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IMPACTS OF GREY SEALS ON FISH POPULATIONS IN EASTERN CANADA

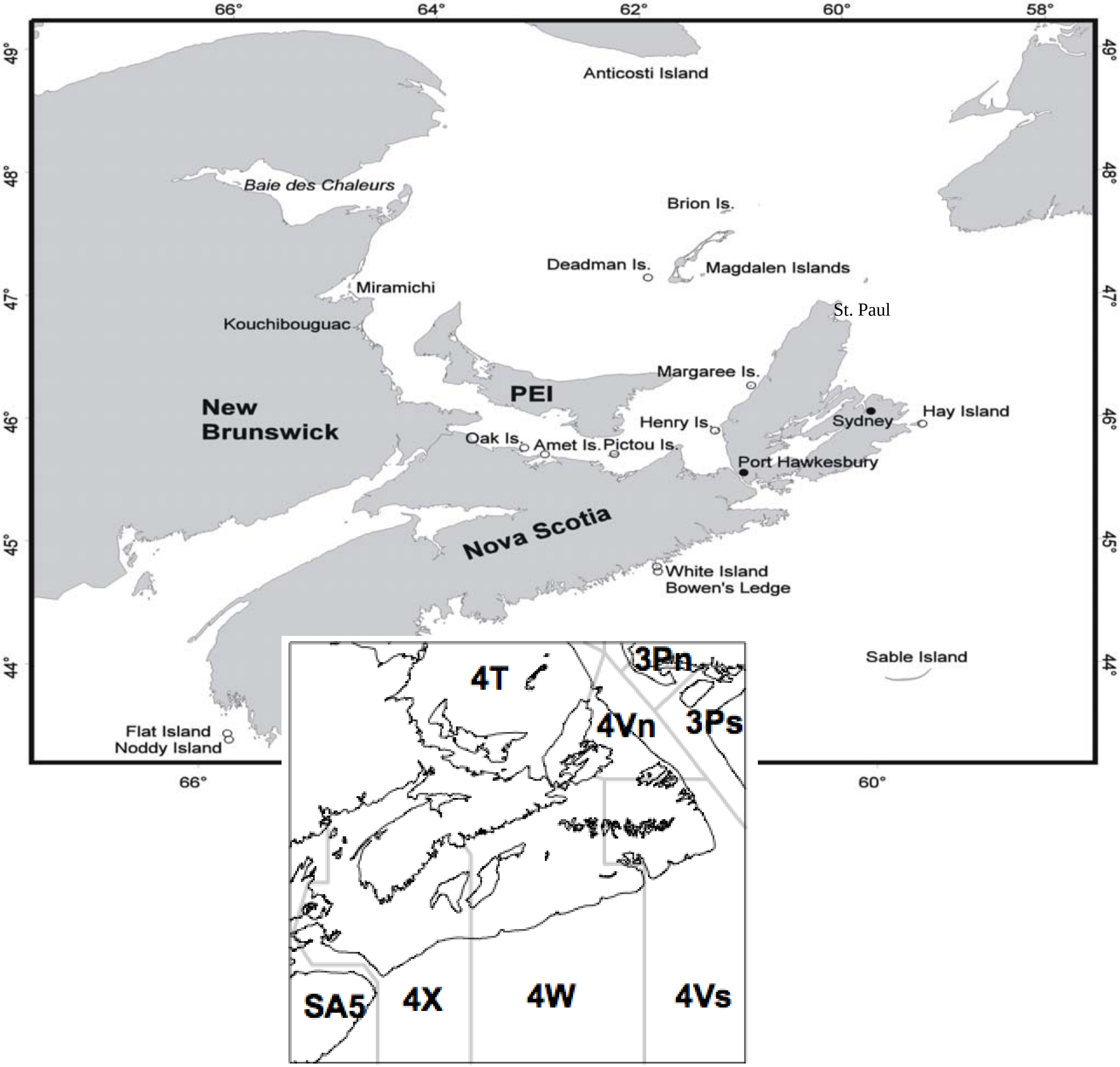

Figure 1. Map showing locations of main pupping colonies in Atlantic Canada and NAFO fishery management areas (inset).

Context

There is ongoing debate about the possible negative impacts of seal predation on fish populations of commercial and conservation interest (e.g. Atlantic cod). One factor contributing to this debate is the growth in grey seal populations in eastern Canadian waters over the past five decades and the concurrent decline or in some cases collapse of several fish populations in the 1990s to the point where fishing has been stopped. Natural mortality of adult fish has been estimated to be unusually high in these collapsed and non-recovering fish populations.

Seals are hypothesized to have five possible kinds of negative effects on prey populations: 1) predation, 2) competition for food, 3) transmission of parasites causing increased mortality of fish, 4) disruption of spawning causing reduced reproductive success, and 5) other indirect effects on prey productivity caused by changes in fish behaviour to reduce the risk of seal predation.

An external review commissioned by the Canadian Department of Fisheries and Oceans (Report of the Eminent Panel on Seal Management 2001) dealt with predation effects in great detail, but other types of hypothesized effects were not considered within the terms of reference of the review. The results of the Eminent Panel stated that the interaction between seals, groundfish and other species is complex and variable and that there was little evidence that seal predation was having a major impact on most commercial fish stocks. Since the Eminent Panel submitted their findings, considerable new research has been conducted on seal population size, changes in the natural mortality of fish and the impacts of predation.

The Canadian Department of Fisheries and Oceans (DFO) hosted a recent two-part workshop to review the impacts of seals on Atlantic cod stocks in eastern Canadian waters. The first workshop focused on the nature and quality of available data, and identified data analyses and modeling studies that could be carried out with existing data to more fully address the issue of seal impacts on recovery of commercial fisheries (DFO Proceedings 2008/021). The second workshop reviewed these new analyses (DFO Proceedings 2009/020). The overall objectives of the two workshops were: 1) to review research on the trophic interactions (e.g. impacts of predation) between seals and Atlantic cod stocks in eastern Canada, with a focus on grey and harp seals, 2) to review similar research conducted elsewhere that may provide insight into the effects of grey and harp seal predation on Atlantic cod stocks, 3) to review research on the effects of seal transmitted parasites as a source of fish mortality, 4) to review research on the possible negative non-trophic indirect effects of seals on spawning success and feeding behaviour of fish, 5) to review available information on the possible impacts of reductions in seal population size on fish population size and exploitable biomass, and the economics of seal management, and 6) to consider the design of experimental or other research that would clarify the impact of seals on the dynamics of cod stocks.

Several hypotheses to explain the population declines and high levels of natural mortality of Atlantic cod stocks in eastern Canada were examined at the second workshop, including unreported catches (i.e., the mortality is due to fishing, not natural mortality), disease, contaminants, starvation (i.e., poor condition), life-history change, impacts of increased seal abundance (predation, parasites, other impacts) and increased predation by other predators. The workshop concluded that the weight of indirect evidence suggested that grey seal predation could account for much of the high natural mortality of southern Gulf cod. The most recent southern Gulf cod advice also states that predation by grey seals is considered to be a significant component of cod natural mortality in the southern Gulf, and at current rates of natural mortality, stock growth is not likely unless productivity increases well above levels observed in the past decade. For 2009-10 and beyond, the Minister announced a targeted removal program for grey seals that would be expected to be preying on concentrations of the southern Gulf cod stock.

SUMMARY

- Grey seals are found in three linked Canadian Atlantic marine ecosystems south of the Laurentian Channel. The southern Gulf of St. Lawrence (4T) is a shallow semi-enclosed sea that is very productive in summer but freezes in winter, and many fish populations, including cod, migrate and overwinter in the warm deeper waters off Cape Breton (4Vn). The cod stocks in the two Scotian Shelf ecosystems (4VsW and 4X), do not conduct extensive migrations and are larger at age than 4T cod. A small resident cod stock is also found in 4Vn but no analyses were reviewed for this stock. Grey seal is a highly mobile species foraging in waters from Georges Bank to the northern Gulf of St. Lawrence. Over this broad geographic range, grey seals encounter different prey assemblages, with differing depth distribution and geographic extent. All of these factors are known to influence grey seal foraging behaviour and diet, and coupled with the different dynamics of the Gulf, Sable Island, and coastal Nova Scotia grey seal herds and their prey species, suggest that the influence of grey seals on prey populations such as cod varies by ecosystem.

- There have been dramatic changes in these ecosystems over the past several decades. Groundfish resources and fisheries once characteristic of the southern Gulf have been replaced by small-bodied demersal fishes and invertebrate fisheries. Like the southern Gulf, the eastern Scotian Shelf ecosystem supported active groundfish fisheries until the early 1990s, which have now been replaced by fisheries on invertebrate species such as shrimp and crab. On the western Scotia Shelf and in the Bay of Fundy, invertebrate fisheries have also increased to unprecedented levels, but some fishing for groundfish continues with cod as a bycatch in fisheries directed towards other species.

- The size of the Canadian grey seal population is estimated by a model incorporating estimates of pup production, reproductive rates and information on removals. Trends in abundance from four population models were presented at the meeting. These models make slightly differing assumptions about adult mortality rates, the effects of increasing density on population growth rate and ice-related mortality of seal pups in the southern Gulf. When these assumptions are taken into account, the population is estimated to have increased from approximately 10,000 animals in 1960 to about 330,000-410,000 animals in 2010, depending on which model is used.

- For management purposes the grey seal population is divided into three herds based upon pupping sites. The herds feed in coastal and offshore waters of 3Pn, 3Ps, 4R, 4T, 4Vn, 4VsW, 4X and 5Z. The largest herd numbering some 260,000 to 320,000 seals, depending on model assumptions, occurs on Sable Island. The rate of increase of this herd has slowed from 12.8% during the 1980s to approximately 4% in the last 5 years. It is uncertain if this reduction in population growth rate is due to changes in age-specific reproduction, young of the year mortality rates, or both. The southern Gulf of St. Lawrence (Gulf) herd numbers around 55,000-71,000 animals, depending on model assumptions, and although apparently increasing, the rate of increase varies with mortality of young due to poor ice conditions. The coastal Nova Scotia herd is the smallest of the three, numbering around 20,000-22,000 animals. Although the majority of these animals are born on Hay Island along the eastern Shore, there is an increasing abundance and new breeding colonies being established in southwest Nova Scotia with a contribution by immigration from the Sable Island herd. Seals from each of these herds range widely throughout the year while foraging and may contribute to colonization of new breeding sites. Reasons for the large increase in the number of grey seals are not fully understood, but reduction in hunting and an increase in ice-breeding habitat in the Gulf are likely to have contributed. Although little is known about historical abundance, current population size is the largest measured in the past several hundred years.

- There are distinct cod stocks in each of the three ecosystems. All stocks have shown declines of at least 80% in abundance and all remain low today. Overfishing reduced the stocks in 4T, 4Vn, and 4VsW to low abundance by the early 1990s. Overfishing also contributed to the lesser decline in the 4X stock up to the mid 1990s. Fisheries have been closed or greatly reduced on all these stocks for the past two decades.

- Despite the severely reduced fishing mortality, survival of adult cod in 4T has remained at a very low level over this period, and the stock has continued to decline. If current levels of productivity and natural mortality were to persist, the stock is estimated to decline to levels near extirpation within 40-50 years. Similar elevated levels of natural mortality are observed in other large demersal fishes in 4T such as winter skate and white hake, which have also declined to very low abundance, and are continuing to decline. The 4Vn resident cod stock has remained very low since the 1980s. The 4VsW cod stock fell rapidly in the late 1980s leading to collapse, followed by fishery closure in 1993. Stock biomass remained low for over a decade but has recently shown an increase and improved survivorship of young cod. The 4X cod stock also experienced high stock mortality and continued to decline after the mid 1990s when fisheries were restricted.

- For 4T cod, a number of the potential causes of the increased adult mortality were examined, including unreported catch, emigration, disease, contaminants, parasites, poor fish condition, life history change and predation due to seals and other predators. A review of the weight of evidence for each cause supported a conclusion that predation by grey seals was likely the greatest contributor to increased mortality in large southern Gulf cod. Changes in the species and size composition of the southern Gulf fish community are consistent with changes in mortality similar to those observed for cod. Grey seal predation is also considered an important component of the high natural mortality of winter skate and white hake, two species at high risk of extirpation in the southern Gulf.

- Determining the diet of grey seals relies mostly on indirect methods because there are limited opportunities to directly observe what they eat. The methods used are based on recovery of hard parts such as fish ear bones from stomach contents, intestines, and feces, and the analysis of blubber chemistry in seals and their prey. Each of these methods has strengths and weaknesses. In addition to challenges in determining what a grey seal has eaten, it is also difficult to obtain a representative sample of the diet from grey seals because they range widely and their diet varies by sex, season, area and other factors. Analyses of the above data sources indicate a wide range of values for the percentage of cod in the diet of grey seals; an overall average of 2-7% in 4VsW, and in 4T, from 1% for females in summer to 24% for the only sample of males in winter. All of these methods make assumptions that may be violated to a greater or lesser extent, but it is believed that the estimates are reasonable representations of the diet in the areas that have been sampled.

- In order to estimate consumption, the various estimates of diet must be extrapolated to the entire area and over the entire year. However, gaps in sampling greatly increase the uncertainty of the consumption estimates and may introduce bias. In particular, consumption of large cod may be underestimated because of current spatial and seasonal gaps in diet sampling during periods when cod are aggregated.

- Energetic models indicate that individual grey seals require approximately 1-2 tonnes of prey annually (3-6 kg/day), depending on seal age and sex, and energy content of the prey mixture in their diet. This variability in energy content of prey affects the stock-specific estimates of cod consumed by seals (see paragraph 8). Our best estimate of grey seal consumption of cod in recent years lies within the range of 4,500 to 20,000 tonnes per year for 4T, and between 3,000 to 11,000 tonnes per year for 4VsW. These estimates themselves have high variance and their wide ranges reflect uncertainty attributable to the assumptions made to address gaps in sampling in 4T and the treatment of the diet data in 4VsW.

- In 4T, grey seals are considered a significant source of mortality for large cod (>35cm) and other adult, bottom-dwelling fish. Southern Gulf cod occur in dense aggregations during seasonal migrations, spawning and on the overwintering grounds. Satellite tracking indicates that some grey seals, in particular males, forage where these aggregations occur. Digestive tract samples from seals foraging on overwintering aggregations of cod contain a relatively high proportion of cod (about 24% in males and 10% in females, based on intestine samples), and a high proportion (58%) of these cod were greater than 35cm in length. Seals are also considered a source of high mortality on winter skate and white hake, species considered by Committee on the Status of Endangered Wildlife in Canada (COSEWIC) to be at heightened risk of extirpation.

- For 4VsW cod, seal predation is also noteworthy, but its magnitude compared to other sources of mortality varies with model assumptions. Most models leave a large portion of mortality unaccounted for and attribute only a small (less than 17%) portion of total cod mortality to seal predation. Comparable information is not available for the mortality inflicted by grey seals on cod in 4X and 4Vn.

- Grey seals transmit a parasite, larval sealworm, which accumulates in the flesh of cod and other groundfish species resulting in increased processing costs and reduced marketability. In 2008-09, sealworm abundances in 4T cod increased dramatically, reaching levels greatly exceeding those reported in 4VsW and 4X cod in 2006. Infection appears to have little impact on the condition of 4T cod.

- Models that make a variety of assumptions were used to estimate the reductions in seal abundance that would be required to reverse the declines of 4T cod. Results of the models differed greatly, reflecting uncertainties about interactions between seals and cod. Consequently, it is not possible to specify a level of reduction that would be necessary or sufficient to reverse the cod decline. Given one set of assumptions about how to fill data gaps, the proportion of mortality due to seal predation is estimated to be so low that total elimination of this mortality source would not be sufficient to allow recovery of cod. Given other assumptions about how to fill data gaps that would produce mortality estimates consistent with the weight of evidence (paragraph 7), seal removal could reduce cod mortality enough to allow recovery, but the necessary reductions would be substantial. This model estimates that in order to lower natural mortality of cod to 0.4, the number of seals foraging in the southern Gulf area would need to be reduced by 70% to 31,000 seals. Currently, there are estimated to be 104,000 seals that forage in the southern Gulf, including 36,000 seals from Sable Island, 5,000 seals from the eastern Shore and 63,000 seals from the southern Gulf. Given current productivity and in the absence of fishing, cod could recover at a natural mortality of 0.4. Removals of this magnitude are also predicted to decrease natural mortality of winter skate such that their abundance could stabilize and perhaps increase but this number of removals would be insufficient to halt the ongoing population decline of white hake. If particular seals specialize in predation of cod and it is possible to target these seals for removal (e.g., males in areas of high overlap with cod such as Cabot Strait in winter), then the required removals could be much lower. Likewise, targeting grey seals that feed in areas where winter skate or white hake aggregate

(Northumberland Strait, Laurentian channel) would likely require considerably smaller removals for comparable reductions in their mortality rates.

