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Grey Seal Abundance in Canadian Waters and Harvest Advice

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Foreword

This series documents the scientific basis for the evaluation of aquatic resources and ecosystems in Canada. As such, it addresses the issues of the day in the time frames required and the documents it contains are not intended as definitive statements on the subjects addressed but rather as progress reports on ongoing investigations.

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ABSTRACT

Here we introduce a new integrated population model (IPM) to provide harvest advice for the Gulf of St. Lawrence (Gulf), Coastal Nova Scotia (CNS) and Sable Island grey seal herds, and compare model outputs with estimates from a deterministic model used in previous assessments. The IPM was fit to the pup production estimates for the Scotian Shelf (CNS and Sable Island combined) and the Gulf. As with the previous assessment model, the new model was fit to both pup production and pregnancy rates, and includes an index for ice-related pup mortality in the Gulf. The new model includes both density-dependent and density-independent pup mortality, and fits to sighting histories of individually marked seals at the breeding colony on Sable Island to estimate sex- and age-specific survival and recruitment to the breeding colony. The model estimated that total pup production increased slightly from 92,300 (95% CI = 86,700–100,100) in 2016 to 99,300 (90,900–107,700) in 2021, while total abundance increased slightly from 339,400 (317,900–361,500) in 2016 to 366,400 (317,800–409,400) in 2021. The rate of growth of the population has continued to slow, declining from approximately 4% during the last assessment period, to 1.5% per year between 2016 and 2021. The updated population estimate from the previously accepted deterministic population model was 363,600 (298,700–450,000) for 2021, which is very similar to the estimate of abundance generated using the IPM. Although the population continues to grow, the current estimate is below that presented during the 2016 assessment. The difference is due to changes in the structure of the new population model and higher estimates of juvenile mortality produced by the model fit to the 2021 pup production estimates. Additional information on juvenile survival and how it responds to changes in abundance (density-dependent) and environmental (density independent) variation is needed as it represents a significant gap to our understanding of the dynamics of this population and of large marine mammals in general. Total allowable removals depend on age structure of the harvest and whether the harvests are conducted in winter at the breeding colonies, or at other times of the year when animals from all herds are mixed. Using an integrated model incorporates many of the inputs in a unified framework that allows for uncertainty to be propagated throughout the analyses.

Keywords: grey seal, population model, abundance, harvest

INTRODUCTION

Pinniped populations, have responded strongly to reductions of commercial hunting and culling, with about half of worldwide populations increasing in abundance (Magera et al. 2013) and some now at record levels (Thomas et al. 2019; Rossi et al 2021). The rapid recovery of pinniped populations may be due to their early maturity and high reproductive rates relative to other marine mammals, their occurrence in coastal waters, which enabled the early detection of declining populations compared to whales, or their relatively isolated breeding sites (Magera et al. 2013). While recent trends in abundance are well established for some populations, the future size of pinniped populations remains highly uncertain, partly because we lack abundance and demographic data prior to widespread depletion, so population responses to high density are unknown.

The grey seal (*Halichoerus grypus*) is distributed throughout the north Atlantic. The northwest Atlantic population ranges from Cape Chidley in the north to Nantucket Sound in the south. Little is known of historical abundance or harvests of grey seals in Atlantic Canada, but grey seals appear to have been abundant throughout the region during the 16th and 17th centuries. By the 18th century, their numbers had declined markedly due to high levels of harvesting for oil. In the late 1800s, Gilpin (1874) speaks of herds of only 20 or 30 seals on Sable Island, and in the early 1950s, they were rare throughout eastern Canada (Fisher 1955; Lavigueur and Hammill 1993; Bowen 2011). Government-sponsored culls and a bounty program may have slowed grey seal recovery in the 20th century (Bowen and Lidgard 2012), but over the last five decades the Canadian grey seal population has been estimated to have increased from approximately 15,000 animals in the early 1960s to approximately 400,000 by 2017 (Mohn and Bowen 1996; Hammill et al 2017; Rossi et al 2021).

Northwest Atlantic grey seals form a single genetic population (Boskovic et al. 1996; Wood et al. 2011). Within Canadian waters, the grey seal population has at different assessments been subdivided into two or three herds for management considerations: Sable Island, coastal Nova Scotia (CNS) and the Gulf of St. Lawrence (Gulf; Figure 1). Sable Island is home to the largest breeding colony of grey seals in the world (Bowen et al. 2007). The second largest breeding colony in Atlantic Canada occurs in the Gulf, where grey seals have their young on the pack ice in the southern Gulf or on small islands (Figure 1). Historically, the CNS herd consisted of a relatively small number of animals breeding on isolated islands along what has traditionally been referred to as the Eastern Shore, which includes Hay Island (Mansfield and Beck 1977). In the CNS area, significant culling efforts, particularly in the Basque Island area, limited pup production to the low 100s during the 1970s; commercial hunting has occurred on Hay Island over the last decade. In the early 1990s, a small colony appeared along the southwestern shore of Nova Scotia on Flat and Noddy Islands. These were included in the CNS area as well. Satellite telemetry and flipper tag returns show that, outside of the breeding season, there is overlap in the distribution of animals from the different colonies (e.g., Lavigueur and Hammill 1993; Breed et al. 2006, 2009, 2013; Harvey et al. 2008). Grey seal pupping also occurs in the northeastern United States (Wood et al. 2007, 2011) with an estimated pup production of around 6,500 animals in 2016 (den Heyer et al. 2020).

In this assessment, the estimates of pup abundance from colonies along the Atlantic coast of Nova Scotia, the area previously referred to as CNS have been grouped with the Sable Island estimates to form a Scotian Shelf herd. The Gulf herd has been retained as a separate management unit. The herds in the two regions have had different population trajectories. Prior to 1997, pup production increased at a rate of 13% per year on Sable Island (Bowen et al. 2011). Between 1997 and 2016, the rate of increase slowed to about 4%, suggesting that the population may be facing resource limitation (Bowen et al. 2011; den Heyer et al. 2020). Pup

production in the Gulf has been much more variable than on Sable Island due to higher and more variable removals associated with bounty, culling and commercial harvests (Hammill et al. 1998), and higher mortality rates associated with pupping on the pack ice (Thomas et al. 2007; Hammill and Stenson 2011; Hammill et al. 2017).

McLaren et al. (2001) identified a need to manage seals under a framework that incorporated benchmarks and harvest control rules. In 2003, Fisheries and Oceans Canada implemented a management approach, referred to as the Atlantic Seal Management Strategy (ASMS), which incorporated the precautionary approach into the management of Atlantic seals. Grey seals are currently classified as being 'Data Rich'. For such species, the framework identifies a precautionary reference level at 70% of the largest population size. A secondary reference level is set to 50% while the critical reference limit is identified at 30% of the largest population size (Hammill and Stenson 2007, 2013). The primary goal of the management framework is to ensure that the population does not decline to levels where it falls below the critical reference level (N_{30}) and as such, is considered to have suffered serious harm. To minimize the risk, the population is normally managed around the precautionary reference level (N_{70}).

Resource Management requested information on the status and trend of the overall population, and the three herds. However, as outlined above, the CNS herd comprises only a small proportion of the total number of seals along the Atlantic coast of Nova Scotia. We provide abundance estimates for Sable Island, because it is such a large colony, but for the purposes of advice, the Sable and CNS herds were combined, to form a Scotian Shelf herd, with a second herd comprising animals born in the Gulf. Resource Management also requested information on the maximum sustainable harvest for the next five years (2022–2027) that ensures with an 80% confidence that the population remains above N_{70} for each of the following scenarios for age composition of the harvest:

- 5% age 1+ / 95% Young of the Year (YOY);
- 10% age 1+ / 90% YOY; and
- 50% age 1+ / 50% YOY.

The dynamics of grey seals in Canadian waters have been modelled by fitting a deterministic model that incorporates information on age-specific reproductive rates and harvests to survey estimates of pup production (Hammill et al. 2017). The model has been fitted to observed aerial survey estimates of pup production by adjusting the start population size, adult mortality rates, and carrying capacity (K; Hammill et al. 2017). In this model, juvenile mortality was set to 15 times the adult mortality rate. den Heyer and Bowen (2017) showed that mature male grey seals had lower survival rates than mature females, and that the differences increased with age. At the previous assessment, an ad hoc approach was used to take this into account. Assuming a stable age distribution, the M:F sex ratio was 0.69:1. This ratio was applied to the 1+ component of the population, resulting in an estimated total abundance of 424,000 animals (Hammill et al. 2017).

Here, we describe the dynamics of the grey seal population in Canadian waters using the deterministic model along with results from a new herd-, sex-, and age-structured integrated population model (IPM) developed by Rossi et al (2021). This IPM model, which operates within a Bayesian framework, will replace the previously used deterministic model and is used to provide harvest advice. We fitted the IPM to observations of pup production, reproductive rate, removals, and sighting histories of marked seals, then projected future abundance under different harvest strategy assumptions.

MATERIALS AND METHODS

We apply the new IPM model to the entire time series and compare model estimates with those from the deterministic model used in previous assessments (Hammill et al. 2017), as well as estimates from Rossi et al. (2021), which included data up until 2016. Details of the deterministic model are outlined in Hammill et al. (2017).

INTEGRATED POPULATION MODEL (IPM)

The IPM consists of three components:

1. a demographic model describing sex-specific maturity-at-age,

2. a population dynamics model structured by age a, sex s, and herd h, and

3. a mark-recapture model describing the sighting and survival probabilities of marked individuals within the population.

Natural mortality (M), density-dependence scale (D) and shape (θ), age-at-50% maturity ($a^{(50\%)}$), age-at-95% maturity ($a^{(50\%)}$), initial abundance ($N^{(1)}$), and the probability of sighting branded seals (p) are estimated. The model operates on an annual time step from 1960 to 2021 and is fit to pup production, pregnancy samples and sighting histories. Model notation and equations are listed in Tables 1 and 2. Additional details on the IPM are given in Rossi et al. (2021).

Maturity was modelled using sex-specific logistic functions of age (T2.1–T2.3). Reproductive rates were the product of maturity-at-age and the probability of reproduction among mature females (γ; T2.5).

The abundance of seals aged less than 1 year old (young of the year or YOY) was modelled as a function of births, early mortality and harvesting. Births were calculated assuming each pregnant female gave birth to one pup (T2.10). We then accounted for pre-weaning mortality (5%, estimated from studies of Sable Island pups [Bowen et al. 2007; 2011, den Heyer et al. 2017]; T2.11), and ice-related mortality (T2.11; Table 7) to provide an estimate of post-weaning abundance. Weaned animals can then be harvested (removals [T2.12]). The number of YOY remaining after harvesting are termed "recruits".

Survival from recruitment to age 1 was divided into density-independent ($S^{(I)}$) and density-dependent ($S^{(D)}$) components. $S^{(D)}$ was modelled as a generalized Beverton-Holt (GBH) function of either recruitment (termed the "R model") or total abundance (the "N model") (Maynard Smith and Slatkin 1973). The generalized Beverton-Holt is a flexible function that can assume a range of convex or concave shapes. Rossi et al. (2021) assumed the density-independent mortality rate for recruits ($M^{(I)}$) was 0.1 yr^{-1} based on Sable Island mark-recapture data when population density was low. In this analysis, we additionally tested a set of models (termed R-DI and N-DI) in which $M^{(I)}$ was estimated with a normal prior centered on 0.1 with a standard deviation of 0.05.

Survival of age-1+ seals was assumed to be density-independent (T2.16). The total mortality of age-1+ seals (Z) was the sum of anthropogenic mortality *(F)* due to hunting, culling, nuisance killing or scientific sampling, plus natural mortality (*M*). Z, F, and *M* are instantaneous with units yr^{-1} (T2.6). Here, unreported anthropogenic mortality would contribute to *M*. We estimated a sex-specific, herd-invariant *M* for six age classes (ages 1–9, 10–14, 15–19, 20–24, 25–30, 30+), under the constraint that *M* increased with age class. *F* was calculated from the Baranov catch equation by assuming removals were known without error (Ricker 1975). The oldest age class accumulated all seals aged 30 years or older (T2.17).

The mark-recapture component of our IPM was based on a parameterization of the Jolly-Seber model (Schwarz and Stobo 2000) that estimated sightings of animals marked as young from parameters for:

1. apparent survival,
2. age-specific recruitment to the breeding population,
3. juvenile survival rate, and
4. resighting probabilities (T2.20–T2.28).

Parameters (i)–(iii) were linked to population model quantities (T2.22, T2.4, T2.21), leaving only resighting parameters to be estimated.

ESTIMATION AND MULTIMODEL APPROACH

We fitted each IPM (Table 3) by assuming that pup production indices arose from log-normal distributions, pregnancy rates and resightings arose from binomial distributions, and initial sightings arose from multinomial distributions. Weakly-informative prior distributions were set for all parameters (except $M^{(I)}$, which had an informative prior in R-DI and N-DI), which were used to regularize the MCMC algorithm by ruling out implausible parameter values, but did not otherwise affect estimates. Posterior distributions for parameters and predictive distributions for unobserved quantities of interest were generated using a Hamiltonian Monte Carlo algorithm implemented in Template Model Builder (Hoffman and Gelman 2014; Monnahan and Kristensen 2018).

We assessed the fit and estimates from each model and also considered ensemble estimates (Millar et al. 2015), which were constructed by combining posterior samples from the four IPMs. We only considered an unweighted ensemble (i.e., each individual IPM contributed an equal number of samples to the ensemble) since each model was considered equally plausible *a priori*, and we did not expect the data to be informative regarding the four YOY survival hypotheses represented by the models.

PROJECTIONS

For the projections, nuisance and cull removals varied between 10 and 40 animals only. Ice-related mortality was set to 0 for the entire projection period (i.e., pupping was assumed to occur on land). Projections were initialized using 500 randomly-drawn posterior samples from each model.

We tested the effects of three harvest strategies on projected seal dynamics. The maximum sustainable harvest for the next five years (2022–2027) that ensures with an 80% confidence that the population remains above N_{70} is presented for each of the following scenarios for age-composition of the harvest:

- 5% age 1+ / 95% YOY;
- 10% age 1+/ 90% (YOY);
- 50% age1+ / 50% YOY.

