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Emmanuel Chassot[1,2,*], Daniel Duplisea[1], Mike Hammill[1], Amanda Caskenette[1], Nicolas Bousquet[3], Yvan Lambert[1], and Garry Stenson[4]

[1]*Fisheries and Oceans Canada, Institut Maurice-Lamontagne, 850 route de la Mer, Mont-Joli, QC, G5H 3Z4, CANADA*

[2]*IRD, CRH, Avenue Jean Monnet, BP 171, 34 203 Sète Cedex, FRANCE (present address)*

[3]*Département de Mathématiques et Statistiques, Université Laval, Pavillon Alexandre-Vachon, QC, G1K 7P4, CANADA*

[4]*Fisheries and Oceans Canada, Northwest Atlantic Fisheries Centre, PO Box 5667, St. John's, NF, A1C 5X1, CANADA*

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Correspondence: Emmanuel Chassot

Telephone: +33(0)4 99 57 32 24
Fax: +33(0)4 99 57 32 95
Email: Emmanuel.Chassot@ird.fr

ABSTRACT: A statistical catch-at-age model was developed to assess the effects of predation by the northwest Atlantic harp seal population on northern Gulf of St. Lawrence cod by estimating the relative importance of different sources of mortality that affected the stock during a period of collapse and non-recovery. Cod recruitment at age 1 is modeled via a non-linear stock-recruitment relationship based on total egg production and 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 linkage between seals and cod is modeled through a multi-age functional response that was derived from the reconstruction of the seal diet using morphometric relationships and stomach contents of more than 200 seals collected between 1998 and 2001. The model was fitted following a maximum likelihood estimation approach to a scientific survey abundance index (1984-2006). Model results show that the collapse of the northern Gulf of St. Lawrence cod stock was mainly due to the combination of high fishing mortality rates and poor environmental conditions in the early to mid-1990s contributing to the current state of recruitment overfishing. The increase in harp seal abundance during 1984-2006 was reflected by an increase in predation mortality for the young cod age-groups targeted by seals. Although current levels of predation mortality affect cod spawning biomass, the lack of recovery of the NGSL cod stock seems mainly due to the situation of very poor recruitment.

Keywords : cod, harp seal, functional response, model, predation, recovery

INTRODUCTION

During the early 1990s, there was an almost simultaneous collapse among most of the Atlantic cod (*Gadus morhua* L.) fisheries in eastern Canada, leading to severe restrictions or moratoria on commercial fishing (Myers et al. 1997, Rice et al. 2003). The northern Gulf of St. Lawrence (NGSL) cod stock (NAFO divisions 3Pn4RS; Fig. 1) was historically the second largest cod population in the Western Atlantic with a spawning stock biomass (SSB) of 380,000 t in the early 1980s, supporting a fishery of more than 100,000 t in 1983 (MPO 2007). By the late 1980s, the population and fishery declined to such an extent that a moratorium was imposed in 1994, leaving a SSB of only about 10,000 t. Subsequently, the population increased quite rapidly and in 1997, a small fishery reopened, although the stock has remained at about 50% of its minimum conservation biomass limit (B_{lim}) of about 80-90,000 t.

There has been considerable debate concerning the causes for the decline in cod abundance and subsequent lack of recovery (Hutchings 1996, Shelton & Healey 1999, Shelton et al. 2006). Overfishing has been identified as the main factor that contributed to the collapse due to several interrelated common factors including underestimated discarding and misreporting (Myers et al. 1996, Myers et al. 1997, Savenkoff et al. 2004). For the NGSL cod stock, it has been suggested that changes in environmental conditions in the early 1990s also played a role in the fishery collapse through a decline in condition, which consequently resulted in reduced growth and recruitment (Lambert & Dutil 1997a, Dutil et al. 1999, Dutil & Lambert 2000). Poor condition is also suspected to have led to an increase in natural mortality through starvation and enhanced vulnerability to predation (Dutil et al. 1999). The current poor productivity of the stock associated with ongoing fishing activity has been proposed as a major factor explaining the lack of recovery for NGSL cod (Dutil et al. 2003, Shelton et al. 2006).

During the last 3 decades, there has been a marked increase in abundance of many pinniped populations in the northwest Atlantic (Hammill et al. 1998, Hammill & Stenson 2005). Higher natural mortality resulting from increased predation has also been put forward as a plausible hypothesis explaining the collapse and failure of northwest Atlantic groundfish populations

to recover (Bundy 2001, DFO 2003, Rice et al. 2003). In particular, harp seals (*Pagophilus groenlandicus*), the most abundant pinniped in the northwest Atlantic, have increased from less than 2 million in the early 1970s to almost 6 million today (Hammill & Stenson 2005). Harp seals summer in the Arctic, but migrate south along the Labrador coast in late autumn to overwinter off northeastern Newfoundland and in the NGSL (Fig. 2). The majority of the seals overwinter off the southeastern Labrador-northeastern Newfoundland coast (NAFO Divisions 2J3KL), while approximately 25-33% of the harp seals move into the NGSL (Stenson et al. 2002, 2003). Harp seals are generalist predators characterized by a diverse diet of fish and invertebrates (e.g. Lawson et al. 1998, Hammill & Stenson 2000). Stomach samples collected during the winter and spring in the NGSL indicate that their diet is highly variable both seasonally and geographically with average of approximately 5% made up by cod, mainly in the size range of 15-25 cm, although in some samples this proportion may be as high as 45% (Hammill & Stenson 2004, Stenson & Hammill 2004).

The correspondence between the decline of NGSL cod and the large increase in harp seal abundance (Fig. 3) has led to a hypothesis that harp seal predation may play a significant role in the cod lack of recovery (McLaren et al. 2001, DFO 2003). Seal predation on cod has been examined using bioenergetic models that derive cod annual consumption estimates by taking into account seasonal changes in feeding and variability in seal abundance, distribution and diet composition (Stenson et al 1997, Hammill & Stenson 2000, Stenson & Hammill 2004). However, because of the variable nature of the diets, these models have assumed an average proportion of cod in the diet, in spite of the marked changes in cod biomass that have been documented over the last 3 decades (MPO 2007). Assumptions about how predation changes in response to variations in prey abundance have been shown to be critical in predicting impacts of predators on commercially important prey (Yodzis 1994, Mackinson et al. 2003). However, individual and population level phenomena among predators and prey alike, such as search image, difficulty in finding prey, aggregation, and dispersion of predator and prey, can lead to significant departures from the linear assumptions about the relationship between prey abundance and the proportion of prey in the diet (Koen-Alonso 2006). In addition, harp seals can display strong preference for specific prey, although they have been shown to be neutrally

selective toward Atlantic cod (Lawson et al. 1998, Lindstrøm et al. 1998, Wathne et al. 2000). Modeling non-linear processes of the functional response of harp seals to cod appears therefore to be a key to modeling predation over a wide range of prey abundance such as observed in NGSL cod.

As described above, hypotheses related to fishing, seal predation, and environment have been proposed for the decline of NGSL cod but few studies have attempted to simultaneously address these hypotheses to determine which processes were at play at different times and how synergistic forcing could have led to the cod collapse. Here, a predator-prey model was constructed for NGSL cod, with mortality partitioned into components caused by harp seal predation and by other processes including an explicit influence of an integrated environmental forcer. The impact of seals on cod was modelled through a non-linear multi-age functional response similar to a multi-species functional response (Smout & Lindstrøm 2007). Cod condition was used as an index for the cumulative and lagged effects of environmental conditions related to factors such as food availability and temperature experienced by cod (Lambert & Dutil 1997a-b, Rātz & Lloret 2003). Changes in cod condition were assumed to affect natural mortality (Dutil & Lambert 2000) and fecundity, i.e. potential recruitment strength (Marteinsdottir & Begg, 2002). The main objective of the analysis was to determine the relative impact of fishing, seal predation, and environment on the decline of NGSL cod by integrating these processes into a single consistent modeling framework. Such a framework is essential to both understand what happened to the stock and serve as a springboard for determining future states in the context of cod recovery and providing advice on exploitation of NGSL harp seal and cod populations.

COD POPULATION MODEL

Cod population dynamics were modelled through a separable statistical catch-at-age analysis (Fournier & Archibald 1982) without process error, where mortality was derived from three sources; the fishery, harp seal predation, and natural mortality due to causes other than harp seal predation (other predation, disease, virus, etc.). The Seal IMpact on Cod ABundance (SIMCAB) model considers 13 age classes of cod from 1 to 13 and 100% mortality occurs at

end of the 13th age class for all cohorts. Following Pope's approximation (1972), mortality processes were modelled as successive steps, i.e. removals of cod by harp seal predation were taken instantaneously at the beginning of the year, fishing removals were taken instantaneously in the middle of the year, and residual mortality occurred between the 2 portions of the year (Table 2, D9-D11). The NGSL cod fishery changed considerably in the last decades, particularly after the 1994 moratorium when the winter mobile fishery dominated by otter trawlers was closed (Fréchet et al. 2003a). To account for changes in fishing pattern, 2 periods of distinct fishery selectivity (partial recruitment) were considered: 1984-1993 and 1994-2006. For consistency with knowledge available on NGSL cod dynamics and because of the convergence property of the virtual population analysis (VPA), the initial population age-structure was based on cod numbers estimated in 1984 from VPA (MPO 2007) and the model was run for the period 1984-2006. The parameters and variables used and the process and observation equations are given in Tables 1 and 2 respectively.

A condition-dependent reproduction function

Recruitment, i.e. fish numbers at age 1, was modelled through a Beverton and Holt (1957) stock-recruitment relationship based on an index of the reproductive potential of cod that was developed from an estimate of total egg production of the stock (TEP) (Table 2, D3). TEP accounted for yearly changes in cod numbers-at-age, sex ratio-at-age, the proportion of mature females-at-age, fecundity-at-age through length-at-age and condition factor of the fish. Previous studies have shown that length and condition factor have significant effects on the fecundity of cod in the NGSL (Lambert & 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 2006 (Lambert 2008).

Sex ratio and maturity ogive data were derived from winter surveys conducted with the MV "Gadus Atlantic" (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 Sen-

tinel Fisheries Program (1995-2007), and supplementary research surveys conducted during the pre-spawning period in 1994, 1995, 1997, and 1998 (Dutil et al. 2003, Fréchet et al. 2007).

A multi-age functional response of harp seals to cod

To account for effects of prey abundance on predation, assuming no predator interference in the predation process, a multi-age functional response (FR), i.e. the number of cod consumed per seal per year, was considered (Table 2, D4). The FR of seal to cod is comprised of a maximum consumption rate for cod (J_{max}), attack rates-at-age (ζ_a), and age-structured cod population. The shape parameter m of the FR determines the FR type, i.e. $m = 1$ corresponds to a hyperbolic type 2 relationship and $m > 1$ corresponds to a sigmoid shaped type 3 response (Koen-Alonso 2006).

