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ARTICLE

Continued decline of a collapsed population of Atlantic cod (*Gadus morhua*) due to predation-driven Allee effects[1]

Rachel D. Neuenhoff, Douglas P. Swain, Sean P. Cox, Murdoch K. McAllister, Andrew W. Trites,
Carl J. Walters, and Mike O. Hammill

Abstract: Most stocks of Atlantic cod (*Gadus morhua*) in the Northwest Atlantic collapsed in the early 1990s, with little sign of recovery since then. In the southern Gulf of St. Lawrence (sGSL), the failed recovery is due to severe increases in the natural mortality of adult Atlantic cod. We examined the role of predation by grey seals (*Halichoerus grypus*) in this failed recovery by directly incorporating grey seal predation in the population model for Atlantic cod via a functional response. Estimated predation mortality of adult Atlantic cod increased sharply during the cod collapse and has continued to increase, comprising the majority of mortality since the late 1990s. While predation by grey seals appeared to play a minor role in the collapse of Atlantic cod, we found it to be the main factor preventing recovery. Our results are consistent with the hypothesis that failed recovery is due to predation-driven Allee effects, a demographic effect due to the decline in cod abundance and an emergent effect resulting from increasing grey seal abundance. Under current conditions, extirpation of sGSL Atlantic cod appears likely unless there is a large decline in the abundance of grey seals.

Résumé : La plupart des stocks de morue (*Gadus morhua*) dans le nord-ouest de l'océan Atlantique se sont effondrés au début des années 1990, montrant peu d'indices de rétablissement depuis. Dans la partie sud du golfe du Saint-Laurent (sGSL), cette absence de rétablissement est due à d'importantes augmentations de la mortalité naturelle des morues adultes. Nous examinons le rôle de la prédation par les phoques gris (*Halichoerus grypus*) dans ce processus en incorporant directement cette prédation dans le modèle démographique pour la morue sous la forme d'une réaction fonctionnelle. La mortalité par prédation estimée des morues adultes a connu une augmentation marquée durant l'effondrement des stocks de morue et continue d'augmenter, expliquant la majorité de la mortalité depuis la fin des années 1990. Si la prédation par les phoques gris semble avoir joué un rôle limité dans l'effondrement de la morue, nous constatons qu'il s'agit du principal facteur empêchant son rétablissement. Nos résultats concordent avec l'hypothèse voulant que l'absence de rétablissement soit due à des effets d'Allee induits par la prédation, un effet démographique découlant de la baisse d'abondance des morues et un effet émergent découlant de l'abondance croissante des phoques gris. Dans les conditions actuelles, la disparition de la morue du sGSL semple probable à moins d'une importante diminution de l'abondance des phoques gris. [Traduit par la Rédaction]

Introduction

Most stocks of Atlantic cod (*Gadus morhua*) in the Northwest Atlantic collapsed to very low levels of abundance in the late 1980s and early 1990s. Since then, abundance of these stocks has remained low, due partly to continued fishing at low levels (Shelton et al. 2006). However, for two of these stocks, Atlantic cod on the Eastern Scotian Shelf (ESS) and in the southern Gulf of St. Lawrence (sGSL), failed recovery reflects sharp declines in population productivity, resulting from large increases in the natural mortality of older fish (ages 5 years and older; Swain and Mohn 2012; Swain and Benoît 2015; Sinclair et al. 2015). Under current productivity conditions, the sGSL stock of Atlantic cod is expected to decline to extirpation by the middle of this century, even in the absence of fishing (Swain and Chouinard 2008).

A number of hypotheses have been suggested for causes of these estimated increases in natural mortality, in particular life-history changes in response to fishing (e.g., early maturation; Hutchings 2005; Jørgensen and Fiksen 2010; but see Swain 2011), poor fish condition due to harsh environmental conditions (e.g., cold ocean temperature; Lambert and Dutil 1997; Dutil and Lambert 2000), predation by grey seals (*Halichoerus grypus*) (Chouinard et al. 2005; O'Boyle and Sinclair 2012), and mortality due to unreported catch (mistakenly attributed to natural mortality (e.g., Bousquet et al. 2010). These and other hypotheses were evaluated for Atlantic cod in the sGSL by Swain et al. (2011*a*). They concluded that unreported catch and mortality associated with early maturation and poor fish condition may have been contributing factors in the 1980s and early to mid-1990s, but the only hypothesis with support since the late 1990s was predation by grey seals.

Grey seals are the predominant piscivorous pinniped on the ESS and in the sGSL (Hammill and Stenson 2000). Their numbers have

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R.D. Neuenhoff,* M.K. McAllister, A.W. Trites, and C.J. Walters. Institute for the Oceans and Fisheries, Aquatic Ecosystems Research Lab, The University of British Columbia, 2202 Main Mall, Vancouver, BC V6T 1Z4, Canada.
D.P. Swain. Fisheries and Oceans Canada, Gulf Fisheries Centre, Moncton, NB E1C 9B6, Canada.
S.P. Cox. School of Resource and Environmental Management, Simon Fraser University, Burnaby, BC V5A 1S6, Canada.
M.O. Hammill. Fisheries and Oceans Canada, Maurice Lamontage Institute, Mont-Joli, QC G5H 3Z4, Canada.
Corresponding author: Douglas P. Swain (email: doug.swain@dfo-mpo.gc.ca).
*Present address: Environmental Resources Branch, USACE Portland District, US Army Corps of Engineers, 333 SW First Ave., Portland, OR 97208-2946, USA.

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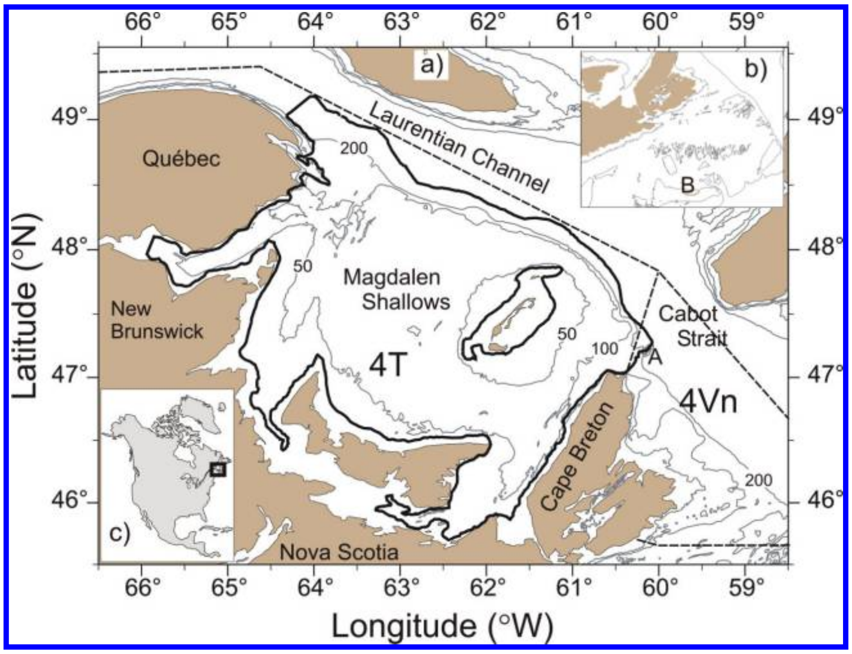
Fig. 1. The southern Gulf of St. Lawrence (sGSL) and place names mentioned in the paper. In the main panel (*a*) grey lines show the 50, 100, and 200 m depth contours; the heavy black line shows the boundaries of the bottom-trawl survey area; "A" indicates St. Paul's Island. The dashed lines delineate the Northwest Atlantic Fisheries Organization areas occupied by the sGSL stock of Atlantic cod: Division 4T and Subdivision 4Vn in November to April. Inset (*b*) shows the neighbouring Eastern Scotian Shelf, with Sable Island denoted by "B". Inset (*c*) shows the location of the study within North America.



increased exponentially in the last 60 years from 8000 animals in 1960 to 500 000 by 2014 (Hammill et al. 2014*a*). Atlantic cod are known to be an important prey of grey seals and remain so in the sGSL despite the severely depleted abundance of cod in this ecosystem (Hammill et al. 2014*b*). This appears to reflect their dense aggregation in predictable areas in certain seasons. For example, high fishery effort and catch rates confirm the presence of dense aggregations of migrating Atlantic cod off the west coast of Cape Breton Island in spring and fall in recent decades (e.g., Poirier 2001). Aggregations of grey seals have been observed in the vicinity of these migrating cod (D.P. Swain, personal observation), but their diet has not been sampled. On the other hand, an immense aggregation of Atlantic cod from the sGSL occurs each winter off of St. Paul's Island in the Cabot Strait (e.g., Comeau et al. 2002*a*). Foraging by adult male grey seals is concentrated in the vicinity of this aggregation (Harvey et al. 2012), and Atlantic cod dominate the diet of these seals (Hammill et al. 2014*b*). The average contribution of Atlantic cod to the grey seal diet is uncertain. But based on the energetic requirements of grey seals and their spatiotemporal overlap with sGSL Atlantic cod, Benoît et al. (2011) concluded that predation by grey seals could plausibly account for a high proportion of the natural mortality of sGSL cod. This was the case even if they contributed only 15% of the average grey seal diet. Furthermore, recent shifts in Atlantic cod distribution out of areas of high risk of predation by grey seals into lower risk areas also support the hypothesis that grey seals are major predators of Atlantic cod in the sGSL (Swain et al. 2015*a*). Based on this and other evidence, Swain and Benoît (2015) suggested that the elevated natural mortality of Atlantic cod in the sGSL reflects a "predator pit" or predation-driven Allee effect, resulting from the severely depleted abundance of cod and the high and increasing abundance of grey seals.

An Allee effect occurs when productivity at low population sizes exhibits positive density dependence, with the per capita rate of population growth declining as abundance decreases (Courchamp et al. 1999; Stephens and Sutherland 1999). This contrasts the increasing per capita rate of population growth at low abundance (i.e., negative density dependence) that is normally expected to result from decreases in intraspecific competition at low population size (Nicholson 1933). Allee effects (also termed depensation) increase extinction risk at low population sizes and can reduce the rate of recovery of depleted populations and increase its uncertainty (Kuparinen et al. 2014). Early studies of population dynamics were dominated by consideration of negative density dependence (Courchamp et al. 1999), but as anthropogenic effects drive many populations to small sizes, the importance of Allee effects is receiving increasing attention (Hutchings 2014, 2015).

Two types of Allee effects have been distinguished: demographic effects and emergent effects (Courchamp et al. 1999; Hutchings and Rangeley 2011). Demographic effects refer to declines in the per capita rate of population increase that result from low population size per se. Many possible causes of demographic Allee effects have been proposed, but the one that has received the most attention, particularly in fishes, is low reproductive success at small population sizes (Myers et al. 1995; Liermann and Hilborn 1997; Keith and Hutchings 2012). There is evidence for this effect in some fishes when population size has been sufficiently reduced (Keith and Hutchings 2012), but the prevalence of this effect may be quite low, or difficult to detect, at many prevailing depletion levels (Hilborn et al. 2014). Another potential cause of demographic Allee effects is predation. Given many models of predator–prey interaction, the prey exploitation rate imposed by an individual predator increases as prey abundance declines (Gascoigne and Lipcius 2004). Increases in adult mortality due to predation can result in an Allee effect even when recruitment dynamics are compensatory (Kuparinen and Hutchings 2014). A number of examples of predator-driven Allee effects have been reported, primarily in mammals and birds (e.g., Sinclair et al. 1998*b*; Angulo et al. 2007). An emergent Allee effect occurs when a population is exposed to changes (e.g., environmental or ecosystem changes) to which an increasingly depleted population is increasingly vulnerable (Courchamp et al. 2008). An example would be increases in predator abundance that are sustainable when prey are at high abundance but not when prey are depleted (Hutchings and Rangeley 2011; Hutchings 2014; Swain and Benoît 2015).

