

Recruitment variation of eastern Bering Sea crabs: Climate-forcing or top-down effects?

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Abstract

During the last three decades, population abundances of eastern Bering Sea (EBS) crab stocks fluctuated greatly, driven by highly variable recruitment. In recent years, abundances of these stocks have been very low compared to historical levels. This study aims to understand recruitment variation of six stocks of red king (*Paralithodes camtschaticus*), blue king (*P. platypus*), Tanner (*Chionoecetes bairdi*), and snow (*C. opilio*) crabs in the EBS. Most crab recruitment time series are not significantly correlated with each other. Spatial distributions of three broadly distributed crab stocks (EBS snow and Tanner crabs and Bristol Bay red king crab) have changed considerably over time, possibly related in part to the regime shift in climate and physical oceanography in 1976–1977. Three climate-forcing hypotheses on larval survival have been proposed to explain crab recruitment variation of Bristol Bay red king crab and EBS Tanner and snow crabs. Some empirical evidence supports speculation that groundfish predation may play an important role in crab recruitment success in the EBS. However, spatial dynamics in the geographic distributions of groundfish and crabs over time make it difficult to relate crab recruitment strength to groundfish biomass. Comprehensive field and spatially explicit modeling studies are needed to test the hypotheses and better understand the relative importance and compound effects of bottom-up and top-down controls on crab recruitment.

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1. Introduction

Crab population abundances and catches in Alaska have fluctuated greatly over time (Zheng et al., 1995, 1996; Zheng et al., 1998b; Kruse et al., 2000). The abundance of commercial-sized red king crab (*Paralithodes camtschaticus*) in the Gulf of Alaska peaked in 1965 with a catch of 51,427 t. During the last 20 years,

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population size was a small fraction of abundances observed in the 1960s and 1970s, and fisheries on almost all Gulf of Alaska red king crab stocks have been closed since the early 1980s. Bristol Bay red king crab support the longest existing crab fishery in Alaska, with small commercial fisheries starting in the 1930s. Commercial-sized red king crab abundance in Bristol Bay peaked in 1979, and its fishery peaked in 1980, with a catch of about 59,000 t. Since 1982, the annual catch of Bristol Bay red king crab has been less than 20% of its peak value. Adak red king crab produced an average annual catch of over 7000 t from 1963 to 1972 and has supported an average catch of less than 3% of that amount during the last 10 years. Tanner crab (*Chionoecetes bairdi*) catch in the Gulf of Alaska peaked in the 1970s with an average annual catch of 20,537 t, and most of these Tanner crab stocks have been closed for fishing since the early 1990s due to low population abundance. Eastern Bering Sea (EBS) Tanner and snow crab (*Chionoecetes opilio*) abundances and catches also experienced sharply up-and-down cycles, and both population abundances are currently at the low end of observed ranges.

Most crab population fluctuations are caused by recruitment variability. In a closed population, abundance increases through recruitment and decreases due to catch and natural mortality. When recruitment exceeds catch and natural mortality, the population abundance increases. If recruitment is periodic, as in Alaskan crab populations (Zheng and Kruse, 2000), population abundance increases quickly during a period of strong recruitment and peaks right after the poor recruitment period begins. Even without fishing, the population will decline if recruitment is less than natural mortality. Crab recruitment varies greatly over time. Among the crab recruitment indices calculated for 15 stocks in Alaska, corresponding to brood years 1963 to 1994, ratios of the highest to lowest recruitment for each stock ranged from 6 to 1697, and most ratios exceeded 29 (Zheng and Kruse, 2000). Periodic and variable recruitment causes fluctuating crab population abundances and creates unstable fisheries.

Recruitment variation may be explained by changes in spawning biomass, environmental factors, competition, and predation. If recruitment is density-dependent, it will be related to spawning biomass, and the stock-recruitment relationship will explain part of recruitment variation (Ricker, 1954; Beverton and Holt, 1957; Cushing, 1973). Environmental factors like temperature, wind, barometric pressure, or overall environmental conditions may affect food availability and larval transport, growth and survival (e.g., Shepherd et al., 1984; Koslow, 1984; Koslow et al., 1987; Hollowed and Wooster, 1992, 1995; Hare and Mantua, 2000), thus affecting recruitment strength. Predation on eggs, larvae, or juveniles will also affect recruitment strength.

Spawning biomass explains only a small portion of recruitment variation for crab stocks in the EBS (Zheng and Kruse, 2003). Among all crab stocks in the EBS, the strongest density-dependent stock-recruitment relationship found so far is for Bristol Bay red king crab. For this stock, strong recruitment generally occurred at intermediate levels of effective spawning biomass (a measure of the biomass of mated mature females in any given year), and very weak recruitment was associated with extremely low levels of effective spawning biomass (Zheng and Kruse, 2003). However, the year classes are highly autocorrelated, thus implicating effects of environmental factors on recruitment. For Bristol Bay Tanner crab, recruits were not strongly associated with effective spawning biomass; both weak and strong recruitment occurred with both low and high effective spawning biomass (Zheng and Kruse, 2003). The association between recruitment and effective spawning biomass for EBS snow crab was even weaker than for Tanner crab; effective spawning biomass explained <21% of recruitment variation (Zheng and Kruse, 2003).

Many hypotheses about oceanic food webs have been proposed in recent years to explain marine ecosystem regulation and population variations. Common hypotheses invoke bottom-up (Beamish and Bouillon, 1993) and top-down controls (Springer et al., 2003; Worm and Myers, 2003) or combinations of both (Hunt et al., 2002). Changes in nutrients affecting the productivity of the lowest trophic levels (e.g., primary producers), which affect population abundance at the next higher trophic level (e.g., herbivores), and associated trends of populations at other trophic levels in an ecosystem are considered bottom-up control. Top-down control often functions through predation, fishing or hunting, and may result in trophic cascades with opposite trends in population abundances between two trophic levels. For instance, reductions in carnivores may release herbivores from predation pressure, thus allowing for increases in herbivore populations to the detriment of populations of primary producers. A classic example of this phenomenon is the denuding of kelp forests in Alaska owing to unregulated herbivory by sea urchins (*Strongylocentrotus* spp.) following the near extinction of sea otters (*Enhydra lutris*) by Russian fur traders in Alaska in the 18th Century (Estes and Palmisano, 1974). Both

bottom-up and top-down controls can affect recruitment strength by regulating larval and juvenile survival rates.

In this study, we examine the effects of climate forcing and top-down control on crab recruitment variation in the EBS. Climate forcing can change food abundance and availability for larvae and juvenile crabs, functioning as the bottom-up control. Climate forcing or human activities can also change predator abundances and their spatial overlap with their prey, thus affecting the degree of top-down control. We compare the trends of crab recruitments and climate indices, examine the spatial distributions of crabs and their main predators, groundfish, over time, and discuss hypotheses as potential areas for more comprehensive future research to explain crab recruitment variation in the EBS.

2. Data and methods

Summer bottom trawl survey data for king, Tanner and snow crabs in the EBS from 1972 to 2004 were obtained from the National Marine Fisheries Service (NMFS). Before 1978, the survey covered a limited area that does not fully represent the EBS snow crab and St. Matthew blue king crab (*Paralithodes platypus*) stocks. The survey employs a systematic design where a 20×20 nautical mile grid was overlaid on the EBS (Fig. 1). One 0.5-h trawl tow was usually made per 400 square nautical miles. Typically, two tows have been conducted for a single station for small areas around the Pribilof Islands and St. Matthew Island. Multiple tows were occasionally conducted at stations with an extremely high catch of red king crab or blue king crab. Surveys occurred from May 20 to September 3, primarily during June–July. In this study, we averaged crab abundance for stations with multiple tows in a given year. Annual female abundance indices by size and maturity were mapped by station to identify spatial patterns. Annual centers of distribution for different groups of females were calculated by averaging locations (in longitude and latitude) weighted by abundance to illustrate changes in distribution over time.