- For 4VsW, the models reviewed provided a wide range of results reflecting uncertainty about seal-cod interactions in recent years. Many of the model scenarios found that seal predation is not an important component of cod mortality, and do not predict a large response of the 4VsW cod stock to changes in seal abundance. If an intervention were to be made, the consequences for cod of a reduction in the seal population would depend on the age and sex of the seals removed. As the Sable Island seal herd is about 5 times larger than the Gulf herd, an intervention to significantly reduce this population would need to be much larger than that described for 4T in paragraph 14. Removal or contraception of adult females is the most effective intervention, followed by removal of pups and then adult males. A predator control or a contraception program on the order of 10,000 seals per year for 5 years would have a very low probability of having a detectable consequence for cod.

- The magnitude of removals of grey seals foraging in the southern Gulf (described in paragraph 14) was not considered to pose a risk of irreversible harm to the seal population. By contrast, if productivities of cod, winter skate and white hake in 4T remain at their present levels, further declines would be expected in these populations, which COSEWIC has determined are at an elevated risk of extirpation.

- Culling is widely practiced as a means to limit predation on livestock and wildlife and can be effective at reducing predator abundance. Culling also has been used to reduce seal species. Nevertheless, although widely practiced, the extent of seal population reduction and the response of targeted prey populations to culls have rarely been evaluated, such that their effectiveness is poorly understood. Further, results from other predator control programs indicate that unintended consequences in food webs, that will be difficult to predict, are nonetheless commonly observed. Thus, any intervention in the southern Gulf would first require a thorough investigation of the likely multi-species impacts of a cod-seal interaction in this ecosystem, and second would require a carefully designed program that would include clearly-stated objectives and rigorous monitoring of the seal and cod populations and the ecosystem to evaluate the consequences.

- There are several protocols and monitoring requirements that should be followed to effectively design and evaluate a predator control program. Key among these are clear statements of objectives and expected benefits and use of performance measures that provide a quantitative interpretation of the extent to which objectives have been met and benefits realized. To be informative, the control program should be planned and conducted in an adaptive management framework.

INTRODUCTION

The purpose of the CSAS workshop held in Halifax, NS, October 4-8, 2010, was to review a series of working papers on the subject of interactions between grey seals and cod and other large demersal fish species and to develop and provide scientific advice on questions posed by Ecosystems and Fisheries Management (EFM), specifically: How many grey seals would have to be removed over five years to measurably lower natural mortality on southern Gulf cod and other cod stocks that are experiencing high natural mortality? What might be the ecosystem responses (e.g. abundance of other predators and prey) to grey seal targeted removal, particularly as they may impact cod recovery?

In initiating this review, the Department organized a steering committee in February 2010 to develop objectives and a time frame for preparing and reviewing the material. The steering committee recognized the importance of including industry, non-governmental organizations, academia and expertise from other countries in this review. The review addressed the following questions:

1) Direct evidence for cod consumption by grey seals
2) Indirect evidence for cod consumption by grey seals
3) Minimum decrease in natural mortality to restore cod populations to reference levels
4) Changes in grey seal abundance, distribution and ecology
5) Grey seals reduction scenarios to restore cod populations
6) Examples of control of large marine predators in other parts of the world
7) Design of a controlled experiment to test impact of grey seal targeted removal on mortality of southern Gulf cod

Background information relevant to the review was provided for the grey seal population, the Atlantic cod stocks of interest and the three ecosystems where these species are found together.

The Ecosystems

Southern Gulf of St Lawrence - 4T

The southern Gulf of St. Lawrence (Northwest Atlantic Fisheries Organization [NAFO] management divisions 4T, see Figure 1) is a shallow semi-enclosed sea covering an area of about 80,000 km^2. The runoff from the St. Lawrence River brings considerable nutrients into the system and a nutrient gradient exists from the estuary to the southern GSL. In summer, three water layers occur in the southern GSL: a warm surface layer extending to depths less than 30 m, a cold intermediate layer (CIL) extending between depths of 30 and 100 m, and a warmer deep layer. The CIL covers the bottom over much of the southern GSL. In winter, the surface waters cool and much of the area is typically ice-covered. The demersal fish community has been dominated by large populations of Atlantic cod and American plaice while herring and mackerel dominate the pelagic system. Snow crab and lobster are abundant in the southern GSL. Most of the larger-bodied fish species undertake seasonal migrations to avoid cold winter temperatures, either exiting the Gulf completely or moving to deeper and slightly warmer waters in the Laurentian Channel. A dramatic shift in the composition of the fish community occurred in the early 1990s, marked by dramatic declines in the biomass of large demersal fishes and increases in the biomass of small-bodied fishes. The initial change in community composition appears to reflect direct and indirect effects of overfishing, but its persistence following severe reductions in fishing effort in the early 1990s must be due to some other factor(s).

Eastern Scotian Shelf - 4VsW

The eastern Scotian Shelf (NAFO management division 4VsW, see Figure 1) is a broad continental shelf made up of a number of shallow offshore banks and deeper inner basins. It extends from the Laurentian Channel in the northeast to a line from Halifax south to the shelf break in the southwest, encompassing an area of approximately 110,000 km^2. The physical environment of the eastern Scotian Shelf is governed by its complex topography and proximity to major ocean currents. The fish community was composed of large populations of groundfish such as cod, haddock, plaice, silver hake and white hake, but several analyses have indicated that the demographic structure of the 4VsW ecosystem has been profoundly altered from its state in the 1980s, with historical declines in the biomass of most groundfish including cod along with an exponential increase in grey seals and increases in forage species such as shrimp and sand lance (based on increased research vessel survey abundance estimates and area of occupancy, although pelagic organisms have been shown to be highly susceptible to changes in vertical distribution affecting their catchability) and other invertebrates such as snow crab, bivalves and lobster. The declines in groundfish biomass were accompanied by large-scale reductions in age and size structure, and decreased condition of many fish populations. There has been a long term reduction in the number of large fish and in the mean weight of individual fish.

Southwestern Scotian Shelf - 4X

The southwestern Scotian Shelf (NAFO management division 4X, see Figure 1) extends southwest from the Halifax line and into the Bay of Fundy, and is contiguous with the Gulf of Maine and Georges Bank in US waters and has an area of approximately 80,000 km^2. The deep basins on the central shelf are directly influenced by the slope water, where the water properties are determined by interactions between the Labrador Slope Water Current originating from the north, and the Gulf Stream, originating from the south. Consequently, the central and western parts of the Scotian Shelf are generally warmer than the eastern Scotian Shelf. The defining characteristic of the Bay of Fundy is the magnitude of tides, ranging from a mean height of 6 meters (maximum 8 m) in the outer bay to a mean height of 11.9 m (maximum 16 m) in the inner bay, the highest in the world. This area has a similar exploitation history to the eastern Scotian Shelf, but the decline of groundfish stocks was less in 4X; however many species, including cod, remain at low levels of abundance and have high mortality rates. Other species such as dogfish, redfish and winter flounder have increased, while others (e.g. black-bellied rosefish) have moved onto the shelf from deeper water. There has been a long term reduction in the number of large fish and in the mean weight of individual fish. Some groundfish also exhibit similar decreases in condition and growth rates to those observed in 4VsW.

The Grey Seal Population

The Canadian grey seal forms a single population that is subdivided into three groups for management considerations based on the locations of concentrations (colonies or herds) of breeding animals: Sable Island, Gulf of St. Lawrence (Gulf), and eastern Shore components. Outside of the breeding season, there is some overlap in the distribution of animals from the different colonies.

The grey seal population in Atlantic Canada has increased over the last 50 years from around 13,000 animals in 1960 to about 330,000 to 410,000 in 2010. Additional grey seals also occur in the northeastern United States where they have established new breeding colonies. The reasons for such a recovery are not understood, but likely result from an improvement in breeding habitat conditions and a reduction in removals. A reduction in predators of seals (sharks and killer whales) may also have played some role in this recovery, but it is not considered to be important.

Improvements in breeding conditions in the southern Gulf could be related to changes in ice conditions. Beginning in the mid-1950s, the Cape Breton Causeway was built, linking the island of Cape Breton to the Nova Scotia mainland. Prior to the causeway, ice drifted through the channel past Port Hawkesbury into the Atlantic where ice destruction would have been rapid and mortality among young seals would have been high. Construction of the Causeway blocked the exit of ice from the area forcing ice to move north and around the coast of Cape Breton Island, allowing a buildup in the Canso Strait and St. George’s Bay areas and increasing the availability of pupping habitat for Gulf herd grey seals. This change would have allowed for earlier formation of stable ice in these areas of the southern Gulf. Over the last decade, there has been a general decline in the quality and quantity of ice cover in the southern Gulf. In response to poor ice conditions, an increasing proportion of pupping now occurs on islands. Throughout the year, grey seals tend to occupy the outermost islands where pupping colonies occur because there are few inhabitants and animals are rarely disturbed (e.g. Anticosti Island, Deadman Island), or disturbance is benign (Sable Island, Pictou Island). Changes in ice conditions cannot explain increases in pup production of the Sable herd.

For all herds, a reduction in cull and bounty efforts, limited commercial harvesting and a change in human behaviour (less overall shooting) have also likely favoured recovery of grey seals.

Total abundance of grey seals is estimated using a population model that incorporates estimates of pup production obtained from direct counts or surveys (Table 1), information on fecundity (Table 2), removals (Table 3) and ice-related mortality of young-of-the-year seals. The model is fitted separately to independent estimates of pup production for each herd by adjusting the starting population size and adult mortality. Reproductive rates were assumed not to have changed. Natural mortality of females was assumed to be the same for all herds at M=0.05. Natural mortality of males was assumed to equal females until age 9, then the rate was doubled for animals aged 10 years and older. Density dependence was assumed to occur on the Sable Island herd and to act on both the number of pups born and the mortality of young in their first year. The coefficient reflecting the strength of density-dependence was set at 2.4 and carrying-capacity was set at 600,000 animals with a coefficient of variation (CV) of 10%.

The model fit to the Gulf survey data was very poor. Surveys of this herd are complicated by the long pupping season and the apparent poor ability of grey seal mothers and pups to adjust to breaking ice. Grey seals also appear to be poorly adapted to cold-water exposure at the first moult (beater stage), suggesting that pupping on ice is an indication of this animal's flexibility to adjust to environmental conditions, rather than evidence of its long term evolution in this environment. A positive relationship was observed between good ice conditions and pup production.

The grey seal population in Atlantic Canada has likely increased by 30-fold since the 1960s based on pup counts and current models (Figure 2). The current population of approximately 330,000-410,000 animals is likely the highest observed in over 200 years.

There is considerable uncertainty in projecting future grey seal herd population abundance. Gulf pup production is highly variable, perhaps due to ice conditions, and there is currently no evidence of density dependence. For the Sable herd, the evidence for density dependence is just emerging, being based upon the 2007 and 2010 estimates of pup abundance. Grey seal abundance in Coastal Nova Scotia (4VWX) and Gulf of Maine area appears to be growing. These trends suggest that projections of grey seal abundance after 2020 are highly speculative.

Table 1. Estimates of pup production in the southern Gulf of St. Lawrence. Sable Island and eastern Shore herds. [1] In early studies there was no estimate of the standard error, which was assigned as equal to the estimate.

	Southern Gulf		Sable Island		Eastern Shore	
	Estimate	SE	Estimate	SE	Estimate	SE
1962					130	200[1]
1963			400	400[1]	180	200[1]
1964			550	550[1]	190	200[1]
1965			660	660[1]	230	200[1]
1966	900	500[1]			180	200[1]
1967			580	580[1]	270	200[1]
1968			700	700[1]		
1969			800	800[1]		
1970			800	800[1]	100	200[1]
1971			1000	1000[1]	130	200[1]
1972			950	950[1]		
1973			1200	1200[1]		
1974			1250	1250[1]	135	200[1]
1975	3800	3800[1]			180	200[1]
1976			2000	2000[1]	130	200[1]
1977	3900	3900[1]	2181	173		
1978			2687	192		
1979			2933	201		
1980			3344	214		
1981			3143	208		
1982			4489	248		
1983			5435	273		
1984	7169	911	5856	283	142	200[1]
1985	6706	795	5606	277	135	200[1]
1986	5588	679	6301	294	151	200[1]
1987			7391	318	179	200[1]
1988			8593	343		
1989	9352	1756	9712	365	179	200[1]
1990	9176	649	10451	575		
1993			15500	463		
1996	10717	1306			395	74
1997	6839	800	25400	750	1061	121
2000	5260	910			799	105
2004	14210	1200	41100	4381	2469	76
2007	11413	1077	54482	1288	3017	40
2010	11329	6442	62,054	587	2,960	236

Table 2. Age specific reproductive rates from Gulf grey seals used in the model (SE=standard error).

Age	Estimate	SE
4	0.167	0.051
5	0.607	0.082
6	0.849	0.037
7	0.906	0.018
8	0.888	0.021

Table 3. Removals of grey seals from the Gulf of St. Lawrence.

Year	Total Sable	Total Gulf	Total Eastern	Year	Total Sable	Total Gulf	Total Eastern
1960	0	0	0				
1961	0	0	0	1986	0	812	0
1962	0	0	0	1987	0	1298	0
1963	0	0	293	1988	46	767	0
1964	0	0	6	1989	477	1883	24
1965	0	0	1	1990	197	152	9
1966	0	0	0	1991	0	50	0
1967	0	0	229	1992	6	310	0
1968	0	0	256	1993	0	56	0
1969	0	644	136	1994	0	89	0
1970	45	92	575	1995	0	55	0
1971	13	406	479	1996	24	83	6
1972	0	271	440	1997	7	75	0
1973	0	166	467	1998	0	70	0
1974	2	636	533	1999	1849	119	0
1975	22	1686	599	2000	1967	139	82
1976	9	96	546	2001	2054	89	1301
1977	69	981	407	2002	2204	150	0
1978	0	324	380	2003	2346	63	0
1979	0	414	314	2004	3002	143	0
1980	0	1330	326	2005	3105	591	494
1981	69	1794	278	2006	3437	1055	830
1982	0	2040	387	2007	3373	966	868
1983	214	2547	394	2008	3334	210	1261
1984	20	243	114	2009	3381	0	263
1985	0	254	0	2010	2933	83	0

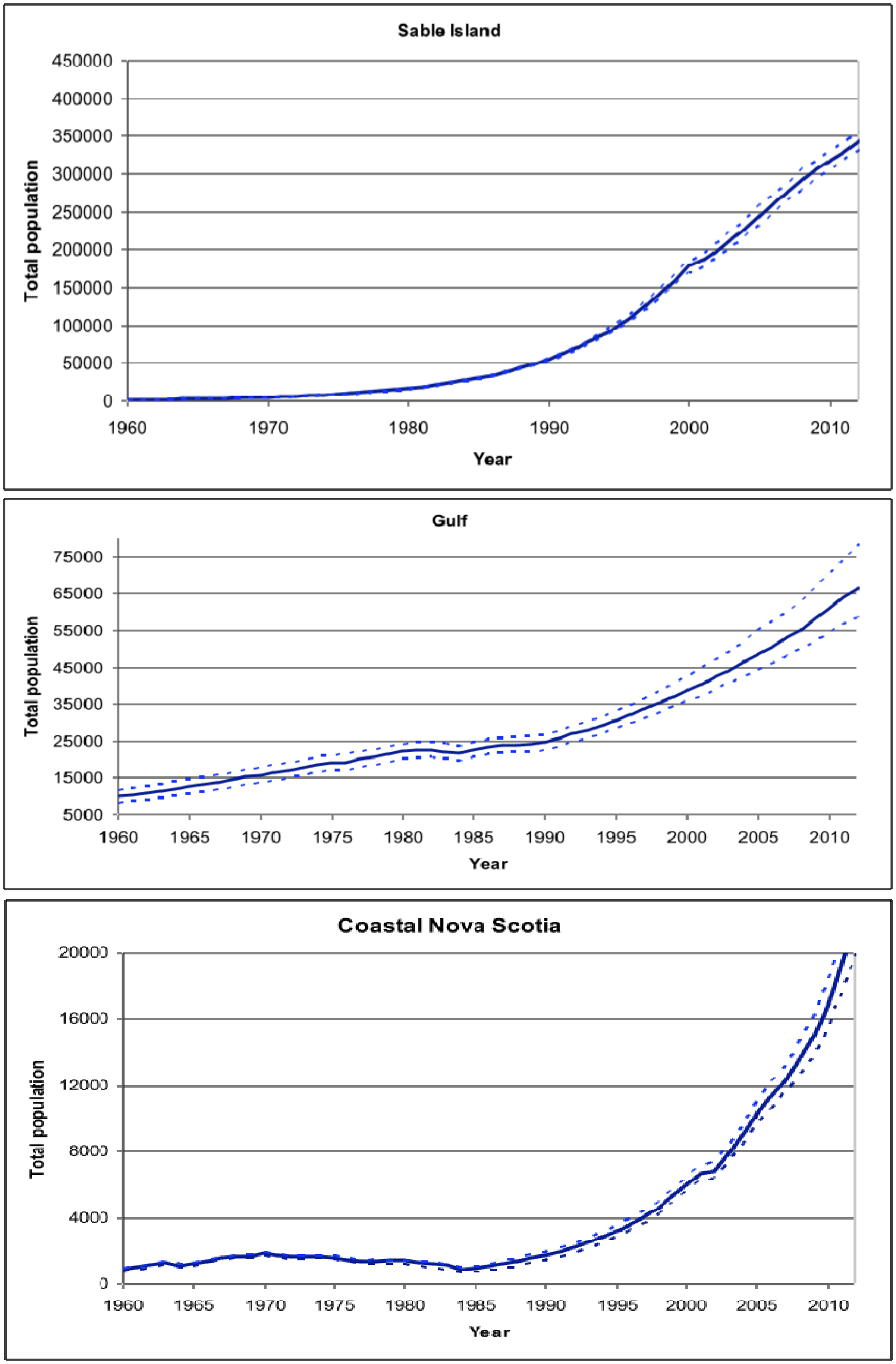

Figure 2. Trajectories (mean±95% confidence interval) of the total population for the three grey seal herds in Eastern Canada.

