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A model of predation by harp seals (*Phoca groenlandica*) on the northern Gulf of St. Lawrence stock of Atlantic cod (*Gadus morhua*)

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Document de recherche 2007/066

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Un modèle de prédation des phoques du Groenland (*Phoca groenlandica*) sur les stocks de morue (*Gadus morhua*) du nord du golfe du Saint-Laurent

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TABLE OF CONTENTS

List of Tables

List of Figures

Abstract

A dynamic model was developed to examine harp seal predation on Atlantic cod in the northern Gulf of St. Lawrence. The model describes the energetic requirements of the seal population by accounting for sex, age-structure and seal growth. The linkage between seals and cod is modeled through a functional response (FR) that was derived from the reconstruction of the seal diet using morphometric relationships and a large database of seal stomach contents. The FR then allows us to quantify the impact of seal predation on the cod population, based on age-structure attack rates and accounting for changes in cod size-at-age with time. Cod recruitment (age 1) is modeled via a linear stock-recruitment relationship based on total egg production that accounts for changes in female length at maturity and cod condition. Natural mortality other than seal predation also depends on cod condition used as an integrative index of changes in environmental conditions.

The model was fitted following a maximum likelihood estimation approach to a consistent time-series of abundance indices taking into account changes in DFO research vessels over the last 23 years (1984-2006). Results were consistent with the most recent DFO stock assessment of the northern Gulf of St. Lawrence cod stock, explaining the history of the stock. Predation mortality, despite an increase in the mid-1990s, was a minor proportion of total mortality for ages targeted by harp seals, *i.e.* ages 1-4. Total cod biomass removed by seals showed higher interannual variability and greater decrease in the early 2000s than for modeling approaches based on a constant ratio diet. The type of FR–II or III– has a strong impact on the biomass removed, especially when the cod abundance is low. Sensitivity analyses were performed to assess the robustness of the results. The next step will be to project the model in to the future to evaluate repercussions of predation mortality rates on cod recovery.

Résumé

Un modèle dynamique a été développé pour analyser la prédation des phoques du Groenland sur la morue franche du nord du golfe du Saint-Laurent. Le modèle décrit les besoins énergétiques de la population de phoques en prenant en compte le sexe, la structure d'âge et la croissance des phoques. Le lien entre les phoques et les morues est modélisé au moyen d'une réponse fonctionnelle (RF) dérivée de la reconstruction du régime des phoques à partir de relations morphométriques et d'une grande base de données de contenus stomacaux de phoques. La RF nous permet ensuite de quantifier l'impact de la prédation des phoques sur la population de morue, se basant sur des taux d'attaque structurés en âge et prenant en compte les changements de longueur aux âges des morues. Le recrutement des morues (âge 1) est modélisé via une relation stock-recrutement linéaire basée sur la production totale d'oeufs qui tient compte des changements de longueur à maturité des femelles et la condition des morues. La mortalité naturelle autre que la prédation par les phoques tient également compte de la condition des morues.

Le modèle a été ajusté suivant une approche d'estimation du maximum de vraisemblance à une série temporelle cohérente d'indices d'abondance qui tient compte des changements de navires de recherche du MPO au cours des 23 dernières années (1984-2006). Les résultats sont cohérents avec l'évaluation la plus récente faite par le MPO du stock de morue du nord du golfe du Saint-Laurent, expliquant l'histoire passée du stock. La mortalité par prédation, malgré une augmentation dans le milieu des années 1990, a constitué une part mineure de la mortalité totale pour les âges ciblés par les phoques, c.-à-d. les âges 1-4. La biomasse totale de morue consommée par les phoques a montré une variabilité importante et une plus grande diminution au début des années 2000 que pour les approches de modélisation basées sur un régime à ratio constant. Le type de RF –II ou III – a un impact fort sur la biomasse prélevée, particulièrement quand l'abondance de morue est faible. Des analyses de sensibilité ont été conduites pour évaluer la robustesse des résultats. La prochaine étape sera de faire des projections dans le futur avec le modèle pour évaluer les répercussions des taux de mortalité par prédation sur la reconstitution du stock de morue.

1 Introduction

Most of the Atlantic cod (*Gadus morhua* L.) fisheries off Atlantic Canada collapsed almost simultaneously in the early 1990s and moratoria were declared on commercial exploitation in the mid-1990s (Myers et al 1996). There has been considerable debate regarding the causes for the decline in cod abundance and subsequent lack of recovery (*e.g.* Shelton and Healey 1999). The possibility that the collapse for the northern cod fishery off Newfoundland and Labrador (*i.e.* Northwest Atlantic Fisheries Organisation (NAFO) divisions 2J3KL) was due to an interaction between fishing and a deteriorating environment was rejected (Hutchings and Myers 1994, Hutchings 1996) and overfishing was alleged to be the main factor that contributed to the collapse, due to several interrelated common factors (Myers et al 1997). By contrast, for the northern Gulf of St. Lawrence (NGSL) cod stock (NAFO divisions 3Pn4RS), it has been suggested that changes in environmental conditions, namely lower temperature, played a role in the fishery collapse through a decline in growth and consequently recruitment (Dutil et al 1999) that coincided with poor individual condition in the early 1990s (Lambert and Dutil 1997, Dutil and Lambert 2000). Poor cod condition could also cause an increase in natural mortality through starvation, and enhanced vulnerability to predation through lower swimming activity (Dutil et al 1999).

In spite of the fishing moratoria in place on the different cod stocks, there has been limited sign of recovery (DFO 2003; Rice et al 2003) and recent updated assessments indicate most of the stocks are still outside safe biological limits (*e.g.* MPO 2007). More than 40 alternative hypotheses have been put forward to explain the lack of recovery of cod stocks (DFO 2003; Rice et al 2003). Current reasons include: low recruitment success linked to poor prerecruit survival (Swain and Sinclair 2000, Fu et al 2001); increased natural mortality on mature cod associated with increased grey seal (*Halichoerus grypus*) predation (Fu et al 2001, Chouinard et al 2005) and continuing fishing activity under lower productivity (Shelton et al 2006).

As large predators, marine mammals may play an important role in the structure and function of marine ecosystems through both direct and indirect impacts on prey populations (Yodzis 1998; Morissette et al 2006). However, these relationships may be complex, and with the exception of the sea otter, where ecosystem effects are quite evident, the role of marine mammals in structuring marine ecosystems remains unclear (Bowen 1997). To evaluate the role that seal predation may play in the recovery of Atlantic groundfish stocks, an understanding of the structure and function of ecosystem components is needed along with the role that marine mammal predation may play as a component of natural mortality.

The collapse and failure of Northwest Atlantic groundfish stocks to recover, coincides with marked increases in seal populations, for example the northwest Atlantic harp seal (*Phoca groenlandica*) population that has increased from less than 2 million in the 1970s to almost 6 million today (Hammill and Stenson 2005). This has led to some statements, that higher mortality resulting from increased predation mortality by seals might be limiting cod recovery. However, few studies have attempted to either support or refute this hypothesis. Here we examine the role that harp seal predation may play in the recovery of Atlantic groundfish stocks. We present a Seal Impact on Cod Abundance (SIMCAB) model that examines this impact in detail, using the simplified assumption that changes in mortality levels from harp seals will have immediate and direct impacts on the recovery of cod in the NGSL (Duplisea and Hammill 2006).

2 Materials and Methods

2.1 General model

SIMCAB was developed as a predator/prey model where the dynamics of the cod population are impacted by harp seal predation via a functional response (FR). The population model for the northern Gulf cod is an age-based cohort model where mortality is derived from three sources; the fishery, harp seal predation and, natural mortality due to other causes than harp seal predation (disease, virus, etc.). In this respect, the model is similar to a multispecies virtual population analysis (MSVPA) (Magnússon 1995), where natural mortality on a population age-class for a species is partitioned into predation and residual components. The population model for the northern Gulf population of harp seals is an age-structured model that was initially developed by Roff and Bowen (1983, 1986) and recently updated by Hammill and Stenson (2005). A FR of harp seal to cod based on age-structured attack rates estimated in 1998-2001 was used to model the predation relationship between both models (Fig. 1). SIMCAB was written in the program language R (R Development Core Team 2007). A summary of notations and equations is given in Appendix A.

2.2 Cod population model

The cod model was setup as a Leslie matrix model which is an efficient way to model age-structured populations, which multiplies a population abundance at age vector, n (length n), by a survivorship matrix, A (n X n), to give a new n (Leslie 1945, Caswell 1998). We extend the Leslie matrix models in two respects. First, an explicit observation model describes how the hidden state or latent process is observed, linking the available data to the underlying dynamics. Second, we use a separate model for each population process to specify cod population dynamics, *i.e.* recruitment, predation mortality and natural mortality other than predation. The cod model considers 13 age classes of cod from 1 to 13. The number of individuals in each class is modelled, accounting for losses in each year from the fishery,

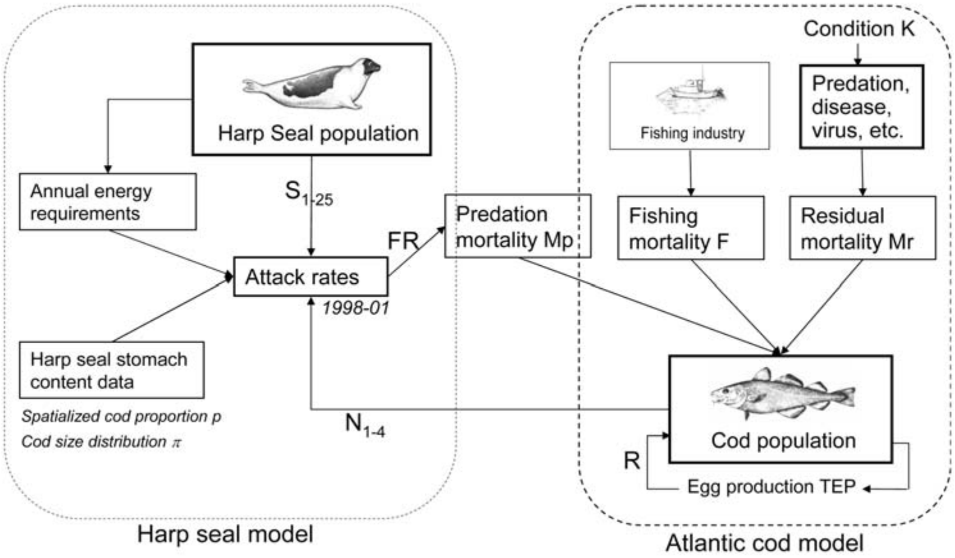

FIG. 1 – Conceptual scheme of the harp seal -cod model. R = recruitment at age 1; N = number of cod; S = number of seals

harp seal predation and, other mortality sources. Recruitment occurs at age 1 following through all age classes. There is 100% mortality at end of the 13th age class for all cohorts. The A matrix is dynamic, with survivorship changing in each time step in accordance with the impact resulting from harp seal predation on cod.

2.2.1 Cod recruitment

In the model, recruitment, *i.e.* fish numbers at age 1, was estimated by accounting for yearly changes in sex ratio, sexual maturation of the gonads, length-at-age and condition. An index of the reproductive potential of cod was developed from an estimate of total egg production (TEP). TEP was estimated each year t following:

$$TEP_t = \sum_{a_m}^{A+} N_{a,t} \times s_{a,t} \times \phi_{a,t} \times f_{a,t} \tag{1}$$

where a is the age, a_m is the age at maturity, s is the sex ratio, $A+$ is the last age-group, *i.e.* 13+, φ is the proportion of maturing females, and f is the potential fecundity.

A linear TEP-recruitment relationship incorporating a lognormally distributed random deviation was used to calculate fish numbers at age 1 in year t:

$$R_t = r \times TEP_{t-1} \times e^{u_t} \qquad \mu_t \sim N(0,\sigma_R) \tag{2}$$

where *r* is the recruitment per million of eggs parameter estimated through the fitting process (see section 3) and assumed constant in time. Multiplicative lognormal process errors e^{u_t}, where the μ_t are independent random variables normally distributed with mean 0 and standard deviation σ_R, represent the stochasticity of recruitment processes.

Sex ratio (*s*) and maturity ogive (ϕ) data were derived from winter surveys conducted with the MV "Gadus Atlantica" (1984-1994) and spring samples available from the Groundfish Sentinel Fisheries Program (http://www.osl.gc.ca/pse/en/). Fulton's condition factor (Fulton 1902) based on length and weight data was also obtained from the winter surveys (1984-1994), the Sentinel Fisheries Program (1995-2007), and supplementary research surveys conducted during the pre-spawning period in 1994, 1995, 1997, and 1998 (Y. Lambert unpublished data). Fulton's condition factor was applied to mean length-at-age to obtain condition factor-at-age.

