

Life history schedule and periodic recruitment of female snow crab (*Chionoecetes opilio*) in the eastern Bering Sea

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Abstract: Snow crab (*Chionoecetes opilio*) populations have fluctuated cyclically in eastern Canada and the eastern Bering Sea, where recruitment to the mature female pool has occurred over a period of three decades (1978–2007) in pulses with a mean period of 7 years. It has been hypothesized that this was the result of a parent–offspring relation between sequentially linked strong cohorts of mature primiparous females, which requires that periodicity matches the time lapsed between egg extrusion by the maternal broodstock and the offspring reaching maturity. We show that female age at maturity (post-settlement) varies between 4.5 and 7.5 years, with most females maturing at 5.5–6.5 years (7–8 years after egg extrusion). Pulses of female recruitment to the mature population do not show a latitudinal trend, consistent with uniformity in age-at-maturity. Results of tracking crab abundance and size–frequency distributions in cod stomach and trawl samples between successive pulses of the cycle are consistent with the hypothesis of serial linkage among pulses. Periodicity is reflected in trends of clutch fullness and average shell condition and in the negative correlation between the strength of primiparous female cohorts and the mean size of their members.

Résumé : Les populations de crabes des neiges (*Chionoecetes opilio*) varient de manière cyclique dans l'est du Canada et dans l'est de la mer de Béring; le recrutement vers le pool des femelles matures s'est produit par vagues d'une période moyenne de 7 ans durant trois décennies (1978–2007). On a émis l'hypothèse selon laquelle ce phénomène s'explique par une relation parents–rejets entre de fortes cohortes de femelles matures primipares ilées de manière séquentielle, qui requiert que la périodicité corresponde au temps écoulé entre l'extrusion des œufs par le stock reproducteur maternel et l'atteinte de la maturité par les rejets. Nous démontrons que l'âge des femelles à la maturité (après leur établissement) varie de 4,5 à 7,5 années et que la majorité des femelles atteignent la maturité à l'âge de 5,5–6,5 années (7–8 ans après l'extrusion des œufs). Les vagues de recrutement de femelles vers la population mature ne suivent pas de tendance latitudinale, ce qui est en accord avec l'uniformité de l'âge à la maturité. Les résultats de la surveillance des abondances et des distributions de fréquence des tailles des crabes dans les estomacs de morue et dans les échantillons de chalutage entre les vagues successives du cycle sont compatibles avec l'hypothèse qui veut qu'il y ait un lien séquentiel entre les vagues. La périodicité se reflète dans les tendances de l'ampleur de masses d'œufs et de la condition moyenne de la coquille, ainsi que dans la corrélation négative entre la force des cohortes de femelles primipares et la taille moyenne des individus qui la composent.

[Traduit par la Rédaction]

Introduction

Cycles in animal populations have attracted the attention of population biologists ever since the seminal work of Elton (1924), prompting a wealth of research, speculation, and theoretical developments (Kendall et al. 1999). Beyond their intrinsic scientific interest, cycles of abundance in marine harvested stocks have significant implications for management, well exemplified by cycling in Dungeness crab (*Cancer magister*) and the fishery that it supports along the west coast of North America (Botsford and Hobbs 1995). Recent research has highlighted the significance of cycles in subarctic

stocks and fisheries of snow crab (*Chionoecetes opilio*) from eastern Canada (Sainte-Marie et al. 2008) and the eastern Bering Sea (Orensanz et al. 2007; Parada et al. 2010). In the latter, recruitment to the mature female stock has occurred over a period of three decades (1978–2007) in pulses with a mean frequency of 7 years and primarily in the Middle Domain (50–100 m depth, Fig. 1a) (Orensanz et al. 2007; Parada et al. 2010). These fluctuations in the reproductive female stock punctuated a contraction of the range of mature females in the Middle Domain, from southeast to northwest (Zheng et al. 2001; Orensanz et al. 2004). While the contraction has been addressed by the Environmental Ratchet Hy-

Received 28 January 2011. Accepted 15 November 2011. Published at www.nrcresearchpress.com/cjfas on 23 February 2012. J2011-0033

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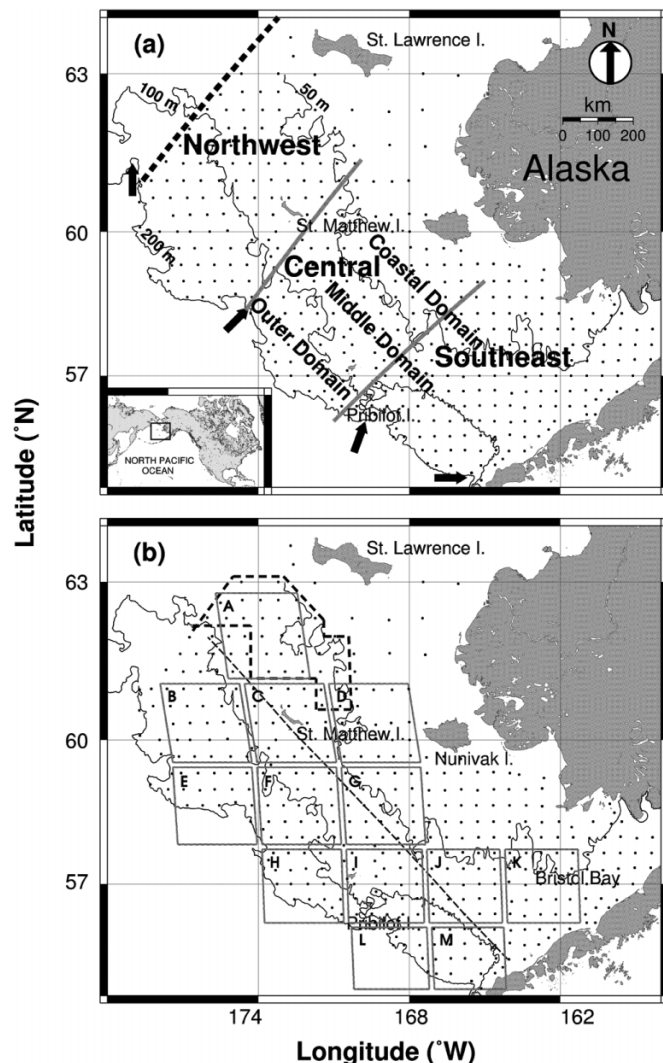
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Fig. 1. The eastern Bering Sea Shelf. (a) Sections (northwest, central, and southeast) and domains (Coastal, Middle, and Outer). Arrows point to four major constrictions of the Outer Domain. (b) “Quadrants” defined to track cohorts of female snow crab (same as in Orensanz et al. 2007). Straight broken line represents the orientation of the main axis of the shelf. Dots indicate stations of the trawl summer surveys conducted by the National Marine Fisheries Service. Dotted polygon bounds the “northern stations”. Broken line indicates the international boundary between the United States and Russia.



pothesis (ERH, Orensanz et al. 2004), the coetaneous periodic recruitment to the mature female stock remains unexplained. These two coincidental but distinct phenomena, contraction and periodicity, may be related to the decline of the snow crab stock from the eastern Bering Sea Shelf (EBS), which has supported one of the largest and most lucrative crab fisheries in the world. Over the last two decades, landings declined dramatically from a maximum of nearly 150 000 t in 1991 to historical lows on the order of 12 000 t during the early 2000s (North Pacific Fishery Management Council 2010).

Because of circulation patterns and the structure of the water column during the summer, the ERH postulated that the Middle Domain of the EBS shelf (Fig. 1a) is a suitable

environment for the retention, survival, and settlement of pelagic larvae, while the Outer Domain (deeper than 100 m) appears to be a much more advective environment (Orensanz et al. 2005). It is in the Middle Domain that female snow crabs reach maturity (at their terminal molt), mate for the first time, and produce their first batch of eggs (first-time breeders are called primipara). Shortly after, the primipara start an ontogenetic migration towards the outer shelf (Ernst et al. 2005; Parada et al. 2010), and eggs hatch somewhere along the way. This sequence of events prompted Parada et al. (2010) to hypothesize that periodic recruitment to the mature female stock could be the result of serial linkage among pulses; a pulse of strong “pseudocoherents” (i.e., all primipara recruited to the mature stock in a given year, from one or more year-classes) would be the maternal stock of strong pseudocoherents some time later. This conjecture requires consistency in the times lapsed (1) from one pulse to the next in the sequence and (2) between oviposition by a pseudocoherent and terminal molt of their offspring. It has been assumed (Orensanz et al. 2004) that the latter is on the order of 6 years (post-settlement) by analogy with female snow crab life history schedules compiled for stocks from eastern Canada (Alunno-Bruscia and Sainte-Marie 1998; Comeau et al. 1998), but in the EBS this still requires empirical validation. Other aspects of female periodic recruitment are also unresolved. The crests of the pulses consist of one to three strong pseudocoherents (Ernst et al. 2005; Parada et al. 2010), but it is not clear whether this results from autocorrelation in year-class strength (implying correspondence between year-classes and pseudocoherents) or from a year-class giving origin to multiple pseudocoherents. Intriguingly, Orensanz et al. (2007) reported a significant and negative correlation between pseudocoherent strength and the mean size of pseudocoherent members, mirroring similar observations in eastern Canada (Sainte-Marie et al. 1996, 2008).

This study addresses the phenomenon of periodic recruitment to the mature female pool and concomitant aspects of female life history. We combined insights from recent work in the EBS and eastern Canada, with data collected by the Food Habits Sampling Program (Lang et al. 2005), survey data generated by the US National Marine Fisheries Service (NMFS) trawl surveys, and size–frequency distribution analysis to (1) assemble a synthetic schedule of female life history events, (2) elucidate the origin and structure of pulses of pseudocoherent strength, and (3) investigate the relation between the relative strength of pseudocoherents and the mean size of their members. The emerging picture is coherent, in spite of the limitations inherent to some of the pieces of information utilized in the inquiry. Finally, we combine old and new evidence to evaluate a hypothesis advanced earlier, aimed at explaining the processes that drive periodic recruitment to the mature female population.

Conventions and notation

A year-class is considered to be formed by all the crab that hatch, undergo pelagic life, and settle during a given year. Age at terminal molt has been expressed in terms of time post-hatching (e.g., Robichaud et al. 1989) or post-settlement (e.g., Alunno-Bruscia and Sainte-Marie 1998), which differ by approximately a half year (e.g., 4.5 years for post-settlement vs.

5 years for post-hatching). We use post-settlement age as our standard.

Instars are conventionally identified with Roman numerals. Here we separate immature and mature crabs in the same instar through the use of, respectively, lower- and upper-case characters (e.g., instar viii vs. instar VIII). Size is always expressed in terms of carapace width (CW), in millimetres. For some analyses, size–frequency distributions (SFDs) were sliced into size brackets that correspond approximately to instars. Those categories (termed “pseudoinstars” by Orensanz et al. 2007) are denoted here as “instar ~ x” (e.g., instar ~ viii or instar ~ VIII).

We denote as CY1 the calendar year during which members of a year-class hatch, undergo pelagic larval life, settle, and molt into instar i. The calendar year of egg extrusion by the maternal broodstock would be, by implication, CY0 or CY1, respectively, for annual and biennial brooders. Studies conducted in Newfoundland (Comeau et al. 1998) and the northwestern Gulf of St. Lawrence (Alunno-Bruscia and Sainte-Marie 1998) consistently concluded that crab go through instars ii–iii during CY2 and through instars iv and v during CY3. Afterwards immature crab molt only once a year, during the winter: from instar v to vi in CY4, from instar vi to vii in CY5, etc. We refer to this as the “eastern Canadian pattern” and use it as a basis for comparative discussion.