The attack rates (ζ_a) were expressed relative to baseline attack rates (ζ_a^0) through a scaling factor (ϱ) that was estimated in the fitting process (see section 'Fitting the model'). Baseline attack rates were derived from cod biomass requirements for the NGSL harp seal population, cod abundance based on the matrix of numbers-at-age derived from virtual population analysis (MPO 2007), that was extended to ages 1-2 based on preliminary runs of the model without predation, and proportion and age-structure of cod in the seal diet in 1998-2001.

First, harp seal energetic requirements to maintain the seal population were estimated based on the daily gross energy intake of an individual harp seal derived from the allometric Kleiber equation that scales animal's metabolic rate to the 3/4 power of the animal's mass, and the age-structure of the seal population (Hammill & Stenson 2004, Stenson & Hammill 2004). 25% of the northwest harp seal population was assumed to move into the Gulf of St. Lawrence each year to spend on average 150 days per year in its northern part (Stenson et al. 2002, 2003). The biomass of cod consumed in 1998-2001 was then estimated based on the average energy of cod in winter, set equal to 4.96 kJ g^{-1} (Lambert & Dutil 1997a), and on the annual average proportion of cod in seals diet during November-March 1998-2001 (Table 3). The relative energetic contribution of cod to seal's diet was based on recovered otoliths and accounted for

harp seal population residency in the areas 4Ra-c, 4Rd-3Pn, and 4S of the NGSL (Fig. 2; Hammill & Stenson 2004). The annual number of cod consumed was then estimated based on the mean mass of cod consumed by harp seals and reallocated between cod age-groups based on information available from the analysis of seal stomach contents (Lawson et al 1998; Hammill & Stenson 2004). Lengths of cod ingested were estimated from otoliths found in seal stomachs and published fish length - otolith length regression equations (Hammill & Stenson 2004). Fish lengths were based on 671 otoliths found in 140 seal stomachs collected during November to March, 1989-2001 in the Gulf of St. Lawrence (Chassot et al. 2007). Harp seal size ranged from 102-166 cm. Otoliths collected from stomach contents were assumed to represent the size distribution of cod eaten. Proportions were estimated by fitting a mixture model of normal distributions to the prey size-frequency histogram by applying a constraint on the variance of cod size derived from DFO summer survey (Chassot et al. 2007).

The maximum consumption rate J_{max} was calculated based on the energy requirements of the NGSL harp seal population in 1998-2001 and a maximum value of cod proportion in seal stomachs derived from diet information available. Following the same approach as described above, fish biomass required to maintain the NGSL seal population was first calculated. Based on a maximum proportion of cod of 18.3% derived from the maximum proportions of cod in seals diet observed since 1980 and the relative residency time in each area of the NGSL, the potential maximum number of cod eaten per seal per year J_{max} was calculated. The baseline attack rates-at-age were finally calculated from the number of cod-at-age consumed per seal and cod numbers-at-age derived from the VPA in 1998-2001 (Table 2, D4). Since the baseline attack rates were based on a number of cod eaten calculated from the mean weight of cod in the reference period 1998-2001, the mass ratio $\left(\frac{\overline{W_t}}{\overline{W_0}}\right)$, an index of cod weight, was included to account for yearly fluctuations in the mean mass of cod when calculating the number of cod predated by seals (Table 2, D5).

In order to illustrate the multi-age functional feeding response to changes in cod availability, a large range of levels of cod abundance were simulated for 2 distinct age-structures of the cod population. For each age-structure, cod-at-age consumed per seal per year were calculated

based on the model fitting results.

Removals by natural mortality other than harp seal predation

The rate of natural mortality excluding harp seal predation, i.e. residual mortality was modelled as an age-dependent function, in the form of a decreasing exponential as a function of age with a condition-dependent asymptote (Table 2, D6). The asymptote was modelled as a decreasing linear function of cod condition based on results of laboratory experiments relating natural mortality to cod condition (Dutil & Lambert 2000, Chassot et al. 2007). The condition factor which is an indicator of the energy content of cod was used here as an integrative index of environmental conditions (Lambert & Dutil 1997b). Alternative values for the asymptote of the residual mortality curve, i.e. a constant value of 0.4 y^{-1} and a time-dependent natural mortality derived from stock assessment models (MPO 2007), were considered to assess the impact on the results through the Akaike Information Criterion (AIC; Akaike 1974).

Effects of seal predation vs. fishing on the reproductive potential

Because seal predation and fishing are mortality sources for different cod age groups, a unit of mortality from each does not have the same impact on the population. Similarly to a multi-fleet biomass-per-recruit analysis, effects of changes in harp seal predation vs. fishing mortality were investigated by calculating the spawning stock biomass per recruit (SSB/R) for different levels of mortality. Such an analysis focuses on the long-term survival of a recruit and does not consider the linkage between the reproductive potential and recruitment at age 1. Based on the mortality rates estimated and averaged over the period 2002-2006 and assuming all else constant, we examined the relative importance of seal predation mortality and fishing mortality on the long-term stock reproductive potential under two scenarios: a high productivity environment and a low productivity environment. Considering a range of fishing mortality multipliers from 0 to 2, cod SSB/R was calculated at equilibrium for distinct levels condition because condition was assumed to affect the asymptote ϑ of the residual natural mortality in

the model. 3 levels of seal predation mortality were considered corresponding to 0.5, 1, and 1.5 times the average harp seal predation mortality estimated in 2002-2006. 2 scenarios of conditions represented different environmental conditions for the cod population, with values of $\vartheta = 0.26$ and $\vartheta = 0.35$ corresponding to a high and a low productivity regime scenario, respectively.

FITTING THE MODEL

Abundance and catch data

Stratified random bottom-trawl surveys have been conducted in the NGSL annually, in summer months, since 1984. A consistent time-series of numbers-at-age, accounting for the changes in research vessels, was used as abundance indices for cod for the period 1984-2006 (Bourdages et al. 2003, 2007, Chassot et al. 2007).

The catch-at-age matrix of cod (in numbers) 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. In the present analysis, reported landings were considered as the "true" catch despite potential discarding and misreporting in the fishery (Fréchet et al. 2003b, Savenkoff et al. 2004).

Statistical estimation approach

Maximum likelihood methods were used to estimate SIMCAB parameters. The likelihood function of the model was derived from assumptions on the statistical distribution of the 4 datasets acquired from independent sampling processes: total abundance index in number, proportion-at-age for the abundance indices, total catch in number, and proportion of catch-at-age (Fournier & Archibald 1982, Quinn & Deriso 1999) (Table 5).

A stochastic observation equation accounting for correlated errors among ages was considered to link the abundance indices to the population model (Myers & Cadigan 1995) (Table 5, S1). For some years, some abundance indices-at-age for very young (age 1) or old cod (ages 11-13) were not observed during the surveys. For these years, total survey indices were considered as right-censored data, providing less information to the likelihood component than real observations (Lawless 2003). This is true for the sum over ages of the logarithms of the survey indices since these indices are extrapolated to the scale of the NGSL and are positive numbers greater than 1. The observed likelihood of total surveys indices was then composed of a product of densities and survival functions, where a survival function is defined as 1 minus the distribution function (Table 6, L1). The survival factor in the likelihood represents the integration, over all its possible values, of the probability that a random total survey index is higher than an underreported observation. It is a common way of including partial data information in a statistical analysis, but rarely used in fisheries analysis (for a notable exception see Hammond and Trenkel 2005).

Proportion-at-age for the abundance indices and catch data were assumed to follow dirichlet distributions to account for correlations among age groups (Fournier & Archibald 1982) (Table 5, S2 and S3). Total catch observed were considered mainly dependent on the fishing year and assumed measured with lognormal observation errors (Table 5, S4). The assumption of log-normal error distributions for survey and catch data was checked through the residuals.

The maximum likelihood estimates were found by minimizing the negative sum of the log of the 4 likelihood components (i.e. objective function) given in Table 6. Minimizations were performed with the Nelder-Mead simplex non-linear optimization algorithm implemented in the R package (R Development Core Team 2008). The parameter space θ to estimate included 37 parameters from 644 observations, an observation being a survey index or catch number for a given age group in a given year: 2 for the TEP-recruitment relationship (R_{max} and r), 2 for the FR (m and ϱ), 2 for the residual mortality curve (α and β), 1 for the survey catchability (q), 6 for the selectivity of survey and fishing gears (γ_s, δ_s, γ_c^1, δ_c^1, γ_c^2, δ_c^2), 23 for the fishing mortality rates (F_t), and 1 for the standard deviation of the observation error in

the total survey data (ψ) (see Table 1 for definition). The maximum likelihood estimate of the observation error variance in the total catch data (σ_c^2) was:

$$\sigma_c^2 = 2\left(\sqrt{1 + \frac{1}{T}\sum_{t=1}^{T}\left(\log\frac{C_t^*}{C_t}\right)^2} - 1\right) \quad (1)$$

Where the notations used are given in table 4.

Confidence statements about parameters were inferred using parametric bootstrap methods accounting for bias (Efron & Tibshirani 1998). 100 bootstrap replicate samples with the same dimensions as the datasets described above were generated by drawing from the probability distributions characterised by the parameters estimated at the maximum likelihood. Replicate samples were then submitted to the estimation procedure to obtain bootstrap replicates of the estimator and calculate percentiles of the distribution.

Sensitivity analysis

To complete the bootstrap analysis that only considered uncertainty in the catch and survey data, a sensitivity analysis was performed to account for uncertainty in some input parameters of the predation model and harp seal population in the NGSL (Hammill & Stenson 2004, Stenson & Hammill 2004). In a first step, the sensitivity of the results was examined by independently increasing parameter values by 10% from a baseline value (values from the standard run), re-fitting the model to observations for each sensitivity run, and assessing the change between the new and baseline results through a measure of relative sensitivity (Stenson & Hammill 2004, Mohn & Bowen 1996). The sensitivity to 5 parameters was investigated: the proportion of the northwest Atlantic population of harp seals moving into the NGSL, the average proportion of cod in seal's diet in 1998-2001, the maximum proportion of cod in seal's diet, the average energy of cod, and the Kleiber multiplier used as a constant multiplicative parameter in the Kleiber equation (Table 7). In order to summarize the model results and because predation by harp seals was the main focus of the analysis, only results for mean cod

biomass removed by seals and mean predation mortality rate for ages 1-4 during 1984-2006 were presented. In a second step, the impacts of setting the value of the functional response type m to 1, i.e. a hyperbolic type 2 relationship, were examined.

RESULTS

Age-structure of cod in seal's diet

The size frequency histogram showed that 95% of cod found in harp seal stomachs were less than 38 cm (Fig. 4). The mixture model fitted well the cod size-frequency data as indicated by the significance level for the goodness-of-fit test ($p > 0.05$), based on the chi-square approximation to the likelihood ratio statistic (Du 2002). The model showed that cod consumed were young cod, with ages 1-4 representing 26.5%, 48.5%, 18%, and 7% of the cod in the diet, respectively (Fig. 4).

