Fisheries and Oceans Canada
Science

Pêches et Océans Canada
Sciences

C S A S

Canadian Science Advisory Secretariat

S C C S

Secrétariat canadien de consultation scientifique

Research Document 2011/016

Quebec Region

Document de recherche 2011/016

Région du Québec

A preliminary evaluation of the impacts of Grey Seal, (*Halichoerus grypus*), predation on the 4T ecosystem and possible effects of their removal on cod (*Gadus morhua*) recovery

Évaluation préliminaire des impacts de la prédation par le phoque gris, (*Halichoerus grypus*), sur l'écosystème 4T et des effets possible d'un abattage sur le rétablissement des stocks de morue (*Gadus morhua*)

Lyne Morissette[1,2] and Mike O. Hammill[1]

[1]Department of Fisheries and Oceans, Regional Science Branch, Institut Maurice-Lamontagne,
P.O. Box 1000, Mont-Joli, Québec G5H 3Z4, Canada

[2]Institut des sciences de la mer de Rimouski, Université du Québec à Rimouski, 310, Allée des Ursulines,
P.O. Box 3300, Rimouski, Québec G5L 3A1, Canada

ISSN 1499-3848 (Printed / Imprimé)
ISSN 1919-5044 (Online / En ligne)

Correct citation for this publication:

Morissette, L. and Hammill, M.O. 2011. A preliminary evaluation of the impacts of Grey Seal, Halichoerus grypus, predation on the 4T ecosystem and possible effects of their removal on cod recovery. DFO Can. Sci. Advis. Sec. Res. Doc. 2011/016. iv + 27 p.

ABSTRACT

In this research document, we use an Ecopath with Ecosim (EwE) model to examine the trophic role of grey seals in the southern Gulf of St. Lawrence ecosystem and assess their direct and indirect impacts on Atlantic cod populations and other species interconnected with them. We assumed different feeding scenarios for grey seals, and simulated to which extent reducing their population is likely to affect the recovery of Atlantic cod. 11 harvest scenarios were tested. Our results suggest that the removal of seals could help the recovery of cod in some circumstances, but additional work is needed to tune the model to better mimic the decline in the southern Gulf of St. Lawrence cod stock, to examine how long recovery might take, to examine a strategy where seals in areas of high overlap with cod could be targeted, examine the impacts of removals on other depleted stocks of hake, and skate and potential effects on other ecosystem components including other fisheries. Additional scenarios need to be examined to explore a more complete range of possible outcomes under different grey seal removal strategies.

RÉSUMÉ

Dans ce document de recherche, nous utilisons un modèle *Ecopath with Ecosim* (EwE) pour examiner le rôle trophique des phoques gris dans le sud du Golfe du Saint-Laurent et se pencher sur leurs impacts directs et indirects sur les populations de morue franche et d’autres espèces y étant associées. Nous avons testé différents scénarios d’alimentation pour les phoques gris, et simulé dans quelle mesure une réduction de leur population pourrait affecter la reprise des populations de morue franche. 11 scénarios de capture ont été testés. Nos résultats suggèrent qu’un abattage de phoques pourrait aider à la reprise des populations de morues dans certaines circonstances, mais plus d’efforts sont nécessaires afin de peaufiner le modèle afin qu’il reproduise plus précisément le déclin du stock de morue dans le sud du Golfe du Saint-Laurent, pour examiner combien de temps serait nécessaire pour une éventuelle reprise, pour envisager une stratégie où les phoques situés dans des zones de grand chevauchement avec la morue pourraient être ciblés par l’abattage, pour examiner les effets de telles mesures sur les faibles stocks de merlus et de raies, et les effets potentiels sur les autres composantes de l’écosystème incluant les autres pêcheries. Des scénarios additionnels doivent être examinés afin d’explorer une gamme plus complète d’effets possibles pour différentes stratégies de réduction de la population de phoques gris.

INTRODUCTION

Several Atlantic cod stocks collapsed in the early 1990s and have shown limited signs of recovery since then. The reasons for the decline in cod and other groundfish stocks have been attributed to over-fishing whereas the reasons for the lack of recovery are uncertain and appear to vary between stocks. In the southern gulf of St. Lawrence, the lack of recovery is due to unusually high mortality among large (adult) cod. Several hypotheses have been proposed including predation by grey seals.

Over the last four decades populations of harp seals and grey seals have increased substantially. Maximum rates of increase for seal populations that do not have immigration are estimated to be as high as about12% per year or doubling roughly every 6 years. Harp seal numbers have increased from just under 2 million animals in 1970 to almost 7 million in 2009 (Hammill and Stenson 2010). Among grey seals the increase has been more dramatic with the Northwest Atlantic population increasing from approximately 13,000 animals in 1960 to roughly 400,000 animals in 2010 (Hammill and Stenson, 2011).

In the southern Gulf of St. Lawrence, the weight of evidence suggests that grey seal predation is limiting the recovery of the 4T cod stock as well as other species such as white hake and skate populations. This evidence includes a strong correlation between natural mortality rates (M) among large cod, large hake and skate and grey seal abundance, the high contribution of cod and hake to diet, strong overlap between grey seals and overwintering concentrations of cod, and hake, shifts in the distribution of skate and the timing of migration and distribution of hake and cod (Chouinard et al. 2005; Swain and Chouinard 2008; Swain et al. 2009; Harvey et al. 2011; Hammill, 2011; Stenson et al. 2011; Swain et al. 2011). This has led to calls for a reduction in the grey seal population to favour recovery of the cod population (FRCC 2004).

Marine mammals are generally considered as apex predators that may play an important role in the structuring of marine ecosystems (Bowen 1997; Morissette et al 2006). Little is known about the ecological consequences of reducing seal populations, but the general consensus is that removing top predators reduces ecosystem resilience (Yodzis 2000, 2001; Morissette et al. 2010).

Over the last century, ecosystems throughout the world have experienced a dramatic shift in structure as a result of the removal of top predators and extensive fishing activities often with unintended consequences (Pauly et al. 1998; Myers and Worm 2003; Estes et al. 2007). When complex trophic interactions are taken into consideration, within a simulation environment, it has been shown in a number of cases that culling of marine mammals would not necessarily lead to recovery of fish stocks, nor otherwise benefit the commercial fishery (Punt and Butterworth 1995; Morissette 2007). In some circumstances, by feeding on other species that could be competing with fisheries, marine mammals and other high-level predators may, in fact, actually be increasing fisheries catches (Punt and Butterworth 1995, Walters and Kitchell 2001). Therefore it is important that direct and indirect trophic linkages be examined to evaluate the role that a predator may play within the ecosystem, and the possible impacts that a reduction in predator abundance may have on ecosystem function (Bax 1998; Morissette et al. 2006). Evaluating the role that a predator may play in an ecosystem within a simulation environment provides a cost-effective and non-invasive approach to identifying the potential impacts predator reduction may have on ecosystem function.

Ecopath with Ecosim, is a mass balance trophic model that has been widely used to describe ecosystem structure (*Ecopath*), and when combined with *Ecosim* has been used to simulate the impacts of fishing, environmental disturbances and potential management activities (Christensen and Walters 2004). EwE has successfully reproduce ecosystem states, including the Baltic Sea (Harvey et al. 2003), Eastern Bering Sea (National Research Council 2003), the Benguela upwelling system (Shannon et al. 2004), Newfoundland–Labrador Shelf (Bundy 2001), and the Gulf of Thailand (Christensen 1998).

Here we use an *Ecopath with Ecosim* (*EwE*) model to examine the trophic role of grey seals in the southern Gulf of St. Lawrence ecosystem assuming different feeding scenarios, and to simulate the potential effect that would be achieved by reducing their population to favour the recovery of Atlantic cod..

METHODOLOGY

MODELLING APPROACH

Describing trophic interactions in the ecosystem (*Ecopath*)

Ecopath is a mass balance modeling approach that has been widely used to explore ecosystem structure and function (Christensen and Pauly, 1992; Christensen et al., 2005). The model assumes mass-balance, i.e., that we account for all flows in a food web. Hence, its parameters can change. In its simplest form, the master equation of Ecopath defines the mass-balance between consumption, production, and net system exports over a given time period for each functional group (i) in an ecosystem (Christensen and Pauly, 1992):

$$B_i \left(\frac{P}{B}\right)_i EE_i = Y_i + \sum_j B_j \left(\frac{Q}{B}\right)_j DC_{ji} \qquad \text{Eq. 1}$$

where B_i and B_j are biomasses (the latter pertaining to *j*, the consumers of *i*); P/B_i is the ratio of production to biomass, equivalent to total mortality under most circumstances (Allen, 1971); EE_i is the ecotrophic efficiency which is the fraction of production (i.e., $P_i = B_i(P/B)_i$) that is consumed within, or caught from the system (by definition between 0 and 1); Yi is equal to the fisheries catch (i.e., $Y_i = F_iB_i$); Q/B_j is the food consumption per unit of biomass of *j*; and DC_{ji} is the contribution of *i* to the diet of *j*, and the sum is over all predators *j*. Biomass accumulation and migration can also be added to the right hand side of the equation. Each group can have an unknown parameter (B or EE; P/B or Q/B) that can be estimated by the model. Most often, when the datasets are relatively complete, the EE is left unknown and is then used as a verification parameter to see which compartment of the model does not meet mass balance constraints.

Ecopath also allowed us to quantitatively assess the impact of grey seals in SGSL. Ecosim converts the trophic flows of Ecopath into dynamic, time-dependent predictions (full details of the *EwE* modelling approach and equations are available from http://www.ecopath.org). We used the mixed trophic impacts (MTI) routine from EwE's network analysis to quantify direct and indirect interactions between all trophic groups of the foodweb. It synthesizes the effects that a small change in the biomass of a group will have on the biomass of other groups in a system (Ulanowicz and Puccia, 1990). The approach is derived from the Leontief economic input-output analysis, and quantifies all the direct and indirect trophic impacts of all groups in the system based on the assumption that the direct impact between group *i* and group *j* can be estimated from the difference between the proportion that group *i* contributes to the diet of group *j*, and the proportion that group i takes from the production of group j (Christensen et al. 2005). The MTI for living groups is calculated by constructing a matrix, where the i,jth element representing the interaction between the impacting group *i* and the impacted group *j* is:

$$MTI_{ij} = DC_{ij} - FC_{j,i} \qquad \text{Eq. 2}$$

where DC_{ij} is the diet composition term expressing how much *j* contributes to the diet of *i*, and $FC_{j,i}$ is a host composition term giving the proportion of the predation on *j* that is due to *i* as a predator. When calculating the host compositions, the fishing fleets are included as "predators".

Beneficial predation is calculated as the percentage of the overall trophic impact by marine mammals that is positive for any prey group of this predator.

Dynamic simulations (*Ecosim*)

Ecosim provides temporal simulations using the initial parameters of the *Ecopath* master equations. This tool uses differential equations to estimate biomass fluxes as follows:

$$dB_i/dt = g_i \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M_i + F_i + e_i)B_i \qquad \text{Eq. 3}$$

where dB_i/dt is the biomass growth rate of group *i* during the interval dt, g_i is the net growth efficiency (production/consumption ratio), I_i is the immigration rate, M_i and F_i are natural and fishing mortality rates of group *i*, and e_i is emigration rate (Walters et al. 1997; Christensen et al. 2004; 2005).

To account for differences in vulnerability of different trophic groups to their predators, we adjusted vulnerability settings based on available information about the specific ecology of each species and by fitting to time series of biomass for each species or trophic group for which data was available.