Following Comeau et al. (1998), we categorize females as “immature” or “mature” depending on whether they have been through their terminal molt; the more explicit categories defined by Sainte-Marie et al. (2008) cannot be specified with data available for the EBS population. Females carrying their first batch of eggs are collectively designated as “primipara”, and those that have spawned at least two broods (the second one while already in hard-shell condition) as “multipara”. Following Ernst et al. (2005) a “pseudocohort” of mature females is defined as a group of females that undergo their terminal molt (i.e., recruit to the mature population) during a given year. Notice that members of a pseudocohort can belong to multiple year-classes and instars and that a given year-class can contribute to multiple pseudocohorts.

A shell condition index (SCI) and a clutch fullness index (CFI) are recorded for females sampled during summer surveys (described below). SCI scores range from 0 to 5: 0, ready to molt or molting; 1, soft shell (carapace soft and pliable, molted within recent weeks); 2, relatively clean, newer shell; 3 old shell; and 4 and 5, very old shell (5 corresponds to advanced deterioration). Mature females in SCI category 2 (denoted as SCI 2) are considered primiparous and assumed to have molted to maturity during the winter prior to summer surveys (Ernst et al. 2005). When sampled during their second year of post-terminal molt life, they have reached SCI 3. In later years shell condition continues to deteriorate, but correspondence between SCI and post-terminal molt age blurs. Mature SCI 3+ females includes the pool of multiparous females, plus those primiparous females on a biennial brooding schedule that are in their second brooding year. Mature females in SCI 0 and SCI 1, very infrequent in the surveys (on average 0.26% of all mature females), were considered primiparous. CFI is expressed as a percentage of maximum CFI conditioned on female size (Orensanz et al. 2005; Ernst et al. 2008).

Previous work (Orensanz et al. 2007; Parada et al. 2010) showed that four pulses of pseudocohort strength (equivalent to “waves”, sensu Sainte-Marie et al. 2008) occurred at approximately 7-year intervals between 1978 and 2003; these events have been referred to as pulses I–IV (“core years” being 1980, 1988, 1994, and 2001), and here we adhere to that convention. Following Sainte-Marie et al. (2008), the series of weak and strong pseudocohorts in the cycle are denoted as, respectively, troughs and crests.

Material and methods

Surveys and field sampling

Time series of data have been collected during trawl surveys conducted by the NMFS since 1975 (annual reports available from <http://www.afsc.noaa.gov/publications>). Surveys follow a systematic sampling design; stations are regularly spaced over a 20 nmi × 20 nmi grid (1 nmi = 1.852 km) and were sampled every year (Fig. 1b). The 1975–1977 surveys were not included in the analyses because they covered only the southern end of the geographic range of interest. Coverage of the shelf south of 61°N has been reasonably consistent after 1978, and the area surveyed has been standardized since 1990 (Rugolo et al. 2006). Parts of the northwestern shelf, particularly the Middle Domain north of 61°N, were surveyed only during a few years (1979, 1982, 1991, and 1994). In 2001 and 2004–2006 a polygon covering approximately half of the Middle Domain of the northwest sector of the shelf under US jurisdiction (northern stations, Fig. 1b) was added to the survey (Rugolo et al. 2006, pp. 24–26), but data from 2004–2006 were not available for this study. The core temporal window of the surveys is June–July, but in some years work started in May or ended in August. Near-bottom temperature (NBT) has been regularly recorded since the initiation of the survey program. Several observations were made on each individual crab caught in a haul or from a subsample when the catch was too large. These included CW, SCI, and, in the case of females, maturity and CFI.

Fish stomachs were also sampled during the surveys. Stomach contents were fixed onboard and processed at the laboratory. Crabs in each stomach were identified, counted, measured (CW, with variable precision, 1 mm or higher), and weighed (bulk). The Food Habits Sampling Program started in 1984, although some data were collected in 1981 (Livingston 1989; Livingston et al. 1993; Lang et al. 2005). The database also contains information obtained as part of the observer program. Although several species of groundfish prey on snow crab, Pacific cod (*Gadus macrocephalus*) is far more important than the rest. The database contained information on 44 412 cod stomachs (as of November 2007). Of these, 5958 cod stomachs contained 18 511 snow crabs. In most cases, for reasons of consistency, we utilized only data collected in the course of the surveys during June and July. The geographic range of the data utilized in the analyses was truncated (mile 100, defined later), omitting a few data outside the confirmed range of occurrence of immature snow crab; those specimens could correspond to misidentified immature individuals of Tanner crab (*Chionoecetes bairdi*). Information on the geographical distribution of (mostly immature) snow crab derived from the analysis of cod stomach samples is inevitably constrained by the range of distri-

bution of the cod population. Stomach contents of two flatfishes, flathead sole (*Hippoglossoides elassodon*) and yellowfin sole (*Limanda aspera*), yielded some additional qualitative information on the early instars of snow crab.

The size selectivity of sampling gear, including trawls and foraging cod, constrains the information retrievable from the data. Size selectivity by fish predators is a function of fish size (Chabot et al. 2008, their Fig. 2; Armstrong et al. 2010, their Fig. 1) and the availability of alternative prey. Trawl efficiency is presumably size dependent (Somerton and Otto 1999). In both cases (trawl and fish stomach content samples), the presence of a given stage in a sample is informative, but its absence has to be interpreted cautiously.

In addition to data from the NMFS surveys, we reanalyzed a data set collected as part of the Outer Continental Shelf Environmental Assessment Program (OCSEAP) around the Pribilof Islands in August 1983, which includes measurements of juveniles made with a precision of 0.1 mm (Armstrong et al. 1990). Samples were obtained with a 3 m beam trawl, mostly close to the 60 m isobath.

Data aggregation and processing

Data were parsed and analyzed using scripts in AWK stream editor (Robbins 2001) and standard Microsoft Access database software. Graphical analysis was conducted using GMT (Generic Mapping Tool) graphical software (Wessel and Smith 1998). Some graphs required surface plots, which implied the additional calculation of regular station grids over the entire distributional area. This was accomplished by using a near-neighbor algorithm.

The EBS shelf was partitioned in various ways for the analysis of size and abundance of different categories of females. Partitions include domains (Coastal, Middle, Outer) defined bathymetrically (Schumacher and Stabenro 1998), transversal sections of the shelf (northwest, central, southeast; Parada et al. 2007), and quadrants (Fig. 1). A fringe area of the Coastal Domain, southwest of Nunivak Island, is functionally part of the Middle Domain, both oceanographically and biologically (Orensanz et al. 2004; Parada et al. 2010). Following Orensanz et al. (2007), the region of interest was partitioned into 13 rectangular quadrants (Fig. 1b). Quadrant A (Middle Domain of the northwest sector of the shelf) was not consistently surveyed before 1988, when a cluster of stations located on its southwest quarter became part of the standard area surveyed. The northern stations polygon (introduced earlier), added to the regular survey in 2001 and 2004–2006, covered the entire quadrant A, but only data from 2001 were available for this study.

Following exploratory analysis, we singled out pulse III of pseudocohort recruitment, which was centered around 1994 and extended from 1992 to 1996, to piece together a tentative life history schedule. Pulse III was selected for three reasons: (1) it is fully contained within the frame of the time series of data. Females of pulse I were already joining the mature female population by 1979, while pulse II could not be backtracked in the northwest section of the shelf, which was not covered by the earlier surveys. (2) Pulse III was detected in all sections of the shelf; pulse IV was not detectable in the southeast section. (4) At least over part of its geographic range, pulse III was the most clearly defined among the four

pulses; it was selected by Ernst et al. (2005) to investigate post-terminal molt longevity, for the same reason.

To show variation of abundance of mature females in time and space we aggregated survey data in slices orthogonal to a reference straight line running along the main axis of the shelf (Fig. 1b), with a northwest–southeast direction; distances along the reference line were calculated starting from its interception with the Alaska Peninsula. Locations of interest along the axis are identified by mile number. Sections of the shelf introduced earlier (northwest, central, southeast) are separated approximately at miles 220 and 425. Quadrant G is spread between miles 226 and 354, and quadrant C between miles 382 and 495.

Estimation of abundance indices by category

Based on survey data, indices of abundance of different categories of interest were estimated, analyzed, and mapped as described by Ernst et al. (2005). Categories of interest were defined on the basis of sex, maturity, size, or shell condition. Catch per haul was used to estimate an abundance index (“density”) using swept-area methods (Sparre and Venema 1998). Mean density by cell was estimated as

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

where D_t^S is density at station S in year t , n_t^S is the total number of hauls associated with station S in year t , $A_{t,i}^S$ is the area swept by haul i associated with station S during year t (in nmi^2), and $d_{t,i}^S$ is the number of crabs caught by haul i in station S in year t . Survey stations are at the center of the 20 $\text{nmi} \times 20 \text{ nmi}$ grid cells. Multiple tows were occasionally conducted in a cell associated with a single station when abundance of a target species (e.g., king crab) was very high. Additionally, some trawling experiments were occasionally conducted in some areas, which increased the number of hauls for particular stations. Density estimates by station and time were rendered into total abundance by grid cell (q), using a constant area expansion factor:

$$(2) \quad N_t^q = (20^2) D_t^S$$

We consider this only as an index of abundance because no correction for gear efficiency (see Somerton and Otto 1999) was used in the analysis. NMFS abundance estimates using survey data has been traditionally based on design-based estimators, although recently model-based (geostatistic) analysis has been proposed as an alternative. We used the traditional approach to obtain abundance indices, and our results are similar to those of NMFS. NMFS does not report estimates based on maturity condition, but on arbitrary size cuts.

In each cell the mean number of immature crab (<35 mm CW) per cod stomach (N_{35t}^S) was computed as

$$(3) \quad N_{35t}^S = \frac{c_{35t}^S}{ST_t^S}$$

where c_{35t}^S is the total number of snow crabs with CW <35 mm as measured in stomachs sampled in station S and year t and ST_t^S is the total number of Pacific cod stomachs

sampled in station S and year t . Spatially explicit information was integrated along the shelf axis to compose a time (years) – distance (nautical miles) plot. Data were split into size categories (introduced below) for some analyses.

Size–frequency distributions

SFDs of immature crab were assembled with data from three sources: NMFS survey trawl samples, cod stomach content samples, and the OCSEAP survey conducted around the Pribilof Islands in August 1983. SFDs assembled with data from NMFS survey samples were not used in the estimation of size at instar owing to concerns about insufficient precision and likelihood of errors derived from onboard recording. SFDs from the OCSEAP survey and cod stomach contents were analyzed using the approach described by Orensanz et al. (2007). Size at instar is not expected to differ significantly between males and females for crabs smaller than 35 mm, corresponding to instars i–vii (Kon and Sinoda 1992; Co-meau et al. 1998). Sexes were pooled for the analysis of SFDs of crabs in that size range.

In some analyses SFDs were sliced into size brackets that correspond approximately to instar categories. Size cut-points for instars ~ iv, v, vi, and vii (9, 14, 19, 25, 34 mm) were based on results of SFD decomposition indicated above (see Results section). Cut-points for instars ~ VIII, IX, X, and XI (40, 46, 55, 65, max. CW) were based on results from Orensanz et al. (2007). Cut-points for instars ~ ix and x (43, 55, 65 mm) were based on a projection and inspection of the SFDs from quadrant G.

Inspection of composite sequences of SFDs indicates that quadrant G was the one most consistently represented as pulse III developed and vanished and for that reason was selected for detailed scrutiny. Also, quadrant G is conveniently located in the central section of the shelf. Quadrant C was used for comparison, to investigate geographic variation in life history schedules.