Cod population dynamics

The model fitted the survey and catch data well and the minimum value for the objective function was 6,149.6, corresponding to an AIC value of 12,373 (Figs. 5-6). The variances of the observation errors in the survey and catch data were low, the values of ψ and σ_c used as proxies of coefficients of variation in the case of lognormal likelihoods being 5.0% and 2.7%, respectively. Consequently, confidence intervals around parameters estimated by bootstrap analysis were small (Table 1). Considering a constant asymptote of 0.4 y^{-1} and a variable asymptote for the residual mortality curve led to higher values of AIC (12,583 and 12,696 respectively) than for a condition-dependent asymptote, indicating a better fit of the model when residual mortality was related to cod condition.

SIMCAB estimates indicated a strong decline in cod abundance for all age-groups from 1984 to 1993, consistent with the collapse of the northern Gulf cod stock in the mid-1990s (Fig. 5).

Abundance indices for ages 4-8 then remained quite stable from the mid-1990s to the early 2000s, the stock showing no clear sign of recovery despite the moratoria on fishing implemented in 1994-1996 and 2003 (Fig. 5). By contrast, abundance indices for cod aged 10-13 displayed increasing trends from the mid-1990s to the 2000s; these age-groups representing a very small proportion of the stock abundance but about 10% of the SSB on average for the period 1984-2006 (Fig. 5). The declines in abundance were accompanied by a decrease in SSB from more than 330,000 t in the early 1980s to a minimum of less than 30,000 t in 1994 and showed a small increase thereafter. SSB estimates were thus below the conservation biomass limit of 80-90,000 t and indicated a clear case of recruitment overfishing for the stock.

The number of cod caught showed a strong decrease from the 1980s to the mid-1990s for ages 5-10 that represent the large majority of the biomass harvested (Fig. 6). SIMCAB predictions appeared bumpy in the 1980s with catches underestimated in 1986 and 1988 for all age-groups (Fig. 6). This mismatch between catch observed and predicted seems mostly due to the exceptional and somewhat surprising abundance indices for ages 4-10 in 1987 (Fig. 5).

Mortality components in different age-groups

Total mortality divided into age-groups showed that sources and magnitude of mortality varied in time and age (Fig. 7). Young cod aged 1-2 experienced high natural mortality, varying between about 1.9 y^{-1} in the mid-1980s to more than 2.4 y^{-1} in the mid-1990s (Fig. 7a). Predation mortality by harp seals only represented a low proportion of mortality for ages 1-2 throughout the period 1984-2006 but increased from about 6% in the 1980s to more than 12% in the mid-2000s.

In addition to seal predation and residual natural mortality, cod aged 3-6 were subject to fishing mortality, mainly in the 1980s (Fig. 7b). The decrease in fishing mortality from the mid-1990s coincided with the change in fishing pattern, i.e. the commercial fishery after 1994 was only conducted by fixed gears (longlines, gill nets, and hand lines) targeting larger cod. Residual natural mortality showed an increase from the 1980s to the mid-1990s associated with

lower condition during this period; the rates in the most recent years were similar to the levels estimated in the mid-1980s. Seal predation mortality for ages 3-6 remained quite stable during 1984-2006 with its proportion in total mortality increasing to more than 20% in the 2000s due to the decrease in fishing and residual natural mortality.

Cod aged 7-10 not preyed upon by harp seals showed high total mortality, particularly in the mid-1980s and early 1990s with rates higher than 1.0 y^{-1} (Fig. 7c). The high interannual variability in mortality rates was mainly due to the strong variations in fishing mortality that represented more than 65% of the total mortality in some years (Fig. 7c). The low fishing mortality values estimated in 1986 and 1988 could be due to the high abundance indices observed in 1987 (Fig. 5). As for ages 3-6, residual natural mortality was the highest in the mid-1990s, corresponding to a low-condition period for cod. Although fishing mortality rates showed a decreasing trend in the 2000s, the values remained high for some years relative to the low abundance of the stock, particularly in 2005.

Harp seal predation

Predation mortality rates for cod aged 1-4 showed a steady increase alongside the increase in harp seal abundance from 0.1 y^{-1} in 1984 to more than 0.3 y^{-1} in 2000 (Fig. 8). The rates then decreased to remain quite stable around 0.25 y^{-1} in the most recent years. Cod biomass removed annually by seal predation was estimated to be around 10,000 t from 1985 to 1995. Removals then showed an increasing trend with a peak above 30,000 t in 2000 and a temporally averaged median of 16,000 t in the 2000s. The high interannual variability in biomass removed was mainly due to the variations in abundance of cod aged 1-2 that represent the major age-groups preyed upon by harp seals.

The exponent of the multi-age functional response fitted to the data was estimated to be 2.13 ($\pm$ 0.015), indicating a sigmoid shaped type 3 response characteristic of sharp changes in the relative importance of the cod age-groups consumed as the result of a relatively small change in their availability in the environment. The changes in biomass removed by seal predation were

then related to both changes in seal population energy requirements and changes in relative cod abundance between age-groups. For instance, the predicted multi-age functional response showed that cod age 2 would be the main target of harp seals when considering different levels of cod abundance described by the 1984 population age-structure (Fig. 9). Considering an age-structure similar to low abundance year of 1995, characterized by a high proportion of cod aged 1 in the population, would lead to a very different response of seals with age-1 cod becoming the major prey and the other age-groups quickly reaching their respective maximum in seal consumption (Fig. 9).

Sensitivity analysis

The sensitivity analysis showed that the results of the model concerning harp seal predation were robust to the assumptions made about the average energy of cod and the values of contribution of cod to seal's diet (Table 7). Increasing the contribution of cod to seal's diet in 1998-2001 did not affect the total biomass removed but led a relatively small increase in predation mortality rates by decreasing the cod population. Although the increase in maximum cod consumption led to an increase in the maximum rate of cod consumption J_{max}, it poorly affected harp seal predation. Predation appeared quite sensitive to a change in the size of the seal population and the Kleiber multiplier of the bioenergetic model (Table 7). Changes in input parameters could be counter-intuitive due to the complexity and non-linearity of the model; hence, the biomass removed by predation during 1984-2006 was decreased by an increase in average energy of cod while it led to an increase in the predation mortality rates. The relative sensitivity of predation rates could have a different sign than the sensitivity of biomass removed since predation rates depend both on the cod biomass removed and cod numbers-at-age.

Constraining the predation model to follow a hyperbolic type 2 relationship strongly affected the results of the model and resulted in a lower quality of fit than for the standard run (AIC = 12,697). Setting the shape parameter of the functional feeding response to 1 led to reduced harp seal predation and increased cod numbers-at-age and spawning stock biomass.

Effects of seal predation vs. fishing on the reproductive potential

The SSB/R curves showed that the reproductive potential of the NGSL cod was affected differently by changes in seal predation and fishing mortality (Fig. 10). The distinct productivity regimes represented by 2 levels of residual mortality modified the values of SSB/R, with low productivity leading to lower values of SSB. In both cases of productivity regimes, the nearly horizontal curves indicated that changes in SSB/R would be poorly modified by changes in fishing mortality while variations in seal predation mortality would have a higher effect on SSB/R (Fig. 10). This result was mainly due to the low fishing mortality rate of 0.15 y^{-1} estimated during 2002-2006. Considering the harp seal predation mortality estimated in 2002-2006 and a low residual mortality (i.e. a high productivity regime), the SSB/R was estimated to be equal to 129 g (Fig. 10 - intermediate dashed line curve). In this case and for a fishing mortality fixed at the level of 2000-2006, a decrease in the predation mortality rate from the mean value of 0.26 y^{-1} in 2000-2006 to a level around 0.13 y^{-1} observed in the mid-1980s would allow almost doubling the SSB/R (Fig. 10 - upper dashed line curve). Changes in fishing mortality assuming constant predation mortality would be less beneficial to the SSB, a decrease from the fishing mortality rate of 0.15 y^{-1} in 2002-2006 to a low rate of 0.03 y^{-1} increasing the SSB from 129 g to 171 g per recruit. Considering a low productivity regime strongly decreased the SSB/R that was estimated to be 73 g in 2000-2006, due to the higher residual mortality decreasing the probability of young cod to reach maturity (Fig. 10 - intermediate solid line curve). In this case, the SSB/R for a predation mortality of 0.13 y^{-1} and constant fishing mortality would only be 131 g (Fig. 10 - upper solid line curve). For the 2002-2006 predation mortality, a decrease in fishing mortality would slowly increase the SSB/R to a maximum of 97 g in the situation of a moratorium.

DISCUSSION

The SIMCAB statistical catch-at-age model was developed to assess the effects of predation by the northwest Atlantic harp seal population on NGSL cod by estimating the relative im-

portance of different sources of mortality that affected the stock during a period of collapse and non-recovery. SIMCAB is a consistent modeling framework which combines the effects of fishing, predation mortality and environment (through the condition index) on cod population dynamics. SIMCAB showed that the increase in harp seal abundance during 1984-2006 resulted in an increase in predation mortality for cod age-groups targeted by seals. Despite the increasing importance of harp seal predation in cod mortality, the collapse of the NGSL cod stock appears mainly due to the combination of high fishing mortality rates and poor environmental conditions that affected the productivity of the population in the early to mid-1990s and led to the current state of recruitment overfishing. SIMCAB results also show, however, that current levels of predation mortality could increase stock rebuilding time by decreasing the probability of fish to reach maturity. Although cod condition has improved in recent years, the current lack of recovery of the NGSL cod seems due mainly to the very low spawner biomass, driven both by the fishery inherently targeting larger fish and increased harp seal predation. Within an ecosystem perspective, management scenarios based on a decline in seal population to promote stock rebuilding should however consider environmental conditions, prey availability for seals and other cod predators of the NGSL that all affect cod productivity and might give rise to unexpected outcomes with a decline in seal abundance.

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 (Andersen & Ursin 1977). This is particularly important in the context of multispecies management as predator control has been proposed for some time as a beneficial tool for fisheries (Flaaten 1988, FRCC, 1999). Multispecies models are useful tools to address the issues raised about the effects of marine mammals on fisheries (Yodzis 1998). In particular, predator-prey models have been used to evaluate the effects of fur seal (*Arctocephalus pusillus pusillus*) predation on hakes (*Merluccius capensis* and *Merluccius paradoxus*) in the Benguela system (Punt & Butterworth 1995) and more recently the effects of northwest Atlantic grey seal (*Halichoerus grypus*) predation on cod population dynamics and causes of collapse and non recovery on the eastern Scotian shelf (ESS) have been

explored (Mohn & Bowen 1996, Fu et al. 2001, Trzcinski et al. 2006). In the Benguela system, modeling the biological interaction between cape fur seals and the cape hakes suggested that an initial reduction in seal numbers would be beneficial, but the resulting decrease in seal consumption would also result in increased predation by a less commercially important hake species *M. capensis* on the more commercially important hake *M. paradoxus*, resulting in little net benefit (Punt and Butterworth 1995). Among northwest Atlantic grey seals, the first modeling approach included predation mortality explicitly in cohort analysis and showed that grey seals had little effect on the collapse of cod on the ESS (Mohn & Bowen 1996). By contrast, more recent analyses suggested that increasing predation mortality since the 1990s could affect the survival of immature cod and contribute to the failure of the ESS and southern Gulf of St. Lawrence cod stocks to recover (Fu et al. 2001, Chouinard et al. 2005, Trzcinski et al. 2006).

