VARIATION OF FEMALE SIZE AND STAGE AT MATURITY IN SNOW CRAB (*CHIONOECETES OPILIO*) (BRACHYURA: MAJIDAE) FROM THE EASTERN BERING SEA

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ABSTRACT

We investigated geographic variation in size and stage (instar) at maturity of snow crab (*Chionoecetes opilio*) on the eastern Bering Sea shelf. Size-frequency distribution analysis showed that females can reach maturity at four different instars, presumably Instars VIII to XI. Geographic variation in instar structure generates clinal variation in size at maturity, from small size at high latitudes (colder) to large size at low latitudes (warmer). Different pieces of evidence support the hypothesis that geographic variation in mature female size is a phenotypic response to environmental conditions governed by a single reaction norm. Clinal variation conforms to the "inverse Bergmann's rule". We argue that a single macroecological rule should not be expected to explain all latitudinal size gradients observed in marine invertebrates. Size at maturity fluctuated cyclically, and was negatively and significantly cross-correlated with strength in the recruitment of females to the mature population. Cycles in the latter were manifested as four commensurate and regularly spaced pulses over the last three decades. Mechanisms that may underlay this intriguing phenomenon, including density-dependent growth rate, require further scrutiny.

INTRODUCTION

Patterns of geographical variation of phenotypic characters, including the absence of pattern, have long attracted the attention of biologists (Blackburn et al., 1999; Ashton, 2001). They have inspired the formulation of imaginative hypotheses (Conover and Schultz, 1995; van Voorhies, 1996; Atkinson and Sibly, 1997), and challenged their predictions (Mousseau, 1997; Partridge and Coyne, 1997; Blanckenhorn and Hellriegel, 2002; Knouft, 2002). Characters related to life-history processes are particularly interesting; maximum size, and size, stage or age at maturity, are noticeable examples (Bernardo, 1993). A significant literature has accumulated on the latitudinal variation of these traits in marine animals (Conover and Schultz, 1995; Partridge and Coyne, 1997), including crabs (Hines, 1989). Among the latter, majid crabs are remarkable in one particular sense; because they stop growing after reaching morphological maturity (Elner and Beninger, 1992), age, stage and size at morphological sexual maturity, and maximum size, are all coincidental for any given individual. Maturity is easily recognizable on the basis of external secondary characters and the transition is irreversible, which effectively overcomes indeterminacies associated with the characteristics of other marine animals. Therefore, majid crabs offer valuable systems for the investigation of phenotypic variation in relation to reproductive maturity.

Clinal geographic variation in size at maturity has been documented for the females of two closely related species of the majid genus *Chionoecetes*, namely snow crab, *C. opilio* (O. Fabricius, 1780) and tanner crab, *C. bairdi* Rathbun,

1924, whose combined latitudinal range along shelf areas of the northeastern Pacific Ocean spans over 22 latitudinal degrees, from slope depths off Oregon to the Chukchi Sea (Hosie, 1974; Paul et al., 1997), and beyond into the Arctic Ocean. Because of this wide range, and majid crab characteristics indicated earlier, this system is exceptionally well suited to investigate the geographic variation of significant life history traits. Over the eastern Bering Sea (EBS) shelf, in particular, mean female size-at-maturity shows a remarkable latitudinal cline, from ca. 70 mm at 55°N to only 40 mm at 63°N (Somerton, 1981a, b; Otto, 1998; Zheng et al., 2001; Otto and Pengilly, 2002; Ernst et al., 2005). Published size-frequency distributions show two major modal groups, with a steep geographic transition between regions in which one or the other is predominant (Fig. 2 in Somerton, 1981b). Somerton (1981b, p. 173) was puzzled by these modes given that there are no abrupt changes in environmental gradients associated with the areas of steep transition. This led him to speculate on the hypothetical existence of distinct populations in which the size at maturity might be genetically determined (see also Otto and Pengilly, 2002). The obvious alternative hypothesis is environmental control (Somerton, 1981a, p. 28; 1981b, p. 172; Zheng et al., 2001, p. 241). These are the two basic hypotheses recurrently invoked to explain geographic variation in life-history traits.

Whichever factors are behind clinal variation, its very manifestation suggests that parameters related to life history should not be expected to be invariant, yet Somerton (1981b, p. 170) speculated that "changes in growth [over time] may not be important [in the EBS]". Temporal trends
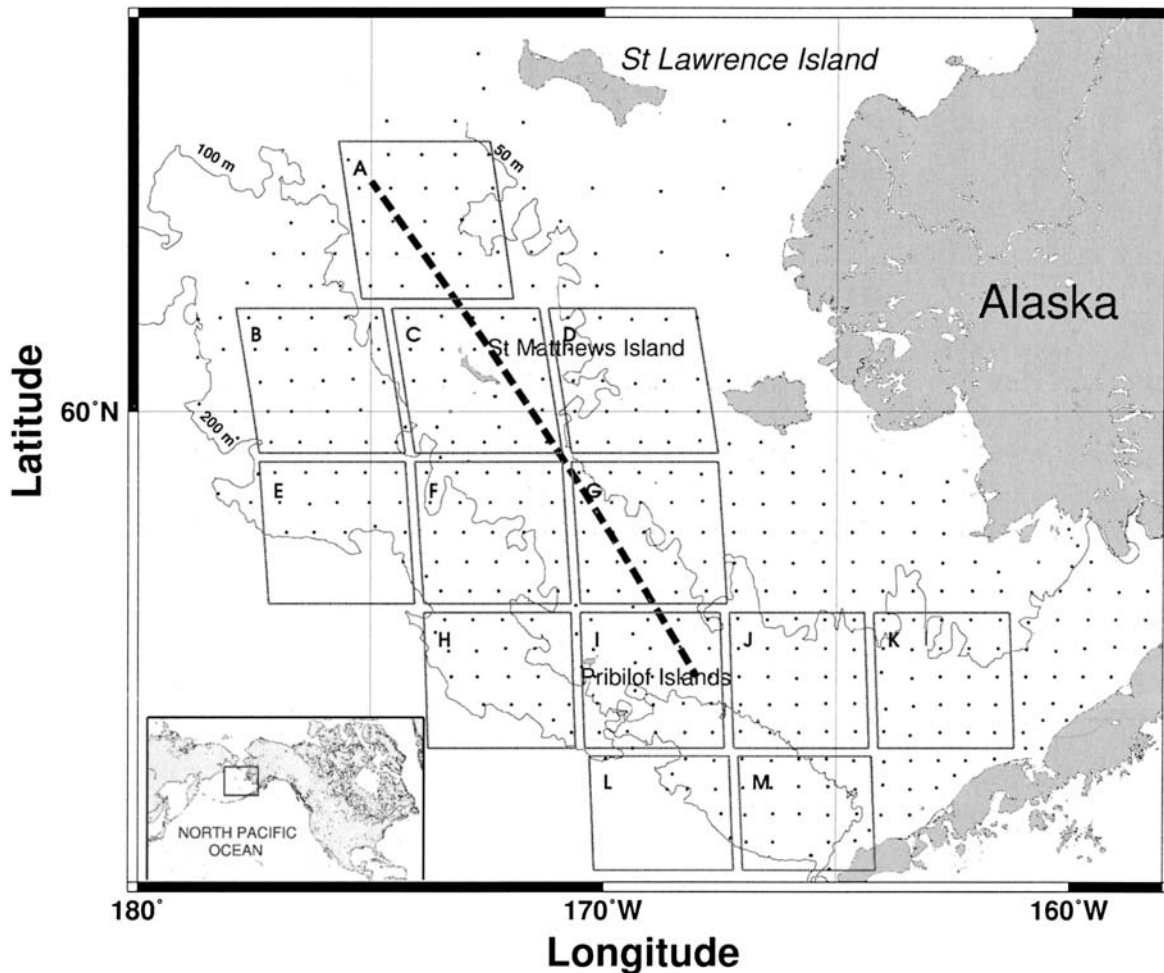
Fig. 1. The eastern Bering Sea shelf. Lettered rectangles indicate "quadrants" defined to investigate geographic patterns and time-series of size-at-maturity. The dashed line connects four quadrants aligned along the Middle Domain (shelf between the 50 m and 100 m isobaths), where most primiparous females are found. Dots indicate stations of the annual survey conducted by the National Marine Fisheries Service.

have been documented, however, in other regions. In two locations from the Sea of Japan (off Wakasa Bay and Yamato Bank) the mean size of adult females increased steadily over decades (Kon et al., 1996). These trends remain unexplained. Sainte-Marie et al. (1996) observed that fluctuations in instar structure (and consequently size structure) of the mature female population of *C. opilio* in the Gulf of St. Lawrence, Canada, are intriguingly associated with an alternation of periods of low and high recruitment. Ernst et al. (2005) reported a cyclical pattern in the recruitment of females to the mature population, and so comparable covariation could exist in the EBS population.

Here we revisit variation of size-at-maturity in female snow crab from the EBS. Size frequency distributions are reanalyzed and a new interpretation of modal structure is offered. Assumptions underlying the hypotheses proposed for this system are made explicit and evaluated. Temporal trends in female size-at-maturity are investigated over a 25-year period, particularly to determine if, as found in eastern Canada, they are related to recruitment cycles. Finally, the observed cline is discussed in relation to predictions of general hypotheses proposed to explain latitudinal

gradients in life-history-related characters of marine poikilotherm animals.