Clutch fullness index

Mean CFI was calculated using NMFS survey data for all years and for SCI categories 2, 3, and 4⁺ (Orensanz et al. 2005; Ernst et al. 2008). The survey protocol specifies seven categories of clutch fullness: (1) empty, (2) traces to 12.5%, (3) 25%, (4) 50%, (5) 75%, (6) 100%, and (7) over-full (“eggs bulging outside tail flap”). In the protocol followed before 1992, assignment to fullness categories was subjective. Between 1991 and 1993, a photo-chart was designed and tried in the field with the purpose of making observations more objective (Orensanz et al. 2005). Comparison of mean CFI estimated objectively (volumetry) and semisubjectively (using the photo-chart) (Rugolo et al. 2005) showed that the latter performs very well, both for the entire sample and for individual CFI categories (Ernst et al. 2008, p. 61). Interpretation of mean levels of CFI before the photo-chart was introduced requires some caution (Ernst et al. 2008, p. 64).

Results

Cyclic variation in the abundance of mature females

The aggregated abundance of mature females showed strong fluctuations during the study period; prominent fea-

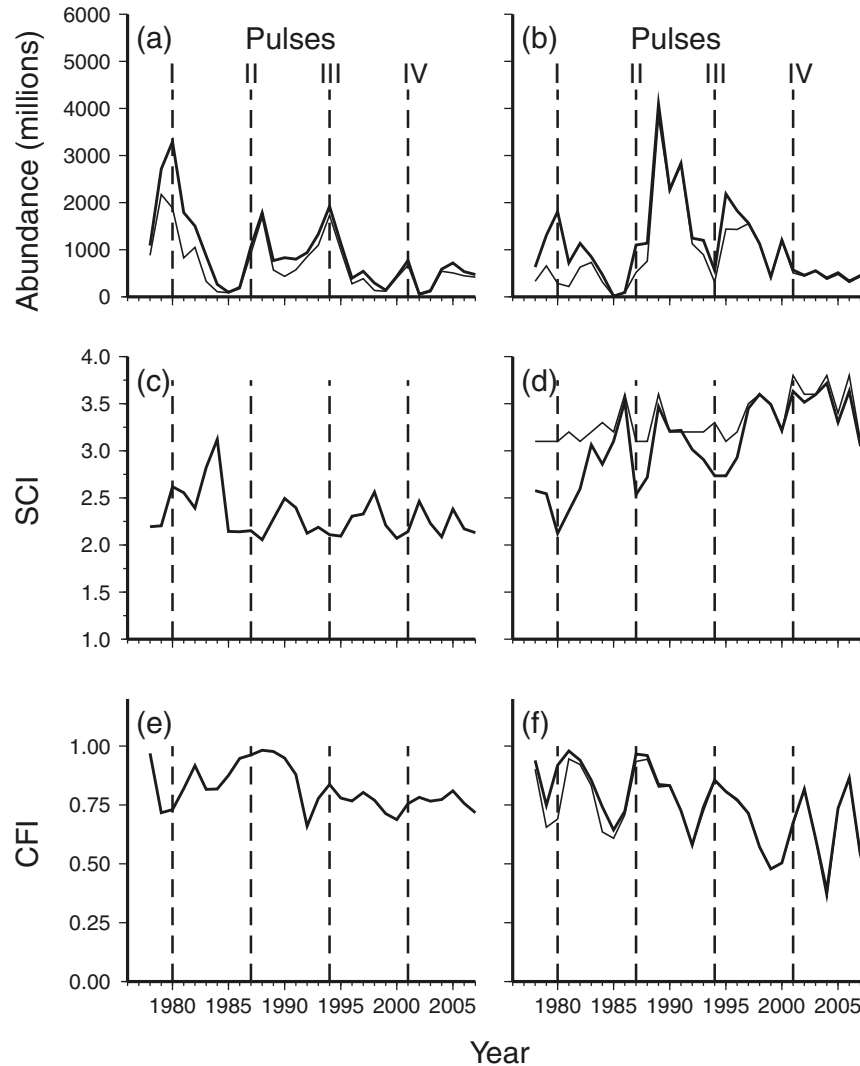
tures included maxima in 1980 and 1989, a consistent historical minimum in 1985–1986, and a declining trend after 1989. The mature female population was dominated by SCI 2 females (primipara) in the Middle Domain (Fig. 2a) and by SCI 3⁺ females in the Outer Domain (Fig. 2b). Segregation has been consistent over time, although SCI 2 females constituted a significant fraction of the mature female stock of the Outer Domain during short intervals (1980–1982, 1987–1988, 1995). The latter match peaks of abundance of SCI 2 females in the Middle Domain, described below.

Crests of the pulses of SCI 2 females (primipara) extended over 1–3 years (1979–1980, 1987–1988, 1993–1995, and 2001), and interspersed troughs lasted approximately 4–6 years (Fig. 2a). Pulses developed synchronously along the northwest–southeast axis of the shelf (Figs. 3a, 3b), spreading approximately 550 nmi and 7° of latitude (Fig. 1b). Local foci sometimes occurred 1 year before or after the core year, as best illustrated by pulse III north of St. Matthew, but variability in timing did not appear to be related to latitude. Pulse IV was not detected in the southeast shelf. When information was aggregated by quadrants, pulses were most easily detected and traceable in quadrants A (in the northwest section of the shelf), C (centered around St. Matthew Island), and G (north of the Pribilof Islands), which are aligned along the main axis of the Middle Domain (Fig. 1b). Secondary events of recruitment to the mature population, most traceable to patches of immature females in preceding years, were spatially localized and sporadic, with typically one identifiable lesser event interspersed between two successive pulses in at least some quadrants. Localized patches of abundance of SCI 2 females in the central section of the shelf, north of the Pribilof Islands, were detected in 2005–2007 (Fig. 3b). These patches, while modest, are remarkable given that substantial presence of primipara had not been observed in that sector since 1995.

Abundance of SCI 3⁺ mature females trailed abundance of primipara pseudocohorts, but periodicity deteriorates in this group (Figs. 3c, 3d) owing to the accumulation of multiple pseudocohorts. Peaks of aggregated annual abundance are interspersed with pulses of primipara recruitment. Tracking the relative strength of single pulses from the Middle Domain (as primipara) to the Outer Domain (as SCI 3⁺ mature females) (Figs. 3a, 3c) reveals some apparent anomalies. Pulse I was the strongest among the primipara, but was comparatively weak in the Outer Domain. The reason is that in this particular case, many SCI 3⁺ mature females remained in the Middle Domain during the years 1979–1982 (Figs. 2a, 2b). Pulse II, on the other hand, was disproportionately strong in the Outer Domain. A high concentration of SCI 3⁺ mature females near the northwest end of the survey geographical frame (Fig. 3d) indicates that these females immigrated from outside the geographical frame of the survey.

Sequential linkage between pulses should be reflected in the cross-correlation between abundance of mature females in the Middle Domain (presumed to have a preponderant role in stock renewal) and recruitment to the mature female population (Fig. 4a). That relation is best captured by expressing the abundance of recruits in relative terms, for example, as the fraction of the mature female stock that corresponds to the primipara. This preserves periodicity in the time series while removing much of the effect of variation in amplitude

Fig. 2. Abundance, mean shell condition index (SCI), and mean clutch fullness index (CFI) of mature females in the eastern Bering Sea Shelf, 1978–2008; left: Middle Domain, right: Outer Domain. (a, b) Abundance of mature females; thick line: total abundance; thin line corresponds to SCI 2 females in (a) and to SCI 3+ in (b). (c, d) Trends in SCI. (e, f) Trends in CFI. Thin line in (d) and (f) corresponds to SCI 3+ females.



(allegedly modulated by extrinsic factors). We used a standard cross-correlation function (XCORR, available from MATLAB software) to estimate the cross-correlation between two random jointly stationary sequences at different time steps; data were pre-processed by subtracting the mean and detrending the series. Cross-correlation was highest at lags of 6 and 13 years (Fig. 4b). Correspondence between the two raw series at a lag of 6 years was lost, as the cycle vanished following pulse IV, the last and weakest in the series (Fig. 4a). The trajectory of the relation between the two series (a crude form of spawner–recruit relation), with a 6-year lag, takes the form of a series of loops, each corresponding to a pulse (Fig. 4c). The cross-correlation coefficient (r^2) between the raw time series was 0.68 for a 6-year lag.

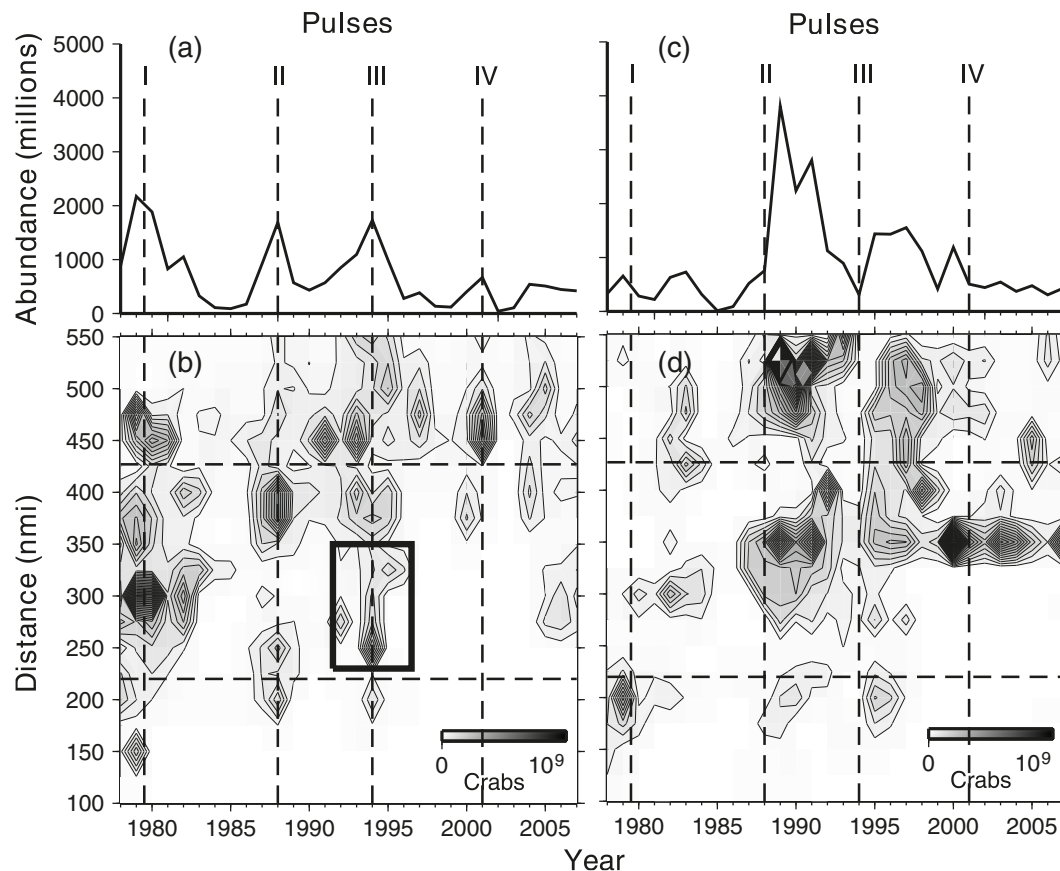
Cross-correlation between abundance of females in the Middle Domain and relative abundance of primipara (highest at a lag of 6 years) is largely driven by autocorrelation in the abundance of primipara (highest at a lag of 7 years), as the latter form the bulk of the mature female stock found in the Middle Domain, where most primipara recruit. The difference of 1 year in the period of these two relations reflects

the fact that the relative abundance of primipara of a given pulse is influenced by the attrition rate of members of the preceding pulse; maximum life span beyond terminal molt is on the order of 6–7 years, but few females are expected to reach that limit.

