ADVECTION AND RETENTION OF LARVAL DUNGENESS CRAB *CANCER MAGISTER* IN GLACIER BAY AND ADJACENT AREAS

A

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Abstract

Spatial and temporal variations of larval abundance of Dungeness crabs were investigated as indications of larval advection and retention in southeastern Alaska. Larvae were collected in five transects: upper Chatham, Icy Strait, Cross Sound, and Icy Point, May to September 1997-2004 and Cape Edward in June 1998-1999. Larval densities were higher in inland water transect and lowest in offshore transects. In all transects, larval densities were highest in June. Zoeae I (ZI) were predominant with a small portion of later larval stages (ZII to ZV) in May. In May and June, late stages (ZIV and ZV) co-occurred with ZI. Later larval hatching in 1997 and 2002 and earlier larval hatching in 1998 may have been related to water temperature during the egg incubation period. Late larval stages that co-occurred with early larval stages can be transported from southern parts of their range where hatching occurs earlier.

Mixing, loss, and distribution of larval Dungeness crabs were investigated inside and outside of Glacier Bay, southeastern Alaska, biweekly from late May to mid-September and monthly in Icy Strait from late May to late August in 2004. Larvae were collected from two different portions of the water column: above and below the thermocline and at four stations in Icy Strait. Larval loss was markedly high for ZI, ZIV, and ZV, and relatively low for ZII and ZIII. ZI occurred from late May to late July. Larval stages progressed seasonally from ZI to ZV and density decreased from ZI through ZV. The larval densities at the inner and outer bay stations and at the shallow and deep depths were similar.

Co-occurrence of late and early larval stages and larvae with different rostrum lengths may be evidence of mixing of larvae incubated in different thermal regimes. The pattern of larval stages in Alaskan sites was markedly different from other parts of the species range: many of the early and intermediate stages occurred within inland waters, as opposed to increasing abundance of later stages with distance offshore.

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General Instruction

Planktonic larval stages are critical components of the life histories of many benthic marine invertebrates (Thorson 1950). Dungeness crab larvae undergo five zoeal stages and a megalopal stage (Poole 1966); the larval period varies with latitude and lasts from 3-4 months in California (Reilly 1983) to more than 5 months in Glacier Bay, southeastern Alaska, defined as the period from the first occurrence of zoeae I (ZI) until the first peak of megalopal abundance (Fisher 2006). The long larval period may be conducive to extensive larval dispersal on the west coast of North America and may result in high natural mortality. Larval natural mortality may be high due to a combination of predation (Thomas 1985) and scarcity or low quality of food (Lough 1976; Armstrong 1983). Prolonged starvation results in lower survival and a longer duration of the larval period (Sulkin et al. 1998). Larval survival also decreases with increasing temperature fluctuations in the ocean (Wild 1980; Sulkin and McKeen 1996).

Because crabs are ectothermic, temperature affects their reproductive biology (Hartnoll 1982). Water temperature affects the rate of embryonic and larval development of Dungeness crabs (Wild 1980). Embryonic development and intermolt periods of crabs increase with colder water temperature in all stages (Reed 1969; Sulkin and McKeen 1989). Warmer water temperature during the egg incubation period accelerates growth rate and reduces larval size in Dungeness crabs (Shirley et al. 1987). Variation in water temperature along the west coast of North America results in differential timing of reproductive events along the distributional range. Reproductive events of Dungeness crabs in the southern part of their range occur earlier than the same events in the northern part of their range as a result of warmer water temperatures in the south. Off the coast of California, crab mating occurs during March and June, and zoeae hatch from December to March (Wild 1980, Reilly 1983). In southeastern Alaska, adult crabs mate and extrude eggs mainly during September and November, and zoeae are released mostly from May to June although zoeae I collected later in the summer suggest that some hatching occurs later (Shirley et al. 1987; Fisher 2006).

Crab populations in aquatic systems are sustained by the recruitment of larvae that undergo ontogeny near hatching locations or by returning larvae that emigrate to the coastal region for ontogeny after hatching (Cronin and Forward 1979; McConaugha 1988; Christy and Morgan 1998). Many crab larvae control their vertical distribution in the tidally-driven currents for advection from and return to nearshore and estuaries. Zoeae I of *Callinectes sapidus* in Chesapeake Bay (Provenzano et al. 1983) and Delaware Bay (Epifanio 1995) and *Pachygrapsus crassipes* in San Diego Bay (DiBacco et al. 2001) are positioned at the surface water during ebb tides when they emigrate. After undergoing ontogeny on the shelf or offshore areas, crab megalopae return to nearshore and estuaries (Dittel and Epifanio 1982; Little and Epifanio 1991). Alternatively, larvae which are retained in estuaries display no migratory patterns or reverse migratory behavior to surface water to avoid offshore advection during ebb tides (Lambert and Epifanio 1982; DiBacco et al. 2001). Zoeae I of *Rhithropanopeus harrisii* in Delaware Bay are found near bottom during flood tides when they are transported upriver (Lambert and Epifanio 1982). *Lophopanopeus* spp., which are retained in San Diego Bay, do not migrate vertically (DiBacco et al. 2001).

Zoeae I of Dungeness crabs off the coasts of Oregon and California are distributed in the upper tens of meters of the water column in inshore waters and larvae can be dispersed hundreds of kilometers offshore (Lough 1976; Reilly 1983). Progressively older stage larvae are found at farther distances from the coast (Lough 1976; Reilly 1983). Dungeness crab larvae may be transported offshore by estuarine run-off and upwelling that moves near-surface water offshore (Lough 1976; Reilly 1983). Megalopae can be transported onshore by internal waves associated with tides and bottom topography (Shanks 1995; Johnson and Shanks 2002), tidal rhythms (Shanks 1995; Johnson and Shanks 2002; Miller and Shanks 2004), surface currents (McCounnaughey et al. 1992; Shanks 1995), and surface winds (McCounnaughey et al. 1992, 1994; Roegner et al. 2003; Miller and Shanks 2004). Off the coasts of California to British Columbia, the Southern California Current and Davidson Current aid the advection of early stage larvae along the coasts northward (Jamieson and Armstrong 1991; McConnaughey et al. 1992). Landward and northward flow characterized by near-surface circulation results in larval retention along a "coastal landing strip" off the coast of Washington (McConnaughey et al. 1994). In the spring transition in April, the California Current moves inshore and southward in the upper layer and the deeper water moves northward (Hickey and Banas 2003). Larvae can be transported back near their hatching location by means of southward currents (Jamieson and Armstrong 1991). However, larval recruitment varies with ocean currents, wind stress and upwelling events. Weak northward currents, strong landward transport (McConnaughey et al. 1994), and upwelling relaxation events (Wing et al. 1995; Botsford 2001) are closely related with recruitment success. In southeastern Alaska, the Alaska Current flows northward throughout the year. A strengthened Alaska Gyre in winter moves coastward off southeastern Alaska and results in a faster flowing Alaska Current (Dodimead et al. 1963). Northward winds in winter result in surface water moving landward. Larvae hatched in British Columbia and Washington coasts can be transported to and along the coast of southeastern Alaska by these currents (Park et al. 2007).

Dungeness crabs are distributed along the west coast of North America from the Aleutian Islands and Pribilof Islands, Alaska to Magdalena Bay, Mexico (Hart 1982; Jensen 1995). Within their range, Dungeness crabs support an important commercial fishery. The Dungeness crab commercial fishery in 2004-5 was worth approximately 141.5 million U.S. dollars in the United States and Canada (Pacific Fishing 2005). The commercial harvest of Dungeness crabs fluctuates throughout the range of the species (Jamieson 1986; Orensanz et al. 1998). These fluctuations result from endogenous and exogenous forces (Higgins et al. 1997). Intense fishing effort for legal-sized crabs (Orensanz et al. 1998), juvenile mortality resulting from cannibalism by larger crabs (Botsford and Wickham 1978), and juvenile mortality from predatory fish (Armstrong et al. 1995), have been proposed as factors influencing the fluctuation of fishery harvest. Also, variations in larval survival in the ocean and subsequent recruitment to the populations have been proposed as factors contributing to the fluctuation. Off British Columbia, Washington, Oregon and California, the variability of coastal currents and wind stress associated with upwelling events affects larval survival and subsequent fishery recruitment (Peterson 1973; Jamieson and Phillips 1988; Hobbs et al. 1992; McConnaughey et al. 1992).

The commercial fishery for Dungeness crabs in southeastern Alaska supports approximately 9% of the total harvest for Dungeness crabs along the west coast of North America (Pacific Fishing 2004) although the proportion varies with the long term cycles of abundance of the species. The cycles of abundance of Dungeness crabs are not in phase throughout the species range, with the cycles increasing in length with increasing latitude. Hence the contribution of the Alaska fishery to the coast-wide catch varies interannually. Since the commercial fishery of Dungeness crabs was initiated in southeastern Alaska in 1916, commercial harvests fluctuated as a result of natural fluctuations (Botsford and Hobbs 1995; Botsford 2001; Higgins et al. 1997) with declines perhaps also as a result of fishing (Orensanz et al. 1998) and reintroduction of sea otters to the outer waters of southeastern Alaska (Shirley et al. 1996). Despite the likely importance of larval recruitment as a possible factor for the fishery fluctuations in southeastern Alaska, little research has been conducted.

The goal of my study is to understand larval advection and retention of Dungeness crabs within embayments and the inshore waters of the deep and comparatively wide straits of southeastern Alaska. To understand larval advection and retention, I explored interannual variations in hatch timing and abundance of Dungeness crab larvae. Also, I postulated whether Dungeness crab larvae were advected into and out of Glacier Bay, or retained within Glacier Bay by scrutinizing larval distribution at shallow and deep depths during ebb and flood tides and by examining differences in larval morphology, as an indicator of incubation temperatures.

This dissertation is divided into three chapters. In chapter 1, I investigated the spatial and temporal variation of density and hatch timing of Dungeness crab larvae to indicate larval advection and retention and climate effects on larval hatch timing. Larvae and sea surface temperature (SST), sea surface salinity (SSS), zooplankon biomass (displacement volume), and Chlorophyll *a* (Chl *a)* were examined at 16 stations along four transects, upper Chatham Strait, Icy Strait, Cross Sound, and Icy Point, in southeastern Alaska by the SouthEast Coastal Monitoring (SECM) survey conducted by NOAA's Auke Bay Laboratory from late May to late September during 1997-2004. Spatial and temporal variations of larval densities and SST, SSS, zooplankon biomass, and Chl *a* were examined by exploratory data analysis using Geographic Information System (GIS). Larval densities were compared with SST, SSS, Chl *a*, and zooplankton biomass to explore any relationships between larval density and oceanographic data. Larval densities were compared between transects and stations within the transect.

In chapter 2, I investigated patterns of development, loss, mixing, distribution of Dungeness crab larvae in Glacier Bay and neighboring bodies of water. Larvae and salinity and temperature data were collected during daylight hours at three inside and two outside stations of Glacier Bay for two different portions of the water column: above and below the thermocline, or the zone of greatest temperature change in the water column. Zooplankton samples were collected biweekly from late May to mid September 2004, and at four stations in Icy Strait from a depth of 200 m or within 10 m of the bottom to the surface, double-obliquely monthly from late May to late August 2004. The distribution pattern between shallow and deep depths, seasonal occurrence, and loss of Dungeness crab larvae were explored as an indication of larval advection and retention. In particular, the rostrum lengths of ZI were investigated as indications of mixing of ZI with different origins incubated in different temperatures.

In chapter 3, I explored the hypothesis that Dungeness crab larvae hatched from northern Washington and British Columbia coasts could be transported to southeastern Alaska. Dungeness crab larvae were collected in offshore transects, Cape Edward and Icy Point and inland water transect, Icy Strait, in May and June from 1997-2004. To support the hypothesis, I investigated monthly changes of Chl *a* concentrations and northward SST progression, and provided supporting evidence from drift buoy tracks.

Literature Cited

Armstrong, D. A. 1983. Cyclic crab abundance and relationship to environmental causes, p. 102-110. *In* W. Wooster [ed.], From year to year: interannual variability of the environment and fisheries of the Gulf of Alaska. Univ. Wash. Sea Grant Rep. WST-WO 83-3. Seattle.

Armstrong, J. L., D. A. Armstrong, and S. D. Mathews. 1995. Food habits of estuarine staghorn sculpin, *Leptocottus armatus*, with focus on consumption of juvenile Dungeness crab, *Cancer magister*. Fish. Bull. **93:** 456-470.

Botsford, L. W. 2001. Physical influences on recruitment to California Current invertebrate populations on multiple scales. ICES J. Mar. Sci. **58:** 1081-1091.

Botsford, L. W., and R. C. Hobbs. 1995. Recent advances in the understanding of cyclic behavior of Dungeness crab (*Cancer magister*) populations. ICES Mar. Sci. Symp. **199:** 157-166.

Botsford, L. W., and D. E. Wickham. 1978. Behavior of age-specific density-dependent models and the northern California Dungeness crab (*Cancer magister*) fishery. J. Fish. Res. Board Can. **35:** 833-843.

Christy, J. H., and S. G. Morgan. 1998. Estuarine immigration by crab postlarvae: mechanisms, reliability and adaptive significance. Mar. Ecol. Prog. Ser. **174:** 51-65.

Cronin, T. W., and R. B. Forward Jr. 1979. Tidal vertical migration: an endogenous rhythm in estuarine crab larvae. Science **204:** 1020-1022.

DiBacco, C., D. Sutton, and L. McConnico. 2001. Vertical migration behavior and horizontal distribution of brachyuran larvae in a low-inflow estuary: implications for bay-ocean exchange. Mar. Ecol. Prog. Ser. **217:** 191-206.

Dittel, A. I., and C. E. Epifanio. 1982. Seasonal abundance and vertical distribution of crab larvae in Delaware Bay. Estuaries **5:** 197-202.

Dodimead, A. J., F. Favorite, and T. Hirano. 1963. Salmon of the North Pacific Ocean. Part II. Review of oceanography of the subarctic Pacific region. Int. North Pac. Fish Comm. Bull. 33

Epifanio, C. E. 1995. Transport of blue crab (*Callinectes sapidus*) larvae in the waters off Mid-Atlantic States. Bull. Mar. Sci. **57:** 713-725.

Fisher, J. L. 2006. Seasonal timing and duration of brachyuran larvae in a high-latitude fjord. Mar Ecol Prog Ser **323:** 213-222

Hart, J. F. L. 1982. Crabs and their relatives of British Columbia. British Columbia Prov. Museum Handbook **40**.

Hartnoll, R. G. 1982. Growth, p. 111-196. *In* L. G. Abele [ed.], The biology of Crustacea. Vol. 2 Embryology, morphology, and genetics. Academic Press, New York.

Hickey, B. M., and N. S. Banas. 2003. Oceanography of the U.S. Pacific Northwest coastal ocean and estuaries with application to coastal ecology. Estuaries **26:** 1010-1031.

Higgins, K., A. Hastings, J. N. Sarvela, and L. W. Botsford. 1997. Stochastic dynamics and deterministic skeletons: Population behavior of Dungeness crab. Science **276:** 1431-1435.

Hobbs, R. C., L. W. Botsford, and A. Thomas. 1992. Influence of hydrographic conditions and wind forcing on the distribution and abundance of Dungeness crab, *Cancer magister*, larvae. Can. J. Fish. Aquat. Sci. **49:** 1379-1388.

Jamieson, G. S. 1986. Implications of fluctuations in recruitment in selected crab populations. Can. J. Fish. Aquat. Sci. **43:** 2085-2098.

Jamieson, G. S., and D. A. Armstrong. 1991. Spatial and temporal recruitment patterns of Dungeness crab in the northeast Pacific. Mem. Queens Mus. **31:** 365-381.

Jamieson, G. C., and A. Phillips. 1988. Occurrence of *Cancer* crab (*C. magister* and *C. oregonensis*) megalopae off the west coast of Vancouver Island, British Columbia. Fish. Bull. **86:** 525-542.

Jensen, G. C. 1995. Pacific coast crabs and shrimps. Sea challengers, Monterey, California.

Johnson, J., and A. L. Shanks. 2002. Time series of the abundance of the post-larvae of the crabs *Cancer magister* and *Cancer* spp. on the southern Oregon coast and their cross-shelf transport. Estuaries **25:** 1138-1142.

Lambert, R., and C. E. Epifanio. 1982. A comparison of dispersal strategies in two genera of brachyuran crab in a secondary estuary. Estuaries **5:** 182-188.

Little, K. T., and C. E. Epifanio. 1991. Mechanism for the reinvasion of the estuary by two species of brachyuran megalopae. Mar. Ecol. Pro. Ser. **68:** 235-242.

Lough, R. G. 1976. Larval dynamics of the Dungeness crab, *Cancer magister* off the central Oregon coast, 1970-71. Fish. Bull. **74:** 353-375.

McConaugha, J. R. 1988. Export and reinvasion of larvae as regulators of estuarine decapod populations, 90-103. *In* M. P. Weinstein [ed.], Workshop on Larval Fish and Shellfish Transport, Ocean Springs, MS Amer. Fish. Soc. Symp. **3**.

McConnaughey, R. A., D. A. Armstrong, B. M. Hickey, and D. R. Gunderson. 1992. Juvenile Dungeness crab (*Cancer magister*) recruitment variability and oceanic transport during the pelagic larval phase. Can. J. Fish. Aquat. Sci. **49:** 2028-2044.

McConnaughey, R. A., D. A. Armstrong, B. M. Hickey, and D. R. Gunderson. 1994. Interannual variability in coastal Washington Dungeness crab (*Cancer magister*) populations: larval advection and the coastal landing strip. Fish. Oceanogr. **3:** 22-38.

Miller, J. A., and A. L. Shanks. 2004. Ocean-estuaries coupling in the Oregon upwelling region: abundance and transport of juvenile fish and of crab megalopae. Mar. Ecol. Prog. Ser. **271:** 267-279.

Orensanz, J. M., J. Armstrong, D. Armstrong, and R. Hilborn. 1998. Crustacean resources are vulnerable to serial depletion-the multifaceted decline of crab and shrimp fisheries in the Greater Gulf of Alaska. Rev. Fish Biol. Fish. **8:** 117-176.

Pacific Fishing. 2004. Pacific fishing yearbook. March. FIS Publishing, Inc. Seattle, WA.

Pacific Fishing. 2005. Pacific fishing yearbook. March. FIS Publishing, Inc. Seattle, WA.

Park, W., D. C. Douglas, and T. C. Shirley. 2007. North to Alaska: Evidence for conveyor belt transport of Dungeness crab larvae along the west coast of the United States and Canada. Limnol. Oceanogr. **52:** 248-256.

Peterson, W. T. 1973. Upwelling indices and annual catches of Dungeness crab, *Cancer magister*, along the west coast of the United States. Fish. Bull. **71:** 902-910.

Poole, R. L. 1966. A description of the laboratory-reared zoeae of *Cancer magister* Dana, and megalopae taken under natural conditions (Decapoda, Brachyura). Crustaceana **11:** 83-97.

Provenzano, A. J., J. R. McConaugha, K. Phillips, D. F. Johnson, and J. Clark. 1983. Vertical distribution of first stage larvae of the blue crab, *Callinectes sapidus*, at the mouth of Chesapeake Bay. Estuar. Coast. Shelf Sci. **16:** 489-500.

Reed, P. H. 1969. Culture methods and effects of temperature and salinity on survival and growth of the Dungeness crab (*Cancer magister*) larvae in the laboratory. J. Fish. Res. Board Can. **26:** 389-397.

Reilly, P. N. 1983. Dynamics of the Dungeness crab, *Cancer magister*, larvae off central and northern California, p. 57-84. *In* P. W. Wild and R. N. Tasto [eds.], Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California fishery resource. Cal. Dept. Fish Game **172**.

Roegner, G. C., D. A. Armstrong, B. M. Hickey, and A. L. Shanks. 2003. Ocean distribution of Dungeness crab megalopae and recruitment patterns to estuaries in southern Washington state. Estuaries **26:** 1058-1070.

Shanks, A. L. 1995. Orientated 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, S. M., T. C. Shirley, and S. D. Rice. 1987. Latitudinal variation in the Dungeness crab, *Cancer magister*, zoeal morphology explained by incubation temperature. Mar. Biol. **95:** 371-376.

Shirley, T.C., G. Bishop, C. E. O'Clair, S. J. Taggart, and J. L. Bodkin. 1996. Sea otter predation on Dungeness crabs in Glacier Bay, Alaska, p 563-576. *In* High Latitude Crabs: Biology, Management, and Economics. Lowell Wakefield Fisheries Symposium. Alaska Sea Grant College Program Report AK-SG-96-02,

Sulkin, S. D., and G. L. McKeen. 1989. Laboratory study of survival and duration of individual zoeal stages as a function of temperature in the brachyuran crab *Cancer magister*. Mar. Biol. **103:** 31-37.

Sulkin, S. D., and G. L. McKeen. 1996. Larval development of the crab *Cancer magister* in temperature regimes simulating outer-coast and inland-water habitats. Mar. Biol. **127:** 235-240.

Sulkin S, A. Blanco, J. Chan, and M. Bryant. 1998. Effects of limiting access to prey on development of first zoeal stage of the brachyuran crabs *Cancer magister* and *Hemigrapsus oregonensis*. Mar. Biol. **131:** 515-521.

Thomas, D. H. 1985. A possible link between coho (silver salmon) enhancement and a decline in central California Dungeness crab abundance. Fish. Bull. **83:** 682-691.

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev. **25:** 1-45.

Wild, P. W. 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.

Wing, S. R., L. W. Botsford, J. L. Largier, and L. E. Morgan. 1995. Spatial structure of relaxation events and crab settlement in the northern California upwelling system. Mar. Ecol. Prog. Ser. **128:** 199-211.

Chapter 1

Spatial and temporal variation of larval density and hatch timing of Dungeness crabs in southeastern Alaska: indications for larval advection and retention and climate effects

Wongyu Park[1] and Thomas C. Shirley

Abstract

Dungeness crab larvae and oceanographic data were collected in southeastern Alaska during May to September 1997-2004 to investigate larval advection and retention, and climate effects on larval hatch timing. Spatial and temporal variations of larval densities and oceanographic data were examined. Larval densities were highest in a transect near the mouth of Glacier Bay, moderate in other transects, and lowest in an offshore transect. Larval densities were highest in June in all transects. Zoeae I (ZI) predominated in May; thereafter ZI decreased and late zoeal stages occurred. In May and June, small numbers of unusually late stage larvae co-occurred with ZI in three transects. These late stage larvae appear to have hatched and been advected from more southern areas. The timing of ZI occurrence varied interannually and was related to water temperature during the egg incubation period. Later larval hatching occurred in years when temperatures were colder (1997 and 2002), while earlier larval hatching occurred in years when temperatures were warmer (1998). Whether locally-produced larvae were advected or retained within Icy Strait or adjacent areas is not definitive from our data; data supporting both alternatives are discussed. Indeed, the appearance of late stage larvae early in the season strongly suggests that larval Dungeness crab populations within Alaskan inland

waters may represent a metapopulation of both allochthonous and locally produced larvae. The temporal and spatial patterns of distribution of Dungeness larvae in southeastern Alaska are markedly different from those reported from other areas of the species range, with larvae occurring much later in the year, and late stage larvae occurring in inland waters.

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Introduction

Crab populations in estuaries or bays are maintained by larvae that undergo larval development within the systems (Cronin & Forward 1979) or by larvae advected from the hatching sites to the coastal region for larval development, which then return as megalopae (McConaugha 1988, Christy & Morgan 1998). For crab larvae that are retained, all larval stages are present within the bay. In such systems, the larvae display no migratory behavior or reverse migratory behavior in which larvae are located near bottom at ebb tide and in the upper water column during flood tide (Lambert & Epifanio 1982, DiBacco et al. 2001). For crab larvae which are advected, first stage zoeae (ZI) but not post ZI larvae are found within the bay (McConaugha 1988, DiBacco et al. 2001). Off the coast of Delaware and North Carolina, *Callinectes sapidus* and *Uca* spp. megalopae are transported by flood tides to settlement sites after offshore larval development (Epifanio et al. 1984, Tankersley & Forward 1994, Welch et al. 1999, Welch & Forward 2001).

The commercial harvest of Dungeness crabs from Alaska to California has multi-year cyclic fluctuations (Methot 1988, Botsford & Hobbs 1995, Higgins et al. 1997, Orensanz et al. 1998). Combinations of predation, oceanographic fluctuations, or low food quality and quantity, influence the larval mortality of Dungeness crabs (Lough 1976). Starvation results in lower larval survival and longer stage duration (Sulkin et al. 1998). Fluctuation of ocean temperatures during the egg incubation period results in high egg mortality and declines of fishery harvests (Wild 1980). Strong upwelling events promote larval advection offshore while upwelling relaxation events increase larval retention onshore, and subsequently, increase in fishery harvests (Peterson 1973, Wing et al. 1995).

The timing of reproductive events of Dungeness crabs occurs progressively later with increasing latitude. Off the California coast, adult Dungeness crabs mate from March to June, and zoeae hatch from late December to March (Wild 1980, Reilly 1983). Along the Oregon coast, zoeae hatch in January to March (Reed 1969, Lough 1976). In Washington waters, mating occurs in May and June, and hatching occurs during January to mid-March (Cleaver 1949, McConnaughey et al. 1994). Along the British Columbia coast, adult crabs mate during April to September, and zoeae hatch during December to June, but mainly in January and February (MacKay 1942, Butler 1956). In southeastern Alaska, adult Dungeness crabs extrude eggs mainly from September to November, and zoeae hatch mostly during May and June (Swiney 1999, Shirley et al. 1987, Fisher 2006). Large female Dungeness crabs in southeastern Alaska extrude eggs in alternate years or less often (Swiney & Shirley 2001, Swiney et al. 2003).

El Niño-Southern Oscillation (ENSO) events, occurring every 2 to 7 years and lasting 8 to 15 months, affect oceanographic conditions (Philander 1989, Fiedler 2002). Warm water temperatures associated with these climate changes accelerate the rate of embryonic and larval development of Dungeness crabs, but decrease larval survival, thus further influencing population fluctuations (Wild 1980). Also, increased or decreased temperatures can reduce or prolong larval duration, which may alter the susceptibility of the larvae to predation or starvation (Moloney et al. 1994).

The larval period of Dungeness crabs lasts 45-158 d, varying with latitude and water temperature (Lough 1976, Reilly 1983, Jamieson & Phillips 1988, Sulkin & McKeen 1989). In late winter when Dungeness crab larvae hatch, the California Undercurrent, which flows northward over the continental slope beneath the southward-flowing California Current at approximately 100-400 m depths, transports warm and saline water, larval fish and invertebrates. The Southern California Countercurrent, a surface current that flows northward in winter, may be connected to Davidson Current along the coast of northern California. The Davidson Current contributes water mass movements northward and inshore in the upper layers and offshore beneath the upper layers from California to British Columbia (Hickey & Banas 2003). Wind-driven currents are also onshore at the surface (Halliwell & Allen 1987). Off the coasts of California and Oregon, the ZI of Dungeness crabs are located in the upper tens of meters of the water column in inshore waters (Lough 1976, Reilly 1983); this location and the prevailing currents may contribute to long distance transportation northward. Landward and northward surface transport by northward and northeastward winds aids in the larvae being retained onshore and transported to the coastal landing strip off the coast of Washington (McConnaughey et al. 1994). In spring and summer the California Current moves inshore and southward in the upper layer; the deeper water below this upper layer moves northward (Hickey & Banas 2003). Dungeness crab larvae can be transported back toward their hatching location by means of the southward currents (Jamieson & Armstrong 1991).

In the Gulf of Alaska, off the coasts of northern British Columbia and southeastern Alaska, flow patterns are dominated by Alaska Current throughout the year

(Dodimead et al. 1963). During the larval season for Dungeness crabs in British Columbia and southeastern Alaska winds blow mainly to the north or northeast (Thomson 1981, Park et al. 2007). Ekman transport driven by winds aids surface water coastward. When Ekman transport moves surface waters coastward, the water piles up on the coast and sinks, generating downwelling. The downwelling areas are found from Queen Charlotte Sound in British Columbia along the entire Alaskan coast from southeastern Alaska to the Aleutian Islands (Ware & McFarlane 1989). The northward flowing Alaska Current and the coastward flowing Ekman transport may contribute to Dungeness crab larvae being retained on the coast and being transported northward. Larvae hatched off the coasts of British Columbia and Washington can be transported to southeastern Alaska, as a result of these northward and coastward currents (Park et al. 2007).

Alternately, Dungeness crab larvae may be dispersed offshore by estuarine runoff, or upwelling events that move surface water offshore (Lough 1976, Reilly 1983). Off the coasts of California and Oregon, upwelling occurs when winds blow from the north. In the northern hemisphere, surface water is transported 90° the right of the northerly components of winds. Larvae released near shore can be transported offshore by this surface water transport. Megalopae may be transported inshore by wind-driven surface currents (McCounnaughey et al. 1992, 1994, Shanks 1995, Roegner et al. 2003, Miller & Shanks 2004) or internal waves, tides, and geostrophic flow (Shanks 1995). Weak upwelling events may also aid in megalopae being returned inshore (Peterson 1973).

Dungeness crab larvae have stage-specific depth positioning and migratory behavior (Lough 1976). Zoeae I are positioned generally in the upper layer of the water column while late zoeal stages are distributed in deeper layers (Lough 1976). Megalopae are abundant at the surface at night (Jamieson & Philips 1988, Jamieson et al. 1989). Dungeness crab larvae have crepuscular migration in which larvae ascend at dawn and dusk and descend at midnight and during the day (Hobbs & Botsford 1992, Park & Shirley 2005).

The spring phytoplankton bloom in high latitudes is a pulsed event and may be followed by smaller blooms when nutrients are re-supplied from deeper waters by protracted wind events (Ziemann et al. 1991). Because grazers may consume a high proportion of the carbon produced during primary production (Ziemann et al. 1993), the annual production and duration of the spring bloom are critical to survival of larval fish and zooplankton (Coyle & Paul 1990, Coyle et al. 1990, Paul et al. 1990a).

The SouthEast Coastal Monitoring (SECM) survey has been conducted by Auke Bay Laboratory (ABL), National Fisheries Marine Service (NMFS) since 1997 to study the early ecology of the oceanic phase of Pacific salmon (*Oncorhynchus* spp.). The SECM survey investigates causal linkages between Pacific salmon production and climate changes, and attempts to assess marine growth, survival, distribution, migration, and ocean carrying capacity for salmon in southeastern Alaska. Zooplankton and hydrographic data are collected during the SECM survey.

We investigated the spatial and temporal distribution of Dungeness crab larvae to determine whether Dungeness crab larvae in southeastern Alaska were advected to the Gulf of Alaska, or were retained and underwent ontogeny within the SECM survey area at 16 stations along four transects in southeastern Alaska. Also, we explored spatial and temporal distribution of sea surface temperature (SST), sea surface salinity (SSS), Chlorophyll *a* (Chl *a*), and zooplankton biomass and compared with larval densities. We also investigated the effects of temperature on the timing of larval hatching of Dungeness crabs.

Materials and Methods

Larval Data

Zooplankton and hydrographic data were collected monthly at 16 stations arrayed along four transects in upper Chatham Strait, Icy Strait, Cross Sound, and Icy Point in southeastern Alaska (Figure 1.1, Table 1.1) by the NOAA vessel, *RV John N. Cobb*, during the last 10 days of each month from May to September, 1997-2004. Four sampling stations, approximately equidistant apart were sampled in each transect and labeled A to D. Hence, ISA is a notation of station A in the Icy Strait transect (Figure 1.1). All sampling occurred during daylight, between 0700 and 2000 h, Alaska Standard Time. SST and SSS were measured to the precision of 0.1 at 1 m depth with an onboard thermosalinograph (Sea-Bird SBE 21); salinity is reported as practical salinity.

At each station, a 60-cm diameter bongo net with 505 and 333 μm mesh was deployed once to a depth of 200 m, or to within 10 m of the bottom, with a double oblique tow. Here, we report on samples collected with the 333 μm mesh net. A General Oceanics model 2031 or Rigosha flow meter was placed inside the nets for measurement of filtered water volumes. Zooplankton samples were preserved in 5% buffered formalin aboard the vessel and transported to the laboratory. Zooplankton biomass (DV, displacement volume as ml per m^3) was used as a proxy for standing stock of zooplankton when Dungeness crab larvae were collected. All Dungeness crab larvae were sorted and identified to zoeal stage following Poole (1966). Larval density was calculated as individuals per 100 m^3 based on the filtered water volumes. Displacement volume and Chl *a* were obtained from the Auke Bay Laboratory (M. Sturdevant, Auke Bay Lab, NMFS).

Larval stages were grouped into three categories: ZI, ZII (zoeal stage II) and ZIII (zoeal stage III) for the intermediate stage, and ZIV (zoeal stage IV), ZV (zoeal stage V) and M (megalopal stage) for the late larval stage. Larval data were viewed in Stack shape in ArcGIS 9.1 (2001). For the oceanographic data, the mean value for each month during the sampling period was selected to represent seasonal oceanographic features of the area. Oceanographic data were averaged and contoured with a Radius Base Function in ArcGIS. Although there were insufficient data points to evaluate spatial autocorrelations for geostatistical interpolation, the Radius Base Function was used because oceanographic data were assumed to be continuous over the study areas and the function was deterministic. In addition, because the contours of the areas between transects did not indicate oceanographic features of the area, the contours of the images between transects were not presented.

Statistical Analysis

Significance levels for all analyses in the study were 0.05. For all statistical analyses, the Kolmogorov-Smirnov test (hereafter K-S test) was used to test normality. Data that did not show normality were log- or square root-transformed. Larval densities of only inland water stations each month were compared to DV, SST, SSS, and Chl *a* using Pearson's product-moment correlation coefficient because most larval densities in the IP transect were low or zero, particularly stations farther than closer to the coast. Larval densities, SSS, and SST only from May to July were used for the analysis because larval densities during August to September were extremely low, or zero. To compare larval densities between transects and stations within the transect, the Kruskal Wallis test (hereafter K-W test) was used. To compare differences in larval densities between transects, the total density of each station for each month was used. To compare differences in larval density between stations in each transect, the total densities for all of months from May to July were used.

Results

Larval Data

Water volume filtered per each sampling ranged from 70 to 270 m^3. Two thousand Dungeness crab larvae were collected during the sampling period, 1997-2004: ZI = 712; ZII = 549; ZIII = 393; ZIV = 246; ZV = 85; M = 15 (Fig 1.2-1.5). Low larval densities occurred in the Icy Point transect throughout the sampling period. Larval densities in the Icy Point transect were significantly higher in stations near the coast than stations farther from the coast (K-W test, $\chi^2 = 8.062$, df = 3, p = 0.046). In the inland transects, larval densities were higher in the IS transect than the CS and UC transects in all months: May (K-W test, $\chi^2 = 20.59$, df = 2, p < 0.001); June (K-W test, $\chi^2 = 6.031$, df = 2, p = 0.049); July (K-W test, $\chi^2 = 11.557$, df = 2, p = 0.003). In inland transects, larval densities between stations were similar in the Cross Sound (K-W test, $\chi^2 = 0.03$, df = 3, p = 0.999) and upper Chatham (K-W test, $\chi^2 = 2.812$, df = 3, p = 0.413) transects, except those of the Icy Strait transect. Larval densities at the ISA were highest (K-W test, $\chi^2 = 21.167$, df = 3, p < 0.001). In all transects, larval densities in June were higher than those in other months: Icy Strait (K-W test, $\chi^2 = 14.204$, df = 2, p < 0.001), upper Chatham (K-W test, $\chi^2 = 11.547$, df = 2, p = 0.003), Cross Sound (K-W test, $\chi^2 = 20.696$, df = 2, p < 0.001), and Icy Point (K-W test, $\chi^2 = 8.563$, df = 2, p = 0.018).

In May, ZI was the predominant larval stage in all years (Figure 1.2). However, unusually late larval stages (ZIV-M) co-occurred with ZI and intermediate stages (ZII and ZIII) at ISA and ISB in the Icy Strait transect in 1998 and at CSA and CSC in the Cross Sound transect in 1999, and IPA in 2003 and 2004 in the Icy Point transect. In particular, all larvae which occurred at the IPA, IPB, and IPC in 2001 were late larval stages.

In June, intermediate stages were predominant in all years except 1997 and 2002 (Figure 1.3). Zoea I was the most abundant stage in 1997 and in 2002. In 2000, late larval stages (ZIV-M) at ISA comprised 35 % of larval collections. Larval densities at ISA in 2000 (88.9 100 m^{-3}) and 2002 (81.4 100 m^{-3}) were high.

In July, larval densities dropped to below 10 100 m^{-3} at most stations (Figure 1.4). Zoeae I occurred in the Icy Strait and Cross Sound transects in 1997, upper Chatham transect in 2001, and Icy Strait transect in 2002. In August, larval densities were extremely low in all years except 2002 and 2004, when no larvae were collected (Figure 1.5). In September, a megalopa was collected at IPD in 1997.

Larval densities were not significantly correlated with any oceanographic data including SSS, SST, Chl *a*, and zooplankton biomass (Table 1.2).

Oceanographic Data

Monthly mean SST was coldest in May, increased throughout the summer, and decreased in September (Figure 1.6). The SST were coldest in the Cross Sound transect, intermediate in the upper Chatham and Icy Strait transects, and warmest in the Icy Point transect. Monthly variation of SST in the Cross Sound transect had relatively narrow ranges from 6.7 to 9.3°C while those in the Icy Point transect varied widely from 7.1 to 15.0°C.

Monthly mean SSS varied seasonally in the upper Chatham and Icy Strait transects, while SSS was relatively stable in the Cross Sound and Icy Point transects (Figure 1.7). The SSS of northern stations in the upper Chatham and Icy Strait transects decreased throughout the summer months and increased in September.

Monthly mean Chl *a* was highest in May and decreased thereafter (Figure 1.8). Chl *a* in the upper Chatham and Icy Strait transects were relatively higher in May and June than those in the Cross Sound and Icy Point transects. In May, mean Chl *a* (3.1-6.6

mg m^{-3}) was highest at the northernmost stations in the upper Chatham and Icy Strait transects. In the Icy Strait transect, mean Chl *a* concentrations were lower, and ranged from 1.3 to 2.3 mg m^{-3}. From July to September, mean Chl *a* concentrations at all stations were below 2.0 mg m^{-3}.

Mean zooplankton biomass was highest in the Icy Strait transect and lowest in the Icy Point transect throughout the sampling period (Figure 1.9). In May, mean zooplankton biomass ranged from 0.6 to 0.9 ml m^{-3} except at CSC, CSD and in the Icy Point transect. In particular, in the Icy Point transect, zooplankton biomass was relatively low, ranging from 0.2-3.0 ml m^{-3}.

Discussion

The decrease in SSS in the Icy Strait and upper Chatham transects throughout the summer likely resulted from increased freshwater discharge from Glacier Bay and small rivers near the study areas owing to seasonal melt of ice and snow and rainfall. In the Cross Sound transect, the narrow mouth (Figure 1.1) and shallow depth (Table 1.1) may have resulted in upwelling of deep, cold, saline water to the surface associated with tidal currents, as suggested by Cokelet et al. (2007).

The increase in SST throughout the summer months is related to the seasonal increase in surface heating. In the Cross Sound transect, mean currents are of an estuarine type, flowing out in the upper 100 m, and flowing in below the 100 m depth (P. Stabeno, Pacific Marine Environmental Laboratory, NOAA, pers. comm.). Vertical mixing of cold deeper waters associated with the narrow mouth (Figure 1.1) and shallow depth of the Cross Sound transect (Table 1.1) may explain why the Cross Sound transect is generally cooler than other transects in the sampling area.

