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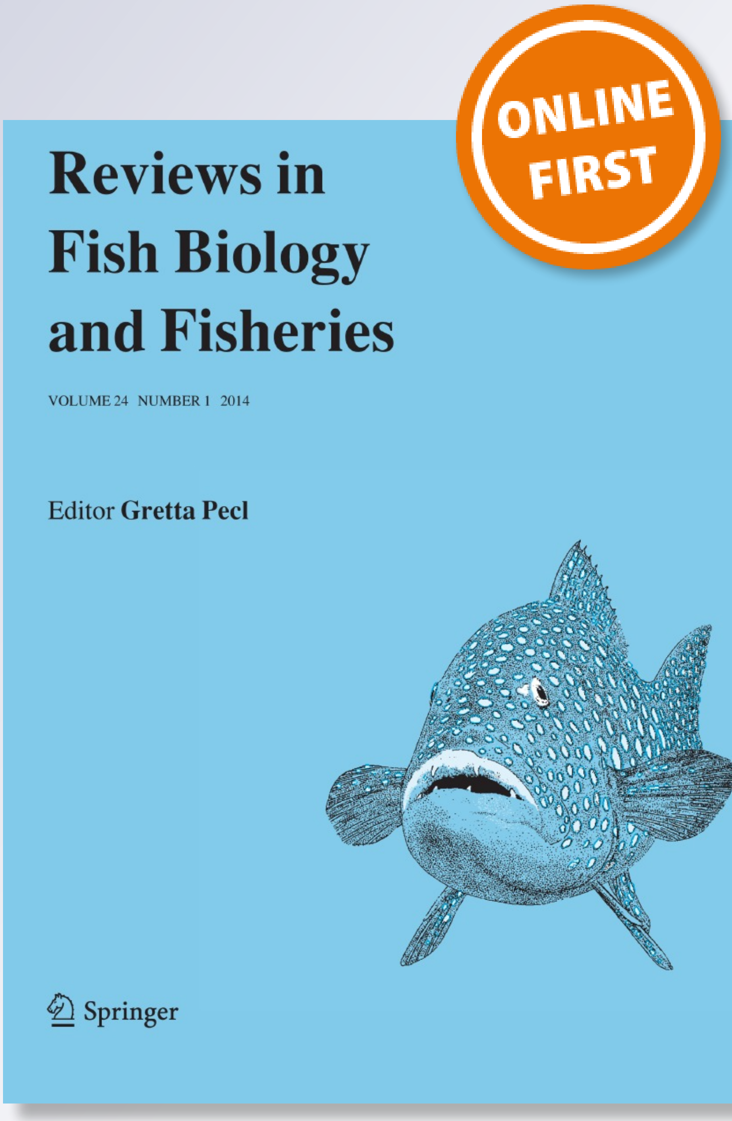

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REVIEWS

A review of factors contributing to the decline of Newfoundland and Labrador snow crab (*Chionoecetes opilio*)

Darrell R. J. Mullowney · Earl G. Dawe · Eugene B. Colbourne · George A. Rose

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Abstract The Newfoundland and Labrador (NL) snow crab resource, presently the basis of the most important commercial fishery in the region, is in decline. Short-, mid-, and long-term recruitment prospects are deemed poor in most areas. Fishery declines have been most apparent in the north, beginning in the mid- to late 2000s, but are expected to begin in the more productive southern areas in the near future. A multitude of emergent theories to explain the resource decline have been hypothesized as contributing factors, including fishing, trawling impacts, seismic activities, disease, predation, and increasing temperature. This study comprehensively reviews and qualitatively relates the results of recent research and literature on each of these factors. We find that several factors may be contributing to a lack of recruitment in the stock, but diminishing productivity resulting from a warming oceanographic regime is the primary cause of the resource decline. Further, we postulate that trends occurring in the snow crab stock are indicative of a broader-scale ecological regime shift occurring along the NL shelf.

Keywords Snow crab · Newfoundland and Labrador · Regime shift · Atlantic multidecadal oscillation

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Introduction

From the mid- 1980s to early 1990s many fished and non-fished pelagic and groundfish species declined in abundance and exhibited shifts in distribution in the waters of the Northwest Atlantic off Newfoundland and Labrador (NL). On July 2, 1992, the Canadian Government imposed a fishery moratorium on the rapidly declining and formerly dominant "northern" Atlantic cod (*Gadus morhua*) stock off the northeast coast of Newfoundland and southern Labrador (Rose 2007). Within a year all cod stocks in the region, along with other important fish stocks such as American Plaice (*Hippoglossoides platessoides*), were under similar closures. These events constituted the most significant event in the history of these fisheries, which had served as the socio-economic mainstay of the region since the early 1,500 s. The 30,000 workers displaced by the moratorium constituted the single largest mass lay-off in Canadian history. It appeared that after nearly 500 years the primary industry of the

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Northwest Atlantic, the fishery, was about to end. However, largely unknown to science, industry, and the general public, a species with much higher commercial value was rapidly increasing in these same waters and the fishery was on the verge of transition to one based primarily on 'crab' (Snow Crab—*Chionoecetes opilio*).

Since the mid 1990s, the NL shelf has supported the world's largest snow crab fishery (Mullowney and Dawe 2009). Although initial abundance levels are uncertain, it is certain that the stock and fishery grew rapidly following a cooling phase and collapse of finfish stocks in the late 1980s and early 1990s (see Fig. 3 in Dawe et al. 2012a). Participation and value peaked in the mid-2000s, with over 3,500 active licences and landed values exceeding $300 million per year (DFO unpublished data). However, after 2 decades of prosperity, the NL snow crab industry is now in decline, with recently contracting levels of activity in both the harvesting and processing sectors. In recent years, several hundred licence holders have exited the fishery and seven of the forty-four crab processing plants have closed. At the root of the industry decline is a resource decline. The resource and industry declines have been most apparent in northern areas (i.e. Northwest Atlantic Fisheries Organization (NAFO) Divisions 2HJ3K, Fig. 1), beginning in the mid-late 2000s, but recent survey data suggest an imminent decline in the more productive southern areas (i.e. Divisions 3LNOPs), where the scale of prosecution is much higher (Mullowney et al. 2013). The impacts of a widespread downturn in the crab fishery may parallel the collapse of the cod fishery, with potential far-reaching socio-economic ramifications.

As with the collapse of the cod stocks, many hypotheses have been advanced by science and industry as causes for the decline in snow crab. Foremost among them are overfishing, trawling impacts, seismic activities, disease, predation, and increasing water temperatures. This study reviews literature on these diverse hypotheses, both in NL and other areas where snow crab occurs, in an attempt to better understand and predict the future state of the ecosystem, its community composition, and the likely impacts on the fishery. The objective of this paper is to qualitatively review, synthesize, and apply these recent findings to broad-scale trends occurring in the NL snow crab resource.

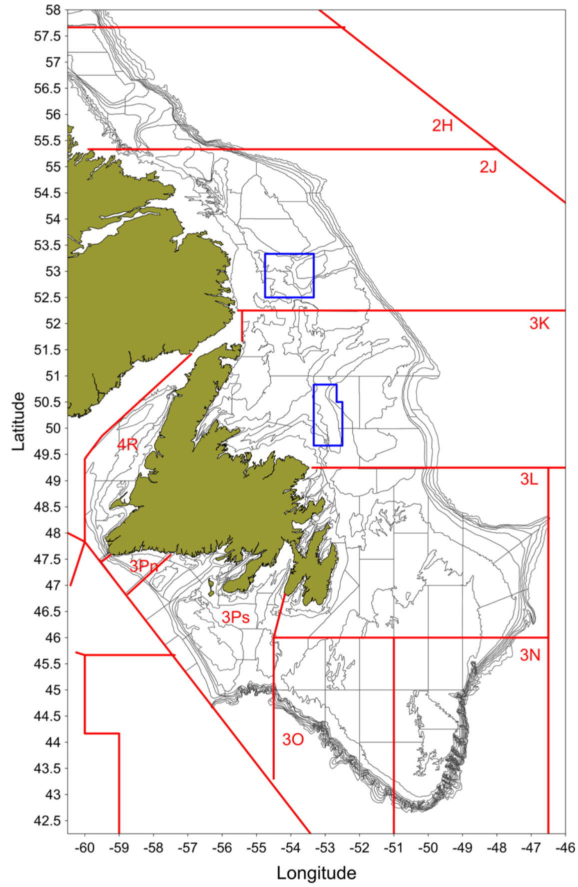


Fig. 1 Map of the Newfoundland shelf showing Northwest Atlantic Fisheries Organization Divisions (NAFO-*red*), Trawl Closures (*blue*), and depth strata of the multi-species trawl surveys (*grey*)

