

# SPATIAL DYNAMICS OF SNOW CRAB (*CHIONOECETES OPILIO*) IN THE EASTERN BERING SEA—PUTTING TOGETHER THE PIECES OF THE PUZZLE

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## ABSTRACT

Landings of the snow crab *Chionoecetes opilio* (J. C. Fabricius, 1788), which supports a lucrative fishery in the eastern Bering Sea (EBS), dropped to historical lows by 2000, and the geographic range of reproductive females contracted to the northwest. Resilience of the mature female range through larval advection may be hampered because hatching now occurs downstream. These changes have been punctuated by four pulses of recruitment, with a remarkably regular period of 6–7 yrs. Major pulses of the fishery, during the 1990s, were sustained by recruitment pulses that originated in regions of the northwest section of the EBS shelf beyond the reach of the fishery. Here we present, for the first time, a conceptual model of snow-crab spatial dynamics that integrates empirical information with new results from modeling of circulation and larval transport. The geographic region of interest, defined by means of biophysical modeling and tracking ontogenetic migrations, consists of the middle and outer domains of the EBS shelf, bounded by the 50- and 200-m isobaths. Connectivity analysis highlights the significance of subsystems in the southeast and northwest sections of the EBS's middle domain. Predicted settlement regions match historical regions of abundance of immature crabs and are consistent with observed fields of suitable near-bottom temperature. Our study, together with others, highlights the significance of climate change for the fate of important high-latitude fisheries.

Scenarios of climate change have prompted concerns about the future of high-latitude fisheries (Perry et al., 2005; Grebmeier et al., 2006; Mueter and Litzow, 2008). Snow crabs [*Chionoecetes opilio* (J. C. Fabricius, 1788)] from the eastern Bering Sea (EBS) shelf, which have supported one of the largest and most lucrative crab fisheries in the world, are a case in point. Over the last two decades landings have declined dramatically, from a maximum of nearly 150,000 metric tons (mt) in 1991 to historical lows on the order of 12,000 mt by 2000 (Danner, 2007) (Fig. 1). The EBS snow crab stock was declared “overfished” in 1999 because the survey estimate of mature biomass was below the minimum stock-size threshold. A rebuilding plan was implemented in 2000; model estimates of the biomass of commercial-size males continued to decline through 2003, then increased after 2006 (NPFMC, 2007; Fig. 1). Compared to that three decades earlier, the current geographic range of the snow-crab spawning female stock has contracted dramatically to the north (Zheng et al., 2001; Orensanz et al., 2004). This phenomenon has been addressed by the environmental-ratchet hypothesis (ERH) (Table 1; Orensanz et al., 2004), a conjecture postulating that the contraction is a process difficult to reverse, because of a combination of factors such as circulation patterns, spatial dynamics of benthic stages, increased near-bottom temperature (NBT), and predation by fish (mostly cod).

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Table 1. Components of the environmental ratchet hypothesis, and consistency with results from recent studies (including the one reported here). Significant insights gained from the biophysical model correspond to components 2, 3, and 5. The coastal domain is shoreward from the 50-m isobath, the middle domain is between the 50- and 100-m isobaths, and the outer domain is between the 100-m isobath and the shelf break.

Components of the environmental ratchet hypothesis, as stated by Orensanz et al. (2005)	Consistency with recent findings
1. Snow crabs 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.	The first element is upheld. Hypothesized favorable conditions for larval growth and survival in the middle domain, particularly in relation to the ice edge, remain untested.
2. Larval retention in the middle domain is favored because of weak currents.	The role of the middle domain is upheld, but the mechanisms involved are different. Results from the individual-based model highlight (i) retention systems east of the Pribilof Islands and north of St. Matthew Island, (ii) northwestward transport along the middle domain, and (iii) northward transport from the outer domain into the middle domain.
3. The region of seabed suitable for settlement is circumscribed by the 2 °C near-bottom temperature (NBT) isotherm, that is, the cold pool, which expands over the middle domain to the southeast during cold years.	Consistency between individual-based-model predictions and field data upheld this element and placed new emphasis on the middle domain of the northwestern section of shelf.
4. The lagged northward shift of female pseudocohorts associated with warming during the 5-yr period 1975–1979 indicates a corresponding northward shift in recruitment to the benthic population (settlement and early benthic survival). Two hypothetical reasons are that appropriate conditions for larval growth and survival are associated with spring blooms that develop under colder conditions and that early juvenile stages are stenothermic, requiring a NBT below 2 °C.	The first rationale remains untested (see also component 1). The second is upheld by consistency between field data and results from the individual-based model of larval transport (see also component 3)
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 downstream.	This component is fully consistent with results from the individual-based model of larval transport.
6. Repopulation of depleted regions to the southeast of the middle domain may be hampered because routes of ontogenetic migration channel females offshore, toward the outer domain, in both cold and warm years, reflecting the dominant direction of environmental gradients tracked during the migration (depth, NBT).	This component is fully consistent with our new explorations and data on ontogenetic migrations.
7. After contraction of the stock to the north, cod predation on juveniles controlled the southward expansion of the range of immature females.	This component is consistent with recent results on cod predation (Julián Burgos, University of Washington, Seattle, pers. comm.)
8. Population resurgence on the southeastern shelf after a return to prewarming conditions, might, depending on the residual local reproductive stock, be hampered by the small size of the latter.	So far, this hypothesis has not been contradicted.

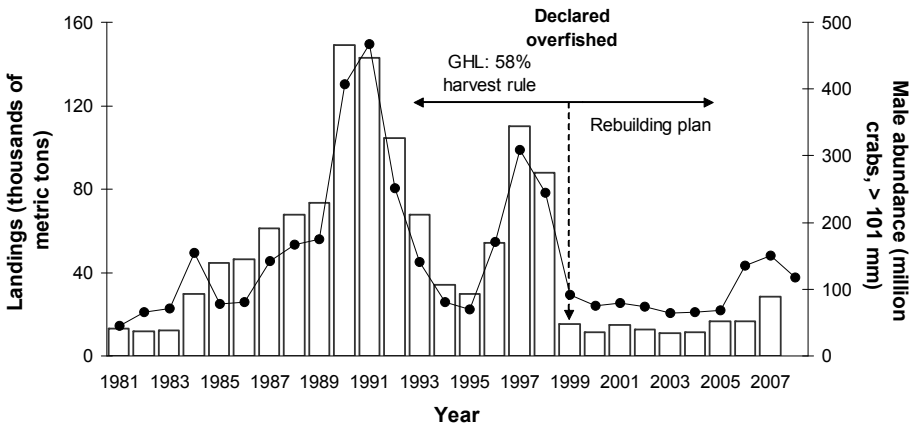


Figure 1. Annual landings of snow crab (*Chionoecetes opilio*) from the eastern Bering Sea (bars) and estimates of commercial-size males based on survey data (dots and line). GHL, guideline harvest level.

Evidence of connections between climate and stock dynamics often consists of cross-correlations between time series of environmental and fisheries or ecological observations. The complex and highly structured spatial dynamics of the snow crab introduces the opportunity for exploration of mechanistic hypotheses, because specific processes take place at different loci on the spatial/environmental template where the life cycle unfolds (Ernst et al., 2005; Orensanz et al., 2004, 2008). Substantial gaps remain, however, in knowledge about the snow crab population from the EBS, particularly regarding pelagic larvae and early benthic stages. Asymmetries in larval dispersion related to circulation patterns, a central tenet of the ERH, remain untested. Speculation about connectivity and conditions encountered in potential settlement regions has not been substantiated by either field research or modeling.

Our study brought together recent results pertaining to the pelagic and benthic stages of this population. Potential connectivity between areas of virtual larval release and settlement were examined by means of a biophysical model of snow-crab early life history and geographical information systems (GIS) tools. The ERH was evaluated in light of the new results, particularly those related to potential connectivity and virtual larval retention. Finally, we introduced a conceptual model that coherently brought together the pieces of a complex spatial puzzle and discuss its implications for fisheries management.

#### DATA, TERMS, AND MODELS

**ANNUAL SURVEYS CONDUCTED BY THE NMFS.**—Time series of data on snow crab juveniles and adults have been collected during bottom trawl surveys conducted by the U.S. National Marine Fisheries Service (NMFS) since 1975 (Otto, 1998; Rugolo et al., 2006; Chilton et al., 2008a,b). Surveys follow a systematic sampling design; primary stations are regularly spaced over an orthogonal grid, and stations, spaced 20 nautical miles from each other, are sampled every year (Fig. 2A). 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

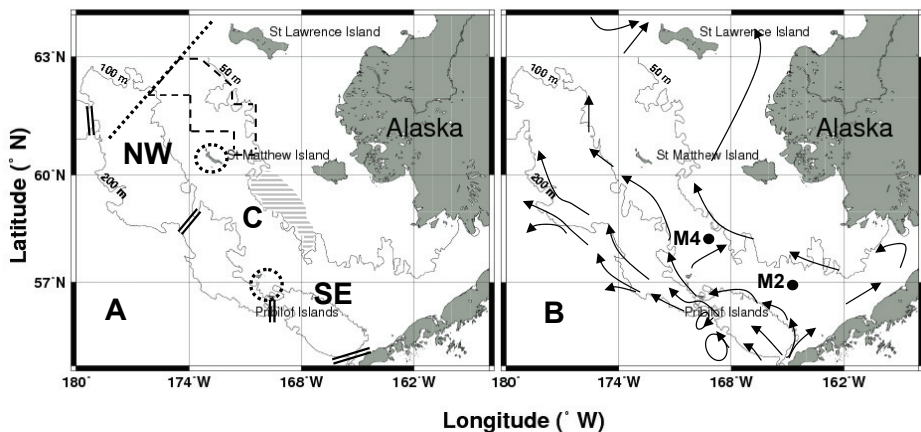


Figure 2. The eastern Bering Sea shelf. (A) major geographic features relevant to the spatial dynamics of benthic stages of snow crabs. Sections of the shelf: northwest (NW), central (C), and southeast (SE). Double bars: constrictions that naturally divide sections of the outer domain; separation between central and southeast sections corresponds to the Pribilof Canyon. Dotted circles highlight St. Matthew Island and the Pribilof Islands, main geographical features of the middle domain. Dots: stations of the annual survey (not all have been consistently occupied every year). Shading: fringe region of the coastal domain. Dashed polygon: region covered by the “northern stations.” Dotted line: boundary of the region surveyed. (B) General pattern of circulation in the eastern Bering Sea (modified from Stabeno et al., 2001). M2 and M4: mooring stations.

spatial coverage after 1978. Additional stations located to the north were covered sporadically in a few years (1979, 1985, 1991). In 2001 and 2004–2006 a sector of the northeast shelf (“northern stations,” data not available for our study) was added to the survey according to the standard design (Fig. 2A). The core temporal window of the surveys is June–July, but in some years sampling started in May or ended in August. NBT has been regularly recorded since the initiation of the survey program. Observations were made on each individual caught in a haul or, when the catch was too large, from a subsample. Carapace width (CW, measured to the nearest mm) and a shell-condition index (SCI) were recorded for both males and females (Ernst et al., 2005). Also recorded for females was sexual maturity based on relative width of the abdomen. Starting in 1989, propodus height of the claw was recorded in a subsample of males.

