



Top-down interactions and temperature control of snow crab abundance in the northwest Atlantic Ocean

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ABSTRACT: In much of the northwest Atlantic Ocean, commercially important snow crab *Chionoecetes opilio* stocks have increased in abundance since the decline and collapse of major groundfish stocks such as Atlantic cod *Gadus morhua*. We examined 3 hypotheses to explain variation in the abundance of snow crabs across 10 regions: (1) climate control of both species, (2) top-down control of snow crab by cod and (3) bottom-up control of cod by snow crab. We tested these hypotheses by analyzing time series data of cod and crab abundance indices and temperature via meta-analysis of full and partial correlation coefficients. We found that temperature had an opposing effect on the 2 species: snow crab abundance was negatively correlated with temperature at 7 to 10 yr lags, whereas cod and temperature were positively related at 1 to 7 yr lags. Controlling for the effect of temperature, our meta-analysis revealed significant negative correlations of snow crab and cod abundance, with cod leading snow crab by up to a 5 yr lag. This suggests a top-down effect on older juvenile and subadult snow crab. We found no evidence of a bottom-up effect of snow crab on cod. Negative correlations between cod and crab abundance were observed both at the warmer and colder portions of their ranges. These results suggest that snow crab abundance is largely influenced by temperature during the early postsettlement years and becomes increasingly regulated by top-down mechanisms during the years approaching fishery recruitment. The method presented in this paper is generally useful to test ecological hypotheses from time series data, particularly where multiple causal mechanisms are suspected.

KEY WORDS: Predation · Species interactions · Climate · Snow crab · *Chionoecetes opilio* · Atlantic cod · *Gadus morhua* · Meta-analysis

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INTRODUCTION

The decline and collapse of Atlantic cod *Gadus morhua* stocks in the NW Atlantic Ocean over the last 2 to 3 decades, and coinciding increases in various crustacean species since, have resulted in a changed ecosystem and a sharp transition in fishing effort from large groundfish species to invertebrates (Worm & Myers 2003, Frank et al. 2005, Anderson et al. 2008). Fisheries for American lobster *Homarus americanus*, snow crab *Chionoecetes opilio* and northern shrimp *Pandalus borealis* are currently the most valuable fisheries in Atlantic Canada (DFO 2009a). Snow crab populations experienced large interannual variation with sustained increases over much of the 1990s (e.g. Conan

et al. 1996, Sainte-Marie et al. 1996, Tremblay 1997, Caddy et al. 2005; Fig. 1). It is unclear which ecological factors influenced this variation and whether they relate to population dynamics. Such factors could include density dependence and cannibalism (e.g. Sainte-Marie et al. 1996, Lovrich & Sainte-Marie 1997, Sainte-Marie & Lafrance 2002), species interactions (e.g. predation; Bailey 1982, Tremblay 1997, Chabot et al. 2008), environmental forcing (e.g. temperature fluctuations; Taylor et al. 1993, Conan et al. 1996, Tremblay 1997) or a combination of these.

The relative importance of these factors in the NW Atlantic Ocean cannot be resolved from an analysis of single time series owing to their limited length (20 to 31 yr) and confounding factors (e.g. sample size, vari-

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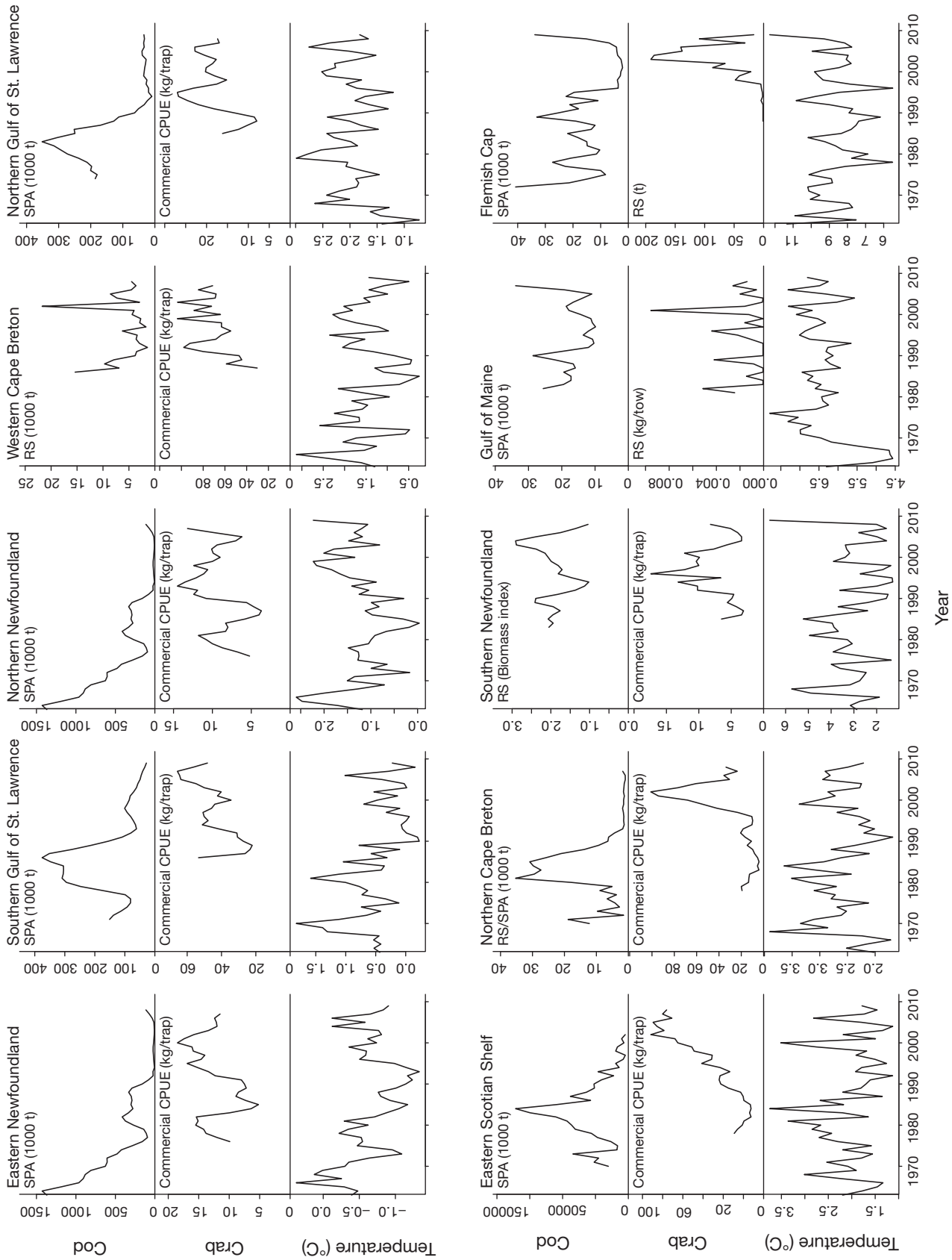


Fig. 1. Time series data. Atlantic cod *Gadus morhua* biomass indices ($\times 1000$ t, top row), snow crab *Chionoecetes opilio* abundance indices (kg trap⁻¹, centre row) and temperature (°C, bottom row) in the regions of study (see Fig. 2) were plotted over time and arranged by temperature from the area with the coldest median water temperature (eastern Newfoundland) to the warmest (Flemish Cap). CPUE (fishery-independent): catch per unit effort; RS (fishery-independent): research surveys; SPA: sequential population analysis. Refer to Table 2 for full details about the cod and crab time series. Temperature data was obtained from the DFO Hydrographic Climate Database (Gregory 2004)

ability), both of which limit statistical inference. When analyzed together, replicated time series in multiple regions can provide insight into food-web interactions (e.g. Worm & Myers 2003). Here we introduce an extended meta-analytic approach to explore the causes of variation in snow crab abundance and to test multiple ecological hypotheses about the structuring factors of marine ecosystems.

