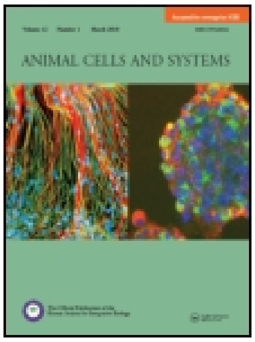

Animal Cells and Systems

ISSN: 1976-8354 (Print) 2151-2485 (Online) Journal homepage: https://www.tandfonline.com/loi/tacs20

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To cite this article: Wongyu Park & Thomas C. Shirley (2008) Variations of abundance and hatch timing of dungeness crab larvae in southeastern Alaska: Implications for climate effect, Animal Cells and Systems, 12:4, 287-295, DOI: 10.1080/19768354.2008.9647184

To link to this article: https://doi.org/10.1080/19768354.2008.9647184

Published online: 15 Nov 2010.

Animal Cells and Systems 12: 287-295, 2008

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Variations of Abundance and Hatch Timing of Dungeness Crab Larvae in Southeastern Alaska: Implications for Climate Effect

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Abstract: Variations of larval abundance and hatch timing of Dungeness crabs, *Cancer magister* Dana 1852, were investigated. Dungeness crab larvae were monthly collected at 16 stations arrayed in four transects, Upper Chatham, Icy Strait, Cross Sound, and Icy Point, in southeastern Alaska from May to September 1997-2004. Larval abundance at all transects was the highest in June except in the Icy Point transect. Larval abundance was the highest in the Icy Strait transect, moderate in the Upper Chatham and Cross Sound transects, and the lowest in the Icy Point transect. Zoeae I (ZI) was predominated in May; thereafter ZI decreased and late zoeal stages occurred. In May and June, small numbers of late stage larvae unusually co-occurred with ZI in three transects. These late stage larvae may have been transported from where hatching occurs earlier. The timing of ZI occurrence varied interannually and was related to degree-days during the egg incubation period of Dungeness crabs: later larval hatching in 1997 and 2002 when temperatures were colder, while earlier larval hatching in 1998 when temperatures were warmer. The distribution patterns of Dungeness crab larvae in southeastern Alaska were markedly different from those reported from other areas of the species distribution ranges: larvae occurring much later in the year, and late stage larvae occurring in inland waters.

Key words: Dungeness crab larvae, spatial and temporal variation, *Cancer magister*, southeastern Alaska

INTRODUCTION

The Dungeness crab, *Cancer magister* Dana 1852, supports important commercial fisheries along the west coast of North America from California to Alaska (Pacific Fishing, 2004). In southeastern Alaska, the Dungeness crab fishery supports approximately 9% of the total landings of the west coast of North America (Pacific Fishing, 2004). The crab harvests in their distribution ranges have multi-year cyclic fluctuations (Methot, 1988; Botsford and Hobbs, 1995; Higgins et al., 1997). Recruitment variability caused by differential larval survival has been implicated as a possible factor explaining harvest fluctuations in southern areas (Jamieson, 1986; McConnaughey et al., 1992; Botsford et al., 1994). Fluctuation of ocean temperatures during the egg incubation period results in high egg mortality and declines of the fishery harvest (Wild, 1980). Combinations of predation, oceanographic fluctuations, or low food quality and quantity, promote the larval mortality of Dungeness crabs (Lough, 1976).

Dungeness crabs exhibit a diverse life history along their broad latitudinal distribution. The larval period of Dungeness crabs lasts 45-158 d, varying with latitude and water temperature (Lough, 1976; Reilly, 1983; Jamieson and Phillips, 1988; Sulkin and McKeen, 1989). In general, reproductive events for crab populations in the southern areas occur earlier than those in the northern areas. Off the California coast, zoeae hatch from the late of December to March (Wild, 1980; Reilly, 1983). In southeastern Alaska, adult Dungeness crabs begin extruding eggs mainly from September to November, and zoeae hatch mostly during May and June (Fisher, 2006; Park and Shirley, 2005).

Zoeae I (ZI) 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 to the offshore by estuarine run-off and upwelling that moves near-surface water offshore (Lough, 1976; Reilly, 1983).

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Megalopae can be transported to the 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; Miller and Shanks, 2004).

Climate changes associated with El Niño-Southern Oscillation (ENSO) events, which irregularly reverse every 3 to 7 years and have episodes lasting 8 to 15 months (Philander, 1989; Fiedler, 2002), reduce primary and secondary productivity (Brodeur and Ware, 1992; Roemmich and McGowan, 1995; Mackas et al., 1998). Biomass and species composition changes are coincident with climate changes (Batten and Welch, 2004). In southeastern Alaska, a strong El Niño in 1997-8 and a local cold event in 2002 decreased copepod biomass (Park et al., 2004). Water temperature variation derived from climate changes could affect the rate of embryonic and larval development of Dungeness crabs (Wild, 1980).

