EXPLAINING VARIATION IN AMERICAN LOBSTER (*HOMARUS AMERICANUS*) AND SNOW CRAB (*CHIONOECETES OPILIO*) ABUNDANCE IN THE NORTHWEST ATLANTIC OCEAN

by

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Signature of Author

To the memory of my uncles (and guardians), Martin and Kelly Boudreau

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Abstract:

In this thesis I assessed the causes of long-term changes in two large, commercially important decapod crustacean populations, American lobster (*Homarus americanus*) and snow crab (*Chionoecetes opilio*) in the northwest (NW) Atlantic. By combining available time-series data, including commercial landings, research surveys, and local ecological knowledge, I explored the causes of an observed ecosystem shift in the NW Atlantic (~1950–2009) which entailed a region-wide decline of groundfish and an increase in benthic invertebrates, including these decapods. Three main ecological hypotheses were examined to explain the increase in decapod abundance: 1) the predation hypothesis, whereby a decrease in predatory groundfish led to an increase in their decapod prey species (top-down effects); 2) the climate hypothesis, whereby changes in temperature or other climatic variables helped to increase decapod numbers (bottom-up effects); and 3) the anthropogenic hypothesis, whereby changes in fishing pressure drove decapod population dynamics. I explored these hypotheses separately for lobster and snow crab, potentially under different selective pressures both ecologically and commercially.

First I investigated the interactions between predatory groundfish and lobster in the inshore region of southwest (SW) Nova Scotia. Long-term fisheries-independent abundance indices for lobsters and their predators are available for Gulf of Maine (GOM) waters under American jurisdiction, but not Canadian. To address research gaps I designed and executed a survey to collect local ecological knowledge of lobster fishermen in SW Nova Scotia fishing in the Canadian GOM. Forty-two fishermen were interviewed. Corresponding survey results from the USA were compared to the expert knowledge results. Both sources provided evidence for a top-down effect (predation release), contributing to observed increases in GOM lobster abundance and landings. Second, I explored relationships between lobster abundance and landings in the NW Atlantic as they may relate to temporal changes in predators, temperature, climate (North Atlantic Oscillation Index, NAOI), and fishing. Available landings data and fisheries-independent abundance estimates were collated to investigate trends in lobster abundance and catch. Links between American lobster, groundfish, temperature and climate indices were explored using mixed effects models. Results offered partial support for the predation hypothesis, namely in the waters off Newfoundland, Nova Scotia, and southern New England as well as broad support for a climate effect on early life stages. This effect appeared related to a region-wide climate signal, the NAOI, but was independent of changes in water temperature. Fishing effort appeared to be following lobster abundance, rather than regulating abundance in a consistent way.

Third, variation in snow crab abundance in the NW Atlantic was examined through meta-analysis of time-series data of cod and crab abundance indices and temperature. Temperature had an opposing effect on the two species: snow crab abundance was negatively correlated with temperature whereas cod and temperature were positively related. Controlling for the effect of temperature, the meta-analysis revealed significant negative correlations of snow crab and cod abundance, with cod leading snow crab up to a five-year lag. Results indicate that snow crab abundance is largely influenced by temperature during early post-settlement years and becomes increasingly regulated by top-down mechanisms as they approach fishery recruitment.

List of Abbreviations and Symbols Used

^{o}C	degrees Celcius
AIC	Akaike Information Criterion
ASMFC	Atlantic States Marine Fisheries Commission
CAD	Canadian dollars
CI	confidence interval
CL	carapace length
cm	centimetres
CPUE	catch per unit effort
CT	Connecticut
CW	carapace width
DFO	Department of Fisheries and Oceans Canada
ESS	Eastern Scotian Shelf
ENL	Eastern Newfoundland
FC	Flemish Cap
GB	Georges Bank
GOM	Gulf of Maine
kg	kilogram
L	length
LEK	local ecological knowledge
LFA	lobster fishing area
m	metres
MA	Massachusetts
MFO	mean frequency of occurrence
mm	millimetres
mt	metric tonnes
N	sample size

NAFO	Northwest Atlantic Fisheries Organization
NCB	Northern Cape Breton
NEFSC	Northeast Fisheries Science Center
NGSL	Northern Gulf of St. Lawrence
NL	Newfoundland and Labrador
NMFS	National Marine Fisheries Service
NNL	Northern Newfoundland
NS	Nova Scotia
PFI	partial fullness index
r	correlation coefficient
RI	Rhode Island
RS	research survey
SPA	sequential population analysis
SGSL	southern Gulf of St. Lawrence
SNE	southern New England
SNL	Southern Newfoundland
t	tonnes
USD	American (United States) dollars
WCB	Western Cape Breton
yr	year

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Three favourite RAM-isms;

“Being busy isn’t an excuse for not doing other things”
“If it was easy, someone would have already done it”
“It’s not that hard, but not exactly non-trivial”

Chapter 1

Introduction

1.1 General Introduction:

> *'To do science is to search for repeated patterns'*
>
> \- Robert H. MacArthur, Geographical Ecology, 1972

This thesis presents an ecological analysis of recent changes in the abundance of large crustaceans in the northwest (NW) Atlantic. In accordance with the above quote, the research approach entailed a search for repeated patterns in the abundance and distribution of these species and others that interact with them. Much of this work was motivated by the observation that the decline and collapse of the NW Atlantic cod and associated groundfish stocks in the 1980s and 1990s (Myers *et al.* 1997, Frank *et al.* 2005) coincided with a perceived increase in several decapod crustacean species, which have since become increasingly important to commercial fisheries in the region (Worm and Myers 2003, DFO 2007, Anderson *et al.* 2011). The American lobster (*Homarus americanu*s, Fig.1) and snow crab (*Chionoecetes opilio*, Fig. 2) in particular are currently the most valuable commercially fished species in the NW Atlantic, and there is a large reliance on the continuing health of these stocks (Steneck *et al.* 2011). American lobster populations range from North Carolina to Newfoundland and Labrador (Lawton and Lavalli 1995), whereas snow crab occur from the Gulf of Maine to northern Labrador (Tremblay 1997, DFO 2007). In the last 20 to 30 years, there have been remarkable changes in lobster and snow crab abundance throughout their ranges though the mechanisms for this change are not clear. Lobster landings remain far above historical averages, particularly in southwest Nova Scotia, and total landings have been increasing since the 1980s and have been relatively constant or increasing through the 1990s with the exception of a decline in the southern Gulf of St. Lawrence and southern New England. Snow crab landings and abundance, while high, are more variable overall, possibly due to episodic pulses of recruitment (Sainte-Marie *et al.* 1996). Landings increased in all snow crab managed areas beginning in the 1980-90s until 2002, when decreases in biomass and catches around Cape Breton, eastern Newfoundland, and the southern Gulf of St. Lawrence began. It is also evident that as groundfish stocks declined, lobsters, snow crab and Northern shrimp (*Pandalus borealis*) all increased steeply in catches, and in the case of shrimp also in abundance (Worm and Myers 2003).

One widely held hypothesis is that a decline in groundfish predation on larval and sub-adult lobsters and snow crab has contributed to the observed lobster and snow crab population increases (i.e. Fogarty 1995, Chabot *et al.* 2008). Both species are indeed susceptible to predation at various stages in their life cycle. Eggs are brooded attached to the female's abdomen for approximately two years, after which planktonic larvae hatch in spring or summer. The larvae moult through three stages while in the plankton and settle to the bottom about two months later. Once benthic, the animal moults many times. As larvae, lobsters may fall prey to schooling pelagic fish such as herring (*Clupea harengus*), and as juveniles or moulting adults they may be vulnerable to groundfish predation. It is often assumed that recently moulted adults are more vulnerable to predation than those post-moult (Fogarty 1995, Chabot *et al.* 2008). However, besides laboratory and tethering studies (Steneck and Wilson 2001), there is little direct evidence of natural predation on lobster by groundfish. Hanson and Lanteigne (2000) reviewed published reports of Atlantic cod (*Gadus morhua*) diets in the southern Gulf of St. Lawrence and found very few incidences of lobster in cod stomachs. They also examined the stomach contents of nine other demersal fish species, and found lobster in white hake (*Urophysis tenuis*), shorthorn sculpin (*Myoxocephalus scorpius*) and cunner (*Tautoglabrus adspersus*) stomachs. However, fishermen do report that predation can be important in certain areas (i.e. inshore cobble habitats) or at specific times of the year (i.e. when lobsters are moulting). In some regions (e.g. LFA 34 and Monhegan Island, ME), fishermen have frequently reported lobsters in the stomachs of cod, both historically and recently. There is more direct evidence of groundfish predation on snow crab. Snow crab have been documented as a common component of Atlantic cod (i.e. Hanson and Chouinard 2002, Chabot *et al.* 2008) and thorny skate (*Amblyraja radiata*) (Robichaud *et al.* 1991) diets. In addition to the direct effects of predation on lobster populations there could also be behaviourally-mediated indirect interactions between large groundfish and lobsters or snow crab (Dill *et al.* 2003).

A second hypothesis about groundfish predation states that the loss of this predation has allowed lobsters to expand into different habitat types, particularly those that offer limited shelter from predators. Anecdotally, fishermen have reported finding lobsters at greater depths and on softer bottom-types than has historically been the case. Regardless of the potential predation by groundfish on juvenile lobsters, large adult lobsters (and snow crab) may have few natural predators (Tremblay and Smith 2001, Geraldi *et al.* 2009). In contrast to lobsters, snow crab are typically found on soft sediments or other bottom types that offer limited physical structure, with the exception of earlier life stages or those in soft-shell or newly moulted condition. Water temperature is believed to be the primary factor determining snow crab distribution, and it is possible that lower bottom temperatures since the mid-1980s may have contributed to an expansion of the habitat available to the species (Tremblay 1997). Seven degrees Celsius appears to be an upper limit above which some metabolic functions are compromised (Foyle *et al.* 1989) though the species is occasionally found in warmer waters as well (i.e. Tremblay 1997). Temperature is particularly important during the more sensitive early life stages, up to benthic instar IV (e.g. Lovrich *et al.* 1995, Dionne *et al.* 2003) at approximately 17 months of age (Sainte-Marie *et al.* 1995). Snow crab live upward of 15 years and do not moult throughout their lifetime, but have a terminal moult to maturity (Conan and Comeau 1986).

Lobsters are believed to moult throughout their lifetime, with intervals between moulting events becoming longer over time, and evidence suggests they can live for more than 40 years. Temperature plays an important role throughout the lifecycle of the lobster, from the development of early life stages, to moulting, spawning, and susceptibility to disease (Aiken and Waddy 1986). In the past, lobster landings have been correlated with water temperature at the time of settlement in Maine (Steneck and Wilson 2001). Temperature is also believed to influence recruitment (Aiken and Waddy 1986, Hudon 1994), and plays a role in seasonal migrations from shallow to deeper waters (Lawton and Lavalli 1995 and references therein). Hence, changes in water temperature as well as predation could potentially drive some of the observed changes in lobster and snow crab abundances or availability to the fishery.

The Canadian lobster fishery is divided into regional management areas, the so-called lobster fishing areas (LFAs). LFAs are managed by the DFO, not using a quota system but by using input controls such as restricted fishing seasons, limited number of licenses, minimum size restrictions, protection of ovigerous females, and vessel and gear restrictions (Miller 1995). The American lobster fishery is similarly managed through input controls by the Atlantic States Marine Fisheries Commission (ASMFC, state waters 0-3 miles from shore) and the National Marine Fisheries Service (NMFS, federal waters 3-200 miles from shore) (ASMFC 2006). There are three main lobster stocks recognised by the ASMFC and NMFS: the Gulf of Maine, Georges Bank and southern New England stocks. In addition to the abovementioned input controls, US management agencies further protect brood stock with a maximum size restriction, but not by restricting fishing seasons (ASMFC 2006). The snow crab fishery is managed similarly to that of lobster (i.e. gear restrictions, size limits, crab fishing areas, seasons) but it only takes place in Atlantic Canada, it is managed under a quota system, and only males are retained in the fishery. In 2010, USA lobster landings were 52,729 mt and valued at $400 million USD, with more than 80% (43,321 mt) landed in Maine (NMFS 2012). Canadian lobster landings were 64,117 mt (DFO 2012a), valued at $396 million CAD (DFO 2012b), and with slightly over half landed in Nova Scotia (35,760 mt, DFO 2012a). By comparison, 84,396 mt (DFO 2012a) of snow crab were landed, mostly from Newfoundland and Labrador (52,229 mt, DFO 2012a), and valued at $281 million (DFO 2012b). Commercial fishing can in essence be considered the apex predator of lobster and snow crab. Lobster in particular experiences large fishing mortality throughout the majority of their range and most of the snow crab's distribution is exploited (Tremblay 1997, DFO 2009). Their abundance may be driven in part by fishing or fishing effort.

1.2 Objectives:

The overarching goal of this research was to assess possible causes of long-term changes in lobster and snow crab populations in the NW Atlantic, occurring as part of a reported ecosystem shift that entailed a region-wide decline of groundfish resources and an increase in benthic invertebrates. This was achieved through compilation and analysis of available time-series data, including commercial landings, research surveys, catch per unit effort (CPUE), and local ecological knowledge. As there is abundant evidence for multiple causalities explaining population trends in different ecosystems (Krebs 2001), it is expected that no one variable will explain lobster or snow crab population trends on its own. Instead, a combination of variables may act together in producing changes in lobster abundance and distribution. I have explored multiple hypotheses relating to the causes of this shift, namely changes in climate, temperature, predation and fishing. Finally, I have assessed the possible ecosystem consequences of changes in large decapod populations through a comprehensive literature review, presented as Chapter 2 of this thesis.

1.3 Hypotheses:

(1) The predation hypothesis, whereby a decrease in predatory groundfish led to an increase in their decapod prey species (top-down effects);

(2) the climate hypothesis, whereby changes in temperature or other climatic variables helped to increase decapod numbers (bottom-up effects); and

(3) the anthropogenic hypothesis, whereby changes in fishing pressure drove decapod population dynamics (top-down effects).

1.4 Data Chapter Summaries:

In Chapter 3 I assessed the above stated hypotheses through a survey of the expert knowledge of lobster fishermen in southwest Nova Scotia fishing in the Canadian Gulf of Maine (GOM) region. This region was selected for its importance to the industry, as ~40% of Canada's lobster landings originate from its waters. To explore a documented shift in groundfish and lobster abundance in the immediate inshore region, 42 fishermen were interviewed. Additionally, research survey results from the National Marine Fisheries Service were analysed and compared to the expert knowledge results. Both data sources provided evidence for a top-down mechanism contributing (at least in part) to observed increases in lobster abundance and landings in the Gulf of Maine.

In Chapter 4 I expanded on the results of Chapter 3, exploring linkages between American lobster catches and abundance, groundfish abundance, temperature, climate (North Atlantic Oscillation), and fishing effort. Specifically, I examined time-series data of lobsters, their predators, temperature and climate though mixed-effects models that share information across the different regions where the species occur. Results again offered partial support for the predation hypothesis, namely in Newfoundland, Nova Scotia, and southern New England, as well as broad support for a climate effect on lobster recruitment and early development. This effect appeared related to a region-wide climate signal, the North Atlantic Oscillation Index, but was independent of changes in water temperature. Fishing effort appeared to be following lobster abundance, rather than regulating abundance in a consistent way.

In Chapter 5 my goal was to explain the variation in snow crab abundance in the NW Atlantic. Time series data of cod (stock assessments) and crab abundance indices (catch per unit effort) and temperature were analysed via meta-analysis of full and partial correlation coefficients between the time series. Results suggest that snow crab abundance is largely influenced by temperature during early post-settlement years and may become increasingly regulated by top-down mechanisms as the species approaches the age of recruitment to the fishery.

Figure 1.1. American lobster. *Homarus americanus* (Milne-Edwards, 1837). Phylum: Arthropoda, Subphylum: Crustacea, Class: Malacostraca, Order: Decapoda, Family: Nephropidae (Photo S.A. Boudreau)

Figure 1.2. Snow crab (also called Queen crab in Canada). *Chionoectes opilio* (Fabricius, 1788). Phylum: Arthropoda, Subphylum: Crustacea, Class: Malacostraca, Order: Decapoda, Infraorder: Brachyura, Family: Oregoniidae (Photo S.A. Boudreau)

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Chapter 2

The Ecological Role of Large Benthic Decapods in Marine Ecosystems

Stephanie A. Boudreau and Boris Worm (2012) *Marine Ecology Progress Series*.

In revision

2.1 Abstract:

Invertebrates, including large benthic decapods, play an increasingly important role for commercial fisheries worldwide, yet their roles in the marine ecosystem are less well defined. A synthesis of existing evidence for four 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 the possible ecosystem consequences of decapod fisheries.

The reviewed decapod species are prey items for a wide range of invertebrates and vertebrates, including other crustaceans, octopus, sea stars, fish, seabirds, and marine mammals. They are typically omnivorous but typically prefer molluscs and crustaceans as prey. Experimental studies have shown how decapods can contribute to the structuring of benthic infaunal or epifaunal communities. They occasionally play a keystone role by regulating habitat structure via suppression of powerful herbivores or space competitors. For example, decapods which prey heavily on urchins, snails, or mussels are implicated in trophic cascades that contribute to the maintenance of kelp forest, marsh grass, and algal turf habitats, respectively. Non-consumptive interactions that are commonly documented 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 for conservation and population recovery, and species introductions influence these ecosystem roles by decreasing (exploitation) or increasing (conservation, introductions) decapod densities, often with measurable effects on prey communities.

A number of studies have investigated particular ecosystem effects of large benthic marine decapods, but there are few examples of species that have been comprehensively studied in an ecosystem context. Thus - while the available evidence is used here to derive a simplified synthetic framework for interpreting ecosystem roles of large decapods, more experimental and long-term observational studies are needed to fully elucidate mechanisms, and long-term consequences of decapod fisheries, respectively.

2.2 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 which now dominate commercial landings and value (Worm and Myers 2003, Frank *et al.* 2005). Globally, commercial catches of crustaceans have increased ~5-fold since 1950 and are the only invertebrate group which 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 *Chionoecetes opilio*, have become particularly important commercial species in the Northwest 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 and Worm 2009, Estes *et al.* 2011). One of the commonly described ecosystem effects of fishing marine predators, which has been an increase in benthic invertebrates, including large decapod crustaceans (Baum and Worm 2009, Boudreau and Worm 2010). On occasion large decapods may replace large fish (i.e. Atlantic cod) as the dominant predator, the impacts of which are poorly understood (e.g. Steneck *et al.* 2011). These changes may have further effects on benthic habitats, for example through increased decapod predation on benthic resource species (Quijon and Snelgrove 2005b). 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. There is much experimental evidence that 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 such studies have focused on large decapods. Decapod predators are typically quite mobile, undergo ontogenetic habitat changes over their life cycle, and show a progressive dietary shift with increasing size (Sainte-Marie and 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) non-consumptive 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.

2.3 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 core of this review.

Available publications employed a variety of methods including, decapod exclusion experiments in the field (e.g. Quijon and Snelgrove 2005b), experimental transplants of species (e.g. Robles and Robb 1993), tethering experiments (e.g. Silliman and Bertness 2002), and diet studies (e.g. Jewett and 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 for example, observations on collected animals (e.g. Dvoretsky and 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 and 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).

2.4 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 9-10cm (Klassen and Locke 2007). Originally native to Europe it was introduced to eastern North America in the 19th century (Grosholz and 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 over 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 northwest Atlantic Ocean and the European lobster *Homarus gammarus* in the northeast Atlantic. Clawless lobsters include several species of spiny lobster, such as *Panulirus interruptus* (California), the spiny rock lobster *Jasus edwardsii* (New Zealand), the western Australian rock lobster *P. cygnus*, spiny lobster *P. marginatus* (Hawaii), Caribbean spiny lobster *P. argus* (Florida, Bahamas) and rock lobster *J. lalandii* (South Africa).

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

2.5 Ecosystem Effects:

2.5.1. 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 and Herrnkind 2009) which both prey on the Caribbean spiny lobster (*P. argus*), Pacific cod (*Gadus macrocephalus*) prey on snow crabs *Chionoecectes* spp. (Jewett 1982), and sculpins (*Myoxocephalus* spp.) consume benthic stages of American lobsters (e.g. Hanson and Lanteigne 2000, Hanson 2009, Boudreau and Worm 2010). Cephalopods are also reported to prey on decapods, for example the Caribbean reef octopus *Octopus briareus* occasionally consumes *P. argus* (e.g. Berger and Butler 2001, Butler and Lear 2009) as do sharks, such as the leopard shark *Triakis semifasciata* on Dungeness crab (third most important prey item, Ebert and Ebert 2005).

Avian predators such as the herring gull *Larus agentatus* and ring-billed gull *L. delawarensis* commonly feed on crabs, for example green or rock crabs (e.g. Dumas and 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) however decapods have not been identified as a major dietary component of seals or sea lions (Goodman-Lowe 1998, Beck *et al.* 2007, Boudreau and 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 two incidences of *C. opilio* males holding dead, recently moulted mature females which were being consumed by whelks *Buccinum undatum*. Additional dead females and immature female exuviae were observed being consumed by lysianassoid amphipods (Sainte-Marie and 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 and Able 1996, Steneck 1997, Boudreau and 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 harrengus*, 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 settle at higher densities than lobster and are 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 *P. argus* increased on artificial patch reefs from which groupers *E. striatus* were removed (Eggleston *et al.* 1997). One interesting study documented that the rock lobster *J. lalandii* could be overwhelmed and ingested by whelks *Burnupena* spp., reversing the typical predator-prey relationship between these two species (Barkai and McQuaid 1988).

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.

2.5.2. 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 and Feder 1982, Wieczorek and Hooper 1995, Squires and Dawe 2003) Their diet may include gastropods, bivalves, chitons, crustaceans, sea urchins, sea stars, polychaetes, algae and occasionally, fish (e.g. Jewett and Feder 1982, Elner and Campbell 1987, Lawton 1987, Robles 1987, Wieczorek and Hooper 1995, Cox *et al.* 1997, Squires and Dawe 2003, Hanson 2009). Other decapods and even conspecifics are also consumed, including their moulted exoskeletons (e.g. Jewett 1982, Elner and Campbell 1987, Wieczorek and Hooper 1995, Hanson 2009). Prey size tends to increase, and species preferences change with the size of the animal (e.g. Robles *et al.* 1990, Sainte-Marie and Chabot 2002, Squires and 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 defences of their prey, for example by crushing mussel shells (Robles *et al.* 1990). Decapods also frequently share particular prey items 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 have also been shown to be 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, 53% for the largest, Sainte-Marie and Chabot 2002).

American lobster and rock crab are typically found in highly structured hard-bottom habitats, however in regions characterized by soft substrates (e.g. southern Gulf of St. Lawrence), rock crab were also an important diet item in the stomachs of lobsters >40 mm CL (45-68% 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 and 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 and Snelgrove 2005a). Hence crab fisheries may have indirect effects on benthic community structure (abundance, composition and diversity) by reducing crab predation on infauna (Quijon and Snelgrove 2005a, b).

Decapods are often effective predators utilizing a variety of behavioural strategies. For example, in Southern California, spiny lobsters *P. interruptus* like most decapods, are intolerant to exposure, and hence forage on intertidal mussels *Mytilus californianus* 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 however, eventually all available individuals were consumed (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 (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.* (2005), 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

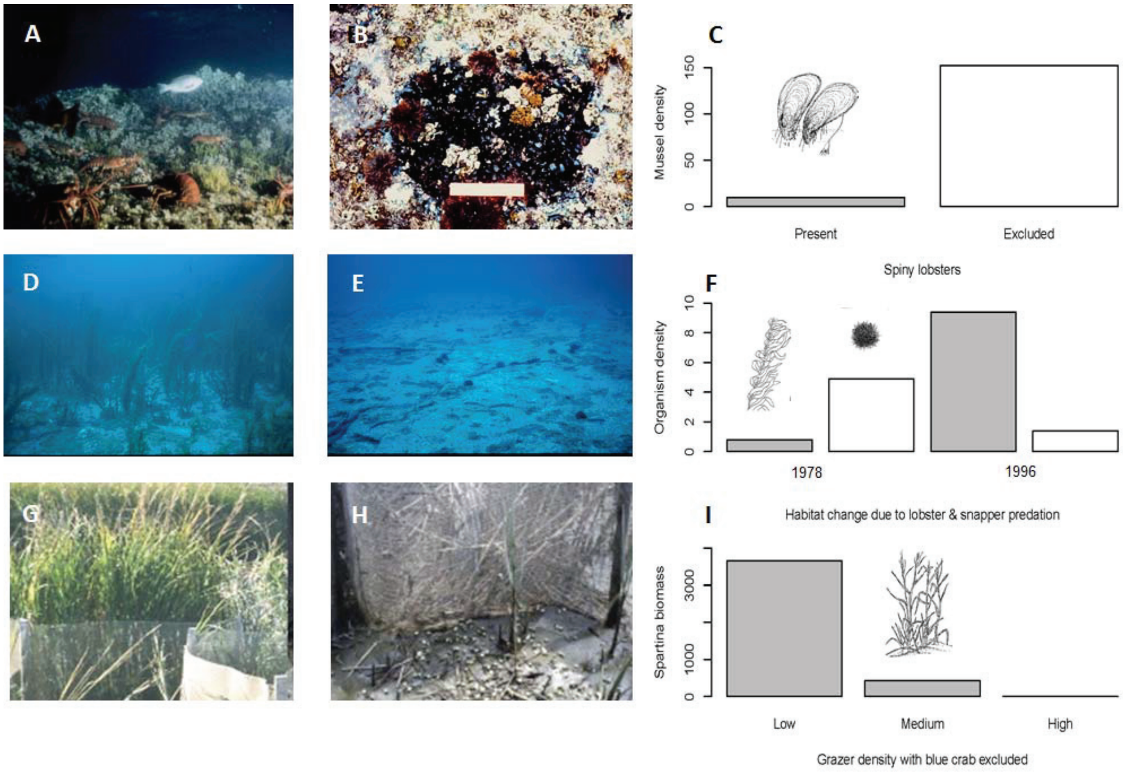

Figure 2.1. Case studies exemplifying strong ecosystem effects of large decapods. Images illustrate effects of decapod presence (left column) versus absence (right column). (A) Spiny lobster *Panulirus interruptus*, preying on mussels in the wave-exposed rocky intertidal in California. (B) Exclusion of lobster caused algal turf to be replaced by mussels (C) Mean number of mussels per 230 cm^2 sample after 10 months, where lobsters were present (shaded) or excluded (open) (after Robles and Robb 1993, Robles *et al.* 2001). (D) Lush kelp habitat resulting from the recovery of spiny lobster *Jasus edswardii* and snapper *Pagurus auratus* populations in Leigh Marine Reserve, New Zealand. (E) Urchin barrens, dominated by the sea urchin *Evechinus chloroticus,* at the same site prior to establishment of the reserve. (F) Habitat shift at Leigh from 1978 to 1996 with kelp (shaded bars), and urchins (open) densities in numbers per m^2 (After Babcock *et al.* 1999, Babcock 2003) (G) *Spartina* marsh grass in the tall zone with blue crab *Callinectes sapidus* predators excluded, and low densities of grazing *Littoraria irrorata* plot versus (H), high-densities of the same species in the same zone. (I) *Spartina* biomass (g dry wt m^{-2}) in the tall marsh zone after 8 months of blue crab exclusion, in relation to *Littoraria* density (after Silliman and Bertness 2002).

the regulation of marsh grass cover through a three-level trophic cascade (Silliman and Bertness 2002). Prior to this study, salt marshes had been mostly described as bottom-up regulated systems driven by nutrient inputs (e.g. Valiela and 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. 1GHI). 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 and Bertness 2002).

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

American lobsters were also long believed to be a keystone predator of NW Atlantic subtidal kelp forests (Elner and 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. However, Elner and 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 and 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) were 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 urchins 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. *P. 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 weight), crustaceans (mainly barnacles, 31.4%) and fish (12.7%) (Jewett and 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 *C. opilio* were also frequently consumed (Squires and Dawe 2003). In

Bonne Bay, NL large crabs were more likely to scavenge on dead fish (e.g. discarded bait) and smaller crabs more likely to ingest shrimp (Wieczorek and Hooper 1995).

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 *P. 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 (35-60m) 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 and Robb 1993) to deep waters (i.e. Smith *et al.* 2011). 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 and 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 and Vadas 1990).

2.5.3. 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.

2.5.3.1. 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.* 1997 a, 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 and Shulman 2008).

2.5.3.2. Competition for Habitat

To avoid predation, many decapods are nocturnal, and seek protective shelter during the day. American lobster is sympatric with two species of *Cancer* crab, which compete for suitable shelter, but are often displaced by lobster when shelter is limiting (Richards and 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 and 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 and Smith 2001, Geraldi *et al.* 2009), this might signal a habitat expansion due to lower abundances of predatory groundfish (Boudreau and Worm 2010). Also, lobsters have a limited capacity for creating shelter in soft sediments by burrowing bowl-like depressions (Tremblay and Smith 2001).

2.5.3.3. 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 and 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 and 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 and Zisserson 2008) and female blue crab (e.g. Haefner Jr. and Shuster Jr. 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 and Kuris 1990) and amphipods (e.g. Dvoretsky and 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).

2.6. Anthropogenic Factors

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

2.6.1. Commercial Fishing

Decapods have become increasingly important to commercial fisheries, often as a result of declining groundfisheries (e.g. Pauly *et al.* 1998, Anderson *et al.* 2008, 2011, Choi and Zisserson 2008). Emerging or already established invertebrate fisheries often operate under scarce ecological and life-history information (e.g. natural mortality rates, nursery habitats) and without proper stock assessments being 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 and 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 NE United States and Atlantic Canada 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 and Worm 2010, Steneck 2011). Yet, this lobster population is not without potential threats, as the nominal fishing effort has been increasing (Gendron and Archambault 1997, Gendron *et al.* 2000, Pezzack *et al.* 2001, DFO 2006), and there has been a trend of fishing of larger lobster in deeper water. Whether these individuals are essential broodstock and how their removal will be affect recruitment, and hence the future of the population has yet to be determined (DFO 2006, Boudreau and 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 decapod predators (e.g. Atlantic cod) or prey (e.g. rock crab) species or by altering habitat (e.g. scallop dredges, Kaiser *et al.* 2006). These interactions can have important implications for multispecies management. For example, in the literature it is often noted that rock crab is important to the diet of American lobster (e.g. Sainte-Marie and 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 other studies reviewed here.

Another potentially important interaction between decapods and fishers is 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 *et al.* 2008). In Western Australia, stable isotope analysis and gut contents analysis indicated that bait inputs contributed between 30-80% of the diet of rock lobster *P. 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 and 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 and Tlusty 2009). Finally, it is not clear how an increase of bait in lobster diets may affect predation rates by lobsters on their regular prey species.

2.6.2. Conservation and Protected Areas

The potentially large effects of fishing on decapods often become most apparent when this influence is removed, in what J. 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 and Babcock 2002). Reserves have been shown to successfully protect and increase spiny lobster populations (i.e. Kelly *et al.* 2000) which had strong cascading effects throughout the ecosystem (Fig. 2). 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 two reserves when compared with adjacent unprotected areas. The spiny lobster *J. 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 approximately 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. 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 lead to increased primary and secondary productivity in marine reserves as a consequence of protection (Babcock *et al.* 1999).

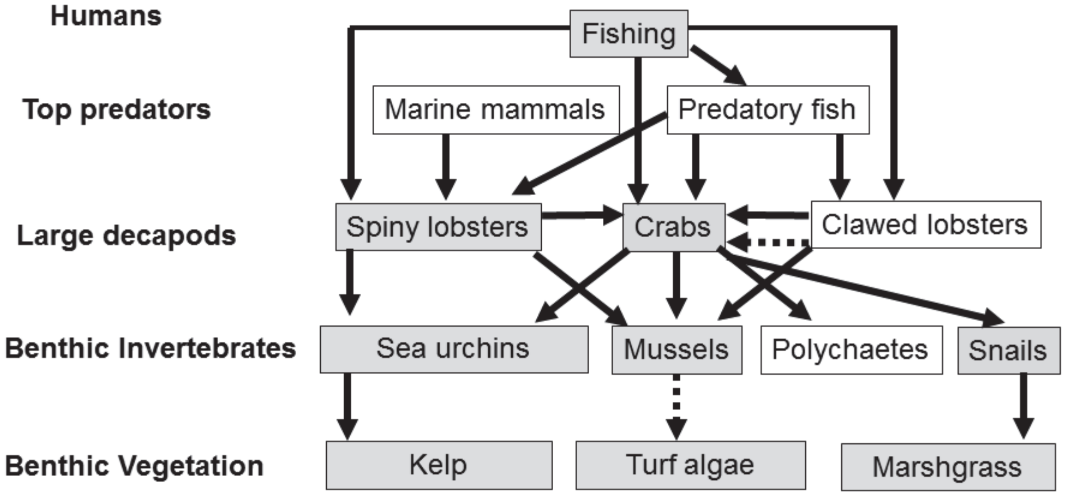

Figure 2.2 Conceptual synthesis. Major documented ecosystem interactions of large decapods include predatory (solid arrows) and competitive (dotted arrows) interactions. Cannibalistic interactions occur in crabs and lobster, but are not shown here. Species that are strongly implicated in trophic cascades are highlighted in grey. Note that this represents a simplified scheme, other interactions may well occur depending on species diets and other ecological traits in particular regions.

