

Spatial dynamics of female snow crab (*Chionoecetes opilio*) in the eastern Bering Sea

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Abstract: Snow crab (*Chionoecetes opilio*) migrations in the eastern Bering Sea have long been ignored. Based on preliminary information, we hypothesized that females undergo an extensive ontogenetic migration, tracking down environmental gradients. We analyzed a 25-year time series of survey data and defined ontogenetic stages in terms of a "shell condition index" calibrated with radiochemical methods. "Pseudo-cohorts" of mature females (groups of females that undergo puberty molt in a given year) "recruit" to the mature female pool in the Middle Domain (50–100 m) of the intermediate shelf. Females undergo puberty molt and primiparous mating in winter. Over the next year, they migrate an average net distance of 73.5 nautical miles towards the shelf edge following a predominantly northeast–southwest direction. Maximum post-terminal molt life span is 6–7 years. Results support the hypothesis that the variable tracked is near-bottom temperature. Although near-bottom temperature fields vary from year to year, the corresponding vector field is a conservative template, which explains the consistency observed in the pattern of migration. Elucidation of the life history schedule of mature female snow crabs in the eastern Bering Sea revealed that it is very similar to that reported for eastern Canada, although patterns of migration may differ substantially between the two systems.

Résumé : L'étude des migrations du crabe des neiges (*Chionoecetes opilio*) dans l'est de la mer de Béring a longtemps été négligée. Sur la base de données préliminaires, nous posons l'hypothèse selon laquelle les femelles complètent une importante migration ontogénique, en suivant des gradients environnementaux. Nous avons analysé une série temporelle de 25 années de données d'inventaire et nous avons défini les stades ontogéniques d'après un « indice de condition de la carapace » calibré au moyen de méthodes radiochimiques. Des « pseudo-cohortes » de femelles matures (des groupes de femelles qui subissent la mue de puberté dans une même année) s'incorporent comme « recrues » dans le pool de femelles adultes dans le domaine central (50–100 m) de la plate-forme intermédiaire. Les femelles complètent leur mue de puberté et leur accouplement de primipare au cours de l'hiver. Dans l'année qui suit, elles migrent sur une distance moyenne nette de 73,5 milles marins vers la marge de la plate-forme, en s'orientant dans une direction surtout nord-est et sud-est. La longévité maximale après la mue terminale est de 6–7 ans. Nos résultats appuient l'hypothèse qui veut que la variable qui est suivie soit la température près du fond (NBT). Bien que les champs de NBT varient d'une année à l'autre, le champ vectoriel qui en résulte a une structure relativement stable, ce qui explique la constance qui existe dans les patrons de migration. L'élucidation du calendrier du cycle biologique des crabes des neiges femelles matures dans l'est de la mer de Béring montre qu'il est très semblable à celui qui a été signalé dans l'est du Canada, bien que les patrons de migration puissent différer considérablement entre les deux systèmes.

[Traduit par la Rédaction]

Introduction

Over recent years, there has been considerable interest in exploring the spatial dimensions of population dynamics and of the fishing process (Kruse et al. 2001), which are of particular significance in the case of benthic organisms (Orensanz and Jamieson 1998). The implications of ignoring the spatial structure of benthic stocks, a usual simplification made in model applications under the unit stock paradigm and the dynamic pool assumption (Caddy 1975), need to be better understood. The snow crab (*Chionoecetes opilio*) fish-

ery of the eastern Bering Sea (EBS) is an interesting case in point.

Snow crabs are distributed over the extensive shelf of the EBS (Fig. 1), where it has supported one of the largest crab fisheries in the world (Otto 1989; Stevens et al. 2002). Annual harvest quotas are calculated on the basis of aggregated estimates of abundance using data from systematic summer trawl surveys that have been conducted by the US National Marine Fisheries Service (NMFS) since 1975 (Stevens et al. 2002). The snow crab population of the EBS is assessed and managed as a unit stock (Zheng et al. 2002), although spatial

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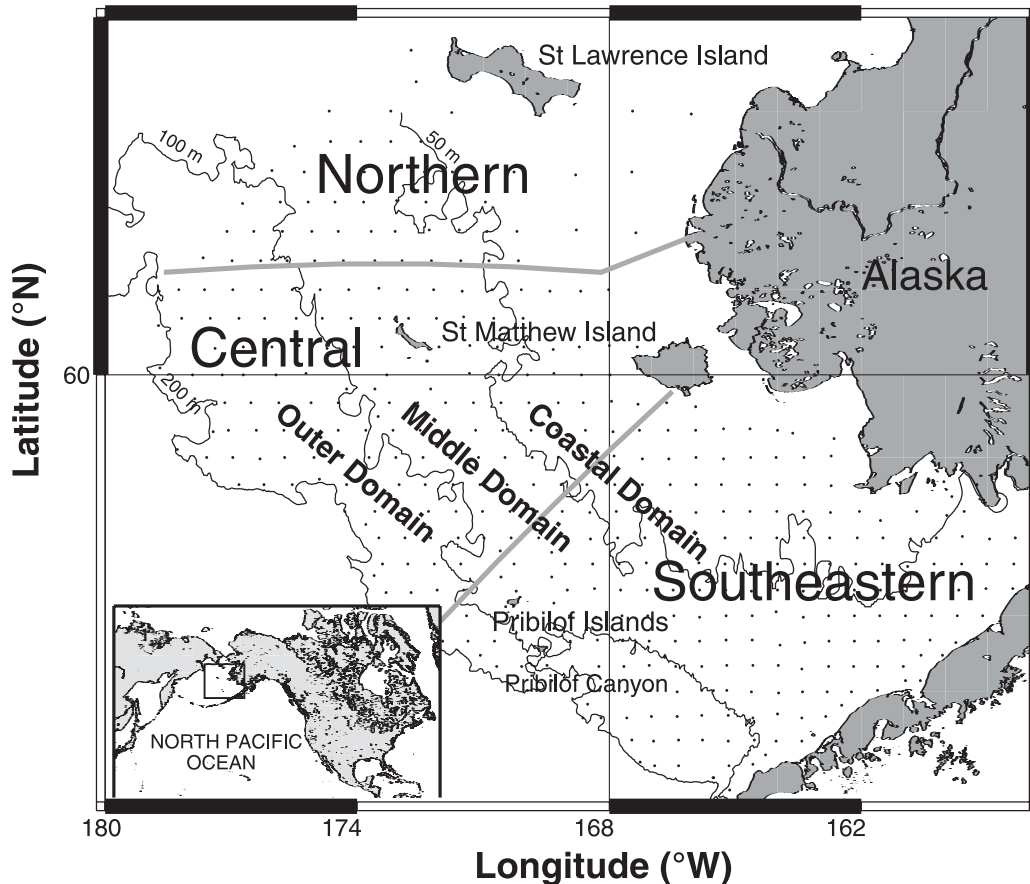
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Fig. 1. Presence of snow crabs (*Chionoecetes opilio*) in the eastern Bering Sea based on the 1975–2001 NMFS trawl surveys. Dots represent stations where snow crabs were caught at least once. The thin lines correspond to the 50-, 100-, and 200-m isobaths.



effort allocation in the male-only fishery (nowadays restricted to the winter months) is constrained by ice cover. The less mobile the individuals and (or) the more spatially structured the population, the less appropriate this assessment/management framework would be. It has been traditionally held that snow crab migrations in the EBS are negligible, if present at all. Somerton (1981a, p. 170) concluded that “short-term changes due to crab migration appear not to be important”, and Incze et al. (1987, p. 1143) pointed out that here is no indication that either [snow or Tanner crab] undertake large seasonal migrations in this region. Yet, paradoxically, differential patterns of distribution of snow crab life history stages in the EBS have long been recognized. Data from the trawl surveys show a striking pattern, early noticed by Somerton (1981b): some areas contain many immatures but few adults and vice versa. The distribution of different types of females shows an offshore shift in location along a progression of life history stages, suggesting a large-scale ontogenetic female migration with a northeast-southwest orientation (Orensanz and Armstrong 1997; Zheng et al. 2001, their fig. 1). The same may apply to males, but this is less clear because of the fact that most of the data do not discriminate between morphologically immature and mature males. The determinants of the hypothetical migration have not been investigated.

Understanding the spatial dynamics of female snow crabs has significant implications for conceptual and formal mod-

els of stock dynamics. Reproductive success of the mature female population is not simply related to the size of the spawning stock but also to (i) the relative spatial distribution of mature males and females and (ii) females hatching their eggs at locations that, given the pattern of water circulation, are appropriate as potential “sources”.

Most studies dealing with the distribution of benthic organisms in relation to environmental variables focus on the absolute magnitude of those factors. The geographic distribution of the variables is usually represented in the form of isolines or contour plots (e.g., Somerton 1981a), and the relationship between environmental factors and organisms has been investigated by means of correlation analysis, multivariate methods, generalized additive models (Swartzman et al. 1992), cumulative distributions along environmental axes (Perry and Smith 1994), etc. Spatial gradients have received little attention, although vector fields are the “roadmaps” that individual crab “see” while trekking over the seabed. An individual that settles away from locations best suited to its environmental preferences may never reach those locations if near-bottom gradients do not lead it in the right direction. The geographic distribution of environmental variables and their aggregate association with abundance are insufficient to understand the patterns of spatial distribution of slow-moving benthic marine organisms.

This study deals with the life history of females after their terminal molt, once they have “recruited” to the mature pop-

ulation and stop growing. Crabs cannot be aged, and the females molting into maturity in any given year are likely to belong to more than one year class. Thus, correspondence between year classes and cohorts of females entering the mature pool cannot be established with certainty. To avoid confusion, we refer to all female crabs entering the mature pool during a given year as a “pseudo-cohort”. Here, we present strong evidence indicating that female pseudo-cohorts undergo an ontogenetic migration in the EBS, hypothesize that this movement is accomplished by following conservative patterns of near-bottom environmental gradients, and explore ways to depict the corresponding gradient fields.

Study system

EBS shelf

The extensive shelf of the EBS, more than 500 km wide, ends seawards in a shelf break (generally coincidental with the 200-m isobath) that spreads along the northwest–southeast direction; the two main geographical features are the St. Matthew and Pribilof islands (Fig. 1). The shelf is conveniently partitioned into three sectors (Schumacher and Stabeno 1998, their fig. 27.1): northern, central, and south-eastern. The latter two, ranging (combined) from the Alaska Peninsula in the southeast to north of St. Matthew Island, constitute the geographic setting of our study. Three zones or domains are usually recognized (Schumacher and Stabeno 1998): Inner or Coastal (shoreward 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 into two naturally discrete segments (southeast and northwest) by the Pribilof Canyon. The Pribilof and St. Matthew islands are located within the Middle Domain; their surrounding shallows are considered here as part of the Middle Domain even though depth is less than 50 m. Up to 75% of the EBS shelf water is covered by ice in late fall – early spring. The advance and retreat of ice average about 1700 km north–south and is the most extensive such process in Arctic regions (Niebauer 1999).