This study explores climate effects on hatch timing of Dungeness crab larvae in southeastern Alaska, and relates ZI occurrence of Dungeness crabs to the degree-days during the egg incubation period in southeastern Alaska. This study also investigates the spatial and temporal occurrence of Dungeness crab larvae in southeastern Alaska.

MATERIALS AND METHODS

Larval data

Zooplankton were collected monthly at 16 stations arrayed along four transects in upper Chatham Strait (UC), Icy Strait (IS), Cross Sound (CS), and Icy Point (IP) in southeastern Alaska (Fig. 1; Table 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, were apart approximately equidistant in each transect and labeled A to D. Hence, ISA is a notation of station A in the Icy Strait transect (Fig. 1). All sampling was conducted during daylight, between 0700 and 2000 h, Alaska Standard Time. SST was measured to the precision of 0.1 at 1 m depth with an onboard thermosalinograph (Sea-Bird SBE 21).

Daily SST of Auke Bay, southeastern Alaska (58º22N, 134º44) was obtained from Dr. B. Wing (Auke Bay Lab, NMFS, NOAA, 11305 Glacier Highway, Juneau, Alaska 99801-8626, USA). As a high correlation (r^2=0.801, p= 0.001) exists during the spring and summer months for SST between Auke Bay and Icy Strait, located in the center of our sampling area, SST in Auke Bay was used for calculating the degree-days during the egg incubation period for Dungeness crabs in the study area. Degree-days were converted by summing daily temperature measurements

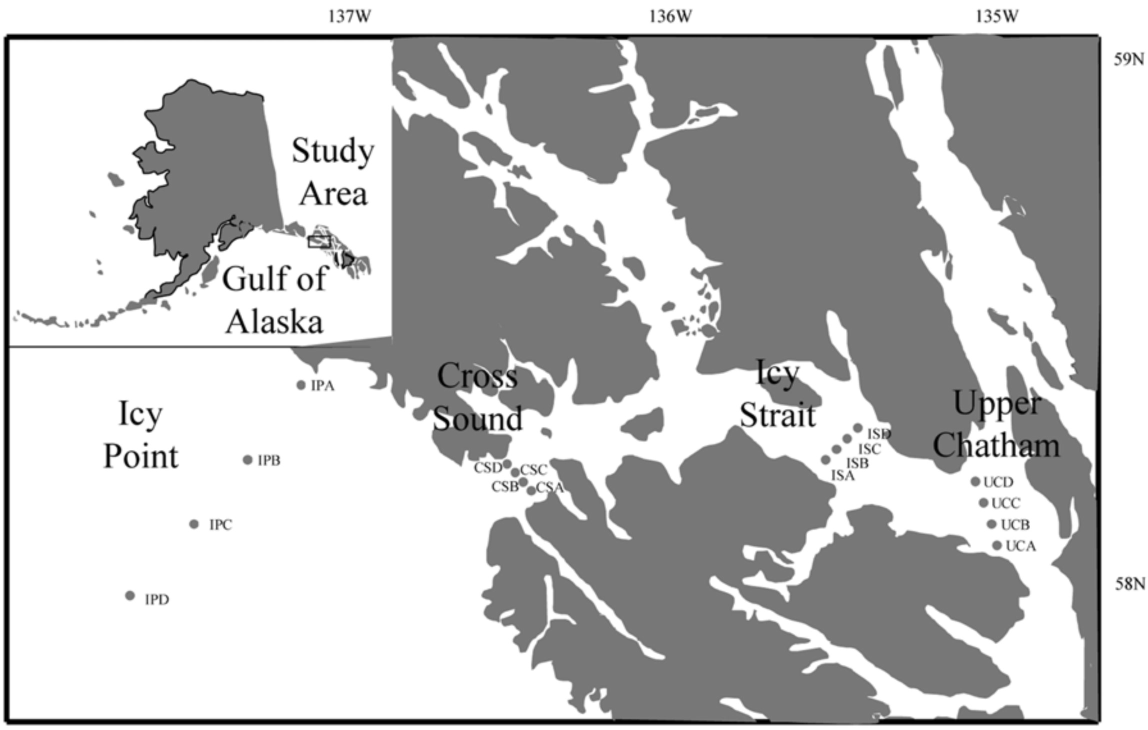

Fig. 1. Zooplankton survey stations sampled monthly in southeastern Alaska, May-September 1997-2004.

Table 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	UCA	58°04'57N	135°00'08W	3.2	400
Strait	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

from 1 September in the preceding year of larval sampling to 30 April in the year of larval sampling. The calendar was used because in southeastern Alaska mating and egg extrusion occur from September to November and mainly larvae release begins in May (Fisher, 2006).