DATA INPUT

Pup production

The model was fit to independent estimates of pup production (Table 4). We are fitting to the new 2021 pup production estimates and have made some changes to the historical data (see den Heyer et al. 2020). Here, we fit the model(s) to the Gulf and Scotian Shelf herds. The latter is composed of Sable Island animals and the CNS breeding colonies. Notably, there were two pup production estimates for Sable Island in 1989 and 1990. Here, we are using the aerial survey in 1990 and total count in 1989 as has been done in previous assessments. The estimates of pup production from the largest colonies were based on aerial surveys in 2016 and 2021, and have been adjusted for pups born after the survey (Hammill et al. 2017; den Heyer et al. 2020; den Heyer et al. 2023).

Pregnancy rates

Late-term pregnancy data are available from sampling programs conducted in the Gulf (Hammill and Gosselin 1995). Samples were collected between August and November. These samples represent late-term pregnancy rates since they were collected only a few months prior to pupping in December. It was assumed that there were no abortions after the samples were taken. Pregnancy was determined by the presence of a corpus luteum. To the extent that abortions could occur, these late-term rates may over-estimate birth rates. The mean birthdate was assumed to be the first of January, and the age of all animals advances by one year on this date. Females enter the model at their age on the first of January of each year. There are gaps in the time series of reproductive data, and in some years sample sizes are small (Table 5). The method used to handle these cases are indicated in Hammill et al. (2017) and Rossi et al. (2021) for the deterministic model and the IPM, respectively.

Removals

Data on removals from the herds are available since 1960. There are five types of removals: the Canadian commercial harvest (Fisheries and Oceans Canada, Statistics Branch): those from nuisance seal licenses, bounty kills, culls, science sampling programs and incidental catches from commercial fisheries (Appendix A). However, we have no information on incidental catches of grey seals in commercial fisheries. The Canadian commercial hunt consists of 99% YOY. All harvests were corrected for estimates of seals struck and killed, but not landed or reported. The commercial hunts and culls occur on land or on the ice. For these hunts, all animals were assumed to have been recovered. For scientific collections, animals are shot in the water. Based on shot samples for science, the struck-and-loss rate is set to 30%, but we do not have information on struck-and-loss rates from contract hunters. We did not correct reports of nuisance seal harvests for struck and loss, since there is no requirement to recover the animal. There are no data available for incidental catches. These losses are subsumed in estimates of natural mortality.

There is considerable uncertainty about the reporting of animals shot as nuisance seals. Roughly 400 nuisance licenses were issued, mostly in the Maritimes Region, between 1999 and 2019. During that time period, the reporting rate from the licenses was low, varying from 0 to 47% per year, with an overall mean of 9.3%. The mean number of grey seals taken per report varied from 0 to 14.7, with an overall mean of 5.5 per license. To maintain the removals time series, we estimate the total number of removals associated with nuisance licenses between 2005 and 2019 based on a take rate of 7.9 (SE = 0.6) removals per license established in 2011 (Table 5; DFO 2011). Since 2020, DFO no longer issues nuisance licenses, so we estimate 0 removals since then.

Adult and juvenile survival

More than 8,000 seals have been individually marked as part of the Sable Island mark-resighting program. The sightings of these individually marked seals at the Sable Island breeding colony are used to monitor adult and juvenile survival. The new integrated population model fits to the 2,313 individual sighting histories (male = 474, female = 1,739) marked at weaning on Sable Island between 1969 and 2002 (Table 6). Most seals were seen in multiple breeding seasons (min = 1, max = 33, median = 14). The recruitment of seals marked at weaning in 1985–1989 and 1998–2002 provides an estimate of juvenile (age 0–4) survival and estimates of age of maturity (den Heyer and Bowen 2017; den Heyer et al. 2013; Schwarz and Stobo 1997). The 1998–2002 cohorts recruited almost a year later than the 1985–1989 cohorts, and the 1998–2002 survival rate (0.33) was almost half the survival rate of the 1985–1989 cohorts (0.76). Based on sightings from 1978–2016, average adult survival was estimated to be 0.943 (95% CI 0.937–0.948) for males and 0.976 (95% CI 0.974–0.978) for females (Schwarz and Stobo 1997; den Heyer et al 2013; Rossi et al. 2021). Males had lower survival at all ages and there was no change in survival of adult males or females over time. The cohorts of weaned pups marked between 2014 and 2016 have not fully recruited and are not used in the current analysis.

Ice-related mortality of YOY in the Gulf

Grey seals in the Gulf give birth on the ice as well as on islands. In heavy ice years, most animals are born on the ice, whereas in years of light ice, a greater proportion of pups are born on the islands (Figure 2; Hammill and Stenson 2011). Pup mortality appears to be higher in the Gulf herd than on Sable Island and, in poor ice years, we have observed that pups disappeared during the surveys (e.g., 1997, 2010) although the numbers have been difficult to quantify. An ice mortality index has traditionally been incorporated into the assessment (Table 7), but in recent years there has been almost no ice, and nearly all pups were born on land. Since the last assessment, ice-related mortality has been assumed to be zero (Figure 2; Hammill et al. 2017).

RESULTS

DETERMINISTIC ASSESSMENT MODEL – THE "OLD" MODEL

Reproductive rates

A smoother used in the Deterministic model fitted to the reproductive data provided a means of interpolating for missing years and attempting to characterize inter-annual variability (Figure 3). Overall, there has been a decline in reproductive rates for animals aged 4 and 5 years, but reproductive rates remain high and are less variable for animals aged 6 years and older (Table 5; Figure 3).

Model estimates

On Sable Island, fitting the deterministic model to the pup production estimates and taking into account removals, pup production increased from 300 animals in 1960 to 81,100 in 2016, and since then has levelled off at 82,800 (95% CI = 68,900–98,300). Estimated total abundance increased from 1,500 animals in 1960 to 289,000 in 2016, and appears to have levelled off in 2021 at 291,300 (247,400–337,200), assuming a sex ratio of 1:1. The model provided an estimated carrying capacity (K) of 319,300 (SE = 23,000) and an adult mortality rate of 0.0368 (SE = 0.005; Table 8).

Combining abundance estimates from Sable Island and the coastal islands to produce a Scotian Shelf estimate resulted in pup production increasing from 600 animals in 1960 to 85,400 in 2016, then increasing only slightly to 87,200 (73,100–103,400) in 2021. Total population for the Scotian Shelf herd increased from 2,700 animals in 1960 to 302,500 in 2016 and 304,600 (259,200–354,100) in 2021. The population appears to be leveling off as it approaches estimated carrying capacity (Figure 4, Table 8).

In the Gulf of St. Lawrence, pup production has increased from an estimated 1,200 in 1960 to 17,400 (12,800–23,000) in 2021. The model suggests that the Gulf population may also be leveling off, but estimates of adult mortality and carrying capacity for this area are highly uncertain (Table 8). The Gulf population increased from 5,100 animals in 1960 to 59,000 (39,500–95,900) in 2021 (Figure 4). Combining the estimates from the Scotian Shelf with the estimates from the Gulf, results in a total estimated grey seal abundance of 363,600 (298,700–450,000).

Over time, there has been a decline in the ratio of number of 1+ animals to pups in the population. Initially, this ratio fluctuated markedly, reflecting the effects of the variable removals from all herds as well as variable ice conditions impacting juvenile survival in the Gulf. Since approximately year 2000, the 1+-to-pup ratio has declined from approximately 4.5 to 2.5 due to an estimated decline in juvenile survival (Figure 5).

Harvest advice

Harvest levels estimated using the deterministic model that respected the management objective, and assuming an age composition of the harvest of 95% young of the year (YOY), 90% YOY, and 50% YOY were: 9,250, 8,000, and 4,000 individuals, respectively for a winter harvest in the Gulf; 49,000, 42,000 and 20,000, respectively for a winter harvest on the Scotian Shelf; and 58,250, 50,000 and 24,000 individuals, respectively in total.

INTEGRATED POPULATION MODEL (IPM) – THE NEW MODEL

Model fits

Four different formulations of the IPM were run. The models differed in how density-dependent survival of the YOY was configured to be affected by YOY abundance or total abundance, and whether density-independent mortality was fixed or estimated (Table 3). We did not detect convergence problems in any of the four IPMs (e.g., the potential scale reduction factor on rank-normalized split chains ($\hat{R}$) was less than 1.01 for each parameter, the effective sample size of the rank-normalized draws was sufficiently high for each chain, and the rank plots of posterior samples was approximately uniform for all parameters and chains).

Each IPM approximated the mean observed pregnancy rates reasonably well, though fits in some years were poor due to high interannual variability in the data and low sample sizes (Figure 6).

Each IPM fit the Shelf pup production relatively closely, except for early in the time-series when standard errors around the observations were large (Figure 7). The *R* and *N* models fit the Shelf pup production similarly, with model-estimated production lower than adjusted survey estimates between 2007 and 2016. In contrast, estimated pup production from *R-DI* and *N-DI* models was higher than adjusted survey estimates between 2004 and 2010, but lower in 2016. Each model fit the 2021 adjusted survey estimate of Shelf pup production closely.

IPM fits to Gulf pup production were more variable (Figure 7), though this was expected given the high degree of noise in the Gulf data caused by factors that we are unable to fully account

for in our model. Each IPM fit the Gulf data similarly, except for early in the time series. Despite large residuals in some years, there did not appear to be any underlying pattern to the residuals. Model-predicted Gulf pup production exceeded the 2010 and 2016 adjusted survey estimate, but was lower than the 2021 adjusted survey estimate.

There was little overlap between the prior and posterior distributions for $M^{(I)}$. The estimates of $M^{(I)}$ from both the *R-DI* and *N-DI* versions of the model were nearer the right tail of the prior distribution (Figure 8). Estimates of $M^{(I)}$ were slightly larger in the *N-DI* model than in the *R-DI* model.

Abundance estimates

The four IPMs estimated similar changes in abundance over much of the time series, but the models identified contrasting trends for each herd beginning around 2010. The R and N models indicated that pup production and total abundance on the Scotian Shelf has continued to grow in recent years (Figures 9–11), although the rate of increase has slowed. In contrast, the R-DI and N-DI models suggest that pup production and total abundance on the Shelf has recently levelled off. In the Gulf, the R and R-DI models indicate that pup production and total abundance have been steady since 2010, whereas the N and N-DI models suggest slightly increasing trends for both pup production and total abundance. Median ensemble estimates of abundance and pup production indicate continued growth for both herds.

In 2021, median ensemble pup production on the Scotian Shelf was 83,700 (95% CI = 5,500–91,900) and median ensemble total abundance was 310,200 (262,600–351,600). The median ensemble pup production in the Gulf was 15,600 (13,800–17,500) and total abundance was 56,000 (48,600–64,600). The model estimated total abundance has increased from a few thousand animals in 1960 to 366,400 (317,800–409,400) in 2021.

Survival estimates

IPMs with fixed $M^{(I)}$ and estimated $M^{(I)}$ estimated contrasting density-dependence relationships. Estimated values of $M^{(I)}$ in *R-DI* and *N-DI* were higher than the fixed value of $M^{(I)}$ in *R* and *N*. As a result, density-dependent recruit survival in the *R* and *N* models declined more steeply at low density, whereas density-dependent recruit survival in the *R-DI* and *N-DI* models were relatively more stable at low density (Figures 12, 13). Differences between IPMs with fixed $M^{(I)}$ and estimated $M^{(I)}$ were more pronounced for the Shelf herd than the Gulf herd. Current estimates suggest that the grey seals are at relatively high density (i.e., current abundance is more than twice as high as *D*), therefore future increases in grey seal abundance are not expected to reduce survival as much as has occurred in the past.

Juvenile survival (i.e., the proportion of each cohort that survives from weaning to age 4) has declined since the 1960s in response to density-dependence in recruit survival and was estimated to currently be less than 0.2 for both herds (Figure 14). Estimates of juvenile survival from previous tagging analyses (den Heyer et al. 2013) broadly match the juvenile survival estimates from the IPMs.

To examine differences in survival rates between females and males, survival in the IPM was estimated in six age classes:

1. ages 1–9,
2. ages 10–14,
3. ages 15–19,
4. ages 20–24,
5. ages 25–29, and
6. ages 30+.

Estimated female survival was higher than male survival for all age classes, with male survival rates declining at a faster rate than female survival rates, particularly after 24 years of age (Figure 15). Survival estimates from the IPM were similar to those obtained from standalone mark-recapture analyses (e.g., den Heyer and Bowen 2017).

Comparison to previous IPM

To evaluate the impact of including recent pup survey estimates, pregnancy rate observations and mark-recapture data from 2017–2021 in the IPM, we compared the estimates from the current IPMs to estimates from the R and N model previously fitted to data up to 2016 (Rossi et al. 2021). The new estimates of abundance for 2016 were about 17% lower for the Scotian Shelf and about 10% higher for the Gulf (Table 9).

Estimated relationships between recruit survival and abundance were also affected by the addition of the new data. For the Shelf herd, the density-dependence relationship became slightly steeper, resulting in recruit survival rates about 10% lower at moderate to high abundance (Figure 16). For the Gulf herd, the addition of new data resulted in a much lower survival rate at low densities, though survival at high densities was slightly higher (Figure 16). Sensitivity in the density-dependence relationship when the Gulf herd was at low abundance is not surprising given the large degree of uncertainty around Gulf pup production survey estimates early in the time series, and given uncertainties regarding ice-related mortality of Gulf pups.

Projections and harvest advice

Harvest levels that respected the management objective are presented in Figure 17 and Table 10. A harvest composition of 95% young of the year (YOY), 90% YOY and 50% YOY would be 68,600, 60,200 and 22,500, respectively for the Scotian Shelf and 8,700, 7,100 and 1,700 for the Gulf (Figure 16 and Table 10).