Snow crab biology and management

The snow crab is a stenothermal subarctic species inhabiting cold waters of about −1.5 to 4 °C (Dawe and Colbourne 2002; Dawe et al. 2012b). The species is sexually dimorphic with males achieving larger sizes than females. Maximum size in Atlantic Canada is about 95 mm carapace width (CW) for females and 150 mm CW for males (Sainte-Marie and Hazel 1992; Sainte-Marie et al. 1995). To help maintain reproductive potential, fishery regulations prohibit the retention of all females and males under 95 mm CW. Growth is a stepwise process associated with molting, which ceases after a terminal molt (Conan and Comeau 1986). This can occur at sizes as small as 30 or 40 mm CW for females and males respectively. Molt frequency is highest during early ontogeny but slows to a near-annual occurrence at larger sizes (Sainte-Marie et al. 1996). Mating and molting normally occurs during spring, but first-time mating (primiparous) females can be mated during winter. For females, the terminal molt into adulthood is the puberty molt, but for males the puberty molt occurs before the terminal molt, with crabs being sexually mature adolescents for a variable number of years before terminally molting into adulthood. Following a molt, crabs are in a soft-shelled condition and it can take up to a year for shells to harden and meat content to progress to a commercially acceptable level. During terminal molt males develop enlarged chela, a trait likely beneficial in competition for food or mates. Maximum longevity following terminal molt is about 7–8 years (Fonseca and Sainte-Marie 2008). Bottom temperature relates negatively to abundance (Marcello et al. 2012) and positively to size (Dawe et al. 2012b). Snow crab appear to follow a fitness strategy of settlement in shallow cold areas to maximize early-life survival followed by ontogenetic migrations to deep warm areas to maximize size. The fishery focuses primarily upon deep areas in bays and between offshore banks where large males are most commonly distributed (Dawe and Colbourne 2002).

Much of the management focus for snow crab is on minimizing the capture of soft-shell crabs, which are commercially undesirable and represent future recruitment to the fishery. Mortality associated with capturing and releasing soft-shell crabs is unknown but thought to be high (Mullowney et al. 2012, 2013). Historically, the fishery was prosecuted during the summer and fall, but in recent years it has shifted to spring and early summer to minimize the capture of soft-shell crabs, which become increasingly mobile over the summer as shells harden.

The stock assessment for snow crab in NL is conducted annually, during late winter, with quotas subsequently allocated for the spring fishery within 44 small-scale management areas. The minimum required mesh size in the pots is 5.25″, intended to allow the escapement of under-sized male and all female crabs, but 5.5″ gear has become increasingly commonplace in the fishery. Other pertinent management measures include mandatory observer coverage for all fleet sectors, the use of vessel monitoring systems (VMS) in offshore fleet sectors, mandatory completion of logbooks, a dockside monitoring program for landings, and a soft-shell protocol whereby fishing grids are closed for the duration of the season when soft-shell crabs constitute 15 % (Divisions 3LNO) or 20 % (Divisions 2HJ3KPs4R) of the observed catch.

Resource status

The stock assessments incorporate a variety of fishery dependent and independent information (Mullowney et al. 2013). A depth-stratified random trawl survey occurring each fall in NAFO Divisions 2HJ3KLNO (Fig. 1) forms the primary basis for estimation of exploitable and pre-recruit biomass indices and advice. Biomass estimates are derived from swept area extrapolation of catch rates to depth-based strata that cover most of the NL Shelf (Smith and Somerton 1981, and see Mullowney et al. 2013 for further details). The exploitable biomass of crabs comprises adult males ≥95 mm CW, while pre-recruits are adolescent males ≥76 mm CW, which are deemed capable of achieving exploitable size following another molt. The capture efficiency of snow crab by the survey trawl is known to be low for all sizes of crab, but is most inefficient for smallest individuals and on hardest substrates (Dawe et al. 2010a). Accordingly, the exploitable and pre-recruit indices are known to be underestimates of true abundance and biomass. No stock-recruitment relationship is evident for this stock, which could reflect inefficient survey performance or intrinsic or extrinsic biological factors.

Overall, the exploitable and pre-recruit biomass indices are both currently in decline, after peaks in the late 1990s and between 2008 and 2010 (Fig. 2). The latter peak was smaller than the earlier one, but improved management and fishing practices likely contributed to maximizing more of the resource potential, as fishery landings have been maintained at 50,000–60,000 t since 1999 (Mullowney et al. 2013). As quotas are allocated annually, much of the scientific and management focus tends to be centred on short-term recruitment prospects and available exploitable biomass. However, in recent years it has become increasingly apparent that recruitment prospects are diminishing and more attention has been given to predicting long-term outcomes. The most recent stock assessments have concluded that short-, mid-, and long-term recruitment prospects are unfavourable across the entire NL shelf (Mullowney et al.

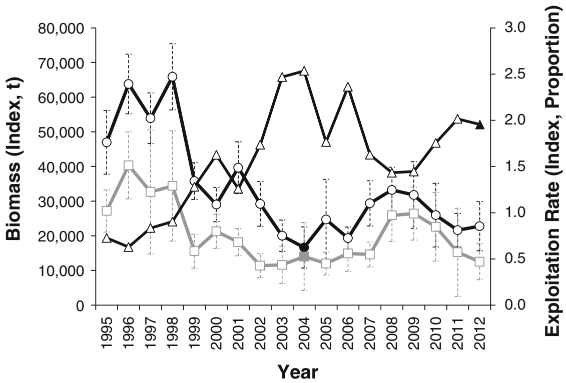


Fig. 2 Exploitable biomass (*black circles*), Pre-recruit biomass (*gray squares*), and exploitation rate (*black trianges*) indices for divisions 2HJ3KLNO. *Error bars* are 95 % confidence intervals. The 2012 exploitation rate point estimate assumes the entire 2013 quota will be taken. The solid symbols in 2004 indicate incomplete surveys

2013). Diminishing recruitment prospects are reflected in trawl survey size frequency distributions of males (Fig. 3), which show reduced abundance of all sizes in recent years. Of particular concern is the paucity of small crabs (i.e. <50 mm CW) in the survey since 2003. Furthermore, there has been a marked decrease in the abundance of mature females, to historical lows for the survey time series, in the past 3 years (Fig. 4). Overall, the prognosis for the resource and fishery is reduced production and a smaller fishery in the coming decade.

The concerns of science and the fishing industry about what is occurring to cause or promote the decline of snow crab have elevated in recent years. Compared to the situation with cod in the late 1980s, there is more broadly accepted consensus that the resource is declining, but as with the cod collapse, the

