

Historical changes in the abundance and distribution of ovigerous red king crabs (*Paralithodes camtschaticus*) in Bristol Bay (Alaska), and potential relationship with bottom temperature

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ABSTRACT

Distribution and abundance of ovigerous female red king crabs (*Paralithodes camtschaticus*) in the southeast Bering Sea from 1975 to 2001 were investigated using data collected during National Marine Fisheries Service annual trawl surveys. Peak abundance of ~140 million crabs was observed in 1978, and declined rapidly to a low of just over 6 million in 1986. Abundance fluctuated from ~6 to 22 million from the late 1980s through 2001, with a single strong recruitment event that resulted in ~35 million ovigerous females observed in 1998. Changes in abundance were accompanied by changes in distribution. During the late 1970s the population was typified by high abundance to the southwest, along the northern shore of Unimak Island and the Alaska Peninsula. By the mid-1980s the population's average center of abundance shifted substantially to the northeast and was found in central Bristol Bay. The distribution remained similar throughout the 1990s. Changes in distribution during the late 1970s and early 1980s coincided with changes in early summer near-bottom temperature. The 1970s were typified by a pool of very cold water (<1°C) within central Bristol Bay. This retreated in ~1978, and was not observed in consecutive summers during the remainder of the time series. The northeastward shift in the population, measured as the distance between Unimak Pass and the average center of abundance, showed a negative correlation with the geographic extent the cold-pool. Abundance calcula-

ted for smaller spatial strata indicate that changes in distribution were not simply the result of relative abundance phenomena or solely generated by mortality in southwestern Bristol Bay, but also reflected regional increases in absolute abundance. Total broodstock abundance declined after 1978, but abundance in the western and northern areas of the region increased until at least 1982. The fact that distribution patterns change over time may have implications for population dynamics and fishery management. Changes in spatial population structure may affect recruitment patterns via changes in larval dynamics, and management might benefit if the causes of geographic displacement can be identified and predicted.

Key words: distribution, ovigerous, *Paralithodes camtschaticus*, red king crab, water temperature

INTRODUCTION

Spatio-temporal variation in the distribution of marine populations is a common occurrence that can have important economic and ecological ramifications. The collapse of the southern Newfoundland winter fixed gear fishery for Atlantic cod (*Gadus morhua*) provides a classic example demonstrating that fisheries can be particularly sensitive to temperature-dependent changes in distribution. Between 1983 and 1991, a period of extensive cooling, the mean wintertime bottom temperature in the shallow coastal waters of southwest Newfoundland decreased by about 2°C. Over the same period the proportion of the cod stock observed in nearshore waters fell from around 60% to nearly 0%. As a result, the stock became unavailable to a fleet comprised of relatively small vessels operating along the coast and total landings fell from a long-term mean of ~5000 t to complete fishery failure in 1991 (Fréchet and Gagnon, 1993). While the large-scale stock decline in northwest Atlantic cod has been largely attributed to overfishing (e.g. Hutchings, 1996), the initial dynamics of the inshore fishery demonstrated

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Received 18 July 2002

Revised version accepted 7 September 2004

considerable vulnerability to shifts in distribution driven by environmental conditions.

In addition to the direct impact that shifting stocks can have on local fisheries, important indirect effects may also occur. The distribution of spawners can influence recruitment by determining regional larval abundance and subsequent recruitment strength (Jackson *et al.*, 2001). Spatial patterns of larval release can influence survivorship because of the predator conditions into which the larvae are released (Ince *et al.*, 1987) or alter larval delivery patterns (Rothlisberg *et al.*, 1994). The results may be persistent for species with limited mobility (McGarvey *et al.*, 1993), or whose larvae are attracted to adult conspecifics at settlement (Jensen, 1991). Stock distribution may also determine fishery conflicts and bycatch (e.g. Armstrong *et al.*, 1993), and have implications for the effectiveness of spatially structured management options such as area closures, exclusion zones, and Marine Protected Areas.

In the southeast Bering Sea, a striking decline in the abundance of red king crabs (*Paralithodes camtschaticus*) in the late 1970s was accompanied by changes in population spatial structure. The commercial red king crab fishery harvests only males, and between 1978 and 1983 mature male abundance declined by roughly an order of magnitude, from >80 million to <10 million crabs (Fig. 1). Commercial catch during the same period closely followed male abundance (Fig. 1), while the abundance of large females (>90 mm carapace length) declined from ~130 million to <10 million individuals (Stevens *et al.*, 1994). Dramatic stock declines resulted in complete closure of the fishery in 1983, and later a management plan aimed at rebuilding the population (Zheng *et al.*, 1997). Despite substantially reduced harvests since the closure, the population has not rebounded to historical abundance. Maximum observed abundance of harvestable males has remained

fairly low and stable since the late 1980s, peaking in 1998 because of a strong year class that settled in 1990 (Loher *et al.*, 2001). Despite lower male abundance in 2003, commercial harvest was very similar to 1998 because of nuances of harvest strategy and incremental changes in the applied exploitation rates (Bowers, 2003).

The mechanisms that presently regulate the abundance of Bristol Bay red king crabs remain largely unknown, but the importance of spatial dynamics deserves more consideration. A shift in the geographic distribution of females occurred concurrently with the stock decline (Hsu, 1987; Armstrong *et al.*, 1993), and it is possible that a functional link exists between spatial abundance patterns and recruitment. It has been hypothesized that a late 1970s northeastward shift in female distribution altered larval production and delivery patterns, changing the relative importance of different regions in generating recruitment (Hsu, 1987; Armstrong *et al.*, 1993). Yet, the causes and impacts of the spatial shifts remain unknown, and the persistence of the changes has not been addressed since Hsu (1987). In this study, we examine changes in spatial distribution of ovigerous red king crabs in the southeast Bering Sea from 1975 to 2001, with attention to potential temperature-dependent responses, and with attention to the possibility that changes might represent density-dependent responses.

MATERIALS AND METHODS

Data

Bering Sea red king crab abundance is monitored by the National Marine Fisheries Service (NMFS) via annual trawl surveys. Data for 1975–2001 were obtained from NMFS, and for our analyses Bristol Bay was defined as Bering Sea waters east of 166.0°W Lon and south of 59.4°N Lat. The survey has consistently

