CONTRACTION OF THE GEOGRAPHIC RANGE OF DISTRIBUTION OF SNOW CRAB (*CHIONOECETES OPILIO*) IN THE EASTERN BERING SEA: AN ENVIRONMENTAL RATCHET?

J. (LOBO) ORENSANZ
Centro Nacional Patagónico
9120 Puerto Madryn
Argentina
lobo@cenpat.edu.ar

BILLY ERNST
Departamento de Oceanografía
Universidad de Concepción
Concepción, Chile

DAVID A. ARMSTRONG
School of Aquatic and Fishery Sciences
University of Washington
Seattle, Washington 98195

PHYLLIS STABENO
Pacific Marine Environmental Laboratory, NOAA
7600 Sand Point Way NE
Seattle, Washington 98115

PAT LIVINGSTON
Alaska Fisheries Science Center, NOAA
7600 Sand Point Way NE
Seattle, Washington 98115

ABSTRACT

Over the last three decades the geographic range of distribution of snow crab (*Chionoecetes opilio*) from the eastern Bering Sea (EBS) has contracted dramatically to the north. An increase in near-bottom temperature (NBT) during 1975–1979 was accompanied by a northward contraction of the cold pool (bound by the 2°C NBT isotherm) that extends over the Middle Domain during the summer. Warming was tracked with a 6-year lag by a contraction to the north of the mature female's range. Snow crab settle and grow to maturity in the Middle Domain. Successful recruitment during cold regimes may result from the occurrence of spring blooms and the stenothermy of early benthic instars. However, recruitment to the mature female population did not expand back to the southern shelf after the mid-1990s, despite some years when NBT was low. Cross-correlation of year-to-year shifts in geographic distribution of cod (*Gadus macrocephalus*) and immature snow crab during the 1990s suggests that the northward expansions of cod controlled the southern boundary of snow crab's distribution range. Reestablishment of crab populations in the south may be hindered by cod predation. Also, because spawning females are now located "up-current," advection of larvae to the south is unlikely. Contraction to the north may not be followed by an expansion back to the south after a change in regime. We refer to this suggested asymmetry as the environmental ratchet hypothesis and discuss it in the context of other conceptual models of the EBS ecosystem.

INTRODUCTION

The geographical range of snow crab contracted to the north in the eastern Bering Sea (EBS) during the 1980s and 1990s (Zheng et al. 2001; Ernst et al. 2005). Estimated abundance and catch quotas declined, reaching historically low levels by 2000–2003 (Stevens et al. 2002). Since this is one of the largest crab fisheries in the world, the economic implications of the trend are significant; consequently, federal disaster relief funds have been directed toward studies of population dynamics and life history. It has been proposed that a possible cause of the contraction in range and reduction in abundance of snow crab is the regime shift that occurred in 1976–1977 (Adams and Bond 1999). During the ensuing period of intensification, seawater was generally warmer, and this could cause snow crab to concentrate in the colder northern shelf (Zheng et al. 2001). But the possible mechanisms linking climate to the contraction of the snow crab's range have not been considered.

This range contraction and abundance reduction is not an isolated phenomenon: during the same period other significant changes have been documented in the EBS ecosystem. Many economically significant stocks have fluctuated dramatically, and there has been much concern about disruptions of commercial fisheries (e.g., red king crab, *Paralithodes camtschaticus*; Loher 2001) and declining populations of some marine birds and mammals (Hunt et al. 2002). A growing understanding of the EBS pelagic ecosystem has led to the formulation of rich conceptual models and complex testable hypotheses, such as the oscillating control hypothesis (Hunt et al. 2002; Hunt and Stabeno 2002).

While changes in the pelagic subsystem have received considerable attention, changes in the benthic subsystem remain poorly understood. Unlike fish, benthic invertebrates are sedentary or move slowly, so their spatial response to environmental change has a different tempo. Because spatial structure is comparatively persistent in benthic populations (Orensanz and Jamieson 1998), a spatially explicit approach to investigating the system is necessary and can be revealing.

Crab stocks of the EBS have been surveyed with a consistent design during the last three decades (Zheng et al 2001; Stevens et al. 2002). Only recently has this rich data set been used to explore their spatial dynamics (Zheng et al 2001; Ernst et al. 2005). In this study we use that data set and several pieces of environmental information to investigate the dramatic contraction to the north of the snow crab population. We address possible
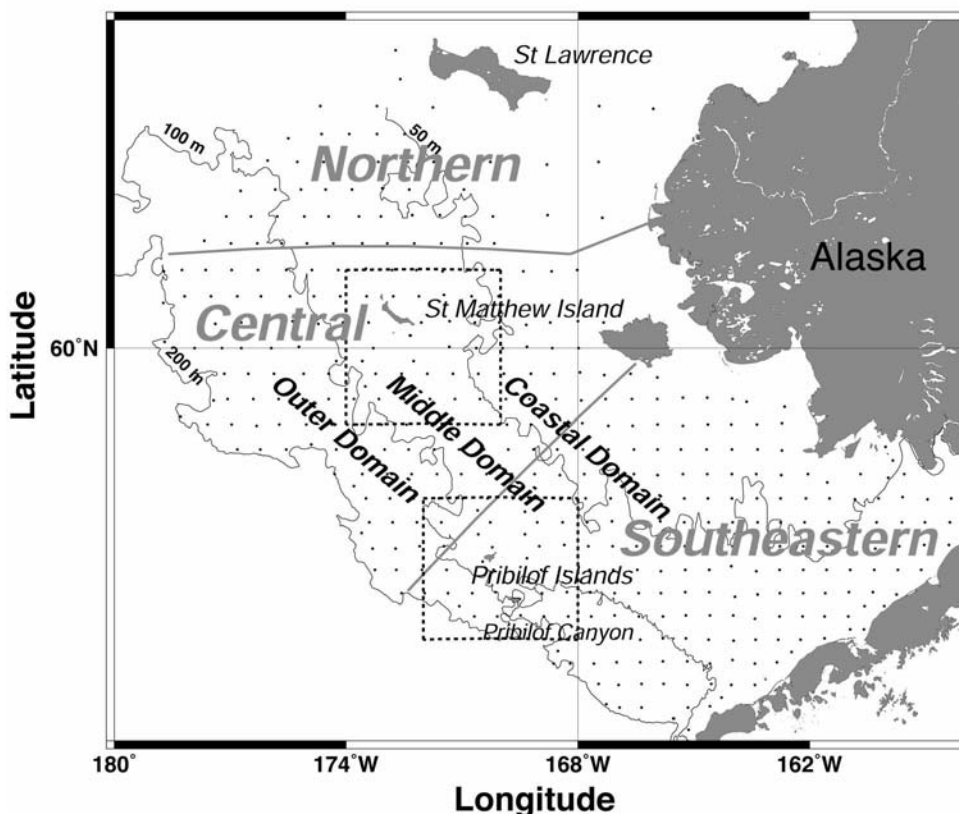
Figure 1. The eastern Bering Sea (EBS). Dots indicate NMFS survey stations where snow crab was observed at least once during surveys conducted between 1975 and 2001. Dashed rectangles around the Pribilof ("south") and St. Matthew ("north") Islands indicate windows that were defined to calculate time series of average near bottom temperature (NBT).

effects of the environment and predators on different life history stages and propose a composite hypothesis (the environmental ratchet hypothesis) to explain the contraction and to link the phenomenon to other oceanographic and ecological processes in the EBS.

BRIEF DESCRIPTION OF THE STUDY SYSTEM

The EBS Shelf

The extensive shelf of the EBS, more than 500 km wide, ends seaward in a shelf-break (generally coincidental with the 200 m isobath) that spreads northwest to southeast. The two main geographical features are St. Matthew Island and the Pribilof Islands (fig. 1). The shelf is conveniently partitioned in three sectors (Schumacher and Stabeno 1998, their fig. 27.1): northern, central, and southeastern. The central and southeastern sectors, the geographic setting of our study, extend from the Alaska Peninsula in the southeast to north of St. Matthew Island. Three zones or domains are usually recognized (Schumacher and Stabeno 1998): inner or coastal (shorewards from the 50 m isobath), middle (between the 50 and 100 m isobaths), and outer (between the 100 m isobath and the shelf-break). The Outer

Domain is cut in two naturally discrete segments (southeast and northwest) by the Pribilof Canyon (fig. 1). Up to 75% of the EBS shelf water is covered by ice in late fall to early spring. The advance and retreat of ice averages about 1,700 km and is the most extensive process of this type in Arctic regions.