The SIMCAB model is an age-structured population dynamics model structurally similar to the models used for grey seals on the ESS but it differs in several important points. A major difference with the models from Mohn & Bowen (1996) and Fu et al. (2001) but addressed by Trzcinski et al. (2006) concerns the linkage between cod abundance and seal consumption through the functional feeding response. The form of the FR is a key issue in multispecies modeling, especially at low abundance, because it defines how predators impact their prey as a function of prey abundance (Yodzis 1994, Mackinson et al. 2003). Most multispecies models such as the Multi-Species Virtual Population Analysis (MSVPA; Magnússon 1995) are based on hyperbolic type 2 functional relationships between prey abundance and predation rates (for a review see Pláganyi 2007). These models assume constant ration formulations where per-capita consumption is set equal to the predator's required daily ration, consistent with the interpretation that feeding selectivities are independent of prey abundance. A sigmoidal functional response is however likely more appropriate when modeling generalist predators (Magnússon & Pálsson, 1991) and recent analyses based on field data tend to support a type 3 relationship (Middlemas et al. 2006, Kempf et al. in press). In Ecopath with Ecosim models (Walters et al. 1997), the functional form of interactions is based on the 'foraging arena' concept that allows exploring alternative forms of functional response but biological

and ecological justifications about this concept remain controversial (Pláganyi 2007).

In the present analysis, cod age-groups were considered distinct prey, consistently with the opportunistic behaviour of harp seals (Hammill & Stenson 2000) and the size-based structure of marine food webs that regulates predation processes (e.g. Shin & Cury 2004). The multi-age FR fitted to the data was a sigmoid shaped type 3 response, suggesting that the response of seals to changes in cod abundance might be complex and highly non-linear, due to predator preferences and potential for prey switching as a function of the relative abundance of prey types in the environment. A sigmoidal shape for the FR would be consistent with the available knowledge on the spatio-temporal and vertical distribution of cod that differs between cod age-groups, juvenile cod being generally found in shallower waters and closer to the shore than adult cod (e.g. Castonguay et al. 1999). Based on survey conducted on board the MV "Gadus Atlantica" in winter from 1978 to 1994, young cod age-groups have been shown to occupy different depths and areas in the NGSL (DFO unpublished data), which could favor the emergence of a type 3 FR. Cod migration and distribution patterns might also change in time in relation to changes in environmental conditions affecting their habitat (Castonguay et al. 1999).

The sensitivity analysis showed that a type 2 FR would be less consistent with both the data and outputs from other predation models (Hammill & Stenson 2004, Duplisea & Hammill 2006). Although cod predation removals were of the same order of magnitude as those found with models based on linear assumptions about seal consumption (Hammill & Stenson 2004, Duplisea & Hammill 2006), the use of a FR led to different conclusions by accounting for changes in cod age-groups abundance in time. Our results are consistent with Middlemas et al. (2006) who provided empirical support for a type 3 FR of seals to Atlantic salmon in an estuarine system in Scotland; however, in a multispecies or multi-age context, the interpretation of the FR type is not straightforward as the changes in alternative prey abundance influence the response of the predator to the availability of any prey (Smout & Lindstrøm 2007). This will be important for harp seals who have been shown to show strong preference for pelagic species such as capelin (*Mallotus villosus*) but are neutrally selective towards cod (Lawson et

al. 1998). Attempts to estimate statistical parameters of a FR have revealed the difficulty of relating microscale observations of stomach contents to the effective feeding responses of marine species at the macroscale (Pláganyi 2007). This is further complicated in the case of harp seal because biomass estimates of important alternative prey such as capelin, sandlance (*Ammodytes* sp), Arctic cod (*Boreogadus saida*) and krill (*Euphausidae* sp) are not available for the NGSL. New data collection, experiments, and analyses such as conducted by Kempf et al (in press) may help clarify harp seal sigmoidal feeding behaviour since modeling such non-linear processes is key to explore the potential impact of management scenarios based on a decline in seal population.

Cod population dynamics

Despite major differences with the current method used to assess the cod stock status (e.g. no commercial data included in the analysis), SIMCAB estimates of cod abundance, fishing mortality, and SSB accorded with the last assessment of the northern Gulf cod (MPO 2007). Results were consistent with the collapse of the stock in the late 1980s and the current lack of recovery (MPO 2007). In the present analysis, cod abundance in the initial year 1984 was based on the numbers-at-age provided by VPA results, considering that the convergence property of this method would give reliable estimates of abundance in the past (Jones 1961). Setting the initial cod numbers helped in the estimation of the parameters linking cod abundance to survey abundance indices, i.e. catchability and selectivity. Although a statistically 'optimal' solution was obtained through the fitting process, the information provided to the model was insufficient to distinguish between the level of residual mortality and magnitude of recruitment at age 1, i.e. there could be a correlation between the maximum recruitment (R_{max}) and the residual mortality parameters (α and β). Such a correlation could affect the absolute values of residual mortality at age 1 but would not modify the model results for the other cod age-groups for which information is provided through survey data.

A novel aspect of our cod population model is a stock-recruitment relationship based on egg production, which for cod is considered a better measure of the true reproductive potential

of the stock than spawning biomass (Marshall et al. 2006). The high interannual variations in abundance indices for cod aged 1-2 included both natural survival variability of cod larvae and juveniles, and sampling noise associated with the research vessel gear that does not well select very small cod (< 15 cm) predated by seals. In the context of trophic interactions where small fish form the bulk of the diet of many predators, collecting data on fish larvae and juveniles abundance appears as a key issue to explain the factors driving prerecruit survival and recruitment.

In addition, total egg production in our model was derived from a statistical model that related egg production to length-at-maturity and condition of mature females (Lambert 2008). 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 harp seal predation was assumed age- and condition-dependent based on a comparative analysis between laboratory feeding experiments and wild cod collected in the Gulf of St. Lawrence in the 1990s (Lambert & Dutil 1997a). The residual natural mortality term for old ages was consistent with temporal patterns estimated with virtual population analysis (Grégoire & Fréchet 2005). Accounting for effects of condition on residual mortality led to a better fit of the model and suggested that the decline in the condition and energy reserves of cod during the 1990s may have lowered the productivity of the stock and contributed to its collapse (Lambert & Dutil 1997a).

In contrast to the VPA, SIMCAB allows the separation of seal predation mortality from fishing mortality and other mortality through time and accounts for environmental influences on mortality and cod fecundity. Modeling the mechanistic processes involved in predation is a valuable alternative to the classic assumption of constant natural mortality rates to include some ecosystem components in stock assessment methods (e.g. Lindstrøm et al. 2002) and progressively move toward ecosystem-based fishery management (Pikitch et al. 2004). This seems particularly critical for conducting stock projections to evaluate the expected effects of fishery management rules (e.g. Hollowed et al. 2000) in a context where predation is suspected to delay the NGSL cod stock recovery.

Cod recovery within an ecosystem perspective

The impact of changes in predation and fishing mortality on the SSB/R was assessed for different values of residual natural mortality assumed here to represent different environmental conditions. Diagnostics about a decline in seal predation were then shown to be dependent on the productivity of the stock related to the environment (Dutil et al. 2003). Residual mortality affecting young cod was shown to be more important than harp seal predation but not explicitly modelled in the present analysis. Predation mortality has been shown to be the dominant source of mortality for small cod ($\leq$ 35 cm) in the 1990s and 2000s, representing about 95% of total mortality (Savenkoff et al. 2006). In the NGSL, small cod have been shown to be preyed upon by large cod through cannibalism, other large demersals (e.g. white hake *Urophycis tenuis*), grey seals and boreal cetaceans including mysticetes such as minke whale (*Balaenoptera acutorostrata*) and odontocetes such as white-beaked dolphins (*Lagenorhynchus albirostris*) (Morissette et al. 2006, Savenkoff et al. 2004, 2006, 2007). While cannibalism decreased in the last decades due to the decline in adult stock biomass, it still represented an important component of mortality for small cod in the early 2000s (Savenkoff et al. 2007). A high proportion of the total mortality of cod aged 3-10 was also not explained by harp seal predation or fishing and attributed to residual mortality. This residual mortality includes both a predation mortality component due to large cod predators such as grey seals and another mortality component that could involve starvation, disease, and parasites (Savenkoff et al. 2004, 2006). In SIMCAB, mortality linked to these latter factors was related to cod condition through the asymptote of residual mortality, assuming that fish in bad condition would have little energy reserves to survive over the winter months or critical stages of their life cycle (Lambert and Dutil 1997, Dutil et al. 1999).

Based on the large database of cod stomachs collected by Fisheries and Oceans Canada during numerous research and commercial fishing-vessel surveys since the mid-1980s, modelling explicitly cannibalism within SIMCAB could help separating the components of residual mortality for small cod. Following the one-way interaction modelled between harp seal and cod, predation by other species than harp seals such as grey seals could also be included in the

model if suitable data are available. The use of ecosystem models such as mass-balanced and end-to-end models (Travers et al. 2007) in complement to SIMCAB would allow to represent the full complexity of the food web, to identify the major factors affecting cod mortality, to include bottom-up effects of prey availability on production and mortality, and eventually to compare simulation outputs for assessing the robustness of the results.

Long-term projections based on the SSB/R analysis did not consider issues of recruitment in a context where the low reproductive potential of the stock associated with a low productivity are major factors explaining its lack of recovery (Dutil et al. 2003, Shelton et al. 2006). Projections performed with SIMCAB to estimate recovery time should also account for the effects of condition on recruitment (Lambert et al. 2000, Marteinsdottir & Begg 2002) and growth (Dutil et al. 1999) that would also modify the response of the cod population to the implementation of management rules based on a decline in seal population. Considering alternative projection scenarios based on different harvest control rules for the commercial cod fishery and different environmental regimes is important to determine the utility of managing seals to increase the recovery rate of the NGSL cod population.

CONCLUSION

The main objectives of this study were to examine the relative impacts of fishing, environmental conditions and seal predation on the decline and recovery of the NGSL cod population within a consistent modeling framework. Within this framework harp seals could play an important role in the recovery of NGSL cod. This framework lends itself to adding additional components which might result in different conclusions. For example, harp seals are generalist predators and their impact will be affected by the availability of alternative prey. Elsewhere it has been shown that incorporating even only a few other prey alternatives may result in different and unexpected outcomes (Punt & Butterworth 1995, Morissette et al. 2006, Matthiopoulos et al. 2007). Therefore, although harp seals may have an important impact on recovery of NGSL cod population, efforts to manage seals with this objective in mind may not achieve the expected

outcomes because of other components within the NGSL marine ecosystem.

