



Absence of predator control increases cod extirpation risk in a Northwest Atlantic ecosystem: inference from multispecies modelling

Steven P. Rossi^{1,3,*}, Sean P. Cox¹, Hugues P. Benoît²

¹School of Resource and Environmental Management, Simon Fraser University, Burnaby, British Columbia V5A 1S6, Canada

²Maurice Lamontagne Institute, Fisheries and Oceans Canada, Mont-Joli, Quebec G5H 3Z4, Canada

³Present address: LGL Limited, Sidney, British Columbia V8L 3Y8, Canada

ABSTRACT: Atlantic cod *Gadus morhua* in the southern Gulf of St. Lawrence (sGSL) declined to low abundance in the early 1990s and have since failed to recover due to high natural mortality, which has been linked to predation by grey seals *Halichoerus grypus*. Increased grey seal harvests have been suggested to improve cod survival; however, predicting the response of cod to changes in seal abundance in the sGSL is complicated by a hypothesized triangular food web involving seals, cod, and small pelagic fishes, wherein the pelagic fishes are prey for cod and grey seals, but may also prey on young cod. Grey seals may therefore have an indirect positive effect on pre-recruit cod survival via predation on pelagic fish. Using a multispecies model of intermediate complexity fitted to various scientific and fisheries data, we found that seal predation accounted for the majority of recent cod mortality and that cod will likely be extirpated without a strong and rapid reduction in grey seal abundance. We did not find evidence that reducing grey seal abundance will impair cod recovery by causing large increases in pelagic biomass so long as pelagic fishing mortality continues at historical levels.

KEY WORDS: Atlantic cod · *Gadus morhua* · Grey seal · *Halichoerus grypus* · Predator control · Seal cull · Ecosystem-based fisheries management

Resale or republication not permitted without written consent of the publisher

1. INTRODUCTION

Human societies have actively managed mammalian predator abundance for at least 2 millennia (Reynolds & Tapper 1996). Reducing predator abundance has sometimes been a means to improve human and livestock safety, whereas in other cases, it has been aimed at improving the survival of wild species of interest ('target' species). In this latter case, predator-reduction initiatives often implicitly assume that ecosystems can be reduced to simple predator–prey systems in which reducing predator abundance results in sustained increases in prey survival; however, reducing predator abundance may result in a wide range of unintended consequences (Bax 1998, Yodzis 2001, Bowen & Lidgard 2013). For instance, removing a top predator from an ecosystem may improve the short-term survival of

not only the target species, but all species consumed by that predator. If one or more of these other species are predators of the target species, then the long-term, total predation mortality of the target species may increase or remain constant in the absence of the top predator due to the improved survival of other predators. It is therefore important to consider wider ecosystem implications when forecasting the impact of predator reductions on target species.

Marine mammal predation on commercially valuable fish stocks is increasingly used to justify predator-control programmes, especially where marine mammal populations (particularly pinnipeds) are growing in response to reduced exploitation. For example, predation by recovering pinnipeds on several sockeye *Oncorhynchus nerka* and Chinook salmon *O. tshawytscha* stocks in the northeast Pacific likely now accounts

*Corresponding author: srossi@lgl.com

for more mortality than all sources of fishing combined (Magera et al. 2013, Wargo Rub et al. 2019, Walters et al. 2020). Similarly, in the northwest Atlantic, where grey seal *Halichoerus grypus* abundance has grown especially large, natural mortality (M) of numerous fish stocks has increased to the point where some stocks, particularly in the southern Gulf of St. Lawrence (sGSL), are being evaluated by the Committee on the Status of Endangered Wildlife in Canada for enhanced risk of extirpation (e.g. Swain et al. 2019). While targeted pinniped reductions have been suggested as a possible means of recovering these threatened fish stocks (e.g. FRCC 2011, SSCFO 2012), the wider implications of such interventions for the sGSL ecosystem are unknown.

Developing quantitative models of interactions between predators and target species is an important step toward understanding the responses of target species to changes in predator abundance. The specific approach used to model species interactions should be linked to scientific goals (i.e. understanding seal predation impacts) and management objectives (i.e. recovering threatened fish populations). 'Food web' or 'whole ecosystem' models, such as ECOPATH with ECOSIM (Polovina 1984, Christensen & Pauly 1992, Walters et al. 1997, 2000) and ATLANTIS (Fulton et al. 2004), consider populations across all trophic levels of an ecosystem. These models are often complex and are intended for strategic use (i.e. broad-scale, long-term planning). In contrast, models of intermediate complexity or 'minimum-realistic models' include only species considered to have important interactions with the species of interest and are more tactically focused, with outputs that can potentially be used in short-term decision making (Plagányi et al. 2014). Models of intermediate complexity are well suited for investigating interactions among higher trophic level species, as these species require relatively fewer linkages than lower trophic level species. In particular, these models are useful for understanding the effects of pinniped predation on fish M and forecasting responses to pinniped abundance changes while accounting for indirect effects (e.g. Punt & Butterworth 1995).

In this paper, we investigate the extirpation risk for Atlantic cod *Gadus morhua* in the sGSL (Atlantic Canada, Northwest Atlantic Fisheries Organization [NAFO] Division 4T) via a multispecies population model consisting of Atlantic cod, Atlantic herring *Clupea harengus*, and Canadian-origin grey seals (hereafter referred to as 'cod', 'herring', and 'seals', respectively). The sGSL encompasses the Magdalen Shallows, with depths mostly less than 100 m, and the Laurentian Channel, with depths up to 500 m (Fig. 1). Cod and herring reside in the sGSL from the spring to fall, where they spawn and feed, while adult herring and all stages of cod overwinter in the Cabot Strait (NAFO Subdivision 4Vn). Cod in the sGSL form a single spawning stock, while herring consist of genetically distinct spring- and fall-spawning components (Lamichhane et al. 2017), the latter of which is further disaggregated by region within the sGSL (North, Middle, and South) for management purposes to account for strong spawning-site

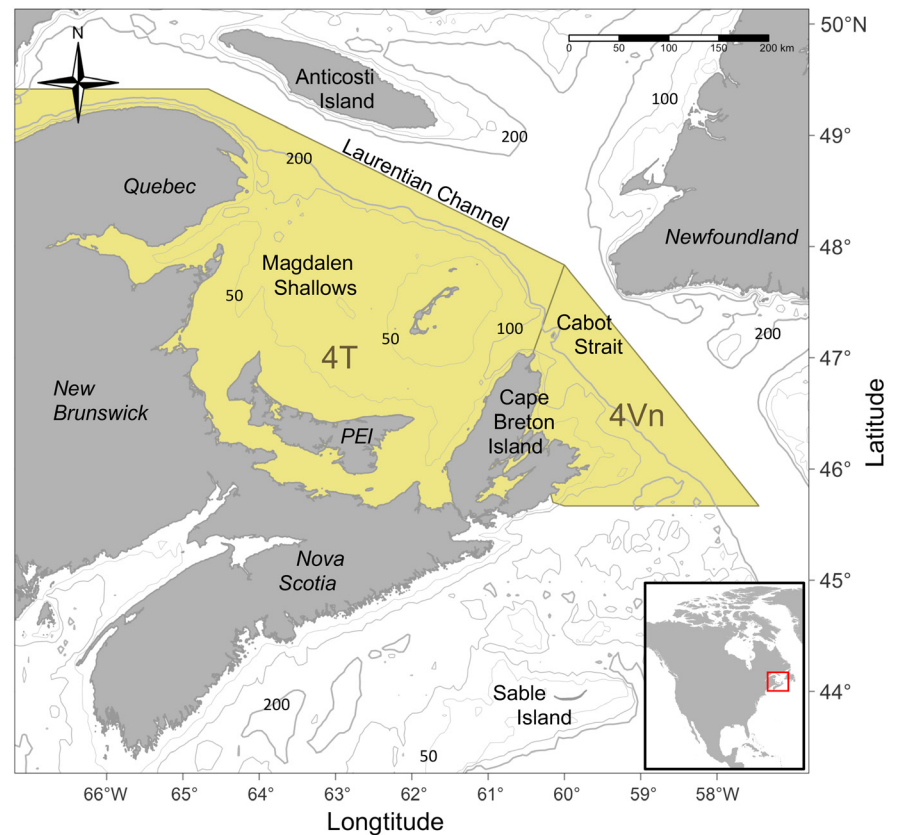


Fig. 1. Southern Gulf of St. Lawrence (sGSL) and place names mentioned in the paper. Grey lines indicate the 50, 100, and 200 m depth contours; yellow-shaded regions indicate Northwest Atlantic Fisheries Organization (NAFO) Divisions occupied by the sGSL stocks of cod and herring (4T and 4Vn). Bathymetric depth contours were obtained from the ETOPO 2022 database (NOAA National Centers for Environmental Information 2022) using the 'marmap' package (Pante et al. 2023) in R (R Core Team 2019). PEI: Prince Edward Island

fidelity (DFO 2018). Grey seals in the Northwest Atlantic form a single population but are subdivided in Canadian waters into Scotian Shelf and Gulf of St. Lawrence herds (hereafter referred to as 'Shelf' and 'Gulf' herds, respectively) for management purposes. The Shelf herd consists of seals from Sable Island, the largest grey seal colony in the world, as well as seals from smaller whelping grounds along coastal Nova Scotia. Gulf-herd seals pup on pack-ice and small islands in the Gulf of St. Lawrence. Grey seals forage widely within their range, including within the sGSL and on cod/herring overwintering grounds (Breed et al. 2006, Harvey et al. 2011, Swain et al. 2015a).

Cod were fished to low abundance in the early 1990s and have failed to recover due to an increase in M among older cod (Swain & Benoît 2015), which is concurrent with a rapid increase in seal abundance (Hammill et al. 2017a). Early maturation, environmental conditions, parasites, and unreported catch were investigated as possible causes of elevated M among older cod from the mid-1990s to present, but none was found to be an important contributing factor (Swain et al. 2011). In contrast, the hypothesis that seal predation has driven increases in cod M has been supported by bioenergetic models, shifts in cod distribution to areas with lower seal abundance, and population models linking cod M to seal abundance (Benoît et al. 2011, Swain et al. 2015a,b). Specifically, increased cod M appears to be the result of a predation-driven Allee effect, suggesting that the extirpation of cod is likely without large reductions in seal predation (Neuenhoff et al. 2019).

Predicting ecosystem responses to grey seal abundance reductions in the sGSL is complicated by a hypothesized triangular food web involving seals, cod, and pelagic fishes such as herring and mackerel *Scomber scombrus* that are important prey for seals (Bowen et al. 1993, Hammill et al. 2007, 2014) and cod (Hanson & Chouinard 2002, Hanson 2011). Cod recruitment success in the sGSL has a strongly negative relationship with pelagic fish biomass, potentially resulting from predation or competition by pelagics with early life history stages of cod (Swain & Sinclair 2000). Thus, seals may have an indirect positive effect on pre-recruit cod survival via predation on pelagics, suggesting that reducing seal abundance could result in reduced recruitment success for cod. For instance, Punt & Butterworth (1995) analysed a pinniped cull in a 3-species food web in the Benguela ecosystem and found that reducing pinniped abundance had a neutral or negative effect on the target species due to the resulting increased

abundance of an intermediate species that consumes the target species. Alternatively, pelagics released from seal predation may instead be consumed by recovering cod, resulting in improved cod survival through cultivation effects (Walters & Kitchell 2001). Management actions aimed at reducing cod mortality may be the only means of recovering cod in the sGSL, so it is critical to better understand the importance of these processes and their relative impacts on the efficacy of potential management actions.

We developed a multispecies, age-structured population model to evaluate the effects of changes in seal and/or herring abundance on cod survival and recruitment in the sGSL. Compared to existing cod-seal modelling approaches for northwest Atlantic ecosystems (Mohn & Bowen 1996, Fu et al. 2001, Trzcinski et al. 2006, Neuenhoff et al. 2019), our approach allows for indirect effects of seal reductions on cod survival via other species to be explicitly evaluated. Our model linked cod mortality to local seal abundance and herring mortality to the local abundance of both cod and seals (Fig. 2). Additionally, we modelled cod recruitment as a function of herring biomass to account for herring effects (predation, competition) on pre-recruit cod. Under this model formulation, seal abundance reductions have a positive direct effect on adult cod survival and an uncertain, potentially negative indirect effect on cod recruitment. The net effect of seal reductions on cod productivity is therefore unknown and may be negative if reduced seal predation on adult cod is sufficiently offset by increased predation on and/or competition with young cod. This model may therefore

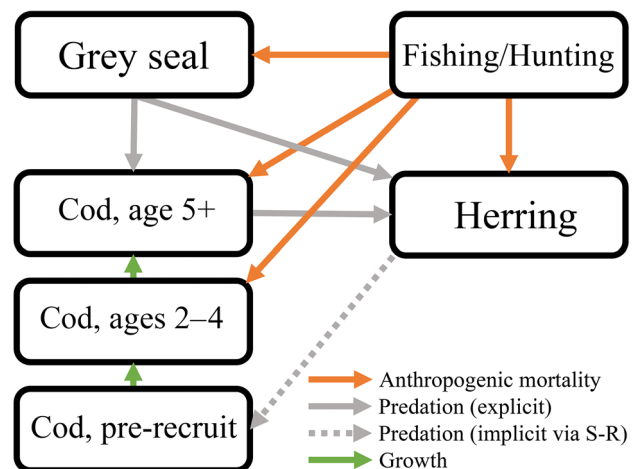


Fig. 2. Seal–cod–herring triangular food web model. Predation was modelled by explicitly incorporating predation into mortality rates (solid grey lines) and implicitly by including a predator as a covariate in a stock–recruitment (S-R) function

yield a range of outcomes for cod depending on the net effect of reduced seal abundance. Our results over a wide range of model assumptions and sensitivity tests suggest that cod recovery in the sGSL is highly unlikely without rapid reductions in seal abundance.