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. 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.

Larval stages were grouped into three categories for graphing: ZI (zoeae I), ZII (zoeae II) and ZIII (zoeae III) for the intermediate stage, and ZIV (zoeae IV), ZV (zoeae V) and M (megalopae) for the late larval stage. Larval data were viewed in Stack shape in ArcGIS 9.1 (2001).

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. 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 densities between stations in each transect, the total densities for all of months from May to July were used. Interannual variability of larval stage occurrence from the IS transect was analyzed using multivariate analysis of variance (MANOVA) with year as a factor, and the six larval stages as variables.

RESULTS

Larval densities (K-W test, χ^2=68.46, df=3, p<0.001) between transects were significantly different. Larval densities was the highest in the IS transect, moderate in the UC and CS transects, and the lowest in the IP transect. The degree-days during the egg incubation period for Dungeness crab was the highest in 1998 (1887 degree-days) and lower in 1997 (1655 degree-days) and 2002 (1650 degree-days) (Fig. 2).

Upper Chatham (UC)

The density of Dungeness crab larvae in the UC transect varied seasonally and interannually (0-10.4/100 m^3; Figs. 3-6). In general, larval density was the highest in June and lower in May and August except in 1998. Larvae in the northern stations, UCC and UCD, were more abundant than those of the southern stations, UCA and UCB. However, larval abundance did not vary significantly between stations (K-W test, χ^2=1.28, df=3, p=0.734). In 1997, larvae hatched later than in other years. In September, a megalopa was collected at IPD in 1997.

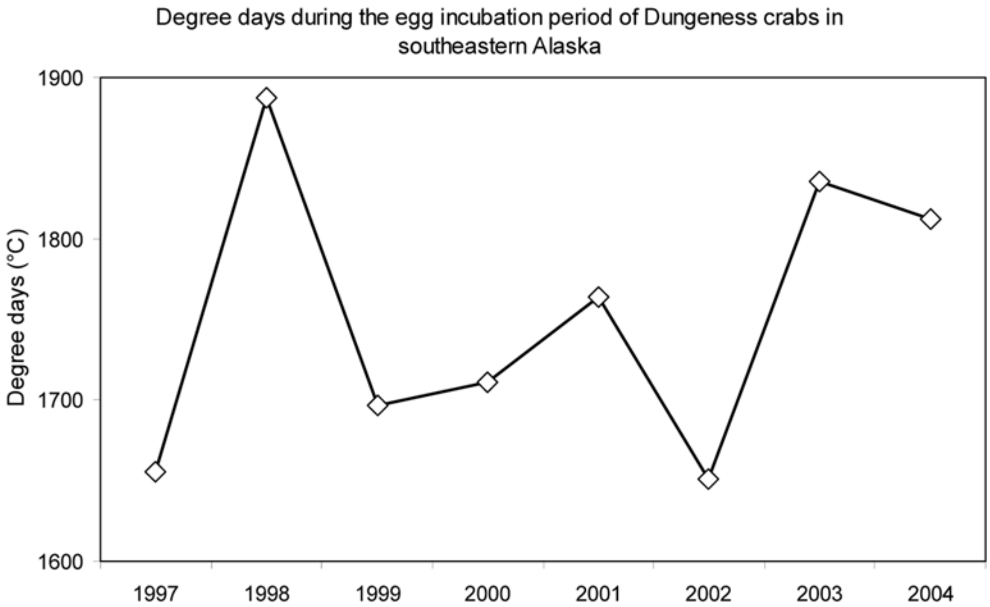

Fig. 2. Adopted degree days during the egg incubation period of Dungeness crabs in Icy Strait, southeastern Alaska. Sea surface temperature (SST) collected in Auke Bay by Dr. B. Wing, Auke Bay Lab, NOAA Fisheries, was used based a high correlation (r^2=0.801, df=35, p=0.001) of the SST in summer, 1997-2004 between Auke Bay and Icy Strait.

Icy Strait (IS)

Larval density was relatively the lowest in 1997 and 1998 (3.0 and 3.1/100 m^3, respectively), while it was the highest in 2002 and 2004 (13.8 and 12.0/100 m^3, respectively). In general, larval density was the highest in June except 1998 (Figs. 3-6). Variability of larval stage and larval density in IS transect was significantly different between years (MANOVA, F=3.752, p=0.002). Overall, larval stage changed seasonally during all years; the average larval stage changed as the summer progressed. Larval abundance varied significantly between stations (K-W test, χ^2= 11.605, df=3, p=0.009); among the stations of the IS transect, the larval density of ISA was the highest. The larvae in May and June 1997 occurred relatively later, while those in May and June 1998 occurred earlier than any other year.