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 over 12 months led to a change from crustose coralline algae to macroalgal canopies that mimic habitats now commonly found in the reserves (Shears and 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 and 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 1950's have been replaced by urchin barrens that have persisted at least since the 1970's (Kerr and Grace 2005).

In a similar example from Southern California, large spiny lobsters *P. interruptus* prey on the purple *Strongylocentrotus purpuratus* (Tegner and Levin 1983) and red sea urchins *S. franciscanus* (Tegner and Dayton 1981). The predatory seastar *Pycnopodia helianthoides* is important at cold-water sites where lobsters are rare (Duggins 1983). A large fish, the sheepshead *Semicossyphus pulcher*, can also reduce urchin densities in southern California (Cowen 1983) and in combination with *P. interruptus* structure the sea urchins' size frequency distributions (Tegner and Dayton 1981). Sixteen sites in and around the Anacapa marine reserve in Channel Islands National Park, CA, were sampled. 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 could also affect urchins by promoting disease (Lafferty 2004).

In the Atlantic Ocean, one short-term study of American lobsters in a reserve exists from Bonavista Bay, Newfoundland (Rowe 2002). The researcher documented increases in body size and density after three years 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 United Kingdom'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 were tagged in a Skagerrak coast (Norway) reserve, and 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.

2.6.3. 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 be lead to changes in habitat, and the 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 in to a region, indigenous species may indirectly facilitate its spread. For example by feeding on mussels, Jonah crabs *C. 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 and 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 and Witman 2004).

One important case study concerns red king crab, which were 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 and by 1976 there were at least 100 records and the introduction was considered a success (Orlov and Ivanov 1978). This population is now believed to be actively invading coastal waters through migration by 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 larger than 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 (Jorgensen 2005). Scallops made up 73-97% 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 5-8 yrs (Jorgensen 2005) however the first red king crab was already recorded four years after (Jorgensen and Primicero 2007).

In addition to intentional introductions, the Arctic and Antarctic are now being exposed to species invasions from lower latitudes due to global warming. 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 ybp) 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.* 2011).

There could also other unintended impacts from other 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 Dungeness crab, and increased the risk of being trapped in marsh grass and exposed at low tide (Holsman *et al.* 2010).

2.7 Discussion:

This review indicates that large decapods can 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 any particular 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, and (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 and grey boxes in Fig. 2). These trophic cascades took place in a variety of temperate habitats, from the rocky intertidal (Robles and Robb 1993), to saltmarshes (Silliman and Bertness 2002) and subtidal reefs (Babcock *et al.* 1999). In these cases, large decapods were essential in the maintenance of benthic vegetation (kelp forests, marshgrass, 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 and Robb 1993, Babcock *et al.* 1999), or whelks (e.g. Robles and Robb 1993). The interaction between sea urchins and spiny lobsters and sea urchins and crab was demonstrated to be significant, however an interesting observation is that such a relationship has not 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. Quijon and Snelgrove 2005 a, 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 *P. argus* (Eggleston *et al.* 1997). It has been shown that 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 and Myers 2003, Steneck *et al.* 2004, Frank *et al.* 2005, Zhang and Chen 2007, Boudreau and 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 (including large decapods and their predators, Fig. 2), influencing species interactions, and in some cases leading to cascading changes throughout the ecosystem (e.g. Dill *et al.* 2003, Baum and 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, 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 (Fig 1 and 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 available evidence suggests 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 mobile and sedentary in- and epifauna 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, which 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 and Chouinard 2002, Zhang and 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 and Chouinard 2002). These methods can be useful, for example, to examine the possible consequences of complex ecosystem shifts (e.g. for the GOM, Zhang and Chen 2007), but cannot replace long-term empirical studies and experimental mechanisms.

Long-term studies could be of great value for creating a baseline as fishing, climate change, and other impacts that continue to alter oceans 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 in 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 and Shulman 2008). Occasionally, new taxonomic discoveries can be made by examining decapods, for example the new Phylum Cycliophora was discovered on the mouthparts of the commercially important Norway lobster *Nephrops norvegicus* (Funch and Kristensen 1995). Such complexities highlight the fact that an ecosystem-based approach to understanding and managing these valuable resources would be informative.

As more decapods populations are of increasing socio-economic importance and continue to be harvested more widely on a global scale (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 to maintain critical trophic interactions, and prevent overexploitation in an ecosystem context.

Table 2.1: Examples of studies examining ecological roles of large marine decapods. Indicated are the region of study, common and scientific names of the decapod species, the type of interaction, the nature of the evidence, and the citation. Listed alphabetically by scientific name.

Region	Common name(s)	Scientific name(s)	Interaction	Mechanism	Methods	Reference
Beaufort Inlet, North Carolina, NW Atlantic	blue crab	*Callinectes sapidus*	Host	Barnacles (*Octolasmis mulleri*) living on gills	Lab, Field	Walker 1974
Back Sound, North Carolina, NW Atlantic	blue crab	*Callinectes sapidus*	Predator	Crabs consumed more clams (*Mercenaria mercenaria*) at vegetated sites possibly avoiding bird predation	Field	Micheli 1997, Micheli & Peterson 1999
Sapelo Island, Georgia, NW Atlantic	blue crab	*Callinectes sapidus*	Keystone predator	Crabs control periwinkle capable of overgrazing salt marsh vegetation	Field	Silliman & Bertness 2002
Casco Bay, ME to Chesapeake Bay, VA, NW Atlantic	blue crab	*Callinectes sapidus, Carcinus maenas*	Predator, Prey	Blue crab predation limits abundance and range of invasive green crab	Lab, Field	DeRivera *et al*. 2005
Monterey Peninsula, CA NE Pacific	Cancer crab	*Cancer* spp.	Prey	*Cancer* spp. crab are a dietary component of the general consumer, the sea otter	Field	Estes et al. 2003
NE Newfoundland, NW Atlantic	snow crab	*Chionoecetes opilio*	Predator	Predation on juvenile snow crab, polychaetes, shrimp and fishes	Lab, Field	Squires & Dawe 2003
Bonne Bay, Newfoundland, NW Atlantic	snow crab	*Chionoecetes opilio*	Predator	Predation influenced composition, abundance, and diversity of benthic infauna	Lab, Field	Quijon & Snelgrove 2005b
Bonne Bay, Newfoundland, NW Atlantic	snow crab	*Chionoecetes opilio*	Predator	Predation on algae, fish, polychaetes, crustaceans, molluscs, echinoderms	Field	Wieczorek & Hooper 1995

Region	Common name(s)	Scientific name(s)	Interaction	Mechanism	Methods	Reference
Alaska, Japan, Russia (North Pacific), Gulf of St Lawrence (NW Atlantic)	snow, tanner crab	*Chionoecetes opilio, C. bairdi*	Prey	*Chionoecetes* prey for species of: 7 invertebrates, 24 fish, 2 skates, 4 marine mammals	Review	Jewett 1982
Bonne Bay, Newfoundland, NW Atlantic	snow, rock crab	*Chionoecetes opilio, Cancer irroratus*	Predator	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
Gulf of Maine, NW Atlantic	American lobster, rock, green crab	*Homarus americanus, Cancer irroratus, Carcinus maenas*	Predator	Nocturnal feeding on crabs, mussels, periwinkles. Believed to migrate up to prey on green crabs	Lab, Field	Jones & Shulman 2008
SW Nova Scotia, NW Atlantic	American lobster	*Homarus americanus*	Predator	65 prey taxa identified, mostly echinoderms, molluscs, crustaceans and polychaetes	Lab, Field	Elner & Campbell 1987
Narragansett Bay, Rhode Island, NW Atlantic	American lobster, Jonah crab	*Homarus americanus, Cancer borealis*	Competitor	Jonah crab choose to utilize alternative shelter when lobster present	Lab, Field	Richards & Cobb 1986
Isle of Shoals, New Hampshire, NW Atlantic	American lobster, Jonah crab	*Homarus americanus, Cancer borealis*	Predator	Crabs and lobster significant predators of sea urchins, indirect effects on ascidians and mussels	Field	Siddon & Witman 2004
Gulf of Maine, NW Atlantic	American lobster, rock crab	*Homarus americanus, Cancer irroratus*	Niche segregation	Rock crab densities higher on kelp fronds when lobsters were present	Lab, Field	Wells *et al*. 2010
Passamaquoddy Bay, New Brunswick, NW Atlantic	American lobster, rock crab	*Homarus americanus, Cancer irroratus*	Predator	Sea urchins avoided rock crabs and lobsters, no aggregations formed when decapods present	Lab, Field	Vadas *et al.* 1986

Region	Common name(s)	Scientific name(s)	Interaction	Mechanism	Methods	Reference
Northumberland Strait, Southern Gulf of St Lawrence, NW Atlantic	American lobster, rock crab	*Homarus americanus, Cancer irroratus*	Predator, Prey	Fish predation on lobster uncommon. Lobster mainly prey on crab, sea stars and lobster	Stomachs	Hanson 2009
Magdalen Islands, Gulf of St Lawrence, NW Atlantic	American lobster, rock crab	*Homarus americanus, Cancer irroratus*	Predator, Prey	Diet shift with increased size of lobster. Rock crab was part of diet at all sizes	Stomachs	Sainte-Marie & Chabot 2001
Magdalen Islands, Gulf of St Lawrence, NW Atlantic	American lobster, rock crab	*Homarus americanus, Cancer irroratus*	Predator, Prey	Lobsters condition, growth and development increased with increasing amounts of rock crab in their diet	Lab	Gendron *et al.* 2001
Southern Gulf of St. Lawrence, NW Atlantic	American lobster, rock crab	*Homarus americanus, Cancer irroratus*	Host, Vector	Non-indigenous ascidians, *Botrylloides violaceus* were found on rock crabs, *Botryllus schlosseri* was found on lobster	Lab, Field	Bernier *et al.* 2009
Southern Gulf of St. Lawrence, NW Atlantic	American lobster, green crab	*Homarus americanus, Carcinus maenas*	Competitor	Green crab outcompeted juvenile lobster for food	Lab	Rossong *et al.* 2006, Wiliams et al. 2006
Lundy no-take zone, United Kingdom, NE Atlantic	European lobster	*Homarus gammarus*	Abundance	Increased abundance and legal-sized lobster inside the NTZ, spillover of sublegal lobster.	Field	Hoskin *et al*. 2011

Region	Common name(s)	Scientific name(s)	Interaction	Mechanism	Methods	Reference
Tawharnui & Mimiwhangata Marine Parks, New Zealand, SW Pacific	spiny rock lobster	*Jasus edwardsii*	Trophic cascade	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
Leigh Reserve, New Zealand, SW Pacific	spiny rock lobster	*Jasus edwardsii*	Trophic cascade	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
Saldanha Bay Reserve, South Africa, SE Atlantic	rock lobster	*Jasus lalandii*	Predator, Prey	Rock lobsters prey on whelks and settling mussels. Transferred lobsters to other island were overwhelmed, consumed by whelks.	Lab, Field	Barkai & McQuaid 1988
Antarctic Bellingshausen Sea, Southern Ocean	king crabs	*Lithodes spp, Paralomis spp,* *Neolithodes spp.*	Predator	Lithodid crabs recolonizing Antarctica may restructure the benthic community via predation and bioturbation.	Field	Thatje *et al.* 2005, Smith *et al*. 2011
Bamfield, Britsh Columbia, NE Pacific	Dungeness crab	*Metacarcinus magister*	Predator	*Cancer* spp. including Dungeness, are able to exert biting forces (claws) greater than most other animals.	Lab	Taylor 2000
Willipa Bay, Washington, NE Pacific	Dungeness crab	*Metacarcinus magister*	Behaviour	Invasive cord grass restructured habitat, altered movement and foraging behaviour of indigenous Dungeness crab.	Lab, Field	Holsman *et al*. 2010

Region	Common name(s)	Scientific name(s)	Interaction	Mechanism	Methods	Reference
Humbolt Bay, California, NE Pacific	Dungeness crab	*Metacarcinus magister*	Prey	Dungeness crab had an 11.6% index of relative importance in the diet of female leopard sharks	Stomachs	Ebert & Ebert 2005
Florida Bay, Florida, NW Atlantic	Caribbean spiny lobster	*Panulirus argus*	Prey	Octopus is assumed predator of lobster. Lobster detected chemical cues to avoid octopus dens.	Lab, Field	Berger & Butler IV 2001
Florida Keys National Marine Sanctuary, Florida NW Atlantic	Caribbean spiny lobster	*Panulirus argus*	Prey	Juvenile lobsters preyed upon by Caribbean reef octopus	Field	Butler IV & Lear 2009
Lee Stocking Island, Bahamas NW Atlantic	Caribbean spiny lobster	*Panulirus argus*	Prey	Abundance of small lobsters was highest in small reefs where Nassau grouper were experimentally removed.	Field	Eggleston *et al.* 1997
Florida Keys, Florida, NW Atlantic	Caribbean spiny lobster	*Panulirus argus*	Prey	Grey triggerfish preyed on tethered lobsters	Lab, Field	Lavalli & Herrnkind 2009
Western Australia, E Indian Ocean	western rock lobster	*Panulirus cygnus*	Predator	Stable isotope analysis showed amphipods, isopods, crabs, bait, foliose red algae and sponges in lobster diet	Lab, Field, Stomachs	Waddington *et al.* 2008
Santa Catalina Island, California, NE Pacific	spiny lobster	*Panulirus interruptus*	Predator	Exclusion of lobsters from upper shore increases in density, size of mussels and herbivorous molluscs, decrease algae	Lab, Field	Robles 1987
Channel Islands National Park, California, NE Pacific	spiny lobster	*Panulirus interruptus*	Trophic cascade	Fishing of lobster led to increase in sea urchins, overgrazing of kelp forests	Field	Lafferty 2004

Region	Common name(s)	Scientific name(s)	Interaction	Mechanism	Methods	Reference
Santa Catalina Island, California, NE Pacific	spiny lobster	*Panulirus interruptus*	Keystone predator	Exclusion of lobsters (keystone) from wave-exposed rocky intertidal sites caused algal turf to be replaced by mussels	Field	Robles & Robb 1993, Robles 1997
Northwestern Hawaiian Islands, NE Pacific	spiny lobster	*Panulirus marginatus*	Prey	Hawaiian monk seals were observed foraging on spiny lobster, but not a major prey item	Field	MacDonald 1982, Goodman-Lowe 1998
Barents Sea, Arctic Ocean	red king crab	*Paralithodes camtschaticus*	Predator	Predation by crabs decreased sea urchin, sea stars, Iceland scallop abundance	Lab	Jorgensen 2005, Jorgensen & Primicerio 2007
Kodiak Island, Alaska NE Pacific	red king crab	*Paralithodes camtschaticus*	Predator	Stomach contents revealed molluscs and arthropods to be preferred prey	Stomachs	Jewett & Feder 1982
Barents Sea, Arctic Ocean	red king, northern stone crab	*Paralithodes camtschaticus,* *Lithodes maia*	Host	Hydrozoans, polychaetes, bivalves, amphipods, cirripedes, bryozoans were described on both species of crab	Field	Dvoretsky & Dvoretsky 2008

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Chapter 3

Top-down Control of Lobster in the Gulf of Maine: Insights from Local Ecological Knowledge and Research Surveys

Stephanie A. Boudreau and Boris Worm (2010) *Marine Ecology Progress Series*.
403: 181-191

3.1 Abstract:

American lobster (*Homarus americanus*) landings in the Gulf of Maine (GOM) have been steadily increasing since the 1980s. As a result, lobsters now support one of the most important fisheries in the United States of America (USA) and Canada. One hypothesis for this pattern is that lobsters have been released from predation as groundfish stocks declined, expanding both in abundance and habitat. Lobster habitat is typically rocky substrate of the inshore region, which is difficult to sample. Some long-term fisheries-independent abundance indices for lobsters and their predators are available for the GOM in the USA but not in Canada. To try and fill those research gaps, we designed a local ecological knowledge (LEK) survey. Semi-structured interviews of 42 fishermen in southwest Nova Scotia, Canada revealed consistent trends of the depletion of large groundfish, particularly Atlantic cod (*Gadus morhua*). Eighty-three percent of fishermen concluded this depletion was the main reason for an observed increase in lobster abundance. They also reported the expansion of lobsters to new habitats and depths. We further show that the proposed top-down control mechanism is independently supported by USA research trawl surveys, which revealed a negative

correlation ($p < 0.05$) between the summed abundance indices of five groundfish predators of lobster and lobster abundance (kg tow^{-1}) at time lags ranging from zero to nine years. Survey-based diet data also corroborated direct observations by fishermen on lobster predation by groundfish. These results suggest that LEK may be a useful supplementary tool to investigate the ecosystem effects of fishing, particularly in data-poor situations.

3.2 Introduction:

Commercially harvested invertebrate populations often exhibit abrupt declines under intense fishing pressure and can be slow to recover. Alaskan red king crab (*Paralithodes camtschaticus*, Orensanz *et al.* 1998), abalones (*Haliotis* spp., Tegner and Dayton 2000), green sea urchins (*Strongylocentrotus droebachiensis*, Berkes *et al.* 2006) and oysters (e.g. *Crassostrea virginica*, Kirby 2004) are well-documented examples of this phenomenon. American lobster (*Homarus americanus*) in the Gulf of Maine (GOM) of the northwestern (NW) Atlantic Ocean, however, shows a different trend characterized by long-term sustainability and recent increases in reported landings (ASMFC 2006, Steneck 2006).

Here we focus on lobster fishing area (LFA) 34 in southwest Nova Scotia, which is part of the Canadian GOM. It is one of the most productive lobster fishing areas in the world, accounting for approximately 40% of Canadian lobster landings every year. The annual lobster fishing season in LFA 34 lasts from late November to the end of May, with an estimated 70-90% of fishable biomass removed every year with baited traps. The fishery is managed by limiting licences, gear and vessel regulations, minimum carapace size and protection of egg-bearing females (DFO 2006a).

Despite intense fishing pressure, the lobster population in the GOM has been increasing since the 1980s, and in the 2004-05 fishing season, LFA 34 landings were approximately five times higher than in 1980-81 (Fig. 1A). Likewise, there have been documented increases in landings, abundance indices and recruitment of lobster in the United States' part of the GOM (Fig. 1B, C). Observed increases in landings, abundance, and recruitment are unique to this region as there has been an observed decline of lobster landings in areas south of the GOM, and also in the Northumberland Straight (LFA 25) and parts of Newfoundland (ASMFC 2006, DFO 2006b, 2007), Canada. The reason for this increase is not well understood; one hypothesis is that the increase in lobster landings is partially explained by the rapid decline in predatory groundfish stocks, such as Atlantic cod (*Gadus morhua*), in the NW Atlantic, leading to a predatory release (Frank *et al.* 2005, Steneck 2006, Zhang and Chen 2007, Collie *et al.* 2008). For example, as cod spawning stock biomass in the Canadian GOM decreased from 65000 MT in 1980 to 9000 MT in 2008 (Clark and Emberley 2009), the lobster population was increasing.

The NW Atlantic is assumed to have been a top-down dominated ecosystem before being subjected to exploitation (Worm and Myers 2003, Steneck *et al.* 2004, Frank *et al.* 2007). Fishing has altered this by removing most of the larger predators, which in turn has led to significant ecological change (Lotze and Milewski 2004, Steneck *et al.* 2004). For example, the GOM is thought to have gone through three phase shifts in

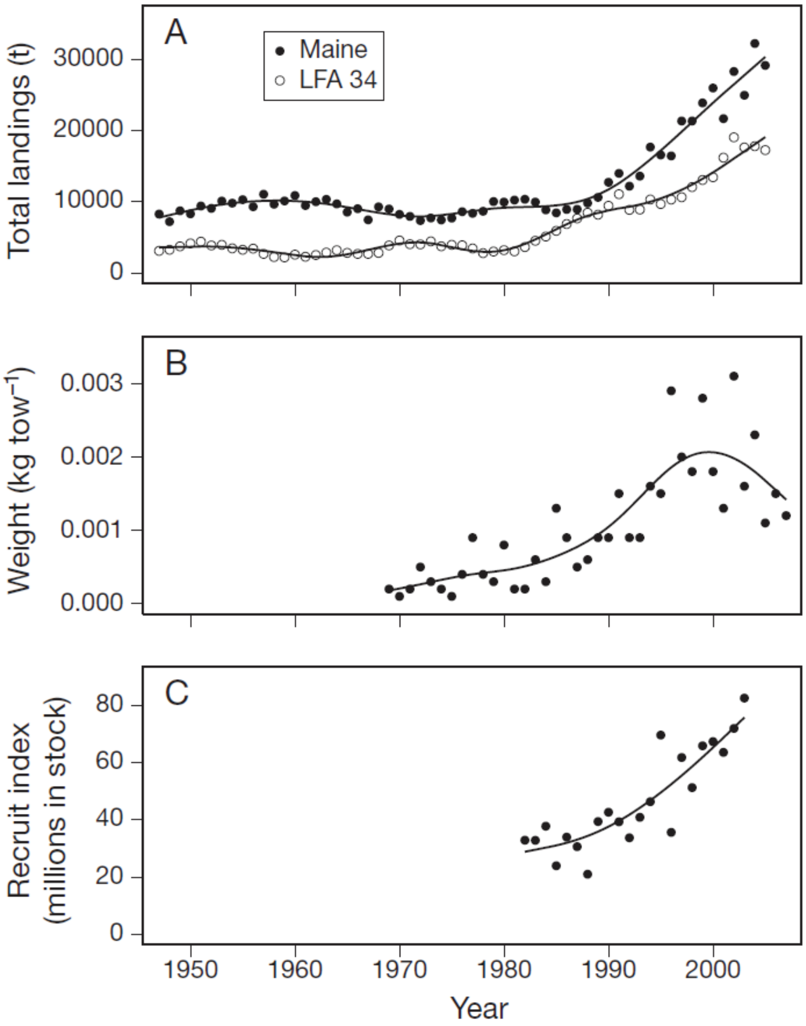

Figure 3.1. American lobster trends in the Gulf of Maine: (A) from 1947 to 2005, lobster landings (t) in Maine from Maine's Department of Marine Resources (solid circles) and lobster fishing area (LFA) 34 from the Canadian Department of Fisheries and Oceans (open circles), (B) from 1969 to 2007, lobster abundance indices (kg tow–1) from the National Marine Fisheries Service research surveys, and (C) from 1983 to 2003, lobster recruit abundance index (millions in stock) from the Atlantic States Marine Fisheries Commission. Trend lines on all panels were derived from a general additive model.

nearshore habitats, from a dominance of predatory groundfish (e.g. Atlantic cod, haddock [*Melanogrammus aeglefinus*], Atlantic halibut [*Hippoglossus hippoglossus*] and wolffish [*Anarhichas lupus*]), to herbivorous invertebrates (sea urchins), to predatory invertebrates (*Cancer* spp., lobster) (Steneck *et al.* 2004). Another study documented a trophic cascade from large groundfish to pelagic forage fish, plankton, marine mammals, and benthic invertebrates on the Scotian Shelf (Frank *et al.* 2005); it was thought to be a consequence of overfishing, possibly mediated by changes in temperature and stratification. An example of an invertebrate population being released from predation is provided by a meta-analysis of cod and shrimp (*Pandalus borealis*) biomass in the North Atlantic Ocean (Worm and Myers 2003). Cod and shrimp biomass, as estimated by research trawl surveys, were found to be inversely correlated, leading to large increases in shrimp abundance as cod stocks declined. Collectively, these results lead to interesting questions about ecosystem-based management and the number of predators that can be removed from a system before forcing it into another ecological state (Frank *et al.* 2007).

A second hypothesis for the observed increase in lobster landings is the advancement of effective fishing effort. The nominal fishing effort in LFA 34 has remained relatively constant over the last few decades; there has been an established fishing season since the 1900s, trap limits have remained between 375 and 400 per fisherman, and no new licences have been issued since 1968 (Pezzack *et al.* 2001). However, there have been changes to effective fishing effort in terms of improvements to fishing technology, vessels, and expansion of the area fished (FRCC 1995, 2007, DFO 2006a). Prior to the mid 1970s, lobster fishing in LFA 34 occurred in nearshore waters, less than 55 metres in depth, and then began to expand to the midshore, a trend which continued through the 1990s (Pezzack *et al.* 2001). These changes are not unique to LFA 34; in the Magdalen Islands of the northern Gulf of St. Lawrence, Canada, fishing capacity expansion coincided with an increase in lobster landings (Gendron and Archambault 1997, Gendron *et al.* 2000). In addition, fishermen interviews documented an increase in vessel size and width to facilitate the transport of more traps (Gendron and Archambault 1997). Advanced technologies for navigation and depth sounding were quickly adopted and spurred the discovery of new lobster grounds. The results from the study suggested that the increase in catch per unit effort in the Magdalen Islands resulted both from an increase in lobster biomass and improved fishing technology (Gendron *et al.* 2000).

Here we were interested in learning how interactions among predatory groundfish and lobsters may have played out in the inshore region of southwest Nova Scotia. Recent recruitment of lobsters in this region is strong (ASMFC 2006) implying that environmental conditions have been favourable for early lobster life stages. However, currently there are no long-term fisheries-independent estimates of lobster abundance in LFA 34 and lobsters have only recently been recorded in the Canadian Department of Fisheries and Oceans (DFO) research trawl surveys. The research surveys typically cover offshore regions, but most lobster habitat is located inshore at depths less than 55 m. In order to fill some of the knowledge gaps for this inshore ecosystem, we designed a local ecological knowledge (LEK) survey for fishermen of LFA 34. The goals of the survey were to record the LEK of fishermen of the coastal LFA 34 ecosystem, with respect to lobsters and groundfish, and compare available fisheries-independent data from the USA to the survey results. We were further interested in the possible effects of climate, disease, changes in prey abundance, and fishing effort on lobster abundance and catches, as recorded by these local experts.

3.3 Methods:

Local ecological knowledge is ‘the knowledge held by a group about their local ecosystem’ (Olsson and Folke 2001) and considers humans as part of the ecological system (Murray *et al.* 2006). Trends from LEK interviews can be quantified on an ordinal scale and may be used to complement scientific information for resource management (Neis *et al.* 1999b).

LFA 34 was selected for the interviews as it is commercially important to Atlantic Canada and has shown a striking increase in landings since the 1980s (Fig. 1A, DFO 2006a). Forty-two lobster fishermen, four of whom were retired, out of approximately 937 lobster fishing licence holders in LFA 34 (DFO 2006a) were interviewed from June to October 2007 during the LFA’s seasonal closure.

3.3.1. Survey Design and Questions

A consent form and semi-structured interview were designed and approved by Dalhousie University’s Social Sciences Research Ethics Board. Questions were formulated from ecological hypotheses linked to the fluctuations in the American lobster population in the NW Atlantic. Specifically, the survey addressed the observed increase of lobster abundance and landings in LFA 34. It was structured around six different variables: predation, conservation, climate, prey abundance, disease, and fishing effort.

Several recent studies (Neis *et al.* 1999ab, Hutchings and Ferguson 2000, Davis and Wagner 2003, Sáenz-Arroyo *et al.* 2005ab) were used as references for the design. Further advice on design and execution was sought from a number of experts in ecological knowledge surveys. The fishermen were contacted first by telephone and arrangements were made to be interviewed in person. The interview began with fishermen signing the consent form, then an explanation of the research, which lead in to the interview questions about the fisherman and their experiences. The survey ended with a free form question where the interviewee could discuss any topics not mentioned. There were two versions of the respondent's consent form, the first mentioned our interest in the loss of groundfish as a potential mechanism for the increased lobster landings and the second did not.

Three main questions of interest about the inshore ecosystem were:

(1) Why do you think there are so many more lobsters in the last 20 years in LFA 34 than there have been since the 1950s?

(2) In your experience, what fish have you cut open and found lobster in its stomach?

(3) Have you observed any other changes in fish or invertebrate species abundance since 1980 in the inshore region?

3.3.2. The Participants

The goal was to target a certain demographic of the licence holders, predominantly middle-aged fishermen with a relatively long history of fishing in the inshore region of LFA 34. To create an initial list of potential participants we consulted the LFA 34 fishermen's representative, community members, and DFO who identified local experts of the inshore ecosystem. However, the majority of participants were identified by their peers through recommendations at the end of the interviews (Davis and Wagner 2003). Such snowball sampling schemes (also called chain referral or reputational sampling, Neuman 2000) are useful in situations where the information desired is perceived as 'sensitive' and finding individuals willing to participate in the survey is a challenge (Lopes *et al.* 1996). This non-random sampling methodology is used in the social sciences (Neuman 2000) and has been used successfully in similar marine LEK studies (e.g. Neis *et al.* 1999ab, Hutchings and Ferguson 2000).

3.3.3. Data Analysis

The various responses to each question were tallied and percentages with 95% confidence intervals (CIs) were calculated. The prop.test command in R was used to create proportions, and CIs were calculated using a modified Wilson's method, correcting for the assumption of normality, with the Yates correction for continuity, which is appropriate for discrete data (Newcombe 1998, R Development Core Team 2008). This method also allows for asymmetrical CIs bounded between zero and one.

To test for possible age-related biases among the respondents' answers, a series of logistic regression analyses were performed with "years of fishing experience" as the explanatory variable. Answers that were not originally recorded binomially were grouped and converted. For example, if the fishermen reported first starting to fish the midshore in the 1980s or before (i.e. before the observed increase in landings), it was assigned zero, if it was in the 1990s and after it was assigned one.

Data from research trawl surveys were compared with average responses from our LEK survey where available. For predator diet data, we compiled occurrences of lobster from the stomach content databases of the Northeast Fishery Science Center (NEFSC) in Woods Hole, MA (Table 1) and the Maine and New Hampshire inshore research trawl survey (Maine Department of Marine Resources, DMR) were tallied and converted to proportions, with 95% CIs calculated as above. We selected five groundfish species with available abundance indices that were identified as predators of lobster from both the LEK survey results and stomach contents database; Atlantic cod, longhorn sculpin (*Myoxocephalus octodecimspinosus*), wolffish, cusk (*Brosme brosme*) and monkfish (*Lophius americanus*). The groundfish and lobster abundance indices (kg tow^{-1}) in the GOM from the National Marine Fisheries Service (NMFS) research trawl survey were log-transformed for normality and correlated using linear regression (Fig. 3). Conventionally, these data are analyzed with time lags to reflect the average time of recruitment for GOM lobster in to the fishery and the predation of groundfish on various life-stages of lobster. It takes lobsters in LFA 34 seven to eight years to grow to minimum legal size (DFO 1997). To address this, correlograms were constructed with lags from zero to ten years. Lobster landings for Maine were accessed from the DMR website (www.maine.gov/dmr/rm/lobster/lobdata.htm).

3.4 Results:

Interviewed fishermen were thoughtful in their replies, had an average of 35 years of fishing experience (Range: 16-51 years), were on average 55 years old (Range: 34-84 years), and 91% of their income came from the lobster fishing industry (Range: 30-

100%). The average fisherman interviewed possessed five different fishing licences or permits (Range: two to eight). The majority of the fishermen interviewed were from Yarmouth County (26), followed by Digby County (9) and Shelburne County (7). Fishermen from a total of 20 harbours were surveyed, with between 1 and 9 of the fishermen interviewed fishing from a particular harbour. Contact with fishermen was initiated in Yarmouth County and, as a result, it was more difficult to snowball-sample fishermen in the other two counties. The location of the interviewee did not necessarily reflect his home harbour.

When asked why lobster landings had increased over the last 20 years, 83% of respondents said that the loss of predators was the major reason, 33% also attributed increased landings to recent increases in fishing effort and the expansion to deeper waters, and 21% thought that conservation measures, such as gear restrictions and the protection of egg-bearing females, were helping to increase the population (Fig. 2A). Finally, 19% identified a different factor that may have influenced the increase, such as changes in climate or water temperatures. Seventy-four percent were concerned that the population may eventually decline due to increasing fishing effort, the targeting of large lobster and the depletion of brood stock. Fifty-two percent mentioned that they would be supportive of a maximum legal size limit to preserve the large individuals.

Of the 17 fishermen that received the first version mentioning our interest in the decline of groundfish abundance as a mechanism for the increase in lobster landings, 82% mentioned that the “loss of predators” was, in their view, a mechanism for increased lobster landings. Of the 25 individuals that received the second version, 84% gave the same reply. Fisher's exact test for count data revealed no significant difference ($p = 1$).

3.4.1. Predator Diet

To examine the potential mechanism of the hypothesized predator release effect, fishermen were asked which fish they had dressed in their careers and found a lobster in its stomach contents (Fig. 2B). Large-bodied predators, such as cod (95% reported finding a lobster in stomach contents), wolffish (74%) and cusk (38%), were listed, in addition to sculpin (most likely longhorn sculpin, 81%). To complement the fishermen's observations of lobster predators, two stomach content databases derived from trawl surveys were examined. The NEFSC stomach contents database (North Carolina to Nova Scotia, 1973-2005, Table 1) revealed that smooth dogfish (*Mustelus canis*), which is rarely observed in the GOM (Branstetter 2002), and cod had the highest proportions of lobster found in their stomachs. Longhorn sculpin, haddock and various hakes (*Urophycis* spp., *Merluccius bilinearis*) also preyed upon lobster. A much smaller inshore research trawl survey, conducted by the Maine DMR (2005-07, not shown), found one lobster in a cod ($N = 668$ stomachs examined) and another in a monkfish ($N = 289$).