2. MATERIALS AND METHODS

2.1. Data

Annual fishery landings of cod (1971–2018) in the sGSL included directed fishing from fixed and mobile gears, as well as cod bycatch from other groundfish fisheries but not from invertebrate fisheries, as landings of commercial-size cod in these fisheries were negligible (Swain et al. 2011). Landings of spring- and fall-spawning herring included catches from fixed (gillnet) gear fisheries on spawning grounds in Div. 4T and mobile (purse seine) gear fisheries in Div. 4T and Subdiv. 4Vn. Fall-spawning herring landings were aggregated across spatial subpopulations from 1971 to 1977 but were disaggregated thereafter.

Fisheries and Oceans Canada (DFO) has monitored relative cod abundance in the sGSL using stratified-random bottom-trawl research vessel (RV) surveys each September since 1971. Changes in fishing efficiency by different RVs were accounted for by applying conversion factors estimated using results of comparative fishing experiments. We also obtained cod abundance indices from a sentinel longline survey, conducted each summer and fall (1995–2017) at fixed sites, and from a mobile sentinel bottom-trawl survey, conducted each August since 2003 using the same stratified-random design as the RV survey (Swain et al. 2019).

Herring catch per unit effort (CPUE) time-series (1986–2018) were constructed for each subpopulation from commercial gillnet catch and effort data. We also used spring herring relative abundance data (1994–2017) from DFO acoustic surveys in the western portion of Div. 4T each fall. Subpopulation-specific herring data prior to 1978 were unavailable, so we used total biomass estimates from an assessment model as biomass indices for 1971–1977 (Cleary 1982).

Counts of newly weaned seals at the main breeding colonies in Canadian waters (1971–2016; den Heyer et al. 2017, Hammill et al. 2017b), corrected for pups that were unseen or died prior to surveying, were used to infer seal abundance. We used samples of age and reproductive status from seals in the Gulf of St. Lawrence between late May and November in intermittent years (1982–2015; Hammill & Gosselin 1995).

We also used estimates of seal removals from the Canadian commercial harvest, nuisance licence kills, bounty kills/culls, and scientific sampling (Hammill et al. 2017a). Removals were aggregated into young-of-year (YOY) and age 1+ bins.

We used seal and cod diet samples to estimate consumption rates and size-selectivity of herring. The seal diet was inferred from prey hard parts found in the digestive tracts of grey seals collected (1) in coastal areas of the sGSL between late spring and August (1985–2004; Hammill et al. 2007), (2) from the west coast of Cape Breton Island between September and January (1996–2011; Hammill et al. 2014), and (3) in the Cabot Strait, mostly between October and December (2010–2011; Hammill et al. 2014). Seals were sampled on or near shore, and the inferred diets likely reflect feeding that occurred near (~30 km) the sampling site (Benoît et al. 2011). The available diet information was assumed to be spatially representative. Cod in the sGSL have been sampled for diet information since 1959 (Hanson & Chouinard 2002, Benoît & Rail 2016). Samples were taken throughout the sGSL and at different times of year when cod were either aggregated or dispersed. Herring consumed by grey seals ranged between 9 and 39 cm, with 50% of consumed herring between 25 and 30 cm. Cod tended to consume smaller herring than seals (50% of consumed herring between 13 and 23 cm, range: 7–29 cm). Length frequencies of herring in predator diets were converted to age frequencies using annual, subpopulation-specific herring age–length keys, which were based on fishery catch-at-age (gillnet and purse seine combined; F. Turcotte unpubl. data).

The movement of seals has been tracked using satellite telemetry since the mid-1990s (Breed et al. 2006, Harvey et al. 2008, Benoît & Rail 2016). We used these data to infer the monthly seal presence in areas occupied by cod and herring (defined as Div. 4T from May to October and both Div. 4T and Subdiv. 4Vn from November to April), which we then averaged into annual foraging rates (Table 1).

2.2. Multispecies model

Our analysis had 3 steps. First, the multispecies model was fitted to commercial fishery and survey catch-at-age data for cod and herring, as well as pup production and reproductive data for grey seals, to estimate intraspecific parameters for each species. Intraspecific parameters estimated for cod and herring included recruitment, initial abundance, fishery/survey selectivity, and catchability, while those for seals were

Table 1. Proportion of time spent by satellite-tracked grey seals in areas occupied by southern Gulf of St. Lawrence (sGSL) cod or herring (from Benoît & Rail 2016). 4T: Northwest Atlantic Fisheries Organization (NAFO) Division 4T; 4T+4Vn: combined area of NAFO Division 4T and Subdivision 4Vn. 'Gulf' and 'Shelf' refer to seals from the Gulf of St. Lawrence and Scotian Shelf herds, respectively

Month	Area	Gulf Male	Gulf Female	Shelf Male	Shelf Female
January	4T+4Vn	0.647	0.534	0.020	0.091
February	4T+4Vn	0.577	0.417	0.059	0.017
March	4T+4Vn	0.441	0.208	0.000	0.000
April	4T+4Vn	0.553	0.302	0.000	0.000
May	4T	0.522	0.226	0.000	0.000
June	4T	0.876	0.606	0.000	0.035
July	4T	0.798	0.615	0.031	0.065
August	4T	0.801	0.605	0.067	0.055
September	4T	0.842	0.549	0.056	0.045
October	4T	0.908	0.562	0.046	0.055
November	4T+4Vn	0.946	0.582	0.012	0.045
December	4T+4Vn	0.841	0.707	0.003	0.045
Mean		0.729	0.493	0.024	0.038

maturity rates, initial abundance, the scale and shape of the density dependence relationship, and the maximum reproductive rate. The model was also simultaneously fitted to bioenergetically derived consumption rates and observed age composition of herring in seal and cod diets to estimate parameters for per capita consumption and age/size preference by seals and cod. Second, functional responses and the stock–recruitment relationships were post-fitted to model estimates of prey consumption and abundance/biomass. Finally, the fitted model, functional responses, and stock–recruitment relationships were projected in stochastic simulations for 50 yr under a range of seal and herring harvest levels. These simulations accounted for parameter uncertainty (via random parameter draws from Bayes joint posterior distributions) as well as uncertainty about future variability in natural processes (i.e. recruitment, non-predation mortality, etc.). We provide a general overview of the model below. A complete list of model equations and notations are given in Supplement 1 at www.int-res.com/articles/suppl/m746p099_supp.pdf.

2.2.1. Population modelling

2.2.1.1. Abundance. The model consisted of an age-structured model for each species (indexed by i ; 1 = seal, 2 = cod, 3 = herring) in which abundance N decayed exponentially according to an annual instantaneous total mortality rate Z (yr^{-1}):

$$N_{i,x,a,t} = N_{i,x,a-1,t-1} \exp(-Z_{i,x,a-1,t-1}) \quad (1)$$

where x , a , and t are index subpopulation, age, and year, respectively. Each combination of herd and sex was considered a separate grey seal subpopulation. Herring had separate subpopulations for spring spawners (Spring) and fall spawners in each region: North (Fall-N), Middle (Fall-M), and South (Fall-S) (DFO 2015).

Seal pup production was the product of female abundance and pregnancy rates (Table S1.2 in Supplement 1, Eqs. S24 & S25), the latter of which were a logistic function of age (Eqs. S1–S4). Seal recruitment at age 1 was then pup production from the previous year adjusted for mortality arising from weaning, poor ice condition (Eq. S26), harvest (Eq. S27), and density dependence, which was modelled as a generalized Beverton-Holt function of abundance (Eqs. S28 & S29). Fish ($i > 1$) recruitment at age 2 for each subpopulation was modelled as a temporal random walk:

$$N_{i,x,2,t} = N_{i,x,2,t-1} \exp(\epsilon_{i,x,t}^{(R)}) \quad (2)$$

2.2.1.2. Mortality rates. We defined Z as the sum of fishing/hunting mortality F and natural mortality M :

$$Z_{i,x,a,t} = F_{i,x,a,t} + M_{i,x,a,t} \quad (3)$$

where M may arise from predation by one of the predators in our model ($M^{(P)}$) or from other sources ($M^{(O)}$):

$$M_{i,x,a,t} = M_{i,a,t}^{(P)} + M_{i,x,a,t}^{(O)} \quad (4)$$

Cod $M^{(O)}$ for ages 5+ was assumed to be constant until 1978 and was subsequently varied as a random walk to account for non-predation factors (poor growth/condition, unreported catch) that led to elevated cod M after 1978 (Bousquet et al. 2010, Swain et al. 2011). Cod $M^{(O)}$ for ages 2–4 was estimated as a single, time-invariant parameter. While some degree of interannual variability in juvenile cod survival can be expected, significant correlation between juvenile survival and recruitment can arise when both quantities are allowed to vary over time, causing estimates to be unreliable. Underlying shifts in juvenile survival will therefore be interpreted by the model as changes in recruitment (i.e. the model will account for a spike in juvenile mortality by estimating lower than expected recruitment). Herring $M^{(O)}$ was estimated as separate random walks for ages 2–6 and ages 7–11+. To increase model tractability, we assumed herring $M^{(O)}$ in the first time step at 0.4 yr^{-1} for all ages.

We explicitly modelled 3 predation links: (1) grey seal predation on cod aged 5–12+ yr (hereafter '5+ cod'), (2) grey seal predation on all ages of herring,

and (3) cod predation on all ages of herring. We did not consider a reciprocal effect of prey on predators, such as increased predator M when consumption rates were low, as cod and grey seals are largely generalist predators and thus decreased predation on one species may be compensated by increased predation on other species in the ecosystem. Additionally, the grey seal population has demonstrated an ability to continue expanding despite low abundance of cod, herring, and mackerel across their range.

For each prey species ($i > 1$), the instantaneous predation mortality rate ($M^{(P)}$) was calculated as:

$$M_{i,a,t}^{(P)} = \sum_j \sum_y \sum_b N_{j,y,b,t} m_{j,y,b,i,a,t}^{(P)} \quad (5)$$

where j , y , and b are index predator species, predator subpopulation, and predator age, respectively, while $m_{j,y,b,i,a,t}^{(P)}$ represents the annual instantaneous mortality rate imposed on prey i of age a by an individual predator j,y at age b . We calculated $m^{(P)}$ as:

$$m_{j,y,b,i,a,t}^{(P)} = S_{j,i,a}^{(P)} f_{j,y} \varphi_{j,y,i,t} \rho_{j,b} \quad (6)$$

where $S_{j,i,a}^{(P)}$ is the age-selectivity of the prey i to predator j ($0 \leq S^{(P)} \leq 1$), f is the proportion of each year that the range of predator j,y overlaps with the range of prey, φ is the maximum per capita rate (across predator ages) at which predator j,y consumes prey i , and ρ is the relative consumption-at-age for each predator ($0 < \rho \leq 1$). We included ρ to account for the different rates at which predators of different ages consume prey (i.e. older/larger predators consume more prey than younger/smaller predators). All 5+ cod were assumed to be fully vulnerable to seal predation (i.e. $S_{j=1,i=2,a}^{(P)}$ for $\alpha \geq 5$). We did not explicitly model predation on younger cod ($S_{j=1,i=2,a}^{(P)}$ for $\alpha < 5$), so predation mortality for these ages is implicitly subsumed into $M^{(O)}$. While grey seals do consume younger Atlantic cod, there is no evidence that natural mortality of younger cod increased in the 1990s and 2000s (Swain et al. 2015b), perhaps due to reduced predation by collapsed piscivorous fishes offsetting increased seal predation (Savenkoff et al. 2007, Benoît & Swain 2008). The age-selectivity of herring to seal predation was assumed to be a logistic function of herring age, i.e.:

$$S_{j=1,i=3,a}^{(P)} = \left[1 + \exp \left(\frac{-\log(19)(a-b^{50})}{b^{95}-b^{50}} \right) \right]^{-1} \quad (7)$$

where $b^{50\%}$ and $b^{95\%}$ are estimated parameters representing the herring ages at which selectivity to herring predation is 0.50 and 0.95, respectively. The age-selectivity of herring to cod predation was assumed to be proportional to a gamma distribution, i.e.:

$$S_{j=2,i=3,a}^{(P)} \propto \frac{1}{\Gamma(k)\theta^k} \theta^{k-1} \exp\left(-\frac{a}{\theta}\right) \quad (8)$$

where k and θ are estimated parameters representing the shape and scale, respectively, of the selectivity function. Γ represents the gamma function. We chose these distributions after initial trials using a range of selectivity functions suggested that herring selectivity to seal predation was a monotonically increasing function of age, whereas selectivity to cod predation was dome-shaped. We assumed that cod and herring had complete spatial overlap throughout the year, while spatial overlap between seals and both fish species was set equal to the mean of the monthly proportion of time that satellite-tracked seals in each herd and for each sex spent near cod and herring (Table 1). Per capita predation rates were assumed to vary as a temporal random walk with shared annual deviations between predator subpopulations (e.g. Cook & Trijoulet 2016), i.e.:

$$\varphi_{j,y,i,t} = \varphi_{j,y,i,t-1} \exp\left(\varepsilon_{j,i,t}^{(\varphi)}\right) \quad (9)$$

Relative consumption (ρ) was modelled as a logistic function of predator age:

$$\rho_{j,y,b} = \left[1 + \exp \left(\frac{-\log(19)(b-\rho_{j,y}^{50})}{\rho_{j,y}^{95}-\rho_{j,y}^{50}} \right) \right]^{-1} \quad (10)$$

where $\rho_{j,y}^{50\%}$ and $\rho_{j,y}^{95\%}$ are estimated parameters representing the ages at which consumption reaches 50 and 95% of peak levels, respectively.