Cross Sound (CS)

Larval occurrence varied seasonally and interannually (Figs. 3-6). In general, larval density in June was higher than any other month. Larval density did not vary significantly between stations (K-W test, χ^2=0.073, df=3, p =0.995). Larvae collected in 1997 were mostly ZI, whereas those in other years belonged to a variety of stages.

Icy Point (IP)

Larval density was relatively much lower than that reported for other transects. Larval abundance at the stations closer to the coastline (IPA and IPB) was higher than larval abundance at the more distal stations (IPC and IPD; Figs. 3-6).

In several years, unusually late larval stages co-occurred with younger larval stages in May and June (Figs. 3-6). In IPA, zoeae V (ZV) and megalopae (M) were collected in May and June 2001 and 2004 along with ZI and ZII. At IPB, ZIV and ZV were captured in May 2001. At IPC, ZIV and ZV were captured in May and June 2001. At IPD, ZV was sampled in June 2000 and 2001. These late stage larvae are unusually transported from southern areas where they hatch earlier (Park et al., 2007).

DISCUSSION

Temperature changes resulting from climate variation have affected the developmental rate of copepods (Mackas et al., 1998) and biomass of zooplankton (Brodeur and Ware, 1992; Francies et al., 1998; Park et al., 2004) in the subarctic Pacific Ocean. In this study, the timing of the appearance of larval stages was related to the degree-days during the egg incubation period of Dungeness crab in southeastern Alaska, probably because temperature affected developmental rates during the incubation and thereby the timing of hatching of Dungeness crab larvae. Water temperatures during the egg incubation period of Dungeness crab from fall 1996 to spring 2004 were not measured at our sampling sites. However, the ocean temperatures during the egg incubation periods in our sampling area may be approximated from published and unpublished values from adjoining areas (Schwing et al., 2002; Etherington et al., 2004; unpubl. data, B. Wing, Auke Bay Laboratory, NMFS, NOAA, USA). Etherington et al. (2004) averaged air temperatures from 1993 to 2002 from six weather stations

