Fisheries and Oceans Canada
Pêches et Océans Canada

Ecosystems and Oceans Science
Sciences des écosystèmes et des océans

Canadian Science Advisory Secretariat (CSAS)

Research Document 2020/057

Newfoundland and Labrador Region

Updated Estimates of Reproductive Rates in Northwest Atlantic Harp Seals and the Influence of Body Condition

G.B. Stenson, A.D. Buren, and G.L. Sheppard

Fisheries & Oceans Canada
Science Branch
P.O. Box 5667
St. John's, Newfoundland A1C 5X1

December 2020

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.

Published by:

Fisheries and Oceans Canada
Canadian Science Advisory Secretariat
200 Kent Street
Ottawa ON K1A 0E6

http://www.dfo-mpo.gc.ca/csas-sccs/
csas-sccs@dfo-mpo.gc.ca

ISSN 1919-5044

Correct citation for this publication:

Stenson, G.B., Buren, A.D., and Sheppard, G.L. 2020. Updated Estimates of Reproductive Rates in Northwest Atlantic Harp Seals and the Influence of Body Condition. DFO Can. Sci. Advis. Sec. Res. Doc. 2020/057. iv + 22 p.

Aussi disponible en français :

Stenson, G. B., Buren, A.D. et Sheppard, G.L. 2020 Estimations actualisées des taux de reproduction des phoques du Groenland dans l’Atlantique Nord-Ouest et influence de l’état corporel. Secr. can.de consult. sci. du MPO. Doc. de rech. 2020/057. iv + 22 p.

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ABSTRACT

Obtaining accurate estimates of reproductive rates is critical for describing the population dynamics of a species. Since the 1950s, fecundity rates of Northwest Atlantic harp seals have declined while inter-annual variability has increased. These highly variable reproductive rates have continued although the very low fecundity rates observed in 2010 and 2011 have not occurred again. High fecundity rates were observed in 2014 and 2015 associated with a period of extensive ice and relatively high capelin abundance. A previous study has shown that while the general decline in fecundity is a reflection of density-dependent processes associated with increased population size, the large inter-annual variability is due to varying rates of late-term abortions which are related to changes in capelin abundance (focal forage species of the system), and mid-winter ice coverage (which reflects environmental conditions that influence a variety of species). We hypothesize that the impact of changing prey availability influences reproductive rates through changes in body condition. We found that the average relative condition of pregnant females was high throughout four decades, whereas that of non-pregnant and immature females varied considerably and showed a general decline since 2000. While condition did not appear to influence fecundity rates directly, it affected the rate of late-term abortions. Relatively small reductions in average condition resulted in much higher abortion rates. This suggests that as overall condition in the population declines, females that are able to attain sufficient energy maintain their pregnancy while those that cannot terminate it prematurely. The relative influences of mid-winter ice coverage, capelin abundance, and body condition could not be resolved as these are different metrics of the amount of energy available for pupping. Capelin biomass is influenced by the timing of the ice retreat from the Newfoundland Shelf. In the short term (i.e., the next two years), capelin biomass is predicted to decline, and this will likely affect reproductive rates. In the long term, there is great uncertainty as to how the predicted changes in timing of ice formation and retreat will impact capelin, and hence reproductive rates of harp seals.

Key words: harp seal, *Pagophilus groenlandicus*, reproductive rates, fecundity, abortions

INTRODUCTION

Understanding fecundity and the factors that influence the proportion of females that successfully complete a pregnancy are crucial for understanding the dynamics of a population. Reproductive rates are influenced by a combination of density-dependent and density-independent factors in response to changes in abundance and their environment (e.g., Eberhardt 1977, Gaillard et al. 2000, de Little et al. 2007, Stenson et al 2016). Harp seals are the most abundant marine mammal in the North Atlantic and the subject of extensive study due to the importance of their ecological role and as the target of a commercial seal hunt. Based upon collections of animals in southern Labrador and northeastern Newfoundland, the reproductive rates of Northwest Atlantic harp seals have been studied since the 1950s (Fisher 1954) with a more systematic programme initiated in the 1980s that continues today (Sjare and Stenson 2010, Stenson et al. 2016). During this period, the population declined to less than 2 million and then increased to over 7 million (Hammill et al. 2015). The northwest Atlantic ecosystem also went through significant changes due to a regime shift that occurred in the early 1990s and ongoing climate change (e.g., McLaren et al. 2001; Drinkwater 2004; Buren et al. 2014).

Bowen et al. (1981) observed that as the population declined during the 1950s and 1960s, the pregnancy rate of mature females increased from 85 to 95 %. They considered this likely to be a density-dependent response to population reductions. As the population increased, reproductive rates have generally declined although with considerable interannual variability (Stenson et al. 2016). Since the late 1980s, there have also been indications that some females terminated their pregnancies prematurely during the winter feeding period prior to pupping in March. Stenson et al. (2016) analysed changes in fecundity and abortion rates to determine the factors influencing reproductive rates in harp seals. They found that while the general decline in fecundity was associated with increased population size, the interannual variability in the fecundity rates could be explained by including the rate of late-term abortions as an explanatory factor in the model. Changes in abortion rates were described by a model that incorporated capelin biomass and mid-winter ice cover (likely a proxy for ecosystem changes in overall prey abundance). It appears that harp seals respond to relatively small variations in environmental conditions when they are at high population levels.

As a capital breeder, harp seals must build up energy reserves that can be used during the breeding and molting periods. Chabot and Stenson (2002) found that male harp seals returned from their high-latitude feeding grounds heavier, in better condition, and with a thicker blubber layer than when they left the area the previous spring. However, they continued to put on weight and blubber until late February. A similar trend was observed in females; a significant proportion of the energy used during reproduction was attained during the winter period when they were off the coast of Newfoundland (Chabot and Stenson, unpublished data). Therefore, changes in prey availability in the southern portion of their annual range are likely to have a major impact on the condition of the females and their ability to complete a pregnancy successfully.

The objective of this study is to update the reproductive rates presented in Stenson et al. (2016) and present preliminary analysis of condition data for females during the pre-pupping period.

METHODS

REPRODUCTIVE RATES

Data to 2012 were taken from Stenson et al. (2016) although there were small updates to some of the data. The data and methods of collection are summarized in Sjare and Stenson (2010) and Stenson et al. (2016). Female reproductive tracts and jaws were collected from harp seals collected around Newfoundland and southern Labrador since 1979. Sampling has focused upon a core area along the northeast coast of Newfoundland which is adjacent to key winter and spring feeding habitat. Samples were collected by experienced seal hunters, and Department of Fisheries and Oceans (DFO) personnel under licenses issued by DFO. To minimize potential sampling biases among years, a core group of hunters from different areas of the province obtained a sample of seals over the entire period. Reproductive tracts were either preserved in 10 % formalin or frozen in the field; in the laboratory, ovaries were cut into 2.0 mm thick serial sections for examination.

Ages were determined to the nearest year by sectioning a lower canine tooth and counting dentine annuli (Fisher 1954; Bowen and Sergeant 1983, Frie et al. 2011). Females were considered immature if the ovaries were small and contained only inactive follicles with no corpus luteum (CL) or corpus albicans (CA) (Fisher 1954; Bowen et al. 1981). If there was evidence of a CL and/or CA in either ovary, the seal was considered mature. Mature females were considered pregnant if the ovary contained a large, fully luteinized CL in one of the ovaries and, since 1985, the presence of a foetus. Mature non-pregnant females lacked an active CL, but showed evidence of having ovulated previously (i.e., a CA was present). As in previous studies, all seals less than three years of age were considered immature (Sjare and Stenson 2010).

For ovaries collected after 1984, the size of all CA and CL were measured in two directions and the mean recorded. For ovaries prior to 1985, the maximum diameter was recorded. Seals that lacked a developing foetus but had a CL ≥13 mm or CA ≥12 mm, a rugose uterus and a large difference in uterine horn width (~15.0 mm), were assumed to have pupped recently (i.e., less than a month, Stenson et al. 2014). For seals collected prior to February 20th, it was assumed that those pups did not survive and that this represented a premature birth (i.e., late-term abortion). For seals collected after February 20th, it was assumed that there was a high probability that these pups contributed to the population that year. It was also assumed that if a female had an active CL and foetus on the day of collection, she would have completed the pregnancy successfully.

Fecundity rates, defined as the proportion of mature females that are pregnant, and age specific pregnancy rates were calculated as per Stenson et al. (2016). Late-term pregnancy, fecundity, and abortion rates were estimated from seals collected between October and February although the vast majority of seals were collected after November.

CONDITION

Standard morphometric measurements (length, total weight, sculp weight, blubber depth) are available for a subsample of the females collected during the December through February period. Using these data, we calculated a relative condition index for each female as CI = W/Wˆ, where W is the observed body weight and Wˆ is the predicted body weight from a length-weight relationship (Le Cren 1951). We subtracted the weight of the foeti from pregnant females prior to fitting the length-weight relationship. Because weights increase as seals put on blubber during the winter to store energy for pupping and moulting, we estimated the expected weights separately for December, January, and February.