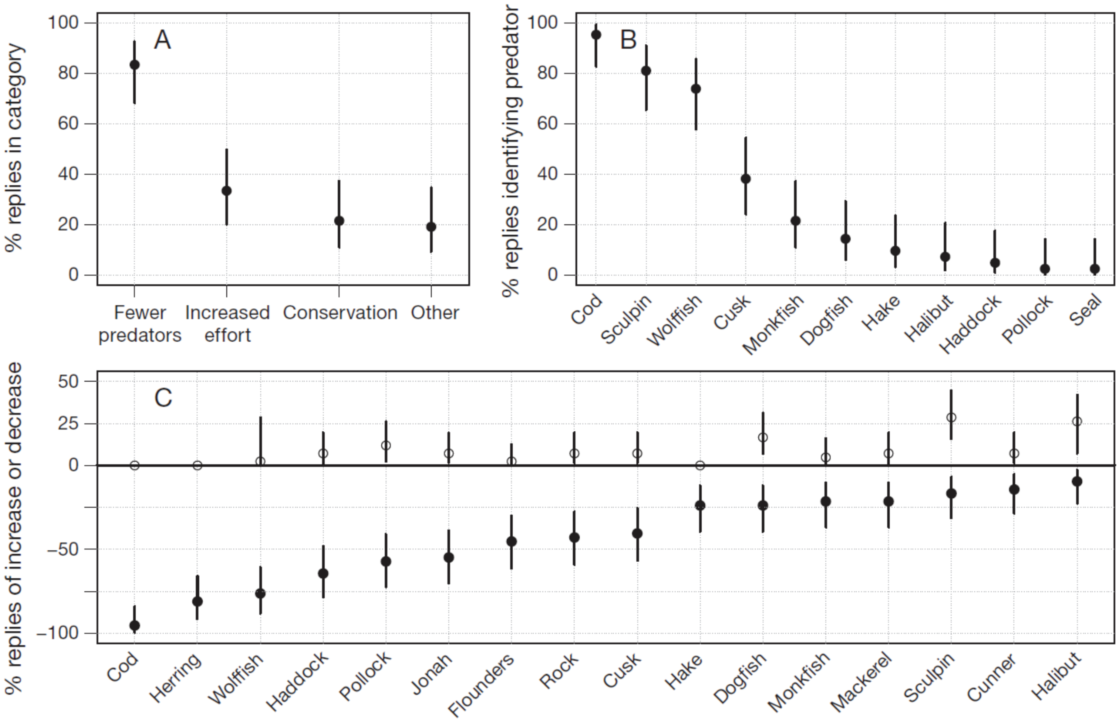

Figure 3.2. Average responses, with 95% CI, to the 3 main survey questions (see Section 3.3.1. of Methods): (A) reasons given by the fishermen for the increase in lobster landings since 1980, (B) the percentage of fishermen who identified particular predators of lobsters based on their own sampling of stomach contents: Atlantic cod *Gadus morhua*, sculpin (Cottoidea), wolffish *Anarhichas lupus*, cusk *Brosme brosme*, monkfish *Lophius americanus*, spiny dogfish *Squalus acanthias*, hake *Urophysis* spp. and *Merluccius bilinearis*, Atlantic halibut *Hippoglossus hippoglossus*, haddock *Melanogrammus aeglefinus*, pollock *Pollachius virens* and grey seal *Halichoerus grypus* and (C) the percentage of fishermen who reported that a species has decreased (solid circles) or increased (open circles) in the inshore ecosystem throughout their careers; species not mentioned above: Atlantic herring *Clupea harengus*, Jonah crab *Cancer borealis*, flounders (Pleuronectidae), rock crab *Cancer irroratus*, Atlantic mackerel *Scomber scombrus* and cunner *Tautogolabrus adspersus.*

Table 3.1: **Species found with lobster in their stomachs** from the NEFSC stomach contents database (1973-2005), ordered by percentage with 95% CIs.

Predator	Species name	Lobsters	Stomachs	%	95% CI
Smooth Dogfish	*Mustelus canis*	25	7145	0.35	0.23 - 0.52
Atlantic Cod	*Gadus morhua*	58	18818	0.31	0.23 - 0.40
Atlantic Halibut	*Hippoglossus hippoglossus*	1	365	0.27	0.01 - 1.52
Thorny Skate	*Raja radiate*	5	3279	0.15	0.05 - 0.36
Smooth Skate	*Raja senta*	1	869	0.12	0.00 - 0.64
Longhorn Sculpin	*Myoxocephalus octodecimspinosus*	9	11116	0.08	0.04 - 0.15
Haddock	*Melanogrammus aeglefinus*	6	8132	0.07	0.03 - 0.16
Spiny Dogfish	*Squalus acanthias*	43	63837	0.07	0.05 - 0.09
Little Skate	*Raja erinacea*	16	25818	0.06	0.04 - 0.10
Sea Raven	*Hemitripterus americanus*	4	6693	0.06	0.02 - 0.15
Red Hake	*Urophycis chuss*	8	16802	0.05	0.02 - 0.09
White Hake	*Urophycis tenuis*	5	13883	0.04	0.01 - 0.08
Monkfish	*Lophius americanus*	3	9573	0.03	0.01 - 0.09
Winter Skate	*Raja ocellata*	4	16358	0.02	0.01 - 0.06
Winter Flounder	*Pseudopleuronectes americanus*	1	7966	0.01	0.00 - 0.07
Spotted Hake	*Urophycis regia*	1	12084	0.01	0.00 - 0.05
Silver Hake	*Merluccius bilinearis*	1	45646	0.00	0.00 - 0.01

3.4.2. Predator Abundance

The fishermen were asked to reflect on any population, besides lobster, that had undergone an increase or decrease in the inshore fishing grounds during their careers. Consistently, large-bodied fish, such as cod (95%), wolffish (76%), and haddock (64%) were reported to have declined (Fig. 2C). There was no consensus, however, as to when precisely the cod populations had started to decline in the nearshore areas: 2% thought that the decline began in the 1970s or before, 19% found this had happened in the early 1980s, and 29% answered late 1980s. Similarly, in the 1990s, 19% observed cod abundance declining nearshore early in the decade, and 17% late. Only sculpins and Atlantic halibut were identified more commonly as increasing, rather than decreasing (Fig. 2C).

3.4.3. Trawl Survey Estimates

Regression analyses between the NMFS trawl surveys for combined groundfish predators ($R^2 = 0.3615$, $p < 0.0001$, Fig. 3A), cod ($R^2 = 0.3616$, $p < 0.0001$, Fig. 3C) and groundfish without cod ($R^2 = 0.1996$, $p = 0.0026$, Fig. 3E) with lobster abundance indices all revealed negative and significant correlations. These negative correlations were largely driven by cod, with lobster increasing as cod abundance indices decreased in the trawl surveys. This negative correlation is also evident at time lags of six to ten years, and usually strongest at around zero to four years (Fig 3).

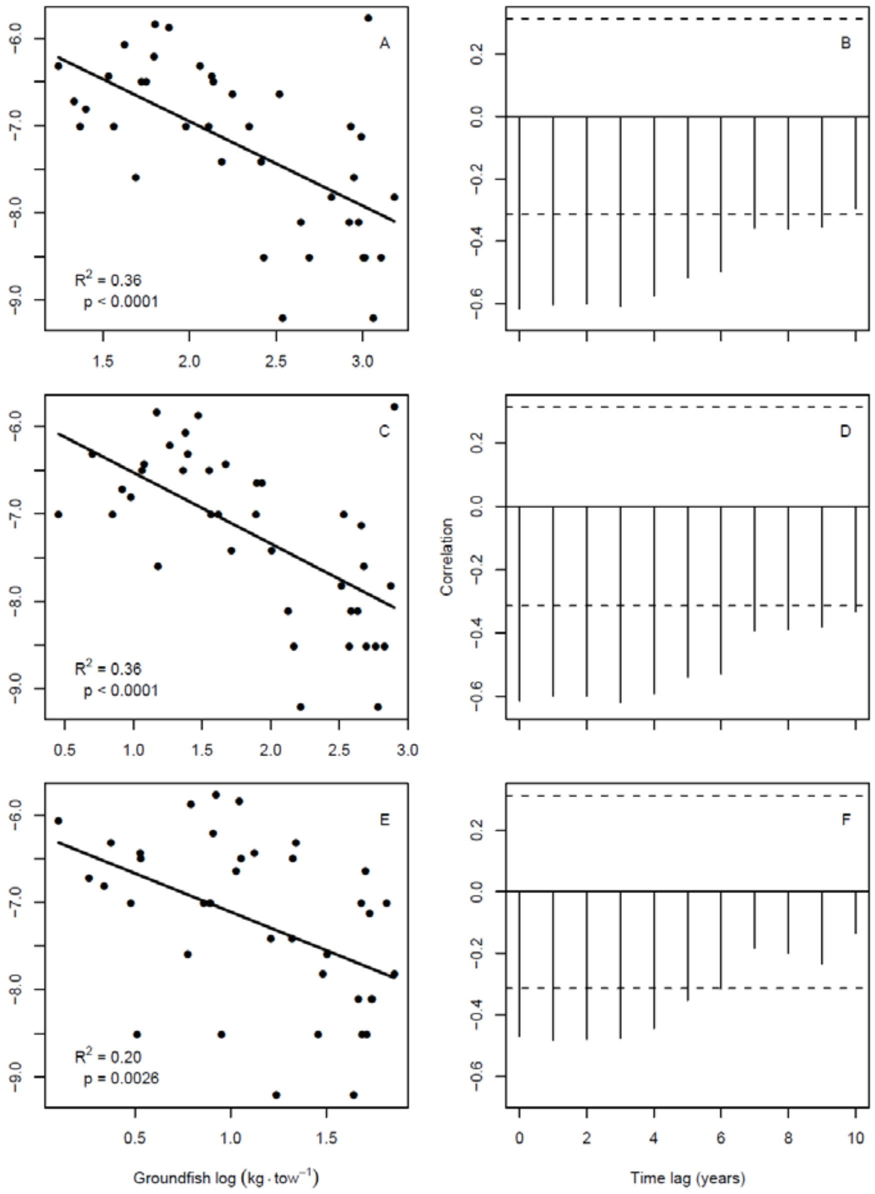

Figure 3.3. Negative correlations between research trawl survey estimates of Gulf of Maine groundfish and lobster. National Marine Fisheries Service abundance indices (kg tow^{-1}) were log-transformed, and correlations were tested at time lags from 0 to 10 yr. (A,B) Lobster abundance versus combined survey estimates of Atlantic cod, cusk, longhorn sculpin, monkfish and wolffish, (C,D) Atlantic cod and lobster, and (E,F) 4 groundfish predators of lobster, as above, but without cod. Dashed lines indicate 95% confidence intervals. Trendline and test statistics are from a linear regression on log-transformed data.

When predators other than cod were examined individually with lobster, longhorn sculpin correlated positively ($R^2 = 0.4742$, $p < 0.0001$), monkfish ($R^2 = 0.1929$, $p = 0.0030$) and cusk ($R^2 = 0.2731$, $p = 0.0004$) negatively, and wolffish trended negatively but without statistical significance ($R^2 = 0.0251$, $p = 0.1708$).

3.4.4. Changes in Fishing Effort

The increase in landings in LFA 34 could in part be due to changes in fishing effort, such as expansion into deeper waters (FRCC 1995, Pezzack *et al.* 2001, DFO 2006a). The region referred to as the 'inshore' is composed of the nearshore and midshore areas. The traditional 'nearshore' grounds are less than 55 m deep, with the expansion in fishing effort, documented since the 1980s, taking place in the deeper waters of the 'midshore'. The midshore ends at the boundary with LFA 41, which is considered the 'offshore' (DFO 2006a). Accordingly, 79% of interviewed fishermen have recently been fishing in deeper waters, with 60% of them starting to fish in these areas in the early 1980-2000s. However, 60% still spend some time fishing nearshore and 19% spend their entire season there. There have been several reasons for this redistribution in fishing effort: 43% report more lobster in deeper water, 29% prefer to avoid competition in nearshore waters, and 24% are following the lobsters as they migrate seasonally from shallow to deeper water. Seventy-six percent were concerned that the increase in effective fishing effort would eventually cause the lobster population to decline and 33% mentioned illegal fishing practices. The fishermen identified several ways to reduce fishing effort, such as lower trap limits, restricting fishing to daylight hours, closing the fishery for part of the season or one day of the week. Traditionally lobster were found mostly on highly structured hard substrates, such as boulder fields, but over the past ten years 71% of interviewed fishermen have been recording lobster expanding to other bottom types, such as soft sediments or mud (60%).

There was no evidence for respondents' answers being biased in some way by their age and experience. The only statistically significant result was that their years of fishing experience correlated with when they started fishing midshore ($p = 0.0194$). This result is intuitive as the more years of experience a fisherman had at the time of the interview, the earlier they could have started fishing midshore.

3.4.5. Other Factors

Temperature plays a major role throughout the lobster's life cycle (Aiken and Waddy 1986). Fifty-five percent of the fishermen surveyed replied that the water temperature stays colder for longer into the spring and 76% said that it is warmer into the fall. Nineteen percent felt that wind direction and strength had no effect on lobster landings, while 79% said that catch decreases with high winds.

In 1999, a parasitic paramoeba caused a massive lobster mortality event in Long Island Sound, USA (Mullen *et al.* 2004). The effects of this disease were likely exacerbated by hypoxia and higher water temperatures (ASMFC 2006). Lobsters in the northeastern USA have also shown an increase in the incidence of shell disease in recent years, which largely causes deformations in lobsters being held for market but is occasionally fatal (ASMFC 2006). Forty percent of interviewed fishermen voiced a general concern about disease affecting the lobster population, however 95% had never or very rarely seen evidence of a diseased animal in their catch.

As for changes in prey abundance, two species of *Cancer* crab are known prey of juvenile and adult lobster (Elner and Campbell 1987, Lawton and Lavalli 1995). Fifty percent of the fishermen surveyed were concerned that lobsters in LFA 34 were becoming food limited due to their high population density, and to commercial catches of Jonah crab (*Cancer borealis*) by those with permits and for use as bait (DFO 2000). *Cancer* spp. were two of the top five species mentioned as being captured most commonly with lobster; cod (98%), sculpin (88%), Jonah crab (86%), rock crab (*Cancer irroratus,* 83%) and cusk (64%).

It has been suggested that the large input of lobster bait (mostly herring, *Clupea harengus*) into the GOM has been subsidizing high lobster abundances (Saila *et al.* 2002). This argument is based on the fact that many lobsters exit the trap after feeding on bait (Karnofsky and Price 1989, Jury *et al.* 2001). The average herring bait to lobster ratio in adjacent LFA 33 has been estimated to be as high as 1:1.9 (Harnish and Willison 2009). While 40% of the fishermen in this study felt that they were to some extent feeding lobsters with bait during the fishing season, for the majority of those interviewed it was not considered as a principal reason for the increase of lobsters in LFA 34.

3.5 Discussion:

This local ecological knowledge survey provided evidence in support of the hypothesis that inshore lobster populations in the GOM have been released from predation, which may in part explain their high recruitment, abundance, and landings. Despite high exploitation rates, whereas most of the new recruits are being caught every year, landings continue to be high. According to the fishermen interviewed, this may be explained partially by the extraordinary peak in lobster abundance and recruitment (Fig. 1) and partially by increased effort, conservation measures, and possibly other factors (Fig. 2A). Fishermen's observations of predator diet and changes in abundance (Fig. 2B, C) as well as the observed decline in cod abundance and increase in lobster abundance, are all consistent with the hypothesized-top down mechanism (Fig. 3, Table 1).

These results are adding further support to the notion that the collapse of demersal predator populations, such as northwest Atlantic cod, has released a suite of species from predation, and contributed to a reorganization of the NW Atlantic inshore and shelf ecosystems (Worm and Myers 2003, Steneck *et al.* 2004, Frank *et al.* 2005). More broadly, there is increasing evidence that top-down interactions and cascading ecosystem effects of fishing may be quite important both in nearshore and oceanic food webs (Heithaus *et al.* 2008, Baum and Worm 2009). These interactions are typically mediated both by changes in prey density and behaviour (Heithaus *et al.* 2008). In this case, there is some evidence for both mechanisms leading to increased abundance of lobster, and the reported expansion towards previously risk-prone habitats. The observation that lobsters are venturing from structured hard substrates onto soft sediments has been independently confirmed by scientific studies which report that catch rates of lobster in trap surveys were higher on soft sediments than hard substrates; however, lobster densities from diver surveys were higher on hard than soft bottom types (Tremblay and Smith 2001, Geraldi *et al.* 2009). Lobsters originally caught and released on soft substrate travelled significantly farther than those caught on hard substrate indicating that the animals move faster over sediment in order to find more suitable habitat (Geraldi *et al.* 2009).

According to this survey, factors other than predation and fishing may play a limited role in regulating lobster populations in the GOM. Only 19% of fishermen observed that climate, disease, or changes in prey abundance were influential. Water temperature is often hypothesized to play a major role in the increased lobster landings in Maine and Nova Scotia. In Maine (1946-86), 54% of the variance in lobster landings could be explained by the sea surface temperature (SST) at the time of larval settlement (Steneck and Wilson 2001). In Nova Scotia (1929-70), 68% of the variance in landings was explained by the SST in St. Andrews, New Brunswick in addition to the previous year's catch (Flowers and Saila 1972). Drinkwater and colleagues (1996) on the other hand, were not able to link SST with the increase in lobster landings throughout the American lobster's range in the 1980s and early 1990s, although they acknowledged a potential role of SST in the past. From the present LEK survey it is evident that the fishermen pay close attention to changes in water temperature, which affects lobster movement, moulting and spawning, and they are keenly aware of environmental cycles. However, water temperature did not emerge in the replies as a main driver of the increase of lobster.

Likewise, bait inputs were not considered as a major mechanism to boost lobster populations in LFA 34, though 40% agreed that lobsters were likely eating bait during the fishing season from late November to the end of May. Bait inputs may be more substantial on the USA side of the GOM, where trap density is higher and the fishery operates year-round (Myers *et al.* 2007, Grabowski *et al.* 2009). Despite the higher bait input, however, the relative increase in lobster landings has been less pronounced in the USA compared with Canadian waters (Myers *et al.* 2007) and in the eastern portions of the GOM, bait is not believed to subsidize lobster populations (Grabowski *et al.* 2009).

Ecological knowledge surveys may best be used in combination with other data sources, such that fishermen's observations could be verified independently. One contrasting example comes from the southern Gulf of Saint Lawrence (sGSL; Davis *et al.* 2004) where fishermen were concerned that research survey protocols were insufficient to document the predation of white hake on juvenile lobster. Fishermen did provide accurate details of hake distribution, yet stomach sampling revealed that contrary to the belief of fishermen, white hake did not ingest lobster (N = 3080). In our study, the fishermen revealed detailed insights into potential predators of lobsters and other aspects of the coastal ecosystem, such as shifts in species composition, water temperatures, habitat expansion, and the incidence of disease. By comparing their replies with the trawl survey-derived stomach content and abundance data, it seems evident that LEK in LFA 34 reflects some of the ecosystem changes in the GOM. Interviewees consistently reported that large fish had declined in abundance and that those same large fish were predators of lobster. Atlantic cod stood out as the species that was most consistently reported as having declined, and as a predator of lobster. While the proportion of lobsters found in fish stomachs is small overall (Table 1), the predation of a large cod stock upon lobsters could still have had a significant effect, particularly when considering the historical biomass of cod in the GOM and Scotian Shelf area (Steneck 1997, Rosenberg *et al.* 2005).

In a study of the sGSL, Atlantic cod reportedly ingested lobster at a much lower rate than those in this study, with lobster being found in 0.05% of cod stomachs during 1990-96. Most size classes of cod, however, overlapped spatially with lobster in the sGSL only during June and October. There were no significant relationships between cod and lobster abundance indices (1950-96) for time lags of zero to seven years indicating that cod did not control lobster abundance in the sGSL. However, the study identified shorthorn sculpin *(Myoxocephalus scorpius)*, cunner (*Tautogolabrus adspersus*) and white hake (*Urophycis tenuis*) as potential predators of lobster (Hanson and Lanteigne 2000). A second study in the northeastern USA collected more than 15000 cod stomachs from the NEFSC seasonal bottom trawl survey between Cape Hatteras, North Carolina and southwest Nova Scotia from 1973-98. Commercially valuable decapods were determined to be an important component of Atlantic cod's diet; however, American lobster was not identified as a major prey item. The study concluded that cod were opportunistic generalists and that it was not likely that cod exerted predatory control on all of its prey populations in the USA northwestern Atlantic (Link and Garrison 2002).

One of the key challenges of LEK surveys is determining whether or not the respondent is giving a reply that they think the interviewer wants to hear, potentially by being lead by the interviewer. To address this, there were two versions of the respondent's consent form, the first mentioned the loss of groundfish as a potential mechanism for the increased lobster landings and the second did not. No differences were found between responses to the two versions, indicating respondents were not lead by the consent form. Another potential challenge in this study was our relatively small sample size; roughly 4.5% of the license owners were interviewed, coming close to our goal of 5%. As a comparison, Hutchings and Ferguson (2000) interviewed 47 fishermen of a similar demographic in two sectors of Newfoundland's fixed-gear cod fishery. Their sample represented 1% of 4677 fishermen, yet they were able to establish patterns in the harvesting of cod from 1980-91 that were consistent with the hypothesis that Newfoundland's inshore cod stock decline was gradual. We targeted fishermen with decades of experience who were viewed as local experts by their peers. The considerable agreement between respondents for most answers indicated that a higher sample size would not likely have changed the results.

It is possible for a respondent to reply in such a way that serves personal motives, particularly if the interviewee has a high stake in the outcome (Gendron *et al.* 2000). We note, however, that this survey did not question fishermen about the abundance of lobsters (which was assumed to be high), or their personal catches and that the ecological hypotheses we explored would not necessarily influence lobster management. In an effort to minimize any further potential for personal biases we targeted experienced fishermen, some of whom would be near retirement. These fishermen were often very candid and forthcoming, and there was little sense of hesitation, bias, or staged answers.

In conclusion, we suggest that LEK surveys are a useful method to learn more about how fisheries may affect ecosystems, especially when they can complement independently collected scientific data. Canadian fisheries are now largely dependent on lower trophic levels (Pauly *et al.* 2001), with a heavy emphasis on benthic invertebrates. Unfortunately, the knowledge base for many of these fisheries is slim, and fisheries-independent data or proper assessments are often not available (Anderson *et al.* 2008). It seems prudent in this case to use all of the available information, including fishermen's expert knowledge as one possible line of evidence, to evaluate both ecological interactions, and to inform the management process.

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Chapter 4

Linking American Lobster Abundance and Landings with Predators, Temperature, and Climate in the Northwest Atlantic Ocean

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4.1 Abstract:

Over the past three decades, the abundance of American lobster (*Homarus americanus*) in the northwest (NW) Atlantic Ocean has undergone large changes, the driving mechanisms of which have not yet been examined across the species' range. Here we analysed all available time-series data of lobster abundance and landings, together with data on the abundance of their teleost and elasmobranch predators, as well as changes in temperature and climate (North Atlantic Oscillation Index, NAOI) through mixed-effects models across nine regions in the Northwest Atlantic. This analysis covered the entire range of the species, and addressed competing hypotheses about the bottom-up (climate, temperature) versus top-down (predation, fishing) regulation of lobster populations. Results offered partial support for the predation hypothesis, namely Newfoundland, Nova Scotia, Massachusetts, and southern New England showed evidence of a negative effect at lags 0 to 4, suggestive of effects on sub-adult lobster. However, this effect was not seen in the other regions. Independently of region-specific predation effects, there was broad support for a climate effect on lobster recruitment and early development across all regions. This was consistent with a large-scale influence of NAOI on lobster early life stages, as the strongest effect was found at lag 6-7 years. The mechanism of this effect remained unclear, as changes in temperature did not emerge as a

major predictor of lobster abundance and landings. Likewise, fishing effort appeared to be following lobster abundance, rather than regulating abundance in a consistent way. This analysis provides evidence that predation and climate both play some role in regulating lobster abundance in the NW Atlantic, but that they act on different life stages in the population.

4.2 Introduction:

Crustaceans are caught in major commercial fisheries worldwide and are presently the only major invertebrate group which continues to rise in global catches (Anderson *et al.* 2011). It is currently unclear how much of this is forced by increasing fishing effort, or by shifts in community and ecosystem structure, respectively. For example, in the northwest (NW) Atlantic Ocean ecosystem there has been a well-documented ecosystem shift from large bodied groundfish to invertebrates, including both small and large crustaceans (Worm and Myers 2003, Frank *et al.* 2005). Several lines of evidence suggests that the decline of predatory groundfish in the NW Atlantic has released large decapods, namely American lobster (*Homarus americanus*) and snow crab (*Chionoectes opilio*) from predation, at least in some areas (Boudreau and Worm 2010, Boudreau *et al.* 2011). An increase in lobster commercial landings and abundance is evident along the species' range, however the timing of this trend varies. Furthermore, while American lobster populations have steadily increased since the 1980s, and continue to generate large catches, these abundance trends have since reversed in the more southern regions where the species occurs (ASMFC 2009). With the exception of an epizootic disease event in the late 1990s (Mullen *et al.* 2004), which dramatically impacted the southern New England stock, it is presently unclear which factors are driving the waxing and waning of each population.

Often Atlantic cod (*Gadus morhua*) is hypothesized to be a major predator on lobster, however it is likely that other groundfish species (such as dogfish, sculpin, and wolffish, see Boudreau and Worm 2010) could also play a role. While the decline of cod likely represents the largest and most influential single-species change from the Gulf of Maine northwards, cod are rarer or absent in ecosystems further south. In this study we focus on lobster populations along the species' range in the NW Atlantic ecosystem, ranging from Newfoundland (North) to Connecticut (South), exploring linkages between American lobster, groundfish, temperature and climate variability (proxied by the North Atlantic Oscillation Index, NAOI), where data is available. Our goal was to examine four competing hypotheses to explain variation in lobster abundance: Top-down effects as, (1) predation by groundfish, resulting in negative relationships between lobster and various groundfish species abundances, or (2) fishing control whereas increasing effort reduces lobster abundance. Alternatively these species may be regulated primarily by bottom-up forces such as (3) temperature or (4) climate, resulting in positive or negative relationships with regional bottom temperatures or NAOI. We tested these hypotheses in isolation as well as in combination, allowing for possible interactions between bottom-up (climate, temperature) and top-down (predation, fishing) forces on lobster abundance.

Where possible, we utilized fishery-independent scientific survey data to answer these questions. In contrast to various regions in the United States, however, there are presently no long-term fisheries-independent lobster abundance indices available in Atlantic Canada. Hence, we tested the additional hypothesis that lobster landings can be

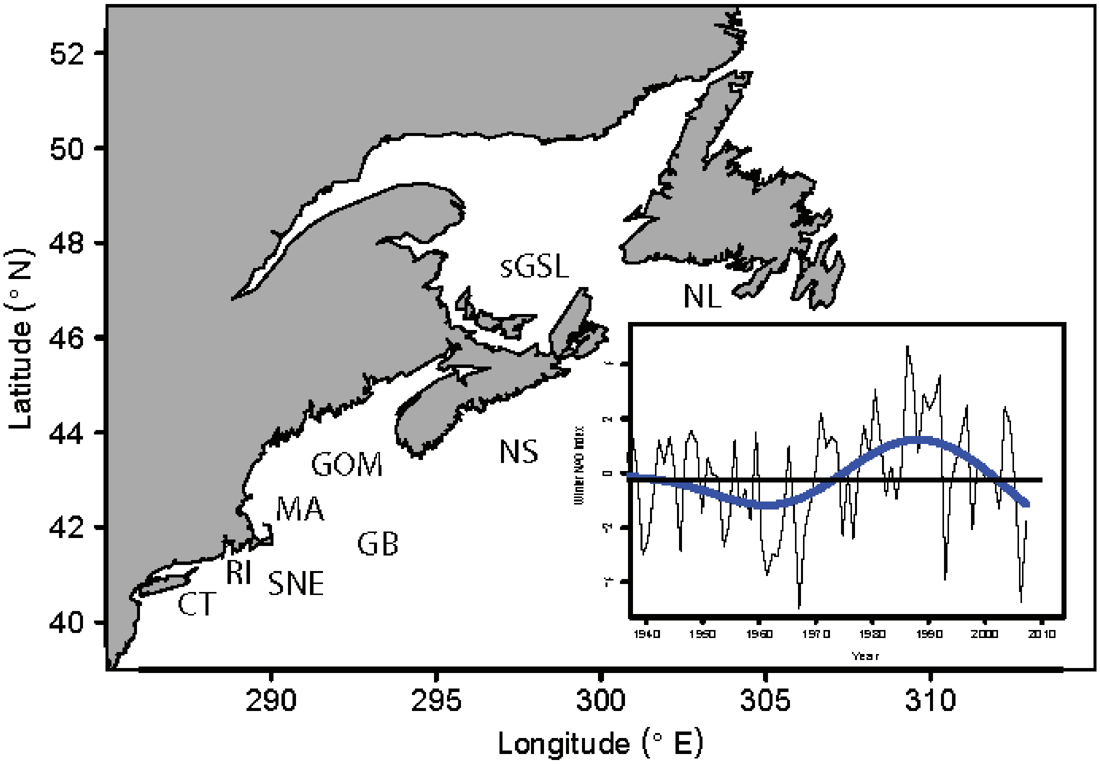

Figure 4.1. Study regions. SGSL; southern Gulf of St. Lawrence, NL; Newfoundland, NS; Nova Scotia/Bay of Fundy, GOM; Gulf of Maine, GB; Georges Bank, SNE; southern New England, MA; Massachusetts, RI; Rhode Island, and CT; Connecticut. Insert (lower right hand corner) is Climate data. Shown is the winter (December-March) index of the NAO based on the difference of normalized sea level pressure between Lisbon, Portugal and Stykkisholmur/Reykjavik, Iceland. Trend line is derived from a generalized additive model.

4.3 Methods:

4.3.1 Data

To explore statistical relationships between lobster, groundfish predators, temperature, climate and fishing we compiled available lobster abundance indices and paired them with appropriate predator, temperature, NAOI and fishing effort time-series. Data were compiled for all major lobster fishing regions in the NW Atlantic, including both the United States Eastern seaboard and Eastern Canada (Fig. 1, Table 1). The Canadian regions included Nova Scotia (NS), specifically the Scotian Shelf and Bay of Fundy (lobster fishing areas [LFA] 27-36, 38, 39), south east Newfoundland (NL) (LFAs 10 and 11), and the southern Gulf of St. Lawrence (SGSL) (LFAs 23-26A and 26B). The US Eastern seaboard included three larger regions for which trawl surveys and assessments are conducted, namely the Gulf of Maine (GOM), Georges Bank (GB), and Southern New England (SNE) (Fig. 1). The SNE lobster time series was paired with groundfish trawl survey estimates from the mid-Atlantic Bight, hence the spatial overlap may be less complete than in the other regions. In addition, several states have conducted long-term nearshore trawl surveys; included in this study are time series from Massachusetts (MA), Rhode Island (RI) and Connecticut (CT). In Canada, fisheries-independent lobster abundance indices are only available from 1999 to 2010, hence long-term trends in lobster abundance have to be inferred from commercial landings (tonnes). Prior to using landings data for inference, we tested the hypothesis that variation in landings is positively related to variation in abundance. We regressed lobster landings against existing abundance and biomass indices from trawl surveys in a linear model to test the hypothesis that abundance can be predicted from landings data.   We included available fishery-independent data (1999-2010) from NS, as well as longer-term data from NMFS research survey abundance for SNE, GOM, and GB. For state-run surveys in MA, RI, and CT the standardized survey abundance index was similarly correlated with landings recorded by these states. All survey indices were log-transformed.

For the main analysis, we spatially and temporally matched measures of lobster abundance (USA) and landings (Canada) with estimates of predator abundance from research surveys conducted by the National Marine Fisheries Service (NMFS) and the Canadian Department of Fisheries and Oceans (DFO). Specifically in US regions, we matched lobster abundance with predator research survey abundance (#/tow). For Canadian regions we matched lobster landings with predator research survey biomass (kg/tow). In the USA, long-term fisheries-independent abundance indices are available for lobster populations. In MA, RI, and CT, a survey-based index of abundance is available from the Atlantic States Marine Fisheries Commission (ASMFC, mean catch per tow summed for 53-228 mm carapace length). For the Gulf of Maine, Southern New England and Georges Bank, a proper fisheries assessment is conducted, which provides an estimate of total abundance (million individuals). Here we used output from the University of Maine model, which integrates trawl survey and landings data to estimate numbers of lobster in a range of size groups by sex and season (Chen *et al.* 2005, ASMFC 2009).