Circulation in the EBS 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 counterclockwise 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 high within the Bering Slope Current ($5\text{--}20\text{ cm}\cdot\text{s}^{-1}$), slower nearshore along the Peninsula ($1\text{--}5\text{ cm}\cdot\text{s}^{-1}$), and very weak within the Middle Domain (Kinder and Schumacher 1981), where there is virtually no net directional flow. Oceanographic and satellite data have revealed an eastward flow ($2\text{--}3\text{ cm}\cdot\text{s}^{-1}$) across the shelf north of the Pribilof Islands (Schumacher and Stabeno 1998). Flow over the Outer Domain is moderate ($4\text{--}8\text{ cm}\cdot\text{s}^{-1}$), following the 100-m isobath towards 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, and this upper layer is heated, which results in stratification of the water column. Crab larvae develop in the upper layer where higher temperature and greater food production benefit growth rate (Incze et al. 1987). The stratified water column “traps” an extensive “cold pool” layer (water $<2\text{ }^{\circ}\text{C}$) 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). Following a warm winter, there may be virtually no cold pool over the EBS – Bristol Bay region (e.g., 1979), or the cold pool may cover most of this region following a very cold winter (e.g., 1995) (B. Ernst, J.M. Orensanz, and D.A. Armstrong, unpublished data). 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.

Ontogeny and reproductive ecology of female snow crab in the EBS

Following Alunno-Bruscia and Sainte-Marie (1998), we use the terms “immature” for sexually immature females, “prepubescent” for females in the instar previous to puberty (terminal) molt, and “mature” for postpuberty females. Females stop growing after the puberty molt, when they reach adulthood; somatic growth is primarily an aspect of the immature life history period. At the puberty molt, there is a dramatic, readily recognizable change in the relative width of the abdominal flap or pleon. Because the molt to maturity is terminal, the best depiction of size at maturity is the size–frequency distribution of mature females (Somerton 1981a). Grand mean carapace width (CW) of mature female snow crab was estimated by Otto (1998) at 56 mm for the EBS (data from 1989–1994 NMFS surveys); most mature females are in the range 35–80 mm (exceptionally down to 26 mm or up to 89 mm). Mean size of mature females varies geographically in the EBS. Somerton (1981b), based on data from the 1979 NMFS survey, explored geographical gradients, finding that mean size decreases northward from approximately 70 mm at 55°N to only 40 mm at 63°N . Otto (1998), based on 1989–1994 NMFS survey data, and Zheng et al. (2001), based on 1978–1999 NMFS survey data, showed the same basic pattern. Instar and age at maturity have not been identified in the EBS. In eastern Canada, females reach maturity at instars ranging from IX to XI, rarely VIII (Alunno-Bruscia and Sainte-Marie 1998; Comeau et al. 1998); maturity is reached at 4.5–6.5 years postsettlement age (Alunno-Bruscia and Sainte-Marie 1998) in the Gulf of St. Lawrence and at 7–8 years in Bonne Bay, Newfoundland (Comeau et al. 1998). The two size modes illustrated by Somerton (1981b) may correspond to instars IX and X or X and XI, implying that in the EBS, most females grow through seven to nine immature instars and the prepubescent instar before maturity. Mating behavior and ecology of snow crabs are very complex and have received considerable attention

(Elner and Beninger 1995). Experimental work conducted in eastern Canada has demonstrated that females can mate after the puberty molt while still in a soft-shell condition or (in subsequent years) while in a hard-shell condition; presumably, this is the case in the EBS as well. The first are termed “primiparous” and the second “multiparous”. The calendar of reproductive events is not well established for the EBS. Hatching/oviposition (and by implication multiparous mating) starts in March and is completed by July (Somerton 1981b, p. 32).

Materials and methods

Survey data

Time series of data were collected during trawl surveys conducted by the NMFS between 1975 and 2001 (Otto 1998; Stevens et al. 2002). Surveys follow a systematic sampling design, where stations are regularly spaced over a 20 nautical mile (nmi) \times 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. The systematic sampling surveys had a consistent spatial coverage after 1978 (Fig. 1). The core temporal window of the surveys is June–July, but in some years, work started in May (1975–1981 and 1999–2000) or ended in August (1975–1976, 1978–1979, 1982–1986, and 1988–1992). Near-bottom temperature (NBT) has been regularly recorded since the initiation of the survey program. Several observations were made on each individual caught in a haul or from a subsample when the catch was too large (“Manual of crab sampling methods for the trawl survey in the eastern Bering Sea”; available from NMFS, Alaska Fisheries Science Center, P.O. Box 1638, Kodiak, AK 99615-1638, USA). In the case of females, these included CW (millimetres), shell condition (see next section), sexual maturity (immature/mature), and various related reproductive variables.

Shell condition index (SCI)

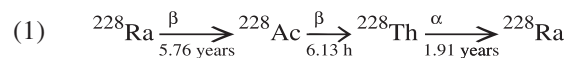
After terminal molt, condition of the shell changes as time passes owing to wear and colonization by epibionts. Subjective SCIs have been devised as a rough correlate of shell age. We used the SCI categories routinely utilized by NMFS as follows. (0) Ready to molt or molting; (1) “soft shell”: carapace soft and pliable, duration very short (weeks); (2) “new hard shell”: carapace firm to hard, clean, brick red to yellow brown on the topside; (3) “old shell”: carapace hard, topside usually yellowish brown, thoracic sternum and underside of legs yellow with numerous scratches, pterygostomial and branchial spines worn and polished, spines on the meri and metabranchial region rounded, epifauna (barnacles and leech cases) usually (but not always) present; (4) carapace hard, topside yellowish brown to dark brown, thoracic sternum and undersides of legs yellow with many scratches and dark stains, pterygostomial and branchial spines rounded with the tips sometimes worn off, dactyli very worn, sometimes flattened at the tip, spines on meri and metabranchial region worn smooth, sometimes completely gone, epifauna most always present (large barnacles and bryozoans); (5) conditions observed in 4 much advanced, large epifauna almost completely covers the crab, carapace

is worn through in metabranchial regions, along pterygostomial branchial spines, or on the meri, dactyli flattened, sometimes worn through, mouth parts and eyes sometimes immobilized by barnacles. Categories 4 and 5 are collectively labeled as “very old shell” and sometimes subsumed under the old shell category for reporting. We refer to this pool as “4+”. Females in SCI 0 and SCI 1 (ready to molt or molted just before capture) are very uncommon in the surveys (on average 0.26% of all mature females) and were not included in our analyses.

For the radiochemical calibration of SCI as an index of time past terminal molt (see section below), we introduced two subcategories: SCI 0⁺ for crabs with extremely soft bodies and SCI 2⁺ for crabs classified as SCI 2 that were closest to conditions defining SCI 3. SCI 0⁺, the softest crabs caught (intermediate between categories 0 and 1), are valuable because they allow validation of assumptions on initial conditions made in radiometric calculations. While it is reasonable to assume that SCI 2 crabs molted within recent months, SCI 2⁺ crabs are expected to help put an upper bound on the duration of that period.

Radiochemical calibration of SCIs

The results presented here (Table 1) correspond to an extension of a previous study by Nevisi et al. (1996) to which we refer for information about field collection and laboratory methods. The estimation is based on the determination of naturally occurring $^{228}\text{Th}/^{228}\text{Ra}$. The basic assumptions for radiometric age determination are that (i) during molting, virtually all of the calcium and associated nuclides are lost by the animal and that (ii) the new carapace is calcified rapidly enough after molting so that (iii) addition or removal of radionuclides during the intermolt period is negligible. When the new carapace is formed, radium is incorporated with calcium into the exoskeleton and with time declines to thorium:



^{228}Th accumulates with time and the activity of ^{228}Th to ^{228}Ra will lead to an age estimate according to

$$(2) \quad \frac{A_{^{228}\text{Th}}}{A_{^{228}\text{Ra}}} = 1.4925(1 - e^{-0.2444t})$$

where t is time expressed in years.

All of the data ($n = 21$) correspond to male individuals, including 17 specimens of snow crab and four specimens of the closely related Tanner crab (*Chionoecetes bairdi*). Assignment of specimens to SCI categories followed consultation with the NMFS expert onboard during the 1992 survey (Dr. Brad Stevens, US National Marine Fisheries Service, P.O. Box 1638, Kodiak, AK 99615-1638, USA). All of the specimens analyzed were males, and the data are utilized under the presumably mild assumption that shells of males and females deteriorate at a similar rate over time. One of the reasons to do measurements on males is that females in SCI 1 are almost never caught in the trawl surveys, but that stage is very important in the calibration of SCIs.

Table 1. Radiometric estimates of shell age in male snow crabs (*Chionectes opilio*) and Tanner crabs (*Chionoecetes bairdi*) ($n = 21$) collected in the eastern Bering Sea during the NMFS survey of 1992.

Shell condition	CW (mm)	Age (years)	Error (years)	Coordinates	Depth (m)	Species
0 ⁺	121	0.05	0.26	59°20'N, 171°49'W	43	<i>C. opilio</i>
0 ⁺	110	0.11	0.27	59°20'N, 171°49'W	43	<i>C. opilio</i>
0 ⁺	132	0.11	0.19	59°20'N, 171°49'W	43	<i>C. opilio</i>
1	118	0.15	0.26	59°20'N, 171°49'W	43	<i>C. opilio</i>
1	130	0.23	0.27	59°20'N, 171°49'W	43	<i>C. opilio</i>
1	116	0.25	0.24	59°20'N, 171°49'W	43	<i>C. opilio</i>
2 ⁺	93	0.33	0.28	57°00'N, 167°43'W	42	<i>C. bairdi</i>
2 ⁺	122	0.42	0.26	57°00'N, 167°43'W	42	<i>C. bairdi</i>
2 ⁺	97	0.66	0.30	59°00'N, 171°47'W	46	<i>C. opilio</i>
2 ⁺	123	0.78	0.32	59°00'N, 171°47'W	46	<i>C. opilio</i>
2 ⁺	121	0.85	0.27	57°00'N, 167°43'W	42	<i>C. opilio</i>
2 ⁺	66	1.07	0.29	59°00'N, 171°47'W	46	<i>C. opilio</i>
3	117	0.92	0.34	59°00'N, 171°47'W	46	<i>C. opilio</i>
3	69	1.04	0.28	59°00'N, 171°47'W	46	<i>C. opilio</i>
3	78	1.10	0.30	59°00'N, 171°47'W	46	<i>C. opilio</i>
4	100	4.43	0.33	57°21'N, 167°45'W	39	<i>C. opilio</i>
4	93	4.89	0.37	58°20'N, 171°38'W	52	<i>C. bairdi</i>
4	100	6.60	0.33	57°00'N, 167°43'W	42	<i>C. opilio</i>
5	111	2.70	0.44	58°60'N, 169°12'W	28	<i>C. opilio</i>
5	100	4.21	0.34	59°00'N, 171°47'W	46	<i>C. bairdi</i>
5	110	6.85	0.58	58°60'N, 169°12'W	28	<i>C. opilio</i>

Analysis of NMFS survey data

Index of abundance

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

$$(3) \quad D_t^S = \frac{1}{n_t^S} \sum_{i=1}^{n_t^S} \frac{d_{t,i}^S}{A_{t,i}^S}$$

where D_t^S is density at station S in year t , n_t^S is the total number of hauls for station S in year t , $A_{t,i}^S$ is the area swept by haul i in station S and year t , and $d_{t,i}^S$ is the number of crabs caught by haul i in station S and year t . We refer to this as “relative abundance” because no gear efficiency correction was used in the analysis. The original database contains approximately 200 000 mature female records.

Parsing and graphics

The data were parsed and analyzed using scripts in AWK stream editor (Robbins 2001). Graphical analysis was conducted using Generic Mapping Tools 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.

