The roles of capelin, climate, harp seals and fisheries in the failure of 2J3KL (northern) cod to recover

by

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Abstract

The Atlantic cod (*Gadus morhua*) fishery sustained the way of life of Newfoundlanders during centuries. Its collapse in the early 1990s represented a socio-economic and cultural crisis. Despite the fishing moratorium imposed in 1992, the northern cod stock (NAFO Divs 2J3KL) is still a shadow of its former self. Several hypotheses have been offered to explain this lack of recovery, many involving ecological interactions between harp seals (*Pagophilus groenlandicus*) and cod. However, these contentions are based on indirect evidence, while formal assessments are lacking. Availing of long term data series, I addressed the two simplest ways in which harp seals might impede cod's recovery: predation and competition for food resources, particularly for the major forage fish in the system: capelin (*Mallotus villosus*). I found no supporting evidence for either hypothesis. The biomass dynamics of northern cod during the period 1985-2007 were driven by an interplay between fisheries removals and food (capelin) availability, and potentially affected by water temperature. Harp seal predation was not an important driver of the stock. I provide evidence that a regime shift occurred on the Newfoundland and Labrador Shelf ecosystem during the early 1990s, linking community reorganization to physical perturbations. The capelin stock is regulated by bottom-up processes: ocean climate and the regime shift, acting via food availability. I found also that Atlantic cod did not change its diet following the regime shift. In addition, the diet of Atlantic cod overlapped to a greater extent with the diet of Greenland halibut than with harp seals' diet. These findings constitute mounting evidence against the consumptive competition hypothesis. The results presented in this thesis are important for the development of ecosystem approaches to fisheries management and raise questions as to the potential impacts of climate change on the structure and productivity of the Newfoundland and Labrador Shelf marine ecosystem. Also, this suggests that reductions in the harp seal population are unlikely to enhance the rebuilding of the northern cod stock; management efforts should be focused on protecting cod itself and the lower trophic levels.

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Chapter 1

Introduction

Most marine ecosystems can be considered perturbed, and many of their resources are often subject to exploitation rates beyond sustainability (Hilborn et al., 2003). Although overfishing is pervasive, the impact of human activities goes beyond target species; the entire system is impacted by exploitation. These systemic perturbations have altered, sometimes in conjunction with long term environmental variability and change, the structure of many marine communities.

Atlantic Canada's marine ecosystems (Figure 1.1) are good examples of such changes; during the 1990s the composition of the fish communities across the Eastern Scotian Shelf (Northwest Atlantic Fisheries Organization (NAFO) Divisions 4VW), southern (NAFO Divisions 4T) and northern Gulf of St. Lawrence (NAFO Divisions 4RS) and in the Newfoundland and Labrador Shelf (NAFO Divisions 2J3KL) changed from being dominated by large-bodied demersal fish to being dominated by small demersal and pelagic fish species and benthic macroinvertebrates (Gomes et al., 1995;

Haedrich and Barnes, 1997; Rice, 2002; Worm and Myers, 2003; Lilly et al., 2003; Choi et al., 2005; Koen-Alonso et al., 2006; Savenkoff et al., 2007; Benoît and Swain, 2008). Given the decline of large piscivorous fish, that humpback and fin whales have increased 3 to 4 % over the last 2 to 3 decades (J. Lawson, pers. comm.), and the concurrent increases in the large populations of grey (*Halichoerus grypus*) and harp seals (*Pagophilus groenlandicus*) off the coasts of eastern Canada (Hammill and Stenson, 2011; Thomas et al., 2011; Hammill et al., 2013), marine mammals have become prominent predators in these systems.

Particularly noticeable were the collapses of six Atlantic cod (*Gadus morhua*) stocks throughout Atlantic Canada (Myers et al., 1997). The northern cod stock (NAFO Divisions 2J3KL) was the largest of these stocks and had supported a large commercial fishery since the 16^{th} Century. A fishing moratorium was put in place in July 1992, following the stock collapse. Despite the severely reduced fishing the stock has experienced in the last 20 years, it has not recovered to its former levels due to the high levels of mortality the offshore component of the stock has experienced (DFO, 2008*b*). A plethora of hypotheses have been proposed to explain this high level of mortality (summary in DFO, 2009) including direct (predation) and indirect effects (competition for food resources) of harp seals on cod. However, claims as to the role of harp seals on the non-recovery of the northern cod are usually made on the basis of lack of evidence to explain the high mortality via other mechanisms (e.g. DFO, 2003*a*,*b*).

1.1 Newfoundland-Labrador Shelf Ecosystem and Species Background

The Newfoundland-Labrador Shelf Ecosystem is a sub-Arctic system whose dynamics are strongly influenced by the cool waters of the Labrador Current and by the seasonal sea ice that drifts into the system in winter. The system is moderately productive, with a major pulse occurring in spring and a reduced peak in the autumn. The system may be characterized as species poor, with the dominant species achieving large abundances. The calanoid copepods *Calanus finmarchicus*, *C. glacialis* and *C. hyperboreus* are key secondary producers in the region (Pepin et al., 2011) and represent important prey for forage fish (e.g. O'Driscoll et al., 2001). The most numerous fish species in the system have historically been Atlantic cod and capelin (*Mallotus villosus*) (Bundy et al., 2000). Arctic cod (*Boreogadus saida*) and sandlance (*Ammodytes* sp.) are also important forage species (Bundy et al., 2000). Since the 1980s, Greenland halibut (*Reinhardtius hippoglossoides*) has gained importance in the system (Link et al., 2011*a*). The most abundant marine mammals are by far the harp seals (Hammill and Stenson, 2011; Thomas et al., 2011; Hammill et al., 2013), while hooded seals (*Cystophora cristata*) are also numerous (Stenson and Hammill, 2006). Among the large cetaceans the migratory pilot (*Globicephala melas*), fin (*Bal-*

aenoptera physalus) and humpback (*Megaptera novaeangliae*) whales are the most abundant (Lawson and Gosselin, 2009). Large numbers of seabirds inhabit the system year-round, or seasonally, e.g. Leach's storm-petrels (*Oceanodroma leucorhoa*), common murres (*Uria aalge*), northern gannets (*Morus bassanus*), Atlantic puffins (*Fratercula arctica*), dovekies (*Alle alle*), northern fulmar (*Fulmarus glacialis*) (Montevecchi, 2014).

1.1.1 Capelin

Capelin is a small (maximum recorded length: 25 cm), short-lived (rarely exceeds 5 years of age), pelagic schooling fish with a circumpolar distribution in Arctic and sub-Arctic regions (Vilhjálmsson, 1994). It is an energetically rich forage fish (Lawson et al., 1998), and it acts as a link between zooplankton and large vertebrates (i.e. marine birds, mammals and large fish) in the Newfoundland-Labrador Shelf Ecosystem (Lavigne, 1996). Capelin feed in the fall building up their somatic lipid reserves which reach their maximum at the end of the year (Montevecchi and Piatt, 1984). Copepods, mainly *Calanus finmarchicus*, are the most important prey species for capelin in the Northwest Atlantic (Gerasimova, 1994; O'Driscoll et al., 2001). During the winter period (January-March), capelin do not feed and are concentrated in large, inactive schools in cold water (Winters, 1970). During spring, they resume feeding, mature rapidly and undergo extensive migrations from offshore feeding grounds to inshore areas and northward along the coast to spawning areas (Nakashima, 1992), during which time they are fed upon by migrating Atlantic cod (Rose, 1993). During the summer, capelin spawn along the Newfoundland and Labrador coasts, on beaches (Templeman, 1948; Jangaard, 1974) or on demersal spawning sites (Templeman, 1948; Davoren et al., 2006). Post-spawning capelin have a low survival rate (Templeman, 1948; Jangaard, 1974; Shackell et al., 1994), with female survival possibly a little higher than that of males (Shackell et al., 1994).

1.1.2 Atlantic cod

Atlantic cod is widely distributed in shelf ecosystems of the North Atlantic. It has historically been the dominant large predatory fish in much of its range. The northern cod stock was the largest Canadian cod stock and one of the largest in the world along with the Icelandic and Barents Sea cod. Cod are a long-lived species (they may live for 25 years), and exhibiting continuous body growth, they can attain very large sizes (up to 200 cm total length and 96 kg body weight). Cod eats an array of prey species although it usually relies upon energy rich prey to sustain large investments in growth and reproduction. In temperate ecosystems (e.g. the North Sea and the Gulf of Maine) this prime prey is generally Atlantic herring (*Clupea harengus*), while in colder systems this prey is capelin. Maturation in Newfoundland waters usually occurred around 6 years of age, with most 7-year old individuals being mature. Since the early 1990s, however, this pattern has shifted toward younger ages, with most fish being mature by age 6 (Lilly et al., 2003). The northern cod stock mostly spawns in relatively warm waters ($2 - 4\,^{\circ}$C) of the offshore Banks. Prior to spawning (i.e. during winter) cod are densely aggregated in offshore areas. In spring the aggregations undergo spawning migrations along warm water trenches toward inshore areas, while following and feeding on the capelin spring spawning migration (Rose, 1993). After spawning cod must replenish its energy reserves; aggregations in the offshore move shoreward, and inshore aggregations seaward, in search of capelin.

1.1.3 Harp seal

The harp seal is the most abundant pinniped species in the Northern Hemisphere. It is a medium-sized, monomorphic seal. Although weight varies seasonally (Chabot and Stenson, 2002), adults weight about 130 kg just prior to the breeding season. The harp seal is widely distributed throughout the North Atlantic and Arctic oceans (Sergeant, 1991). There are 3 populations, each of which uses specific breeding grounds: Barents Sea/White Sea in the White Sea (Russia), Greenland Sea off eastern Greenland (north of Jan Mayen Island) and the most numerous of the three, the Northwest Atlantic. It is a pagophilic (ice loving) species, it requires ice for a critical period of its life cycle. The Northwest Atlantic population summers in the Canadian Arctic and during winter they migrate south along the Labrador coast to whelp (pup) at the "Front" (southern Labrador and northeast Newfoundland) and in the Gulf of St Lawrence. They remain in the area until after moulting, which occurs shortly after the mating period in the spring. Harps seals consume a wide range of prey species. In the Northwest Atlantic, their main prey are pelagic fish such as Arctic cod and capelin. They also consume large amounts of invertebrates such as shrimp (*Pandalus* spp.). Although Atlantic cod represents a minor portion of their diet, there have been speculations that, given the large population, its consumption may be enough to produce a marked impact on the depressed cod stocks off Atlantic Canada.

1.1.4 Major changes to the ecosystem in the early 1990s

Rapid and drastic changes occurred in marine ecosystems off Atlantic Canada during the late 1980s and early 1990s; Atlantic cod and other groundfish stocks collapsed throughout the eastern seaboard.

The Newfoundland and Labrador marine ecosystem, in particular, underwent a major restructuring. The decline of the northern cod was particularly acute; compared to the maximum estimates for which data are available, at the time of the collapse spawner biomass had declined 99% (Myers et al., 1997), leading to a 20-year period of severely reduced fishing effort. The collapse has been attributed to overfishing by some authors (e.g. Hutchings and Myers, 1994), although others have speculated that climate effects have played a role too (Rose et al., 2000; Drinkwater, 2002; Halliday and Pinhorn, 2009). During the late 1980s and early 1990s the water temperature was the coldest in 40 years, reaching their lowest values in 1991 (Drinkwater, 1996). Concurrently, most commercial and many non-commercial demersal species also declined (Gomes et al., 1995; Haedrich and Barnes, 1997; Rice, 2002; Koen-Alonso et al., 2006) while some shellfish species increased in abundance (Lilly et al., 2003; Worm and Myers, 2003). Some demersal predatory fish species such as Atlantic cod and Greenland halibut changed their diets during the mid-1990s to include a larger proportion of invertebrate prey (Dwyer et al., 2010; Dawe et al., 2012). There was also a major reduction in capelin biomass in 1991, from which the stock has not recovered (DFO, 2010). In addition to this reduction in biomass, its spawning was delayed up to four weeks and protracted (Nakashima and Wheeler, 2002; DFO, 2010). Size and age at maturity, and somatic condition were reduced (Carscadden and Nakashima, 1997; Carscadden and Frank, 2002) and distribution shifted to occupy deeper waters (Mowbray, 2002) and a southward expansion (Frank et al., 1996; Carscadden and Nakashima, 1997). Over the past decades, the harp seal population grew from circa 2 million individuals in the mid-1970s to circa 7 million in the late 2000s (Hammill et al., 2013). Changes in seabird diets, phenology and populations in the NW Atlantic have been recorded in concert with oceanographic and food web changes (Gaston et al., 2009).

Although overfishing and likely climate change were partly responsible for some of the changes observed in the system (Rice, 2002), the reasons behind this major rearrangement are still not fully understood.

1.2 History of exploitation of marine resources in Newfoundland and Labrador

The history of exploitation of marine resources in Newfoundland and Labrador has been described by Lear (1998), Sergeant (1991), and Rose (2007). Exploitation of marine resources in waters off Newfoundland commenced shortly after John Cabot came upon vast cod stocks on the Grand Banks and the Newfoundland Shelf in 1497. Fishing in Newfoundland has meant for centuries fishing for Atlantic cod. Cod are simply referred to as "fish".The early history of exploitation was marked by intermittent eras of fishing and dispute among the Portuguese, French, Spanish and British fleets. Given the proximity of Newfoundland to the Old World, the fishing operations were carried out by migratory fleets that sailed to Newfoundland in the spring and returned to Europe in the fall with cargoes of salted fish. This mode of operation persisted until the late 18th Century. Traditionally, the fishery was carried out in inshore areas using handlines. During the 18th and early 19th centuries English fishing settlements began to spread as the banker vessel, which fished the Grand Banks and brought the fish to land for curing, was introduced. Also during the 18th Century the northern cod fishery was supplemented by the exploitation of other natural resources such as Atlantic salmon (*Salmo salar*) and harp seals. Three innovations were introduced into the fishery during the 19th Century: the cod trap, the long line (a long buoyed fishing line with baited hooks closely placed), and steam power. This last innovation was initially introduced into the seal fishery, but quickly made its way into the Labrador fishery as well. During the mid-19th Century the seal fishery was at its historical height, catching an average of 400 000 animals annually (with reported removals of over 500 000 animals occurring in several years between 1828 and 1873) on the ice off the coast of Labrador and northeast Newfoundland. A gradual decrease in the amount of animals removed ensued in the later part of the 19th Century. This large removal level impacted the harp seal population, bringing it from a pristine state (around 11 million animals during the 18th Century; Hammill et al., 2011) to a depressed state by the late 19th Century (approximately 1.6 million animals in 1918; Hammill et al., 2011).

The turn of the 20th Century brought further innovations into the Newfoundland and Labrador cod fishery: the gasoline engine and the use of draggers, although these innovations were not rapidly adopted in a widespread fashion. Dragging operations were restricted for many years as the perception was that the introduction of efficient fishing units would reduce employment. The growth of urban centres during the early 20th Century, in addition to the development of transportation and refrigerated fish handling facilities, opened markets for fresh and frozen fish products, which impacted the output of salted fish from Newfoundland. Nevertheless, the drop in European fish supplies during World War I bolstered the production of salted dried codfish to fill the demand in Europe. The European market for Newfoundland salt codfish shrank when the war ended and European countries restored, and expanded, their production. The development in New England of quick freezing and filleting at source of production during the 1920s led to an expansion of the fresh fish trade, although Newfoundland lagged behind in these developments. World War II brought about lowered fishing rates in waters off Newfoundland and throughout the North Atlantic, which tripled the value of Newfoundland salt cod within a decade. Once World War II was over, fishing operations increased again and the fishing capacity of many European nations was greatly increased. At the same time, United States and Iceland were legally protecting their continental shelves placing them under national jurisdiction.

During the period 1948 to 1965 many of the great fish populations on the Grand Banks and continental shelf off Newfoundland and Labrador came under intensive exploitation: haddock (*Melanogrammus aeglefinus*), redfish, grenadier (family Macrouridae), American plaice (*Hippoglossoides platessoides*) and Atlantic cod. Large fishing fleets of European nations (Russia, France, Portugal and Spain) fished the offshore waters, while the inshore fisheries carried out by Newfoundland and Labrador fishermen saw a nearly 50% decline in catch per man. During the 1950s stern trawls and factory freezing were introduced into the fishing industry. The large fleets and technological capabilities meant a sharp increase in fish catches, during the 1960s, followed by a decrease in the 1970s. The catch of northern cod in particular, which from 1850 to 1950 had averaged about 250 000 tons, increased to an average of 580 000 tons during the 1960s with a sharp peak of 800 000 tons in 1968 (Rose

2004; Figure 2 in Hutchings and Rangeley 2011). The catch declines of the 1970s mirrored declines in fish populations.

Concern over declining abundances of fish stocks throughout the Northwest Atlantic following World War II led to the establishment in 1950 of the International Commission of the Northwest Atlantic Fisheries (ICNAF), an international fisheries management body in charge of the assessment and management of fish stocks outside of national jurisdictions. ICNAF imposed catch quota regulations in the 1970s for several fish stocks, including northern cod, although they were ineffective as they were set too high. The imposition of the 200 mile limit fisheries jurisdiction in 1977 arrested the stock decline and led into a limited rebuilding of the stock. The rebuilding of fish stocks during the second half of the 1970s led to optimism about their capacity to sustain large catches and subsequently large investments on fishing vessels and plants were made which translated into large overcapacity in the Atlantic Canadian fishing industry. During the 1980s northern cod was managed on a quota system, and catches averaged about 225 000 tons. Most of the catches were by Canadian fleets, although some fishing by foreign fleets was carried out in the “nose”and “tail”of the Grand Banks, regions beyond the 200 mile limit jurisdiction. Catch rates during the late 1980s were unsustainable from a biological standpoint. Unsustainable fishing rates and environmental changes, and variability, led to the collapse of most groundfish stocks (Hutchings and Myers, 1994; Rose et al., 2000;

Drinkwater, 2002; Halliday and Pinhorn, 2009), the fishing moratoria imposed in the early 1990s, and the restructuring of the ecosystem described above. Since then, the main targets of the fishing industry in waters off Newfoundland and Labrador are invertebrate species such as shrimp and snow crab (*Chionoecetes opilio*).

The War periods saw a largely decreased sealing industry, while the average catches during the inter-war period was around 160 000 animals. The harp seal catch following World War II averaged around 200 000 animals, which brought an already depressed population to its historical low in 1971. That same year a quota came into force. Since the introduction of quotas, the population has been recovering and now appears to be close to historical levels (Hammill et al., 2011). Harp seal catches averaged 52 000 animals between 1983 and 1995, increasing significantly to a range of 226 000 to 366 000 animals between 1996 and 2006 (DFO, 2011*a*). Large reductions in catch have occurred since 2007 and since then the industry has not been able to meet the quotas set by Fisheries and Oceans Canada (DFO) due to shortages of demand in international markets.

1.3 Science in support of Ecosystem Based Fisheries Management in the Northwest Atlantic

Historically, fisheries resources have been managed focusing solely on maximizing the catch of a single target species, not explicitly considering the target species' habitat, predators, prey and other ecosystem components and interactions. This approach has led to an increasing worldwide percentage of overexploited stocks and a large proportion of fully exploited stocks (FAO, 2005, 2012).

The realization of the limitations of this mode of management has prompted considerable interest in ecosystem-based fisheries management (EBFM) during the last two decades (Larkin, 1996; Link, 2002; Garcia et al., 2003; Smith et al., 2007; Beamish and Rothschild, 2009; Levin et al., 2009; McLeod and Leslie, 2009; Essington and Punt, 2011; Rice, 2011; Fulton et al., 2014). The objective of EBFM is to maintain valued ecosystem goods and services, identifying potential conflicting management objectives and explicitly considering trade-offs among them, while accounting for the requirements of other ecosystem components (e.g., nontarget species, protected species, habitat considerations, and trophic interactions) (Pikitch et al., 2004; Essington and Punt, 2011).

Levin et al. (2009) defined a formal framework (Integrated Ecosystem Assessment (IEA)) in which information on natural and socio-economic factors can be analysed in relation to ecosystem management objectives. An important component of this framework is the implementation of a management strategy evaluation (MSE), a simulation-based approach used to explore alternative management options and to identify trade-offs across a range of management objectives (for an example see Fulton et al., 2014). Our ability to simulate ecosystem dynamics (unperturbed and when exposed to perturbations, e.g. climate and/or fishing) lies at the heart of the MSE approach. Therefore, it is crucial to understand the modes of regulation of energy flow, and the dynamic relationships among important components of the ecosystem of interest.

The regulation of energy flows in marine ecosystems is usually described as either bottom-up, top-down or wasp-waist control (Cury et al., 2003). Control is defined as bottom-up if the supply of energy and nutrients influences the amount of energy that flows to higher trophic levels. On the other hand, control is top-down if predation and grazing by higher trophic levels regulate components lower in the food web. In marine ecosystems that have a wasp-waist structure there is a single species (or at most a handful) that dominates an intermediate trophic level (it is usually a plankton-feeding pelagic fish). These key species exert both top-down control on zooplankton and bottom-up control on top predators (Cury et al., 2003; Bakun, 2006). Although these may be good representations of the control of energy flow of any particular system at a given time, we must not lose sight that ecosystems are dynamic and thus ecosystem control is likely variable in both, space and time (Frank et al., 2006).

Link et al. (2011*a*,*b*) describe the advances made on the provisioning of science advice toward EBFM in the Northwest Atlantic, encompassing several ecosystems from the Mid Atlantic Bight in the south to the Newfoundland and Labrador Shelf in the northern range. In particular for the Newfoundland-Labrador Shelf marine ecosystem, there have been several studies that can guide the development of EBFM strategies. Three mass-balance biomass models were developed, following two different approaches (Ecopath approach (Bundy et al., 2000; Pitcher et al., 2002); inverse modelling approach (Savenkoff et al., 2001)). Results from the Ecopath models were later imported into Ecosim to produce dynamic simulations of the system with particular emphasis on the relative roles of fishing pressure and harp seal consumption on the dynamics of Atlantic cod (Bundy, 2001; Bundy et al., 2009).

Recently, several papers resulted from international workshops that analysed the relative importance of fisheries, trophodynamics, and environmental change and variability in the regulation of 13 Northern Hemisphere marine ecosystems. Although all papers from the Theme Section (Gaichas et al., 2012; Link et al., 2012) are relevant to science development in support of EBFM, 3 studies in particular analysed different aspects of the dynamics of the Newfoundland and Labrador Shelf ecosystem (Bundy et al., 2012; Holsman et al., 2012; Pranovi et al., 2012). Pranovi et al. (2012) analysed biomass accumulation curves across trophic levels in the Newfoundland-Labrador Shelf Ecosystem and 9 other marine ecosystems of the Northern Hemisphere. These curves can be used as indicators of shifts in community structure beyond normal observed ranges. Bundy et al. (2012) carried out a comparative analysis of aggregate surplus production models across 12 ecosystems, from which they derived a fisheries yield rule of thumb: maximum sustainable yield (MSY) appears to vary between 1 and 5 t km^{-2} in exploited Northern Hemisphere marine ecosystems. Holsman et al. (2012) compared cod and herring production dynamics models across 13 ecosystems and found that including environmental and/or ecological covariates consistently improved model fits, suggesting the importance of considering these drivers when developing models to provide scientific advice.

1.4 Cod-seals conflict

The presence of marine mammals in the waters utilized by fisheries is often perceived as detrimental. The interaction between marine mammals and the species targeted by the fishery in usually portrayed as “predation” or “competition”. Predation occurs if marine mammals prey upon species targeted by the fishery (Figure 1.2a), while competition takes place if both marine mammals and commercial species depend on a shared and limited food source (Figure 1.2b).

Based on these depictions, and usually in the midst of discussions on fisheries management and policy decision, the diverse community of people linked to the fisheries, from stakeholders and industry representatives to managers, politicians and scientists, often put forward arguments along the following lines:

- if predation is at work, removal of marine mammals will make the amount of commercially valuable fish that they would have consumed available to fisheries,

or

- if competition is acting, removing marine mammals will enhance the food supply for commercial fish species, increasing their productivity, and consequently fisheries yields.

However, the depictions in Figure 1.2 only capture the two simplest ways in which marine mammals and fisheries may interact. Thus, recommendations of removals of marine mammals would only fulfil the expectations that guide them with certainty if the world were as simple as Figure 1.2. Food webs are complex networks with many pathways connecting any two species (e.g. Lavigne, 1996; Yodzis, 1998); some can be short (e.g. Figure 1.2) but much longer pathways also exist. All pathways need to be considered to properly determine the output of the interaction between any pair of species (Yodzis, 2000). Still, the effects travelling through short pathways are felt sooner (Yodzis, 1996), and strong interactions tend to be associated with short loops within the network (Neutel et al., 2002).

In this context, considering simple configurations like the ones illustrated in Figure 1.2 is a reasonable starting point. On one hand, this literally evaluates the interactions as envisioned by many of the people involved (i.e. a scientific evaluation of a fisherman's perception), and on the other it focuses on the configurations that would likely have the highest odds of showing a significant interaction. If such an analysis cannot detect strong interactions, it is unlikely that more realistic food web models will render significant effects of marine mammals on fisheries resources. Conversely, if effects are detected, then a more complex food web model would be required to assess if the detected effect persists strong as more realism is added.

1.4.1 The conflict in Atlantic Canada

The collapses of the Atlantic cod stocks off Eastern Canada (COSEWIC, 2010) and concomitant increases in abundance of harp and grey seals (*Halichoerus grypus*) (Hammill and Stenson, 2011; Thomas et al., 2011; Hammill et al., 2013) spurred debates along the lines described above. The debate has been on mainstream media since the collapse of the stocks and it is still current today (e.g. CBC, 1992, 1995*b*,*a*, 2011, 2012). There have been multiple calls for seal culls to enhance cod stocks made by the Fisheries Resources Conservation Council to the Minister of Fisheries and Oceans (FRCC, 1994, 1999, 2011). In 2001 the Minister of Fisheries and Oceans appointed an Eminent Scientific Panel to provide advice on the best strategies for management of seal populations in Eastern Canada, addressing the issue of seal culls to protect groundfish (McLaren et al., 2001). DFO also hosted two recent international workshops to assess the impacts of seals on fish populations in Eastern Canada (DFO, 2008*a*, 2009). Despite these efforts, the role of seals in the non-recovery of groundfish off eastern Canada is still not fully resolved. Furthermore, the results of using seal culls as management tools are highly uncertain and may even end being detrimental to the targeted fish stocks (e.g. Punt and Butterworth, 1995; Yodzis, 1998, 2001).

The effects of seal consumption on the 4 cod populations off Atlantic Canada differ among stocks. There is debate around the role of grey seal predation on the non-recovery of the Eastern Scotian Shelf (ESS) cod stock. Some studies indicate the possibility that grey seal predation may be hindering the recovery of the stock (Trzcinski et al., 2006; Koen-Alonso and Bundy, 2009), while a recent study concluded that grey seal predation constitutes a small component of the total mortality of cod on the ESS (Trzcinski et al., 2009).

A weight of evidence analysis suggests that grey seal predation is the most plausible hypothesis to explain the lack of recovery of the southern Gulf of St Lawrence cod stock (Swain et al., 2011).

The failure to recover of the northern Gulf of St Lawrence cod stock seems to be mainly associated to very poor recruitment (Chassot et al., 2009). Predation by harp seals may impact recruitment under favourable environmental conditions, while under poor environmental conditions the effects of other factors prevail in limiting recruitment (Chassot et al., 2009).

The lack of recovery of the northern cod stock has been attributed to the high levels of mortality that the offshore components of the stock have experienced throughout the mid-1990s and the early 2000s (DFO, 2008*b*). Predation by harp seals is a hypothesis commonly proposed to explain the high mortality, either based on lack of evidence that the high mortality experienced may be explained differently (e.g. DFO, 2003*a*,*b*) or on results from simulations based on a whole system model (Bundy, 2001). However, the accepted view of the trajectory of the capelin stock has changed since that simulation study was carried out, and simulation results would likely have been different if the accepted view of the trajectory of the capelin stock (DFO, 2010, 2013*a*) had been considered.

This fact and the extended time series we can now avail of several years later merit a re-evaluation of the cod-seals conflict in waters off Newfoundland and Labrador.

1.5 Thesis Objectives and Chapter Outlines

In this context, the general objective of this thesis is to explore the potential role harp seals may have played in the collapse and non-recovery of the Atlantic cod stock off the Southern Labrador and Newfoundland Shelf (NAFO Divisions 2J3KL, Figure 1.1), i.e. the "northern cod". In particular, I explore the predation and competition hypotheses. I tackle the predation hypothesis by investigating if harp seal consumption is an important driver of northern cod's biomass dynamics. The consumptive competition hypothesis implies that capelin is a fundamental driver of cod's population dynamics, and that harp seal consumption limits the amount of capelin available to cod, thereby impeding stock recovery.

The objective of Chapter 2 is to explore the possibility that harp seals competed for food resources with cod in the periods that preceded and followed the groundfish collapse. Competition for food resources, particularly the energetically rich capelin, is often cited as one of the potential ways through which harp seals may be impeding the recovery of the northern cod stock. However, formal assessments of this hypothesis are lacking. I therefore analysed the diets and compared the degree of dietary overlaps among Atlantic cod, harp seals and a third prominent predator on the system, Greenland halibut over 10 years comprising pre- and a post-collapse periods (1986-1996).

In Chapter 3, I examine the factors that regulate the population biomass and timing of spawning of capelin in the Northwest Atlantic ecosystem. The objectives of this Chapter are to assess the occurrence of a regime shift during the early 1990s on the Newfoundland-Labrador Shelf marine ecosystem, and examine the effects of sea ice on capelin population biomass and timing of spawning to probe the hypothesis that capelin is environmentally regulated via food availability. Forage species sustain many species of marine wildlife, and therefore represent a crucial link in ocean food webs (Pikitch et al., 2012). Capelin plays the role of the major forage fish in the ecosystem, providing the link between the lower trophic levels and top predators such as large fish, marine mammals and seabirds (Lavigne, 1996). However, the processes that regulate the population are not well understood. In this chapter I appraise the likelihood that population regulation is exerted through bottom-up forces, thus gaining insight into the second premise of consumptive competition, i.e. does harp seal consumption limit the amount of capelin available to cod?

In Chapter 4 I address the predation hypothesis: the particular objective of the Chapter is to test competing hypotheses on the relative contributions of fisheries removals, predation by harp seals, and food availability (as indexed by capelin) on the lack of recovery and dynamics of the northern cod stock, and to explore the mechanisms through which the main drivers may affect the stock's dynamics. The northern cod stock collapsed in the early 1990s, and has since been under either a fishing moratorium or severely reduced fishing effort. Although the stock showed some signs of biomass recovery through the mid and late 2000s, the overall stock remains a mere shadow of its former self (DFO, 2011*b*, 2013*b*). Overfishing was clearly one of the main causes for the collapse of the stock, while a changing climate may have also played a role in its demise. However, it is still not clear why the stock has not recovered despite the low fishing mortalities it has experienced for 20 years. Many hypotheses have been put forward to explain the non-recovery, mainly invoking harp seal predation or the effects of an impoverished environment as explanations. Nevertheless, a synthesis and assessment of the empirical support for these different hypotheses is lacking. In this chapter I integrate available information on fisheries catches, consumption by harp seals, and available biomass of cod's main prey, capelin, in a bioenergetic-allometric modelling framework that allowed testing multiple hypotheses on the relative importance that these proposed drivers have on the dynamics of the stock. This chapter therefore addresses the popular notion that harp seal consumption is impeding the recovery of the stock and assesses its empirical support against that of alternative hypotheses.

Chapter 5 summarizes my findings, discusses limitations of the studies, proposes directions for future research, and emphasizes the management implications of my thesis.

This Thesis has been written in a manuscript format, i.e. Chapters 2-4 were written as stand-alone research chapters. There are therefore some redundancies among chapters, particularly in the introduction sections.

1.6 Co-authorship Statement

I am the major intellectual contributor and principal author of all chapters presented in this thesis. Most of the data used in this thesis consist of long time series collected by Fisheries and Oceans Canada and other institutions such as Environment Canada and the United States of America National Oceanic and Atmospheric Administration (NOAA). Acknowledgement to these sources is made throughout the thesis chapters. I am responsible for all data analysis, interpretation, and manuscripts preparation. The work could not have been completed without the collaborative contribution of many individuals, particularly my supervisors Dr Mariano Koen-Alonso and Dr William Montevecchi, and committee member Dr Garry Stenson.

I prepared the manuscripts and revised them based on the advice and comments from my co-authors.

Chapter 2. Buren AD, Koen-Alonso M and Stenson GB. Is competition with harp seals and Greenland halibut a parsimonious hypothesis for the non-recovery of northern cod? Diet overlap and changes following the stock collapse will be submitted to Marine Biology Research.

Chapter 3. Buren AD, Koen-Alonso M, Pepin P, Mowbray F, Nakashima B, Stenson GB, Ollerhead N and Montevecchi WA. Bottom-up regulation of capelin, a keystone forage species, has been published in PLoS ONE.

Buren AD, Koen-Alonso M, Pepin P, Mowbray F, Nakashima BS, Stenson GB, Ollerhead N, Montevecchi WA (2014) Bottom up regulation of capelin, a keystone forage species. PLoS ONE 9(2): e87589. doi:10.1371/journal.pone.0087589.

Chapter 4. Buren AD, Koen-Alonso M. and Stenson GB. The role of harp seals, fisheries and food availability in driving the dynamics of northern cod, is in press in Marine Ecology Progress Series. doi: 10.3354/meps10897.

1.7 References

Bakun, A. (2006). ‘Wasp-waist populations and marine ecosystem dynamics: Navigating the ”predator pit” topographies’, *Prog Oceanogr* 68, 271–288.

Beamish, R. J. and Rothschild, B. J. (2009), *The Future of Fisheries Science in North America*, Springer.

Benoît, H. P. and Swain, D. P. (2008). ‘Impacts of environmental change and direct and indirect harvesting effects on the dynamics of a marine fish community’, *Can J Fish Aquat Sci* 65, 2088–2104.

Bundy, A. (2001). ‘Fishing on ecosystems: the interplay of fishing and predation in Newfoundland-Labrador’, *Can J Fish Aquat Sci* 58, 1153–1167.

Bundy, A., Bohaboy, E., Hjermann, D., Mueter, F., Fu, C. and Link, J. (2012). ‘Common patterns, common drivers: comparative analysis of aggregate surplus production across ecosystems’, *Mar Ecol Prog Ser* 459, 203–218.

Bundy, A., Heymans, J. J., Morissette, L. and Savenkoff, C. (2009). ‘Seals, cod and forage fish: A comparative exploration of variations in the theme of stock collapse and ecosystem change in four Northwest Atlantic ecosystems’, *Prog Oceanogr* 81, 188–206.

Bundy, A., Lilly, G. R. and Shelton, P. A. (2000). 'A mass balance model of the Newfoundland-Labrador shelf', *Can Tech Rep Fish Aquat Sci* 2310.

Carscadden, J. and Frank, K. (2002). 'Temporal variability in the condition factors of Newfoundland capelin (*Mallotus villosus*) during the past two decades', *ICES J Mar Sci* 59, 950–958.

Carscadden, J. and Nakashima, B. S. (1997), Abundance and changes in distribution, biology and behavior of capelin in response to cooler water of the 1990s, *in* 'Forage fishes in marine ecosystems. Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program Rep. No. AK-SG-97-01.', University of Alaska Fairbanks, Fairbanks, Alaska, pp. 457–468.

CBC. (1992). 'Seals, cod and the Atlantic fisheries'.
URL: *http://www.cbc.ca/archives/categories/economy-business/business/pelts-pups-and-protest-the-atlantic-seal-hunt/who-had-cod-for-dinner.html*

CBC. (1995*a*). 'The seal hunt makes a comeback'.
URL: *http://www.cbc.ca/archives/categories/economy-business/business/pelts-pups-and-protest-the-atlantic-seal-hunt/the-seal-hunt-makes-a-comeback.html*

CBC. (1995*b*). 'Tobin says seals slow down cod recovery'.
URL: *http://www.cbc.ca/archives/categories/economy-business/business/pelts-*

pups-and-protest-the-atlantic-seal-hunt/tobin-says-seals-slow-down-cod-recovery.html

CBC. (2011). 'Seals hurting cod recovery: DFO'.
URL: *http://www.cbc.ca/news/canada/new-brunswick/seals-hurting-cod-recovery-dfo-1.1007853*

CBC. (2012). 'To cull, or not to cull'.
URL: *http://www.cbc.ca/fisheriesbroadcast/episodes/2012/12/11/to-cull-or-not-to-cull/*

Chabot, D. and Stenson, G. (2002). 'Growth and seasonal fluctuations in size and condition of male Northwest Atlantic harp seals Phoca groenlandica: an analysis using sequential growth curves', *Mar Ecol Prog Ser* 227, 25–42.

Chassot, E., Duplisea, D., Hammill, M., Caskenette, A., Bousquet, N., Lambert, Y. and Stenson, G. (2009). 'Role of predation by harp seals *Pagophilus groenlandicus* in the collapse and non-recovery of northern Gulf of St. Lawrence cod *Gadus morhua*', *Mar Ecol Prog Ser* 379, 279–297.

Choi, J. S., Frank, K. T., Petrie, B. and Leggett, W. (2005). 'Integrated assesment of a large marine ecosystem: a case study of the devolution of the Eastern Scotian Shelf, Canada', *Oceanogr Mar Biol: Ann Rev* 43, 47–67.

COSEWIC. (2010). 'COSEWIC assessment and status report on the Atlantic Cod *Gadus morhua* in Canada'.

Cury, P. M., Shannon, L. and Shin, Y.-J. (2003), The functioning of marine ecosystems: a fisheries perspective, *in* **M. Sinclair and G. Valdimarsson**., eds, 'Responsible fisheries in the marine ecosystem', number 7, Food and Agriculture Organization of the Unoted Nations (FAO) and CABI Publishing, pp. 103–123.

Davoren, G. K., Anderson, J. T. and Montevecchi, W. A. (2006). 'Shoal behaviour and maturity relations of spawning capelin (*Mallotus villosus*) off Newfoundland: demersal spawning and diel vertical movement patterns', *Can J Fish Aquat Sci* 63, 268–284.

Dawe, E., Koen-Alonso, M., Chabot, D., Stansbury, D. and Mullowney, D. (2012). 'Trophic interactions between key predatory fishes and crustaceans: comparison of two Northwest Atlantic systems during a period of ecosystem change', *Mar Ecol Prog Ser* 469, 233–248.

DFO. (2003*a*). 'Northern (2J+3KL) cod stock status update', *Can Sci Advis Secretar Stock Stat Rep* 2003/018.

DFO. (2003*b*). 'Proceedings of the Zonal Assessment Meeting - Atlantic Cod', *Can Sci Advis Secretar Proc Ser* 2003/021.

DFO. (2008*a*). 'Proceedings of the National Workshop on the Impacts of Seals on Fish Populations in Eastern Canada (Part 1); 12-16 November 2007', *Can Sci Advis Secretar Proc Ser* 2008/021.

DFO. (2008*b*). 'Stock assessment of Northern (2J3KL) cod in 2008', *Can Sci Advis Secretar Adv Rep* 2008/034.

DFO. (2009). 'Proceedings of the National Workshop on the Impacts of Seals on Fish Populations in Eastern Canada (Part 2)', *Can Sci Advis Secretar Proc Ser* 2009/020.

DFO. (2010). 'Assessment of capelin in SA2+Div. 3KL in 2010', *Can Sci Advis Secretar Adv Rep* 2010/090.

DFO. (2011*a*). 'Current status of Northwest Atlantic harp seals, (*Pagophilus groenlandicus*)', *Can Sci Advis Secretar Adv Rep* 2011/050.

DFO. (2011*b*). 'Stock assessment of Northern (2J3KL) cod in 2011', *Can Sci Advis Secretar Adv Rep* 2011/041.

DFO. (2013*a*). 'Assessment of capelin in SA2 + Div. 3KL in 2013', *Can Sci Advis Secretar Adv Rep* 2013/11.

DFO. (2013*b*). 'Stock Assessment of Northern (2J3KL) Cod in 2013', *Can Sci Advis Secretar Adv Rep* 2013/014.

Drinkwater, K. F. (1996). 'Atmospheric and oceanic variability in the Northwest Atlantic during the 1980s and early 1990s', *J Northw Atl Fish Sci* 18, 77–97.

Drinkwater, K. F. (2002), A review of the role of climate variability in the decline of northern cod, *in* **N. McGinn**., ed., 'American Fisheries Society Symposium', American Fisheries Society, Symposium 32, Bethesda, Maryland, pp. 113–129.

Dwyer, K. S., Buren, A. D. and Koen-Alonso, M. (2010). 'Diet of Greenland halibut in the Newfoundland Shelf, Northwest Atlantic, from 1978-2003: reflections of a changing ecosystem', *J Sea Res* 64, 436–445.

Essington, T. E. and Punt, A. E. (2011). 'Implementing Ecosystem-Based Fisheries Management: Advances, Challenges and Emerging Tools', *Fish Fisheries* 12, 123–124.

FAO. (2005). 'Review of the state of world marine fishery resources', FAO Fish Tech Pap 457.

FAO. (2012). 'The state of world fisheries and aquaculture 2012', Rome, 209 pp.

Frank, K., Carscadden, J. and Simon, J. (1996). 'Recent excursions of capelin (*Mallotus villosus*) to the Scotian Shelf and Flemish Cap during anomalous hydrographic conditions', *Can J Fish Aquat Sci* 53, 1473–1486.

Frank, K., Petrie, B., Shackell, N. L. and Choi, J. S. (2006). 'Reconciling differences in trophic control in mid-latitude marine ecosystems', *Ecol Lett* 9, 1096–1105.

FRCC. (1994). 'Conservation - stay the course : Fisheries Resource Conservation Council, report to the Minister of Fisheries and Oceans : 1995 conservation measures for Atlantic groundfish', *Fisheries Resource Conservation Council* FRCC 94.R4E.

FRCC. (1999). 'Fisheries Resource Conservation Council, report to the Minister of Fisheries and Oceans: 1999 Conservation requirements for the Gulf of St. Lawrence groundfish stocks and cod stocks in Divisions 2GH and 3Ps', *Fisheries Resource Conservation Council* FRCC 99.R.1.

FRCC. (2011). 'Fisheries Resource Conservation Council, report to the Minister of Fisheries and Oceans: Towards recovered and sustainable groundfish fisheries in Eastern Canada', *Fisheries Resource Conservation Council* FRCC 11.R1.

Fulton, E. A., Smith, A. D. M., Smith, D. C. and Johnson, P. (2014). 'An integrated approach is needed for ecosystem based fisheries management: Insights from Ecosystem-Level Management Strategy Evaluation', *PLoS ONE* 9(1), e84242.

Gaichas, S., Gamble, R., Fogarty, M., Benoît, H. P., Essington, T., Fu, C., Koen-Alonso, M. and Link, J. (2012). 'Assembly rules for aggregate-species production models: simulations in support of management strategy evaluation', *Mar Ecol Prog Ser* 459, 275–292.

Garcia, S., Zerbi, A., Aliaume, C., Do Chi, T. and Lasserre, G. (2003). 'The ecosystem approach to fisheries: issues, terminology, principles, institutional foundations, implementation and outlook', *FAO Fish Tech Pap* No. 443.

Gaston, A., Bertram, D. J., Boyne, A. W., Chardine, J., Davoren, G., Diamond, A. W., Hedd, A., Montevecchi, W., Hipfner, J., Lemon, M. J., Mallory, M. L., Rail, J.-F. and Robertson, G. (2009). 'Changes in Canadian seabird populations and ecology since 1970 in relation to changes in oceanography and food webs', *Environ Rev* 17, 267–286.

Gerasimova, O. (1994). 'Peculiarities of spring feeding by capelin (*Mallotus villosus*) on the Grand Bank in 1987-90', *J Northw Atl Fish Sci* 17, 59–67.

Gomes, M. d. C., Haedrich, R. L. and Villagarcia, M. (1995). 'Spatial and temporal changes in the groundfish assemblages on the north-east Newfoundland/Labrador Shelf, north-west Atlantic, 1978-1991', *Fish Oceanogr* 4, 85–101.

Haedrich, R. and Barnes, S. (1997). 'Changes over time of the size structure in an exploited shelf fish community', *Fish Res* 31, 229–239.

Halliday, R. and Pinhorn, A. (2009). 'The roles of fishing and environmental change in the decline of Northwest Atlantic groundfish populations in the early 1990s', *Fish Res* 97, 163–182.

Hammill, M. and Stenson, G. B. (2011). 'Modelling grey seal abundance in Canadian waters', *Can Sci Advis Sec Sci Res Doc* 2011/014.

Hammill, M., Stenson, G. B., Doniol-Valcroze, T. and Mosnier, A. (2013). 'Estimating carrying capacity and population trends of Northwest Atlantic harp seals, 1952-2012', *DFO Can Sci Advis Sec Sci Res Doc* 2012/148.

Hammill, M., Stenson, G. B. and Kingsley, M. (2011). 'Historical abundance of Northwest Atlantic harp seals (*Pagophilus groenlandicus*): influence of harvesting and climate', *DFO Can Sci Advis Sec Sci Res Doc* 2011/100.

Hilborn, R., Branch, T. A., Ernst, B., Magnussson, A., Minte-Vera, C. V., Scheuerell, M. D. and Valero, J. L. (2003). 'State of theworld's fisheries', *Annu Rev Environ Resour* 28, 359–399.

Holsman, K., Essington, T., Miller, T., Koen-Alonso, M. and Stockhausen, W. (2012). 'Comparative analysis of cod and herring production dynamics across 13 northern hemisphere marine ecosystems', *Mar Ecol Prog Ser* 459, 231–246.

Hutchings, J. A. and Myers, R. A. (1994). 'What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador', *Can J Fish Aquat Sci* 51, 2126–2146.

Hutchings, J. A. and Rangeley, R. W. (2011). 'Correlates of recovery for Canadian Atlantic cod (*Gadus morhua*)', *Can J Zool* 89, 386–400.

Jangaard, P. (1974). 'The capelin (*Mallotus villosus*): biology, distribution, exploitation, utilization, and composition', *Bull Fish Res Board Can* 186, 1–70.

Koen-Alonso, M. and Bundy, A. (2009). 'Trophodynamic modeling of core species of the eastern scotian shelf marine community', *Can Sci Advis Secretar Proc Ser 2009/20* .

Koen-Alonso, M., Mowbray, F. and Lilly, G. R. (2006), Changes in the fish community of the Newfoundland Shelf (NAFO Divisions 2J3KLNO) in the period 1981-2005: Signals and trends from the Canadian multi-species bottom trawl survey, *in* 'NAFO Symposium', Dartmouth, NS, Canada.

