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Top-down vs. bottom-up drivers of recruitment in a key marine invertebrate: investigating early life stages of snow crab

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Many snow crab fisheries have fluctuated widely over time in a quasi-cyclic way due to highly variable recruitment. The causes of this variability are still debated. Bottom-up processes related to climate variability may strongly affect growth and survival during early life, whereas top-down predator effects may be a major source of juvenile mortality. Moreover, intrinsic density-dependent processes, which have received much less attention, are hypothetically responsible for the cycles in recruitment. This study explored how climate, larval production, intercohort cannibalism and groundfish predation may have affected recruitment of early juvenile snow crab in the northwest Gulf of St Lawrence (eastern Canada) over a period of 23 years. Abundance of early juvenile snow crabs (2.5–22.9 mm in carapace width), representing the first 3 years of benthic life, came from an annual trawl survey and was used to determine cohort strength. Analyses revealed a cyclic pattern in abundance of 0^+ crabs that may arise from cohort resonant effects. This pattern consisted of three recruitment pulses but was reduced to two pulses by age 2^+, while the interannual variability of cohort strength was dampened. This reconfiguration of the earliest recruitment pattern was dictated primarily by bottom water temperature and cannibalism, which progressively overruled the pre-settlement factors of larval production and surface water temperature that best explained abundance of 0^+ crabs. The results strongly suggest that bottom-up and density-dependent processes prevail over top-down control in setting the long-term trends and higher-frequency oscillations of snow crab early recruitment patterns.

Keywords: cannibalism, climate, groundfish predation, larval production, population dynamics, recruitment, snow crab.

Introduction

Recruitment of many marine species is a complex process, being the culmination of a sequence of pre- and post-settlement events during which a diverse set of environmental factors operate and interact at different spatial and temporal scales (Pineda *et al.*, 2009). The factors determining the strength of recruitment may be classified as either bottom-up (Beaugrand *et al.*, 2003) or top-down (Köster and Möllmann, 2000). Both types of factors are influential in the marine environment, yet top-down effects appear very strong in some ecosystems where the removal of apex predators has led to a major restructuring of the community and foodweb (e.g. Frank *et al.*, 2005; Halpern *et al.*, 2006). Nevertheless, debate about the relative importance of top-down vs. bottom-up controls in marine ecosystems continues. Early life stages are especially sensitive to bottom-up effects (e.g. Koeller *et al.*, 2009). Predation may also be one of the most significant sources of mortality for these small life stages (Houde, 2008), suggesting that top-down effects are likely to act soon in life history (Munch *et al.*, 2005). Thus, direct knowledge of population dynamics during the early life period is paramount to understanding recruitment; however, the early life stages of many marine species either are not sampled or, the case arising, are sampled often inefficiently due to their small size and patchy distribution (Hunt and Scheibling, 1997; Gallego *et al.*, 2012).

The snow crab (*Chionoecetes opilio* O. Fabricius; Majoidea, Oregoniidae) has been a centerpiece of debate on bottom-up vs. top-down controls in northern hemisphere cold marine environments (Mueter *et al.*, 2012). This species is a large and abundant invertebrate predator, a key structurer of coastal marine benthic communities (Quijón and Snelgrove, 2005a, b), and a major fishery resource of the North Atlantic and north Pacific (FAO, 2013). Snow crab fisheries have fluctuated greatly over time due to highly variable recruitment (Sainte-Marie *et al.*, 1996; Caddy *et al.*, 2005; Zheng and Kruse, 2006). Abundance surveys, mostly of intermediate and late life history stages, indicate that snow crab populations are characterized by groups of strong and weak cohorts that are apparently fixed in early life and alternate in a quasi-cyclic manner (e.g. Caddy *et al.*, 2005; Ernst *et al.*, 2012). This strongly suggests that egg (larval) production, settlement intensity, and/or survival of early benthic stages are highly variable among years (Conan *et al.*, 1996; Sainte-Marie *et al.*, 1996). Snow crab is a cold-stenothermic species (Foyle *et al.*, 1989; Dionne *et al.*, 2003) and bottom-up processes related to climate variability may strongly influence the survival of early life stages. Predation by cod (*Gadus* spp.), the main vertebrate predator of snow crabs, may also be a major source of juvenile mortality (Orensanz *et al.*, 2004; Chabot *et al.*, 2008; Burgos *et al.*, 2013).

Although multiple explanations for snow crab recruitment variability have been proposed, its causes remain uncertain. Previous studies that investigated snow crab recruitment variability were based on data aggregated over vast spatial domains, such that important processes operating at smaller spatial scales may be obscured (Windle *et al.*, 2012; Burgos *et al.*, 2013). Furthermore, the recruitment index was most commonly the catch per unit effort of commercial fisheries that target large males at post-settlement ages of ~9–13 years (Sainte-Marie *et al.*, 1995), and so the supporting correlative analyses invoked multiyear (up to 12 years) time lags (e.g. Boudreau *et al.*, 2011) that can potentially mask the effects of the earliest pre- and post-settlement processes and produce spurious correlations. In the remaining cases, the recruitment index was based on intermediate prefishery stages (4–5 years post-settlement age) whose abundance was modelled or obtained from surveys (e.g. Marcello *et al.*, 2012; Szuwalski and Punt, 2013).

Rather opposing views affirming the primacy of bottom-up or top-down control of snow crab recruitment emerged from these studies. On one hand, some authors concluded that snow crab recruitment at various sizes/ages is primarily related to the extent of sea ice cover before the larval phase and to water temperature during early benthic life, and found no evidence of regulation by groundfish predation (Somerton, 1982; Dawe *et al.*, 2008; Marcello *et al.*, 2012). On the other hand, Frank *et al.* (2005) associated the increased abundance of legal-size snow crab (i.e. males ≥95 mm carapace width) on the eastern Scotian Shelf (Nova Scotia, Canada) in the early 1990s with the decline of groundfish biomass and inferred a top-down control through cod predation on snow crab fishery recruits. More generally across eastern Canada, Boudreau *et al.* (2011) provided evidence that abundance of legal-size snow crab was mainly influenced by water temperature during early benthic life and by cod predation 0–5 years before fishery recruitment. However, the inference that cod prey extensively and intensively on snow crab late life history stages is inconsistent with factual evidence showing that snow crabs are most susceptible to cod predation during the first 4 years of benthic life and that large snow crabs are rarely eaten by cod (Chabot *et al.*, 2008; Burgos *et al.*, 2013).

Recruitment variability in snow crab may also occur as a result of intrinsic density-dependent processes (Sainte-Marie *et al.*, 1996; Caddy *et al.*, 2005). For one, snow crab is highly cannibalistic (Sainte-Marie and Lafrance, 2002; Squires and Dawe, 2003; Kolts *et al.*, 2013) and predation on early benthic stages by older conspecifics is potentially a major source of post-settlement mortality (Lovrich and Sainte-Marie, 1997; Sainte-Marie and Lafrance, 2002). For another, the documented high and autocorrelated interannual variability of snow crab female spawning biomass (Ernst *et al.*, 2012) and egg production (Drouineau *et al.*, 2013) may contribute to year-class strength at settlement, and stage population episodes of high and low cannibalism intensity which operate in the first few post-settlement years (Sainte-Marie *et al.*, 1996; Lovrich and Sainte-Marie, 1997). Yet, to date, none of the studies examining recruitment variability of snow crab has formally tested both the effects of intercohort cannibalism and spawning biomass, although Caddy *et al.* (2005) suggested that density-dependent effects were preponderant over groundfish predation and temperature in determining snow crab fishery recruitment patterns.

The goal of this study was to investigate bottom-up, top-down, and density-dependent effects on recruitment of snow crab early benthic stages. We documented the annual abundance of the first three age classes of snow crab in a long-term (1990–2012) survey in the northwest Gulf of St Lawrence (GSL), eastern Canada. We then investigated the relative influence of a set of abiotic and biotic factors that are most likely to act on these early life history stages and shape snow crab recruitment patterns. We examined the effects of regional climate variability (sea ice cover, surface, and bottom water temperature), larval production, intercohort cannibalism, and groundfish predation during the settlement year of each life history stage. We also investigated the cumulative effects of bottom water temperature, cannibalism, and groundfish predation over time spent on the bottom.

Material and methods

Study species

The snow crab is a cryophilic species that is widely distributed in cold coastal or bathyal waters of the northern hemisphere (Alvsvåg *et al.*, 2009; FAO, 2013). In eastern Canada, the egg incubation period is determined by water temperature and lasts 1 year at >0.75–1°C or 2 years at <0.75–1°C (Sainte-Marie *et al.*, 2008; Kuhn and Choi, 2011). Depending on geographic location and temperature, larvae emerge between April and June and spend ~3–5 months in the plankton, passing through two zoea stages and one megalops stage (Davidson and Chin, 1991; Lovrich *et al.*, 1995). Compared with other marine benthic invertebrates, the snow crab planktonic phase is long and potentially allows for broad dispersal of larvae by surface currents. Snow crab in Atlantic Canada shows no significant genetic spatial structure, suggesting gene flow between populations via the planktonic phase (Puebla *et al.*, 2008).

In the north GSL, snow crab transition from the plankton to the benthos annually from August to October when larvae settle and metamorphose into the first benthic stage (i.e. instar I; Lovrich *et al.*, 1995; Conan *et al.*, 1996). The narrow temperature and substrate preferenda of settling or recently settled snow crabs lead to their concentration into spatially limited nursery areas for the first few years of benthic life (Lovrich *et al.*, 1995; Dionne *et al.*, 2003). Instars I–V are not equally abundant year-round because their intermoult period is ~6 months (Sainte-Marie *et al.*, 1995; Comeau *et al.*, 1998). Snow crab benthic life stages are separated into an immature or juvenile phase (before onset of physiological maturity), a transitional male adolescent and female prepubescent phase during which testes and vasa deferentia become functional or ovaries are developing, and the fully mature adult phase (Sainte-Marie *et al.*, 1995; Alunno-Bruscia and Sainte-Marie, 1998). Herein, the juvenile and transitional phases are collectively called subadults. Juvenile snow crab growth per moult is considered to be conservative and largely independent of temperature because size-at-instar appears similar across occupied geographic ranges (e.g. Comeau *et al.*, 1998; Orensanz *et al.*, 2007). The duration of intermoult in early benthic and later life history stages, however, may vary among geographic locations or years because it is inversely related to temperature (Dawe *et al.*, 2012a; B. Sainte-Marie, unpublished data). Snow crabs moult at most once a year from instar VI and up, until they undergo the terminal moult to adulthood (Sainte-Marie *et al.*, 1995; Comeau *et al.*, 1998).