We used the 1985-1987 *EwE* model to fit the projected biomass trends to observed biomass data collected for commercially important fish groups from 1985-2009 (Hugues Benoît, pers. comm.). This was done by adjusting the vulnerabilities of all groups. Vulnerabilities are factors describing how a change in a given predator biomass will impact predation mortality for a given prey. Low vulnerability factors imply that an increase in predator biomass will not cause any noticeable increase in the predation mortality the predator will cause on the given prey. High vulnerability factors oppositely indicate that if the predator biomass is for instance doubled, it will cause close to a doubling in the predation mortality rate on a given prey. This then relates directly to assumptions about the carrying capacity for the predator in question (Christensen et al. 2005). Other parameters representing detailed ecological features related to marine mammals, seal and cod groups were also adjusted: prey-switching effects, prey-handling time, and changes in foraging time. The maximum relative feeding time was set from 2.0 (default) to 10.0 for all marine mammals, given that these species can spend more time searching for their prey if they are scarce (Piroddi 2008). Feeding time adjustment rate was set to 0.5 for marine mammals and to 0.0 for other groups, because seals and cetaceans may change their feeding time as food availability varies (Heymans 2005, Piroddi 2008). Finally, assuming that seals can be opportunistic foragers and adapt their diet depending on prey availability, the switching power was set to 2.0 for these groups and left at 0.0 (default) for other trophic groups (Piroddi 2008). The model was driven by fishing effort obtained from all commercially important species in the SGSL (data from Hugues Benoît, pers. comm.) from 1985 to 2009.. Then, we let the model run for an additional 25 years, so until 2035. Once the model was fitted, we used Ecosim to investigate how a potential harvest of seals might impact the biomass of commercially important fish.

Grey seal harvesting scenarios

Different exploitation patterns were applied to the grey seals trophic group to simulate a harvest in SGSL. Starting in 2010, we examined the impact of different removal levels of grey seals on the cod stock (Table 1). We then compared biomass trends of other trophic groups (mainly cod) during simulations before and after the removal of seals.

Table 1: *Harvesting scenarios used for grey seal population in the southern Gulf of St. Lawrence*

Seal diet	Grey seal harvesting scenarios	Equivalent in grey seal abundance (approx.)	Scenario #
Generalist, 3% large cod in the diet	2x initial harvest effort	30,000 seals total over 25 yrs	1
	3x initial harvest effort	40,000 seals total over 25 yrs	2
	4x initial harvest effort	60,000 seals total over 25 yrs	3
	eradication	all seals removed	4
Generalist, 3% large cod in the diet	One year cull (2010) and back to normal for upcoming years	15,000 seals removed	5
		50,000 seals removed	6
		100,000 seals removed	7
Cod-specialist 50% large cod in the diet (St. Paul Island data)	2x initial harvest effort	30,000 seals total over 25 yrs	8
	3x initial harvest effort	40,000 seals total over 25 yrs	9
	4x initial harvest effort	60,000 seals total over 25 yrs	10
	eradication	all seals removed	11

MODELLED ECOSYSTEM

Study area

The southern Gulf of St. Lawrence (SGSL; Northwest Atlantic Fisheries Organization [NAFO] division 4T) is a relatively shallow shelf (generally < 60 m deep; maximum depth 130 m), with a total area of 64,075 km^2 (Figure 1), characterized by pronounced seasonal variation in surface waters, which are almost entirely covered by ice during winter and may reach 15˚C or more during summer (Strain, 1988). In our model, we defined the study area to include depths between 15 and the 200 m. The nearshore region was excluded from the models because it is not sampled research vessel bottom-trawl surveys and because exchanges between the infra-littoral and offshore zones are still poorly understood.

The southern Gulf of St. Lawrence system a high diversity of organisms. The mesozooplankton community is characterized by small copepod species (mainly *Oithona similis*, *Temora longicornis*, *Pseudocalanus* spp.), while the shrimp community is dominated by *Argis dentata*, *Pandalus montagui*, and *Eualus macilentus* and the abundance of large shrimp is insufficient to support a commercial fishery (Hanson and Lanteigne, 1999). Snow crabs (*Chionoecetes opilio*) are an important component of the benthic community on the SGSL, where they support a large fishery. Prior to an increase in the biomass of capelin (*Mallotus villosus*) in the 1990s, Atlantic herring (*Clupea harengus*) and Atlantic mackerel (*Scomber scombrus*) were the dominant pelagic fishes in the SGSL, whereas capelin was the most important forage fish in NGSL in both the 1980s and 1990s (DFO, 2001; Savenkoff et al., 2004a,b). Deep-water species (e.g., redfish [Sebastes spp.] and Greenland halibut [*Reinhardtius hippoglossoides*]) are important components of the fish community in the northern Gulf of St. Lawrence (NGSL), but are rare in the SGSL (Ni, 1982; DFO, 2002). In contrast, mid- and shallow-water flatfish species (e.g., American plaice [*Hippoglossoides platessoides*], winter flounder [*Pseudopleuronectes americanus*], yellowtail flounder [*Limanda ferruginea*]) are important components of the fish community and fisheries in the SGSL, but are rare in the deep waters of the NGSL during the summer feeding season. Atlantic cod have been an important component of both ecosystems, but studies have indicated that very little mixing occurs between the cod populations from the two areas (Gascon et al., 1990; Swain et al., 2001). The only other large gadoid species in both systems is white hake (*Urophycis tenuis*), which has morphologically distinct populations in the NGSL and the SGSL (Hurlbut and Clay, 1998). Other large commercially-fished gadoids, haddock (*Melanogrammus aeglefinus*) and pollock (*Pollachius virens*) are uncommon in both ecosystems. Four species of pinnipeds occur in the Gulf of St. Lawrence: harp seals (*Pagophilus groenlandica*), grey seals (*Halichoerus grypus*), hooded seals (*Cystophora cristata*), and harbour seals (*Phoca vitulina*). Harp and grey seals are the most abundant pinnipeds in the Gulf. Both ecosystems also have

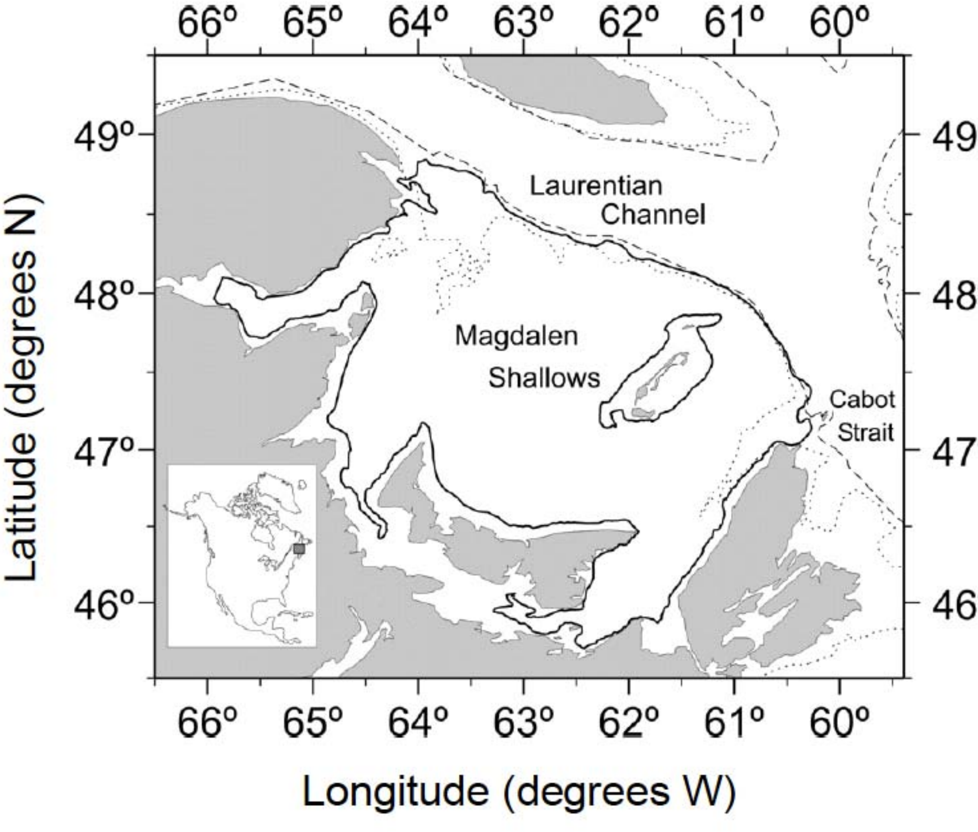

Figure 1: Study area (solid line) in the southern Gulf of St. Lawrence (NAFO division 4T) between 15 and 200 meters deep equivalent to a total area of 64,075 km2 (from Savenkoff et al. 2004)

boreal cetaceans species, ranging from large and medium size misticeti (baleen whales) and odontceti (toothed whales) to small odontoceti such as porpoises and dolphins.

Trophic structure of the model

The SGSL ecosystem was aggregated into 32 trophic groups. Species were grouped on the basis of their commercial significance and importance as predators or prey. We distinguished seven marine mammal groups (including two seals species where adults and pups were treated separately), one seabird group, 14 fish groups, six invertebrate groups, two zooplankton groups, one phytoplankton group, and one detritus group (Table 1). Some compartments such as large pelagic fishes and large demersal fishes were aggregated on the basis of similarity of size and ecological role of their species. Atlantic cod and American plaice were separated into large and small individuals based on diet, age/size at first capture, and age/size at maturity. Smaller animals prey mainly on invertebrates whereas larger animals prey mainly on fish. These changes tend to occur gradually with increasing length, but for our models, a sudden change was assumed to occur at 35 cm for Atlantic cod (Lilly, 1991) and at 35 cm for American plaice (Pitt, 1973). To also account for the microbial loop, bacteria were included in the detritus compartment.

DATASETS & MODIFICATIONS TO THE ORIGINAL 4T MODEL

Information on species, biomass, production, consumption, diet and catch for each trophic group was obtained from various sources given in Savenkoff *et al.* (2004). Biomass estimates for demersal fishes were obtained from annual bottom trawl surveys in the two ecosystems. Survey biomass estimates from these surveys were adjusted to total biomass based on catchability coefficients from Harley and Myers (2001) and Savenkoff et al. (2004).

Overall, considerable effort was expended to obtain biomass, production, consumption, diet, and catch data from the study areas during the periods of interest. However, biomass, production, consumption, and diet information on several groups (e.g., forage species, benthic invertebrates, and zooplankton) was sparse or non-existent; in these situations, data were obtained either from the literature or from different period of the same area.

Changes to the model to incorporate multistanza methodology

The multi-stanza option of Ecosim allows us to create a set of biomass groups representing life history stages or stanzas for species that have complex trophic ontogeny. Mortality rates (M0, predation, fishing) and diet composition are assumed to be similar for individuals within each stanza (e.g. larvae having high mortality and feed on zooplankton, juveniles having lower mortality and feed on benthic insects, adults having still lower mortality and feed on fish) (Christensen et al. 2008) The data needed for this feature are baseline estimates of total mortality rate Z and diet composition for each stanza, then biomass, Q/B, and BA for one “leading” stanza only. Two groups were split using the multistanza methodology incorporated into Ecosim: Altantic cod and American plaice. With this feature, mortality rates (Mo, predation, fishing) and diet composition are assumed to be similar for individuals within each stanza and the baseline estimates of total mortality rate ‘Z’ and diet composition for each stanza need to be entered, while the biomass, Q/B ratio, and biomass accumulation are only entered for adults. Total mortality (Z) is entered for each stanza-group and used to replace the Ecopath’s P/B ratio for that group. For each of the groups, the von Bertalanffy’s growth parameter ‘k’, is needed, as well as the age in months at transition, and the ratio of the weight at maturity to asymptotic weight (W_{mat}/W_{inf}). Because of the particular nature of their harvest, harp and grey seals should also be tested with multistanza in future research. However, some exploration tests done for this working paper showed that this didn't seem to affect the outcomes of the simulations.

Harp seals

The time series of harp seals removals was taken from the Atlantic resource management landing reports (Stenson 2009) and we used the 1985-2008 time series of the front and gulf herds to represent the trends of catches in 4T (Figure 2). Each year class of harp seals was weighted by average body mass (Hammill and Stenson 2000) to get a time series of catches in biomass.