2.2.1.3. Total consumption. Annual per capita consumption (in numbers) by predator j (of subpopulation y and age b) of prey i (of age a) was calculated from the Baranov catch equation as:

$$\hat{c}_{j,y,b,i,x,a,t}^{(N)} = \frac{m_{j,y,b,i,a,t}^{(P)}}{Z_{i,x,a,t}} N_{i,x,a,t} \left(1 - \exp(-Z_{i,x,a,t}) \right) \quad (11)$$

We scaled per capita consumption by prey weight-at-age and summed over prey subpopulations to obtain the total consumption in weight per predator for each predator/prey pair:

$$\hat{c}_{j,y,b,i,a,t} = \sum_x \hat{c}_{j,y,b,i,x,a,t}^{(N)} w_{i,x,a,t} \quad (12)$$

where $w_{i,x,a,t}$ is the annual weight-at-age for each prey subpopulation.

The age composition of consumed prey was calculated by converting total consumed numbers-at-age to proportions-at-age:

$$\hat{u}_{j,a,t}^{(P)} = \frac{\sum_y \sum_b \sum_x \hat{c}_{j,y,b,i,x,a,t}^{(N)} N_{j,y,b,t}}{\sum_a \sum_y \sum_b \sum_x \hat{c}_{j,y,b,i,x,a,t}^{(N)} N_{j,y,b,t}} \quad (13)$$

2.2.1.4. *Catch.* The abundance of cod or herring that were vulnerable to the commercial fishery ($g = 1$) or surveys ($g > 1$) was calculated as:

$$V_{g,i,x,a,t} = N_{i,x,a,t} S_{g,i,x,a,t}^{(F)} \exp\left(-d_{g,i,x} Z_{i,x,a,t}\right) \quad (14)$$

where $S^{(F)}$ is age-selectivity of the fishery and d is the timing of the fishery (expressed as the approximate ordinal date of the fishery divided by 365). We estimated F for each fish species and subpopulation by iteratively solving the Baranov catch equation:

$$C_{i,x,t}^{(F)} = \sum_a \frac{F_{i,x,t}}{Z_{i,x,a,t}} V_{g=1,i,x,a,t} w_{g=1,i,x,a,t}^{(F)} \left(1 - \exp\left(-Z_{i,x,a,t}\right)\right) \quad (15)$$

For seals, we separately solved the Baranov catch equation for YOY and age 1+ seals. All 1+ seals were assumed to have equal selectivity.

2.2.1.5. *Predicted indices and age composition.* We calculated model-predicted cod and herring biomass indices ($g > 1$) as the product of vulnerable biomass and fishery/survey catchability (q):

$$\hat{I}_{g,i,t} = q_{g,i,x,t} \sum_a V_{g,i,x,a,t} w_{g,i,x,a,t}^{(F)} \quad (16)$$

We assumed that q was time-invariant for all cod surveys. For the herring gillnet CPUE indices, q varied as a random walk to allow for changes in q that are expected to arise from stock and fishery changes. For instance, q is expected to increase as a stock declines and occupies smaller areas (Winters & Wheeler 1985), though time/area closures implemented since 2010 are expected to decrease q (Swain 2016). Cod and herring age composition was calculated by converting vulnerable numbers-at-age to proportions-at-age, i.e.:

$$\hat{u}_{g,ix,a,t}^{(F)} = \frac{V_{g,i,x,a,t}}{\sum_a V_{g,i,x,a,t}} \quad (17)$$

2.2.1.6. *Grey seal foraging effort.* The total abundance of grey seals near sGSL cod, termed 'foraging effort', was summarized as the product of seal abundance and the spatiotemporal overlap between seals and cod:

$$E_{y,t} = f_{j=1,y} \sum_a N_{i=1,y,a,t} \quad (18)$$

2.2.2. Model fitting

Cod and herring biomass indices were assumed to arise from lognormal distributions, while age proportions of cod and herring in fishery and survey catches were assumed to arise from logistic-normal distributions (Schnute & Haigh 2007, Francis 2014). Process errors in fish recruitment, prey consumption, and her-

ring catchability were assumed to arise from zero-mean lognormal distributions. Grey seal pup production observations were also assumed to arise from lognormal distributions, while the number of pregnancies were assumed to arise from age-specific binomial distributions.

Stock assessment models with predation may be fit to total estimates of prey consumption as a means of bounding the model consumption within a plausible range (e.g. Cook et al. 2015). Without priors or external information about consumption, predation mortality may absorb statistical noise and produce biologically impossible estimates of prey consumption. Total prey consumption has previously been estimated for the species under consideration by first calculating per capita consumption and then scaling by predator abundance as estimated by single-species population models (e.g. Benoît & Rail 2016). We could not incorporate these estimates into the model, as the predator abundance estimates were based on the same data that are used in our analysis. Instead, we fit the model to external per capita consumption-at-age estimates (c), which were based on estimated bioenergetic consumption (Table 1), the spatiotemporal overlap between predator and prey species, and the proportional contribution of prey to predator diets (Supplement 2). For each predator subpopulation and each associated prey species, we assumed a lognormal distribution for prey consumption at predator age b , centred on c , i.e.:

$$\ln \sum_a \hat{c}_{j,y,b,i,a,t} \sim N\left(\ln c_{j,y,b,i,t}, \sigma_{c,j}^2\right) \quad (19)$$

We chose $\sigma_{c,j} = 1$ for seal predation based on a bootstrap analysis in which 10 000 samples of c were calculated using proportional diet contributions that were randomly drawn from beta distributions centred on the mean estimated diet contribution of each species across months (cod: 0.26, herring: 0.12) and a CV of 1.5. This approach allows for the contribution of species to the grey seal diet to vary over time but remain within biologically plausible ranges. In contrast, we more tightly constrained cod consumption ($\sigma_{c,j} = 0.1$), in part because a nonstationary diet contribution was assumed in the estimation of c , and in part because initial trials revealed that large values of $\sigma_{c,j}$ produced unreliable output. Sensitivity analyses are provided in Supplement 3 to show how model outputs respond to alternative values of $\sigma_{c,j}$.

We also fit the model to the observed age-composition of herring in seal and cod diets from diet studies. The subpopulations-of-origin of herring in the diet composition analyses were unknown, so we converted the entire set of length frequencies from these

studies into a separate set of age frequencies for each subpopulation using age–length keys. We then aggregated age frequencies across subpopulations to create a single set of age frequencies for each predator. We assumed a logistic-normal likelihood for the age-composition of herring in predator diets. All data sets used in model fitting or in the definition of prior distributions are summarized in Table 2.

The model was implemented using the 'Template Model Builder' (Kristensen et al. 2016) package within R version 3.6.3 (R Core Team 2019). Model estimates and uncertainty were based on Hamiltonian Monte Carlo (HMC) samples from the joint posterior distribution. We ran 4 HMC chains for 2000 iterations each, discarding the first half of each chain as a warm-up. Starting values for each chain were randomly sampled based on maximum likelihood estimates and associated standard errors. We monitored convergence using the potential scale reduction factor on rank-normalized split chains (\hat{R}) and the effective sample size of the rank-normalized draws (Vehtari et al. 2021).

2.2.3. Extirpation risk projections

To evaluate the effects of seal and herring abundance changes on sGSL ecosystem dynamics, we projected the model forward in time (50 yr) under a range

of seal and herring harvest strategies. For each posterior sample, we post-fitted functional responses and stock-recruitment functions, then projected the model based on the posterior sample, the post-fitted structural forms, and a harvest plan for seals and herring. We post-fitted functional response and stock–recruitment relationships to model estimates rather than estimating them within the model to avoid imposing structure on relationships for which the data are typically uninformative (Cook & Trijoulet 2016). For cod and each seal subpopulation, we fitted the relationship between prey density and the consumption rate by predators with a functional response (dropping predator species and subpopulation indices for simplification):

$$\varphi_{i,t} = \frac{\eta_i B_{i,t}^{\lambda_i - 1}}{1 + \sum_j (\eta_j h_j B_{j,t}^{\lambda_j})} \quad (20)$$

where $\varphi_{i,z}$ is the annual consumption rate of prey species i per unit of prey i biomass, $B_{i,t}$ represents the biomass of prey i (summed across subpopulations) available to the predator, η_i represents the rate at which the predator encounters prey i , h_i represents the time the predator spends consuming prey i (the 'handling time'), and λ_i determines the shape of the functional response. This equation describes a multi-species functional response for seals and a single-species response for cod. The biomass of prey species not explicitly included in our analysis is implicitly as-

Table 2. Summary of data used in the population model. AI: abundance index; RS: reproductive status; BE: bioenergetic estimate; AC: age composition; BI: biomass index; FI: fishery independent; FD: fishery dependent; g : survey index; CPUE: catch per unit effort. (–) in the 'Ages (Yr)' column indicates that the data is not age-specific with respect to the predator. (–) in the ' g ' column means the data is not assignable to a specific g

Source	Data type	Ages (yr)	Years	g	Comment
Grey seal					
Pup production survey	AI	0	1971–2016	1,2	Herd-specific (1 = Shelf, 2 = Gulf)
Reproductive survey	RS	4–8+	1982–2015	–	Gulf samples only
Per capita consumption of cod and herring	BE	0–30	1971–2018	–	Year-invariant (see Supplement 2)
Herring-at-age in diet	AC	–	1986–2011	–	Year-, herd-, and age-invariant
Atlantic cod					
Commercial fishery	Catch, AC	2–12	1971–2018	1	FD
Bottom trawl (RV) survey	BI, AC	2–11	1971–2018 ^a	2	FI
Mobile sentinel (MS) survey	BI, AC	2–11	2003–2018	3	FI
Longline (LL) sentinel survey	BI, AC	5–11	1995–2017	4	FI
Per capita consumption of herring	BE	2–12	1978–2018	–	See Supplement 2
Herring-at-age in diet	AC	–	1990–2013	–	
Atlantic herring					
Commercial fishery	Catch, AC	2–11	1971–2018	1	FD, stock-specific
Gillnet CPUE	BI, AC	4–10	1986–2018 ^b	2	FD, stock-specific
Acoustic survey	BI, AC	4–8	1994–2017	3	FI, spring
Assessment biomass series	BI, AC	4–11	1971–1977	4	Fall aggregated across subpops

^aNo data in 2003; ^bSpring data start in 1990

sumed to be constant over time. This assumption, which was also made by Neuenhoff et al. (2019), is supported for cod by a mass-balance ecosystem model for the sGSL, which estimated that the biomass of other prey, defined as pelagic fish and demersal fish other than large cod, before and after the collapse was approximately the same (19.7 t km⁻² in the mid-1980s vs. 19.6 t km⁻² in the mid-1990s; Savenkoff et al. 2007).

We characterized the cod stock–recruitment relationship in the projections using an extended Ricker function that accounted for a herring effect on pre-recruit cod (Minto & Worm 2012):

$$N_{i=2,x=1,a=2,t} = \hat{R}_t = \beta_0 C_{t-2} \exp\left(-\beta_C C_{t-2} - \beta_H \sum_x H_{x,t-2}\right) \quad (21)$$

where C_t and $H_{x,t}$ are the spawning biomasses of cod and herring, respectively, in year t , β_0 and β_C are standard Ricker parameters representing fecundity and density-dependence, respectively, and β_H represents the strength of herring predation on or competition with pre-recruit cod. For each posterior sample, we fitted the full extended Ricker model, as well as a standard Ricker version of the extended Ricker in which the herring effect (β_H) was fixed at 0. Ricker models were fitted to posterior estimates of cod recruitment (R) assuming lognormal errors, i.e.:

$$\ln R_t = \ln \hat{R}_t + \varepsilon_t \quad (22)$$

The residuals ε were either independent and identically distributed (*iid*; $\varepsilon_t \sim N(0, \sigma_\varepsilon^2)$) or AR(1) auto-correlated ($\varepsilon_t \sim N(\phi\varepsilon_{t-1}, \sigma_\varepsilon^2)$), where the variance σ_ε^2 was estimated. We used Durbin-Watson tests to determine whether projections should be based on either *iid* or AR(1) models. We similarly projected herring recruitment for each subpopulation using a standard Ricker function, though we considered Beverton-Holt recruitment as a sensitivity analysis (Supplement 4).