**BASICS OF SNOW CRAB LIFE HISTORY.**—In the EBS survey information on immature snow-crab instars came from cod stomachs (CW > 10 mm, primarily instars IV–VIII) and survey samples (CW > 25 mm, primarily instars VII–IX) (Orensanz et al., 2008); virtually no information is available for instars I–III, corresponding to the first year of benthic life. Male and female snow crabs stop growing after the “terminal molt,” a transition recognizable in the relative width of the abdominal flap in females and in the relative size of the claws in males. After terminal (“puberty”) molt females mate for the first time (undergo “primiparous” mating) while still in a soft-shelled condition. In subsequent years females spawn in a hard-shelled condition. Females carrying their first batches of eggs are collectively known as “primipara,” and those that have spawned at least two broods (the second one in a hard-shelled condition) as “multipara.” Multiparous females may mate soon after hatching of a brood. Following Sainte-Marie et al. (2008), we refer to males as “immature” (sexu-

ally immature), "adolescent" (physiologically mature not having been through terminal molt), or "adult" (having been through terminal molt, entirely mature); the term "mature" is applied to all sexually mature males, including adolescents and adults. Male physiological maturity, recognizable by the presence of spermatophores in the vas deferens, occurs over the size range 33–38 mm CW in eastern Canada (Comeau and Conan, 1992; Sainte-Marie et al., 1995), but may occur at smaller sizes at higher latitudes, e.g., in the Chukchi Sea, where males mature over the size range 20–30 mm CW (Paul et al., 1997). Following Comeau et al. (1998) we categorize females as "immature" or "mature" depending on whether or not they have been through their terminal molt. The more detailed categories defined by Sainte-Marie et al. (2008) cannot be delineated with available survey data from the EBS.

Following Ernst et al. (2005), we refer to all female crabs entering the mature pool during a given year as a "pseudocohort" and to the corresponding event as "recruitment to the mature female pool" or "pseudocohort recruitment." Because of variation in age at maturity, members of a pseudocohort can belong to more than one year class. Mature females in SCI category "2" (denoted "SCI 2"; relatively clean, newer shell) are considered to be primiparous, having molted to maturity during the winter before the survey (Ernst et al., 2005). When sampled by the survey during their second year after terminal molt, they have reached SCI 3. In later years the condition of their shells continues to deteriorate, but correspondence between SCI and post-terminal-molt age is gradually lost. "Mature SCI 2+ females" include all females in SCI category 2 and higher, i.e., the pool of mature females. Mature SCI 3+ females include the pool of multiparous females, plus those primiparous females on a biennial brooding schedule that are in their second brooding year.

**MAPPING ABUNDANCE AND TRACKING PSEUDOCOHORTS.**—Indices of abundance of different stages, based on survey data, were estimated, analyzed, and mapped as described by Ernst et al. (2005). Graphical analysis was conducted with Generic Mapping Tools graphical software (Wessel and Smith, 1998). The surface plots required by some graphs, which implied the additional calculation of regular station grids over the entire distributional region, were accomplished by means of a nearest-neighbor algorithm. Aggregated spatial patterns of environmental conditions and crab distribution include data from years 1978 to 2002, the same period for which larval transport was simulated (see below).

Aggregations of mature SCI 2 females in year  $i$  can be tracked to SCI 3 in year  $i+1$  on the basis of survey data (Ernst et al., 2005; Orensanz et al., 2004, 2008). Graphic renditions of the post-terminal-molt migration have been presented before for six out of the 30 pseudocohorts represented in the time series of NMFS surveys (1978–2007): 1985 and 1986 (Orensanz et al., 2004, their fig. 7), 1988 (Ernst et al., 2005, their fig. 11), 1980, 1991, and 1992 (Ernst et al., 2008a, their figs. 6 and 9). According to the same approach, average migration vectors were compiled for the 25 pseudocohorts recruited to the mature female pool during the period 1978–2002.

**INDIVIDUAL-BASED MODEL OF LARVAL TRANSPORT.**—An individual-based model (IBM) of snow-crab early life history was developed to simulate larval transport from source areas of interest to potential spring and summer settlement areas. The IBM was coupled to a hydrodynamic model of the Bering Sea Regional Ocean Model System (ROMS), run with a 10-km grid from 1978 to 2002 (northeast Pacific, Curchitser et al., 2005). Geographic patterns of NBT predicted by ROMS for the period

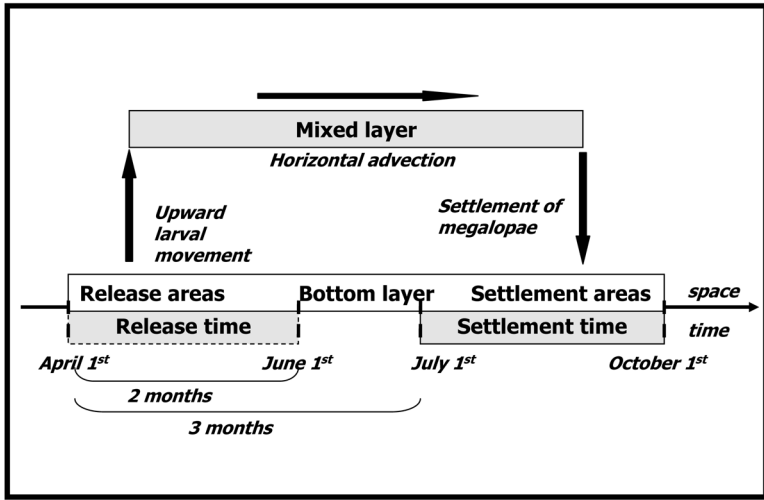


Figure 3. Conceptual model of snow crab larval transport.

June–July match very closely those observed during the NMFS summer surveys but have (on average) a systematic upward bias of 1 °C for exact dates and locations. Consequently, predicted NBT was adjusted by subtraction of 1 °C. Adjusted NBT predicted for the period July–October was used to investigate the thermal suitability of potential settlement regions.

Virtual particles representing larvae were released near the bottom and soon afterwards were made to migrate upward to the mixed layer, remaining there until they reached the megalopa stage (Fig. 3). Virtual larvae are capable of vertical movement and variable swimming speed. In the simulations reported here, larvae swam randomly up or down within the mixed layer. Release time was set to occur between 1 April and 1 June; “settlement” took place 90 d later. Note that, in the context of the model, “settlement” is defined as the time at which the megalopa stage is reached and larvae are presumed to become demersal or hyperbenthic. The duration of the megalopa stage is unknown; spatial dispersal of the megalopae is presumed to be negligible in view of the geographic scale of the patterns investigated here. In this Lagrangian application, the trajectory of each particle was tracked through time and space. Variables such as temperature, salinity, depth, position, and stage were recorded along the trajectory of each virtual particle. Exploration of the effects of variable duration of the pelagic stages, hatching date, and exact hatching location is beyond the scope of this study and will be the subject of forthcoming contributions. The position of each particle at the time of virtual settlement and the associated NBT, as well as the location of origin of the particle, were recorded at the end of the simulation. This information was used to construct an average connectivity matrix (1978–2002); connectivity between source  $x$  and a sink  $y$  was calculated as the fraction of the virtual larvae originating in source region  $x$  that settled in sink region  $y$ .

## INTERLINKING PROCESSES

**SIGNIFICANT FEATURES OF THE EASTERN BERING SEA SHELF.**—The extensive shelf of the EBS (Fig. 2A), more than 500 km wide, ends seaward in a shelf break (generally coincidental with the 200-m isobath) that spreads along the NW–SE direction. Three zones or domains are usually recognized on the southeast shelf on the basis of bathymetry and oceanographic conditions (Schumacher and Stabeno, 1998; Stabeno et al., 2008): 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 southeast section 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). We used the same bathymetric boundaries to define domains in the central and northwest sections of the EBS shelf, although the oceanographic correlates of those partitions are not as well understood as in the southeast. In the middle domain, the main features are St. Matthew Island and the Pribilof Islands. In the outer domain, the Pribilof Canyon isolates the expanses to the southeast, whereas the northwest and central sections of the EBS are naturally separated by constrictions at about 59°N and 61–62°N (Fig. 2A). The bathymetric definition of the middle domain is amended to include a fringe region of the coastal domain southwest of Nunivak Island (CD fringe, Fig. 1) on the basis of extension of the cold pool and the distribution of immature snow crabs (Orensanz et al., 2004).

Circulation in the EBS (Fig. 2B) is dominated by the Alaska Coastal Current, which enters from the Gulf of Alaska through Unimak Pass and other passes along the Aleutian island chain (Reed and Stabeno, 1996). Much of the Alaska 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 Alaska 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 ( $5\text{--}20\text{ cm s}^{-1}$ ), slower near shore along the peninsula ( $1\text{--}5\text{ cm s}^{-1}$ ), and very weak within the middle domain (Kinder and Schumacher, 1981). Oceanographic and satellite data have detected an eastward flow ( $2\text{--}3\text{ cm s}^{-1}$ ) across the shelf north of the Pribilof Islands (Reed and Stabeno, 1996; Schumacher and Stabeno, 1998), although this was not observed in recordings at mooring site 4 (Fig. 2B) by Stabeno et al. (2007). Data from mooring sites 2 and 4 (Fig. 2B) reveal a weak mean flow with a southern component from April to September (Stabeno et al., 2007). Flow over the outer domain is moderate ( $4\text{--}8\text{ cm s}^{-1}$ ) and follows the 100-m isobath toward the NW.

Up to 75% of the EBS shelf water is covered in most years by ice from late fall through early spring. As ice melts in spring, the less saline water “floats” over higher-salinity marine water, this upper layer is heated, and stratification of the water column results. The stratification “traps” an extensive “cold pool” of water (summer NBT  $< 2^\circ\text{C}$ ) down to the seafloor over a large part of the middle domain. South of St. Matthew Island, the southeast reach of the cold pool varies from year to year. After a warm winter (e.g., 1979), it may be virtually absent over the EBS–Bristol Bay region; in contrast the cold pool may cover most of this region after a cold winter (e.g., 1995) (Orensanz et al., 2004).