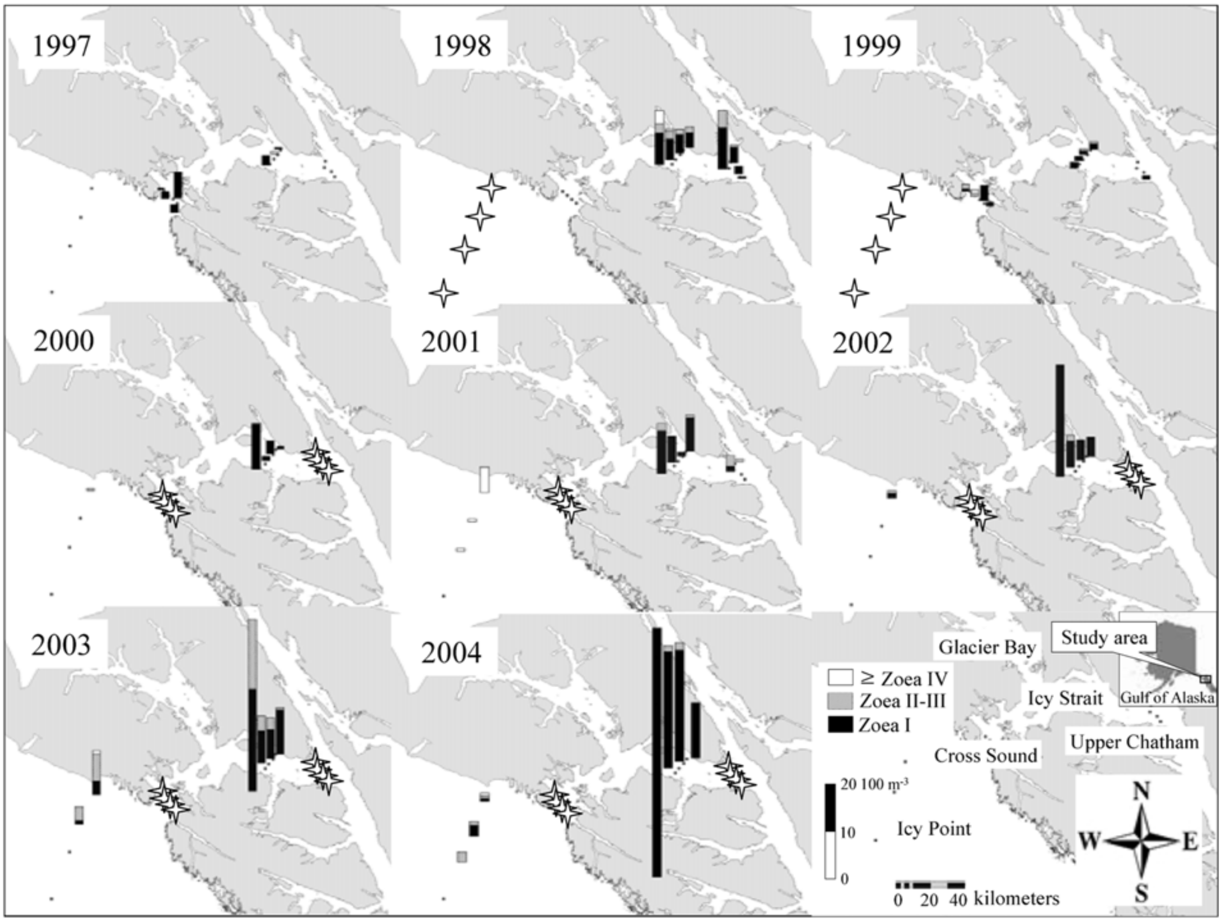

Fig. 3. Interannual larval density of Dungeness crabs in May. Sampling period varied with transects: Icy Point in 1997, 2000-2004; Cross Sound during 1997-2000; Icy Strait during 1997-2004; Upper Chatham during 1997-2001. Height of the scale bar at middle left in the legend map indicates the density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

in southeastern Alaska: Yakutat Airport, Elfin Cove, Hoonah, Barlett Cove (Glacier Bay), Gustavus Airport, Auke Bay, Juneau Airport, and Haines. The monthly mean air temperatures for 1997-2002 from September to April, corresponding to the egg incubation period for Dungeness crabs in southeastern Alaska, were 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 Etherington et al. (2004). Sea surface temperature measured in Auke Bay had the same pattern as the air temperature (unpubl. data, B. Wing, Auke Bay Laboratory, NMFS, NOAA, USA). The mean SST during the egg incubation period was the coldest in 1997 and 2002 and the highest in 1998, similar to that reported for the air temperature from the six weather stations in southeastern Alaska. Also, in the northeastern Pacific Ocean, the possible effects of an El Niño occurred in the summer 1997 and persisted until spring1998 (Schwing et al., 2002; Batton and Welch, 2004). Thus, a cold event during the egg incubation period for larvae occurring in the spring 1997 and 2002 may have slowed embryonic development and subsequent later first appearance of ZI and a longer ZI presence in the water column over the spring and the summer in 1997 and 2002. Conversely, the El Niño in 1997-1998 may have resulted in elevated water temperature and subsequently early larval hatching in the spring 1998. Elevated SST by El Niño, which occurred in the summer 1997 and lasted until the summer 1998, may have resulted in earlier hatching of Dungeness crab larvae in 1998. Previous studies clarified temperature effects on pre-post larval development (Wild, 1980; Sulkin and McKeen, 1989) and juvenile growth of Dungeness crabs (Sulkin et al., 1996). In addition, decreased water temperature during the incubation period for embryos to hatch in the summer 1997 (Figs. 3-6) may have resulted in the continuous occurrence of ZI during the summer months; i.e., embryonic development slowed and Z1 occurred in the water column during a longer period.

Larvae off the coasts of British Columbia, Washington, Oregon, and California are capable of being transported hundreds of kilometers between hatching and settling location by coastal currents and winds along the uninterrupted and