We projected the model under all combinations of the following 4 controls:

- (1) annual seal quota (thousands of seals): (0, 1, 2, ..., 20)
- (2) proportion of quota allocated to YOY seals: (0.5, 0.75)
- (3) length of seal harvest (yr): (5, 10)
- (4) constant herring F (yr⁻¹): (0, 0.1, 0.2, ..., 1.0)

To simulate the effect of a short-term increase in seal harvest, the seal quota was taken only in the initial projection years (i.e. quota from a 5 yr harvest was taken only in the first 5 yr of the projection). Additionally, the quota was only taken from the Gulf herd, as these seals spend significantly more time foraging near sGSL cod and herring than Shelf seals. The

additional quota in initial years and the targeting of seals in the sGSL are consistent with an adaptive management approach proposed a decade ago as part of a review of grey seal impacts in eastern Canada (DFO 2011, Hammill & Swain 2011). Annual Shelf harvest levels in the projections, as well as annual Gulf harvest levels after the initial harvest period, were randomly sampled from historical harvest observations. Seal harvests were applied to sex- and age-classes in the projections, as in the historical model, in proportion to the relative abundance of those classes. We assumed no commercial fishery landings of cod in the projections consistent with the moratorium on directed fishing in place for the stock since 2009. The random walks in recruitment and consumption in the model were replaced by the post-fitted recruitment and consumption relationships. Specifically, Eq. (9) was replaced by Eq. (20), while Eq. (2) was replaced by Eq. (21) for cod and Eq. (C.1) in Supplement 4 for herring.

To evaluate cod recovery potential, we compared cod spawning stock biomass (SSB) at the end of the projection period with a limit reference point (LRP) of 80 kt, which was based on the lowest SSB from which the stock has recovered (Chouinard et al. 2003).

3. RESULTS

3.1. Historical dynamics

Overall, the model fitted the seal pup production and reproductive data, as well as cod and herring fishery and survey catch-at-age, about as closely as accepted assessment models for those species, and we did not detect issues with convergence (Fig. 3; Supplement 5). Estimated seal abundance increased from approximately 15 000 in 1971 to 457 000 in 2018, corresponding to a rise in foraging effort in the sGSL from approximately 6000 seal-years to nearly 44 000 seal-years over that time frame (Fig. 4a). Foraging effort in the sGSL grew more slowly than overall seal abundance because overall abundance was primarily driven by Shelf seals who spend relatively less time foraging in the sGSL. Estimated predation M for 5+ cod grew from 0.02 yr⁻¹ in the early 1980s to 0.95 yr⁻¹ in 2018 (Fig. 4b). Estimated other M for 5+ cod rose from 0.2 yr⁻¹ in the 1970s to 0.40 yr⁻¹ in the early 1990s and has since declined to 0.15 yr⁻¹ (Fig. 4b). Estimated cod M for ages 2–4 was 0.57 yr⁻¹. Estimated cod fishing mortality ranged from 0.42 to 0.53 yr⁻¹ between 1972 and 1976, before declining to around 0.20 yr⁻¹ in the late 1970s and early 1980s. Estimated F rose steadily

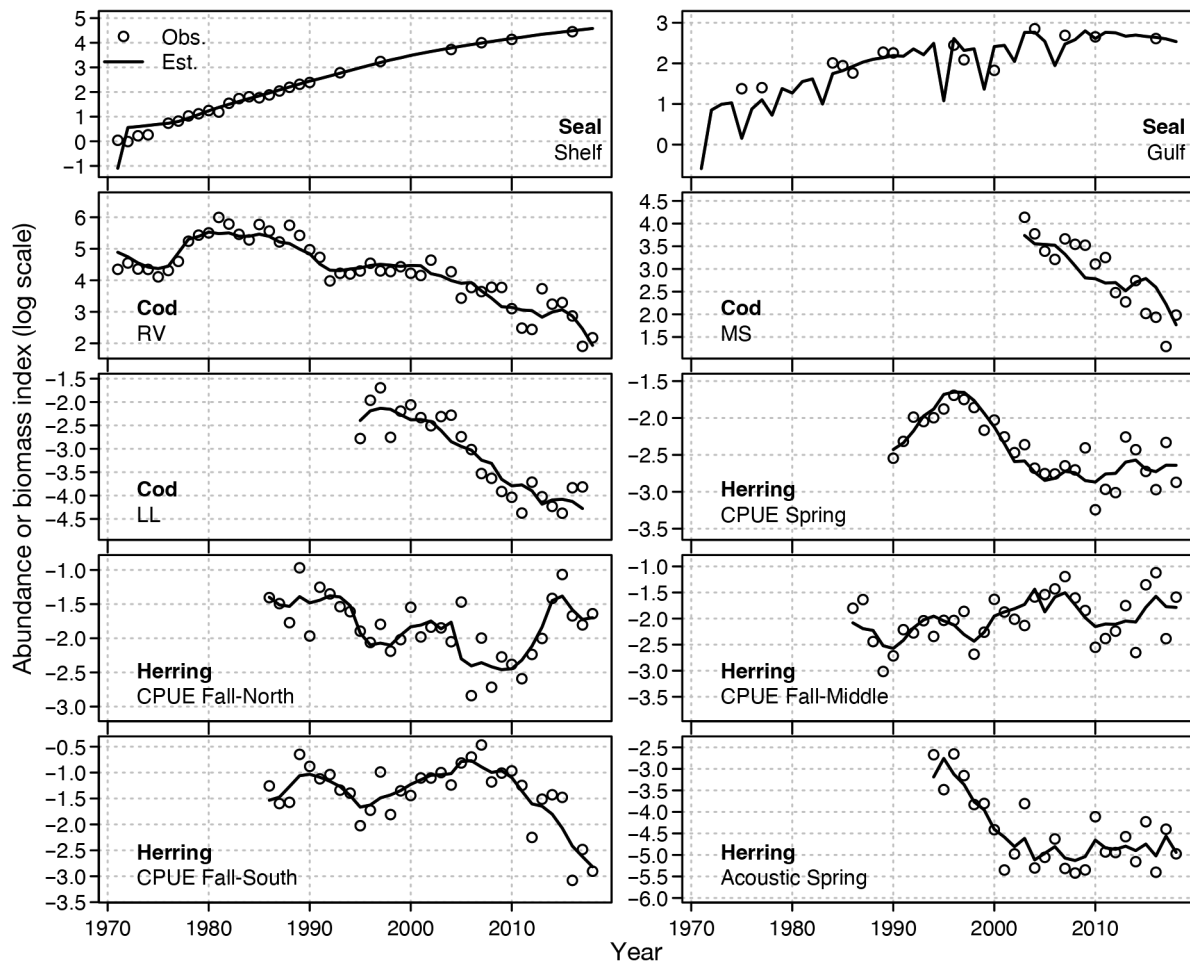


Fig. 3. Model fits (posterior modes; lines) to observed abundance or biomass indices (circles) for each modelled species. The abundance index represents pup production for grey seals and survey-selected biomass for cod and herring. Note that fits to the 1971–1977 assessment model biomass estimates are not shown. RV: bottom-trawl research vessel; MS: mobile sentinel; LL: longline; CPUE: catch per unit effort

throughout the 1980s and exceeded 0.50 yr^{-1} in the early 1990s as the cod population was collapsing (Fig. 4b). Fishing was a minor source of cod mortality from 1993 to 2008 and was negligible thereafter (Fig. 4b). Estimated annual cod consumption by seals rose from less than 3 kt in the early 1970s to 27 kt in the mid-2000s and subsequently declined to 9 kt (Fig. 4c). Estimated annual cod consumption by seals has exceeded cod fishery landings since 1993 (Fig. 4c). Estimated cod SSB grew rapidly in the late 1970s and remained high until the mid-1980s before declining to low levels (Fig. 4d). Cod SSB has declined precipitously in recent years, falling from 31 kt in 2016 to 14 kt in 2018. Estimated cod recruitment has steadily declined from nearly 1.1 billion in the early 1980s to less than 45 million in recent years (Fig. 4e). The estimated cod recruitment rate (age 2 abundance divided by SSB 2 yr earlier) rose dramatically in the late 1970s to more

than 8000 recruits per tonne of SSB, contributing to the rapid recovery of cod during this time (Fig. 4f). The cod recruitment rate doubled from the early 1990s to the early 2010s but has since declined (Fig. 4f).

Seal and cod predation represented moderate sources of mortality for herring at various periods. Seals preferentially selected for larger herring, while cod selected for moderately sized (ages 3–7) herring (Fig. 5). Seal predation mortality for herring rose steadily from less than 0.04 yr^{-1} in the 1970s to more than 0.20 yr^{-1} in recent years (Fig. 6a). Cod predation was an appreciable source of herring mortality in the mid- to late-1980s but has since declined to negligible levels (Fig. 6a). Other herring M for ages 2–6 increased steadily from 0.43 yr^{-1} in the mid-1980s to more than 0.65 yr^{-1} in recent years, while other M for ages 7–11+ ranged between 0.17 and 0.21 yr^{-1} over that period (Fig. 6b). Fishery landings of herring were

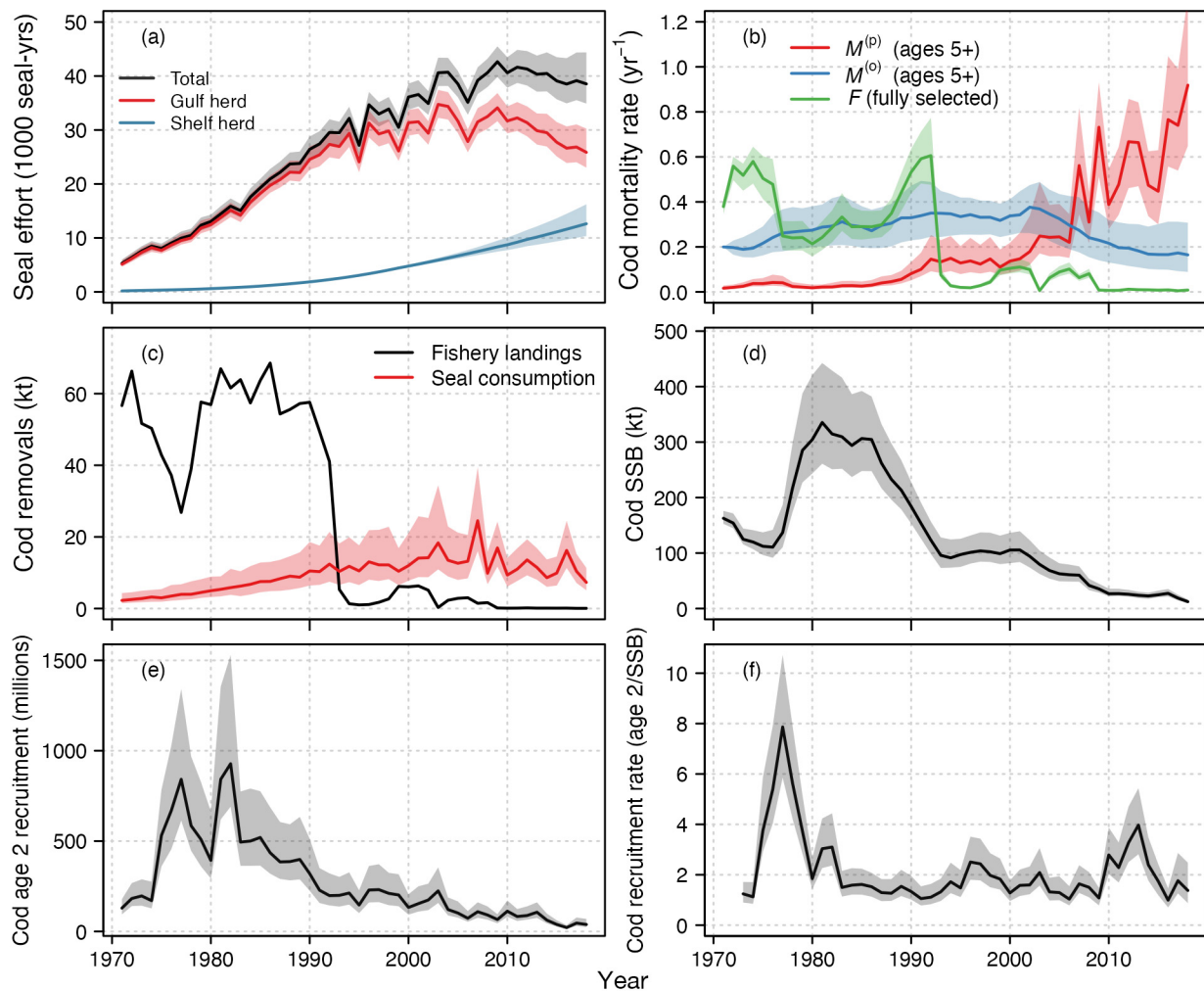


Fig. 4. Model estimates of (a) grey seal foraging effort in the sGSL, (b) instantaneous cod mortality rates, (c) cod removals from fisheries (observed) and seal consumption (estimated), (d) cod spawning stock biomass (SSB) on 1 January, (e) cod recruitment, and (f) cod recruits per spawner. Lines represent posterior modes (except for fishery landings in (c), which were observed) and shaded regions represent central 95% uncertainty intervals

generally larger than estimated seal and cod consumption in all years except for the mid-1980s during the peak years of cod predation (Fig. 6c). Herring F for 2010–2018 was lower for the Spring subpopulation (0.27 yr^{-1}) than for the Fall subpopulations (North: 0.71 yr^{-1} ; Middle: 0.48 yr^{-1} ; South 0.68 yr^{-1}). Total herring SSB rapidly increased from 120 kt in 1977 to more than 375 kt in 2006 before gradually declining to less than 200 kt in recent years (Fig. 6d). Rapid cod population growth in the late 1970s overlapped with a period of low and declining herring SSB.