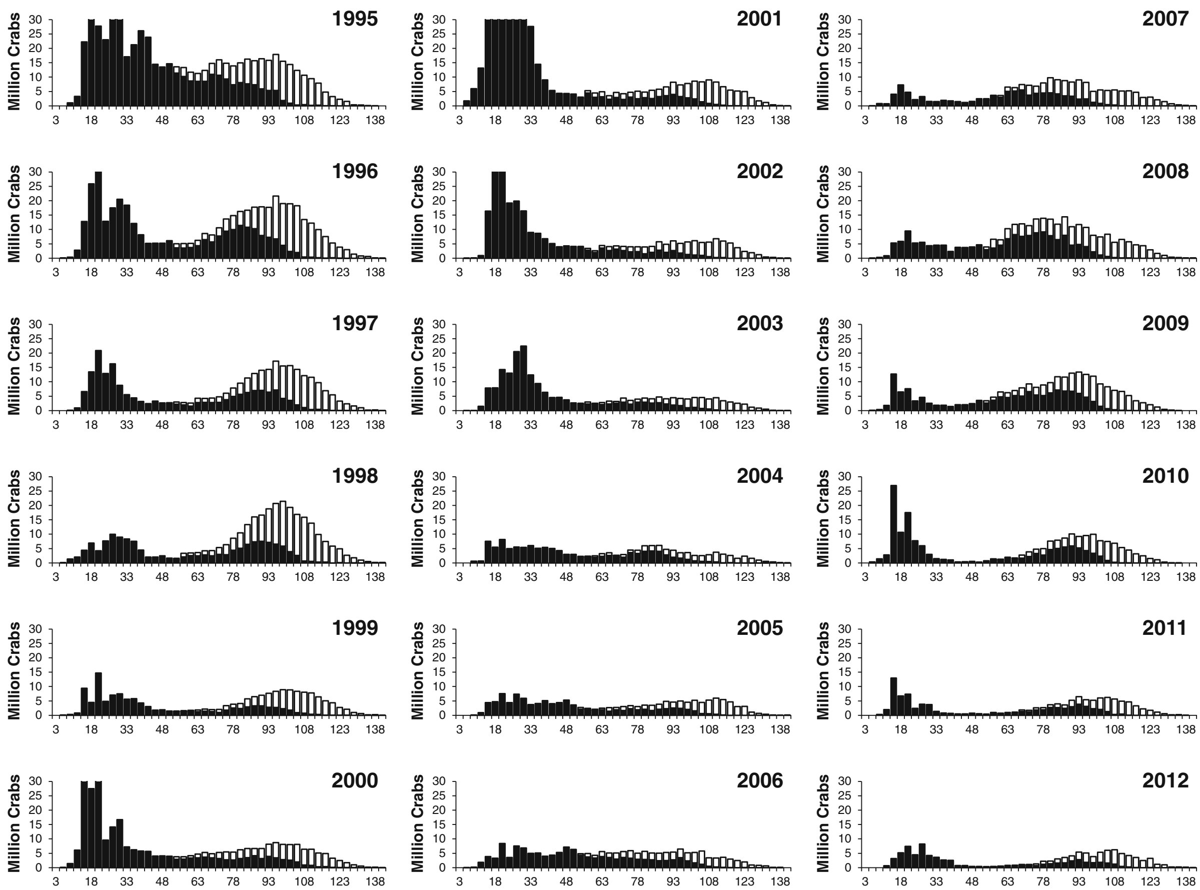


Fig. 3 Annual divisions 2HJ3KLNO fall trawl survey abundance indices of male snow crab by size. Adolescents in *black* and adults in *white*. X-axis units are carapace width (CW)

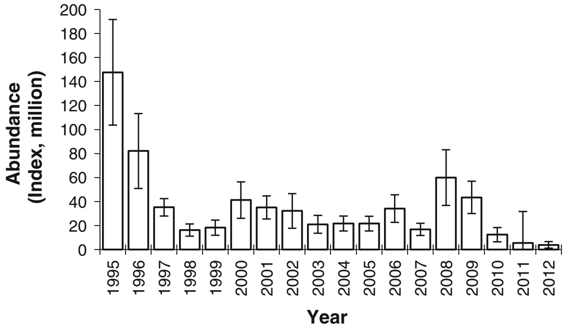


Fig. 4 Annual Divisions 2HJ3KLNO abundance index of mature female snow crab. *Error bars* are 95 % confidence intervals

impact on the fishery is likely to have enormous ramifications. The subsequent sections highlight the results of recent research and qualitatively evaluate information on potential contributing factors.

Analysis

Fishing

Anthropogenically-driven top-down impacts from fishing are always a possibility when fishery resources go into decline. Fishing has the potential to impact present and future stock abundance and productivity, with the mechanisms of harm and full breadth of repercussions rarely understood. In the NL snow crab fishery, large mesh pots are used, thereby restricting the catch to large males. Hence, the probability of inflicting direct mortality or serious harm to females and small males is low, with sexual dimorphism in this species imputing some inherent resilience to fishing. The greatest concern for top-down fishery impacts is over-exploitation of large and pre-recruit-sized males.

It is possible that long-term productivity could be impacted by the removal of too many large males, although there is no known relationship between large male abundance and recruitment potential. Interestingly, however, recent work on Red King Crab (*Paralithodes camtschaticus*) in Norway found that the removal of high numbers of large males can lead to a coincidental reduction in the size of ovigorous females, either due to decreased post-molt protection from large males or increased rates of capture in the fishery, and that sperm limitation can become an issue when largest breeding males are removed (Hjelset et al. 2012; Hjelset 2013). Nevertheless, there is no evidence of fecundity issues in NL snow crab, with >80 % of mature females consistently carrying full clutches of viable eggs in all areas since 1995 (Mullowney et al. 2013). Long-term effects of fishery exploitation remain open to question.

In the short- to medium- terms the management of snow crab stocks typically aims to maintain production by protecting females and a portion of the largest adult males, as well as all small adult and adolescent males. This strategy relies on assumptions that females need only be mated once to produce several clutches of viable eggs with stored sperm (Sainte-Marie and Hazel 1992), and that strong recruitment has been evident in years with seemingly low abundance of large males. This could reflect differences in mating and fishery timing, with the spring-summer fishery occurring later than the mating period.

The trend in the exploitation rate index for Divisions 2HJ3KLNO, calculated as the ratio of landings to the exploitable biomass index from the previous survey, is inversely related to the trend in exploitable biomass (Fig. 2). This indicates that landings have remained constant relative to fluctuations occurring in the exploitable biomass. The exploitation rate index was lowest in the late 1990s, highest in the early 2000s, at a secondary low in the late 2000s, and at a secondary high in the past 3 years.

The overall trends in the exploitable and pre-recruit biomass indices incorporate division-specific variability within them. There has been a general pattern of a spatiotemporal cline with events occurring first in the north and following in succession southward. For example, the most recent peaks in exploitable biomass occurred in Divisions 2HJ in 2006–2007, in Division 3 K in 2007–2008, and in Divisions 3LNO and Subdivision 3Ps in 2009 (Mullowney et al. 2013). The fishery has exhibited a similar clinal pattern, with catch rates most recently peaking in Divisions 2HJ and 3K in 2007–2008 versus 2009 in Subdivision 3Ps. However, Divisions 3LNO have countered the trend, with increasing fishery catch rates in recent years. This is thought to reflect a lower level of exploitation in Divisions 3LNO compared to other Divisions and consequently a higher residual component to the exploitable biomass (i.e. less dependent upon immediate recruitment each year). This phenomenon largely accounts for the cessation of decline in the overall

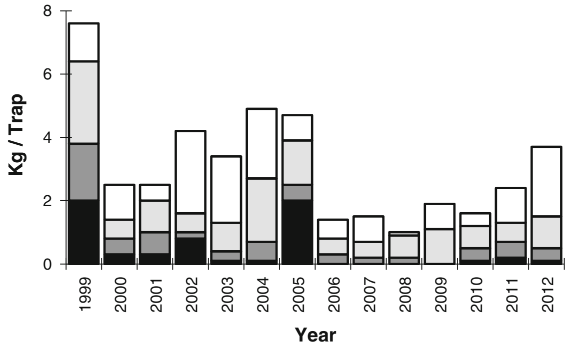


Fig. 5 Annual observed catch rates of soft-shell crab in the fishery by NAFO Division (2 J-*white*, 3 K-*light gray*, 3LNO-*dark gray*, 3Ps-*black*)

exploitable biomass index from 2011 to 2012 (Fig. 2), with Divisions 3LNO most significantly weighting the data. However, of particular concern is that the declining trend in the pre-recruit biomass index has been increasingly weighted by Divisions 3LNO in the past 2 years, with declines in other Divisions beginning earlier.

Apart from the obvious effect of direct removals by fishing, the issue of greatest concern is the capture and release of soft-shell crabs, with incidence in the fishery reflecting both seasonality and large male density (Mullowney et al. 2012). Soft-shell prevalence normally increases throughout the summer, as crabs that molted in the spring become increasingly mobile, but becomes accelerated when the density of large hard-shelled males is reduced. This likely reflects an increased catchability of soft-shell crabs due to a decreased level of competition for baited pots. As such, high prevalence of soft-shell crabs can serve as a direct indicator of overfishing as it signifies a low density of large competitive males. A continuation of fishing activities during periods of high soft-shell prevalence has the potential to reduce the numbers of pre-recruits and consequently impact near-future fisheries. Soft-shell crab incidence, based on at-sea observer sampling throughout the year, is consistently highest in Division 2J, tends to be relatively high in Division 3K, is consistently very low in Divisions 3LNO, and arises only occasionally in Subdivision 3Ps (Fig. 5). Overall, with the exception of a high catch rate in Division 2J in 2012, soft-shell crab catch rates have been lower in recent years relative to pre-2006 levels. This trend is consistent with the management shift toward earlier (spring) fisheries since the mid-2000s. The highest incidence consistently occurs in northern Divisions (2J3 K), where the biomass is low relative to Divisions 3LNO (Mullowney et al. 2013), and is not consistent with soft-shell mortality being a primary driver of the overall declining trends in the broader-scale pre-recruit and exploitable biomass indices (Fig. 2).

In summary, although fishing pressure is higher now than during the most recent resource peak it cannot be ascribed as the primary driver of broad-scale resource trends. The overall exploitation rate is moderate relative to historical levels, especially in the most important areas (i.e. 3LNO), and soft-shell crab prevalence in the catch is relatively low in recent years. It is possible that overfishing could be exacerbating the decline or prohibiting recovery in some areas (i.e. 2HJ3K), but it does not account for the broad-scale and prolonged decline occurring in the stock as a whole.

Shrimp trawling

Other human activities occurring on the snow crab grounds have been postulated to have driven the crab decline in some areas. One such activity that has garnered considerable attention is shrimp trawling.

