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THEME SECTION

Effects of climate and predation on subarctic crustacean populations

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INTRODUCTION

Subarctic fish and crustacean populations — climate effects and trophic dynamics

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ABSTRACT: This Theme Section reviews the ecological role of large marine decapods, presents selected case studies, and features comparative analyses of the dynamics of fish and crustacean populations and their interactions across several subarctic ecosystems. Collectively, the studies described here highlight the role of climate and predation in regulating fish and crustacean populations in these systems. The Theme Section has resulted from the activities of ESSAS (Ecosystem Studies of Sub-Arctic Seas) Working Group 4 on 'Climate Effects at Upper Trophic Levels'.

KEY WORDS: Subarctic · Crustacea · Gadoids · Climate · Predation · Trophic dynamics

Background

The Ecosystem Studies of Sub-Arctic Seas (ESSAS) program was established in 2005 to examine how climate change affects marine ecosystems of the Sub-Arctic Seas. The hallmark of ESSAS has been a comparative approach that seeks a better understanding of subarctic ecosystems by identifying commonalities and differences among multiple systems. This Theme Section is the product of ESSAS Working Group 4 (WG4) 'Climate Effects at Upper Trophic Levels', which assesses the effects of climate variability, predation, and fishing on major commercial fishes and crustaceans across multiple subarctic marine ecosystems.

Gadoid fishes, flatfishes and crustaceans are integral parts of subarctic ecosystems (Livingston & Tjelmeland 2000, Aydin & Mueter 2007) and support important commercial and subsistence fisheries, as well as large populations of marine birds and mammals (Hunt & Drinkwater 2007). Sustainability and management of these fisheries in a changing climate requires a better understanding of the effects of climate variability on the target stocks, on interactions among stocks, and on the ecosystems of which they are a part.

Observations from several high-latitude marine ecosystems in both the Atlantic and Pacific oceans indicate the existence of alternating states dominated by crustaceans or large predatory fishes (primarily gadoids and flatfishes), respectively (Anderson & Piatt 1999, Choi et al. 2004, Lilly et al. 2008). However, the effects of climate variability, exploitation, and predation on the transition between states remain controversial.

To address this issue, WG4 brought together experts on fishes and crustaceans in 8 subarctic ecosystems. Initial workshops were held in conjunction with the ESSAS Annual Science Meetings in Seattle, USA, in September 2009 and in Reykjavik, Iceland, in September 2010. These workshops featured case studies from selected subarctic seas and laid the foundation for collaborative analyses of long-term fishery and survey data, as well as time series of ocean climate variables. A third workshop to focus on cross-system comparisons was held in conjunction with the second ESSAS Open Science Meeting (OSM) in Seattle in

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May 2011 on 'Comparative studies of climate effects on polar and sub-polar ocean ecosystems: progress in observation and prediction' (Drinkwater et al. 2012). Members of WG4 chaired a scientific session on 'Interactions between gadoids and crustaceans: the roles of climate, predation and fisheries' during the OSM.

Major findings

This Theme Section includes a review of the ecological role of large marine decapods and several case studies, as well as comparative analyses of trophic interactions between predatory fishes and crustaceans and comparisons of recruitment dynamics of snow crabs *Chionoecetes opilio* across several subarctic ecosystems. Boudreau & Worm (2012, this volume) conclude that more experimental studies and long-term observations are needed to understand the mechanisms driving variability in large marine decapods and to manage their fisheries sustainably. Other papers in the Theme Section draw on long-term observations, often from multiple systems, to shed new light on the dynamics of, and interactions between, predatory fishes and crustaceans. Diet studies in the Gulf of Alaska indicate that Tanner crabs *Chionoecetes bairdi* are the most important prey of Pacific cod *Gadus macrocephalus*, whereas shrimp represent an important component of the diet of walleye pollock *Theragra chalcogramma* (Urban et al. 2012, this volume). Pandalid shrimp are important in the diet of Atlantic cod *Gadus morhua* off Iceland, but their prevalence varies greatly between inshore and offshore waters (Jónsdóttir et al. 2012, this volume), highlighting the importance of spatial considerations in analyses of trophic dynamics. The diets of Atlantic cod off Newfoundland and Labrador and of Greenland halibut *Reinhardtius hippoglossoides* in the Gulf of St. Lawrence both shifted from capelin *Mallotus villosus* in the 1980s to shrimp since the mid-1990s, following the collapse of capelin and other fish stocks (Dawe et al. 2012a, this volume). Snow crabs are of lesser importance in the diets of predatory fishes, consistent with evidence across systems that predation does not control their dynamics (Marcello et al. 2012, this volume, Dawe et al. 2012a), although spatial interactions between cod and crustaceans off Newfoundland were locally stronger for snow crabs than for northern shrimp (Windle et al. 2012, this volume).

Climate variability has important effects on the dynamics of snow crab and shrimp populations in a number of subarctic systems. Warm temperatures have consistent negative effects on the survival of early benthic stages of snow crabs (Boudreau et al. 2011, Marcello et al. 2012, this volume), but adults achieve a higher molting frequency and larger size at terminal molt under higher temperatures (Dawe et al. 2012b, this volume). These effects on growth imply that low temperatures reduce recruitment into the fishery because fewer males recruit to harvestable size. However, the overall effect of lower temperatures on recruitment is positive (Marcello et al. 2012), implying that positive effects on early survival dominate recruitment dynamics. In contrast, northern shrimp off West Greenland benefit from warmer surface layer temperatures, presumably due to enhanced food availability for the larvae, as long as bottom temperatures are also warmer to ensure a match between the time of hatching and the plankton bloom (Koeller et al. 2009, Ouellet et al. 2011, Wieland & Siegstad 2012, this volume).

Conclusions

Collectively, papers in this Theme Section provide new evidence for the importance of climate effects on the dynamics of subarctic crustacean populations. In particular, there is strong evidence that climate controls snow crab populations (Marcello et al. 2012), although predation may impede recovery when abundances are low (Orensanz et al. 2004). Climate also interacts with predation in regulating some northern shrimp populations (Wieland & Siegstad 2012). Spatial dynamics regulating the relative overlap of predatory fishes and crustaceans are key to understanding the temporal dynamics of crab and shrimp stocks (Orensanz et al. 2004, Wieland et al. 2007, Parada et al. 2010, Wieland & Siegstad 2012, Windle et al. 2012). These findings will contribute to the sustainable management of fish and shellfish populations in subarctic ecosystems.

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Contribution to the Theme Section 'Effects of climate and predation on subarctic crustacean populations'

Ecological role of large benthic decapods in marine ecosystems: a review

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ABSTRACT: Large benthic decapods play an increasingly important role in commercial fisheries worldwide, yet their roles in the marine ecosystem are less well understood. A synthesis of existing evidence for 4 infraorders of large benthic marine decapods, Brachyura (true crabs), Anomura (king crabs), Astacidea (clawed lobsters) and Achelata (clawless lobsters), is presented here to gain insight into their ecological roles and possible ecosystem effects of decapod fisheries. The reviewed species are prey items for a wide range of invertebrates and vertebrates. They are omnivorous but prefer molluscs and crustaceans as prey. Experimental studies have shown that decapods influence the structuring of benthic habitat, occasionally playing a keystone role by suppressing herbivores or space competitors. Indirectly, via trophic cascades, they can contribute to the maintenance of kelp forest, marsh grass, and algal turf habitats. Changes in the abundance of their predators can strongly affect decapod population trends. Commonly documented non-consumptive interactions include interference-competition for food or shelter, as well as habitat provision for other invertebrates. Anthropogenic factors such as exploitation, the creation of protected areas, and species introductions influence these ecosystem roles by decreasing or increasing decapod densities, often with measurable effects on prey communities. Many studies have investigated particular ecosystem effects of decapods, but few species were comprehensively studied in an ecosystem context. A simplified synthetic framework for interpreting ecosystem roles of decapods was derived from the available evidence; however, more experimental and long-term observational studies are needed to elucidate mechanisms and shed light on the long-term consequences of decapod fisheries.

KEY WORDS: Lobster · Crab · Trophic cascade · Keystone · Ecosystem effects · Anthropogenic effects · Species interactions

INTRODUCTION

Large crustaceans are becoming increasingly important to coastal and continental shelf fisheries (Anderson et al. 2011, Steneck et al. 2011). For example, in eastern North America, a well-documented shift has occurred from groundfish, such as Atlantic cod *Gadus morhua*, to invertebrates that now dominate commercial landings and value (Worm & Myers 2003, Frank et al. 2005). Globally, commercial catches of crustaceans have increased ~5-fold since 1950 and are the only invertebrate group that continues to trend upward in recent years (Anderson et al. 2011). Yet, when compared to finfish, there is a much smaller knowledge base available from which to manage these fisheries, particularly in an ecosystem context (Anderson et al. 2008). Large mega-decapods, defined here as decapod crustaceans with a carapace length (CL) or width (CW) of >10 cm, such as American lobster *Homarus americanus* and snow crab

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Chionoecetes opilio, have become particularly important commercial species in the Northwest (NW) Atlantic region and elsewhere. Decapod crustaceans have a global distribution and can be found in most habitats, ranging from intertidal to deep water regions. Their importance to humans is well documented and frequently discussed (Steneck et al. 2011), however we are only beginning to understand the role that decapods play in marine ecosystems, and how exploitation might modify this role.

Interest in the ecological effects of fisheries often tends to focus on large apex predators and their role in the ecosystem (e.g. Pauly et al. 1998, Jackson et al. 2001, Frank et al. 2005, Heithaus et al. 2008, Baum & Worm 2009, Estes et al. 2011). One of the commonly described ecosystem effects of fishing marine predators has been an increase in benthic invertebrates, including large decapod crustaceans (Baum & Worm 2009, Boudreau & Worm 2010). On occasion large decapods may replace large fish (e.g. Atlantic cod) as the dominant predator, the ecological impacts of which are poorly understood (e.g. Steneck et al. 2011). One well-documented example is a shift in the NW Atlantic ecosystem's trophic structure in the 1980s to 90s due to the depletion of top predators. Here, an observed decline in groundfish abundance (largely due to overexploitation) was followed by a large increase in benthic decapods and other prey species, likely because of predation release (Steneck et al. 2004, Worm & Myers 2003, Frank et al. 2005). In contrast, the North Pacific Ocean currently yields low decapod abundance (e.g. king crab *Paralithodes camtschaticus*, snow crab *Chionoecetes opilio*, and shrimp *Pandalus* spp.) due to population collapses in the early 1980s (Orensanz et al. 1998). These populations have since been slow to recover. As decapod stocks were low in Alaska, the biomass of groundfish (i.e. Walleye pollock *Theragra chalcogramma*) increased to an all-time high (Ianelli et al. 2011). This suggests that there may be a suite of conditions within an oceanic system that, once altered by fishing, are better suited for supporting decapod crustaceans or large-bodied groundfish (Worm et al. 2007). Yet, the broader ecological consequences of such changes in decapod populations on the benthic ecosystem are less well understood.

Many studies have focused on the diet of large marine decapods, but little is known about the strength of predatory interactions, their cascading, and overall ecosystem effects. Predation generally plays a strong role in structuring marine benthic communities (Shurin et al. 2002), ranging from intertidal shores (e.g. Paine 1994) to the deep sea (e.g. Micheli et al. 2002), but few experimental studies have focused on large decapods. Decapods are typically quite mobile, undergo ontogenetic habitat changes over their life cycle, and show a progressive dietary shift with increasing size (Sainte-Marie & Chabot 2002). It is therefore likely that they would affect a range of habitat and prey types over their life cycle.

In this paper we attempt to synthesize what is known about the role of large benthic decapods (lobsters and large crabs) in marine ecosystems. Specifically we review their multiple roles as (1) prey, (2) predators and keystone species, as well as (3) nonconsumptive interactions. Finally, given the large role humans play in modifying natural systems (Estes et al. 2011), we ask how anthropogenic factors modify the ecosystem role of decapods, and how future research efforts could provide deeper insights into these questions.

METHODS

The above questions are addressed by synthesizing the existing evidence from mega-decapod populations worldwide. A literature search was conducted using the Web of Knowledge database and the following keywords: decapod ecosystem effect (52 results), lobster ecosystem effect (109), crab ecosystem effect (347), lobster diet (456), and crab diet (1570). These papers, as well as references cited therein, form the basis of this review. Specifically, we were interested in case studies of the different roles all species of mega-decapod (CL or CW >10 cm) play in oceanic ecosystems. However, the majority of the mega-decapods studied in the literature were of commercial value, hence this review is necessarily biased towards those species.

Available publications employed a variety of methods including decapod exclusion experiments in the field (e.g. Quijon & Snelgrove 2005b), experimental transplants (e.g. Robles & Robb 1993), tethering experiments (e.g. Silliman & Bertness 2002), and diet studies (e.g. Jewett & Feder 1982). These were used primarily to gain mechanistic insights into potential predator–prey mechanisms and interactions. Experiments in the laboratory were also used, often in concert with field observations and surveys. Non-consumptive interactions were studied using similar methods as those listed above, e.g. observations on collected animals (e.g. Dvoretsky & Dvoretsky 2008), field (e.g. Novak 2004) and lab experiments to observe interactions (e.g. Williams et al. 2006), or a combination of field and lab studies (e.g. Jones & Shulman 2008). At larger spatial and temporal scales, time series analyses were used to complement smaller-scale mechanistic studies. These might examine ecosystem changes occurring in the wake of decapod exploitation (e.g. Lafferty 2004, Shears et al. 2006) or recovery (e.g. Babcock et al. 1999).

SPECIES

The species addressed in this paper are large benthic invertebrates of the order Decapoda, belonging to the following infraorders: Brachyura (true crabs), Anomura (king crabs), Astacidea (clawed lobsters) and Achelata (clawless lobsters). Most of these species are well known, largely due to their commercial value (Table 1).

Most of the brachyurans included in this review, with the exception of the tanner crab *Chionoecetes bairdi* and Dungeness crab *Metacarcinus magister* (formerly *Cancer magister*) (north Pacific Ocean), are native to the northwestern Atlantic Ocean, such as the blue crab *Callinectes sapidus,* snow crab *Chionoecetes opilo* (co-occurs in the north Pacific), and the rock crab *Cancer irroratus*. Also mentioned are the Jonah crab *Cancer borealis* and green crab *Carcinus maenas*. The green crab is the smallest decapod described here, reaching a maximum CW of 9 to 10 cm (Klassen & Locke 2007). Originally native to Europe it was introduced to eastern North America in the 19th century (Grosholz & Ruiz 1996) and has since been identified as one of the world's most invasive marine species (Lowe et al. 2000). Part of its success may be due to lower rates of parasitism and larger size in its introduced range (Torchin et al. 2001). The green crab's range, habitat, and prey field overlaps with important commercial species in the NW Atlantic, namely American lobster, rock and Jonah crabs. Its interactions will be discussed within this context.

King crabs (Family Lithodidae) belong to one of the youngest decapod families (Thatje et al. 2005) and may have originally evolved from hermit crabs (Cunningham et al. 1992). Red king crab *Paralithodes camtschaticus* is possibly one of the largest extant arthropods; large individuals can weigh >10 kg and measure up to 22 cm in CL. This species is native to the northeastern Pacific Ocean where it is commercially harvested. It has also been introduced into the Barents Sea. Other lithodids discussed here include the northern stone crab *Lithodes maja*, stone crab *Paralomis* spp., and *Neolithodes* spp.

Clawed lobsters discussed here are the American lobster *Homarus americanus* native to the NW Atlantic Ocean and the European lobster *H. gammarus* in the northeast Atlantic. Clawless lobsters include several species of spiny lobster, such as *Panulirus interruptus* (California), *P. marginatus* (Hawaii), and Caribbean *P. argus* (Florida, Bahamas), and the spiny rock lobsters *Jasus edwardsii* (New Zealand), *P. cygnus* (western Australia), and *J. lalandii* (South Africa).

There are important morphological differences between the crabs, clawed and clawless lobsters included in this study. Whether a species has claws influences how it interacts with habitat, conspecifics, predators and prey. For example, the American lobster's claws allows it to manipulate substrates for shelter, establish rank, capture prey and defend itself (Lawton & Lavalli 1995). Clawed lobsters are often aggressive (Scrivener 1971), and form dominance hierarchies (Karnofsky & Price 1989, Atema & Voight 1995). In clawless lobsters, defensive structures are limited to their robust antenna and armoured carapace (Atema & Cobb 1980, Barshaw et al. 2003), and they are often associated with conspecifics (Herrnkind 1969).

ECOSYSTEM EFFECTS

Mega-decapods as prey

Most of the large decapods considered here (Table 1) have relatively few predators once they become adults due to their large size and armoured carapaces; yet they can be very vulnerable to predation at earlier life stages. In addition to humans, some fish, birds, marine mammals and cephalopods are known to prey on these species at various stages.

Examples of fish predators include the Nassau grouper *Epinephelus striatus* (Eggleston et al. 1997) and grey triggerfish *Balistes capriscus* (Lavalli & Herrnkind 2009), which both prey on the Caribbean spiny lobster *Panulirus argus*; Pacific cod *Gadus macrocephalus* prey on snow crabs *Chionoecetes* spp. (Jewett 1982); and sculpins *Myoxocephalus* spp. consume benthic stages of American lobsters (e.g. Hanson & Lanteigne 2000, Hanson 2009, Boudreau & Worm 2010). Cephalopods and sharks are also reported to prey on decapods, for example the Caribbean reef octopus *Octopus briareus* occasionally consumes *P. argus* (e.g. Berger & Butler 2001, Butler & Lear 2009) and the leopard shark *Triakis semifasciata* preys on Dungeness crab (third most important prey item; Ebert & Ebert 2005).

Table 1. Examples of studies examining ecological roles of large marine decapods. Indicated are regions of study, common and scientific names of the decapod species, type of interaction, nature of the evidence, and sources. Listed alphabetically by scientific name

Region	Common name(s)	Scientific name(s)	Interaction
Beaufort Inlet, North Carolina; NW Atlantic	Blue crab	*Callinectes sapidus*	Host
Back Sound, North Carolina; NW Atlantic	Blue crab	*Callinectes sapidus*	Predator
Sapelo Island, Georgia; NW Atlantic	Blue crab	*Callinectes sapidus*	Keystone predator
Casco Bay, Maine to Chesapeake Bay, Virginia; NW Atlantic	Blue crab, green crab	*Callinectes sapidus, Carcinus maenas*	Predator, prey
Chesapeake Bay, Maryland; NW Atlantic	Blue crab	*Callinectes sapidus*	Cannibalism
Monterey Peninsula, California; NE Pacific	Cancer crab	*Cancer* spp.	Prey
NE Newfoundland; NW Atlantic	Snow crab	*Chionoecetes opilio*	Predator
Bonne Bay, Newfoundland; NW Atlantic	Snow crab	*Chionoecetes opilio*	Predator
Bonne Bay, Newfoundland; NW Atlantic	Snow crab	*Chionoecetes opilio*	Predator
Alaska, Japan, Russia; North Pacific Gulf of St. Lawrence; NW Atlantic	Snow crab, tanner crab	*Chionoecetes opilio, C. bairdi*	Prey
Bonne Bay, Newfoundland; NW Atlantic	Snow crab, rock crab	*Chionoecetes opilio, Cancer irroratus*	Predator
Gulf of Maine; NW Atlantic	American lobster, rock crab, green crab	*Homarus americanus, Cancer irroratus, Carcinus maenas*	Predator
SW Nova Scotia; NW Atlantic	American lobster	*Homarus americanus*	Predator
Narragansett Bay, Rhode Island; NW Atlantic	American lobster, Jonah crab	*Homarus americanus, Cancer borealis*	Competitor
Isle of Shoals, New Hampshire; NW Atlantic	American lobster, Jonah crab	*Homarus americanus, Cancer borealis*	Predator
Gulf of Maine; NW Atlantic	American lobster, rock crab	*Homarus americanus, Cancer irroratus*	Niche segregation
Passamaquoddy Bay, New Brunswick; NW Atlantic	American lobster, rock crab	*Homarus americanus, Cancer irroratus*	Predator
Northumberland Strait, Southern Gulf of St. Lawrence; NW Atlantic	American lobster, rock crab	*Homarus americanus, Cancer irroratus*	Predator, prey
Magdalen Islands, Gulf of St. Lawrence; NW Atlantic	American lobster, rock crab	*Homarus americanus, Cancer irroratus*	Predator, prey
Magdalen Islands, Gulf of St. Lawrence; NW Atlantic	American lobster, rock crab	*Homarus americanus, Cancer irroratus*	Predator, prey
Southern Gulf of St. Lawrence; NW Atlantic	American lobster, rock crab	*Homarus americanus, Cancer irroratus*	Host, vector
Southern Gulf of St. Lawrence; NW Atlantic	American lobster, green crab	*Homarus americanus, Carcinus maenas*	Competitor
Lundy no-take zone, UK; NE Atlantic	European lobster	*Homarus gammarus*	Abundance
Tawharnui and Mimiwhangata Marine Parks, New Zealand; SW Pacific	Spiny rock lobster	*Jasus edwardsii*	Trophic cascade
Leigh Reserve, New Zealand; SW Pacific	Spiny rock lobster	*Jasus edwardsii*	Trophic cascade
Saldanha Bay Reserve, South Africa; SE Atlantic	Rock lobster	*Jasus lalandii*	Predator, prey
Antarctic Bellingshausen Sea, Southern Ocean	King crab	*Lithodes* spp., *Paralomis* spp., *Neolithodes* spp.	Predator
Bamfield, Britsh Columbia; NE Pacific	Dungeness crab	*Metacarcinus magister*	Predator
Willipa Bay, Washington; NE Pacific	Dungeness crab	*Metacarcinus magister*	Behaviour
Humbolt Bay, California; NE Pacific	Dungeness crab	*Metacarcinus magister*	Prey
Gray's Harbor, Washington; NE Pacific	Dungeness crab	*Metacarcinus magister*	Predator
Florida Bay, Florida; NW Atlantic	Caribbean spiny lobster	*Panulirus argus*	Prey
Florida Keys National Marine Sanctuary, Florida; NW Atlantic	Caribbean spiny lobster	*Panulirus argus*	Prey
Lee Stocking Island, Bahamas; NW Atlantic	Caribbean spiny lobster	*Panulirus argus*	Prey
Florida Keys, Florida; NW Atlantic	Caribbean spiny lobster	*Panulirus argus*	Prey
Western Australia; E Indian Ocean	Western rock lobster	*Panulirus cygnus*	Predator
Santa Catalina Island, California; NE Pacific	Spiny lobster	*Panulirus interruptus*	Predator
Channel Islands National Park, California; NE Pacific	Spiny lobster	*Panulirus interruptus*	Trophic cascade
Santa Catalina Island, California; NE Pacific	Spiny lobster	*Panulirus interruptus*	Keystone predator
Northwestern Hawaiian Islands; NE Pacific	Spiny lobster	*Panulirus marginatus*	Prey
Barents Sea, Arctic Ocean	Red king crab	*Paralithodes camtschaticus*	Predator
Kodiak Island, Alaska; NE Pacific	Red king crab	*Paralithodes camtschaticus*	Predator
Barents Sea, Arctic Ocean	Red king crab, Northern stone crab	*Paralithodes camtschaticus, Lithodes maia*	Host

Table 1 (continued)

Mechanism	Method	Sources
Barnacles *Octolasmis mulleri* living on gills	Lab, field	Walker (1974)
Crabs consumed more clams *Mercenaria mercenaria* at vegetated sites possibly avoiding bird predation	Field	Micheli (1997), Micheli & Peterson (1999)
Crabs control periwinkle capable of overgrazing salt marsh vegetation	Field	Silliman & Bertness (2002)
Blue crab predation limits abundance and range of invasive green crab	Lab, field	DeRivera et al. (2005)
Cannibalism by large blue crabs was 75–97% of mortality of juveniles	Lab, field	Hines & Ruiz (1995)
Cancer spp. crab are a dietary component of the general consumer, the sea otter	Field	Estes et al. (2003)
Predation on juvenile snow crab, polychaetes, shrimp and fishes	Stomachs	Squires & Dawe (2003)
Predation influenced composition, abundance, and diversity of benthic infauna	Lab, field	Quijon & Snelgrove (2005b)
Predation on algae, fish, polychaetes, crustaceans, molluscs, echinoderms	Field, stomachs	Wieczorek & Hooper (1995)
Chionoecetes prey for 7 invertebrates, 24 fish, 2 skates, and 4 marine mammal species	Review	Jewett (1982)
Rock crab decreased infaunal species richness. Infaunal density and diversity increased with the exclusion of the crabs. Clear effect on species composition	Lab, field	Quijon & Snelgrove (2005a)
Nocturnal feeding on crabs, mussels, periwinkles. Believed to migrate up into the intertidal zone to prey on green crabs	Lab, field, stomachs	Jones & Shulman (2008)
65 prey taxa identified, mostly echinoderms, molluscs, crustaceans and polychaetes	Stomachs	Elner & Campbell (1987)
Jonah crab choose to utilize alternative shelter when lobster present	Lab	Richards & Cobb (1986)
Crabs and lobster significant predators of sea urchins, indirect effects on ascidians and mussels	Field	Siddon & Witman (2004)
Rock crab densities higher on kelp fronds when lobsters were present	Lab, field	Wells et al. (2010)
Sea urchins avoided rock crabs and lobsters, no aggregations formed when decapods present	Lab, field	Vadas et al. (1986)
Fish predation on lobster uncommon. Lobster mainly prey on crab, sea stars and lobster	Stomachs	Hanson (2009)
Diet shift with increased size of lobster. Rock crab was part of diet at all sizes	Stomachs	Sainte-Marie & Chabot (2002)
Lobsters condition, growth and development increased with increasing amounts of rock crab in their diet	Lab	Gendron et al. (2001)
Non-indigenous ascidians *Botrylloides violaceus* were found on rock crabs, *Botryllus schlosseri* was found on lobster	Field	Bernier et al. (2009)
Green crab outcompeted juvenile lobster for food	Lab	Rossong et al. (2006), Williams et al. (2006)
Increased abundance and legal-sized lobster inside the NTZ, spillover of sublegal lobster	Field	Hoskin et al. (2011)
In no-take area, lobster abundance increased 11 times and biomass 25 times since establishment. Lower densities of sea urchins and expanding kelp forest in no-take reserves	Field, time series	Shears et al. (2006)
Protection of lobsters and fish resulted in higher predation on urchins resulting in increased kelp cover	Field, time series	Babcock et al. (1999), Babcock (2003)
Rock lobsters prey on whelks and settling mussels. Lobsters transferred to other island were overwhelmed, consumed by whelks.	Lab, field	Barkai & McQuaid (1988)
Lithodid crabs recolonizing Antarctica may restructure the benthic community via predation and bioturbation	Field	Thatje et al. (2005), Smith et al. (2011)
Cancer spp. including Dungeness, are able to exert biting forces (claws) greater than most other animals.	Lab	Taylor (2000)
Invasive cord grass restructured habitat, altered movement and foraging behaviour of indigenous Dungeness crab	Lab, field	Holsman et al. (2010)
Dungeness crab had an 11.6% index of relative importance in the diet of female leopard sharks	Stomachs	Ebert & Ebert (2005)
First year crabs preyed on bivalves, small crustaceans (incl. conspecifics). Second and third year preyed upon *Crangon* spp. and fish	Stomachs	Stevens et al. (1982)
Octopus is assumed predator of lobster. Lobster detected chemical cues to avoid octopus dens.	Lab, field	Berger & Butler IV (2001)
Juvenile lobsters preyed upon by Caribbean reef octopus	Field	Butler IV & Lear (2009)
Abundance of small lobsters was highest in small reefs where Nassau grouper were experimentally removed	Field	Eggleston et al. (1997)
Grey triggerfish preyed on tethered lobsters	Lab, field	Lavalli & Herrnkind (2009)
Stable isotope analysis showed amphipods, isopods, crabs, bait, foliose red algae and sponges in lobster diet	Lab, field, stomachs	Waddington et al. (2008)
Exclusion of lobsters from upper shore results in increases in density/size of mussels and herbivorous molluscs, and decrease in algae	Field	Robles (1987)
Fishing of lobster led to increase in sea urchins, overgrazing of kelp forests	Field	Lafferty (2004)
Exclusion of lobsters (keystone) from wave-exposed rocky intertidal sites caused algal turf to be replaced by mussels	Field	Robles & Robb (1993), Robles (1997)
Hawaiian monk seals were observed foraging on spiny lobster, but not a major prey item	Field	MacDonald (1982), Goodman-Lowe (1998)
Predation by crabs decreased abundance of sea urchin, sea stars, and Iceland scallop	Lab	Jørgensen (2005), Jørgensen & Primicerio (2007)
Stomach contents revealed molluscs and arthropods to be preferred prey	Stomachs	Jewett & Feder (1982)
Hydrozoans, polychaetes, bivalves, amphipods, cirripedes, bryozoans were described on both species of crab	Field	Dvoretsky & Dvoretsky (2008)

Avian predators such as the herring gull *Larus agentatus* and ring-billed gull *L. delawarensis* commonly feed on crabs, e.g. green or rock crabs (e.g. Dumas & Witman 1993); likewise herons were observed to prey on blue crabs (Micheli 1997). Marine mammals, for example the Hawaiian monk seal *Monachus schauinslandi*, occasionally feed on various crustaceans including spiny lobsters *P. marginatus* (MacDonald 1982, Goodman-Lowe 1998). Decapods have not been identified as a major dietary component of seals or sea lions (Goodman-Lowe 1998, Beck et al. 2007, Boudreau & Worm 2010). Similarly, *Cancer* spp. crabs are found in the diet of sea otters *Enhydra lutris* in the Pacific (Estes et al. 2003).

Of course most decapod species have multiple predators across their life cycle. Crabs of the genus *Chionoecetes*, for example, are known to be consumed by at least 7 species of invertebrates (including conspecifics, red king crab, and the sea star *Asterias amurensis*), 24 species of bony fish, 2 species of skate and 4 species of marine mammals. Most of these interactions were reported from the North Pacific, with the exception of predation by Atlantic cod on *C. opilio* (as well as cannibalism in *C. opilio*) in the Gulf of St. Lawrence (Jewett 1982 and references therein). In the northwest Gulf of St. Lawrence, SCUBA divers observed 2 incidences of *C. opilio* males holding dead, recently moulted mature females that were being consumed by whelks *Buccinum undatum*. Additional dead females and immature female exuviae were observed being consumed by lysianassoid amphipods (Sainte-Marie & Hazel 1992).

Likewise, a number of bony fish and elasmobranchs prey on American lobster, *Cancer* spp., snow crab, and blue crab, at varying rates (e.g. Moss 1972, Robichaud et al. 1991, Rountree & Able 1996, Steneck 1997, Boudreau & Worm 2010, Boudreau et al. 2011). Some predators may be more important than others; in the soft substrates of the Southern Gulf of St. Lawrence, the shorthorn sculpin *Myoxocephalus scorpius* was the only demersal fish to consume large amounts of American lobsters (2.6% frequency of occurrence, 28.9% biomass). Small amounts of lobster larvae were detected in pelagic fishes such as herring *Clupea harengus*, American shad *Alosa sapidissima*, and rainbow smelt *Osmerus mordax*; amounts were roughly proportional to their availability in the water column, suggesting random uptake of lobster larvae while filter-feeding zooplankton (Hanson 2009).

Predation risk is often increased at the post-settlement stage, when pelagic larvae recruit to benthic habitats. Substrate choice can have strong effects on species vulnerabilities to predation at this stage. For example, rock crabs settled at higher densities than lobster and were less selective of substrate, as they were found on both cobble and sandy substrate, whereas lobster clearly preferred cobble (Palma et al. 1998, 1999). Densities of post-settlement rock crabs, but not lobsters, increased in predator exclusion experiments (Palma et al. 1998, 1999).

In studies of spiny lobsters, early benthic phase individuals were vulnerable to predation and suffered high mortality from fishes and motile invertebrates (crabs and octopus) (Butler et al. 2006). Experiments confirmed that the abundances of juvenile lobster *Panulirus argus* increased on artificial patch reefs from which groupers *Epinephelus striatus* were removed (Eggleston et al. 1997). One interesting study documented that rock lobster *Jasus lalandii* could be overwhelmed and ingested by whelks *Burnupena* spp., reversing the typical predator–prey relationship between these 2 species (Barkai & McQuaid 1988). Another demonstrated that Dungeness crab feeding switched from fish to crustaceans in the late spring, specifically preying upon the newly settled first instar conspecifics (Stevens et al. 1982).

We conclude that decapods form a supplementary food source for a wide variety of predators, ranging from gastropods to mammals, but that most species appear to be used opportunistically. There is little evidence that any predator species largely depends on the mega-crustaceans in their diet, with the exception of decapods preying on each other, which will be explored in the following section.

Mega-decapods as predators

Lobsters and crabs are often assumed to be detritivores and scavengers, yet in reality they exhibit a wide range of feeding strategies and behaviours. In fact, all species considered in this study actively prey on a variety of benthic invertebrates. Most studies have found that they are generalists that feed at more than one trophic level (omnivory), with preferences of particular prey species dependent on the area in which they are foraging (e.g. Jewett & Feder 1982, Wieczorek & Hooper 1995, Squires & Dawe 2003) Their diet may include gastropods, bivalves, chitons, crustaceans, sea urchins, sea stars, polychaetes, algae and occasionally, fish (e.g. Jewett & Feder 1982, Stevens et al. 1982, Elner & Campbell 1987, Lawton 1987, Robles 1987, Wieczorek & Hooper 1995, Cox et al. 1997, Squires & Dawe 2003, Hanson 2009). Other decapods and even conspecifics are also consumed, including their moulted exoskeletons (e.g. Jewett 1982, Stevens et al. 1982, Elner & Campbell 1987, Wieczorek & Hooper 1995, Hanson 2009). Prey size tends to increase, and species preferences change with the size of the animal (e.g. Stevens et al. 1982, Robles et al. 1990, Sainte-Marie & Chabot 2002, Squires & Dawe 2003, Hanson 2009), likely reflecting their changing ability to manipulate larger and better defended organisms as they grow. Large decapods can often overpower the defenses of their prey, for example by crushing mussel shells (Robles et al. 1990). Decapods often have prey species in common with other invertebrates and fish (e.g. Robles 1987). There is a large body of literature documenting the range of diet items consumed by crabs and lobsters (Table 1), but much less is known about their effects on prey populations and communities.

The sympatric American lobster and rock crab are often studied in comparison. Rock crab consistently emerges in the literature as the lobster's preferred prey. Additionally, rock crab are also important to the somatic and gonadal growth of the American lobster (Gendron et al. 2001). This important dietary component for lobster is consistent and evident throughout its ontogenesis, but the contribution of crab, as well as their average size, increase with the size of the lobster (from 7% of stomach volume contents for the smallest lobster to 53% for the largest; Sainte-Marie & Chabot 2002).

While American lobster and rock crab are typically found in highly structured hard-bottom habitats, they are also present in regions characterized by soft substrates, such as the southern Gulf of St. Lawrence (SGSL), NW Atlantic. In the SGSL, rock crab were an important diet item in the stomachs of lobsters >40 mm CL (45 to 68% of prey biomass, 30% moulted carapaces, according to Hanson 2009). Additional prey items were small sea stars *Asterias vulgaris* (3.8–10.5% prey biomass) and lobsters (0.7–12.9% of prey biomass, 70% were moulted carapaces) with molluscs, polychaetes and fish remains (cunner *Tautogolabrus adspersus*, three-spined stickleback *Gasterosteus aculeatus*, and herring) not exceeding 7.5% of the prey biomass (Hanson 2009).

Rock crab themselves were suggested to play an important role in structuring benthic communities, by influencing species composition and abundance, for example in Bonne Bay, Newfoundland (Quijon & Snelgrove 2005a,b). Both rock and snow crab were reported to be the most abundant and frequently encountered predators in Bonne Bay. When the crabs were experimentally excluded from the benthos, the polychaete *Pholoe tecta* and the clam *Macoma calcarea* came to dominate the benthic infauna, resulting in increased species richness overall (Quijon & Snelgrove 2005a). Hence, crab fisheries may have indirect effects on benthic community structure (abundance, composition and diversity) by reducing crab predation on infauna (Quijon & Snelgrove 2005a,b).

Decapods are often effective predators utilizing a variety of behavioural strategies. For example, in Southern California, spiny lobsters *Panulirus interruptus* like most decapods are intolerant to exposure, and hence forage on intertidal mussels *Mytilus* spp. on the evening high tide (Robles et al. 1990). There were shore-level differences in the mussels described in the study, with low-shore mussels having thinner shells than those in the upper zone. Large lobsters were observed to use trial and error to kill lower shore mussels before the thicker-shelled forms (Robles et al. 1990). When spiny lobsters were experimentally excluded from the upper shore, a significant increase in the density and size of mussels and herbivorous molluscs was observed, which indirectly decreased understory algal cover (Fig. 1A–C) (Robles 1987). Hence, lobster predation on mussels had multiple direct and indirect effects on this intertidal ecosystem.

Occasionally, decapod predators have been suggested to be keystone species (Table 1, Fig. 1) sensu Power et al. (1996), i.e. having a strong impact on the community, which is disproportionally large relative to their abundance. In the NW Atlantic, blue crabs were described as the keystone predators in salt marshes by being responsible for the regulation of marsh grass cover through a 3-level trophic cascade (Silliman & Bertness 2002). Prior to this study, salt marshes had been mostly described as bottom-up regulated systems driven by nutrient inputs (e.g. Valiela & Teal 1979), however a series of field experiments provided evidence that salt marshes may also be controlled by consumers. Blue crabs preyed on the herbivorous periwinkle *Littoraria irrorata* preventing it from decimating marsh grass *Spartina* spp., which would convert the complex habitat to mudflats (Fig. 1D–F). Using a variety of experimental methods, this cascade was found to occur when the periwinkle was at moderate to high densities. Based on these experimental findings, overfishing of blue crab was proposed as a possible mechanism contributing to the massive die-off of salt marshes in the southeast USA (Silliman & Bertness 2002).

Similar drastic effects were observed at wave-exposed rocky intertidal sites along Santa Catalina

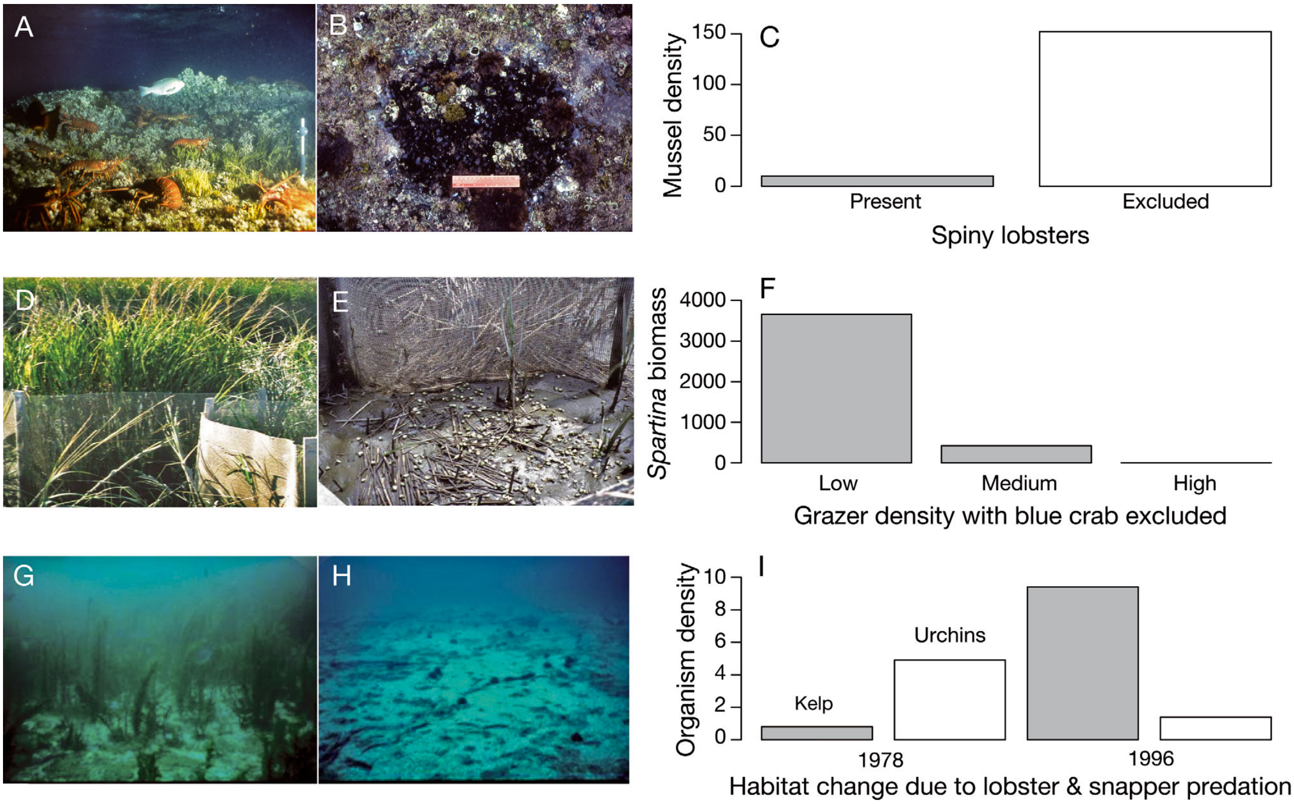

Fig. 1. Case studies exemplifying strong ecosystem effects of large decapods. Images: effects of decapod presence (left column) versus absence (right column). (A) Spiny lobster *Panulirus interruptus* preying on mussels in the wave-exposed rocky intertidal in California. (B) Exclusion of lobster caused algal turf to be replaced by mussels. (C) Mean number of mussels per 230 cm^2 sampled after 10 mo, where lobsters were present (shaded) or excluded (open) (after Robles & Robb 1993, Robles et al. 2001). (D) *Spartina* marsh grass in the tall zone with blue crab *Callinectes sapidus* predators excluded and low densities of grazing *Littoraria irrorata* versus (E) high densities of the same species in the same zone. (F) *Spartina* biomass (g dry wt m^{-2}) in the tall marsh zone after 8 mo of blue crab exclusion, in relation to *Littoraria* density (after Silliman & Bertness 2002). (G) Lush kelp habitat resulting from the recovery of spiny lobster *Jasus edswardii* and snapper *Pagurus auratus* populations in Leigh Marine Reserve, New Zealand. (H) Urchin barrens, dominated by the sea urchin *Evechinus chloroticus* at the same site prior to establishment of the reserve. (I) Habitat shift at Leigh from 1978 to 1996 with kelp (shaded bars) and urchin (open) densities in numbers m^{-2} (after Babcock et al. 1999, Babcock 2003)

Island, California, where the exclusion of spiny lobsters *Panulirus interruptus* resulted in the complete and persistent replacement of a red algal turf by mussel *Mytilus* spp. beds; an example of keystone predation (Fig. 1A–C). At wave-protected sites, however, the lobsters were foraging on mussels jointly with carnivorous fishes and whelks; this was called diffuse predation (Robles & Robb 1993). Notably, at wave-protected sites, the lobster and fish removals produced significant community changes only in combination with whelk removals (Robles & Robb 1993).

American lobsters were also long believed to be a keystone predator of NW Atlantic subtidal kelp forests (Elner & Vadas 1990). Specifically, it was hypothesized that lobsters controlled sea urchin populations through predation, and in turn prevented the destructive grazing of kelp forests by urchins, which commonly results in so-called 'urchin barrens' devoid of frondose macroalgae (Fig. 1G–I). However, Elner & Campbell (1987) observed that lobster in both macroalgal and barren habitats did not preferentially prey on sea urchins. Their rank in the diet of lobster was variable and always surpassed by mussels. These observations did not support the hypothesis that lobster predation regulates sea urchins and indirectly maintains macroalgal habitats (Elner & Campbell 1987). A subsequent extensive review on the topic found that there was a general lack of experimental testing and that contradictory evidence (e.g. lobster preferring crab to sea urchins) was discounted without explanation in the available literature. Since then the attention has shifted from lobsters to large crabs, which may be able to control sea urchin densities at the juvenile stage, which would make them an effective top predator in the Gulf of Maine (GOM) ecosystem (reviewed by Steneck et al. 2004).

The diet of most large decapods appears to be mostly, but not exclusively carnivorous, with heavy emphasis on crustaceans or molluscs. *Panulirus interruptus* from the intertidal zone of Santa Catalina Island, California was found to have *Mytilus* spp. (88% of the total sample of lobsters contained this prey item), other bivalves (96%) and limpets (15%) in their stomach contents (Robles 1987). Red king crab from inshore and offshore habitats around Kodiak Island, Alaska, mostly fed on molluscs (bivalves, 31.3% wet wt), crustaceans (mainly barnacles, 31.4%) and fish (12.7%) (Jewett & Feder 1982). For snow crab in Newfoundland, the most frequently occurring prey items were polychaetes (81–90%) and bivalves (43–48%). With respect to prey biomass, however, shrimp (22–65%) and fish (capelin *Mallotus villosus*, Atlantic spiny lumpsucker *Eumicrotremus spinosus*, redfish *Sebastes* spp.; 5–35%) were more important. Crabs, mostly small *Chionoecetes opilio*, were also frequently consumed (Squires & Dawe 2003). In Bonne Bay, Newfoundland, large crabs were more likely to scavenge on dead fish (e.g. discarded bait) and smaller crabs more likely to ingest shrimp (Wieczorek & Hooper 1995). The most important prey item in the diet of Dungeness crab in Gray's Harbor, Washington, was the shrimp *Crangon* spp.; however, first year (small) *Metacarcinus magister* preferred small bivalves or small crustaceans, including conspecifics (Stevens et al. 1982). Of note in this study was the importance of teleost fish to the diet of second and third year crab.

Stable isotope analysis has been used to determine the trophic position of decapods (e.g. Grabowski et al. 2009). An analysis of western rock lobsters *Panulirus cygus* from the west coast of Australia revealed that they were highly omnivorous, with diets consisting of amphipods, isopods, crabs, bait, foliose red algae and sponges (Waddington et al. 2008). The proportional contributions differed widely among locations, but bait (4–79%), crabs (0–76%) and amphipods or isopods (0–54%) were important in most cases while algae and sponges were less important. On average lobsters occupied the trophic position of a first-order predator. Lobsters in the deep coastal zone (35 to 60 m) were primarily carnivorous and this did not vary with sex, size or location (Waddington et al. 2008).

We conclude that the decapod species reviewed here actively prey on a range of organisms in a variety of benthic habitats, ranging from the intertidal zone (i.e. Robles & Robb 1993) to deep waters (i.e. Smith et al. 2012). Their preferred prey items appear to be other decapods and molluscs, namely mussels. The wider impacts of their foraging can be substantial (for example keystone predation by spiny lobster and blue crab; Figs. 1 & 2). Experiments where decapod predators were excluded consistently reported an increase in benthic infaunal or epifaunal density, changes in species composition, and sometimes cascading effects affecting various epifauna and vegetation. Collectively, the available evidence suggests that large decapods can play important roles in structuring benthic communities; however it is not clear how general these roles are and to which extent they can be assumed across species (e.g. American lobster; Elner & Vadas 1990).

Non-consumptive interactions

Decapods are not only involved in predator–prey interactions, but also compete with other species for food and habitat, as well as providing and altering habitat themselves. These non-consumptive interactions have received somewhat less attention than predatory ones, but may nevertheless represent an important aspect of decapod ecology.

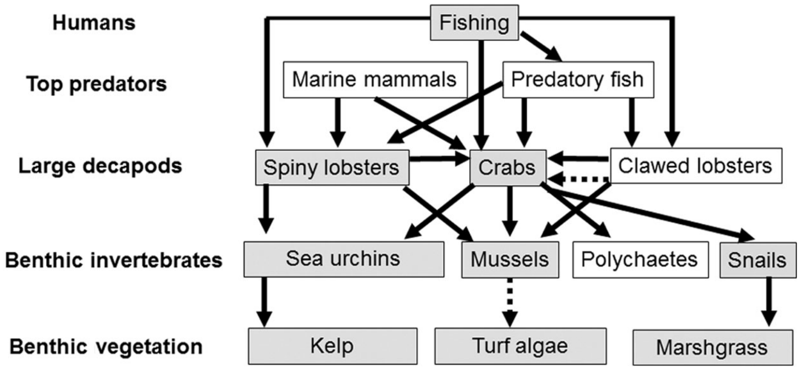

Fig. 2. Conceptual synthesis. Major documented ecosystem interactions of large decapods include predatory (solid arrows) and competitive (dotted arrows) interactions. Cannibalistic interactions occur in crabs and lobster, but are not shown here. Grey: species that are strongly implicated in trophic cascades. Note this represents a simplified scheme; other interactions may well occur depending on species diets and other ecological traits in particular regions

Interference competition. Negative, direct interactions between organisms trying to access the same resource are called interference competition. In decapods, agonistic displays, visual displays or combat may play a role during disputes over limited resources such as food or shelter (Rossong et al. 2006), depending on the species in question, and its life stage. For example, American lobsters use agonistic displays first, while green crabs tend to go immediately to combat (Sneddon et al. 1997a,b). Green crabs are able to outcompete and ingest juvenile lobsters (Rossong et al. 2006), and compete with sub-adult lobsters for resources (Williams et al. 2006); however, they are often preferred food for adult lobster (Jones & Shulman 2008).

Competition for habitat. To avoid predation, many decapods are nocturnal and seek protective shelter during the day. The American lobster is sympatric with 2 species of *Cancer* crab, which compete for suitable shelter, but are often displaced by lobster when shelter is limited (Richards & Cobb 1986). Crabs, however, were more flexible in their requirements for shelter than lobster and had an ability to rapidly burrow and use a wider variety of crevice configurations in the field. Shelter appeared to be more important to lobster survival than to crab, implying that habitat limitation could be detrimental to lobster by exposing them to increased predation mortality (Richards & Cobb 1986, Wells et al. 2010). However, shelter does become relatively less important to lobster as their size increases, and relative predation risk decreases (Wahle 1992). Recently, American lobster have been observed more frequently in predation-prone habitats such as soft-bottoms where effective shelter is rare (Tremblay & Smith 2001, Geraldi et al. 2009), this might signal a habitat expansion due to lower abundances of predatory groundfish (Boudreau & Worm 2010). Also, lobsters have a limited capacity for creating shelter in soft sediments by burrowing bowl-like depressions (Tremblay & Smith 2001).

Habitat provision. Most decapods do not only use habitat, but can provide habitat for other invertebrates, for example barnacles *Balanus* spp., polychaetes, bivalves, crustaceans and gastropods that may settle on them (e.g. Bernier et al. 2009, Dvoretsky & Dvoretsky 2009). For example, red king and snow crabs carry sea leach adults *Johanssonia arctica* and their egg cases in the North Pacific and Barents Sea (Dvoretsky & Dvoretsky 2008), and barnacles *Octolasmis mulleri* have been found growing on the gills of blue crab in North Carolina (Walker 1974). The high mobility of many mega-decapods is beneficial to suspension feeders, and also to mobile epifauna, as they gain protection in addition to access to scraps from feeding. This shelter is often only temporary as decapods moult their exoskeleton, hence most suitable for fast-growing, short-lived epifaunal species. However, as the animal ages, moulting frequency slows, often reaching a terminal moult, for example in snow crab (e.g. Sainte-Marie et al. 1995, Choi & Zisserson 2008) and female blue crab (e.g. Haefner & Shuster 1964). These species can gradually become debilitated under an increasing load of epizoites (Walker 1974). Brooding female decapods may also provide food in terms of eggs to nemerteans (e.g. Wickham 1986, Wickham & Kuris 1988) and amphipods (e.g. Dvoretsky & Dvoretsky 2010) living on them. Decapods with epibionts can also act as vectors for the spread of invasive species. For example, rock crab and American lobster were discovered to carry invasive tunicates (*Botrylloides* sp., *Botryllus* sp.) (Bernier et al. 2009).

ANTHROPOGENIC FACTORS

Fishing, marine protected areas, and species introductions may be changing the way large crustaceans are distributed and play out their ecosystem roles. We will examine each of these potential factors in detail.

