

FLUCTUATIONS IN RANGE AND ABUNDANCE OF SNOW CRAB (*CHIONOECETES OPILIO*) FROM THE EASTERN BERING SEA: WHAT ROLE FOR PACIFIC COD (*GADUS MACROCEPHALUS*) PREDATION?

*Julian Burgos, Billy Ernst, David Armstrong,
and JM (Lobo) Orensanz*

ABSTRACT

Fluctuations in abundance of commercially valuable crustacean stocks in sub-Arctic ecosystems have been variously attributed to the effects of climatic forcing, fishing pressure, and predation, mostly by gadoid fishes. Landings of snow crab, *Chionoecetes opilio* (J. C. Fabricius, 1788), from the eastern Bering Sea declined after the early 1990s, reaching historical lows a decade later. At the same time, two phenomena became apparent in the dynamics of the primiparae (first-time female breeders): their geographic range contracted to the northwest along the middle shelf (50–100 m depth), and the contraction was punctuated by periodic recruitment to the mature female pool, with a period of approximately 7 yrs and declining amplitude. The first phenomenon has been addressed by the environmental ratchet hypothesis, which attributes the contraction to a combination of an ontogenetic female migration, circulation patterns, the spatial dynamics of benthic stages in relation to near-bottom temperature, and predation by Pacific cod, *Gadus macrocephalus* Tilesius, 1810. Mortality due to cod predation in the Middle Domain, apparently related to near-bottom temperature, increased after 1995, contributing to the ratchet effect and the disappearance of periodic pulses of primipara abundance. Cod predation does not, however, appear to have controlled the frequency of periodic recruitment fluctuations. On the other hand, amplitude of fluctuations of primipara abundance in the Middle Domain, purportedly the “engine” of renewal of this stock, do appear to be affected by both predation and climate, whose interaction is complex but perhaps interpretable.

Top-down control of commercially valuable crustacean stocks from subarctic ecosystems, mostly with regard to predation by cod (*Gadus* spp.), has been the subject of much attention in recent years (Frank et al. 2005, Link et al. 2009). Those interactions are significant because of their role in the functioning of shelf ecosystems, their large spatial scale, and the economic significance of the species involved, both predators and prey (Worm and Myers 2003). Snow crab, *Chionoecetes opilio* (J. C. Fabricius, 1788), for example, is preyed upon by Atlantic cod, *Gadus morhua* Linnaeus, 1758, in eastern Canada (Chabot et al. 2008) and by Pacific cod, *Gadus macrocephalus* Tilesius, 1810, in the Bering Sea (Livingston 1989, Orensanz et al. 2004). Over the last two decades landings of snow crab have declined dramatically in the eastern Bering Sea (EBS; Fig. 1A), from a maximum of nearly 150,000 t in 1991 to historical lows on the order of 12,000 t during the early 2000s (NPFMC 2010). The stock, declared “overfished” in 1999, has recently been considered to be rebuilt. These fluctuations of abundance, variously attributed to climate, fishing, and predation, have

been a subject of much interest (Zheng and Kruse 2006) and of concern to managers (NPFMC 2010).

The spatial dynamics of the EBS snow-crab population is highly structured by a rather rigid life-history program: conservative size-at-stage and molting schedule, directed ontogenetic migrations, and a complex mating system. Conditioned on the constraints imposed by life history, spatial processes are modulated by recurrent oceanographic phenomena, including expansions and contractions of the cold pool, cross-shelf vectors of near-bottom temperature, and patterns of circulation (Orensanz et al. 2004, Ernst et al. 2005, 2012, Parada et al. 2010). The fishery, historically one of the most lucrative crab fisheries of the world, harvests only large adult males and operates only on the outer shelf (deeper than 100 m), mostly during the winter. A combination of strong spatial structure in major life-history events, their oceanographic drivers, and the fishing process may allow the separation of the effects of climate, predators, and fishing on the fluctuations of the population (Parada et al. 2010).

The vast expanses of the EBS are naturally partitioned into domains defined by frontal systems and conventionally demarcated by bathymetry (Hunt et al. 2010). The 50-m isobath separates the Inner and Middle domains, and the 100-m isobath the Middle and Outer domains; the latter extends to the shelf break (200 m). Snow crab transition from immature benthic stages to the terminal molt that marks attainment of adulthood (in both males and females) occurs primarily in the Middle Domain (Parada et al. 2010, Ernst et al. 2012). After attaining adulthood, both females and large males migrate to the Outer Domain; no evidence indicates that they ever return to the Middle Domain (Ernst et al. 2005). Over recent decades the range of first-time breeding females, collectively known as “primiparae,” has contracted dramatically from southeast to northwest (Orensanz et al. 2004). The contraction has been punctuated by four periodic pulses of recruitment, with average intervals of 7 yrs. The last pulse, centered in 2001, was also the weakest in the series (Ernst et al. 2012).

Orensanz et al. (2004) postulated the environmental ratchet hypothesis (ERH) to explain the contraction. According to the ERH, recruitment in the Middle Domain and expansion of the distribution range of immature snow crab are favored after cold periods, when a cold-water pool extends close to the bottom and far into the southeastern shelf during the summer. Experimental and field studies conducted in eastern Canada (Dionne et al. 2003) showed that early benthic stages are cryophilic and prefer temperatures between 0 and 2 °C (the conventional boundary of the cold pool; Wyllie-Echeverria and Wooster 1998). Also, cod predation, believed to be a major source of immature-crab mortality (Livingston 1989, Livingston et al. 1993), is expected to relax during cold summers. In contrast, during warm years the cold pool does not expand to the south of St. Matthew Island, and the thermal habitat is not favorable to early snow-crab instars. At the same time, cod foraging on immature snow crab intensifies over the Middle Domain. Orensanz et al. (2004) hypothesized that expansions and contractions of the geographic range of cod “chop off” the southern fringe of juvenile/immature snow crab. According to the ERH, contraction toward the northwest after warm periods is not easily reversed during cold periods because of the predominant direction of residual circulation over the shelf (southeast to northwest, particularly over the Outer Domain), which places the depopulated grounds upstream of the remnant female reproductive stock.

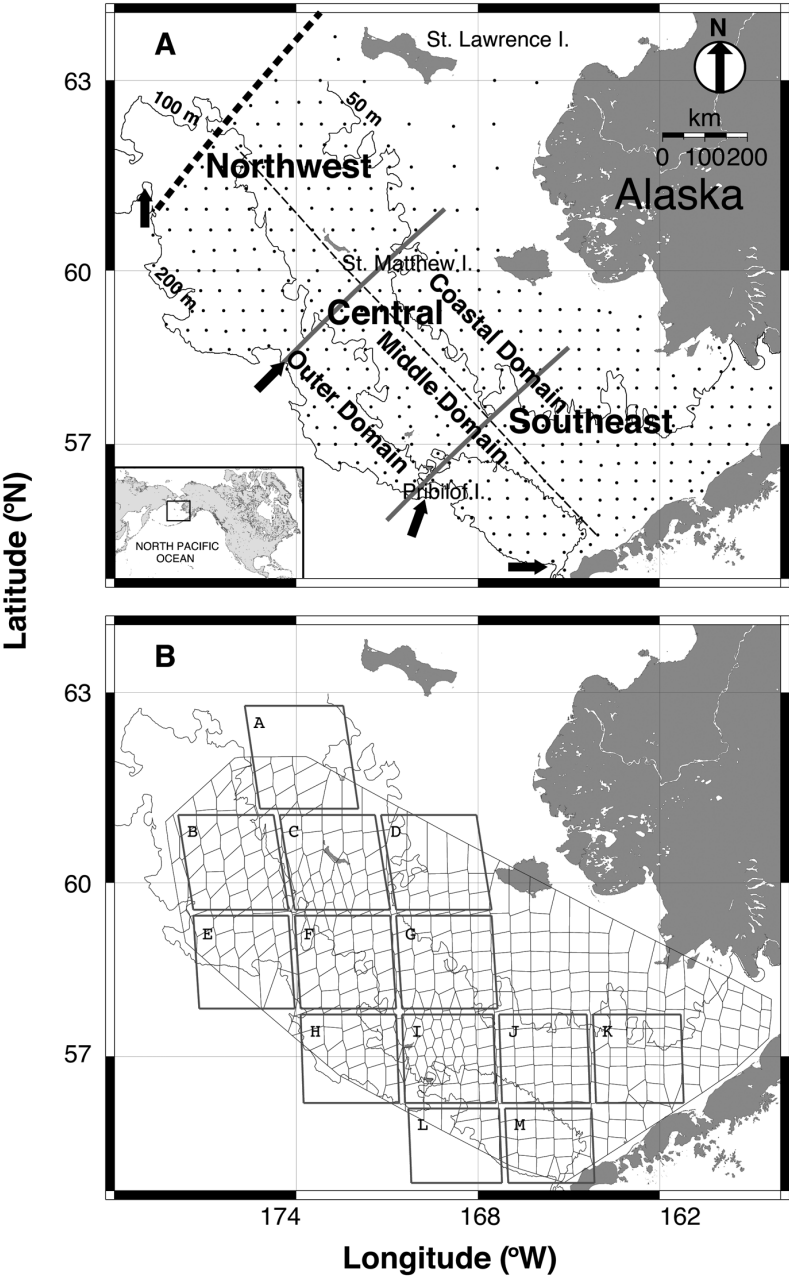


Figure 1. The eastern Bering Sea Shelf. (A) Sections (northwest, central, and southeast) and domains (Coastal, Middle, and Outer). Arrows point to four major constrictions of the Outer Domain. The straight dashed line (running from northwest to southeast) corresponds to the main axis of the Middle Domain. Dots indicate stations of the summer bottom trawl surveys conducted by the National Marine Fisheries Service. The thick dotted line indicates the international boundary (US-Russia). (B) Voronoi tessellation tiles identifying the area associated with each sampling station of the trawl survey (exemplified with the 2000 survey). Each of the larger tiles on the edges of the survey area was assigned an area of 400 nmi². The larger spatial grid defining the quadrants A–M is also shown.

Here we address the predator-prey interaction between Pacific cod and snow crab in the EBS using the information available and insights gained from recent studies of snow-crab population biology. We investigated the size and instar specificity of cod predation on snow crab, geographic patterns and temporal trends of cod consumption, and indices of immature crab survival. More specifically, we focused on the possible role of cod predation in the disappearance of reproductive females from the Middle Domain of the southeast shelf after 1995 and the end of a sequence of periodic pulses of recruitment.