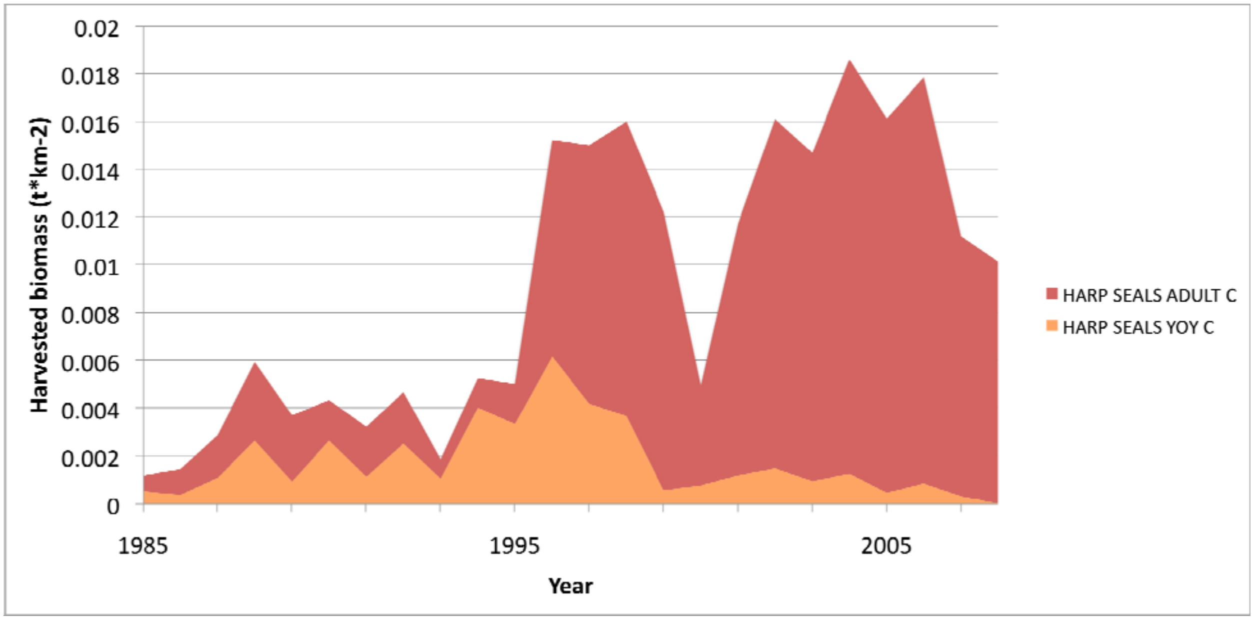

Figure 2. *Total harp seals removals from the front and gulf herds (in biomass).*

Grey seals

For the simulations we used the "ice" model data for the Gulf herd (Hammill and Stenson, 2011) (Figure 3). The eastern shore herd consists of animals born along the Nova Scotia coast, outside of the Gulf. For now we add them into the Sable herd when describing seasonal changes in distribution. The Eastern shore herd is small, and will not mean much for 4T, but it may mean more for 4Vn, the area where the 4T cod overwinter.

We transformed the grey seal population numbers into an age structure matrix for each of the different grey seal herds (M. Hammill, unpublished data). We used the 1985-2009 time series of the Eastern, Sable Island, and Gulf herds to represent the trends of biomass in 4T. Each year class of grey seals was weighted by average body mass (Hammill and Stenson 2000) to transform abundance data into a time series of biomass.

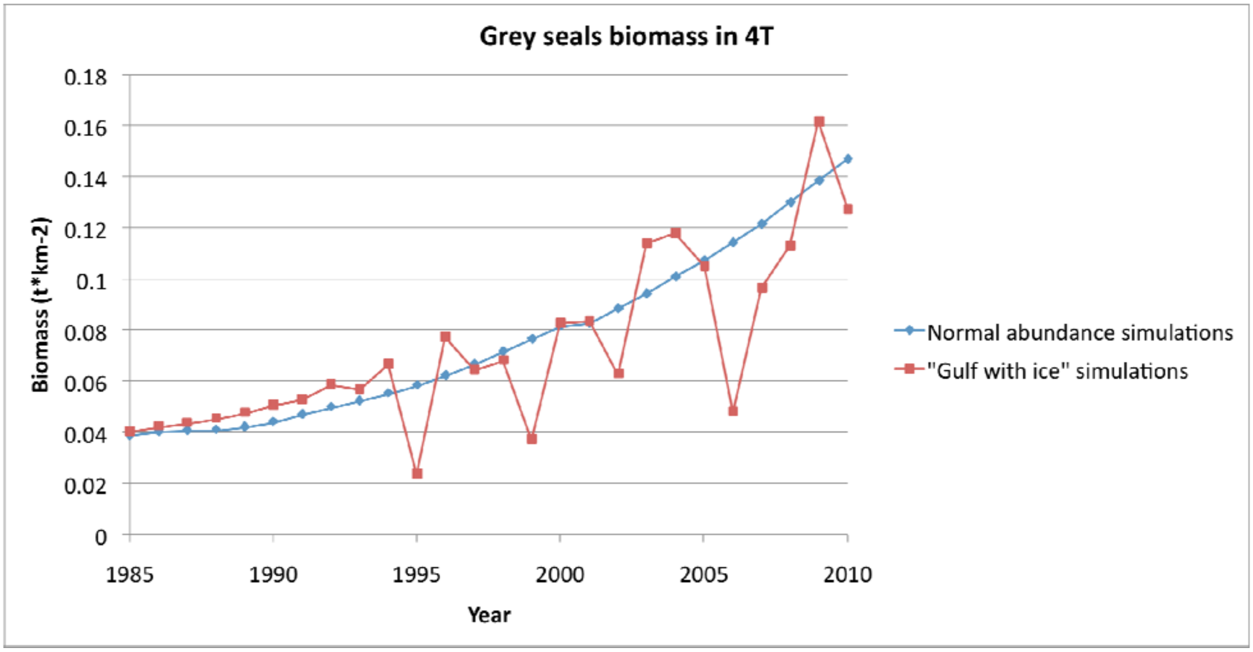

***Figure 3**: Biomass estimates for grey seals in 4T based on different models (with and without ice mortality).*

Diet of grey seals were analyzed by stomach contents and intestine contents (hard parts remains, adjusted for digestibility). In either case, cod was an important part of the diet, representing between 1 and 5% of grey seals' diet (in weight).

Depending on the season, the proportion of cod in grey seals' diet changes. Therefore, we created a forcing function based on these diet proportion changes. It is not yet possible in *EwE* to address diet changes directly. Therefore, the algorithm describing the change in diet towards cod (Figure 4) was used to drive the vulnerability of cod to grey seal predation.

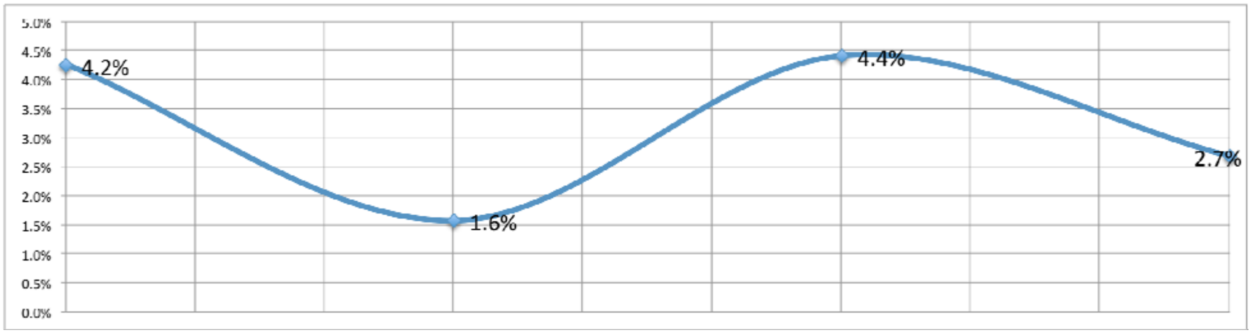

***Figure 4:** Cod proportion changes in the diet of Grey seals in 4T over a year.*

Saint. Paul Island winter diet

Based on stomach samples from 49 grey seals collected during the winter 2008 near St. Paul Island, cod comprised nearly 50% of the diet by weight (Table 2) (Stenson et al. 2011). Broken into size classes, grey seals were consuming, in terms of abundance, 75% large cod and 25% small cod (Figure 5). However, in terms of biomass, this represents 98.3% large cod and 1.7% small cod for the same samples.

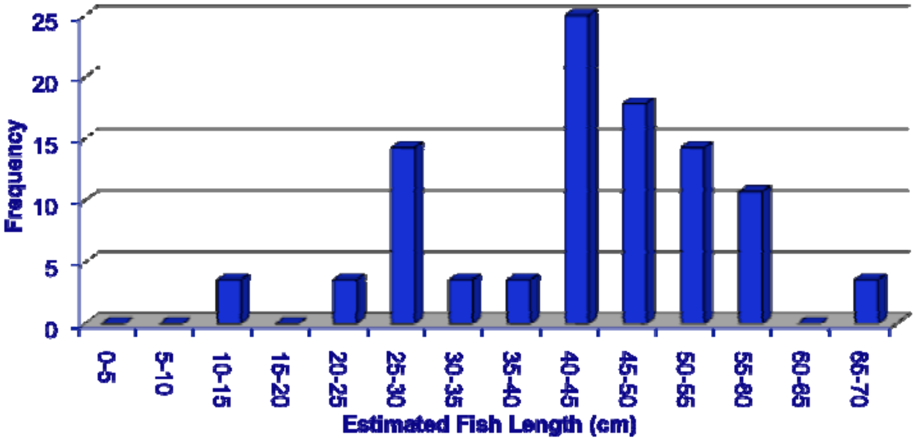

Figure 5. *Size distribution of Atlantic cod in grey seals stomachs during winter in St. Paul Island.*

Applying the 98.3%/1.7% ratio of cod diet to these St. Paul island's stomach contents gives us a winter diet of :

Table 2: *Grey seal diet composition for St. Paul island winter samples (n. 49 seals)*

Ecopath group	**Name**	**Diet proportion (%)**
7	Large Atlantic cod	59.13
8	Small Atlantic cod	1.02
12	Flounders	9.66
15	Large demersals	13.07
16	Small demersals	0.01
17	Capelin	0.11
19	Piscivorous Small pelagics	2.48
20	Planktivorous Small pelagics	14.52
21	Shrimp	8.64
22	Large crustaceans	< 0.01

We used this diet as an "extreme" scenario for our simulations (later referred to as St. Paul's diet).

Adding this new diet to the original model from Morissette et al. 2009 created a slight imbalance for the large demersals group (their ecotrophic efficiency, which should usually be below 1.00, was 1.32). To compensate for this, we set the EE to 0.95 and let the model calculate the biomass needed by the model to reach a balanced solution. This generated a biomass of 0.472 $t*km^{-2}$ (instead of the 0.340 we started with) for the group, which falls within the range of possible values for large demersal biomass in 4T (Savenkoff et al. 2004).

Cod

For cod we set the age at transition (i.e., when the cod started being caught) at 36 months, to get the same general biomass and Q/B estimated for the juveniles as in the previous model (Savenkoff et al. 2004). The P/B (0.464 & 0.563 yr^{-1}), biomass for adults (5.250 & 3.653 $t•km^{-2}•year^{-1}$), and Q/B (1.553 & 2.668 yr^{-1}) for large and small cod, were based on the previous model (Savenoff et al. 2004).

The weight at maturity/asymptotic weight was calculated as the 1985-1987 average provided by Swain et al. (2009) (Table 23).

***Table 3**: growth parameters of Atlantic cod in 4T for years 1985-1987 (adapted from Swain et al. 2009).*

	Wmat (kg)	**Winf (kg)**	**W_{mat}/W_{inf}**
1985	0.50	12.66	0.039
1986	0.51	11.55	0.044
1987	0.42	15.66	0.026
AVERAGE			**0.037**

A von Bertalanffy K value of 0.290 was given in FishBase (based on Sinclair 2001), while the asymptotic weight weight at age 4 (Table 2) were obtained from the stock assessment report for 4T cod (Swain et al. 2009).

American plaice

For American plaice we set the age at transition (i.e., when the fish started being caught) at 35 cm, which, for years 1985-1987, represents about 8 year-old (96 months). We used the same general biomass, P/B and Q/B estimated for the juveniles as in the previous model (Savenkoff et al. 2004).

