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Grey Seal Pup Production in Canada

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Canada

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

To estimate Grey Seal (*Halichoerus grypus*) pup production, digital-photographic aerial surveys were conducted of the major Grey Seal breeding colonies in Canadian waters in January 2021. Where there were multiple counts from a colony, the largest count was used to estimate total pup production. A total of 72,209 pups were counted on digital imagery from Sable Island, the largest breeding colony. The pup counts at Brion Island and Pictou Island, the two largest breeding colonies in the Gulf of St. Lawrence, were 5,151 and 3,604 individuals, respectively. Reconnaissance flights identified a small number of pups at new locations in the Gulf of St. Lawrence, but no new colonies along the Atlantic coast of Nova Scotia, New Brunswick and Newfoundland.

Pup developmental stage surveys were undertaken on the ground or from helicopter at the seven largest breeding colonies to describe the birth distribution and correct the pup count for the estimate of pups born after the aerial photographic survey. Two models were used to estimate the proportion of pups born on the day of the survey: the accepted Myers Birth Distribution model, which uses the developmental stage duration estimated from known-age pups sighted daily on Sable Island; and a new Bayesian approach that uses the stage durations estimated from the known-age pups as priors but allows for the model to estimate stage duration for each colony. At all colonies, the pup production estimated by the Myers Birth Distribution was higher than the Bayesian birth distribution model. To maintain the time series, estimates of pup production are provided using the Myers Birth Distribution model. The estimated number of pups born on Sable Island was 76,600 (SE = 2,900), for Coastal Nova Scotia it was 4,700 (SE = 550) and for Gulf of St. Lawrence it was 16,900 (SE = 2,400) for a total production of 98,200 pups (SE = 5,800). For Sable Island, this is the first estimate of pup production since the 1960s that has not been a significant increase. Sable Island accounts for 77.5% of total pup production in Canada, and the change in trend in pup production on Sable Island is reflected in the trend in total pup production. Pup production in the Gulf of St. Lawrence continues to fluctuate with little evidence of trend over the past several decades, while at the more recently-established breeding colonies in southwest Nova Scotia, pup production continues to increase.

INTRODUCTION

Grey Seal breeding colonies in the northwest Atlantic currently range over a north–south distance of some 1,400 km encompassing several ecosystems (Frank et al. 2006). Over this broad geographic range, the northwest Atlantic population has grown rapidly, and new breeding colonies have been established both in eastern Canada and north-eastern United States (Mansfield and Beck, 1977, Wood et al. 2011, 2019, den Heyer et al. 2021). Outside of the breeding season, Grey Seals disperse broadly throughout the continental shelf of the northwest Atlantic but mature animals show philopatry to breeding sites (Breed et al. 2006, 2009, Harvey et al. 2008).

Grey Seals are iteroparous capital breeders that haul out on land or sea-ice to pup. In the northwest Atlantic, pupping occurs in the winter from early December to mid-February but there is variation among colonies and over time, with increasing evidence for pupping becoming earlier (Bowen et al. 2020, Mosnier et al. 2023). Female Grey Seals mature between four and roughly 12 years of age and reproduce into their late 30s or early 40s (Hammill and Gosselin 1995, Bowen et al. 2006). Females stay with their pup in one location on the breeding colony. The lactation period averages 16 to 18 days (Bowen et al. 1992, Iverson et al. 1993, Baker et al. 1995). Weaning is abrupt, with females leaving the colony and returning to sea. Weaned pups undergo a post-weaning fast that varies in duration from a few days to several weeks (Noren et al. 2008).

There are few systematic time series of pup production for pinnipeds which are sufficient in duration and sampling frequency to support robust investigations of long-term trends. One of the longest series comes from the Canadian northwest Atlantic, where pup production of Grey Seals has been periodically estimated since the 1960s. The last pup production estimate was in 2016. At that time total pup production in Canadian waters was just over 101,500 pups, which had increased for more than 50 years from approximately 1,000 pups/year in the 1960s (den Heyer et al. 2021). The northwest Atlantic Grey Seal is considered to form a single population (Boskovic et al. 1996), but within Canadian waters, Grey Seals are subdivided into two herds for management considerations: Scotian Shelf and Gulf of St. Lawrence (Gulf) (Figure 1). The two herds have had very different population trajectories. The Scotian Shelf herd includes breeding colonies on the Atlantic coast of Nova Scotia and Sable Island, which is the largest single breeding colony of Grey Seals in the world. Pup production on Sable Island increased rapidly from less than 2,000 pups in 1975 to over 25,000 pups in 1997, with a maximum annual rate increase of 14% (Bowen et al. 2003). Since the late 1990s, estimates of pup production, have continued to increase but the rate of increase has slowed (den Heyer et al. 2021). Historically, few pups were born on isolated islands along the Nova Scotia eastern shore, in part due to significant culling efforts that occurred periodically up until the mid-1980s (Mansfield and Beck 1977, Lavigueur and Hammill 1993, Bowen and Lidgard 2013). However, in the 1990s coastal colonies were established on small island at the eastern and western tips of the province. Pup production along the Atlantic Coast of Nova Scotia has increased from several hundred in the 1960s to 9,800 (SE = 2,000) in 2016 (Hammill et al. 2013, 2017b, den Heyer et al. 2021). In the Gulf, most pups have traditionally been born on the pack-ice south of Prince Edward Island with a few being born on beaches and/or small islands in the Northumberland Strait, off western Nova Scotia, and on Deadman Island in the central Gulf. However, with the decline in ice cover in the Gulf, pup production on the ice has declined from nearly 100% to approximately 1% in recent years (Hammill et al. 2017b, den Heyer et al. 2021). Overall, pup production in this region has increased from approximately 200 in the 1960s to around 10,000 by the turn of the century and has remained relatively stable over the last two decades.