The northern shrimp fishery in NL waters occurs from the tip of Labrador in the north to the northern portion of the Grand Bank in the south (Fig. 1; Orr and Sullivan 2012). In general, much of the activity is concentrated on muddy substrates along the slope edges of the continental shelf, where crab fishing effort is minimal. However, in Divisions 2J3K where industry outcry has been particularly strong, about 18–32 % of the fishing grounds of the two fisheries may overlap in any given year (unpublished data). Schwinghamer et al. (1998) found no significant impacts of trawling on snow crab on the Grand Bank, but did note some dead crabs in the tow path of the trawl. Subsequently, two separate collaborative studies carried out by industry and both levels of government (i.e. Federal/Provincial) using secondary retainer bags in the trawl as well as a remotely operated vehicle (ROV) to observe trawl-induced damage and mortality concluded there is no significant impact of trawling on snow crab (FDP 2002; Dawe et al. 2007). The latter and more comprehensive study found no evidence of trawling-induced mortality or damage from post-trawl

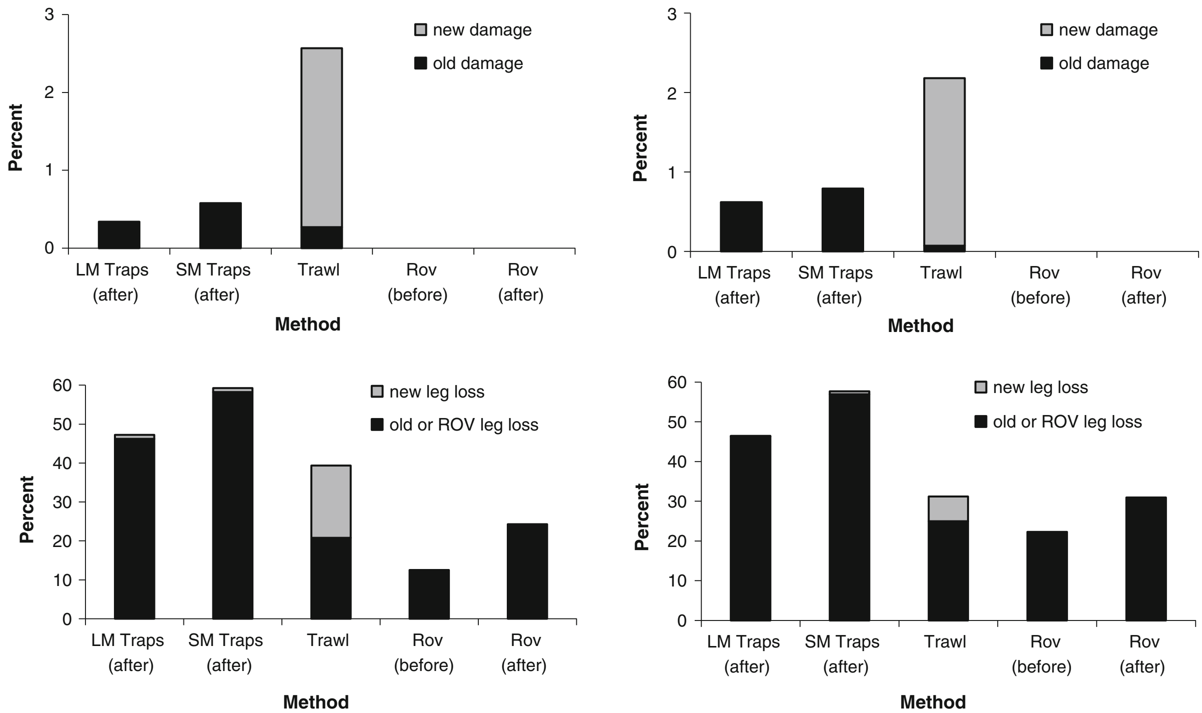


Fig. 6 Crab damage caused by trawling from 2007 St. Mary's Bay experiments. *Top panels* show Carapace damage (*left* = outer corridor, *right* = mid corridor) and *bottom panels* show leg loss (*left* = outer corridor, *right* = mid corridor). *LM* traps indicates large-mesh traps, *SM* indicates small-mesh traps

videos. Similarly, post-trawl trapping using both large- and small-mesh pots found no evidence of carapace damage or leg loss in crabs where trawling had occurred (Fig. 6). Crab specimens captured in the trawl showed elevated levels of new carapace damage and leg loss (Fig. 6), which was attributed to post-capture damage inside the trawl itself (Dawe et al. 2007).

Two large areas closed to trawling and other bottom impact fisheries were established during 2002–2005 as precautionary measures to protect snow crab from potential harm (Fig. 1). The effectiveness of the larger and initially established Hawke Box in Division 2J was reviewed by Mullowney et al. (2012), who found that any potential positive outcomes from the cessation of trawling had been masked by excessive crab fishing activity following the closure. No formal studies have been done on the Funk Island Deep closure, but the most recent stock assessments suggest it has had a similar outcome (Mullowney et al. 2013). In both cases, pre-closure fishery catch rates of snow crab were generally higher inside the areas, relative to adjacent fishing grounds, but since closure catch rates

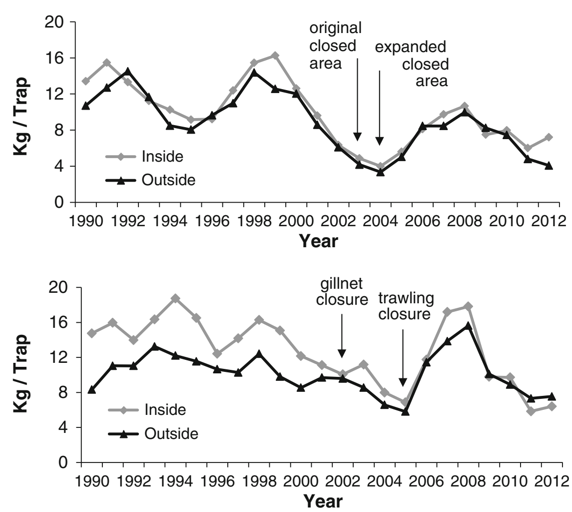


Fig. 7 Annual logbook-based catch rates of snow crab inside versus outside trawling closure areas. Hawke Box (Division 2 J—above) and Funk Island Deep Box (Division 3 K—below)

have come together and shown no difference (Fig. 7). Neither closure has been successful in protecting pre-recruit crabs from mortality because the crab fishery itself has imposed a higher level of mortality on the resource than shrimp trawling. These results, however, do not preclude the notion that productivity of snow crab may have increased within the closed areas, with this aspect currently under investigation in an independent study.

The shrimp trawling fishery has the largest potential for by-catch of snow crab in the region, with pelagic and benthic hook and line fisheries not likely to capture high numbers of snow crab. Dawe et al. (2007) estimated bycatch in shrimp trawls to average 1–2 kg/tow and total removals by the large-vessel shrimp fleet, which receives 100 % at-sea observer coverage, to total about 0.25–2 tonnes per year. The removals by the small-vessel shrimp fleet are unknown, but with such low by-catch in the large vessel fishery there appears little cause for concern of any significant effect from direct removals of snow crab by shrimp boats.

Trawls with rockhopper footgear used in NL, including for scientific surveys, are known to have low capture efficiencies for snow crab (Dawe et al. 2010a; Mullowney et al. 2013). Despite low capture efficiency, a recent study using video observations on the footrope of a bottom trawl demonstrated that about 50 % of large crabs experienced direct contact with the gear before passing beneath it (personal communication, Dr. Paul Winger, Marine Institute of Memorial University, St. John's, Canada), demonstrating the potential for interaction.

The evidence currently compiled does not suggest that shrimp trawling is the main factor driving recent snow crab resource declines. Although there is a potential for some mortality and damage, studies to date suggest it is relatively minor, with other factors such as crab fishing itself exhibiting greater impacts. Nonetheless, the issue of shrimp trawling impacts on snow crab remains a contentious one in NL and further studies on the matter are on-going.

Seismic activities

To date, potential impacts of seismic activities on snow crab have received only limited formal study, with few published papers on the topic. In a review on the effects of seismic and marine noise on invertebrates, Moryiasu et al. (2004) cautioned that because of the predominance of gray literature that general consensus conclusions of invertebrates being robust to seismic noise should be treated cautiously.

Christian et al. (2003) and DFO (2004) found no immediate or latent mortality or effects on a variety of haematological and histopathological parameters for snow crab exposed to seismic guns at distances of 2–4 m, but did suggest latent developmental effects could occur in larvae. Payne et al. (2007) found no immediate or delayed effects of damage or mortality to American Lobster (*Homarus americanus*) in lab and field experiments when Gulf of St. Lawrence lobsters were exposed to seismic noise. In a study directed at crab larvae, Pearson et al. (1994) exposed early stage Dungeness Crab (*Cancer magister*) to maximum sound levels encountered during seismic surveys, with the air gun as close a 1 m, and found no immediate or latent mortality. Similarly, preliminary results from tank-based observations of exposure to seismic noise on snow crab have suggested there is no impact on egg development or immediate or latent mortality from episodic exposure to high sound levels [personal communication, Dr. Jerry Payne (DFO)].