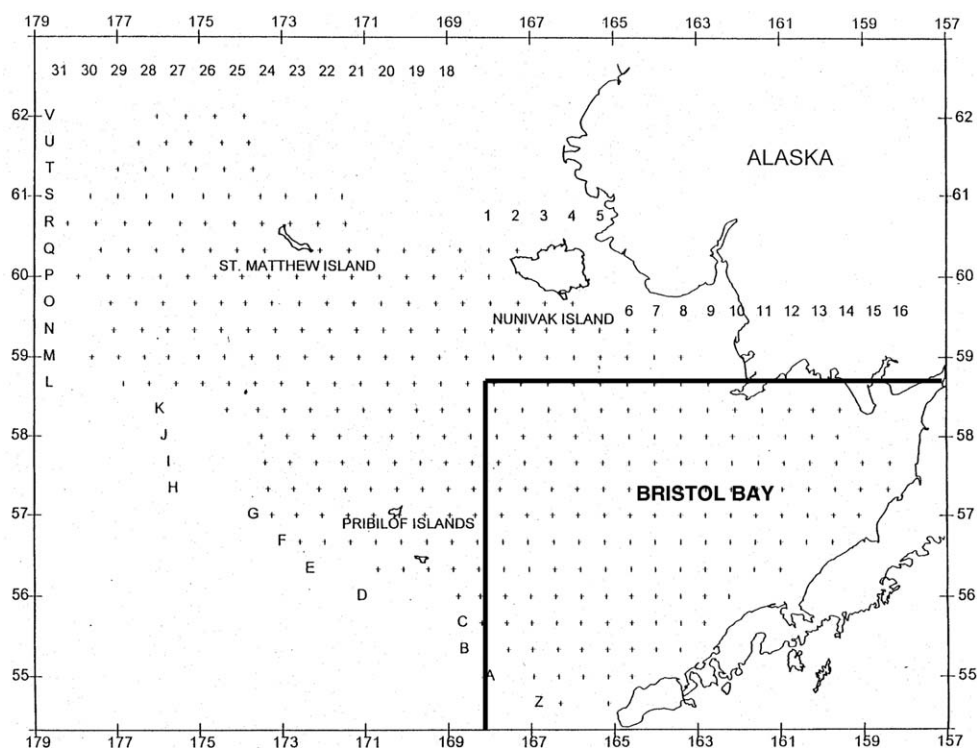


Fig. 1. NMFS EBS crab survey area. Symbols “+” indicate survey stations. (From Stevens et al., 2000.)

Biomass per unit effort data for groundfish stocks in the summer trawl surveys in the EBS were also obtained from 1982 to 2004. The groundfish data before 1982 were not used due to potential changes in survey catchability (Gary Walters, NMFS, 7600 Sand Point Way, NE, Seattle, WA 99115, personal communication). Groundfish species include skates (*Raja* and *Bathyraja* spp.) and commercially important species: walleye pollock (*Theragra chalcogramma*), Pacific cod (*Gadus macrocephalus*), Pacific halibut (*Hippoglossus stenolepis*), yellowfin sole (*Pleuronectes asper*), northern rock sole (*Lepidopsetta polyxystra*), flathead sole (*Hippoglossoides elassodon* and *H. robustus*), Alaska plaice (*Pleuronectes quadrituberculatus*) and arrowtooth flounder (*Atheresthes stomias*). Spatial distributions of each of these species and their changes over time were mapped to identify their spatial overlap with crab distributions. Routine examination of stomach contents of a few commercially important groundfish species in the EBS shows that Pacific cod are the primary crab consumer (Livingston, 1991; Livingston et al., 1993; Livingston and deReynier, 1996; Lang et al., 2003). All the other groundfish listed above also consume crabs in the EBS, but not as consistently as Pacific cod.

Time series of recruitment were obtained for six crab stocks from length-based analyses and catch-survey analyses (Zheng et al., 1995; Vining and Zheng, 2004) of assessment survey data. Unlike fish, crabs cannot be aged morphologically, and crab ages have to be approximated from growth information obtained from tagging data. We define recruits and recruitment with reference to the modeled components of populations, i.e., newshell (molted within the past 12 months) male crabs that first enter the modeled populations. This recruitment is assumed to represent year-class strength in this study. The recruitment definition used here differs from the one commonly used in fishery management, where recruitment is defined with reference to the fishery as the number of male crabs first molting to a legal size. The recruitment to the fishery is about 1–5 years older than the recruitment to the model. Length-based analyses provided recruitment estimates for Bristol Bay red king crab from 1973 to 2004 (Vining and Zheng, 2004), Norton Sound red king crab from 1978 to 2003 (Zheng et al., 1998a), Tanner crab from 1976 to 2004 (Zheng et al., 1998b), and snow crab from 1978 to 2002 (Jack Turnock, NMFS, 7600 Sand Point Way NE, Seattle, WA 99115, personal communication). Estimates for blue king crab from 1975 to 2004 for the Pribilof stock and from 1978 to 2004 for the St. Matthew stock were based on catch-survey analyses (Vining and Zheng, 2004).

Based on growth data, crab recruitment was lagged 7 years for king and Tanner crabs and 4 years for snow crab, back to the year of hatching, to represent year classes. It is assumed that hatching occurs one year after mating. Recruitment was also log-transformed to minimize the effects of extreme year classes and measurement error (Zheng, 1996; Pyper and Peterman, 1998). A LOWESS (locally weighted regression scatter plot smoothing) procedure with bandwidth of 0.3 was used to reveal time trends. Pearson's product-moment correlation coefficients were calculated using all available data (log-transformed without smoothing) for each pair of stocks to check whether the underlying associations were statistically significant. Two-tailed *t*-tests were conducted with the effective number of degrees of freedom to account for autocorrelation in the time series (Pyper and Peterman, 1998).

We examined a predation hypothesis about crab-groundfish relationships in the EBS: i.e., H_0 : Increased predation by groundfish caused declines in crab recruitment. We obtained biomass estimates for two groundfish stocks in the EBS from the same annual bottom trawl survey used to estimate crab abundance. Stock synthesis models incorporate these survey data, as well as other catch sampling and fishery data, to provide biomass estimates for Pacific cod (Thompson and Dorn, 2003) and yellowfin sole (Wilderbuer and Nichol, 2003). To test the predation hypothesis, time series of groundfish biomass were compared with indices of crab year-class strength lagged to ages 0–4. Crabs of ages 0–4 are more vulnerable to predation than other age groups (Livingston, 1991; Livingston et al., 1993; Livingston and deReynier, 1996; Lang et al., 2003). Because Pacific cod is the main known crab predator and their spatial distribution overlaps with those of five crab stocks (Bristol Bay red king crab, EBS Tanner crab, EBS snow crab, and two blue king crabs), Pacific cod biomass was compared with the recruitment of these five crab stocks. A long time series of yellowfin sole biomass was available; spatial distribution of yellowfin sole overlaps with Bristol Bay red king crab. Thus, yellowfin sole biomass was correlated against Bristol Bay red king crab recruitment. For each crab-groundfish species pair, a one-tailed *t*-test was conducted using all available data to determine whether the correlation coefficient, *r*, was significantly ($\alpha = 0.05$) less than zero. The effective number of degrees of freedom was computed using Pyper and Peterman's (1998) approach to account for autocorrelation in the time series of biomass and log-transformed recruitment.

Four environmental factors were considered in this study: near-bottom temperatures, proportion of ice coverage, Aleutian Low Pressure Index (ALPI), and Pacific Decadal Oscillation (PDO). Temperature data were provided by Dr. Steven Hare (International Pacific Halibut Commission, Seattle, Washington) for the period 1934–1997 and by Dr. Gary Walters (National Marine Fisheries Service, Seattle, Washington) for the period 1998–2004. The temperature data were collected by numerous researchers and are consistently available only during summer months. Based on the main distributions of three crab stocks, we averaged the temperature data during June and July within the area bounded by 56.0–57.99°N and 158.0–166.99°W for Bristol Bay red king crab; 56.0–57.99°N and 160.0–174.99°W for EBS Tanner crab; and 57.0–60.99°N and 167.0–176.99°W for EBS snow crab. The ice coverage index in the Bering Sea is a combination of several highly correlated variables (Hare and Mantua, 2000) and was obtained from the Bering Climate page (<http://www.beringclimate.noaa.gov/>). Values of the PDO from 1900 to 2004 were also obtained from the Bering Climate page (<http://www.beringclimate.noaa.gov/>). Values of the ALPI from 1900 to 2004 were obtained from <http://www.pac.dfo-mpo.gc.ca/sci/sa-mfpd/downloads/alpi.txt>. The ALPI measures the relative intensity of the Aleutian Low pressure system of the north Pacific (December through March) and is calculated as the mean area (km²) with sea level pressure ≤ 100.5 kPa and expressed as an anomaly from the 1950–1997 mean (Beamish et al., 1997). To smooth the environmental data, we used 3-year running averages for all three environmental factors. To update the relationship between Tanner crab recruitment and northeast winds in Rosenkranz et al. (2001), we obtained the 60° component of the average May–June wind vector during 1969–1995 at St. Paul Airport in the Pribilof Islands from Rosenkranz et al. (2001) and computed the index after 1995 from the wind data obtained from oceanographic data archives of the University of Alaska Fairbanks Institute of Marine Science.

3. Results and discussion

3.1. Crab recruitment variation

Recruitment over time was highly variable for all six crab stocks (Fig. 2). There was some concurrence of strong and weak year classes among the six stocks (Fig. 2). Strong recruitment occurred from brood years in the late 1960s for all four stocks for which we have data from this period. Although year classes in the late 1960s were not estimated for EBS snow crab and St. Matthew Island blue king crab, mature snow crab abundance in the survey was very high in the mid- and late-1970s and survey mature blue king crab abundance was also high in the late 1970s, implying some strong year classes in the late 1960s. The other common recruitment features are the strong similarity for the two blue king crab stocks, a similar recruitment trend for the two red king crab stocks in the 1990s, and weak year classes for blue king, Tanner and snow crab stocks in the 1990s. Differences in recruitment patterns include a long-term decline during the 1970s and 1980s for Bristol Bay red king crab, two very weak year classes of Norton Sound red king crab in the early 1970s, and strong recruitment of snow crab and St. Matthew blue king crab in the late 1980s (Fig. 2).