Previous studies showed that length and condition factor had significant effect on the fecundity of cod in the NGSL (Lambert and Dutil 2000, Lambert et al. 2000). This dependence of fecundity on length and condition factor was used to develop a generalized linear model to determine the variation in the fecundity between 1984 and 2005. The fecundity model was developed using individual values of fork length, condition factor and potential fecundity for cod sampled in 1995, 1998, 2001 and 2002. Mean length-at-age and condition factor-at-age obtained as described above were used in the model to obtain fecundity-at-age.

2.2.2 Fishing removals

The catch-at-age matrix of cod (in numbers) used was obtained from the last updated stock assessment carried out in February 2007 (MPO 2007). All quantities caught and landed for both commercial and recreational fisheries, excluding discards, were included in the data.

2.2.3 Natural mortality excluding harp seal predation

The Atlantic cod population in the NGSL is subjected to multiple sources of mortality other than fishery catches and seal predation, mainly predation by other fish species, disease, and starvation (*e.g.* Savenkoff et al 2004, Savenkoff et al 2007). Assessment models usually consider only a constant rate of instantaneous mortality (*M*) at age and this value is often set at 0.2 y^{-1}. Here, as we model all age-groups it is important to consider the high mortality experienced by fish before they recruit to the fishery. Therefore, the rate of natural mortality excluding harp seal predation (*Mr*) was modelled as an age-dependent function to capture the mortality regime experienced by a fish throughout its life.

$$M_{r_{a,t}} = \vartheta_t + (\alpha - \vartheta_t) \times \exp - \left(\frac{a}{\beta} \right) \tag{3}$$

where ϑ is the asymptote of M_r that depends on cod condition (see below), α is the intercept, *i.e.* the residual natural mortality at age 0, and β is the ramping down slope of the function.

In addition, *M* estimates based on sequential population analysis (SPA) using the ADAPT software (Gavaris 1988) showed variations in natural mortality with time (Benoît and Chouinard 2004, Grégoire and Fréchet 2005). Consequently, M_r was assumed time-dependent and expressed as a function of interannual variations in cod condition (Lambert and Dutil 1997a). The Fulton's condition factor has been shown to be a good indicator of total available energy reserves in cod and is related to feeding intensity, growth, maturation, fecundity, and survival (Lambert and Dutil 1997b). It is therefore an integrative indicator for environmental conditions and prey availability (Lambert and Dutil 1997b, Rätz and Lloret 2003). Condition plays a major role in mortality, the lower the condition of the cod the less adept they will be when faced with circumstances that could lead to mortality (Dutil and Lambert 2000). The closure of several Northwest Atlantic cod fisheries in the mid-1990s was an unique opportunity to show that the instantaneous natural mortality rates (M) of the cod stocks were close or higher than 0.4 y-^{1} in recent years (Sinclair 2001, Shelton et al 2006). Time trends in M estimated with the sequential population analysis (SPA) were consistent with the hypothesis of a current rate of natural mortality close to 0.4 y^{-1} for the large cod in the NGSL (Grégoire and Fréchet 2005) in the early 1990s whereas it was considered to be 0.2 y^{-1} in the late 1970s and early 1980s (MPO 2007). ϑ was thus assumed to be comprised between 0.2 y^{-1} and 0.4 y^{-1} and modelled as a decreasing linear function of cod condition:

$$\vartheta_t = b - a \times K_t \tag{4}$$

where the parameters *a* and *b* are set according to values of low condition (K_{low}) and high condition (K_{high}) cut-offs that correspond to a value of ϑ of 0.4 and 0.2 respectively (Fig. 2).

Mean condition factor was estimated for ages 5-13 each year. K_{low} was set at 0.66, corresponding to the upper limit of the condition distribution of Atlantic cod during starvation laboratory experiments (Dutil and Lambert 2000). K_{high} was set at 0.9 that corresponded to the mean condition of fed cod used as controls in the laboratory experiments (Dutil and Lambert 2000). For the period 1984-2006, the asymptote ϑ had an average of 0.30 (stan-

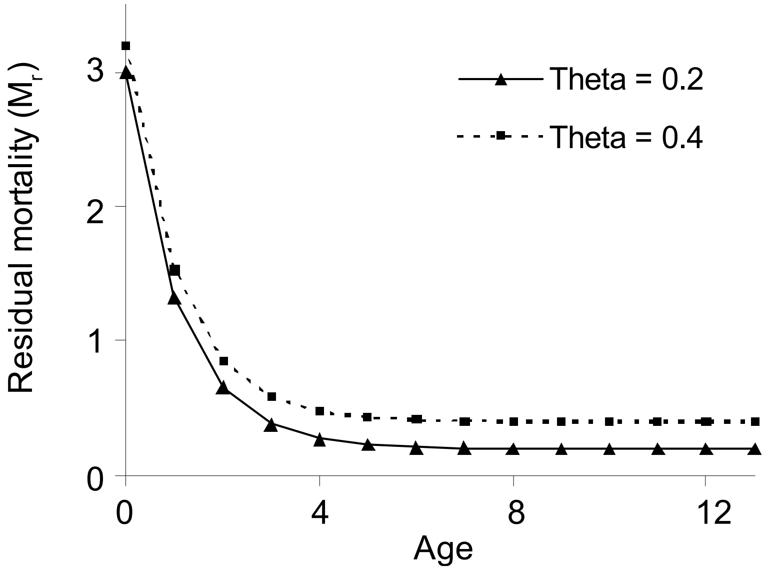

FIG. 2 – Decreasing function with age of the rate of natural mortality M_r excluding harp seal predation for two values of the asymptote ϑ of 0.2 and 0.4

dard deviation of 0.04) with a maximum of 0.38 in 1993 and a minimum of 0.19 in 2005. Constant values of 0.2 and 0.4 were also considered for the asymptote ϑ and the impact on the results was assessed through the Akaike Information Criterion (AIC), that is based on penalized likelihoods.

2.3 Harp seal population model

2.3.1 Harp seals in the northern Gulf of St. Lawrence

Northwestern Atlantic harp seals summer in the Arctic, but move into southern waters off northeastern Newfoundland and into the Gulf of St. Lawrence in early November where they overwinter (Sergeant 1992). Breeding occurs on the pack ice in March. Animals moult during April then return to the Arctic, exiting the Gulf by late May. A few animals may also summer in the Gulf of St. Lawrence. Approximately 25-33% of the harp seal moves into the Gulf, with the remainder of the population remaining off the southeastern Labrador-northeastern Newfoundland coast (Stenson et al 2002, 2003) (Fig. 3).

The Northwest Atlantic harp seal population size was estimated using a two-parameter population model that incorporates information on pup production, removals from the population, and age-specific reproductive rates since 1980 (Hammill and Stenson 2005; Fig. 4). This model estimates unreported mortality (*i.e.* natural mortality plus unreported anthropogenic mortality) and an initial abundance to fit to independent field estimates of pup production.

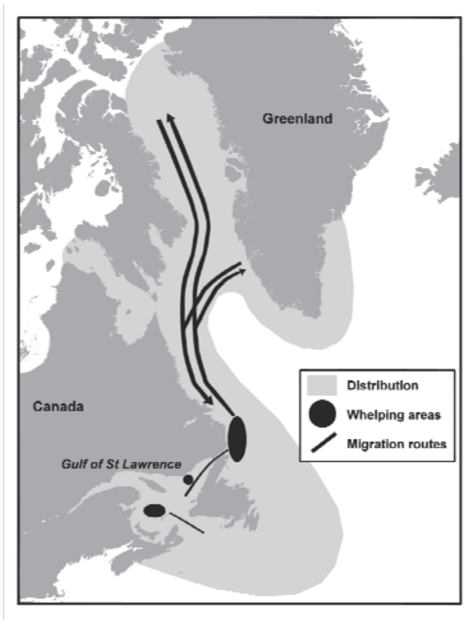

FIG. 3 – Migration of the Northwest Atlantic harp seal population

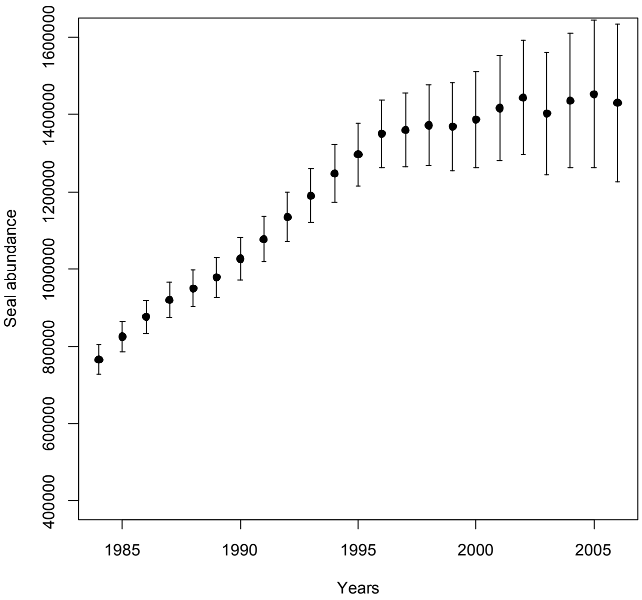

FIG. 4 – Harp seal abundance (±standard error) in the northern Gulf of St. Lawrence

2.3.2 Annual cod biomass requirements for harp seals

Cod consumed by harp seals are required to derive the age-structured attack rates of the FR of harp seal to cod (see section 2.4). The period 1998-2001 was considered to estimate the FR of harp seals to cod because the populations of harp seals and cod were relatively stable from 1998-2001 and a large number of seal stomachs were collected at that time. Estimates of annual biomass of cod consumed during 1998-2001 were obtained by considering annual energy requirements for the harp seal population, proportion of cod in seal's diet, and seal distribution in the NGSL (see Hammill and Stenson 2004).

The daily gross energy intake ($GEI_{d,a}$, kJ d^{-1}) of an individual harp seal was estimated as:

$$GEI_{d,a} = \frac{AF \times GF_a \times 293 \times BM_a^{0.75}}{ME} \tag{5}$$

where *d*, and *a* index day and age respectively. The body mass at-age (BM_a; kg) was derived from the average of male and female seal body mass estimates (Hammill and Stenson 2005). Metabolizable energy (*ME*), the percent of *GEI* available to the seal, was estimated at 83% based on experimental work done by Ronald et al (1984). The growth factor (*GF*) is the additional energy required at age *a* by young seals (<6 years). *GF* was set at 1.8, 1.6, 1.4, 1.3, 1.1, 1.1, and 1.0 for animals aged 0, 1, 2, 3, 4, 5, and >6 years respectively (Olesiuk, 1993). The activity factor (*AF*) was estimated at 2 following Worthy (1999). The Kleiber equation $293 \times BM_a^{0.75}$ represents the relationship between body mass and the metabolic rate (Kleiber 1975).

The amount of biomass needed to maintain seal growth ($S\,G_a$, tons) was calculated as:

$$SG_a = \frac{GEI_{d,a} \times \rho}{AE} \times 10^{-6} \tag{6}$$

The average energy (*AE*) of 5.04 kJ g^{-1} was derived from the energy values for 55 prey found in the stomachs of harp seals in the northern Gulf (M Hammill unpublished data). ρ = 150 represents the number of feeding days in Gulf each year (see section 2.3.1).

The total biomass ($T\,B_a$; tons) of prey consumed by the seal population per year was calculated as:

$$TB_{a,t} = S\,G_a \times S_{a,t} \tag{7}$$

where t indexes the year (1998-2001) and S_a represents the updated population numbers-at-age of harp seals found in the NGSL (Hammill and Stenson 2005).

The biomass of cod consumed (E_t; tons) was then found as:

$$E_t = TB_{a,t} \times p_t \tag{8}$$

where p_t is the annual average proportion of cod in seals diet weighted by the residency of the seal population in the areas 4Ra-c, 4Rd-3Pn, and 4S of the NGSL during November-March (Hammill and Stenson 2004). For the area 4S, a mean proportion of cod of 0.02% was considered for the period 1998-2001 and also included 18 seal stomachs collected in 1996 in Godbout in order to increase sample size.