Field sampling

Snow crab abundance indices were estimated from the annual beam trawl survey conducted by the Department of Fisheries and Oceans in Baie Sainte-Marguerite (Figure 1), an $\sim$400 km^2 bay located in the northwest GSL. In April–May of each year since 1989, snow crabs were collected with a 3 m wide beam trawl fitted with 15 mm mesh netting in the codend from at least three randomly selected sites in each of three depth strata: 4–20, 20–80, and 80–140 m. Early benthic instars were uncommon deeper than 140 m (Dionne *et al.*, 2003). Tows lasted on average 10 (3–36 min) at a mean speed of 2.4 (2.0–2.9 knots) and start-end positions were recorded with GPS or other means to determine the surface area sampled by the trawl.

Trawl contents were sorted on-board ship and snow crabs were identified. Snow crab sex was determined from abdomen shape (triangular in males, oval to rounded in females), except for crabs $<$6–7 mm carapace width (*CW*), which could not be differentiated visually. Carapace width was measured to the nearest 0.01 mm using a vernier caliper. Shell condition was rated 1 (clean-soft), 2 (clean-hard), 3 (intermediate), 4 (dirty-hard), or 5 (dirty-soft) following criteria in Sainte-Marie *et al.* (1995). These categories reflect gradual changes in the exoskeleton with time elapsed since the last moult (Fonseca *et al.*, 2008). The height of the right chela excluding spines was measured to the nearest 0.01 mm on all males $>$35 mm CW. These males were then classified as adolescent (relatively small chelae) or adult (relatively large chelae) using the site-specific discriminant function of chela height on *CW* from Sainte-Marie and Hazel (1992). Females were categorized visually as subadult (narrow, oval abdomen) or adult (broad, rounded abdomen). Adult females were further classified based on their appearance as primiparous (first brood: shell condition 1–2, no mating scars) or multiparous (second or subsequent brood: shell condition 3–5, mating scars; Alunno-Bruscia and Sainte-Marie, 1998). In Baie Sainte-Marguerite, however, most females have a biennial reproductive cycle (Sainte-Marie, 1993) and at the time of the survey primiparous females starting their second year of brooding or preparing to release their larvae could not be consistently distinguished from young multiparous females because of similar shell condition (Drouineau *et al.*, 2013).

To assess escapement of early benthic stages, in 2001 the trawlnet was separated lengthwise into two equal sections, one lined with the regular (15 mm) mesh and the other with a 5 mm mesh. On average (45 tows), the number of snow crabs retained by the regular mesh relative to the 5 mm mesh was $\sim$30% at 3 mm mean *CW* (instar I), 55% at 5 mm mean *CW* (instar II), 83% at 7 mm mean *CW* (instar III), and almost 100% at 10 mm mean *CW* (instar IV). Therefore, snow crabs were considered to be fully selected by the regular mesh at a *CW* of $>$10 mm. Although abundance of instars I–IV was certainly underestimated due to trawl

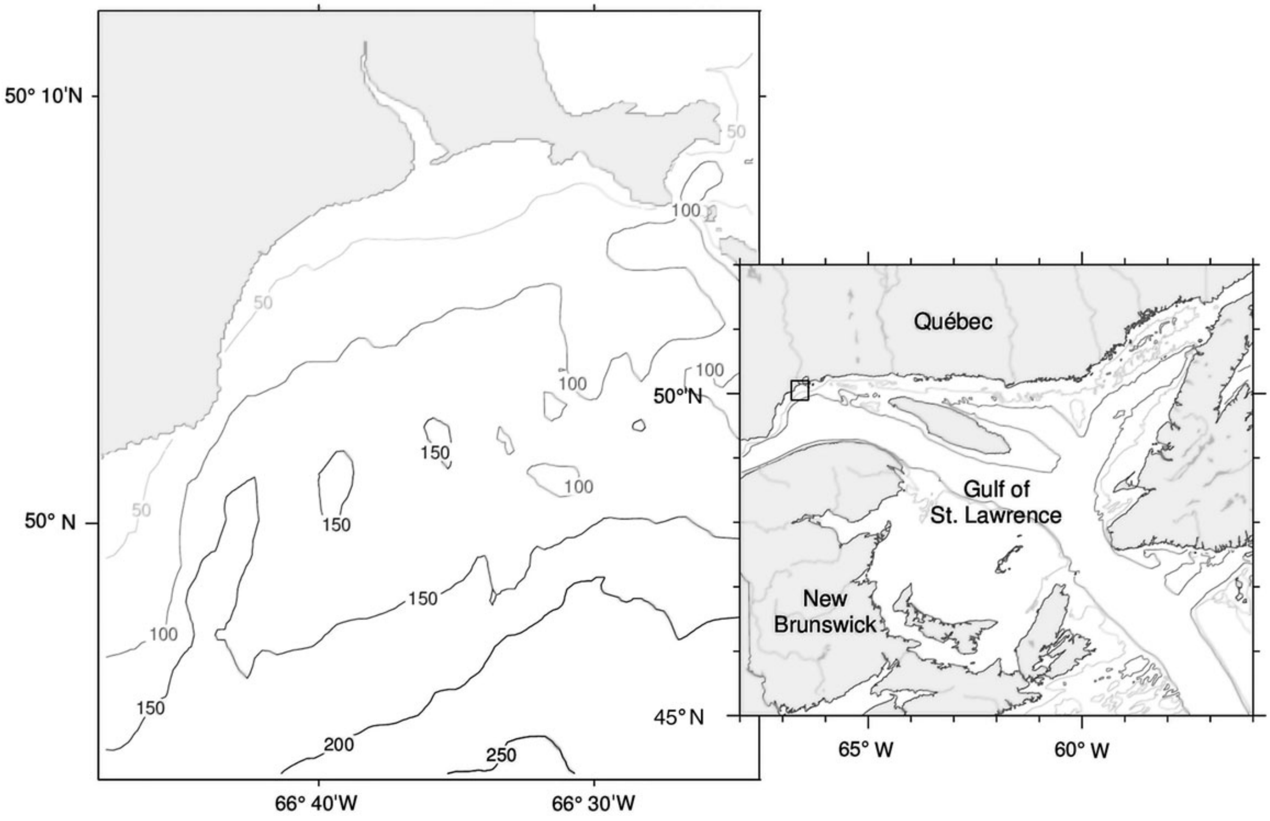

Figure 1. Map of the Gulf of St Lawrence (right) with box indicating Baie Sainte-Marguerite, enlarged at left.

selectivity and some difficulty of detecting instars I–III when sorting trawl contents, we assume that trawl capture and sorting efficiency were constant after the survey start-up year (see Data analyses) so that the recorded numbers of instars I–IV are a reliable relative index of their actual abundance.

Snow crab demographics

Bay-wide abundances of snow crabs were estimated by sex, maturity (subadult or adult), and 0.02 $\log_{10}$ *CW* size classes. First, crab numbers in each tow were standardized to a constant surface area (number of crabs per km^2) based on the area swept by the trawl. Crab densities from all tows within each depth stratum were then averaged and expanded to depth stratum area. Bay-wide abundances were obtained by summing the abundance estimates from each depth stratum. Because the sex ratio of early benthic stages is close to 1 : 1 (Brêthes *et al.*, 1987; Lovrich *et al.*, 1995, this study), the sexually non-differentiated crabs were equally distributed between males and females. Abundance indices in 2001 were calculated only for crabs captured in the trawl-half rigged with the regular mesh net then doubled to be equivalent to the usual sampling method.

We examined the aggregated $\log_{10}$ *CW*-abundance distributions of all sampling years (1989–2012, Figure 2) for female and male snow crabs to make sure that modes in the distributions, each interpreted to be an instar, were distinct. Logarithmic transformation of *CW* had the advantage of making modes more prominent and stabilizing variance about the mean. We also generated annual $\log_{10}$ *CW*-abundance distributions by sex to estimate yearly abundances of female and male instars I–VI (first 3 years of benthic life). In most years, the lower and upper *CW* boundary values for each instar in *CW*-abundance distributions were clear and delimited visually, and the total abundance within these boundaries was calculated. In some years, however, the mode representing instar VI was less conspicuous and abundance could not be estimated by visual assessment alone. To address this issue, we used the NORMSEP method in FiSAT II software (version 1.2.2, Gayanilo *et al.*, 2005) to estimate the mean and standard deviation (*SD*) of the normal distribution of instar VI mode from the aggregated *CW*-abundance distribution (Figure 2) then calculated its 99% confidence interval. This *CW* interval was used to measure abundance of instar VI only in years when its mode in annual *CW*-abundance distributions was not clearly discernible. The lower confidence limit of instar VI mode was adjusted upwards to avoid double counting when it overlapped with the upper *CW* boundary value of instar V. During the April–May period of the survey, snow crabs belonging to instars I, III, and V may be preparing to or undergoing moult to the next instar, and crabs in instars II, IV, and VI may have recently moulted from the previous instar (Sainte-Marie *et al.*, 1995; Alunno-Bruscia and Sainte-Marie, 1998). We therefore calculated annual cohort abundances by summing for each survey year (y) the abundance indices of instars I and II for cohort 1 (age 0^+, settlement in $y-1$), instars III and IV for cohort 2 (age 1^+, settlement in $y-2$), and instars V and VI for cohort 3 (age 2^+, settlement in $y-3$).