STUDY SYSTEM

The Eastern Bering Sea Shelf (EBS)

The extensive shelf of the EBS (Fig. 1), more than 500 km wide, ends seawards in a shelf break (generally coincidental with the 200-m isobath) that spreads along the northwest-southeast direction; the two main geographical features are St. Matthew and the Pribilof islands. Three zones or domains are usually recognized (Schumacher and Stabeno, 1998): an Inner or Coastal (shoreward from the 50-m isobath), a Middle (between the 50- and 100-m isobaths), and an Outer (between the 100-m isobath and the shelf break) Domain. In most years up to 75% of the EBS shelf water is covered by ice from late fall through early spring. The southeastern sector of the shelf is divided by a series of three fronts into two interfrontal zones that correspond to the Middle and Outer domains (Coachman, 1986). As ice melts in spring, the less saline water "floats" over higher salinity marine water, and this upper layer is heated, which results in
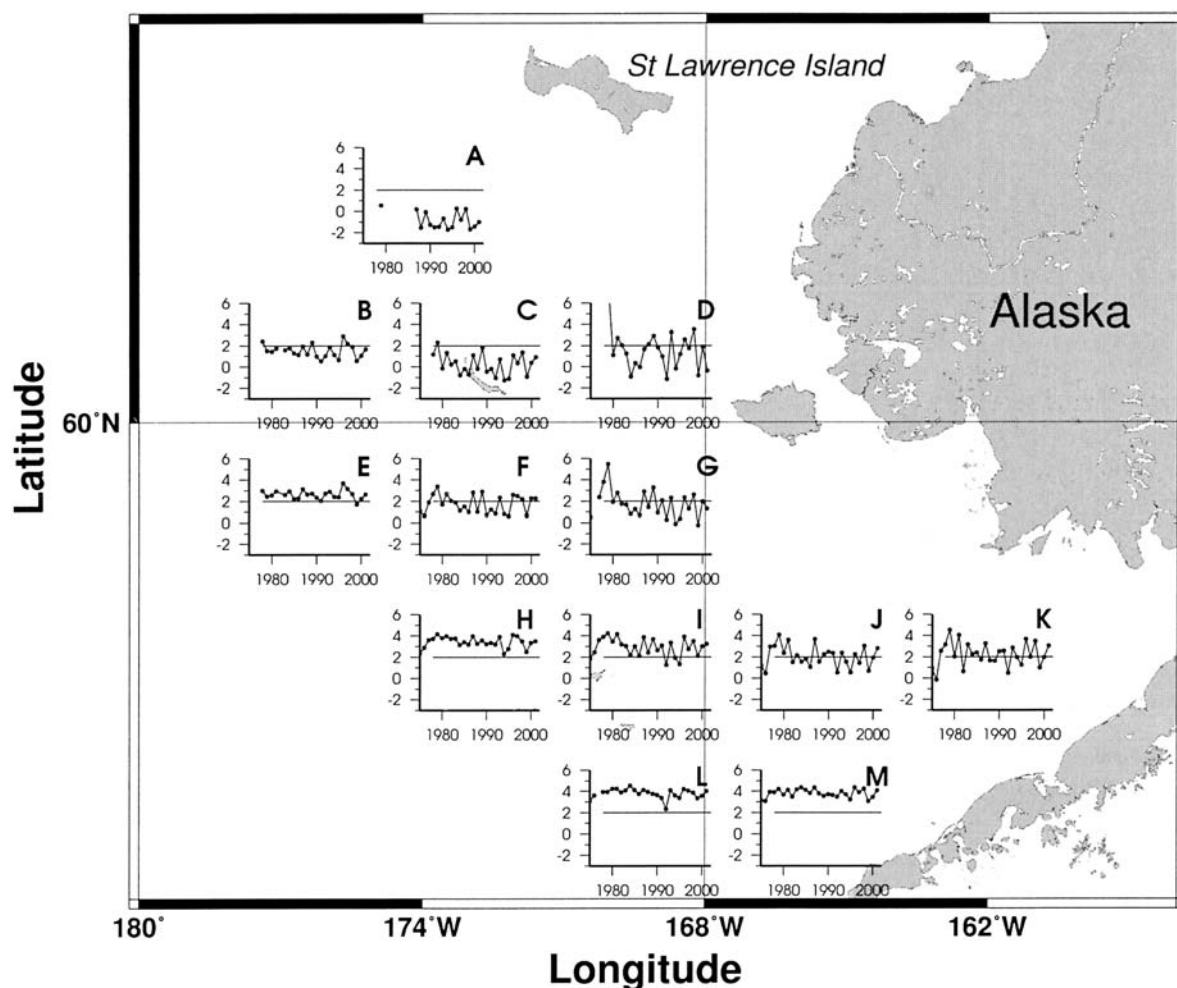
Fig. 2.   Trends in near-bottom temperature in June and July, averaged for each of the quadrants indicated in Fig. 1. The horizontal line corresponds to 2°C.

stratification of the water column. The stratified water column "traps" an extensive "cold pool" of water (near-bottom temperature < 2°C) down to the seafloor over a large area of the EBS. Following a warm winter, there may be virtually no cold pool over the EBS-Bristol Bay region, e.g., 1979, or the cold pool may cover most of this region following a very cold winter, e.g., 1995, (Orensanz et al., 2004). Due to this phenomenon, summer near-bottom temperature (NBT) has a minimum in the Middle Domain, increasing towards the coast and the shelf break (Orensanz et al., 2004). For this study we partitioned the EBS shelf into 13 rectangular "quadrants" (Fig. 1). Spatial and temporal patterns were well captured by a time series of summer NBT averaged by quadrant (Fig. 2). Summer NBT in quadrant A, at the northern end of the survey area, has been lowest, regularly below 0°C since 1987 (when the survey expanded into that region). In quadrant C, historically the core of the cold pool, average summer NBT was virtually always below 2°C. In quadrants F and G, where the cold pool often expands over the Middle Domain, average summer NBT has oscillated around 2°C. Towards the SE (Quadrants L and M, where summer NBT is highest) and along the shelf-break (Quadrants E and H) average summer NBT was always above 2°C.

Mature Snow Crab Females

Two species of *Chionoecetes* coexist in the EBS shelf, widely overlapping in their spatial distribution: *C. opilio* (snow crab) and *C. bairdi* (tanner crab). The two are morphologically similar but can be distinguished by eyestalk color, the contour of the epistome and the outline of the carapace (Urban et al., 2002). The range of size-at-maturity of females is 35-80 mm (exceptionally down to 26 mm or up to 89 mm) in snow crabs vs. 65-105 mm for tanner crabs (Somerton, 1981b; Otto, 1998). Members of the two species can mate and produce hybrids, which display a mixture of characters, including an intermediate body size range (Karinen and Hoopes, 1971). The geographic ranges of the two species overlap over a broad, presumably, secondary hybrid zone that extends over the southeastern end of the EBS shelf and along the shelf break.

Following Alunno-Bruscia and Sainte-Marie (1998), we use the terms "immature" for morphologically and sexually immature females, "prepubescent" for females in the instar previous to puberty (terminal) molt, and "mature" for post-puberty females. In eastern Canada, females reach maturity at instars ranging from IX to XI, rarely VIII (Robichaud et al., 1989; Alunno-Bruscia and Sainte-Marie, 1998; Comeau

Table 1. Pulses of recruitment of mature females (SCI 2) to the mature snow crab population from the eastern Bering Sea. The first two occurred before the period studied by us (Ernst et al., 2005).

Pulses (pseudo-cohorts)	Observations	Source of information	Modal components
1969	Strong group in SCI 2 observed during the spring	Somerton (1981a, fig. 10 and table 4)	Size range corresponds to modal component x, but SFD appears bimodal in Somerton's figure
1975-1976	Pseudo-cohort persisted through at least 1979	Somerton (1981a, fig. 10 and table 4)	Bimodal. Small modal component recruited in 1975, large component in 1976
1979-1980	Pseudo-cohort persisted through 1985	Zheng et al. (2001, fig. 9); Ernst et al. (2005, fig. 4); this study	Small modal component (Instar VIII) present in Quadrant A
			Large modal component (presumably Instar X) present in Quadrant E
1987-1988		Zheng et al. (2001, fig. 9); Ernst et al. (2005, fig. 4); this study	Small modal component (Instar VIII) represented in quadrant A
			Large modal component (presumably Instar X) represented in Quadrants G, H, I
1993-1995		Zheng et al. (2001, fig. 9); Ernst et al. (2005, fig. 4); this study	Basically similar to pooled pattern
2001		Ernst et al. (2005, fig. 4); this study	Basically similar to pooled pattern

et al., 1998). Most females mature at post-settlement ages of 5.5 to 6.5 years (a few at age 4.5 years, in Instar VIII) in the Gulf of St. Lawrence (Alunno-Bruscia and Sainte-Marie, 1998) and at post-hatching ages of 7 to 8 years in Bonne Bay, Newfoundland (Comeau et al., 1998). In both cases Instar X is the most important, and is reached at the average post-settlement age of 6.5 years. Growth ceases following the puberty molt; growth of body size is primarily an aspect of the immature-prepubescent life history period. Females mate for the first time after undergoing the terminal molt, while still in a soft-shell condition (primiparous) or in subsequent years while in a hard-shell condition following egg-hatching (multiparous). Following Ernst et al. (2005) a "pseudo-cohort" of mature females is defined as a group of females that undergo puberty molt (recruit to the mature population) during a given year. In the EBS recruitment of pseudocohorts occurs primarily in the Middle Domain (Ernst et al., 2005). Females undergo their puberty molt and primiparous mating in winter. Over the next year they migrate an average lineal distance of 70+ nautical miles towards the shelf edge, following a predominantly northeast-southwest direction, and presumably tracking NBT gradients. Estimated maximum life span after the terminal molt is 6-7 years (Ernst et al., 2005).

The mean size of mature snow crab females varies geographically in the EBS. Somerton (1981b), based on data from the 1979 NMFS survey, examined geographical gradients, finding that mean size decrease northward from approximately 70 mm at 55°N to only 40 mm at 63°N. Otto (1998; based on the 1989-1994 NMFS surveys). Zheng et al. (2001; 1978-1999 surveys), and Ernst et al. (2005; 1975-2001 surveys) showed the same basic pattern. None of these studies identified instar- or age-at-maturity for snow crab from the EBS.

Over the last three decades the geographic range of the snow crab population from the EBS has contracted dramatically to the north (Zheng et al., 2001; Orensanz et al., 2004). An increase in NBT during 1975-1979 was accompanied by a northward contraction of the cold pool. Warming was tracked with a 6-year lag by a contraction to the north of the mature female's range (Orensanz et al., 2004). However, recruitment to the mature female population did not expand back to the southern shelf after the mid-1990s, despite some

years when NBT was low. Recruitment to the mature female population has fluctuated in a remarkable cyclical pattern (Ernst et al., 2005). The cycle is the result of commensurate and regularly spaced pulses of recruitment (Table 1), presumably corresponding to strong year-classes.