The Atlantic Cod Stocks in 4TVn, 4VsW and 4X

Southern Gulf of St. Lawrence cod (4TVn)

The southern GSL cod population is a migratory stock, overwintering along the slope of the Laurentian Channel in the Cabot Strait area (NAFO subdivision 4Vn). In spring (April-May), it migrates into the southern GSL to spawn and then disperses throughout the area to feed before migrating back to the overwintering grounds in late fall.

Trends in relative abundance of this stock are monitored by an annual bottom-trawl survey. Additional information on relative abundance is obtained from catch rates in the commercial fishery (prior to 1993) and a number of surveys conducted in collaboration with the fishing industry (since 1995). Indices of relative abundance are scaled to absolute abundance using population models that incorporate data on fishery catch-at-age and estimated or assumed values for natural mortality (M). The last assessment of this stock (Feb 2009) used a population model with M aggregated over all ages (2+yr). The assessment model assumed that 2+ M was 0.2 in the 1970s and estimated M in blocks of years after the 1970s. Work conducted since that review has indicated that the trends in M differ between young cod (ages 2-4 yr) and older cod (ages 5+ yr). Models which incorporate separate M trends for young and old cod provide much better fits to the abundance indices for this stock. One of these models was chosen to provide the advice at this meeting. This model fixed M at 0.1 for cod aged 5 years and older (based on the results of earlier studies) and at 0.5 for younger cod in 1971-1976, and estimated M separately for the two age groups in blocks of subsequent years. CVs on the estimates of abundance at the beginning of 2010 from this model are 45% for age 3, 32% for age 4, 29% for age 5, and 20-24% for older ages. Results of this model for 2009 are:

Age group (yr)	Mid-year biomass (t)	Natural mortality (M)	Cod biomass loss to M
2-4	33,872	0.28 ± 0.126 SE	9,544
5+	35,017	0.63 ± 0.038 SE	22,384

Landings of southern GSL cod increased substantially following the introduction of otter trawling in the late 1940s. The exploitation rate on the stock increased from the early 1950s to the mid 1970s (Figure 3). Stock biomass declined during this period of increasing exploitation (Figure 4). Cod biomass recovered rapidly in the late 1970s despite continued fishing. Biomass then decreased sharply in the early 1990s. The directed fishery was closed in September 1993, and fishing effort has remained at a very low level since then. Despite very low fishing mortality, cod biomass continued to decline throughout the 1990s and 2000s. The striking contrast between the rapid recovery in the late 1970s despite continued fishing and the lack of recovery in the 1990s and 2000s despite severely limited fishing reflects a dramatic decline in the productivity of this resource between the 1970s and the 1990s. All components of production (recruitment, individual growth and natural mortality) contribute to this decline in productivity. However, the most important factor in the rapid recovery in the 1970s was unusually strong recruitment while the most important factor in the lack of recovery in the 1990s and 2000s is unusually high natural mortality. The strong recruitment between the mid 1970s and the early 1980s is thought to have resulted from the unusually low abundance of pelagic fishes (herring and mackerel) at that time. Herring and mackerel are potential predators of cod eggs and larvae. Herring biomass in the southern Gulf has been at a relatively high level since the mid-1980s. Possible causes of the high natural mortality in the 1990s and 2000s are examined below. If the current low productivity conditions were to persist, the stock would be expected to continue to decline even with no fishing. The directed fishery for this stock was closed in 2009 and 2010.

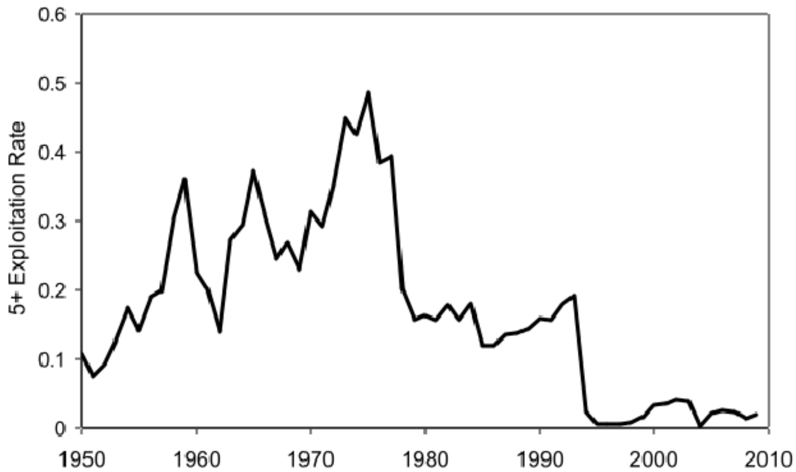

Figure 3. Estimated exploitation rate (ages 5+ yr) for the southern GSL cod stock.

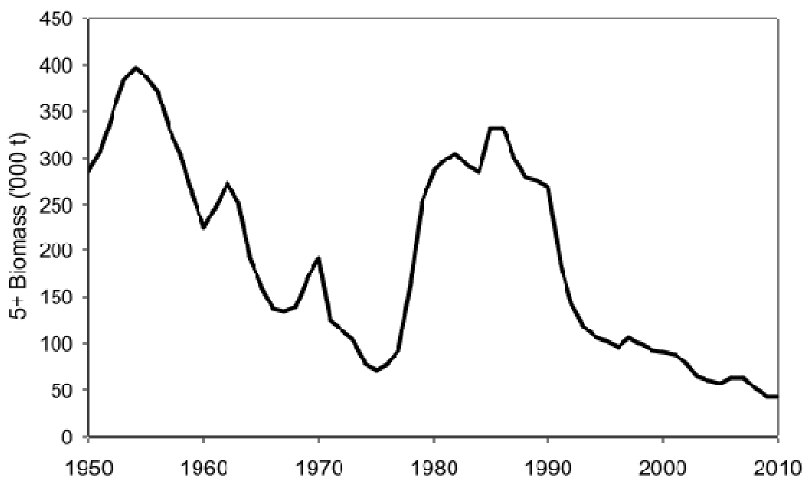

Figure 4. Estimated biomass (ages 5+ yr) of the southern GSL cod stock.

Eastern Scotian Shelf cod (4VsW)

The last CSAS assessment of this stock (DFO, 2003) suggested that natural mortality on both adults and juveniles was extremely high and there were no indications of stock recovery. Since then, a number of analyses have been undertaken to model population dynamics of 4VsW cod (e.g. Trzcinski et al, 2006; 2009). Current (2009) estimates of biomass, natural mortality and cod biomass loss due to M are given in the table below. The range in values reflects uncertainty in the estimates reflected through different cod–seal modeling assumptions.

Length group	Mid-year biomass (t)	Natural mortality (M)	Cod biomass loss to M
<35cm	15,200 - 83,700	0.2 - 0.8	3,500 - 52,600
>35cm	13,600 - 68,200	0.2 - 0.7	10,300 - 18,800

Southwestern Scotian Shelf cod (4X)

At the last CSAS assessment for 4X stock (Feb 2009), it was concluded that natural mortality had remained unchanged for small cod (<age 4) but had increased since the mid-1990s from 0.2 to 0.7 for large cod. If current productivity patterns continue, the stock is expected to increase slowly at current fishery removals (TAC in 2009 = 3,000t). If natural mortality is not reduced, spawning stock biomass is unlikely to reach the reference level of 25,000t.

Length group	Mid-year biomass (t)	Natural mortality (M)	Cod biomass loss to M
<35cm	500	0.2	160
>35cm	10,000	0.7	4,000

ASSESSMENT

1. Direct evidence for cod consumption by grey seals

1.1 What are the estimated diets of grey seals?

Grey seals are generalist predators that consume a wide range of fish species and some invertebrate species. Their diets are influenced by a number of factors including sex and age. In addition, grey seal diets vary in response to seasonal and geographic differences in the abundance and distribution of their prey. A review of grey seal diets in the northeast and northwest Atlantic indicated that cod was commonly found in the diet of grey seals.

Diets have been estimated from stomach contents (Stomach), intestinal contents (Intestine), fecal samples (Scat) and fatty acid signatures obtained from the seal blubber (FA) (Table 4).

Table 4. Availability of grey seal diet data. NR indicates where data are not required to estimate cod consumption. Components where data are not available are indicated with X.

	Jan-April	May-June	July-Oct	Nov-Dec
Southern Gulf				
4Vn	Stomach Intestine	NR	NR	X
Inshore 4T	Stomach Intestine	Stomach Intestine	Stomach Intestine	Stomach Intestine
Offshore 4T	X	X	X	X
Scotian Shelf				
Nearshore	FA	FA	Stomach, FA	Stomach, FA
Offshore	FA	FA	FA	FA
Sable	Stomach, FA	Stomach, FA	Stomach, FA, Scat	Stomach, FA, Scat

In the eastern Scotian Shelf, diet composition has been estimated primarily from analyses of fish otoliths recovered from more than 1,300 scats (feces) and from the composition of fatty acids stored in about 740 blubber samples. Similar prey species (> 30 species) are detected by both methods, but the estimated contributions of each prey to the diet differ. One reason for this difference is that fatty acids represent feeding over a period of weeks or months whereas scats represent only the last few meals. All methods indicate that sand lance is a dominant prey eaten by grey seals on the Scotian Shelf. Other species consumed include several species of flatfish (e.g. American plaice), cod, pollock, redfish, herring, capelin, mackerel, sculpins, skates, silver hake and squids. The relative importance of these species in a seal's diet differs according to the method used.

Diet composition for grey seals in the southern Gulf of St. Lawrence was estimated using otoliths recovered from 470 digestive tracts. Forty-six different prey taxa were identified. The main prey species were sand lance, herring, hake, and winter flounder. Cod was an important prey in both the western and eastern Gulf, but was only a minor prey item in the Northumberland Strait area where cod rarely occur. Male seals showed greater diet diversity than females and young-of-the-year (<6 months old). Cod was an important prey item for males in some areas, but was much less important to females.

Our understanding of the diet of grey seals in the Gulf during the winter is based upon a single sample of 100 animals collected between Cape Breton and St. Paul islands in October-December 2008: 50 animals had food in their stomachs; and, 91 animals had intestines containing prey items. Intestines are considered to be less biased and therefore able to provide a better estimate of diet than stomachs. The most important prey item in intestines was flatfish. Adjusting these data using numerical correction factors to account for the differential loss of species with small, fragile otoliths, the percentage of cod in the diet was 16.2% for male seals and 2.6% for females. Including otoliths recorded as unidentified cod-like fishes, which were very likely to be Atlantic cod, the percentages increased to 24.1% for male seals and 10.4% for females. The stomach contents of males and females differed greatly. Males (n=35) fed primarily on Atlantic cod, herring, winter flounder, white hake, sand lance and capelin. No cod was found in females (n=15) which fed mainly on herring, white hake and flatfish. No cod DNA was found in seal stomachs that did not contain cod otoliths, suggesting that if seals were feeding on soft parts of cod (i.e. 'belly biting'), it was not common in this area.

1.2 What are the estimates of the proportions and the size distributions of cod eaten by grey seals?

The mean percentage of cod in seal diets was calculated for the different samples and the results are shown below in Table 5.

Table 5: Estimated percentage of cod in the diet by weight for samples collected in different areas and seasons. Estimates for males and females are shown separately. Note that no samples were collected in area 4X.

Area	Year	Season	Method	% Cod male seals	% Cod female seals
4Vn	2008	Oct-Dec	Intestine	24	10
4T (inshore)	1994-2008	June - Nov	Intestine	7	1
4VsW	1991-2010	Spring, summer, fall, winter	Scat	7	7
4VsW	1996-2005	Spring, summer, fall, winter	Fatty acid	2	2
4X	na	na	na	na	na

The majority of studies indicate that when grey seals feed on cod, they feed primarily upon small cod. Otoliths collected from scats in 4VsW indicate that grey seals generally consume young cod less that 35 cm in size, but that older cod are also eaten (Figure 5). These samples are based upon foraging in proximity to Sable Island, where DFO trawl surveys indicate that small cod occur preferentially in abundance over larger cod. Thus, the size composition of cod in a seal's diet based on scat samples is likely biased. On the other hand, the fatty acid analyses suggest indicate that cod longer than 35 cm contribute more to the diet. The mean length of cod consumed by grey seals in 4T between June and November was 23.8 cm (SD=11.0, N=94), see Figure 6.

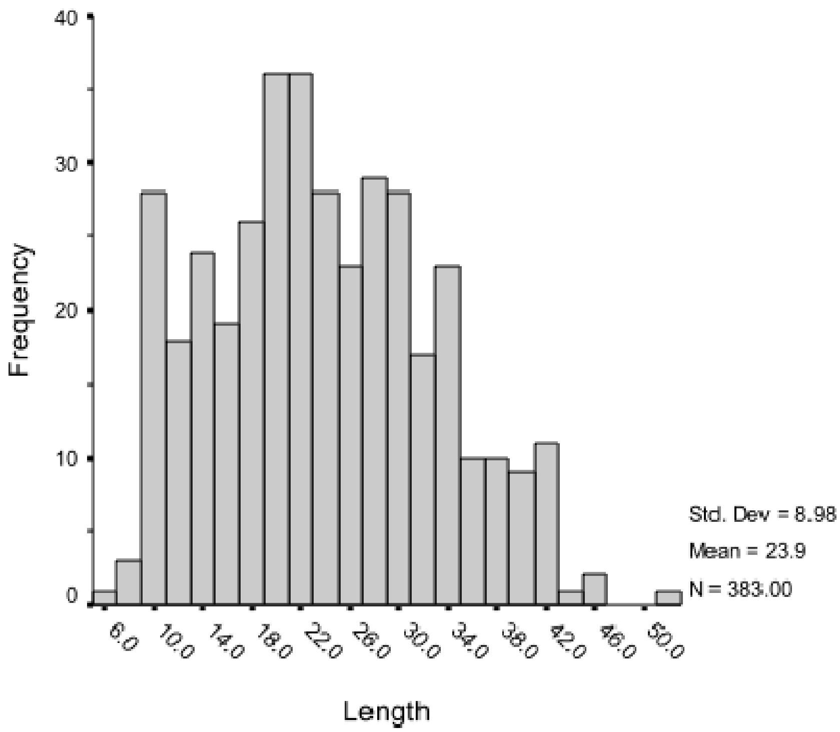

Figure 5. Length frequency of Atlantic cod, in 2 cm classes, consumed by grey seals in 4VsW presented as frequency of occurrence.