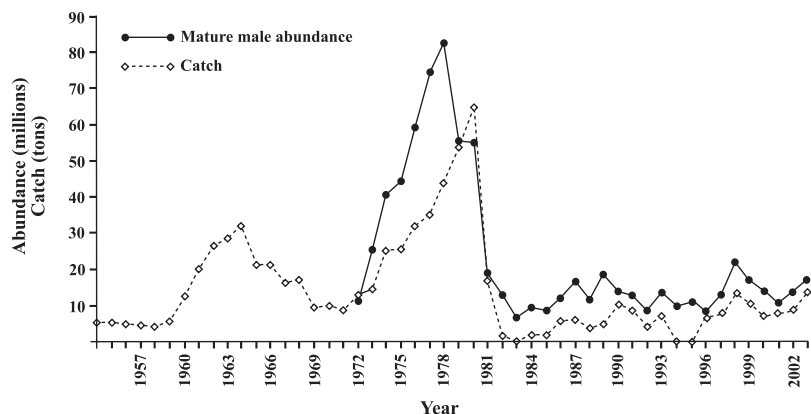


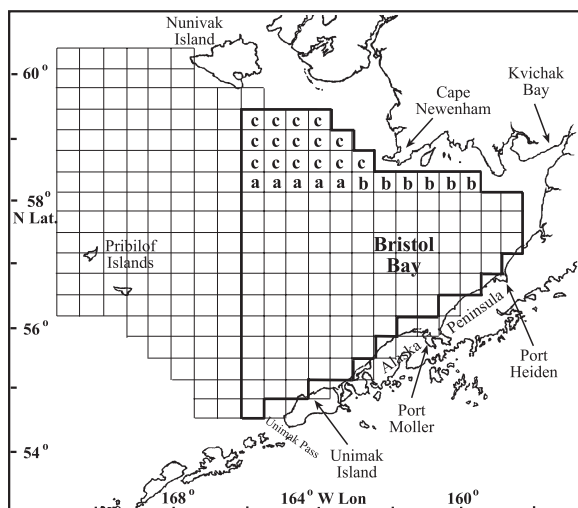
Figure 1. Abundance of mature male red king crabs estimated from area swept methods and directed fishery catch in the Bristol Bay region (adapted from Zheng and Kruse, 1999; Granath, 2002; Bowers, 2003).

visited 119 stations in this area covering $\sim 160\,000\text{ km}^2$ (Fig. 2). Fourteen additional stations, mostly along the Alaska Peninsula, have been visited only sporadically; we did not include these 14 stations in our analyses. All analyses only include females that carried an egg clutch (i.e. ovigerous 'broodstock') at the time of the survey, because we aim to describe changes that might have resulted in altered larval production patterns.

Population abundance, density, and geographic range

A distinction is made between 'abundance' and 'density': density refers to number of crabs per square kilometer, whereas abundance is the estimated total number of crabs in an area of specified extent. Abundance is reported for the entire region, as well as for smaller areas (strata) comprised of a number of stations. Population structure was examined by comparing abundance and density to geographic range, where range was defined as the proportion of survey stations inhabited by broodstock. Relationships between range, density and abundance were examined using ordinary least squares regression with tests of serial autocorrelation via the Durbin–Watson statistic

Figure 2. Geography of the southeast Bering Sea and coverage of the National Marine Fisheries Service eastern Bering Sea groundfish trawl survey. Tows are normally conducted near the center of each quadrant, each of which measures $\sim 1372\text{ km}^2$. The dark outline indicates the 119 stations typically visited in the Bristol Bay region. Note that 1979 was the first year all 119 stations were sampled; northern station-lines were not visited earlier, nor in 1981. Stations (a) were not visited during 1975, 1976 or 1978; stations (b) were not visited from 1975 to 1978; stations (c) were not visited from 1975 to 1978, nor in 1981.



(Montgomery *et al.*, 2001). Effective sample size (i.e. degrees of freedom) was adjusted prior to significance testing (Bence, 1995) because autocorrelation was detected in all time series.

Population density at each station (station CPUE) was estimated as number of crabs captured divided by area swept, station abundance as CPUE multiplied by quadrant area (1372 km^2), and total abundance within larger areas as the summed abundance of the quadrants comprising them. In most years, only one tow was conducted at each station, but stations were occasionally re-sampled within years. In cases where a station was re-sampled over the course of a few days, CPUE was calculated as mean CPUE of all tows. If a station was re-sampled in late summer following the May/June survey, only the earliest sampling date was used to avoid bias associated with re-sampling mobile fauna.

To determine if annual distributions were statistically different from one another, pairwise year-by-year comparisons were conducted using a Monte Carlo analysis developed by Syrjala (1996). Test statistics and *P*-values were calculated based on both the Cramer–von Mises (C–vM) and Kolmogorov–Smirnov (K–S) non-parametric test for a difference between two univariate probability distribution functions (Conover, 1980). Results of both are reported, but the K–S test is more sensitive to rare, large density observations (Syrjala, 1996). The C–vM test is preferred because of the contagious distribution of red king crabs. C–vM is less likely to yield significance when distributions do not differ (Syrjala, 1996). Comparisons were conducted using QuickBasic GeoDistn (S.E. Syrjala, NMFS-WASC, Seattle, WA, USA), with 1000 simulations per test.

Average central weighted distribution and dispersion

Changes in geographic displacement were examined using an 'Average Central Weighted Distribution' (ACWD) representing the annual center of abundance. ACWD was calculated by averaging the latitude and longitude of all stations where crabs were captured, weighted by abundance at those stations. Spatial distribution was further investigated using a dispersion index (McConnaughey, 1995) representing the CPUE-weighted average distance between individuals and the ACWD. Dispersion is a composite of a number of population attributes, including the extent of the population relative to total abundance (i.e. mean population density), the shape of the distribution, and patterns of aggregation within the population. Dispersion was calculated as:

$$\text{dispersion} = \left\{ \frac{\sum_1^i (\text{CPUE}_i \times \text{Dist}_{i(\text{station}_i, \text{ACWD})})}{\sum_1^i \text{CPUE}_i} \right\}$$

where, $\text{CPUE}_i = \text{CPUE}$ (crabs km^{-2}) at station i , $\text{Dist}_{i(\text{station}_i, \text{ACWD})} = \text{distance}$ (km) between station i and the population ACWD.

As with the bivariate relationships described previously, relationships between dispersion, year and abundance were examined using ordinary least squares following adjustment for serial autocorrelation.

Interannual variability in Bristol Bay early summer near-bottom temperatures

Summer near-bottom temperature data were obtained from NMFS Bering Sea trawl surveys. Data were available for other seasons, but these data were generally restricted to the shelf break and did not provide reasonable coverage of Bristol Bay. NMFS survey data provided complete coverage throughout the period of interest. Early summer temperatures were used as a proxy for conditions during the preceding winter and spring. Cold bottom water is generated during sea ice formation, becomes insulated from surface heating by the spring thermocline, and persists throughout the following summer (Azumaya and Ohtani, 1995; Wyllie-Echeverria and Ohtani, 1999). Thus, interannual variation in summer bottom temperature is strongly correlated with atmospheric conditions the preceding winter (Azumaya and Ohtani, 1995). Analyses were restricted to short time spans to avoid incorporating temporal biases because spurious spatial trends could be generated by vessels moving in a set direction across the region over a protracted sampling period. Data were selected over the shortest period that provided reasonable spatial coverage, centered on June 15. The selected period was typically 3–5 weeks. Temperature plots were constructed using Surfer 6.04 (Keckler, 1994), with isotherms interpolated via kriging using a linear variogram model.