Predator data from trawl surveys had to be compiled differently in different regions, as species composition of lobster predators varied along the species' range. The predator species included in the present analysis were selected from existing stomach content databases (i.e. the top 10 lobster predator species in Boudreau and Worm 2010, Hanson and Lanteigne 2000, Comeau *et al*. 2008), with some additional species selected because they were identified as predators on lobster by regional scientists or fishermen (Table 2). The abundance indices of the selected predatory species were summed for each region to produce a synthetic abundance index. The suite of predators of lobster included teleost groundfish, small demersal sharks, and skates. Individual species correlations with lobster abundance were also explored at time lags 0 to 10 in order to investigate how different species may contribute to the main predator effect in the analyses.

Bottom temperature data were either extracted from the DFO hydrographic climate database (Gregory 2004) or directly from the trawl surveys (RI, CT). For those series queried from the database, the depth ranges for the GOM, SNE, NS, SGSL, were 0-50m. Since MA is divided into GOM and SNE stock groups the temperature series for this state was calculated as an average of the GOM and SNE time series. We used 0-40m for NL and 100-300m for GB - depth ranges which reflect the distribution of lobsters in these regions from the fisheries assessments. Broad-scale climate conditions were assumed to relate to the North Atlantic Oscillation Winter Index (NAOI, December-March), which represents the difference of normalized sea level pressure between Portugal and Iceland (Hurrell 1995). The index from 1950-2011 was accessed from the National Center for Atmospheric Research' Climate Analysis Section website (http://www.cgd.ucar.edu/cas/jhurrell/nao.stat.winter.html), see Hurrell (1995) for further details.

Table 4.1: **Data sources for lobster and groundfish predators abundance analyses**. Lobster indices are from stock assessment or landings. Predator indices from research trawl survey estimates of abundance.

	Lobster			Predators			Temperature (^{o}C)	
Region	Source	Range	Index	Source	Range	Index	Source	Range
SNE	ASMFC 2009	1982-2007	UMaine Model Abundance Index	NMFS	1965-2007	Abundance	DFO	1950-2009
GOM	ASMFC 2009	1982-2007	UMaine Model Abundance Index	NMFS	1963-2007	Abundance	DFO	1950-2009
GB	ASMFC 2009	1982-2007	UMaine Model Abundance Index	NMFS	1963-2007	Abundance	DFO	1950-2010
RI	ASMFC 2009	1982-2007	Abundance Index	RIDEM	1979-2007	Abundance	RIDEM	1979-2006
MA	ASMFC 2009	1981-2007	Abundance Index	MADMF	1978-2006	Abundance	DFO	1950-2010
CT	ASMFC 2009	1985-2007	Abundance Index	CTDEP 2010	1984-2009	Abundance	CTDEP	1991-2009
SGSL	DFO	1984-2009	Landings	DFO	1971-2007	Biomass	DFO	1950-2009
NS	DFO	1950-2007	Landings	DFO	1970-2006	Biomass	DFO	1950-2009
NL	DFO	1976-2011	Landings	DFO	1951-1995	Biomass	DFO	1950-2009

Table 4.2: **Included groundfish predators of lobster** for each study region.

Predator	Species name	GOM	SNE	GB	RI	MA	CT	NL	SGSL	NS
Atlantic cod	*Gadus morhua*	X	X	X	X	X		X	X	X
Cunner	*Tautogolabrus adspersus*				X	X	X		X	X
Cusk	*Brosme brosme*									X
Haddock	*Melanogrammus aeglefinus*	X	X	X		X		X	X	X
Atlantic halibut	*Hippoglossus hippoglossus*			X				X	X	X
Little skate	*Leucoraja erinacea*	X	X	X			X			X
Longhorn sculpin	*Myoxocephalus octodecemspinosus*	X	X	X	X	X	X	X	X	X
Monkfish	*Lophius americanus*	X	X	X	X	X		X		X
Sea raven	*Hemitripterus americanus*	X	X	X			X	X	X	X
Shorthorn sculpin	*Myoxocephalus scorpius*								X	
Smooth dogfish	*Mustelus canis*		X	X	X	X	X			
Smooth skate	*Malacoraja senta*	X		X				X	X	X
Spiny dogfish	*Squalus acanthias*	X	X	X	X	X	X	X	X	X
Striped bass	*Morone saxatilis*						X			
Tautog	*Tautoga onitis*				X	X	X			
Thorny skate	*Amblyraja radiata*	X		X				X	X	X
White hake	*Urophycis tenuis*								X	
Wolffish	*Anarhichas lupus*	X				X		X	X	X

In order to analyse the effects of fishing, the number of reported traps (ASMFC 2009) were used as a proxy for fishing effort in the USA. In Canada, the total number of traps allowed was used for the Southern Gulf of St. Lawrence, Nova Scotia, and Newfoundland. The Canadian data represent an upper limit of actual fishing effort, as not all allowable traps may be fished each season.

4.3.2 Statistical Analyses

We used a multimodel averaging framework (Burnham and Anderson 2002, Mazerolle 2011) to simultaneously consider the strength of evidence for multiple hypothesized drivers of lobster abundance. We log-transformed the lobster, predator, effort, and temperature data to improve the normality of the residuals in our model fits. Further, to make the magnitude of the model coefficients approximately comparable, we standardized all data within each region by subtracting the mean and dividing by 2 standard deviations (Gelman 2008). We lagged the lobster time series by 0-11 years to reflect probable effects of temperature or predation on early life stages of lobster that would be detected later in the catch or trawl survey time series. Changes in fishing effort (measured as the number of lobster traps) should have an immediate impact on lobster abundance and so were included without a time lag.

We built predictive models of lobster abundance using linear mixed-effects models (fitted with the lme4 package; R and lme4, Bates *et al*. 2011) and estimating random-effects slopes for ‘predators’, ‘temperature’, and ‘climate’ by region and a fixed effect for ‘fishing effort’. Candidate mixed-effect models were fitted using maximum likelihood and the resulting coefficients averaged according to their Akaike weights based on AICc (small-sample-size-corrected Akaike Information Criterion; Sugiura 1978, Burnham and Anderson 2002). The resulting mixed-effects model (after Zuur 2009) can be expressed as:

$$\mathbf{Y}_i = \mathbf{X}_i \times \beta + \mathbf{Z}_i \times \mathbf{b}_i + \varepsilon_i$$

where $\mathbf{Y}_i$ represent the estimated lobster abundance index for each region, $\mathbf{X}_i \times \beta$ represent the fixed effects, and $\mathbf{Z}_i \times \mathbf{b}_i$ the random effects where $\mathbf{b}_i$ are the normally distributed residuals with a mean of 0 and a given variance; ε_i represents the normally-distributed error term. To assess model fit we plotted predicted lobster abundance versus observed, and test statistics were generated for the top candidate models for each set of analyses.

Our mixed-effect analysis assumes that there exists an underlying distribution of the effects of predators, temperature, climate, and fishing effort on lobster abundance across regions — the regions are considered samples from a larger population of regions. We tested the inclusion of both a fixed and random effect for fishing effort, however as results were similar we present models with effort as a fixed effect for simplicity of interpretation and computation. We reasoned that effort would likely have a consistent effect on lobster abundance across regions. In addition to mixed-effect-model fits we also show the results of separate linear regressions of lobster abundance against each predictor variable for each region.

Since temperature and NAOI may capture some of the same climate-induced variability, we included them in separate analyses. We therefore considered four sets of models: those that included temperature or NAOI, and those with effort (264 candidate models, considering all combinations of time lags, variables, and their interactions) or without (529 candidate models). The same predator time series were included in all analyses. Since allowable traps (our effort metric in Canadian regions) were constant for NS, we excluded NS from the analyses with effort. We did not mix or include lags of the same variable in any of the candidate models, that is, each variable only appears once per candidate model.

4.4 Results:

The available lobster abundance time series spanned several decades, approximately 25 years in the USA, and between 25 to 50 years in Canada (Fig. 2). Over much of the observed period, lobster populations in the NW Atlantic have increased in abundance, which is remarkable given that they were fished intensively over much of this time. Particularly the more southern regions (Georges Bank southwards) have also shown recent declines, while abundance trends and landings appear mostly stable or are still increasing in the Gulf of Maine northwards (Fig. 2). Predator time-series spanned between ~20 to 40 years. Over this time, the total abundance of lobster predators has declined over time, with the exception of the Gulf of Maine and Georges Bank regions, which have shown large increases in dogfish populations, and more recent recovery of haddock and some other groundfish (Murawski *et al.* 2000). Temperature has generally increased across regions, with the exception of the SGSL and RI (Fig. 2). Fishing effort measured as the number of traps generally appeared to track increasing abundance trends (Fig. 2). The NAOI (Fig. 1, see insert) has been predominantly in a ‘high’ (above average) phase since 1980. It reached a peak in the early 1990s and has since decreased.

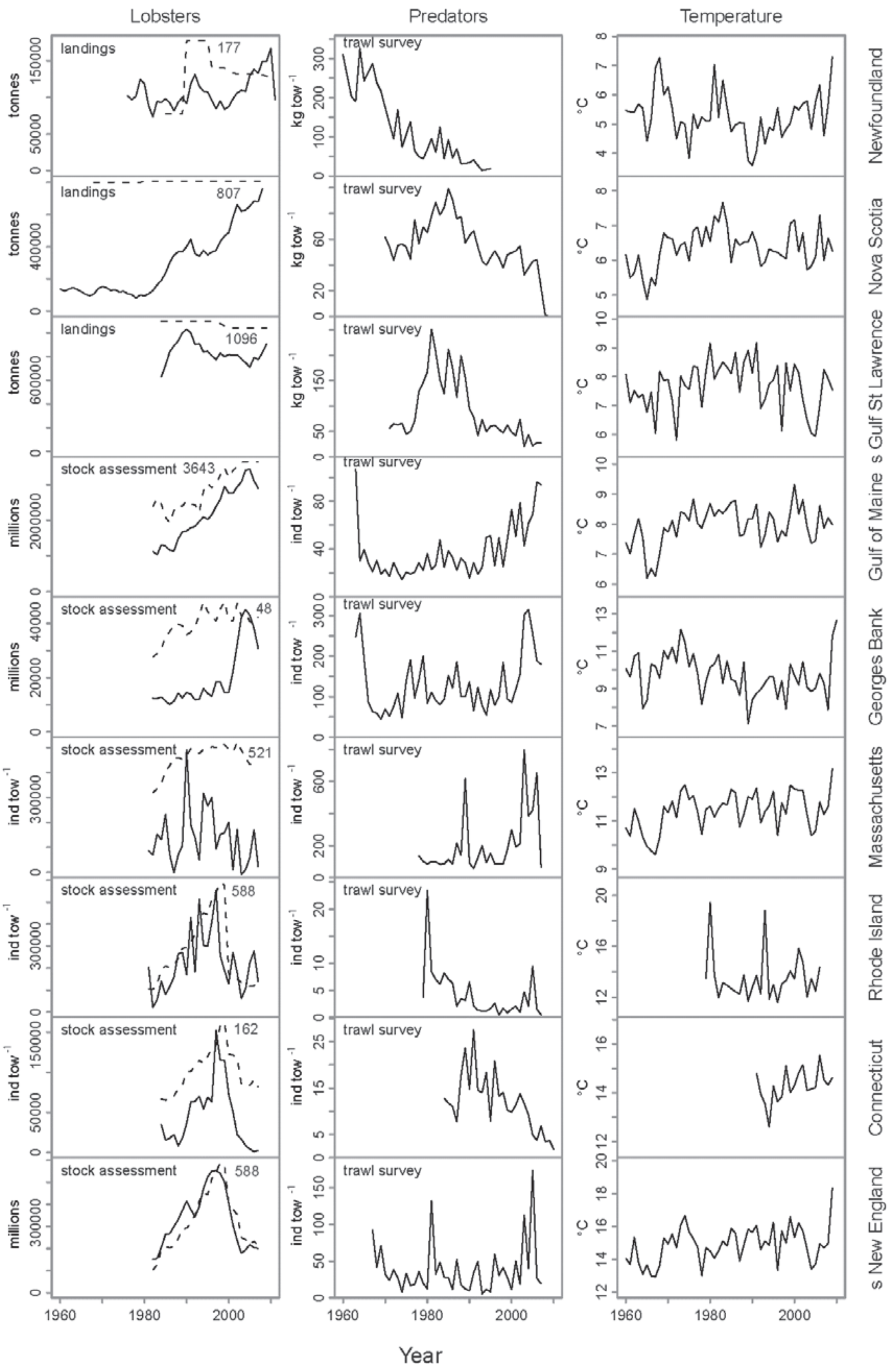
Lobsters
Predators
Temperature
landings
177
807
1096
stock assessment
3643
48
521
588
162
588
trawl survey
tonnes
millions
ind tow -1
kg tow -1
°C
Newfoundland
Nova Scotia
s Gulf St Lawrence
Gulf of Maine
Georges Bank
Massachusetts
Rhode Island
Connecticut
s New England
1960
1980
2000
Year

Figure 4.2. Time series data. Shown are untransformed abundance index data for lobsters (solid line) as well as fishing effort (dashed line), groundfish predators (see Table 2 for species), and temperature (^{o}C). Regions are arranged from coldest (Newfoundland) to warmest (southern New England). The y-axes for lobster and predators are anchored at 0 and the value printed on the lobster abundance panels indicates the maximum number of traps (in 1000s, dashed line).

Most of the lobster abundance indices examined trended significantly positively with landings (Fig, 3). One exception was Nova Scotia where landings were not statistically significantly related to survey abundance (R^2= 0.07098, p-value= 0.2449, note low sample size of N=10 years), but they were to survey biomass (R^2=0.4339, p-value=0.0320). For the larger regions of GOM, SNE and GB, landings correlated exceptionally well with the University of Maine stock assessment model estimates, maybe in part because landings are included in the model inputs. However, similarly strong relationships were seen between landings and survey abundance of lobster. Specifically, SNE landings and University of Maine index (R^2=0.8770, p-value <0.0001) and research survey (R^2= 0.1234, p-value=0.0407) were positively correlated, as were GB landings and University of Maine index (R^2= 0.5175, p-value <0.0001) but not with research survey abundance (R^2= 0.0074, p-value=0.2851). The GOM landings and University of Maine index showed similar trends (R^2= 0.9303, p-value <0.0001) as did research survey (R^2 =0.3074, p-value= 0.0016). For individual States nearly all correlations were positive and significant, with the exception of RI landings and abundance index (R^2= 0.08385, p-value= 0.0779), however landings and research survey index were significantly correlated (R^2 =0.2006, p-value= 0.0098). In CT, landings and abundance index (R^2= 0.6175, p-value <0.0001), landings and research survey index (R^2=

0.6926, p-value=0.0001) were all statistically significant. In MA landings and abundance index (R^2= 0.2552, p-value= 0.0042), landings and research survey index (R^2= 0.3016, p-value= 0.0012) were also highly correlated.

Figures 4 through 6 display the relationships between lobster abundances and individual explanatory variables at appropriate lags. Slope estimates from mixed effects models generally show a more conservative slope (solid line) than the simple linear regressions (dashed line). Lobsters and predators time series (Fig. 4) often showed no relationship or are correlated positively, except at shorter lags (0-4 years) in SNE, MA, NS, NL where they were negative. Overall, temperature (Fig. 5) did not appear to have strong effects on lobster abundance or landings over most of the observed time lags, although there were some negative trends across regions at lags 7-9 years. The relationship between lobsters and NAOI (Fig. 6) was consistently positive across all regions at lags 5-8 years. Effort closely followed most abundance trends (Fig. 1) and hence was positively correlated at time lag of 0, except on GB where effort trended slightly negative with abundance.

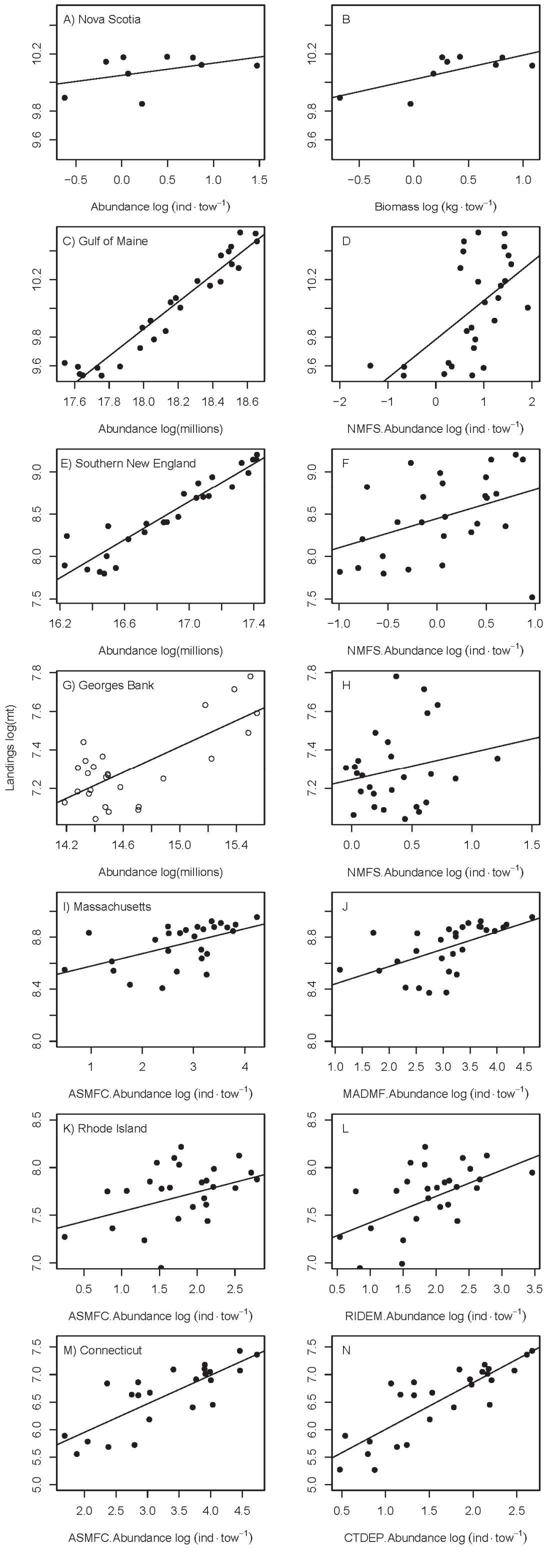

Figure 4.3. Lobster landings in relation to abundance estimates. Regions are ordered from north to south, acronyms as in Figure 1. Linear regression (line) of commercial landings against NS trawl survey abundance #/tow (A) and biomass kg/tow (B), for the GOM (C-D), SNE (E-F), and GB (G-H), lobster abundance data were derived from the University of Maine stock assessment model (millions, left panels), or research surveys (#/tow, right panels). For individual States MA (I-J), RI (K-L), CT (M-N) research trawl-based indices of abundance available from the Atlantic States Marine Fisheries Commission (mean catch per tow summed for 53-228 mm carapace length, left panels) and state-run trawl survey (#/tow, right panels) are correlated with landings reported by those states.

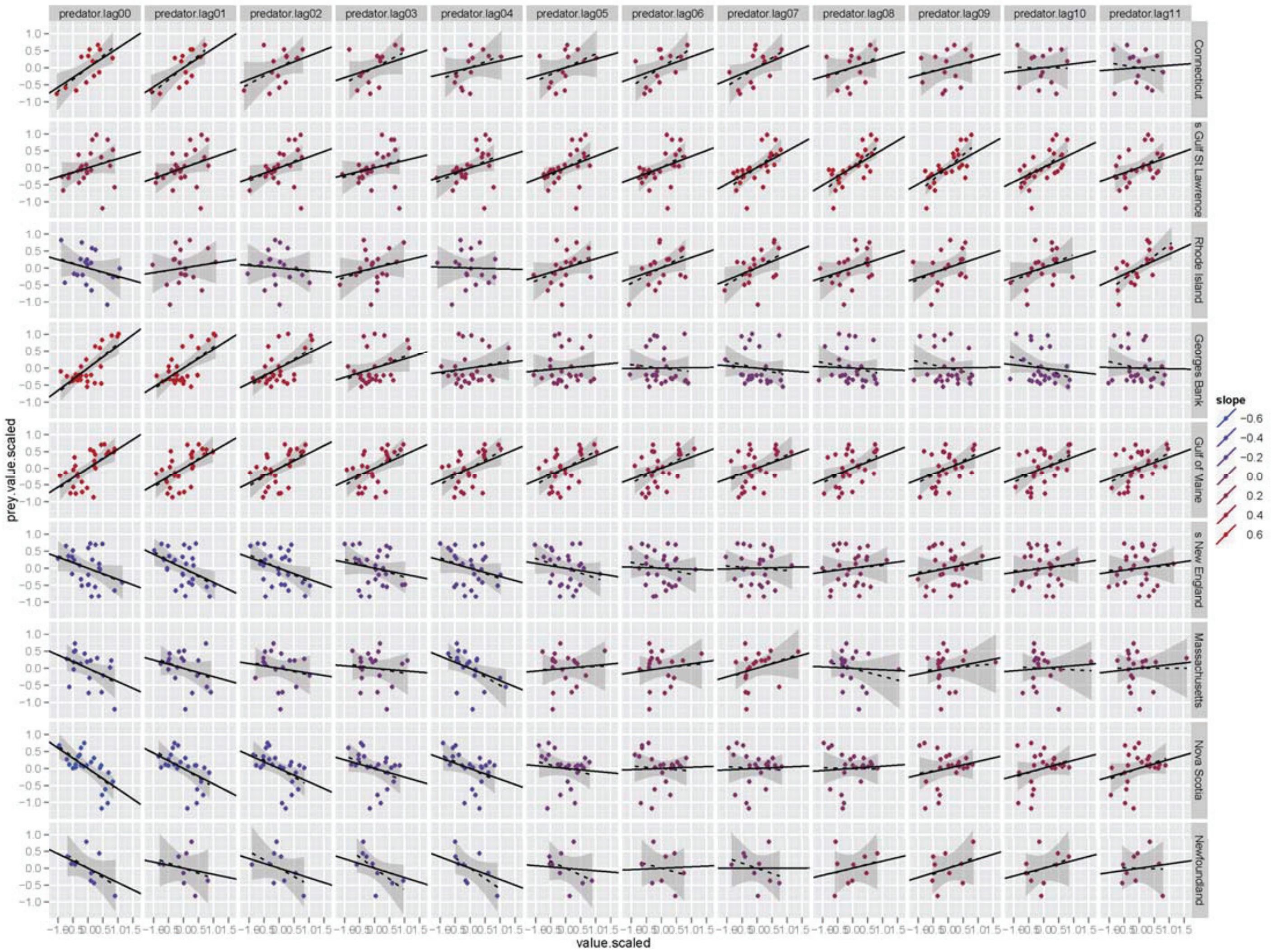

Figure 4.4. Relationships between lobsters (prey) and groundfish (predators) across regions at different time lags. Solid line is derived from a mixed effects model, dashed line from a simple linear model with 95% confidence intervals. Regions are arranged from warmest to coldest, and data points are colour-coded by the steepness of the mixed-effects slope.

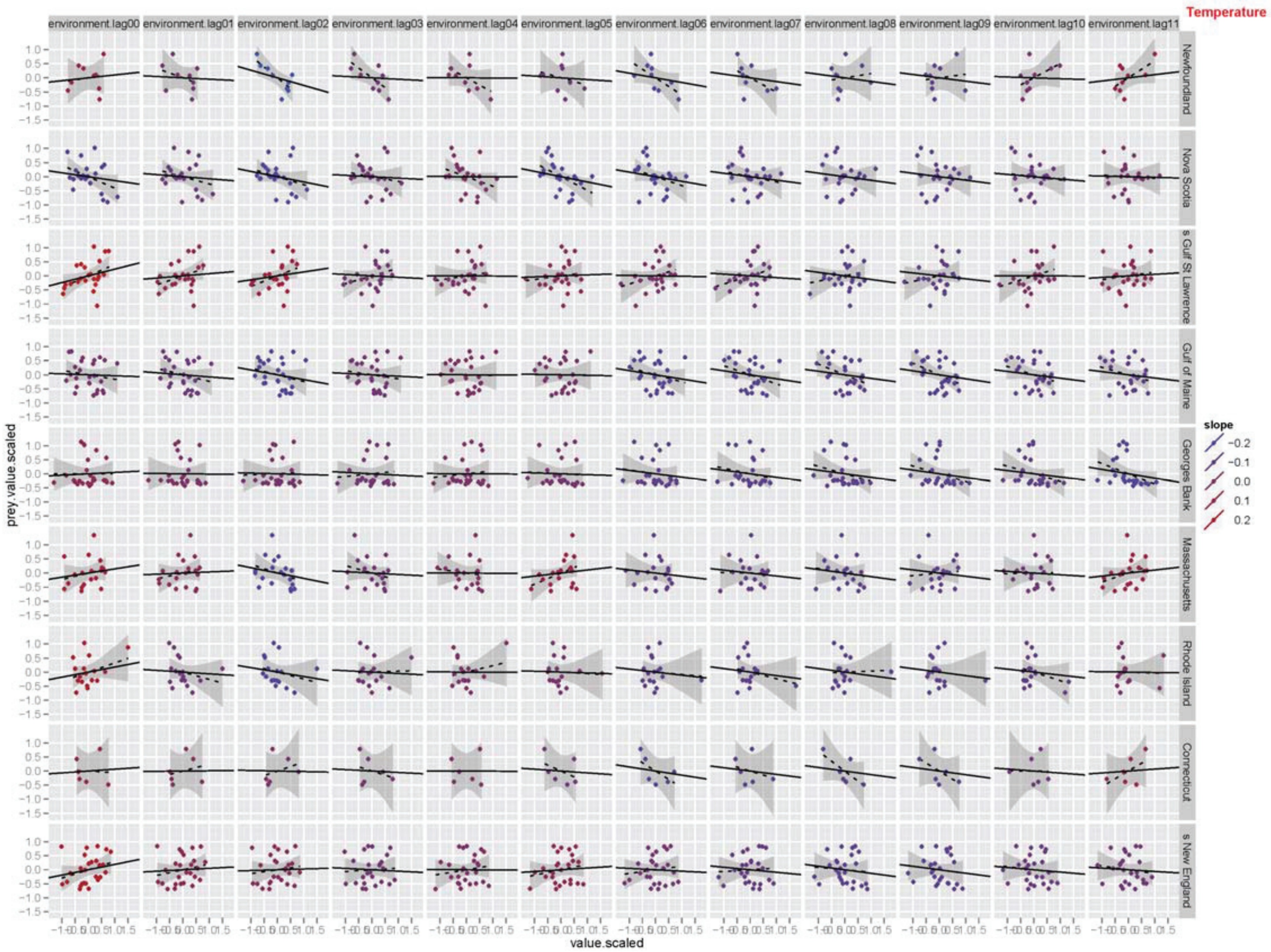

Figure 4.5. Relationships between lobsters and temperature across regions at different time lags. Solid line is derived from a mixed effects model, dashed line from a simple linear model with 95% confidence intervals. Regions are arranged from coldest to warmest, and data points are colour-coded by the steepness of the mixed-effects slope.

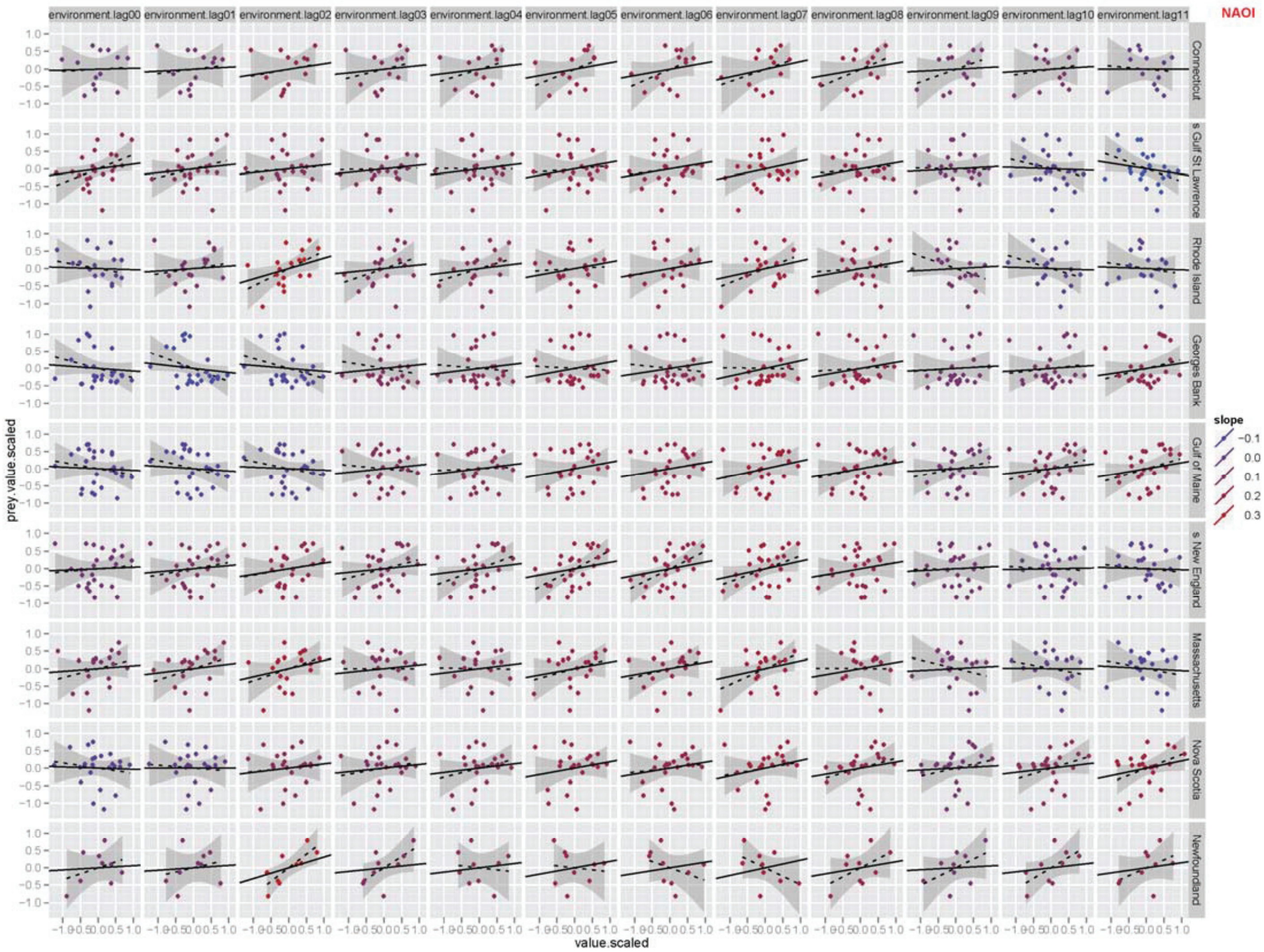

Figure 4.6. Relationships between lobsters and NAOI across regions at different time lags. Solid line is derived from a mixed effects model, dashed line from a simple linear model with 95% confidence intervals. Regions are arranged from coldest to warmest, and data points are colour-coded by the steepness of the mixed-effects slope.

Based on their AIC weights and ΔAIC_c, the resultant candidate models (Table 3) with the most weight and a $\Delta\ AIC_c < 2$ included predators at a range of time lags, including 0 to 1 (Table 3), and 5 and 9 (Fig. 7) years. Temperature was not found to be a strong predictor of lobster abundance and was not included in any of the top candidate models (Table 3). Significant interactions occurred between climate and predators. In models including NAOI, the effects of NAOI at a lag of 7 were slightly stronger when they interacted with predators at a lag of 0 (Table 3, Fig. 8). When effort was included (Table 3, Fig 7C-D), the model averaging strongly supported as positive effect of the number of traps in the model. While most top candidate models were statistically significant (Table 3) they did not explain much of the observed variability in lobster abundance (Fig. 9), with R^2 ranging from 0.08 (Predators-NAOI) to 0.41 (Predators-NAOI-Effort). The positive NAOI effect was consistent across regions and was found to be driving the interaction with predators (Fig. 8). Individual predators region by region (Fig. 10, lag 0 years) correlated at varying degrees with lobster abundance indices, however did not vary much over the explored 0 to 10 year time lags. Consistent with previous studies in the regions of the GOM and NS, cod, wolffish, thorny skate, and cusk were negatively correlated with lobster. Cod, haddock and monkfish were also negatively correlated with lobster in NL.