Larkin, P. (1996). 'Concepts and issues in marine ecosystem management', *Rev Fish Biol Fish* 6, 139–164.

Lavigne, D. (1996), Ecological interactions between marine mammals, commercial fisheries and their prey: unravelling the tangled web, *in* **W. A. Montevecchi**., ed., 'Studies of high-latitude seabirds. 4. Trophic relationships and energetics of endotherms in cold ocean systems', Can Wildl Serv Ocass Pap 91, pp. 59–71.

Lawson, J. W., Anderson, J. T., Dalley, E. L. and Stenson, G. B. (1998). 'Selective foraging by harp seals *Phoca groenlandica* in nearshore and offshore waters of newfoundland, 1993 and 1994', *Mar Ecol Prog Ser* 163, 1–10.

Lawson, J. W. and Gosselin, J.-F. (2009). 'Distribution and preliminary abundance estimates for cetaceans seen during Canada's marine megafauna survey - A component of the 2007 TNASS', *DFO Can Sci Advis Sec Sci Res Doc* 2009/031, –.

Lear, W. (1998). 'History of fisheries in the Northwest Atlantic: the 500-year perspective', *J Northw Atl Fish Sci* 23, 41–73.

Levin, P. S., Fogarty, M. J., Murawski, S. A. and Fluharty, D. (2009). 'Integrated ecosystem assessments: developing the scientific basis for ecosystem-based management of the ocean', *PLoS Biology* 7(1), e1000014.

Lilly, G. R., Shelton, P. A., Brattey, J., Cadigan, N. G., Healey, B. P., Murphy, E., Stansbury, D. and Chen, N. (2003). 'An assessment of the cod stock in NAFO Divisions 2J+3KL in February 2003', *Can Sci Advis Secretar Res Doc* 2003/023.

Link, J., Gaichas, S., Miller, T., Essington, T., Bundy, A., Boldt, J., Drinkwater, K. and Moksness, E. (2012). 'Synthesizing lessons learned from comparing fisheries production in 13 northern hemisphere ecosystems: emergent fundamental features', *Mar Ecol Prog Ser* 459, 293–302.

Link, J. S. (2002). 'Ecological considerations in fisheries management: when does it matter?', *Fisheries* 27, 10–17.

Link, J. S., Bundy, A., Overholtz, W. J., Shackell, N., Manderson, J., Duplisea, D., Hare, J., Koen-Alonso, M. and Friedland, K. (2011*a*), Northwest Atlantic ecosystem-based management for fisheries, *in* **A. Belgrano and C. W. Fowler**., eds, 'Ecosystem-based management for marine fisheries', number 2, Cambridge University Press, pp. 32–112.

Link, J. S., Bundy, A., Overholtz, W. J., Shackell, N., Manderson, J., Duplisea, D., Hare, J., Koen-Alonso, M. and Friedland, K. D. (2011*b*). 'Ecosystem-based fisheries management in the Northwest Atlantic', *Fish Fish* 12, 152–170.

McLaren, I., Brault, S., Harwood, J. and Vardy, D. (2001). 'Report of the Eminent Panel on Seal Management', *Report to the Department of Fisheries and Oceans* Available from Fisheries and Oceans at http://publications.gc.ca/collections/Collection/Fs23-405-2001E.pdf.

McLeod, K. and Leslie, H. (2009), *Ecosystem-Based Management for the Oceans*, Island Press, Washington DC, USA.

Montevecchi, W. A. (2014), *Seabird capitals. The ecological seabird reserves of Newfoundland and Labrador*, Flanker Press. In prep.

Montevecchi, W. A. and Piatt, J. (1984). 'Composition and energy contents of mature inshore spawning capelin (*Mallotus villosus*): implications for seabird predators', *Comp Biochem Physiol A: Physiol* 78, 15–20.

Mowbray, F. (2002). 'Changes in the vertical distribution of capelin (*Mallotus villosus*) off Newfoundland', *ICES J Mar Sci* 59, 942–949.

Myers, R. A., Hutchings, J. A. and Barrowman, N. J. (1997). 'Why do fish stocks collapse? The example of cod in Atlantic Canada', *Ecol Appl* 7, 91–106.

Nakashima, B. S. (1992). ‘Patterns in coastal migration and stock structure of capelin (*Mallotus villosus*)’, *Can J Fish Aquat Sci* 49, 2423–2429.

Nakashima, B. S. and Wheeler, J. P. (2002). ‘Capelin (*Mallotus villosus*) spawning behaviour in Newfoundland waters - the interaction between beach and demersal spawning’, *ICES J Mar Sci* 59, 909–916.

Neutel, A.-M., Heesterbeek, J. A. and de Ruiter, P. C. (2002). ‘Stability in real food webs: weak links in long loops’, *Science* 296, 1120–1123.

O’Driscoll, R., Parsons, M. and Rose, G. A. (2001). ‘Feeding of capelin (*Mallotus villosus*) in Newfoundland waters’, *Sarsia* 86, 165–176.

Pepin, P., Maillet, G. L., Fraser, S., Shears, T. and Redmond, G. (2011). ‘Optical, chemical, and biological oceanographic conditions on the Newfoundland and Labrador Shelf during 2009 and 2010’, *Can Sci Advis Secretar Res Doc* 2011/074.

Pikitch, E., Boersma, P., Boyd, I., Conover, D., Cury, P. M., Essington, T. E., Heppell, S., Houde, E., Mangel, M., Pauly, D., Plagányi, E., Sainsbury, K. and Steneck, R. (2012), *Little fish: big impact: managing a crucial link in ocean food webs*, Lenfest Ocean Program, Washington, DC.

Pikitch, E., Santora, C., Babcock, E., Bakun, A., Bonfil, R., Conover, D., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E., Link,

J., Livingston, P., Mangel, M., McAllister, M., Pope, J. and Sainsbury, K. (2004). 'Ecosystem-Based Fishery Management', *Science* 305(5682), 346–347.

Pitcher, T. J., Heymans, J. J. and Vasconcellos, M. (2002). 'Ecosystem models of Newfoundland for the time periods 1995, 1985, 1900, and 1450', *Fisheries Centre Research Reports* 10(5), 1–74.

Pranovi, F., Link, J., Fu, C., Cook, A., Liu, H., Gaichas, S., Friedland, K., Rong, U. K. and Benoît, H. P. (2012). 'Trophic-level determinants of biomass accumulation in marine ecosystems', *Mar Ecol Prog Ser* 459, 185–201.

Punt, A. and Butterworth, D. S. (1995). 'The effects of future consumption by the Cape fur seal on catch rates of the Cape hakes. 4. Modelling the biological interactions between Cape fur seals *Arctocephalus pusillus* pusillus and the Cape hakes *Merluccius capensis* and *M. paradoxus*', *S Afr J Mar Sci* 16, 255–285.

Rice, J. (2002), Changes to the large marine ecosystem of the Newfoundland-Labrador shelf, *in* **K. Sherman and H. Skjoldal**., eds, 'Large marine ecosystems of the North Atlantic', number 3, Elsevier Science B.V., Amsterdam, Netherlands, pp. 51–103.

Rice, J. (2011). 'Managing fisheries well: delivering the promises of an ecosystem approach', *Fish Fish* 12(2), 209–231.

Rose, G. A. (1993). 'Cod spawning on a migration highway in the north-west Atlantic', *Nature* 366, 458–461.

Rose, G. A. (2004). 'Reconciling overfishing and climate change with stock dynamics of Atlantic cod (*Gadus morhua*) over 500 years', *Can J Fish Aquat Sci* 61, 1553–1557.

Rose, G. A. (2007), *Cod: an ecological history of the North Atlantic fisheries*, Breakwater Books, St John's, NL.

Rose, G. A., deYoung, B., Kulka, D., Goddard, S. and Fletcher, G. (2000). 'Distribution shifts and overfishing the northern cod (*Gadus morhua*): a view from the ocean', *Can J Fish Aquat Sci* 57, 644–663.

Savenkoff, C., Castonguay, M., Chabot, D., Hammill, M. O., Bourdages, H. and Morissette, L. (2007). 'Changes in the northern Gulf of St. Lawrence ecosystem estimated by inverse modelling: Evidence of a fishery-induced regime shift?', *Estuar Coast Shelf Sci* 73, 711 – 724.

Savenkoff, C., Vézina, A. F. and Bundy, A. (2001). 'Inverse analysis of the structure and dynamics of the whole Newfoundland-Labrador Shelf ecosystem', *Can Tech Rep Fish Aquat Sci* 2354, –viii+56 p.

Sergeant, D. (1991). 'Harp seals, man and ice', *Can Spec Publ Fish Aquat Sci* 114, 1–153.

Shackell, N. L., Shelton, P. A., Hoenig, J. and Carscadden, J. (1994). 'Age- and sex-specific survival of Northern Grand Banks capelin (*Mallotus villosus*)', *Can J Fish Aquat Sci* 51, 642–649.

Smith, A. D. M., Fulton, E. J., Hobday, A. J., Smith, D. C. and Shoulder, P. (2007). 'Scientific tools to support the practical implementation of ecosystem-based fisheries management', *ICES J Mar Sci* 64(4), 633–639.

Stenson, G. B. and Hammill, M. (2006). 'Quantifying uncertainty in estimates of Atlantic cod (*Gadus morhua*) consumption by harp seals (*Phoca groenlandica*)', *Can Sci Advis Secretar Res Doc* 2004/089.

Swain, D., Benoît, H. P., Hammill, M., McClelland, G. and Aubry, . (2011). 'Alternative hypotheses for causes of the elevated mortality of cod (*Gadus morhua*) in the southern Gulf of St Lawrence; the weight of evidence', *DFO Can Sci Advis Sec Sci Res Doc* 2011/036, –.

Templeman, W. (1948). 'The life history of the caplin (*Mallotus villosus* O. F. Müller) in Newfoundland waters', *Bull Nfld Gov Lab* 17, 1–151.

Thomas, L., Hammill, M. and Bowen, W. (2011). 'Estimated size of the Northwest Atlantic grey seal population 1977-2010', *DFO Can Sci Advis Sec Sci Res Doc* 2011/017, 1–23.

Trzcinski, M., Mohn, R. and Bowen, W. (2006). 'Continued decline of an atlantic cod population: how important is gray seal predation?', *Ecol Appl* 16, 2276–2292.

Trzcinski, M., Mohn, R. and Bowen, W. (2009). 'Estimating the impact of grey seals on the Eastern Scotian Shelf and Western Scotian Shelf cod populations', *DFO Can Sci Advis Sec Sci Res Doc* 2009/052, 1–19.

Vilhjálmsson, H. (1994). 'The Icelandic capelin stock', *Rit Fiskideildar* 13(1), 1–281.

Winters, G. (1970). 'Biological changes in coastal capelin from the over-wintering to the spawning condition', *J Fish Res Board Can* 27, 2215–2224.

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

Yodzis, P. (1996), Food webs and perturbation experiments: theory and practice, *in* **G. A. Polis and K. O. Winemiller**., eds, 'Food webs: integration of patterns and dynamics', Chapman and Hall, New York, pp. 192–200.

Yodzis, P. (1998). 'Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem', *J Anim Ecol* 67, 635–658.

Yodzis, P. (2000). 'Diffuse effects in food webs', *Ecology* 81, 261–266.

Yodzis, P. (2001). 'Must top predators be culled for the sake of fisheries?', *Trends Ecol Evol* 16, 78–84.

1.8 Figures

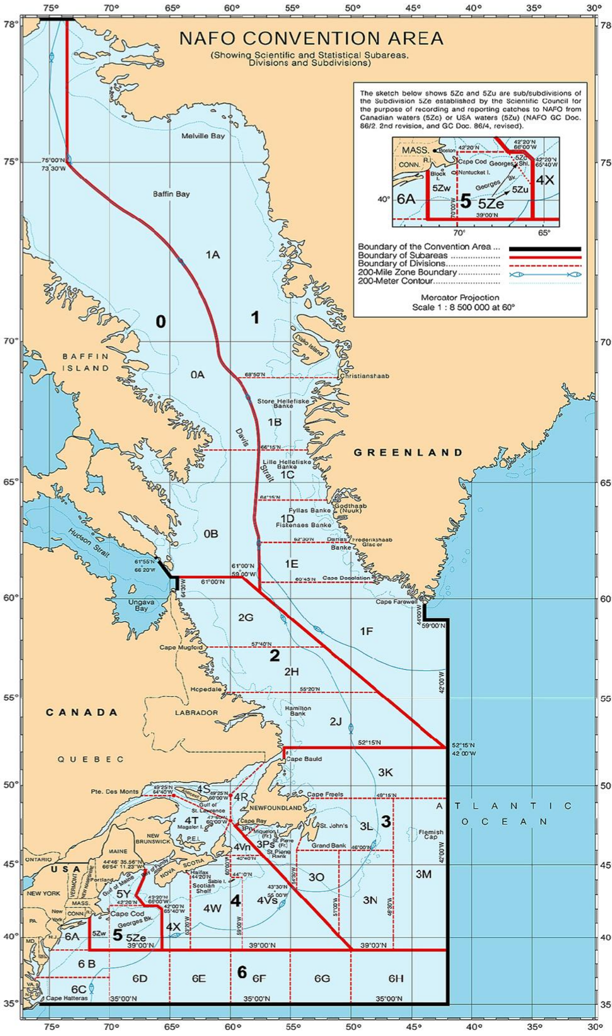


Figure 1.1: Map of the Northwest Atlantic Fisheries Organization (NAFO) Convention area. Original map from NAFO, www.nafo.int

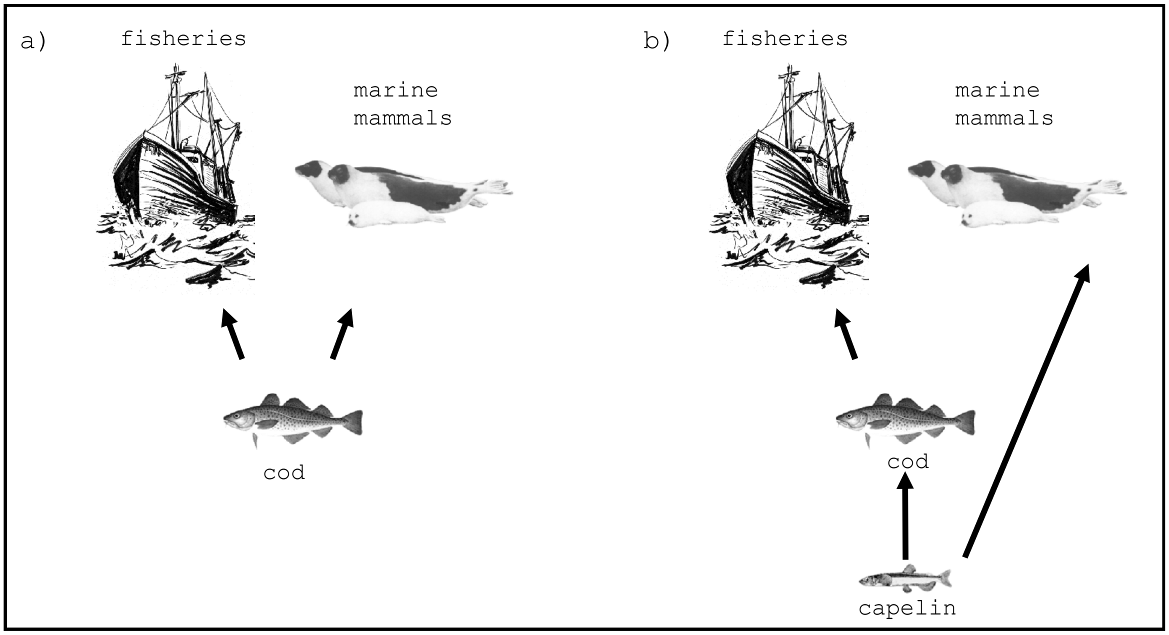


Figure 1.2: The simplest plausible hypotheses that might explain the non-recovery of cod stocks due to the effect of harp seals in waters off Newfoundland, a) “predation” and b) “competition”. Note that competition for target species (cod) between marine mammals and fisheries is also implied in these representations.

Chapter 2

Is competition with harp seals and Greenland halibut a parsimonious hypothesis for the non-recovery of northern cod?

Diet overlap and changes following the stock collapse

2.1 Abstract

Competition between marine mammals and other top predators for their resource base can influence their abundances and the composition of the natural communities in which they are embedded. The Newfoundland and Labrador Shelf (NAFO Divs 2J3KL) marine community underwent drastic changes during the late 1980s and early 1990s, including the continuing increase of the large harp seal herd, the collapse of several groundfish species (including the notorious case of Atlantic cod), and the collapse of the main forage fish in the system - capelin. Despite over two

decades of severely reduced fishing effort, the Atlantic cod stock has not recovered. In this chapter I explore the hypothesis that competition with harp seals may be the reason for the non-recovery. I analysed the diets of harp seal, Atlantic cod and a third prominent top predator, Greenland halibut, and assessed their similarity. All three predators relied heavily on capelin, but cod's diet showed a higher consistency over time, indicating low trophic plasticity. This low plasticity could not only be a contributing factor in the lack of recovery of cod, but also suggests that other predators may be better positioned for utilizing a changing resource base. Furthermore, the diet of Atlantic cod was more similar to Greenland halibut's diet than to harp seal's diet. This low degree of dietary overlap suggests that consumptive competition with harp seals is unlikely to be a relevant factor in the non-recovery of the northern cod stock.

2.2 Introduction

The structure of natural communities is determined and regulated by both environmental and biological factors. Among the latter, competition has always been considered a major structuring force although its relative importance compared to that of predation and disturbance is still unresolved (Sih et al., 1985; Wilbur, 1987; Stokstad, 2009). As is the case for all indirect effects in ecosystems, detecting competitive ecological interactions and assessing their magnitude remains a challenge (Wootton, 2002; Krivtsov, 2008). Doing this requires a wealth of information on the abundance and distribution in space and time of the resource and potential competitors, as well as on the dynamics of the study system.

In the marine realm, a competitive interaction that has received much attention is that of commercial fisheries with marine mammals for their prey base or the primary production needed to sustain such prey base (e.g. Harwood and Croxall, 1988; Trites et al., 1997; Matthiopoulos et al., 2008). The general perception that the presence of marine mammals is detrimental to commercial fisheries, either through consumption of target species or through competition with target species for food resources, has frequently resulted in calls for culling marine mammals (e.g. Wickens et al., 1992; FRCC, 2011), and in some cases culls have actually occurred (Lavigne, 2003).

The ecosystem off the Newfoundland and Labrador Shelf sustained extensive fisheries for centuries. The main commercial species, Atlantic cod *Gadus morhua*, collapsed in the early 1990s due to the joint effects of overfishing (Hutchings and Myers, 1994) and environmental variability (Drinkwater, 2002; Halliday and Pinhorn, 2009).This collapse was part of a major restructuring that occurred in the marine community during the late 1980s and early 1990s; most commercial and many non-commercial demersal fish species declined (Gomes et al., 1995; Rice, 2002; Koen-Alonso et al., 2010; NAFO, 2010; DFO, 2012), shellfish biomass increased (Lilly et al., 2003; Worm and Myers, 2003), and there was a major reduction in acoustic offshore abundance estimates of the main forage fish in the system (capelin *Mallotus villosus* (DFO, 2010)), which also exhibited pronounced changes in its biology and ecology (Carscadden and Nakashima, 1997; Carscadden and Frank, 2002; Nakashima and Wheeler, 2002; DFO, 2010). In addition, the harp seal *Pagophilus groenlandicus* population increased rapidly from circa 2 million individuals in the mid-1970s to circa 7 million in the late 2000s (Hammill et al., 2013).

Following the collapse of the northern cod stock, a fishing moratorium was put in place in 1992 to help the stock rebuild, and to date there have not been any major commercial harvests on this stock. However, despite the drastically reduced fishing effort, the stock has not recovered due to the high levels of mortality experienced by the offshore components throughout the mid-1990s and the early 2000s (DFO, 2008, 2011). Given the size of the harp seal herd, there have been arguments put forth that harp seals are impeding the recovery of the stock through either predation or competition for food resources (DFO, 2003*a*,*b*; Rice et al., 2003). The competition hypothesis finds support in the argument that low abundance of capelin, the most energetically dense of cod's prey in the Northwest Atlantic (Lawson et al., 1998), led to poorer condition, and reduced reproductive potential therefore hindering cod's recovery (Rose and O'Driscoll, 2002; Sherwood et al., 2007). Testing this hypothesis is extremely difficult as two premises must be met, namely that capelin must be a fundamental driver of cod's population dynamics and that harp seal consumption limits the amount of capelin available to cod. A first step in assessing if consumptive competition exists is to assess the degree of dietary overlap of the potential competitors.

The most important top predators of the Northwest Atlantic ecosystem have historically been Atlantic cod and harps seals; with Greenland halibut *Reinhardtius hippoglossoides* gaining importance towards the late 1980s. All three predators have a varied diet and rely to some extent on capelin (Stenson and Perry, 2001; Link et al., 2009; Dwyer et al., 2010). If harp seals were strong competitors with cod, one would expect that their diet would show a large degree of overlap, much larger than the degree of cod's diet with other important predators (i.e. Greenland halibut). In this study I explore the possibility that harp seals competed for food resources with cod in the periods that preceded and followed the groundfish collapse. I analysed the diets and compared the degree of dietary overlaps among Atlantic cod, harp seals and Greenland halibut over 10 years comprising pre- and a post-collapse periods (1986-1996).

2.3 Materials & Methods

2.3.1 Study Area

The study area comprised the Northwest Atlantic Fisheries Organizations Divisions (NAFO) 2J, 3K and 3L, range of the 'northern' cod stock (Figure 2.1).

2.3.2 Data collection

Atlantic cod and Greenland halibut were captured during Fisheries and Oceans Canada (DFO) fall bottom trawl research surveys. These surveys occurred during September-December, occasionally extending into January. Details on the annual DFO bottom trawl survey are in McCallum and Walsh (1996) and Brodie and Stansbury (2007).

A total of 3 stomachs per length group (10 cm for Atlantic cod and 5 cm for Greenland halibut) per research tow were collected in each Division. The stomachs were excised and preserved at sea using 10% formalin until 1993 in the case of Atlantic cod and 1995 in the case of Greenland halibut, and by freezing thereafter.

Stomach content collection of Atlantic cod took place during 1986-1996 with annual sample sizes ranging from 266 to 4100 (Table 2.1). Stomach collection of Greenland halibut was not carried out in 1989, 1990 or 1994. Annual sample sizes ranged from 2025 to 4004 (Table 2.1).

Harp seals were collected by professional sealers or DFO personnel using methods outlined in the Fisheries Act to ensure they were killed humanely. Stomachs from seals collected between April and September are regularly designated as summer samples and those taken between October and March as winter samples (Lawson et al., 1995). Stomachs were removed from the seals soon after death and either frozen at $-20\,^{\circ}\mathrm{C}$ or preserved in a 70% ethanol solution (see methods in Lawson et al., 1995).

Stomachs were collected for the period 1986-1996, annual sample sizes ranging from 177 to 540 (Table 2.1).

2.3.3 Stomach content analysis

In the laboratory, food items were sorted and identified to the lowest possible taxonomic level. When analysing the diets of groundfish, prey items were blotted with paper towel to remove excess moisture, counted and the total of each item weighed to the nearest 0.1g. In the case of harp seals, prey lengths and masses were recorded whenever possible and reconstructed using allometric regressions of hard parts for most prey items. See Lawson et al. (1995) for a full description of the methods used.

2.3.4 Spatio-temporal distribution of predators

The bottom trawl survey covered the offshore area of the continental shelf of NAFO Divisions 2J3KL (Figure 2.1). Coverage was limited in the nearshore area (within ˜30 km of the coastline) due to vessels' capabilities. Cod was caught throughout the entire area, at depths generally shallower than 400m (Figure 2.1a). Greenland halibut was also caught throughout NAFO Divisions 2J and 3K, while catches in Division 3L were quite minor compared to those of cod. Greenland halibut was caught in waters deeper than 1000m, although the majority of the catches were restricted to depths between 100 and 600 m (Figure 2.1b). Hence there was a high degree of spatio-temporal overlap of the groundfish considered in this study.

Most harp seal samples were collected in the nearshore area, with fewer samples taken in the offshore throughout the 3 NAFO Divisions (Figure 2.1c). However, this is a reflection of sampling effort, not of harp seal distribution. Harp seals are highly migratory; Northwest Atlantic harp seals summer on feeding grounds in the Canadian Arctic and/or West Greenland. During the fall and winter, seals move southward along the Labrador coast. Some of these seals (~20%-30%) enter the Gulf of St Lawrence while the remaining overwinter in waters off Northeast Newfoundland and Southern Labrador (i.e. NAFO Divs 2J3KL). In the spring, the animals migrate back to the feeding grounds (Sergeant, 1991; Stenson and Sjare, 1997). While on the wintering grounds, harp seals spend much of the time in offshore waters (Sergeant, 1991; Stenson and Sjare, 1997). As a result, a large proportion (~80%-90%) of the energy seals require is acquired in the offshore areas of NAFO Divisions 2J3KL (Hammill and Stenson, 2000).

Thus, spatial overlap among groundfish and harp seals, and hence potential for competition, in Newfoundland waters peaks in the offshore area of 2J3KL during the fall and winter seasons.

2.3.5 Factors affecting diet composition

The effects on diet composition of year, season, predator length class (age class for harp seals), sex, depth and NAFO Division were evaluated using a multinomial regression model (Agresti, 2002) (Table 2.2).

Predator size variability is associated with ontogenic changes in the diet (e.g. behaviour, changes in energetic requirements, learning). Diets of fish predators were estimated by size class (small, medium or large). To determine the cut offs between classes I first looked at diet descriptions per 3 cm bin and looked for the sizes where the diet transitioned from small invertebrates to mainly fish and considered that the transition size from small to medium (21 cm in Atlantic cod and 18 cm in Greenland halibut). To determine the transition size from medium to large I looked for the size where diet became more variable and the predators consumed prey usually consumed by larger individuals (Link et al., 2009; Dwyer et al., 2010) (90 cm in Atlantic cod and 65 cm in Greenland halibut). Diets of harp seals were described in terms of age classes: Young of the year (YOY), Juveniles (1-4 years old) and Adults (5 years and older) (Lawson et al., 1995; Lawson and Stenson, 1997; Stenson, 2012). Time variability can be considered as a surrogate for changes in prey availability over time. These changes can be seasonal or long-term (prey population dynamics). In the case of harp seals, both year and season effects were included in the model while for fish predators only a year effect was included as the data collection was carried out only during the fall. Variability due to sex is usually associated with different foraging behaviours or energetic requirements. Geographical variability is associated with foraging habitat and the spatial structure of prey assemblages. This variability can involve both latitudinal changes (e.g. north-south clines) and depth-related changes (e.g. inshore and offshore areas).

The multinomial regression analysis relies on identifying a main prey category (by weight) for each individual stomach and assuming that each one of these observations is the result of a multinomial experiment, where the observed main prey category in the stomach belongs to one among a pre-defined set of 13 possible prey categories. This analysis is a generalization of a binomial logistic regression, with many potential outcomes instead of only two.

Analyses were carried out using the multinom function in the nnet package (Venables and Ripley, 2002) in R Language and Environment for Statistical Computing (R Core Team, 2012).

2.3.6 Diet description

I compared the diets of the predators in the offshore area of 2J3KL during the fall (fish) and winter (seals) seasons. Given the paucity of seal offshore diet samples, I employed a method that allows filling gaps in a data set by making use of all available data and extrapolating to the combinations of space-time of interest. This method was initially described in ICES (2008) and successfully implemented by Dwyer et al. (2010). To compare diets described using a common methodology I modelled diet composition for all predators.

The method for describing diet is a reparametrization of the classical proportion by weight (e.g. Hyslop, 1980), considering only the main prey in the stomach of each individual predator. This approach is based on the fact that the classical calculation of proportion by weight in the diet can also be represented in terms of probability of finding a given prey in a stomach and the mean weight of that prey in the stomach when it is present. For example, if N is the total number of predators in a sample, n_i is the number that actually contains a given prey i, and B_i is the total biomass of i in the collection, then the relative proportion of i in the diet (w_i) can be calculated as:

$$w_i = \frac{B_i}{\sum\limits_J B_j} = \frac{B_i/N}{\sum\limits_J B_j/N} = \frac{(n_i/N)(B_i/n_i)}{\sum\limits_J (n_j/N)(B_j/n_j)} = \frac{p_i m_i}{\sum\limits_J p_j m_j} \tag{2.1}$$

with $p_j = n_j/N$ and $m_j = B_j/n_j$

and where p_i is the probability that prey i is the main prey in a stomach and m_i is the mean weight of i in a stomach when i is actually present. The usefulness of this reparametrization is that allows for estimating p_i and m_i independently. Under the assumption that each prey species in a stomach is consumed independently, using the above parametrization when considering all prey species in a stomach or just one of them should render similar results if the sample size is large enough. Buren et al. (2008) tested this concept using harp seal diet data by comparing the classical diet analysis (e.g. Hyslop, 1980) with the proportions obtained by only considering the most important prey in biomass in each stomach, and found that the approach was sensible. Buren et al. (2008) conducted a randomization test to compare diet descriptions from a classical and the multinomial regression approach and found that both are similar with moderate to large sample sizes. The main advantages of using this method over the classical diet analysis are: *1*) The probability that prey i is the main prey in a stomach can be estimated using multinomial regression models, and therefore the method accounts for variability due to statistically significant factors, and *2*) it allows to fill in data gaps. Buren et al. (2008) assessed how well the model performs at filling in data gaps by removing subsets of data and predicting diet composition for the said subset and contrasted those results to a diet description using the entire data set, and found that the predicted and observed diet composition were quite similar.

For each predator I expressed the percentage weight that a given prey species i ($\%w_i$) represents in terms of two factors; the probability that prey i is the main prey in a stomach (p_i) and its mean weight when it actually is the main prey (m_i)s:

$$\%w_i = 100 \frac{p_i m_i}{\sum_I p_i m_i} \tag{2.2}$$

The probabilities (p_i) were estimated using the multinomial regression model. The range of prey sizes the predators consume increase several fold during their lifetime, thus I estimated a mean weight prey per length/age class of the predator ($m_{i,l}$).
I split the time series in 2 periods; pre-collapse (1986-1991) and post-collapse (1992-1996). I compared the diets between the periods to assess the predators' responses to the restructuring the ecosystem suffered.

2.3.7 Comparison of predators' diets

To visualize the similarities of the predators' diets I mapped them using multivariate techniques. The data used for this analysis were the diets in terms of percentage by weight ($\%w_i$) of each trophic group (species-size; e.g. small cod) in a given year. The similarity matrix was built using Bray-Curtis dissimilarity coefficients (Clarke and Warwick, 2001). A non-metric Multi-Dimensional Scaling (MDS) plot (Clarke and Warwick, 2001) was used to visualize the relative distances between pairs of samples based on the ranks of the Bray-Curtis dissimilarity matrix. Points that are closer together represent very similar diets, and points that are far apart correspond to dissimilar diets. This analysis provides a visual representation of the predators' trophic plasticity over the study period; a large spread of the data points of a given trophic group corresponds to a high degree of trophic plasticity (i.e. the predator is capable of having more dissimilar diets) while a smaller spread corresponds to a low degree of plasticity (similar diets over time).

Hierarchical cluster analysis (Clarke and Warwick, 2001) was used to classify trophic groups based on their diet similarities. Results are overlaid on top of the MDS graph. Multivariate analyses were carried out using the vegan package (Oksanen et al., 2013) in R (R Core Team, 2012).

2.4 Results

All explanatory variables included in the multinomial regressions had significant effects on the diet compositions of all predators, with the exception of sex (Table 2.3). The later only had a significant effect on the diet composition of Greenland halibut. Dwyer et al. (2010) argue that the sex effect is related to different maximum sizes (females grow larger) and distribution and/or behavioural changes this entails. Although results will be mainly described in terms of period and ontogeny, it is pertinent to briefly indicate here some differences in diet composition related to the other factors. In terms of depth: *a*) Greenland halibut consumed relatively more redfish *Sebastes* spp., gadiformes, other fish and other invertebrates and less amphipods, capelin, Atlantic cod and Arctic cod in deep waters than on the shelf, *b*) Atlantic cod consumed relatively more capelin, gadiformes and zooplankton, and less sandlance *Ammodytes* sp., flatfishes (Pleuronectidae), and amphipods in deep waters than on the shelf, and *c*) although there were differences in the diets of harp seals in terms of depth, I only considered diets in the offshore as this is where the spatio-temporal overlap with fish predators is maximum. In terms of a north-south cline (NAFO Division): *a*) Greenland halibut consumed relatively more zooplankton in NAFO Divisions 2J3K, more flatfish in NAFO Division 2J, more capelin in NAFO Division 3K, and more redfish in NAFO Division 3L (Figure 2.2), *b*) Atlantic cod consumed relatively more shrimp and flatfishes in the north (NAFO Division 2J), more capelin on NAFO Division 3K and more sandlance in the south (NAFO Division 3L) (Figure 2.3), and *c*) Harp seals consumed relatively more amphipods, shrimp and Arctic cod in the north (NAFO Divisions 2J3K), and more capelin, sandlance and flatfishes in the south (NAFO Division 3L) (Figure 2.4).

In terms of time period and size/age class: the diet of small Greenland halibut during 1986-1991 was dominated by amphipods, zooplankton and other invertebrates, with a minor contribution of capelin, shrimp *Pandalus* sp. and unidentified fish. Capelin comprised over 50 %*w* of the diet of medium sized Greenland halibut. Redfish, flatfishes, unidentified fish and other invertebrates made up the bulk of the remaining diet. The diet of large Greenland halibut was almost exclusively piscivorous (>98 %*w*), with redfish (˜35 %*w*) and flatfish (21 %*w*) as the main prey items. Capelin, Atlantic cod, other fish, and unidentified fish were the other important prey items (Figure 2.5).

There were major changes in the diet of Greenland halibut from 1986-1991 to 1992-1996. In general, the diet was more diverse with no particular prey item dominating the diet composition as it did in the pre-collapse period (with the exception of small Greenland halibut). The contribution of other invertebrates to the diet of small Greenland halibut increased (from 13.4 %*w* to 21.4 %*w*) at the expense of capelin (from 11 %*w* to 3.5 %*w*). The importance of capelin during the post-collapse period dropped from >50 %*w* to 29.5 %*w*, and the importance of redfish dropped from ˜11 %*w* to 3%*w*. The contributions of Arctic cod *Boreogadus saida*, gadiformes, other fish, unidentified fish, shrimp and other invertebrates increased after 1991. The diet of large Greenland halibut remained almost exclusively piscivorous, although the most important prey items changed. The major prey item was gadiformes (29 %*w*), with important contributions of Arctic cod, flatfishes, redfish (yet the latter two exhibited greatly decreased importance since the first period), other fish and unidentified fish (Figure 2.5).

The diet of harp seal YOY during the pre-collapse period was heavily dominated (˜85 $\%w$) by pelagic fish: sandlance, capelin and Arctic cod. Shrimp and amphipods were the prey items that comprised most of the remaining diet. Juvenile harp seals also relied on pelagic fish, though not the extent that YOY did (>60 $\%w$). Shrimp, amphipods and other invertebrates completed the diet of juvenile harp seals. Pelagic fish were also the main prey items of adult harp seals (>60 $\%w$), though sandlance only comprised 5 $\%w$ of the diet. Other important prey items were shrimp, flatfish and other fish (Figure 2.5).

Harp seals changed their diet following the collapse of the groundfish assemblage, though not to the extent that Greenland halibut did. The importance of Arctic cod and shrimp decreased while the importance of sandlance increased for the three age classes. There was a moderate increase in the importance of capelin in the diet of juvenile and adult harp seals (Figure 2.5).

The diet of small Atlantic cod during 1986-1991 was mainly composed of invertebrates (77.5 $\%w$). The main prey items were amphipods, zooplankton, shrimp and other invertebrates. The most important fish prey species was capelin (˜10 $\%w$). The diet of medium sized cod was largely dominated by capelin (57 $\%w$); sandlance (5 $\%w$) and unidentified fish (10 $\%w$) were the other important fish prey items. Among the invertebrates, shrimp (4 $\%w$), amphipods (4 $\%w$) and other invertebrates (10 $\%w$) were important prey items. Large Atlantic cod relied almost exclusively on fish (96 $\%w$). The most important prey items were capelin (30 $\%w$), gadiformes (20

%*w*), flatfishes (18 %*w*), and Atlantic cod (13.8 %*w*), with minor contributions of redfish, other fish, unidentified fish and other invertebrates (Figure 2.5).

The diet of Atlantic cod remained virtually unchanged from the pre-collapse to the post collapse period, for all three size classes. The only changes observed were an increase in the importance of shrimp (15.3 %*w* vs 30.8 %*w*) and a minor decrease in the importance of amphipods (31 %*w* vs 24.8 %*w*) in the diet of small cod. Changes in the importance of prey items in the diet of medium and large cod were less than 5 %*w* (Figure 2.5).

Fish predators showed typical ontogenic changes in diet, with small individuals feeding mainly on crustaceans and these being gradually replaced by fish. Large fish predators consumed almost exclusively fish prey items. The diet of harp seals was mainly piscivorous for all age classes, though all age classes consumed a non-negligible amount of invertebrates. The diets of YOY and adult harp seals were comprised of ˜85 %*w* fish, while that of juveniles was ˜70 %*w* fish (Figure 2.6). I observed temporal variability in the ratio of fish/invertebrates in the diets of harp seals and Greenland halibut, but no change in the diet of Atlantic cod. During the post collapse period harp seals consumed more fish and Greenland halibut less fish than during the pre-collapse (Figure 2.6).

The diets of the 9 trophic groups assemble in 4 distinct clusters: 1. small Atlantic cod and Greenland halibut, 2. large Atlantic cod and Greenland halibut, 3. harp seal YOY and 4. medium sized Atlantic cod and Greenland halibut and juvenile and adult harp seals. These clusters showed a large degree of similarity (50 % or larger) and were clearly distinct in MDS space (Figure 2.7). The trophic groups within the last cluster (medium sized fish and juvenile and adult harp seals) represent the major proportion of their respective population biomasses and thus merit a closer evaluation. There are two distinct clusters; one comprised by medium Atlantic cod and Greenland halibut (60 % similarity) and the second one by juvenile and adult harp seals (60 % similarity) (Figure 2.8). The diets of medium Greenland halibut during the pre-collapse period were particularly similar (75 %) to the diets of medium Atlantic cod (Figure 2.8).

The diets of Greenland halibut showed the largest degree of separation in MDS space, while the diets of harp seals showed moderate and the diets of Atlantic cod low, separation (Figure 2.7 and Figure 2.8).

2.5 Discussion

Has consumptive competition by harp seals hindered the recovery of the northern cod in the period immediately following its collapse? The first step in the assessment of consumptive competition is to assess differences and similarities in the composition of the diets of the predators of interest. Although dietary overlap does not necessarily imply competition among predators, it is a required condition to infer the occurrence of competition (Link and Auster, 2013).

The diets of Greenland halibut and harp seals changed following the restructuring of the system in the early 1990s, following different strategies for coping with the extensive changes in the system, while the diet of northern cod remained virtually unchanged. By the mid-1990s, northern cod did change its diet to rely more on *Pandalus* shrimp, a prey with a much lower energy density, particularly in the northern part of its range (Dawe et al., 2012; DFO, 2012; Krumsick and Rose, 2012). These results suggest that cod's continued decline and lack of recovery during the early 1990s may have been, at least partially, due to its inability to quickly adapt to a changing environment.

Given that the diet composition of all predators is spatially variable, a potential source of bias in this analysis would be if sample sizes would not be balanced among NAFO Divisions between time periods. Although more samples were collected in the pre-collapse period (Table 2.1), the proportion of samples coming from each NAFO Division remained fairly stable between periods, with the exceptions of a larger proportion of Greenland halibut, harp seals and small Atlantic cod caught in NAFO Division 3L in the post-collapse period (Figure 2.9). Despite these differences, the proportion of medium sized Atlantic cod and Greenland halibut and juvenile and adult harp seals remained fairly stable. Therefore, if any biases exist in the temporal comparison of diet compositions due to spatial difference, these were minimized by virtue of maintaining relatively constant proportional sample sizes. In addition, given that I compared modelled diet descriptions, the percent weights $\%w_i$ are not affected by the sample sizes within each NAFO Division *per se* (the multinomial model makes use of all data to estimate the probabilities of being a main prey p_i). I compared diets of the three predators in the areas and seasons where the intensity of potential competition would peak, i.e. the offshore area of NAFO Divs 2J3KL during the fall and winter seasons. Due to logistical constraints, seal samples from the offshore are relatively low compared to the inshore region. I therefore modelled the diet employing a method that makes uses of all the available data. The main criticism that could be made of such approach would be that the model would 'make up' prey items where there were not supposed to show up (e.g. typical inshore prey appearing in the offshore due to extrapolation). Buren et al (in DFO, 2009) carried out a cross-validation of this model by excluding portions of the data set (e.g. adults offshore for 7 years or adults inshore for different 7 years) and checking how well the model would fill that given gap, using the harp seal data set as working example. They found that with moderate to large sample sizes (in the order of hundreds to thousands of individuals), the method for estimating diet compositions and filling in data gaps was robust. In case the resulting diet descriptions I used in this paper were biased, given the large sample sizes (Table 2.1) I would expect these biases to be minimal.

The most important food resource in the system has historically been capelin, due to its high energy content (Lawson et al., 1998) and its former high abundance (Mowbray, 2012). The three predators considered in this study relied to differing degrees on this resource. I found that despite a marked reduction in its availability, capelin remained an important prey item in the diets of the three predators, particularly so in the case of Atlantic cod. Although harp seals and Greenland halibut consumed capelin during the post-collapse period, it was not as important as for Atlantic cod and they exhibited an ability to switch diets earlier. On the other hand, capelin remained Atlantic cod's main prey item, comprising ˜60 $\%w$ of the diet of medium sized Atlantic cod (Figure 2.5). The apparent increase in the percentage of capelin consumed by juvenile and adult harp seals can be explained by the sharp decrease in importance of Arctic cod. Given that the diet metric is proportional to the total biomass of all prey species, if the importance of a given prey species decreases, it will be compensated by increases in other prey species (e.g. capelin). Given that the availability of capelin was markedly reduced (Mowbray, 2012), not switching its main prey must have imposed an energetic burden for Atlantic cod as more time and effort may have been needed to obtain similar amounts of energy from the capelin consumed. It is also plausible that Atlantic cod maintained its diet composition, but may have not maintained consumption rates, therefore potentially contributing to lowered somatic condition during the period immediately following the cod collapse (Buren et al., 2014).

I found high similarities among the diets of the trophic groups that represent the largest proportion in biomass of the 3 predators (medium sized fish and juvenile and adult seals). The diet of Atlantic cod was particularly similar to that of Greenland halibut. Given that high dietary overlap on the same prey stocks indicates shared resource use and therefore high potential for interspecific competition (Link and Auster, 2013), this suggests that if consumptive competition were actually at play, Greenland halibut's pressure on cod could be higher than that of harp seals.

Although assessing diet similarities is a clear step toward understanding the forces that shape the ecosystem, it does not equate with assessing consumptive competition among species. The next step in assessing the components for a competitive interaction among the predators considered in this paper would be evaluating the impact that the consumption of important prey species (e.g. capelin) by one of the predators has on the availability of that species for the other predators.

The literature on competition between marine mammals and fisheries is quite rich; it usually centres on consumptive competition for target species or the primary production needed to sustain the target species (e.g. Harwood and Croxall, 1988; Crespo et al., 1997; Trites et al., 1997; Yodzis, 2001; Matthiopoulos et al., 2008; Plagányi and Butterworth, 2009). However, marine mammals-groundfish competition literature is not as extensive. Merrick (1997) proposed that large population declines of apex predators of the Eastern Bering Sea and Aleutian Islands ecosystems (Steller sea lions *Eumetopias jubatus*, murres *Uria aalge* and *U. lomvia* and kittiwakes *Larus brevirostris* and *L. tridactyla*) from the early 1970s to the mid 1990s occurred due to a large decline in the abundance, or availability, of their preferred prey (pelagic fish). He hypothesized that high abundance of adult walleye Pollock *Theragra chalcogramma* resulted in a systematic reduction of the abundance of marine mammal and seabird prey. Merrick (1997) also suggested that declines in several components of the Barents Sea ecosystem (cod, capelin, Atlantic herring *Clupea harengus*, harp seals and seabirds) during the late 1980s was due to three large cod year classes depleting the resource base and causing a restructuring of the ecosystem.

The results from this study suggest that Atlantic cod showed a delayed trophic response (cod eventually changed its diet during the late 1990s, see Dawe et al., 2012; DFO, 2012; Krumsick and Rose, 2012) to the drastic changes in its environment in the early 1990s. It likely spent more energy searching for prey in the period following the collapse than in the period preceding it, potentially affecting its somatic condition and therefore contributing to the non-recovery. In terms of competitive pressures from other important predators, I found that if competition was indeed a factor in slowing the recovery, and based on their diet overlaps, cod and Greenland halibut were more likely to be stronger competitors than cod and its more commonly hypothesized competitor - the harp seal.

2.6 References

Agresti, A. (2002), *Categorical data analysis*, Vol. 2, John Wiley & Sons, Hoboken, New Jersey, USA.

Brodie, W. and Stansbury, D. (2007). 'A brief description of Canadian multispecies surveys in SA2+Divisions 3KLMNO from 1995-2006', *NAFO SCR Research Document* NAFO SCR Res. Doc. 07/18.

Buren, A. D., Koen-Alonso, M. and Stenson, G. B. (2008), Reconstructing diet composition using a multinomial regression approach, *in* 'ICES-NAFO-NAMMCO Symposium on the Role of Marine Mammals in the Ecosystem in the 21st Century. 29 September - 1 October 2008, Dartmouth, Canada.'.

Buren, A., Koen-Alonso, M. and Stenson, G. (2014). 'The role of harp seals, fisheries and food availability in driving the dynamics of northern cod', *Mar Ecol Prog Ser* 511, 265–284.

Carscadden, J. and Frank, K. (2002). 'Temporal variability in the condition factors of Newfoundland capelin (*Mallotus villosus*) during the past two decades', *ICES J Mar Sci* 59, 950–958.

Carscadden, J. and Nakashima, B. S. (1997), Abundance and changes in distribution, biology and behavior of capelin in response to cooler water of the 1990s, *in* 'Forage fishes in marine ecosystems. Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program Rep. No. AK-SG-97-01.', University of Alaska Fairbanks, Fairbanks, Alaska, pp. 457–468.

Clarke, K. and Warwick, R. (2001), *Change in marine communities: an approach to statistical analysis and interpretation*, PRIMER-E Limited, Plymouth, UK.