Temperatures warmer than 15°C have been correlated with high mortality of late stage zoeae (Lough 1976, Sulkin & Mckeen 1989) while megalopal distribution and abundance were not correlated with water temperature (Hobbs et al. 1992). Dungeness crab larvae do not develop successfully in laboratory cultures at temperatures warmer than 20-21.5°C (Reed 1969, Sulkin & McKeen 1989). In our study, the warmest SST was 15.6°C but rarely exceeded 14 °C during 1997-2004. Temperatures below 6°C reduce survival (Reed 1969) and may result in cessation of larval development (Jamieson & Phillips 1993), but temperatures below 6°C were not observed in our study. Thus, temperatures may not have affected larval survival or distribution in our study site.

Warmer temperatures accelerate embryonic and larval development (Wild 1980, Sulkin & McKeen 1989). Water temperatures were not collected during the egg incubation period of Dungeness crabs from fall 1996 to spring 2004 at our sampling sites. However, temperatures during egg incubation in our sampling area were approximated from published and unpublished values from adjoining areas (Schwing et al. 2002, Etherington et al. 2004, B. Wing, Auke Bay Laboratory, NMFS, unpubl. data.). Etherington et al. (2004) averaged air temperatures from 1993 to 2002 from six weather stations in southeastern Alaska: Yakutat Airport, Elfin Cove, Hoonah, Barlett Cove (Glacier Bay), Gustavus Airport, Auke Bay, Juneau Airport, and Haines (Figure 3 of Etherington et al. 2004). The monthly mean air temperatures for 1997-2002 from September to April, corresponding to the egg incubation period for Dungeness crabs in southeastern Alaska, was colder than average in 1997 and 2002 and warmer than average in 1998. The Northern Oscillation Index (NOI), a climate index for the Northeast Pacific, indicated the same pattern as air temperatures reported by Etherington et al. (2004). Sea surface temperature measured in Auke Bay had the same pattern as air temperature (B. Wing, Auke Bay Laboratory, NMFS, unpubl. data). During the study period from 1997 to 2004, the mean of SST degree-days during the likely egg incubation period, from the previous September to April, was 1428°C. The SST degree-days during the same egg incubation period were colder in 1997 (1283.4°C, 10.1%) and 2002 (1380°C, 3.3% colder) and warmest in 1998 (1533°C, 7.3% warmer), similar to values reported for the air temperature patterns from the six weather stations in southeastern Alaska. Also, in the northeastern Pacific Ocean, an El Niño occurred in summer 1997 and persisted until spring1998 (Schwing et al. 2002, Batten & Welch 2004, Zamon & Welch 2005). Thus, a cold event during the egg incubation period for larvae that occurred in spring 1997 and 2002 may have slowed embryonic development and subsequent later first appearance of ZI and a longer ZI duration in the water column over the spring and summer in 1997 and 2002. Conversely, the El Niño in 1997-1998 may have resulted in elevated water temperature and subsequently earlier larval hatching in spring 1998.

Monthly changes of Chl *a* and zooplankton biomass in the SECM survey area were dissimilar to those of adjacent Glacier Bay. Chl *a* and zooplankton biomass in Glacier Bay were high throughout the spring and summer months (Etherington et al. 2004) while Chl *a* of the SECM survey displayed relatively high values only in May and decreased thereafter. In Glacier Bay, Chl *a* and zooplankton biomass were lowest near the mouth of the bay, except for the very distal portion of both arms; both Chl *a* and zooplankton biomass were higher in mid bay and upper bay (Etherington et al. 2004). Because the waterway of Glacier Bay is directly connected to Icy Strait, Chl *a* and zooplankton might be dispersed into Icy Strait. Conversely, Chl *a* and zooplankton could be retained within the bay.

Dungeness crab larvae are omnivores (Lough 1976) but little is known about their diets in situ. In laboratory experiments, Dungeness crab larvae consumed nauplii of *Artemia salina* and *Balanus grandula* and developed normally (Poole 1966, Reed 1969, Sulkin et al. 1998). Dungeness crab larvae also feed on dinoflagellates (Hinz et al. 2001, Moore 2003, Perez & Sulkin 2005) and diatoms (Hartman & Letterman 1978). In Auke Bay, large diatoms such as *Thalassiosira* spp. and *Chaetoceros* spp. are predominant during the primary bloom in April; another large diatom, *Skeletonema costatum,* a relevant food for Dungeness crab larvae (Hartman & Letterman 1978), is frequently the most abundant phytoplankter in June (Ziemann et al. 1993). Under laboratory conditions, *Skeletonema costatum* or mixed foods with *Skeletonema costatum* allowed Dungeness crab larvae to develop to ZIV or ZV stages (Hartman & Letterman 1978). Nauplii of barnacles, including *Balanus grandula* which is densely distributed in the intertidal areas of southeastern Alaska (O'Clair & O'Clair 1998), hatch following the primary spring bloom in southeastern Alaska. The euphausiid *Thysanoessa raschii* and small copepods *Pseudocalanus* spp. also have similar hatching patterns (Coyle & Paul 1990, Paul et al. 1990a,b). These nauplii of small crustaceans, along with phytoplankton species such as *Skeletonema costatum,* which occurs as a later successional phytoplankter, may be pertinent foods for Dungeness crab larvae. Thus, many potential prey of Dungeness crab larvae occur in our study area. However, the sizes of these prey items are small so that they would have passed through the 333 μm mesh net used in our sampling. Also, we do not know the contribution of Chl *a* from each diatom species. Actual numbers of these potential prey items were likely underestimated with the larger mesh sizes used in our sampling; phytoplankton and small nauplii may have passed through the mesh. A few incidentally caught nauplii were counted in the laboratory (pers. obs.). Accordingly, a significant relationship between zooplankton biomass or Chl *a* and larval densities of Dungeness crabs should not be expected because of the sampling biases of the large mesh net and the lack of knowledge of Chl *a* contribution by the different phytoplankton species.

Late larval stages (ZIV, ZV and megalopae) that co-occurred with ZI at individual stations in the Icy Point, Cross Sound, and Icy Strait transects in May might have overwintered, hatched earlier and developed faster, or been transported from other habitats where larvae hatched earlier. In high latitudes the spring primary bloom is initiated when light is not limiting and when the water column stabilizes to create a shallow mixing depth (Sverdrup 1953, Ziemann et al. 1991, 1993, Hunt et al. 2002). In the Gulf of Alaska (Park et al. 2007) and Glacier Bay and Auke Bay (Ziemann et al. 1991, Etherington et al. 2004), the Chl *a* concentration is extremely low during the winter. During winter, several fish species release larvae in the Gulf of Alaska and inland waters in southeastern Alaska (Wing 1997, Wing, B. pers. comm.), although many fish species spawn larvae synchronously with or after the spring phytoplankton bloom

(Haldorson et al. 1993). In the Gulf of Alaska and southeastern Alaska little information exists on what prey items are consumed by those larvae spawned during winter. In Long Island Sound, NY, American sandlance, *Ammodytes americanus* spawn herbivorous larvae during winter but the larvae do not feed until the spring phytoplankton bloom (Monteleone et al. 1987). However, it is unlikely that Dungeness crab larvae off the California and Oregon in winter hatch in food limited conditions. Lough (1976) did not indicate the precise amount of food exactly in the water column but stated that relevant amount of foods for Dungeness crab larvae occurred between 3 and 20 miles offshore in Oregon. Off the coast of California Chl *a* concentrations were sustained at approximately 1.0 mg m^{-3} or higher during the larval period (Croll et al. 2005) while Chl *a* was lower than 0.5 mg m^{-3} in the Gulf of Alaska until the spring phytoplankton bloom (Park et al. 2007). In southeastern Alaska Dungeness crab larvae are released mostly in May and June (Shirley et al. 1987, Fisher 2006) long after the peak phytoplankton bloom, but when alternative prey such as small crustacean nauplii occur (Coyle & Paul 1990, Paul et al. 1990a,b). Without sufficient food, planktonic larvae reach a PNR (Point of No Return) in which larvae cannot molt to the next stage because of the lack of energy necessary for development (McConaugha 1985). Dungeness crabs are planktonic, have few stored energy reserves, and will not develop without feeding (Hartman & Letterman 1978, Sulkin et al. 1998).

Temperatures during winter may be most critical for survival of Dungeness crab larvae. Temperatures during larval periods in the southern parts of the Dungeness crab distribution (Lough 1976, Reilly 1983) are similar to the summer temperature of southeastern Alaska. In several bays in southeastern Alaska, the SST in November through March is approximately 2-5°C (Matthews 1981, Wing & Pella 1998, Etherington et al. 2004). Temperatures below approximately 6°C are deleterious to larval survival (Reed 1969) and development of Dungeness crabs (Jamieson & Phillips 1993). Thus, cold temperatures and scarce prey during winter in our study area preclude for larvae to overwintering or early hatching of Dungeness crab larvae.

It is more likely that late stage larvae are advected from more southerly locations where they hatch earlier. Larvae hatch 3-4 months earlier off the coasts of British Columbia and northern Washington than in our study area in southeastern Alaska (Cleaver 1949, Butler 1956, McConnaughey et al. 1994). The time required to complete larval development is about 4 months at 9-13°C off the coasts of California, Oregon and British Columbia (Lough 1976, Reilly 1983, Jamieson & Phillips 1988), and 111 days at 10.5°C in the laboratory (Poole 1966) and 70 days at 10°C from ZI to ZV (Sulkin & McKeen 1989). Late-stage larvae hatch off the Washington and British Columbia coasts in January and February (Cleaver 1949, Jamieson & Phillips 1988) and may have been transported to southeastern Alaska during their larval period by the Alaska Current flowing northward throughout the year (Reed & Schumacher 1986). The Alaska Current flows northward in winter and in early spring flows faster in a narrower width and deeper depth (Reed & Schumacher 1986). Buoy drift tracks and wind patterns support the contention that larvae hatched off the coasts of Washington and British Columbia can be transported to off southeastern Alaska (Park et al. 2007). In addition, larvae transported a long distance from off the coasts of Washington and British Columbia could be advected into inland waters such as Icy Strait. Strong tidal water movement based on the velocity measured with an Acoustic Current Depth Profiler (ACDP) was reported within our study area (Cokelet et al. 2007). According to a case model conducted with buoys, a tidal movement from Cross Sound into Glacier Bay during a flood tide transported a buoy 43 km (Hooge &Hooge 2002). Tidal movements may have transported unusually late stage larvae into inland waters such as Icy Strait.

However, unusually late stage larvae did not occur in consistent density annually (Figure 1.2). The pathway for larval transport from northern Washington and British Columbia to southeastern Alaska contains many temporary baroclinic eddies and meanders including the Sitka eddy (Tabata 1982, Swaters & Mysak 1985). These eddies and meanders can deviate the paths of larval transport or entrap larvae in eddies for the remainder of their larval life. Some buoys remained in the eddies until their batteries were depleted while others drifted offshore (David Douglas, USGS, Juneau, unpubl. data). Only 7 of 49 buoys deployed off Washington and British Columbia coasts arrived in off southeastern Alaska (Park et al. 2007); this inconsistency of currents explains internannual variability of abundance of larvae that might have been transported to southeastern Alaska.

Dungeness crab larvae could be advected into our study area from relatively short distances. Southeastern Alaska encompasses numerous inland waterways that have nontidal currents flowing in one direction as a result of freshwater discharge (Haight 1926). Nontidal currents from Wrangle Narrows to a point near the western end of Icy Strait through Chatham Strait was observed by spar buoys (Figure 1, Haight 1926). Also, two drift bottles that were deployed off the northwestern Queen Charlotte Island were transported to Icy Strait (Dodimead et al. 1963). Dungeness crabs inhabit bays, estuaries and open-ocean coasts (Hoopes 1973) from the intertidal (Hart 1982) to 200 m depth (Scheding 2004) on many kinds of substrates, but prefer sandy and muddy areas (Scheding 2004). Dungeness crabs are harvested in many bays, estuaries and the entire opencoast of the Gulf of Alaska in southeastern Alaska (Koeneman 1985, Stone & O'Clair 2001) and British Columbia (Jamieson 1985). Larvae hatched in inland waters may have been transported to our study area through the Chatham Strait, a 240 km long and narrow passage that separates Chichagof Island and Baranof Island from Admiralty Island (Fig. 1, Haight 1926). Also, larvae hatched from the population along the open coast of southeastern Alaska could be transported to our study area by the northward following Alaska Current. If larvae were transported from a closer site to our study site with similar hatch timing, allochthonous and local produced larvae could not easily be discerned because of their similar larval stages. Larvae with different rostrum lengths resulting from different incubation temperatures might provide evidence of larval advection from relatively closer distances. Different rostrum lengths at the same sampling stations are discussed in detail in the chapter 2.

Larvae hatched in our study area may be advected to other areas. Several locations within our study sites contain large aggregations of ovigerous females (O'Clair et al. 1996, Scheding et al., 2001, Stone & O'Clair 2002, Scheding 2004). Numerous larvae are produced from these females and might be advected by the strong tidal currents. Repeated tidal exchanges may disperse larvae that hatched within our study sites to coastal areas. If larvae are advected offshore from the Cross Sound, Icy Strait, Upper Chatham transects and from Glacier Bay, larval densities in the Icy Point transect should have been high throughout the sampling period. However, high densities did not occur at any stations in the Icy Point transect. A few larvae were collected in the Icy Point, the only offshore transect in our study site, which extended to 65 km from the coast (Table 1.1). Northward winds contribute surface water to landward so that larvae may be transported landward. Also, larvae that were advected from inland waters might be immediately entrained by the Alaska Coastal Current so that the larvae might not be dispersed far offshore, but instead transported northward. However, although the Alaska Coastal Current is a fast flowing current that is unidirectional throughout the year (Schumacher et al. 1989), fronts and eddies are generated by wind forces (Stabeno et al. 1996) and wave-current interaction (Liu et al. 1994). Walleye Pollock eggs and larvae were retained in the coastal area (Stabeno et al. 1996, Bailey et al. 1999). Similarly, Dungeness crab larvae that might be advected from inland waters and coastal areas in southeastern Alaska might be entrained by these fronts and eddies on the coast. However, mechanisms by which larvae would be advected back to inland waters cannot be easily addressed.

Dungeness crab larvae have been reported to be dispersed long distances offshore in California, Oregon, Washington and British Columbia (Lough 1976, Reilly 1983, Jamieson & Phillips 1988, 1993, Jamieson et al. 1989, Jamieson & Armstrong 1991). The general pattern of larval distribution when larvae are dispersed offshore is that the ZI occurs near shore and post ZI are found progressively offshore (Lough 1976, Reilly

1983). No ZI were found within 20 km seaward of the Golden Gate Bridge in San Francisco Bay, California, but maximum densities occurred 25-30 km seaward when the plume was located about 15 to 20 km seaward (Reilly 1983). Late intermolt stage megalopae predominate inshore (Hatfield 1983, Jamieson & Phillips 1988, 1993, Eggleston & Armstrong 1995, Miller & Shanks 2004). In our study, a different pattern in larval abundance was observed. ZI were collected at every station, and subsequent stages occurred at the same stations except those of the Icy Point transect until July. In sharp contrast, in California and Oregon larvae were dispersed offshore for ontogeny (Lough 1976, Reilly 1983).

A few late stage larvae were found in our study sites in the upper 20 m from the surface at day and night in August, but no larvae were collected in September (Park & Shirley 2005). The low density of late stage larvae throughout our study, particularly in July and August and Park & Shirley (2005) may have resulted from stage-specific larval behavior in which ZV are positioned at deeper depths (Lough 1976; Reilly 1983). Almost all (98.8 %) of ZV were collected deeper than 915 m (Reilly 1983). Although our study site is not deep (Table 1.1), ZV may have been located at depths deeper than our samples, resulting in a sampling bias. Vertical migration of larval Dungeness crab to cold and deep water may delay larval development and the timing of settlement (Jamieson & Phillips 1993). ZV residing at cold and deep depths may delay their larval development during the summer and their molt to megalopae in September. In addition, the lack of megalopae collections in September 1997-2000 in our study and Park & Shirley (2005) presents a sharp contrast to the high abundance found in the light traps in

Glacier Bay (G. Eckert, University of Alaska Southeast, unpubl. data). Megalopal abundance in Glacier Bay was extremely pulsed in late September and October; our sampling was only two days and we might miss the pulse, and we did not sample in October, a period of higher megalopal concentration. This difference in megalopal abundance may have resulted from the use of different sampling gear. Neuston nets, light traps, and night time sampling can be more effective for sampling photopositive organisms (Choat et al. 1993) than vertical tows with conical nets, as megalopae are strong swimmers (Jamieson & Phillips 1988, Hobbs & Botsford 1992, Fernandez et al. 1994). Collection of megalopae by means of oblique plankton tows was poor in other larval studies of Dungeness crabs (Lough 1976, Reilly 1983, Porter et al. in press). Light traps collected significantly more megalopae than plankton tows, however plankton tows collected more zoeae (Porter et al. in press). If Bongo nets were an adequate sampling gear to collect megalopae, megalopae should have been collected in high abundance in September from 1997 to 2000 in our study and Park & Shirley (2005). Also, daytime sampling for megalopae may not be optimal for accurate estimation of relative megalopal abundance because of net avoidance (Jamieson et al. 1989).

Our grouping of larval stages for some analyses may have smoothed the complexity that resulting from having many larval stages with low densities at the same station. Grouping larval stages implies the combining of larval durations of two or more stages, however we used ZI along, but combined ZII and ZIII as intermediate stages and grouped ZIV, ZV, and megalopae as late larval stages. Because Dungeness crab larvae vertically migrate (Park & Shirley 2005, Hobbs & Botsford 1992) and have stage specific depth positioning (Lough 1976), we do not know the temperature at which larvae were located. We cannot estimate the duration of each larval stage or the combined larval stages. Monthly changes in temperature alter the duration of larval stages. Even if larvae were the same stage, larvae occurred in warmest summer have shortest larval duration.

Overall, we cannot definitely state whether larvae were advected or retained in our study area. However, larvae appear to have been advected into our study sites from distant sites where hatching had occurred earlier. The pattern of distribution of larval stages in our study area was markedly different from what has been reported from the coastal waters of California, Oregon, Washington and British Columbia. This alternate life history pattern merits further research and consideration.

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Literature Cited

ArcGIS9.1 (2001) ArcGIS Geostastitical Analyst. ESRI, Redlands, CA

Bailey KM, Bond NA, Stabeno PJ (1999) Anomalous transport of walleye Pollock larvae linked to ocean and atmosphric patterns in May 1996. Fish Oceanogr 8:264-273

Batten SD, Welch DW (2004) Changes in oceanic zooplankton populations in the north-east Pacific associated with the possible climatic regime shift of 1998/1999. Deep Sea Res II 51:863-873

Botsford LW, Hobbs RC (1995) Recent advances in the understanding of cyclic behavior of Dungeness crab (*Cancer magister*) populations. ICES Mar Sci Symp 199:157-166

Butler TH (1956) The distribution and abundance of early larval stages of the British Columbia commercial crab. Fish Res Board Can Prog Rep 99:3-5

Choat JH, Doherty PJ, Kerrigan BA, Leis JM (1993) A comparison of towed nets, purse seine, and light-aggregation devices for sampling larvae and pelagic juveniles of coral reef fishes. Fish Bull 91:195-209

Christy JH, Morgan SG (1998) Estuarine immigration by crab postlarvae: mechanisms, reliability and adaptive significant. Mar Ecol Prog Ser 174:51-65

Cleaver FC (1949) Preliminary results of the coastal crab (*Cancer magister*) investigation. Washington State Biol Rep 49:49-82

Cokelet ED, Jenkins AJ, Etherington LL (2007) A transport of Glacier Bay ocean currents measured by Acoustic Doppler Current Profiler (ADCP). In: Piatt JF, 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, D. C., p 74-77

Coyle KO, Paul AJ (1990) Abundance and biomass of meroplankton during the spring bloom in an Alaskan Bay. Ophelia 32:199-210

Coyle KO, Paul AJ, Ziemann DA (1990) Copepod populations during the spring bloom in an Alaskan subartic embayment. J Plank Res 12:759-779

Croll DA, Marinovic B, Benson S, Chavez FP, Black N, Ternullo R, Tershy BR (2005) From wind to whales: trophic links in a coastal upwelling system. Mar Ecol Prog Ser 289:117-130.

Cronin TW, Forward RB Jr (1979) Tidal vertical migration: an endogenous rhythm in estuarine crab larvae. Science 205:1020-1022

DiBacco C, Sutton D, McConnico L (2001) Vertical migration behavior and horizontal distribution of brachyuran larvae in a low-inflow estuary: implications for bay-ocean exchange. Mar Ecol Prog Ser 217:191-206

Dodimead AJ, Favorite F, Hirano T (1963) Salmon of the North Pacific Ocean. Part II. Review of oceanography of the subarctic Pacific region. Int North Pac Fish Comm Bull 33

Eggleston DB, Armstrong DA (1995) Pre- and post-settlement determinants of estuarine Dungeness crab recruitment. Ecol Monogr 65:193-216

Epifanio CE, Valenti CC, Pembroke AE (1984) Dispersal and recruitment of blue crab larvae in the Delaware Bay. Est Coast Shelf Sci 18:1-12

Etherington LL, Hooge PN, Hooge ER (2004) Factors affecting seasonal and regional pattern of surface water oceanographic properties within a fjord estuarine system: Glacier Bay, AK. U.S. Geological Survey, Alaska Science Center, Gustavus, AK

Fernandez M, Iribane OO, Armstrong DA (1994) Swimming behavior of Dungeness crab, *Cancer magister*, megalopae in still and moving water. Estuaries 17:271-275

Fiedler PC (2002) Environmental change in the eastern tropical Pacific Ocean: review of ENSO and decadal variability. Mar Ecol Prog Ser 244:265-283

Fisher JL (2006) Seasonal timing and duration of brachyuran larvae in a high-latitude fjord. Mar Ecol Prog Ser 323:213-222

Haight FJ (1926) Nontidal currents in southeastern Alaska. Geograph Rev 16:642-646

Haldorson L, Pritchett M, Sterritt D, Watts, J (1993) Abundance patterns of marine fish larvae during spring in a southeastern Alaskan Bay. Fish Bull 91:36-44

Halliwell GH, Allen JS (1987) Large-scale coastal wind field along the west coast of North America, 1981-1982. J Geophys Res 92:1861-1884

Hart JFL (1982) Crabs and their relatives of British Columbia. British Columbia Prov Museum Handbook 40

Hartman M, Letterman G (1978) An evaluation of three species of diatoms as food for *Cancer magister* larvae. In: Avault JW (ed) Proc 9th Annual Meeting of World Mariculture Society. Louisiana State University Press, Lafayette, p 272-276

Hatfield SE (1983) Distribution of zooplankton in association with Dungeness crab, *Cancer magister*, larvae in California. In: Wild PW, Tasto RN (eds.) Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California fishery resource. Cal Dep. Fish Game, Long Beach, CA. Fish Bull 172, p 97-124

Hickey BM, Banas NS (2003) Oceanography of the U.S. Pacific Northwest coastal ocean and estuaries with application to coastal ecology. Estuaries 26:1010-1031

Higgins K, Hastings A, Sarvela JN, Botsford LW (1997) Stochastic dynamics and deterministic skeletons: Population behavior of Dungeness crab. Science 276:1431-1435

Hinz S, Sulkin S, Strom S, Testermann J (2001) Discrimination in ingestion of protistan prey by larval crabs. Mar Ecol Pro Ser 222:155-162

Hobbs RC, Botsford LW (1992) Diel vertical migration and timing of metamorphosis of larvae of the Dungeness crab *Cancer magister*. Mar Biol 112:417-428

Hobbs RC, Botsford LW, Thomas A (1992) Influence of hydrographic conditions and wind forcing on the distribution and abundance of Dungeness crab, *Cancer magister,* larvae. Can J Fish Aquat Sci 49:1379-1388

Hooge PN, Hooge ER (2002) Fjord oceanographic processes in Glacier Bay, Alaska. USGS Alaska Biological Science Center, Anchorage, AK

Hoopes DT (1973) Alaska's fishery resources: the Dungeness crab. NMFS. Fishery Facts 6

Hunt GL, Stabeno P, Walters G, Sinclair E, Brodeur RD, Napp JM, Bond NA (2002) Climate change and control of the southeastern Bering Sea pelagic ecosystem. Deep-Sea Res II 49:5821-5853

Jamieson GS (1985) The Dungeness crab, *Cancer magister*, fisheries of British Columbia In: Proc Symp on Dungeness crab biology and management. University of Alaska, Sea Grant College Program Report 85-3, p 37-60

Jamieson GS, Armstrong DA (1991) Spatial and temporal recruitment patterns of Dungeness crab in the northeast Pacific. Mem Queens Mus 31:365-381

Jamieson GS, Phillips AC (1988) Occurrence of *Cancer* crab (*C. magister* and *C. oregonensis*) megalopae off the west coast of Vancouver Island, British Columbia. Fish Bull 86:525-542

Jamieson GS, Phillips AC (1993) Megalopal spatial distribution and stock separation in Dungeness crab (*Cancer magister*). Can J Fish Aquat Sci 50:416-429

Jamieson GS, Phillips AC, Huggett WS (1989) Effects of ocean variability on the abundance of Dungeness crab (*Cancer magister*) megalopae. In: Beamish RJ, McFarlane GA (eds) Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. Can Spec Publ Fish Aquatic Sci 108, p 305-325

Koeneman TM (1985) A brief review of the commercial fisheries for *Cancer magister* in southeast Alaska and Yakutat waters, with emphasis on recent seasons. In: Proc Symp on Dungeness crab biology and management. University of Alaska, Sea Grant College Program Report 85-3, p 61-83

Lambert R, Epifanio CE (1982) A comparison of dispersal strategies in two genera of brachyuran crab in a secondary estuary. Estuaries 5:182-188

Liu AK, Peng CY, Schumacher JD (1994) Wave-current interaction study in the Gulf of Alaska for detection of eddies by synthetic aperture radar. J Geophys Res 99:10075-10085

Lough RG (1976) Larval dynamics of the Dungeness crab, *Cancer magister* off the central Oregon coast, 1970-71. Fish Bull 74:353-375

MacKay DG (1942) The Pacific edible crab, *Cancer magister*. Fish Res Board Can Bull 62:1-32

Matthews JB (1981) The seasonal circulation of the Glacier Bay, Alaska fjord system. Est Coast Shelf Sci 12:679-700

McConaugha JR (1985) Nutrition and larval growth. In: Wenner AM (ed) Larval growth, Crustacean Issue 2. Balkema, Rotterdam, Netherlands, p 127-154

McConaugha JR (1988) Export and reinvasion of larvae as regulators of estuarine decapod populations. Amer Fish Soc Symp 3:90-103

McConnaughey RA, Armstrong DA, Hickey BM, Gunderson DR (1992) Juvenile Dungeness crab (*Cancer magister*) recruitment variability and oceanic transport during the pelagic larval phase. Can J Fish Aquat Sci 49:2028-2044

McConnaughey RA, Armstrong DA, Hickey BM, 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

Methot RD (1988) Management of a cyclic resource: the Dungeness crab fisheries of the Pacific Coast of North America. In: Caddy JF (ed) Marine invertebrate fisheries: their assessment and management. John Wiley & Sons, Rome, Italy, p 205-223

Miller JA, 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

Moloney CL, Botsford LW, Largier JL (1994) Development, survival and timing of metamorphosis of planktonic larvae in a variable environment: the Dungeness crab as an example. Mar Ecol Prog Ser 113:61-79

Monteleone DM, Peterson WT, Williams GC (1987) Interannual fluctuations in the density of sand lance, *Ammodytes americanus*, larvae in Long Island Sound, 1951-1983. Estuaries 10:246-254

Moore NM (2003) Temporal patterns of ingestion of the dinoflagellate *Prorocentrum micans* by newly-hatched brachyuran crab larvae. MS thesis, Western Washington University, WA

O'Clair RM, O'Clair CE (1998) Southeast Alaska's Rocky Shores: Animals. Plant Press, Juneau, AK

O'Clair CE, Shirley TC, Taggart SJ (1996) Dispersion of adult *Cancer magister* at Glacier Bay, Alaska: Variation with spatial scale, sex, and reproductive status. In: High Latitude Crabs: Biology, Management, and Economics. Lowell Wakefield Fisheries Symposium. Alaska Sea Grant College Program Report AK-SG-96-02, p 209-227

Orensanz JM, Armstrong J, Armstrong D, Hilborn R (1998) Crustacean resources are vulnerable to serial depletion-the multifaceted decline of crab and shrimp fisheries in the Greater Gulf of Alaska. Rev Fish Biol Fisher 8:117-176

Park W, 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

Park W, Douglas DC, Shirley TC (2007) North to Alaska: Evidence for conveyor belt transport of Dungeness crab larvae along the west coast of the United States and Canada. Limnol Oceanogr 52:248-256

Paul AJ, Coyle KO, Ziemann DA (1990a) Variation in egg production rates by *Pseudocalanus* spp. in a subarctic Alaskan bay during the onset of feeding by larval fish. J Crust Biol 10:648-658

Paul AJ, Coyle KO, Ziemann DA (1990b) Timing of spawning of *Thysanoessa raschii* (Euphausiacea) and occurrence of their feeding-stage larvae in an Alaskan bay. J Crust Biol 10:69-78

Perez MF, Sulkin SD (2005) Palatability of autotrophic dinoflagellates to newly hatched larval crabs. Mar Biol 146:771-780

Peterson WT (1973) Upwelling indices and annual catches of Dungeness crab, *Cancer magister*, along the west coast of the United States. Fish Bull 72:902-910

Philander G (1989) El Niño and La Niña. Amer Sci 77:451-459

Poole RL (1966) A description of the laboratory-reared zoeae of *Cancer magister* Dana, and megalopae taken under natural conditions (Decapoda, Brachyura). Crustaceana 11:83-97

Porter SS, Eckert GL, Byron CJ, Fisher JL (in press) Comparison of light traps and plankton tows for sampling Brachyuran crab larvae in an Alaskan Fjord. J Crust Biol

Reed PH (1969) Culture methods and effects of temperature and salinity on survival and growth of Dungeness crab (*Cancer magister*) larvae in the laboratory. J Fish Res Board Can 26:389-397

Reed PK, Schumacher JD (1986) Physical Oceanography. In: Hood DW, Zimmerman ST (eds) The Gulf of Alaska: Physical environment and biological resources. Ocean assessment division, NOAA, p 57-75

Reilly PN (1983) Dynamics of the Dungeness crab, *Cancer magister*, larvae off central and northern California. In: Wild PW, Tasto RN (eds) Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California fishery resource. Cal Dept Fish Game, Long Beach, CA. Fish Bull 172, p 57-84

Roegner GC, Armstrong DA, Hickey BM, Shanks AL (2003) Ocean distribution of Dungeness crab megalopae and recruitment patterns to estuaries in southern Washington State. Estuaries 26:1058-1070

Scheding KA (2004) Dungeness crab depth distribution: effects of sea otters. MS thesis, University of Alaska, Fairbanks, AK

Scheding K, Shirley T, O'Clair CE, Taggart SJ (2001) Critical habitat for ovigerous Dungeness crabs. In: Kruse GH, Bez N, Booth A, Born MW, Hills S, Lipcius RN, Pelletier D, Roy C, Smith SJ, Witherell D (eds) Spatial processes and management of marine populations. 17th Lowell Wakefield Fisheries Symposium. University of Alaska Sea Grant College Program AK-SG-01-02, p 431-445

Schumacher JD, Stabeno PJ, Roach AT (1989) Volume transport in the Alaska Coastal Current. Cont Shelf Res 9:1071-1083.

Schwing FB, Murphree T, Green PM (2002) The Northern Oscillation Index (NOI): a new climate index for the Northeast Pacific. Prog Oceanogr 53:115-139

Shanks AL (1995) Orientated 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, Rice SD (1987) Latitudinal variation in the Dungeness crab, *Cancer magister*: zoeal morphology explained by incubation temperature. Mar Biol 95:371-376

Stabeno PJ, Schumacher JD, Bailey KM, Brodeur RD, Cokelet ED (1996) Observed patches of walleye Pollock eggs and larvae in Shelikof Strait, Alaska: their characteristics, formatin and persistence. Fish Oceanogr 5:81-91

Stone RP, O'Clair CE (2001) Seasonal movements and distribution of Dungeness crabs *Cancer magister* in a glacial southeastern Alaska estuary. Mar Ecol Prog Ser 214:167-176

Stone RP, O'Clair CE (2002) Behavior of female Dungeness crabs, *Cancer magister*, in a glacial southeast Alaska estuary: homing, brooding-site fidelity, seasonal movement, and habitat use. J Crust Biol 22:481-492

Sulkin SD, McKeen GL (1989) Laboratory study of survival and duration of individual zoeal stages as a function of temperature in the brachyuran crab *Cancer magister*. Mar Biol 103:31-37

Sulkin S, Blanco A, Chan J, Bryant M (1998) Effects of limiting access to prey on development of first zoeal stage of the brachyuran crabs *Cancer magister* and *Hemigrapsus oregonensis*. Mar Biol 131: 515-521

Sverdrup HU (1953) On conditions for the vernal blooming of phytoplankton. J Con Perm Int Explor Mer 18:287-295

Swaters GE, Mysak LA (1985) Topographically-induced baroclinic eddies near a coastaline, with application to the Northeast Pacific. J Phys Oceanogr 15:1470-1485

Swiney KM (1999) Reproductive cycle of the Dungeness crab, *Cancer magister*, in southeastern Alaska. MS thesis, University of Alaska Fairbanks, AK

Swiney KM, Shirley TC (2001) Gonad development of southeastern Alaska Dungeness crab, *Cancer magister*, under laboratory conditions. J Crust Biol 21:897-904

Swiney KM, Shirley TC, Taggart SJ, O'Clair CE (2003) Dungeness crab, *Cancer magister*, do not extrude eggs annually in southeastern Alaska: an in situ study. J Crust Biol 23:280-288

Tabata S (1982) The anticyclonic, baroclinic eddy off Sitka, Alaska, in the northeast Pacific Ocean. J Phys Oceangr 12:1260-1282

Tankersley RA, Forward RB Jr (1994) Endogenous swimming rhythms in estuarine crab megalopae: implications for flood-tide transport. Mar Biol 118: 415-423

Thomson RE (1981) Oceanography of the British Columbia coast. Can Spec Publ Fish Aquat Sci 56

Ware DM, McFarlane GA (1989) Fisheries production domain in the Northeastern Pacific Ocean. In: Beamish RJ, McFarlane (eds) Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. Can Spec Publ Fish Aquat Sci 108, p 359-379

Welch JM, Forward RB Jr (2001) Flood tide transport o blue crab, *Callinectes sapidus*, postlarvae: behavioral responses to salinity and turbulence. Mar Biol 139:911-918

Welch JM, Forward RB Jr, Howd PA (1999) Behavioral responses of blue crab *Callinectes sapidus* postlarvae to turbulence: implications for selective tidal transport. Mar Ecol Prog Ser 179:135-143

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

Wing BL (1997) Distribution of Sablefish, *Anoplopoma fimbria*, larvae in the eastern Gulf of Alaska: Neuston-net tows versus oblique tows. NOAA Technical Report NMFS 130:137-150.

Wing SR, Largier JL, Botsford LW, Quinn JF (1995) Settlement and transport of benthic invertebrates in an intermittent upwelling region. Limnol Oceanogr 40:316-329

Wing BL, Pella JJ (1998) Time series analyses of climatological records from Auke Bay, Alaska. U.S. Commer NOAA Tech Memo NMFS-AFSC-91

Zamon JE, Welch DW (2005) Rapid shift in zooplankton community composition on the northeast Pacific shelf during the 1998-1999 El Niño-LaNiña event. Can J Fish Aquat Sci 62:133-144

Ziemann DA, Conquest LD, Olaizola M, Bienfang PK (1991) Interannual variability in the spring phytoplankton bloom in Auke Bay, Alaska. Mar Biol 109:321-334

Ziemann DA, Bienfang PK, Fulton-Bennett KW, Kottenmeier W, Conquest LD (1993) Carbon budget for the spring bloom in Auke Bay, Alaska. Mar Biol 115:509-521

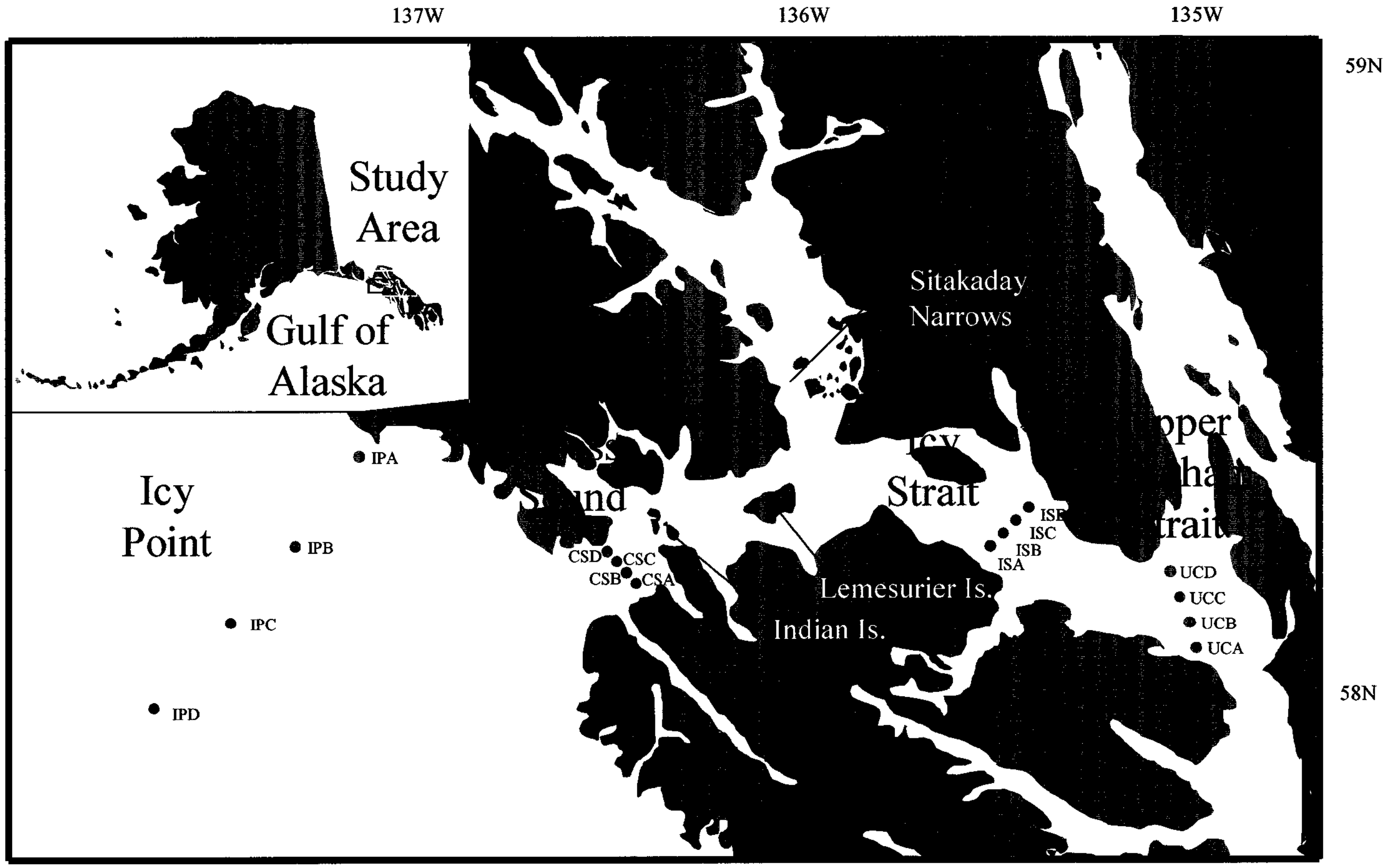


Figure 1.1. Zooplankton sampling stations in southeastern Alaska, May-September 1997-2004.