MATERIAL AND METHODS

CONVENTIONS AND NOTATION FOR SNOW CRAB LIFE HISTORY.—Crab instars are conventionally identified with Roman numerals. We distinguish immature from mature crabs in the same instar through the use of, respectively, lower and upper case characters (e.g., instar viii and instar VIII). When instar composition was approximated by means of knife-edged size intervals, we add the tilde (~) symbol (e.g., instar ~viii). Size is always expressed in terms of carapace width (CW) in millimeters. Following Comeau et al. (1998), we categorized females as “immature” or “mature” depending on whether they had been through their terminal molt, a condition easily evaluated by visual inspection of the abdominal flap and regularly recorded during the surveys. Females carrying their first batch of eggs are collectively designated “primiparae,” and those that have spawned at least two broods (the second one while already in hard-shell condition) as “multiparae.” A “shell condition index” (SCI) was recorded for females scored during summer surveys (described below). SCI scores range from 0 to 5. Mature females in SCI category 2, corresponding to a clean new shell, were considered primiparous and assumed to have molted to maturity during the winters before the summer surveys (Ernst et al. 2005). As by Ernst et al. (2005), a “pseudocohort” of mature females is defined as the group of females that underwent their terminal molt (i.e., recruited to the mature population) during the same year. Members of a pseudocohort can belong to multiple year classes and instars, and a given year class can contribute to multiple pseudocohorts (Ernst et al. 2012). 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-yr intervals between 1978 and 2003; these events have been referred to as pulses I–IV (the “core years” were 1980, 1988, 1994, and 2001), and here we adhere to that convention.

SURVEY DATA.—Indices of abundance of Pacific cod and selected categories of snow crab (immature females and primiparae) from the EBS shelf were estimated from data obtained during annual bottom-trawl surveys (BTSS) conducted by the National Marine Fisheries Service (annual reports available from <http://www.afsc.noaa.gov/Publications>). BTSS started in 1975, but 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 since 1978, and the area surveyed has been standardized since 1990 (Rugolo et al. 2006). BTSS follow a systematic sampling design, with sampling stations located at the nodes of a 20 × 20-nmi grid; additional sampling stations were located around the Pribilof and St. Matthew islands. Most sampling stations were occupied between June and July, although in some years the BTS started in May or ended in August. Near-bottom temperature (NBT) has been regularly recorded since the initiation of the survey program. The catch, or a subsample if the catch was too large, was sorted, and the components were identified to the lowest taxonomic level possible, counted, and weighed; fork length (FL) was measured from a representative subsample of each fish species. Several observations were recorded for each individual crab, including CW, SCI, and in the case of females, maturity.

STOMACH-CONTENT DATA.—Fish stomach-content data used in our study were provided by the Resource Ecology and Ecosystem Modeling Program, Alaska Fishery Science Center

(National Marine Fisheries Service). The sampling program started in 1984; stomach contents from major groundfish species were collected concurrently with the BTSs (Livingston 1989, Livingston et al. 1993, Lang et al. 2005). Additional samples were obtained from observers in commercial vessels (some data were collected by observers during 1981–1983, before the BTS sampling routine was implemented). Stomachs were removed at sea, labeled, preserved in 10% buffered formalin, and later transferred to 70% ethyl alcohol. Prey items were identified to the lowest taxonomic level possible, enumerated, weighed (blotted wet mass), and in the case of snow crab, measured to the nearest millimeter (Lang et al. 2005). Lang et al. (2005), on the basis of 5 yrs of data, estimated that Pacific cod accounts for at least 75% of the snow crab biomass removed by predatory fishes; other predatory fishes are flathead sole, *Hippoglossoides elassodon* Jordan and Gilbert, 1880, Alaska or walleye pollock, *Theragra chalcogramma* (Pallas, 1814), Pacific halibut, *Hippoglossus stenolepis* Schmidt, 1904, northern rock sole, *Lepidopsetta polyxystra* Orr and Matarese, 2000, skates (Rajidae), Alaska plaice, *Pleuronectes quadrituberculatus* Pallas, 1814, and yellowfin sole, *Limanda aspera* (Pallas, 1814). The number of Pacific cod stomachs collected per year ranged from 12 to 2730. No cod stomachs were collected in 2004 north of 57°N; that year was excluded from the analyses. The database contained information on 46,919 cod stomachs (as of December 2008). Of these, 6190 contained 14,679 snow crabs. The geographic range of the snow crab data used in the analyses was truncated (mile 150, defined below), excluding a few data outside the confirmed range of occurrence of immature stages; those specimens could correspond to misidentified immature individuals of Tanner crab, *Chionoecetes bairdi* M. J. Rathbun, 1924.

DATA AGGREGATION AND PROCESSING.—Data were parsed and analyzed and plotted by means of scripts in AWK stream editor (Robbins 2001), R statistical environment (R Development Core Team 2011), and standard MS-ACCESS database software. Spatial analysis was conducted with 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, accomplished by means of a near-neighbor algorithm.

The EBS shelf was partitioned in various ways: domains (Coastal, Middle, Outer) defined bathymetrically (Schumacher and Stabeno 1998) and transversal sections of the shelf (northwest, central, southeast; Fig. 1A). The region of interest was partitioned into 13 rectangular “quadrants” (Fig. 1B; Orensanz et al. 2007) for the purpose of aggregating information above the station level. To show variation in variables of interest (crab and cod abundance, cod consumption) in time and space, we aggregated survey data into slices orthogonal to a reference straight line running northwest–southeast along the main axis of the shelf (Fig. 1A); distances in nautical miles along the reference line were measured from its intersection 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.

ESTIMATION OF CRAB ABUNDANCE INDICES.—From survey data, indices of abundance in the Middle Domain of two categories of interest were estimated, analyzed, and mapped as described by Ernst et al. (2005). Categories of interest were immature females in the size range 35–50 mm (corresponding approximately to instars viii–ix) and primiparae. Catch per haul was used to estimate an abundance index (“density”) by swept-area methods (Sparre and Venema 1998). Average density by cell was estimated as

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

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_{it}^s is the number of crabs caught by haul i at station S in year t . Survey stations are at the centers of the 20×20 -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. In addition, some trawling experiments were occasionally conducted in some areas, increasing the number of hauls for particular stations. Density estimates by station and time were rendered into total abundance by grid cell (q), with a constant area expansion factor,

$$N_t^q = (20^2) \cdot D_t^s$$

We consider this value to be only an index of abundance because no correction for gear efficiency (see Somerton and Otto 1999) was used in the analysis. Geographic patterns of distribution of nonjuvenile snow crab, corresponding to spatial processes with an operating scale larger than the station grid of BTSs, are remarkably consistent (Ernst et al. 2005, 2012, Murphy et al. 2010, Parada et al. 2010). Spatial processes with an operating scale smaller than the mesh of the grid, best exemplified by reproductive aggregates, cannot be captured with the data available. The broad-scale patterns that we are interested in are not affected by reproductive aggregations that occur during March–May, concurrently with the multiparous mating season, which is over when the BTSs are conducted.

ESTIMATION OF COD ABUNDANCE INDICES.—Cod catch per unit of effort (CPUE) expressed in numbers and mass (kilograms caught per square kilometer swept), respectively n CPUE and w CPUE, was calculated as an index of abundance. The area-swept method described for the estimation of crab abundance indices was also used in the case of cod n CPUE and w CPUE. Given that prey preference and daily ration are size-dependent, size-specific estimates of Pacific cod abundance were required for estimation of a snow-crab consumption index. We used the size-frequency distribution of cod captured in the BTSs to partition the w CPUE of Pacific cod into 100-mm size classes. Given that the number of cod measured at each sampling station was not large enough to permit estimation of the relative abundance in every size class, we pooled all fish measured in each quadrant and used the resulting size distribution to partition w CPUE in each sampling station within the quadrant. The estimated mass CPUE from size class i at sampling station S and year t ($w\text{CPUE}_{it}^S$) was estimated as

$$w\text{CPUE}_{it}^S = w\text{CPUE}_t^S \cdot \frac{N_{i,q,t} \cdot w_i}{\sum_i (N_{i,q,t} \cdot w_i)} \cdot (2 - sel_i)$$

where $w\text{CPUE}_t^S$ is the mass CPUE at sampling station S and year t , $N_{i,q,t}$ is the number of cod of size class i collected at all stations within quadrant q (that includes sampling location S) in year t , w_i is the mean cod mass at size class i , and sel_i is the selectivity of the BTS for size class i . BTS selectivity was derived from the 2009 Pacific cod stock assessment (Thompson et al. 2009, table 2.22b). Mean cod mass at each size class i was calculated as

$$w_i = (5.774 \times 10^{-6} FL_i)^{3.165}$$

where FL_i is fish length (FL , in millimeters) at the center of interval i . Coefficients in this equation are from the 2008 Pacific cod stock assessment (model B1; Thompson et al. 2008).

ANALYSIS OF STOMACH-CONTENT DATA.—On the assumption that at least some fish over the entire size range of interest had full stomachs when sampled, the 99th quantile regression (Cade et al. 1999) between FL and stomach content mass (in grams; both on logarithmic scale) was considered to represent the relationship between FL and full stomach mass (FST). A stomach-fullness index was defined as the ratio between the observed stomach content mass and the calculated FST . Fish with fullness index $<0.1\%$ were considered to have empty stomachs. Two indices were used to examine the importance of snow crabs in the diet of

Pacific cod: Pw , defined as the ratio between the mass of snow crabs in the stomach and total stomach-content mass, and Pfw , defined as the ratio between the mass of snow crabs in the stomach and the estimated mass of the content of the full stomach. Following Chabot et al. (2008), we described the relationship between predator and prey sizes using quantile regressions at the 1%, 50%, and 99% quantiles.

In each of the cells described above, the average number of immature crabs (<35 mm CW) per cod stomach ($N_{35_t^s}$) was computed as

$$N_{35_t^s} = \frac{C_{35_t^s}}{St_t^s}$$

where $C_{35_t^s}$ is the total number of snow crabs <35 mm CW measured in stomachs sampled at station s in year t , and st_t^s is the total number of Pacific cod stomachs sampled at station s in year t . Data were split into size categories (described below) for some analyses.

INDEX OF CRAB CONSUMPTION.—An index of crab consumption by cod was calculated for all sampling locations for the period 1984–2005 ($n = 9583$ stations, between 354 and 376 stations yr^{-1}). The index, which has the general form of an estimate of daily consumption rate for the area represented by each sampling location, allowed integration of several pieces of size-specific information on cod: CPUE, an estimate of daily ration, the proportion of stomachs containing snow crab, and the proportion of snow crab in the those stomachs.