Calculation of centroids

Centroids of density for each ontogenetic group in a particular year were computed as weighted averages of longitudinal and latitudinal components:

$$(4) \quad C_t^\phi = \frac{\sum_{i=1}^{n_t^T} \phi_i^S D_i^S}{\sum_{i=1}^{n_t^T} D_i^S}$$

and

$$(5) \quad C_t^\theta = \frac{\sum_{i=1}^{n_t^T} \theta_i^S D_i^S}{\sum_{i=1}^{n_t^T} D_i^S}$$

where C_t^θ is the latitudinal component of the density centroid in time t , C_t^ϕ is the longitudinal component, n_t^T is the total number of stations for year t , ϕ_i^S is the average longitude of station S (across hauls) in time t , and θ_i^S is the average latitude of station S (across hauls) in time t .

Angle and distance of migration

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 relative to the north for specified pairs of stages (e.g., mature females in SCI 2 in year i and SCI 3 in year $i + 1$; see the Results section for rationale):

$$(6) \quad \tau_t = [(\text{SCI}^2 C_t^\theta - \text{SCI}^3 C_{t+1}^\theta)^2 + \{\cos(0.5 \text{ABS}(\text{SCI}^2 C_t^\phi - \text{SCI}^3 C_{t+1}^\phi)) (\text{SCI}^2 C_t^\phi - \text{SCI}^3 C_{t+1}^\phi)\}^2]^{1/2}$$

for southeast migration

$$(7) \quad \Gamma_t = 180^\circ - \arctg \left[\frac{\cos(0.5 \text{ABS}(\text{SCI}^2 C_t^\theta - \text{SCI}^3 C_{t+1}^\theta))}{\text{ABS}(\text{SCI}^2 C_t^\theta - \text{SCI}^3 C_{t+1}^\theta)} \right]$$

for southwest migration

$$(8) \quad \Gamma_t = 180^\circ + \arctg \left[\frac{\cos(0.5 \text{ABS}(\text{SCI}^2 C_t^\theta - \text{SCI}^3 C_{t+1}^\theta))}{\text{ABS}(\text{SCI}^2 C_t^\theta - \text{SCI}^3 C_{t+1}^\theta)} \right]$$

where τ_t is the average migration distance from time t to time $t + 1$ and Γ_t the average angle of migration with respect to true north from year t to year $t + 1$.

Mean size at maturity

Mean values were computed as a weighted average by sampling station (weights proportional to density of each size class in each sample). Equal weight was given to the average size at maturity per station when integrating over time. Size selectivity of the survey gear has not been assessed; immature females smaller than 35 mm CW are poorly represented in the samples. It is assumed that vulnerability is the same for all mature females.

Mapping of environmental gradients

Temperature and depth information was also retrieved from the NMFS trawl survey data set. Given our interest in gradient information, we transformed the original data (temperature and depth) into gradient (vector) fields. To that end, we followed three steps. First, data points for gradient calculation were selected based on the full complement of eight associated observations. Second, overall directional latitudinal and longitudinal components were estimated at each point with respect to the eight immediate neighbor stations in the grid. Third, angle and magnitude of the gradients were computed from vectorial north–south and east–west components.

Results

Aggregated pattern of geographical distribution

Records of snow crab in the NMFS survey data cover virtually the entire grid surveyed between 1978 and 2001 in the EBS shelf, ranging from Bristol Bay and off the Alaska Peninsula to the vicinity of St. Lawrence Island (Fig. 1). The aggregated spatial distribution of females (1978–2001 surveys, data pooled) indicates, however, that significant abundance of mature females has been historically concentrated in the Middle and Outer domains of the Central Shelf (Fig. 2). The boundaries of the aggregated distribution are well captured to the east, west, and south, but the female stock extends farther to the north and northwest over the North Shelf (Paul et al. 1997). The latter has not been regularly surveyed.

The aggregated pattern (1978–2001, data pooled) varies for females in different life history stages. Immature females are remarkably concentrated in the Middle Domain of the Central Shelf and adjacent fringe sectors of the Coastal Domain with hotspots around St. Matthew Island, while mature females in SCI 2 (Fig. 2b) (largely primiparous) are spread over the same region plus the shallower fringes of the Outer Domain. Females in SCI 3 and SCI 4⁺ (Figs. 2c and 2d) (mostly multiparous) are progressively displaced towards the Outer Domain.

The aggregated distribution of mature females (Figs. 2b–2d) shows two broad clusters, roughly separated by the 59°N parallel, each containing a variable number of local maxima. The latter reflect localized pulses of abundance (recruitment to the mature population in the case of SCI 2 females) in particular years. The southern cluster is distributed to the east, north, and northwest of the Pribilof Islands, the southern half of the Central Shelf. The northern cluster is distributed in the northern part of the Central Shelf around St. Matthew Island, where the Outer Domain expands to the west. In some cases, we analyze the two clusters separately using the 59° N parallel as a convenient and reasonable (albeit somewhat arbitrary) line for the partition.

Trends in recruitment to the mature population

By the time of the year when the surveys were conducted, all pubescent females had undergone their terminal molt to primiparous status, and almost all multiparous females were carrying a new clutch of eggs. This conclusion is based on two facts. First, out of a total of 195 366 mature females sampled and checked between 1975 and 2001, 98.5% had yellow/orange eggs. Virtually all SCI 2 egg-carrying females had yellow/orange eggs (0.24% had brown eggs and 0.31% were not carrying eggs). Second, females in SCI 1 were reported in very low numbers during the surveys. Given that the NMFS surveys are conducted once the puberty molt season is over, the abundance of females in SCI 2 reflects the annual recruitment to the mature female population. These females constitute a cohort, but we prefer to use here the term “pseudo-cohort” because the term “cohort” is often equated with “year class”. We did not attempt to trace pseudo-cohorts back into the immature female pool because the latter is possibly a mixture of individuals in different instars that may recruit into the mature population over more than one year.

The trend in pseudo-cohort strength shows well-defined pulses in the two clusters (north and south sectors of the Central Shelf) during the period 1975–2001 (Fig. 3). Recruitment rose to a maximum in 1980 and then dropped to a minimum in 1984 in both clusters. Recruitment was stronger in the south cluster before 1983, but the relationship reversed afterwards, remaining generally stronger in the north cluster during the 1983–2001 period. During this period, although there is some coherence in fluctuations between the two clusters, there are also noticeable differences. During the late 1990s, recruitment dropped sharply in both regions but recovered in 2000–2001 in the north while remaining close to zero in the south during the 5-year period 1997–2001. While peaks in recruitment generally coincide between regions after the 1985 minimum, peaks in the south are dominated by a single pseudo-cohort (1988, 1992, and 1994), while in the north, they are spread over 2 or 3 years (1987–1988 and 1993–1995, respectively). This could reflect differences in year-class strength and (or) differences in age at maturity between the two regions. Although deserving further research, this subject is beyond the scope of our study.

Calibration of shell condition

Females in SCI 2 (virtually all carrying yellow/orange eggs) are presumed to be primarily primiparous, having molted a few months before the survey. Past SCI 2, the meaning of

Fig. 2. Three-dimensional illuminated surface plots of female snow crab (*Chionoecetes opilio*) relative abundance by life history stage: (a) immature, (b) SCI 2, (c) SCI 3, and (d) SCI 4⁺, all integrated over time from 1978 to 2001. In the two-dimensional panels at the bottom, shading is proportional to density. Isobath lines are 50, 100, and 200 m.

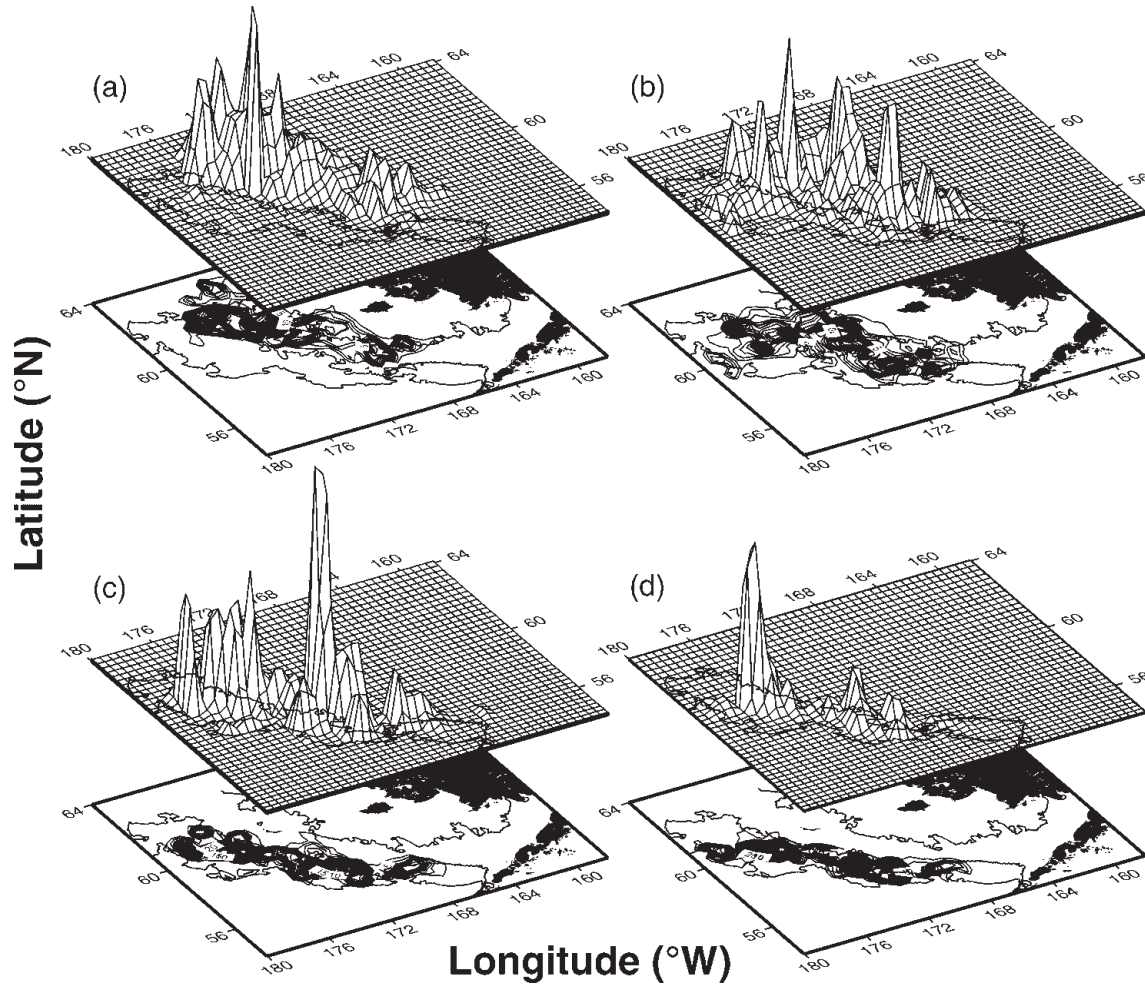
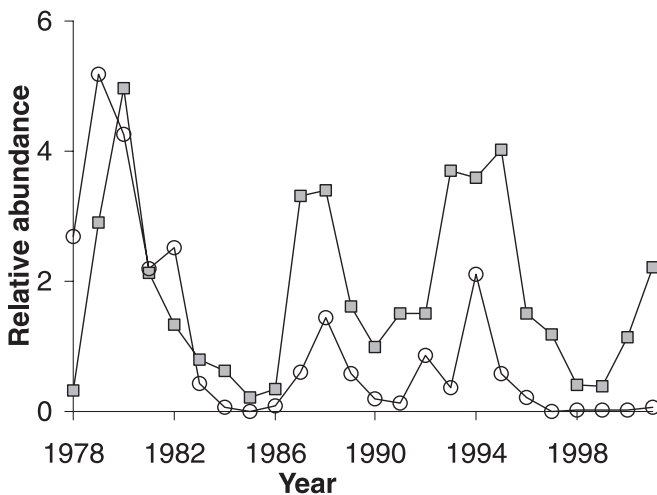


Fig. 3. Recruitment to the mature female snow crab (*Chionoecetes opilio*) population north (shaded squares) and south (open circles) of 59°N in the eastern Bering Sea expressed as an index of abundance of females in SCI 2 during the summer NMFS surveys.



the SCI is unclear. We calibrated it as an index of time past puberty molt in two different ways.