Commercial fishing

Decapods have become increasingly important to commercial fisheries, often as a result of declining groundfisheries (e.g. Pauly et al. 1998, Worm & Myers 2003, Anderson et al. 2008, 2011, Choi & Zisserson 2008). Many invertebrate fisheries operate under scarce ecological and life-history information (e.g. natural mortality rates, nursery habitats) and without having proper stock assessments conducted (Anderson et al. 2008). Fisheries by their nature remove a certain proportion of the population and in absence of appropriate biological reference points there is a risk of overexploitation (Jennings & Kaiser 1998, Worm et al. 2009). This is particularly true for some highly valued invertebrate fisheries, where particular populations have declined abruptly and shown slow recovery (e.g. Alaskan red king crab; Orensanz et al. 1998). However, there are well-known exceptions to this pattern, for example the American lobster fishery in the NW Atlantic has exhibited an increase in abundance and landings that began around 1980 and potentially replaced large fish as the dominant predator in the ecosystem, which may have in turn influenced various prey species (Pezzack 1992, ASMFC 2006, DFO 2006, Steneck 2006, Boudreau & Worm 2010, Steneck et al. 2011). Yet, this lobster population is not without potential threats, as the nominal fishing effort has been increasing (Gendron & Archambault 1997, Gendron et al. 2000, Pezzack et al. 2001, DFO 2006), and there has been a trend of fishing larger lobster in deeper water. Whether these individuals are essential broodstock and how their removal will affect recruitment, and hence the future of the population, has yet to be determined (DFO 2006, Boudreau & Worm 2010).

In addition to these population-level impacts, fishing operations may also affect species interactions (Estes et al. 2011, Steneck et al. 2011) by removing predators of decapods (e.g. Atlantic cod) or prey (e.g. rock crab) species, and by altering habitat (e.g. scallop dredges, Kaiser et al. 2006). These interactions can have important implications for multispecies management. For example, rock crab is important to the diet of American lobster (e.g. Sainte-Marie & Chabot 2002). Given that lobster has a far higher commercial value, the fishery for rock crab should be managed conservatively in order to leave sufficient high-quality prey for lobsters (e.g. Gendron et al. 2001). It is not clear, however, how these findings relate to other species; while studies on American lobster or snow crab often mention their interactions with sympatric species of crab, such associations were largely absent from studies on other species reviewed here.

Another potentially important interaction between decapods and fishers are mediated by bait inputs. There is some evidence that bait losses as well as discards have the potential to subsidize decapod populations, for example, in the GOM American lobster fishery (Saila et al. 2002, Grabowski et al. 2009) and the Western Australia rock lobster fishery (Waddington & Meeuwig 2009). In Western Australia, stable isotope analysis and gut contents analysis indicated that bait inputs contributed between 30 and 80% of the diet of rock lobster *Panulirus cygnus*. However, the amount of bait available depends on the length of the fishing season (Waddington et al. 2008). In the Western GOM, year-round fishing and its bait inputs, may have significant effects on lobster (Saila et al. 2002, Grabowski et al. 2009), whereas this is probably not the case in the Eastern GOM, where the fishing season is limited to winter and bait inputs are considerably lower (Grabowski et al. 2009, Boudreau & Worm 2010).

The long-term effects of decapods being fed large amounts of bait are unclear. There is some evidence that American lobsters in New Brunswick, where bait is available only in winter, outgrew those in Maine where bait is available year round (Grabowski et al. 2009). It is also possible that a diet that largely relies on herring bait affects the physiological condition of those animals (Myers & Tlusty 2009). Finally, whether an increase of bait in lobster diets has resulted in a reduction of predation rates by lobsters on their regular prey species, has yet to be tested.

In conclusion, fisheries may have a range of effects on the ecosystem. Removal of groundfish or other decapod predators can lead to population increases and shifts in trophic structure. Additionally, fishing may decrease the abundance of key prey items (e.g. rock crab for American lobster) or supplement decapod diets through bait.

Conservation and protected areas

The potentially large effects of fishing on decapods often become most apparent when this influence is removed, in what Castilla (1999) has termed a 'human exclusion experiment'. Marine reserves where fishing is excluded can be valuable in this regard, in testing ecosystem level effects of fished species at ecologically relevant scales (Shears & Babcock 2002). Reserves have been shown to successfully protect and increase spiny lobster populations (e.g. Kelly et al. 2000), which had strong cascading effects throughout the ecosystem (Fig. 1G–I). In northeastern New Zealand, Taharanui Marine Park (established 1981, implemented 1983) and Leigh Marine Reserve (established in 1975) are no-take reserves, whereas Mimiwhangata Marine Park (established 1984, commercial fishing phased out by 1993) allows recreational fishing. Several studies documented the development of benthic communities inside and outside these reserve sites. In the Leigh Marine Reserve and Taharanui Marine Park, trends post-reserve revealed that the most common demersal predatory fish, the Cockney snapper *Pagrus auratus*, was 5.8 and 8.7 times more abundant and considerably larger inside these 2 reserves when compared with adjacent unprotected areas. The spiny lobster *Jasus edwardsii* showed similar trends (1.6 to 3.7 times more abundant, as well as increased mean size). In one of the reserves, densities of the dominant sea urchin *Evechinus chloroticus* (not of significant commercial value) had declined from 4.9 to 1.4 m^{-2} since 1978. Consequently, kelp forests were less heavily grazed and more extensive in cover in 1998 than they were at the time of reserve creation. Macroalgal primary productivity was estimated to be ~58% greater within the Leigh reserve in 1998 than it was in 1980. Urchin-dominated barrens occupied only 14% of available reef substratum in reserves as opposed to 40% in unprotected areas (Fig. 1G–I). These changes in community structure, which have persisted since at least 1994, suggest a trophic cascade from lobsters and fish to urchins and kelp that led to increased primary and secondary productivity in marine reserves as a consequence of protection (Babcock et al. 1999).

Interactions between lobsters and sea urchins continue to be of importance. In the no-take marine parks and at sites outside the reserves mentioned above, field experiments during 1998–99 revealed that lobsters preyed on a range of sea urchins. Tethering experiments suggested that lobster were responsible for at least 45% of predation on urchins in the reserve sites; the rest was attributed to snapper and potentially to several slow-moving predators such as the sea star *Coscinasterias muricata*, or the gastropod *Charonia lampax*. Predation on urchins was significantly (6.9 times) higher inside the reserve than outside. Consequently, the density of adult sea urchins grazing on barrens within reserve sites was significantly lower than outside. Experimental removal of sea urchins >12 mo led to a change from crustose coralline algae to macroalgal canopies that mimic habitats now commonly found in the reserves (Shears & Babcock 2002). Such changes in habitat are believed to affect a host of other species. For example, in the Leigh Marine Reserve, lower density of the limpet *Cellana stellifera* and higher densities of the turbinid gastropod *Cookia sulcata* are thought to be responses to changes in the habitat structure indirectly resulting from the increased density of urchin predators (Shears & Babcock 2003).

Not just commercial exploitation, but limited recreational fishing may also affect these interaction chains. In Taharanui and Mimiwhangata Marine Park lobster densities were similar prior to the creation of the parks. After full protection in Taharanui, the abundance of legal-sized lobster increased 11-fold and biomass increased 25-fold. Mimiwhangata Park, in contrast, allowed recreational fishing and showed no significant change in the abundance or biomass of legal size lobsters, nor any spatial difference to fully fished areas adjacent to the park. Likewise, other urchin predators have not recovered following partial protection in Mimiwhangata (Shears et al. 2006). Consequently, kelp forest habitats that dominated on shallow reefs up until the 1950s have been replaced by urchin barrens that have persisted at least since the 1970s (Kerr & Grace 2005).

In a similar example from Southern California, large spiny lobsters *Panulirus interruptus* prey on the purple *Strongylocentrotus purpuratus* (Tegner & Levin 1983) and red sea urchins *S. franciscanus* (Tegner & Dayton 1981). By contrast, in cold water sites such as Torch Bay, Alaska, where lobsters are absent, the predatory seastar *Pycnopodia helianthoides* is an important urchin predator (Duggins 1983). In southern California, a large fish, the sheepshead *Semicossyphus pulcher*, can also reduce urchin densities (Cowen 1983) and in combination with *P. interruptus,* structure the sea urchins' size frequency distributions (Tegner & Dayton 1981). Sampling in and around the Anacapa marine reserve in Channel Islands National Park, California, revealed that where the main predators on urchins were fished, urchin populations increased to such an extent that they overgrazed algae and starvation eventually limited urchin population growth (Lafferty 2004). Individual growth rates were also reduced and epidemics were 4 times more frequent outside the reserve than inside. However, the availability of food and temperature did not appear to influence disease. It was inferred that overfishing the spiny lobster, and therefore releasing urchins from predation, could in turn promote disease transmission as urchin density increased (Lafferty 2004).

In the Atlantic Ocean, one short-term study of American lobsters in a reserve exists from Bonavista Bay, Newfoundland (Rowe 2002). Increases in body size and density were documented after 3 yr of protection. There was evidence to suggest that the creation of these no-take reserves would benefit fisheries by increasing lobster survival (Rowe 2001, 2002); however, no wider ecosystem effects were examined. In the northeast Atlantic, European lobster abundance and size rapidly increased after the establishment of the UK's first no-take zone (NTZ) in 2003. Evidence also indicated a 'spillover' into areas adjacent to the NTZ where an increase of sub-legal lobsters was observed (Hoskin et al. 2011). In contrast, European lobster tagged in a Skagerrak coast reserve (Norway) were observed to remain in the reserve or near the boundary (Moland et al. 2011).

We conclude that it is possible to observe strong species interactions and trophic cascades due to the recovery of spiny lobsters, as well as other predators in some marine reserves. Urchins seem to be particularly important in mediating these ecosystem-wide effects. Again, it is unclear whether and how these results transfer to other species, such as large crabs and clawed lobsters. Marine reserves, especially when replicated at different sites and during different time periods, create an excellent opportunity to study the potential direct and indirect effects of fishing on benthic communities.

Decapod introductions and invasions

Introductions and invasions lead to the establishment of a species in a habitat where it was not formerly found. As such, these events provide quasi-experimental context in which to examine the ecosystem role of particular species. Marine invasive species have been described as important drivers of ecological change. They are often viewed as being irreversible and their impacts can lead to changes in habitat and displacement of native species via predatory or competitive interactions (Bax et al. 2003). However, it is often quite difficult to quantify these ecosystem consequences in the marine environment.

Once a non-indigenous organism has been introduced into a region, indigenous species may indirectly facilitate its spread. For example, by feeding on mussels, Jonah crabs *Cancer borealis* had a positive indirect effect on the abundance of an introduced ascidian *Diplosoma* sp., by facilitating bare substrate for settlement and successful colonization of the invader (Siddon & Witman 2004). American lobster, when present, reduced the foraging effectiveness of the crabs on mussels. The authors were concerned that the harvesting of lobsters may lead to increased crab predation on mussels and in turn, an increase in *Diplosoma* sp. cover in the GOM (Siddon &Witman 2004).

One important case study concerns red king crab, which was introduced to the Barents Sea by the former Soviet Union from 1961 to 1969 to establish a commercial fishery. In 1974, a first berried female was found; by 1976, there were at least 100 records, and the introduction was considered a success (Orlov & Ivanov 1978). This population is now believed to be actively invading coastal waters through migration of mature crabs and passive dispersal of larvae (Pedersen et al. 2006). Red king crabs are currently abundant along the Finmark coast of Northern Norway with an estimated population of 3.5 million crabs >70 mm CL in 2003 (Hjelset et al. 2003).

Like most mega-decapods, adult red king crabs are opportunistic omnivores (Cunningham 1969). There is great concern that these crabs will decimate the native Iceland scallop *Chlamys islandica*, a slow-growing, commercially important species with a depth distribution that overlaps with the invasive king crab population. Laboratory studies suggested that even small king crabs would have an impact on the scallop community by removing sea urchins, sea stars, and scallops (Jørgensen 2005). Scallops made up 73 to 97% of the prey weight (g) foraged by the crabs. The benthic community impacts associated with the migratory medium-sized to large crabs may extend to other species as well; for example, horse mussels and common whelks were crushed and consumed by these individuals. This invasion is progressing rapidly: in 2001, a non-invaded control bed was selected for long term monitoring in Porsanger fjord, Norway. Invasion was expected within 5 to 8 yr (Jørgensen 2005); however, the first red king crab was already recorded 4 yr later (Jørgensen & Primicero 2007).

In addition to intentional introductions, the Arctic and Antarctic are now being exposed to species invasions from lower latitudes due to climate change. For example, king crabs (*Lithodes* spp., *Paralomis* spp., *Neolithodes* spp.) have recently been recorded in the Antarctic Ocean for the first time since an extinction event in the Miocene (~15 million yr BP) that is thought to have occurred due to Antarctic cooling. Migration from the deep sea is the most likely mechanism for recolonization (Thatje et al. 2005). These species also have larvae that are well-adapted to low temperatures and low levels of plankton productivity (Anger et al. 2003). As king crabs re-establish, they may impact the rich fauna of large amphipods and isopods found in this region and could further affect benthic communities by consuming echinoderms and crustaceans (Thatje et al. 2005) and altering sediments through locomotive and feeding activities (Smith et al. 2012).

There could also be other unintended impacts from introduced species on indigenous decapods. For example, in the north Pacific (Washington, USA), the introduced Atlantic smooth cordgrass *Spartina alterniflora* has transformed previously unstructured habitats to highly structured marsh meadows. This ecosystem transition has altered the movement and foraging behaviour of the Dungeness crab and increased its risk of being trapped in marsh grass and exposed at low tide (Holsman et al. 2010).

We conclude that mega-decapods, once introduced to a new region, can become successfully established and have the potential to dramatically alter the benthic community through predation. They are vulnerable to the establishment of non-indigenous vegetation, which can restructure their habitat. Additionally, indigenous mega-decapods may facilitate the dispersal of non-indigenous sessile organisms by providing habitat and also indirectly by preying upon bivalves resulting in bare substrate upon which other invasives may settle. As climate change continues to increase average ocean temperature, invasions may increase in frequency as species expand their distributions.

DISCUSSION

This review indicates that large decapods play an important role in benthic communities, ranging from intertidal to deep waters (Table 1). These effects are mediated by the following mechanisms (Fig. 2): (1) Decapods are prey for a large range of vertebrate (humans, marine mammals and fish) and invertebrate (mostly other decapods) predators; however, they did not appear to be a key dietary component for non-decapod species. (2) They are successful and versatile predators, preying at more than one trophic level, mostly on benthic invertebrates, but occasionally consuming algae or detritus. Some species, especially spiny lobsters and blue crabs, have demonstrated large effects on benthic community structure, either as keystone species or by inducing trophic cascades. (3) Decapods interact with the habitat and its inhabitants in a variety of ways, including providing habitat for smaller invertebrates, and competing for food and shelter.

For the species and ecosystems reviewed here, one of the most striking interactions was that of regulating trophic cascades (Fig. 1, grey boxes in Fig. 2). These trophic cascades took place in a variety of temperate habitats, from the rocky intertidal (Robles & Robb 1993) to saltmarshes (Silliman & Bertness 2002) and subtidal reefs (Babcock et al. 1999). In these cases, large decapods were essential in the maintenance of benthic vegetation (kelp forests, marsh grass, or turf algae), and therefore habitat complexity and productivity by regulating the grazing community (e.g. gastropods, sea urchins). Often predatory decapods were joined in this function by fish (Robles & Robb 1993, Babcock et al. 1999) or whelks (e.g. Robles & Robb 1993). Predatory interactions between spiny lobsters and crabs on sea urchins were demonstrated to be important; however, no such relationship has become evident for American (or European) lobsters. Instead, American lobster appear to prefer crabs in their diet, and it is possible that these observed differences could be due to their claws allowing them to be more effective at capturing and consuming mobile and well-defended prey. Exclusion experiments (e.g. Quijón & Snelgrove 2005a,b) often supported the hypothesis of strong ecosystem effects of decapods on benthic fauna (molluscs, polychaetes), even if no trophic cascade was observed.

Decapods themselves may be commonly regulated in their abundance by predators (Fig. 2). Exclusion of fish predators allowed decapod populations to increase, for example in the case of Nassau grouper preying on juvenile *Panulirus argus* (Eggleston et al. 1997). A similar release from (mostly gadoid) fish predation has contributed to observed increases in the abundance of American lobster and snow crab in the NW Atlantic (e.g. Worm & Myers 2003, Steneck et al. 2004, Frank et al. 2005, Zhang & Chen 2007, Boudreau & Worm 2010, Boudreau et al. 2011). This body of evidence adds to a growing concern that commercial fisheries have the potential to affect ecosystem function through the removal of certain predators (Fig. 2), influencing species interactions, and in some cases leading to cascading changes throughout the ecosystem (e.g. Dill et al. 2003, Baum & Worm 2009, Estes et al. 2011).

It has become evident from the research reviewed here that decapods have evolved to become efficient predators of other shelled organisms (mostly bivalves, gastropods, echinoderms, and crustaceans) due largely to their uniquely strong claws (Taylor 2000). They prey on these items across a broad range of habitats and are capable of controlling strong space competitors, such as mussels, to maintain algal growth or mobile herbivores (sea urchins, snails) grazing on algae (kelp, sea grass, turf algae), with strong indirect effects on habitat structure and (likely) primary productivity (Figs. 1 & 2). Furthermore, if teleost predators of decapods become overharvested, those decapods typically increase in abundance, and hence in their importance in the ecosystem, where they can become the dominant predator in some cases (Steneck et al. 2011).

While the focus of this review has been largely on predatory (top-down) species interactions, it is important to note that other mechanisms are also present in the ecosystem. Environmental variables, such as temperature and hydrodynamics (e.g. Higgins et al. 1997), and density-dependent mechanisms (e.g. Wahle 2003) are common bottom-up factors that explain changes in mega-decapod abundance. For example, Dungeness crab *Metacarcinus magister* exhibit cycles of recruitment linked to spring oceanographic conditions that influence currents and larval transport, directly affecting early life stages (Shanks

& Roegner 2007). Crab such as *Chionoecetes opilio* (Conan et al. 1996, Caddy et al. 2005) and *Callinectes sapidus* (Hines & Ruiz 1995) display strong density-dependent population regulation (i.e. via cannibalism), which may partly explain observed population cycles. Thus, while the top-down mechanisms displayed in Figs. 1 & 2 are undoubtedly important, other factors will come into play when considering decapods in a full ecosystem context.

Although the available evidence does suggest that large marine decapods play a role in structuring benthic communities, this literature review also exposed some clear knowledge gaps. For example, comprehensive long-term studies of benthic communities documenting changes in mobile and sedentary in- and epi-fauna are scarce. It appears that most studies examine one particular interaction (e.g. decapods as predators) and rarely consider the species in a full ecosystem context. Recently fisheries scientists and managers have been considering ecosystem-based approaches that take into account trophic interactions and human as well as natural sources of mortality (e.g. Garcia et al. 2003). Towards this goal, scientists have been using sophisticated modeling techniques, such as multispecies virtual population analyses and mass-balance models (e.g. Walters et al. 1997, Hanson & Chouinard 2002, Zhang & Chen 2007). These models are parameterized using available dietary studies (such as those described in this paper) and population time series summarized for a given ecosystem (Walters et al. 1997, Hanson & Chouinard 2002). These methods can be useful, for example, to examine the possible consequences of complex ecosystem shifts (e.g. for the GOM; Zhang & Chen 2007), but cannot replace long-term empirical and experimental studies.

Long-term studies could be of great value for creating a baseline as fishing, climate change and other impacts continue to alter ocean ecosystems. A diverse range of other benthic community members such as fish, sea stars or even amphipods and isopods interact with mega-decapods. Thus, detailed time series of these species could be beneficial in understanding and predicting broader ecosystem change. Time series, however, cannot uncover mechanisms; hence detailed mechanistic studies are equally essential. For example, several predator exclusion experiments reviewed here provided valuable insights into the mechanisms by which large decapods affect community structure across a range of benthic habitats. Results from such experiments may also be used to parameterize ecosystem-based models. However, interactions with benthic fishes were not covered in much detail in the literature and we suggest that this could be further examined.

Many of the factors and interactions examined in this paper are linked: consider for example the complex mechanisms of interference-competition (Rossong et al. 2006, Williams et al. 2006) and predation at different life stages between an indigenous commercially harvested decapod (American lobster) and non-indigenous competitors (green crab) and prey (Jones & Shulman 2008). Such complexities highlight the fact that an ecosystem-based approach to understanding and managing these valuable resources would be informative.

As more decapod populations are of increasing socio-economic importance and continue to be harvested more widely (Anderson et al. 2011), it is important that we expand our knowledge of ecological interactions that affect the abundance of these species, their prey, and habitat. It is our hope that this knowledge may ultimately help managers maintain critical trophic interactions and prevent overexploitation in an ecosystem context.

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Contribution to the Theme Section 'Effects of climate and predation on subarctic crustacean populations'

Food habits of Pacific cod and walleye pollock in the northern Gulf of Alaska

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ABSTRACT: Seasonal variations in the diets of Pacific cod *Gadus macrocephalus* and walleye pollock *Theragra chalcogramma* were examined from fish collected during 5 sampling periods from August 1998 to June 1999 in the Kodiak Island area in the Gulf of Alaska. Both species were shown to be generalist predators, eating a wide variety of fish and invertebrates. Pollock, which are limited to pelagic prey, can be considered more specialized than cod. Cod consumed 78 prey items, and pollock consumed 45 prey items, with 28 items shared by both species. Individual pollock, however, typically concentrated on a single prey item, while individual cod stomachs contained a wider variety of prey. The principal prey of Pacific cod was Tanner crab *Chionoecetes bairdi*, comprising >28% of the cod diet by weight. The most common prey item for walleye pollock was the euphausiid *Thysanoessa.* Over the 5 sampling periods, the prey evenness and niche width occupied by the 2 species were similar, but seasonal differences were evident.

KEY WORDS: Pacific cod · Ealleye pollock · Tanner crab · Northern shrimp · predator/prey · Gulf of Alaska

INTRODUCTION

Food habits have long been an important topic in fisheries science (e.g. Faber 1829), helping to define the niche that a fish occupies (Hutchinson 1957, Sargeant 2007) and also playing a key role in the development of basic ecological theory (MacArthur & Levins 1967, MacArthur 1972, Chesson 2000). Numerous indices based on food habits have been developed which attempt to quantify and analyze the different dimensions of a species' niche such as niche overlap, niche width, and the evenness of resource use (Smith & Wilson 1996, Krebs 1999).

The present study examines the seasonal food habits of 2 co-occurring gadids, Pacific cod *Gadus macrocephalus* and walleye pollock *Theragra chalcogramma*. Their diets, which have been relatively well studied across their shared range in the North Pacific (Jewett 1978, Bailey & Dunn 1979, Dwyer et al. 1987, Yamamura et al. 2002, Yang 2004, Yang et al. 2006, Adams et al. 2007, Poltev & Stominok 2008), have shown that both Pacific cod and walleye pollock (hereafter cod and pollock) are upper trophic level, generalist predators that consume a number of the same prey items (Jewett 1978, Adams et al. 2007, Aydin et al. 2007).

Standard diet indices including niche width, diet overlap, diet richness, and diet evenness were used to compare the food habits of these 2 commercially important predators. Niche width is a measure of how broad a spectrum of prey items are utilized by a predator. Diet overlap quantifies the overlap in prey items. Diet richness is simply a count of the number of different prey items consumed, while diet evenness attempts to quantify how equally prey items are targeted (Krebs 1999). This study compares cod and pollock food habits both seasonally and with ontogeny, with the goal of inferring differences in the role of these predators in the ecosystem, including their potential effects on prey populations and their relative susceptibility to ecosystem changes.

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MATERIALS AND METHODS

Data collection

The Alaska Department of Fish and Game (ADF&G) conducted 5 trawl surveys at 31 stations in Marmot Bay on the northeast corner of Kodiak Island (Fig. 1): 24–29 August 1998, 26–31 October 1998, 7–17 January 1999; 30 March–5 April 1999, and 19–23 June 1999. These sampling periods covered the full seasonal range of temperatures and reproductive cycles of predators and prey in the area. The vessel made 1 tow per station during each sampling period. Cod and pollock were captured by the ADF&G RV 'Resolution' towing a 400-Eastern otter trawl net targeting soft substrates. The net was constructed with 102 mm stretch mesh in the mouth, 89 mm stretch mesh in the body, and a 32 mm stretch mesh liner in the codend (Pengilly et al. 1999). This net catches cod and pollock approximately 5 cm in length and larger, although the catchability at size is unknown. Stomachs were collected at sea and preserved in 10% formalin and later transferred to 70% ethyl alcohol.

A total of 699 cod stomachs and 882 pollock stomachs were collected during the 5 sampling periods (Table 1). For cod 40 to 85 cm fork length (FL) and pollock 30 to 70 cm FL, significant differences were found in the size distributions between sampling periods, but the differences were <3 cm and not considered biologically important. Use of those size ranges excluded 27 cod stomachs and 54 pollock stomachs from the calculation of the diet evenness, diet richness, and niche width indices. Diet overlap was calculated for 3 size classes of fish: 20–50 cm, 51–60 cm, and 61–80 cm. Due to the small numbers of cod in the smallest category, calculation of diet overlap by sample period was not possible and only an overall value could be calculated. Seven cod stomachs and 20 pollock stomachs were excluded from the diet overlap calculations.

Fish that showed signs of either ingesting prey during the capture process or with signs of prey regurgitation were not collected. Stomach content analysis was conducted at the National Marine Fisheries Service, Alaska Fisheries Science Center's Resource Ecology and Fisheries Management Division (REFM) laboratory in Seattle, Washington (Yang 1993). Contents were identified to the lowest taxonomic level possible, and commercially important species were enumerated and measured. Predator length and sex were recorded. Wet weights of prey items were recorded to the nearest 0.1 g after the contents were blotted with paper towels.

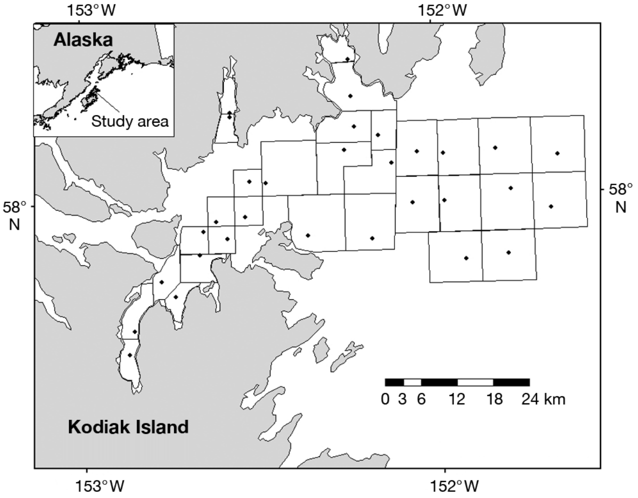


Fig. 1. Study location in Marmot Bay in the central Gulf of Alaska. The boxes indicate station boundaries; the solid dots represent the haul locations. One haul was made at each station during each of 5 sampling periods (see Table 1)

Table 1. *Gadus macrocephalus*, *Theragra chalcogramma*. Summary of sample sizes and fish lengths for cod and pollock in different sampling periods

	Sample size	Fish length (cm) Avg.	Range
24–29 Aug 1998			
Cod	136	62.5	26–86
Pollock	206	52.1	20–74
26–31 Oct 1998			
Cod	103	63.7	25–87
Pollock	185	48.7	9–87
7–17 Jan 1999			
Cod	135	64.3	10–95
Pollock	151	49.5	10–73
30 Mar–5 Apr 1999			
Cod	128	60.1	35–80
Pollock	164	50.5	24–67
19–23 Jun 1999			
Cod	103	62.8	37–84
Pollock	105	50.5	26–81
Overall			
Cod	605	61.4	10–95
Pollock	811	47.6	9–87

Data analysis

Calculations of diet overlap, niche width, diet richness, and diet evenness indices were made for each sampling period and for the entire study based on the sum of the prey weights of the individual fish. The combined prey items of both species were used to calculate the indices.

It is well known that both cod and pollock diets change with ontogeny (Dwyer et al. 1987, Yamamura et al. 2002, Yang et al. 2006, Poltev & Stominok 2008), so calculation of diet indices can be confounded if differing predator sizes are combined (Bolnick et al. 2002). Predator size distributions by sampling period were analyzed using a Kolmogorov-Smirnov test (Sokal & Rohlf 1995) to insure no significant differences existed in size distributions between periods when calculating diet evenness, niche width, and diet richness. Diet overlap was calculated for 3 different size classes of cod and pollock. Historical diet summaries (Yang 1993, Yang & Nelson 2000, Yang et al. 2006) were examined to identify the fish lengths at which shifts in diet occurred (Garrison & Link 2000).

The overlap by period between the diets of similarly sized cod and pollock were calculated using the Schoener similarity measure (Krebs 1999) as:

$$P_{jk} = \left[\sum_{i=1}^{n}(\text{minimum } p_{ij}, p_{ik})\right] \qquad (1)$$

where P_{jk} is the proportion of overlap between species j and species k, p_{ij} is the proportion of the diet represented by i used by species j, p_{ik} is the proportion resource i of the total resources used by species k, and n is the total number of prey items considered. Percentage overlap has the advantage of ease of calculation and interpretation (Krebs 1999). Overlap >0.60 is considered biologically significant, overlap between 0.30 and 0.60 moderate, and overlap <0.30 low (Høines & Bergstad 1999, Guedes & Araújo 2008). A 2-sample *t*-test assuming unequal variances was used to determine the significance of the differences in interspecific differences in prey size.

Niche width of each species was calculated using Hurlbert's (1978) measure. He argues that the relative abundance of the prey resources, not only the proportions of the resource actually used, should be considered when calculating niche width. When proportional abundance is applied to prey use by species, the niche width can be calculated as:

$$B' = \frac{1}{\Sigma(p_j^2 / a_j)} \qquad (2)$$

where B' is Hurlbert's niche width, p_j is the proportion of individuals using prey item j, and a_j is the proportion of the total prey items utilized consisting of prey item j. Variance of the estimate was calculated using the delta method (Krebs 1999). As described by Seber (1973), Smith (1982), and Krebs (1999), the delta method is a standard method for deriving standard errors based on the Taylor expansion (Odibat & Shawagfeh 2007).

Evenness and richness are 2 related components used to describe the diversity of resource use where richness is the number of resources being utilized and evenness is a measure of how equally the prey items are distributed between samples. With large sample sizes, a reasonable approximation of diet richness is simply a count of the number of prey items utilized (Krebs 1999). Evenness reaches a maximum value of 1 when the abundance values of all prey items are equally used by the population, indicating a generalist predation pattern.

$$E_{1/\hat{D}} = \frac{1/\hat{D}}{s} \quad \text{and} \quad \hat{D} = \Sigma p_i^2 \qquad (3)$$

where $E_{1/\hat{D}}$ is Simpson's measure of evenness, s is the number of species in the sample, and p_i is the proportional abundance of each prey species. Values approaching zero can be interpreted as more specialized predation focusing on a limited range of prey items (Smith & Wilson 1996, Krebs 1999). In order to establish broad patterns of resource use, especially as it related to predation on crustaceans, evenness was calculated using the top 5 prey items of cod and pollock plus a grouping of all other prey items. The evenness value of the individual stomachs was used to calculate the variance of the estimate.

RESULTS

Prey composition

Cod diet overall contained a mixture of 59% benthic prey and 41% pelagic prey by weight, while pollock *Theragra chalcogramma* were limited to pelagic prey for 95% of their diet. Tanner crab *Chionoecetes bairdi* was the main prey item of cod, comprising from 20 to 45% of the diet (Fig. 2, Table 2), but they were virtually non-existent in pollock stomachs. The principal prey item of pollock was euphausiids. Those euphausiids that could be identified were primarily in the genus *Thysanoessa* (Fig. 2, Table 2). The proportion of pollock in the diets of both cod and pollock was similar at 13.5 and 15.0%, respectively, but pollock preyed on pollock almost entirely during the October sampling period, consuming fish which averaged 9.4 cm which corresponds to the size of young-of-the-year fish (Ciannelli et al. 1998). Cod preyed on pollock during all sampling periods and consumed fish that were in a broader size range, averaging 29.3 cm in length. Both species overall consumed fish other than pollock for approximately 15% of their diets, with pollock feeding mainly on Pacific sandlance, while cod fed largely on a variety of flatfish.

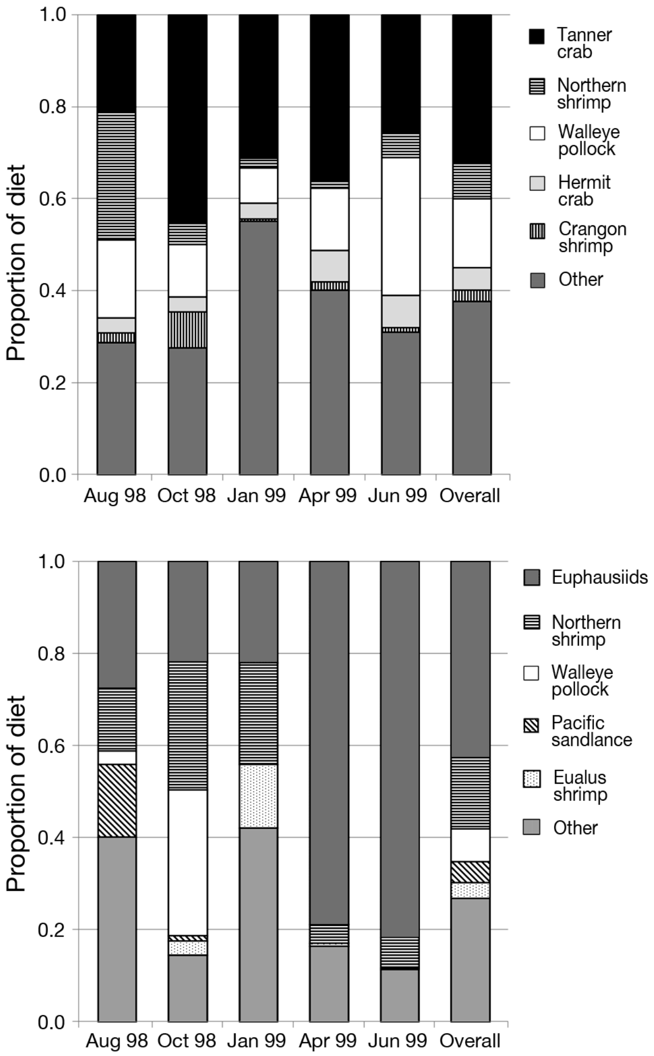


Fig. 2. *Gadus macrocephalus*, *Theragra chalcogramma*. Proportions by weight of the major diet items of cod (upper panel) and pollock (lower panel) by sampling period

Table 2. *Gadus macrocephalus*, *Theragra chalcogramma*. Percent weight of taxa and percent frequency of occurrence (FO) in the diets of cod and pollock. Only taxa which comprised >1 % of the diet by weight are included

Taxon	Weight (%)	FO (%)
Cod diet		
Chionoecetes bairdi	28.3	56.9
Theragra chalcogramma	13.5	5.9
Pandalus eous	10.3	40.8
Paguridae	5.1	19.7
Crangon spp.	3.4	33.5
Caridea	2.7	19.0
Pleuronectidae	2.1	9.3
Atheresthes stomias	2.1	3.1
Aphroditidae	2.0	5.3
Lithodidae	1.9	0.4
Polychaeta	1.6	25.5
Hippoglossoides elassodon	1.6	3.4
Teleostei	1.3	11.6
Natantia	1.2	5.0
Reptantia	1.1	10.9
Pollock diet		
Thysanoessa sp.	20.1	12.7
Euphausiidae	16.0	57.7
Pandalus eous	15.3	37.4
Theragra chalcogramma	15.0	15.4
Thysanoessa spinifera	4.4	7.3
Ammodytes hexapterus	4.2	1.2
Hippolytidae	3.2	6.0
Eualus spp.	2.6	1.7
Caridea	2.5	6.1
Teleostei	1.9	4.4
Echiurus echiurus	1.5	1.1
Argis lar	1.5	0.8
Mysidacea	1.2	5.8
Crangon communis	1.1	2.6
Atheresthes stomias	1.1	0.3

The seasonal proportion of shrimp in the diet of cod and pollock showed very different patterns (Fig. 2, Table 3). During the August sampling period 47 % of the cod diet by weight was shrimp, but the percentage of shrimp fell to <5 % in the following periods. The proportion of shrimp in the pollock diet in August, November, and January was similar (range: 16 to 25 %), but then declined when pollock concentrated on euphausiids in the April and June periods.

Overall, shrimp occurred less frequently in pollock diets than in cod diets. When pollock were consuming shrimp, however, shrimp constituted a much greater proportion of the prey items in their stomachs (Table 3). For example, in April 1999, 8 % of cod were eating shrimp, which made up 6 % of the stomach contents. Only 3.6 % percent of pollock were eating shrimp during this period, but those shrimp represented 77 % by weight of the stomach contents.

Niche indices

Cod diets (78 distinct prey items) contained greater prey richness than pollock diets(45 prey items), with 28 items shared by both species (Fig. 3). The diet overlap of cod and pollock was moderate for fish larger than 50 cm, but low in fish smaller than 50 cm (Fig. 4). Northern shrimp *Pandalus eous* was the main contributor to the diet overlap. Population niche width was significantly narrower in pollock than in cod overall (Fig. 3), indicating that cod were utilizing a broader spectrum of the available food resources than pollock.

Table 3. *Gadus macrocephalus*, *Theragra chalcogramma*. Percent of *Pandalus eous* in the diets of cod and pollock by frequency of occurrence (FO), percent of the overall diet by weight, and percent of the diet by weight of only those fish which were eating shrimp

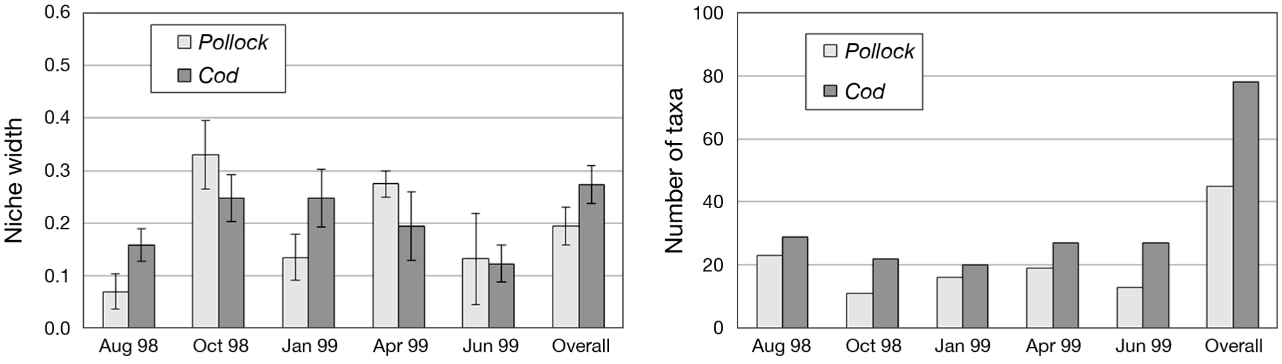
Sampling period	FO (%)		Diet weight (%)		Shrimp in stomach (%)	
	Cod	Pollock	Cod	Pollock	Cod	Pollock
Aug 1998	81.1	9.2	47.0	16.9	53.0	68.6
Nov 1998	35.1	28.6	2.7	25.3	6.7	54.2
Jan 1999	25.6	2.0	4.0	22.3	16.8	38.3
Apr 1999	8.0	3.6	0.4	3.9	6.2	76.6
Jun 1999	10.9	12.0	3.7	6.9	38.4	27.8
Overall	43.5	14.0	11.6	14.7	36.1	50.0

Cod and pollock also showed differing patterns of evenness of prey utilization. Simpson's measure of evenness for cod varied within a relatively small range from 0.49 to 0.58, while pollock diet evenness varied from 0.35 to 0.67, although the overall evenness measures for the 2 species were not significantly different (Fig. 3). The least even resource use occurred in April and June of 1999, when pollock were feeding almost exclusively on euphausiids (>80% of the diet).

Both cod and pollock changed their food habits with increasing size, but with somewhat different patterns. Tanner crab, the main food of cod, were consumed in relatively constant proportions by fish larger than 40 cm. Pollock gradually excluded their main food, euphausiids, from their diets at the largest fish sizes (Fig. 5). Shrimp, primarily northern shrimp, remained at approximately 35% by weight in the larger pollock diets, while the proportion of shrimp in cod diets declined with fish size to 5% in the largest cod (Fig. 5). The largest cod and pollock both consumed increasing proportions of pollock.

DISCUSSION

Marmot Bay has a history of trawl surveys dating back to 1972; these have shown that cod and pollock coexist in all parts of the bay (Jackson 2005, Spalinger 2010). Both fish were found to consume a large variety of prey items, which is consistent with food habit studies in other parts of their range (Bailey & Dunn 1979, Albers & Anderson 1985, Kooka et al. 1998, Yamamura et al. 2002, Yang 2004, Napazakov 2008). A third of the prey items were shared by both species. The ability of these similar species to coexist appears to be at least partially based on differing foraging strategies. It is thought that the protruding



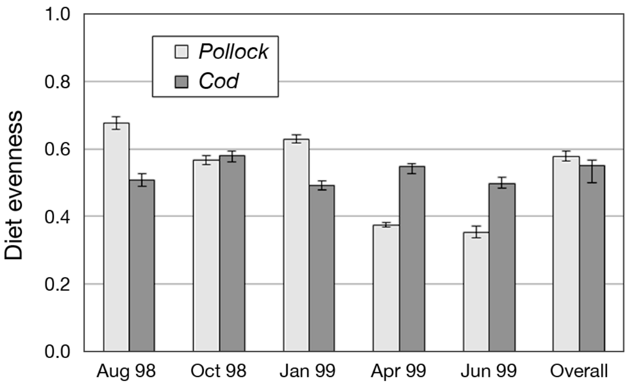


Fig. 3. *Gadus macrocephalus*, *Theragra chalcogramma*. Niche width, Simpson's measure of diet evenness, and diet richness of cod and pollock. Simpson's evenness index was calculated for the top 5 prey items, which, for Pacific cod, were *Chionoecetes bairdi*, *Pandalus eous*, *Theragra chalcogramma*, Paguridae, and *Crangon* spp. For walleye pollock the top 5 prey items were Euphausiidae, *Pandalus eous*, *Theragra chalco gramma*, *Ammodytes hexapterus*, and *Eualus* spp. Error bars represent the 95% confidence interval

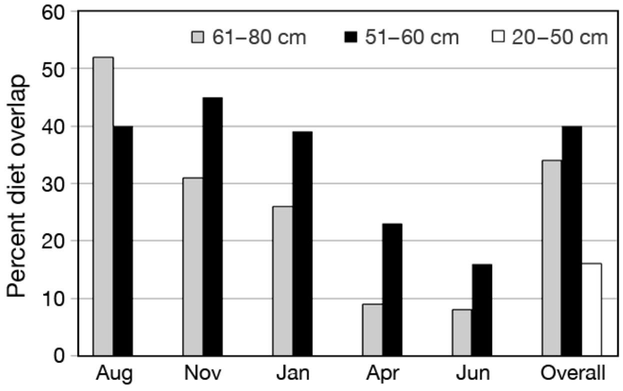


Fig. 4. *Gadus macrocephalus*, *Theragra chalcogramma*. Interspecific seasonal diet overlap between cod and pollock by fish size. Overlap of <30% is considered low; 30 to 60%, moderate; and >60%, high (Høines & Bergstad 1999, Guedes & Araújo 2008)

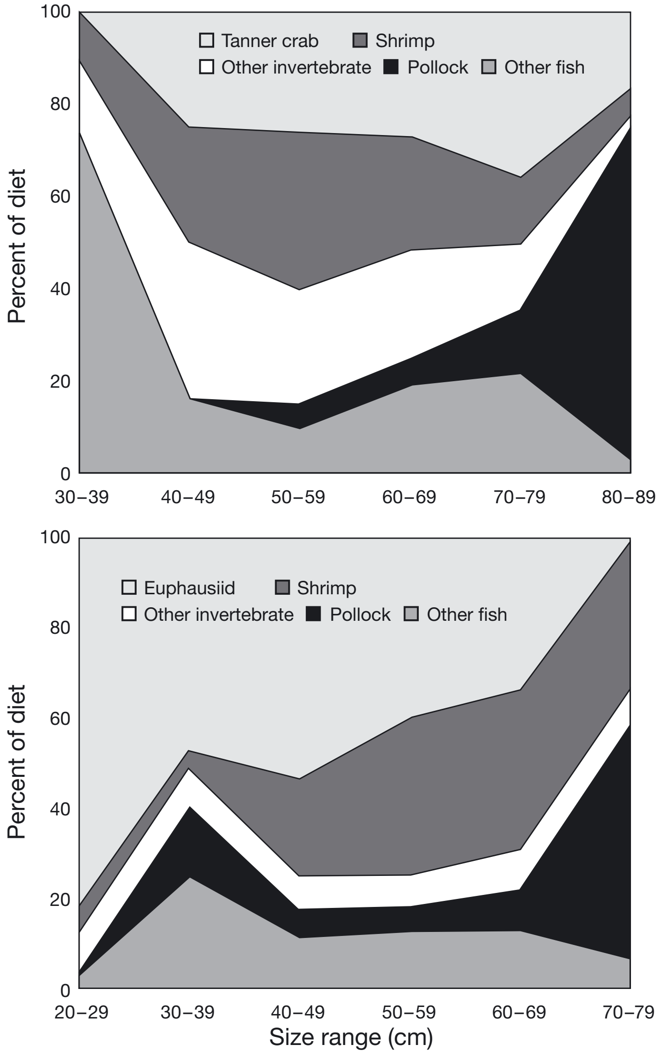


Fig. 5. *Gadus macrocephalus*, *Theragra chalcogramma*. Changes in diet by weight and fish size of cod (upper panel) and pollock (lower panel). Note differences in the size range of fish represented

lower jaw of pollock prevents them from effective benthic foraging, limiting them to a largely pelagic diet (Yamamura et al. 2002). Cod, however, are able to forage both benthically and pelagically. As larger fish, with a larger gape size, they have the ability to feed on a wider variety of prey items. While individual pollock tended to specialize on a single prey item, individual cod typically fed on a variety of prey items.

The present study confirms the findings of other studies that Tanner crab is a main prey item of cod during all seasons (Jewett 1978, Albers & Anderson 1985, Yang 2004, Yang et al. 2006, Poltev & Stominok 2008). At the same time, Tanner crab as a benthic species is virtually absent from pollock diets (Bailey & Dunn 1979, Clausen 1983, Dwyer et al. 1987, Yamamura et al. 2002, Yang 2004, Yang et al. 2006, Adams et al. 2007), although the gape size of pollock does not necessarily preclude them as a prey item. Pollock have a strong seasonal component to their diets, most notably with a spring focus on euphausiids. While euphausiids were preyed upon by pollock during all seasons, the concentration on euphausiids during the April and June sampling periods was likely due to the targeting of spawning aggregates of euphausiids which form in the northern Gulf of Alaska during these months (Pinchuk et al. 2008). Cod also preyed on euphausiids in large numbers during those periods, but the weight of euphausiids consumed was <1% of the diet. This study highlights the importance of sampling throughout the year to obtain a clear understanding of the overall diet patterns of these gadid predators.

Marmot Bay has been shown to be a productive marine environment, with species distributions that vary both temporally and spatially (Jackson 2005, Urban & Vining 2008, Spalinger 2010). The period of this study was no exception, as the North Pacific Ocean was in the midst of the 1998/1999 regime shift to a warmer environment (Curchitser et al. 2005), although it did not prove to be as strong or long lasting as the major shift in 1976/1977 (Litzow 2006). There have been no major trends in gadid populations, which have increased only slightly in recent years. There have been no strong trends either in Tanner crab or shrimp populations, which are near their 15 yr average. While there is some evidence that cod in Marmot Bay may regulate Tanner crab populations (Urban 2010), elsewhere in Alaska climate effects on crab larval survival have been used to explain crab recruitment variability (Zheng & Kruse 2006). Examination of the relationship between cod and shrimp biomass has supported the idea of the ‘top-down’ regulation of shrimp populations across the North Atlantic (Worm & Meyers 2003, Palsson & Bjornsson 2011). In Marmot Bay, however, there has actually been a slight positive correlation between shrimp biomass with cod and pollock biomass over the last 10 yr, so any conclusions about top-down regulation remain elusive. While the potential exists for cod to affect Tanner crab populations and for pollock and cod to impact shrimp populations, the interactions between climate, fishing, and food web dynamics in the Gulf of Alaska and other areas in the North Pacific Ocean are still poorly understood (Gaichas et al. 2011).

Both of these predators occupy a broad niche width but exhibit different foraging patterns. Cod are more generalist, with a diverse diet including relatively rare prey items, while individual pollock show a high level of specialization on a single prey category, for example, euphausiids or northern shrimp. Given their more diverse diet and ability to forage both benthically and pelagically, cod would be expected to be more resilient to changes in the marine community of Marmot Bay (Smith et al. 2011), while pollock could be more drastically affected by a collapse in the shrimp or euphausiid populations. The possibility remains, however, given the diversity of pollock prey items throughout their range, that changes in the marine community could make more prey species available to pollock.

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Contribution to the Theme Section 'Effects of climate and predation on subarctic crustacean populations'

Predation by Atlantic cod *Gadus morhua* on northern shrimp *Pandalus borealis* in inshore and offshore areas of Iceland

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ABSTRACT: Northern shrimp *Pandalus borealis* is found in both inshore and offshore areas around Iceland, where it has supported an important commercial fishery. However, in the past 15 yr the northern shrimp population has decreased in size and collapsed in most of the inshore areas. In this study, the importance of Atlantic cod *Gadus morhua* on northern shrimp stock dynamics was studied by comparing stomach contents of cod between 2 different habitats, inshore and offshore northern shrimp fishery areas. Many prey items were observed in cod stomachs, but only a few dominated. The most important prey types, in decreasing order of importance, included northern shrimp, fish and euphausiids in the inshore area, as opposed to capelin *Mallotus villosus*, other fish species, northern ambereye *Hymenodora glacialis* and northern shrimp in the offshore area. Low northern shrimp biomass was observed during periods of high cod density, suggesting that predation by cod affected northern shrimp biomass in both areas.

KEY WORDS: Northern shrimp · Cod · Predation · Species interaction · Temperature

INTRODUCTION

Northern shrimp *Pandalus borealis* is targeted by commercial fisheries and is also of great importance as prey in the marine food web. Various fish species, mammals, sea birds and invertebrates, feed on shrimp (Parsons 2005). Demersal fishes, especially Atlantic cod *Gadus morhua*, are important predators on northern shrimp throughout Atlantic waters (Stefánsson et al. 1998, Berenboim et al. 2000, Sousa et al. 2006, Fraser et al. 2008, Campbell et al. 2011). Close linkage has been described between northern shrimp and cod, and predation can have strong effects on the development of shrimp stocks (Worm & Myers 2003). The biological interactions between gadoids and northern shrimp are, however, poorly understood. Valuable information into the stock dynamics may be gained by comparing predation between areas.

Predation by cod on demersal stages of northern shrimp has been well documented in various geographical areas (Albers & Anderson 1985, Magnússon & Pálsson 1989, Lilly et al. 2000). These studies have demonstrated the importance of northern shrimp in the diet of cod, but have also noted that the contribution by northern shrimp to the cod diet can vary greatly with area (Rose & O'Driscoll 2002), time of year (Pálsson & Björnsson 2011) and size of cod (Albers & Anderson 1985, Berenboim et al. 2000). The consumption of northern shrimp by cod can also be quite variable over years (Mehl 1989, Pálsson & Björnsson 2011), and sometimes it may represent a greater source of mortality than commercial fishing pressure (Savenkoff et al. 2007).

Northern shrimp are considered to represent localized populations in inshore and offshore Icelandic areas, with genetic differences and limited connectivity during adult stages (Jónsdóttir et al. 1998). In the 1980s and 1990s northern shrimp was one of the most important commercial species in Icelandic waters. However, in the past 15 yr the northern

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shrimp populations have declined and most of the inshore populations have collapsed (Anonymous 2010). Northern shrimp fishing is regulated by area-specific total allowable catches, which are determined based on results from annual surveys. Due to a poor state of the stocks, all but 2 inshore areas around Iceland are now closed for northern shrimp fishing. The northern shrimp resource in the offshore area north/northeast of Iceland was not as severely impacted as were the inshore resources, but it did experience major depletion after 1996, following a rapid increase in cod biomass in the northern shrimp grounds.