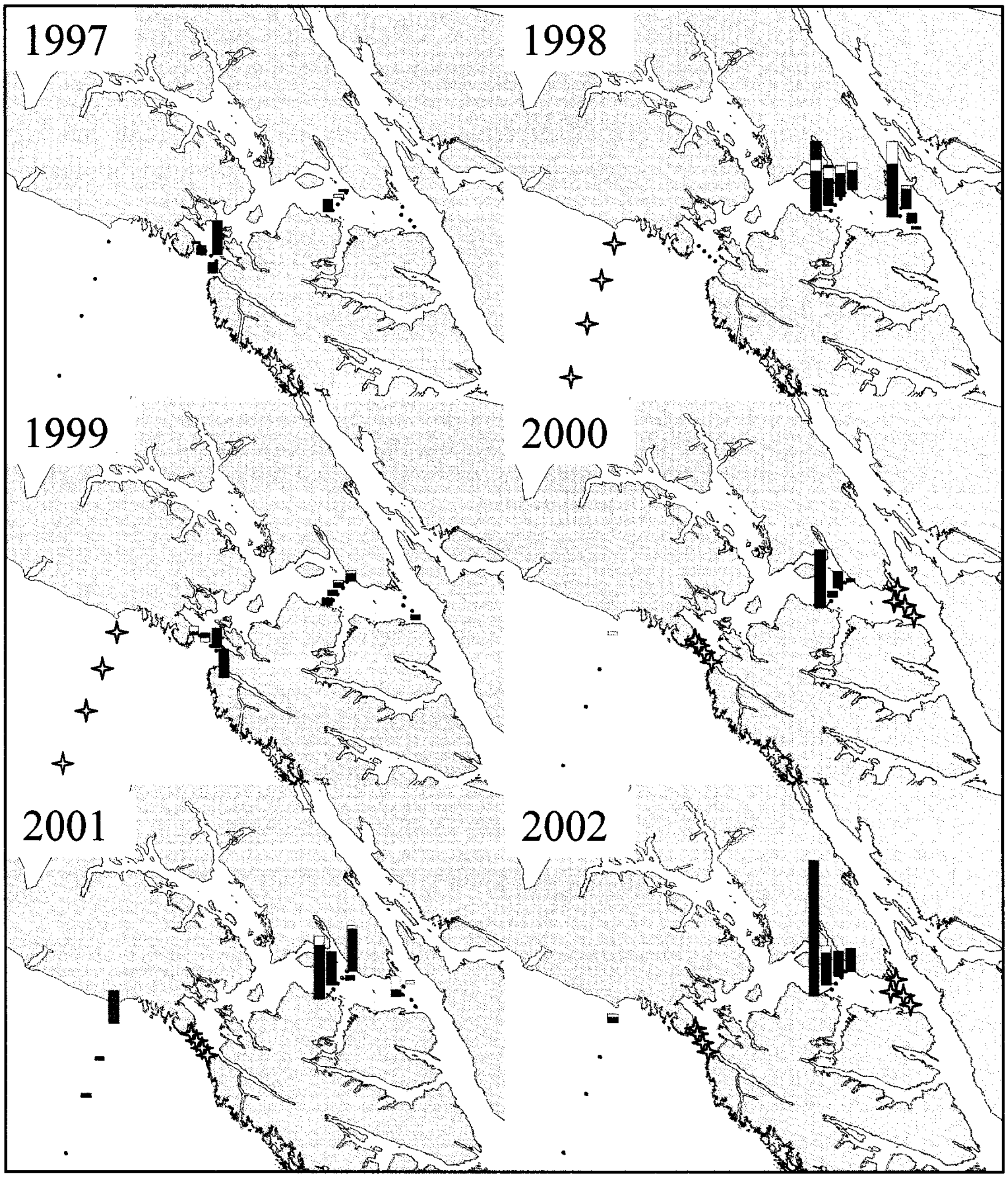
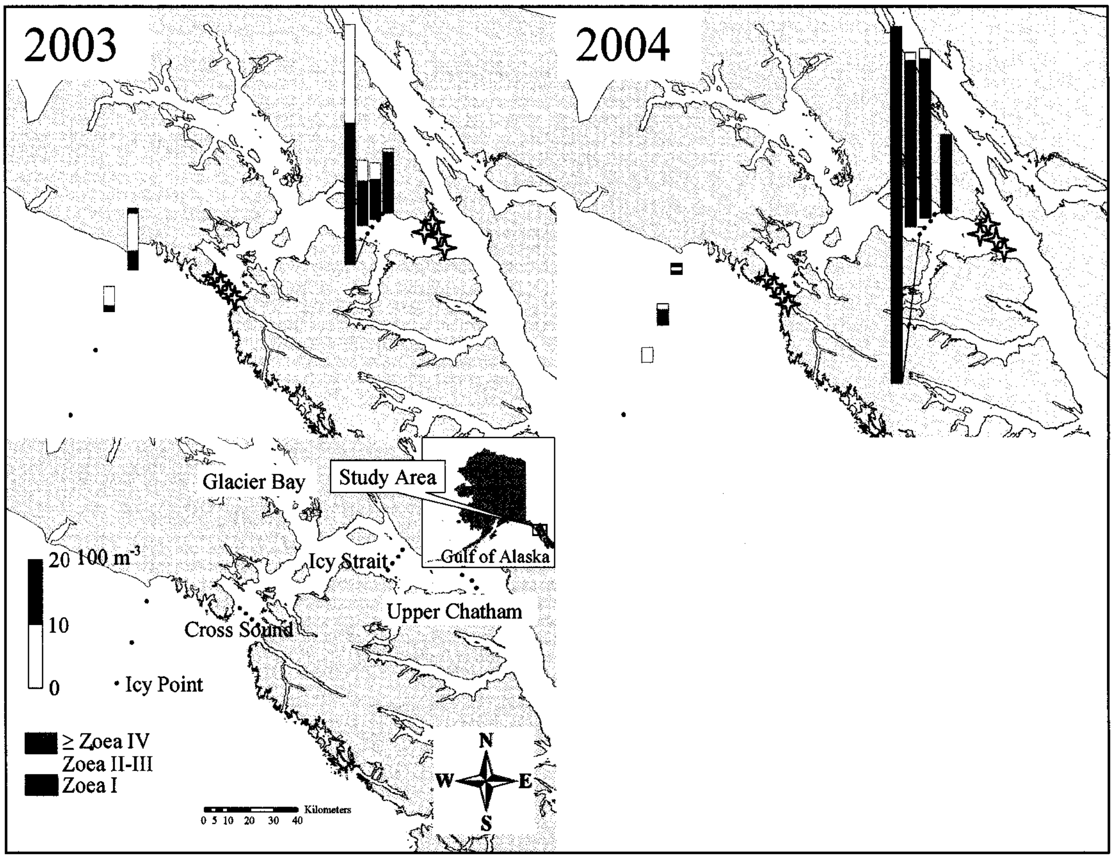


Figure 1.2. Interannual larval density of Dungeness crabs in May. Sampling period varied with transects: Icy Point in 1997, 2000-2004; Cross Sound during 1997-2000; Icy Strait during 1997-2004; Upper Chatham during 1997-2001. Height of the scale bar at middle left in the legend map indicates the density of Dungeness crab larvae (no 100 m^{-3}). Star symbols indicate no sampling.



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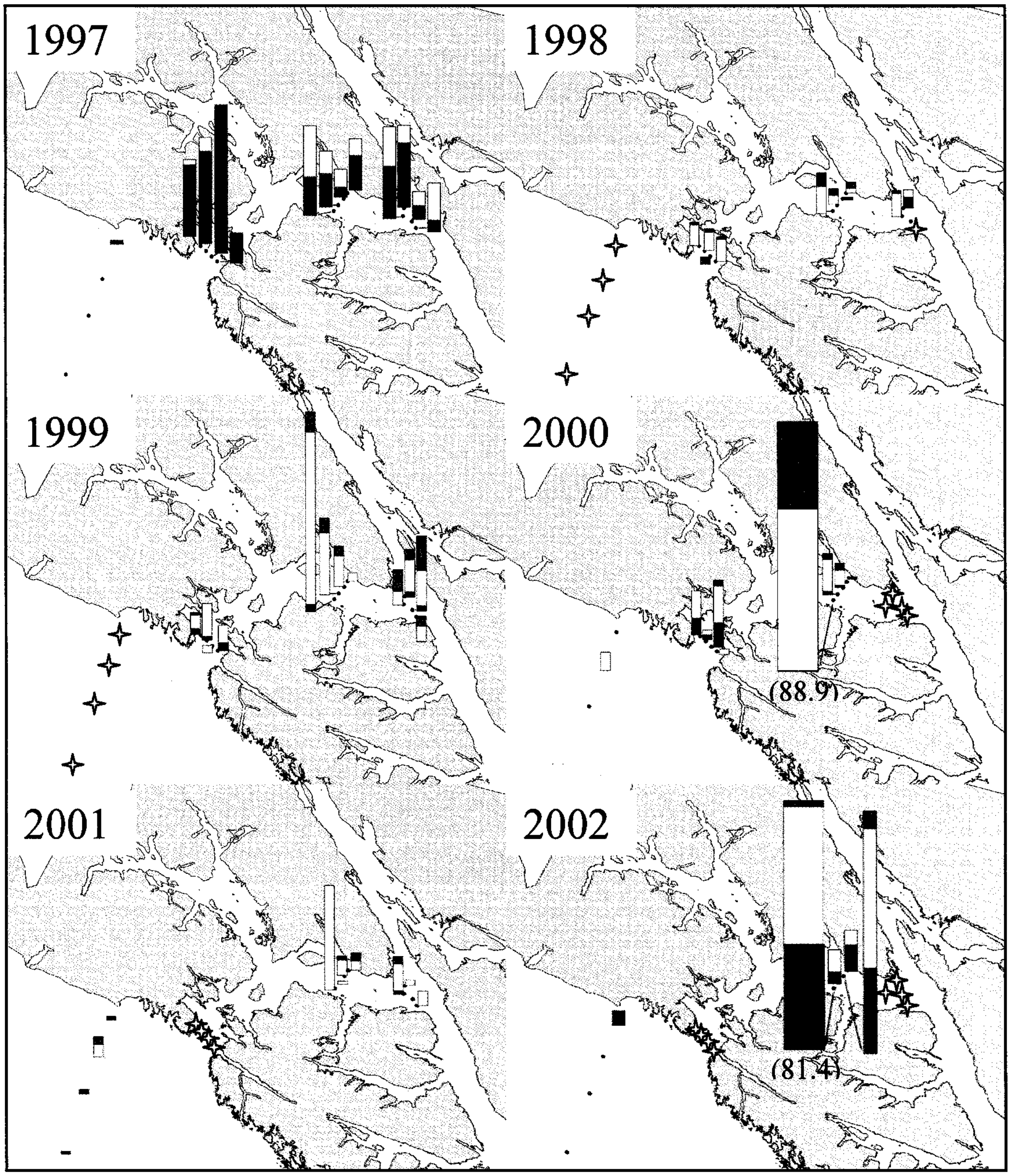
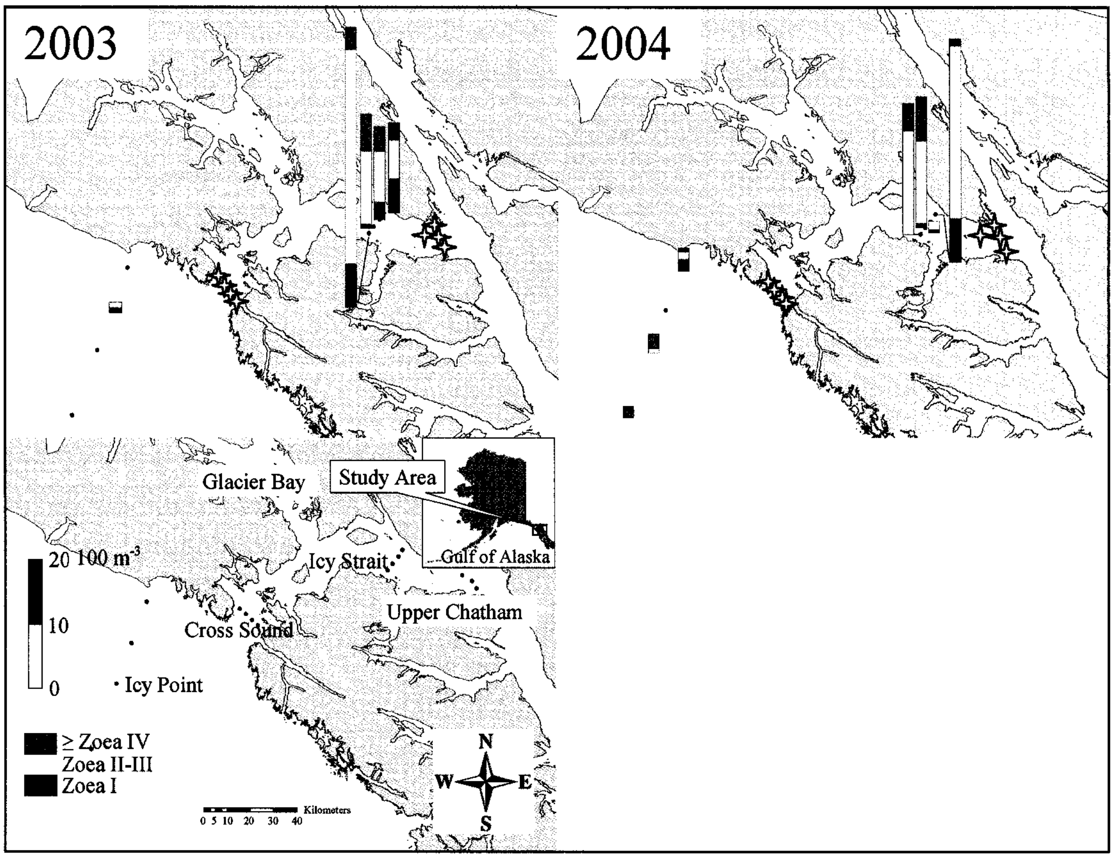


Figure 1.3. Interannual larval density of Dungeness crabs in June. Sampling period varied with transects: Icy Point in 1997, 2000-2004; Cross Sound during 1997-2000; Icy Strait during 1997-2004; Upper Chatham during 1997-2001. Height of the scale bar at middle left in the legend map indicates the density of Dungeness crab larvae (no 100 m^{-3}). Numbers below wide bars denote larval density. Star symbols indicate no sampling.



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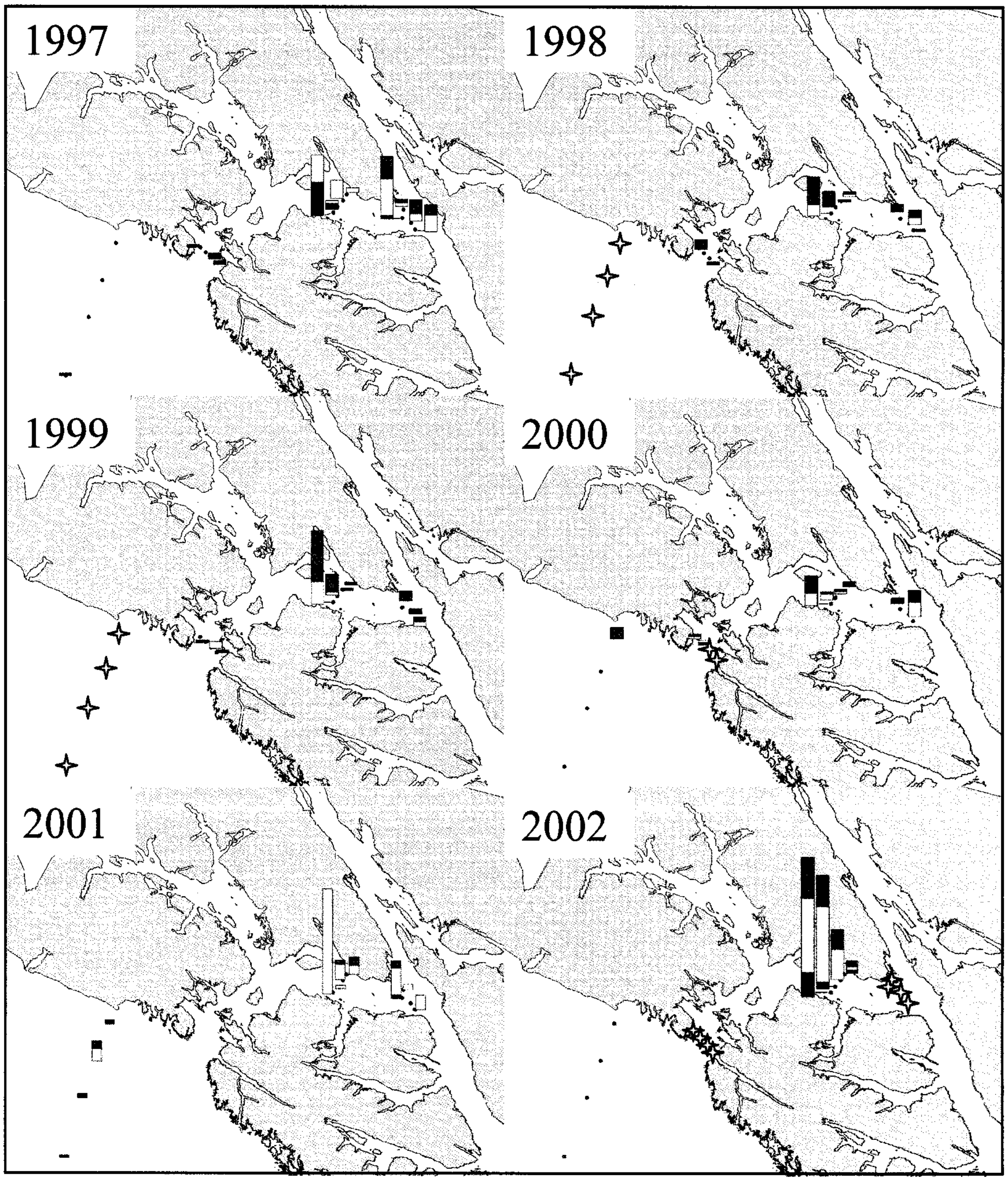
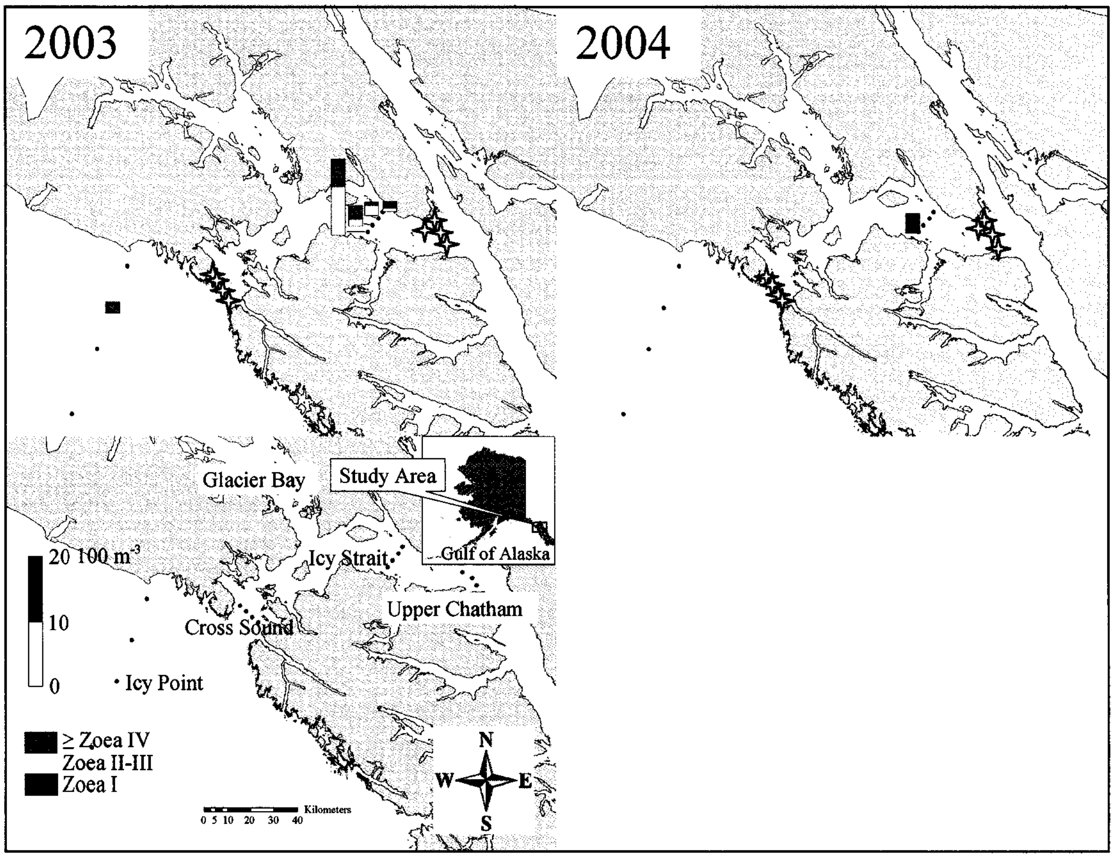


Figure 1.4. Internannual larval density of Dungeness crabs in July. Sampling period varied with transects: Icy Point in 1997, 2000-2004; Cross Sound during 1997-2000; Icy Strait during 1997-2004; Upper Chatham during 1997-2001. Height of the scale bar at middle left in the legend map indicates the density of Dungeness crab larvae (no 100 m^{-3}). Star symbols indicate no sampling.



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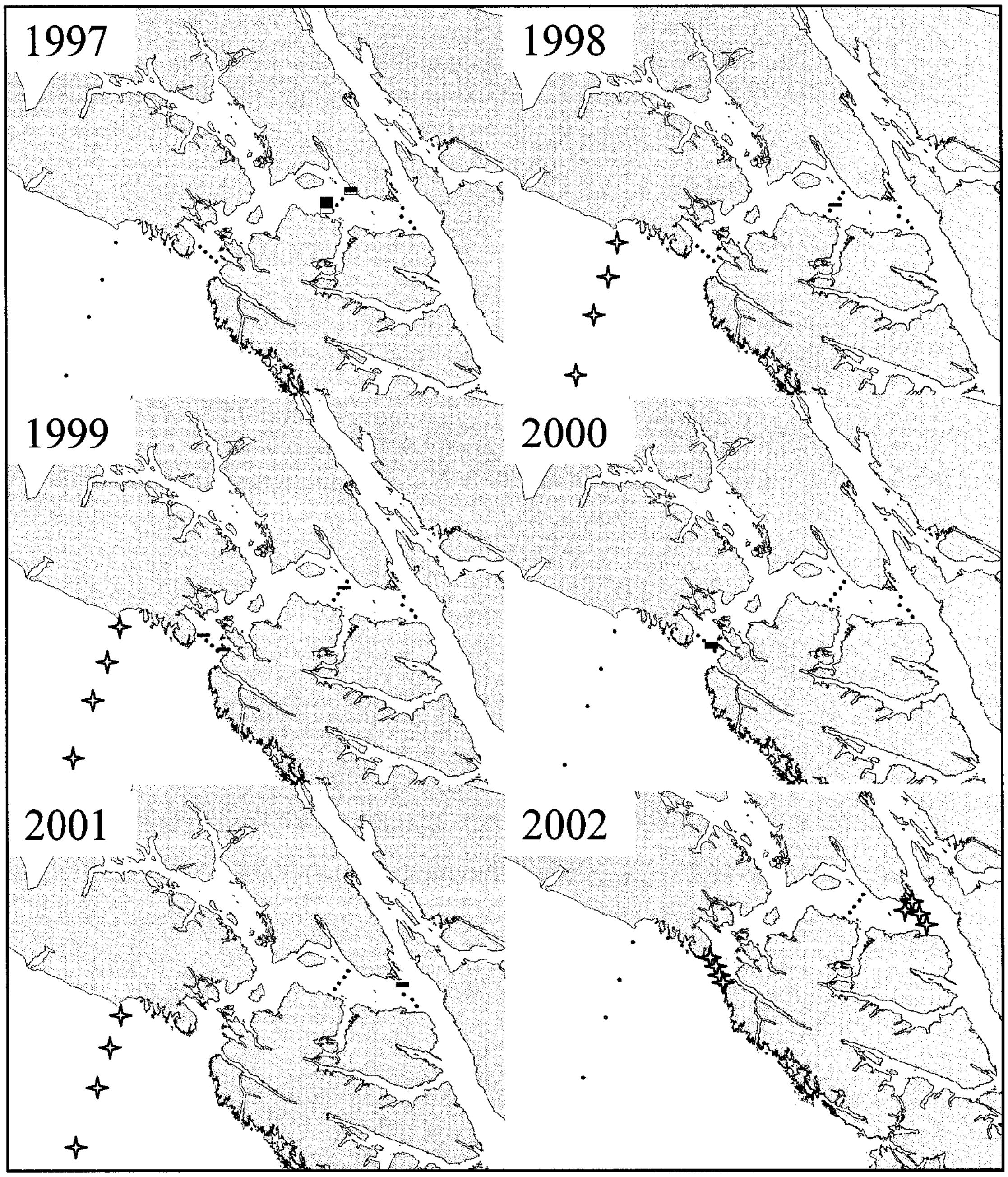
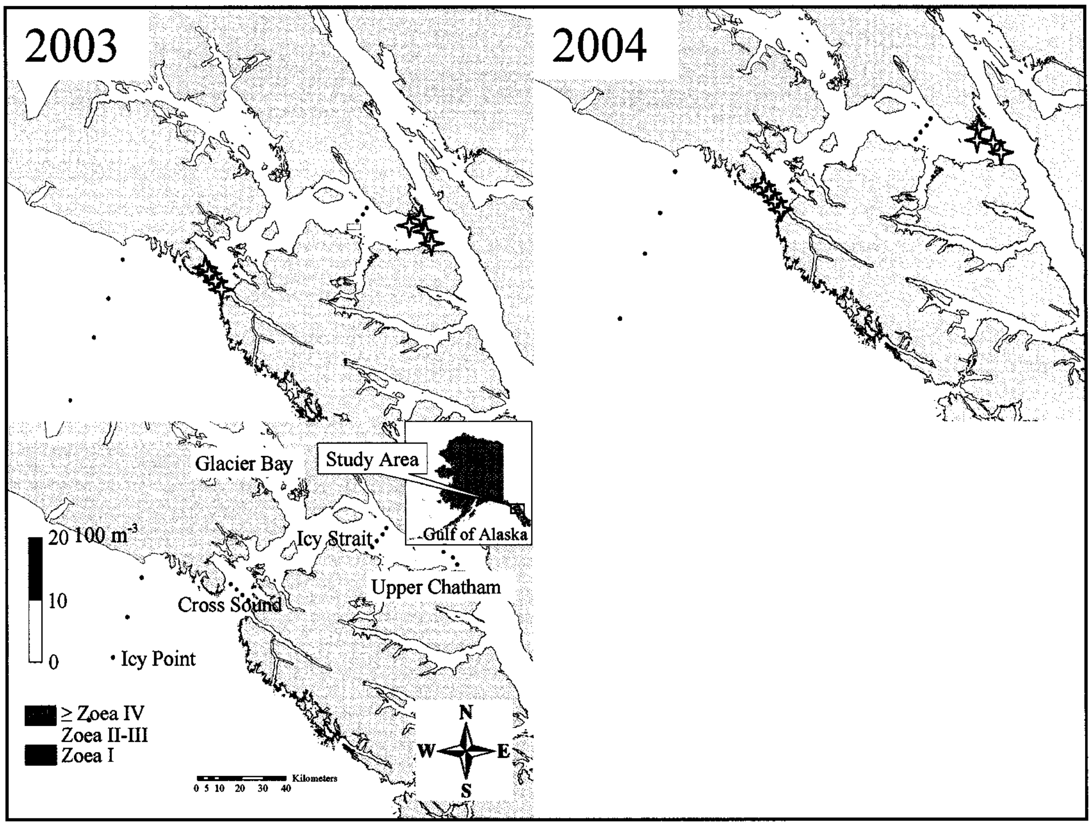


Figure 1.5. Interannual larval density of Dungeness crabs in August. Sampling period varied with transects: Icy Point in 1997, 2000-2004; Cross Sound during 1997-2000; Icy Strait during 1997-2004; Upper Chatham during 1997-2001. Height of the scale bar at middle left in the legend map indicates the density of Dungeness crab larvae (no 100 m^{-3}). Star symbols indicate no sampling.



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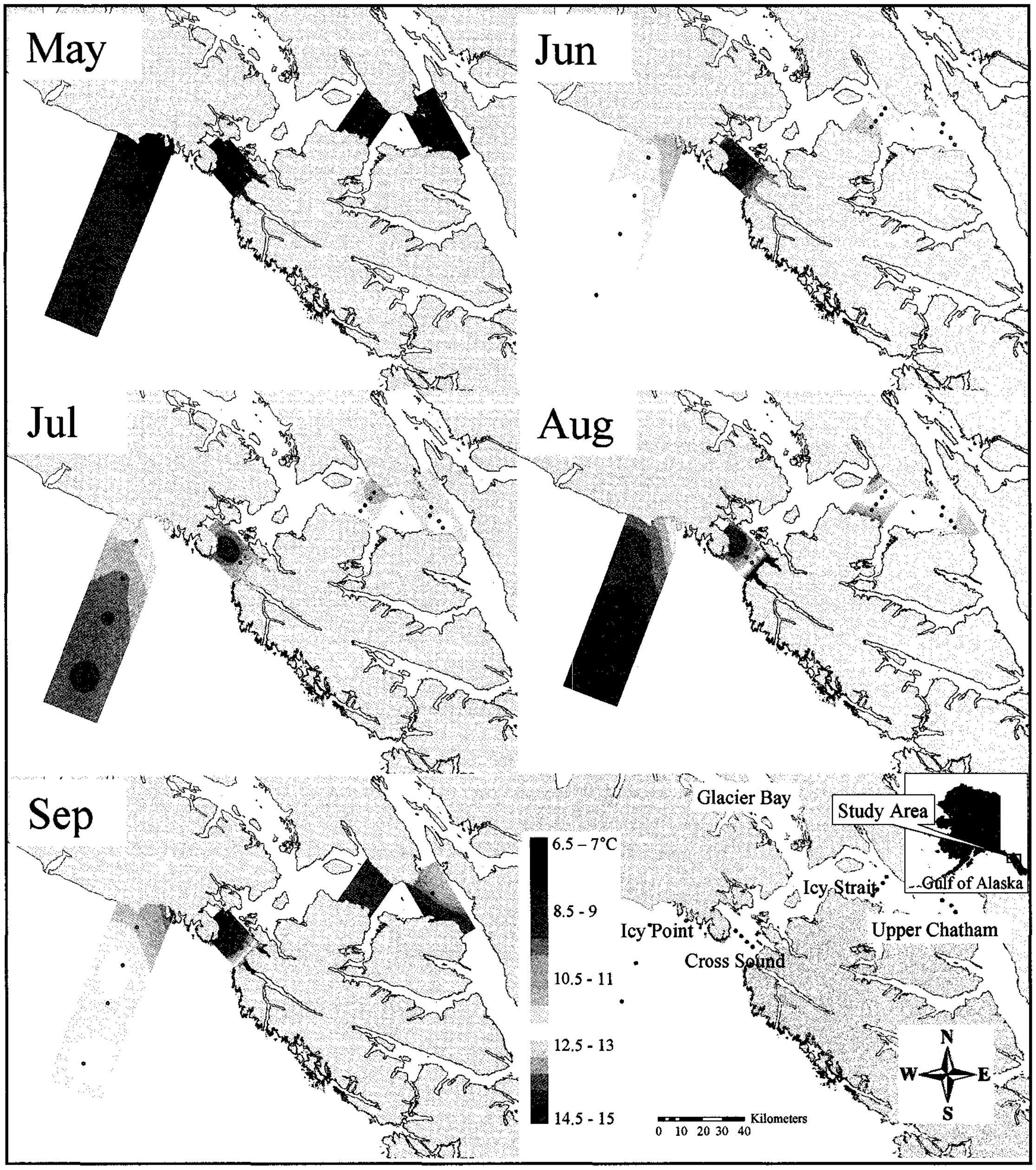

Figure 1.6. Seasonal change of sea surface temperature (SST) during 1997-2004. Sea surface temperatures were measured at 1 m depth using CTD (conductivity, temperature and depth). SSTs were averaged by month and imaged by Radius Base Functions in the geostatistical analyst extension of ArcGIS 9.1.

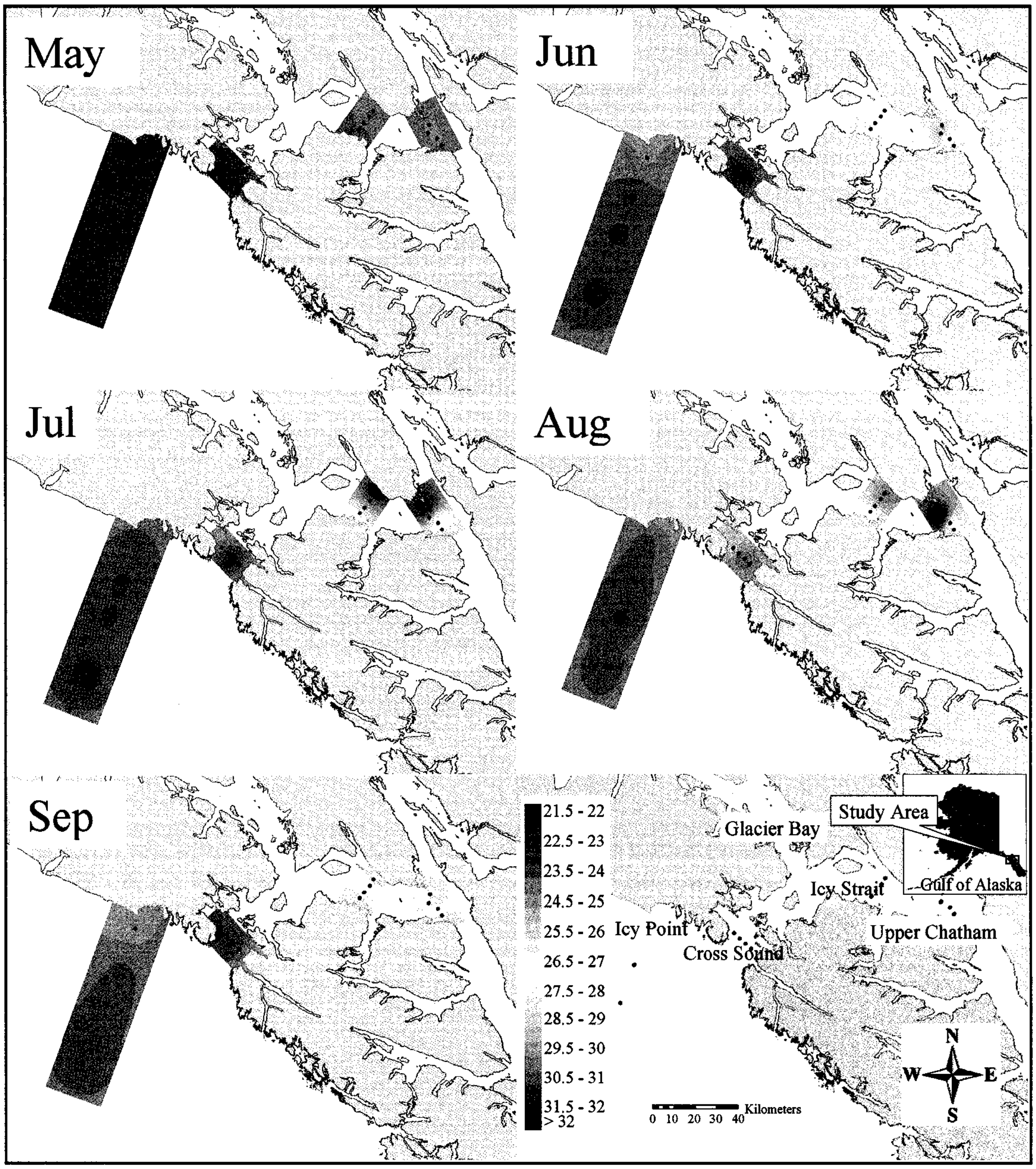

Figure 1.7. Seasonal change of sea surface salinity (SSS) during 1997-2004. Sea surface salinities were measured at 1 m depth using CTD (conductivity, temperature and depth). SSSs were averaged by month and imaged by Radius Base Functions in the geostatistical analysis extension of ArcGIS9.1.

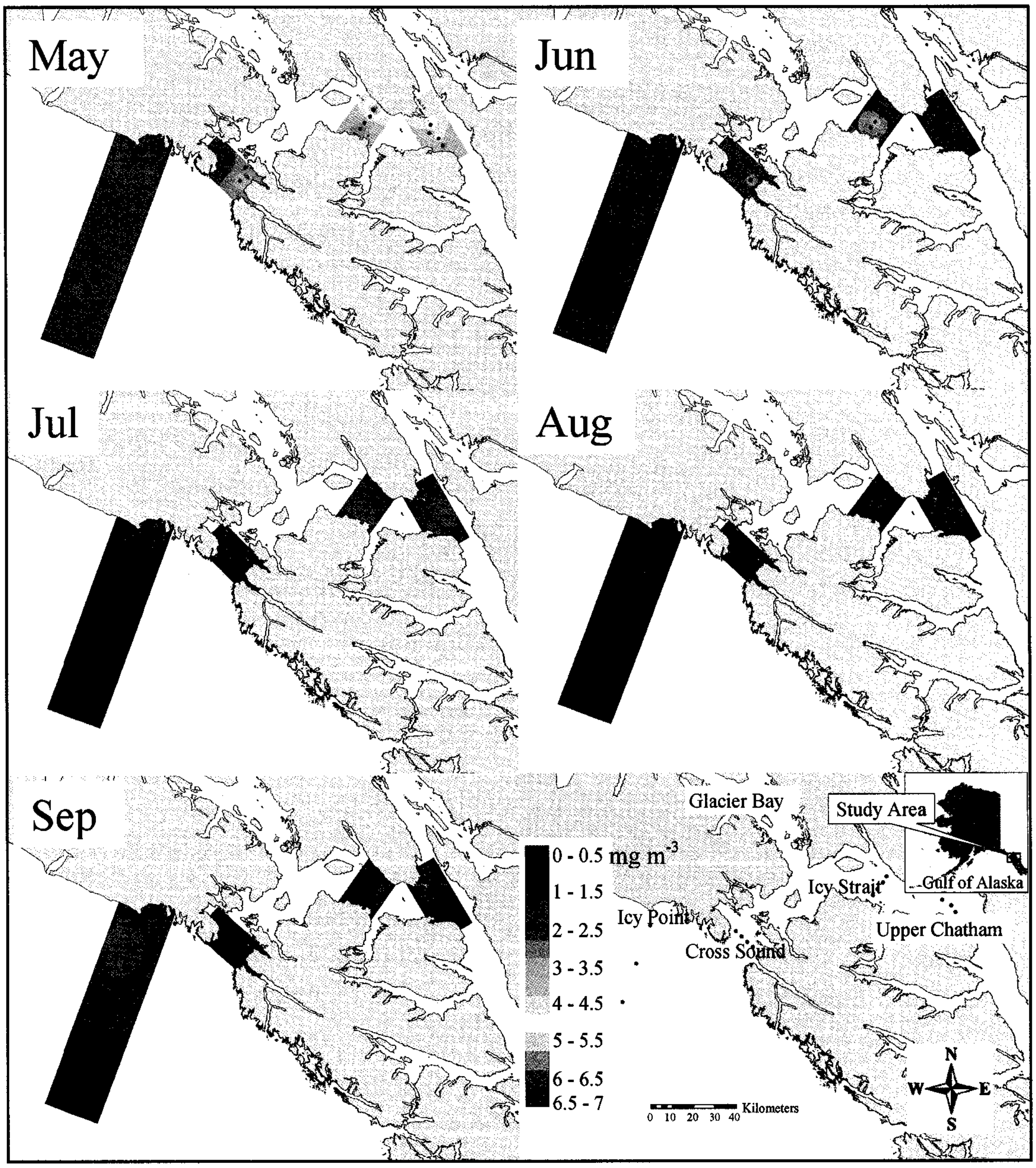

Figure 1.8. Seasonal change of Chl *a* during 1999-2004. Chl *a* was averaged by month and imaged by Radius Base Functions in the geostatistical analyst extension of ArcGIS 9.1.