TAB. 1 – Proportion (*p*) of Atlantic cod in harp seal diet weighted by their relative residency in each area during the period November-March. *n* = number of samples

Year	n			p
	4Ra-c	rRd-3Pn	4S	
1998	27	21	-	0.0506
1999	28	22	24	0.0538
2000	25	39	29	0.0382
2001	30	16	-	0.0377

2.4 A functional response of harp seal to cod

A FR is essential to accurately model the energy requirements and consumption rates according to the method of predation and prey density (Koen-Alonso 2006). Harp seals are generalist predators that prey on many fish species (Lawson et al 1998). Generalist predators can exhibit different predation patterns in response to prey density. These can be explained using a type II or a type III FR (Holling 1959; Fig. 5). The type II FR is typical of predators that specialize on a few prey, whereas with type III, predators exhibit prey switching and/or concentrate feeding on prey that are abundant (Koen-Alonso 2006).

The FR of seal to cod is comprised of an attack rate, asymptotic attack rate, and age-structured cod and seal populations (Trzcinski et al 2006). The FR is based on cod biomass requirements for harp seals (see above), abundance of cod, and age-structure and proportion of cod in the seal diet in the reference period 1998-2001. The FR was converted between type II and type III by changing the exponent for cod abundance. Both types were applied in the model and criteria were used to determine the best fit.

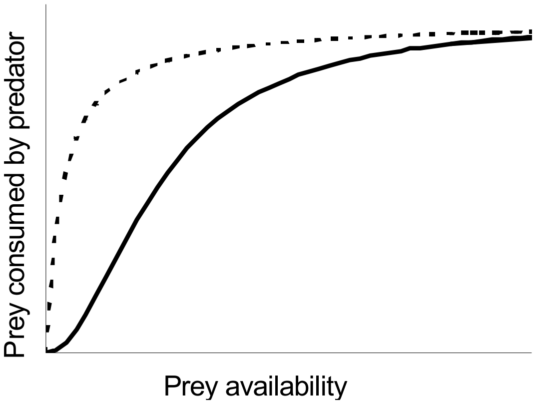

FIG. 5 – Typical type II (dashed line) and type III (solid line) functional responses

2.4.1 Estimating the age-structure of cod in seal diet

Cod biomass removed by harp seal predation during 1998-2001 (section 2.3.2) was reallocated between cod age-classes based on information available from the analysis of seal stomach contents (Lawson et al 1998; Hammill and Stenson 2004). Lengths of cod ingested were estimated from otoliths found in seal stomachs and published fish length -otolith length regression equations (Hammill and Stenson 2004). Fish lengths were based on 671 otoliths found in 140 seal stomachs collected during November to March, 1989-2001 from four regions: West coast of Newfoundland, Godbout, Harrington Harbour and Magdalen Islands (Appendix B, Table 8). Harp seal size ranged from 102-166 cm. We assumed that otoliths collected from stomach contents represent the size distribution of cod eaten.

Mean length-at-age for cod in the population was estimated based on DFO survey data. Large samples of length-age data were available from readings of cod otoliths collected each year from 1987 to 2003 during the DFO summer survey conducted first with the MV "Lady Hammond" (1987-1989) and then with the "NGCC Alfred Needler" (1990-2003) (Appendix C, Table 9). No cod otoliths were sampled during "Lady Hammond" surveys for the period 1984-1986 (Fréchet and Schwab 1989). Although technical characteristics (*e.g.* fishing gear) of the "Lady Hammond" and RV "NGCC Alfred Needler" differ, vessel catchability for cod with size comprised between 20 and 40 cm is very similar (H. Bourdages unpublished data). By contrast, length data for the period 2004-2006 were not considered due to the large differences in cod selectivity between the "NGCC Alfred Needler" and the "NGCC Teleost".

We considered that the mean length-at-age estimated in summer months by the survey data characterize their mean length throughout the year. Cod consumed at the beginning (January to March) or at the end of the year (November to December) would average to the

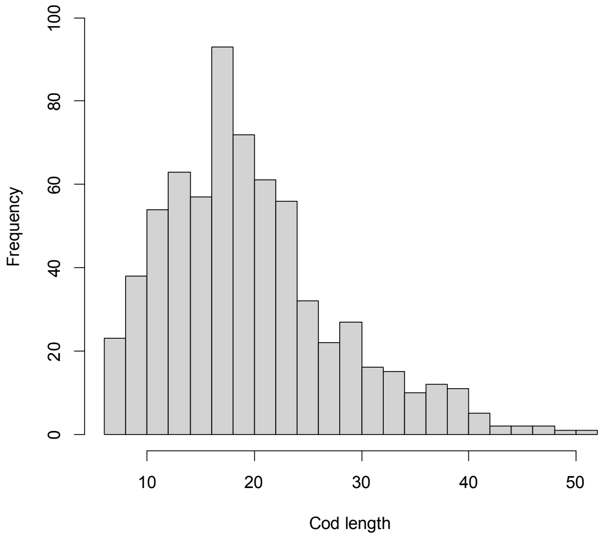

FIG. 6 — Size-frequency histogram of cod ingested derived from otoliths collected in seal stomachs

mean length in the summer. Although the selectivity of bottom trawls might bias upward the mean length by selecting fish that grow faster, the impact of this is lessened as age-1 fish are consumed at the end of their first year. Summer survey data were therefore assumed to adequately represent the mean length of age-1 fish.

Cod length-at-age in the NGSL has been shown to vary in time due to changes in environmental conditions and density-dependent effects (Dutil et al 1999, Swain et al 2003). In addition, size-selective fishing could explain observed changes in growth associated with changes in life history traits for several Northwest Atlantic cod populations (*e.g.* Olsen et al 2004, Hutchings 2005). To account for possible changes and/or shifts in mean length of cod with time, a sequential regime shift detection method was performed as a preliminary analysis (Rodionov and Overland 2005). This method enabled us to estimate the magnitude of the shift through a regime shift index (RSI). The algorithm has user-specified criteria, *e.g.* cut-off time-scale (l) that determines the minimum duration to qualify as a regime. The key concept is that there must be significant shifts in mean value relative to the within-regime variance in order to detect a new regime. In the present analysis, cut-off length was set to 4-12 years and probability level at $p = 0.1$. The significance level p is the level at which the null hypothesis that the mean values of the two regimes are equal is rejected by the two-tailed Student t-test. A probability level of 0.05 was also used for sensitivity analysis. The method was applied to the 1987-2003 time-series of mean length for ages 2-4.

The proportion (π) of each cod age-class consumed by harp seals was estimated by fitting a mixture of distributions to the prey size-frequency histogram. Estimating the mixing proportions and the parameters of the component distributions generally requires applying constraints on the parameters because the model may be over-parameterized (Macdonald and Pitcher 1979).Based on a consistent time-series of length (*i.e.* no major change) defined by the regime shift method, mean length-at-age was fixed as a constraint for the fitting procedure. We used the Rmix package developed by Du (2002) that allows applying constraints on the parameters and combines an expectation-maximization algorithm (Dempster et al 1977) and a Newton-type method for maximum likelihood estimation. We assumed a normal distribution for size-frequency data at each age.

2.4.2 Attack rates and functional response

The attack rates and asymptotic attack rates were generated from biomass of prey required (section 2.3.2) and cod age-structure in seal diet (see above). FR parameters were averaged over the period 1998-2001 and then assumed time-independent.

The number of cod consumed at-age ($nc_{a,t}$) was estimated following:

$$nc_{a,t} = \frac{E_t}{\overline{W_t}} \pi_a \tag{9}$$

where E_t is the biomass of cod consumed (Eq. 8), $\overline{W_t}$ represents the mean mass of a cod aged 1-4 in the ocean in tons and π_a is a vector which represents the proportion of cod consumed at-age (Table 2). $\overline{W_t}$ was derived from the length-at-age data collected from DFO summer surveys and then converted to mass using length-weight relationships for each year (Appendix C, Table 10).

The attack rate of seals on cod was averaged from the yearly attack rate ($\zeta_{a,t}$) calculated as:

$$\zeta_{a,t} = \frac{nc_{a,t}}{S_t \left(\frac{\rho}{365}\right) N_{a,t}^m} \tag{10}$$

where $N_{a,t}$ represents the mean number of cod-at-age and S_t represents the sum of seals in the NGSL per year. The exponent m determines the FR type, m = 1 for type II and m = 2 for type III.

The asymptotic attack rate, *i.e.* maximum consumption rate, was averaged from the yearly asymptotic attack rate ($\zeta_{\max_{a,t}}$) calculated as:

$$\zeta_{\max_{a,t}} = \frac{nc_{\max_{a,t}}}{S_t \left(\frac{\rho}{365}\right)} \tag{11}$$

with $nc_{max_{a,t}}$ calculated following equations (8-9) using a maximum value of p, p_{max} equal to 7.6% and assumed constant for the years 1998-2001. p_{max} was derived from the maximum proportions of cod in seals diet observed in time in each area of the northern Gulf, *i.e.* 12% in 1999 in 4Ra-c, 93% in 1989 in 4Rd-3Pn, and 2% in 1996-2000 in 4S (Hammill and Stenson 2004).

The FR was then calculated as:

$$FR_{a,t} = \frac{\zeta_a \times N_{a,t}^m}{1 + \frac{\zeta_a \times N_{a,t}^m}{\zeta_{\max_a}}} \tag{12}$$

where m is the exponent that determines the FR type, $m = 1$ for type II and $m = 2$ for type III.

2.4.3 From individual to population level

The individual FR was projected to the population level determining the total number of Atlantic cod removed by seal predation for each year. The number consumed ($NC_{a,t}$) was calculated as:

$$NC_{a,t} = FR_{a,t} \times S_t \times \frac{\rho}{365} \times \left(\frac{\overline{W}_t}{\overline{\overline{W}}} \right) \tag{13}$$

where S represents the abundance of harp seals, $\overline{W}$ represents the mean mass of cod in the reference years (1998-2001), ρ is the number of feeding days spent by seals in Gulf each year, 365 is the number of days each year, and the mass ratio $\left(\frac{\overline{W}_t}{\overline{\overline{W}}} \right)$, an index of cod weight, accounts for yearly fluctuations in the mean mass of cod.

Similarly to the Baranov catch equation, the predation mortality rate Mp due to harp seals was expressed as:

$$Mp_{a,t} = \frac{NC_{a,t} \times Z_{at}}{N_{at} \times (1 - \exp(-Z_{at}))} \tag{13}$$

where Z is the total mortality rate and N is the cod abundance.

3 Fitting process

3.1 Survey data

Stratified random bottom-trawl surveys have been conducted annually, in summer months, since 1984. Sampling procedures and equipment were maintained as consistent as possible throughout the time period to minimize variation in the population estimates due to sampling. However, three different vessels have been used through the period 1984-2006 that resulted in differences concerning fishing power and fish catchability (Bourdages et al 2007, H Bourdages unpublished data).

Comparative fishing experiments were conducted between vessels each time there was a change and conversion factors were applied to catch rates estimates when warranted (Bourdages et al 2007). Since some strata within the DFO survey design (Doubleday 1981) were not sampled in some years, and given variations in sampling were different from year to year, a multiplicative model was used to consider the biomass of the missing strata, thereby making the entire surface of the studied area consistent (Bourdages et al 2003). Otoliths were removed from a length-stratified sub-sample for age determination. Catch-at-age was estimated for each tow by applying a survey-wide age-length key to the length distribution of each catch. For the period 1984-1986, an age-length key based on 1987-1988 survey data was used.

Waters shallower than 50 fathoms (*i.e.* 91.44 m) were not sampled by the surveys carried out with the “Lady Hammond” for the period 1984-1989. Indices of abundance were extrapolated for this depth stratum based on the rather stable proportion of cod numbers in deep waters for the period 1990-2006, *i.e.* 63% ±14%. This assumption was supported by the consistent patterns between abundance indices in deep waters (>50 fathoms (91.44 m)) vs. indices in the total water column for the period 1990-2006 (Fig. 7).