MATERIALS AND METHODS

Survey Data

Time series of data were collected during trawl surveys conducted by the U.S. National Marine Fisheries Service (NMFS) since 1975 (Otto, 1998; Stevens et al., 2002). Surveys follow a systematic sampling design, where stations are regularly spaced over a 20 nmi × 20 nmi grid, and sampled every year. The 1975-1977 surveys were not included in most of the analyses because they covered only the southern end of the geographic range of interest. The systematic sampling surveys have had an extensive spatial coverage after 1978 (Fig. 1). Most of the survey activity is conducted in June and July, but in some years work started in May (1975-1981, 1999-2000) or ended in August (1975-1976, 1978-1979, 1982-1986, 1988-1992). NBT has been regularly recorded since the initiation of the survey program. Several observations were made on each individual caught in a haul, or from a sub-sample when the catch was too large. For further information on the sampling protocol see the "Manual of crab sampling methods for the trawl survey in the Eastern Bering Sea", available from the NMFS, Alaska Fisheries Science Center, PO Box 1638, Kodiak, AK 99615-1638, U.S.A. In the case of females observations recorded included carapace width (CW, 1 mm precision), an index of shell condition (SCI) and sexual maturity (immature/mature). Size was expressed as CW. Following Ernst et al. (2005) females in SCI category "2" (denoted as "SCI 2") are considered as primiparous, having molted into maturity during the winter prior to the survey. Mature SCI 2^+ females denotes the sum of all females SCI category 2 and higher, i.e., the pool of mature females. Mature SCI 3^+ females correspond to the pool of multiparous females.

Mean Size-at-Maturity and Size-Frequency Distributions

Mean size and the size frequency distributions (SFDs) were investigated at the scale of the quadrants (Fig. 1). Mean values were computed as a weighted average by sampling station (weights proportional to density of each size class in each sample) for the period 1978-2001. Equal weight was given to the average size-at-maturity per station when integrating over time. It is assumed that vulnerability is the same for all mature females. Mean CW was mapped for primiparous (SCI 2) and multiparous (SCI 3+) females, and "iso-CW" lines were traced at 50 mm and 60 mm. The number of stations per quadrant varied depending on geographical location and year, with a minimum of 9 and maximum of 25. The total number of measured mature females recorded in the NMFS data-base for the period was 144,440.

Modal Decomposition and Model Selection

SFDs (calculated as proportions) were computed for each quadrant by pooling stations and years. We implemented a statistical modal

Table 2. Descriptive statistics for mature female size, by quadrant (see Fig. 1). Data pooled for the period 1978-2001.

Quadrant	Mean Latitude	Mean NBT (°C)	N	Mean CW (mm)	CW 5% and 95% percentiles (mm)	SD	CV	Skewness
A	61.7	−1.0	3717	49.8	43, 59	5.02	0.10	0.55
B	60.3	1.5	23820	51.1	44, 59	4.76	0.09	0.48
C	60.2	0.2	17875	51.9	43, 61	5.51	0.11	0.15
D	60.0	1.7	4020	51.3	44, 60	5.01	0.10	0.46
E	59.0	2.6	3846	55.6	47, 68	6.52	0.12	0.85
F	58.7	1.8	22625	52.9	45, 63	5.53	0.10	0.58
G	58.6	1.7	7961	54.6	45, 67	6.68	0.12	0.40
H	57.2	3.5	15483	54.4	46, 66	5.97	0.11	0.71
I	57.1	2.9	16768	57.6	48, 68	6.27	0.11	0.24
J	57.0	2.2	3934	60.0	52, 70	5.43	0.09	0.55
K	56.9	2.4	202	64.4	55, 75	6.29	0.10	0.45
L	55.7	3.8	466	65.1	56, 74	6.08	0.09	0.00
M	55.5	3.8	925	66.9	57, 78	6.88	0.10	0.31

decomposition analysis to extract modal components from female snow crab length-at-maturity data (MacDonald and Pitcher, 1979). Each mode (i) was modeled by a Gaussian parametric function (Ψ^i) and described by the following equation:

$$\Psi^i_{(l|\mu_i,\sigma_i{}^2)} = \frac{1}{\sqrt{2\pi}\,\sigma_i} e^{-\left[\frac{(l-\mu_i)^2}{2\sigma_i{}^2}\right]}$$

with parameters mean size-at-instar (μ_i) and variance (σ^2_i). The predicted SFD of mature females corresponded to the sum of size-at-instar modes (ranging from one to three),

$$P = \sum_{i=1}^{n} p_i \Psi^i,$$

where p_i is the proportion of mode i in the mixed probability density function (P).

We used a maximum likelihood parameter method with a robust normal likelihood function for proportions (Fournier et al., 1998), which we coded in ADMB (Otter Research Ltd. 2001). The likelihood model is described by the following equation:

$$L_P = \prod_l \frac{1}{\sqrt{2\pi(\xi_l + .1/n_l)}\tau^2} \exp\left(-\frac{(P_l^O - P_l^P)^2}{2(\xi_l + .1/n_l)\tau^2}\right),$$

where l denotes size (CW), ξ_l is $P_l^O(1 - P_l^O)$ and $\tau^2 = 1/n$ (n = min(sample size, 1000)); O and P indicate, respectively, observed and predicted. We optimized the following negative log-likelihood model (constant terms were omitted):

$$-\log(L_P) = \sum_l \left[0.5\log(\xi_l + .1/n_l) - \log\left(\exp\left[-\frac{n(P_l^O - P_l^P)^2}{2(\xi_l + .1/n_l)}\right] + 0.01\right)\right]$$

Model selection was based on likelihood ratio tests (Casella and Berger, 2002) to assess the number of modes present in each SFD. The rejection area in the hypothesis testing was established by a threshold Chi-square value of $\chi_{1-\alpha,\rho}$, were α is the significance level and ρ is the additional number of parameters between the simple and full model.

In a second step of the analysis, SFDs were inspected for each [quadrant × year] combination. In many cases the sample size was too small to allow any statement or further analysis. When sample size was appropriate, we analyzed SFDs to identify occurrences of instars that could be transiently present in a quadrant, but whose signal could have been lost in the pooled SFD data.

Gradients and Trends

We focused on the geographic size gradient for SCI 2 females. When the annual NMFS survey is conducted (June-July), primiparous females are carrying the first clutch of eggs in their lifetime, having gone through their terminal molt during the previous winter (Ernst et al., 2005). Among mature females, the primiparous are found closest to the geographical region where they reached maturity, and so may best reflect the environmental conditions associated with that stage. The time series of near-bottom temperature were
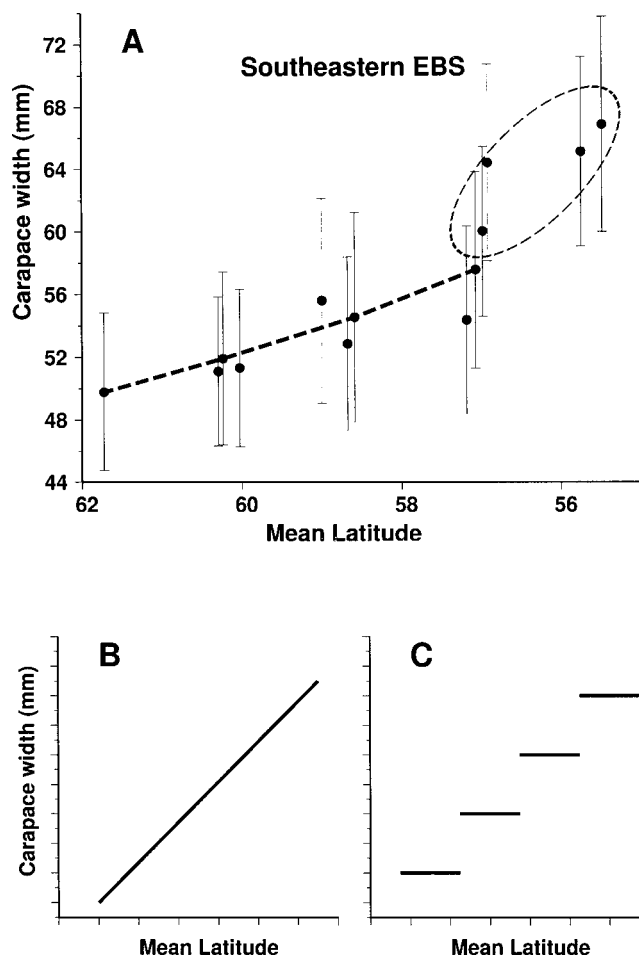

Fig. 3. A: Latitudinal cline in mature female size, averaged by quadrants (see Fig. 1), all years and SCI categories pooled; dashed line connects quadrants A, C, G and I, aligned along the Middle Domain (shelf between the 50 m and 100 m isobaths). Vertical lines indicate one standard deviation above and below the mean; standard errors are narrower than the diameter of the symbols. Bottom: schematic representation of two non-exclusive hypotheses that may explain the pattern (each solid line represents mean size of a hypothetical instar-at-maturity): clinal variation in size-at-instar (B) and in instar-at-maturity (C).

computed for each quadrant by averaging over space. Time series of average size of SCI 2 females by quadrant were estimated by considering sample sizes at the haul and station levels (Ernst et al., 2005). Series of abundance and weighted-standardized mean size were calculated for Quadrants B, C, D, F and G, which together incorporate most of the historical core area of recruitment to the mature population. To remove geographical gradients in mean CW we subtracted the overall quadrant mean from each mean CW in the time series, thus allowing for analysis of temporal variation in mean size.

Parsing and Graphics

The data were parsed and analyzed using scripts in AWK stream editor (Robbins, 2001). Graphical analysis was conducted using GMT (Generic Mapping Tool) graphical software (Wessel and Smith, 1998).