Trends in clutch fullness and shell condition index

In the Middle Domain mean SCI of mature females fluctuated regularly; minima were (as expected) coincidental with crests of pseudocohort strength (Fig. 2c) owing to the overwhelming relative abundance of primipara (SCI 2 mature females). This regularity and the absence of a long-term trend are indicative of a persistent role of the Middle Domain in pseudocohort recruitment. Maxima in SCI (1984, 1990, 1998, 2002) were coincidental with troughs of the pseudocohort strength cycle, when the relative abundance of the residual population of SCI 3+ females increased. The cycle is less clear in the Outer Domain (Fig. 2d), where the accumulation and attrition of pseudocohorts of variable strength influence short-term variability. Prominent minima (centered in 1980, 1987, 1994–1995) are coincidental with pulses of pseudoco-

Fig. 3. Abundance of mature females, 1978–2007. (a, b) Primipara (SCI 2 mature females) in the Middle Domain. (c, d) SCI 3⁺ mature females in the Outer Domain. (a, c) Aggregated abundance; (b, d) abundance along the main axis of the shelf (northwest to southeast). Vertical broken lines indicate core of pulses of pseudocohort recruitment. Horizontal lines run across Pribilof and St. Matthew islands, approximately separating the southeast, central, and northwest sectors of the Middle Domain.



hort strength, when there was a detectable presence of primipara in the Outer Domain (Figs. 2b, 2d). Mean SCI increased after 1997, perhaps reflecting a period of low pseudocohort strength.

The trend of mean CFI in the Outer Domain showed two distinct components: a decline over the 30-year study period and a cycle related to pulses of pseudocohort strength (minima in 1979, 1984, 1992, and 2000; Fig. 2f). Pulses of mean CFI developed with a recurrent pattern: a steep 1–2 year increase followed by a declining trend lasting approximately 4 years (Fig. 2f). Maxima of mean CFI (1981–1983, 1987–1988, 1994–1995, 2002) trail pulses of pseudocohort strength in the Middle Domain with an approximate lag of 1 year, reflecting the offshore migration of the primipara. High mean CFI reflects the abundance of SCI 3 females, a mixture of primipara on a biennial brooding schedule that are in their second year of brooding, and first-time multipara. During the decline phase of the pulse the relative abundance of older multipara (SCI 4⁺) increased relative to immigrants originating in the Middle Domain. The result is a decline in mean CFI, since CFI declines with post-terminal molt age due primarily to senescence. There was no clear trend in mean CFI in the Middle Domain. An apparent downward shift during the early 1990s (Fig. 2e) may reflect a change in the survey protocol (see Materials and methods), which had the greatest impact in the case of SCI 2 females.

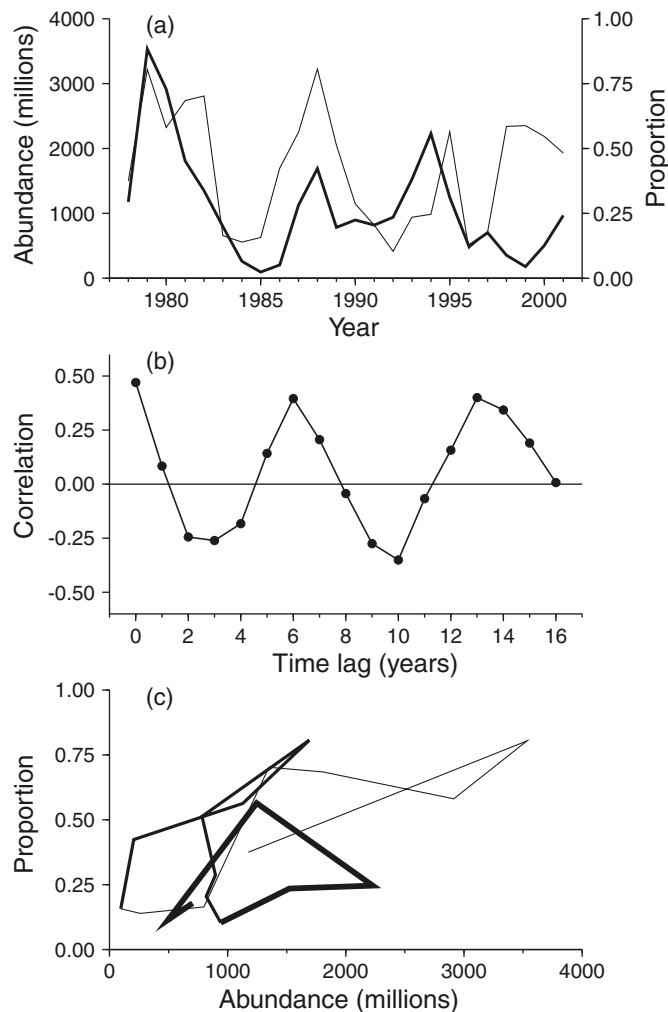
Size-stage structure of immature females

It is generally assumed that immature females molt at least once every year and so are not expected to be in SCI 3 or higher. The database contains some records of immature females listed as SCI 3⁺ (413 out of 82 357 for the period considered here, or 0.5%). The size range is 20–74 mm (mean: 45.4 mm), and the records do not show a clear pattern of geographical distribution. They could represent real but rare cases of skip-molting or may simply correspond to observation error, for example, barren mature females that were mis-coded as immature (at least towards the larger end of the range).

The aggregate SFDs (all years pooled) of immature crab from cod stomach samples (sexes pooled) and immature females from trawl samples overlap significantly over a relatively narrow size range (Fig. 5). Most of the immature crab obtained from cod stomachs are smaller than 35 mm, while most of those trawled during summer surveys are larger than 25 mm. The size range of immature females observed in survey trawl samples corresponds to instars vi–x, but most are in the size range expected for instars viii–ix. Very few crab putatively corresponding to instars i and ii (expected mean CW approximately 3 and 5 mm, respectively) have ever been sampled and reported from the EBS.

The stomach content database (including observer data) contains few records of snow crab ≤ 6 mm as prey: 40 from

Fig. 4. Relation between abundance of mature females in the Middle Domain and relative abundance of primipara in subsequent years, 1978–2007. (a) Time series of abundance of mature females in the Middle Domain (thick line) and relative abundance of primipara (“Proportion”, thin line) 6 years later. (b) Cross-correlogram of the two series. (c) Trajectory of the relative abundance of primipara as a function of abundance of mature females in the Middle Domain 6 years earlier; thickness of the lines (from thin to thick) corresponds to pulses II–IV of pseudocohort strength.



cod and 21 from flatfish stomachs. Virtually all were sampled between June and October. Immature females in the range 6–35 mm CW sampled from cod stomach contents ($n = 11\,568$) show five clear modal components, which correspond to instars iii–vii (Table 1; Fig. 6a). Analysis of the SFD of immature snow crab ($n = 234$ individuals <20 mm CW, sexes pooled) from the Pribilof Islands collected in August 1983 (measured with a precision of 0.1 mm) shows two clear modal components that correspond to instars iv and v (Table 1; Fig. 6b).

Tracking the abundance and distribution of immature stages

The mean number of immature crabs per cod stomach (sexes pooled) was calculated for crab prey in the size range 9–34 mm, corresponding approximately to instars iv–vii (the ones best represented in cod stomach contents; Table 1;

Fig. 6a). Cod predation on crab is size selective, but the mean size of cod sampled for stomach contents during the summer surveys in the Middle Domain and in the latitudinal range of interest (north of 56°N) did not vary much (mean: 45.4 cm, range: 41.7 cm (1990) – 51.0 cm (1987)). Crabs from samples collected during the summer surveys were partitioned into three size brackets: 9–19, 19–25, and 25–34 mm, which correspond to (respectively) instars ~ iv–v, vi, and vii (Fig. 6).

Instars ~ iv–v generally co-occurred in cod stomachs and were pooled for that reason. Their spatial distribution was very patchy; main patches were detected in 1988, 1989–1990, 1997, and 2003 (no data for 2004). In those years, mostly 2–3 years after pulses of primipara pseudocohort strength, the relative abundance of crabs in instars iv–v was overwhelmingly high. Within-year variation in the proportion of instars iv and v was investigated using the pool of cod stomach content samples (including data collected through the observers program), by month and for the period of the year during which molting is expected to occur (late spring to early winter). To that end we fixed mean sizes-at-instar and standard deviations (estimates shown in Table 1) and calculated the proportions using the numerical approach described earlier. The proportion of instar iv declined gradually and monotonically from 74% in May to 6% in November–December.

Occurrence in cod stomachs of crabs in instars ~ vi and vii showed similar patterns of geographic and temporal variation, but patterns were more consistent in the case of instar ~ vii; we focus on the latter for that reason. The mean number of crabs per cod stomach varied periodically (Fig. 7a), with crests and troughs resembling those observed in time series of aggregated primipara abundance (Fig. 3a). Crests peaked in 1991, 1998, and 2005 (no data available for 2004), 4 years after core years of pulses II–IV of pseudocohort strength. Occurrence in cod stomachs of crabs in instars ~ vi and vii virtually vanished from the southeast and central sections of the shelf during the period 2002–2008 (latest data available) (Fig. 7b).

More than 90% of the immature females sampled during the summer surveys originated in the Middle Domain and the Coastal Domain fringe. We focused on the size interval 35–50 mm, which includes the core of the immature females sampled during the surveys (Fig. 5) and corresponds to instars ~ viii–ix. The aggregated abundance of that group varied periodically (Fig. 7c), with crests and troughs analogous to those observed in trends of pseudocohort strength (Fig. 3a) and occurrence of instar ~ vii crabs in cod stomachs (Fig. 7a). Abundance peaked in 1979, 1987, 1993–1994, and 2004–2005; the first three peaked slightly earlier than pseudocohort strength of pulses I–III (Fig. 7d); pulse IV was slightly anticipated in 2000–2001. While crab in instars ~ vi and vii occurred extensively in cod stomachs sampled in the three sections of the Middle Domain between 1994 and 2001 (Fig. 7b), abundance of immature females in instars ~ viii–ix and primipara forming pulse IV was confined to the north-west section of the shelf (Figs. 7d and 3b).

Based on results presented in the two preceding sections, pulse III could be tracked from instars ~ iv–v (1988–1990) and instar ~ vii (1991–1992, Fig. 7a) in cod stomachs, through instars ~ viii–ix (1993–1994, Fig. 7c), primipara in

Fig. 5. Aggregated size–frequency distributions (SFDs) of pooled samples of immature crabs. (□) Cod stomach samples (males and females pooled, 1978–2005), (○) immature females from trawl samples (1981–2005).