In this context, the overfishing and collapse of NW Atlantic cod stocks (Myers et al. 1996, 1997a) may be viewed as the replicated realization of a large-scale predator removal experiment. Analyses of stomach contents demonstrate that various crabs, including snow crab, are important prey of cod in the Atlantic Ocean (see Table 1). However, previous analyses have yielded conflicting conclusions about the role Atlantic cod plays in regulating snow crab abundance. Bailey (1982) found strong evidence of a predator–prey relationship whereas Waiwood & Elner (1982) did not. Chabot et al. (2008) found that snow crab comprised less than 10% of stomach content mass in Atlantic cod from the Gulf of St. Lawrence (GSL). By comparison, northern shrimp comprises from 5.0 to 9.3% of cod stomach contents (averaged across studies), and cod appears to exert strong top-down control of shrimp stocks (Worm & Myers 2003 and references therein). Further, this interaction was found to be temperature dependent, with stronger evidence of top-down control in colder temperatures (Worm & Myers 2003, Frank et al. 2007).

Snow crabs in Atlantic Canada are generally found at temperatures between -0.5 and 5°C (Elner 1982, Tremblay 1997), and bottom temperature is thought to be an important determinant of snow crab distribution. Along the Scotian Shelf, snow crabs are predominantly found in areas where the bottom temperature does not exceed 7°C (Tremblay 1997). At 7°C energetic restrictions come into play for mature males as metabolic costs begin to rise faster than energy inputs (Foyle et al. 1989). A decline in mean bottom temperature from -0.6 to -1.4°C in the 1980s off southeastern Newfoundland is thought to have interrupted the moult cycle of the snow crab, and the absence of newly moulted recruits contributed to a collapse of the crab fishery (Taylor et al. 1993). Though environmental conditions may not fully explain the cyclical nature of snow crab populations (Conan et al. 1996, Sainte-Marie et al. 1996), it is possible that lower temperatures after 1984 may have contributed to an expansion in habitat (e.g. Tremblay 1997) (Fig. 1). Water temperature and substrate are also thought to be important for the survival of early life stages of snow crab (e.g. Lovrich et al. 1995, Dionne et al. 2003).

By expanding on the meta-analytic methods established by Worm & Myers (2003), we attempted to test

both predation and climate hypotheses by correlating snow crab abundance, Atlantic cod biomass, and ocean temperature. Specifically, our goal was to examine 3 competing hypotheses to explain variation in snow crab abundance: (1) climate control, which should result in correlations with environmental variables such as ocean temperature; (2) top-down control, which should result in negative correlations between cod (predator) and crab (prey); and (3) bottom-up control, which should result in positive correlations between cod and crab abundance if both populations are driven by factors regulating productivity. We examine these hypotheses simultaneously, accounting for possible time lags, for 10 regions ranging from the northern to the southern limits of snow crab populations on the NW Atlantic continental shelf.

METHODS

Species. In the NW Atlantic Ocean, male and female snow crabs can reach a maximum carapace width (CW) of 150 and 80 mm, respectively, after their terminal moult (Chabot et al. 2008) to maturity (Conan & Comeau 1986). Only males with a CW greater than 95 mm are harvested commercially (Sainte-Marie et al. 1996, Choi & Zisserson 2008) and females are not retained (Miller 1976). On the Scotian Shelf, snow crabs are usually most abundant between 100 and 250 m depth and are found at cold temperatures between <1 and 3°C (Tremblay 1997). It takes approximately 9 (postsettlement) to 11 (postegg extrusion) yr for male snow crab to reach the minimum CW, and after the terminal moult, their life expectancy is approximately 5 to 8 yr (Sainte-Marie et al. 1995, Choi & Zisserson 2008, Fonseca et al. 2008). In the GSL, snow crabs migrate to shallow (<35 m) waters to moult in the early spring (Sainte-Marie & Hazel 1992, Lovrich et al. 1995). Both sexes separate by depth and aggregate according to maturity, shell condition and size. Primiparous females and small adult males are generally found in shallower water whereas multiparous females and large adult males are found in deeper water (Sainte-Marie & Hazel 1992).

Atlantic cod are highly migratory (ICES 2005) and feed opportunistically on benthic crustaceans and other invertebrates before becoming increasingly piscivorous with size (Hanson & Chouinard 2002, Link & Garrison 2002). Atlantic cod can be as large as 150 cm, live 20+ yr and occupy depths from 1 to 600 m (Pálsson 1994). Atlantic cod in the NW Atlantic Ocean are found at a range of depths and temperatures. For example, on the Flemish Cap (FC) they can be found from 150 to 500+ m at temperatures ranging between 3.5 and 4.5°C (ICES 2005). On Georges Bank (in the Gulf of

Maine [GOM]) they are found at their upper range of temperatures from 10 to 14°C (annual mean at 100 m) (ICES 2005). In eastern Newfoundland (ENL) they are found at their lower range of temperatures from <0 to 6°C (ICES 2005). Stomach sampling confirms that Atlantic cod prey on snow crab and that their ranges overlap (Table 1).

Data. We compiled all available time series of Atlantic cod and snow crab abundances in the NW Atlantic Ocean (Table 2, Fig. 2 for study regions). For cod populations, we used biomass estimates derived from random stratified research surveys (RS) and from sequential population analyses (SPA) as presented in the official Canadian Department of Fisheries and Oceans (DFO) stock assessments (Table 2). In Canada, snow crabs were not recorded consistently in the standard trawl surveys in most of the east coast regions until the mid-1990s (Table 2). Therefore, in our analyses, we used fishery catch per unit effort (CPUE) data (catch per trap haul) for those regions. For snow crabs in the FC and GOM we used data from otter trawl surveys in which all sizes of crab encountered were recorded and included in the present data set and analysis (i.e. not only legal-sized males). These surveys are variable owing to the low densities of snow crab but can still be used to examine long-term population trends.

In Canada, localized exploitation of snow crab began in the 1960s through incidental catch by groundfish fleets (Bailey & Elner 1989, DFO 2009b,c). Directed fishing with baited traps was introduced in the late 1960s (Bailey & Elner 1989, DFO 2009c) and fishing pressure intensified and expanded from the mid-1970s (Bailey & Elner 1989) through the mid-1990s, with a decline in catches through the 1980s (Tremblay 1997, DFO 2009b,c,d). By the early 1990s, fishers were exploiting most of the snow crab's distribution along the Scotian Shelf (Tremblay 1997, DFO 2009b) and expanding to offshore regions in Newfoundland (DFO 2009c).