Most crab recruitment time series are not significantly correlated with each other (Table 1). As shown in Fig. 2, the most closely related recruitment series are two blue king crab stocks ($R^2 = 0.52$, Table 1). Norton Sound red king crab recruitment was negatively related to the recruitment of two blue king crab stocks; however, explanatory mechanisms for such relationships are unclear. If large-scale physical forcing affects these stocks, they may not affect each stock in the same way, as suggested by poor correlations among the stocks.

3.2. Environmental conditions and Bristol Bay red king crab recruitment

The ALPI and PDO indices show similar trends, which are opposite to the ice coverage index (Fig. 3). These indices exhibit decadal-scale variability. The deviates of the smoothed ALPI were negative from the mid-1960s to the mid-1970s, positive from the late 1970s to the late 1980s, briefly negative in 1989 and 1990, and generally positive in recent years (Fig. 3). The weak ALPI before 1977 was associated with generally low near-bottom temperatures and high ice coverage (Fig. 3). The trends of near-bottom temperatures for areas for Bristol Bay red king crab, EBS Tanner crab and snow crab are similar (Fig. 3). The temperatures were low during the 1970s and high in the early 1980s.

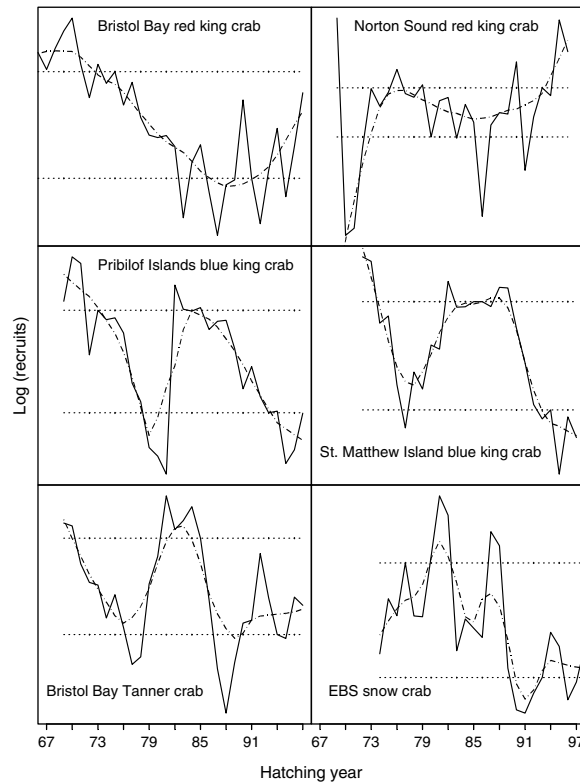


Fig. 2. Time series of log-transformed recruitment (solid line) for six crab stocks in the EBS. Dashed lines are LOWESS smoothed lines, and dotted lines are limits for the 25% lower and upper quartiles of recruitment.

Table 1

Pairwise correlation coefficients (r , upper triangle) on log-transformed recruitment for six crab stocks in the EBS and levels of statistical significance of two-tailed t -test (lower triangle)

	1	2	3	4	5	6
1. Bristol Bay red king crab		0.27	0.02	0.19	0.04	−0.01
2. Pribilof Is. blue king crab	ns		0.72	0.16	0.12	−0.44
3. St. Mat. Is. blue king crab	ns	*		0.18	0.33	−0.50
4. Bristol Bay Tanner crab	ns	ns	ns		0.09	−0.16
5. EBS snow crab	ns	ns	ns	ns		−0.05
6. Norton Sound red king crab	ns	*	*	ns	ns	

Lower triangle: ns for $p > 0.05$; * for $p < 0.05$.

Among the six stocks, Bristol Bay red king crab recruitment trends appear to relate best to decadal shifts in physical oceanography: all strong year classes occurred before 1977 when the Aleutian Low was weak (Fig. 4). The largest year class during the last 20 years, the 1990 year class, was also coincidental with the weak ALPI during 1989–1991. Specific mechanisms linking Bristol Bay red king crab recruitment and the physical oceanography are unclear. Zheng and Kruse (2000) hypothesized that the strength of the Aleutian Low affects food availability for red king crab larvae. Strong Aleutian Lows may have effects on species composition of the spring bloom that are adverse for red king crab larvae. Diatoms such as *Thalassiosira* are important food for first-feeding red king crab larvae (Paul et al., 1989), and they predominate in the spring bloom in years of light winds when the water column is stable (Ziemann et al., 1991; Bienfang and Ziemann, 1995). Years of strong wind mixing associated with intensified Aleutian Lows may depress red king crab larval survival and subsequent recruitment. Yet, the recruitment trends of other crab stocks cannot be consistently explained by the decadal-scale variability of these environmental data. Possibly, red king crab in Norton Sound are too

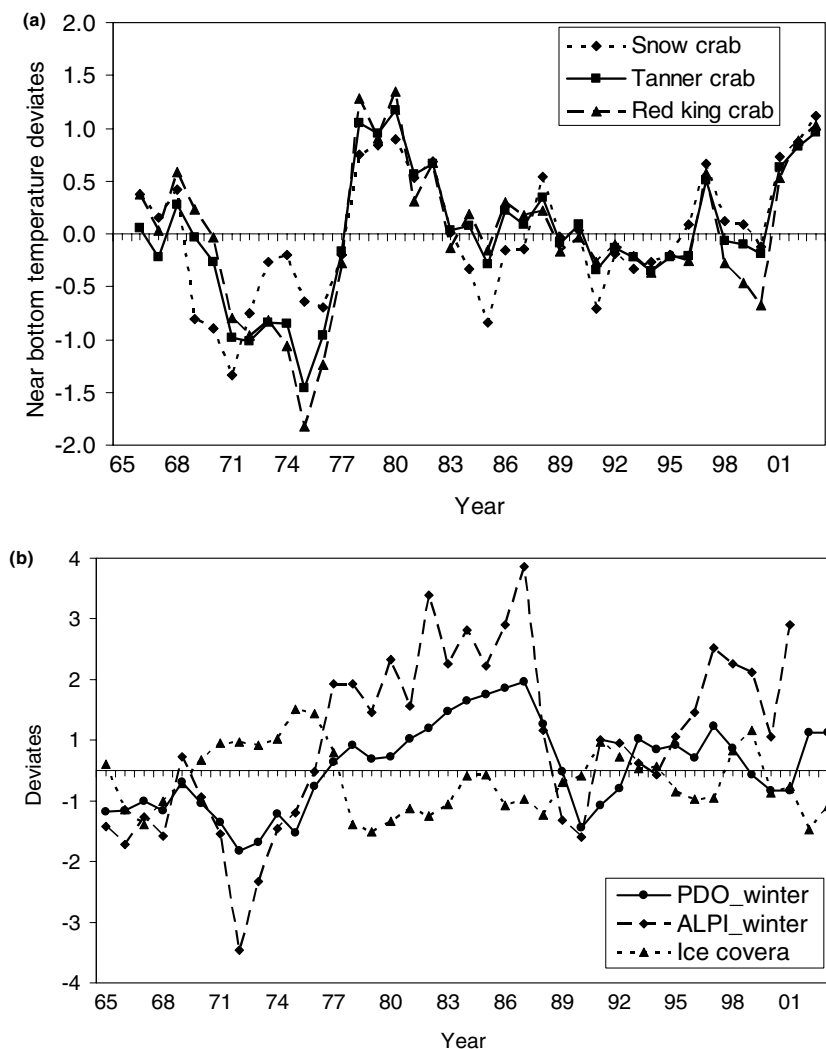


Fig. 3. Time series of anomalies of (a) summer near-bottom temperature (June–July) in the EBS and (b) winter ALPI and PDO indices (December–March), and Bering Sea ice coverage index. All indices and near-bottom temperatures are three-year-running averages. Temperatures were averaged within the area of 56.0–57.99°N and 158.0–166.99°W for Bristol Bay red king crab, the area of 56.0–57.99°N and 160.0–174.99°W for EBS Tanner crab, and the area of 57.0–60.99°N and 167.0–176.99°W for EBS snow crab.

far north to be significantly affected by Aleutian Low dynamics; different mechanisms (explained later) may affect other crab stocks.