Temperature, broodstock distribution, and spatially stratified abundance

Annual measures of mean temperature throughout the whole of Bristol Bay and mean temperatures experienced by crab were calculated for the entire time series. Whole-area mean temperature is simply the average of survey values observed at each trawl station. Mean temperature experienced by ovigerous crabs was calculated by weighting each temperature observation by the observed density of ovigerous females at that survey station. Comparisons were also conducted

between broodstock distribution and extent of cold bottom water. Annual isothermal plots were digitized to estimate the region inundated by water $\leq 2^\circ\text{C}$, and these areas were compared to the geographic distance between that year's ACWD and Unimak Pass. Isothermal plots were then qualitatively examined for spatio-temporal patterns suggestive of persistent or extreme conditions that might shape crab distribution. This suggested a number of discrete regions (strata) with respect to the thermal environment. Abundance was calculated for each stratum and compared with the trend for all strata combined (i.e. the 'composite' population).

RESULTS

Population abundance, density, and geographic range

Estimated broodstock abundance (Fig. 3) peaked in 1978 at ~ 140 million and declined to ~ 6 million individuals by 1986. From 1987 to 2001, abundance remained comparatively low and stable, fluctuating between ~ 6.4 and ~ 35.3 million crabs. During the 1970s large concentrations of females were located along the Alaska Peninsula, from Unimak Pass to east of Port Moller (Fig. 4), but beginning in ~ 1980 , the population retreated from Unimak while shifting offshore. The early 1980s were typified by distributions that rarely extended west of $\sim 164^\circ\text{W}$ Lon, and by the early 1990s the distribution became consistently restricted to central Bristol Bay. The population displayed little qualitative change in distribution over the last 12–15 yr.

A strongly positive relationship was observed between abundance and mean population density

Figure 3. Estimated abundance of broodstock (ovigerous females), 1975 to 2001, using area-swept methods and National Marine Fisheries Service survey data. Open symbols connected by dashed lines indicate years during which the survey coverage was of lesser extent than the other years in the time series.

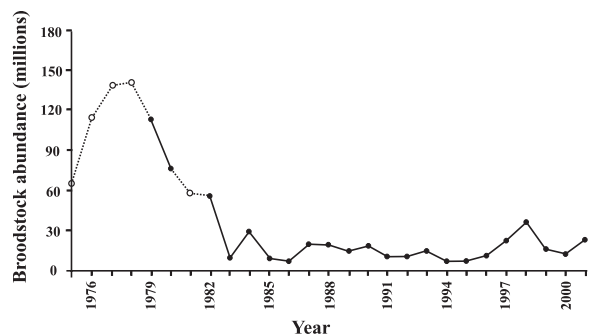


Figure 4. Distribution of broodstock (ovigerous females) plotted as population density surfaces. Note that vertical axes represent different scales, because the maximum population density observed during each year was variable; all plots have been scaled to a uniform height.

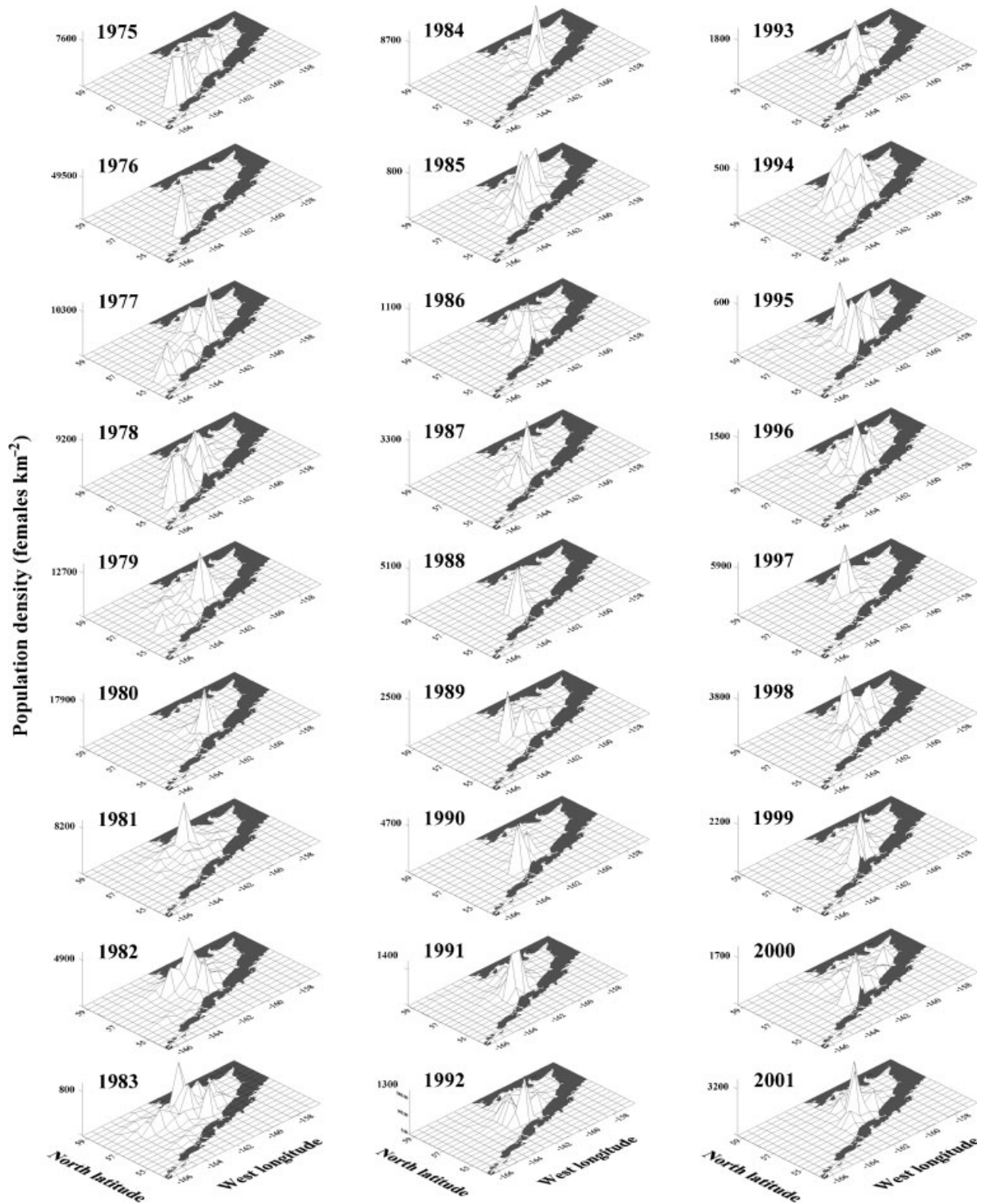


Figure 5. Relationship between total broodstock abundance and mean population density (a), and between abundance and the range of the stock (b), where range was the proportion of survey stations at which broodstock was captured.