Table 4.3: Summary of the candidate mixed-effects models contributing to lobster abundance using predators and temperature or NAOI, with and without effort (traps). The models are ordered according to decreasing weight and only those with a Δ $AIC_c < 2$ are shown. Pearson's correlation coefficient (r) and p-value for the top model are also reported. K= parameters, $\Delta AIC_c = (AIC_{c(i)} - AIC_{c(min)})$

Candidate Model	K	AIC_c	ΔAIC_c	AIC_c Weight	Log likelihood	Top model r	Top model p-value
Predators-Temperature							
Predators (lag0)	6	218.48	0.00	0.67	-102.99	0.0525	0.489
Predators-Temperature-Effort							
Predators (lag1)+Effort	7	144.02	0.00	0.48	-64.62	0.6304	< 0.001
Predators-NAOI							
Predators(lag0)*NAOI(lag7)	11	230.89	0.00	0.46	-103.68	0.2862	< 0.001
Predators-NAOI-Effort							
Predators(lag0)*NAOI(lag9) *Effort	12	149.12	0.00	0.15	-61.51	0.6430	< 0.001
Predators(lag0)*NAOI(lag6) *Effort	7	149.29	0.17	0.14	-61.59		
Predators(lag1)+Effort	7	149.50	0.38	0.12	-67.38		
Predators(lag0)+Effort	7	150.21	1.09	0.09	-67.74		
Predators(lag0)*NAOI(lag7) *Effort	12	150.47	1.35	0.08	-62.18		
Predators(lag1)*NAOI(lag4) *Effort	12	151.12	2.00	0.06	-62.51		

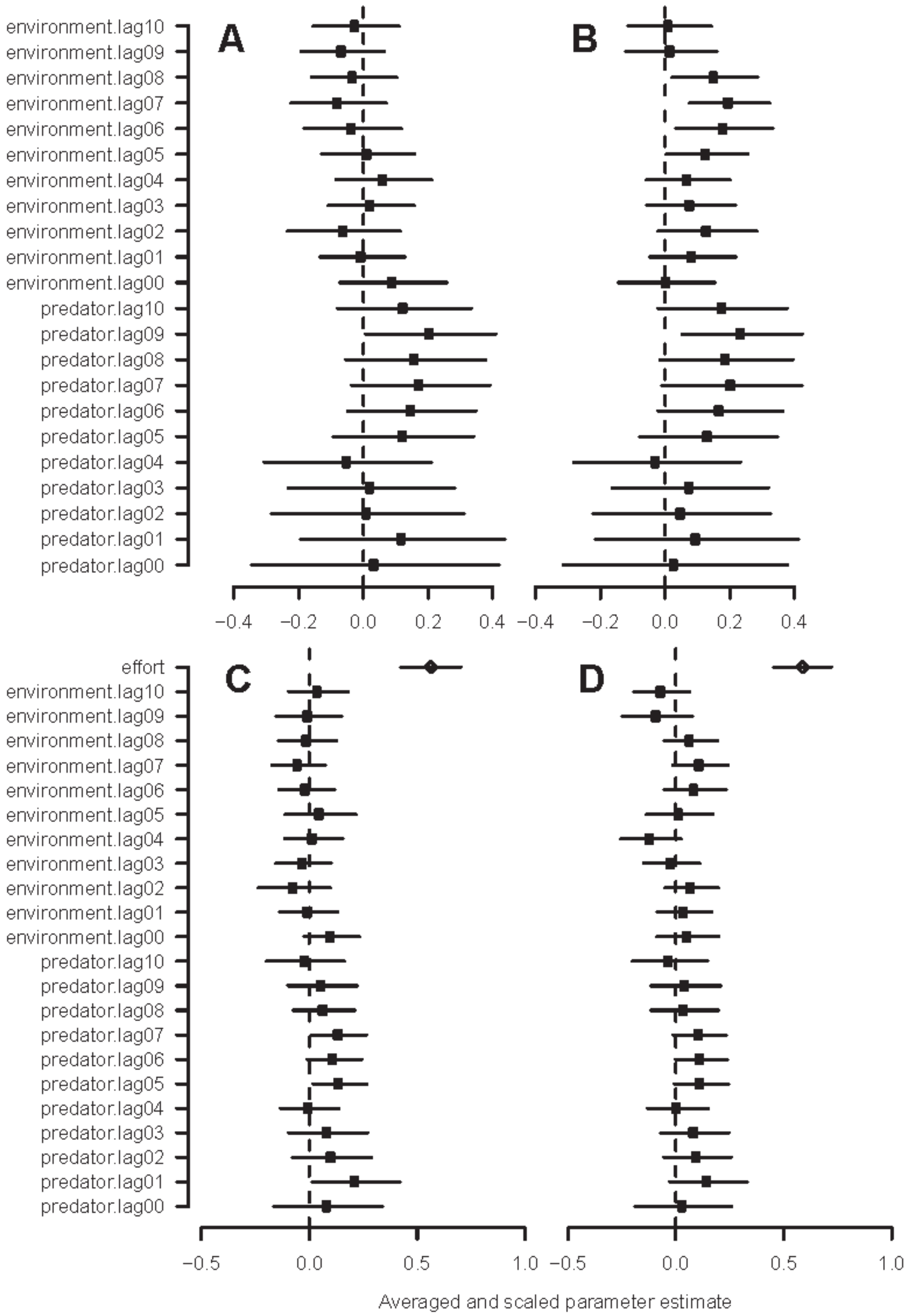

Figure 4.7. Multimodel AIC averaged coefficients with 95% CIs for the effects of predators and, A) temperature, B) NAOI, C) temperature with effort, D) NAOI with effort on lobster abundance at various lags. The approach takes all of the candidate models into account, but does not include interactions.

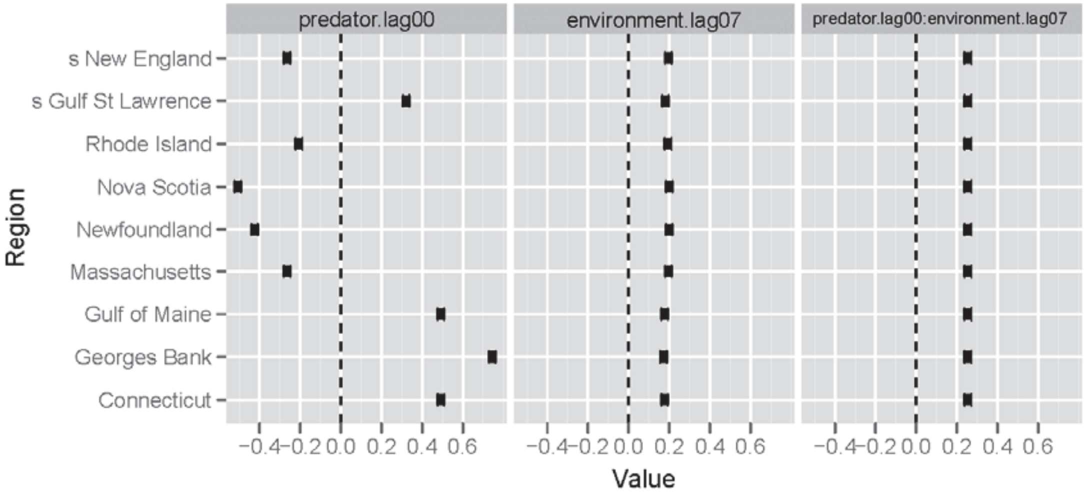

Figure 4.8. Region-specific parameter estimates of the best mixed-effects model with the lowest AICc to explain lobster abundance across regions. Shown are parameter estimates for the effects of predators at lag 0 and effects of NAOI at lag 7 separately (left and centre), and their interaction (far right).

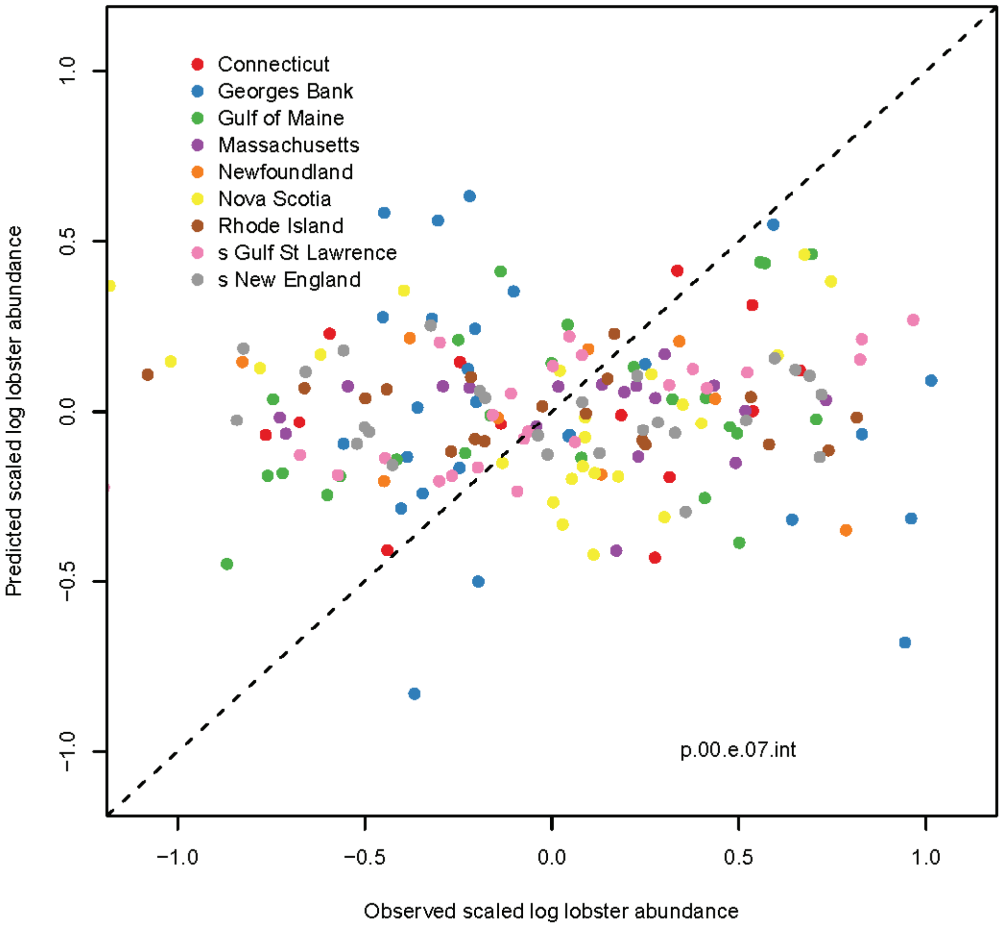

Figure 4.9. **Model fits of the mixed-effects model with the lowest AICc to explain lobster abundance by region, the interaction of predators at lag 0 with NAOI at lag 7** (p.00.e.07.int), plotted as predicted lobster abundance estimates vs observed lobster abundance estimates. Colour coded by region and the dashed line refers to the 1:1 line.


Connecticut
littleskate.abund
smoothdog.abund
tautog.abund
strbass.abund
cunner.abund
longhorn.abund
searaven.abund
spinydog.abund
Georges Bank
spinydog.abund
had.abund
longsculp.abund
littlesk.abund
cod.abund
searaven.abund
thorny.abund
smoothdog.abund
monk.abund
smoothsk.abund
hal.abund
Gulf of Maine
spinydog.abund
had.abund
longsculp.abund
cod.abund
thorny.abund
monk.abund
smsk.abund
searaven.abund
littlesk.abund
wolf.abund
Massachusetts
spinydog.abund.all.fall
cod.abund.gom.spring
longsculp.abund.gom.spr
cod.abund.gom.fall
longsculp.abund.gom.fall
spinydog.abund.all.spring
smoothdog.abund.sne.fall
tautog.abund.sne.spr
cun.abund.all.spr
cun.abund.all.fall
had.abund.gom.fall
tautog.abund.sne.fall
had.abund.gom.spr
smoothdog.abund.sne.spring
monk.abund.all.fall
monk.abund.all.spr
wolf.abund.gom.spr
wolf.abund.gom.fall
Newfoundland
cod.bio
thsk.bio
wolf.bio
longsculp.bio
monk.bio
had.bio
searaven.bio
spinydog.bio
hal.bio
smsk.bio
Nova Scotia
had.bio
cod.bio
spinydog.bio
thorny.bio
monk.bio
wolf.bio
cusk.bio
longsculp.bio
hal.bio
searaven.bio
smsk.bio
littlesk.bio
cun.bio
Rhode Island
longhorn.abund.spr
cod.abund.spr
cunner.abund.spr
tautog.abund.fall
cunner.abund.fall
tautog.abund.spr
smoothdog.abund.fall
monk.abund.spr
spinydog.abund.spr
spinydog.abund.fall
smoothdog.abund.spr
monk.abund.fall
cod.abund.fall
longhorn.abund.fall
s Gulf St Lawrence
cod.bio
spinydog.bio
whhake.bio
thsk.bio
longsculp.bio
had.bio
hal.bio
searaven.bio
wolf.bio
shortsculp.bio
smsk.bio
cun.bio
s New England
spinydog.abund
had.abund
littlesk.abund
smoothdog.abund
longsculp.abund
monk.abund
searaven.abund
cod.abund
pred.name
-0.5
0.0
0.5
r
r
-0.5
0.0
0.5

Figure 4.10. Correlations (r) between lobster abundance indices and individual groundfish predators in each region with 95% CIs at lag 0. See Table 4.2 for predator species.

4.5 Discussion:

This analysis provides evidence that predation and climate both play some role in regulating lobster abundance in the NW Atlantic. The effects of predation were not consistent across regions (Fig. 10) however, with limited negative effects of predators on lobster detected in Newfoundland, Nova Scotia, Massachusetts, and southern New England at lags 0 to 4 but not in other regions. Climate variation captured by the NAOI was positively correlated with lobster abundance across all regions, consistent with previously documented region-wide influences of NAOI climate forcing (Hurrell 1995, Otterson *et al.* 2001). The strongest effect was found at lag 6 to 8 (Fig. 6 and 7B), indicating some climate-driven effect on recruitment. This effect however did not appear to be explained by temperature variation, as temperature did not play a consistent role in the analysis. Fishing effort, proxied by the number of traps appeared important, as the candidate models with the lowest AIC_c values (Table 3, Fig. 7C,D) always included effort, in addition to the effects of NAO (7 lag, Table 3, Fig. 8), and predation (Table 3: lag of 0,1; Fig. 7A-C: lag 5,9). As the effect of effort on lobster was consistently positive (Fig. 7C,D), it does not appear that fishing is driving down lobster abundance (top-down), but rather that fishing effort tracks (responds positively to) increases in abundance (Fig. 2).

In Atlantic Canada, there are presently no long-term fisheries-independent abundance indices available. In lieu of estimates of abundance, landings are assumed to approximate population trends as fishing pressure tends to remove a large and relatively constant fraction of new recruits each year (Fogarty 1995). It is assumed that high landings indicate high population abundance, with the understanding that landings are also a function of fishing effort, catchability, and the distribution of the lobster population any given time (DFO 2001). The only Canadian region where fishery-independent abundance indices were available was Nova Scotia (1999-2010), and while abundance (#/tow) was not closely linked with landings, biomass (kg/tow) was. In the United States fisheries-independent abundance indices exist from trawl surveys conducted by NMFS and state departments (ASMFC 2009) which are used to estimate abundance trends, including spawning stock and recruitment, and to parameterize population models, such as the University of Maine's (Chen *et al.* 2005, ASMFC 2009). For Southern New England, Gulf of Maine and Georges Bank, model-predicted abundance and research trawl survey abundance indices were consistently and highly correlated with landings (Fig. 3), with the exception of the research survey index on GB. As the University of Maine model also includes landings information, strong positive correlations are not unexpected. The interesting case again is the offshore area of GB where the relationship was noticeably weaker than in the GOM and SNE. It is likely that fishing effort on GB is not as high and constant as in the more nearshore regions, and hence changes in landings may be less tightly coupled to changes in abundance. The landings from individual states also trended positively with standardized NMFS survey abundance as well as state-employed trawl survey estimates, with the exception of landings RI which were more closely linked with the near shore survey (10-50 m depth; Lynch pers. comm.). Generally however, this evidence (Fig. 3) suggests that landings may be used as abundance proxies for American lobster, particularly in nearshore areas.

The North Atlantic Oscillation Index (NAOI, Fig. 1 inset) is the fluctuation in atmospheric pressure between Iceland and the Azores. It affects the dominant weather pattern in the North Atlantic region (Hurrell 1995) and is associated with decadal trends in climate and physical oceanography. The NAOI has been in a high phase for the past two decades (Fig. 1), which appears to coincide with the increase in lobster abundance in the Gulf of Maine (both U.S. and Canadian portion), however a direct mechanism has yet to be discovered (Fogarty and Gendron 2004). Support of the NAO's influence on ecological processes however has been building over the last decades (Greene and Pershing 2000, Ottersen *et al.* 2001, Visbeck *et al*. 2001, Drinkwater *et al.* 2003, Fogarty and Gendron 2004). During years with a high NAO index, warm slope water (as opposed to cold Labrador slope water) flows towards the Northeast Channel between Georges Bank and Nova Scotia and infuses the Gulf of Maine with warm, salty water (GoMOOS 2005). Lobster abundance off Nova Scotia's Atlantic coast is thought to be influenced strongly by large-scale oceanographic factors and the high landings in southwest Nova Scotia may be related to warm, stable water temperatures (Hudon 1994). Larval lobsters are planktivores (Harding *et al*. 1983), hence their feeding success could depend on the NAOI's influence on plankton communities. For example, in Narragansett Bay, RI, shifts in phytoplankton species were believed to be due to a warming SST and an increasing NAOI (Durbin and Durbin 1992). In the Gulf of Maine, *Calanus finmarchicus* abundance (1961-1991) showed a positive relationship with NAOI (Conversi *et al.* 2001). In Narragansett Bay and Rhode Island Sound a shift (1980-2005) from benthic to pelagic species strongly correlated with an increase in winter NAOI and a reduction in chlorophyll *a* concentration (Collie *et al.* 2008). It might also be useful to examine NAOI influences on lobster predators, as Drinkwater (2002) linked >

50% of the variability in NL cod (ages 3-5 years) growth with NAOI (Drinkwater *et al.* 2003). Finally, it is conceivable that climatic conditions (including wind, currents and onshore transport) associated with a high NAO phase favour the retention and growth of lobster larvae, and subsequent settlement, resulting in a greater abundance of commercially harvestable sized lobster in the following years (~7 year time lag to allow for growth and recruitment to the fishery). If this was generally true, it would allow prediction of changes in lobster abundance from NAOI up to 7 years ahead.

Postlarval supply and settlement are believed to be major drivers of adult lobster population size (Incze *et al*. 2000, Wahle *et al*. 2004, Incze *et al*. 2006) and, as mentioned above, favourable environmental conditions have been proposed as a mechanism for observed increases in lobster abundance and recruitment. There are many factors which play a role in settlement success including, the transport of the larvae, the distribution of the brooding females (and larval release), temperature, advection, and turbulence (Incze *et al*. 2000, 2003, 2006, 2010, Chasse and Miller 2010). Within a region there can be hot (i.e. outercoast westward Penobscot Bay, ME) and cold (i.e. NE corner of Penobscot Bay) spots of lobster larval settlement (Steneck and Wilson 2001), with the eastern Maine coast experiencing lower larval supply and therefore lower recruitment than other regions in the GOM (Incze and Naimie 2000). As lobster larvae are near the surface (neustonic), coastal wind patterns can move postlarva in- or offshore (Incze and Naimie 2000, Xue *et al*. 2008), which is important because successful settlement typically occurs in coastal zones at depths < 25m (Wahle and Steneck 2001, Incze *et al*. 2006). Further, larvae arriving in mid-coast Maine likely travel down the eastern coast, drifting northeast to southwest, with the Gulf of Maine Coastal Current (Incze and Naimie 2000, Incze *et al*. 2006). Given that many environmental factors are important in lobster settlement success, the role of the NAOI on lobster abundance patterns could be mechanistically complex.

We specifically examined the hypothesis that temperature at the depths were lobster occur could explain some of the observed variation. Temperature plays an important role on the American lobster throughout its many life stages, from egg through adulthood. Hatching occurs over the summer months (late May through September) with larval stages in the plankton appearing at sea surface temperatures (SST) around 12.5 °C (Ennis 1995). Lobsters settle out of the plankton as a stage IV postlarva (after approximately18 to 38 days, Incze and Naimie 2000), and in the past, lobster landings have been correlated with water temperature at the time of settlement in Maine and Nova Scotia. From 1946-1986 in Maine, 54% of the variance in lobster landings could be explained by a positive relationship with SST at the time of larval settlement (Acheson and Steneck 1997). In Nova Scotia (1929-1970), 68% of the variance in landings was explained by the SST in St. Andrews, NB in addition to the previous year's catch (Flowers and Saila 1972). While it is difficult to correctly age lobsters, there is a consensus that recruitment into the fishery occurs at around age 7 and that it is therefore necessary to incorporate time lags of 6 to 9 years into predictive models that relate larval or settlement processes to catches or changes in adult abundance (Flowers and Saila 1972, Drinkwater *et al.* 1996, Acheson and Steneck 1997). Drinkwater *et al.* (1996) on the other hand, were not able to link SST with the increase in lobster landings throughout the American lobster's range in the 1980s and early 1990s, although they acknowledged a potential role of SST in the past. This could mean that different factors influenced lobster populations through time (i.e. multiple or changing causalities). Temperature may also affect survival in the first year of life, though if a lobster survives to settlement, natural mortality in general decreases (Wahle and Steneck 1992). Lobsters migrate offshore in the winter to seek out warmer water temperatures (Hudon 1994) and are less available to the fishery when they are moulting (Miller 1990, Tremblay and Smith 2001). Thus temperature may also affect catchability in the recruited size classes and temperature and catchability together have the potential to influence abundance (i.e. Tremblay and Smith 2001). For any given effort, if catchability increases, a larger proportion of a fished population is removed, and this could result in a population decline.

As American lobster populations experience high fishing mortality over most of their range (ASMFC 2009), their abundance may be driven in some significant part by fishing. Yet our results imply that overfishing is not occurring, as effort does not seem to be driving down lobster abundances over the range of observed values. Instead, effort appears to be following lobster abundance, resulting in a strong positive effect in the analysis. Although trap and license limits have been in effect in Atlantic Canada since 1968 (Pezzack *et al.* 2006) the number of traps has generally increased along with landings in the US while the number of fishing licenses is decreasing (ASMFC 2009). Changes in trap design over time and associated changes in catchability could also have an influence on effort, yet this is difficult to quantify over time (Miller 1990). Also, there has been a spatial expansion of the fishery with a well-documented redirection of fishing effort from the nearshore into offshore regions (Acheson and Steneck 1997, Gendron and Archambault 1997, Pezzack *et al*. 2001). The full effects of this shift in effort are not yet known but are of concern as offshore regions are believed to support larger lobsters acting as broodstock (DFO 2006).

The observed positive correlation between trap densities and lobster abundance could also relate the input of lobster bait, which is believed to help fuel the increase in lobster abundance in the Gulf of Maine, where effort is extremely high (millions of traps deployed year round), and massive bait inputs may help to ‘farm’ lobsters (i.e. Grabowski *et al.* 2009). However, this is not believed to explain increased abundance in other regions, such as southwest Nova Scotia (Boudreau and Worm 2010) which features lower trap densities, only half as long a season, and yet similarity increasing abundance trends as the GOM (Myers *et al.* 2007, Grabowski *et al.* 2009). Our results here indicate that the (positive) relationship of traps with lobster abundance is very consistent despite the varying trap densities in the different study regions. It appears more likely that fishermen (particularly in the USA) are adjusting their effort as abundance changes, and that any possible ‘farming’ effect is more local.

Lobsters, like most decapods, undergo ontogenic habitat shifts. Early benthic stages are largely dependent on sheltering habitats to minimize predation risk (Wahle 1992, Wahle and Steneck 1992). At later stages, they might be outgrowing most of their predators and becoming less dependent on shelter (Wahle 1992, Wahle and Steneck 1992). Negative correlations between individual groundfish predators and lobster occurred predominantly in the colder regions (Fig. 10) as previously reported, however the strength of these interactions did not change much over a range of plausible time lags (0-10 years). According to the model averaging (Fig.7A,B) predators are having an impact on early life stages ~9 years before recruitment to the fishery but are positively correlated, indicating predators would be boosting lobster abundance, contrary to our prediction. The underlying mixed effects models however (Fig. 4) show that half of the regions show negative relationships with predators over lags 0 to 4 years (NS, NL, SNE, MA). While we are not sure of the body sizes represented, the lags are less biologically plausible but similar to results from Chapter 3 of this thesis (i.e. negative correlations at short time lags, Boudreau and Worm 2010).

There are a number of uncertainties which affect our analyses. For example, while we have made an effort to compare lobster abundance indices that represent similarly sized lobsters, average sizes of lobsters caught in the state-run surveys (MA, RI, CT) are not presently reported. Two additional challenges in our analyses are that we are often using relative abundances estimates; this is particularly problematic when combining different predators from trawl survey data, as these might differ in their catchability, hence our composite predator index may not accurately reflect the absolute abundance of predators in the ecosystem. This is why we explored and included information on individual species and their correlations with lobster abundance (Fig. 10). The results presented here are consistent with those of Boudreau and Worm (2010) who found negative effects of a more limited suite of predatory groundfish on lobsters (Atlantic cod, cusk, longhorn sculpin, monkfish and wolffish). However, the direct evidence of predation on lobster from the literature continues to remain fairly limited. Finally there is a possibility that variation in lobster (and other invertebrate abundance) is better explained by changes in the body size of their groundfish predators (resulting in changes in their average food spectrum), and not necessarily in their abundance (Shackell *et al.* 2010).

One key factor not accounted for in our study was the epizootic disease contributing to the sudden decline in SNE lobster abundance in the late 1990s (Fig. 2) (Wahle *et al*. 2009). Another difficulty with our method is that the results depend upon where and how the data were taken. Fisheries-independent surveys are conducted primarily offshore, while most of the lobster catch is taken inshore. The Canadian trawl survey for example, does not cover much lobster habitat (Tremblay *et al.* 2007). It is possible that predator abundance data from the offshore only gives a skewed picture of what occurs in terms of changes in predation inshore. Similarly, most temperature data are taken further offshore and may imperfectly reflect conditions in the core lobster habitat.

Despite the inherent limitations discussed above, we conclude that there is evidence for an effect of predators and large-scale climate (NAOI) on lobster abundance indices in the NW Atlantic, however the strength and importance of these variables appear to change with region (at least for predators) and lobster life stage (climate affecting recruitment, predation a variety of life stages). In addition we found that landings are likely an appropriate proxy for abundance in most regions and that it does not appear that lobster populations are currently being driven down by excessive fishing pressure. We propose that future studies continue to examine the regional variation in climate-forcing on recruitment, as this process is potentially important, yet not well understood. As NW Atlantic fisheries are largely dependent on crustaceans (Anderson *et al*. 2011), it is important we continue to add to the knowledge-base (Anderson *et al*. 2008) that allows us to gauge lobster population dynamics, their ecological interactions, and the potential impacts of their harvest.

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Chapter 5

Top-down Interactions and Temperature Control of Snow Crab Abundance in the Northwest Atlantic Ocean

Stephanie A. Boudreau, Sean C. Anderson, Boris Worm (2011) *Marine Ecology Progress Series*. 429: 169-183

5.1 Abstract:

In much of the northwest Atlantic, commercially important snow crab *Chionoecetes opilio* stocks have increased in abundance following the decline and collapse of major groundfish stocks such as Atlantic cod *Gadus morhua*. We examined 3 hypotheses to explain variation in the abundance of snow crab across 10 regions: (1) climate control of both species, (2) top-down control of snow crab by cod, and (3) bottom-up control of cod by snow crab. We tested these hypotheses by analyzing time series data of cod and crab abundance indices and temperature via meta-analysis of full and partial correlation coefficients. We found that temperature had an opposing effect on the 2 species: snow crab abundance was negatively correlated with temperature at 7- to 10-year lags whereas cod and temperature were positively related at 1- to 7-year lags. Controlling for the effect of temperature, our meta-analysis revealed significant negative correlations of snow crab and cod abundance, with cod leading snow crab by up to a 5-year lag. This suggests a top-down effect on older juvenile and sub-adult snow crab. We found no evidence of a bottom-up effect of snow crab on cod. Negative correlations between cod and crab abundance were observed both at the warmer and colder portions of their ranges. These results suggest that snow crab abundance is largely influenced by temperature during the

early post-settlement years and becomes increasingly regulated by top-down mechanisms during the years approaching fishery recruitment. The method presented in this paper is generally useful to test ecological hypotheses from time series data—particularly where multiple causal mechanisms are suspected.

5.2 Introduction:

The decline and collapse of Atlantic cod *Gadus morhua* stocks in the northwest (NW) Atlantic over the last 2 to 3 decades, and coinciding increases in various crustacean species since then, have resulted in a changed ecosystem and a sharp transition in fishing effort from large groundfish to invertebrates (Worm and Myers 2003, Frank *et al.* 2005, Anderson *et al.* 2008). Fisheries for American lobster *Homarus americanus*, snow crab *Chionoecetes opilio* and northern shrimp *Pandalus borealis* are currently the most valuable fisheries in Atlantic Canada (DFO 2009a). Snow crab populations experienced large interannual variation with sustained increases over much of the 1990s (Fig. 1; e.g. Conan *et al.* 1996, Sainte-Marie *et al.* 1996, Tremblay 1997, Caddy *et al.* 2005). It is unclear which ecological factors influenced this variation and whether they relate to population dynamics (density dependence, cannibalism; e.g. Sainte-Marie *et al.* 1996, Lovrich and Sainte-Marie 1997, Sainte-Marie and Lafrance 2002), species interactions (predation; e.g. Bailey 1982, Tremblay 1997, Chabot *et al.* 2008), environmental forcing (temperature fluctuations; e.g. Taylor *et al.* 1993, Conan *et al.* 1996, Tremblay 1997), or a combination of these.

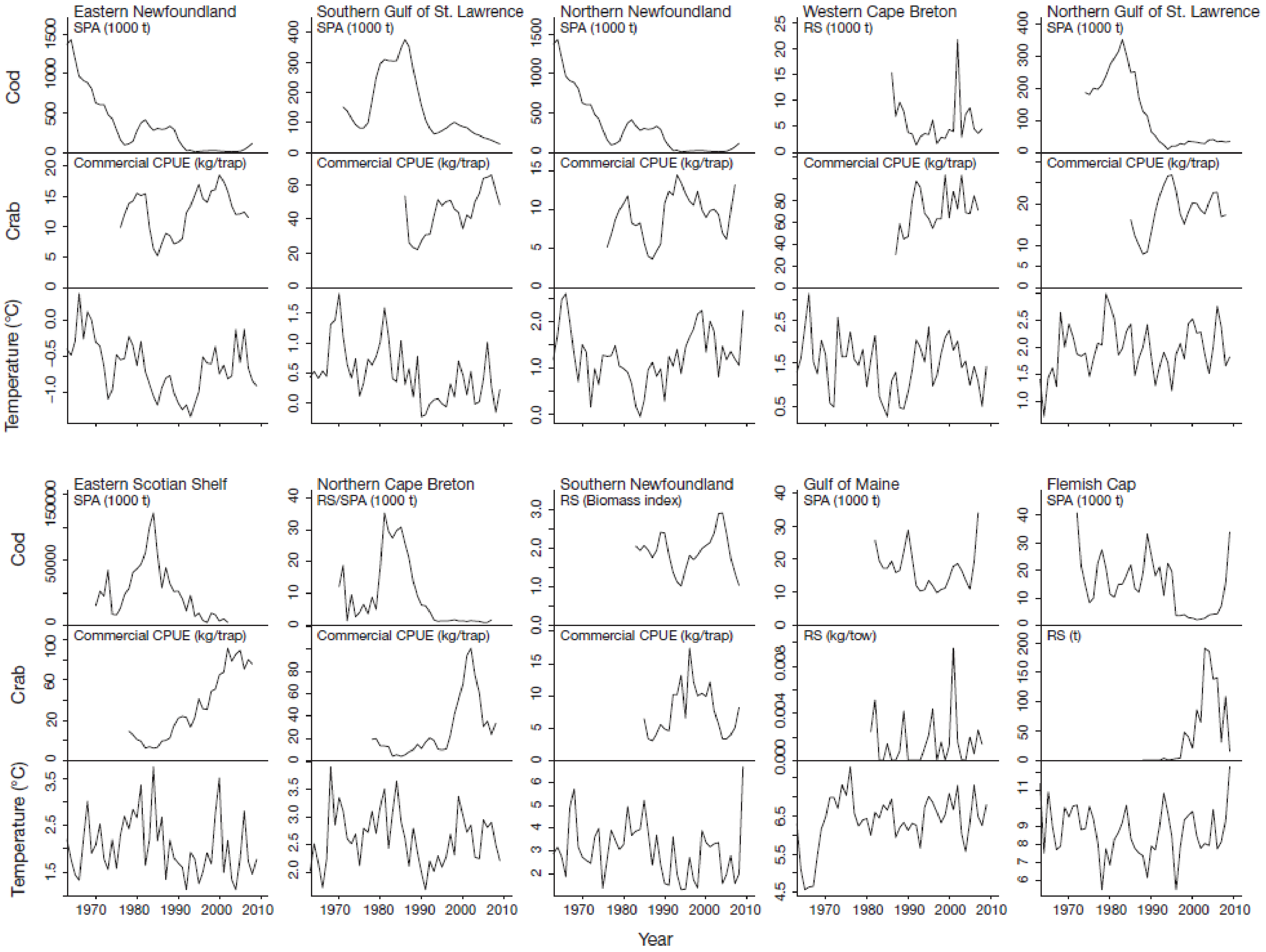
Eastern Newfoundland
SPA (1000 t)
Southern Gulf of St. Lawrence
SPA (1000 t)
Northern Newfoundland
SPA (1000 t)
Western Cape Breton
RS (1000 t)
Northern Gulf of St. Lawrence
SPA (1000 t)
Commercial CPUE (kg/trap)
Cod
Crab
Temperature (°C)
Eastern Scotian Shelf
SPA (1000 t)
Northern Cape Breton
RS/SPA (1000 t)
Southern Newfoundland
RS (Biomass index)
Gulf of Maine
SPA (1000 t)
Flemish Cap
SPA (1000 t)
RS (kg/tow)
RS (t)
1970
1980
1990
2000
2010
Year

Figure 5.1. **Time series data**. Atlantic cod *Gadus morhua* biomass indices (× 1000 t, top row), snow crab *Chionoecetes opilio* abundance indices (kg trap^{-1}, centre row) and temperature (°C, bottom row) in the regions of study (see Fig. 2) were plotted over time and arranged by temperature from the area with the coldest median water temperature (eastern Newfoundland) to the warmest (Flemish Cap). CPUE (fishery-dependent): catch per unit effort; RS (fishery-independent): research surveys; SPA: sequential population analysis. Refer to Table 2 for full details about the cod and crab time series. Temperature data was obtained from the DFO Hydrographic Climate Database (Gregory 2004).