Circulation in the EBS (fig. 2) is dominated by the Alaskan Coastal Current, which enters from the Gulf of Alaska through Unimak Pass and other passes along the Aleutian Island chain (Reed and Stabeno 1999) and moves east onto the EBS shelf as a cyclonic gyre. Much of the Alaskan Coastal Current that enters through Unimak Pass flows to the northwest (Bering Slope Current); a second branch slowly flows counter-clockwise within the Coastal Domain, first along the north side of the Alaskan Peninsula, then across the mouth of Bristol Bay, and finally to the north. Long-term average speeds are relatively fast within the Bering Slope Current ($5–20 \text{ cm} \cdot \text{s}^{-1}$), slower nearshore along the peninsula ($1–5 \text{ cm} \cdot \text{s}^{-1}$), and very weak within the Middle Domain (Kinder and Schumacher 1981), where there is virtually no net directional flow (Loher 2001). Oceanographic and satellite data have revealed an eastward flow ($2–3 \text{ cm} \cdot \text{s}^{-1}$) across the shelf north of the
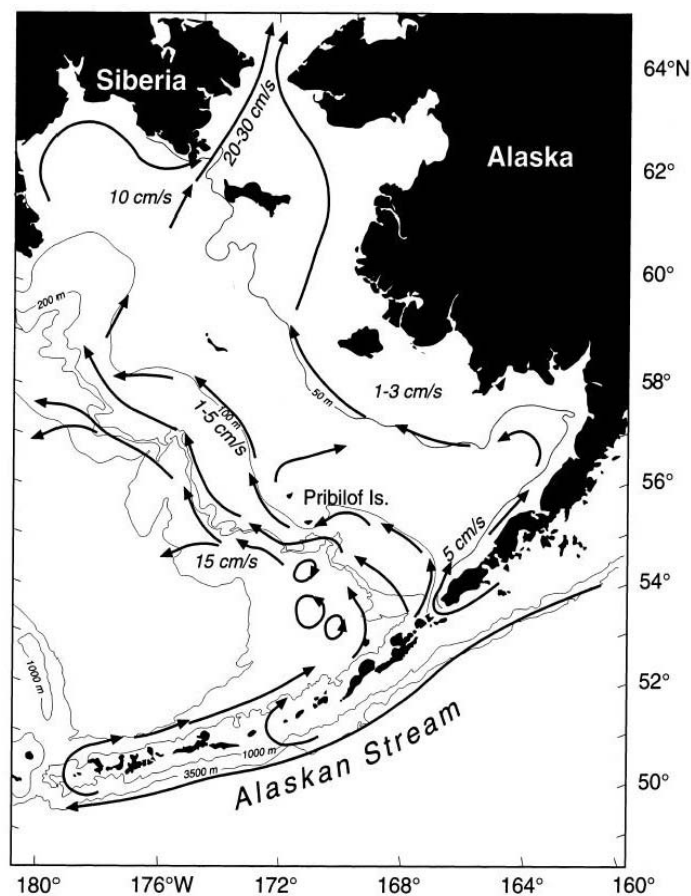
Figure 2. Schematic of mean circulation in the EBS shelf (modified from Stabeno et al. 2001).

Pribilof Islands (Schumacher and Stabeno 1998). Flow over the Outer Domain is moderate (4-8 cm·s⁻¹), following the 100 m isobath toward the northwest.

The southeastern sector of the shelf is divided by a series of three fronts into two interfrontal zones that correspond to the Middle and Outer Domains (Coachman 1986). Many biological phenomena can be conveniently conceptualized in this framework (Iverson et al. 1979), although the location and dynamics of the fronts are not clearly established for the central shelf (Schumacher and Stabeno 1998). As ice melts in spring, the less saline water "floats" over higher salinity marine water; this upper layer is heated, causing stratification of the water column. The stratified water column "traps" an extensive "cold pool" layer (water < 2°C) down to the seafloor over a large area of the EBS. In summer this cold pool averages 200 km north-south and 500 km east-west (Wyllie-Echeverria and Wooster 1998). The cold pool may persist over larger or smaller areas of the EBS for several consecutive years (Loher 2001), and the degree of spatial coverage influences the abundance and distribution of fishes and invertebrates.

Life History of Snow Crab in the EBS

Hatching and oviposition for the snow crab in the EBS start in March, peak in April, and are over in July (Somerton 1981, p. 32). Strong stratification of the water column in the Middle Domain during the summer (when larvae are in the plankton) provides a productive habitat for larval growth, which progresses through two zoeal and a megalops stage (Incze et al. 1987; Loher 2001). Immature females become vulnerable to the NMFS (National Marine Fisheries Services) survey gear when they reach a size range (30–60 mm carapace width) that is roughly equivalent to the three instars preceding the terminal (pubertal) molt to maturity. This pool of immature females is concentrated in the Middle Domain (Ernst et al. 2005). Female snow crab stop growing after the puberty molt, a transition recognizable in the relative width of the abdominal flap. Female age-at-maturity is unknown for the EBS; in eastern Canada it has been reported to range between 4.5 and 7.5 years after settlement (Alumno-Bruscia and Sainte-Marie 1998; Comeau et al. 1998). To avoid confusion, we refer to all female crabs entering the mature pool during a given year as a "pseudocohort." Female recruits to the mature population (SCI-2, shell-condition index value; see "Sources of Information—NMFS Survey Data," below) are also concentrated in the Middle Domain of the central shelf but slightly displaced toward the Outer Domain by comparison to immature females. It is in the Middle Domain that the life-history events from the pelagic larval stage to maturity occur. Older females appear displaced toward the Outer Domain. Ernst et al. (2005) hypothesized that during their directed ontogenetic migration female snow crab track environmental gradients, such as depth and near-bottom temperature.

Males also experience a morphological transformation related to reproductive maturity: the propodus becomes proportionally larger (in relation to carapace width) at the terminal molt (Conan and Comeau 1986). Since allometric changes in the claws are generally associated with sexual maturity, males with proportionally large claws are usually known as "morphometrically mature" (as opposed to morphometrically immature). Maximum post-terminal molt lifespan is 6–7 years (Ernst et al. 2005). According to Ernst et al. (2005), the terminal molt of males is likely to take place in winter and early spring (February–May); they hypothesized that the pseudocohorts of morphologically mature males that are seen as recently molted (SCI-1) during the summer surveys are likely to migrate offshore, becoming available to the fishery in the Outer Domain during the next winter as "clean shell" crab.

Mating behavior and ecology of snow crab are very complex (Elner and Beninger 1995). Studies conducted in eastern Canada show that females can mate after the

67

puberty molt while still in a soft-shell condition or (in subsequent years) while in hard-shell condition. The first are termed "primiparous," and the second "multiparous." Somerton (1982) proposed the "bipartite mating hypothesis" on the basis of field observations on tanner crab (*Chionoecetes bairdi*) in the Gulf of Alaska: primiparous females would mate with morphometrically immature, sexually mature males in shallow water, and multiparous females would mate with morphometrically mature males in deeper regions. Consistent with this hypothesis extensive experimental work conducted in eastern Canada has shown that morphometrically immature males are able to mate with primiparous females but not with multiparous ones, whereas morphometrically mature males can mate with both primi- and multiparous females (Conan et al. 1990).

INFORMATION SOURCES

NMFS Survey Data

Most of the information used in this study consists of time-series data collected during trawl surveys conducted by NMFS between 1975 and 2001 (Otto 1998; Stevens et al. 2002). Surveys follow a systematic sampling design in which stations are regularly spaced over a 20 nmi by 20 nmi grid and sampled every year. The 1975–1977 surveys were not included in the analyses because they covered only the southern end of the geographic range of interest. Systematic sampling surveys had a consistent spatial coverage after 1978 (fig. 1), with some variation north of 61°N; a cluster of northern stations was consistently occupied after 1988. The core temporal window of the surveys is June–July, but in some years work started in May (1975–1981, 1999–2000) or ended in August (1975–1976, 1978–1979, 1982–1986, 1988–1992). Information is collected on environmental variables and stocks of crab and groundfish. The environmental information used in this study consists of depth and near-bottom temperature (NBT), which has been regularly recorded since the initiation of the survey program.

Several observations are made on each individual crab caught in a haul or from a subsample when the catch is too large (for further information on the sampling protocol, see the "Manual of crab sampling methods for the trawl survey in the eastern Bering Sea"[1]). These observations include carapace width (CW, in millimeters), a shell condition index, sexual maturity (immature/mature, females only), color of the eggmass (if present), and height of the cheliped's propodus (males only, recorded only in recent years). After the terminal molt, shell condition changes as a result of wear and colonization by epibionts.

[1] Available from NMFS, Alaska Fisheries Science Center, P.O. Box 1638, Kodiak, AK 99615-1638.

Subjective "shell condition indexes" (SCIs) have been devised as a rough correlate of shell age. We used the SCI categories routinely recorded by NMFS and interpreted them following Ernst et al. (2005). Roughly, SCI-1:2 correspond to crab that molted very recently (during the survey's calendar year), SCI-3 to crab that molted during the preceding year, and SCI-4+ to individuals that molted two or more years earlier. In the case of females, SCI-2 and SCI-3 largely correspond to, respectively, primiparous recruits to the female pool and first-time multiparous breeders.