The estimated predation rate imposed on age 5+ cod per seal was largely steady until the 2000s, at which point it increased sharply (Fig. 7). The predation rate imposed on herring per seal declined steeply in the early 1980s and has increased steadily since then

(Fig. 7). Functional responses fit the model estimates of prey consumption by seals closely and exhibited strongly hyperbolic patterns consistent with a Type II functional response (Fig. 7). The relationship between cod predation and herring biomass was less clear; the shape parameter was greater than 1 (indicating a sigmoidal or Type III functional response) for 90% of posterior samples, while a hyperbolic functional response emerged in other samples (Supplement 5).

Durbin-Watson tests for the *iid* stock–recruitment models indicated the presence of lag-1 autocorrelation in residuals, so inference was based on the AR(1) models. Cod recruitment in the extended Ricker AR(1) model was negatively associated with herring biomass. For instance, an increase in herring SSB from the mean estimated level (256 kt) to the maxi-

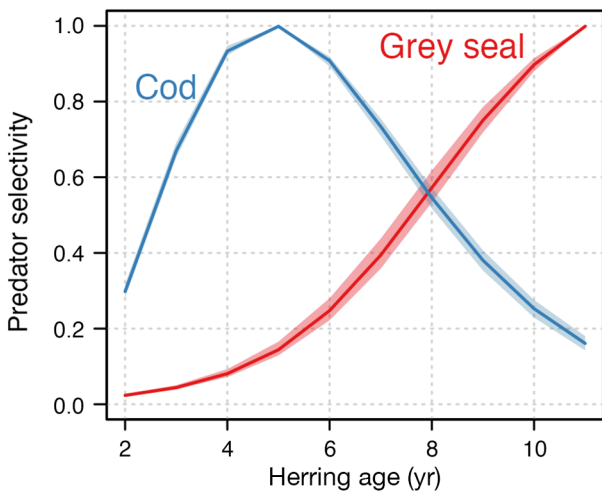


Fig. 5. Estimated selectivity-at-age functions for grey seal (red) and cod (blue) predation on herring. Lines represent posterior modes, while shaded regions represent central 95% posterior intervals

imum estimated level 365 kt) corresponded to a 30% decrease in cod recruitment in the extended Ricker AR(1) model, while a decrease in herring SSB from the mean level to the minimum level (122 kt) corresponded to a 57% increase in cod recruitment (Fig. 8).

3.2. Projections

Cod failed to recover in nearly all projection scenarios in which annual seal quotas were below 5000 seals (Fig. 9). Five-year harvests were less effective than 10 yr harvests at facilitating cod recovery, as 5 yr harvests required extremely high quotas (e.g. >15000 seals) and required a sufficiently high proportion of age 1+ seals to be targeted, to adequately reduce grey seal predation on cod (Fig. 9). There was a positive relationship between herring F and cod recovery; cod were generally unlikely to recover when herring

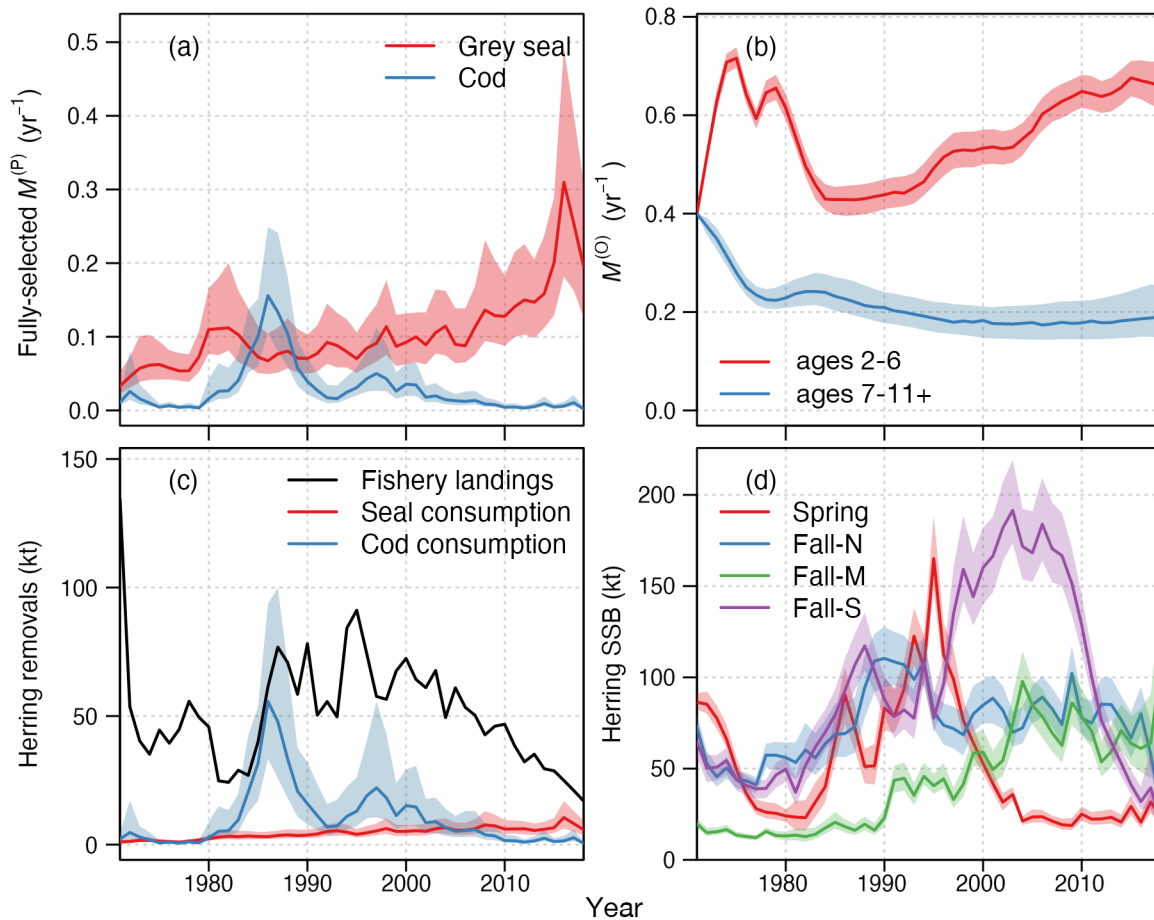


Fig. 6. Model estimates of herring dynamics including (a) fully selected predation mortality imposed by grey seals and cod, (b) natural mortality from sources other than predation, (c) removals by fisheries (observed) and predation (estimated), and (d) spawning stock biomass (SSB) on 1 January. Lines represent posterior modes (except for fishery landings in (c), which were observed) and shaded regions represent central 95% uncertainty intervals

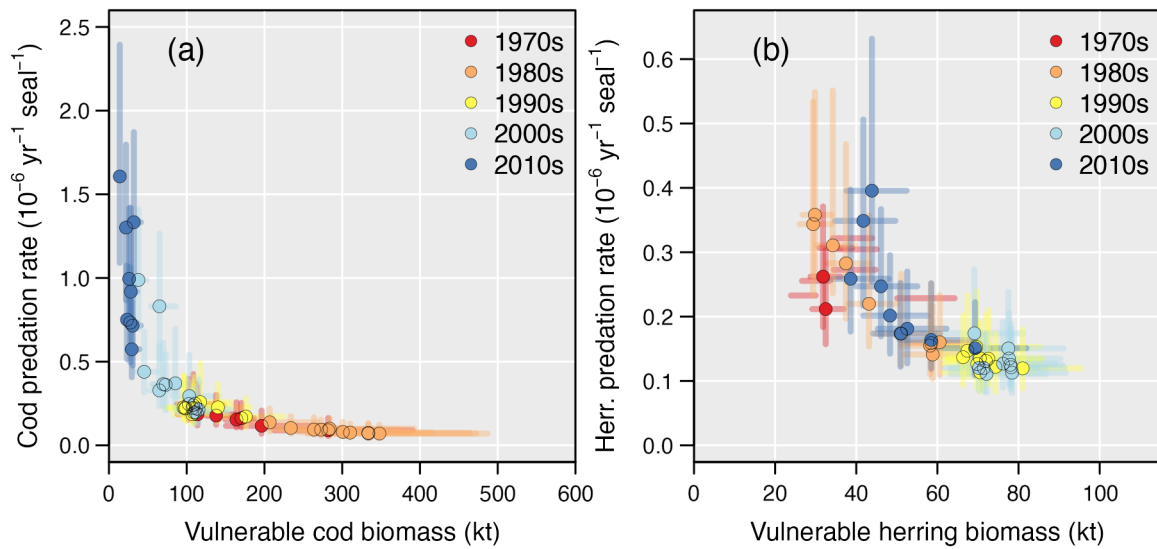


Fig. 7. Model estimates of per capita consumption by male grey seals from the Shelf herd on (a) cod and (b) herring. Circles represent posterior modes, while vertical and horizontal coloured lines represent central 95% uncertainty intervals. Herring biomass is aggregated across subpopulations

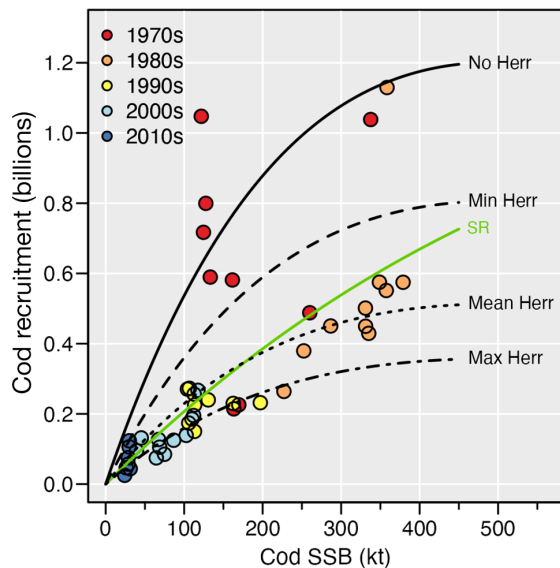


Fig. 8. Posterior modes of cod recruitment and cod spawning stock biomass (SSB; circles), with fitted standard Ricker (green line) and extended Ricker stock–recruitment function under 4 levels of herring SSB (no herring [0 kt], and the minimum [120 kt], mean [256 kt], and maximum [365 kt] model-estimated levels for 1971–2018). Stock–recruitment models were fitted for illustrative purposes (in projections, we fitted a separate stock–recruitment function to each posterior sample)

F was less than 0.2 yr^{-1} (Fig. 9). Targeting higher proportions of YOY seals was relatively ineffective in decreasing seal predation on cod, as quotas for YOY seals quickly exceeded the number of pups being born, leaving much of the quota unfilled.

Even in the most optimistic cod projections, cod SSB continued to decline for 10 yr and did not surpass the LRP for more than 20 yr. We consider harvest strategies that set an annual quota of 12 000 seals targeting 50% YOY for either 5 or 10 yr, with either low (0.1 yr^{-1}) or high (0.6 yr^{-1}) herring F , as this set of strategies produces a range of outcomes for each species that can be generalized (Fig. 10). Cod recovery was only likely under longer (10 yr) seal harvests (Fig. 10c) that rapidly removed the entire Gulf herd (Fig. 9a). The Gulf herd quickly recovered after shorter (5 yr) seal harvests in which it was not driven to zero abundance (Fig. 10a), resulting in predation mortality rates that the still-collapsed cod stock was unable to withstand (Fig. 10d). Following 5 yr seal harvests, seals still imposed high predation mortality rates despite reduced abundance due to the hyperbolic functional response, which specifies exponentially increasing mortality with declining prey abundance. Seal foraging effort increased in years following 10 yr seal harvests due to the growing Scotian Shelf herd; however, it took more than 50 yr for seal foraging effort in the sGSL to recover to pre-harvest levels (Fig. 10b), by which point cod had sufficiently recovered to levels that could sustain seal predation (Fig. 10c). Seal harvests that enabled cod recovery were negative for herring if herring abundance was low, as increased predation from recovered cod outweighed reduced predation from seals (Fig. 10e). In contrast, reductions in seal predation slightly decreased overall herring mortality when herring biomass was large (Fig. 10e). High herring biomass