Radiochemical methods

The radiometric technique indicated a postmolt life of 1 month on average ($n = 3$) for male crabs in SCI 0⁺. Considering the measurement error surrounding the estimates (Table 1), the conclusion (consistent with our expectation and assumptions) is that crabs collected in SCI 0⁺ had molted very recently (down to the day when the sample was taken). Estimated postmolt life of SCI 1 males was 1.8–3 months (2.5 months on average, $n = 3$) (Table 1). Since the males sampled were morphologically mature, this implies that the male terminal molt extends approximately from March through May. Our results support assumptions about the initial condition made in radiometric calculations. Radiometric ages calculated for the oldest looking crab that would be classified as SCI 2 by an expert ranged between 4 months and 1 year, with a mean radiometric age of 8.2 months (Table 1). Considering that (i) during the period of the surveys (May–August), females were very rarely found in SCI 1, (ii) the condition SCI 2⁺ was observed in males but not in females (SCI 2 females were mostly on the “new-looking”

end of the SCI 2 range), and (iii) the minimum radiometric age of SCI 2⁺ was 4 months, we conclude that the SCI 2 category corresponds to primiparous females that molted (on average) 3–4 months before the survey. This indicates that female terminal molt and primiparous mating in the EBS occur during the winter (February–March).

The radiometric age of three SCI 3 males collected in June was, on average, 1 year (11–13 months) (Table 1; Fig. 4a), which puts their last molting event slightly after the inferred peak of the male terminal molt season (March–May). Shells of females in SCI 3 should be slightly older, approximately 1.5 years on average, which implies that they correspond to the first-time multiparous group assuming an annual reproductive cycle. The radiometric age of shells in SCI 4 and SCI 5 ranges from 2.7 to 6.8 years. Our results suggest that SCI 4 and higher are poorly correlated (if at all) with shell age (Fig. 4a). Since crabs in SCI 5 included some of the ones in the poorest condition collected during the 1992 survey, it is reasonable to conclude that maximum life span after terminal molt is on the order of 6–7 years.

Tracking an isolated pseudo-cohort

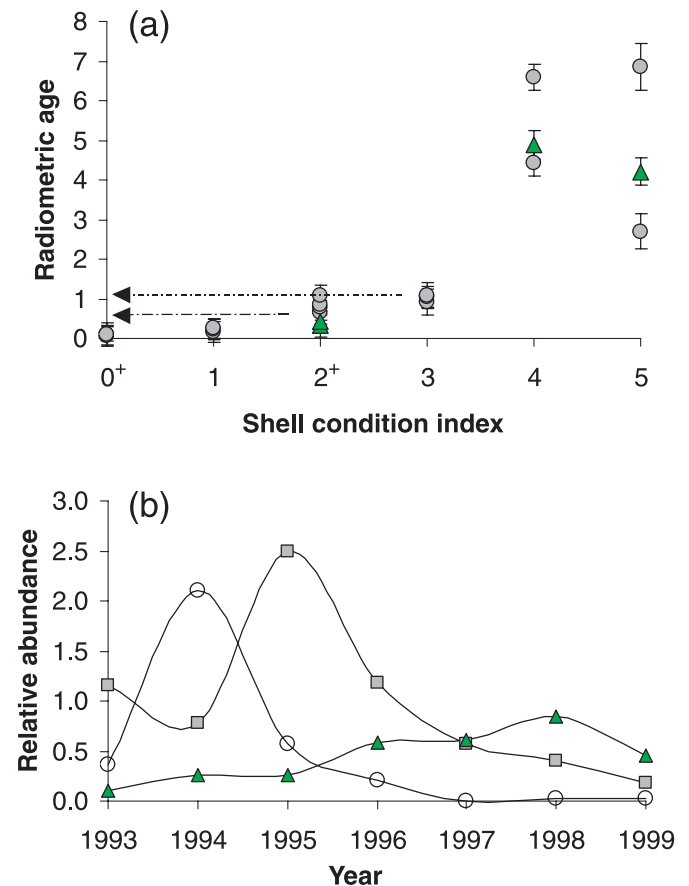
One possible way of calibrating the SCI is to track the abundance of females in each SCI over a few years after the recruitment of a strong pseudo-cohort. Ideally, this should not be immediately preceded or followed by other strong pseudo-cohorts so that transitions can be clearly established. The 1994 pseudo-cohort in the southern cluster best satisfies these criteria: it was preceded by a much weaker pseudo-cohort and, more importantly, was followed by 7 years of insignificant recruitment (Fig. 4b). A clear peak in the abundance of females in SCI 2 in 1994 was followed 1 year later (1995) by a peak of females in SCI 3. The abundance of SCI 4 females gradually increased between 1996 and 1998, declining afterwards. Abundance of females in SCI 5 was negligible throughout the period. This pattern is consistent with the hypothesis that the transition between SCI 2 and SCI 3 takes 1 year. Females in SCI 4 appear to comprise a pool of individuals that were mostly 2 or more years past their puberty molt.

Tracking of an individual pseudo-cohort and radiometric data both suggest that females in SCI 2 and SCI 3 are definable in terms of time past the puberty molt but that females in SCI 4 and SCI 5 correspond to a pool of females that molted 2–6 years before. Thus, in subsequent analyses, we consider only three groups: SCI 2, SCI 3, and SCI 4⁺. These are assumed to have had their terminal molt, respectively, shortly before the time of the survey, 1 year earlier, or 2 or more years before. Given the very low relative abundance of mature females in SCI 4⁺, natural mortality after the second year past terminal molt must be very high; most SCI 4⁺ females are likely to be only 2 years past terminal molt.

Shifts in the geographic distribution of pseudo-cohorts

In a preceding section, we illustrated geographical shifts in the distribution of pooled mature females along the progression of SCI categories (Fig. 2). These shifts are better appreciated when individual pseudo-cohorts are tracked over time, as illustrated with the 1992 pseudo-cohort (Fig. 5). Immature females (prerecruits) were widely distributed in the

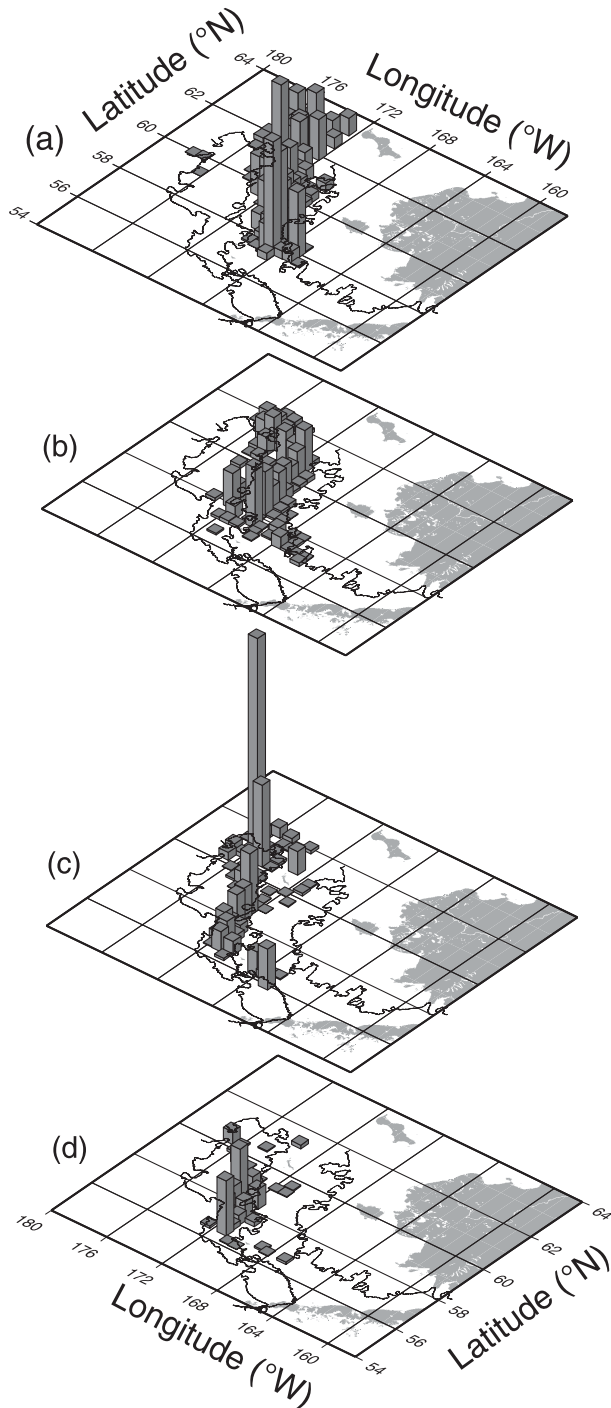
Fig. 4. (a) Radiometric shell age (in years) estimated for males in SCI 0 through SCI 5. Circles, *Chionoecetes opilio*; triangles, *Chionoecetes bairdi*. Vertical bars represent measurement error. Horizontal arrows show the approximate mean age of SCI 2 and SCI 3. (b) Time series of abundance of females in the south, 1993–1999, by SCI. Circles, SCI 2; squares, SCI 3; triangles, SCI 4⁺.



Middle Domain of the Central Shelf during the summer of 1991 (Fig. 5a), a pattern that is typical for that stage. One year later (summer of 1992), the range of SCI 2 females (necessarily originating from a subset of the 1991 immature pool) had shifted from that of the 1991 immatures in several ways (Fig. 5b): (i) at the northern end of the Central Domain, the range contracted southwards, (ii) in the Middle Domain of the Central Shelf, the range contracted on the east, while on the west, it expanded into adjacent sectors of the Outer Domain, and (iii) at the southeastern end of the Middle Domain of the Central Shelf (north of the Pribilof Islands), there was an eastward expansion along the 50-m isobath.