Grey Seals are managed under an Integrated Fisheries Management Plan that seeks to maintain the population above a precautionary reference level of 70% of the largest population estimated or inferred (referred to as N70). Fisheries Management has requested advice on acceptable catch levels that would continue to respect the objectives of the management plan. As part of the assessment, aerial surveys to estimate Grey Seal pup production in Canadian waters were flown during December 2020 to February 2021. Here, we provide new estimates of Grey Seal pup production in Canada, based upon these surveys. The new estimates lengthen the time series of pup production, which are the key indices of abundance to which the population assessment models are fit.

MATERIALS AND METHODS

A well-established survey design (Bowen et al. 2003, 2007, Hammill et al. 2013, 2017b, den Heyer et al. 2017, 2021) was used to complete a comprehensive survey of Grey Seal pup production at all breeding colonies in Canada (Figure 1, Table 1). Several methods were used to complete counts, with larger established colonies being surveyed with a vertical large-format camera mounted in a fixed-wing aircraft and a helicopter with a pod-mounted camera. For the smallest colonies visual counts were completed from a helicopter with supplementary counts provided by DFO Conservation and Protection Branch (DFO C&P) infrared video.

UNCORRECTED COUNTS

Reconnaissance aerial surveys

Grey Seal pups were observed during reconnaissance aerial surveys flown along the southern coast of Newfoundland, in the Gulf, and along the Atlantic coast of Nova Scotia and New Brunswick during December, January and February 2021. Along the Atlantic coast of Nova Scotia and New Brunswick, directed surveys were conducted at an altitude of 500 ft from a Bell 429 helicopter as well as opportunistic searches from helicopter during transit to and from survey work at the established coastal colonies (Figure A1). In addition, DFO C&P used infrared video to opportunistically observe the coast of Nova Scotia and New Brunswick and provided video of seal haul outs and breeding colonies. Along the southern coast of Newfoundland, visual observations for seals were conducted by staff from the Newfoundland Region's Marine Mammal Section on DFO C&P Super King Air and Dash-8 fixed wing aircraft (Figure A2). Forward-looking infrared video was also used to identify seals, and images were recorded for post-flight analysis to determine species and assess the presence of pups. Fog was encountered during some flights, which resulted in parts of St. George's Bay not being searched. Similarly in the Gulf, DFO C&P used infrared video to opportunistically observe the coastline, and provided images to count seals at established and new breeding locations. The Gulf was also searched throughout the breeding season by the Quebec and Newfoundland staff that were completing surveys at the numerous coastal colonies and developing ice.

Large-format vertical fixed wing aerial surveys

A Microsoft Vexcel UCX camera with a motion compensation camera housing and an integrated in-flight GPS were used to provide 3 cm ground resolution digital imagery. The camera was installed in a purpose-modified aircraft operated by The Airborne Sensing Corporation (www.airsensing.com) and flew at a target altitude of approximately 418 m (1,370 ft). The imagery at each island or set of islands was taken on a single flight to minimize error introduced by the movement of seals between adjacent photographs. A series of parallel transects with 60% forward and 20% lateral overlap among adjacent photographs were used for all colonies. Transects were planned to be parallel to beaches so that high density areas would be covered

by fewer transects. Optimal conditions for imagery are mid-day and with high cloud to reduce shadows.

A single mosaic was constructed for each colony using a digital surface model and INPHO OrthoMaster software to orthorectify images. All orthorectified images were projected in UTM Zone 20 or UTM Zone 21 depending on their location. During seam editing, mosaic seams were adjusted so that entire animals appeared on just one side of the seam. For Sable Island, the photographic mosaic was broken into 600 m × 600 m tiles for ease of analysis, and care was taken to ensure pups appeared in only one tile. Pup counts were taken on each mosaic or tile using ArcGIS (ESRI ArcView 10.2.2) or QGIS (QGIS.org, v3.18) with each pup marked to avoid double counting. Original photos were used to confirm counts in areas where the mosaic or tile was unclear.

Helicopter surveys

Helicopter surveys were flown to provide data on the developmental stages of pups, based on pelage and body shape, to inform birth distribution models and to provide an estimate of the number of pups born at the time of the survey. At several colonies, multiple photographic surveys were completed using a 36.3 megapixel digital SLR Nikon D800 camera with a 35 mm lens (Zeiss, Distagon T* 2/35). The camera was mounted in a pod under the nose of a Bell 429 helicopter. Surveys were flown at altitudes between 30 and 156 m. Low-level flights were used to determine pup stage, and to detect brands and signs of scarring from shark attacks. High-level flights were used to count pups restricted to coastal beaches or to fly parallel transects over larger colonies to obtain complete coverage. Imagery was stitched together using Pix4Dmapper to create mosaics and terrain models. Live pups were counted in QGIS (QGIS.org, v3.18). Dead pups were identified by wounds often at the umbilical and/or eyes and were often attended by a seagull. The dead pups were marked but not included in the count, as a mortality adjustment is applied subsequently.

Infrared video

DFO C&P infrared video from surveillance flights was used to locate new colonies. Notably for a few colonies, infrared imagery was used to estimate the abundance of seals. In this imagery pups are hardly distinguishable from adults, so the total counts of Grey Seals for Anticosti and Margaree Islands were adjusted using the estimated proportion of total animals counted that were pups from the vertical large-format imagery of Saddle, Brion, Pictou and Hay Islands, i.e., 0.44 (SD = 0.017). For Deadman Island, where both helicopter and DFO C&P infrared surveys were flown on the same date (January 15), this proportion was 0.34.