In this paper we examine the role of predation by grey seals in the lack of recovery of Atlantic cod in the sGSL. First, using a population model that does not explicitly incorporate predation by grey seals, we describe historical trends in the biomass of this Atlantic cod stock and in its rates of natural and fishing mortality. We then go beyond previous work by explicitly estimating predation mortality using the diet data for grey seals foraging in the sGSL and a model that incorporates a functional response for grey seals preying on Atlantic cod. Our models indicate that predation by grey seals accounts for most of the elevated natural mortality of cod in this ecosystem since the late 1990s and that the continued decline of this cod population is due to predation-driven Allee effects.

Methods

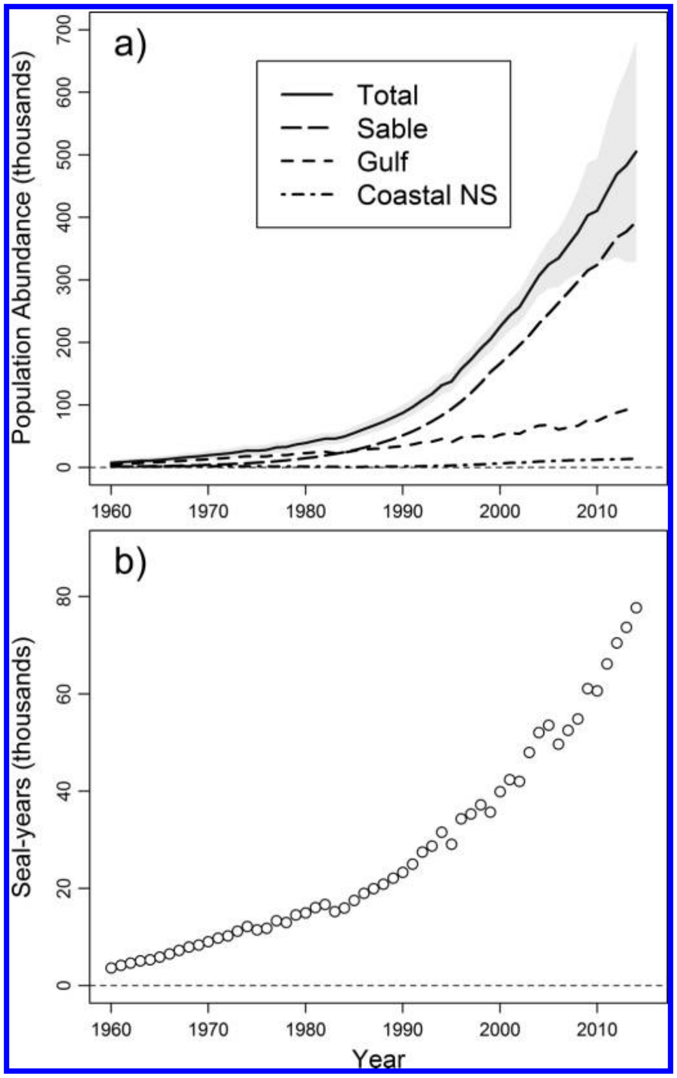
Data

The relative abundance of Atlantic cod in the sGSL has been monitored by a stratified-random bottom-trawl survey conducted by Fisheries and Oceans Canada (DFO) each September since 1971 (Fig. 1). The target fishing procedure was a 30 min tow at 3.5 knots (1 knot = 1.852 $\text{km}\cdot\text{h}^{-1}$) in all years. When there was a change in the research vessel (RV, 1985, 1992, 2004), trawl (1985), or survey protocol (1985), comparative fishing experiments and other analyses were conducted to test for changes in fishing efficiency. When necessary, survey catch rates were adjusted to maintain a consistent time series (Benoît 2006). An uncalibrated vessel was used in the 2003 survey, which was thus excluded as a data input in this study. In addition, abundance indices for Atlantic cod were also obtained from two sentinel programs conducted in collaboration with the fishing industry. A sentinel bottom-trawl survey has been conducted each August since 2003 using the same stratified-random design as the RV survey. A sentinel longline program has been conducted each summer and fall since 1995. In this program, fixed sites are fished on several occasions throughout the summer and fall using standardized protocols. Standardized abundance indices were obtained using a statistical model with terms for year, month, and site. See online Supplementary Material 1[2] for further details on data inputs and the study area.

Annual fishery landings (metric tonnes, t) of Atlantic cod were another data input. Bycatch of Atlantic cod in fisheries targeting other groundfish must be reported and are included in the landings. Length and age composition of the fishery catch was based on length–frequency distributions and length-stratified subsamples of ageing material (otoliths) obtained by port samplers and at-sea observers. Bycatch of commercial-sized Atlantic cod ($\geq$43 cm total length) in fisheries for invertebrates (lobster, snow crab, scallop and shrimp) appears to be negligible (Swain et al. 2011*a*), as is the catch in recreational fisheries (Swain et al. 2015*b*).

Grey seals in Atlantic Canada consist of three herds breeding on Sable Island, in the Gulf of St. Lawrence, and along coastal Nova Scotia. Abundance estimates for each herd were obtained by Hammill et al. (2014*a*) using population models fit to estimates of pup abundance (Fig. 2*a*). Satellite telemetry indicates that these seals move substantial distances and that individuals from all three herds contribute to those foraging in the sGSL (Breed et al. 2006; Harvey et al. 2008). Based on the satellite telemetry, Benoît and Rail (2016) estimated the monthly proportions of grey seals from each herd that occurred in the regions occupied by sGSL Atlantic cod. Combining these proportions and the annual abundance estimates yielded estimates of grey seal abundance (seal-years) in the sGSL. Estimated abundance increased from 9795 seal-years in 1971 to 60 612 seal-years in 2010 (Fig. 2*b*).

Fig. 2. The abundance of grey seals in Atlantic Canada. (*a*) Total abundance (shading shows ±2 standard errors) and abundance by herd (data from Hammill et al. 2014); (*b*) estimated number of seal-years spent in the southern Gulf of St. Lawrence, based on data from Benoît and Rail (2016).



Grey seals are primarily piscivorous. Their diet in the sGSL is estimated based on the otoliths (ear bones) found in their stomach and intestines. Estimated size composition of their prey is based on relationships between otolith size and fish length. Based on the size distributions of Atlantic cod otoliths found in grey seal digestive tracts, the length composition of consumed cod was estimated and converted to age composition using the stock assessment age–length keys obtained from catches in the annual RV survey. Only otoliths with little indication of erosion due to digestion were used in this analysis.

Until recently, data on diets of grey seals foraging in the sGSL have been limited to samples collected from nearshore areas mostly between spring and early fall (Hammill et al. 2007). Cod are absent in some of these areas and in the remaining areas occur at lower densities than in areas further offshore, particularly for larger cod. The average contribution of 5+ cod to the diet is 8% by

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[2] Supplementary data are available with the article through the journal Web site at http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2017-0190.

mass based on these inshore summer samples (Supplementary Material 2[2]). Recently, diet samples have also been obtained from seals feeding heavily in the vicinity of overwintering aggregations of sGSL cod. The contribution of Atlantic cod, in particular larger cod, to the diet was much greater in these samples than in those collected in the nearshore areas in summer (Hammill et al. 2014*b*). The average contribution of 5+ Atlantic cod to the diet based on these winter samples is 41% by mass (Supplementary Material 2[2]).

Population modelling

Time-varying natural mortality

Studies using data from the 1970s and earlier estimated that the instantaneous rate of natural mortality (M) of commercial-sized Atlantic cod in the sGSL was in the range of 0.1 to 0.2 (Dickie 1963; Beverton 1965; Myers and Doyle 1983). However, following the initial closure of the Atlantic cod fishery in 1993, it became evident that M had increased to a higher level (Sinclair 2001). Assessment models for this stock have incorporated time-varying M since 1998 (Sinclair et al. 1998*a*), initially as a fixed value increasing from 0.2 to 0.4 in 1986. Subsequently, M was estimated in the assessment model in blocks of ages and years following an initial period with M fixed at 0.2 (Chouinard et al. 1999). Alternative hypotheses that catchability to the RV survey had increased, selectivity had changed, or availability had decreased due to movement of Atlantic cod to regions outside of the survey area were rejected (Sinclair et al. 1998*a*; Swain et al. 2011*a*; Swain and Benoît 2015; Supplementary Material 1[2]).

In this study, we used a statistical catch-at-age model to estimate temporal variation in M. This model (named here the RW (random walk) model) estimated M as independent random walks for two age groups (1–4 and 5 to 12+ years, hereinafter abbreviated as 5+). The RW model resembled the statistical catch-at-age model used in the latest assessment of this stock (Swain et al. 2015*b*) and provided estimates of time-varying M free of any constraints associated with assumptions about the causes of changes in natural mortality. Thus, this “baseline” model was considered to provide the best approximation of reality and was used to evaluate the performance of models directly incorporating effects of predation by grey seals.

The RW model extended over 40 years (1971–2010) and from ages 1 to 12+. Model notation and parameters are given in Table 1, equations defining the process model (i.e., the population dynamics) and the observation models are described in Table 2, priors are given in Table 3, and components of the total negative log-posterior density function G are described in Table 4. On the log scale, abundance at age 1 in year y, $\log(N_{1,y})$, was the sum of log average recruitment, $\bar{R}$, and a normally distributed recruitment deviate (eqs. T2.6, T2.9, T3.1, T3.2). Abundance at other ages in year 1 was similarly obtained, discounting recruitment by mortality from age 1 to age a (eqs. T2.7 and T2.8). For ages 2 years and older in years after 1971, cod abundance was assumed to decay exponentially based on the instantaneous rate of total mortality Z, the sum of fishing mortality F and natural mortality M (eqs. T2.4, T2.5, T2.10, T2.11). Selectivity-at-age to the fishery and to the surveys was modelled as a logistic curve (eq. T2.1). For the fishery, this is consistent with the partial recruitment vectors estimated using virtual population analysis (VPA; D.P. Swain, unpublished analyses). For the RV survey and sentinel programs, this was consistent with the VPA estimates of catchability-at-age, which showed no indication of a dome for any of the indices, including the longline index (Swain 2012). For the fishery, the selectivity function was estimated independently for three time blocks (1971–1981, 1982–1993, and 1994–2010) to account for important changes in the fishery. For each age group, M in 1971 was estimated with a Normal prior (eqs. T2.2 and T3.3). The prior mean was based on the estimates of M for the 1970s and earlier for the older age group and on relationships between M and length and growth characteristics of marine fishes (Gislason et al. 2010) for the younger age group. For later years, M was assumed to follow a random walk, estimated independently for each age group (eq. T2.3). The choice of values for the standard deviations (SD) of the priors for initial M (eq. T3.3) and for the process error in the random walks in M (eq. T3.4) was guided by the sensitivity analyses in Swain and Benoît (2015). The Baranov catch equation (eq. T2.14) was solved iteratively to estimate fully recruited fishing mortality, F_y.

Observation models are described by eqs. T2.13 and T2.24 for the RV survey and sentinel biomass indices and by eq. T2.25 for the age proportions of the fishery, survey, and sentinel catches. The biomass indices were assumed to be distributed lognormally. Calculation of their negative log-likelihoods is described by eqs. T4.1 to T4.5. Age proportions were assumed to be obtained from multivariate logistic distributions, with their negative log-likelihood obtained following eqs. T4.6 to T4.9 (see Schnute and Richards 1995; Martell and Stewart 2014). Priors for M in 1971 (eq. T4.12), the process errors in M (eq. T4.14), and the recruitment process errors (eqs. T4.16, T4.17) also contributed to the negative log-posterior density for the RW model, G_{RW} (eq. T4.18).