Compared with SCI 2 females in 1992, during the summer of 1993, females in SCI 3 were displaced towards the Outer Domain (Fig. 5c), but the direction of the shift varied regionally: (i) over much of the Central Shelf, the shift was from northeast to southwest into the Outer Domain, (ii) at the southern end of the Central Shelf, west of the Pribilof Islands, the shift was to the south into the Outer Domain, and (iii) at the southeastern end, east of the Pribilof Islands, the shift was also southwards from the 50- to the 100-m

Fig. 5. Snow crab (*Chionoecetes opilio*) pseudo-cohort of 1992. Relative spatial density of life history stages over the eastern Bering Sea. (a) Immature females in 1991; (b) mature females in SCI 2 (1992); (c) mature females in SCI 3 (1993); (d) mature females in SCI 4⁺ (1994). Notice the geographic progression of immature and SCI 2 females in the Middle Domain to older stages in the Outer Domain. Isobaths are 50, 100, and 200 m.



isobath, east of the Pribilof Islands. In 1994, the range of the SCI 4⁺ pool (integrated by females of the 1992 pseudo-cohort and older) was generally similar to that of SCI 3 females in 1993, except that it had shrunk southward towards

the northern end of the Outer Domain of the Central Shelf (Fig. 5d). Contraction of the range could be the result of mortality, movements, or a combination of both; the data do not allow examination of these alternative hypotheses.

To investigate these shifts across pseudo-cohorts, we used the centroids of the geographic range of each pseudo-cohort calculated by SCI (2 and 3). We calculated centroids for the entire region covered by the NMFS surveys and for the northern and southern partitions of the Central Shelf (defined earlier) separately. We focus on the centroids for females in SCI 2 and SCI 3 because (i) the average transition time between these is consistently 1 year, (ii) most of the mature females sampled in the surveys (86.3 %) were in either SCI 2 or SCI 3, and (iii) most of the shift in geographical distribution between SCI groups occurs in the transition between SCI 2 and SCI 3. To track and summarize shifts in the distribution of pseudo-cohorts, we connected the centroids for females in SCI 2 in year i and SCI 3 in year $i + 1$. When the whole region is considered (Fig. 6a), all vectors (Table 2) are rooted north of 58°N, reflecting the significance of the northern part of the Middle Domain for recruitment. Most vectors are oriented towards the southwest, the most notable exception being the three earlier pseudo-cohorts followed in the study (1978–1980), which had their recruitment (SCI 2) centroid located north of the Pribilof Islands and shifted to the south–southeast. The mean angle of the vectors (Fig. 6a, inset) was 200° clockwise from the north, and the average length of the vectors' moduli was 73.5 nmi (range 37–128 nmi).

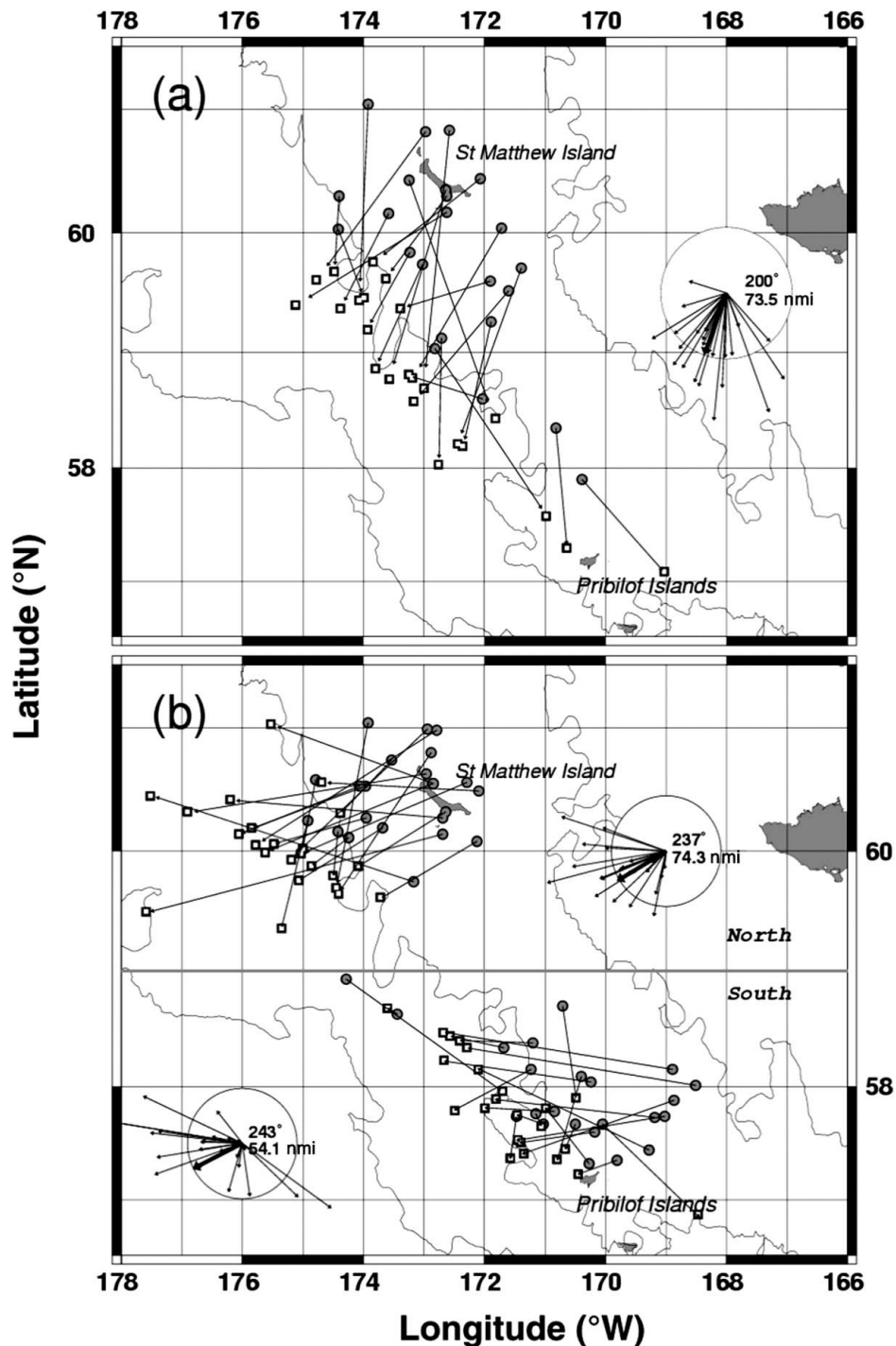
Centroids calculated separately for the northern and southern partitions of the Central Shelf are shown in Fig. 6b. Vectors in the northern partition point predominantly to the southwest (186–290° clockwise from the north), with a mean angle of 237° and a mean modulus of 74.3 nmi (range 22.9–152.7 nmi). In the southern partition, the pointing direction of the vectors is more variable, but the mean orientation is (as in the northern partition) towards the southwest (mean angle 243° clockwise from the north, mean modulus 54.1 nmi). Whether the Central Shelf is partitioned into northern and southern sectors or not, (i) the vectors point (on average) to the southwest of the SCI 2 centroid, (ii) the centroids for SCI 2 females are virtually always located in the Middle Domain, and (iii) the centroids of SCI 3 females are always located in the Outer Domain or near the border between the Middle and Outer domains.

During the study period, there was a pronounced shift to the north and west of the centroids of geographic distribution of females in SCI 2 and SCI 3 between 1978 and 1985 that continued in a more gradual fashion thereafter (Fig. 7). Between 1978 and 2000, the centroid of SCI 2 females shifted from 58°N in 1978 to north of 60°N in 1998–2000 (120 nmi), mostly between 1978 and 1985. The northward shift of SCI 3 females was steep during the latter period, but the position of the centroid fluctuated around 59°N afterwards. The westward shift (Fig. 7) was sharper in the case of SCI 3 females and (as in the case of the latitudinal shift) occurred mostly between 1978 and 1985.

Environmental gradients

Bottom temperature in the EBS during the summer was investigated using data from the NMFS surveys, which were

Fig. 6. Centroids of abundance of mature snow crab (*Chionoecetes opilio*) females in SCI 2 (circles) and SCI 3 (squares) by pseudo-cohort. Thin arrows connecting centroids represent average annual migration (distance and azimuth). Inset circles summarize the migration pattern; the thick arrows represent average migration pattern; the thick arrows represent average migration pattern. (a) Centroids and migration computed for the entire Central Shelf; (b) Central Shelf divided into northern and southern sectors at 59°N.



conducted mostly during late spring – early summer. Although these data provide a good representation of the distribution of bottom temperature over the entire area of interest, there is one important caveat: temperatures were always recorded over a 2- to 3-month period while the surveys progressed from east to west. Thus, there is room for some

confounding of within-season temporal trends and spatial pattern.

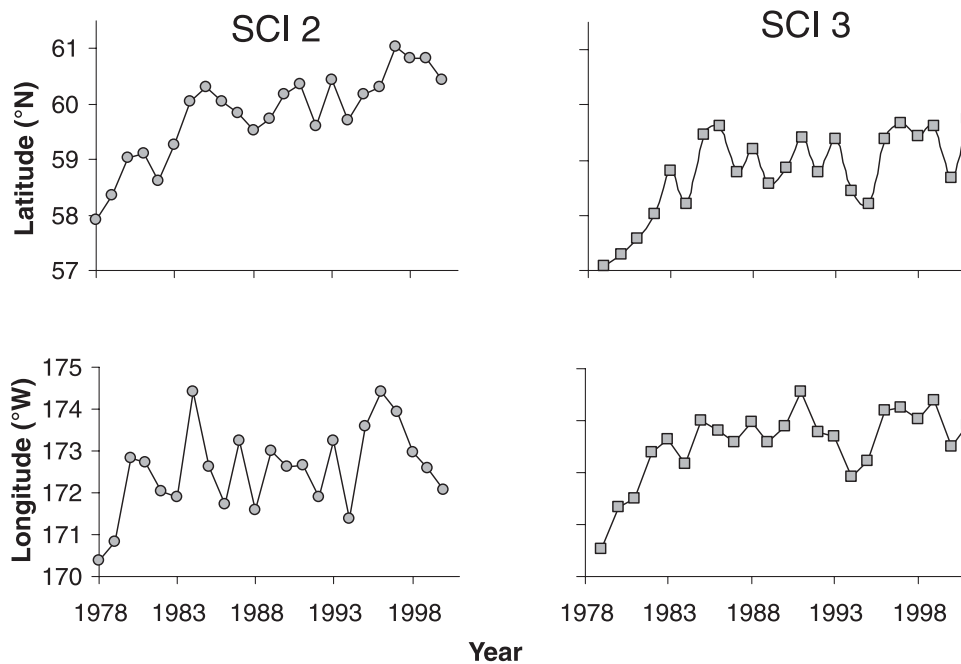
The typical distribution of NBT during the summer is illustrated for 1996 in Fig. 8a. A most significant feature in the context of this study is the cold pool of the Middle Domain. From there, NBT increases towards the Coastal

Table 2. Distance between centroids of snow crab (*Chionoecetes opilio*) mature females in SCI 2 during the summer of year *i* and in SCI 3 during the summer of year *i* + 1 (annual pseudo-cohorts 1978–2000).