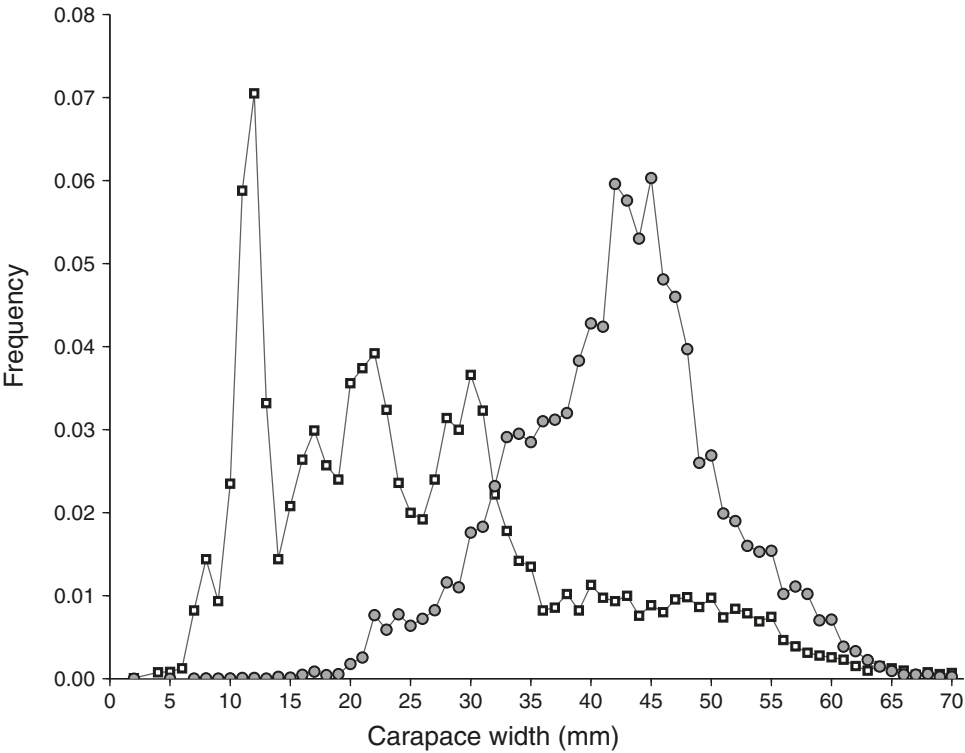


Table 1. Estimated mean instar sizes and standard deviations (SD) of the modal components, instars iii–vii, and comparable parameters from other studies.

Instar	Sample dredged in the Pribilof I. region (OCSEAP) (<i>n</i> = 234, sexes pooled)		Samples from cod stomach contents (pooled, 1981–2005) (<i>n</i> = 11 568)		Gulf of St. Lawrence		Newfoundland		Japan Sea
	Mean CW (SE) (mm)	SD	Mean CW (SE) (mm)	SD	Mean CW (mm)	SD	Mean CW (mm)	SD	Mean CW (mm)
iii			7.9 (0.76)	0.87	Males: 6.6 Females: 6.6	0.38 0.39	Males: 7.0 Females: 9.7	0.52 0.76	6.5
iv	11.2 (0.32)	0.71	11.6 (0.31)	1.05	Males: 9.7 Females: 9.7	0.64 0.65	Males: 9.8 Females: 14.7	0.72 1.05	9.7
v	15.8 (0.53)	1.20	16.4 (1.44)	1.63	Males: 14.1 Females: 14.1	0.92 0.91	Males: 14.9 Females: 20.9	1.32 1.77	13.5
vi			21.4 (1.28)	1.86	Males: 20.0 Females: 20.2	1.33 1.35	Males: 21.6 Females: 27.3	1.63 1.99	Males: 19.6 Females: 19.0
vii			29.6 (1.24)	3.65	Males: 26.9 Females: 27.3	1.90 2.01	Males: 28.0 Females: 27.7	1.79 1.87	Males: 27.3 Females: 27.9

Note: Sources of data: Gulf of St. Lawrence: Sainte-Marie et al. 1995; Alunno-Bruscia and Sainte-Marie 1998; Newfoundland: Comeau et al. 1998; Japan: Kon and Sinoda 1992.

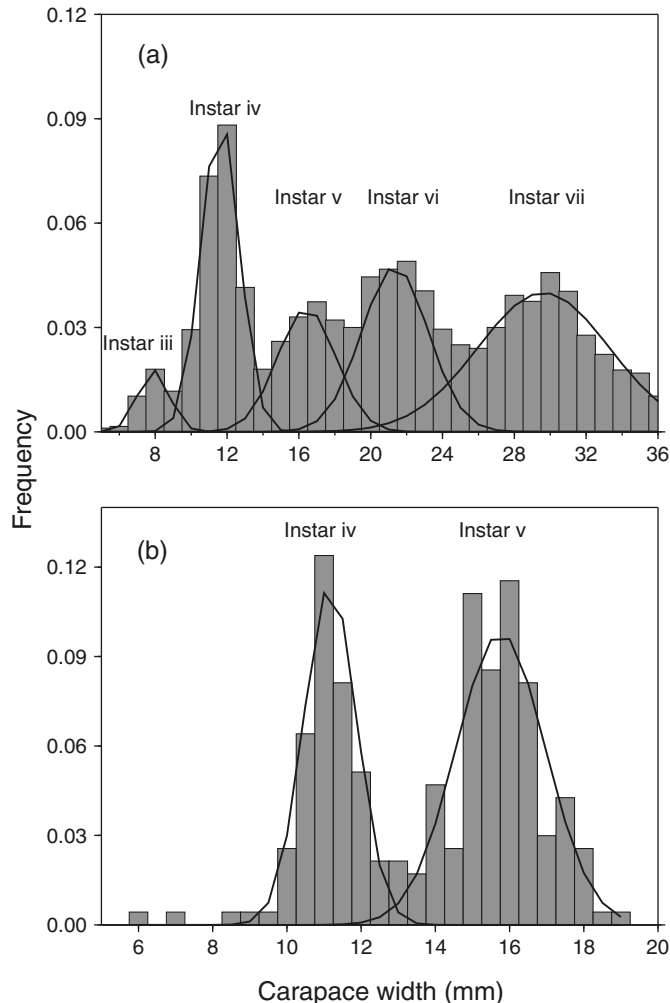
the Middle Domain (1994, Fig. 3a), and SCI 3+ mature females in the Outer Domain (1995–1998, Fig. 3c) in survey samples.

Tracking pseudocohorts and pulses over sequences of size–frequency distributions

The development and decline of pulse III could be tracked in more detail in quadrant G through sequential SFDs. Immature crab in instars iv–vii were observed in cod stomach content samples during June–July of 1988–1991 (*n* = 738). Modal components corresponding to instars iv–v were identifiable in 1988–1990, and those corresponding to instar vii in

1989–1991 (Fig. 7b, Fig. 8), suggesting that settlement contributing to pulse III extended over a period of at least 3 years. Crabs in instars iv–v occurred in stomach contents from two nonoverlapping locations: to the north (miles 308–322), in the fringe area of the Coastal Domain in 1988, and to the south (miles 238–266), in the Middle Domain, in 1989–1990. Crab of year-classes traceable to pulse III first became detectable in SFDs of trawl samples from quadrant G in 1991, in a size range that corresponds to instars vi–ix (Fig. 8). This was the only year in which a given instar (instar vii) was represented in both cod stomach and trawl samples. In 1991–1992, trawl samples contained members of

Fig. 6. Size–frequency distributions of immature crab. (a) Aggregated samples from cod stomachs ($n = 11\,568$). Continuous lines corresponds to the distributions fitted to the modal components identified. (b) Sample of immature snow crab measured with 0.1 mm precision ($n = 234$), collected in the Pribilof Islands region in August 1983 (OCSEAP).



weak pseudocohersts recruited between pulses II and III, including instar $\sim x$ in 1991 and instar $\sim XI$ in 1992 (Fig. 8); this group became undetectable after 1992 (Fig. 7d), as its members underwent terminal molt and presumably emigrated from the Middle Domain. From 1993 on, all females from quadrant G were, for all practical purposes, assignable to the year-classes that contributed to pulse III (Fig. 3b). From 1992 to 1995, females in the size range corresponding to instars $\sim VIII$ – X included mature and immature individuals. Mature females present in the samples corresponded to instars $\sim VIII$ – XI in 1993, $\sim IX$ – XI in 1994, $\sim X$ – XI in 1995, and $\sim XI$ in 1996. A few large individuals sampled in 1997–1998 were excluded from the analysis; they may indicate the rare occurrence of instar $\sim XII$. Events tracked in survey samples from quadrant C trailed quadrant G with a 1–2 year delay, from the first occurrence of immature females assignable to year-classes contributing to pulse III (instars vi–vii 1992 vs. 1991) through their vanishing from the immature pool (1998 vs. 1996) (Fig. 8).

Qualitative instar composition of cod stomach and trawl

samples corresponding to pulse III in quadrant G, described above, is summarized for ease of interpretation (Fig. 9). Instars observed in each year are superimposed on the eastern Canadian pattern (see Conventions and notation section), showing that in general the latter matches the information recovered from the data (Fig. 9a).

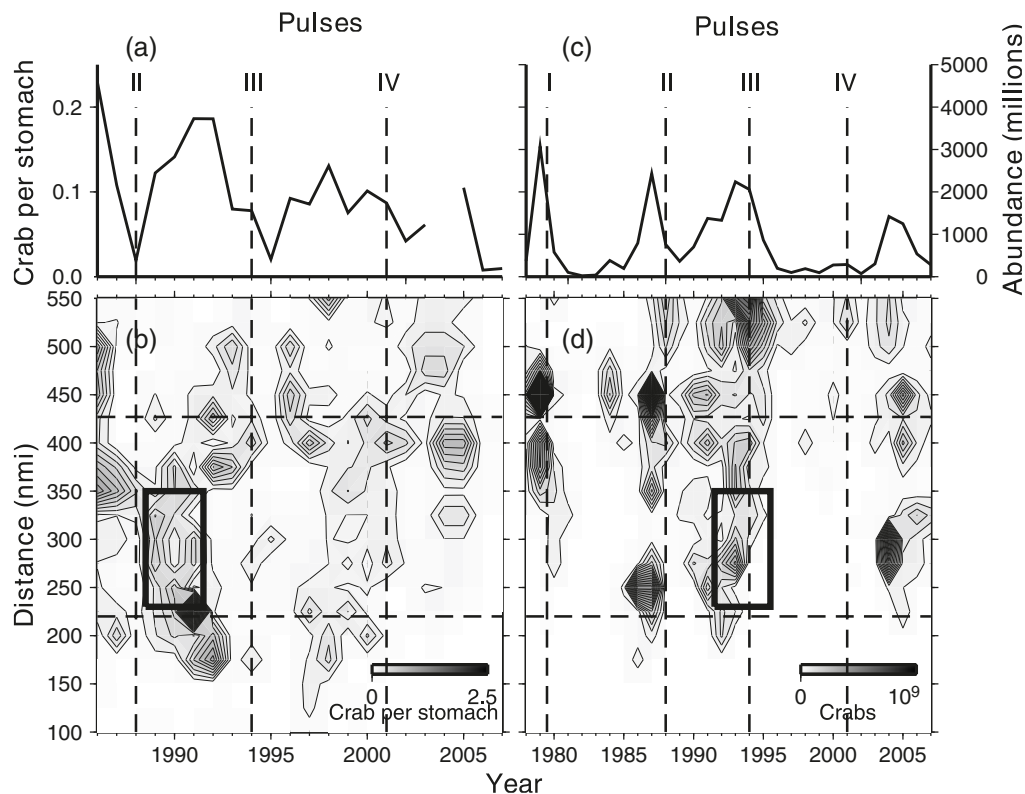
Matching is virtually complete if at least some individuals are allowed to molt twice during CY3, for example, from instar iv to v during early spring and from instar v to vi during late fall (Fig. 9b). This hypothesis would be consistent with the absence of instar vi in samples of cod stomachs collected during the summer, which are dominated by instars iv and vii. Females in instars $\sim VIII$ – X observed in 1993 in quadrant G would belong to the 1986–1988 year-classes and would be maturing at the approximate age of 4.5–5.5 years (Fig. 9b). Absence of instars $\sim VIII$ – IX in 1991–1992 may reflect insufficient sampling of relatively weak year-classes.