The model was implemented in AD Model Builder (Fournier et al. 2012). Model estimates and their uncertainty were based on Markov chain Monte Carlo (MCMC) sampling of the posterior distribution. MCMC sampling was run for 2.5 million iterations with every 750th sample retained. The model was informally checked for convergence and adequate thinning by examining the posterior distribution of each model parameter using plots of autocorrelation along MCMC chains, cumulative quantile plots and density plots comparing the first and last halves of the MCMC chain. Model estimates reported here are medians of the posterior distribution, and uncertainty is described using 95% credible limits (i.e., the 2.5th and 97.5th percentiles of the posterior distribution).

Mortality due to predation by grey seals

The RW model was modified to incorporate predation by grey seals. Estimation of the effects of grey seal predation was restricted to 5+ Atlantic cod, the age group with elevated natural mortality (Swain et al. 2015*b*). Grey seals also consume younger Atlantic cod but, unlike 5+ fish, there is no evidence that natural mortality of younger cod increased in the 1990s and 2000s (Swain et al. 2015*b*). This may reflect decreased predation on young fish by collapsed piscivorous fishes (Benoit and Swain 2008), compensating for the increase in predation by grey seals (Savenkoff et al. 2007). To avoid the need to account explicitly for changes in mortality of young Atlantic cod due predation by both piscivorous fishes and seals, we continued to model their natural mortality using a random walk.

This revised model, termed the FR model, incorporated a type II functional response (Holling 1959) for grey seals preying on the 5+ age group of Atlantic cod (eq. T2.20). The functional response included a term Ho to account for the handling time of prey other than 5+ Atlantic cod (eq. T2.21). The derivation of Ho is given in the online Supplementary Material 3[2]. Ho was assumed to be constant, implying constant total biomass of other prey. There is some support for this assumption. Savenkoff et al. (2007) compared the sGSL ecosystem between the mid-1980s and mid-1990s (i.e., before and after the collapse of Atlantic cod). The estimated demersal fish biomass (excluding large Atlantic cod) averaged 9.5 and 6.6 t·km^{-2} before and after the collapse, while pelagic fish (Atlantic herring and capelin) averaged 10.2 and 13.0 t·km^{-2} in the two periods. Thus, the total biomass of alternate prey was estimated to be about the same before (19.7 t·km^{-2}) and after (19.6 t·km^{-2}) the cod collapse.

In the FR model, 5+ M consisted of M due to predation by grey seals (Mp) and M due to other causes (Mo) (eq. T2.19). Like 5+ M in the RW model, Mp was modelled as a random walk beginning from the estimated initial Mp (eqs. T2.15, T2.16). However, unlike

Table 1. Model notation and parameters.

Symbol	Description	Value	Model
Indices			
A	Plus group age	12+	Both
Y	Total number of years	40	Both
K	No. of natural mortality age blocks	2 (1–4, 5–12+)	Both
G	No. of fisheries–surveys	4	Both
a	Age index	1, 2, …, A	Both
y	Time index	1, 2, …, T	Both
k	Age-block index	1, 2	Both
g	Fishery–survey index: 1 = commercial; 2 = RV survey; 3 = sentinel trawl; 4 = sentinel longline	1, 2, 3, 4	Both
a_g^{min}	Minimum age for index g 1–4:	2, 2, 2, 5	Both
a_g^{max}	Maximum age for index g 1–4:	12, 11, 11, 11	Both
y_g^{min}	First year for index g 1–4:	1, 1, 33, 25	Both
y_g^{max}	Last year for index g 1–4:	40, 40, 40, 40	Both
Population dynamics variables			
$\bar{R}^a$	Log mean recruitment (log numbers)		Both
$\varepsilon_a^{ri}{}^a$	Recruitment process errors to initialize abundance at age in year 1		Both
$\varepsilon_y^{r}{}^a$	Recruitment process errors $y \in \{2, 3, \ldots, T\}$		Both
σ^r	Recruitment process error standard deviation	0.5	Both
$m_k{}^a$	Initial natural mortality for age block k (year^{-1})		Both
μ_k^m	Prior mean for initial natural mortality (year^{-1})	0.5, 0.15	Both
σ_k^m	Prior standard deviation for initial natural mortality	0.1, 0.05	Both
$\varepsilon_{k,y}^{M}{}^a$	Natural mortality process errors		Both^b
σ_k^M	Natural mortality process error standard deviation	0.075, 0.075	Both^b
q_g	Catchability for fishery g = 2, 3, 4		Both
C_y	Catch of Atlantic cod in year y (t)		Both
$N_{a,y}$	Abundance of Atlantic cod at age in year y (numbers)		Both
B_y^S	Spawning biomass in year y (t)		Both
$B_{g,y}^E$	Exploitable biomass for fishery–survey G in year y (t)		Both
$Z_{a,y}$	Instantaneous total mortality rate at age in year y (year^{-1})		Both
F_y	Fully recruited instantaneous fishing mortality in year y (year^{-1})		Both
Fi^a	Fully recruited fishing mortality for initializing abundance at age in year 1		Both
$s_{g,a,y}$	Selectivity at age in year y for fishery g		Both
$s_{50,g,y}{}^a$	Age at 50% selectivity for fishery g in year y		Both
$s_{95,g,y}{}^a$	Age at 95% selectivity for fishery g in year y		Both
$w_{a,y}^B$	Beginning-of-year mass-at-age (t)		Both
$w_{g,a,y}^G$	Mass-at-age for fishery–survey g		Both
$P_{a,y}^{\mathrm{mat}}$	Proportion mature at age in year y		Both
d_g	Survey date (month/12)	0, 0.75, 0.67, 0.75	Both
$M_{a,y}$	Instantaneous natural mortality rate at age in year y (year^{-1})		Both
Mp_y	M due to grey seal predation for age class k = 2 ($a \geq 5$)		FR
Mo_y	M due to other causes for age class k = 2 ($a \geq 5$)		FR
$m_p{}^a$	Mp_1 (prior mean and variance the same as for m_2)		FR
$m_o{}^a$	Mo_1		FR
μ^{m_o}	Prior mean for m_o (year^{-1})	0.15	FR
σ^{m_o}	Prior standard deviation for m_o	0.03	FR
y_O^{min}	First year for random walk in Mo	7 (1977)	Both
y_O^{max}	Last year for random walk in Mo	32 (2002)	Both

Table 1 (*concluded*).

Symbol	Description	Value	Model
$\varepsilon_y^{Mo\,a}$	Process errors for *Mo* $y \in \{7, 8, \ldots, 32\}$		FR
σ_y^{Mo}	Process error standard deviation for *Mo* $y \in \{7, 8, \ldots, 32\}$	—[c]	FR
Functional response variables			
$\log(q')^a$	$\log_e$ encounter rate between grey seals and Atlantic cod 5 years and older		FR
n_y^{k2}	Per capita consumption of age-block 2 Atlantic cod by grey seals (numbers)		FR
N_y^{k2}	Abundance of age-block 2 Atlantic cod (numbers)		FR
Ho	Handling time of prey other than age-block 2 Atlantic cod		FR
w_y	Average mass of 5+ cod (t)		FR
$C_{\max}$	Maximum annual consumption by grey seals (t)	2.0	FR
$N_{y^*}^{k2}$	Abundance of age-block 2 Atlantic cod in reference year y^* (numbers)	53×10^6	FR
w_{y^*}	Mean mass of age-block 2 Atlantic cod in reference year y^* (t)	0.00092	FR
$P_{y^*}^{\text{diet}}$	Proportional contribution by age-block 2 Atlantic cod by mass to the average grey seal diet in reference year y^* (2010)		FR
Ce_y	Age-block 2 Atlantic cod eaten by seals in year *y* (numbers)		FR
Observation model variables			
S_y	Observed grey seal foraging effort (seal-years)		FR
$\hat{S}_y$	Predicted grey seal foraging effort (seal-years)		FR
σ^S	Observation error standard deviation for seal abundance	0.1	FR
$B_y^{S^{\text{RW}}}$	Spawning biomass estimates by model RW for year *y* (t) (for eq. T4.11)		FR
$B_y^{S^{\text{FR}}}$	Spawning biomass estimates by model FR for year *y* (t) (for eq. T4.11)		FR
σ^{B^S}	Observation error standard deviation for SSB (for eq. T4.11)	0.1	FR
$I_{g,y}$	Observed biomass index		Both
$\hat{I}_{g,y}$	Predicted biomass index		Both
$p_{g,a,y}$	Observed proportions at age		Both
$\hat{u}_{g,a,y}$	Predicted proportions at age		Both

Note: The last column identifies the model(s) incorporating each variable: the RW model (*M* modelled as random walks), the FR model (*M* due to seal predation explicitly modelled using a functional response), or both models.

[a] Estimated parameters.

[b] In the FR model, $\varepsilon_{2,y}^M$ applies to predation mortality only. σ_2^M was increased to 0.1 due to additional constraints on time-varying *M* for age group 2.

[c] Time-varying σ for process error in *Mo*: {0.025, 0.05, 0.075, 0.1, 0.2, 0.3, …, 0.3, 0.2, 0.1, 0.075, 0.05, 0.025, 0.02}.

in RW, this random walk was constrained by the functional response as follows (eqs. T2.22, T2.23, T2.26, T4.10, T4.11). The number of 5+ Atlantic cod eaten by grey seals in year *y* (Ce_y) was estimated based on Mp_y and the catch equation (eq. T2.22). Ce_y can also be obtained using the functional response and the estimated seal abundance in year *y*, S_y (eq. T2.23). Re-arranging eq. T2.23, seal abundance can be predicted based on the functional response and the estimate of Ce_y derived from eq. T2.22 (eq. T2.26). The discrepancy between the model prediction ($\hat{S}_y$) and the independently estimated seal abundance (S_y) was included as a component of the model objective function (eq. T4.10).

Parameters of the functional response included q', $C_{\max}$, w_y, and the additional variables needed to calculate *Ho* (i.e., $N_{y^*}^{k2}$, w_{y^*}, and $P_{y^*}^{\text{diet}}$). A value of 2.0 t was used for $C_{\max}$ based on the estimate by Benoît et al. (2011). Differences in results were negligible using a value of 1.5 or 2.5 t (Supplementary Material 4[2]). The mean mass of 5+ Atlantic cod in year *y* (including y^*) was based on the RV survey data for that year. Because information on winter diets was available only for 2010 and 2011, 2010 was chosen as y^*. Abundance of 5+ Atlantic cod in 2010 was based on the estimate from the RW model for that year. Initial trials indicated that the estimates for $P_{y^*}^{\text{diet}}$ and $\log(q')$ were highly correlated (–0.95). Thus, we used a fixed value for $P_{y^*}^{\text{diet}}$. This value was based on the two area–season combinations for which diet data were available, the average contributions in inshore areas in summer (8% by mass) and offshore in winter (41%). Based on these data, $P_{y^*}^{\text{diet}}$ was assumed to be 0.20. This value is lower than the mean of the two available estimates (0.245) and was considered a reasonable choice (see Discussion). Nonetheless, we also conducted sensitivity analyses using a range of values for $P_{y^*}^{\text{diet}}$ between 0.05 and 0.30 (Supplementary Material 5[2]).

Initial trials indicated that there was little information in the data to estimate $\log(q')$, and the posterior distribution for this parameter was far from convergence even after 2.5 million MCMC iterations. Furthermore, there was no information to develop an informative prior for this parameter. However, we noticed a relationship between the estimate for q' and the estimates for spawning stock biomass (SSB). Despite this relationship there was no strong correlation between q' and any other estimated parameter, likely because the value of SSB depends in a complex way on many parameters. To accelerate convergence of $\log(q')$, we included a likelihood component based on the discrepancy between estimates of SSB by the FR versus RW models (eq. T4.11). If there is a difference between estimates from the FR and RW models, it is likely that the RW estimates are closer to the true values, as argued above. Thus, FR model estimates that departed from those of the RW model were penalized.

A fixed prior was provided for *Mo* (eqs. T2.17, T3.5) based on the independent estimates of 5+ *M* for the 1970s and earlier. However, we allowed *Mo* to follow a random walk from 1977 to 2002. Factors other than grey seal predation appeared to contribute to elevated

Table 2. Equations defining the population dynamics and observation models for the RW and FR models applied to Atlantic cod in the southern Gulf of St. Lawrence.