The relative importance of these factors in the NW Atlantic cannot be resolved from an analysis of single time series due to their limited length (20–31 years) and confounding factors (e.g. sample size, variability), both of which limit statistical inference. When analyzed together, replicated time series in multiple regions can provide insight into food-web interactions (e.g. Worm and Myers 2003). Here we introduce an extended meta-analytic approach to explore the causes of variation in snow crab abundance and to test multiple ecological hypotheses about the structuring factors of marine ecosystems.

In this context, the overfishing and collapse of NW Atlantic cod stocks (Myers *et al.* 1996, 1997a) may be viewed as the replicated realization of a large-scale predator removal experiment. Analyses of stomach contents demonstrate that various crabs, including snow crab, are important prey of cod in the Atlantic (Table 1). However, previous analyses have yielded conflicting conclusions about the role Atlantic cod plays in regulating snow crab abundance. Bailey (1982) found strong evidence of a predator-prey relationship whereas Waiwood and Elner (1982) did not. Chabot *et al.* (2008) found that snow crab comprised less than 10% of stomach content mass in Gulf of Saint Lawrence (GSL) Atlantic cod. By comparison, northern shrimp comprises from 5.0 to

9.3% of cod stomach content (averaged across studies), and cod appears to exert strong top-down control of shrimp stocks (Worm and Myers 2003 and references therein). Further, this interaction was found to be temperature dependent, with stronger evidence of top-down control in colder temperatures (Worm and Myers 2003, Frank *et al.* 2007).

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

By expanding on the meta-analytic methods established by Worm and Myers (2003), we attempt to test both predation and climate hypotheses by correlating snow crab abundance, Atlantic cod biomass, and ocean temperature. Specifically, our goal was to examine 3 competing hypotheses to explain variation in snow crab abundance: (1)

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

5.3 Methods:

5.3.1. Species

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

Atlantic cod are highly migratory (ICES 2005) and feed opportunistically on benthic crustaceans and other invertebrates before becoming increasingly piscivorous with size (Hanson and Chouinard 2002, Link and Garrison 2002). Atlantic cod can be as large as 150 cm, live 20+ years, and occupy depths from 1 to 600 m (Pálsson 1994). Atlantic cod in the NW Atlantic are found at a range of depths and temperatures. For example, on the Flemish Cap (FC) they can be found from 150 to 500 + m at temperatures ranging between 3.5 and 4.5 °C (ICES 2005). On Georges Bank (in the Gulf of Maine [GOM]) they are found at their upper range of temperatures from 10 to 14 °C (annual mean at 100 m) (ICES 2005). In eastern Newfoundland (ENL) they are found at their lower range of temperatures from < 0 to 6 °C (ICES 2005). Stomach sampling confirms that Atlantic cod prey on snow crab and that their ranges overlap (Table 1).

Table 5.1: Atlantic cod *Gadus morhua* predation on snow crab *Chionoecetes opilio*. The mean proportion of snow crab in the diet of cod is expressed by 3 measures: percent by mass of stomach contents (Mass), percent of mean frequency of occurrence (MFO), and a partial fullness index (PFI, see Lilly 1984). To demonstrate the range of crab ingested by cod, the number of cod stomachs (N cod) examined, the number of crab measured in the stomach contents (N crab), the carapace width of the snow crab (CW), the length of cod sampled (Cod L) and cod age are reported when available. Ranges of values are in brackets following the mean values and data has been pooled across available years. Sources: 1- Lilly (1984), 2- Robichaud et al. (1991), 3- Chabot et al. (2008), 4- Waiwood & Elner (1982), 5- Hanson & Chouinard (2002), 6- Waiwood & Majkowski (1984).

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

+ Newly moulted males, ++ hard-shelled ovigerous females, +++ juveniles both sexes

^ Estimated ceiling of hard-shelled snow crab ingested by large cod

* Value reflects only the crabs actually measured in the cod stomachs

5.3.2. Data

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

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

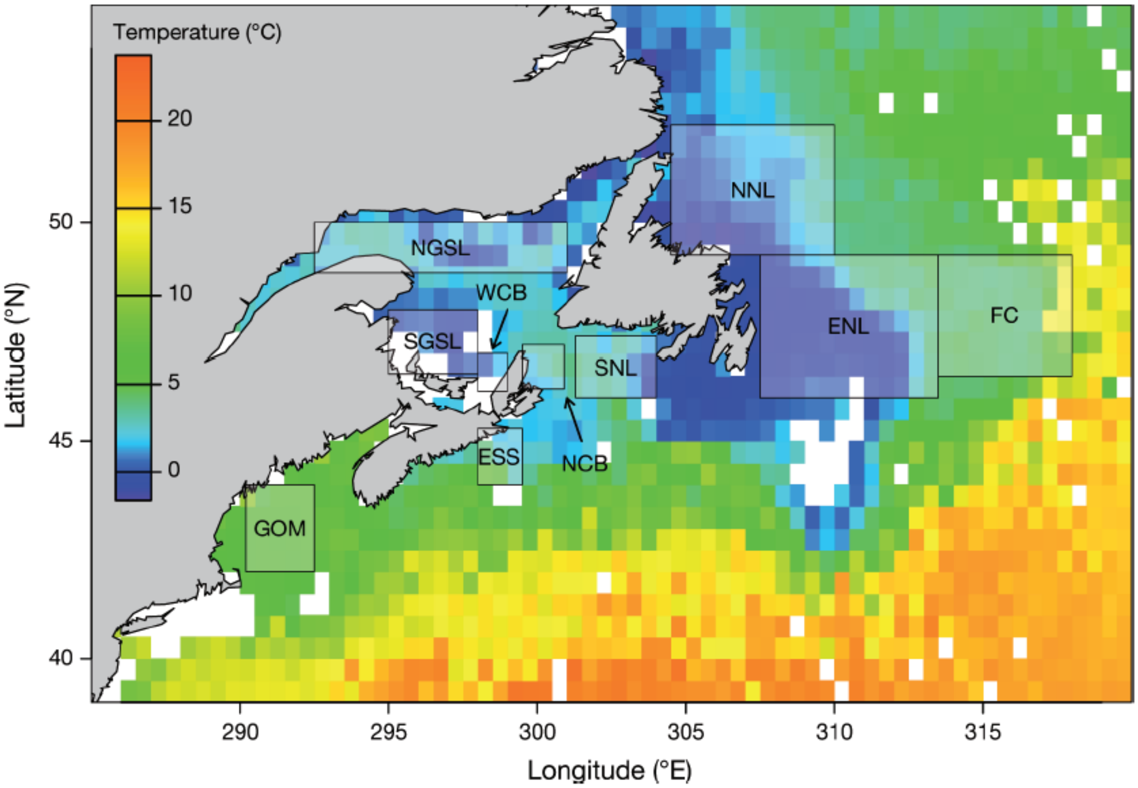

Figure 5.2. Study regions. To illustrate temperatures regimes we underlayed the median temperature across all available samples from 1 January 2005 to 1 January 2010 at 150 ± 75 m depth at 0.5° × 0.5° resolution. NNL: northern Newfoundland; ENL: eastern Newfoundland; SNL: southern Newfoundland; FC: Flemish Cap; NSGL: northern Gulf of St. Lawrence; SGSL: southern Gulf of St. Lawrence; WCB: western Cape Breton; NCB: northern Cape Breton; ESS: eastern Scotian Shelf; GOM: Gulf of Maine.

Table 5.2: Data sources for Atlantic cod Gadus morhua and snow crab Chionoecetes opilio abundance estimates from stock assessments. Assessment methods included sequential population analysis (SPA), catch per unit effort (CPUE) and research surveys (RS).

	Atlantic cod			**Snow crab**		
	Reference	**Data range**	**Assessment**	**Reference**	**Data range**	**Assessment**
Northern Newfoundland (NNL)	Bishop et al. 1994	1962–1994	SPA	R. J. Miller pers. comm.	1976–1980	CPUE
	Lilly et al. 2006	1995–2005	SPA	E. G. Dawe pers. comm.	1981–2007	CPUE
	Brattey et al. 2009	2006–2008	SPA	DFO 2009c	1995–2008	RS
Eastern Newfoundland (ENL)	Bishop et al. 1994	1962–1994	SPA	E. G. Dawe pers. comm.	1976–2007	CPUE
	Lilly et al. 2006	1995–2005	SPA	DFO 2009c	1995–2008	RS
	Brattey et al. 2009	2006–2008	SPA			
Southern Newfoundland (SNL)	DFO 2009g	1983–2008	RS	DFO 2007	1981–2008	CPUE
Flemish Cap (FC)	Vázquez & Cervino 2002	1972–1987	SPA	A. Vázquez pers. comm.	1988–2009	RS
	Gonzalez-Troncoso & Fernandez 2009	1988–2009	SPA			
Northern Gulf of St. Lawrence (NGSL)	DFO 2009f	1974–2009	SPA	B. Sainte-Marie pers. comm.	1985–2008	CPUE
				DFO 2009e	1996–2008	RS
Southern Gulf of St. Lawrence (SGSL)	Swain et al. 2009	1971-2009	SPA	Hébert et al. 2001	1986–2000	CPUE
				DFO 2010a	2001–2009	CPUE
				DFO 2010a	1988–2009	RS

	Atlantic cod			Snow crab		
	Reference	**Data range**	**Assessment**	**Reference**	**Data range**	**Assessment**
Western Cape Breton (WCB)	Chouinard et al. 2001	1986–2001	RS	Hébert et al. 2008	1987–2007	CPUE
	D. P. Swain pers. comm.	2002–2008	RS	DFO 2010	1993–2009	RS
Northern Cape Breton (NCB)	G. M. Fowler pers. comm.	1970–1980	RS	Biron et al. 2001	1978–1996	CPUE
	G. M. Fowler pers. comm.	1981–2007	SPA	DFO 2009b	1997–2008	CPUE
				DFO 2009b	1998–2008	RS
Eastern Scotian Shelf (ESS)	Fanning et al. 2003	1970–2002	SPA	Biron et al. 2001	1978–1996	CPUE
				DFO 2009b	1997–2008	CPUE
				DFO 2009b	1999–2008	RS
Gulf of Maine (GOM)	NEFSC 2008	1982–2007	SPA	R. W. Brown pers. comm.	1981–2008	RS

R. W. Brown pers. comm. Branch Chief, Ecosystem Surveys Branch, Northeast Fisheries Science Center, National Oceanic and Atmospheric Administration Fisheries, Woods Hole MA, USA

E. G. Dawe pers. comm. Research Scientist, Science Branch, Northwest Atlantic Fisheries Centre, Department of Fisheries and Oceans, St. Johns NL, Canada

G. M. Fowler pers. comm. Population Ecology Division, Bedford Institute of Oceanography, Department of Fisheries and Oceans, Dartmouth NS, Canada

R. J. Miller pers. comm. Emeritus Scientist, Bedford Institute of Oceanography, Department of Fisheries and Oceans, Dartmouth NS, Canada

B. Sainte-Marie pers. comm. Head and Research Scientist, Marine Invertebrate Biology and Conservation, Maurice Lamontagne Institute, Department of Fisheries and Oceans, Mont-Joli QC, Canada

D. P. Swain pers. comm. Research Scientist, Gulf Fisheries Centre, Department of Fisheries and Oceans, Moncton NB, Canada

A. Vázquez pers. comm. Instituto de Investigaciones Marinas, Consejo Superior de Investigaciones Científicas, Eduardo Cabello 6, 36208 Vigo, Spain

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

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

5.3.3. Statistical Analysis

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

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

We conducted meta-analyses at a variety of time lags to test a suite of hypotheses. It takes snow crab approximately 9 years post-settlement to moult to legal size and they recruit one year after their terminal moult (Sainte-Marie *et al.* 1995). Twelve years encompasses both the larval and embryonic life stages (Sainte-Marie 1993, Comeau *et al.* 1999). We therefore examined lags of 0 to 12 years for each species with temperature, and both positive and negative lags up to 12 years for species interactions. We explored the partial correlations by controlling for the effect of temperature at several lags (5–9 years) approximating the year of fishery recruitment. In the final analysis, we controlled for the effect of temperature at a 7-year lag, as suggested by the maximum correlation in our meta-analysis of temperature with cod and crab abundance (see Results). At positive lags (cod leading snow crab), negative correlations would suggest top-down control of cod on crab. Positive correlations (at negative or positive lags) would suggest bottom-up control by factors affecting the productivity of both species. At negative lags (snow crab leading cod), positive correlations would suggest bottom-up control, potentially by crab as prey for cod.

Recruitment among fish populations within 500 km is frequently correlated (Myers *et al.* 1997b). Therefore, we tested the sensitivity of our conclusions to potential spatial correlation by repeating our analysis after removing the data from the southern Gulf of St. Lawrence (SGSL), western Cape Breton (WCB), northern Cape Breton (NCB), and ENL, such that all remaining regions were > 500 km apart. We further tested for robustness by grouping some of the regions which demonstrated similar trends and repeating the analyses. The regional groupings tested were: (a) SGSL and NGSL, (b) Northern Newfoundland (NNL) and ENL, (c) ENL, SGSL and NNL, (d) NCB and Southern Newfoundland (SNL), (e) NCB, SNL and FC, and (f) all regions excluding the GOM and FC (i.e. using only fishery-dependent CPUE).

5.4 Results:

5.4.1. Diet Studies

A literature survey confirmed that snow crab is an important component of Atlantic cod diet (Table 1). A wide range of carapace sizes (2.2–107 mm CW) were found in Atlantic cod of 18–106 cm length. Snow crab were found in 4.5–15.4% of cod stomachs and contributed 2.1–16.5% of cod stomach content by weight (Table 1 and references therein). In cases where the ingested snow crab were measured, most were juveniles and a larger range of snow crab sizes were recorded as cod length increased. In NW Cape

Breton, 3 groups of snow crab were found in cod stomachs: juveniles were most common (ranging from 6–44 mm CW in cod 33–82 cm in length), a second group consisted of larger hard-shelled ovigerous females (49–70 mm CW in cod 67–106 cm), and a third group of mainly large soft-shelled (recently moulted) adult males (77–107 mm CW in cod 49–66 cm) (Robichaud *et al.* 1991). In the GSL most of the ingested snow crab ranged from 5 to 30 mm CW. Hard-shelled crab larger than ~60–70 mm CW may not be vulnerable to predation by Atlantic cod in the GSL (Waiwood and Elner 1982, Robichaud *et al.* 1991, Chabot *et al.* 2008). These larger hard-shelled crabs are likely not taken because they aggressively confront and may fend off even large cod (Chabot *et al.* 2008).

5.4.2. Data Trends

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

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

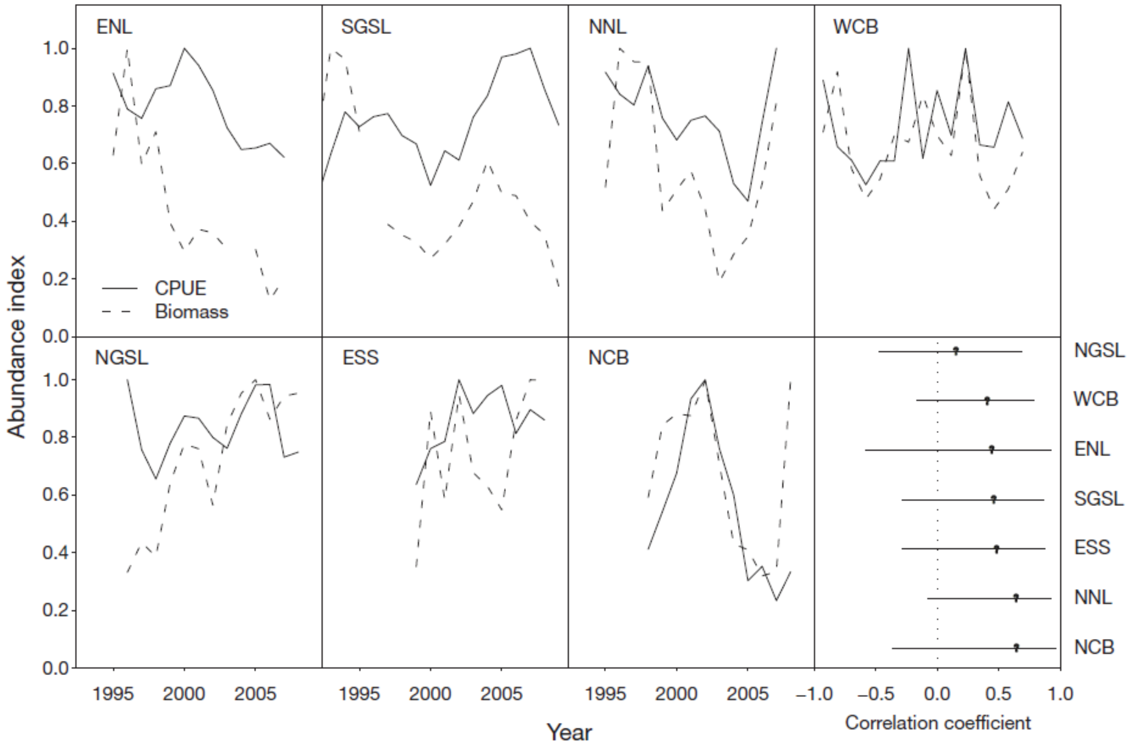

Figure 5.3. *Chionoecetes opilio* abundance estimates. We compared fishery-independent abundance indices (dashed lines) and snow crab fishery CPUE data (kg trap haul–1, solid lines). Data are scaled relative to the time series maximum. Ranges and units of the fishery-independent biomass indices vary by region: northern Newfoundland (NNL) and eastern Newfoundland (ENL), 1995 to 2006, fishable biomass of mature hard-shelled legal sized males (t); southern Gulf of St. Lawrence (SGSL), 1988 to 2009, biomass of post-fishery legal sized males (t); western Cape Breton (WCB), 1993 to 2009, biomass of postfishery legal sized males (t); northern Gulf of St. Lawrence (NGSL), 1996 to 2008, CPUE of postfishery legal sized crabs (kg trap haul–1); eastern Scotian Shelf (ESS), 1999 to 2008, fishable biomass (t); and northern Cape Breton (NCB), 1998 to 2008, fishable biomass (t). The correlation coefficients of log-transformed fishery CPUE and fishery-independent snow crab indices for each region are displayed in the lower right panel along with 95% CIs (horizontal bars) corrected for temporal autocorrelation.

5.4.3. Meta-analysis

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

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

A sensitivity analysis of data with all regions > 500 km apart did not alter these conclusions. Additional meta-analyses of separate regional groupings produced results that were remarkably consistent with the full analyses (see supplementary material in Appendix). Significant negative correlations remained at the shorter time lags (cod leading snow crab) and were consistent when the GOM and FC (fishery-independent indices) were included and excluded. One difference concerned the meta-analyses of temperature with cod. When NNL and ENL were the only regions retained in the analyses (Fig. S2, supplement), the significantly positive correlations between cod and temperature occurred at longer time lags (10 and 11 years). Similarly, when NNL, ENL, and SGSL were the only regions retained (Fig. S3), cod and temperature were significantly positive at lags of 8 to 12 years. These results may be attributed to cod maturing later in Newfoundland than in the rest of Atlantic Canada (ICES 2005).

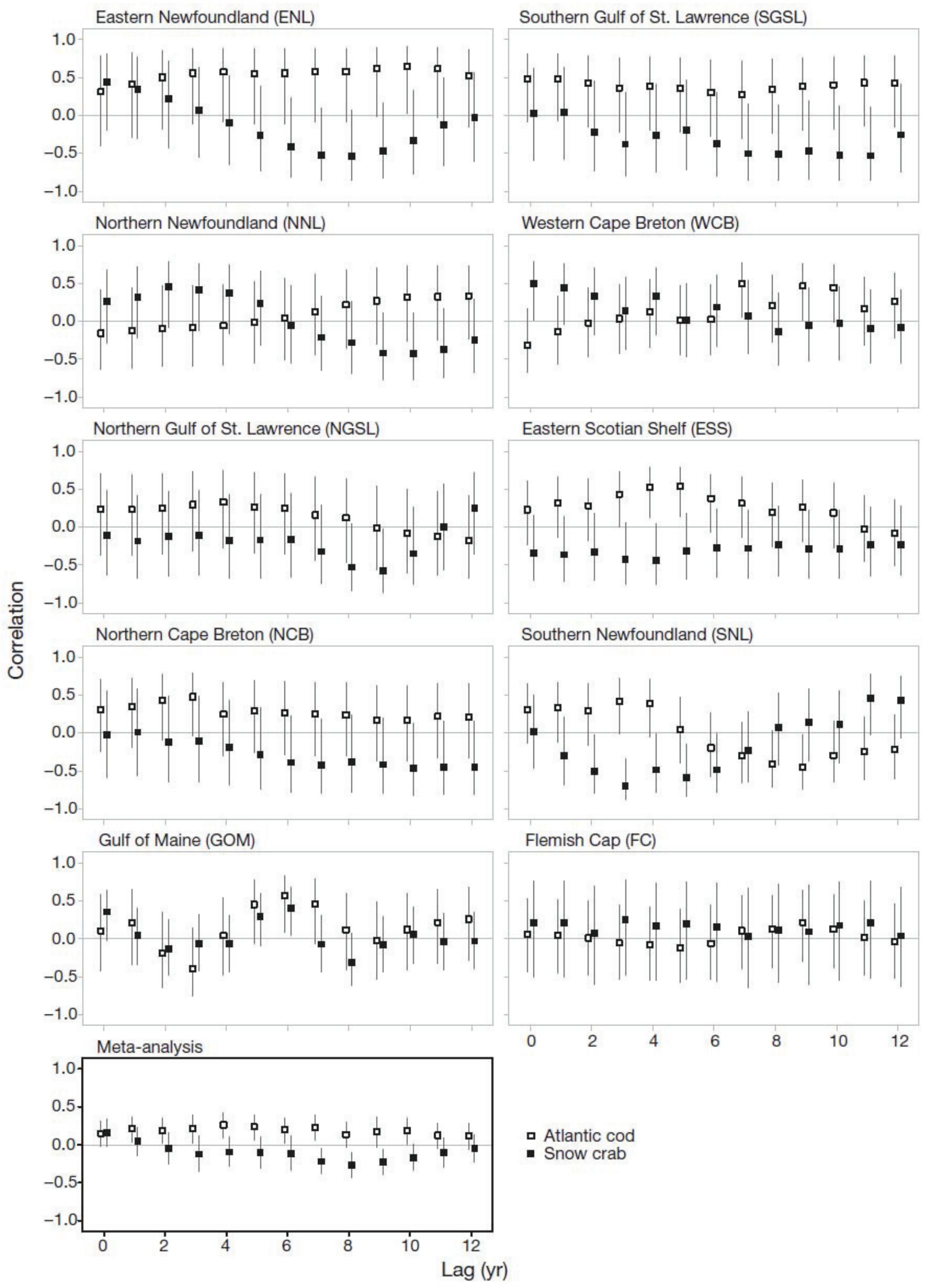

Figure 5.4. *Gadus morhua* and *Chionoecetes opilio*. Temperature analysis. Shown are the correlation coefficients at various lags between time series of temperature and Atlantic cod, and temperature and snow crab. Vertical bars illustrate 95% CIs corrected for autocorrelation. Study regions are arranged from the coldest (eastern Newfoundland) to the warmest (Flemish Cap) median water temperatures. Meta-analysis results are presented in the lower left panel. We explored lags up to 12 yr, which reflects the maximum time it takes for snow crab to recruit into the fishery.

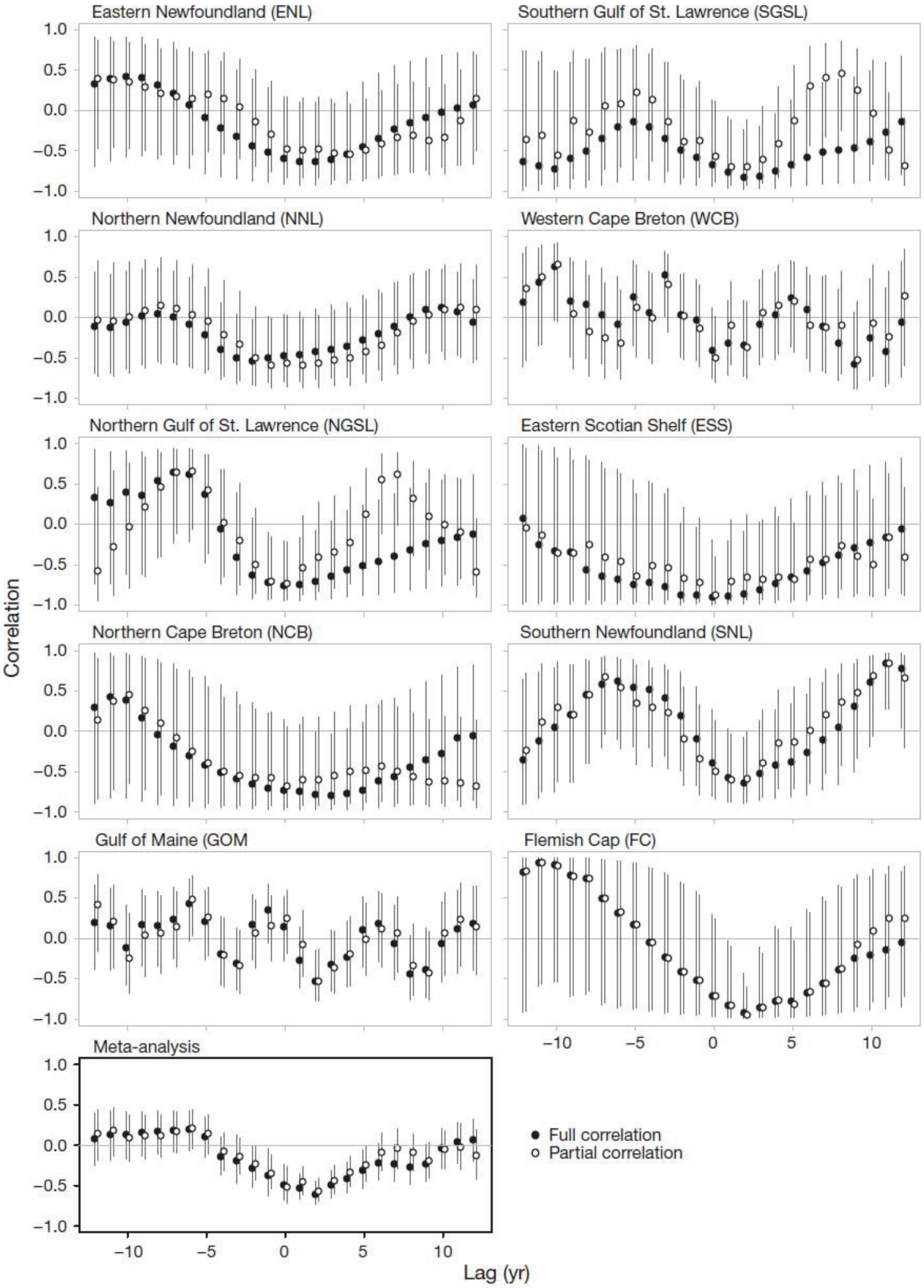

Figure 5.5. *Gadus morhua* and *Chionoecetes opilio*. Analysis of Atlantic cod–crab interactions. Shown are the full and partial correlation coefficients of snow crab biomass indices with lagged cod biomass indices, along with 95% CIs (vertical bars) corrected for autocorrelation. Study regions are arranged from the coldest (eastern Newfoundland) to the warmest water temperatures (Flemish Cap). Meta-analysis results are presented in the lower left panel. The partial correlations have been corrected for the effects of temperature at a 7 yr lag.

5.5 Discussion:

We tested 3 hypotheses examining the variation in snow crab abundance in the NW Atlantic. We present evidence that snow crab is influenced by both ocean temperature and Atlantic cod predation. Increases in crab abundance and CPUE were seen following the collapse of cod stocks. The meta-analyses suggested opposite effects of temperature on cod and snow crab, but still revealed significant negative correlations between cod and crab after accounting for the effect of temperature on each species. There was no clear evidence of a bottom-up effect of snow crab on Atlantic cod. These results suggest that both species interactions and environmental forcing play a role in regulating snow crab abundance in the NW Atlantic.

The strength of the meta-analytic correlation coefficients at different lags suggests that the effect of climate and predation on snow crab varies with life stage. Snow crab abundance was significantly negatively correlated with temperature between lags of 7 and 10 years, with the strongest correlation at a lag of 8 years (Fig. 4). This approximates the time of recruitment to the fishery, and may indicate that temperature plays a strong role in the early juvenile stages, i.e. the first 3–4 years post-settlement. All life stages of snow crab are sensitive to temperature fluctuations (Foyle *et al.* 1989, Taylor *et al.* 1993, Conan *et al.* 1996); however, early juveniles may be the most affected due to their narrow range of preferred temperatures (Dionne *et al.* 2003). Cod abundance was positively correlated with temperature at lags of 1 to 7 years, which is consistent with research demonstrating adverse effects of cold temperature on cod growth and condition (e.g. Purchase and Brown 2001, Dutil and Brander 2003).

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

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

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

Other studies provide some evidence that Atlantic cod could influence abundance of snow crab. In the SGSL, Bailey (1982) found a negative correlation between commercial-sized snow crab (landings) and the biomass of Atlantic cod at a 3–6 year lag. He suggested that snow crab were vulnerable to predation during their first 3 years post-settlement, although this result was based on short time series. A later study in the same region found a significant negative correlation (r = - 0.66) between snow crab landings and cod abundance at a lag of 10 years, yet concluded that density-dependent mechanisms were more likely responsible for the variation in snow crab abundance (Caddy *et al.* 2005). A third study reported that snow crab is vulnerable to predation by Atlantic cod for the first ~5 years post-settlement in the GSL, which could be detected in the snow crab fishery 6 to 11 years later (Chabot *et al.* 2008). On the ESS, Frank *et al.* (2005) found a strong negative correlation (r = - 0.70) between benthic fish biomass and snow crab abundance, without assuming a time lag. Further, Shackell *et al.* (2009) presented evidence that the declining individual size of predators on the Scotian Shelf could have top-down effects that are independent of changes in total biomass. The study notes that according to trawl surveys, the aggregated biomass of ‘large-bodied’ predatory fish had been stable for 4 decades while the biomass of their prey species had doubled in

11 years. Declines in predator body size largely accounted for the increase in aggregate prey biomass, suggesting a potential reduction in predator energy requirements and their maximum potential size of prey. This pattern of decline in average cod length is not unique to the Scotian Shelf and has been recorded in much of the NW Atlantic (Worcester *et al.* 2009). We note that these results from individual ecosystems could be further tested by the meta-analytic approach presented here.

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

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

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

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

C. opilio is also found in the north Pacific where researchers examined various hypotheses, including the top-down and bottom-up (climate control) mechanisms explored in the present study, to explain abundance trends for snow crab populations in Alaska, USA. Commercial crab stocks showed highly variable recruitment in Alaska, which is reflected in their population abundance (Zheng and Kruse 2006). In the eastern Bering Sea (EBS), snow crab recruitment has been weakly negatively correlated with sea surface temperature (Zheng and Kruse 2000). There is also evidence that the range of snow crab in the EBS has contracted to the north due to large-scale warming in the late 1970s, and although the water has since cooled, their range has not re-expanded south. Orensanz *et al.* (2004) suggested that currents preventing the advection of larvae to the southern EBS or predation on pre-recruits by Pacific cod *Gadus macrocephalus* might be preventing the snow crab's re-expansion. While Pacific cod prey upon snow crab (Livingston 1989), their regulatory role is also debated as Pacific cod did not emerge as a driving factor in explaining EBS snow crab recruitment variability (time lags of 0 to 4 years) (Zheng and Kruse 2000, 2006). There is therefore some evidence that bottom-up (climate forcing) and top-down (groundfish predation) mechanisms jointly control commercial crab recruitment in the EBS (Zheng and Kruse 2000, 2006, Orensanz *et al.* 2004). However, these studies were based on single time series analyses, and therefore the meta-analytic approach employed in the present analysis may be a more powerful tool to evaluate these general hypotheses by addressing the regulation of species abundances across several large marine ecosystems. We note that any meta-analytic approach represents a trade-off between generality and local detail, as individual regions may vary in their responses and averaged results may be of limited value to predict local response to changes in the environment.