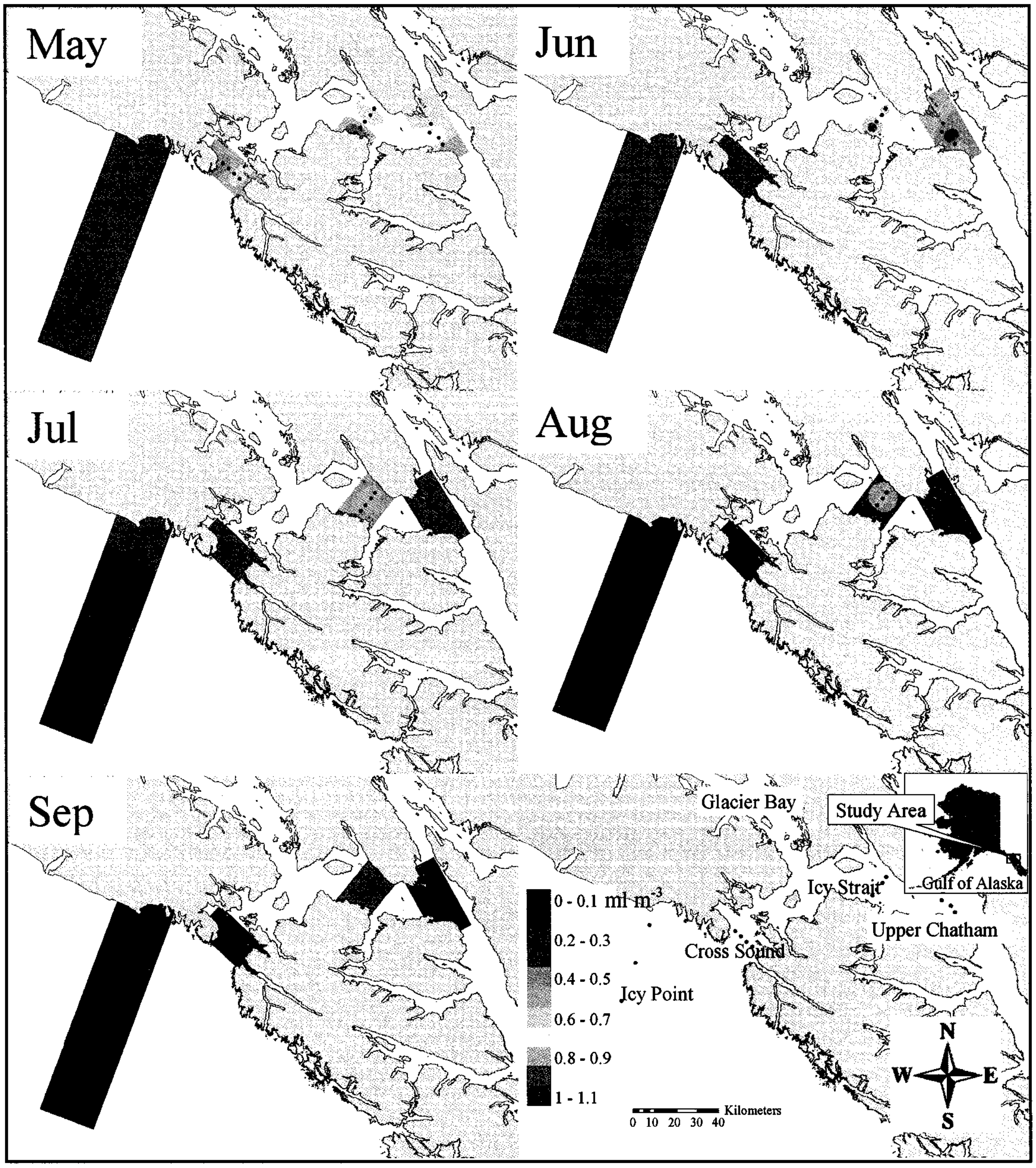

Figure 1.9. Seasonal change of zooplankton biomass during 1997-2004. Zooplankton biomasses were averaged by month and imaged by Radius Base Functions in the geostatistical analyst extension of ArcGIS 9.1.

Table 1.1. Localities and coordinates of monthly zooplankton sampling stations in southeastern Alaska. Zooplankton were collected at 16 stations belonging to four transects in marine waters of the northern region in southeastern Alaska, May-September 1997-2004.

Locality	Station	Latitude	Longitude	Offshore distance(km)	Bottom depth (m)
Upper Chatham Strait	UCA	58°04'57N	135°00'08W	3.2	400
	UCB	58°06'22N	135°00'91W	6.4	100
	UCC	58°07'95N	135°04'00W	6.4	100
	UCD	58°09'64N	135°02'52W	3.2	200
Icy Strait	ISA	58°13'25N	135°31'76W	3.2	128
	ISB	58°14'22N	135°29'26W	6.4	200
	ISC	58°15'28N	135°26'25W	6.4	200
	ISD	58°16'38N	135°23'98W	3.2	234
Cross Sound	CSA	58°09'53N	136°26'96W	3.2	300
	CSB	58°10'91N	136°28'68W	6.4	60
	CSC	58°12'39N	136°30'46W	6.4	200
	CSD	58°13'84N	136°32'23W	3.2	200
Icy Point	IPA	58°20'12N	137°07'16W	6.9	160
	IPB	58°12'71N	137°16'96W	23.4	130
	IPC	58°05'28N	137°26'75W	40.2	150
	IPD	57°53'50N	137°42'60W	65.0	1300

Table 1.2. Pearson's product moment correlation coefficients between Dungeness crab larval density and oceanographic variables. Dungeness crab larvae were compared with SST, SSS, Chl *a*, and zooplankton biomass. All data were collected from the SouthEast Coastal Monitoring (SECM) survey conducted during May to September 1997-2004. Data that did not show normality was log- or square root- transformed.

			SST	SSS	Chl *a*	Biomass
		r^2	0.04	<0.001	0.11	0.01
	May	*df*	44	44	24	44
		p	0.187	0.937	0.104	0.537
		r^2	0.01	0.02	0.002	0.04
Larvae	June	*df*	59	59	29	59
		p	0.570	0.244	0.813	0.129
		r^2	0.03	0.02	0.07	0.01
	July	*df*	53	53	23	52
		p	0.194	0.334	0.192	0.415

Chapter 2

Patterns of development, loss, mixing, and distribution of Dungeness crab larvae in Glacier Bay and neighboring straits[1]

Wongyu Park[1] and Thomas C. Shirley

Abstract

Patterns of development, loss, mixing, and distribution of the larvae of Dungeness crab, *Cancer magister*, were investigated inside and outside of Glacier Bay, southeastern Alaska, biweekly from late May to mid-September and monthly in Icy Strait from late May to late August in 2004. Larvae, salinity, and temperatures were collected during daylight hours at three inner and two outer Glacier Bay stations for two different portions of the water column: above and below the thermocline or at the zone of greatest temperature change in the water column, and at four stations in Icy Strait from a depth of 200 m or within 10 m of the bottom to the surface. Larval loss was high for three larval stages, zoeae I (ZI), zoeae IV, and zoeae V (ZV), and relatively low for zoeae II and zoeae III. In late May, ZI predominated at all stations and ZI density gradually decreased thereafter. Zoeae I were collected from late May to 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. Rostrum lengths varied, indicating that larvae, which had incubated at different temperatures, appeared to be mixed in our study area. The pattern of spatial distribution of larval stages for the inland waters encompassed by Icy Strait was

markedly different than the pattern reported for Dungeness crab larvae from other parts of the species range: many of the early and intermediate stages occurred within inland waters, as opposed to increasing in abundance with distance offshore.

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Introduction

Estuarine crab larvae 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).

Alternately, 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 harrisii* 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, *Rhithropanopeus harrisii* 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 *P.*

crassipes 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 crabs are found within tens of kilometers of shore while post ZI and megalopae are found progressively further offshore, and late intermolt stage 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). Alongshore transport of Dungeness crab larvae on the west coast of North America has been hypothesized to occur by different mechanisms: in the wintertime, the northward flowing Davidson Current and the Southern California Countercurrent, and by strong alongshore winds (Lough 1976; McConnaughey et al. 1994). Landward and northward flow characterized by near-surface circulation contributes to Dungeness crab larvae being retained near the coast and retained in the coastal landing strip off the coast of Washington (McConnaughey et al. 1994). Strong recruitment of Dungeness crabs off the coast of Washington is related to weak northward and strong landward transport (McConnaughey et al. 1994) and upwelling relaxation events (Peterson 1973; Wing et al. 1995).

The coasts of British Columbia and southeastern Alaska are influenced by the northward flowing Alaska Current throughout the year (Reed and Schumacher 1986). The Alaska Current may transport Dungeness crab larvae hatched in northern

Washington and British Columbia to southeastern Alaska (Park et al. 2007).

Water temperature affects embryo development rate and timing of larval hatching, and the morphology of Dungeness crab ZI (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, which encompasses a wide temperature range, occurs progressively later from California, where it occurs in December and January (Wild 1980; Reilly 1983), to Alaska where it occurs in late April and May (Swiney 1999; Shirley et al. 1987; Fisher 2006) to late July (discussed herein). Spine lengths of Dungeness crab ZI incubated at 5° C were significantly longer than those at 15° C (Shirley et al. 1987). Hence, larval morphology is an indicator of incubation temperature and perhaps of geographic origin of the larvae incubated in different water temperatures.

Glacier Bay is located approximately 50 km west of Juneau, Alaska. Glacier Bay is a semi-enclosed, fjord estuarine system consisting of many glaciers and glacial rivers that discharge a high volume of glacial meltwater and glacial sediments (Hooge and Hooge 2002). Freshwater discharge by glacial meltwater and precipitation influence temperature and salinity gradients throughout the bay system (Matthews 1981; Etherington et al. 2004). In general, water temperature in the lower bay is warmer than in the upper bay (Taggart et al. 2003). But, local variability of salinity and temperature is characterized by mixing of fresh water and deep saline water associated with bottom topographical features, such as sills, throughout the bay (Hooge and Hooge 2002;

Etherington et al. 2004). 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). During ebb tides, the predominant currents from Icy Strait and Glacier Bay flow to Cross Sound, resulting in a portion of water from Glacier Bay being transported to Icy Strait (Hooge and Hooge 2002). During flood tides, currents from Cross Sound flow into Icy Strait and into Glacier Bay (Cokelet et al. 2007). Strong semi-diurnal tidal currents inside and outside of the bay result in the exchange of zooplankton and changes of temperature and salinity between the bay and adjacent straits.

We investigated the mixing of ZI of different origins and incubation temperatures within our study sites. We explored the loss and the hatch timing of larvae. We examined the larval distribution patterns between shallow and deep depths during ebb and flood tides to postulate 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 adjacent to Glacier Bay, fortnightly, from late May to mid September 2004, and at four stations in Icy Strait, located approximately 30 km east of the mouth of Glacier Bay, monthly from late May to late August 2004 (Fig. 2.1). Zooplankton at the four stations in Icy Strait were collected with the same methods and materials as chapter 1. Three stations located within Glacier

Bay were defined as inner bay stations while six stations, including two stations positioned near the mouth of the bay, and the four stations within the Icy Strait transect, were defined as stations outside the bay. 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 (2003), 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 surface to within 10 m of the bottom. A multiple open-closing Tucker trawl (= NIO net) with 1 m^2 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. 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 times 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, or near the largest change in temperature if no pronounced thermocline occurred; 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. The water volume filtered varied with stations and thermocline depths: approximately 33.0 m^3 was filtered in the shallow tows, with a range from 10.3 to 77.7 m^3, and 120.1 m^3 volume was filtered in the deep tows with a range of 69.5 to 209.2 m^3.

Two replicate collections were made at each station. General Oceanics Co., model 2031 flowmeters were installed inside the nets to measure the water volume filtered. 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. For this analysis, densities of each zoeal stage during the entire sampling period were summed.

The rostrum length of ZI collected on 27-28 May and 14 June inside and outside of Glacier Bay and on 19 May in the Icy Strait transect were measured to investigate the possible mixing of Dungeness crab larvae. For the measurements of rostrum lengths, 50 or all ZI collected only in the deep depth at each station were measured; ZI collected in the shallow depths were omitted because of the small number collected. Zoeae I were placed under a Wild M5A stereomicroscope, and digital images made at 50x magnification with an Olympus DP12 camera. The larval images were analyzed with Carnoy 2.0 (2001), a program for measuring digital images. The rostrum lengths in the images were measured to the nearest 0.001 mm. The rostrum lengths were measured from the tip to an indentation of the spine between the eyes, visible from a dorsal view.

Statistical Analysis

The significance level used for all statistical analysis in our study was 0.05. The Kolmogorov-Smirnov test (hereafter K-S test) was used to test normality. If the p-value was smaller 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 Tides and Currents for windows 2.1 (Nautical software Inc., 1993). Larval densities of Z1 on 27-28 May and 14 and 29 June were included in the analysis because ZI were 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 shallower depths. All larvae were included in the analysis.

Results

Hydrographic Patterns

On 19 and 27-28 May and on 14 and 29 June 2004, the water column of all sampling stations was nearly isothermal from the surface to the bottom, except at station 2 on 28 May and station 5 in 14 and 29 June (Fig. 2.2-2.3). Thermocline depths varied at each sampling station and date (Table 2.1). In July, the water column at all stations was strongly stratified. In August, the water column at stations 2 and 5 was strongly stratified, while at other stations the water column was nearly isothermal. In September, the thermocline at all sampling stations was inconspicuous, except at station 2. SST of the stations during the sampling period ranged from approximately 7°C to 15°C and was highest from July to mid-August, and lowest on 27-28 May and 14 June (Fig. 2.2-2.3). Salinity stratification in the water column had a pattern similar to water temperature (Fig. 2.2-2.3). On 27-78 May and June, the water column was isohaline from the surface to the bottom, except at stations 2 and 5.

Rostrum Length of Zoeae I

The range of rostrum lengths at each station varied widely based on sampling stations and dates from 0.14 mm (station 2 on 29 May 2004) to 0.06 mm (station 3 on 14 June) (Fig. 2.4). Mean length of rostrums slightly varied with stations and the coefficients of variations at each station were small (Table 2.2).

Distributions and Loss of Larvae

A total of 2874 zoeae and 1 megalopa of Dungeness crabs was collected during the sampling period. Larval loss was high for three larval stages: ZI (66 %), ZIV (77 %), and ZV (99%) while it was relatively low for ZII (46 %) and ZIII (37 %) (Fig. 2.5). The densities of ZI at shallow and deep depths at all stations were not significantly different (Fig. 2.6; Table 2.3). 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 not significantly different. Larval density was highest on 27-28 May and ZI (92.4%) predominated; larval abundance gradually decreased thereafter. Larval stages shifted seasonally from ZI to the fifth zoeal stage (ZV); density decreased from ZI through ZV (Fig. 2.7). The densities of each zoeal stage in the inner and outer bay stations were similar (Fig. 2.7; Table 2.2). There was no significant difference in mean density of any larval stage above and below the thermocline (Fig. 2.8; Table 2.2).

Larval densities varied from 0 to 359.4 100 m^{-3} in the shallow tows and from 18.1 to 187.9 100 m^{-3} in the deep tows on 27-28 May (Fig. 2.9). Larvae were predominantly ZI in both shallow and deep depths at all stations. The proportion of the second zoeal stage (ZII) was highest in the shallow tows at station 2 (18%, 63.1 100 m^{-3}), while the ZII were fewer than 2 % at all other stations. In the deep tows, ZII (3-11%) occurred at each station except for station 3. Two weeks later, the larval stages became more diverse, with mainly ZI and ZII occurring at all stations (Fig. 2.10). On 29 June, ZV occurred for the first time and ZIII were predominant (Fig. 2.11). On 14 July, larval abundances diminished to less than 10 100 m^{-3} in the shallow tows and ZIV predominated during this sampling period (Fig. 2.12). On 29 July and 14 August, extremely low larval densities occurred (Fig. 2.13-2.14). No larvae were found in zooplankton samples collected on 29 August and 9 September.

Discussion

In general, water temperature is colder in upper Glacier Bay and gradually increases along a gradient to lower Glacier Bay (Hooge and Hooge 2002; Etherington et al. 2004). Strong gradients in water temperatures exist between Glacier Bay and adjacent areas (Hooge and Hooge 2002; Taggart et al. 2003). In Glacier Bay and adjacent areas, ovigerous female crabs aggregate at discrete locations at 2 to 5.5 m depths and mostly occur in less than 10 m in depth (O'Clair et al. 1990, 1996; Scheding et al. 2001). However, we do not know the locations or incubation temperatures of the ZI from our study, however, the variation in rostrum length was regarded as evidence of the advection and mixing of larvae with different embryonic incubation temperatures.

Tidal flows that support the hypothesis that ZI were mixed between Glacier Bay and Icy Strait have been reported by Acoustic Doppler current profiler (Cokelet et al. 2007). At ebb tides, water masses from Icy Strait move into Glacier Bay and Cross Sound, while at flood tides, water masses that flow from Glacier Bay and reside near the mouth or in Cross Sound can extend to Icy Strait and into Glacier Bay (Cokelet et al. 2007). In addition, southeastern Alaska encompasses a wide range of bays, estuaries, and islands. Water temperatures at different locations in southeastern Alaska vary (Williamson 1965; Jones 1978). Dungeness crabs are distributed in various locations in southeastern Alaska (Koeneman 1985; O'Clair and Freese 1988; Stone and O'Clair 2002) and may have variable reproductive schedules because of local climate patterns affected by river flows and glacial meltwater. Larvae hatched from these various areas with different incubation temperatures could be transported into our study sites. Possible transportation of larvae through the coastal Gulf of Alaska from northern Washington to southeastern Alaska may occur (Park et al. 2007). Also, possible transport of larvae through inland channels in southeastern Alaska can be demonstrated by nontidal current (Haight 1926) and drift bottle records from northern Queen Charlotte Island to Icy Strait via Chatham Strait (Dodimead et al. 1963).

Temperature variation during the incubation period affects morphology of ZI; e.g., spine lengths increase with decreasing incubation temperature (Shirley et al. 1987; Webb et al. 2006). Rostrum lengths of Dungeness crab ZI incubated at 5°C were approximately 19% longer than those at 15°C (Shirley et al. 1987). Thus, differences in morphology of ZI strongly suggest the larvae had different incubation temperatures. In general, rostrum lengths of ZI in our study area were distributed around mean values at each station. However, the range of rostrums was relatively large. Wide ranges of rostrum lengths at our sampling sites suggest that larvae with different incubation temperatures were mixed in our study area.

Our measurements of rostrum lengths were slightly different than those of Shirley et al. (1987), resulting in approximately 2% shorter. Shirley et al. (1987) measured rostrum lengths from a lateral view while we measure them from a dorsal view, resulting in the different values. Considering only rostrum lengths, an 0.804 mm rostrum length in our study corresponds to a 0.820 (SD±0.01) mm length in Shirley et al. (1987); a 0.770 (SD±0.02) mm at 5°C in Shirley et al. (1987) corresponds to a 0.755 mm in our study. If ZI rostrum lengths were influenced by only incubation temperatures, approximately 94% of the ZI in our study were incubated at lower than 5°C in mean temperature in incubation period.

Relatively higher loss 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, ZI are found but post ZI and megalopae are not

(Reilly 1983; Epifanio 1995; DiBacco et al. 2001). Within our study area, advection of Dungeness crab larvae may occur. At Sidakaday Narrows in Glacier Bay (Fig. 2.1), a high density of ZI and low density of post ZI were found (Fisher 2006). Although larval densities of post ZI in our study area in May and June were relatively higher than those reported by Fisher (2006), the lack of later stage larvae during July and August in our study area support the hypothesis that Dungeness crab larvae may have been 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. The predominance of megalopae collected by other sampling methods in Glacier Bay in September and October (Herter 2006) should have been preceded by high abundances of late zoeal stages in the same areas if the larvae had been retained.

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 at near bottom than near the surface where net transport is upstream (Sandifer 1973). Ovigerous females of *Callinectes sapidus* 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 were advected after hatching from our study site to coastal areas for development, the ZI should occur 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 may suggest that ZI in our study area did not follow the pattern of emigrating larvae.

However, the thermocline depth or the zone of greatest temperature change in water column varied with sampling stations and times, so that the use of only two sampling depths 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). Previous research conducted close to our sampling sites indicated strong vertical migration pattern of ZI at dawn and dusk (Park and Shirley 2005). Our coarsely separated depths for shallow and deep samplings may have biased results.

In general, ZI occur near shore and post ZI are found progressively further offshore (Lough 1976; Reilly 1983). Late intermolt stage megalopae are dominant 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 different pattern in larval densities in comparison to previous studies (Lough 1976; Reilly 1983) in which larvae were advected offshore for development. If larvae are advected offshore, larval abundance should be higher offshore, but larval densities off southeastern Alaska were low during all sampling months (Chapter 1). Also, the relatively high loss of ZV and megalopae may have resulted from different behaviors of each larval stage in the water column. 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 M are stronger swimmers and should be able to more readily avoid nets. Accordingly, ZV and M could be less easily collected than ZI-ZIV by vertical net tows.

Light attracting sampling gear such as light traps may be more effective 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. in press).

Overall, we cannot verify whether the decrease in densities of subsequent larval stages in our study was a result of natural mortality or larval advection to other areas. We cannot determine the magnitude of Dungeness crab larvae that were advected or retained within the study sites. Out data support the contention that larvae incubated at different temperatures were mixed within our study area. Perhaps more importantly, the pattern of distribution of larval stages in southeastern Alaska is markedly different than the distributional pattern reported from other parts of the range of Dungeness crabs.

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Literature Cited

Booth, J., A. Phillips, and G. S. Jamieson. 1985. Fine scale spatial distribution of *Cancer magister* megalopae and its relevance to sampling methodology, p 273-286. *In* Proceedings of the symposium on Dungeness crab biology and management. University of Alaska, Sea Grant College Program Report 85-3.

Carnoy 2.0. 2001. Lab of plant. K.U. Leuven, Begium.

Cokelet, E. D., A. J. Jenkins, and L. L. Etherington. 2007. A transport of Glacier Bay ocean currents measured by Acoustic Doppler Current Profiler (ADCP), p 74-77. *In* Piatt, J. F., and Gende, S. M. [eds], Proceedings of the fourth Glacier Bay science symposium, 2004. U.S. Geological Survey, information and technology report USGS/BRD/ITR-2007-5047, Washington, D. C.

Cronin, T. W., and R. B. Forward Jr. 1979. Tidal vertical migration: an endogenous rhythm in estuarine crab larvae. Science **205:** 1020-1022.

DiBacco, C., D. Sutton, and L. McConnico. 2001. Vertical migration behaviour and horizontal distribution of brachyuran larvae in a low-inflow estuary: implications for bay-ocean exchange. Mar. Ecol. Pro. Ser. **217:** 191-206.

Dodimead, A. J., F. Favorite, and T. Hirano. 1963. Salmon of the North Pacific Ocean. Part II. Review of oceanography of the subarctic Pacific region. Int. North Pac. Fish. Comm. Bull. **33:** 1-195.

Eggleston, D. B., and D. A. Armstrong. 1995. Pre- and post-settlement determinants of estuarine Dungeness crab recruitment. Ecol. Monogr. **65:** 193-216.

Epifanio, C. E. 1995. Transport of blue crab (*Callinectes sapidus*) larvae in the waters off mid-Atlantic states. Bull. Mar. Sci. **57:** 713-725.

Etherington, L. L., P. N. Hooge, and E. R. Hooge. 2004. Factors affecting seasonal and regional pattern of surface water oceanographic properties within a fjord estuarine system: Glacier Bay, AK. U.S. Geological Survey, Alaska Science Center, Gustavus, AK.

Fisher, J. L. 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.

Haight, F. J. 1926. Nontidal currents in southeastern Alaska. Geograph. Rev. **16**: 642-646.

Hatfield, S. E. 1983. Internolt staging and distribution of Dungeness crab, *Cancer magister*, megalopae, p. 85-96. *In* P. W. Wild and R. N. Tasto [eds.], Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California fishery resource. Calif. Fish. Game Fish. Bull. **172**.

Herter, H. L. 2006. Transport of Dungeness crab (*Cancer magister*) megalopae into Glacier Bay, Alaska. MS thesis, Univ. of Alaska Fairbanks.

Hobbs, R. C., and L. W. Botsford. 1992. Diel vertical migration and timing of metamorphosis of larvae of the Dungeness crab *Cancer magister*. Mar. Biol. **112:** 417-428.

Hooge, P. N., and E. R. Hooge. 2002. Fjord oceanographic patterns in Glacier Bay National Park. USGS Alaska Biological Science Center. Final Rep. 130 pp.

Jamieson, G. S., A. Phillips, and W. S. Hugget. 1989. Effects of ocean variability on the abundance of Dungeness crab larvae. Can. Spec. Publ. J. Fish. Aquat. Sci. **108:** 305-325.

Jones, J. D. 1978. Southeastern Alaska sea surface temperatures, 1964-1974. U.S. Dep. Commer., NWAFC Processed Rep., Auke Bay Lab. Nat'l. NMFS, NOAA, Juneau, AK, 67 p.

Koeneman, T. M. 1985. A brief review of the commercial fisheries for *Cancer magister* in southeast Alaska and Yakutat waters, with emphasis on recent seasons, p 61-83. *In* Proceedings of the symposium on Dungeness crab biology and management. University of Alaska, Sea Grant College Program Report 85-3.

Lambert, R., and C. E. Epifanio. 1982. A comparison of dispersal strategies in two genera of brachyuran crab in a secondary estuary. Estuaries **5:** 182-188.

Little, K. T., and C. E. Epifanio. 1991. Mechanism for re-invasion of an estuary by two species of brachyuran megalopae. Mar. Eco. Prog. Ser. **68:** 235-242.

Lough, R. G. 1976. Larval dynamics of the Dungeness crab, *Cancer magister*, off the central Oregon coast, 1970-71. Fish. Bull. **74:** 353-375.

Matthews, J. B. 1981. The seasonal circulation of the Glacier Bay, Alaska fjord system. Est. Coast. Shelf Sci. **12:** 679-700.

McConnaughey, R. A., D. A. Armstrong, B. M. Hickey, and D. R. Gunderson. 1994. Interannual variability in coastal Washington Dungeness crab (*Cancer magister*) populations: larval advection and the coastal landing strip. Fish. Oceanogr. **3:** 22-38.

Miller, J. A., and A. L. Shanks. 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.

O'Clair, C. E., and J. L. Freese. 1988. Reproductive condition of Dungeness crabs, *Cancer magister*, at or near log transfer facilities in southeastern Alaska. Mar. Environ. Res. **26:** 57-81.

O'Clair, C. E., R. P. Stone, and J. L. Freese. 1990. Movements and habitat use of Dungeness crab in the Glacier Bay fishery, p. 74-77. *In* Milner, A. M. and Wood, J. D. Jr [eds.], Proceedings of the Second Glacier Bay Science Symposium. Gustavus, Glacier Bay National Park & Preserve, AK, U.S. National Park Service.

O'Clair, C. E., T. C. Shirley, and S. J. Taggart. 1996. Dispersion of adult *Cancer magister* at Glacier Bay, Alaska: variation with spatial scale, sex, and reproductive status, p. 209-227. *In* High latitude crabs: biology, management, and economics, Anchorage, Alaska Sea Grant. AK-SG-96-02.

Park W., and T. C. Shirley. 2005. Diel vertical migration and seasonal timing of the larvae of three sympatric cancrid crabs, *Cancer* spp., in southeastern Alaska. Estuaries **28:** 266-273.

Park W., D. C. Douglas, and T. C. Shirley. 2007. Evidence of conveyor belt transport of Dungeness crab larvae along the west coast of the United States and Canada. Limnol. Oceanogr. **52:** 248-256.

Peterson, W. 1973. Upwelling indices and annual catches of Dungeness crab, *Cancer magister*, along the west coast of the United States. Fish. Bull. **71:** 902-910.

Porter, S. S., G. L. Eckert, C. J. Byron, and J. L. Fisher. (In press). Comparison of light traps and plankton tows for sampling brachyuran crab larvae in a n Alaskan fjord. J. Crust. Biol.

Provenzano, A. J., J. R. McConaugha, K. B. Philips, D. F. Johnson, and J. Clark. 1983. Vertical distribution of first stage larvae of the blue crab, *Callinectes sapidus*, at the mouth of Chesapeake Bay. Estu. Coast. Shelf Sci. **16:** 489-499.

Reed, P. K., and J. D. Schumacher. 1986. Physical Oceanography, p 57-75. *In* D. W. Hood and D. W. Zimmerman ST [eds.], The Gulf of Alaska: Physical environment and biological resources. Ocean assessment division, NOAA.

Reilly, P. N. 1983. Dynamics of the Dungeness crab, *Cancer magister*, larvae off central and northern California, p. 57-84. *In* P. W. Wild and R. N. Tasto [eds.], Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California fishery resource. Calif. Fish. Game Fish. Bull. **172**.

Sandifer, P. A. 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, P. A. 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. Mar. Sci. **3:** 269-279.

Scheding, K. A., T. C. Shirley, C. E. O'Clair, and S. J. Taggart. 2001. Critical habitat for ovigerous Dungeness crabs, p. 431-445. *In* G. H. Kruse, N. Bez, A. Booth, M. W. Dorn, S. Hills, R. N. Lipcius, D. Pelletier, C. Roy, S. J. Smith, and D. Witherell [eds.], Spatial Processes and Management of Marine Populations. Alaska Sea Grant. AK-SG-01-02.

Shanks, A. L. 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, S. M., T. C. Shirley, and S. D. Rice. 1987. Latitudinal variation in the Dungeness crab, *Cancer magister* zoeal morphology explained by incubation temperature. Mar. Biol. **95:** 371-376.

Stone, R. P., and C. E. O'Clair. 2002. Behavior of female Dungeness crabs, *Cancer magister*, in a glacial southeast Alaska estuary: homing, brooding-site fidelity, seasonal movements, and habitat use. J. Crust. Biol. **22:** 481-492.

Swiney, K. M. 1999. Reproductive cycle of the Dungeness crab, *Cancer magister*, in southeastern Alaska. MS thesis, Univ. of Alaska, Fairbanks, AK.

Taggart, S. J., P. N. Hooge, J. M., Mondragon, E. R. Hooge, and A. G. Andrews. 2003. Living on the edge: the distribution of Dungeness crab, *Cancer magister*, in a recently deglaciated fjord. Mar. Ecol. Prog. Ser. **246:** 241-252.

Tides and currents for Windows 2.1. 1993. Nautical software Inc. Denver, CO.

Webb, J. B., G. L. Eckert, T. C. Shirley, and S. L. Tamone. 2006. Changes in zoeae of the snow crab, *Chionoecetes opilio*, with variation in incubation temperature. J. Exp. Mar. Biol. Ecol. **339:** 96-103.

Wild, P. W. 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.

Williamson, R. S. 1965. Southeastern Alaska sea surface temperature, 1959-1963. U.S. Fish Wildl. Serv. Data Rep. **8**, 41 p.

Wing, S. R., J. L. Largier, L. W. Botsford, and J. F. Quinn. 1995. Settlement and transport of benthic invertebrates in an intermittent upwelling region. Limnol. Oceanogr. **40:** 316-329.

Yannicelli, B., L. R. Castro, A. Valle-Levinson, L. Atkinson, and D. Figueroa. 2006. Vertical distribution of decapod larvae in the entrance of an equatorward facing bay of central Chile: implications for transport. J. Plankton Res. **28:** 19-37.

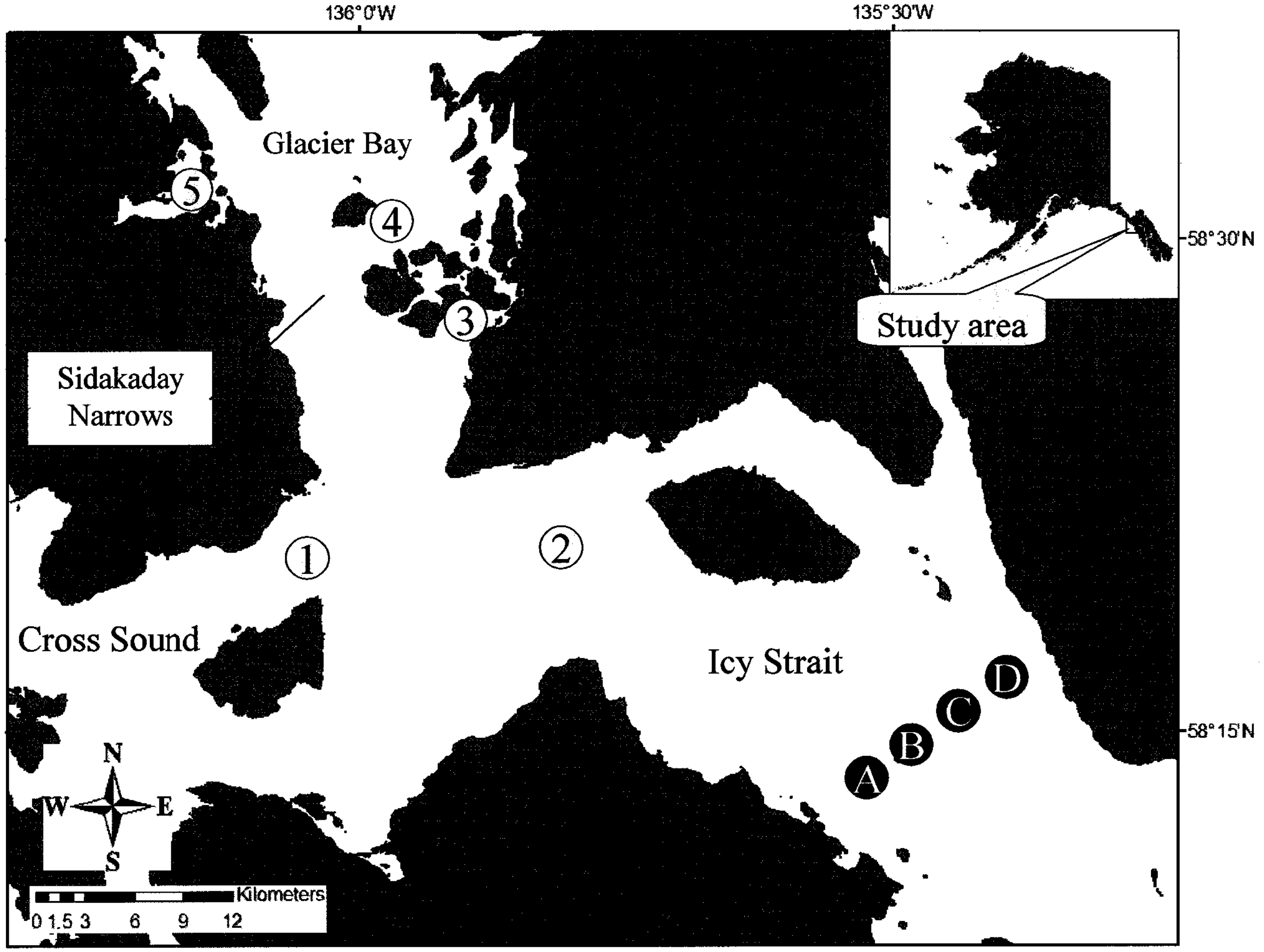

Fig. 2.1. Map of sampling stations. Zooplankton at stations 1 to 5 were collected fortnightly from late May to mid September 2004. Zooplankton at stations ISA through ISD were collected monthly from late May to late August 2004.

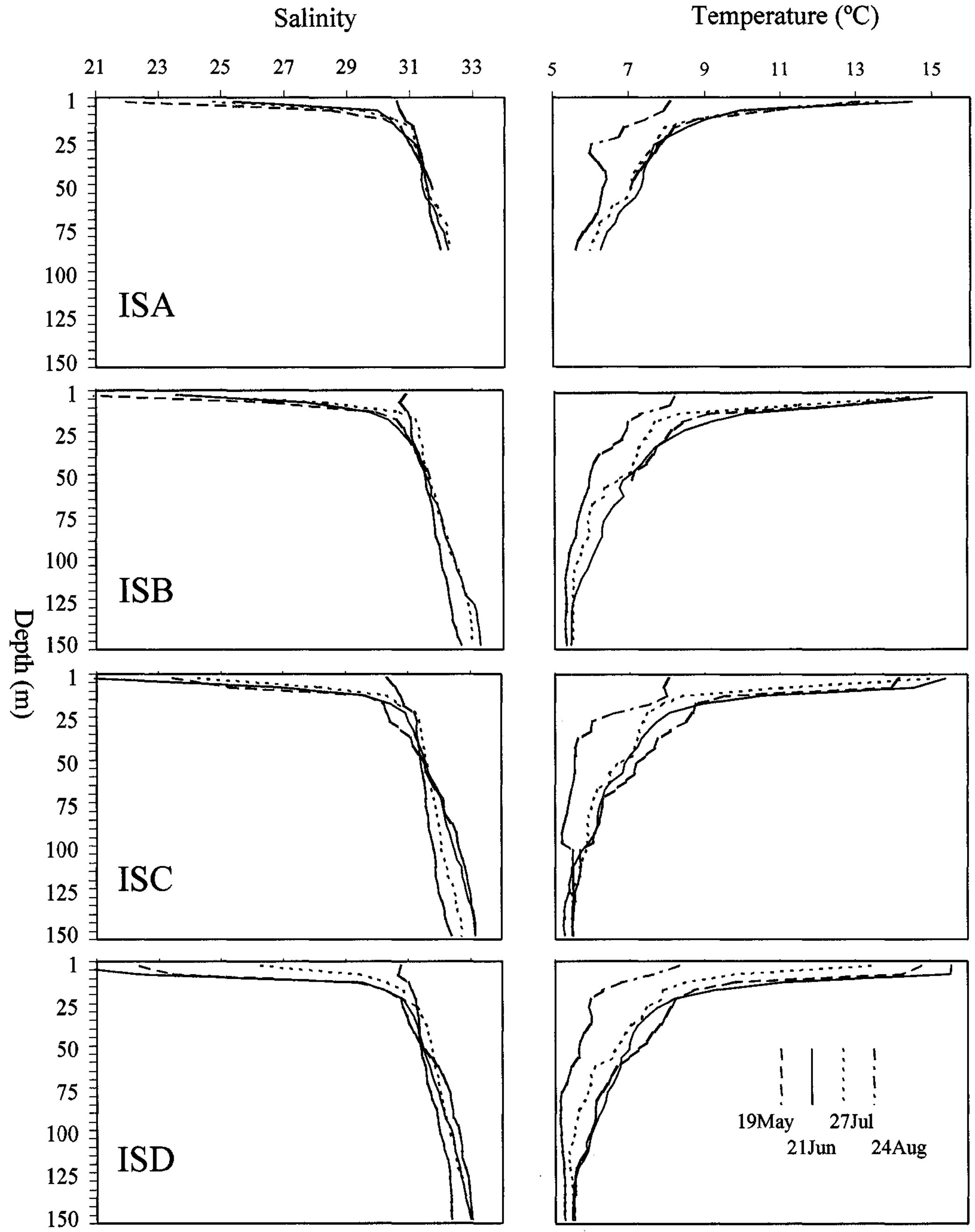

Fig. 2.2. Salinity and temperature profiles in Icy Strait. Salinity and temperature were collected in Icy Strait by SECM survey, Auke Bay Lab, NFMS, monthly within last 10-11 days from late May to late August 2004. Dates below bars indicate sampling dates of month.