Crespo, E., Pedraza, S. N., Dans, S., Koen-Alonso, M., Reyes, L. M., Garcia, N. A., Coscarella, M. and Schiavini, A. C. (1997). 'Direct and indirect effects of the highseas fisheries on the marine mammal populations in the northern and central Patagonian coast', *J Northw Atl Fish Sci* 22, 189–207.

Dawe, E., Koen-Alonso, M., Chabot, D., Stansbury, D. and Mullowney, D. (2012). 'Trophic interactions between key predatory fishes and crustaceans: comparison of two Northwest Atlantic systems during a period of ecosystem change', *Mar Ecol Prog Ser* 469, 233–248.

DFO. (2003*a*). 'Northern (2J+3KL) cod stock status update', *Can Sci Advis Secretar Stock Stat Rep* 2003/018.

DFO. (2003*b*). 'Proceedings of the Zonal Assessment Meeting - Atlantic Cod', *Can Sci Advis Secretar Proc Ser* 2003/021.

DFO. (2008). 'Stock assessment of Northern (2J3KL) cod in 2008', *Can Sci Advis Secretar Adv Rep* 2008/034.

DFO. (2009). 'Proceedings of the National Workshop on the Impacts of Seals on Fish Populations in Eastern Canada (Part 2)', *Can Sci Advis Secretar Proc Ser* 2009/020.

DFO. (2010). 'Assessment of capelin in SA2+Div. 3KL in 2010', *Can Sci Advis Secretar Adv Rep* 2010/090.

DFO. (2011). 'Stock assessment of Northern (2J3KL) cod in 2011', *Can Sci Advis Secretar Adv Rep* 2011/041.

DFO. (2012). 'Results and recommendations from the Ecosystem Research Initiative - Newfoundland and Labrador's Expanded Research on Ecosystem Relevant but UnderSurveyed Splicers', *Can Sci Advis Secretar Adv Rep* 2012/058.

Drinkwater, K. F. (2002), A review of the role of climate variability in the decline of northern cod, *in* **N. McGinn**., ed., 'American Fisheries Society Symposium', American Fisheries Society, Symposium 32, Bethesda, Maryland, pp. 113–129.

Dwyer, K. S., Buren, A. D. and Koen-Alonso, M. (2010). 'Diet of Greenland halibut in the Newfoundland Shelf, Northwest Atlantic, from 1978-2003: reflections of a changing ecosystem', *J Sea Res* 64, 436–445.

FRCC. (2011). 'Fisheries Resource Conservation Council, report to the Minister of Fisheries and Oceans: Towards recovered and sustainable groundfish fisheries in Eastern Canada', *Fisheries Resource Conservation Council* FRCC 11.R1.

Gomes, M. d. C., Haedrich, R. L. and Villagarcia, M. (1995). 'Spatial and temporal changes in the groundfish assemblages on the north-east Newfoundland/Labrador Shelf, north-west Atlantic, 1978-1991', *Fish Oceanogr* 4, 85–101.

Halliday, R. and Pinhorn, A. (2009). 'The roles of fishing and environmental change in the decline of Northwest Atlantic groundfish populations in the early 1990s', *Fish Res* 97, 163–182.

Hammill, M. and Stenson, G. B. (2000). 'Estimated prey consumption by harp seals (*Phoca groenlandica*), hooded seals (*Cystophora cristata*), grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) in Atlantic Canada', *J Northw Atl Fish Sci* 26, 1–23.

Hammill, M., Stenson, G. B., Doniol-Valcroze, T. and Mosnier, A. (2013). 'Estimating carrying capacity and population trends of Northwest Atlantic harp seals, 1952-2012', *DFO Can Sci Advis Sec Sci Res Doc* 2012/148.

Harwood, J. and Croxall, J. P. (1988). 'The assessment of competition between seals and commercial fisheries in the North Sea and the Antarctic', *Mar Mamm Sci* 4, 13–33.

Hutchings, J. A. and Myers, R. A. (1994). 'What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador', *Can J Fish Aquat Sci* 51, 2126–2146.

Hyslop, E. (1980). ‘Stomach content analysis - a review of methods and their application’, *J Fish Biol* 17, 411–429.

ICES. (2008). ‘Report of the working group on multispecies assessment methods (WGSAM)’, International Council for the Exploration of the Sea CM 2008/RMC:06.

Koen-Alonso, M., Pepin, P. and Mowbray, F. (2010). ‘Exploring the role of environmental and anthropogenic drivers in the trajectories of core fish species of the Newfoundland-Labrador marine community’, *NAFO Sci Coun Res Doc* 10/37.

Krivtsov, V. (2008), Indirect Effects in Ecology, *in* **E. J. Sven and F. Brian**., eds, ‘Encyclopedia of Ecology’, Academic Press, Oxford, UK, pp. 1948–1958.

Krumsick, K. J. and Rose, G. A. (2012). ‘Atlantic cod (*Gadus morhua*) feed during spawning off Newfoundland and Labrador’, *ICES J Mar Sci* 69, 1701–1709.

Lavigne, D. (2003), Marine mammals and fisheries: the role of science in the culliing debate, *in* **N. Gales, M. Hindell and R. Kirkwood**., eds, ‘Marine mammals: fisheries, tourism and management issues’, CSIRO Publications, Collingwood, Australia, pp. 31–47.

Lawson, J. W., Anderson, J. T., Dalley, E. L. and Stenson, G. B. (1998). ‘Selective foraging by harp seals *Phoca groenlandica* in nearshore and offshore waters of newfoundland, 1993 and 1994’, *Mar Ecol Prog Ser* 163, 1–10.

Lawson, J. W. and Stenson, G. B. (1997). ‘Diet of northwest Atlantic harp seals (*Phoca groenlandica*) in offshore areas’, *Can J Zool* 75, 2095–2106.

Lawson, J. W., Stenson, G. B. and McKinnon, D. G. (1995). ‘Diet of harp seals (*Phoca groenlandica*) in nearshore waters of the northwest Atlantic during 1990-1993’, *Can J Zool* 73, 1805–1818.

Lilly, G. R., Shelton, P. A., Brattey, J., Cadigan, N. G., Healey, B. P., Murphy, E., Stansbury, D. and Chen, N. (2003). ‘An assessment of the cod stock in NAFO Divisions 2J+3KL in February 2003’, *Can Sci Advis Secretar Res Doc* 2003/023.

Link, J. S. and Auster, P. J. (2013). ‘The challenges of evaluating competition among marine fishes: who cares, when does it matter, and what can one do about it?’, *Bull Mar Sci* 89(1), 213–247.

Link, J. S., Bogstad, B., Sparholt, H. and Lilly, G. R. (2009). ‘Trophic role of Atlantic cod in the ecosystem’, *Fish Fish* 10(1), 58–87.

Matthiopoulos, J., Smout, S., Winship, A. J., Thompson, D., Boyd, I. and Harwood, J. (2008). ‘Getting beneath the surface of marine mammal fisheries competition’, *Mamm Rev* 38, 167–188.

McCallum, B. and Walsh, S. (1996). ‘Groundfish survey trawls used at the Northwest Atlantic Fisheries Centre, 1971-present’, NAFO SCR Res. Doc. 96/50.

Merrick, R. L. (1997). 'Current and historical role of apex predators in the Bering Sea ecosystem', *J Northw Atl Fish Sci* 22, 343–355.

Mowbray, F. (2012). 'Some results from spring acoustic surveys for capelin (*Mallotus villosus*) in NAFO Division 3L between 1982 and 2010', *Can Sci Advis Secretar Res Doc* 2012/143, 1–34.

NAFO. (2010). 'Report of the NAFO Scientific Council Working Group on Ecosystem Approachesto Fisheries Management (WGEAFM)', *NAFO Sci Coun Summ Doc* 10/19.

Nakashima, B. S. and Wheeler, J. P. (2002). 'Capelin (*Mallotus villosus*) spawning behaviour in Newfoundland waters - the interaction between beach and demersal spawning', *ICES J Mar Sci* 59, 909–916.

Oksanen, J., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Simpson, G. L., Solymos, P., Stevens, M. H. H. and Wagner, H. (2013), *vegan: Community Ecology Package.* R package version 2.0-9.

Plagányi, E. and Butterworth, D. S. (2009), Competition with fisheries, *in* **W. F. Perrin, B. Würsig and J. Thewissen**., eds, 'Encyclopedia of marine mammals', Vol. 2nd, Academic Press, San Diego, California, pp. 269–275.

R Core Team. (2012), *R: A Language and Environment for Statistical Computing*, R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.

Rice, J. (2002), Changes to the large marine ecosystem of the Newfoundland-Labrador shelf, *in* **K. Sherman and H. Skjoldal**., eds, 'Large marine ecosystems of the North Atlantic', number 3, Elsevier Science B.V., Amsterdam, Netherlands, pp. 51–103.

Rice, J., Shelton, P. A., Rivard, D., Chouinard, G. A. and Fréchet, A. (2003). 'Recovering Canadian Atlantic cod stocks: the shape of things to come?', *ICES CM Document* U:06.

Rose, G. A. and O'Driscoll, R. L. (2002). 'Capelin are good for cod: can the northern stock rebuild without them?', *ICES J Mar Sci* 59, 1018–1026.

Sergeant, D. (1991). 'Harp seals, man and ice', *Can Spec Publ Fish Aquat Sci* 114, 1–153.

Sherwood, G. D., Rideout, R. M., Fudge, S. B. and Rose, G. A. (2007). 'Influence of diet on growth, condition and reproductive capacity in Newfoundland and Labrador cod (*Gadus morhua*): Insights from stable carbon isotopes (δ^{13}C)', *Deep Sea Res Pt II* 54(23-26), 2794–2809.

Sih, A., Crowley, P., McPeek, M., Petranka, J. and Strohmeier, K. (1985). 'Predation, competition, and prey communities: a review of field experiments', *Annu Rev Ecol Syst* 16(1), 269–311.

Stenson, G. B. (2012). 'Estimating consumption of prey by harp seals (*Pagophilus groenlandicus*) in NAFO Divisions 2J3KL', *Can Sci Advis Secretar Res Doc* 2012/156.

Stenson, G. B. and Perry, E. (2001). 'Incorporating uncertainty into estimates of Atlantic cod (*Gadus morhua*), capelin (*Mallotus villosus*) and Arctic cod (*Boreogadus saida*) consumption by harp seals (*Pagophilus groenlandicus*) in NAFO Divisions 2J3KL', *Can Sci Advis Secretar Res Doc* 2001/074.

Stenson, G. B. and Sjare, B. (1997). 'Seasonal distribution of harp seals, *Phoca groenlandica*, in the Northwest Atlantic', *ICES CM Document* CC:10.

Stokstad, E. (2009). 'On the origin of ecological structure', *Science* 326(5949), 33–35.

Trites, A. W., Christensen, V. and Pauly, D. (1997). 'Competition between fisheries and marine mammals for prey and primary production in the Pacific Ocean', *J Northw Atl Fish Sci* 22, 173–187.

Venables, W. and Ripley, B. (2002), *Modern Applied Statistics with S. Fourth Edition*, Springer, New York.

Wickens, P., Japp, D., Shelton, P., Kriel, F., Goosen, P., Rose, B., Augustyn, C., Bross, C., Penney, A. and Krohn, R. (1992). 'Seals and fisheries in South Africa - competition and conflict', *S Afr J Mar Sci* 12, 773–789.

Wilbur, H. M. (1987). ‘Regulation of Structure in Complex Systems: Experimental Temporary Pond Communities’, *Ecology* 68, 1437–1452.

Wootton, J. (2002). ‘Indirect effects in complex ecosystems: recent progress and future challenges’, *J Sea Res* 48, 157–172.

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

Yodzis, P. (2001). ‘Must top predators be culled for the sake of fisheries?’, *Trends Ecol Evol* 16, 78–84.

2.7 Tables

Table 2.1: Annual sample sizes of Atlantic cod, Greenland halibut and harp seals stomachs, discriminated by ontogenic state and NAFO Divisions.

Predator	NAFO Div	Ontogeny	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996
Atlantic Cod	2J	Small	2	4	30	4	9	1	0	0	1	74	22
		Medium	989	946	832	1020	778	529	253	86	59	241	251
		Large	0	0	0	0	0	0	0	0	0	1	0
	3K	Small	15	18	71	87	41	3	4	1	2	63	44
		Medium	1060	1119	872	1619	1149	1060	521	324	87	273	420
		Large	4	12	0	0	0	1	0	0	0	0	0
	3L	Small	6	9	12	9	10	5	2	0	0	53	49
		Medium	1140	1250	1424	1348	1122	1168	929	308	117	192	332
		Large	19	14	17	13	21	13	5	0	0	0	0
Greenland Halibut	2J	Small	47	24	20	0	0	48	74	25	0	138	226
		Medium	966	827	703	0	0	561	931	721	0	661	821
		Large	206	144	83	0	0	5	2	1	0	0	16

Continued on next page

Table 2.1 – *Continued from previous page*

Predator	NAFO Div	Ontogeny	1986	1987	1988	1989	1990	1991	1992	1993	1994	1995	1996
Greenland Halibut	3K	Small	103	44	77	0	0	89	155	112	0	99	206
		Medium	1179	1748	1189	0	0	1347	1705	1656	0	1061	1684
		Large	29	61	18	0	0	11	2	7	0	1	11
	3L	Small	0	0	0	0	0	0	0	0	0	0	86
		Medium	0	0	0	0	0	0	0	0	0	65	944
		Large	0	0	0	0	0	0	0	0	0	0	10
Harp Seal	2J3K	Young of the Year	26	30	19	3	3	1	27	1	0	0	5
		Juvenile	277	208	193	184	125	123	116	212	117	120	154
		Adult	93	191	85	81	78	93	66	146	126	84	94
	3L	Young of the Year	0	6	1	1	0	3	19	9	0	4	2
		Juvenile	19	0	9	4	11	10	50	61	50	35	40
		Adult	0	0	1	0	1	3	20	16	28	9	4

Table 2.2: Description of the variables used in the multinomial regression models to explain the diet compositions of Atlantic cod, Greenland halibut and harp seals in the Northwest Atlantic.

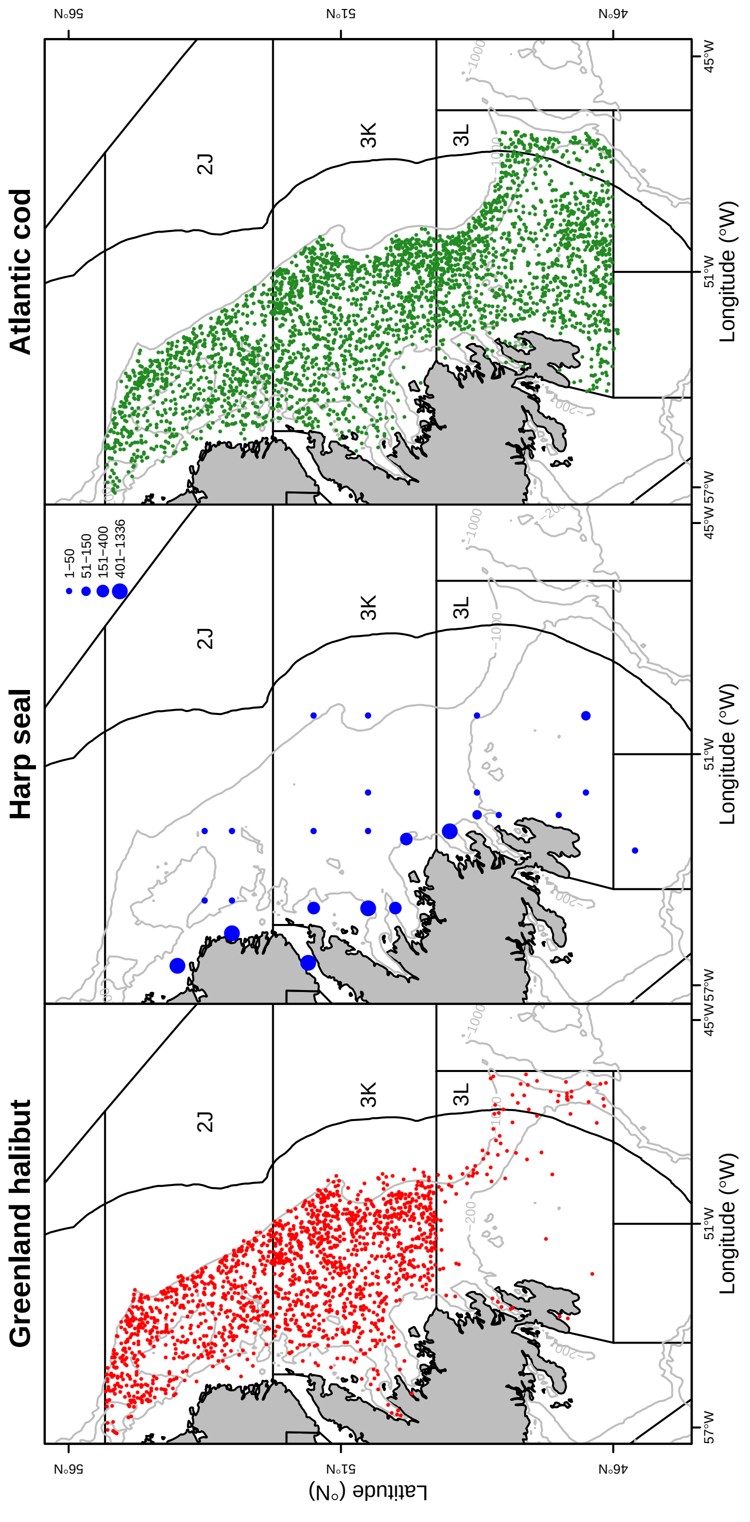
Factor	Atlantic cod	Greenland Halibut	Harp Seal
Ontogeny	Small Medium Large		Young of the year Juvenile Adult
NAFO Division	2J 3K 3L		2J3K 3L
Depth	Shelf(> -400 m) Deep(≤ -400 m)		Inshore Offshore
Season	NA		W(Oct-Mar) S(Apr-Sep)
Sex	Male Female		
Year	1986-1996		

Table 2.3: Analysis of effects from the multinomial regression models

Predator	Factor	df	Wald Chi-Square	p-value
Atlantic Cod	Ontogeny	24	511.2	<0.0001
	NAFO Division	24	876.2	<0.0001
	Depth	12	150.9	<0.0001
	Season	NA	NA	NA
	Sex	12	20.4	0.0596
	Year	12	907.2	<0.0001
Greenland Halibut	Ontogeny	24	1230.3	<0.0001
	NAFO Division	24	805.2	<0.0001
	Depth	12	821.1	<0.0001
	Season	NA	NA	NA
	Sex	12	52.1	<0.0001
	Year	12	1243.8	<0.0001
Harp Seal	Ontogeny	24	372.3	<0.0001
	NAFO Division	12	174.1	<0.0001
	Depth	12	185.3	<0.0001
	Season	12	348.1	<0.0001
	Sex	12	11.2	0.5104
	Year	12	695.1	<0.0001

2.8 Figures

Figure 2.1 *(following page)*: Study area and sampling locations of (a) Greenland halibut, (b) harp seals, and (c) Atlantic cod. In the case of Atlantic cod and Greenland halibut, each dot represents a fishing set and in the case of harp seals they represent approximate sampling location. Relative sizes indicate sample size.


Greenland halibut
Harp seal
Atlantic cod
2J
3K
3L
1–50
51–150
151–400
401–1336
200
1000
56°N
51°N
46°N
Latitude (°N)
57°W
51°W
45°W
Longitude (°W)

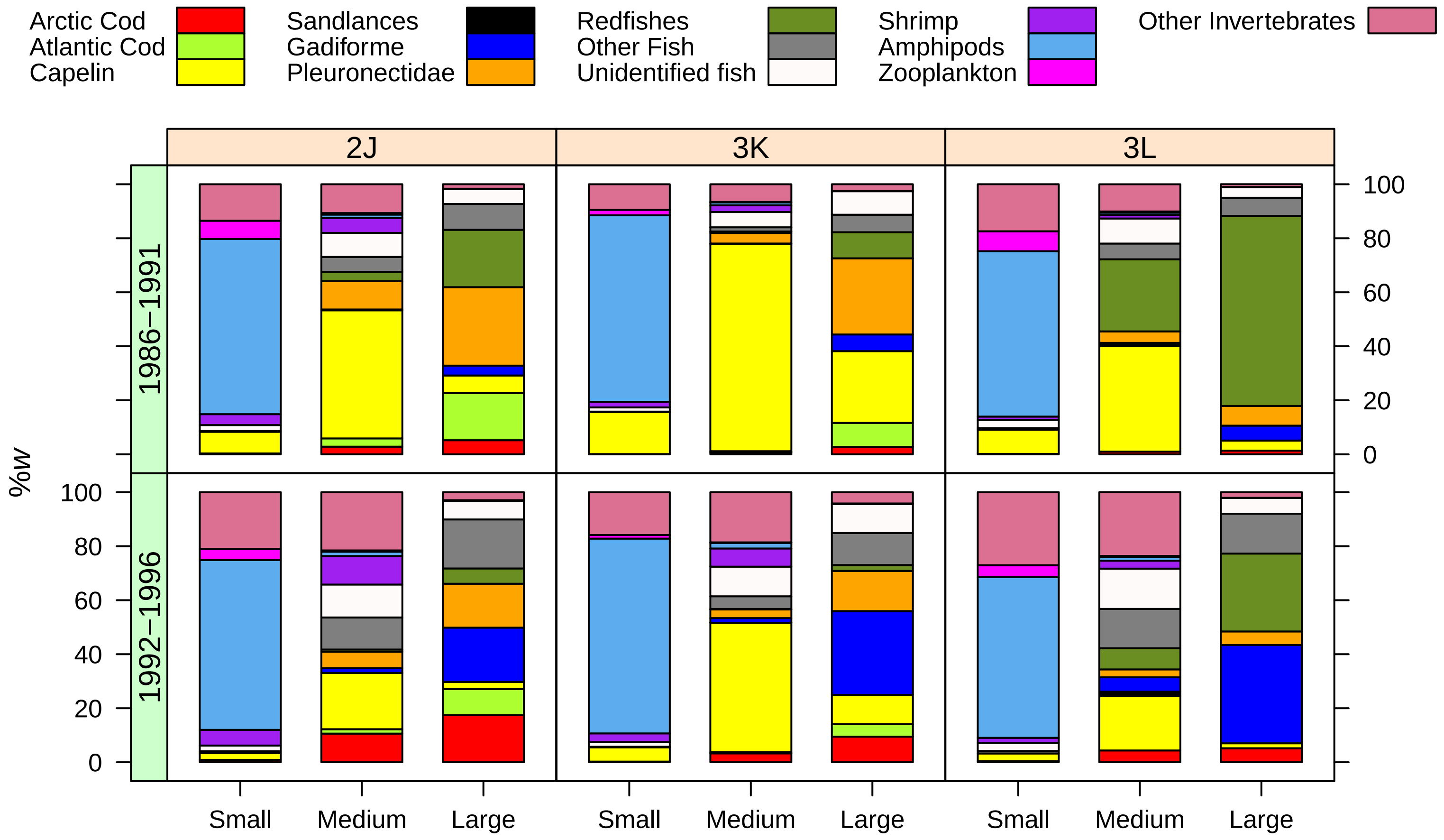


Figure 2.2: Diet composition of Greenland halibut (described in terms of main prey) by NAFO Division, expressed in terms of percentage mass, in the periods preceding and following the groundfish collapse.

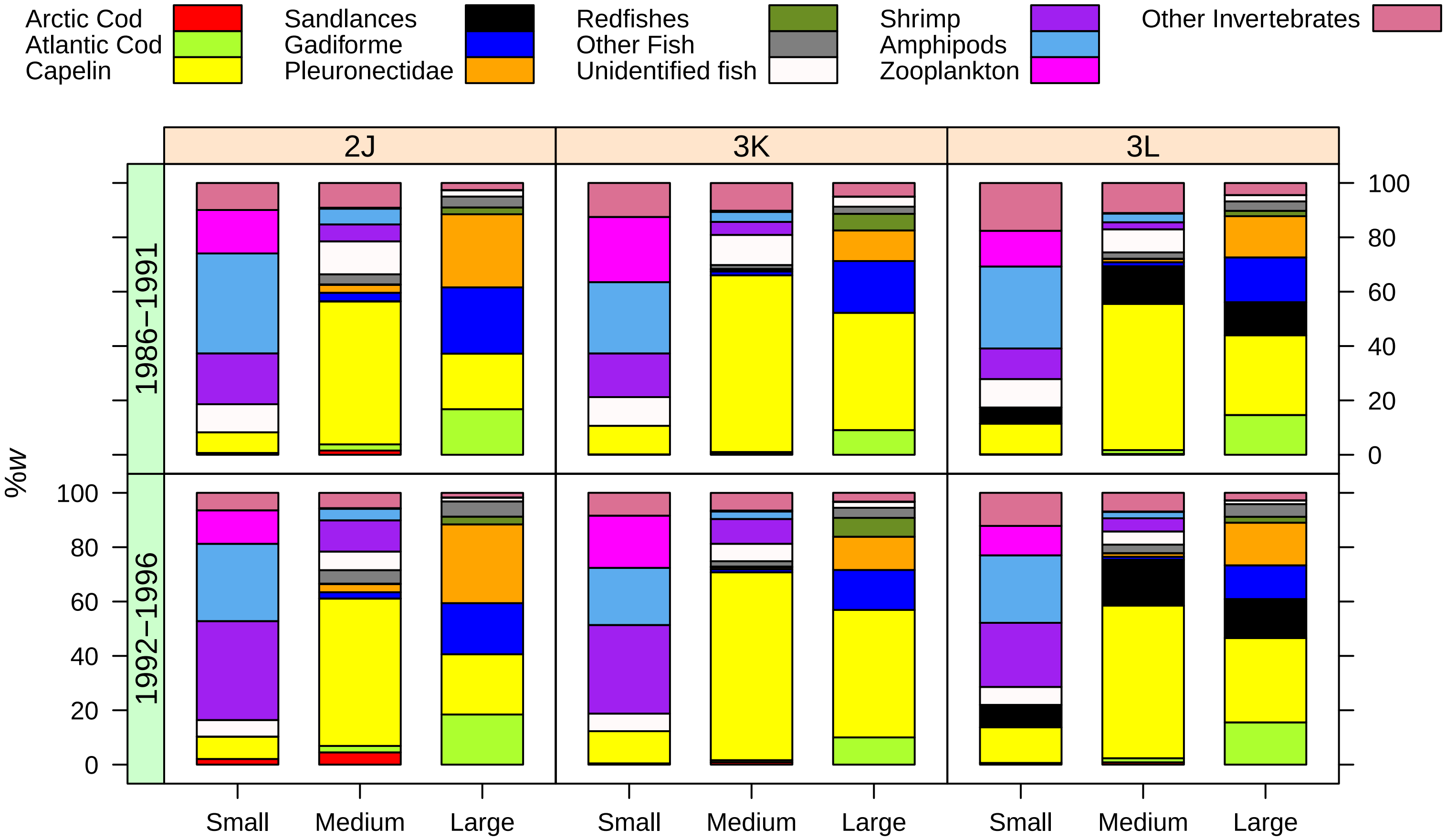


Figure 2.3: Diet composition of Atlantic cod (described in terms of main prey) by NAFO Division, expressed in terms of percentage mass, in the periods preceding and following the groundfish collapse.

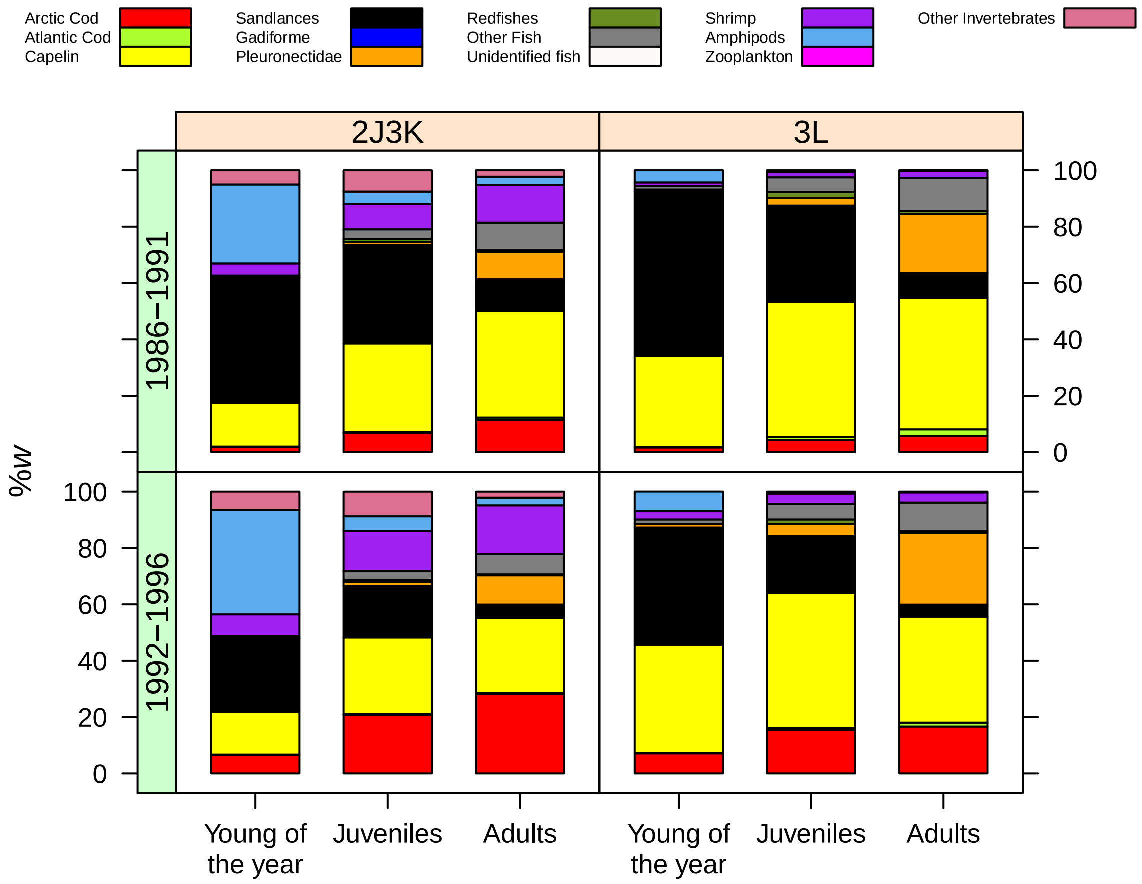


Figure 2.4: Diet composition of harp seals (described in terms of main prey) by NAFO Division, expressed in terms of percentage mass, in the periods preceding and following the groundfish collapse.

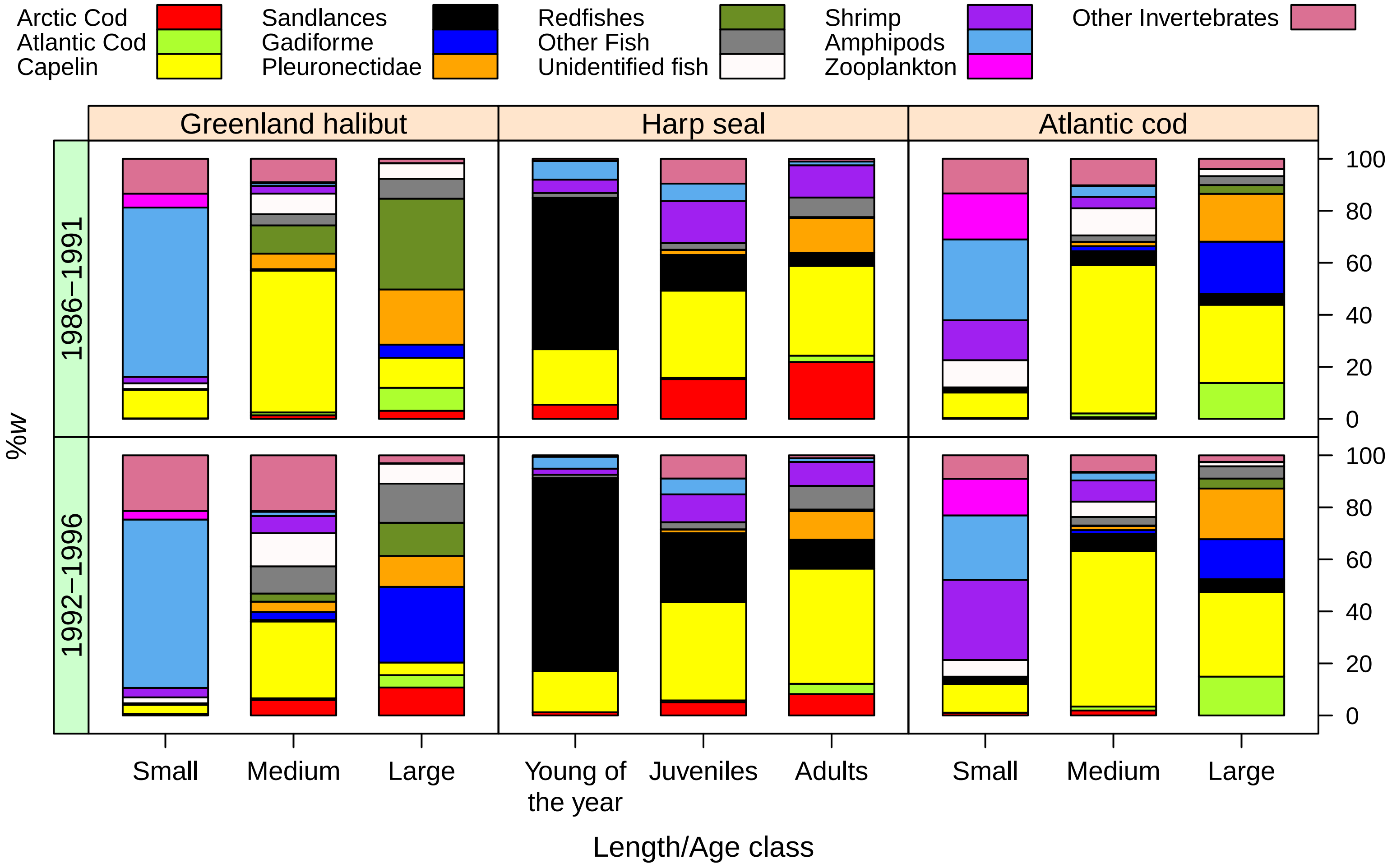


Figure 2.5: Diet composition of Greenland halibut, harp seal and Atlantic cod (described in terms of main prey), expressed in terms of percentage mass, in the periods preceding and following the groundfish collapse.

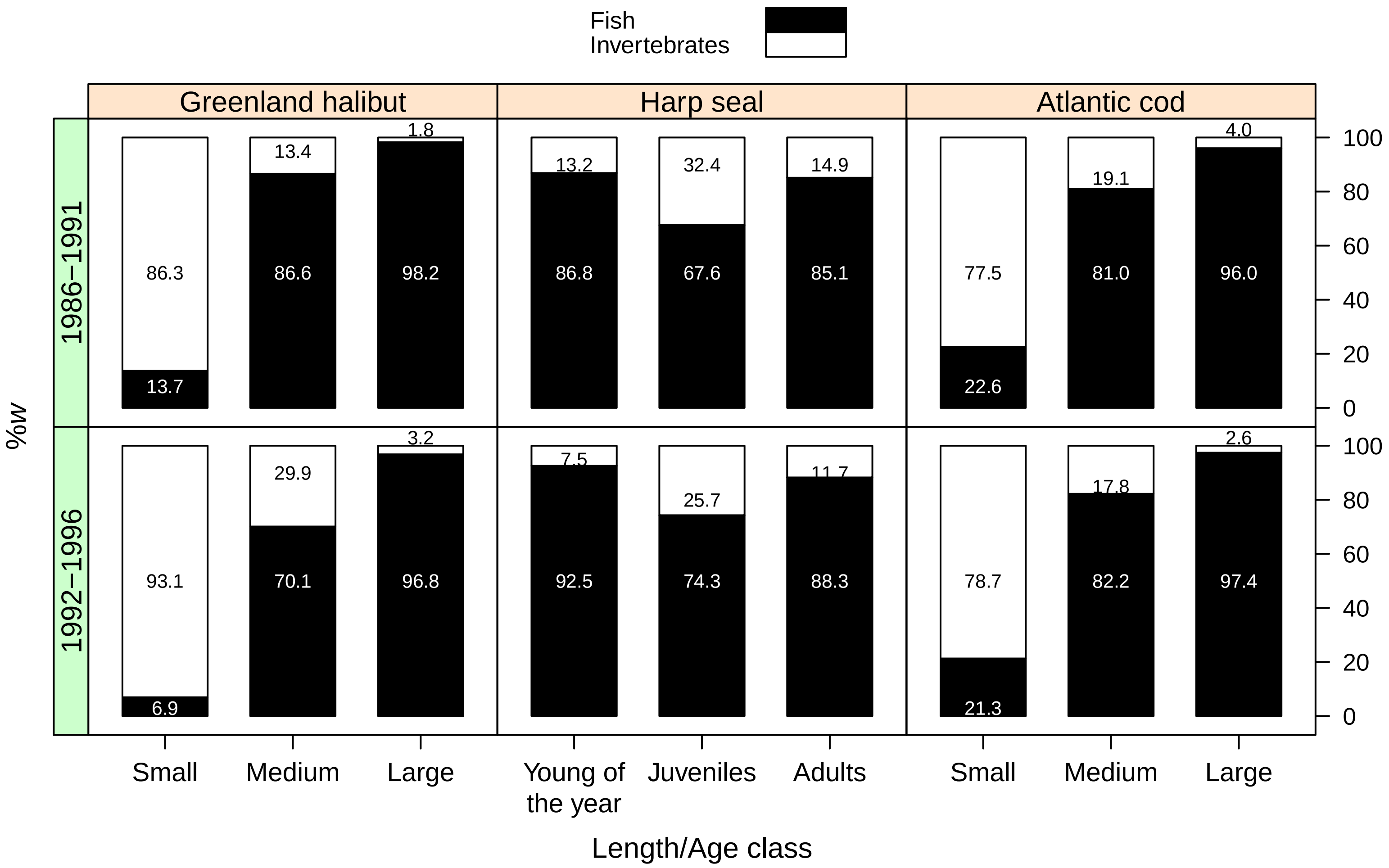


Figure 2.6: Diet composition of Greenland halibut, harp seal and Atlantic cod (described in terms of main prey), expressed in terms of zoological groups, in the periods preceding and following the groundfish collapse. The figures inside or just above the bars represent the percentage weight that the zoological group z ($\%w_z$) represents in th diet.

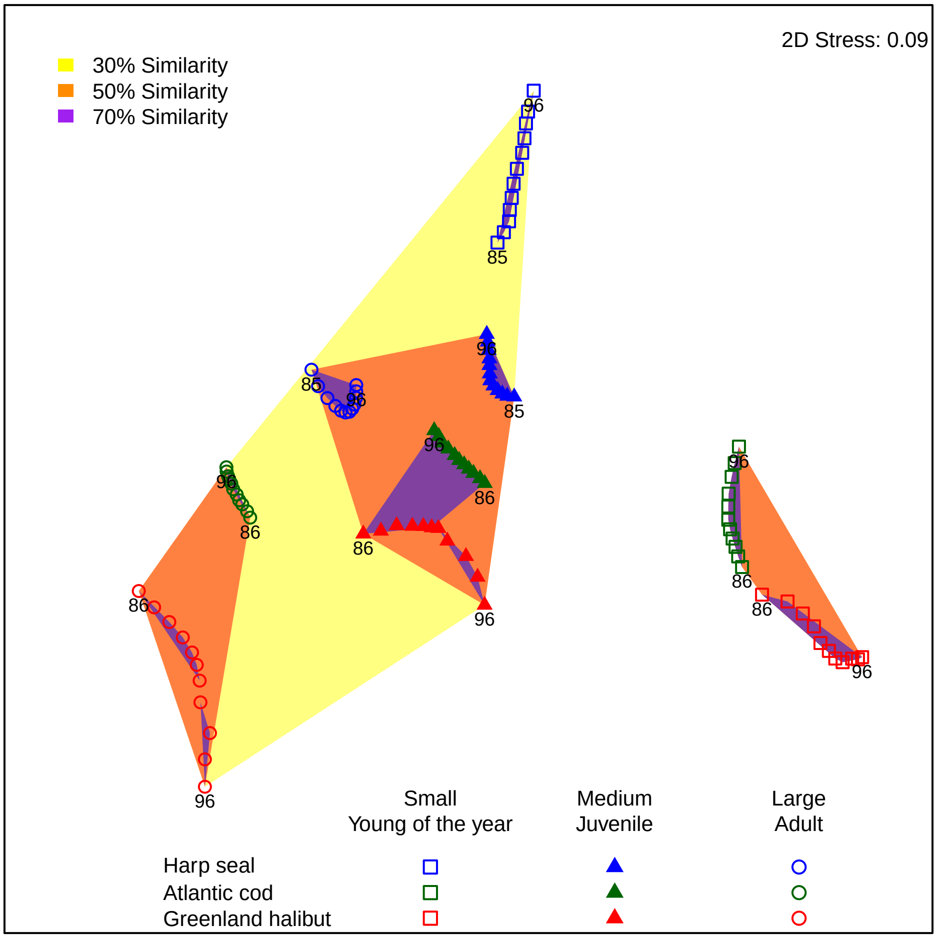


Figure 2.7: Two-dimensional non-metric multidimensional scaling (MDS) ordinations of the diet description of Atlantic cod, Greenland halibut and harp seals discriminated by size/age class and year, based on Bray-Curtis dissimilarity measures (stress=0.09). The first and last years for each trophic group (species-size) are noted below each data point. Hulls represent similarity coefficients calculated by hierarchical clustering.

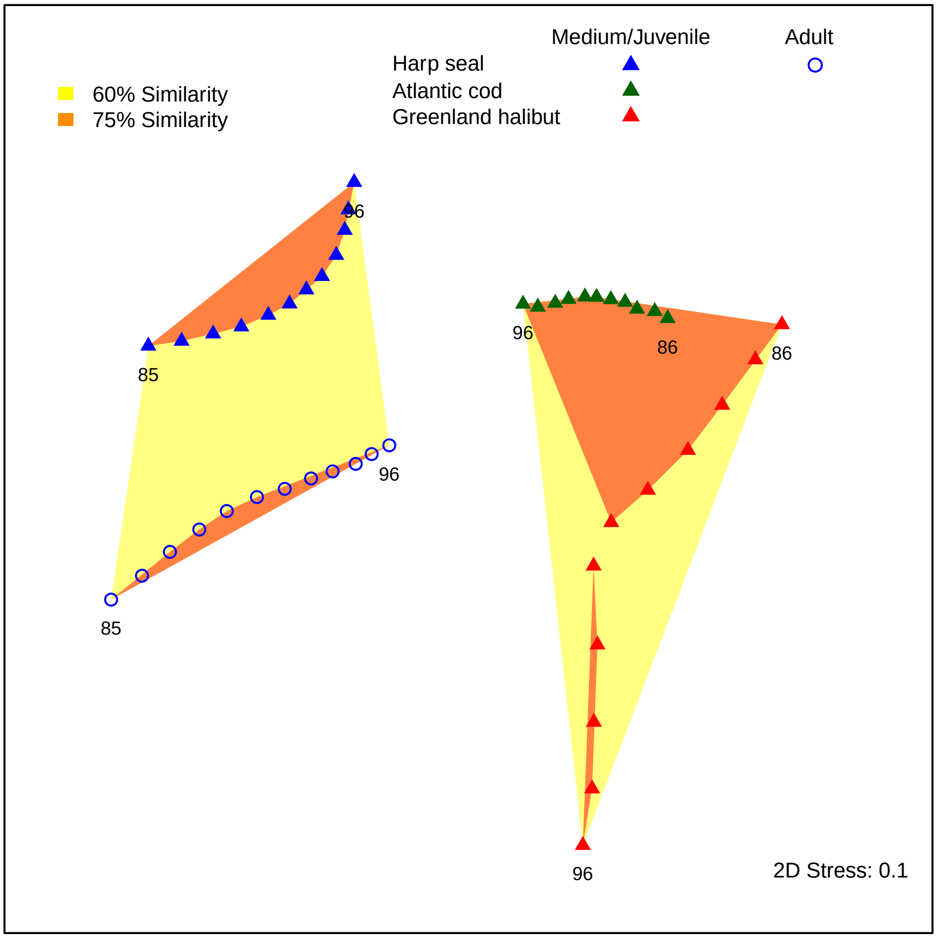


Figure 2.8: Two-dimensional non-metric multidimensional scaling (MDS) ordinations of the diet description of the size/age classes of Atlantic cod, Greenland halibut and harp seals that represent the major proportion of their respective populations, discriminated by year (stress=0.1). The first and last years for each trophic group (species-size) are noted below each data point. Hulls represent similarity coefficients calculated by hierarchical clustering.

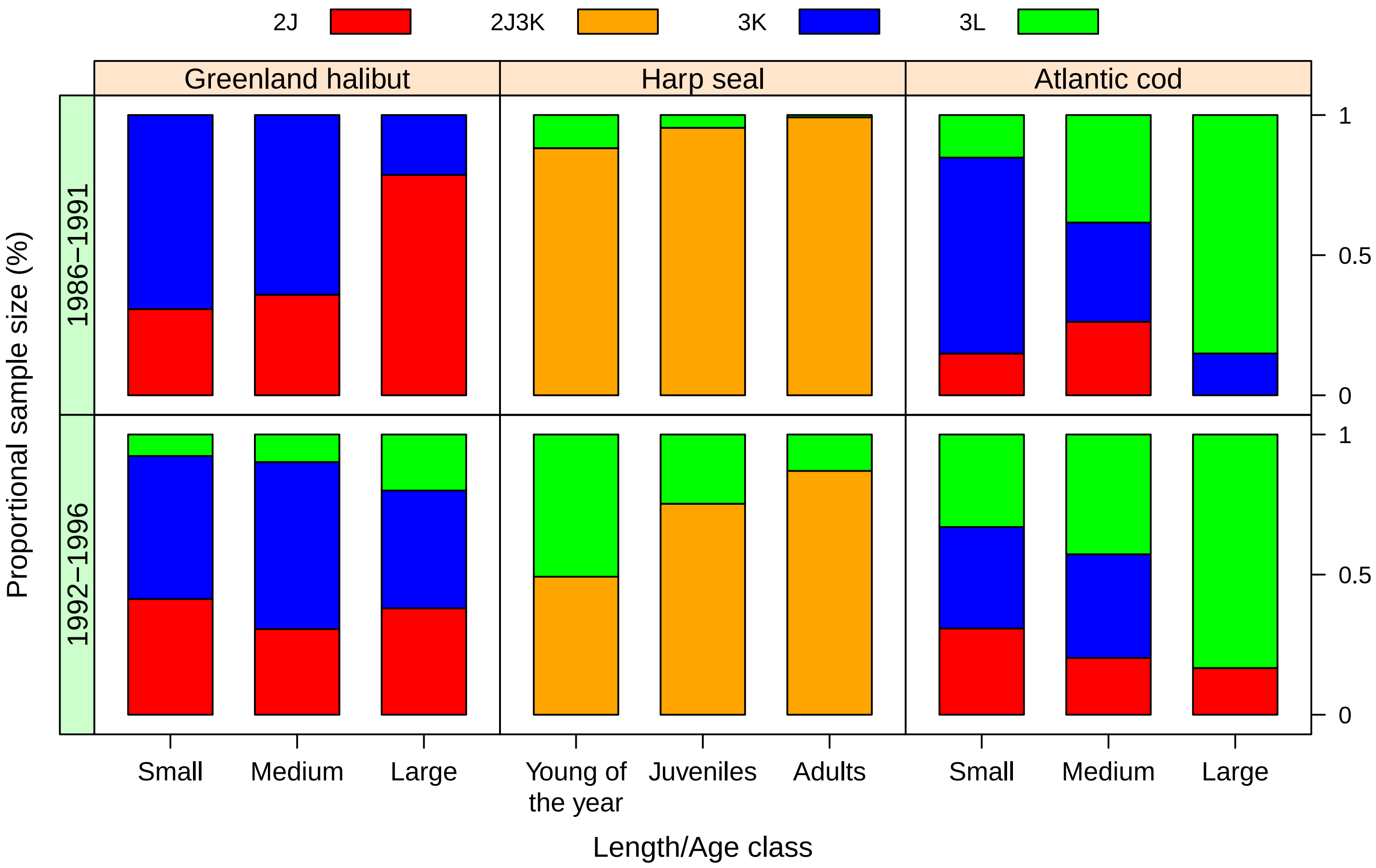


Figure 2.9: Sample sizes expressed as proportion of the total samples collected by predator, time period, length/age class and NAFO Division.