	Combined		North		South	
	Azimuth	Distance (nmi)	Azimuth	Distance (nmi)	Azimuth	Distance (nmi)
1978	138	65.69	288	137.00	134	70.37
1979	175	63.43	255	152.73	251	21.86
1980	146	104.78	194	54.95	202	14.25
1981	181	65.42	233	22.91	242	45.58
1982	288	40.19	238	49.15	156	7.12
1983	193	65.84	240	55.70	188	22.42
1984	160	36.47	186	22.16	126	99.94
1985	217	50.95	238	51.08	172	48.47
1986	211	87.97	247	88.57	276	84.43
1987	209	44.24	255	47.36	295	99.78
1988	221	74.38	275	104.67	261	78.95
1989	204	58.20	248	63.99	262	39.93
1990	238	88.58	261	118.56	273	36.76
1991	197	98.89	248	88.89	278	77.66
1992	253	47.44	290	83.82	196	45.63
1993	160	128.00	224	36.18	322	37.43
1994	200	96.08	214	82.73	251	84.65
1995	207	53.27	250	59.80	290	14.73
1996	183	37.54	191	34.34	282	28.57
1997	183	96.20	191	81.91	279	120.93
1998	217	90.56	227	91.86	303	5.83
1999	186	129.33	238	104.50	279	121.24
2000	232	66.96	273	76.63	272	38.26
Average	200	73.50	237	74.33	243	54.12

Note: Calculations are presented for the entire Central Shelf and for partitions north and south of 59°N. Azimuth is measured clockwise from the north in degrees and the length of the modulus in nautical miles (nmi) (1 nmi corresponds to a latitudinal minute).

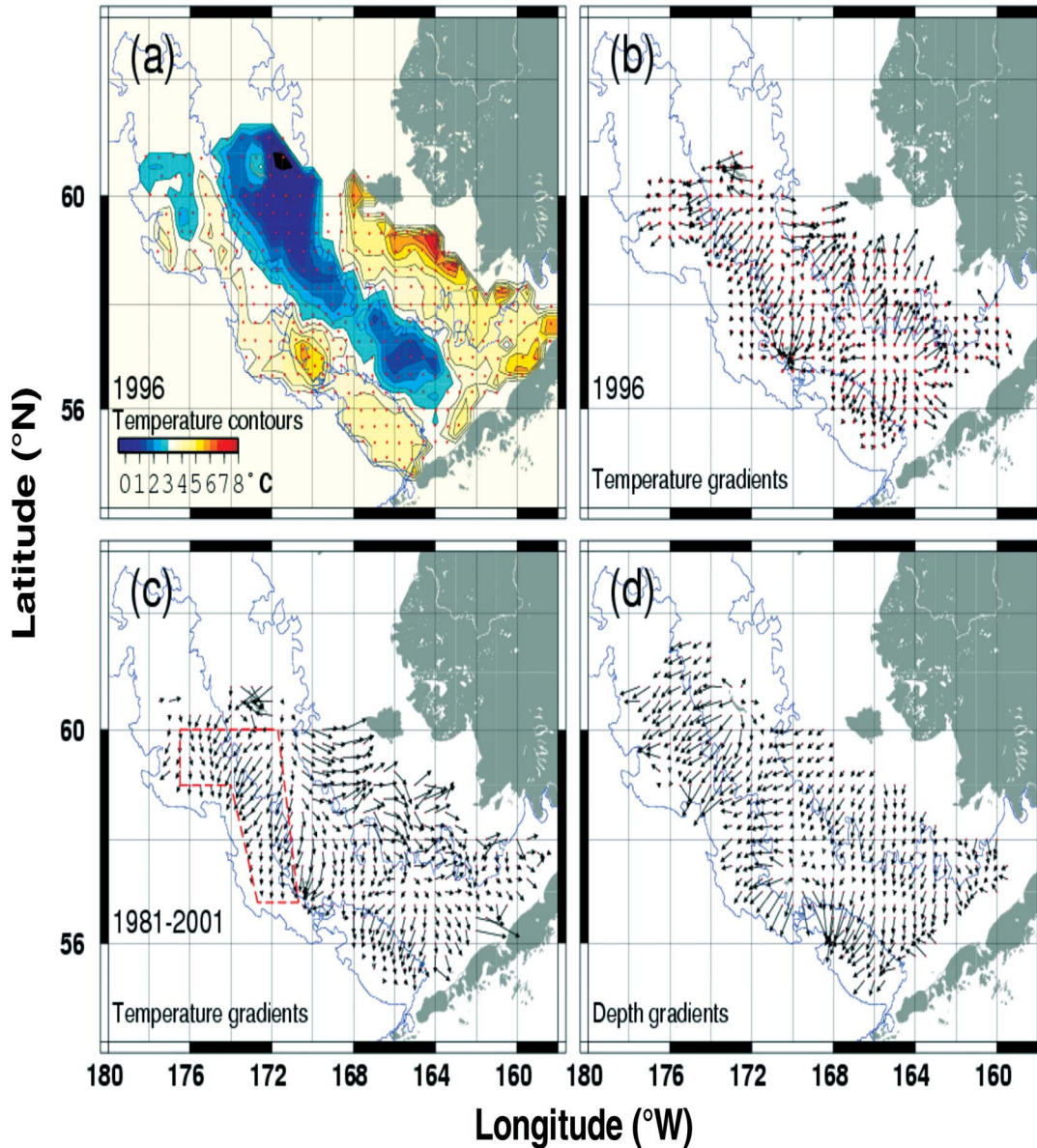
Fig. 7. Time series of centroids of abundance for snow crab (*Chionoecetes opilio*) females in different life history stages.



Domain (to the northeast) and towards the Outer Domain and shelf break (to the southwest). Small patches of relatively warm water surround the Pribilof Islands and to a

lesser extent St. Matthew Island. This pattern governs the shape of NBT gradients in the Central Shelf, shown as vector fields for 1996 (Fig. 8b) and for the average of 1981–

Fig. 8. Summer NBT and depth in the eastern Bering Sea. Points correspond to actual survey stations. (a) The 1996 summer NBT contours; (b) gradients of NBT during the summer of 1996; (c) average gradients of NBT during the summer, period 1981–2001; the polygon shows the station data set used to study environmental variables and migration shown in Fig. 9; (d) depth gradients.



2001 (Fig. 8c, data for 1975–1980 surveys lack information for many stations). There is a “plateau” (low steepness) region coincidental with the cold pool at the core of the Middle Domain. From there, gradients pointing off the Central Domain (from cold to warm) are grouped into several main vector fields (Figs. 8b and 8c): (1) towards the Coastal Domain, steep gradients point “downstream” from the west or the northwest, (2) towards the Outer Domain, between St. Matthew and the Pribilof Islands, gradients point to the southwest, (3) in the southeast, east of the Pribilof Islands, gradients pointing to the Outer Domain are oriented to the south, and (4) centripetal gradient fields develop around the Pribilof and St. Matthew islands.

Depth gradients (pointing from shallow to deep) (Fig. 8d) are similar to NBT gradients in the case of gradient field 2 but opposite in the case of 1 and 4, as temperature increases towards both the shelf break (deeper) and the coast (includ-

ing the islands, shallower). As is the case for temperature, steepness of the gradients is minimal over the Central Domain.

Compared with temperature fields (captured by isotherms) (Fig. 8a), NBT gradients based on NMFS survey data are likely to be more insensitive to the east–west progression of the survey because the group of neighboring stations used to calculate a vector (typically one central point and its eight nearest neighbors) are generally occupied within a few days. Gradient fields are more conservative than temperature itself, their general configuration being the same during warm and cold years.

Correspondence between environmental gradients and inferred migration route

Let us consider only the region of the Central Shelf where evidence of an ontogenetic migration is stronger, i.e., the

Middle and Outer domains, north of the Pribilof Islands and west and south of St. Matthew Island (enclosed in a dashed polygon in Fig. 8c). There is remarkable correspondence of circular (azimuthal) distributions between (i) the proportion of average inferred migration vectors (centroids of SCI 2 in year i to SCI 3 in year $i + 1$) and (ii) the proportion of average NBT gradients in the Middle Domain quadrant (Fig. 9). There is less matching between either of the two and the circular distribution of depth gradients (which, of course, constitutes a fixed template). In other words, inferred migrations tend to follow the predominant orientation of NBT gradients rather than the fixed topographic gradient template.

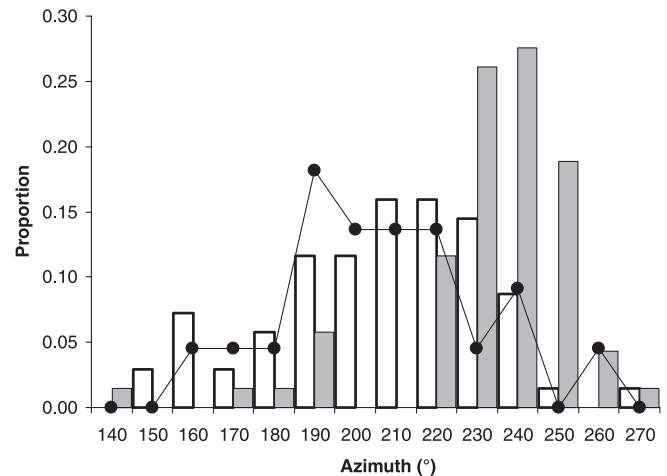
Geographic patterns in the size structure of the mature female population

The existence of a geographical gradient in the average size of mature females in the EBS is shown using the pool of all females sampled in the surveys (Fig. 10). Mature females range in average from more than 70 mm CW at the southeastern end of the range to less than 50 mm CW towards the north, between St. Matthew and St. Lawrence islands. Given that growth stops at the puberty molt (time of recruitment to the mature female pool), geographic patterns in the distribution of average size of pseudo-cohorts should be informative about ontogenetic migration routes. An area where females in SCI 2 are small in year i should be connected (through migration) to an area where females in SCI 3 are correspondingly small in year $i + 1$. Provided that there are consistent geographical patterns in the size of mature females, average size could be used as a tracer. The 1988 pseudo-cohort offers a unique opportunity to investigate this hypothesis. In that year, most of the recruits (SCI 2 females) were very concentrated in a large patch located to the southeast of St. Matthew Island (Fig. 11a). One year later (summer of 1989), SCI 3 females were concentrated in a dense patch located to the southwest of the 1988 SCI 2 patch (Fig. 11b) into the Outer Domain. Average female size contours for the two years (1988–1989) pooled show an intrusion of relatively small females along a corridor that would correspond to the migration path of the 1988 pseudo-cohort (Fig. 11c). The corridor has the same orientation as NBT vectors in the same region during the summer of 1988 (Fig. 11d).

Discussion

As the members of a snow crab female pseudo-cohort age, there are few ways to track them through time. Under some assumptions (see Materials and methods), radiometric techniques can provide an estimated time since last (in this case terminal) molt. There are several variations of these techniques; radiochemical methods (used by us) take long and are time-consuming. More recently, the use of gamma spectroscopy (a relatively fast technique) has allowed the analysis of large samples (e.g., Gardner et al. 2002), but it requires special facilities (not available to us) and is expensive. In either case, radiometric methods are valuable for calibration purposes but impractical to age large samples. A second method is based on subjective (qualitative) indices of shell deterioration (“condition”), including colonization by epibionts. Among the latter, barnacles can be aged, providing a

Fig. 9. Distribution of the orientation of depth gradients (shaded bars), temperature gradients (open bars), and ontogenetic migration (SCI 2 to SCI 3) around the azimuth (in degrees with respect to true north) (circles). The frequency of temperature and depth gradients was computed for the area indicated in Figs. 8c and 8d, which overlaps most with inferred routes of ontogenetic migration.