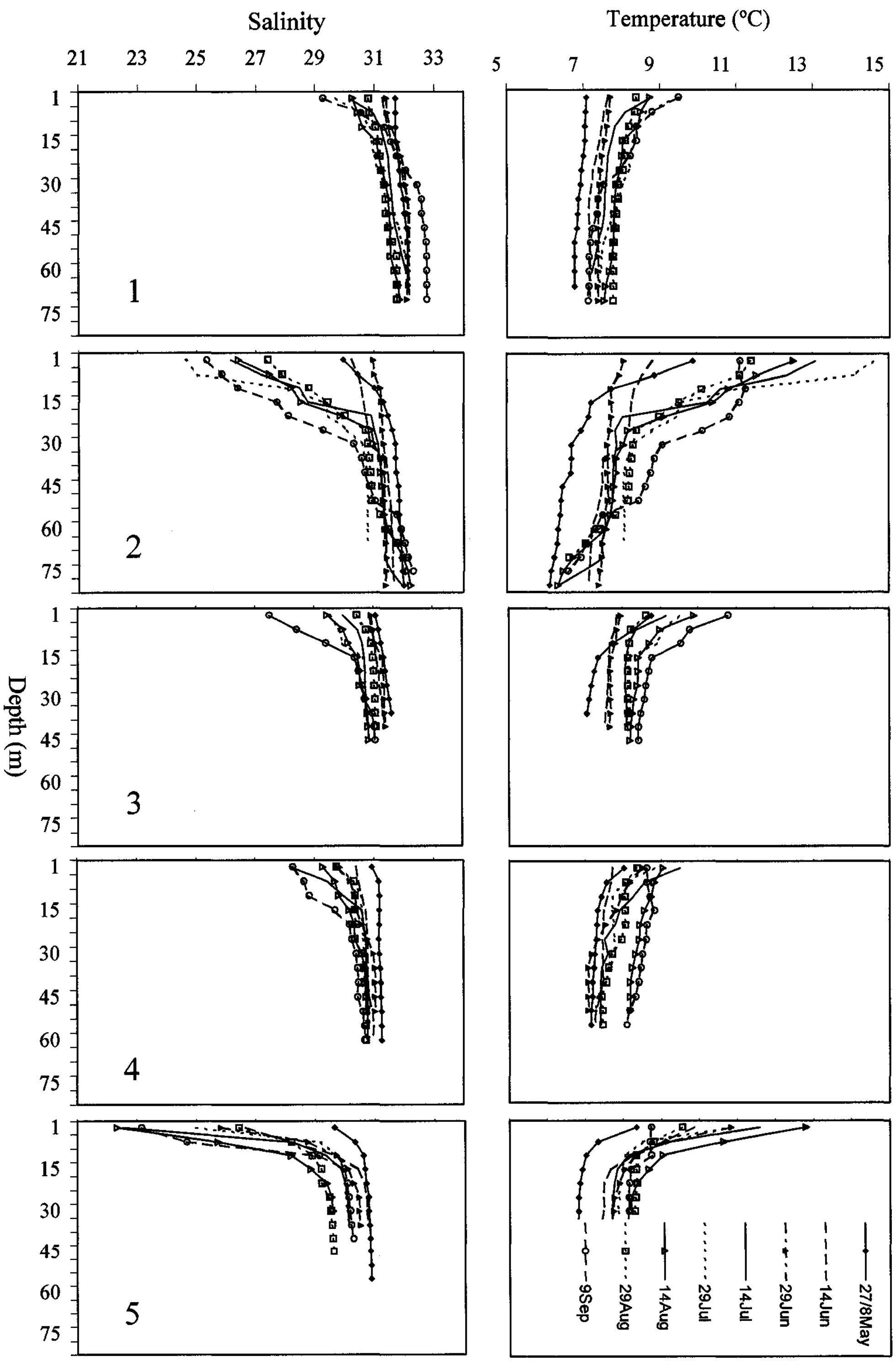

Fig. 2.3. Salinity and temperature profiles inside and outside of Glacier Bay. Salinity and temperature were collected fortnightly at inner and outer Glacier Bay stations from late May to mid September 2004. Dates below bars indicate sampling dates.

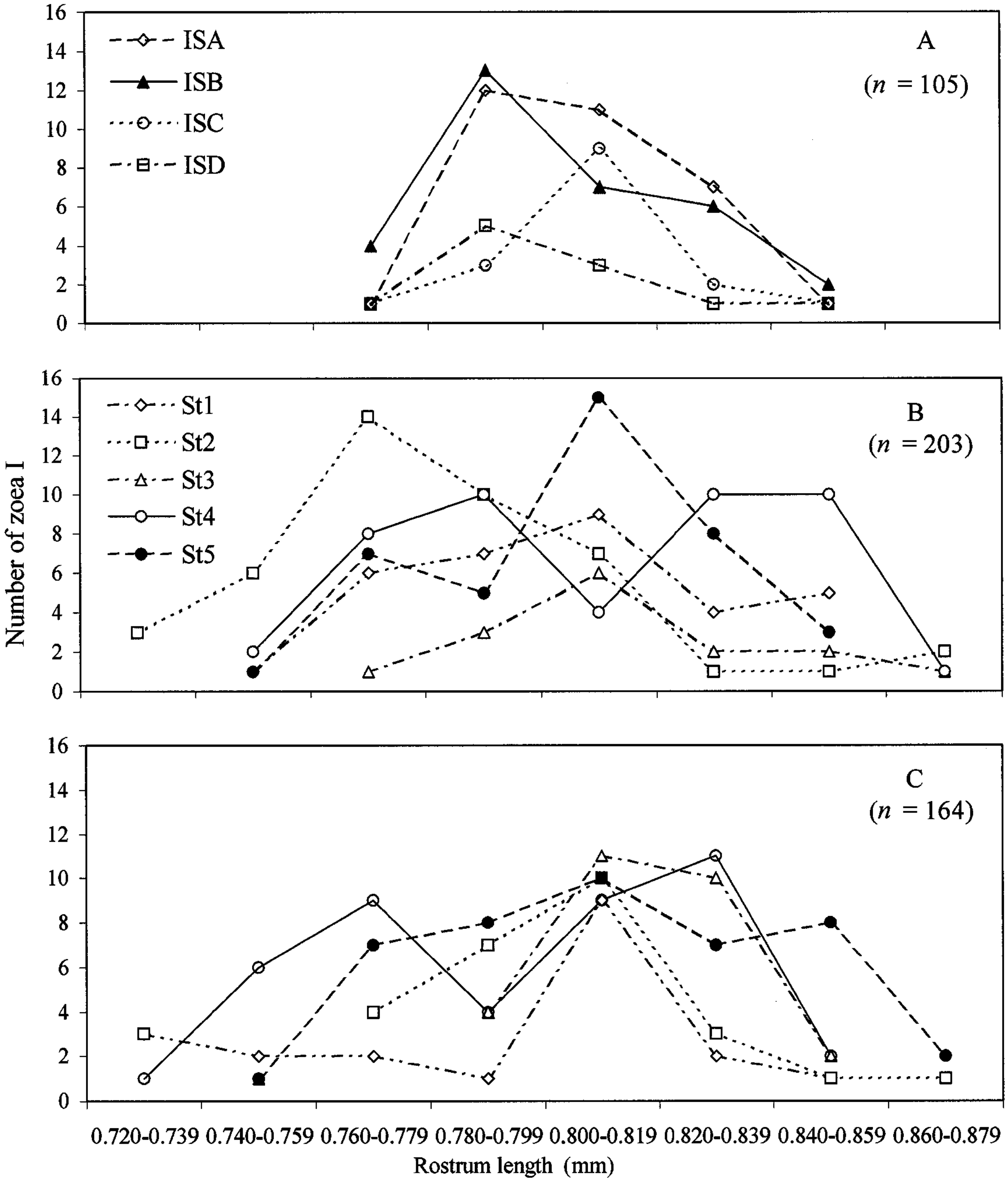

Fig. 2.4. Rostrum lengths of zoeae I of Dungeness crabs. A) Zoeae I were collected in Icy Strait transect on May 19, 2004. B and C) Zoeae I were collected inside and outside of Glacier Bay on May 27-28 and June 14, 2004, respectively.

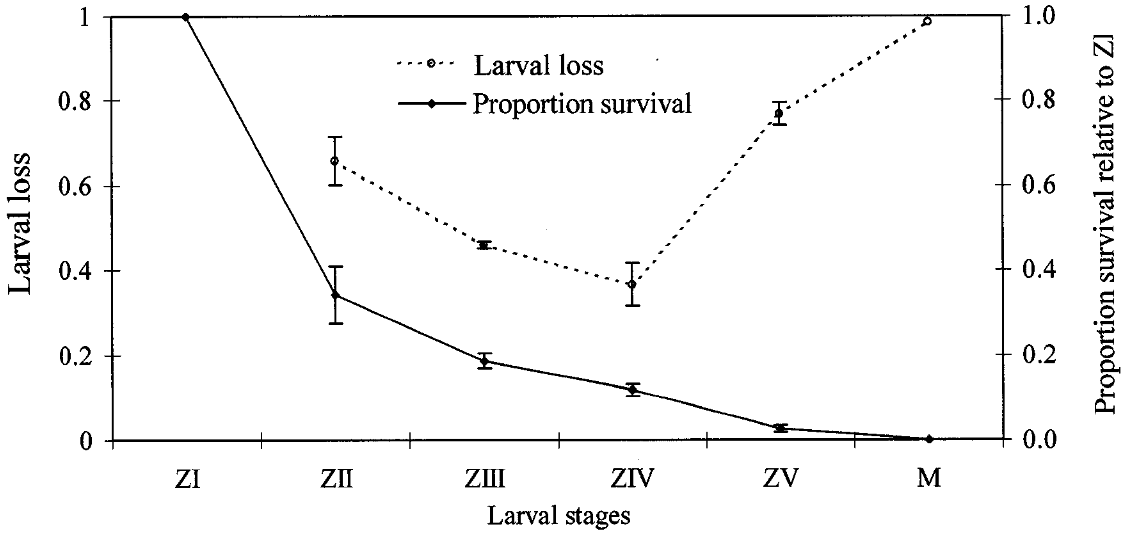

Fig. 2.5. Larval loss and proportion survival relative to zoeae I. Error bars indicate standard error between inner and outer Glacier Bay stations.

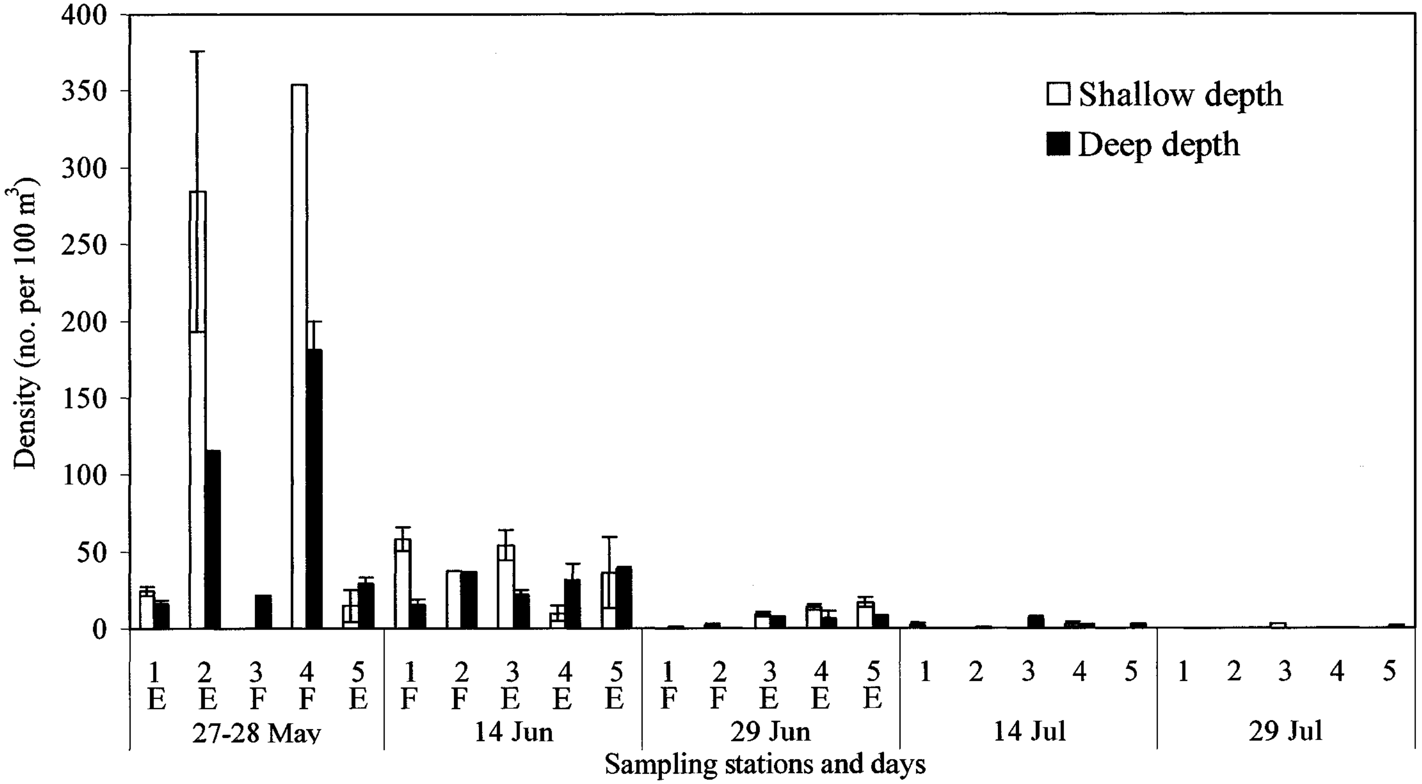

Fig. 2.6. Comparison of zoea I density between shallow and deep depths. Zoea I collected at inner and outer Glacier Bay stations between shallow and deep depths are compared. Error bars indicate standard errors of zoea I densities between replicates at each station. No error bars indicate no replicate 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. E and F indicate ebb and flood tides, respectively.

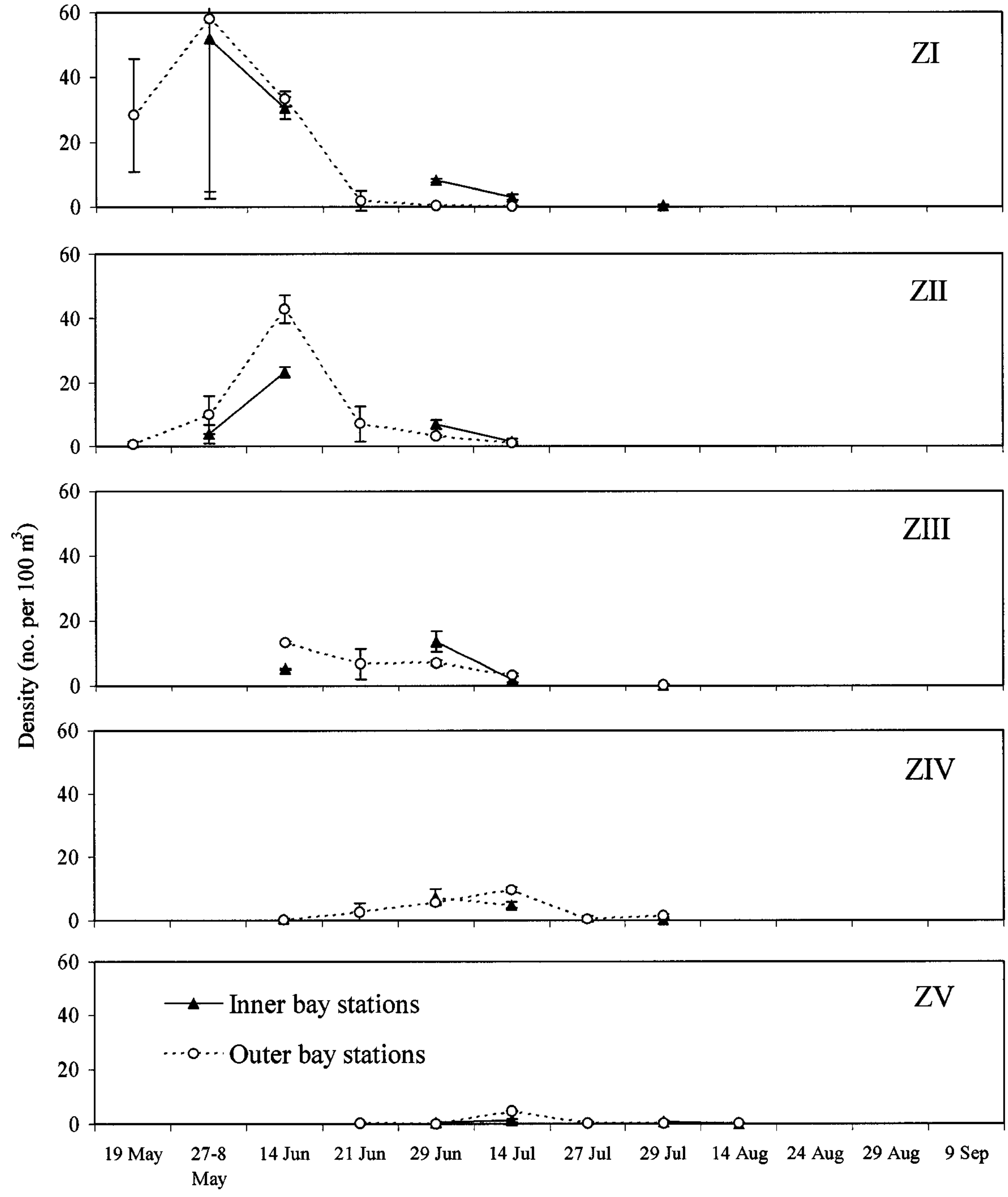

Fig. 2.7. Comparison and seasonal changes of mean larval density between inner and outer Glacier Bay stations. Mean larval density of Dungeness crabs between inner and outer bay stations are compared. All sampling stations are included. Fortnightly sampling dates near mouth and within Glacier Bay in 2004 were on 27-8 May, 14 Jun, 29 Jun, 14 Jul, 29 Jul, 14 Aug, 29 Aug, and 9 Sep. Monthly sampling dates in Icy Strait in 2004 were on 19 May, 21 Jun, 27 Jun, and 24 Aug. Vertical bars represent standard error of larval densities between stations.

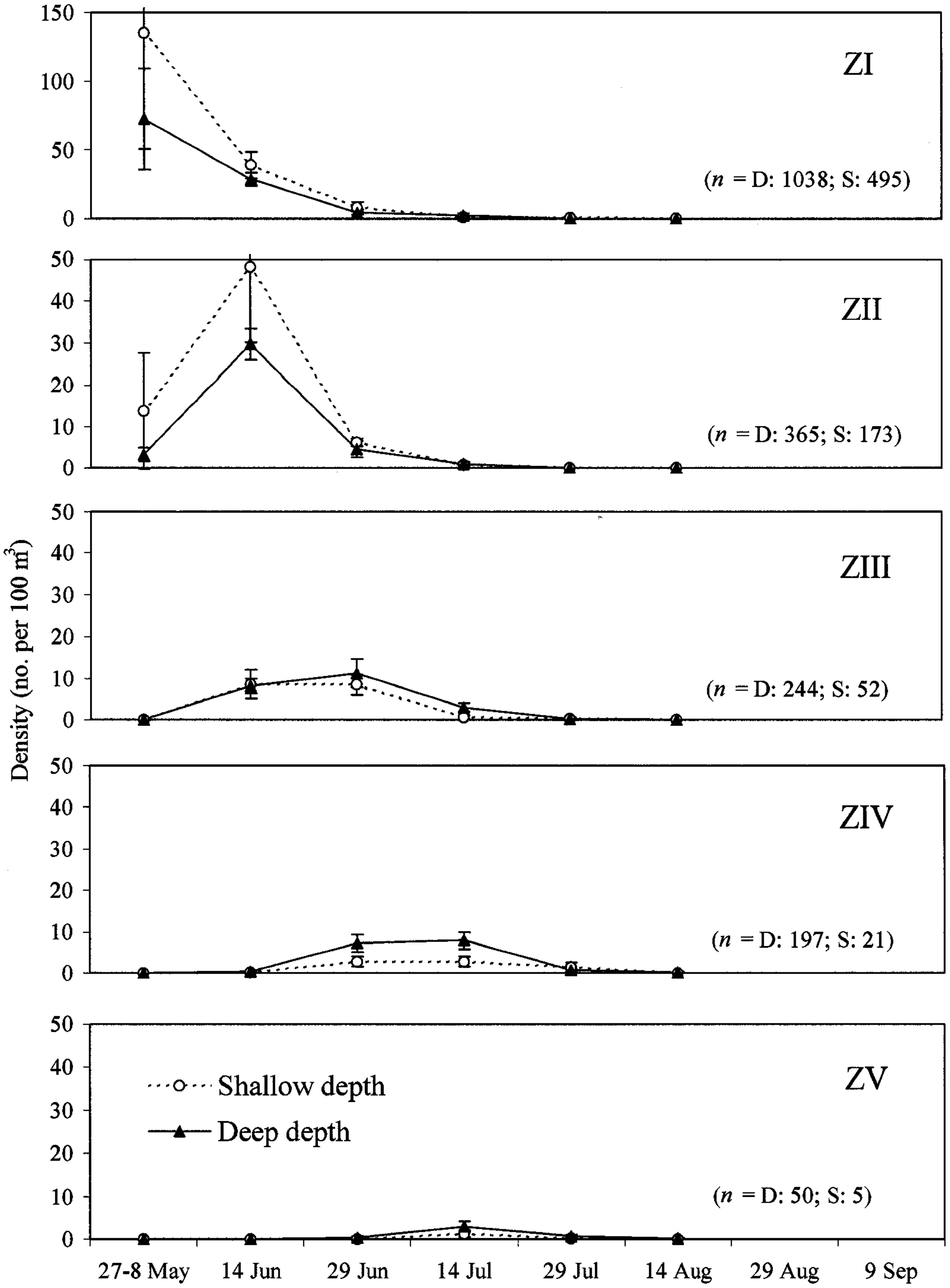

Fig. 2.8. Comparison of mean larval density between shallow and deep depths. Mean larval density of Dungeness crabs between shallow and deep depths are compared. Dungeness crab larvae were collected fortnightly near mouth and within Glacier Bay in 2004. Note differences in scale for ZI.

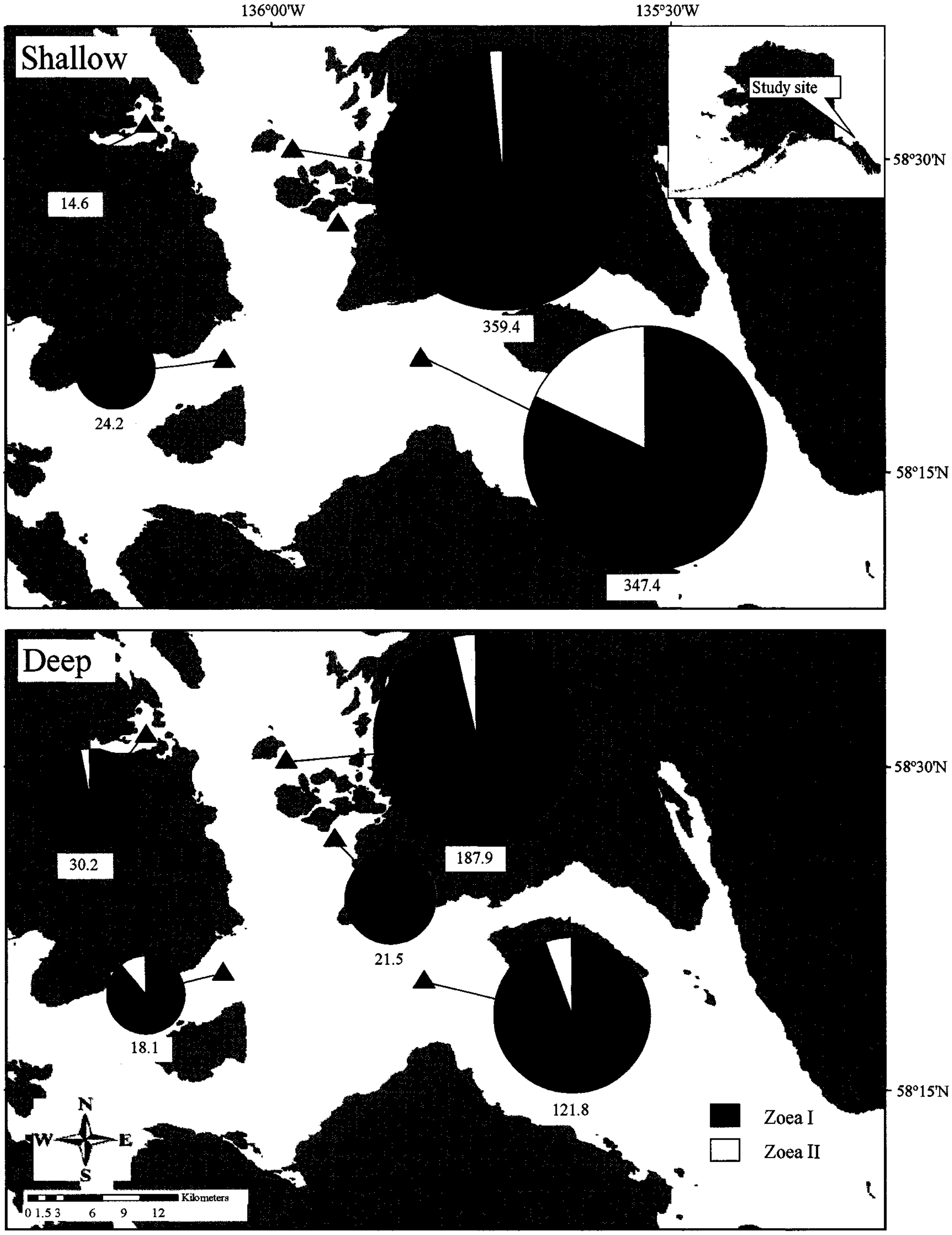

Fig. 2.9. Spatial variation of larval densities of Dungeness crabs on 27-28 May 2004. Larval Dungeness crabs, *Cancer magister*, were collected inside and outside of Glacier Bay, southeastern Alaska. Triangles indicate sampling stations. No larvae were found at the shallow depth at station 3. The numbers below the pie charts are larval density (no. per 100 m^3) at each station. Sizes of pie charts denote relative abundance of larvae.

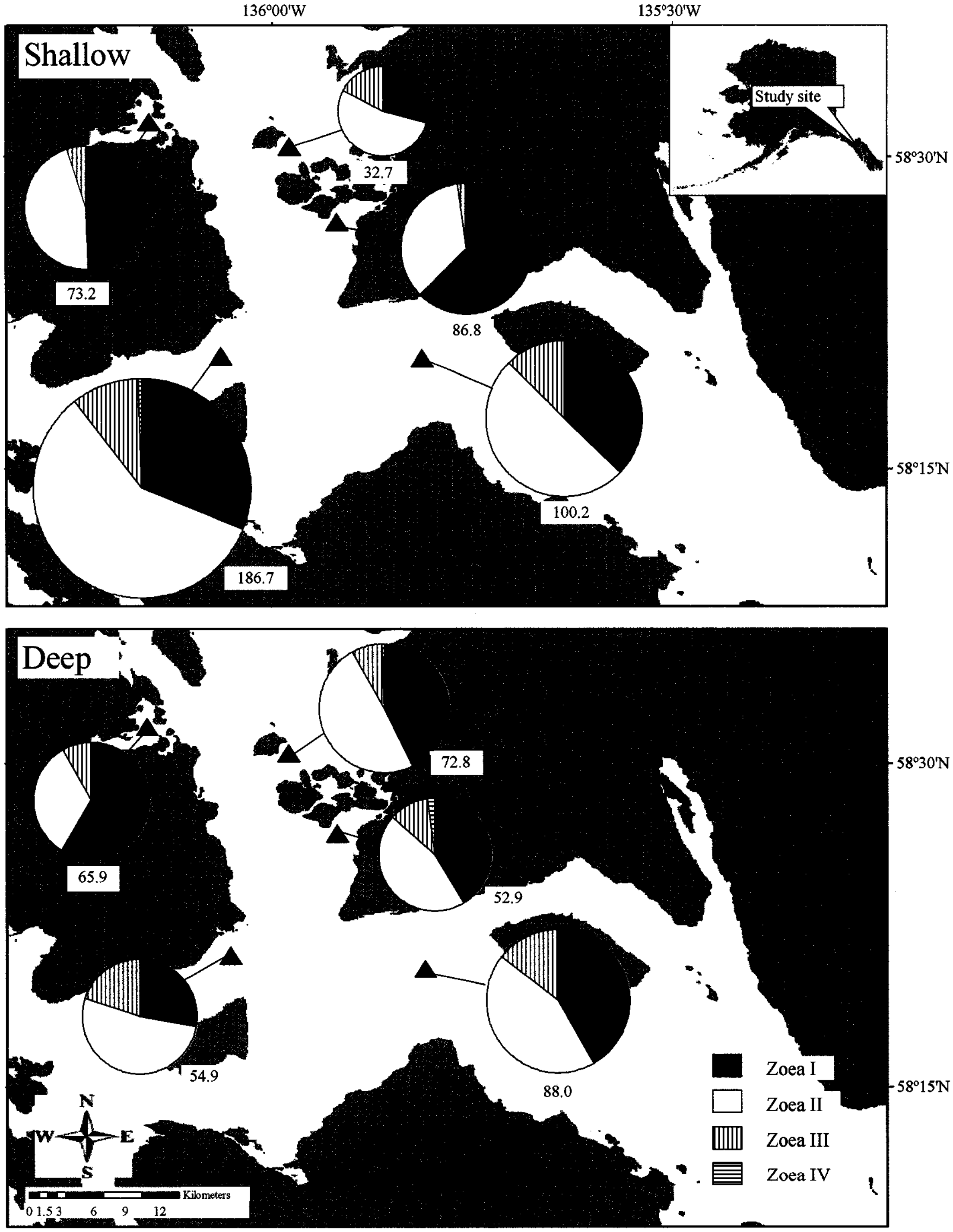

Fig. 2.10. Spatial variation of larval densities of Dungeness crabs on 14 June 2004. Larval Dungeness crabs, *Cancer magister*, were collected inside and outside of Glacier Bay, southeastern Alaska. Triangles indicate sampling stations. The numbers below the pies are larval density (no. per 100 m^3) at each station. Sizes of Pie charts indicate relative abundance of larvae.

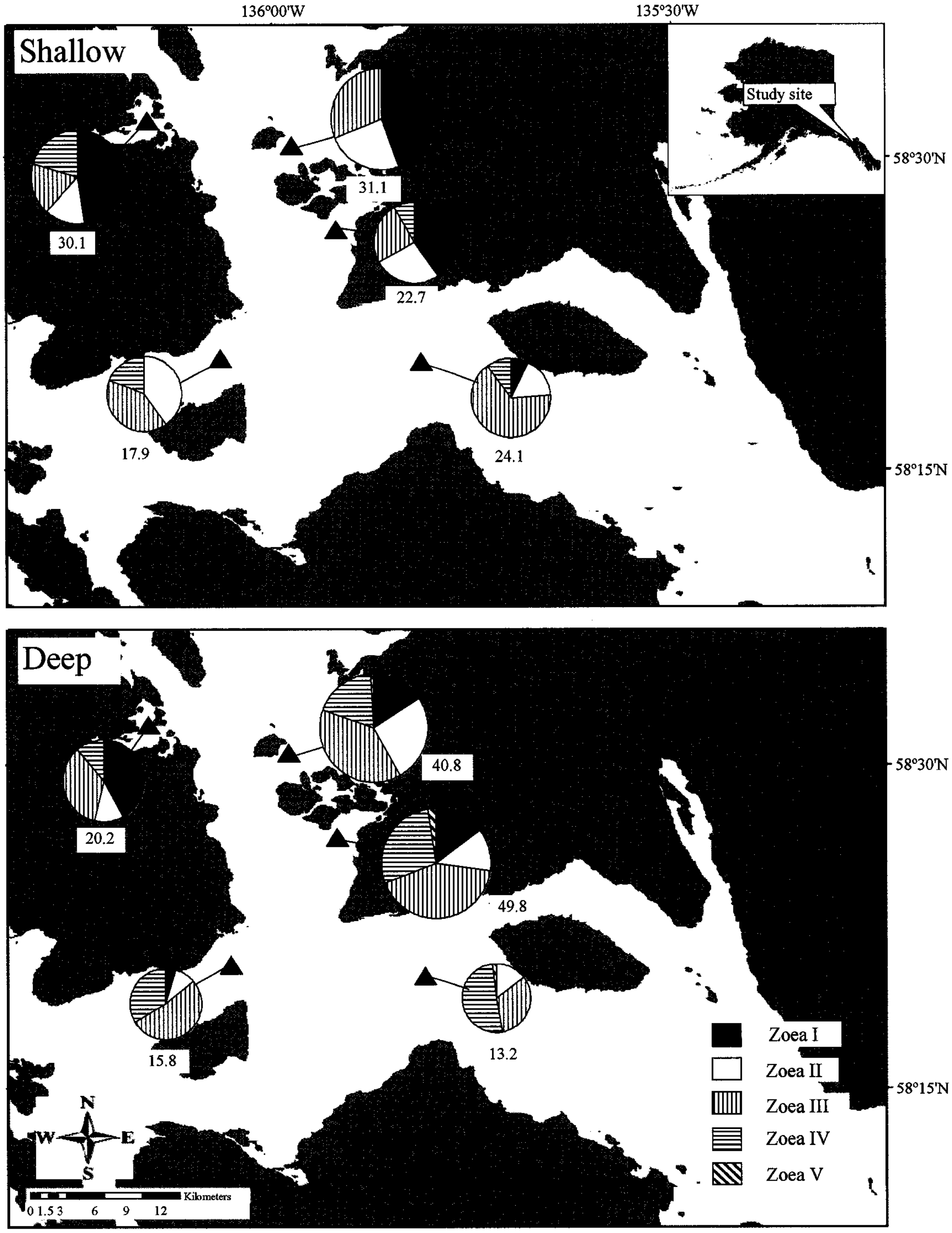

Fig. 2.11. Spatial variation of larval density of Dungeness crabs on 29 June 2004. Larval Dungeness crabs, *Cancer magister*, were collected inside and outside of Glacier Bay, southeastern Alaska. Triangles indicate sampling stations. The numbers below the pies are total larval density (no. per 100 m^3) at each station. Sizes of pie charts denote relative abundance of larvae.

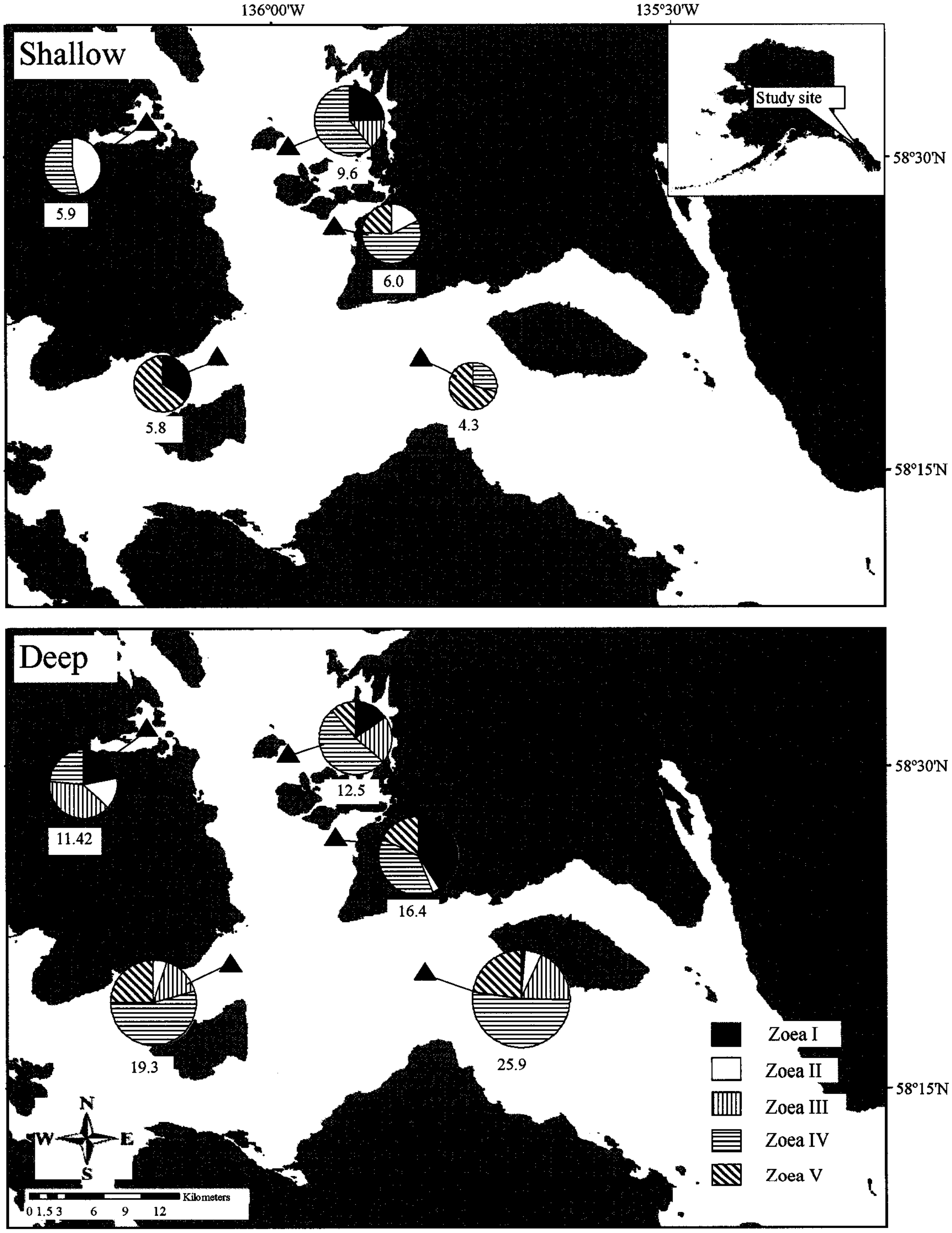

Fig. 2.12. Spatial variation of larval densities of Dungeness crabs on 14 July 2004. Larval Dungeness crabs, *Cancer magister*, were collected inside and outside of Glacier Bay, southeastern Alaska. Triangle indicates sampling stations. The numbers below the pies are total larval density (no. per 100 m^3) at each station. Sizes of pie charts indicate relative abundance of larvae.