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

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Chapter 6

Thesis Conclusions

6.1 Discussion:

The main objective of this thesis was to explain the marked patterns of variation in lobster and snow crab abundance in the northwest (NW) Atlantic Ocean, with an emphasis on relating temporal increases since ca. the 1980s to bottom-up (climate, temperature) and top-down (predators, fishing) forcing. In Chapter 2, I reviewed the literature to discover the roles of these and other large decapods in marine ecosystems and to glean insight into potential ecosystem effects of observed changes in some decapod populations. This chapter assessed and synthesized existing studies to describe the known ecological roles of large benthic marine decapods and to assess the wider ecosystem effects of harvesting decapods, their predators and prey. The literature revealed evidence of complex trophic and non-trophic interactions, including several examples of trophic cascades. This suggests that large decapods are not only important to fisheries, but also influential in the ecosystems in which they are embedded. In particular, lobsters were implicated in maintaining macroalgal canopy and marsh grass cover by preying on herbivores (sea urchins) or space competitors (mussels), while crabs were playing a predatory role in regulating sedimentary infauna. This information is important in the context of ecosystem management because fishing certain decapod predators can have very visible effects on structural species (‘foundation species’ *sensu* Grime 1998), with associated impacts on primary productivity, habitat provision, and other ecosystem functions.

In order to investigate changes in lobster abundance in the Gulf of Maine (Chapter 3), I interviewed 42 lobster fishermen to learn about potential changes in the inshore ecosystem that cannot be readily gleaned from offshore survey data. Results from this knowledge survey were then compared with abundance indices from offshore research trawl surveys and stomach sampling data. The fishermen reported lobsters being found increasingly in deeper waters and on soft bottom types. Eighty-three percent of the fishermen believed that the increase in lobster was mainly due to a decrease in groundfish predators that occurred at a similar time as the observed changes in lobster populations. Large-bodied groundfish such as cod, sculpin, and wolffish (all previously common in inshore NW Atlantic ecosystems) were identified as the top three predators of lobster, and it was asserted that these predators had decreased in abundance in the inshore regions that were most heavily fished for lobster. These observations were consistent with a top-down view of coastal ecosystems (Estes *et al.* 2011) whereas human predation of large predators has decreased predation pressure on their crustacean prey species, leading to large increases in crustacean abundance. This view of the inshore ecosystem were also statistically supported by offshore trawl-survey indices, which showed negative correlations between the abundance of lobster and identified groundfish predators over a wide range of plausible time lags (0–9 years). Bottom temperature did not emerge as a major driver of lobster abundance in the interviews, but fishing of lobster, and some established conservation measures in particular, were seen as important in affecting their abundance trends as well. This research suggests that local ecological knowledge can be used as an important complementary tool when investigating commercially harvested species and ecosystem change, particularly when data from those ecosystems (inshore subtidal areas) are scarce or lacking.

In Chapter 4 I directly analysed all available time-series data from the NW Atlantic region for the individual and combined effects of groundfish predation, climate (NAOI), temperature, and fishing effort (number of traps fished) on lobster abundance indices. Again there was some evidence for the predation hypothesis, particularly in Newfoundland, Nova Scotia and southern New England, where a negative association between lobsters and predators was found at short time lags (0 to 4 years). However, this mechanism was not supported for other regions. The NAO index was positively associated with lobster abundance across all regions, and the strongest correlations were found at 6–8 year lags, suggestive of a climate-driven effect on lobster recruitment. Bottom temperature overall did not emerge as a major predictor of changes in lobster abundance though, suggesting that climate forcing may be mediated by other variables (possibly in some combination with temperature). Fishing effort (tested at 0 lag) was also included in the best candidate models. The effects of effort on lobster, however, were consistently positive, which is not indicative of a top-down mechanism, but rather suggests that the number of traps has increased as lobster abundance has increased.

In Chapter 5 all available time series data was compiled to explain variation in snow crab abundance in the NW Atlantic. In a meta-analysis of partial correlation coefficients, temperature had an opposing effect on the two species: snow crab abundance was negatively correlated with temperature whereas cod and temperature were positively correlated. Controlling for the effect of temperature, the analysis revealed significant negative correlations of snow crab and cod abundance, with cod leading snow crab up to a five-year lag. Results indicate that snow crab abundance is largely influenced by temperature during early post-settlement years and becomes increasingly regulated by top-down mechanisms as fishery recruitment is approached.

Drawing from the results of the research outlined above, there is some evidence that decreases in predator populations can lead to observed increases at lower trophic levels and changes in ocean temperature and climate can affect both predators and prey, as well as the strength of their interactions. Specifically, my results suggest lobster and snow crab have been released from predation in some regions of the NW Atlantic, particularly towards the northern part of the range where groundfish stocks collapsed very suddenly in the early 1990s. These results are broadly consistent with the view that top-down control may be more prevalent in colder, boreal regions that are characterized by simpler food webs (Worm and Myers 2003, Frank *et al.* 2007). The results imply that different life stages would be vulnerable to predators, specifically the juvenile and sub-adult for snow crab, and a range of life stages for lobster. There are also differing results for the effect of temperature on lobster (little evidence) and snow crab (evidence for effects on pre-adult life stages). Lobster are less restricted by water temperature than snow crab which are limited to colder water, though changes in temperature have been shown to be very important to early life stages for both species (i.e. Aiken and Waddy 1986, Dionne *et al.* 2003). My analyses did not provide insight into the direct role of temperature on lobster abundance; however snow crab was negatively correlated with temperature at long time lags. This result reflects the importance of temperature during the early life stages of that species, which is consistent with other published evidence (Lovrich *et al.* 1995). Regional climate variability, proxied by the NAOI, however, was positively correlated with lobster abundance at longer time lags, also reflecting the importance of environmental variables during early life stages.

As for the effects of predation the sudden decline and collapse of Atlantic cod stocks has been among the largest changes observed in the NW Atlantic ecosystem, cod have never been overly abundant south of the Gulf of Maine, and the effects of predation appear less visible there. Shackell *et al.*'s (2010) hypothesis that a reduction in predator body-size, not necessarily abundance, is the mechanism releasing decapods from top-down control is an exciting new theory which warrants more exploration. A logical next step would be to examine the sizes of fish predators described in this work in relation to their capacity to ingest decapod prey.

With regards to future research on these topics, I believe the next steps would be to create or find surveys which have better spatial and temporal resolution between predators and prey in order to test, for example, when groundfish predators and moulting snow crab would overlap in space and time to determine if this directly impacts the population. Additionally, the research trawl surveys rarely cover the inshore lobster habitat and do not give an accurate representation of predator-prey relationships there. Some efforts along these lines are underway; these include for example, the Fishermen and Scientist Research Society's lobster trap survey (DFO 2006) and the deployment of passive collectors for lobster settlement in collaboration with DFO scientists. These efforts will provide important information on changes in lobster abundance and settlement in the immediate inshore region. It is also possible that over time, environmental variables (bottom-up forces) and predatory-forcing (top-down) may have changed in their relative importance. Presently there is some interest within the research community to examine this at smaller scales to gain insight into when possible shifts in dominant mechanisms have taken place (Steneck *et al*. 2004).

Much ecological research has focused on the roles of large marine, freshwater, and terrestrial vertebrate predators on ecosystem structure and processes (Estes *et al.* 2011 for an overview). I believe that there is great opportunity to broaden this perspective and include large invertebrates, which have become increasingly abundant, and presumably ecologically important, in some ecosystems. It is important both from the perspective of striving for greater understanding of lobster and snow crab populations and improving our capacity to manage fisheries, to continue uncovering the ecological interactions that involve these and other fished invertebrates, which as of yet are managed on a comparatively slim knowledge base (Anderson *et al.* 2008). In contrast to the NW Atlantic, the north Pacific Ocean currently yields low decapod abundance (king i.e. *Paralithodes camtschaticus*, and snow crab *Chionoecetes opilio*, and shrimp *Pandalus* spp.) due to population collapses in the early 1980s which were largely mediated by overexploitation (Oresanz *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 which, once altered by fishing, are better suited for supporting crustaceans (and benthic species) or large bodied groundfish, respectively (Worm *et al.* 2007). Yet, with respect to American lobsters and snow crab, there is still only sparse knowledge as to what the broader ecological consequences of increases in their populations are, and what the larger impacts of fishing these decapods in the NW Atlantic might be (see Chapter 2). For this thesis I considered it important to use all available lines of evidence, such as trends on landings, multiple survey abundance, and fishermen's ecological knowledge, across different regions. This was done in order to derive a comprehensive understanding that is founded in multiple analyses and sources of information. Yet, there remains much to be learned; for example through controlled experimental manipulations that may shed more light on underlying mechanisms of ecosystem change, something that correlative studies, such as those presented here, cannot provide. Given the present dependence on invertebrates in Canadian fisheries such further work would likely have significant pay-offs for management. In particular we should work to improve our ability to anticipate changes in stock status relative to a given suite of variables or predictors, as this would improve confidence in the sustainability of these fisheries, and support the development of robust ecosystem-based models. It is my hope that this thesis can make a contribution towards this goal.

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Appendix A: Local Ecological Knowledge Survey Questionnaire

Documenting lobster harvesters' local ecological knowledge in LFA 34 to detect ecosystem changes.

Date: ____________________

Fisherman: ________________

What is the name of the harbour or wharf from which you are currently fishing?
____

What year were you born? ______________________

What year did you start fishing for a living? ________________________

Are you currently still fishing? ____________________________

™ If no, what year did you retire? ____________________

™ What was your position when you retired? _____________________

What is the name of the vessel on which you currently fish? __________________

What is your current position on the crew? ___________________________

Which commercial fishing or harvesting licenses do you hold?

a. a lobster license
b. a snow crab license
c. other crab license
d. a marine plant license
e. an eel license
f. a herring license
g. a mackerel license
h. a groundfish license
i. none
j. no answer
k. Other:

What percentage of your income comes from lobster?

a. < 50%
b. 50%
c. 75%
d. 90%
e. 100%
f. Don't know
g. No answer

Hypothesis 1: Is temperature affecting lobster catches?

1A) In your experience has the time when the water temperature turns warm or cold changed?

1- Yes, it stays cold longer in the fishing season (spring).
2- Yes, it gets cold sooner in the season (fall).
3- Yes, it stays warmer longer (fall).
4- Yes, it gets warmer sooner (spring).
5- Yes, it has become more unpredictable when the water is going to warm up and cool down.
6- No, water temperature is always variable from one year to the next.
7- Don't know
8- No answer

Hypothesis 2: Is large-scale climate affecting lobster abundance/catches?

2A) In your experience, does wind direction and wind strength have an effect on lobster catches?

1- Yes, they increase in years with strong onshore winds
2- Yes, they increase in years with strong offshore winds
3- Yes, they decrease when there are high winds.
4- Yes, they increase when there are high winds.
5- Yes, but the increase is delayed by a few years after a year of strong onshore winds.
6- Yes, but the increase is delayed by a few years after a year of strong offshore winds.
7- No effect
8- Don't know
9- No answer

2B) In years where there are a lot of storms, do you a notice a change in lobster catches?

1- Yes, they increase
2- Yes, they go down
3- No, winter storms do not affect lobster populations
4- Don't know
5- No answer

2C) Do you think Hurricane Juan (2003) had an effect on the lobster population?

1- Yes, they have increased
2- Yes, they have decreased
3- No, there has been no change.
4- Not sure, too soon to tell.
5- Don't know
6- No answer

Hypothesis 3: Is disease affecting lobster catches?

3A) Are you concerned about disease affecting lobsters in the wild?

1- Not at all
2- Yes
3- Yes, it is already present
4- Don't know
5- No answer

3B) Have you seen evidence of disease in lobsters coming fresh out of the ocean?

1- Never
2- Very rarely (1% or less)
3- Sometimes (1-10%)
4- Quite often (>10%)
5- Don't know
6- No answer

Hypothesis 4: Are changes in groundfish or invertebrate abundance affecting lobster catches?

4A) Are you concerned that lobsters may be running out of food?

1- Yes
2- No
3- Don't know
4- No answer

4B) Do you think that you are 'farming' lobsters due to the amount of bait that is used in the fishery?

1- Yes
2- No
3- Don't know
4- No answer

4C) In your experience, when did you observe cod populations start to decline in the inshore areas?

1- Early 70s or before
2- Late 70's
3- Early 80's
4- Late 80's
5- Early 90's
6- Late 90's
7- Don't know
8- No answer

4D) Have you observed any other changes in species abundance in since 1980? Nearshore (N) < 20 nm or < 36 km from shore/ < 55 m or 30 fm? Midshore (M)?

Common Name	Increase	Decrease	No Change	Notes
Haddock				
Wolffish				
Herring				
Monkfish				
Cunner				
Pollock				
Cusk				
Silver Hake				
White Hake				
Red Hake				
Shorthorn Sculpin				
Longhorn Sculpin				
Sculpin unident.				
Spiny Dogfish				
Winter Flounder				
American Plaice				
Witch Flounder				
Flatfish unident.				
Halibut				
Mackerel				
Jonah Crab				
Rock Crab				
Green Crab				
Jellyfish				
Snow Crab				

4E) In your experience, what species are caught with lobsters the most often? Which season?

Common Name	Most Often	Fall	Spring	Notes
Cod				
Haddock				
Wolffish				
Herring				
Monkfish				
Cunner				
Pollock				
Cusk				
Silver Hake				
White Hake				
Red Hake				
Shorthorn Sculpin				
Longhorn Sculpin				
Sculpin unident.				
Spiny Dogfish				
Winter Flounder				
American Plaice				
Witch Flounder				
Flatfish unident.				
Halibut				
Mackerel				
Jonah Crab				
Rock Crab				
Green Crab				
Jellyfish				
Snow Crab				

4F) In your experience, what eats lobster?

Common Name	Perceived Predation	Observed Predation	Lobster in Fish Gut	Notes – What sized lobster in fish gut
Cod				
Haddock				
Wolffish				
Herring				
Monkfish				
Cunner				
Pollock				
Cusk				
Silver Hake				
White Hake				
Red Hake				
Shorthorn Sculpin				
Longhorn Sculpin				
Sculpin unident.				
Spiny Dogfish				
Winter Flounder				
American Plaice				
Witch Flounder				
Flatfish unident.				
Halibut				
Mackerel				
Jonah Crab				
Rock Crab				
Green Crab				
Jellyfish				
Snow Crab				

Hypothesis 5: Are changes in fishing effort influencing lobster catches?

5A) In the past 10 years have you been routinely fishing lobsters in deeper water?

1- Yes
2- No
3- Don't know
4- No answer

5B) In the past 10 years have you been finding and fishing lobster on new bottom types?

1- Yes
2- No
3- Don't know
4- No answer

5B.1) If yes, what kind?
1- Sandy
2- Cobble
3- Mud (or soft)
4- Rocky
5- Other:
6- Don't know
7- No answer

5C) If your distribution of fishing effort has changed, what is the reason?

5D) In the following time frames, how much time you spent fishing in each region:

Time frame	Nearshore <55m (30 fm) OR < 36km (20 nm) from shore	Midshore 36 km (20 nm) from shore to LFA 41	Notes
Early 1950s			
Late 1950s			
Early 1960s			
Late 1960s			
Early 1970s			
Late 1970s			
Early 1980s			
Late 1980s			
Early 1990s			
Late 1990s			
Early 2000s			

™ Don't Know
™ No Answer

5E) What was the largest lobster you ever caught? What year? Where?

Hypothesis 6: Do all of the above have something to do with the increase in lobster catches?

6A) Are you concerned that the lobster population may decline?

1- Yes
2- Yes, in the next 5 years
3- Yes, in the next 10 years
4- Yes, in the next 15 years
5- Yes, in the next 20 years
6- Not concerned
7- Don't know
8- No answer

6B) Why do you think that there are so many more lobsters in the last 20 years in LFA 34 than there has been since the 1950s?

6C) Is there anything that I've missed that you feel affects the lobster population either positively or negatively?

7) Other than yourself, who would you say knows the most about the local fishing ground?

1)
2)
3)

8) Are there any other persons currently fishing or retired from fishing who you think are very knowledgeable about the fishing ground?

1)
2)
3)
4)
5)

NOTES:

The following supplement accompanies the article

Exploring bottom-up and top-down control of snow crab abundance in the northwest Atlantic

Stephanie A. Boudreau[1]*, Sean C. Anderson[1], Boris Worm[1]

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We tested for robustness by grouping some of the regions that demonstrated similar trends and repeating the analyses. The regional groupings tested were: (a) southern Gulf of St. Lawrence and northern Gulf of St. Lawrence, (b) northern Newfoundland & Labrador and eastern Newfoundland & Labrador, (c) eastern Newfoundland & Labrador, southern Gulf of St. Lawrence, and northern Newfoundland & Labrador, (d) northern Cape Breton and southern Newfoundland & Labrador, (e) northern Cape Breton, southern Newfoundland & Labrador and Flemish Cap, and (f) all regions excluding the Gulf of Maine and Flemish Cap (i.e. using only fishery-dependent CPUE).

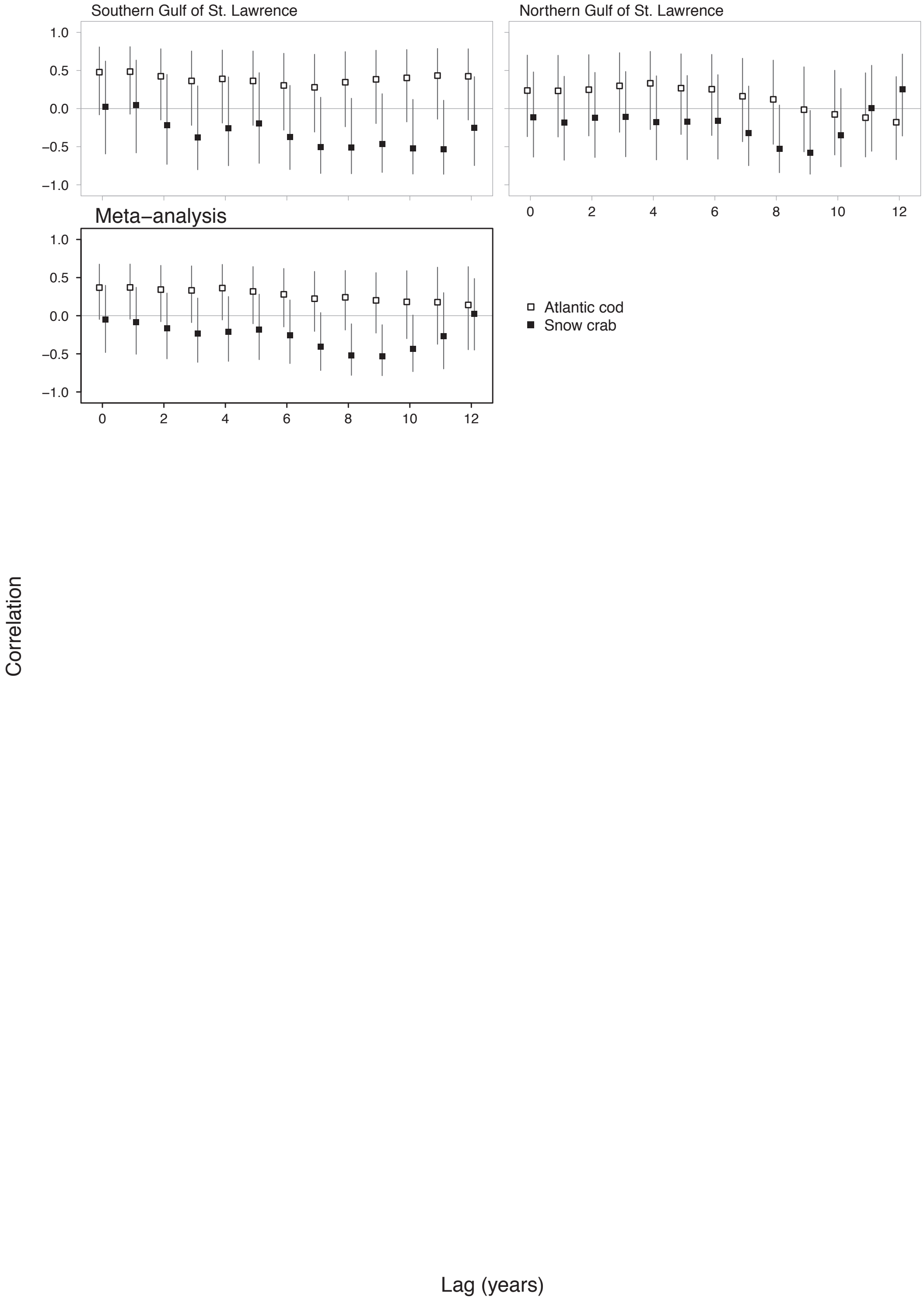

Figure S1: Temperature analysis **for southern and northern Gulf of St. Lawrence only**. Shown are the correlation coefficients at various lags between time series of temperature and Atlantic cod (open squares), and temperature and snow crab (closed squares). Error bars illustrate 95% confidence intervals corrected for autocorrelation. Meta-analysis results are presented in the final panel.

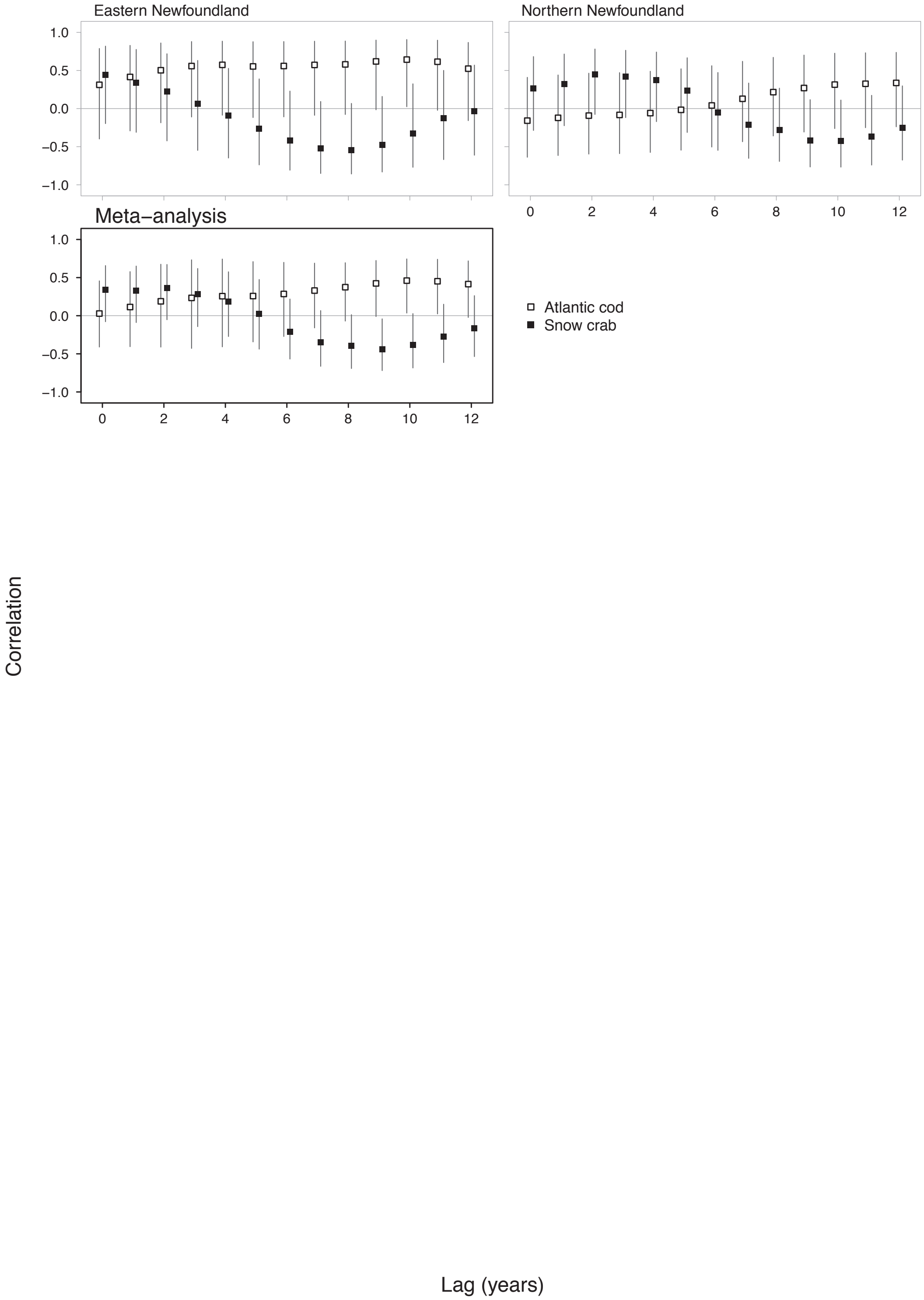

Figure S2: Temperature analysis **for eastern and northern Newfoundland only**. Shown are the correlation coefficients at various lags between time series of temperature and Atlantic cod (open squares), and temperature and snow crab (closed squares). Error bars illustrate 95% confidence intervals corrected for autocorrelation. Meta-analysis results are presented in the final panel.

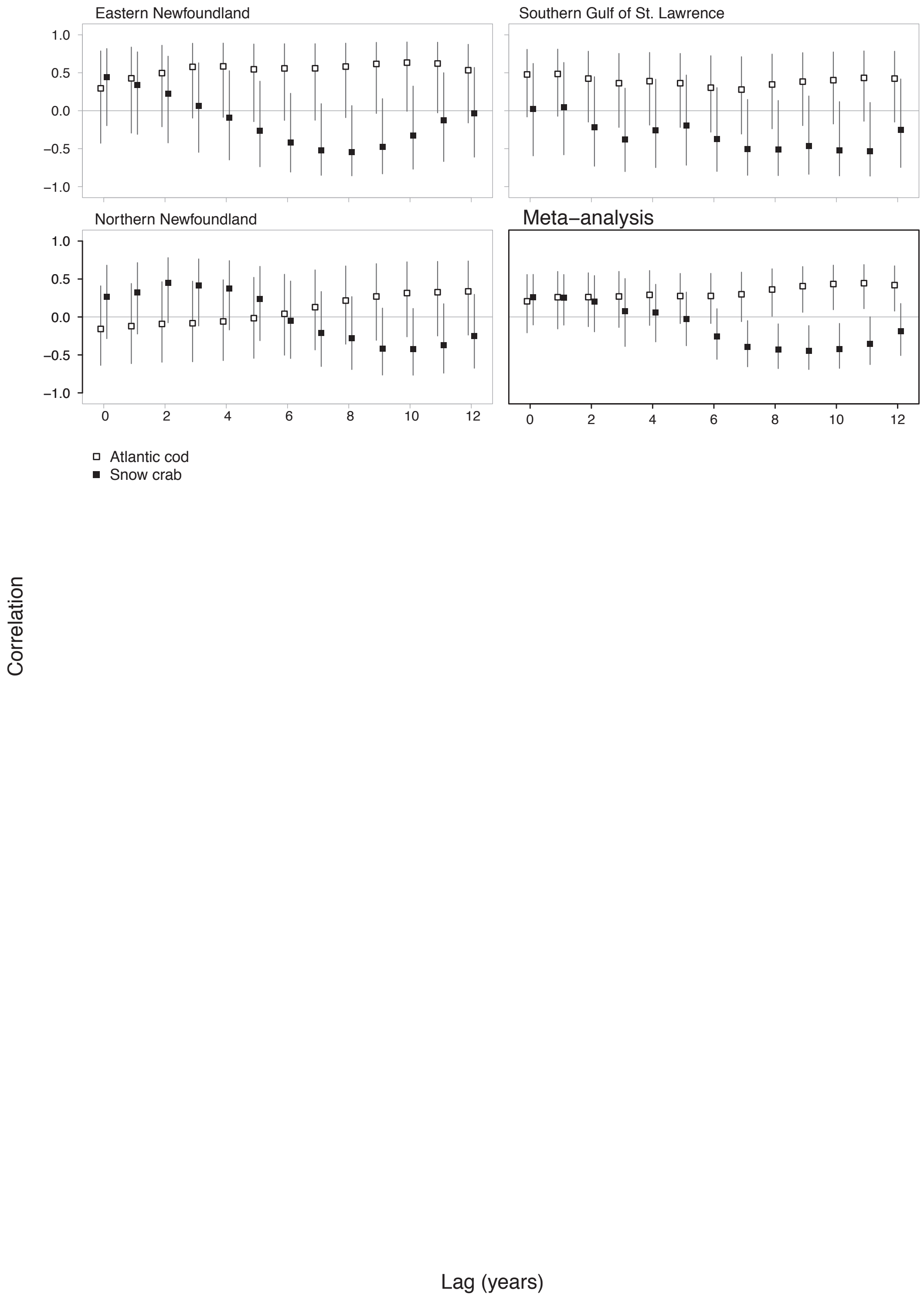

Figure S3: Temperature analysis **for eastern Newfoundland, southern Gulf of St. Lawrence, and northern Newfoundland only**. Shown are the correlation coefficients at various lags between time series of temperature and Atlantic cod (open squares), and temperature and snow crab (closed squares). Error bars illustrate 95% confidence intervals corrected for autocorrelation. Meta-analysis results are presented in the final panel.

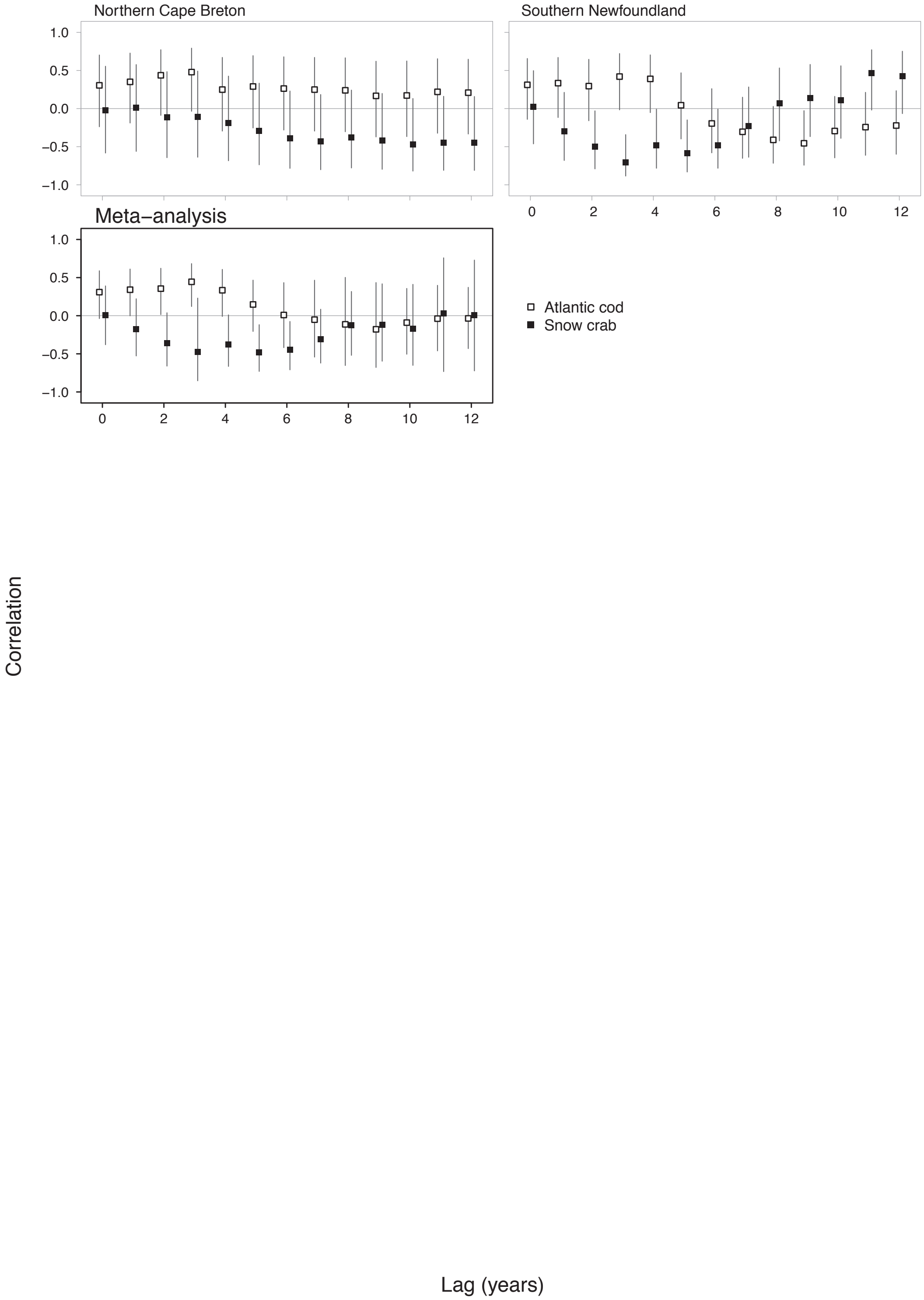

Figure S4: Temperature analysis **for northern Cape Breton and southern Newfoundland only**. Shown are the correlation coefficients at various lags between time series of temperature and Atlantic cod (open squares), and temperature and snow crab (closed squares). Error bars illustrate 95% confidence intervals corrected for autocorrelation. Meta-analysis results are presented in the final panel.