Based on the results presented above, a schematic of events in the life history of female snow crab from the central section of the EBS shelf is shown (Fig. 10). Let us start with a strong pseudocoherst recruited to the mature pool in year x . A pseudocoherst may include females on annual and biennial brooding schedules, thus contributing to two year-classes that will settle in years $x+1$ and $x+2$, respectively. Below we consider only the first; the other proceeds through the same stages with a 1-year delay. The age threshold for the onset of maturity is reached in year $x+6$ (post-settlement age ~ 4.5 years), as some members in each year-class molt into maturity, from instar vii to instar VIII. Previous research (Orensanz et al. 2007) has shown that instar $\sim IX$ is overwhelmingly dominant in quadrant G, and so the strongest pseudocoherst, composed primarily of females in instar IX, is expected to occur at year $x+7$; pseudocohersts of declining strength would recruit to the mature pool over the next 2 years ($x+8$ and $x+9$). Thus, considering both possible daughter year-classes, the progeny of the original pseudocoherst (year x) would be spread over four instars (VIII–XI) and 5 years ($x+6$ to $x+10$); abundance would peak in years $x+7$ and $x+8$.

Correlation between the strength of pseudocohersts and the size of their members

As pulse III developed and vanished in the Middle Domain (quadrants A, C, D, G; Fig. 11a) between 1992 and 1998 (Figs. 3a, 3b), pseudocoherst strength (Fig. 11b) and the mean size of its members (Fig. 11c) was negatively correlated (Fig. 11d). Inspection of sequential SFDs capturing the development of pulse III reveals that the size of immature females increased over time (Fig. 8). This reflects the fact that, in the absence of skip-molting, those females that did not molt to maturity progressed towards larger immature instars. Since pulses of pseudocoherst strength are dominated by one or two strong year-classes, intrayear-class size-related molting should result in a negative correlation between pseudocoherst strength and the mean size of its members. This pattern would not exist in the absence of strong fluctuations of pseudocoherst strength. When the pulse starts to develop, the mean size of pseudocoherst members may increase (e.g., Fig. 11d, quadrants A and C) or decrease (e.g., Fig. 11d, quadrants D and G, 1992–1994), depending on the relative contribution of large recruits from previous (ageing) year-

Fig. 7. Geographic distribution and abundance of immature crab in the Middle Domain. (a, b) Mean number of crab in instar ~ vii (sexes pooled) per cod stomach, 1986–2007. (c, d) Abundance of immature females in instars ~ viii–ix (35–50 mm carapace width), 1978–2007. (a, c) Aggregated time series; (b, d) variation along the main axis of the shelf (northwest to southeast). Vertical broken lines indicate core of pulses of pseudocohort recruitment. Horizontal lines run across Pribilof and St. Matthew islands, approximately separating the southeast, central, and northwest sectors of the Middle Domain.



classes to pseudocohort strength being, respectively, small or large.

Discussion

Life history schedule of immature female snow crab in the eastern Bering Sea Shelf

There is an interval of approximately 2 years in the early life history of snow crab from the EBS, for which there is little information available. That interval includes (1) hatching, which occurs during the spring, before summer surveys are conducted (Somerton 1981, 1983; Incze et al. 1987); (2) pelagic stages, lasting 3–5 months, which are not routinely monitored (Incze et al. 1987; Kon and Sinoda 1992); (3) settlement and megalopae molting into instar i (mean CW ~3 mm), which presumably occur in late summer to early fall, after the surveys are completed (Incze et al. 1987; this study); and (4) instars ii–iii (mean CW ~5–7 mm), for which there is virtually no available information on molting schedule. The only regular source of information on instars iv–v are cod stomach contents, while instars vi–vii are represented both in stomach contents and trawl survey samples. The latter are the only consistent source of information for instars viii and higher.

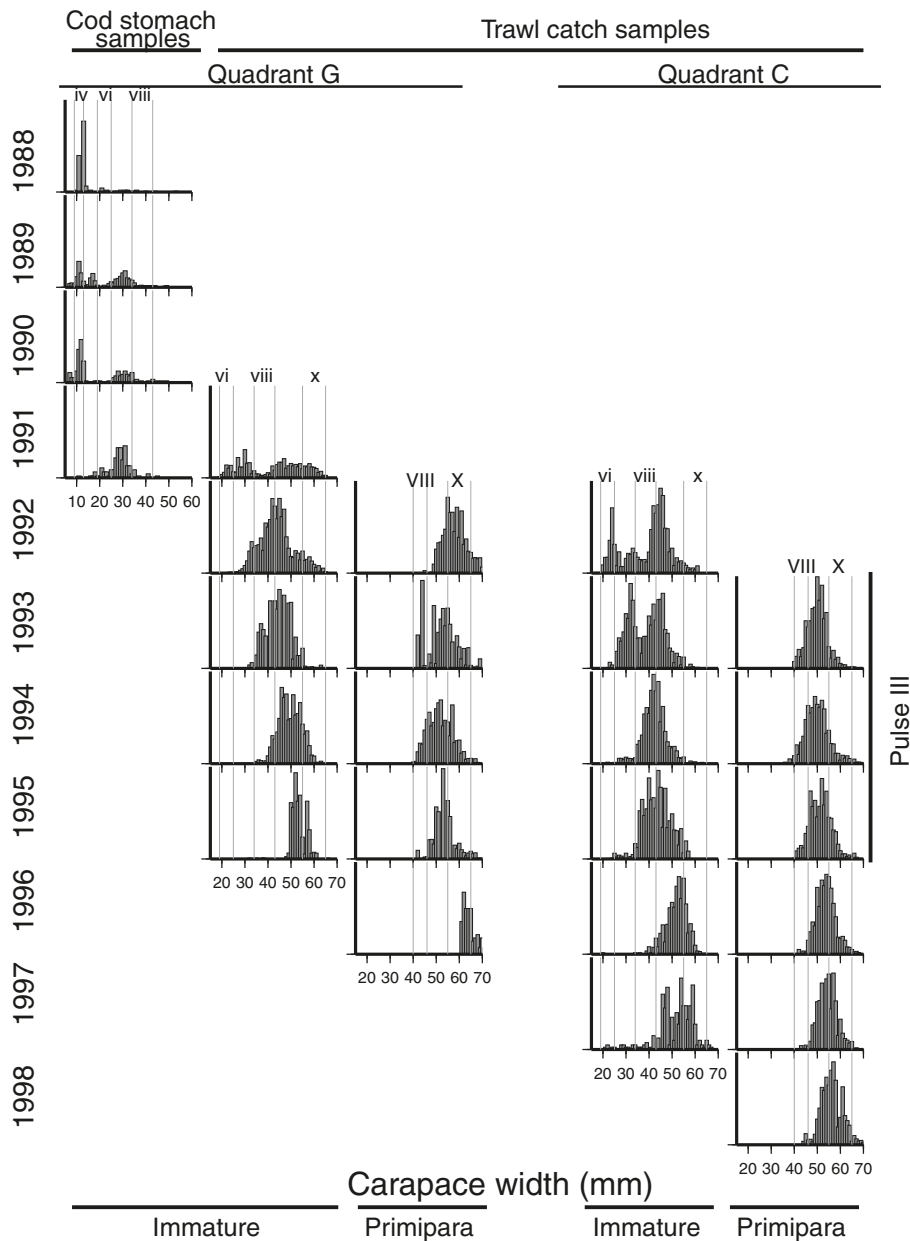
The mean sizes-at-instar estimated by us for instars iii–vii are comparable to those from other regions (Alunno-Bruscia and Sainte-Marie 1998; Comeau et al. 1998; Orensanz et al. 2007), albeit slightly larger. The difference, while consistent,

is not statistically significant and could be the result of observation error. Size overlap among modal components is relatively broad when compared with SFDs compiled in studies from other regions. The likely reason is that specimens from stomach contents are inevitably deteriorated, which increases measurement error. Also, precision is variable and often low (1 mm). Aspects of the molting schedule of immature females that could be inferred from the fragmentary information available are comparable to those determined for Newfoundland (Comeau et al. 1998) and the northwestern Gulf of St. Lawrence (Alunno-Bruscia and Sainte-Marie 1998). This is the case for molting between instars iv and v, a key event that proceeds from May to October in the EBS, between May and September in Newfoundland (Comeau et al. 1998), and between April and June in the Gulf of St. Lawrence (Alunno-Bruscia and Sainte-Marie 1998).

Variability of age at maturity

Alunno-Bruscia and Sainte-Marie (1998) concluded that in the northern Gulf of St. Lawrence females may reach maturity at instars VIII–XI, but most of them at instars IX–X, at ages of, respectively, 5.5 and 6.5 years. Our results for the central sector of the EBS shelf are remarkably consistent with theirs. Contribution by a year-class to several pseudocohorts is fully consistent with results on lipofuscin analysis reported by Shirley and Bluhm (2005) for the EBS, implying that terminal molt may occur over an absolute range of about 5 years of age. Considering that molting into maturity of

Fig. 8. Tracking relative size–frequency distributions corresponding to the progression of pulse III in quadrants G (north of the Pribilof Islands) and C (St. Matthew Island region), between 1988 and 1998. Only immature and primipara (SCI 2) are included. Vertical lines correspond to approximate mean instar size boundaries, added to facilitate comparative discussion. Sexes were pooled in cod stomach samples.



members of a year-class at a given location extends over at least 4 years, and assuming that maximum life after terminal molt is on the order of 7 years, inferred maximum longevity would be 11.5–14.5 years, a range comparable to the mean of 13 years (post-hatching age) estimated by Comeau et al. (1998) for Bonne Bay, Newfoundland. Our results strengthen the notion of a conservative life history program for snow crab across a vast geographical realm.

Studies of size-at-maturity (and by implication of instar- and age-at-maturity) in female snow crab from the extensive EBS shelf have dealt, implicitly or explicitly, with two different problems: regional variation and variation among individuals from a single location. Orensanz et al. (2007) referred to those patterns of variation as “geographical” versus “local” and concentrated on the first. They investigated a latitudinal

cline in size-at-maturity (larger towards lower latitudes), which, they conjectured, would result from the interaction of latitudinal variation in NBT, temperature-dependent molting frequency of early instars, a rigid size-at-instar vector, and conservative age at which the members of a year-class start to mature; the latter was hypothetical. Clinal variation in size-at-maturity would thus be the result of higher mean instar-at-maturity towards lower latitudes (i.e., warmer habitats). This hypothesis received support from work conducted on snow crab populations from Greenland (Burmeister and Sainte-Marie 2010). Notice that it is not implied that all females reach maturity at the same age, but rather that there is relative invariance in the age at which the transition to maturity begins. This hypothesis also implies that the geographical coherence of pulses of pseudocohort recruitment observed in

Fig. 9. Schematic representation of the approximate instar composition (actual or inferred presence) of samples from quadrant G. Connecting arrows: (a) eastern Canadian pattern superimposed on the data; (b) molting between instars v and vi allowed in CY3.