Number of cod in the six 100-mm size classes of focal interest (200–800 mm FL) ranged between 4283 and 8995. Because of the relatively low number of stomach samples from small (FL ≤ 200 mm, $n = 3294$) and large (FL > 800 mm, $n = 2679$) cod, data for those two size categories were combined with the adjacent intervals in the calculations of the proportion of stomachs with snow crabs and the proportion by mass of snow crab in the stomach contents. Total biomass of snow crab consumed per day by Pacific cod of size class i in the area represented by sampling station S during year t ($C_{i,t}^s$) was calculated as

$$C_{i,t}^s = DR_i \cdot wCPUE_{i,t}^s \cdot A_t^s \cdot Pc_{i,q,t} \cdot Pw_{i,q,t}$$

where DR_i is an estimate of daily ration of cod of size class i (expressed as a proportion of body mass), $wCPUE_{i,t}^s$ is the estimated $wCPUE$ from size class i at sampling station S and year t , A_t^s is the area represented by sampling location S at year t , $Pc_{i,q,t}$ is the proportion of stomachs of cod size class i at quadrant q (containing sampling location S) containing snow crabs, and $Pw_{i,q,t}$ is the proportion by mass of snow crab in the stomach contents of Pacific cod of size class i at quadrant q and year t (computed only from cod with snow crabs in their stomachs). We used the daily ration estimates used by the REFM (Resource Ecology & Fisheries Management) program (Lang et al. 2005), which were obtained by calculating daily growth in mass of cod of each size group from annual growth increments by length and from a length-mass relationship. Daily ration, defined as the amount of food required to produce the observed growth, was calculated on the assumption of a gross conversion efficiency of food to somatic tissue of 25% for adult fish and 10% for juvenile fish. Estimated daily rations, expressed as fraction of body mass, were 0.012, 0.009, and 0.007 for Pacific cod of, respectively, <300, 300–500, and >600 mm FL. These values match well laboratory-based estimates of 0.013–0.003 obtained by Paul et al. (1990). The area represented by sampling location S at year t (A_t^s) was calculated by means of a Voronoi tessellation (Okabe et al. 2000), which divided the survey area into tiles on the basis of the spatial proximity to the sampling locations (Fig. 1B). Locations within each tile were closer in space to that station than to any other station in the survey area. This approach was used to accommodate the two spatial resolutions of the bottom trawl survey (an overall 20×20 -nmi resolution and a higher resolution around the Pribilof and St. Matthew islands). Each tile in the periphery of the sampling area was assigned an area of 400 nmi^2 . The median area attributed to each station was 1352.75 km^2 , roughly 400 nmi^2 (range 526.08 – 4967.70 km^2).

The crab-consumption index was calculated as the total biomass of snow crab consumed at station S and year t (C_t^S) by all cod size classes:

$$C_t^S = \sum_i C_{t,i}^S$$

The index is basically a weighted form of cod CPUE that better reflects its significance from the viewpoint of crab consumption. Its use requires some caveats. First, the calculation applies only to the time interval in which the stomach samples were taken. We avoided expanding the results to calculate annual consumption. Second, crabs found in stomachs are assumed to have been eaten during the previous 24 hrs. This assumption would probably lead to overestimates of consumption because stomachs with moderate amounts of prey usually take longer to empty (Knutzen and Salvanes 1991). In addition, gastric evacuation takes longer for crustaceans than for fish items (Andersen 2001, Andersen and Beyer 2005). Finally, the index was not adjusted for temperature, although gastric evacuation increases with ambient temperature (Bromley 1994). These limitations do not affect the use of the index as such. We avoided its use in absolute terms, even when its form and dimensions are interpretable as estimates of daily crab consumption by cod.

The calculations described above are similar to those used by the REFM program to estimate consumption rate (Lang et al. 2005) but had a higher spatial resolution. In addition, we replaced the mean proportion of snow crab in all cod stomachs by the product of the proportion of stomachs containing crab and the mean proportion of snow crabs in stomachs containing crabs. This change is analogous to the use of the delta-gamma model to describe the stomach content of Atlantic cod proposed by Stéfanússon and Pálsson (1997). Their rationale was that the presence of a particular prey item in the stomachs and the actual amount (in number, mass, or proportion of total mass) of that prey item represent distinct processes: prey selection, determined in part by the spatial overlap between predator and prey, and prey consumption, determined partially by ease of capture of the prey and the predator's metabolic needs. In addition, and from a statistical point of view, the proportion of crabs in cod stomachs calculated from all stomachs has a skewed distribution for which the mean value is not the best descriptor. Our estimated index was in most cases somewhat larger than the corresponding daily consumption rate obtained by the REFM program (Lang et al. 2005). This difference can be attributed to the higher spatial resolution of our analysis, to our use of gear selectivity information to estimate cod biomass (smaller size classes prey more heavily on snow crab), and to the use of the two-step approach.

IMMATURE CRAB SURVIVAL INDEX.—To construct an index of survival of immature crab before they are detected by the BTSs, we fitted a linear relation between (1) average number of crabs in cod stomachs in size intervals 9–19 mm (instars ~iv–v) and 19–34 mm (instars ~vi–vii) and (2) abundance of immature females in BTSs surveys in the size interval 35–50 mm (instars ~viii–ix), with lags of 2 and 1 yrs, respectively. Residuals around the regression line correspond to the difference between the abundance of immature females (CW 35–50 mm) observed during the BTSs and the abundance expected from observations of cod stomach contents 1 or 2 yrs earlier. A negative index is an indicator of low survival before a year class of snow crab is first detected by the survey. Immigration of immature crabs from regions beyond the boundaries of the area surveyed by the BTSs is assumed to be negligible; this assumption is justified by the distances involved and the occurrence of long-range ontogenetic migrations only after terminal molt is reached (Ernst et al. 2005, Parada et al. 2010).

RESULTS

TRENDS AND PATTERNS OF COD ABUNDANCE.—In the Middle Domain and during the summer, Pacific cod were distributed in three very well-defined zones (referred to

below as “cod zones” or simply “zones” for brevity), separated approximately by miles 150 and 350 along the shelf axis (Fig. 2B,D). The southeastern cod zone (southeast of mile 150), adjacent to the Alaska Peninsula, was outside our geographical realm of interest (as defined by the range of distribution of immature snow crabs). The central zone (between miles 150 and 350) was centered around the Pribilof Islands, and the third cod zone (northwest of mile 350) was located around St. Matthew Island. In the Outer Domain, cod abundance during the summer was significant only in the northwestern section of the shelf (Fig. 2B).

Trends in abundance in the sectors of interest show some strong patterns. Abundance in the Middle Domain (Fig. 3B) was punctuated by pulses that to some extent parallel observed pulses of female snow-crab pseudocohort strength (Fig. 3A). Two pulses of cod abundance exactly match pulses III and IV of female crab pseudocohort strength, in both timing and relative strength, whereas an earlier pulse of cod abundance (1986) coincided with the end of a deep trough of female snow-crab pseudocohort strength (1984–1986), shortly before crab pulse II (1987–1988).

During the study period, relative summer distribution of cod among the zones of interest changed significantly. A rearrangement occurred during 1994–1995, as abundance (on average) declined in the northwestern part of the Outer Domain (Fig. 2A,B) and the Pribilof zone of the Middle Domain, while it increased in the St. Matthew zone of the Middle Domain (Fig. 2C,D).

Summer distribution of cod in the region of primary interest (Middle Domain, northwest of mile 150) is correlated with summer NBT (Fig. 4A), as revealed by significant correlation between time series of summer NBT in quadrant C (centered around St. Matthew Island) and the proportion of cod abundance observed in the St. Matthew zone (northwest of mile 350) relative to abundance in the region of interest (northwest of mile 150; Fig. 4C, $r^2 = 0.35$, $P < 0.01$.) Matching between the first-order difference of the two series was high (three sign mismatches out of 25 observations, Fig. 4B). In synthesis, this result means that proportionally more cod reach the St. Matthew zone when summer NBT is relatively high.

SIGNIFICANCE OF SNOW CRAB IN THE DIET OF PACIFIC COD.—The summer diet of Pacific cod in the EBS shifts in the course of ontogeny from being composed primarily by benthic invertebrates (hermit crabs, octopus, polychaetes and echiuran worms, king crab, etc.) and pandalid shrimp at small sizes to piscivory at large sizes; on average, fish prey add up to 50% of the stomach contents at an approximate size of 650 mm (FL; Fig. 5B). The amount of snow crab in the diet peaks at an approximate cod size of 550 mm (Fig. 5A), at which it constitutes 20% of the mass of the stomach content (Fig. 5B). The relative amount of snow crab in the diet decreases gradually toward large and small cod sizes (Fig. 5B). The average size of cod with snow crabs in their stomachs fluctuated within a narrow range (480–575 mm) between 1984 and 2000, increasing to 607–670 mm in 2006–2008 (Fig. 3C).

The estimated relationship between cod length (FL, cm) and the mass of the content of a full cod stomach (FST, Fig. 6) was

$$\log(FST) = -7.850 + 3.740 \cdot \log(FL)$$

Only 462 stomachs (1.23%) were empty. Snow crabs were found in 16.5% of nonempty stomachs. The average fraction contributed by snow crabs to stomach content mass

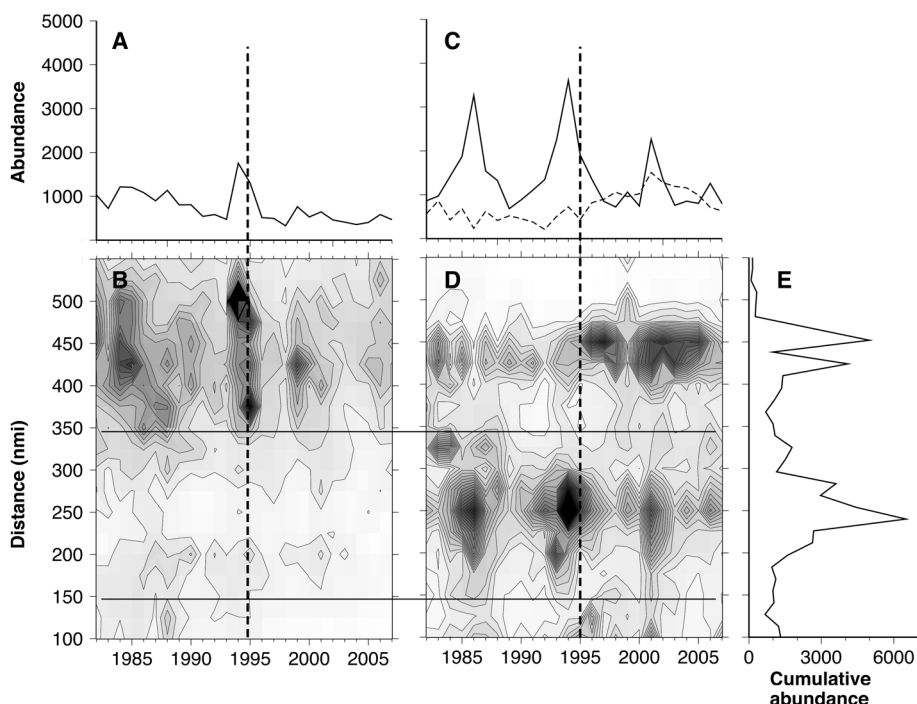


Figure 2. Pacific cod abundance (nCPUE, in number km^{-2}), 1982–2007. (A,B) Outer Domain; (C,D,E) Middle Domain. (A,C) Aggregated abundance; (B,D) abundance along the main axis of the shelf (see Fig. 1A); (E) abundance aggregated over the entire study period. Horizontal lines (miles 150 and 350) separate natural zones of cod distribution along the shelf; vertical lines highlight the 1995–1996 shifts in summer distribution.

fluctuated in the range of 4%–22% between 1984 and 2003 but was consistently lower in 2006–2008 (5%–6%, Fig. 3E), coincident with the indicated increase in the average size of crab-eating cod during those years. When Pacific cod preyed on snow crabs, their relative importance as prey could be high. In stomachs with at least one snow crab, ratio Pw ranged between 0.001 and 1 and was higher than 0.5 in 45.5% of the stomachs (Fig. 7A). The ratio Pfw ranged between 0.019 and 1; 95% of observations lay between 0.021 and 0.589 (Fig. 7B). The relationship between cod length (FL, mm) and ratio Pw was modeled with a LOESS smoothing fitted only to stomachs with snow crabs. The proportion of snow crab in cod stomachs containing crab was rather flat in relation to size (0.44 on average), peaking at 650 mm FL (0.5) and gradually decreasing for larger fish (0.4 at 1000 mm FL).