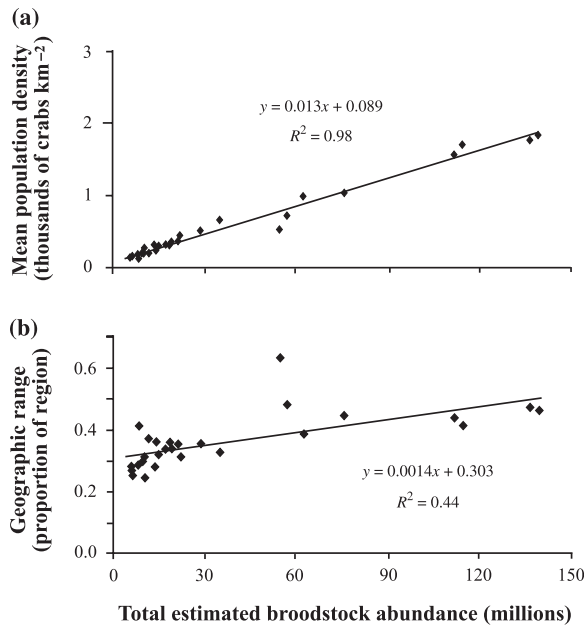
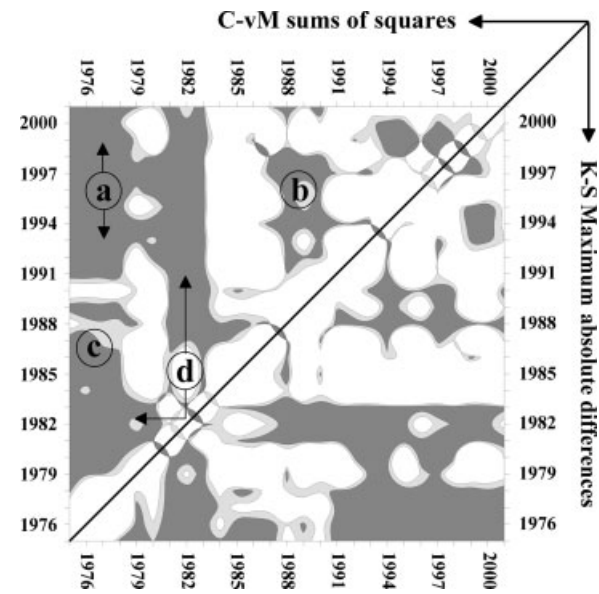


Table 1. Statistics for linear least squares regressions presented in Figs 5 and 8.

Comparison	R ²	F	Residual df*	P-value
Density versus abundance	0.98	772.92	17	<<0.0005
Range versus abundance	0.44	9.40	12	<0.01
Dispersion versus year	0.28	5.01	13	<0.05
Dispersion versus abundance	0.41	12.39	18	<0.0025

(Fig. 5a; Table 1). A weak positive relationship was observed between abundance and total geographic range, with a 20-fold decrease in abundance resulting in only ~20% reduction in range (Fig. 5b; Table 1). Statistical analysis of annual spatial distributions (Fig. 6) indicated numerous pairwise differences, but only seven of 26 comparisons between consecutive years were significant at the 0.05 level. Rather, larger-scale temporal patterns were apparent in which groups of years were similar to one another and different from other periods (Fig. 6). Four regions of contrast were apparent: (1) distributions in the 1970s differed from those after 1990; (2) distributions in the late 1980s differed from those after 1990; (3) 1985–89 differed from 1975–78; (4) 1981–83 contrasted with most other years.

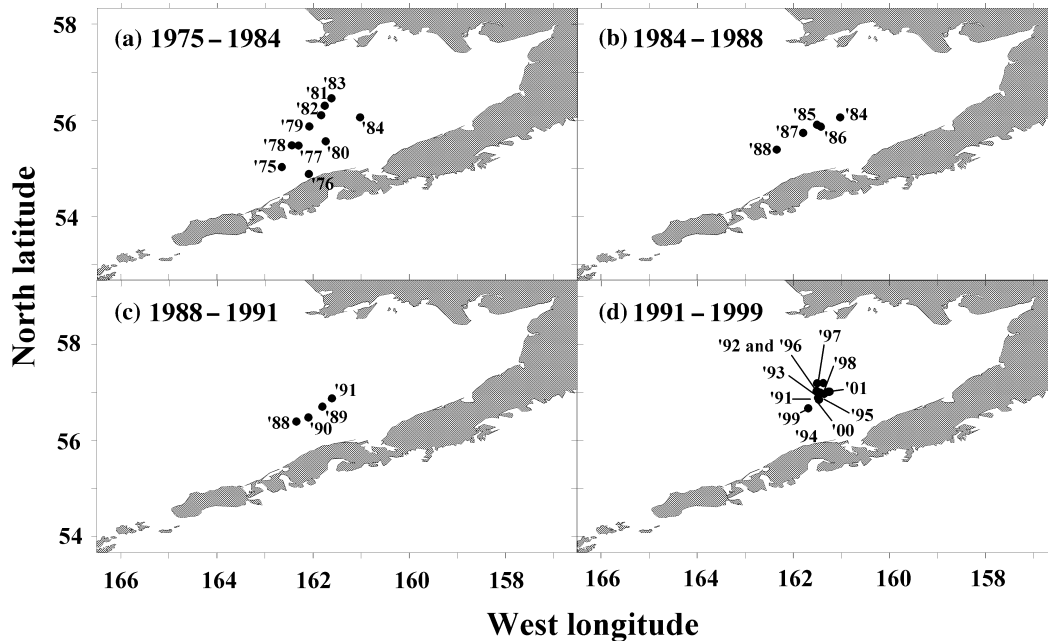
Figure 6. Significance of year-versus-year comparisons of broodstock distribution in Bristol Bay, determined via Geo-Distn (Syrjala, 1996). Smoothed isolines were drawn around values of equal significance: dark fill, $P < 0.05$; light fill, $0.05 \leq P \leq 0.10$; open, $P > 0.10$. The upper half represents results determined from the Cramer–von Mises method; the lower half displays the Kolmogorov–Smirnov test. Four regions have been noted: (a) distributions from the 1970s tended to differ from those after 1990; (b) distributions during the late 1980s differed from those after 1990; (c) 1985–89 contrasted with 1975–78; (d) 1981–83 tended to differ from other years.



Average central weighted distribution and dispersion

Over the 27-yr time series the population underwent four periods of population shift; these shifts are depicted in Fig. 7, which represents an update of an analysis presented in Armstrong *et al.* (1993). Substantial displacement toward the northeast occurred from 1974 to 1984, with the most rapid displacement from 1975 to 1981. The ACWD reached its most northerly location in 1983, and most easterly in 1984 (Fig. 7a). Total displacement between 1975 and 1984 was ~150 km, after which the ACWD drifted ~110 km back to the southwest (Fig. 7b), reaching a location in 1988 that was nearly equivalent to that observed in 1977. From 1988 to 1992 the population shifted ~85 km northeastward (Fig. 7c), and remained relatively stationary thereafter (Fig. 7d). Dispersion was highest during the 1970s, and somewhat lower throughout the 1980s and 1990s (Fig. 8a; Table 1). Highest dispersion was observed in 1977 and the lowest in 1997, and weak but significant decrease was observed across the time series. A

Figure 7. Average Central Weighted Distribution of broodstock, demonstrating displacement over time. The number placed beside each point indicates the year. The population shifted to the northeast from the mid-1970s through the early-1980s (a), back to the southeast during the late-1980s (b), returned to central Bristol Bay by the early-1990s (c), and remained there through 2001 (d).



slightly stronger positive relationship existed between dispersion and broodstock abundance (Fig. 8b; Table 1).