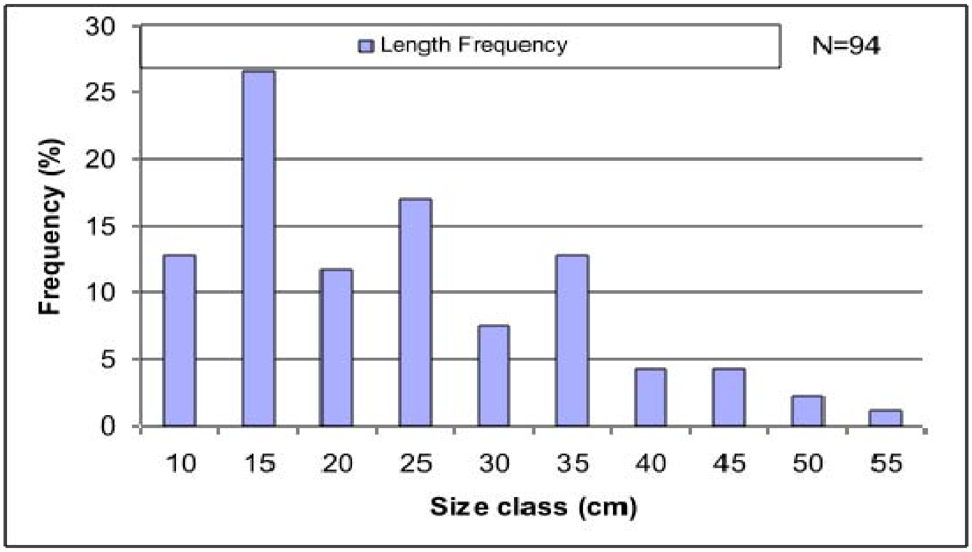

Figure 6. Length frequency of cod consumed by grey seals in the southern Gulf of St. Lawrence presented as frequency of occurrence. Length class 10 cm, includes fish 5 cm to 9.9 cm long, class 15 includes fish 10 cm to 19.9 cm long.

Based on one sample of animals collected over a two-month period in 2008, grey seals eat larger cod during the winter in Cabot Strait than observed in other studies., The average length of cod consumed was 38.6 cm (std = 14.3 cm) and 58% of the cod consumed were greater than 35 cm in length (Figure 7), based upon the length of undigested cod otoliths in the stomachs and intestines.

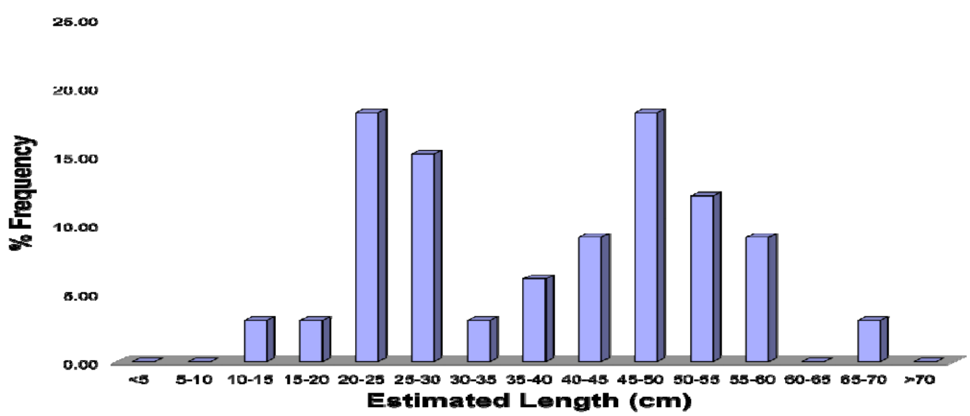

Figure 7. Length frequency of cod consumed by grey seals in the Cabot Strait presented as frequency of occurrence.

The size of cod eaten by seals has important implications for the estimation of grey seal predation mortality, and in particular, for explaining the high levels of M on large cod (i.e., >35 cm). While the majority of studies indicate that grey seals mainly eat small cod, studies in the Gulf and Cabot Strait show that large cod are also eaten and may be preferentially selected. If grey seals prefer large cod, i.e., large cod occur in the diet to a greater extent than would be expected based on their relative abundance where seals are feeding, they would be more likely to account for the high M on large cod. The Cabot Strait estimate of the diet provides some indication that large cod might be preferred in overwintering concentrations. In addition, the size composition of cod consumed in summer diet samples closely matches the population size distribution over the 15-65 cm length range (Figure 8). This observation might be interpreted as indicating that grey seals consume cod of different sizes in proportion to their availability. However, these diet samples are difficult to interpret as they were obtained from inshore foraging areas where the proportion of cod that are large (>35 cm) is lower than in the population as a whole, suggesting selective predation on the larger, less available cod. Nevertheless, quantitative estimates of the size-selectivity of predation on cod by seals are currently not available. This situation is because the size composition of cod has not yet been estimated at the temporal and spatial scales used by foraging grey seals.

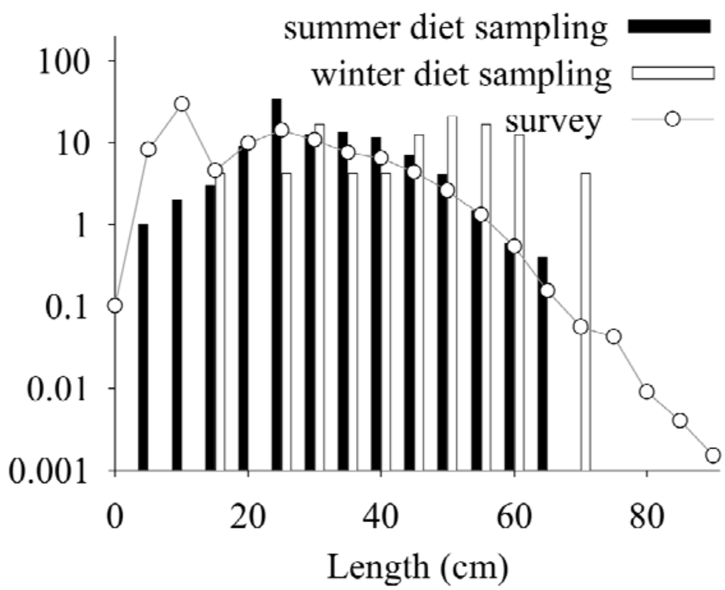

Figure 8. Frequency distribution of southern GSL cod lengths in the 2005 population, and in spring/summer and winter grey seal diet samples. The population frequency distribution is based on catchability-adjusted estimates from the annual September survey. Note that the percentage axis is on the log-scale.

1.3 What are possible sources of bias and uncertainty in estimates of grey seal diets?

1.3.1 Analysis of hard parts

The following points list the assumptions of using otoliths recovered from scats, intestines and stomachs to estimate diet, the violation of which could introduce bias.

1.3.1.1 Scats or gastro-intestinal (GI) tracts should be representative of the population diet

If some foraging occurs sufficiently far from sites where seals are sampled such that prey remains are defecated at sea, the diet represented in samples may not be representative of the entire diet and bias could result. Bias could also result if samples are not representative of the age and sex distribution in the seal population. Sample collection and analysis need to be stratified seasonally and regionally to account for this source of variation. It should be noted that because diets are expressed as a proportion, an underestimate in one prey species will result in an overestimate of all others.

1.3.1.2 Prey remains in samples should be representative of the prey being sampled

All prey consumed should have recoverable remains to avoid bias. Bias could be caused by ‘false absences’ if some prey do not have otoliths or other recoverable body parts (e.g. cartilaginous fish), if seals eat some fish without consuming the head or if the hard parts are small or fragile and cannot be identified. Although some otoliths recovered may be from secondary prey, this source of bias is not thought to be important. Digestion and retention of otoliths in stomachs varies between prey species and recovered remains may not be representative of ingested prey. For example, larger and more robust otoliths or other hard parts may be retained in the stomach while small, fragile otoliths may be digested or pass through the digestive system more quickly. Generally, large, robust otoliths are more likely to be over-represented in relation to small otoliths causing bias. Finally, if prey are digested and move out of the stomach at different rates, highly-digested stomach contents may not reflect the total diet. The degree to which this is an issue when examining intestines is not clear. If adequate sampling is carried out, differences in retention times should not be a problem in scats.

1.3.1.3 Measurements of prey remains

All relevant prey remains should be recovered, correctly identified and measured to avoid bias. If the partial or complete digestion of otoliths is not accounted for in samples from stomachs, intestines and scats, then prey size will be underestimated and estimates of diet composition may be biased. If available, species-specific digestion coefficients (DC), ideally digestion-grade-specific, can be used to correct measurements. Alternatively, if only un-eroded otoliths are measured it can be assumed that their size is representative of all partially-eroded otoliths by species. However, the greater degree of erosion may be because the otoliths were originally smaller on average than un-eroded ones (i.e. retained longer in the stomach) which would create a bias towards larger estimates of fish length.

Otoliths may be completely digested during passage through the gut. If this phenomenon is not accounted for, the number of prey items eaten will be underestimated. Assuming that some otoliths of a particular species do remain, species-specific number correction factors (NCFs) can be used to correct samples. If stomach contents are highly digested, NCFs may also be appropriate although such stomach-specific correction factors have not been developed.

It is assumed that digestion coefficients and NCFs, which are estimated in laboratory studies, are appropriate to represent wild samples. However, DC and NCFs are only available from relatively few studies and for some species. Therefore, it must be assumed that correction factors can be applied to species that have not been examined. Erosion-grade-specific coefficients ensure a better extrapolation than single values because lab-based studies are unlikely to fully mimic what occurs in the wild.

1.3.2 Fatty acid analysis

The following points list the assumptions of using fatty acids to estimate diet the violation of which could introduce bias.

1.3.2.1 Prey species must have distinct fatty acids signatures

To date, most prey appear to have distinct fatty acid signatures; however, prey species without distinct signatures cannot be reliably estimated and either false-positive or false-negative results would occur. A large sample of prey needs to have been chemically analyzed to properly characterize the fatty acid composition of the prey and its within species variability. Prey not included in the model cannot be estimated. Therefore, it is important to adequately sample prey species from the ecosystem under study.

1.3.2.2 Calibration coefficients must be determined by experiment

Calibration coefficients are used to account for differential metabolism of prey fatty acids which influence their deposition in predator fat stores, such as blubber. Estimates of diet are sensitive to these coefficients and the best results are obtained from the use of species-specific coefficients if available. The use of the wrong coefficient may lead to errors in the estimated diet.

1.3.2.3 Fat content of prey species

Estimated diets are dependent on the estimated fat content of prey. Fat content determines the weighting given to different prey species. Variability in fat content should include seasonal changes in prey.

1.3.2.4 Estimating diet composition from quantitative fatty acid signature analysis (QFASA)

QFASA is a statistical model with the limitation that the number of prey species used in the model cannot exceed the number of fatty acids. Fatty acids derived solely or largely from diet are used in the model. The set of fatty acids selected can influence the estimated diet.

1.3.2.2 Integration time

Fatty acids integrate diets over a period of weeks or even months. This method provides an advantage in that it can indicate diets for seals that forage far away from sampling locations. However, it may also pose difficulties in estimating diets in specific small areas for highly mobile species such as seals, because the diet estimated from fatty acid may be an integration of feeding over an area larger than the one of interest.

1.3.3 Estimating population consumption

An energetic model is used to estimate daily calorific requirements of grey seals. The model results should be unbiased with respect to: sex and age differences in energy requirements; seasonal differences in energy requirements and energy densities of prey; estimates of seasonal distribution that incorporate potential sex and age differences; and, diets for each of the age, sex, spatial and seasonal components in the model. Estimates of population size should also be unbiased.

1.3.4 Uncertainty

To the extent possible, uncertainty in all components of the model should be taken into account when estimating total consumption The following points describe ways of quantifying uncertainty in estimates of grey seal diet and consumption:

- In estimating diet composition from a sample (scat or GI tract) parametric bootstrapping of digestion coefficients, NCFs and coefficients of allometric relationships between otolith size and prey size can be used.
- When many samples are available, non-parametric bootstrap re-sampling of samples (scat or GI tract) can be carried out in order to estimate sampling variability.

- Uncertainty in estimates of consumption by individual animals can be estimated from parametric bootstrapping of the parameters of the energetic model to estimate daily calorific requirements.
- Where diet estimates are used to calculate the food requirements of the whole seal population, uncertainty in estimates of population size must also be taken into account. This may involve considering alternative population models, model selection, and uncertainties in the parameters of these models.

1.4 What is the temporal and spatial overlap of grey seals and cod and what are possible sources of bias and uncertainty in estimates of the seasonal distribution of the grey seal and cod populations?

Temporal and spatial overlap between grey seals and Atlantic cod, and other potential prey, provide insight into the opportunity for predation, but in themselves such overlap provides no evidence that predation has occurred. Locations from satellite telemetry data were used to identify where grey seals overlapped in their distribution with different prey species. The fish distribution data were obtained from synoptic groundfish surveys.

In the southern Gulf of St. Lawrence, grey seals using haul-out sites along the coast of northern New Brunswick spent 85% of their time within 50 km of the coast. In August, grey seals were estimated to overlap more with small cod, large winter flounder, and less with sand lance at distances of 10-30 km compared 50-100 km. In September, the probability of co-occurrence between seals and medium cod, large cod, and winter flounder was higher at a distance greater than 50 km from the coast than between 30-50 km from the coast.

Grey seals and many commercial fish species leave the Gulf to overwinter in the Cabot Strait area. Satellite data indicate that grey seals were concentrated in areas of less than 200 m deep, to the west of the Laurentian channel although there were differences in the distribution of males and females. In early winter, males concentrated their foraging effort around St. Paul Island where they overlapped with medium and large cod, and herring. In late winter, the distribution of foraging males shifted to the southeast part of the 4Vn area where the abundance of large turbot, medium cod and small winter flounder was less.

As observed in the southern Gulf during the summer, the concentration and therefore presumed foraging effort of seals decreased with distance from Sable Island. Fish species that overlapped with the spatial distribution of seals at close proximity to Sable Island differed from those that overlapped with presumed foraging patches of seals further offshore. In July, female grey seals co-occurred with medium size cod and small silver hake, while no significant co-occurrence with cod was observed among males. Co-occurrence of females decreased with an increased abundance of small silver hake during March, contrasting with that observed in July. Also during March, the probability of co-occurrence between male seals and medium (pre-2000) and large cod (post 2000) was significant, but this association declined gradually with distance from the Island.

There were strong herd, sex and stage-specific differences in grey seal movements. Juvenile and adult male grey seals from the Gulf herd overlapped most with southern Gulf cod, with a mean monthly average of 16% of individuals overlapping with cod. Overlap between seals from Sable Island and 4T cod was smaller (<1%).

1.4.1 Potential bias and uncertainty

Movement patterns of seals are inferred from a small number of tagged seals, particularly given the need to account for sex and stage-specific differences in grey seal movements. Because of this low sample size, there is considerable uncertainty in the inferred distribution of seals. Unfortunately, the sample size of tagged seals is especially low during some periods when cod are aggregated (winter, spawning, migration).

There are also likely spatial biases for seal tagging in the Gulf of St. Lawrence with respect to haul-out sites that may affect population-level inferences on grey seal distribution. Also, there has been no satellite tagging of grey seals that breed on the eastern Shore of Nova Scotia or that spend the summer in areas such as Newfoundland. Thus, movements of grey seals in these areas are therefore not well characterized. However, outside of the Gulf the number of seals using these areas represent a small fraction of the population and therefore any resulting bias is small.

Overlap analyses in Cabot Strait suffer from having no current survey information on the winter distribution of cod and other fish species. More generally, in all areas, estimates of the spatial abundance of fish are available at rather coarse scales which may not be relevant to the scales used by seals in making decisions on what prey to consume. In addition, estimates of pelagic fish abundance and distribution from bottom-trawl surveys are biased by trends in availability to the trawl, thus biasing their abundance trends relative to cod and other groundfish.

1.5 What are the estimated rates and trends in grey seal predation mortality on cod and to what extent can these estimates explain size-specific natural mortality of cod?