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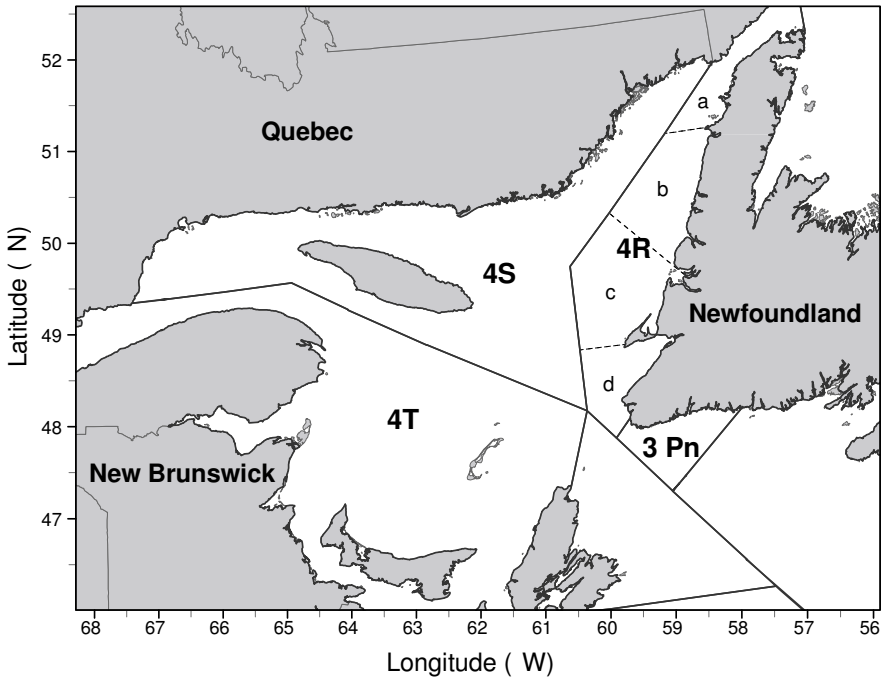

Figure 1: Location of the northern Gulf of St. Lawrence (NAFO divisions 4RS)

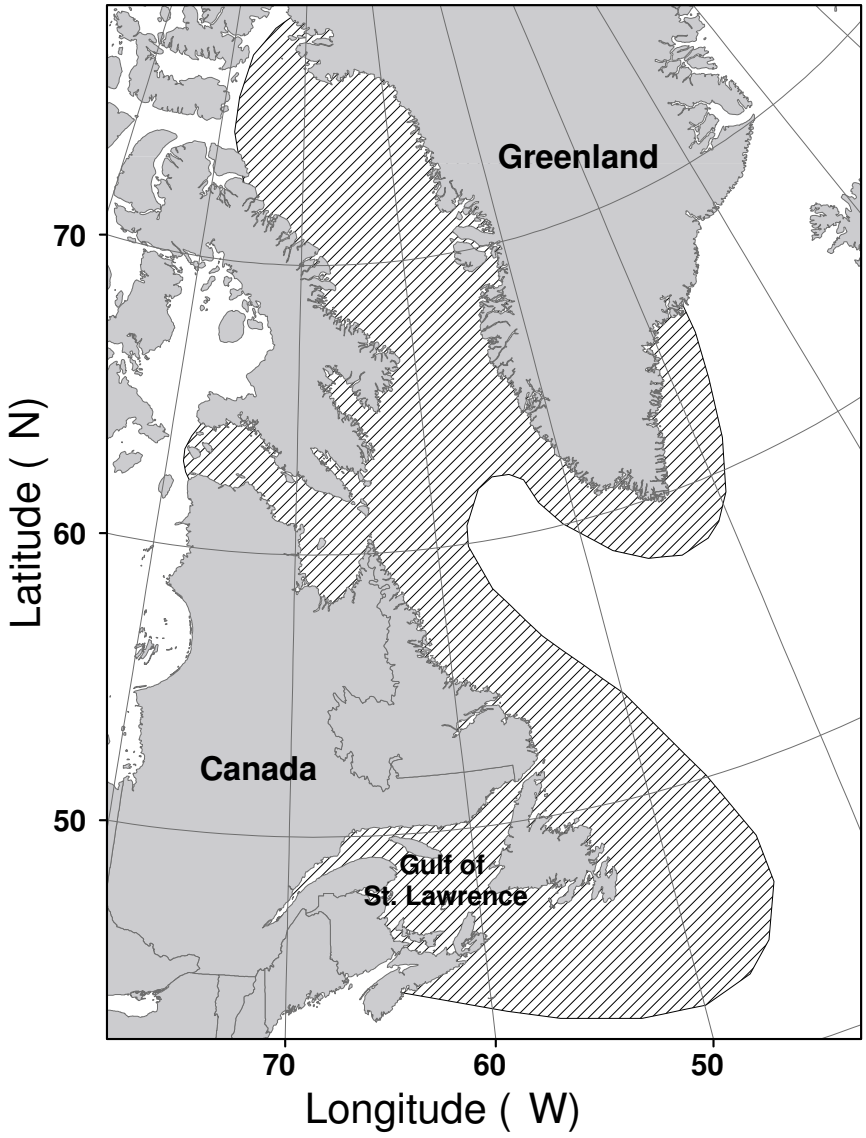

Figure 2: Distribution area of northwest Atlantic harp seals (*Pagophilus groenlandicus*)

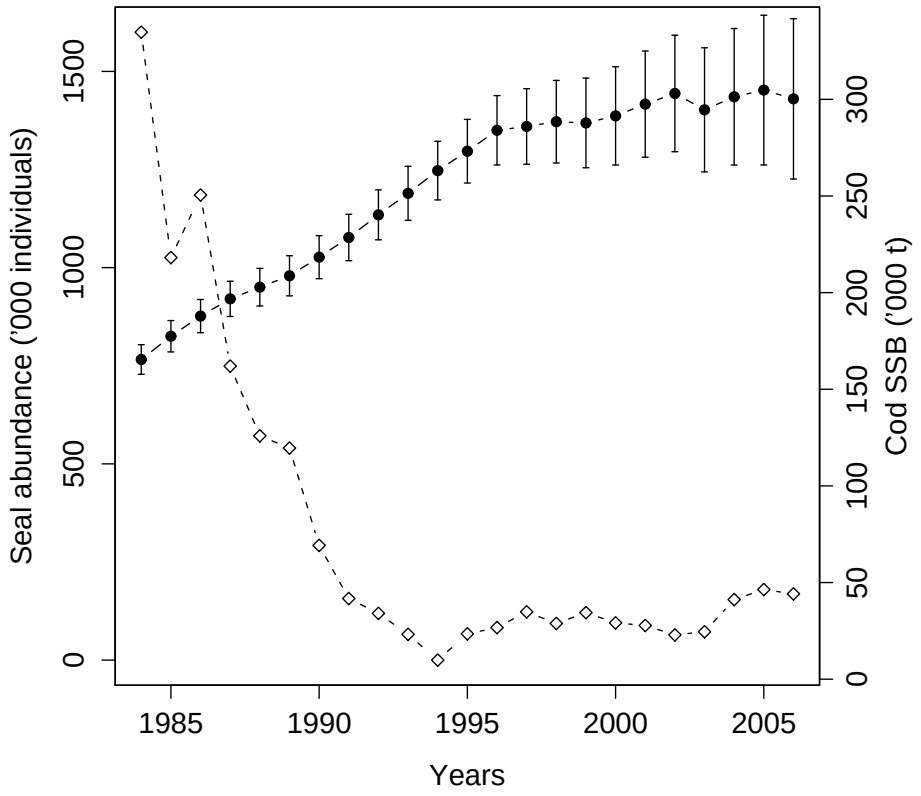

Figure 3: Harp seal abundance (black dots) (± standard deviation) derived from the model of Hammill and Stenson (2004) and cod spawning stock biomass (white diamonds) derived from virtual population analysis (MPO 2007) in the northern Gulf of St. Lawrence during 1984-2006

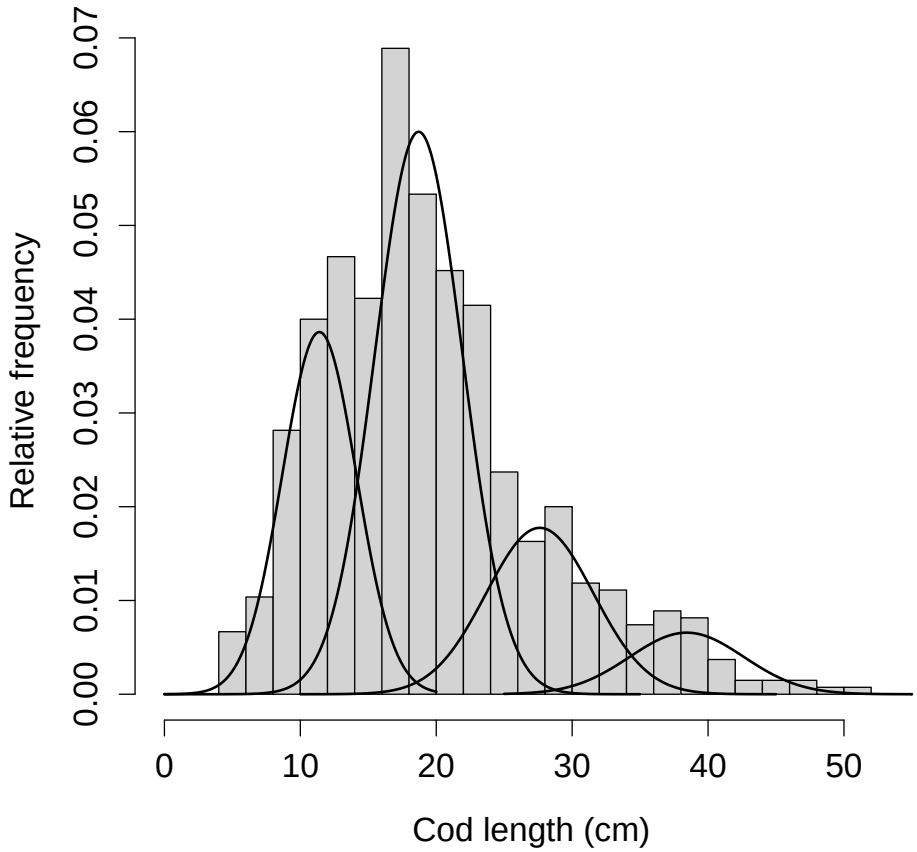

Figure 4: Size-frequency histogram of cod ingested derived from otoliths collected in seal stomachs with fitted mixture distribution representing cod of age 1-4