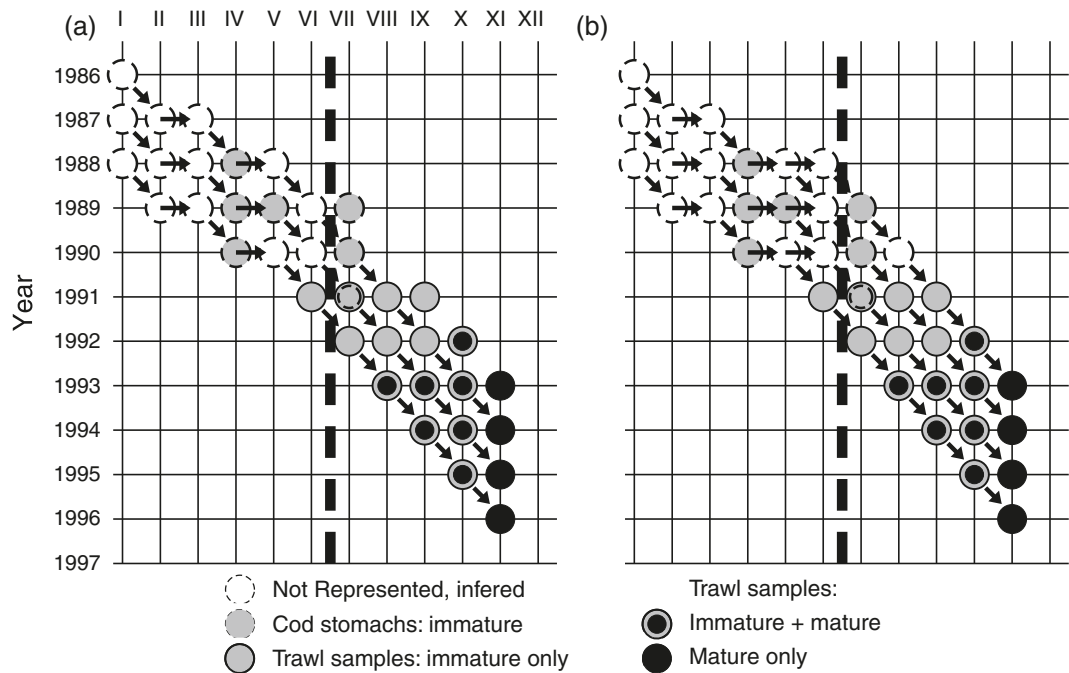
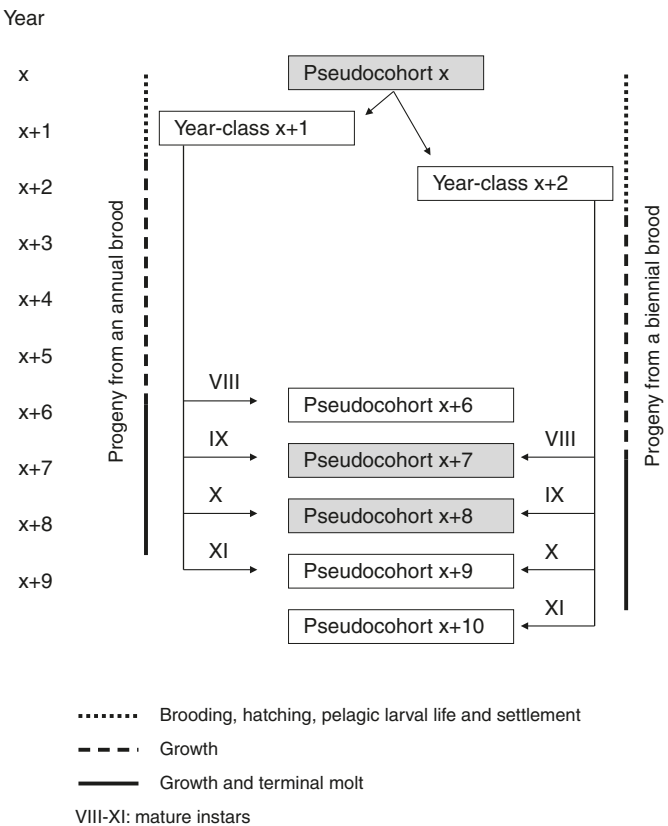


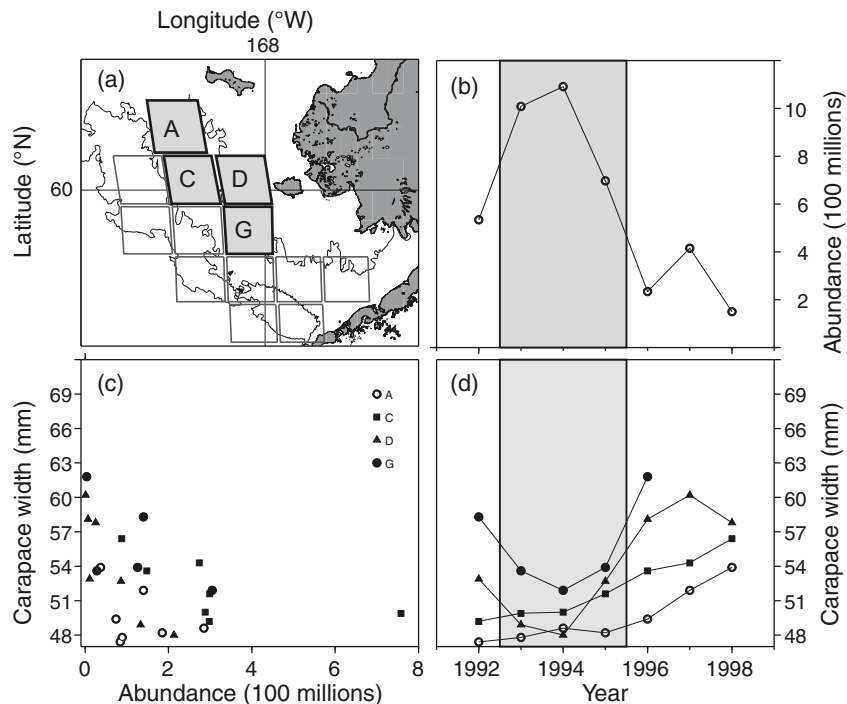
Fig. 10. Schematic representation of the sequential correspondence between a strong pseudocohort and the spread of its progeny among year-classes and pseudocohorts, based on the analysis of pulse III. Shaded boxes: strong pseudocohorts.



the EBS is a result of them being formed by one or two year-classes over a wide latitudinal range, along which there is significant variation in NBT and, consequently, size- and instar-at-maturity (Orensanz et al. 2007).

Orensanz et al. (2007) documented local variation in size- and instar-at-maturity. Here we showed that the variation is largely related to age-at-maturity, as members of a year-class reach terminal molt over a period of approximately 4 years (generally 4.5–7.5 years of post-settlement age), giving origin to consecutive pseudocohorts of incremental instar composition (generally instars VIII–XI). Orensanz et al. (2007) also showed that instars ~ IX–X form the bulk of the mature female population over most of the EBS, implying that the second and third pseudocohorts originating from a given year-class are, on average, the strongest. Instar ~ IX was overwhelmingly dominant in quadrants A, C, D, and G, used here to investigate the relation between the strength of pseudocohorts and the mean size of their members. This, combined with the fact that crests of pulses of pseudocohort strength are sharply defined (clear maxima formed by one or two pseudocohorts), implies that pulses are likely to be dominated by one or at most two consecutive year-classes. As members of a strong year-class reach maturity, two processes co-occur: (1) strength of contributed pseudocohorts increases from the first (weak, typically age 4.5 years and instar VIII) to the second (typically age 5.5 years and instar IX), then declines; based on aggregated SFDs, the fourth contributed pseudocohort (typically age 7.5 years, instar XI) is expected to be very weak. (2) Mean size of the members of successive pseudocohorts increases. If the pulse of pseudocohort strength is dominated by one or two year-classes (as we claim is the case), negative correlation between the strength of pseudocohorts and the mean size of their members is to be expected. Results from tracking pulse III are consistent with this expectation. The same phenomenon was observed

Fig. 11. Trends in mean size of primipara and pseudocohort strength as pulse III developed and vanished in quadrants A, C, D and G, 1992–1998. (a) Quadrants where pulse III was strongest, selected for the analysis. (b) Trend in pseudocohort strength. (c) Relation between pseudocohort strength and mean size of primipara. (d) Trends in mean size of primipara. (○) quadrant A, (■) quadrant C, (▲) quadrant D, (●) quadrant G. Shaded area in (b) and (d) highlights the core of the pulse (1993–1995).



in previous studies of cycling populations (Sainte-Marie et al. 1996, p. 461; Orensanz et al. 2007; Sainte-Marie et al. 2008, their Fig. 2). Notice that correlation would vanish in the absence of periodic pseudocohort recruitment.

Geographical variation in observed size-at-maturity and inferred age-at-maturity fits “pattern B” in the conceptual model of Wenner et al. (1985; see Orensanz et al. 2007, their Table 4), under which fast- and slow-growing phenotypes attain maturity at the same mean age, but fast-growing phenotypes (low latitude in the case of snow crab from the EBS) reach a larger terminal size (Fig. 12). Alunno-Bruscia and Sainte-Marie (1998) found that the fastest growing females in a year-class are the first to undergo terminal molt. Thus, local variation would fit “pattern C”: fast-growing phenotypes mature at a smaller size and earlier (Fig. 12). In synthesis, age-at-maturity appears to have two components: one is age dependent, which governs the onset of maturity in a year-class; the other is dependent on growth phenotype (expressed by size), which regulates the tempo of transition to maturity among members of the year-class. They are manifest in, respectively, geographical (e.g., clinal) and local variation in the size–stage (instar) structures of the mature female population. The nature of the interaction between age and size in setting the pace of transition to maturity in snow crab populations remains unresolved.

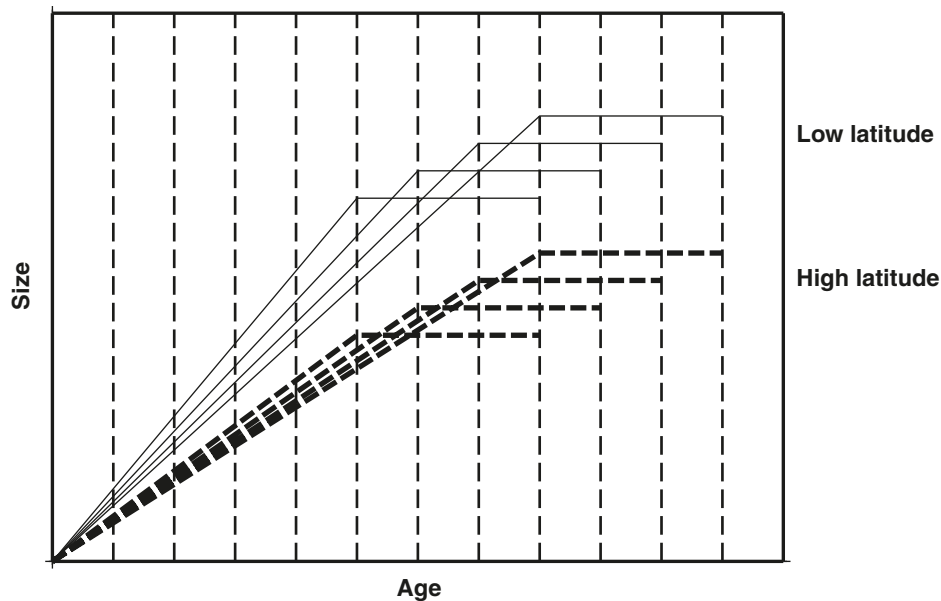
Periodic variation in pseudocohort strength

Factors driving fluctuations of recruitment to the mature female snow crab population could possibly be intrinsic (e.g., some relation between spawning stock and recruitment), extrinsic (e.g., predation or environmental variables), or a combination thereof (Sainte-Marie et al. 2008). Several

ongoing inquiries (e.g., Marcello et al. 2010; Hinckley et al. 2011; S. Danielson, University of Alaska, Institute of Marine Science, Fairbanks, Alaska, personal communication 2011) are exploring empirical relations between a multiplicity of drivers (both intrinsic and extrinsic) and recruitment, showing preliminary evidence of a role for environmental factors (temperature, ice-edge blooms, etc.). These statistical analyses are based on highly aggregated variables, either spatially or in terms of the life history stages involved (e.g., not differentiating multipara and primipara). Intrinsic and extrinsic factors are likely to interact in complex ways. We have explored hypotheses formulated a priori that invoke mechanistic explanations linking spatially explicit aspects of life history to spatial and temporal environmental variation. Along these lines we advanced the ERH (Orensanz et al. 2004; see also Zheng and Kruse 2006, p. 201, their hypothesis 2), which postulates that a contraction of the female spawning stock towards the northwest over recent decades was ultimately driven by NBT in the Middle Domain (via early benthic survival) and patterns of oceanographic circulation (via larval dispersal).