DISCUSSION

The Canadian grey seal population has been increasing since the 1960s. Pup production increased rapidly on the ice in the Gulf, coastal colonies in eastern Nova Scotia and Sable Island until the late 1990s. Since the turn of the century, Gulf pup production has been quite variable owing to variable ice conditions, while pup production on the Scotian shelf, particularly Sable Island, continued to increase, albeit at a slower rate. In this assessment, we document the first pup production estimate from Sable that is not larger than the previous estimate.

In Canada, population models for grey seals have been fitted to the time series of pup production estimates and life history data from sampling in the Gulf. In the 2016 assessment,

survival rate information gathered from the mark-resighting program at the Sable Island breeding colony were used to set the multiplier value for juvenile survival in a deterministic population model. The model assumed a 1:1, sex ratio which was adjusted post hoc, assuming a stable age distribution. This resulted in a male:female sex ratio of 0.69:1 (Hammill et al. 2017). The new integrated population model consists of three components:

1. a population dynamics model structured by age a, sex s, and herd h,

2. a demographic model describing sex-specific maturity-at-age, and

3. a mark-recapture model describing the sighting and survival probabilities of marked individuals within the population (Hammill et al. 2017; Rossi et al. 2021).

Overall, the IPM provides similar estimates of abundance to the more ad hoc deterministic model, and offers an advancement over the deterministic model because it incorporates many of the inputs into a unified framework. It uses the mark-resight information to estimate juvenile survival on the Scotian shelf and guide model fitting to estimate Gulf abundance. The unified framework allows for uncertainty to be propagated throughout.

Both models showed similar trends, and considerable overlap in estimates of both pup production and total abundance. Both models underlined a greater level of uncertainty associated with the model fit to the Gulf data than in the model fit to data from the Scotia Shelf, and both models pointed towards a slowing in the rate of increase of the northwest Atlantic grey seal population. The deterministic model suggests that the Gulf population continues to increase, while the Scotian Shelf population is levelling off sharply. The IPM estimates that the Gulf herd has levelled off, while the Scotian Shelf herd continues to increase. The differences in suggested trends are due to the use of the theta-logistic curve to describe density-dependent changes in the deterministic model, versus the generalized Beverton-Holt curve used to describe density-dependent changes in the IPM (see below). However, given the much higher level of uncertainty associated with the deterministic model, the differences between the two models in predicted trajectories are not significant.

In the IPM model, juvenile survival estimates for Gulf animals from the ensemble model were lower than estimates for Scotian Shelf animals. The reasons for this difference are not clear since over the last decade, there has been a shift in pupping in the Gulf, from ice breeding to land breeding as ice cover has declined. This would be expected to result in improved juvenile survival. The absence of improved juvenile survival may result from the model sharing parameters across the two herds (e.g., fixed density-independent mortality in R and N models). Alternatively, because data for pregnancy rates and adult survival estimates remain high, the model can only adjust juvenile survival rates in order to fit the observed changes in pup production estimates from the surveys.

The slowing in the growth rate of the northwest Atlantic grey seal population is likely due to density-dependent factors, operating on the dynamics of the population. Early indications of density-dependent regulation are expected to be reflected by changes in individual growth, followed by juvenile mortality, age at maturity, reproduction, and finally, adult mortality (Eberhardt and Siniff 1977; Stenson et al. 2016; Hammill and Sauvé 2017). From our sampling programs, we have documented a slowing of individual growth rates through changes in length and mass-at-age (Dussault 2007; Hammill and Sauvé, unpublished data). The Eberhardt paradigm also identifies changes in reproduction as a density-dependent response. However, apart from a decline in productivity of animals aged 4 and 5 years, productivity of older animals has remained high over the 50-year time series. Mansfield (1977), when the population was much smaller, estimated pregnancy rates on Sable Island to be 0.85, which is close to the overall rate of 0.89 from the sampling program in the Gulf of St. Lawrence. Since 1969, more

than 8,000 grey seals have been individually marked on Sable Island. Using sighting data from 1978 to 2016, the transition probabilities between the observed (pregnant) and unobserved (non-pregnant) state animals has varied, but without trend, also indicating no apparent change in the pregnancy rate (den Heyer and Bowen 2017). However, there has been no direct comparison of pregnancy rate estimates from the fall sampling program, which occurs 3 months prior to pupping, and the apparent pregnancy rates determined from the brand-sighting program conducted during the breeding season. Such a comparison may not be possible due to sample size limitations, but it may indicate if there is significant intra-uterine mortality in the last trimester in some years as has been reported in other species. Among harp seals, declines in pregnancy rates have been linked to density-dependent changes in abundance and density-independent environmental changes, which operate through a mechanism of increased late-term abortion rates when conditions are poor (Stenson et al. 2016). Variable and sometimes high rates of intra-uterine mortality have also been reported in walrus, Weddell seals, harbour seals, and Steller sea lions (summarized in Testa 1987). However, in the UK, the grey seal population has also expanded rapidly, but in recent years growth has slowed, most likely a result of a marked decline in juvenile survival, rather than a change in productivity (Thomas et al 2019).

Data on juvenile survival among northwest Atlantic grey seals is limited to information from the brand re-sighting program on Sable Island. In the deterministic model, juvenile mortality is assumed to be a multiplier of the adult mortality rate. In the last assessment, an ad hoc approach determined that juvenile mortality rates are approximately 15 times adult rates. The deterministic model adjusts the carrying capacity (K) and adult mortality rate to fit the model to the survey estimates of pup production, assuming a relationship described by the theta-logistic equation. This relationship was assumed not to have changed since the last assessment. Using this formulation, juvenile mortality increases slowly with increasing abundance, but then increases more rapidly as population abundance approaches K. Within the IPM, density-dependent changes in juvenile survival are described using a generalized Beverton-Holt function. Juvenile mortality initially increases rapidly as population abundance increases, but this rate of increase in mortality rates slows as K is approached. Unfortunately, we do not have sufficient information on the pattern of juvenile mortality to understand how it should be specified in the population model.

We have proposed that the slowing in the growth rate of the population is due to a density-dependent response to increasing resource competition acting on juvenile survival. Emigration may also be contributing to the decline in the rate of increase of the population. However, we feel that it is not a major factor, given the few sightings of Sable Island-branded animals in other colonies during the breeding season, the slow rate of increase in other colonies, and the slow rate at which new colonies are forming.

The previous estimate of grey seal abundance was 424,300 (95% CI= 263,600–578,300) with the population increasing at an annual rate of 4.4% (Hammill et al. 2017). The IPM ensemble provided a slightly lower estimate of 339,400 (95% CI = 317,900–361,500) in 2016, increasing at roughly 4% per year (Rossi et al 2021). In this assessment, the model estimated that total pup production grew from 92,300 (95% CI = 86,700–100,100) in 2016 to 99,300 (95% CI = 90,900–107,700) in 2021, while total abundance grew from 339,400 (95% CI=318,00–361,600) in 2016 to 366,400 (95% CI = 317,800–409,400) in 2021. The rate of increase from 2020 to 2021 was 2.6% (0.5–3.6%). The apparent paradox of a smaller population that continued to increase, does not appear to result from changes in reproduction rates, which remained high although some sample sizes were small. Instead, the revisions of the estimates resulted from changes in the assessment model, and revisions to our assumptions of how juvenile mortality may be operating on this population, resulting in a declining adult-to-pup ratio

in the population (Figure 5), as has been observed among grey seals in the UK (Thomas et al. 2019). This points to a need to improve our understanding of the functional relationship of juvenile survival within the context of density-dependent and environmental change if we are to improve our understanding of the grey seal dynamics and the role that grey seals play in the dynamics of marine ecosystems in eastern Canada.

For many years, a sex ratio of 1:1 was assumed for the northwest Atlantic grey seal population. While the sex ratio at birth is 1:1, in the northeast Atlantic, it has been found that juvenile males have higher mortality than females (Hall et al. 2001). However, recent analysis of the mark-sighting data from Sable Island has shown that males have similar mortality rates to females from birth until 25 years of age, but thereafter male survival decreases significantly (den Heyer and Bowen 2017). Assuming a constant age structure in population, the male and female survival estimated from mark-resighting analysis of individually marked seals on Sable Island suggested that there are 0.69 males for every female (den Heyer and Bowen 2017). However, given the until recently rapid increase in abundance and variable history of removals and ice-related mortality, it is unlikely the age distribution in the population is stable. Based on 5-year age-class bins, the IPM suggests that the sex ratio more likely approaches that of 0.93 M:F, which is close to the 1:1 sex ratio assumed in the deterministic model. Smaller age-class bins may indicate a more disparate sex ratio, but may be limited by sample sizes among the older age classes.

Northwest Atlantic grey seals form a single population (Wood et al. 2011). In recent years, there has been a rapid expansion in grey seal abundance in the northeastern United States, (den Heyer et al 2020) and grey seals are known to disperse to American waters, where some remain while others return seasonally to Canadian waters. However, this has not been included in the current assessment. In the present study, we provided estimates of total number of Canadian removals from the Canadian grey seal population and the probabilities that the population would decline below 70% of the maximum population size (N_{max}) which, for all areas, is the current population size. While there is no information on bycatch of grey seals in Canadian waters, there is a significant bycatch in fisheries located in the Gulf of Maine in the United States, which we have also not accounted for in this assessment. A recent study (Punt et al. 2021) has attempted to model this high bycatch and its impact on the grey seal population in the United States, but has been limited by the paucity of abundance information from that area and information on the movement of animals between the two countries. Overall, bycatch and other sources of anthropogenic removals such as the nuisance seal program, which were poorly documented, are subsumed into the model estimates of natural mortality (e.g., Hammill et al. 2015). While permits are no longer issued under the nuisance seal program, the absence of information on bycatch may impact our estimates of density-dependent changes in juvenile mortality as well as developing measures to reduce bycatch in fisheries. Future research should consider including grey seals in a common assessment model to evaluate the impact of directed harvests and removals due to incidental catches in commercial fisheries from both countries.

The model identified total harvest levels of 24,200 to 77,300 animals, depending on the age structure of harvested animals that respected the management objective to ensure an 80% probability that the population remains above N_{70}. These estimates of total removals are associated with several caveats. Currently, the population model fitted to the aerial survey estimates and the projection model assume that both the population sex ratio and the sex ratio of the harvest are close to 1:1. Also, as outlined above, four different model formulations for juvenile survival were used. The different formulations did have an impact on estimates of abundance and trend, and would impact sustainable harvest estimates. However, the data were not sufficiently informative to indicate which model was best. Consequently, an ensemble abundance estimate was derived by pooling the posterior samples from the four models, then

considering the quantiles of those pooled samples. Harvest mortality was treated as an additional source of mortality, but some of the animals that would be harvested would not have survived, particularly animals in their first year, which would reduce the actual impact of harvest mortality on the population. Additional uncertainties include the assumptions that future reproductive rates will remain unchanged. It is also assumed that there is no unusual mortality event occurring over the projection period. We have provided advice by herd based on harvesting in winter at the breeding colonies. Excessive harvests over several years at particular colonies could affect the long-term viability of these colonies. Outside of the breeding season, there is considerable movement of animals between the Scotian Shelf and the Gulf. For winter harvests the herd-specific harvests should be considered, but for harvesting at other times of the year, harvesting based on a combined total would be more reasonable.

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Table 1. Notation for grey seal population dynamics model and likelihood equations. Values used in the grey seal case study are given in parentheses. (*) indicates a parameter that was estimated.

Indices

Symbol	Description
A	Plus group age-class ($A = 30$)
T	Final model year ($T = 2016$)
h	Herd (1 = Scotian Shelf; 2 = Gulf)
a	Age index (yr) ($a = \{0, \ldots, A\}$)
s	Sex (1 = male; 2 = female)
t	Year ($t = \{1960, 1961, \ldots, T\}$)
i	Marking year ($I = \{1985, 1986, 1987, 1989, 1998, 1999, \ldots, 2002\}$)
j	Resighting year ($j = \{1978, 1979, \ldots, T\}$)

Inputs

Symbol	Description
$I_{h,t}$	Pup production for herd h in year t
$C_{h,t}^{(0)}$	Age-0 removals from herd h in year t
$C_{h,t}^{(1+)}$	Age-1+ removals from herd h in year t
$n_{h,a,t}$	Number of age-a seals sampled for reproductive status from herd h in year t
$k_{h,a,t}$	Observed number of age-a pregnancies in herd h in year t
$Q_{s,i,j}$	Number of seals of sex s from cohort i that were sighted in year j
$r_{s,i,j}$	Number of seals of sex s from cohort i sighted in year j that were subsequently resighted
$x_{s,i,j}$	Number of seals of sex s from cohort i sighted in year j that had previously been sighted
γ	Annual reproductive rate among mature females (0.92)
$p_{h,t}^{(\text{ice})}$	Proportion of pupping occurring on pack ice for herd h in year t
$S_{h,t}^{(\text{ice})}$	Survival rate for pups born on pack ice for herd h in year t

Parameters

Symbol	Description
$N_h^{(1)}$	Age-1 abundance in first model year (*)
$M_{h,s,a}$	Instantaneous natural mortality rate (yr^{-1}) (*)
$M^{(I)}$	Instantaneous density-independent age-0 natural mortality rate (yr^{-1})
D_h	Parameter representing either density-dependent M in SBH equation or half-saturation in the GBH equation (*)
θ_h	Shape of density dependence in the GBH equation (*)
$a_{h,s,t}^{(50\%)}$	Age-at-50% maturity (*)
$a_{h,s}^{(95\%)}$	Age-at-95% maturity (*)
γ	Reproductive rate among mature females (*)
$p_{s,i,j}$	Probability that a branded seal of sex s in cohort i will be sighted in *year j* (*)

Latent population variables

Symbol	Description
$N_{h,s,a,t}$	Abundance by herd, sex, age, and year
$m_{h,s,a,t}$	Proportion mature by herd, sex, age, and year
P_a	Reproductive rate-at-age
$F_{h,t}$	Instantaneous age 1+ hunting rate (yr^{-1})
$Z_{h,s,a,t}$	Instantaneous total mortality rate (yr^{-1})
$S_h^{(I)}$	Density-independent recruit survival rate
$S_{h,t}^{(D)}$	Density-dependent recruit survival rate

Latent mark-recapture variables

Symbol	Description
$u_{s,i,j}$	Number of marked seals of sex s from cohort i that were first sighted in year j
$b_{s,a}$	Probability that a marked seal of sex s that survives until it returns to breed for the first time will return to breed at age a
$\varphi_{s,i,j}$	Probability that a seal of sex s in cohort i will survive year j
$\psi_{s,i,j}$	Probability that a previously unsighted seal of sex s in cohort i will be present at breeding ground in year j
$\lambda_{s,i,j}$	Probability that a seal of sex s in cohort i is resighted after year j
$\tau_{s,i,j}$	Probability that a seal of sex s in cohort i will be sighted in year j given that it was sighted on or after year j

Table 2. Integrated population dynamics model.