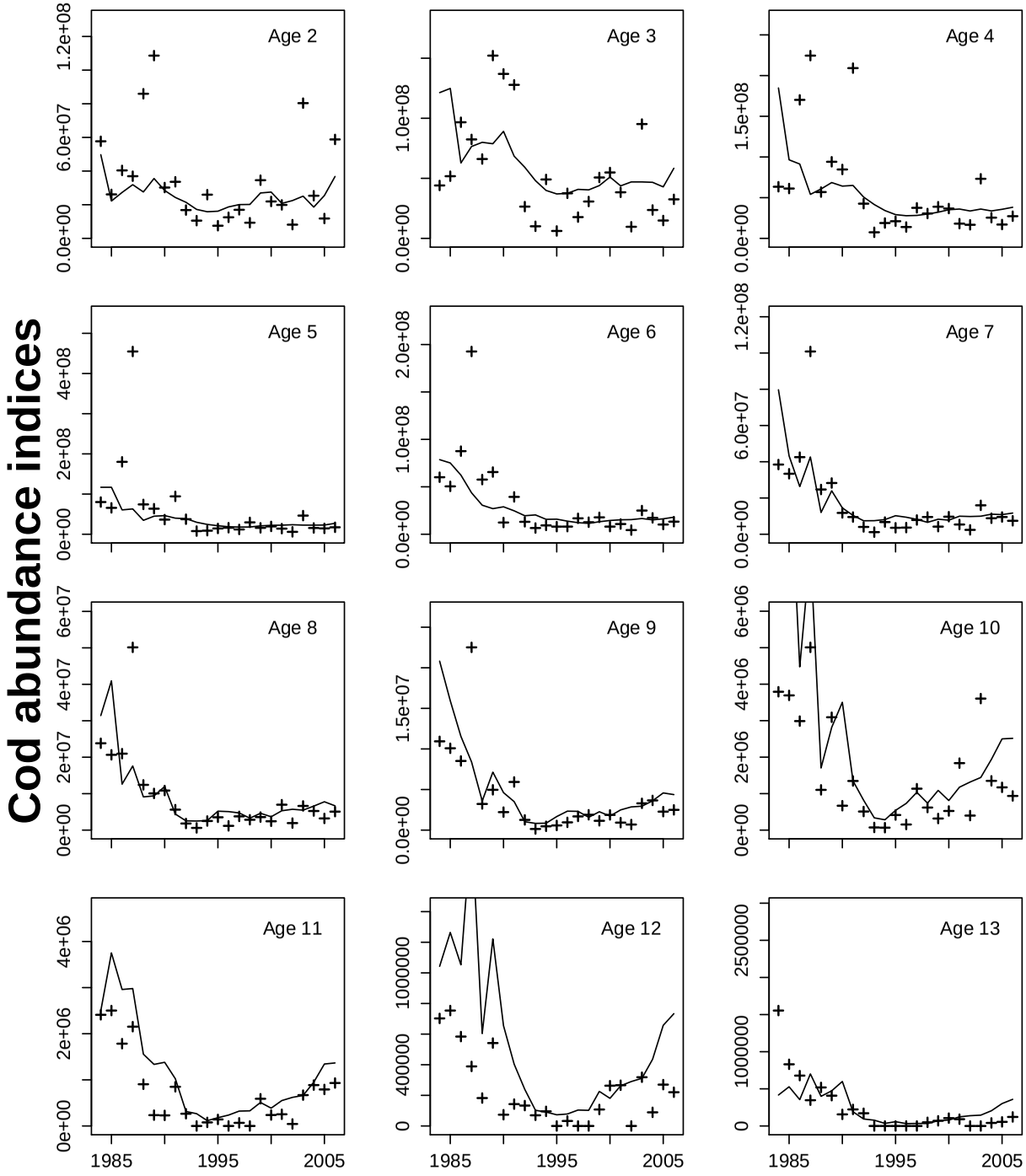

Figure 5: Survey numbers-at-age observed (cross) and predicted by the SIMCAB model (solid line). Scales were selected for readability along y-axes

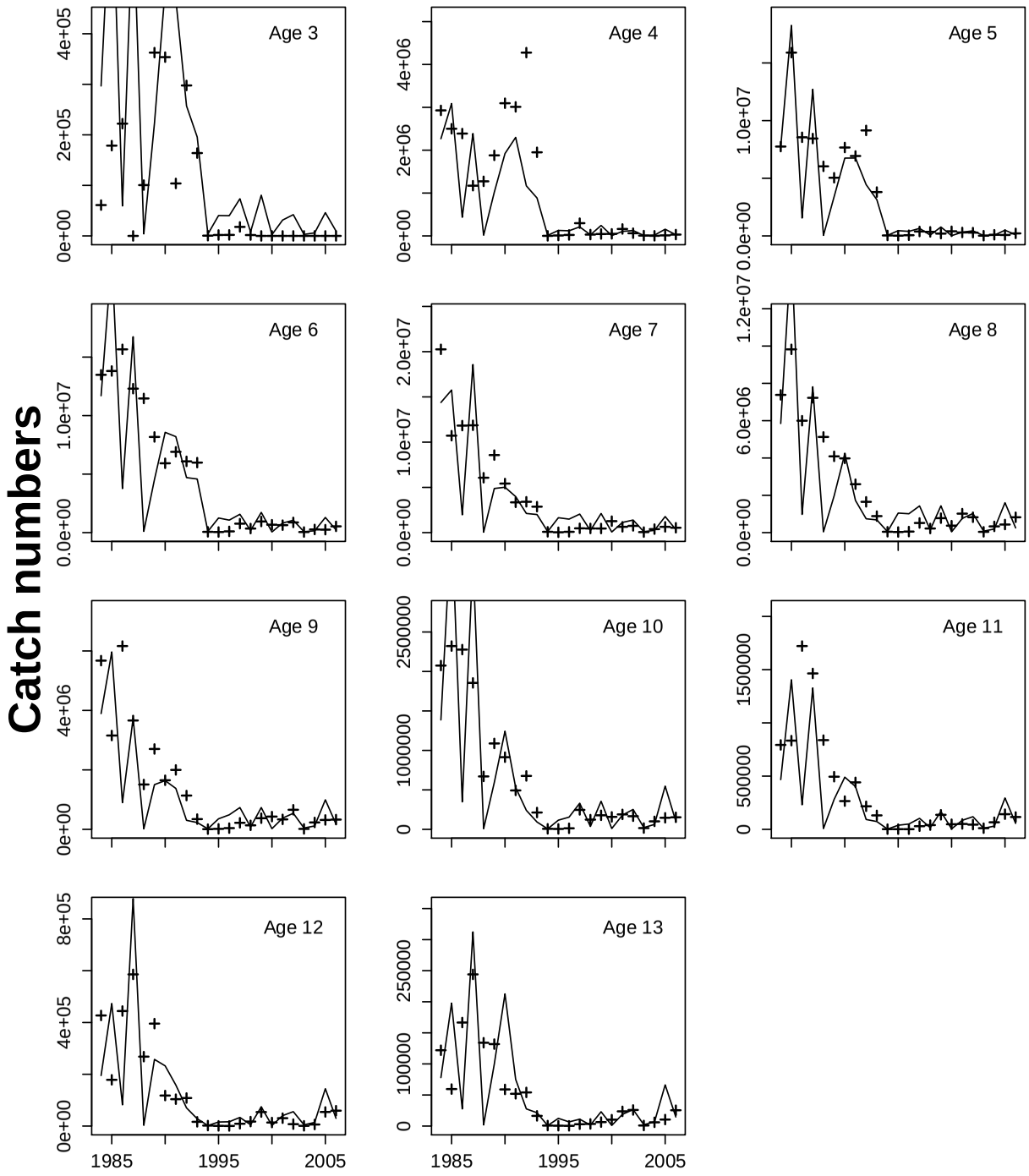

Figure 6: Catch-at-age observed (cross) and predicted by the SIMCAB model (solid line). Scales were selected for readability along y-axes

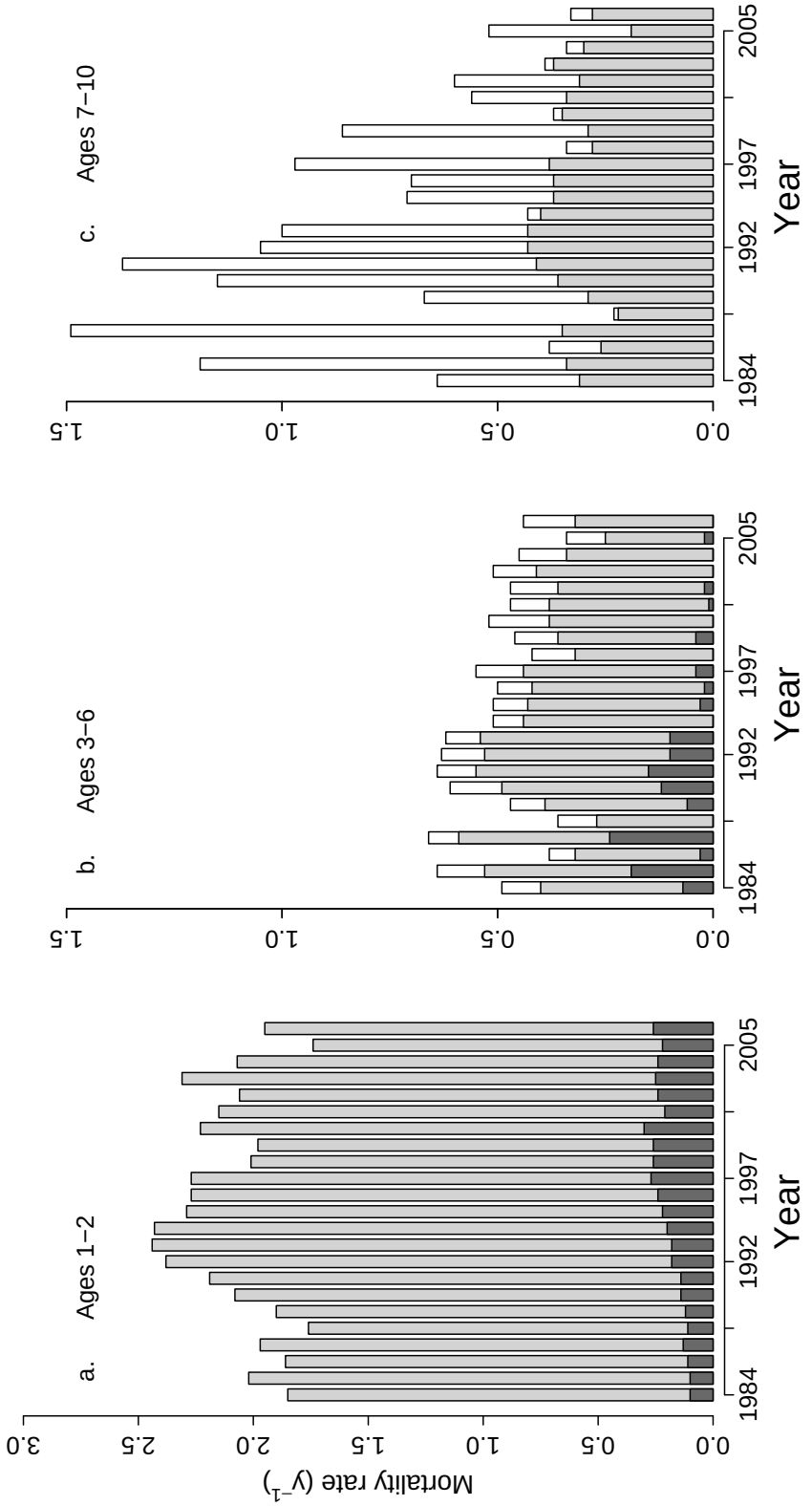

Figure 7: Cumulative annual mortality rates for cod aged (a) 1-2, (b) 3-6, and (c) 7-10. Dark grey: seal predation mortality; light grey: natural mortality other than seal predation; white: fishing mortality. Scales were selected for readability along y-axes