Equation	Formula
Selectivity	
T2.1: selectivity	$s_{g,a,y} = \{1 + \exp[-\log(19)(a - s_{50,g,y})/(s_{95,g,y} - s_{50,g,y})]\}^{-1}$
Mortality	
T2.2[a]: instantaneous rate of natural mortality, $y = 1$	$M_{a,1} = m_i, \quad a \in k_i$
T2.3[a]: instantaneous rate of natural mortality, $y > 1$	$M_{a,y} = M_{a,y-1}\exp(\varepsilon^{M}_{k_i,y}), \quad a \in k_i$
T2.4: instantaneous rate of fishing mortality	$F_{a,y} = s_{1,a,y}F_y$
T2.5: instantaneous rate of total mortality	$Z_{a,y} = M_{a,y} + F_{a,a}$
State dynamics	
T2.6: abundance $a = 1$, $y = 1$	$N_{1,1} = \exp\left(\bar{R} + \varepsilon^{ri}_{1}\right)$
T2.7: abundance at $a \in \{2, 3, \ldots, A-1\}$, $y = 1$	$N_{a,1} = \exp\left[\bar{R} + \varepsilon^{r1}_{a} - \sum_{a=1}^{a-1}(s_{1,a,1}Fi + M_{a,1})\right]$
T2.8: abundance at $a = A$, $y = 1$	$N_{A,1} = \dfrac{\exp\left[\bar{R} + \varepsilon^{r1}_{A} - \sum_{a=1}^{A-1}(s_{1,a,1}Fi + M_{a,1})\right]}{1 - \exp[-(s_{1,A,1}Fi + M_{A,1})]}$
T2.9: abundance $a = 1$, $y > 1$	$N_{1,y} = \exp\left(\bar{R} + \varepsilon^{r}_{y}\right)$
T2.10: abundance $a \in \{2, 3, \ldots, A-1\}$, $y > 1$	$N_{a,y} = N_{a-1,y-1}\exp(-Z_{a-1,y-1})$
T2.11: abundance $a = A$, $y > 1$	$N_{A,y} = N_{A-1,y-1}\exp(-Z_{A-1,y-1}) + N_{A,y-1}\exp(-Z_{A,y-1})$
T2.12: spawner biomass	$B^{S}_{y} = \sum_{a=1}^{A} P^{\mathrm{mat}}_{a,y} w^{B}_{a,y} N_{a,y}$
T2.13: exploitable biomass	$B^{E}_{g,y} = \sum_{a=a^{\min}_{g}}^{a=a^{\max}_{g}} w^{G}_{g,a,y} s_{g,a,y} N_{a,y}\exp(-d_g Z_{a,y})$
T2.14: total fishery catch	$C_y = \sum_{a=1}^{12+} \dfrac{s_{1,a,y}F_y}{Z_{a,y}} N_{a,y} w^{C}_{a,y}[1 - \exp(-Z_{a,y})]$
FR model equations that differ from RW model equations	
T2.15: M due to predation by grey seals $a \in b_2$, $y = 1$	$Mp_1 = m_2$
T2.16: M due to predation by grey seals $a \in b_2$, $y > 1$	$Mp_y = Mp_{y-1}\exp(\varepsilon^{M}_{2,y})$
T2.17: M due to other causes, $a \in b_2$, $y \in \{1, \ldots, 6, 33, \ldots, 40\}$	$Mo_1 = m_o$
T2.18: M due to other causes, $a \in b_2$, $y \in \{7, \ldots, 32\}$	$Mo_y = Mo_{y-1}\exp(\varepsilon^{Mo}_{y})$
T2.19: $M_{a,y}$, $a \in k_2$	$M_{a,y} = Mp_y + Mo_y$
T2.20: type II Holling disc	$n^{k2}_{y} = \dfrac{q'N^{k2}_{y}}{1 + \left(\dfrac{Ho + q'N^{k2}_{y}w_y}{C_{\max}}\right)}$
T2.21: handling time of other prey	$Ho = q'N^{k2}_{y^*}w_{y^*}\left[\left(\dfrac{1}{P^{\mathrm{diet}}_{y^*}}\right) - 1\right]$
T2.22: 5+ Atlantic cod eaten by grey seals (calculation 1)	$Ce^{c1}_{y} = \sum_{a=5}^{12+} N_{a,y}[1 - \exp(1 - Z_{a,y})]\left(\dfrac{Mp_y}{Z_{a,y}}\right)$
T2.23: 5+ Atlantic cod eaten by grey seals (calculation 2)	$Ce^{c2}_{y} = \dfrac{q'N^{k2}_{y}S_y}{1 + q'\left[N^{k2}_{y^*}w_{y^*}\left(\dfrac{1}{P^{\mathrm{diet}}_{y^*}} - 1\right) + N^{k2}_{y}w_y\right]\Big/ C_{\max}}$
Observation models	
T2.24: biomass indices	$\hat{I}_{g,y} = q_g B^{E}_{g,y}$
T2.25: proportions at age in fishery–survey catches	$\hat{u}_{g,a,y} = \dfrac{N_{a,y}s_{g,a,y}\exp(-d_g Z_{a,y})}{\sum_{a=a^{\min}_{g}}^{a=a^{\max}_{g}} N_{a,y}s_{g,a,y}\exp(-d_g Z_{a,y})}$
T2.26: grey seal abundance (from eqs. T2.22 and T2.23)	$\hat{S}_y = \dfrac{Ce^{c1}_{y}}{q'N^{k2}_{y}}\left\{1 + q'\left[N^{k2}_{y^*}w_{y^*}\left(\dfrac{1}{P^{\mathrm{diet}}_{y^*}} - 1\right) + N^{k2}_{y}w_y\right]\Big/ C_{\max}\right\}$

Note: RW is a model incorporating random walks in the natural mortality (M) of two age groups (ages 1–4 years and 5+ years). FR is a model like RW except that it incorporates a functional response for predation by grey seals on 5+ Atlantic cod and models 5+ M as the sum of M due to predation by grey seals and M due to other causes.

[a] Equations T2.2 and T2.3 do not apply to age group 2 in the FR model.

Table 3. Prior distributions for the population models RW and FR.

Parameter	Prior distribution
T3.1: ε_a^{ri}, lognormal recruitment deviates to estimate $N_{a,1}$	$\sim\mathrm{N}(0, \sigma_r)$, $\sigma_r = 0.5$
T3.2: $\varepsilon_{1,y}^{r}$, lognormal recruitment deviates to estimate $N_{1,y}$, $y > 1$	$\sim\mathrm{N}(0, \sigma_r)$, $\sigma_r = 0.5$
T3.3[a]: m_k, M in year 1 for age group k	$\sim\mathrm{N}(\mu_k, \sigma_k)$, $\mu_1 = 0.5$, $\sigma_1 = 0.1$, $\mu_2 = 0.15$, $\sigma_2 = 0.05$
T3.4[a]: $\varepsilon_{k,y}^{M}$, process error in M for age group k	$\sim\mathrm{N}(\mu_k, \sigma_k)$, $\mu_1 = \mu_2 = 0$, $\sigma_1 = \sigma_2 = 0.075$
T3.5: m_0, Mo in year 1	$\sim\mathrm{N}(\mu, \sigma)$, $\mu = 0.15$, $\sigma = 0.03$
T3.6: ε_y^{Mo}, process errors for Mo $y \in \{7, \ldots, 32\}$	$\sim\mathrm{N}(\mu, \sigma)$, $\mu = 0$, σ (see footnote c, Table 1)

[a] For $k = 2$ in the FR model, this prior is for predation mortality only. For eq. T3.4 in the FR model, $\sigma_2 = 0.1$.

Table 4. Components of the total negative log-posterior density function G.

Likelihoods and priors
Biomass indices
T4.1: $\Delta_{g,y} = \log I_{g,y} - \log B_{g,y}^{E}$
T4.2: $\log \hat{q}_g = \frac{1}{n_{I,g}}\sum_{y=1}^{n_{I,g}}\Delta_{g,y}$,
where $n_{I,g} = y_g^{\max} - y_g^{\min} + 1$
T4.3: $D_{I,g} = \sum_{y=1}^{n_{I,g}}(\Delta_{g,y} - \log \hat{q}_g)^2$
T4.4: $\hat{\tau}_{I,g}^2 = \frac{1}{n_{I,g} - 1}D_{I,g}$
T4.5: $l_I = \sum_{g=2}^{G}(n_{I,g} - 1)\log \hat{\tau}_{I,g}^2$
Age composition
T4.6: $H_{g,a,y} = \log p_{g,a,y} - \log \hat{u}_{g,a,y} - \frac{1}{n_{P,g}}\sum_{a=1}^{n_{P,g}}(\log p_{g,a,y} - \log\hat{u}_{g,a,y})$,
where $n_{P,g} = a_g^{\max} - a_g^{\min} + 1$
T4.7: $D_{P,g} = \sum_{y=y_g^{\min}}^{y_g^{\max}}\sum_{a=1}^{n_{P,g}}H_{g,a,y}^2$
T4.8: $\hat{\tau}_{P,g}^2 = \frac{1}{n_{P,g}}D_{P,g}$
T4.9: $l_P = \sum_{g=1}^{G}n_{P,g}\log \hat{\tau}_{P,g}^2$
T4.10: $l_S = \frac{1}{2(\sigma^S)^2}\sum_{y=1}^{nT}(S_y - \hat{S}_y)^2$
T4.11: $l_B = \frac{1}{2(\sigma^{B^S})^2}\sum_{y=1}^{nT}\left(B_y^{S^{\mathrm{RW}}} - B_y^{S^{\mathrm{FR}}}\right)^2$
T4.12: $l_{m_k} = \sum_{k=1}^{2}\left[(m_k - \mu_k)^2/\left(2\sigma_k^2\right)\right]$
($l_{m_2} = l_{m_p}$ in the FR model)
T4.13: $l_{m_o} = \frac{1}{2(\sigma^{m_o})^2}\left(m_o - \mu^{m_o}\right)^2$
T4.14: $l_{M_k} = \frac{1}{2\left(\sigma_k^M\right)^2}\sum_{y=2}^{nT}\left(\varepsilon_{k,y}^{M}\right)^2$
($l_{M_2} = l_{M_p}$ in the FR model)
T4.15: $l_{M_O} = \sum_{y=y_O^{\min}}^{y_O^{\max}}\left[\frac{1}{2\left(\sigma_y^{Mo}\right)^2}\left(\varepsilon_y^{Mo}\right)^2\right]$
T4.16: $l_{ri} = \frac{1}{2(\sigma^r)^2}\sum_{a=1}^{A}\left(\varepsilon_a^{ri}\right)^2$
T4.17: $l_r = \frac{1}{2(\sigma^r)^2}\sum_{y=2}^{nT}\left(\varepsilon_y^{r}\right)^2$
T4.18: $G_{\mathrm{RW}} = l_I + l_P + l_{m_k} + l_{M_k} + l_{ri} + l_r$
T4.19: $G_{\mathrm{FR}} = l_I + l_P + l_S + l_{m_1} + l_{m_P} + l_{m_O} + l_{M_1} + l_{M_P} + l_{M_O} + l_B + l_{ri} + l_r$

Note: l_I, l_P, l_S, and l_B are the negative log-likelihood functions for the biomass indices (I), the age-proportion data (P), the seal abundance data (S) and $B^{S^{\mathrm{FR}}}$ given $B^{S^{\mathrm{RW}}}$ (B, FR model only), respectively. l_{m_k}, l_{m_1}, l_{m_P}, and l_{m_o} are the contributions of the priors for the initial value for natural mortality for age block k (m_k) in the RW model or m_1, m_P, and m_o in the FR model. The remaining terms are the contributions of process error in M (l_{M_k} in RW; l_{M_1}, l_{M_P}, and l_{M_o} in FW) or in recruitment (l_{ri}, l_r).