To determine if condition has an influence on fecundity rate (defined as proportion of mature females that were considered pregnant), the data presented in Stenson et al. (2016) was reanalysed including condition as a potential explanatory variable. As in Stenson et al. (2016) and given that rates assume values in the standard unit interval (0; 1), we modelled abortion rates using fixed-dispersion, beta-regression models (Ferrari and Cribari-Neto 2004; Cribari-

Neto and Zeileis 2010) using the betareg package (Cribari-Neto and Zeileis 2010) in the Statistical Language R (R Development Core Team 2012). The model had the form:

fecundity rate ~ population size + abortion rate + mean relative condition

Given the nonlinear functional relationship between abortion rate and relative condition (see below), abortion rate was modelled as a Generalized Additive Model (GAM, Wood 2006) of the form:

abortion rate ~ s(mean relative condition)

GAMs were fit using the package mgcv (Wood 2011) in the Statistical Language R.

Using the beta regression model, Stenson et al. (2016) found that the most parsimonious model to describe abortion rates included mid-winter (January 29) ice and capelin biomass (from the fall bottom trawl surveys). We reanalysed these data to determine if the fit of the model improved with the addition of condition or by using condition alone (GAM model).where

Meancond is the mean condition,

Capt1 is the capelin biomass, lagged by 1 year, and

Ice.1y.jan is the on January 29

Finally, condition was modelled as a Generalized Additive Model (Wood 2006) of the form:

abortion rate ~ s(Mid-winter Ice) - adjusted r-squared=0.42

or

abortion rate ~ s(Mid-winter Ice) + s(Capelin) - adjusted r-squared=0.44

We built all possible candidate models (without including interactions) and ranked and selected the best model based on the Akaike Information Criterion corrected for small sample sizes (AICc) (Burnham and Anderson 2002) and the derived measure evidence ratio (Emin,i) (Anderson 2008).

RESULTS

REPRODUCTIVE RATES

Age-Specific Pregnancy Rates

Sampling effort has varied throughout the sampling period, with large numbers of animals collected in some years while in others considerably fewer were obtained (Table 1). After a period of relatively low sample sizes, samples sizes for seals eight years of age and older (8+) have generally been in the order of 50-150 since the early 2000s, although they were smaller in some years. Sample sizes for younger seals are quite small in most years throughout the time series. They were especially rare in sampling since the mid-1990s although there is an indication that sample sizes of young seals may be increasing since 2016.

Overall, there is a shift in the age of the majority of samples (Table 2, Fig. 2). Prior to 1990 approximately 80% of the samples were seals less than eight years of age while only 10% were above the age of 13. This has shifted with the proportion of young seals declining while the proportion of samples that have come from the oldest age group of seals has increased. In the most recent period (2015-2018) less than 60% of the seals were less than eight (the majority being 1 or 2), while over 30% of the samples came from seals 14 years of age and older. More than 10% of the samples were from seals twenty (20) years of age and older.

Because of the small sample sizes, there is no new data on pregnancy rates for seals less than eight years of age. Pregnancy rates for 3-year olds were very low, while 4 and 5 year olds appeared to have slightly higher reproductive rates during the late 1970s and early 1980s than either before or after. Pregnancy rates for 6-year olds have been low (<67%) since the mid-1990s when compared with earlier years when rates averaged around 80%. However, virtually no 6-year old seals have been sampled since the mid-2000s. Very few 7-year olds have been sampled over the past decade and pregnancy rates vary greatly as expected with small sample sizes.

Among the 8+ animals, pregnancy rates were high (80–90%) until the mid-1980s (Table 1, Fig 3). Pregnancy rates declined in the late 1980s although sample sizes in the mid-1980s were small which makes it difficult to determine exactly when the change occurred. Since 2000, pregnancy rates have averaged ~62% although they have varied considerable from approximately 20% in 2011 to over 85% in 2014 (Table 1). Since the last assessment in 2013, pregnancy rates have generally been high, averaging 78%.

Given the older ages of the samples, we checked for senescence among the females. Of the approximately 2,260 mature females examined, twelve (12) appear to be senescent with no indication of recent reproductive activity. These females were collected between 1987 and 2017 and ranged in age from 24 to 42 years of age. The majority were in their late 20s or early 30s. We also compared reproductive rates for various age groups to determine if the changing age structure impacted the estimated pregnancy rates, but no difference was observed between females of different age classes with respect to their annual pregnancy rates.

Fecundity and Abortion Rates

The estimated fecundity and abortion rates of seals collected in Newfoundland waters are shown in Table 3. The estimated fecundity rates are very similar to the pregnancy rates of females eight years of age and older as the only difference is the addition of a few younger seals that were mature. In keeping with Stenson et al. (2016), the criteria for identifying late-term abortions was based upon the observed diameters of CL and CA in seals identified as being pregnant with the absence of an implanted foetus.

Until the late 1970s, more than 85% of the mature females were pregnant each year. Since then fecundity rates have been highly variable, but with a declining trend (Table 3, Fig. 3). The lowest rate in the time series occurred in 2011 (19.6%) while the rates in 2014 (85.5%) was the highest seen in recent years and similar to rates seen prior to the 1980s.

While previously (Stenson et al. 2016) it appeared that no late-term abortions were detected in females collected prior to 1987, reanalysis of some of the earlier samples indicated that a few females showed signs of having had premature births in 1979 and 1981(Table 3, Fig. 4). Since 1987, abortions appear to have occurred in almost every year although the rate varies greatly. Generally, the rate of abortion appeared to be higher in years with lower overall fecundity (Fig. 4). For example, the highest abortion rates (0.196 and 0.233) occurred in 2004 and 2010 which were years with some of the lowest fecundity rates.

Condition

The monthly regressions for expected condition for a given length are shown in Fig. 5 and the yearly relative condition of pregnant, non-pregnant and immature females is shown in Fig. 6. With few exceptions, the average condition of pregnant females remained at, or above 1.

Condition in 2018 appears lower but these data are still preliminary. In contrast, the average relative condition of non-pregnant females appears to have declined and generally, has been below 1 since 2000. The average condition of non-pregnant females was lower than among pregnant females in virtually all years. The average relative condition of immature females followed a similar pattern to that of non-pregnant seals with condition being below average since 2000.

Fecundity Rate and Condition

Stenson et al. (2016) found that the most parsimonious model to describe the fecundity rate included population size and abortion rate as explanatory variables. This model had considerable support (pseudo r^2=0.824,) relative to the second best model, which included only population size as explanatory variable (pseudo r^2=0.49 E_{min},i=17,676). Adding body condition as one of the explanatory variables to the model that provided the best fit previously did not improve the model fit very much (pseudo r^2=0.841). The fit of the two models is almost identical (Fig. 7).

Abortion Rate and Condition

There is a non-linear relationship between the annual abortion rate and condition (Fig. 8). A slight decrease in condition may result in a considerable increase in the rate of premature births.

In the previous analyses abortion rates were best described by the model that included only ice coverage in late January and capelin biomass as explanatory variables (Stenson et al. 2016). The addition of body condition as an explanatory variable in the beta regression model did not improve the model fit significantly. Although the most parsimonious model was one that included all three variables (mid-winter ice cover, capelin biomass, and mean body condition), this model could not be distinguished from the original model (ice and capelin) or one that included capelin and condition (Table 4). The relationships between abortion rate and ice, capelin, and mean condition were all negative.

When using the GAM, however, the model that included only mean body condition was the most parsimonious (Table 4, Fig. 9). It had approximately four times more support than the models that included either ice and condition, or capelin and condition.

The close relationship among models that include a combination of mid-winter ice (January 29th), capelin biomass the previous autumn and condition are not surprising as ice, or ice and capelin are explanatory variables to describe condition (Fig. 10).

DISCUSSION

Stenson et al. (2016) concluded that the overall decline in reproductive rates since the 1980s was related to density dependent factors as the population increased in abundance. However, the interannual variability was related to environmental factors such as capelin and mid-winter ice extent. They felt that ice was an indicator of overall environment conditions and acted as a proxy for prey availability. In the northwest Atlantic, harp seals build up their energy stores during the winter just prior to pupping and moulting (Chabot et al. 1996). If they do not gain sufficient energy, they abort their foetus to improve their likelihood of survival (Stenson et al. 2016). We found that the average relative condition of pregnant females does not appear to vary while that of non-pregnant and immature females varied considerably and showed a general decline since 2000. This suggests that as overall condition in the population declines, females that are able to attain sufficient energy maintain their pregnancy while those that cannot, abort.

While condition did not appear to influence fecundity rates directly they did affect the rate of late-term abortions. Relatively small reductions in average condition resulted in much higher abortion rates. It is difficult to separate the influence of mid-winter ice, capelin biomass and condition on abortion rates since they are essentially different measure of the amount of energy available for pupping. Capelin are a major prey of harp seals (Lawson and Stenson 1995, Lawson et al. 1997) while ice conditions reflect environmental conditions that influence a variety of species (Koen-Alonso, pers. comm.). Condition is simply the integration of prey availability and energy expenditures. Hammill and Sauvé (2017) who reported a similar decline in condition of harp seals that was negatively related to reproductive rates the previous year and ice breakup in the Gulf of St. Lawrence.