Catch per haul was used to estimate density using swept-area methods (Sparre and Venema 1998). Average density for each station was estimated as

$$D_t^S = \frac{1}{n_t^S} \sum_{i=1}^{n_t^S} \frac{\mathrm{d}_{t,i}^S}{\mathrm{A}_{t,i}^S},$$

where

D_t^S is density of station S in year t,

n_t^S is total number of hauls for station S in year t,

$\mathrm{A}_{t,i}^S$ is swept area of haul i in station S in year t,

$\mathrm{d}_{t,i}^S$ is number of specimens (crab or fish) of haul i in station S in year t.

We refer to this as "relative abundance," because no gear efficiency correction was used in the analysis.

The data were parsed and analyzed using scripts in AWK stream editor (Robbins 2001). Graphical analysis was conducted using GMT (Generic Mapping Tool) graphical software (Wessel and Smith 1998). Some graphs required surface plots, which implied the additional calculation of regular station grids over the entire distributional area. This was accomplished by using a near-neighbor algorithm (Wessel and Smith 1998). Centroids of density for a given category (species, sex, ontogenetic group) in a particular year were computed as weighted averages of latitudinal and longitudinal components, as described by Ernst et al. (2005). In the case of crab, the geographical location of pairs of centroids of consecutive life-history stages allowed us to estimate time series of mean migration distances and angles of migration for specified pairs of stages (e.g., mature females in SCI-2 in year i and SCI-3 in year i+1). We refer to Ernst et al. (2005) for details of the calculation.

We used temperature and depth records to calculate and map gradient (vector) fields as described by Ernst et al. (2005). The earliest surveys included in the NMFS database (1975–1977) were circumscribed to the southeastern part of the EBS. That period, however, is very
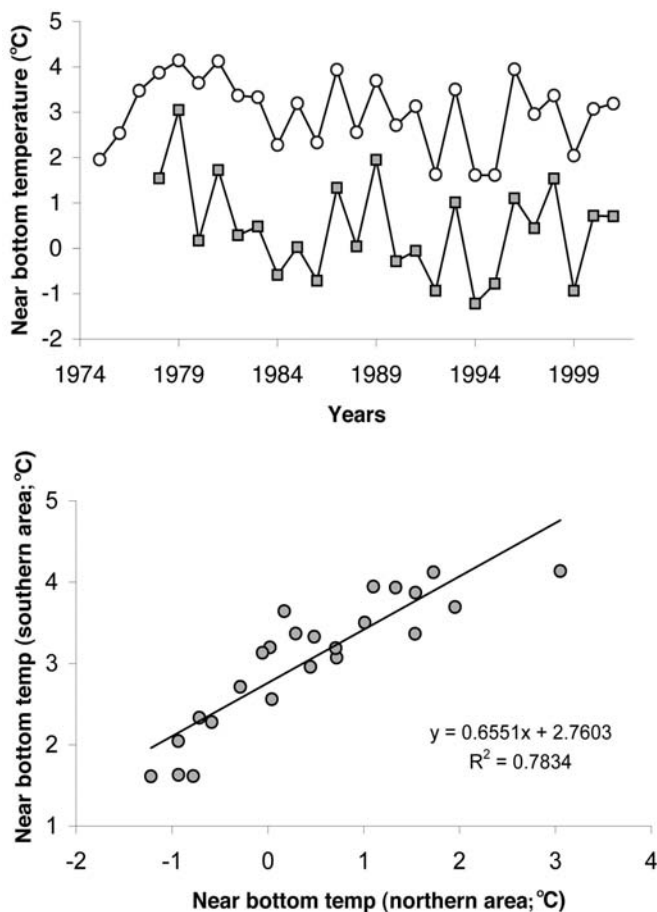
Figure 3.   Upper panel shows time series of average NBT calculated for the northern (*rectangles*) and southern (*circles*) areas (see fig. 1); lower panel shows the correlation between the two time series.

significant for our study, so we explored NBT in two windows centered on St. Matthew Island (north; 59°–61°N, 186°–190°W) and the Pribilof Islands (south; 56°–58°N, 188°–192°W) (fig. 1). Trends are very similar in the two windows (fig. 3; cross-correlation coefficient is 0.78), so trends observed in the south window in 1975–1977 were most likely paralleled in the north window.

Fish Stomach Content Data

Data on cod predation and cod CPUE from the NMFS surveys were available for the period 1981–2000; for details we refer to Livingston (1989) and Livingston et al. (1993). Centroids of cod CPUE were computed as weighted averages. Predation centroids were computed from an index of predation, calculated as the proportion (in weight) of snow crab in the diet of cod at a particular site and time.

Crab Fishery Data

Fishery data were provided as a database ("Catch/effort by statistical area for the eastern Bering Sea snow crab from 1969 to 2002") by Gail Smith.[2] Centroids of the fishery were computed based on numeric abundance (not biomass) and as the weighted average of the landings by statistical area.

Ice–Edge Data

The National Ice Center, Anchorage, Alaska, made data on ice coverage in the EBS available. Ice concentration is recorded on a relative scale from 0 to 10 and reported on a spatial grid of 0.25 latitude degrees by 0.27 longitude degrees. Lines illustrated here (based on these data) correspond to maximum extension of ice coverage for specific dates and were constructed by including cells where concentration was ≥ 5/9.

RESULTS

The cold pool, as observed through the summer NMFS surveys, expands and contracts, tracking the extension of ice cover during the preceding winter. A comparison of consecutive "cold" (e.g., 1986) and "warm" (e.g., 1987) years makes this clear (fig. 4). In 1986, a typically "cold" year, the ice was spread along the outer border of the Middle Domain in the southeast and along the Outer Domain in the northwest (fig. 4c). During the summer, the outer boundary of the cold pool matched rather well the maximum reach of the ice edge during the preceding winter (fig. 4a). In 1987, a typically "warm" year, the maximum reach of the ice edge ran from east to west at 59°–60°N (fig. 4d), again matching the summer extension of the cold pool (fig. 4b). Year-to-year expansions and contractions of the cold pool are a Middle Domain phenomenon that takes place primarily between the 50 m and 100 m isobaths and along the northwest-southeast direction. There are two noticeable exceptions. First, the southeast outer fringe of the Middle Domain (MDf), ranging from ~59°N to the southeast and including the area around the Pribilof Islands, does not overlay the Cold Pool even during "cold" years (fig. 4a). Second, an expanse of the Coastal Domain located to the southwest of Nunivak Island (CDf) overlays the cold pool even in "warm" years (figs. 4b).