Demographic rates

Equation	Formula
T2.1: Proportion mature-at-age, $a < 4$	$m_{s,a} = 0$
T2.2: Proportion mature-at-age, $a \geq 4$	$m_{s,a} = \left(1 + \exp\left[\dfrac{-\ln(19)\left(a - a_s^{(50\%)}\right)}{a_s^{(95\%)} - a_s^{(50\%)}}\right]\right)^{-1}$
T2.3: Proportion mature-at-age, $a \geq 4$	$m_{s,a} = 1$
T2.4: Proportion maturing-at-age, $a \geq 4$	$b_{s,a} = m_{s,a} - m_{s,a-1}$
T2.5: Annual reproductive rate-at-age	$P_a = \gamma m_{2,a}$
T2.6: Total mortality rate, $a > 0$	$Z_{h,s,a,t} = M_{h,s,a} + F_{h,t}$

Initial abundance

Equation	Formula
T2.7: Age-1 abundance, $t = 0$	$N_{h,s,1,1} = N_h^{(1)}/2$
T2.8: Abundance, $a > 1$, $t = 0$	$N_{h,s,a,1} = N_{h,s,a-1,1}\exp\left(-M_{h,s,a-1}\right)$
T2.9: Weaned pup abundance, $t = 0$	$\hat{I}_{h,t} = 0.95\sum_{a=4}^{A} N_{h,2,a,1}P_a$

YOY dynamics

Equation	Formula
T2.10: Births	$B_{h,t} = \sum_{a=4}^{A-1} N_{1,2,a,t-1}P_a$
T2.11: Weaned pup abundance, $t > 0$	$\hat{I}_{h,t} = 0.95\left(B_{2,t}p_{h,t}^{(ice)}S_{h,t}^{(ice)} + B_{2,t}\left[1 - p_{h,t}^{(ice)}\right]\right)$
T2.12: Recruitment	$R_{h,t} = \hat{I}_{h,t} - C_{h,t}^{(0)}$
T2.13: Density-independent recruit survival rate	$S^{(I)} = \exp\left(-M^{(I)}\right)$
T2.14: Density-dependent recruit survival rate	$S_{h,t}^{(D)} = \begin{cases} \dfrac{D_h^{\theta_h}}{D_h^{\theta_h} + R_{h,t}^{\theta_h}}, & R \text{ model} \\ \dfrac{D_h^{\theta_h}}{D_h^{\theta_h} + \left(R_{h,t} + \sum_{a=1}^{A} N_{h,s,a,t}\right)^{\theta_h}}, & N \text{ model} \end{cases}$
T2.15: Age-1 abundance	$N_{h,s,1,t} = R_{h,t-1}S^{(I)}S_{h,t-1}^{(D)}/2$

Age 1+ dynamics

Equation	Formula
T2.16: Abundance $a \in \{2,3,\dots,A\text{-}1\}$	$N_{h,s,a,t} = N_{h,s,a-1,t-1}\exp\left(-Z_{h,s,a-1,t-1}\right)$
T2.17: Plus group abundance $a = A$	$N_{h,s,A,t} = \sum_{a=A-1}^{A} N_{h,s,a,t-1}\exp\left(-Z_{h,s,a,t-1}\right)$
T2.19: Removals	$C_{h,t}^{(1+)} = \sum_{s} \sum_{a=1}^{A} \frac{F_{h,t}}{Z_{h,s,a,t}} N_{h,s,a,t}\left[1 - \exp\left(-Z_{h,s,a,t}\right)\right]$

Mark-Resighting

Equation	Formula
T2.20: First sightings in year j	$u_{s,i,j} = Q_{s,i,j} - x_{s,i,j}$
T2.21: Probability of surviving year j	$\phi_{s,i,j} = \exp\left(-Z_{1,s,j-i,j}\right)$
T2.22: Probability that a previously uncaptured seal returned to breed at age 4	$\psi_{s,i,i+4} = b_{s,4}$
T2.23: Probability that a previously uncaptured seal returned to breed in year j, $j > i+4$	$\psi_{s,i,j} = \psi_{s,i,j-1}\left(1 - p_{s,i,j}\right)\phi_{s,i,j-1} + b_{s,j-i}$
T2.24: Probability of capture after year j, $j < T$	$\lambda_{s,i,j} = \psi_{s,i,j}p_{s,i,j+1} + \psi_{s,i,j}\left(1 - p_{s,i,j+1}\right)\lambda_{s,i,j+1}$
T2.25: Probability of capture after year T	$\lambda_{s,i,T} = 0$
T2.26: Probability of capture in year j given capture in or after year j	$\tau_{s,i,j} = \dfrac{p_{s,i,j}}{p_{s,i,j} + \left(1 - p_{s,i,j}\right)\lambda_{s,i,j}}$

Table 3. Four integrated population models fitted in this analysis based on unique configurations of density-dependent and density-independent survival from recruitment to age 1. YOY = Young of Year; recruitment = animals successfully weaned; N(0.1, 0.05) means that the prior had a normal distribution with a mean of 0.1 and a standard deviation of 0.05.

Model name	Density affecting YOY survival	Density-independent YOY mortality (yr^{-1})
R	Recruitment	Fixed at 0.1
N	Total abundance	Fixed at 0.1
R-DI	Recruitment	Estimated with N(0.1, 0.05) prior
N-DI	Total abundance	Estimated with N(0.1, 0.05) prior

Table 4. Pup production estimates used as input into the population models. Estimates from the Sable Island colony (1962–1971), CNS (1962–1989) and Gulf colonies (1962–1984) are very uncertain. The SEs for these periods are assumed values and reflect considerable uncertainty (bold italic).

Year	Sable Island		CNS		Gulf		Scotian Shelf	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
1962	-	-	130	*400*	-	-	-	-
1963	400	**400**	180	*400*	-	-	400	**400**
1964	550	**550**	190	*400*	-	-	550	**550**
1965	660	**660**	230	*400*	-	-	660	**660**
1966	-	-	-	-	900	*2,000*	-	-
1967	580	**580**	212	*400*	-	-	792	**580**
1968	700	**700**	134	*400*	-	-	834	**700**
1969	800	**800**	104	*400*	-	-	904	**800**
1970	800	**800**	450	*400*	-	-	1,250	**800**
1971	1,000	**1,000**	382	*400*	-	-	1,382	**1,000**
1972	950	**950**	408	*400*	-	-	1,358	**950**
1973	1,200	**1,200**	431	*400*	-	-	1,631	**1,200**
1974	1,250	**1,250**	482	*400*	-	-	1,732	**1,250**
1975	-	-	-	-	3,300	*3,800*	-	-
1976	2,000	**2,000**	466	*400*	-	-	2,466	**2,000**
1977	2,181	173	370	*400*	3,900	*3,900*	2,551	173
1978	2,687	192	290	*400*	-	-	2,977	192
1979	2,933	201	269	*400*	-	-	3,202	201
1980	3,344	214	115	*400*	-	-	3,459	214
1981	3,143	208	197	*400*	-	-	3,340	208
1982	4,489	248	276	*400*	-	-	4,765	248
1983	5,435	273	152	*400*	-	-	5,587	273
1984	5,856	283	80	*400*	7,169	911	5,936	283
1985	5,606	277	125	*400*	6,706	795	5,731	277
1986	6,301	294	144	*400*	5,588	679	6,445	294
1987	7,391	318	179	*400*	-	-	7,391	318
1988	8,593	343	-	-	-	-	8,593	343
1989	9,712	365	179	*400*	9,352	1,756	9,712	365
1990	10,451	575	-	-	9,176	649	10,451	575
1993	15,500	463	-	-	-	-	15,500	463
1994	-	-	-	-	-	-	-	-
1996	-	-	-	-	10,717	1,306	-	-
1997	25,400	750	1,061	242	6,839	800	26,461	750
2000	-	-	-	-	5,260	910	-	-
2004	41,500	4,381	2,471	76	14,556	1,200	43,971	4,457
2007	54,482	8,909	3,023	57	11,413	1,077	57,505	8,966
2010	62,054	4,973	2,959	136	11,229	6,442	65,013	5,109
2016	87,495	13,560	4,783	683	9,833	1,820	92,278	14,243
2021	76,600	2,900	4,700	550	16,900	2,400	81,300	3,000

Table 5. Year, age (years), number of females collected between 1969 and 2012 (n) and number of females pregnant (Preg). Note that age 8 refers to females aged 8 years and older.

Year	Age	N	Preg rate	Age	N	Preg rate	Age	N	Preg rate	Age	N	Preg rate	Age	N	Preg rate
1970	4	12	0.25	5	7	0.71	6	9	1.00	7	6	1.00	8	36	0.81
1983	4	4	0.00	5	4	0.75	6	8	0.88	7	1	1.00	8	48	0.90
1987	4	4	0.25	5	2	1.00	6	4	0.75	7	7	0.86	8	34	0.94
1988	4	7	0.14	5	10	0.50	6	8	0.63	7	9	0.67	8	71	0.94
1989	4	7	0.29	5	14	0.71	6	10	0.90	7	5	0.80	8	57	0.89
1993	4	16	0.06	5	16	0.75	6	13	0.92	7	7	0.86	8	32	0.91
1994	4	0	-	5	0	-	6	0	-	7	1	0.00	8	0	-
1995	4	1	0.00	5	3	0.00	6	1	1.00	7	2	1.00	8	1	1.00
1997	4	0	-	5	0	-	6	1	1.00	7	0	-	8	0	-
1998	4	0	-	5	1	0.00	6	0	-	7	0	-	8	5	0.80
1999	4	0	-	5	0	-	6	1	0.00	7	1	1.00	8	9	0.78
2000	4	0	-	5	2	0.00	6	2	1.00	7	2	1.00	8	13	0.92
2001	4	5	0.40	5	3	0.67	6	6	-	7	2	1.00	8	18	0.89
2002	4	1	0.00	5	0	-	6	1	1.00	7	1	1.00	8	8	0.88
2003	4	7	0.71	5	4	0.75	6	3	1.00	7	7	0.86	8	20	0.90
2004	4	2	0.00	5	4	1.00	6	3	1.00	7	0	-	8	8	0.88
2005	4	5	0.20	5	7	1.00	6	3	0.33	7	4	0.75	8	39	1.00
2006	4	1	0.00	5	3	1.00	6	1	1.00	7	0	-	8	1	1.00
2007	4	1	0.00	5	0	-	6	0	-	7	0	-	8	0	-
2008	4	1	0.00	5	3	1.00	6	3	1.00	7	0	-	8	10	0.90
2009	4	0	-	5	0	-	6	6	1.00	7	5	1.00	8	9	0.78
2011	4	2	0.00	5	2	0.50	6	3	0.67	7	4	0.50	8	11	1.00
2012	4	5	0.20	5	10	0.20	6	8	0.63	7	5	1.00	8	16	0.75
2013	4	0	-	5	3	0.00	6	2	0.50	7	4	0.25	8	14	1.00
2014	4	3	0.00	5	1	0.00	6	0	-	7	1	1.00	8	6	0.83
2015	4	1	1.00	5	2	0.00	6	5	1.00	7	4	1.00	8	23	0.96
2016	4	2	0.50	5	5	0.80	6	5	0.80	7	0	-	8	12	1.00
2017	4	4	0.00	5	4	0.25	6	2	1.00	7	2	1.00	8	19	1.00
2018	4	3	0.00	5	2	1.00	6	2	1.00	7	4	1.00	8	25	0.96
2019	4	3	0.00	5	2	0.50	6	2	1.00	7	0	-	8	13	1.00
2020	4	4	0.00	5	1	1.00	6	1	1.00	7	2	1.00	8	9	1.00

Table 6. Number of individually marked seals by cohort and sex, the number resighted between 1978 and 2021.

Cohorts	Individually Marked			Resighted 1978–2021		
	Male	Female	Total	Male	Female	Total
1969	100	100	200	30	67	97
1970	100	100	200	48	102	150
1973	100	100	200	74	112	186
1974	300	700	1,000	45	69	114
1985	100	400	500	45	250	295
1986	100	400	500	57	240	297
1987	100	400	500	36	257	293
1989	10	500	510	5	301	306
1998	145	156	301	36	51	87
1999	243	258	501	78	96	174
2000	252	249	501	43	64	107
2001	235	267	502	32	61	93
2002	252	252	504	45	69	114
2014	323	378	701	1	31	32
2015	311	389	700	-	7	7
2016	314	388	702	-	1	1
Total	**2,985**	**5,037**	**8,022**	**575**	**1,778**	**2,353**

Table 7. Survival coefficient (S_{ice}) used to account for ice-born pups drowning before surveys were completed in the Gulf.

Year	Survival	Year	Survival	Year	Survival
1960	1.0	1980	0.8	2000	0.7
1961	1.0	1981	1.0	2001	0.7
1962	1.0	1982	1.0	2002	0.4
1963	1.0	1983	0.5	2003	1.0
1964	1.0	1984	1.0	2004	1.0
1965	1.0	1985	1.0	2005	0.7
1966	1.0	1986	1.0	2006	0.1
1967	1.0	1987	1.0	2007	0.5
1968	1.0	1988	1.0	2008	0.6
1969	0.8	1989	1.0	2009	1.0
1970	1.0	1990	1.0	2010	0.6
1971	1.0	1991	0.9	2011	1.0
1972	0.9	1992	1.0	2012	1.0
1973	1.0	1993	0.8	2013	0.7
1974	1.0	1994	1.0	1014	0.9
1975	0.4	1995	0.2	2015	0.8
1976	0.8	1996	1.0	2016–2021	1.0
1977	1.0	1997	0.7	-	-
1978	0.6	1998	0.7	-	-
1979	1.0	1999	0.2	-	-

Table 8. Estimated mean mortality rates, and estimated mean carrying capacity (K) for Sable Island, the Scotian shelf (Sable and coastal colonies combined) and the Gulf of St. Lawrence (Gulf). Standard errors (SE) are shown in parenthesis and 95% confidence intervals (CI) in square brackets. K has been rounded to the nearest 100).