The highly variable reproductive rates reported by Sjare and Stenson (2010) and Stenson et al. (2016) have continued although the very low fecundity rates observed in 2010 and 2011 have not occurred again. In fact, extremely high fecundity rates were observed in 2014 and 2015. These periods correlate with a warm period with little ice in 2010 and 2011 (Stenson and Hammill 2014) and a cooler period with more extensive ice in 2014 and 2015 (Canadian Ice Service). The environmental changes that occurred over the past decade impacted the abundance of prey for harp seals. Although the capelin stock off Newfoundland collapsed in the early 1990s (Buren et al. 2019), the estimates of capelin biomass in the spring acoustic survey reached their lowest level in 2010 (23,000 tonnes). In contrast, the 2014 biomass rose to 982,000 tonnes in the cooler environment. This close relationship between harp seal reproductive rates and prey availability observed by Stenson et al. (2016) appears to be continuing. The higher than usual fecundity rates in past few years are associated with relatively high capelin abundance as indicated by the spring acoustic survey (Fig. 11).

In the previous analysis, there were no indication of abortions in seals collected before 1987. However, with the re-examination of the earlier samples, it appears that some females collected earlier may have terminated their pregnancies prior to the usual pupping time. Many of these females were from 1981 which was an extremely poor year for ice. Considerable pup mortality occurred in 1981 and conditions were very similar to those observed in 2010 and 2011 when fecundity rates were low and abortion rates among the highest.

There has been a considerable shift in the age structure of the females we have sampled. Although it may represent a change in the distribution of harp seals, there is no evidence to indicate such a change. The distribution and timing of migrations of adult harp seals equipped with satellite transmitters in 2004 were very similar to those of seals tagged with satellite transmitters in the mid-1990s and reports of the distribution of seals along the Newfoundland coast are similar over the entire time period. Therefore, we feel that the changes in age structure of the samples likely reflect changes in the age structure of the population. In the 1980s the vast majority of samples (~80%) were from seals less than eight years of age. However, with the resumption of the large commercial hunt in the mid-1990s (Stenson and Upward 2019) and the increase in number of years with ice related mortality (e.g., Hammill et al. 2015), a number of cohorts between 1995 and 2012 were reduced. Examining the age frequency of the samples suggests that these cohorts were lacking in the population while females born before 1995 dominated the samples. It is only in the last few years that younger females (2-6 years) are reappearing in the sampling. This is consistent with the perception that these cohorts may be stronger.

The increased number of older seals we are able to examine allow us to begin to get a better understanding of senescence in harp seals. Although we have yet to work out the exact proportion of females that appear to have ended their reproductive life, it appears to be a rare occurrence. A number of females well into their 30s are still actively completing successful pregnancies.

The data we have presented here indicates that, generally, reproductive rates of northwest Atlantic harp seals continue to be highly variable in response to their changing environment and prey availability. If females obtain the energy necessary to give birth and nurse their pup, they can reach an adequate condition level and complete the pregnancy successfully. If not, they will terminate the pregnancy early. Since 2012, pregnancy rates have been relatively high, likely as a result of increased capelin abundance. However, capelin biomass is influenced by the timing of ice retreat (Buren et al 2014, Lewis et al 2019) and based upon ice retreat in 2019 and larval production during 2017-2018, capelin biomass is predicted to decrease in the next two years (DFO 2019). This may result in lower reproductive rates in the next few years. Using a regional climate change model, Han et al. (2019) predicted that there will be large changes in the timing of ice formation and retreat by 2040, and that southern Labrador may be virtually ice free by 2100. What this means for capelin and subsequently harp seals, is unknown.

ACKNOWLEDGEMENTS

We thank the late B. Sjare for providing the historical data, D. Wakeham for examining ovaries for many years, W. Penny and B. Stockwood for aging, P. Upward and P. Goulet for providing some of the figures, and W. Penney, D. McKinnon, J. Foley, G. Furey, and B. Stockwood for sample collections. We would also like to thank the many collectors who provided us with samples and helped us carry out our work. Support for this work was provided through the Department of Fisheries and Oceans’ Center of Excellence for Marine Mammalogy.

REFERENCES CITED

Anderson, D.R. 2008. Model based inference in the life sciences: a primer on evidence. Springer, New York, USA.

Bowen, W.D., and D.E. Sergeant. 1983. Mark-recapture estimates of harp seal pup (*Phoca groenlandica*) production in the northwest Atlantic. Can. J. Fish. Aquat. Sci. 40: 728-742.

Bowen, W.D., Capstick, C.K., and D.E. Sergeant. 1981. Temporal changes in the reproductive potential of female harp seal, *Pagophilus groenlandicus*. Can. J. Fish. Aquat. Sci. 38: 495–503.

Buren, A.D., Koen-Alonso, M., Pepin, P., Mowbry, F., Nakashima, B., Stenson, G., Ollerhead, N., and W.A. Montevecchi. 2014. Bottom-up regulation of capelin, a keystone forage species. PLoS One 9(2):e87589. Doi:10.1371/journal.pone.0087589.

Buren, A.D., Murphy, H.M., Adamack, A.T., Davoren, G.K., Koen-Alonso, M., Montevecchi, W.A., Mowbray, F.K., Pepin, P., Regular, P.M., Robert, D., Rose, G.A., Stenson, G.B., and D. Varkey. 2019. The collapse and continued low productivity of a keystone forage fish species. Mar. Ecol. Prog. Ser. 616:155-170.

Burnham, K.P. and D.R. Anderson. 2002. Model selection and multimodel inference. A practical Information-theoretic approach. Springer, New York, USA.

Chabot, D., and G.B. Stenson. 2002. Growth and seasonal fluctuations in size and condition of male Northwest Atlantic harp seals (*Phoca groenlandica*): An analysis using sequential growth curves. Mar. Ecol. Prog. Ser. 227:25-42.

Chabot, D., Stenson, G.B., and N.B. Cadigan. 1996. Short-and long-term fluctuations in the size and condition of harp seal (*Phoca groenlandica*) in the northwest Atlantic. NAFO Sci. Coun. Stud. 26:15-32

Cribari-Neto, F., and A. Zeileis. 2010. Beta regression in R. Journal of statistical software 34: 1-24.

de Little, S.C., Bradshaw, C.J.A., McMahon, C.R., and M.A. Hindell. 2007. Complex interplay between intrinsic and extrinsic drivers of long-term survival trends in southern elephant seals. BMC Ecology 2007, 7:3 doi:10.1186/1472-6785-7-3

DFO. 2019. Assessment of 2J3KL Capelin in 2018. DFO Can. Sci. Advis. Sec. Sci. Advis. Rep. 2019/048.

Drinkwater, K.F. 2004. Atmospheric and sea-ice conditions in the Northwest Atlantic during the decade, 1991–2000. J. Northw. Atl. Fish. Sci. 34: 1-11.

Eberhardt, L.L. 1977. Optimal policies for conservation of large mammals, with special reference to marine ecosystems. Environ. Conserv. 4: 205–212.

Ferrari, S.L.P., and F. Cribari-Neto. 2004. Beta regression for modelling rates and proportions. J. Appl. Stat., 31: 799-815.

Fisher, H.D. 1954. Studies on reproduction in the harp seal *Phoca groenlandica* Erxleben in the Northwest Atlantic. Fish. Res. Board Can. MS Report 588. 109 pp.

Frie, A.K., Fagerheim, K.-A., Hammill, M.O., Kapel, F.O., Lockyer, C., Stenson, G.B., Rosing-Asvid, A., and V. Svetochev. 2011. Error patterns in age estimation of harp seals (*Pagophilus groenlandicus*): results from a transatlantic, image-based blind-reading experiment using known-age teeth. ICES J. Mar. Sci. 68:1942-1953.

Gaillard, J.M., Festa-bianchet, M., Yoccoz, N.G., Loison, A., and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annu Rev Ecol Syst 31: 367–393.

Hammill, M.O., and C. Sauvé. 2017. Growth and condition in harp seals-evidence of density dependent and density independent influences. ICES J. Mar. Sci. 74:1395-1407

Hammill, M.O., Stenson, G.B., Doniol-Valcroze, T., and A. Mosnier. 2015. Conservation of Northwest Atlantic harp seals: past success, future uncertainty? Biol. Conserv. 192:181-191.

Han, G., Ma, Z., Long, Z., Perrie, W., and J. Chasse. 2019. Ocean and Sea-Ice Model Under an A1B Forcing Scenario 2011–2069, Atmosphere-Ocean, 57: 3-17.

Lawson, J.W., and G.B. Stenson. 1997. Diet of northwest Atlantic harp seals (*Phoca groenlandica*) in offshore areas. Can J. Zool. 75:2095-2106.

Lawson, J.W., Stenson, G.B., and D. McKinnon. 1995. Nearshore diet of harp seals (*Phoca groenlandica*) in the northwest Atlantic during 1990-1993. Can. J. Zool. 75:1805-1818.