5+ M in the 1980s and 1990s (Swain and Benoît 2015). The condition of Atlantic cod was low in the sGSL in the early to mid-1980s due to density-dependent effects and in the late 1980s to mid-1990s due to harsh environmental conditions (Swain et al. 2011*b*). Unreported catch during the intense fishery of the late 1980s and early 1990s also appeared to contribute to the mortality attributed to natural causes during this period (Bousquet et al. 2010). However, it is unlikely that these factors have been an important source of mortality since the mid-1990s. The condition of Atlantic cod returned to higher levels as intraspecific competition declined following the collapse of cod and water temperatures warmed in the late 1990s (Swain et al. 2011*b*). It likewise is implausible that unreported catch has been more than a negligible source of mortality since the mid-1990s. Fishing effort for groundfish declined to very low levels after 1993, as annual landings dropped from about 60 000 t in the late 1980s to 1300 t during the fishing moratorium in the mid-1990s and 125 t during the current moratorium (Supplementary Material 1[2]; Swain et al. 2015*b*). When the fishery was temporarily re-opened in 1998, new measures were put in place to improve catch monitoring (e.g., mandatory hail-out and hail-in, mandatory dock-side monitoring), both in fisheries directing for Atlantic cod and in those directing for other species. Furthermore, additional measures were taken to reduce bycatch of Atlantic cod in fisheries targeting other species. Given this enhanced catch monitoring and the massive reduction in fishing effort, impacts of unreported catch on estimated M must now be slight. For example, if 35% of the true catch were unreported in 1991, this unreported catch would account for about 25% of the mortality attributed to natural causes (Swain et al. 2011*a*). On the other hand, if 50% of the catch were unreported in 2008, this would account for only 5% of the estimated M (Swain et al. 2011*a*). Thus, we assumed that Mo had returned to the early 1970s value by 2003. In the intervening period (1977–2002), Mo was allowed to vary via a random walk (eq. T2.18). A large value was chosen for σ_y^{Mo} (0.3) for 1982–1996 when evidence for these effects was greatest (Swain et al. 2011*a*). σ_y^{Mo} ramped down to small values over years at the margins of this period (Table 1).

The observation error SD for the SSB likelihood component was set at 0.1 based on the coefficient of variation of the SSB estimates from the RW model. A similar calculation could not be made for the seal abundance estimates, and we chose to also set SD = 0.1 for this likelihood component. G_{FR} also included all the additional terms in G_{RW}, except that the priors for initial 5+ M and process error in 5+ M were replaced by the corresponding priors for both Mp and Mo (eq. T4.19).

Projections

To estimate the impact of grey seal abundance on recovery potential of this stock, we used the FR model to project the population forward under various scenarios for future grey seal abundance, with $P_{y^*}^{\mathrm{diet}} = 0.2$. Projections were conducted during MCMC sampling while fitting the population model and thus incorporated uncertainties in the parameter estimates. We assumed that components of productivity other than predation mortality remained at recent levels during the projection period. Fishing mortality during the projection period was assumed to be 0, near recent values (e.g., $F = 0.002$ for ages 5–8; Swain et al. 2015*b*), and *Mo* was assumed to remain at the constant "background" level used in 1971–1976 and 2003–2010. Recruitment rate, juvenile *M*, and mean mass at age of cod have fluctuated without trend since the mid- to late 1980s (Swain et al. 2015*b*). For each year in each MCMC simulation, a recruitment rate, juvenile *M*, and a vector of mean mass at age were randomly selected from those estimated over the past 20 years. Four scenarios were examined: seal abundance was held constant at the most recent estimated level (2014), or seal abundance declined from the 2014 level by 25% over 6 years, 50% over 8 years, or 65% over 10 years.

These projections should not be considered actual forecasts of future stock status because they depend on assumptions about future productivity (i.e., rates of recruitment, individual growth, natural mortality of ages 1–4 years, and 5+ mortality due to causes other than seal predation). Instead, these projections give the likelihood of different future states conditional on these assumptions, as well as other model assumptions.

Allee effects

Plots of surplus production per unit of biomass (*P*/*B*) versus biomass were inspected for evidence of Allee effects, characterized by a positive relationship between *P*/*B* and *B* when *B* is below some threshold. Surplus production was calculated as follows:

$$P_y = B_{y+1} - B_y + C_y \tag{1}$$

where B_y and C_y are, respectively, 2+ biomass and fishery catch in year *y*. C_y, and thus P_y, are expected to be biased low in 1989 to 1992 (Bousquet et al. 2010). To identify possible causes of any observed Allee effects, relationships between recruitment rate (*R*/SSB, where *R* is age 2 recruit abundance) and SSB were examined, as were relationships between the survival rate associated with either total natural mortality *M* or predation mortality *Mp* of 5+ cod and their biomass B_{5+}.

Results

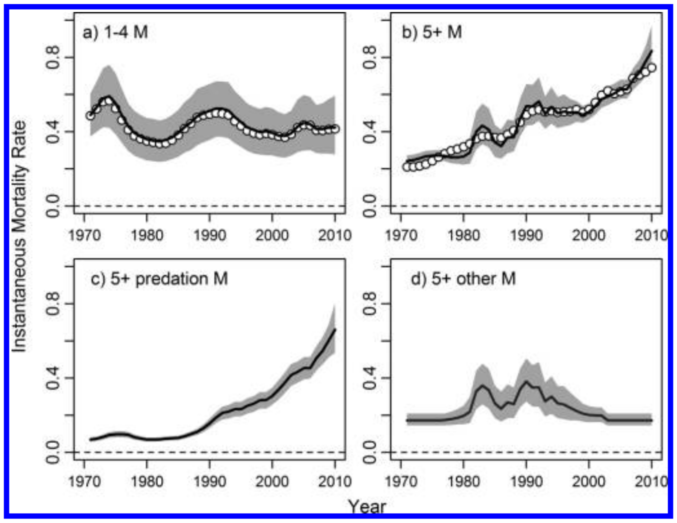
Model fits and estimates

Both the FR and RW models provided good fits to the biomass indices and the proportions at age in the fishery and index catches (Supplementary Material 6[2]). Fits were nearly identical between the two models.

The two models provided similar estimates of *M* of cod aged 1–4 years and indicated no long-term trend in *M* for this age group (Fig. 3*a*). In contrast, both models indicated a progressive increase in *M* of 5+ cod over the 1971–2010 period, with *M* in recent years dramatically higher than the values in the early 1970s (Fig. 3*b*). Estimates of 5+ *M* by the FR model fluctuated around those by the RW model in the 1970s and 1980s and were very similar to the RW estimates from the late 1980s to 2009, with the 2010 estimate slightly greater than the RW estimate. Based on the FR model, *M* of 5+ cod due to predation by grey seals averaged 0.08 (7.7% annually) from the early 1970s to the mid-1980s and then progressively increased, reaching 0.66 (48% annually) in 2010 (Fig. 3*c*). The initial value of *Mo* was estimated to be 0.17, consistent with the independent estimates of 5+ *M* for the early 1970s (Fig. 3*d*). Between 1977 and 2003, estimated *Mo* increased to peaks near 0.35 in 1982–1984 and 1988–1994 and then progressively declined from 1995 to 2003. These estimates are consistent with the observed poor body condition of sGSL Atlantic cod in the early to mid-1980s and early to mid-1990s and the estimated discarding of fishery catch in the late 1980s and early 1990s (see above).

Both the RW and FR models led to the same conclusions about stock status (Fig. 4). Estimates of both SSB and 5+ *F* were nearly identical between the two models. This was partly due to the constraint on SSB in the FR model (eq. T4.11), though estimated trends in SSB and in 5+ *F* were similar between the two models in initial trials without this constraint. The SSB estimates from both models show the same trends over time, with SSB recovering rapidly in the late 1970s from low biomass in the early to mid-1970s but then declining rapidly in the late 1980s and early 1990s (Fig. 4*a*). This decline was initially arrested by the closure of the cod-directed fishery in late 1993 (Fig. 4*b*), but a slower decline resumed in the early 2000s despite very low fishing mortality. The most recent estimates of SSB were the lowest levels observed in the 40-year time series.

Fig. 3. Instantaneous rates of natural mortality (*M*) for Atlantic cod aged 1–4 years (*a*), 5 years and older (5+) (*b*), 5+ Atlantic cod due to predation by grey seals (*c*), and 5+ Atlantic cod due to other causes (*d*). Line shows the median and shading the 95% credible interval based on MCMC sampling using the model incorporating a functional response for predation by grey seals on 5+ Atlantic cod. In panels (*a*) and (*b*), circles show the median estimates from the random walk model.



The estimated functional response of grey seals preying on 5+ cod was strongly density-dependent, with the exploitation rate exerted on 5+ cod per seal increasing sharply as the abundance of 5+ cod declined (Fig. 5). Holding average 5+ cod mass at the long-term mean, the predicted exploitation rate exerted per seal increased 3.4-fold as 5+ cod abundance declined from 440 million to 49 million.

Sensitivity analyses

Sensitivity analyses were conducted with $P_{y^*}^{\text{diet}}$ varying between 0.05 and 0.30 (Supplementary Material 5[2]). Model fit and estimates were about the same with $P_{y^*}^{\text{diet}}$ set at 0.2 or 0.3. With $P_{y^*}^{\text{diet}}$ set at 0.15, results were close to those obtained with the higher values of $P_{y^*}^{\text{diet}}$ (Fig. 6). With lower values for $P_{y^*}^{\text{diet}}$ (0.05–0.1), model fit and correspondence with the RW estimates of *M* were poor, especially when the background level of *Mo* was constrained to a plausible level consistent with independent estimates of 5+ *M* in the early 1970s. Estimated 5+ predation mortality averaged 87%, 66%, and 37% of the values at $P_{y^*}^{\text{diet}} = 0.2$ when $P_{y^*}^{\text{diet}}$ was set at 0.15, 0.10, and 0.05, respectively. In conclusion, the FR model provided a good fit to the data, with estimates that closely matched those of the RW model, when $P_{y^*}^{\text{diet}}$ was set at 0.20 or higher. Results were nearly as good with $P_{y^*}^{\text{diet}} = 0.15$. In both cases, predation by grey seals was estimated to be the main source of mortality of 5+ Atlantic cod in the 2000s. At values of 0.10 or lower for $P_{y^*}^{\text{diet}}$, fits to the data and consistency with the RW results were poor.

Fig. 4. Estimated spawning stock biomass (SSB, (*a*)) and the mean instantaneous rate of fishing mortality (*F*) for 5+ Atlantic cod (*b*). Lines show the median and shading the 95% credible interval based on the functional-response model. Circles show the median estimates from the random walk model.