Table 1. Predation by Atlantic cod *Gadus morhua* on snow crab *Chionoecetes opilio*. The mean proportion of snow crab in the diet of Atlantic cod is expressed by 3 measures: (1) percent by mass of stomach contents (Mass), (2) percent of mean frequency of occurrence (MFO) and (3) a partial fullness index (PFI, see Lilly 1984). To demonstrate the range of snow crab ingested by Atlantic cod, the number of cod stomachs (Cod N) examined, the number of snow crabs measured in the stomach contents (Crab N), the carapace width of the snow crab (CW), the length of cod sampled (Cod L) and cod age are reported when available. Ranges of values are in brackets following the mean values and data have been pooled across available years. Sources: 1: Lilly (1984); 2: Robichaud et al. (1991); 3: Chabot et al. (2008); 4: Watwood & Elner (1982); 5: Hanson & Chouinard (2002); 6: Waiwood & Majkowski (1984)

Region	Data range	Cod (N)	Crab (N)	Mass (%)	MFO (%)	PFI	CW (mm)	Cod L (cm)	Cod age (yr)	Source
NE Newfd. (NAFO 2J, Hamilton Bank)	1977–1982	1650	–	–	–	0.04 (0–0.10)	–	30–69	–	1
NE Newfoundland (NAFO 2J3K)	1978, 1980–1982	5739	–	–	–	0.03 (0.01–0.05)	–	30–69	–	1
NE Newfoundland (NAFO 2J3K)	1982	3077	–	8.4	15.3	0.08	–	–	–	1
NE Newfoundland (NAFO 2J3K)	1986	2125	–	3.8	8.7	0.05	–	–	–	1
NW Cape Breton	1981–1982	933	–	16.5 (0–66.2)	15.4 (0–52.5)	–	–	–	–	2
NW Cape Breton	1981–1982	–	10	–	–	–	77–107 ^a	49–66	–	2
NW Cape Breton	1981–1982	–	7	–	–	–	46–70 ^b	67–106	–	2
NW Cape Breton	1981–1982	–	–	–	–	–	6–44 ^c	33–82	–	2
Gulf of St. Lawrence	–	–	–	–	–	–	65.1 ^d	>80	–	3
N Gulf of St. Lawrence (NAFO 3Pn4RS)	1993–2003	16672	2667 ^e	3.5 (0–10.86)	9.1 (0–18.8)	0.05 (0–0.16)	2.2–62.4	7.5–92.5	–	3
S Gulf of St. Lawrence (NAFO 4T)	1987, 1990–1995, 1999–2003	14301	626 ^e	2.1 (0–7.17)	4.5 (0–12.8)	0.03 (0–0.12)	~3.3–51	7.5–92.5	–	3
S Gulf of St. Lawrence (NAFO 4T)	1959–1973, 1980–1981	–	–	–5 (0–34)	–	–	–	–	7–15	4
S Gulf of St. Lawrence	1987, 1991, 1995, 1997	–	–	5–7	–	–	–	–	–	5
S Gulf of St. Lawrence	1980	–	–	17	–	–	–	46–60	–	5
S Gulf of St. Lawrence	1962, 1970, 1991, 1999	–	–	>5	–	–	–	61–75	–	5
S Gulf of St. Lawrence	1980	1880	–	10.6 (1–22)	–	–	–	61–75	–	5
S Gulf of St. Lawrence	1980	–	–	–	–	–	–	33.9–80.8+	3.4–11+	6

^aNewly moulted males; ^bHard-shelled ovigerous females; ^cJuveniles, both sexes; ^dEstimated ceiling of hard-shelled snow crab ingested by large cod; ^eValue reflects only the crabs actually measured in the cod stomachs

Table 2. Data sources for Atlantic cod *Gadus morhua* and snow crab *Chionoecetes opilio* abundance estimates from stock assessments. Assessment methods included sequential population analysis (SPA), catch per unit effort (CPUE) and research surveys (RS)

Atlantic cod			Snow crab		
Reference	Data range	Assessment	Reference	Data range	Assessment
Northern Newfoundland	Bishop et al. (1994)	SPA	R. J. Miller (pers. comm.)	1976–1980	CPUE
	Lilly et al. (2006)	SPA	E. G. Dawe (pers. comm.)	1981–2007	CPUE
Eastern Newfoundland	Bratley et al. (2009)	SPA	DFO (2009c)	1995–2008	RS
	Bishop et al. (1994)	SPA	E. G. Dawe (pers. comm.)	1976–2007	CPUE
	Lilly et al. (2006)	SPA	DFO (2009c)	1995–2008	RS
Southern Newfoundland	Bratley et al. (2009)	SPA	DFO (2007)	1981–2008	CPUE
Flemish Cap	DFO (2009g)	RS	A. Vázquez (pers. comm.)	1988–2009	RS
Northern Gulf of St. Lawrence	Vázquez & Cervino (2002)	SPA	B. Sainte-Marie (pers. comm.)	1985–2008	CPUE
	Gonzalez-Troncoso & Fernandez (2009)	SPA	DFO (2009e)	1996–2008	RS
	DFO (2009f)	SPA	Hébert et al. (2001)	1986–2000	CPUE
Southern Gulf of St. Lawrence	Swain et al. (2009)	SPA	DFO (2010a)	2001–2009	CPUE
			DFO (2010a)	1988–2009	RS
Western Cape Breton	Chouinard et al. (2001)	RS	Hébert et al. (2008)	1987–2007	CPUE
	D. P. Swain (pers. comm.)	RS	DFO (2010a)	1993–2009	RS
Northern Cape Breton	G. M. Fowler (pers. comm.)	RS	Biron et al. (2001)	1978–1996	CPUE
	G. M. Fowler (pers. comm.)	SPA	DFO (2009b)	1997–2008	CPUE
Eastern Scotian Shelf	Fanning et al. (2003)	SPA	DFO (2009b)	1998–2008	RS
			Biron et al. (2001)	1978–1996	CPUE
Gulf of Maine	NEFSC (2008)	SPA	DFO (2009b)	1997–2008	CPUE
			DFO (2009b)	1999–2008	RS
			R. W. Brown (pers. comm.)	1981–2008	RS

Pers. comms: R. W. Brown, NEFSC, NOAA Fisheries, Woods Hole, MA, USA; E. G. Dawe, NAFC, DFO, St. Johns, NL, Canada; G. M. Fowler, DFO, Bedford Institute of Oceanography, Dartmouth, NS, Canada; R. J. Miller, DFO, Bedford Institute of Oceanography, Dartmouth, NS, Canada; B. Sainte-Marie, Maurice Lamontagne Institute, DFO, Mont-Joli, QC, Canada; D. P. Swain, Gulf Fisheries Centre, DFO, Moncton, NB, Canada; A. Vázquez, Instituto de Investigaciones Marinas, CSIC, Vigo, Spain

CPUE may not always reflect changes in species abundance (e.g. Harley et al. 2001) and could be sensitive to changes in fishing efficiency (e.g. Myers & Cadigan 1995, Hutchings 1996, Swain & Wade 2003) and target species catchability (e.g. Murray & Seed 2010). Still, CPUE is commonly used as an index of abundance when fisheries-independent data are unavailable. CPUE in the northern Gulf of St. Lawrence (NGSL) is the only time series that has been standardized by the DFO to account for season, gear type and soak time (DFO 2009e). Where possible, we examined how well fishery CPUE tracked biomass estimates from research surveys using linear regression.

To consider the effect of temperature on both cod and crab populations we assembled temperature time series at depths where cod and crab distributions overlap (150 ± 75 m depth; 350 ± 100 m depth for the FC). We obtained temperature data from the DFO Hydrographic Climate Database (Gregory 2004) and used generalized linear models with year and month as independent variables to derive adjusted mean annual temperature trends.