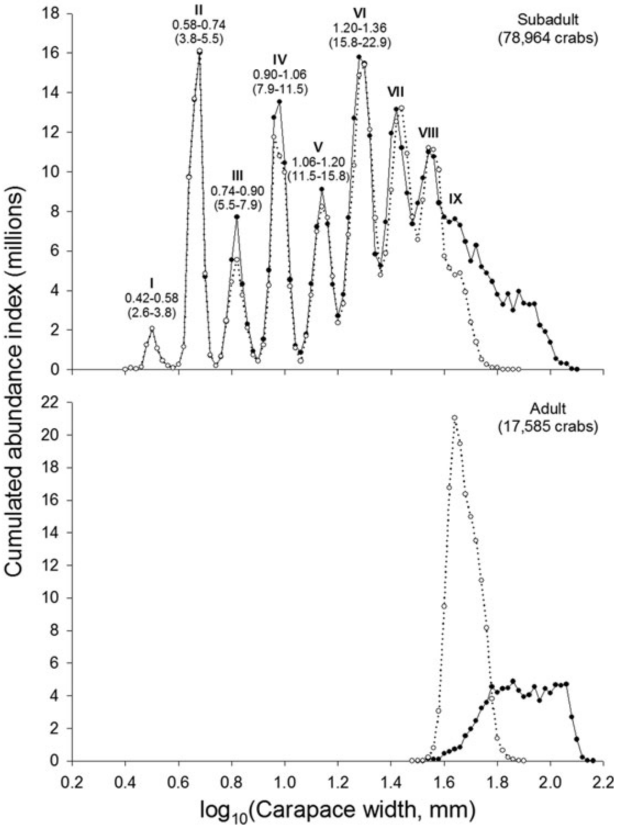

Figure 2. *CW*-abundance distribution aggregated over 24 years (1989–2012) for subadult and adult snow crabs collected annually by beam trawl in Baie Sainte-Marguerite. Males (black circles, full line) and females (white circles, dotted line) are shown separately. Roman numerals above modes represent instars. Range of $\log_{10}$ *CW* and mm CW (in parentheses) for instars I–VI are also reported. Cumulated abundance of adult females exceeded that of any subadult female instar because individual adults may be represented in the same size class over several annual surveys due to cessation of growth after terminal moult; adult males do not reach similarly high levels of cumulated abundance because they achieve terminal moult over more instars (size classes) and are subject to direct and indirect fishing mortality.

Climate variables

Three regional climate variables were considered in this study: ice maximum volume and water temperature at surface and bottom. All variables were estimated for the northwest GSL (region 2, Figure 2 in Galbraith *et al.*, 2012a) for the period 1986–2011, with 1986 corresponding to year of hatch and settlement of cohort 3 surveyed in 1989. The maximum observed ice volume (km^3) during each winter was estimated from digitized charts of ice cover and development stage obtained from the Canadian Ice Service, for which standard ice thicknesses are attributed to each ice development stage. While ice volume is strongly correlated with ice cover area, volume is used here as it circumvents the issue of the occasional complete but temporary ice cover by newly formed thin ice.

Surface water temperature was calculated using National Oceanic and Atmospheric Administration Advanced Very High Resolution Radiometer satellite images, available at 1 km resolution from the Maurice Lamontagne Institute remote sensing laboratory. Surface temperatures are representative of the surface mixed layer in which snow crabs spend their zoeal life (Conan *et al.*, 1996; P. Ouellet, Maurice Lamontagne Institute and B. Sainte-Marie, unpublished data). Regional average surface temperatures were calculated for the months of June, July, and August, the main period of snow crab larval development in the northwest GSL. June is a warming period with a 1986–2011 climatological mean temperature of 9.2°C (1.0°C *SD*) while July and August climatological means are closer to the maximum of the annual cycle at 13.3°C

(1.0°C *SD*) and 13.6°C (0.9°C *SD*), respectively (Galbraith *et al.*, 2012a).

We estimated bottom water temperature from the Department of Fisheries and Oceans CTD data collected at a depth of 100 m, where most crabs settle and spend ∼2–3 years before migrating to shallower waters (Dionne *et al.*, 2003). Bottom temperature is presented as an annual mean of all monthly means from May to November (no recordings in most other months). The climatological cycle of the water temperature at 100 m depth shows a minimum occurring in May followed by warming until at least November (Galbraith *et al.*, 2012a). Therefore, the annual May–November mean was computed using data from all available months and was then adjusted to represent August conditions using a climatological warming rate of 0.1°C per month to avoid biases that could occur in years when temperature data were sampled earlier or later in the season.

Biotic variables

To test the effect of snow crab female spawner abundance on recruitment, we used a proxy of larval production. Adult females recorded as primiparous during the survey were not included in the estimation of this variable as they do not contribute to larval production in the survey year, so we considered only females recorded as multiparous (thus including primiparous females releasing larvae in the survey year). Using the linear regression of fecundity (i.e. number of eggs per brood) on *CW* estimated by Sainte-Marie (1993) for multiparous females in Baie Sainte-Marguerite ($\log_{10}$ fecundity $= 2.616 \log_{10} CW + 0.062$), we calculated potential fecundity for each multiparous female size class at the midpoint of the size class and multiplied the fecundity estimate by the corresponding multiparous female abundance index to obtain total fecundity by size class. The proxy of larval production was obtained by summing total fecundity estimates for all size classes and halving the sum to reflect the biennial reproductive cycle (Sainte-Marie, 1993). Although larvae from other populations undoubtedly contribute to snow crab recruitment in Baie Sainte-Marguerite, our proxy likely provided a reasonable estimate of relative larval abundance because female spawner abundance was positively correlated between our study site and neighbouring GSL localities (data not shown).

To explore the effects of intercohort cannibalism on cohort 1, we calculated abundances of subadult and adult crabs belonging to instars VIII and IX (respectively ∼40 and 50 mm mean *CW* and 4.3 and 5.7 years of post-settlement age; Sainte-Marie *et al.*, 1995; Alunno-Bruscia and Sainte-Marie, 1998) for the 1989–2012 period. Cannibalism in snow crab is size-selective and instars VIII and IX are the most potent predators of instar I crabs (see Figure 6 in Lovrich and Sainte-Marie, 1997). Cannibal abundance indices were calculated in the same way as for instars I–VI, using *CW* boundary values (99% confidence interval) from the aggregate *CW*-abundance distribution. An annual index that reflects the potential intensity of cannibalism on cohort 1 was obtained by summing the abundance estimates of instars VIII and IX each year. We also derived an index of potential cannibalism on each of cohorts 2 and 3 by calculating the annual abundance of instars IX and X and of instars X and XI, respectively, in reflection of the fact that the size of the most potent predators increases with increasing prey size (Dutil *et al.*, 1997; Lovrich and Sainte-Marie, 1997). Abundance indices of instars X–XI were estimated using mean *CW* at instar obtained from the Hiatt growth model for adolescent and adult males reported in Sainte-Marie *et al.* (1995).

We also investigated top-down effects by examining the relationship between groundfish predators and abundance of cohorts 1–3. A broad size range of cod and skates (∼20–90 cm length) have been identified as important predators of juvenile snow crab (Robichaud *et al.*, 1991; Chabot *et al.*, 2008). We obtained annual biomass of Atlantic cod (*Gadus morhua*), smooth skate (*Malacoraja senta*) and thorny skate (*Amblyraja radiata*) from the Department of Fisheries and Oceans multispecies survey that has been conducted in the GSL in August of each year since 1990 (Bourdages *et al.*, 2010). Biomass estimates were derived from sampling stations located only in the northwest GSL. Cod and skate biomasses were summed each year to obtain an annual groundfish predator biomass index.

Data analyses

Abundance estimates of cohorts 1–3 for 1989 were very low, likely because sampling, sorting, and identification of early benthic stages in the start-up year of the survey were less efficient than in subsequent years, and were therefore excluded from analyses. The proxy of larval production and cannibalism indices for 1989 were nevertheless included because they were apparently well estimated. Cohorts 1–3 abundance, larval production, cannibalism index, and groundfish predator biomass, or derived indices (see below), were $\log_{10}$ transformed before analyses.

We performed spectral analyses (PROC SPECTRA in SAS) to detect cyclic patterns in the smoothed abundance (moving average, mean = 3) of cohorts 1–3 and used the Bartlett's Kolmogorov–Smirnov statistic (K–S) to test the null hypothesis of no cycle. Smoothing has the advantage of making long-term fluctuations stand out more clearly by reducing random noise (Ao, 2010). The modified Mann–Kendall test for autocorrelated data (mkTrend function from the fume package in R; Santander Meteorology Group, 2012) was used to detect significant temporal trends in cohort abundance and climate variables.

Correlation then multiple regression were used to examine relationships between cohort abundance and climate and biotic variables operating: (i) from hatch to settlement time (called at-settlement effects for simplicity) and (ii) only from settlement on (called cumulated effects for simplicity). For analyses of at-settlement effects, we lagged all climate and biotic variables by 1, 2 or 3 years to coincide with the larval phase and settlement year of cohorts 1, 2 and 3, respectively (Table 1). For cumulated effects, we calculated new indices of bottom temperature (BT_C) and groundfish predator biomass ($PRED_C$) that were the mean of values estimated in years $y-1$ and y for cohort 1, in years $y-2$ to y for cohort 2, and in years $y-3$ to y for cohort 3. A new index for cumulated effects of cannibalism ($CANNIB_C$) was calculated as the mean of abundance of instars VIII and IX in years $y-1$ and y for cohort 1; abundance of instars VIII and IX in years $y-2$ and $y-1$ and abundance of instars IX and X in year y for cohort 2; abundance of instars VIII and IX in years $y-3$ and $y-2$, abundance of instars IX and X in year $y-1$ and abundance of instars X and XI in year y for cohort 3 (Table 1).

For each cohort, Pearson correlation coefficients (r) between crab abundance and all climate and biotic variables with the *a priori* selected time lags were calculated. Because the abundance of a cohort in a given year may be related to its abundance in the previous year, the abundance of cohorts 2 and 3 was also compared with 1-year lagged abundance of cohorts 1 and 2, respectively. The correlation matrices were built for exploratory purposes only and all coefficients with p-values < 0.05 (uncorrected for multiple

Table 1. Pearson correlations between $\log_{10}$ cohorts 1 – 3 snow crab abundance indices measured annually in Baie Sainte-Marguerite from 1990 to 2012 and all potential explanatory variables operating before or at settlement, and after settlement.

	Cohort (*y*)		
Variable	**1**	**2**	**3**
Effects at settlement	$y - 1$	$y - 2$	$y - 3$
LP	0.424^{*}	0.350	0.112
Ice	0.094	-0.080	-0.076
ST	-0.593^{**}	-0.437^{*}	-0.523^{**}
BT	-0.036	-0.034	-0.371
CANNIB	-0.227	-0.355	-0.750^{***}
PRED	0.189	0.269	0.437
Cumulated post-settlement effects	$[(y - 1) + y] / 2$	$[(y - 2) + (y - 1) + y]/3$	$[(y - 3) + (y - 2) + y - 1) + y]/4$
BT_C	-0.139	-0.342	-0.698^{***}
$CANNIB_C^{a}$	-0.001	-0.138	-0.584^{**}
$PRED_C$	0.254	0.293	0.224

Climate variables include ice maximum volume (Ice), surface water temperature (*ST*), and bottom water temperature (*BT*). Biotic variables include $\log_{10}$ larval production (*LP*), $\log_{10}$ cannibalism index (*CANNIB*), and $\log_{10}$ groundfish predator biomass (*PRED*). All variables were lagged 1, 2, or 3 years to coincide with the larval period and settlement year of cohorts 1 – 3. A cumulated index of bottom temperature (BT_C), cannibalism index ($CANNIB_C$), and groundfish predator biomass ($PRED_C$) was calculated as the mean value of *BT*, *CANNIB*, and *PRED*, respectively, over the years spent on the bottom by each cohort. Only raw *p*-values (unadjusted for multiple testing) are reported.