Location	Mortality (SE) [95% CI]	K (SE) [95% CI]
Scotian shelf	0.0354 (0.0056) [0.0231–0.0449]	332,900 (24,200) [285,300–380,500]
Gulf	0.0254 (0.0115) [0.0200–0.0423]	88,800 (110,800) [42,500–584,600]
Sable	0.0368 (0.0051) [0.0258–0.0455]	319,300 (23,000) [274,300–365,300]

Table 9. IPM estimates (posterior modes) of total abundance and the density-dependence scale (D) and shape (θ). D represents the density (recruitment in the R models and total abundance in the N models) at which the density-dependent survival is 0.5.

Fitted to data up to 2016 (Rossi et al., 2021)

Model	2016 Shelf abundance	2016 Gulf abundance	Shelf D	Gulf D	Shelf θ	Gulf θ
R	341,500	47,680	22.5	5.3	0.70	2.57
N	349,700	51,680	116.2	28.9	0.75	2.60

Fitted to data up to 2021

Model	2016 Shelf abundance	2016 Gulf abundance	Shelf D	Gulf D	Shelf θ	Gulf θ
R	286,800	52,558	17.1	3.0	0.97	1.22
N	289,000	54,600	85.8	15.2	1.11	1.29
R-DI	278,000	53,000	31.9	3.9	1.74	1.30
N-DI	280,400	55,100	163.0	20.2	2.68	1.38

Table 10. Harvest levels that have an 80% probability of remaining above N_{70} for the Scotian Shelf (Shelf) and Gulf of St. Lawrence (Gulf).

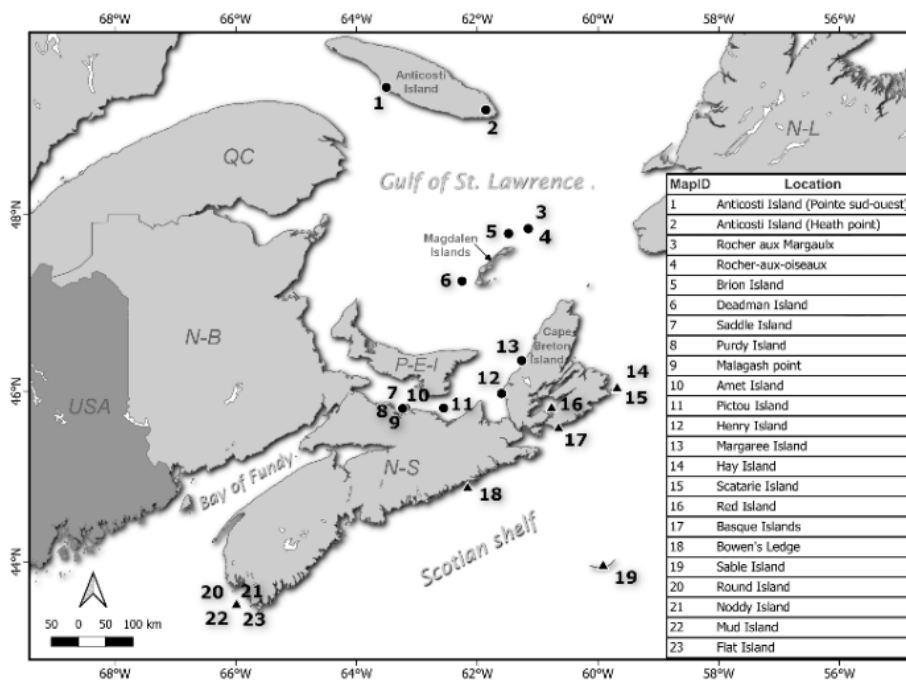| Proportion pups in harvest	Shelf	Gulf	Total
0.50	22,500	1,700	24,200
0.90	60,200	7,100	67,300
0.95	68,600	8,700	77,300

FIGURES

Figure 1. Southern Gulf of St. Lawrence and Scotian Shelf showing the locations of Sable Island, coast of Nova Scotia (▲) and Gulf of St. Lawrence (●) grey seal colonies.
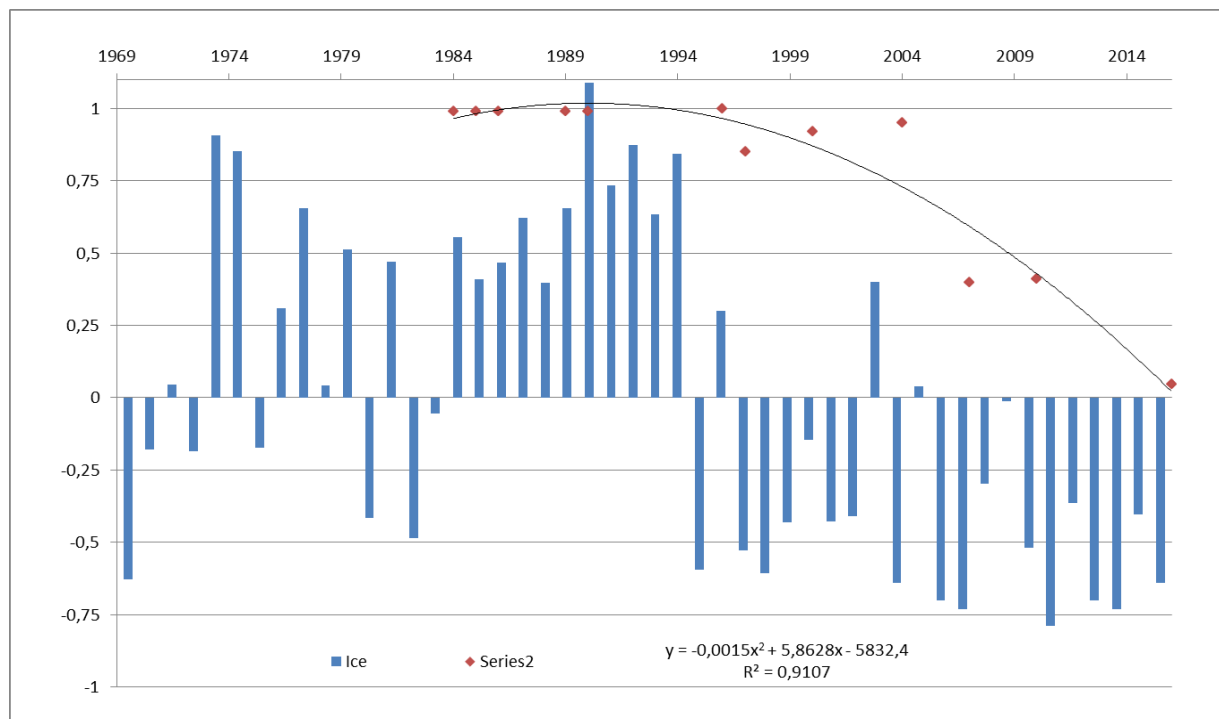