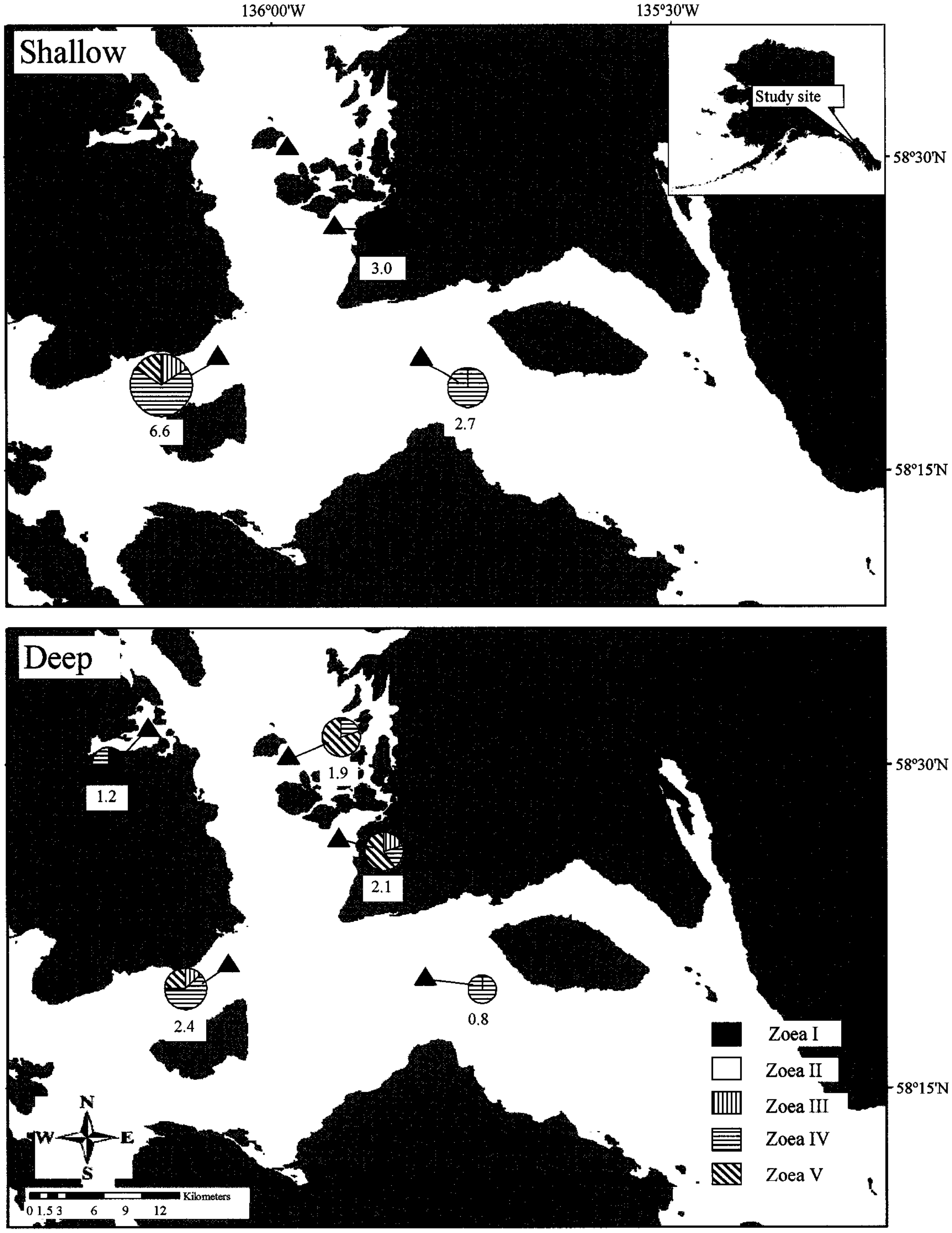

Fig. 2.13. Spatial variation of larval densities of Dungeness crabs on 29 July 2004. Larval Dungeness crabs, *Cancer magister*, were collected inside and outside of Glacier Bay, southeastern Alaska. Triangles indicate sampling stations. The numbers below the pies are total larval density (no. per 100 m^3) at each station. Sizes of pie charts denote relative abundance of larvae.

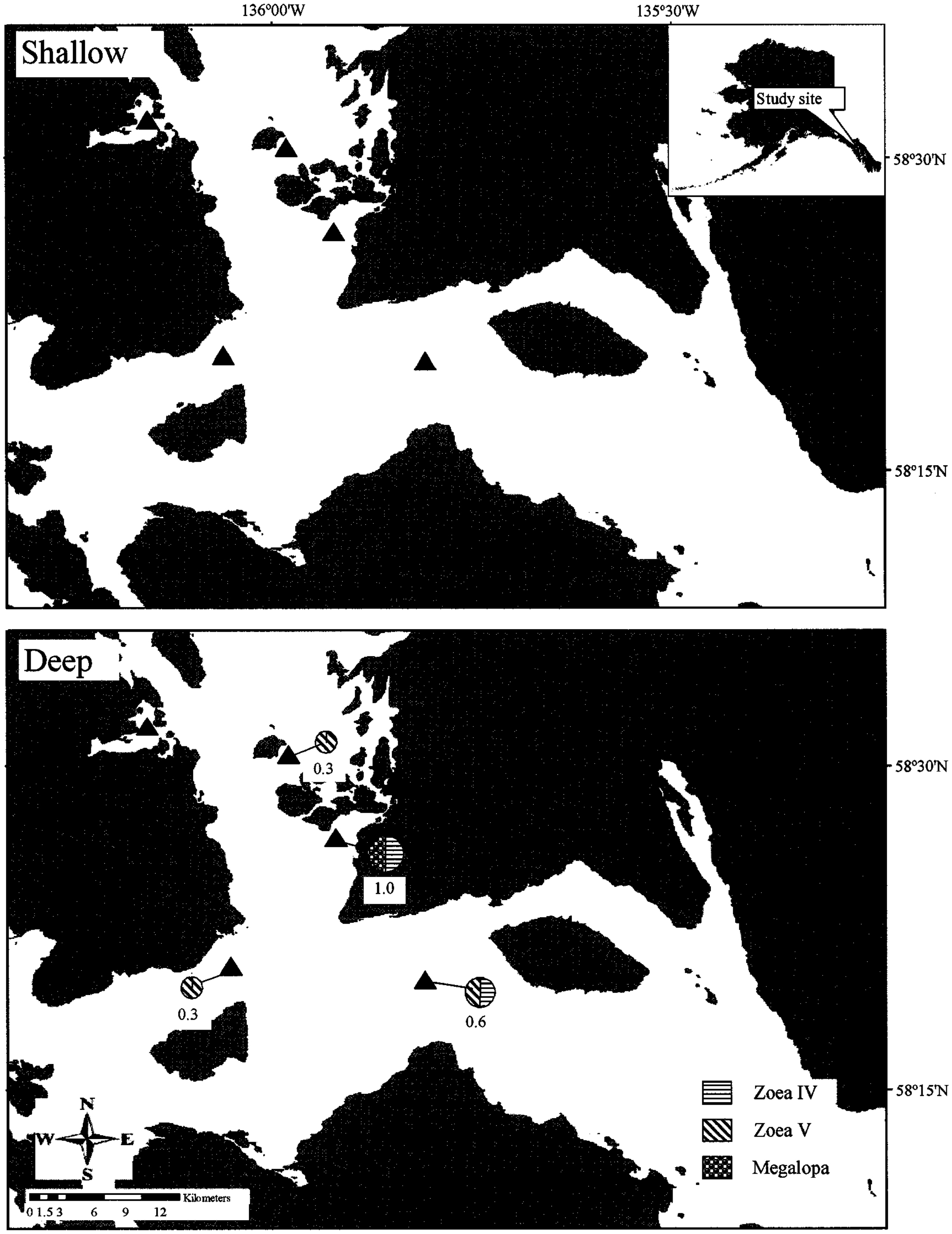

Fig. 2.14. Spatial variation of larval density of Dungeness crabs on 14 August 2004. Larval Dungeness crabs, *Cancer magister*, were collected inside and outside of Glacier Bay, southeastern Alaska. Triangles indicate sampling stations. The numbers below the pies are total larval density (no. per 100 m^3) at each station. Sizes of pie charts denote relative abundance of larvae.

Table 2.1. Depths (m) of thermocline in Glacier Bay from May to September 2004. Thermocline (zone of rapid change in temperature) was used to separate shallow water and deep water plankton tows collected biweekly in Glacier Bay and neighboring straits, southeastern Alaska, from May to September, 2004. Depths in parentheses indicate bottom depths at the sampling stations. Asterisks indicate that the water column was not stratified, but these depths separated the sampling strata. Question marks note data were unavailable. On September 9, only surface water was sampled.

(Depth in meters)

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

Table 2.2. Mean, standard deviation, and coefficient of variation for rostrum lengths of Zoeae I (ZI). Mean, standard deviation, and coefficient of variation for rostrum lengths of ZI were calculated to compare distributions across stations based on samples collected on each sampling date. Stdev = standard deviation, CV = coefficient of variation.

May 19, 2004					
Station	ISA	ISB	ISC	ISD	
Mean	0.806	0.801	0.812	0.800	
Stdev	0.019	0.021	0.018	0.021	
CV	0.023	0.026	0.023	0.027	
May 27-28, 2004					
Station	1	2	3	4	5
Mean	0.804	0.785	0.815	0.810	0.805
Stdev	0.028	0.033	0.024	0.033	0.026
CV	0.035	0.042	0.029	0.041	0.032
June 14, 2004					
Station	1	2	3	4	5
Mean	0.785	0.791	0.814	0.795	0.810
Stdev	0.040	0.039	0.023	0.032	0.030
CV	0.051	0.049	0.028	0.040	0.037

Table 2.3. Kolmogorov-Smirnov test (K-S test) results for the difference in densities of Dungeness crab larvae. Difference of the density of each larval stage between shallow upper thermocline and deep (below thermocline) depths and between inner and outer bay stations were tested with K-S test. Stations located outside of Glacier Bay (1, 2, ISA, ISB, ISC, and ISD) 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

Chapter 3

North to Alaska: Evidence for conveyor belt transport of Dungeness crab larvae along the west coast of the United States and Canada

Wongyu Park[1], David C. Douglas, and Thomas C. Shirley

Abstract

We propose and evaluate the hypothesis that Dungeness crab (*Cancer magister*) larvae from the northwestern coast of the United States and Canada can be transported northward to southeastern Alaska. Larvae collected in southeastern Alaska during May and June 1997-2004 had abundances and stages that varied seasonally, interannually, and spatially. An unexpected presence of late stage larvae in spring raises a question regarding their origin, and the most plausible explanation is that they hatched off the northern Washington and British Columbia coasts and were transported to southeastern Alaska. Buoy drift tracks support the hypothesis that larvae released off the northern Washington and British Columbia coasts during the peak hatching season can be physically transported to southeastern Alaska, arriving as late stage larvae in May and June when local larvae are only beginning to hatch. A northward spring progression of monthly mean 7°C SST isotherms and phytoplankton blooms provide further evidence that environmental conditions are conducive for larval growth and metabolism during the transport period. The proposed larval transport suggests possible unidirectional gene flow between southern and northern populations of Dungeness crabs in southeastern Alaska.

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[1] Park, W., D. C. Douglas, and T. C. Shirley. 2007. North to Alaska: Evidence for conveyor belt transport of Dungeness crab larvae along the west coast of the United States and Canada. Lomnol. Oceanogr. **52(1):** 248-256.

Introduction

Dungeness crabs, as do many crab species, form metapopulations composed of subpopulations connected by dispersing larvae (Botsford et al. 1998). Although adult Dungeness crabs have relatively small movements of up to tens of kilometers (Gotshall 1978; Stone and O'Clair 2001), the species has broad latitudinal and habitat distributions. The long planktonic period of Dungeness crabs of more than three months along the west coast of North America contributes to long distance dispersion (Jamieson and Armstrong 1991), aided by ocean currents and winds (McConnaughey et al. 1994). As part of a long term zooplankton sampling study in southeastern Alaska (Park et al. 2004), we discovered strikingly anomalous larval stages. Late stage Dungeness crab larvae (zoeae IV, V and megalopal stages) were present in plankton samples, even though local Dungeness crab populations were only beginning to release their larvae. In this manuscript we review buoy drift tracks and hydrographic data, and the abundance pattern of larval stage to explore the potential that the larvae may have been advected long distances from southern populations, and consider alternate explanations.

The North Pacific Current (NPC), also known as the Subarctic Current or West Wind Drift, bifurcates at approximately 45°N into the southward flowing California Current (CC) and the northward flowing Alaska Current (AC) (Dodimead et al. 1963). The AC forms the eastern branch of the broad scale wind-driven cyclonic circulation in the Gulf of Alaska (GOA) (Tabata 1982). The coastal waters off southeastern Alaska are always dominated by the northward flowing AC, which was suggested by Wickett (1967) to transport zooplanktors to the northwestern coast of America.

Despite the CC southward flow throughout the year, off the coasts of California, Oregon, and Washington, the wintertime northward flowing Davidson Current, and Southern California Countercurrent, as well as strong alongshore winds, aid Dungeness crab larvae in northward and onshore transport (Lough 1976; McConnaughey et al. 1994). Landward and northward flow characterized by the near-surface circulation contributes to Dungeness crab larvae being retained on the coast and to the coastal landing strip off the coast of Washington (McConnaughey et al. 1994). This current reversal results in upwelling and subsequent offshore larval transport, so that the larvae may not return to their natal origins (Jamieson and Armstrong 1991).

Ideally, the northward flowing Davidson Current and the Southern California Countercurrent during January and February could transport larvae hatched in northern California as far north as Washington, or even British Columbia, before the currents reverse and transport the larvae back to northern California. Arguably, some portion of the larvae could be retained in northern locations. Owing to these dynamic hydrographic processes, larvae hatched at different locations appear to be mixed, resulting in gene flow throughout the coastal areas below 45°N (L. Parr, unpubl. data, San Jose University). At the mouth of Juan de Fuca Strait and along the continental shelf of Vancouver Island and northern Washington, northward currents prevail until the spring reversal (Thomson et al. 1989), hence providing opportunity for Dungeness crab larvae that hatched off the coasts of northern Washington and British Columbia, and potentially some larvae hatched as far south as northern California, to enter the AC.

Marine invertebrate populations are sustained by self-recruitment or by recruitment of larvae from other populations. In particular, allochthonous larvae can affect the gene flow and sustainability of populations even if the long distance dispersal is insufficient to sustain or rebound a population (Strathmann et al. 2002). Understanding the connectivity afforded by hydrography and the dispersal of larvae between metapopulations of commercial species is pivotal to fisheries management (Botsford et al. 2004). Based on the dispersal capabilities of larvae, proper locations and numbers of marine reserves can be proposed to help sustain or rebound marine populations (Shanks et al. 2003; Botsford et al. 2004), thereby assisting fishery management.

Dungeness crabs have a complex life history with a reproductive strategy aligned with their broad latitudinal distribution. Off the Washington coast eclosion (hatching or zoeal release) occurs during January through mid-March (Cleaver 1949). Off the British Columbia coast, peak hatching occurs in January and February (MacKay 1942); in southeastern Alaska, hatching occurs mostly in May and June (Shirley et al. 1987).

The timing of larval hatching of Dungeness crabs may be related to the timing of the primary spring phytoplankton bloom along the west coast of North America, although a disparity occurs between these two events. The high latitude spring bloom has a narrow temporal window, but produces approximately 50% of annual primary production (Chester and Larrance 1981; Ziemann et al. 1991). Approximately 70% of the carbon produced in the spring bloom is consumed by primary consumers, although the amounts vary greatly interannually (Ziemann et al. 1993). A prolonged phytoplankton bloom can provide sufficient time for the majority of primary consumers to feed and reproduce (Ziemann et al. 1991).

Planktonic larval stages are critical to the life histories of many benthic marine invertebrates (Thorson 1950). Natural mortality of Dungeness crab larvae may be high due to combinations of predation, excessive temperature fluctuations, a scarcity of food, or low food quality (Lough 1976). Prolonged starvation results in lower larval survival and longer stage duration (Sulkin et al. 1998).

Dungeness crab larvae have stage-specific depth positioning and diel vertical migration. All larval stages of Dungeness crab have a strong crepuscular vertical migration; larvae ascend to the surface at dawn and dusk and descend to deeper depths at midnight and during daytime (Jamieson et al. 1989; Hobbs and Botsford 1992; Park and Shirley 2005). In general, zoeae I are positioned near the surface while later zoeal stages reside deeper in the water column (Lough 1976).

This paper explores the plausibility that Dungeness crab larvae hatched from southern regions (northern Washington and British Columbia) are being transported to southeastern Alaska, a direct distance of up to 1,500 km. We investigate temporal changes of Chl *a* concentrations and northward sea surface temperature (SST) progression to support our hypothesis, and provide supporting evidence from drift buoy tracks. Further, we explore the consequences of this larval transport, e.g., a unidirectional gene flow from southern to northern populations to northern populations of Dungeness crabs in southeastern Alaska.

Materials and Methods

To investigate the potential of larval transport over such a long distance, we examined the progression of Chl *a* concentrations that would serve as food for larvae during their northward transport period. We also examined SST progression to the north, as temperature would affect larval development during their transportation, and we examined buoy tracks from off the coasts of northern Washington and British Columbia to the larval collection locations. We also examined the pattern of occurrence of larval stages in the Alaskan study locations.

Study Sites

The Icy Strait (IS) transect is within a fjord system, surrounded by snowfields, glaciers, and densely forested mountains in the Alexander Archipelago of southeastern Alaska (Fig. 3.1). The area is approximately 50 km west of Juneau and includes the Glacier Bay ecosystem and supports a productive Dungeness crab fishery. Four stations were sampled at the 12 km long IS transect. The southernmost station on the IS transect is 70 m deep, while the others were 200-250 m in depth. The typical mean tidal range in IS was approximately 4 m with a maximum range to 7 m.

Two offshore transects were also sampled: Icy Point (IP) and Cape Edward (CE), approximately parallel with IS in latitude (Fig. 3.1). The IP and CE transects each contained four sampling stations along transects of 65 and 47 km lengths, respectively. The landward three stations of IP are 130-160 m in depth. The farthest station from the coastline is approximately 1,300 m in depth. The CE transect becomes drastically deeper from the coastline to offshore: 90 to 1,800 m. We combined the stations of the two offshore transects into a single entity, the Offshore Transect (OT) because of the limited samples in CE in June 1998 and 1999 and two missing years of data in 1998 and 1999 in IP, and because both transects were directly influenced by the northward flowing AC throughout the year.

Environmental Data

Several data sources were utilized to assess if environmental conditions in the eastern GOA during late winter and spring were conducive to long-distance transport and survival of Dungeness crab larvae. Larval growth and survival require suitable water temperature and food supply, while physical transport requires sufficient velocity and directionality.

Spring SST dynamics in the eastern GOA were investigated using Advanced Very High Resolution Radiometer (AVHRR) multichannel estimates disseminated in the 4 km pixel-resolution AVHRR Pathfinder Oceans SST Version 5.0 data sets (http://podaac.jpl.nasa.gov/). Monthly averaged daytime (ascending) Pathfinder SST data were acquired for February-May 1985–2003, and then averaged within months over the 19-year record. SST estimates with implausible magnitude, probable cloud contamination, or unacceptable satellite zenith angle (i.e. Pathfinder data quality indices <4) were removed prior to calculating the long-term means. Average geographic location of the 7°C SST isotherm was derived for each month by contouring the respective gridded long-term averages. The 7°C SST isotherm was chosen because its spatiotemporal progression roughly coincides with the peak period of local larval hatching of Dungeness crabs.

Primary production during spring in the eastern GOA was evaluated using Chl *a* concentration estimates derived from Sea-Viewing Wide Field-of-View Sensor (SeaWiFS) satellite imagery. Level-3 standard-mapped files of Chl *a* monthly climatology were obtained for March, April, and May 1998-2005, and June 1998-2004, from the Ocean Color Web, SeaWiFS Reprocessing #5.1 (http://oceancolor.gsfc.nasa.gov).

Trajectories of Argos-tracked Lagrangian drifters were examined to empirically evaluate the transport capabilities of AC. Drifters passing through coastal waters in the eastern GOA during January through May were extracted from a standardized global drifter velocity data set (Pazan and Niiler 2004) obtained from Scripps Institution of Oceanography, La Jolla, CA. Most drifters carried "holey sock" drogues that extended 18 m below the ocean surface. As part of the Scripps' standardized data processing, corrections for wind slip and leeway drift had been applied to compensate for movements of drifters without drogues, or those that had lost their drogues. We constructed daily and weekly drift vectors from the original 6 h vectors. Characteristics of some drift tracks were qualitatively compared with mesoscale geostrophic velocity vectors derived from sea surface height anomaly data by the Near-Real-Time Altimetry Data Group at the Colorado Center for Astrodynamics Research (Boulder, CO, http://argo.colorado.edu/~realtime/global_realtime/geovel.html).

Prevailing surface wind directions and velocities along the path of AC were summarized using monthly averaged 1,000 mb u-v wind velocities from the National Center for Environmental Prediction/National Center for Atmospheric Research (NCEP/NCAR) reanalysis data set (http://www.cdc.noaa.gov/). Data were extracted for each of 5 months (January-May) over a 57-year period (1948–2004) at four 2.5-degree resolution grid cells that parallel the eastern GOA coastline (50°N 130°W, 52.5°N 132.5°W, 55°N 135°W, 57.5°N 137.5°W). Surface wind vectors (speed and direction) were derived for each of the monthly averaged u-v wind velocity pairs ($n = 1140$).

Zooplankton and Oceanographic Sampling

The SouthEast Coastal Monitoring (SECM) survey has been conducted by the Auke Bay Laboratory, National Marine Fisheries Service, since 1997. The SECM survey investigates causal linkages between salmon production and climate changes, and attempts to assess marine growth, survival, distribution, migration, and ocean carrying capacity for Pacific salmon in southeastern Alaska. The Dungeness crab larval samples analyzed in this study were collected in conjunction with SECM.

Zooplankton and oceanographic data were collected in the IS, IP, and CE transects (Fig. 1) during the latter 10 days of each month, May to September 1997-2004. We report here only those samples collected in May and June. All sampling occurred during daylight, between 07:00 and 20:00 h. At each station, a 60 cm diameter bongo net (505 and 333 μm mesh) was deployed a single time in a double oblique tow. We report here on samples collected with the 333 μm mesh net. The bongo was deployed and retrieved at a 45° wire-angle with a descent rate of 1.0 m s^{-1}, a 30-second pause at maximum depth (to 200 m or within 10 m of the bottom at shallow stations), and an ascent rate of 0.5 m s^{-1}. General Oceanics model 2031, or Rigosha flow meters were placed inside the bongo nets for calculation of filtered water volumes. Plankton samples were preserved in 5 % buffered formalin aboard the ship and transported to the laboratory where Dungeness crab larvae were sorted and identified to larval stage.

Mean density of each larval stage across the transects was calculated as individuals per 100 m^3. Data from the IC and CE transects were pooled, and hereafter are referred to as OT. Mean transect densities were computed across years and months by averaging among the respective sample stations. Mean and proportional transect densities by larval stage were also computed.

Results

Hydrographic Conditions

On average, the 7°C SST isotherm was established between Queen Charlotte Island and Vancouver Island in February and March, and progressed to the northern part of Queen Charlotte Island in April (Fig. 3.1). Spring progression of the 7°C SST isotherms generally coincided with the timing of local peak hatching of Dungeness crab larvae. Surface Chl *a* concentrations followed a similar spatiotemporal evolution (Fig. 3.2). In March, surface Chl *a* was primarily concentrated in localized areas near the coast of northern Washington and Vancouver Island. In April, Chl *a* concentrations expanded throughout most coastal zones, with prominent phytoplankton blooms along British

Columbia and the northern GOA near Prince William Sound. During May, the concentrations continued to propagate northward and offshore, with notable blooms commencing in the coastal fjord systems of southeastern Alaska. In June, surface Chl *a* concentration remained elevated throughout most coastal zones along the British Columbia and southeastern Alaska.

Tracking histories of all Lagrangian drifters that had ever passed through northeastern GOA ($n = 49$) were initially examined to empirically evaluate transport velocities of the AC during late winter and spring. Only a small subset of drift tracks ($n = 7$) met requirements of originating in late winter near the southernmost extent of the AC. Many drifters were entrained far offshore in the cyclonic GOA gyre, while others were rejected because they tracked the AC during a different season. Among the drifters that originated in Washington and British Columbia during late winter and successfully reached southeastern Alaska by spring, three passed through coastal waters of the eastern GOA (Fig. 3.3A) and two moved primarily along nearshore waters (Fig. 3.3B). Two cases of drifters that failed to reach the vicinity of larval sampling near OT by spring are shown in Fig. 3.3C. Northward progression for one of these impeded drifters was clearly prolonged by entrainment in two persistent eddies (Fig. 3.3D) that are common to the coastal and shelf waters of southeastern Alaska and British Columbia (Okkonen et al. 2001). Monthly mean surface winds along the eastern GOA coastline during January-May are predominately northward (Fig. 3.3D), indicating that the prevailing spring wind direction is commensurate with the AC.

Larval Sampling

A larger proportion of late stage Dungeness crab larvae, such as zoea IV (ZIV), zoea V (ZV) and megalopa (M), were collected in OT during May with a small proportion of late stage larvae in IS (Fig. 3.4). In IS, early larval stages, such as zoea I (ZI) and zoea II (ZII), occurred in May during most of the study period. In May and June 2001, most OT larvae were uniquely late stage, notably different from all other years.

Monthly and interannual larval density and stages varied considerably at both OT and IS (Fig. 3.5); however, as stated above, a greater proportion of late-stage larvae were captured in OT. Overall, larval densities were an order of magnitude less in OT compared to IS (10 fold), and greater larval densities were observed in both transects during the more recent years of the study (Fig. 3.5).

Discussion

The ontogeny of Dungeness crab larvae is influenced by water temperature (Shirley et al. 1987; Sulkin and McKeen 1989). Local variability in the timing of life history events such as embryonic development rates and larval hatching is attributed to differences in water temperatures. Different larval stages occurring simultaneously in the same area may be a result of embryos being exposed to different temperature regimes during incubation (i.e., brooding females occupying colder fjords versus warmer waterways). Studies of Dungeness crab populations in southeastern Alaska over several decades argue against the possibility that the anomalously late stage larvae reported here resulted from early hatching of local populations because females that had hatched eggs during mid-late winter have never been observed (Shirley et al. 1987; Shirley and Shirley 1988; Taggart et al. 2004). Also, Dungeness crab larvae have never been reported to overwinter, and the cold water temperatures and limited food availability during winter months in southeastern Alaska further argue against the possibility that the advanced-stage larvae were born locally in the previous year.

A much higher proportion of late stage larvae were found in OT, whereas mostly early stages with a small fraction of late stages were found in IS (Fig. 3.4). We postulate that the late-stage larvae in OT did not hatch locally and that the late-stage larvae in IS were brought from the outer coast by flood tides. For example, the OT larvae in May 2001 were much older than those collected in June (Fig. 3.5A). Considering that larval duration exceeds 5 months in southeastern Alaska (Shirley et al. 1987), ZV that were found in OT in May 2001 should have hatched approximately four months earlier. Although the timing of ZI appearance varied interannually, perhaps affected by local variations in water temperature, ZV that were found in May should have hatched in January. However, in southeastern Alaska, the mean water temperature in March is approximately 3°C and phytoplankton blooms do not occur until April. Thus, the probability that the late stage larvae present in May originated in southeastern Alaska is low. The early larval stages collected in June are assumed to have hatched locally because the June larval stages in OT were more similar to those larvae found in IS. However, the stages collected in OT were often mixed with both late and early stages. In addition, the two stations most distant from the coast in OT had late larval stages at relatively low concentrations, while the two stations closer to the coast in OT had a mixed composition of early and late larval stages.

Buoy drift records empirically document that larvae hatched along the Washington or British Columbia coasts could passively drift to southeastern Alaska during the spring season (Fig. 3.3). Prevailing wind patterns would also facilitate northward transport during late winter and spring, particularly since most larval stages of Dungeness crab are found in the upper portion of the water column (for review see Park and Shirley, 2005). It is also likely that flow of the AC in the upper 18 m emulates the general flow of a much thicker (40-100 m) upper surface layer (Murray et al. 1999). In addition to the necessary mechanisms for physical transport, the spatiotemporal progression of water temperature (Fig. 3.1) and primary production (Fig. 3.2) in the eastern GOA are consistent with conditions necessary to sustain metabolic activity and zoeal development during their advection. Thus, at the time when local Dungeness crab larvae had only recently hatched, we conclude that the unusually late stage larvae in the OT originated from more southern populations.

Disparity in the chronology of larval stage development arises between the crab larvae found at OT and the larvae occurring concurrently in Washington and British Columbia. Peak settling of Dungeness crab megalopae in Washington and British Columbia occurs in May and June (Jamieson and Armstrong 1991). The late stage larvae collected at OT, which we assume to have been transported from the northern Washington and British Columbia coasts, were in earlier stages of development, namely ZIV, ZV, and M. But because of the northward progression of 7°C SST (Fig. 3.1), larvae that were transported northward were maintained in consistently cooler water, while members of the same cohort that remained near the Washington and British Columbia coasts would have experienced increasingly warmer water temperatures. When members of a single cohort are incubated under different ambient water temperature regimes, larvae grown in warmer water have accelerated development compared to those maintained in cooler conditions (Sulkin and McKeen 1989). Hence, the larvae advected northward would be expected to develop more slowly than their resident cohorts along the Washington and British Columbia coasts.

The densities of late stage larvae in the OT varied interannually. To account for this variability, biotic and abiotic conditions must be considered. The buoy drifters that were passively transported from the Washington and British Columbia coasts had different pathways. Some drifters traveled more directly to southeastern Alaska while others were periodically trapped in eddies (Fig. 3.3), and many were permanently advected offshore into the GOA (not shown). Hence, the variety of spatial pathways of larval Dungeness crab transport from Washington and British Columbia coasts to southeastern Alaska could result in the temporal variability of larval densities and stages found at OT. Furthermore, the coasts of Washington and British Columbia support abundant Dungeness crab populations across a broad latitudinal gradient which have a wide range of hatch timing. Hence, if advected to southeastern Alaska, larvae from southern populations would be expected to arrive in different stages and abundances due to variable transport pathways and hatch dates.

Our assessment of Dungeness crab larval hatch chronologies along the west coast of North America, the trajectories of ocean buoys, and the coincident progression of isotherms and phytoplankton blooms in the eastern Pacific, all collectively suggest that advection and survival of Dungeness crab larvae from Washington and British Columbia to southeastern Alaska is feasible. The transport hypothesis readily explains the presence of anomalously late stage larvae in the coastal waters of southeast Alaskan during May and June, while alternative explanations such as early hatching or overwintering of local populations lack supporting evidence and biological rationale.

The coastal Northeast Pacific is divided into three major production domains that are strongly influenced by the North Pacific Current (NPC): the Coastal Downwelling Domain (CDD) in the north, Coastal Upwelling Domain (CUD) in the south, and the Transition Zone (TZ) near British Columbia (Ware and McFarlane 1989). The likelihood that Dungeness crab larvae hatched from the coasts of northern Washington and British Columbia are being transported to southeastern Alaska invites consideration that unidirectional gene flow may be occurring from southern populations of Dungeness crabs to those in southeastern Alaska. The British Columbia coast is a transitional area where the genomes of CUD and CDD populations are mixed (L. Parr, unpubl. data, San Jose University). Subsequent advection of larvae from British Columbia to southeastern Alaska would again disperse the genotypes of CUD populations, and further promote a northward gene flow among Dungeness crab populations along the west coast of North America.

Our study benchmarks a potential distance and direction of larval dispersal of Dungeness crabs in the eastern North Pacific. While most marine invertebrate dispersal capabilities are unknown or may vary with local hydrography, our study highlights the role of hydrographic connectivity over broad geographic scale. Since larval export is a primary goal of many marine reserves, understanding dominant trajectories of larval dispersal is a key element in establishing a reserve. Hence, our findings can assist in evaluating the appropriate location, number, and size of reserves (Shanks et al. 2003; Botsford et al. 2004) in the eastern North Pacific.

Alaska serves as the terminus for northward larval advection, and hence the endpoint of a unidirectional gradient of gene flow between southern and northern crab populations. Among adult Dungeness crabs of southeastern Alaska, 22% of their genetic variation is attributed to allochthonous genotypes (L. Parr, San Jose University, unpubl. data). Probably any nearshore marine species in the eastern North Pacific Ocean with a wide latitudinal range, long-lived and dispersive larvae, and adults with limited movements, may be exposed to this unidirectional conveyor belt of larval transport and genetic dispersion. We emphasize that the unique, unidirectional current flow in the eastern Pacific invites the assessment of genetic structure of populations in southeastern Alaska in comparison with their conspecifics in British Columbia and the west coast of the United States, and in the design of marine reserve and international resource management between Canada and United States.

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Literature Cited

Botsford, L. W., C. L. Moloney, J. L. Largier, and A. Hastings. 1998. Metapopulation dynamics of meroplanktonic invertebrates: the Dungeness crab (*Cancer magister*) as an example, p. 295-306. *In* G. S. Jamieson and A. Campbell [eds.], Proceedings of the North Pacific symposium on invertebrate stock assessment and management. Can. Spec. Publ. Fish. Aquat. Sci. **125**.

Botsford, L. W., D. M. Kaplan, and A. Hastings. 2004. Sustainability and yield in marine reserve policy. Amer. Fish. Soc. Symp. **42:** 75-86.

Chester, A. J., and J. D. Larrance. 1981. Composition and vertical flux of organic matter in a large Alaskan estuary. Estuaries **4:** 42-52.

Cleaver, F. C. 1949. Preliminary results of the coastal crab (*Cancer magister*) investigation. Wash. State Biol. Rep. **49:** 49-82.

Dodimead, A. J., F. Favorite, and T. Hinano. 1963. Review of oceanography of the subarctic Pacific region. Int. N. Pac. Fish. Comm. Bull. No. **13:** 1-195.

Gotshall, D. W. 1978. Northern California Dungeness crab *Cancer magister* movements as shown by tagging. Bull. Cal. Dep. Fish Game **64:** 234-254.

Hobbs, R. C., and L. W. Botsford. 1992. Diel vertical migration and timing of metamorphosis of larvae of the Dungeness crab, *Cancer magister*. Mar. Biol. **112:** 417-428.

Jamieson, G. S., and D. A. Armstrong. 1991. Spatial and temporal recruitment patterns of Dungeness crab in the northeast Pacific. Mem. Queens Mus. **31:** 365-381.

Jamieson, G. S., A. C. Phillips, and W. S. Hugget. 1989. Effects of ocean variability on the abundance of Dungeness crab larvae, p. 305-325. *In* R. J. Beamish and G. A. McFarlane [eds.], Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. Can. Spec. Publ. Fish. Aquat. Sci. **108**.

Lough, R. G. 1976. Larval dynamics of the Dungeness crab, *Cancer magister* off the central Oregon coast, 1970-71. Fish. Bull. **74:** 353-375.

MacKay, D. G. 1942. The Pacific edible crab, *Cancer magister*. Fish. Res. Board Can. Bull. **62:** 1-32.

McConnaughey, R. A., D. A. Armstrong, B. M. Hickey, and D. R. Gunderson. 1994. Interannual variability in coastal Washington Dungeness crab (*Cancer magister*) populations: larval advection and the coastal landing strip. Fish. Oceanogr. **3:** 22-38.

Murray, C. P., S. L. Morey, and J. J. O'Brien. 1999. Interannual variability of upper ocean vorticity balances in the Gulf of Alaska. J. Geophys. Res. **106:** 4479-4491.

Okkonen, S. R., G. A. Jacobs, E. J. Metzger, H. E. Hurlburt, and J. F. Shriver. 2001. Mesoscale variability in the boundary currents of the Alaska Gyre. Continental Shelf Res. **21:** 1219-1236.

Park W., D. C. Douglas, and T. C. Shirley. 2007. Evidence of conveyor belt transport of Dungeness crab larvae along the west coast of the United States and Canada. Limnol. Oceanogr. **52:** 248-256.

Park, W., M. Sturdevant, J. Orsi, A. Wertheimer, E. Fergusson, W. Heard, and T. Shirley. 2004. Interannual abundance patterns of copepods during ENSO events in Icy Strait, southeastern Alaska. ICES J. Mar. Sci. **61:** 464-477.

Pazan, S. E., and P. Niiler. 2004. New global drifter data set available. Eos Trans. **85:** 17-18.

Shanks, A. L., B. A. Grantham, and M. H. Carr. 2003. Propagule dispersal distance and the size and spacing of marine reserves. Ecol. Appl. **13:** S159-S169.

Shirley, S. M., and T. C. Shirley. 1988. Appendage injury in Dungeness crabs, *Cancer magister*, in southeastern Alaska. Fish. Bull. **86:** 156-160.

Shirley, S. M., T. C. Shirley, and S. D. Rice. 1987. Latitudinal variation in the Dungeness crab, *Cancer magister*, zoeal morphology explained by incubation temperature. Mar. Biol. **95:** 371-376.

Stone, R. P., and C. E. O'Clair. 2001. Seasonal movements and distribution of Dungeness crabs *Cancer magister* in a glacial southeastern Alaska estuary. Mar. Ecol. Prog. Ser. **214:** 167-176.

Strathmann, R. R., T. P. Hughes, A. M. Kuris, K. C. Linderman, S. G. Morgan, J. M. Pandolfi, and R. R. Warner. 2002. Evolution of local recruitment and its consequences for marine populations. Bull. Mar. Sci. **70:** 377-396.

Sulkin, S. D., and G. L. McKeen. 1989. Laboratory study of survival and duration of individual zoeal stages as a function of temperature in the brachyuran crab *Cancer magister*. Mar. Biol. **103:** 31-37.

Sulkin, S., A. Blanco, J. Chan, and M. Bryant. 1998. Effects of limiting access to prey on development of first zoeal stage of the brachyuran crabs *Cancer magister* and *Hemigrapsus oregonensis*. Mar. Biol. **131:** 515-521.

Tabata, S. 1982. The anticyclonic, baroclinic eddy off Sitka, Alaska, in the Northeast Pacific Ocean. J. Phys. Oceanogr. **12:** 1260-1282.

Taggart, S. J., T.C. Shirley, C.E. O'Clair, and J. Mondragon. 2004. Dramatic increase in the relative abundance of large male Dungeness crabs, *Cancer magister*, following closure of commercial fishing. Amer. Fish. Soc. Symp. **42:** 243-253.

Thomson, R. E., B. M. Hickey, and P. H. LeBlond. 1989. The Vancouver Island Coastal Current: fisheries barrier and conduit, p. 265-296. *In* R. J. Beamish and G. A. McFarlane [eds.], Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. Can. Spec. Publ. Fish. Aquat. Sci. **108**.

Thorson, G. 1950. Reproductive and larval ecology of marine bottom invertebrates. Biol. Rev. **25:** 1-45.

Ware, D. M., and G. A. McFarlane. 1989. Fisheries production domains in the northeast Pacific Ocean, p. 359-379. *In* R. J. Beamish and G. A. McFarlane [eds.], Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. Can. Spec. Publ. Fish. Aquat. Sci. **108**.

Wickett, W. P. 1967. Ekman transport and zooplankton concentration in the North Pacific Ocean. J. Fish. Res. Bd. Can. **24:** 581-594.

Ziemann, D. A., L. D. Conquest, M. Olaizola, and P. K. Bienfang. 1991. Interannual variability in the spring phytoplankton bloom in Auke Bay, Alaska. Mar. Biol. **109:** 321-334.

Ziemann, D. A., P. K. Bienfang, K. W. Fulton-Bennett, W. Kottenmeier, and L. D. Conquest. 1993. Carbon budget for the spring bloom in Auke Bay, Alaska. Mar. Biol. **115:** 509-521.