[a] Definition of cannibals changes with lag, see Material and methods.

$^{*}p \leq 0.05$; $^{**}p \leq 0.01$; $^{***}p \leq 0.001$.

comparisons) were considered to reflect potentially strong associations. We ran sensitivity analyses to ensure the robustness of our results to possible changes in snow crab growth rate. Correlation analyses were repeated using cohort abundance indices composed of different combinations of instars that assumed a faster growth rate than documented by Sainte-Marie *et al.* (1995) during the cold 1991–1992 period. For example, we tested an extreme scenario that included instars I–III in cohort 1, instars IV and V in cohort 2, and instar VI in cohort 3. The resulting changes in cohort abundance did not radically change the results (not shown) as the direction and strength of the correlations remained similar for all variable pairs.

We fitted multiple linear regression models with the ordinary least-squares method to cohort 1–3 abundances using all climate and biotic variables. For bottom water temperature, cannibalism and groundfish predator biomass, only the cumulated indices were used in regression. The variables that contributed most to explaining cohorts 1–3 abundances were selected by Best Subsets procedure using the corrected Akaike Information Criterion. Using all possible combinations of explanatory variables is considered a reasonable approach to selecting a subset of important variables, as opposed to stepwise variable selection (Quinn and Keough, 2002). Two-way interactions between selected variables were evaluated and retained only if statistically significant. To reduce multicollinearity, interaction terms were computed as the product of the two centred variables. The relative importance of each explanatory variable (i.e. contribution of each variable to the amount of explained variance, R^2) within each final regression model was measured with the calc.relimp function (metric LMG) from the relaimpo package in R (Grömping, 2006).

We examined scatterplots between cohorts 1–3 abundances and selected climate variables to assess the nature of the relationships. When relationships appeared non-linear, climate variables were $\log_{10}$ transformed. If linearity was not improved with a transformation, a quadratic polynomial term expressed as the square of the variable that showed a non-linear relationship with cohort abundance was added to the regression model. Climate variables were Mean-centred before generating the squared term. A partial *F*-test was performed to determine whether adding a polynomial term significantly improved model fit (Quinn and Keough, 2002).

We used Cook's distance to detect influential observations. We tested for residual normality using Shapiro-Wilk's test and validated homoscedasticity with the studentized Breusch–Pagan test. No action was taken when residuals deviated slightly from normality because linear regression is considered fairly robust to departures from normality (Vittinghoff *et al.*, 2005). We examined multicollinearity among selected explanatory variables with the variance inflation factor and used the Durbin–Watson statistic to test for positive autocorrelation in residuals at time lags of 1–3 years. If autocorrelated, errors from the regression model were allowed to contain autocorrelation. Statistical analyses were carried out using SAS 9.3 (SAS Institute Inc., Cary, NC, USA) and R 2.15.3 (R Development Core Team, 2012).

Results

Snow crab demographics

The aggregated *CW*-abundance distribution included 96,549 snow crabs captured in Baie Sainte-Marguerite from 1989 to 2012 (Figure 2). Subadult crabs showed eight conspicuous modes designated instars I–VIII and one less distinct mode designated instar IX. The fading of modal structure at larger subadult sizes and in adults is the result of (i) the increasing modal variance with instar, (ii) the reduction in size differences between consecutive adult instars owing to the tendency of larger individuals within a given instar to terminally moult sooner than smaller individuals, and (iii) for adults the consequent mixing of several year-classes with different sizes at moult (Alunno-Bruscia and Sainte-Marie, 1998; Orensanz *et al.*, 2007).

Smoothed abundance of cohort 1 varied interannually by two orders of magnitude, but this extreme variability was somewhat dampened over the following 2 years of benthic life (Figure 3). Abundance of most year-classes increased from age 0^+ to age 2^+, as revealed by median values for cohorts 1–3 (Figure 3), and this most likely reflected an increase in capture and sorting efficiency

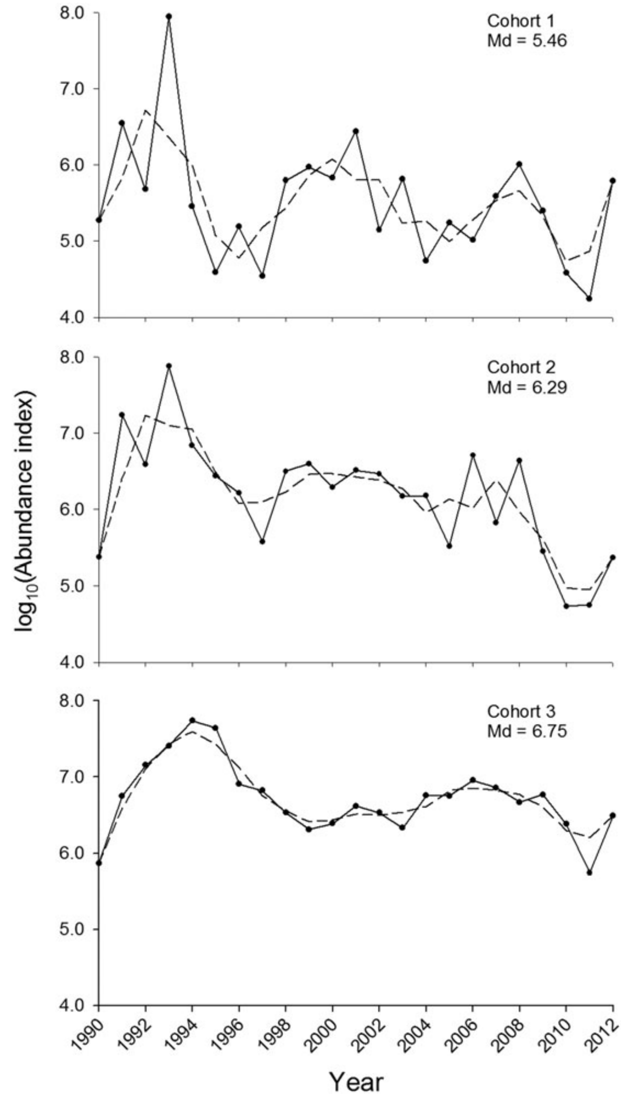

Figure 3. Bay-wide abundance indices of snow crab cohorts 1 (instars I and II, age 0^+), 2 (instars III and IV, age 1^+), and 3 (instars V and VI, age 2^+) in Baie Sainte-Marguerite from 1990 to 2012. Abundance indices were smoothed by taking 3-year moving averages (dashed lines). Median (Md) of $\log_{10}$ abundance indices by cohort are reported.

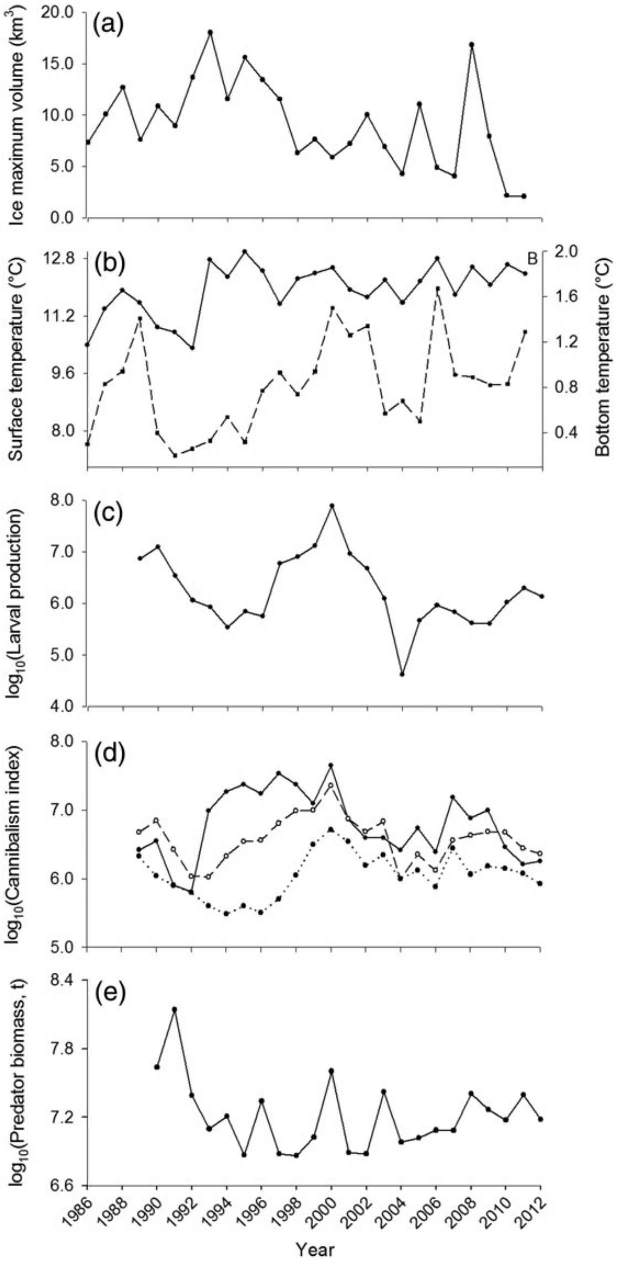

Figure 4. Time series of climate and biotic variables used to test effects of ice maximum volume (a), surface water temperature (b, full line), bottom water temperature (b, dashed line), larval production (c), intercohort cannibalism (d), and groundfish predator biomass (e) on the abundance of snow crab early juvenile stages in Baie Sainte-Marguerite. The cumulated cannibalism index for cohort 1 (d, black circles and full line), cohort 2 (d, white circles and dashed line), and cohort 3 (d, black circles and dashed line) are shown separately.

of crabs from 3 to 10 mm CW. The cohorts alternated between periods of low and moderate to high abundance in a near-cyclic pattern which is best illustrated by the smoothed abundance indices. Peaks in smoothed abundance of cohort 1 occurred around 1993, 2001 and 2008. A cycle of 7.7 and 11.5 years was detected in the smoothed abundance of cohorts 1 and 3, respectively (K–S = 0.61–0.71, $p < 0.001$), while no cycle was found in the smoothed abundance of cohort 2. This change in cycle length reflects the reduction from three recruitment pulses in cohort 1 to only two clear pulses in cohort 3 (Figure 3). The three cohorts had highest abundances in the first half of the 1990s and showed a negative trend in abundance over the study period (tau = − 0.19– − 0.42) that was significant only for cohort 2 ($p = 0.003$).