Figure 2. The proportion of animals pupping on the ice compared to the ice anomaly (ice index; Hammill et al. 2017). Ice data are from Environment Canada.
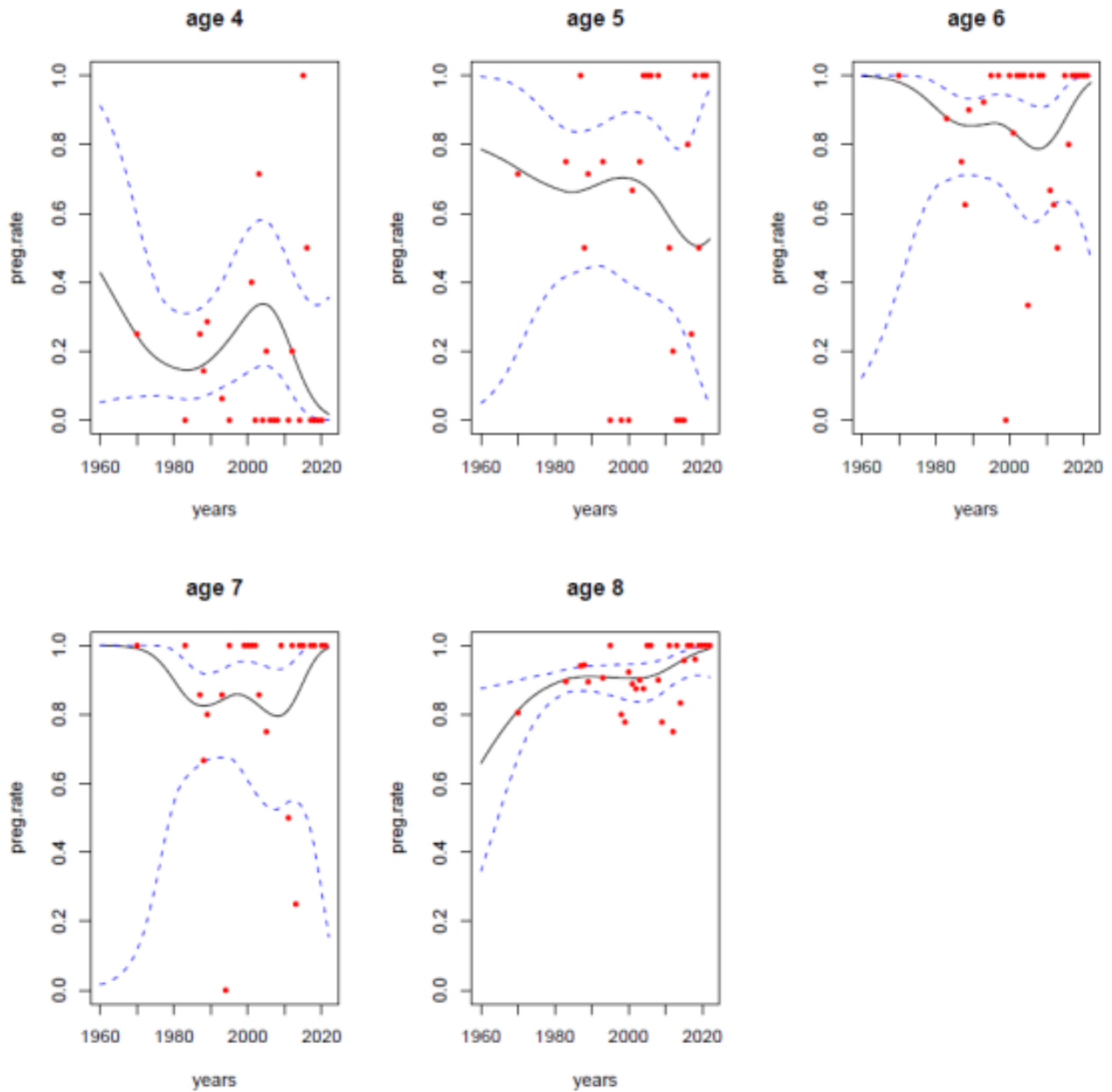
Figure 3. Age-specific reproductive rates (red circles) and non-parametric smoothed rates (solid line) for the period of 1969–2020 for ages 4–8+ years when animals were collected. Dotted lines represent 95% CI.
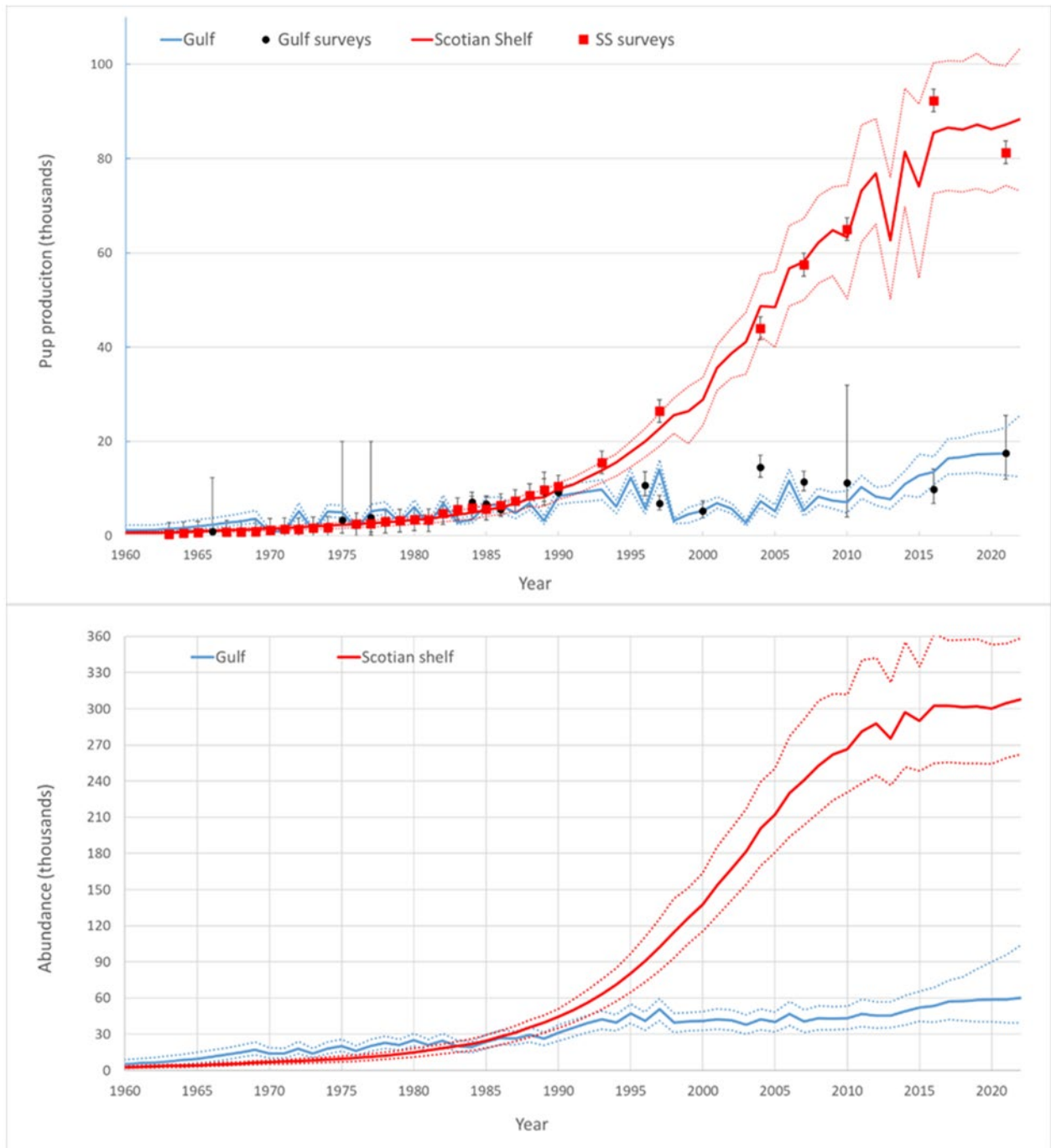
Figure 4. Deterministic model estimates of pup production for the Scotian Shelf and Gulf of St. Lawrence (top) and total abundance estimates (lower), with 95% CI as dotted lines) and survey estimates (points and squares, with 95% CI as error bars).
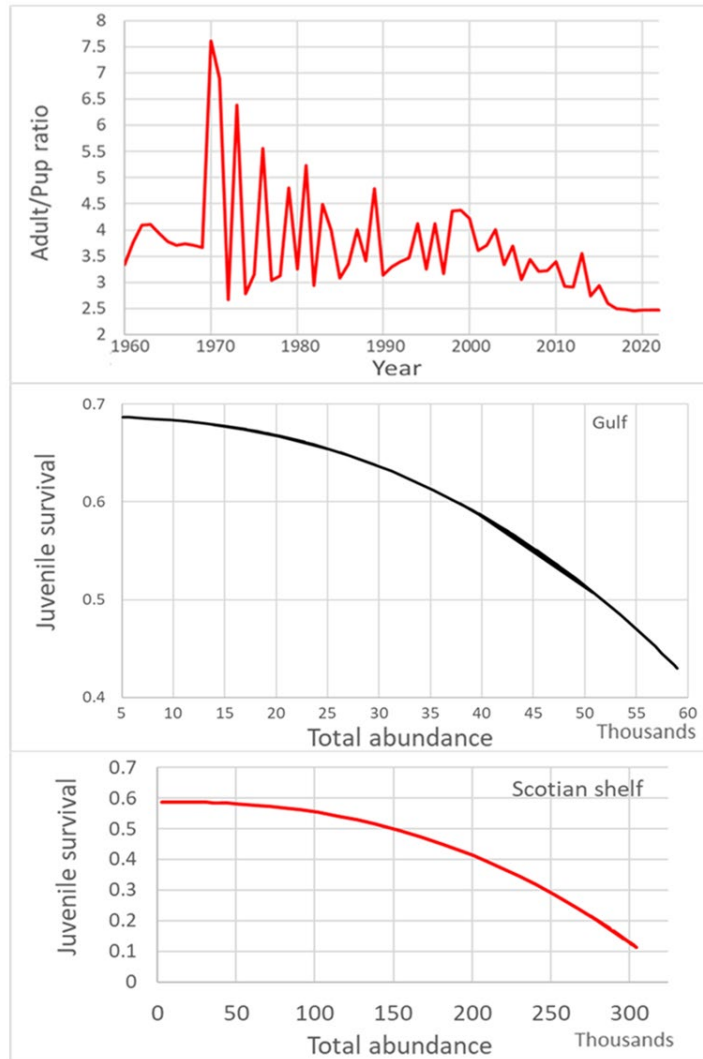
Figure 5. Change in the estimated ratio of 1+ animals to pups in the population from 1960 to 2021, based on the deterministic population model (top). Change in juvenile survival with changes in abundance related to density-dependent factors in the Gulf (middle) and changes in density-dependent survival of juveniles on the Scotian Shelf (bottom).
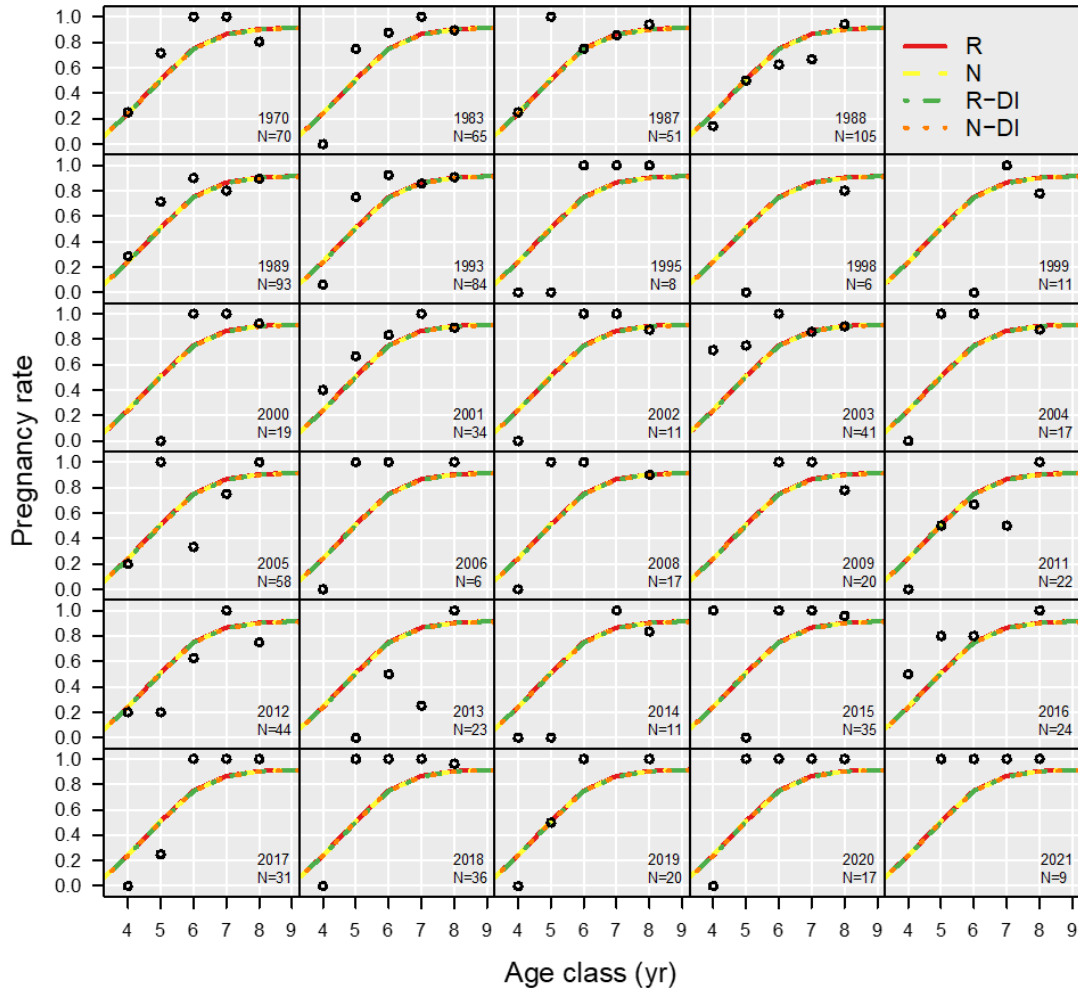
Figure 6. Integrated population model (IPM) fits (lines) to observed pregnancy rates (circles) from samples collected in the Gulf of St. Lawrence for years with sample size (N) greater than 1. Model runs: R = density-dependent survival affected by abundance of weaned animals (recruitment), density-independent mortality fixed (Table 3); N = density-dependent survival affected by total abundance, density-independent mortality fixed; R-DI = recruitment density-dependent survival, density-independent mortality estimated; N-DI = density-dependent survival affected by total abundance, density-independent mortality estimated.
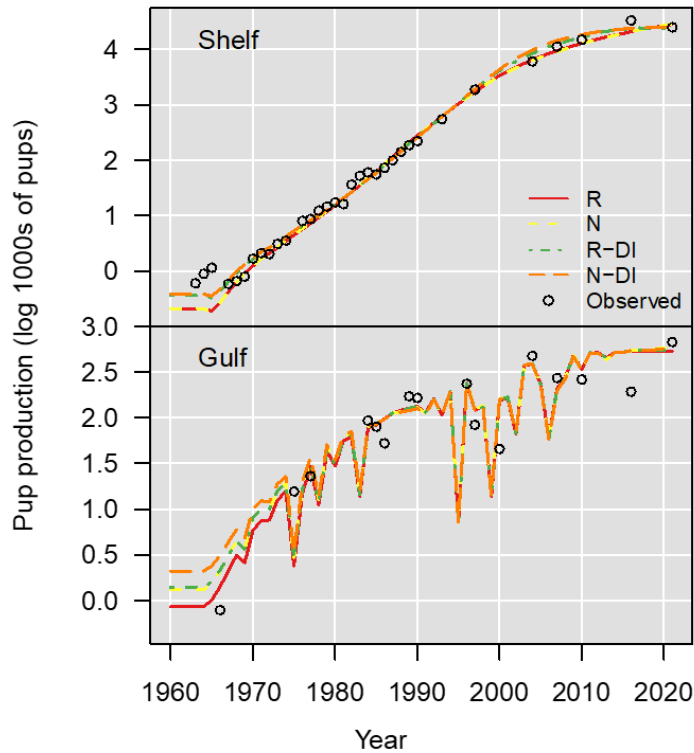
Figure 7. Integrated population model (IPM) fits (lines) to the Scotian Shelf (top) and the Gulf of St. Lawrence (bottom) pup production survey estimates (circles), 1960–2021. Model runs: R = density-dependent survival affected by abundance of weaned animals (recruitment), density- independent mortality fixed (Table 3); N = density-dependent survival affected by total abundance, density-independent mortality fixed; R-DI = recruitment density-dependent survival, density-independent mortality estimated; N-DI = density-dependent survival affected by total abundance, density-independent mortality estimated.
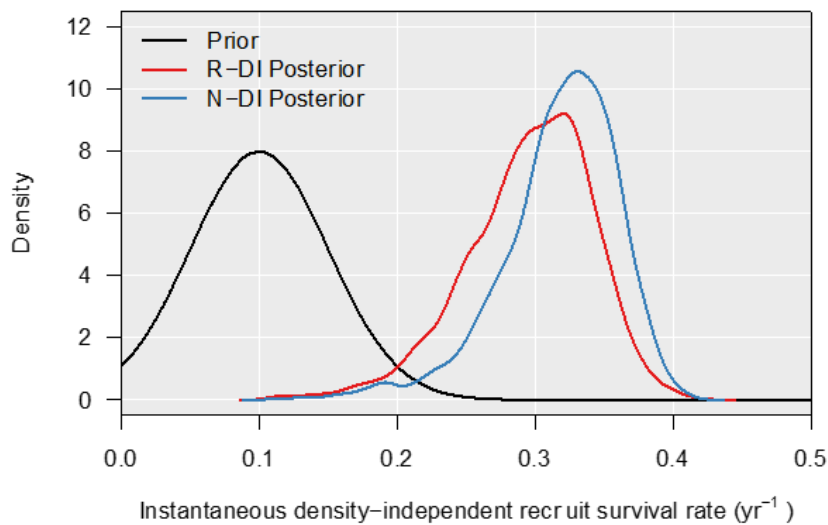

Figure 8. Prior and posterior distributions for the rate of density-independent survival from recruitment to age 1. Model runs: R = density-dependent survival affected by abundance of weaned animals (recruitment), density-independent mortality fixed (Table 3); N = density-dependent survival affected by total abundance, density-independent mortality fixed; R-DI = recruitment density-dependent survival, density-independent mortality estimated; N-DI = density-dependent survival affected by total abundance, density-independent mortality estimated.
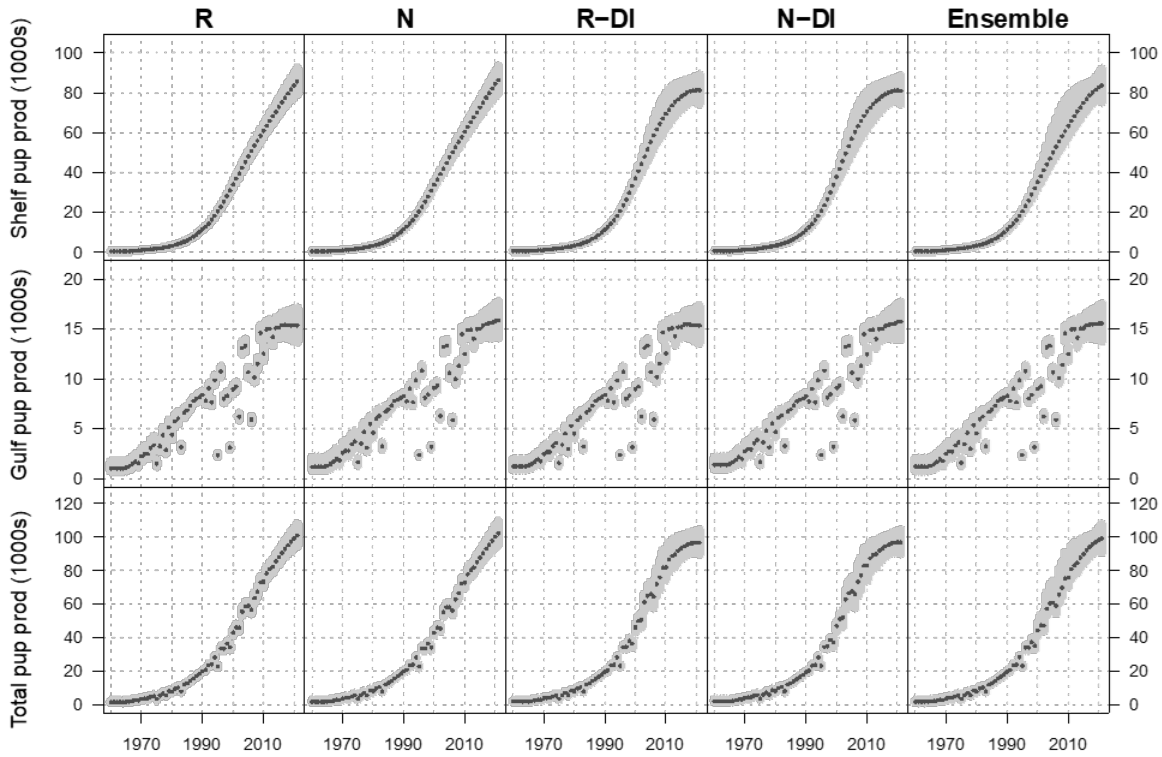
Figure 9. IPM estimates of pup production for the Shelf herd (top row), Gulf herd (middle row), and total population (bottom row). Points represent posterior modes while shaded regions represent the central 95% uncertainty interval. Model runs: R = density-dependent survival affected by abundance of weaned animals (recruitment), density-independent mortality fixed (Table 3); N = density-dependent survival affected by total abundance, density-independent mortality fixed; R-DI = recruitment density-dependent survival, density-independent mortality estimated; N-DI = density-dependent survival affected by total abundance, density-independent mortality estimated.