Interannual variability in Bristol Bay early summer near-bottom temperatures

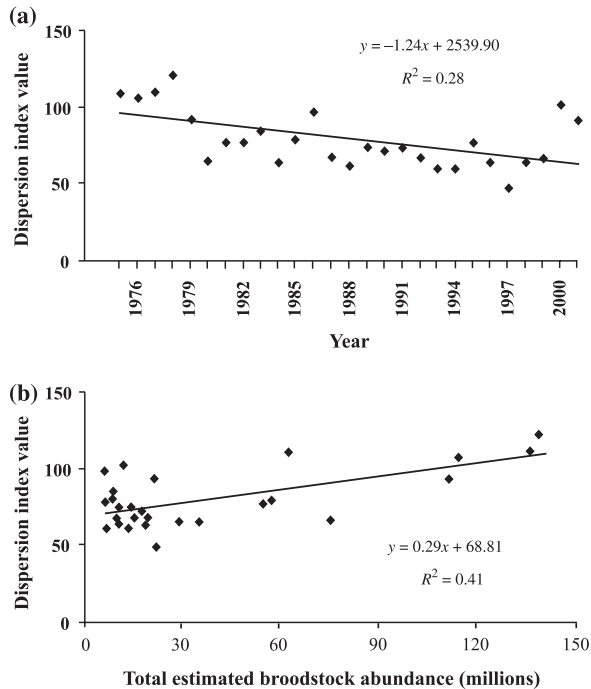
Mean temperature was coldest during the mid-1970s, reaching a low of $\sim 0.5^{\circ}\text{C}$ in 1976 (Fig. 9). Average conditions experienced by broodstock, as a density-weighted mean, actually remained above 2°C during the 1970s, owing to the population's shoreward and southwesterly distribution. During all years, warmer temperatures were found along the coastline than in central Bristol Bay and the northwest (Fig. 10). In some years the central cold-water region was comprised of sub-zero temperatures, apparently representing a tongue of cold pool waters intruding from the northwest. At the cold-tongue's greatest extent (e.g. 1975, 1976, and 1999), temperatures $<1^{\circ}\text{C}$ were observed nearshore, along the Alaska Peninsula from about Port Moller through Port Heiden. Unimak Pass to southeast of the Black Hills did not experience these extreme early summer conditions at any time. Interannual variability in the thermal regime was considerable. In some years temperatures of -1°C were common (e.g. 1976) whereas in others (e.g. 1979) temperatures below 3°C were not observed at any location.

Temperature, broodstock distribution, and spatially stratified abundance

During 1976, the coldest year in the time series, nearly 80% of the region was estimated to have experienced near-bottom temperatures $\leq 2^{\circ}\text{C}$. At the same time, the population displayed its most southerly and shoreward location (refer to Figs 4, 7 and 10). The northeasterly shift in broodstock distribution observed during the late 1970s was coincident with the retreat of the cold-pool from the region. Between 1975 and 1981 the population's mean distance from Unimak Pass increased markedly while the extent of near-bottom temperatures $\leq 2^{\circ}\text{C}$ rapidly declined (Fig. 11).

Six spatial strata were identified that appeared relevant to the dynamics of cold-tongue intrusion, as indicated by the 3-yr mean early summer near-bottom temperature profile constructed for the coldest period observed, 1974–76 (Fig. 12). These strata were as follows: (1) Southwest: coastal waters from Unimak Pass to just south of Port Moller, characterized by mean temperatures of $0\text{--}5^{\circ}\text{C}$; (2) Southeast: coastal waters from just south of Port Moller to Port Heiden; mean temperatures $1\text{--}2^{\circ}\text{C}$; (3) West Central: core of the cold-tongue; mean temperatures $0.5\text{--}1.5^{\circ}\text{C}$; (4) Central: eastern tip of the cold-tongue; mean temperatures of $0\text{--}1.5^{\circ}\text{C}$; (5) Northeast: coastal waters

Figure 8. Change in population dispersion displayed by Bristol Bay red king crab broodstock. Highest dispersion was observed in the 1970s and decreased significantly thereafter (a; Table 1). A significant positive relationship existed between dispersion and total broodstock abundance (b; Table 1).



from Kvichak Bay through Cape Newenham; mean temperatures similar to the Southwest stratum; (6) Northwest: waters west of Cape Newenham and north of the cold-tongue; mean temperatures of 0–2°C.

Estimated broodstock abundance trajectories were similar across strata in the sense that peak abundance was observed early in the time series, fell by the mid-1980s, and remained low thereafter (Fig. 13). However, the timing of peak abundance was different in

each stratum. Whereas peak abundance of the composite broodstock occurred in 1978 (refer to Fig. 3), this was only matched in the central strata. Peak abundance was observed earlier in the south and later in the north. It was not possible to determine precise timing in the northern strata because of incomplete survey coverage from 1975 to 1978 and in 1981 (refer to Fig. 2). However, peak abundance in the Northeast stratum occurred in either 1981 or 1982, at least 3–4 yr later than the composite broodstock peak. A substantial increase in broodstock abundance was observed in the West Central stratum in 1984, and the relatively strong recruitment of 1997–98 was observed primarily in the Southeast, Central, and West central strata.

DISCUSSION

Shift in distribution

The shifts in distribution first documented by Hsu (1987) and presented in Armstrong *et al.* (1993) proved significant and persistent. During the late 1970s and early 1980s, a potentially important component of the broodstock population located along the north shore of Unimak Island essentially disappeared (refer to Fig. 4). Subsequently, the majority of broodstock has been located to the northeast, near the center of Bristol Bay. An apparent redistribution towards the southwest in late 1980s was only transient. Since 1989 the population has remained relatively stationary with the majority of individuals found north of Port Moller. It should be noted that early in the time series the NMFS trawl survey did not visit the most northerly stations and so distributions may be artificially biased toward southerly locales. However, in 1979 no crabs were found in the four northernmost survey lines indicating that the 1975–78 metrics were probably accurate. In 1980, <0.3% of the ovigerous

Figure 9. Mean bottom temperature for the entire Bristol Bay region (solid line and open circles) and the density-weighted mean temperature experienced by ovigerous red king crabs (dashed line and solid diamonds), 1975–2001 (data source: National Marine Fisheries Service Bering Sea trawl surveys).