ESTIMATES OF PUP PRODUCTION

The estimation of pup production from live counts follows the approach developed by Myers and Bowen (1989). Total pup production (N) was estimated as follows:

$$N = count \cdot g/(1-d) \cdot p$$

where count is the number of live pups on the images, g is the correction for pups missed in the imagery, p is the estimated proportion born prior to the time of the survey and d is the estimated proportion of pups that had died prior to the day of the photographic survey. Pups are missed on the photographs for several reasons, which include poor quality images, reader error, pup mortality and loss from imagery, births that occur after the survey images are captured or pups leave the survey area before the survey. Standard error of total pup production was calculated from the estimated variances of correction factors using a delta method implementation for

Jensen's inequality and prediction uncertainty for independent random variables (Lyons, 1991) using the deltavar function from the R package “emdbook” (Bolker 2016).

Sable Island is the largest breeding colony and is readily accessible by researchers housed on the island. This allows for the collection of data over the breeding season to estimate pup stage duration and pup mortality on the breeding colony. At larger colonies (i.e., Sable Island, Pictou Island, and Brion Island), where a minimum of three visual surveys to determine the developmental stage composition were completed, birth distribution models were fit to adjust the count for the proportion of pups born after the survey. At other colonies, where this was not possible, the highest count was considered a minimum estimate of pup production.

Correction for missed pups

Owing to the high quality of the large-format photographic images, a correction for pups not detectable on the images was deemed unnecessary. However, improved image quality would facilitate counting and this is more important where snow, wooden debris or cobble and rock habitat makes the identification of pups more challenging. Bias in counting may occur if pups are not counted on the images because they are missed by the readers, or if readers mis-identify objects or juvenile or adult seals as pups. One reader read all imagery of Sable Island. A second reader read the imagery of Brion, Saddle and Pictou Island, and both readers read Hay, Round, Noddy, Mud and Flat Islands. Thirty randomly-selected transects from two of the largest colonies, Sable (Figure 2a) and Brion Islands, were counted by both readers to estimate counting accuracy. A consensus pup count was established using a third reader when the two primary readers’ counts were not the same. Bias was estimated by comparing a reader’s count to the consensus count for each transect.

Correction for pup mortality

A portion of pups born on the breeding colony die before the aerial survey is flown. These pups are often covered by sand and snow or swept out to sea before the aerial survey is flown, and thus are missed in the counts. On Sable, where access to the colony allows for identifying dead pups throughout the breeding season, pup mortality prior to the aerial survey was estimated in 2007, 2010, and 2016 using the pup mortality plots (Bowen et al. 2007, 2011, den Heyer et al. 2017). In 2021, the proportion of pups that died prior to the vertical aerial photographic survey was estimated at eight locations throughout the colony. GPS locations of the vertices of the chosen locations were recorded so they could be plotted on the photographs. The areas chosen encompassed areas of high pup abundance and the polygon boundaries were set in areas of low abundance using natural features such as dune edges, such that the number of pups close to the boundaries was a small proportion of the pups within the boundary. GPS locations were used to create polygons in ArcGIS and the total pup count in the polygon was compared to the dead pups counted and marked. Surveys for dead pups occurred roughly every three days between December 20, 2020, and January 11, 2021. Estimates of pre-survey pup mortality are not available for the other large colonies due to limited access throughout the breeding season.

Temporal birth distribution

The breeding season for Grey Seals in the northwest Atlantic spans six to eight weeks at individual colonies and varies geographically and inter-annually. It is necessary to correct the pup production estimate for the number of pups born after the pup photographic survey is completed. At the larger colonies where it was possible to conduct multiple developmental staging transects a model of the temporal distribution of births was fit to estimate the proportion of pups born up to and including the date of the aerial survey (Reed and Ashford, 1968, Myers and Bowen, 1989, Bowen et al. 2003, 2007). The distribution of births was estimated from stage

duration, the change over time in the proportion of each developmental stage on the breeding colony, and an estimate of the first birth at the colony. Grey Seal pups were classified into five developmental stages based on pelage colour and body shape (Table 2, Radford et al. 1978, Kovacs and Lavigne, 1986, Bowen et al. 2003). On Sable Island, developmental staging transects were completed by a single observer weekly between December 17, 2020 and January 27, 2021 (Table 3). As noted above, developmental staging surveys on coastal islands were completed by visual surveys from the Bell 429 helicopter.

Two models were fit to the pup staging transects. The first model, referred to as the Myers Birth Distribution (MBD) model has been used in previous surveys (Myers and Bowen, 1989, Bowen et al. 2003, 2007, den Heyer et al. 2017, 2021) and is described below. A new Bayesian model was also applied to the pup staging surveys to provide an estimate of the proportion of pups born at the time surveys were flown (Mosnier et al. 2023). The Bayesian model includes stage duration (Stages 1–4) and the start date for the birth distribution curves as priors, and has two unobserved stages, the Stage 0, which defines the birth curve and Stage 6, which allows for loss from the breeding colony from Stage 5. This model is described in detail in Mosnier et al. (2023).