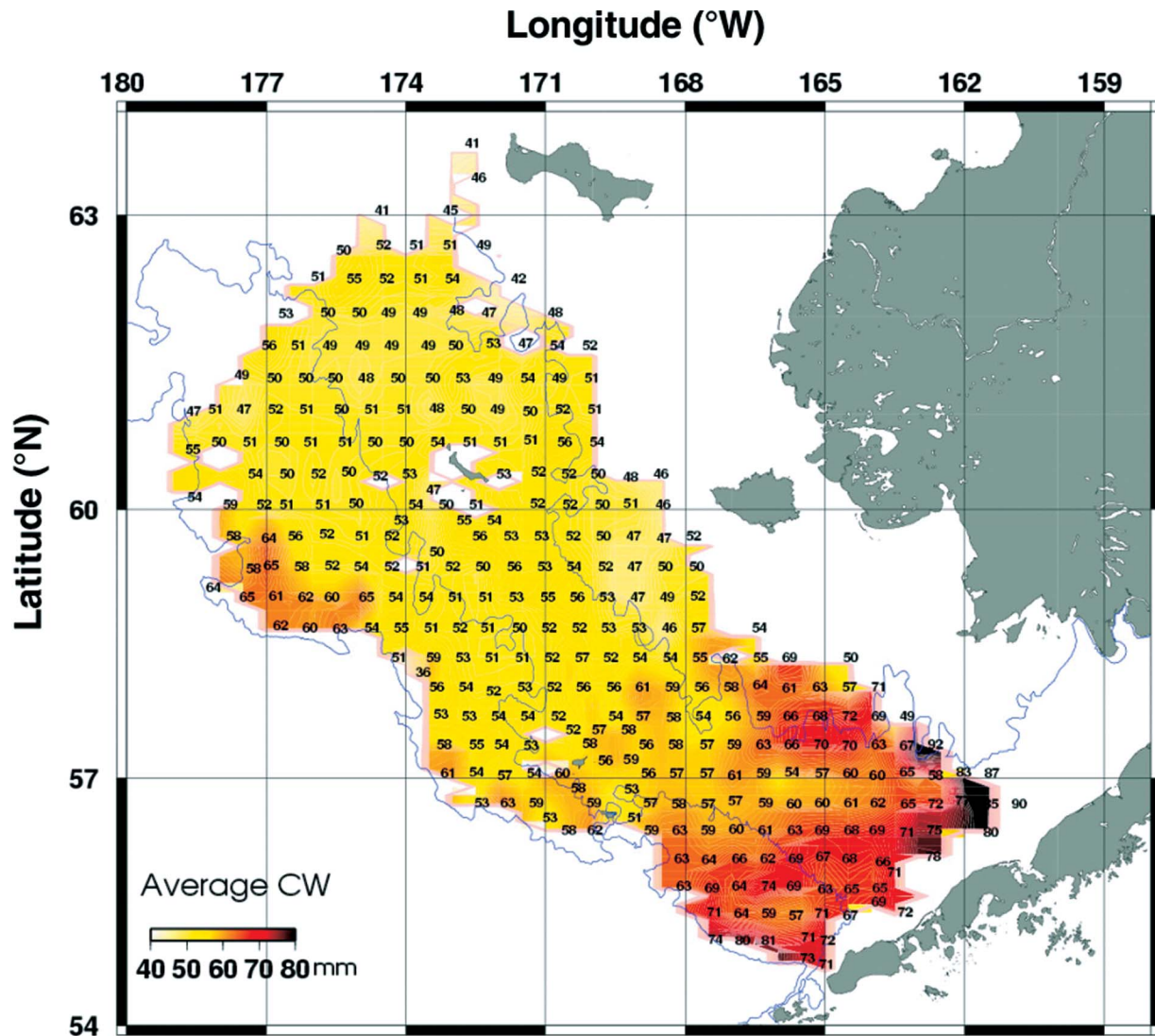


lower boundary estimate of the age of the host's shell (e.g., Paul and Paul 1986). We disregarded this alternative because of the fact that barnacles were present on only 20% of the females processed in the laboratory. We used the radiometric analyses to provide a calibration and also attempted tracking identifiable pseudo-cohorts through time. The results of the two methods coincide: SCI 2 and SCI 3 largely correspond to, respectively, females that molted during the current calendar year and during the previous one. Thus, SCI 2 females are the primiparous recruits to the female pool. In the case of an annual reproductive cycle, SCI 3 females would be first-time multiparous.

The life history schedule of mature females in the EBS is poorly known. The timing of the puberty molt has not been documented in the EBS, although it is over by the time the annual NMFS survey is conducted (May–August). Our radiometric results indicate that the female terminal molt (and consequently primiparous mating) in the EBS must occur during the winter (February–March). Interestingly, this is also the case for eastern Canada, where it occurs in February–April, beginning before the ice breakup (Moriyasu et al. 1987; Sainte-Marie 1993; Sainte-Marie et al. 1995 and references therein). In the EBS, hatching and subsequent oviposition start in March and are completed by July (Somerton 1981b). This, too, is comparable with eastern Canada, where hatching of mature eggs, mating, and subsequent extrusion of new eggs occur in April–June (Taylor et al. 1985; Sainte-Marie 1993; Comeau et al. 1999). Thus, as is also the case in eastern Canada, primiparous mating takes place 2–3 months earlier than multiparous mating. For the same reason, primiparous females carry eggs for a longer period than multiparous females (approximately 14 versus 12 months in the case of an annual reproductive cycle).

In eastern Canada, the timing of the terminal molt of males has been observed in aquaria in winter and early spring (February – late April; Conan et al. 1990) and was inferred

Fig. 10. Average CW of mature snow crab (*Chionoecetes opilio*) females, all SCIs and 1978–2001 surveys combined. Individual numbers correspond to average CW at each NMFS survey station.

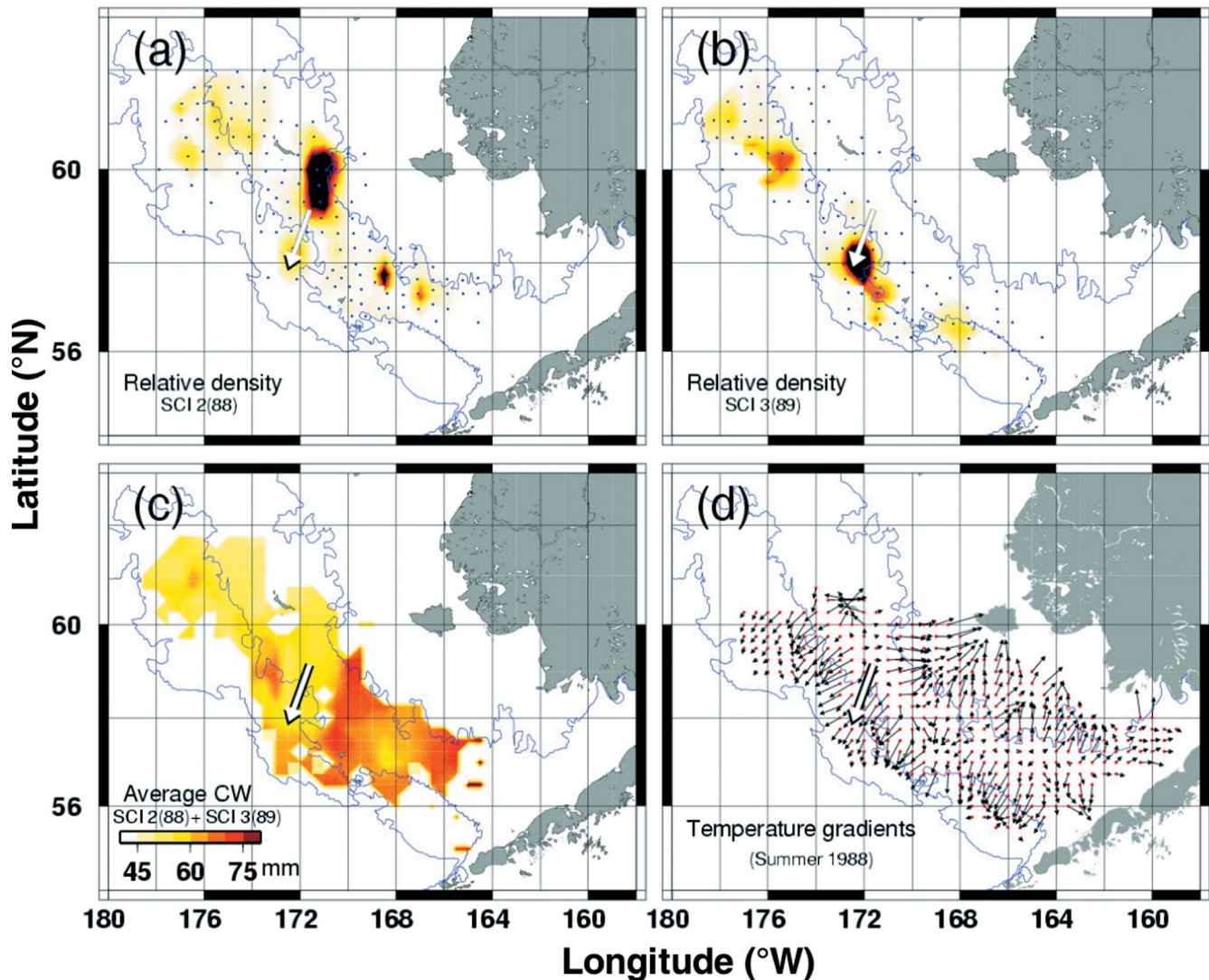


to peak in the field during the spring (March–May) (Sainte-Marie et al. 1995 and references therein; Conan et al. 1996). Consequently, the puberty molt of females peaks before the terminal molt of males, possibly allowing the latter to mate with primiparous females before molting into morphological maturity. The timing appears to be the same in the EBS (B. Ernst, J.M. Orensanz, and D.A. Armstrong, unpublished data), as the proportion of recently molted (SCI 1) large males (CW > 102 mm, presumably morphologically mature) caught by the NMFS surveys (aggregated data) peaks in June and July (23.8% and 21.9%, respectively, of the large males). According to our radiometric results, those SCI 1 males should have molted up to 3 months earlier. We hypothesize that the pseudo-cohorts of morphologically mature males that were 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” crabs. A very similar phenomenon has been proposed for eastern Canada populations. After males and females molt into maturity in shallow water dur-

ing late winter and spring, a radiotelemetry study showed that while females remained in shallow water, males moved offshore (Conan et al. 1996). If disturbed, morphologically mature males can move several miles in a few days. These observations are consistent with the hypothesis that recruitment of large males to deep coastal fishing grounds occurs following a down-slope movement of recently molted males (Coulombe et al. 1985; Bouchard et al. 1986; Sainte-Marie and Hazel 1992).

Somerton (1981b) was the first to track a pseudo-cohort of snow crab mature females in the EBS. He tracked the 1969 pseudo-cohort through the early 1970s and concluded that maximum life after terminal molt is approximately 5 years. Both radiometric methods (Nevisi et al. 1996; this study) and tracking of an identifiable pseudo-cohort (this study) suggest that maximum post-terminal molt life span in the EBS is on the order of 6–7 years. This, again, is in line with estimates from eastern Canada, where it has been estimated by means of tagging (Sainte Marie et al. 1996) and radiometry (Conan et al. 1996). These studies indicate that it

Fig. 11. Tracking of the 1988 snow crab (*Chionoecetes opilio*) pseudo-cohort. Dots correspond to NMFS survey stations with recorded abundance. The large arrow indicates the direction of movement of the core of the pseudo-cohort distribution. (a) Abundance of SCI 2 females in 1988; (b) abundance of SCI 3 females in 1989; (c) surface plot of CW of individuals of SCI 2 in 1988 and SCI 3 in 1989 combined; (d) NBT gradients during the summer of 1988.



can reach a maximum of 5–6 years. We conclude that the annual schedule of life history events from the terminal molt onwards is virtually the same in eastern Canada and the EBS for both females and males.