Climate variables

The three regional climate indices varied considerably over the period 1986–2011 (Figure 4). Ice maximum volume reached its highest values in 1993 and 2008 (16.8–18.0 km^3), and its lowest values in 2010–2011 (2.1–2.2 km^3). Ice volume showed a significant negative trend over the study period (tau = − 0.37; $p = 0.003$). Water temperatures were especially low in the early 1990s and were never as cold thereafter (Figure 4b), with the lowest surface and bottom temperatures occurring in 1991–1992 with mean temperatures of 10.3 and 0.2°C, respectively. Surface temperature was the warmest in 1995 (13.4°C) and bottom

Table 2. Regression models describing interannual variability of the abundance of snow crab cohorts 1–3 sampled annually in Baie Sainte-Marguerite from 1990 to 2012.

Cohort	*n* (year)	Selected variables	Coefficients (standard error)	Relative importance	R^2	*F* (*p*)
1	23	ST	−0.33 (0.17)	0.20	0.72	11.39 (<0.001)
		ST^2	0.51 (0.15)	0.30		
		LP	0.39 (0.14)	0.15		
		$ST \times LP$	0.62 (0.27)	0.07		
2	23	ST	−0.46 (0.21)		0.19	4.94 (0.037)
3	23	BT_C	−0.94 (0.35)	0.30	0.82	28.57 (<0.001)
		$CANNIB_C$	−0.41 (0.15)	0.18		
		$COH2$	0.29 (0.06)	0.34		

R^2 values describe the proportion of variation in cohort abundance that was explained by each regression model. *F* statistics (and associated *p*-values) test the overall significance of the regression models. Relative importance decomposes the full model R^2 into contributions from each variable (ST, surface water temperature; LP, $\log_{10}$ larval production; BT_C, $\log_{10}$ cumulated bottom water temperature; $CANNIB_C$, $\log_{10}$ cumulated cannibalism index; $COH2$, $\log_{10}$ cohort 2 abundance).

temperature reached its maximum in 2006 (1.7°C). Interannual variability of bottom water temperature exceeded the climatological seasonal variability (data not shown). Surface and bottom temperature both showed a significant positive trend over the study period (tau = 0.28–0.29, $p < 0.023$). In fact, closer scrutiny of surface temperature revealed that the northwest GSL shifted from a cooler state before 1993 (1986–1992 mean: 11.0°C) to a warmer state after (1993–2011 mean: 12.4°C), consistent with the observations of Galbraith *et al.* (2012b) for the GSL as a whole.

Biotic variables

All three biotic factors were highly variable over the study period (Figure 4). Larval production was relatively high at the beginning of the survey and during the period 1997–2002 with a maximum reached in 2000, but remained moderately low thereafter with an exceptionally weak value in 2004. The cannibalism index for cohort 1 (i.e. instars VIII–IX as predators) alternated between low (1989–1992, 2002–2006 and 2010–2012) and moderate-to-high values (1993–2000 and 2007–2009). Instars VIII and IX were at least twice more abundant during 1993–2000 than during 2007–2009, which is consistent with the very high larval production and cohort 1 abundance that occurred in the early 1990s (Figures 3 and 4c). The cannibalism index for cohorts 2 and 3 exhibited similar oscillation over the study period but with a positive lag of ~1 and 2 years, respectively, relative to the cohort 1 cannibalism index. Groundfish predator biomass in 1991 was at least three times higher than in other years and oscillated between relatively low and moderate values thereafter.

Correlation and regression analyses

Changes in annual abundance were very similar between cohorts 1 and 2 ($r = 0.71$, $p < 0.001$) and similar between cohorts 2 and 3 ($r = 0.58$, $p = 0.003$). The correlation between cohorts 1 and 2 was weakened when a 1-year lag was applied to cohort 1 ($r = 0.40$, $p = 0.064$), but applying a 1-year lag to cohort 2 improved its association with cohort 3 ($r = 0.66$, $p < 0.001$). The correlation between cohort 1 abundance lagged 2 years and cohort 3 abundance was weak ($r = 0.38$, $p = 0.093$).

Cohort abundance was positively correlated with larval production, but the association was strong only for cohort 1 and the correlation coefficient weakened progressively from cohorts 1 to 3 (Table 1). Abundance of the three cohorts was negatively correlated with surface water temperature during larval development, but was not correlated with ice volume during winter before the larval phase (Table 1). Abundance of cohorts 1–3 was not correlated with bottom water temperature during the settlement year, but the negative correlation coefficient between abundance and cumulated bottom temperature strengthened notably with cohort age (Table 1). Abundance of all cohorts was negatively associated with the cannibalism index at settlement and cumulated over time, and the intensity of correlation increased with cohort age (Table 1). The correlations between cohort abundance and groundfish predator biomass were weak and unexpectedly positive (Table 1).

In regression analysis, one or more climate and biotic variables contributed to explain interannual variation in the abundance of cohorts 1–3 (Table 2). Cohort 1 abundance was best explained by the combination of larval production the previous year and surface water temperature during larval development (Table 2, Figure 5). Abundance of cohort 1 declined exponentially with surface water temperature even after log transformation of this climate variable, and the addition of a squared term in the final model significantly improved model fit ($F_{1,19} = 11.82$, $p = 0.003$). Surface water temperature accounted for most of the variance explained by the model (Table 2) and there was a significant interaction between this climate variable and larval production ($t_{18} = 2.28$, $p = 0.035$). Examination of the interaction revealed that the negative effect of surface water temperature on cohort 1 abundance was strong when larval production was low, while surface water temperature had no effect on cohort 1 abundance when larval production was high. For cohort 2, only surface water temperature during the planktonic larval phase was selected as the variable best explaining abundance fluctuations over time (Table 2).

The interannual variation in cohort 3 abundance was best explained by changes in cumulated bottom water temperature (log transformed) and the cumulated cannibalism index, as well as cohort 2 abundance in the previous year (Table 2, Figure 6). Among these three variables, cumulated bottom temperature contributed most to the large amount of variation (82%) explained by the model. Dropping only cohort 2 abundance still resulted in a satisfactory model with 61% of variance explained. However, when only temperature and cohort 2 were considered, there remained a strong quasi-cyclic pattern in the model residuals that was not apparent in the full model with cannibalism included (Figure 6c).

Discussion

This study investigated the factors controlling recruitment of the earliest benthic stages of snow crab (cohorts 1–3, representing age

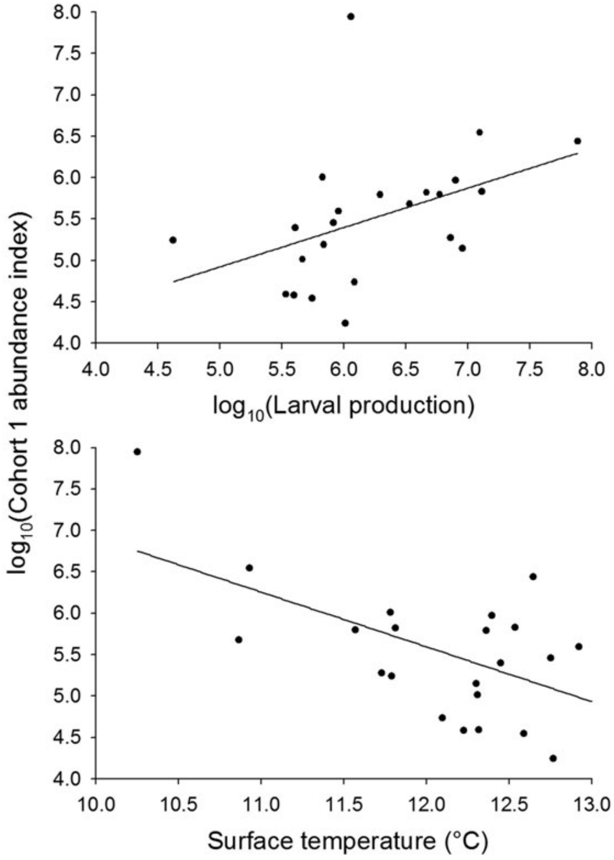

Figure 5. Relationship between larval production and cohort 1 abundance (upper panel) and between surface water temperature and cohort 1 abundance (lower panel). Larval production and surface temperature were lagged 1 year to coincide with the larval period of cohort 1.