Chapter 3

Bottom-up regulation of capelin, a keystone forage species

3.1 Abstract

The Northwest Atlantic marine ecosystem off Newfoundland and Labrador, Canada, has been commercially exploited for centuries. Although periodic declines in various important commercial fish stocks have been observed in this ecosystem, the most drastic changes took place in the early 1990s when the ecosystem structure changed abruptly and has not returned to its previous configuration. In the Northwest Atlantic, food web dynamics are determined largely by capelin (*Mallotus villosus*), the focal forage species which links primary and secondary producers with the higher trophic levels. Notwithstanding the importance of capelin, the factors that influence its population dynamics have remained elusive. I found that a regime shift and ocean climate, acting via food availability, have discernible impacts on the regulation of this population. Capelin biomass and timing of spawning were well explained by

a regime shift and seasonal sea ice dynamics, a key determinant of the pelagic spring bloom. My findings are important for the development of ecosystem approaches to fisheries management and raise questions on the potential impacts of climate change on the structure and productivity of this marine ecosystem.

3.2 Introduction

The Northwest Atlantic is a highly productive low-Arctic ecosystem that has supported commercial fishing activities for more than half a millennium. The structure of the food web is best described as a wasp-waist pattern, in which a crucial intermediate trophic level is dominated by a single species (Bakun, 2006). The dynamic properties of wasp-waist food webs are critically determined by the species at the waist (Rice, 1995). Capelin (*Mallotus villosus*) fulfils this role in the Northwest Atlantic, acting as a link between zooplankton and large vertebrates (Lavigne, 1996). Consequently, elucidating the mechanisms that regulate capelin populations is important to understanding the dynamics of the system. Trophic control of ecosystems is often described in terms of bottom-up (resource-driven) or top-down (consumer-driven) regulation, though these are just extremes on a continuum; the most parsimonious description is that control is spatially and temporally variable (Frank et al., 2006).

The marine community off the Newfoundland and Labrador Shelf underwent a series of radical changes during the early 1990s; abundance of Atlantic cod (*Gadus morhua*), the dominant groundfish and major predator of the system collapsed (Hutchings and Myers, 1994; Rose et al., 2000; Rice, 2002) while much of the demersal fish community suffered an overall decline (Gomes et al., 1995; Rice, 2002; Koen-Alonso et al., 2010; NAFO, 2010; DFO, 2012), and shellfish biomass increased (Lilly et al., 2000; Worm and Myers, 2003). These changes were accompanied by the ongoing rebuilding of the harp seal (*Pagophilus groenlandicus*) population (Healey and Stenson, 2000; Hammill et al., 2011), and shifts in the diets, phenologies and population trends of seabirds (Montevecchi and Myers, 1997; Gaston et al., 2009). The capelin stock suffered a major biomass decline in 1991, from which it has not yet recovered (DFO, 2010); spawning became protracted and was delayed up to four weeks (Nakashima and Wheeler, 2002; DFO, 2010), while size and age at maturity, and somatic condition declined (Carscadden and Nakashima, 1997; Carscadden and Frank, 2002).

Extensive, and sudden, changes in marine ecosystems such as those observed during the early 1990s on the Newfoundland-Labrador Shelf are usually linked to regime shifts (Hare and Mantua, 2000; Beaugrand, 2002; Chavez et al., 2003; Lees et al., 2006). These are defined as rapid, pervasive, and persistent changes in system structure forced by environmental or anthropogenic (e.g. fishing) perturbations that alter key energy pathways (deYoung et al., 2004). A climate-induced regime shift occurred in the North Atlantic during the 1920s and 1930s, when significant changes in several marine ecosystems of the northern North Atlantic were linked to general ocean warming (Drinkwater, 2006). During 1991, a pulse of fresh water flowing from the

Arctic (Greene et al., 2008) created unusual climatic conditions in the area; the water temperature was the coldest in 50 or more years, reaching a centennially significant nadir (Drinkwater, 1996). The synchrony of this perturbation in the climatic record with the restructuring of the community raises the possibility that they are related.

In this chapter I focus on the regulating mechanisms of the keystone forage species in the system, punctuated by the extreme events of the early 1990s. Despite its role as the main channel of energy flow between basal trophic levels and top predators, little is known about the factors that regulate the capelin population. Given the sudden nature of the changes in capelin during the 1990s, the small magnitude of the capelin fishery (DFO, 2010), and the expected predation release from a declining groundfish assemblage, changes in capelin were likely driven by bottom-up effects, though the mechanisms involved are unknown. Year-class strength is, however, regulated by meteorological and hydrographical variables (Leggett et al., 1984).
Copepods, mainly *Calanus finmarchicus*, are the most important prey species for capelin in the NW Atlantic (Gerasimova, 1994; O'Driscoll et al., 2001). At high latitudes, calanoid copepods accumulate large lipid reserves (Sargent and Falk-Petersen, 1988), which likely fuel the growth of predators (e.g. capelin). Copepod production is regulated by physical and biological variables, though their relative strengths are heterogeneous in space and time (Plourde et al., 2009; Neuheimer et al., 2010). *Calanus finmarchicus* production off Newfoundland is affected by temperature and cannibal-

ism by adult females (Neuheimer et al., 2010), which increases when phytoplankton abundance is low (Head et al., 2013). Thus, food availability in spring is likely a limiting factor for *C. finmarchicus* production on the Newfoundland–Labrador Shelf. The spring bloom on the shelf follows the retreat of seasonal sea ice. During winter, pack ice rapidly extends southward from the northern Labrador to the northern Newfoundland coast mainly as a result of local ice formation (Tang, 1991). During early spring accelerated melting causes the ice edge to retreat northward and the freshwater runoff is advected by the Labrador Current onto the Grand Banks, causing rapid stratification of the water column and promoting phytoplankton growth in the shallow mixed layer (Wu et al., 2007).

The objectives of this chapter are to assess the occurrence of a regime shift during the early 1990s on the Newfoundland-Labrador Shelf marine ecosystem, and to examine the effects of sea ice on capelin population biomass and timing of spawning to evaluate the hypothesis that capelin is environmentally regulated via food availability.

3.3 Materials and Methods

3.3.1 Data series

3.3.1.1 Climate

To assess environmental patterns linked to the climatic perturbation of the 1990s, I examined 5-year running means of air temperature anomalies and their cumulative sums - the methodology used previously to describe the climate forcing associated with the North Atlantic regime shift of the 1920s and 1930s (Drinkwater, 2006). I examined air temperatures anomalies (from the long-term mean; since 1874) recorded at the monitoring station in St. John's, Newfoundland (Figure 3.1) (`http://www.meds-sdmm.dfo-mpo.gc.ca/isdm-gdsi/azmp-pmza/climat/airTemp-eng.asp?stn=STJOHNS`). I also examined the Atlantic Multidecadal Oscillation (AMO) anomalies and their cumulative sums (from the long-term mean; since 1856) (121-month smoothed estimates as provided by NOAA `http://www.cdc.noaa.gov/Timeseries/AMO`). The AMO is an ongoing series of oscillatory changes in basin-wide North Atlantic sea-surface temperature with a period of 65-70 years (Schlesinger and Ramankutty, 1994).

3.3.1.2 Sea ice

Weekly data on sea ice concentration of various thicknesses for 1969-2010 were obtained from the Canadian Ice Service (CIS) (`http://www.ice-glaces.ec.gc.ca/`). Two parameters were derived from each map: southernmost position of the ice edge (10% total ice concentration) and ice-covered area south of 55 °N. Occasionally, ice sheets which are clearly not part of the ice pack that drift southward from the Arctic are retained in Notre Dame Bay (Figure 3.1), and were thus not considered in the derivation of the sea ice parameters. The maximum value of ice area south of 55 °N was then extracted for each year (A_{ice}) , and start time of ice retreat (t_{ice}) was considered to be the day when the ice edge reached the southern-most latitude in a given ice season (November-July).

3.3.1.3 Capelin

I used a capelin stock biomass index derived from Fisheries and Oceans Canada's (DFO) spring acoustic survey (methodological details in Mowbray, 2002). Given its typical pelagic behaviour, standard random-stratified bottom trawl surveys are not the best method to estimate capelin abundance; although the introduction of the Campelen gear in DFO's research surveys in the region in 1995 (Warren, 1997; Warren et al., 1997) significantly improved the survey performance for small fishes, including capelin. Notwithstanding these improvements, the most reliable method for estimating capelin abundance is acoustic integration supported by directed trawling (O'Driscoll et al., 2002). In this context, there are no reliable estimates of spring spawning biomass for the entire stock that spans before and after the 1991 biomass decline, but an index covering the core of the historical spring distribution area is available from the DFO's spring acoustic survey (DFO, 2010). Since this survey has only partial coverage of the entire stock area, the estimates it provides are considered to be minimum biomass estimates. Nonetheless, the estimates from this survey show a high degree of internal consistency, and thus the relative biomass index for the capelin stock in the region can be considered reliable (Mowbray, 2012). Directed trawling is used to assess the age structure of the stock being measured acoustically. Due to gear's size dependent catchability, age 1 capelin has been poorly represented and, age 2, followed by age 3 fish accounted for the majority of fish caught in most years (Mowbray, 2012). Historically, the spawning populations were composed of mainly three and four year old fish. However, since the early 1990s spawning populations have consisted predominantly of two and three year old fish, with the percent maturing of two year-old reaching almost as high as 80% (Mowbray, 2012; DFO, 2013). Capelin biomass estimates from DFO's spring acoustic survey are available for the years 1982, 1985-1992, 1996, 1999-2005 and 2007-2010. Monte Carlo simulations were implemented to estimate 95% confidence intervals (methodological details in Mowbray, 2012). Raw acoustic data were not available for years prior to 1988; hence confidence limits could not be calculated.

To examine the difference in the timing of spawning, I used a long term data set from two beach sites in Newfoundland (methodological details in Carscadden et al., 1997). The Annual date of peak spawning has been recorded systematically at Bryant's Cove, 1978-2010 and Bellevue Beach, 1990-2010 (Figure 3.1) (DFO, 2010).

3.3.1.4 Prey of Capelin

Abundance estimates of adult *Calanus finmarchicus* (6^{th} copepodite stage) were based on collections from DFO Atlantic Zone Monitoring Programme (AZMP) (`http://www.meds-sdmm.dfo-mpo.gc.ca/isdm-gdsi/azmp-pmza/index-eng.html`) along two oceanographic sections on the Newfoundland-Labrador Shelf (Figure 3.1). Data are available from 1999-2010 only, and thus effects of *C. finmarchicus* availability on capelin biomass and/or timing of spawning could not be assessed directly. Complete details of field and laboratory protocols are available in Mitchell et al. (2002). I focussed analyses on the abundance of the adult stages (6^{th} copepodite stage, CVI) of *C. finmarchicus* because capelin feed predominantly on these larger copepods (O'Driscoll et al., 2001) which are most abundant, in terms of numbers and overall proportion of the population, in the late autumn and early spring (i.e. prior to the surveys from which capelin abundance are derived). Annual estimates (1999-2010) of water column inventories of adult *Calanus finmarchicus* from the Shelf stations (depth $<$ 400m) along the Bonavista and Seal Island lines were based on general linear models of the form ln(Density)˜year+station+season for each oceanographic section, where Density is in units of m^{-2}, based on type III sums of squares estimates of overall year effect (Pepin et al., 2011).

3.3.2 Analyses

Given the abrupt changes observed in the Newfoundland and Labrador Shelf ecosystem in the early 1990s, I included in all analyses a categorical variable “period” to all the analytical models to discriminate the conditions in the last 2 decades (1991-2010) from those before 1991. The timing of peak spawning at Bryant’s Cove and Bellevue Beach and capelin biomass index were described as functions of “period” and ice parameters. In all cases, ice parameters used were the annual maximum extent of ice (A_{ice}) and start time of ice retreat (t_{ice}), although I only show the ice-capelin relationships with the parameters that yielded the best fit to the data.

3.3.2.1 Capelin biomass

To describe the variations in capelin biomass as a function of the timing of the onset of the spring bloom (triggered by sea ice retreat), I fitted a linear model and two different formulations of a dome-shaped model. I discarded the linear model given that it did not impose an upper bound on the estimated capelin biomass, i.e. as the spring bloom occurred later in the year capelin biomass grew unbounded to extremely high levels. There must be an optimum timing of the spring bloom that yields a maximum of capelin biomass, with either an early or late spring bloom negatively affecting biomass. The difference between the dome-shaped models I used resides in the descending limbs of the functions (i.e. during summer and autumn); if the start time of ice retreat occurs past the optimum, capelin biomass in one of the functions declines to some extent, while in the second it eventually reaches zero . Given that the explanatory variable I am using is a proxy for the timing of the spring bloom, I only have information on the ascending limbs of the functions and thus it is not possible to inform the model with respect to the effect of the start time of ice retreat on capelin biomass if the retreat occurs either in summer or fall. The models had an almost identical fit (not shown here) and thus I decided to present the model where capelin biomass reaches zero, based on the premise that if the bloom does not occur by fall, there will be no food supply available for capelin and thus the biomass will drop to zero. Therefore, the dome-shaped model I used to capture the patterns of variation in capelin biomass had the form:

$$ln(CapelinBiomass) = \begin{cases} \alpha * t_{ice} * \left(1 - \frac{t_{ice}}{\beta}\right) & \text{if } year < 1991 \\ \alpha * t_{ice} * \left(1 - \frac{t_{ice}}{\beta}\right) * \delta & \text{if } year \geq 1991 \end{cases} \tag{3.1}$$

where α and β are the parameters that determine the shape of the dome and δ is a scale parameter that represents the effect of “period”. The optimum start time of ice retreat (i.e. timing that results in maximum capelin biomass) is $\beta/2$. I assumed a normal multiplicative observation error (on the logarithmic scale), and fit the model by minimizing the negative log-likelihood function using the ”nlminb” function in R (R Core Team, 2012). The maximum likelihood estimates of the parameters were used to produce a hindcast of capelin biomass predicted from the values of (A_{ice}) since 1972. These predictions were compared with estimates of capelin biomass on January 1st 1972-1980 produced by sequential capelin abundance models (SCAM; Carscadden, 1983). These models are similar to VPA and cohort analysis, and were used in the past to provide management advice (Carscadden, 1983). I also forecast the capelin biomass and compared the prediction to the acoustic estimate for 2011.

3.3.2.2 Capelin spawning

To describe the relationship between spawning timing and sea ice, I fitted a general linear model of the form peakdate˜ A_{ice}+ beach + period, where beach is either Bryant's Cove or Bellevue Beach. I did not include the peak spawning date in 1990 at Bellevue Beach, as this was the only datum available for the period pre-1991. To assess the significance of A_{ice}, I constructed an empirical frequency distribution by bootstrapping the residuals within each period and beach ($n_{boot} = 500000$). Maximum likelihood parameter estimates were used to produce forecast spawning dates in 2011, and these were compared to field observations.

3.3.2.3 Prey availability

If capelin is regulated by bottom-up processes from the base of the food web, I would expect to find a relationship between the timing of retreat of sea ice (as a proxy of the timing of onset of the spring bloom) and the abundance of capelin's main prey, *C. finmarchicus.* To explore this relationship, I fitted a general linear model of the form ln(abundance Calfin)˜ A_{ice} + line, where line refers to the AZMP lines where abundance was estimated: Seal Island and Bonavista (Figure 3.1). To assess the significance of A_{ice}, I constructed an empirical frequency distribution by bootstrapping the residuals within each line ($n_{boot} = 500000$).

3.4 Results

3.4.1 Climate

Air temperature at St John's (Figure 3.2) was relatively cool during the latter part of the 19th century and the beginning of the 20th, compared to temperatures during the mid-20th century and especially compared to the latter part of the 20th and beginning of the 21st centuries. The cumulative sum of air temperature anomalies abruptly changed sign in 1929 (Figure 3.2). During the early 1990s, air temperature was substantially colder than average, though by 1996 it increased rapidly and has since remained at above average values.

The AMO shows a periodicity of ˜65 years (Figure 3.2). Notably, the minimum points of the cumulative sum of the AMO cycle (when the system switches from a cool to a warm phase) coincided with the transitional periods in the air temperature time series (Figure 3.2).

3.4.2 Sea ice

Maximum annual extent of sea ice is highly variable, ranging from ˜150,000 to ˜475,000 km^2 (Figure 3.3a), with the exception of 2010 and 2011, when (A_{ice}) was at its minimum at 88,000 and 101,000 km^2 respectively. Variability in (A_{ice}) has however been declining since the mid-1990s (Figure 3.3a).

The timing of the retreat of sea ice varies between late January and mid-April (Figure 3.3b). In only a few years (1981, 1984, 1991, 1996, 2006, 2010) the retreat of sea ice occurred before February 19 (day 50 of the year). The southernmost extent of ice occurred in 1991, when a narrow ice tongue extended as far south as Boston, USA (42°28′N), and there was ice present off St John's until mid-May. It is noteworthy that both the earliest (January 30) and latest (April 23) ice retreat dates occurred in 2006 and 2007 respectively (Figure 3.3b).

3.4.3 Capelin biomass

Acoustic estimates of capelin biomass (Figure 3.4A) range from 466,000 tonnes (1982) to 5,783,000 tonnes (1990) in the pre-1991 time series. In 1991, the acoustic estimate dropped to 138,000 tonnes (˜10% of historical values) and oscillated around 100,000 tonnes until 2007 when it increased slightly to 300,000 tonnes and remained at a similar level until 2010 when it declined to the lowest estimate in the time series (23,000 tonnes, ˜1% of historical values) (Figure 3.4a).

I found that variations in capelin stock biomass estimates from spring acoustic surveys were well explained by the dome-shaped model (Figure 3.4a,r=0.95, n=21). Maximum capelin biomass occurs when the sea ice retreats northward in early April ($\beta/2$ =93.95=April 4); low biomasses are expected if ice retreats earlier than February 19 (Figure 5). Capelin biomass hindcasts for 1972-1980 agreed well with earlier estimates obtained from SPA analyses (Figure 3.4a). Considering that these earlier estimates were produced with a different methodology and for the beginning of the year (Carscadden, 1983) (unlike the acoustic surveys modelled by my analysis, which are carried out during May-June), the fact that both sets of model predictions show similar trends is important and reassuring. Moreover, the model forecast for 2011 (196,000 tonnes) and the survey acoustic estimate for that year (210,000 tonnes, not used to fit the model) also showed excellent concurrence.

3.4.4 Capelin spawning

Capelin's peak spawning date at Bryant's Cove during the first years of the time series (until 1990) ranged from June 7 (1979) to June 30 (1984) (Figure 3.4b). In the later period, peak spawning date was delayed by about a month, ranging from July 1 (2005) to July 30 (1994). The peak spawning date at Bellevue Beach reflected that at Bryant's Cove, occurring on July 2 (1990) and ranging between July 1 (1994) and August 5 (2009). Peak spawning occurred particularly late in 1993, August 8 (Figure 3.4b).

A large proportion of the variability in the date of peak spawning at Bellevue

Beach and Bryant's Cove was explained by the general linear model (Figure 3.4b, $p(A_{ice})$=0.000008, $r^2 = 0.76$, n=48). Furthermore, there was strong agreement between the predicted and observed dates of peak spawning for 2011, a 1- and 4-day difference for Bellevue Beach and Bryant's Cove, respectively (Figure 3.4b).

3.4.5 Prey availability

I found a positive and significant relationship between the density of adult C. finmarchicus and the timing of retreat of sea ice (Figure 3.4c , $p(t_{ice})$=0.01, $r^2 = 0.65$, n=23).

3.5 Discussion

Capelin exhibited an abrupt state change in the early 1990s that is consistent with a regime shift (see below). I further show that physical factors in the form of seasonal sea ice dynamics regulate the timing of spawning and the population biomass trajectory of capelin in the Northwest Atlantic.

In my analysis of a long-term time series ($>$ 20 years) of capelin population biomass and time of peak spawning in waters off Newfoundland, I explained the time of peak spawning as a linear function of the maximum annual extent of sea ice (A_{ice}) and capelin biomass as a dome-shaped function of the start time of ice retreat (t_{ice}). In both cases I included a break at the year 1991 to account for the extensive changes that occurred in the marine community on the Newfoundland-Labrador Shelf. It is noteworthy that seasonal sea ice dynamics (although different characteristics) drive both biomass and timing of spawning, and that in both cases the year-to-year relationships are not changed after the tipping point in 1991; rather they are merely shifted down in the case of biomass and toward later dates in the case of timing of peak spawning. This suggests that, despite the drastic changes in capelin in particular and the system in general, the mechanisms that modulate timing of peak spawning and stock biomass have remained unchanged.

Carscadden et al. (1997, 2001) proposed that capelin spawning time could be explained by a combination of fish length and an integration of the temperature in the upper 20 m of the water column during February-June (TEMPSUM). These authors hypothesized that temperature modulates spawning time via its effect on zooplankton abundance and on the rates of gonadal development. My explanation of the impact of the environment on spawning time differs from Carscadden et al.'s (1997; 2001) hypothesis (based on data through 1994). I assessed the relationship between timing of spawning at Bryant's Cove and TEMPSUM including data from 1978 to 2009 and found that the relationship breaks down (r=0.06, data not shown), rejecting the hypothesis that temperature regulates spawning timing via accelerated gonad development in warmer years. My analyses indicate that timing of spawning can be described by a combination of the maximum annual extent of sea ice (A_{ice}) and a categorical variable "period", which effectively separates pre-1991 data from the last 20 years of the time series. I found that (A_{ice}) and TEMPSUM are negatively correlated (r=-0.75, data not shown), i.e. the annual maximum extent of sea ice is larger in colder years, which explains the transient positive relationship between temperature and timing of spawning Carscadden et al. (1997) found. They reported lengths in the 160-180 mm range prior to 1991 and 140-160 mm range thereafter (Figure 5 in Carscadden et al., 1997). Subsequent analysis indicates that lengths have remained in the 140-160 mm range (DFO, 2010) suggesting that a shift occurred in 1991, rather than a continuous relationship between spawning timing and capelin length. Though the mechanisms that regulate the timing of spawning are yet not clear, it is likely that fall (which determine the amount of energy reserves maturing capelin accumulate) and spring feeding conditions (which are related to the way sea ice impacts the phytoplankton spring bloom) interact to influence spawning time.

The biomass model captured biomass values very well and, most importantly, the temporal trends (Figure 3.4a). The only year when the model behaved somewhat poorly was 1999. A number of unusual biological events occurred in 1999 (Ouellet et al., 2003; Smith et al., 2003; Head et al., 2005), including the occurrence of the Pacific diatom *Neodenticula seminae* on the Labrador Shelf for the first time in 800,000 years (Reid et al., 2007).

The reliability of the capelin biomass model was explored by a) generating a hindcast and contrasting these predictions with existing estimates of a sequential capelin abundance model and, b) forecasting the 2011 biomass (196,000 tonnes) which could be compared to the acoustic estimate (210,000 tonnes). The reasonable agreement between the data and hindcast and good agreement with the forecast projections support the identification of plausible mechanisms that regulate capelin biology. That is 1) a regime shift in the early 1990s, and 2) seasonal sea ice dynamics as a regulator of primary production on the Newfoundland and Labrador Shelf (its impact percolating through the food web via *Calanus finmarchicus* to capelin).

3.5.1 The regime shift

In addition to continuous state changes, ecosystems may undergo punctuated, drastic shifts when environmental conditions cross a threshold tipping point (Scheffer et al., 2001). In this chapter I used a variable "period" to explain the biological changes that occurred in the Northwest Atlantic. Here I link this sudden change in biological variables to environmental forcers, and, propose that a regime shift occurred on the Newfoundland-Labrador Shelf during the early 1990s.

Two clear breaks occurred in the data series of meteorological patterns I analysed (late 1920s and early 1990s). In addition, the largest annual decline in the North Atlantic Oscillation (NAO) was recorded in 1996 (Drinkwater, 2004), synchronously with the second break. This suggests the occurrence of two regime shifts, the first in the late 1920s which is consistent with Drinkwater's (2006) description, and the second during the early to mid-1990s, characterized by a brief period (1991-1995) of transient climatic forcing. The concomitant restructuring of the system described above (collapse of groundfish stocks, increase in shellfish, extensive changes in capelin biology, rebuilding of harp seal population, changes in seabirds' biology), and the persistence of this new state are consistent with the definition of regime shifts.

I interpret the 1990s regime shift as the result of synergistic climatic and anthropogenic forcers. The system has been intensively exploited for centuries, targeting top predators (e.g. Atlantic cod) significantly reducing their stock sizes (Steele et al., 1992). Apex predators link multiple sub-systems in complex food webs conveying system stability (McCann et al., 2005; Rooney et al., 2006). Thus, these large removals likely eroded the system's resilience, possibly paving the way for major changes when exposed to a punctuated extreme event (Scheffer et al., 2001). Climate change altered Arctic circulation patterns leading to enhanced low-salinity export into the Northwest Atlantic (Greene et al., 2008). A major pulse of surface water flowed from the Arctic through the Canadian archipelago reaching the Northwest Atlantic in 1991, causing a regime shift in the Georges Bank ecosystem (Greene and Pershing, 2007; Greene et al., 2008). This rare event, acting on a system already under stress, likely affected the state of the Newfoundland-Labrador Shelf ecosystem, moving it to a different configuration (Koen-Alonso et al., 2010; NAFO, 2010; DFO, 2012). The reversal in the trend of atmospheric variables by the mid-1990s (Figure 3.2) potentially affected the currently dominant ecosystem configuration.

3.5.2 The capelin regulating mechanism

I hypothesize that the mechanistic linkage between sea ice and the modulation of capelin is a match/mismatch phenomenon between the timing of the onset of the spring bloom, triggered by the retreat of sea ice (Wu et al., 2007), and the abundance of emergent *Calanus finmarchicus* (capelin's main prey) from diapause, with its effects percolating to capelin via nutritional stress.

Capelin feed in the late summer and autumn, building up their somatic lipid reserves which reach their maximum by the end of the year (Montevecchi and Piatt, 1984, Figure 3.6). During winter (January-March) capelin do not feed and concentrate in large, inactive schools in cold water (Winters, 1970). Gonad development and maturation begins in early April, when capelin concentrations move toward warming surface waters to feed. Somatic lipid reserves are moved to the gonads, decreasing somatic condition through the spring, and reaching a minimum prior to spawning (Figure 3.6), making this a key period in their phenology. The timing of the DFO acoustic capelin surveys (May-June, Figure 3.6) is ideal for capturing the realisation of processes that occur during spring. I hypothesize that if capelin do not find an abundant food source during this critical stage, it would lead to augmented natural mortality either via starvation or enhanced susceptibility to predation and reduced competitive abilities.

An alternative explanation would be that as a result of low *Calanus* abundance (during years when the ice retreats early) capelin may redistribute. Distribution and migratory patterns of Barents Sea capelin depend on stock size, as a large stock leads to food depletion and consequent relocation to meet higher food demands (Fauchald et al., 2006; Ingvaldsen and Gjøsæter, 2013). As a result of relocating, capelin may either not spawn at all or spawn elsewhere and the resulting progeny would be lost to the stock, along with the progenitors due to the high level of post spawning mortality (Templeman, 1948; Jangaard, 1974; Shackell et al., 1994; Flynn et al., 2001).

Calanus finmarchicus feed intensively on phytoplankton during summer accumulating large lipid stores. Later in the season they sink into deep water and undergo diapause, a phase of arrested development and reduced metabolism (Conover and Huntley, 1991). In spring, the dormant stages re-emerge and migrate to surface waters taking advantage of the spring phytoplankton bloom to support high reproductive rates (Conover, 1988). Emergence on the Newfoundland-Labrador Shelf is highly variable and begins before the spring chlorophyll peak (Johnson et al., 2008), from late February to late April (Head et al., 2013). Adult and offspring *Calanus* survival will be enhanced if this period coincides with the peak spring bloom; adults will have an improved body condition and offspring will be subjected to lowered rates of cannibalism. If, on the other hand, the onset of the bloom occurs too early in the season, *Calanus* will likely emerge too late to fully utilize the high chlorophyll concentrations during the bloom, resulting in low *Calanus* biomass. The timing of the spring bloom on the Newfoundland-Labrador Shelf is determined by the timing of retreat of seasonal sea ice from the area (Wu et al., 2007). If match/mismatch were the regulating mechanism, I would expect the positive relationship between timing of retreat of sea ice and *C. finmarchicus* abundance in the spring which was observed (Figure 3.4c).

These results indicate that the energy flow in the Newfoundland Shelf ecosystem seems to be controlled by bottom-up processes. This finding is consistent with the form of regulation of many forage fish, which show strong and rapid population responses to environmental variability (Schwartzlose et al., 1999; Cury et al., 2000; Chavez et al., 2003; Alheit and Niquen, 2004; Pikitch et al., 2012). My bottom-up regulation hypothesis contrasts with Frank et al.'s (2006) proposal that the control is exerted from the top-down. The foundation for their assertion is a negative correlation between the abundance of benthic and forage fish species from 1970-1994, as measured by scientific bottom trawl surveys (their Figure 3). They describe the abundance of forage fish as oscillating until the mid-1980s and increasing thereafter. Because capelin is the most abundant forage fish in the system, their "forage fish" signal must be driven primarily by the abundance of capelin, so this figure contradicts the accepted view of capelin's history (Figure 3.4a) (DFO, 2010). The reason for this discrepancy lies in the methodology used to estimate capelin abundance on the Newfoundland-Labrador Shelf. Frank et al. (2006) estimated forage fish abundance from bottom trawl survey data, but the Campelen trawl, which improved the ability of Newfoundland and Labrador DFO bottom trawl surveys to estimate small fishes, was only introduced in 1995. Prior surveys in the region, which were the ones used by Frank et al. (2006), used the Engels trawl, which has a known poor performance for catching small fishes, making them an unreliable source for estimating capelin abundance.

Capelin is a key prey for many predators in the system, such as cod (Lilly, 1987, 1991; Rose and O'Driscoll, 2002), harp seals (Stenson, 2012), Greenland halibut (*Reinhardtius hippoglossoides*) (Dwyer et al., 2010), whales (Lawson and Stenson, Fisheries and Oceans, unpublished data) and seabirds (Davoren and Montevecchi, 2003; Montevecchi, 2007; Buren et al., 2012). Although these predators consume large amounts of capelin annually (Bundy et al., 2000; Barrett et al., 2006; Stenson, 2012), the trends in capelin abundance and consumption are not consistent with the theory of top down control. Further, predator consumption does not change instantly and therefore cannot account for the sudden change in capelin abundance observed during the 1990s. Based upon the biomass model, the effects of bottom-up environmental forcers account for over 90% of the variation in the time series of stock biomass indicating that the capelin population is not regulated by top-down mechanisms.

The Newfoundland-Labrador Shelf ecosystem is similar in some respects to the Norwegian and Barents Seas and the Iceland basin that are influenced by Atlantic and Arctic currents, and have relatively simple structures, with one main group of zooplankton *Calanus* spp., pelagic forage fish (capelin, herring, blue whiting (*Micromesistius poutassou*)), and demersal fish (most prominently Atlantic cod), marine mammals, and seabirds at the top of the food web. As in the Newfoundland-Labrador Shelf ecosystem, physical forcers play substantial roles in regulating these northern marine ecosystems. Large bottom-up driven bio-geographical shifts have been recorded in the Iceland basin, and changes in the strength and extent of the subpolar gyre have been associated with changes in four trophic levels – phytoplankton, zooplankton, blue whiting and pilot whales (*Globicephala melas*) (Hatún et al., 2009). The ecosystems of the Barents and Norwegian Seas are controlled by top-down and bottom-up forces: climate variability influences fish distribution, abundance, production, and growth rates. In addition, fish abundance is also controlled by complex interspecific interactions among fish species, particularly cod, capelin and herring, and their zooplanktonic prey, and predation by marine mammals (Loeng and Drinkwater, 2007). The Barents Sea capelin stock underwent three collapses in the last 3 decades. The effects of the collapses propagated up and down the food web; zooplankton abundance increased due to release from predation pressure, and predators (cod, harp seals and seabirds) suffered negative consequences due to nutritional stress (Gjøsæter et al., 2008).

The role of sea ice in the regulation of ecosystem function has been highlighted in the pelagic ecosystem of the eastern Bering Sea, where the timing of primary production is determined by the timing of ice retreat, but secondary (zooplankton) production is sensitive to water temperature (Hunt Jr. et al., 2002).

In this chapter I have described the bottom-up forcers that regulate capelin in the Newfoundland-Labrador Shelf ecosystem. Although not a full account of energy flow regulation in the system, having advanced our understanding of the mechanisms that regulate the key forage species is a step in the right direction.

3.6 Concluding remarks

I have provided evidence for bottom-up control of energy flow in a wasp-waist marine ecosystem, the Newfoundland and Labrador Shelf, driven by physical factors through at least three trophic levels: from primary producers to zooplankton to forage species. Given the central role of capelin as a keystone species, it is expected that the bottom-up control would reverberate through the food web to the major predatory species. The implications of this finding are far-reaching in terms of achieving sustainable fisheries at the ecosystem level, i.e. not just for better defining capelin management practices, but also for delineating strategies that would promote recovery for higher trophic level species (Hutchings et al., 2012). Traditional fisheries management has focused on target species, assuming that the main driving forces of exploited stocks are the fisheries themselves. Rarely are changes in productivity state and interactions among ecosystem components considered. My results indicate that incorporating the impacts of environmental forcing on ecosystem productivity is a fundamental basis on which to develop Ecosystem-Based Management approaches (Pikitch et al., 2004). My findings are also relevant under the light of climate change predictions of general warming in the area (IPCC, 2007). It is unclear how the dynamics of seasonal sea ice will be affected and in turn how this will affect the system's primary productivity. Climate change may elicit non-linear responses affecting patterns of synchrony among system components that can fundamentally change the energy flow and structure of the Northwest Atlantic food web.

3.7 References

Alheit, J. and Niquen, M. C. (2004). ‘Regime shifts in the Humboldt Current ecosystem’, *Prog Oceanogr* 60(2-4), 201–222.

Bakun, A. (2006). ‘Wasp-waist populations and marine ecosystem dynamics: Navigating the ”predator pit” topographies’, *Prog Oceanogr* 68, 271–288.

Barrett, R. T., Chapdelaine, G., Anker-Nilssen, T., Mosbech, A., Montevecchi, W. A., Reid, J. B. and Veit, R. R. (2006). ‘Seabird numbers and prey consumption in the North Atlantic’, *ICES J Mar Sci* 63(6), 1145–1158.

Beaugrand, G. (2002). ‘The North Sea regime shift: Evidence, causes, mechanisms and consequences’, *Prog Oceanogr* 60(2-4), 245–262.

Bundy, A., Lilly, G. R. and Shelton, P. A. (2000). ‘A mass balance model of the Newfoundland-Labrador shelf’, *Can Tech Rep Fish Aquat Sci* 2310.

Buren, A., Koen-Alonso, M. and Montevecchi, W. (2012). ‘Linking predator diet and prey availability: common murres and capelin in the Northwest Atlantic’, *Mar Ecol Prog Ser* 445, 25–35.

Carscadden, J. (1983), ‘Population dynamics and factors affecting the abundance of capelin (*Mallotus villosus*) in the Northwest Atlantic’.

Carscadden, J. and Frank, K. (2002). 'Temporal variability in the condition factors of Newfoundland capelin (*Mallotus villosus*) during the past two decades', *ICES J Mar Sci* 59, 950–958.

Carscadden, J., Frank, K. and Leggett, W. (2001). 'Ecosystem changes and the effects on capelin (*Mallotus villosus*), a major forage species', *Can J Fish Aquat Sci* 58, 73–85.

Carscadden, J. and Nakashima, B. S. (1997), Abundance and changes in distribution, biology and behavior of capelin in response to cooler water of the 1990s, *in* 'Forage fishes in marine ecosystems. Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program Rep. No. AK-SG-97-01.', University of Alaska Fairbanks, Fairbanks, Alaska, pp. 457–468.

Carscadden, J., Nakashima, B. S. and Frank, K. (1997). 'Effects of fish length and temperature on the timing of peak spawning in capelin (*Mallotus villosus*)', *Can J Fish Aquat Sci* 54, 781–787.

Chavez, F. P., Ryan, J., Lluch-Cota, S. E. and Niquen, M. C. (2003). 'From anchovies to sardines and back: multidecadal change in the Pacific Ocean', *Science* 299(5604), 217–221.

Conover, R. (1988). ‘Comparative life histories in the genera *Calanus* and *Neocalanus* in high latitudes of the northern hemisphere’, *Hydrobiologia* 167-168, 127–142.

Conover, R. and Huntley, M. (1991). ‘Copepods in ice-covered seas–Distribution, adaptations to seasonally limited food, metabolism, growth patterns and life cycle strategies in polar seas’, *J Mar Syst* 2(1-2), 1–41.

Cury, P., Bakun, A., Crawford, R. J., Jarre, A., Quiñones, R. A., Shannon, L. J. and Verheye, H. M. (2000). ‘Small pelagics in upwelling systems: patterns of interaction and structural changes in ”wasp-waist” ecosystems’, *ICES J Mar Sci* 57(3), 603–618.

Davoren, G. K. and Montevecchi, W. A. (2003). ‘Signals from seabirds indicate changing biology of capelin stocks’, *Mar Ecol Prog Ser* 258, 253–261.

deYoung, B., Harris, R., Alheit, J., Beaugrand, G., Mantua, N. and Shannon, L. (2004). ‘Detecting regime shifts in the ocean: data considerations’, *Prog Oceanogr* 60, 143–164.

DFO. (2010). ‘Assessment of capelin in SA2+Div. 3KL in 2010’, *Can Sci Advis Secretar Adv Rep* 2010/090.

DFO. (2012). ‘Results and recommendations from the Ecosystem Research Initiative - Newfoundland and Labrador’s Expanded Research on Ecosystem Relevant but UnderSurveyed Splicers’, *Can Sci Advis Secretar Adv Rep* 2012/058.

DFO. (2013). ‘Assessment of capelin in SA2 + Div. 3KL in 2013’, *Can Sci Advis Secretar Adv Rep* 2013/11.

Drinkwater, K. F. (1996). ‘Atmospheric and oceanic variability in the Northwest Atlantic during the 1980s and early 1990s’, *J Northw Atl Fish Sci* 18, 77–97.

Drinkwater, K. F. (2004). ‘Atmospheric and sea-ice conditions in the Northwest Atlantic during the decade 1991-2000’, *J Northw Atl Fish Sci* 34, 1–11.

Drinkwater, K. F. (2006). ‘The regime shift of the 1920s and 1930s in the North Atlantic’, *Prog Oceanogr* 68(2-4), 134–151.

Dwyer, K. S., Buren, A. D. and Koen-Alonso, M. (2010). ‘Diet of Greenland halibut in the Newfoundland Shelf, Northwest Atlantic, from 1978-2003: reflections of a changing ecosystem’, *J Sea Res* 64, 436–445.

Fauchald, P., Mauritzen, M. and Gjøsæter, H. (2006). ‘Density dependent migratory waves in the marine pelagic ecosystem’, *Ecology* 87(11), 2915–2924.

Flynn, S., Nakashima, B. and Burton, M. (2001). ‘Direct assessment of post-spawning survival of female capelin, *Mallotus villosus*’, *J Mar Biol Assoc UK* 81, 307–312.

Frank, K., Petrie, B., Shackell, N. L. and Choi, J. S. (2006). ‘Reconciling differences in trophic control in mid-latitude marine ecosystems’, *Ecol Lett* 9, 1096–1105.

Gaston, A., Bertram, D. J., Boyne, A. W., Chardine, J., Davoren, G., Diamond, A. W., Hedd, A., Montevecchi, W., Hipfner, J., Lemon, M. J., Mallory, M. L., Rail, J.-F. and Robertson, G. (2009). 'Changes in Canadian seabird populations and ecology since 1970 in relation to changes in oceanography and food webs', *Environ Rev* 17, 267–286.

Gerasimova, O. (1994). 'Peculiarities of spring feeding by capelin (*Mallotus villosus*) on the Grand Bank in 1987-90', *J Northw Atl Fish Sci* 17, 59–67.

Gjøsæter, H., Bogstad, B. and Tjelmeland, S. (2008). 'Ecosystem effects of the three capelin stock collapses in the Barents Sea Published in collaboration with the University of Bergen and the Institute of Marine Research, Norway, and the Marine Biological Laboratory, University of Copenhagen, Denmark', *Mar Biol Res* 5, 40–53.

Gomes, M. d. C., Haedrich, R. L. and Villagarcia, M. (1995). 'Spatial and temporal changes in the groundfish assemblages on the north-east Newfoundland/Labrador Shelf, north-west Atlantic, 1978-1991', *Fish Oceanogr* 4, 85–101.

Greene, C. H. and Pershing, A. J. (2007). 'Climate drives sea change', *Science* 315(5815), 1084–1085.

Greene, C. H., Pershing, A. J., Cronin, T. M. and Ceci, N. (2008). 'Arctic climate change and its impacts on the ecology of the North Atlantic', *Ecology* 89(sp11), S24–S38.

Hammill, M., Stenson, G. B., Doniol-Valcroze, T. and Mosnier, A. (2011). ‘Northwest Atlantic harp seals population trends, 1952-2012’, *DFO Can Sci Advis Sec Sci Res Doc* 2011/099, –.

Hare, S. R. and Mantua, N. J. (2000). ‘Empirical evidence for North Pacific regime shifts in 1977 and 1989’, *Prog Oceanogr* 47(2-4), 103–145.

Hatún, H., Payne, M., Beaugrand, G., Reid, P., Sand, A., Drange, H., Hansen, B., Jacobsen, J. and Bloch, D. (2009). ‘Large bio-geographical shifts in the north-eastern Atlantic Ocean: From the subpolar gyre, via plankton, to blue whiting and pilot whales’, *Prog Oceanogr* 80(3-4), 149–162.

Head, E., Brickman, D. and Harris, L. (2005). ‘An exceptional haddock year class and unusual environmental conditions on the Scotian Shelf in 1999’, *J Plankton Res* 27, 597–602.

Head, E. J., Melle, W., Pepin, P., Bagøien, E. and Broms, C. (2013). ‘On the ecology of *Calanus finmarchicus* in the Subarctic North Atlantic: a comparison of population dynamics and environmental conditions in areas of the Labrador Sea-Labrador/Newfoundland shelf and Norwegian Sea Atlantic and Coastal waters’, *Prog Oceanogr* 114, 46–63.

Healey, B. P. and Stenson, G. B. (2000). ‘Estimating pup production and population size of the Northwest Atlantic harp seal (*Phoca groenlandica*)’, *Can Sci Advis Sec Sci Res Doc* 2000/081.

Hunt Jr., G. L., Stabeno, P., Walters, G., Sinclair, E., Brodeur, R. D., Napp, J. M. and Bond, N. A. (2002). 'Climate change and control of the southeastern Bering Sea pelagic ecosystem', *Deep-Sea Res Pt II* 49(26), 5821 – 5853.

Hutchings, J. A., Côté, I. M., Dodson, J. J., Fleming, I. A., Jennings, S., Mantua, N. J., Peterman, R. M., Riddell, B. E., Weaver, A. J. and VanderZwaag, D. L. (2012). 'Sustaining Canadian marine biodiversity: responding to the challenges posed by climate change, fisheries, and aquaculture. Expert panel report prepared for the Royal Society of Canada'.

Hutchings, J. A. and Myers, R. A. (1994). 'What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador', *Can J Fish Aquat Sci* 51, 2126–2146.

Ingvaldsen, R. B. and Gjøsæter, H. (2013). 'Responses in spatial distribution of Barents Sea capelin to changes in stock size, ocean temperature and ice cover', *Mar Biol Res* 9, 867–877.

IPCC. (2007), Summary for Policymakers, *in* **S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. Averyt, M. Tignor and H. Miller**., eds, 'Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change', Cambridge, United Kingdom and New York, NY, USA, pp. –.

Jangaard, P. (1974). 'The capelin (*Mallotus villosus*): biology, distribution, exploitation, utilization, and composition', *Bull Fish Res Board Can* 186, 1–70.

Johnson, C. L., Leising, A. W., Runge, J. A., Head, E. J., Pepin, P., Plourde, S. and Durbin, E. G. (2008). 'Characteristics of *Calanus finmarchicus* dormancy patterns in the Northwest Atlantic', *ICES J Mar Sci* 65, 339–350.

Koen-Alonso, M., Pepin, P. and Mowbray, F. (2010). 'Exploring the role of environmental and anthropogenic drivers in the trajectories of core fish species of the Newfoundland-Labrador marine community', *NAFO Sci Coun Res Doc* 10/37.

Lavigne, D. (1996), Ecological interactions between marine mammals, commercial fisheries and their prey: unravelling the tangled web, *in* **W. A. Montevecchi**., ed., 'Studies of high-latitude seabirds. 4. Trophic relationships and energetics of endotherms in cold ocean systems', Can Wildl Serv Ocass Pap 91, pp. 59–71.