Le Cren, E.D.L. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in the perch (*Perca fluviatilis*). J Anim Ecol 20: 201-219

Lewis, K.P., Buren, A.D., Regular, P.M., Mowbray, F.K., and H.M. Murphy. 2019. Forecasting capelin *Mallotus villosus* biomass on the Newfoundland shelf. Mar. Ecol. Prog. Ser. 616:171-183.

McLaren, I.A., Brault, S., Harwood, J., and D. Vardy. 2001. Report of the eminent panel on seal management. 146p.

R Development Core Team 2012. R: A language and environment for statistical computing. R Foundation for Statistical Computing.

Sjare, B., and G.B. Stenson. 2010. Changes in the reproductive parameters of female harp seals (*Pagophilus groenlandicus*) in the Northwest Atlantic. ICES J. Mar. Sci. 67: 304 315.

Stenson, G.B., and M.O. Hammill. 2014. Can ice breeding seals adapt to habitat loss in a time of climate change? ICES J. Mar. Sci. 71:1977-1986.

Stenson, G.B., Buren, A.D., and M. Koen-Alonso. 2016. The impact of changing climate and abundance on reproduction in an ice-dependent species, the Northwest Atlantic harp seal, *Pagophilus groenlandicus*. ICES. J. Mar. Sci. 73:250-262.

Wood, S. 2006. Generalized additive models: an introduction with R. Chapman and Hall/CRC Press, Boca Raton.

Wood, S.N. 2011. Fast stable restricted maximum likelihood and marginal likelihood estimation of semiparametric generalized linear models. J. Royal Statistical Soc. (B) 73(1):3-36.

TABLES

Table 1. Age-specific pregnancy rates of female harp seals sampled in Newfoundland and Labrador waters 1954 to 2018. Rates are based on the proportion of pregnant females in a particular age class regardless of maturity status.

Age	-	3	-	-	4	-	-	5	-
Year	n	No Preg	Preg rate	n	No Preg	Preg rate	n	No Preg	Preg rate
1954	4	0	0	3	1	0.333	3	2	0.667
-	-	-	-	-	-	-	-	-	-
1964	11	0	0	9	1	0.111	2	1	0.500
1965	30	1	0.033	44	5	0.114	37	20	0.541
1966	7	0	0	9	1	0.111	17	6	0.353
1967	10	0	0	19	4	0.211	33	20	0.606
1968	27	0	0	19	6	0.316	20	14	0.700
1969	25	1	0.040	25	4	0.160	16	7	0.438
1970	13	0	0	13	3	0.231	12	6	0.500
-	-	-	-	-	-	-	-	-	-
1978	40	1	0.025	38	23	0.605	20	18	0.900
1979	21	5	0.238	15	8	0.533	5	5	1.000
1980	2	0	0	2	1	0.500	1	1	1.000
1981	5	1	0.200	4	3	0.750	2	1	0.500
1982	4	0	0	5	2	0.400	1	1	1.000
-	-	-	-	-	-	-	-	-	-
1985	4		0	3	1	0333	5	2	0.400
1986	1	1	1.000	0	-	-	2	1	0.500
1987	12	2	0.167	8	3	0.375	9	7	0.778
1988	17	2	0.118	6	1	0.167	3	3	1.000
1989	8	0	0	9	0	0	6	2	0.333
1990	8	0	0	7	1	0.143	3	1	0.333
1991	10	0	0	11	2	0.182	7	4	0.571
1992	10	2	0.200	11	3	0.273	9	4	0.444
1993	11	1	0.091	17	2	0.118	7	0	0
1994	23	1	0.043	16	2	0.125	14	6	0.429
1995	10	0	0	13	6	0.462	4	2	0.500
1996	8	0	0	6	0	0	4	1	0.250
1997	6	0	0	4	0	0	10	3	0.300
1998	6	0	0	10	3	0.300	9	2	0.222
1999	6	0	0	7	0	0	18	4	0.222
2000	1	0	0	9	3	0.333	6	4	0.667
2001	2	0	0	0	0	-	2	2	1.000
2002	2	0	0	4	1	0.250	5	3	0.600
2003	1	0	0	3	2	0.667	2	1	0.500
2004	2	0	0	5	0	0	5	1	0.200
2005	9	1	0.111	9	0	0	13	2	0.154
2006	2	0	0	0	0	-	0	-	-
2007	1	0	0	5	0	0	3	1	0.333
2008	6	0	0	3	0	0	2	0	0
2009	2	0	0	1	0	0	1	0	0
2010	3	0	0	0	-	-	0	-	-
2011	5	0	0	3	0	0	2	0	0
2012	0	-	-	2	0	0	1	0	0
2013	6	0	0	1	0	0	0	-	-
2014	4	0	0	2	0	0	0	-	-
2015	4	0	0	0	-	-	1	0	0

Age	-	3	-	-	4	-	-	5	-
Year	n	No Preg	Preg rate	n	No Preg	Preg rate	n	No Preg	Preg rate
2016	16	0	0	7	0	0	4	1	0.250
2017	8	0	0	7	0	0	8	0	0
2018	5	0	0	10	0	0	6	0	0

Table 1 con't.

Age	-	6	-	-	7	-	-	8+	-
Year	n	No Preg	Preg rate	n	No Preg	Preg rate	n	No Preg	Preg rate
1954	16	12	0.750	4	3	0.750	29	26	0.897
-	-	-	-	-	-	-	-	-	-
1964	4	3	0.750	5	5	1.000	20	17	0.850
1965	38	27	0.711	33	28	0.848	76	68	0.895
1966	11	8	0.727	8	7	0.875	41	36	0.878
1967	29	28	0.966	3	20	0.870	100	89	0.890
1968	12	11	0.917	11	9	0.818	44	39	0.886
1969	28	23	0.821	9	27	0.931	136	119	0.875
1970	10	9	0.900	19	18	0.947	88	74	0.841
-	-	-	-	-	-	-	-	-	-
1978	9	6	0.667	10	7	0.700	31	28	0.903
1979	9	8	0.889	4	4	1.000	7	16	0.941
1980	0	-	-	2	2	1.000	10	7	0.700
1981	7	6	0.857	0	-	-	17	14	0.824
1982	4	3	0.750	0	-	-	3	1	0.333
-	-	-	-	-	-	-	-	-	-
1985	3	3	1.000	0	-	-	1	1	1.000
1986	1	-	0	1	1	1.000	6	6	1.000
1987	4	4	1.000	1	1	1.000	23	14	0.609
1988	0	-	-	3	2	0.667	16	12	0.750
1989	3	2	0.667	2	2	1.000	20	20	1.000
1990	1	0	0	0	-	-	10	6	0.600
1991	3	1	0.333	3	1	0.333	26	17	0.654
1992	8	6	0.750	2	2	1.000	30	19	0.633
1993	5	4	0.800	3	2	0.667	32	15	0.469
1994	7	3	0.429	5	5	1.000	36	29	0.806
1995	5	2	0.400	0	-	-	24	14	0.583
1996	1	1	1.000	0	-	-	35	24	0.686
1997	2	2	1.000	2	1	0.500	34	26	0.765
1998	4	2	0.500	9	6	0.667	27	16	0.593
1999	15	6	0.400	9	7	0.778	50	30	0.600
2000	5	2	0.400	6	3	0.500	37	26	0.703
2001	3	0	0	3	3	1.000	36	23	0.639
2002	17	10	0.588	7	4	0.571	65	36	0.554
2003	3	2	0.667	4	2	0.500	87	57	0.655
2004	1	0	0	8	5	0.625	68	26	0.382
2005	7	0	0	6	1	0.167	80	54	0.675
2006	0	-	-	5	3	0.600	114	64	0.561
2007	2	2	1.000	2	1	0.500	82	63	0.768
2008	0	0	-	4	1	0.250	57	44	0.772
2009	1	0	0	1	1	1.000	105	59	0.562
2010	0	-	-	1	0	0	114	35	0.307
2011	0	-	-	0	-	-	153	30	0.196
2012	0	-	-	0	-	-	28	17	0.607

Age	-	6	-	-	7	-	-	8+	-
Year	n	No Preg	Preg rate	n	No Preg	Preg rate	n	No Preg	Preg rate
2013	0	-	-	1	0	0	11	6	0.630
2014	1	0	0	1	0	0	76	65	0.855
2015	0	-	-	3	0	0	15	15	1.000
2016	6	2	0.333	4	3	0.750	93	69	0.742
2017	0	-	-	2	0	0	50	29	0.580
2018	3	1	0.333-	2	1	0.500	69	51	0.739

Table 2. Proportion of reproductive samples from various age groups for five year sampling blocks.

Age	**1980-84**	**1985-89**	**1990-94**	**1995-99**	**2000-04**	**2005-09**	**2010-14**	**2013-18**
1-7	0.80	0.82	0.77	0.78	0.71	0.57	0.38	0.53
8-13	0.09	0.06	0.09	0.10	0.13	0.11	0.02	0.05
14-19	0.06	0.05	0.05	0.06	0.10	0.20	0.15	0.03
20+	0.04	0.07	0.08	0.06	0.05	0.11	0.45	0.40

Table 3: Annual late-term fecundity (#pregnant/# mature) and abortion (#abortions/#mature) rates of female harp seals, October through February, 1954-2019.