Gradient fields of NBT in the EBS are best documented for the summer period, when the summer NMFS survey has been conducted since 1975. Regional NBT fields show some remarkable regularity. South of St. Matthew Island, the axis of the cold

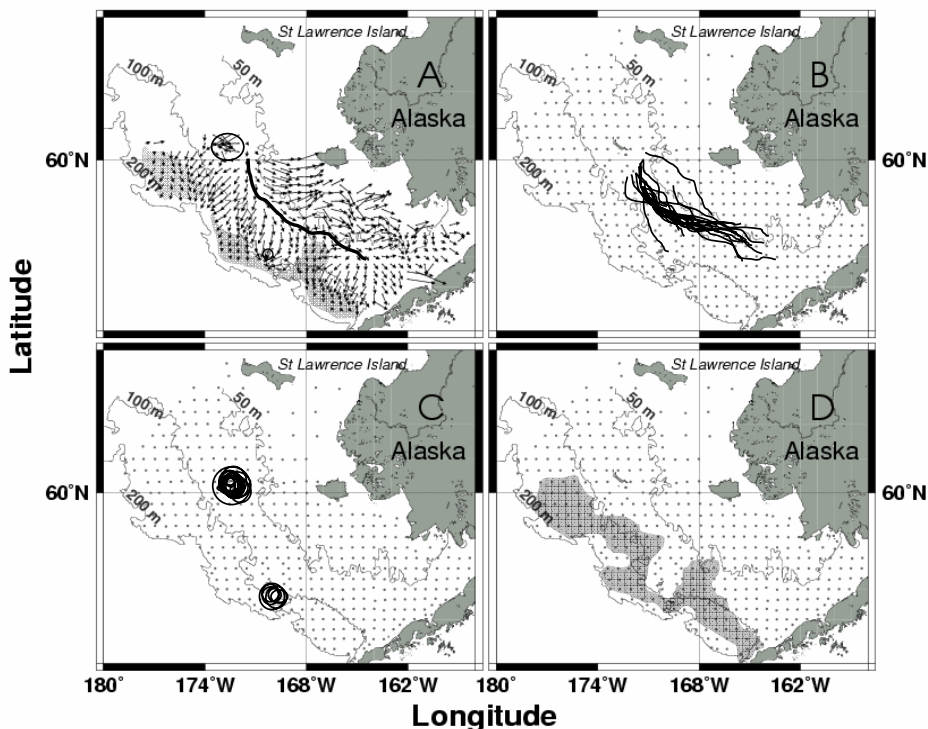


Figure 4. Thermal bottomscapes of the eastern Bering Sea shelf during the summer (June–July, 1978–2002). Arrows: vectors of near-bottom temperature (NBT, one per station), pointing from low to high. Solid lines: position of the NBT divide (axis of the cold pool). Circles: centripetal vector fields around St. Matthew Island and the Pribilof Islands. Shading: regions where NBT vectors are close to 0. (A) Average conditions for the entire period. (B) Variability in the location of the NBT divide (one per summer). (C) Centripetal vector fields in the middle domain. (D) Maximum extension of the regions where NBT gradients become negligible.

pool can be visualized as dividing the vector fields running along the middle domain; from it, summer NBT increases offshore (toward the outer domain) and onshore (toward the inner domain) (Fig. 4A). The position and length of the NBT divide vary from year to year (Fig. 4B), but the general pattern is very consistent. At least during the summers, NBT vectors vanish in most of the outer domain and in a sector of the middle domain northeast of Pribilof Canyon (Figs. 4A,D), where the NBT gradient is close to zero. The main anomalies are centripetal vector fields centered on St. Matthew and the Pribilof Islands, effectively coastal enclaves in the middle domain (Fig. 4C). Gradient fields are poorly documented north of St. Matthew, but some evidence indicates that they are weak in both the middle and outer domains, probably because winter ice covers both domains in most years. Although fields of NBT change dramatically from year to year, reflecting the extent of the cold pool, gradient fields are very conservative in their spatial structure.

**FROM SETTLEMENT TO ADULTHOOD.**—The pool of immature females observed through the surveys is virtually confined to the middle domain (Fig. 5; Ernst et al., 2005); their range in the northwest section of the shelf has not been completely covered by the standard survey grid. The ecological responses of snow crabs to temperature provide a rationale for the analysis of the spatial dynamics of snow crabs



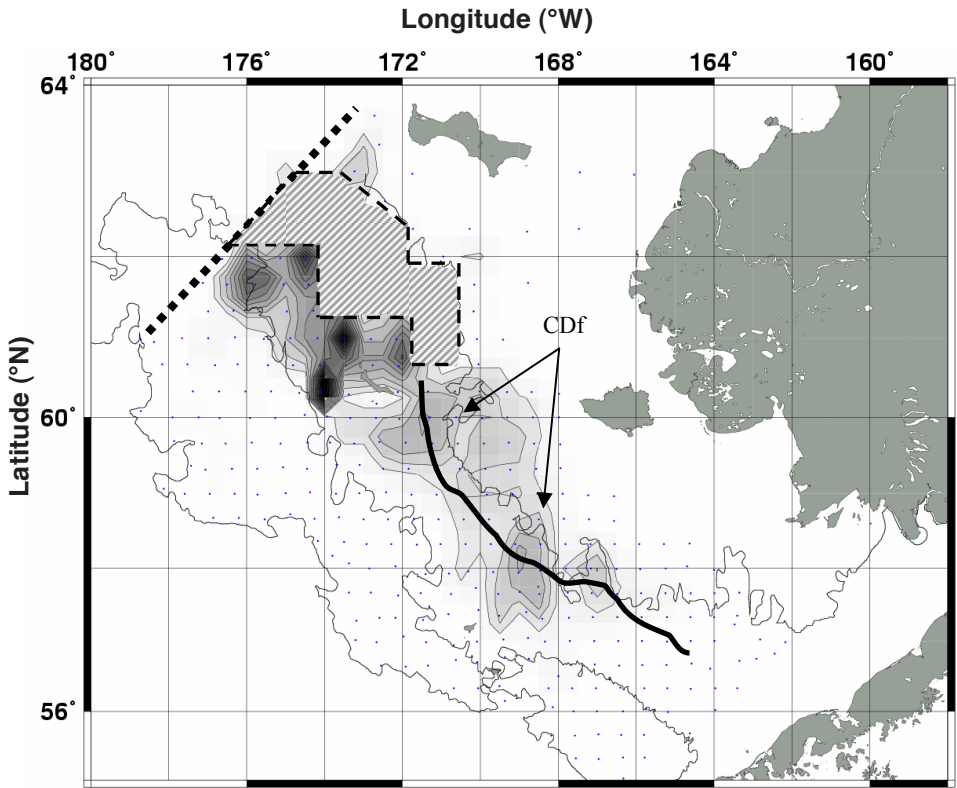


Figure 5. Average catch per unit effort of immature female snow crabs, 1978–2002 (modified from Orensanz et al., 2004). Dotted line: boundary of the region surveyed by the U.S. National Marine Fisheries Service during the summers. Cross-hatched region: “northern stations” polygon. CDF: fringe region of the coastal domain (see also Fig. 2). Solid line: average position of the summer NBT divide (axis of the cold pool), 1979–2001 (see also Fig. 4).

in relation to NBT (Ernst et al., 2005; Orensanz et al., 2004, 2007). South of 60°N, where the cold pool develops seasonally, the match between regions of historical abundance of immature females and the cold pool is remarkable (compare Figs. 4, 5); NBT in the latter (below 2 °C) corresponds to the purported thermopreference of early benthic instars (Dionne et al., 2003). Field data and experimental studies suggest an ontogenetic trend of higher temperature preferences. Postsettlement movement patterns have been well documented in the Gulf of St. Lawrence, eastern Canada (Lovrich et al., 1995); early benthic stages (instars I–V) are sedentary, and movements of immature females would be negligible for the observational scale of our study. The region where immature females are observed during the surveys may therefore reflect the geographic patterns of settlement and juvenile survival.

Molting to maturity (terminal molt) and primiparous mating occur during the winter (February–March; Ernst et al., 2005). Females that molt into maturity during the winter are observed as SCI 2s during the subsequent summer survey. Most females mature at a postsettlement age of 5.5–6.5 yrs (Orensanz et al., 2008), similar to ages that have been reported for the Gulf of St. Lawrence (Alunno-Bruscia and Sainte-Marie, 1998). Despite within-year-class variation, average age at maturity appears to be conservative (Orensanz et al., 2007). Combined with temperature depen-

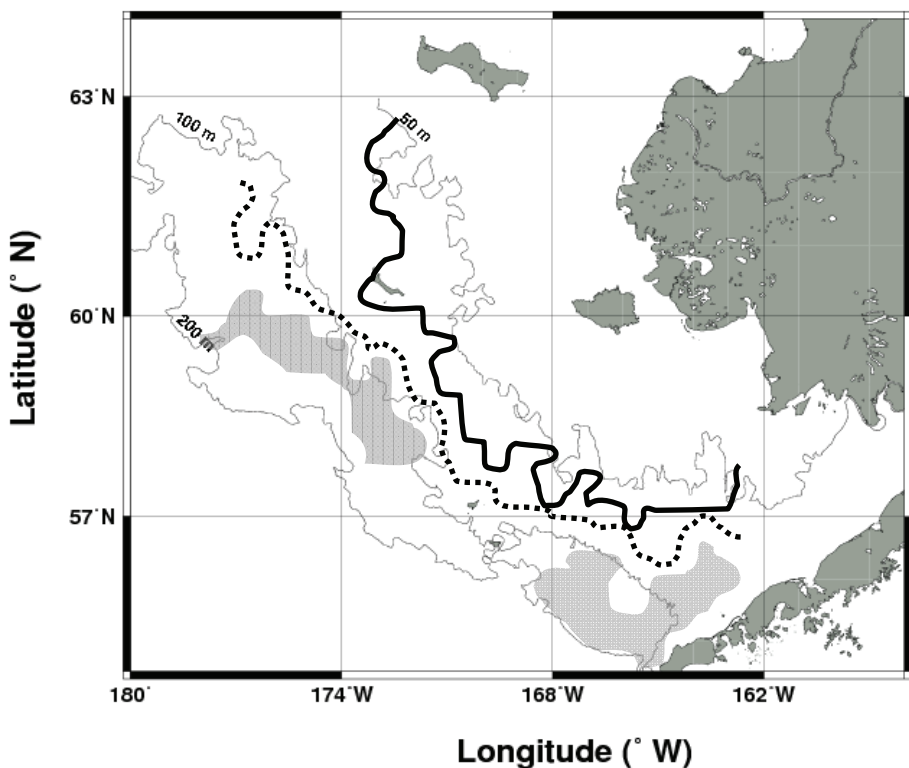


Figure 6. Isolines of average shell condition index (SCI), 1978–2002. Solid line, average SCI 2.0; dotted line, average SCI 2.5; shaded regions, contour corresponds to SCI 3.0.

dency of molting frequency during early ontogeny, conservation of age at maturity should result in clinal variation of average size and instar at maturity (Orensanz et al., 2007). Clinal variation in average size at maturity, from small size at high latitudes (ca. 40 mm CW at 63°N) to large size at low latitudes (ca. 70 mm CW at 55°N) is well documented for the EBS (Somerton, 1981a,b; Otto, 1998; Zheng et al., 2001; Ernst et al., 2005). In the EBS females can reach maturity at instars VIII–XII; females from a single year class in a given region can be spread over up to four pseudocohorts (Orensanz et al., 2007, 2008). This pattern is consistent with results on lipofuscin accumulation suggesting that terminal molt occurs over an age range of four years (Shirley and Bluhm, 2005). Average size at maturity continues to decline northward of the region covered by the annual NMFS survey, into the northeast Bering and Chukchi seas (Jewett, 1981; Stevens and MacIntosh, 1986; Paul et al., 1997).