A von Bertalanffy K value of 0.340 was given in FishBase, and the asymptotic weight weight of 6.4 kg (Fishbase), this vives us a Wmat/Winf ratio of 0.3 for the American plaice stanzas.

Fisheries time series

Fisheries catch data were obtained from the Department of Fisheries and Oceans – Maritime region database (Hugues Benoît, DFO, pers. comm.) for NAFO area 4T (Figure 6). Time series of effort (F) were available only for cod, therefore we used the catch data to extrapolate effort as F=C/B.

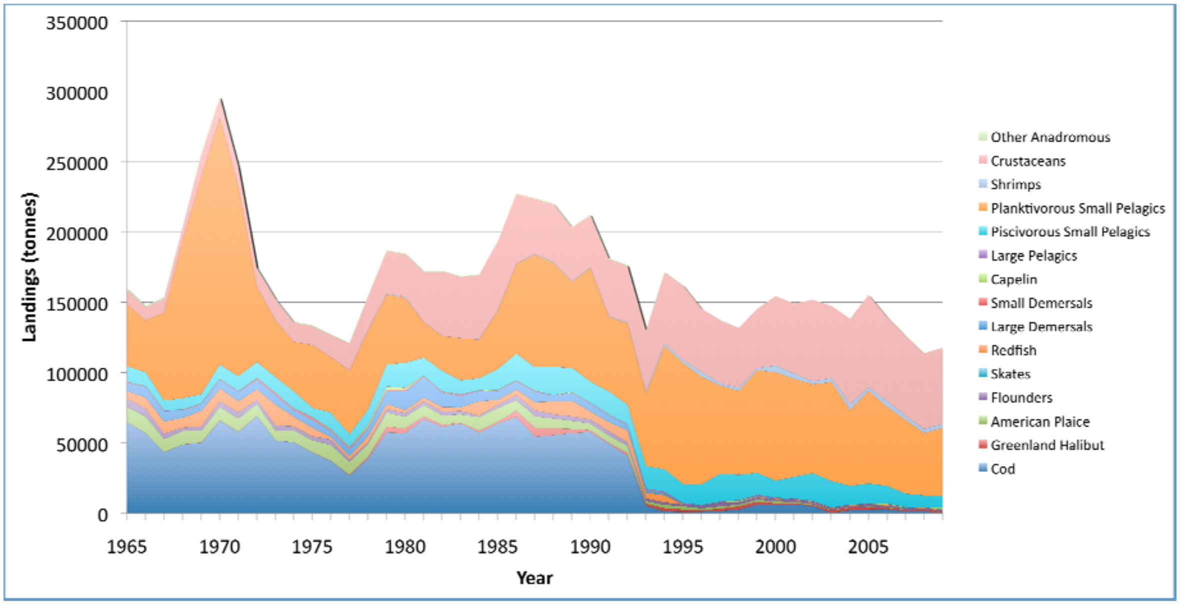

Figure 6: *total landings (tonnes) by trophic group in the southern Gulf of St. Lawrence.*

RESULTS

While there are a number of ecosystem modeling approaches available (Plagányi 2007), we chose *EwE* over other approaches (e.g., Minimum realistic model) because we are interested in potential impacts of grey seal predation on a wide-range of other ecosystem components (eg white hake, winter flounder, skate, herring) in addition to cod, and we wanted to be able to compare our results with other models developed using similar approaches for neighbouring ecosystems eg Scotian-shelf, northern gulf of St. Lawrence (Bundy et al. 2009). This approach allows for the representation of several predator-prey interactions and the inclusion of different routines takes into account of the estimated uncertainty associated with model inputs (Plagányi et Butterworth, 2004). We used the version 6.1.0.625 of EwE to estimate mortality (due to fishing, predators, and other sources), the basic emergent properties and network analysis indices for the two time periods, and estimates of the associated uncertainties. In EwE, several system's indices are computed to describe the food web, its complexity, and the way trophic groups interact with one another. The software also allows making dynamic simulations based on Ecosim, a dynamic modelling application for exploring past and future impacts of fishing and environmental disturbances (Christensen and Walters 2004). Ecosim converts the trophic flows of Ecopath into dynamic, time-dependent predictions (full details of the EwE modelling approach and equations are available from http://www.ecopath.org).

TROPHIC STRUCTURE AND FUNCTIONS OF THE SGSL ECOSYSTEM

The SGSL area is an ecosystem dominated by marine mammals and demersal organisms (Figure 7), where most primary production was consumed by zooplankton and benthic invertebrates, which is then transferred to demersal species. Species are highly interconnected in SGSL, with a connectance index of 0.285 and a system omnivory index of 0.121, which is in the upper range of marine ecosystem models (n = 392 models; L. Morissette, unpublished data).

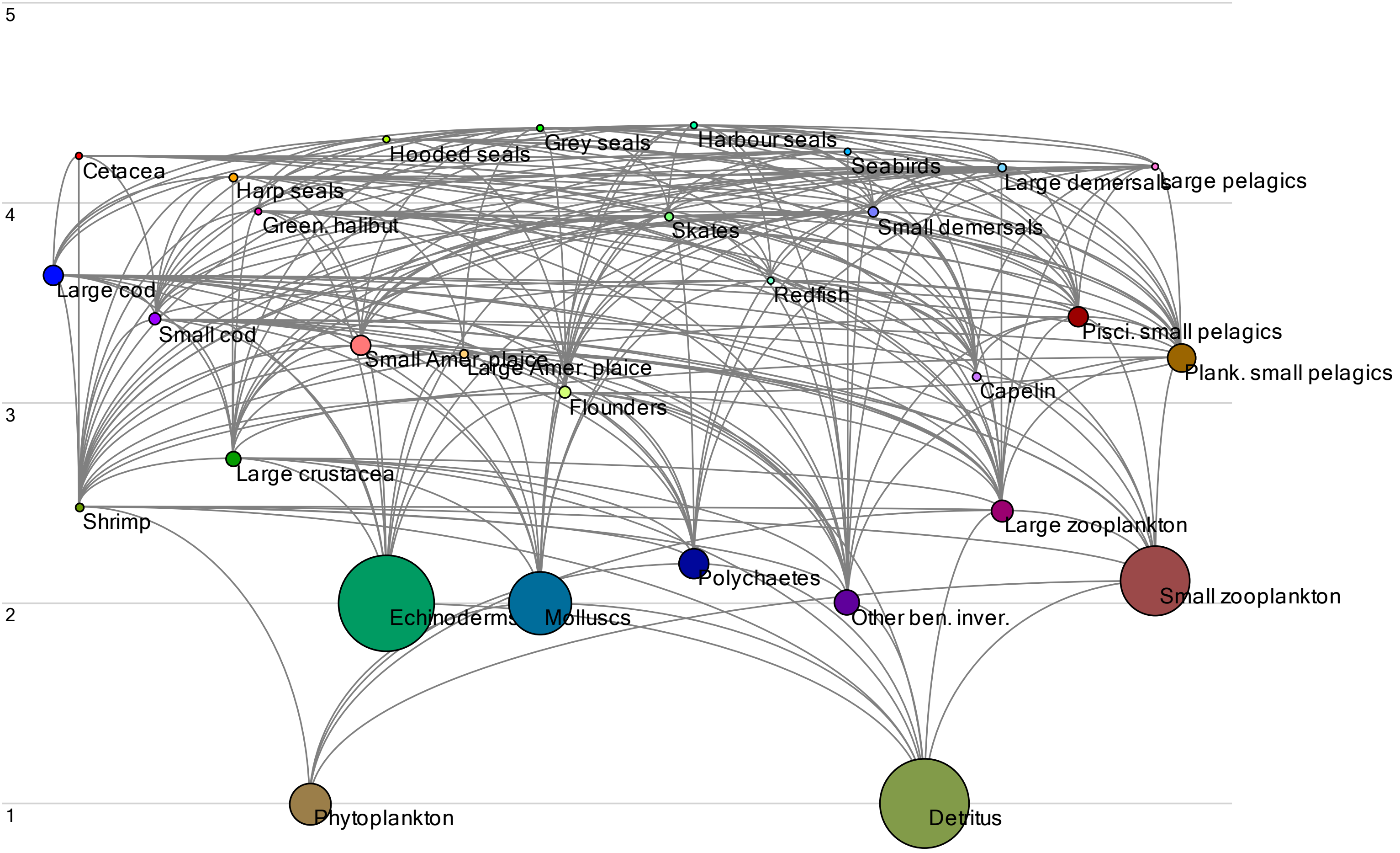

Figure 7: *Overview of the trophic interactions in the Southern Gulf of St. Lawrence for recent years (after the collapse of cod). Circle size indicates the biomass of each trophic group. Trophic levels are in y-axis.*

ABILITY OF THE MODEL TO EXPLAIN BIOMASS TRENDS

In spite of the many indirect factors driving the changes in most fish populations in the SGSL, the model performed relatively well at reproducing basic trends in relative biomass for most commercially important trophic groups (Figures 8 A-G). Model fitting allowed us to minimize sum of squares (SS) by adjusting vulnerabilities, prey-switching, prey-handling, and foraging for all species ($SS_{default}$ = 1264; $SS_{fitted\ best\ model}$ = 312). The model was unable to duplicate the collapse of cod adequately (period 1985-1990), but in this initial examination we did not fully explore the impacts of unreported catch which was extensive at this time (Bousquet et al. 2010; Swain et al. 2011), nor possible changes in natural mortality due to changes in life-history traits (Swain 2010). Spatial overlap and recent diet studies indicate that grey seals may consume larger cod than considered traditionally (Harvey et al. 2011; Hammill, 2011; Stenson et al. 2011), and results from the St Paul's diet indicate that grey seal diets at certain times of the year or in certain areas can certainly consist of more large cod (Stenson et al. 2011) then generally considered. Thus the potential contribution of seal predation to natural mortality of cod during earlier periods needs to be explored. In preliminary runs when using the St. Paul Island's grey seal diet data for our model, the fitting for cod biomass was better, indicating that grey seals might have changed their diet before the collapse of cod, and this increased consumption by seals, added to extensive fishing effort, seemed to reproduce the observed biomass trends for cod in SGSL.

MIXED TROPHIC IMPACTS OF GREY SEALS IN SGSL

The SGSL is a complex ecosystem and species are interconnected through direct and indirect interactions, as shown in Figure 7. The MTI analysis shows us that species at the top of the foodweb (such as grey seals) largely have a negative impact on the rest of the ecosystem (Figure 9). Species showing an overall positive impact on other species are usually of lower trophic level. However, slight positive impacts are also occurring from top predators, even on their prey, through indirect interactions. While grey seals seem to have one of the strongest impacts on the SGSL ecosystem, the most impacted species are grey seals (intraspecific competition), skates and large demersal fish. Large cod and small cod (to a lesser extent) are also impacted by grey seals in SGSL.

When we look more closely at the species impacted by grey seals before the collapse of cod (mid-1980s; Figure 10), we see that most higher trophic level species are negatively impacted by grey seals, but lower trophic levels (small pelagics, shrimp, crab, invertebrates) show a slight positive impact by their presence in the ecosystem. One exception to this is redfish, a relatively high trophic level being positively impacted by their predator, through indirect interactions.

Cod is also an important top-predator in the SGSL ecosystem. Consequently, the MTI of grey seals in scenarios where they eat more cod (Figure 10) result in more groups being positively impacted by seals (because they eat cod which is a predator of many species). This includes a positive impact on small cod, because grey seals mainly consume large cod, which in turn may also consume juveniles of their own species. However, this needs to be examined further, because the incidence of cannibalism is rare among cod from the southern Gulf of St. Lawrence ecosystem (Hanson and Chouinard 2002).