Year	# Mature Females	Fecundity Rates	Abortion Rates
1954	51	0.863	0
-	-	-	-
1964	32	0.844	0
1965	161	0.925	0
1966	59	0.983	0
1967	163	0.988	0
1968	85	0.929	0
1969	187	0.968	0
1970	116	0.948	0
-	-	-	-
1978	88	0.943	0
1979	51	0.941	0
1980	14	0.786	0
1981	32	0.781	0.094
1982	9	0.778	0
-	-	-	-
1985	11	0.727	0
1986	10	0.900	0
1987	46	0.696	0.022
1988	26	0.769	0.038
1989	32	0.781	0.125
1990	15	0.533	0.067
1991	38	0.684	0.026
1992	56	0.643	0.071
1993	47	0.469	0.085
1994	60	0.767	0.033
1995	37	0.676	0.081
1996	39	0.667	0
1997	42	0.762	0.119
1998	44	0.636	0.023
1999	81	0.568	0.025
2000	54	0.704	0.019
2001	42	0.667	0.048
2002	93	0.581	0.032
2003	96	0.656	0.052
2004	80	0.300	0.238
2005	95	0.611	0.011
2006	119	0.521	0.109
2007	90	0.744	0.022
2008	62	0.726	0.000
2009	105	0.571	0.124
2010	114	0.307	0.228
2011	153	0.196	0.124
2012	28	0.627	0.036
2013	12	0.500	0.167
2014	76	0.855	0.013

Year	# Mature Females	Fecundity Rates	Abortion Rates
2015	17	0.882	0.000
2016	100	0.750	0.040
2017	50	0.580	0.100
2018	72	0.736	0.042
2019	110	0.727	0.064

Table 4. Model selection statistics for the abortion rates analyses. The delta Akaike Information Criterion corrected for small sample sizes (Δ AICc) and the derived measure evidence ratio ($E_{min,i}$) for each model are included.

BETA REGRESSION MODEL SELECTION TABLE

model	N	K	pseudorsquared	LH	deltaAICc	$E_{min,i}$
ice.1y.jan + Capt1 + meancond	16	4	0.79	40.04	0.00	1.00
Capt1 + meancond	16	3	0.67	37.62	0.48	1.27
ice.1y.jan + Capt1	16	3	0.69	37.41	0.90	1.57
ice.1y.jan	16	2	0.52	32.49	7.10	34.85
meancond	16	2	0.47	32.35	7.37	39.92
ice.1y.jan + meancond	16	3	0.59	33.70	8.31	63.85
Capt1	16	2	0.17	27.78	16.52	3862.25

GAM MODEL SELECTION TABLE

model	N	K	adjrsquared	LH	deltaAICc	$E_{min,i}$
s(meancond)	16	2	0.68	18.02	0.00	1.00
Capt1 + s(meancond)	16	3	0.67	18.41	2.76	3.97
ice.1y.jan + s(meancond)	16	3	0.68	18.76	3.00	4.48
ice.1y.jan + Capt1 + s(meancond)	16	4	0.67	19.09	6.16	21.73
ice.1y.jan	16	2	0.40	12.37	6.66	27.91
ice.1y.jan + Capt1	16	3	0.45	13.58	7.87	51.21
Capt1	16	2	0.01	8.33	14.73	1580.29

FIGURES

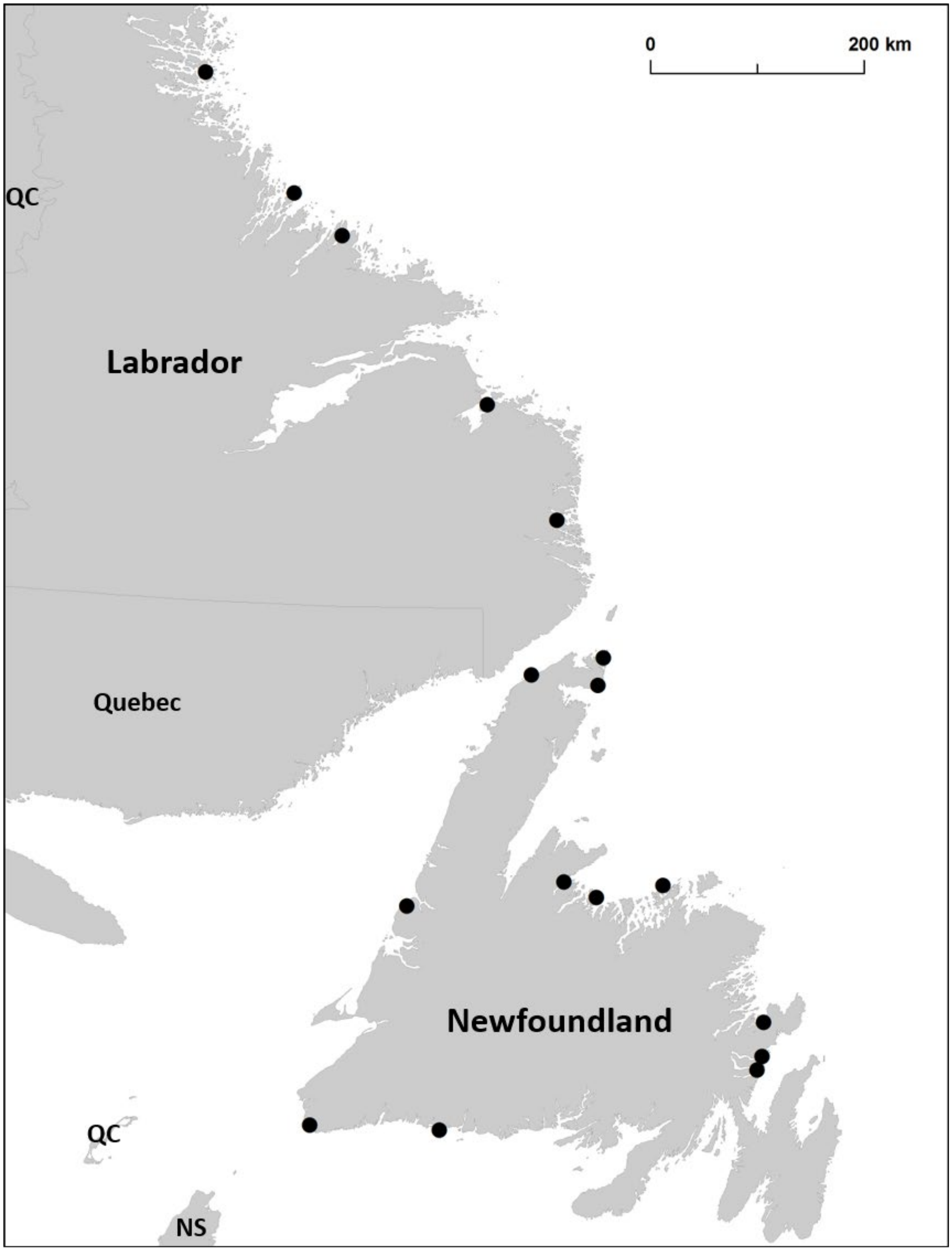

Figure 1. Location of collections of reproductive samples from the Newfoundland Region collection program.