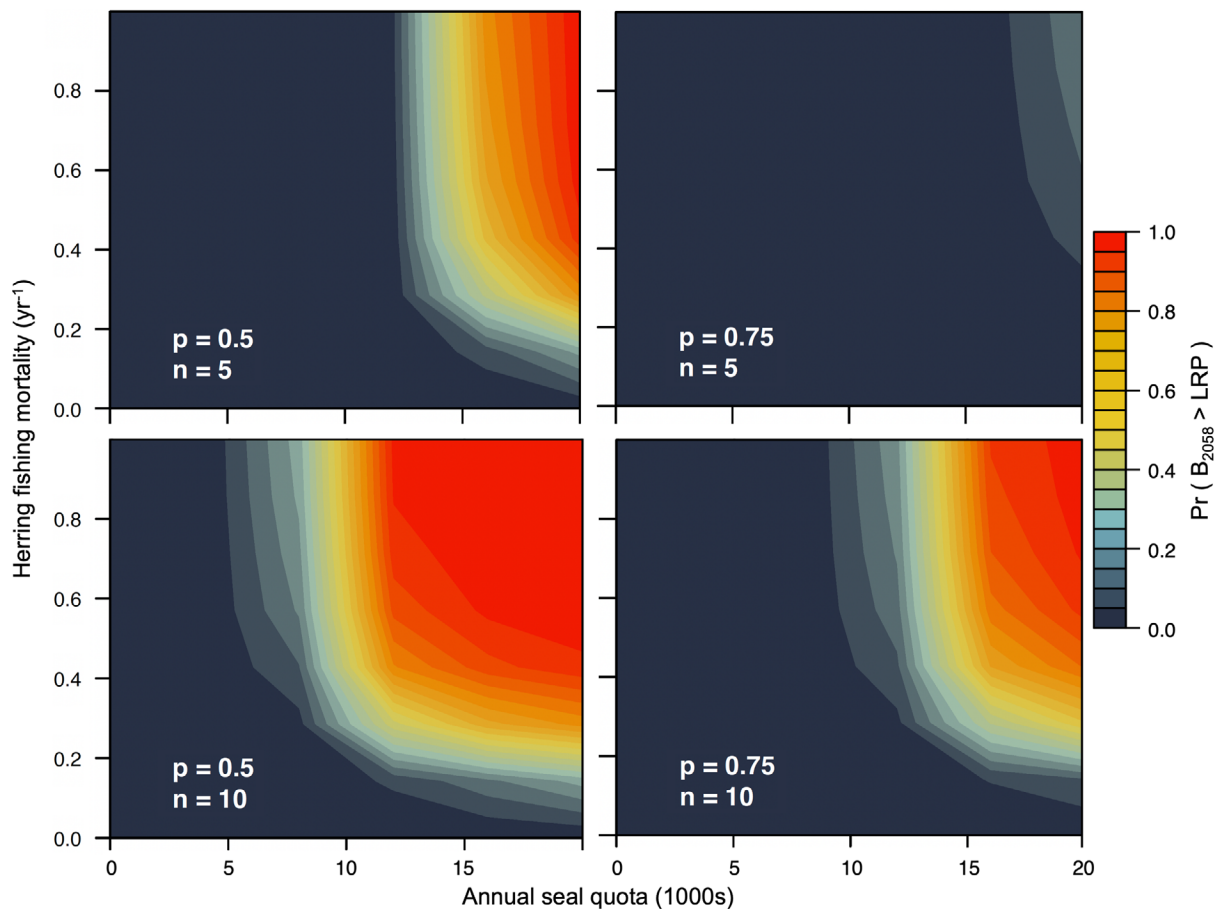


Fig. 9. Probability of cod spawning stock biomass in 2058 exceeding the limit reference point (LRP = 80 kt) given varying levels of seal quota (x-axis) and herring fishing mortality (y-axis), and 4 combinations of the proportion of young-of-year (YOY) seals targeted for removal (p) and the length of the seal harvest period (n ; number of years)

significantly impaired cod productivity (Fig. 10f) and prevented recovery in most samples, regardless of the length of the seal harvest.

Model estimates were relatively insensitive to the choice of consumption prior for seal predation (Supplement 3). Additionally, using Beverton-Holt functions to project herring recruitment instead of Ricker functions had negligible impacts on projections (Supplement 4).

4. DISCUSSION

Many studies have linked reduced survival of cod in the sGSL to increases in seal predation (e.g. Benoit et al. 2011, Swain et al. 2015a, Neuenhoff et al. 2019). In this paper, we analysed a triangular food web of seals, cod, and herring in the sGSL and found that cod failed to recover in the absence of grey seal abundance reductions. The seal quotas required to

sufficiently reduce predation mortality on cod to allow for the chance of cod survival were significantly higher than current removal levels and would likely collapse the grey seal herd in the Gulf of St. Lawrence. Herring biomass had a negative relationship with cod recruitment; however, seal predation accounted for a smaller proportion of herring mortality than fishing or other sources of natural mortality, so herring did not increase greatly in abundance in response to grey seal reductions. Additionally, while our analysis suggests that cod may rebound in response to sufficiently severe grey seal reductions, cod spawning biomass continued to decline for about a decade in these scenarios to less than 1500 t and was not projected to be at the LRP for several decades. During this period, cod would be vulnerable to extirpation by environmental stochasticity and/or processes not captured by our model.

Grey seal impacts on sGSL cod were last evaluated by Neuenhoff et al. (2019), who found that the extir-

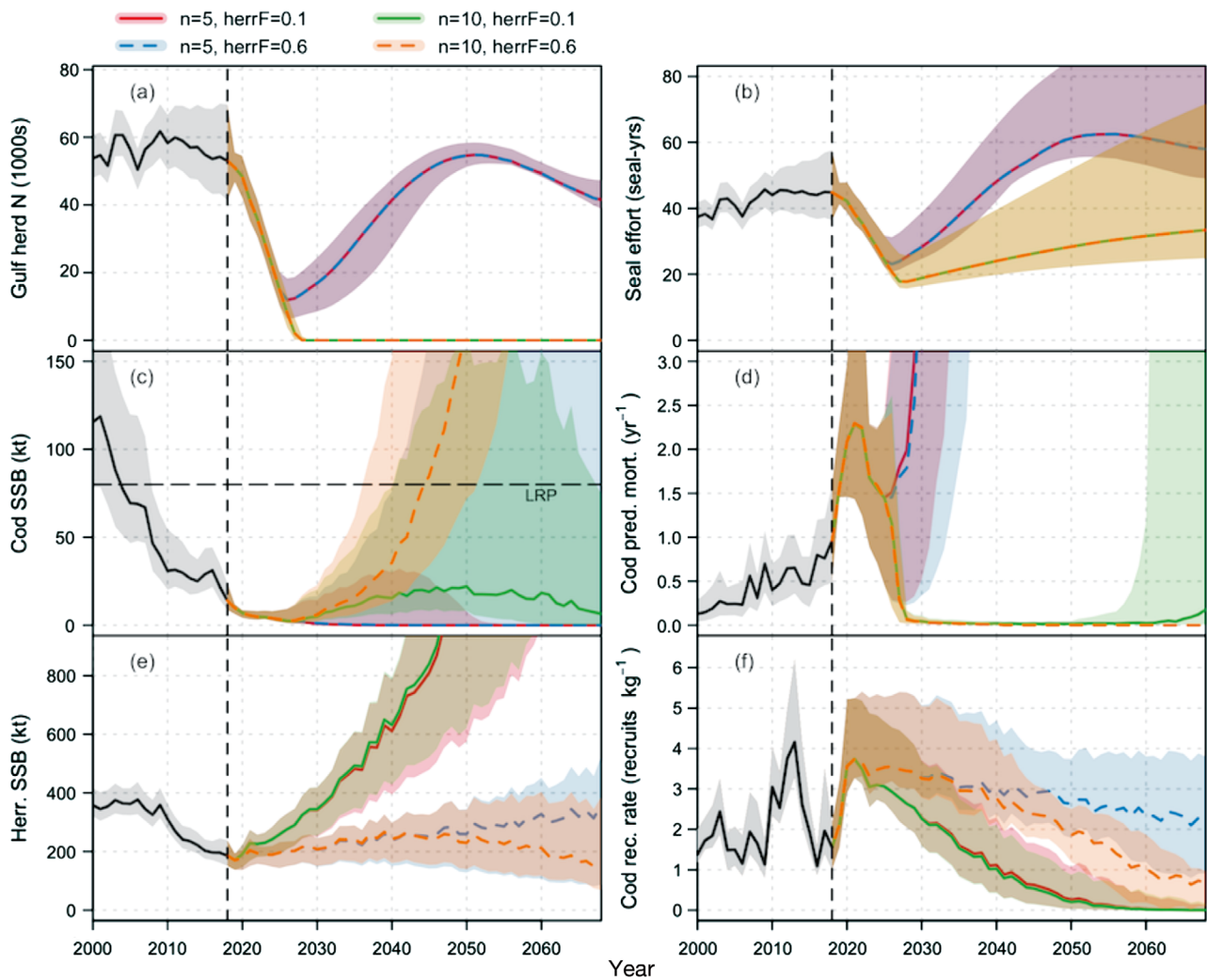


Fig. 10. Model projections with annual quotas of 12 000 seals targeting 50% YOY under 4 combinations of seal harvest period (n ; years) and herring fishing mortality ($herrF$; yr^{-1}), including (a) Gulf herd abundance, (b) seal foraging effort, (c) cod spawning stock biomass, (d) cod predation mortality, (e) herring spawning stock biomass, and (f) cod recruitment rate. Lines represent posterior modes while shaded regions indicate the central 95% uncertainty interval. Black lines and grey shaded regions represent historical estimates, while coloured lines and shaded regions represent projections. SSB: spawning stock biomass; LRP: limit reference point (80 kt)

pation of sGSL cod was likely without a strong and rapid reduction in seal abundance ($E < 27\,000$ seal-years by 2024). In comparison to Neuenhoff et al. (2019), our analysis (1) added 8 yr of cod removals in fisheries directed to other stocks and survey catch-at-age data that indicated further population decline (e.g. the cod RV biomass index fell by 60% between 2010 and 2018), (2) incorporated an updated grey seal population dynamics model with new pup production observations in 2016 and several years of new reproductive data (Rossi et al. 2021), rather than simply fitting to output from the seal assessment, (3) incorporated herring dynamics, and (4) estimated parameters for all species under consideration in a single inte-

grated framework. Adding the 2016 Gulf grey seal pup production observation to the model changed the perception of the Gulf population from one that was growing to one that had reached its carrying capacity and stabilized. The change in Gulf estimates was not a result of changes in assumptions between our model and the previous grey seal assessment model, as similar estimates were obtained when the 2016 pup production observations were added to that assessment model (Hammill et al. 2017a). Our estimates of seal foraging effort varied from those used by Neuenhoff et al. (2019), particularly in the last 2 decades, for which our model predicted that seal foraging effort levelled off around 41 000 seal-years,

while the foraging effort estimates used by Neuenhoff et al. (2019) continued to increase rapidly to nearly 78 000 seal-years in 2014. Despite these differences, as well as differences in modelling approaches, our estimates of cod abundance and predation mortality broadly matched those of Neuenhoff et al. (2019).

Extending the cod–seal analysis of Neuenhoff et al. (2019) to include population models for grey seals and herring allowed us to test hypotheses about the effect of management actions aimed at grey seals or herring on cod recovery in a single framework, avoiding ad hoc procedures for propagating uncertainty from one species to another, and without modelling the entire ecosystem. However, despite these benefits, the model was time-consuming to construct and tune, and still required many simplifying assumptions. In particular, the inclusion of herring in the model was challenging given that herring (1) consisted of multiple subpopulations in the sGSL, (2) had more volatile dynamics than seals or cod, and (3) had noisy and/or conflicting data. Accounting for non-stationarities in herring catchability, selectivity, and natural mortality increased model complexity and run time. Multiple biomass indices existed for each herring subpopulation, and these indices were difficult to reconcile with one another, leading to the exclusion of some fishery-independent herring data. Moreover, the herring data we included for 1971–1977, which are excluded from assessment models (DFO 2018), were less reliable and coarser than the 1978–2018 data; however, we needed to include herring data prior to 1978 since it was important to capture this period when cod rebounded from low abundance. The model estimated that a very large herring population could weaken cod recruitment, but it is difficult to imagine that the herring population would grow to such levels given that M is currently elevated for young herring and the population is actively fished. We also note that our analysis was applied to an ecosystem that has been closely studied for decades, and for which an array of data exists for each species under consideration, including relative abundance-at-age, diet composition, and spatiotemporal predator foraging behaviours. While gaps exist in our data, these types of data may be entirely unavailable for species of concern in other, less studied ecosystems, making our approach difficult to apply to other systems.

Hyperbolic (Type II) functional responses for seal consumption of both cod and herring emerged from multispecies model estimates. This functional response states that per capita consumption of prey increases exponentially as prey abundance declines,

even when prey are at low abundance. These dynamics lead to the extirpation of the target prey species if the abundance of that species falls below some critical threshold. Sigmoidal (Type III) functional responses could emerge at lower prey densities if seals switch to alternative prey. In this case, the primary prey species may be trapped at low abundance in a ‘predator pit’, i.e. the prey species would not be extirpated by predation, since predation mortality decreases at very low prey abundance, but the prey species also fails to recover, since increases in abundance are countered by increased predation mortality. Evidence for prey switching by seals in the literature is mixed; fine spatial and temporal scale analysis of North Sea grey seals diet showed evidence of prey switching at low prey density (Smout et al. 2014), whereas population modelling of grey seal predation on West of Scotland cod suggested that the functional response was hyperbolic (Cook et al. 2015). A hyperbolic functional response was also observed in harbour seal *Phoca vitulina* predation on salmon (Middlemas et al. 2006). While it is difficult to predict if prey switching will occur for grey seals preying on cod or herring in the sGSL, we note that cod are already at extremely low abundance and their aggregative behaviour while overwintering suggests that seals may continue to target cod even as cod abundance further declines. A hyperbolic functional response is also plausible for herring, given that herring aggregate during the winter (Chouinard & Hurlbut 2011), and also while spawning when they are particularly energy dense. Additionally, herring occupy coastal waters where seals are more likely to occur.