Recruitment to the mature snow crab population takes place over the Middle Domain. Little is known about distribution and abundance of early instars, which are too small to be captured in the NMFS survey gear. The only category of information available about the large-scale distribution of early snow crab instars is stomach content data from fish, primarily cod. Most of the snow crab sampled from cod stomachs are 6–35 mm CW (fig. 5) in size. The cumulative geographic distribution of snow crab sampled from cod stomachs gives
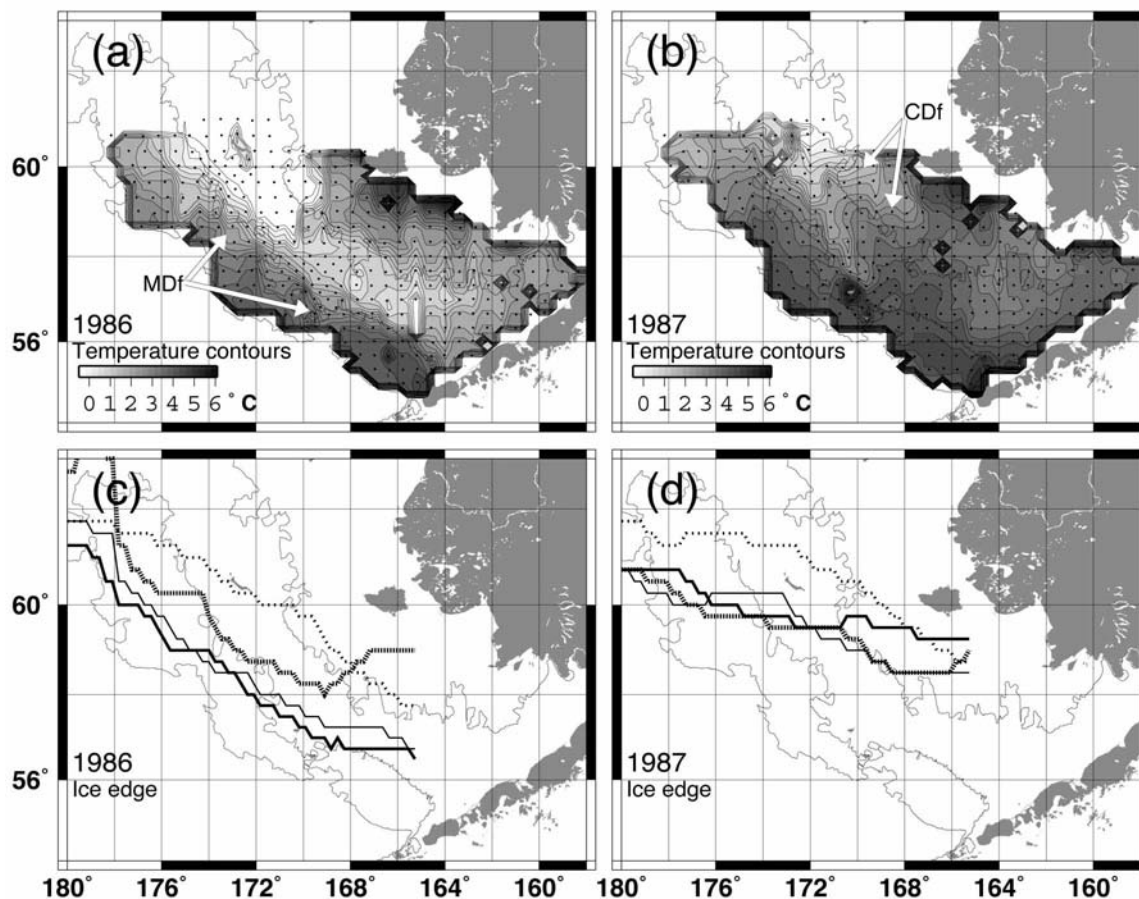
Figure 4. Extension of the cold pool during the summer (*a* and *b*) and position of the ice edge (*c* and *d*) in cold (*a* and *c*) and warm (*b* and *d*) consecutive years (1986 and 1987, respectively). In 1986, ice edge was calculated on 4 Feb. (c1), 25 Mar. (c2), 1 Apr. (c3), and 29 Apr. (c4); in 1987, on 3 Feb. (d1), 3 Mar. (d2), 31 Mar. (d3), and 21 Apr. (d4). CDf = Coastal Domain southwest of Nunivak Island; MDf = southwest fringe of Middle Domain.
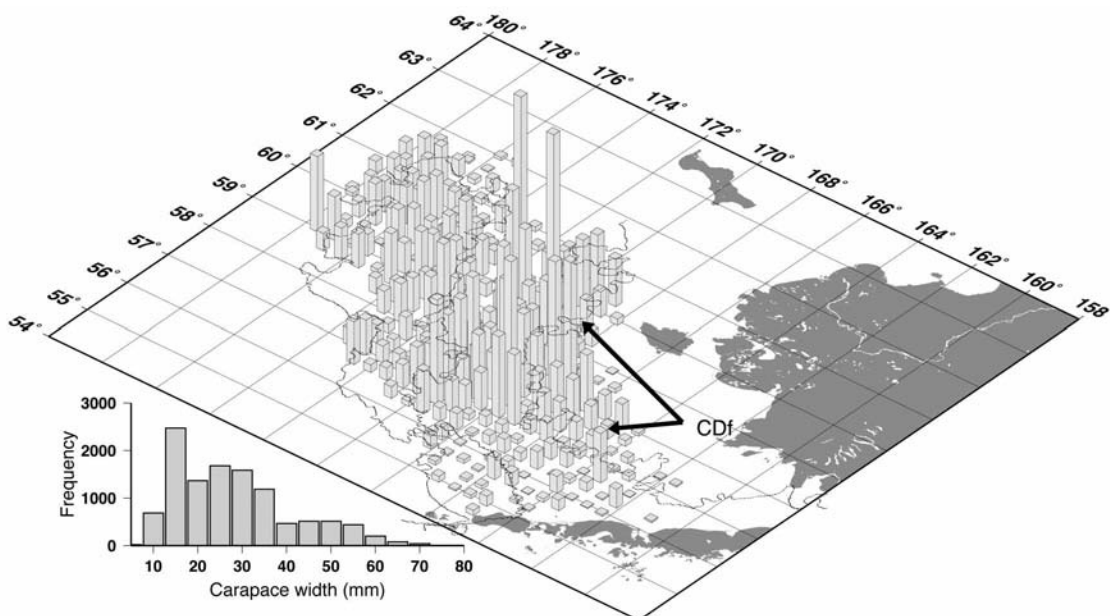

Figure 5. *Upper panel*, aggregated distribution (1981, 1984–1999) of cod predation on snow crab in the EBS; bar height is proportional to the count of individual cod with snow crab in their stomach that were sampled in each cell of the grid. *Lower panel*, size-frequency distribution of all snow crab sampled from cod stomachs.
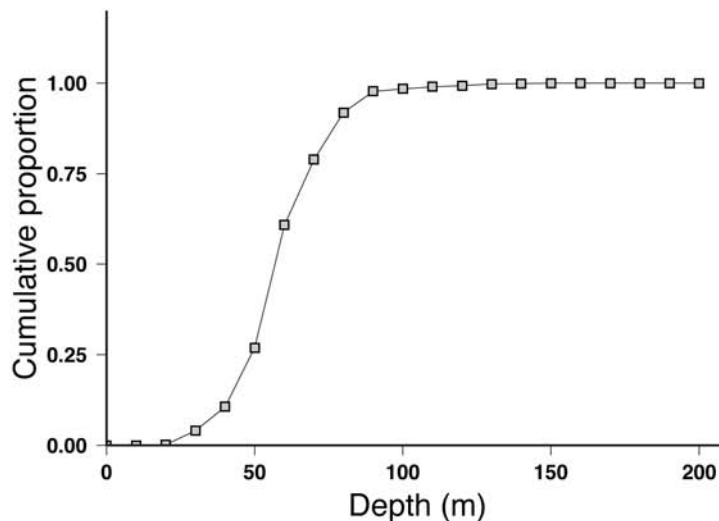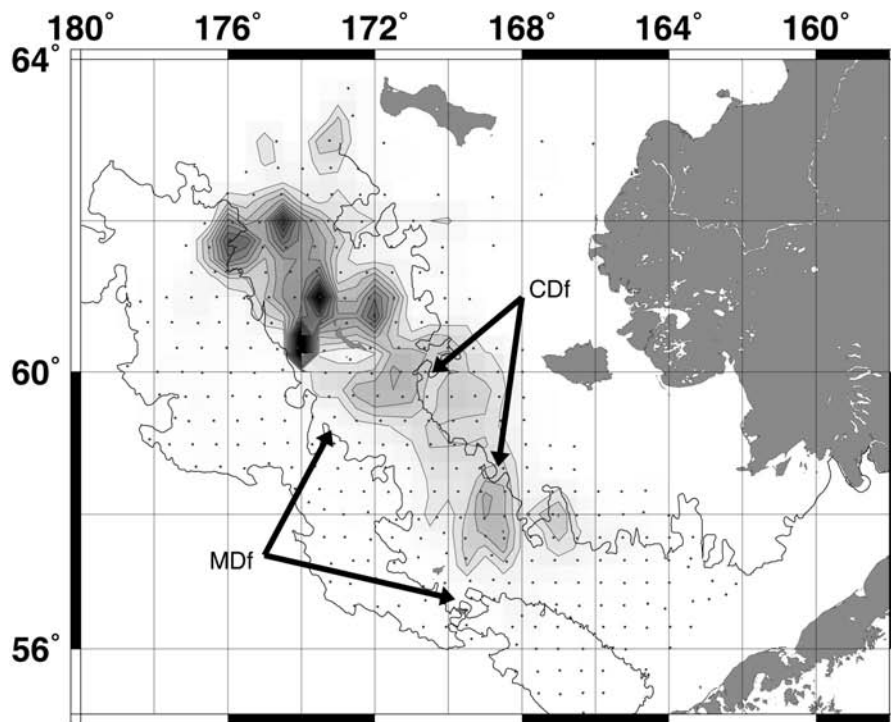
Figure 6.   *Upper panel*, relative density (survey CPUE) of immature female snow crab integrated over time from 1978 to 2001. *Lower panel*, cumulative proportion of immature females (number sampled weighted by abundance) relative to depth (NMFS survey data).

at least a qualitative idea of the distribution of younger age classes (fig. 5). Juveniles are distributed primarily throughout the Middle Domain, spreading also eastward over the CDf (fig. 5) and (in smaller numbers) in areas of the Outer Domain west of 174°W and north of St. Matthew Island. This information must be considered qualitative because it is biased by cod behavior and geographic distribution. Immature females sampled during the summer NMFS surveys are 30–60 mm in size (intermediate between cod prey and mature females).