3.3. Spatial distributions and implications on the role of advection in crab recruitment

The spatial distribution of red king crab in the EBS changed profoundly during the last three decades (Figs. 5 and 6a). Hsu (1987) first documented the shifts in spatial distribution of Bristol Bay red king crab in the 1970s, and Loher and Armstrong (2005) updated these spatial dynamics and tried to link the shifts to oceanographic conditions. Generally speaking, red king crab abundance in southern Bristol Bay was high during the 1970s, declined, and was extremely low after 1979. Female red king crab were found primarily in central Bristol Bay during 1980–1987 and 1992–2004. The distribution centers of mature females moved south slightly during 1988–1991 but did not reach the southern locations previously occupied in the 1970s. Small immature females occurred primarily along the shore and in northeastern Bristol Bay, and mature females occurred in the deeper water and offshore (Fig. 6a). With ontogeny, young red king crab tend to move from inner Bristol

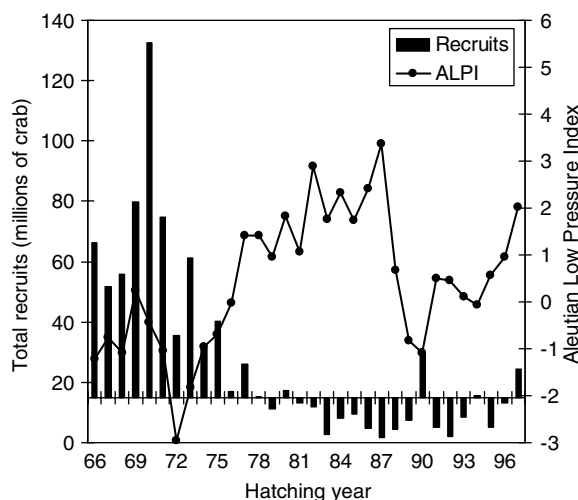


Fig. 4. Recruits of Bristol Bay red king crab and 3-year-running average anomalies of the ALPI (December–March, 3-year moving average). A 7-year lag from hatching to recruitment was applied to match recruits to climate conditions during hatching.

Bay in a southwesterly direction along the north shore of the Alaska Peninsula to central or southern Bristol Bay as mature females.

Centers of distribution of Tanner crab in the EBS were highly variable during the past 30 years (Fig. 5). During 1978–1983, most females (Fig. 6b) and the centers of distribution for mature females (Fig. 5) occurred primarily west of the Pribilof Islands. During 1984–1986, a low abundance period, female Tanner crab were quite evenly distributed throughout their range. From 1987 to 1991, female Tanner crab were concentrated within Bristol Bay. Few crab were found in northeastern Bristol Bay during 1992–2004 (Fig. 6b). Small immature females occurred primarily between 100 and 200 m depth west of the Pribilof Islands and between 50 and 200 m depth east of the Pribilof Islands (Fig. 6b). Generally, small, immature female crab were located in deeper waters than were mature females (Fig. 6b).

The spatial distribution of female snow crab also changed over time (Figs. 5 and 6c). Zheng et al. (2001) documented these changes, and Ernst et al. (2005) further examined their spatial dynamics. It appears that the centers of distribution of mature females have moved gradually to the northwest since the 1970s; as a contrast, oldshell mature females were found primarily east of or around the Pribilof Islands during 1978–1980 and northwest of the Pribilof Islands during 1996–2004. Newshell mature females also shifted from a broad distribution during 1978–1980 to one primarily confined to the northwest portion of the standard survey area during 1996–2004. Immature females generally occur in the northeastern part of the EBS in relatively shallow water. With increasing age and size, crab appear to move in a southwest or cross-shelf direction to the outer continental shelf. Oldshell mature females mostly occur in deep water and concentrate within a smaller area than other groups of crab.

Changes in spatial distributions of crab abundance in the EBS may be related to the regime shifts during the last 30 years. The shifts of distributions for large mature female red king crab in Bristol Bay occurred right after the 1976/77 regime shift, while the shifts of mature female snow crab occurred from the mid-1970s to early 1980s (Fig. 5). Loher and Armstrong (2005) hypothesized that changes in near bottom temperatures associated with the 1976/77 regime shift were the cause for spatial shifts of red king crab female distributions, and Orensanz et al. (2004) proposed a similar hypothesis to explain spatial changes for snow crab. Orensanz et al. (2004) further suggested that the lagged northward shift of mature females associated with warming during the 5-year period 1975–1979 was indicative of a corresponding northward shift in larval settlement. Both studies attributed spatial shifts of crab distributions to changes in the cold pool, a body of cold ($<2^{\circ}\text{C}$) subsurface water that occurs in summer as a remnant of winter conditions. In the early to mid-1970s sea ice extended more consistently into the southeastern Bering Sea where average bottom temperatures were $0.5\text{--}3^{\circ}\text{C}$ colder than in the late 1970s and early 1980s, when the cold pool retreated north (Wyllie-Echeverria and Wooster, 1998). During the late 1970s and early 1980s when near bottom temperatures were high, the distribution centers of mature

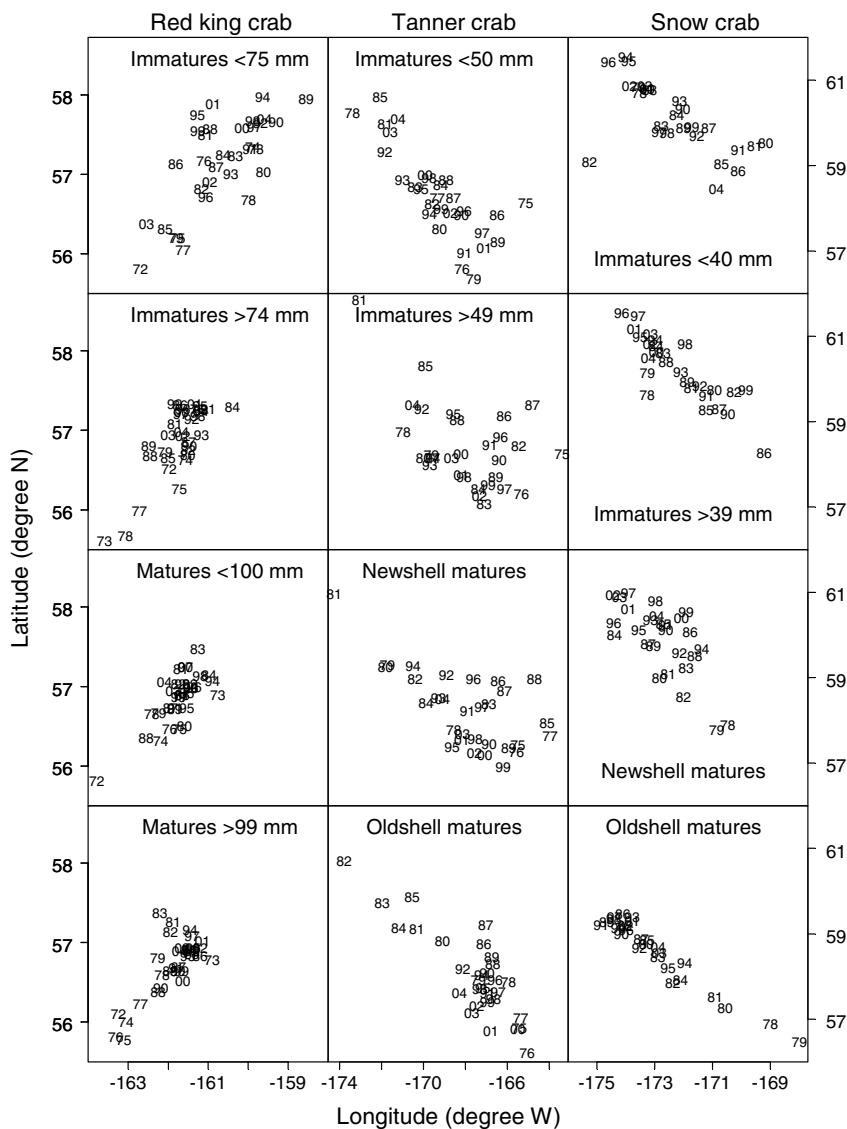


Fig. 5. Distribution centers of female abundance for Bristol Bay red king crab and EBS Tanner and snow crabs. The left Y-axis is for red king and Tanner crabs, and the right Y-axis is for snow crab.

female Tanner crab were primarily west of the Pribilof Islands (Fig. 5), and few female Tanner crab were found in central Bristol Bay after the regime shift in 1989 (Fig. 6b).

Overall, after the regime shift in 1976/77, EBS crab stocks have been stronger in the northern than southern habitats. For two red king crab stocks, the northern stock (Norton Sound) has recovered more completely from previous lows during the last 15 years than has the Bristol Bay stock. Within the Bristol Bay stock, the southern component has almost disappeared, whereas the northern component is rebuilding (Fig. 6a). For two blue king crab stocks, the mature abundance of the St. Matthew Island stock (northern stock) was relatively high until 1999 whereas the Pribilof Islands stock has been depressed since the early 1980s (Vining and Zheng, 2004). The abundance of mature female snow crab has been extremely low in their southern range during the last 10 years (Fig. 6c).