Analysis. To stabilize variances we log-transformed all cod and crab time series. We corrected for autocorrelation by adjusting the effective degrees of freedom of the correlation coefficients using the modified Chelton method (Pyper & Peterman 1998). We applied a Fisher's z transformation to the correlation coefficients before combining them to normalize their distribution and stabilize their variance (Stuart & Ord 1987, Worm & Myers 2003). Corrected correlation coefficients were combined by means of random-effects inverse-variance-weighted meta-analysis (Hedges 1994, Worm & Myers 2003). When the assumption of homogeneous effect sizes is violated, e.g. when comparing populations from substantially different habitats, the random-effects approach is more realistic than the fixed-effects approach (Hedges 1994).

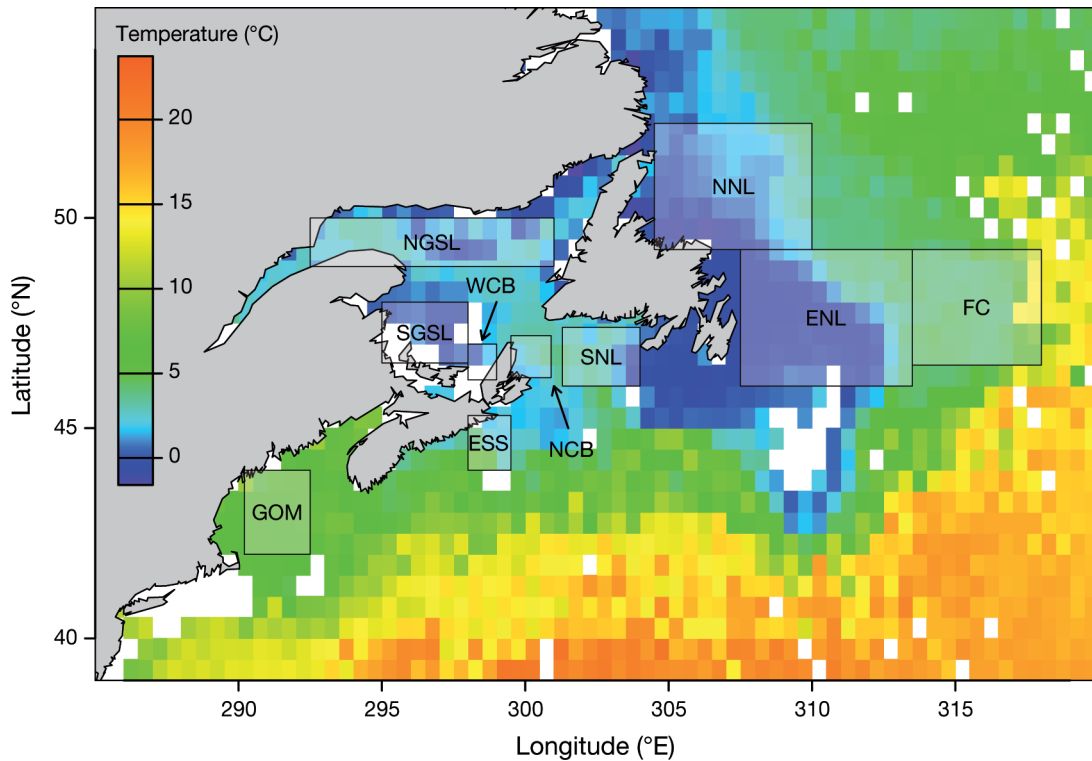


Fig. 2. Study regions. To illustrate temperatures regimes we underlayed the median temperature across all available samples from 1 January 2005 to 1 January 2010 at 150 ± 75 m depth at $0.5^\circ \times 0.5^\circ$ resolution. NNL: northern Newfoundland; ENL: eastern Newfoundland; SNL: southern Newfoundland; FC: Flemish Cap; NSGL: northern Gulf of St. Lawrence; SGSL: southern Gulf of St. Lawrence; WCB: western Cape Breton; NCB: northern Cape Breton; ESS: eastern Scotian Shelf; GOM: Gulf of Maine

We extended the meta-analytic approach of Worm & Myers (2003) to include testing for the effect of cod biomass on crab abundance after accounting for the effect of water temperature. We therefore conducted 4 separate meta-analyses. To test the hypothesis that changes in population abundance were related to climate, we separately analyzed correlations between (1) cod biomass and (2) crab abundance with temperature. To test the top-down and bottom-up species interaction hypotheses, we analyzed correlations between cod biomass and crab abundance. We show meta-analyses of both the (3) full correlations (without taking into account the effect of temperature) and (4) partial correlations (taking into account the effect of temperature). Therefore, for the partial correlations, we first regressed cod and crab series with temperature separately and then regressed the residuals from those models against each other.

We conducted meta-analyses at a variety of time lags to test a suite of hypotheses. It takes snow crab approximately 9 yr postsettlement to moult to legal size and they recruit 1 yr after their terminal moult (Sainte-Marie et al. 1995). The larval and embryonic life stages span 12 yr (Sainte-Marie 1993, Comeau et al. 1999). We therefore examined lags of 0 to 12 yr for each spe-

cies with temperature and both positive and negative lags up to 12 yr for species interactions. We explored the partial correlations by controlling for the effect of temperature at several lags (5 to 9 yr) approximating the year of fishery recruitment. In the final analysis, we controlled for the effect of temperature at a 7 yr lag, as suggested by the maximum correlation in our meta-analysis of temperature with cod and crab abundance (see 'Results'). At positive lags (cod leading snow crab) negative correlations would suggest top-down control of cod on crab. Positive correlations (at negative or positive lags) would suggest bottom-up control by factors affecting the productivity of both species. At negative lags (snow crab leading cod) positive correlations would suggest bottom-up control, potentially by crab as prey for cod.

Recruitment among fish populations within 500 km is frequently correlated (Myers et al. 1997b). Therefore, we tested the sensitivity of our conclusions to potential spatial correlation by repeating our analysis after removing the data from the southern Gulf of St. Lawrence (SGSL), western Cape Breton (WCB), northern Cape Breton (NCB) and ENL, such that all remaining regions were >500 km apart. We further tested for robustness by grouping some of the regions

that demonstrated similar trends and repeating the analyses. The regional groupings tested were: (a) SGSL and NGSL, (b) Northern Newfoundland (NNL) and ENL, (c) ENL, SGSL and NNL, (d) NCB and Southern Newfoundland (SNL), (e) NCB, SNL and FC and (f) all regions excluding the GOM and FC (i.e. using only fishery-dependent CPUE).

RESULTS

Diet studies

A literature survey confirmed that snow crabs are an important component of Atlantic cod diet (Table 1). A wide range of carapace sizes (2.2 to 107 mm CW) were found in Atlantic cod of 18 to 106 cm length. Snow crabs were found in 4.5 to 15.4% of cod stomachs and contributed 2.1 to 16.5% of cod stomach content by weight (Table 1 and references therein). In cases where the ingested snow crabs were measured, most were juveniles, and a larger range of snow crab sizes were recorded as cod length increased. In NW Cape Breton, 3 groups of snow crabs were found in cod stomachs: juveniles were most common (ranging from 6 to 44 mm CW in cod 33 to 82 cm in length), a second group consisted of larger hard-shelled ovigerous females (49 to 70 mm CW in cod 67 to 106 cm) and a third group of mainly large soft-shelled (recently moulted) adult males (77 to 107 mm CW in cod 49 to 66 cm) (Robichaud et al. 1991). In the GSL most of the ingested snow crabs ranged from 5 to 30 mm CW. Hard-shelled crab larger than ~60 to 70 mm CW may not be vulnerable to predation by Atlantic cod in the GSL (Waiwood & Elner 1982, Robichaud et al. 1991, Chabot et al. 2008). These larger hard-shelled crabs are probably not taken because they aggressively confront and may fend off even large cod (Chabot et al. 2008).