1.5.1 Southern Gulf of St. Lawrence

In 4T, a predator-prey model, consisting of three components (a seal consumption model, a fish demographic and energy model, and seal-fish spatial/temporal overlap model) was used to examine the impacts of grey seals on cod. Due to large spatial and seasonal gaps in the distribution of diet samples (see section 1.6), it was difficult to quantify the consumption of southern GSL cod by grey seals. Different assumptions to fill these data gaps produced very different estimates of annual cod consumption, ranging from 4,500 to 20,000 t for recent years. For the large (>35 cm) cod with high natural mortality, estimates of their consumption accounted for about 10 to 50% of total natural mortality in recent years, depending on the assumptions used to fill data gaps.

Given the difficulties in quantifying consumption of southern GSL cod by grey seals due to the gaps in the diet sampling, the plausibility that seal predation could account for cod M was also examined using inverse modeling. This approach calculated how much cod could be consumed by seals given the data on the spatial overlap between seals and cod and the energy requirements of seals. As with any model, the degree to which the results reflect reality depends on the extent to which model assumptions are met. Using this approach, predation can likely explain up to 30-50% of natural mortality of adult (5+) cod even if these cod comprise a small percentage of grey seal diets (<15%). If seals consume some of these fish only partially, by selectively feeding on soft tissues, the plausibility of predation accounting for a particular percentage of M increases substantially.

Inverse modeling was also used to examine potential consumption of white hake and winter skate by grey seals. In the simulation, consumption of whole age 3+ white hake by grey seals explained approximately 45% and 25% of M with respective probabilities of 0.5 and 0.95. The 0.5 probability was achieved with white hake comprising around 8% of the diet of overlapping seals and 2.5% and <0.5% of the respective mean diets of the Gulf and Sable Island populations. Predation of white hake was heavily constrained by considerable spatial overlap with adult cod and the assumption of a proportional functional response. If white hake comprised 13% and 4% of the diets of overlapping and Gulf population grey seals, then it would account for all of the natural mortality above the level of around 0.2. All of winter skate M was explained by predation in every simulation undertaken. To explain all natural mortality, adult winter skate must comprise no more than 0.7% of the diet of the grey seals that overlap spatially with them, and no more than 0.2% and <0.05% of the respective mean diets of the Gulf and Sable Island populations.

1.5.2 Eastern Scotian Shelf

Most models estimated that grey seal predation accounted for a small portion of the total mortality of cod on the eastern Scotian Shelf (4VsW). Because of uncertainty in both the percentage of cod in the grey seal diet and the size of cod eaten, a number of scenarios were explored, four of which were: 1) 7% cod in seal diet and age distribution of cod eaten estimated from scats; 2) 7% cod in seal diet and age distribution of cod eaten shifted to older cod using data on the size of cod caught in the annual research vessel (RV) survey; 3) 2% cod in seal diet as indicated by analyses of fatty acids and age distribution of cod eaten estimated from scats; and, 4) 2% cod in seal diet from fatty acids and age distribution of cod eaten shifted to older cod using RV survey data. The estimated pattern of seal predation mortality differed among scenarios (Figure 9). In 2009, the model results indicate that grey seals imposed a low level of instantaneous mortality (scenarios 1-4, respectively: 0.013, 0.021, 0.087, 0.166), which ranges from approximately 2 to 22% of the total mortality.

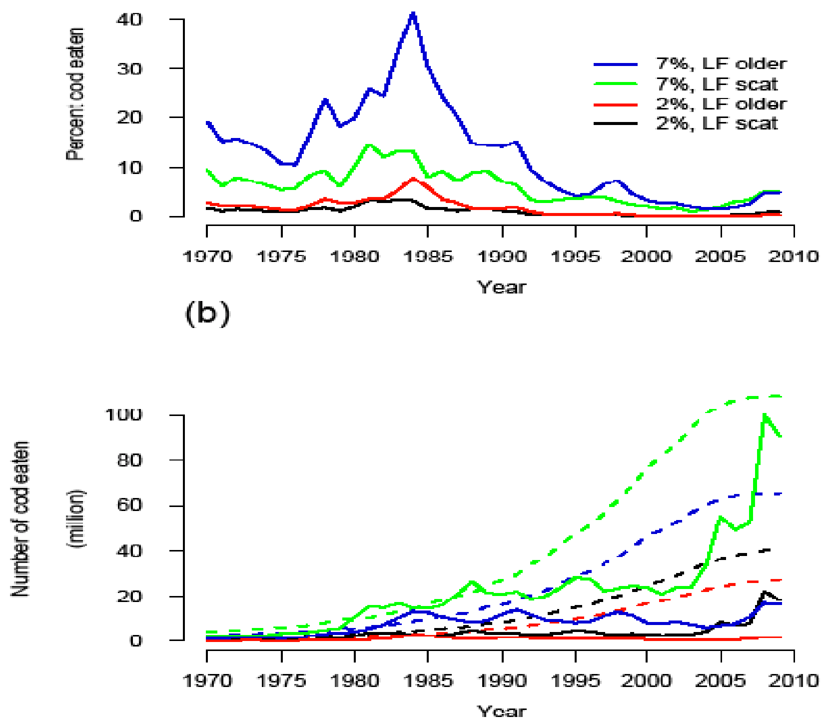

Figure 9. Trends in seal predation mortality under 4 different scenarios. Annual mortality rate for cod is plotted against year. The colours of the curves represent the different assumptions used in calculating mortality, which are: 7% cod in seal diet and age distribution of cod eaten estimated from scats (green curve); 7% cod in seal diet and age distribution of cod eaten shifted to older cod using data on the size of cod caught in the annual research vessel survey (blue curve); 2% cod in seal diet from fatty acids and age distribution of cod eaten estimated from scats (black curve); and, 2% cod in seal diet from fatty acids and age distribution of cod eaten shifted to older cod using RV survey data (red curve). Solid lines are for the functional response models and the dashed lines represent the constant ration models. The reference year for 2% and 7% scenarios is 1993.

These models assumed that cod total mortality has remained high (0.6 – 0.8) since the mid-1990s.

Another set of models estimated that total cod mortality has declined since the early 2000s to about 0.2 in 2009. Total mortality in the DFO summer survey also declined during this period. The results suggest that a major component of natural mortality of cod since the mid-1990s has been due to seal predation, if the proportion of cod in the diet is assumed to be twice the value estimated from scat samples. The range in model scenarios highlights the uncertainty in understanding the cod-grey seal interaction in 4VsW.

1.6 What is the sensitivity of the results in topic 1.5 to the possible biases and uncertainties identified in 1.3 and 1.4?

The estimates of mortality on southern Gulf cod are highly dependent upon assumptions about diet, size of fish taken and the seasonal distribution of cod. Unfortunately, there are spatial and seasonal gaps in the distribution of diet samples in 4T. Samples are predominantly from nearshore areas, from late spring to fall, and represent foraging in areas where cod are not abundant and where cod tend to be smaller (<35 cm). Satellite tracking indicates that seals forage in other areas where large cod are more abundant. Diet sampling in such an area, during a time of spatial aggregation in both small and large cod, indicates a higher proportion of cod in the diet and that the majority (58%) of cod consumed are large cod (>35+ cm). Existing diet sampling cannot account for possible partial consumption of prey if otoliths are not ingested (‘belly-biting’). Because of the data gaps, it is difficult to reliably quantify the consumption of cod by seals. Therefore, different approaches were taken to fill the data gaps, and depending on the approach, estimated consumption of large cod accounted for 15% to 50% of the natural mortality of adult cod in this stock.

In the extrapolation of diet composition to estimated consumption for the southern Gulf, it is necessary to assume that the current spatial distribution of southern Gulf cod in months other than August and September is the same as that seen during surveys that took place 15-20 years ago. Data from sentinel fisheries and limited commercial fishing in the area suggest that there has not been a major change in distribution since the earlier surveys although these sources are also limited in time and space. Thus, current distribution is poorly known during some months, such as during cod migration. Furthermore, monthly changes in distribution are not well defined due to changes in the timing of spring and fall migrations.

There is a large uncertainty in the consumption of cod by grey seals on the eastern Scotian Shelf. The uncertainty in the number of seals foraging on the eastern Scotian Shelf was small (CV 6%) compared with the uncertainty associated with energy requirements of grey seals (CV 30%) and with the uncertainty in the percentage of cod in the diet (CV 150%). Uncertainties in the abundance and total mortality of cod are also large and have a considerable impact on the level of predation mortality imposed by grey seals. How the consumption of cod by grey seals responds to changes in cod abundance is also highly uncertain. Estimates of natural mortality due to grey seal predation are very sensitive to uncertainty in this functional response. Uncertainty in the functional response is also a source of uncertainty in seal-cod interactions elsewhere, including the southern Gulf of St, Lawrence.

2. Indirect evidence for cod consumption by grey seals

2.1 What are the trends in natural mortality in cod and other relevant fish species in each ecosystem?

2.1.1 Southern Gulf of St. Lawrence

Population models indicate that the trend in natural mortality (M) differs between young (ages 2-4 years) and older (ages 5+ years) cod in the southern GSL population (Figure 10). Using data from the 1970s and earlier, previous studies estimated that M of older cod was about 0.1. Estimated M of 5+ cod increased slightly (by about 0.1-0.2) in the 1980s. A sharp increase in estimated M occurred between the late 1980s and the early 1990s. Estimated M of 5+ cod has remained high (near 0.6) since then. In contrast, estimated M of younger cod declined between the late 1980s and the early 1990s, and has remained relatively low since then.

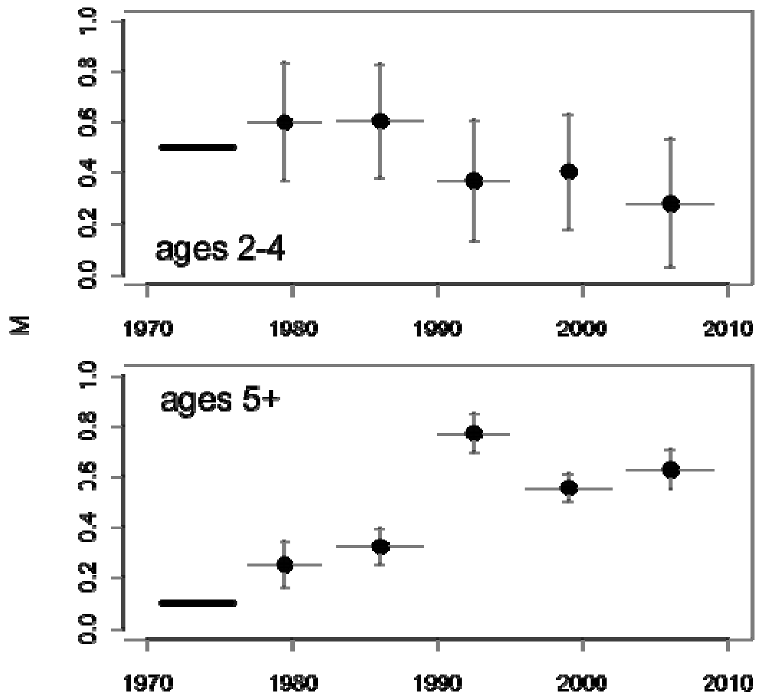

Figure 10. The instantaneous rate of natural mortality (M) of southern GSL cod aged 2-4 or 5+ years. Heavy horizontal lines are assumed values. Light horizontal lines indicate the time period for each estimated value (circles). Vertical lines are ± 2SE.

Similar trends in natural mortality appear to be widespread throughout the southern GSL fish community, with mortality increasing to high levels in the 1990s and 2000s for large fish and declining to low levels for smaller fish. Total mortality of adult white hake increased throughout the 1990s, reaching extremely high levels in the 2000s (Figure 11). Mortality is now so high that few hake live to an age of 7 years; no hake older than 7 years have been caught since 2000, whereas hake as old as 12-15 years were caught in surveys in the mid 1980s. The directed fishery for white hake has been closed since 1995, and fishing mortality has been at a very low level since then (Figure 11). Thus, the current high mortality of adult white hake is due to high natural mortality, with estimated M increasing from about 0.1-0.2 prior to 1985 to about 2.0 during the 2000s. In contrast to adults, mortality of juvenile white hake appears to have declined to a low level based on the high recruitment rates observed in the 2000s.

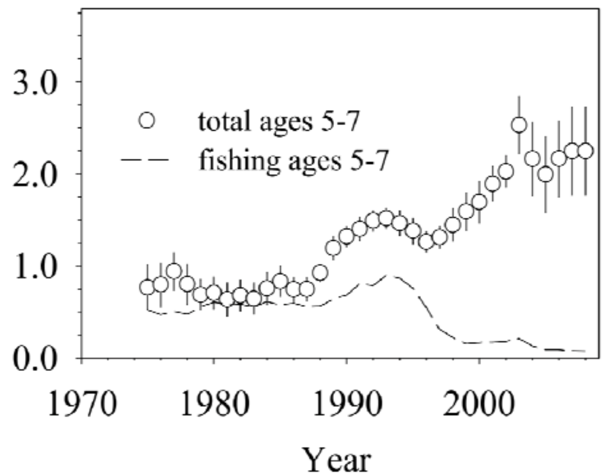

Figure 11. Total mortality of adult white hake (ages 5-7 years) estimated in moving 7-yr windows, and estimated fishing mortality for the same periods. Vertical lines are ± 2SE.

For all three skate species common in the southern GSL (winter, thorny and smooth skate), population models indicate that adult mortality increased to a very high level in the 1990s and 2000s whereas juvenile mortality decreased to low levels during this period (Figure 12). There is no directed fishery for skates in the southern GSL, and overall fishing effort declined to a very low level in this area in the 1990s and 2000s. This suggests that the increase in adult mortality reflects an increase in natural mortality. This is confirmed for winter skate by population models incorporating estimates of winter skate bycatch in fisheries for other groundfish. These models indicate that fishing mortality of adult winter skate declined to a low level in the 1990s whereas their natural mortality was at a high level during this period. Population models also indicate that M of American plaice (ages 4+ years) was at a high level (>0.5) throughout the 1990s and 2000s.

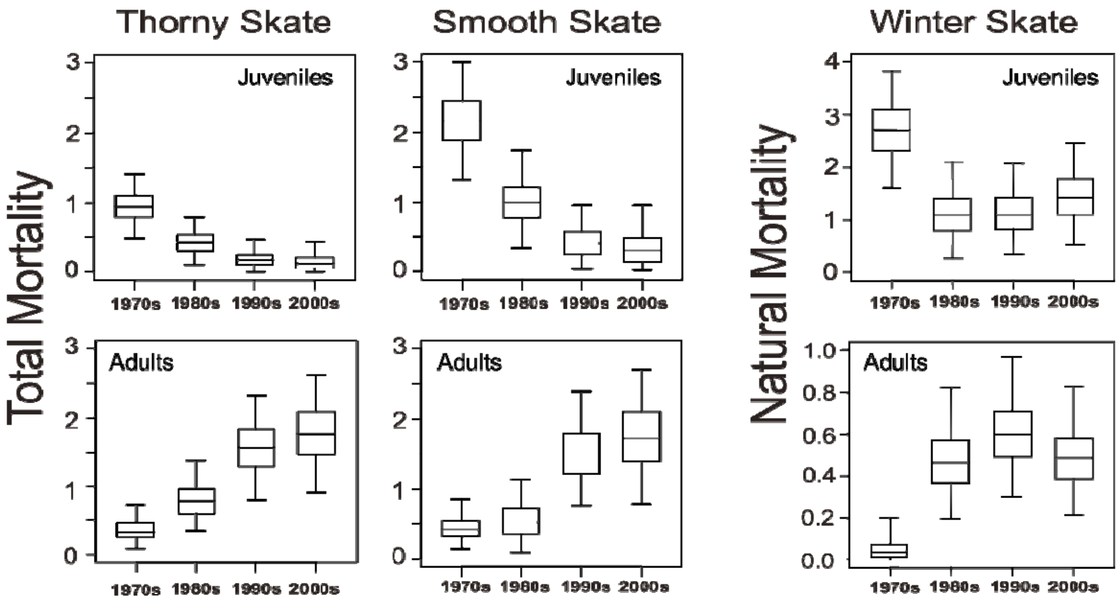

Figure 12. Decadal variation in estimated total mortality of juvenile and adult thorny and smooth skate, and natural mortality of juvenile and adult winter skate in the southern Gulf of St. Lawrence. Juveniles are defined as skates less than 54 cm (thorny skate), 48 cm (smooth skate) or 45 cm (winter skate) in total length. Box plots show the 2.5th, 25th, 50th, 75th and 97.5th percentiles of the posterior distributions for mortality parameters.