Lees, K., Pitois, S., Scott, C., Frid, C. and Mackinson, S. (2006). 'Characterizing regime shifts in the marine environment', *Fish Fish* 7(2), 104–127.

Leggett, W., Frank, K. and Carscadden, J. (1984). 'Meteorological and hydrographic regulation of year-class strength in capelin (*Mallotus villosus*)', *Can J Fish Aquat Sci* 41, 1193–1201.

Lilly, G. (1987). 'Interactions between Atlantic cod (*Gadus morhua*) and capelin (*Mallotus villosus*) off Labrador and eastern Newfoundland: a review', *Can Tech Rep Fish Aquat Sci* 1567, 1–37.

Lilly, G. R. (1991). 'Interannual variability in predation by cod (*Gadus morhua*) on capelin (*Mallotus villosus*) and other prey off southern Labrador and northeastern Newfoundland', *ICES Mar Sci Symp* 193, 133–146.

Lilly, G. R., Parsons, D. and Kulka, D. (2000). 'Was the increase in shrimp biomass on the northeast Newfoundland shelf a consequence of a release in predation pressure from cod?', *J Northw Atl Fish Sci* 27, 45–61.

Loeng, H. and Drinkwater, K. (2007). 'An overview of the ecosystems of the Barents and Norwegian Seas and their response to climate variability', *Deep Sea Res Pt II* 54, 2478–2500.

McCann, K., Rasmussen, J. and Umbanhowar, J. (2005). 'The dynamics of spatially coupled food webs', *Ecol Lett* 8(5), 513–523.

Mitchell, R. M., Harrison, G., Pauley, K., Gagné, A., Maillet, G. and Strain, P. (2002), 'Atlantic Zone Monitoring Program sampling protocol'.

Montevecchi, W. A. (2007). 'Binary dietary responses of northern gannets *Sula bassana* indicate changing food web and oceanographic conditions', *Mar Ecol Prog Ser* 352, 213–220.

Montevecchi, W. A. and Myers, R. A. (1997). 'Centurial and decadal oceanographic influences on changes in Northern Gannet populations and diets in the Northwest Atlantic: Implications for climate change', *ICES J Mar Sci* 54, 608–614.

Montevecchi, W. A. and Piatt, J. (1984). ‘Composition and energy contents of mature inshore spawning capelin (*Mallotus villosus*): implications for seabird predators’, *Comp Biochem Physiol A: Physiol* 78, 15–20.

Mowbray, F. (2002). ‘Changes in the vertical distribution of capelin (*Mallotus villosus*) off Newfoundland’, *ICES J Mar Sci* 59, 942–949.

Mowbray, F. (2012). ‘Some results from spring acoustic surveys for capelin (*Mallotus villosus*) in NAFO Division 3L between 1982 and 2010’, *Can Sci Advis Secretar Res Doc* 2012/143, 1–34.

NAFO. (2010). ‘Report of the NAFO Scientific Council Working Group on Ecosystem Approachesto Fisheries Management (WGEAFM)’, *NAFO Sci Coun Summ Doc* 10/19.

Nakashima, B. S. and Wheeler, J. P. (2002). ‘Capelin (*Mallotus villosus*) spawning behaviour in Newfoundland waters - the interaction between beach and demersal spawning’, *ICES J Mar Sci* 59, 909–916.

Neuheimer, A., Gentleman, W., Pepin, P. and Head, E. (2010). ‘Explaining regional variability in copepod recruitment: Implications for a changing climate’, *Prog Oceanogr* 87, 94–105.

O’Driscoll, R., Parsons, M. and Rose, G. A. (2001). ‘Feeding of capelin (*Mallotus villosus*) in Newfoundland waters’, *Sarsia* 86, 165–176.

O'Driscoll, R., Rose, G. and Anderson, J. (2002). 'Counting capelin: a comparison of acoustic density and trawl catchability', *ICES J Mar Sci* 59, 1062–1071.

Ouellet, P., Grgoire, F., Harvey, M., Head, E. J., Morin, B., Robert, G., Savard, L., Smith, S., Starr, M. and Swain, D. P. (2003). 'Exceptional environmental conditions in 1999 in Eastern Canadian waters and the possible consequences for some fish and invertebrate stocks', *AZMP Bull* 3, 21–27.

Pepin, P., Maillet, G. L., Fraser, S., Shears, T. and Redmond, G. (2011). 'Optical, chemical, and biological oceanographic conditions on the Newfoundland and Labrador Shelf during 2009 and 2010', *Can Sci Advis Secretar Res Doc* 2011/074.

Pikitch, E., Boersma, P., Boyd, I., Conover, D., Cury, P. M., Essington, T. E., Heppell, S., Houde, E., Mangel, M., Pauly, D., Plagányi, E., Sainsbury, K. and Steneck, R. (2012), *Little fish: big impact: managing a crucial link in ocean food webs*, Lenfest Ocean Program, Washington, DC.

Pikitch, E., Santora, C., Babcock, E., Bakun, A., Bonfil, R., Conover, D., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E., Link, J., Livingston, P., Mangel, M., McAllister, M., Pope, J. and Sainsbury, K. (2004). 'Ecosystem-Based Fishery Management', *Science* 305(5682), 346–347.

Plourde, S., Maps, F. and Joly, P. (2009). 'Mortality and survival in early stages control recruitment in *Calanus finmarchicus*', *J Plankton Res* 31, 371–388.

R Core Team. (2012), *R: A Language and Environment for Statistical Computing*, R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0.

Reid, P., Johns, D., Edwards, M., Starr, M., Poulin, M. and Snoeijs, P. (2007). 'A biological consequence of reducing Arctic ice cover: arrival of the Pacific diatom *Neodenticula seminae* in the North Atlantic for the first time in 800 000 years', *Glob Change Biol* 13, 1910–1921.

Rice, J. (1995), Food web theory, marine food webs, and what climate change may do to northern marine fish populations, *in* **R. J. Beamish**., ed., 'Climate change and northern fish populations', Vol. 121, National Research Council of Canada, Ottawa, pp. 561–568.

Rice, J. (2002), Changes to the large marine ecosystem of the Newfoundland-Labrador shelf, *in* **K. Sherman and H. Skjoldal**., eds, 'Large marine ecosystems of the North Atlantic', number 3, Elsevier Science B.V., Amsterdam, Netherlands, pp. 51–103.

Rooney, N., McCann, K., Gellner, G. and Moore, J. C. (2006). 'Structural asymmetry and the stability of diverse food webs', *Nature* 442(7100), 265–269.

Rose, G. A., deYoung, B., Kulka, D., Goddard, S. and Fletcher, G. (2000). 'Distribution shifts and overfishing the northern cod (*Gadus morhua*): a view from the ocean', *Can J Fish Aquat Sci* 57, 644–663.

Rose, G. A. and O'Driscoll, R. L. (2002). 'Capelin are good for cod: can the northern stock rebuild without them?', *ICES J Mar Sci* 59, 1018–1026.

Sargent, J. and Falk-Petersen, S. (1988). 'The lipid biochemistry of calanoid copepods', *Hydrobiologia* 167-168(1), 101–114.

Scheffer, M., Carpenter, S., Foley, J. A., Folke, C. and Walker, B. (2001). 'Catastrophic shifts in ecosystems', *Nature* 413(6856), 591–596.

Schlesinger, M. E. and Ramankutty, N. (1994). 'An oscillation in the global climate system of period 65-70 years', *Nature* 367(6465), 723–726.

Schwartzlose, R., Alheit, J., Bakun, A., Baumgartner, T., Cloete, R., Crawford, R., Fletcher, W., Green-Ruiz, Y., Hagen, E., Kawasaki, T., Lluch-Belda, D., Lluch-Cota, S., MacCall, A., Matsuura, Y., Nvarez-Martnez, M., Parrish, R., Roy, C., Serra, R., Shust, K., Ward, M. and Zuzunaga, J. (1999), 'Worldwide large-scale fluctuations of sardine and anchovy populations'.

Shackell, N. L., Shelton, P. A., Hoenig, J. and Carscadden, J. (1994). 'Age- and sex-specific survival of Northern Grand Banks capelin (*Mallotus villosus*)', *Can J Fish Aquat Sci* 51, 642–649.

Smith, P. C., Flagg, C. N., Limeburner, R., Fuentes-Yaco, C., Hannah, C., Beardsley, R. C. and Irish, J. D. (2003). 'Scotian Shelf crossovers during winter/spring 1999', *J Geophys Res* 108.

Steele, D., Andersen, R. and Green, J. (1992). 'The managed commercial annihilation of northern cod', *Newfoundland and Labrador Studies* 8(1), 34–68.

Stenson, G. B. (2012). 'Estimating consumption of prey by harp seals (*Pagophilus groenlandicus*) in NAFO Divisions 2J3KL', *Can Sci Advis Secretar Res Doc* 2012/156.

Tang, C. L. (1991). 'A two-dimensional thermodynamic model for sea ice advance and retreat in the Newfoundland marginal ice zone', *Journal of Geophysical Research: Oceans* 96(C3), 4723–4737.

Templeman, W. (1948). 'The life history of the caplin (*Mallotus villosus* O. F. Müller) in Newfoundland waters', *Bull Nfld Gov Lab* 17, 1–151.

Warren, W. G. (1997). 'Report on the comparative fishing trial between the Gadus Atlantica and the Teleost', *NAFO Scien Coun Res Doc* 96/28.

Warren, W. G., Shelton, P. A. and Stenson, G. B. (1997). 'Quantifying some of the major sources of uncertainty associated with estimates of harp seal prey consumption Part I: Uncertainty in the estimates of harp seal population size', *J Northw Atl Fish Sci* 22, 289–302.

Winters, G. (1970). 'Biological changes in coastal capelin from the over-wintering to the spawning condition', *J Fish Res Board Can* 27, 2215–2224.

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

Wu, Y., Peterson, I. K., Tang, C. C., Platt, T., Sathyendranath, S. and Fuentes-Yaco, C. (2007). 'The impact of sea ice on the initiation of the spring bloom on the Newfoundland and Labrador Shelves', *J Plankton Res* 29, 509–514.

3.8 Figures

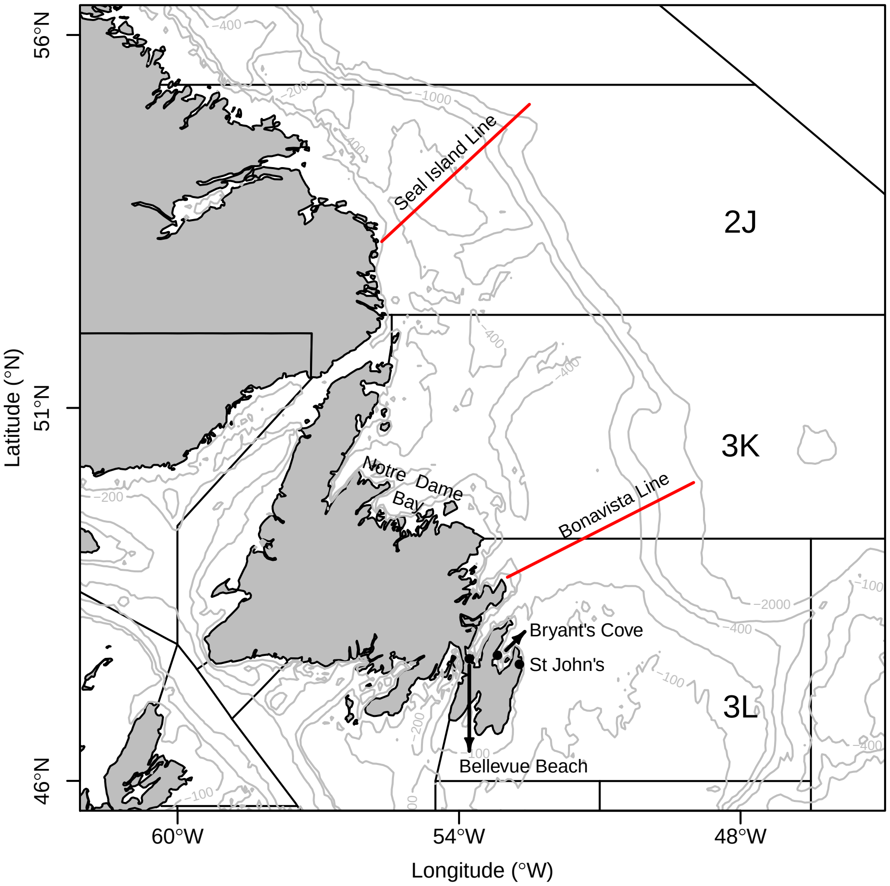
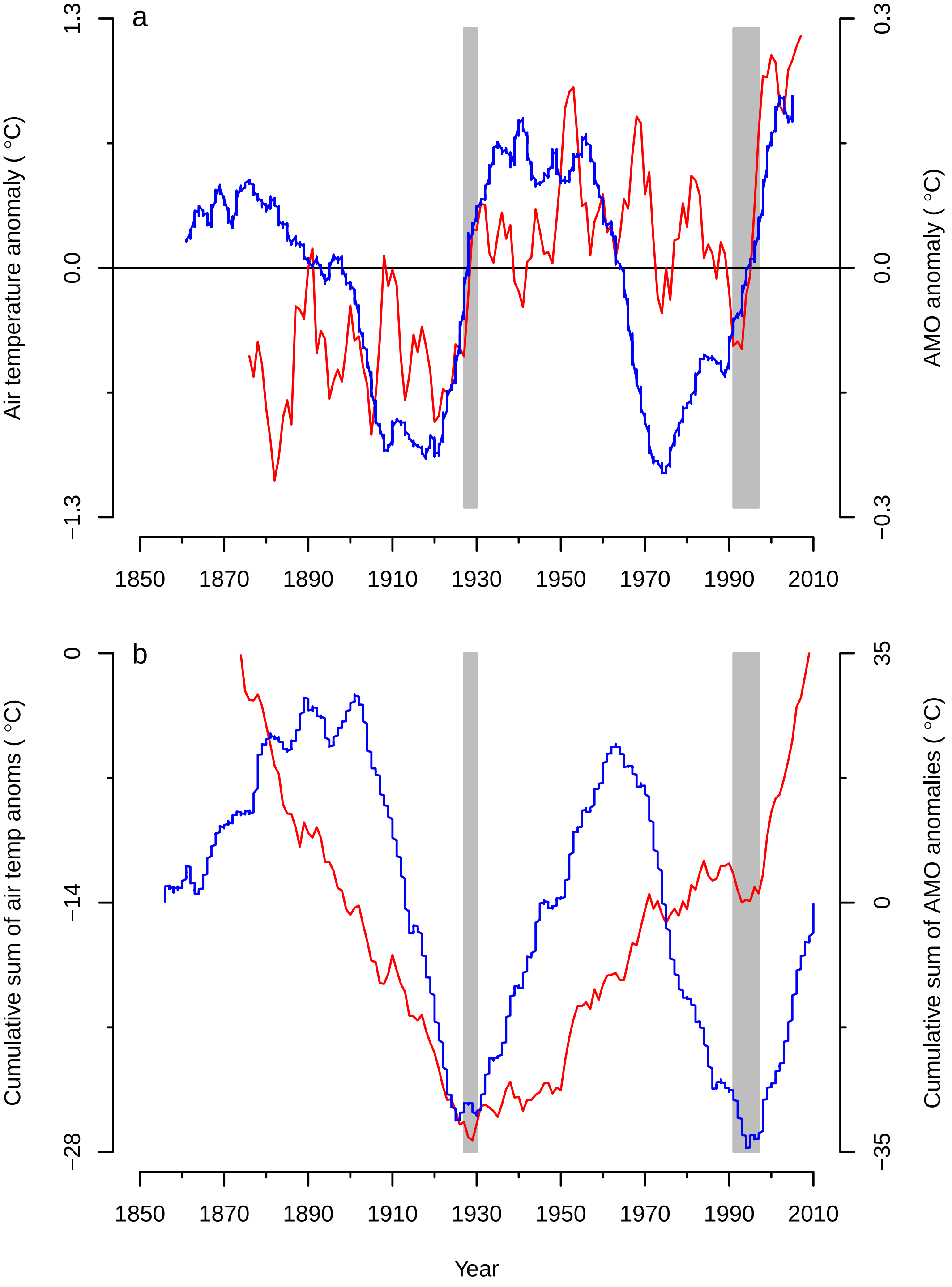


Figure 3.1: Study area. Capelin stock area, NAFO Divisions 2J3KL. The locations of St John's, Bryant's Cove, Bellevue Beach, Notre Dame Bay, and the Atlantic Zone Monitoring Program (AZMP) lines Seal Island and Bonavista are indicated.

Figure 3.2 *(following page)*: Climatic patterns. (a) 5-year running mean of air temperature anomalies in St John's (red line) and 121-month smoothed Atlantic Multidecadal Oscillation (AMO) anomalies (from long term means), (b) Cumulative sums of air temperature anomalies in St John's (red line) and Atlantic Multidecadal Oscillation anomalies (blue line). Shaded portions represent periods when regime shifts occurred.


a
b
Air temperature anomaly (°C)
AMO anomaly (°C)
1.3
0.0
−1.3
0.3
0.0
−0.3
Cumulative sum of air temp anoms (°C)
Cumulative sum of AMO anomalies (°C)
0
−14
−28
35
0
−35
1850
1870
1890
1910
1930
1950
1970
1990
2010
Year

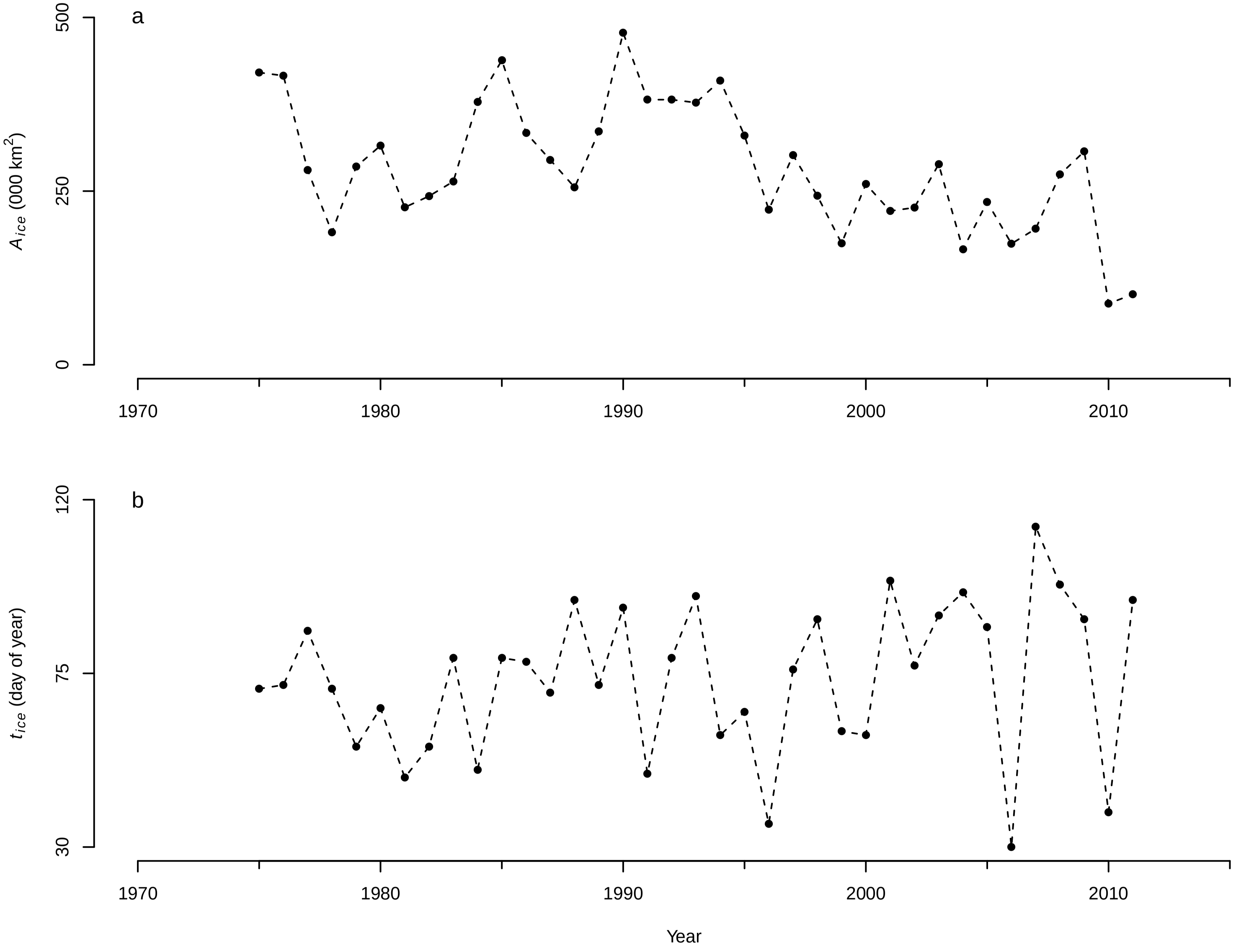
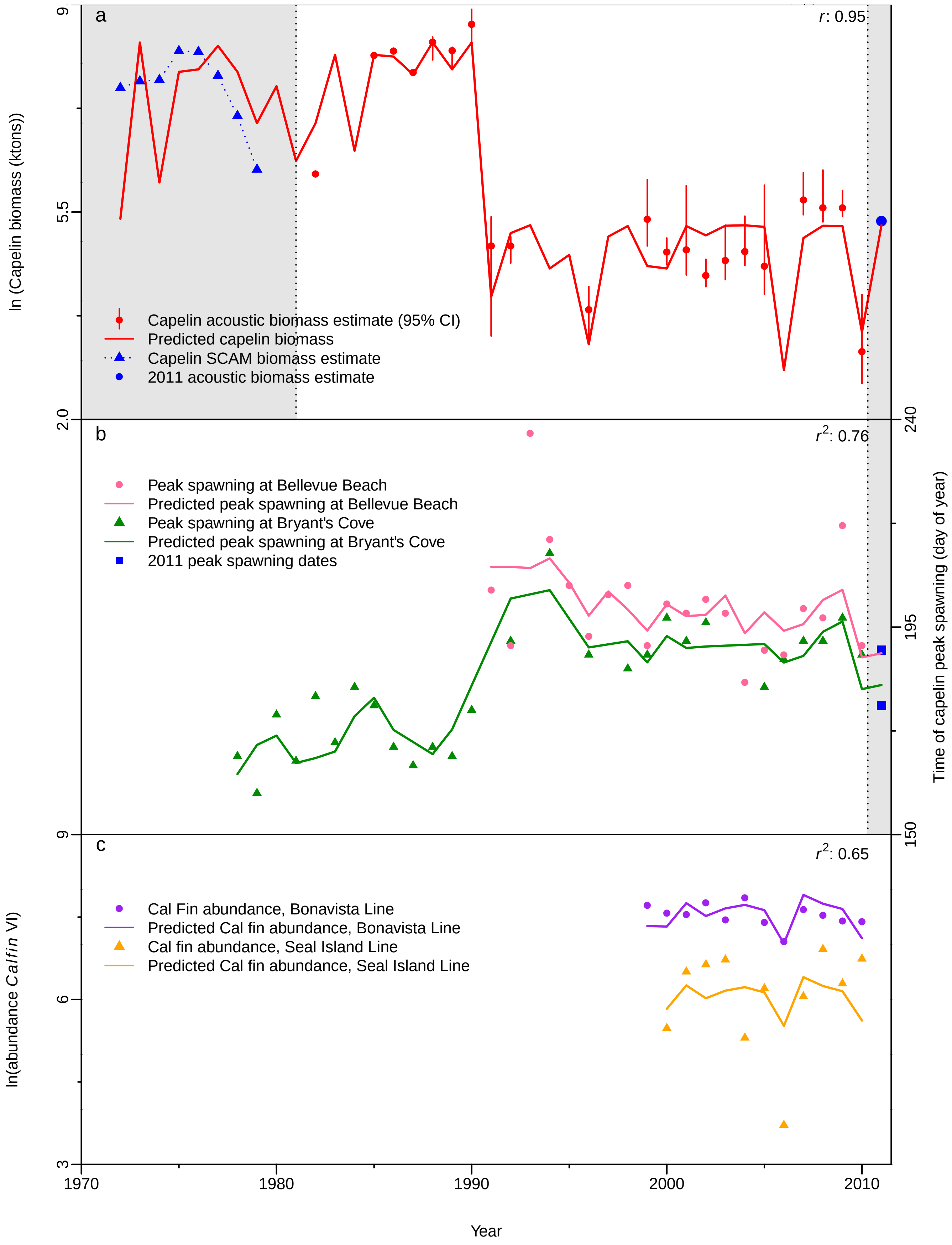


Figure 3.3: Sea ice properties. (a) Maximum annual extent of sea ice (A_{ice}, (b) start time of ice retreat (t_{ice}.

Figure 3.4 *(following page)*: Relationship between biological variables, ice characteristics and period. Capelin and *Calanus finmarchicus* characteristics explained by ice properties and period. (a) Capelin biomass. (b) Timing of capelin peak spawning date at Bryant's Cove and Bellevue Beach. (c) Abundance of adult *C. finmarchicus* (Calfin VI) on the Newfoundland-Labrador Shelf. Shaded portions indicate models forecasts and hindcast contrasted to independent data.


a
r: 0.95
9.
5.5
2.0
ln (Capelin biomass (ktons))
Capelin acoustic biomass estimate (95% CI)
Predicted capelin biomass
Capelin SCAM biomass estimate
2011 acoustic biomass estimate
b
r2: 0.76
240
195
150
Time of capelin peak spawning (day of year)
Peak spawning at Bellevue Beach
Predicted peak spawning at Bellevue Beach
Peak spawning at Bryant's Cove
Predicted peak spawning at Bryant's Cove
2011 peak spawning dates
c
r2: 0.65
9
6
3
ln(abundance Calfin VI)
Cal Fin abundance, Bonavista Line
Predicted Cal fin abundance, Bonavista Line
Cal fin abundance, Seal Island Line
Predicted Cal fin abundance, Seal Island Line
1970
1980
1990
2000
2010
Year

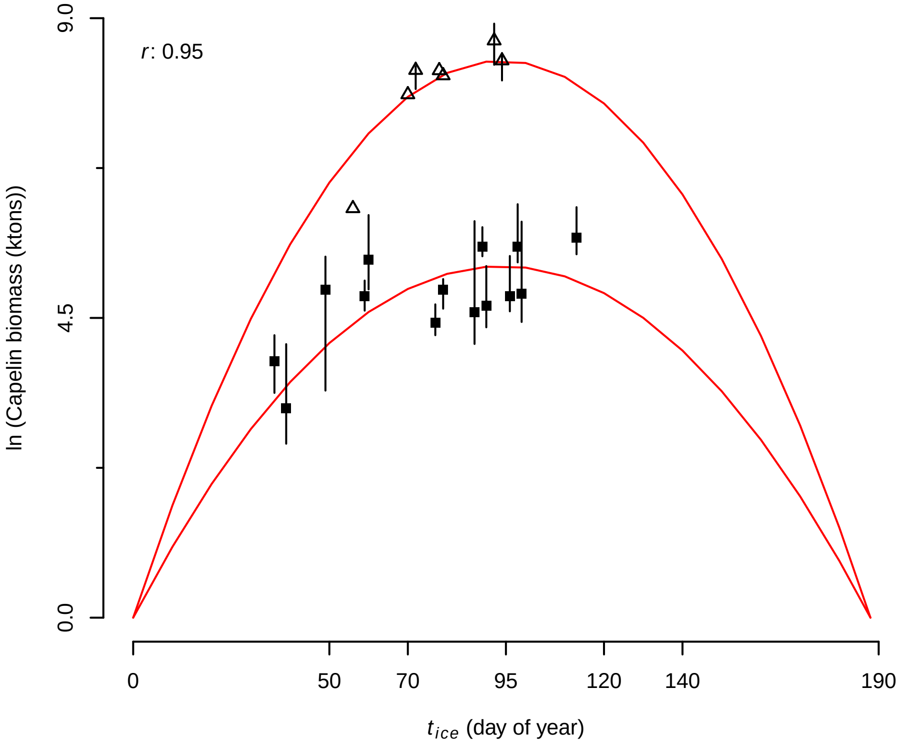


Figure 3.5: Fit of the dome-shaped capelin biomass model. Open triangles denote capelin acoustic biomass estimates prior to 1991 and filled squares during the post 1990 period. Bars denote 95% confidence intervals. Note that y-axis is in logarithmic scale.

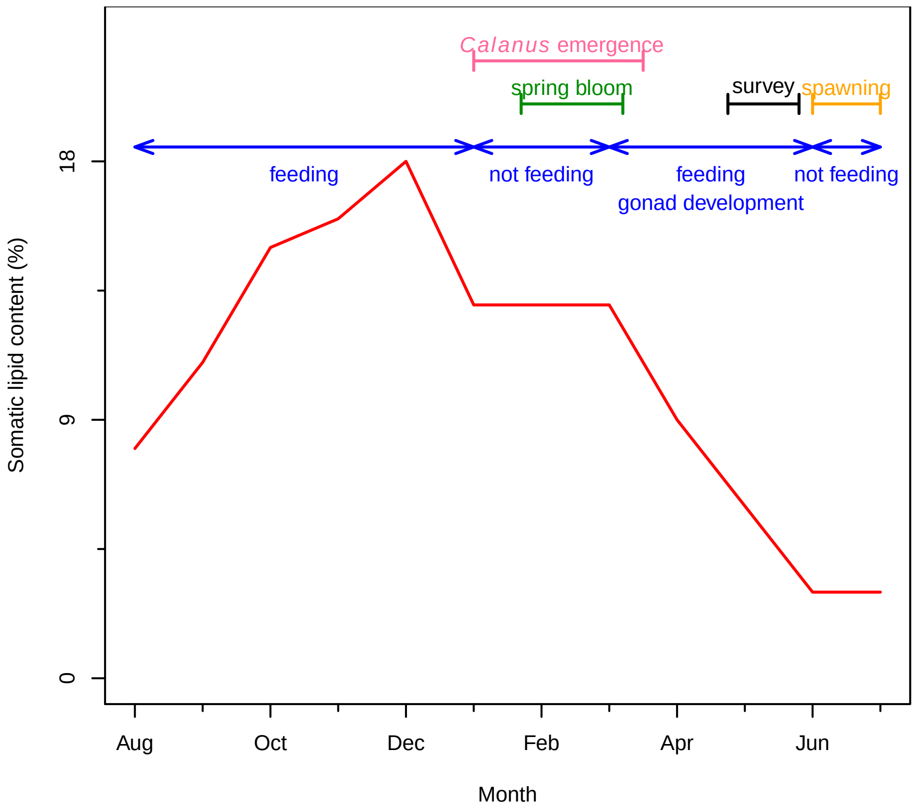


Figure 3.6: Schema of chronology of events relevant to the phenology of capelin. Somatic lipid contents of adult capelin (red line) (redrawn from Table 1 in Montevecchi and Piatt, 1984), periods of capelin feeding and gonadal development (blue line) (Winters, 1970), timing of the spring bloom (green line) (Wu et al., 2007), timing of *Calanus finmarchicus* emergence from dormancy (pink line) (Johnson et al., 2008), timing of capelin spawning (orange) and timing of capelin acoustic survey (black line).

Chapter 4

The role of harp seals, fisheries and food availability in driving the dynamics of northern cod

4.1 Abstract

Atlantic cod (*Gadus morhua*) off Newfoundland collapsed in the early 1990s due to over-exploitation, and despite marked reduction in fishing effort the stock remains depressed. Harp seal (*Pagophilus groenlandicus*) predation has been repeatedly proposed as an explanation for this lack of recovery, but other hypotheses include reduced prey availability and/or food quality (i.e. lack of capelin *Mallotus villosus*), as well as fisheries catches and environmental effects. Using a bioenergetics-allometric model, I gauged the relative contributions of these drivers on the lack of recovery and dynamics of the northern cod stock. Biomass dynamics were best explained by a combination of fisheries removals and capelin availability, whereas seal consumption

was found not to be an important driver of the northern cod stock. Prey availability is linked to reduced somatic condition during the 1990s and 2000s. I discuss evidence that suggests that cod may be experiencing depensatory dynamics, but not related to a 'predator pit effect'. This chapter suggests that trophic control is bottom-up and that a depressed capelin stock could be a serious impediment for cod rebuilding.

4.2 Introduction

The Atlantic cod *Gadus morhua* stocks off eastern Canada once sustained one of the world's largest fisheries and supported the livelihoods of many generations. During the late 1980s and first half of the 1990s, six populations of Atlantic cod throughout Atlantic Canada collapsed. These stock collapses and subsequent failures to recover and concomitant increases in the abundance of grey *Halichoerus grypus* and harp seals *Pagophilus groenlandicus* off the coasts of eastern Canada (Hammill and Stenson, 2011; Thomas et al., 2011; Hammill et al., 2013) prompted enquiries to assess if these were related (Bundy, 2001; McLaren et al., 2001; DFO, 2003*a*,*b*; Trzcinski et al., 2006; DFO, 2008*a*; Trzcinski et al., 2009; Chassot et al., 2009; DFO, 2009; Benoît et al., 2011; DFO, 2011*a*; Swain et al., 2011). Trophic interactions between marine mammals and fisheries, particularly the potential detrimental effects that top predators may have on fish stocks, have been considered for decades (e.g. May et al., 1979; Flaaten, 1988; Northridge, 1991; Harwood, 1992; Yodzis, 1994; Punt and Butterworth, 1995; Lavigne, 1996; Bowen, 1997; Trites et al., 1997; Yodzis, 1998; Goldsworthy et al., 2003; Ruzicka et al., 2013). The argument that marine mammals can limit the growth and/or recovery of prey populations that are also commercially harvested has led to calls for culls of marine mammals (e.g. Wickens et al., 1992; FRCC, 2011). However, where the effects of a marine mammal cull on fisheries was analysed (proposed cull of Cape fur seals *Arctocephalus pusillus pusillus* to enhance Cape hakes *Merluccius capensis* and *M. paradoxus* fisheries off the South African coast), simulation studies indicated that a cull would likely be detrimental to fisheries yields (Punt and Butterworth, 1995; Yodzis, 1998).

The northern cod stock off eastern Newfoundland and Labrador (NAFO Divisions 2J3KL, Figure 4.1) was by far the largest of the Atlantic Canadian stocks. Continued overexploitation led to a stock collapse in the early 1990s (Hutchings and Myers, 1994; Steele et al., 1992), though environmental variability may also have played an important role in this collapse (Drinkwater, 2002; Halliday and Pinhorn, 2009). Despite 20 years of markedly reduced fishing effort, this stock has not recovered to pre-collapse levels. This lack of recovery has been attributed to the high levels of mortality that the offshore components of the stock have experienced throughout the mid-1990s and the early 2000s (DFO, 2008*b*). Shelton et al. (2006) argued that fishing mortality under low productivity during the last half of the 1990s delayed the recovery of the stock. Potential hypotheses to explain the elevated natural mortality include diseases and parasites, contaminants, starvation and/or poor condition, changes in life history and predation by marine mammals, all with differing degrees of empirical support (summary in DFO, 2009). An explanation commonly offered for the non-recovery of the stock is predation by harp seals, either based on model simulations (Bundy, 2001) or on lack of evidence that the high mortality experienced may be explained by alternative mechanisms (e.g. DFO, 2003*a*,*b*).

Harp seals are the most abundant marine mammal in the Northwest Atlantic, with an estimated population size of 7.1 million animals (Hammill et al., 2013). Harp seals undergo extensive migrations between the Arctic, where they summer, and the waters off Newfoundland and Labrador and the Gulf of St Lawrence, where they whelp and moult during the winter, thus effectively spending half the year in the area of interest (Stenson and Sjare, 1997). Feeding is intensive in winter and summer, less intensive during spring and autumn migration, and in spring during whelping and moult (Sergeant, 1973). In Newfoundland waters, they feed on an array of prey species, including cod. Although cod is neutrally or negatively selected by harp seals (Lawson, Anderson, Dalley and Stenson, 1998), cod consumption estimates are in the order of hundreds of thousand tons annually (Stenson, 2012).

Capelin *Mallotus villosus* is the core forage species in this ecosystem (Lavigne, 1996). It is an energy rich fish (Lawson, Magalhães and Miller, 1998) that has historically been cod's main prey (Lilly, 1987, 1991). In 1991 there was a major reduction in capelin biomass on the Newfoundland-Labrador shelf, and to date the stock has not recovered (DFO, 2010). In addition, spawning was protracted and delayed up to four weeks (Nakashima and Wheeler, 2002; DFO, 2010), size and age at maturity and somatic condition were reduced (Carscadden and Nakashima, 1997; Carscadden and Frank, 2002), vertical distribution shifted (Mowbray, 2002) and episodic occurrences outside of their normal range, on the Scotian Shelf and Flemish Cap, were recorded (Frank et al., 1996; Carscadden and Nakashima, 1997). In Chapter 3 (Buren et al., 2014) I proposed that the capelin biomass trajectory is driven by a regime shift and the dynamics of seasonal sea ice via the synchrony of the phytoplankton bloom and *Calanus finmarchicus*' (capelin's main prey) timing of emergence from diapause.

The abundance of capelin has been related to cod's fecundity on the Grand Banks (NAFO Divs 3NO, Figure 4.1) (Rideout and Morgan, 2010), and diets rich in capelin have been correlated with high body and liver condition, and increased spawning potential of cod, thus suggesting that capelin is key to the productivity and recovery potential of the northern cod (Rose and O'Driscoll, 2002; Sherwood et al., 2007). However, Lilly et al. (2003) report that mean somatic condition of northern cod in the northern portion of the range (NAFO Divs 2J3K) declined in the early 1990s and returned to approximately normal during the second half of the decade, while the mean somatic condition in the southern portion (NAFO Div 3L) remained relatively unchanged.

The objectives of this chapter are to test competing hypotheses on the relative contributions of fisheries removals, predation by harp seals, and food availability (as indexed by capelin) on the lack of recovery and dynamics of the northern cod stock, and to explore the mechanisms through which the main drivers may affect the stock's dynamics.

4.3 Materials and methods

4.3.1 The Data

The time series of Atlantic cod biomass to which the model was fitted was based on the research vessel (RV) survey index (Figure 4.2a) derived from the Fisheries and Oceans Canada (DFO) annual autumn bottom trawl surveys of Northwest Atlantic Fisheries Organization (NAFO) Divisions 2J, 3K and 3L (Figure 4.1).

In 1995 DFO changed the survey gear from an Engel otter trawl to a Campelen shrimp trawl and comparative fishing trials were carried out to develop conversion factors for catches at length (Warren, 1997; Warren et al., 1997). As my model is biomass-based, I do not need to make the assumptions these authors made to develop these length-based conversions, and therefore I used the data from the comparative fishing trials to produce a biomass-based conversion factor. The median ratio of Campelen/Engel cod swept area biomass was 3.3642 (Figure 4.3). Therefore the survey data prior to 1995 was corrected using this factor, producing a "gear corrected" time series (Figure 4.2a). The entire cod biomass "gear corrected" time series was assumed to be an index with a time invariant catchability, q. I also used the converted time series using the length-based conversions (Warren, 1997; Warren et al., 1997), and the results were qualitatively identical (results not shown).

Fisheries catches of Atlantic cod for NAFO Divisions 2J3KL (Figure 4.2b) were obtained from (Brattey et al., 2011).

Acoustic estimates of capelin availability (Miller, 1997; DFO, 2010; Mowbray, 2012) from the Fisheries and Oceans Canada (DFO) annual spring survey of NAFO Division 3L were used as an index of capelin availability (Figure 4.2c). Since this survey has only partial coverage of the entire stock area, the estimates it provides are considered to be minimum biomass estimates. Nonetheless, the estimates from this survey show a high degree of internal consistency, and thus the relative biomass index for the capelin stock in the region can be considered a reliable index of abundance for the 2J3KL capelin stock (Mowbray, 2012). Capelin surveys were carried out during the years 1985-1992, 1996, 1999-2005, 2007. For those years when a capelin survey was not carried out, the value of biomass was linearly interpolated between the 2 surveys closest in time.

Prey (Atlantic cod) consumption by Northwest Atlantic harp seals (Figure 4.2d) was estimated using a bioenergetics model that incorporates seal population size, seal seasonal and spatial distribution, energy requirements of seals, energy content of prey, and geographical and seasonal variation in diet composition (Stenson, 2012).

Uncertainty in each of these components carries through into the consumption estimates. Of all these, the biggest contributor to uncertainty in consumption of Atlantic cod is diet composition (Shelton et al., 1997). To account for this uncertainty I estimated consumption of cod using 3 different diet compositions as inputs for the consumption model and, during fitting of the cod dynamic model, I allowed the consumptions to scale up or down via a scaling parameter. In this fashion I allowed cod consumption to take 3 different shapes (Figure 4.2d) and cover a wide range of potential consumption magnitudes. The diet descriptions used as input for the consumption model were:

i. ‘average’ description,

ii. reconstructed diet taking a multinomial regression approach (Koen-Alonso et al., 2009), and

iii. ‘inshore annual’.

Diet composition (and prey consumption) is described in 8 spatio-temporal blocks; prey consumption is then integrated to provide annual consumption in the study area. The blocks are defined to contemplate seasonal (summer vs winter), and spatial differences in diet. Geographical variability in diet composition is considered in terms of both, latitudinal (NAFO Divs 2J3K vs NAFO Div 3L) and depth related (inshore vs offshore) differences. The ‘average’ description considers diet variability in the 8 blocks described above, but it does not allow for inter-annual differences in the diet, which masks potential changes in diet over time. The 'multinomial regression' approach fills in data gaps and produce yearly estimates of diet composition for each of the area/season blocks. The resulting diet estimate yielded a larger proportion of cod in the offshore diet than seen in the raw data. Given the weight that the offshore area bears (˜90% offshore vs ˜10% inshore) in the consumption, this resulted in likely overestimation of the total cod consumption. The diet data were collected annually in nearshore areas from 1982-2008. The 'inshore annual' diet description considers yearly differences in the diet composition in the inshore areas, and assumes a constant diet composition in the offshore. Sample sizes in the offshore are not sufficient to resolve inter-annual variability. This description led to cod consumption that had greater inter-annual variability than the other 2 cases (Figure 4.2d).

4.3.2 The model

I implemented a bioenergetic-allometric cod biomass dynamic model (Yodzis and Innes, 1992).

$$\frac{dB_{cod}}{dt} = B_{cod,t}\left(-T + P_t\right) - L_t \tag{4.1}$$

where $\frac{dB_{cod}}{dt}$ is the rate of change of cod biomass, $B_{cod,t}$ is the cod stock biomass at time t, T is mass-specific respiration rate of the population, P_t is a mass-specific gross production rate at the metabolizable level at time t (i.e. the net production rate is given by (-T+ P_t)), and L_t is the rate of loss of biomass at time t due to causes other than starvation.

The mass-specific gross production rate of the population P_t is expressed as

$$P_t = (1 - \delta)\, J_t \tag{4.2}$$

where δ is the fraction of ingested energy that is lost as feces and urine and J_t is the mass-specific ingestion rate of the population at time t.

The specific ingestion rate J_t depends on the resource density and I expressed it as a function of capelin availability at time t, $I_{capelin,t}$. Note that the availability of capelin is used as a proxy for the quality of the prey field at time t, i.e. years when capelin biomass is high represent a time when a high quality prey field is available to cod.

$$J_t = J_{max} \frac{I^2_{capelin,t}}{I^2_0 + I^2_{capelin,t}} \tag{4.3}$$

The constant J_{max} is the asymptotic saturation rate of ingestion, and I_0 is the resource density at which half the saturation ingestion rate is attained (half-saturation density). Given that the value of the exponent of $I_{capelin,t}$ is two, this ingestion rate has the form of a Holling Type III functional response.

The biomass losses of the population at time t, L_t, were expressed as the sum of natural mortality ($mB^{\psi}_{cod,t}$), consumption by harp seals ($H_{seal,t}$) and fisheries catches ($H_{fisheries,t}$).

$$L_t = mB^{\psi}_{cod,t} + H_{seal,t} + H_{fisheries,t} \tag{4.4}$$

I fitted the model with two different types of natural mortality: linear (Ψ=1; density independent) and quadratic (Ψ=2; density-dependent).

The constants T and J_{max} were calculated:

$$T = a_T \left(\overline{w_{cod}}\right)^{-0.25} \tag{4.5}$$

where $(\overline{w_{cod}}$ is the average body mass of an individual cod and a_T is the allometric coefficient of the mass-specific respiration rate of ectothermic vertebrates (Yodzis and Innes, 1992), and

$$J_{max} = a_J \left(\overline{w_{cod}}\right)^{-0.25} \tag{4.6}$$

where a_J is the allometric coefficient of the maximum physiological capacity to metabolize food of ectothermic vertebrates (Yodzis and Innes, 1992). I assumed $\overline{w_{cod}} = 1kg$.

Thus, the cod biomass dynamic model consists of 2 equations: the first is the dynamic equation for which the full expression is

$$\begin{aligned} \frac{dB_{cod}}{dt} =& B_{cod,t}\left[-a_T\overline{w_{cod}}^{-0.25} + (1-\delta)\, a_J\overline{w_{cod}}^{-0.25}\frac{I^2_{capelin,t}}{I_0^2 + I^2_{capelin,t}}\right] \\ & - mB^{\psi}_{cod,t} - \theta H_{seal,t} - H_{fisheries,t} \end{aligned} \tag{4.7}$$

where θ is a scaling parameter for the time series of consumption by harp seals. The second equation relates the Index of cod biomass from the survey $I_{cod,t}$ with the stock biomass at time t, $B_{cod,t}$ through the catchability q

$$B_{cod,t} = \frac{I_{cod,t}}{q} \tag{4.8}$$

Thus, the model has estimable parameters q, m, I_0, δ, θ and an initial cod stock biomass $B_{cod,1985}$ while $H_{seal,t}$, $H_{fisheries,t}$ and $I_{capelin,t}$ are external forcers (Figure 4.2).

4.3.3 Model implementation

The model was fitted by minimizing the -log-likelihood function. A lognormal observation error was assumed.

The model was written in Fortran 77. The ordinary differential equation (equation 4.7) was solved using the Runge-Kutta method (subroutine IVMRK in IMSL, 2006). In order to achieve global convergence, minimization of the model's -log-likelihood function was performed using the Enhanced Simulated Annealing (ESA) algorithm (Siarry et al., 1997), implemented in a multi-start scheme where each model was run 100 times, starting each run from a random point within the possible parameter space.

In order to run, the model requires a complete set of predictor variables for every year in the time series. Linearly interpolated capelin biomass values are used as input, and will affect the model behaviour. In order to reduce (but not fully eliminate) the impact of these interpolated values, I estimated model parameters in two ways, by defining two alternative likelihood functions:

i. 'full likelihood': all available survey indices of cod biomass within the 1985-2007 period were included in the calculation of the likelihood.

ii. 'restricted likelihood': only survey indices of cod biomass corresponding to years within the 1985-2007 period when actual survey-based capelin data were available were included in the calculation of the likelihood.