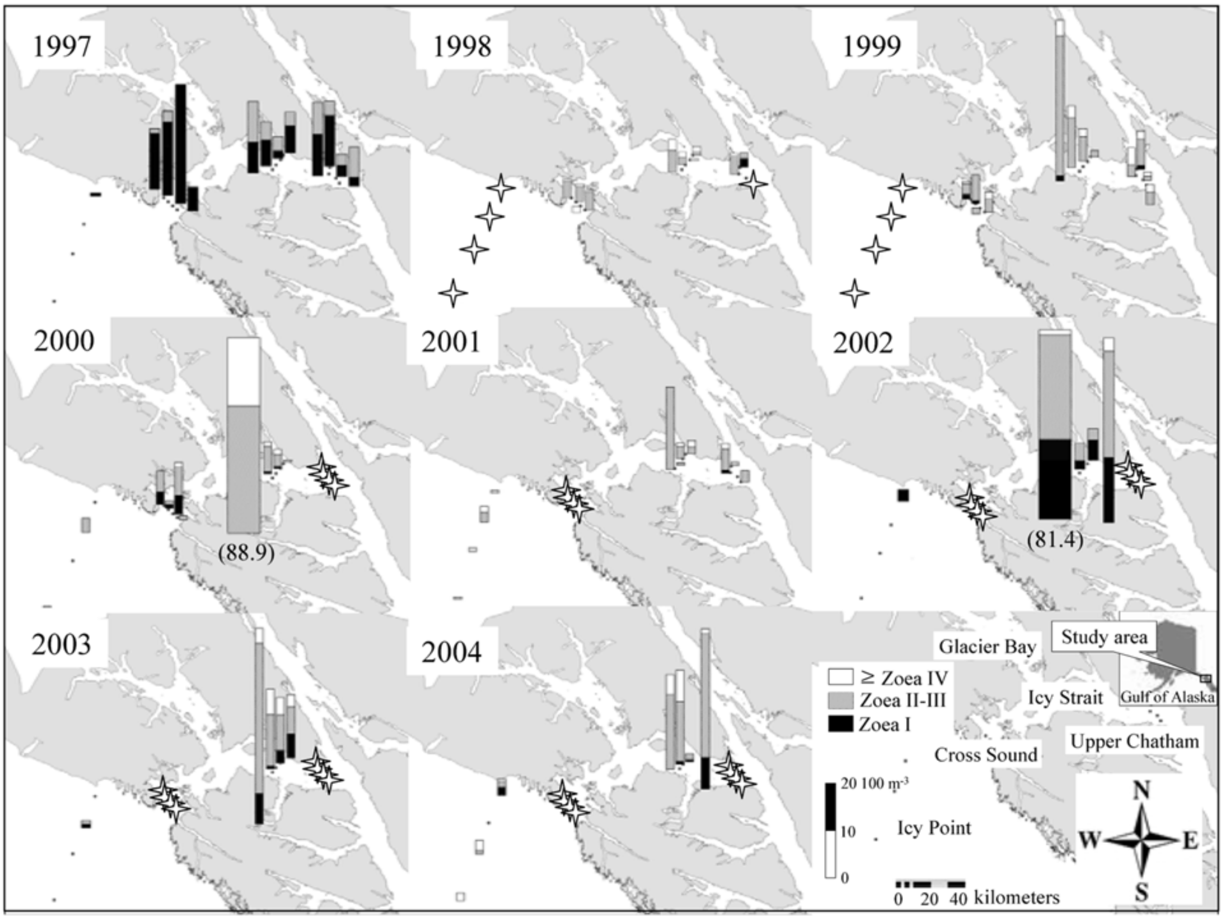

Fig. 4. Interannual larval density of Dungeness crabs in June. Sampling period varied with transects: Icy Point in 1997, 2000-2004; Cross Sound during 1997-2000; Icy Strait during 1997-2004; Upper Chatham during 1997-2001. Height of the scale bar at middle left in the legend map indicates the density of Dungeness crab larvae (inds./100 m^3). Numbers below wide bars denote larval density to the bars. Star symbols indicate no sampling.

simple coastline (Lough, 1976; Reilly, 1983; Jamieson and Phillips, 1988; McConnaughey et al., 1992). However, the hydrography of bays and fjords in southeastern Alaskan may limit larval advection to the offshore and aid retention of larvae in inland water systems. Our study sites were located within inside straits except for those stations on the Icy Point transect. In our study, ZI occurred at every station, and subsequent stages followed at the same stations except those of IP transect. However, the abundances of early stages including ZI and ZII were strongly higher than late stages such ZIV or ZV. This may be resulted from different behavior of each larval stage in the water column. ZI is strongly phototaxic and stay near the surface (Lough, 1976; Park and Shirley, 2005) so that ZI may be more easily collected than late zoeal stages that are photo-negative or photo-neutral and reside in the deeper water close to the bottom. In addition, Dungeness crab larvae do a strong diel vertical migration (Reilly, 1983; Hobbs and Botsford, 1992; Park and Shirley, 2005), particularly a crepuscular migration; larval abundance peaked in early morning and evening (Park and Shirley, 2005). Larval abundance during daytime is greatly lower than that during nighttime while ZI abundance occupies higher proportion during the daytime. However, late stage larvae such as ZIV and ZV stay deeper water (Reilly, 1983; Jamieson and Armstrong, 1991). Accordingly, relative abundances of late larval stages such as ZIV or later could be less collected than early stages such as ZI and ZII. Despite lack of evidence about the larval behavior described above in the study area, we document this progression of larval appearance lends support to the hypothesis that Dungeness crab larvae are retained and undergo ontogeny near their hatching area within our study sites.