The immature group is definable only for females because observers note the condition of the abdominal flap. In the case of males, it is not possible, with the data at hand, to separate morphologically mature and immature individuals in most of the survey data. Data pooled over all surveys shows that immature females are circumscribed to the Middle Domain (fig. 6, top), with the noticeable exception of the two fringe areas of the Coastal and Middle Domains described above (fig. 4a,b; fig. 6). In general, the region where immature females are found
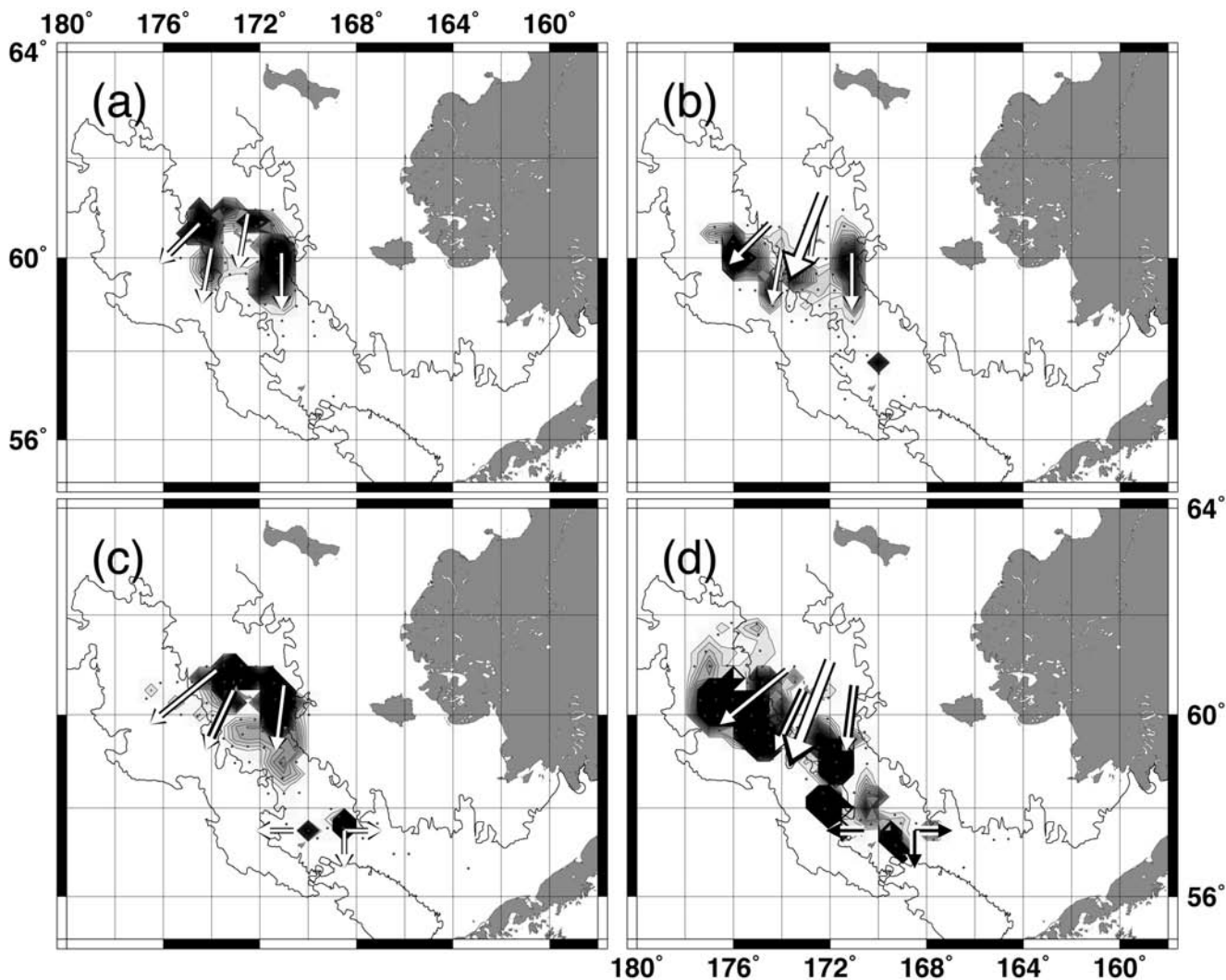
Figure 7. Relative abundance (survey CPUE) of mature females of two pseudocohorts. 1985 pseudochort: *a*, SCI-2 in 1985; *b*, SCI-3 in 1986. 1986 pseudocohort: *c*, SCI-2 in 1986; *d*, SCI-3 in 1987. Notice that 1986 and 1987 are the consecutive cold and warm years, respectively, shown in fig. 4. Large arrows in *b* and *d* indicate the azimuth of net large-scale migration; smaller arrows indicate apparent vectors of local, small-scale migration.

corresponds to the maximum extension of the NBT isotherm of 2°C, which bounds the Middle Domain. Over 25 years of surveys, more than 90% of the immature females sampled came from depths in the 50–100 m range that bathymetrically defines the Middle Domain (fig. 6, bottom).

Most females recruit to the mature population (that is, undergo their terminal molt) within the Middle Domain, then migrate to the south and to the west (for supporting evidence and details, see Ernst et al. 2005). The resultant direction (from northeast to southwest) is rather conservative, irrespective of whether years are "cold" or "warm" (fig. 7). The core of the ontogenetic migration takes place during the first year after the terminal molt, as females change from SCI-2 to SCI-3. This transition is often traceable at the level of large patches in the population, as Figure 7 shows for the

1985–1986 and 1986–1987 post-terminal molt ontogenetic migrations. Notice the similarities in distribution of the main pool of females in SCI-2 in 1985 and 1986, probably reflecting the fact that immature females in the source pool molt into maturity over more than 1 year.

While this general sequence of ontogenetic events appears to have persisted after 1981, the geographic range of the mature female population has contracted from southeast to northwest (fig. 8). During the 5-year period 1978–1982 the mature population was spread over the entire EBS shelf, with large concentrations in the southeast and northwest (roughly located in the region of, respectively, Pribilof Island and St. Matthew Island). In contrast, during the 5-year period 1998–2001, the southeast concentration had disappeared, and nearly all the mature population was concentrated north of 58°N (fig. 8). Between these two periods there were some
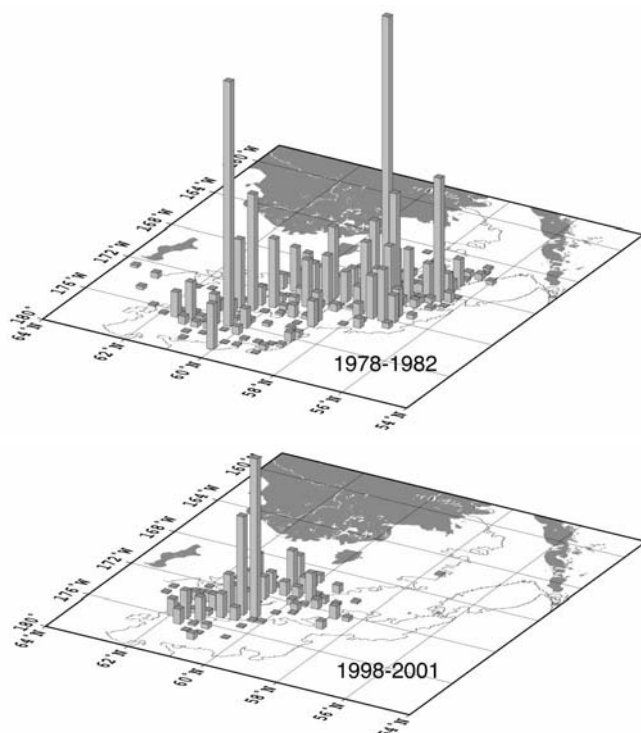
Figure 8.   Aggregated abundance of mature females in SCI-2 at the beginning (*top*, 1978–1982) and toward the end (*bottom*, 1998–2001) of the study period. Bar height is proportional to abundance (survey CPUE) in each cell, aggregated for the period indicated.

Figure 9.   Time series of average near bottom temperature in the south window (*circles*; see fig. 1 for location) and latitudinal component of the centroid of distribution of primiparous (SCI-2) mature females (*diamonds*), the latter lagged by 6 years. The vertical line shows the change from an autocorrelated cycle of NBT to a period dominated by year-to-year variation.

transient expansions of the mature female stock, discussed below. Contraction to the north was accompanied by a long-term decline in abundance, punctuated by periodic pseudocohort recruitment (centered around 1980, 1987, 1994, and 2001).[3]

If temperature had an effect on settlement or recruitment, it is likely that the corresponding phenomenon relates to spawning, the pelagic larval phase, or early benthic instars, stages that are in the first calendar year of life. Age at female maturity has not been established for the EBS, but in eastern Canada it ranges from 4.5 to 7.5 years. Considering that life-history schedules are similar in the two regions (Ernst et al. 2005), 6 years is a reasonable guess for the EBS. Recruitment of female pseudocohorts is the most proximate estimate of year-class strength for snow crab in the EBS. Following these considerations, we compared the time series of average NBT and the latitudinal component of the centroids of distribution of females in SCI-2, the latter with a 6-year lag (fig. 9). Expansions and contractions of the cold pool, described above, are well captured by average NBT during the summers (NMFS survey data). The median NBT over that period is about 3°C (fig. 9). Figure 9 reveals a significant pattern : annual mean NBT during the summer rose continuously during the 5-year
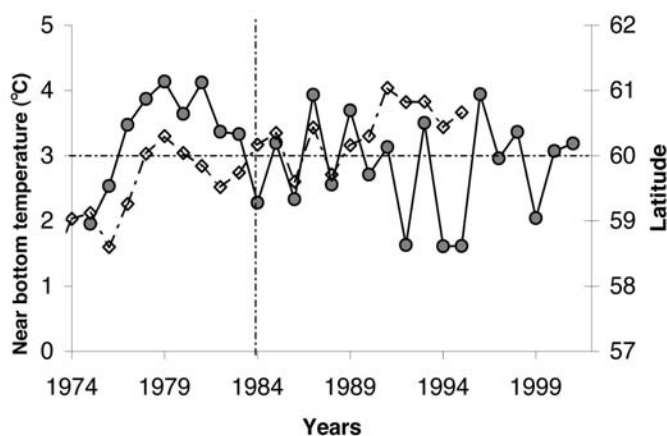
period 1975–1979. The summer of 1979 was the warmest for the study period, with the entire Coastal Domain experiencing NBT higher than 6°C and the cold pool not extending beyond the northern shelf. Once average NBT rose above the median, it stayed relatively warm (above 3°C) during the 7-year period 1977–1983. After 1980, change was dominated by year-to-year variation.