Trends

In all areas, snow crab abundance and CPUE varied markedly, but generally increased after cod stocks declined. These changes occurred throughout the 1990s at varying times in different regions (Fig. 1). The increase of snow crab abundance in the 1990s occurred both at the warmer (FC) and the colder (NNL) limits of its range, suggesting the increase was not a simple effect of temperature. Temperature varied interannually in all regions (Fig. 1), and a sustained and gradual cooling of waters in ENL, SGSL and NNL leading up to the 1990s was apparent. Atlantic cod biomass recently increased in the warmer regions of the FC and GOM.

Fishery-independent abundance estimates for snow crabs were available in all regions, with the exception of SNL, but were generally of shorter duration (9 to 21 yr) than fishery CPUE series (20 to 31 yr) (Table 2, Fig. 3). Despite the shortness of the time series, the fishery CPUE and fishery-independent snow crab time series showed similar trends (Fig. 3). The 2 time series were consistently but weakly positively correlated; however, after accounting for autocorrelation, none of the regions were statistically significant (Fig. 3).

Meta-analysis

The meta-analytic summaries of the correlation of temperature on Atlantic cod and snow crab (Fig. 4) showed that for cod, the effects of temperature appeared weakly positive at most lags and significant at lags of 1 to 7 yr. For snow crabs, the correlation with temperature was negative at most lags and significant at lags of 7 to 10 yr (Fig. 4). This basic pattern was particularly evident in the colder regions (ENL, the GSL, and the eastern Scotian Shelf [ESS]), and less so in warmer regions (GOM and FC). Both species had significant correlations with temperature at Year 7 in the meta-analytic summary.

Since Atlantic cod biomass and snow crab abundance respectively correlated with temperature positively and negatively, the potential exists to create spurious negative correlations when correlating time series of both species. Hence, we tested for a relationship between Atlantic cod and snow crab by comparing partial correlations (controlling for temperature at a 7 yr lag), and full correlations among time series of the 2 species (Fig. 5). Controlling for the effect of temperature, our meta-analysis revealed significant negative correlations with cod leading snow crab up to 5 yr. The full correlations (not accounting for temperature) were statistically significant at positive lags of 0 to 5 and 8 yr, and in both the full and partial correlation analyses the strongest effect was observed at a lag of 2 yr, with cod leading snow crab (Fig. 5). Negative correlations at positive lags of 1 to 3 yr were consistent across all individual regions. There was no clear evidence for a bottom-up effect as positive correlations were not statistically significant.

A sensitivity analysis of data with all regions >500 km apart did not alter these conclusions. Additional meta-analyses of separate regional groupings produced results that were remarkably consistent with the full analyses (see the supplement at www.int-res.com/articles/suppl/m429p169_suppl.pdf). Significant negative correlations remained at the shorter time lags (cod leading snow crab) and were consistent when the GOM and FC (fishery-independent indices) were

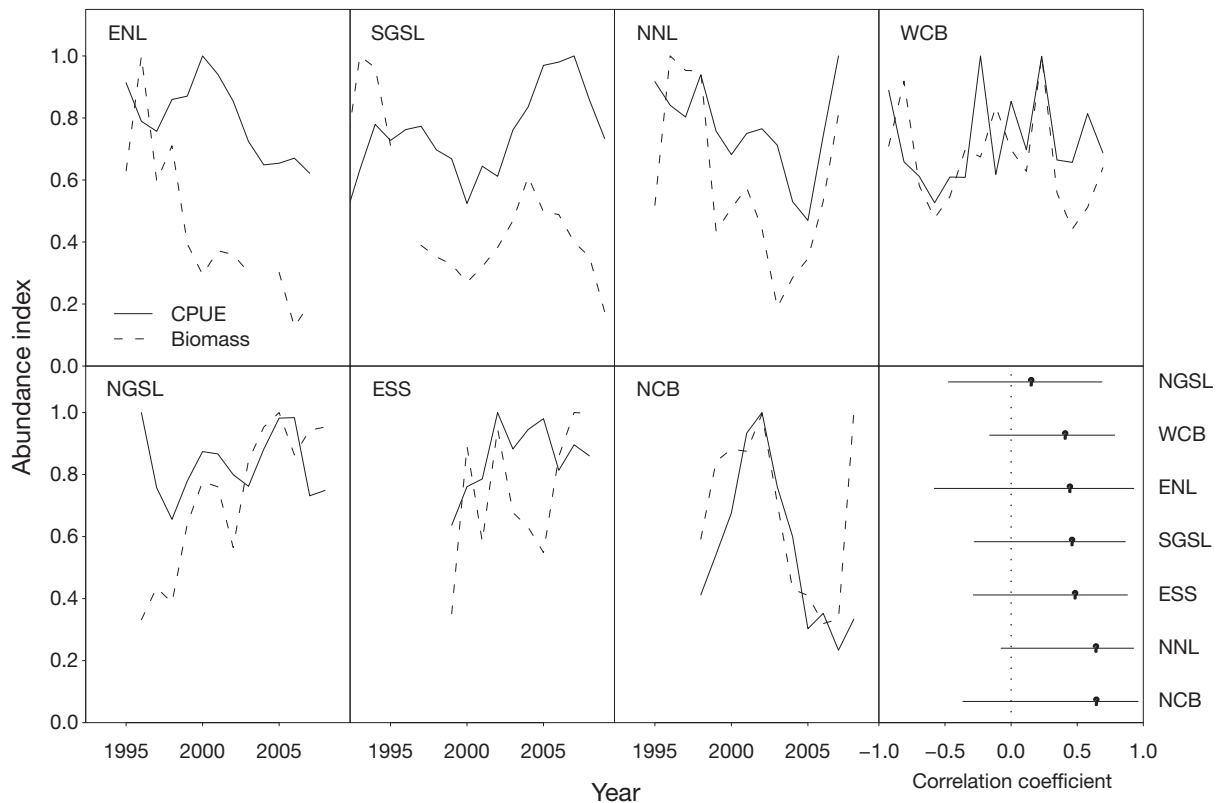


Fig. 3. *Chionoecetes opilio* abundance estimates. We compared fishery-independent abundance indices (dashed lines) and snow crab fishery CPUE data (kg trap haul⁻¹, solid lines). Data are scaled relative to the time series maximum. Ranges and units of the fishery-independent biomass indices vary by region: northern Newfoundland (NNL) and eastern Newfoundland (ENL), 1995 to 2006, fishable biomass of mature hard-shelled legal sized males (t); southern Gulf of St. Lawrence (SGSL), 1988 to 2009, biomass of post-fishery legal sized males (t); western Cape Breton (WCB), 1993 to 2009, biomass of postfishery legal sized males (t); northern Gulf of St. Lawrence (NGSL), 1996 to 2008, CPUE of postfishery legal sized crabs (kg trap haul⁻¹); eastern Scotian Shelf (ESS), 1999 to 2008, fishable biomass (t); and northern Cape Breton (NCB), 1998 to 2008, fishable biomass (t). The correlation coefficients of log-transformed fishery CPUE and fishery-independent snow crab indices for each region are displayed in the lower right panel along with 95% CIs (horizontal bars) corrected for temporal autocorrelation

either included or excluded. One difference concerned the meta-analyses of temperature with cod. When NNL and ENL were the only regions retained in the analyses (Fig. S2 in the supplement), the significantly positive correlations between cod and temperature occurred at longer time lags (10 and 11 yr). Similarly, when NNL, ENL and SGSL were the only regions retained (Fig. S3), cod and temperature were significantly positive at lags of 8 to 12 yr. These results may be attributed to cod maturing later in Newfoundland than in the rest of Atlantic Canada (ICES 2005).