Cod have however been shown to change their vertical distribution in the water column according to interannual fluctuations in sea temperature and prey availability (Swain and Kramer 1995, Castonguay et al 1999). Changes in northern Gulf cod distribution in shallow nearshore waters during the oceanic cooling in the mid-1980s were not fully analysed by Castonguay et al (1999) but these authors detected little depth, temperature, or latitudinal changes in cod distribution in summers 1984-1995 for the portion of the stock surveyed in water deeper than 50 fathoms (91.44 m). In addition, the median occupied depth in August did not exhibit trends and remained in the 144-181 m range and there was no apparent age-related difference of depth distribution in summer. These results were not modified when shallow stations were included for the period 1991-1994 (Castonguay et al 1999), supporting our assumption of stable proportion of deep water component in the northern

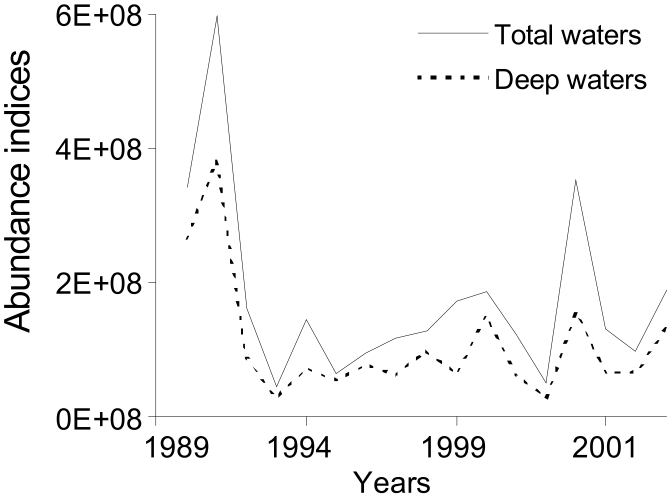

FIG. 7 — Comparison between the indices of abundance (fish numbers for all ages) in the deep water (>50 fathoms, *i.e.* 91,44 m) and the whole water column for the period 1990-2006

Gulf stock. After standardisation, random stratified mean catches per tow at age were used as a relative index of population abundance.

3.2 Catchability and selectivity

We partitioned the global catchability of the research vessel into an age-dependent (selectivity; ς) and a time-independent component (catchability; *q*) since corrections were made for changes in catchability with time between the three successive research vessels (Bourdages et al 2007, H Bourdages unpublished data).

Selectivity for the research-survey gear at age *a* was modelled as a logistic curve (see for a review Millar and Fryer 1999):

$$\varsigma_a = \frac{1}{1 + \exp(-\gamma \times (a - \delta))} \tag{15}$$

where γ is the shape parameter and δ is the age at which 50% of the individuals are vulnerable to research survey gear. Both parameters were assumed time-independent.

The expected numbers-at-age *a* for research surveys were calculated assuming they were measured with lognormal observation errors:

$$I_{a,t} = q \times \varsigma_a \times N_{a,t} \times e^{n_t} \qquad n_t \sim N(0,\sigma_s) \tag{16}$$

where the catchability q was arbitrarily set to a fixed value and the η_t are independent and identically distributed normal random variables with zero mean and constant variance (σ_s). A sensitivity analysis was conducted to evaluate the impact of other catchability values on the results.

3.3 Statistical estimation approach

Six parameters were estimated including the selectivity parameters for DFO research survey γ and δ, the M_r parameter β, the recruitment parameter r, and the standard deviations on the recruitment process (σ_R) and on the survey observation errors (σ_s). The cod population model was fitted to observed data using an iterative maximum likelihood estimation approach. The statistical model consists of two likelihood components (L_i) and a penalty term (P). The likelihood components represent process errors on recruitment and observation errors on abundance indices respectively. The penalty term was included as a constraint to smooth the selectivity curve (Brodziak 2002). The model objective function (Λ) is the sum of the negative log-likelihood components and the penalty term:

$$\Lambda = \sum_{i=1}^{2} - log(L_i) + P \tag{17}$$

The first likelihood component (L_1) describes the assumption of lognormal process error on recruitment that accounts for random fluctuations around the mean (Eq. 2):

$$L_1 = \prod_t \frac{1}{\sigma_R\sqrt{2\pi}\log(R_t)} \exp\left(-\frac{\log(R_t) - \log(TEP_{t-1} \times r))^2}{2\sigma_R^2}\right) \tag{18}$$

The second likelihood component (L_2) describes the assumption of lognormal observation errors on abundance indices derived from survey data (Eq. 16):

$$L_2 = \prod_t \prod_a \frac{1}{\sigma_s\sqrt{2\pi} log(N_{at})} \exp\left(-\frac{(log(I_{at}) - log(q\varsigma_a\ N_{a,t}))^2}{2\sigma_s^2}\right) \tag{19}$$

The penalty term (P) describes the assumption of a smooth selectivity curve without adding any degrees of freedom:

$$P = \sum_{a=1}^{11} (\varsigma_a - 2\varsigma_{a+1} + \varsigma_{a+2})^2 \tag{20}$$

The estimates of model parameters were obtained by minimizing Λ:

$$\Lambda \propto \quad \frac{at}{2} log(\sigma_s^2) + \frac{1}{2\sigma_s^2} \sum_a \sum_t log(I_{at}) log(q\varsigma_a N_{at}))^2 \tag{21}$$

$$+ \quad \frac{t}{2} log(\sigma_R^2) + \frac{1}{2\sigma_R^2} \sum_t log(R_t) - log(TEP_{t-1} \times r))^2 \tag{22}$$

$$+ \quad \sum_{a=1}^{11} (\varsigma_a - 2\varsigma_{a+1} + \varsigma_{a+2})^2 \tag{23}$$

Minimizations were performed with the Nelder-Mead simplex (Nelder and Mead 1965) non-linear optimization algorithm implemented in the R package (R Development Core Team 2007).

The asymptotic covariance matrix of the maximum likelihood estimator equals negative the inverse of the expected value of the matrix of second derivatives of the log-likelihood. However, as in many cases the expected values of the derivatives are difficult to compute and the observed values were therefore approximated by minus the inverse of the Hessian matrix.

3.4 Parameterizing the model

3.4.1 Estimating an initial cod population matrix

Cod abundance for ages 3-13 was derived from the numbers-at-age matrix estimated by virtual population analysis (VPA) during the last updated cod stock assessment working group held in February 2007 (MPO 2007). The model without predation mortality by seals was then fit for ages 3-13 for the period 1984-2006 to estimate the natural mortality curve and derive numbers-at-age 1-2. The model fit the data well and numbers-at-age estimated followed close to those of the VPA. Although the model relied on different data (only DFO summer survey considered) and assumptions than the VPA (*i.e.* a stock recruitment relationship and an age-and condition-dependent natural mortality), SIMCAB results were consistent with VPA outputs in terms of total numbers and biomass, numbers-at-age, and fishing mortality (not shown). In this model without predation, the residual mortality represented the total mortality for cod aged 1-2. Commercial fisheries do not target ages 1-2, therefore the residual mortality curve estimated in this fitting for ages 3-13 was used to derive the abundance of ages 1-2. The complete matrix of cod numbers-at-age 1-13 was constructed by adding ages 1-2 to VPA numbers 3-13. This matrix was then used to initialize the vector of abundance (1984) and the attack rates for the FR. In the model fittings the resulting matrix of cod numbers was also used to replace the initial matrix through an iteration process, for all years except for 1984, in order for the FR to be independent of the VPA data.

3.4.2 Estimating research vessel catchability for cod

The catchability *q* cannot be estimated with sufficient accuracy simultaneously with natural mortality (*M*), and it is better to keep *q* at a given level while estimating *M* each year (Fu et al 2001). Therefore, the value of catchability (*q*) estimated by the model without predation in the age 3-13 fitting was assumed constant for age and time and was fixed for all subsequent model fittings. The parameters for selectivity remained free to scale the value and allow flexibility for when the younger age classes were included.

3.4.3 Testing different functional responses

The reference model was fitted considering FR of type III. A FR of type II was also considered in order to assess how the response type affects the cod biomass removed by seals. The quality of the fit was assessed using AIC to determine the type best suited to explain harp seal predation. In both cases, the biomass removed by seal predation was compared to the results found by Stenson and Hammill (2004) for the NGSL, which are based on constant proportion of cod in the seal diet.

3.5 Sensitivity analysis

The sensitivity analysis was conducted by altering parameter values in increasing (+20% to +80%) and decreasing (-20% to -80%) increments from a baseline value (values from the standard run), running the model and assessing the change between the new and baseline results.

3.5.1 Sensitivity statistic

The exact variable assessed for the sensitivity analysis standardised the proportional change in the variables of interest from the baseline values by the absolute value of the proportional change in the parameter value:

$$sens = \frac{\left(\frac{V_{new} - V_{baseline}}{V_{baseline}}\right)}{\left|\frac{par_{new} - par_{baseline}}{par_{baseline}}\right|} \tag{24}$$

where *sens* is the relative sensitivity, *par* is the parameter value and *V* is the result of interest. The subscripts 'baseline' and 'new' denote the baseline values and the new values, respectively. If a parameter and number are linearly related then *sens* will be the same for any new parameter value chosen in any one direction (*e.g.* if the parameter value changes by -10% from the baseline value and the relationship is linear, then a change of -20% will produce the same *sens* value). However, most parameters are not linearly related to the results of interest and the examination of a range of deviations in parameter values will uncover the degree of non-linearity in the model of a parameter. As $V_{baseline}$ approaches 0 while V_{new} is greater than 0, *sens* will approach infinity.

3.5.2 Variables and results of interest

A sensitivity analysis was performed for the main parameters of the model: the recruitment per million of eggs (r), the slope parameter for residual mortality (β), the shape parameter for selectivity (γ), the age at which 50% of the individuals are vulnerable to gear (δ), the intercept of the M_r curve (α), the attack rate (ζ) and maximum attack rate (ζ_{max}). Changes in the attack rates would allow to cover the uncertainty associated with estimates of proportion of cod in diet and assumptions on the residency of the seal population in the subareas of the NGSL.

Variability of harp seal numbers derived from the seal population dynamic model (Hammill and Stenson 2005) was not taken into account. Hence, variations in the results were examined considering seal abundance ± standard error.

We focused on the last 5 years 2002-2006 in order to assess the robustness of the results. This is further relevant in preparation for projecting the model 5-15 years to investigate alternative simulation scenarios for management. The variables of interest were the total cod biomass, cod biomass removed by seals, and mean predation mortality rate for ages 1-2 (see Table 4).

4 Results

4.1 Changes in cod length-at-age in seal diet samples

Cod mean length for ages 2-4 for the period 1987-2003 showed 1-3 regime shifts according to cut-off length considered. A significant positive shift in mean length was found in 1995 for cut-off lengths of 4, 5, 9, 10, and 11 years. The maximum value of RSI equal to 6.4 was found for a cut-off length of 10 years. Two distinct periods in the mean length-at-age were then found, *i.e.* the period 1987-1994 was characterized by a lower mean length for ages 2-4 (305 mm) than the period 1995-2003 (328 mm) (Figure 8).

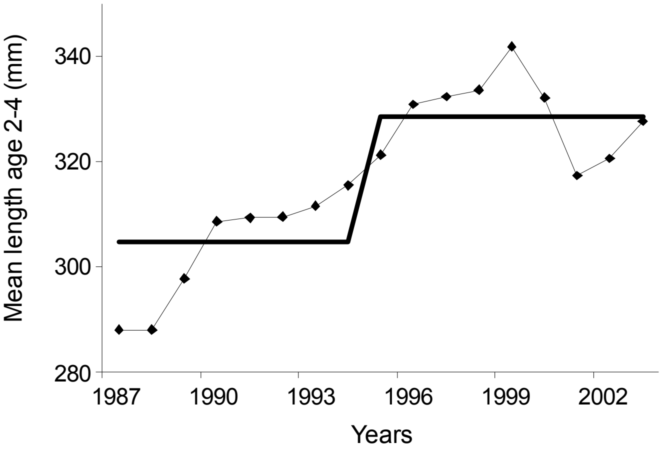

FIG. 8 – Detection of a regime shift in 1995 in cod mean length for ages 2-4

The detection of the regime shift was relatively sensitive to the cut-off length as regime shifts associated with lower magnitude were detected in 1993 for l = 6 (RSI = 1.2), 1994 for l = 7 (RSI = 1.5) and l = 8 (RSI = 1.1), and 1996 for l = 12 (RSI = 4.2). The results were consistent with a probability value of 0.05, with a maximum value of RSI of 5.7 found for l = 10. Hereafter, we considered 2 distinct periods corresponding to different mean length-at-age for cod, *i.e.* 1984-1994 and 1995-2006.

Following the regime shift in mean length of cod in 1995, two mixture models were fitted for the periods 1984-1994 and 1995-2006. The same dataset of cod lengths was used in both cases, assuming that size of cod consumed reflect size-selection predation by harp seals. Length-at-age data available from DFO surveys were pooled for the periods 1987-1994 and 1995-2003. A von Bertalanffy growth function (von Bertalanffy 1938) was fitted to each dataset in order to estimate the mean length for ages 0-4 in each period (Appendix C, Fig. 18). Mean length for ages 0-4 in years 1984-1986 and 2004-2006 were then assumed equal to the mean lengths estimated in 1987-1994 and 1995-2003, respectively (Table 2).