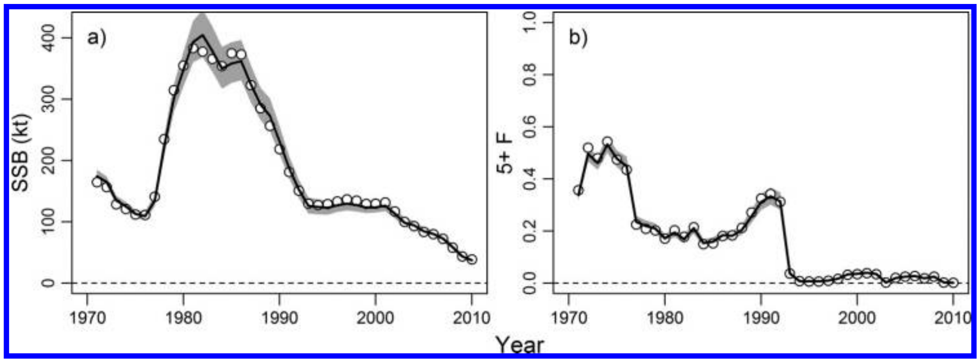
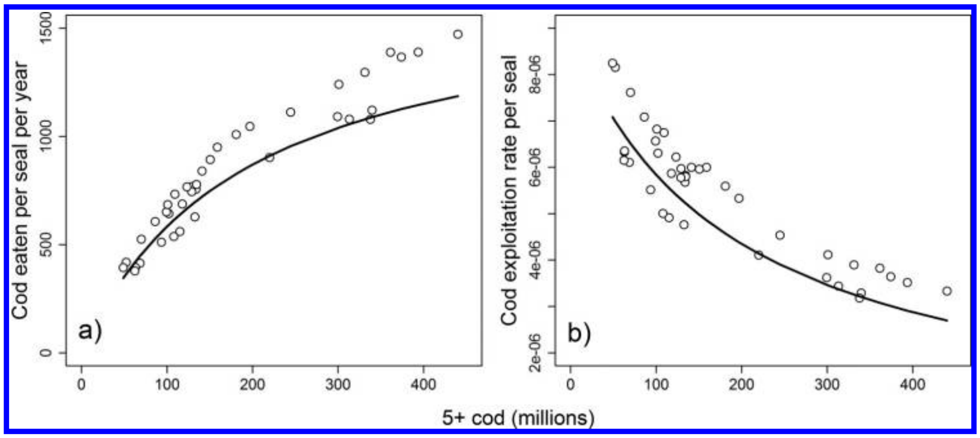


Fig. 5. Estimated functional response of grey seals preying on 5+ Atlantic cod (*a*) and the resulting exploitation rate on 5+ cod per seal (*b*). Circles are the estimates incorporating interannual variation in the mean mass of 5+ Atlantic cod. Lines show the predicted values using the global (1971–2010) mean mass of 5+ Atlantic cod in all years.



Allee effects

Relationships between production rate and biomass were similar for the RW and FR models (Fig. 7). There was some evidence for negative density dependence (compensation) in the 1970s, but density dependence has been positive since the late 1970s. The production rate became negative at biomasses below about 200 kt, indicating the occurrence of a strong Allee effect. The stock–recruit relationship appeared to be strongly compensatory in the 1970s (Fig. 8*a*), but has been unrelated to density since then. Survival rates associated with both 5+ *M* and *M* due to seal predation were positively related to 5+ biomass since the early 1980s, indicating depensation (Figs. 8*b*, 8*c*). The slope of this relationship became steeper at biomasses below about 100 kt, particularly for survival rates associated with *Mp* (Fig. 8*c*). These results suggest that compensatory rates of production in the 1970s reflected high recruitment success when SSB was low, whereas the strong Allee effect observed in recent years reflected high rates of natural mortality, in particular mortality due to predation by grey seals.

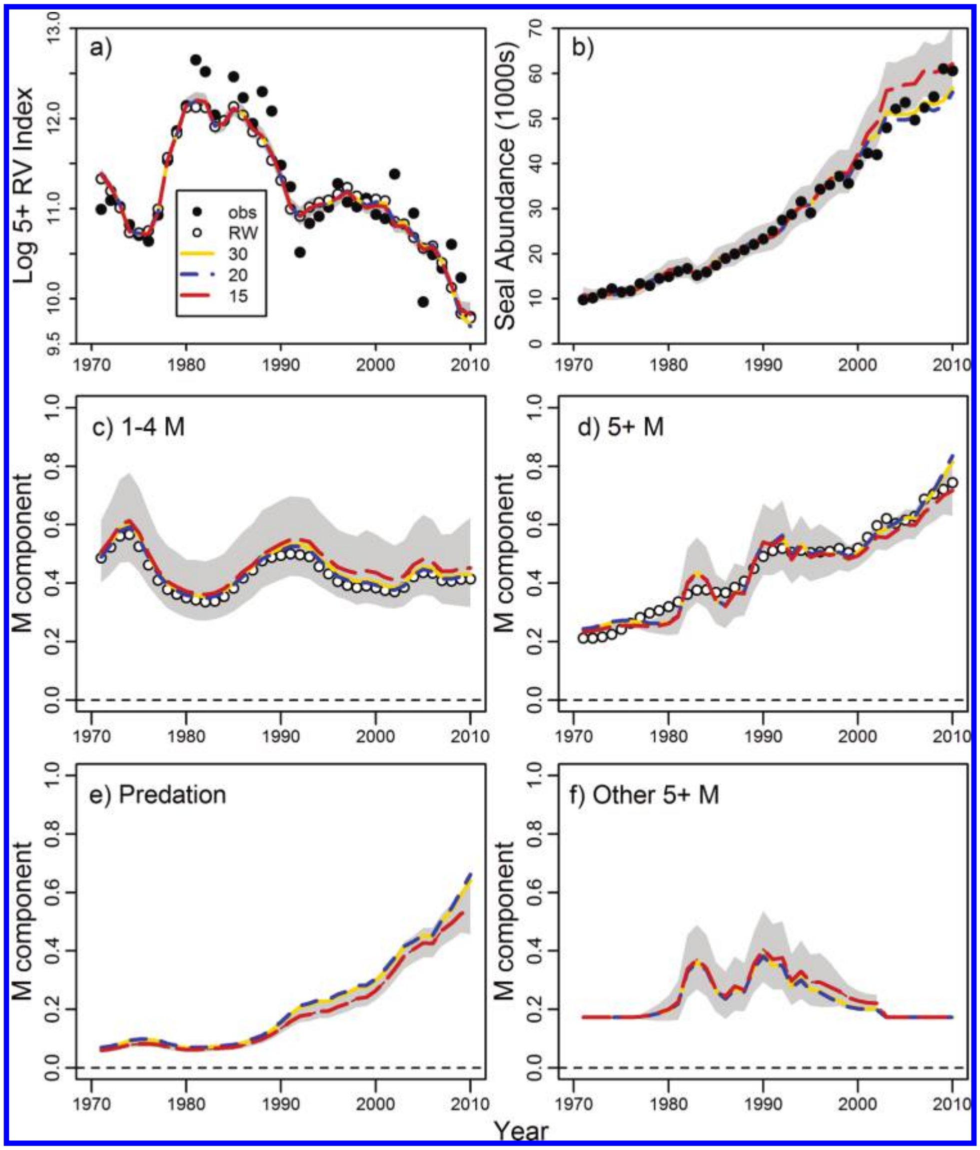
Projections

In the projection at the 2014 level of grey seal abundance, the Atlantic cod population continued to decline rapidly to extirpation (Fig. 9). Under the assumptions of this projection, there was a 99% probability that SSB would be below 1000 t by 2051 and below 100 t by 2064 (Fig. 10). SSB continued to decline although at slower rates, even when grey seal abundance was reduced by 25% or 50%. With a 25% reduction in grey seal abundance, the probabilities that SSB would be below 1000 or 100 t reached 99% by 2082 or 2108, respectively. Even with a 50% reduction, these probabilities were 88% and 63%, respectively, at the end of the 100-year projection. In each of these cases, there was a small probability (0.2%, 0.7%, and 4.2%, respectively) that SSB would exceed the limit reference point (LRP) at the end of the projection. The LRP is the level below which a stock is considered to have suffered serious harm to its productivity. Even with a 65% decline in grey seal abundance, the SSB of Atlantic cod continued to slowly decline at the end of the 100-year projection, though the probabilities that SSB would be below 1000 or 100 t were reduced to 16% or 0.4%, respectively, whereas the probability of exceeding the LRP increased to 23%.

Discussion

The collapse of Atlantic cod stocks and other groundfish resources in the Northwest Atlantic in the late 1980s and early 1990s is among the most dramatic of fishery failures on record (Kurlansky 1997). Causes of the collapse and the subsequent failure of many of these stocks to recover have been the subject of much debate (e.g., Shelton et al. 2006; Swain and Mohn 2012; Swain and Benoît 2015; Sinclair et al. 2015). Atlantic cod in the sGSL and on the ESS have failed to recover despite low to negligible fishing mortality for over 20 years. The failed recovery of these two stocks is due to unprecedented increases in the natural mortality of adult (ages 5+) Atlantic cod (Swain and Benoît 2015; Sinclair et al. 2015). In this paper, we have shown that predation by grey seals can explain this elevated mortality for Atlantic cod in the sGSL, particularly since the late 1990s when predation by grey seals was estimated to be the main source of mortality. Although ultimately due to overfishing, elevated "natural" mortality (i.e., mortality not attributable to reported fishery catches) also contributed to the collapse of sGSL cod (Swain et al. 2015*b*). However,

Fig. 6. Model fit to the research vessel (RV) biomass index for Atlantic cod aged 5 years and older (*a*) and to independently estimated grey seal abundance (*b*) and model estimates of components of natural mortality of Atlantic cod: *M* of ages 1–4 years (*c*), *M* of ages 5+ years (*d*), 5+ *M* due to predation by grey seals (*e*), and 5+ *M* due to other causes (*f*). Solid circles are observed values, open circles are median estimates from the random walk (RW) model and lines are median estimates from functional response (FR) models with $P_{y^*}^{\mathrm{diet}}$, the percent contribution of 5+ Atlantic cod (by mass) to the average grey seal diet in year *y**, set at 15%, 20%, or 30%. Shading shows the 95% credible limits for estimates with $P_{y^*}^{\mathrm{diet}} = 0.15$.

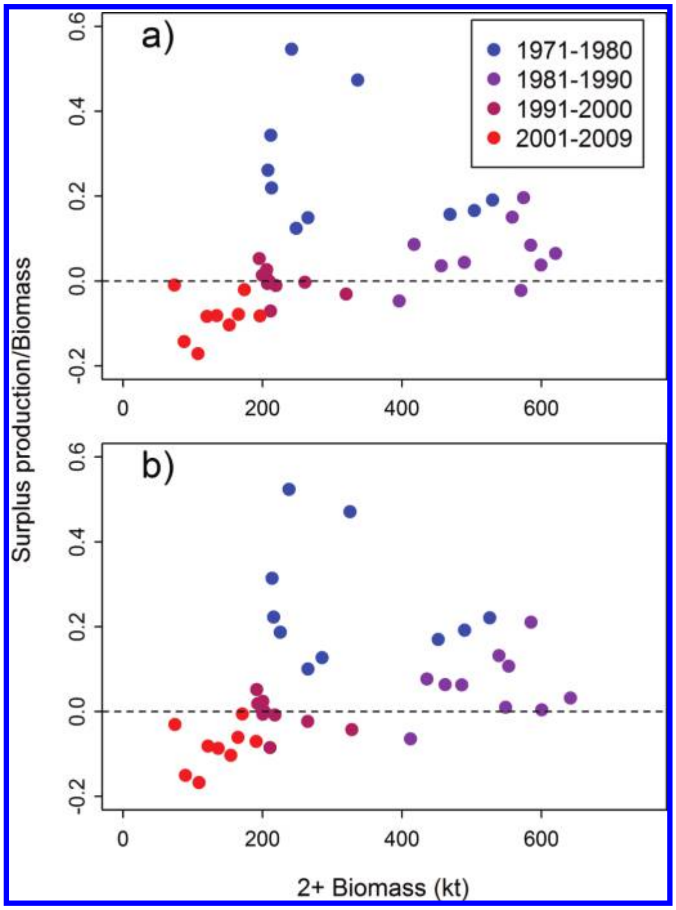


grey seal predation was estimated to be a minor component of increases in natural mortality prior to and during the collapse in the late 1980s and early 1990s (Fig. 3). Instead, other factors such as unreported catch (mistakenly attributed to natural mortality) and poor fish condition appeared to be involved in these earlier increases in adult mortality (Swain et al. 2011*a*, 2011*b*; Bousquet et al. 2010; Dutil and Lambert 2000).