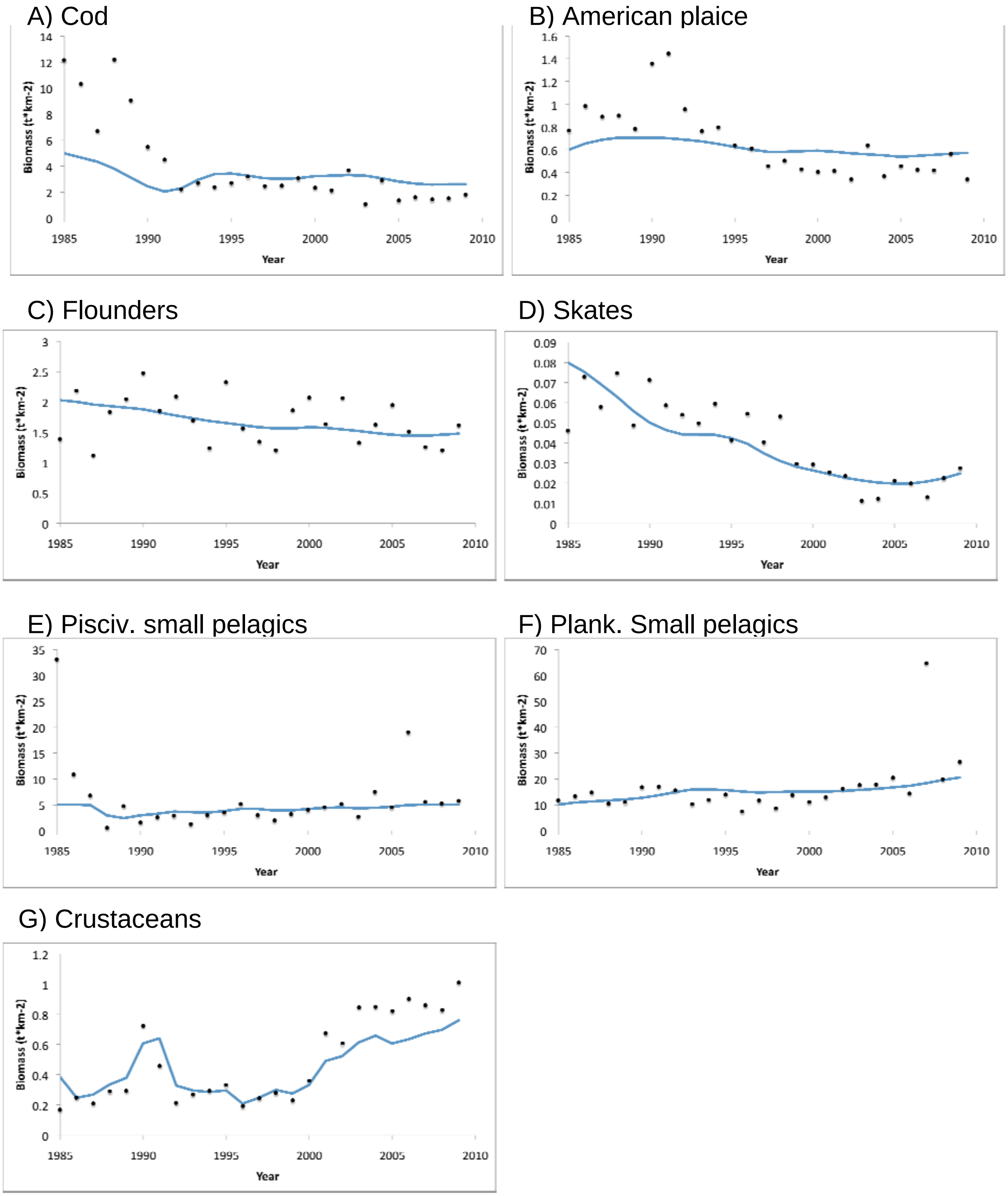

***Figure 8.** Ecosim outputs for biomass (line) were fitted to observed time series of biomass (dots) for most commercially important species in the southern Gulf of St. Lawrence.*

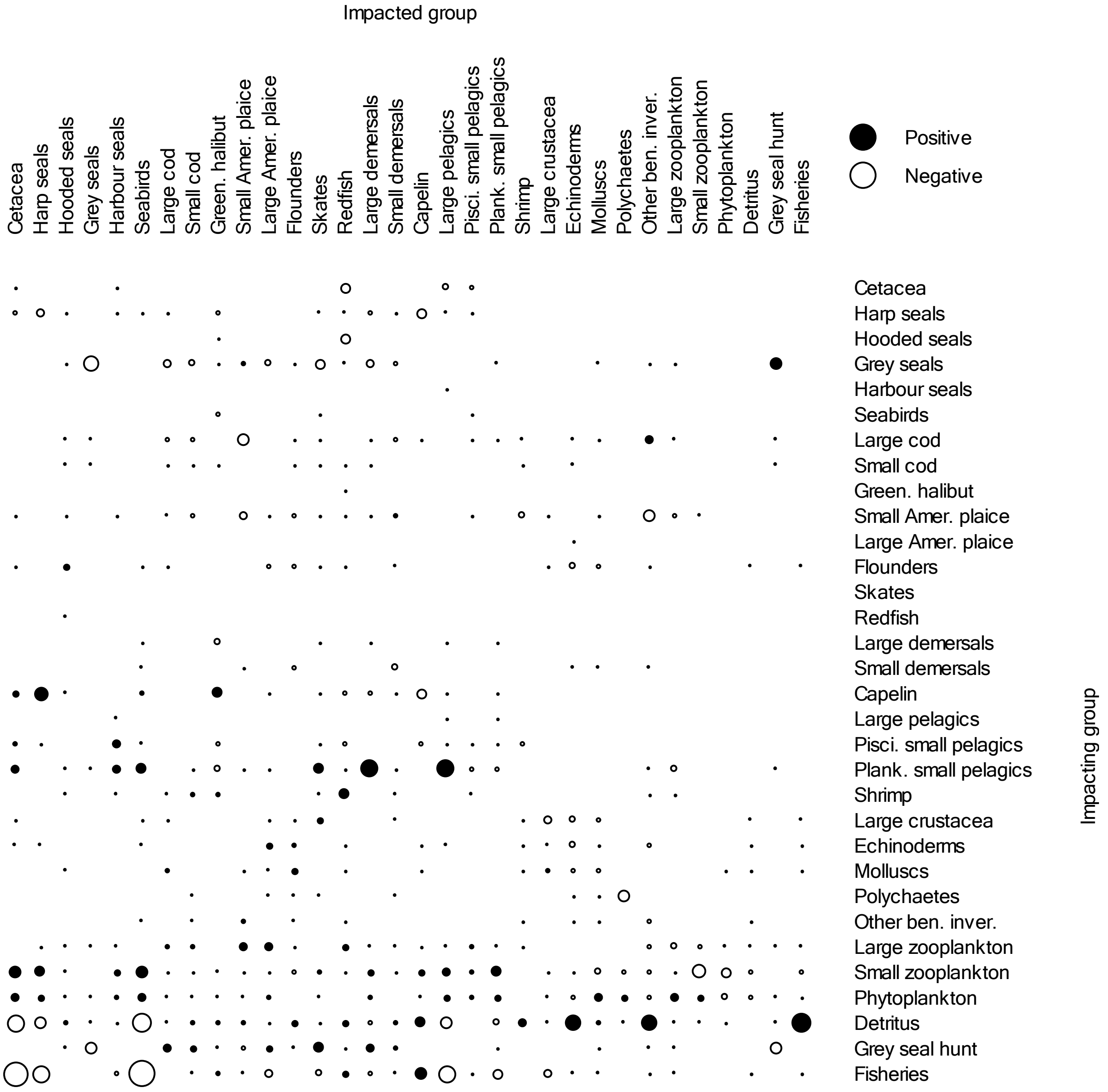

Figure 9: *Mixed trophic impacts of the different trophic groups in Southern Gulf of St. Lawrence, for the recent years.*

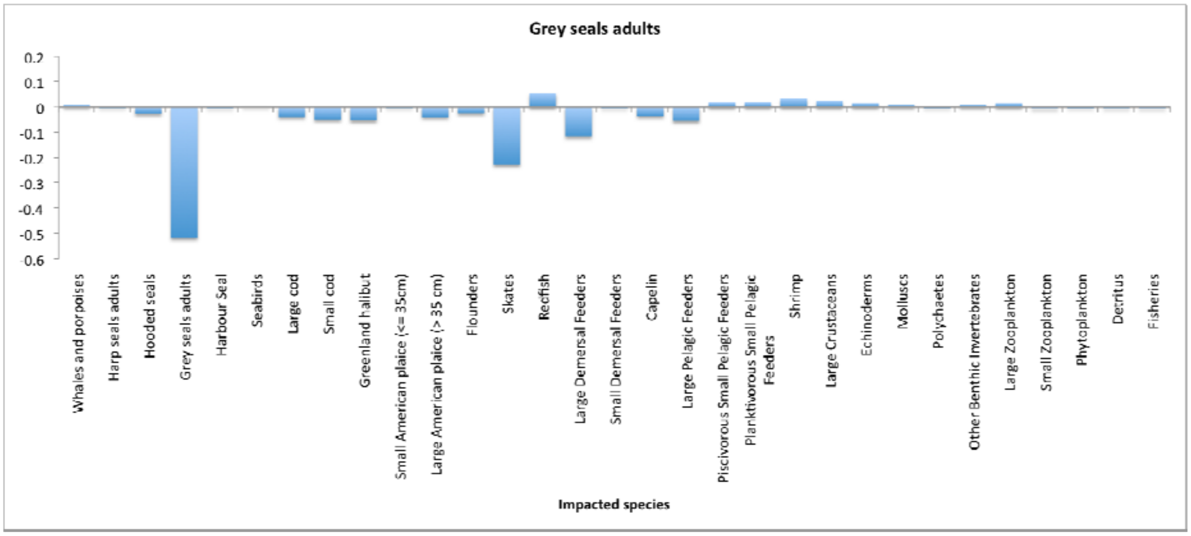

Figure 9: *Mixed trophic impacts of grey seals in SGSL for the 1980s based on best available diet information. A positive MTI means that grey seals have an overall positive effect on impacted species and that increasing their biomass would benefit the impacted species. A negative MTI means the grey seals have an overall negative effect on impacted species and that increasing their biomass would reduce the biomass of impacted species.*

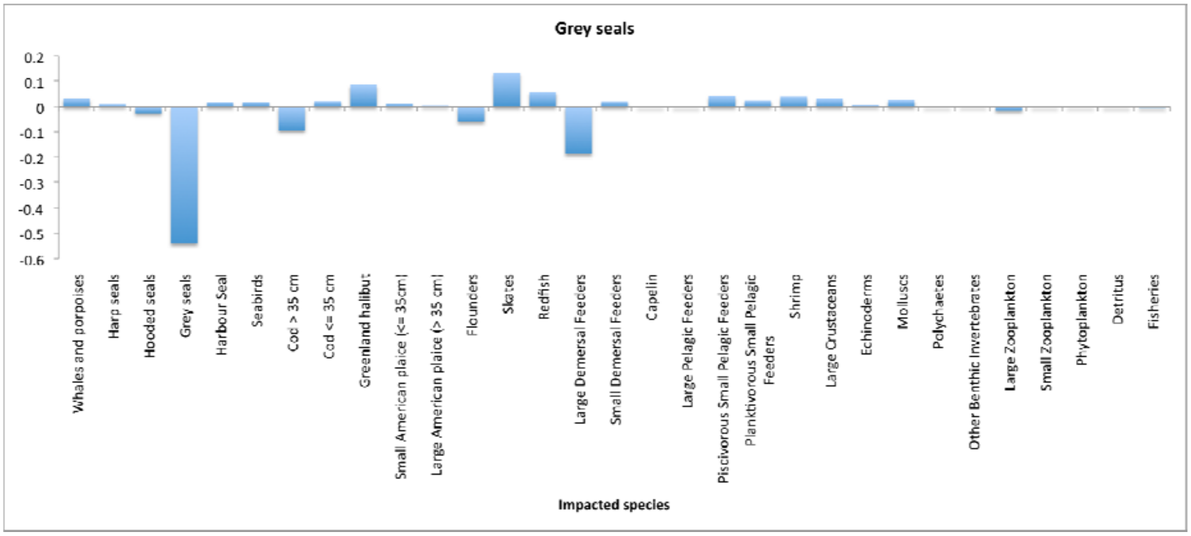

Figure 10: *MTI of grey seals in SGSL for the 1980s based on St. Paul island's diet scenarios (50% of large cod in the diet). A positive MTI means that grey seals have an overall positive effect on impacted species and that increasing their biomass would benefit the impacted species. A negative MTI means the grey seals have an overall negative effect on impacted species and that increasing their biomass would reduce the biomass of impacted species.*

After the collapse of groundfish stocks in the SGSL (mid-1990s), the negative impact of grey seals is stronger (Figure 11), as a consequence of the increased grey seal population affecting severely reduced fish stocks. However, here again, if we assume grey seal eat a higher proportion of cod (St. Paul Island's diet), then their overall impact on the whole structure of the foodweb changes with for example, grey seals having a positive impact on small cod, and small Greenland halibut under these circumstances. More species seem to be positively impacted by seals when they eat more cod, because cod remain a major top-predator of the system. However, this needs to be examined within an ecosystems services context to evaluate the distribution of benefits.