Figure 10. IPM estimates of abundance for the Shelf herd (top row), Gulf herd (middle row), and total population (bottom row). Points represent posterior modes while shaded regions represent the central 95% uncertainty interval. Model runs: R = density-dependent survival affected by abundance of weaned animals (recruitment), density-independent mortality fixed (Table 3); N = density-dependent survival affected by total abundance, density-independent mortality fixed; R-DI = recruitment density-dependent survival, density-independent mortality estimated; N-DI = density-dependent survival affected by total abundance, density-independent mortality estimated.
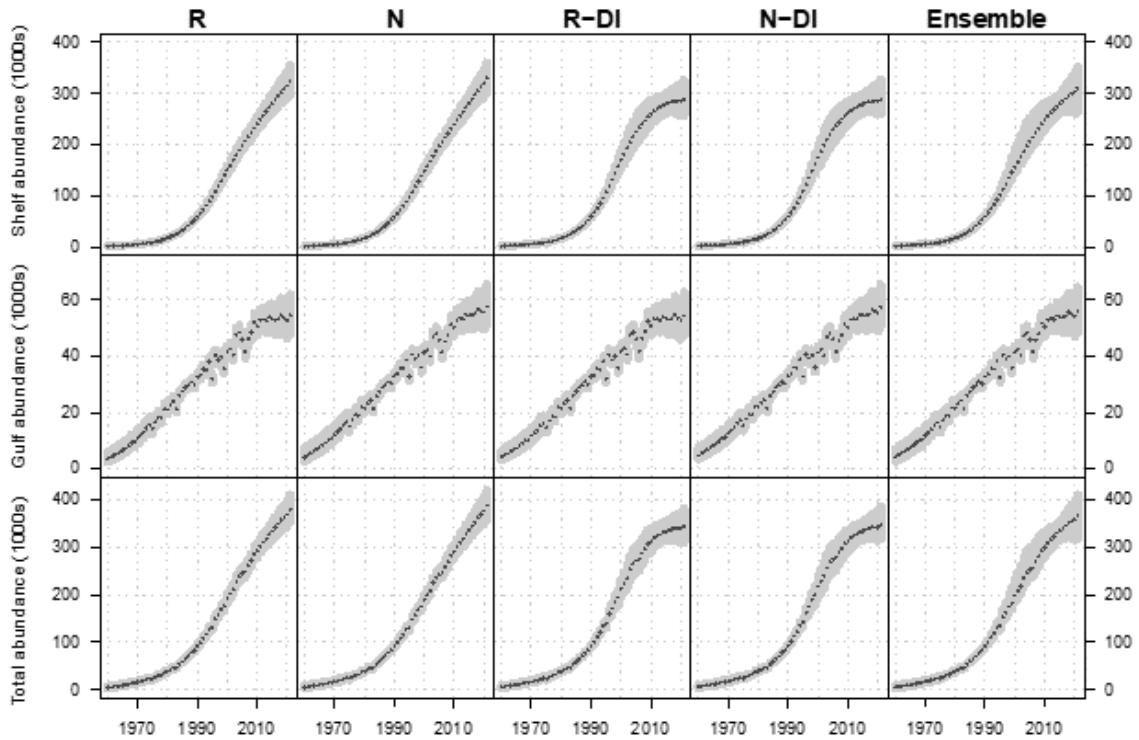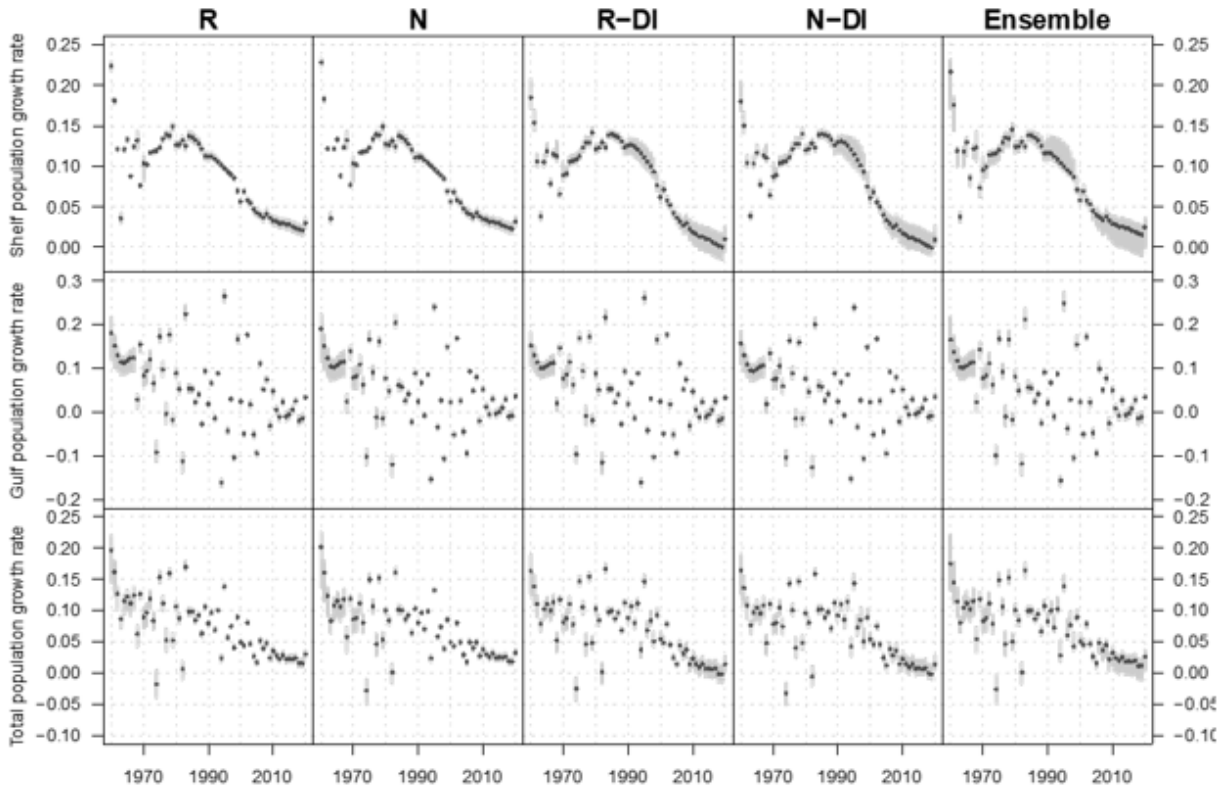
Figure 11. IPM estimates of the rate of population increase for the Shelf herd (top row), Gulf herd (middle row), and total population (bottom row). Points represent posterior modes while shaded regions represent the central 95% uncertainty interval. Model runs: R = density-dependent survival affected by abundance of weaned animals (recruitment), density-independent mortality fixed (Table 3); N = density-dependent survival affected by total abundance, density-independent mortality fixed; R-DI = recruitment density-dependent survival, density-independent mortality estimated; N-DI = density-dependent survival affected by total abundance, density-independent mortality estimated. Ensemble = combined estimates from all models.
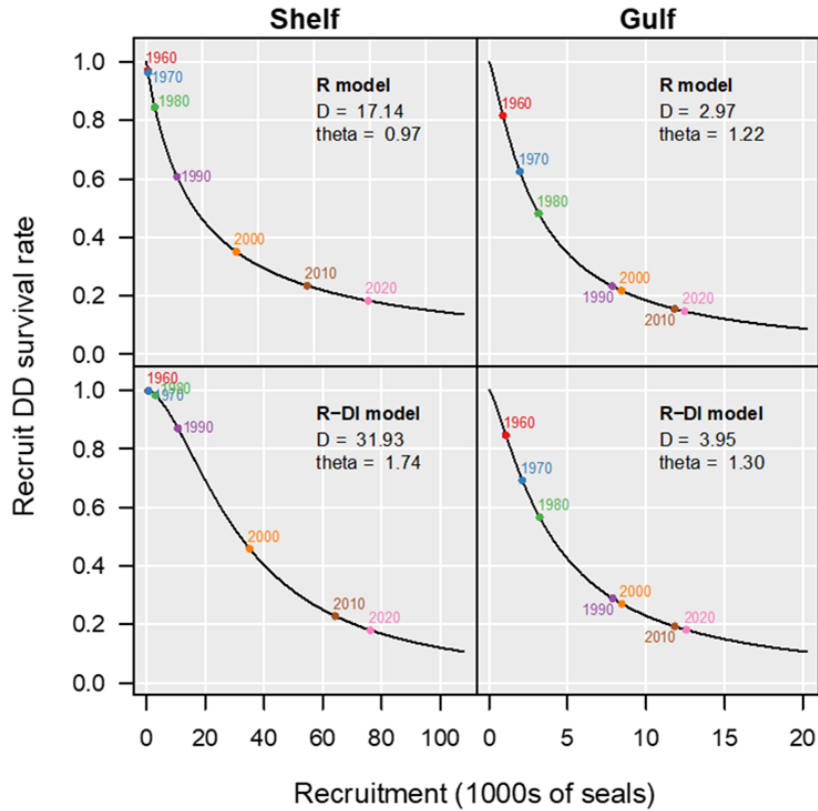
Figure 12. Estimated relationship between grey seal recruitment (YOY abundance after weaning and hunting/science/nuisance/bycatch/culling removals) and the density-dependent component of recruit survival for each herd (columns) by the R model (top row) and the R-DI model (bottom row). Points on the curves represent estimates from individual years. Model runs: R = density-dependent survival affected by abundance of weaned animals (recruitment), density-independent mortality fixed (Table 3);
N = density-dependent survival affected by total abundance, density-independent mortality fixed;
R-DI = recruitment density-dependent survival, density-independent mortality estimated;
N-DI = density-dependent survival affected by total abundance, density-independent mortality estimated.
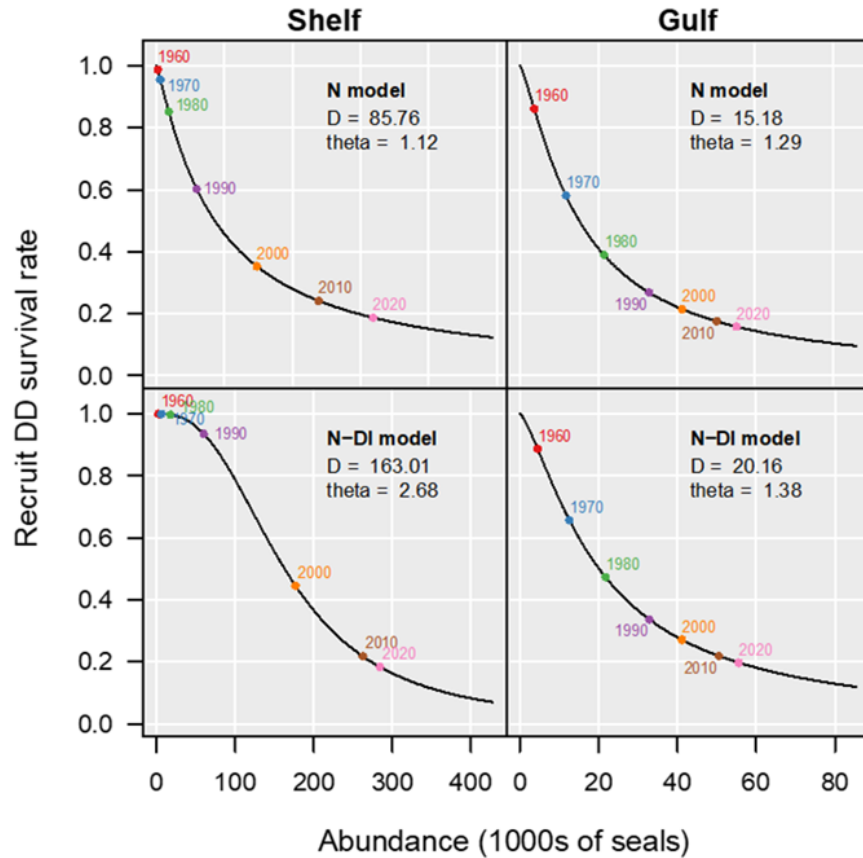
Figure 13. Estimated relationship between grey seal abundance and the density-dependent component of recruit survival for each herd (columns) by the N model (top row) and the N-DI model (bottom row). Points on the curves represent estimates from individual years. Model runs: R = density-dependent survival affected by abundance of weaned animals (recruitment), density-independent mortality fixed (Table 3); N = density-dependent survival affected by total abundance, density-independent mortality fixed; R-DI = recruitment density-dependent survival, density-independent mortality estimated; N-DI = density-dependent survival affected by total abundance, density-independent mortality estimated.
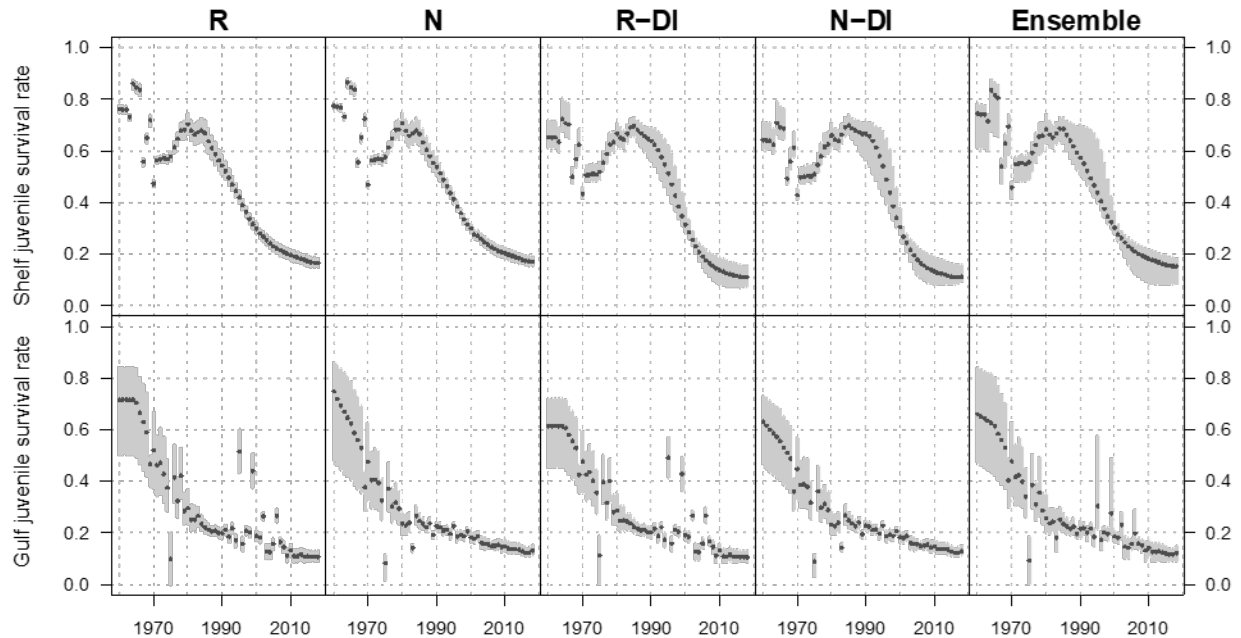
Figure 14. Estimated proportion of each cohort that survived from weaning to age 4. Shaded regions represent posterior modes. Model runs: R = density-dependent survival affected by abundance of weaned animals (recruitment), density-independent mortality fixed (Table 3); N = density-dependent survival affected by total abundance, density-independent mortality fixed; R-DI = recruitment density-dependent survival, density-independent mortality estimated; N-DI = density-dependent survival affected by total abundance, density-independent mortality estimated. Ensemble = combined estimates from all models.