Changes in the species composition within the southern GSL fish community are consistent with an increase in mortality for large fish and a decrease in mortality for small fish. Large-bodied species generally declined to a low level of abundance in the early 1990s and have remained at low abundance since then. In contrast, small-bodied species were generally at high levels of abundance in the mid to late 1990s and the 2000s. Within large-bodied species, abundance has generally declined to low levels for large individuals but has increased or remained relatively high for small individuals. At the community level, abundance of small fish increased to a high level in the 2000s whereas abundance of large fish has been declining since the early 1990s reaching record low levels in the most recent period (Figure 13).

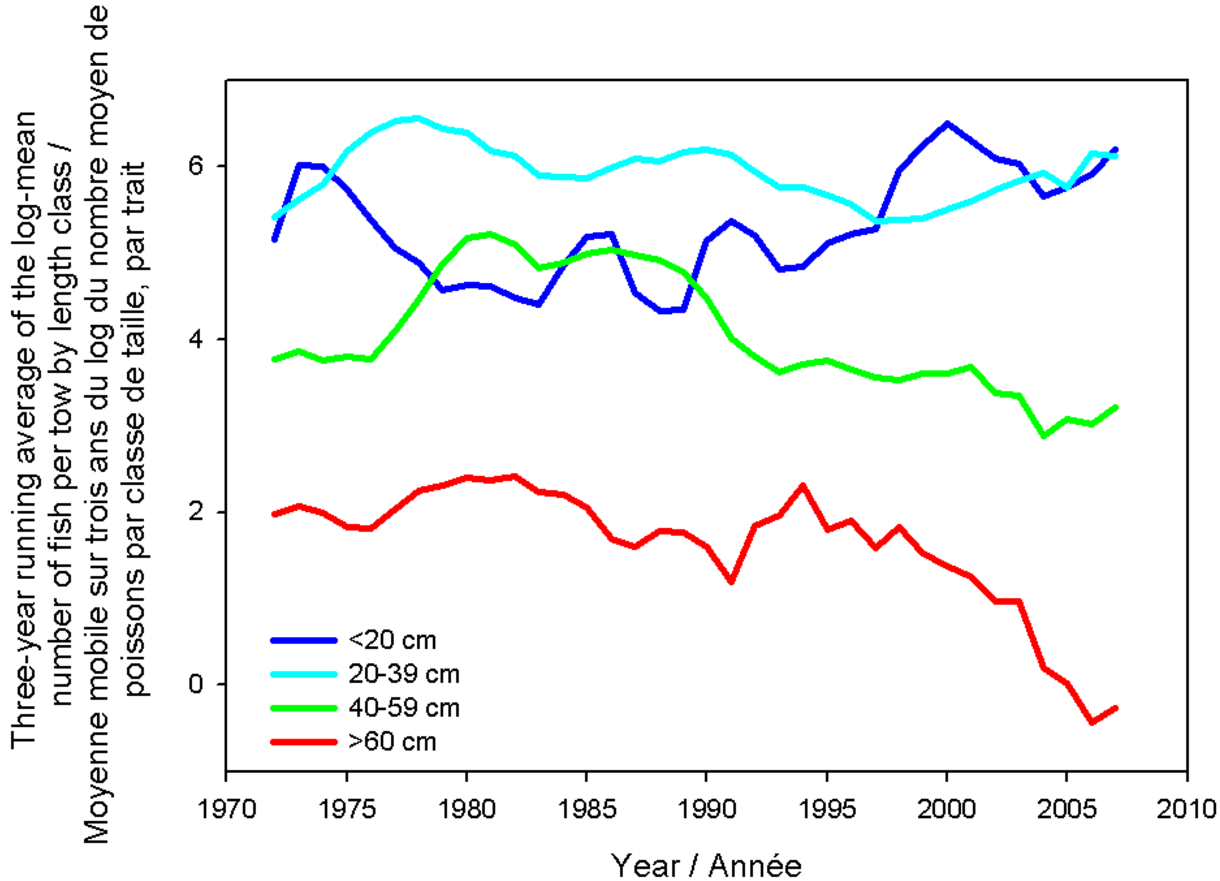

Figure 13. Three-year running average of abundance (log-transformed mean number per tow) of southern GSL fish in four size categories (irrespective of species) in the annual survey.

The improved survival of small fish in the 1990s and 2000s is consistent with release from predation following the sharp declines in the abundance of large demersal fish in the late 1980s and early 1990s. Declines in the abundance of larger fish may be related to fishing and predation by grey seals. The overall intensity of fishing on groundfish species increased in the late 1980s and early 1990s, declined sharply with the closure of the cod fishery in 1993, and has been at a very low level since then. Decreases in the abundance of larger fish coincident with the increase in fishing intensity during the late 1980s and early 1990s is consistent with a direct effect of fishing, though failure of those populations to recover despite the recent period of little fishing is not. Species that have failed to recover are all known grey seal prey.

2.1.2 Eastern Scotian Shelf

The 4VsW cod stock fell rapidly in the late 1980s leading to collapse, followed by fishery closure in 1993. Stock biomass remained low for over a decade but has recently shown an increase and improved survivorship of young cod. Since the beginning of the time series (1950s), cod has exhibited strong reductions in length at 50% maturity. A similar trend has been observed for haddock. The changes in maturity for both species seem to have preceded the observed changes seen in natural mortality and growth.

2.1.3 Southwestern Scotian Shelf

Survey data indicate there was in increase in natural mortality for large cod (age 4+) in the mid-1990's. Modeling of this change indicated that there was an increase of M from 0.2 to 0.7 in 1996. A similar change in natural mortality (from 0.2 to 0.5) has been estimated for large cod in Georges Bank. Trends in natural mortality have not been formally investigated for other fish species in 4X; however, exploratory analyses for pollock also suggest an increase in natural mortality in the mid-1990s.

The major predators for cod are other cod. Seal abundance has increased in 4X. It seems likely that grey seals contribute to the natural mortality of 4X cod but the extent of their interaction remains unclear as there are no estimates of grey seal diets in 4X.

2.2 What are the alternative hypotheses for causes of elevated natural mortality for the species for which it is observed (cod and others)?

The alternative hypotheses that were examined for 4T cod were: 1) unreported catch, 2) emigration, 3) disease, 4) contaminants, 5) poor fish condition, 6) life-history change (increased mortality cost to reproduction due to maturation at an earlier age or smaller size and, evolution of early senescence), 7) parasites, and 8) predator pit due to predation by grey seals, harp seals and other predators.

2.3 Based on a weight-of-evidence approach, which of these hypotheses are most likely to contribute to the observed increases in natural mortality?

A weight of evidence approach was used to examine a suite of alternate hypotheses for the causes of the elevated natural mortality of older (ages 5+ yr) southern Gulf cod. The other cod stocks were not examined.

2.3.1 Unreported catch

Estimated M incorporates all sources of mortality other than mortality due to reported fishery catch. Thus, in addition to mortality due to natural causes, M would include mortality due to any unreported catch. It is thought that catch misreporting increased as the cod fishery intensified in the late 1980s and early 1990s, and recent analyses have estimated that unreported catch was substantial during this period. Thus, a significant portion of the losses attributed to M in the late 1980s and early 1990s may instead be due to unreported catch.

Fishing effort for groundfish dropped dramatically in the southern Gulf in the early 1990s, and has remained very low since then. In addition, catch surveillance increased substantially, and management measures were taken to reduce cod bycatch in other fisheries. By-catch of cod in non-groundfish fisheries in the southern GSL is very low. Thus, unreported catch of cod must be very low since the mid 1990s. Even if the true catch was twice the reported catch, which is very unlikely, the effect on estimates of M would be negligible. This hypothesis can be rejected for the recent period (mid 1990s to present).

2.3.2 Emigration

This hypothesis supposes that, instead of dying, the missing fish have emigrated to another area. The stocks neighbouring the southern Gulf stock are the northern Gulf stock (3Pn4RS), the 4Vn stock, and the 4VsW stock. Southern GSL cod can be distinguished from cod in these other stocks by their small size-at-age and low vertebral number. Based on tagging studies and a stock mixing study conducted in the mid 1990s, emigration of significant quantities of southern GSL cod across the Laurentian Channel to the northern GSL stock can be ruled out. Extensions of the annual September survey of 4T into 4Vn in 1994, 1995 and 2006 determined that only a negligible portion of the southern GSL stock (<3%) occurred in 4Vn in those years. The estimated number of 5+ cod lost to M each year in the southern GSL stock is about four times an estimate of the number of 5+ fish in the 4VsW stock. Thus, the influx of a substantial portion of the fish thought to be lost to M in the southern GSL stock would have been noticed in assessments of the 4VsW stock. M is also estimated to be very high in the 4VsW stock. This would not be expected if abundance at older ages in the 4VsW stock was being supplemented by immigration from 4T. This hypothesis can be rejected.

2.3.3 Disease

There are no confirmed detections of bacterial or viral pathogens in cod screened from the southern Gulf, and no reports of sick or diseased cod from fish harvesters or processors, or from samplers on the annual survey (who have examined over 31000 individual cod since 1995). While data are limited, there is no evidence to support the hypothesis that disease is a major contributor to the elevated M.

2.3.4 Contaminants

Levels of contaminants are very low in the Gulf outside of the St. Lawrence Estuary. The Gulf is less contaminated than other semi-enclosed seas such as the Baltic and North Seas. Contaminant concentrations are much lower in cod from the Gulf than in those from the Baltic Sea. Despite their higher contaminant loads, M does not appear to be elevated in Baltic Sea cod; assessments of Baltic Sea cod use an M of 0.2. North Sea cod stock assessments do use an increasing trend in M for older ages (3-6 years), but the rationale for this increase in M is estimated increases in mortality due to seal predation, not contaminant-induced mortality. The evidence does not support the hypothesis that contaminant-induced mortality is a significant component of elevated M.

2.3.5 Poor fish condition

Cod in the southern Gulf exhibit a marked seasonal cycle in condition, with lowest condition in the spring, following the overwintering period when little feeding occurs. It has been proposed that poor fish condition in spring, resulting from harsh (cold) environmental conditions, contributed to increased M in the northern Gulf cod stock in the early 1990s. Based on seasonal monitoring conducted since 1991, southern Gulf cod are in better condition in spring than was reported for the northern Gulf stock in the early to mid 1990s. The proportion of cod at increased risk of mortality due to poor condition was much lower in the southern Gulf stock than in the northern Gulf stock in spring in the early 1990s. Condition of southern Gulf cod in spring increased substantially in the early 2000s and has been at a relatively high level since then. Based on long-term monitoring (in September, 1971-2010), condition of southern Gulf cod was lowest in the late 1970s to mid 1980s and was near the long-term average throughout the 1990s and 2000s.

Bottom water temperature in the southern Gulf was below normal in the early to mid 1990s, but has since warmed and has been above average throughout the 2000s. In contrast, the ambient temperature of southern Gulf cod (i.e., the bottom temperature in areas occupied by cod) in September (during the feeding season) was lowest in the early to mid 1980s and has been near average levels throughout the 1990s and 2000s.

Based on the data on the condition of cod and the trends in environmental conditions, the hypothesis that poor fish condition is an important cause of the high M of southern Gulf cod can be rejected, at least for the 2000s. Although there is no direct evidence, poor fish condition may have been a more important cause of M in the early to mid 1980s, when both the ambient temperature of cod and their condition were relatively low in September, or in the early 1990s, when bottom water temperature was below normal and cod condition in spring was lower than the levels observed in the 2000s.

2.3.6 Life history change

2.3.6.1 Early maturation

In most situations, a decline in age and size at maturation is the expected evolutionary response to the increase in mortality that is imposed by fishing. Survival costs to reproduction are expected to increase as age and size at maturity decline. This has led to suggestions that fisheries-induced declines in age and size at maturation may contribute to high M.

Age and length at maturity declined dramatically in cohorts of southern Gulf cod produced in the 1950s and 1960s but have changed little since then. Contrary to the predictions of this hypothesis, M remained low in the 1970s following the sharp decline in length at maturity, and subsequent increases in M occurred over a period when size at maturity changed little (Figure 14). Costs to reproduction may be more evident under stressful physiological or ecological conditions. Cod condition was at a low level in the early to mid 1980s. Thus, interacting effects of early maturation and harsh conditions may contribute to the increase in M observed then. If so, a decline in M due to this cause would be expected when conditions improved. Because cod condition has been at a high level throughout the 2000s, an interactive effect of early maturation and harsh conditions does not appear to be an important factor in the current high level of M.

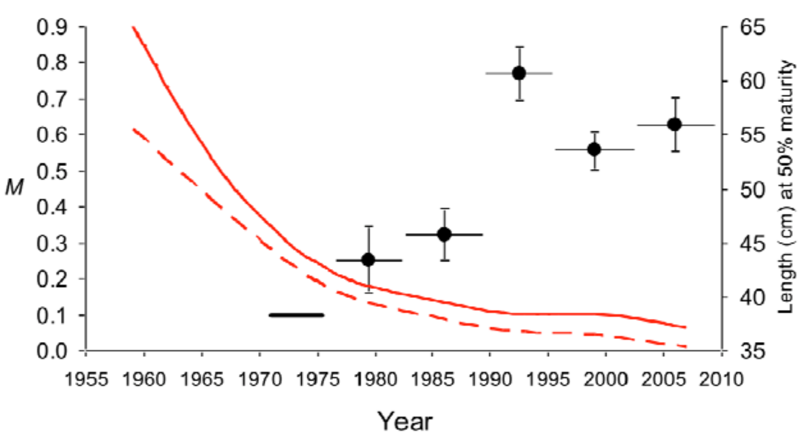

Figure 14. Trends in length at 50% maturity of female (solid line) and male (dashed line) southern Gulf cod and assumed (black line) and estimated (circles) M of 5+ cod.

2.3.6.2 Early senescence

A hypothetical effect of high mortality is the evolution of earlier or more rapid senescence, though some life-history theories yield alternate predictions. This hypothesis is not supported as a cause of the high M of southern GSL cod. There is no indication of a decrease in reproductive investment in old cod, as would be expected in senescent individuals. Furthermore, both early senescence and early maturation can be rejected as the main cause of the current high M because they would be expected to evolve only if mortality were high due to some external factor like fishing or predation, and would not evolve if they themselves were the main cause of this high mortality.

2.3.7 Parasites

Relationships between parasite infection and fish condition were examined in about 4000 southern Gulf cod. Results indicated that any negative effect of parasite infection on cod condition was weak relative to other factors affecting condition. Because sub-lethal effects should become apparent before lethal effects, these results suggest that parasite-induced mortality related to direct damage to organs and tissues or depletion of energy reserves is small in this population. However, it is possible that parasite infection may contribute to elevated M by increasing the susceptibility of heavily infected fish to predators but this hypothesis has not been examined.

2.3.8 Predation

The sharp increase in M of 5+ cod as their abundance collapsed in the late 1980s and early 1990s is consistent with the hypothesis that they entered a “predator pit” as their abundance declined. Given the diets, distributions and abundances of potential predators of large cod, grey seals are most likely to be their predominant predator. The available diet information indicates that grey seals consume large cod (>35-40 cm in length), that they appear to show positive selection for large cod over small cod, and that when foraging in the vicinity of overwintering cod aggregations, large cod can comprise a significant component of the diet. Due to data gaps, the quantity of large cod consumed by grey seals is uncertain. However, under some assumptions for filling data gaps, consumption estimates could account for a high proportion of the M of 5+ cod.

It might be argued that a close positive correlation should be observed between cod M and grey seal abundance if grey seal predation is an important cause of high M. M was at a high level throughout the 1990s and 2000s, and did not increase with increasing seal abundance during this period. A number of factors may contribute to this apparent inconsistency. First, grey seal predation may have accounted for a lower proportion of M in the 1990s than in the 2000s. For example, it is likely that unreported catch accounted for a substantial portion of estimated M in the early to mid 1990s, but was a negligible component of M in more recent years. Secondly, a simple linear relationship between prey mortality and predator abundance may not occur for a number of reasons, such as prey switching when abundance of the focal prey declines to very low levels or abundance of alternate prey increases. However, there is no evidence that prey switching has or has not occurred.