RESULTS

Clinal Variation in Mean Female Size at Maturity

The mean size of mature female snow crabs in the EBS shelf (data fom the 1978-2001 surveys pooled) shows a well defined cline (Table 2; Figs. 3, 4). Mean female size (all
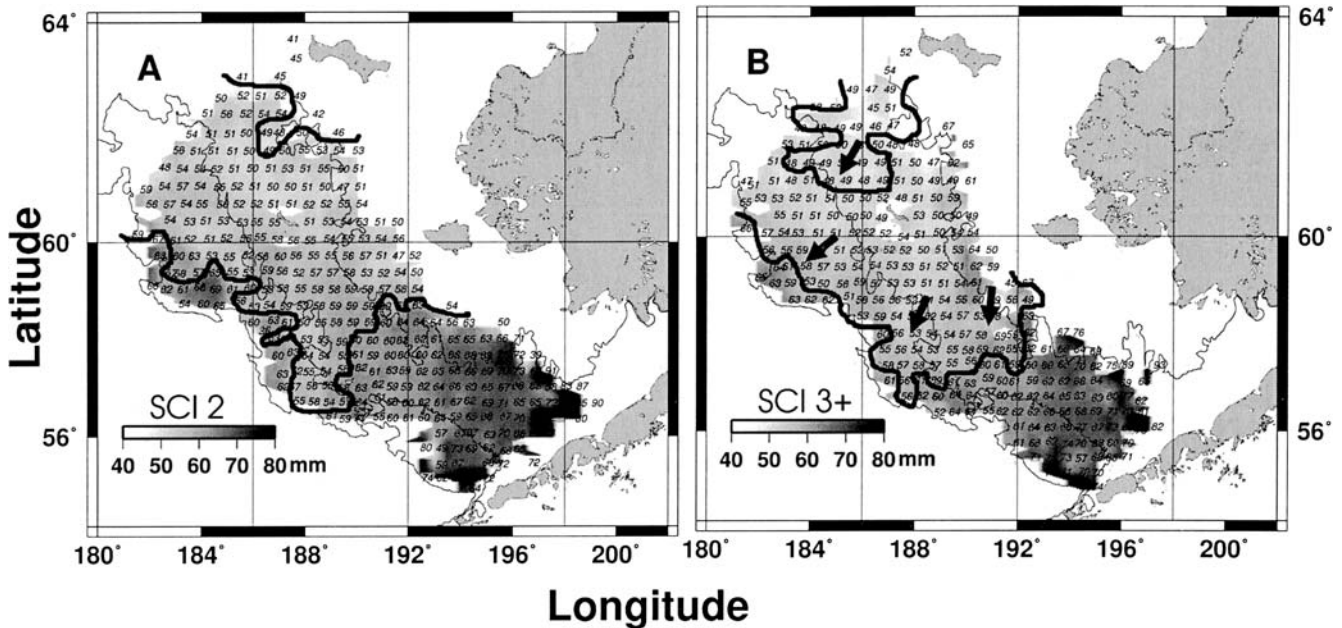
Fig. 4. Gradients of mean size of mature female size over the eastern Bering Sea shelf; all years pooled. Thick lines correspond to mean size (carapace width) isolines (50 mm and 60 mm) for the primiparous (A) and multiparous (B) groups. Arrows highlight the direction in which the multiparous isolines are displaced with respect to the primiparous isolines.

years pooled) is generally in the range 50-52 mm in the north shelf (Quadrants A-D) and 60-67 mm in the southeast shelf (Quadrants J-M), with a broad transition zone along the main axis (NW to SE) of the central shelf. The gradient is very clear and quasi-linear for the four quadrants aligned along the main axis of the Middle Domain (A, C, G, I; Fig. 1), connected by a dashed line in Fig. 3 (top). There is also a consistent increase in size towards the deeper fringes of the range of distribution, well into the Outer Domain (Fig. 4). The cline persists if SCI 2 females (primiparous, distributed primarily over the Middle Domain) and SCI 3^+ females (multiparous, distributed primarily over the Outer Domain) are considered separately (Fig. 4). Inspection of iso-CW lines traced at 50 and 60 mm indicated that, relative to SCI 2 females, large SCI 3^+ females are displaced towards the outer fringes of the geographic range, and to the south (Fig. 4). We did not consider finer patterns, which could be a result of non-measurement observation error.

We used the CW corresponding to the 5% and 95% percentiles of the observed distribution as a surrogate of the absolute range, which can be distorted by outlier values. The relative range (expressed as a fraction of mean CW) did not show a latitudinal trend, but had a local maximum around the intermediate latitude of 59°S (Quadrants E-G; Table 2). The SD increased gradually from north to south, but the CV showed a pattern very similar to that of the range. The skewness of the observed distribution did not show a consistent geographical pattern (Table 2).

Analysis of SFDs of Mature Females

SFDs pooled for all surveys were unimodal for most quadrants, but clearly bimodal in the case of the southeastern EBS (quadrants K-L, also likely in M; Fig. 5). This bimodality was observed only during the earlier surveys. Afterwards the range of the female mature population contracted to the north, and SCI 2 females vanished from the southeast shelf. Quadrants along the fringes of the Outer Domain (E, H) show the possible insinuation of a secondary mode (Fig. 5, arrows); a similar but weaker signal is observable in Quadrants A, F and J. SFD analysis shows statistically significant bimodality ($\chi^2 \geq 7.81$) only in the case of Quadrants E, K and L (Table 3; Fig. 6), but the calculated χ^2 value is reasonably high in two other quadrants, H and M. In Quadrant H a secondary mode appears to be obscured by the primary mode. Consistently, the skewness coefficient of observed unimodal distributions ranged from 0.84 (highest) in Quadrant E, to 0.71 (second highest) in Quadrant H, to 0.55-0.57 (relatively high) in Quadrants A, F and J (Table 2). Skewness seems to be a good indicator of the presence of cryptic secondary modal components.

SFD analysis for individual [quadrant × year] combinations was not possible in most cases due to small sample size. In order to refine the analysis while avoiding this problem, we examined SFDs by quadrant for the four pulses of recruitment to the mature female population that are represented in the survey samples (1979-1980, 1987-1988, 1993-1995, 2001; Table 1). Inspection of the SFDs revealed the transient presence of modal components that were unidentifiable in the pooled SFDs. A spiky component of small crabs (modal CW = 43 mm) was consistently identifiable in quadrant A during the 1979-1980 and 1987-1988 pulses only (Fig. 7, left). A secondary mode at 53 mm (Fig. 7, bottom left) may correspond to a third component, but sample size is too small for conclusive identification. Insinuation of the presence of a secondary modal component of small crabs showed up in other quadrants as well, but in general was not statistically separable. SFDs of
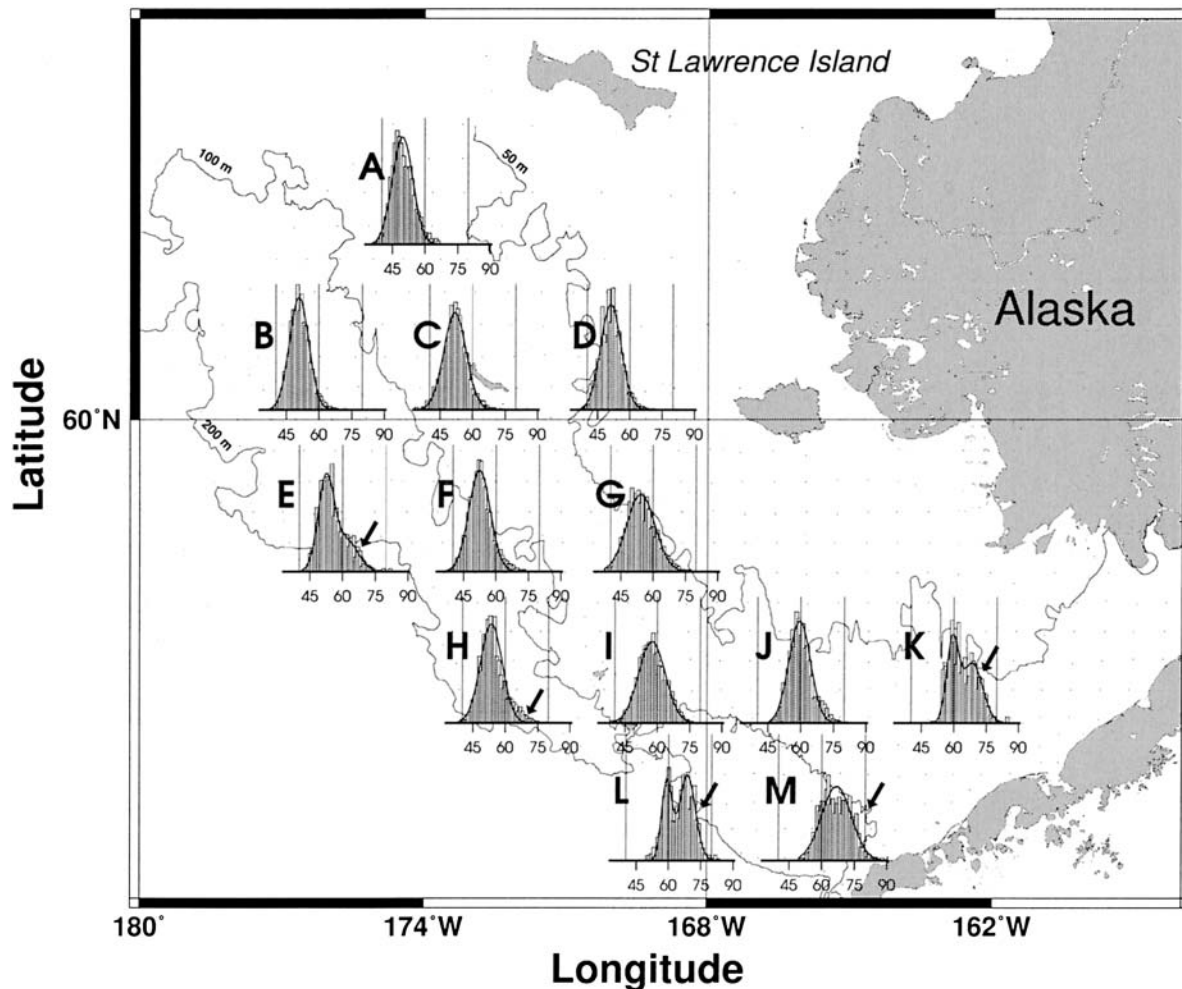
Fig. 5.   Size-frequency distributions of mature females pooled for the period 1978-2001, by quadrant, and model fit. Arrows indicate cases where there is significant evidence or insinuation of bimodality.

quadrants B, C, D and F were always unimodal, with no significant evidence of other modal components. A secondary modal component of larger crabs was definitely represented in quadrant E during the 1979-1980 pulse, and in quadrants G, H, I and J during the 1987-1988 pulse. This "anomaly" is illustrated with quadrant I, pseudocohorts of 1987-1988 (Fig. 7, right); the average size of the two major modal components was 56.8 mm (SD = 5.17) and 66.5 mm (SD = 4.57). During the 1993-1995 and 2001 pulses, the SFDs were unimodal and similar to the pooled data in all quadrants. Thus, quadrants fall into four regional groups, which from north to south are: [1] a secondary mode of relatively small crabs sporadically present (Quadrant A); [2] SFD always unimodal (Quadrants B, C, D and F); [3] a secondary mode of large crabs sporadically present (Quadrants E, G, H, I and J); and [4] SFDs bimodal before the contraction of the female population to the north (Quadrants K and L, and presumably M as well).

Means of dissected modal components show a pattern of clinal variation similar to that described earlier for the pool of mature females. Mean size of the primary modal component increases linearly with average NBT along the main axis of the Middle Domain (Quadrants A, C, G, I, L; Fig. 8). Mean size of the secondary component (larger crabs; Table 3, Fig. 8) was smaller along the warm, deep fringes of the Outer Domain than in the southeastern end of the EBS, and may be even smaller in other parts of the Middle Domain and the northern shelf, where it is likely to constitute a small fraction of the mature female population.