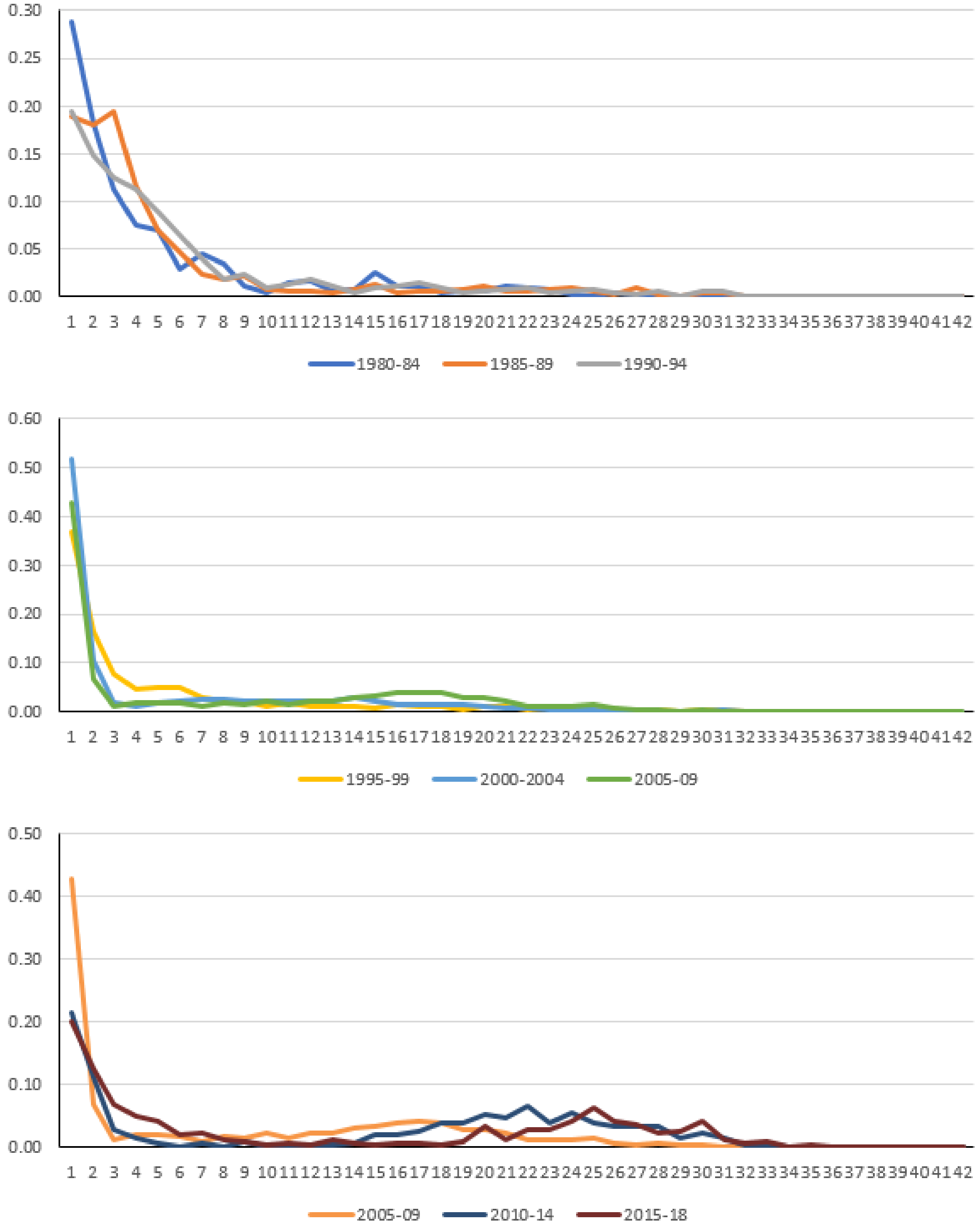

Figure 2. Age of females collected during five-year periods of reproductive sampling. Only four years of data are available for the final period.

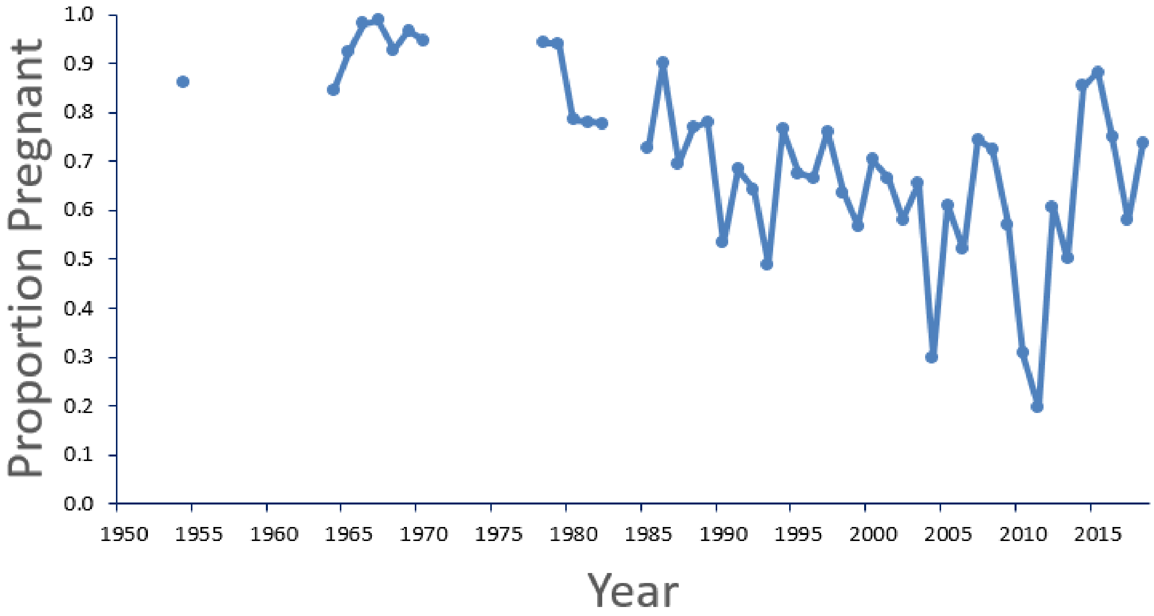

Figure 3. Proportion of seals eight years of age and older that were considered pregnant in each year of sampling.

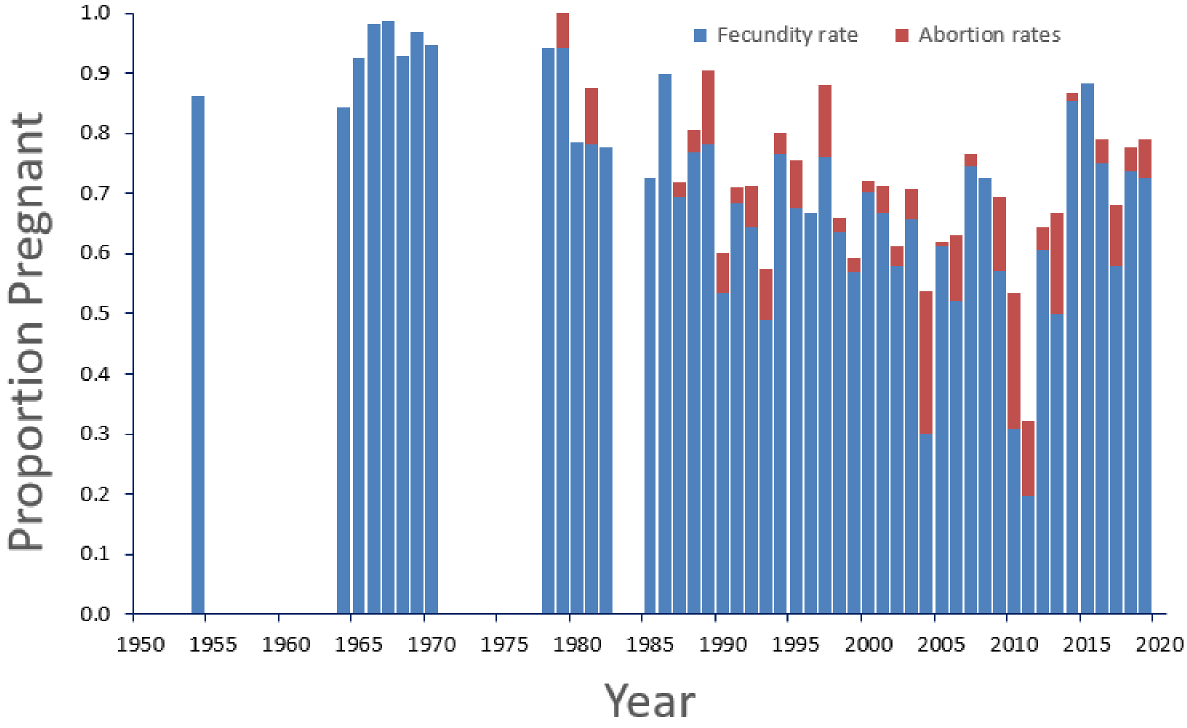

Figure 4. Proportion of mature females collected in December through mid-February that were pregnant or showed indications of having aborted their foetus within the past month.

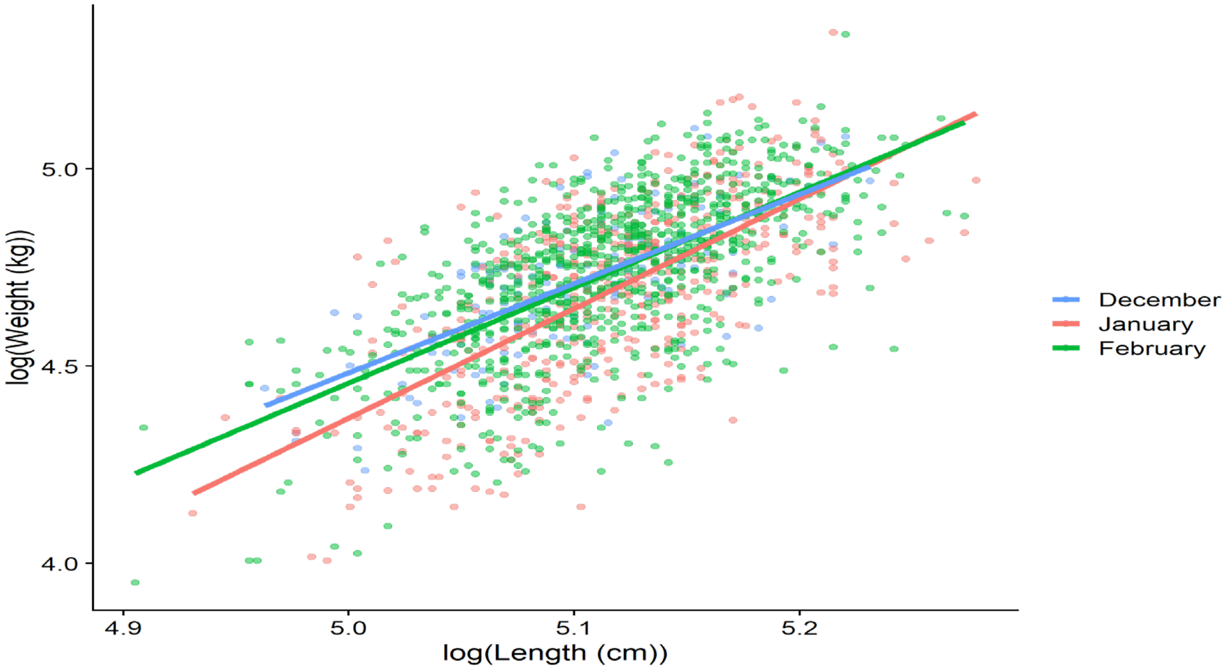

Figure 5. Relationship be between log length and log weight for female harp seals collected during December, January, and February in Newfoundland waters.