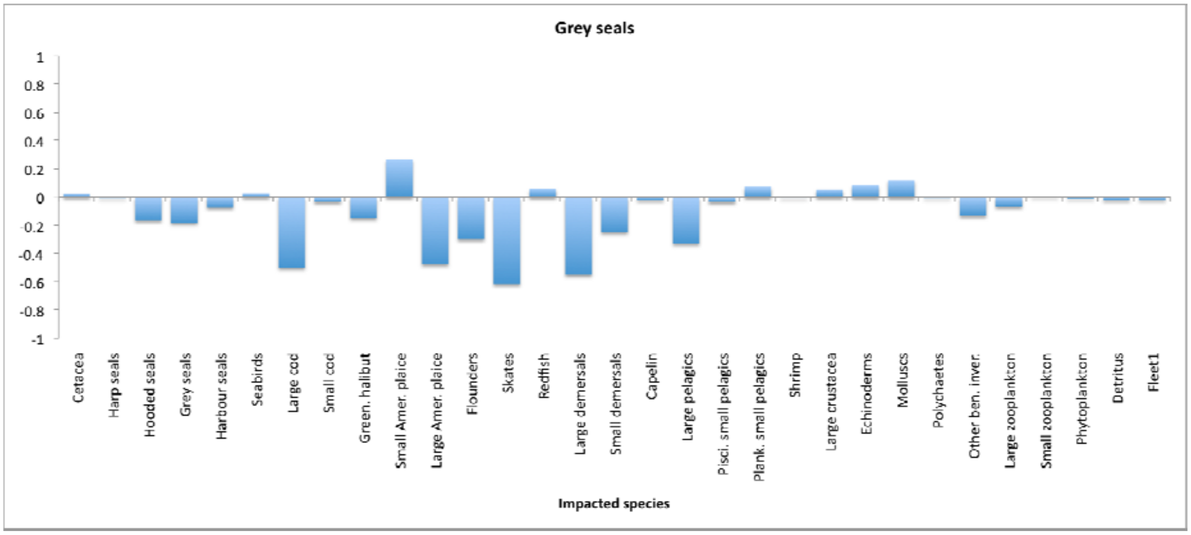

Figure 11: *MTI of grey seals in SGSL for the 1990s based on best available diet information. A positive MTI means that grey seals have an overall positive effect on impacted species and that increasing their biomass would benefit the impacted species. A negative MTI means the grey seals have an overall negative effect on impacted species and that increasing their biomass would reduce the biomass of impacted species.*

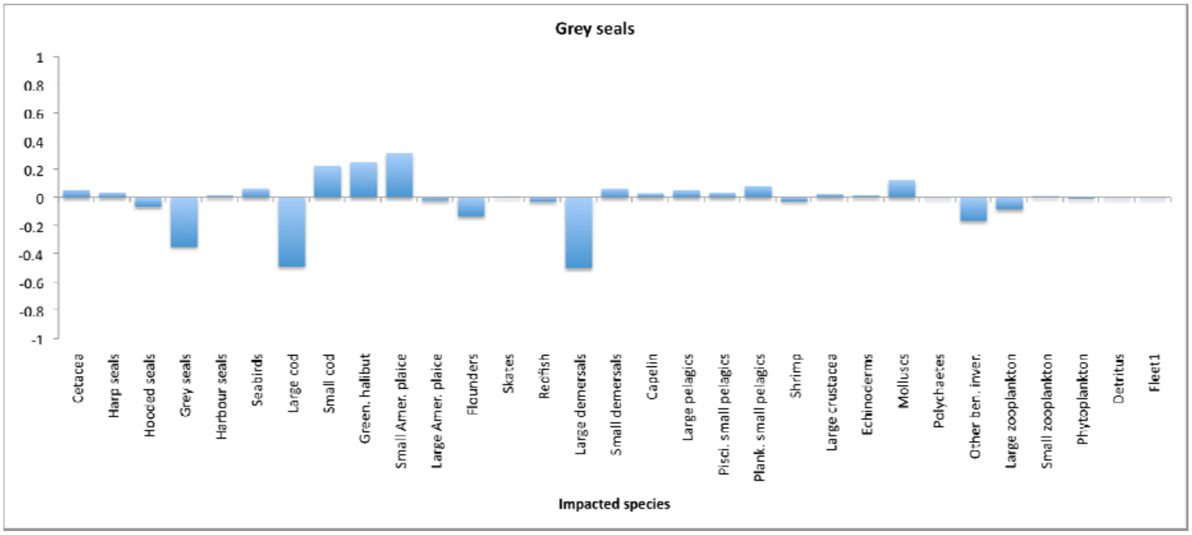

Figure 12: *MTI of grey seals in SGSL for the 1990s based on St. Paul Island's diet scenarios (50% of large cod in the diet). A positive MTI means that grey seals have an overall positive effect on impacted species and that increasing their biomass would benefit the impacted species. A negative MTI means the grey seals have an overall negative effect on impacted species and that increasing their biomass would reduce the biomass of impacted species.*

SIMULATIONS OF GREY SEALS REMOVALS

In the “normal diet” model, where a general removal of grey seals were to occur, the different seal harvest scenarios produced some increase in cod biomass after 25 years of simulation. Multiplying grey seal harvest effort by 2 or 3 (scenarios 1 & 2, which represent a cull of about 30,000 or 40,000 seals over the modeling period) does not seem to be enough to stop the decline of large cod biomass that is occurring right now in the SGSL. Removing the grey seal population by maintaining a harvest effort that is 4 times higher than the actual rate (scenario #3) would slightly increase the biomass of cod, and would allow recovery to about 40% of what it was before the collapse in 1985 (about 125,000 tonnes of cod). Only a total eradication of grey seals would achieve a real gain of biomass of cod in the SGSL. Impacts on small cod population are very similar.

We also tested a single synoptic grey seal cull over only one year. In scenarios # 5 and #6 (removing 15,000 and 50,000 seals in 2010, respectively), there was an increase in cod biomass for about 10 years but then the cod stock collapsed, putting it back to the levels observed prior to the cull. Removing 100,000 seals in 2010 would create an increase of cod biomass that would last longer before beginning to decline, but as grey seals recovered, the cod biomass would decline accordingly.

Assuming an ecosystem where grey seals eat a much higher proportion of cod (based on St. Paul Island’s diet) did not produce results as clear as the previous models (Scenarios 8, 9 & 10; Figure 15). The high consumption by grey seals drives large cod population to low levels that make it almost impossible to recover, whatever the number of seals that are removed from the system. Only by multiplying the grey seal harvest by 4 (Scenario #10, harvesting about 60,000 seals over 25 years, reducing their population to less than 0.2 $t*km^{-2}$) seemed to stop the collapse, with the cod population reaching a level of 6% of the large cod biomass we had in the mid-1980s. However there is considerable uncertainty surrounding these model outcomes.

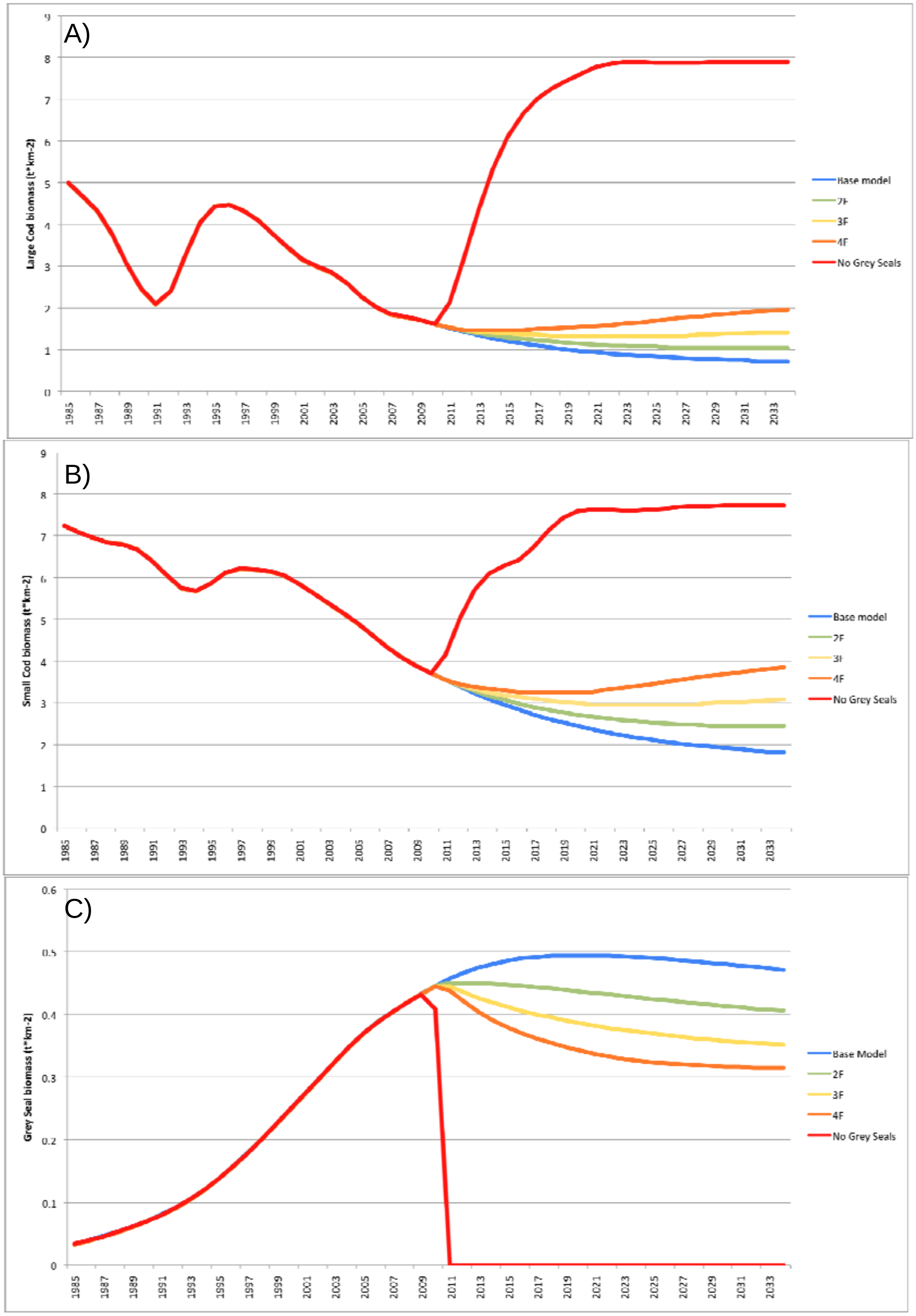

***Figure 14**: Changes in biomass trends for large cod (A) and small cod (B) under different grey seal hunt scenarios (C). Base model = no additional harvest, 2F= 2x harvesting effort, 3F= 3x harvesting effort, 4F = 4x harvesting effort, “No Grey Seals” = eradication of grey seal population.*