A displacement of the centroids of SCI-2 females toward the north during the 4-year period 1982–1985 matches the increase in average NBT 6 years earlier (fig. 9), even though the magnitude of the displacement is probably underestimated because between 1983 and 1986 the survey did not extend north of 60°N. The latitudinal position of lagged centroids tracked average NBT between 1976 and 1988 but afterward remained north of 60°N for 6 years. During the early 1990s, there were some short-lived expansions of the mature female population to the south. The centroids of 1992 and 1994 were well displaced to the south, tracking (as before with a 6-year lag) the cold years 1986 and 1988. This resulted in a transient expansion to the south of the mature female population that lasted until 1997, after which the 1992 and 1994 pseudocohorts vanished from the population. After 1988, the cold years 1992, 1994, and 1995 were not followed by a rebound of pseudocohort recruitment in 1998 and 2000, but they were followed by a small peak in the north in 2001. The latitudinal component of the lagged centroids did not track the year-to-year fluctuations of NBT that have been characteristic of the 1990s.

Tracking year classes or pseudochorts is more difficult for males than for females, in part because morphologically immature and mature males cannot be discriminated in the NMFS survey data. Ernst el al. (2005) hypothesized that large males (CW > 102 mm,

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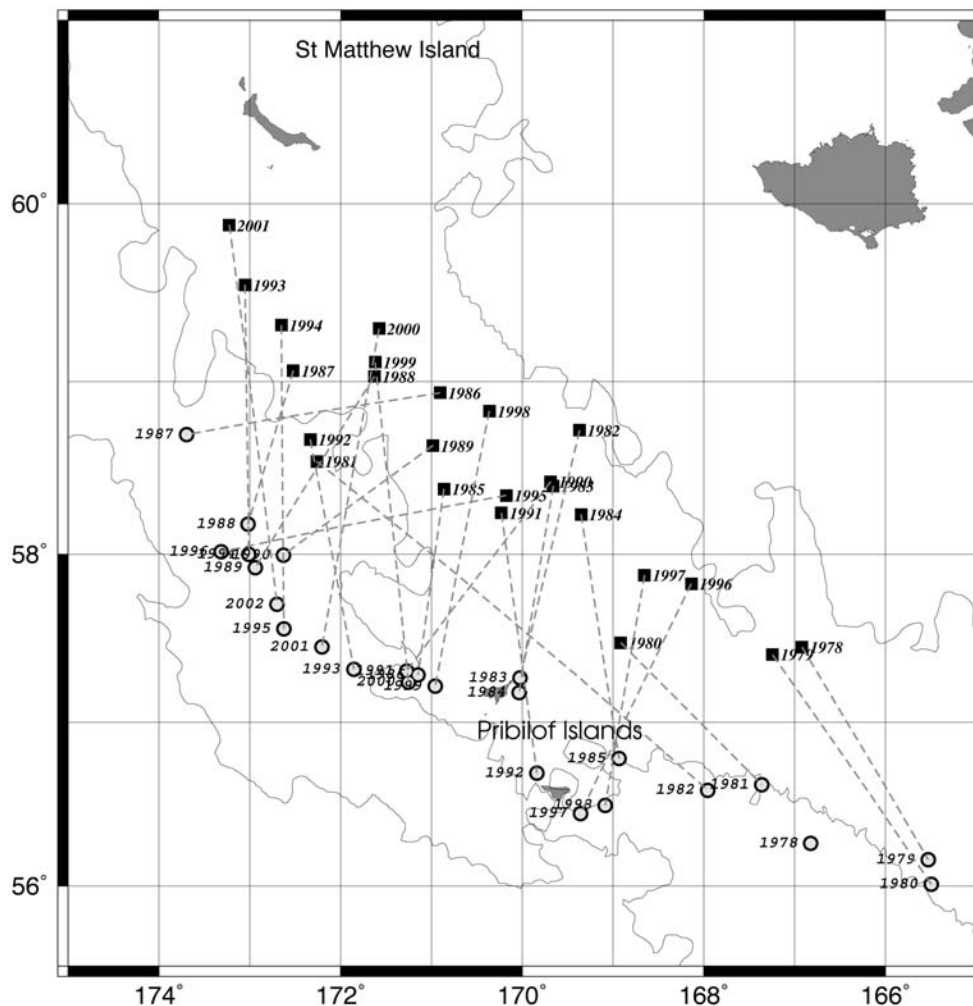[3]B. Ernst, D. A. Armstrong, and J. M. Orensanz, unpubl. results.

Figure 10. Centroids of large male abundance (CW > 102 mm) in SCI-1:2 (large new-shell crab, *squares*) and the fishery (*circles*). Dashed lines connect centroids for large new-shell crab observed during the summer surveys with centroids of the commercial catch during the following winter.

which corresponds to commercial size, virtually all morphologically mature) molting during the survey's calendar year (SC 1-2) correspond to the "clean crab" caught by the fishery in the Outer Domain during the subsequent winter fishing season. Winter fishery centroids are always located to the south of the large, recently molted crab centroids of the previous summer (fig. 10). This could be explained by two hypotheses: (1) male crab move offshore and southward (into the Outer Domain) after molting into maturity in the Middle Domain, or (2) males do not migrate, and the fishery is simply constrained by ice cover so that only the outer fringe of the large crab population is accessible to the fishery. Hypothesis (2) is falsified by two facts: first, during the early years of the series the fleet was not seasonally constrained by regulation, yet the observed pattern was the same, and, second, crabs molting to maturity are confined to the Middle Domain at the time of the summer survey.

If hypothesis (1) is correct (males move southward), then two predictions follow: first, the spatial allocation of fishing effort during the winter (captured by the location of the fishery centroids) should track the spatial distribution of large males reaching morphological maturity during the preceding calendar year (captured by centroids calculated with the NMFS spring/summer surveys), and, second, the fishery centroids should be located to the south of the centroids calculated with survey data. Both predictions hold remarkably well (fig. 11). Notice that the longitudinal separation of the centroids is relatively small compared to more obvious differences in latitudinal separation of these events, consistent with the notion of a southward migration to the fishing grounds after molting. As in the case of females, the centroids of males molting into maturity during the summer show a net northward displacement over the 25-year study period, from 57.5°N in 1978 to 60°N in 2001. While centroids of the survey and the fishery are well
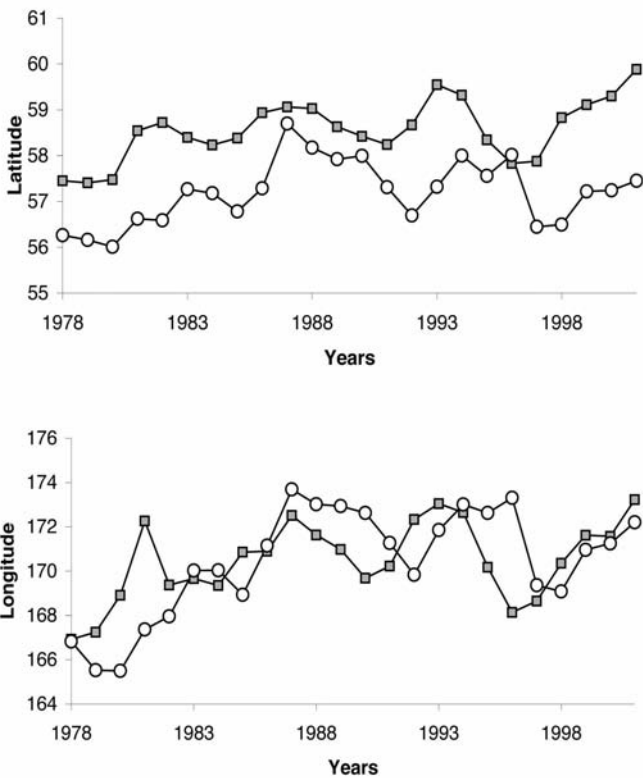
74

Figure 11. Latitudinal (*top*) and longitudinal (*bottom*) components of the summer centroids of large-male abundance (CW > 102 mm) in SCI-1:2 (new-shell large crab, *squares*) and the subsequent winter fishery (*circles*).

cross-correlated (with a 1-year lag), the fishery centroids moved northward between 1978 and 1987 (fig. 11, top) but fluctuated afterward between 56°N and 58°N. As a result, the shift between the summer centroids of stock abundance (survey data) and the fishery during the following winter has increased steadily over the 7-year period 1995–2001. This parallels a similar trend in SCI-2 females, which remained north of 60°N during the same period.