The on-going work on snow crab is suggesting it is possible they become stressed from exposure to seismic noise, as interpreted from a drop in blood parameters following exposure. American Lobsters experienced similar stress following exposure, with a drop in serum enzymes, protein, and calcium, and changes in feeding behaviour (increased consumption). Wale et al. (2013) recently showed that noise from lower level sources such as ships altered behaviour in the shallow water European Shore Crab (*Cancer Maenus*) by disrupting feeding, slowing reaction time to threats, and hastening turn-over times for crabs placed on their backs. They inferred that such behavioural alterations could increase the susceptibility to starvation or predation in the wild.

In summary, the evidence compiled to date does not suggest that seismic activities have significantly contributed to recent snow crab resource declines. Although it is possible that seismic noise could induce physiological or behavioural changes in crabs, no studies to date have found any direct or latent damage or mortality from noise exposure. Any mortality associated with post-exposure physiological or behavioural alterations is theoretical and undemonstrated. Nonetheless, many crab harvesters remain concerned about seismic exploration along the NL shelf.

Disease

Disease-induced mortality may regulate a population. Along the NL shelf, the only known disease fatal to snow crab is bitter crab disease (BCD). BCD is a hemo-parasitic affliction caused by infective dinoflagellates of the genus *Hematodinium*. The increased metabolic load stemming from infection normally results in respiratory and/or organ dysfunction and subsequent death. Parasitic transmission is typically associated with host molting (Eaton et al. 1991; Stentiford and Shields 2005), thus in snow crab infection likely occurs during spring. Infected crabs may be identified visibly by fall and death likely occurs over winter. BCD prevalence has been monitored by macroscopic analyses from the fall multi-species trawl surveys since 1995. These macroscopic diagnostics are known to underestimate true prevalence (Dawe et al. 2010b; Mullowney et al. 2011), but an ongoing study has confirmed trends are consistent with those determined through more sensitive polymerase chain reaction DNA sequencing (unpublished data).

Dawe et al. (2010b) reported that ocean circulation features and host population dynamics influenced distribution of BCD along the NL shelf. The highest infection rates were typically associated with shallow areas, such as the top of offshore banks, where small crabs are most common (Dawe and Colbourne 2002). Shields et al. (2005, 2007) studied BCD prevalence and distribution dynamics in snow crab from Conception Bay in inshore Division 3L, and concluded that the disease was positively related to ocean temperature. They predicted future warming would lead to increased prevalence and distribution, and consequently elevated natural mortality levels in NL snow crab. However, counter to this, as the ocean climate along the NL shelf has warmed since the mid 1990s (Colbourne et al. 2012) overall BCD prevalence levels have decreased (Mullowney et al. 2013).

Mullowney et al. (2011) studied BCD in snow crab from bays in Division 3K and found no direct relationship with ocean temperature. In contrast, they found the disease was density regulated, with infection rates reflecting the relative abundance of small and intermediate-sized crabs. The disease was deemed to alter populations most during periods of high recruitment. Moreover, they found that BCD prevalence levels could be used as an index of long-term recruitment potential for the fishery. The relationship with temperature was found to be indirect, with temperature regulating small crab abundance, which in turn largely determined overall disease prevalence. Accordingly, as the relationship between temperature and small crab abundance is negative, they argued that reduced BCD prevalence and subsequent mortality in the snow crab would be expected as ocean temperatures increased.

The two groups of male crabs most commonly infected are new-shelled adolescents ranging 40–59 and 60–75 mm CW (Mullowney et al. 2013). An examination of annual trends in these groups shows that the prevalence of BCD has indeed decreased in recent years (Fig. 8). In Division 2J, prevalence was exceptionally high in 1999 and has been low since, while in Division 3K there has been a gradual decline in annual prevalence levels since 1997. The 2010 observations in Division 3K were deemed anomalous due to mis-classification (Mullowney et al. 2013). In Divisions 3LNO, an increase during the 2003–2005 period reflected the progression of a recruitment pulse through those sizes, which has subsequently progressed into the exploitable biomass and become manifest in recent high fishery catch rates (Mullowney et al. 2013).

In summary, the overall decreased prevalence of BCD in recent years indicates that mortality from this disease is not the primary driver of recent declines in the crab resource. However, a broad-scale reduction in BCD is consistent with other data in suggesting a low level of production and recruitment.

Predation

Along the NL shelf, the historically dominant predator in the ecosystem was Atlantic Cod (*Gadus morhua*). Other predators with the potential to influence snow crab abundance include Wolffishes (Northern (*Anarhichas denticulatus*), Spotted (*A. minor*), and Atlantic (*A. lupus*)), Greenland Halibut (*Reinhardtius hippoglossoides*), Thorny Skate (*Amblyraja radiate*), and Harp Seals (*Pagophilus groenlandicus*).

The cod stocks surrounding Newfoundland and southern Labrador (Divisions 2J3KL) were once among the world's largest (Rose 2007). However, during the late 1980s and early 1990s they collapsed, along with most of the finfish community, leading to the commercial fishing moratorium. Concomitant

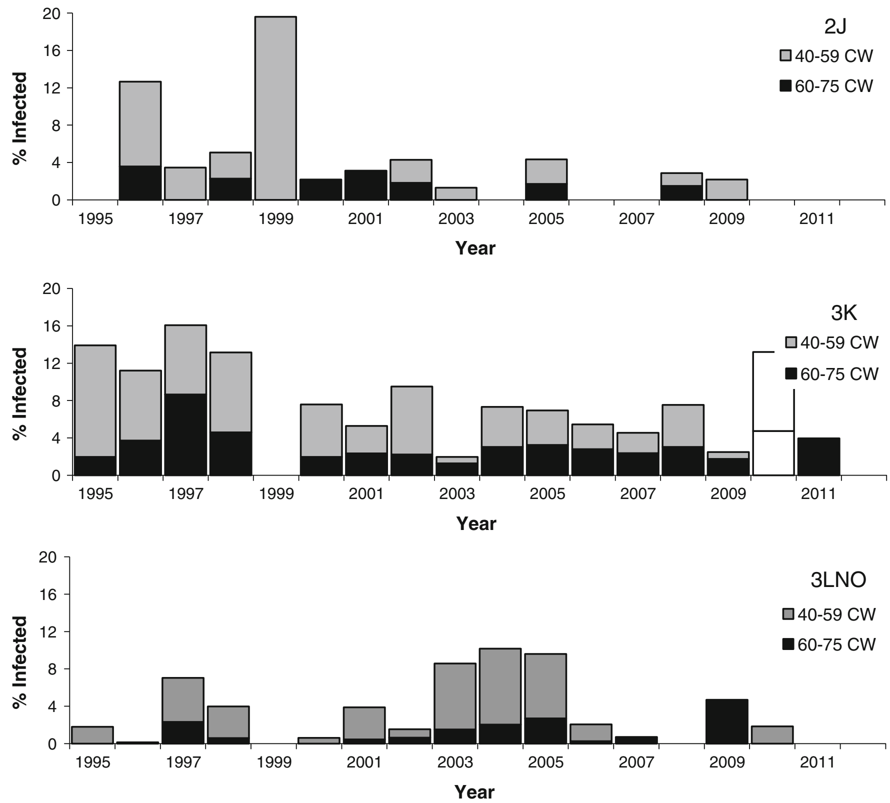


Fig. 8 Annual trends in Prevalence of Bitter Crab Disease from fall multi-species trawl surveys. 2010 value in Division 3 K deemed anomalous (see Analysis—Disease section of text)

decreases in size- and age-at maturity and condition were associated with high levels of natural mortality during and subsequent to the collapse. However, some recovery has occurred in recent years (Rose et al. 2011), and some crab harvesters claim that cod is now exerting top-down control and contributing to the decline of the resource. Based on a meta-analysis of cod and crab correlation coefficients, Boudreau et al. (2011) concluded that cod predation can exert a top-down regulating influence on large juvenile and sub-adult snow crab, lending support to the observations of some crab harvesters that increasing numbers of cod are causing declines in crab.