Even though interpolated capelin values are always used to fit the model, the implementation of the restricted likelihood focuses the parameter estimation process on those years which have a full suite of drivers available, and reduces the influence of mismatches between cod observations and model prediction for those years without actual capelin data. The assumption here is that any “misdirection” occurring because of the interpolated capelin will affect more severely the year for which the capelin was interpolated than any subsequent year. Thus, a set of results is presented for the ‘full likelihood’ and a second set for the ‘restricted likelihood’ models. These are not directly comparable because the cod biomass data set used to estimate the parameters of the latter models is a subset of the larger data set used to estimate the parameters of the former models.

4.3.4 Model comparison and selection

On the basis of the generic model (equation 4.7), scenarios were explored by fitting different versions to the observed DFO RV survey series for northern cod (Table 4.1). These scenarios resulted from a combination of

i. removing each forcer from the model independently, and

ii. using the different estimates of harp seal consumption derived from the three diet descriptions considered.

In addition, due to their high uncertainty, consumption time series were allowed to scale up or down according to a scaling parameter (θ) estimated during the fitting process. Each scenario represents a hypothesis of which are the main drivers of the cod stock.

The Akaike information criterion corrected for sample size (AICc) (Burnham and Anderson, 2002) was used to select the model that provided the best fit. Models that deserved further exploration were identified through the delta AICc ($\Delta AICc_i$) (Burnham and Anderson, 2002). As a general rule, models having $\Delta AICc_i$ >10 have either essentially no empirical support, or at least those models fail to explain some substantial explainable variation in the data (Burnham and Anderson, 2002), and may thus be omitted from further consideration. The relative empirical support the models had was assessed using evidence ratios ($E_{min,i}$), which is a measure of the support that a given model i has on the data relative to the best model (Anderson, 2008).

I carried out this exercise considering two different time spans; I implemented the models using data from 1985 to 2007 as a representation of the cod biomass dynamics and the period 1992-2007 to specifically pinpoint the drivers of the cod dynamics during the period of non-recovery.

4.3.5 Somatic condition

To explore the mechanisms through which food availability could impact the dynamics of the cod stock, I compared the distribution curves of somatic condition from 1978 until 2006. I used Fulton's condition factor (K) as indicator of cod condition.

It was expressed as: $K = 100\,{}^{W}\!/_{L^3}$ where W is total weight (g) and L is fish length (cm).

Atlantic cod exhibit marked seasonal variations in energy reserves, with maximum levels reached in fall and minimum levels in spring during the spawning period. Given that the research surveys occur in the fall, data collected during these periods reflect top condition. I used Lambert's (2011; 2012) equation that relates K calculated from total mass in January to K calculated from somatic mass in the following month of May in the northern Gulf of St. Lawrence to estimate a condition factor for the spring period (K_s), the most critical time of the year. The condition of Atlantic cod in Newfoundland remains virtually constant during the fall and into January (Mello and Rose, 2005), thus allowing the use of fall condition as independent variable in Lambert's (2011; 2012) equation.

I present the distribution of the condition factor during spring (K_s), and use as benchmarks for comparisons threshold values found in starvation and feeding experiments (Lambert and Dutil, 1997). In these laboratory settings, prolonged fasting resulted in condition factors below 0.7 and feeding in values above 0.85 (Lambert and Dutil, 1997).

I restricted the size range of fish analysed to 30-55 cm, the size range used in the starvation experiments (Lambert and Dutil, 1997).

Fulton's condition factor suffers from an important shortcoming; the value of the condition factor is dependent on the length of the fish, given that an exponent of 3 is assumed in the length-weight relationship and the instances were that is true are rare. To overcome this, it is common practice to calculate a relative condition factor $K_r = {}^{W}/_{\hat{W}}$, where $\hat{W}$ is the predicted body weight from a length-weight relationship (Le Cren, 1951). I calculated K_r and the patterns obtained are identical to those observed when K is examined. I therefore present the results only in terms of Fulton's condition factor (K).

4.4 Results

4.4.1 Model Selection

Model selection statistics for the time span 1985-2007 are presented in Tables 4.2 (restricted likelihood) and 4.3 (full likelihood), and for the time span 1992-2007 in Tables 4.4 (restricted likelihood) and 4.5 (full likelihood). Model fits are compared across scenarios and expressions of natural mortality (Ψ=1: density independent or Ψ=2: density dependent).

Only a few models had enough empirical support to deserve further consideration (i.e. $E_{min,i} < 10$), considering both the 1985-2007 and 1992-2007 time spans. For the 1985-2007 time span; only 2 models (out of 36) in the case of restricted likelihood (Table 4.2) and 3 in the case of the full likelihood (Table 4.3) had reasonable empirical support. For the 1992-2007 time span, 3 models in each likelihood considered had an $E_{min,i}$ value smaller than 10 (Tables 4.4 and 4.5). The rest of the models had very little empirical support and were therefore concluded not to be valid depictions of cod biomass dynamics.

A clear pattern arises from examining the tables (Tables 4.2, 4.3, 4.4 and 4.5) concurrently: all models worth considering contained fishery removals and/or capelin availability and none had consumption by harp seals as important drivers of the dynamics, considering the entire time period or only the period of non-recovery.

It is interesting to note that the 'Only fisheries' model ranked either first or second when considering the post-1991 period, despite severely reduced fishing effort. However, the level of removals was still significant, compared to the stock biomass (~10%).

Given that the patterns described above were identical when considering the entire time span and the the time span for the non-recovery, I will hereafter discuss only the models fit to the entire time span (1985-2007), as these are better representations of the cod biomass dynamics.

In the case of the restricted likelihood the model that best fit the data was the 'No seals (Ψ=2)' model which had 5 times the weight of evidence relative to the second best model, 'Only capelin (Ψ=2)' ($E_{noseals,onlycapelin}=5$).

In the case of the full likelihood the best model was the 'Only fisheries (Ψ=2)' model with double the weight of evidence as the second best 'Only fisheries (Ψ=1)' and 5, 11 and 16 times the weight of evidence than the rest of the models that had a value of ΔAICc smaller than 10 ('No seals (Ψ=2)', 'No seals (Ψ=1)' and 'Only capelin

(Ψ=2)'), respectively.

4.4.2 Model Fits

The fit of the 2 models from the restricted likelihood set are virtually identical (Figure 4.4), which indicates that capelin availability is the driver that has most influence on the behaviours of the models in this set. These models capture well the plateau in stock biomass during the 1980s and also track well the dynamics of the stock in the later part of the time series, when the biomass has been very low but nevertheless show a fair amount of variation (best seen in logarithmic scale). The characteristic of the time series these models fail to represent well is the timing of the collapse during the early 1990s, predicting that the collapse would have occurred later than it actually did: the stock reached its minimum biomass in 1994 whereas the expected biomass under these models reaches its minimum in 1997. It is important to note however that during the 1990s there were several years (1993-1995, 1997-1998) when capelin surveys were not carried out and given the influence that capelin availability has on the behaviour of these models it is not entirely unexpected that the stock biomass is not well captured during this period.

On the other hand, the fit of the 4 best models from the full likelihood set (Figure 4.5) (those that include fisheries and/or capelin availability) are mainly driven by fisheries removals.

This group of models predicted that the cod stock decreased since the beginning of the time series, earlier than it actually did, but capturing well the timing of the minimum, during 1993-1994. The dynamics of the stock since the 1990s are not well captured by these models, predicting less inter year variability than observed. This group of models includes 2 models with density independent and 2 with density dependent mortality. The behaviour of these models is very similar; the most conspicuous difference between them is that the expected biomass at the beginning of the time series is larger in the models that show density dependence.

4.4.3 Model Projections and hindcast

Using the maximum likelihood estimates from the best model in each set (restricted and full likelihood), and the data on fisheries removals and capelin availability I produced forecasted stock biomass for the years 2008-2010 (Figure 4.6). These two projections fail in opposite directions: the best model from the restricted likelihood set (No seals) overestimates the stock biomass whereas the best model from the restricted full set (Only fisheries) underestimates it (Figure 4.6). This is an indication that the dynamics of the stock might be driven by an interplay of both these variables, rather than being dominated by one as the projections represent.

4.4.4 Balancing the effects of fisheries removals and capelin availability on cod dynamics

The parameter that controls the relative contribution of fisheries removals and food availability within the model is the half-saturation density I_0. If I_0 is too low, then the ingestion rate is quickly saturated and the model does not respond to the availability of capelin (I_0 estimated in the No seals (Ψ=2) model of the full likelihood set was 11 ktons) (Figure 4.7). If, on the other hand I_0 is too large the ingestion rate does not reach saturation and the model is very responsive to the capelin levels (I_0 estimated in the No seals(Ψ=2) model of the restricted likelihood set was 111 ktons) (Figure 4.7). I explored intermediate values of I_0 by creating a likelihood profile (Hilborn and Mangel, 1997), allowing I_0 to vary between 20 and 100 ktons (Figure 4.7). To break correlation among parameters, I fixed the value of the catchability parameter q at the level I observed in the 7 models discussed above, q=1. For each fixed level of I_0 I looked for the best fit and produced a forecast for 2008-2010 and a hindcast for 1969-1984. The capelin biomass used to produce these hindcasts was taken from the ice-capelin model I developed in Chapter 3 (Buren et al., 2014). Hindcasts were contrasted with the output of the missing fish sequential population analysis (SPA) (Shelton and Lilly, 2000; Smedbol et al., 2002), which spans from 1962 to 2001.

I found that at a level of I_0=80 ktons the 2008-2010 predictions agree quite well with the observed level of stock biomass (Figure 4.8). In addition, the hindcast agreed very well with the SPA in both the trends and the magnitudes of the stock biomass (Figure 4.8). The major difference between these two is that the SPA predicts a biomass peak during the mid-1980s whereas my model hindcast predicts a plateau throughout the 1980s, which is more consistent with the RV data. It is worth noting that both the SPA and my most parsimonious model predict lower stock biomass during the 1980s than the index derived from the RV survey. This is not unexpected given that the "gear corrected" time series is an index and thus it is concordance in trends, rather than absolute values, which is most reassuring.

4.4.5 Mortality

I calculated the net losses at time t from the model (Z_{model}), and contrasted it to the total mortality rate of cod aged 4-6 calculated using data from the autumn RV surveys in the offshore of 2J3KL (DFO, 2011*b*). Z_{model} was estimated for the most parsimonious model, i.e. 'No seals(Ψ=2, q=1,I_0=80)', and defined as:

$$Z_{model} = Losses_t - Gains_t = B_{cod,t}T + L_t - B_{cod,t}P_t \qquad (4.9)$$

where $Losses_t$ represent biomass losses from the cod population at time t due to all sources (i.e. metabolic loss, natural mortality and fisheries removals) and $Gains_t$ represents the biomass gain of the cod population at time t from somatic growth and reproduction.

There was very good correspondence between the net losses from the model and the total mortality rate calculated using RV data, except in 1991 (Figure 4.9). If the year 1991 is not considered, the correlation coefficient between the variables is r=0.65.

4.4.6 Somatic condition

Condition of Atlantic cod was variable both in terms of space and time (Figure 4.10). During most years the median somatic condition was below the value considered as excellent condition (i.e. $K_s < 0.85$), with part of the distribution falling below the condition of starved fish (i.e., $K_s < 0.7$). During the late 1970s and 1980s there was a spatial progression in fish condition, from better condition in northern areas (NAFO Div 2J) to poorer conditions in the south (NAFO Div 3L) (Figure 4.10). As time progressed into the 1990s and 2000s, median condition was lower than during the 1980s, and noticeably the distributions of conditions curves were more leptokurtic. These responses were gradual in terms of space; the decrease in condition over time was more noticeable in the north (NAFO Div 2J), smaller in NAFO Div 3K and less noticeable in the south of the study area (NAFO Div 3L) (Figure 4.10). In addition, the median of the distribution during the late 1970s and 1980s was quite variable. During the 1990s and 2000s all the condition distribution curves tended to be centred on a very similar median value (Figure 4.10).

4.5 Discussion

The northern cod stock that once sustained one of the largest fisheries worldwide collapsed in the early 1990s and has not recovered despite 20 years of highly reduced fishing. Intense fisheries exploitation was certainly an important factor in the collapse, although it is less clear if other factors also contributed to the collapse and why the stock has been kept suppressed despite low exploitation rates.

In this chapter I gauged the relative roles that fisheries removals, capelin availability and consumption by harp seals play in driving the dynamics of the stock through the implementation of a bioenergetic-allometric cod biomass dynamic model. This framework allowed us to test multiple hypotheses on the roles of each of the drivers (Table 4.1) simultaneously and weight their relative empirical support (Table 4.2 and Table 4.3). I assumed the average weight of cod to be equal to 1 kg. It is expected that the average weight of cod changed during the period considered due to the truncation of the size structure of the population (Lilly et al., 2003). However, given that bioenergetics-allometric models (Yodzis and Innes, 1992) consider body sizes that range from unicellular organisms to vertebrates, I would not expect relatively minor changes in mean weight to have a large impact on the model results. In fact, I have fitted the models using 0.5 and 4 kg as cod's average weight and found similar results (not shown).

4.5.1 Main drivers of northern cod dynamics

The results of this modelling exercise indicate that during the period considered (1985-2007) the main drivers of the northern cod stock were capelin availability and fisheries removals, and that consumption by harp seals has not been a major forcer of the cod dynamics.

The interplay between the two drivers could not, however, be fully resolved. This was likely due to missing capelin surveys during the 1990s (1993-1995, 1997, 1998) and 2006, and/or the fact that both drivers showed a sharp decrease during the early 1990s making the task of disentangling their effects very challenging from a modelling perspective. Looking to balance the effects of fisheries and capelin, I found that the most parsimonious model was the 'No seals' model with a half saturation rate (I_0) of 80 ktons.

The good correspondence between quantities predicted from my most parsimonious model and three different independent data sources suggests that the model captures the most significant drivers of the northern cod stock biomass dynamics. The comparisons I carried to validate the model were:

i. forecasted biomass levels for 2008-2010 vs biomass estimated by the research vessel surveys (Figure 4.8),

ii. hindcasted biomass levels for 1969-1984 vs an accepted view of the trajectory of the stock's biomass, the output of the missing fish sequential population analysis (SPA) (Shelton and Lilly, 2000; Smedbol et al., 2002) (Figure 4.8), and

iii. a proxy for annual mortality rate from my model vs mortality rates estimated from the research survey data (DFO, 2011*b*) (Figure 4.9).

4.5.1.1 Fisheries removals as a driver

As expected, my analyses indicated that fisheries removals has been an important driver of the northern cod stock's dynamics during the period considered (1985-2007). The mechanisms through which fishing affects the dynamics of northern cod have been studied extensively (Hutchings and Myers, 1994; Hutchings, 1996; Myers et al., 1996, 1997; Rose, 2004; Shelton et al., 2006; Lilly et al., 2008; Hilborn and Litzinger, 2009). My study reinforces the notion that fisheries removals was an important factor in the collapse of Atlantic cod off Newfoundland during the early 1990s.

4.5.1.2 Capelin availability as a driver

The role of capelin availability in driving the dynamics of the northern cod stock is likely linked to individual energy allocation. In this study I have used capelin availability as a proxy for the quality of the prey field; high abundances of capelin represent a good quality and low abundances a poor quality prey field. The rationale for this is that capelin is the most energetically dense of cod's important prey in the Northwest Atlantic (Lawson, Magalhães and Miller, 1998). I therefore expected that the changes in capelin biology and ecology that took place during the 1990s and most importantly its severe abundance decline must have represented a serious burden. Northern cod's diet composition changed from a heavy reliance on capelin during the 1980s and early 1990s to rely more on *Pandalus* shrimp, a prey with a much lower energy density, during the late 1990s and 2000s; this shift was more marked in the northern regions (Dawe et al., 2012; DFO, 2012; Krumsick and Rose, 2012). I used Lambert's (2011; 2012) simple linear regression relating Atlantic cod's somatic condition during January to somatic condition during May in the northern Gulf of St Lawrence, to convert fall to spring somatic condition (when it is at its minimum). This allowed us to compare spring condition to threshold values found in starvation and feeding experiments (Lambert and Dutil, 1997). This rescaling only lowers the condition of each fish considered, but does not change the shape of the condition curves obtained. Thus, even in the case that Lambert's (2011; 2012) relationship did not hold for cod in 2J3KL, conclusions drawn from the shapes of the condition curves would still stand.

All organisms face a trade-off between reproduction, growth and survival. These trade-offs are mediated through the allocation of energy toward stores or growth; stored energy determines fecundity if reproduction occurs and survival in the event of low prey availability (Jørgensen et al., 2006). The growth rate of northern cod is influenced by both, food availability and environmental temperature (Krohn et al., 1997; Brander, 2007). Thus cod's ability to utilize growth as currency in this trade-off is likely limited. On the other hand, iteroparous fish may skip spawning, favouring growth or survival in a given year. Thus, if female cod in poor condition invest their energy in reproduction they do it at the cost of increasing their risk of mortality (Lambert and Dutil, 2000). The most commonly reported cause of skipped spawning in fish is poor nutrition (Rideout et al., 2005). The distribution of the condition factor over time suggests a decrease in somatic condition during the 1990s and early 2000s in NAFO Div 2J, and to some extent in NAFO Div 3K (Figure 4.10). This is consistent with reports of low growth, somatic condition, liver index and age-at-maturity associated with diets dominated by *Pandalus* shrimp (Sherwood et al., 2007; Krumsick and Rose, 2012). The distribution curves were more leptokurtic as time progressed (Figure 4.10). In probabilistic terms, this would mean that there was a larger chance of finding individuals in poor condition during the 1990s and early 2000s than during the 1980s. Also, the medians of the condition factor distributions showed a higher inter-annual variability during the 1970s and 1980s (Figure 4.10), thus the effects of a large proportion of fish being in poor condition in any given year would be buffered by smaller proportions in other years. This 'buffer' effect was lost during the 1990s and early 2000s when the median condition of fish was poor for several consecutive years. In this context, skipping spawning during a bad year may not have been a successful strategy. The frequency of skipped spawning in the offshore component of the stock was very low during the period 1978-2004 (2J: 0.33%, 3K: 3.45%, 3L: 8.11%), with no apparent trend in the proportion of fish that skipped spawning (Rideout et al., 2006). In contrast, cod in the large inshore aggregation of Smith Sound, which fared well in terms of spawning biomass during the last half of the 1990s and first half of the 2000s, suppressed reproduction in a significant proportion in the years 1999-2004 (Rideout and Rose, 2006). Thus, cod in the inshore has apparently invested energy toward survival forgoing reproduction while cod in the offshore may have been investing its compromised energy reserves toward reproduction, in detriment to survival. The effects of a fish in poor condition spawning will not only be felt in terms of its own survival, but also in terms of the quantity and quality of the eggs produced (affecting the probability of larvae to survive to maturity). Consistent with this idea, there have been reports of reduced average productivity and cumulative individual egg production per recruit of the northern cod stock (Shelton et al., 2006; Fudge and Rose, 2008).

Lilly et al. (2003) reported that no problems had been identified in the offshore component of the stock during the regular autumn research surveys. However, these authors only analysed trends in mean condition, and thus would not have been able to detect differences in distribution of condition over time. Notwithstanding, they reported concern that there might not be sufficient capelin available to restore the northern cod stock to its former level of abundance. My interpretation is that although cod can survive without capelin, having a lipid rich diet (such as that provided by capelin) gives cod the edge needed to not only survive in the harsh environment of the Northwest Atlantic but also to afford producing strong progeny in terms of both numbers and quality.

4.5.1.3 Harp seal consumption as a driver

Notably, the significant drivers of the stock do not include consumption by harp seals. In this study I included a variety of plausible shapes that the trajectory of cod consumption by seals could take, as a result of using three different descriptions of the diet utilized to estimate consumption levels. In addition, I allowed the consumptions to scale up or down during model fitting. I therefore addressed uncertainty in terms of the form of seal consumption and in terms of the magnitude of the consumption. Thus, the evidence leads to reject the hypothesis that seal predation has been an important driver of the stock.

Nonetheless, one might wonder if the residual variation not explained by my models could be explained by harp seal consumption. As fisheries removals had an unquestionable role on the dynamics of cod, I present the residuals from the 'Only fisheries' models (both likelihoods), the 'No seals' models (both likelihoods) and from my most parsimonious model 'No seals (Ψ=2, I_0=80)' in Figure 4.11. The most conspicuous feature of the residuals in the arithmetic scale is that they show large fluctuations in the pre-collapse period and afterwards the variation is overshadowed because of the large differences in magnitude of the biomass estimates. When the residuals are examined in the logarithmic scale, a quasi-sinusoidal pattern clearly emerges, reaching the lowest point in 1994 particularly for the models that were fitted considering the restricted likelihood. There is no plausible way in which to reconcile this pattern with cod consumption by harp seals. Plausible drivers that could account for this pattern would be the effect of other food items or an environmental forcer such as temperature. I found good correspondence between the residuals of the best ('No seals (Ψ=2)') and the most parsimonious 'No seals (Ψ=2, I_0=80)' models and the mean annual bottom (depth $\leq$ -150 m) temperature at Station 27 (Figure 4.12), although there seems to be an offset in this relationship during the 1980s, compared to subsequent years. Thus, this modelling exercise suggests that environmental conditions may also influence the dynamics of the northern cod. Drinkwater (2002) provided evidence that environmental variability plays a role on the dynamics of the northern cod stock, via its effects on individual growth rates, displacements of the stock, and likely lower recruitment, although these effects have not yet been integrated into a dynamic model. This warrants further study into the mechanistic links between temperature and the rate of change of the northern cod stock biomass.

Bundy (2001) explored whether the relative effects of fishing and predation could account for the collapse of the northern cod and other groundfish stocks. This author modelled 31 functional components of the Newfoundland-Labrador Shelf marine ecosystem and found support for the hypothesis that the recovery of the northern cod was being retarded by harp seals predation. However, at the time Bundy (2001) conducted her study capelin biomass estimates were derived from an assortment of sources that included bottom trawl surveys, commercial catch data, an aerial survey and data on capelin egg deposition on beaches, and the view at the time was that the stock biomass had been steadily increasing since 1980 through to 1996 (Nakashima and Winters, 1997). After the publication of Bundy's (2001) study, a comparative analysis (O'Driscoll et al., 2002) concluded that bottom trawl surveys are unlikely to provide a reliable index of capelin abundance, and acoustic integration, supported by directed trawling, is the most reliable method for estimating capelin abundance. Applying this later methodology, the currently accepted view is that the capelin stock suffered a drastic decline in 1991 from which it has not yet recovered (Figure 4.2c, DFO, 2010). If today's perspective on capelin status and trend during the 1990s were to be considered, it is possible that simulations like the ones carried out by Bundy (2001) would render different outcomes. This possibility suggests that an updated multispecies modelling study for the Newfoundland-Labrador marine ecosystem would be of both scientific and management value.

Predator pit effect Shelton and Healey (1999) suggest that the northern cod stock may have depensatory dynamics caused by harp seal consumption (i.e. a 'predator pit'). A population's dynamics are depensatory if the per-capita rate of growth decreases as the density decreases to low levels (Liermann and Hilborn, 2001). Several mechanisms can lead to depensation: reduced probability of fertilization, impaired group dynamics, conditioning of the environment and predator saturation (Liermann and Hilborn, 2001). The concepts of depensation and predator pit are illustrated in Figure 4.13: the part of the curve of growth rate between the minimum and unstable equilibrium (B_B) is considered depensatory. If the biomass falls below B_B it will be driven to even lower levels and eventually to the lower stable equilibrium (B_A). If these dynamics are caused by predation mortality, biomasses lower than B_B represent the predator pit. A predator pit occurs when the predation probability decreases above and below an intermediate level of prey abundance (Bakun, 2006, the concept is identical if abundance is replaced by biomass) (Figure 4.13a). The predation probability decreases above an intermediate level of prey biomass due to predator saturation, and thus if the prey biomass exceeds this critical point it can break out from the pit. The probability of predation decreases below a critical level because of prey 'refuges' at low density.

Considering this; what is the evidence that the dynamics of northern cod are depensatory?

To assess if the dynamics are depensatory, I calculated the net rate of increase following Sinclair et al. (1998) using the survey biomass instead of numbers as follows: $r_{net} = ln({}^{B_{cod,t+1}}/_{B_{cod,t}})$, and present the point estimates with a fitted loess curve in order to visualize trends in the data (I excluded years influenced by the anomalously high biomass recorded in 1986) (Figure 4.13b).

The shape of the resulting curve suggests that the dynamics are depensatory and that the magnitude of the unstable equilibrium B_B is ˜450 kt, the level observed throughout the 1980s.

Is depensation caused by harp seal predation mortality, i.e. is cod in a harp seal predator pit?

I calculated the mortality rate due to predation by harp seals as the ratio of the consumption by harp seals in a given year to the biomass of cod in that year, and present the point estimates with fitted loess curves.

The shape of the mortality rate predation curves are best described as exponentially decreasing (Figure 4.13b), and thus bear no resemblance with the shape of the mortality rates needed to create a predator pit.

As a consequence, I agree with Shelton and Healey (1999) that the northern cod may have depensatory dynamics. However, I disagree as to the mechanisms that may prompt these dynamics. The evidence suggests that the northern cod is not in a predator pit. Nonetheless, it seems that the biomass of northern cod would have to be pushed beyond roughly ˜500 kt for it to break out from the depensatory dynamics. It may take one or several good year-classes to produce this level of recruitment. However, year-class strength in the offshore has been very poor since 1990 (DFO, 2011*b*). The issue of depensatory dynamics in northern cod warrants further investigation.

4.6 Concluding remarks

In this chapter I have provided evidence that the biomass dynamics of the northern cod stock have been driven by the fishery and the abundance of lipid-rich capelin. Taking into account that capelin seems to be environmentally driven (Chapter 3, Buren et al., 2014), my findings here reinforce the notion that bottom-up regulation is important in this system through multiple trophic levels, including the possibility that cod's dynamics may be explained from physical drivers. My study clearly supports the view that system-wide production and the regulatory mechanisms that forage species play in the ecosystem are fundamental to the development of Ecosystem Based Fisheries Management approaches.

4.7 References

Anderson, D. (2008), *Model based inference in the life sciences: a primer on evidence*, Springer, New York, USA.

Bakun, A. (2006). 'Wasp-waist populations and marine ecosystem dynamics: Navigating the "predator pit" topographies', *Prog Oceanogr* 68, 271–288.

Benoît, H. P., Swain, D., Bowen, W., Breed, G., Hammill, M. and Harvey, V. (2011). 'Evaluating the potential for grey seal predation to explain elevated natural mortality in three fish species in the southern Gulf of St. Lawrence', *Mar Ecol Prog Ser* 442, 149–167.

Bowen, W. (1997). 'Role of marine mammals in aquatic ecosystems', *Mar Ecol Prog Ser* 158, 267–274.

Brander, K. M. (2007). 'The role of growth changes in the decline and recovery of North Atlantic cod stocks since 1970', *ICES J Mar Sci* 64, 211–217.

Brattey, J., Cadigan, N. G., Dwyer, K. S., Healey, B. P., Morgan, M., Murphy, E., Maddock Parsons, D. and Power, D. (2011). 'Assesment of the cod (*Gadus morhua*) stock in NAFO Divisions 2J+3KL in 2010', *Can Sci Advis Secretar Res Doc* 2010/103.

Bundy, A. (2001). 'Fishing on ecosystems: the interplay of fishing and predation in Newfoundland-Labrador', *Can J Fish Aquat Sci* 58, 1153–1167.

Buren, A. D., Koen-Alonso, M., Pepin, P., Mowbray, F., Nakashima, B. S., Stenson, G. B., Ollerhead, N. and Montevecchi, W. (2014). 'Bottom-up regulation of capelin, a keystone forage species', *PLoS ONE* 9(2), e87589.

Burnham, K. and Anderson, D. (2002), *Model selection and multimodel inference. A practical Information-theoretic approach*, Springer, New York, USA.

Carscadden, J. and Frank, K. (2002). 'Temporal variability in the condition factors of Newfoundland capelin (*Mallotus villosus*) during the past two decades', *ICES J Mar Sci* 59, 950–958.

Carscadden, J. and Nakashima, B. S. (1997), Abundance and changes in distribution, biology and behavior of capelin in response to cooler water of the 1990s, *in* 'Forage fishes in marine ecosystems. Proceedings of the International Symposium on the Role of Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Program Rep. No. AK-SG-97-01.', University of Alaska Fairbanks, Fairbanks, Alaska, pp. 457–468.

Chassot, E., Duplisea, D., Hammill, M., Caskenette, A., Bousquet, N., Lambert, Y. and Stenson, G. (2009). 'Role of predation by harp seals *Pagophilus groenlandicus* in the collapse and non-recovery of northern Gulf of St. Lawrence cod *Gadus morhua*', *Mar Ecol Prog Ser* 379, 279–297.

Dawe, E., Koen-Alonso, M., Chabot, D., Stansbury, D. and Mullowney, D. (2012). 'Trophic interactions between key predatory fishes and crustaceans: comparison of two Northwest Atlantic systems during a period of ecosystem change', *Mar Ecol Prog Ser* 469, 233–248.

DFO. (2003*a*). 'Northern (2J+3KL) cod stock status update', *Can Sci Advis Secretar Stock Stat Rep* 2003/018.

DFO. (2003*b*). 'Proceedings of the Zonal Assessment Meeting - Atlantic Cod', *Can Sci Advis Secretar Proc Ser* 2003/021.

DFO. (2008*a*). 'Proceedings of the National Workshop on the Impacts of Seals on Fish Populations in Eastern Canada (Part 1); 12-16 November 2007', *Can Sci Advis Secretar Proc Ser* 2008/021.

DFO. (2008*b*). 'Stock assessment of Northern (2J3KL) cod in 2008', *Can Sci Advis Secretar Adv Rep* 2008/034.

DFO. (2009). 'Proceedings of the National Workshop on the Impacts of Seals on Fish Populations in Eastern Canada (Part 2)', *Can Sci Advis Secretar Proc Ser* 2009/020.

DFO. (2010). 'Assessment of capelin in SA2+Div. 3KL in 2010', *Can Sci Advis Secretar Adv Rep* 2010/090.

DFO. (2011*a*). 'Impacts of grey seals on fish populations in Eastern Canada', *Can Sci Advis Secretar Science Adv Rep* 2010/071.

DFO. (2011*b*). 'Stock assessment of Northern (2J3KL) cod in 2011', *Can Sci Advis Secretar Adv Rep* 2011/041.

DFO. (2012). 'Results and recommendations from the Ecosystem Research Initiative - Newfoundland and Labrador's Expanded Research on Ecosystem Relevant but UnderSurveyed Splicers', *Can Sci Advis Secretar Adv Rep* 2012/058.

Drinkwater, K. F. (2002), A review of the role of climate variability in the decline of northern cod, *in* **N. McGinn**., ed., 'American Fisheries Society Symposium', American Fisheries Society, Symposium 32, Bethesda, Maryland, pp. 113–129.

Flaaten, O. (1988), *The economics of multispecies harvesting. Theory and application to the Barents Sea fishery*, Springer-Verlag, Berlin, Germany.

Frank, K., Carscadden, J. and Simon, J. (1996). 'Recent excursions of capelin (*Mallotus villosus*) to the Scotian Shelf and Flemish Cap during anomalous hydrographic conditions', *Can J Fish Aquat Sci* 53, 1473–1486.

FRCC. (2011). 'Fisheries Resource Conservation Council, report to the Minister of Fisheries and Oceans: Towards recovered and sustainable groundfish fisheries in Eastern Canada', *Fisheries Resource Conservation Council* FRCC 11.R1.

Fudge, S. B. and Rose, G. A. (2008). 'Life history co-variation in a fishery depleted Atlantic cod stock', *Fish Res* 92, 107–113.

Goldsworthy, S. D., Bulman, C., He, X., Larcombe, J. and Littnan, C. (2003), Trophic interactions between marine mammals and Australian fisheries: an ecosystem approach, *in* **N. Gales, M. Hindell and R. Kirkwood**., eds, 'Marine Mammals. Fisheries, tourism and management issues', CSIRO Publishing, Collingwood, Australia, pp. 62–99.

Halliday, R. and Pinhorn, A. (2009). 'The roles of fishing and environmental change in the decline of Northwest Atlantic groundfish populations in the early 1990s', *Fish Res* 97, 163–182.

Hammill, M. and Stenson, G. B. (2011). 'Modelling grey seal abundance in Canadian waters', *Can Sci Advis Sec Sci Res Doc* 2011/014.

Hammill, M., Stenson, G. B., Doniol-Valcroze, T. and Mosnier, A. (2013). 'Estimating carrying capacity and population trends of Northwest Atlantic harp seals, 1952-2012', *DFO Can Sci Advis Sec Sci Res Doc* 2012/148.

Harwood, J. (1992). 'Assessing the competitive effects of marine mammal predation on commercial fisheries', *S Afr J Mar Sci* 12, 689–693.

Hilborn, R. and Litzinger, E. (2009). 'Causes of decline and potential for recovery of Atlantic cod populations', *Open Fish Sci J* 2, 32–38.

Hilborn, R. and Mangel, M. (1997), *The ecological detective. Confronting models with data*, Princeton University Press, Princeton, New Jersey, USA.

Hutchings, J. (1996). 'Spatial and temporal variation in the density of northern cod and a review of hypotheses for the stock's collapse', *Can J Fish Aquat Sci* 53(5), 943–962.

Hutchings, J. A. and Myers, R. A. (1994). 'What can be learned from the collapse of a renewable resource? Atlantic cod, *Gadus morhua*, of Newfoundland and Labrador', *Can J Fish Aquat Sci* 51, 2126–2146.

IMSL. (2006), *IMSL MATH/LIBRARY User's Manual, Version 6.0*, Houston, TX.

Jørgensen, C., Ernande, B., Fiksen, Ø. and Dieckmann, U. (2006). 'The logic of skipped spawning in fish', *Can J Fish Aquat Sci* 63, 200–211.

Koen-Alonso, M., Buren, A. D. and Stenson, G. B. (2009). 'A multinomial regression approach to reconstruct diet composition', *Can Sci Advis Secretar Proc Ser 2009/20* .

Krohn, M., Reidy, S. and Kerr, S. (1997). 'Bioenergetic analysis of the effects of temperature and prey availability on growth and condition of northern cod (*Gadus morhua*)', *Can J Fish Aquat Sci* 54 (Supplement 1), 113–121.

Krumsick, K. J. and Rose, G. A. (2012). 'Atlantic cod (*Gadus morhua*) feed during spawning off Newfoundland and Labrador', *ICES J Mar Sci* 69, 1701–1709.

Lambert, Y. (2011). 'Environmental and fishing limitations to the rebuilding of the northern Gulf of St. Lawrence cod stock (*Gadus morhua*)', *Can J Fish Aquat Sci* 68, 618–631.

Lambert, Y. (2012). 'Erratum: Environmental and fishing limitations to the rebuilding of the northern Gulf of St. Lawrence cod stock (*Gadus morhua*)', *Can J Fish Aquat Sci* 69, 612–612.

Lambert, Y. and Dutil, J.-D. (1997). 'Can simple condition indices be used to monitor and quantify seasonal changes in the energy reserves of cod (*Gadus morhua*)?', *Can J Fish Aquat Sci* 54(S1), 104–112.

Lambert, Y. and Dutil, J.-D. (2000). 'Energetic consequences of reproduction in Atlantic cod (*Gadus morhua*) in relation to spawning level of somatic energy reserves', *Can J Fish Aquat Sci* 57, 815–825.

Lavigne, D. (1996), Ecological interactions between marine mammals, commercial fisheries and their prey: unravelling the tangled web, *in* **W. A. Montevecchi**., ed., 'Studies of high-latitude seabirds. 4. Trophic relationships and energetics of endotherms in cold ocean systems', Can Wildl Serv Ocass Pap 91, pp. 59–71.

Lawson, J. W., Anderson, J. T., Dalley, E. L. and Stenson, G. B. (1998). 'Selective foraging by harp seals *Phoca groenlandica* in nearshore and offshore waters of newfoundland, 1993 and 1994', *Mar Ecol Prog Ser* 163, 1–10.

Lawson, J. W., Magalhães, A. M. and Miller, E. H. (1998). 'Important prey species of marine vertebrate predators in the northwest Atlantic: proximate composition and energy density', *Mar Ecol Prog Ser* 164, 13–20.

Le Cren, E. (1951). 'The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*)', *J Anim Ecol* 20, 201–219.

Liermann, M. and Hilborn, R. (2001). 'Depensation: evidence, models and implications', *Fish Fish* 2, 33–58.

Lilly, G. (1987). 'Interactions between Atlantic cod (*Gadus morhua*) and capelin (*Mallotus villosus*) off Labrador and eastern Newfoundland: a review', *Can Tech Rep Fish Aquat Sci* 1567, 1–37.

Lilly, G. R. (1991). 'Interannual variability in predation by cod (*Gadus morhua*) on capelin (*Mallotus villosus*) and other prey off southern Labrador and northeastern Newfoundland', *ICES Mar Sci Symp* 193, 133–146.

Lilly, G. R., Shelton, P. A., Brattey, J., Cadigan, N. G., Healey, B. P., Murphy, E., Stansbury, D. and Chen, N. (2003). 'An assessment of the cod stock in NAFO Divisions 2J+3KL in February 2003', *Can Sci Advis Secretar Res Doc* 2003/023.

Lilly, G. R., Wieland, K., Rothschild, B. J., Sundby, S., Drinkwater, K. F., Brander, K. M., Ottersen, G., Carscadden, J. E., Stenson, G. B.,

Chouinard, G. A., Swain, D. P., Daan, N., Enberg, K., Hammill, M., Rosing-Asvid, A., Svedöng, H. and Vázquez, A. (2008), Decline and recovery of Atlantic cod (*Gadus morhua*) stocks throughout the North Atlantic, *in* **G. Kruse, K. F. Drinkwater, J. Ianelli, J. S. Link, D. Stram, V. Wespestad and D. Woodby**., eds, 'Resiliency of gadid stocks to fishing and climate change', Alaska Sea Grant College Program, Fairbanks, pp. 39–66.

May, R. M., Beddington, J. R., Clark, C. W., Holt, S. J. and Laws, R. M. (1979). 'Management of multispecies fisheries', *Science* 205(4403), 267–277.

McLaren, I., Brault, S., Harwood, J. and Vardy, D. (2001). 'Report of the Eminent Panel on Seal Management', *Report to the Department of Fisheries and Oceans* Available from Fisheries and Oceans at http://publications.gc.ca/collections/Collection/Fs23-405-2001E.pdf.

Mello, L. and Rose, G. (2005). 'Seasonal growth of Atlantic cod: effects of temperature, feeding and reproduction', *J Fish Biol* 67(1), 149–170.

Miller, D. (1997), Results from an acoustic survey for capelin (*Mallotus villosus*) in NAFO Divisions 3KL in the spring of 1996, *in* **Anon**., ed., 'Capelin in SA2 + Div 3KL', Can Sci Advis Secretar Res Doc 97/29, pp. 84–90.

Mowbray, F. (2002). 'Changes in the vertical distribution of capelin (*Mallotus villosus*) off Newfoundland', *ICES J Mar Sci* 59, 942–949.

Mowbray, F. (2012). 'Some results from spring acoustic surveys for capelin (*Mallotus villosus*) in NAFO Division 3L between 1982 and 2010', *Can Sci Advis Secretar Res Doc* 2012/143, 1–34.

Myers, R. A., Hutchings, J. A. and Barrowman, N. (1996). 'Hypotheses for the decline of cod in the North Atlantic', *Mar Ecol Prog Ser* 138, 293–308.

Myers, R. A., Hutchings, J. A. and Barrowman, N. J. (1997). 'Why do fish stocks collapse? The example of cod in Atlantic Canada', *Ecol Appl* 7, 91–106.

Nakashima, B. S. and Wheeler, J. P. (2002). 'Capelin (*Mallotus villosus*) spawning behaviour in Newfoundland waters - the interaction between beach and demersal spawning', *ICES J Mar Sci* 59, 909–916.

Nakashima, B. S. and Winters, G. (1997), Multiplicative trends of biomass, cohort abundance and recruitment of capelin, *Mallotus villosus*, *in* 'Capelin in SA2 + Div 3KL', Can Sci Advis Secretar Res Doc 97/29, pp. 74–83.

Northridge, S. (1991). 'An updated world review of interactions between marine mammals and fisheries', *FAO Fish Tech Pap* 251, Supplement 1.

O'Driscoll, R., Rose, G. and Anderson, J. (2002). 'Counting capelin: a comparison of acoustic density and trawl catchability', *ICES J Mar Sci* 59, 1062–1071.

Punt, A. and Butterworth, D. S. (1995). 'The effects of future consumption by the Cape fur seal on catch rates of the Cape hakes. 4. Modelling the biological interactions between Cape fur seals *Arctocephalus pusillus* pusillus and the Cape hakes *Merluccius capensis* and *M. paradoxus*', *S Afr J Mar Sci* 16, 255–285.

Rideout, R. and Morgan, M. (2010). 'Relationships between maternal body size, condition and potential fecundity of four north-west Atlantic demersal fishes', *J Fish Biol* 76, 1379–1395.

Rideout, R., Morgan, M. and Lilly, G. (2006). 'Variation in the frequency of skipped spawning in Atlantic cod (*Gadus morhua*) off Newfoundland and Labrador', *ICES J Mar Sci* 63, 1101–1110.

Rideout, R. M. and Rose, G. A. (2006). 'Suppression of reproduction in Atlantic cod *Gadus morhua*', *Mar Ecol Prog Ser* 320, 267–277.

Rideout, R. M., Rose, G. A. and Burton, M. P. (2005). 'Skipped spawning in female iteroparous fishes', *Fish Fish* (1), 50–72.

Rose, G. A. (2004). 'Reconciling overfishing and climate change with stock dynamics of Atlantic cod (*Gadus morhua*) over 500 years', *Can J Fish Aquat Sci* 61, 1553–1557.

Rose, G. A. and O'Driscoll, R. L. (2002). 'Capelin are good for cod: can the northern stock rebuild without them?', *ICES J Mar Sci* 59, 1018–1026.

Ruzicka, J. J., Steele, J. H., Ballerini, T., Gaichas, S. K. and Ainley, D. G. (2013). 'Dividing up the pie: Whales, fish, and humans as competitors', *Prog Oceanogr* 116, 207–219.

Sergeant, D. E. (1973). 'Feeding, growth, and productivity of Northwest Atlantic harp seals (*Pagophilus groenlandicus*)', *J Fish Res Board Can* 30, 17–29.

Shelton, P. A. and Healey, B. P. (1999). 'Should depensation be dismissed as a possible explanation for the lack of recovery of the northern cod (*Gadus morhua*) stock?', *Can J Fish Aquat Sci* 56, 1521–1524.

Shelton, P. A. and Lilly, G. R. (2000). 'Interpreting the collapse of the northern cod stock from survey and catch data', *Can J Fish Aquat Sci* 57, 2230–2239.

Shelton, P. A., Sinclair, A. F., Chouinard, G. A., Mohn, R. and Duplisea, D. E. (2006). 'Fishing under low productivity conditions is further delaying recovery of Northwest Atlantic cod (*Gadus morhua*)', *Can J Fish Aquat Sci* 63, 235–238.

Shelton, P. A., Warren, W. G. and Stenson, G. B. (1997). 'Quantifying Some of the Major Sources of Uncertainty Associated with Estimates of Harp Seal Prey Consumption. Part II: Uncertainty in Consumption Estimates Associated with Population Size, Residency, Energy Requirement and Diet', *J Northw Atl Fish Sci* 22, 303–315.

Sherwood, G. D., Rideout, R. M., Fudge, S. B. and Rose, G. A. (2007). 'Influence of diet on growth, condition and reproductive capacity in Newfoundland

and Labrador cod (*Gadus morhua*): Insights from stable carbon isotopes (δ^{13}C)', *Deep Sea Res Pt II* 54(23-26), 2794–2809.

Siarry, P., Berthiau, G., Durbin, F. and Haussy, J. (1997). 'Enhanced simulated annealing for globally minimizing functions of many-continuous variables', *ACM Trans Math Softw* 23(2), 209–228.

Sinclair, A., Pech, R., Dickman, C., Hik, D., Mahon, P. and Newsome, A. (1998). 'Predicting Effects of Predation on Conservation of Endangered Prey', *Cons Biol* 12, 564–575.

Smedbol, R., Shelton, P. A., Swain, D., Frchet, A. and Chouinard, G. A. (2002). 'Review of population structure, distribution and abundance of cod (*Gadus morhua*) in Atlantic Canada in a species-at-risk context', *Can Sci Advis Secretar Res Doc* 2002/082.

Steele, D., Andersen, R. and Green, J. (1992). 'The managed commercial annihilation of northern cod', *Newfoundland and Labrador Studies* 8(1), 34–68.

Stenson, G. B. (2012). 'Estimating consumption of prey by harp seals (*Pagophilus groenlandicus*) in NAFO Divisions 2J3KL', *Can Sci Advis Secretar Res Doc* 2012/156.

Stenson, G. B. and Sjare, B. (1997). 'Seasonal distribution of harp seals, *Phoca groenlandica*, in the Northwest Atlantic', *ICES CM Document* CC:10.

Swain, D., Benoît, H. P., Hammill, M., McClelland, G. and Aubry, . (2011). 'Alternative hypotheses for causes of the elevated mortality of cod (*Gadus morhua*) in the southern Gulf of St Lawrence; the weight of evidence', *DFO Can Sci Advis Sec Sci Res Doc* 2011/036, –.

Thomas, L., Hammill, M. and Bowen, W. (2011). 'Estimated size of the Northwest Atlantic grey seal population 1977-2010', *DFO Can Sci Advis Sec Sci Res Doc* 2011/017, 1–23.

Trites, A. W., Christensen, V. and Pauly, D. (1997). 'Competition between fisheries and marine mammals for prey and primary production in the Pacific Ocean', *J Northw Atl Fish Sci* 22, 173–187.

Trzcinski, M., Mohn, R. and Bowen, W. (2006). 'Continued decline of an atlantic cod population: how important is gray seal predation?', *Ecol Appl* 16, 2276–2292.

Trzcinski, M., Mohn, R. and Bowen, W. (2009). 'Estimating the impact of grey seals on the Eastern Scotian Shelf and Western Scotian Shelf cod populations', *DFO Can Sci Advis Sec Sci Res Doc* 2009/052, 1–19.

Warren, W. G. (1997). 'Report on the comparative fishing trial between the Gadus Atlantica and the Teleost', *NAFO Scien Coun Res Doc* 96/28.