RELATIONSHIP BETWEEN PREY (CRAB) AND PREDATOR (COD) SIZE.—Size of captured cod ranged from 70 to 1400 mm, and size of crabs found in cod stomachs from 2 mm to 106 mm, although 95% ranged between 8 and 57 mm. Snow crabs <7 mm CW were rarely observed in stomachs ($n = 56$).

The median, minimum, and maximum sizes of ingested snow crab increased with Pacific cod size (Fig. 8B):

Median (50% quantile) CW = $0.073 \text{ FL} - 16.358$

Minimum (1% quantile) CW = $0.018 \text{ FL} - 2.282$

Maximum (99 % quantile) CW = $0.098 \text{ FL} + 8.461$

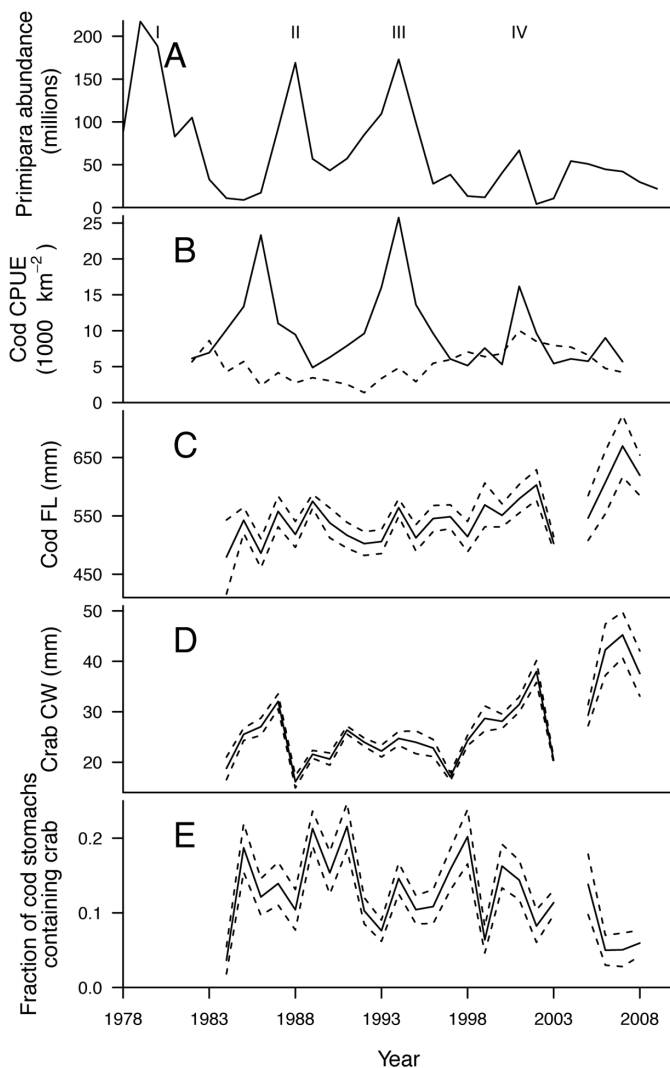


Figure 3. Time series of selected variables on interest in the Middle Domain northwest of mile 150 (see Fig. 2). (A) Female pseudocohort strength (estimated primipara abundance, in millions). (B) Cod abundance (mean nCPUE, in thousands km^{-2}). Solid line, southeastern zone; dashed line, central zone (see Fig. 2). (C) Average size of sampled cod with snow crab in the stomach content (fork length, FL). (D) Average size of snow crabs found in cod stomachs (carapace width, CW). (E) Fraction of stomach content mass corresponding to snow crab. In A, roman numerals indicate pulses of pseudocohort strength. In C–E the solid line corresponds to the mean, and the dashed lines bound the 95% confidence interval.

With the exception of the minimum and maximum intercepts, all parameters in the quantile regressions were highly significant ($P < 0.01$).

Most ingested snow crabs were in the size range corresponding to instars iv–viii, which correspond to the second to fourth years of benthic life (Fig. 8A). The average size of snow crabs in stomachs fluctuated between 19 and 32 mm between 1984 and 2001 (Fig. 3D), but was significantly higher during 2006–2008 (38–45 mm). Average size of crab prey and predatory cod were significantly cross-correlated ($R^2 = 0.63$, $P < 0.01$).

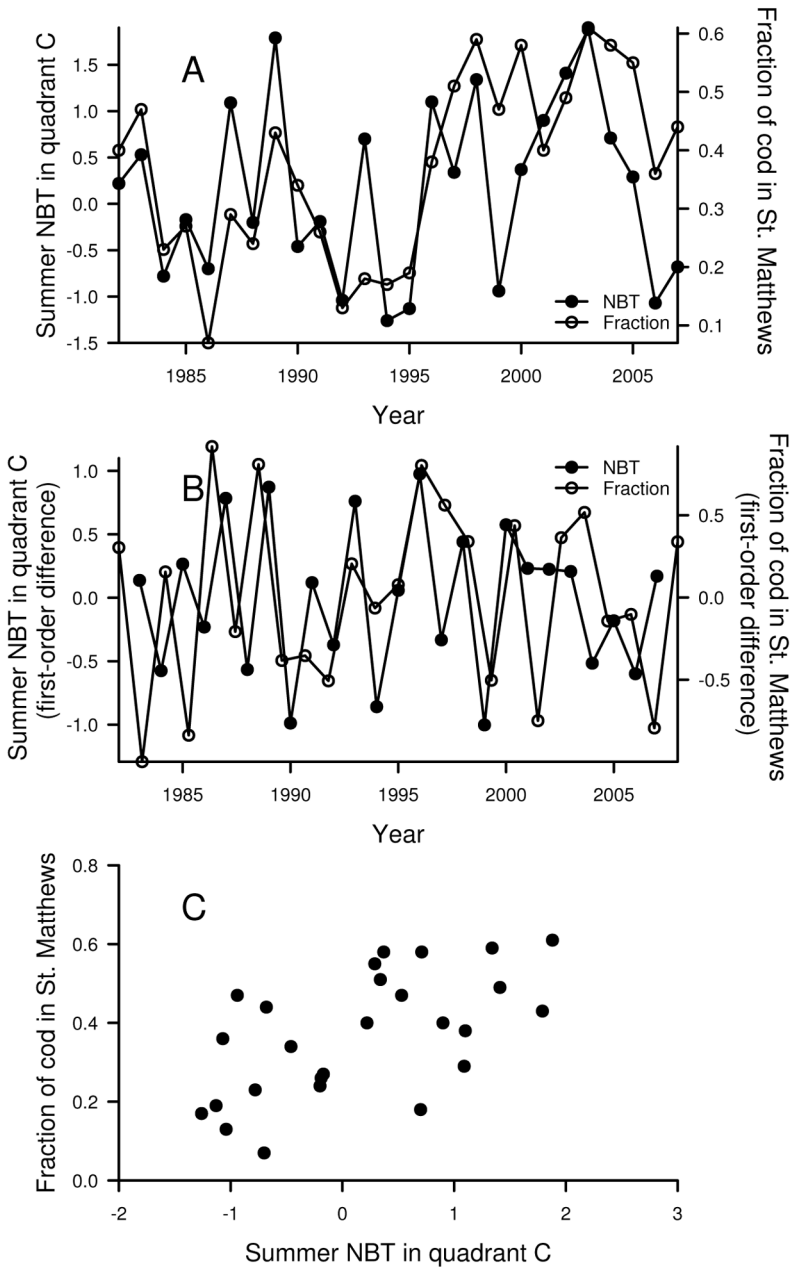


Figure 4. Relation between the summer distribution of cod in the Middle Domain of the eastern Bering Sea shelf (northwest of mile 150) and near-bottom temperature (NBT, expressed as average summer NBT in quadrant C, centered around St. Matthew Island). (A) Time series of NBT (solid line) and the fraction of cod observed in the St. Matthew zone (thin line). (B) Time series of the first-order difference between the two series shown in A (normalized). (C) Cross-correlation between the two series shown in A.

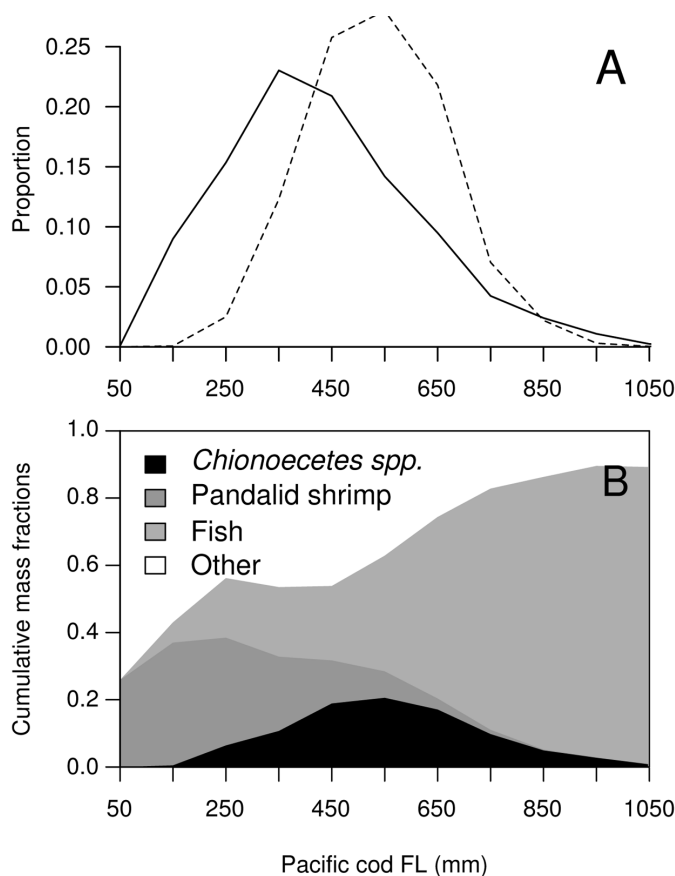


Figure 5. Cod size and diet composition (years pooled). (A) Size-frequency distributions of cod with (dashed line) and without (solid line) snow crabs in their stomachs. (B) Composition of stomach contents by major components (as cumulative fractions), in relation to cod size.

CONSUMPTION OF SNOW CRABS BY PACIFIC COD.—The distribution of daily consumption of snow crabs was highly skewed, with a mean of 138.29 kg d^{-1} per sampling station (75th quantile = 1116.2 kg d^{-1} , 95th quantile = $15,642.7 \text{ kg d}^{-1}$). Estimated consumption was zero at 3423 sampling stations, in most cases ($n = 3022$) because sampled cod stomachs contained no snow crabs. The temporal/spatial pattern of estimated crab consumption by cod (Fig. 9) generally mirrored cod abundance (Fig. 2), with the noticeable exception of the Middle Domain southeast of mile 150, which is outside the range of distribution of immature cod in the EBS. Aggregated consumption increased after 1994, coincidentally with the shift in the relative abundance of cod in the Pribilof and St. Matthew zones after 1995 (Fig. 4A). Consumption rate dropped sharply in the St. Matthew zone during the exceptionally cold summer of 1999. In 2006–2007 the consumption index dropped to historically low levels (Fig. 9C), because of an increase in the average size of cod (Fig. 3C) rather than greater cod abundance (Fig. 2C).