Molting of large (commercial-size) males into maturity lags 4–5 yrs behind that of the primipara (Ernst et al., 2008b). Estimated maximum life span after the terminal molt is on the order of 7 yrs (Ernst et al., 2005; Shirley and Bluhm, 2005; Fonseca et al., 2008). Accordingly, maximum total longevity would be higher for males than for females, consistent with results from lipofuscin accumulation (Shirley and Bluhm, 2005).

**ONTOGENETIC MIGRATIONS AND GEOGRAPHICAL STRUCTURE OF THE FEMALE REPRODUCTIVE STOCK.**—Recruitment of pseudocohorts to the mature female stock

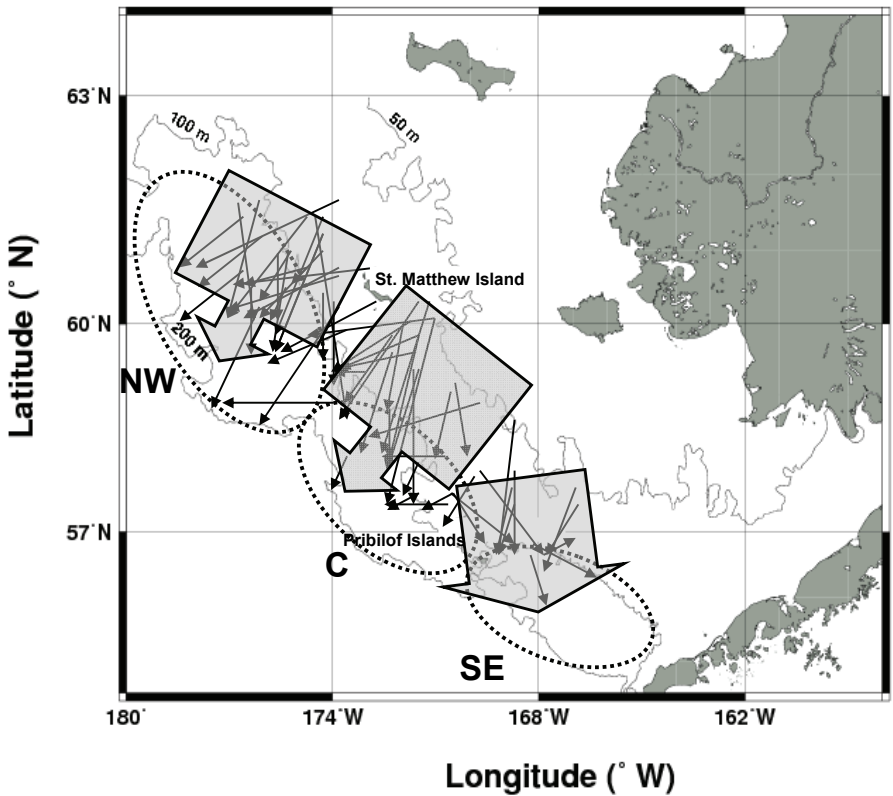


Figure 7. Patterns of female ontogenetic migration. Shaded arrow-blocks indicate major patterns (northwest, central, southeast). Simple arrows connect major aggregations of mature females of SCI 2 in year  $i$  and of SCI 3 in year  $i + 1$ , 1978–2002. Dotted ellipses: natural partitions of the outer domain (northwest, central, southeast; see Fig. 1)

occurs primarily in the middle domain. After mating, the primipara start an ontogenetic migration toward the shelf edge, presumably tracking NBT gradients (Ernst et al., 2005); over the year after terminal molt they migrate an average linear distance of 130+ km. Females of SCI 3+ are found primarily in the outer domain. This pattern is clearly captured by the isolines of average SCI (Fig. 6); the 2.5 isoline matches the boundary between the middle and outer domains. Older females (mean SCI 3+) congregate in the relatively warm regions of the outer domain, where NBT gradients are weakest (compare Figs. 4A, 6).

When migration vectors connecting aggregations of mature females of SCI 2 in year  $i$  and SCI 3 in year  $i + 1$  are compiled for the period 1978–2002 and superimposed, pattern emerges. Migration routes out of the middle domain are diverted by St. Matthew and the Pribilof Islands, the dominant geographic features. For brevity, the three resulting vector clusters are designated the NW, central, and SE patterns of female ontogenetic migration (Fig. 7). The NW and central patterns, oriented from NE to SW, were well captured by the analysis of aggregate centroids (Ernst et al., 2005). Pseudocohort tracking consistently indicated that, on the southeast shelf, females migrated in a N/NW to S/SE direction, converging toward the boundary region between the middle and outer domains NE/E of the Pribilof Islands and the

Pribilof Canyon, as exemplified well by the 1980 pseudocohort (Ernst et al., 2008a, their fig. 6).

Males also appear to move offshore after reaching adulthood (Otto, 1998), as strongly suggested by comparison of the distribution of males molting into adulthood during the summer (observed during the surveys as SCI 1–2) and “new shells” captured by the fishery during the subsequent winter season (Orensanz et al., 2004, their fig. 10).

**POTENTIAL MATING OPPORTUNITIES.**—According to Somerton’s “bipartite mating hypothesis” (Somerton, 1982b, originally formulated for Tanner crab, *Chionoecetes bairdi* Rathbun, 1924), and extensive experimental work conducted in eastern Canada on snow crab (Sainte-Marie et al., 2008), all mature males (both adolescent and adult) are potential mates for the primipara. Primiparous mating in the middle domain during the winter could therefore involve all the mature males available (males  $\geq 40$  mm CW can safely be assumed to be mature) and primiparous females (seen as SCI 2 mature females during the surveys). Given that adult males migrate offshore after molting during the summer, they must, if they are to be available as potential mates for the primipara, engage in seasonal back-and-forth migrations. This phenomenon is well documented in the Gulf of St. Lawrence (Lovrich et al., 1995) but cannot be fully investigated in the EBS with the data currently available. Females mating in the outer domain are primarily multiparous; experimental work conducted in eastern Canada shows that multiparous females can mate only with adult males (Sainte-Marie et al., 2008).

Because the fishery concentrates on large adult males in the outer domain during the winter season, the impact of the fishery on males available as mates for the primipara depends on an eventual inshore migration of the adult males that escape capture. Small adult males (together with adolescents) could be significant in the pool of prospective mates if, as has been demonstrated in eastern Canada, movement rate of males during the post-terminal-molt offshore migration were size dependent. If the primipara in the middle domain did depend on a pool of small adults and adolescent males as prospective mates, then the fishery would have little effect on stock dynamics, as the contribution of the multipara fertilized by adult males (target of the fishery) and whose eggs hatch in the outer domain might make a limited contribution to recruitment in the middle domain. This would be the case even if, as suggested by IBM simulations, part of the larval output were advected northward to the middle domain.

**HATCHING AND LARVAL STAGES.**—The hatching season starts in March and ends in June, but most hatching in the EBS occurs in April–May (Somerton, 1981a, 1982a; Incze et al., 1987). The egg incubation period can extend over 1–2 yrs (Rugolo et al., 2005; Orensanz et al., 2008), as previously reported for the Gulf of St. Lawrence (Sainte-Marie, 1993). The factor determining the developmental mode of crab embryos is the temperature to which they are exposed during early embryogenesis (Rugolo et al., 2005; Sainte-Marie et al., 2008).

The proportion of larvae contributed by the primipara that hatch in the middle domain is not well understood. Primiparous females are collected by the surveys during the summer after their puberty molt, at least 8 mo before the onset of the hatching season. During that period the primipara have initiated their offshore migration, which will take them to the outer domain, where they are collected during

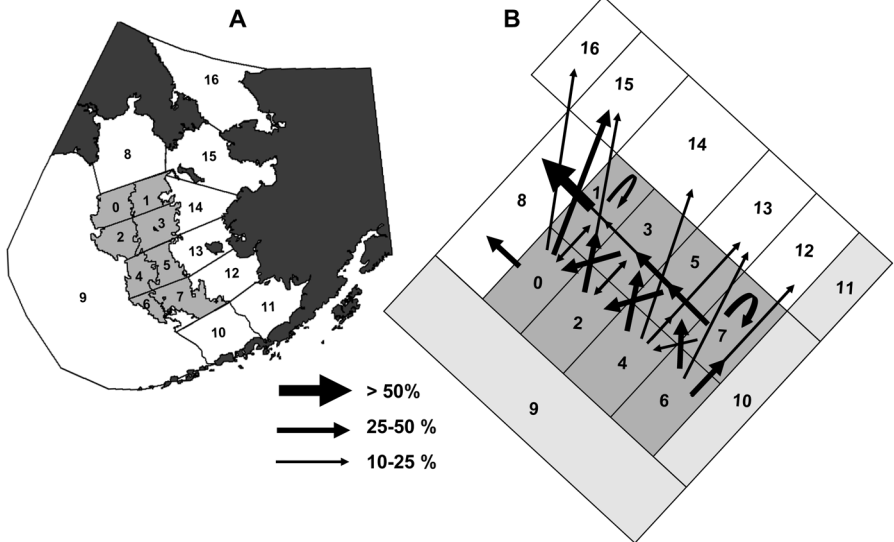


Figure 8. Patterns of connectivity predicted by the biophysical model. (A) Areas defined for simulations of snow-crab larval transport with an individual-based model (IBM areas); shading, eight larval release IBM areas, capturing the historical distributions of the mature female stock surveyed by the U.S. National Marine Fisheries Service; IBM areas 8–16 are treated only as “sinks.” (B) Schematic summary of connectivity patterns. Width of the arrows indicates the strength of connectivity; connectivity below 10% not represented (see Table 3). Horizontal hatching (IBM areas 9–11), areas outside the region of interest; dark shading, core region of interest.

the summer survey as SCI 3s. This group is a mixture of multipara (annual brooders) and biennial primipara in their second year of brooding, so the larvae of at least some primipara hatch in the outer domain (Ernst et al., 2008a). Simulations with initial realistic, year-specific conditions (source areas) based on survey data may illuminate this problem, but that inquiry is beyond the scope of the study reported here.

Pelagic larval stages include two zoeae and a megalopa. Incze et al. (1987) found that, on the southeastern shelf, zoeae are concentrated in the upper 20 m of the water column, in both daylight and darkness. Duration of the zoeal stages depended on temperature in experimental studies conducted on the stock from the Japan Sea (Kon and Sinoda, 1992: 187). At the temperatures to which they are exposed in the EBS, average duration would be on the order of 3 mo. This conclusion is very tentative, as the Japanese results were obtained in an experimental setting and correspond to a stock that experiences a thermal regime very different from that of the EBS. Megalopae may gradually become demersal or hyperbenthic (Kon and Sinoda, 1992: 200–201). The duration of the megalopa stage was on the order of 1 mo in the Japanese experiments, but this finding can be complicated (in addition to the reasons indicated for the zoeae) by the ability of many crab species to delay settlement according to environmental conditions other than NBT. Settlement of megalopae in the EBS probably peaks during late summer or early fall.