Spatial distributions of mature and small juvenile female Tanner crab mostly overlap, with the distribution centers of juveniles generally being southwest of those of the mature females, whereas distribution centers of small juvenile red king and snow crabs are generally located downstream of the mature females (Fig. 7). Thus,

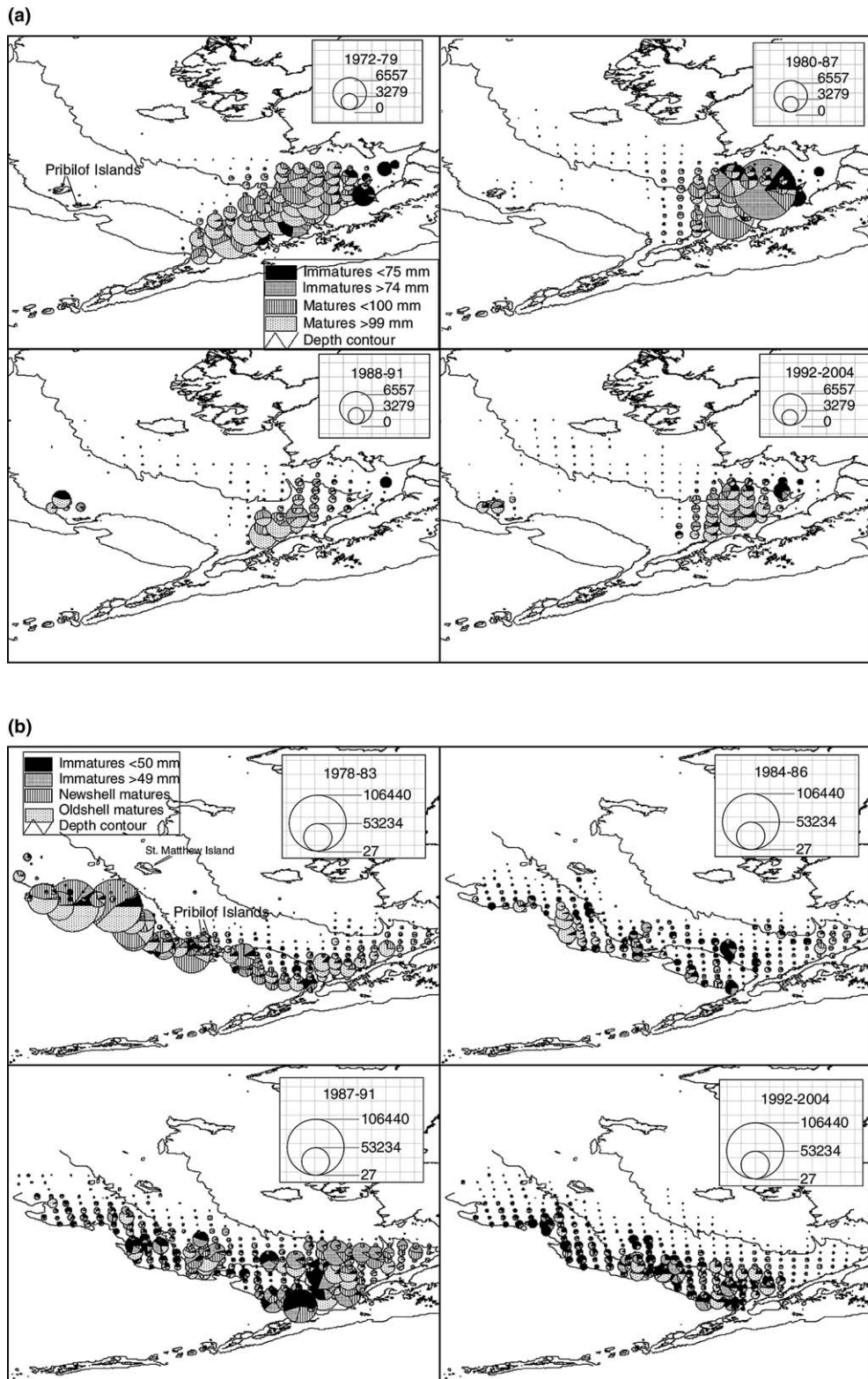


Fig. 6. Geographic distributions of immature and mature female (a) red king crab from 1972 to 2004, (b) Tanner crab from 1978 to 2004, and (c) snow crab from 1978 to 2004 in the EBS derived from NMFS summer trawl survey data. The diameter of each pie represents crab density expressed as the number of crab per square nautical mile. Three depth contour lines are 50, 100, and 200 m.

(c)

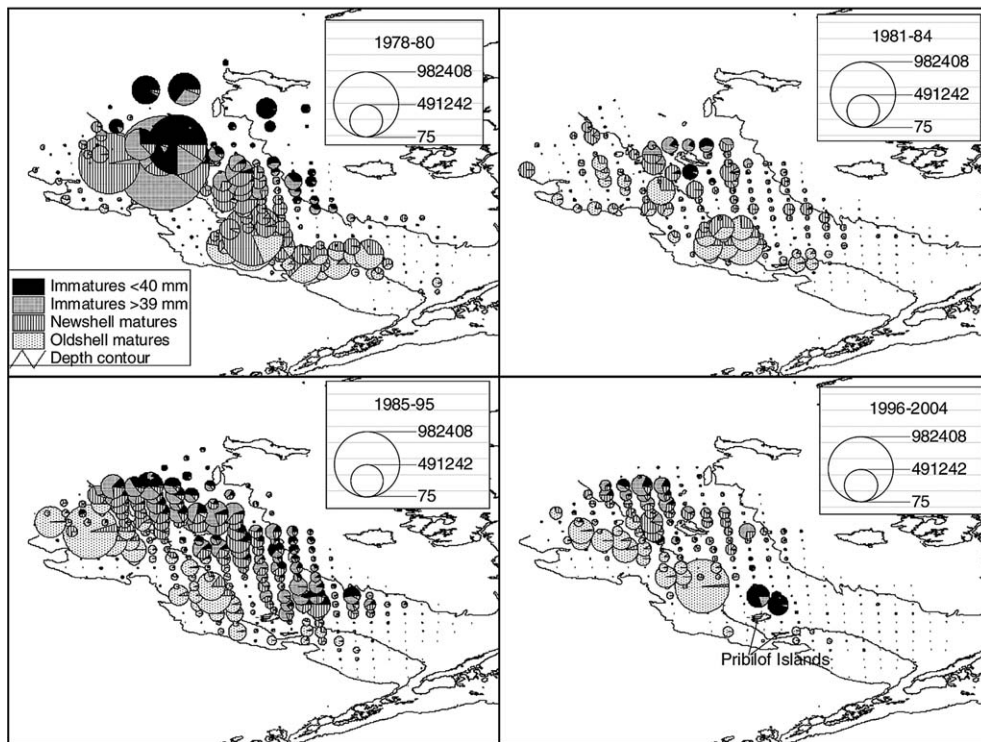


Fig. 6 (continued)

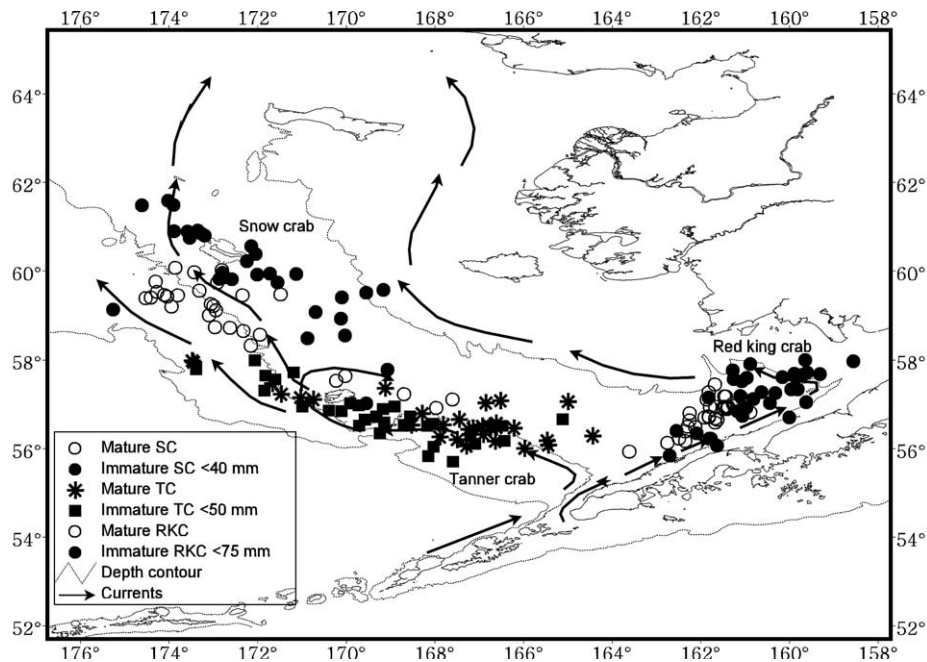


Fig. 7. Centers of distributions (one point per year) of small immature and mature female red king (RKC, 1972–2004), Tanner (TC, 1975–2004), and snow (SC, 1978–2004) crabs in the EBS derived from NMFS summer trawl survey data. Points east of 164°W are for red king crab. Arrows show long-term average flow patterns of the currents. The three depth contour lines are 50, 100, and 200 m.

advection appears to be an important process for red king and snow crabs, whereas, in general, retention appears to be important to Tanner crab.