The mixture models fitted for the two sets of mean length-at-age were composed of different distributions (Table 2). The significance levels (p-values) for the goodness-of-fit test, based on the chi-square approximation to the likelihood ratio statistic (Rao 1965), were 0.24 and 0.23 for the periods 1984-1994 and 1995-2006, respectively. This indicated that both the mixture models were consistent with the data. In both periods, cod of ages 1 and 2 represented more than 80% of the cod consumed by seals (Table 2). The changes in mean length-at-age of cod throughout the period affected the mixing proportions of age-groups consumed, shifting cod towards younger ages.

TAB. 2 – Mean and standard deviation (SD) of the normal size-frequency distributions for ages 0-4 and corresponding percentage (π) of cod age-groups consumed by harp seals

Period	Age	Mean	SD	π
1984-1994	0	10.2	0.9	3.1%
	1	15.6	4.8	56.4%
	2	23.4	6.6	33.7%
	3	30.8	2.8	0.0%
	4	37.7	5.9	6.8%
1995-2006	0	9.1	1.0	2.4%
	1	16.0	4.9	63.4%
	2	25.5	7.6	29.4%
	3	33.6	8.7	3.8%
	4	40.6	4.4	1.0%

4.2 SIMCAB fittings

The likelihood component for recruitment was not informative to the fitting when the ages 1-2 were included, succeeding only to add noise, and was not used in subsequent analyses. This might be due to the poor selectivity of the DFO survey gear for small cod aged 1. Recruitment estimates from the model differed from the temporal trends in survey data for cod age 1. Recruitment estimates showed a decreasing trend from 1984 to 2006 whereas DFO survey data did not display any clear trend throughout the time period.

The model fitted the survey data well and the minimum value for the objective function Λ was -355.1, corresponding to an AIC value of -700.2 (Fig. 9). The variance of the observation error was low with a value close to 0.2 (Table 3). The 95% confidence intervals around the parameter values estimated at the maximum likelihood were narrow, indicating a good precision of the parameters (Table 3).

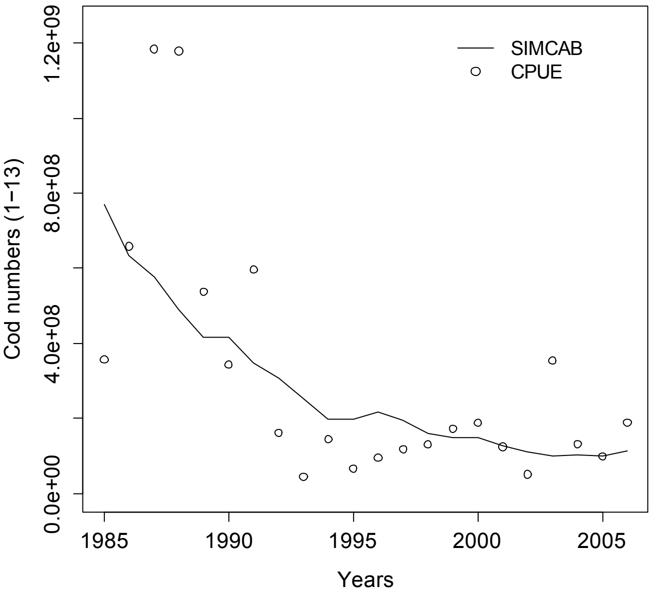

FIG. 9 – Fitting of the model to the DFO survey data for ages 1-13

TAB. 3 – Parameter values with 95% confidence intervals derived from the Hessian matrix

	Lower	Value	Upper
r	5.51	14.97	24.44
β	0.90	1.14	1.38
γ	0.27	0.35	0.44
δ	6.43	7.27	8.11
σ_S^2	0.16	0.18	0.19

4.3 Cod population dynamics

Cod numbers for ages 3-13 showed a continuous decreasing trend from the mid-1980s to the 2000s, consistent with the collapse of the northern Gulf cod in the late 1980s and the current lack of recovery of the stock (Fig. 10). Our results were in accordance with the last stock assessment (MPO 2007) and showed similar trends in time although our estimates were generally higher than VPA results and the decline in cod abundance appeared less pronounced. Cod numbers 3-13 were closer in the 2000s.

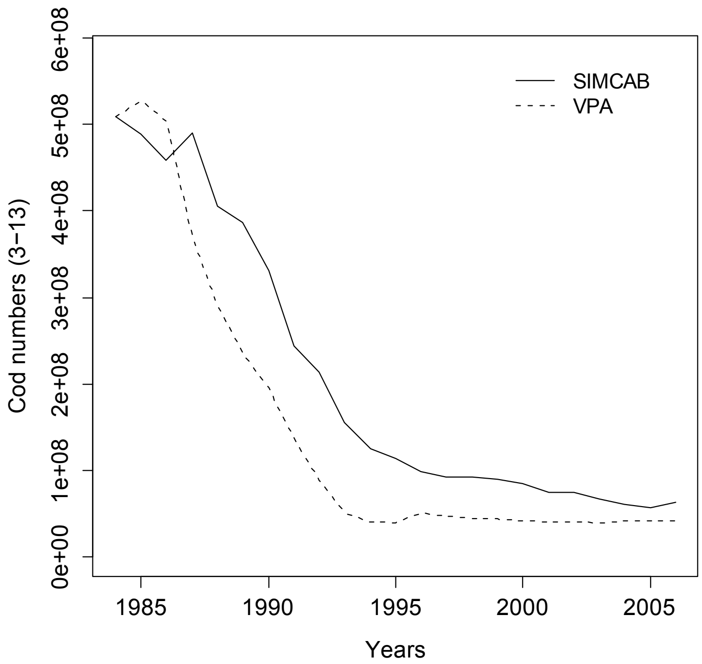

FIG. 10 – Cod numbers for ages 3-13 estimated with SIMCAB and with the VPA

Although recruitment at age 1 was modelled as a linear function of total egg production (TEP), the relationship between cod aged 3 and TEP departed from linearity due to non-linear effects of predation and residual mortality affecting young cod (Fig. 11). Our results were close to the TEP-recruitment (age 3) relationship derived from VPA (MPO 2007), indicating good consistency between our approach and current knowledge on numbers of cod aged 3 (Fig. 11).

The sources of mortality – fishing, seal predation, and residual mortality – were split over age groups in order to compare mortality rates where they were inflicted. Ages 1-2 are not targeted by cod fisheries and residual mortality represented more than 75% of the total mortality for 1984-2006 (Fig. 12 -left graph). Mortality rates due to seal predation increased until 1997 to reach more than 0.4 y-^{1} after which they declined and maintained a lower rate around 0.25.

For ages 3-6, residual mortality also represented a major proportion of the total mortality, on average 0.36 y-^{1} (Fig. 12 -middle graph). Predation mortality showed a similar pattern to ages 1-2 and remained a minor part of the total mortality for ages 3-6 throughout the total period. The part of predation in total mortality however increased from 4% in the mid-1980s to reach 14% in the 2000s due to the decrease in fishing mortality. Fishing mortality steadily increased until the year prior to the 1994-1996 moratorium. Thereafter, the fishing mortality rate remained very low.

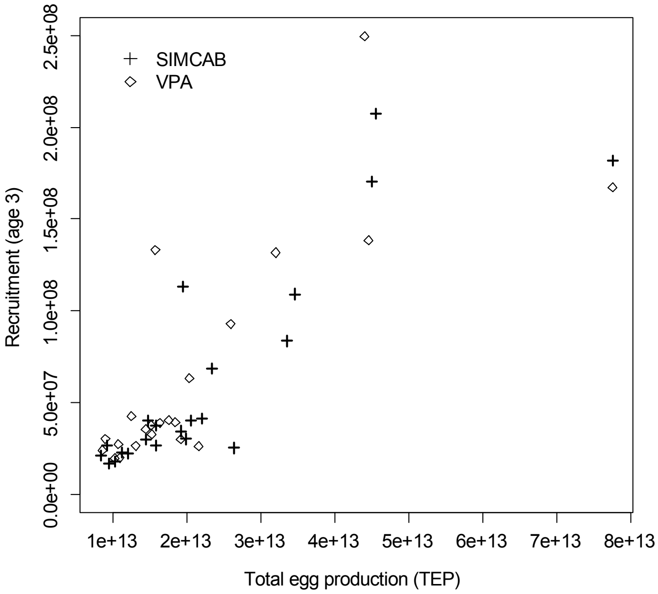

FIG. 11 – Relationship between total egg production (TEP) and cod numbers at age 3 estimated with SIMCAB and with the VPA

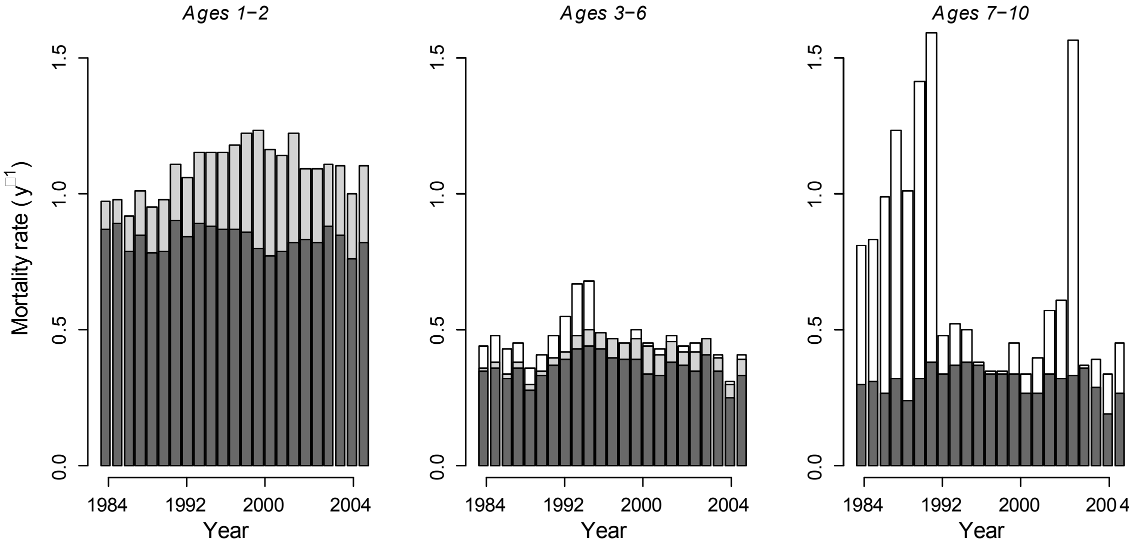

FIG. 12 – Total mortality rates for ages 1-2 (left-graph), 3-6 (middle-graph), and 7-10 (right-graph). Dark grey; residual natural mortality M_r; light grey: harp seal predation mortality M_p; white: fishing mortality F

By contrast, residual mortality for ages 7-10, *i.e.* natural mortality, was not the main component of total mortality for several years of the period 1984-2006 since fishing mortality exceeded natural mortality throughout the 1980s (Fig. 12 -right graph). The natural mortality varied from around 0.3 y^{-1} in the early 1980s to around 0.4 y^{-1} in the early 1990s before decreasing at the end of the period to 0.25 y^{-1}. Fishing mortality showed high inter-annual variations during the period with major peaks in the late 1980s and in 2002, with values exceeding 1.2 y^{-1}.

The mean residual mortality for ages 7-10, weighted by the numbers-at-age, equals natural mortality since they represent older cod not consumed by harp seals. The mean natural mortality rates were consistent with the pattern followed by the natural mortality rates used in the VPA, the highest mortality rates being observed in the early 1990s (Fig. 13a). The natural mortality for the model was higher at the beginning and end of the time series. The mortality rates estimated by the model showed higher variability than the VPA as they were estimated each year based on the index of condition. Considering constant asymptotes of 0.2 and 0.4 for the residual mortality curve led to higher values of AIC (-594 and -680 respectively) than for a condition-dependent asymptote (-700.2), indicating a better fit of the model when residual mortality was related to cod condition.