We did not model an effect of prey on seal mortality or reproductive success. This assumption is appropriate, as grey seals are highly mobile generalist predators and are therefore less sensitive to changes in the biomass of a specific prey compared to predators that are more stationary and/or have more specialized diets. On the other hand, the seal model in our analysis assumes no exchange between herds and therefore that no recolonization takes place once the Gulf herd reaches zero abundance. This assumption is more tenuous, given the large number of grey seals in adjacent ecosystems and the slowing of growth on Sable Island, suggesting that seals from Sable Island may be seeking less crowded whelping grounds. However, the data needed to characterize grey seal colonization are unavailable.

Several sources of fishery-independent data that were available for herring were excluded from the model. Catch-at-age from experimental gillnets was initially included but was challenging to tractably

model given the time-varying, dome-shaped selectivity patterns evident in those data and which conflicted with other data. We similarly attempted to include acoustic and RV survey catch-at-age for the Fall subpopulation, although these data conflicted mutually and with CPUE. Given these conflicts, we retained the longer-term commercial catch-at-age data instead of the experimental gillnet, Fall acoustic, and RV survey data. The downside to this approach is that fishery-dependent CPUE is known to be hyperstable, i.e. catch rates may remain high as abundance declines since commercial fisheries do not randomly sample the population but instead target high densities. Model population estimates may therefore be biased, particularly for the Fall subpopulations, for which commercial fisheries provide the only source of abundance data.

We aimed for the herring component of the model to match the accepted assessment model for herring as closely as possible, although our inclusion of data for 1971–1977 and our exclusion of some survey data suggest that notable differences between the 2 models are likely. Indeed, the model estimated smaller overall biomass than the assessment model throughout the time series. Additionally, the model estimated an increasing trend in herring M for ages 2–6, with terminal values greater than 0.70 yr^{-1} , whereas the assessment model estimated a fairly stable trend in M for the spring subpopulation and decreasing trends in the fall subpopulations, terminating at 0.05 yr^{-1} . It is not surprising that M estimates for young fish could diverge between the 2 models, as juvenile M is correlated with recruitment and is therefore difficult to reliably estimate. Given that M of 0.05 yr^{-1} is anomalously low for small fish that are eaten by numerous predators (e.g. Benoît & Rail 2016), we considered the multispecies model estimates to be more plausible. Furthermore, we note that the increasing trend for other M in juvenile herring since the early 1980s estimated by the multispecies model is consistent with the increase in predators in the ecosystem that feed on herring of these sizes, notably northern gannets *Morus bassanus*, cormorants (*Phalacrocorax auratus* and *P. carbo*), and bluefin tuna *Thunnus thynnus* (Benoît & Rail 2016). We also note that, while the assessment model includes several sources of fishery-independent data that we excluded from our model, it fits these data poorly (DFO 2022).

A shortcoming of multispecies models is that the appropriate degree of complexity (e.g. number of species or interactions) is unknown *a priori*. Yodzis (1998) demonstrated that ignoring feeding links accounting for more than 10% of consumption by or for

a species in a Benguela ecosystem food web model led to unreliable model estimates. In our model, seal predation accounts for about 80% of cod mortality, and there is no evidence that other suspected cod predators are important drivers of the remaining mortality. Studies of pinniped diets in Atlantic Canada found no evidence of piscivory in the sGSL among harp seals *Phoca groenlandica* and hooded seals *Cystophora cristata* and found harbour seals to be a minor predator of sGSL cod (Hammill & Stenson 2000). Expanding the model to include harbour seals would be difficult, as these seals are not regularly surveyed in Atlantic Canada and their abundance is unknown (e.g. Mosnier et al. 2023). Juvenile white sharks *Carcharodon carcharias* use the sGSL and are piscivorous, but the population is generally considered depleted. Atlantic bluefin tuna use the sGSL (Block et al. 2019), but cod are a minor prey (Pleizier et al. 2012, Varela et al. 2020).

We chose herring to represent pelagic fish in the hypothesized triangular food web for sGSL cod, as age-structured herring data were available; however, indirect effects of seal reductions on cod survival could also be expressed through mackerel, the other common pelagic species in the system (Swain & Sinclair 2000). We tested cod stock–recruitment models that included mackerel spawning biomass as a covariate using estimates from DFO (2023), but found a negligible effect compared to the effect of herring.

We fitted the model to data up to 2018. Cod showed minor signs of improvement in 2020 and 2021 RV surveys, increasing in biomass in consecutive years; however, by the 2023 RV survey, cod biomass had again declined to near record-low biomass (DFO pers. comm.). The accepted cod assessment model fitted to data up to 2023 predicts that cod will be reduced below the extinction proxy of 1 kt by 2044 with 0.50 probability and by 2065 with 0.95 probability (DFO 2024). A 2021 survey of grey seal pup production observed fewer pups on Sable Island than the previous survey in 2017, suggesting a slowing of growth in that herd. However, a record number of pups (nearly 17 000) were observed in the Gulf in the 2021 survey. Revised estimates of grey seal foraging effort near sGSL cod from the grey seal assessment model fitted to 2021 (Hammill et al. 2023) are 20% higher than the multispecies model in the 1990s and 9% higher than the multispecies model in recent years. Fishery and survey data collected for herring since 2018 suggest continuing trends of poor productivity (DFO 2022).

Evaluating the logistics of grey seal predator control was outside the scope of this analysis; however,

large-scale reductions of the grey seal population may be infeasible. The difficulty of hunting and recovering grey seals renders many potential commercial hunts unprofitable, so scaling up commercial harvests would likely require government subsidies. Indeed, recent commercial quotas have gone unfilled and most hunting licenses are inactive. Additionally, the status of Brion Island, which is a provincial sanctuary and largest grey seal colony in the Gulf of St Lawrence, and Sable Island National Park, precludes hunting at these locations where predator-control programmes would likely be most effective. Similar barriers exist for managing the growing grey seal colonies in US waters. The US Marine Mammal Protection Act generally prohibits the use of hunting in managing seal populations in US waters, although the lethal removal of California sea lions *Zalophus californianus* predating upon Pacific salmon and steelhead (*Oncorhynchus* spp.) below the Bonneville Dam has recently been authorized (NOAA 2019). More generally, current reference points under the precautionary approach for grey seals result in a narrow scope for removals that might facilitate rebuilding in sGSL cod (Rossi et al. 2021).

When ecosystems have been altered and one species of interest is at risk of extinction due at least partly to a newly abundant predator and/or competitor, natural resource managers are confronted with a choice between active control of the predator/competitor, passive controls such as reducing anthropogenic impacts, or 'letting nature run its course' (Lessard et al. 2005). There may also be calls for further research to better understand predation impacts and indirect impacts of active controls before making decisions. In the case of cod in the sGSL, there are few options for passive controls, as directed fishing has already been curtailed and unreported catch is likely minor. Letting nature run its course will likely lead to the extirpation of cod from this ecosystem (Swain & Chouinard 2008, Neuenhoff et al. 2019; this study). Our study demonstrates that there are opportunity costs associated with further research, as was recommended as part of a large review of grey seal predation impacts in Atlantic Canada (DFO 2011, Hammill & Swain 2011). In the time it has taken to collect additional data on seal diets, establish predation links to cod, and analyse the indirect effects of a seal cull via pelagics, the cod population has declined to critically low levels with little potential for recovery. Although calling for a better understanding of ecosystem dynamics may appear to be a safe or neutral option, a risk therefore exists that the conflict under investigation may rapidly intensify to the point where

the problem becomes intractable and beyond the means of resource managers to address. In other ecosystems where cod mortality and seal abundance are both elevated (O'Boyle & Sinclair 2012, Rossi et al. 2019), such as the Scotian Shelf and Georges Bank, significantly less is known about seal foraging behaviours and diets (e.g. Rossi et al. 2024), so developing multispecies models to analyse potential responses seal population management in these ecosystems would be more difficult than for the sGSL. Decisions between active, passive, or no ecosystem controls for these ecosystems will therefore need to be made without a full understanding of the possible effects.

Data availability. The data underlying this article are available at <https://doi.org/10.5281/zenodo.13822551>

Acknowledgements. We thank Doug Swain for providing feedback at each stage of the analysis. We also thank Michael Bradford for helpful discussion and François Turcotte for providing herring age–length keys. Funding for this research was provided by Fisheries and Oceans Canada's International Governance Strategy (IGS 2014-2-12) and DFO Deputy Minister Priority Results funding for ecosystem approach implementation. The present work was part of S.R.'s PhD thesis.

LITERATURE CITED

- ✦ Bax NJ (1998) The significance and prediction of predation in marine fisheries. *ICES J Mar Sci* 55:997–1030
- ✦ Benoît HP, Rail JF (2016) Principal predators and consumption of juvenile and adult Atlantic herring (*Clupea harengus*) in the southern Gulf of St. Lawrence. *DFO Can Sci Advis Sec Res Doc* 2016/065
- ✦ Benoît HP, Swain DP (2008) Impacts of environmental change and direct and indirect harvesting effects on the dynamics of a marine fish community. *Can J Fish Aquat Sci* 65:2088–2104
- ✦ Benoît HP, Swain DP, Bowen WD, Breed GA, Hammill MO, Harvey V (2011) Evaluating the potential for grey seal predation to explain elevated natural mortality in three fish species in the southern Gulf of St. Lawrence. *Mar Ecol Prog Ser* 442:149–167
- ✦ Block BA, Whitlock R, Schallert RJ, Wilson S, Stokesbury MJW, Castleton M, Boustany A (2019) Estimating natural mortality of Atlantic bluefin tuna using acoustic telemetry. *Sci Rep* 9:4918
- ✦ Bousquet N, Cadigan N, Duchesne T, Rivest LP (2010) Detecting and correcting underreported catches in fish stock assessment: trial of a new method. *Can J Fish Aquat Sci* 67:1247–1261
- ✦ Bowen WD, Lidgard D (2013) Marine mammal culling programs: review of effects on predator and prey populations. *Mammal Rev* 43:207–220
- ✦ Bowen WD, Lawson JW, Beck B (1993) Seasonal and geographic variation in the species composition and size of prey consumed by grey seals (*Halichoerus grypus*) on the Scotian Shelf. *Can J Fish Aquat Sci* 50:1768–1778