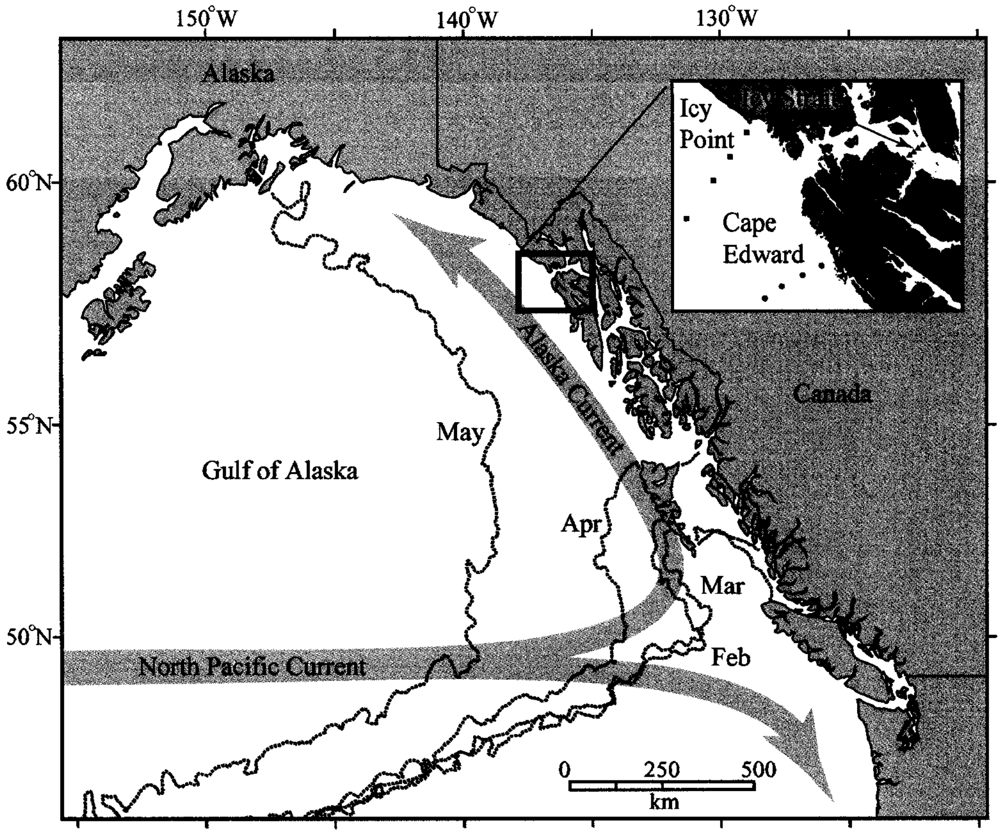

Fig. 3.1. Northward progression of 7°C SST isotherm. The generalized northwesterly flow of the Alaska Current and the northwesterly spring progression of the monthly mean (1985-2003) 7°C SST isotherm were indicated in eastern Gulf of Alaska. Inset demarcates the 8 offshore (Icy Point and Cape Edward) and 4 inside passage (Icy Strait) sampling sites of Dungeness crab larvae.

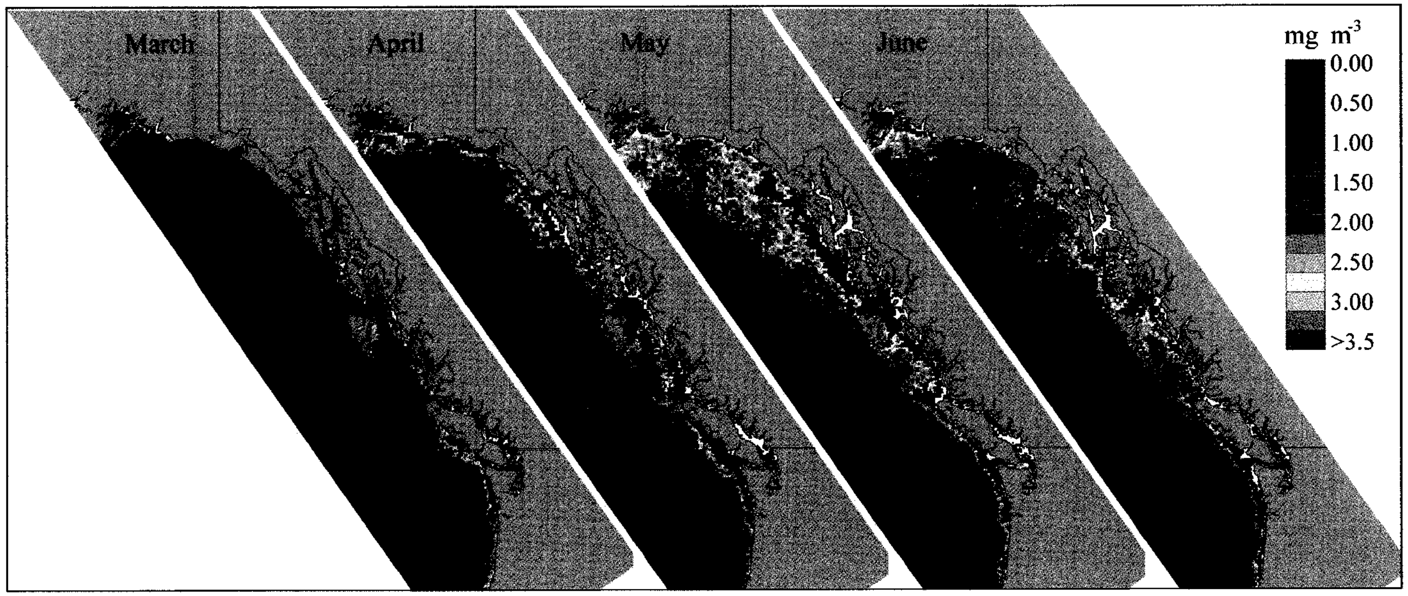

Fig. 3.2. Satellite-derived (SeaWiFS) Chl *a* concentration estimates. Satellite-derived (SeaWiFS) Chl *a* concentration estimates for March, April, and May (1998-2005), and June (1998-2004) in the eastern Gulf of Alaska were averaged.

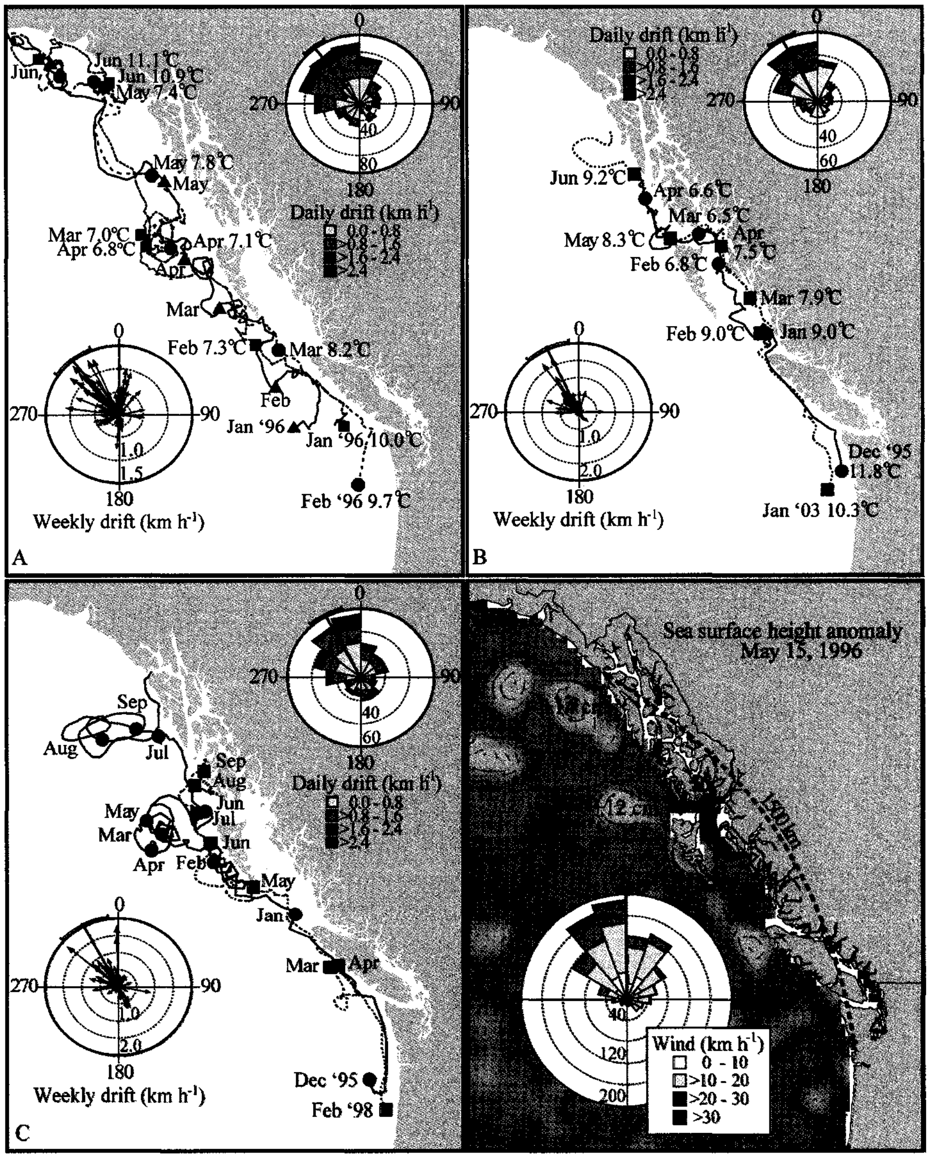

Fig. 3.3. Trajectories of 7 Lagrangian drifters that progressed through the Alaska Current during January-June. Symbols denote buoy positions at the beginning of each labeled month, followed by SST data when available. Circular histogram insets (in panels A-C) illustrate the direction and speed of drift vectors at weekly and daily intervals. (A) Three drifters that moved primarily along the outer coast (drifter Ids: 9524454 (square), 9524486 (circle), 9422213 (triangle)); (B) two drifters that moved primarily along near shore waters (35899 (square), 9524427 (circle)); (C) two drifters (9730562 (square), 9524421 (circle)) that propagated northward more slowly; (D) sea surface height anomalies on 15 May 1996 with superimposed geostrophic velocity vectors showing two persistent anticyclonic eddies that entrained buoy 9524421 during March-May and July–September; (D-inset) frequency histogram of the directions and speeds of all monthly averaged wind vectors for January-May 1948–2004.

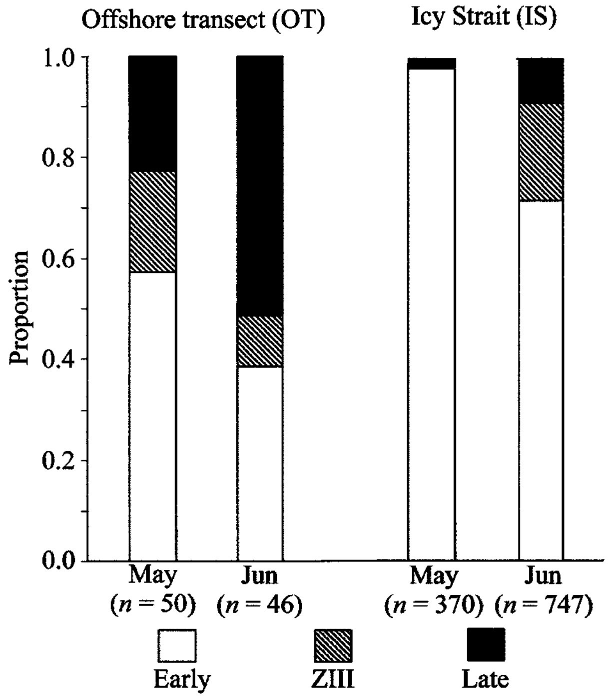

Fig. 3.4. Mean monthly proportions of Dungeness crab larval stages. Mean monthly proportions of Dungeness crab larval stages between the offshore transect versus Icy Strait in May and June 1997-2004 were compared. Zoea I and II were grouped as 'Early', and zoea IV, V, and megalopa were grouped as 'Late'.

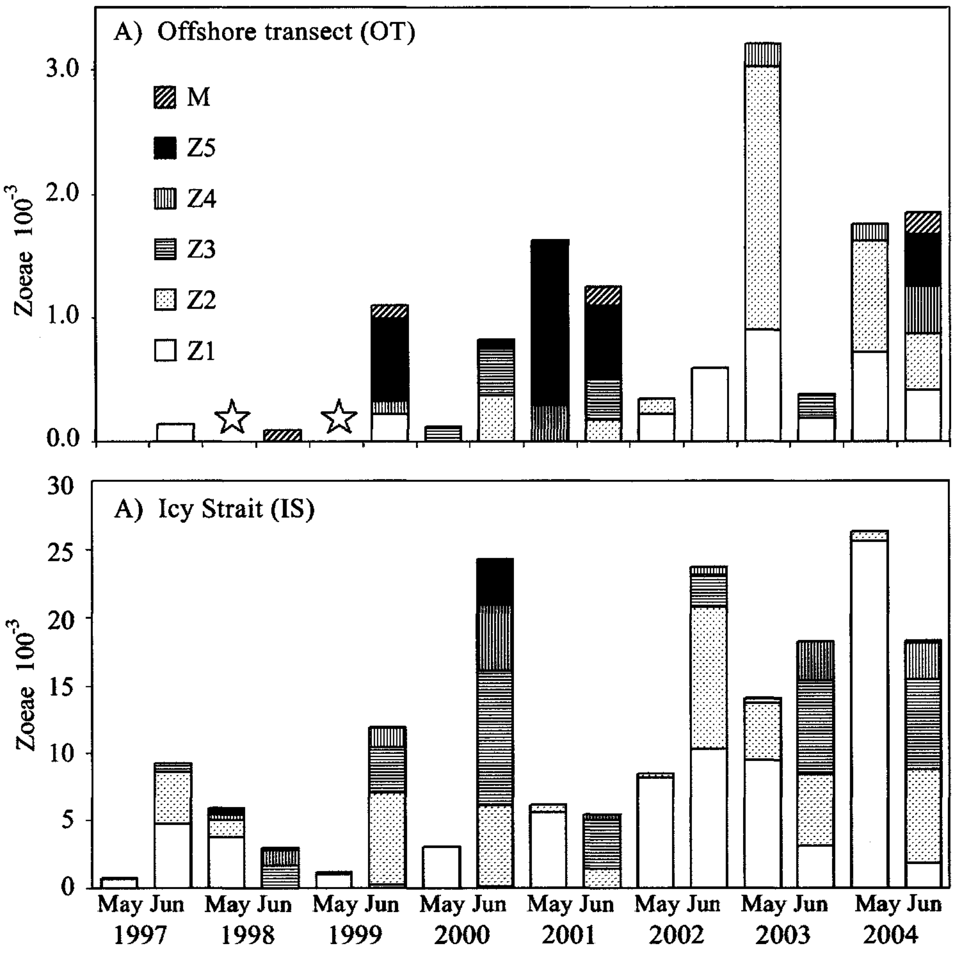

Fig. 3.5. Comparison of larval densities between the offshore and Icy Strait transects. Dungeness crab larval densities by larval stage in the (A) offshore transect, and (B) Icy Strait transect, in May and June 1997–2004 were compared. Star-symbol indicates no data.

General Conclusions

I examined the spatial and temporal pattern of the distribution of Dungeness crab larvae and oceanographic data collected at various locations in southeastern Alaska to indicate whether Dungeness crab larvae in southeastern Alaska hatched and were advected to different locations after hatching or retained within near hatched locations,.

I investigated the spatial and temporal variation of larval abundance and hatch timing of Dungeness crabs in Chapter 1. Dungeness crab larvae and oceanographic data were examined at 16 stations along four transects collected by the SouthEast Coastal Monitoring (SECM) survey in southeastern Alaska from May to September during 1997-2004: upper Chatham strait (UC), Icy Strait (IS), Cross Sound (CS), and Icy Point (IP).

In general, zoeae I (ZI) predominated in May and the densities of ZI decreased and later stage larvae increased thereafter. Larval densities were higher in inland waters than offshore waters. Many of the early and intermediate stages were found within inland waters. This is a different pattern of larval distribution than in the southern parts of the range of the species where larvae are dispersed offshore after hatching (Lough 1976; Reilly 1983). Co-occurrence of ZI and later stage larvae suggested that larvae hatched earlier in more southern parts of the distribution range were transported to southeastern Alaska by the Alaska Current which flows northward throughout the year (Reed and Schumacher 1986).

The timing of ZI occurrence varied interannually. Water temperatures during the embryonic development were correlated to ZI hatch timing. ZI hatched earlier in 1998 when water temperatures during the egg incubation period were warmer, while they hatched later in 1997 and 2002 when water temperatures were colder (Etherington et al. 2004). This result coincided with previous studies of the effects of temperature on larval developments (Wild 1980; Shirley et al. 1987).

In Chapter 2, I examined the distribution and mortality of Dungeness crab larvae and the rostrum length of ZI from a relatively small area in southeastern Alaska. Larvae were collected at five stations inside and outside of Glacier Bay at two different depth ranges, biweekly from late May to mid-September, 2004 and at four stations in Icy Strait, southeastern Alaska, monthly from late May to late August 2004.

ZI was predominant at all stations in May and gradually decreased thereafter. Larval densities decreased gradually from ZI to ZV. This is a different pattern from a previous study conducted at nearby locations in which late stage zoeae were missing but a high abundance of ZI occurred (Fisher 2006). The densities of larvae in shallow and deep depths of the water column during ebb and flood tides were similar. The lack of differences in ZI densities during ebb and flood tides in the water column is not similar to the pattern of larval advection in which ZI that are advected to other areas concentrate at the surface during ebbing tides (Provenzano et al. 1983). Total larval loss increased from ZI to ZV. The loss of Dungeness crab larvae in this study is slightly higher than that of *Paralithodes camtschatica* larvae from Auke Bay, southeastern Alaska (Shirley and Shirley 1989), in which the larvae of the red king crab are thought to be retained.

ZI with different rostrum lengths at the same locations co-occurred. This may be evidence of larval advection and mixing. Spine lengths of Dungeness crab ZI incubated at cold temperatures are longer than those at warmer temperatures (Shirley et al. 1987).

Tidal movements in Glacier Bay and neighboring straits (Hooge and Hooge 2002) and nontidal currents (Haight 1926) may have resulted in mixing of ZI incubated at different temperatures or possibly other biological factors.

In chapter 3, we investigated the possible sources of unusually late stage larvae which co-occurred with early stage larvae, collected at inshore and offshore transects during May and June 1997-2004. Unusually late stage larvae that co-occurred with early stage larvae might be transported from more southern areas where larval hatching occurred 3-4 months earlier. To support the hypothesis, buoy drift tracks, wind directions, SST, and food conditions during transportation were analyzed. These late stage larvae most likely were not larvae that overwintered or larvae that hatched earlier in the year and developed faster; the lack of adequate prey (Coyle et al. 1990; Paul et al. 1990a,b) and cold water temperatures during winter months (Etherington et al. 2004, B. Wing, Auke Bay Laboratory, NMFS, unpubl. data) argue against these alternate explanations. Larvae that released off the northern Washington and British Columbia coasts in January through March can be physically transported to southeastern Alaska, arriving as late stage larvae in May and June. A northward spring progression of monthly mean 7°C SST isotherms and phytoplankton blooms provide further evidence that environmental conditions are conducive for larval growth and metabolism during the transport period. Interannual variation of larval densities of late stage larvae may have resulted from interannual variations in eddies and meanders during the transportation route (Tabata 1982).

Overall, the patterns of development and spatial distribution of larval stages for the inland waters in southeastern Alaska were markedly different from the patterns reported for Dungeness crab larvae from southern parts of the species range: many intermediate larval stages were collected, as opposed to the lack of post ZI in estuaries and coastal areas from California through Washington and British Columbia (Reilly 1983). Although I cannot definitely ascertain whether Dungeness crab larvae locally hatched are advected or retained within my study sites, I can report that late stage larvae occur in May, and co-occurrence of different rostrum lengths provide evidence of the mixing of larvae with different origins and incubation temperatures.

Literature Cited

Coyle, K. O., A. J. Paul, and D. A. Ziemann. 1990. Copepod populations during the spring bloom in an Alaskan subartic embayment. J. Plank. Res. **12:** 759-779.

Etherington, L. L., P. N. Hooge, and E. R. Hooge. 2004. Factors affecting seasonal and regional pattern of surface water oceanographic properties within a fjord estuarine system: Glacier Bay, AK. U.S. Geological Survey, Alaska Science Center, Gustavus, AK, 83 pp.

Fisher, J. L. 2006. Seasonal timing and duration of brachyuran larvae in a high-latitude fjord. Mar. Ecol. Prog. Ser. **323:** 213-222.

Haight, F. J. 1926. Nontidal currents in southeastern Alaska. Geogr. Rev. 16: 642-646.

Hooge, P. N., and E. R. Hooge. 2002. Fjord oceanographic patterns in Glacier Bay National Park. USGS Alaska Biological Science Center. Final Rep. 130 pp.

Lough, R. G. 1976. Larval dynamics of the Dungeness crab, *Cancer magister* off the central Oregon coast, 1970-71. Fish. Bull. **74**: 353-375.

Paul, A. J., K. O. Coyle, and D. A. Ziemann. 1990a. Variation in egg production rates by *Pseudocalanus* spp. in a subarctic Alaskan bay during the onset of feeding by larval fish. J. Crust. Biol. **10:** 648-658.

Paul, A. J., K. O. Coyle, and D. A. Ziemann. 1990b. Timing of spawning of *Thysanoessa raschii* (Euphausiacea) and occurrence of their feeding-stage larvae in an Alaskan bay. J. Crust. Biol. **10:** 69-78.

Provenzano, A. J., J. R. McConaugha, K. B. Phillips, D. F. Johnson, and J. Clark. 1983. Vertical distribution of first stage larvae of the blue crab, *Callinectes sapidus*, at the mouth of Chesapeake Bay. Estu. Coast. Shelf Sci. **16:** 489-499.

Reed, P. K., and J. D. Schumacher. 1986. Physical Oceanography, p 57-75. *In* D. W. Hood and D. W. Zimmerman ST [eds.], The Gulf of Alaska: Physical environment and biological resources. Ocean assessment division, NOAA.

Reilly, P. N. 1983. Dynamics of the Dungeness crab, *Cancer magister*, larvae off central and northern California, p. 57-84. *In* P. W. Wild and R. N. Tasto [eds.], Life history, environment, and mariculture studies of the Dungeness crab, *Cancer magister*, with emphasis on the central California fishery resource. Calif. Dept. Fish Game **172**.

Shirley, S. M., and T. C. Shirley. 1989. Interannual variability in density, timing and survival of Alaskan red king crab *Paralithodes camtschatica* larvae. Mar. Ecol. Prog. Ser. **54:** 51-59.

Shirley, S. M., T. C. Shirley, and S. A. Rice. 1987. Latitudinal variation in the Dungeness crab, *Cancer magister*: zoeal morphology explained by incubation temperature. Mar. Biol. **95**: 371-376.

Tabata, S. 1982. The anticyclonic, baroclinic eddy off Sitka, Alaska, in the Northeast Pacific Ocean. J. Phys. Oceanogr. **12:** 1260-1282.

Wild, P. W. 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.

Appendix 1. Salinity and temperature in southeastern Alaska in May-September, 1997-2004. Salinity and temperature were measured at 2 m depth in southeastern Alaska, May-September 1997-2004. Data were collected by SouthEast Coastal Monitoring (SECM) survey, Auke Bay Lab, NMFS, NOAA.

	Icy Strait							
Sampling date	Salinity				Temperature (°C)			
	ISA	ISB	ISC	ISD	ISA	ISB	ISC	ISD
5/24/1997	30.8	29.9	29.9	29.4	8.1	8.5	8.6	9.0
6/26/1997	27.6	27.4	27.7	27.9	12.2	12.9	12.4	13.0
7/21/1997	24.1	20.3	20.2	20.4	12.0	13.2	13.5	13.9
8/22/1997	27.0	26.1	24.5	23.7	11.2	11.5	12.3	12.8
10/5/1997	29.0	28.4	28.0	26.6	8.6	8.7	8.8	9.0
5/16/1998	30.6	30.7	30.6	30.4	7.7	7.8	8.0	8.1
6/27/1998	28.8	27.9	28.6	28.8	11.1	11.2	11.2	11.1
7/21/1998	24.1	22.6	20.9	20.2	13.2	13.4	14.2	13.9
8/25/1998	30.0	29.6	28.8	27.8	9.1	10.0	10.9	11.7
10/6/1998	26.9	26.4	25.0	24.2	8.8	8.8	9.1	9.1
5/21/1999	31.0	31.0	30.8	30.6	6.5	6.5	7.3	7.7
6/29/1999	30.2	29.1	27.3	26.7	8.4	10.3	11.1	11.5
7/27/1999	28.2	27.8	26.6	26.1	11.1	12.0	12.1	12.5
8/22/1999	26.8	21.4	17.9	18.3	11.0	12.9	13.4	13.4
9/27/1999	29.4	29.3	28.1	25.4	8.3	8.3	8.7	9.2
5/20/2000	31.4	31.2	31.0	30.9	6.6	7.2	7.0	7.9
6/29/2000	25.8	26.2	25.7	31.6	12.6	12.2	12.5	12.5
7/20/2000	27.9	28.2	27.4	26.0	11.6	11.5	12.7	13.2
8/30/2000	27.1	26.7	21.1	27.5	11.5	11.6	11.8	12.0
9/27/2000	28.8	28.3	27.0	27.0	8.6	8.9	9.3	9.4
5/20/2001	31.2	31.3	31.1	31.0	7.2	7.2	7.0	7.1
6/28/2001	28.2	26.9	23.6	24.1	12.2	11.0	12.3	12.2
7/29/2001	19.2	29.0	25.8	22.6	10.2	11.0	12.1	12.8
8/27/2001	22.3	24.5	21.5	23.3	12.7	12.4	12.8	12.6
9/27/2001	28.5	28.1	28.3	27.9	8.8	9.0	9.1	9.2
5/23/2002	31.7	31.8	31.5	31.5	7.0	6.1	6.9	6.4
6/22/2002	30.5	29.2	25.0	25.1	9.1	9.8	11.8	12.0
7/23/2002	28.2	27.2	24.9	23.9	10.2	11.1	12.3	12.8
8/23/2002	28.5	26.2	25.9	26.1	9.7	10.8	10.9	10.9
5/22/2003	31.3	31.4	31.3	31.0	8.0	7.7	7.6	8.4
6/23/2003	30.0	29.6	30.3	29.0	11.1	10.7	9.6	11.1
7/24/2003	25.7	25.6	25.0	25.4	13.6	13.6	14.0	13.7
8/22/2003	29.3	26.9	25.6	25.0	10.8	11.9	12.2	13.1
5/19/2004	30.0	29.9	29.8	29.7	8.2	8.6	8.1	8.3
6/22/2004	23.2	22.3	24.0	24.8	14.5	14.7	14.7	15.6
7/25/2004	25.1	23.7	19.4	19.1	14.7	15.1	15.5	15.6
8/24/2004	26.9	21.7	23.3	22.5	12.0	14.3	14.2	14.5

Appendix 1 (cont'd)

	Upper Chatham							
Sampling date	Salinity				Temperature (°C)			
	UCA	UCB	UCC	UCD	UCA	UCB	UCC	UCD
5/21/1997	28.6	28.0	28.7	28.8	9.4	8.7	7.8	7.9
6/23/1997	22.4	22.5	22.5	22.1	14.3	12.9	12.9	13.2
7/19/1997	23.1	23.3	17.1	16.1	13.6	13.7	13.1	13.2
8/23/1997	28.5	28.2	26.3	28.1	11.2	11.3	12.5	12.0
10/6/1997	29.4	ns	ns	ns	8.7	ns	ns	ns
5/17/1998	29.5	29.6	30.1	30.4	7.9	8.0	8.0	8.2
6/29/1998	28.8	27.9	28.6	28.8	12.7	12.9	12.9	12.9
7/22/1998	24.1	22.6	20.9	20.2	12.3	12.9	13.4	13.5
8/26/1998	30.0	29.6	28.8	27.8	10.0	10.2	11.2	11.2
5/22/1999	30.3	31.1	30.8	30.8	6.5	6.3	7.1	7.1
7/1/1999	29.1	26.6	28.9	26.9	10.9	10.2	11.2	11.4
7/29/1999	29.5	29.1	29.0	25.0	10.6	11.2	12.8	12.5
8/21/1999	24.7	23.8	18.8	18.6	12.7	12.9	13.4	13.3
10/1/1999	25.0	26.1	23.5	24.0	9.0	9.0	8.9	8.9
5/20/2000	30.6	30.4	30.4	30.5	7.0	7.5	7.7	7.4
6/30/2000	22.5	23.0	24.0	24.5	13.4	13.2	12.7	12.5
7/21/2000	27.0	28.9	28.1	27.4	12.8	10.8	12.5	12.0
8/29/2000	24.0	22.7	23.0	20.5	11.6	11.6	11.3	11.6
9/28/2000	29.8	29.5	28.1	27.6	8.5	8.6	9.2	9.5
5/19/2001	30.0	30.8	30.7	30.7	7.1	7.4	7.8	7.0
6/26/2001	26.4	26.1	26.3	28.1	11.9	12.3	12.9	10.9
7/29/2001	26.9	25.7	23.3	25.4	12.1	12.6	12.5	11.9
8/26/2001	26.4	27.0	25.6	21.1	12.2	11.8	12.4	12.5
9/26/2001	28.9	28.1	27.8	27.4	9.0	9.5	9.4	9.4

Appendix 1 (cont'd)

			Cross Sound					
Sampling date	Salinity				Temperature (°C)			
	CSA	CSB	CSC	CSD	CSA	CSB	CSC	CSD
5/23/1997	31.4	31.4	31.7	31.8	6.9	6.6	6.6	6.5
6/24/1997	31.1	31.6	31.8	31.8	9.8	8.2	7.4	7.3
7/24/1997	30.9	31.7	31.6	30.9	11.3	8.2	8.3	8.0
8/26/1997	30.8	30.9	30.5	30.1	15.2	10.7	10.2	9.4
10/4/1997	31.3	31.6	31.7	31.3	11.6	9.1	8.2	8.3
5/dd/1998	ns	ns	ns	ns	ns	ns	ns	ns
6/28/1998	31.7	31.7	32.0	31.7	8.4	8.4	7.7	7.6
7/27/1998	31.0	31.4	31.3	31.4	12.1	9.6	9.7	8.5
8/29/1998	30.9	30.8	30.8	30.8	12.3	12.2	9.4	10.1
10/7/1998	31.7	31.9	31.8	31.6	10.1	7.5	7.7	7.6
5/22/1999	31.6	31.9	31.9	31.9	7.9	6.9	7.0	6.8
6/28/1999	30.8	31.8	32.0	31.0	8.8	7.8	7.5	7.5
7/26/1999	31.7	31.8	31.8	31.5	11.3	7.7	7.8	7.8
8/23/1999	29.0	29.8	30.1	29.2	10.4	9.8	9.9	9.5
9/29/1999	31.3	31.5	30.9	31.1	8.5	8.6	7.8	7.8
5/21/2000	31.6	31.9	31.9	31.9	7.4	7.0	6.9	6.8
6/28/2000	31.4	31.7	31.5	31.6	11.6	7.9	8.1	8.0
7/23/2000	ns	ns	30.3	26.0	ns	ns	8.7	7.3
8/27/2000	30.7	31.7	31.0	27.5	10.9	7.9	8.2	7.9
9/29/2000	ns	ns	ns	31.5	ns	ns	ns	8.0

Appendix 1 (cont'd)

			Icy Point					
Sampling date	Salinity				Temperature (°C)			
	IPA	IPB	IPC	IPD	IPA	IPB	IPC	IPD
5/22/1997	30.8	31.2	31.3	31.3	8.2	8.7	9.1	9.4
6/25/1997	30.9	31.4	31.5	31.5	11.2	12.4	13.4	13.3
7/25/1997	30.9	31.2	31.4	31.9	13.9	14.5	14.4	14.6
8/25/1997	31.0	30.7	31.1	31.1	15.0	14.1	15.0	16.3
10/3/1997	29.9	31.1	31.0	31.0	11.2	12.5	12.4	12.3
5/23/2000	31.6	31.6	31.7	32.0	8.7	8.1	7.8	8.4
6/27/2000	29.3	31.0	31.4	31.8	12.9	13.2	13.0	12.9
7/24/2000	31.4	31.3	31.1	31.6	13.1	12.9	13.4	14.1
8/28/2000	31.4	31.5	31.5	31.5	12.5	13.2	13.0	12.5
9/26/2000	30.9	30.9	31.1	31.8	11.5	11.6	11.6	11.9
5/24/2001	31.9	31.9	32.1	32.2	7.1	7.4	7.8	7.6
6/27/2001	32.0	31.9	32.1	32.0	12.6	11.5	12.1	11.7
7/28/2001	31.7	31.7	32.0	32.0	13.6	13.3	13.8	14.1
8/dd/2001	ns	ns	ns	ns	ns	ns	ns	ns
9/dd/2001	ns	ns	ns	ns	ns	ns	ns	ns
5/22/2002	31.5	32.0	32.2	32.2	7.6	8.0	8.3	8.4
6/23/2002	31.7	31.4	31.8	31.9	10.8	11.9	11.7	11.5
7/29/2002	31.1	31.6	31.9	31.9	10.1	12.4	13.8	13.9
8/25/2002	31.5	31.6	31.7	31.5	13.5	13.0	13.8	13.8
5/21/2003	31.8	31.7	31.7	31.9	8.8	10.0	9.7	10.2
6/22/2003	31.7	31.5	31.3	32.0	9.7	11.0	11.3	11.7
7/23/2003	31.1	31.7	31.6	31.0	13.2	14.9	14.7	15.8
8/dd/2003	ns	ns	ns	ns	ns	ns	ns	ns
5/22/2004	30.9	31.0	31.0	30.9	7.3	8.2	8.9	9.1
6/21/2004	31.3	31.6	31.6	31.6	12.8	12.9	13.3	13.0
7/24/2004	31.2	31.3	31.3	31.4	14.4	15.6	15.3	15.7
8/23/2004	30.3	31.3	31.3	31.3	14.8	17.2	16.8	17.4

Appendix 2. Zooplankton displacement volume (ml m^{-3}) and number of larval Dungeness crabs in 1997-2004. Zooplankton displacement volume (DV) and larval Dungeness crabs were collected in southeastern Alaska in May-September, 1997-2004. Data were collected by SouthEast Coastal Monitoring (SECM) survey, Auke Bay Lab, NMFS, NOAA. FWV=filtered water volume (m^3), DV=zooplankton displacement volume.