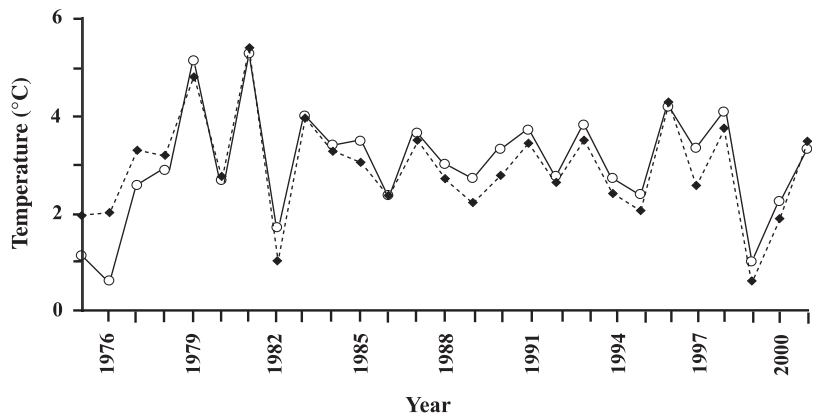


Figure 10. Early summer near-bottom temperature patterns constructed for the Bristol Bay region, 1974–2001. Each year’s plot represents a sampling period of 3–5 weeks, grouped around a target date of June 15.

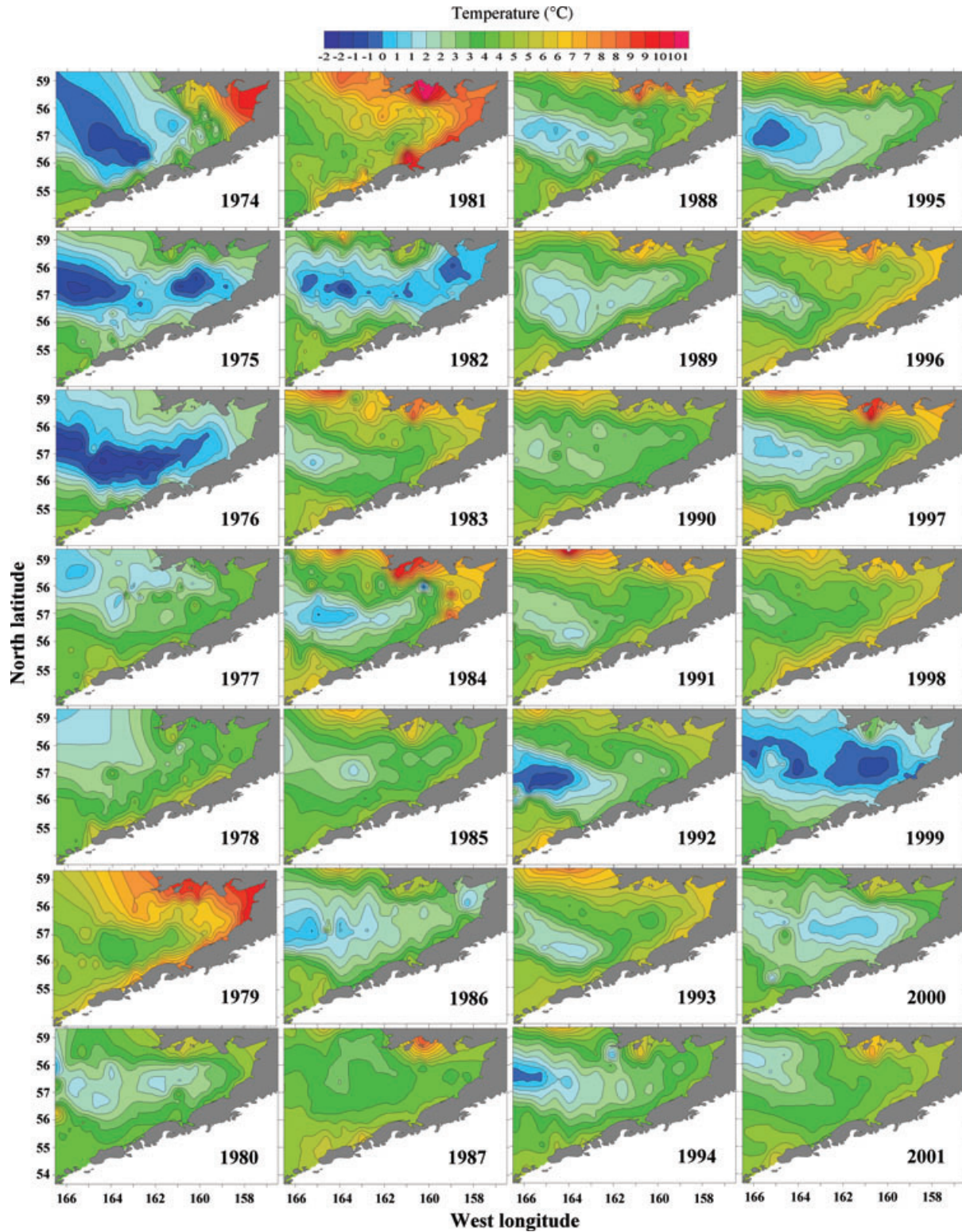
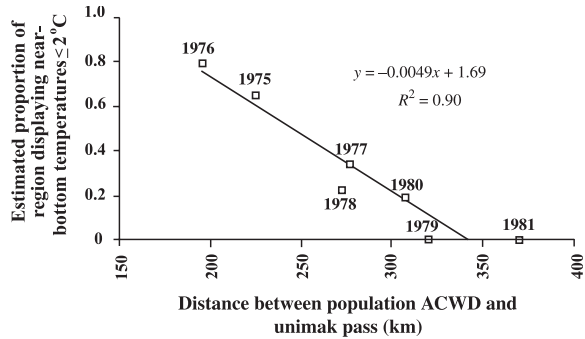


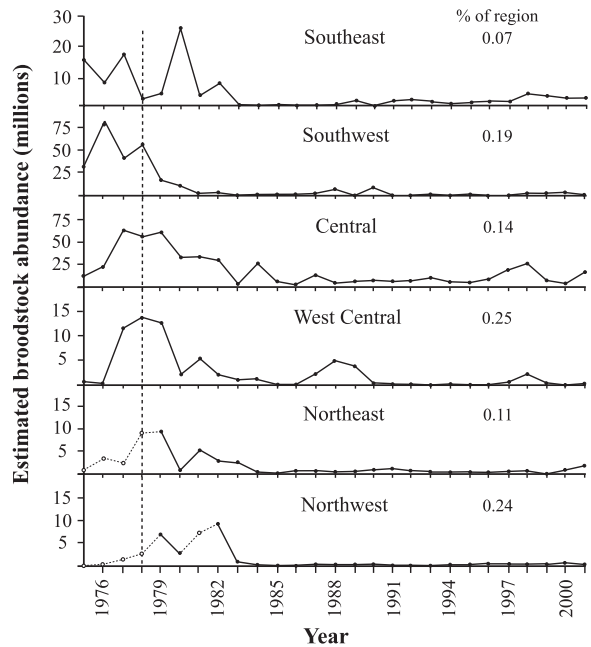
Figure 11. Relationship between the proportion of the Bristol Bay region experiencing near-bottom temperatures $\leq 2^{\circ}\text{C}$, and the northeasterly shift of the broodstock population from 1976 to 1981, expressed as the geographic distance between Unimak Pass ($54.5^{\circ}\text{N Lat} \times 165.0^{\circ}\text{W Lon}$) and the population's Average Central Weighted Distribution.



population was located in the three northernmost survey lines (the stations omitted in 1981), whereas in 1982 ~5% of broodstock was located at these stations. It is reasonable to suspect that 1981 abundance was slightly underestimated, but it is highly unlikely that overall abundance trends or the northward shift in distribution were artifacts of survey design.