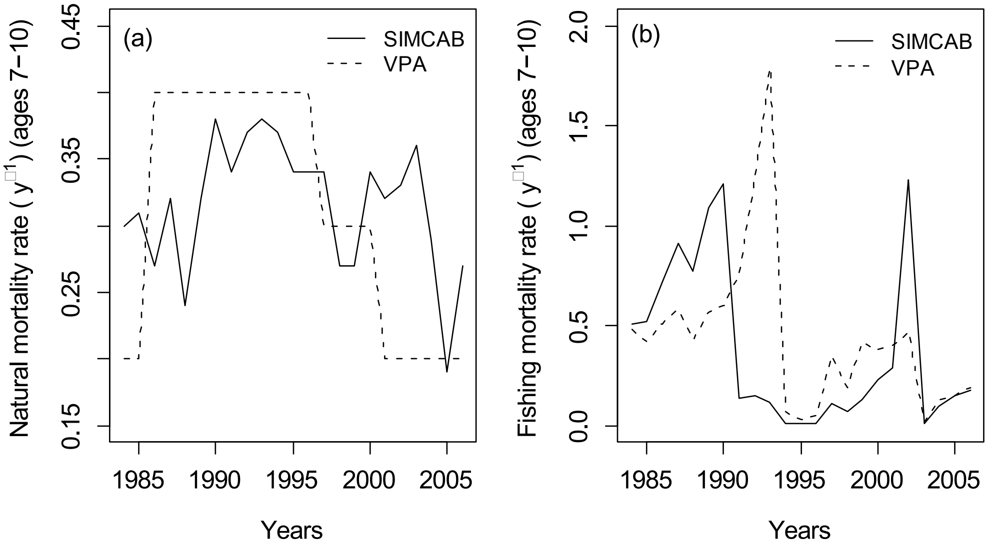

FIG. 13 – (a) Weighted mean natural mortality for ages 7-10 (b) Weight mean fishing mortality for ages 7-10, estimated with SIMCAB and with the VPA

Fishing mortality rates for the model were consistent with those of the VPA for the majority of the times series (Fig. 13b). Rates estimated with SIMCAB were lower than VPA results in the 1990s because numbers-at-age were higher (Fig. 10). The mortality rates for the model increased from the mid-1980s to reach a peak in 1990 compared to the peak in 1993 found by the VPA; both reflected the strong decline in the cod population that led to the moratorium in 1994. A second peak occurred in the early 2000s right before the moratorium in 2003. The model and VPA showed fishing mortality values close to zero for both moratoriums periods, 1994-1996 and 2003. For the last 4 years the fishing mortality matched that of the VPA.

4.4 Impact of seal predation on cod

4.4.1 Cod removals

Predation removals were different for each cod age-group and showed high interannual fluctuations for the period 1984-2006 (Fig.14). Ages 1-2 represented the majority of the removals according to the proportions derived from size-frequency distribution in seal stomachs used to estimate the attack rates. Cod recruitment and age 0 removals exhibited different trends due to the FR but peaks in removals generally matched peaks in recruitment. Aged 2 cod showed similar patterns with age 0 removals but showed a 1-year lag with recruitment.

Relative stability in consumption displayed between 1984 and 1995 was followed by a large increase in the late 1990s with a steady decline from then on. The relative stability may be explained by an increase in seal abundance compensating for the decline of cod observed in the NGSL. The decline in the amount of cod consumed from the mid-1990s could be accounted for by the stabilization of the seal population and the low cod abundance.

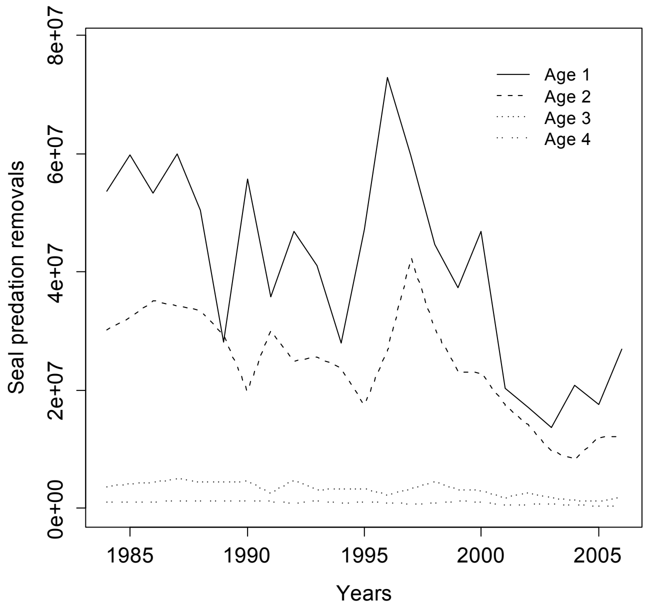

FIG. 14 – Removals of cod numbers by seals for each age 1-4

The total biomass of cod removed varied around 5,000 tonnes from 1984 to 1995 and then increased to reach around 10,000 tonnes in the late 1990s (Fig. 15). The biomass removed then showed a rapid decrease to reach a minimum value of 2,500 tonnes which remained steady in the early 2000s. These results are consistent with the orders of magnitude of removals found in the constant ration models of Stenson and Hammill (2004) based on 2 alternative assumptions of consumption. However, cod biomass removed with our model showed higher interannual variability throughout the period and was much lower in the early 2000s, accounting for the changes in cod abundance.

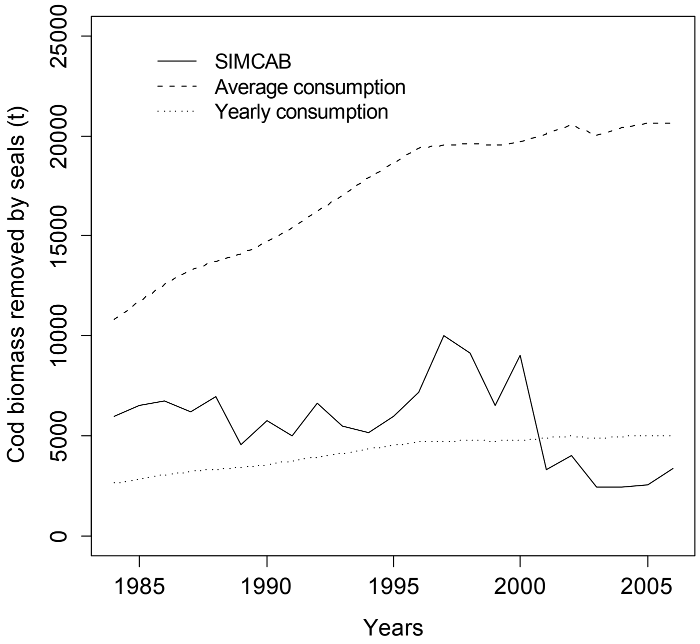

FIG. 15 – Cod biomass removed by harp seals estimated with SIMCAB and with a constant ration model based on 2 alternative assumptions of consumption models for harp seals (Stenson and Hammill 2004)

4.4.2 Impact of different functional responses

FR type did not have a large impact on the temporal patterns of cod biomass removed however it strongly affected the magnitude of cod numbers removed each year. For a high abundance of prey corresponding to the early 1980s, cod removed by seal predation were lower for a type II than for type III FR (Fig. 16). By contrast, the type II FR led to higher removals than type III when cod abundance was low (Fig. 16). In the early 2000s when cod abundance was particularly low, the FR type led to strong differences in cod numbers removed, with type II resulting in an average biomass removed of more than 4,000 tonnes whereas the average type III removal was around 2,500 tonnes. The best fit for the model with a type II FR was obtained for a minimum value of the model objective function (Λ)

equal to -350.6, *i.e.* an AIC value of -691. This value was higher than the value obtained with a type III FR (-700.2), indicating a better fit of the model in this latter case.

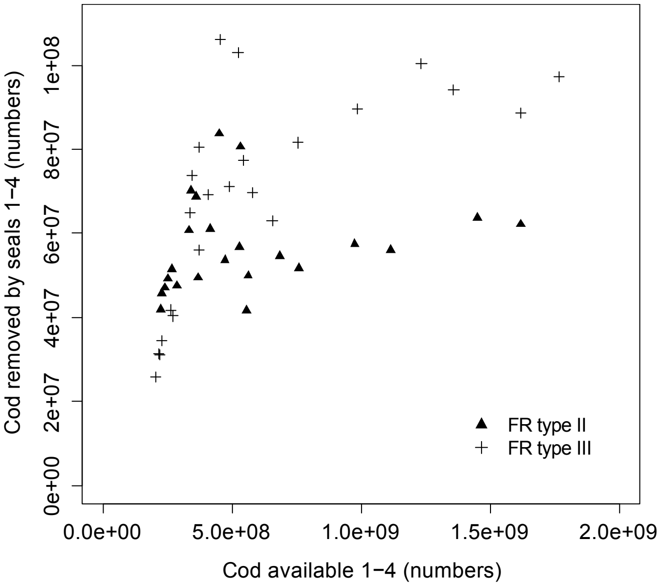

FIG. 16 – Cod numbers removed by harp seals (t) estimated with SIMCAD using type II and type III functional response (FR)

4.5 Sensitivity Analysis

Cod biomass estimated in the model was quite sensitive to the recruitment per million of eggs parameter (*r*) and residual mortality parameters, intercept αand slope *β* (Table 4). An increase in *r* led to an increase in cod biomass accompanied by an increase in seal predation due to changes in small cod availability. Effects on the predation rate were less straightforward due to the non linearity of the FR but positive or negative changes in *r* generally led to a decrease in predation mortality. Decreasing *β* decreased the residual mortality on cod and therefore increased cod biomass, leading to higher removals by predation. Variations in αhad similar effects on the outputs of the model. Selectivity parameters γ and δ did not have a strong impact on the results (Appendix E, Table 11). In particular, the biomass removed by seal predation in the 2000s was not sensitive to variations in the selectivity parameters. Changes in attack rates did not strongly affect the total biomass, biomass removed and predation rates (Appendix E, Table 11). Increasing the attack rate ζ decreased the total biomass and hence the cod removals, leading to an increase in predation mortality. Again, effects on predation mortality rates could be counter-intuitive as they emerged from non-linear FR. Variations in maximum attack rate ζ_{max} led to similar results as for attack rate although increasing values of ζ_{max} decreased predation mortality.

TAB. 4 – Qualitative summary of the sensitivity analysis of the model to the value of its main parameters on the total biomass (*B*), the biomass removed (*BR*) by seals, and the predation mortality rate for cod aged 1-2 (M_p1-2) for the period 2002-2006. Arrows indicate increasing or decreasing increments from a baseline value (see section 3.5). Complete table of results is given in Appendix E

Param.	Definition	*B*		*BR*		$M_p(1\text{-}2)$	
		↗	↘	↗	↘	↗	↘
r	Recruitment per million of eggs	+	-	+	-	-	-
α	Intercept of the Mr curve	-	+	-	+	-	-
β	Slope of the Mr curve	-	++	-	++	-	-
δ	Age50 of the selectivity	-	+	0	0	+	-
γ	Shape parameter of the selectivity	-	+	0	0	+	-
ζ	Attack rate	-	+	-	+	+	-
$\zeta_{\max}$	Maximum attack rate	-	+	-	+	-	-

0 = no effect, + = positive effect, and - = negative effect

The coefficient of variation associated with seal abundance estimates was relatively low through the period 1984-2006 and increased from 5% in the early 1980s to about 11% in the 2000s (Stenson and Hammill 2005; Fig. 4). Uncertainty associated with the seal population model did not affect the outputs of the model. Cod total biomass (not shown) and biomass removed by seals were relatively insensitive when changing the seal population size by its standard error (Fig. 17).