Any discussion of cod predation on snow crab must consider that impacts will be lagged in the fishery or exploitable biomass by several years because cod gape limitations render small crabs most susceptible to consumption and largest crabs virtually immune. For example, Chabot et al. (2008) demonstrated that nearly all consumed crabs were less than about 40 mm CW. Large cod of about 80 cm fork length (FL) or more are able to consume an intermediate-sized crab of about 65 mm CW. Dawe et al. (2012a) showed only marginal consumption of crab by cod for the past two decades (Fig. 9), but the study did not include data after 2009 and during the time of the study few large cod were present in the major crab grounds (Brattey et al. 2010). A study incorporating cod diet data up to 2011 when larger fish were present also reported few snow crabs in the stomach contents from various stocks in NL waters (Krumsick and Rose 2012). Hence, the general absence of large cod in the previous decades and the lack of crab in more recent cod diet studies of primarily smaller cod suggests that predation by cod is not broad-based and any regulating effect on snow crab recruitment or adult mortality is likely to be minor. It is noteworthy, nonetheless, that recent increases in the abundance of large cod in some areas (i.e. Division 3K) (Rose, unpublished data) may have elevated the potential for cod to impact some crab groups.

The weight of the evidence suggests that cod predation is not responsible for the presently observed recruitment declines or adult mortality in snow crab. This is not to say that predation could not reduce crab populations, but until recently the abundance of large

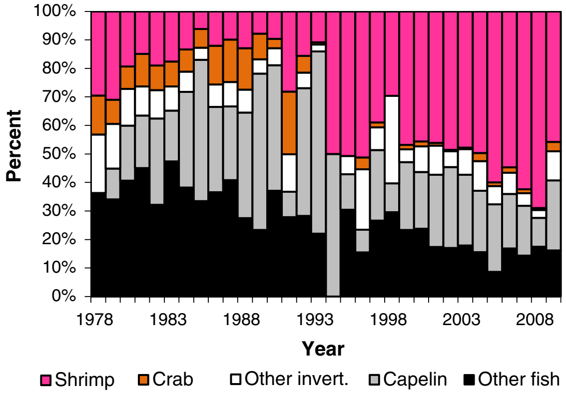


Fig. 9 Annual composition of northern cod diet from fall multi-species trawl surveys in Divisions 2J3KL. Data taken from Dawe et al. (2012a). The y-axis is the percentage contribution by weight. Sampling of stomachs was length-stratified for all sizes of cod. Further details available in Dawe et al. (2012a)

(i.e. age 5+) cod has been near-universally too low in the NL ecosystems to have significant impact. None-theless, the increasing numbers of larger cod in some areas could exacerbate rates of decline. Indeed, recently increased predation could partially explain the increased rate of decline in mature female crab abundance in the past 3 years (Fig. 4). In the Eastern Bering Sea, Orensanz et al. (2004) described a situation whereby cod predation was prohibiting female snow crab from re-establishing their distributional range to the south, following a climate-induced northward contraction, providing evidence of the potential for cod to impact snow crab stocks.

Other finfish species might also prey on snow crab and influence their numbers. Greenland halibut abundance along the NL shelf did not decline as precipitously as most other predatory finfish species during the late 1980s and early 1990s, and this species maintained a higher potential to regulate crab than most other top predators. However, the diet of Greenland halibut has been highly piscivorous since the late 1970s, with little consumption of snow crab (Dwyer et al. 2010; Dawe et al. 2012b).

Thorny skate and wolffishes might also feed on snow crab, but long-term population abundance has likely been too low for these species to account for long-term declines in snow crab. These species' have been reviewed by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) in recent years (Simpson et al. 2011, 2012), with northern and spotted wolfish deemed threatened and Atlantic wolfish and thorny skate of special concern. Moreover, the diet of thorny skate in the Northwest Atlantic is varied, consisting mainly of small pelagic fishes, crabs (including snow crab), cephalopods, polychaetes, and amphipods (Templeman 1982). There is limited information available on the diet of wolffishes along the NL shelf, but some on-going work has shown it to be highly varied with no single species dominating and low consumption of snow crab (Simpson et al. 2013).

The abundance of harp seals along the NL shelf has steadily increased since the early 1970s and has sustained itself near a historical high since the mid 1990s (Stenson et al. 2009). This species may have been the top predator exerting top-down influence in the NL shelf ecosystem since the collapse of cod (Lilly et al. 2008; Bundy et al. 2009). There have been increased accounts by fish harvesters in some northern areas in recent years of seeing snow crab on the surface ice during winter and spring, which has been attributed to seal predation. However, analyses of the offshore diet of harp seals has shown virtually no snow crab consumption during winter and summer sampling since the mid 1980s (Stenson et al. 2009).

In summary, predation by cod is unlikely to account for long-term and broad-scale declines that have occurred in snow crab. Nevertheless, recent increases in large cod may increase predation and exacerbate the rate of crab decline. There is little evidence that Greenland halibut or harp seals have any regulating effect on snow crab.

Ocean climate

Zoogeographic evidence shows that snow crab is restricted to subarctic ecosystems where cold water persists. Three recent independent studies using data on the few variables with sufficient time series (i.e. temperature, predator abundance) for modeling from our region have reported similar results, with temperature key to distribution and abundance of snow crab. First, Boudreau et al. (2011) concluded, based on an Atlantic Canadian-wide meta-analysis of correlation coefficients of crab, cod, and temperature, that temperature exerts a bottom-up influence on small crab with cold conditions favourable. Subsequently, in a multivariate regression analysis Marcello et al. (2012) compared the effects of temperature in relation to cod predation and crab spawning stock biomass on crab recruitment along the NL shelf, in the southern Gulf of

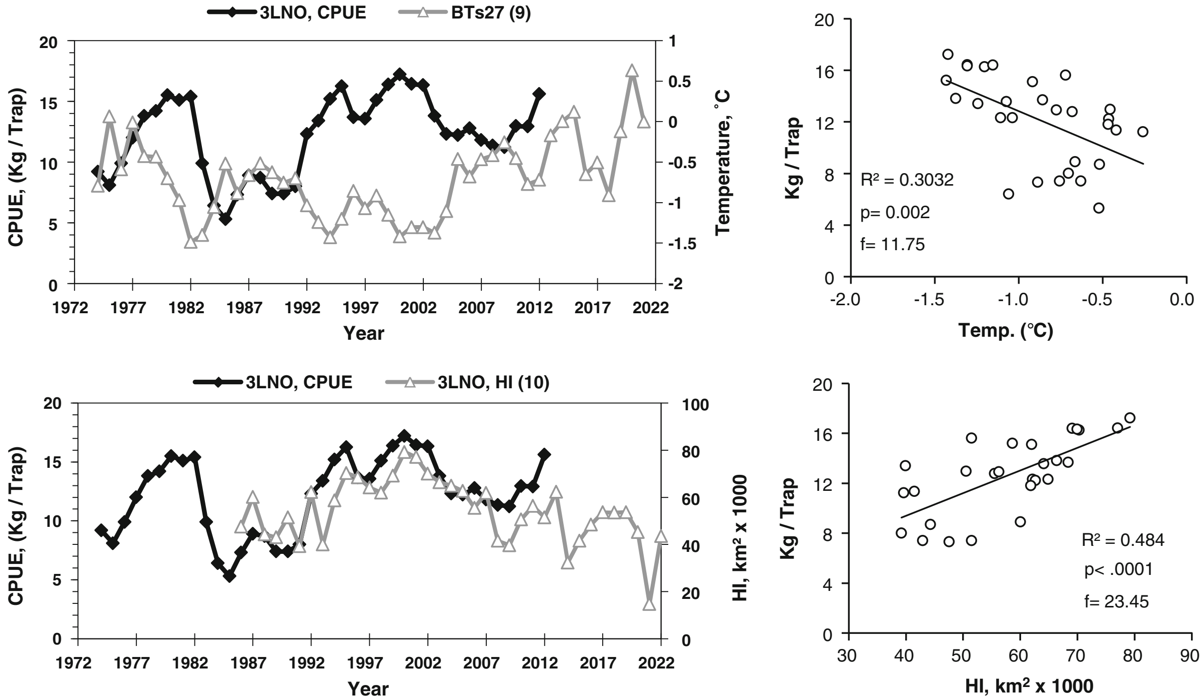


Fig. 10 Lagged relationships of Station 27 fall bottom temperature versus division 3LNO snow crab CPUE. *Top panels* show relationship of fishery CPUE versus raw bottom temperature and *bottom panel* shows relationship of fishery CPUE versus areal extent of < 1 °C water (*HI* habitat index). *Right panels* show linear relationships and significance

St. Lawrence, and in the Eastern Bering Sea. They found that cold ocean conditions during early ontogeny was the only factor consistently associated with strong recruitment. Finally, in a multi-species study on the NL Shelf using geographic weighted regressions, Windle et al. (2012) found that snow crab abundance was better predicted by environmental variables (i.e. temperature) than predator abundance.