Cod predation is the main source of natural mortality of snow crab prerecruits so far identified in the EBS. The centroids of cod abundance (as indicated by CPUE observed in the NMFS surveys) showed a steady shift toward the north between 1979 and 1983. This closely paralleled (with a 4-year lag) the increase in average summer NBT observed between 1975 and 1979 and was 2 years ahead of a corresponding shift to the north of crab's range of distribution (indicated by the centroids of abundance of mature female pseudocohorts; figs. 8 and 9). After 1984 cod CPUE centroids fluctuated around 58°N (fig. 12, right), with no apparent relation to average NBT. Indexes of cod predation have been calculated for the period 1984–2000. During the 11-year period 1991–2001, the latitudinal component of the centroids of cod CPUE, abundance of immature females (the group sampled during the NMFS surveys that is closest to the size range of cod prey), and the index of cod predation (fig. 12, left)
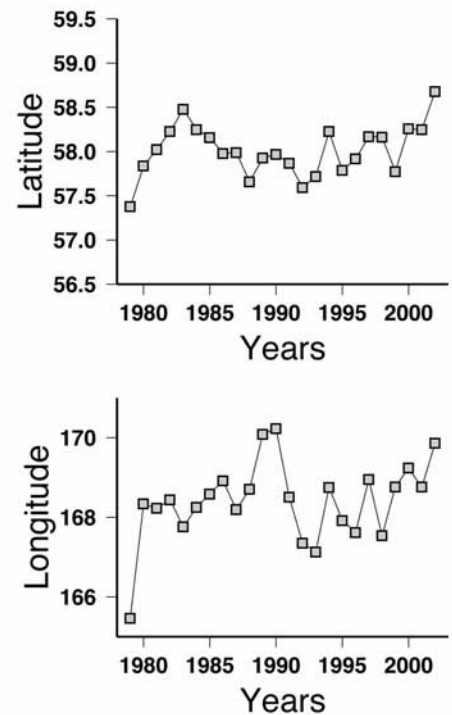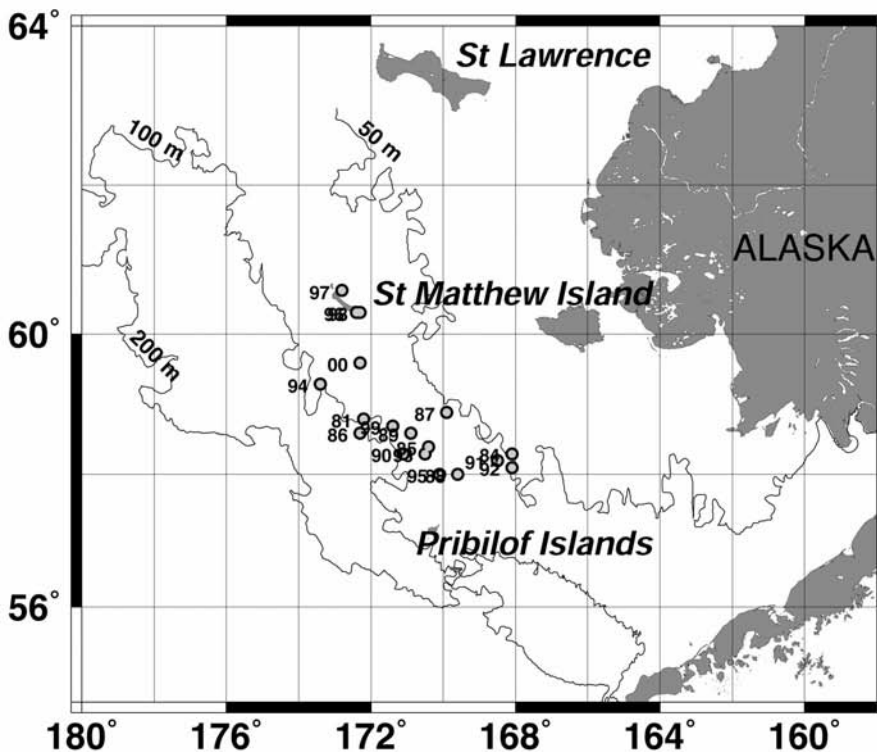

Figure 12. *Left*, centroids of cod predation calculated for 1981 and 1984–1999, weighted by cod CPUE. Right, time series of the latitudinal (*top*) and longitudinal (*bottom*) component of centroids of cod relative abundance distribution (survey CPUE).
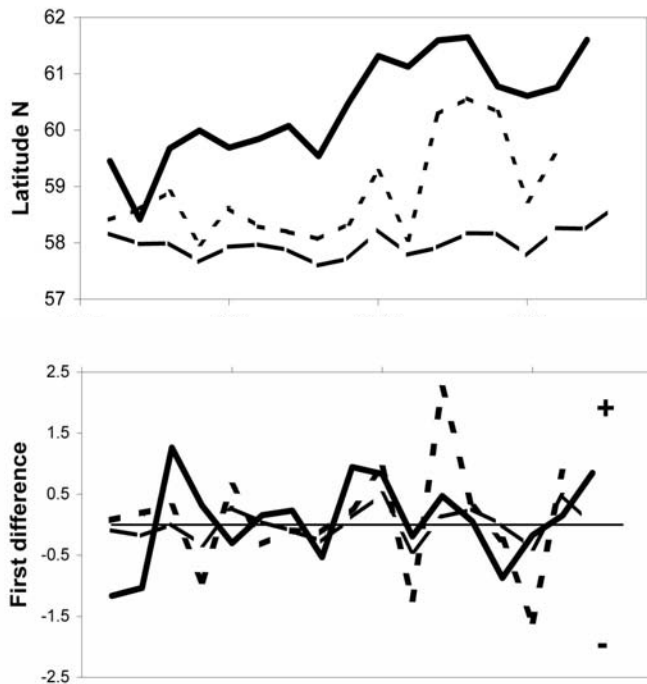
Figure 13. *Top*, time series of the latitudinal component of centroids of distribution (survey CPUE) of immature females (*solid line*), cod (*dashed line*), and predation index (*dotted line*). *Bottom*, first-order difference of the series shown in the top panel.

have fluctuated in a very consistent way: the first-order difference of the three series showed the same sign in every year (fig. 13). Cod CPUE centroids were located, on average, 1.5° latitude to the south of centroids of immature female abundance. This gap can be anticipated when Figures 6 (top) and 12 (left) are compared.

DISCUSSION

During the 24-year period 1978–2001, recruitment to the snow crab stock of the EBS (as indicated by the abundance of female pseudochorts) declined; the fishery reached historically low levels in 2002–2003 under the current rebuilding plan (Stevens et al. 2002). At the same time, the geographic range of the population (males and females) showed a significant long-term shift toward the north. Here, we suggest that these changes are, at least in part, related to climatic forcing, and we advance what we term the "environmental ratchet hypothesis." The elements of the hypothesis are as follows:

1. Snow crab settle and grow to maturity in the Middle Domain. Pelagic larvae find a favorable environment in the upper layer of the water column, strongly stratified during the summer between the middle and inner shelf fronts, foraging on phytoplankton blooms that develop in spring along the ice edge.

2. Larval retention in the Middle Domain is favored because of lack of a strong current pattern.

3. The area of seabed suitable for settlement is circumscribed by the 2°C NBT isotherm, that is, the cold pool, that expands over the Middle Domain to the southeast during cold years.

4. The lagged northward shift of female pseudochorts associated with warming during the 5-year period 1975–1979 indicates a corresponding northward shift in recruitment to the benthic population (settlement and early benthic survival). There are two reasons: Appropriate conditions for larval growth and survival are associated with spring blooms that develop under colder conditions, and early juvenile stages are stenothermic, requiring a NBT below 2°C.

5. Once the reproductive stock had contracted to the north, relaxation to the south tracking year-to-year fluctuations in NBT was made difficult by the current pattern: The reproductive stock had effectively contracted "up-current."

6. Females are not likely to repopulate depleted areas to the southeast of the Middle Domain, because routes of ontogenetic migration take them offshore toward the Outer Domain, whether years are cold or warm, reflecting the dominant direction of environmental gradients tracked during the migration (depth, NBT).

7. After contraction of the stock to the north, cod predation on juveniles controlled the southward expansion of the range of immature females.

8. Resurgence in the south based on the local reproductive stock is unlikely because of the small size of the stock and because of persistent cod predation on juvenile crab.