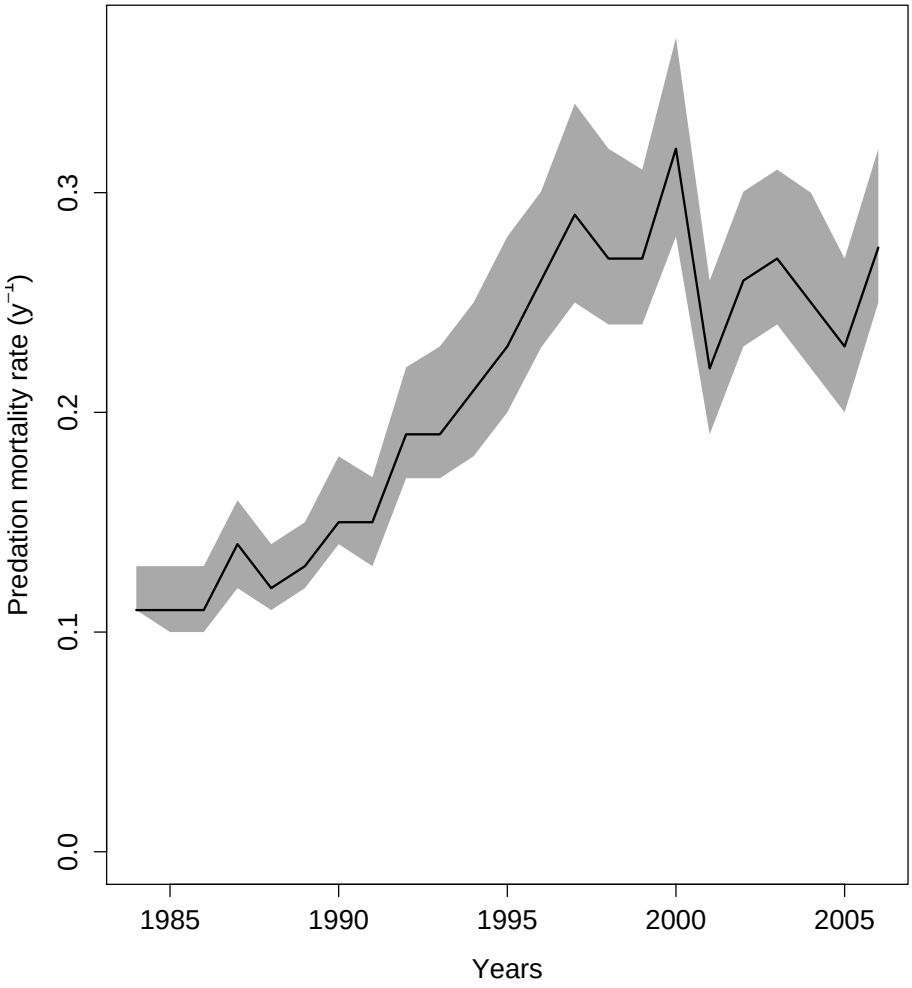

Figure 8: Annual predation mortality rate for cod aged 1-4 with 90% bootstrap confidence intervals

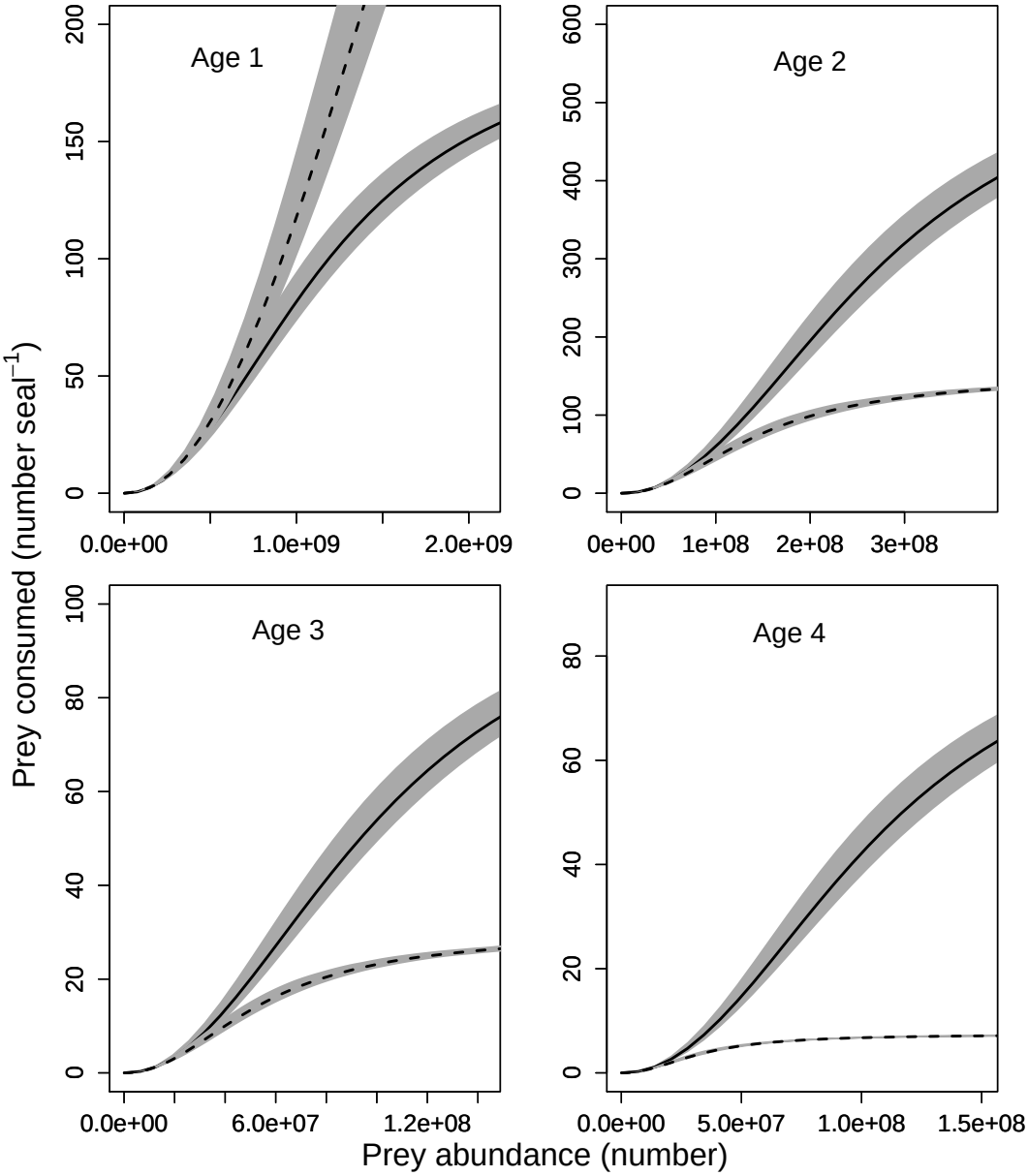

Figure 9: Predicted multi-age functional response of harp seal to cod for 2 distinct age-structures of the population. Solid line corresponds to the age-structure of the year 1984; dashed line corresponds to the age-structure of the year 1995 characterized by a high abundance of cod aged 1. Grey area represents 90% bootstrap confidence intervals. Scales were selected for readability along y-axes

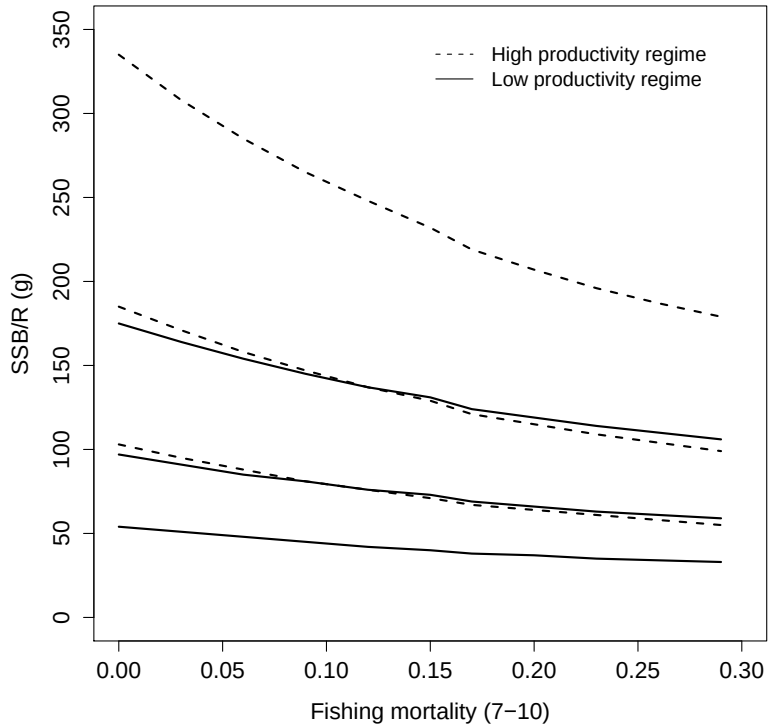

Figure 10: Spawning stock biomass per recruit (SSB/R) as a function of fishing mortality for 3 different levels of harp seal predation and 2 distinct productivity regimes (see text for details)

Table 1: Parameters and variables used in SIMCAB. NS: not shown

Notation	Definition	Origin	Value	Equation
B	Cod biomass (t)	Calculated	NS	D1
N	Cod numbers (number)	Calculated	NS	D1-D5,D9,D11-D12
w_a	Cod weight-at-age (t)	Fixed	NS	D1-D2
SSB	Spawning stock biomass (t)	Calculated	NS	D2
TEP	Total egg production (number)	Calculated	NS	D3,D8
ξ	Sex ratio	Fixed	NS	D3
ϕ	Proportion of maturing females	Fixed	NS	D1,D3
f	Fecundity (number of eggs cod^{-1})	Fixed	NS	D3
A	Last age-group	Fixed	13	D3
λ	Functional response of harp seals to cod (number seal^{-1} year^{-1})	Calculated	Fig. 9	D4,D5
ζ	Attack rate (number seal^{-1} year^{-1})	Calculated	NS	D4
ζ^{ref}	Reference attack rate (number seal^{-1} year^{-1})	Calculated	NS	D4
ϱ	Scaling factor of the attack rates	Estimated	0.021 (0.003)	D4
J_{max}	Maximum consumption rate (number seal^{-1} year^{-1})	Calculated	996	D4
m	Shape parameter defining the functional response type	Estimated	2.13 (0.015)	D4
ρ	Number of feeding days spent by seals in Gulf each year	Fixed	150	D5

Table 1: Parameters and variables used in SIMCAB (continued)