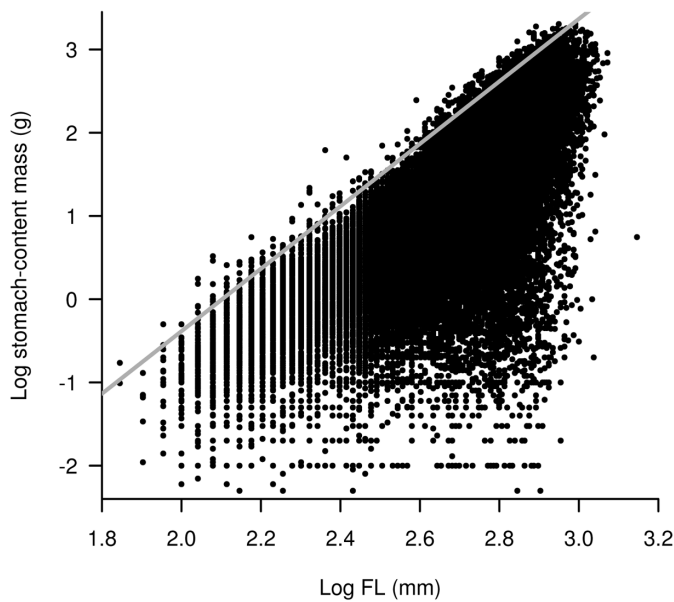


Figure 6. Relationship between cod size (FL) and total stomach content. The line indicates the 99th percentile regression assumed to represent the relationship between cod size and stomach-content mass when the stomach is full.

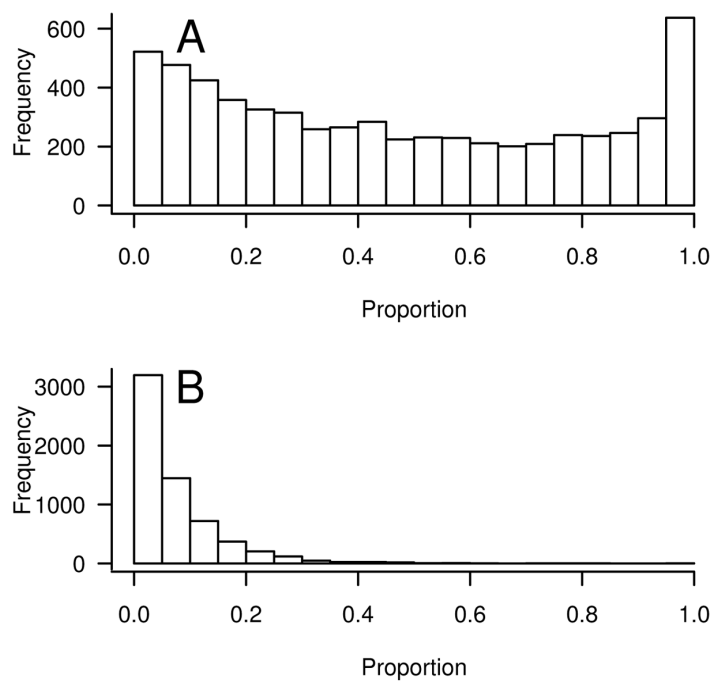


Figure 7. Importance of snow crab in the composition of crab-containing cod stomachs. (A) Distribution of the ratio between snow-crab mass and total stomach-content mass (P_w). (B) Distribution of the ratio between snow-crab mass and estimated full-stomach mass (P_{fw}).

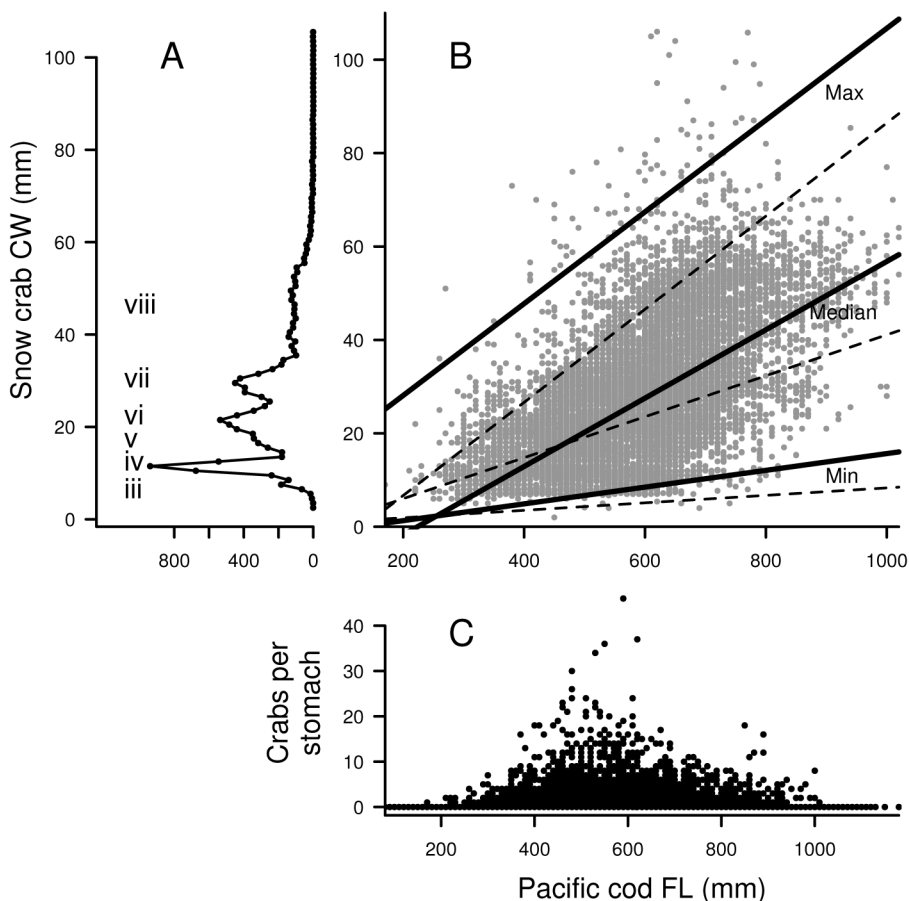


Figure 8. Number and size of snow crabs in cod stomach contents in relation to cod size. (A) Size-frequency distribution of crabs from stomach contents, indicating correspondence between modes and instars. (B) Relationship between cod size and crab size; solid lines indicate the estimated 1 (Min), 50 (Median), and 99 (Max) percentile quantile regressions; broken lines correspond to quantile regressions reported by Chabot et al. (2008, fig.2a using all data) for snow crabs ingested by Atlantic cod off eastern Canada. (C) Observations of number of crabs per stomach in relation to cod size.

TRENDS AND GEOGRAPHIC PATTERNS OF CRABS PER STOMACH.—The number of crabs in crab-containing stomachs ranged between 1 and 46, although 95% had 8 crabs or fewer (Fig. 8C); the highest values were recorded for cod in the size range 500–600 mm. Most cod with snow crab in their stomach contents were caught at stations where NBT was between -1.8 and 6°C (Fig. 10). Record numbers of crabs per stomach and highest frequencies of cod containing crab in their stomachs were observed at NBT ranging from 0 to 4°C .

Patterns of spatial/temporal distribution of the average number of crab per cod stomach were investigated separately for crab in the size intervals 9–19 mm (instars ~iv–v) and 19–34 mm (instars ~vi–vii; Fig. 11A, B). The aggregated trend for instars ~iv–v peaked in 1988–1989, 1997, and 2003 (Fig. 11A), 1–3 yrs after the peaks of pulses II–IV of primipara pseudocohort strength. The corresponding trend for instars ~vi–vii have peaks 1–2 yrs later, in 1991, 1998, and 2005 (Fig. 11B). In addition,

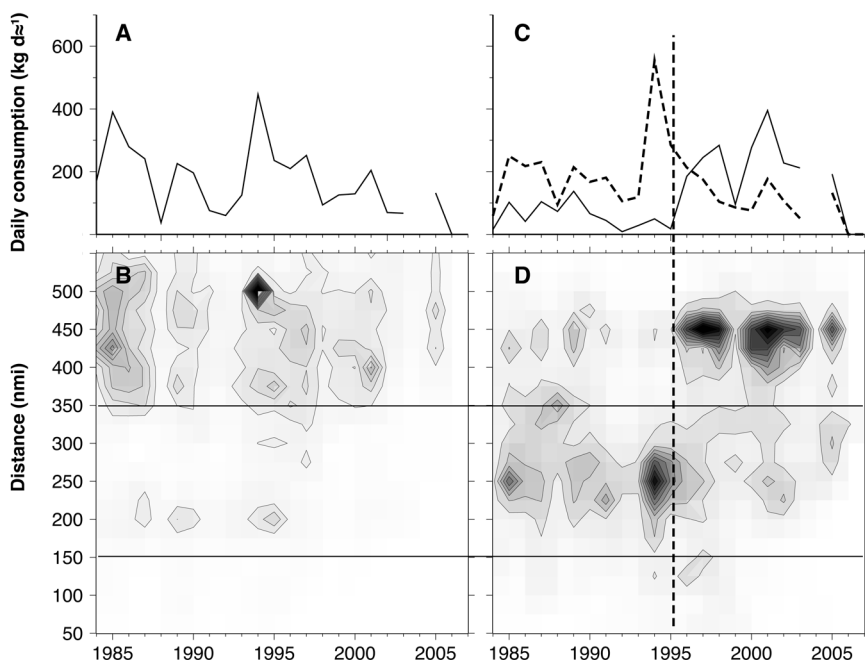


Figure 9. Daily consumption of snow crabs by Pacific cod in the Middle Domain, during the summer (kg d⁻¹), 1982–2007. (A,B) Outer Domain; (C,D) Middle Domain. (A,C) Aggregated consumption; (B,D) consumption along the main axis of the shelf (northwest to southeast, see Fig. 1A). Horizontal lines (miles 150 and 350) separate natural zones of cod distribution along the shelf; the vertical line highlights the 1995–1996 shift in summer daily consumption of snow crabs in the Middle Domain.

a peak that could not be tracked back developed in 1986 (Fig. 11B). The sequences could be tracked in the BTS-based indices of abundance of immature females in instars ~viii–x; aggregated peaks occurred in 1987, 1993, 2001, and 2004–2005 (Fig. 11C), the first three corresponding with pulses II–IV of pseudocohort strength (Fig. 11D). Abundance of immature females (instars ~viii–ix, Fig. 11C) in 2004–2005 could be tracked to a modest increase in primipara abundance in 2004–2006 (Fig. 11D). Peaks in the number of crabs per stomach corresponding to instars ~iv–v in 1997 and instars ~vi–vii in 1998 signal the early development of pulse IV. In both cases crabs were found in the stomachs of cod caught in all sections of the Middle Domain, whereas abundance of instars viii–ix in trawl samples from the 2000–2001 BTSs was low and confined to the northwestern sector of the shelf. The latter was also the case for the primiparae. A pulse of primipara abundance in the making is anticipated by the abundance of immature females observed during the 2009–2010 BTSs, so far circumscribed to the northwestern shelf (Fig. 11C). Unlike the other cases, this episode was not preceded by corresponding abundance of crab in cod stomachs during previous years.