Impacts of grey seals on the population dynamics of Atlantic cod have been modelled in a number of other ecosystems, sometimes with conflicting results. Mohn and Bowen (1996), Fu et al. (2001), and Trzcinski et al. (2006) modelled the impact of grey seals on Atlantic cod on the ESS. Based on the size distribution of Atlantic cod otoliths found in scats, these studies inferred that the Atlantic cod consumed by grey seals were almost entirely juveniles. Thus, these studies suggest that grey seals play a negligible role in the elevated natural mortality of adult Atlantic cod and in their failure to recover from overfishing. In contrast, O'Boyle and Sinclair (2012) concluded that the increases in natural mortality of Atlantic cod on the ESS have been due in large part to predation by grey seals. Recent studies also indicate an important impact by grey seals on the Atlantic cod stock in the West of Scotland, with predation mortality increasing as the stock declined and currently impairing recovery potential (Cook et al. 2015; Cook and Trijoulet 2016). Our results are consistent with the findings of the latter studies.

In large part, the divergence between studies reflects differences in estimates of the sizes of Atlantic cod consumed by grey seals. The early ESS studies concluded that most of the Atlantic cod consumed by grey seals were less than 30 cm in length (≤ age 3; Mohn and Bowen 1996). O'Boyle and Sinclair (2012) suggested that the seal diets used in the earlier studies were biased, under-representing the importance of large Atlantic cod in the seal diet. They attributed this to the collection of otoliths from areas such as Sable Island where juvenile Atlantic cod were dis-

Fig. 7. The per capita rate of surplus production as a function of population biomass (ages 2+) for southern Gulf of St. Lawrence Atlantic cod. Symbol colour denotes decade. (*a*) RW model; (*b*) FR model.



proportionately abundant. In recent decades, this bias has increased because large Atlantic cod have shifted their distribution further offshore from Sable Island as grey seal abundance increased (Harvey and Hammill 2011). In contrast with the conclusions in the early ESS studies, the estimated selectivity curve for grey seals preying on West of Scotland Atlantic cod peaked at 50 cm (Cook et al. 2015). At this length, Atlantic cod are predominantly 5–6 years old on the ESS and 6–8 years old in the sGSL. Based on the otoliths collected from grey seals in inshore areas of the GSL (Hammill et al. 2007) and from the Atlantic cod overwintering grounds near the Cabot Strait (Hammill et al. 2014), the sizes of Atlantic cod consumed by grey seals in the sGSL are consistent with the size selectivity curve for grey seals preying on cod in the West of Scotland. Estimated sizes were much larger than the estimates from the ESS; the percentage of Atlantic cod in the diet estimated to be greater than 30 cm in length was 39% in the inshore samples and 66%–80% in the offshore winter samples. Based on these samples, 56% of the Atlantic cod consumed by grey seals in inshore areas were 5 years of age or older (by mass), as were 66%–87% of the Atlantic cod consumed on the overwintering grounds (Supplementary Material 2[2]).

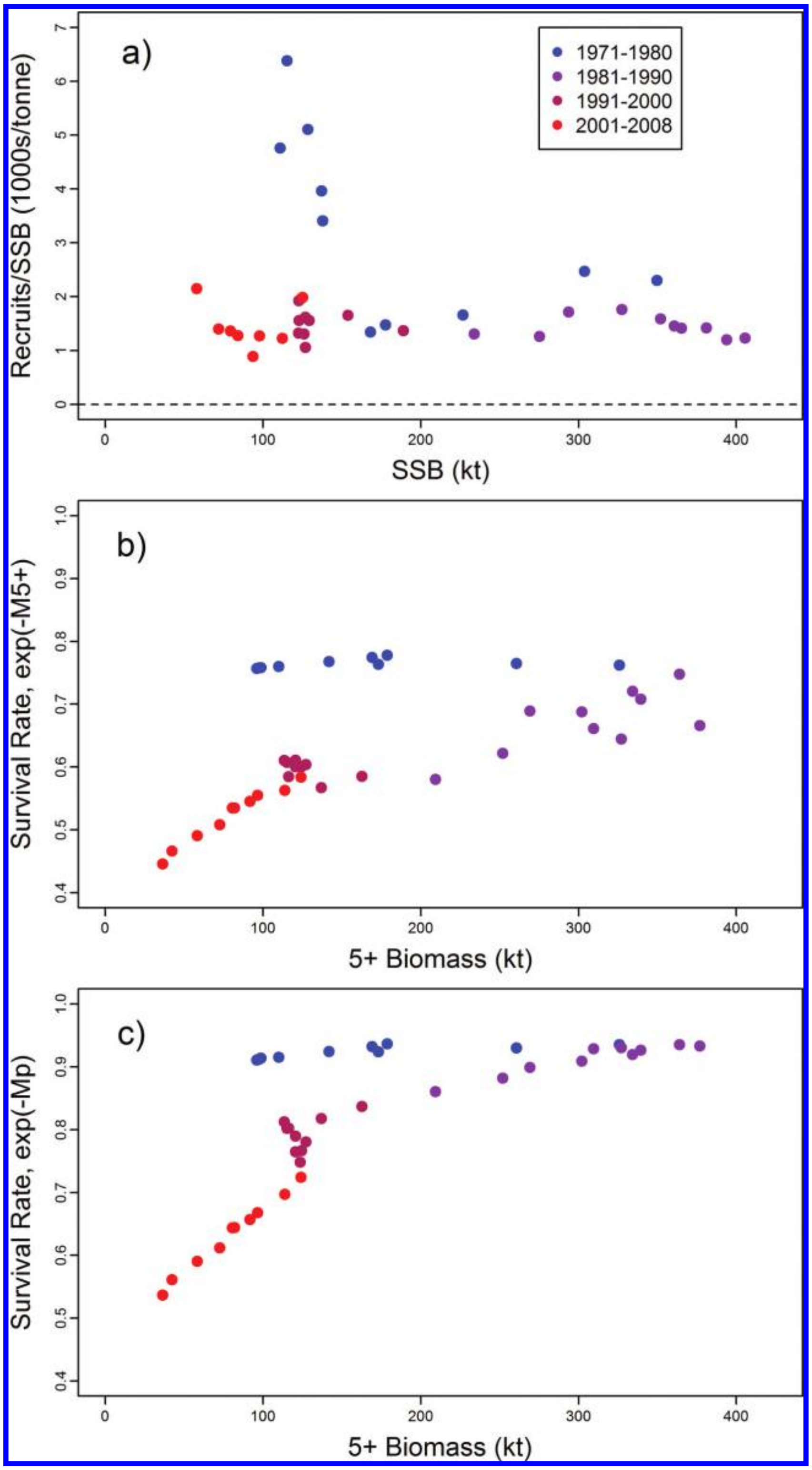
As noted by O'Boyle and Sinclair (2012) and Cook and Trijoulet (2016), predation on older cod will be underestimated if their otoliths are not always consumed due to partial consumption of larger fish. Fish harvesters have frequently reported "belly-biting" of large Atlantic cod and white hake (*Urophycis tenuis*) by grey seals, including cases with no gear in the vicinity (personal communications to the authors; O'Boyle and Sinclair 2012). Selective rejection of fish heads has been documented in a number of seal species (e.g., Roffe and Mate 1984; Moore 2003; Hauser et al. 2008; Phillips and Harvey 2009). Partial consumption of blue sharks (*Prionace glauca*) by Cape fur seals (*Arctocephalus pusillus pusillus*) has also been recently reported (Fallows et al. 2015). When preying on large cod, partial consumption of the energy-rich abdomen (belly-biting) may be an optimal foraging strategy where cod are locally abundant (Supplementary Material 2[2]).

The contribution of Atlantic cod to the average grey seal diet is an important source of uncertainty in this and other studies of the impact of predation by grey seals on cod populations. The diet of grey seals varies widely among seasons, areas, and individuals. Our best estimate of the contribution of 5+ Atlantic cod to the average annual diet was the mean of the inshore summer and offshore winter diets (24.5%). There is no indication that this is an overestimate. The prevalence of 5+ cod in inshore areas in summer is lower than in many of the unsampled areas and seasons, such as offshore areas in summer and early fall (Swain 1993) and areas in the vicinity of cod aggregations during the spring and fall migrations and spawning in May and June. Nonetheless, even if the percentage of Atlantic cod in the diet in 2010 ($P_{y^*}^{\text{diet}}$) is fixed at a value as low as 15%, estimated predation mortality of 5+ cod rises to high values from 1990 to 2010. The estimates obtained since 2000 with $P_{y^*}^{\text{diet}}$ fixed at 15% average 90% of the estimates with $P_{y^*}^{\text{diet}}$ fixed at 20% (Fig. 6*e*).

Our use of a single-species FR required the assumption that the biomass of alternate prey was constant over time. While there is some support for this assumption (Savenkoff et al. 2007), it could be avoided by using a multispecies FR (e.g., Smout et al. 2014). However, even in their case, Smout et al. (2014) aggregated a subset of prey, assuming that their abundance was constant over time. They justified this assumption by noting that the abundance of these "other prey" is the aggregate of many near independent time series whose total is unlikely to vary systematically on average. Finally, using either approach (single-species or multispecies FR), the aggregative response of predators to prey should ideally also be taken into account. In our case, the data required to incorporate a multispecies FR and the predator aggregative response are not available. These approaches are thus beyond the scope of our paper. Nonetheless, our results for the recent period are not dependent on the above assumption because *Ho*, the parameter accounting for impacts of alternate prey, was estimated based on recent conditions. The recent period is of greatest interest due to the large increase in 5+ *M* occurring in this period. The model estimates of cod consumption in earlier periods (the 1970s and 1980s) may be biased due to changes in the relative abundance of alternate prey; these estimates are yet consistent with the natural mortality estimates from the RW model.

In this study, we have assumed that predation by grey seals on adult cod can be represented by a type II functional response. This type of functional response was also assumed in studies of predation by grey seals on ESS cod (Trzcinski et al. 2006; O'Boyle and Sinclair 2012), emerged in population modelling of the impact of grey seal predation on West of Scotland cod (Cook et al. 2015), and was observed in harbor seals (*Phoca vitulina*) preying on salmon (Middlemas et al 2006). In our case the close correspondence between estimates of natural mortality obtained using a type II functional response and those obtained using a random walk supports the use of this type of functional response. However, in an analysis at fine spatial and temporal scales, Smout et al. (2014) found evidence for prey-switching by grey seals at low prey abundance (a type III functional response). This may not be evident at the larger spatial (ecosystem) and temporal (annual diets) scales of population-level analyses because of the aggregative behavior of cod. During overwintering, seasonal migrations and spawning, cod occur in dense aggregations (e.g., Comeau et al. 2002*b*). Thus, even when population abundance is low, cod densities can be locally high, providing attractive foraging opportunities for pred-