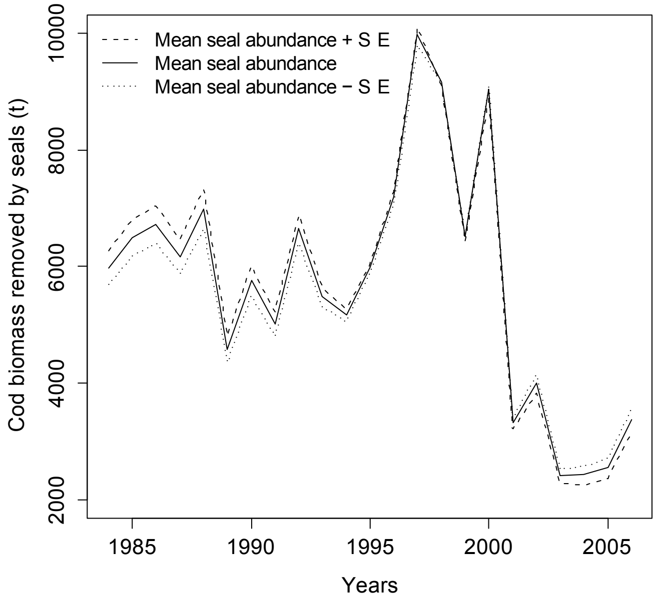

FIG. 17 – Cod biomass removed by harp seals (t) estimated with SIMCAD using ± standard error (SE) around the mean abundance of harp seals estimated by Stenson and Hammill (2005)

5 Discussion

Our approach is the first attempt to dynamically model the impact of harp seal predation on the NGSL cod stock. The SIMCAB model is an extended Leslie matrix that explicitly links a consistent long time-series of CPUE data to the latent state variables through an observation equation. Despite major differences with the current methods used to assess the cod stock status (*e.g.* TEP-recruitment relationship), our model was able to mimic the results of the VPA. Using SIMCAB we estimated the relative importance of different sources of mortality that affected the northern Gulf cod stock for the period 1984-2006. Our main results indicate that predation removals accounted for only a minor proportion of the total mortality on the ages targeted by seals, while fishing was the main source of total mortality affecting ages 7-10 in the mid-1980s before the stock collapse. Although predation mortality by seals increased in the 1990s, overall predation removals decreased in the early 2000s despite the increase in seal abundance. Only the type III functional response accounts for active prey switching, while our results indicate a decrease for both FR models, suggesting that seal predation declines after 2000 for other reasons, *e.g.* low cod abundance.

5.1 Multispecies modeling and functional response

Separating the sources of mortality affecting animal populations is a major issue in ecology and has a long history in fisheries science (*e.g.* Andersen and Ursin 1977). This is particularly important in the context of multispecies management as marine mammals culling (Yodzis 2001, Lavigne 2003) has been proposed for some time as a beneficial tool for fisheries. Predator/prey modeling has been used to quantify the impact of grey seal predation on cod population dynamics and explain causes of collapse and non recovery on the eastern Scotian shelf (ESS) (Mohn and Bowen 1996, Fu et al 2001, Trzcinski et al 2006). The first modelling approach included predation mortality explicitly by seals in a VPA and showed that grey seals had little effect on the collapse of cod on the ESS (Mohn and Bowen 1996). By contrast, more recent statistical catch-at-age population models suggest that increasing predation mortality since the 1990s could affect the survival of immature cod and contribute to the failure of the stock to recover (Fu et al 2001, Trzcinski et al 2006).

Our model is an age-structured population dynamics model structurally similar to the models used for grey seals but it differs in several important points. A major difference with the models from Mohn and Bowen (1996) and Fu et al (2001) and addressed by Trzcinski et al (2006) concerns the linkage between cod abundance and seal consumption through the means of a FR. The form of the FR is a key issue in multispecies modelling, especially at low abundance, because it defines how predators impact their prey as a function of prey abundance (Koen-Alonso 2006). In the present analysis, we used a large dataset of seal stomach contents to derive age-structured attack rates and define a FR following Trzcinski et al (2006) approach. The use of a FR led to different conclusions in terms of predation removals of cod by seals than based on constant ration models and suggested a decrease in cod consumption in the 2000s. Therefore, the form of the FR can have major consequences when assessing the impact of seals on cod recovery. The type III FR led to a better fit of the model than the type II and had a large impact on the predation removals. Several mechanisms have been proposed for explaining type III FR, mainly prey switching between alternative food sources and existence of prey refuges (Koen-Alonso 2006). Harp seals are generalist predators that exhibit seasonal and interannual variations in diet but they have also been shown to actively choose their prey in waters off Newfoundland (Lawson et al 1998). Strong modifications in the trophic structure of the northern Gulf ecosystem during the last 3 decades have led to changes in the most important prey of harp seals, suggesting prey switching (Savenkoff et al 2007). In addition, recent findings of seal predation on salmonids in an estuarine system in Scotland provided empirical support for a type III FR (Middlemas et al 2006). The FR of a predator to prey density might however be affected by the presence of alternative prey and development of a multispecies functional response for harp seal could improve our understanding of cod/seal interactions in the NGSL (Smout and Lindstrøm 2007; Tschanz et al 2007). In absence of a better knowledge on the form of the FR of harp seals to changes in cod abundance, the use of both types II and III allows us to define a potential range of cod removals by seals.

5.2 Cod population dynamics

A novel aspect of our cod population model is a stock-recruitment relationship based on total egg production, which for cod is considered a better measure of the true reproductive potential of the stock than spawning biomass (Tara-Marshall et al 1998). In addition, TEP in our model was derived from a statistical model that related egg production to length-at-maturity and condition of mature females (Y Lambert unpublished data). Hence, recruitment in the model accounted for changes in growth of cod that could be density and/or temperature dependent (Swain et al 2003), as well as changes in environment that could affect egg productivity through cod condition.

Natural mortality other than seal predation was assumed age-dependent and estimated in the model through the slope of the curve. To disentangle the effects of catchability and natural mortality in the model, it was necessary to fix the catchability at a given level (see Fu et al 2001). Changes in catchability poorly modified the quality of the fit and the qualitative results of the model but did affect the magnitude of the predation mortality and hence the biomass removed by seal predation. This clearly remains a part of the model to improve and knowledge on natural mortality affecting cod larval and juvenile stages and on age-specific catchability (Harley and Myers 2001) could be used as auxiliary information in a Bayesian version of the model for the estimation of these parameters.

Results were also sensitive to the intercept of the curve that was fixed based on preliminary runs of the model without predation. Nevertheless, age-specific values of M estimated were in good agreement with values used for the southern Gulf cod stock (Mohn and Bowen 1996). Residual mortality was also modelled as a function of cod condition to take into account temporal changes in M. Indeed, condition has been shown to affect the natural mortality of cod in laboratory experiments (Dutil and Lambert 2000). Values of natural mortality for ages 7-10 estimated were consistent with temporal patterns of M estimated with VPA (Benoît and Chouinard 2004, Grégoire and Fréchet 2005). Sources of natural mortality other than harp seal predation have been shown to vary in time and were mainly due to predation by grey seals and large cod in the 2000s (Savenkoff et al 2007). Based on similar data but on different model structures and assumptions, our results were consistent with the findings of Savenkoff et al (2007) who showed a slight increase in total mortality on small cod from the mid-1990s to the early 2000s.

5.3 Cod consumption by harp seals

The proportion of cod in seal diets was based on the reconstruction of diet composition from recovered hard parts from animals sampled from different sites in the gulf and during different seasons. Although this approach provides valuable information on potential prey consumed by harp seals, several studies have suggested that they present a biased perception of population diet composition. Difficulties with the hard parts diet reconstruct-tion include: stomachs and faecal samples may only represent the composition of the last meal consumed and close to the sampling site; variable retention and digestion of hard parts or failure to ingest hard parts (*e.g.* belly biting) may result in certain prey being over-represented in the diet, while others are under-represented; small sample sizes and considerable individual variability in prey choice will also influence our final perception of diet composition (see references in Hammill et al 2005). Further assumptions are also needed to link the spatial distribution of diet samples to the distribution of animals in order to estimate population consumption. Unfortunately, fine scale movement data are not available; therefore, residency of animals in the Gulf was determined using information from tag returns, aerial surveys and the location of traditional seal fisheries (Hammill and Stenson 2000, 2006). New analyses based on stable isotopes and quantitative fatty acid signatures are in progress and should improve our knowledge on cod fraction in harp seal diet.

In our analysis, age distributions of cod consumed by harp seals were derived from mixtures of length-at-age distribution fitted for 2 different time periods to take into account major changes in cod growth during 1984-2006. Although the detection of a clear regime shift was not straightforward, the detection method allowed us to show important changes in length-at-age for young cod between the 1980s-early 1990s and the late 1990s-2000s. Our approach led to quite different results than obtained with fixed age-length keys (Banville 2003; Hammill and Stenson 2004). According to our results, most of the cod eaten by harp seals were aged 1 and 2 and the maximum age found in seal stomachs was 4 compared to ages 10 and 7 for Banville (2003) and Hammill and Stenson (2004), respectively. Differences in the results stem both from the method and data used. Compared to Banville (2003), we included a larger dataset of cod otoliths collected in winters of 1989-2001 in the different areas of the NGSL. Our mean length-at-age for cod was based on von Bertalanffy growth functions fitted for the periods 1987-1994 and 1995-2003 and differed from Hammill and Stenson (2004) who used grouped Needler data. In SIMCAB, age proportions of cod consumed by harp seals were used to define the age-structure attack rates of the functional response based on reference years. Cod numbers removed by seal predation in the model were then corrected by a weight ratio to account for yearly changes in cod length.

5.4 Perspectives

The next steps in our modelling approach will deal with SIMCAB projections in the future under a set of different management scenarios for cod and seals. These projections will enable us to assess how predation mortality on small cod (ages 1-3) eventually affects recruitment to the fishery, *i.e.* how much are harp seals responsible for the non-recovery of the cod population in the NGSL. Projections will also include recovery scenarios addressing the most effective measures that could achieve recovery above reference points. In addition, a dynamic version of a mass-balanced model (Ecopath with Ecosim) applied to the northern Gulf (Morissette et al 2006) is currently under progress to compare SIMCAB with Ecosim projections in order to assess the robustness of our results. Similar questions will then be addressed by transposing our model to the case study of grey seals and cod in the southern Gulf of St. Lawrence, another case-study where seal population control measures have been proposed to rebuild the cod population (DFO 2005).

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7 Appendix

A. Notations and model equations

TAB. 5 – Parameters and variables used in the SIMCAB model

Notation	Definition	Equation
B	Cod biomass	(D1)
w_a	Cod mean weigh at age	(D1,2)
SSB	Spawning stock biomass	(D2)
TEP	Total egg production	(D3)
s	Sex ratio	(D3)
ϕ	Proportion of maturing females	(D3)
f	Fecundity	(D3)
l	Length	(D3)
K	Fulton's condition index	(D3,5)
M_p	Predation mortality by harp seals	(D4)
ζ	Attack rate	(D4)
$\zeta_{\max}$	Maximum attack rate	(D4)
ρ	Number of feeding days spent by seals in Gulf each year	(D4)
$\overline{W}_t$	Cod mean weight for ages targeted by seals in year t	(D4)
$\overline{W}$	Cod mean weight for ages targeted by seals in years (1998-2001	(D4)
S	Seals numbers	(D4)
m	Parameter defining the functional response type	(D4)
M_r	Residual natural mortality	(D5)
α	Intercept of the M_r curve	(D5)
β	Slope of the M_r curve	(D5)
ϑ	Asymptote of the M_r curve	(D5)
F	Fishing mortality	(D6)
R	Recruitment	(D7)
r	Recruitment per million of eggs	(D7)
N	Cod numbers	(D8)
ς	Selectivity at age	(D9)
γ	Shape parameter	(D9)
δ	Age at which 50% of the individuals are vulnerable to gear	(D9)
q	Catchability	(D10)
I	Index of abundance	(D10)
σ_R	Standard deviation of the process on recruitment	(S1)
Σ_N	Standard deviation of the process on numbers	(S2)
Σ_s	Standard deviation of the observation error	(S3)

TAB. 6 – Deterministic equations defining the process and observation equations in the SIMCAB model. *a* and *t* index age and time respectively. *F* and *G* represent specific functions

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State moments

(D1) $$B_t = \sum_{a=0}^{A} w_a N_{a,t}$$

(D2) $$SSB_t = \sum_{a=0}^{A} w_a N_{a,t} \phi_{at}$$

(D3) $$TEP_t = \sum_{a_m}^{A+} N_{a,t} S_{a,t} \phi_{a,t} f_{a,t} \text{ with } f_{a,t} = F(l_{a,t}, K_t)$$

Mortality components

(D4) $$Mp_{a,t} = \frac{\dfrac{\zeta_{a,t} N_{a,t}^{m}}{1 + \dfrac{\zeta_{a,t} N_{a,t}^{m}}{\zeta_{\max_{a,t}}}} \left(\dfrac{\overline{W_t}}{\overline{W}} \right) S_t \dfrac{\rho}{365}}{N_{a,t}}$$

(D5) $$Mr_{a,t} = \vartheta_t + \alpha \exp - \left(\frac{a}{\beta} \right) \text{with } \vartheta_t = G(K_t)$$

(D6) $$F_{a,t} = \frac{C_{a,t}}{N_{a,t}}$$

Process function

(D7) $$R_t = TEP_{t-1} r$$

(D8) $$N_{a,t} = N_{a-1,t-1} \exp - (Mp_{a-1,t-1} + Mr_{a-1,t-1} + F_{a-1,t-1})$$