INDEX OF CRAB SURVIVAL.—The most prominent feature in the time series of indices of crab survival between stages primarily eaten by cod (instars iv–viii) and those consistently detected by BTSs (instars ~viii–ix; Fig. 11C) is a transition from relatively high to low survival regimes in 1995–1996 (Fig. 12). A transient increase

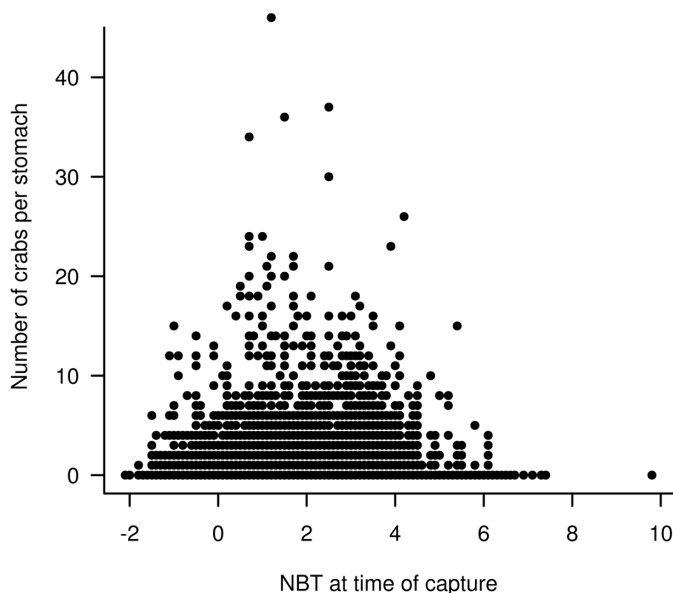


Figure 10. Number of snow crabs per cod stomach in relation to near-bottom temperature (NBT) at the moment of capture.

in the indices in 2000 may be related to relaxed predation on immature crab during the very cold summer of 1999, when consumption rate dropped sharply. Relative survival was also relatively low at the time when the stomach content sampling program started to be informative (1985–1986).

DISCUSSION

SIZE-DEPENDENT PATTERNS OF PACIFIC COD PREDATION ON SNOW CRAB.—Eastern Canada and the EBS are generally similar in composition and size spectrum of snow crabs in cod diets, but they differ in some consistent ways. Pacific cod from the EBS, like Atlantic cod (Link and Garrison 2002), experiences an ontogenetic shift in diet: small cod feed primarily on small benthic invertebrates, whereas large individuals are piscivorous (Livingston et al. 1993, Lang et al. 2005). Snow crab appears to be more common in the diet of Pacific cod from the EBS (where it adds up to 20% for some size classes) than in the Gulf of St. Lawrence Atlantic cod (where it never exceeds 10% for any size class, Chabot et al. 2008). Like those in the Gulf of St. Lawrence, cod <20 mm eat almost no snow crab in the EBS. Some cod in the size range 600–800 mm contained male crabs >90 mm CW (up to 106 mm) in their stomach contents, similar to a pattern observed in the Gulf of St. Lawrence. In the Gulf of St. Lawrence these large individuals corresponded to soft-shell (recently molted) large males, “compacted into a pliable ball in the stomach” (Robichaud et al. 1991, p. 671). This was probably also the case in the EBS, but shell condition was not recorded for crabs from stomach contents. Large males molt during the summer in the Middle Domain of the EBS, making their occurrence likely in samples of cod stomach contents collected in the course of the summer BTSS.

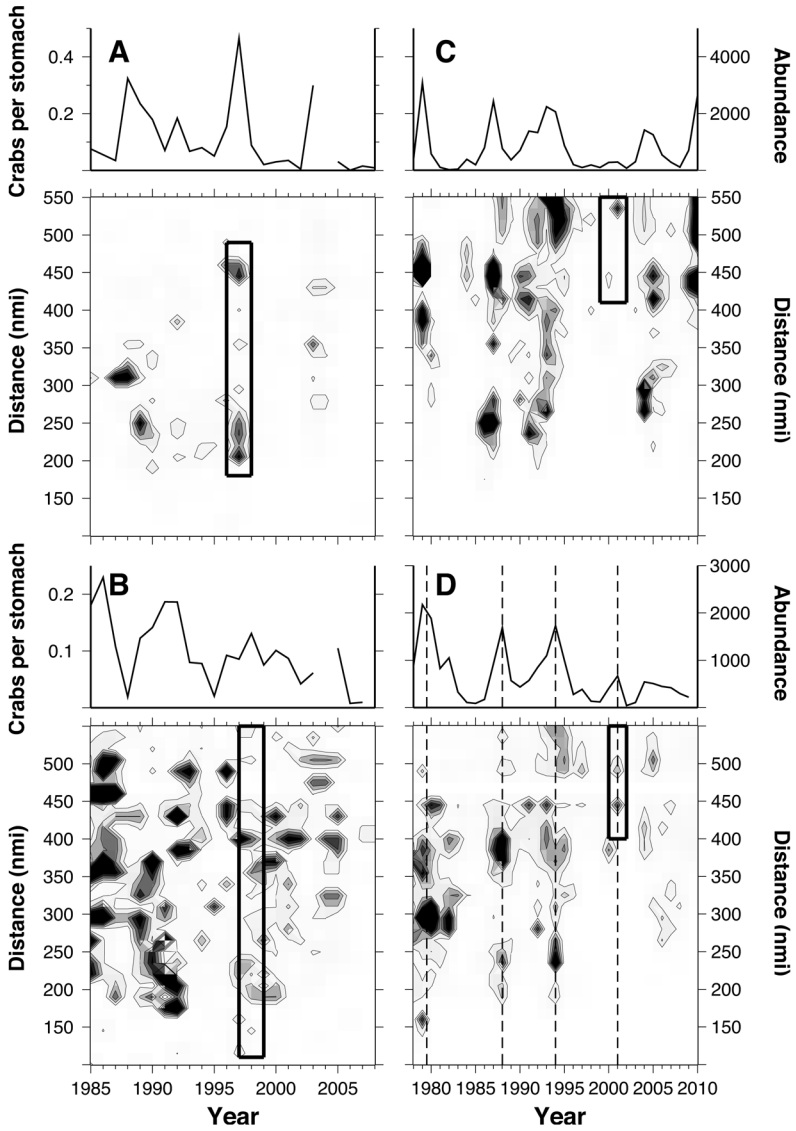


Figure 11. Tracking the development of pulses of snow crab pseudocohort strength (primipara abundance) through cod-stomach and trawl-survey samples. (A,B) average number of snow crabs per cod stomach for crab size in, respectively, size ranges 9–19 mm (instars ~iv–v) and 19–34 mm (instars ~vi–vii). (C,D) abundance in trawl survey samples of, respectively, immature females in the range 35–50 mm (instars ~viii–ix) and primiparae. In each case the top element shows the trend in the aggregated variable, and the bottom element the distribution along the main axis of the shelf (northwest to southeast; see Fig. 1A), over the period of interest. Vertical lines in D: core years of Pulses I–IV. Rectangles highlight the development of Pulse IV.

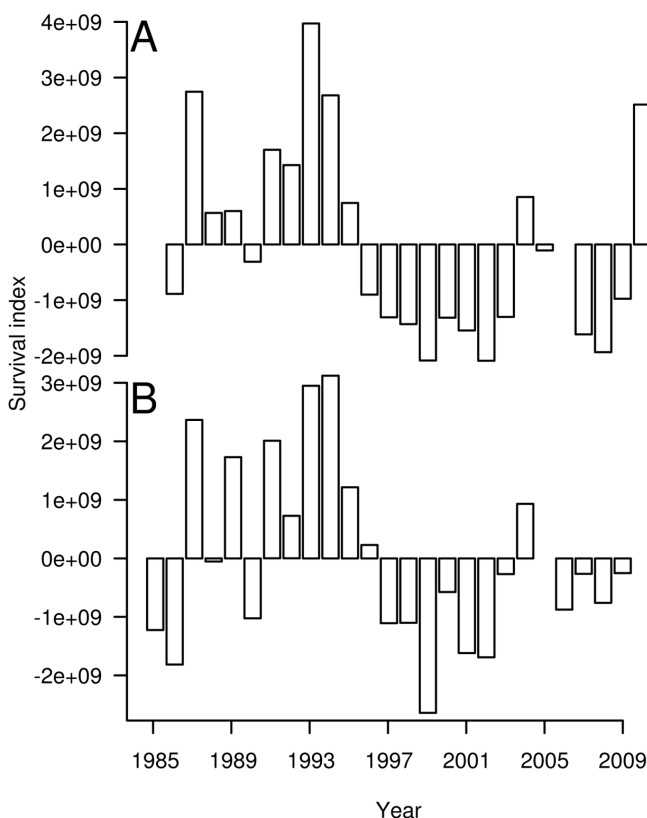


Figure 12. Trends in snow-crab survival index between observation in cod stomach contents and detection (35–50 mm immature females) in trawl samples, based on crabs from stomach contents in size ranges (A) 9–19 mm and (B) 19–39 mm. Time lags between stomach-content and trawl-sample observations are, respectively, 2 and 1 yrs.

Comparison (with the same statistical technique) of snow-crab size distribution in cod diet conditioned on cod size showed that, for any given predator size, Pacific cod from the EBS eat significantly larger snow crabs than Atlantic cod from the Gulf of St. Lawrence (as reflected by the 99%, median, and 1% quantile regressions). This pattern is best seen in the number of snow crabs in stomachs of Pacific cod from the EBS that are above the 99% quantile regression line estimated by Chabot et al. (2008) for Atlantic cod. Consistently, the cod size range over which importance of crabs in cod diet is highest was lower in Pacific cod from the EBS (500–600 mm) than in Atlantic cod from the Gulf of St. Lawrence (700–800 mm, Chabot et al. 2008).

An interspecific comparative study of the relation between size-specific mouth gap in cod and size of snow crabs in the diet (along the lines of the inquiry by Chabot et al. 2008) would be interesting from the viewpoint of the evolution of these analogous predator-prey systems and relevant to understanding of the effects of cod predation on snow-crab population dynamics. The spectrum of snow-crab instars preyed upon by Pacific cod in the EBS (primarily instars iv–vii) is comparable to that of Atlantic cod in the northern Gulf of St. Lawrence (primarily instars iii–vi; Chabot et al. 2008). This pattern is obviously related to the size-dependence of cod predation (discussed above), but given that snow crab populations of the central shelf of the EBS and the

northern Gulf of St. Lawrence are remarkably similar in life history (Ernst et al. 2005, 2012), cod predation in the latter is likely to occur at an earlier average age than in the EBS.