**POTENTIAL SOURCES, SINKS, AND PATTERNS OF CONNECTIVITY.**—For our study, the Bering Sea was partitioned into 17 IBM areas (Fig. 8A). Release regions were located in the middle (IBM areas 1, 3, 5, and 7) and outer (IBM areas 0, 2, 4, and 6) domains of the EBS shelf (Fig. 8A), selected according to the historical geographical

Table 2. Pattern of average connectivity. Each cell corresponds (see Fig. 8) to the average percentage of larvae produced in a source area (columns) that ends up (“settles”) in a given destination (rows). Averages are calculated for the period 1978–2002.

Destinations	Source							
	0	1	2	3	4	5	6	7
0	1.1	10.4	2.1	39.0	1.8	7.2	0.1	0.5
1	15.4	14.9	30.5	21.0	4.6	3.7	0.1	0.0
2	0.1	0.4	0.5	13.4	2.5	33.2	1.1	3.2
3	0.8	0.5	15.1	9.1	35.3	35.9	9.8	11.3
4	0.2	0.0	0.0	0.0	0.0	6.8	0.7	14.5
5	0.2	0.0	0.2	0.0	11.7	8.8	27.0	33.2
6	0.2	0.0	0.0	0.0	0.0	0.0	0.2	2.8
7	0.3	0.0	0.0	0.0	0.5	0.2	31.0	30.1
8	36.6	62.6	8.8	11.1	0.1	0.1	0.0	0.0
9	0.6	6.8	0.1	2.6	0.0	0.6	0.0	1.4
10	0.4	0.0	0.0	0.0	0.0	0.0	0.3	0.9
11	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
12	0.5	0.0	0.0	0.0	0.3	0.0	15.3	1.2
13	0.5	0.0	0.8	0.0	18.0	1.4	13.8	0.8
14	4.1	0.6	23.5	3.1	24.3	1.9	0.6	0.1
15	29.2	3.6	16.0	0.6	0.9	0.0	0.0	0.0
16	10.8	0.4	2.4	0.0	0.0	0.0	0.0	0.0

range of mature females (Ernst et al., 2005). The other nine areas are treated only as sinks. Although the presence of mature females has been documented in the north-eastern Bering Sea and Norton Sound (IBM area 15; Stevens and MacIntosh, 1986), the Chukchi Sea (IBM area 16; Paul et al., 1997), the Gulf of Anadyr (IBM area 8; Sample and Nichol, 1994), and the fringes of the coastal domain in the EBS (IBM areas 12–14; Ernst et al., 2008a), we assume, given what is known about their distribution and abundance, that their relative significance for recruitment in the EBS shelf is negligible. Patterns of mean connectivity (1978–2002) between release and potential settlement areas predicted by the IBM of larval transport, including retention within release areas, are summarized in Figure 8B and Table 2. Some results are noteworthy: (1) negligible retention of virtual larvae released in the outer domain; (2) substantial northward transport along the middle domain and westward transport from the middle domain (IBM areas 3, 5, 7) to the outer domain (IBM areas 0, 2, 4); (3) consistent northeastward (onshore) transport from the outer domain (IBM areas 2, 4, 6) to the middle domain (IBM areas 1, 3, 5); (4) substantial retention of virtual larvae in two areas of the middle domain (15%–20% northwest St. Matthew, IBM area 1) and 25%–30% east of the Pribilof Islands, IBM area 7); (5) consistent eastward transport from IBM area 6 (outer domain) to IBM area 7 (middle domain), east of the Pribilof Islands; (6) transport from the core region to the coastal domain (IBM areas 12–14) and to subarctic regions north of St. Lawrence Island (IBM area 15), even into the Chukchi Sea (IBM area 16) (the model highlights IBM area 15 as an important sink); (7) substantial transport from northwest of the core region (IBM areas 0 and 1) to the Gulf of Anadyr (IBM area 8) (55%–60% in the case of transport from IBM area 1 to IBM area 8); (8) virtually no offshore transport (i.e., to IBM area 9) from the core

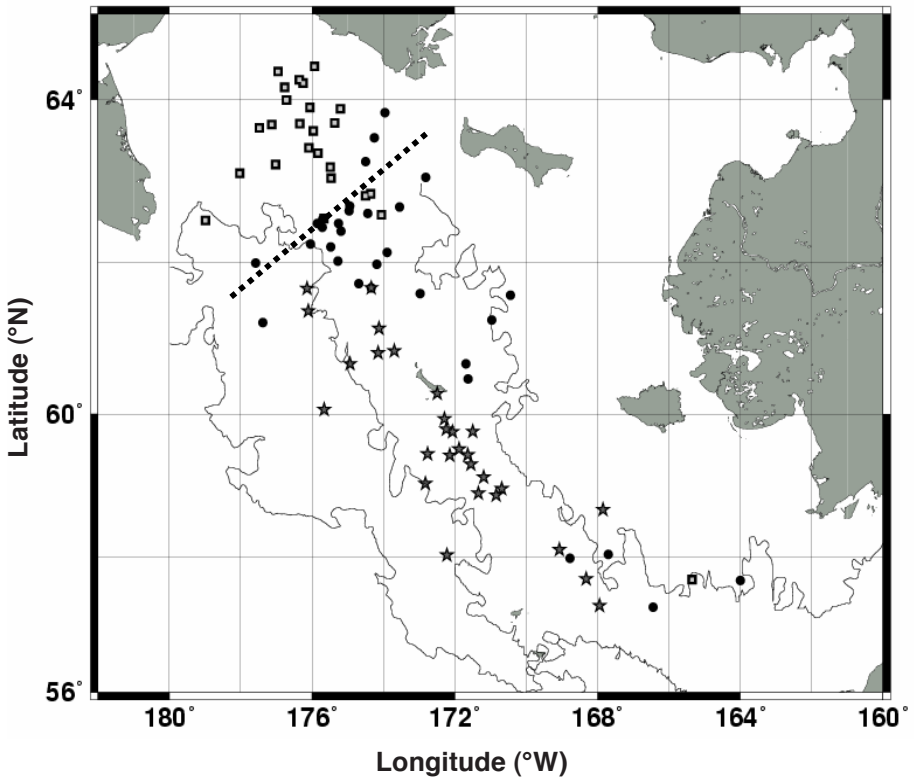


Figure 9. Centroids of regions of potential larval settlement in simulations conducted with the individual-based model of larval transport (1978–2002). Centroids were calculated for each year and for each adjusted NBT interval of interest; squares, below 0 °C, circles, 0–2 °C (two centroids calculated in some years), stars, 2–4 °C. Dotted line, boundary of the region surveyed by the U.S. National Marine Fisheries Service during the summers.

region; and (9) virtually no southward (including southeastward and southwestward) transport throughout the entire geographic region of interest.

Regions of potential settlement by virtual larvae were stratified according to the adjusted NBT predicted for July–October; three strata were defined: less than 0 °C, 0–2 °C, and 2–4 °C. Centroids for each stratum, calculated for years 1978–2002 as by Ernst et al. (2005), are located mainly in the middle domain or near its boundaries. Few exceptions show centroids located in the outer domain. The 0–2 °C stratum usually consists of two geographically separate components, the main one in the middle domain of the northwestern section of the shelf and the other north of the Pribilof Islands (Fig. 9); centroids were estimated separately for each sector. In total, therefore, five centroids were calculated for each year: below 0 °C, 0–2 °C on the northwest shelf, 0–2 °C north of the Pribilof Islands, 2–4 °C on the northwest shelf, and 2–4 °C north of the Pribilof Islands (Fig. 9). The 0–2 °C stratum should be an indicator of the thermopreferendum for the stenothermic early snow-crab instars, which is in that range (Dionne et al., 2003). Interestingly, the region defined by the centroids of the adjusted NBT 0–2 °C stratum matches the region where high concentrations of immature snow crabs have been observed during the NMFS surveys (compare Figs. 5, 9). Centroids corresponding to the coldest stratum, below the purported thermo-

preferendum of early benthic stages, are located in the Gulf of Anadyr (IBM area 8), out of reach of the NMFS surveys. That region is a potentially important destination for larvae originating in IBM areas 0 and (mostly) 1.

**SUBSYSTEMS.**—The geographic/oceanographic configuration of the EBS, in conjunction with the determinate ontogenetic schedule of the species and larval retention mechanisms in the middle domain, create two scenarios for population persistence. Below, we refer to them as the SE and NW subsystems.

At the core of the SE subsystem, a sector of the middle domain located to the northeast of the Pribilof Islands (coincident with IBM area 7) showed the highest potential for larval retention (Fig. 8; Parada et al., 2007). That region is also characterized by a local minimum of NBT predicted by the ROMS and observed during several surveys (Fig. 9); summer NBT in that sector is often in the 0–2 °C range, the presumed thermopreferendum of early benthic instars. Consistently with potential for larval retention and a local minimum of NBT (two favorable conditions), immature crabs were recurrently observed in that region (Fig. 5), particularly during the period 1985–1993.

South of the SE subsystem, the ontogenetic migration of mature females followed the SE pattern (Fig. 7). Females molting into maturity to the north of the Pribilof Islands (IBM area 7) migrate southward, most of them ending up in the southeast section of the outer domain (IBM area 6), southeast of the Pribilof Canyon (Fig. 7). Primipara in IBM area 7 released larvae at the core of the SE subsystem, and the model also predicts strong onshore transport of larvae released by the multipara in adjacent IBM area 6 of the outer domain, which are advected to IBM area 7. This pattern is consistent with the observation of a weak, local cross-shelf eastward flow at 57.5°N (Fig. 2B; Schumacher and Stabeno, 1998; Stabeno et al., 2001; Flint et al., 2002), probably an extension of anticyclonic circulation around the Pribilof Islands (Stabeno et al., 2007). A weak mean flow with a southern component was detected at mooring sites 2 and 4 (Fig. 2B) from April to September (Stabeno et al., 2007). Mooring site 2 is outside the region of interest to us; the time series of observations at mooring site 4 is relatively short but consistent with observations at site 2. The significance of this flow for larval retention in IBM area 7 or for transport from IBM area 5 to IBM area 7 is uncertain but could certainly increase the importance of the SE subsystem.

The NW subsystem corresponds to the northwest section of the middle domain (Fig. 2A), which includes the “northern stations” polygon, and to IBM area 1. Simulation results indicate substantial larval retention, as well as incoming transport from the outer domain (IBM areas 2 and 4) and from the expanses of the middle domain to the southeast (Fig. 9). The NW subsystem therefore has substantial potential for concentration and retention of larvae. Consistently, the middle domain of the northwestern section of the shelf has been, historically, the most important in terms of abundance of immature snow crabs (Fig. 5). Primiparous females migrate southward toward the northwestern section of the outer domain (Fig. 7), and the life history cycle is closed when a substantial part of their larvae are advected back to the middle domain.