Visual inspection of the results from SFD analysis (Table 3; Fig. 8) suggests two ways of grouping the means of modal components. In the first, two groups correspond to the objectively dissected primary and secondary modes. The two groups show clear latitudinal clinal variation, as described earlier for the entire female population (smaller towards the north to larger towards the southern end). According to the second approach the modal groups objectively identified fall into three clusters, with mean size ranging from 49 to 54 mm (primary mode in Quadrants A to G), from 56.9 to 61.3 mm (primary mode in Quadrants I to L, and secondary mode in Quadrant E), and from 68.0 to 71 mm (secondary mode in Quadrants K-L). The major axes of the three clusters are parallel, but do not show a latitudinal cline in mean size.

Table 3. Modal decomposition of size-frequency distributions of mature females; data pooled for the period 1978-2001 (see Fig. 5). Models investigated include one and two modal components. Estimated mean and standard deviation for two components are presented only for cases in which model selection resulted in statistically significant support for that hypothesis. In the case of Quadrant M, the bimodal hypothesis was rejected (see Fig. 6) but parameters are shown because inspection of the SFD suggests otherwise.

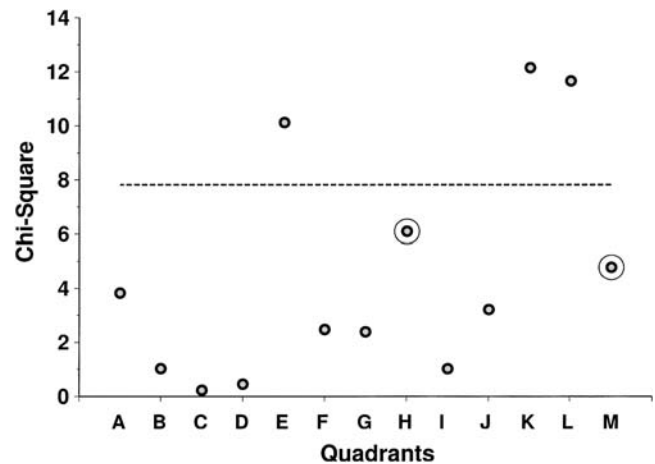|	First modal component		Second modal component		
Quadrant	Mean CW	SD	Mean CW	SD	Chi sq.
A	49.0	6.6	—	—	3.8
B	50.3	6.3	—	—	1.0
C	51.3	7.3	—	—	0.2
D	50.6	6.8	—	—	0.5
E	51.8	5.2	61.3	7.5	10.1
F	51.8	7.1	—	—	2.5
G	53.8	9.3	—	—	2.4
H	53.0	7.2	—	—	6.1
I	56.9	8.7	—	—	1.0
J	59.0	7.0	—	—	3.2
K	58.8	3.9	68.0	6.7	12.2
L	58.6	3.3	68.2	5.3	11.7
M	61.0	5.3	71.0	5.9	4.8

Fig. 6. Chi-square values corresponding to the hypothesis of two modal groups in the size-frequency distributions of mature females (Fig. 5). The dashed line indicates level chosen for rejection. Circled values highlight cases in which there is evidence of two modal components in spite of no statistical significance.

Temporal Trends in the Size of Primiparous Females

Mean size of mature female pseudo-cohorts (SCI 2) fluctuated around the long-term average (1978-2001) in all quadrants (Fig. 9). Much of the variability in each series was non-informative (noisy) due to small sample size, e.g. in quadrants where SCI 2 females were uncommon, or during years of low recruitment to the mature population. In a few cases (Fig. 9, arrows) negative (quadrant A) or positive (quadrants E, G, H, I) "anomalies" reflect an identifiable secondary modal component (see earlier section). Mean size and abundance indices were estimated for the pool of quadrants B, C, D, F and G, which together incorporated an important fraction of the historical core area of recruitment to the mature population. Abundance showed peaks similar to those reported by Ernst et al. (2005) for the shelf north of 59°N. Mean size index of SCI 2 females fluctuated in the opposite direction: mean size of recruiting pseudo-cohorts tended to be small during recruitment pulses (Fig. 10:A). Pseudo-cohort strength and the mean size of SCI 2 mature females (primiparous recruits to the mature population) were negatively cross-correlated ($r^2 = 0.27$, $P \ll 0.01$) (Fig. 10, bottom).

DISCUSSION

Clinal Variation in Female Size-at-Maturity in the Eastern Bering Sea (EBS)

Latitudinal clinal variation in the size of mature female snow crabs over the EBS shelf was well characterized by Somerton (1981b) with data from the 1979 NMFS survey, and further documented by Zheng et al. (2001), Ernst et al. (2005) and in this study using the entire survey time series. Mean terminal size continues to decline northward of the area covered by the annual NMFS survey, into the northeast Bering and Chukchi Seas (Jewett, 1981; Stevens and MacIntosh, 1986; Paul et al., 1997). Comparable clinal variation has been reported for the Gulf of Saint Lawrence, Canada (Sainte-Marie and Gilbert, 1998), where the cline is longitudinal rather than latitudinal; the overall size range of mature females recorded in the EBS (Table 2) and the Gulf of St. Lawrence (39-85 mm, exceptionally up to 95 mm; Sainte-Marie and Hazel, 1992) are similar to each other.

We showed that the cline is present in both primiparous and multiparous females. While the two groups are not expected to differ in size, large primiparous females were displaced towards the outer fringes and the southern part of their combined geographic range. This result was expected. As a result of a generally NE to SW ontogenetic migration (Ernst et al., 2005), primiparous females that molt into maturity in the Middle Domain end up a year later as multiparous females towards the Outer Domain (Ernst et al., 2005). For a typical location, incoming females originating towards the N and the NE are expected to be smaller than outgoing females that will end up in regions towards the S and the SW. The mismatch could be exacerbated if the migration rate of females were size-dependent, as larger females would end up further away from their sites of origin as compared to smaller ones.

Instar Composition

Two non-exclusive hypotheses can explain the observed cline (Fig. 3, bottom): 1) there is a gradient in size-at-instar (larger at lower latitudes), or 2) females undergo extra molts towards lower latitudes.

According to Hypothesis 1 the modal components objectively identified by us in the EBS could be interpreted as corresponding to two different instars, each of them showing marked clinal variation (Fig. 8A, straight lines). Most mature females in the EBS would belong to a single instar. Towards the southeastern end of the gradient (and to a lesser extent along the shelf-break, as far as 59°N) a significant proportion of the females would undergo an extra molt before reaching maturity, while at the northern end some females would reach maturity at a smaller instar,
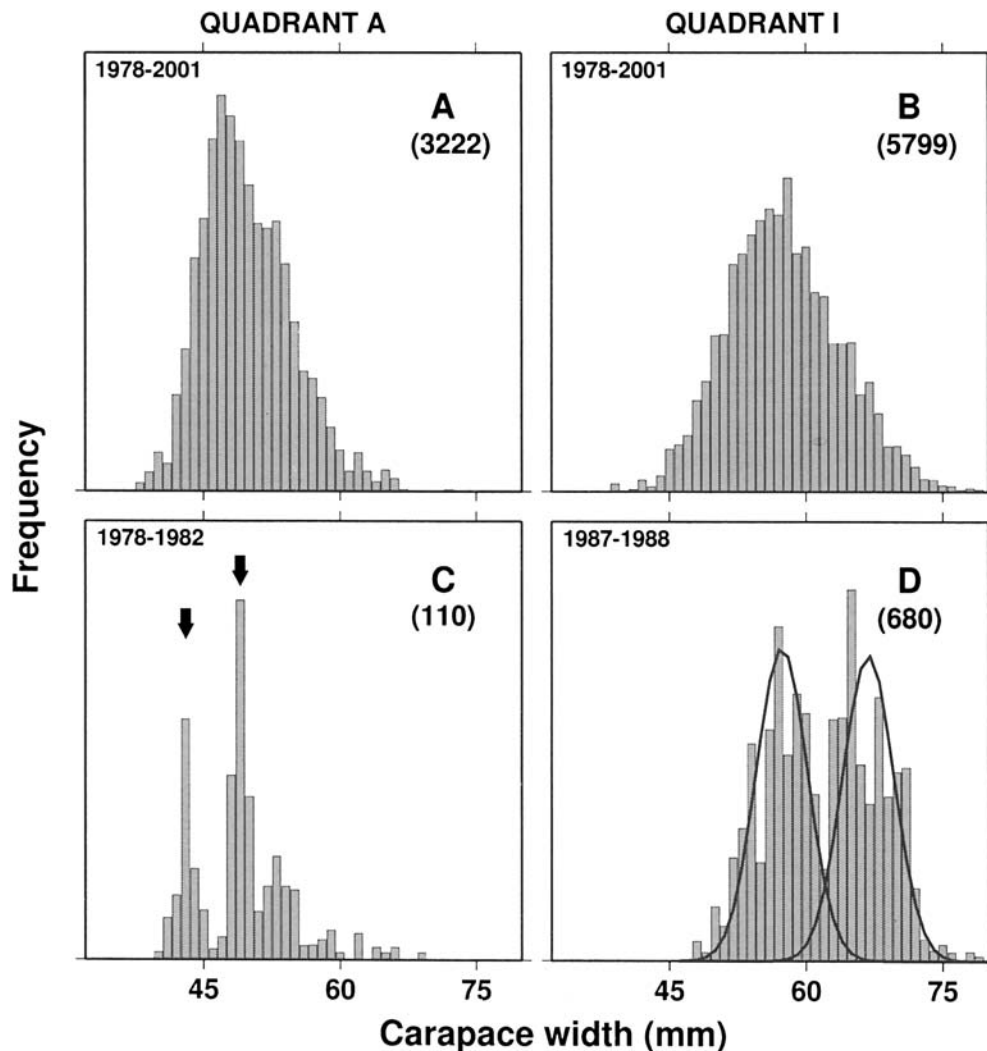
Fig. 7. Analysis of two "anomalies" in the size frequency distribution of primiparous females. A and B, size-frequency distributions pooled for the period 1978-2001 for, respectively, Quadrants A and I. C and D, size-frequency distributions for "anomalous" size frequency distributions in the same quadrants; C, pulse of 1978-1982 in quadrant A (arrows indicate modes). D, pulse of 1987-1988 in quadrant I (continuous lines represent model fit).

observed mostly in Quadrant A (Fig. 7C). Thus, the cline would result from size-at-instar and number of instars at maturity, both resulting in larger size at lower latitudes, where mean NBT is higher. The relationship between size-at-instar and temperature has been investigated experimentally in other brachyurans, with variable results (Hartnoll, 1982, and references therein): no relation within the range investigated, amplification of increments-at-molt with an increase of temperature, or the opposite, which was the most frequent outcome (see also Mohamedeen and Hartnoll, 1990; Fisher, 1999; Hartnoll and Bryant, 2001). The latter has been related to the abbreviation of the intermolt period at higher temperatures, which would permit the accumulation of limited reserves for size increase at molt (Hartnoll, 1982). Laboratory results cited above would predict larger size-at-instar at higher latitudes, the converse of the pattern implied by Hypothesis 1. In experimental studies, however, the frequency of molting was not constrained by the duration of a growth season. If the number of molting events by year were constrained, then the length of the

growth season and -consequently- the accumulation of mass during the intermolt period could decrease at higher latitudes, causing the cline in size-at-instar observed in mature snow crab females from the EBS under Hypothesis 1. There is, however, no indication of a growth season for juvenile snow crab. In fact, early benthic instars are known to molt in winter (Sainte-Marie et al., 1995; Alunno-Bruscia and Sainte-Marie, 1998).