In this study we compare the diet of cod between inshore and offshore areas of Iceland. To evaluate the potential effect of predation by cod on northern shrimp populations in different habitats, stomach contents of cod were compared between an inshore area (Ísafjardardjúp, northwest of Iceland) and the offshore shrimp fishing area north/northeast of Iceland. Data were available from northern shrimp surveys from 1999 to 2010, allowing both annual and spatial comparisons.

MATERIALS AND METHODS

The data used in the present study were collected during annual shrimp surveys of both inshore and offshore areas. The purpose of the surveys was to provide an index of the overall northern shrimp *Pandalus borealis* stock biomass to inform fishery management. The standardized surveys have been conducted every year since 1988, whereas cod *Gadus morhua* stomach examination has only been conducted since 1998 and 1999 in the offshore and inshore areas, respectively, and so only data since 1999 were used in this study.

The inshore area chosen for this study, Ísafjardardjúp, is the largest fjord on the Westfjord peninsula in the northwest of Iceland (Fig. 1). The fjord is 75 km long, and the width at the mouth is approximately 20 km. The depth in the middle of the fjord is 110 to 130 m, but closer to the coast it is about 40 to 60 m. Ísafjardardjúp does not have a sill near the mouth, and the water exchange into the fjord is fairly unrestricted. During September and October, the survey utilizes a standard shrimp bottom trawl of 1000 meshes in standard tows of 2 nautical miles, during daylight hours only, at a tow speed of 2.0 to 2.2 knots. The codend has an open mesh size of 37 mm (42 mm whole mesh size). The distance between the wing ends is 14.7 m, and the mean (±SD) vertical opening is 4.6 ± 0.3 m. In order to sample fish of all size classes, a sorting grid is not used. The survey includes 54 fixed stations annually at 39 to 155 m depth (Fig. 1). In 2006, 2009 and 2010, the sampling was reduced to 28 to 31 stations.

The offshore survey takes place in July to August (starting in June in 2004) north, northeast and east of Iceland at depths ranging from 200 to 700 m (Fig. 1). The survey trawl is a standard shrimp bottom trawl of 1400 meshes, towed during daylight hours only, at a speed of 2.1 to 2.3 knots. The codend has a diamond mesh, with a mesh size of 37 mm open mesh (whole mesh size is 40 mm). The distance between the wing ends is 17 m, and the mean (±SD) vertical opening is 6.0 ± 0.4 m. Approximately 190 stations were sampled each year from 1999 to 2005, but only 92 fixed stations have been sampled annually in more recent years (Fig. 1). Despite reduced coverage the overall survey area has remained unchanged. Tow length was reduced from 1.5 to 2.5 nautical miles from 1999

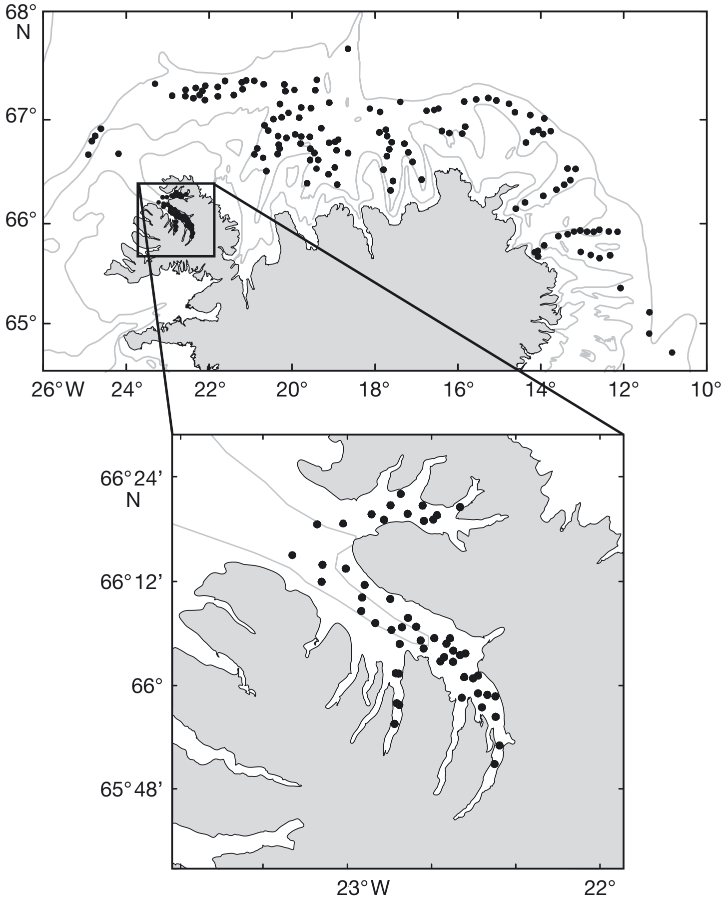

Fig. 1. Sampling locations in the annual shrimp surveys. Depth contours at 100, 200 and 500 m. The inshore area is within the box and enlarged. Depth contours in inshore area at 100 m

to 2003 to between 1.5 and 2.0 nautical miles in subsequent years. In order to sample fish of all size classes a sorting grid is not used.

Sea bottom temperature is determined at each station using a pre-calibrated trawl sensor (Scanmar) attached to the trawl headline. Sea bottom temperature was not determined in 2006 in the inshore area due to failure in the equipment. Each study area was divided into several sub-areas based on northern shrimp distribution. The northern shrimp stock biomass index was calculated using the sum of the mean biomass estimates per square kilometre, which was calculated for each sub-area using the swept-area method described by Sparre & Venema (1989).

When available up to 5 Atlantic cod (>15 cm) were randomly sampled at each station for detailed analysis onboard. Total length (TL) of each cod was measured to the nearest centimetre, whole and gutted weight recorded, and otoliths removed for age determination. The stomachs were cut open, and the contents were macroscopically identified with all prey items classified to the lowest taxonomic level possible. To avoid possible bias from fish swallowing food items in the trawl, any prey items not displaying signs of digestive action were discounted. The number of individuals of each prey type was counted, and their wet weights were measured to the nearest whole gram. Data were reduced to 7 prey categories or groups, including the most prominent prey species, northern shrimp *Pandalus borealis*, northern ambereye *Hymenodora glacialis* and capelin *Mallotus villosus*. Other prey types were pooled into 4 main groups: (1) fish, (2) other shrimps, (3) euphausiids, and (4) all other prey types including other crustaceans, echinoderms, annelids, molluscs and unidentified items. The weight of each prey group was expressed as a percentage of the total weight of the stomach content. Furthermore, the mean total stomach fullness (TF) was calculated as:

$$\mathrm{TF} = \frac{1}{N}\sum\left(\frac{W_\mathrm{f}}{(\mathrm{TL_f})^3}\times 10^4\right)$$

and the mean shrimp stomach fullness (SF) as:

$$\mathrm{SF} = \frac{1}{N}\sum\left(\frac{W_\mathrm{if}}{(\mathrm{TL_f})^3}\times 10^4\right)$$

where N is the total number of fish, W_f is the total stomach content weight from each fish, W_if is the weight of northern shrimp from each fish and $\mathrm{TL_f}$ is the total length of cod in centimetres (Nielsen & Andersen 2001). The stomach fullness data were not normally distributed, and the values were not normally distributed after natural-log transformation of the data. Therefore, a non-parametric test, the Kruskal-Wallis test, was used to test for differences in mean stomach fullness (TF and SF) among years for both inshore and offshore areas.

RESULTS

Biomass trends

The northern shrimp *Pandalus borealis* biomass index in the inshore area decreased continuously from 1990 to 2004, while it increased in the offshore area until 1996, after which it declined (Fig. 2). High indices in 1990 and 1996 in the inshore and offshore areas, respectively, could be due to year-effects. In both areas, the indices declined sharply after 2001 and reached historically low levels in 2004. The populations recovered slightly in the following years, and, while the offshore population has been relatively stable in the past 5 yr, the inshore northern shrimp biomass index was again very low in 2009 and 2010 (Fig. 2).

The density index, based on catch rate of cod *Gadus morhua* (number of cod caught per trawling hour) was calculated separately for small (≤15 cm) and large cod (>15 cm). The density of small cod was much higher in the inshore than the offshore area,

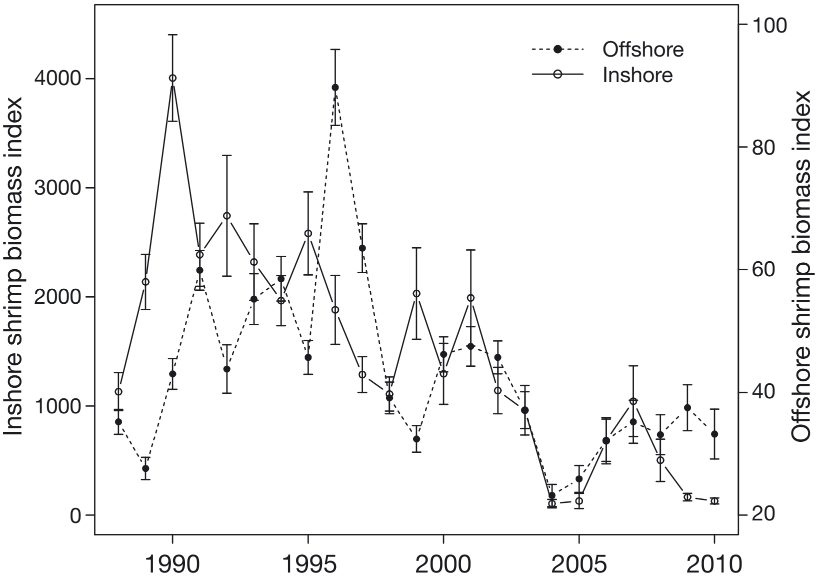

Fig. 2. *Pandalus borealis*. Northern shrimp biomass indices (±CV, the coefficient of variation of the stock size estimate) for inshore and offshore areas

where they were almost absent (Fig. 3A). The density of small cod in the inshore area varied without trend from 1988 to 2000, but it has been very low since 2001 (Fig. 3A).

The density of large cod was very low in the offshore area from 1988 to 1995, but was generally higher from 1996 to 1998 in both areas (Fig. 3B). This was followed by 2 yr of low catch rates before large cod density again increased; since 2003 it has remained much higher than between 1988 and 1995 (Fig. 3B).

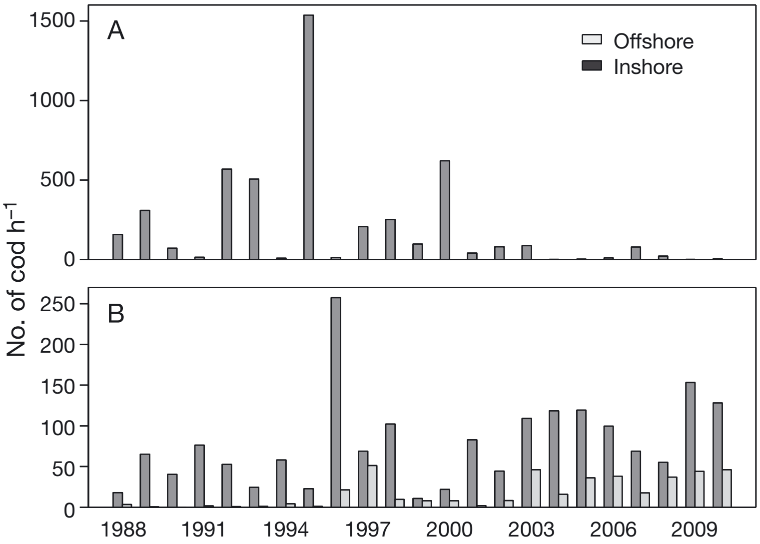

Fig. 3. *Gadus morhua.* Number of (A) small (≤15 cm) and (B) large (>15 cm) cod caught per hour in inshore and offshore northern shrimp surveys from 1988 to 2010

Diet composition

Cod in the inshore area was on average smaller (mean length: 23.5 cm) than in the offshore area (mean length: 56.6 cm). Stomach content was not analysed in small cod, and the mean length of cod used for stomach analysis was 44.1 and 62.6 cm in the inshore and offshore areas, respectively.

From 1999 to 2010, a total of 2062 and 4859 cod stomachs were examined in the inshore and offshore areas, respectively. The percentage of cod with empty stomachs (Table 1) was higher in the inshore area (15 to 34 %) than in the offshore area (6 to 17 %).

The stomach contents were quite variable, with 65 and 105 prey items identified in the inshore and offshore areas, respectively. There were 3 main prey groups for inshore cod and 4 main groups for offshore cod (Fig. 4). For inshore cod, the main prey group was fish, including cod, haddock *Melanogrammus aeglefinus*, snake blenny *Lumpenus lampretaeformis*, spotted snake blenny *Leptoclinus maculates* and herring *Clupea harengus*. The second main prey group was northern shrimp, and the third main prey group was euphausiids. An obvious shift in prey preference of inshore cod was observed in 2006, when the main prey group became northern shrimp and at the same time the proportion of various fishes decreased (Fig. 4). The main prey group for offshore cod (as for inshore cod) was fish, including *Lumpenus* spp., *Lycodes* spp. and long rough dab *Hippoglossoides platessoides*. The second main prey group was capelin, and the last 2 main prey groups were the 2 shrimp species, northern ambereye and northern shrimp.

The TF values for both inshore and offshore cod differed significantly among years (Kruskal-Wallis test; $p < 0.001$) and were generally inversely related (Fig. 5A). The TF for inshore cod declined from 1999 to 2003 and has since been highly variable. The TF

Table 1. *Gadus morhua* and *Pandalus borealis.* Number of cod sampled in the inshore and offshore northern shrimp areas each year. Percentage of cod observed with empty stomachs, and percentage of cod observed with northern shrimp in the stomach

	n	Empty cod stomachs (%)	Northern shrimp in cod stomachs (%)
Inshore			
1999	78	30.8	48.7
2000	164	34.1	22.0
2001	178	20.2	37.6
2002	151	19.2	28.5
2003	165	33.3	29.7
2004	253	28.5	29.6
2005	248	31.0	20.6
2006	115	23.5	33.9
2007	208	15.9	48.6
2008	234	15.4	52.6
2009	133	24.8	35.3
2010	135	22.2	49.6
Offshore			
1999	422	5.7	61.8
2000	338	12.7	53.8
2001	253	8.3	57.3
2002	351	7.4	63.2
2003	724	11.5	56.8
2004	552	12.5	53.4
2005	514	15.4	38.9
2006	367	7.6	45.5
2007	305	15.1	47.2
2008	350	15.7	41.7
2009	340	17.1	40.6
2010	343	14.6	41.1

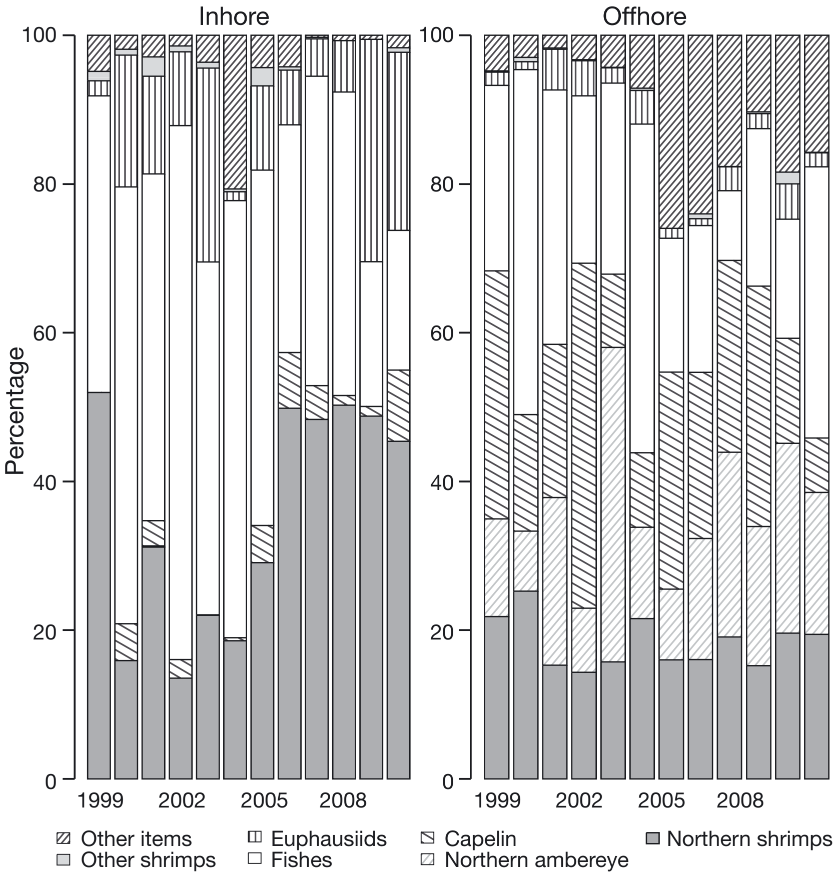

Fig. 4. *Gadus morhua*. Proportion (% of total stomach content by mass) of the 7 main prey groups of cod in inshore and off-shore areas from 1999 to 2010

for offshore cod showed clear differences between 2 periods (Fig. 5A). It was much higher than for inshore cod from 1999 to 2003. However, it decreased sharply in 2004 (when the TF for inshore cod increased sharply) and has remained at its lowest level since 2006 (Fig. 5A).

An inverse relationship in SF was also observed between inshore and offshore cod (Fig. 5B). SF increased in the inshore, but decreased in offshore cod (Fig. 5B). Hence, from 2000 to 2003, the SF was higher in offshore cod, but, since 2004, it has been consistently much higher (and more highly variable) in inshore cod.

Higher percentages of cod included northern shrimp in their diet in the offshore area (39 to 63%) than in the inshore area (21 to 53%) (Table 1). The percentage of cod stomachs containing northern shrimp did not change significantly with increasing cod length in the inshore area ($r^2 = 0.0089$, $p = 0.405$; Fig. 6A). It did, however, increase significantly with increasing cod length in the offshore area ($r^2 = 0.302$, $p < 0.001$; Fig. 6A). The percentage by weight of northern shrimp in the cod diet decreased significantly with increasing cod length in both inshore and offshore areas (inshore: $r^2 = 0.501$; offshore: $r^2 = 0.766$; $p < 0.001$; Fig. 6B).

The relationship between the number of cod caught per hour and the shrimp biomass index was not clear in either the inshore or offshore area (Fig. 7). High cod density did, however, appear to be related to shrimp biomass in both areas. Above average cod catch rates tended to be associated with below average shrimp biomass levels (Fig. 7). In contrast, when cod catch rates were below average, it was equally likely that the shrimp biomass would be below or above average (Fig. 7). Negative effects of

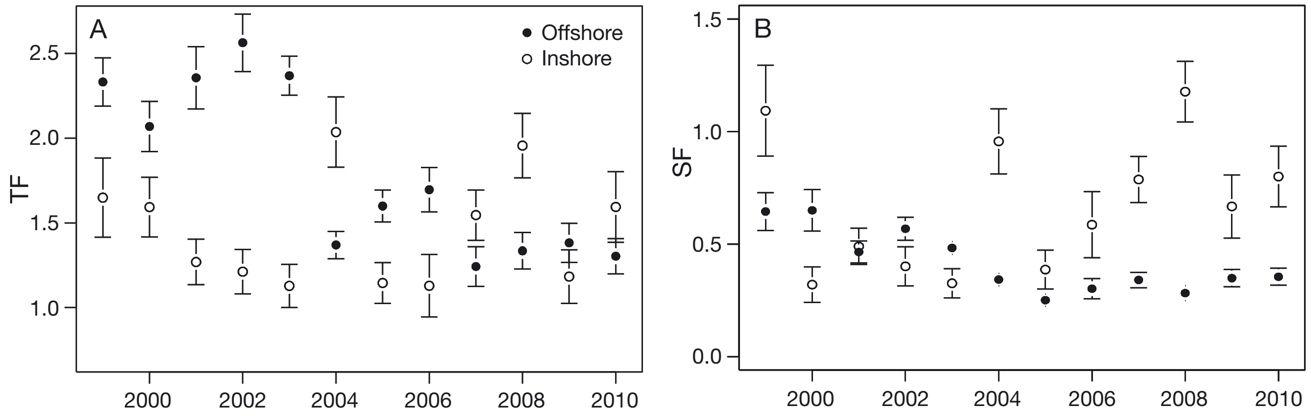

Fig. 5. *Gadus morhua* and *Pandalus borealis.* (A) Mean total stomach fullness (TF) and (B) mean shrimp stomach fullness (SF) for cod in inshore (○) and offshore (●) northern shrimp areas off Iceland

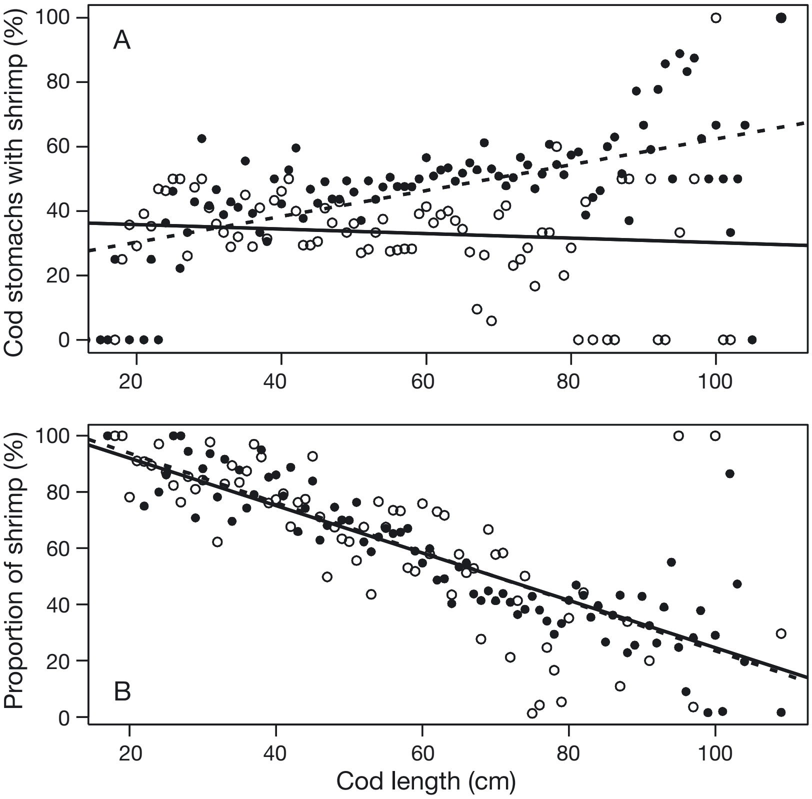

Fig. 6. *Gadus morhua* and *Pandalus borealis.* (A) Proportion of cod that had consumed northern shrimp in inshore (○, —) and offshore (●, - - -) northern shrimp areas. (B) Proportion by weight of northern shrimp in the stomach of cod (cod with no shrimp in the stomach were excluded)

predation on prey biomass are often observed with a lag of 1 yr, but the relationships described here did not become clearer when the shrimp biomass index was compared with the cod catch rate in the previous year.

DISCUSSION

Prey composition

The main prey types of cod *Gadus morhua* differed between the 2 areas, but it is common to see diet differences between areas (Lee & Khan 2000, Rose & O'Driscoll 2002). Fish size is the most likely candidate factor for explaining the variation in the diet of Icelandic cod (Jaworski & Ragnarsson 2006). The most important prey types included northern shrimp *Pandalus borealis*, fish and euphausiids in the inshore area, as opposed to capelin *Mallotus villosus*, other fish species, northern ambereye *Hymenodora glacialis* and northern shrimp in the offshore area. Differences between areas in relative importance of the principal prey types was likely due to differences in cod size, with small cod in the inshore area feeding on smaller prey, such as euphausiids, while larger cod in the offshore area prey more heavily on large prey types such as capelin. Euphausiids are known to be of greater importance to small than to large cod (Dalpadado & Bogstad 2004, Pálsson & Björnsson 2011). In the inshore area, euphausiids were found in dense groups, a pattern also observed in a nearby fjord, where euphausiids were an important food source for cod (Björnsson et al. 2011).

Prey types are of variable quality, and food of low quality may negatively influence growth, condition and reproductive potential of the fish (Rose & O'Driscoll 2002). Although cod may be considered opportunistic feeders, they do exhibit distinct prey preferences, and the results of this present study showed indications of selective feeding. From 2006 to 2010, a relatively high biomass of large cod was observed in the inshore area. At the same time, a low percentage of fish (other than capelin) was found in cod stomachs, and high SF was observed despite low shrimp biomass. This could indicate that cod selectively preyed upon northern shrimp when cod density was relatively high and the preferred fish prey was unavailable. In the offshore area, cod seemed to select for capelin and northern ambereye. Capelin is one of the most important prey for cod, and cod liver condition is related to capelin availability (Rose & O'Driscoll 2002). Northern ambereye is a deepwater, lipid-rich shrimp, with total lipids representing about 44 % of the dry mass, which they accumulate to survive periods of low food supply (Kreibich et al. 2010). Hence, northern ambereye is an energy-rich food item. For comparison, total lipids of northern ambereye are twice as high as in northern krill *Meganyctiphanes norvegica* (Kreibich et al. 2010). Northern ambereye is not very abundant in the offshore survey. However, cod are observed with full stomachs of northern ambereye, indicating selective feeding by cod. As northern ambereye is not found in high abundance in the offshore survey, cod feed on them either in the water column or at greater depths than those sampled in the survey. The reason for the

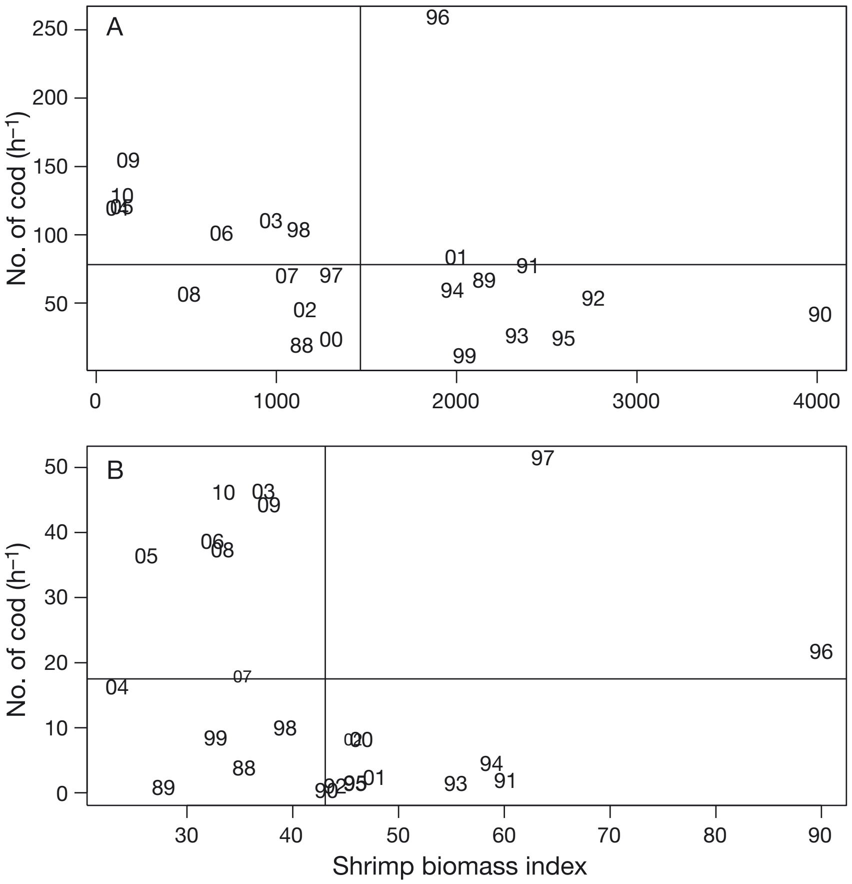

Fig. 7. *Gadus morhua* and *Pandalus borealis.* Relationship between shrimp biomass index and number of cod caught per hour in (A) inshore and (B) offshore northern shrimp areas. Lines represent mean shrimp biomass index and mean number of cod caught per hour in each area. Numbers represent sampling years

high frequency of occurrence of euphausiids in cod stomachs, despite their relatively low lipid content, could be that euphausiids are found in dense patches and little foraging time and energy is used for hunting.

The cod diet generally reflects prey availability, and the overlap between cod and its prey is reflected in the diet. Therefore, cod may be categorized as opportunistic feeders. In 2004, there were some changes in the offshore area; a high proportion of cod had empty stomachs, and the TF decreased sharply. At the same time, the proportion of fish (except capelin) decreased in cod stomachs and the proportion of other prey types increased. Comparison of the diet of northwest Atlantic cod with prey distribution has shown that most major prey species were consumed when they were abundant and their distribution overlapped with that of cod (Link & Garrison 2002). As the diet of predatory fishes partly reflects the prey availability in the area (Fahrig et al. 1993), changes in diet composition may indicate shifts in distribution and/or abundance of prey species. The observed changes in the present study, along with the fact that northern shrimp biomass was at historically low levels in 2004, may indicate some changes in the ecosystem north of Iceland during this time.

Prey consumption

Two factors, cod size and sea temperature, are most important when comparing prey consumption between the 2 study areas. Cod inhabiting the 2 areas were of different size classes. Small cod were most common in the inshore area, while cod were larger in the offshore area. The inshore area is a known nursery area, while various offshore and inshore areas are feeding areas. The 2 areas, therefore, play different roles in the life history of the cod. Even though the proportion of cod consuming northern shrimp increased with increasing fish length (in the offshore area), the importance of northern shrimp in the diet of cod decreased with length in both areas. These results are in accordance with earlier studies in Icelandic waters (Pálsson & Björnsson 2011), the Barents Sea (Berenboim et al. 2000) and Pavlof Bay, Alaska (Albers & Anderson 1985). That does, however, not necessarily mean lower consumption of northern shrimp by large than by small cod, as large cod have a greater total consumption than small cod and may therefore consume more shrimp. Further, large cod (>35 cm TL) is the main predator on northern shrimp in Icelandic waters (Jaworski & Ragnarsson 2006), and, before the collapse of the northern Gulf of St. Lawrence cod stock, large cod was also the main predator in that area (Savenkoff et al. 2007). Stomach examination was not conducted for small (<15 cm TL) cod in this study, but other studies have shown that northern shrimp is not an important prey type for such small cod in other areas (Lilly et al. 2000, Dalpadado & Bogstad 2004).

There are substantial differences in bottom temperature between the 2 areas, with annual near-bottom temperatures ranging from 0.4 to 1.8°C in the offshore area and 6.8 to 9.1°C in the inshore area.

Due to the inflow of the cold water masses of the East Greenland Current, the area north and northeast of Iceland is the coldest around the country (Stefánsson 1962, Malmberg & Valdimarsson 2003). Consumption may be significantly different between areas due to the different temperature regimes. The rate of handling, eating and digesting a meal increases with temperature (Wootton 1998, Grigoriou & Richardson 2008), escalating the energy demand in areas with high temperature. Furthermore, experimental studies have shown that the stomach evacuation rate and, hence, consumption, increases with temperature (dos Santos & Jobling 1991). Consumption is therefore expected to be lower in the offshore area than in the inshore area. Little change in bottom temperature has been observed in the offshore area, but it did increase in the inshore area during the study period, leading to increased food requirements in recent years. Furthermore, laboratory experiments have demonstrated that gastric evacuation of small cod is faster than that of large cod when fed similar-sized meals relative to their body weight (dos Santos & Jobling 1995). This would suggest a greater food requirement and greater consumption per body weight for inshore than for offshore cod.

Effects of predation by cod on northern shrimp

In this study the predation by cod on northern shrimp was studied in 2 different areas off Iceland. Even though some of the main prey groups differed between the 2 areas, northern shrimp was one of the major prey types of cod in both the inshore and offshore areas. Low northern shrimp biomass has been evident in both areas in recent years, while cod density has remained high, implying that predation by cod had a negative effect on northern shrimp biomass.

Given the importance of northern shrimp as prey for cod, top-down control might be expected. The results of the present study suggest that cod had an adverse effect on northern shrimp abundance in both areas, as northern shrimp biomass was more likely to be below average in years when cod abundance was above average. The impact of cod predation on northern shrimp populations has been ambiguous. Several studies have suggested that cod control shrimp populations (Berenboim et al. 2000, Worm & Myers 2003), and the abundance of northern shrimp has been noted to increase markedly following the collapse of demersal fish populations, such as on the northeast Newfoundland shelf (Lilly et al. 2000) and in Greenland (Hamilton et al. 2003). In the Gulf of Alaska, cod predation has played a role in keeping the reduced shrimp stocks from rebuilding (Albers & Anderson 1985). Consumption by cod has also been noted as the main cause of shrimp mortality in the Gulf of St. Lawrence (Savenkoff et al. 2007), and a positive relationship was found between northern shrimp consumption by cod and shrimp biomass in Icelandic waters (Pálsson & Björnsson 2011). However, other studies have demonstrated that shrimp populations are not regulated entirely by cod predation (Lilly et al. 2000, Mueter & Norcross 2000).

Predation by other species

Northern shrimp is an important prey for other fish species (Pálsson 1983, Parsons 2005), and the consumption by cod is only a part of the total removals by all predators. Greenland halibut *Reinhardtius hippoglossoides* is the most important bycatch in the offshore northern shrimp fishery in Icelandic waters and is an important predator on shrimp (Haug & Gulliksen 1982, Solmundsson 2007). In the period from 1987 to 1989, a feeding study of Greenland halibut on the offshore northern shrimp grounds revealed that northern shrimp contributed 6% by weight to the total diet (Solmundsson 2007). Another possibly important predator that is common in the offshore survey is eelpout *Lycodes* spp. In a study in West Greenland waters, northern shrimp contributed 81.5% by weight to the total diet of eelpouts (Pedersen & Riget 1991). Furthermore, in a study from 1993 in the offshore area, >70% of the diet of the largest eelpouts (*L. eudipleurostictus* and *L. vahlii*) were shrimps, euphausiids and mysids (Valtýsson 1997). In the inshore area, haddock *Melanogrammus aeglefinus* abundance increased after 1997 (Skúladóttir et al. 2001) and whiting *Merlangius merlangus* after 2001 (Anonymous 2010). Northern shrimp is not a major prey type of haddock (Björnsson et al. 2011, Pálsson & Björnsson 2011), but has been noted in the stomach of both haddock and whiting.

Conclusions

The results of the present study suggest that cod had an adverse effect on northern shrimp abundance in both areas, as northern shrimp biomass was more likely to be below average in years when cod abundance was above average. Northern shrimp was a more important prey type of cod in the inshore than in the offshore area, and in some years it represented about 50% of the diet. Other important prey types, such as capelin and northern ambereye, which cod selectively feed on in the offshore area, were rare in the inshore area. Higher temperature in the inshore than offshore area implies a greater food requirement and higher consumption. Accordingly, cod is likely to have a greater impact on northern shrimp in the inshore than in the offshore area.

Although cod predation has an impact on northern shrimp biomass, other factors, such as fishing (Savenkoff et al. 2007), ocean climate variability (Wieland 2005, Ouellet et al. 2011), size of areas of suitable habitat and larval transport (Koeller 2000) may also be important factors in regulating shrimp abundance. Further work is needed to evaluate how northern shrimp may respond to changes in predator abundances in relation to other factors, such as temperature, other ocean climate variables, abundance of other prey, and the distribution of predators and prey.

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Contribution to the Theme Section 'Effects of climate and predation on subarctic crustacean populations'

Trophic interactions between key predatory fishes and crustaceans: comparison of two Northwest Atlantic systems during a period of ecosystem change

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ABSTRACT: This study shows that a sharp ecosystem transition in dominant communities during the early 1990s, from finfish to crustaceans, was common to the 2 northernmost Northwest Atlantic ecosystems, the Newfoundland–Labrador shelf (NL) and the northern Gulf of St. Lawrence (nGSL). Fishery and survey data show that populations of Atlantic cod *Gadus morhua*, typical of most finfish species, collapsed during the late 1980s to early 1990s in both systems, while Greenland halibut *Reinhardtius hippoglossoides* populations changed little. Biomass of northern shrimp *Pandalus borealis* increased following the collapse of cod in both systems, likely due, at least in part, to release of predation pressure. Predation appeared to have relatively little effect on biomass of snow crab *Chionoecetes opilio*. Shrimp replaced capelin as the principal prey in the diet of NL cod and nGSL Greenland halibut in the mid-1990s. The contribution of shrimp to the predator diets was generally highest when neither capelin nor other suitable prey (fish or squid) were available. We conclude that the NL and nGSL ecosystems are similar in form and function, differing from Canadian Atlantic ecosystems further south. The implications of a change in predominant forage species from capelin to shrimp in these systems are unknown, but could conceivably include changes in the pathway and efficiency of energy flow.

KEY WORDS: Canadian Atlantic · Predation · Atlantic cod · Greenland halibut · Northern shrimp · Snow crab

INTRODUCTION

Many subarctic marine ecosystems have experienced transitions to altered states of structure and functioning, associated with pronounced shifts in oceanographic regimes ('regime shifts'; Choi et al. 2004, Frank et al. 2006, 2007, Mueter et al. 2009, Shackell et al. 2010). Clearest examples of such transitions include Northeast Pacific and Northwest Atlantic ecosystems. In the Northeast Pacific (eastern Bering Sea and Gulf of Alaska), a shift from a cold to a warmer regime in the mid-1970s was associated with a change in predominant communities and commercial fisheries from decapod crustaceans to demersal fishes (Litzow & Ciannelli 2007, Mueter et al. 2009). In contrast, in the Northwest Atlantic (the Newfoundland-Labrador shelf, NL; Gulf of St. Lawrence, GSL; and eastern Scotian Shelf, ESS) a prolonged cold period during the 1980s and early 1990s was associated with a transition from demersal fish to decapod crustacean communities (Lilly et al. 2000, 2008, Choi et al. 2004, Frank et al. 2006, 2007, Lilly 2008, Bundy et al. 2009, Dwyer et al. 2010). In both oceans, the transitions were initially attributed either

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exclusively or primarily to excessive exploitation leading up to the transition (e.g. Hutchings & Myers 1994, Armstrong et al. 1998). It is now generally believed, for the Northwest Atlantic, that shifts in ocean climate regime played an important role in those transitions, with fishing pressure representing a strong forcing factor (Lilly 2008, Lilly et al. 2008).

It has been argued that bottom-up control is the primary basic controlling mechanism for species abundance, and that ecosystems become vulnerable to top-down control following perturbation, particularly in the ocean climate regime (Litzow & Ciannelli 2007). It has also been proposed that cold, low-diversity, high-latitude ecosystems are more susceptible to top-down control following perturbation than are warmer ecosystems at lower latitudes, with higher diversity (Frank et al. 2006, 2007). The underlying rationale is that low diversity in high-latitude functional groups such as demersal fishes limits the community capability to compensate for the removal of dominant species.

In the Northwest Atlantic, the change in community dominance from demersal (predatory) fishes to decapod crustaceans was characterized by the collapse of Atlantic cod *Gadus morhua* and most other commercially important demersal fish stocks (Koen-Alonso et al. 2010); only a few stocks, primarily of arctic species such as Greenland halibut *Reinhardtius hippoglossoides*, did not collapse. This collapse occurred during a prolonged cold oceanographic period, from about 1982 to 1995 at NL, the longest such cold period within the 50 yr monitoring time series (Colbourne & Anderson 2003, Colbourne et al. 2009). It is believed that the unfavorably cold conditions adversely affected survival of pre-recruit fish (Colbourne & Anderson 2003). Abundances declined for the entire fish community, including non-commercial species (M. Koen-Alonso unpubl. data). This collapse was concurrent with (or followed by) increases in abundance of commercially important decapod crustaceans, especially northern shrimp *Pandalus borealis* and snow crab *Chionoecetes opilio*. The relative effects of ocean climate variability, exploitation, and changes in predation pressure on this transition remain controversial (Lilly et al. 2000, 2008, Worm & Myers 2003, Choi et al. 2004, Frank et al. 2005, 2006, 2007, 2011, Chabot et al. 2008, Dawe et al. 2008, Petrie et al. 2009, Boudreau et al. 2011). Populations of Atlantic cod and other demersal fishes have not recovered despite the persistence of warm oceanographic conditions (Colbourne & Anderson 2003, Colbourne et al. 2009) and a moratorium on fishing in some areas for the past 15 yr.

In this study, we investigated the effects of changes in relative abundance of predatory demersal fishes and their crustacean prey in severely perturbed high-latitude Northwest Atlantic ecosystems. We adopted a comparative approach between the northern GSL (nGSL) and NL ecosystems, drawing inferences from trends in abundance based on fishery and survey data, trends in diets of principal predators, and trends in spatial interactions between predators and their prey. Our specific objectives included evaluating the degree of similarity in ecosystem transition between our study systems. We also address the role of predation, relative to other forcing factors, in regulating the abundance of dominant and commercially important crustacean populations (northern shrimp and snow crab) in both systems. We then very generally compare our results from the 2 most northern Northwest Atlantic ecosystems to recent changes in predator–prey dynamics in more southern Canadian ecosystems, the southern GSL (sGSL) and the ESS. Finally, we discuss the possible effects of such relative changes in Northwest Atlantic systems on ecosystem structure and function.

MATERIALS AND METHODS

Study areas and species

We selected the nGSL and NL ecosystems for this comparative study, as they represent the northernmost ecosystems in the Northwest Atlantic for which survey abundance and biomass data, as well as predator diet data, are available. We selected Atlantic cod and Greenland halibut as our indicators of predation by demersal fish primarily because diet data are available for both of these predators from both ecosystems. Also, Atlantic cod was historically the most abundant predator, known to prey on both northern shrimp and snow crab (Lilly 1984, 1991), and the collapse of its stocks reflects the collapse of most stocks of predatory demersal fishes (Koen-Alonso et al. 2010). Greenland halibut is an important predator on northern shrimp in both ecosystems (Parsons 2005a,b, Savenkoff et al. 2006, Dwyer et al. 2010) and is currently the most abundant demersal predatory fish species in both ecosystems.

For the NL ecosystem, we selected an area from the southern Labrador shelf to the northern Grand Bank (North Atlantic Fisheries Organization, NAFO, Div. 2J3KL, Fig. 1), as it represents an ecologically distinct subunit from the southern Grand Bank (NAFO Div. 3NO, Fig. 1; Koen-Alonso et al. 2010).

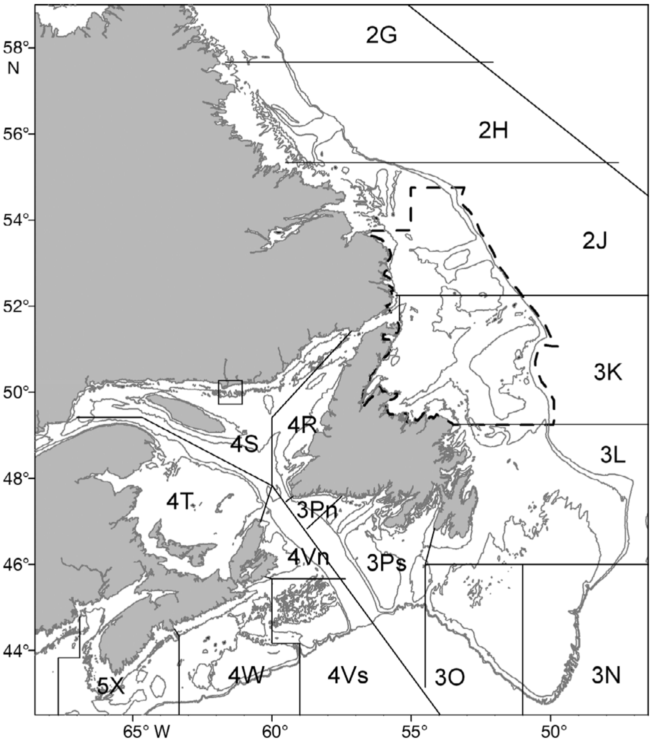

Fig. 1. North Atlantic Fisheries Organization (NAFO) Divisions and dominant bathymetric features on the Newfoundland–Labrador shelf and the Gulf of St. Lawrence, Canada. Shrimp fishing area 6 is bounded by the dashed line. The approximate location of snow crab management area 15 is indicated by the small square

This area also represents the historical distribution of the northern cod stock. Our other study species have broader spatial distributions that include this area. The nGSL ecosystem includes NAFO Div. 3Pn4RS and the deep northwestern portion of Div. 4T (Fig. 1).

Fishery and survey data and indices

Data on commercial landings (kg) for NL were obtained from the Statistics Division, Policy and Economics Branch, Newfoundland Region of Fisheries and Oceans Canada. Landings for nGSL were available from the Division of Fisheries Science and Aquaculture, Maurice Lamontagne Institute (Mont-Joli, Québec).

Catch rates, biological data, and stomach data were obtained from bottom trawl surveys in each ecosystem. Survey data for NL were available from fall (September to December) multispecies depth-stratified surveys conducted by 2 research vessels from southern Labrador to the tail of the Grand Bank (Div. 2J3KLNO, Fig. 1). This survey series began in Div. 2J3K in 1978 and extended to the more southern divisions in 1981. The survey trawl was changed in 1995 from the Engel 145 Hi-Lift Otter Trawl to a Campelen 1800 shrimp trawl (McCallum & Walsh 1996, Walsh & McCallum 1996). The Engel Hi-Lift Otter Trawl is a large-meshed (160–180 mm) trawl fitted with a 28.5 mm codend liner. It has a wingspread of 17 to 22 m and a vertical opening of 4 to 6 m. It has a steel bobbin and rubber roller footgear and was deployed throughout the diel cycle in standard tows of 30 min duration at a tow speed of 3.5 knots. The Campelen 1800 survey trawl is a small-meshed (80, 60, and 44 mm) shrimp trawl that is fitted with a 12.7 mm mesh codend liner. It has an average wingspread ranging from 15 to 18 m and an average vertical opening of 4 to 5 m. It has rockhopper footgear featuring 355 mm diameter rubber disks spaced at 200 mm intervals along the 19.6 m footrope. Survey tows, executed throughout the diel cycle at depths of about 50 to 1500 m, were standardized to 15 min duration at a tow speed of 3.0 knots. A conductivity, temperature, and depth (CTD) sensor was mounted on the trawl head rope, and a SCANMAR acoustic net monitoring system was used to monitor trawl performance at each station. Unsuccessful tows were repeated at the same or alternate stations. The annual coverage of survey strata was variable, with inshore strata and strata deeper than 750 m along the slope edges not surveyed in all years, including the most recent years. Conversion factors between the 2 survey trawls, based on comparative fishing experiments in 1995 and 1996, only exist for a few commercially important fish species, including Atlantic cod and Greenland halibut (Warren 1996, Warren et al. 1997). Catches from the Engel trawl for most species were converted to Campelen equivalents. The Campelen trawl catches more shrimp and crabs than the Engel trawl, such that the survey series for northern shrimp and snow crab begins in 1995. Further details on the treatment of survey data and biological sampling for northern shrimp and snow crab can be found in Orr et al. (2011) and Dawe et al. (2011), respectively.

Data were available for the nGSL from August to early September surveys conducted throughout Div. 3Pn4RS and deep 4T (Fig. 1) during 1990 to 2010. This survey area encompassed the spatial distribution of the Div. 3Pn4RS cod stock in the northern gulf. The survey followed a stratified random sampling plan according to predetermined depth strata. It was conducted from 1990 to 2003 on the CCGS ‘Alfred Needler’ with a 81′/114′ URI (GOV) 44 mm stretched mesh shrimp bottom trawl equipped with a 19 mm codend liner (Bourdages et al. 2003). In 2004, ship and gear changed and the survey was conducted on the CCGS 'Teleost' equipped with a 4-panel shrimp trawl, the Campelen 1800, as described above and by Bourdages et al. (2004). The duration of a standard tow conducted at a speed of 3 knots was 24 min on the 'Needler' and 15 min on the 'Teleost.' The corrections made for differences in catchability between the 'Needler' and the 'Teleost' are described by Bourdages et al. (2007). The 4 species discussed here had higher catchability on the 'Teleost,' and the 'Needler' data (from the URI trawl) were converted into 'Teleost' (with Campelen trawl) equivalents.

Survey methodology in both study areas included determination of total catch number and weight by species. Biological sampling of all commercially important species includes determination of individual size, sex, and maturity. Size was represented by total length (cm) for the fishes and by carapace width (mm) and length (mm) for snow crab and northern shrimp, respectively. For all 4 study species, except nGSL snow crab, biomass indices were generated by areal expansion methods, for various population components, including the exploitable biomass. More detailed information is available elsewhere regarding collection and treatment of survey data for NL cod (Brattey et al. 2010), nGSL cod (Fréchet et al. 2009), Greenland halibut (Bourdages et al. 2010, Healey 2011), northern shrimp (Savard & Bourdages 2010, Orr et al. 2011), and NL snow crab (Dawe et al. 2011).

In some cases where survey data series were lacking (nGSL snow crab) or limited (NL northern shrimp and snow crab), we used longer time series of fishery catch per unit effort (CPUE), as an alternate exploitable biomass index. Snow crab CPUE (kg [trap haul]$^{-1}$) was estimated from commercial landings (kg) and fishing effort (number of trap hauls) obtained from vessel logbooks. These data, from NL, were compiled by the Statistics Division, Policy and Economics Branch, Newfoundland Region of Fisheries and Oceans Canada. The longest time series of CPUE data (from NAFO Div. 3L, Fig. 1) was selected to illustrate trends in snow crab biomass at NL. This CPUE series is unstandardized in that it does not account for variation in fishing practices (e.g. soak time and mesh size). A standardized CPUE series was obtained for Management Area 15 to illustrate trends in nGSL snow crab (Fig. 1). Northern shrimp standardized CPUE (kg h^{-1}) from Shrimp Fishing Area 6 at NL (Fig. 1) was selected for our purpose, as that area includes Div. 3K and southern Div. 2J, representing the central portion of our NL study area.

Stomach collection, examination, and diet analysis

Length-stratified sampling of stomachs from both cod and Greenland halibut was conducted during the NL fall bottom trawl surveys. In early years, stomachs were fixed and preserved using formaldehyde in seawater solution, but after 1995, they were frozen onboard; stomach contents of both predators were later examined in detail in the laboratory. Data from detailed stomach analysis for cod were available for 1978 to 1996 and 2008 to 2009. Further details on methods of collecting and examining Atlantic cod stomachs during 1978 to 1996 can be found in Lilly (1991) and Lilly et al. (2000). Data from detailed examination of Greenland halibut stomachs were available for the period 1978 to 2003, but no data were collected for 5 years within that period (1980, 1989, 1990, 1994, and 2002). Further details on methods of collecting and examining Greenland halibut stomachs can be found in Dwyer et al. (2010).

In years when stomachs were not taken for detailed examination, routine onboard sampling included quickly opening stomachs and identifying the dominant prey type (qualitative stomach contents). To fill in the large gap in the cod detailed diet series (1997 to 2008) and the missing years in the Greenland halibut series, the diet was reconstructed by combining the frequency of occurrence of prey types as dominant prey, by weight, in a stomach (based on qualitative stomach contents), and its mean weight when they were a dominant prey type in a stomach (based on detailed stomach analysis). The basic rationale for this approach is described in ICES (2008). The more continuous time series of modeled diets will be used in describing trends for NL predators. Although there are some differences in relative contribution by prey categories between stomach sampling methods, the major trends in diet composition were similar between methods (M. Koen-Alonso unpubl. data).

In the nGSL, stomachs of both predator species were excised and frozen at sea. Atlantic cod stomachs were collected according to a length-stratified design during the annual August survey. Up to 3 stomachs were collected from each 10 cm length class in each set in 1993 and 1994. From 1995 until 2005, 3 stomachs were collected from each 3 cm length class per set. This was changed to 2 stomachs per 3 cm length class in 2006 to 2009. It is assumed, for both areas, that predator diets at the time of the surveys are broadly representative of diets throughout the year.

The stomach sampling protocol for nGSL Greenland halibut was the same as for cod in 1993 to 1996. In 1997, up to 3 Greenland halibut stomachs were collected for each 3 cm length class for each set in Div. 3Pn4R, but only for odd set numbers in Div. 4S. In 1998, stomachs were collected from 1 male and 1 female for each 1 cm length class (2 cm length class in 1999) for each odd-numbered set for the entire survey area. No Greenland halibut stomachs were collected in 2000. In 2001, stomachs were collected from 1 male and 1 female for each 3 cm length class for each odd-numbered set, except in strata 801 and 812 to 814 in Esquiman Channel, where all sets were sampled. The same protocol was followed in 2002 to 2009, but all sets from the estuary (strata 411 to 414) were sampled. Starting in 2008, 2 males and 2 females were sampled per 3 cm length class above 49.1 cm, if available, to increase sample size for large fish.