There is also indirect (correlative) evidence that grey seal predation plays a role in the elevated M of adult cod and other large demersal fish. Levels of cod M and grey seal abundance are correlated among ecosystems. Within the southern Gulf ecosystem, increased grey seal abundance is also correlated with increased mortality of several large demersal fishes in addition to cod (e.g., white hake and three skate species). Changes in species composition of the southern Gulf fish community is associated with a measure of the susceptibility of those species to grey seal predation. As grey seal abundance increased over the 1971-2005 period, the community shifted from one dominated by species common in grey seal diets to one dominated by species rare in grey seal diets. Shifts in the spatial distribution of large cod also suggest that grey seals are an important predator of these cod; as grey seal abundance increased from the 1970s to the 2000s, the distribution of large cod has shifted away from areas where the risk of predation by grey seals is high.

The hypothesis most strongly supported by the weight of evidence is that predation by grey seals is an important component of the current high M of 5+ southern Gulf cod. Other factors, such as unreported catch and early maturation interacting with poor fish condition, may have contributed to elevated M in earlier periods but do not appear to have been important factors in the 2000s.

In the analyses presented above, each hypothesis advanced to account for the high M in older 4TVn cod is considered alone. When considered alone, none of these, excepting the grey seal predation hypothesis, is thought to be an important factor. However, the cumulative impact of multiple small effects has not been considered. While there are indications that some factors may have been more important in the past (unreported catch in the early 1990s, early maturation combined with poor condition in the early to mid 1980s), there are no indications that any of these factors contribute to the high M in the 2000s. This suggests that a consideration of cumulative impacts with respect to high M would not significantly change conclusions about the importance of grey seal predation.

3. Minimum decrease in natural mortality to restore cod populations to reference levels

3.1 Southern Gulf of St. Lawrence cod - 4TVn

A conservation limit reference point (LRP) has been established for the 4TVn stock, based on the spawning stock biomass (SSB) below which the probability of poor recruitment is high. The LRP is estimated to be 80,000 t. Current SSB is estimated to be well below this level. Population projections were conducted to determine the reduction in 5+ M required to restore SSB to the LRP, assuming that other components of productivity remain at the current levels. These projections took into account uncertainty in estimated abundance-at-age in 2010 and in estimated natural mortality, as well as the variability in weight-at-age and recruitment rate observed over the past 20 years. Fishery removals were assumed to be zero in these projections.

At the current levels of M and other components of productivity, SSB is projected to decline exponentially, reaching levels near extirpation (SSB<1000 t) in about 40-50 years (Figure 15). In order to have a high probability (70%) of SSB increasing to the LRP within 20 years, 5+ M would have to decrease to 0.4 or lower if other components of productivity remain unchanged.

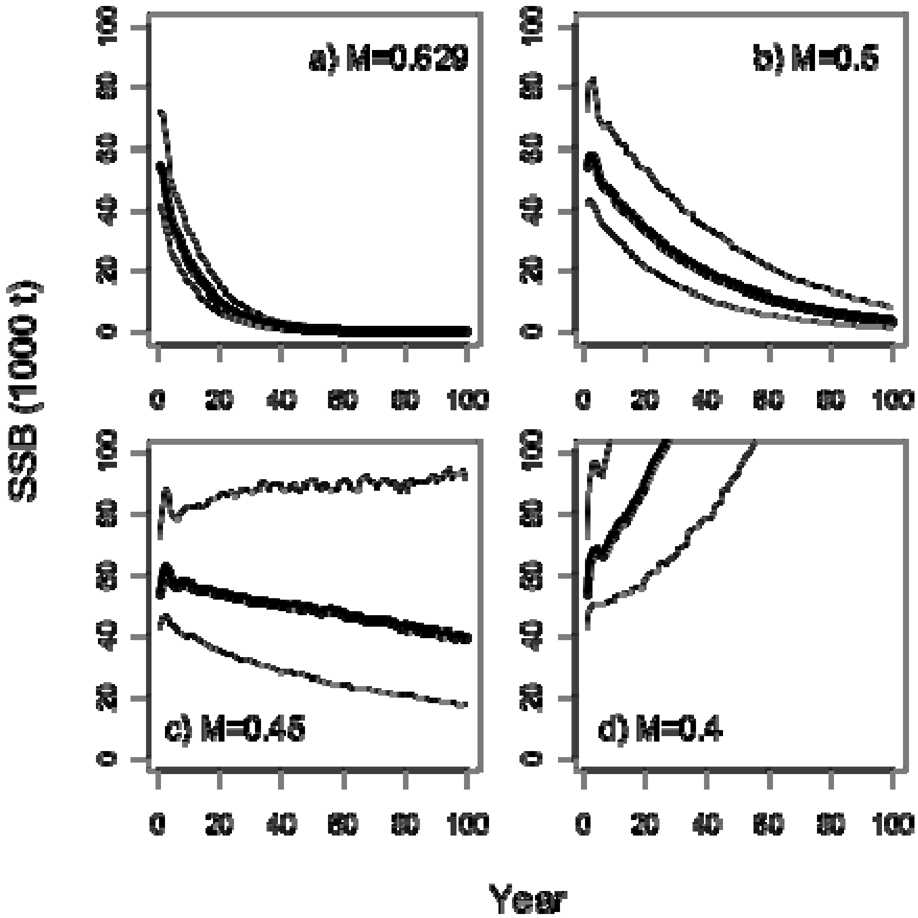

Figure 15. Projected SSB of southern Gulf cod at 4 levels of M for cod aged 5 years and older. Heavy line is the median projection and light lines are the 2.5th and 97.5th percentiles.

3.2 Eastern Scotian Shelf cod- 4VsW

Production is a combination of survivorship, growth and recruitment. Instantaneous growth rate is approximately 0.9 for young cod (<35cm) and approximately 0.4 for old cod (>35cm). Natural mortality for young cod has dropped by about a factor of two. This and the good growth have resulted in increased biomass in recent years. Cod recruitment remains low compared to the 1970s and early 1980s lessening the increase in biomass. Thus, minimum reductions in M would be required to restore this cod population to its reference level.

4. Changes in grey seal abundance, distribution and ecology

4.1 What factors may have played a role in any increased impact of grey seals on fish prey in general and/or cod in particular? Include a historical review of changes in the ecology, distribution and natural predators of grey seals.

Although rare during most of the early part of the last century, grey seals were once abundant enough to be hunted by indigenous tribes and by early European explorers. Grey seals have inhabited the northwestern Atlantic for millennia. Archeological data in the Quoddy region of the Bay of Fundy reveal grey seal bones dating from 2200–350 yr BP and further south, grey seals have been found from about 4000–400 yr BP at archeological sites in Maine and Massachusetts. Although historical abundance of grey seals is not well understood, the first quantitative estimates of grey seal abundance on Sable Island were of several hundred individuals in the mid-1800s. The current population size is the highest observed in the past two centuries.

Hunting can account for the rarity of grey seals for the better part of a century, prior to the 1960s. But why the population began to increase in the early 1960s is not well understood. One hypothesis is that the increase in the size of the grey seal population during the 1960s might have been attributed to reduced shark predation caused by a decrease in shark populations as a result of overfishing and bycatch in the swordfish and other fisheries.

Presumably because of their large size, grey seals have few predators in eastern Canada. Killer whales (*Orcinus orca*) and the walrus (*Odobenus rosmarus*) are known predators of pinnipeds and also certainly would have taken grey seals historically. Walrus went extinct long ago and given killer whale numbers and distribution, it seems unlikely that a reduction in killer whale predation on grey seals contributed to the increase in the grey seal population in the southern Gulf of St. Lawrence and on the Scotian Shelf. Shark species that might be considered or are known predators of grey seals include the white shark (*Carcharodon carcharias*), blue shark (*Prionace glauca*) and probably shortfin mako shark (*Isurus oxyrinchus*) and Greenland shark (*Somniosus microcephalus*). Potential shark predators have declined in abundance, but there are few data on the diet of potentially the most important predator, white sharks. Although release from shark predation may have played a role, admittedly scant data suggest this role was minor.

Perhaps more important was the change in the harbour seal bounty system in 1949 when the presentation of jaws became mandatory, which resulted in a reduction of hunting effort on grey seals and a corresponding increase in their survival. Construction of the Canso Causeway in 1955 resulted in an increase in the area and stability of ice habitat in St George's Bay used by grey seals for rearing offspring. Both of these factors should have had a positive impact on the productivity of grey seals. Changes in ecosystem structure may have also contributed to the growth of the population by providing more abundant high quality food.

4.2 Are any of these factors amenable to management actions, including population control actions?

As suggested in part 4.1, a number of factors have presumably contributed to the increase in the size of the grey seal population in eastern Canada over the past half century. However, the importance of these factors is poorly understood. Ecosystem changes (predator and food abundance) that may have favoured an increase in grey seal abundance are to some extent amenable to management actions in so far as we chose to modify human impacts on those ecosystems. Similarly, some aspects of habitat use and quality could be affected by management actions, but others, such as the availability of ice-breeding habitat and prey availability may be more strongly influenced by climate variability and trends. Without clear evidence for the influence of a factor on the rate of grey seal population growth, any management action other than direct control of population numbers (either through culling or contraception) would be difficult if not impossible to evaluate with respect to its effect on the population.

5. Grey seals reduction scenarios to restore cod populations

- Considering if grey seal predation is a factor in M, what would be the minimum reduction in grey seals necessary to be 50% certain of attaining a detectable increase in productivity to the level that the population will increase in the absence of fishing (if this were the only management measure taken)?
- Given the data and different assumptions about the diet of grey seals, what might be the consequences of 10%, 20% and 40% reductions of the grey seal population on direct consumption of cod and other fish prey and how would they translate into changes in natural mortality?
- What might be the consequences of taking no action?

5.1 Southern Gulf of St. Lawrence – 4T

Analyses focussed on three species considered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) to be at an elevated risk of extirpation, namely Atlantic cod, winter skate and white hake. Southern Gulf cod are part of a unit assessed by COSEWIC in 2010 as Endangered, a category more serious than that of Special Concern, the status assigned to 4T cod in 2003. In 2005, COSEWIC assessed winter skate in the southern Gulf as Endangered. Because winter skate in the southern Gulf may constitute a distinct species that has yet to be fully described, this assessment is particularly serious. Although COSEWIC has yet to assess the status of white hake, the Committee recently (October 2010) identified the species as one for which it requires a status report. This will re-start the initial stages of the assessment process for white hake, which has been delayed since the initial draft report for the species was prepared in the mid 2000s. Given that the Species at Risk Act identifies one of the functions of COSEWIC to “determine when wildlife species are to be assessed, with priority given to those more likely to become extinct” (section 15(b)), it can be concluded that the Committee considers white hake to be at an elevated risk of extirpation.

5.1.1 Cod

In order to estimate impacts of grey seal reductions on 4T cod, it is necessary to estimate the abundance of grey seals preying on 4T cod and the amount of cod consumed by these seals. It was assumed that reductions would target grey seals foraging in the 4T area or in 4Vn in winter (December-April), the areas in which 4T cod occur. The focal year for the analysis was 2009. Based on the distribution of satellite-tagged seals, it was estimated that 36,000 Sable Island seals, 5,000 eastern Shore seals and 63,000 Gulf seals forage in these areas at some time in the year (or in winter in the case of 4Vn), for a total of 104,000 seals in 2009. Given these estimates of seal abundance and estimates of 5+ cod consumption, the number of seals that would need to be removed to reduce 5+ cod natural mortality (M) to 0.4 was calculated. Given this level of 5+ M and current levels for other components of productivity, the cod population would be expected to increase in the absence of fishing.

Due to spatial and seasonal gaps in the diet sampling, it is difficult to quantify the consumption of 4T cod by grey seals. Two different approaches were used to fill these data gaps. One approach yielded a consumption estimate of 2500 t of 4T cod 38 cm or more in length (corresponding to ages 5 years and older). Consumption at this level accounts for 11% of 5+ M. Given this level of consumption, it is not possible to reduce 5+ M to 0.4 by removal of grey seals. Under the assumptions of this approach, 5+ M due to factors other than predation by grey seal amounts to 0.56, a level that is too high to allow population recovery under current productivity conditions.

A second approach yielded a consumption estimate of 11,000 t of 4T cod in the 38 cm and larger length range, accounting for 49% of 5+ M. This second approach is more consistent with the conclusion, based on weight of evidence, that predation by grey seals is a major component of the current high M of 5+ cod. Given this level of consumption, 5+ M would decline to 0.4 if the number of seals foraging in the areas occupied by 4T cod were reduced to 31,000 animals. If grey seals show diet specialization, with a fraction of seals specializing in predation on large cod, and it is possible to target these seals for removal, then fewer seals would need to be removed to promote cod recovery. For example, if all the consumption of 5+ 4T cod was due to half the seals foraging in the areas occupied by the stock, and it was possible to target those seals for removal, then the required removals would be half as large, i.e. the number of seals preying on 4T cod would need to be reduced by 36,000 animals.

5.1.2 Winter skate and white hake

Elevated adult M in both these species is resulting in population declines, with extirpation possible within a few decades if current productivity conditions were to persist. For winter skate, a decline in adult M by 57% would be expected to halt the population decline, but adult M would need to be reduced by 75% to have a 50% chance of reaching abundance levels comparable to those of the 1980s in 50 years. For white hake, adult M needs to be reduced by 55-68% (depending on model assumptions) to halt the population decline and by about 75% to allow recovery to the abundance levels observed in the 1970s and 1980s.

Based on a weight-of-evidence approach like that described above for 4T cod, predation by grey seals appears to be contributing significantly to the elevated M of both winter skate and white hake, though evidence for a predation effect is largely indirect. Assuming that predation by grey seals contributes 90% of the adult M of winter skate, the number of grey seals foraging in the 4TVn area would need to be reduced by 45% (about 45,000 animals) to achieve a 57% reduction in M, the reduction needed to halt the decline in the winter skate population. Because winter skate are highly aggregated in the western portion of the Northumberland Strait in summer and early autumn, it may be possible to reduce the number of grey seals that need to be removed using more precisely targeted removals. For example, if winter skate comprise 1% of the diet of grey seals in the area and approximately half of annual feeding by seals takes place during summer and early autumn, approximately 1700 grey seals foraging in the western portion of the Northumberland Strait would need to be removed to stabilize the winter skate population.

Predation by grey seals was assumed to account for all of the adult M of white hake above a level of 0.05-0.15. In order to have a 50% chance of achieving a 3+ population of 6 million hake by 2020 (i.e., near the average level in the 2000s), the number of seals preying on white hake would need to be reduced by 51-76%. It may be possible to reduce the required removals by targeting seals foraging in areas of white hake aggregation, i.e., year round in the Laurentian Channel and Cape Breton Trough, and in St. George’s Bay in summer. Depending on diet assumptions, this could reduce the required removals to about 13,000 animals.

5.1.3 Risk Analysis

A risk analysis framework was used to evaluate the ecological risks associated with undertaking, or not, a grey seal population reduction, under the weight-of-evidence hypothesis that predation by grey seals is the greatest contributor to elevated and unsustainable adult M in sGSL cod, white hake and winter skate. Risks associated with the broader ecological, social, political or economic consequences of undertaking a seal population reduction or those resulting from the perception of allowing extirpation of the marine fish populations were not considered as part of the science-led process.

5.1.3.1 The hypothesis is correct; no seal management action is taken

Trends in NW Atlantic grey seal populations are such that the populations are projected to continue to increase, though perhaps at a reduced rate at Sable Island. Based on current levels of productivity, the three fish species are at heightened risk of extirpation. Because elevated adult natural mortality is the main contributor to the ongoing declines in these species, failure to reduced predation mortality by grey seals may likely result in the loss of these populations within a few decades. Because winter skate in the southern Gulf may actually be a distinct species that has yet to be fully described, this loss may constitute extinction. Alternatively, theory on the predator pit phenomenon suggests that the populations may simply be reduced to considerably smaller levels than observed today, given present trends. Such abundance levels would heighten the vulnerability of these populations to extirpation by other causes.

5.1.3.2 The hypothesis is correct; appropriate seal management actions are taken

Reduction of the seal herd will affect the three fish species directly, via reduced predation, and indirectly via changes occurring in other parts of the food web. The direct effects are reasonably clear; reducing the number of grey seals that consume the fish species will reduce their M and thereby reduce the risk of extirpation. Substantial decreases in M could even lead to population recovery in as little as 15-30 years for cod and white hake.

It is likely impossible to anticipate all of the possible indirect ways that a grey seal population reduction could affect the three fish species, and consequently only key pathways were explored. The focus in this report is on negative effects, not because they are necessarily more likely but because they would contribute to heightened risk to the status of the fishes.