The ERH, however, did not address the fact that over a period of three decades (1978–2007) the contraction was punctuated by four pulses of pseudocohort strength, which declined in amplitude and (or) geographical spread. We tracked the abundance of immature females conducive to those pulses using the limited information available. Some robust patterns emerged from the analysis. Year-class strength is already established early in benthic life history. Pulses of pseudocohort strength could be back-tracked to the third year of benthic life in survey samples of immature females and to the second year in immature crab samples from

Fig. 12. Schematic representation of geographical versus local variation in growth and size at maturity in female snow crab; vertical broken lines separate years.



cod stomach contents. Periodic pseudocohort recruitment (mean period ~7 years) is commensurate with the length of two significant periods in female life history: (1) the mean time lapsed between egg extrusion by females of a pseudocohort and terminal molt of primipara originating from those eggs (this study) and (2) maximum life span beyond terminal molt (Ernst et al. 2005; Fonseca et al. 2008). These two aspects of female life history, combined, enhanced periodicity in the relative abundance of the primipara, because members of a given pulse had gradually vanished from the population by the time when the next one developed. Periodic variation in pseudocohort strength drives multiple aspects of mature female reproductive dynamics, including mean size of the primipara (discussed earlier), mean post-terminal molt age, mean clutch size, and, by implication, mean per capita reproductive contribution. Our reconstruction of the post-larval life history schedule of female snow crab in the EBS and the observed period between crests of pulses of pseudocohort strength (6–8 years) are consistent with the hypothesis of sequential linkage, according to which pseudocohorts forming a pulse would be the parental stock of pseudocohorts forming the subsequent one. Variability in the period and amplitude of the cycle is to be expected because (1) pulses can be formed by more than one pseudocohort and (2) the progeny of a pseudocohort is spread among multiple pseudocohorts owing to variation in the duration of brooding and of age at maturity; besides, success of descendent pseudocohorts may vary owing to extrinsic factors.

The timing of life history events was examined in more detail in quadrants G and C, tracking the development of pulse III. Results are informative in spite of the high uncertainty inevitably associated with the data available. Considering the location of quadrant G, and given known patterns of brooding (Ernst et al. 2008) and potential larval connectivity (Parada et al. 2010), settlers in that region are likely to originate from annual broods. The strongest and most consistent of the three year-classes detected, which reached instar vii in

1991 (observed both in cod stomachs and trawl samples), would correspond to the 1988 year-class. It would have been, in turn, the progeny of the strong 1987 pseudocohort. The 1-year lag in the occurrence of life history events in quadrants C relative to quadrant G, observed in trawl samples, could have different causes: (1) same parental pseudocohort but different year-classes owing to difference in the length of the brooding period (incidence of bienniality increases with latitude; Ernst et al. 2008), (2) different parental pseudocohorts (e.g., being the progeny of the strong 1988 pseudocohort), and (3) same year-class but different frequency of molting during early benthic life (frequency expected to decrease with latitude; Orensanz et al. 2007). The latter is consistent with the observed combination of geographic coherence in pseudocohort strength (this study) and clinal variation in mean size-at-maturity (Orensanz et al. 2007). The other two year-classes (detected as instars iv–v in 1988–1989), presumably corresponding to 1986–1987, were not observed in quadrant C or (as instars ~vi–vii) in trawl samples from either quadrant. They were probably weak or spatially confined. Crabs in instars iv–v sampled from cod stomach contents in 1988 originated from an atypical location, within the fringe area of the Coastal Domain. The 1986–1987 year-classes would be the progeny of the 1985–1986 pseudocohorts, which were among the weakest in the time series. The trough centered in 1985–1986 was anomalous for two reasons: (1) a historical minimum of mature female abundance, including primipara and multipara in the two domains, and (2) the later than expected development of pulse II, observed as an abrupt increase in pseudocohort strength between 1985–1986 and 1987–1988. These anomalies may be the end result of the warming that culminated in exceptionally high near-bottom temperature and contraction of the cold pool during the summer of 1979 (Orensanz et al. 2005). The first apparent effect of that phenomenon was a dislocation of the usual pattern of segregation of primipara and multipara by domain in 1979–1981 (crest of pulse I),

which preceded the extreme trough of 1985–1986. A plausible hypothesis to explain the magnitude and extent of the trough is that at that time mature females were distributed outside the survey sampling frame.

Even if the sequential linkage hypothesis did hold true, it is unlikely that a simple functional relation will be ever found between an aggregated “spawning stock” and “recruitment”, at least if these are not carefully specified. Zheng and Kruse (2003), for example, found only weak evidence of overcompensation. Cross-correlation between the abundance of mature females in the Middle Domain and the relative abundance of primipara some years later is a crude form of spawner–recruit relation. It is crude because it ignores possible contributions of females in the Outer Domain to recruitment, as well as the fact that the progeny of a group of spawners (e.g., a pseudocohort) is spread over several pseudocohorts. The relation does not account for other effects, like the environmental factors that allegedly governed the amplitude of fluctuations along the declining trend of pseudocohort strength during the time interval of interest. Those effects are preserved, and the lagged cross-correlation vanishes, if the absolute (instead of the relative) abundance of primipara (“recruits”) is considered. This is the case of the “circular pattern” noticed by Zheng and Kruse (2003, their Figs. 8–10) in the relation between spawning stock (variously defined) and recruitment (immature crab in the range 25–39 mm CW, 3–5 years lag). We intentionally avoid proposing a formal model of the relation between spawning stock and recruitment, although we see our inquiry as a step in the direction of modeling the dynamics of this population.

A cycle in pseudocohort strength resulting from sequentially linked pulses opens two questions: what triggered the initiation of the sequence, and how long can the latter be expected to last. A likely trigger would be a period of exceptionally good conditions for larval retention or for the survival of early benthic stages. The latter are stenothermic and cryophilic, with a thermal preferendum in the range of 0–2 °C (Dionne et al. 2003). In the EBS this corresponds to the cold pool that expands over the Middle Domain during the spring and summer, its southeast reach being related to ice cover during the preceding winter (Stabeno et al. 2007). Years with an extended cold pool are believed to favor the survival of early benthic stages (Orensanz et al. 2004) and may be the reason for an inverse relation between temperature and recruitment (Marcello et al. 2010). Members of the exceptional pulse of pseudocohort recruitment of 1979–1980 (pulse I) are likely to have originated from larvae that settled around 1973–1974, during the exceptionally cold period 1971–1976 (Azumaya and Ohtani 1995; Stabeno et al. 2007). The cold pool contracted and NBT rose sharply in the Middle Domain during 1977–1979. That exceptional warming event was followed 7 years later by a historical minimum in pseudocohort strength (1984–1986). Thus, this sequence of exceptionally cold and warm periods is a candidate to have triggered and delineated pulse I, initiating a sequence that vanished in strength and geographical spread during the early 2000s. Pulse IV was the weakest in the series, virtually confined to the northwest sector of the shelf, and developed before a protracted warm period (2000–2005), which combined may be conducive to the vanishing of the sequence. Analysis of cod stomach contents indicates

that immature crab corresponding to pulse IV (instars iv–vii) were widely distributed in the Middle Domain, but were already confined to the northwest shelf when detected (as instars viii–ix) in trawl samples. This suggests that the demise of pulse IV was the result of cod predation, an explanation consistent with an element of the ERH (Orensanz et al. 2004) claiming that cod predation on immature snow crab constrains the geographic spread of the stock towards the southeast end of the range. A more comprehensive enquiry of the predator–prey interaction between cod and snow crab in the EBS is the subject of a forthcoming contribution.

The EBS has experienced dramatic climate fluctuations over the past decade, as observed in trends of NBT: an exceptionally cold year in 1999, warming during 2000–2005 (Stabeno et al. 2007), and a cold period afterwards, with the cold pool extending again deep into the southeast shelf in 2006–2010 (Zador and Gaichas 2010, their Fig. 22). Analysis of the behavior of the stock following these exceptional environmental fluctuations will provide an opportunity to investigate the resiliency of the stock. Along these lines, it is worth noticing that the modest but significant event of pseudocohort recruitment of 2005–2007, in the central section of the shelf (where substantial presence of primipara had not been observed since 1994), occurred 6–8 years after the exceptional expansion of the cold pool in 1999. Phenomena of particular interest following the cold period that started in 2006 would be an eventual return of primipara to the southeast section of the shelf or a strong recruitment event (analogous to pulse I) that could eventually lead to a new pulse of strong recruitment.

As mentioned earlier, periodic recruitment has been documented in the Gulf of St. Lawrence (eastern Canada), where the period of the cycle may range between 6 and 12 years. Sainte-Marie et al. (2008, p. 140) identified egg and larval production and density-dependent cannibalism as candidate intrinsic causative factors. Alternative hypotheses on the role of cannibalism have emphasized predation by large hard-shelled males on large pre-recruits (Comeau and Conan 1992) and of early benthic instars by larger conspecifics (Lovrich et al. 1995; Sainte-Marie et al. 1995, 1996). The first could not possibly generate cyclic recruitment in the EBS because year-class strength is established early in life history, which is also the case in the Gulf of St. Lawrence (Sainte-Marie et al. 1996). In the case of the EBS, cannibalism hypotheses may be, by themselves, insufficient to explain cyclic pseudocohort recruitment given the large geographical scale of the phenomenon and the spatial heterogeneity of abundance (large-scale patchiness) among year-classes. Movements by larger immature crab and mature females could, however, spread the geographic impact of cannibalism, diluting the effects of patchy settlement.

Implications

The hypothesis postulating that each pulse of primipara recruitment constitutes the spawning stock leading to the next in the sequence (introduced earlier) assumes that larval inputs to the Middle Domain originating in other regions (including the adjacent Outer Domain) are of secondary significance. If that were the case, renewal of the snow crab population from the EBS would be dependent on events taking place in the Middle Domain and sustained to a large extent by the repro-

ductive output from the primipara (Parada et al. 2010). Besides its basic theoretical appeal, the complexity of the renewal process of snow crab in the EBS has significant implications for stock assessment and management. In the stock assessment that currently supports management decisions, spawning stock is defined and estimated in terms of adult ("morphologically mature") males, assuming that adult "newshells" have not entered the reproductive stock (North Pacific Fishery Management Council 2010). Paradoxically, if (as we hypothesize) the primipara have a major role in the renewal of the stock, the males available to them as mating partners in the Middle Domain during the mating season (winter) are overwhelmingly adolescents (functionally mature even if morphologically immature; Sainte-Marie and Carrière 1995).

Acknowledgements

This study was supported by North Pacific Research Board (NPRB) project 508. Assistance of Carrie Eischens and Francis Wiese during all stages of their execution is acknowledged. Claire Armistead, Robert Foy, and Louis Rugolo (NMFS, Kodiak) made every possible effort to satisfy our requests of survey data. Pat Livingston (AFSC–NMFS, Seattle) made cod stomach content data available. Arni Thomson (Alaska Crab Coalition) provided sustained encouragement and orientation on aspects of the fishery. Finally, support received from our home institutions is acknowledged by all of us. Thorough criticism by Gordon Kruse (U. of Alaska, Juneau), Bernard Sainte-Marie (DFO, Mont Joli), and two anonymous referees helped improve the original manuscript.

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