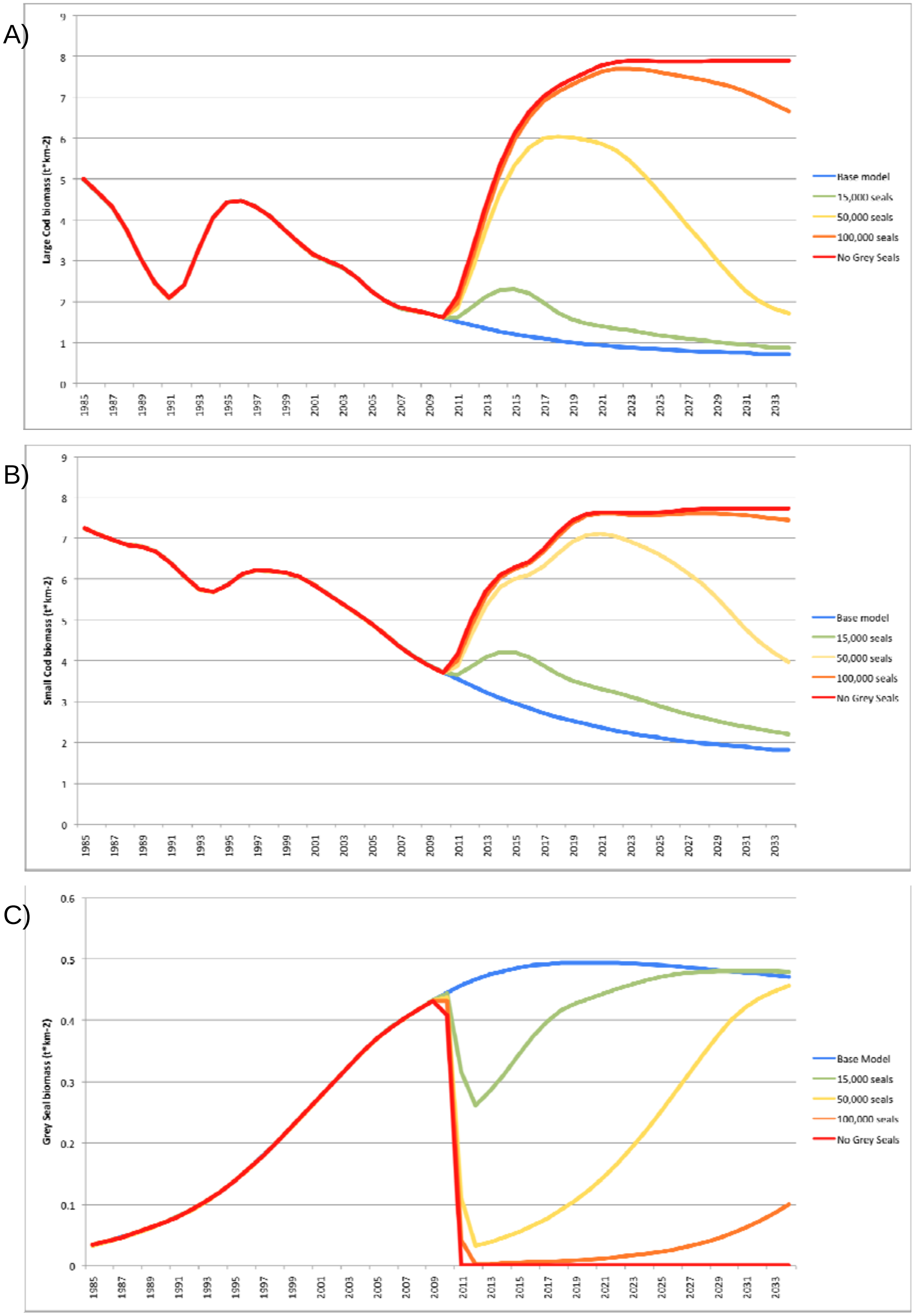

***Figure 15**: Changes in biomass trends for large cod (A) and small cod (B) under different scenarios of a one-year "pulse" harvest of grey seals (C): no additional harvest, 15,000, 50,000, or 100,000 seals removed in 2010 and going back to normal harvest the following years.*

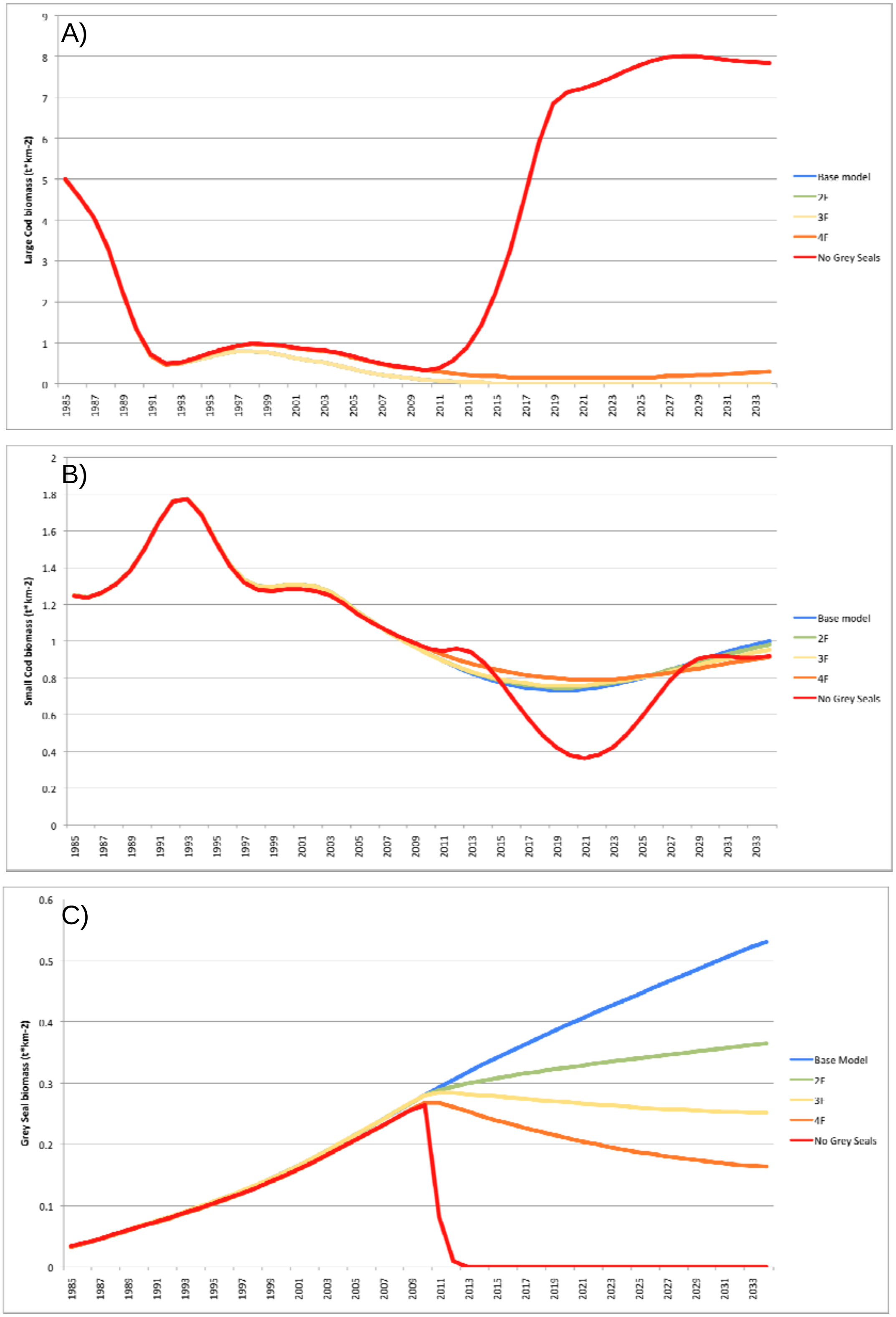

***Figure 16**: Changes in biomass trends for large cod (A) and small cod (B) under different grey seal hunt scenarios (C), assuming a higher proportion of cod in their diet (St. Paul Island). Base model = no additional harvest, 2F= 2x harvesting effort, 3F= 3x harvesting effort, 4F = 4x harvesting effort, "No Grey Seals" = eradication of grey seal population.*

DISCUSSION & CONCLUSIONS

Although preliminary, the model and analyses presented here indicate that the removal of grey seals is likely to be beneficial to the recovery of cod in the southern Gulf of St. Lawrence. However, this needs to be explored further through more explicit testing of scenarios to identify the potential range of outcomes, including possible unintended consequences. Within the context of cod we assumed that the removal of seals occurred across the population under 11 harvest scenarios and two diets, a low and a high cod diet. We also assumed that all seals had the same diet and removals occurred uniformly across the herd without any consideration for spatial-temporal specialization in seal predation on cod. However, the St. Paul Island diet showed that in areas of cod aggregations, where seals overlapped with these aggregations (Stenson et al. 2011; Harvey et al. 2011), that large cod made a significant contribution to the male grey seal diet; this sample also shows that the contribution of cod may be higher than what has generally been considered based on the summer samples alone. The diet sampling (Hammill, 2011; Stenson et al. 2011) also identified that cod comprised a larger component of the male diet than the female diet. Therefore, scenarios need to examine the effects of removing seals that were targeting cod ie sampling in areas of high overlap and removing more males than females as identified by Swain et al. (2011).

Additional scenarios need to examine how long removals should continue, whether at some point cod recovery may reach such a level that grey seals and cod might co-exist. Other scenarios also need to examine at levels grey seal removals may lead to significant changes in ecosystem structure and to identify what other fisheries might be affected and to what level. For example, in this study, cod were identified as the species of most interest, but severe declines in Hake, winter flounder and skate populations in the southern Gulf, have also occurred and can be strongly linked to grey seal predation (Benoit et al. unpublished manuscript; Swain et al. 2010) and it is important that the impact of grey seals within this modeling framework be examined. Additional scenarios could include an evaluation of how long it would require cod to recover under different levels of removals. Although the continued need to remove animals while cod recover might represent a weakness in the cull approach, it also provides a measure of protection by allowing removal levels to be adjusted to minimize the probability that grey seal abundance will decline below management plan objectives, while ensuring cod recovery.

In this analysis we presented two extremes for diet composition, however, results presented at the meeting (Benoit et al. unpublished manuscript; Hammill. 2011) indicate that spatial differences in diet composition do occur. In addition to improving the approach to focusing or targeting removals of different components of the seal population, we could also examine the importance of a spatial component (Ecospace) for our EwE model of the southern Gulf.

Size structure of fish in most NW Atlantic ecosystems has now shifted to a dominance of medium-sized fish all competing for the same food resources (Fisher et al. 2010). The SGSL is probably no different: cod is now smaller than before, and therefore has to compete with new species such as herring and mackerel for similar food resources. These new competitors are also new predators for the juvenile cod, increasing even more their impact on the cod population.

It is generally considered that the removal of top predators will alter the overall structure of the ecosystem and ultimately weaken it, or in other words, make it less resilient to perturbations (Morissette et al. unpublished data). In the context of the SGSL ecosystem, large cod, which was an important predator, has been removed by overfishing and replaced by marine mammals, particularly seals. The current SGSL ecosystem is the result of a fisheries-induced regime shift with a structure that may be weaker than what we had before. Within this context, it is tempting to suggest that the reduction of seal populations, to favour recovery of cod and other demersal fish populations may further weaken the structure of this ecosystem. However, throughout the 19th and early 20th centuries, grey seal numbers were quite low (Lavigueur and Hammill 1993) These low populations sizes of grey seals coincided with low cod biomass during the 1970s, were followed by rapid recovery of cod. Thus this system has already experienced periods when major predators such as cetaceans, seals and cod had been removed at different times over the last 200 years. These were followed by strong recoveries in cod eg during the 1980s or by grey seals (2000s). Reducing grey seals within the context of a closely monitored experiment may lead to a more rapid recovery of SGSL cod, which in combination with a healthy grey seal population, would more closely resemble ecosystem conditions observed in previous centuries.

The Canadian grey seal population has undergone a rapid expansion since the 1960s, increasing from approximately 13,000 animals in 1960 to roughly 400,000 animals today. The reasons for this increase are not well understood, but are probably linked in part to a reduction in removals over the last two decades (Hammill and Stenson, 2011). Throughout this period there have been major changes in demersal fish abundance, with low abundance during the 1970s, high abundance during the 1980s followed by a decline in demersal abundance in the 1990s and continuing into the current century. With the reduction in cod abundance, a major predator has been removed from the ecosystem. Perhaps another scenario to examine is how a reduction in cod biomass may have favoured the recovery of grey seals.