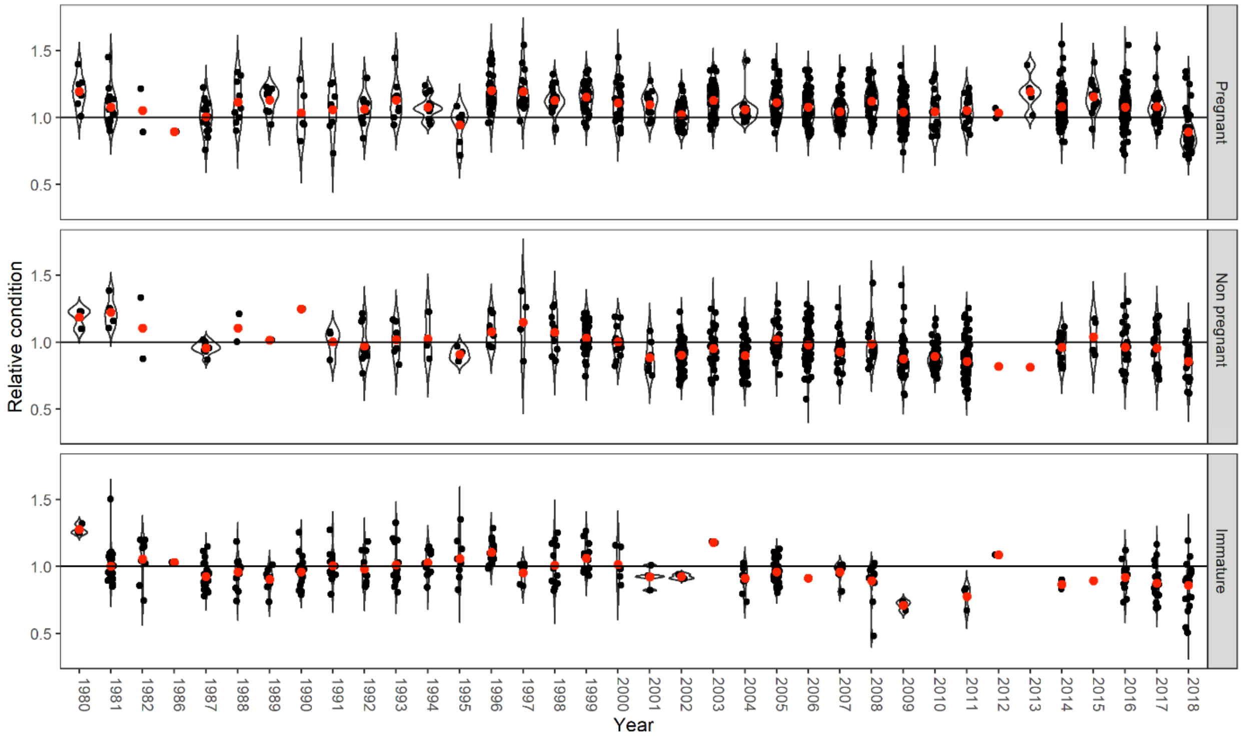

Figure 6. Distribution of annual relative condition of pregnant, mature non-pregnant (including females that abort their pups prematurely) and immature female harp seals collected between December and February 1980-2018. Black dots represent individual data points while the red dot indicates the annual mean.

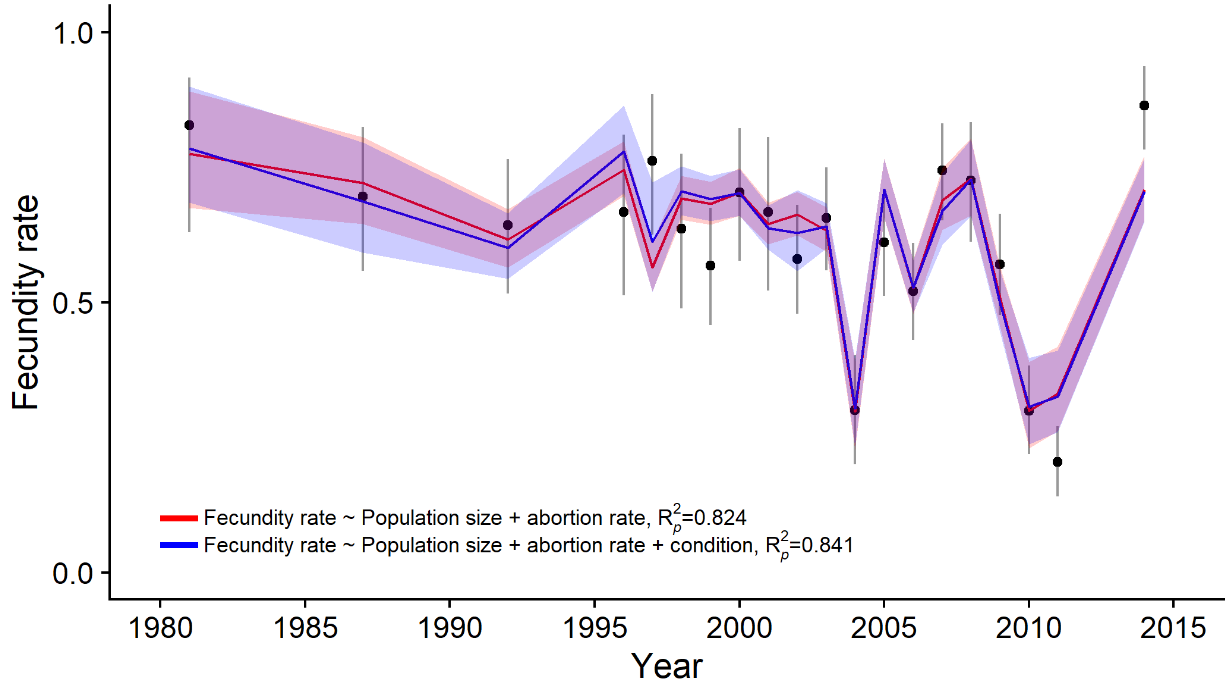

Figure 7. Fit of a model to describe fecundity rate using relative condition as an explanatory parameter

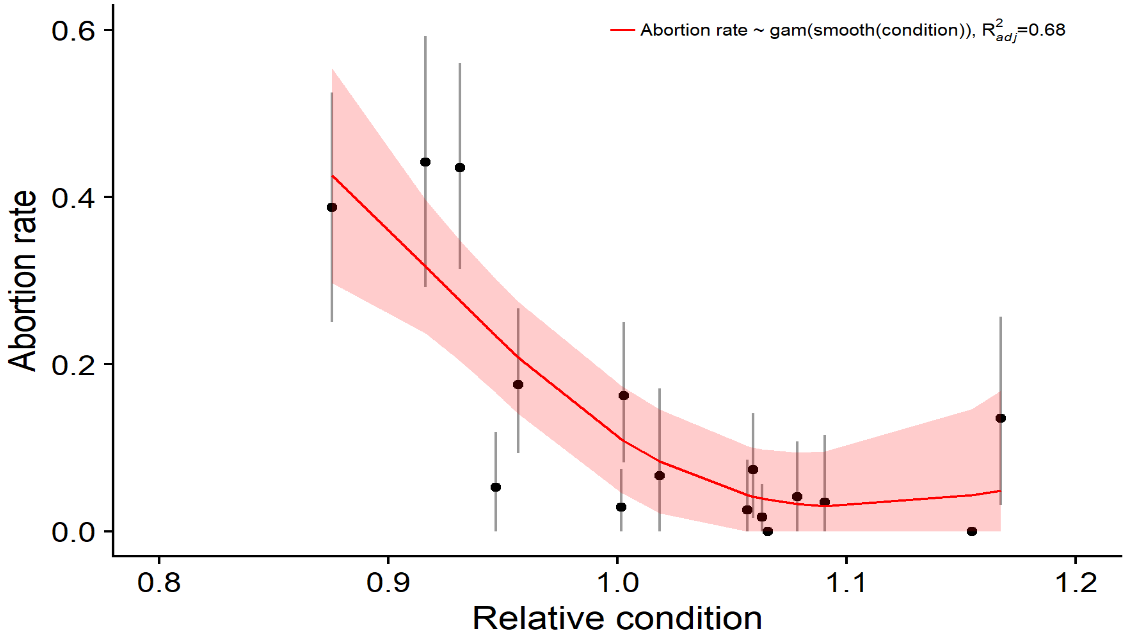

Figure 8. Relationship between mean yearly condition index and abortion rate of northwest Atlantic harp seals, 1980-2013.