According to the Fretwell–Lucas theory (Fretwell, 1972) a population's distribution should be a function of habitat suitability and abundance. If individuals choose location based upon habitat suitability, areas of greatest suitability will define the center of the range and, in the face of competition, increased abundance will cause marginal habitats to become more attractive. The resultant population expansion has been likened to water rising in a basin (MacCall, 1990),

Figure 13. Spatially stratified estimates of broodstock abundance. The value on the upper right of each plot indicates the relative size of each stratum, expressed as the percentage of the Bristol Bay region it comprises. The vertical dashed line indicates the year of maximum observed composite abundance. Open symbols connected by dashed lines indicate years during which trawl survey coverage was of lesser extent than the other years in the time series; abundance may be underestimated for these years.



where similar habitat suitability over broad distances causes individuals to spread rapidly across the landscape. The slope of a population's dispersion–abundance (D–A) relationship has been used as a metric of

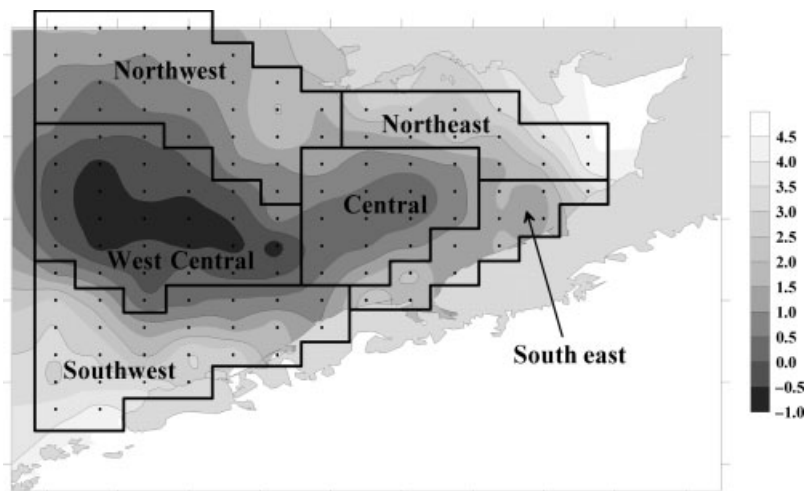


Figure 12. Spatial strata derived for the Bristol Bay region based on average thermal conditions during coldest period in the time series: 1974–76.

the tendency for range to expand, contract, or resist change as abundance changes. A positive relationship indicates a species prone to range expansion and a negative relationship a static population. Positive D–A is considered standard for marine fish (MacCall, 1990), and has been documented in Atlantic cod (Swain and Wade, 1993), haddock (Marshall and Frank, 1995), and some flatfishes (McConnaughey, 1995).

The Bristol Bay red king crab broodstock population displayed a weakly positive D–A relationship implying a tendency for range to contract and individuals to become more concentrated at low abundance. However, this is somewhat deceptive. Dispersion is a composite including mean density, distribution shape, and aggregation patterns. Treatment of each factor is beyond the scope of this manuscript, but was presented elsewhere: positive D–A in Bristol Bay red king crabs was primarily generated by a change in distribution shape, not by interactions between range and mean density (Loher, 2001). In fact, the population was actually more concentrated (i.e. displayed much higher population density) at high abundance, which would generate negative D–A if distribution shape remained stable. While Bristol Bay broodstock was reduced to <10% of its former abundance between 1979 and 1984, the population continued to occupy a range that was ~90% of its maximum observed size. Range declined modestly, but the large concurrent decrease in mean population density indicates a stock that may be somewhat resistant to density-dependent shifts, and whose range remains relatively constant over large variations in abundance. This contrasts with spatial dynamics of Kodiak Island red king crabs over approximately the same period: an order of magnitude decrease in female abundance from 1977 to 1986 (Scott *et al.*, 1990) was met with nearly complete retreat of the population from Kodiak shelf waters (Greene and Lock, 1990).

In the Bristol Bay broodstock population, change in distribution was not so much shrinkage in range as it was a large-scale displacement. By looking at late 1970s distributions one would be led to conclude that Unimak represented preferred habitat and was the center of the population's 'basin'. Under MacCall's theory, the population would have been expected to become even more concentrated around Unimak in the face of decreased abundance. But by the early 1980s the bulk of the population had become displaced either to areas of formerly low relative abundance (central Bristol Bay), or to where no broodstock had been previously detected (the northwest Bay). If

the population remained centered upon preferred habitat throughout that transition, then the location of that habitat must also have changed over time.

Relationship to bottom temperature and other potential causes

A comparison of broodstock redistribution and temperature suggests that water temperature may be an important physical feature structuring distribution. Nakanishi (1987) reported that embryo development is optimized at 3–8°C, and observed very slow development at lower temperature. This may represent a preferred temperature range for ovigerous females, and persistent cold may impede egg development and brood failure may occur if females remain in very cold water throughout incubation. Thus, the population may have selected the Unimak region as a refuge from the influence of the 1970s cold pool. During the mid-1970s, broodstock experienced temperatures that were warmer than the regional mean, by virtue of the population's southwesterly distribution (see Fig. 9). Following the retreat of the cold-pool the population invaded central Bristol Bay, and remained there throughout the 1990s. No long periods of cold-pool inundation were observed thereafter.

While it is difficult to empirically test the hypothesis that Bristol Bay red king crabs responded to temperature, redistribution in response to cold-pools has been observed in other species. Temperature reportedly alters distribution of a fish species in the Bering Sea, including yellowfin sole (*Limanda aspera*), walleye pollock (*Theragra chalcogramma*), and Arctic cod (*Boreogadus saida*) (Koto and Maeda, 1965; Wyllie-Echeverria, 1995). The range of Arctic cod expands northward during years of greatest cold pool extent, while walleye pollock move southward (Wyllie-Echeverria, 1995). Also, similar to red king crabs, the distribution of mature female snow crabs (*Chionoecetes opilio*) shifted northward in the southeast Bering Sea during the late 1970s and early 1980s (Zheng *et al.*, 2001). Average centers of abundance during the late 1970s were located northeast of the Pribilof Islands, but by 1984 had shifted 250 km to the northwest and remained stationary throughout the 1990s. In eastern Canada, expansion of the cold pool on the Scotian Shelf was accompanied by range expansion in snow crabs (Tremblay, 1997; Sainte-Marie and Gilbert, 1998). Absence of snow crabs on the Labrador Shelf has been associated with sub-zero temperatures from the previous year's sea ice (Dawe *et al.*, 2001). It seems plausible that redistribution of Bristol Bay female red king crabs might, in part, be a response to thermal forcing.