Myers birth distribution (MBD) model

On Sable Island, where daily access to the breeding colony is possible, stage duration was estimated from pups that were staged daily from Stage 1 (newborn) to Stage 5. As in the previous pup production estimates, the mean and variance of the duration (days) for Stage 1 to 4 was estimated by fitting the semi-Markov transition model with a gamma distribution for stage duration. We fit the model with either a common shape parameter for all stages, or a more flexible model that allowed for a separate shape parameter for all stages. The rate at which pups enter the stage *j* over time, $m_1(t)$, is a function of the transition functions, $\varphi_j(\tau)$, and the time spent in stage *j*, τ.

$$m_j(t) = \int_0^\infty m_{j-1}(t-\tau)\varphi_{j-1}(\tau)d\tau \;\; j = 1 \ldots, k$$

Following methodology of Myers and Bowen (1989) and Bowen et al. (2003), the predicted proportion of each stage present on each day, P_{ij}, is estimated with gamma and Weibull distributions, with the scale parameter, ρ, and shape parameter, κ. The proportion of pups that will be observed in stage *j* at time *t*, $n_j(t)$, is

$$n_j(t) = \int_0^\infty m_j(t-\tau)\left[1 - \int_0^\tau \varphi_j(s)ds\right] d$$

This equation assumes no pup mortality, no emigration, and that pups of all stages have equal probability of being sighted in pup transects on the colony. We selected models with the lowest Akaike's Information Criterion (AIC). Variance of the parameters and proportion born was estimated with a jackknife of stage transects (Myers and Bowen, 1989, Bowen et al. 2003, 2007).

RESULTS

RECONNAISSANCE SURVEYS

The areas where pupping is known to occur in Northumberland Strait, and around Cape Breton Island were searched for Grey Seal pups frequently during January and February. All major haul out sites and habitat thought suitable for pupping in the Bay of Fundy and on the coast of Nova Scotia were checked for pups (Figure A1). Experienced marine mammal observers aboard a King Air operated by DFO C&P completed reconnaissance surveys along the south and west

coasts of Newfoundland in late January and early February. Haul outs of both Grey and Harbour Seals were observed, but no pups were seen.

New colonies were detected at Pointe Sud-ouest on Anticosti Island, on Purdy Island on beaches facing the breeding colony on Saddle Island in the southern Gulf, on the Rocher aux Oiseaux/Rocher aux Margaulx, near the Magdalen Islands and on Scatarie Island on beaches facing the Hay Island breeding colony (Figure 1, Table 1). Notably, some pups have been observed on Scatarie Island before, but not consistently. There was no ice in the southern Gulf at the start of the survey. Near the end of January, some ice formed in Northumberland Strait and the occasional pups seen on the ice were located between Amet Island and Pictou Island. On the Eastern Shore of Nova Scotia, a small number of pups were observed on Bowen's Ledge and Basque Island (max count n = 11), where once there were established breeding colonies. For the more recently established breeding colony in the Bras D'Or Lakes on Red Island, the maximum number of pups counted was 66 on January 22.

UNCORRECTED PUP COUNTS

Sable Island

Eighteen transects were flown over Sable Island on January 11, 2021, between 10:29 and 12:45 PM (Eastern Standard Time) resulting in 1,313 photographs (Table A1). Image quality was high over most of the island (Figure A3), although the orthorectified tile (ECW files) was more blurry than the original imagery. The original imagery was used to evaluate the identification of a pup when there was uncertainty. A total of 72,209 pups was counted on the large format vertical digital imagery taken on Sable Island on January 11, 2021 (Table 1, Figure 2).

Coastal Nova Scotia

The large format survey for the southwest Nova Scotia (SWNS) islands, Mud, Round, Noddy and Flat, was completed with seven transects (Table A1) and 228 of photographs on January 16 (Table 3). The coastal photographs and orthorectified images from the large format fixed wing surveys (Table A1) was of similar quality to that of Sable Island. A total of 2,246 live pups were counted at the islands in SWNS (Table 1, Figure 2b). On Hay Island, a total of 1,619 live pups were counted on the large format imagery of January 11, 2021 (Figure 2c, Table A1). Three additional surveys were flown (January 13, 16 and 22) by helicopter and the largest estimate from these surveys was 1,705 pups (Table 1). Another 121 pups were counted on Scatarie Island (Table 1), which is proximate to Hay Island (Figure 1).

Gulf of St. Lawrence

At Brion Island a total of 4,987 pups was counted on large format vertical digital imagery flown on January 13, 2021 (Table 1, Table A1). There were two other counts of helicopter pod imagery for Brion Island on January 15 and 20, with the maximum count of 5,151 pups on January 15.

For Pictou Island, 2,792 pups were counted on large format vertical digital imagery on January 16, 2021 (Table 1, Table A1). There were two other counts of helicopter pod imagery for Pictou Island on January 21 and 23, with the maximum count of 3,604 pups on January 23. Similarly, for Saddle Island, there were 2,530 pups counted on large format vertical digital imagery on January 16, with three other counts of helicopter pod imagery for Saddle Island on January 13, 19 and 23, with the maximum count of 3,155 pups on January 23.

Finally, the number of pups on Henry Island was counted during three helicopter surveys on January 13, 20 and 22, with a maximum count of 1,447 pups on January 22.

ESTIMATES OF PUP PRODUCTION

Correction for missed pups

For Sable Island large-format photographs, the comparison between the reader's counts and the consensus counts differed by an average of 0.6% (SE = 0.27) (Table 4). A similar pattern was observed for Brion Island, with reader's counts slightly lower, 0.4% (SE = 0.36), than the consensus count. Thus, a small correction was applied for missed pups for each reader.

Correction for pup mortality

On Sable Island, eight sites from a range of habitats across the island were used to estimate the proportion of pups that had died prior to the aerial survey. The mean percentage that had died was 4.7% (SE = 1.4) (Table 5). Owing to small number of pup mortality plots and low numbers of pups in these plots in 2021, pup mortality on the breeding colony prior to the aerial survey has been estimated based on the surveys completed since 2007 (Bowen et al. 2007, 2011, den Heyer et al. 2017). The correction based on several years (mean = 0.04, Var = 0.0001) has been applied to all major colonies for which a birth distribution correction is applied.