Under Hypothesis 2, three subjective clusters of objectively estimated modal components (Fig. 8A, dotted ellipses) could be informative about instar structure. Complete size-at-instar series have been compiled for morphologically immature and mature female snow crab in the northwestern (Sainte-Marie et al., 1995; Alunno-Bruscia and Sainte-Marie, 1998) and southeastern (Robichaud et al., 1989) Gulf of St. Lawrence, Newfoundland (Comeau et al., 1998), the Okhotsk Sea (Ito, 1970) and the Japan Sea (Kon, 1980). Instars X-XII in the latter two studies may correspond to Instars XI-XIII (Sainte-Marie, personal communication). Results from these studies,
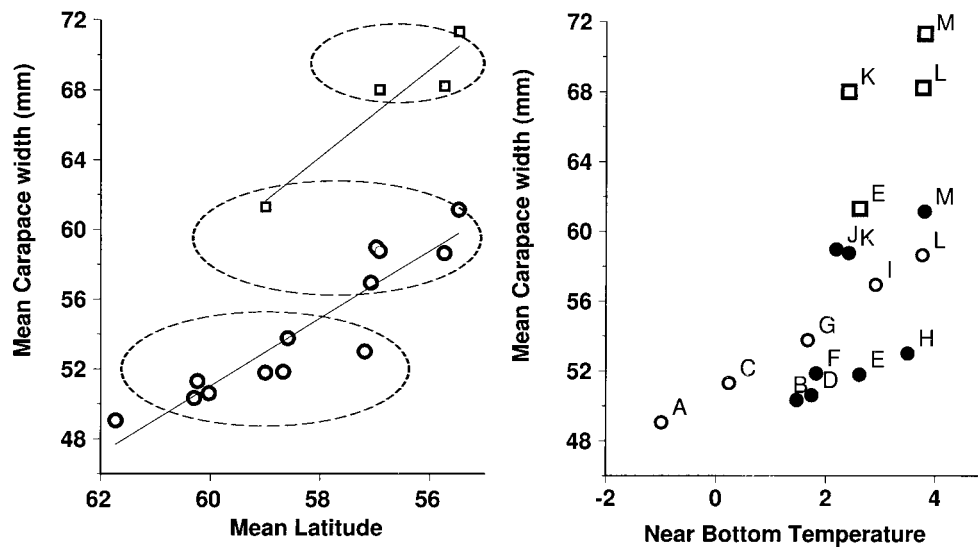
Fig. 8.   Relation between mean size of modal components identified through size-frequency distribution analyses with (A) mean latitude of the survey stations and (B) average summer near-bottom temperature (data pooled for the period 1978-2001). Circles: first modal component, squares: second modal component (when present). Straight lines in A indicate latitudinal trends in the groups of modal components; dashed lines encircle apparent clusters of modal components. Open circles in B correspond to quadrants aligned along the Middle Domain (Quadrants A, C, G., I, connected by dashed line in Fig. 1).

conducted in widely separated regions, are remarkably consistent with each other (Fig. 11), suggesting that size-at-instar of snow crab is highly conservative. The pattern is expectedly blurred in the transition to morphological maturity (Alunno-Bruscia and Sainte-Marie, 1998). The reason is that the mature female group can be composed of individuals belonging to different instars, which combined with size-dependence in the probability of molting to maturity (large, fast growing females molting into maturity earlier; Alunno-Bruscia and Sainte-Marie, 1998) results in reduced identifiability of instar components in SFDs. Inspection of SFDs indicated that the unimodal SFDs observed in some quadrants are composed by more than one instar: a secondary mode is insinuated in the aggregate SFDs of Quadrants G-H and J, and transient modal components became evident when individual recruitment pulses were scrutinized. Unimodal instar mixtures, or "pseudo-instars", tend to be dominated by a primary instar component. For that reason the mean of a pseudo-instar is expected to be close to that of the primary instar component, but the standard deviation should be larger. Consistent with this expectation, the standard deviations of pseudo-instars from the EBS (Table 2, Quadrants A-J, average: 5.7) are about one third larger compared to the standard deviation of instar size observed by Alunno-Bruscia and Sainte-Marie (1998, their Table 3) in the Gulf of Saint Lawrence and by Comeau et al. (1998) in Newfoundland. Also, because we integrated information for an area much larger and over a period much longer than all previous studies, variability in size-at-instar is expected to be higher even when the latter is relatively conservative in snow crab. Growth projections using parameters estimated from data presented by Alunno-Bruscia and Sainte Marie (1998, their Table 3) indicate that SFDs of mature females observed by them and by us can be composed of two or three instars, and can be uni- or bimodal depending on the relation between mean size of the last

purely juvenile instar and minimum size-at-maturity. Instar components in unimodal mixtures may be unidentifiable in SFDs, regardless of the precision of size measurements, choice of CW classes and/or sampling effort. According to Hypothesis 2 the three apparent groups of modal components (Fig. 8A, circled) can be interpreted as pseudo-instars dominated by Instars IX, X and XI, well identified in eastern Canada (Sainte-Marie et al., 1995; Comeau et al., 1998; Alunno-Bruscia and Sainte-Marie, 1998 (Fig. 11).

The small modal component detected in Quadrant A during at least two pulses of recruitment is indicative of sporadic molting into maturity at a relatively small instar, most likely Instar VIII, in the northern end of the region surveyed. This conclusion holds irrespective of the hypothesis considered.

The two hypotheses discussed above make different predictions about the number of instars present in the mature female population of the EBS (3 under Hypothesis 1, 4 under Hypothesis 2), and the relative significance of variation in mean size-at-instar (high under Hypothesis 1, negligible under Hypothesis 2). Elucidation of this issue will require investigation of growth in juvenile snow crab from the EBS. Both hypotheses are, however, coincidental in stressing variation in instar-at-maturity as the primary factor governing clinal variation in the size of mature females.

Possible Causes of Variability in Instar-at-Maturity

Somerton (1981b, p. 172) observed that in the EBS there are "extensive areas with gradual clinal variation separated by narrow transition regions in which size increases abruptly. Clinal variation in adult size is clearly related to the distribution of temperature, but transition regions are not always associated with temperature discontinuities". He hypothesized that the observed pattern could be related to genotypic variation. Actually, the pattern can be explained
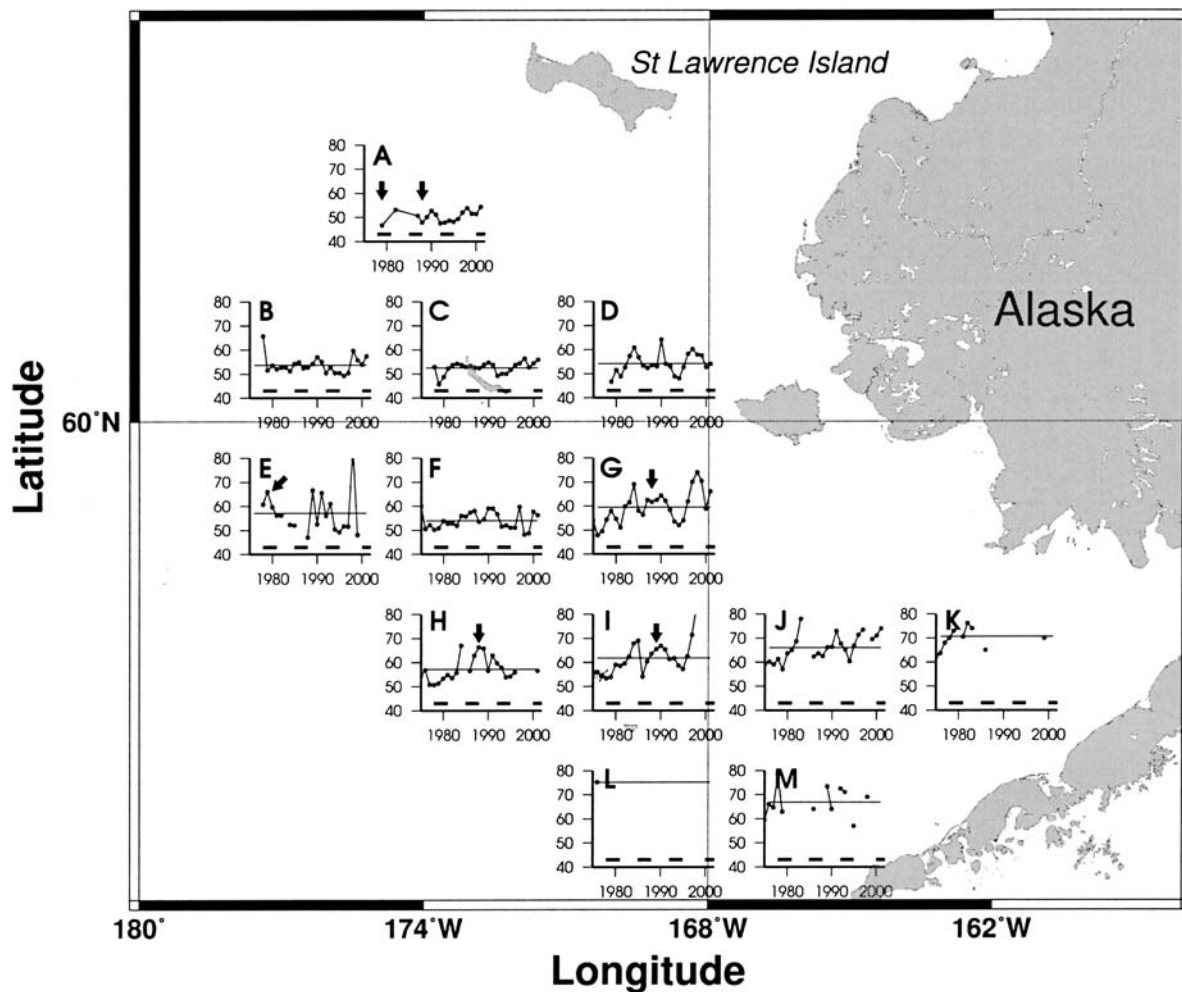
Fig. 9. Trends in mean size-at-maturity of primiparous females by quadrants (see Fig. 1). Horizontal lines indicate mean size for each quadrant. Thick dashes indicate the timing of pulses of recruitment to the mature female pool. Arrows point to anomalies (negative in the case of A, positive in the other quadrants) due to the transient occurrence of secondary instars.

by several alternative hypotheses: [I] an artifact caused by observation error, [II] the expression of geographical genotypic variation, [III] introgression of genes from the closely related *C. bairdi*, and [IV] phenotypic variation controlled by a single reaction norm.