Detailed examination of stomachs in both ecosystems involved determination of the total mass of the contents of each stomach. Prey composition was determined to the lowest taxonomic level possible, and weight of each prey type was determined. Analysis of the diet composition involved determining the percentage by mass that each prey type contributed to the total diet. The raw length-stratified data were summarized to facilitate comparison of annual trends in prey composition between the detailed nGSL series (1993 to 2009) and the reconstructed NL series (1978 to 2009). In order to facilitate comparisons and identify main patterns among species and ecosystems, prey composition was summarized into 5 primary categories; capelin *Mallotus villosus*, other fishes, shrimps, crabs, and other invertebrates.

Spatial interactions

Spatial interactions between predators and their crustacean prey were analyzed by first identifying, based on the literature and our own data, the size groups of each fish predator and crustacean prey that are most important in each pairwise predator–prey interaction (Table 1). No information was available regarding sizes of Greenland halibut that may be capable of preying upon crabs, because crabs are only very rarely found in Greenland halibut stomachs. Therefore, the same size groups identified for Atlantic cod–snow crab predation were used to explore spatial interactions of snow crab with potential Greenland halibut predators. Survey catches (numbers) of each predator and prey group at each set location were used to calculate the global index of co-location (GIC, Bez & Rivoirard 2000, Wieland et al. 2007) for each predator–prey pair. This method estimates the center of gravity (CG) and inertia (extent of horizontal distribution in the form of an ellipse around the CG) for each population to determine the overlap between 2 populations. The GIC can range from 0, reflecting no overlap between populations, to 1, indicating fully sympatric populations.

Table 1. *Gadus morhua* and *Reinhardtius hippoglossoides*. Size relationships in the predation by Atlantic cod and Greenland (G.) halibut on crabs and shrimp

Predator	Size (cm)	Prey	Source
Cod	(50–80)	Crab <50 mm	Lilly (1984, 1991), Chabot et al. (2008)
	(20–65)	Shrimp all	Lilly (1984, 1991)
G. halibut	(50–80)	Crab <50 mm	Dwyer et al. (2010)
	(20–50)	Shrimp all	Dwyer et al. (2010)

RESULTS

Trends in fisheries

Trends in commercial landings (Fig. 2) imply that the timing of the final collapse of Atlantic cod stocks was similar between NL and nGSL. Landings declined precipitously from 269 000 t in 1988 at NL and 106 000 t in 1983 at nGSL to 40 956 and 28 000 t, respectively, in 1992. A moratorium on commercial fishing was imposed in NL in 1992 and in the nGSL in 1994. Since 1995, cod landings have remained below 9000 t at NL and 7000 t at nGSL. While there has been some inshore commercial and recreational cod fishing at NL since the moratorium was imposed, no directed offshore commercial cod fishery has remained at NL. However, the nGSL commercial cod fishery was re-opened during 1997 to 2002 and 2004 to 2010.

While the timing of this cod fishery collapse was comparable between areas, its magnitude was much greater at NL than at nGSL. The NL fishery collapsed (in 2 phases) from a historical level of about half a million tons during the 1960s (Fig. 2). In contrast, the nGSL fishery collapsed from a historically high level of about 100 000 t.

While the collapse in the cod fishery typifies similar collapses in most other groundfish stocks, Greenland halibut represents a notable exception in both areas

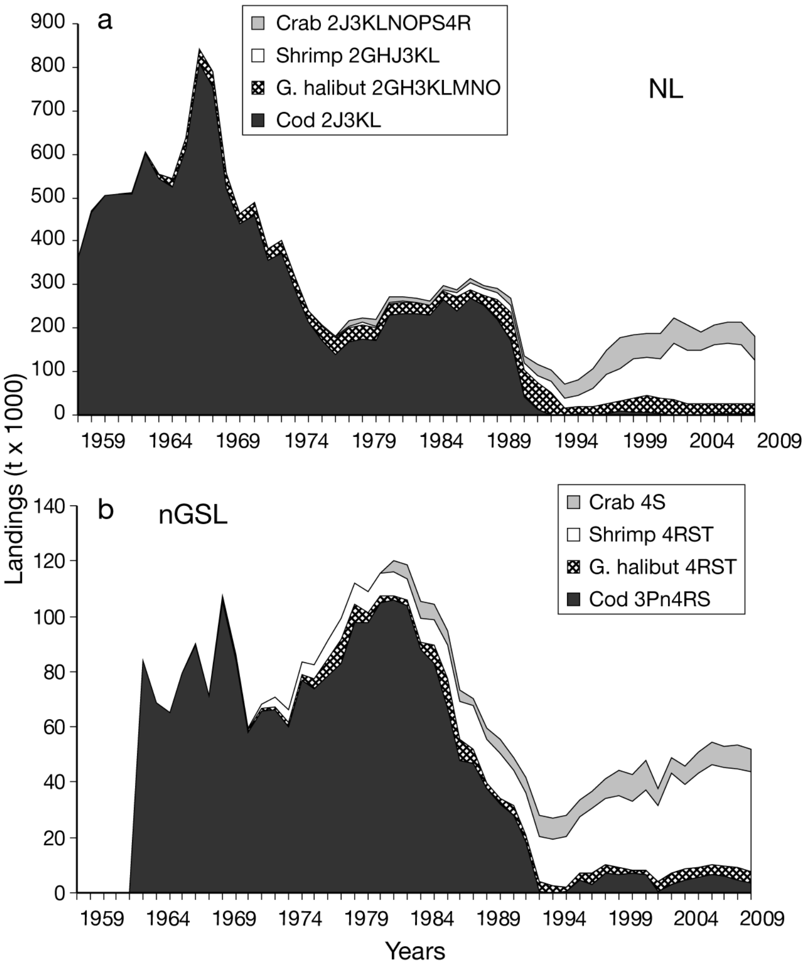

Fig. 2. Annual trends in landings by stock area (stacked in graphs) of snow crab, northern shrimp, Greenland G. halibut, and Atlantic cod (a) on the Newfoundland–Labrador shelf (NL) and (b) in the northern Gulf of St. Lawrence (nGSL)

(Fig. 2). Landings at NL increased from very low levels (<5000 t) in the early 1960s, varying at a higher level of about 20 000 to 70 000 t since 1990. At nGSL, Greenland halibut landings have varied between 1000 and 4000 t in most years since the late 1970s.

Northern shrimp landings (Fig. 2) at NL increased from less than 5000 t prior to the mid-1980s to peak at 138 000 t in 2007, before decreasing in 2009. Northern shrimp landings at nGSL increased from less than 10 000 t sprior to the mid-1980s to about 40 000 t in recent years.

Snow crab landings (Fig. 2) at NL increased from <15 000 t during the 1980s to peak at 69 000 t in 1999. They have since varied between 44 000 and 59000 t. Snow crab landings at nGSL varied between 3000 and 6000 t during 1983 to 1993 and between 6000 and 10 000 t during 1994 to 2010 (Fig. 2).

Trends in biomass

Annual changes in biomass are uncertain due to sampling variability, particularly due to annual changes in survey trawl efficiency. However, some general trends are evident and consistent with fishery trends. For example, survey biomass trends for NL show that the northern cod biomass collapsed during the early 1990s from a level of about 1.0 to 1.5 Mt in the 1980s to only about 7000 t in 1993. Meanwhile, Greenland halibut biomass has varied without any clear trend since 1978. Northern shrimp and snow crab biomass indices are available only for the period since the northern cod collapse (Fig. 3). Shrimp biomass increased from 1999 to 2006, as reflected by more than doubling of annual biomass indices despite increasing fishery removals (Fig. 2), but then apparently decreased to 2009. Snow crab biomass was highest during 1996 to 1998 and has since varied at a lower level (Fig. 3).

The relatively short survey series for groundfish from nGSL (Fig. 3) does not capture the final collapse of the Div. 3Pn4RS cod stock that is reflected in the landings trend (Fig. 1). Cod biomass estimates generally remained below 20 000 t during 1978 to 2002 but were slightly higher during more recent years (Fig. 3). Greenland halibut biomass estimates have fluctuated greatly around an overall level of about 80 000 to 100 000 t. Northern shrimp biomass showed a similar general trend to that at NL, increasing by about a factor of 4 from the early 1990s to 2004/2005, despite increasing fishery removals (Fig. 2), but then apparently decreased to 2010.

Because of the unavailability of a reliable nGSL survey series for snow crab biomass and the short time series of survey biomass for NL crustaceans, longer time series of fishery CPUE, for both snow crab (NL and nGSL) and northern shrimp (NL), were examined in relation to predator biomass trends (Fig. 4). Northern shrimp CPUE at NL was highly variable during the final years of the cod collapse (1989 to 1994), but then increased by about 60% to 2008. NL shrimp CPUE decreased in 2009 (Fig. 4), as did shrimp survey biomass (Fig. 3). Snow crab CPUE trends displayed fairly regular oscillations over time in both systems (Fig. 4). While these 2 CPUE series were of differing lengths, it is clear that these oscillations were maintained at NL

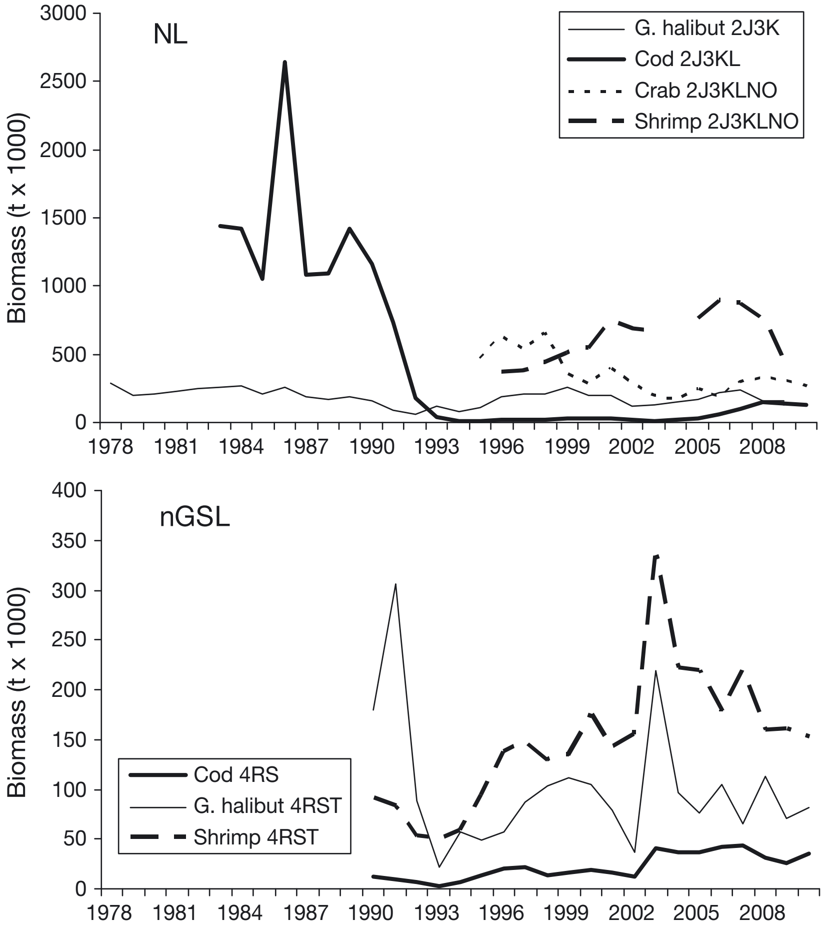

Fig. 3. Annual trends in survey biomass indices of snow crab (Newfoundland–Labrador shelf, NL, only, scaled up by an order of magnitude), northern shrimp, Greenland G. halibut, and Atlantic cod on (a) the NL and (b) the northern Gulf of St. Lawrence (nGSL)

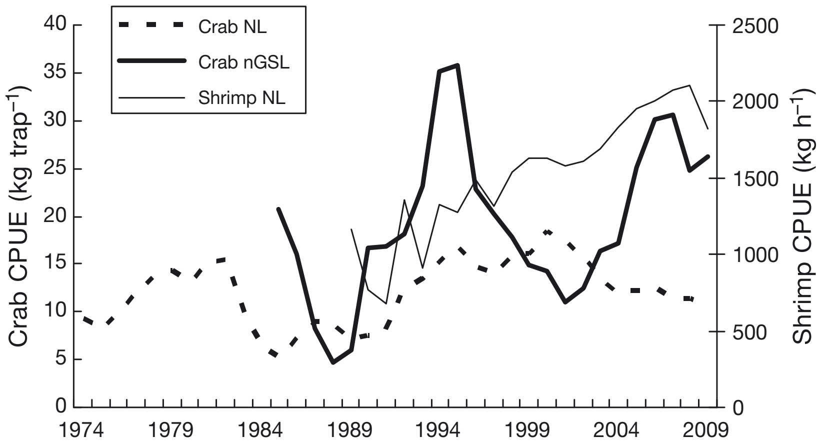

Fig. 4. *Chionoecetes opilio* and *Pandalus borealis*. Annual trends in catch per unit effort (CPUE) of snow crab from NAFO Div. 3L and northern shrimp from shrimp fishing area 6 on the Newfoundland–Labrador shelf (NL) and of snow crab from management area 15 in the northern Gulf of St. Lawrence (nGSL)

throughout the period of the final cod collapse. The trends showed a peak in CPUE at NL in 1982, prior to the final collapse of cod, that was generally of comparable magnitude to post-collapse peaks. The nGSL snow crab CPUE declined sharply during 1985 to 1988 and then continued to oscillate regularly while the biomass of cod remained at relatively low levels and that of Greenland halibut varied with no clear trend.

Predator–prey spatial interactions

The spatial distribution of each size-specific predator and prey pair is illustrated for 2009, as an example (Fig. 5). The location of the CG for each predator and prey group (Fig. 6) generally reflects the more detailed survey distributions. For example, the CGs for nGSL cod reflect a distribution that is concentrated close to the west coast of Newfoundland, well east of the CGs of their shrimp prey, mostly in the western portion of the northern gulf, as seen in the detailed 2009 distributions (Fig. 5). It is uncertain to what extent annual variation in the location of the CG reflects shifts in the geographic distribution of each size-specific predator and prey species, independent of changes in horizontal dispersion (Fig. 6), versus random sampling variability. For example, the annual CGs for shrimp in both areas and for both size groups of Greenland halibut in nGSL are tightly clustered, reflecting virtually no annual shifts in the distributions. In contrast, large predators of both species show highly variable locations of their CGs at NL (Fig. 6), reflecting low abundance and patchy distributions of populations of large fish that are not well sampled by the surveys. Annual variation in location of CGs in the nGSL was more pronounced for snow crab than for any of the other 3 species, likely reflecting low and annually variable capture efficiency of small crabs by the survey trawl.

Differences in GIC values between NL and nGSL (Fig. 7) must be interpreted with caution. The higher values at NL,

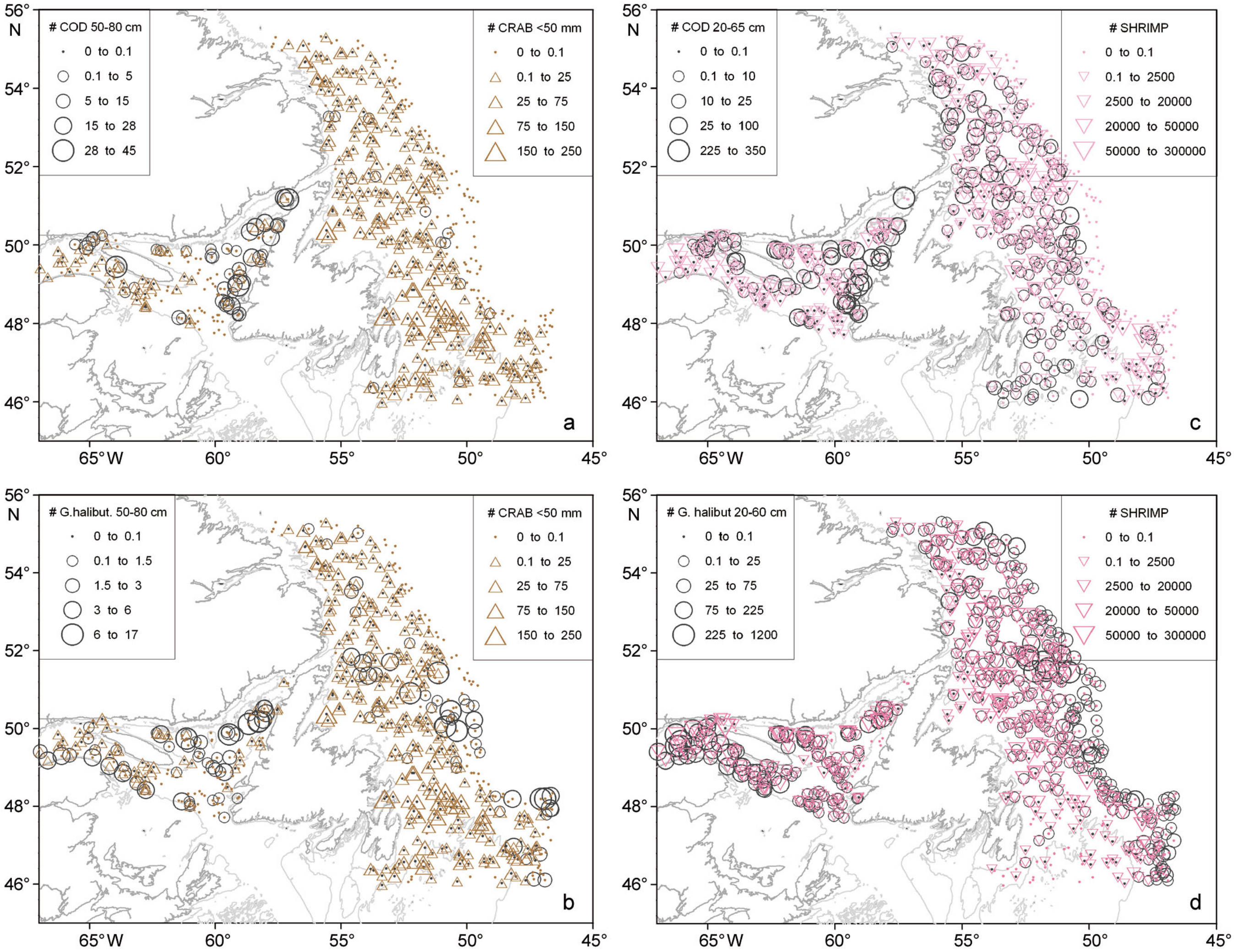

Fig. 5. Distribution of size-specific predator–prey pairs involving (a,c) Atlantic cod, (b,d) Greenland (G.) halibut, (a,b) snow crab and (c,d) northern shrimp from surveys on the Newfoundland–Labrador shelf and in the northern Gulf of St. Lawrence. Size of symbols represents catch numbers per survey set within species

especially for shrimp and its predators, may largely be an artifact of broader and more uniformly distributed populations at NL than at nGSL.

Examination of the raw survey catches for our 2009 example year (Fig. 5) shows that northern shrimp overlap more extensively (and evenly) with cod at NL than at nGSL, where cod are most concentrated in the eastern portion of the nGSL, and partially avoid the deep channels, possibly because of hypoxia (Chabot 2004). By contrast, northern shrimp overlap with Greenland halibut more extensively at nGSL than at NL, where the Greenland halibut distribution is concentrated along the deep slope, overlapping with the eastern portion of the shrimp distribution. The lower GIC values for shrimp–Greenland halibut at nGSL than at NL is likely an artifact of the existence of 4 major concentrations of nGSL adult shrimp, with likely very little movement of adults across concentrations (DFO 2012). Notwithstanding these concerns, both predators overlap extensively with at least a portion of the northern shrimp distribution in both areas. Therefore, it is appropriate to make only relative comparisons of GIC between areas.

General comparisons of GIC within areas are appropriate. For example, the GIC for crab and its potential predators at NL was generally lower and more variable than for shrimp and its predators (Fig. 7). At nGSL, the cod–crab GIC was low throughout the short 2004 to 2010 time series, fluctuating between about 0.4 and 0.7. The closest pairwise interaction at nGSL was between crab and Green-

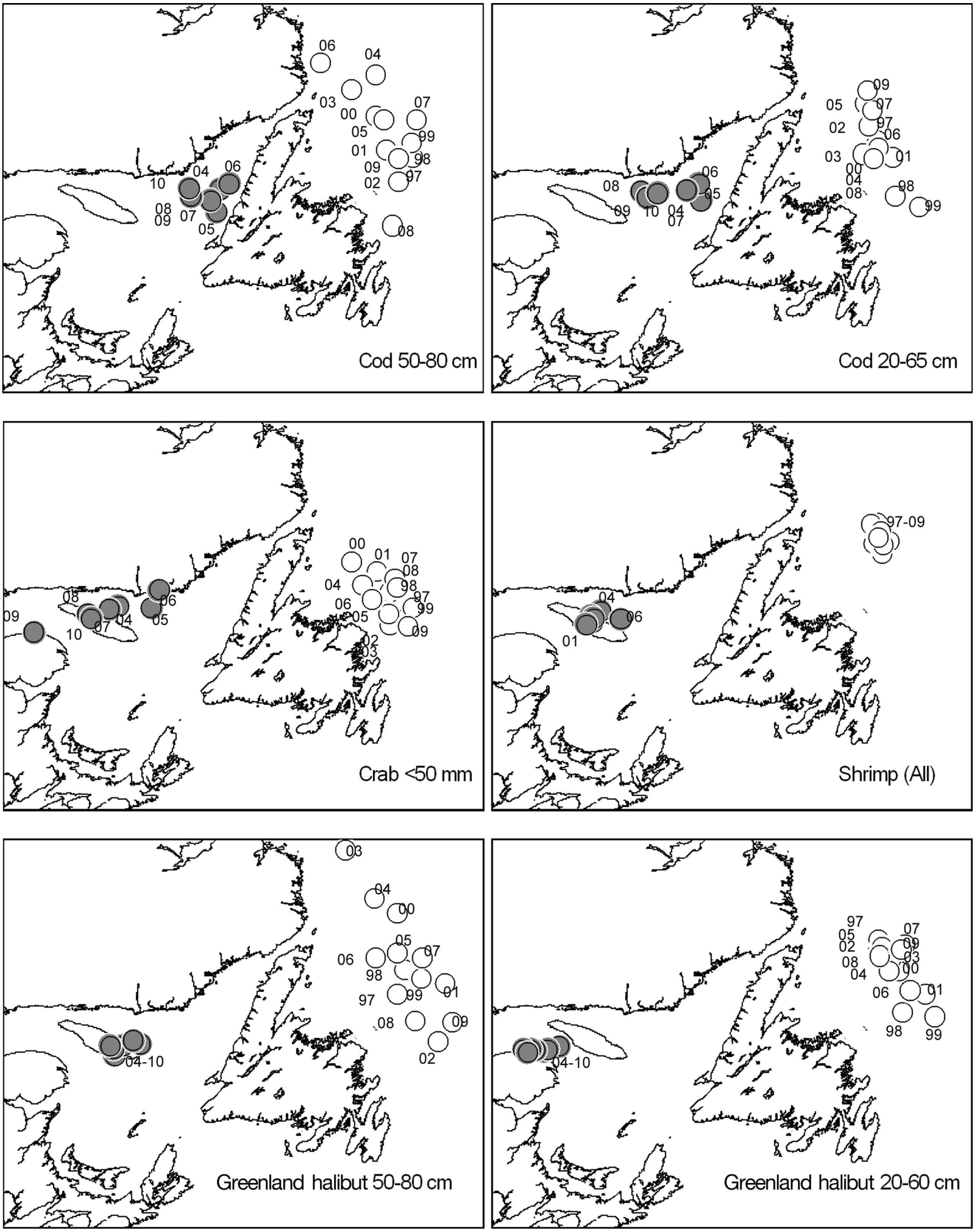

Fig. 6. Yearly variation in location of the center of gravity (CG; numbers indicate years) on the Newfoundland–Labrador shelf (white circles) and the northern Gulf of St. Lawrence nGSL (grey circles) for size-specific predators and prey relative to predation on snow crab (left column) and on northern shrimp (right column)

land halibut, with the GIC exceeding 0.9 in all but 1 year (Fig. 7). This close spatial interaction, combined with a lack of crab in Greenland halibut diets, indicates that large Greenland halibut select against available small snow crab as prey.

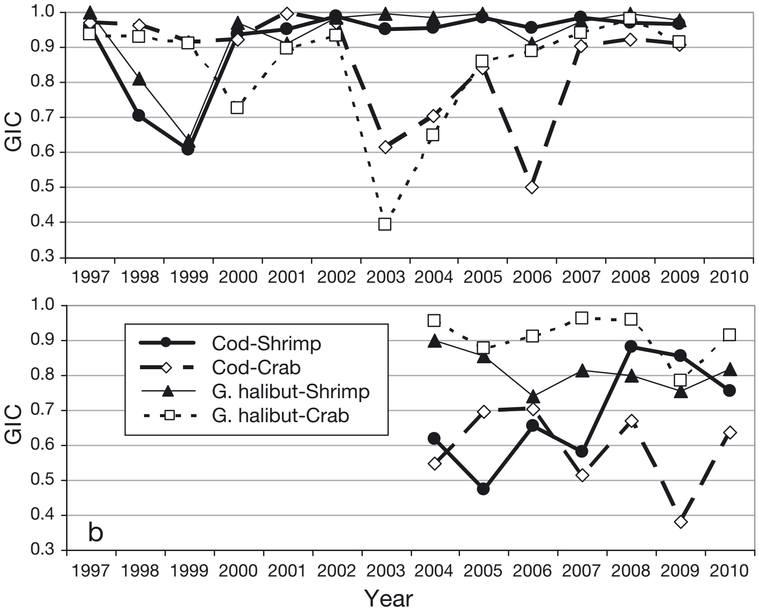

Fig. 7. Annual trends in the global index of co-location (GIC) for each size-specific predator–prey pair on (a) the Newfoundland–Labrador shelf and (b) the northern Gulf of St. Lawrence. Size groups are as described in Table 1

Annual trends in predator diets

Atlantic cod

Capelin represented the predominant prey type of cod prior to the early 1990s at NL (Fig. 8) and during the first 2 yr of the limited time series at nGSL. The capelin contribution to the cod diet dropped sharply at both NL and nGSL from about 60% in 1993 to about 10% in 1995 and has since remained low. The NL cod diet became heavily dependent on shrimp at NL following the decline in capelin prey (Fig. 8), with the shrimp contribution increasing to about 50% in 1994 and has since remained high. In contrast, at nGSL, other fish prey remained an important component of the cod diet following the drop in capelin prey, varying between about 20 and 55% (Fig. 8). Meanwhile, the shrimp contribution changed little and remained low, seldom exceeding 20%. The shrimp contribution to the nGSL cod diet increased in 2008 and 2009 as the contribution of other fish decreased (Fig. 8). This coincided with an increase in spatial interaction between shrimp and cod (Fig. 7), due to a westward shift in the cod distribution (Fig. 6), suggesting that cod may actively seek shrimp as prey only when preferred fish prey becomes unavailable.

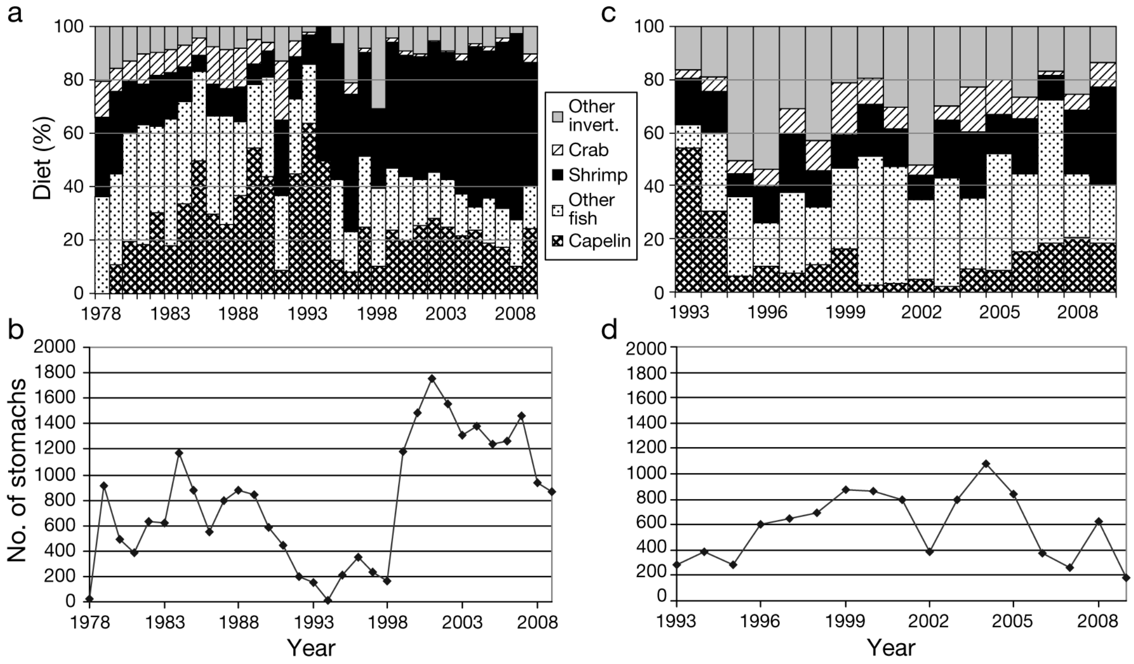

Fig. 8. *Gadus morhua*. (a,c) Annual trends in percentage contribution by weight for each of 5 prey categories to the diet of Atlantic cod, with (b,d) number of stomachs examined from (a,b) the Newfoundland–Labrador shelf (reconstructed diet) and (c,d) the northern Gulf of St. Lawrence (detailed diet)

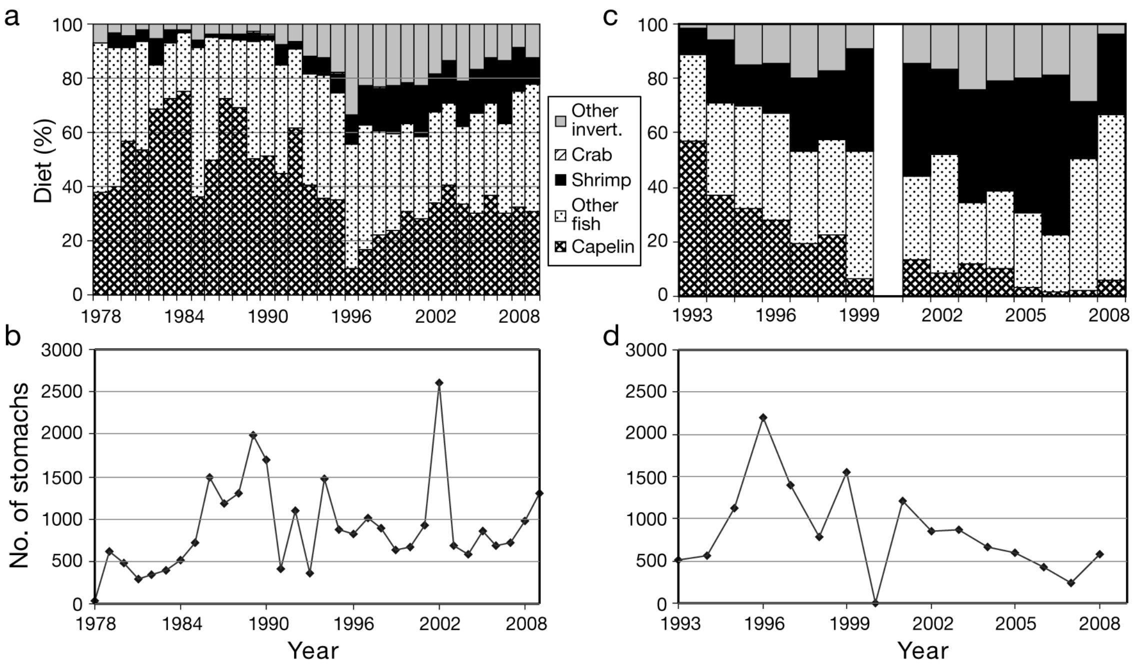

Fig. 9. *Reinhardtius hippoglossoides.* (a,c) Annual trends in percentage contribution by weight for each of 5 prey categories to the diet of Greenland halibut, with (b,d) number of stomachs examined from (a,b) the Newfoundland–Labrador shelf (reconstructed diet) and (c,d) the northern Gulf of St. Lawrence (detailed diet)

The crab contribution to the NL cod diet was generally below 15% during 1978 to 1990, decreased to 0% in 1994, and has since remained virtually absent (Fig. 8). The occurrence of crab in the nGSL cod diet showed no clear trend, ranging between 2 and 20%. This difference between systems in the importance of crab in cod diets is undoubtedly due to greater prevalence of large (>50 cm) cod at nGSL than at NL (Fig. 5). The contribution by other invertebrates was much more important at nGSL than at NL. The importance of other invertebrates since 1995 varied without trend at NL, but declined at nGSL.

Greenland halibut

The contribution of capelin to the Greenland halibut diet decreased substantially in the early 1990s in both systems, as it did in the cod diet (Fig. 9). However, the drop in capelin was not as sharp in the Greenland halibut diet as it was in the cod diet. The capelin contribution to the NL Greenland halibut diet dropped sharply in 1996, 1 yr later than its sharp drop in the cod diet (Fig. 8). It increased gradually to about 40% in 2003 (Fig. 9) and has since varied little. Capelin also declined greatly at nGSL in the 1990s (Fig. 9). Capelin in the nGSL Greenland halibut diet declined from 57% in 1993 to 7% in 1999, and has since remained low.

Greenland halibut did not rely as heavily on shrimp as did Atlantic cod at NL following the decline in the capelin contribution around 1995, with other fish remaining an important component of the diet. A reduction in the NL capelin component was compensated for by increases in shrimp and other invertebrates (Fig. 9).

At nGSL (as at NL) other fish remained relatively important in the Greenland halibut diet as capelin declined, ranging between 21 and 61% and the decline in the capelin component was compensated for by increases in shrimp and other invertebrates. However, the diet became more highly dependent on shrimp than did the diet of NL Greenland halibut (Fig. 9) or of nGSL cod (Fig. 8). At nGSL, shrimp increased steadily from 10% in 1993 to 59% in 2006. Snow crab was virtually absent from the Greenland halibut diet in both areas, at 0% in most years and never achieving 1% (Fig. 9).

DISCUSSION

Effects of predation on crustacean populations

Our results suggest that, at the present time, snow crab populations are not controlled by top-down effects of predation by these 2 fish species. Crabs were virtually absent from the Greenland halibut diet in both areas. Crabs (including snow crab) were never a major component of the Atlantic cod diet in either area, and since the groundfish collapse, they have been virtually absent from the NL cod diet. This is no doubt a result of the very low abundance of large cod at NL in recent years due to the much reduced abundance of older (>age 5), larger (>about 50 cm) fish (DFO 2007). It is reasonable to assume that prior to the collapse, during the 1960s and 1970s, predation by large cod populations may have played some role in limiting snow crab abundance. However, snow crab catch rates have maintained regular oscillations in abundance throughout the study period in both systems, including before the final collapse at NL, which is unexplained by the hypothesis of strong top-down control proposed by Boudreau et al. (2011). Other possible controlling mechanisms include density-dependent processes that influence egg production or settlement success (Conan et al. 1996, Sainte-Marie et al. 1996, Sainte-Marie & Lafrance 2002, Caddy et al. 2005). The most convincing recent evidence, across multiple ecosystems, is that that snow crab populations are controlled by bottom-up processes associated with temperature (Orensanz et al. 2004, Dawe et al. 2008, Marcello et al. 2012, this volume)

It seems more likely that northern shrimp, rather than snow crab, populations may be regulated, at least in part, by predation pressure. Although our results were inconclusive because our time series of biomass indices are too short, survey and fishery CPUE trends suggest that northern shrimp biomass in both areas increased following the final groundfish collapse. Lilly et al. (2000) concluded that an initial increase in NL shrimp during the early to mid-1980s was not related to changes in cod, but that a larger increase in shrimp biomass in the 1990s was, at least in part, related to the collapse of cod. They noted that coarse estimates of consumption suggested that consumption of shrimp by cod in the 1980s was lower than fishery removals in the late 1990s, and more than an order of magnitude lower than estimated biomass levels in the late 1990s. They further concluded that consumption of shrimp by cod at NL was very low after 1991 and that this reduction in consumption contributed to the increase in shrimp biomass, which was a function of increased shrimp density as well as area of distribution. They suggested that the fishery has become a more important source of shrimp mortality than predation by cod since the 1990s, when shrimp biomass increased. However, they recognized that total removals by all predators would be higher than that by cod alone.

Besides Atlantic cod and Greenland halibut, redfish *Sebastes mentella* represents another important predator of northern shrimp (Parsons 2005a,b, Savenkoff et al. 2006). No data are available on redfish diet from our NL study area, but the population trajectory of NL redfish is well-represented by that of northern cod (Koen-Alonso et al. 2010). A study in the nGSL showed that predation has been by far the main source of northern shrimp mortality from the mid-1980s to the early 2000s (Savenkoff et al. 2006). Over this time period, Greenland halibut replaced cod and redfish as the main shrimp predator. Total consumption of northern shrimp decreased from the mid-1980s to the mid-1990s and was believed to be playing an important role in controlling the shrimp population in that area. Consumption of shrimp increased in the early 2000s, but remained below the mid-1980s level. It is therefore likely that predation in the early 2000s (primarily by Greenland halibut) continued to play an important role in regulating shrimp abundance. This seems especially likely given that in our study, nGSL northern shrimp represented about 40 % of shrimp (all species combined) in the cod diet, but about 80 % of the shrimp in the Greenland halibut diet. This generally agrees with results of studies across multiple ecosystems that trends in shrimp abundance are, at least in part, related to changes in predation pressure (Worm & Myers 2003).

Regardless of the role of predation in affecting northern shrimp biomass up to the early 2000s, the apparent recent declines in biomass in both areas cannot be attributed primarily to effects of predation. Northern shrimp biomass indices declined by half from 2006 to 2009 at NL and by about one-third from 2004 to 2010 at nGSL. The changes in biomass of cod and Greenland halibut during this recent period are uncertain and marginal in both systems.

There is growing evidence across multiple ecosystems that northern shrimp populations are affected by bottom-up effects associated with temperature and primary productivity (Ouellet et al. 2007, Koeller et al. 2009). Our results further support the idea that there was a major transition in both ecosystems associated with the collapse of the demersal fish community, where northern shrimp abundance appeared to have increased to a higher level as a consequence of release from predation pressure. However, it is unlikely that any population is regulated by a single process, and it is reasonable to assume that ocean climate continues to play a role in affecting shrimp abundance, as the recent drop in survival during early life in many areas of nGSL suggest (DFO 2012). A recent study at West Greenland found that both ocean climate variability and predation by Greenland halibut were significant determinants of northern shrimp abundance (Wieland & Siegstad 2012, this volume).

Comparison across Northwest Atlantic ecosystems

We found that both predators had ready access to both crustacean prey species throughout the time series. In general, we conclude that our trends in diets reflect overall changes in relative availability of forage species in both systems, since both predators are considered to be opportunistic (Lilly 1991, Hanson & Chouinard 2002, Dwyer et al. 2010), and in the case of Greenland halibut in NL, positive correlations between diet and prey trajectories have actually been found (Dwyer et al. 2010). The sharp change in prey composition in both systems was due to both a decrease in capelin and increase in shrimp availability. Our data suggest that shrimp consumption is modulated both by shrimp availability and the availability of fish prey. Hence the pronounced shift from capelin to shrimp as principal prey type for NL cod, but not for nGSL cod, could be the result of a greater availability of alternate fish prey in nGSL, where increases in the proportion of Atlantic herring *Clupea harengus* and pleuronectids were observed in the cod diet. Conversely, NL Greenland halibut increased predation upon other fish (especially grenadiers) and bathypelagic gonatid squid (Dwyer et al. 2010) as capelin availability declined, whereas nGSL Greenland halibut relied on shrimp. This suggests that cod and Greenland halibut are not truly opportunistic, consuming shrimp only when other more suitable prey is not available. This could be due in part to the lower energy content of shrimp (approximately 5 kJ g^{-1}, Lawson et al. 1998, D. Chabot unpublished data), compared with capelin (4 to 5 kJ g^{-1} in spring and early summer, 8 to 10 kJ g^{-1} in autumn and winter, Montevecchi & Piatt 1984, Perez 1994, Lawson et al. 1998, Anthony et al. 2000). This difference in energy density is likely amplified by the fact that gastric evacuation rates can be slower for prey with a carapace that resists digestion (Jobling 1987, dos Santos & Jobling 1992, Bromley 1994, Andersen 2001, Couturier 2003).

Although there may be some concerns with relying upon reconstructed diets for the NL predators, when detailed stomachs and reconstructed diets based on similar principles to the ones used here have been compared, the differences between methods have been minor for the most part; both approaches provide similar overall pictures of the diet and its major changes over time (Dwyer et al. 2010). Particularly convincing for NL cod is that the detailed stomach analysis data, available for 1978 to 1996, clearly showed the sharp transition during 1994 to 1996 from capelin to shrimp as principal prey type that was also evident in the qualitative data. These datasets also agreed that shrimp remained the principal prey type in the 2 most recent years. Nonetheless, care must be taken when analyzing these types of results to avoid over-interpreting minor variations in diet composition that a coarse-grain approach like this should not be expected to reflect with high accuracy.

Overall, the major trends we described in predator diets (shift from capelin to shrimp prey since 1995) would be expected to reflect a transition common to both ecosystems. The increase in shrimp in both systems is supported by recent trends in survey and fishery biomass indices. The decrease in capelin abundance at NL is supported by results of hydroacoustic surveys (DFO 2010, 2011a) and mass balance modeling (Bundy et al. 2009).

Support for the decline in nGSL capelin is unavailable, due to scanty and conflicting diet-independent information. Bundy et al. (2009) concluded that there has been little change in capelin abundance at nGSL based on mass balance modeling. By contrast, bottom trawl survey data indicate an increase in capelin dispersion and catch rate since 1990 in the nGSL as well as in the sGSL (DFO 2011b). It has been cautioned, however, that these increases may be due to an increase in the depth of capelin distribution, as occurred at NL during the early 1990s (DFO 2010), and consequent increased availability to the survey bottom trawl (McQuinn 2009, Swain & Mohn 2012). Also, capelin has not featured prominently in the diet of sGSL cod, where the principal prey shifted from euphausiids during 1959 to 1980 to herring *Clupea harengus* during 1987 to 2000 (Hanson & Chouinard 2002). We conclude, based on the great similarity that we found in annual trends in capelin prevalence within our predator diets between systems, that capelin abundance decreased in both systems in the mid-1990s and has since remained low. This is further supported by great similarities between these systems in trends in capelin size and other biological and behavioral characteristics (DFO 2011b).

Trends in our study areas support the conclusion of Bundy et al. (2009) that the most northern NL and nGSL ecosystems are similar in form and function, whereas the shallow sGSL system has closer affinity to the most southern ESS ecosystem. Whereas planktivorous forage fishes remain in low abundance in the northern systems, they have recently increased in both the sGSL (Hanson & Chouinard 2002, Bundy et al. 2009) and on the ESS (Frank et al. 2006, Bundy et al. 2009). Bundy et al. (2009) concluded that both the NL and nGSL ecosystems have experienced similar recent changes, with common decreases in many ecosystem parameters including total production, biomass, consumption, and total system throughput.

Current theory holds that depletion of apex predators in subarctic ecosystems has resulted in trophic cascades throughout the ecosystem (Frank et al. 2005), the most immediate effect being an increase in the primary forage species, as appeared to occur on the ESS (Frank et al. 2006). However, in the most northern Northwest Atlantic ecosystems (NL and nGSL), it is clear (especially for NL) that depletion of predators did not result in an increased abundance of the primary forage species, but rather that capelin declined as part of a collapse of the entire finfish community. In these most northern ecosystems, it could be argued that the increase in northern shrimp abundance represented such a cascading effect. However, even shrimp abundance is not simply the result of top-down effects only. Recent declines in shrimp stocks, without any noticeable change in predator abundance, suggest that changes in ocean climate conditions are also affecting shrimp productivity. In any case, these declines do not appear to be linked with strong rebuilding of fish stocks, casting doubts about the trophic cascade hypothesis for these northern ecosystems.

The ultimate effect of the replacement of a historical primary forage fish (capelin) in the ecosystem by crustaceans (shrimp) remains unclear, but unavailability of suitable prey (capelin) has been proposed as one of many factors that may be contributing to high natural mortality and failure of NL cod to recover (Rose & O'Driscoll 2002, Lilly 2008, DFO 2009, 2011a). The switch from a pelagic planktivorous fish to an omnivorous crustacean as primary prey type may imply a change in the pelagic–demersal coupling within the ecosystem. Conceivably, an increased portion of the ecosystem energy flow might go directly from surface to the bottom, to benefit the benthic community, rather than be channeled through the pelagic domain into traditionally dominant groundfish species.

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Contribution to the Theme Section 'Effects of climate and predation on subarctic crustacean populations'

Effects of temperature and gadid predation on snow crab recruitment: comparisons between the Bering Sea and Atlantic Canada

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ABSTRACT: Snow crabs *Chionoecetes opilio* are found in many subarctic ecosystems, where they are important components of marine food webs and support large commercial fisheries. Snow crab abundance is highly variable, but the causes of large changes in year-class strength are poorly known. We used a regression approach to examine the effects of snow crab spawning stock biomass, bottom water temperature, cold area or sea ice extent, and predation by Pacific cod *Gadus macrocephalus* or Atlantic cod *G. morhua* on snow crab recruitment in each of 3 ecosystems: the eastern Bering Sea, the Newfoundland-Labrador Shelf, and the southern Gulf of St. Lawrence. Comparing results across systems showed that cold ocean conditions during early life history were associated with increased snow crab recruitment or recruitment indices in all 3 ecosystems. However, we found no consistent evidence that spawning stock or gadid biomasses were significantly related to subsequent snow crab recruitment. Our results underscore the value of comparing multiple ecosystems and demonstrate the importance of ocean conditions in driving variability in snow crab populations.

KEY WORDS: Snow crab · Recruitment · Environment · Predation · Spawning stock biomass · Eastern Bering Sea · Newfoundland-Labrador Shelf · Southern Gulf of St. Lawrence

INTRODUCTION

Snow crabs *Chionoecetes opilio* are found in shelf and slope areas of several subarctic ecosystems in the Pacific and Atlantic Oceans (Sainte-Marie et al. 2008). They serve an important trophic role in these systems and support large male-only commercial fisheries. Rational management of these important resources requires a sound understanding of factors that affect their population dynamics.

Snow crab abundance can be highly variable and is believed to be driven largely by changes in the strength of incoming year classes (Zheng & Kruse 2006). However, the drivers of fluctuations in production and survival of these early life history stages, before snow crab are first detected by survey gear, are poorly known. Spawning stock biomass influences production levels (Zheng & Kruse 2003, 2006) but relationships with recruitment are unclear because of large variations in spawner to recruit survival. Cannibalism on newly settled juveniles by previously settled year classes may influence survival and contribute to cyclical recruitment (Sainte-Marie et al. 1996, Sainte-Marie & Lafrance 2002). Bottom-up effects from ocean-climate variability may affect recruitment and abundance in snow crab (Zheng &

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Kruse 2006, Dawe et al. 2008, Boudreau et al. 2011). Snow crab generally inhabit regions of very cold water (Sainte-Marie et al. 2008), especially during early benthic and juvenile stages (Dawe & Colbourne 2002, Orensanz et al. 2004), and are energetically confined to cold areas (Foyle et al. 1989). Hence, their distribution and abundance, as well as survival, may be limited by the spatial extent of cold bottom waters. Alternatively, snow crab population dynamics and subarctic ecosystem structure may also be regulated by predation pressure from upper trophic levels ('top-down' effects) (Frank et al. 2005, Link et al. 2009). In particular, recent increases in snow crab biomass in Atlantic Canada have been attributed to declines in biomass of groundfish predators (Frank et al. 2005). Changes in snow crab recruitment and abundance may be influenced by the above factors or others, such as disease (Morado et al. 2010, Mullowney et al. 2011) and resource competition.

By comparing snow crab dynamics across similar ecosystems, we may be able to gain a better understanding of what drives ecosystem processes (Murawski et al. 2010). Subarctic ecosystems in both the North Pacific and North Atlantic Oceans share many commonalities including the presence of commercially important snow crab and large gadid predators. This study compares population dynamics of snow crab in the eastern Bering Sea (EBS), the southern Gulf of St. Lawrence (SGSL), and 2 regions in the Newfoundland-Labrador Shelf (NL) ecosystem to address the following question: Is snow crab abundance governed by analogous factors across subarctic ecosystems or do snow crab in each ecosystem respond to important drivers in different ways?

Specifically, we investigate how the spawning stock biomass, the environment (water temperature or cold area extent), and the biomass of gadoid fishes impact snow crab recruitment or recruitment indices. Three hypotheses were tested for each of 3 ecosystems: (H_{A1}) snow crab recruitment shows an increasing or compensatory (e.g. asymptotic or dome-shaped) response to spawning stock biomass (density dependence); (H_{A2}) colder conditions, represented by lower temperatures, a larger spatial extent of cold bottom temperatures, or more extensive ice cover will result in increased recruitment; and (H_{A3}) increased biomass of potential predators will be associated with decreased snow crab recruitment. These hypotheses were tested in a statistical modeling framework relating estimates or indices of snow crab recruitment to variability in predation, spawning stock biomass, and the environment.

MATERIALS AND METHODS

Study areas

We examined snow crab dynamics in 3 subarctic ecosystems that are characterized by a high degree of seasonality in ice cover and sunlight and by large influxes of freshwater (Hunt & Drinkwater 2007). Snow crab generally inhabit shelf or slope areas and are typically associated with a cold pool of water (Dawe & Colbourne 2002, Sainte-Marie et al. 2008). Relationships between snow crab recruitment or recruitment indices and potential explanatory variables were modeled for 4 regions in 3 large marine ecosystems: (1) EBS, (2) SGSL, Northwest Atlantic Fisheries Organization (NAFO) Division 4T, and 2 regions in NL, (3) NAFO Division 3K (NAFO 3K) and (4) NAFO Division 3L (NAFO 3L) (Fig. 1). The 2 NL regions were modeled separately because snow crab abundance trends and thermal regimes differed between the regions. Data are aggregated at the division level before being combined for the NL system as a whole (DFO 2010); area NAFO 3K corresponds to the relatively deep and warm northeast Newfoundland Shelf, while NAFO 3L is over the shallow colder Grand Bank.