Correction for birth distribution

Stage durations

Stage duration was estimated from 47 pups sighted daily between December 18, 2020 and January 27, 2021 on Sable Island. Of these pups, five had not reached Stage 5 before the end of field program. Pup stage duration data were also available from 153 pups that were staged daily from Stage 1 to Stage 5 at the Sable Island colony in 1997, 2007, and 2010 by different observers. The stage durations estimated in 2021 were different from earlier years, with Stage 2 being almost a day longer on average and Stage 3 a few days shorter. The most notable difference was in the duration of Stage 4, which was much longer in 2021 (Table 6, Figure A4 and 5). The differences in duration may reflect inter-annual variation in stage duration and also the differences in observer scoring. The transition to and from Stage 4 is defined by the presence of lanugo as is expected to have less variability in observer scoring, therefore we suspect that the variation reflects interannual variation in the pup shedding of lanugo. The 2021 breeding season was unusually warm, and this might have influenced the shedding of the lanugo. For 2021, the same observer completed the individual pup follows and the developmental stage transects on Sable, so the stage durations estimated from 2021 were used in the birth distribution models for Sable Island. Although the separate shape model had the lowest AIC in 2021 (Table A2), the separate shape model did not describe Stage 4 well (Figure A5), so the common shape model was used to fit the birth distribution curve on Sable Island. For coastal colonies, where the stage transects were estimated from helicopter by an experienced observer, the stage duration estimates from 1997 to 2010 were used because the variation in observers that estimated the stages and variation of stage duration across the years was more likely to encompass the stage duration for the coastal colonies and the observer effect. Here, the separate shape model was preferred and provided good fit of the stage duration models (Figures 3.1 and 3.2) and the Bayesian models (Mosnier et al. 2023).

Birth distributions

To estimate how the proportion in each developmental stage changed over time, we fitted the birth distribution model to the visual stage surveys completed on the ground on Sable Island

and from the helicopter for the coastal colonies (Table 3). As in previous years, the total count for Mud, Round, Noddy and Flat Islands in southwest Nova Scotia were adjusted using the combined staging transects from all four islands. Similarly, with the expansion of the Hay Island breeding colony to adjacent Scatarie Island, a single birth distribution was fit to the staging surveys on Hay and Scatarie Islands. A single birth distribution curve was also fit to Saddle Island and adjacent Purdy Island. At all colonies the highest count was used to estimate pup production.

Sable Island

The date of first birth on Sable Island was estimated to be December 3, 2020 based on the oldest pups seen in the first days of the field season that started on December 10. For Sable Island, each week over the course of the breeding season one observer recorded pup developmental stages at each of 14 widely distributed areas (Table 3, Figures 3.1 and 3.2). For the MBD model, the Weibull distribution provided the best fit (Table 7). The estimated proportion of pups born before the survey was flown using this latter model was similar to the estimate from the Bayesian model, as the adjusted estimates of the pup production were only different by 220 pups (less than 1% of the total). Using the MBD model, estimated pup production for the Sable Island colony (rounded to the nearest hundred) was 76,600 (SE = 2,900) pups (Table 8).

Brion Island

The date of first birth on Brion Island was estimated to be December 20, 2020. Five developmental stage surveys were completed between January 15 and February 1 (Table 3, Figures 3.1 and 3.2). The gamma curve was the preferred model for birth distribution using the MBD model (Table 7). There were three aerial survey counts and correction for pups born after the surveys for the MBD model were very similar for the survey counts on January 13 and 15 (Table 8). However, for the last survey on January 20, both the counts and the estimated pup production were lower suggesting that some of the pups had possibly left the colony. Notably, the estimate from the Bayesian model, that allows for loss of Stage 5 pups, was less impacted by the later survey. The estimate for pup production on Brion was 6,100 (SE = 400) pups based on the MBD model, which was 500 pups (8% higher) than the pup production estimated from the Bayesian model (Table 8).

Henry Island

The date of first birth on Henry Island, was estimated to be December 21, 2020. To estimate the distribution of births, the developmental stage of 4,395 pups was recorded along six ground transects covering the island between January 5 and February 9 (Figure 3, Table 3). The gamma curve was the preferred distribution for birth distribution for the MBD model (Table 7). There were four total counts for Henry Island; January 5, 13, 20, and 22. Both the MBD and Bayesian models estimated highest pup production based on the January 22 survey, which also had the highest counts (Table 8). The MBD model estimated total pup production from Henry Island to be 1,600 (SE = 110) pups, which 84 pups (5%) more than the Bayesian model.

Pictou Island

The date of first birth on Pictou Island, was estimated to be December 16, 2020. To estimate the distribution of births, the developmental stage of 10,648 pups was recorded along seven ground transects covering the Island between January 5 and February 9 (Table 3, Figures 3.1 and 3.2). The preferred birth distribution for the MBD model was a Weibull curve (Table 7). There were three counts available to estimate the pup production. There were large adjustments to the counts, as the distribution of births at Pictou was later than other colonies (Mosnier et al. 2023). The MBD model applied to the first photographic survey resulted in the largest estimates of the number of pups produced, which suggests that later surveys underestimated pup production

due to the loss of pups from the island which is not accounted for by the MBD model. The Bayesian model included loss from the colony and estimated the highest pup production from the count on January 23, again suggesting that loss from the colony may be important at this location. The total pup production estimated for Pictou based on the MBD model from the raw count of 3,604 pups January 23 was 4,700 (SE = 1,400) (Table 8).