Because total abundance dropped markedly at the same time, it is also possible that the northwest shift could represent relative abundance, generated solely by southern mortality. However, absolute abundance actually increased in the northwest from 1978–1982 (refer to Fig. 13) in contrast to declining total abundance (Fig. 3). Increased abundance to the north appears to have resulted from either movement from southern strata or from local prerecruits maturing into the ovigerous population. Age-specific analyses conducted elsewhere indicate that northern abundance increases were primarily comprised of cohorts already recruited to the reproductive population: prerecruit size-classes were generally absent from northern strata in years prior to the increases (Loher, 2001). Thus, it is difficult to support the hypothesis that increases observed to the north were driven by spatially explicit recruitment.

But could red king crabs actually move across Bristol Bay in 3–5 yr? Adult males are known to migrate from wintering grounds to mating areas each spring (Powell, 1964; Vinogradov, 1968). Tagging studies indicate annual round trip spawning migrations of 40–60 km near Kodiak Island (Powell, 1964), and 50–150 km on the Kamchatka shelf (Vinogradov, 1968). Bristol Bay tagging (Simpson and Shippen, 1968) has indicated a mean rate of movement of 0.67 km day^{-1} , with single-year movement of as much as 425 km, from Unalaska to Port Heiden. While these studies were conducted for male crabs, some females may undergo similar movements. It is generally thought that males migrate to deeper water for energetic reasons, in order to reduce food requirements throughout the year, while ovigerous females must remain within warmer waters to incubate eggs. If true, one might expect prereproductive females to partake in migrations that are similar to those of males. Regardless of the nuances, migration of broodstock from southwestern to northeastern Bristol Bay over a 3-yr period ($\sim 100 \text{ km yr}^{-1}$) is well within the range of movements documented for this species.

While movement must be invoked to explain some changes in spatial population structure, there were likely multiple processes in operation. In particular, spatially-explicit mortality cannot be ignored. The hypothesis that ovigerous crabs actively move to avoid cold conditions does little to explain the disappearance of the southwestern component of the population. Between 1976 and 1981, broodstock abundance declined by $\sim 94\%$ in the Unimak region, representing nearly 80 million crabs. While some probably relocated, the majority disappeared. Recruitment modeling (Zheng *et al.*, 1995) has indicated high mortality

during the stock decline, and the present analyses suggest particularly high mortality around Unimak. Whether this mortality was natural or anthropogenic remains an open question. High trawl bycatch mortality has been suggested as a mortality agent during the decline (Dew and McConnaughey, 2005), and although the directed fishery harvests males, high female bycatch associated with high discard mortality could also have been a factor.

Broodstock responses may also be linked to other unknown population components and it must be noted that broodstock are only a portion of a larger puzzle. Have mature males moved in similar ways to broodstock? If dynamics exists between adult males and females, perhaps in the context of spawning, then changes in female distribution may also contain a social component reflecting male distribution, and vice versa. Similarly, has the spatial distribution of juvenile recruitment changed, and if so, are shifts in spatial recruitment linked to changes in adult distribution? Prerecruits might be expected to have similar food requirements as adults and generate some degree of resource competition. Analysis of density-dependent causes should include all age classes and treatment of potential competitive interactions. A complete understanding of the spatial dynamics of the population ultimately hinges upon our understanding of a host of other potential influences, most of which are beyond the scope of what is presented here, combined to form a coherent model for the species as a whole.

Implications of broodstock distribution shifts on larval ecology

Regardless of the causes, shifts in spatial population structure have ecological implications. Movement of broodstock may alter numerical and spatial recruitment patterns by impacting larval survivorship and growth, or by altering advection to settlement habitat. The highest levels of phytoplankton productivity in Bristol Bay occur to the south, concentrated along a 'green belt' at the shelf edge and extending into the bay north of Unimak Island (Springer *et al.*, 1996). Primary productivity in the green belt may be an order of magnitude greater than to the north, and the phytoplankton community may govern growth and survivorship of first stage king crab larvae (Paul *et al.*, 1990). Somerton (1981) hypothesized that *Chionoecetes* larvae released into the spring ice-edge phytoplankton bloom would experience high survival, and Incze *et al.* (1987) concluded that depressed larval abundance could be attributed to poor feeding and growth conditions. Plankton predators may also vary in space and time. For example, the biomass of gela-

tinous zooplankton increased during the late 1980s and mid-1990s, primarily in central Bristol Bay and northwest (Brodeur *et al.*, 1997), the present center of abundance for the spawning population.

Furthermore, it has been demonstrated for other crustacean species that the location of larval release relative to critical settlement habitat may have a substantial impact on total recruitment strength (White *et al.*, 1988; McConnaughey *et al.*, 1994). Early benthic phase red king crab are known to have very specific habitat needs (Loher and Armstrong, 2000) that appear to be met in only limited areas of Bristol Bay (Armstrong *et al.*, 1993; Loher, 2001). Thus, large-scale shifts in broodstock that translate into shifts in the location of the larval pool relative to regional circulation patterns might have considerable impacts on subsequent adult population dynamics.

Management implications

From a pragmatic standpoint, changing broodstock distribution can have important implications for management. Management tools must match spatial population structure in order to be effective. An obvious example is trawl exclusion areas. Bristol Bay has a long and complex history of trawl exclusion, much of which has been established to protect red king crabs or their fishery. For example, early exclusion zones were, at least in part, aimed at reducing gear conflicts, the Red King Crab Savings Area (RKCSA) designed to protect spawning stock, and the Nearshore Bristol Bay Trawl Closure Area to protect benthic habitat critical to early juvenile survival. It is clear that the precise location of these areas has been designed to match crab distribution at the time of their implementation, but a broader understanding of historical patterns might be of value to future deliberations. For instance, under the influence of another prolonged period of cold water inundation, will broodstock move back toward Unimak? If so, will they be subjected to high bycatch as they move across the southwestern boundary of the RKCSA? While the event was too short in duration to provide conclusive support for our distributional hypothesis, it is interesting to note that during 1999 broodstock displayed their most southwesterly central distribution for over a decade, coincident with the cold tongue's strongest intrusion since the early 1980s. Knowing that crabs have historically occupied the Unimak area in great abundance and that they may respond to temperature, we might predict future shifts and provide managers with the necessary information to alter trawl exclusion boundaries incrementally, in advance of the crab population, thereby reducing future bycatch issues.

ACKNOWLEDGEMENTS

This research builds on the work of C.-C. Hsu conducted during the early 1980s at the University of Washington, School of Fisheries. The authors wish to thank B.G. Stevens, L. Rugolo, and C.B. Dew for their help in obtaining NMFS trawl survey data. Near-bottom temperature data from NMFS surveys were obtained with help from S.R. Hare and G.E. Walters. S.E. Syrjala provided statistical assistance in analyzing interannual differences between geographic distributions. This work was supported in part by the University of Washington, School of Aquatic and Fishery Sciences, through a Victor and Tamara Loosanoff Fellowship, and by NMFS via Saltenstall-Kennedy Grant#NA76FD0036.

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