**FLUCTUATIONS IN ABUNDANCE OF THE REPRODUCTIVE STOCK.**—Four pulses of recruitment to the mature female population occurred in the middle domain at 6- to 7-yr intervals between 1978 and 2005 (1979–1980, 1987–1988, 1993–1995, 2001;



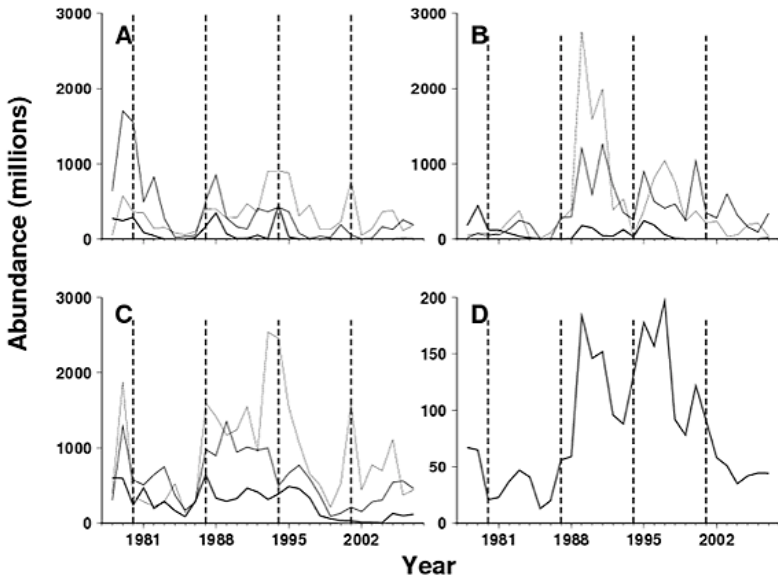


Figure 10. Fluctuations in abundance of reproductive snow crabs on the eastern Bering Sea shelf (1978–2007). Left, middle domain; right, outer domain. Thickness of the lines indicates shelf sections: thin, northwest; intermediate, central; thick southeast. (A) Females of SCI 2 (primiparous females that molted into adulthood during the winter preceding the summer survey). (B) Females of SCI 3+. (C) Males larger than 40 mm (carapace width). (D) Males of SCI 3+ larger than 40 mm (sections of the shelf pooled). Vertical dashed lines, at intervals of 7 yrs, indicate the pulses I–IV of female pseudocohort recruitment to the mature female stock.

Orensanz et al., 2007, 2008); we refer to these events as pulses I–IV and to 1980, 1987, 1994, and 2001 as their “core years” (Fig. 10A; Table 3). As compared to background years, pulses of recruitment to the mature population were accompanied by dramatic but short-lived expansions in the geographic range of SCI 2 females, shown in Figure 11 for pulse III. A recurrent feature of the range expansions during the first three pulses was the occurrence of SCI 2 females in the southeastern section of the shelf, which, however, has not been observed since 1995 (Fig. 11) (Ernst et al., 2008a).

Pseudocohort strength shows the same general pattern when analyzed by shelf section, although consistent regional variation is observed (Fig. 10A; Table 3). Pseudocohort strength was always lowest in the southeastern section, where pulse IV was not detected (Figs. 10A, 11). In the central section pseudocohort strength declined from pulse I to pulse IV. In view of connectivity patterns predicted by the IBM, abundance in the central shelf may have depended on the input of larvae originating in the SE subsystem. The relative significance of the northwestern section, where pulse III was strongest, increased over the same period. The geographic spread of the pulses of pseudocohort recruitment was foreshadowed by the distribution of immature females in previous years (Fig. 11 for pulses III and IV).

Pulses of multipara in the outer domain were delayed and appeared protracted by comparison to corresponding pulses of primipara in the middle domain (compare Figs. 10A,B). This result might be expected because mature females of SCI 3+ observed in a given year are the sum of a series of surviving pseudocohorts, whereas most mature females observed in the middle domain in a given year correspond to a

Table 3. Pulses of recruitment of mature females (shell-condition index, SCI, 2) to the mature snow-crab population from the eastern Bering Sea, 1978–2003.

Pulse	Core year (duration)	Source of information	Observations
I	1980 (1979–1980)	Zheng et al. (2001: fig. 9); Ernst et al. (2005: fig. 4); Orensanz et al. (2007)	Strongest in the central section of the shelf; vanished in all sections during the transition to SCI 3+, otherwise expected to occur in the outer domain with a 1–2 yr lag (compare Figs. 10A and 10B).
II	1987 (1987–1988)	Zheng et al. (2001: fig. 9); Ernst et al. (2005: fig. 4); Orensanz et al. (2007)	Mature females of SCI 2 peaked in the middle domain in 1987–1988, and SCI 3+ females in the outer domain 2 yrs later (1989–1991) (Fig. 10A,B)
III	1994 (1993–1995)	Zheng et al. (2001: fig. 9); Ernst et al. (2005: fig. 4); Orensanz et al. (2007)	Strongest in the northwest section of the shelf. Mature females of SCI 2 peaked in the middle domain in 1993–1995, and SCI 3+ females in the outer domain 2 yrs later (1995–1997) (Fig. 10A,B)
IV	2001	Ernst et al. (2005: fig. 4); Orensanz et al. (2007)	Not detected in the southeastern section of the shelf.

single pseudocohort. Development of pulses II and III during the periods 1986–1990 and 1992–1997 was dominated by the NW pattern of female migration. In the first case, observed regions of concentration were apparently truncated to the north by the coverage of the survey. This truncation is clearly seen when the period 1983–1986, when the survey stopped at 61°N, is compared to 1987–1990, when it extended to 62°N: in the latter period substantial abundance of SCI 2 females was detected between 61° and 62°N (Ernst et al., 2008a, their fig. 5). Interestingly, during the same period, SCI 2 females were concentrated along the outer fringes of the middle domain. The great strength of the outer domain pulse II (and to a lesser extent pulse III) of multipara in the central and northwestern sections of the outer domain, particularly in the latter, is probably a result of immigration of mature females from beyond the region covered by the survey.

If SCI 3 mature females appearing in the outer domain of the northwestern shelf did come from regions to the north and northeast, partly beyond the region covered by the regular surveys (i.e., including the “northern stations” polygon and the sector of the northwestern shelf beyond U.S. jurisdiction, Figs. 2A, 11), then, in view of clinal variation in the size of mature females (Orensanz et al., 2007), they should be expected to be comparatively small in size. This prediction is consistent with the intrusion by small SCI 3 mature females (Orensanz et al., 2007, their fig. 4). Rugolo et al. (2006: 26 and their table 5) observed that females smaller than 50 mm CW were most abundant at the northern stations (2004–2006) and larger females in the rest of the region surveyed. They also interpreted this pattern as evidence of southward ontogenetic migration, but their preliminary analysis did not separate immature from mature females or SCI categories of the latter.

Although most easily discernible in the pseudocohort strength of the primipara, cyclic variation was equally apparent in male recruitment to the mature population (Orensanz et al., 2008; Fig. 10C). Abundance of adult males can be estimated only

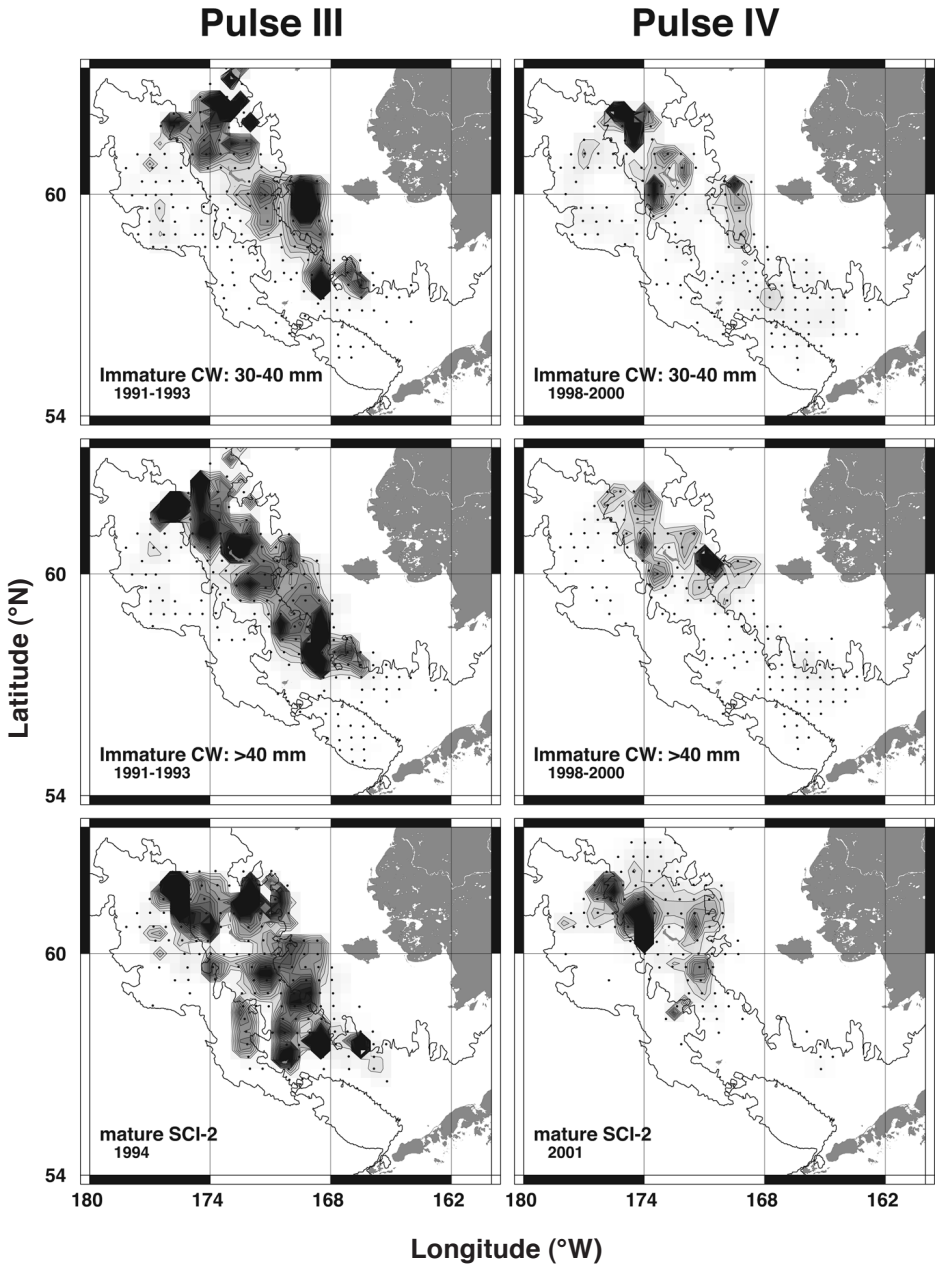


Figure 11. Geographical distribution of primiparous females (SCI 2) in 1994 and 2001, core years of pulses III and IV, and of immature females during the preceding 3 yrs.

for years after 1989, when claw size began to be recorded, but the abundance of SCI 3+ males larger than 40 mm CW is a reasonable surrogate (Fig. 10D; Ernst et al., 2008b). Exclusion of SCI 1–2 males of all sizes leaves out those that had molted during the current year, either to a new adolescent instar (probably during the winter) or into adulthood (during spring and summer). In either case they were adolescent and largely confined to the middle domain at the time of the multiparous mating season (Ernst et al., 2008b).