While differential patterns of distribution of snow crab life history stages in the EBS have long been recognized (Somerton 1981b), it has been traditionally held that migrations in the EBS are negligible, if present at all (Somerton 1981a; Incze et al. 1987). However, there is growing evidence of an extensive ontogenetic migration of both males and females from shallower to deeper waters (Otto 1998), with a predominant northeast–southwest direction (Orensanz and Armstrong 1997; Zheng et al. 2001). This can be inferred from the spatial shifts in the distribution of SCI categories, whether cohorts are pooled or not. Tagging experiments conducted in the EBS between 1978 and 1982 showed an average displacement of 75 km for males (McBride 1982).

In this study, we expanded from those preliminary indications. Females become vulnerable to the NMFS survey gear

when they reach a size range (30–60 mm CW) that is roughly equivalent to the three instars preceding the terminal molt, presumably owing to size selectivity of the trawl gear. This pool of immature females is concentrated in the Middle Domain and adjacent fringe of the Coastal Domain of the Central Shelf. For smaller crabs, the only piece of information available on a regional scale comes from fish stomach contents, predominantly Pacific cod (*Gadus macrocephalus*) caught during the same NMFS surveys (Livingston 1989). Livingston (1989) found that snow crabs (size range 3–87 mm but predominantly smaller than 35 mm, her fig. 6) tend to occur in stomachs of Pacific cod caught in the Middle Domain or adjacent sectors of the Coastal Domain (her fig. 3). This is virtually the same geographical range observed for immature females caught in the surveys.

Female recruits to the mature population (SCI 2) are also concentrated in the Middle Domain of the Central Shelf but slightly displaced towards the Outer Domain in comparison with immatures. Females in SCI 3 (1 year past terminal

molt) appear displaced towards the Outer Domain, a pattern that emerges both in the aggregated data and when individual pseudo-cohorts are tracked (e.g., the 1992 pseudo-cohort). The consistency and recurrence of the pattern could not be possibly explained by mechanisms other than an ontogenetic migration (e.g., differential survival). Errors in the assignation of individuals to SCI categories may affect the estimated rate of annual migration but not the basic pattern or the orientation of the migration. Assignation errors would result in an underestimation of the annual rate of migration, as centroids for the two groups would be pulled closer to each other. Older females (SCI 4⁺ pool) are concentrated in the Outer Domain. The transition between SCI 2 and SCI 3 is the most significant in terms of the average distance of the migration (approximately 75 nmi) and the reproductive contribution of the stages involved. The reproductive contribution of older females (SCI 4⁺ pool) is likely to be of limited significance owing to mortality (only 13.7% of the mature females caught over 25 years were in that group) and reduced fecundity related to senescence.

Given that females stop growing after terminal molt and that there is variation in size at maturity between pseudo-cohorts, strong pulses composed of exceptionally large or small individuals could be tracked in time and space, as they contrast with the background population (pool of other pseudo-cohorts). In the case of males, this edge was utilized by Otto (1998), who was able to track a strong pseudo-cohort of morphologically mature males, identifiable because of its small size, as it vanished from shallow areas (<80 m) after 1990, showing up in deeper water in 1991. In a similar way, we were able to track a strong, localized pulse of small-sized recruits of the 1988 pseudo-cohort as they intruded (with a southwest direction) across a background region characterized by larger females.

An ontogenetic unidirectional offshore migration has been also reported for shelf/slope populations of *Chionoecetes tanneri* (Pereyra 1966) and snow crabs of Japan (Ito 1968; Kon 1969; Yamasaki and Kuwahara 1993). In the latter, females molt to maturity and mate at a depth of 200–300 m. Males and females migrate offshore afterwards, the male migration being far more reaching; males, on average, end up in deeper areas than females, apparently not returning to shallower areas.

The ontogenetic migration of female snow crabs in the EBS, as seen through the “window” of NMFS’ summer surveys, appears to be unidirectional. We hypothesize that during their directed ontogenetic migration, female snow crabs track environmental gradients. Two possibilities are depth and NBT. These variables are often illustrated in the form of isolines (isobaths and isotherms), but the resulting charts are of limited value in the interpretation of crab movements, as the latter do not “see” a map integrating information for a large region but, rather, respond to conditions in their immediate vicinity. Considering their sensorial complement, crabs are more likely to follow temperature than depth gradients, although the latter could be correlated with other factors, such as sediment composition or temperature itself. Experiments conducted by Dionne et al. (2003) demonstrated that juvenile snow crabs make active choices based on water temperature and substrate. Starting from the Middle Domain (low temperature and intermediate depth) where the offshore

ontogenetic migration of mature females begins, summer NBT and depth gradients do not run in the same direction offshore (towards the Outer Domain, deeper and warmer water) and onshore (towards the Coastal Domain, shallower and warmer water). Considering summer gradients only, and given that there is no evidence of an inshore migration into the Coastal Domain, the most parsimonious assumption would be that females track the depth gradient, which would consistently lead them offshore. During the winter, however, as the ice cover develops, water in the Coastal Domain becomes colder and the gradient, although not well documented for that time of the year, reverses its direction (Phyllis Stabeno, National Marine Fisheries Service, 7600 Sand Point Way Northeast, Seattle, WA 98115, USA, personal communication). From the Middle Domain towards the Outer Domain, the gradient of NBT is colder to warmer year-round. Orientation of the integrated annual migration of primiparous females (SCI 2 females in year i to SCI 3 females in year $i + 1$) is remarkably similar to summer NBT gradients observed between the Middle and Outer domains. The distribution of migration vectors matches the distribution of NBT gradients better than it does the depth gradient template. We hypothesize that snow crabs in the EBS generally track NBT gradients and that onshore movements away from the Middle Domain are prevented by the winter cooling and excessive summer warming of the Coastal Domain. Alternatively, it could be hypothesized that mature primiparous females move onshore during the fall and return during the spring. This seasonal migratory cycle is unlikely given that SCI 3 females (the presumable condition of females migrating back to the Middle Domain during the spring) are virtually absent during the summer from fringe areas of the Middle Domain adjacent to the Coastal Domain.

A relationship between snow crab distribution and temperature has been documented for the EBS (Somerton 1981b), the Sea of Japan (Yosho and Hayashi 1994), and eastern Canada (Tremblay 1997). Temperature-related shifts in spatial distribution have been documented for eastern Canada. Dionne et al. (2003) argued that early benthic stages of snow crab (instars I–IV) are stenothermic, occurring in the northwest Gulf of St. Lawrence immediately above and below the core of the cold intermediate layer at NBT > 0 °C. Consistently, the thermopreferendum observed in laboratory experiments was in the range 0–1.5 °C. The thermopreferendum shifted in the laboratory to a warmer range (1.0–4.5 °C) at instars III and V (Dionne et al. 2003). A similar relationship could exist in the EBS with the cold pool (NBT < 2 °C) that develops over the Middle Domain during the spring and summer (Somerton 1981b; Livingston 1989).

Seasonal migrations between the Outer and Middle domains of the EBS could not be investigated because surveys are conducted only during the summer. Although an eventual offshore–onshore seasonal component superimposed to the offshore ontogenetic migration of females cannot be captured through the “windows” available (the NMFS summer survey), it seems to exist in males (B. Ernst and J.M. Orensanz, unpublished data). If seasonal migrations did exist, then seasonal female “onshore” (to shallower water) net displacements should be shorter than the subsequent “offshore” displacements. The result, as observed through the summer window, would still be a unidirectional ontogenetic migra-

tion. A phenomenon of this type was documented by Brêthes and Coulombe (1990) for males off the north shore of the Gulf of St. Lawrence. Snow crab seasonal offshore–onshore migrations have been well documented in the Gulf of St. Lawrence ecosystem (eastern Canada), where male and female crabs are present in shallow waters during late winter and early spring (Taylor et al. 1985; Sainte-Marie and Hazel 1992; Conan et al. 1996). Some adult males move into the shallow waters in December (coincident with the start of the pubescent female molting period), while the abundance of adolescent males increases over the winter, suggesting a slightly later arrival (Lovrich et al. 1995). The conditions that elicit seasonal aggregation in shallow-water locations are unknown; they have been variously interpreted as the result of a directed reproductive migration or, more generally, tracking temperature gradients following stage-specific thermopreferenda (Sainte-Marie and Hazel 1992). Crabs move away from the shallow coastal area during the summer, when surface temperature begins to warm and exceeds the core temperature of the cold intermediate layer.

Our hypothesis about the ontogenetic migration being driven by NBT implies the assumption of no upper limit to thermal preference (at least within the geographic domain of interest). Seasonal reversals in the prevalent direction of migration would require a more complex hypothesis, including ontogenetic changes in the thermopreferendum (e.g., as in Dionne et al. 2003) and (or) the nonlinearity of thermal preference.

A full comparative discussion with eastern Canadian scenarios is not possible because environmental variables are unevenly documented and have not been analyzed in the same way in the different systems. It is likely, however, that while the timing of life history events appears to be very similar between eastern Canada and the EBS, this may not apply to patterns of migration. Resultant directionality of the ontogenetic migration and onshore–offshore seasonality may be different in the two systems owing to the different ways in which NBT gradients are structured, in particular relative to the cold intermediate layer in the Gulf of St. Lawrence and the cold pool in the EBS. In the EBS, there is no indication of a seasonal migration into the Coastal Domain, which would be analogous to seasonal migrations to shallow waters in the Gulf of St. Lawrence (Lovrich et al. 1995). Ontogenetic migration is directed, instead, towards the deeper and warmer waters of the Outer Domain. Migration towards deeper waters for access to warm water is not a viable option for juvenile snow crabs in the Gulf of St. Lawrence, considering the severity of hypoxia at depth (Dionne et al. 2003).

The ecosystem in which snow crabs evolved is unknown and so the original adaptive significance of behavioral characters observed in extant populations cannot be interpreted with certainty to provide an explanation for movements in the EBS. The various systems that now harbor snow crab populations on both sides of North America are relatively recent, as all originated after the retreat of ice during the last postglacial period. It is not likely that in such a brief time, local populations were fine-tuned by natural selection in characters such as the nature of the environmental gradients tracked during migrations. More likely, snow crabs may prosper in different systems with the same basic repertoire of rel-

atively simple behavioral responses, a possible result being that crabs end up doing different things at different locations, yet for the same reasons.

Whichever the case, we show that the female population of snow crabs of the EBS has strong spatial structure and a directed ontogenetic migration, but the latter cannot be invoked to justify homogeneity assumptions. At a reasonably large scale (on the order of kilometres), a perturbation of the mating system at a given location (e.g., removal of males by the fishery) may be compensated by down-gradient migration in one direction (e.g., northeast–southwest) but not by cross-gradient displacements in the orthogonal direction (e.g., northwest–southeast).

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