Warren, W. G., Shelton, P. A. and Stenson, G. B. (1997). 'Quantifying some of the major sources of uncertainty associated with estimates of harp seal prey consumption Part I: Uncertainty in the estimates of harp seal population size', *J Northw Atl Fish Sci* 22, 289–302.

Wickens, P., Japp, D., Shelton, P., Kriel, F., Goosen, P., Rose, B., Augustyn, C., Bross, C., Penney, A. and Krohn, R. (1992). 'Seals and fisheries in South Africa - competition and conflict', *S Afr J Mar Sci* 12, 773–789.

Yodzis, P. (1994). 'Predator-prey theory and management of multispecies fisheries', *Ecol Appl* 4, 51–58.

Yodzis, P. (1998). 'Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem', *J Anim Ecol* 67, 635–658.

Yodzis, P. and Innes, S. (1992). 'Body size and consumer-resource dynamics', *Am Nat* 139, 1151–1175.

4.8 Tables

Table 4.1: Description of the scenarios used to test the effects of the proposed drivers on the dynamics of the northern cod stock and the parameters that are estimated in each case.

Scenario	Cod stock drivers	Diet description	Estimated parameters
All effects, average	Capelin, fisheries, seals	Average	q, m, δ, $B_{cod,1985}$, I_0
All effects, average, ASC	Capelin, fisheries, seals	Average	q, m, δ, $B_{cod,1985}$, I_0, θ
All effects, MR	Capelin, fisheries, seals	MR	q, m, δ, $B_{cod,1985}$, I_0
All effects, MR, ASC	Capelin, fisheries, seals	MR	q, m, δ, $B_{cod,1985}$, I_0, θ
All effects, annual inshore	Capelin, fisheries, seals	Annual Inshore	q, m, δ, $B_{cod,1985}$, I_0
All effects, annual inshore, ASC	Capelin, fisheries, seals	Annual Inshore	q, m, δ, $B_{cod,1985}$, I_0, θ
No capelin, average, ASC	Fisheries, seals	Average	q, m, δ, $B_{cod,1985}$, I_0, θ
No fishery, average, ASC	Capelin, seals	Average	q, m, δ, $B_{cod,1985}$, I_0, θ
No capelin, MR, ASC	Fisheries, seals	MR	q, m, δ, $B_{cod,1985}$, I_0, θ
No fishery, MR, ASC	Capelin, seals	MR	q, m, δ, $B_{cod,1985}$, I_0, θ
No capelin, annual inshore, ASC	Fisheries, seals	Annual Inshore	q, m, δ, $B_{cod,1985}$, I_0, θ
No fishery, annual inshore, ASC	Capelin, seals	Annual Inshore	q, m, δ, $B_{cod,1985}$, I_0, θ
No Seals	Capelin, fisheries	NA	q, m, δ, $B_{cod,1985}$, I_0
Only seals, average, ASC	Seals	Average	q, m, δ, $B_{cod,1985}$, θ
Only seals, MR, ASC	Seals	MR	q, m, δ, $B_{cod,1985}$, θ
Only seals, annual inshore, ASC	Seals	Annual Inshore	q, m, δ, $B_{cod,1985}$, θ
Only capelin	Capelin	NA	q, m, δ, $B_{cod,1985}$, I_0
Only fisheries	Fisheries	NA	q, m, δ, $B_{cod,1985}$

Note: MR: multinomial regression, ASC: adjusted seal consumption (parameter θ is estimated)

Table 4.2 *(following page)*: Model selection statistics for models fitted considering the restricted likelihood, for the period 1985-2007. Model fits are compared across scenarios and types of natural mortality (Ψ=1: linear mortality, Ψ =2: quadratic mortality).

		$\Delta AICc$		$E_{min,i}$	
Scenario	K	Ψ=1	Ψ=2	Ψ=1	Ψ=2
No Seals	5	28.9	0	2 E+06	1
Only capelin	5	33.2	3.1	2 E+07	5
No fishery, average, ASC	6	50.2	13	8 E+10	674
All effects, average, ASC	6	44.7	13.4	5 E+09	798
All effects, annual inshore, ASC	6	49.9	17.7	7 E+10	7 E+03
No fishery, annual inshore, ASC	6	53.5	19.6	4 E+11	2 E+04
All effects, average	5	62.8	21.9	4 E+13	6 E+04
All effects, MR, ASC	6	53.2	24.7	4 E+11	2 E+05
Only fisheries	4	25.7	25.6	4 E+05	4 E+05
No fishery, MR, ASC	6	59.2	26.8	7 E+12	7 E+05
All effects, MR	5	68.6	36.2	8 E+14	7 E+07
All effects, annual inshore	5	65.5	36.8	2 E+14	1 E+08
No capelin, average, ASC	5	40.3	40.5	6 E+08	6 E+08
Only seals, average, ASC	5	45.3	41	7 E+09	8 E+08
No capelin, annual inshore, ASC	5	45	43.3	6 E+09	2 E+09
Only seals, annual inshore, ASC	5	48.6	45.1	4 E+10	6 E+09
No capelin, MR, ASC	5	49	48.2	4 E+10	3 E+10
Only seals, MR, ASC	5	54.2	49	6 E+11	4 E+10

Table 4.3 *(following page)*: Model selection statistics for models fitted considering the full likelihood, for the period 1985-2007. Model fits are compared across scenarios and types of natural mortality (Ψ=1: linear mortality, Ψ =2: quadratic mortality).

		$\Delta AICc$		$E_{min,i}$	
Scenario	K	Ψ=1	Ψ=2	Ψ=1	Ψ=2
Only fisheries	4	1.4	0	2	1
No Seals	5	4.7	3.1	10.5	4.7
Only capelin	5	22.7	5.5	9.00E+04	15.7
No capelin, average, ASC	5	19.4	13	2.00E+04	667.5
All effects, average, ASC	6	17.4	13.8	6.00E+03	986.2
No fishery, average, ASC	6	37	16	1.00E+08	3.00E+03
All effects, MR, ASC	6	26.2	17.4	5.00E+05	6.00E+03
No fishery, annual inshore, ASC	6	43.2	17.4	2.00E+09	6.00E+03
All effects, annual inshore, ASC	6	24.7	18.1	2.00E+05	8.00E+03
No fishery, MR, ASC	6	45	18.5	6.00E+09	1.00E+04
All effects, average	5	45.6	21.2	8.00E+09	4.00E+04
No capelin, MR, ASC	5	26.3	22.3	5.00E+05	7.00E+04
All effects, annual inshore	5	52.8	25.5	3.00E+11	4.00E+05
Only seals, average, ASC	5	33.3	26.6	2.00E+07	6.00E+05
All effects, MR	5	55.3	26.7	1.00E+12	6.00E+05
No capelin, annual inshore, ASC	5	25.7	28.7	4.00E+05	2.00E+06
Only seals, annual inshore, ASC	5	38.3	31.9	2.00E+08	8.00E+06
Only seals, MR, ASC	5	41.3	34.3	9.00E+08	3.00E+07

Table 4.4 *(following page)*: Model selection statistics for models fitted considering the restricted likelihood, for the period 1992-2007. Model fits are compared across scenarios and types of natural mortality (Ψ=1: linear mortality, Ψ =2: quadratic mortality).

		$\Delta AICc$		$E_{min,i}$	
Scenario	K	Ψ=1	Ψ=2	Ψ=1	Ψ=2
Only capelin	5	0	0.2	1	1.1
Only fisheries	4	3.5	10.1	5.7	158
All effects, average	5	8.3	42.2	6.24E+01	1.00E+09
No Seals	5	8.6	14.6	7.20E+01	1.00E+03
No capelin, average, ASC	5	13.8	21.4	1.00E+03	4.00E+04
Only seals, average, ASC	5	14.2	23	1.00E+03	1.00E+05
No capelin, annual inshore, ASC	5	15.7	26	3.00E+03	4.00E+05
Only seals, annual inshore, ASC	5	15.9	27.4	3.00E+03	9.00E+05
All effects, average, ASC	6	16.4	34.6	4.00E+03	3.00E+07
No fishery, average, ASC	6	19.6	28.3	2.00E+04	1.00E+06
All effects, annual inshore, ASC	6	19.8	39.5	2.00E+04	4.00E+08
Only seals, MR, ASC	5	20.1	29.6	2.00E+04	3.00E+06
No capelin, MR, ASC	5	20.2	30.1	2.00E+04	4.00E+06
No fishery, annual inshore, ASC	6	22	35.7	6.00E+04	6.00E+07
All effects, MR, ASC	6	24	43.8	2.00E+05	3.00E+09
No fishery, MR, ASC	6	26	39.2	4.00E+05	3.00E+08
All effects, annual inshore	5	27.4	44.2	9.00E+05	4.00E+09
All effects, MR	5	33.9	48	2.00E+07	3.00E+10

Table 4.5 *(following page)*: Model selection statistics for models fitted considering the full likelihood, for the period 1992-2007. Model fits are compared across scenarios and types of natural mortality (Ψ=1: linear mortality, Ψ =2: quadratic mortality).

		$\Delta AICc$		$E_{min,i}$	
Scenario	K	Ψ=1	Ψ=2	Ψ=1	Ψ=2
Only fisheries	4	1.5	0	2.1	1
Only capelin	5	7.8	0.5	50	1.3
No Seals	5	9.9	5.2	1.43E+02	1.30E+01
Only seals, average, ASC	5	9.1	5.7	9.60E+01	1.70E+01
No capelin, average, ASC	5	10.9	6.1	2.39E+02	2.10E+01
All effects, average, ASC	6	11.7	7.1	3.47E+02	3.50E+01
No fishery, average, ASC	6	14.4	7.4	1.00E+03	4.10E+01
All effects, annual inshore, ASC	6	15.7	7.6	3.00E+03	4.40E+01
No fishery, annual inshore, ASC	6	17.7	7.7	7.00E+03	4.80E+01
Only seals, annual inshore, ASC	5	15.1	7.8	2.00E+03	4.90E+01
No capelin, annual inshore, ASC	5	13.3	8.1	7.58E+02	5.70E+01
All effects, average	5	43.9	8.4	3.00E+09	6.50E+01
Only seals, MR, ASC	5	20.3	10.8	3.00E+04	2.24E+02
No capelin, MR, ASC	5	20.4	11.3	3.00E+04	2.83E+02
No fishery, MR, ASC	6	21	11.7	4.00E+04	3.41E+02
All effects, MR, ASC	6	22.3	11.8	7.00E+04	3.56E+02
All effects, annual inshore	5	45.4	26.6	7.00E+09	6.00E+05
All effects, MR	5	51.3	31.3	1.00E+11	6.00E+06

4.9 Figures

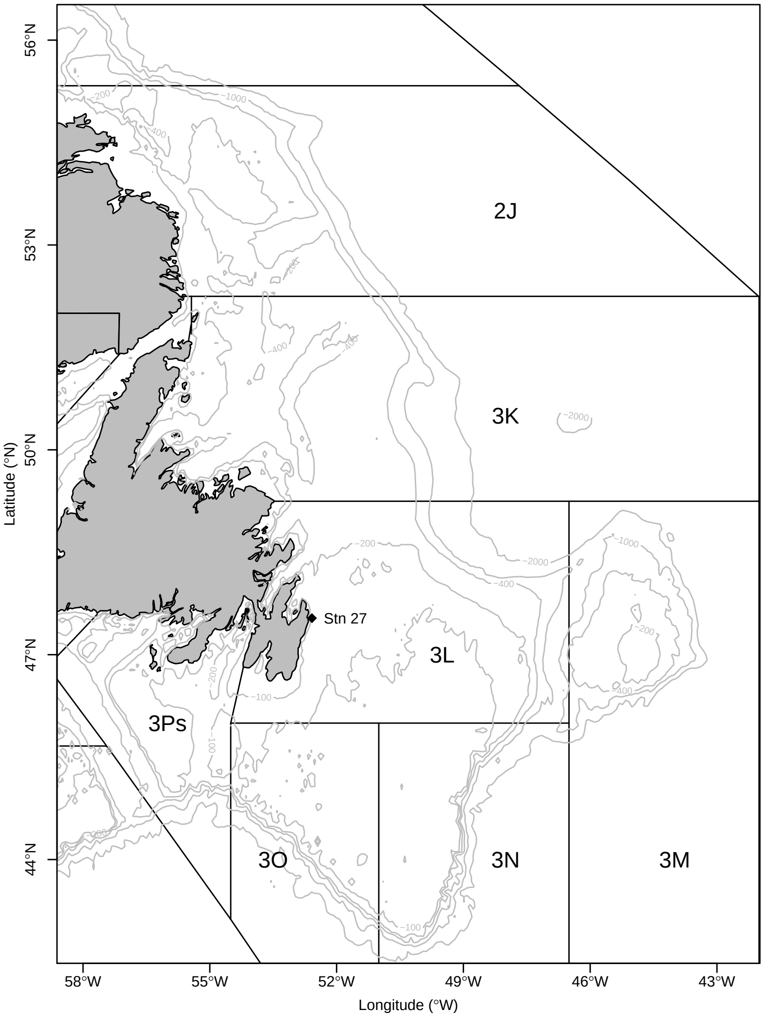
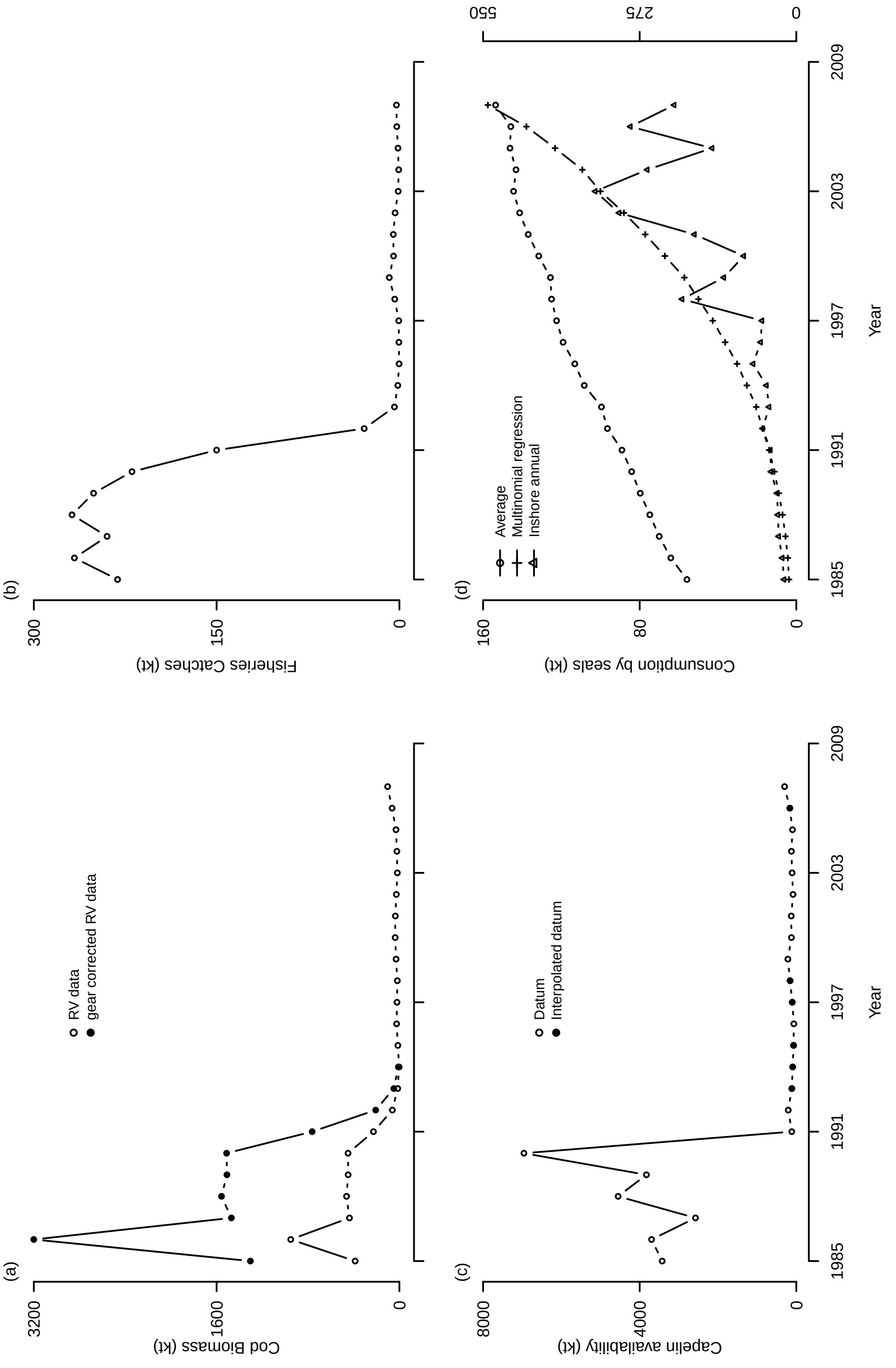


Figure 4.1: Study area. The northern cod inhabits NAFO Divisions 2J3KL. The position of Station 27 is indicated.

Figure 4.2 *(following page)*: Input data for the model (a) Atlantic cod biomass index in NAFO Divs 2J3KL, derived from RV surveys and corrected due to change in gear using the biomass conversion factor developed in this study (see Figure 4.3) (b) fisheries catches of Atlantic cod in NAFO Divs 2J3KL, (c) Acoustic estimate of capelin availability index from the DFO annual spring survey in Div 3L and (d) Atlantic cod consumption by harp seals, estimated using average (left axis), multinomial regression and inshore annual diets (both on right axis).


(a)
Cod Biomass (kt)
3200
1600
0
RV data
gear corrected RV data
(b)
Fisheries Catches (kt)
300
150
0
(c)
Capelin availability (kt)
8000
4000
0
Datum
Interpolated datum
(d)
Consumption by seals (kt)
160
80
0
550
275
0
Average
Multinomial regression
Inshore annual
1985
1991
1997
2003
2009
Year

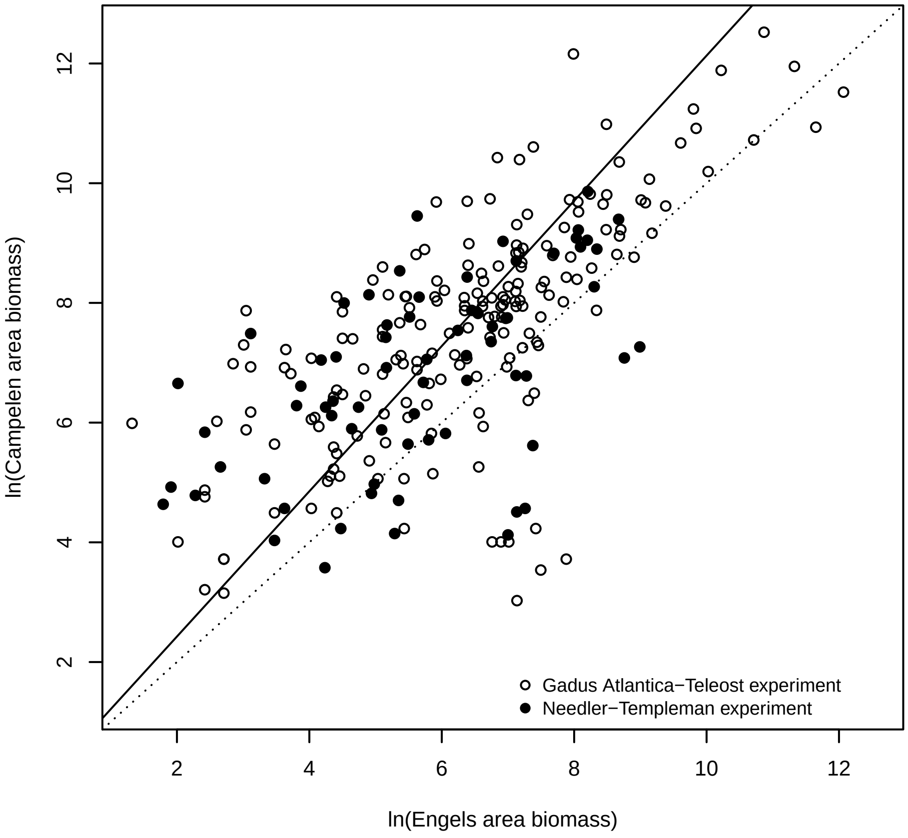


Figure 4.3: Paired tows from comparative fishing trials to assess differences in catchability of cod between Engels and Campelen gears and fishing procedures. Dotted line represents a 1:1 relationship, solid line has a slope of ln(3.3642)

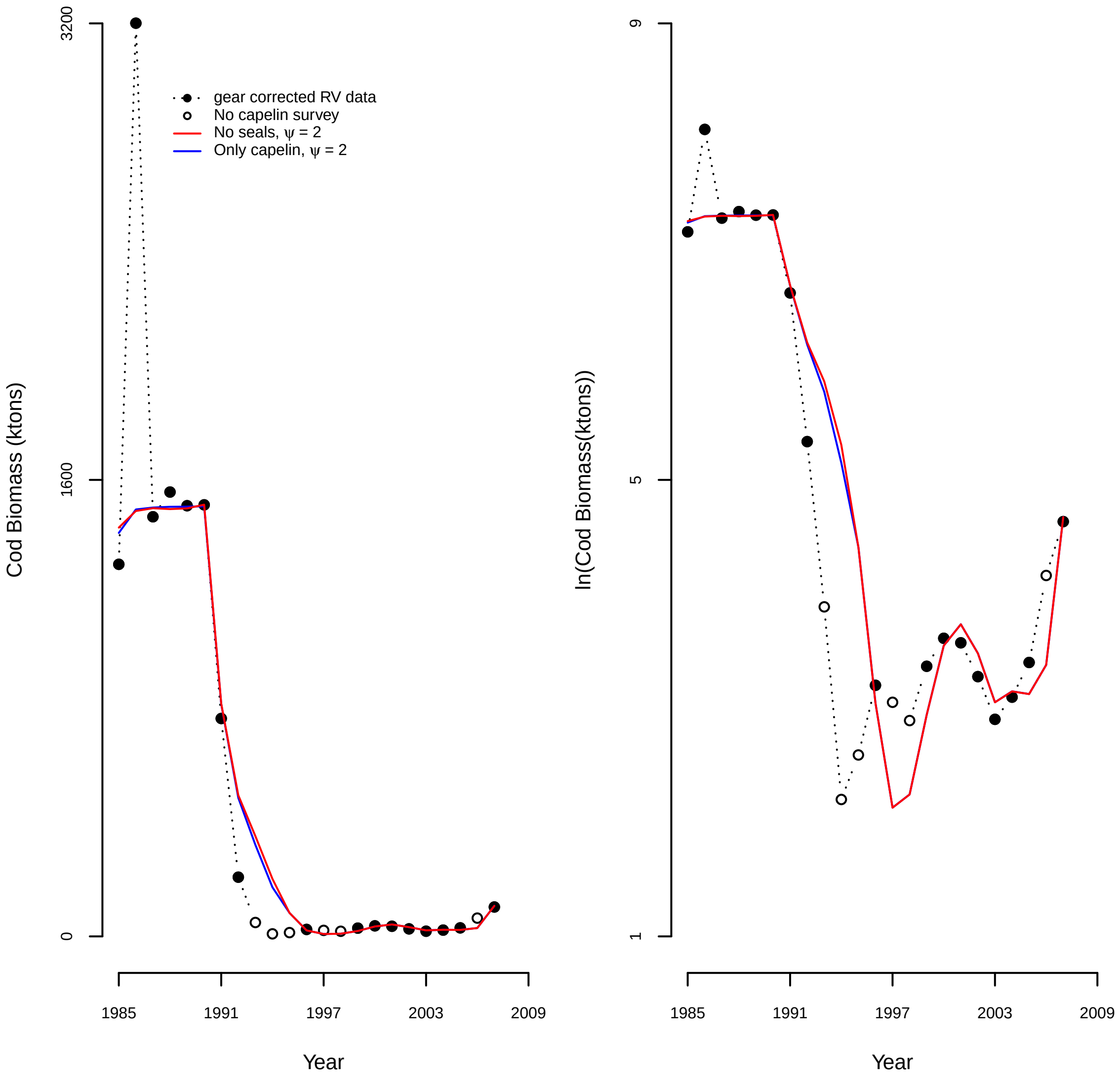


Figure 4.4: Fit of the best 2 models of the restricted likelihood set. Filled circles denote years when a capelin survey was carried out and open circles years when a survey was not carried out. Models are listed in descending order of empirical support (see Table 4.2). Left panel: cod stock biomass in arithmetic scale, right panel: cod stock biomass in logarithmic scale.

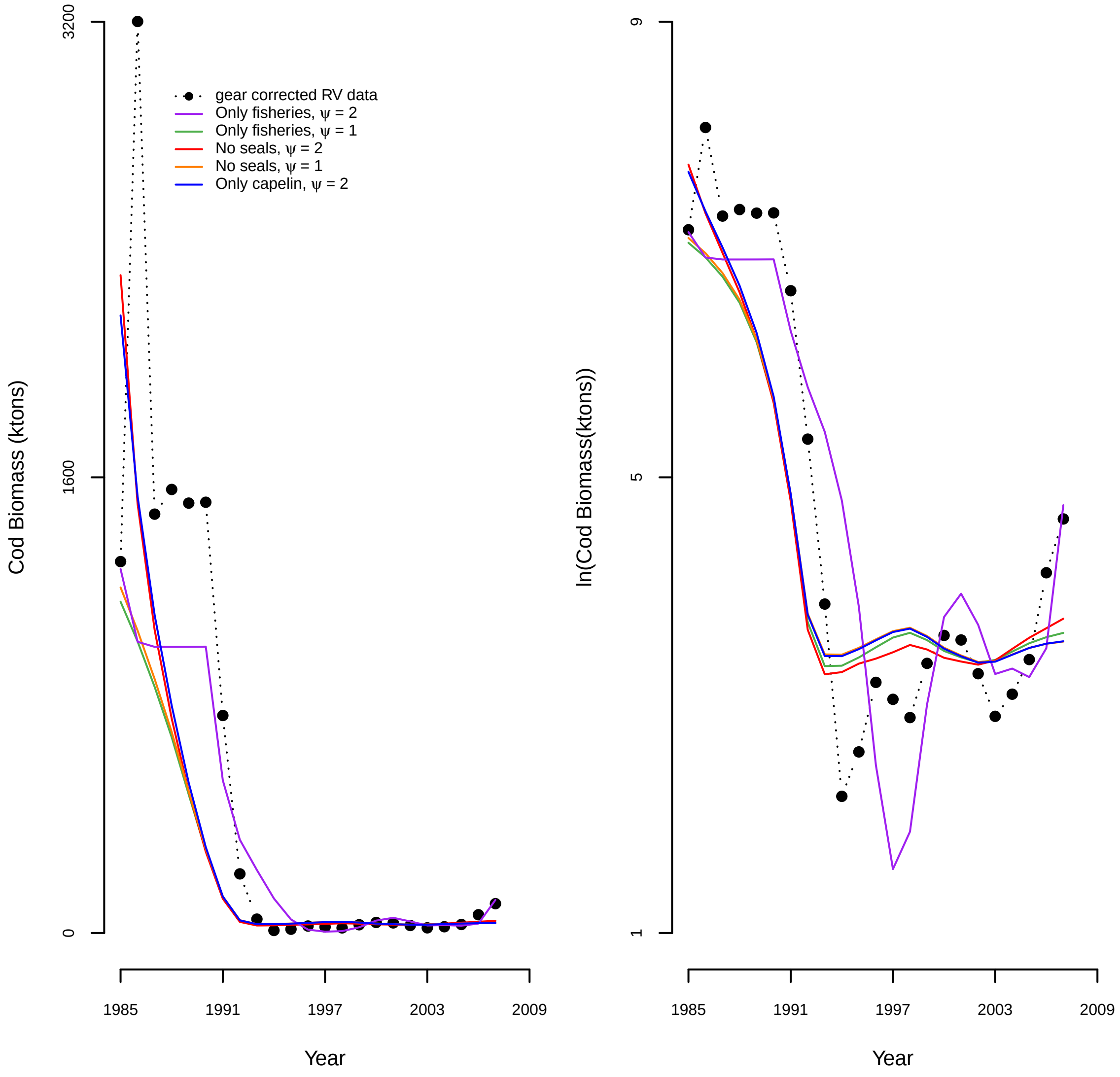


Figure 4.5: Fit of the best 5 models of the full likelihood set. Models are listed in descending order of empirical support (see Table 5). Left panel: cod stock biomass in arithmetic scale, right panel: cod stock biomass in logarithmic scale.

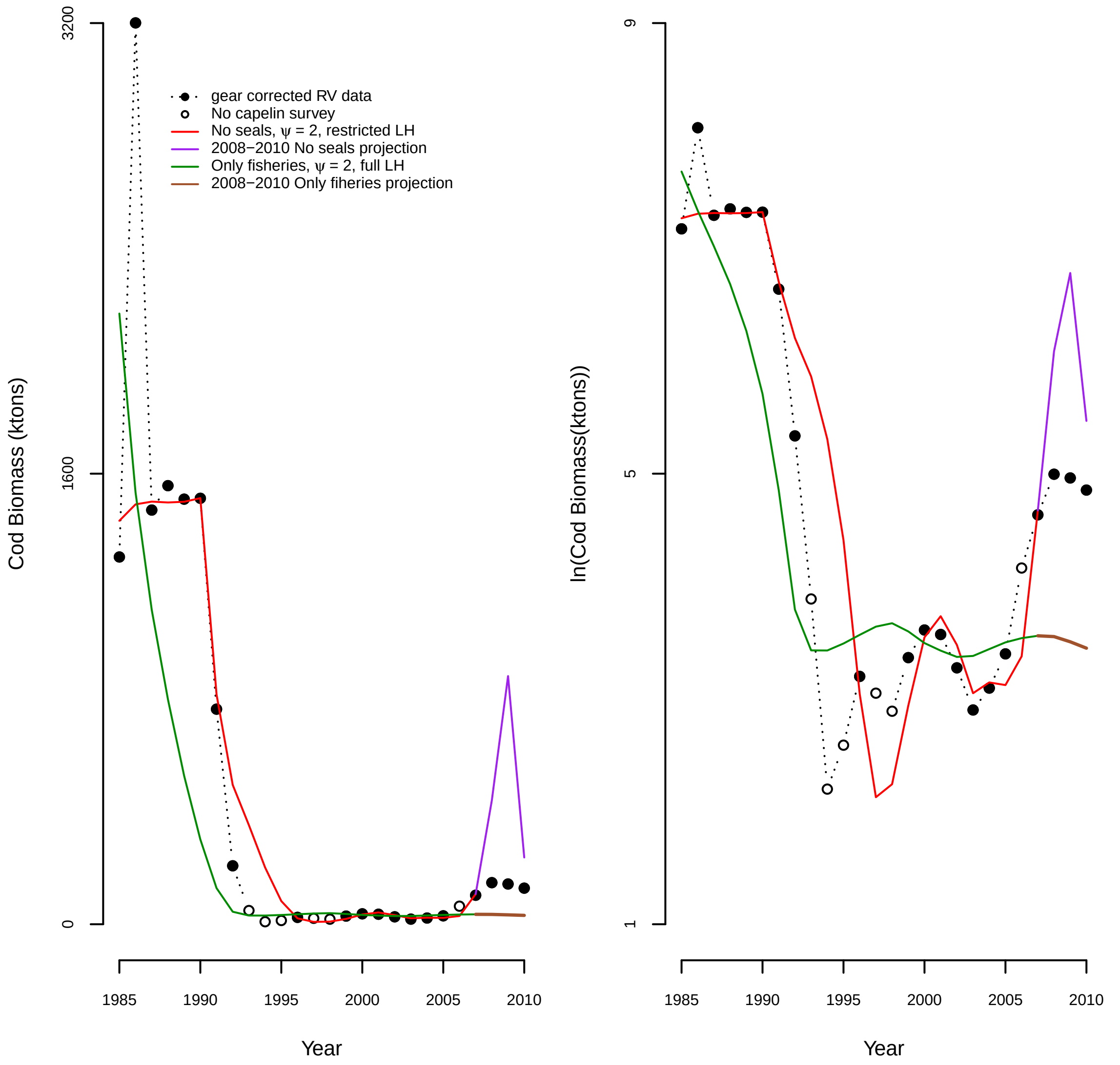


Figure 4.6: Projection for 2008-2010 of the best model of the restricted (No seals (Ψ=2), red and purple lines) and full (Only fisheries (Ψ=2), green and brown lines) likelihood sets. Filled circles denote years when a capelin survey was carried out and open circles years when a survey was not carried out Left panel: cod stock biomass in arithmetic scale, right panel: cod stock biomass in logarithmic scale.

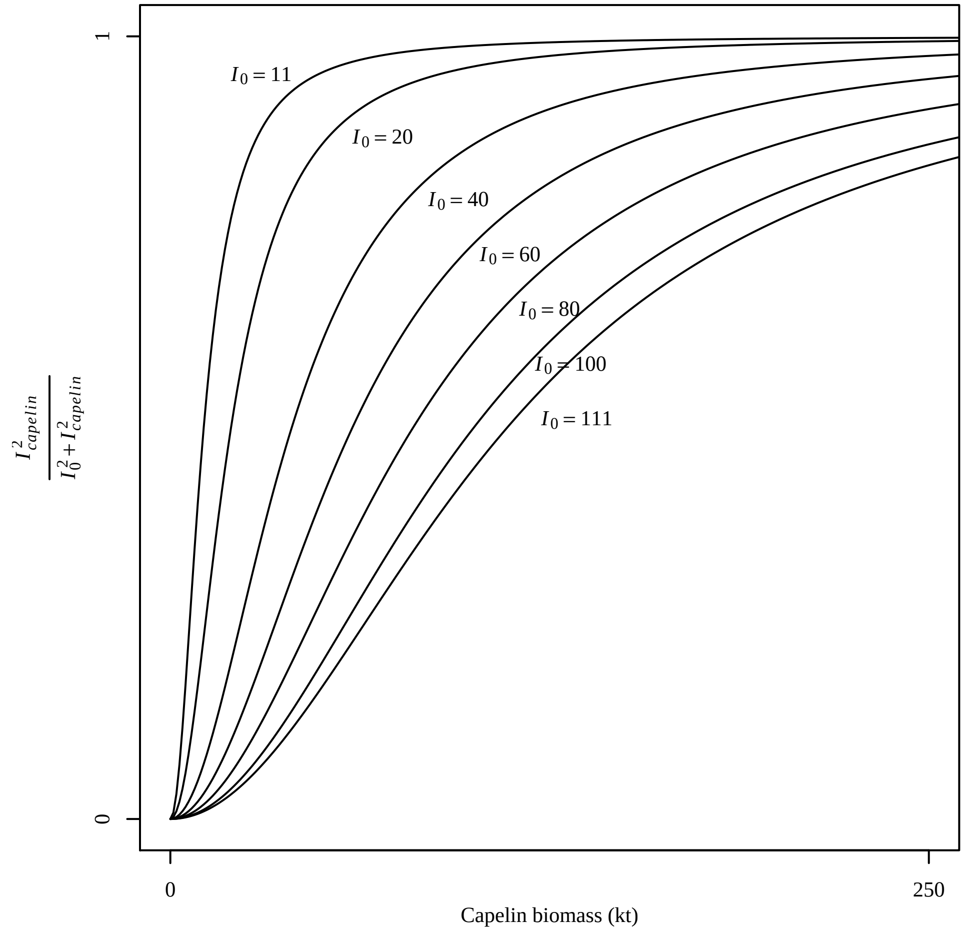


Figure 4.7: Ingestion rate of Atlantic cod as a function of resource density and half-saturation density (I_0).

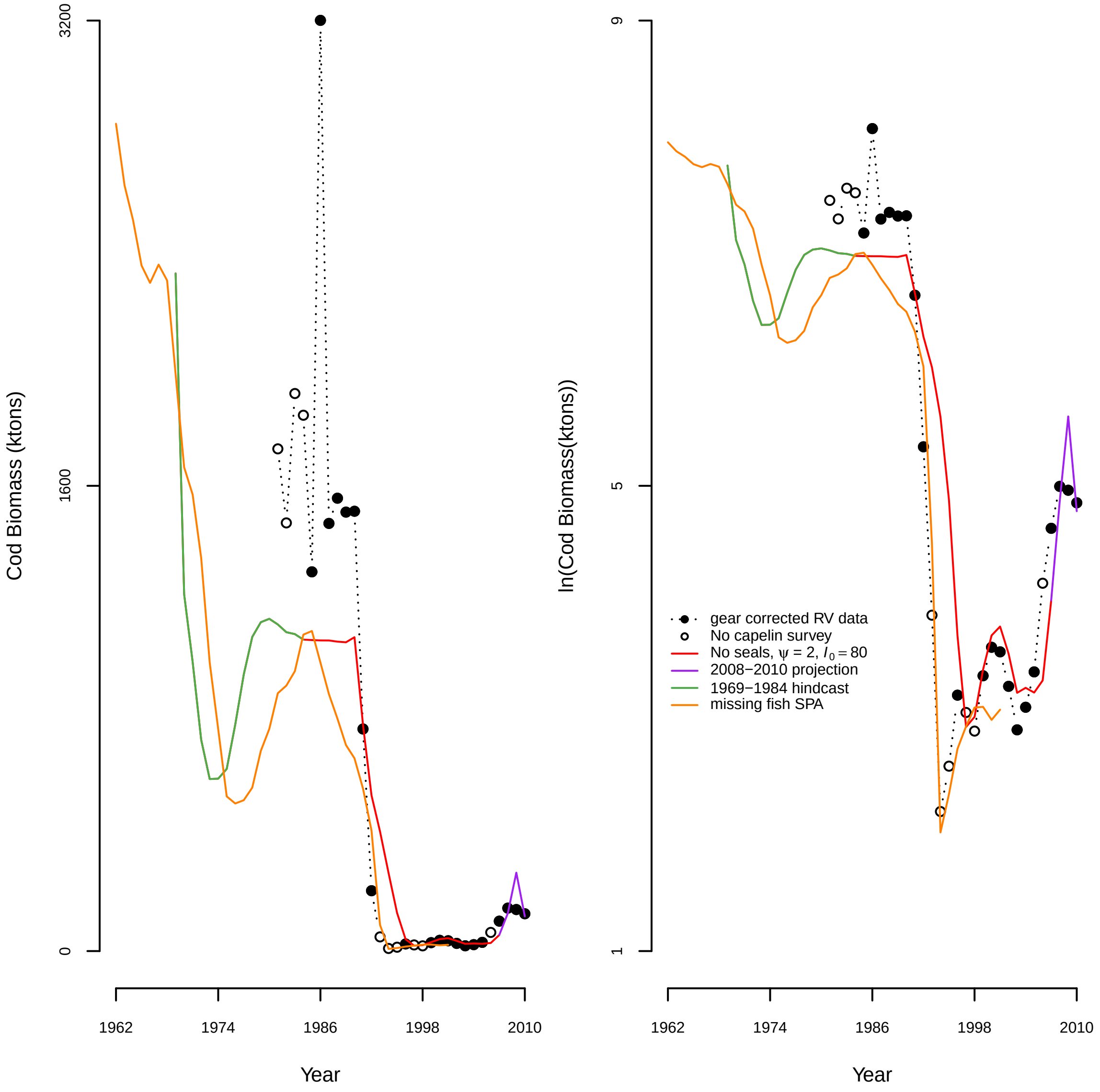


Figure 4.8: Projection for 2008-2010 (purple line) and hindcast 1969-1984 (green line) for the most parsimonious model No seals(Ψ=2, q=1, I_0=80) (red line), and output of the missing fish sequential population analysis for the years 1962-2001 (orange line). Filled circles denote years when a capelin survey was carried out and open circles years when a survey was not carried out. Left panel: cod stock biomass in arithmetic scale, right panel: cod stock biomass in logarithmic scale.

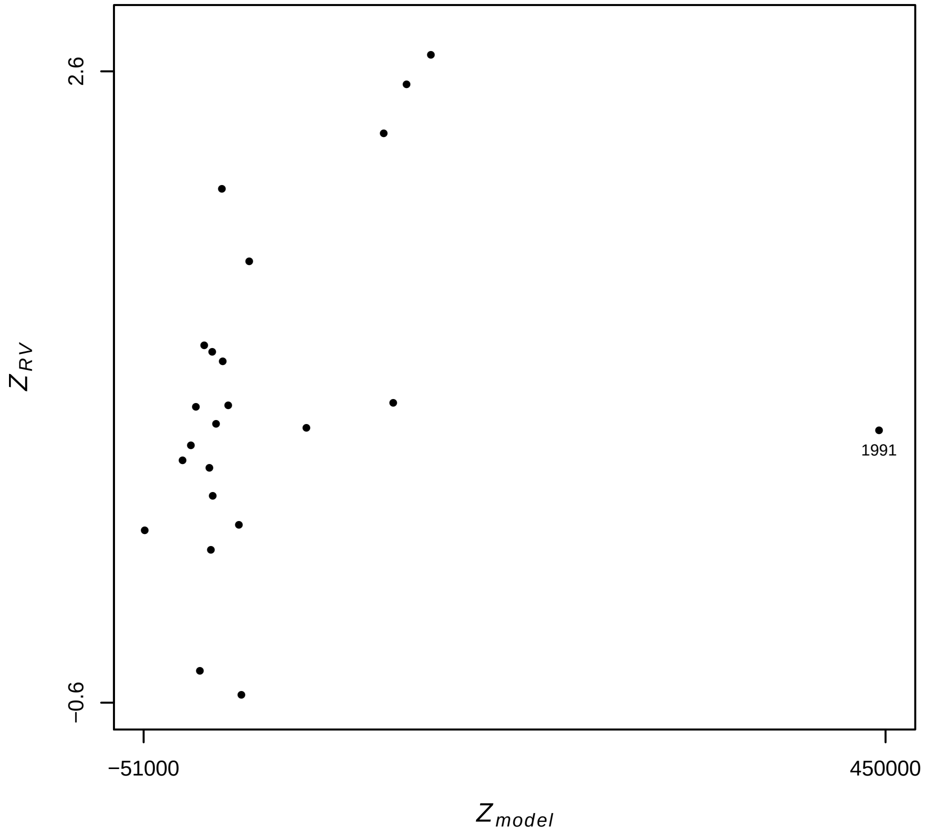
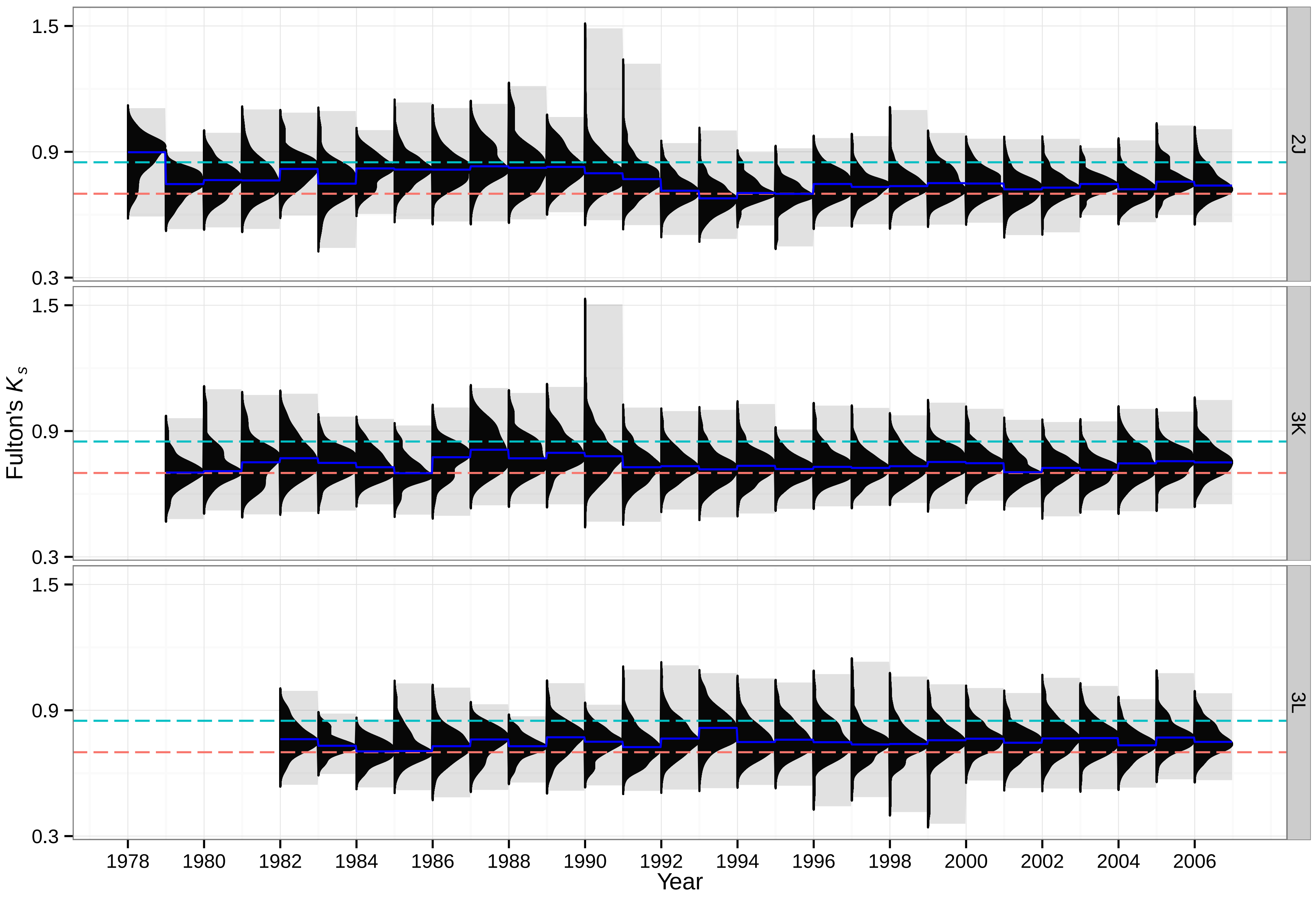


Figure 4.9: Scatterplot of net losses from the most parsimonious model No seals(Ψ=2, q=1, I_0=80) (Z_{model}) and total mortality rate of cod aged 4-6 calculated using data from the autumn RV surveys (Z_{RV}) (DFO 2011).

Figure 4.10 *(following page)*: Frequency distributions of somatic condition of Atlantic cod (Fulton's K) during spring, by year and NAFO Division. The top panel represents NAFO Division 2J, middle panel NAFO Division 3K and bottom panel NAFO Division 3L. Horizontal green and red dashed lines indicate values of K_s for excellent (0.85) and starved (0.7) condition, horizontal blue solid lines represent median observed condition values and shaded envelopes represent the 95 % central range of the frequency distributions.