			Icy Strait						
Date	Station	FWV	DV	ZI	ZII	ZIII	ZIV	ZV	M
5/24/1997	ISA	94.5	99.0	2	0	0	0	0	0
5/24/1997	ISB	201.2	109.0	0	0	0	0	0	0
5/24/1997	ISC	202.3	129.0	0	1	0	0	0	0
5/24/1997	ISD	197.2	154.0	1	0	0	0	0	0
6/26/1997	ISA	94.6	48.0	6	6	2	0	0	0
6/26/1997	ISB	185.8	112.0	10	6	1	0	0	0
6/26/1997	ISC	240.6	175.0	4	7	0	0	0	0
6/26/1997	ISD	247.5	143.0	14	7	0	0	0	0
7/21/1997	ISA	90.4	21.0	5	3	1	1	0	0
7/21/1997	ISB	198.4	93.0	2	0	1	0	0	0
7/21/1997	ISC	237.8	156.0	0	0	3	0	0	0
7/21/1997	ISD	252.6	137.0	0	2	0	0	0	0
8/22/1997	ISA	109.7	29.0	0	0	1	1	1	0
8/22/1997	ISB	223.4	87.0	0	0	0	0	0	0
8/22/1997	ISC	283.6	363.0	0	0	0	0	0	0
8/22/1997	ISD	244.8	162.0	0	1	0	1	1	0
10/5/1997	ISA	85.3	32.0	0	0	0	0	0	0
10/5/1997	ISB	212.0	101.0	0	0	0	0	0	0
10/5/1997	ISC	264.9	113.0	0	0	0	0	0	0
10/5/1997	ISD	239.4	67.0	0	0	0	0	0	0
5/16/1998	ISA	104.2	68.0	7	2	0	1	2	0
5/16/1998	ISB	225.4	105.0	10	4	0	1	0	0
5/16/1998	ISC	255.6	107.0	10	2	1	0	0	0
5/16/1998	ISD	225.2	85.0	7	3	0	0	0	0
6/25/1998	ISA	90.1	62.0	0	0	4	2	0	0
6/25/1998	ISB	205.8	141.0	0	0	3	2	0	0
6/25/1998	ISC	225.6	153.0	0	0	0	1	0	0
6/25/1998	ISD	442.5	220.0	0	1	2	2	2	0
7/21/1998	ISA	108.8	23.0	0	0	2	4	1	0
7/21/1998	ISB	226.6	135.0	0	0	0	3	2	1
7/21/1998	ISC	281.5	127.0	0	0	0	1	0	0
7/21/1998	ISD	235.9	61.0	0	0	1	0	1	0
8/25/1998	ISA	96.2	13.0	0	0	0	0	0	0
8/25/1998	ISB	181.2	82.0	0	0	0	0	0	0
8/25/1998	ISC	240.6	79.0	0	0	0	0	1	0
8/25/1998	ISD	235.5	40.0	0	0	0	0	0	0

Appendix 2 (cont'd)

			Icy Strait						
Date	Station	FWV	DV	ZI	ZII	ZIII	ZIV	ZV	M
10/6/1998	ISA	86.7	17.0	0	0	0	0	0	0
10/6/1998	ISB	211.9	60.0	0	0	0	0	0	0
10/6/1998	ISC	251.3	71.0	0	0	0	0	0	0
10/6/1998	ISD	238.6	54.0	0	0	0	0	0	0
5/21/1999	ISA	108.9	135.0	1	0	0	0	0	0
5/21/1999	ISB	216.2	130.0	2	0	0	0	0	0
5/21/1999	ISC	251.2	115.0	2	1	0	0	0	0
5/21/1999	ISD	255.8	65.0	3	1	0	0	0	0
6/29/1999	ISA	180.3	55.0	2	36	15	6	0	0
6/29/1999	ISB	207.1	55.0	0	11	10	5	0	0
6/29/1999	ISC	257.4	181.0	0	7	6	3	1	0
6/29/1999	ISD	230.0	185.0	0	3	0	0	0	0
7/27/1999	ISA	84.4	30.0	0	0	3	5	2	0
7/27/1999	ISB	204.9	92.0	0	0	1	5	1	0
7/27/1999	ISC	256.1	148.0	0	0	0	1	0	0
7/27/1999	ISD	237.9	88.0	0	0	0	1	0	0
8/22/1999	ISA	90.3	18.0	0	0	0	0	0	0
8/22/1999	ISB	200.5	53.0	0	0	0	0	0	0
8/22/1999	ISC	266.4	145.0	0	0	0	0	1	0
8/22/1999	ISD	255.5	122.0	0	0	0	0	0	0
9/27/1999	ISA	92.8	4.0	0	0	0	0	0	0
9/27/1999	ISB	200.6	72.0	0	0	0	0	0	0
9/27/1999	ISC	255.6	89.0	0	0	0	0	0	0
9/27/1999	ISD	245.2	80.0	0	0	0	0	0	0
5/20/2000	ISA	95.0	52.0	9	0	0	0	0	0
5/20/2000	ISB	194.1	188.0	2	0	0	0	0	0
5/20/2000	ISC	223.6	143.0	6	0	0	0	0	0
5/20/2000	ISD	169.0	165.0	1	0	0	0	0	0
6/29/2000	ISA	90.0	212.0	0	20	32	16	12	0
6/29/2000	ISB	190.6	173.0	1	2	8	2	0	0
6/29/2000	ISC	242.4	192.0	1	4	2	3	0	0
6/29/2000	ISD	234.0	215.0	0	0	0	1	0	0
7/20/2000	ISA	105.5	58.0	0	2	0	3	0	0
7/20/2000	ISB	235.0	175.0	0	0	2	1	0	0
7/20/2000	ISC	283.8	155.0	0	0	1	0	1	0
7/20/2000	ISD	244.4	110.0	0	0	0	1	1	0
8/26/2000	ISA	97.7	15.0	0	0	0	0	0	0
8/26/2000	ISB	199.8	98.0	0	0	0	0	0	0
8/26/2000	ISC	251.4	147.0	0	0	0	0	0	0
8/26/2000	ISD	245.6	104.0	0	0	0	0	0	0
9/27/2000	ISA	116.2	70.0	0	0	0	0	0	0
9/27/2000	ISB	199.8	82.0	0	0	0	0	0	0
9/27/2000	ISC	232.7	87.0	0	0	0	0	0	0
9/27/2000	ISD	271.4	77.0	0	0	0	0	0	0

Appendix 2 (cont'd)

			Icy Strait						
Date	Station	FWV	DV	ZI	ZII	ZIII	ZIV	ZV	M
5/20/2001	ISA	67.4	91.0	6	1	0	0	0	0
5/20/2001	ISB	127.7	172.0	7	0	0	0	0	0
5/20/2001	ISC	132.1	179.0	1	0	0	0	0	0
5/20/2001	ISD	169.5	185.0	12	1	0	0	0	0
6/28/2001	ISA	92.7	71.0	0	5	11	0	0	0
6/28/2001	ISB	196.8	252.0	0	0	1	0	0	0
6/28/2001	ISC	283.6	288.0	0	4	3	2	0	0
6/28/2001	ISD	215.5	304.0	0	0	3	3	0	0
7/29/2001	ISA	109.6	40.0	0	0	1	0	0	0
7/29/2001	ISB	186.1	104.0	0	1	0	4	0	0
7/29/2001	ISC	213.6	176.0	0	0	1	0	0	0
7/29/2001	ISD	217.0	178.0	0	0	0	3	1	0
8/27/2001	ISA	106.0	33.0	0	0	0	0	0	0
8/27/2001	ISB	161.6	141.0	0	0	0	0	0	0
8/27/2001	ISC	215.4	150.0	0	0	0	0	0	0
8/27/2001	ISD	241.7	126.0	0	0	0	0	0	0
9/27/2001	ISA	102.5	9.0	0	0	0	0	0	0
9/27/2001	ISB	197.4	86.0	0	0	0	0	0	0
9/27/2001	ISC	245.0	89.0	0	0	0	0	0	0
9/27/2001	ISD	228.3	89.0	0	0	0	0	0	0
5/23/2002	ISA	80.4	72.0	18	0	0	0	0	0
5/23/2002	ISB	169.8	104.0	9	2	0	0	0	0
5/23/2002	ISC	211.4	122.0	9	0	0	0	0	0
5/23/2002	ISD	207.4	138.0	8	0	0	0	0	0
6/24/2002	ISA	95.9	82.0	33	34	9	2	0	0
6/24/2002	ISB	161.0	132.0	3	6	0	0	0	0
6/24/2002	ISC	242.8	178.0	34	46	10	6	1	0
6/24/2002	ISD	206.1	122.0	9	5	0	0	0	0
7/24/2002	ISA	74.7	35.0	3	5	4	5	0	0
7/24/2002	ISB	268.8	147.0	3	5	28	12	2	0
7/24/2002	ISC	222.1	155.0	0	0	11	6	0	1
7/24/2002	ISD	358.5	170.0	1	0	1	1	1	0
8/24/2002	ISA	103.0	51.0	0	0	0	0	0	0
8/24/2002	ISB	197.6	170.0	0	0	0	0	0	0
8/24/2002	ISC	227.3	81.0	0	0	0	0	0	0
8/24/2002	ISD	218.8	108.0	0	0	0	0	0	0
5/22/2003	ISA	103.8	69.0	22	14	1	0	0	0
5/22/2003	ISB	193.6	72.0	13	5	1	0	0	0
5/22/2003	ISC	198.9	111.0	12	5	0	0	0	0
5/22/2003	ISD	186.1	132.0	17	1	0	0	0	0
6/23/2003	ISA	62.8	83.0	4	9	11	2	0	0
6/23/2003	ISB	147.1	143.0	1	7	9	8	0	0
6/23/2003	ISC	187.4	170.0	5	6	8	7	0	0
6/23/2003	ISD	156.6	166.0	8	3	6	4	0	0

Appendix 2 (cont'd)

				Icy Strait					
Date	Station	FWV	DV	ZI	ZII	ZIII	ZIV	ZV	M
7/24/2003	ISA	97.2	64.0	0	0	7	4	0	0
7/24/2003	ISB	185.7	127.0	0	1	1	3	1	0
7/24/2003	ISC	202.3	134.0	0	0	3	1	0	0
7/24/2003	ISD	203.4	140.0	0	0	1	1	1	0
8/22/2003	ISA	100.5	47.0	0	0	1	0	0	0
8/22/2003	ISB	194.0	116.0	0	0	0	0	0	0
8/22/2003	ISC	269.9	155.0	0	0	0	0	0	0
8/22/2003	ISD	226.6	141.0	0	0	0	0	0	0
5/19/2004	ISA	85.0	73.0	45	0	0	0	0	0
5/19/2004	ISB	161.8	122.0	40	2	0	0	0	0
5/19/2004	ISC	161.1	83.0	19	0	0	0	0	0
5/19/2004	ISD	67.5	53.0	16	1	0	0	0	0
6/22/2004	ISA	97.1	135.0	0	7	8	4	0	0
6/22/2004	ISB	169.5	160.0	1	10	11	10	1	0
6/22/2004	ISC	228.3	205.0	1	2	1	0	0	0
6/25/2004	ISD	193.5	131.0	14	31	25	2	0	0
7/25/2004	ISA	103.1	85.0	0	0	0	2	1	0
7/25/2004	ISB	199.6	131.0	0	0	0	0	0	0
7/26/2004	ISC	231.1	142.0	0	0	0	0	0	0
7/26/2004	ISD	233.7	141.0	0	0	0	0	0	0
8/24/2004	ISA	105.1	20.0	0	0	0	0	0	0
8/24/2004	ISB	218.9	80.0	0	0	0	0	0	0
8/24/2004	ISC	224.3	90.0	0	0	0	0	0	0
8/24/2004	ISD	239.6	97.0	0	0	0	0	0	0

Appendix 2 (cont'd)

			Upper Chatham						
Date	Station	FWV	DV	ZI	ZII	ZIII	ZIV	ZV	M
5/21/1997	UCA	208.5	129.0	0	0	0	0	0	0
5/21/1997	UCB	217.8	105.0	0	0	0	0	0	0
5/21/1997	UCC	142.3	91.0	0	0	0	0	0	0
5/21/1997	UCD	123.7	54.0	0	0	0	0	0	0
6/23/1997	UCA	263.9	89.0	5	15	2	0	0	0
6/23/1997	UCB	174.8	44.0	4	3	1	0	0	0
6/23/1997	UCC	152.5	37.0	13	7	3	0	0	0
6/23/1997	UCD	133.6	60.0	14	3	1	0	0	0
7/19/1997	UCA	249.7	156.0	0	0	7	4	0	0
7/20/1997	UCB	258.9	108.0	0	1	2	6	0	0
7/19/1997	UCC	254.4	150.0	1	2	8	6	0	0
7/19/1997	UCD	170.9	65.0	0	0	1	1	0	0
8/23/1997	UCA	251.4	160.0	0	0	0	0	0	0
8/23/1997	UCB	199.2	49.0	0	0	0	0	0	0
8/23/1997	UCC	178.6	32.0	0	0	0	0	0	0
8/23/1997	UCD	82.5	31.0	0	0	0	0	0	0
10/6/1997	UCA	267.8	52.0	0	0	0	0	0	0
5/17/1998	UCA	262.2	112.0	1	0	0	0	0	0
5/17/1998	UCB	252.6	105.0	4	0	0	0	0	0
5/17/1998	UCC	161.6	89.0	14	6	0	0	0	0
5/17/1998	UCD	209.8	149.0	7	1	0	0	0	0
6/29/1998	UCA	225.3	ns	0	0	0	0	0	0
6/29/1998	UCB	166.3	41.0	0	0	0	0	0	0
6/29/1998	UCC	184.6	149.0	0	2	5	1	0	0
6/29/1998	UCD	174.2	74.0	3	1	1	0	0	0
7/22/1998	UCA	281.3	62.0	0	0	0	0	1	0
7/22/1998	UCB	166.6	19.0	0	0	2	1	1	0
7/22/1998	UCC	161.5	15.0	0	0	0	2	0	0
7/22/1998	UCD	165.2	24.0	0	0	0	0	0	0
8/26/1998	UCA	264.5	39.0	0	0	0	0	0	0
8/26/1998	UCB	157.3	6.0	0	0	0	0	0	0
8/26/1998	UCC	168.8	16.0	0	0	0	0	0	0
8/26/1998	UCD	182.6	16.0	0	0	0	0	0	0
5/22/1999	UCA	251.8	81.0	2	0	0	0	0	0
5/22/1999	UCB	190.2	61.0	0	0	0	0	0	0
5/22/1999	UCC	161.3	90.0	0	0	0	0	0	0
5/22/1999	UCD	151.6	77.0	0	0	0	0	0	0
7/1/1999	UCA	243.0	172.0	0	1	5	4	0	0
7/1/1999	UCB	165.2	72.0	1	3	6	8	1	0
7/1/1999	UCC	171.8	67.0	0	0	4	5	1	0
7/1/1999	UCD	115.1	68.0	1	1	5	2	0	0

Appendix 2 (cont'd)

			Upper Chatham						
Date	Station	FWV	DV	ZI	ZII	ZIII	ZIV	ZV	M
7/29/1999	UCA	243.9	110.0	0	1	1	0	2	0
7/29/1999	UCB	250.3	66.0	0	0	0	1	1	0
7/29/1999	UCC	201.0	35.0	0	0	0	0	0	0
7/29/1999	UCD	188.9	32.0	0	0	0	3	0	0
8/21/1999	UCA	286.6	92.0	0	0	0	0	0	0
8/21/1999	UCB	159.2	39.0	0	0	0	0	0	0
8/21/1999	UCC	179.7	86.0	0	0	0	0	0	0
8/21/1999	UCD	133.7	13.0	0	0	0	0	0	0
10/1/1999	UCA	253.6	38.0	0	0	0	0	0	0
10/1/1999	UCB	251.3	39.0	0	0	0	0	0	0
10/1/1999	UCC	181.7	27.0	0	0	0	0	0	0
10/1/1999	UCD	193.5	23.0	0	0	0	0	0	0
5/20/2000	UCA	161.7	148.0	Discarded					
5/20/2000	UCB	188.3	142.0	Discarded					
5/20/2000	UCC	125.1	148.0	Discarded					
5/20/2000	UCD	135.7	113.0	Discarded					
6/30/2000	UCA	254.5	158.0	Discarded					
6/30/2000	UCB	163.7	65.0	Discarded					
6/30/2000	UCC	107.9	40.0	Discarded					
6/30/2000	UCD	131.0	57.0	Discarded					
7/21/2000	UCA	271.3	107.0	Discarded					
7/21/2000	UCB	164.1	11.0	0	3	1	3	0	0
7/21/2000	UCC	197.3	34.0	Discarded					
7/21/2000	UCD	211.3	33.0	0	0	0	2	0	0
8/29/2000	UCA	262.2	39.0	0	0	0	0	0	0
8/29/2000	UCB	246.3	42.0	0	0	0	0	0	0
8/29/2000	UCC	167.1	11.0	0	0	0	0	0	0
8/29/2000	UCD	330.8	28.0	0	0	0	0	0	0
9/28/2000	UCA	233.8	43.0	0	0	0	0	0	0
9/28/2000	UCB	201.9	32.0	0	0	0	0	0	0
9/28/2000	UCC	155.8	9.0	0	0	0	0	0	0
9/28/2000	UCD	179.5	59.0	0	0	0	0	0	0
5/19/2001	UCA	210.3	151.0	0	0	0	0	0	0
5/19/2001	UCB	93.7	164.0	0	0	0	0	0	0
5/19/2001	UCC	91.8	84.0	1	2	0	0	0	0
5/19/2001	UCD	176.3	146.0	0	1	0	0	0	0
6/26/2001	UCA	243.5	303.0	0	3	3	0	0	0
6/26/2001	UCB	251.5	ns	Discarded					

Appendix 2 (cont'd)

			Upper Chatham						
Date	Station	FWV	DV	ZI	ZII	ZIII	ZIV	ZV	M
6/26/2001	UCC	157.5	71.0	1	4	3	1	1	0
6/26/2001	UCD	223.4	146.0	0	1	0	0	0	0
7/29/2001	UCA	235.7	68.0	0	0	0	0	2	0
7/27/2001	UCB	217.9	173.0	0	0	0	1	0	0
7/27/2001	UCC	142.9	20.0	0	0	1	3	0	0
7/27/2001	UCD	148.6	24.0	0	0	0	1	0	0
8/26/2001	UCA	229.5	81.0	0	0	0	0	0	0
8/26/2001	UCB	140.1	9.0	0	0	0	0	0	0
8/26/2001	UCC	182.7	49.0	0	0	0	0	0	0
8/26/2001	UCD	148.3	18.0	0	0	0	0	1	0
9/26/2001	UCA	233.5	58.0	0	0	0	0	0	0
9/26/2001	UCB	142.5	7.0	0	0	0	0	0	0
9/26/2001	UCC	164.2	11.0	0	0	0	0	0	0
9/26/2001	UCD	123.8	3.0	0	0	0	0	0	0

Appendix 2 (cont'd)

			Cross Sound						
Date	Station	FWV	DV	ZI	ZII	ZIII	ZIV	ZV	M
5/23/1997	CSA	172.7	41.0	3	0	0	0	0	0
5/23/1997	CSB	72.9	20.0	4	0	0	0	0	0
5/23/1997	CSC	135.4	39.0	2	0	0	0	0	0
5/23/1997	CSD	226.6	56.0	1	0	0	0	0	0
6/24/1997	CSA	184.2	41.0	9	0	0	0	0	0
6/24/1997	CSB	69.7	15.0	17	0	0	0	0	0
6/24/1997	CSC	172.1	38.0	26	4	0	0	0	0
6/24/1997	CSD	233.0	67.0	27	2	0	0	0	0
7/24/1997	CSA	167.8	48.0	1	0	0	0	0	0
7/24/1997	CSB	97.9	10.0	0	0	0	0	0	0
7/24/1997	CSC	192.4	33.0	2	0	0	0	0	0
7/26/1997	CSD	249.8	46.0	0	0	0	0	0	1
8/26/1997	CSA	164.5	21.0	0	0	0	0	0	0
8/26/1997	CSB	75.0	7.0	0	0	0	0	0	0
8/26/1997	CSC	171.7	17.0	0	0	0	0	0	0
8/26/1997	CSD	282.0	52.0	0	0	0	0	0	0
10/4/1997	CSA	262.4	16.0	0	0	0	0	0	0
10/4/1997	CSB	67.6	3.0	0	0	0	0	0	0
10/4/1997	CSC	144.4	5.0	0	0	0	0	0	0
10/4/1997	CSD	229.4	17.0	0	0	0	0	0	0
5/dd/1998	CSA	ns	ns	ns	ns	ns	ns	ns	ns
5/dd/1998	CSB	ns	ns	ns	ns	ns	ns	ns	ns
5/dd/1998	CSC	ns	ns	ns	ns	ns	ns	ns	ns
5/dd/1998	CSD	ns	ns	ns	ns	ns	ns	ns	ns
6/28/1998	CSA	247.1	53.0	0	3	6	1	0	0
6/28/1998	CSB	83.0	22.0	0	0	0	1	0	0
6/28/1998	CSC	163.8	40.0	0	3	2	1	0	0
6/28/1998	CSD	236.2	65.0	0	3	5	1	0	0
7/27/1998	CSA	202.4	41.0	0	0	0	0	0	1
7/27/1998	CSB	76.1	14.0	0	0	0	0	0	0
7/27/1998	CSC	162.8	29.0	0	0	0	0	0	0
7/27/1998	CSD	255.1	37.0	0	0	0	3	1	0
8/29/1998	CSA	221.2	58.0	0	0	0	0	0	0
8/29/1998	CSB	154.6	30.0	0	0	0	0	0	0
8/29/1998	CSC	81.4	24.0	0	0	0	0	0	0
8/29/1998	CSD	230.5	58.0	0	0	0	0	0	0
10/7/1998	CSA	208.8	22.0	0	0	0	0	0	0
10/7/1998	CSB	74.0	3.0	0	0	0	0	0	0
10/7/1998	CSC	166.9	25.0	0	0	0	0	0	0
10/7/1998	CSD	228.9	24.0	0	0	0	0	0	0

Appendix 2 (cont'd)

			Cross Sound						
Date	Station	FWV	DV	ZI	ZII	ZIII	ZIV	ZV	M
5/22/1999	CSA	114.6	94.0	4	0	0	0	1	0
5/22/1999	CSB	62.2	21.0	2	0	0	0	0	0
5/22/1999	CSC	142.4	77.0	0	1	0	0	1	0
5/22/1999	CSD	211.4	86.0	1	0	1	0	0	0
6/28/1999	CSA	203.5	56.0	2	4	2	0	0	0
6/28/1999	CSB	81.3	14.0	0	0	1	0	0	0
6/28/1999	CSC	170.8	71.0	1	4	5	0	0	0
6/28/1999	CSD	225.8	79.0	2	5	0	1	0	0
7/26/1999	CSA	258.4	187.0	0	0	0	0	0	1
7/26/1999	CSB	89.3	64.0	0	0	1	0	0	0
7/26/1999	CSC	209.9	ns	0	0	0	1	0	0
7/26/1999	CSD	237.8	68.0	0	0	0	0	0	0
8/23/1999	CSA	193.5	33.0	0	0	0	0	0	0
8/23/1999	CSB	77.9	31.0	0	0	0	0	0	0
8/23/1999	CSC	237.0	47.0	0	0	0	0	0	0
8/23/1999	CSD	262.5	31.0	0	0	0	0	1	0
9/29/1999	CSA	118.2	14.0	0	0	0	0	0	0
9/29/1999	CSB	92.4	13.0	0	0	0	0	0	0
9/28/1999	CSC	252.2	44.0	0	0	0	0	0	0
9/28/1999	CSD	257.3	40.0	0	0	0	0	0	0
5/21/2000	CSA	ns	ns	ns	ns	ns	ns	ns	ns
5/21/2000	CSB	ns	ns	ns	ns	ns	ns	ns	ns
5/21/2000	CSC	ns	ns	ns	ns	ns	ns	ns	ns
5/21/2000	CSD	ns	ns	ns	ns	ns	ns	ns	ns
6/28/2000	CSA	110.7	18.0	0	1	0	0	0	0
6/28/2000	CSB	102.5	45.0	4	5	1	0	1	0
6/28/2000	CSC	132.0	60.0	1	1	0	0	0	0
6/28/2000	CSD	229.4	80.0	6	8	2	0	0	0
7/23/2000	CSC	267.8	35.0	0	0	0	0	0	0
7/23/2000	CSD	242.4	40.0	0	0	0	0	0	0
8/27/2000	CSA	122.4	23.0	1	0	1	0	0	0
8/27/2000	CSB	89.2	4.0	0	0	1	1	0	0
8/27/2000	CSC	203.9	17.0	0	0	0	0	0	0
8/27/2000	CSD	226.1	28.0	0	0	0	1	0	0
9/29/2000	CSD	218.7	45.0	0	0	0	0	0	0

Appendix 2 (cont'd)

			Icy Point						
Date	Station	FWV	DV	ZI	ZII	ZIII	ZIV	ZV	M
5/22/1997	IPA	176.1	26.0	0	0	0	0	0	0
5/22/1997	IPB	140.2	33.0	0	0	0	0	0	0
5/22/1997	IPC	136.2	29.0	0	0	0	0	0	0
5/22/1997	IPD	262.6	95.0	0	0	0	0	0	0
6/25/1997	IPA	169.8	33.0	1	0	0	0	0	0
6/25/1997	IPB	125.4	13.0	0	0	0	0	0	0
6/25/1997	IPC	205.2	12.0	0	0	0	0	0	0
6/25/1997	IPD	307.0	57.0	0	0	0	0	0	0
7/25/1997	IPA	177.4	41.0	0	0	0	0	0	0
7/25/1997	IPB	139.9	16.0	0	0	0	0	0	0
7/25/1997	IPC	144.6	27.0	0	0	0	0	0	0
7/25/1997	IPD	277.1	19.0	0	0	0	0	0	1
8/25/1997	IPA	143.3	29.0	0	0	0	0	0	0
8/25/1997	IPB	138.8	29.0	0	0	0	0	0	0
8/25/1997	IPC	134.3	10.0	0	0	0	0	0	0
8/25/1997	IPD	241.2	49.0	0	0	0	0	0	0
10/3/1997	IPA	168.7	13.0	0	0	0	0	0	0
10/3/1997	IPB	138.0	15.0	0	0	0	0	0	0
10/3/1997	IPC	131.4	17.0	0	0	0	0	0	0
10/3/1997	IPD	264.7	11.0	0	0	0	0	0	1
5/23/2000	IPA	206.8	62.0	0	0	1	0	0	0
5/23/2000	IPB	135.5	45.0	0	2	2	0	0	0
5/23/2000	IPC	146.8	44.0	0	0	0	0	0	0
5/23/2000	IPD	290.7	77.0	0	0	0	0	0	0
6/27/2000	IPA	190.5	38.0	0	0	0	0	0	0
6/27/2000	IPB	143.6	20.0	0	0	0	0	0	0
6/27/2000	IPC	168.8	18.0	0	0	0	0	0	0
6/27/2000	IPD	286.8	49.0	0	0	0	0	1	0
7/24/2000	IPA	207.4	25.0	0	0	0	0	0	4
7/24/2000	IPB	131.8	3.0	0	0	0	0	0	0
7/24/2000	IPC	163.3	6.0	0	0	0	0	0	0
7/24/2000	IPD	254.7	18.0	0	0	0	0	0	0
8/28/2000	IPA	162.3	22.0	0	0	0	0	0	0
8/28/2000	IPB	137.8	15.0	0	0	0	0	0	0
8/28/2000	IPC	153.0	19.0	0	0	0	0	0	0
8/28/2000	IPD	244.2	22.0	0	0	0	0	0	0
9/26/2000	IPA	172.2	11.0	0	0	0	0	0	0
9/26/2000	IPB	126.8	4.0	0	0	0	0	0	0
9/26/2000	IPC	137.8	4.0	0	0	0	0	0	0

Appendix 2 (cont'd)

			Icy Point						
Date	Station	FWV	DV	ZI	ZII	ZIII	ZIV	ZV	M
9/26/2000	IPD	246.6	25.0	0	0	0	0	0	0
5/24/2001	IPA	217.4	82.0	0	0	0	0	0	0
5/24/2001	IPB	164.5	34.0	0	0	0	1	0	0
5/24/2001	IPC	157.8	54.0	0	0	0	1	0	0
5/24/2001	IPD	281.2	146.0	0	0	0	0	0	0
6/27/2001	IPA	168.2	35.0	0	0	0	0	9	0
6/27/2001	IPB	152.7	116.0	0	1	2	0	2	0
6/27/2001	IPC	146.2	19.0	0	0	0	0	1	0
6/27/2001	IPD	255.1	34.0	0	0	0	0	1	0
7/28/2001	IPA	160.1	41.0	0	0	0	0	0	1
7/28/2001	IPB	139.5	23.0	0	0	0	0	0	0
7/28/2001	IPC	149.9	12.0	0	0	0	0	0	0
7/28/2001	IPD	255.4	19.0	0	0	0	0	0	0
8/dd/2001	IPA	ns	ns	ns	ns	ns	ns	ns	ns
8/dd/2001	IPB	ns	ns	ns	ns	ns	ns	ns	ns
8/dd/2001	IPC	ns	ns	ns	ns	ns	ns	ns	ns
8/dd/2001	IPD	ns	ns	ns	ns	ns	ns	ns	ns
5/22/2002	IPA	244.7	71.0	2	1	0	0	0	0
5/22/2002	IPB	127.3	32.0	0	0	0	0	0	0
5/22/2002	IPC	162.8	84.0	0	0	0	0	0	0
5/22/2002	IPD	257.1	45.0	0	0	0	0	0	0
6/23/2002	IPA	166.8	48.0	4	0	0	0	0	0
6/23/2002	IPB	115.0	37.0	0	0	0	0	0	0
6/23/2002	IPC	135.8	21.0	0	0	0	0	0	0
6/23/2002	IPD	218.7	18.0	0	0	0	0	0	0
7/29/2002	IPA	174.6	32.0	0	0	0	0	0	0
7/29/2002	IPB	127.2	11.0	0	0	0	0	0	0
7/29/2002	IPC	122.2	6.0	0	0	0	0	0	0
7/29/2002	IPD	227.9	20.0	0	0	0	0	0	0
8/25/2002	IPA	159.8	14.0	0	0	0	0	0	0
8/25/2002	IPB	142.6	23.0	0	0	0	0	0	0
8/25/2002	IPC	129.7	12.0	0	0	0	0	0	0
8/25/2002	IPD	225.0	27.0	0	0	0	0	0	0
5/21/2003	IPA	141.7	27.0	4	8	0	1	0	0
5/21/2003	IPB	127.8	52.0	1	0	0	0	0	0
5/21/2003	IPC	121.1	8.0	0	0	0	4	11	0
5/21/2003	IPD	265.0	106.0	0	0	0	0	1	0
6/22/2003	IPA	184.9	19.0	0	0	0	0	0	0
6/22/2003	IPB	130.9	36.0	1	0	1	0	0	0
6/22/2003	IPC	145.9	23.0	0	0	0	0	0	0

Appendix 2 (cont'd)

			Icy Point						
Date	Station	FWV	DV	ZI	ZII	ZIII	ZIV	ZV	M
6/22/2003	IPD	243.1	41.0	0	0	0	0	0	0
7/23/2003	IPA	155.1	17.0	0	0	0	0	0	0
7/23/2003	IPB	127.4	11.0	0	0	0	1	0	1
7/23/2003	IPC	130.2	12.0	0	0	0	0	0	0
7/23/2003	IPD	214.5	16.0	0	0	0	0	0	0
5/22/2004	IPA	178.9	75.0	1	1	0	1	0	0
5/22/2004	IPB	127.8	38.0	3	1	0	0	0	0
5/22/2004	IPC	134.6	72.0	0	3	0	0	0	0
5/22/2004	IPD	248.5	72.0	0	0	0	0	0	0
6/21/2004	IPA	179.8	22.0	3	2	0	0	1	0
6/21/2004	IPB	131.0	9.0	0	0	0	0	0	0
6/21/2004	IPC	141.3	51.0	0	1	0	1	1	1
6/21/2004	IPD	241.3	73.0	0	0	0	2	1	0
7/24/2004	IPA	172.4	28.0	0	0	0	0	0	0
7/24/2004	IPB	126.3	8.0	0	0	0	0	0	0
7/24/2004	IPC	129.2	16.0	0	0	0	0	0	0
7/24/2004	IPD	253.9	42.0	0	0	0	0	0	0
8/23/2004	IPA	174.2	24.0	0	0	0	0	0	0
8/23/2004	IPB	164.2	ns	0	0	0	0	0	0
8/23/2004	IPC	179.4	26.0	0	0	0	0	0	0
8/23/2004	IPD	251.0	14.0	0	0	0	0	0	0

			Cape Edward						
Date	Station	FWV	DV	ZI	ZII	ZIII	ZIV	ZV	M
6/27/1998	CEA								
6/27/1998	CEB								
6/27/1998	CEC	256.4							1
6/27/1998	CED								
6/30/1999	CEA	112.1						1	
6/30/1999	CEB	254.6							1
6/30/1999	CEC	226.0						2	
6/30/1999	CED	229.4					1	2	

Appendix 3. Localities and coordinates of stations near Glacier Bay in 2004. Larval Dungeness crabs were collected inside and outside of Glaceir Bay, southeastern Alaska in May-September 2004.

		Larval sampling		
Locality	Station	Longitude	Latitude	Depth (m)
West Icy Strait	1	136°03'16"W	58°20'34"N	90
East Icy Strait	2	135°48'06"W	58°19'05"N	110
Bartlett Cove	3	135°54'37"W	58°27'15"N	50
South Beardslee Is.	4	135°59'00"W	58°30'00"N	65
Berg Bay	5	136°09'32"W	58°31'23"N	50
Icy Strait	ISA	135°31'76"W	58°13'25"N	128
	ISB	135°29'26"W	58°14'22"N	200
	ISC	135°26'25"W	58°15'28"N	200
	ISD	135°23'98"W	58°16'38"N	234

Appendix 4. Salinity and temperature at 1 m depth in Glacier Bay in 2004. Salinity and temperature were measured at inner and outer stations of Glacier Bay in 2004.

Date	Station 1	Station 2	Station 3	Station 4	Station 5
		Temperature (°C)			
5/28/2004	7.1	9.9	8.8	8.0	8.3
6/14/2004	7.7	8.8	7.9	7.7	9.9
6/29/2004	7.7	8.0	7.8	8.2	9.2
7/14/2004	8.8	13.1	9.2	9.5	11.6
7/29/2004	9.5	14.6	9.5	8.8	10.9
8/14/2004	8.7	12.5	9.9	9.1	12.8
8/29/2004	8.4	11.4	8.6	8.4	9.6
9/9/2004	9.5	11.1	10.8	8.6	8.7
		Salinity			
5/28/2004	31.7	30.0	31.1	30.9	29.6
6/14/2004	31.3	30.2	30.9	30.4	26.7
6/29/2004	31.4	31.0	30.9	29.8	25.8
7/14/2004	30.2	26.2	30.0	28.2	22.5
7/29/2004	29.7	24.6	29.5	29.9	25.0
8/14/2004	30.3	26.4	29.5	29.3	22.3
8/29/2004	30.8	27.4	30.4	29.7	26.4
9/9/2004	29.3	25.3	27.5	28.3	23.1

Appendix 5. Number of Dungeness crab larvae collected in Glacier Bay in 2004. Larval Dungeness crabs were collected at inner and outer stations of Glacier Bay in 2004. FWV=filtered water volume (m^3), D= deep, S=shallow.

Date	Station	Replicate	Depth	FWV	Z1	Z2	Z3	Z4	Z5	M
5/28/2004	1	1	D	133.6	26	3	0	0	0	0
5/28/2004	1	2	D	124.9	16	2	0	0	0	0
5/28/2004	2	1	D	109.7	127	13	0	0	0	0
5/28/2004	2	2	D	110.2	126	13	0	0	0	0
5/27/2004	3	1	D	Failed	ns	ns	ns	ns	ns	ns
5/27/2004	3	2	D	93.0	20	0	0	0	0	0
5/27/2004	4	1	D	79.6	165	11	0	0	0	0
5/27/2004	4	2	D	Failed	ns	ns	ns	ns	ns	ns
5/27/2004	5	1	D	97.9	34	2	0	0	0	0
5/27/2004	5	2	D	121.6	29	0	0	0	0	0
6/14/2004	1	1	D	82.4	17	24	5	0	0	0
6/14/2004	1	2	D	81.2	8	40	13	0	0	0
6/14/2004	2	1	D	125.8	46	45	16	0	0	0
6/14/2004	2	2	D	Failed	ns	ns	ns	ns	ns	ns
6/14/2004	3	2	D	79.7	21	21	5	1	0	0
6/14/2004	3	3	D	85.7	15	18	5	1	0	0
6/14/2004	4	1	D	114.4	53	39	7	1	0	0
6/14/2004	4	2	D	105.7	17	17	5	0	0	0
6/14/2004	5	1	D	84.0	31	17	4	0	0	0
6/14/2004	5	2	D	86.6	35	18	5	0	0	0
6/29/2004	1	1	D	117.9	0	3	9	6	0	0
6/29/2004	1	2	D	145.8	2	2	13	8	0	0
6/29/2004	2	1	D	209.2	0	3	12	14	1	0
6/29/2004	2	2	D	178.1	0	4	5	12	0	0
6/29/2004	3	1	D	122.6	8	7	17	6	1	0
6/29/2004	3	2	D	111.6	9	8	31	26	2	0
6/29/2004	4	1	D	154.8	20	13	28	15	1	0
6/29/2004	4	2	D	120.7	0	14	16	7	0	0
6/29/2004	5	1	D	107.3	9	5	7	3	0	0
6/29/2004	5	2	D	116.3	10	3	9	2	0	0
7/14/2004	1	1	D	116.6	0	1	6	17	8	0
7/14/2004	1	2	D	109.5	0	1	1	7	3	0
7/14/2004	2	1	D	116.3	0	4	6	17	7	0
7/14/2004	2	2	D	138.8	1	1	6	17	8	0
7/14/2004	3	1	D	75.5	6	1	0	7	2	0
7/14/2004	3	2	D	92.0	5	0	0	3	3	0
7/14/2004	4	1	D	81.2	2	0	2	4	0	0
7/14/2004	4	2	D	72.5	1	0	2	6	2	0
7/14/2004	5	1	D	94.5	2	1	3	1	0	0
7/14/2004	5	2	D	69.5	2	3	4	3	0	0
7/29/2004	1	1	D	155.1	0	0	1	2	1	0
7/29/2004	1	2	D	172.9	0	0	0	3	1	0

Appendix 5 (cont'd)

Date	Station	Replicate	Depth	FWV	Z1	Z2	Z3	Z4	Z5	M
7/29/2004	2	1	D	164.9	0	0	0	1	0	0
7/29/2004	2	2	D	Failed	ns	ns	ns	ns	ns	ns
7/29/2004	3	1	D	117.4	0	0	0	0	1	0
7/29/2004	3	2	D	Failed	ns	ns	ns	ns	ns	ns
7/29/2004	4	1	D	131.0	0	0	0	1	4	0
7/29/2004	4	2	D	124.0	0	0	0	0	0	0
7/29/2004	5	1	D	171.6	3	0	0	1	0	0
7/29/2004	5	2	D	170.3	0	0	0	0	0	0
8/14/2004	1	1	D	71.0	0	0	0	0	0	0
8/14/2004	1	2	D	174.4	0	0	0	0	1	0
8/14/2004	2	1	D	173.9	0	0	0	1	0	0
8/14/2004	2	2	D	178.6	0	0	0	0	1	0
8/14/2004	3	1	D	95.6	0	0	0	1	0	1
8/14/2004	3	2	D	108.4	0	0	0	0	0	0
8/14/2004	4	1	D	146.4	0	0	0	0	1	0
8/14/2004	4	2	D	146.1	0	0	0	0	0	0
8/14/2004	5	1	D	122.0	0	0	0	0	0	0
8/14/2004	5	2	D	114.7	0	0	0	0	0	0
5/28/2004	1	1	S	40.5	8	0	0	0	0	0
5/28/2004	1	2	S	27.9	8	0	0	0	0	0
5/28/2004	2	1	S	53.4	83	8	0	0	0	0
5/28/2004	2	2	S	50.1	207	25	0	0	0	0
5/27/2004	3	1	S	31.9	0	0	0	0	0	0
5/27/2004	3	2	S	37.1	0	0	0	0	0	0
5/27/2004	4	1	S	14.7	52	2	0	0	0	0
5/27/2004	4	2	S	Failed	ns	ns	ns	ns	ns	ns
5/27/2004	5	1	S	10.3	3	0	0	0	0	0
5/27/2004	5	2	S	11.7	0	0	0	0	0	0
6/14/2004	1	1	S	46.9	22	17	5	1	0	0
6/14/2004	1	2	S	40.6	28	41	11	0	0	0
6/14/2004	2	1	S	40.1	15	16	5	0	0	0
6/14/2004	2	2	S	Failed	ns	ns	ns	ns	ns	ns
6/14/2004	3	1	S	24.9	10	12	1	0	0	0
6/14/2004	3	2	S	17.6	12	4	0	0	0	0
6/14/2004	4	2	S	41.6	1	10	2	0	0	0
6/14/2004	4	3	S	29.9	5	4	2	0	0	0
6/14/2004	5	1	S	27.6	19	8	2	0	0	0
6/14/2004	5	2	S	26.7	1	2	0	0	0	0
6/29/2004	1	1	S	29.1	0	4	2	2	0	0
6/29/2004	1	2	S	25.9	0	2	2	0	0	0
6/29/2004	2	1	S	20.8	0	3	3	1	0	0
6/29/2004	2	2	S	28.5	1	2	5	0	0	0
6/29/2004	3	1	S	26.8	3	2	3	1	0	0
6/29/2004	3	2	S	14.0	1	0	0	0	0	0
6/29/2004	4	1	S	35.4	4	3	3	0	0	0

Appendix 5 (cont'd)

Date	Station	Replicate	Depth	FWV	Z1	Z2	Z3	Z4	Z5	M
6/29/2004	4	2	S	18.4	3	2	2	0	0	0
6/29/2004	5	1	S	14.1	3	2	1	0	0	0
6/29/2004	5	2	S	16.1	2	1	0	2	0	0
7/14/2004	1	1	S	25.1	1	0	0	0	1	0
7/14/2004	1	2	S	27.3	0	0	0	0	1	0
7/14/2004	2	1	S	31.8	0	0	1	0	0	0
7/14/2004	2	2	S	39.9	0	0	0	1	1	0
7/14/2004	3	1	S	24.2	0	0	0	1	0	0
7/14/2004	3	2	S	34.3	0	1	0	1	1	0
7/14/2004	4	1	S	42.7	2	0	0	5	0	0
7/14/2004	4	2	S	35.1	0	0	1	0	0	0
7/14/2004	5	1	S	15.7	0	0	0	1	0	0
7/14/2004	5	2	S	12.8	0	2	0	0	0	0
7/29/2004	1	1	S	39.6	0	0	0	1	0	0
7/29/2004	1	2	S	46.4	0	0	1	3	1	0
7/29/2004	2	1	S	37.3	0	0	0	1	0	0
7/29/2004	2	2	S	Failed	ns	ns	ns	ns	ns	ns
7/29/2004	3	1	S	33.1	1	0	0	0	0	0
7/29/2004	3	2	S	Failed	ns	ns	ns	ns	ns	ns
7/29/2004	4	1	S	32.3	0	0	0	0	0	0
7/29/2004	4	2	S	34.1	0	0	0	0	0	0
7/29/2004	5	1	S	25.2	0	0	0	0	0	0
7/29/2004	5	2	S	36.5	0	0	0	0	0	0
8/14/2004	1	1	S	47.3	0	0	0	0	0	0
8/14/2004	1	2	S	57.1	0	0	0	0	0	0
8/14/2004	2	1	S	22.6	0	0	0	0	0	0
8/14/2004	2	2	S	39.4	0	0	0	0	0	0
8/14/2004	3	1	S	77.9	0	0	0	0	0	0
8/14/2004	3	2	S	46.6	0	0	0	0	0	0
8/14/2004	4	1	S	59.3	0	0	0	0	0	0
8/14/2004	4	2	S	37.3	0	0	0	0	0	0
8/14/2004	5	1	S	45.0	0	0	0	0	0	0
8/14/2004	5	2	S	36.5	0	0	0	0	0	0

* No Dungeness crab larvae were collected on August 29 and September 9, 2004