This composite hypothesis subsumes several single hypotheses on the dynamics of snow crab populations in the EBS. Each component hypothesis is supported by empirical evidence but can also be challenged on empirical grounds, making the composite hypothesis a useful framework for further inquiry. At the core of the hypothesis is the notion of an "environmental ratchet": given the nature of hydrographic features and the spatial behavior of crab and their predators, change in geographical range is asymmetrical. According to the hypothesis, contraction to the north during warm regimes is more likely than expansion back to the south during cold years.

Important elements of our hypothesis are based on a general oceanographic model of the EBS shelf, inferred largely from detailed long-term studies conducted over the southeastern shelf. Far less documented are the oceanographic processes for the central and northern parts of the shelf (Schumacher and Stabeno 1998), the main ambit of snow crab dynamics. Similarly, studies on

snow crab larval ecology have been circumscribed to the southeastern part of its range (Incze et al. 1987). Further work focusing on the central and north portions of the shelf is needed to validate the rationales of the environmental ratchet hypothesis.

The 25-year study period (1976–2001) can be clearly partitioned in two segments in terms of the patterns of variation of average summer NBT, which, as noted earlier, is correlated with the extension of the cold pool. Following an extremely cold period (1974–1975; Azumaya and Ohtani 1995), NBT increased monotonically during 5 consecutive years; average summer NBT in this study's south window doubled from 2°C in 1976 to 4°C in 1979 (see also Loher et al. 2001, their fig. 9). Somerton (1981) hypothesized that successful larval development and settlement are related to spring blooms that develop near the ice-edge in early to mid-April, accompanying salinity changes during ice melting and subsequent stabilization of the water column. This could explain why the southern boundary of female snow crab distribution is approximately coincidental with the mean southern extent of sea ice in April. Hunt et al. (2002) proposed the oscillating control hypothesis as a conceptual model for the functioning of the pelagic ecosystem in the EBS. This hypothesis predicts alternation between primarily bottom-up control in cold regimes and primarily top-down control in warm regimes. According to the model, "the timing of spring primary production is determined predominantly by the time of ice retreat: late ice retreat (late March or later) leads to an early, ice-associated bloom in cold water, whereas no ice, or early retreat of ice before mid-March, leads to an open-water bloom in May or June." Coupling between holopelagic mesozooplankton and phytoplankton is probably weak in cold years, when primary production is dominated by spring blooms. In cold years the reproduction and growth of holoplankton (which are controlled by temperature) are retarded, the spring phytoplankton bloom is not controlled by zooplankton grazing (Napp et al. 2000), and phytoplanktonic production sinks ungrazed to the bottom. The case of meroplankton is different. Since the timing of larval hatching in snow crab is constrained by the reproductive cycle of benthic adults, which peaks in April, crab larvae are likely to thrive during cold years, consistent with Somerton's (1981) hypothesis. Interestingly, Comeau et al. (1991) and Starr et al. (1994) hypothesized that the trigger for snow crab eggs to release larvae in Bonne Bay (eastern Canada) is linked to the phytoplankton bloom and rain of organic particulate matter that follows.

Beyond pelagic larval life, association of recruitment with the cold pool could result from the stenothermy of early benthic stages. Experimental and field work by Dionne et al. (2003) in the Gulf of St. Lawrence (eastern Canada) showed that the preferendum for snow crab instars I–III is in the 0.0–1.5°C range, that this is the most stenothermic stage in snow crab life history, and that the most important factor constraining its distribution appears to be temperature. Because of narrow habitat requirements, they concluded, early juvenile instars could represent the weakest link in the snow crab's life cycle. Even if other factors influence trends in snow crab abundance and spatial distribution in the EBS, spread of the cold pool during the first year of life could easily determine the southern boundary of a cohort's range.

Somerton's (1981) hypothesis and juvenile stenothermy are consistent with the northward contraction of snow crab's range during the late 1970s and early 1980s, but they cannot explain why there was not a return to previous conditions during the 1990s. Fish predation, mostly by small Pacific cod (*Gadus macrocephalus*) on juvenile benthic stages, is the main source of snow crab natural mortality identified in the EBS (Livingston 1989). Three species of flatfish also prey on juvenile snow crab: yellowfin sole (*Pleuronectes asper*), rock sole (*P. bilineatus*), and flathead sole (*Hippoglossoides elassodon*). Livingston (1989) analyzed 3 years of cod stomach content data (1981, 1984, 1985) that suggest that the geographic distribution of young snow crab in cod stomach contents is related to the maximum extent of winter ice cover, which in turn is correlated with the extension of the cold pool during the following summer. This could not be explained by a link between changes in the geographic pattern of snow crab settlement and climate (e.g., Somerton's hypothesis, introduced earlier), because cod prey on snow crab of age 1+ and older (Livingston 1989, p. 821). Postsettlement migrations of juveniles tracking year-to-year changes in the geographic pattern of NBT can be ruled out, given the distances involved and what is known about snow crab migrations (Ernst et al. 2005).

Cod accounts for up to 64% of the aggregate total finfish predation on snow crab in the EBS; up to 84–95% of age 1+ snow crab can be consumed by Pacific cod (Livingston 1989; Livingston et al. 1993). Though tentative, these figures give an idea of the possible magnitude of predation based on what is known about cod and immature crab abundance and estimated cod consumption rate. During 1991–2001 (for which an index of cod predation is available), cross-correlated year-to-year variation in the location of the centroids of cod CPUE, cod predation index, and immature snow crab abundance strongly suggests that cod distribution controlled the spread of crab recruitment to the south in the Middle Domain of the central shelf. The index of predation indicates that when cod distribution shifts toward the north, the relative importance of snow crab as an item in cod diet also increases. We propose that expansions and contractions of the geographic range of

cod results in "chopping off" the southern fringe of juvenile/immature snow crab. During warm years, the centroid of cod abundance moves northward, the amount of snow crab in cod diet is amplified as cod make a deeper dent into the snow crab's range, and the geographic range of juvenile/immature snow crab contracts accordingly, owing to predation. Bailey (1982) hypothesized that cod predation controls snow crab abundance in the Gulf of St. Lawrence (eastern Canada), but later studies failed to find consistency in population fluctuations of the two (Elner and Bailey 1986). Our results suggest that Bailey's hypothesis should be reexamined.

Resurgence of the mature female stock in the south requires at least one of three mechanisms: active displacement of females to the south, resurgence of the population in the south through retention of larvae produced locally by the residual stock, or southward transport of pelagic larvae produced in the north. Ernst et al. (2005) and results from this study indicate that females maturing in the Middle Domain of the central and northern shelves undergo an ontogenetic migration toward the Outer Domain, with a predominant northeast-southwest direction. This pattern has predominated in the postwarming years, starting with the 1981 female pseudo-cohort. However, some southward migration takes place within the Middle Domain in two regions: west of the CDf and to the northeast of the Pribilof Islands. The latter was significant during the late 1970s (1975–1979) and occurred occasionally afterward, whereas southward migration in the central shelf, near the Coastal Domain, occurs when patches of immature crab reach maturity to the east of the axis of the cold pool.[4] These alternative routes are insufficient for a significant southward migration originating in the northern shelf.

Southward transport of larvae produced in the central and northern parts of the shelf appears unlikely. Primiparous (SCI-2) females now spawn primarily in the Middle Domain north of 60°N, where flow is insignificant. There is no evidence of spawning in the Coastal Domain, and the larvae from multiparous females hatching in the Outer Domain are likely to be transported to the northwest, advected by a $1–5 \text{ cm} \cdot \text{s}^{-1}$ flow along the 100 m isobath that becomes increasingly stronger toward the shelf edge, where it reaches $15 \text{ cm} \cdot \text{s}^{-1}$. The implications of some local oceanographic phenomena for snow crab larval retention in the south are not understood, however. An eastward flowing current north of the Pribilof Islands could possibly advect larvae produced in the Outer Domain (otherwise likely to be flushed to the northwest) toward the Middle Domain. Clockwise circulation around the Pribilof Islands and Canyon (Kowalik and Stabeno 1999) may retain larvae

produced in that region, as has been suggested before for blue king crab, *P. platypus* (Armstrong et al. 1985). Such phenomena could possibly create unforeseen favorable conditions for resurgence of the population in the southern part of the geographic range of distribution of snow crab in the EBS.

Many elements of the environmental ratchet hypothesis are based on phenomena (like the regime shift of 1976–1977) that have been observed only once. Future monitoring, as well as research in the less known parts of the EBS, will undoubtedly contribute to a better understanding of snow crab dynamics as well as the combined effects of fishing and climate. Increasingly integrated hypotheses on the functioning of this ecosystem are needed to frame further inquiry. The environmental ratchet hypothesis complements more comprehensive conceptual models, such as the oscillating control hypothesis (Hunt et al. 2002), by contributing a benthic perspective that emphasizes the spatial aspects of population structure and dynamics.

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