DISCUSSION

We tested 3 hypotheses examining the variation in snow crab abundance in the NW Atlantic Ocean. We presented evidence that snow crab is influenced by both ocean temperature and Atlantic cod predation. Increases in crab abundance and CPUE were seen

after the collapse of cod stocks. The meta-analyses suggested opposite effects of temperature on cod and snow crab, but still revealed significant negative correlations between cod and crab after accounting for the effect of temperature on each species. There was no clear evidence of a bottom-up effect of snow crab on Atlantic cod. These results suggest that both species interactions and environmental forcing play a role in regulating snow crab abundance in the NW Atlantic Ocean.

The strength of the meta-analytic correlation coefficients at different lags suggests that the effect of climate and predation on snow crab varies with life stage. Snow crab abundance was significantly negatively correlated with temperature between lags of 7 and 10 yr, with the strongest correlation at a lag of 8 yr (Fig. 4). This approximates the time of recruitment to the fishery and may indicate that temperature plays a strong role in the early juvenile stages, i.e. the first 3 to 4 yr postsettlement. All life stages of snow crab are

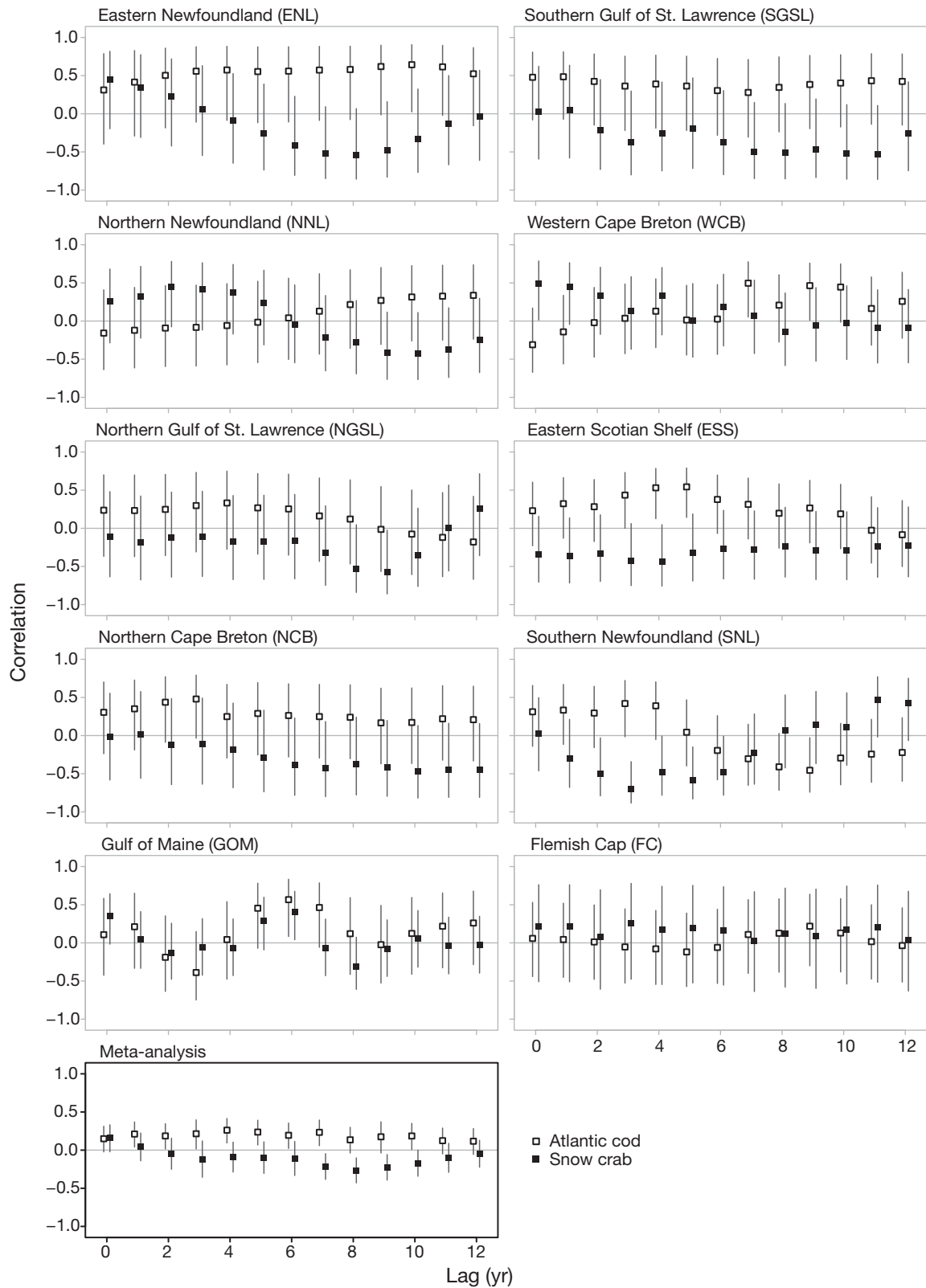


Fig. 4. *Gadus morhua* and *Chionoecetes opilio*. Temperature analysis. Shown are the correlation coefficients at various lags between time series of temperature and Atlantic cod (□), and temperature and snow crab (■). Vertical bars illustrate 95% CIs corrected for autocorrelation. Study regions are arranged from the coldest (eastern Newfoundland) to the warmest (Flemish Cap) median water temperatures. Meta-analysis results are presented in the lower left panel. We explored lags up to 12 yr, which reflects the maximum time it takes for snow crab to recruit into the fishery