Hypothesis [I] would hold in the case of significant misclassification of small mature *C. bairdi* or [*C. opilio x C. bairdi*] hybrids (both being generally larger than snow crab females) as large mature female snow crabs during the NMFS surveys. Size overlap between the large modal component of snow crab and the small modal component of tanner crab is, however, very small (Somerton, 1981b, his fig. 2). This, combined with the fact that the two species are easily distinguished by a trained observer, makes misclassification unlikely. The case of hybrids is more problematic. Biologists specializing in the identification of *Chionoecetes* species can identify unknown samples based on morphological traits consistently with allozyme-based identifications, but fisheries observer trainees produced identifications inconsistent with allozyme data up to 45% of the time in the case of hybrids (Urban et al., 2002). Morphological and genetic surveys indicate, however, that

hybrids of any generation are rare, less than 10% in the hybrid zone (Smith et al., 2005). Therefore, misclassification is, by itself, unlikely to generate the observed pattern.

According to Hypothesis [II], advanced by Somerton (1981b, p.173), geographic variation could result from multiple genotypes selected in response to conditions encountered in different sectors of the species range within the EBS (see Partridge and Coyne, 1997, for cases involving various invertebrates). Hypotheses in this type are unlikely to apply in the case of the snow crab population from the EBS, which is continuously distributed over an extensive shelf, with no apparent geographic barriers that might create the conditions for the evolution of local adaptations. Considering that pelagic larvae spend at least three months in the water column (Incze et al., 1987), the potential for dispersal must be high even if residual circulation were comparatively small, as appears to be the case in the upper layer of the intermediate shelf where larvae concentrate (Kinder and Schumacher, 1981). Extensive ontogenetic migrations (Ernst et al., 2005) may also contribute to gene flow. Further, Merkouris et al. (1998) did not find significant geographic differentiation using allozyme analyses
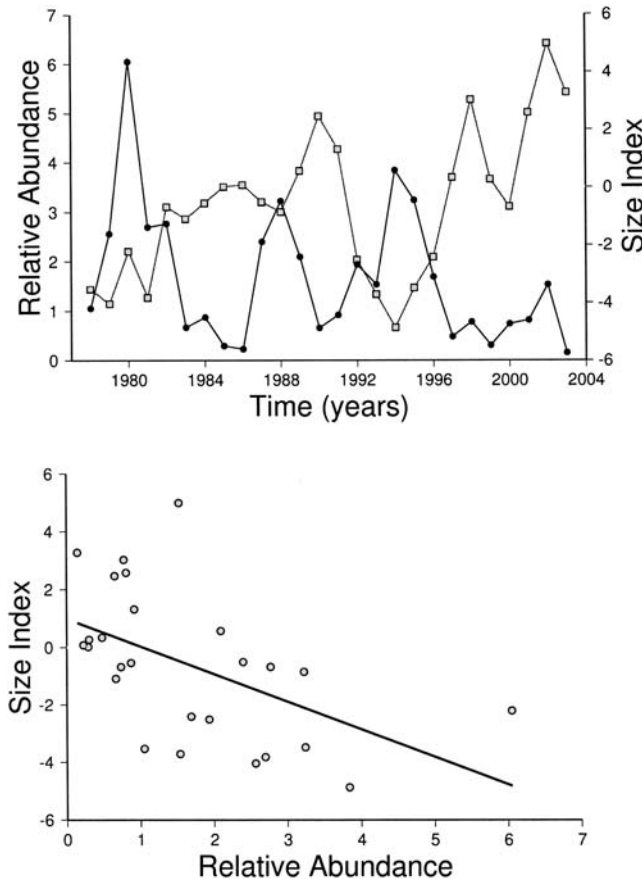
Fig. 10. A: trends in (i) pseudocohort abundance (dots) and (ii) a standardized-weighted size index for primiparous females (squares) at the historical core of the range of distribution of primiparous females (quadrants B, C, D, F, G). B: cross-correlation between the two series.
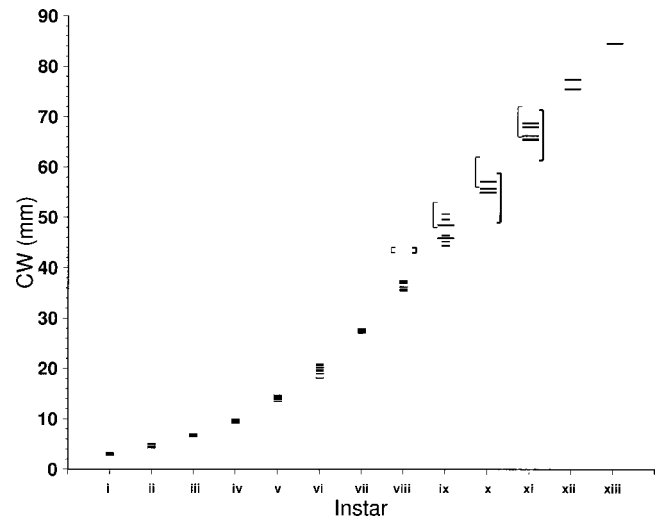

Fig. 11. Size-at-instar in several populations of snow crab (horizontal segments) and ranges estimated in this study under two alternative hypotheses. Short segments: means of juvenile instars, long segments: means of mature female instars. Data from Sainte-Marie et al. (1995) and Alunno-Bruscia and Sainte-Marie (1998, northwestern Gulf of St. Lawrence), Robichaud et al. (1989, southeastern Gulf of St. Lawrence); Comeau et al. (1998, Newfoundland), Ito (1970, Okhotsk Sea) and Kon (1980, Japan Sea). Brackets indicate the ranges of mean instar size of mature females estimated by us under two hypotheses. Right brackets: Hypothesis 1, three instars and clinal variation in size at instar. Left brackets: Hypothesis 2, four instars and no clinal variation in size-at-instar.

(34 presumptive loci, n = 539) throughout the commercially important range of snow crab in the EBS. The same study contributed some support for Hypothesis [III], as it found evidence of gene introgression between tanner and snow crab in the hybrid zone, which is largely coincidental with the region in which the bimodal pattern was observed. Most hybrids represent first generation crosses, but F_2 and later generations are also present. Introgression could thus possibly provide a mechanism for the origination of a large-female snow crab phenotype. It is uncertain whether this system fits the "tension zone" model, under which the heterozygotes or hybrid recombinants leave fewer offspring (Hewitt, 1988). Such genotypes tend to be removed from the population by natural selection, leaving pure parental genotypes (Hewitt, 1988). It has been observed that hybrid females appear to have reduced reproductive potential (Karinen and Hoopes, 1971; JMO, personal observation). Many are non-gravid or carry abnormally small egg clutches containing large numbers of dead eggs. Further research to test Hypothesis [III] could investigate the genetic makeup of mature females, including Tanner crab, hybrids, and small and large snow crab mature females.

Hypotheses [I] and [III] cannot explain variability in instar- or size-at-maturity in the northern shelf, nor in Eastern Canada, where snow crabs do not coexist with other congeners. Hypothesis [II] is unrealistic, which does not imply negating likely genetic variation in the response of growth and development to variable environmental conditions. We argue that Hypothesis [IV], phenotypic plasticity (Heino et al., 2002), offers the most parsimonious explanation of variability in size-at-maturity of snow crab females over the EBS shelf. Below we attempt to explain observed variability in this framework.

Plasticity in Size-, Instar- and Age-at-Maturity

Phenotypic plasticity in the transition to maturity can be related to age, development (expressed by instar) and growth (expressed by body size) (Bernardo, 1993). In this study we documented high variability in size- and instar-at-maturity. Variability in age-at-maturity, in contrast, is poorly documented in the EBS due to the intrinsic difficulties of estimating crab age. Size- and instar-at-maturity are the combined result of growth rate and a trigger (related to size, stage and/or age) that stops growth, and that could be tuned by physiological condition or environmental factors. Crustacean growth rate has two components: molting frequency and size-dependent increments per molt. Considering that (as discussed earlier) the size-at-instar schedule is highly conservative in snow crab, molting frequency would be the primary source of variation. Molting frequency in crabs generally increases with temperature (Hartnoll, 1982), and so in snow crabs from the EBS it is likely to increase at lower latitudes (particularly during early ontogeny). Empirical support for this expectation is scarce but consistent: duration of the intermolt period is inversely related to temperature in juvenile males of the closely related *C. bairdi* (Paul and Paul, 2001), and juvenile snow

Table 4. Growth patterns associated with different reaction norms (patterns after Wenner et al., 1991, for the particular case in which size-at-maturity and maximum size are coincidental), with indication of hypotheses under which they are expected, pertinent observations in our study system, and consistency between expectations and observations.

	Pattern	Expectation	Observations	Consistency
A	Maximum size of the fast and slow growing phenotypes is the same; fast growing phenotype matures earlier		Same as for Pattern C	Inconsistent with our data
B	Fast growing phenotype matures at a larger size; both phenotypes mature at the same age			Plausible, some empirical support
C	Fast growing phenotype matures at a smaller size and earlier	Predicted by Bergmann's rule	Fast growing phenotypes reach a larger terminal size (see text)	Inconsistent with our data
D	Fast growing phenotype matures at a larger size and earlier			Plausible, but not supported by empirical evidence
E	Fast growing phenotype matures at a larger size and later	Predicted by optimal life-history theory	Implies that molting frequency of fast growers should be equal or lower than in slow growers	Inconsistent with expected relation between temperature and molting frequency

crabs reared at relatively warm temperature (4°C) by Sainte-Marie and Lafrance (2002) had shorter intermolt periods than observed in the colder natural habitat. Research conducted in eastern Canada indicates that past the first two to three years of life there is one molting event per year before terminal molt is reached; skip-molting in immature crabs is negligible (Sainte-Marie et al., 1995; Comeau et al., 1998; Hébert et al., 2002). This is also likely to be the case in crabs from the EBS. Thus, temperature-dependent molting frequency, the primary determinant of growth rate, can vary only during early ontogeny. The addition of one molt during the first year of life, projected through life time, may have a significant effect on size-at-maturity provided that age-at-maturity is constrained.