Northward shifts and different spatial distributions of mature and juvenile females may partly explain recruitment variation for Bristol Bay red king crab and EBS snow crab. The shifts of spatial distributions of mature females make it difficult to supply larvae to the southern portions of their ranges. This not only reduces the number of suitable habitats to which larvae are delivered (Armstrong et al., 1993; Loher and Armstrong, 2005), but also slows juvenile growth due to relatively low temperatures in the north (Stevens, 1990), thus affecting recruitment strength.

Unlike red king and snow crabs, EBS Tanner crab nursery areas occur offshore on soft sediments. For larvae released offshore, retention may be favorable, but for those released along the Alaska Peninsula, advection helps them to reach their nursery areas. The mechanisms for offshore retention of larval Tanner crab are not entirely clear, as mean currents over the shelf are sluggish with a moderate northwesterly flow, at least over the outer shelf (Schumacher and Reed, 1992). The larvae of Tanner crab spawning near the shelf edge may be retained by clockwise circulation around the Pribilof Islands (Kowalik and Stabenro, 1999), thus facilitating settlement near the adults in that area. Rosenkranz et al. (1998) and Rosenkranz et al. (2001) showed that Tanner crab recruitment may be enhanced by NE winds during the larval period. Winds blowing from the northeast along the Alaska Peninsula during spring (May and June) promote coastal upwelling (perhaps favoring productivity) while advecting larvae offshore to their nursery areas. Years resulting in the two strongest year classes (1981, 1984) featured not only NE wind in spring, but also enhanced forcing of northward transport through Unimak Pass the previous winter, perhaps augmenting supplies of nutrients to the shelf prior to larval release (Bond and Overland, 2005). We updated the relationship between Tanner crab recruitment and NE winds with recent data (Fig. 8). The relationship is still statistically significant but the R^2 has decreased considerably (from 0.27 to 0.17). The weakened relationship may be partly due to the fact that few mature females have occurred in the Bristol Bay area since the early 1990s, so possibly a stock effect may be important now (Fig. 6b).

Two other processes have been proposed for explaining Tanner crab recruitment variation in the EBS (Rosenkranz et al., 1998, 2001): (1) warm bottom temperatures favor Tanner crab gonadal development and egg incubation; and (2) warm sea surface temperatures during spring promote increases in *Pseudocalanus* copepod nauplii, a primary prey of Tanner crab larvae, thus favoring feeding success of Tanner crab larvae due to higher prey densities. Statistically significant correlations exist between Tanner crab year classes and these temperatures (Rosenkranz et al., 1998, 2001).

3.4. Groundfish predation on crabs

During the period from mating to recruitment, many events can modify crab year-class strength. This may explain the weak relationships between recruitment and spawning biomass as well as individual environmental

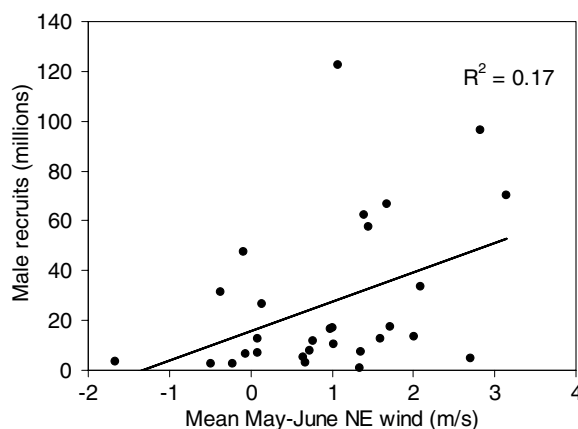


Fig. 8. Relationship between log-transformed male Tanner crab recruitment and the 60° component of the average May–June NE wind for years of hatching corresponding to 1969–1997. The wind was lagged to hatching years (7 years).

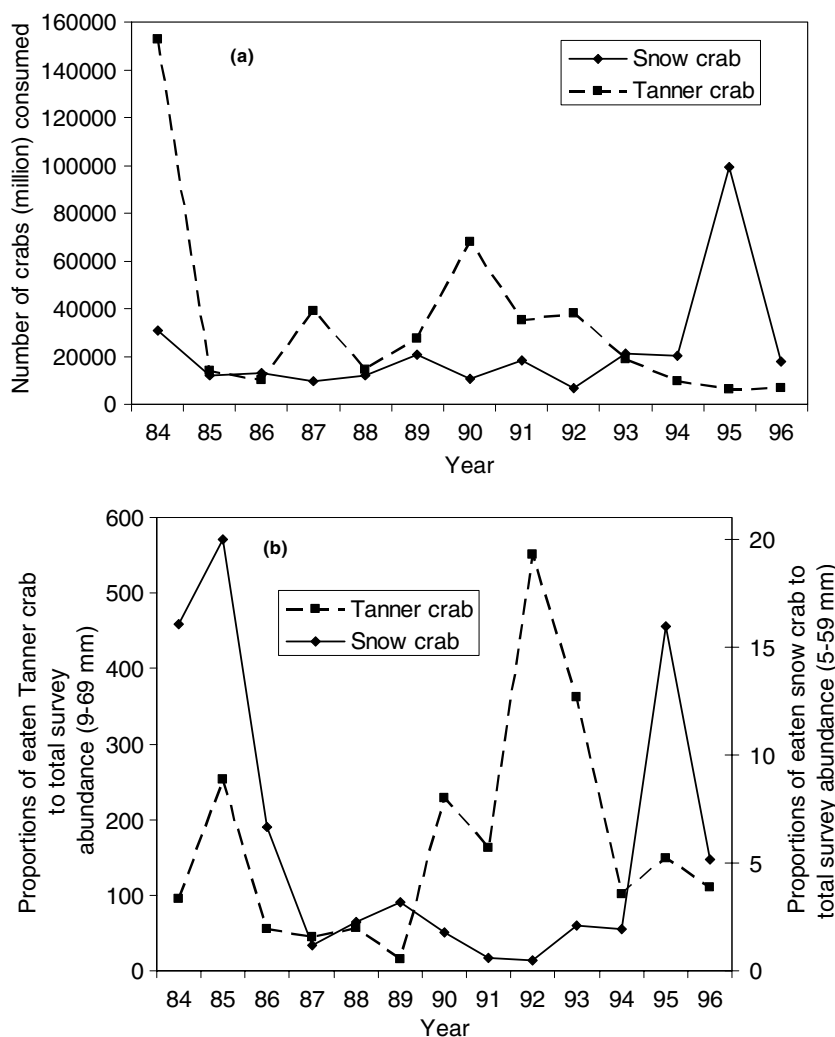


Fig. 9. Estimated number of Tanner (9–69 mm CW) and snow (5–59 mm CW) crabs consumed by groundfish during three months from May to September in the EBS and their proportions to corresponding survey abundances from 1984 to 1996. Data were obtained from Lang et al. (2003).

factors. One such event is groundfish predation. Groundfish consume crabs from the pelagic larval to adult stages. Based on routine examination of stomach contents of some groundfish species (Alaska plaice, arrow-tooth flounder, flathead sole, northern rock sole, Pacific cod, Pacific halibut, skates, walleye pollock, and yellowfin sole) in the EBS, huge amounts of early juvenile Tanner and snow crabs are consumed by groundfish each year during summer months, May to September (Lang et al., 2003). Based on data collected largely during summer, groundfish were estimated to consume up to 600 times the survey abundance of 9–69 mm carapace width Tanner crab and up to 20 times the survey abundance of 5–59 mm carapace width snow crab (Fig. 9). Predation on large crabs usually occurs during molting periods (Blau, 1986), which are generally during spring. Therefore, few large crabs are found in groundfish stomachs during summer months when sampling occurs and most of these are females. Because female red king crab molt later than males, sampling may bias against monitoring of predation on adult male red king crab relative to females. Likewise, juvenile red and blue king crabs are usually found in nearshore, shallow waters, where few samples of groundfish are taken. Thus, data are not available to estimate groundfish predation on juvenile king crabs.

Few statistically significant linear relationships exist between Pacific cod biomass and log-transformed crab recruitment in the EBS (Table 2). Excluding the significant relationships between Pacific cod and two blue king

Table 2

Correlation coefficients of Pacific cod biomass vs. log-transformed crab recruitment for 5 crab stocks in the EBS and levels of statistical significance of one-tailed *t*-test in parentheses

	Lagged to recruitment ages				
	0	1	2	3	4
1. Bristol Bay red king crab	−0.49 (*)	−0.59 (**)	−0.57 (*)	−0.51 (*)	−0.42 (ns)
2. Pribilof Is. blue king crab	0.72 (*)	0.62 (*)	0.39 (ns)	0.18 (ns)	0.02 (ns)
3. St. Mat. Is. blue king crab	0.59 (ns)	0.73 (*)	0.72 (*)	0.54 (ns)	0.37 (ns)
4. Bristol Bay Tanner crab	−0.02 (ns)	0.29 (ns)	0.47 (ns)	0.50 (ns)	0.51 (ns)
5. EBS snow crab	0.03 (ns)	0.15 (ns)	0.26 (ns)	0.29 (ns)	0.38 (ns)

Statistical significance levels are denoted as: ns for $p > 0.05$; * for $p < 0.05$; ** for $p < 0.01$.

crab stocks, which are contrary to our predation hypothesis due to positive sign, the only biologically meaningful, statistically significant correlations with Pacific cod involve Bristol Bay red king crab. Correlations are significant with recruitment time lags from ages 0 to 3 (Table 2). Correlations between yellowfin sole biomass and log-transformed Bristol Bay red king crab recruitment are also statistically significant with recruitment time lags from ages 0 to 2 ($r = -0.85, -0.83, -0.79$, and $p = 0.03, 0.04, 0.04$, respectively). The spatial distribution of yellowfin sole mainly overlaps with Bristol Bay red king crab and has not changed much over time. Higher Pacific cod and yellowfin sole biomass was associated with lower red king crab recruitment (Fig. 10).