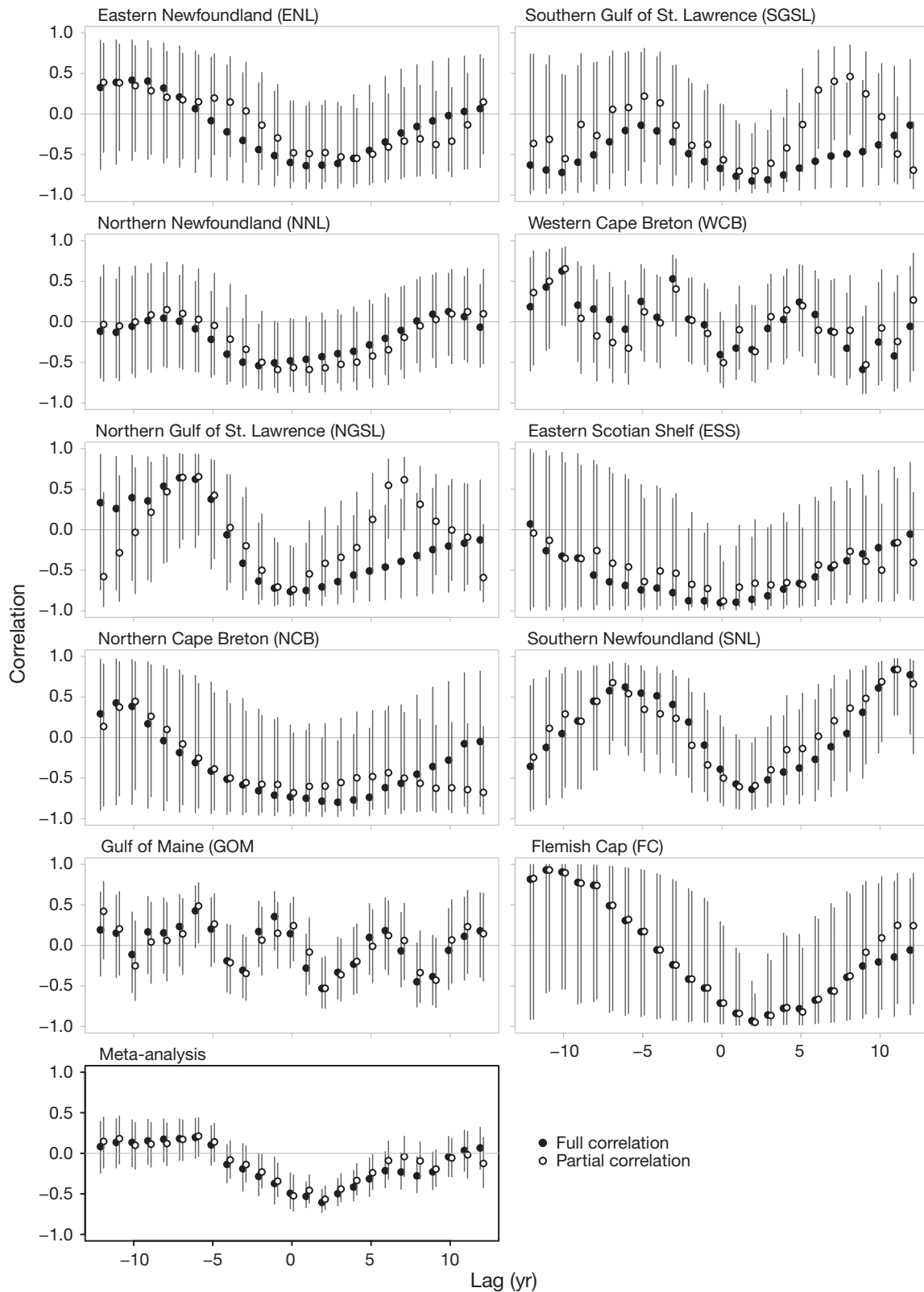


Fig. 5. *Gadus morhua* and *Chionoecetes opilio*. Analysis of Atlantic cod–crab interactions. Shown are the full (●) and partial (○) correlation coefficients of snow crab biomass indices with lagged cod biomass indices, along with 95% CIs (vertical bars) corrected for autocorrelation. Study regions are arranged from the coldest (eastern Newfoundland) to the warmest water temperatures (Flemish Cap). Meta-analysis results are presented in the lower left panel. The partial correlations have been corrected for the effects of temperature at a 7 yr lag

sensitive to temperature fluctuations (Foyle et al. 1989, Taylor et al. 1993, Conan et al. 1996); however, early juveniles may be the most affected owing to their narrow range of preferred temperatures (Dionne et al. 2003). Cod abundance was positively correlated with temperature at lags of 1 to 7 yr, which is consistent with research demonstrating adverse effects of cold temperature on cod growth and condition (e.g. Purchase & Brown 2001, Dutil & Brander 2003).

In contrast, top-down forces appeared to have their greatest effect on older juveniles and subadult snow crab. Negative correlations at long time lags (i.e. >6 yr, Chabot et al. 2008) would have been expected based on the diet data (Table 1); however, the negative relationship between Atlantic cod and snow crab abundance was strongest at relatively short lags, between 0 and 5 yr, with cod leading snow crab (Fig. 5). According to Sainte-Marie et al. (1995), and assuming that the crab were taken by the fishery in their year of moult, those represented at these short time lags (0 to 5 yr) would be juvenile and subadult crab from ~29 mm (Instar VII, 3.3 yr of age at moult) to ~97 mm CW (Instar XII, 8.7 yr of age at moult and recruited to the fishery). Commercial catches (i.e. fishery CPUE) and surveys also include males belonging to Instars XIII and XIV; 0 to 5 yr earlier they would have been recently moulted crab of ~38 to 115 or ~51 to 136 mm CW, respectively (Sainte-Marie et al. 1995). While the negative correlations at relatively short time lags are not consistent with what is presently known of Atlantic cod predation on snow crab, we noted that most of these values fell within the range of the larger snow crab recorded in diet studies (Table 1), with the exception of the largest (115 and 136 mm CW). Our results were robust across alternative combinations of areas (see supplement); however, it is likely that larger crabs (i.e. >65 to 70 mm CW, Table 1) would have to be ingested in postmoult condition (i.e. soft-shelled), as larger hard-shelled crabs are not present in diet studies.

The regions selected for this study all show spatial and temporal overlap between snow crab and Atlantic cod stocks (Table 1); however, predation effects might not play out across their range owing to, for example, seasonal migration of cod (e.g. the GSL, Chabot et al. 2008 and references therein), but may be concentrated on smaller spatial and temporal scales (Link & Garrison 2002). For example, off Labrador (both inshore and offshore) a dietary shift along the coast was observed in Atlantic cod from fish in the south (e.g. capelin *Mallotus villosus*) to crustaceans in the north (e.g. snow crab). This spatial diet shift was attributed to the distribution of their prey species (Lee & Khan 2000). Similar variation may occur over time, for example, if predation occurs on larger, defenseless crab during moulting (Robichaud et al. 1991, Chabot et al. 2008).

In the GSL, large snow crab moult in high-density aggregations during early spring, February to April in the SGSL (Hébert et al. 2002) and March to June in the NGSL (Sainte-Marie & Hazel 1992, Lovrich et al. 1995), in shallow water (<35 m, Sainte-Marie & Hazel 1992, Sainte-Marie 1993, Lovrich et al. 1995), possibly to avoid predation (Lovrich et al. 1995, Comeau et al. 1998, Chabot et al. 2008). Atlantic cod typically begin to migrate back into the SGSL by mid-April (ICES 2005) and into the NGSL in April and May for spawning, and then disperse along the coast (DFO 2010b). Chabot et al. (2008) examined additional SGSL cod stomachs for the presence of soft-shelled crab. They discovered a low incidence (0.9%) of large soft-shelled snow crab (≥ 79 mm CW) in larger cod from the eastern SGSL, in the same locations as in Robichaud et al. (1991) (Table 1). All age classes of cod return to the eastern portion of the SGSL during the spring (by mid-May) (Hanson 1996), increasing the overlap between cod and soft-shell male snow crabs (Chabot et al. 2008). Large male snow crabs recover from postmoult (soft-shelled) condition to a hard carapace in 2 to 3 mo (Watson 1971, O'Halloran & O'Dor 1988, Taylor et al. 1989, Hébert et al. 2002), sometimes longer (Godbout et al. 2002). This would indicate that soft-shelled crabs, especially late-moulting individuals, could be available to Atlantic cod for part of their spring/summer migration. Further research on this issue should focus on the extent of temporal and spatial overlap between Atlantic cod and moulting snow crab as well as cod predation on sublegal and legal sized crabs in soft-shell condition. This may occur, for example, in poorly assessed coastal areas where moulting snow crabs tend to aggregate (Sainte-Marie & Hazel 1992, Lovrich et al. 1995). It is presently unclear how strong a role predation may play in regulating snow crab abundance during this vulnerable life stage.