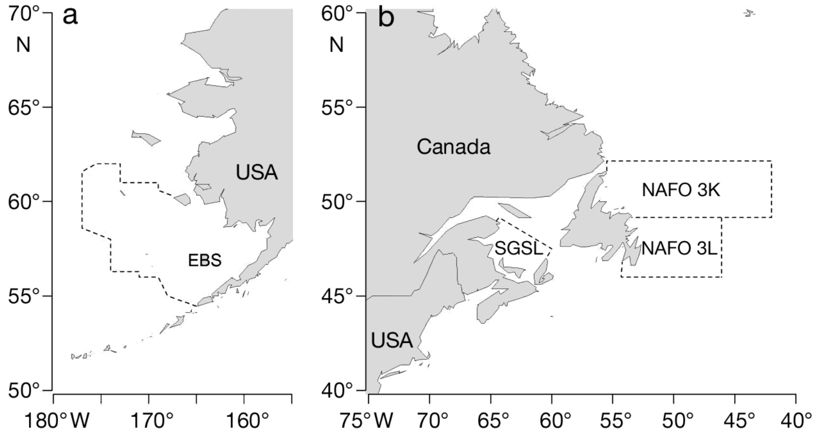

Fig. 1. Study regions used to model the effects of spawners, the environment, and predation by gadoid fishes on snow crab recruitment in (a) the eastern Bering Sea (EBS) and (b) the Northwest Atlantic Fisheries Organization (NAFO) Division 4T in the Gulf of St. Lawrence (SGSL), and NAFO Divisions 3K (NAFO 3K) and 3L (NAFO 3L) off the Newfoundland-Labrador Shelf

Data

Snow crab data

For the EBS and SGSL, time series of estimated recruitment were used as the primary response variables. Hereafter, we use the general term 'recruitment' to refer to the estimated or modeled abundance of a specific size-class, which is smaller than the smallest age group recruiting to the fishery. For the EBS, recruits become vulnerable to survey gear over the size range of 30 to 60 mm carapace width (Orensanz et al. 2004). We used the number of individuals, in millions, between 25 and 40 mm carapace width for the years 1984 to 2007 as estimated from a statistical, size-structured model based on survey and fishery data (Turnock & Rugolo 2010). This represents the best available index of recruitment, although it does not fully account for small crab occurring to the north of the standard survey area. Crabs of this size class are thought to be 4 yr from hatching and 5 yr from fertilization (Turnock & Rugolo 2010). Recruitment of instar VIII snow crab in the SGSL was modeled based on survey data from 1989 to 2009 (DFO 2010) and indexed on a scale from 0 to 100 for this study. The SGSL trawl survey was conducted during fall in Fishing Area 12, which is the largest fishing area in the SGSL. No survey was conducted in 1996 and a model-derived value was substituted for this year (Hébert et al. 1997). SGSL instar VIII snow crab are 30.7 to 34.5 mm carapace width and have been estimated to be 4.3 to 5 yr from hatching (Sainte-Marie et al. 1995, Hébert et al. 2002). Although the SGSL recruits cover a narrower size range than in the EBS, the 2 size classes correspond to approximately the same age range. Snow crab can reach sexual maturity over several different instars, beginning from 35 (Ernst et al. 2005) to 40 mm carapace width (Hébert et al. 2002).

For the 2 NL regions, available trawl survey time series were too short for modeling purposes. However, fluctuations in the exploitable biomass and abundance are largely dependent on the strength of incoming recruitment to the fishery (males larger than 94 mm carapace width) and should reflect the abundance of the youngest year classes entering the fishery (approximately age 10). Therefore, we used catch-per-unit-effort (CPUE in kg trap^{-1} for snow crab >94 mm carapace width) as a crude recruitment index in these regions (1977 to 2008 for NAFO 3K, 1974 to 2008 for NAFO 3L). To validate this approach, we compared fishery CPUE to trawl survey abundance indices for various limited size groups of new-shelled crabs. Convincing direct relationships were found between the CPUE and trawl survey abundance indices at appropriate lags for both NL regions (E. Dawe unpubl. data). Hereafter, we refer to these CPUE series as 'recruitment index.'

The reproductive potential of snow crab influences larval production and this may be reflected in variations in recruitment. To address our first hypothesis linking spawner biomass to later recruitment, we used proxies for spawning stock biomass as measures of reproductive potential (Fig. 2). In the EBS we used an estimate of total mature snow crab biomass (morphometrically mature males plus mature females) based on survey size composition and maturity at size estimated in the stock assessment (Turnock & Rugolo 2010). In all other areas (SGSL, NAFO 3K and 3L), CPUE of male snow crab 95 mm carapace width or larger was used as a proxy for spawning stock biomass, hereafter called 'spawning stock biomass index'. These measures were incorporated at appropriate lags in regression models to assess potential impacts of spawner biomass on recruitment as described below.

Environmental data

To capture the potential effects of ocean climate variability on snow crab recruitment we selected bottom temperatures and cold area extent (measured either as the extent of the cold layer of water that forms as a result of winter cooling and ice cover or as the spatial extent of the sea ice itself) as environmental variables for modeling (Fig. 2).

For the EBS, a long-term proxy for bottom temperature was constructed using the NOAA extended reconstructed sea surface temperature data series (Smith et al. 2008, NOAA 2011). The proxy uses sea surface temperatures averaged over the spring and late summer periods (March, April, May, and August), when water column temperatures were most strongly correlated with average bottom temperatures over the shelf (Pearson's product moment correlation $r = 0.88$) due to vertical mixing. Bottom temperatures in the SGSL were measured annually at Magdalen Shallows during September (Chassé & Pettipas 2010). For both NL areas (NAFO 3K and NAFO 3L), a time series of annual mean bottom temperatures at Stn 27, an oceanographic monitoring station located 7 km from St. John's Harbour (Newfoundland), was selected as a measure of temperature variability in these regions (Dawe et al. 2008).

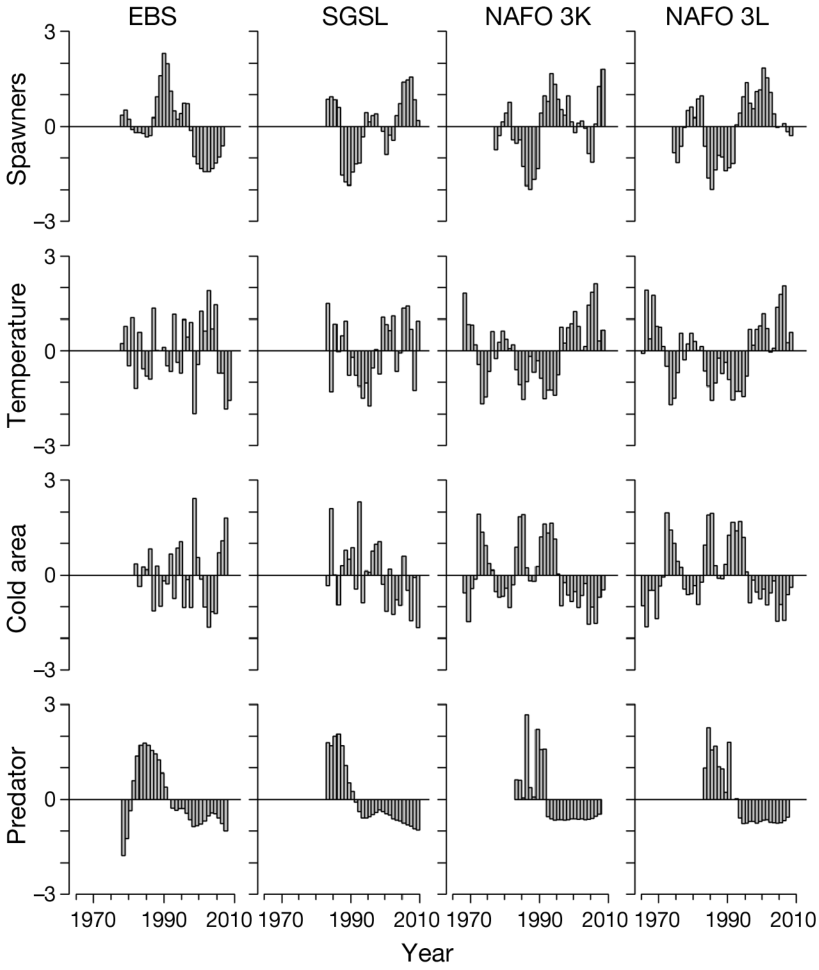

Fig. 2. Normalized anomalies of explanatory variables (snow crab spawning stock biomass, temperature, cold area extent, and Pacific or Atlantic cod biomass) in each region were calculated from raw data, before lags and moving averages were applied. The year range plotted for each region includes the first year used in analysis to the most recent year of data available, thus showing a wider range of data than was used in models. See Fig. 1 for region abbreviations

Seasonal ice cover is an important feature of all the study areas examined here. It determines the spatial extent of the cold pool in the EBS and is related to the area of the cold intermediate layer in Atlantic Canada. Because the spatial extent of these cold waters has important effects on the distribution of snow crab (Dionne et al. 2003, Orensanz et al. 2004), we examined the influence of cold area extent in each region. For the EBS, cold area extent represents the fraction of the National Marine Fisheries Service summer bottom trawl survey area with water less than 2°C (F. Mueter unpubl. data). The SGSL cold area variable represents the area (km^2) of Magdalen Shallows covered by −1 to 3°C bottom water during September (Chassé & Pettipas 2010). For NAFO 3K and NAFO 3L, the annual ice cover area (km^2) from 45 to 55° N on the Newfoundland-Labrador Shelf (Dawe et al. 2008) was used to represent the spatial extent of cold water.

Predators

To examine the potential effects of key predators on snow crab recruitment in each system, and to address hypothesis H_{A3}, suitable estimates of predator biomass were compiled (Fig. 2). Although there are many predators of snow crab, this study focused on predation by gadoid fishes. Walleye pollock *Theragra chalcogramma* dominate gadid biomass in the EBS, but were not included here because snow crab make up a very small proportion of their diet (Aydin et al. 2007). The major gadid predator on snow crab in the EBS is Pacific cod *Gadus macrocephalus* (Livingston 1989), and we used a model-based estimate of the total biomass of Pacific cod age 0+ from the 2007 stock assessment model (Thompson et al. 2010) to quantify potential gadid predation in this system. In both Atlantic Ocean ecosystems, Atlantic cod *Gadus morhua* has historically been a predator of snow crab. In the SGSL, Atlantic cod age 3+ biomass estimates from the 2009 stock assessment model (Swain et al. 2009) were used to examine predation effects. In NL regions NAFO 3K and 3L, estimates of total Atlantic cod biomass from autumn surveys (conducted through 2007) were used.

Analytical approach

A general regression approach was used to examine the effects of snow crab spawning stock biomass, environmental variability, and predation on snow crab recruitment in each ecosystem. The basic modeling structure was as follows:

$$y_t = \beta_0 + \beta_1 \text{spawners}_{t-k1} + \beta_2 \text{environment}_{t-k2} + \beta_3 \text{predator}_{t-k3} + \varepsilon_t \qquad (1)$$

where y_t represents snow crab recruitment (or recruitment index) in year t, βs are regression coefficients, $k1$, $k2$, and $k3$ represent time lags, and the errors ε_t are assumed to be either independent and normally distributed with mean zero and variance σ^2 or first order autocorrelated ($\varepsilon_t = \phi\,\varepsilon_{t-1} + \nu_t$) with autoregressive coefficient ϕ and innovations ν_t that are independent and normally distributed.

Recruitment data often have a skewed distribution and may require a transformation to achieve normality in model residuals. A range of Box-Cox transformations (Box & Cox 1964) were explored to identify the best power transformation for each response variable (y_t) to achieve approximate normality of the residuals. Likelihood profiles indicated that a log transformation was the best possible transformation for the EBS and SGSL recruitment series, while no transformation was necessary for the NAFO 3K and NAFO 3L recruitment indices.

Spawning stock biomass affects larval production, while both predation and the environment may influence survival. Each of these factors would be expected to alter population abundances several years prior to recruitment and the effects may extend over multiple years, necessitating the use of lags and moving averages for the explanatory variables. Available diet studies suggest that early life history stages of snow crab are particularly vulnerable to predation (Livingston 1989, Chabot et al. 2008). For example, in the Gulf of St. Lawrence, 4 size groups of crab were susceptible to Atlantic cod predation (Chabot et al. 2008). These sizes roughly correspond to ages 1 to 4 yr (Hébert et al. 2002), although there can be some variability in growth to each size class. Similarly, environmental conditions including temperature can affect larval and juvenile stages of snow crab by influencing development rate (Moriyasu & Lanteigne 1998), hatch timing (Webb et al. 2007), growth rate, and molt frequency (Orensanz et al. 2007), as well as energy budgets (Foyle et al. 1989). Since effects may range over several life stages and because snow crab cannot be aged reliably, 3 or 4 yr moving averages were applied to time series of both predators and environmental variables to capture their potential effects on multiple age classes of snow crab. Likewise, moving averages were applied to spawning stock biomass series because the time period between fertilization and growth to the recruitment size class varies. The averaged variables were then lagged by k years relative to the response in Year t to correspond to the approximate period when the effect is presumed to occur (Year $t - k$). For example, the recruitment of EBS snow crab is most likely to be influenced by the parental stock 4 to 6 yr prior (Table 1); hence, recruits in 1995 were modeled as a function of the spawning stock biomass averaged over 1989 to 1991. In some cases, several biologically reasonable lags were considered, such as in NL regions NAFO 3K and NAFO 3L, where the recruitment index was based on snow crab of commercial size (>94 mm carapace width). In those areas it was reasonable to consider predation effects over several lags (ranging from 5–8 yr to 7–10 yr prior) due to uncertainty and variability in the age at which snow crab reach commercial size. When multiple lags were considered, the lag that resulted in the lowest p-value in a simple linear regression between the recruitment index or the log of recruits and each explanatory variable was selected for use in regression models. The lags and moving averages used for all variables in each model are listed in Table 1.

Table 1. Explanatory variables used in this study, by region, with lags considered for each variable. Lags denote the time range (in yr) prior to the year when snow crab recruitment (eastern Bering Sea, EBS; southern Gulf of St. Lawrence, SGSL) or recruitment indices (in Newfoundland-Labrador NAFO Divisions 3K and 3L) were measured. Ranges include only those years during which explanatory variables may reasonably be expected to affect snow crab subsequent recruitment. Spawners: snow crab spawners

Region	Explanatory variable	Lags (yr)
EBS	Spawners	4–6
	Temperature	2–4
	Cold area cover	2–4
	Pacific cod	2–4
SGSL	Spawners	4–6
	Temperature	3–5
	Cold area cover	3–5
	Atlantic cod	2–4
NAFO 3K	Spawners	9–11
	Temperature	7–9
	Sea ice extent	7–9
	Atlantic cod	5–8
NAFO 3L	Spawners	9–11
	Temperature	7–9
	Sea ice extent	7–9
	Atlantic cod	7–10

For some ecosystems, the length of overlapping time series was limited once the predator and/or spawner series were lagged appropriately. For these systems both ‘short models’ including all variables and ‘long’ models including fewer variables were tested. For example, the Atlantic cod series in NAFO 3L overlapped with the response variable by only 16 yr, whereas the spawner and environmental variables were available over longer time periods (n = 24 and n = 35 yr, respectively). Results from analyses using the short and long series were then compared for consistency. We considered the results to be consistent when the sign of all explanatory variables remained unchanged regardless of whether the short or the long series were used.

A species may exhibit non-linear, non-additive, or threshold responses to external pressures (Cury et al. 1995, Ciannelli et al. 2007, 2008). To explore potential non-linearities and thresholds we fit exploratory generalized additive models (GAMs) to the data using a cross-validation approach before constructing a corresponding linear model for further analysis. To avoid over-fitting we limited parameter smoothness by constraining the estimated degrees of freedom (EDF) for any variable to 3, corresponding to a biologically realistic set of possible responses (approximately linear, asymptotic, or dome-shaped). Partial fits for each explanatory variable and the estimated degrees of freedom were examined, and a squared term was included in the full linear model for any variable with EDF >1.5. No higher-order polynomial terms were considered as they were not deemed biologically reasonable.

For each ecosystem, both a temperature variable and cold area extent (or sea ice extent) were available for modeling. However, bottom temperatures were strongly correlated with cold area cover and/or sea ice extent in each system (multicollinearity). Therefore, the effects of these variables were modeled separately and compared for consistency. For each system, the initial full linear model included one environmental variable, a cod predator, and spawning stock biomass. We tested for interactions among variables in each full model, and because we found no significant interactions, we did not consider interactions further. We compared the full model with all 3 variables to reduced models with 1 or 2 variables using the small-sample Akaike Information Criterion (AICc). The model with the smallest AICc was selected as the final model when the difference between AIC values, ΔAICc, was >4 (Burnham & Anderson 2002). If differences in AICc were <4, the most parsimonious model was selected as the final model.

Residuals from both the initial (full) model and from the final (AICc-best) model were examined for normality, heteroscedasticity, and autocorrelation. When significant autocorrelation ($p < 0.05$) was present in residuals from the full model according to a Durbin-Watson (DW) test, all model comparisons were based on generalized least squares fits that included a first-order auto-regressive error term. The overall significance of the final (AICc-best) model was tested using the likelihood ratio test (LRT) for generalized least squares models or *F*-test for linear models without autocorrelation.

Program R version 2.9 (R Development Core Team 2011) was used for all analyses and a level of $\alpha = 0.05$ was chosen to assess significance.

RESULTS

In the EBS, cold temperatures were related to increased recruitment, consistent with our hypothesis, but results did not support a predation effect (Tables 2 & 3). The final model included temperature

Table 2. Regression coefficients with p-values (in parentheses) for final model fits of snow crab recruitment or fishery recruitment indices in 4 regions (eastern Bering Sea, EBS; southern Gulf of St. Lawrence, SGSL; NAFO Division 3K, NAFO 3K; and NAFO Division 3L, NAFO 3L). Coefficients denote intercept (β_0) and estimated effects of spawning stock biomass (β_1), temperature or sea ice extent (β_2), predator biomass (β_3), and a first-order autoregressive parameter (φ), if significant. Predators are Pacific cod in the EBS and Atlantic cod elsewhere

Region	Environmental variable	β_0	β_1	β_2	β_3	φ
EBS	Temperature	16.50 (<0.001)	$-5.38\text{x}10^{-3}$ (0.032)	−2.12 (0.006)		0.66
SGSL	Temperature	5.12 (<0.001)		−2.85 (0.020)		0.73
NAFO 3K	Sea ice extent	6.80 (0.035)		4.72 (0.034)		0.91
NAFO 3L[a]	Temperature	20.27 (<0.001)	−0.65 (<0.001)	−2.73 (0.008)	$-9.63\text{x}10^{-3}$ (0.001)	
	Sea ice extent	20.91 (<0.001)	−0.70 (<0.001)	2.98 (0.011)	$-9.63\text{x}10^{-3}$ (0.001)	

[a] Results based on model fit to 16 yr with data for all variables. See section 'Results' for results from longer model (n = 24 yr) that did not include Atlantic cod

Table 3. Summary of estimated effects of snow crab spawning stock biomass, the environment, and predation by cod on snow crab recruitment. For the eastern Bering Sea (EBS) and southern Gulf of St. Lawrence (SGSL) the response variable was the log of the estimated number of recruits at a small size. In the 2 Newfoundland-Labrador systems (NAFO 3K and NAFO 3L), a fishery recruitment index was the response variable. Predators are Pacific cod (EBS) and Atlantic cod (SGSL, NAFO 3K, NAFO 3L).Variables that were significant to the final models are shown in plus or minus signs, while those that are not significant are indicated by NS

	EBS	SGSL	NAFO 3K	NAFO 3L
Spawners	–	NS	NS	–[a]
Temperature	–	–	NS	–
Cold area cover/ sea ice extent	NS	NS	+	+
Predators	NS	NS	+/–[b]	–

[a] Spawners were negatively related to the recruitment index in both short and long models; however, they were only significant in the short model

[b] Results from models including and excluding Atlantic cod were not consistent

and spawning stock biomass; both variables were negatively and linearly related to the log of recruitment (n = 24 yr, LRT = 20.75, $p < 0.001$) and explained approximately 38% of the variability in recruitment (Fig. 3a). The model included a first-order autoregressive term ($\varphi = 0.66$) to account for significant autocorrelation in the residuals (DW = 0.93, $p < 0.001$, Fig. 4a). When replacing temperature with the cold area extent (n = 22 yr) in the full model, its estimated effect was not significant ($t = 1.45$, p = 0.164), but its sign was consistent with a positive effect of cold conditions on recruitment.

In the SGSL we found a negative linear relationship between temperature and the log of recruitment, but neither a predation nor a spawner effect (n = 21 yr, Tables 2 & 3). The final model included the temperature variable (LRT = 20.81, $p < 0.001$, Table 2) and explained about 41% of the recruitment variability (Fig. 3b). A first-order auto-regressive term ($\varphi = 0.73$) was included in the model to account for residual autocorrelation (DW = 0.77, $p < 0.001$, Fig. 4b). The full model for SGSL based on cold area extent rather than temperature was not significant overall (LRT = 4.66, p = 0.32) and contained no significant variables ($p > 0.05$). Therefore, models with cold area extent were dropped from further consideration.

In the NL area, NAFO 3K sea ice extent was positively related to the snow crab recruitment index 7 to 9 yr later (Table 2), meaning sea ice conditions appear to affect snow crab at approximately 1 to 3 yr of age. There was no evidence of an effect of spawner stock biomass index or temperature on snow crab recruitment index and the relationships with Atlantic cod biomass were inconsistent (Table 3). Models for NAFO 3K that included the Atlantic cod series (n = 18 yr) differed substantially from those including just other variables (n = 21 for spawners, n = 32 for temperature or ice area). Specifically, when Atlantic cod biomass was included in these models, the sign and significance of other coefficients changed drastically, most likely as a result of strong correlations between Atlantic cod and the other explanatory variables. Therefore, models including Atlantic cod were not considered further. Spawner stock biomass index was neither significant to the model with bottom temperature nor to the model using sea ice extent as a proxy for the cold area extent. Sea ice extent had a significant positive linear relationship with the snow crab recruitment index (Table 2), though it only explained a small proportion of overall variability (Fig. 3c, n =32 yr, LRT = 33.00, $p < 0.001$, $R^2 = 0.18$). A first-order autoregressive term ($\varphi = 0.91$) was included to account for significant autocorrelation in the residuals (Fig. 4c, DW = 0.45, $p < 0.001$). When using bottom temperature as the environmental variable, none of the variables in the model were significant ($p > 0.05$), but a negative temperature coefficient was consistent with the observed positive effect of extensive ice on the snow crab recruitment index.

In the other NL region, NAFO 3L, cold conditions and low predator biomasses were associated with a high recruitment index in following years. Spawner stock biomass index showed a negative association with the later recruitment index (Tables 2 & 3). Models including Atlantic cod covered a shorter time period (n = 16 yr) than those with spawner stock biomass index (n = 24 yr) or environmental conditions (temperature or sea ice extent, n = 35), but the sign of coefficients for spawner stock biomass index and temperature or sea ice extent remained consistent among models. Temperature or sea ice extent were significant in all models, though spawner stock biomass index was not significant in the longer (n = 24 yr) model. In the short models, spawner and predator biomasses were both negatively related to the subsequent snow crab recruitment index. Likewise, colder conditions were linked with a higher recruitment index. Both model fits explained about 90% of recruitment index variability over the 16 yr modeled (temperature model: $F_{3,12} = 45.62$, p <

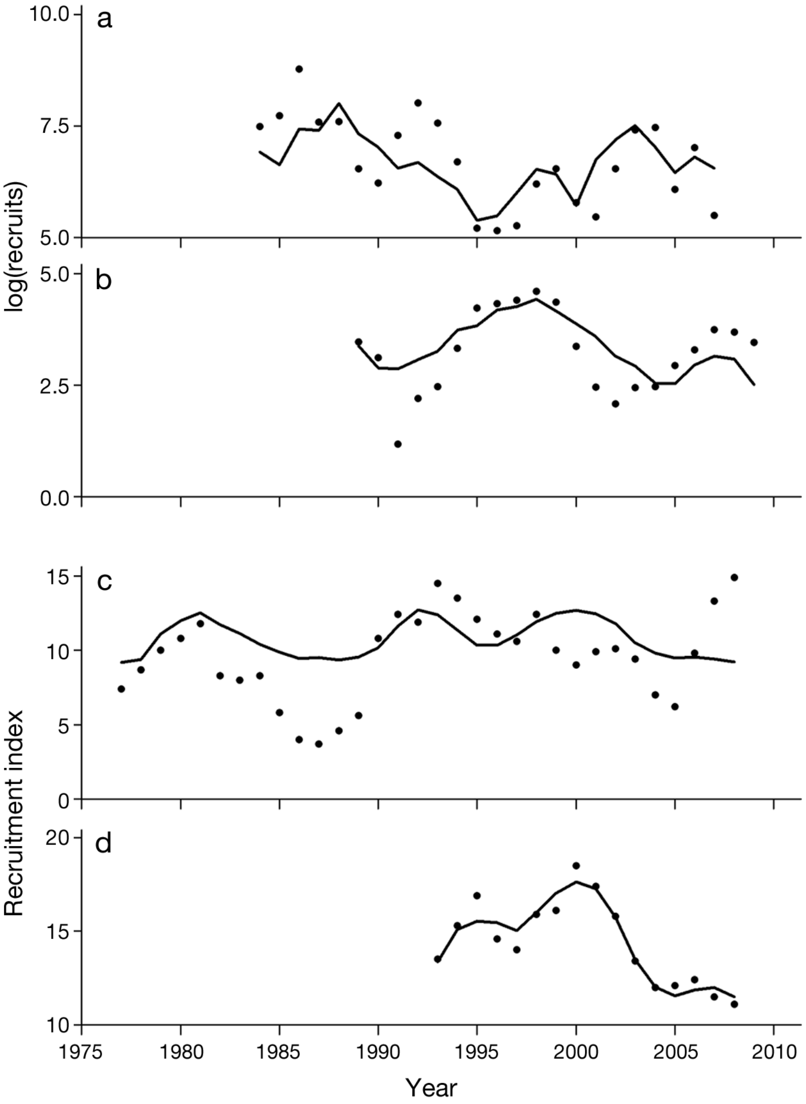

Fig. 3. *Chionoecetes opilio.* Time series of snow crab recruitment or recruitment indices (dots) with predicted values from best-fit models (lines) for (a) the eastern Bering Sea, (b) the southern Gulf of St. Lawrence, (c) Northwest Atlantic Fisheries Organization (NAFO) 3K, and (d) NAFO 3L (sea ice extent model). Best-fit models for each region are described in 'Results' and summarized in Table 2

0.001; sea ice extent model: Fig. 3d, $F_{3,12} = 43.91$, $p < 0.001$), and there was no evidence of first-order autocorrelation in the residuals (temperature model: DW = 2.05, p = 0.22; sea ice-extent model: Fig. 4d. DW = 2.04, p = 0.22).

Significant and pronounced autocorrelation was present in the recruitment or recruitment index residuals in the final models for 3 of 4 regions studied (EBS, SGSL, and NAFO 3K in the NL ecosystem), as was clearly evident in residual plots (Fig. 4). The first-order autoregressive structure of the generalized least squares models accounted for the observed serial correlation and ensured that significance tests and model comparisons are valid. However, clear cyclic patterns with several multi-year runs of alternating positive and negative residuals were evident in both the full models and in the AICc-best models. This suggests that models including environmental variables, predation and/or spawner effects, in combination with random measurement errors, do not fully account for the dynamics of these populations.

DISCUSSION

Overview

This study investigated the effects of 3 factors (spawning stock biomass, environmental conditions, and gadid biomass) on the strength of subsequent recruitment levels in snow crab and compared results across 3 subarctic ecosystems in the Northwest Atlantic and Northeast Pacific (Table 3). Our modeling results showed that ocean climate variability was the only factor that was consistently associated with recruitment in all ecosystems and regions. This strongly supports our hypothesis (H_{A2}) that cold conditions during early life history stages promote subsequent snow crab recruitment (Fig. 5). In contrast, there was little support for a consistent effect of spawning stock or predator biomasses (hypotheses H_{A1} or H_{A3}) on recruitment across systems. Spawning stock biomass was inversely related to recruitment in the EBS and NAFO 3L, possibly indicating a density-dependent effect on recruitment in those areas. Atlantic cod biomass was inversely related to recruitment, consistent with a predation effect, but only in NAFO 3L.

Our study shows that bottom-up processes related to ocean climate conditions appear to have a consistent influence on snow crab recruitment, while the importance of gadid biomass or spawning stock biomass is less clear. This study also highlights the value in comparing multiple ecosystems because con-

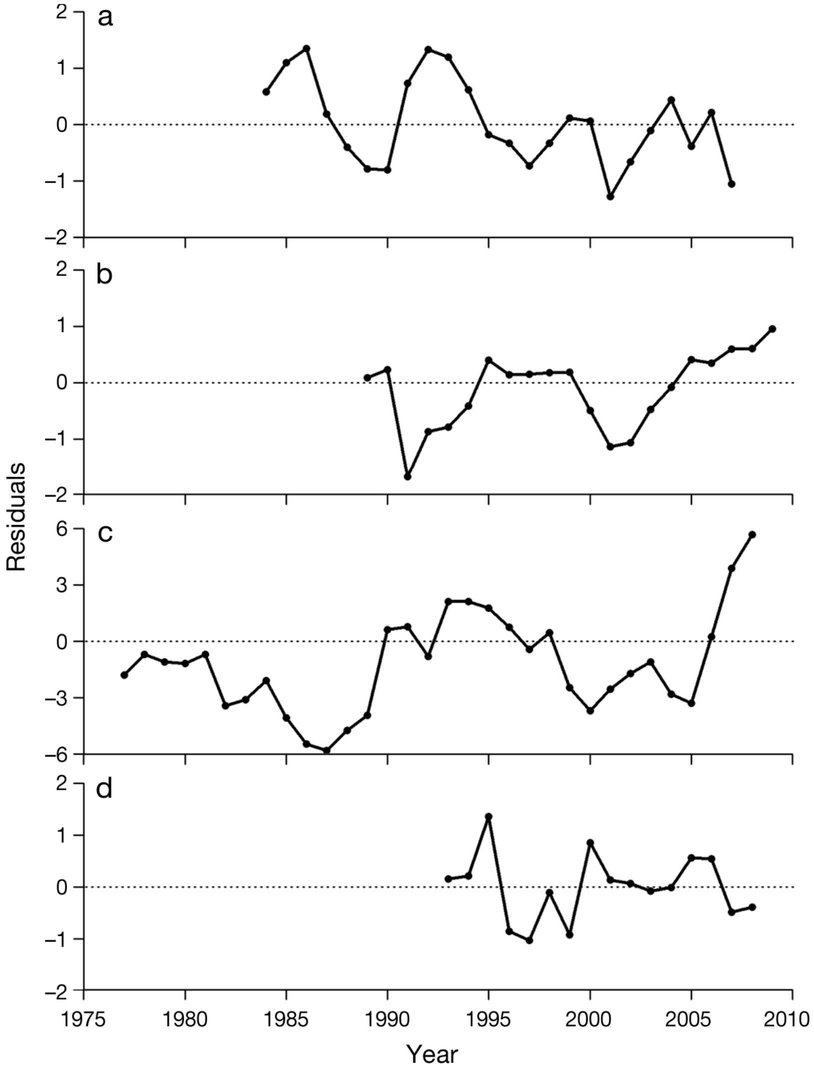

Fig. 4. Model residuals through time for 4 geographic regions: (a) the eastern Bering Sea, (b) the southern Gulf of St. Lawrence, (c) Northwest Atlantic Fisheries Organization (NAFO) 3K, and (d) NAFO 3L (sea ice extent model). Residuals from several models have long runs of negative and positive residuals indicating a possible cyclical pattern in snow crab recruitment

sistent responses across several systems greatly strengthen our conclusions about significant effects of temperature conditions on early life stages of snow crab.

Environment, spawning stock biomass, and predation

Our study suggests that colder conditions during early life are associated with better snow crab recruitment in all of the systems examined. Our indices of ocean climate are closely related, and we did not address mechanisms linking climate to snow crab life history, so it is unclear whether these indices reflect a common regulatory mechanism or if they represent different processes. Climate can be linked to snow crab reproduction and survival in several ways. For example, the hatch timing of larval crab is linked to temperature (Webb et al. 2007) and ice cover can affect stratification and larval feeding conditions in the spring (Orensanz et al. 2004). Recently settled juveniles are thought to be very stenothermic and have low mobility; they could represent the 'weakest link' in snow crab life history because they cannot easily escape unfavorable environmental conditions such as unfavorable temperatures (Dionne et al. 2003). Therefore, the area of cold water during summer may limit the amount of suitable habitat and hence the carrying capacity for early benthic stages (Dawe & Colbourne 2002). In addition, temperature likely affects early survival directly by regulating the energy budget of individual crabs (Foyle et al. 1989). A laboratory experiment found that for mature male snow crab taken from the Scotian Shelf, total metabolic costs exceeded digestible energy intake in waters 7°C or higher and slightly exceeded digestible energy intake in 0 to 1°C water (Foyle et al. 1989). Therefore, snow crab may be excluded from warm waters based on energetic demands (Foyle et al. 1989). Conversely, it is known that cold conditions promote snow crab to terminally molt at a smaller size, which may reduce the proportion of commercially harvestable males in the total adult male population (Dawe et al. 2012b, this volume). Overall, the effects of temperature or cold area extent on early life stages seem to have a dominant effect on recruitment. However, in the present study, mean temperatures in each system varied within a narrow range (roughly 1.5°C), and recruitment responses should not be extrapolated outside of the modeled temperature range. Although temperatures differed substantially among regions, relationships between recruitment and temperature were similar, suggesting that snow crab are adapted to local temperature conditions. Therefore, the effect of a given

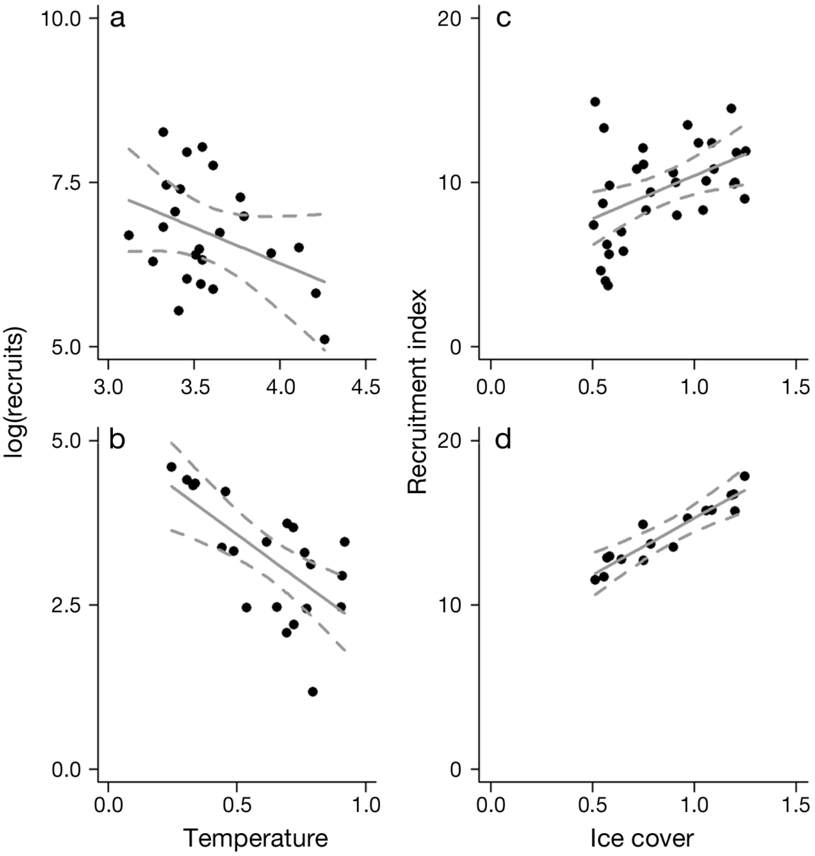

Fig. 5. Partial fits (solid lines) with 95% pointwise confidence intervals (dashed lines) illustrating the estimated effects of temperature and ice conditions on snow crab recruitment, while holding other variables constant at their mean values. Plots show the effect of temperature on recruitment in the (a) eastern Bering Sea and (b) southern Gulf of St. Lawrence and the effect of ice cover on recruitment indices in (c) Northwest Atlantic Fisheries Organization (NAFO) Division 3K and (d) NAFO Division 3L. Note that the axes differ among panels

temperature on recruitment must be evaluated relative to typical conditions for snow crab in each region.

For the cod predators considered in this study, we found a relationship with recruitment only in NAFO 3L in the NL ecosystem. Considering the absence of any such effect in other regions, especially in the adjacent NAFO 3K area, our study found little evidence that cod biomass has exhibited top-down control on larval and juvenile snow crab since the late 1970s. In both the Newfoundland-Labrador Shelf (Lilly 2008) and in the Gulf of St. Lawrence (Ruppert et al. 2010), Atlantic cod populations have crashed from their historic levels and were at low abundances during most of the time period examined here. Consequently, there simply may be too few cod at the present time to exert significant population-level predation effects on young snow crab. The apparent predation effect in NAFO 3L may also result from opposing responses of snow crab and Atlantic cod to ocean climate variability, with snow crab increasing and cod decreasing during a prolonged cold period when cod was also excessively exploited (Dawe et al. 2008). However, our results do not imply that predation has no effect on snow crab recruitment. Previous studies indicate that predation may be important. For example, Livingston (1989) estimated that in the EBS, Pacific cod remove 27 to 57% of Age 1 snow crab from the population. Our results may differ for several reasons. First, the spatial scale of data may influence statistical analyses (Ciannelli et al. 2008, Windle et al. 2012, this volume) and hence our results. Biological data for this study represented large geographic regions and will fail to detect small-scale predator-prey interactions. Second, predation can have indirect effects on snow crab recruitment by limiting their geographic range. Climate conditions may affect predator-prey relationships by altering the spatial distributions of either species (Zheng & Kruse 2006). Also, the EBS snow crab population has contracted northward in recent decades (Orensanz et al. 2004). The environmental ratchet hypothesis proposes that Pacific cod predation may help prevent snow crab from expanding and returning to more southern portions of the eastern Bering Sea shelf that provide favorable spawning habitat (Orensanz et al. 2004). Such spatial dynamics can lead to important predation effects that may not be evident in a relationship between time series of aggregated predator biomasses and prey recruitment. Finally, the diet of both cod species changes with age (Livingston 1989, Chabot et al. 2008), and the age classes of cod which are the most important consumers of snow crab may not be well-represented in aggregated biomass series.

A recent meta-analysis by Boudreau et al. (2011) looked for evidence of top-down and bottom-up controls on snow crab in the northwest Atlantic Ocean. Similar to our study, their results linked colder temperatures during the early years after settlement with higher subsequent snow crab abundances. In contrast to our study, they found statistical evidence of top-down control by Atlantic cod on snow crab 0 to 5 yr later. For crab entering the fishery, these lags would correspond to snow crab approximately 29 to 97 mm carapace width or 3.3 to 8.7 yr of age. Their result including older crab is unexpected because cod generally consume snow crab that are younger than 4.5 yr post-settlement (Chabot et al. 2008), and predation by cod on crabs in the NL ecosystem has been virtually non-existent for 2 decades due to very low abundance of large cod (Dawe et al. 2012a, this volume). However, at the longer lags, which correspond to predation on younger crab, the results of Boudreau et al. (2011) agree with expectations from available diet studies. Our predation results may differ from those found in Boudreau et al. (2011) in part due to methodological approaches. We selected suitable lags corresponding to the crab ages most vulnerable to predation a priori in order to minimize the chance of finding spurious relationships. Boudreau et al. (2011) considered a much larger range of lags (25 yr) since they were examining both the effects of crab on cod and of cod on crab. Furthermore, we used a regression approach that allowed us to consider the combined effects of multiple covariates, including spawning stock biomass, on crab recruitment at once. In contrast, Boudreau et al. (2011) considered pairwise full and partial correlation coefficients.

The lack of an obvious relationship between cod biomass and snow crab recruitment in our study may reflect a true absence of top-down control by cod on snow crab. However, in light of the results from Boudreau et al. (2011) and the aforementioned drawbacks of using biomass as an indicator of overall predation pressure, we cannot discount top-down controls of cod on snow crab.

Spawning stock biomass did not show a consistently positive or dome-shaped relationship with recruitment, as we hypothesized. Rather, it was significantly and negatively correlated to subsequent recruitment in 2 areas (EBS, NAFO 3L in the NL ecosystem). This relationship could occur if our data represented the right (declining) limb of a dome-shaped curve. However, that would imply that the spawner-recruit relationships peak at low spawner biomasses. Also, climate variability and numerous other factors may affect the survival of young crab in the years between fertilization and recruitment. For example, cannibalism may reduce the abundance of recently settled snow crab (Sainte-Marie & Lafrance 2002) and could perhaps confound or even mimic spawning stock biomass effects, particularly in the EBS and SGSL regions where the lag time between spawners and recruits was relatively short. In addition, several elements of snow crab reproductive biology may mask any direct link between adult spawning stock biomass and later recruitment. Female snow crab are able to store sperm and to use these reserves to fertilize ova (Elner & Beninger 1992), so current male or total biomass may not reflect reproductive potential in a given year. In addition, the length of embryonic development (Webb et al. 2007) and the overall reproductive cycle varies and is thought to be influenced by temperature (Kuhn & Choi 2011) and by whether the female is a primiparous or multiparous spawner (Elner & Beninger 1992). A crab that remains on a 1 yr reproductive cycle can produce up to twice as many clutches over its reproductive lifetime than a crab on a 2 yr reproductive cycle (Kuhn & Choi 2011). Therefore, the proportion of crab reproducing on each cycle can have a large impact on a population's overall fecundity. Finally, the geographic distribution of female snow crab may affect reproductive success. For example, in the EBS, female snow crab undergo ontogenetic migrations (Ernst et al. 2005). Parada et al. (2010) used an individual-based model to show that larval retention, and presumably recruitment success, in the EBS varies greatly depending on the location of larval release. They also hypothesize that primiparous females, which aggregate in the middle domain of the EBS, may be the largest source of renewal for the EBS snow crab stock (Parada et al. 2010, Ernst et al. 2012). Hence, we may have failed to detect any relationship between measures of spawning biomass and recruits because spawning biomass is weakly related to total reproductive output.

Another important finding from this study is that the variables we modeled cannot fully explain the observed cycles in recruitment that are characteristic of snow crab and other crab populations. This is evident in the residual patterns for 3 of the regions modeled here (Fig. 4) and is likely to result from internal community dynamics. Such dynamics may be linked to a stronger contribution of primiparous than multiparous females to recruitment (Parada et al. 2010, Ernst et al. 2012) or cannibalism among cohorts within settlement grounds (Sainte-Marie et al. 1996). Alternatively, small-scale changes in climate related to atmospheric circulation like the El Niño could be related to snow crab recruitment cycles (Zheng & Kruse 2003). Residual cycles could also be related to changes in predation pressures owing to the spatial distribution of snow crab or their predators, as discussed earlier.

Implications for stock assessment and management

Reliable stock assessment provides the foundation for successful fisheries management. Stock assessment scientists must make assumptions about recruitment levels to project future snow crab populations, to evaluate the effects of harvesting, and to develop or compare rebuilding plans (NOAA 2001) for depleted stocks. The dominant role of bottom-up climate processes in regulating recruitment and the cyclic patterns we observed in model residuals imply that productivity is not stationary. Incorporating ocean climate effects and population cycles into projections will lead to more reliable predictions of future recruitment that would result in improved management advice. Precautionary reference points, guideline harvest levels, and thresholds for overfishing should be set to reflect variability in production and subsequent recruitment. Further, the current study indicates that warm conditions are linked with poor recruitment. Therefore, if climate change causes bottom conditions to continue to warm, snow crab recruitment will likely decline in our study areas. Studies such as ours, if applied to other important predatory and forage species, can be very important in developing a better basis for ecosystem-based management, especially under a scenario of a changing ocean climate.

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Contribution to the Theme Section 'Effects of climate and predation on subarctic crustacean populations'

Spatio-temporal variations in invertebrate–cod–environment relationships on the Newfoundland–Labrador Shelf, 1995–2009

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ABSTRACT: We examined spatial and temporal relationships between snow crab *Chionocetes opilio*, shrimp *Pandalus* spp., Atlantic cod *Gadus morhua* and the environment (depth, temperature and salinity) on the Newfoundland–Labrador Shelf from 1995 to 2009 using autumn multispecies trawl survey data. First, the core habitat of snow crab and shrimp was determined based on cumulative distribution functions of species abundance over depth and bottom temperature. On average, this method predicted the presence of crab and shrimp at 95 and 99% of trawl locations, respectively, and indicated 90% of crab and shrimp inhabited temperature ranges of −1 to 4 and 0 to 4°C and depths of 100 to 500 and 150 to 450 m, respectively. Then geographically weighted regressions, based on trawl stations where species presence was predicted, indicated spatial non-stationarity between invertebrates and explanatory variables at scales <200 km. Snow crab abundance was best predicted by environmental variables, suggesting bottom-up influences are important, whereas shrimp abundance was influenced by both the environment and cod (predator) abundance. We discuss how averaged ecological relationships within large marine ecosystems central to fisheries management mask processes operating at smaller scales, with reference to the northern cod ecosystem under present conditions of warming waters and increasing cod.

KEY WORDS: Spatial ecology · *Gadus morhua* · *Chionoecetes opilio* · *Pandalus borealis* · Northwest Atlantic · Geographically weighted regression · Species interactions

INTRODUCTION

The need for accurate distribution models of commercial marine species is universal (Planque et al. 2011) and increasingly important under global fishing pressures (Worm et al. 2009) and changing climates (Brander 2007, Halliday & Pinhorn 2009, Lenoir et al. 2011). In the Northwest Atlantic region, marine ecosystems have undergone dramatic changes in recent decades with concurrent large-scale shifts in the abundance and distribution of many species. Following years of sustained overfishing, high mortality, and a period of unusually cold ocean temperatures, the historically important and widely distributed northern cod *Gadus morhua* stock off southern Labrador and eastern Newfoundland, Canada, declined severely in the early 1990s to the point of commercial collapse (Drinkwater 2002, Lilly 2008). This

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decline coincided with a contraction and southward shift in the distribution of the cod stock (deYoung & Rose 1993, Atkinson et al. 1997, Rose et al. 2000) and was mirrored by declines and distributional shifts in several non-commercially exploited species (e.g. capelin *Mallotus villosus*) on the Newfoundland–Labrador Shelf (Gomes et al. 1995, Carscadden et al. 2001). A moratorium on directed cod fishing over most of the range has been in place since July 2, 1992.

The decline of the northern cod stock coincided roughly with a large increase in the abundance of snow crab *Chionoecetes opilio* and northern shrimp *Pandalus borealis* (Lilly 2000), which have comprised the most important fisheries in this region since the mid-1990s. These invertebrate species are favoured by cold ocean regimes (Parsons & Colbourne 2000, Dawe et al. 2008), where their geographic distributions are hypothesized to be largely determined by bottom-up influences requiring colder temperatures (Foyle et al. 1989) and specific habitat requirements for different life stages (Tremblay 1997, Dionne et al. 2003). Additionally, both shrimp and snow crab are prey for cod (Bailey 1982, Lilly 1984, Parsons 2005, Chabot et al. 2008), and top-down predatory control may also influence the distribution and abundance of these species. These population dynamics combined with climate fluctuations have fuelled discussion regarding the relative importance of predation and environmental factors on the abundance and distribution of invertebrates in this region (Worm & Myers 2003, Frank et al. 2006).

A region-wide spatial scale has typically been used to study trends between crustacean–predator and crustacean–environment relationships off Newfoundland–Labrador (Lilly 2000, Worm & Myers 2003, Frank et al. 2006, Boudreau et al. 2011), and, while this approach may elucidate important correlations between factors, it may also mask significant geographic variation (i.e. spatial non-stationarity) in the relationships under study (Windle et al. 2010). Spatial stationarity implies that the parameters of a process (e.g. variance and mean) are independent of location or direction, and is an important assumption for spatial statistics calculated over large regions (Fortin & Dale 2005). Observed spatial patterns of individual marine species and assemblages are the outcome of multiple environmental (exogenous) and biological (endogenous) processes that may operate on different spatial and temporal scales (Planque et al. 2011). The choice of scale is important in ecology, as different spatial patterns and relationships may result from varying the spatial extent and resolution of the analysis (Wiens 1989, Fortin & Dale 2005, Ciannelli et al. 2008). Spatial variation of species–environment interactions within a management area could have important implications for building reliable predictive models as well as for understanding the role of various factors thought to be associated with invertebrate abundance and distribution on a local scale.

Geographically weighted regression (GWR) is a relatively new statistical technique for investigating spatially varying relationships (Fotheringham et al. 2002). GWR differs from other spatial analysis methods such as autoregressive models and regression kriging because it allows model coefficients to vary with location (Fortin et al. 2012). A local regression is performed at each observation point by applying a spatial kernel that gives more weight to nearby observations than to those farther away, and a set of local coefficients and model performance statistics is subsequently generated for each sampling location. Significant variation in the GWR parameter estimates can be indicative of spatial non-stationarity and used to sub-divide a study area for further analysis (Fotheringham et al. 2002). GWR can also be used to explore the scale dependency of ecological interactions by systematically varying the bandwidth size of the spatial kernel at each observation. This technique has been applied to determine the scale at which a species–environment relationship becomes stationary (Osborne et al. 2007, Windle et al. 2010, Miller & Hanham 2011, Gao et al. 2012) and is potentially an important step in building multi-scale predictive models (Graf et al. 2005).

Marine fisheries data are characterized by zero-inflated counts, patchiness, scale dependency, and spatial correlation, all of which present challenges to traditional statistical methods (Ciannelli et al. 2008, Webley et al. 2011). Zero-inflated data distributions, which can result from spatial patchiness within preferred habitat or sampling outside the range of a species, are difficult to normalize using linear transformations and can result in serious violations of statistical assumptions such as normality, homoscedasticity, and parameter inference (Cunningham & Lindenmayer 2005). In the case of linear GWR analysis, non-normal data distributions may conceal spatial non-stationarity of parameter estimates (Yu et al. 2009), and curvilinear relationships between variables may result in false patterns of spatial non-stationarity (Austin 2007). A 2-stage modelling approach has been increasingly used in the ecological literature to cope with zero-inflated data counts, whereby presence/absence is modelled in the first step and abundance is modelled in the second step, conditional on predicted presence being greater than zero (Barry & Welsh 2002, Cunningham & Lindenmayer 2005, Martin et al. 2005, Rooper & Martin 2009, Taylor et al. 2011). When presence/absence and abundance are modelled on important ecological niche limits for survival and growth, the results of both stages can be interpreted in a biologically meaningful way (Guisan & Thuiller 2005, Rooper & Martin 2009).

The goal of this work was to investigate spatio-temporal patterns of invertebrate–predator–habitat associations within the large and heterogeneous seascape of the southern Labrador and eastern Newfoundland Shelf, and to identify characteristic scales at which these relationships achieve spatial stationarity. This study expands on previously published work (Windle et al. 2010) to apply GWR to a 15 yr time series (1995 to 2009) of fisheries survey data in Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J and 3K. We used a 2-stage modelling approach to compensate for the patchy distribution and zero-inflated catches of species in the study area and to improve the linearity of relationships by focussing the analysis on areas where species were expected to be present. Given evidence of the importance of environmental conditions to snow crab and pandalid shrimp distributions (Foyle et al. 1989, Parsons & Lear 2001), as well as the hypothesized top-down control of these invertebrates by large groundfish species (Worm & Myers 2003, Frank et al. 2006, Boudreau et al. 2011), the objectives of this study were to: (1) model crab and shrimp presence and abundance as a function of predator abundance, depth, bottom temperature, and bottom salinity; (2) estimate the spatio-temporal variability of the GWR coefficients; (3) determine scale effects of invertebrate–predator–environment relationships over time; and (4) compare model performances using non-spatial and spatial methods. We interpret the observed spatio-temporal relationships within the context of historical changes on the Newfoundland–Labrador Shelf and existing hypotheses on top-down versus bottom-up influences on snow crab and northern shrimp distribution and abundance.

MATERIALS AND METHODS

Study area

Relationships between invertebrates and explanatory variables were investigated off the eastern coast of Newfoundland–Labrador within the NAFO management divisions 2J, 3K, and 3L (Fig. 1). This region includes a large area (>300 000 km^2) of continental shelf extending from southern Labrador to the northern part of the Grand Banks of Newfoundland, and is characterized by relatively shallow outer banks intersected by several large troughs. The oceanographic regime is heavily influenced by the cold Labrador Current that flows southwards along the Labrador and Newfoundland coastline and at the edge of the continental shelf. Average bottom temperatures over most of the shelf range are from −1.0 to 0.0°C inshore to >3.0°C in the deeper trenches and on shelf slopes (Colbourne et al. 1997).