## CONCLUSIONS AND IMPLICATIONS

**BOUNDING THE GEOGRAPHIC REGION OF INTEREST.**—Results from simulations with the IBM provided objective criteria to bound the region of interest for modeling the snow-crab population of the EBS. Lack of (i) southward transport along the middle and outer domains, (ii) eastward transport into Bristol Bay, and (iii) westward transport off the outer domain effectively leaves IBM areas 9, 10, and 11 (shaded in Fig. 8) out of the geographic region of interest. IBM areas 8 (Gulf of Anadyr), 15 (northeastern Bering Sea), and 16 (Chukchi Sea) are likely sinks for larvae originating in the EBS, but crabs recruited in those down-current regions are unlikely to have a substantial influence on the dynamics of the EBS stock; postsettlement migration to the EBS is highly unlikely in the case of the Chukchi and northeastern Bering seas, and larval advection is not favored in a direction toward the EBS. Information from the Gulf of Anadyr is limited (Sample and Nichol, 1994); so far, no conclusive evidence supports immigration from that region. The coastal domain (IBM areas 12–14) is likely to receive some larvae, and the coastal domain fringe (Figs. 2, 5) is well documented to function effectively as part of the middle domain with respect to NBT and abundance of immature crabs (Orensanz et al., 2004). Otherwise, its significance appears to be limited. The reasons why primiparous females and adult males do not migrate into the coastal domain are still not well understood; a likely reason is a reversal in NBT gradients during the winter, implying relatively low NBT during the winter months. This hypothesis can now be explored with the ROMS model, but that inquiry is beyond the scope of the study reported here. So far as we know, the significance of IBM areas 12 and 13 is marginal; little is known about IBM area 14. In sum, results from the simulations support the notion that the regions of interest for analyzing and modeling the EBS snow-crab stock are the outer and middle domains of the northwestern, central, and southeastern sections of the EBS shelf (IBM areas 0–7; Figs. 2, 8).

**THE ERH IN RETROSPECT.**—Formulation of the ERH was motivated by the observation that an increase in NBT during 1975–1979, and a concomitant weakening of the cold pool, was followed with a 6-yr lag by a northward contraction in the geographic spread of pseudocohorts during 1981–1986 (Orensanz et al., 2004). Consistency between results from recent research and the ERH is summarized in Table 1. The decade that followed the initial contraction was punctuated by two transient range expansions of the mature female population to the south (Orensanz et al., 2008), corresponding to pulses II and III of pseudocohort recruitment. The contraction has intensified since the mid 1990s, as pulse IV of pseudocohort recruitment did not materialize in the southeastern section of the shelf (Fig. 11). The likely reason is a contraction of the cold pool, closely associated with a marked decrease in duration

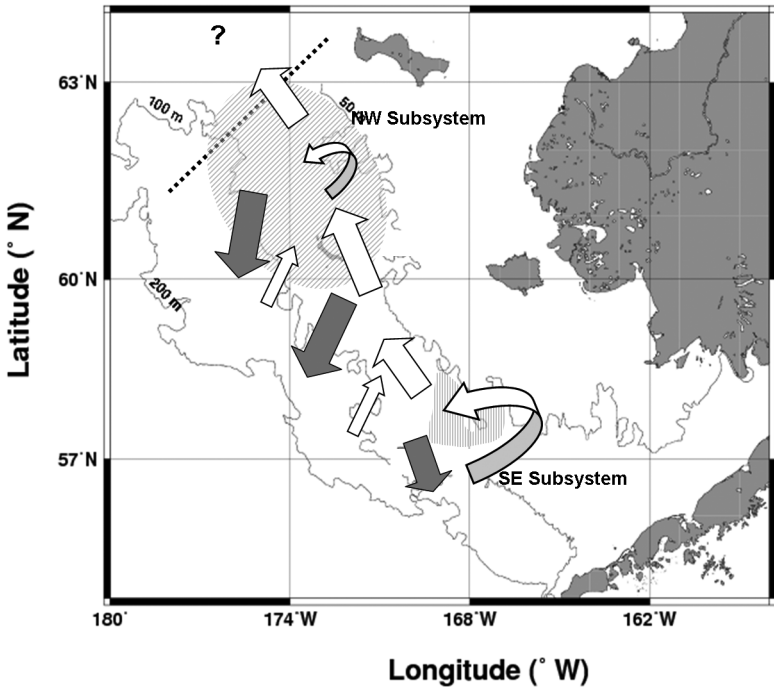


Figure 12. Conceptual hypothesis on shift of snow crab spatial dynamics in the eastern Bering Sea shelf. White arrows show direction of larval transport; curved arrows indicate retention. Shaded arrows indicate ontogenetic migrations. Hatching highlights hypothesized main regions of settlement and recruitment to the mature female stock.

and concentration of winter sea ice over the EBS (Grebmeier et al., 2006). During 2000–2005 the southeastern shelf underwent a warming of approximately 3 °C (Stabeno et al., 2007). Warming of the EBS shelf could have profound influences on the ecosystem, from modification of the timing of the spring phytoplankton bloom to the northward retreat of arctic species (Stabeno et al., 2007), snow crabs being a case in point. More recently (2006–2008) an extended cold pool returned over the central section of the middle domain (Rugolo et al., 2006; Chilton et al., 2008a,b), creating an interesting opportunity to investigate the reversibility of the contraction phenomenon. The potential for a resurgence of the SE subsystem sustained by the residual stock of reproductive females would be most informative about renewal dynamics.

**POPULATION CYCLES AND SUBSYSTEMS.**—The sequence of four regularly spaced pulses of recruitment that has dominated the dynamics of the EBS snow-crab population over three decades is an extraordinary phenomenon, whose significance has been highlighted by recent studies (Orensanz et al., 2007, 2008). Remarkably, the core years of pseudocohort strength are approximately 7 yrs apart, the average time elapsed in the life of an average individual female snow crab between egg extrusion by her mother and terminal molt. That correspondence suggests dynamic linkage between the pulses, in which each one in the sequence becomes the parental stock for the next. This hypothesis would be consistent with a central role of the primipara and the middle domain in the dynamics of renewal. Dynamics driven by linkage between pulses of primipara also imply a strong stock-recruitment relation, one that

would go undetected if the entire mature female stock is aggregated (see, e.g., Zheng and Kruse, 2003).

A second aspect that emerges as most significant for the understanding of snow-crab dynamics in the EBS is a spatial structure that we conceptualize in the form of two major, asymmetrically connected subsystems (Fig. 12). Much of the action driving fluctuations of the stock appear to occur in regions, and to involve stages, that are beyond the reach of the fishery. Immigrants from the northern section of the middle domain, mostly outside the region regularly covered by the surveys, are suspected of giving origin to pulses II and III of SCI 3 female abundance in the outer domain. Perhaps more immediately important from a management viewpoint, large males of the same pulses molting into maturity during the summers of 1989–1991 and 1997–1998 contributed to the high winter landings of the 1990–1992 (historical maximum) and 1998–1999 fishing seasons.

The results reported here tend to support a major role of climate and fishery-independent dynamics in the shift of the system, concurrently with other climate-related changes occurring in the EBS (Grebmeier et al., 2006; Mueter and Litzow, 2008). A combination of the complex and determinate life-history of snow crabs, the strongly structured environment of the EBS, and the modus operandi of the fishery offers valuable opportunities to tease apart the effects of the environment and the fishery, one of the most challenging issues at a time when stocks experience the combined effects of climate change and fishing.

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#### LITERATURE CITED

- Alunno-Bruscia, M. and B. Sainte-Marie. 1998. Abdomen allometry, ovary development, and growth of female snow crab, *Chionoecetes opilio* (Brachyura, Majidae), in the northwestern Gulf of St. Lawrence. *Can. J. Fish. Aquat. Sci.* 55: 459–477.
- Chilton, E. A., C. E. Armistead, and R. J. Foy. 2008a. The 2008 eastern Bering Sea continental shelf bottom trawl survey: results for commercial crab species. U.S. Department of Commerce. NOAA Tech. Memo. NMFS-AFSC-187. 88 p.