It is not clear how size, stage or age trigger maturity and the terminal molt, or how the process is modulated by physiological condition and environmental factors. These questions are difficult to address, but the information avail-able allows narrowing on some specific hypotheses. Wenner et al. (1991) presented six general patterns describing the relationship between size- and age-at-maturity in crusta-ceans, a system which provides a useful framework for the comparative evaluation of possible reaction norms (Table 4). Consider "fast", "intermediate" and "slow" growth rate phenotypes, the difference between them being determined by temperature-dependent frequency of molting during early ontogeny (Fig. 12). Under Wenner et al.'s Pattern B (Table 4) all phenotypes reach maturity at the same age, implying that maturation is triggered by age, and that instar-at-maturity would be higher for the fast, and lower for the slow growing phenotypes. The resulting vertical reaction norm (Fig. 12, vertical dotted rectangle) would be the result of the combination of a relatively inflexible molting schedule governed by an age-related trigger. Limited flexibility in snow crab molting schedule, discussed earlier, is consistent with the fact that pulses of recruitment to the mature female
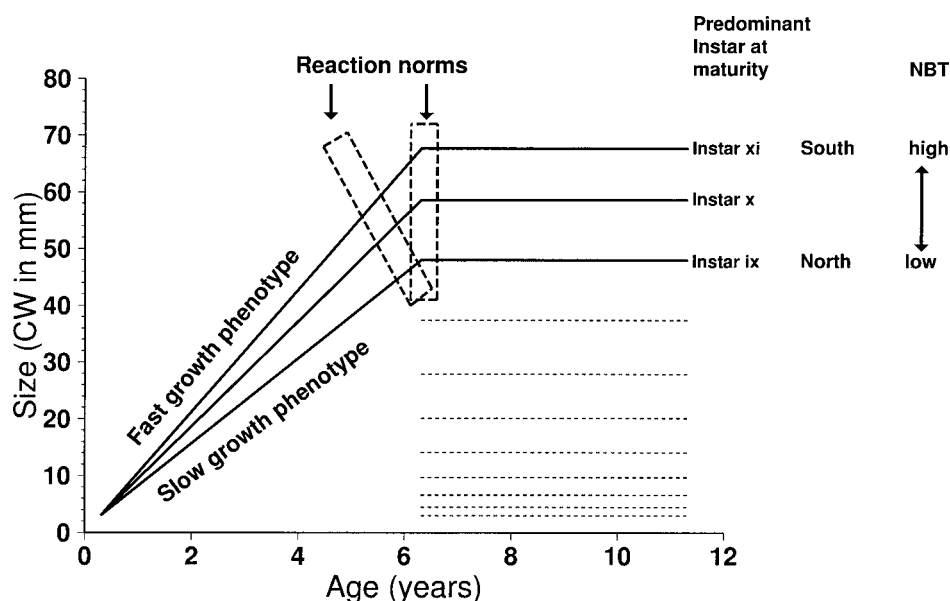

Fig. 12. Hypothetical reaction norm governing size-at-maturity in snow crab from the eastern Bering Sea. The three curves represent fast, intermediate and slow growth phenotypes reaching maturity at the same age (staircase-style representation avoided for clarity). Horizontal dotted lines indicate approximate juvenile sizes-at-instar expected in the central shelf based on the literature. Vertical dotted rectangle: reaction norm if maturity were age-dependent; the tilted reaction norm would reflect a temperature-dependent physiological age effect. NBT: near-bottom temperature.

population of the EBS show much geographical coherence in spite of large variation in size-at-maturity. A hypothetical relation between age and the initiation of events leading to terminal molt is in line with recent results on the molecular basis of "timekeeping" and the timing of developmental transitions in arthropods (Adoutte, 2000; Pasquinelli and Ruvkun, 2002; Sempere et al., 2003).

There is little support for other patterns, their respective reaction norms, or the required triggers. Counter-clockwise rotation of the reaction norm leads to Pattern D (Table 4; tilted rectangle in Fig. 12), in which faster growth phenotypes reach a larger size and mature earlier. This pattern would be expected if molting to maturity were triggered by physiological age (i.e., cumulative degree days) rather than chronological age. It would imply an even higher differential between phenotypes in terms of molting frequency during early ontogeny. Wenner et al.'s Patterns A, C and E are inconsistent with existing information (Table 4).

The preceding discussion addressed deterministic variability in age-at-maturity between growth phenotypes. Related subjects of interest in the context of reaction norms are the variability in age-at-maturity within a given growth phenotype, and in growth phenotype within a given location. Evidence of the first was provided by Alunno-Bruscia and Sainte-Marie (1998), who reported that over the period 1991-1996 females reached maturity at Instars IX and X at the post-settlement age of 5.5 or 6.5 years, respectively. Analogously, Somerton (1981a) showed (his Fig. 10 and Table 4) that small and large female modal components of a strong year class reached maturity in, respectively, 1975 and 1976 in the southeastern Bering Sea. This variability could be genetic in origin, but is different from the hypothetical patterns of geographical genetic variation discussed earlier (Hypotheses II and III). Local variability in growth phenotype is suggested by the observation that mature females can correspond to a mixture of instars even at small spatial scales. Stochasticity in reaction norms is a subject of much current interest (Heino et al., 2002), but remains poorly documented for snow crab.

Temporal Trends in Size-at-Maturity

Fluctuation in the composition by instars (and consequently size structure) of the mature female population can be the result of an alternation of periods of low and high recruitment, as demonstrated by Sainte-Marie et al. (1996, p. 461). They reported that the average size of primiparous females decreased from 57.1 mm in 1991 (weak pseudocohort) to 50.3 mm in 1995 (strong pseudocohort) in the Gulf of St. Lawrence. Sainte-Marie and Lafrance (2002) conducted an experiment in which snow crabs in Instar I were reared at four different densities, and at constant density under six density levels of Instar v crabs. They found that the first and second molts occurred increasingly late as density increased, possibly reflecting poor physiological condition due to starving, the latter resulting from growing agonism and competition. The authors speculated that crowding and the presence of larger conspecifics (environmental stressors) reduces the supply of ecdysteroid levels and diminishes foraging activity, both conductive to delayed molting. The delay of molting in the face of risk is likely to have adaptive significance (Sainte-Marie and

Lafrance, 2002, p. 201). Individually reared crabs showed larger molt increments in size as compared to communally reared crabs. These experimental results provide support to the hypothesis that negative correlation between the strength of female pseudocohorts and the average size of their members may originate from intraspecific interactions. The existence of comparable, negatively cross-correlated cycles of recruitment and size in the Gulf of Saint Lawrence and the EBS (reported here) suggests the operation of strong density-dependence in the dynamics of snow crab populations, modulated by intrinsic characteristics of the life-history of this species.

Clinal Variation in a Macroecological Context

Clinal variation in the size of mature *Chionoecetes* females along shelf areas of the northeastern Pacific and the EBS, from large at low latitude to small at high latitude, holds both at the interspecific level (*C. bairdi* females are larger than those of *C. opilio*) and, at least in the case of snow crabs, also at the intra-specific level. There is an abundant literature dealing with intra- and inter-specific patterns of latitudinal clinal variation in body size, which has been generally considered in the general framework of Bergmann's rule in its broadest definition. Blackburn et al. (1999), after a review of the historical evolution of the concepts embodied in the rule, proposed restricting it to supra-specific patterns, as 'the tendency for a positive association between the body mass of species in a monophyletic higher taxon and the latitude inhabited by those species'. The same authors proposed renaming the intra-specific version as "James's rule". The validity of James' rule for ectotherms has been extensively investigated, with diverging results (Atkinson, 1994; Ashton, 2001). Some empirical studies have shown patterns consistent with the rule (Partridge et al., 1994; James et al., 1995), including some decapod examples (Hines, 1989; Dugan et al., 1991). Coincidentally, experimental studies have consistently shown that ectotherms grow to larger sizes when reared at lower temperatures, a phenotypically plastic response that has been termed 'developmental temperature-size rule' (Atkinson, 1994; Sibly and Atkinson, 1994; Atkinson and Sibly, 1997). A mechanistic explanation for the rule is that clinal variation is simply a physiological byproduct of the effects of temperature on cell division and replication, which results in larger cells, and hence larger organisms from cooler rearing temperatures (Partridge et al., 1994; Van Voorhies 1996; French et al., 1998). The larger size of ectotherms at higher latitudes is also predicted by bioenergetic models (Dugan et al., 1991, p. 77; van der Veer et al., 2003).

Opposite to these empirical and theoretical results, others have supported the 'converse' form of James' rule (Masaki, 1967; Mousseau and Roff, 1989; Mousseau, 1997; Blanckenhorn and Hellriegel, 2002), again including some brachyurans (Somerton, 1981b; Hines, 1989; this study). The converse rule is consistent with a prediction of optimal life history theory (Atkinson and Sibly, 1997, their Box 2). In some invertebrates the converse rule is a direct consequence of the length of the growth season, which conditions the physiological time available for development (Masaki, 1978; Roff, 1980, 1983; Mousseau, 1997).

Any general theory aimed at explaining geographical clines in size-at-maturity in ectotherms, particularly if optimality is assumed, needs to attend to several factors that bound life-history solutions: opportunities for natural selection in different regions of the geographic range, developmental constraints, the menu of triggers that may initiate developmental transformations, and the tempo of metabolic processes being dictated by physiological time (usually related to temperature) rather than chronological time. Summarizing our discussion, we suggest that in snow crab from the EBS: 1) opportunities for the evolution of local adaptations within that geographical region are limited due to larval dispersal and adult migrations; 2) the cline reflects phenotypic plasticity controlled by a single reaction norm; 3) growth rate is constrained by limited flexibility in the molting schedule, either in the form of the frequency of molting during the first 2-3 years of life or, later on, when developmental constraints impose a one-molt-per-year schedule; 4) coincidence of maturity and terminal molt imposes a major developmental constraint; and 5) it is plausible for the latter to be controlled primarily by age.

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