Distributions of cod *Gadus morhua*, crab *Chionoecetes opilio* and shrimp *Pandalus borealis* within the study area vary seasonally, although all 3 species have overlapping habitat preferences. In the 2J3KL area, snow crab are widely distributed across the shelf over a broad range of depths (Dawe & Colbourne 2002) and are generally associated with bottom temperatures between −1 and 4°C. Northern shrimp prefer near-bottom temperatures in the range of 2 to 6°C and muddy substrates (DFO 2010a), and are found in high-density aggregations in the northern range of the study area (2J3K). Atlantic cod are found throughout the study area at low densities, with denser aggregations forming during winter and spring in certain regions (Mello & Rose 2010, Rose et al. 2011) and have a tolerance for large ranges of

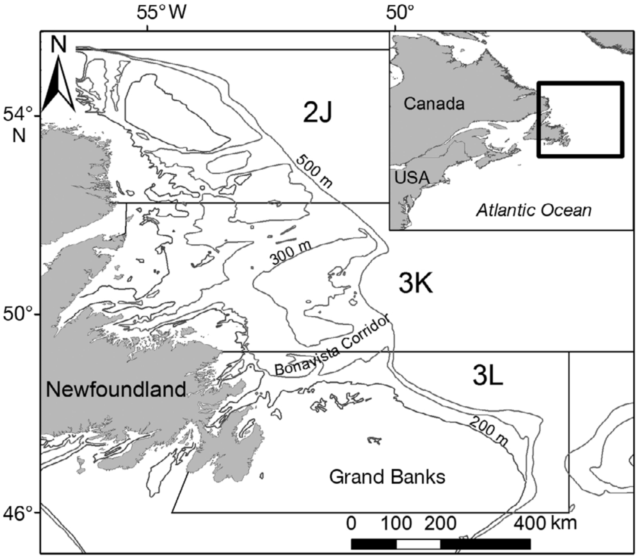

Fig. 1. The continental shelf off Newfoundland and Labrador, Canada (with 200, 300, and 500 m contours identified), showing the locations of the Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J, 3K and 3L, the Grand Banks of Newfoundland, and the Bonavista Corridor. The inset shows the location of the study area

depth (10 to >500 m) and temperatures (−1 to 10°C) (Rose 2005). The highest remaining concentrations of cod are found in the Bonavista Corridor, which spans the border between 3K and 3L (DFO 2010b).

Data sources

Fisheries scientific survey data (1995 to 2009) were obtained from the Department of Fisheries and Oceans Canada (DFO) and were collected during fall multispecies bottom-trawl surveys in NAFO Divisions 2J, 3K, and 3L. The survey employed a Campelen 1800 research bottom trawl and followed a stratified random design (Brodie 2005). Trawl catch weights (kg) and abundances of cod, snow crab, and northern shrimp were standardized according to the area swept (0.8 nautical miles in 15 min with a wing spread of 16.84 m), while mean bottom depth (m), temperature (°C), and salinity (ppt) were recorded for each set. Species weights and abundances were log-normalized to adjust for skewed distributions prior to statistical analyses.

Statistical analyses

The data analysis consisted of 2 steps: (1) identifying the core habitat of crab and shrimp by establishing the important environmental niche dimensions of each species; and (2) modelling the abundances of snow crab and northern shrimp within the identified core areas using bottom temperature, bottom salinity, depth, and Atlantic cod abundance as explanatory variables.

Core habitat identification

Niche theory assumes that a species occupies a theoretical ecological space that is limited by environmental determinants (fundamental niche) and that this niche is reduced further by competition, predation, and disturbance (realized niche) (Hutchinson 1957). Depth and temperature are known to be key factors that determine invertebrate distribution and survival (Foyle et al. 1989), and as such, these variables were chosen to define the habitat models for both species.

To increase the robustness of core habitat identification given the species patchiness, the cumulative distribution function (CDF) of crab and shrimp abundance was randomly resampled over depth and bottom temperature (1000 replicates with replacement) as suggested by Rooper & Martin (2009). The average resampled CDFs were then used to generate habitat limits for each environmental variable for each year to account for changes in species abundance and climate over time. The potential effects of sampling error and outliers were avoided by narrowing the habitat limits to the 5th and 95th percentiles of the cumulative distribution for each species. Trawl locations falling within these percentiles for depth and temperature were considered to be the core habitat of the species over which abundances were modelled in the second stage of the analysis.

Species modelling

GWR was applied to investigate spatial patterns and scale dependency of relationships between invertebrate species and variables hypothesized to be important to their distribution off Newfoundland–Labrador. The abundances of snow crab and northern shrimp within the identified core areas were modelled separately for each year of the time series using bottom temperature, bottom salinity, depth, and Atlantic cod abundance as explanatory variables. The analysis for snow crab abundance used data from 2J, 3K and 3L, while the analysis for northern shrimp was limited to 2J and 3K, due to the more northern distribution of this species at the time of this study. Given the highly correlated relationships between bottom temperature, depth, and salinity, the relationships between crustaceans and predictor variables were paired separately in univariate models to avoid the effects of interactions and multicollinearity on the coefficient estimates (Graham 2003, Wheeler 2007).

The GWR model represents an extension of the traditional linear regression by incorporating a set of geographic locations for each observation point, such that:

$$y_i(u_i,v_i) = \beta_0(u_i,v_i) + \beta_i(u_i,v_i)x_1 + \beta_i(u_i,v_i)x_2 + \varepsilon_i(u_i,v_i) \quad (1)$$

where y_i is the dependent variable, β_0 is the intercept coefficient, x_1 and x_2 are explanatory variables, β_1 and β_2 are the parameter coefficients, ε is the error term, and (u_i,v_i) are spatial coordinates for each location i in space. The statistical background and methodology of GWR is detailed in Fotheringham et al. (2002). The radius of the local GWR model can be determined by a fixed Euclidian distance–decay function or an adaptive kernel function that uses a minimum number of nearest neighbours. A fixed spatial kernel (bandwidth) of 100 km was selected based on optimization of a corrected Akaike information criterion (AICc) (Fotheringham et al. 2002) and was applied to every GWR model to ensure consistency in the time series. The AICc is a relative measure of model performance corrected for the number of parameters, where the model with the smallest AIC represents the closest approximation to reality, and differences in values >3 are assumed to represent a significant improvement (Fotheringham et al. 2002). The bi-square distance decay function took the form:

$$w_{ij} = \exp[-(d_{ij}/b)^2]^2 \tag{2}$$

where d_{ij} is the Euclidean distance between the 2 observation sites i and j and b is the bandwidth in map units.

GWR assumes linear relationships between response and predictor variables, and when this assumption is not met, it can result in spatial patterns of coefficients that are the outcome of model misspecification rather than real ecological phenomena (Austin 2007). Given that species often exhibit curvilinear, skewed, or bimodal responses along environmental gradients that define their habitat (Austin 2002), we investigated this potential source of statistical bias by testing for nonlinear relationships using generalized additive models (GAMs). GAMs represent an extension of the generalized linear model (GLM), and have previously been used in fisheries research for a wide range of species–environment modelling exercises (Murase et al. 2009). A GAM fits a smoothing curve through the data and allows nonlinear response curves to be modelled. In a GAM, a smoothing function (f_i) is used in place of the coefficient β_i, such that:

$$y_i = \beta_0 + f_i x_i + \varepsilon_i \tag{3}$$

where f_i is a non-parametric function describing the effect of x_i on y_i. A Gaussian GAM was fitted using an identity link function and penalized regression splines with automatic smoothness selection (Wood 2006). GAM analyses were carried out in R v. 2.8.1 (R Development Core Team 2012), using the 'mgcv' package V. 1.5-5 (Wood 2006).

In the case where a significant ($p(\chi) < 0.05$) nonlinear relationship was identified in a GAM univariate model, a second-order polynomial transformation was applied to the dependent variable and subsequently tested in the GWR in addition to the log-transformed predictor variable (Miller & Hanham 2011). While it is recognized that species–environmental response curves can take many forms (Austin 2002), our nonlinear analysis was limited to the second-order polynomials as niche theory assumes a symmetric bell-shaped response curve that is more easily interpretable than more complex polynomial transformations. The GWR results from the linear (log) and nonlinear (polynomial) transformations were compared using the AICc.

Maps of GWR coefficient estimates were generated for both the shrimp and crab time series to show how the associations between response and predictor variables varied across the study area and over time. A subset of the time series was chosen to compare the spatial patterns of GWR coefficients during contrasting periods of relatively high/low species abundances and ocean temperatures. These years also had to meet the criteria of having no significantly nonlinear relationships between response and predictor variables. Only significant coefficients (>95%) were displayed, as determined by *t*-values for each local regression (Mennis 2006). GWR analyses were performed in R v. 2.15.0 (R Development Core Team 2012), using the 'spgwr' package (Bivand & Yu 2012), and the results were imported into ESRI's ArcGIS (v. 9.3) for spatial analyses and mapping.

Spatial stationarity in the relationships between invertebrates, temperature, and cod can be expected to vary according to spatial scale. Using progressively larger increments of GWR bandwidth (50, 100, and 200 km), the spatial scale of these relationships was investigated using a spatial stationarity index, where the interquartile range of a given GWR coefficient was divided by twice the standard error (SE) of the same variable from the equivalent global ordinary least-squares regression (Fotheringham et al. 2002). Given that 68% of the global values are within ±1 SE and 50% of the GWR values are within the interquartile range, ratio values >1 suggest spatial non-stationarity between the independent and dependent variables. Stationarity indices for each bandwidth were plotted over time to compare within-year scale differences as well as differences through time.

Finally, the overall ability of GWR models to predict local crab and shrimp abundances per year was tested by combining all explanatory variables in multivariate GWR models at a 100 km bandwidth. The overall spatial patterns of model performance were explored visually by mapping local coefficients of variation (R^2) from all multivariate models per species and creating an interpolated surface using inverse distance-weighting techniques.

RESULTS

Exploratory analysis of mapped species distributions over the time series revealed general geographic trends within the study area. Atlantic cod *Gadus morhua* were widely distributed in low numbers, but concentrated in the Bonavista Corridor area, at the offshore border between NAFO Divisions 3K and 3L (Fig. 1). Crab *Chionoecetes opilio* were also widely distributed, with higher concentrations in 3K and along the northern slopes of the Grand Banks in 3L, with overall capture rates of 79% over the time series. Shrimp *Pandalus borealis* were found in very high densities in the northern extent of the study area (2J and 3K), and were captured in 83% of the trawls in 2J/3K from 1995 to 2009. Pooled catches for crab and shrimp were both positively skewed across all years (skewness = 8.24 and 9.74, respectively) and were dominated by several large catches and many samples without catches or low numbers.

The CDFs, pooled over the time series (1995 to 2009), revealed that 90% of crab were found between −1 and 4°C and at depths between 100 and 500 m, while 90% of shrimp were found between 0 and 4°C and depths of 150 to 450 m (Fig. 2). Over the time series, 88 to 99% of the stations within the core area had crab present (mean = 95%). The percentages of shrimp found at core area locations were similarly high at 96 to 100% (mean = 99%). Habitat models for both species were weak in accurately predicting the absence of each species at trawl locations outside the core areas. This was likely a result of the cumulative distribution functions not accounting for 10% of overall species abundance; therefore, the calculated environmental niche limits were narrower than the actual species tolerances for depth and temperature. However, the habitat models reflected the overall niche dimensions for the majority (90%) of catches for each species, and this was likely the cause of the relatively high percentages of species occurrence within the core areas.

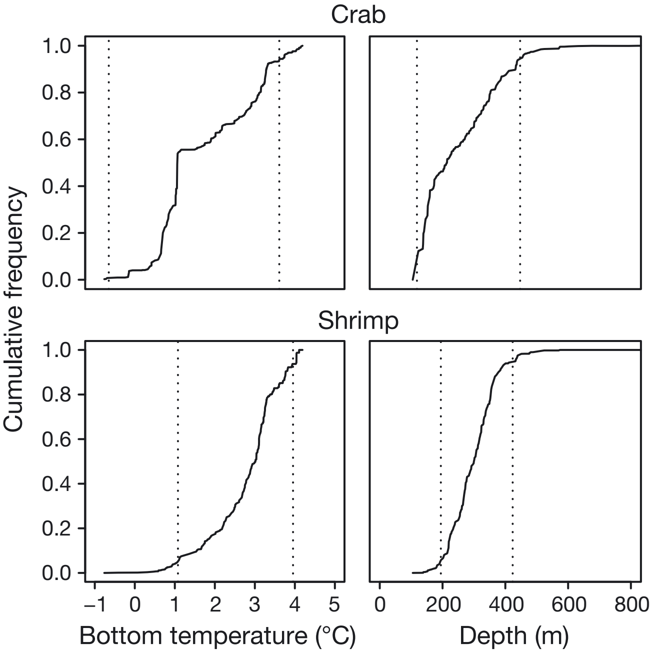

Fig. 2. *Chionoecetes opilio* and *Pandalus borealis.* Examples of the cumulative frequency of snow crab and northern shrimp abundance as a function of bottom temperature (°C) and depth (m), with 5th and 95th percentiles indicated by dotted lines. Data were derived from the 2001 fall multi-species bottom trawl surveys in Northwest Atlantic Fisheries Organization Divisions 2J, 3K, and 3L

GAM and GWR models were fitted to each of the 4 univariate relationships (bottom temperature and salinity, depth, cod abundance) per invertebrate species per year, resulting in a total of 120 models for each of the regression methods. The overall incidence of nonlinearity between crustacean abundance and predictor variables was relatively low for shrimp (6 out of 60 univariate GAM models) and higher for crab (15 out of 60 univariate GAM models). However, out of the 15 models of crab with nonlinear transformations, only 3 performed significantly better (AICc difference > 3) than the equivalent linear model in the GWR analysis (Table 1a). For shrimp, 5 of the 6 nonlinear models performed significantly better than the equivalent linear model (Table 1b). The incidence of nonlinear relationships was spread evenly between crab and environmental predictors over the time series, with no nonlinear relationships found between crab and cod. Of the few nonlinear relationships found between shrimp and the predictor variables, most were found with bottom temperature and salinity and none were found with depth.

Depth was consistently the best, or equivalent to the best, predictor for crab abundance in 13 of 15 yr in the time series (Table 1a). No crab–cod pairings resulted in the best model for any year. Of the 6 crab–depth models with nonlinear relationships, only 2 of the polynomial transformations resulted in significantly better models compared to models using standard linear transformations. Bottom temperature was the most consistently superior predictor of shrimp abundance in 8 out of 15 yr (Table 1b). Cod also performed well as a predictor of shrimp abundance relative to the other variables in 5 of the survey years.

Average GWR coefficients of crab models over the time series revealed a mostly negative relationship with cod abundance, bottom temperature and salinity, and a very weak positive relationship with depth

Table 1. *Chionoecetes opilio* and *Pandalus borealis*. Comparison of fit for univariate geographically weighted regression models used to predict (a) snow crab and (b) northern shrimp abundance in Northwest Atlantic Fisheries Organization Divisions 2J, 3K, and 3L from 1995 to 2009. Relative corrected Akaike information criterion (AICc) values are shown for linear (L) and nonlinear (NonL: second-order polynomial transformation) models, with values relative to the lowest AICc score per year. Independent variables included Atlantic cod *Gadus morhua* abundance, bottom temperature (°C; Temp), bottom salinity (ppt; Sal), and trawl depth (m). Models not used indicated by dash (–)

Year	n	Relative AICc							
		Cod		Temp		Sal		Depth	
		L	NonL	L	NonL	L	NonL	L	NonL
Chionoecetes opilio									
1995	172	14.2	–	0	–	8.26	3.95	5.08	–
1996	257	37.27	–	10.23	–	7.12	12.17	0	5.45
1997	263	26.83	–	28.56	–	20.05	–	0	–
1998	242	22.52	–	17.7	–	5.8	0	10.86	–
1999	253	12.32	–	5.56	–	0	1.91	1.99	–
2000	186	5.92	–	6.62	–	7.11	–	0	–
2001	251	32.06	–	21.73	–	24.57	23.84	0	0.94
2002	238	0.32	–	9.36	11.49	11.64	–	0	–
2003	261	14.8	–	3.86	0	3.12	–	0.71	–
2004	243	13.17	–	8.59	11.47	6.2	–	0	–
2005	308	39.74	–	27.7	–	45.27	–	6.35	0
2006	260	67.34	–	50.53	–	86.2	–	12.32	0
2007	218	49.41	–	39.28	–	65	–	0	2.31
2008	209	37.01	–	27.39	–	38	–	0	–
2009	228	47.59	–	30.34	31.99	55.07	–	0	5.46
Pandalus borealis									
1995	83	6.85	–	0	–	4.4	–	1.38	–
1996	95	18.53	–	6.99	–	8.37	–	0	–
1997	123	39.71	–	38.2	21.35	38.79	0	51.6	–
1998	121	13.75	–	7.43	–	0	–	13.27	–
1999	104	5.16	–	2.21	–	0	–	3.52	–
2000	107	27.87	–	6.86	0	7.69	8.15	25.23	–
2001	122	0	–	11.49	–	10.76	–	8.59	–
2002	125	21.72	–	9.33	–	11.75	–	0	–
2003	122	16.86	–	0	–	4.16	–	3.87	–
2004	114	4.64	–	0	–	5.45	–	2.18	–
2005	136	0	–	4.11	–	5.14	–	5.15	–
2006	119	46.83	0	78.7	–	88.4	–	84.1	–
2007	118	0	–	0.33	–	7.78	–	3.52	–
2008	114	51.79	–	23.01	0	42.33	–	31.13	–
2009	101	1.59	–	0	–	8.36	–	11.49	–

(Fig. 3a). In contrast, GWR coefficients of shrimp models revealed mostly weak positive relationships with temperature, salinity, and depth, and a mostly negative relationship with cod (Fig. 3b). Mean shrimp–cod relationships appeared to alternate between positive and negative coefficients every 3 to 4 yr (Fig. 3b). For both species, salinity and temperature coefficients had the highest variability, while depth and cod coefficients had the lowest over the time series. GWR salinity coefficients showed a marked decrease in variability after 2004 for both species.

The spatio-temporal variation of GWR parameter coefficients was explored visually for each species, resulting in a series of maps that contrast invertebrate–habitat associations in years of different ocean climate conditions and relative overall abundance. GWR coefficients for crab models were mapped for the 1997 and 2008 surveys, which contrasted periods of relatively high/low crab abundance, cooler/warmer bottom temperatures, and lower/higher cod abundance, respectively (Fig. 4). In both periods, the spatial pattern of GWR cod coefficients revealed a very weak and mostly non-significant relationship with crab throughout the study area. Crab–depth associations were positive in the inshore areas of 2J and 3K as well as offshore 3K in 2008, and negative on offshore slopes of the Grand Banks in 2008. GWR salinity and temperature coefficients followed a similar spatial pattern as depth in both years, although these relationships were mostly non-significant. GWR coefficients for shrimp models were mapped for the 1998 and 2007 surveys in 2J and 3K, which contrasted periods of relatively low/high shrimp abundance, cooler/warmer bottom temperatures, and lower/higher cod abundance, respectively. Spatial patterns of coefficients differed greatly between the 2 periods, with mostly weak positive or non-significant relationships between shrimp and predictor variables in 1998, and weak negative or non-significant relationships in 2007 (Fig. 5).

Spatial scaling of the GWR bandwidths (i.e. gradually expanding the local regressions until they approached a global model) revealed that the relationships between both invertebrate species and predictor variables became spatially stationary on average between 100 and 200 km (Fig. 6). The spatial stationarity of GWR cod coefficients was relatively constant in crab models at 100 km, while shrimp–cod associations varied over the time series and achieved stationarity at scales of <100 km in many years. Large fluctuations in spatial non-stationarity were found for relationships with environmental variables at smaller (50 km) and medium (100 km) scales, making it difficult to establish a clear pattern or trend for either species. Nearly all relationships became stationary at the largest bandwidth tested (200 km) (Fig. 6).

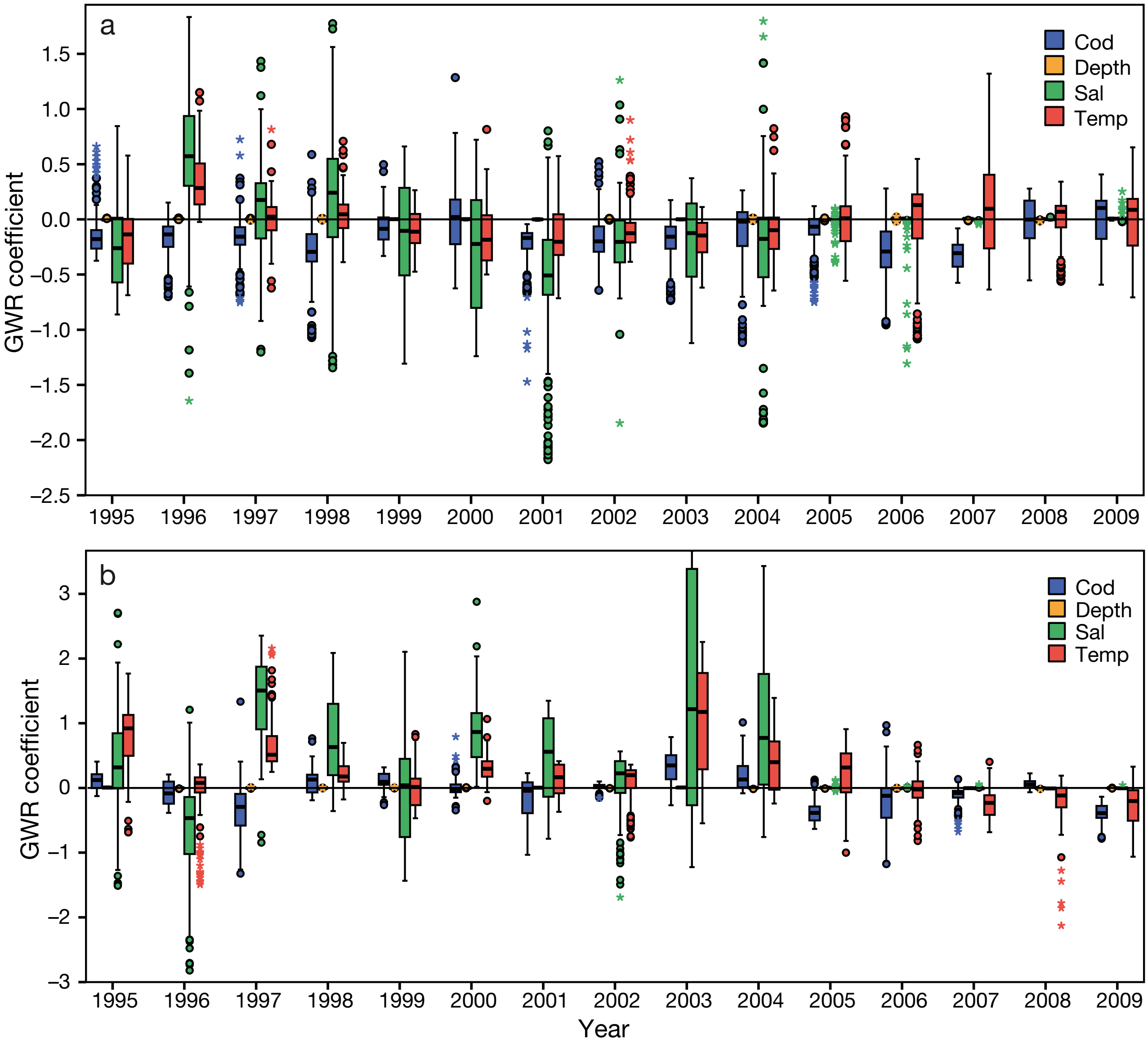

Fig. 3. *Chionecetes opilio* and *Pandalus borealis*. Non-standardized coefficients for univariate geographically weighted regression (GWR) models of (a) snow crab and (b) northern shrimp abundance predicted by cod *Gadus morhua* abundance, depth, bottom salinity (Sal) and bottom temperature (Temp) at 100 km bandwidths. Boxplots show the mean, lower and upper quartiles, and outliers of each GWR coefficient per year for the 1995 to 2009 timeline with outliers shown by star symbols

When all explanatory variables were combined, the amount of variance explained by the GWR models at 100 km bandwidths averaged 37 % for crab and 35 % for shrimp models over the time series (Fig. 7). Model performance for predicting crab abundance appeared to follow a repeating cycle of higher and lower R^2 values every 6 yr, although our ability to establish a clear pattern is limited by the length of the time series. Performance of shrimp models peaked in 1997, with a mean explained variance of 67 %, although much lower R^2 values (22 to 26 %) were observed in other years (Fig. 7). The spatial variability of local R^2 estimates was explored by mapping these results for all years, and revealed that, on average, crab models performed best near the fringes of the study area and more poorly near the centre (Fig. 8). Shrimp models performed best near the inshore area in 3K and throughout 2J, and more poorly throughout the remainder of 3K. Overall, the predictor variables used in this study were better able to model crab compared to shrimp distributions, with higher levels of explained variance throughout the study area.

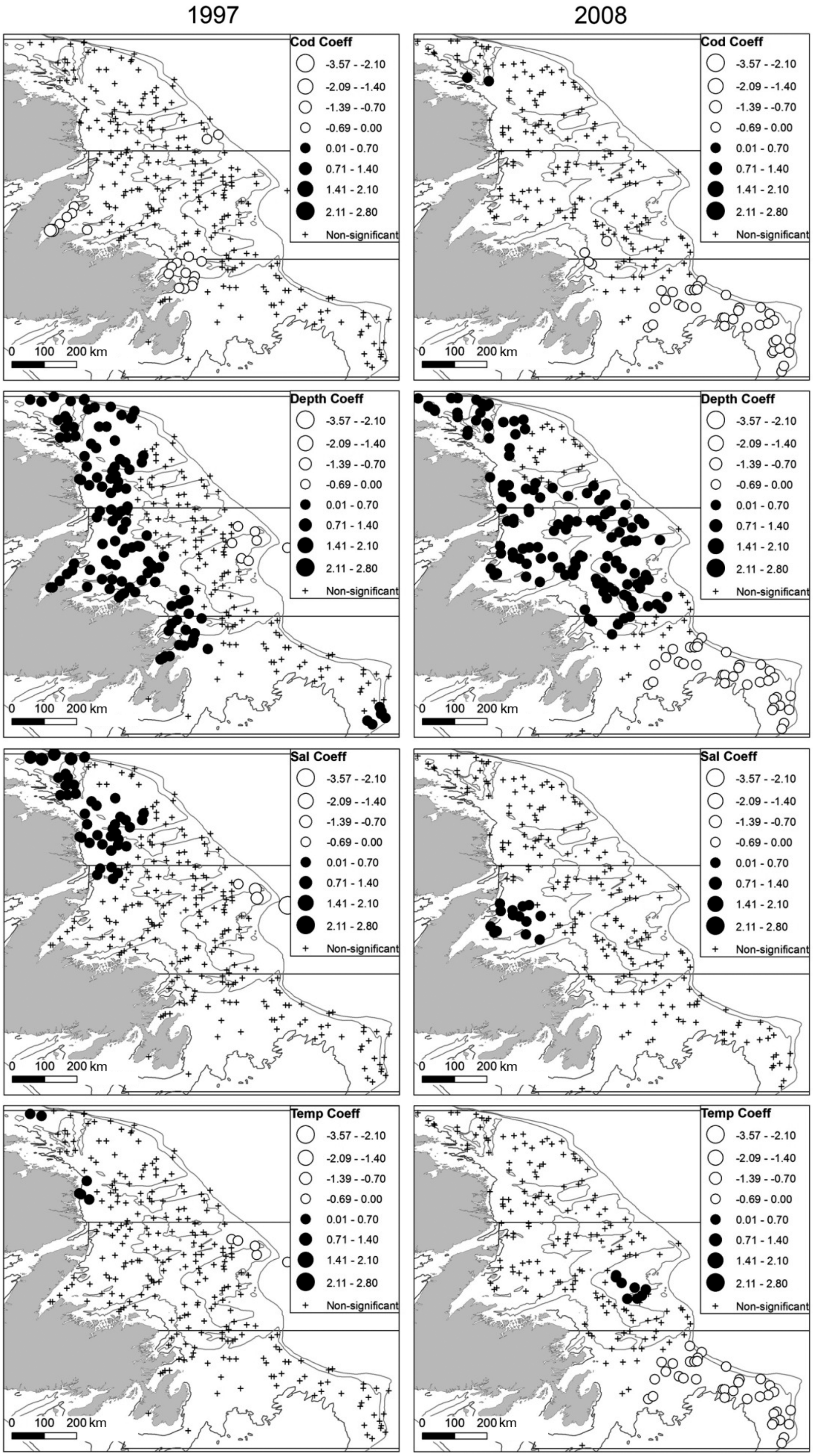

Fig. 4. *Chionoecetes opilio*. Spatial distribution of geographically weighted regression coefficients that were significant in predicting snow crab abundance in 1997 and 2008. The 2 years contrast periods of relatively high/low crab abundance, cooler/warmer bottom temperatures, and lower/higher cod *Gadus morhua* abundance, respectively. Open circles: negative coefficients; closed circles: positive coefficients; crosses: non-significant values. Horizontal lines are NAFO divisions (see Fig. 1)

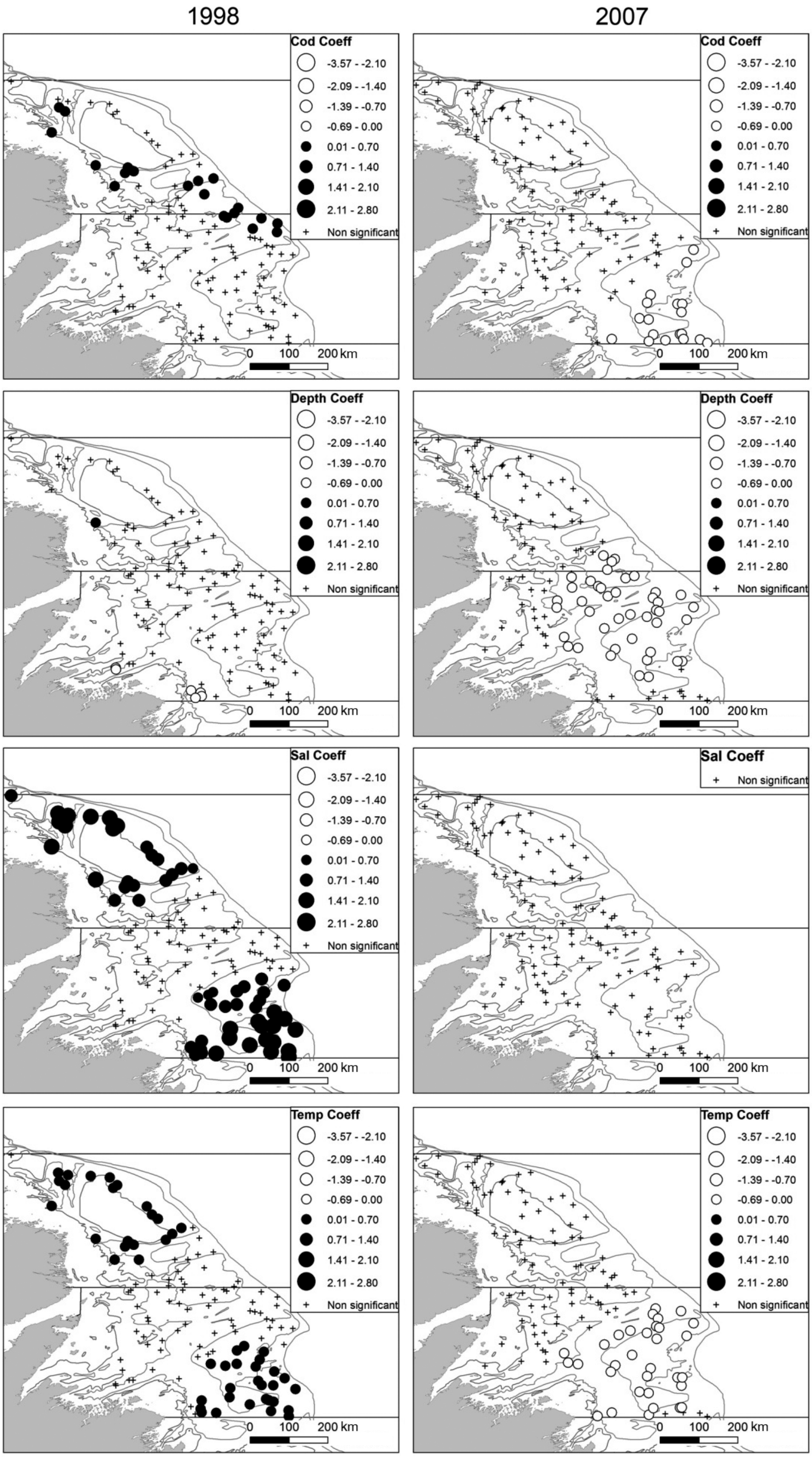

Fig. 5. *Pandalus borealis*. Spatial distribution of geographically weighted regression coefficients that were significant in predicting northern shrimp abundance in 1998 and 2007. The 2 years contrast periods of relatively low/high shrimp abundance, cooler/warmer bottom temperatures, and lower/higher cod *Gadus morhua* abundance, respectively. Open circles: negative coefficients; closed circles: positive coefficients; crosses: non-significant values. Horizontal lines are NAFO divisions (see Fig. 1)

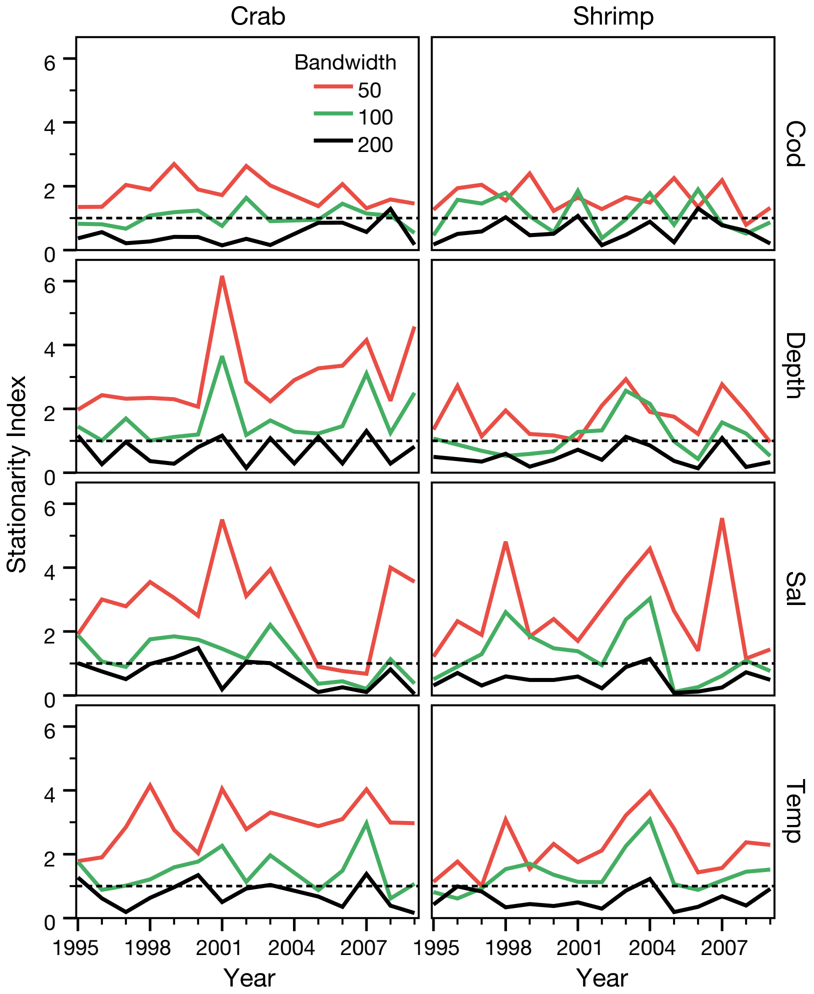

Fig. 6. *Chionoecetes opilio* and *Pandalus borealis.* Spatial stationarity index for geographically weighted regression (GWR) coefficients of cod *Gadus morhua*, depth, and bottom salinity (Sal) and bottom temperature (Temp) used to model snow crab and northern shrimp abundance over multiple bandwidths, from 1995 to 2009. The index is calculated by dividing the interquartile range of a GWR regression coefficient by twice the SE of the same parameter estimate from the global model. Spatial non-stationarity is suggested by values >1 (below dashed line)

DISCUSSION

Our models of spatio-temporal variation of snow crab *Chionoecetes opilio* and shrimp *Pandalus borealis* in the Newfoundland–Labrador region, accounting for both putative top-down (predation by cod) and bottom-up (indexed by depth, temperature, and salinity) factors, indicated both commonalities in factors and differences, and strong spatial dependence. For snow crab, depth was the best predictor of distributions in both linear and nonlinear models, being a proxy for several environmental variables (temperature, salinity, pressure, and sediment type) and consistently outperforming cod *Gadus morhua* as a predictor of crab distribution and abundance. This predominance of environmental effects supports the importance of bottom-up processes for this species (Foyle et al. 1989, Dawe & Colbourne 2002, Dawe et al. 2008, Boudreau et al. 2011). The results of GWR univariate models of shrimp were less definitive in terms of bottom-up and top-down control, as cod was the best predictor of shrimp distribution from 2005 to 2009 in most cases, but environmental factors also were influential. An increasing abundance of cod in the region since 2005 (DFO 2010b), as well as recent warming trends that would impact the availability of suitable habitat for shrimp, may have influenced this result.

GWR time-series analysis revealed that the regression relationships between crab, shrimp, environmental parameters, and cod were spatially non-stationary and varied through time. Hence, globally averaged relationships are likely to mask important spatial variability that occurs across the Newfoundland–Labrador Shelf. Depth, temperature, and salinity are generally strongly correlated in this region (Colbourne et al. 2009), and mapped GWR parameter estimates for these variables tended to follow similar spatial patterns. Where significant, crab tended to have stronger positive associations with nearshore environmental variables and weaker negative associations with offshore environmental parameters. This weak negative association with temperature was more widely distributed in the south during relatively warm years. These patterns fit with the average distribution of bottom temperatures across the shelf, with the cold inshore branch of the Labrador Current flowing south along the coast and over the top of the Grand Banks, and warmer temperatures in the deeper offshore water (Colbourne et al. 1997). Given that crab are seldom found at temperatures >5 to 6°C, the positive association with cold (<0°C) inshore waters is consistent with their temperature range. In contrast, the warmest waters of the offshore basins and trenches have typically been around 4°C, and in recent years have increased to near 5°C (Colbourne et al. 2009),

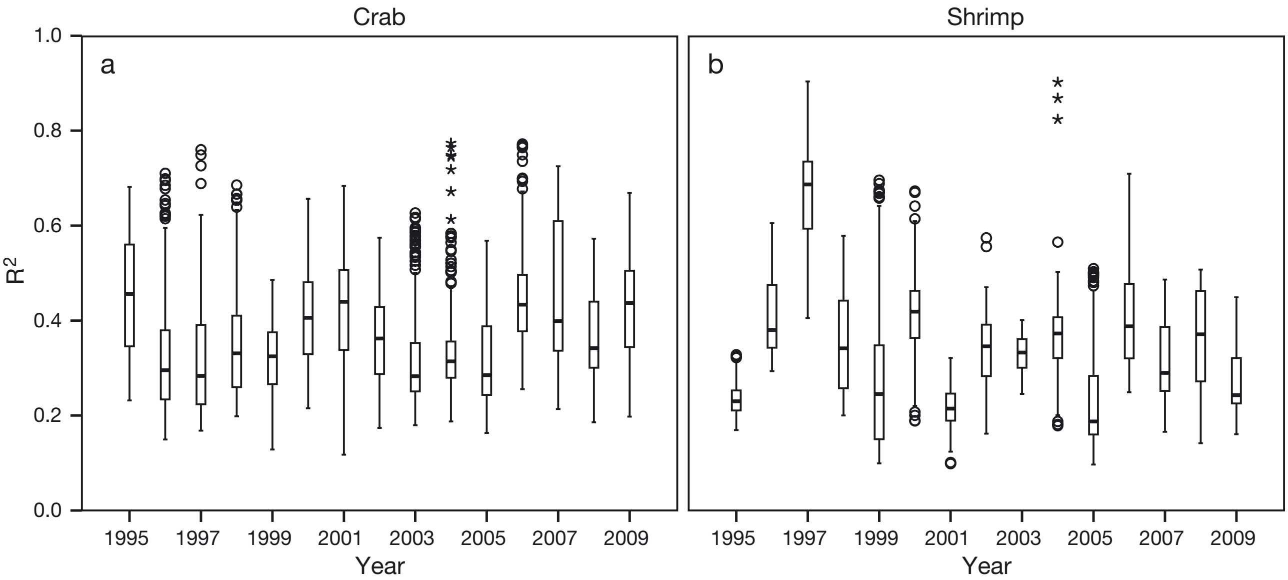

Fig. 7. *Chionoecetes opilio* and *Pandalus borealis*. Explained variance (local R^2) values from geographically weighted regression multivariate models of (a) crab and (b) shrimp abundance as a function of cod *Gadus morhua* abundance, depth, and bottom salinity and bottom temperature, for the period from 1995 to 2009

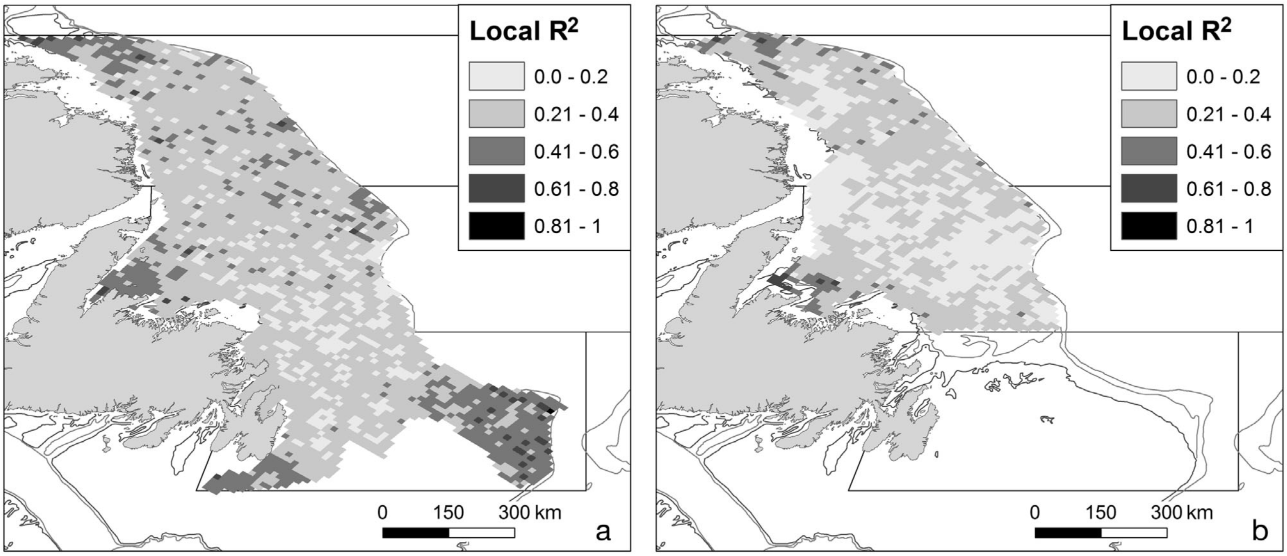

Fig. 8. *Chionoecetes opilio* and *Pandalus borealis*. Mapped distribution of the average explained variance (local R^2) of geographically weighted regression multivariate models of (a) crab and (b) shrimp abundance as a function of cod *Gadus morhua* abundance, depth, and bottom salinity and bottom temperature, for the period from 1995 to 2009. Resolution is at the 10 km × 10 km scale. Black lines show NAFO divisions (see Fig. 1)

which is near the upper range for these crustaceans. We note that crab had a more negative relationship with temperature in the southern offshore area during a relatively warm period and a more positive relationship in the northern inshore area during a cooler period and that this may be indicative of temperature constraints near the edges of preferred habitat. Overall, the temporal and spatial patterns of crab–environment relationships are consistent with known species tolerances and reinforce the importance of ocean climate on the distributions of this species (Foyle et al. 1989). The spatial patterns of shrimp and environmental relationships differed greatly between the beginning and end of the time series, although they tended to follow similar patterns within years. These differences may be the result of an overall warming trend in the ocean conditions over the time series (Colbourne et al. 2009), as well as a large increase in shrimp abundance in this region over the same period (DFO 2010a).

Interpreting predator–prey relationships requires consideration of the environmental variability that may influence overlap between species and potential contact scales (Rose & Leggett 1990, Bailey et al. 2010). Coincident catches of various species may represent similar habitat preferences rather than predator–prey dynamics, and as such we interpret the spatial relationships between invertebrates and cod as complementary to more direct evidence. Diet studies have shown that in the 1970s and 1980s, when cod were more abundant than at present, snow crab comprised a minor proportion of prey for cod (0 to 8% by mass) in most seasons in regions of the Newfoundland–Labrador Shelf (Lilly 1984). In the 1990s and 2000s, the much reduced cod stocks have shown a similar low incidence of feeding on snow crab (Sherwood et al. 2007). Consistent with the diet data, we found that crab and cod had a relatively weak and mostly negative spatial relationship throughout the study area.

The models of spatial association between cod and crab would have benefited from size- or sex-partitioned data, because predation by cod on snow crab is size and sex dependent. Small cod likely avoid the larger male crab, and larger cod feed mainly on smaller size classes of crab, which are mainly females (Chabot et al. 2008). Hence, some of the spatial patterns observed could have resulted from differences in the overlap between size classes of each species. Furthermore, there is evidence that smaller crabs are not always effectively sampled by survey bottom trawls, depending on surficial geology (Dawe et al. 2010), which could bias analyses of crab distribution. Nevertheless, our findings of stronger relationships between crab and environmental predictors and mostly non-significant relationships between crab and cod throughout the study period do not lend support to the theory of a top-down control on snow crab by cod, at least not in the size ranges of crab sampled by the scientific survey.

In contrast to crab, shrimp are a frequent prey item for cod in 2J, 3K and 3L (Parsons 2005, Sherwood et al. 2007). Spatial patterns of GWR coefficients showed an alternating pattern of positive and negative relationships between cod and shrimp throughout the time series, although this association was mostly negative during the warmest years (2005 onwards). On average, the shrimp–cod relationships were negative and were consistent with previously found trends in cod and shrimp interactions (Worm & Myers 2003). Cod and shrimp have similar habitat preferences, and this relationship may indicate opportunistic predation by cod. It is interesting to note that GWR cod coefficients predicting shrimp were mostly non-significant or positive in the northern range during a year of lower shrimp and cod abundance and cooler bottom temperatures and mostly non-significant or negative during a later period of higher shrimp and cod abundance and bottom temperatures. The negative shrimp–cod relationship in 2008 was mostly found near the Bonavista Corridor, where the offshore cod population is concentrated and has increased in recent years (DFO 2010a). Hence, our findings are consistent with the notion that shrimp have been subjected to some degree of top-down control by cod in this relatively simple food web (Worm & Myers 2003, Frank et al. 2005).

The combined ability of all explanatory variables to predict crab and shrimp abundance was generally poor over the time series, suggesting an incomplete set of predictors in the models. Other factors for which data were not available almost certainly influence crustacean distribution and abundance, especially bottom substrate (Tremblay 1997, Dionne et al. 2003). Moreover, both known and unknown factors are almost certain to interact. For example, a suitable substrate becomes an unsuitable habitat if local temperatures diverge from the physiological range of tolerance for the species. Such appears to be the case on the Newfoundland–Labrador Shelf in recent years for the cold-adapted crustaceans as a consequence of a warming ocean, as evidenced by negative temperature relationships in warm years along the southern extent of the study area.

Central to the findings of this study, spatial information and analyses (GWR) enabled the identification of region-wide patchiness not only in species distributions but in the relationships among species, environmental determinants, and predators that would have been masked by traditional global regression methods. Both crab and shrimp had non-stationary relationships with predictor variables at small and medium bandwidths, and generally achieved stationarity at the largest GWR bandwidths, suggesting that an appropriate scale of analysis for these variables is between 100 and 200 km. Spatial non-stationarity was higher at smaller scales for invertebrate–environment relationships compared to invertebrate–cod relationships. This may have resulted from spatial variability in the underlying processes affecting invertebrate distributions, as well as the consistently low abundance of cod throughout the study area during the fall surveys used in this study. It is unclear why certain years exhibited increased non-stationarity at multiple scales compared to multi-year averages. For example, spatial non-stationarity of crab–environment relationships increased from 2000 to 2001 and from 2007 to 2009, perhaps as a result of survey-derived bottom temperatures showing a relatively large decrease in 2000 and an increase from 2006 to 2009. The increased spatial non-stationarity of shrimp–environment relationships in 2004 may be due to reduced survey coverage for this year. We note that shrimp–cod relationships showed an alternating pattern of spatial non-stationarity over the time series, which may be related to the recruitment of shrimp cohorts occurring on similar cycles (DFO 2010a). Spatial and temporal patterns in GWR coefficients such as these could help identify areas for more focused species distribution modelling. In addition, our finding that the scale of stationarity was dynamic over space and time highlights the difficulty of translating locally observed predator–prey interactions to the scale of populations and regions in ecological models (Hunsicker et al. 2011). These results emphasize the utility of GWR as an exploratory method for revealing spatial trends in a dataset that can subsequently be analyzed using other statistical tools more appropriate for inference testing.

Time-series analyses revealed dynamics in abiotic and biotic relationships over a 15 yr period from 1995 to 2009 that are likely to continue if waters continue to warm and cod (and capelin) continue to increase and crustaceans decline. We believe that the 2-stage analysis employed in this paper holds promise to disentangle these relationships, by addressing both the statistical and ecological challenges inherent in modelling such large-scale species distributions and their dynamics. In addition, estimating cumulative abundance frequencies over biologically relevant environmental variables aided the establishment of habitat limits (Rooper & Martin 2009). The cumulative frequency method led to improved predictions of the presence of invertebrates, normality of distributions, and analysis of species distributions in areas with appropriate habitat.

As a final comment, it is worth emphasizing that predator associations with potential prey, and hence any suggestion of top-down control by cod in these large marine ecosystems, were not universal and differed among prey species. Previous studies of cod interactions have focussed on only a single prey, be it shrimp (e.g. Worm & Myers 2003) or crab (Boudreau et al. 2011) and, hence, could not make inter-species comparisons. Unfortunately, spatial data on capelin, formerly and still in some regions the chief prey of cod in Newfoundland–Labrador ecosystems (Link et al. 2009), are not available, but existing survey data indicate that capelin biomass collapsed about the same time as that of cod did, in the early 1990s (DFO 2011). Moreover, diet and isotope studies indicate that cod that formerly fed on capelin switched to shrimp in the 1990s (Sherwood et al. 2007). These findings alone indicate that cod could not have had a top-down influence on their chief prey but that the lack of capelin likely resulted in an increase in shrimp consumption. Overall, these findings suggest that trophic interactions are seldom simple or universal and cannot be expressed for an ecosystem in terms of relationships among a single pair of species. Only a multi-species spatial ecosystem model has the potential to quantify these influences simultaneously, but the present work demonstrates the likelihood that these complexities exist.

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Contribution to the Theme Section 'Effects of climate and predation on subarctic crustacean populations'

Effects of temperature on size-at-terminal molt and molting frequency in snow crab *Chionoecetes opilio* from two Canadian Atlantic ecosystems

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ABSTRACT: The effect of temperature on molting frequency and size-at-terminal molt of the snow crab *Chionoecetes opilio* was investigated and compared between 2 Canadian Atlantic ecosystems based on spring and summer surveys. We found that the size-at-terminal molt was directly related to temperature but that the effect of temperature was much clearer and occurred at smaller sizes for females than for males. By focusing on recently molted (new-shelled) crabs, we showed that size-at-terminal molt is conditioned by temperature over a variable number of instars and intermolt periods leading up to the terminal molt. Crabs of both sexes larger than about 50 mm carapace width (CW), on annual molting schedules, sometimes skipped a molt. The frequency of skip-molting differed between the areas and sexes, and was directly related to size and inversely related to temperature. We develop a hypothesis to explain the relationships of terminal size with temperature and molting frequency that is consistent with life-history theory and snow crab bioenergetics and considers differences between the sexes. The implications to natural mortality and recruitment to fisheries are also discussed.