Process function

D(9) $$\varsigma_a = \frac{1}{1 + \exp(-\gamma \times (a - \delta))}$$

D(10) $$I_{a,t} = q \, \varsigma_a \, N_{a,t}$$

TAB. 7 – Definitions used to extend the deterministic model in Table 6 to a stochastic model

(S1) $\mu_t = \log(R_t) - \log(TEP_{t-1} r)$ $\mu_t \approx normal(0, \sigma_R^2)$

(S2) $\varepsilon_t = \log(N_{a,t}) - \log(N_{a-1,t-1}) + Z_{a-1,t-1}$ $\varepsilon_t \approx normal(0, \sigma_N^2)$

(S3) $\eta_t = \log(I_{a,t}) - \log(q \varsigma_a N_{a,t})$ $\eta_t \approx normal(0, \sigma_s^2)$

B. Otolith data

TAB. 8 – Spatial and temporal coverage of cod otoliths collected in harp seals stomachs. NF = Newfoundland; HH = Harrington Harbour; MI = Magdalene Islands; G = Godbout

	NF	HH	MI	G
1989	2	-	-	-
1990	37	-	-	-
1992	27	-	-	-
1993	18	-	-	-
1994	1	-	-	-
1995	1	-	-	-
1996	153	-	-	1
1997	60	-	-	-
1998	61	-	-	-
1999	105	30	-	-
2000	105	-	-	-
2001	30	22	18	-

C. Cod length and weight-at-age

TAB. 9 – Number of cod sampled during "Lady Hammond" and "NGCC Alfred Needler" summer surveys for ages 0-4 and used in the analysis to estimate cod mean length-at-age

	0	1	2	3	4
1987	-	6	52	95	157
1988	53	83	118	132	105
1989	-	4	69	156	130
1990	11	19	53	176	130
1991	40	32	50	103	179
1992	20	27	79	122	152
1993	-	-	46	77	78
1994	5	7	62	206	120
1995	-	-	25	21	66
1996	-	1	37	146	79
1997	-	5	118	124	162
1998	-	5	48	168	142
1999	1	15	108	157	209
2000	-	72	89	136	94
2001	4	7	58	142	113
2002	-	1	26	69	132
2003	-	2	73	140	176

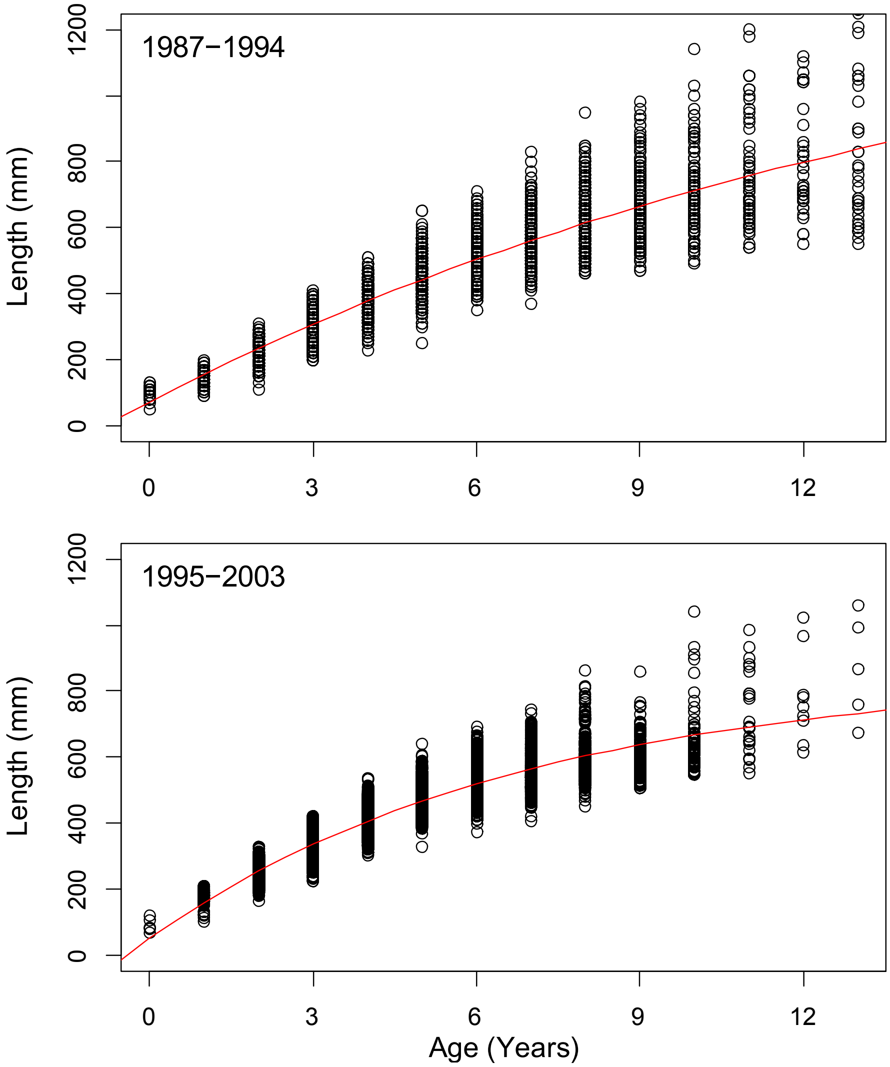

FIG. 18 – Growth functions (von Bertalanffy, 1938) fitted to length-age data for the periods 1987-1994 (top) and 1995-2003 (bottom) in order to estimate mean length for ages 0-4 in the mixture models

TAB. 10 – Weight-at-age (g) for the cod stock of the northern gulf of St. Lawrence derived from length-at-age data converted to mass using length-weight relationships for each year

	1	2	3	4	5	6	7	8	9	10	11	12	13
1984	28.3	102.2	243.7	467.5	783.8	1199.6	1718.4	2341.5	3068.0	3895.6	4820.3	5837.4	6941.5
1985	28.3	102.2	243.7	467.5	783.8	1199.6	1718.4	2341.5	3068.0	3895.6	4820.3	5837.4	6941.5
1986	28.3	102.2	243.7	467.5	783.8	1199.6	1718.4	2341.5	3068.0	3895.6	4820.3	5837.4	6941.5
1987	15.4	95.1	262.8	521.9	865.1	1279.9	1751.9	2266.4	2809.8	3369.9	3936.2	4500.1	5054.3
1988	33.4	107.7	246.6	467.7	786.5	1216.6	1770.1	2457.6	3288.0	4269.2	5407.6	6708.5	8176.1
1989	15.9	86.3	236.2	476.9	809.7	1230.1	1729.2	2296.4	2919.9	3587.9	4289.0	5012.8	5749.9
1990	28.9	113.8	267.1	486.6	762.9	1083.5	1435.6	1806.8	2186.6	2566.3	2938.9	3299.0	3642.8
1991	24.9	98.9	239.6	451.6	731.2	1069.9	1456.4	1879.0	2326.0	2786.8	3252.3	3714.9	4168.1
1992	35.4	127.6	283.7	497.3	756.8	1049.0	1361.7	1684.2	2007.6	2324.9	2631.1	2922.4	3196.5
1993	24.4	115.1	278.1	499.7	760.1	1040.8	1326.2	1604.8	1868.9	2113.6	2336.6	2536.9	2715.0
1994	29.9	122.9	285.3	506.4	769.5	1058.1	1357.5	1656.0	1945.2	2219.0	2473.9	2708.0	2920.5
1995	38.6	144.0	319.3	551.4	822.3	1114.9	1414.5	1710.2	1993.8	2260.2	2506.2	2730.4	2932.7
1996	29.2	138.9	332.9	590.4	885.6	1195.5	1502.8	1795.3	2065.8	2310.6	2528.4	2719.7	2886.0
1997	27.6	155.9	377.4	653.9	949.5	1238.3	1505.2	1742.3	1947.5	2121.6	2267.1	2387.4	2486.0
1998	40.2	166.6	375.6	645.1	950.5	1270.4	1588.7	1893.9	2179.1	2440.1	2675.4	2884.9	3069.7
1999	31.3	147.2	356.5	641.4	975.9	1335.3	1699.1	2052.5	2385.5	2692.2	2969.8	3217.6	3436.4
2000	64.1	184.6	378.1	644.1	977.5	1370.6	1814.6	2300.1	2818.2	3360.3	3918.7	4486.2	5057.0
2001	25.5	112.7	277.3	517.9	824.4	1182.9	1578.5	1997.2	2426.8	2857.1	3279.9	3689.1	4080.1
2002	42.5	145.8	322.9	572.0	884.7	1249.6	1654.5	2087.5	2537.7	2995.6	3453.3	3904.3	4343.5
2003	18.9	119.1	317.6	596.0	924.9	1276.6	1628.7	1965.9	2278.4	2561.3	2812.6	3032.8	3223.5
2004	26.7	132.3	328.2	599.6	922.9	1274.4	1634.1	1986.9	2322.3	2633.9	2918.2	3174.0	3401.4
2005	25.2	123.2	311.6	584.7	926.1	1315.8	1734.5	2165.4	2594.7	3012.3	3410.8	3785.2	4132.8
2006	29.8	134.6	325.9	590.6	906.4	1250.6	1603.8	1950.9	2281.6	2589.2	2870.0	3122.8	3347.8

D. From residual mortality rate to removals

Residual natural mortality rate was expressed in terms of removals in order to estimate the survival rate in the model transition matrix. Following the classic approximation in single-species VPA (Pope 1972), we assumed that cod removals by harp seal predation (*PR*) were made at the beginning of the year and that fishing removals were made in the middle of the year. These assumptions are sustained by the fact that seal predation is mainly concentrated in the months of December-January and fishing activity has mostly been restricted to summer months since the mid-1990s. Removals due to residual natural mortality (*MR*) were then expressed as:

$$Mr_{a,t} = N_{a,t} \times (1 - \exp(-Mr_{a,t})) - C_{a,t} \times (1 - \exp(-Mr_{a,t} / 2)) - PR_{a,t} \times (1 - \exp(-Mr_{a,t})) \qquad (25)$$

where *a* and *t* index age and year, respectively. *N* is cod abundance, *C* is catch, and *Mr* is residual natural mortality rate.

E. Sensitivity analysis

TAB. 11 – Sensitivity analysis of the model to the value of its main parameters (r, α, β, δ, γ, ζ and ζ_{max}) on the total biomass (B), the biomass removed (BR) by seals, and the predation mortality rate for cod aged 1-2 (M_p1-2) for the period 2002-2006

	-80%	-60%	-40%	-20%	+20%	+40%	+60%	+80%
r								
B	-1.25	-1.54	-1.84	-2.14	3.73	6.00	9.43	13.37
BR	-1.25	-1.66	-2.34	-3.41	7.36	9.09	8.18	6.62
M_p(1-2)	-1.25	-1.59	-2.03	-2.44	2.24	0.73	-0.35	-0.69
α								
B	460.36	83.22	16.31	2.33	-3.10	-2.27	-1.66	-1.25
BR	27.41	13.61	8.58	3.52	-4.16	-2.47	-1.67	-1.25
M_p(1-2)	-4.61	-1.97	-0.60	0.51	-2.91	-2.26	-1.60	-1.25
β								
B	180.39	165.26	89.57	29.44	-4.40	-2.50	-1.67	-1.25
BR	6.86	9.14	13.62	23.56	-4.89	-2.50	-1.67	-1.25
M_p(1-2)	-1.18	-1.54	-1.97	-0.39	-4.33	-2.50	-1.67	-1.25
δ								
B	1.77	1.76	1.71	1.62	-1.36	-1.22	-1.09	-0.96
BR	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M_p(1-2)	-0.95	-1.14	-1.40	-1.77	2.83	3.86	5.29	7.33
γ								
B	0.71	0.65	0.60	0.54	-0.43	-0.39	-0.35	-0.32
BR	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
M_p(1-2)	-0.89	-1.04	-1.20	-1.46	2.09	2.60	3.25	4.15
ζ								
B	8.12	2.20	0.78	0.24	-0.74	-0.66	-0.59	-0.54
BR	1.17	0.68	0.33	0.12	-0.47	-0.45	-0.43	-0.41
M_p(1-2)	-2.68	-0.83	-0.31	-0.10	0.24	0.22	0.18	0.15
ζ_{max}								
B	12.46	3.23	0.98	0.26	-0.65	-0.55	-0.48	-0.42
BR	0.83	1.87	1.01	0.33	-0.92	-0.78	-0.68	-0.60
M_p(1-2)	-3.03	-0.35	0.17	0.11	-0.51	-0.45	-0.42	-0.37