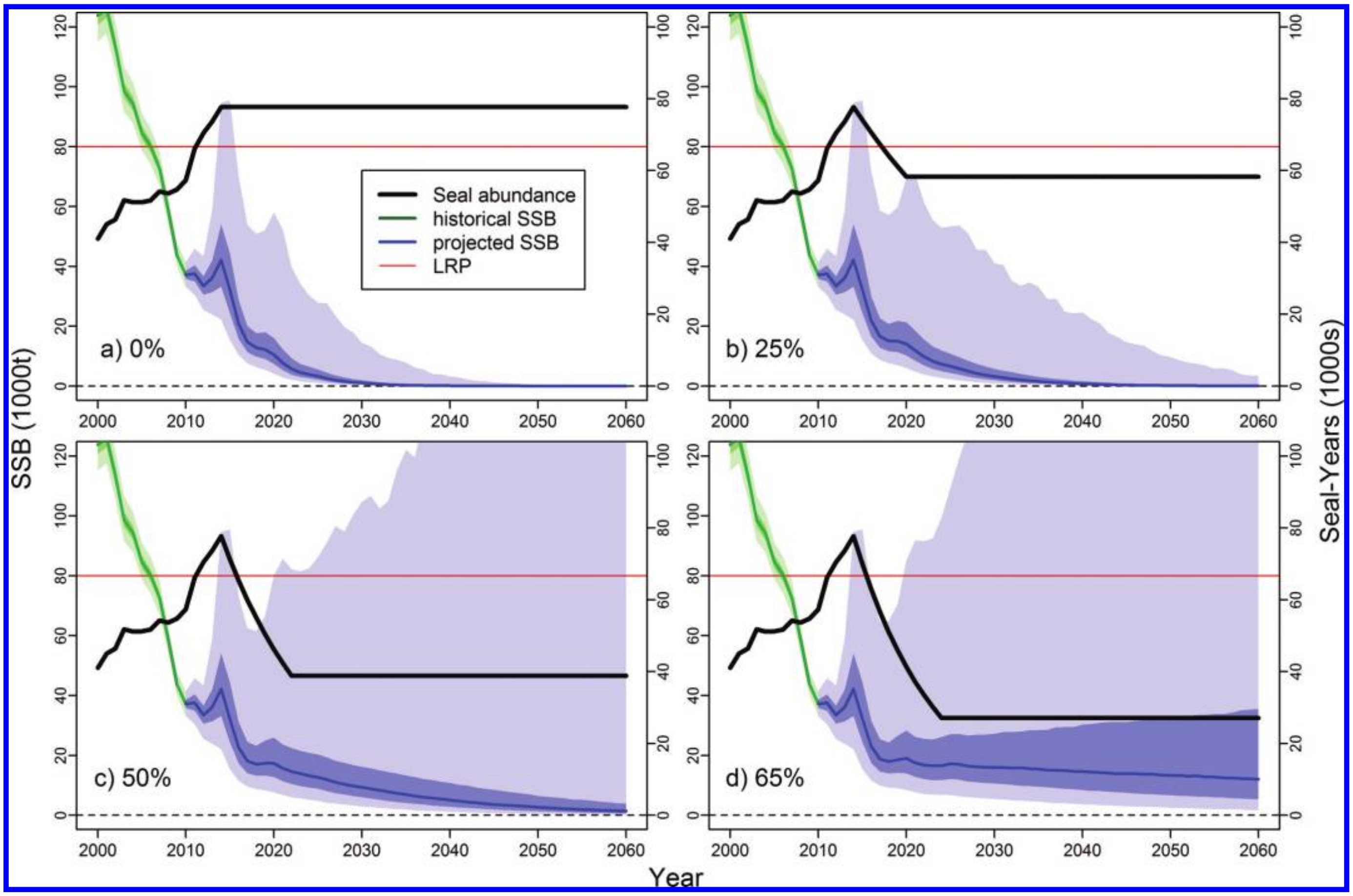
Fig. 8. Relationships between recruitment or survival rates and biomass of southern Gulf of St. Lawrence Atlantic cod. Symbol colour denotes decade. (*a*) Recruitment rate; (*b*) survival rate based on total *M* of 5+ Atlantic cod; (*c*) survival rate based on mortality of 5+ Atlantic cod due to predation by grey seals.



ators. This same behavior allows fishery catch rates to remain high when the population abundance of fish stocks is very low (e.g., Rose and Kulka 1999).

In our model we have assumed that the impact of grey seals on Atlantic cod mortality is restricted to the direct effect of their consumption of cod. However, "nonconsumptive" or risk effects of intimidation by predators can rival or exceed the effects of consumption (Preisser et al. 2005). These effects involve changes in prey traits (e.g., behaviour) that reduce predation mortality at a cost (e.g., reduced energy intake, increased vulnerability to other predators). Strong risk effects have been demonstrated for Atlantic cod in the sGSL, whose distribution has shifted out of habitats

Fig. 9. Projected Atlantic cod SSB under different scenarios for future grey seal abundance. Projections assume that other components of productivity remain at recent levels. Scenarios for seal abundance (heavy black line) are (*a*) constant at the 2014 level; (*b*) a 25% decline over 6 years from the 2014 level, then held constant; (*c*) a 50% decline over 8 years from the 2014 level, then held constant; and (*d*) a 65% decline over 10 years from the 2014 level, then held constant. Lighter solid lines show the median estimate of SSB and dark and light shading show the 50% and 95% credible limits, respectively. The horizontal line shows the limit reference point (LRP, 80 kt), the level below which the stock is considered to have suffered serious harm to its productivity. The historical and projection periods are denoted by green and blue lines and shading, respectively.

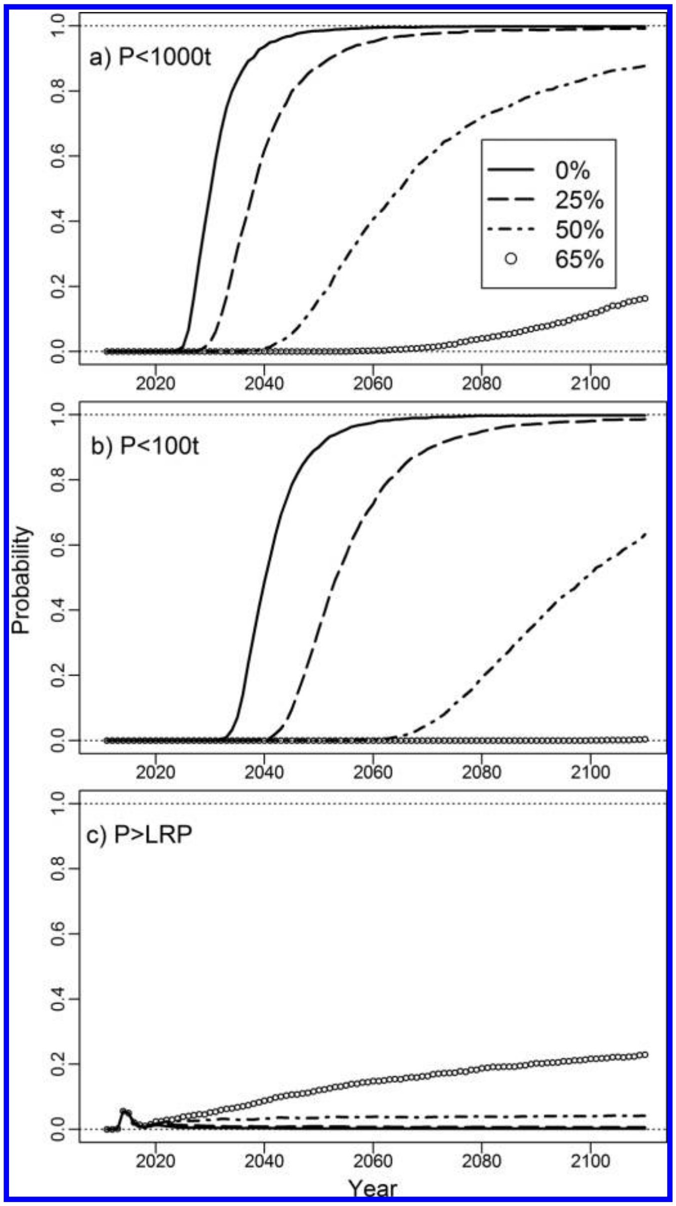


where the risk of predation by grey seals has become high into lower risk but less profitable habitats (Swain et al. 2015*a*). These risk effects may be an important source of mortality not accounted for in our models. Thus, grey seals could account for most of the current high mortality of adult Atlantic cod even if they consume less cod than estimated here.

Atlantic cod in the sGSL are currently experiencing a strong Allee effect, with the rate of surplus production declining to negative values as population biomass has decreased over the past decade. Changes in recruitment dynamics do not appear to be the primary cause of this negative productivity. While there does appear to have been a weakening in recruitment compensation between the 1970s and 1990s (cf. Keith and Hutchings 2012), there is no evidence for depensatory recruitment dynamics in this stock. Furthermore, the high recruitment success of sGSL cod in the 1970s appears to have resulted primarily from reduced predation on Atlantic cod eggs and larvae by collapsed pelagic fish stocks rather than from compensatory recruitment dynamics (Swain and Sinclair 2000). Instead, the positive density dependence of population productivity at low abundance of this stock appears to result from predation-driven Allee effects. Given a type II functional response, the predation mortality generated per predator increases as prey abundance declines, resulting in a demographic Allee effect (Gascoigne and Lipcius 2004). This is reflected in the slight peak in predation mortality in the mid-1970s and the sharp increase in predation mortality as the stock collapsed in the late 1980s and early 1990s (Fig. 2*c*). However, much of the large increase in 5+ *M* in the 1990s and 2000s reflects an emergent Allee effect, resulting from increasing grey seal abundance when Atlantic cod abundance is severely depleted.

It appears that healthy populations of both grey seals and Atlantic cod co-existed prior to the mid-1800s. Increased hunting resulted in severe reductions in grey seal abundance in the mid- to late 1800s, but grey seals were very abundant in prior centuries (Lavigueur and Hammill 1993). Atlantic cod abundance also appears to have been very high then. Rosenberg et al. (2005) estimated that Atlantic cod biomass on the Scotian Shelf in 1852 was 1260 kt, over five times the highest biomass in the modern record (about 240 kt in the early 1980s; Mohn and Rowe 2012; DFO 2015). If cod densities were similar in the sGSL during earlier periods of high seal abundance, biomass would have been about 735 kt based on the relative sizes of the two ecosystems. Given this biomass and the functional response estimated in our modelling, the predation mortality exerted by the current high abundance of grey seals would be less than 0.2, a level considered normal for Atlantic cod. This suggests that even at their current high level of abundance, predation by grey seals would be sustainable at historical levels of cod biomass, in contrast with the current depleted levels of biomass.

Fig. 10. Probability that SSB will be below 1000 t (*a*), below 100 t (*b*), or above the limit reference point (LRP) (80 000 t, (*c*)) at different levels of grey seal reduction, conditional on the assumption that other components of Atlantic cod productivity remain at recent levels.



Based on current grey seal abundance and Atlantic cod productivity, our projections indicate that there is a high probability that Atlantic cod will be locally extinct in the sGSL by mid-century, even in the absence of fishing. Furthermore, only very large reductions in the current abundance of grey seals (e.g., a 65% reduction) would reduce the extinction probability to a low level. However, the realized future trajectory of this population may differ from these projections. For example, a type III functional response may develop at even lower cod abundance, as grey seals engage in prey-switching behaviors. In this case, Atlantic cod may not be driven to local extinction in the sGSL, but would instead be confined to very low abundance in a "predator pit". While this possibility cannot be discounted, a type II functional response adequately accounted for estimated changes in 5+ M despite the decline in cod abundance to very low levels in recent years. Seals may not switch to alternate prey at low cod abundance due to the aggregative behaviour of Atlantic cod.

These projections also assume that there are no indirect effects of declines in seal abundance on Atlantic cod productivity (e.g., Yodzis 2001). These indirect effects could occur if important predators of Atlantic cod are also prey of grey seals. If so, this alternate predator could increase in abundance and prevent cod recovery as grey seals declined. For example, Atlantic herring (*Clupea harengus*) are an important prey of grey seals (Hammill et al. 2007) and of Atlantic cod (Hanson and Chouinard 2002). Atlantic herring are also thought to be an important predator of the early life stages of Atlantic cod in the sGSL (Swain and Sinclair 2000). Thus, released from predation by grey seals, Atlantic herring could increase in abundance and increase predation on the early life stages of Atlantic cod, reducing recruitment success. On the other hand, reduced predation by grey seals could be replaced by increased predation on herring by recovering Atlantic cod. Furthermore, Atlantic herring in the sGSL are currently the target of an important fishery (Swain 2016), and this fishery would likely prevent dramatic increases in herring biomass even in the absence of grey seal predation.

Many marine mammal populations around the world are recovering from past depletions (e.g., Magera et al. 2013). The case of sGSL Atlantic cod emphasizes the importance of maintaining exploited prey of these recovering predators at healthy population levels to avoid Allee effects from which recovery may not be possible. At the current abundance of grey seals, the sGSL cod population is expected to be extirpated by mid-century, even with no fishing and no further increase in seal abundance. We estimate that a very large decrease in current seal abundance would be required to avoid cod extirpation with high probability and allow a slow recovery of the stock.

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