Saddle and Purdy Islands

The date of first birth on Saddle Island was estimated to be December 21, 2020. The developmental stage of 5,307 pups was recorded during six surveys covering the island between January 1 and January 29 (Table 3, Figures 3.1 and 3.2). The gamma curve with the MBD was the preferred birth distribution (Table 7). Four aerial surveys provided pup counts for January 13, 16, 19, and 23. Here, both the Bayesian and MBD models estimated the highest pup production from the last survey. The Bayesian model estimated about 300 fewer pups (8.8% less) than the MBD model. Total pup production at Saddle Island was estimated to be 3,700 (SE = 450) (Table 8). Another 190 (SE = 14) pups were estimated at the adjacent Purdy Island.

Hay and Scatarie Islands

The date of first birth on Hay Island was estimated to be December 14, 2020. To estimate the distribution of births, the developmental stage of 3,120 pups was recorded from eight helicopter visual surveys of Hay and Scatarie Island (Table 3, Figures 3.1 and 3.2). The gamma curve was the preferred distribution for the MBD model (Table 7). There were four surveys of Hay Island and three of Scatarie Island available to estimate total pup production. For Hay Island, the MBD model predicted highest pup production from the second survey (January 16), but there was very little difference between the pup production estimates across survey dates. The Bayesian model also provided very consistent estimates across survey dates, but the highest estimate was on January 16. Total production for Hay Island, not including Scatarie Island, was estimated to be 2,100 (SE = 340) pups (Table 8).

Mud, Round, Noddy, and Flat islands

The date of first birth on Mud Island was estimated to be December 10, 2020, based on a helicopter developmental stage transects completed on December 20, 2020. The distribution of births on Mud, Round, Noddy and Flat Islands were determined from the stage composition of 1,814 pups from a total of 28 transects completed over four dates between December 20 and January 27 (Table 3, Figures 3.1 and 3.2). The preferred distribution for the MBD model was a gamma distribution (Table 7). The adjustment for births after the January 16 photographic survey was small as both birth distribution models estimated that more that 95% of the pups had been born by January 16. Total production for Mud, Round, Noddy and Flat Islands was estimated to be 2,400 (SE = 200) pups (Table 8).

REGIONAL TRENDS

Total Grey Seal pup production at all Canadian colonies in 2021 was 98,200 (SE = 8,500) individuals (Table 9). This estimate is not significantly lower than the 2016 estimates (den Heyer et al. 2021). The 2021 survey marks the first time in 60 years that the estimate of pup production has decreased on Sable Island (Figure 4). Estimated pup production at the coastal Nova Scotia colonies showed a very small increase of less than 200 animals from 4,556 animals to 4,700 (SE = 550) pups in 2021, while in the Gulf, the pup production estimate for 2021 at 16,900 (SE = 2,400) pups is the highest in the time series. Brion, Saddle, Henry and Pictou Islands all saw large increases. For both the Gulf and Scotian Shelf herds, the pup

production estimates in 2021 were not significantly different from the estimates obtained in 2016.

DISCUSSION

After more than 60 years of increase, this is the first Grey Seal pup production survey in Canadian waters where the estimates are virtually unchanged from the last survey. There was considerable variation in pup production among the coastal colonies (Table 1). As with 2016, only a few pups were observed at Bowen's Ledge or the Basque Islands off southern Cape Breton. These were areas that produced several hundred pups in the 1960s and early 1970s (Mansfield and Beck, 1977, Zwanenburg and Bowen, 1990). In the 1990s, new colonies were established on Hay Island, just south of Cape Breton, and a cluster of small islands in southwest Nova Scotia. Pup production on Hay Island rose rapidly until 2004, but estimates have been relatively stable since then, despite the expansion of the breeding colony to the adjacent Scatarie Island. The colonies in southwest Nova Scotia continue to increase, but still represent a small proportion of total pup production. A new colony, discovered on Red Island in the Bras D'Or lakes in 2015, has been reported to have pups every year since, with 66 pups observed in 2021. Reconnaissance flights identified new breeding locations on Anticosti Island (Pointe Sud-Ouest and Heath Point) and on small rocks near Brion Island. Notably, seals have been seen breeding on the rocks near Brion before, but pups were often washed away during storms. The establishment of new small colonies or pupping locations in the Gulf indicates that the population continues to expand its geographic breeding distribution and find new breeding sites as the sea ice becomes increasingly uncommon (Johnston et al. 2005, Stenson and Hammill, 2014). Notably, despite occurrence of summer haul outs and the presence of a small number of adults during the winter, no pupping was observed along the coast of Newfoundland. Brion and Pictou Islands in the Gulf have become the second and third largest breeding colonies in Canadian waters. Perhaps the most significant result of this survey, because it accounts for almost 80% of the total pup production in the northwest Atlantic (den Heyer et al. 2021), was the change in trajectory for Sable Island pup production which until this survey had been increasing since the 1960s (Stobo and Zwanenburg, 1990, Bowen et al. 2003, 2007, den Heyer et al. 2017, 2021).

Both uncorrected counts and the estimates of pup production from Sable Island were lower in 2021 than 2016, although not significantly so. With only one survey estimate that is below the previous estimate, and the uncertainty in these estimates, it is not possible to conclude that there has been a decline in pup production, but it does suggest a change in the trajectory from increasing to stable or declining. A decline or stabilization in pup production may result from unaccounted bias in the survey or reflect the lagged effects of an increase in juvenile mortality rates over the last two decades (den Heyer et al. 2014). There also could have been changes in proportion of females giving birth in 2021 or temporary or permanent emigration from the Sable Island breeding colony. While Grey Seals have high fidelity to breeding colonies, younger animals may be more likely to emigrate as new breeding colonies become established and competition for resources near Sable Island increase. It is notable that some smaller colonies along the coast of Nova Scotia and in the Gulf have been rapidly increasing in size and must be receiving some subsidy from other breeding colonies.