KEY WORDS: Snow crab · Terminal molt · Molting frequency · Size · Temperature · Atlantic Canada

INTRODUCTION

The commercial fishery for snow crab *Chionoecetes opilio* in Atlantic Canada began in the mid-1960s in the southern Gulf of St. Lawrence (sGSL) and rapidly expanded to cover fishing grounds along the Canadian coast and continental shelf from southern Nova Scotia to southern Labrador. These fishing areas are currently divided into 61 management zones with total landings of approximately 84 000 t valued at 280 million Canadian dollars in 2010 (Moriyasu 2011). The snow crab is a highly stenothermal subarctic species, inhabiting very cold waters of about −1.5°C to 4°C (Dawe & Colbourne 2002, Orensanz et al. 2007, Sainte-Marie et al. 2008). Fisheries in the northwest Atlantic are conducted on the Newfoundland and Labrador shelf, in the Gulf of St. Lawrence (GSL), and on the Eastern Scotian Shelf (ESS) (see Fig. 1), with Newfoundland and Labrador and the sGSL accounting for most of the landings in most years (FRCC 2005). All Atlantic Canadian snow crab fisheries target only males, with a minimum legal size of 95 mm carapace width (CW). Snow crabs undergo a terminal molt across a broad size range (Hartnoll et al. 1993, Conan & Comeau 1986). Males terminally molt over a broader size range than females, such that females do not grow to the minimum legal size of the fishery. In Atlantic Canada, the size-at-terminal molt ranges about 40 to 150 mm (postmolt) carapace width (CW) in males (Sainte-Marie & Hazel 1992, Sainte-Marie et al. 1995) compared to about 30 to 95 mm (postmolt) CW in females

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(Alunno-Bruscia & Sainte-Marie 1998). Most males terminally molt at one of 5 successive instars, whereas most females terminally molt (and achieve maturity) at one of 2 successive instars (Alunno-Bruscia & Sainte-Marie 1998, Comeau et al. 1998, Orensanz et al. 2007, Burmeister & Sainte-Marie 2010). The reasons for high variability in terminal size are not fully understood, but the broad size range of both sexes implies that some biotic or abiotic factors affect snow crab growth and maturation (Foyle et al. 1989).

Growth in snow crabs, as in all crustaceans, is a step-wise process between successive stages (instars) and is a function of both molting frequency and the size increase at molting (molt increment), as described by Sainte-Marie et al. (1995) for the northern Gulf of St. Lawrence (nGSL). Early benthic juveniles molt frequently until instar VI, at about 20 mm CW, following which molting occurs on a near annual schedule during spring. At around this size, the first event in sexual maturation of females (i.e. the prepuberty molt) marks the onset of ovary development, and is accompanied by a decrease in molt increment and a large increase in relative growth of the abdomen (Alunno-Bruscia & Sainte-Marie 1998). The first event in sexual maturation of males is the puberty (or 'adolescent') molt, which occurs at about 37 to 38 mm CW and marks the onset of testis/vas deferens development and maturation; this molt is accompanied by a decrease in the molt increment and a modest increase in chela relative growth (Sainte-Marie et al. 1995, Comeau et al. 1998). The decrease in growth rate, reflected in the molt increment, is thus similar between the 2 sexes at the first 'critical' molt, but females initiate maturation about 2 instars before males. The second major event in maturation is the terminal molt (also the pubertal molt in females), which causes a large proportional decrease in carapace molt increment in females. The terminal ('adult') molt of males is associated with only a small proportional decrease in carapace molt increment but a large increase in chela relative growth (Sainte-Marie et al. 1995, Comeau et al. 1998, Hébert et al. 2002).

Males in the nGSL achieve the minimum legal size and recruit to the exploitable biomass at instar XII and about 8.7 years of post-larval age (Sainte-Marie et al. 1995). Some males may continue to molt to instar XII at about 10.7 years of age. Males on annual molting schedules are known to fail to molt in any single year or for 2 consecutive years (Sainte-Marie et al. 1995, Hebert et al. 2002). These 'skip-molters' are identified as immature crabs or adolescent males with relatively old and discolored carapaces. Crabs of both sexes may live about 5 to 7 yr following the terminal molt, during which time the carapace ages and becomes progressively fouled and ultimately deteriorates. Snow crabs, and especially males, may undertake extensive migrations (Biron et al. 2008), including an ontogenic size-related migration (Lovrich et al. 1995, Dawe & Colbourne 2002) and seasonal breeding migrations (Taylor et al. 1985, Maynard & Webber 1987, O'Halloran & O'Dor 1988),

Molting frequency (and age-at-instar) is believed to be much more variable than the molt increment (and size-at-instar) in snow crabs (Orensanz et al. 2007). Therefore, the principal mechanism creating variation in terminal size of snow crabs, as in other majid and oregoniid crabs (Hines 1989, Hartnoll et al. 1993), is believed to be the number of instars achieved (molts experienced) before terminal molt. While several extrinsic (and intrinsic) factors may be influential in regulating size-at-terminal molt (Elner & Beninger 1992, Sainte-Marie et al. 2008), recent studies indicate that temperature is the most important factor. Orensanz et al. (2007) found that a spatial cline in mature female size in the eastern Bering Sea (EBS) was directly related to ambient bottom temperature, while Burmeister & Sainte-Marie (2010) similarly found that spatial variation of mean size of mature females and adult males in isolated West Greenland fjords was a direct function of temperature. Regional differences in minimum size of adult males in the northern Gulf of St. Lawrence was also directly related to temperature (Sainte-Marie et al. 2008)

Improving the understanding of how temperature conditions the size-at-terminal molt has important fishery management implications, particularly under the current scenario of a changing ocean climate. However, there is considerable uncertainty regarding processes involved as there have been limited studies conducted on this subject. Very limited information is available from the northwest Atlantic (Sainte-Marie et al. 2008). Most studies have focused only on females from the EBS (Orensanz et al. 2007, Ernst et al. 2012) with only a single study (from West Greenland) including males (Burmeister & Sainte-Marie 2010). All these studies have been based on associations of size metrics with mean temperature.

Some recent studies have hypothesized that variability in terminal size is primarily a function of conditioning by temperature during early ontogeny (Orensanz et al. 2007, Sainte-Marie et al. 2008, Burmeister & Sainte-Marie 2010), with high temperatures promoting increased molt frequency at early post-settlement stages before the onset on an annual molting schedule at instar VI (about 20 mm premolt CW and 2.3 years post-settlement age (Sainte-Marie et al. 1995). Assuming that terminal molt occurs at a fixed age (Orensanz et al. 2007, Burmeister & Sainte-Marie 2010), this would result in a higher instar-at-age and ultimately larger size-at-terminal molt at high temperatures than at low temperatures. This hypothesis, developed for females in the EBS, was based in part on the observation that skip-molting in EBS females was negligible (Orensanz et al. 2007). While variable molting frequency only during early post-settlement stages may account for variation in terminal size of females, it cannot account for the much greater range in terminal size of males. A more recent study of EBS females (Ernst et al. 2012) asserts that the terminal molt does not occur at a fixed age, but rather terminal size is related to age-at-maturity, with females terminally molting over an absolute range of about 5 years of age.

In this, the first comprehensive study from Canadian waters, we assume that common principles apply between the sexes. Accordingly, we hypothesize that size-at-terminal molt is conditioned by temperature over a variable number of instars and intermolt periods leading up to the terminal molt. We address this hypothesis by modeling size-at-terminal molt as a function of temperature and compare between the sexes for each of 2 segregated Canadian fishery areas. We also describe and invoke the effects of temperature on molting frequency to help explain the effects of temperature on size-at-terminal molt. Our study addresses the possible applicability of existing hypotheses to explain relationships and trends generated from the results. We go on to develop alternative hypotheses to explain the trends observed and address the implications of these findings to mortality and fishery issues, including recruitment and yield per recruit.

MATERIALS AND METHODS

Bottom trawl surveys

Data on near-bottom temperature and snow crab biological characteristics on the southern Newfoundland Shelf (NL) were acquired from multi-species spring bottom trawl surveys on the Grand Bank and St. Pierre Bank (Fig. 1). Depth stratified multi-species surveys (Doubleday 1981) utilizing a Campelen 1800 shrimp trawl (McCallum & Walsh, 1996, Walsh & McCallum, 1996) were conducted each spring from 1999 to 2010. The Campelen 1800 survey trawl is a small-meshed (80, 60 and 44 mm) shrimp trawl that is fitted with a 12.7 mm mesh codend liner. It has an average wing spread ranging from 15 to 18 m and an average vertical opening of 4 to 5 m. It has rock-hopper footgear featuring 355 mm diameter rubber disks spaced at 200 mm intervals along the 19.6 m footrope. Survey tows, executed throughout the diel

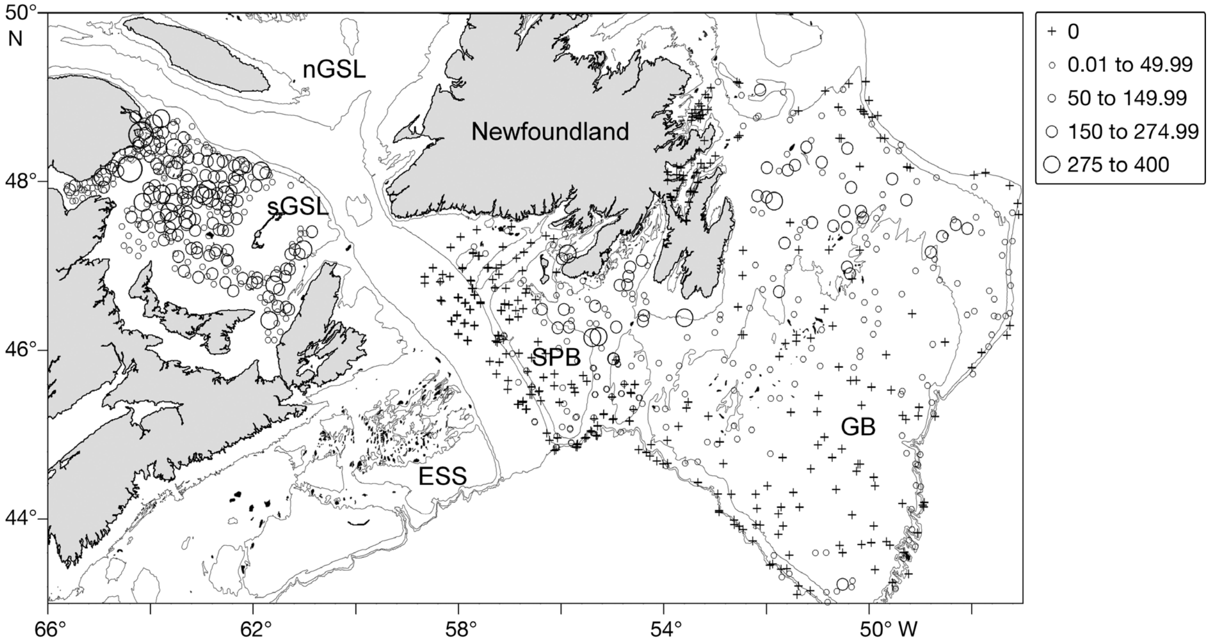

Fig. 1. Distribution of survey sets and snow crab catch rates from the 2005 surveys on the southern Newfoundland shelf and the southern Gulf of St. Lawrence: nGSL, northern Gulf of St. Lawrence; sGSL, southern Gulf of St. Lawrence; ESS, Eastern Scotian Shelf; SPB, St. Pierre Bank; GB, Grand Bank

cycle at depths of about 50 to 1500 m, were standardized to 15 min duration at a tow speed of 3.0 knots. A conductivity, temperature, and depth (CTD) sensor was mounted on the trawl head rope, and a SCANMAR acoustic net monitoring system was used to monitor trawl performance at each station. Unsuccessful tows were repeated at the same or alternate stations. The capture efficiency of snow crabs by this survey trawl is generally poor, especially for small crabs on hard substrates (Dawe et al. 2010). The surveys normally occurred from April to June, but extended into July in some years. The annual coverage of survey strata was variable, with inshore strata and strata deeper than 750 m along the slope edges not surveyed in all years, including most recent years.

In the southern Gulf of St. Lawrence, the annual snow crab post-fishing season trawl survey (1988–2009) has been conducted from July to October since 1988 except for 1996. The survey area includes all areas between the 36 m (20 fathoms) and 365 m (200 fathoms) isobaths. The total number of trawl stations has been increased from 155 during 1988 to 2004 to 355 in more recent years (Hébert et al. 2011). A Bigouden *Nephrops* bottom trawl, originally developed for Norway lobster fisheries in France (Conan et al. 1994) was used (20 m opening with a 27.3 m foot rope and 50 mm mesh in the codend). Tow duration varied between 4 and 6 min at a target speed of 2 knots, depending on the depth, current speed and substrate type. The horizontal opening of the trawl was measured every 4 s with the Netmind (Northstar Technical) distance sensors. All stations were trawled during daylight hours.

Biological sampling

Survey catches from both areas were sorted by species and enumerated at sea. Snow crabs were fully sampled in the sGSL, and either fully- or subsampled at NL based upon magnitude of the catch. Data were collected on sex, size, shell condition, maturity stage (females) and chela allometery (males). Both sexes were measured for carapace width (CW, to nearest 0.1 mm) using vernier calipers. Females were categorized as mature versus immature based on morphometry of the abdomen, while males were sampled for chela height (CH, to nearest 0.1 mm), which was subsequently used in relation to CW to segregate adolescents from adults (Dawe et al. 2011 for NL, Hébert et al. 2011 for sGSL). For both sexes, shell condition was subjectively assigned to one of 5 categories ranging from soft-shelled to very-old shelled (see Table 1), reflecting time elapsed since molting (Dawe et al. 2011 for NL, Hébert et al. 2011 for the sGSL).

Data analysis

The annual distribution of bottom temperature was mapped and kriged (with Surfer 8, Golden Software USA) for both survey areas. We chose 2005 for presentation of near-bottom temperatures as the surveys were spatially almost fully complete in both areas during that year, providing comprehensive broad-scale views. The thermal regime was about average for sGSL in 2005, but was warmer than average for NL. The total survey catch of snow crabs by sex, size, and temperature was plotted and compared to determine the thermal distribution of males and females in each area. We partitioned bottom temperature among 1°C bins with each temperature representing the midpoint of each grouping. For example, the 1°C temperature bin was comprised of temperatures ranging from 0.5 to 1.49°C. Crabs associated with each temperature bin were grouped over 3 mm CW intervals by sex, year, and area. As with temperature, size groupings were represented by the midpoint. Crabs were then pooled over all survey years for each temperature bin by sex and area. All sizes of females were included in the analysis, but males were limited to those larger than 50 mm CW, as the regression model used to segregate adolescents from adults in the NL region was not reliable for smaller sizes (Dawe et al. 1997, 2011). Males with obviously deformed or regenerated chelae were rejected.

We modeled the proportion of all new-shelled crabs that were terminally molted on carapace width by temperature bin, sex and area. Focusing on new-shelled (soft + new hard-shelled) crabs allowed us to best address our hypothesis that size-at-terminal molt is conditioned by water temperature throughout the instars and intermolt periods leading up to the terminal molt. This assumes that capture temperature reflects prevailing temperature conditions during the most recent inter-molt interval. We realize that this assumption is tenuous due to potential effects of changes in thermal regime and crab movement in the interval between terminal molt and capture. Crab movement in particular likely partially masks the true association of terminal size with premolt thermal regime. However, we assume that this association, although likely weakened, is maintained due to some degree of broad-scale spatiotemporal consistency of the thermal regime in each area.

In both areas, initial analyses revealed that logistic models produced the best fits to temperature-specific size-at-maturity distributions for females, while sixth-order polynomial regression models produced better fits to the corresponding male data. To determine the effect of temperature on size at maturity, we used these logistic and polynomial regression models to produce temperature-specific percent mature at size ogives for each area to compare the sizes at which 50% of females were mature and 50% of males were adult (mat50s).

To further investigate whether terminal size is conditioned during early life versus during more recent intermolt periods leading up to the terminal molt, we calculated mean sizes of new-shelled and old-shelled crabs by temperature bin for both mature females and adult males (both terminally molted). Linear regression models were applied to the mean size on temperature data, and regression slopes were compared between shell categories (ANCOVA, SAS 9.2) by sex and area. It was hypothesized that regression slopes would be steeper for new-shelled (most recent terminal molters) than for old-shelled (those terminally molted more than one year before capture) mature females and adult males, indicating conditioning by temperature, with new-shelled crabs remaining closer than old-shelled crabs, in time and space, to the thermal regime at which they most recently molted. New-shelled crabs included those classed as soft and new-hard shelled (see Table 1), whereas old-shelled crabs included those classed as intermediate, old, and very-old shelled from the surveys, and therefore had not molted for more than one year. A few terminally molted adult males may have been misclassified as adolescent due to undetected regeneration of chelae, but this is at a negligible level of less than 0.1% of total crabs sampled (M. Hébert pers. comm.).

The effects of physical and biological variables on the frequency of skip-molting was examined by modeling the proportion of non-terminally-molted crabs (immature crabs plus adolescent males) that had not molted during the most recent molting season on size, by area, sex and temperature bin. All immature and adolescent crabs larger than about 20 mm CW are scheduled to molt annually during spring. Therefore, those with new carapaces during our survey periods represented crabs that molted during the most recent spring molting season. Skip-molters were defined as immature and adolescent crabs with other than new carapaces as described above. Logistic models were applied to the data for proportion skip-molting on carapace width by area, sex, and temperature bin. The significance of the effects of explanatory variables on proportion skip molting was determined, for males only, using a multiple regression model (ANCOVA, SAS 9.2). Size represented the continuous covariate in the logistic regression analysis, grouped into 3 mm increments. Area and temperature were treated as class variables, with temperature grouped into 1°C bins ranging from −1°C to 4°C.

RESULTS

Thermal regime and snow crab distribution

Both areas are characterized by a cold thermal regime, with bottom temperatures ranging from −1 to 6°C (Fig. 2). Virtually no crabs were caught within the very limited area >4°C. The sGSL represented the more homogenous area with respect to both bathymetry and thermal regime, characterized by a

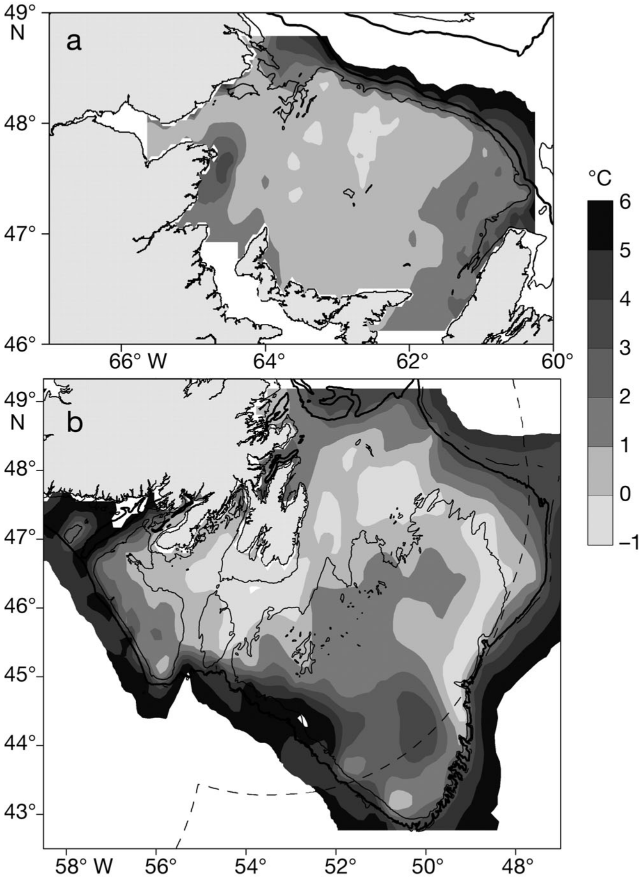

Fig. 2. Example of near-bottom temperature distribution in (a) the southern Gulf of St. Lawrence (summer 2005) and (b) the southern Newfoundland shelf (spring 2005). The dashed line represents the boundary of Canada's 200 n mile exclusive fishery zone

central pool of mostly 0°C water surrounded by smaller areas of 1°C on the periphery. The NL shelf was generally colder, particularly along the northern portion where cold (–1 to 0°C) water was common. Sub-zero temperatures were broadly distributed on the NL shelf, even in 2005, a relatively warm year, whereas they were virtually absent in the sGSL in 2005 within a more typical thermal regime. In both areas the greatest depths down over the slope edges were characterized by warmest water of about 4 to 6°C. The spatial extent of temperature bins other than 0 and 1°C were particularly limited within the sGSL survey area.

Total catch by temperature bin for both sexes (Fig. 3) generally reflected variation in the spatial extent of those temperature intervals (Fig. 2). The majority of females of all sizes captured in spring NL were taken from –1 and 0°C waters, with the catch generally decreasing progressively with temperatures above 0°C (Fig. 3). With a primary mode at 55 to 60 mm CW, the sGSL females were on average much larger than those captured at NL, despite increasing capture efficiency with size by the NL survey trawl (Dawe et al. 2010). Most sGSL females of all sizes were taken at 0 and 1°C, (mainly at 0°C), with relatively few females found at other temperatures. The largest catch of males across the entire size range at NL was at 0°C, with modal groups at smallest (about 15 to 40 mm CW) and largest (70 to 120 mm CW) sizes (Fig. 3). Lowest catches, primarily of largest males (about 80 to 120 mm CW) were at highest temperatures (2 to 4°C). As with females, the majority of the sGSL males of all sizes were taken from 0 and 1°C areas (mainly at 0°C).

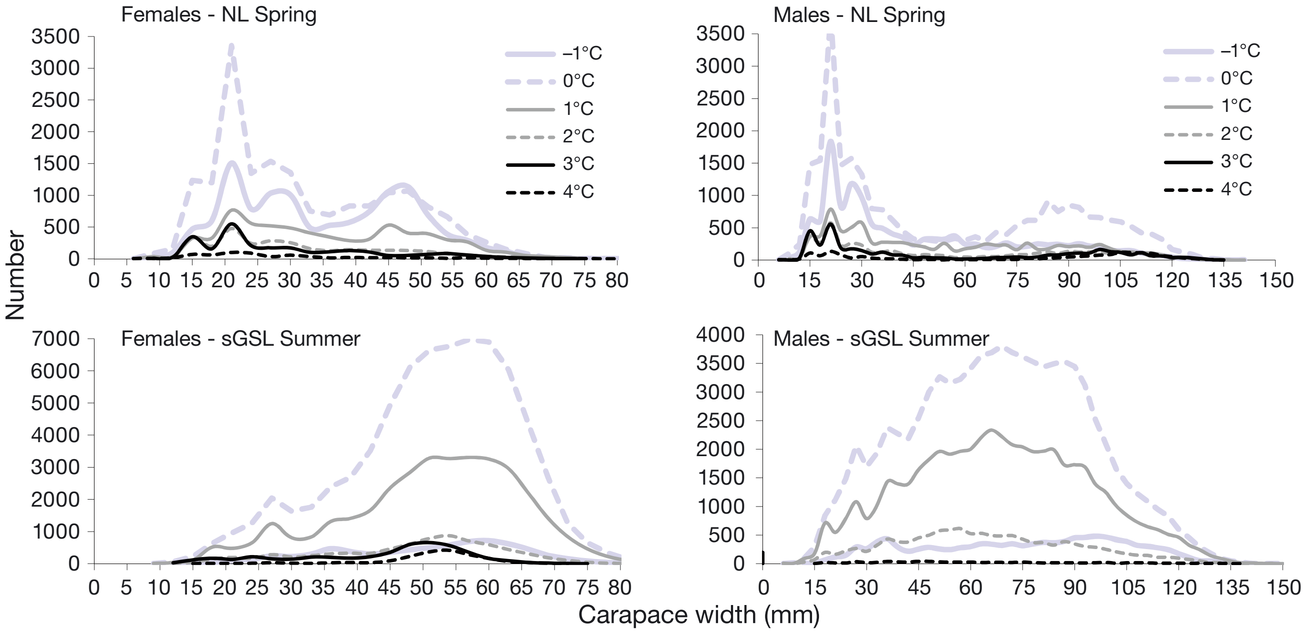

Fig. 3. *Chionoecetes opilio*. Sample size (number) vs. carapace width by sex and temperature bin from surveys on the southern Newfoundland shelf (NL, 1999–2010) and the southern Gulf of St. Lawrence (sGSL, 1988–2009). All shell conditions and maturities are pooled

Table 1. *Chionoecetes opilio*. Snow crab sample size (percentage in parentheses) by sex and reproductive stage from surveys partitioned by shell condition. NL: southern Newfoundland shelf; sGSL: southern Gulf of St. Lawrence

			Soft	New	Intermediate	Old	Very old	Total
NL	M	Adolescent	2611 (5.8)	40015 (88.7)	2133 (4.7)	338 (0.7)	29 (0.1)	45125 (100.0)
		Adult	1955 (15.3)	4490 (35.2)	4197 (32.9)	1971 (15.5)	129 (1.0)	12743 (100.0)
	F	Immature	511 (1.6)	31419 (98.1)	46 (0.1)	43 (0.1)	2 (0.0)	32021 (100.0)
		Mature	665 (5.3)	4751 (38.2)	2206 (17.7)	4247 (34.1)	577 (4.6)	12446 (100.0)
sGSL	M	Adolescent	96168 (83.7)	5062 (4.4)	13083 (11.4)	424 (0.4)	199 (0.2)	114936 (100.0)
		Adult	17784 (34.6)	8712 (17.0)	15079 (29.4)	6467 (12.6)	3283 (6.4)	51325 (100.0)
	F	Immature	46086 (98.8)	145 (0.3)	172 (0.4)	231 (0.5)	28 (0.1)	46662 (100.0)
		Mature	157 (0.2)	19855 (24.5)	28773 (35.5)	26606 (32.8)	5662 (7.0)	81053 (100.0)

The molting history of snow crabs sampled was similar between the areas in most respects (Table 1). Most of the crabs sampled in both areas were new-shelled (soft + new hard-shelled). This was especially true for non-terminally molted crabs, with new-shelled males comprising 88 and 95% of all immature + adolescent males in the sGSL and NL, respectively, and with new-shelled females comprising more than 99% of all immature females in both areas. Interestingly, most of the new-shelled crabs from the sGSL were soft-shelled, whereas most of those from NL were new hard-shelled. For example, 84% of immature + adolescent males and 99% of immature females from the sGSL were soft-shelled, whereas only 6 and 2%, respectively, from NL were soft-shelled. This indicates that most of the non-terminally molted new-shelled crabs from the sGSL summer-fall survey had molted during the immediately past spring, whereas most of those from the spring NL survey last molted almost a year earlier and were yet to molt during the current spring. Old shelled non-terminally molted crabs (old + very old) were uncommon, at <1%, in both areas (Table 1).

Size-at-terminal molt

For new-shelled females, logistic regression models produced very tight fits to the temperature-specific percent mature on size data by area (Fig. 4). However, there was a tendency for the relationships to erode at highest temperatures, most evident at 3 and 4°C in both areas. This reflects the limited spatial distribution of such high temperatures in these areas (Fig. 2) and the consequent small sample sizes (Fig. 3). Nonetheless, these models adequately described the female data in all cases. These temperature-specific models showed that females captured in warm areas matured at larger sizes than those captured in cold areas (Fig. 5). In NL, the size-at-mat50 increased from 45 mm CW at −1°C to 59 mm CW at 4°C. In the sGSL size-at-mat50 increased from 48 mm CW at −1°C to 62 mm CW at 4°C. Similarly, the probability that any molt would be the terminal molt increased with decreasing temperature, for all sizes in both areas. For example, the percent mature at 51 mm CW increased from −1 to 4°C in both areas, from 12 to 84% in NL and from 12 to 62% in the sGSL.

The failure of logistic models to adequately describe the temperature-specific percent adult on size data for males reflects a much more gradual increase in the probability of terminally molting with size than in females (Fig. 6). However, polynomial regression models produced generally adequate fits to these data for males. As with females, there was a tendency for the relationships to erode at extreme temperatures in both areas. Also, the male polynomial models did not fit the NL data well at sizes smaller than about 80 mm CW. The models showed that relatively low proportions of males became adult at sizes smaller than about 90 mm CW, with the elongated lower-end tails of the models reflecting percentages of 10 to 40% terminally molted crabs in most cases. The very gradual increase in probability of terminally molting at small sizes would have been even more evident if we had been able to extend our models to the smallest sizes at which males may terminally molt. Minimum temperature-specific size-at-mat50 values were 88 mm CW in NL and 98 mm CW in the sGSL (Fig. 7). In both areas, the models producing minimum size-at-mat50 values were associated with −1 and 0°C waters. The overall effect of temperature on size-at-maturity was less clear in males than in females, with relatively little separation among the temperature-specific size-at-maturity curves in both areas. Maximum temperature-specific size-at-mat50 occurred at 101 and 103 mm CW in NL and the sGSL respectively, in both cases associated with 3 or 4°C waters.

Comparison of mean sizes between shell condition categories by area and sex (Fig. 8) showed that mean size was more strongly directly related to temperature for new-shelled than for old-shelled terminally molted crabs. As with the size-at-mat50 comparisons, these results were clearer for females than males, and for NL than for the sGSL. Females showed significantly steeper positive slopes of linear regression models for new-shelled than for old-shelled crabs in both areas. Similarly, males from NL also showed significantly steeper regression slopes for new-shelled than for old-shelled crabs. In fact, mean size of the sGSL old-shelled females was inversely related to temperature. Mean size of new-shelled mature females was significantly smaller than that of old-shelled mature females at the lowest temperature. Only for the sGSL males did these relationships not hold, with new-shelled mature males showing an inverse relationship with temperature.

Molting frequency

The logistic regression model did not fit the data for proportion skip-molted vs. CW for NL females (Fig. 9), whereas it provided adequate fits for sGSL

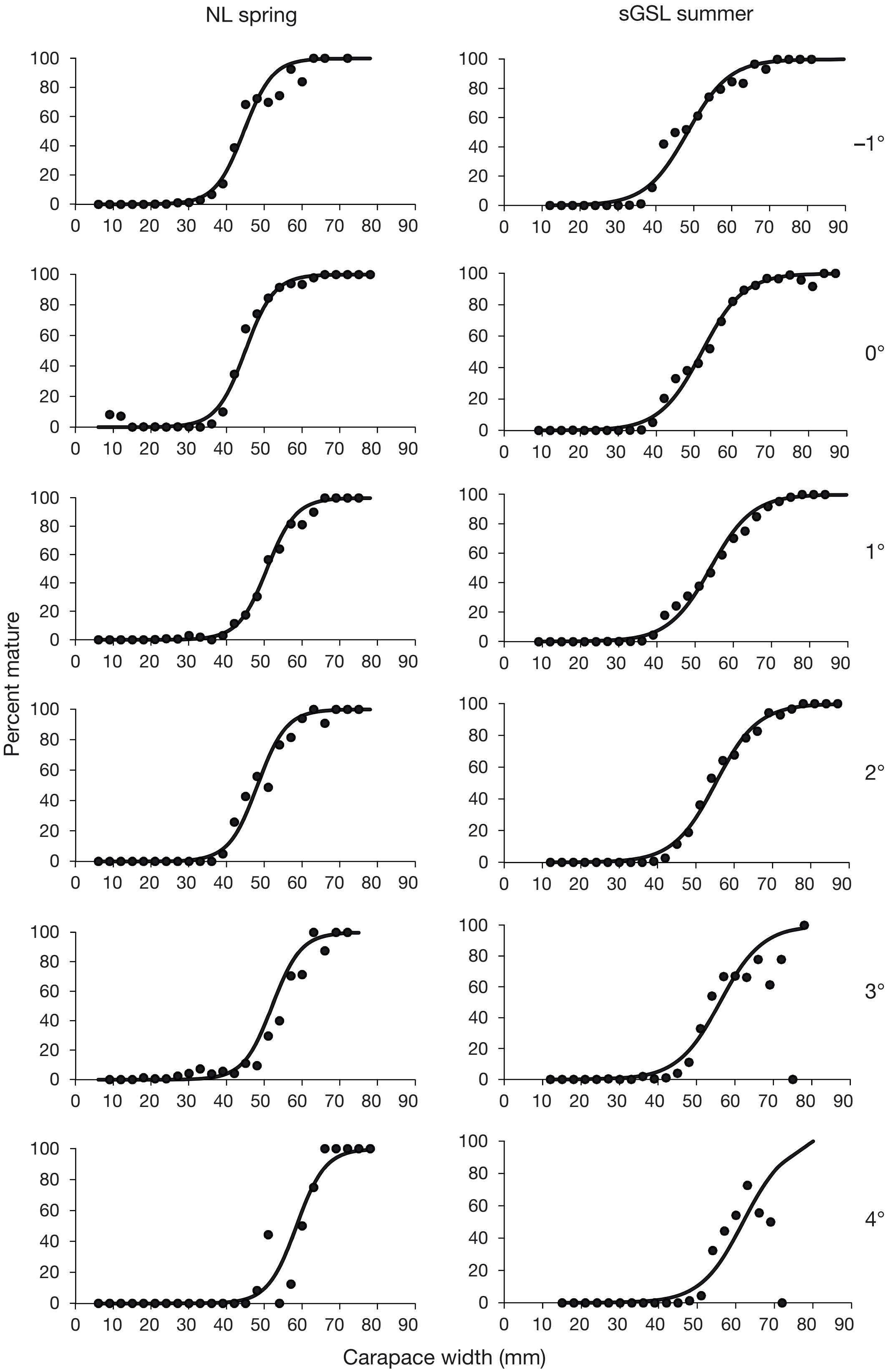

Fig. 4. *Chionoecetes opilio*. Application of logistic regression models to the percentage mature vs. size (carapace width), by temperature bin (°C), for females from the southern Newfoundland shelf (NL) and the southern Gulf of St. Lawrence (sGSL)

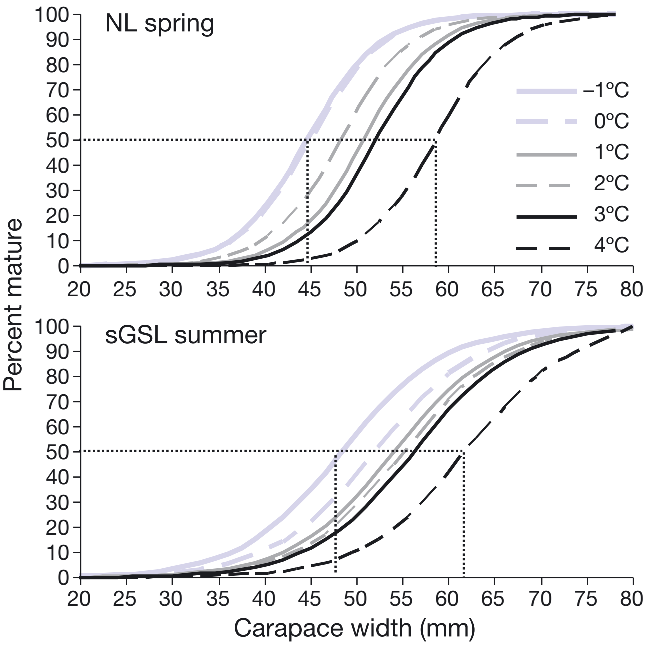

Fig. 5. *Chionoecetes opilio*. Temperature-specific logistic size-at-maturity models for females showing mat50 probits for the southern Newfoundland shelf (NL) and the southern Gulf of St. Lawrence (sGSL)

females and for males from both areas (Fig. 10). There was a much higher level of variability in the distribution of empirical data about the male models from NL than from sGSL (Fig. 10), reflecting greater inconsistency at NL in identifying skip molters. This inconsistency at NL is likely due largely to more variable levels of experience in assigning subjective shell condition stages by personnel sampling during NL multispecies surveys relative to those sampling during the sGSL dedicated snow crab surveys. Also, intermediate- and old-shelled skip-molters are more easily distinguished from new-shelled recent molters at sGSL (mostly soft-shelled) than at NL (mostly new-hard-shelled) (Table 1). The models for males from both areas over-estimated proportion of skip-molting at largest sizes, greater than about 80 to 90 mm CW (Fig. 10), which we attribute to effects of fishery induced mortality on legal-sized males (>95 mm CW) as well as on largest sub-legal sized males that are captured and released in the fishery. A large number, but small percentage of oldest-shelled (old + very old shelled) skip-molters (especially males) from both NL (0.8 % of males) and sGSL (0.6 % of males) represent crabs that skipped 2 or more consecutive molts (Table 1).

Skip-molting was virtually absent in both sexes at sizes smaller than about 50 mm CW (Figs. 9 & 10). It was common in females only in the largest immature individuals that were caught at 0 and 1°C in the sGSL (Fig. 9). At those temperature bins the percentage of skip-molting sGSL females increased sharply from a virtual absence at 50 mm CW to about 50 % at 70 mm CW, a much sharper increase than in comparably-sized males from the same area and thermal regime (Fig. 10).

The multiple regression analysis (Table 2) indicated that the frequency of skip-molting in males was also directly related to size. This very highly significant effect (chi-square = 867.53, $p < 0.0001$) was consistent between areas as well as across all temperature bins (Fig. 11). It increased to maxima of 57 and 58 % respectively in NL and the sGSL. It ranged 22 to 58 % for adolescents larger than 100 mm CW across all temperatures and both areas. The effects of both class variables, area ($p < 0.0001$) and temperature ($p = 0.0019$), were also significant as were most interactions. Skip-molting in males was overall more frequent in the sGSL than in NL. The frequency of male skip molting at the temperatures most common to both areas (0 and 1°C) increased more rapidly with size in the sGSL than at NL (Fig. 11), as reflected in the significant size by area interaction (Table 2).

The effect of temperature was less clear than that of size (Fig. 11), but overall the frequency of male skip molting was inversely related to temperature (chi-square = 9.61, $p < 0.01$, Table 1). The interaction of temperature with size in affecting male skip molting frequency was highly significant (chi-square = 31.77, $p < 0.0001$). For both areas, the highest incidence of skip molting was generally at the lowest temperatures that were most extensive in each area (ie −1 and 0°C at NL versus 0 and 1°C at sGSL), and frequency generally decreased at higher temperatures (excepting 3°C at NL) and the extreme low temperature at sGSL (−1°C) (Fig. 11).

DISCUSSION

Effects of temperature

We confirmed that size-at-terminal molt in both sexes from NL and the sGSL is directly related to temperature, as shown in previous studies from the EBS for females (Orensanz et al. 2007) and from West Greenland for both sexes (Burmeister & Sainte-Marie 2010). Sainte-Marie at al. (2008) reviewed the more limited information available from the nGSL that indicated such a direct effect of temperature on female terminal size (Sainte-Marie & Gilbert 1998) and proposed that temperature may also affect termi-

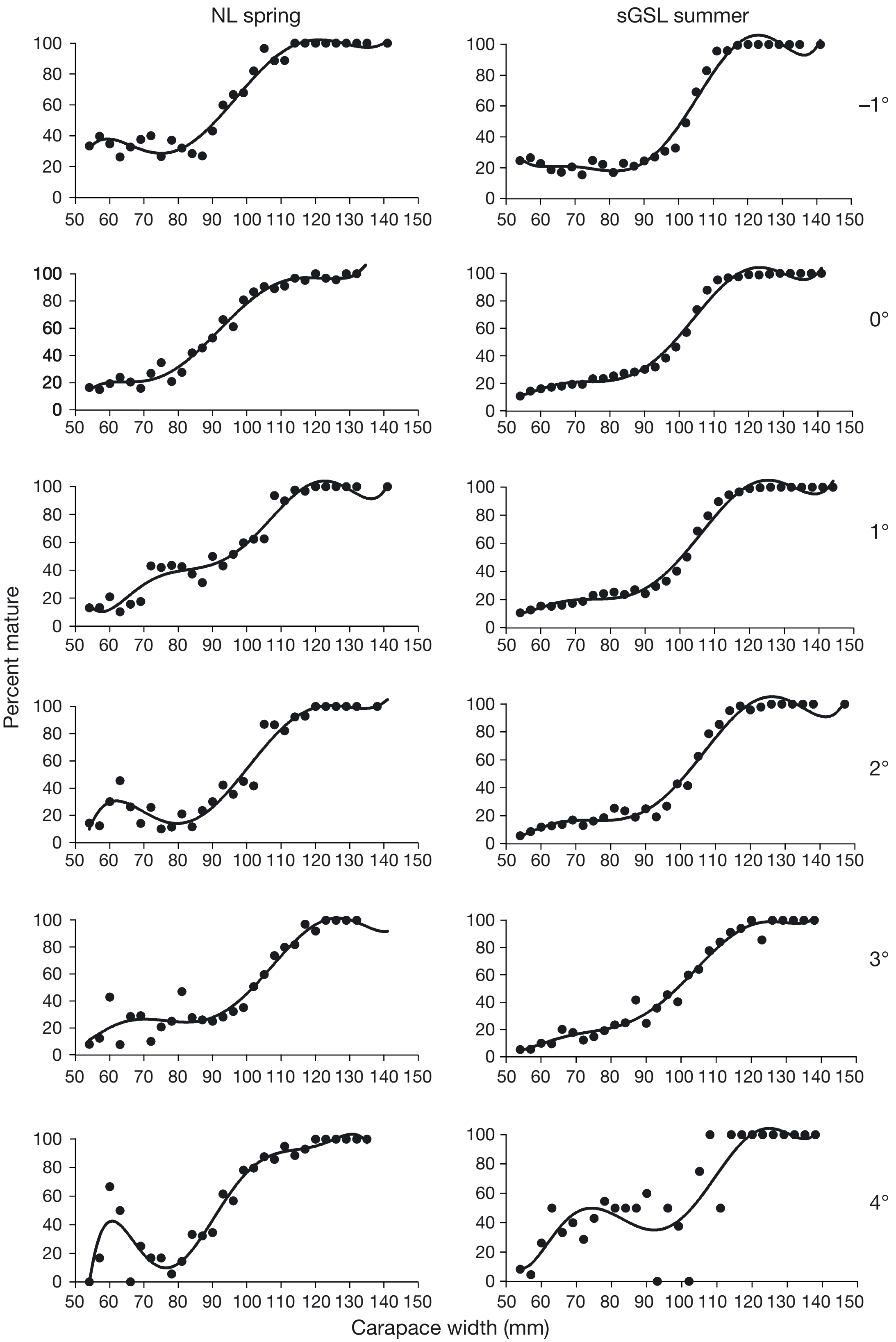

Fig. 6. *Chionoecetes opilio*. Application of sixth-order polynomial regression models to the percentage 'mature' (ie. adult) vs. size (carapace width), by temperature bin (°C) for males from the southern Newfoundland shelf (NL) and the southern Gulf of St. Lawrence (sGSL)

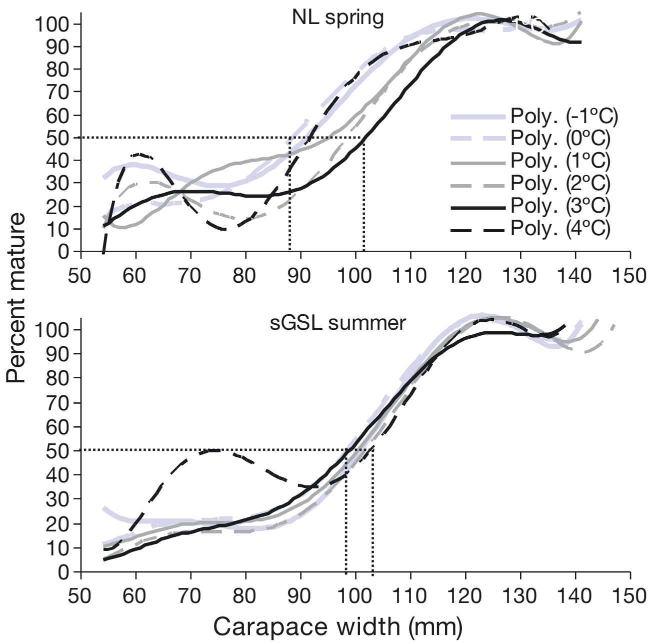

Fig. 7. *Chionoecetes opilio*. Temperature-specific polynomial (poly.) size-at-adulthood models for males showing mat50 probits for the southern Newfoundland shelf (NL) and the southern Gulf of St. Lawrence (sGSL)

nal size of males (Alunno-Bruscia & Sainte-Marie 1998). Those studies, based on size metrics alone, hypothesized that size-at-terminal molt is conditioned by temperature during the first 2 to 3 years of life, prior to the onset of an annual molting schedule and that age ultimately triggers the terminal molt.

We suppose this hypothesis, developed for EBS females, was based on the observation that annually molting females do not skip molts (Orensanz et al. 2007). However, our data, based on both sexes in NL and in the sGSL, show that Canadian snow crabs do skip annual molts and that the frequency of skip-molting is strongly and directly related to body size, although it is also inversely related to temperature. We found that skip-molting is negligible in both sexes at sizes smaller than about 50 mm, such that most females achieve their terminal size without skipping a molt, as found in previous studies (Orensanz et al. 2007, Burmeister & Sainte-Marie 2010, Ernst et al. 2012). However, many of the largest sGSL females (>50 mm CW) skipped a molt at low temperatures before terminally molting to largest sizes of about 75 to 80 mm CW. Accordingly, it is clear from our results that size-at-terminal molt is conditioned

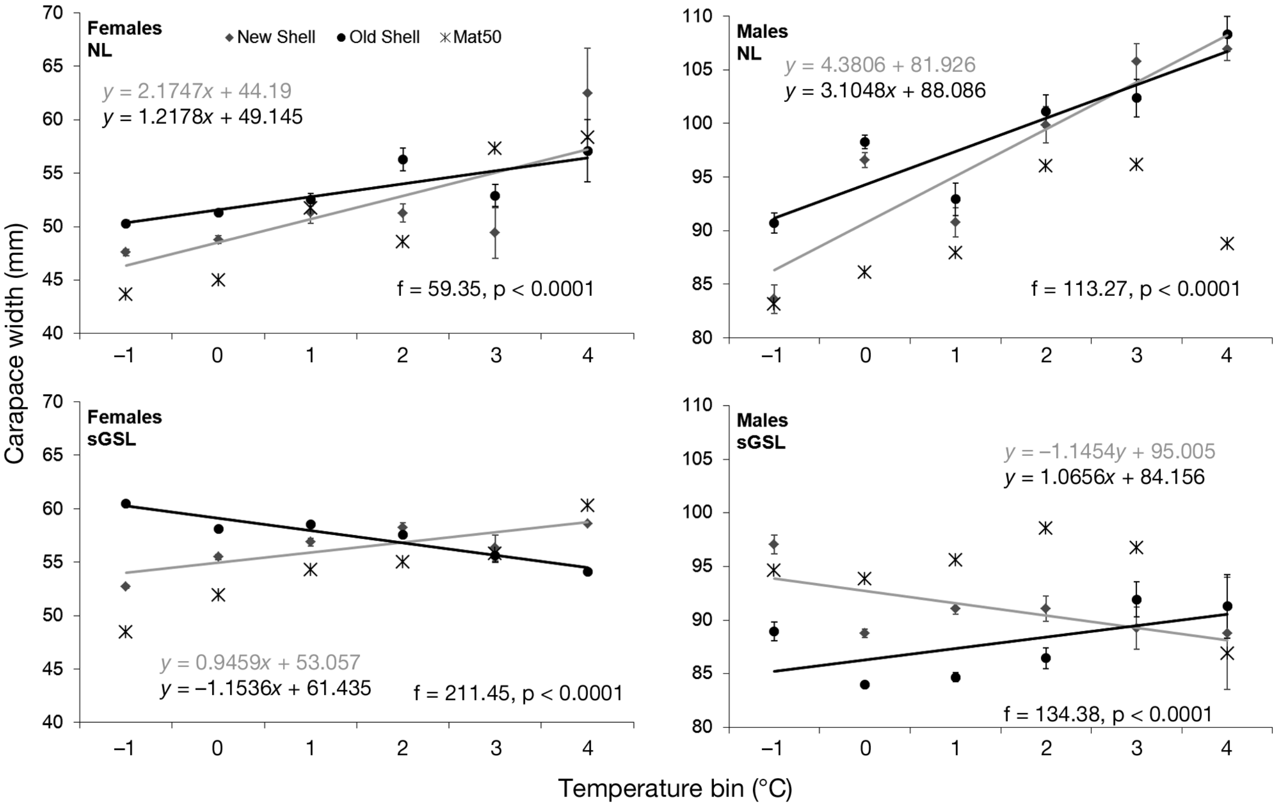

Fig. 8. *Chionoecetes opilio*. Mean (± 2SE) size of new-shelled and old-shelled mature females and adult males from the southern Newfoundland shelf (NL) and the southern Gulf of St. Lawrence (sGSL) with linear regression models and results of the tests of significance of differences between regression slopes (f). Sizes at 50% maturity (females) or adulthood (males) are also shown, as Mat50 for both sexes

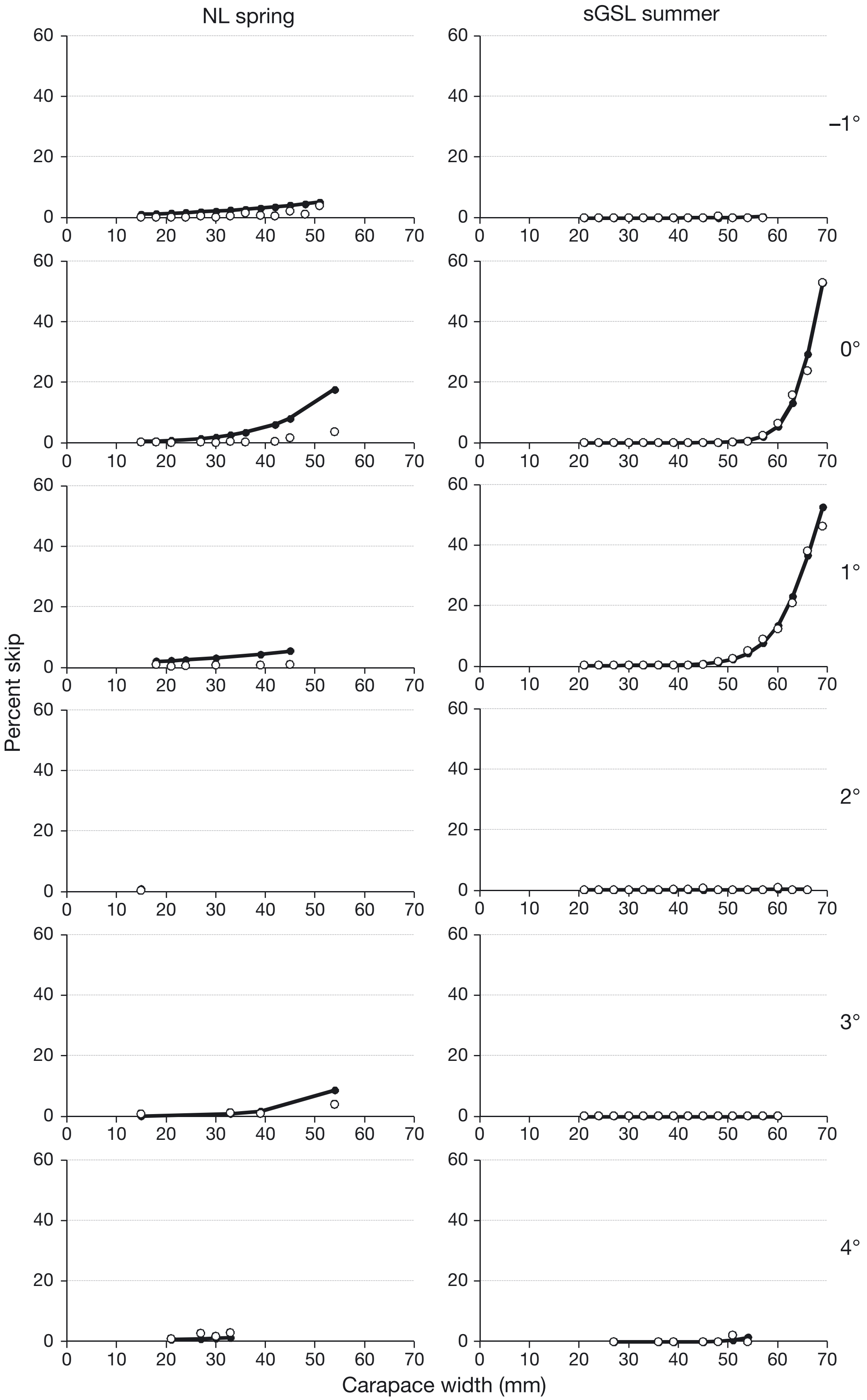

Fig. 9. *Chionoecetes opilio*. Logistic regression models applied to the empirical percentage skip-molting (percent skip) vs. size (carapace width), by temperature bin (°C), for females from the southern Newfoundland shelf (NL) and the southern Gulf of St. Lawrence (sGSL). Filled circles represent predicted values; open circles represent observed values

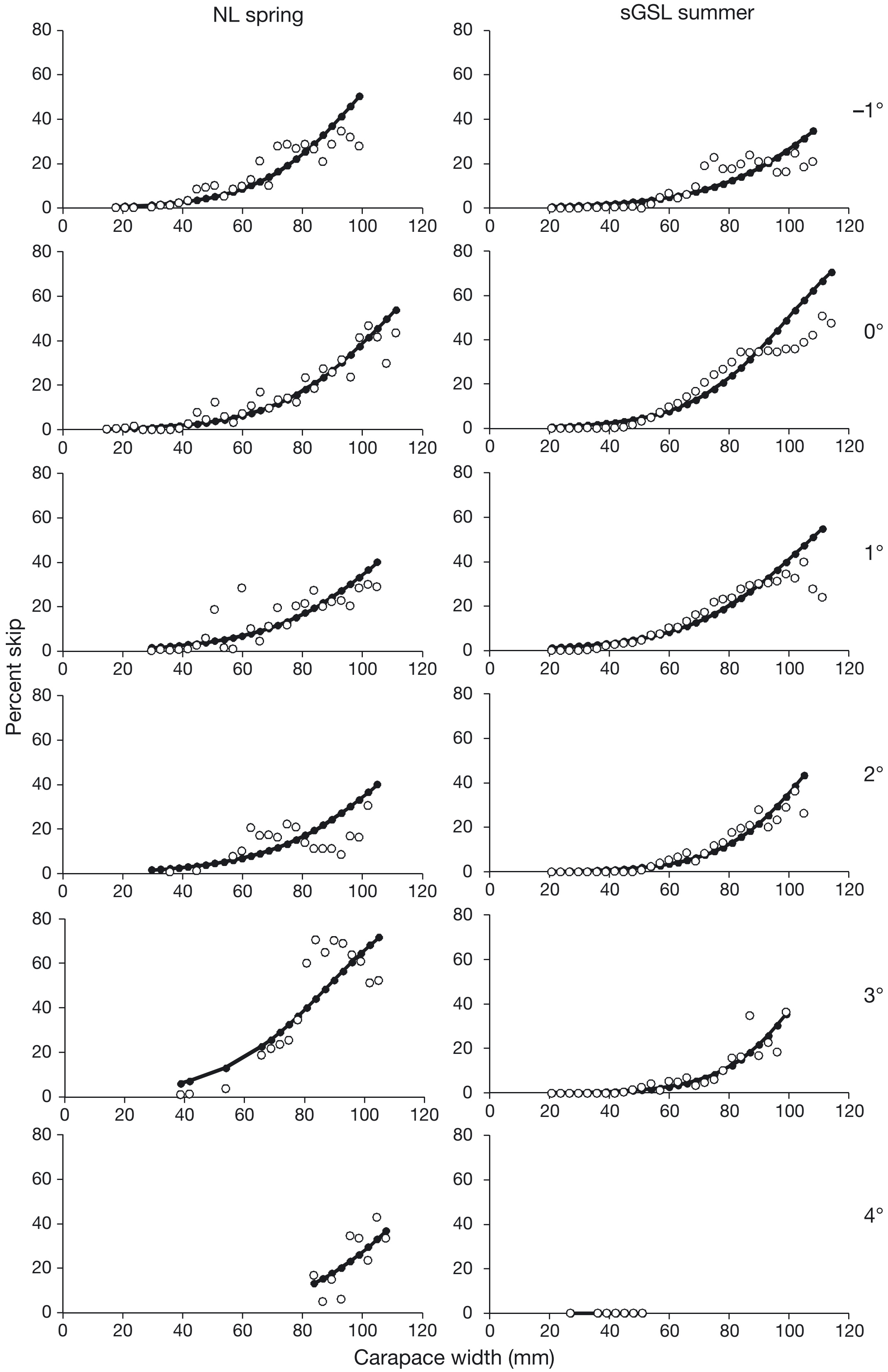

Fig. 10. *Chionoecetes opilio*. Logistic regression models applied to the empirical percentage skip-molting (percent skip) vs. size (carapace width), by temperature bin, for males from the southern Newfoundland shelf (NL) and the southern Gulf of St. Lawrence (sGSL). Filled circles represent predicted values; open circles represent observed values

Table 2. Results of logistic multiple regression analysis of male snow crab percentage skip-molting on size by area and temperature bin (temp). All main effects and significant interaction effects are shown

Parameter	df	Estimate	Standard error	Wald 95 % confidence limits		Wald chi-square	p > chi-square
Intercept	1	−6.5205	0.1548	−6.8239	−6.2171	1774.31	<0.0001
Size	1	0.0616	0.0021	0.0575	0.0657	867.53	<0.0001
Area	1	0.3793	0.0861	0.2106	0.548	19.42	<0.0001
Temp	1	−0.1766	0.057	−0.2883	−0.065	9.61	0.0019
Size*Area	1	−0.0032	0.0011	−0.0054	−0.001	7.87	0.005
Size*Temp	1	0.0027	0.0005	0.0018	0.0037	31.77	<0.0001
Area*Temp	1	−0.0724	0.0229	−0.1173	−0.0275	9.97	0.0016

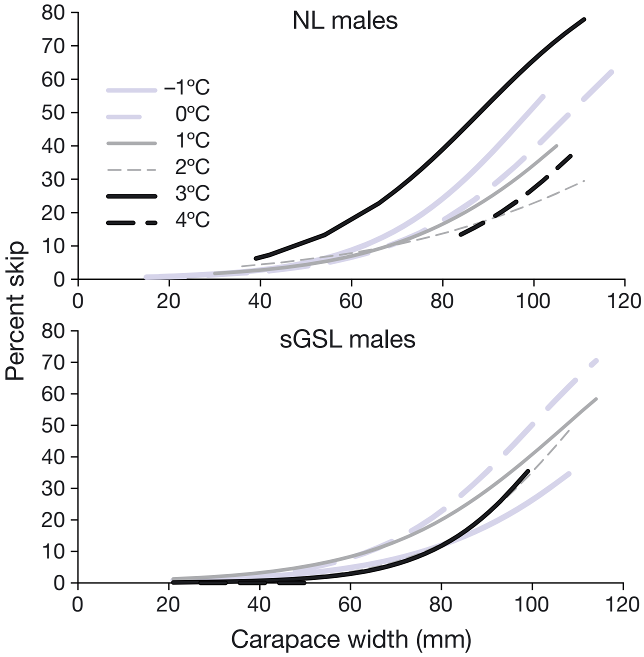

Fig. 11. *Chionoecetes opilio*. Comparison of male logistic regression models describing the percentage skip-molting (percent skip) vs. size (carapace width), across temperature bins for the southern Newfoundland shelf (NL) and the southern Gulf of St. Lawrence (sGSL)

by temperature throughout the life history of both sexes, including the most recent intermolt periods leading up to the terminal molt, and occurs at highly variable ages. This conclusion better accounts for the broad range in terminal size for both sexes (especially males) than does the hypothesis of conditioning only during early ontogeny and an age-related trigger (Orensanz et al. 2007, Burmeister & Sainte-Marie 2010). It more closely agrees with Ernst et al. (2012), who concluded that terminal molt may occur over a range of about 5 yr of age for EBS females, despite negligible skip-molting. While the size and age at terminal molt are highly variable in males, the maximum age at terminal molt is more conservative. Males that skip molts frequently and terminally molt at small size in a cold thermal regime may actually be older than larger adults that skipped fewer molts at higher temperatures. This is consistent with the observation that temperature effects at early benthic stages on subsequent recruitment to fisheries operate over a longer time interval in cold areas than in warm areas (Dawe et al. 2008).