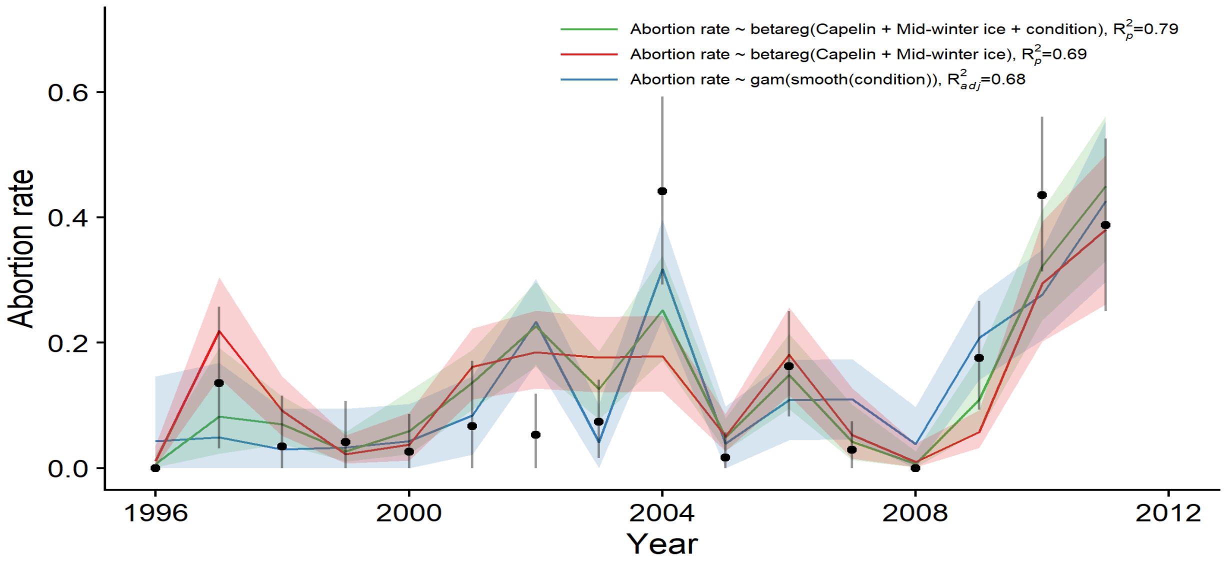

Figure 9. Fits of the most parsimonious models to describe abortion rate in northwest Atlantic harp seals.

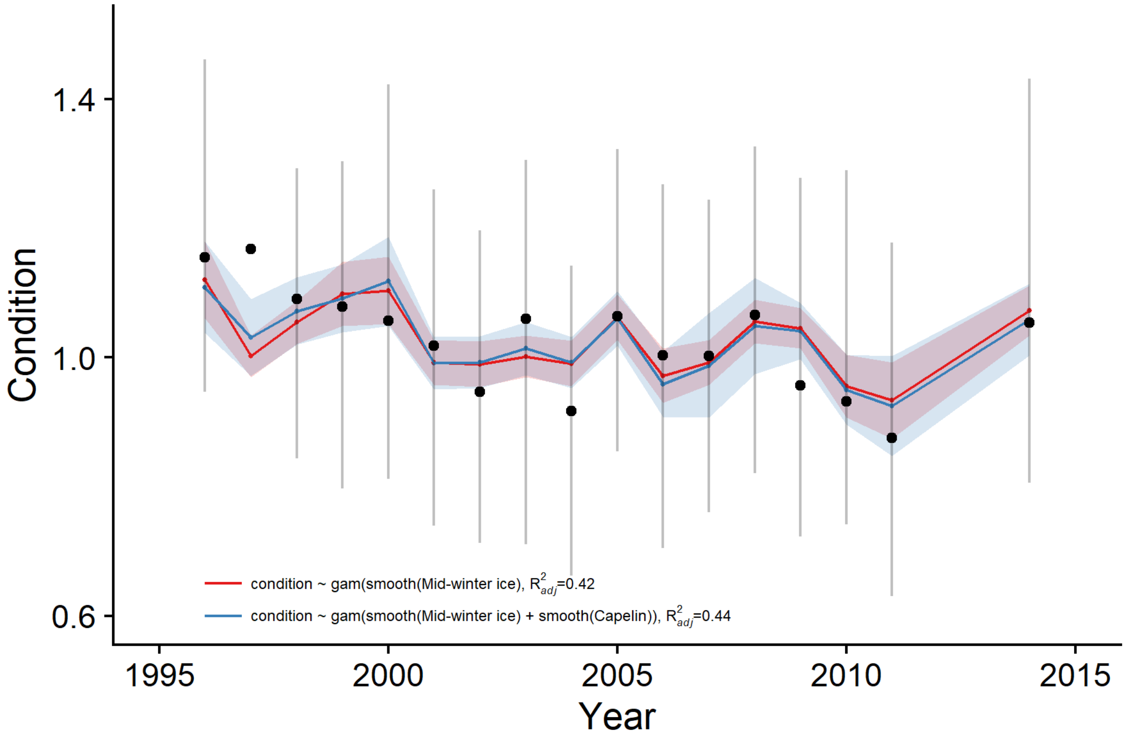

Figure 10. Fits of the two most parsimonious models to describe relative condition in female harp seals.

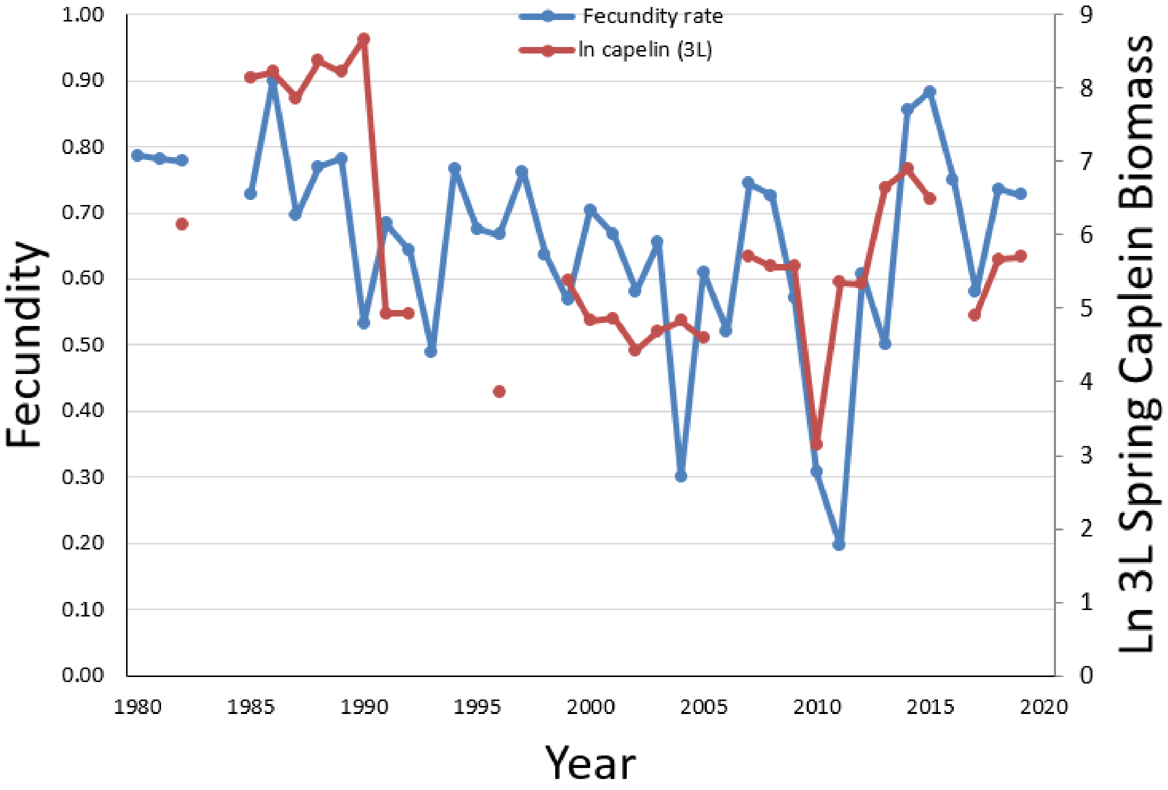

Figure 11. Fecundity rates of northwest Atlantic harp seals and ln capelin abundance from the DFO spring capelin biomass assessment.