The methods to estimate Grey Seal pup production in the northwest Atlantic have changed since the 1960s. Early work on Sable Island and coastal colonies on the eastern shore of Nova Scotia used whole cohort tagging to estimate pup production and garner information of the movement and dispersal of Grey Seals. Mark-recapture methods were also used to estimated pup production in the Gulf from samples of marked pups (Myers et al. 1997, Hammill et al. 1998). Since 1989, aerial photographic surveys have been used to estimate pup production on

Sable Island. The aerial survey methods were extended to Hay Island in 2004, and the cluster of islands in southwest Nova Scotia in 2016. In the Gulf, the aerial survey techniques used to assess harp seals (Stenson et al. 2003) were applied to Grey Seals in 1996 (Hammill et al. 2007). This involved extensive reconnaissance to detect all concentrations of seals on ice, and systematic surveys flown to estimate the number of animals present. Prior to the 2016 survey, pups born on islands in the Gulf were counted visually. For the larger colonies, these visual counts are negatively biased (Hammill et al. 2017a). Beginning in 2016, the use of photographic surveys was expanded in the Gulf and applied at all major colonies in 2021. Here, for a few small colonies, we have also used infrared imagery to count total number of seals and estimated pup production based on the ratio of pups to adults from photographs at the colony or nearby colonies. The pup to adult ratio will vary between colonies and throughout the breeding season. To make better use of the infrared imagery in future surveys, it would be necessary to develop a systematic approach to estimating pup to adult ratios.

Pup counts from aerial survey imagery must be corrected for several factors to estimate total pup production. First, as found in other photographic surveys, some live pups may be missed on the photographs resulting in an underestimate of total count. This problem will be of greater importance in areas where pups move into the cover of trees such as Pictou Island. Second, dead pups may be missed by the imagery if they are buried by snow or sand, washed away, or scavenged. Here we attempted to estimate the proportion of pups that died before the survey and the readers were instructed not to count obviously dead pups. While it was noted that the presence of seagulls were good markers for dead pups, it is possible that recently dead pups would be counted as live pups. Notably, the mortality correction was also only estimated for Sable Island and there may be additional hazards at coastal colonies, from predators that are not observed on Sable Island such as eagles and coyotes. A black bear was also seen on Saddle Island in 2021, but there was no evidence of predation at that time. Third, we expanded the count from the imagery to estimate total pup production over the breeding season by estimating the proportion of pups born on each colony on the day we flew the survey. To minimize the impact of this correction, we attempted to fly the photographic surveys after peak pupping, but before pups begin to enter the water. Surveys flown too early will miss pups born after the survey, and later surveys will miss pups that have died during the season, left the colony or moved to habitats where they cannot be observed (for example treed areas).

Describing the birth distribution on the colonies to adjust the survey count to total pup production is difficult because of both seasonal and inter-annual variation in birth timing. Birthing is also spatially clustered at colonies, so there is considerable spatial variation in pup developmental stage composition within a breeding colony. Although stage composition data at colonies other than Sable Island have been limited in the past, in 2021 there were developmental stage composition surveys for all the breeding colonies with more than 1,000 pups. Further, the helicopter pod-mounted camera also established a digital record that could be used to estimate stage composition from photographs. Subsequent work will be needed to make full use photographs to assess the developmental stage composition. This methodology could provide digital records and should provide an opportunity to develop methods for more standardized evaluation of stages, including those developed through machine learning, which could improve estimates of pup production and help to maintain integrity of the time series.

For Sable Island, we have data on pup stage duration over several years from several observers. In 2021, we had the same observer complete the individual follows and the pup staging transects. However, for coastal colonies, several observers were used to conduct staging from helicopters. For these colonies, we also had fewer stage transects to estimate stage composition and fit the stage distribution models, as well as less information to estimate the first birth. This contributed to greater uncertainty in the birth distribution model and the

estimate of the proportion of pups born on the coastal islands. The implications of this sampling effort are more fully explored by Mosnier et al. (2023). Here, we have presented both the adjusted counts from a new Bayesian birth distribution model and the MBD model with stage duration estimated from the individual pup follows on Sable Island. The two methods provided similar total pup production estimates, but in all cases the pup production estimated by MBD model is larger. The biggest differences in the estimate of total pup production at a colony occurred at Pictou, where the birth timing was the latest and the smallest proportion of pups were born prior to the survey. On Sable Island, a considerable amount of data was collected to describe the birth distribution and account for births that occur after the survey was flown. Our estimates for the proportion of pups born on the day of survey (January 11) are close to 100%, which was higher than the estimated proportion born on the day of the survey (January 12) in 2016, suggesting that the timing of births on the island has continued to advance (Bowen et al. 2020). After weaning, pups undergo a post-weaning fast and slowly begin to leave the island; it is possible that with earlier birth distribution, some pups had already left the colony at the time of the survey. While the new Bayesian birth distribution model, that allows for loss at Stage 5, provided the same estimate of pup production as the MBD model, it estimated that 5 to 6% of pups had transitioned to an unobservable Stage 6 and left the island (Mosnier et al. 2023). The MBD model was used here as it was used to adjust the counts in previous assessments and therefore maintains the time series in pup production estimates. Notably, an improved birth distribution model (Mosnier et al. 2023) could be applied to previous pup production estimates, or the birth distribution model could be integrated into a population model and fit to survey counts. The high uncertainties around the estimates of pup production on Sable in 2016 and at the coastal colonies reflects greater uncertainty in the estimate of the proportion of pups born, and larger adjustments when the aerial survey is flown earlier in the birth distribution. Notably for Sable in 2016, stage duration was not estimated with individual pup follows, so the stage duration from previous years was used to fit the birth distribution models. Improvements in the accuracy and precision of the correction factor for pups born after an aerial survey is flown would improve the interpretation of trends in pup production and the population estimate.