Figure 15. IPM estimates of annual sex-specific survival for six age classes. Points represent posterior modes while lines represent the central 95% posterior interval. Model runs: R = density-dependent survival affected by abundance of weaned animals (recruitment), density-independent mortality fixed (Table 3); N = density-dependent survival affected by total abundance, density-independent mortality fixed; R-DI = recruitment density-dependent survival, density independent mortality estimated; N-DI = density-dependent survival affected by total abundance, density-independent mortality estimated.
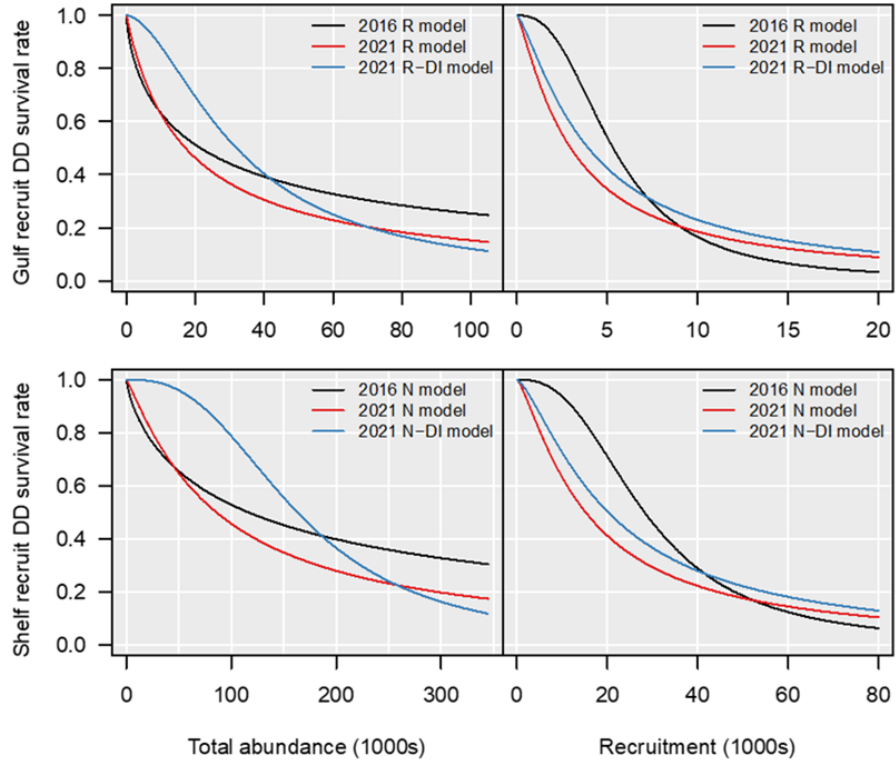
Figure 16. Estimated density-dependence relationships from IPMs fitted to data from 1960–2016 (black line) and 1960–2021 (red and blue lines). Recruitment is the number of YOY animals alive after the winter harvest.
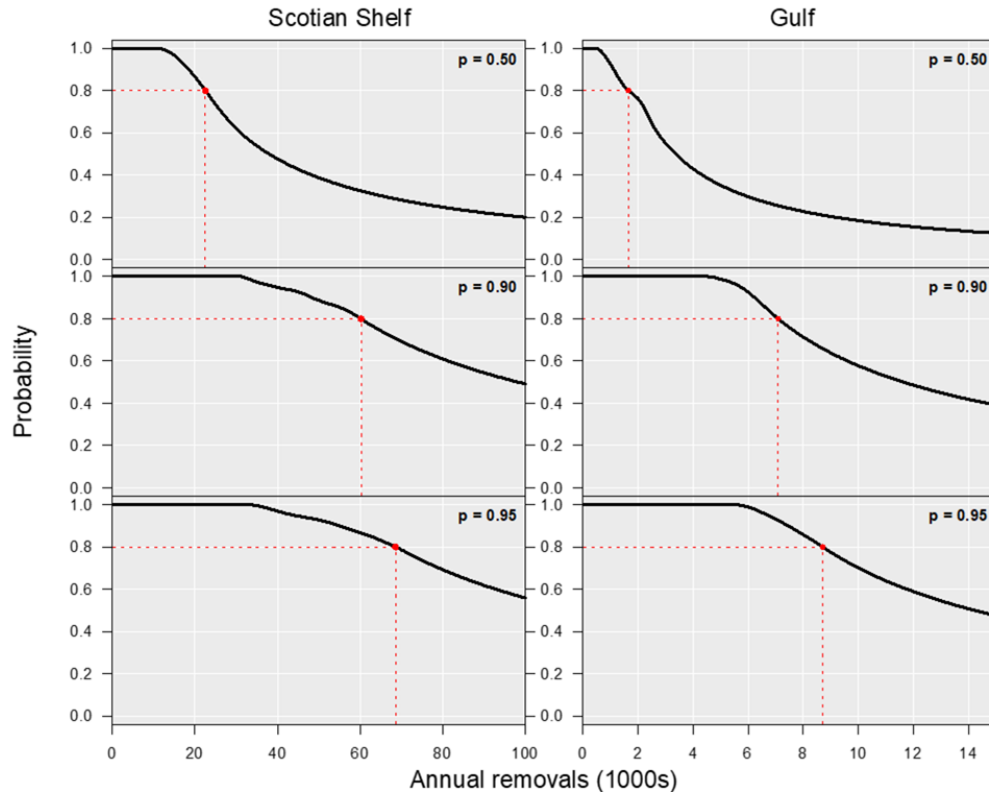
Figure 17. Harvest levels (1000s) that would have an 0.8 (80%) probability that the population would remain above N_{70} for different age compositions of the harvest. The scenarios examined a proportion (p) of: p = 0.95 which represents a harvest comprising 95% YOY / 5% 1+; p = 0.9 representing a harvest comprised of 90%YOY / 10%1+; and p = 0.5, which consists of a harvest of 50% YOY / 50% 1+. YOY is young of the year and 1+ represents animals aged 1 year and older.

APPENDIX A

Table A1. Removals of grey seals. YOY is young of the year and 1+ represents animals aged 1 year and older.

Scotian Shelf

YEAR	Nuisance	Science	YOY	1 plus	Cull 1+	Cull YOY
1960	0	0	0	0	0	0
1961	0	0	0	0	0	0
1962	0	0	0	0	0	0
1963	0	0	0	0	0	0
1964	0	0	0	0	0	0
1965	0	0	0	0	0	0
1966	0	0	0	0	0	0
1967	0	0	0	0	0	0
1968	0	0	0	0	0	0
1969	0	0	0	0	0	0
1970	43	2	0	0	0	0
1971	1	12	0	0	0	0
1972	0	0	0	0	0	0
1973	0	0	0	0	0	0
1974	0	2	0	0	0	0
1975	22	0	0	0	0	0
1976	0	9	0	0	0	0
1977	0	69	0	0	0	0
1978	0	0	0	0	0	0
1979	0	0	0	0	0	0
1980	0	0	0	0	0	0
1981	0	69	0	0	0	0
1982	0	0	0	0	0	0
1983	0	214	0	0	0	0
1984	0	20	0	0	0	0
1985	0	0	0	0	0	0
1986	0	0	0	0	0	0
1987	0	0	0	0	0	0
1988	0	46	0	0	0	0
1989	0	477	0	0	0	0
1990	0	197	0	0	0	0
1991	0	0	0	0	0	0
1992	0	6	0	0	0	0
1993	0	0	0	0	0	0
1994	0	0	0	0	0	0
1995	0	0	0	0	0	0
1996	0	24	0	0	0	0
1997	0	7	0	0	0	0
1998	0	0	0	0	0	0
1999	1,638	0	0	0	0	0
2000	1,743	0	0	0	0	0
2001	1,820	0	0	0	0	0
2002	1,953	0	0	0	0	0
2003	2,079	0	0	0	0	0
2004	2,660	0	0	0	0	0
2005	3,105	0	0	0	0	0
2006	3,437	0	0	0	0	0
2007	3,373	0	0	0	0	0
2008	3,334	0	0	0	0	0
2009	3,381	0	0	0	0	0
2010	3,421	0	0	0	0	0
2011	3,579	0	0	0	0	0
2012	3,681	0	0	0	0	0
2013	3,081	0	0	0	0	0
2014	3,081	0	0	0	0	0
2015	3,200	0	0	0	0	0
2016	3,294	0	0	0	0	0
2017	3,365	0	0	0	0	0
2018	3,460	0	0	0	0	0
2019	3,571	0	0	0	0	0
2020	0	0	0	0	0	0
2021	0	0	0	0	0	0

Gulf

YEAR	Nuisance	Science	YOY	1+	Cull 1+	Cull YOY
1960	0	0	0	0	0	0
1961	0	0	0	0	0	0
1962	0	0	0	0	0	0
1963	0	0	0	0	0	0
1964	0	0	0	0	0	0
1965	0	0	0	0	0	0
1966	0	0	0	0	0	0
1967	0	0	0	0	0	0
1968	0	0	0	0	0	0
1969	0	0	0	0	159	485
1970	0	22	0	0	0	70
1971	0	0	0	0	45	361
1972	0	0	0	0	80	191
1973	0	0	0	0	39	127
1974	0	1	0	0	75	560
1975	0	1	0	0	447	1,238
1976	0	1	0	0	16	79
1977	0	0	0	0	308	673
1978	0	0	0	0	57	267
1979	0	9	0	0	190	215
1980	0	0	0	0	336	994
1981	0	0	0	0	552	1,242
1982	0	199	0	0	880	961
1983	0	12	0	0	814	1,721
1984	0	12	0	0	135	96
1985	0	0	0	0	141	113
1986	0	230	0	0	402	180
1987	0	249	0	0	456	593
1988	0	298	0	0	379	90
1989	0	45	0	0	138	1,700
1990	0	16	50	0	48	38
1991	0	0	50	0	0	0
1992	0	260	50	0	0	0
1993	0	6	50	0	0	0
1994	0	39	50	0	0	0
1995	0	5	50	0	0	0
1996	0	33	50	0	0	0
1997	0	25	50	0	0	0
1998	0	20	50	0	0	0
1999	0	69	50	0	0	0
2000	0	89	50	0	0	0
2001	0	39	50	0	0	0
2002	0	100	50	0	0	0
2003	0	13	50	0	0	0
2004	0	93	50	0	0	0
2005	0	12	579	0	0	0
2006	0	28	1,027	0	0	0
2007	0	87	879	0	0	0
2008	0	100	210	0	0	0
2009	0	0	0	0	0	0
2010	0	150	58	25	0	0
2011	0	186	200	18	0	0
2012	0	102	200	18	0	0
2013	14	51	200	18	5	20
2014	0	91	82	0	0	0
2015	0	63	872	46	0	0
2016	0	72	1,531	81	0	0
2017	3	90	1,350	71	0	0
2018	2	60	61	3	0	0
2019	0	66	1174	62	0	0
2020	0	127	2,023	106	0	0
2021	0	75	222	12	0	0