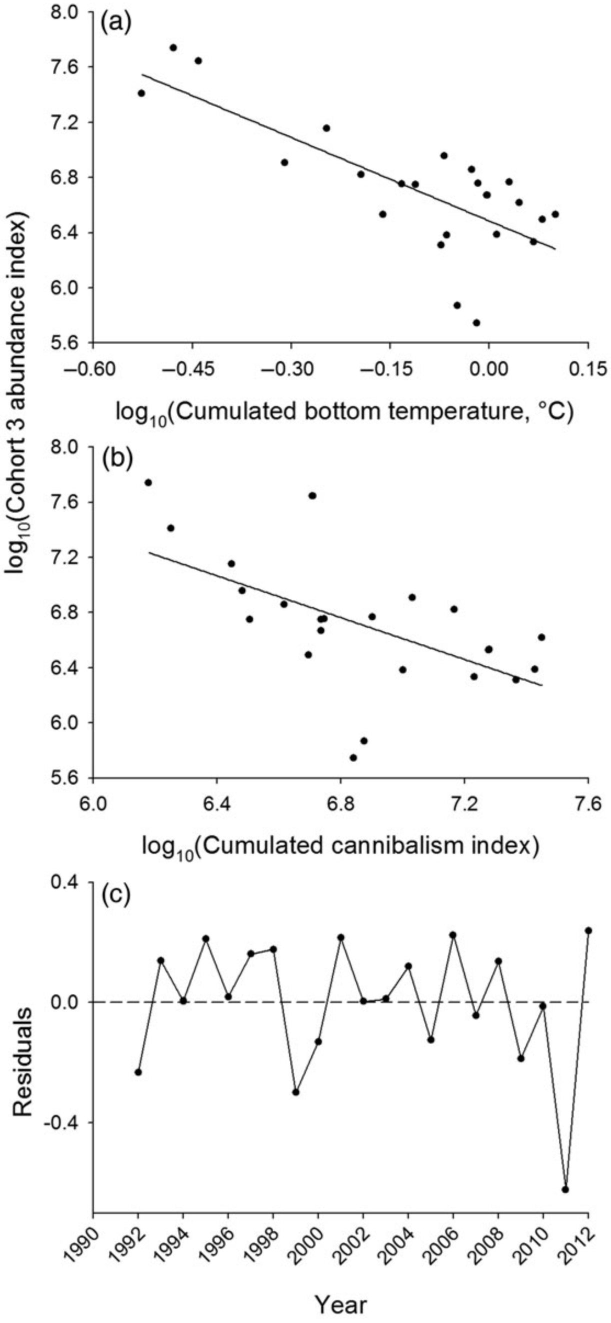

Figure 6. (a) Relationship between cumulated bottom water temperature and cohort 3 abundance. (b) Relationship between cumulated cannibalism index and cohort 3 abundance. Bottom temperature and cannibalism index were averaged over the years spent on the bottom by cohort 3. (c) Residuals of cohort 3 final regression model.

classes 0^+ to 2^+) at a spatial scale relevant to population-level processes. The interannual variability in abundance of these early juveniles was chronicled for the first time, which allowed us in subsequent analyses to invoke only short-time lags (maximum 3 years) when exploring at-settlement and cumulated effects of climate and biotic factors on cohort abundance. Bottom-up and density-dependent factors apparently determined abundance of early juvenile snow crab and explained both cyclicity and longer term trends in recruitment. The initial pattern of recruitment (age 0^+) was shaped largely by pre-settlement factors, whereas the pattern of recruitment-at-age 2^+ was partly decoupled and reconfigured from the initial pattern by the cumulative effects of post-settlement factors.

There was no evidence of a top-down control on early juvenile snow crab. This finding agrees with Chabot *et al.* (2008), who suspected the effect of cod predation on snow crab abundance to be low in the GSL, and with very recent studies concluding that abundance of snow crab is not under top-down control in the northeast Pacific and Northwest Atlantic (Dawe *et al.*, 2012b; Marcello *et al.*, 2012; Windle *et al.*, 2012). Although these studies were conducted at a time when cod populations were at low levels, especially in the Northwest Atlantic, the vast increase in spatial distribution and abundance of snow crab in the Barents Sea in face of the largest cod stock in the world (ICES, 2011; Jørgensen and Spiridonov, 2013) strongly suggests that cod predation is not a major regulatory factor of snow crab populations except perhaps when or where environmental conditions are unfavourable to crab (Orensanz *et al.*, 2004; Burgos *et al.*, 2013). In particular, groundfish predation cannot explain the cyclic fluctuations of snow crab abundance during this study, which furthermore existed even when cod was abundant (Sainte-Marie *et al.*, 1996). It is more likely that groundfish (cod) predation occurs mainly when snow crab are abundant relative to cod's preferred prey (Waiwood and Elner, 1982; Marcello *et al.*, 2012), such that it has a dampening effect on some prominent snow crab year-classes but does not contribute strongly to structure cohorts (Sainte-Marie *et al.*, 1996; Chabot *et al.*, 2008).

Snow crab and northern shrimp (*Pandalus borealis*) are key ecological components and fishery resources of boreal and Subarctic coastal marine environments (Dawe *et al.*, 2012b), and have been considered by some authors to respond similarly to environmental forcings (Worm and Myers, 2003; Frank *et al.*, 2005). Northern shrimp is also influenced by bottom-up processes related to climate variability (Koeller *et al.*, 2009), but, unlike snow crab, it additionally appears under variably strong top-down control by groundfish predators (Lilly *et al.*, 2000; Dawe *et al.*, 2012b; Windle *et al.*, 2012). The difference in susceptibility to groundfish (cod) predation may relate to major size and behavioural differences between the two species. Northern shrimp are small even as adults (most are <32 mm in carapace length), have habitat preferences similar to cod (Windle *et al.*, 2012), and spend substantial time on the sediment surface where they are exposed to predators (Bergström, 2000). In contrast, snow crab prefers colder waters than does cod (Windle *et al.*, 2012) and early juveniles are cryptic whereas older subadults and adult females often bury which makes them much harder for predators to find (Robichaud *et al.*, 1991; Lovrich *et al.*, 1995). Furthermore, snow crab may grow to a size that offers refuge from groundfish predation, and large hard-shelled male snow crabs aggressively confront and can fend off large cod (Chabot *et al.*, 2008; Winger and Walsh, 2011).

Abundance of 0^+ snow crabs fluctuated quasi-periodically over the study period, with stronger year-classes recurring approximately every 8 years. This 8-year period is the same as the cycle length previously reported for snow crab in northwest GSL based largely on historical data (Sainte-Marie *et al.*, 1996) and is similar to the 7-year cycle reported for the eastern Bering Sea (Ernst *et al.*, 2012). Snow crab populations in these two regions are quasi-semelparous because it is mostly the primiparous females (first time spawners) that contribute to recruitment, due either to spatial constraints in the Bering Sea (Ernst *et al.*, 2012) or to high natural mortality in the northwest GSL (Drouineau *et al.*, 2013). This study demonstrated in snow crab a significant spawner-settlement relation and the approximate 8-year recruitment cycle is equivalent to the time interval between a snow crab female's conception (zygote) and her terminal moult and first spawning in the northwest GSL (Alunno-Bruscia and Sainte-Marie, 1998). Abundance cycles of period equal to the mean age of maturation and reproduction may arise from cohort resonant effects, a phenomenon characteristic of some semelparous, age-structured populations in which cohorts interact with each other through cannibalism and intraspecific competition (Bjørnstad *et al.*, 2004; also see Burgos *et al.*, 2013 for a previous discussion of possible cohort resonance effects in snow crab). There is ample laboratory and field evidence supporting the existence of such interactions in snow crab (Dutil *et al.*, 1997; Lovrich and Sainte-Marie, 1997; Sainte-Marie and Lafrance, 2002; Squires and Dawe, 2003).

The obvious weakening of the snow crab settlement pulse of the early 2000s from cohorts 1 to 3 is likely to have resulted largely from intercohort cannibalism and competition. Crabs from the recruitment pulse of the early 2000s were probably cannibalized by older conspecifics belonging to the preceding, exceptionally strong settlement event that occurred in the early 1990s. The progressive and additive effects of cannibalism through time since settlement, between the same interacting year-classes, can explain why the negative correlation between cannibalism at settlement and early juvenile cohort abundance increased in strength with time. In context of the resonant cohort interpretation of the snow crab settlement pattern, it is intriguing that a pulse of 0^+ crabs centred on 2008 was observed despite the local demise of the early 2000s pulse and low larval production in 2007–2009. A reasonable explanation for this paradox, consistent with the metapopulation concept for GSL snow crab (Puebla *et al.*, 2008), is that the Baie Sainte-Marguerite population was partially subsidized by larvae from neighbouring easterly populations where the early 2000s settlement pulse remained strong and generated a large female spawning biomass in the years 2006–2010 (J. Lambert, Maurice Lamontagne Institute, pers. comm.).

Previous studies on snow crab recruitment patterns did not include density-dependent cannibalism and egg/larval production, or for the latter considered only a male or combined male–female spawning index as a proxy of egg/larval production, and could not explain population cyclicity which is a characteristic of snow crab dynamics in many populations. This acknowledged failure was apparent in the fact that models did not well reproduce or account for the low and high extremes of recruitment/abundance and consequently had strong, autocorrelated residual patterns (e.g. Zheng and Kruse, 2003; Marcello *et al.*, 2012). Male or combined male–female spawning indices can be problematic for investigating spawner-settlement relations in snow crab, because variation in female and male spawning biomasses are not synchronous or of the same magnitude due to females maturing at a substantially smaller mean size/age than males (Sainte-Marie *et al.*, 2008). As for cannibalism, the formulation of a representative index presents some difficulties and improvement over this study may be possible. For instance, we did not consider the role of cannibalism between proximate cohorts and did not incorporate seasonality of cannibalism, both demonstrated by Lovrich and Sainte-Marie (1997), focusing only on the abundance of the most potent cannibals of each cohort. Moreover, partial or sublethal cannibalism resulting in limb losses or cannibal avoidance by hiding can lead to declining crab condition, reduced growth rate, and delayed mortality by disease or insufficient foraging (Dutil *et al.*, 1997; Sainte-Marie and Lafrance, 2002). Such lagged effects could further contribute to explain the decoupling of recruitment patterns and the increasingly strong negative correlation between juvenile abundance and cannibalism index at settlement from cohorts 1 to 3. The complex nature of cannibalism and its effects would be best addressed by modelling.

The warming of water may be responsible, at least in part, for declining cohort abundances over the study period, as suggested by Mullowney *et al.* (2014) for Newfoundland and Labrador snow crab. Several studies have now concluded that cold conditions during early snow crab life promote recruitment/abundance (Boudreau *et al.*, 2011; Marcello *et al.*, 2012; Szuwalski and Punt, 2013), consistent with findings indicating that the first few benthic instars are the most stenothermic of all life history stages (Dionne *et al.*, 2003). In this study, cohort abundances were highest in the first half of the 1990s when the coldest temperatures occurred. On one hand, this cold period may have been physiologically optimal for larvae (Yamamoto *et al.*, 2014) and may have contributed to increase food availability in the surface mixed layer, resulting in better larval growth and survival. Water temperature is associated with changes in nutrient availability, which in turn influences the timing, intensity and quality of spring bloom (Bouman *et al.*, 2003). However, the strength of temperature effects during the planktonic phase of snow crab in our study was found to depend on the magnitude of larval production. The negative correlation between surface temperature and abundance of cohort 1 was lost when larval production was high, probably because more larvae were available for settlement than were needed to saturate benthic nurseries despite suboptimal surface conditions. On the other hand, warmer bottom temperatures may be physiologically disadvantageous to early juvenile snow crab (Gravel, 2002) and may intensify competition and cannibalism by shrinking the area of suitable habitat and increasing spatio-temporal overlap of interacting cohorts (Parada *et al.*, 2007).