Our study did not rely on size metrics alone, as did the earlier studies. By modeling size-at-maturity for new-shelled (recently-molted) crabs as a function of temperature we showed that conditioning of terminal size by temperature includes the most recent intermolt period. For example, we showed that at any given size, especially for females, the percentage that had recently terminally molted decreased with increasing temperature at capture. This is further supported by our comparison of mean size by shell condition. We found that mean size was more strongly directly related to temperature for new-shelled than for old-shelled crabs based on differences in slopes of linear regression models.

The effects of temperature on size-at-terminal molt were consistent between the sexes, although they were clearer for females than males. This sex difference is attributed, in part, to poorer fits of size-at maturity models for males than females. Males may be influenced by sample size limitation at small sizes, as well as fishery effects at large sizes. The removal of large adult males by the fishery introduces a bias into the size-at-maturity analysis. Males also undertake more pronounced ontogenetic and seasonal migrations than do females (Ennis et al. 1990, Sainte-Marie & Hazel 1992, Comeau et al. 1998, Dawe & Colbourne 2002), such that temperature at capture may not reflect the thermal conditions throughout the past intermolt period as well as it does for females. Despite these confounding factors, it was clear that sex effects included a stronger response to temperature by females than males, as reflected by the very gradual rate of terminally molting at small male sizes.

The relationships we found between temperature and terminal size generally agreed between study areas but were clearer for NL than for the sGSL, despite the fact that new-shelled crabs sampled during summer-fall from the sGSL (mostly soft-shelled) were more recently molted than those sampled during spring at NL (mostly new-hard-shelled) and so were sampled closer in time to the most recent molt. We attribute this apparent paradox to the much greater size of the NL than the sGSL survey area and greater heterogeneity in its bathymetric and thermal regimes. Despite crab movements and temporal change in thermal regime, crabs are more likely to remain associated with any temperature bin for a longer period at NL than at sGSL.

Several authors have offered possible explanations for skip-molting, including low physiological condition, mating success as adolescents, density-dependence, and temperature (Elner & Beninger 1995, Comeau et al. 1998, Godbout et al. 2002, Sainte-Marie et al. 2008). Our results indicate that skip-molting is a function of an interaction between size and temperature, with highest rates at largest sizes and low temperatures (0 and 1°C). Size exerting the greatest effect on skip-molting frequency is logical in that body size is constrained by an increasing energy requirement with growth. The metabolic rate of well-fed ectotherms, in general, scales as a power function of body mass (van der Meer 2006, Brose 2010) and increases exponentially with temperature (Brown et al. 2004). Skip-molting results in the ability to store somatic energy over an extended intermolt period, thereby facilitating the achievement of a threshold physiological condition necessary to successfully molt at large sizes (Godbout et al. 2002). The decrease in incidence of skip molting with increasing temperature is consistent with increasing molting frequency with temperature in crustaceans generally (Hartnoll 1982), which reflects a direct effect of temperature on metabolic rate. Paul & Paul (2001) found that the intermolt period in Tanner crab (*Chionoecetes bairdii*) is inversely related to temperature, while more recently, Dutil et al. (2010) showed that in the laboratory, snow crabs molt earlier at higher than at lower temperatures.

The direct effect of temperature on snow crab metabolic rate is reflected in studies of snow crab bioenergetics (Foyle et al. 1989, Thompson & Hawryluk 1990). Laboratory studies on relatively large (85 to 95 mm CW) adult male snow crabs (Foyle et al. 1989) indicate that food consumption increases up to 6°C. Metabolic costs increase with temperature and overtake caloric intake at about 7°C. An anomaly to the general effect of temperature was that growth becomes negative at very low temperatures (<1°C), implying that effects of temperature on large adult males may not apply to all other life history stages. This is consistent with the observed distribution of snow crabs at NL (Dawe & Colbourne 2002), in that smallest crabs are mostly distributed on hard substrates at shallowest depths and lowest temperatures, whereas largest males tend to be associated with soft mud substrates at greatest depths and warmest temperatures. The inverse relationship of incidence of male skip-molting with temperature is consistent with snow crab bioenergetics in that the greatest positive energy balance (digestible energy minus metabolic costs) in large adult males occurred at 4°C in the laboratory (Foyle et al. 1989). We feel that this can be explained by variation in habitat suitability in that foraging ability may become limiting for large crabs at low temperatures due to relatively low absolute food availability on hard substrates or increased competition associated with increase in individual growth and population biomass. The ontogenic migration of males (Dawe & Colbourne 2002) is adaptive in that it results in distribution of large males to deep warm areas on soft substrates, where growth potential is maximized. This may also result in an improved feeding regime due to increase in absolute food availability on mud substrates and reduced density and competition.

Mechanism for regulation of size-at-terminal molt

We assume that size-at-terminal molt is regulated by principles that are generally common to both sexes. Accordingly, we offer a most plausible hypothesis for regulation of size-at-terminal molt that also accounts for the observed differences between the sexes. Crabs of both sexes, on annual molting schedules, maintain good physiological condition and rarely skip molts at sizes smaller than about 50 mm CW. Larger crabs have 3 options during each spring molting season; to forego the annual molt (skip molt), undertake a regular molt to remain immature-pubescent (females) or adolescent (males), or to commit to the terminal molt. Molting is highly demanding, such that crabs must commit to one of these options at least 2 to 3 mo prior to the start of actual ecdysis (Sainte-Marie et al. 1995, O'Halloran & O'Dor 1988). We hypothesize that the 'decision' to molt in both sexes is based upon achievement of some threshold physiological condition that enhances the probability of surviving the molt. The height of this threshold differs between the sexes and with type of molt, depending on the energetic cost of molting. The highest threshold is associated with the puberty molt of females, which is also the terminal molt, because of the cumulative high energetic cost associated with development of the ovary over several intermolt periods leading up to the terminal molt with extrusion of the first egg clutch (Alunno-Bruscia & Sainte-Marie 1998). This is supported by the great increase in frequency of skip-molting with size that we found in largest sGSL females. The male puberty molt (to adolescence) is less costly, and least costly is the male terminal molt. These differences in hypothetical thresholds are reflected in the changes in molt increment with each type of molt (Sainte-Marie et al. 1995, 2008). Since maximum size is also constrained by energy requirement, females will commit to the terminal molt as soon as possible, especially at low temperatures. Failure to achieve the threshold physiological condition results in undertaking a molt to remain immature or (at largest immature size) skipping a molt before being forced, by size constraints, to terminally molt over the next 1 to 2 instars. Adolescent males, already sexually mature, may not commit to the terminal molt upon achieving their low physiological threshold, but rather opt to skip annual molts and undertake further adolescent molts until they are finally forced by energetic constraints at large size to undertake the terminal molt. This occurs at largest sizes within energetically-favourable warm regimes.

This proposed mechanism is consistent with life history theory in that the probability of successfully reproducing for females is maximized by terminally molting (and maturing) as early as possible. This also enhances lifetime fitness in that females surviving their first reproductive event may continue to reproduce (as multiparous females) for several years without the energetic demands of molting or (necessarily) re-mating (Elner & Beninger 1992, Sainte-Marie et al. 2008). Conversely, males may successfully first reproduce as sexually mature adolescents, but lifetime fitness is maximized by deferring the terminal molt to very large sizes. Large adult males mate as many females as possible and most females (including virtually all multiparous females) are mated by large adults (Sainte-Marie et al. 1999, 2008). It is unlikely that smallest size at terminal molt in males is related to physiological condition alone. More likely some other density-dependent factor that enhances individual fitness is also involved, such as reproductive success as an adolescent.

Implications for fisheries

This study has important implications for fisheries. High temperatures are clearly positive from an immediate recruitment perspective. Increase in male terminal size with temperature results in a relatively large portion of a cohort achieving the minimum legal size and recruiting to fisheries. It also results in large size at recruitment in that males at high temperatures have a relatively high probability of delaying the terminal molt to sizes as large as about 115 mm CW, and molting to a maximum size of about 140 mm CW. This is reflected in larger mean size of recruited males in deeper warmer areas north of the Grand Bank and on the eastern slope of the Grand Bank than on the cold shallow shelf of the Grand Bank and St. Pierre Bank (Dawe et al. 2011). It also accounts for the very large size of recruited crabs in the warmest Atlantic Canadian fishery area on the eastern Nova Scotian Shelf (Choi & Zisserson, 2007).

While the effects of temperature on probability of recruiting to fisheries and size at recruitment are clear, its overall effect on recruitment level is not. Our study implies that highest temperatures would promote recruitment through positive effects on both size at recruitment and proportion continuing to molt to legal-size. However, recent studies (Dawe et al. 2008, Marcello et al. 2012, this volume) indicate that production and subsequent recruitment are promoted by low temperatures during early life history. Therefore, the positive effects of low temperature on production or early survival are stronger than any potentially negative effects on growth and recruitment in later life.

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Contribution to the Theme Section 'Effects of climate and predation on subarctic crustacean populations'

Environmental factors affecting recruitment of northern shrimp *Pandalus borealis* in West Greenland waters

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ABSTRACT: Survey estimates of northern shrimp *Pandalus borealis* biomass in West Greenland waters increased from about 178 000 t in 1998 to about 598 000 t in 2003. The increase in stock size was preceded by several consecutive years in which recruitment was substantially above average. Recruitment has been poor since then despite record high levels of female stock biomass. Ricker-type stock-recruitment functions did not indicate that the variability in recruitment was related to female biomass. Multiple regression analysis revealed that mean female length, ambient bottom temperature and biomass of Greenland halibut *Reinhardtius hippoglossoides* had the most important effect on the variations of the 'recruit per female biomass' time series for the years 1993 to 2011. Variables which did not contribute significantly to the model included biomass of Atlantic cod *Gadus morhua*. This can be explained by the low stock size of Atlantic cod throughout the major part of the study period. The final model explained 83% of the variation in the recruit per female biomass index. However, the observations for 5 out of the 19 years considered in the present study were outside the 95% confidence interval of the fitted model, possibly due to a mismatch between the timing of larval hatch and the timing of the phytoplankton bloom, which could not adequately be addressed due to data limitations.

KEY WORDS: Pandalid shrimp · Stock–recruitment relationship · Recruitment success · Temperature · Predation · Maternal effects · Subarctic seas

INTRODUCTION

Northern shrimp *Pandalus borealis* feeds on phytoplankton, detritus and small zooplankton (Horsted & Smidt 1956), and serves in turn as important prey for several fish species including Atlantic cod *Gadus morhua* and Greenland halibut *Reinhardtius hippoglossoides* (Parsons 2005a,b). In relation to its trophic level, responses of shrimp abundance to bottom-up and top-down processes have been documented (Fuentes-Yaco et al. 2007, Lilly et al. 2000). The reproductive cycle of northern shrimp has adapted to local temperature conditions so that, under average conditions, the timing of larval hatch matches that of the spring phytoplankton bloom (Koeller et al. 2009). Moreover, upper water column temperature has been identified as a significant factor determining recruitment success of northern shrimp in the Northwest Atlantic (Ouellet et al. 2007, 2011). On the other hand, linkages between population size of Atlantic cod and northern shrimp have been reported for various parts of the North Atlantic (Worm & Myers 2003). Hence, simple stock–recruitment relationships have usually not been found for northern shrimp (Aschan & Ingvaldsen 2009) or other pandalid shrimp species (Hannah 1993, Bergström 2000).

Northern shrimp is a protandric hermaphrodite with a circumpolar distribution in the northern hemi-

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sphere (Shumway et al. 1985, Bergström 2000). In West Greenland waters, the juveniles mature as males at about 3 yr of age, undergo transition to female at an age of 5 to 6 yr (Horsted & Smidt 1956, Wieland 2004), and may attain a maximum age, as female, of more than 8 yr (Savard et al. 1994). Mating and spawning occur during July to September, the egg-bearing period lasts 8 to 10 mo, depending on the temperature in the bottom water, and the larvae hatch in April to June of the following year (Shumway et al. 1985, Bergström 2000). The pelagic larvae undergo a 60 to 90 d development period with 6 stages (Rasmussen & Aschan 2011) and attain a carapace length of about 3.5 mm during summer (Storm & Pedersen 2003) before finally settling at the bottom as postlarvae in autumn where they reach a carapace length of 8 to 9 mm at age 1 in the following summer in West Greenland waters (Wieland 2005).

The fishery for northern shrimp off West Greenland started in the 1970s in Disko Bay (Fig. 1) and an offshore fishery developed thereafter with annual landings of up to 150 000 t. In the offshore areas, the fishery is conducted in all seasons (Hammeken Arboe & Kingsley 2010), and egg-bearing females are subject to the fishery during the winter (Fig. 2). Pronounced fluctuations in female biomass and recruitment of northern shrimp have been reported for the past 2 decades. At the same time, temperature conditions and the latitudinal distribution of northern shrimp changed considerably (Wieland et al. 2007). The present study compares Ricker-type stock-recruitment functions with multiple regression models that include environmental variability in order to identify the most important factors influencing the recruitment of northern shrimp off West Greenland in the years 1993 to 2011.

MATERIALS AND METHODS

The analysis was based on 2 bottom trawl survey series for monitoring fish and shrimp resources and 1 time series of routine observations of the oceanographic conditions off West Greenland. These were a Greenland survey for shrimp and fish carried out annually in summer since 1988 by the Greenland Institute of Natural Resources (GINR) in Nuuk and a German groundfish survey conducted annually in autumn since 1982 by the Institute of Sea Fisheries in Hamburg (ISH). Both surveys follow a stratified-random design. The routine observations of the oceanographic conditions off West Greenland are conducted by the Danish Meteorological Institute (DMI) and provide mean surface layer (0 to 40 m) temperatures based on measurements in mid-June at a standard station on Fylla Bank (Fig. 1) which are considered to represent the general conditions on the West Greenland shelf (Ribergaard 2011).

The GINR survey for shrimp and demersal fish covers the West Greenland shelf between 72° 30′ and 59° 30′ N down to 600 m depth (Fig. 1). The survey area has been expanded and stratification has changed through time but adjustments for these changes, in particular for the missing coverage of the inshore area (Disko Bay and Vaigat) in 1988 to 1990, have been adopted (Kingsley et al. 2011). The fishing

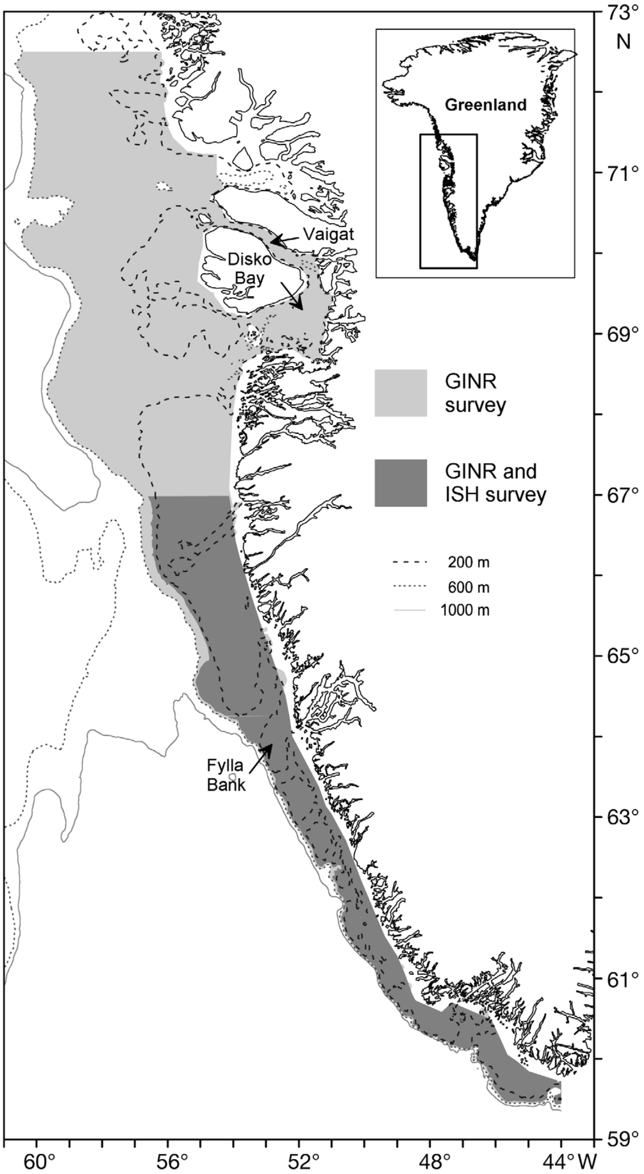

Fig. 1. Area coverage of the Greenland (GINR) and German (ISH) bottom trawl surveys, and location of the oceanographic standard station on Fylla Bank

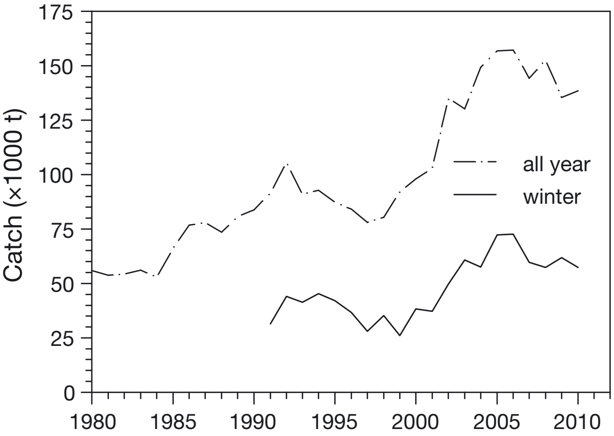

Fig. 2. *Pandalus borealis.* Annual northern shrimp total catch (1980 to 2010) and catch taken during the winter (October to March, 1991 to 2010) off West Greenland (based on Hammeken Arboe & Kingsley 2010)

gear used has a high vertical opening (ca. 14 m), which is essential for catching northern shrimp, and the towing speed is about 2.5 knots. The trawl was changed in 2005 and due to the change in the ground rope from a bobbin chain to a rubber disc rockhopper gear, higher catch rates were observed, particularly of small demersal fish. The survey results were adjusted for the gear change based on a calibration experiment (Kingsley et al. 2008, Nygaard & Jørgensen 2011). The mesh size of the trawl's codend was 44 mm in the early years but a 20 mm codend liner has been used since 1993. Fine meshed (6 mm) juvenile bags were used in only 2 years with full coverage of the survey area and the results indicated that northern shrimp smaller than about 9 mm carapace length (age 1 and younger) are not well retained in the main trawl (Wieland 2002). The primary objective of the GINR survey is to provide an estimate of the fishable biomass and recruitment at age 2 of northern shrimp, and it is considered to be less efficient for Atlantic cod, in particular for the years prior to 2005. Due to the maximum depth of 600 m, the survey catches of Greenland halibut consists mainly of juveniles (<40 cm total length; Nygaard & Jørgensen 2011) as the adults occur predominantly at greater depths and in areas other than that covered by this survey (Jørgensen 1997, Orr & Bowering 1997). The GINR survey provides further area-specific mean bottom temperatures based on measurements logged along the tow path since 1990 (Kingsley et al. 2011). The bottom temperatures were weighted by the density of northern shrimp in the various geographical survey strata to obtain a time series of ambient bottom temperatures during summer.

The ISH survey covers the shelf area outside the 3 nautical mile limit and the continental slope down to a depth of 400 m between 67° 00′ and 59° 30′ N (Fig. 1) off West Greenland. The fishing gear used is a groundfish trawl with a low vertical opening (ca. 4 m) and a fine meshed (10 mm) liner inside the codend, and the towing speed is 4 knots. The ISH survey was originally designed for Atlantic cod, and does not adequately cover the distributional range of northern shrimp and Greenland halibut.

According to the survey specifications, the data for northern shrimp and Greenland halibut were taken from the GINR survey (Kingsley et al. 2011, Nygaard & Jørgensen 2011) and the data for Atlantic cod were based on the ISH survey (Retzel 2011). Both surveys use measurements of swept area to convert catch rates to estimates of abundance and biomass. However, the efficiency of the survey gear and hence the survey catchability is not precisely known and thus the survey estimates should be considered as indices rather than as absolute values.

Relationships between parental stock size (P) expressed as female biomass and recruitment (R) represented by abundance at age 2 for northern shrimp were fitted to the original Ricker model (Ricker 1954):

$$R = \alpha \times P \times \exp(-\beta \times P) \tag{1}$$

where α and β are the coefficients of the density-independent and the density-dependent terms, respectively, and to a modified version which allowed for a non-zero intercept (Frank & Brickman 2000):

$$R = \alpha \times (P - \gamma) \times \exp(-\beta \times (P - \gamma)) \tag{2}$$

where γ is the stock level associated with absolute recruitment failure. A lag of 3 yr between female biomass and abundance at age 2 was applied to take into account that the females found in a summer survey produce offspring that emerge as larvae in the following spring and are first caught in survey 3 yr later, at age 2.

Environmental and ecological variables were added to the linearized form of the standard Ricker function, similar to the approach of Stocker et al. (1985):

$$\begin{aligned}\ln(R/P) = \ln(\alpha) - \beta \times P + \chi \times L + \delta \times S \\ + \phi \times A + \eta \times C + \varphi \times G + \kappa \times E\end{aligned} \tag{3}$$

or

$$\begin{aligned}\ln(R/P) = \ln(\alpha) - \beta \times P + \chi \times L + \delta \times A \\ + \phi \times (S - A) + \eta \times C + \varphi \times G + \kappa \times E\end{aligned} \tag{4}$$

where L is the mean carapace length of northern shrimp females, S and A are surface layer and ambient bottom temperatures respectively, C and G are survey estimates of Atlantic cod and Greenland halibut biomass respectively, E is the catch of northern shrimp during winter (October to March) relative to female biomass in the preceding summer, and χ, δ, ϕ, η, φ and κ are coefficients of the environmental and ecological variables. Female carapace length was lagged by 3 yr with respect to the year in which the recruitment was measured in order to represent the average size of the egg-bearing females in the year of spawning. Surface layer and ambient bottom temperature were lagged by 2 yr so that they correspond to the year in which the larvae hatched and settled. The difference between surface layer and ambient bottom temperature (S–A) lagged by 2 yr was included in the analysis to reflect variations in the match between the timing of larval hatch, which depends on the conditions in the bottom water, and those of the phytoplankton bloom, which depends on the conditions in the surface layer. A time lag of 1 yr was applied for Atlantic cod and Greenland halibut biomass indices representing predation on juvenile northern shrimp at age 1. The biomass indices for Atlantic cod and Greenland halibut were adjusted for the spatial overlap of the distribution of each predator with that of northern shrimp, based on an index of collocation. The index of collocation is a geostatistical tool developed by Bez & Rivoirard (2000) for pelagic species and its application for demersal fish and shellfish is described in Hendrickson & Vázquez (2005), Wieland et al. (2007) and Woillez et al. (2007). Estimates of effective biomass for the 2 predators were obtained by multiplying the original biomass indices with the respective index of collocation. The catch of northern shrimp during winter relative to female biomass in the preceding summer was lagged by 2 yr and used as an indicator for a potential effect of the removal of egg-bearing females in the time period between spawning and larval hatch. The impact of surface layer temperature (S, Eq. 3) and the difference between surface layer and ambient bottom temperature ($S - A$, Eq. 4) were studied separately because a significant correlation between the 2 variables was found (Shapiro-Wilks normality tests passed with $p = 0.637$ and $p = 0.928$, Pearson product moment correlation: $r = 0.657$, $p < 0.01$). Non-significant variables at the 5% level were removed from models (3) and (4) by stepwise (both directions) multiple regression. The residuals were tested for deviation from normality, trends and autocorrelation. Furthermore, the robustness of the final model was investigated using model runs in which single years were sequentially excluded from the analysis and in which the first 3 yr of the recruit per female biomass index were excluded due to concerns about the consistency of the female biomass estimates related to the reduced area coverage of the survey in the early years. The statistical analyses were performed with S-Plus Version 6.1 and SigmaPlot Version 10.2.

RESULTS

Survey estimates of total and female biomass of northern shrimp were fairly stable until the end of the 1990s, increased to record high levels within a few years, and declined subsequently towards average (Fig. 3a). The increase in stock size was preceded by a couple of years with high recruitment (Fig. 3b) and the high values of the abundance at age 2 per female biomass index indicate exceptionally high survival of the pre-recruits in this period (Fig. 3c). At the same time, the mean size of females declined remarkably over a decade and a reversal of this trend has only been evident in the past 5 yr (Fig. 3d). Average bottom temperature for the entire area covered by the GINR survey increased during the end of the 1990s from 1.8 to 3.2°C and remained at this relatively high level thereafter. Surface layer temperature at Fylla Bank also increased during the mid-1990s but colder conditions were recorded for several years thereafter as well (Fig. 3e). Spatial overlap between northern shrimp and Atlantic cod was lower than for northern shrimp and Greenland halibut in all years, in particular for the years 2005 to 2008 (Fig. 3f). The occurrence of Atlantic cod in West Greenland offshore waters has been sporadic (Fig. 3g), and in the period 2005 to 2010 most of its biomass was distributed outside the area inhabited by northern shrimp. The biomass index of Greenland halibut increased steadily from 1990 to 2004 (Fig. 3h) and showed much lower year to year changes than those for Atlantic cod (Figs. 3g,h). The mean latitude of the northern shrimp survey biomass indicates a southward shift of the centre of the distribution during the late 1990s (Fig. 4a). Conversely, in the past 5 yr, northern shrimp has almost disappeared from the southern area where average bottom temperatures regularly exceeded 4°C after the mid 1990s and the mean latitude of the survey biomass increased from 66° N in 2003 to about 68° N from 2005. The ambient bottom temperature during summer reflects this change in distribution with a value of 4.2°C in 1999 decreasing to 2.6°C in 2010 (Fig. 4b). No change in the seasonal pattern of the fishery has been obvi-

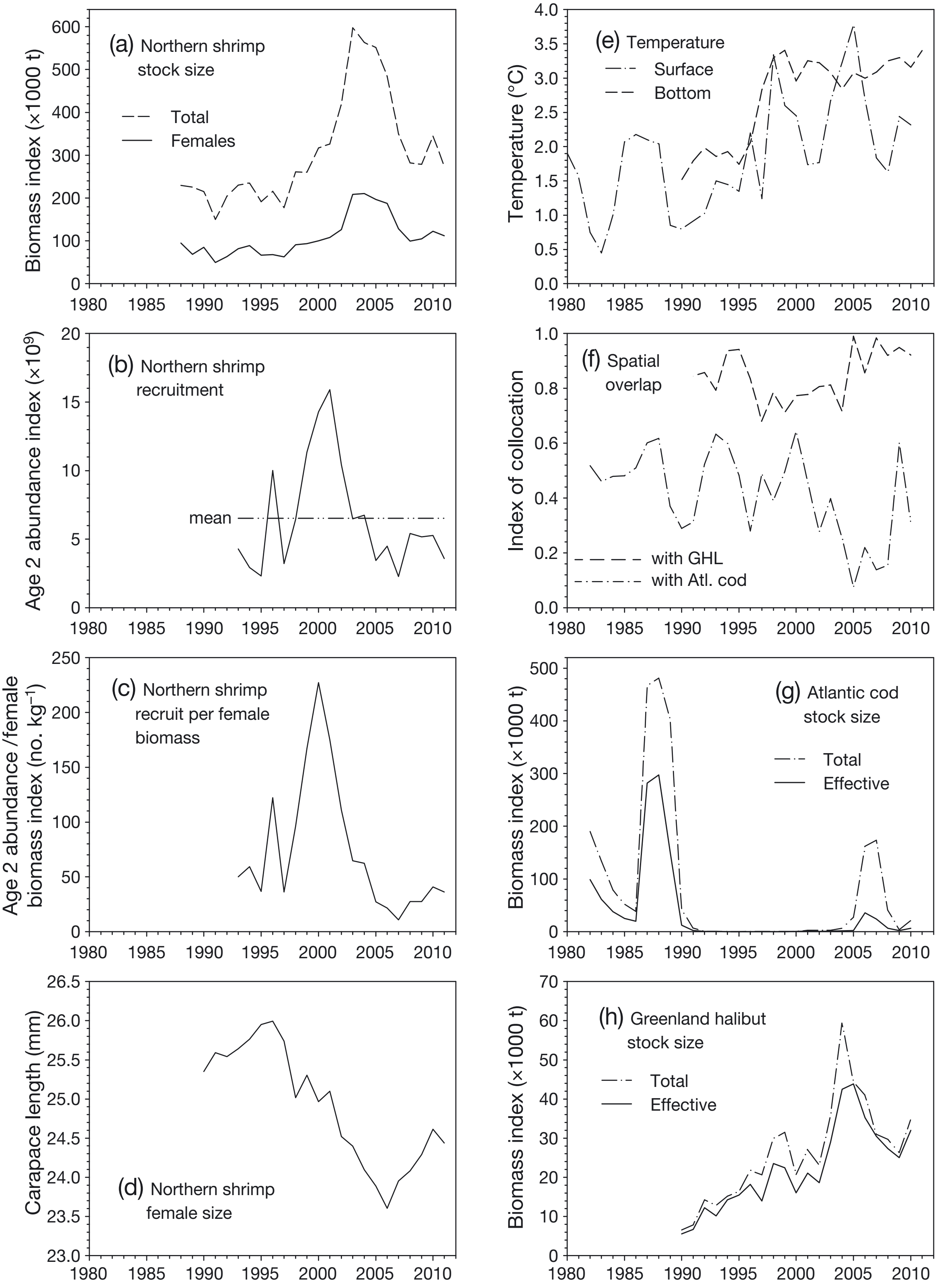

Fig. 3. *Pandalus borealis.* Time series of northern shrimp (a) stock size, (b) recruitment at age 2, (c) recruit per female biomass, (d) mean female length, (e) surface layer and bottom temperature, (f) spatial overlap between northern shrimp and Atlantic cod or Greenland halibut (GHL), and stock size of (g) Atlantic cod and (h) Greenland halibut off West Greenland

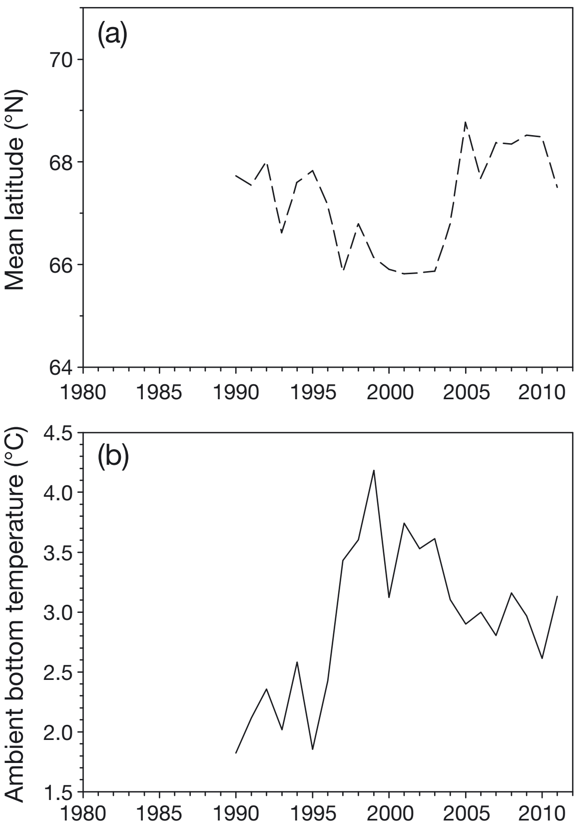

Fig. 4. *Pandalus borealis.* Changes in (a) the latitudinal distribution of northern shrimp and (b) ambient bottom temperature during summer off West Greenland, 1990 to 2011

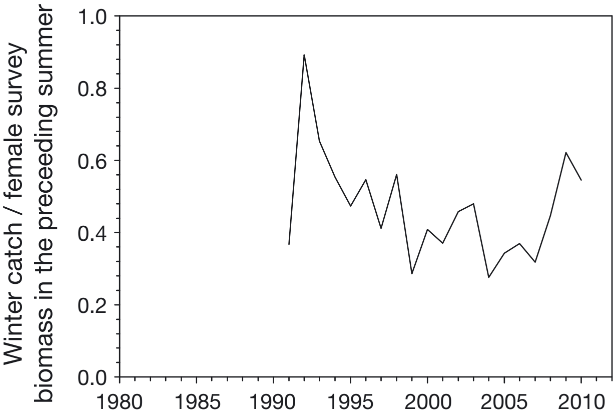

Fig. 5. *Pandalus borealis.* Catch of northern shrimp during winter relative to the female biomass index from the GINR survey in the preceding summer off West Greenland, 1990 to 2010

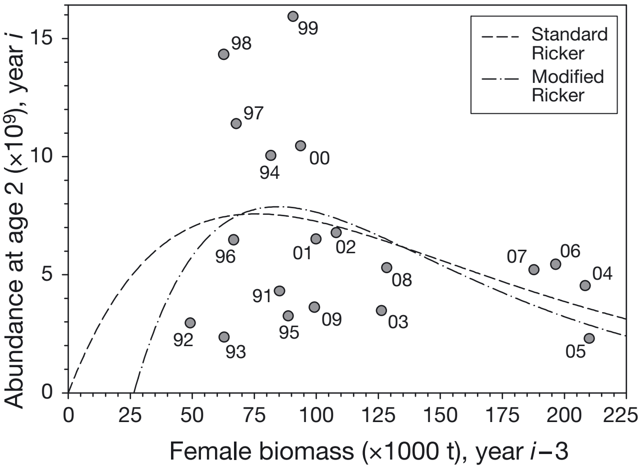

Fig. 6. *Pandalus borealis.* Stock–recruitment plot with fitted Ricker functions for northern shrimp off West Greenland (number at symbol denotes year class)

Table 1. Parameter estimates of the standard and modified Ricker stock–recruitment model for northern shrimp off West Greenland ($n = 19$; standard Ricker: $r^2 = 0.137$, adjusted $r^2 = 0.086$, $p = 0.119$; modified Ricker: $r^2 = 0.147$, adjusted $r^2 = 0.040$, $p = 0.281$)

	Parameter	Coefficient	SE	p
Standard Ricker	α	0.272	0.102	0.016
	β	0.013	0.004	0.002
Modified Ricker	α	0.368	0.194	0.076
	β	0.017	0.007	0.033
	γ	26.382	29.578	0.386

ous (Fig. 1). However, the catch taken by the commercial fishery during winter (October to March) relative to the female biomass index from the survey in the preceding summer was highest in 1991, declined steadily until 2003 and increased slightly again thereafter (Fig. 5), possibly due to annual variation in the proportion of egg-bearing females removed by the fishery.

Female biomass of northern shrimp ranged from about 50 000 to 210 000 t, and highest abundance indices at age 2 were observed at female biomasses between 60 000 and 90 000 t whereas no strong year classes emerged when female biomass was highest (Fig. 6). Standard and modified Ricker functions explained less than 15 % of the recruitment variability (Table 1). Only the density-dependent term (β) of the Ricker functions was significant ($p < 0.05$) in both models; neither the density-independent term (α) nor the offset for the female biomass (γ) were significant in the modified version (Table 1).

Variables that contributed significantly to the final multiple regression model were mean female length in the year of spawning, ambient bottom temperature in the year of larval hatch and settling, and Greenland halibut biomass (Table 2). This was the case irrespective of whether the analysis started with

Table 2. Parameter estimates for the environmental variables in the final multiple regression model for northern shrimp recruitment off West Greenland (n = 19, multiple r^2 = 0.830, adjusted r^2 = 0.796, $p < 0.001$, residual SE = 0.3638 at df = 15; VIF: variance inflation factor)

Variable	Coefficient	SE	VIF	p
(Intercept)	−11.208	3.859	–	0.011
Northern shrimp female length, 3 yr lag	0.550	0.147	1.763	0.002
Ambient bottom temperature, 2 yr lag	0.801	0.147	1.182	< 0.001
Greenland halibut biomass, 1 yr lag	−0.038	0.012	1.965	0.007

model (3) or (4). The multiple r^2 value for the final regression model with 19 yr of observations amounted to 0.830 ($p < 0.001$, adjusted r^2 = 0.796). The residuals did not exhibit trends (Fig. 7), did not deviate significantly from normality (Shapiro-Wilks test passed with p = 0.298) and were not significantly autocorrelated (Pearson product moment correlations with time lags up to 4 yr, $p > 0.05$). The variance inflation factors for the significant variables (Table 2) were below the value beyond which collinearity may cause difficulties in the parameter estimation (Zuur et al. 2010). The coefficient for mean female length was positive, indicating that pre-recruit survival is higher when the offspring are produced by larger females. The coefficient for Greenland halibut biomass lagged by 1 yr was negative and this would represent predation on the pre-recruits of northern shrimp. Excluding single years from the analysis changed neither the selection of the significant variables (r^2 between 0.809 and 0.874, $p < 0.001$ in all cases, adjusted r^2 between 0.767 and 0.846) nor the signs of the estimated coefficients. Similarly, the exclusion of the first 3 years of the time series did not change the structure of the final model (r^2 = 0.854, $p < 0.001$, adjusted r^2 = 0.817). However, 5 observations were outside the 95 % confidence interval associated with the model fit for all available years included, and in particular the high pre-recruit survival in 1996 and the low observed values in 2003 and 2007 were not well represented by the model (Fig. 8).

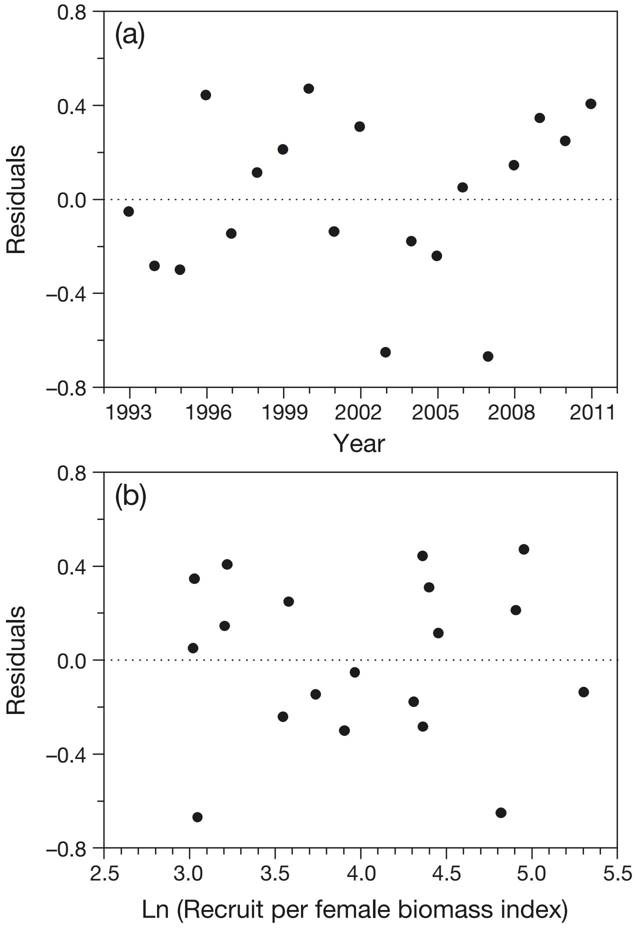

Fig. 7. *Pandalus borealis.* Residuals from the final multiple regression model for northern shrimp recruitment off West Greenland plotted versus (a) year and (b) estimated recruit per female biomass index

DISCUSSION

The results of the present study do not support the existence of a classical stock–recruitment relationship for northern shrimp off West Greenland. Egg

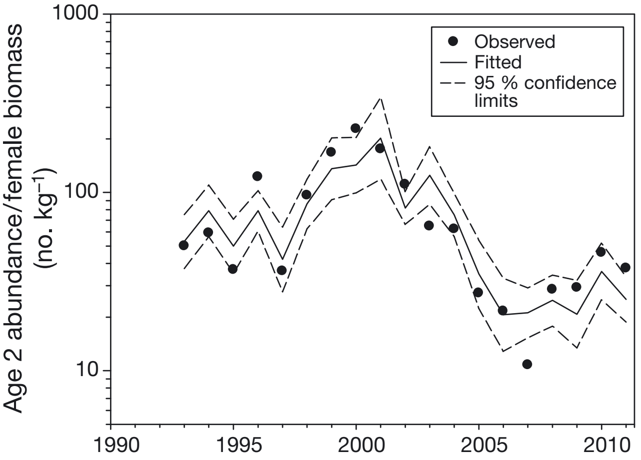

Fig. 8. *Pandalus borealis.* Comparison of the observed recruit per female biomass index with the estimate from the final multiple regression model for northern shrimp off West Greenland

mortality during the egg-bearing period may be due to natural causes such as unfavourable temperature conditions or predation as well as the removal of egg-bearing females from the stock by the fishery in winter. This mortality may result in egg production falling below some threshold level required for the production of a measurable number of recruits. However, using a modified Ricker function, which allows for a non-zero intercept, did not improve the fit, and hence the relevance of such a possible effect could not be demonstrated here.

Both the standard and the modified Ricker models suggested the presence of density-dependence, which justified including female biomass in the initial multiple regression analysis. Female biomass, however, was not significant in the final multiple regression model, which indicates that the low pre-recruit survival at high female biomass was related to unfavourable environmental conditions rather than to density-dependent mechanisms such as limitation of suitable settling areas or cannibalism.

Koeller et al. (2007) reported that decreasing length of northern shrimp off Newfoundland and Labrador was mainly caused by high water temperatures and the fishery could have an accelerating effect through selection of the largest individuals from the population. Off West Greenland, a transition from cold to warm conditions in the late 1990s was related to a decrease in length at sex transition (Wieland 2004). This and the high pre-recruit survival at the same time have likely caused the decline in mean female length observed since the end of the 1990s. Fecundity of northern shrimp is positively correlated with size (Shumway et al. 1985) but changes in mean female length are accommodated when using female biomass instead of abundance as a measure of parental stock size. However, the significance of female length in the multiple regression model on pre-recruit survival suggests that the proportion of large repeat spawners may have an important effect, through egg size and quality, on recruitment success of northern shrimp, as has been postulated for other decapod crustaceans (Moland et al. 2010, Sato & Suzuki 2010).

Warm conditions in the surface layer reduce larval development time and mortality, and will enhance larval growth if food is not limiting (Rasmussen & Tande 1995, Storm & Pedersen 2003). High temperatures shorten the duration of the egg-bearing period but could cause a lower larval size at hatch (Brillon et al. 2005) and a considerably earlier hatching time (Koeller et al. 2009), which may not necessarily match with the timing of the plankton bloom (Ouellet et al. 2007). However, direct observations on the timing of larval hatch and the onset of the phytoplankton bloom on appropriate spatial scales are sparse and have not provided conclusive results for the West Greenland shelf (Ouellet et al. 2011). The timing and succession of the plankton bloom in high latitude areas does not simply depend on temperature alone due to its link to the actual ice conditions (Heide-Jørgensen et al. 2007, Dünweber et al. 2010). The difference between a surface layer temperature measured at a single standard oceanographic station and an overall ambient bottom temperature at 150 to 600 m depth for the entire shelf between 59° 30′ and 72° 30′ N, as used in the present study, may not be the most representative indicator for a match or mismatch of the timing of larval hatch of northern shrimp off West Greenland.

Above and below average recruitment levels of northern shrimp were recorded in the absence of Atlantic cod off West Greenland in the period 1992 to 2004, but strong recruitment was not seen in the presence of Atlantic cod, i.e. in the years 2005 to 2009. Similarly, pre-recruit survival of northern shrimp declined when Greenland halibut biomass increased. Northern shrimp has been identified as an important food item in the diet of Greenland halibut at sizes below 60 cm total length in the Davis Strait (Orr & Bowering 1997) and northern shrimp at sizes down to 6 mm carapace length have been found in Greenland halibut stomachs off West Greenland (Pedersen & Riget 1993). It appears therefore reasonable to conclude that the negative coefficient for the Greenland halibut biomass index lagged by 1 yr in the final multiple regression model represents predation on northern shrimp juveniles at age 1. Feeding on juvenile northern shrimp of 4 to 13 mm carapace length has also been reported for Atlantic cod off Newfoundland and Labrador (Parsons et al. 1986). However, in contrast to Greenland halibut, no significant effect of Atlantic cod predation on northern shrimp recruitment was found, which may be explained by the absence or low abundance of Atlantic cod in West Greenland water during the years considered in the present analysis. However, the impact of Atlantic cod may rapidly become important if its biomass and the spatial overlap with northern shrimp increase as was the case until the beginning of the 1990s when the stock dynamics of the 2 species were linked (Wieland et al. 2007).

So far, modelling results on the advection of northern shrimp larvae off West Greenland have not provided conclusive results on the spatial structure of the stock, and the link between Disko Bay and the adjacent offshore area with respect to larval transport or migration of adults is poorly known (Storm & Pedersen 2003, Ribergaard et al. 2004). Exceptionally high abundance of northern shrimp at age 2 was observed in 1996 and during 1999 to 2002. In 1996, most of these recruits were found in the offshore area between 62° and 66° N, whereas the offshore area between 66° and 69° N and in particular the Disko Bay and Vaigat area contributed the majority of the recruits in the other years (Wieland 2005). The relevant factors for pre-recruit survival may differ between these areas, but spatial effects are at present difficult to incorporate in studies of the processes determining recruitment success of northern shrimp off West Greenland.

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