REFERENCES

Allen, K.R. 1971. Relation between production and biomass. Journal of the Fisheries Research Board of Canada 28: 1573-1581.

Bax, N.J. 1998. The significance and p rediction of predation in marine fisheries. ICES Journal of Marine Sciences 55: 997–1030.

Bousquet, N., N. Cadigan, T. Duchesne, and L.-P. Rivest. 2010. Detecting and correcting underreported catches in fish stockassessment: trial of a new method. Can. J. Fish. Aquat. Sci. 67: 1247-1261.

Bowen,W.D. 1997. Role of marine mammals in aquatic ecosystems. Marine Ecology Progress Series 158:267–274.

Bundy, A. 2001. Fishing on ecosystems: the interplay of fishing and predation in Newfoundland-Labrador. Canadian Journal of Fisheries and Aquatic Sciences 58: 1153-1167.

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

Christensen, V. 1998. Fishery-induced changes in a marine ecosystem: insight from models of the Gulf of Thailand. Journal of Fish Biology 53: 128 - 142.

Christensen, V., and Pauly. D. 1992. Ecopath II: a software for balancing steady-state ecosystem models and calculating network characteristics. Ecological Modelling 61: 169-185.

Christensen, V. and Walters, C.J. 2004. Ecopath with Ecosim: methods, capabilities and limitations. Ecological Modelling 172: 2-438.

Christensen, V. Walters, C.J. and Pauly, D. 2005. Ecopath with Ecosim: a user's guide. Fisheries Centre, University of British Columbia, Vancouver, Canada & International Center for Living Aquatic Resources Management, Penang, Malaysia.

Christensen, V., Walters, C.J., Pauly, D., and Forrest, R. 2008. Ecopath with Ecosim: User Guide. November 2008 version. Lenfest Ocean Futures Project, 235 pp.

Chouinard, G.A., D. P. Swain, M.O. Hammill and G. A. Poirier. 2005. Correspondence between changes in grey seal population abundance and variation in natural mortality of southern Gulf of St. Lawrence cod. Can. J. Fish. Aquat. Sci. 62:1991-2000.

Department of Fisheries and Oceans (DFO). 2001. Capelin of the Estuary and Gulf of St. Lawrence. DFO—Science, Stock Status Report B4-03.

Department of Fisheries and Oceans (DFO). 2002. Gulf of St. Lawrence (4RST) Greenland halibut in 2001. DFO—Science, Stock Status Report A4-03.

Estes, J.A., DeMaster, D.P., Doak, D.F., Williams, T.M., Brownell, R.L. 2007. Whales, whaling, and ocean ecosystems. University of California Press, Berkeley, CA.

Fisher, J., Frank, K., and Leggett, W. 2010. Breaking Bergmann’s rule: truncation of Northwest Atlantic marine fish body sizes. Ecology 91: 2499-2505.

FRCC. 2004. 2004 / 2005 Conservation Requirements for Groundfish Stocks in the Gulf of St. Lawrence (April 2004) (FRCC.2004.R.3). Available at:. http://www.frcc.ca/eindex.htm

Gascon, D., Aparicio, M., Mercille, B., 1990. Estimations du mélange entre les stocks de morue Nord du Golfe du Saint Laurent (Divisions 3Pn4RS) et les stocks adjacents (2J3KL, 3Ps, et 4TVn [Janvier-Avril]) à partir de résultats de marquage. CAFSAC Research Document 90/61.

Hammill, M.O. 2011. Feeding by grey seals in the southern Gulf of St. Lawrence. DFO Can. Sci. Advis. Sec. Res Doc. 2010/130.

Hammill, M.O. and Stenson, G.B. 2000. Estimated prey consumption by harp seals (Phoca groenlandica), hooded seals (Cystophora cristata), grey seals (Halichoerus grypus) and harbour seals (Phoca vitulina) in Atlantic Canada. Journal of Northwest Atlantic Fishery Science 26: 1-23.

Hammill, M.O. and Stenson, G.B. 2011. Pup production of Northwest Atlantic grey seals in the Gulf of St. Lawrence. DFO Can. Sci. Advis. Sec. Res Doc. 2010/122.

Hanson, J.M. and Chouinard, G.A. 2002. Diet of Atlantic cod in the southern Gulf of St. Lawrence as an index of ecosystem change, 1959-2000. Journal of Fish Biology 60: 902-922.

Hanson, J.M., and Lanteigne, M. 1999. Results of an experimental shrimp fishery in Chaleur Bay, southern Gulf of St. Lawrence. North-American Journal of Fisheries Management 19: 713-723.

Harley, S.J., and Myers, R.A. 2001. Hierarchical Bayesian models of length-specific catchability of research trawl surveys. Canadian Journal of Fisheries and Aquatic Sciences 58: 1569-1584.

Harvey, V., Hammill, M.O., Swain, D.P., Breed, G.A., Lydersen, C. and Kovacs, K.M. 2011. Winter foraging by a top predator, the grey seal, in relation to the distribution of prey. DFO Can. Sci. Advis. Sec. Res Doc. 2010/124. iv + 41 p.

Heymans, J.J. .2005. Ecosystem model of the Eastern Aleutians and the Gulf of Alaska in 1963. In: Food Web Models and Data for Studying Fisheries and Environmental Impacts on Eastern Pacific Ecosystems (eds. S. Guénette and V. Christensen). Fisheries Centre Research Reports 13, 83–105.

Hurlbut, T., and Clay, D. 1998. Morphometric and meristic differences between shallow- and deep-water populations of white hake (Urophycis tenuis) in the southern Gulf of St. Lawrence. Canadian Journal of Fisheries and Aquatic Sciences 55: 2274-2282.

Lavigueur, L., and M.O. Hammill. 1993. Distribution and seasonal movements of grey seals, Halichoerus grypus, in the Gulf of St. Lawrence. Canadian Field Naturalist 107: 329-340.

Lilly, G.R., 1991. Interannual variability in predation by cod (Gadus morhua) on capelin (Mallotus villosus) and other prey off southern Labrador and northeastern Newfoundland. ICES Marine Science Symposia 193: 133-146.

Morissette, L. 2007. Complexity, cost and quality of ecosystem models and their impact on resilience: a comparative analysis, with emphasis on marine mammals and the Gulf of St. Lawrence. Ph.D. Thesis, University of British Columbia, Vancouver, BC, Canada.

Morissette, L., Hammill, M.O., and Savenkoff, C. 2006. The trophic role of marine mammals in the Northern Gulf of St. Lawrence. Marine mammal science 22: 74-103.

Morissette, L., Pedersen, T., and Nilsen, M. 2009 Comparing pristine and depleted ecosystems: the Gulf of St. Lawrence, Canada vs. the Sørfjord, Norway. Effects of intense fisheries on marine ecosystems. Progress in Oceanography 81: 174-187.

Morissette, L, Kaschner, K., and Gerber, L. 2010. ‘Whales eat fish’? Demystifying the myth in the Caribbean marine ecosystem. Fish and Fisheries, DOI: 10.1111/j.1467-2979.2010.00366.x

Myers, R.A., and Worm, B. 2003. Rapid worldwide depletion of predatory fish communities. Nature (London) 423: 280-283.

National Research Council. 2003. The decline of Steller Sea Lion in Alaskan waters: Untangling food webs and fishing nets. Committee on the Alaska groundfish fishery and Steller Sea lions. National Academies Press, Washington, D.C.

Ni, I.-H. 1982. Meristic variation in beaked redfish, Sebastes mentella and S. fasciatus, in the Northwest Atlantic. Canadian Journal of Fisheries and Aquatic Sciences 39: 1664-1685.

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., Torres, F.C.Jr. 1998. Fishing down marine food webs. Science 279: 860-863.

Pitt, T. K. 1973. Food of American plaice (*Hippoglossoides platessoides*) from the Grand Bank, Newfoundland. Journal of the Fisheries Research Board of Canada **30**: 1261-1273.

Piroddi, C. 2008. An ecosystem-based approach to study two dolphin populations around the island of Kalamos, Ionian sea, Greece. MSc thesis, University of British Columbia, Canada.

Plagányi, É.E. 2007. Models for an ecosystem approach to fisheries. FAO fisheries technical paper 477. 126 pp.

Plagányi, É.E. and Butterworth, D.S. 2004. A critical look at the potential of Ecopath with Ecosim to assist in practical fisheries management. In Ecosystem Approaches to Fisheries in the Southern Benguela. Shannon, L.J., Cochrane, K.L. and Pillar, S.C. (Eds). African Journal of Marine Science 26: 261-287.

Punt, A.E. and Butterworth, D.S. 1995. The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 4. Modelling the biological interaction between Cape fur seals Arctocephalus pusillus pusillus and the Cape hakes Merluccius capensis and M. paradoxus. South African Journal of Marine Sciences 16: 255-285.

Savenkoff, C., Bourdages, H., Swain, D.P., Despatie, S.-P., Hanson, J.M., Methot, R., Morissette, L., Hammill, M.O., 2004. Input data and parameter estimates for ecosystem models of the southern Gulf of St. Lawrence (mid-1980s and 1990s). Canadian Technical Report of Fisheries and Aquatic Sciences 2529, vi + 105 p.

Shannon, L.J., Christensen, V., and Walters, C.J. 2004. Modelling stock dynamics in the southern Benguela ecosystem for the period 1978 – 2002. Afrian Journal of Marine Science 26: 179-196.

Sinclair, A.F. 2001 Natural mortality of cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. ICES J. Mar. Sci. 58:1-10.

Stenson, G.B. 2009. Total Removals of Northwest Atlantic Harp Seals (Pagophilus groenlandicus) 1952-2009. Canadian Science Advirory Secreteriat, Research Document 2009/112. 34 pp.

Stenson, G.B., Hammill, M.O., and Flight, J. 2011. Winter diet of Greay Seals in Cabot Strait. DFO Can. Sci. Advis. Sec. Res Doc. 2010/128.

Strain, P.M. 1988 (Ed.). Chemical oceanography in the Gulf of St. Lawrence. Canadian Bulletin of Fisheries and Aquatic Sciences 220.

Swain, D.P. 2010. Life-history evolution and elevated natural mortality in a population of Atlantic cod (*Gadus morhua*). Evolutionary Applications, doi:10.1111/j.1752-4571.2010.00128.x.

Swain, D.P. and G.A. Chouinard. 2008. Predicted extirpation of the dominant demersal fish in a large marine ecosystem: Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Can. J. Fish. Aquat. Sci. 65:2315-2319.

Swain, D.P., Frank, K.T., and Maillet, G. 2001. Delineating stocks of Atlantic cod (Gadus morhua) in the Gulf of St. Lawrence and Cabot Strait areas using vertebral number. ICES Journal of Marine Research 58, 253–269.

Swain, D.P., Savoie, L., Hurlbut, T. Surette, T., Daigle, D. 2009. Assessment of the southern Gulf of St. Lawrence cod stock, February 2009. Canadian Science Advisory Secretariat, Research Document 2009/037. 129 pp.

Swain, D.P., Benoît, H.P., Hammill, M.O., McClelland, G. and Aubry, É. 2011. Alternative hypotheses for causes of the elevated natural mortality of southern Gulf cod: the weight of evidence. DFO Can. Sci. Advis. Sec. Res Doc. 2011/036.

Ulanowicz, R.E., Puccia, C.J. 1990. Mixed trophic impacts in ecosystems. Coenoses 5, 7–16.

Walters, C. and Kitchell, J.F. 2001. Cultivation/depensation effects on juvenile survival and recruitment: Implications for the theory of fishing. Canadian Journal of Fisheries and Aquatic Sciences 58: 39-50.

Walters, C., Christensen, V. and Pauly, D. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Reviews in Fish Biology and Fisheries 7: 139-172.

Yodzis, P. 2000. Diffuse effects in food webs. Ecology 81: 261-266.

Yodzis, P. 2001. Must top predators be culled for the sake of fisheries? Trends in Ecology & Evolution 16: 78-84.