Notation	Definition	Origin	Value	Equation
$\overline{W_t}$	Cod mean weight for ages targeted by seals (t)	Calculated	NS	D5
$\overline{W}_0$	Cod mean weight for ages targeted by seals in 1998-2001 (t)	Calculated	288e-6	D5
S	Seal numbers (number)	Fixed	Fig. 3	D5
M	Residual natural mortality rate (y^{-1})	Calculated	Fig. 7	D6
α	Intercept of the M curve (y^{-1})	Estimated	5.03 (0.013)	D6
β	Slope of the M curve (y^{-1} a^{-1})	Estimated	0.90 (0.002)	D6
ϑ	Asymptote of the M curve (y^{-1})	Calculated	NS	D6
F	Fishing mortality rate (y^{-1})	Estimated	Fig. 7	D7
$\varsigma_{a,\,c}$	Partial recruitment	Calculated	NS	D7
γ_c^1	Shape parameter of the partial recruitment (1984-1993)	Estimated	1.95 (0.007)	D7
δ_c^1	Age at which 50% of the individuals are vulnerable to fishing gear (1984-1993)	Estimated	5.39 (0.006)	D7
γ_c^2	Shape parameter of the partial recruitment (1994-2006)	Estimated	1.64 (0.017)	D7
δ_c^2	Age at which 50% of the individuals are vulnerable to fishing gear (1994-2006)	Estimated	6.46 (0.016)	D7
R	Recruitment (number)	Calculated	NS	D8
R_{max}	Maximum number of recruits produced (number)	Estimated	1.9e9 (6.9e6)	D8
r	TEP needed to produce recruitment equal to $R_{max}/2$ (number of eggs)	Estimated	5.3e11 (1.3e11)	D8
N'	Cod numbers in the middle of the year (number)	Calculated	NS	D9-D10
P	Cod numbers predated by the seals (number)	Calculated	NS	D9

Table 1: Parameters and variables used in SIMCAB (continued)

Notation	Definition	Origin	Value	Equation
C	Fishery catch (number)	Calculated	Fig. 6	D10-D11,D14-D15
I	Abundance index (number)	Calculated	Fig. 5	D12
$\varsigma_{a,\,s}$	Survey selectivity-at-age	Calculated	NS	D12
q	Survey catchability	Estimated	1.38 (0.076)	D12
γ_s	Shape parameter of the survey selectivity	Estimated	2.99 (0.028)	D12
δ_s	Age at which 50% of the individuals are vulnerable to the survey gear	Estimated	2.72 (0.007)	D12
$p_{a,\,t,\,s}$	Proportion of number-at-age in the survey	Calculated	NS	D13
$p_{a,\,t,\,c}$	Proportion of catch-at-age	Calculated	NS	D15

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Table 2: Deterministic process and observation equations in the SIMCAB model. a and t index age and time respectively

State moments

(D1) $$B_t = \sum_{a=1}^{A} w_a \, N_{a,\,t}$$

(D2) $$SSB_t = \sum_{a=1}^{A} w_a \, N_{a,\,t} \, \phi_{a\,t}$$

(D3) $$TEP_t = \sum_{a=1}^{A} N_{a,t} \, \xi_{a,\,t} \, \phi_{a,\,t} \, f_{a,t}$$

Mortality components

(D4) $$\lambda_{a,\,t} = \frac{J_{max} \, \zeta_a \, N_{a,\,t}^{m}}{J_{max} + \sum_{i} \zeta_i \, N_{i,\,t}^{m}} \quad \text{with} \quad \zeta_a = \varrho \, \zeta_a^0$$

(D5) $$P_{a,\,t} = \frac{\lambda_{a,\,t} \, N_{a,\,t}}{\left(\frac{\overline{W}_t}{\overline{W}_0}\right) \, S_t \, \frac{\rho}{365}}$$

(D6) $$M_{a,\,t} = \vartheta_t + \alpha \, \exp\left(\frac{-a}{\beta}\right)$$

(D7) $$F_{a,\,t} = \varsigma_{a,\,c}^{k} \, F_t \quad \text{with} \quad \varsigma_{a,\,c}^{k} = \frac{1}{1 + \exp\left(-\gamma_c^k \, (a - \delta_c^k)\right)}$$

Process functions

(D8) $$R_t = \frac{R_{max} \, TEP_{t-1}}{r + TEP_{t-1}}$$

(D9) $$N'_{a,\,t} = (N_{a,\,t} - P_{a,\,t}) \exp(-M_{a,\,t}/2)$$

(D10) $$C_{a,\,t} = N'_{a,\,t} \left(1 - \exp\left(-F_{a,\,t}\right)\right)$$

(D11) $$N_{a+1,\,t+1} = \left(N'_{a,\,t} - C_{a,\,t}\right) \exp(-M_{a,\,t}/2)$$

Observation functions

(D12) $$I_t = \sum_{a=1}^{A} q \, \varsigma_{a,\,s} \, N_{a,\,t} \quad \text{with} \quad \varsigma_{a,\,s} = \frac{1}{1 + \exp\left(-\gamma_s \, (a - \delta_s)\right)}$$

(D13) $$p_{a,\,t,\,s} = \frac{I_{a,\,t}}{\sum_{a=1}^{A} I_{a,\,t}}$$

(D14) $$C_t = \sum_{a=1}^{A} C_{a,\,t}$$

(D15) $$p_{a,\,t,\,c} = \frac{C_{a,\,t}}{\sum_{a=1}^{A} C_{a,\,t}}$$

Table 3: Proportion of Atlantic cod in harp seal diet weighted by their relative residency in each area during the period November-March. The year 1998 refers to the period November 1997-March 1998 and similarly for the other years

Year	Sample size			Proportion
	4Ra-c	4Rd-3Pn	4S	
1998	27	21	-	0.0506
1999	28	22	24	0.0538
2000	25	39	29	0.0382
2001	30	16	-	0.0377

Table 4: Parameters and variables used in the stochastic equations and likelihood components. a, t, s, and c index age, year, survey, and catch respectively

Notation	Definition	Equation
$I^*_{a,\,t}$	Observed abundance index	L1
$J^*_{a,\,t}$	log-observed abundance index	S1
T_1	Number of uncensored data, with $T_1 = \mathrm{Card}(\bar{I})$	L1
Φ	Cumulative standard normal distribution	L1
ψ	Standard deviation of the observation error in the survey data	L1
$n^*_{t,\,s}$	Observed total number of fish taken by the survey vessels	L2
$p^*_{a,\,t,\,s}$	Observed proportion of number-at-age, with $p^*_{a,\,t,\,s} = \dfrac{I^*_{a,\,t}}{\sum_{a=1}^{A} I^*_{a,\,t}}$	L2
$p_{a,\,t,\,s}$	Predicted proportion of number-at-age	L2
T	Number of years	L2-L4
Γ	Gamma distribution	L2-L3
$p^*_{a,\,t,\,c}$	Observed proportion of catch-at-age	L3
$p_{a,\,t,\,c}$	Predicted proportion of catch-at-age	L3
$n^*_{t,\,c}$	Total catch sampled to establish age-proportions	L3
C^*_t	Observed total catch	L4
C_t	Predicted total catch	L4
σ_c	Standard deviation of the observation error in the catch data	L4

Table 5: Definitions used to extend the deterministic model in Table 2 to a stochastic model. iid: independent and identically distributed; $\sim$: distributed as; $\mathcal{N}$: normal distribution; *Dir*: Dirichlet distribution

(S1)	$J_t^* = \sum_{a=1}^{A} J_{a,\,t}^* \overset{iid}{\sim} \mathcal{N}\left(\sum_{a=1}^{A} \log I_{a,\,t}(\theta), \psi^2\right)$	$\psi^2 = A\sigma^2 + A^2\tau^2$
where	$J_{a,\,t}^* = log(I_{a,\,t}^*) = log(I_{a,\,t}) + \epsilon_{a,\,t} + \eta_t$	$\epsilon_{a,\,t} \overset{iid}{\sim} \mathcal{N}(0, \sigma^2)$ $\eta_t \overset{iid}{\sim} \mathcal{N}(0, \tau^2)$
(S2)	$p_{a,\,t,\,s}^* \overset{iid}{\sim} Dir\left(p_{1,\,t,\,s}(\theta), \ldots, p_{A,\,t,\,s}(\theta), n_{t,\,s}^*\right)$	
(S3)	$p_{a,\,t,\,c}^* \overset{iid}{\sim} Dir\left(p_{1,\,t,\,c}(\theta), \ldots, p_{A,\,t,\,c}(\theta), n_{t,\,c}^*\right)$	
(S4)	$\log C_t^* \overset{iid}{\sim} \mathcal{N}\left(\log C_t(\theta) - \frac{\sigma_c^2}{2}, \sigma_c^2\right)$	

Table 6: Likelihood components of the SIMCAB model. The generic notation θ represents the set of parameters to estimate

Equation	Likelihood
(L1)	$L(\{I_{a,\,t}^*\}\|\theta) = \underbrace{\frac{1}{(2\pi)^{\frac{T_1}{2}}\,\psi^{T_1}}\ \exp\left\{-\sum_{t\in\bar{I}} \frac{\left(\sum_{a=1}^{A} \log \frac{I_{a,\,t}^*}{I_{a,\,t}(\theta)}\right)^2}{2\psi^2}\right\}}_{\text{real observations}} \underbrace{\prod_{t\in I}\left\{1 - \Phi\left(\frac{\sum_{a=1}^{A} \log \frac{I_{a,\,t}^*}{I_{a,\,t}(\theta)}}{\psi}\right)\right\}}_{\text{censored observations}}$
(L2)	$L(\{p_{a,\,t,\,s}^*\}\|\theta) = \prod_{t=1}^{T} \Gamma\left(n_{t,\,s}^* + 1\right) \frac{\prod_{a=1}^{A} \left(p_{a,\,t,\,s}^*\right)^{n_{t,\,s}^*\, p_{a,\,t,\,s}(\theta)}}{\prod_{a=1}^{A} \Gamma\left(n_{t,\,s}^*\, p_{a,\,t,\,s}(\theta) + 1\right)}$
(L3)	$L(\{p_{a,\,t,\,c}^*\}\|\theta) = \prod_{t=1}^{T} \Gamma\left(n_{t,\,c}^* + 1\right) \frac{\prod_{a=1}^{A} \left(p_{a,\,t,\,c}^*\right)^{n_{t,\,c}^*\, p_{a,\,t,\,c}(\theta)}}{\prod_{a=1}^{A} \Gamma\left(n_{t,\,c}^*\, p_{a,\,t,\,c}(\theta) + 1\right)}$
(L4)	$L(\{C_t^*\}\|\theta) = \frac{1}{(2\pi)^{\frac{T}{2}}\,\sigma_c^T} \exp\left\{-\frac{1}{2\sigma_c^2} \sum_{t=1}^{T} \left(\log \frac{C_t^*}{C_t(\theta)} - \frac{\sigma_c^2}{2}\right)^2\right\}$

Table 7: Relative sensitivity (%) of biomass removed (BR) by seals and predation mortality rate for cod aged 1-4 (M_p(1-4)) to a 10% increase in input parameters

Parameter	Base value	BR	$M_p(1-4)$
% in the NGSL	25	67	129
% cod contribution to diet 1998-2001	4.53	1	25
% cod maximum contribution to diet	18.3	-6	-2
Average energy of cod (kJ g^{-1})	4.96	-13	40
Kleiber multiplier (kJ)	293	67	129