An important consideration for this study is the reliability of cohort relative abundance estimates. A potential concern is the strong positive correlation between unlagged abundance indices of cohorts 1 and 2. This similarity could result from the precedence of year effects in trawl capture efficiency for instars composing these cohorts and/or mixing of individuals from two consecutive age classes within instars due to reduced or accelerated growth. Year effects are an unlikely reason because they usually result in random year-to-year variation, which is inconsistent with the quasi-cyclic oscillations seen particularly in the smoothed abundance of cohort 1. Some mixing of 0^+ and 1^+ age classes within individual instars, due to differential growth of crabs within or among years, is a more plausible explanation. Indeed, early benthic juvenile snow crabs in Baie Sainte-Marguerite are separated into two subpopulations, one usually minor distributed above and one usually major distributed below the core of the cold intermediate layer (Dionne *et al.*, 2003), that may moult at different rates due to different temperature regimes. This feature is compounded by interannual variability in surface and bottom water temperature which may change the duration of larval development (Yamamoto *et al.*, 2014), the time of settlement, and modify—along with conspecific density—the moulting frequency of early juveniles.

While only recruitment of the earliest benthic stages of snow crab was measured in this study, some authors have suggested that the relative strength of cohorts—or more appropriately pseudo-cohorts, *sensu* Orensanz *et al.* (2007)—is definitively set at the intermediate developmental stages (25–50 mm, instars VII to VIII) and thereafter propagates to the fishery (e.g. Caddy *et al.*, 2005). This is also implicit in all studies concluding that bottom-up processes acting early in life determine abundance of legal males. A next logical step will be to test this hypothesis and therefore assess the importance of early juvenile recruitment and intervening environmental conditions that modify survival and growth for adult population fluctuations and fishery performance.

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References

Alunno-Bruscia, M., and Sainte-Marie, B. 1998. Abdomen allometry, ovary development, and growth of female snow crab, *Chionoecetes opilio* (Brachyura, Majidae), in the northwestern Gulf of St. Lawrence. Canadian Journal of Fisheries and Aquatic Sciences, 55: 459–477.

Alvsvåg, J., Agnalt, A-L., and Jorstad, K. E. 2009. Evidence for a permanent establishment of the snow crab (*Chionoecetes opilio*) in the Barents Sea. Biological Invasions, 11: 587–595.

Ao, S. 2010. Applied time series analysis and innovative computing. Lecture Notes in Electrical Engineering, Volume 59, Springer. 112 pp.

Beaugrand, G., Brander, K. M., Lindley, J. A., Souissi, S., and Reid, P. C. 2003. Plankton effect on cod recruitment in the North Sea. Nature, 426: 661–664.

Bergström, B. I. 2000. The biology of *Pandalus*. Advances in Marine Biology, 38: 55–245.

Bjørnstad, O. N., Nisbet, R. M., and Fromentin, J. M. 2004. Trends and cohort resonant effects in age-structured populations. Journal of Animal Ecology, 73: 1157–1167.

Boudreau, S. A., Anderson, S. C., and Worm, B. 2011. Top-down interactions and temperature control of snow crab abundance in the northwest Atlantic Ocean. Marine Ecology Progress Series, 429: 169–183.

Bouman, H. A., Platt, T., Sathyendranath, S., Li, W. K. W., Stuart, V., Fuentes-Yaco, C., Maass, H., *et al.* 2003. Temperature as indicator of optical properties and community structure of marine phytoplankton: implications for remote sensing. Marine Ecology Progress Series, 258: 19–30.

Bourdages, H., Archambault, D., Bernier, B., Fréchet, A., Gauthier, J., Grégoire, F., Lambert, J., *et al.* 2010. Preliminary results from the groudfish and shrimp multidisciplinary survey in August 2010 in the northern Gulf of St. Lawrence. DFO Canadian Science Advisory Secretariat Research Document 2010/107. 92 pp.

Brêthes, J. C. F., Coulombe, F., Lafleur, P. E., and Bouchard, R. 1987. Habitat and spatial distribution of early benthic stages of the snow crab *Chionoecetes opilio* O. Fabricius off the north shore of the Gulf of St. Lawrence. Journal of Crustacean Biology, 7: 667–681.

Burgos, J., Ernst, B., Armstrong, D., and Orensanz, J. M. 2013. Fluctuations in range and abundance of snow crab (*Chionoecetes opilio*) from the eastern Bering Sea: what role for Pacific cod (*Gadus macrocephalus*) predation? Bulletin of Marine Science, 89: 57–81.

Caddy, J. F., Wade, E., Surette, T., Hebert, M., and Moriyasu, M. 2005. Using an empirical traffic light procedure for monitoring and forecasting in the Gulf of St. Lawrence fishery for the snow crab, *Chionoecetes opilio*. Fisheries Research, 76: 123–145.

Chabot, D., Sainte-Marie, B., Briand, K., and Hanson, J. M. 2008. Atlantic cod and snow crab predator-prey size relationship in the Gulf of St. Lawrence, Canada. Marine Ecology Progress Series, 363: 227–240.

Comeau, M., Conan, G. Y., Maynou, F., Robichaud, G., Therriault, J. C., and Starr, M. 1998. Growth, spatial distribution, and abundance of benthic stages of the snow crab (*Chionoecetes opilio*) in Bonne Bay, Newfoundland, Canada. Canadian Journal of Fisheries and Aquatic Sciences, 55: 262–279.

Conan, G. Y., Starr, M., Comeau, M., Therriault, J.-C., Maynou, F. X., and Robichaud, G. 1996. Life history strategies, recruitment fluctuations, and management of the Bonne Bay Fjord Atlantic snow crab (*Chionoecetes opilio*). *In* High Latitude Crabs: Biology, Management, and Economics, Program Report AK-SG-96-02, pp. 59–97. Ed. by B. Baxter. Alaska Sea Grant College, Anchorage, AK.

Davidson, K. G., and Chin, E. A. 1991. A comparison of the taxonomic characteristics and duration of the laboratory reared larvae of snow crabs, *Chionoecetes opilio* (O. Fabricius), and toad crabs (*Hyas* sp.) from Atlantic Canada. Canadian Technical Report of Fisheries and Aquatic Sciences No. 1762. 21 pp.

Dawe, E. G., Koen-Alonso, M., Chabot, D., Stansbury, D., and Mullowney, D. 2012b. Trophic interactions between key predatory fishes and crustaceans: comparison of two Northwest Atlantic systems during a period of ecosystem change. Marine Ecology Progress Series, 469: 233–248.

Dawe, E. G., Mullowney, D. R., Moriyasu, M., and Wade, E. 2012a. Effects of temperature on size-at-terminal molt and molting frequency in snow crab *Chionoecetes opilio* from two Canadian Atlantic ecosystems. Marine Ecology Progress Series, 469: 279–296.

Dawe, E. G., Parsons, D. G., and Colbourne, E. 2008. Relationships of sea ice extent and bottom water temperature with abundance of snow crab (*Chionoecetes opilio*) in the Newfoundland-Labrador Shelf. ICES CM 2008/B:02. 18 pp.

Dionne, M., Sainte-Marie, B., Bourget, E., and Gilbert, D. 2003. Distribution and habitat selection of early benthic stages of snow crab *Chionoecetes opilio*. Marine Ecology Progress Series, 259: 117–128.

Drouineau, H., Sainte-Marie, B., and Duplisea, D. 2013. Estimating natural mortality and egg production of snow crab *Chionoecetes opilio* adult females. Aquatic Biology, 18: 261–270.

Dutil, J-D., Munro, J., and Péloquin, M. 1997. Laboratory study of the influence of prey size on vulnerability to cannibalism in snow crab (*Chionoecetes opilio* O. Fabricius, 1780). Journal of Experimental Marine Biology and Ecology, 212: 81–94.

Ernst, B., Armstrong, D. A., Burgos, J., and Orensanz, J. M. 2012. Life history schedule and periodic recruitment of female snow crab (*Chionoecetes opilio*) in the eastern Bering Sea. Canadian Journal of Fisheries and Aquatic Sciences, 69: 532–550.

FAO. 2013. Species fact sheets: *Chionoecetes opilio* (O. Fabricius, 1788). www.fao.org/fishery/species/2644/en (last accessed 14 May 2013).

Fonseca, D. B., Sainte-Marie, B., and Hazel, F. 2008. Longevity and change in shell condition of adult male snow crab *Chionoecetes opilio* inferred from dactyl wear and mark-recapture data. Transactions of the American Fisheries Society, 137: 1029–1043.

Foyle, T. P., O'Dor, R. K., and Elner, R. W. 1989. Energetically defining the thermal limits of the snow crab. Journal of Experimental Biology, 145: 371–393.

Frank, K. T., Petrie, B., Choi, J. S., and Leggett, W. C. 2005. Trophic cascades in a formerly cod-dominated ecosystem. Science, 308: 1621–1623.

Galbraith, P. S., Chassé, J., Gilbert, D., Larouche, P., Brickman, D., Pettigrew, B., Devine, L., *et al.* 2012a. Physical oceanographic conditions in the Gulf of St. Lawrence in 2011. DFO Canadian Science Advisory Secreteriat Research Document 2012/023. 85 pp.

Galbraith, P. S., Larouche, P., Chassé, J., and Petrie, B. 2012b. Sea-surface temperature in relation to air temperature in the Gulf of St. Lawrence: interdecadal variability and long term trends. Deep-Sea Research II, 77–80: 10–20.

Gallego, A., North, E. W., and Houde, E. D. 2012. Understanding and quantifying mortality in pelagic, early life stages of marine organisms—old challenges and new perspectives. Journal of Marine Systems, 93: 1–3.

Gayanilo, F., Sparre, P., and Pauly, D. 2005. FAO-ICLARM Stock Assessment Tools II (FiSAT II). Revised version. User's guide. FAO Computerized Information Series (Fisheries) No. 8. FAO, Rome. 168 pp.

Gravel, K. 2002. Bilan énergétique des juvéniles du crabe des neiges, *Chionoecetes opilio*, à différentes températures. MSc thesis. Université du Québec à Rimouski, Rimouski, QC.

Grömping, U. 2006. Relative importance for linear regression in R: the package relaimpo. R package version 2.2-2. Journal of Statistical Software, 17: 1–27.

Halpern, B. S., Cottenie, K., and Broitman, B. R. 2006. Strong top-down control in southern California kelp forest ecosystems. Science, 312: 1230–1232.