The effect of cold bottom temperature on future fisheries is evident from the negative relationship of data from Station 27, adjacent to the Grand Bank, to future catch per unit of effort (CPUE) in Divisions 3LNO at a lag of 9 years ($f = 11.75$, $p = 0.002$). Similarly, a strong positive ($p < 0.0001$) relationship occurs between CPUE and habitat index (areal extent of <1 °C bottom water) at a lag of 10 years (Fig. 10). We chose to present the relationship of CPUE against Station 27 temperature because it is the longest and most consistently sampled oceanographic monitoring site in Northwest Atlantic, and provides the only satisfactorily long time series for cross-correlation when lags necessary to project back from 'fishery-size' to smallest sizes of crabs are applied (i.e. 9–10 years). Similar relationships of CPUE, as well as exploitable biomass, with lagged bottom temperature and habitat indices occur in all areas of the NL Shelf (i.e. Div. 2J3KLNOP4R), albeit with shorter time series (Mullowney et al. 2013). Furthermore, the lags are longer in coldest areas, such as Divisions 3LNO, due to a lower molt frequency (i.e. higher incidence of skip-molting) in cold conditions (Dawe et al. 2012a) and perhaps a longer period of egg retention in cold (i.e. 2 years) versus warm (i.e. 1 year) areas (Mallet et al. 1993; Sainte-Marie 1993).

Relationships between the environment and future fisheries only indirectly address the effects on early-life survival of small crabs. Nevertheless, their consistency across all areas of the NL shelf strongly suggests that thermal mechanisms influence early-life survival. Where survey data allowed, Marcello et al. (2012) more directly addressed the impact of temperature on recruitment in other areas (i.e. Eastern Bering Sea, Southern Gulf of St. Lawrence), similarly finding strong, negative, and consistent relationships between

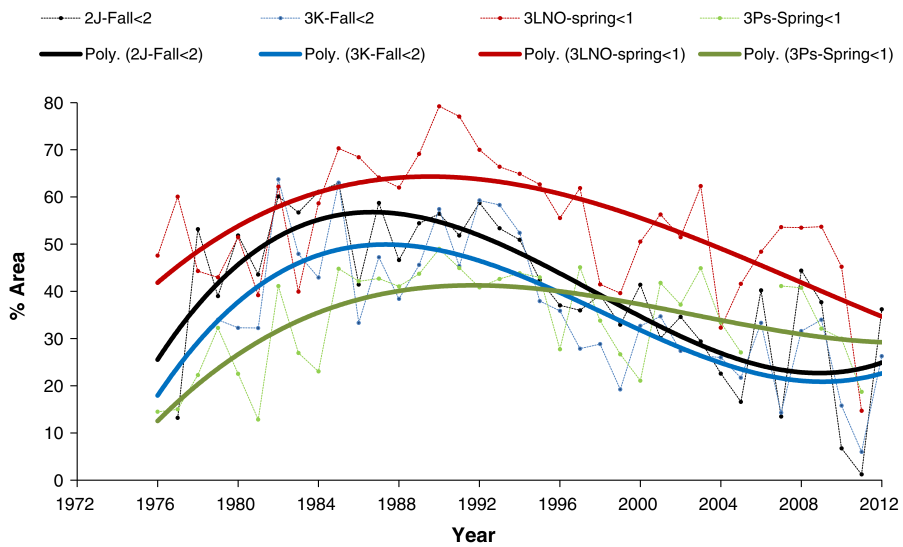


Fig. 11 Snow crab thermal habitat indices by division. Models are 3rd order polynomial regressions fit to annual estimates. *Data* acquired from multi-species trawl surveys

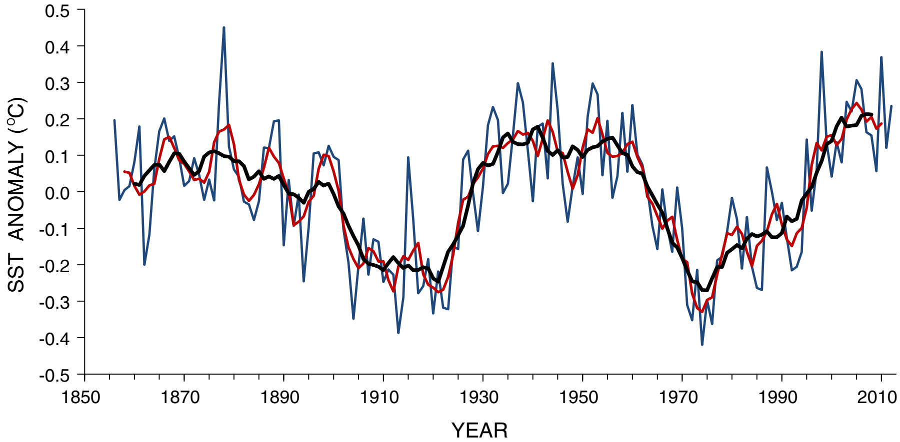
bottom temperature and early-life survival. To test and validate the relationship in NL waters, they used lagged CPUE as a proxy for recruitment due to concerns with the short times series of survey data and poor catchability of snow crab by the Campelen trawl (Fig. 10).

The strength of the argument for a strong direct effect of temperature on early-life survival lies in the consistency seen among major snow crab stocks on a global scale, including different areas of the NL shelf operating under different temperature regimes (i.e. ‘warm’ Divisions 2J3K vs. ‘cold’ Divisions 3LNOPs). Based upon this recently advanced knowledge, stock assessments in NL have included a long-term projection based on thermal habitat indices in each Division (Mullowney et al. 2013). To explicitly focus the temperature analysis on smallest crabs, the division-specific indices are restricted to shallow (i.e. ≤200 m) areas, corresponding tightly with distribution of smallest crabs, which are rarely observed in deep areas (Dawe and Colbourne 2002). Although cold water dominates this small crab habitat, crabs migrate to deeper, warmer areas over the course of life (Dawe and Colbourne 2002; Mullowney et al. 2011). The stratification of the water column, with shallow areas coldest, is a function of the distribution of the cold intermediate layer (CIL), a body of cold water (<0 °C) intermediate in the water column resulting from winter cooling. In the deep northern areas (Divisions 2J3K) there is limited distribution of shallow or <1 °C bottom water and the habitat indices are more loosely defined as bottom water <2 °C from shallowest areas (i.e. ≤300 m).

An examination of smoothed third-order polynomial regression models of the habitat indices for each Division (Fig. 11) shows a clear contraction of the cold water mass across the entire NL shelf since the early 1990s, with expansion to peak levels occurring in the late 1980s in northern Divisions 2J3K and the early 1990s in southern Divisions 3LNOPs. The growth of the cold water mass throughout the 1980s resulted in a highly productive period for the stock that led to unprecedented levels of exploitable biomass in the mid- to late-1990s (Fig. 2). Accordingly, with reductions in cold bottom water occurring across the entire NL shelf for the past two decades, with some Division-specific variability, the long-term outlook for snow crab is unfavourable across the entire NL shelf (Mullowney et al. 2013).

Apart from driving production and recruitment potential, temperature also impacts stock biomass via a direct effect on crab size. Dawe et al. (2012b) showed that size-at-terminal molt is positively related to prevailing thermal conditions, with crabs in warm regions consistently achieving greater sizes than crabs in cold regions. In NL, the deeper and warmer northern areas of the continental shelf (i.e. Divisions 2HJ3K) house crabs that achieve larger sizes on average. However, cold areas are more productive and able to support larger-scale fisheries. Overall, the negative effects of warm conditions on productivity and recruitment are greater than the positive effects on

Fig. 12 The annual Atlantic multi decadal oscillation index (*blue line*). The *red* and *black* lines are the 5 and 9 year running averages



individual size in regulating overall stock biomass (Dawe et al. 2012b).

In summary, a recently warming oceanographic regime is fully consistent with the prolonged and broad-scale decline in productivity and recruitment in NL snow crab.

Discussion

Summary

A prolonged period of low productivity and recruitment has resulted in declines in all components of the NL snow crab resource over the past decade. This is evident in reduced catch rates of all population components. In addition, broad-scale reductions in prevalence of BCD are consistent with declining productivity. The evidence suggests that a warming oceanographic regime underpins the decline in productivity and recruitment. However, other factors such as overfishing and increasing predation may be having localized impacts in some areas and have potential to exacerbate the rate of future decline.