Low megalopal density in our study may be a result of different sampling gears or different sampling times. A neuston net or tucker trawl is more effective in collecting megalopae (Jamieson and Phillips, 1988; Jamieson et al., 1989; Miller and Shanks, 2004) because megalopae are highly associated with the water surface (Reilly, 1983) and photo-positive (Lough, 1976). Megalopal densities collected

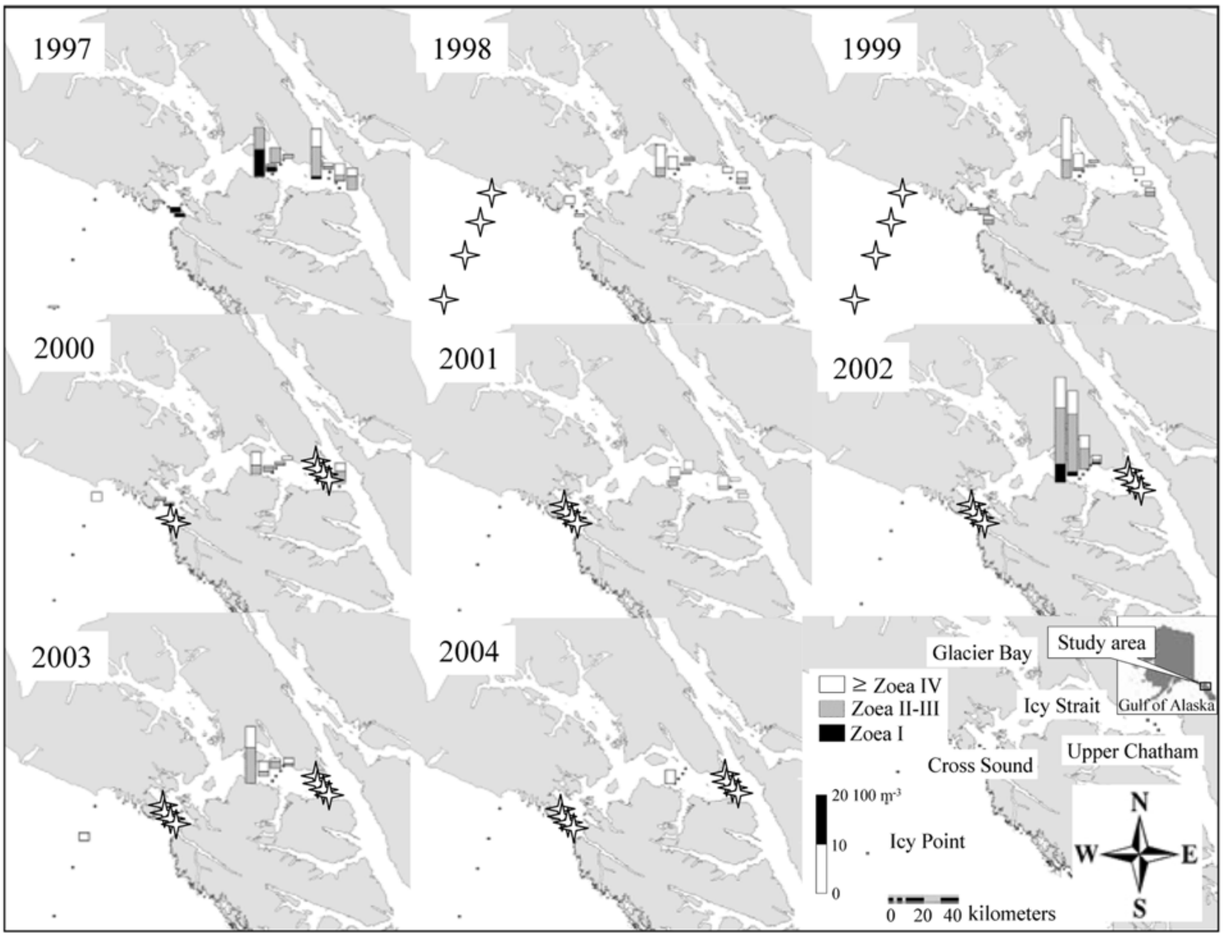

Fig. 5. Internannual larval density of Dungeness crabs in July. Sampling period varied with transects: Icy Point in 1997, 2000-2004; Cross Sound during 1997-2000; Icy Strait during 1997-2004; Upper Chatham during 1997-2001. Height of the scale bar at middle left in the legend map indicates the density of Dungeness crab larvae (inds./100 m^3). Star symbols indicate no sampling.

by light trap at night in the coast of Oregon were extremely high (Miller and Shanks, 2004). Megalopal densities collected in Glacier Bay with light traps near our study sites (Porter et al., 2008) were similarly as high as the megalopal densities reported from southern areas.

Overall, the timing of ZI occurrence varied interannually and was related to water temperature during the egg incubation period: later larval hatching in 1997 and 2002 when temperatures were colder, while earlier larval hatching in 1998 when temperatures were warmer. 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: larvae occurring much later in the year and late stage larvae occurring in inland waters.