Houde, E. D. 2008. Emerging from Hjort's shadow. Journal of Northwest Atlantic Fishery Science, 41: 53–70.

Hunt, H. L., and Scheibling, R. E. 1997. Role of early post-settlement mortality in recruitment of benthic marine invertebrates. Marine Ecology Progress Series, 155: 269–301.

ICES. 2011. Report of the Arctic Fisheries Working Group (AFWG), 28 April–4 May, Hamburg, Germany. ICES CM 2011/ACOM:05. 659 pp.

Jørgensen, L. L., and Spiridonov, V. 2013. Effect from the king- and snow crab on Barents Sea benthos. Results and conclusions from the Norwegian-Russian Workshop in Tromsø 2010. Fisken of Havet nr. 8/2013. Institute of Marine Research, Bergen, Norway. 41 pp.

Koeller, P., Fuentes-Yaco, C., Platt, T., Sathyendranath, S., Richards, A., Ouellet, P., Orr, D., *et al.* 2009. Basin-scale coherence in phenology of shrimps and phytoplankton in the North Atlantic Ocean. Science, 324: 791–793.

Kolts, J. M., Lovvorn, J. R., North, C. A., Grebmeier, J. M., and Cooper, L. W. 2013. Effects of body size, gender, and prey availability on diets of snow crabs in the northern Bering Sea. Marine Ecology Progress Series, 483: 209–220.

Köster, F. W., and Möllmann, C. 2000. Trophodynamic control by clupeid predators on recruitment success in Baltic cod? ICES Journal of Marine Science, 57: 310–323.

Kuhn, P. S., and Choi, J. S. 2011. Influence of temperature on embryo developmental cycles and mortality of female *Chionoecetes opilio* (snow crab) on the Scotian Shelf, Canada. Fisheries Research, 107: 245–252.

Lilly, G. R., Parsons, L. S., and Kulka, D. W. 2000. Was the increase in shrimp biomass on the northeast Newfoundland Shelf a consequence of a release in predation pressure from cod? Journal of Northwest Atlantic Fishery Science, 27: 45–61.

Lovrich, G. A., and Sainte-Marie, B. 1997. Cannibalism in the snow crab, *Chionoecetes opilio* (O. Fabricius) (Brachyura: Majidae), and its potential importance to recruitment. Journal of Experimental Marine Biology and Ecology, 211: 225–245.

Lovrich, G. A., Sainte-Marie, B., and Smith, B. D. 1995. Depth distribution and seasonal movements of *Chionoecetes opilio* (Brachyura, Majidae) in Baie Sainte-Marguerite, Gulf of Saint Lawrence. Canadian Journal of Zoology, 73: 1712–1726.

Marcello, L. A., Mueter, F. J., Dawe, E. G., and Moriyasu, M. 2012. Effects of temperature and gadid predation on snow crab recruitment: comparisons between the Bering Sea and Atlantic Canada. Marine Ecology Progress Series, 469: 249–261.

Mueter, F. J., Dawe, E. G., and Palsson, O. K. 2012. Subarctic fish and crustacean populations—climate effects and trophic dynamics. Marine Ecology Progress Series, 469: 191–193.

Mullowney, D. R. J., Dawe, E. G., Colbourne, E. B., and Rose, G. A. 2014. A review of factors contributing to the decline of Newfoundland and Labrador snow crab (*Chionoecetes opilio*). Reviews in Fish Biology and Fisheries, 24: 639–657.

Munch, S. B., Snover, M. L., Watters, G. M., and Mangel, M. 2005. A unified treatment of top-down and bottom-up control of reproduction in populations. Ecology Letters, 8: 691–695.

Orensanz, J. M., Ernst, B., and Armstrong, D. A. 2007. Variation of female size and stage at maturity in snow crab (*Chionoecetes opilio*) (Brachyura: Majidae) from the eastern Bering Sea. Journal of Crustacean Biology, 27: 576–591.

Orensanz, J. M., Ernst, B., Armstrong, D. A., Stabeno, P., and Livingston, P. 2004. Contraction of the geographic range of distribution of snow crab (*Chionoecetes opilio*) in the eastern Bering Sea: an environmental ratchet? CalCOFI Report, 45: 65–79.

Parada, C., Hinckley, S., Ernst, B., Orensanz, J. M., Armstrong, D. A., Curchitser, E., and Hermann, A. J. 2007. Settlement patterns of snow crab associated with warm and cold years in the eastern Bering Sea. ICES CM 2007/B:12. 14 pp.

Pineda, J., Reyns, N., and Starczak, V. 2009. Complexity and simplification in understanding recruitment in benthic populations. Population Ecology, 51: 17–32.

Puebla, O., Sévigny, J. M., Sainte-Marie, B., Brêthes, J. C., Burmeister, A., Dawe, E. G., and Moriyasu, M. 2008. Population genetic structure of the snow crab (*Chionoecetes opilio*) at the Northwest Atlantic scale. Canadian Journal of Fisheries and Aquatic Sciences, 65: 425–436.

Quijón, P. A., and Snelgrove, P. V. R. 2005a. Differential regulatory roles of crustacean predators in a sub-arctic, soft-sediment system. Marine Ecology Progress Series, 285: 137–149.

Quijón, P. A., and Snelgrove, P. V. R. 2005b. Predation regulation of sedimentary faunal structure: potential effects of a fishery-induced switch in predators in a Newfoundland sub-Arctic fjord. Oecologia, 144: 125–136.

Quinn, G. P., and Keough, M. J. 2002. Experimental design and data analysis for biologists. Cambridge University Press, Cambridge, UK. 537 pp.

R Development Core Team. 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing. Vienna, Austria. www.R-project.org (last accessed 23 January 2014).

Robichaud, D. A., Elner, R. W., and Bailey, R. F. J. 1991. Differential selection of crab *Chionoecetes opilio* and *Hyas* spp. as prey by sympatric cod *Gadus morhua* and thorny skate *Raja radiata*. Fishery Bulletin, 89: 669–680.

Sainte-Marie, B. 1993. Reproductive cycle and fecundity of primiparous and multiparous female snow crab, *Chionoecetes opilio*, in the Northwest Gulf of Saint Lawrence. Canadian Journal of Fisheries and Aquatic Sciences, 50: 2147–2156.

Sainte-Marie, B., Gosselin, T., Sévigny, J. M., and Urbani, N. 2008. The snow crab mating system: opportunity for natural and unnatural selection in a changing environment. Bulletin of Marine Science, 83: 131–161.

Sainte-Marie, B., and Hazel, F. 1992. Moulting and mating of snow crabs, *Chionoecetes opilio* (O. Fabricius), in shallow water of the northwestern Gulf of Saint Lawrence. Canadian Journal of Fisheries and Aquatic Sciences, 49: 1282–1293.

Sainte-Marie, B., and Lafrance, M. 2002. Growth and survival of recently settled snow crab *Chionoecetes opilio* in relation to intra- and intercohort competition and cannibalism: a laboratory study. Marine Ecology Progress Series, 244: 191–203.

Sainte-Marie, B., Raymond, S., and Brethes, J. C. 1995. Growth and maturation of benthic stages of male snow crab, *Chinoecetes opilio* (Brachyura, Majidae). Canadian Journal of Fisheries and Aquatic Sciences, 52: 903–924.

Sainte-Marie, B., Sévigny, J. M., Smith, B. D., and Lovrich, G. A. 1996. Recruitment variability in snow crab (*Chionoecetes opilio*): pattern, possible causes, and implications for fishery management. *In* High Latitude Crabs: Biology, Management, and Economics, Program Report AK-SG-96-02, pp. 451–478. Ed. by B. Baxter. Alaska Sea Grant College, Anchorage, AK.

Santander Meteorology Group. 2012. fume: FUME package. R package version 1.0. http://CRAN.R-project.org/package=fume (last accessed 15 September 2013).

Somerton, D. A. 1982. Effects of sea ice on the distribution and population fluctuations of *C. opilio* in the eastern Bering Sea. *In* Proceedings of the International Symposium on the Genus *Chionoecetes*, Program Report AK-SG-82-10, pp. 159–171. Ed. by B. Metleff. Alaska Sea Grant College, Fairbanks, AK.

Squires, H. J., and Dawe, E. G. 2003. Stomach contents of snow crab (*Chionoecetes opilio*, Decapoda, Brachyura) from the northeast Newfoundland Shelf. Journal of Northwest Atlantic Fishery Science, 32: 27–38.

Szuwalski, C., and Punt, A. E. 2013. Regime shifts and recruitment dynamics of snow crab, *Chionoecetes opilio*, in the eastern Bering Sea. Fisheries Oceanography, 22: 345–354.

Vittinghoff, E., Glidden, D. V., Shiboski, S. C., and McCulloch, C. E. 2005. Regression Methods in Biostatistics: Linear, Logistic, Survival, and Repeated Measures Models. Statistics for Biology and Health, Springer. pp. 340.

Waiwood, K., and Elner, R. W. 1982. Cod predation of snow crab, *Chionoecetes opilio*, in the Gulf of St. Lawrence. *In* Proceedings of the International Symposium on the Genus *Chionoecetes*, Program Report AK-SG-82-10, pp. 499–520. Ed. by B. Metleff. Alaska Sea Grant College, Fairbanks, AK.

Windle, M. J. S., Rose, G. A., Devillers, R., and Fortin, M. J. 2012. Spatio-temporal variations in invertebrate-cod-environment relationships on the Newfoundland-Labrador Shelf, 1995–2009. Marine Ecology Progress Series, 469: 263–278.

Winger, P. D., and Walsh, P. J. 2011. Selectivity, efficiency, and underwater observations of modified trap designs for the snow crab (*Chionoecetes opilio*) fishery in Newfoundland and Labrador. Fisheries Research, 109: 107–113.

Worm, B., and Myers, R. A. 2003. Meta-analysis of cod-shrimp interactions reveals top-down control in oceanic food webs. Ecology, 84: 162–173.

Yamamoto, T. Y., Fujimoto, H., and Hamasaki, K. 2014. Effects of temperature on snow crab (*Chionoecetes opilio*) larval survival and development under laboratory conditions. Journal of Shellfish Research, 33: 19–24.

Zheng, J., and Kruse, G. H. 2003. Stock-recruitment relationships for three major Alaskan crab stocks. Fisheries Research, 65: 103–121.

Zheng, J., and Kruse, G. H. 2006. Recruitment variation of eastern Bering Sea crabs: climate-forcing or top-down effects? Progress in Oceanography, 68: 184–204.

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