A strong indirect effect on adult fish is not anticipated because grey seals are not suppressing any potential predators of these fish. Furthermore, even if the abundance of competitors were to increase, data from the high abundance period for large groundfish in the 1980s does not suggest that there would be large density-dependent consequences for survival resulting from poor condition.

Indirect effects of a seal population reduction, if they occur, may be most likely for juvenile fish. Population increase in species that are both prey of grey seals and predators or competitors with juvenile stages of the three fish species may lead to reduced juvenile survival/performance.

> *Predation on eggs and larvae*: The recruitment rate of cod (but not of white hake and skate) is related to the biomass of pelagic fish, mainly herring and mackerel, in the ecosystem. This is likely due to predation on cod eggs and larvae. The pelagic fish in question are also the focus of important directed fisheries. Possible increases in pelagic fish abundance resulting from release from seal predation would likely lead to increases in fishery total allowable catch, consequently a large increase in predation pressure on cod early life stages is not expected. Winter skate eggs appear to be most susceptible to predation by gastropods. A number of grey seal prey are gastropod predators (e.g., cunner, winter flounder), and increases in their numbers following release from grey seal predation may indirectly increase egg-case survival.

Predation on juveniles: The main predators of these juveniles are large fish. In time, recovery of large adults is expected to reduce the survival of juveniles, thereby slowing population growth. With the collapse of large fish, juvenile mortality has been reduced to very low levels and there is considerable scope for increase to levels that are common in most marine fish populations worldwide and that nonetheless sustained large southern Gulf populations prior to the 1990s.

Competition: Important competitors of juvenile fish are other similar-sized fish. These competitors are also prey for grey seals and for large demersal fish such as adult cod, white hake and skate. These species may therefore not increase in abundance over the long term as fish become their main predators in the ecosystem. It is unclear whether and how competitive interactions would affect juvenile performance, though decreased growth and perhaps increased risk of overwinter mortality are possible consequences. However, increases in mortality resulting from poor condition are expected to be small, relative to the decrease in natural mortality that has occurred over the past three decades.

While this list is far from exhaustive, concrete strong indirect effects that would result in overall worsened population status for sGSL cod, white hake or winter skate were not identified. However, our understanding of the trophic dynamics in this and other coastal marine ecosystems is limited and therefore other unforeseen indirect effects cannot be ruled out either.

Risks to the viability of the NW Atlantic grey seal population resulting from a moderate population reduction were deemed small. Recent trends in the three herds that make up the population suggest that they are highly productive, and could rapidly recover to current levels even with an overall reduction of 50% (10 year recovery time for Sable Island, 18 years in the Gulf), if their productivity remains unchanged.

5.1.3.3 The hypothesis is incorrect; seal management actions are (mistakenly) taken

Trends in adult fish M are predicted to persist. Because there are presently no other suspected causes of adult M that are directly amenable to management actions, nature will be left to take its course. Indirect effects on juveniles noted in section 5.2 may be produced by a grey seal population reduction. Because there is little evidence that adult M would decline substantially in the near future, decreased juvenile survival, if it occurs, would merely speed up the otherwise inevitable extirpation of the populations.

As described in 5.1.3.2, the seal population is likely to rebound when seal population control ceases.

5.1.3.4 The hypothesis is not correct, no seal management action is taken

Trends in adult fish M are predicted to persist. Because there are presently no other suspected causes of adult M that are directly amenable to management actions, nature will be left to take its course.

5.1.3.5 Conclusions of the risk analysis

On balance, the estimated ecological risks related to the population status of NW Atlantic grey seals, and southern Gulf cod, white hake and winter skate, appear to be reduced by undertaking a reduction of grey seals in the NW Atlantic. Such reductions would pose minimal conservation risks to the grey seal population. Under the best case scenario for the fish, reduced adult M will halt population decline and possibly promote recovery. At worst, the fish populations are likely to be extirpated more rapidly than they would otherwise be and a seal cull would lead to unforeseen, unpredictable and unintended consequences for the ecosystem.

The risks can be further minimized by closely monitoring demographic rates in the fish populations. Under scenario 5.1.3.3, evidence of increasing and unsustainable juvenile M resulting from a reduction in seals numbers and failure of adult M to decline should become apparent in approximately 5-10 years of monitoring. Cessation of seal population control would allow the seal populations to rapidly return to the status quo situation, slowing down an accelerated progression to extirpation on the part of the three fish species.

5.2 Eastern Scotian Shelf – 4VsW

For 4VsW, the models reviewed provided a wide range of results reflecting uncertainty about seal-cod interactions in recent years. Some of the models found that seal predation is not an important component of cod mortality, and do not predict a large response of the 4VsW cod stock to changes in seal abundance. Other models indicate that seal predation could account for a large proportion of cod natural mortality, if the proportion of cod in the diet was assumed to be twice corrected estimates based on scat samples. If an intervention were to be made, the consequences to cod for a reduction in the seal population would depend on the age and sex of the seals removed. As the Sable Island seal herd is about 5 times larger than the Gulf herd, an intervention to significantly reduce this population would need to be much larger than that described for 4T. Removal or contraception of adult females is the most effective intervention, followed by removal of pups and then adult males. A predator control or a contraception program on the order of 10,000 seals per year for 5 years would have a very low probability of having a detectable consequence for cod. The consequences of taking no action cannot be predicted with any confidence. The coefficient of variation for spawning stock biomass of 4VsW cod was >100%.

6. Examples of control of large marine predators in other parts of the world

Ecologists have known for some time that predators can have significant effects on terrestrial and aquatic prey populations. Culling is widely practiced as a means to limit predation on livestock and game. Changes in species' distributions and abundance illustrate that culling programs can be very effective at reducing predator density. Culling has also been used to reduce marine mammal populations in many parts of the world. Coastal pinniped species have usually been the target of such programs, but dolphins and large cetaceans have also been culled. Extent of marine mammal population reduction and the response of targeted prey populations to culls have rarely been evaluated.

There are several conclusions that can be drawn from experimental studies in terrestrial systems and more model-based approaches in aquatic systems. First, predator removal can increase productivity and population size of target prey populations, but not always. Second, these studies typically have involved large proportional reduction (>50%) in predator populations, presumably to increase effect size and the statistical power to detect a significant effect. Third, the effects of culling are typically dependent on continued control, and in the absence of control the benefits rapidly disappear. This underscores the need for predator removal to be a long-term management strategy. Fourth, at least in the case of marine mammals, few studies have clearly articulated measurable objectives for prey population recovery or increase and have evaluated the success of the control program with respect to those objectives. Fifth, culling predators often has non-intuitive and unintended consequences for both target and other predator and prey species.

Despite their prevalence, the effectiveness, efficiency and the benefit: cost ratio of culling, programs have been poorly studied.

The requirements for a cull proposal would include:

1. clearly stated objectives and expected benefits,
2. definition of performance measures that provide a quantitative interpretation of the extent to which objectives have been met and the benefits realized,
3. estimation of per capita seal consumption of target species, the resulting seal predation mortality in relation to other sources of mortality, the size, age structure and duration of the proposed cull, predicted population response of the target population to the cull in an ecosystem context (i.e., accounting for response to other strong interactions),
4. sensitivity or robustness of the predicted benefits of the cull to assumptions and uncertainties, and
5. identification of measures used to monitor the target population to evaluate the longer-term consequences of the cull.

7. Design of a controlled experiment to test impact of grey seal targeted removal on mortality of southern Gulf cod

7.1 Design of experiment to test the impact of grey seal control on cod mortality

Based on the answers to Questions 1 through 6, mortality associated with grey seal predation appears to be an important factor inhibiting the recovery of cod and other groundfish stocks (notably white hake and winter skate populations) in the southern Gulf of St. Lawrence where groundfish distributions overlap concentrations of grey seals. This result leads to the hypothesis that the reduction of grey seal numbers especially in overlapping regions of the southern Gulf would lead to a recovery of cod and other groundfish populations there. In the context of science-based, adaptive and precautionary management, it is appropriate to test this hypothesis by undertaking a controlled grey seal stock reduction program in a carefully monitored ecosystem as a system-level experiment. The design of such a program assumes:

1. *Framework for sustainable management* – The program is predicated on well-defined principles of ecosystem-based management.
2. *Groundfish management objectives of reducing M and enhancing spawning stock biomass of cod and other groundfish* – Substantial removals of grey seals will reduce the natural mortality (M) on large cod; M is targeted to decline to 0.4 from the estimated current value of 0.63, which is unsustainable. At an M of 0.4, cod spawning stock biomass (SSB) is projected, with a high probability, to increase to the conservation limit reference point of 80,000 t within 20 years.
3. *Grey seal management objectives of targeted removal of 73,000 grey seals in 4TVn, plus maintenance removals of a number equivalent to the annual production* – Priority of removal is directed towards seals foraging on cod and other groundfish aggregations in 4T during the summer, and 4Vn in winter.

4. *Continuation of the commercial fishing moratorium* – The moratorium on directed fishing remains in place with respect to the recovery objectives for cod and other groundfish stock biomass.
5. *Target aggregation areas and times* – The recovery of groundfish stocks will be enhanced by targeting grey seals that feed in the areas and periods where groundfish are aggregated.
6. *No impact on the sustainability of grey seal populations* – The recommended removal of 73,000+ grey seals will not lead to serious harm to the grey seal population in Atlantic Canada. By this removal program, the total population will not fall below the critical reference level identified under the Canadian Atlantic Seal Management Strategy.

The design of the grey seal removal experiment and management program during this five year trial period would include two steps: i) operational spatial-temporal dynamics of a proposed grey seal stock reduction program, and ii) the management context of this program, whose details would be the subject of a future meeting. Given the assumptions noted above, the elements of operational program design are as follows:

- *Modelling and scenario building* – Impacts of seal removals on cod recovery will be examined within a suite of models designed to improve understanding of predator-prey interactions, outline scenarios that will enhance the effectiveness of management actions, and reduce the domain of possible but unexpected consequences of the removal.
- *Distribution and movement program* – Bio-loggers will be deployed on grey seals and cod to improve our understanding of distribution, and movements. These devices will provide information on geographical and seasonal overlap between the two species and the potential for feeding (seals) and mortality (cod).
- *Focus removals on overlap areas* – Overlapping aggregations of grey seals and cod occur in the summer at Miramichi-Gaspé, Magdalen Islands and Port Hood to Cape North; and, in the fall at Magdalen Islands and Port Hood to Cape North, into Cabot Strait and Sydney Bight. These spatial-temporal characteristics provide the geographic foci of the targeted grey seal removal program in the southern Gulf.
- *Grey seal population monitoring* – Numbers, age and sex composition of the grey seal removals will be monitored to model the dynamics of the seal population. Additional samples from grey seal removals can provide additional necessary information on growth and reproduction rates, parasite loads, and diet composition. Maintain and possibly increase the frequency of grey seal population surveys to understand the impacts of removals on seal dynamics.
- *Groundfish population monitoring* – Use samples from locally and temporally intensified trawl surveys within the experimental ecosystem, as well as the annual multi-species trawl surveys to accurately monitor population parameters of cod and other grey seal prey species in the experimental ecosystem.

7.2 What stock, location, methodology, time frame and degree of control would be required to observe an increase in cod productivity?

The stock, location, methodology, time frame and degree of control required are described below for grey seals and cod over an initial experimental removal period of five years. Life histories of both seals and cod imply that the duration of the experiment may have to be extended in order to derive unequivocal results.

7.2.1 Grey seals

The known distributions of grey seals throughout their life history provide the basis for the targeted removal program. As summarized in Table 6, the main removal activity occurs during the winter and early spring (harvesting of post-lactation adults and juveniles for oil and pelts in rookeries where grey seals are known to whelp), and in the summer and fall at haul out areas in the Gulf and Cabot Strait.

Table 6. Grey seal removal program, showing annual timeline, stock, location, time frame and control mechanism.

	Time frame:	*Winter-Q1*	*Spring-Q2*	*Summer-Q3*	*Fall-Q4*
Stock	*Months:*	*J F M*	*A M J*	*J A S*	*O N D*
Grey seals	Location:	Pictou and Henry islands Magdalen Is. Sable and Hay islands	Pictou and Henry islands Magdalen Is. Sable and Hay islands	Miramichi-Gaspe Magdalen Islands Port Hood to Cape North	Cabot Strait Magdalen Islands Port Hood to Cape North
	Seal activity:	Whelping, lactation	Breeding, dispersal	Feeding, hunting prey	Feeding, hunting prey
	Control:	Targeted removal of males, post-lactation females & juveniles	Targeted removal of juveniles	Removals of all age classes by independent sealers	
	Monitoring:	Tagging of adults	Tagging of juveniles & adults	Tag & jaw bone retrieval Gut sampling	
		Fatty acid sampling	Gut sampling		
Cod	Location:	4Vn	4Vn, 4T	Miramichi-Gaspe Magdalen Islands Port Hood to Cape North	Cabot Strait Magdalen Islands Port Hood to Cape North
	Fish activity:	Overwintering	Migrating, Spawning	Feeding	Feeding, migrating
	Control:	Acoustic tag program	Tag sampling	Food web analysis	Tag sampling
	Monitoring:	Bottom trawl survey	Spring bloom sampling	Annual research vessel survey	Benthic production measures

Legend:
- (yellow) - denotes cod-seal overlap
- (red) - denotes sampling points
- (blue) - denotes targeted removal activity

7.2.2 Cod

The overlap areas for cod and grey seals provide the basis for most effective protection of the cod (and some other groundfish) stocks in the southern Gulf. The overlap areas determine the spatial-temporal domain for the targeted removal of adult grey seals. These areas are identified in Table 6.

Table 6 provides the best available scientific information on the overlaps of cod and grey seals over the course of the calendar year in the southern Gulf of St. Lawrence (4T) and Sydney Bight (4Vn). These broad elements provide the planning basis for efficient reduction of grey seal numbers in the southern Gulf and, accordingly, offer the best opportunity for reducing the natural mortality of cod and other groundfish due to grey seal predation and associated effects.

To be successful, the proposed grey seal reduction program requires a sustainable management framework for the effective governance of human interventions in the ecosystem of the southern Gulf of St. Lawrence. This framework would inform the mechanism, scope, scale, and duration of the grey seal reduction experiment, and prepares for its extension toward successful local recovery of endangered groundfish stocks.

Knowledge Gaps

Seal diet

The spatial and temporal description of the seal diet is inadequate in some areas. A better description may help to reconcile the differences between diet estimated from intestines, scats and chemistry of seal blubber. Minimal attention was paid to variation (in space and time) in the fraction of cod in a seal's prey field, and how this might affect the fraction of cod in the diet. Thus, the functional responses of grey seals to changes in density of cod and other prey are poorly understood.

Cod mortality

The weight of evidence approach suggested that seal predation was the most likely hypothesis for explaining elevated cod mortality than other hypotheses examined in 4T. It is possible that there are sources of mortality not considered among these hypotheses, or that one or more of the other hypotheses examined is a more important source of mortality than was thought. In either of these cases, seal predation may be a less important source of mortality than suggested here.

There is a high natural mortality for cod in 4VsW that is unexplained and additional hypotheses were not examined to determine the importance of other mortality sources. If seals in fact consume more cod than is indicated in the diet analyses, then the contribution of seal predation to M could be much higher.

Ecosystem

Grey seals are generalist feeders and their role in the ecosystem is likely more complex than a simple two-species relationship. This more complex role needs to be more thoroughly investigated with a suite of models ranging in structure and level of system complexity from minimum realistic multi-species to ecosystem-level modeling. Two important aims of such work would be (i) to explore indirect interactions, which might result in outcomes for prey that are not intuitively obvious, and (ii) to improve our understanding of the relationship between changes in

M and the increase in seal populations. This latter point is a concern because the magnitude of adult cod mortality is similar in 4T and 4VsW despite four-fold differences in the relative density of grey seals between the two areas. Thus, we do not know if seals interact with cod in a consistent way throughout their area of overlap and we do not have a method for quantifying grey seal-cod interactions that can provide a consistent result across different combinations of seal and cod abundance.

Environment

Model projections were based on a number of assumptions; most particularly, they assume that productivity remains at the levels observed over the past 20 years. These predictions may be incorrect if environmental conditions change, or if other model assumptions are incorrect. Long-term projections of the impact of grey seal predation on cod are especially unreliable.

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