TEMPORAL AND GEOGRAPHIC VARIATION IN COD PREDATION ON SNOW CRAB.—Coincidental changes appear to have occurred in the Middle Domain between 1994 and 1995. As indicated by previous studies (Parada et al. 2010, p. 433, Ernst et al. 2012), the primiparae gradually disappeared from the central and southeastern sectors of the shelf after 1995, except for a modest patch detected north of the Pribilof Islands in 2006–2008. The disappearance of primiparae from the southeast-central shelf for more than a decade was reflected in the low strength of pulse IV. Confined to the northwestern sector of the EBS shelf, this pulse was the last and weakest of a sequence of pulses of pseudocohort strength occurring with an average frequency of 7 yrs between 1978 and 2003 (Ernst et al. 2012). In 1994–1995, a major rearrangement took place in the summer distribution of cod, which shifted from the Pribilof to the St. Matthew zone along the Middle Domain northwest of mile 150, the region of interest, and from the Outer to the Middle Domain in the northwestern section of the shelf. Coincidentally with the range contraction of the primiparae and shifts in cod distribution, the cod consumption index of snow crab increased after 1995 in the northwestern section of the shelf, remaining high through 2005. Starting in 1996, the abundance of immature females (CW 35–50, instars ~viii–ix) observed during the summer surveys was lower than that expected from the observed occurrences of immature crabs in cod stomach contents 2 and 1 yrs earlier (respectively, instars ~iv–v and ~vi–vii). This is the basis for the calculation of the immature crab survival index, which was below average from 1995–1996 through 2003, implying that immature survival (between the 2nd/3rd and 4th/5th calendar years of postsettlement life) was low during the period 1994–2002.

Events occurring after 1994–1995, including the rearrangement of cod distribution, increased cod consumption of snow crabs in the northwestern section and decrease in the central section of the shelf, disappearance of primiparae from the central and southeastern sections, and negative indices of immature crab survival, were likely to be sequentially and causally related to each other. This sequence may be controlled by year-to-year variation in the summer near-bottom thermal regime. On the basis of analysis of 3 yrs of cod stomach-content data (1981, 1984, 1985), Livingston (1989) suggested that the geographic distribution of young snow crab in cod stomach contents was related to the maximum extent of winter ice cover, which in turn was correlated with the extension of the cold pool during the following summer. Synchronous variation in the latitudinal component of the centroids of cod CPUE, abundance of immature snow crab females in BTSs, and an index of cod predation during the 11-yr period 1991–2001 prompted Orensanz et al. (2004) to hypothesize that cod predation on juveniles is one factor controlling the range of immature females. They concluded that “during warm years the centroid of cod abundance moves northward, the amount of snow crab in cod diet is amplified as cod make a deeper dent into the snow crab’s range, and the geographic range of juvenile/immature snow crab contracts accordingly, owing to predation.” The work reported here confirmed that northward expansions of cod foraging areas in the Middle Domain during the summer are related to NBT and that cod predation (as captured

by the number of crab per stomach) tracks pulses of recruitment. Crab consumption generally tracked cod abundance, even as crab abundance declined after 1995.

A strong pulse of immature female abundance (instars ~viii–ix) observed during the 2009–2010 BTSs on the northwestern shelf was not preceded by a corresponding abundance of small crabs (instars ~iv–vii) in cod stomachs during 2006–2008. During those years, which correspond to a return of the EBS to cool conditions (Zador and Gaichas 2010), the index of crab consumption by cod declined to historically low levels. This phenomenon was due to declining cod abundance on the northwest shelf and increasing average size of cod, which resulted in a sharp drop in the fraction of cod stomachs containing crab, an increase in the average size of crabs eaten by cod, and a high survival index of immature crab in 2010.

COD PREDATION, RANGE CONTRACTION OF SNOW CRAB PRIMIPARAE, AND THE DEMISE OF PERIODIC PSEUDOCOHORT STRENGTH.—Pulses of snow-crab pseudocohort strength in the Middle Domain of the EBS may be serially linked to each other; members of one pulse may be the maternal stock of the next (Parada et al. 2010, p. 433, Ernst et al. 2012). Although we focus here on the dynamics of females, cycles of abundance were mirrored by the male population (Parada et al. 2010). These dynamics represent a case of cohort resonance (Botsford et al. 2011), manifested in its simplest and clearest form in some semelparous populations (see e.g., Myers et al. 1998). The snow-crab stock of the EBS would de facto be quasi-semelparous if, as has been argued, the primiparae were the main contributors to the renewal of the stock (Ernst et al. 2012). Cohort resonance may explain periodicity of pseudocohort strength over three decades (1975–2005), but not the virtual demise of the last pulse in the series (pulse IV). Evidence presented here supports the hypothesis that this phenomenon was the result of increased cod predation in the Middle Domain after 1994, while pulse IV was developing. The core year of pulse III (presumed maternal stock of pulse IV) was 1994. Under annual brooding mode, expected in the central/southeastern sections of the shelf except for eggs hatched during very cold winters (Ernst et al. 2008), their progeny (on average) is expected to have hatched, gone through pelagic larval stages, and settled (molting from megalopa to instar i) around 1995. Most of them probably went through benthic instars ii–iii (infrequent in cod stomach contents) in 1996, instars iv–v in 1997, instars vi–vii in 1998–1999, and instars viii–ix in 2000–2001; the abundance of primiparae peaked in 2001. This expected sequence of life-history events could be effectively tracked and confirmed through cod stomach-content and trawl samples. Occurrence of instars iv–vii in cod stomachs between 1997 and 1999 was high and spread over the entire Middle Domain, whereas abundance of instars viii–ix in trawl samples from the 2000–2001 BTSs was low and confined to the northwestern sector of the shelf. The latter was also the case for the primiparae. The contrast was well captured by the period of low immature crab survival starting in 1995–1996 and extending through 2003, which encompassed the period during which members of pulse IV were most exposed to cod predation. Cod predation on juvenile crabs did not appear to drive observed periodicity in the recruitment of snow crab but did contribute to controlling the southward spread of the range of immature stages over the Middle Domain. This conclusion is consistent with one of the tenets of the ERH (Orensanz et al. 2004).

The nature of the interaction between climate and predation in the regulation of snow-crab abundance has been examined with a variety of approaches. The

correlation among aggregated time series led to the conclusion that snow-crab abundance in eastern Canada is largely influenced by temperature during the early post-settlement years, becoming increasingly regulated by cod predation during the years approaching recruitment to the fishery (Boudreau et al. 2011). The latter was supported by the observation that the negative relationship between Atlantic cod and snow crab in commercial landings was strongest at relatively short lags, between 0 and 5 yrs; cod led snow crab. This mechanism could not possibly apply in the case of the EBS, where Pacific cod preys primarily on small snow crabs (instars iv–vii). Our results and conclusions are, in this sense, very similar to those of Chabot et al. (2008) for Atlantic cod predation on snow crabs in the Gulf of St Lawrence. Significant predation by Atlantic cod on larger snow crabs off eastern Canada may have gone undetected because of limitations of data relative to the spatial behavior of cod and crab (Boudreau et al. 2011). Such a failure of detection would be unlikely in the case of the EBS, where results are based on 25 yrs of extensive summer surveys of cod and snow-crab abundance and cod stomach contents and NBT covering most of the shelf, complemented by observer samples collected at other times of the year. Interaction between climate and predation, exemplified here by the cod-mediated effect of NBT on snow-crab recruitment, cannot be understood without attention to the spatial dimension of the processes of interest, i.e., to “seascapes” as defined by Cianelli and Bailey (2005) in their study of cod predation on capelin in the EBS. Correlations among highly aggregated variables are unlikely to reveal the mechanisms underlying observed patterns of covariation.

Alternation of warming (2001–2005) and cooling (2006–2010) periods during recent years (Stabeno et al. 2007, Zador and Gaichas 2010, fig. 22) offers an exceptional opportunity to explore the interaction of climate and predation as controls on snow-crab recruitment. We hypothesize that a persistent return of an expanded cold pool over the Middle Domain resulted in relaxation of cod predation, which in turn contributed to the abundance of immature females observed during the 2009–2010 BTSs.

ACKNOWLEDGMENTS

This study was supported by North Pacific Research Board (NPRB) projects 508 and 624. Assistance from C Eischens and F Wiese during all stages of its execution is acknowledged. C Armistead, R Foy, and L Rugolo (NMFS, Kodiak) made every possible effort to satisfy our requests for survey data. P Livingston, K Aydin, and G Lang (AFSC/NMFS, Seattle) made cod stomach-content data available. R Lauth (AFSC/NMFS, Seattle) provided cod length data. L Botsford (UC Davis) brought to our attention the concept of cohort resonance. Two anonymous reviewers provided criticism that contributed significantly to improvement of the manuscript; thorough editing by AB Thistle is also greatly appreciated. Finally, support received from our home institutions is acknowledged by all of us.

LITERATURE CITED

Andersen NG. 2001. A gastric evacuation model for three predatory gadoids and implications of using pooled field data of stomach contents to estimate food rations. *J Fish Biol.* 59:1198–1217. <http://dx.doi.org/10.1111/j.1095-8649.2001.tb00186.x>