Statistical significance does not necessarily imply biologically meaningful relationships. Multiple statistical tests increase the probability of Type I error. In a detailed study of predation and population trends, Livingston (1989) concluded that cod predation was not responsible for declines of red king crab in Bristol Bay in the early 1980s. Estimates of red king crab consumed by cod during 1981 and 1983–1996 (Livingston, 1991; Livingston et al., 1993; Livingston and deReynier, 1996; Lang et al., 2003) constitute only a very small proportion of the crab population. Most king crabs in cod stomachs are softshell females >80 mm carapace length (Livingston, 1989)—well beyond the size at which year class strength is determined. However, as noted earlier, the lack of red king crab in groundfish stomachs may also be due to sampling problems. Therefore, the lack of large numbers of early juvenile red king crab in groundfish stomach data obtained during summer months in offshore waters does not necessarily invalidate the apparent negative relationships between red king crab year-class strength and the biomass of Pacific cod and yellowfin sole. Groundfish stomachs must be sampled at the appropriate spatial and temporal scales to resolve questions about groundfish predation on juvenile king crabs. Interestingly, based on Fig. 9, a good case for control by predation exists for Tanner and snow crabs, since juveniles of both species are heavily preyed by Pacific cod. However, strong year classes of both crab species co-occurred with high cod biomass resulting in positive correlations (Table 2).

The lack of general inverse relationships between crabs and groundfish in the Bering Sea is largely attributable to the variety of patterns of year-class strengths among crab stocks (Fig. 2). Many groundfish populations experienced common patterns: strong year classes in the mid-1970s through the 1980s caused large increases in biomass throughout the 1980s, and moderate year classes in the 1990s caused a leveling off or decline in biomass in the 1990s. Year-class strength of most crab stocks declined from the early to mid-1970s, opposite the groundfish trend, but thereafter crab trends are stock specific. Year-class strength of St. Matthew blue king crab increased from the mid-1970s through 1990, whereas year-class strength of the Pribilof Islands stock continued its decline until the early 1980s; since then recruitment has been moderate through 1990. Year-class strength of Tanner crab increased sharply in the late 1970s to early 1980s and has since declined. Snow crab year-class strength was very high in the early and late 1980s but fell off in the early 1990s. Finally, year-class strength of red king crab continued to decline through the 1980s and then started to rebound. Several red king and Tanner crab stocks in the Gulf of Alaska had patterns similar to Bristol Bay red king crab with the exception that, during recent years, the recruitment rebounded somewhat for Bristol Bay red king crab and for some Tanner crab stocks in the Gulf, but there are no signs of rebound for red king crab stocks in the Gulf (Zheng and Kruse, 2000).

Spatial distributions of crabs and groundfish may also play an important role in groundfish predation on crabs. Like crab stocks, spatial distributions of groundfish stocks in the EBS have changed over time (Fig. 11). During recent years, biomass distribution centers of Pacific cod, flathead sole and arrowtooth flounder shifted

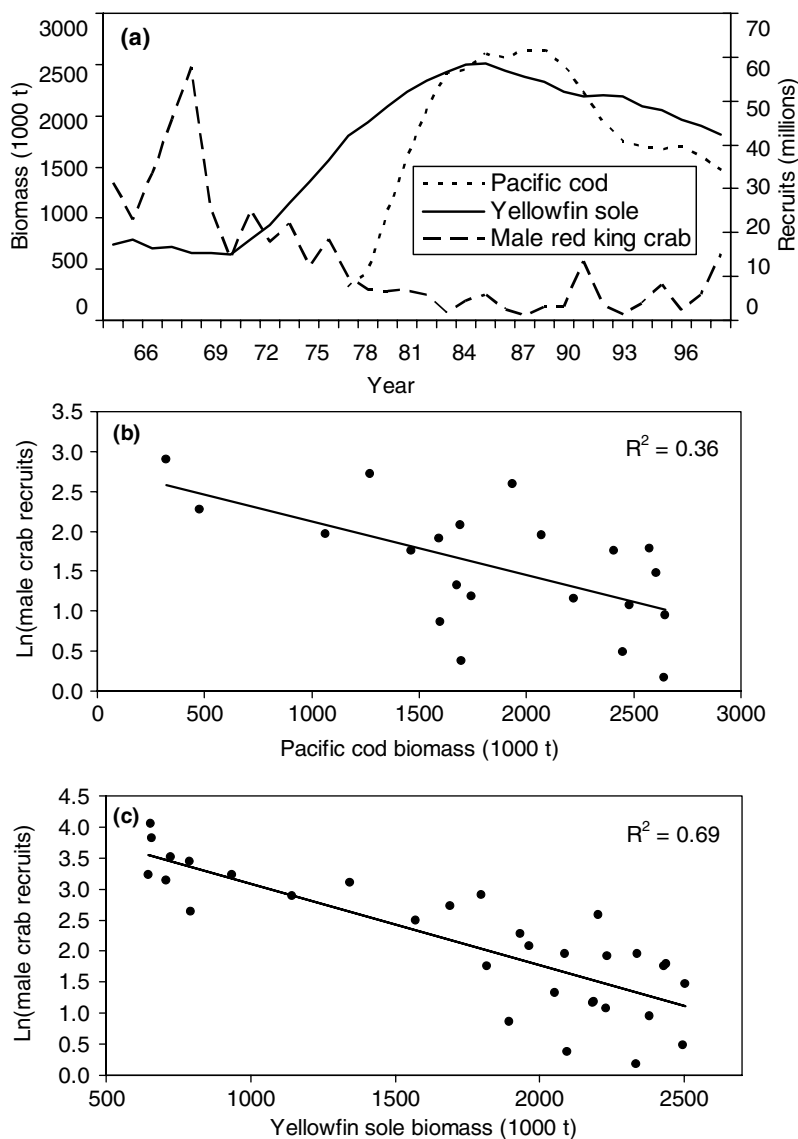
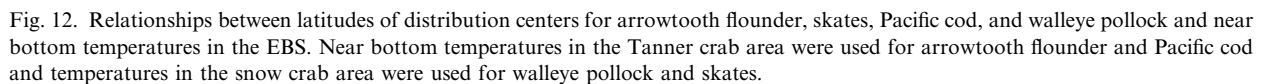
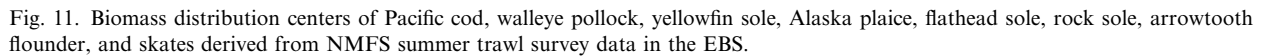


Fig. 10. Time series of (a) Pacific cod and yellowfin sole biomass in the eastern Bering Sea and Bristol Bay male red king crab recruitment, (b) relationship between Pacific cod biomass and log-transformed male red king crab recruitment, and (c) relationship between yellowfin sole biomass and log-transformed male red king crab recruitment.

to the northwest, those of rock sole, skates and Alaska plaice shifted to the northeast, whereas spatial distributions of yellowfin sole remained relatively stable (Fig. 10). The northward expansion for some groundfish seems to relate to warmer bottom temperatures, perhaps producing a northward extension of suitable habitat. With warmer temperatures, the center of groundfish spatial distributions moved farther to the north (Fig. 12).

Changes in spatial distributions of groundfish in the EBS are best illustrated by distributions of Pacific cod biomass from 1982 to 2004 (Fig. 13a). In the early 1980s, Pacific cod mainly occurred in shallow waters, <50 m, in the Bristol Bay area and in deep waters, >100 m, in the northwest of the EBS. However, during 1985–1988 and 1991–1996 the distribution of Pacific cod biomass was widespread across the shelf. In 1989 and 1990, few Pacific cod were found in the areas with juvenile snow crab (north and east of and around St. Matthew Island). In recent years, cod abundance concentrated in the north, around St. Matthew Island, and remained at a relatively low density in Bristol Bay. Pacific cod biomass was low around the Pribilof Islands only during 1982–1984.