- \_\_\_\_\_, L. Rugolo, C. E. Armistead, and R. J. Foy. 2008b. The 2007 eastern Bering Sea continental shelf bottom trawl survey: results for commercial crab species. U.S. Department of Commerce. NOAA Tech. Memo. NMFS-AFSC-186. 85 p.
- Coachman, L. K. 1986. Circulation, water masses, and fluxes on the southeastern Bering Sea shelf. *Continental Shelf Res.* 5: 23–108.
- Comeau, M. and G. Y. Conan. 1992. Morphometry and gonad maturity of male snow crab, *Chionoecetes opilio*. *Can. J. Fish. Aquat. Sci.* 49: 2460–2468.
- \_\_\_\_\_, G. Y. Conan, F. Maynou, G. Robichaud, J.-C. Therriault, and M. Starr. 1998. Growth, spatial distribution, and abundance of benthic stages of the snow crab (*Chionoecetes opilio*) in Bonne Bay, Newfoundland, Canada. *Can. J. Fish. Aquat. Sci.* 55: 262–279.
- Curchitser, E. N., D. B. Haidvogel, A. J. Hermann, E. L. Dobbins, T. Powell, and A. Kaplan. 2005. Multi-scale modeling of the North Pacific Ocean: assessment of simulated basin-scale variability (1996–2003). *J. Geophys. Res.* 110: C11021.
- Danner, S. 2007. Snow and Tanner crabs. Seafood report. Seafood Watch, West Coast Region. Monterey Bay Aquarium, Monterey. 41 p.
- Dionne, M., B. Sainte-Marie, E. Bourget, and D. Gilbert. 2003. Distribution and habitat selection of early benthic stages of snow crab *Chionoecetes opilio*. *Mar. Ecol. Prog. Ser.* 259: 117–128.
- Ernst, B., J. M. Orensanz, and D. A. Armstrong. 2005. Spatial dynamics of female snow crab (*Chionoecetes opilio*) in the eastern Bering Sea. *Can. J. Fish. Aquat. Sci.* 62: 250–268.
- \_\_\_\_\_, \_\_\_\_\_, and \_\_\_\_\_. 2008a. Trends and patterns in the reproductive contribution of female snow crab (*Chionoecetes opilio*) from the eastern Bering Sea. Pages 52–92 in J. M. Orensanz, B. Ernst, D. A. Armstrong, and J. Burgos, eds. Female effective reproductive output of the snow crab stock in the eastern Bering Sea. North Pacific Research Board, Project 508 Final Report. Anchorage, Alaska. Available from: <http://project.nprb.org/view.jsp?id=c1078c9b-3458-4a29-8d21-3430c2eb34b0>. Accessed 6 December 2008.
- \_\_\_\_\_, \_\_\_\_\_, and \_\_\_\_\_. 2008b. Patterns of potential mating opportunities in snow crab (*Chionoecetes opilio*) from the eastern Bering Sea. Pages 125–159 in J. M. Orensanz, B. Ernst, D. A. Armstrong, and J. Burgos, eds. Female effective reproductive output of the snow crab stock in the Eastern Bering Sea. North Pacific Research Board, Project 508 Final Report. Anchorage, Alaska. Available from: <http://project.nprb.org/view.jsp?id=c1078c9b-3458-4a29-8d21-3430c2eb34b0>. Accessed 6 December 2008.
- Flint, M. V., I. N. Sukhanova, A. I. Kopylov, S. G. Poyarkov, and T. E. Whiteledge. 2002. Plankton distribution associated with frontal zones in the vicinity of the Pribilof Islands. *Deep-Sea Res. II* 49: 6069–6093.
- Fonseca, D. B., B. Sainte-Marie, and F. Hazel. 2008. Longevity and change in shell condition of adult male snow crab inferred from dactyl wear and mark-recapture data. *Trans. Am. Fish. Soc.* 137: 1029–1043.
- Grebmeier, J. M., J. E. Overland, S. E. Moore, E. V. Farley, E. C. Carmack, L. W. Cooper, K. E. Frey, J. H. Helle, F. A. McLaughlin, and S. L. McNutt. 2006. A major ecosystem shift in the northern Bering Sea. *Science* 311: 1461–1464.
- Incze, L. S., D. A. Armstrong, and S. L. Smith. 1987. Abundance of larval Tanner crabs (*Chionoecetes* spp.) in relation to adult females and regional oceanography of the southeastern Bering Sea. *Can. J. Fish. Aquat. Sci.* 44: 1143–1156.
- Jewett, S. C. 1981. Variations in some reproductive aspects of female snow crabs *Chionoecetes opilio*. *J. Shellfish Res.* 1: 95–99.
- Kinder, T. H. and J. D. Schumacher. 1981. Hydrographic structure over the continental shelf of the southeastern Bering sea. Pages 31–52 in D. Hood and J. A. Calder, eds. The eastern Bering Sea shelf: oceanography and resources, vol. 1. U.S. Government Printing Office, Washington, D.C.
- Kon, T. and M. Sinoda. 1992. Zuwai crab population. *Mar. Behav. Physiol.* 21: 185–226.

- Lovrich, G. A., B. Sainte-Marie, and B. D. Smith. 1995. Depth distribution and seasonal movements of *Chionoecetes opilio* (Brachyura: Majidae) in Baie Sainte-Marguerite, Gulf of Saint Lawrence. Can. J. Zool. 73: 1712–1726.
- Mueter, F. J. and M. A. Litzow. 2008. Sea ice retreat alters the biogeography of the Bering Sea continental shelf. Ecol. Appl. 18: 309–320.
- NPFMC (North Pacific Fisheries Management Council). 2007. Stock assessment and fishery evaluation (SAFE) report for the king and Tanner crab fisheries of the Bering Sea and Aleutian Islands (BSAI) Regions. The Plan Team for the King and Tanner Crab Fisheries, Anchorage, Alaska. 259 p.
- Orensanz, J. M., B. Ernst, and D. A. Armstrong. 2007. Variation of female size- and stage-at-maturity in snow crab (*Chionoecetes opilio*) (Brachyura: Majidae) from the eastern Bering Sea. J. Crust. Biol. 27: 576–591.
- \_\_\_\_\_, B. Ernst, D. A. Armstrong, and J. Burgos. 2008. Female effective reproductive output of the snow crab stock in the Eastern Bering Sea. North Pacific Research Board, Project 508 Final Report. Anchorage, Alaska. 165 p. Available from: <http://project.nprb.org/view.jsp?id=c1078c9b-3458-4a29-8d21-3430c2eb34b0>. Accessed 6 December 2008.
- \_\_\_\_\_, B. Ernst, D. A. Armstrong, P. Stabeno, and P. Livingston. 2004. Contraction of the geographic range of distribution of snow crab (*Chionoecetes opilio*) in the eastern Bering Sea: an environmental ratchet? CalCOFI Rep. 45: 65–79.
- Otto, R. S. 1998. Assessment of the eastern Bering Sea snow crab, *Chionoecetes opilio*, stock under the terminal molt hypothesis. Pages 109–124 in G. S. Jamieson and A. Campbell, eds. Proc. North Pacific Symp. Invertebrate Stock Assessment and Management. Can. Spec. Publ. Fish. Aquat. Sci. 125.
- Parada, C., S. Hinckley, B. Ernst, J. M. Orensanz, D. A. Armstrong, E. Curchitser, and A. J. Hermann. 2007. Settlement patterns of snow crab associated with warm and cold years in the eastern Bering Sea. ICES CM 2007/B:12. 14 p.
- Paul, J. M., A. J. Paul, and W. E. Barber. 1997. Reproductive biology and distribution of the snow crab from the northeastern Chukchi Sea. Am. Fish. Soc. Symp. 19: 287–294.
- Perry, A. L., P. J. Low, J. R. Ellis, and J. D. Reynolds. 2005. Climate change and distribution shifts in marine fishes. Science 308: 1912–1915.
- Reed, R. K. and P. J. Stabeno. 1996. On the climatological mean circulation over the eastern Bering Sea shelf. Continental Shelf Res. 16: 1297–1305.
- Rugolo, L. J., E. A. Chilton, C. E. Armistead, and J. A. Haaga. 2006. Report to industry on the 2006 eastern Bering Sea crab survey. AFSC Processed Report 2006-17. Alaska Fisheries Science Center, NOAA, National Marine Fisheries Service, Kodiak Laboratory, 301 Research Court, AK 99615. 61 p.
- \_\_\_\_\_, D. Pengilly, R. Macintosh, and K. Gravel. 2005. Reproductive potential and life history of snow crabs in the eastern Bering Sea. In D. Pengilly, coordinator, Bering Sea snow crab fishery restoration research. Alaska Department of Fish and Game, Juneau, Alaska. 324 p.
- Sainte-Marie, B. 1993. Reproductive cycle and fecundity of primiparous and multiparous female snow crab, *Chionoecetes opilio*, in the northwest Gulf of Saint Lawrence. Can. J. Fish. Aquat. Sci. 50: 2147–2156.
- \_\_\_\_\_, S. Raymond, and J.-C. Brethes. 1995. Growth and maturation of the benthic stages of male snow crab, *Chionoecetes opilio* (Brachyura: Majidae). Can. J. Fish. Aquat. Sci. 52: 903–924.
- \_\_\_\_\_, T. Gosselin, J.-M. Sévigny, and N. Urbani. 2008. The snow crab mating system: opportunity for natural and unnatural selection in a changing environment. Bull. Mar. Sci. 83: 131–161.
- Sample, T. M. and D. G. Nichol. 1994. Results of the 1990 U.S.-U.S.S.R. cooperative bottom trawl survey of the eastern and western Bering Sea continental shelf. U.S. Department of Commerce. NOAA Tech. Memo. NMFS-AFSC-34. 173 p.



- Schumacher, J. D. and P. J. Stabeno. 1998. Continental shelf of the Bering Sea coastal segment. Pages 789–822 in A. R. Robinson and K. H. Brink, eds. *The sea*, vol. 11. John Wiley and Sons, Hoboken.
- Shirley, T. C. and B. A. Bluhm. 2005. Development of age-determination methods for snow crabs. In D. Pengilly, coordinator, *Bering Sea snow crab fishery restoration research*. Alaska Department of Fish and Game, Juneau, Alaska. 324 p.
- Somerton, D. A. 1981a. Life history and population dynamics of two species of Tanner crab, *Chionoectes bairdi* and *C. opilio*, in the eastern Bering Sea with implications for the management of the commercial harvest. PhD Dissertation, Univ. Washington, Seattle, Washington. 220 p.
- \_\_\_\_\_. 1981b. Regional variation in the size at maturity of two species of Tanner crab (*Chionoectes bairdi* and *C. opilio*) in the eastern Bering Sea, and its use in defining management subareas. *Can. J. Fish. Aquat. Sci.* 38: 163–174.
- \_\_\_\_\_. 1982a. Effects of sea ice on the distribution and population fluctuations of *C. opilio* in the eastern Bering Sea. Pages 157–172 in *Proc. Int. Symp. Genus Chionoectes*. Lowell Wakefield Symposium Series, Alaska Sea Grant College Program, Publication AK-SG-82-10. Univ. Alaska, Fairbanks, Alaska.
- \_\_\_\_\_. 1982b. Bipartite breeding: a hypothesis of the reproductive pattern in Tanner crabs. Pages 283–289 in *Proc. Int. Symp. Genus Chionoectes*. Lowell Wakefield Symposium Series, Alaska Sea Grant College Program, Publication AK-SG-82-10. Univ. Alaska, Fairbanks, Alaska.
- Stabeno, P. J., N. A. Bond, and S. A. Salo. 2007. On the recent warming of the southeastern Bering Sea Shelf. *Deep-Sea Res. II* 54: 2599–2618
- \_\_\_\_\_, N. A. Bond, N. K. Kachel, S. A. Salo, and J. D. Scumacher. 2001. On the temporal variability of the physical environment over the southeastern Bering Sea. *Fish. Oceanogr.* 10: 81–98.
- \_\_\_\_\_, N. K. Kachel, C. Mordy, D. Righi, and S. A. Salo. 2008. An examination of the physical variability around the Pribilof Islands in 2004. *Deep-Sea Res. II* 55: 1701–1716.
- Stevens, B. G. and R. A. MacIntosh. 1986. Analysis of crab data from the 1985 NMFS survey of the northeast Bering Sea and Norton Sound. Northwest and Alaska Fisheries Center, National Marine Fisheries Service, NWAFC Processed Report 1986-16. Kodiak, Alaska.
- Wessel, P. and W. H. F. Smith. 1998. New, improved version of Generic Mapping Tools released. *EOS Trans. Am. Geophys. U.* 79-47: 579.
- Zheng, J. and G. H. Kruse. 2003. Stock-recruitment relationships of three major Alaskan crab stocks. *Fish. Res. (Amst.)* 65: 103–121.
- \_\_\_\_\_, G. H. Kruse, and D. R. Ackley. 2001. Spatial distribution and recruitment patterns of snow crabs in the eastern Bering Sea. Pages 233–255 in G. H. Kruse, N. Bez, A. Booth, M. W. Dorn, S. Hills, R. N. Lipcius, D. Pelletier, C. Roy, S. J. Smith, and D. Witherell, eds. *Spatial processes and management of marine populations*. Alaska Sea Grant College Program, Report No. AK-SG-01–02. Fairbanks, Alaska.

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