Other studies provide some evidence that Atlantic cod could influence abundance of snow crab. In the SGSL, Bailey (1982) found a negative correlation between commercial-sized snow crab (landings) and the biomass of Atlantic cod at a 3 to 6 yr lag. Bailey (1982) suggested that snow crabs were vulnerable to predation during their first 3 yr postsettlement, although this result was based on short time series. A later study in the same region found a significant negative correlation ($r = -0.66$) between snow crab landings and Atlantic cod abundance at a lag of 10 yr, yet concluded that density-dependent mechanisms were more likely responsible for the variation in snow crab abundance (Caddy et al. 2005). A third study reported that snow crab is vulnerable to predation by Atlantic cod for the first ~5 yr postsettlement in the GSL, which could be detected in the snow crab fishery 6 to 11 yr later (Chabot et al. 2008). On the ESS, Frank et al. (2005)

found a strong negative correlation ($r = -0.70$) between benthic fish biomass and snow crab abundance, without assuming a time lag. Further, Shackell et al. (2009) presented evidence that the declining individual size of predators on the Scotian Shelf could have top-down effects that are independent of changes in total biomass. That study noted that according to trawl surveys, the aggregated biomass of 'large-bodied' predatory fish had been stable for 4 decades while the biomass of their prey species had doubled in 11 yr. Declines in predator body size largely accounted for the increase in aggregate prey biomass, suggesting a potential reduction in predator energy requirements and their maximum potential size of prey. A pattern of decline in average Atlantic cod length is not unique to the Scotian Shelf and has been recorded in much of the NW Atlantic Ocean (Worcester et al. 2009). These results from individual ecosystems could be further tested by the meta-analytic approach presented here.

Our results have focused on Atlantic cod, which in many areas of the NW Atlantic was probably an important predator of snow crab (Table 1); however, the decline of cod coincided with declines of other large groundfishes (Casey 2000, Frank et al. 2005). For example, total groundfish biomass in Newfoundland decreased by nearly an order of magnitude between 1950 and 1995 (Myers & Worm 2003). Some of these other species may have been important predators of crab. For example, some skates may consume more snow crab than do Atlantic cod (Robichaud et al. 1991). Atlantic cod are described as opportunistic generalists, and while they exhibit preferences throughout their ontogeny, it is unlikely that they control the abundance of all potential prey species (e.g. Link & Garrison 2002). Atlantic cod may be opportunistically preying on snow crab in years when juveniles are abundant (Waiwood & Elner 1982, Chabot et al. 2008), and therefore the strength of predator top-down control may vary across time and regions.

We interpret our results as evidence of temperature control on early juvenile snow crab and top-down control on older juvenile and subadult stages. The alternative hypothesis of bottom-up control was not supported by our analysis. Under this scenario, if both populations were primarily influenced by resource availability, we would expect positive correlations across a range of lags. Additionally, we encountered negative meta-analytic correlations at negative lags, which could imply top-down control of snow crab on Atlantic cod. Such a scenario could be plausible because fish are present in the diet of larger snow crab (Wieczorek & Hooper 1995, Lovrich & Sainte-Marie 1997, Squires & Dawe 2003); however, these correlations attenuated quickly towards zero and were marginally significant. It is possible that these correlations are not biologically

meaningful, given that some degree of serial autocorrelation is expected in the cross-correlation between 2 nonrandom time series at successive lags.

Other variables, such as wind-driven upwellings, sea ice coverage (e.g. Conan et al. 1996, Dawe et al. 2008) or density dependence (e.g. cannibalism, Lovrich & Sainte-Marie 1997) could be influencing snow crab populations in ways not accounted for by our analysis. Another possibility could be direct competition between the 2 species, as they both prey on benthic invertebrates such as small crustaceans (i.e. shrimp, crab) and molluscs (Waiwood & Majkowski 1984, Wieczorek & Hooper 1995, Casas & Paz 1996, Lovrich & Sainte-Marie 1997, Hanson & Chouinard 2002, Squires & Dawe 2003). The importance of top-down and bottom-up forces may vary between areas (Figs. 4 & 5), although some mechanistic generalities have emerged from the present analysis.

One important limitation of our study is that much of the inference is based on snow crab fishery CPUE data. Fishery CPUE can underestimate (hyperdepletion) or overestimate (hyperstability) abundance depending on the behaviour and distribution of both fishers and their target species (Harley et al. 2001). In the present study, there are inherent differences in how the abundance indices (i.e. fishery dependent and fishery independent) were collected. Snow crab fishery CPUE (kg trap haul⁻¹) was weakly and not significantly positively correlated with abundance indices in all regions, yet showed trends similar to the fishery-independent survey data (research trawl surveys; t or kg tow⁻¹) (Fig. 1), which supports the use of CPUE in the analysis.

Snow crab is also found in the north Pacific Ocean where researchers examined various hypotheses, including the top-down and bottom-up (climate control) mechanisms explored in the present study, to explain abundance trends for snow crab populations in Alaska. Commercial snow crab stocks showed highly variable recruitment in Alaska, which is reflected in their population abundance (Zheng & Kruse 2006). In the eastern Bering Sea (EBS), snow crab recruitment has been weakly negatively correlated with sea surface temperature (Zheng & Kruse 2000). There is also evidence that the range of snow crab in the EBS has contracted to the north owing to large-scale warming in the late 1970s, and although the water has since cooled, their range has not re-expanded south. Orensanz et al. (2004) suggested that currents preventing the advection of larvae to the southern EBS or predation on prerecruits by Pacific cod *Gadus macrocephalus* might be preventing the snow crab's re-expansion. While Pacific cod prey upon snow crab (Livingston 1989), their regulatory role is also debated as Pacific cod did not emerge as a driving factor in explaining EBS snow crab recruitment variability (time lags of 0 to 4 yr) (Zheng & Kruse 2000,

2006). There is therefore some evidence that bottom-up (climate forcing) and top-down (groundfish predation) mechanisms jointly control commercial crab recruitment in the EBS (Zheng & Kruse 2000, 2006, Orensanz et al. 2004). However, these studies were based on single time series analyses, and therefore the meta-analytic approach employed in the present analysis may be a more powerful tool that can be used to evaluate these general hypotheses by addressing the regulation of species abundances across several large marine ecosystems. Any meta-analytic approach represents a trade-off between generality and local detail, as individual regions may vary in their responses and averaged results may be of limited value for predicting local response to changes in the environment.

In conclusion, based on the available evidence from multiple time series, this analysis supports both the climate and top-down hypotheses. We suggest that the observed fluctuations in snow crab abundance are driven partly by temperature and partly by the variation in Atlantic cod abundance. The results suggest that temperature has a stronger influence on snow crab abundance during the first few years postsettlement and its importance may lessen as top-down mechanisms begin to play a larger regulatory role. In the wake of the groundfish collapse of the 1990s, Atlantic Canadian fisheries have become increasingly dependent on invertebrates, and the snow crab fishery is among the 3 most valuable today. The knowledge gained from this analysis would be useful in a management context when possible changes to snow crab stocks are anticipated as water temperature and groundfish abundance change over time. The meta-analytic approach is a useful tool for detecting general trends from relatively short time series and providing insight into regulating forces across regions. Meta-analysis of partial correlation coefficients may be used more generally to detect the relative effects of a changing climate, as well as the ecosystem effects of fishing, on species communities in the North Atlantic Ocean and elsewhere.

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