Bottom-up versus top-down influences

Snow crab populations are undoubtedly susceptible to forces and interactions associated with many factors. Although this and a number of recent studies have shown bottom-up temperature influences to be the primary mechanism determining year-class strength, other processes certainly influence the subsequent biomass that becomes available to fisheries. This study in no way intends to dismiss their relevance. Among a host of factors, mortality associated with over-exploitation does impact near-future fisheries (i.e. Mullowney et al. 2012), trawl fisheries do interact with snow crab on the seafloor (Paul Winger, unpublished data), disease does kill crabs (i.e. Shields et al. 2005; Mullowney et al. 2011), and large finfish consume snow crab in their diets. Furthermore, cannibalism has been shown to be an important regulator of snow crab populations in the northern Gulf of St. Lawrence, with early instars particularly susceptible to consumption by larger crabs (Lovrich and Sainte-Marie 1997; Sainte-Marie and Lafrance 2002). Further, diet is a possible causative factor that we have not considered. The diet of NL snow crab has not been extensively studied, although Squires and Dawe (2003) highlighted the important contributions of polychaetes, pandalid shrimps, and capelin (*Mallotus villosus*) for individuals inhabiting waters off the northeast coast of Newfoundland. Although the abundance of shrimp has recently declined off the northeast coast (Orr and Sullivan 2012), and capelin abundance has been perpetually low since the stock collapse in the early 1990s (DFO 2011), there are no long-term diet data available from which to assess if these factors have influenced recent crab resource declines.

Despite these other influences on snow crab, the evidence suggesting temperature to be the primary driver of snow crab population dynamics is strong. It is the only factor that is consistent among regions having diverse levels of other factors. For example, in NL, the northernmost areas (i.e. Divisions 2HJ3K) have higher fishery exploitation rates, receive considerable levels of shrimp trawling, and have the highest rates of disease (i.e. BCD). In contrast, the southern areas (i.e. Divisions 3LNOPs) have less trawling, low rates of disease, and cod stocks that did not decline to the same extent as the northern stock. Despite spatiotemporal variability in all these factors, snow crab fishery catch rates have maintained oscillatory patterns linked to the climate signal (i.e. Fig. 10) in all areas (Mullowney et al. 2013). Similar findings have been reported from other regions where large snow crab populations reside, with populations following climate signals despite spatiotemporal variability in other factors (Boudreau et al. 2011; Marcello et al. 2012).

The influences of bottom-up forcing are known to occur over large spatial scales in marine ecosystems (Shackell et al. 2009). In our case, the snow crab resource followed a similar trajectory of growth, and now decline, across all areas of the NL shelf. Declines in cold water coverage began several years earlier in northern Divisions (2J3K), thus it is consistent to expect a delay in fishery impacts in the southern Divisions (3LNOPs). The southern area fisheries have been able to extract greater amounts of crab yet consistently avoid soft-shell encounters (i.e. overfishing) because of higher productivity in the southern areas resulting from the greater expanse of shallow, cold, bottom water. Nevertheless, a decline in recruitment into the exploitable biomass in the southern areas is anticipated as the effects of decadal-long warming begin to come to fruition. A recent recruitment pulse has now near-fully entered into exploitable size in these areas with no subsequent pulses evident (Mullowney et al. 2013).

Although cold water is evidently beneficial for early-life survival, it is debatable exactly what mechanisms govern this process and at exactly what stage the effect(s) occur. Szuwalski and Punt (2013) recently demonstrated a lagged effect of temperature on female snow crab recruitment in the Eastern Bering Sea, hypothesizing that temperature effects were exerted at larval stages, with survival influenced by food availability in the pelagic phase and during subsequent advection to nursery grounds. In contrast, however, our data (based on best fit lags, see Mullowney et al. 2013) infer that the impact of temperature occurs following settlement, and we hypothesize temperature interacts with post-settlement metabolic demand to regulate early-life survival. Whatever the mechanism, it is clear that further research efforts should be directed at understanding this early-life bottleneck for snow crab.

Along with directly influencing year class strength, bottom-up forcing may also impact snow crab recruitment in other ways. For example, increasing temperatures might lead to increased abundance of finfish in cold-water ecosystems (Worm and Myers 2003; Drinkwater 2005, 2006; Wieland and Hovgard 2009), and consequently predator regulation. However, the extent to which the abundance of predatory finfish increases is likely to be driven in indirect as well as direct fashions by temperature. Drinkwater (2005) found that population dynamics of northern cod were largely dependent on processes influencing primary and secondary production, and impacts on potential predator (i.e. deYoung and Rose 1993) and prey (Frank et al. 1994; Rose and O'Driscoll 2002) distributions are well known. Mullowney and Rose (2013) recently showed that a capelin deficiency in the diet has limited the growth of individuals in the northern cod stock, which has reduced growth in stock biomass and possibly recruitment. They posited that a positive response of the northern cod to warming temperatures has been mollified by poor feeding, especially on capelin, their former chief prey. Indeed, bottom-up influences of diet have been shown to be limiting capelin population growth (Obradovich et al. 2013), specifically due to a lack of euphasiids (Dalpadado and Mowbray 2013).

Our overall goals are not only to better understand the dynamics of snow crab in NL waters, but to inform management on fishing and conservation strategies. Management cannot control the influences of bottom-up processes throughout the ecosystem, including the impacts on snow crab recruitment. However, under the scenario of an anticipated decline in snow crab biomass, and a fishing industry that remains largely dependent on crab, it is advisable to focus efforts on controlling potentially influential top-down interferences, even if they are not ascribed as the primary driver of snow crab population dynamics. Clearly, it is within the capability of management to control fishery exploitation rates as well as exert influence on factors such as interactions with trawling and seismic activities. In addition, the impacts of increasing groundfish, especially cod, on snow crab requires additional study. If there is a benefit from the extreme fishery, environmental, and community changes of the past decades, it is that it offers the range of contrasts needed to better understand the mechanisms that impact abundance and distribution of snow crab and other species in this northern shelf ecosystem.

Outlook

The finding of climate as the primary driver of NL snow crab declines necessitates an exploration of events occurring in the environment. The recent broad-scale warming in the northwest Atlantic, coupled with events such as declines in cold water crustaceans like snow crab and northern shrimp (Orr and Sullivan 2012) and increases in many finfish stocks, makes it seem highly plausible that we are on the cusp or in the midst of a regime shift. Regime shifts are rapid reorganizations of ecosystems from one relatively stable state to another. The ability to adapt to or manage regime shifts relies on fundamentally understanding their causes (deYoung et al. 2008). In the marine environment they are often associated with climate shifts (i.e. Biggs et al. 2009; Mueter et al. 2009), with impacts persisting for decades and changes in community productivity and structure occurring over large spatial scales. Fishing may also contribute to or even precipitate shifts, with interactions between climate, productivity, and hence sustainable fishing levels, a given (Rose 2007). Regime shifts have been identified in many northern ecosystems from re-analysis of history (Anderson and Piatt 1999; Hare and Mantua 2000; Beaugrand 2004; Tian et al. 2011) with the most pronounced one in the North Atlantic in the 1920s and 1930s (Drinkwater 2006), whereby warm conditions persisted into the 1950s–1960s. This warming had profound impacts for fisheries throughout the North Atlantic, causing large poleward range extensions for many species (Edwards et al. 2013). It is plausible such a pattern could be repeated if recent warming persists. Trends in the broadest-based climactic indices of sea surface temperature incorporated in the Atlantic multidecadal oscillation (AMO) Index, a naturally occurring signal of low-frequency temperature variability incorporating latitudes north of the equator (Fig. 12), generally reflect the historic patterns of regime shifts described in the literature, with multidecadal variability observed in the order of about 60–80 years (Drinkwater et al. 2013).

The AMO shows that broad-scale warming has recently occurred in the north Atlantic, but the future state of the ocean climate remains uncertain. Edwards et al. (2013) investigated the AMO drivers in a principal components analysis and found that the two warming phases of the twentieth century have had similar hydro-biological impacts but there is a fundamental difference with the current warming being driven more by the increasing monotonic temperature trend in the Northern Hemisphere. They concluded that the key question of when the current warm phase of the AMO will begin to decline remained elusive, as does a clear understanding of the relative future influence of the natural low frequency signal versus the anthropogenic-induced warming phenomenon. Cannaby and Husrevoglu (2009) estimated the peak in the AMO may occur around 2025, roughly based on a 60 year cycle, while Holliday et al. (2011) predicted the AMO has peaked and that coming decades will bring cooling temperatures. If both the natural low-frequency and anthropogenic-forced monotonic warming signals persist, a scenario of possible cooling during the next negative phase could be followed by rapid warming during the next positive phase. Future improvements in capacities to predict ocean climate would greatly help improve expectations and management of the snow crab resource beyond the 8–10 year predictive capacity afforded by current knowledge. Drinkwater et al. (2013) found that many species which have only been researched in recent decades suggest a multi-decadal effect linked to climate, but short time series makes the connections impossible to confirm. Nevertheless, initial indications from all studied ecosystems are that snow crab responds strongly to bottom-up processes with relatively long lead-time to the fished stock. This feature is fundamental to management of the species and has potential importance to studies of climate and shifts in community regimes in northern ecosystems.

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