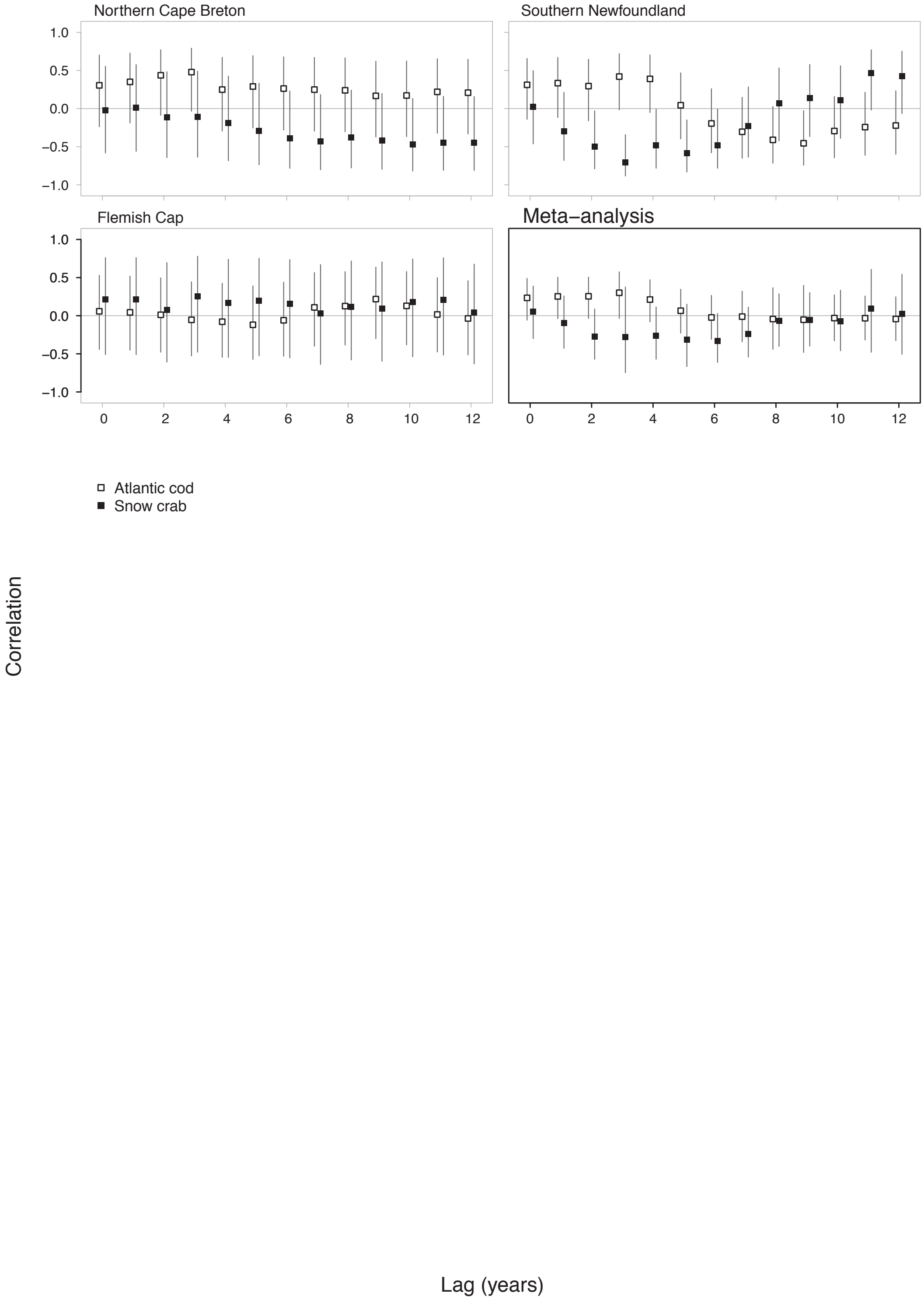

Figure S5: Temperature analysis **for northern Cape Breton, southern Newfoundland, and Flemish Cap only**. Shown are the correlation coefficients at various lags between time series of temperature and Atlantic cod (open squares), and temperature and snow crab (closed squares). Error bars illustrate 95% confidence intervals corrected for autocorrelation. Meta-analysis results are presented in the final panel.

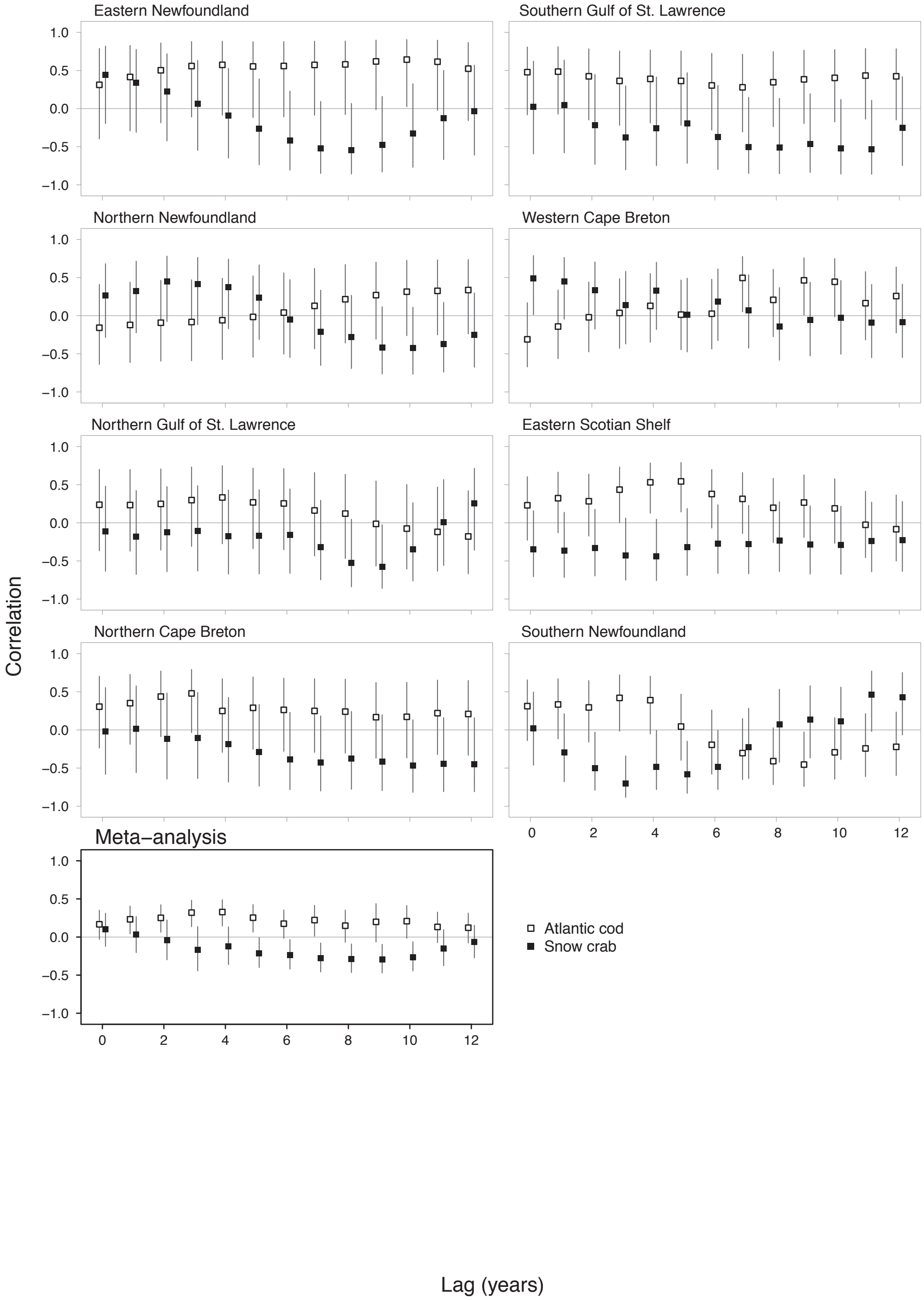

Figure S6: Temperature analysis **for all regions except Flemish Cap and Gulf of Maine**. Shown are the correlation coefficients at various lags between time series of temperature and Atlantic cod (open squares), and temperature and snow crab (closed squares). Error bars illustrate 95% confidence intervals corrected for autocorrelation. Meta-analysis results are presented in the final panel.

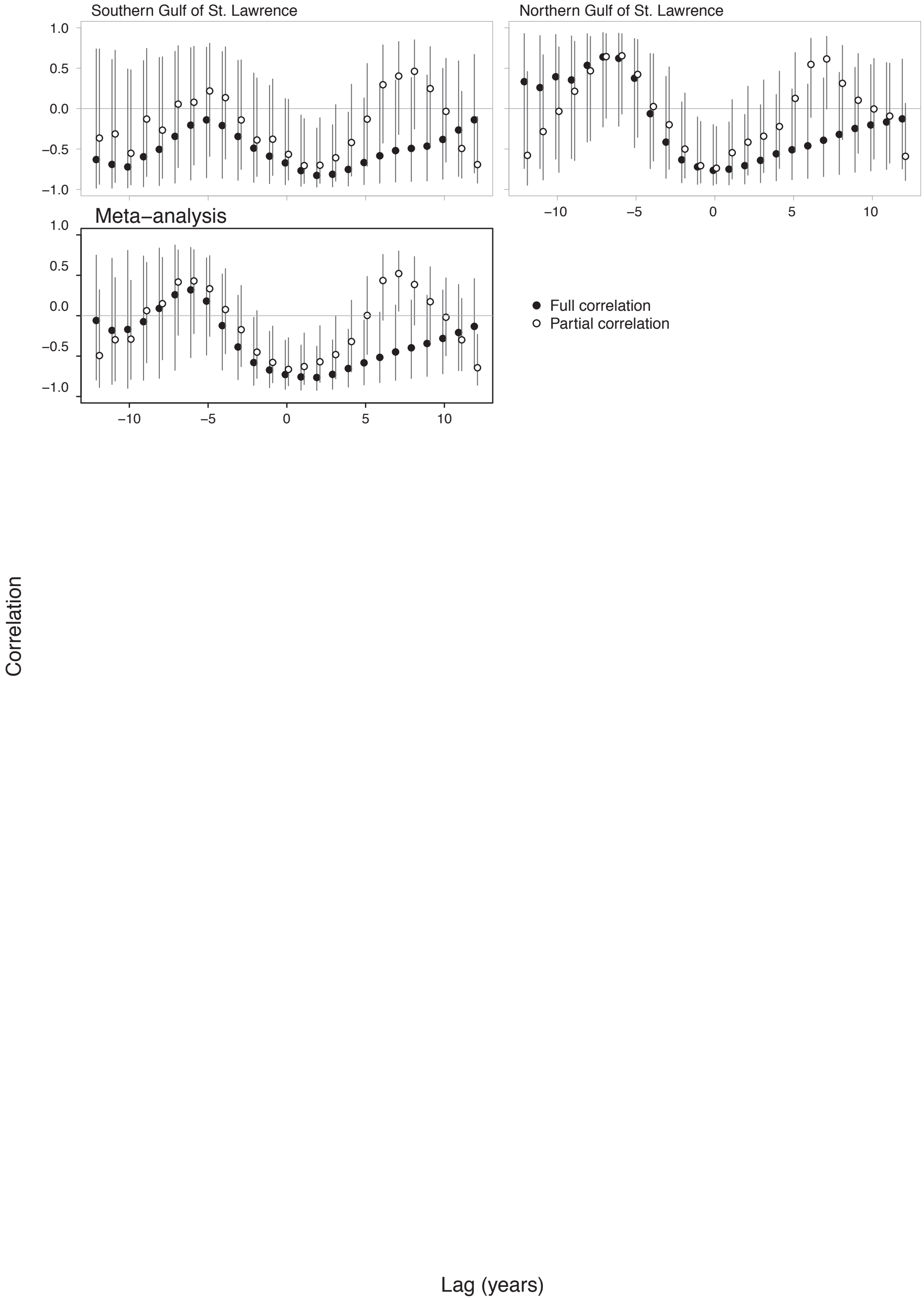

Figure S7: Analysis of cod-crab interactions **for southern and northern Gulf of St. Lawrence only**. Shown are the full (closed circles) and partial (open circles) correlation coefficients of snow crab biomass indices with lagged cod biomass indices, along with 95% confidence intervals corrected for autocorrelation. Meta-analysis results are presented in the final panel. The partial correlations have been corrected for the effects of temperature at a 7-year lag.

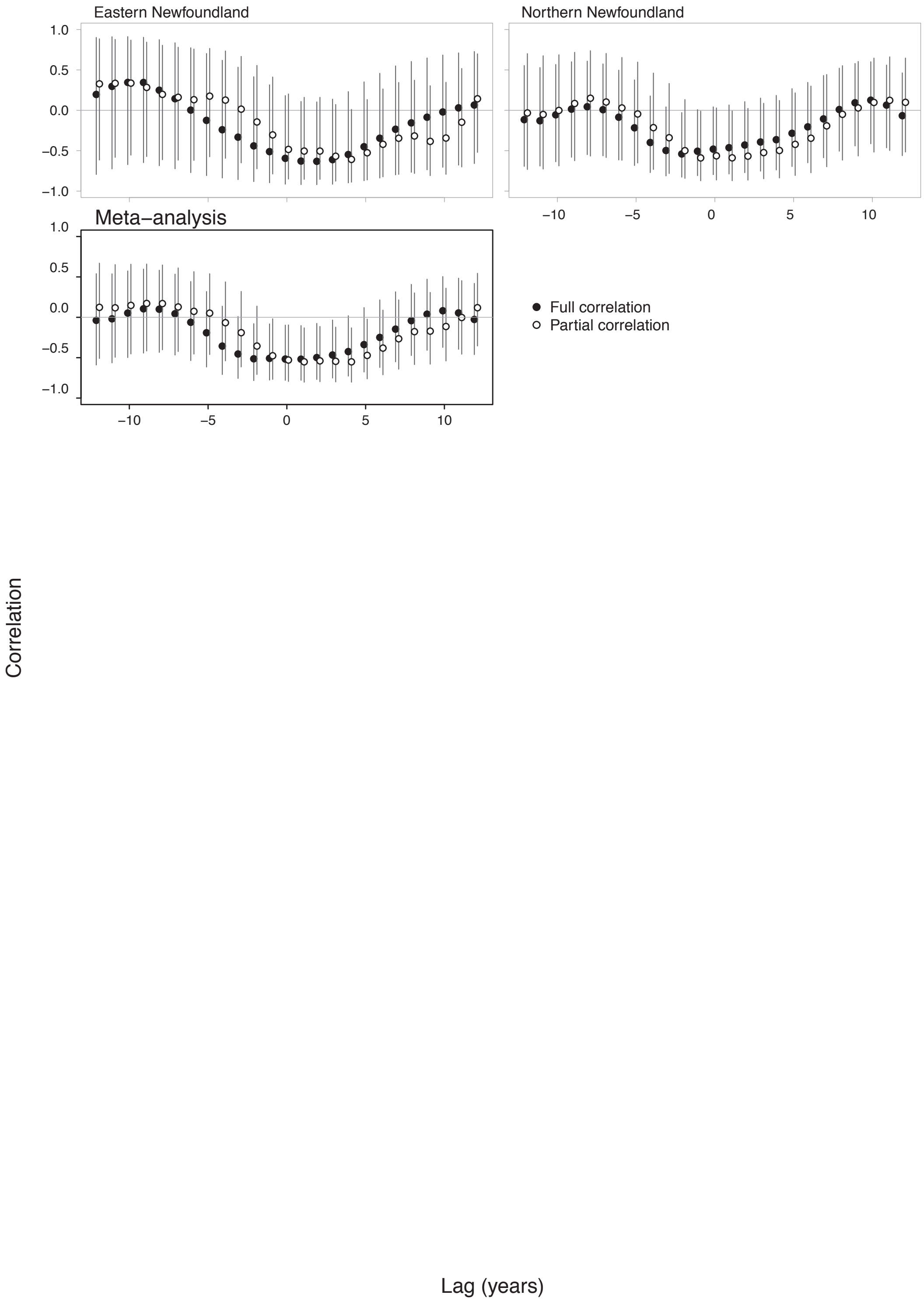

Figure S8: Analysis of cod-crab interactions **for eastern and northern Newfoundland only**. Shown are the full (closed circles) and partial (open circles) correlation coefficients of snow crab biomass indices with lagged cod biomass indices, along with 95% confidence intervals corrected for autocorrelation. Meta-analysis results are presented in the final panel. The partial correlations have been corrected for the effects of temperature at a 7-year lag.

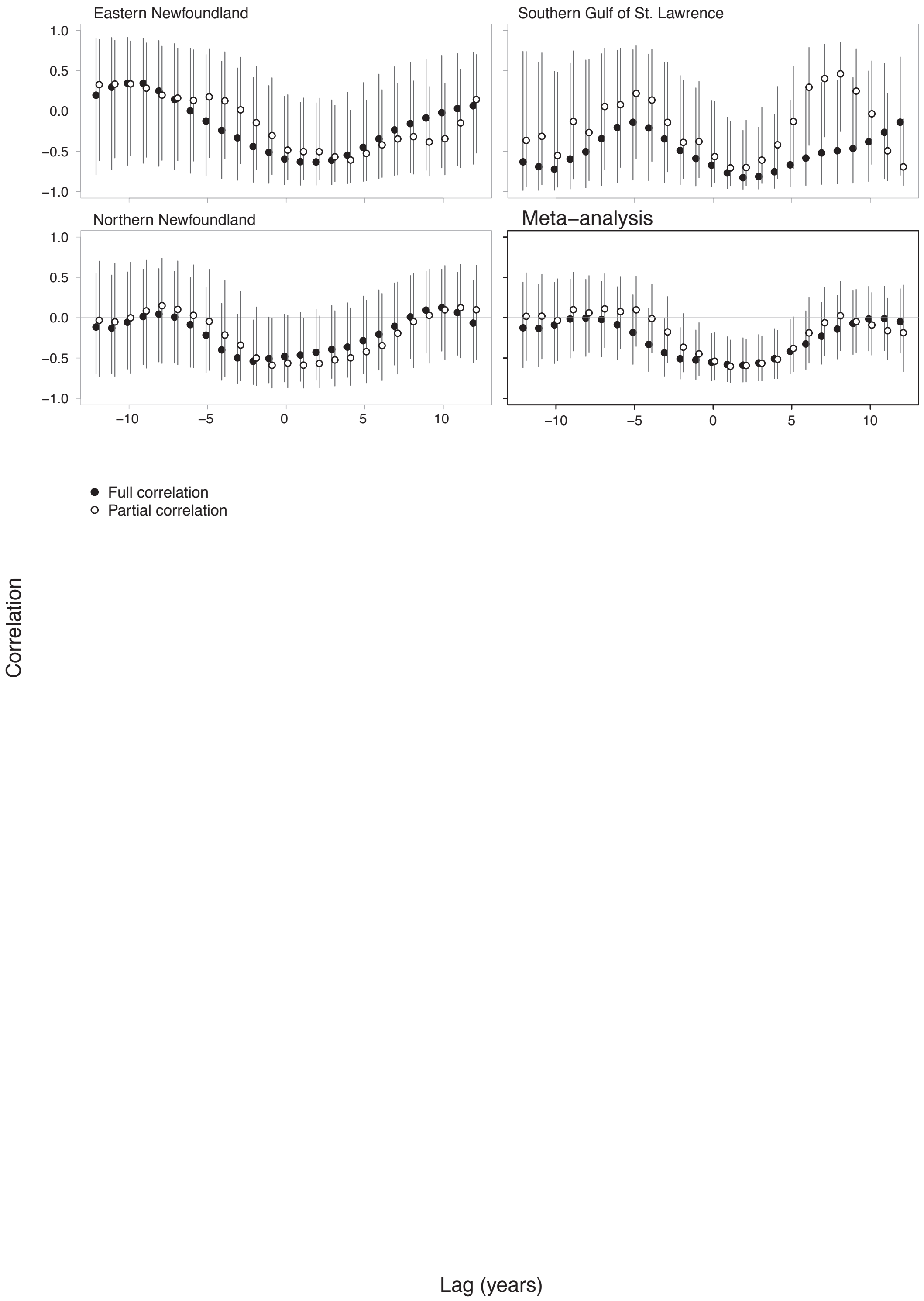

Figure S9: Analysis of cod-crab interactions **for eastern Newfoundland, southern Gulf of St. Lawrence, and northern Newfoundland only**. Shown are the full (closed circles) and partial (open circles) correlation coefficients of snow crab biomass indices with lagged cod biomass indices, along with 95% confidence intervals corrected for autocorrelation. Meta-analysis results are presented in the final panel. The partial correlations have been corrected for the effects of temperature at a 7-year lag.

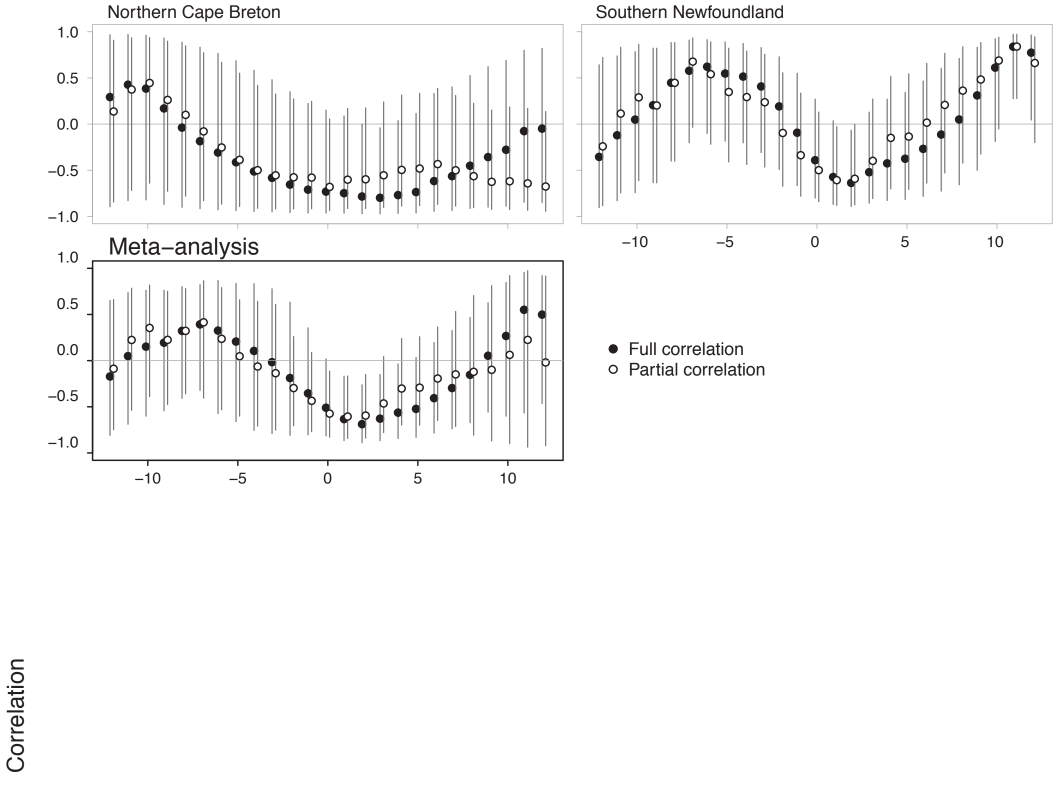

Figure S10: Analysis of cod-crab interactions **for northern Cape Breton and southern Newfoundland only**. Shown are the full (closed circles) and partial (open circles) correlation coefficients of snow crab biomass indices with lagged cod biomass indices, along with 95% confidence intervals corrected for autocorrelation. Meta-analysis results are presented in the final panel. The partial correlations have been corrected for the effects of temperature at a 7-year lag.

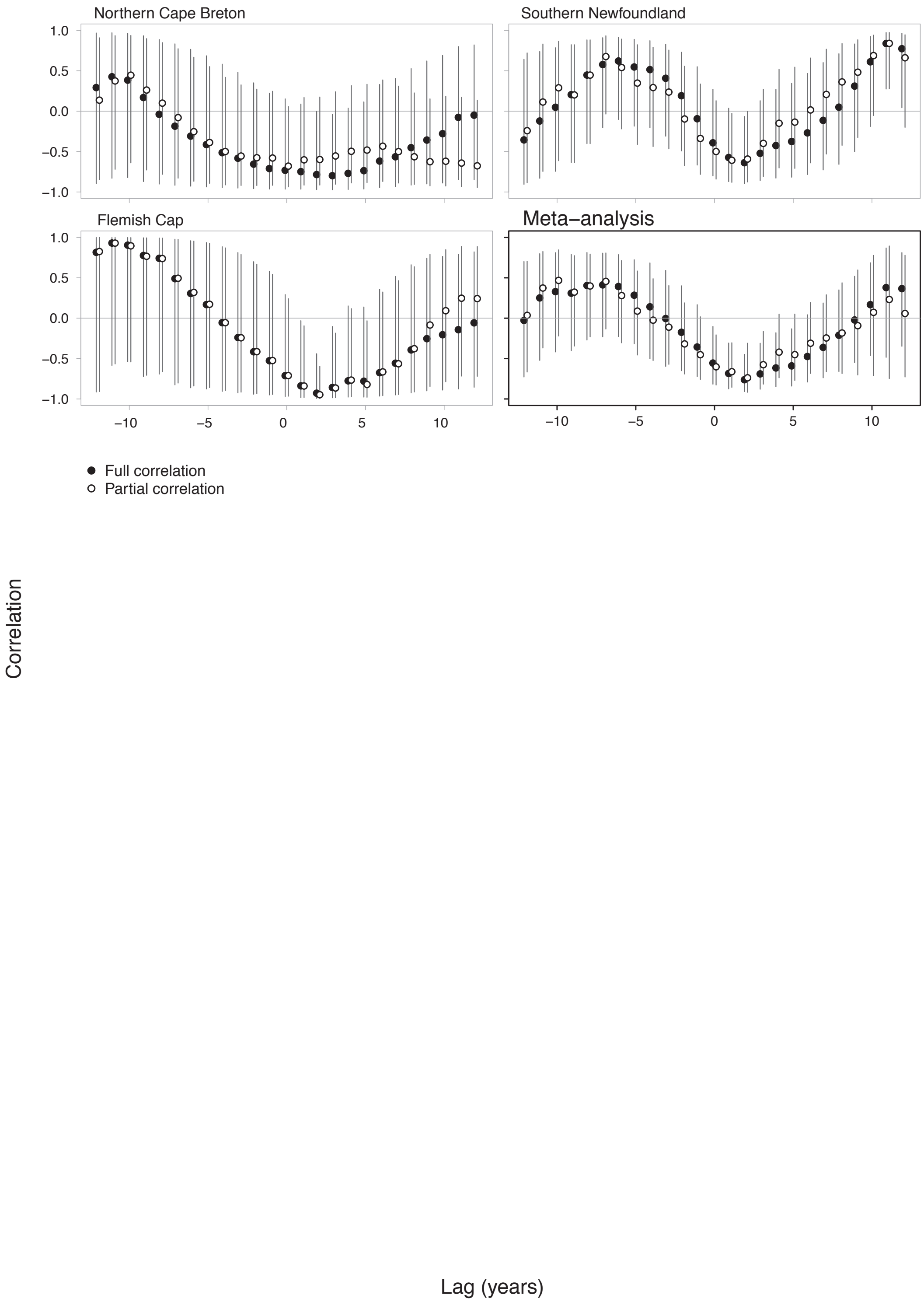

Figure S11: Analysis of cod-crab interactions **for northern Cape Breton, southern Newfoundland, and Flemish Cap only**. Shown are the full (closed circles) and partial (open circles) correlation coefficients of snow crab biomass indices with lagged cod biomass indices, along with 95% confidence intervals corrected for autocorrelation. Meta-analysis results are presented in the final panel. The partial correlations have been corrected for the effects of temperature at a 7-year lag.

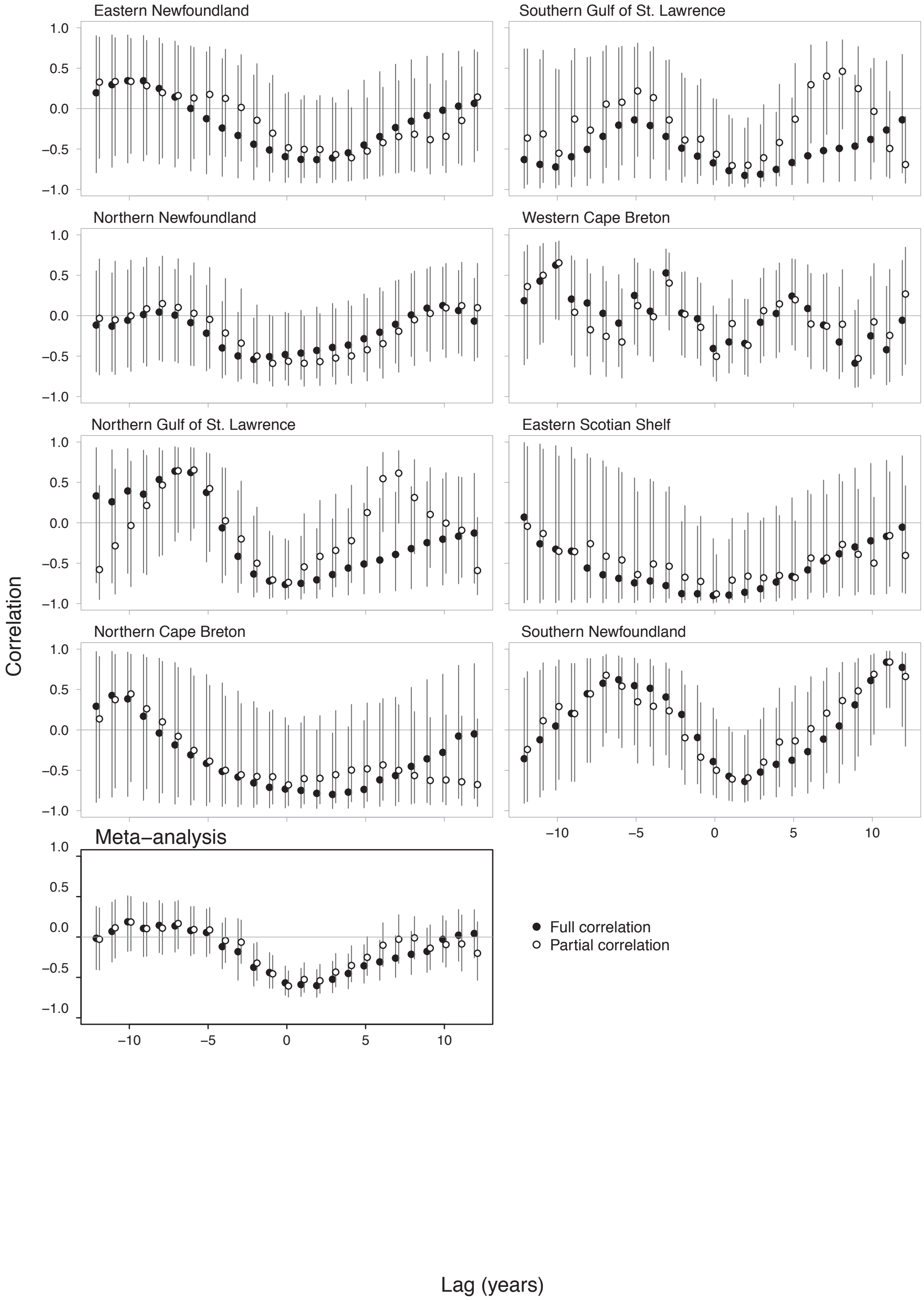

Figure S12: Analysis of cod-crab interactions **for all regions except Flemish Cap and Gulf of Maine**. Shown are the full (closed circles) and partial (open circles) correlation coefficients of snow crab biomass indices with lagged cod biomass indices, along with 95% confidence intervals corrected for autocorrelation. Meta-analysis results are presented in the final panel. The partial correlations have been corrected for the effects of temperature at a 7-year lag.

Appendix C: Copyright Agreement Letter

Subject: Re: ms, copyright permissions
From: Marita Bruns <marita@int-res.com>
Date: 23/11/2011 6:15 AM
To: Stephanie Boudreau <S.Boudreau@dal.ca>

Dear Dr. Boudreau,

We herewith give publisher permission for you to use the articles mentioned below in your PhD thesis, provided proper acknowledgement is being made to the original source of publication.

Kind regards
Marita Bruns
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(1) Boudreau SA, Worm B
Top-down control of lobster in the Gulf of Maine: insights from local ecological knowledge and research surveys
MEPS 403:181-191
(2) Boudreau SA, Anderson SC, Worm B
Top-down interactions and temperature control of snow crab abundance in the northwest Atlantic Ocean
MEPS 429:169-183
(3) Stephanie A. Boudreau, Boris Worm
The ecological role of large benthic decapods in marine ecosystems
under review (# 20111020)