ACKNOWLEDGMENTS

We thank M. Sturdevant, J. Orsi, A. Wertheimer, E. Fergusson, W. Heard, and B. Wing of the Auke Bay Lab, NMFS, NOAA for their field samples collected under the SouthEast Coastal Monitoring (SECM) survey program during 1997-2004. We also gratefully acknowledge the captain and the crew of the F/V *John N. Cobb*. This publication is the result of research sponsored by Alaska Sea Grant with funds from the National Oceanic and Atmospheric Administration Office of Sea Grant, Department of Commerce, under grant no. NA16RG2321 (project no. R/31-12), and from the University of Alaska with funds appropriated by the state.

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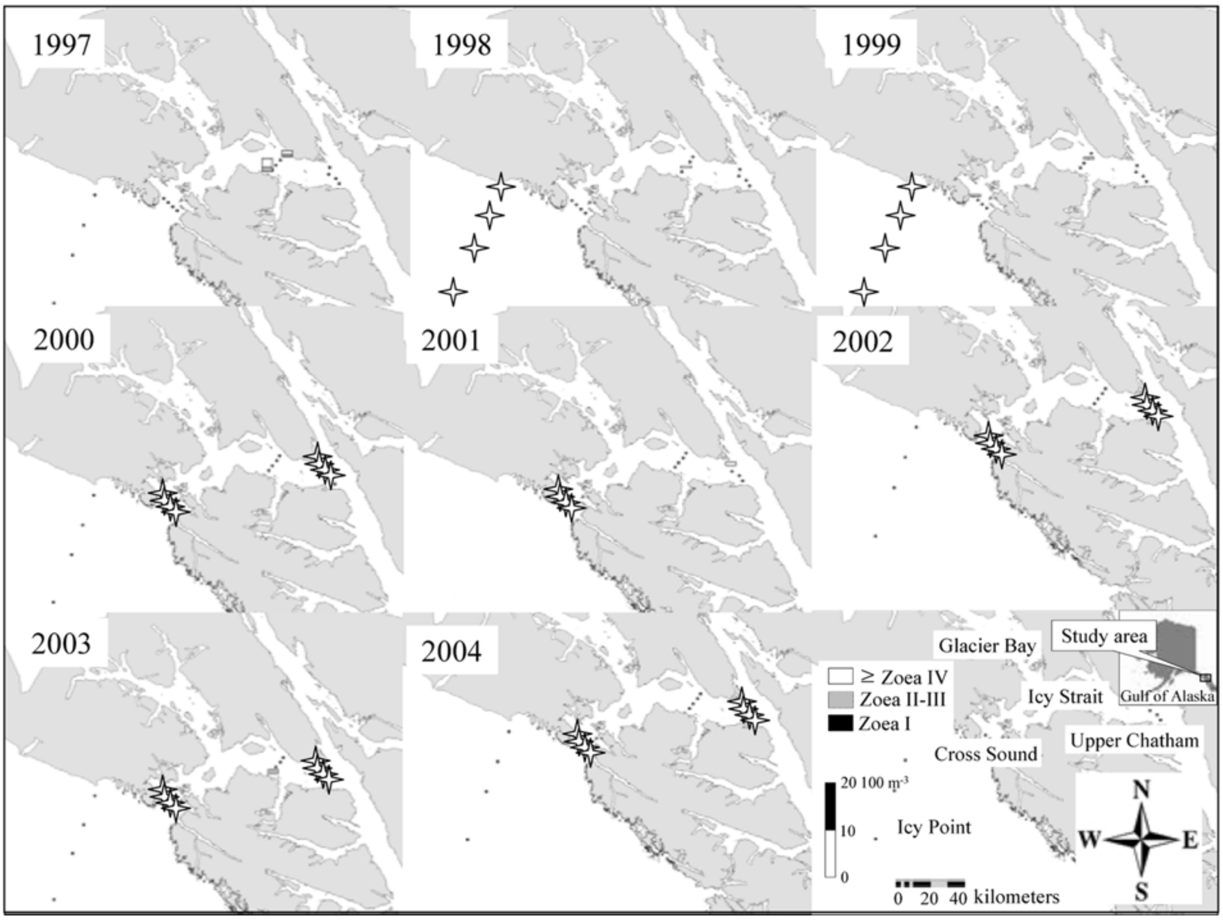

Fig. 6. Interannual larval density of Dungeness crabs in August. Sampling period varied with transects: Icy Point in 1997, 2000-2004; Cross Sound during 1997-2000; Icy Strait during 1997-2004; Upper Chatham during 1997-2001. Height of the scale bar at middle left in the legend map indicates the density of Dungeness crab larvae (inds./100 m^3). Star symbols indicate no sampling.

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[Received October 6, 2008; accepted December 1, 2008]