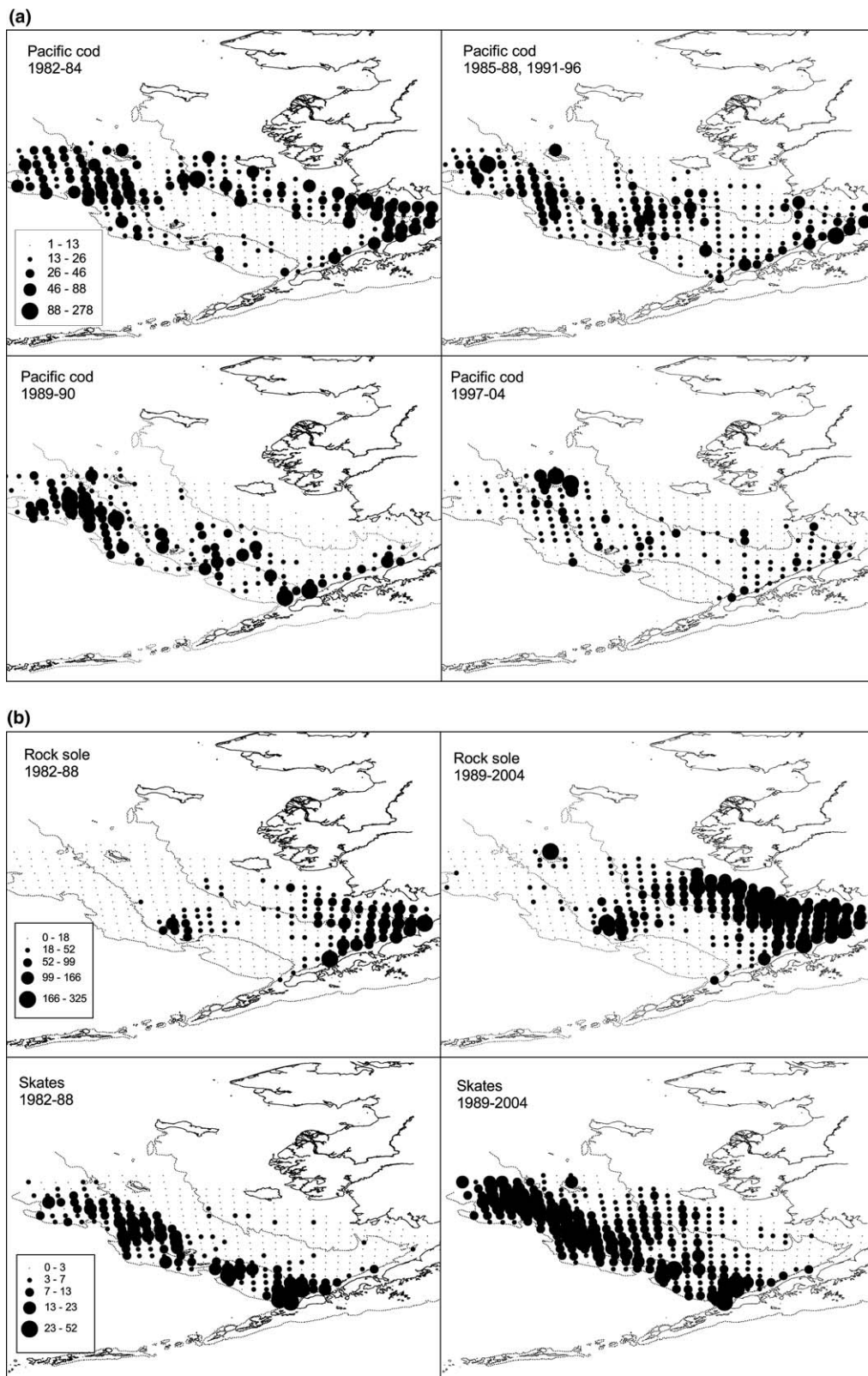


Fig. 13. Distributions of relative biomass of (a) Pacific cod and (b) rock sole and skates in the EBS from 1982 to 2004 derived from NMFS summer trawl survey data. Relative biomass is expressed as kg/ha. Three depth contour lines are 50, 100, and 200 m.

These changes in spatial distributions of Pacific cod may partly explain the weak correlations between Pacific cod biomass and crab recruitment. Even though Pacific cod biomass peaked in the early 1980s (Thompson and Dorn, 2003), they mainly occurred in the areas lacking high densities of juvenile snow and Tanner crabs. Both crab stocks had strong cohorts during the early 1980s. In fact, the strongest year classes of Tanner crab in the last 30 years were juveniles during the early 1980s. Likewise, strong snow crab cohorts in 1987 and 1988 may have benefited from a predominantly deep-water distribution of Pacific cod in 1989 and 1990. Although Pacific cod biomass in the EBS has decreased during the last decade, cod biomass around St. Matthew Island recently has been at its highest since 1982, which may continue to depress snow and St. Matthew blue king crab recruitment. Recent distributions of Tanner crab and Pribilof Islands blue king crab overlap with many groundfish stocks, which may make it difficult for cohorts of settling crab larvae to overcome a gauntlet of groundfish predators.

Other striking examples of changes in spatial distributions are provided by rock sole and skates (Fig. 13b). Rock sole mainly occurred in Bristol Bay and the Pribilof Islands in the 1980s. During the last 15 years, rock sole have expanded northward to St. Matthew Island. The biomass of skates has also increased greatly during the last 20 years and expanded northwards. Among other commercially important species, the biomass of arrowtooth flounder and flathead sole also increased during the 1980s.

4. Conclusions

Crab recruitment is likely to be a function of spawning biomass, fishing effects, larval survival, juvenile cannibalism, and predation. No single factor alone can consistently explain crab recruitment variation in the EBS, in part because most crab stocks have divergent recruitment patterns.

In this study, three hypotheses regarding climate forcing of larval survival were addressed in relation to crab recruitment variation: (1) years of strong wind mixing associated with intensified Aleutian Lows may depress Bristol Bay red king crab larval survival and subsequent recruitment; (2) the shifts of spatial distributions of mature females of Bristol Bay red king and EBS snow crabs make it difficult to supply larvae to the southern portions of their spatial distributions, thereby affecting recruitment strength; and (3) winds from the northeast along the north side of the Alaska Peninsula promote coastal upwelling, serving to advect inshore-hatched Tanner crab larvae offshore to nursery areas of fine sediments. Support for the first hypothesis comes mainly from the general correspondence between strong red king crab year classes prior to the 1976/77 regime shift (period of weak Aleutian lows), and weak year classes since then (period of strong Aleutian lows) with the exception of a strong 1990 year class that also corresponded to a brief (1989–1991) period of weakened Aleutian low intensity. Support for the second hypothesis comes from the fact that snow and red king crab nursery areas (indexed by concentrations of juveniles) occur downstream of centers of distributions of adults and that, since the 1970s, adult red king crab shifted from southern to central Bristol Bay and adult snow crab shifted to the northwest along the middle and outer shelf; both shifts are downstream of prevailing currents in their respective regions. Finally, support for the last bottom-up hypothesis is attributable to a statistically significant relationship between the mean NE wind during the larval period (May–June) and subsequent Tanner crab recruitment, lagged 7 years corresponding to year of hatching.

Groundfish predation may play an important role for crab recruitment success in the EBS. However, dynamic and divergent spatial distributions of groundfish and crabs over time confound our ability to relate crab recruitment strength to groundfish biomass. Support for top-down control includes: (1) crab cohorts in the late 1960s were all strong for six stocks when groundfish biomass was low; (2) statistically significant relationships between Bristol Bay red king crab recruits and Pacific cod biomass and yellowfin sole biomass; and (3) large amounts of Tanner and snow crabs are consumed by groundfish. On the other hand, both snow and Tanner crabs had some strong year classes in the 1980s after groundfish abundance increased, and analyses of groundfish stomach contents indicate that too few red king crab are consumed to explain recruitment fluctuations. However, the weak relationships between snow and Tanner crab recruitment and groundfish abundance may relate to a lack of geographic overlap between groundfish predators and crab prey when groundfish initially increased (1980s), and a lack of groundfish stomach collections in shallow nursery areas for red king crab may explain the low occurrence of juvenile red king crab in sampled groundfish stomach contents.

Based on our exploratory data analyses, available evidence supports a mix of climate forcing and top-down control on EBS crab recruitment. However, these findings remain provisional until these hypotheses can be tested more comprehensively. To do so, we propose the following needed research. Field studies of groundfish predation on young juvenile king crabs are needed during spring in shallow waters of Bristol Bay and around St. Matthew and Pribilof Islands. Rather than additional correlation studies, computer simulations are needed to evaluate the role of ocean currents on crab larval distributions and settlement relative to nursery areas. To test the climate forcing hypotheses, field studies are necessary to document relationships among climate indices, winds, *Thalassiosira* diatom abundance, and red king crab larval feeding success and survival, and among surface temperature, abundance of *Pseudocalanus* copepod nauplii, and Tanner crab larval feeding success and survival in the Bering Sea. Spatially explicit, multi-species models of groundfish predation effects on crabs based on their dynamic distributions may provide understanding of the top-down control on the crab recruitment in the EBS. Additional field studies on the location and habitat characteristics of crab nursery areas would strengthen the advection and predation modeling.

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