- Breed GA, Bowen WD, McMillan JI, Leonard ML (2006) Sexual segregation of seasonal foraging habitats in a non-migratory marine mammal. *Proc R Soc B* 273:2319–2326
- Chouinard GA, Hurlbut TR (2011) An atlas of the January distribution of selected marine fish species in the Cabot Strait from 1994 to 1997. *Can Tech Rep Fish Aquat Sci* 2967
- Chouinard G, Swain D, Currie L, Poirier G and others (2003) Assessment of cod in the southern Gulf of St. Lawrence, February 2003. DFO Can Sci Advis Sec Res Doc 2003/015
- Christensen V, Pauly D (1992) ECOPATH II — a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecol Modell* 61:169–185
- Cleary L (1982) Assessment of the 4T herring stock. CAF-SAC (Canadian Atlantic Fisheries Scientific Advisory Committee) Res Doc 82/47
- Cook RM, Trijoulet V (2016) The effects of grey seal predation and commercial fishing on the recovery of a depleted cod stock. *Can J Fish Aquat Sci* 73:1319–1329
- Cook RM, Holmes SJ, Fryer RJ (2015) Grey seal predation impairs recovery of an over-exploited fish stock. *J Appl Ecol* 52:969–979
- den Heyer CE, Lang SLC, Bowen WD, Hammill MO (2017) Pup production at Scotian shelf grey seal (*Halichoerus grypus*) colonies in 2016. DFO Can Sci Advis Sec Res Doc 2017/056
- DFO (2011) Impacts of grey seals on fish populations in Eastern Canada. DFO Can Sci Advis Sec Sci Advis Rep 2010/071
- DFO (2015) Updated assessment to 2014 of the fall spawning component of Atlantic herring (*Clupea harengus*) in the southern Gulf of St. Lawrence (NAFO Div. 4T) and advice for the 2015 fishery. DFO Can Sci Advis Sec Sci Rep 2015/033
- DFO (2018) Assessment of the southern Gulf of St. Lawrence (NAFO Div. 4T) spring and fall spawner components of Atlantic herring (*Clupea Harengus*) with advice for the 2018 and 2019 Fisheries. DFO Can Sci Advis Sec Sci Advis Rep 2018/029
- DFO (2022) Assessment of the southern Gulf of St. Lawrence (NAFO Division 4TVn) spring and fall spawner components of Atlantic herring (*Clupea harengus*) with advice for the 2022 and 2023 fisheries. DFO Can Sci Advis Sec Sci Advis Rep 2022/021
- DFO (2023) Assessment of the northern contingent of Atlantic mackerel (*Scomber scombrus*) in 2022. DFO Can Sci Advis Sec Sci Advis Rep 2023/015
- DFO (2024) Southern Gulf of St. Lawrence, NAFO Division 4T-4VN (November–April), Atlantic cod (*Gadus morhua*) Stock Assessment to 2023. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2024/026
- Francis RICC (2014) Replacing the multinomial in stock assessment models: a first step. *Fish Res* 151:70–84
- FRCC (Fisheries Resource Conservation Council) (2011) Towards recovered and sustainable groundfish fisheries in eastern Canada. Fisheries Resource Conservation Council, Ottawa
- Fu C, Mohn R, Fanning LP (2001) Why the Atlantic cod (*Gadus morhua*) stock off eastern Nova Scotia has not recovered. *Can J Fish Aquat Sci* 58:1613–1623
- Fulton EA, Fuller M, Smith ADM, Punt A (2004) Ecological indicators of the ecosystem effects of fishing: final report. Rep No. R99/1546. Australian Fisheries Management Authority, Canberra
- Hammill MO, Gosselin JF (1995) Grey seal (*Halichoerus grypus*) from the Northwest Atlantic: female reproductive rates, age at first birth, and age of maturity in males. *Can J Fish Aquat Sci* 52:2757–2761
- Hammill MO, Stenson GB (2000) Estimated prey consumption by harp seals (*Phoca groenlandica*), hooded seals (*Cystophora cristata*), grey seals (*Halichoerus grypus*) and harbour seals (*Phoca vitulina*) in Atlantic Canada. *J Northwest Atl Fish Sci* 26:1–23
- Hammill MO, Swain D (2011) A controlled experiment (Strawman draft) to test the impact of removals of grey seals on the mortality of southern Gulf cod. DFO Can Sci Advis Sec Res Doc 2011/013
- Hammill MO, Stenson GB, Proust F, Carter P, McKinnon D (2007) Feeding by grey seals in the Gulf of St. Lawrence and around Newfoundland. *NAMMCO Sci Publ* 6:135–152
- Hammill MO, Stenson GB, Swain DP, Benoit HP (2014) Feeding by grey seals on endangered stocks of Atlantic cod and white hake. *ICES J Mar Sci* 71:1332–1341
- Hammill MO, den Heyer CE, Bowen WD, Lang SLC (2017a) Grey seal population trends in Canadian waters, 1960–2016 and harvest advice. DFO Can Sci Advis Sec Res Doc 2017/052
- Hammill MO, Gosselin JF, Stenson GB (2017b) Pup production of Northwest Atlantic grey seals in the Gulf of St. Lawrence. DFO Can Sci Advis Sec Res Doc 2017/043
- Hammill MO, Rossi SP, Mosnier A, den Heyer CE, Bowen WD, Stenson GB (2023) Grey seal abundance in Canadian waters and harvest advice. DFO Can Sci Advis Sec Res Doc 2023/053
- Hanson JM (2011) Ontogenetic diet comparison of Atlantic cod and white hake occurring at historically low population abundances. *Trans Am Fish Soc* 140:1070–1077
- Hanson JM, Chouinard GA (2002) Diet of Atlantic cod in the southern Gulf of St Lawrence as an index of ecosystem change, 1959–2000. *J Fish Biol* 60:902–922
- Harvey V, Cote SD, Hammill MO (2008) The ecology of 3-D space use in a sexually dimorphic mammal. *Ecography* 31:371–380
- Harvey V, Hammill MO, Swain DP, Breed GA, Lydersen C, Kovacs KM (2011) Winter foraging by a top predator, the grey seal, in relation to the distribution of prey. DFO Can Sci Advis Sec Res Doc 2010/124
- Kristensen K, Nielsen A, Berg CW, Skaug H, Bell BM (2016) TMB: automatic differentiation and Laplace approximation. *J Stat Softw* 70(5):1–21
- Lamichhane S, Fuentes-Pardo AP, Rafati N, Ryman N and others (2017) Parallel adaptive evolution of geographically distant herring populations on both sides of the North Atlantic Ocean. *Proc Natl Acad Sci USA* 114:E3452–E3461
- Lessard RB, Martell SJ, Walters CJ, Essington TE, Kitchell JF (2005) Should ecosystem management involve active control of species abundances? *Ecol Soc* 10:1
- Magera AM, Mills Flemming JE, Kaschner K, Christensen LB, Lotze HK (2013) Recovery trends in marine mammal populations. *PLOS ONE* 8:e77908
- Middlemas SJ, Barton TR, Armstrong JD, Thompson PM (2006) Functional and aggregative responses of harbour seals to changes in salmonid abundance. *Proc R Soc B* 273:193–198
- Minto C, Worm B (2012) Interactions between small pelagic fish and young cod across the North Atlantic. *Ecology* 93:2139–2154
- Mohn R, Bowen WD (1996) Grey seal predation on the eastern Scotian Shelf: modelling the impact on Atlantic cod. *Can J Fish Aquat Sci* 53:2722–2738

- ✦ Mosnier A, Dispas A, Hammill M (2023) Spatial distribution and count of harbour seals (*Phoca vitulina*) and grey seals (*Halichoerus grypus*) in the Estuary and Gulf of St. Lawrence from an aerial survey conducted in June 2019. Can Tech Rep Fish Aquat Sci 3541
- ✦ Neuenhoff RD, Swain DP, Cox SP, McAllister MK, Trites AW, Walters CJ, Hammill MO (2019) Continued decline of a collapsed population of Atlantic cod (*Gadus morhua*) due to predation-driven Allee effects. Can J Fish Aquat Sci 76:168–184
- ✦ NOAA (2019) Marine mammals; pinniped removal authority; revised authorization. RIN 0648–XE461. Fed Regist 84: 19052–19053
- ✦ NOAA National Centers for Environmental Information (2022) ETOPO 2022 15 Arc-Second Global Relief Model. NOAA National Centers for Environmental Information, <https://doi.org/10.25921/fd45-gt74>
- ✦ O'Boyle R, Sinclair M (2012) Seal–cod interactions on the Eastern Scotian Shelf: reconsideration of modelling assumptions. Fish Res 115:116:1–13
- ✦ Pante E, Simon-Bouhet B, Irissou J-O (2023) marmap: import, plot and analyze bathymetric and topographic data. R package version 1.0.10. <https://cran.r-project.org/package=marmap>
- ✦ Plagányi EE, Punt AE, Hillary R, Morello EB and others (2014) Multispecies fisheries management and conservation: tactical applications using models of intermediate complexity. Fish Fish 15:1–22
- ✦ Pleizier NK, Campana SE, Schallert RJ, Wilson SG, Block BA (2012) Atlantic bluefin tuna (*Thunnus thynnus*) diet in the Gulf of St. Lawrence and the Eastern Scotian Shelf. J Northwest Atl Fish Sci 44:67–76
- ✦ Polovina JJ (1984) Model of a coral reef ecosystem. Coral Reefs 3:1–11
- ✦ Punt AE, Butterworth DS (1995) The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 4. Modelling the biological interaction between Cape fur seals *Arctocephalus pusillus pusillus* and the Cape hakes *Merluccius capensis* and *M. paradoxus*. S Afr J Mar Sci 16:255–285
- R Core Team (2019) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna
- ✦ Reynolds JC, Tapper SC (1996) Control of mammalian predators in game management and conservation. Mammal Rev 26:127–155
- ✦ Rossi SP, Cox SP, Benoît HP, Swain DP (2019) Inferring fisheries stock status from competing hypotheses. Fish Res 216:155–166
- ✦ Rossi SP, Cox SP, Hammill MO, den Heyer CE, Swain DP, Mosnier A, Benoît HP (2021) Forecasting the response of a recovered pinniped population to sustainable harvest strategies that reduce their impact as predators. ICES J Mar Sci 78:1804–1814
- ✦ Rossi SP, Wang Y, den Heyer CE, Benoît HP (2024) Evaluating the potential impacts of grey seal predation and fishery bycatch/discards on cod productivity on the Western Scotian Shelf and in the Bay of Fundy. ICES J Mar Sci 81: 944–960
- ✦ Savenkoff C, Swain DP, Hanson JM, Castonguay M and others (2007) Effects of fishing and predation in a heavily exploited ecosystem: comparing periods before and after the collapse of groundfish in the southern Gulf of St. Lawrence (Canada). Ecol Modell 204:115–128
- ✦ Schnute JT, Haigh R (2007) Compositional analysis of catch curve data, with an application to *Sebastes maliger*. ICES J Mar Sci 64:218–233
- ✦ Smout S, Rindorf A, Hammond PS, Harwood J, Matthiopoulos J (2014) Modelling prey consumption and switching by UK grey seals. ICES J Mar Sci 71:81–89
- ✦ SSCFO (Standing Senate Committee on Fisheries and Oceans) (2012) The sustainable management of grey seal populations: a path toward the recovery of cod and other groundfish stocks. Standing Senate Committee on Fisheries and Oceans, Ottawa
- ✦ Swain DP (2016) Population modelling results for the assessment of Atlantic herring (*Clupea harengus*) stocks in the southern Gulf of St. Lawrence (NAFO Division 4T) to 2015. DFO Can Sci Advis Sec Res Doc 2016/061
- ✦ Swain DP, Benoît HP (2015) Extreme increases in natural mortality prevent recovery of collapsed fish populations in a Northwest Atlantic ecosystem. Mar Ecol Prog Ser 519:165–182
- ✦ Swain DP, Chouinard GA (2008) Predicted extirpation of the dominant demersal fish in a large marine ecosystem: Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Can J Fish Aquat Sci 65:2315–2319
- ✦ Swain DP, Sinclair AF (2000) Pelagic fishes and the cod recruitment dilemma in the Northwest Atlantic. Can J Fish Aquat Sci 57:1321–1325
- ✦ Swain DP, Benoît HP, Hammill MO, McClelland G, Aubrey É (2011) Alternative hypotheses for causes of the elevated natural mortality of cod (*Gadus morhua*) in the southern Gulf of St. Lawrence: the weight of evidence. DFO Can Sci Adv Sec Res Doc 2011/036
- ✦ Swain DP, Benoît HP, Hammill MO (2015a) Spatial distribution of fishes in a Northwest Atlantic ecosystem in relation to risk of predation by a marine mammal. J Anim Ecol 84:1286–1298
- ✦ Swain DP, Savoie L, Cox SP, Aubry É (2015b) Assessment of the southern Gulf of St. Lawrence Atlantic cod (*Gadus morhua*) stock of NAFO Div. 4T and 4Vn (November to April), March 2015. DFO Can Sci Advis Sec Res Doc 2015/080
- ✦ Swain DP, Ricard D, Rolland N, Aubry É (2019) Assessment of the southern Gulf of St. Lawrence Atlantic Cod (*Gadus morhua*) stock of NAFO Div. 4T and 4Vn (November to April), March 2019. DFO Can Sci Advis Sec Res Doc 2019/038
- ✦ Trzcinski MK, Mohn R, Bowen WD (2006) Continued decline of an Atlantic cod population: How important is gray seal predation? Ecol Appl 16:2276–2292
- ✦ Varela JL, Spares AD, Stokesbury MJW (2020) Feeding ecology of Atlantic bluefin tuna (*Thunnus thynnus*) in the Gulf of Saint Lawrence, Canada. Mar Environ Res 161: 105087
- ✦ Vehtari A, Gelman A, Simpson D, Carpenter B, Bürkner PC (2021) Rank-normalization, folding, and localization: an improved \hat{R} for assessing convergence of MCMC (with discussion). Bayesian Anal 16:667–718
- ✦ Walters C, Kitchell JF (2001) Cultivation/densation effects on juvenile survival and recruitment: implications for the theory of fishing. Can J Fish Aquat Sci 58:39–50
- ✦ Walters C, Christensen V, Pauly D (1997) Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Rev Fish Biol Fish 7:139–172
- ✦ Walters C, Pauly D, Christensen V, Kitchell JF (2000) Representing density dependent consequences of life history strategies in aquatic ecosystems: EcoSim II. Ecosystems 3:70–83

-
- ✦ Walters CJ, McAllister MK, Christensen V (2020) Has Steller sea lion predation impacted survival of Fraser River sockeye salmon? *Fisheries* 45:597–604
- ✦ Wargo Rub AM, Som NA, Henderson MJ, Sandford BP and others (2019) Changes in adult Chinook salmon (*Oncorhynchus tshawytscha*) survival within the lower Columbia River amid increasing pinniped abundance. *Can J Fish Aquat Sci* 76:1862–1873
- ✦ Winters GH, Wheeler JP (1985) Interaction between stock area, stock abundance, and catchability coefficient. *Can J Fish Aquat Sci* 42:989–998
- ✦ Yodzis P (1998) Local trophodynamics and the interaction of marine mammals and fisheries in the Benguela ecosystem. *J Anim Ecol* 67:635–658
- ✦ Yodzis P (2001) Must top predators be culled for the sake of fisheries? *Trends Ecol Evol* 16:78–84

*Editorial responsibility: Franz Mueter,
Juneau, Alaska, USA
Reviewed by: B. Bogstad and 3 anonymous referees*

*Submitted: November 11, 2023
Accepted: August 1, 2024
Proofs received from author(s): September 22, 2024*