2J
3K
3L
1.5
0.9
0.3
Fulton's K_s
1978
1980
1982
1984
1986
1988
1990
1992
1994
1996
1998
2000
2002
2004
2006
Year

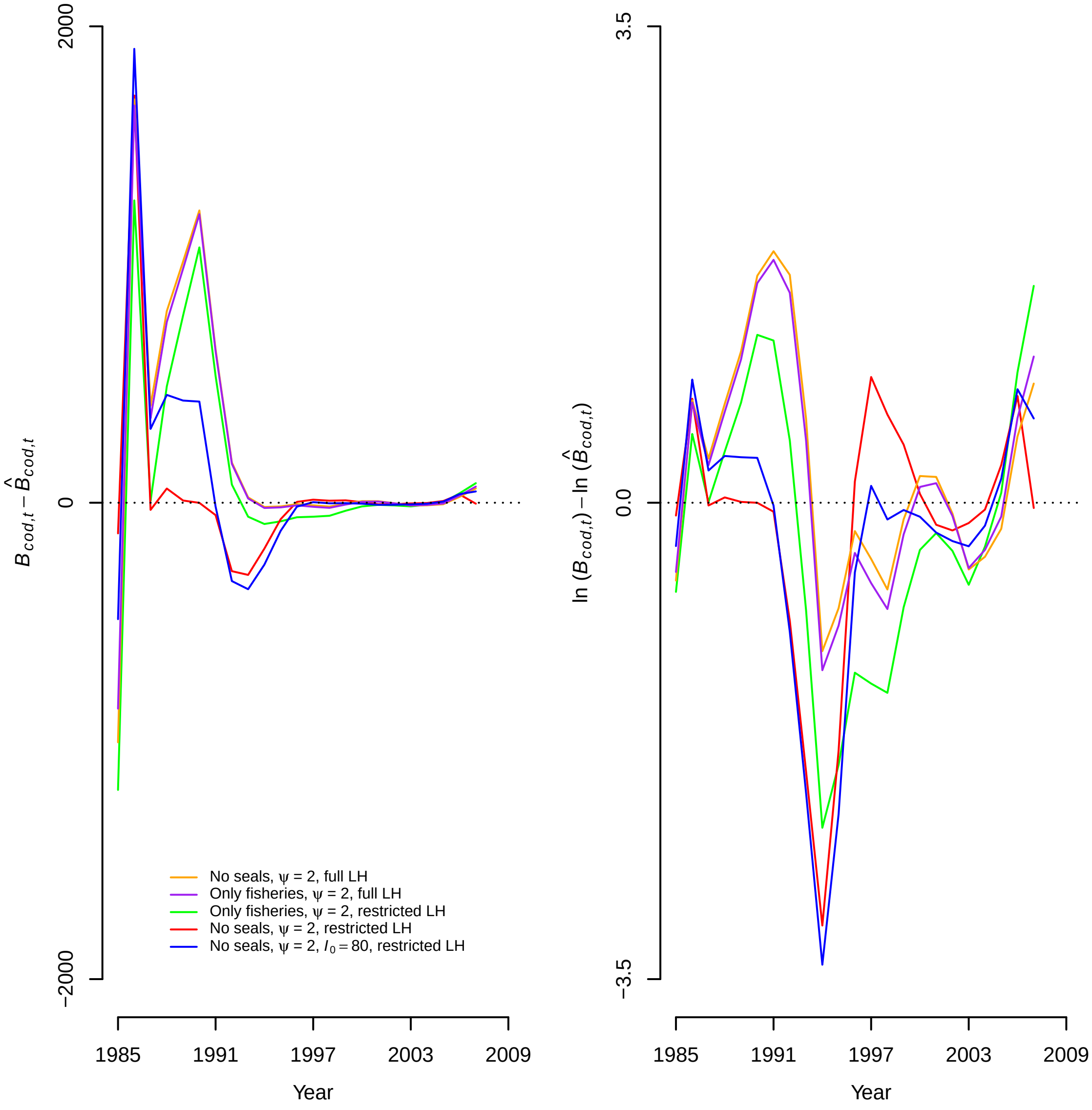
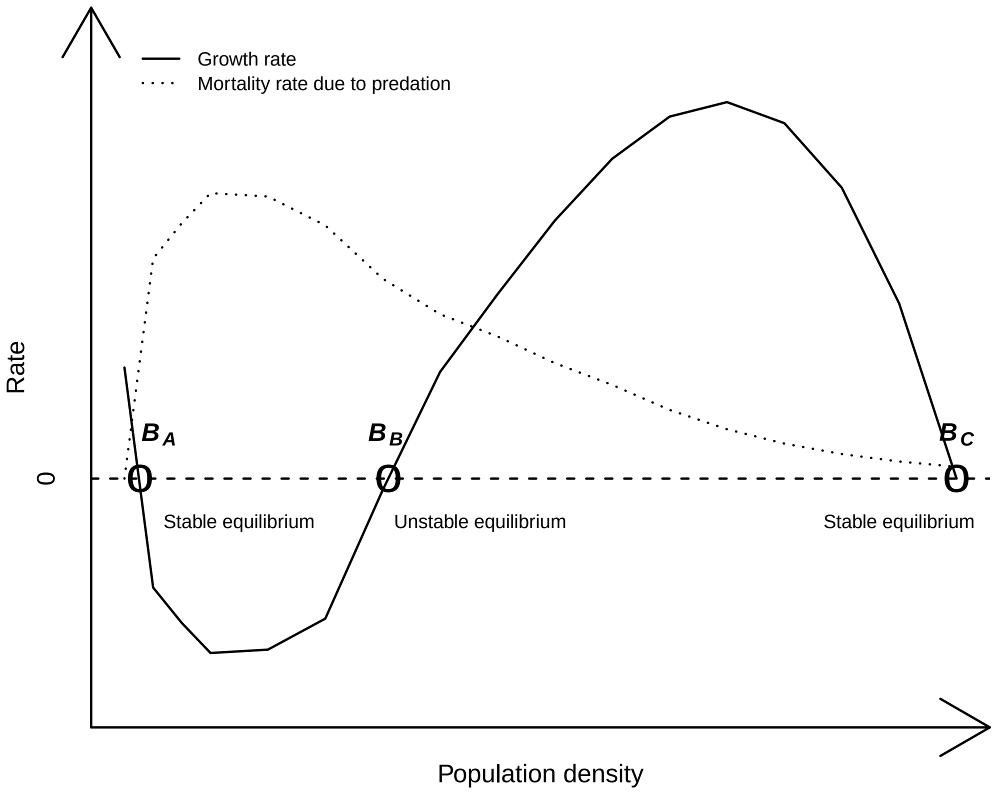
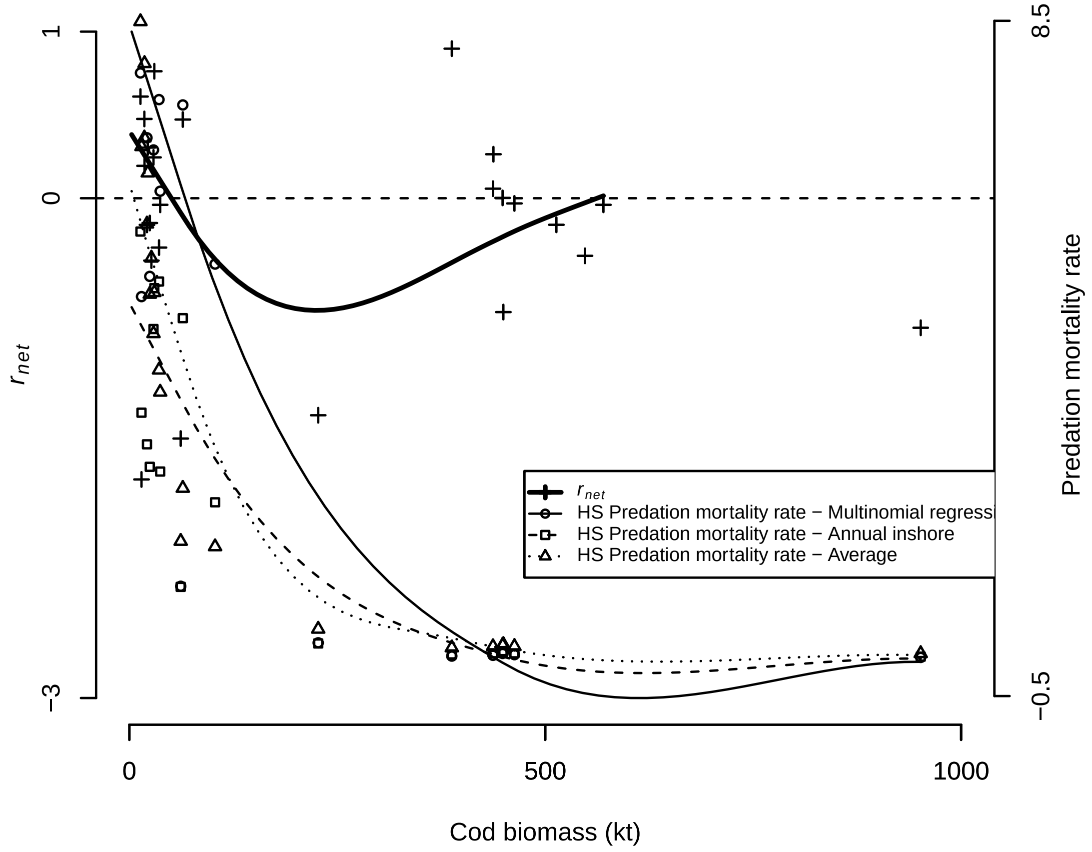


Figure 4.11: Residual from the Only fisheries, No seals and the most parsimonious model No seals(Ψ=2, q=1, I_0=80). Residuals were calculated based in the arithmetic (a), and logarithmic (b) scales.

Figure 4.12: Mean annual bottom (depth ≤ -150 m) temperature at Station 27 and the residuals from the best model (restricted likelihood set): No seals(Ψ=2)and the most parsimonious model No seals(Ψ=2, q=1, I_0=80).

Figure 4.13 *(following page)*: Growth rate and predation mortality as a function of population density. a) Per-capita growth rate (solid line) of a population that exhibits depensation and shape of the mortality rate due to predation needed to cause a predator pit (dotted line). B_A, B_B and B_C are equilibrium biomasses. The part of the curve between the minimum growth rate and B_B is considered depensatory. If depensatory dynamics are caused by predation mortality, biomasses lower than B_B represent the predator pit. b) Net rate of increase (r_{net}, crosses fitted loess curve: bold line) and cod mortality rates due to harp seal predation calculated using the multinomial regression (circles fitted loess curve: solid line), yearly inshore (squares fitted loess curve: dashed line), and classic diets (triangles fitted loess curve: dotted line).


Growth rate
Mortality rate due to predation
Rate
0
B_A
B_B
B_C
Stable equilibrium
Unstable equilibrium
Stable equilibrium
Population density


1
0
−3
r_{net}
8.5
−0.5
Predation mortality rate
r_{net}
HS Predation mortality rate − Multinomial regress
HS Predation mortality rate − Annual inshore
HS Predation mortality rate − Average
0
500
1000
Cod biomass (kt)

Chapter 5

Summary and Synthesis:
Interactions between Harp Seals and Northern Cod

Atlantic cod (*Gadus morhua*) constitutes a defining feature in the history of Atlantic Canada, particularly for Newfoundland and Labrador. It sustained the fishery and way of life of Newfoundlanders during centuries. However, in the early 1990s the cod stock off eastern Newfoundland and Labrador (NAFO Divs 2J3KL), as well as several other stocks off Atlantic Canada, collapsed. Given the social relevance the cod fishery had in Newfoundland, the collapse constituted a socio-economic and cultural crisis. Despite the fishing moratorium imposed in 1992, the stock has not recovered. Several hypotheses have been offered to explain the lack of recovery:

i. fishing, poaching, and by-catch,

ii. environmental effects (e.g.temperature) on stock productivity,

iii. predation by seals,

iv. competition with seals for food sources (e.g. capelin), and

v. food web effects

Interestingly enough, most of these hypotheses involve ecological interactions between seals and cod (direct impact by predation, short pathway indirect effect through competition and long pathways indirect effects through the food web network). However, these contentions have been based on indirect evidence and no formal assessment of these hypotheses has been carried out.

In this thesis I explored the potential role harps seals may have played in the non-recovery of the northern cod stock in waters off Newfoundland and Labrador. I explicitly addressed the predation hypothesis and made an initial examination of the consumptive competition hypothesis.

5.1 Summary and synthesis of research Chapters

5.1.1 Summary

At the cod Zonal Assessment meeting in 2003 (DFO, 2003) it was hypothesized that competitors for juvenile cod food may have reduced its food supply as one of the plausible mechanisms to explain the non-recovery of the northern cod stock.

I addressed this hypothesis in Chapter 2. I compared the diets of the three main predators on the Newfoundland and Labrador Shelf: Atlantic cod, harps seals and Greenland halibut. I examined the diet of Greenland halibut as well as those of harp seals and northern cod for 2 reasons: *i*) it is one of the most abundant predators on the shelf, and as it relies to some extent on capelin (Dwyer et al., 2010), it is a potential important competitor with cod , and *ii*) as a benchmark; if competition between Atlantic cod and harp seals is as intense as to hinder the recovery of the stock, then the degree of dietary overlap with other predators should pale in comparison. However, the most similar diets were those of Atlantic cod and Greenland halibut.

I also found that the three predators showed differing degrees of trophic plasticity and thus ability to rapidly adapt to a changing environment. Greenland halibut showed the most plastic response, followed by harp seals, while Atlantic cod showed no signs of trophic plasticity during the study period considered. The heavy reliance of Atlantic cod on capelin as a main prey item in the post-collapse period implies that cod must have had to invest large amounts of energy to find and consume the same percentage they did prior to the capelin collapse. This energetic encumbrance likely contributed to Atlantic cod's lowered somatic condition during the 1990s described in Chapter 4.

The results from Chapter 2 thus suggest that consumptive competition with harp seals is unlikely to be a relevant factor in the non-recovery of the northern cod stock, and that cod's inability to rapidly adapt to the changing environment during the late 1980s and early 1990s positioned it in disadvantage relative to other predators in the system.

In Chapter 3 I investigated the regulating mechanisms of the focal forage species in the system: capelin. Given the position of capelin at the waist of the food web on the Newfoundland and Labrador Shelf (Lavigne, 1996), and that it has historically been Atlantic cod's main prey (Lilly, 1987, 1991), understanding the mechanisms that regulate capelin is an essential requisite to understand the reasons for the non-recovery of the northern cod stock. I linked the extensive restructuration the system underwent during the early 1990s to physical forcers, thus presenting evidence that a regime shift took place in the system. I proposed that the regime shift was triggered by the synergistic effect of climatic and anthropogenic forcers. Further, I associated the patterns of variation in timing of spawning and stock biomass of capelin with this regime shift and a bottom-up physical forcer, the dynamics of seasonal sea ice. I proposed that the stock biomass is modulated by a match/mismatch mechanism between the timing of the onset of the spring bloom on the shelf (triggered by the retreat of the sea ice from the study area, Wu et al., 2007) and the emergence from diapause of its main prey *Calanus finmarchicus.*

These results suggest that the energy flow in the Newfoundland and Labrador Shelf ecosystem is controlled by bottom-up processes. Given capelin's central role as a keystone species in the ecosystem, it is expected that the bottom-up control would reverberate through the food web to the predatory species.

Seal predation is one of the hypotheses more frequently put forward to explain the lack of recovery of northern cod after the collapse in the early 1990s. However, other hypotheses include reduced prey availability and/or food quality (i.e. lack of capelin), as well as fisheries catches and environmental effects. Chapter 4 evaluates the results from a modelling exercise designed to incorporate all these effects simultaneously.

The results of this modelling exercise indicate that, during the period considered (1985-2007), the main drivers of the northern cod stock were capelin availability and fisheries removals, and that consumption by harp seals has not been a major forcer of the cod dynamics. The interplay between the two drivers could not, however, be fully resolved. In addition, I found good correspondence between the residuals of the most parsimonious model and the mean annual bottom (depth $\leq$ -150 m) temperature at Station 27. Thus, this modelling exercise does not rule out the potential effects of environmental conditions on the dynamics of the northern cod.

I proposed that the low availability of capelin contributed to natural mortality via lowered body condition. When exposed to nutritional stress, iteroparous fish may skip spawning, favouring growth or survival in a given year. Thus, if female cod in poor condition invest their energy in reproduction they do it at the cost of increasing their risk of mortality (Lambert and Dutil, 2000). The most commonly reported cause of skipped spawning in fish is poor nutrition (Rideout et al., 2005). As described in Chapter 2, northern cod maintained capelin as its main prey in the first half of the 1990s, despite the capelin collapse. During the late 1990s and 2000s, cod relied on *Pandalus* shrimp (Dawe et al., 2012; DFO, 2012; Krumsick and Rose, 2012). Despite investing more energy per unit of energy consumed during the first half of the 1990s and consuming a lower quality prey in subsequent years, the frequency of skipped spawning in the offshore component of the stock was very low (Rideout et al., 2006). Given that cod's investment in reproduction did not seem to dwindle, this forcibly meant a lessened investment in body condition. I found evidence of reduced somatic condition during the 1990s and 2000s compared to the 1980s, and a reduced inter-annual variation in condition. This meant that in any given any year during the 1990s and 2000s the probability of finding individuals in poor condition was larger than during the 1980s and that these probabilities remained high year after year, thus losing the potential buffer that a year with good somatic condition represented during the 1980s. Given the loss of this buffer, fish would not have had the choice of skipping spawning during a bad year in order to wait for improved condition to spawn. They were forced to spawn while in poor condition, potentially contributing to a high natural mortality. Spawning while having poor somatic condition would not only affect the individual's survival, but also the quantity and quality of eggs produced (which affects the probability of larvae to survive to maturity).

A hypothesis commonly put forward to explain the non-recovery of cod due to seal predation is that harp seals are keeping the northern cod in a predator pit, i.e. they show depensatory dynamics due to mortality imposed by harp seal predation. I found evidence that the northern cod may have depensatory dynamics. However, the evidence suggests that these dynamics are not caused by mortality imposed by harp seals, thus not supporting the hypothesis that harp seals are keeping cod in a predator pit.

5.1.2 Synthesis

In this thesis I described the bottom up regulation of the sub-Arctic ecosystem of the Newfoundland and Labrador shelf, from physical drivers to primary producers, zooplankton (*C. finmarchicus*), forage fish (capelin) and predatory fish (Atlantic cod), with commercial fisheries playing a role in the regulation of the species in higher trophic levels (Figure 5.1).

The research question that motivated this thesis centred on whether or not the harp seal herd of the Northwest Atlantic is impeding the recovery of the northern cod stock in waters off the Southern Labrador and Newfoundland Shelf (NAFO Divs 2J3KL). I addressed the two simplest mechanisms through which seals could impede or slow the recovery of cod: predation and competition for food resources.

I ruled out the predation hypothesis in Chapter 4, where I found that the biomass dynamics of northern cod are driven by fisheries catches and capelin availability.

Two premises must be met for consumptive competition to take place:

i. the availability of a given prey (capelin) must be a significant driver of the population of a predator (northern cod), and

ii. the status of the prey must be affected by the consumption of a second population of predators (harp seal).

As discussed in Chapter 4, the first premise is clearly met as the dynamics of cod depend on the availability of capelin. However, the capelin stock is modulated by bottom-up processes. I explained over 90% of the variation in capelin biomass in the last 15 years through a combination of seasonal sea ice dynamics and the regime shift that occurred during the early 1990s. This leaves little to no room for harp seals to modulate the biomass of capelin. In addition, in Chapter 2, I showed that the diet of northern cod was more similar to Greenland halibut's diet than to harp seal's diet, thus Greenland halibut is potentially a more important competitor than harp seals. Though this is not a direct test of the consumptive competition hypothesis, it constitutes mounting evidence that competition with harp seals for food resources (capelin) does not appear to be hindering the recovery of the northern cod stock.

Naturally, not finding a direct effect on cod does not mean that harp seals do not affect the fish assemblage; as predators that consume approximately 4.2 million metric tons annually (Stenson, 2012), they necessarily play an important role in the system. It means that the interactions between harp seals and cod are diffused through the food web (*sensu* Yodzis, 2000), i.e. there are likely multiple long pathways through the food web that involve other species connecting them. To address this issue, food web models need to be developed (i.e. coupled multi species models) to assess the extent to which long pathways in the web from harp seals affect cod. However, given that effects travelling through short pathways are felt sooner (Yodzis, 1996), and strong interactions tend to be associated with short loops within the network (Neutel et al., 2002), it is unlikely that this effect would be strong.

5.2 Cod-seals in Atlantic Canada

Although the analyses carried out in this thesis indicate that harp seals are not impeding the recovery of the northern cod off the southern Labrador and northeastern Newfoundland coasts (NAFO Divs 2J3KL), the role of seals in cod recovery varies depending upon the species of seals and dynamics of the cod stock. In Atlantic Canada, the 'cod-seals' issue encompasses 4 different ecosystems and 2 species of seals. The 'problematic' species are grey seals in the systems south and harp seals in the systems north, of the Laurentian Channel.

An analysis of the impacts of harp seals on the cod stock of the northern Gulf of St Lawrence cod stock concluded that the lack of recovery seems mainly associated to very poor recruitment (Chassot et al., 2009). Although under favourable environmental conditions harp seal predation could impact recruitment, under poor environmental conditions the effects of other factors prevail in limiting recruitment (Chassot et al., 2009).

There is debate around the role of grey seal predation in the non-recovery of cod on the Eastern Scotian Shelf (EES). Some modelling exercises indicated that predation by grey seals is contributing to the failure of the stock to recover (Trzcinski et al., 2006; Koen-Alonso and Bundy, 2009). However, Trzcinski et al. (2009) later incorporated new data to their model and concluded that grey seal predation constitutes a small component of the total mortality of cod on the ESS. In addition, it is difficult to reconcile the predation hypothesis on the ESS with recent increases in abundance of cod (Swain and Mohn, 2012). Bundy and Fanning (2005) proposed that cod in the ESS is failing to recover due to predation on juvenile cod by a wide range of predators, along with competition for food with sandlance and pelagic feeders. These authors proposed that the high levels of natural mortality experienced by large cod are a consequence of the poor condition of small cod carried through to adulthood. Along these lines, Frank et al. (2011) proposed that the dynamics of the ESS ecosystem are governed by the oscillatory dynamics of the forage fish complex, and attribute the recent increases in groundfish biomass to larval and juvenile stages of benthic species being released from predation pressure from pelagic species acting in conjunction with increased food availability. Swain and Mohn (2012), however, provided evidence that the recent improvement in the status of the ESS cod is mainly a result of a decline in natural mortality of adults and contend that this is inconsistent with the hypothesis of predation release from forage fish.

One of the main reasons for the lack of recovery of the southern Gulf of St Lawrence (sGSL) cod stock is elevated adult natural mortality (Swain et al., 2009). Taking a weight of evidence approach, Swain et al. (2011) explored alternative hypotheses that may explain the causes of this elevated mortality, and concluded that the most plausible hypothesis is predation by grey seals. This line of enquiry would benefit from modelling approaches that would allow testing multiple hypotheses simultaneously and quantifying their relative empirical support.

5.3 Implications for management and conservation

The results from this thesis have several implications for the management and conservation of the natural marine resources of the Newfoundland and Labrador Shelf.

In first place, results from this thesis reinforce the crucial importance of capelin in the system as a conduit of energy between primary producers and large vertebrates. This implies that developing a large scale fishery for capelin in the region would not be advisable, as it would likely break the flow of energy towards the system's top predators. Another recommendation is to continue, and enhance, the regular (annual) monitoring of capelin abundance, distribution, spawning, and larvae abundance, survival and dispersal.

Second, I have described the regulation of energy flow as bottom-up, from physical drivers to top predators. This means that incorporating the impacts of environmental forcing on ecosystem productivity is a fundamental basis on which to develop Ecosystem-Based Management approaches (Pikitch et al., 2004) for the region. Given the predictions of general warming in the area (IPCC, 2007), it is unknown how the dynamics of seasonal sea ice and thus the system's primary and secondary production will be affected. Therefore, it is important to maintain and enhance monitoring of physical oceanographic variables and the lower trophic levels of the system. This also means that ecosystem considerations in the management of target species such as cod need to consider the regulation of forage species. Assessment reports of groundfish conducted by Fisheries and Oceans currently include sections on oceanographic conditions, important prey and a restricted set of predators, although a synthesis of the system's components is lacking (e.g. DFO, 2011).

Finally, given that the biomass dynamics of the northern cod stock is regulated by fisheries removals, food availability and potentially environmental effects, efforts toward rebuilding the stock should be focused on maintaining very low catches (including bycatch), protecting important spawning grounds as well as protecting key prey species (i.e. capelin). A corollary of the analyses carried out in this thesis is that there is no scientific evidence to suggest that a seal cull would have the desired management effect of rebuilding the northern cod stock.

5.4 Future Directions

As part of this thesis, I have identified several gaps in existing knowledge. In this section I outline how the analyses carried out could be expanded and provide a general view on how I envision this work could be used to guide efforts on multispecies modelling of the Newfoundland and Labrador Shelf marine ecosystem.

The work presented in this thesis can be improved in a number of ways; here I list the ones I believe would substantially enrich the work:

- Include temperature effects on the bioenergetic-allometric model of cod biomass dynamics. Environmental temperature affects the metabolic rates of ectotherms, and as seen in Chapter 4 it likely influences cod's biomass dynamics. This could be achieved following Vasseur and McCann (2005),who have expanded Yodzis and Innes' (1992) bioenergetic allometric framework to include the dependence of vital rates on temperature.
- I have described the main drivers of the northern cod biomass dynamics in Chapter 4. However, as the model I developed is not age structured, it does not allow disentangling the causal relationships between individual-level pro-

cesses and the emergent population dynamics. Age structured models provide insights into mechanistic processes that drive the growth of a population, i.e. individual body growth, mortality, recruitment. Biomass dynamic models of the sort I have used in this thesis capture the realization, but are unable to delve into the details of these demographic processes. However, developing age structured models brings further complications into the picture; most importantly age structured models are "data hungry", i.e. they demand that the input data be resolved for every age of the fish stock being modelled. In the case of the cod model this would mean not only data on age specific biomass and captures of cod, but also age specific consumption by harp seals, and age specific proportions of capelin in cod's diet. Therefore, the cod biomass dynamic model might be more amenable to be developed as a stage-structured biomass model (De Roos et al., 2008), which would account for food- and size-dependent growth.

- Growth and survival are food-dependent functions in the bioenergetic-allometric framework (Yodzis and Innes, 1992). In Chapter 4 I modelled them as a function of capelin availability as this is the main forage fish in the system (Lavigne, 1996), and it has historically been cod's main prey (Lilly, 1987, 1991). Cod, however, shifted its diet to rely more on *Pandalus* shrimp during the late 1990s and 2000s (Dawe et al., 2012; DFO, 2012; Krumsick and Rose, 2012). It would therefore be interesting to include shrimp availability as a further driver to the biomass dynamic model.

- One of the main limitations of the study was that I was not able to assess the second necessary condition for consumptive competition, i.e. that harp seals drive the dynamics of capelin. I attempted to tackle this question by implementing the ice-capelin model in the bioenergetic-allometric framework, as I did for cod in Chapter 4. As such, it was implemented as an ordinary differential equation. I was unable to represent the intra-period (corresponding to the regimes described in Chapter 3) dynamics of capelin without being overshadowed by the abrupt and large jump in capelin's biomass (and it was therefore not presented in the thesis). More effort should be invested toward this end, as this would complement the work presented in this thesis and would provide a more rounded answer to the role of harp seals as competitors of cod and as a potential driving force of the dynamics of capelin.

- It would be very interesting to implement the ice-capelin and capelin-cod models as a system of coupled ordinary differential equations. This would be a synthesis of this thesis, integrating the dynamics from physical drivers through several trophic levels to predatory groundfish. It would potentially allow explaining the dynamics of both, capelin and cod, based on physical drivers of the system, i.e. regime shift in 1991 and seasonal sea ice dynamics.

- it would be desirable to implement the models I used in a framework that would integrate uncertainty from all sources and synthesize it into quantitative measurements of the uncertainty of model results, ideally a Bayesian framework (Gelman et al., 2004).

The work presented in this thesis can be used as a building block for the development of multispecies models for the Newfoundland and Labrador Shelf marine ecosystem. Some of the results from this thesis are of particular importance to guide modelling efforts:

- The regulation of energy flow in the system is driven from the bottom-up. This means that effort should be directed to understanding the processes that define production in the system and to gaining a better understanding of the lower trophic levels, in terms of their composition, trends, and regulating mechanisms.
- Given that seasonal sea ice dynamics determine the timing of the spring bloom, and that temperature is potentially an important driver of cod dynamics, modelling efforts should include environmental forcing.
- Capelin plays a crucial role in regulating the dynamics of the upper trophic levels (e.g. cod, marine mammals, seabirds), and thus must be an important component of any and all models to be developed.

It is important to stress the importance of long-term datasets; it would not have been possible to achieve the insights gained in this thesis if these were not extant.

It is therefore vital to maintain and enhance existing sampling programs of basic physical and biological variables at all trophic levels.

In terms of data needs for the developments of multispecies models, it is not only essential to have datasets on abundance (biomass), distribution, reproduction, and movements of the species of interest, but it is also essential to resolve links within food webs, i.e. estimate flows of energy from species i to species j.

Most trophic studies in the region have been directed toward understanding diet and prey consumption of top predators (e.g. Lilly, 1987; Rose and Leggett, 1990; Lilly, 1991, 1994; Montevecchi and Myers, 1996; Shelton et al., 1997; Stenson et al., 1997; Stenson and Perry, 2001; Rose and O'Driscoll, 2002; Davoren and Montevecchi, 2003; Montevecchi et al., 2006; Stenson and Hammill, 2006; Montevecchi, 2007; Moody and Hobson, 2007; Sherwood et al., 2007; Burke and Montevecchi, 2008; Dwyer et al., 2010; Buren et al., 2012; Dawe et al., 2012; DFO, 2012; Stenson, 2012). Given the importance of long-term datasets, it is necessary to maintain these efforts but it is also essential to expand them to include other predators (e.g. whales, seabirds), as well as species at the middle and the bottom of the food web. Continuing the collection of dietary data of top predators is also important because these can be used as indicators of change in the ecosystem (e.g. Boyd et al., 2006; Dwyer et al., 2010; Buren et al., 2012).

There are various modelling approaches currently in existence, from whole ecosystem models (e.g. Ecopath with Ecosim, Atlantis), to minimum realistic models (e.g.

GADGET, some bioenergetic-allometric models), to extensions of single species assessment models to include predators of the targeted species. Plagányi (2007) provides an excellent overview of the currently available modelling approaches, their assumptions, data requirements, advantages and limitations. Plagányi's (2007) report should be considered a starting point when deciding the scales of detail and resolution needed to address specific questions at the multispecies and ecosystem levels.

5.5 Conclusion

The purpose of this study was to test the general hypothesis that the large Northwest Atlantic harp seal herd is impeding, or slowing, the recovery of the northern cod stock. I addressed the two most commonly hypothesized ways in which harp seals could affect the recovery of cod: predation and consumptive competition for the lipid-rich capelin. My analyses clearly show that harp seal predation has not had a large impact on the biomass dynamics of the northern cod stock during the period 1985-2007. Instead, I show that the combined effects of fisheries removals, food availability (capelin), and potentially environmental effects (temperature) are important drivers of the dynamics of the stock. Therefore, the predation hypothesis is not supported by the data. In terms of the competition hypothesis, I presented evidence in Chapters 2 and 3 that support the view that consumptive competition with harp seals is not a major force impeding the rebuilding of the stock.

A major theme in the thesis is that the regulation of energy flow in the Newfoundland and Labrador Shelf marine ecosystem is regulated from the bottom-up from physical drivers through several trophic levels: primary producers, secondary producers, forage fish, to predatory fish (as illustrated in Figure 5.1). This finding can help aid in the development of both, models to better understand the dynamics of the marine community and policies aimed at achieving sustainable use of natural marine resources in Atlantic Canada.

5.6 References

Boyd, I., Wanless, S. and Camphuysen, C. (2006), *Top predators in marine ecosystems. Their role in monitoring and management*, Cambridge University Press.

Bundy, A. and Fanning, L. (2005). 'Can Atlantic cod (*Gadus morhua*) recover? Exploring trophic explanations for the non-recovery of the cod stock on the eastern Scotian Shelf, Canada', *Can J Fish Aquat Sci* 62, 1474–1489–.

Buren, A., Koen-Alonso, M. and Montevecchi, W. (2012). 'Linking predator diet and prey availability: common murres and capelin in the Northwest Atlantic', *Mar Ecol Prog Ser* 445, 25–35.

Burke, C. and Montevecchi, W. A. (2008). 'Fish and chicks: Forage fish and chick success in two co-existing auks', *Waterbirds* 31, 372–384.

Chassot, E., Duplisea, D., Hammill, M., Caskenette, A., Bousquet, N., Lambert, Y. and Stenson, G. (2009). 'Role of predation by harp seals *Pagophilus groenlandicus* in the collapse and non-recovery of northern Gulf of St. Lawrence cod *Gadus morhua*', *Mar Ecol Prog Ser* 379, 279–297.

Davoren, G. K. and Montevecchi, W. A. (2003). 'Signals from seabirds indicate changing biology of capelin stocks', *Mar Ecol Prog Ser* 258, 253–261.

Dawe, E., Koen-Alonso, M., Chabot, D., Stansbury, D. and Mullowney, D. (2012). 'Trophic interactions between key predatory fishes and crustaceans: comparison of two Northwest Atlantic systems during a period of ecosystem change', *Mar Ecol Prog Ser* 469, 233–248.

De Roos, A. M., Schellekens, T., Van Kooten, T., Van De Wolfshaar, K., Claessen, D. and Persson, L. (2008). 'Simplifying a physiologically structured population model to a stage-structured biomass model', *Theor Popul Biol* 73, 47–62.

DFO. (2003). 'Proceedings of the Zonal Assessment Meeting - Atlantic Cod', *Can Sci Advis Secretar Proc Ser* 2003/021.

DFO. (2011). 'Stock assessment of Northern (2J3KL) cod in 2011', *Can Sci Advis Secretar Adv Rep* 2011/041.

DFO. (2012). 'Results and recommendations from the Ecosystem Research Initiative - Newfoundland and Labrador's Expanded Research on Ecosystem Relevant but UnderSurveyed Splicers', *Can Sci Advis Secretar Adv Rep* 2012/058.

Dwyer, K. S., Buren, A. D. and Koen-Alonso, M. (2010). 'Diet of Greenland halibut in the Newfoundland Shelf, Northwest Atlantic, from 1978-2003: reflections of a changing ecosystem', *J Sea Res* 64, 436–445.

Frank, K. T., Petrie, B., Fisher, J. A. and Leggett, W. C. (2011). 'Transient dynamics of an altered large marine ecosystem', *Nature* 477(7362), 86–89.

Gelman, A., Carlin, J. B., Stern, H. S. and Rubin, D. B. (2004), *Bayesian data analysis*, Vol. Second edition, Chapman & Hall/CRC.

IPCC. (2007), Summary for Policymakers, *in* **S. Solomon, D. Qin, M. Manning, Z. Chen, M. Marquis, K. Averyt, M. Tignor and H. Miller**., eds, 'Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change', Cambridge, United Kingdom and New York, NY, USA, pp. –.

Koen-Alonso, M. and Bundy, A. (2009). 'Trophodynamic modeling of core species of the eastern scotian shelf marine community', *Can Sci Advis Secretar Proc Ser 2009/20* .

Krumsick, K. J. and Rose, G. A. (2012). 'Atlantic cod (*Gadus morhua*) feed during spawning off Newfoundland and Labrador', *ICES J Mar Sci* 69, 1701–1709.

Lambert, Y. and Dutil, J.-D. (2000). 'Energetic consequences of reproduction in Atlantic cod (*Gadus morhua*) in relation to spawning level of somatic energy reserves', *Can J Fish Aquat Sci* 57, 815–825.

Lavigne, D. (1996), Ecological interactions between marine mammals, commercial fisheries and their prey: unravelling the tangled web, *in* **W. A. Montevecchi**., ed., 'Studies of high-latitude seabirds. 4. Trophic relationships and energetics of endotherms in cold ocean systems', Can Wildl Serv Ocass Pap 91, pp. 59–71.

Lilly, G. (1987). ‘Interactions between Atlantic cod (*Gadus morhua*) and capelin (*Mallotus villosus*) off Labrador and eastern Newfoundland: a review’, *Can Tech Rep Fish Aquat Sci* 1567, 1–37.

Lilly, G. R. (1991). ‘Interannual variability in predation by cod (*Gadus morhua*) on capelin (*Mallotus villosus*) and other prey off southern Labrador and northeastern Newfoundland’, *ICES Mar Sci Symp* 193, 133–146.

Lilly, G. R. (1994). ‘Predation by Atlantic cod on capelin on the southern Labrador and Northeast Newfoundland shelves during a period of changing spatial distributions’, *ICES mar Sci Symp* 198, 600–611.

Montevecchi, W. A. (2007). ‘Binary dietary responses of northern gannets *Sula bassana* indicate changing food web and oceanographic conditions’, *Mar Ecol Prog Ser* 352, 213–220.

Montevecchi, W. A., Garthe, S. and Davoren, G. K. (2006), Biophysical influences on seabird trophic assessments, *in* **I. Boyd, S. Wanless and C. Camphuysen.**, eds, ‘Top predators in marine ecosystems. Their role in monitoring and management’, Cambridge University Press, pp. 118–130.

Montevecchi, W. A. and Myers, R. A. (1996). ‘Dietary changes of seabirds reflect shifts in pelagic food webs’, *Sarsia* 80, 313–322.

Moody, A. and Hobson, K. A. (2007). ‘Alcid winter diet in the Northwest Atlantic determined by stable isotope analysis’, *Mar Ornithol* pp. 39–46.

Neutel, A.-M., Heesterbeek, J. A. and de Ruiter, P. C. (2002). 'Stability in real food webs: weak links in long loops', *Science* 296, 1120–1123.

Pikitch, E., Santora, C., Babcock, E., Bakun, A., Bonfil, R., Conover, D., Dayton, P., Doukakis, P., Fluharty, D., Heneman, B., Houde, E., Link, J., Livingston, P., Mangel, M., McAllister, M., Pope, J. and Sainsbury, K. (2004). 'Ecosystem-Based Fishery Management', *Science* 305(5682), 346–347.

Plagányi, E. (2007). 'Models for an ecosystem approach to fisheries', *FAO Fish Tech Pap* 447.

Rideout, R., Morgan, M. and Lilly, G. (2006). 'Variation in the frequency of skipped spawning in Atlantic cod (*Gadus morhua*) off Newfoundland and Labrador', *ICES J Mar Sci* 63, 1101–1110.

Rideout, R. M., Rose, G. A. and Burton, M. P. (2005). 'Skipped spawning in female iteroparous fishes', *Fish Fish* (1), 50–72.

Rose, G. A. and Leggett, W. (1990). 'The importance of scale to predator-prey spatial correlations: an example of Atlantic fishes', *Ecology* 71, 33–43.

Rose, G. A. and O'Driscoll, R. L. (2002). 'Capelin are good for cod: can the northern stock rebuild without them?', *ICES J Mar Sci* 59, 1018–1026.

Shelton, P. A., Warren, W. G. and Stenson, G. B. (1997). 'Quantifying Some of the Major Sources of Uncertainty Associated with Estimates of Harp Seal Prey

Consumption. Part II: Uncertainty in Consumption Estimates Associated with Population Size, Residency, Energy Requirement and Diet', *J Northw Atl Fish Sci* 22, 303–315.

Sherwood, G. D., Rideout, R. M., Fudge, S. B. and Rose, G. A. (2007). 'Influence of diet on growth, condition and reproductive capacity in Newfoundland and Labrador cod (*Gadus morhua*): Insights from stable carbon isotopes (δ^{13}C)', *Deep Sea Res Pt II* 54(23-26), 2794–2809.

Stenson, G. B. (2012). 'Estimating consumption of prey by harp seals (*Pagophilus groenlandicus*) in NAFO Divisions 2J3KL', *Can Sci Advis Secretar Res Doc* 2012/156.

Stenson, G. B. and Hammill, M. (2006). 'Quantifying uncertainty in estimates of Atlantic cod (*Gadus morhua*) consumption by harp seals (*Phoca groenlandica*)', *Can Sci Advis Secretar Res Doc* 2004/089.

Stenson, G. B., Hammill, M. and Lawson, J. W. (1997). 'Predation by harp seals in Atlantic Canada: preliminary consumption estimates for Arctic cod, capelin and Atlantic cod', *J Northw Atl Fish Sci* 22, 137–154.

Stenson, G. B. and Perry, E. (2001). 'Incorporating uncertainty into estimates of Atlantic cod (*Gadus morhua*), capelin (*Mallotus villosus*) and Arctic cod (*Boreogadus saida*) consumption by harp seals (*Pagophilus groenlandicus*) in NAFO Divisions 2J3KL', *Can Sci Advis Secretar Res Doc* 2001/074.

Swain, D., Benoît, H. P., Hammill, M., McClelland, G. and Aubry, . (2011). 'Alternative hypotheses for causes of the elevated mortality of cod (*Gadus morhua*) in the southern Gulf of St Lawrence; the weight of evidence', *DFO Can Sci Advis Sec Sci Res Doc* 2011/036, –.

Swain, D.-P. and Mohn, R.-K. (2012). 'Forage fish and the factors governing recovery of Atlantic cod (*Gadus morhua*) on the eastern Scotian Shelf', *Can J Fish Aquat Sci* 69, 997–1001.

Swain, D., Savoie, L., Hurlbut, T., Surette, T. and Daigle, D. (2009). 'Assessment of the southern Gulf of St. Lawrence cod stock, February 2009', *DFO Can Sci Advis Sec Sci Res Doc* 2009/037, –.

Trzcinski, M., Mohn, R. and Bowen, W. (2006). 'Continued decline of an atlantic cod population: how important is gray seal predation?', *Ecol Appl* 16, 2276–2292.

Trzcinski, M., Mohn, R. and Bowen, W. (2009). 'Estimating the impact of grey seals on the Eastern Scotian Shelf and Western Scotian Shelf cod populations', *DFO Can Sci Advis Sec Sci Res Doc* 2009/052, 1–19.

Vasseur, D. A. and McCann, K. S. (2005). 'A mechanistic approach for modeling temperature-dependent consumer-resource dynamics', *Am Nat* 166, 184–198.

Wu, Y., Peterson, I. K., Tang, C. C., Platt, T., Sathyendranath, S. and Fuentes-Yaco, C. (2007). 'The impact of sea ice on the initiation of the spring bloom on the Newfoundland and Labrador Shelves', *J Plankton Res* 29, 509–514.

Yodzis, P. (1996), Food webs and perturbation experiments: theory and practice, *in* **G. A. Polis and K. O. Winemiller**., eds, 'Food webs: integration of patterns and dynamics', Chapman and Hall, New York, pp. 192–200.

Yodzis, P. (2000). 'Diffuse effects in food webs', *Ecology* 81, 261–266.

Yodzis, P. and Innes, S. (1992). 'Body size and consumer-resource dynamics', *Am Nat* 139, 1151–1175.

5.7 Figures

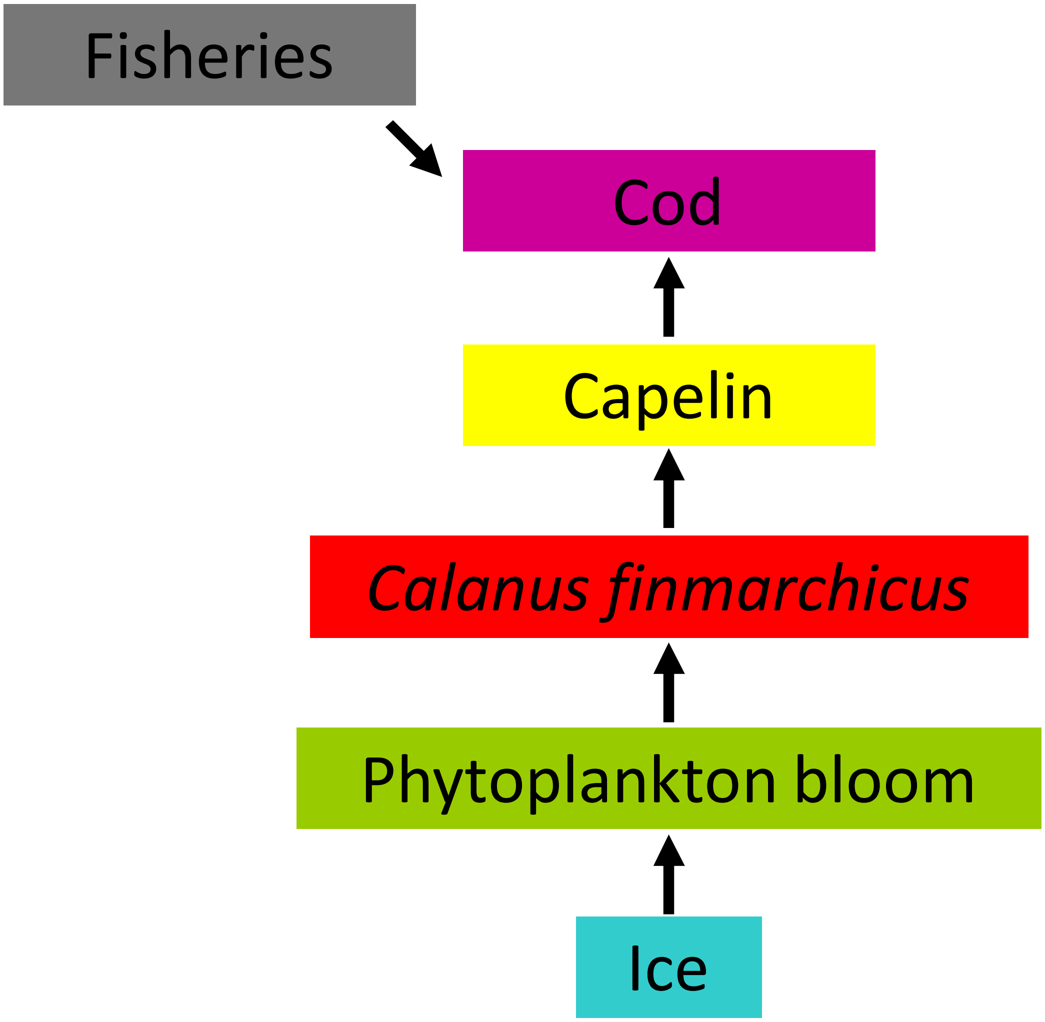


Figure 5.1: Schema of the regulation of some important components of the Newfoundland and Labrador Shelf marine ecosystem.