- Andersen NG, Beyer JE. 2005. Gastric evacuation of mixed stomach contents in predatory gadoids: an expanded application of the square root model to estimate food rations. *J Fish Biol.* 67:1413–1433. <http://dx.doi.org/10.1111/j.0022-1112.2005.00835.x>
- Botsford LW, Holland MD, Samhouri JF, White JW, Hastings A. 2011. Importance of age structure in models of the response of upper trophic levels to fishing and climate change. *ICES J Mar Sci.* 68:1270–1283. <http://dx.doi.org/10.1093/icesjms/fsr042>
- Boudreau SA, Anderson SC, Worm B. 2011. Top-down interactions and temperature control of snow crab abundance in the northwest Atlantic Ocean. *Mar Ecol Prog Ser.* 429:169–183. <http://dx.doi.org/10.3354/meps09081>
- Bromley PJ. 1994. The role of gastric evacuation experiments in quantifying the feeding rates of predatory fish. *Rev Fish Biol Fish.* 4:36–66. <http://dx.doi.org/10.1007/BF00043260>
- Cade BS, Terrell JW, Schroeder RL. 1999. Estimating effects of limiting factors with regression quantiles. *Ecology.* 80:311–323. [http://dx.doi.org/10.1890/0012-9658\(1999\)080\[0311:EEO LFW\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(1999)080[0311:EEO LFW]2.0.CO;2)
- Chabot D, Sainte-Marie B, Briand K, Hanson JM. 2008. Atlantic cod and snow crab predator–prey size relationship in the Gulf of St. Lawrence, Canada. *Mar Ecol Prog Ser.* 363:227–240. <http://dx.doi.org/10.3354/meps07384>
- Ciannelli L, Bailey KM. 2005. Landscape dynamics and resulting species interactions: the cod–capelin system in the southeastern Bering Sea. *Mar Ecol Prog Ser.* 291:227–236. <http://dx.doi.org/10.3354/meps291227>
- Comeau M, Conan GY, Maynou F, Robichaud G, Therriault JC, Starr M. 1998. Growth, spatial distribution, and abundance of benthic stages of the snow crab (*Chionoecetes opilio*) in Bonne Bay, Newfoundland, Canada. *Can J Fish Aquat Sci.* 55:262–279. <http://dx.doi.org/10.1139/f97-255>
- Dionne M, Sainte-Marie B, Bourget E, Gilbert D. 2003. Distribution and habitat selection of early benthic stages of snow crab *Chionoecetes opilio*. *Mar Ecol Prog Ser.* 259:117–128. <http://dx.doi.org/10.3354/meps259117>
- Ernst B, Armstrong DA, Burgos J, Orensanz JM. 2012. Cyclic recruitment and the life history schedule of female snow crab (*Chionoecetes opilio*) in the eastern Bering Sea. *Can J Fish Aquat Sci.* 69:532–550. <http://dx.doi.org/10.1139/f2011-173>
- Ernst B, Orensanz JM, Armstrong DA. 2005. Spatial dynamics of female snow crab (*Chionoecetes opilio*) in the eastern Bering Sea. *Can J Fish Aquat Sci.* 62:250–268. <http://dx.doi.org/10.1139/f04-201>
- Ernst B, Orensanz JM, Armstrong DA. 2008. Trends and patterns in the reproductive contribution of female snow crab (*Chionoecetes opilio*) from the eastern Bering Sea. In: Orensanz JM, Ernst B, Armstrong DA, Burgos J, editors. Female effective reproductive output of the snow crab stock in the eastern Bering Sea. North Pacific Research Board, Project 508 Final Report. Anchorage (Alaska). p. 52–92. Available from: <http://project.nprb.org/view.jsp?id=c1078c9b-3458-4a29-8d21-3430c2eb34b0>. Accessed 25 June, 2011.
- Frank KT, Petrie B, Choi JS, Leggett WC. 2005. Trophic cascades in a formerly cod-dominated ecosystem. *Science.* 308:1621–1623. PMID:15947186. <http://dx.doi.org/10.1126/science.1113075>
- Hunt Jr GL, Allen BM, Angliss RP, Baker T, Bond N, Buck G, Byrd GV, Coyle KO, Devol A, Eggers DM, et al. 2010. Bering Sea. In: McKinnell SM, Dagg MJ, editors. Marine ecosystems of the North Pacific Ocean, 2003–2008. PICES Special Publication 4. Sidney (BC, Canada), North Pacific Marine Science Organization. p. 196–267.
- Knutzen I, Salvanes AGV. 1991. Temperature-dependent digestion handling time in juvenile cod and possible consequences for prey choice. *Mar Ecol Progr Ser.* 181:61–79. <http://dx.doi.org/10.3354/meps181061>
- Lang GM, Livingston PA, Dodd KA. 2005. Groundfish food habits and predation on commercially important prey species in the eastern Bering Sea from 1997 through 2001. NOAA Technical Memorandum (NMFS-AFSC) 158. National Marine Fisheries Service, Seattle.

- Link JS, Bogstad B, Sparholt H, Lilly GR. 2009. Trophic role of Atlantic cod in the ecosystem. *Fish Fish.* 10:58–87. <http://dx.doi.org/10.1111/j.1467-2979.2008.00295.x>
- Link JS, Garrison LP. 2002. Trophic ecology of Atlantic cod *Gadus morhua* on the northeast US continental shelf. *Mar Ecol Prog Ser.* 227:109–123. <http://dx.doi.org/10.3354/meps227109>
- Livingston PA. 1989. Interannual trends in Pacific cod, *Gadus macrocephalus*, predation on three commercially important crab species in the eastern Bering Sea. *Fish Bull US.* 87:807–827.
- Livingston PA, Ward A, Lang GM Yang M. 1993. Groundfish food habits and predation on commercially important prey species in the eastern Bering Sea from 1987 to 1989. NOAA Technical Memorandum (NMFS-AFSC) 11. National Marine Fisheries Service, Seattle.
- Murphy JT, Hollowed AB, Anderson JJ. 2010. Snow crab spatial distributions: examination of density-dependent and independent processes. *In:* Kruse GH, Eckert GL, Foy RJ, Lipcius RN, Sainte-Marie B, Stram DL, Woodby D, editors. *Biology and management of exploited crab populations under climate change.* Alaska Sea Grant, University of Alaska Fairbanks. p. 49–79.
- Myers RA, Mertz G, Bridson JM, Bradford MJ. 1998. Simple dynamics underlie sockeye salmon (*Oncorhynchus nerka*) cycles. *Can J Fish Aquat Sci.* 55:2355–2364. <http://dx.doi.org/10.1139/f98-059>
- NPFMC (North Pacific Fishery Management Council). 2010. Stock assessment and fishery evaluation (SAFE) report for the king and Tanner crab fisheries of the Bering Sea and Aleutian Islands Regions. Anchorage (Alaska). Available from: <http://www.fakr.noaa.gov/npfmc/PDFdocuments/resources/SAFE/CrabSAFE/CRABSAFE2010.pdf>. Accessed 25 June, 2011.
- Okabe A, Boots B, Sugihara K. 2000. *Spatial tessellations: concepts and applications of Voronoi Diagrams*, 2nd ed. New York: Wiley.
- Orensanz JM, Ernst B, Armstrong DA. 2007. Variation of female size- and stage-at-maturity in snow crab (*Chionoecetes opilio*) (Brachyura: Majidae) from the eastern Bering Sea. *J Crust Biol.* 27:576–591. <http://dx.doi.org/10.1651/S-2790.1>
- Orensanz J, Ernst B, Armstrong DA, Stabeno P, Livingston P. 2004. Contraction of the geographic range of distribution of snow crab (*Chionoecetes opilio*) in the eastern Bering Sea: an environmental ratchet? *CalCOFI Rep.* 45:67–79.
- Parada C, Armstrong DA, Ernst B, Hincley S, Orensanz, JM. 2010. Spatial dynamics of snow crab (*Chionoecetes opilio*) in the eastern Bering Sea—putting together the pieces of the puzzle. *Bull Mar Sci.* 86:413–437.
- Paul AJ, Paul JM, Smith RL. 1990. Consumption, growth and evacuation in the Pacific cod, *Gadus macrocephalus*. *J Fish Biol.* 37:117–124. <http://dx.doi.org/10.1111/j.1095-8649.1990.tb05933.x>
- R Development Core Team. 2011. R: a language and environment for statistical computing. Foundation for Statistical Computing, Vienna, Austria. Available from: <http://www.R-project.org>. Accessed 10 November, 2011.
- Robbins A. 2001. *Effective AWK programming*, 3rd ed. Sebastopol, California. O'Reilly & Associates.
- Robichaud DA, Elnor RW, Bailey RFJ. 1991. Differential selection of crab *Chionoecetes opilio* and *Hyas* spp. as prey by sympatric cod *Gadus morhua* and thorny skate *Raja radiata*. *Fish Bull US.* 89:669–680.
- Rugolo LJ, Chilton EA, Armistead CA, Haaga JA. 2006. Report to industry on the 2006 Eastern Bering Sea crab survey. AFSC Processed Report 2006-17. Alaska Fisheries Science Center, National Marine Fisheries Service, Kodiak, Alaska. Available from: <http://www.afsc.noaa.gov/publications/ProcRpt/PR%202006-17.pdf>. Accessed 26 November, 2010.
- Sainte-Marie B, Gosselin I, Sévigny JM, Urbani N. 2008. The snow crab mating system: opportunity for natural and unnatural selection in a changing environment. *Bull Mar Sci.* 83:131–161.
- Schumacher JD, Stabeno PJ. 1998. Continental shelf of the Bering Sea coastal segment. *In:* Robinson AR, Brink KH, editors. *The sea*, vol. 11. New York: John Wiley & Sons. p. 789–822.

- Somerton DA, Otto RS. 1999. Net efficiency of a survey trawl for snow crab, *Chionoecetes opilio*, and Tanner crab, *C. bairdi*. Fish Bull US. 97:617–625.
- Sparre P, Venema SC. 1998. Introduction to tropical fish stock assessment. Part 1. Manual. FAO Fish Tech Paper 306/1, Rev. 2.
- Stabeno PJ, Bond NA, Salo SA. 2007. On the recent warming of the southeastern Bering Sea shelf. Deep-Sea Res II. 54:2599–2618. <http://dx.doi.org/10.1016/j.dsr2.2007.08.023>
- Stefánsson G, Pálsson OK. 1997. Statistical evaluation and modeling of the stomach contents of Icelandic cod (*Gadus morhua*). Can J Fish Aquat Sci. 54:169–181. <http://dx.doi.org/10.1139/f96-246>
- Thompson GG, Ianelli JN, Lauth RL, Gaichas S, Aydin K. 2008. Assessment of the Pacific cod stock in the Eastern Bering Sea and Aleutian Islands area. In: Plan Team for Groundfish Fisheries of the Bering Sea/Aleutian Islands, compiler. Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions. Anchorage, Alaska: North Pacific Fishery Management Council. p. 221–401.
- Thompson GG, Ianelli JN, Lauth RL. 2009. Assessment of the Pacific cod stock in the Eastern Bering Sea and Aleutian Islands area. In: Plan Team for Groundfish Fisheries of the Bering Sea/Aleutian Islands, compiler. Stock assessment and fishery evaluation report for the groundfish resources of the Bering Sea/Aleutian Islands regions. Anchorage, Alaska: North Pacific Fishery Management Council. p. 235–439.
- Wessel P, Smith WHF. 1998. New, improved version of Generic Mapping Tools released. EOS Trans Am Geophys Union. 79:579. <http://dx.doi.org/10.1029/98EO00426>
- Worm B, Myers RA. 2003. Meta-analysis of cod-shrimp interactions reveals top-down control in ocean food webs. Ecology. 84:162–173. [http://dx.doi.org/10.1890/0012-9658\(2003\)084\[0162:MAOCSI\]2.0.CO;2](http://dx.doi.org/10.1890/0012-9658(2003)084[0162:MAOCSI]2.0.CO;2)
- Wyllie-Echeverria T, Wooster WS. 1998. Year-to-year variations in Bering Sea ice cover and some consequences for fish distributions. Fish Oceanogr. 7:159–170. <http://dx.doi.org/10.1046/j.1365-2419.1998.00058.x>
- Zador S, Gaichas S, editors. 2010. Ecosystem considerations for 2011, Appendix C. Anchorage, Alaska: North Pacific Fisheries Management Council. Available from: <http://access.afsc.noaa.gov/reem/ecoweb/Eco2010.pdf>. Accessed 26 November, 2010.
- Zheng J, Kruse GH. 2006. Recruitment variation of eastern Bering Sea crabs: climate-forcing or top-down effects? Prog Oceanogr. 68:184–204. <http://dx.doi.org/10.1016/j.pocean.2006.02.002>

DATE SUBMITTED: 28 November, 2011.

DATE ACCEPTED: 19 June, 2012.

AVAILABLE ONLINE: 8 October, 2012.

ADDRESSES: (JB) Marine Research Institute, Skúlagata 4, 121 Reykjavík, Iceland. (BE) Departamento de Oceanografía, Universidad de Concepción, Concepción, Chile. (DAA) School of Aquatic and Fishery Sciences, University of Washington, Seattle, Washington 98195. (JMO) Centro Nacional Patagónico, 9120 Puerto Madryn, Argentina. CORRESPONDING AUTHOR: (JB) Email: <julian@hafro.is>.