In the northwest Atlantic, Grey Seals were severely depleted by the late 1800s and were considered uncommon or rare well into the middle of the last century (Fisher 1950, Lavigueur and Hammill, 1993). Government culling programs extirpated breeding colonies in both USA and Canada (Lavigueur and Hammill, 1993, Bowen and Lidgard, 2013), but small colonies on Sable Island, coastal islands in eastern Nova Scotia, and on the ice in the Gulf persisted. Despite control efforts that continued into the 1980s, Grey Seal colonies in the Gulf and on Sable Island began to increase in the 1960s. Since the 1990s breeding colonies have been re-established throughout the historical range (Wood et al. 2019, den Heyer et al. 2021). Sable Island became the largest breeding colony in northwest Atlantic in the 1980s and continued to increase until this survey. While, Sable Island still accounts for almost 80% of total Grey Seal pup production in Canada, the rapid increase in pup production at some of the smaller colonies and the detection of new breeding colonies suggests that despite the loss of ice in the Gulf, there remain suitable pupping sites throughout the range of Grey Seals. While there is evidence for limitation of pupping habitat on Hay Island, if the population is resource limited, resources at sea, not pupping habitat, will more likely be limiting. Based on the results of just one survey, it is difficult to interpret the change in the trajectory of pup production on Sable Island. The continuation of the mark-resighting program on Sable Island can provide estimates of inter-annual variability in the proportion of females giving birth and loss of seals from the breeding colony from emigration or increased mortality. It will be important, given the dominance of Sable Island numerically, to conduct another survey of Sable Island as soon as possible, as reliable forecasts of population size depend heavily on knowing if the trajectory of pup production on Sable Island has in fact changed.

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TABLES

Table 1. Grey Seal pup counts at colonies from large format and small format photographic, visual surveys and infrared imagery. Blanks indicate that there were no counts.

Location	Platform	Dates	1st	2nd	3rd	4
Sable						
Sable Island	Large Format	Jan 11	72,209	-	-	-
Gulf of St. Lawrence						
Gulf central						
Brion Island	Large format	Jan 13	4,987	-	-	-
	Helicopter	Jan 15, 20	5,151	4,350	-	-
Anticosti Island - Heath Point	DFO C&P	Jan 11	9	-	-	-
Anticosti Island - Pointe Sud-ouest	DFO C&P Infrared	Jan 12	165	-	-	-
Rocher aux Oiseaux	DFO C&P Infrared	Jan 27	87	-	-	-
Roches aux Margaulx	DFO C&P Infrared	Jan 23	13	-	-	-
Deadman Island	DFO C&P Infrared	Jan 6,7,15, 23	24	51	56	132
	Helicopter	Jan 15, Feb 1	19	0	-	-
Gulf southern coast						
Pictou Island	Large format	Jan 16	2,792	-	-	-
	Helicopter	Jan 21,23	3,452	3,604	-	-
Henry Island	DFO C&P	Jan 5	395	-	-	-
	Helicopter	Jan 13,20,22	1,218	1,397	1,447	-
Saddle Island	Large format	Jan 16	2530	-	-	-
	Helicopter	Jan 13,19,23	1,750	2,873	3,155	-
Purdy Island	Helicopter	Jan 29	169	-	-	-
Margaree Island	DFO C&P	Jan 5	39	-	-	-
Amet Island	Helicopter	Jan 19,23	94	98	-	-
Coastal Nova Scotia						
Eastern Nova Scotia						
Hay Island	Large format	Jan 11 (2 readers)	1,619	-	-	-
	Helicopter	Jan 13,16,22	1,705	1,702	1,637	-
Scatarie Island	Helicopter	Jan 13,16,22	70	107	121	-
Red Island	Helicopter	Jan 16,22	58	66	-	-
Bowen's ledge	Helicopter	Jan 16	2	-	-	-
Basque Island	Helicopter-visual	Jan 13	8	-	-	-
Southwest Nova Scotia						
Round Island	Large Format	Jan 16	560	-	-	-
Mud Island	Large Format	Jan 16	1,456	-	-	-
Noddy Island	Large Format	Jan 16	184	-	-	-
Flat Island	Large Format	Jan 16	46	-	-	-

Table 2. Grey Seal pup developmental stages.

Stage	Description
1	newborn, wet, weak, yellowish (possibly), neck visible
2	tubular shape; body trunk width equals shoulder width, neck visible
3	body trunk is wider than the shoulders, neck not visible, no sign of moulting
4	moulting evident, flippers and nose not included in this criterion
5	completely moulted (>= 95% moulted)

Table 3. Number of Grey Seal pups in different developmental stages recorded during visual surveys flown over coastal breeding colonies and recorded from ground transects on Sable Island.

Colony Date	No Surveys	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Total
Sable Island							
12/17/2020	14	548	703	3	0	0	1,254
12/22/2020	12	212	1469	189	0	1	1,871
12/23/2020	2	100	196	5	0	0	301
12/29/2020	8	302	1172	382	30	3	1,889
12/30/2020	4	55	456	316	22	3	852
12/31/2020	2	19	273	142	25	14	473
1/4/2021	2	7	74	309	45	30	465
1/5/2021	5	35	240	749	46	39	1,109
1/6/2021	5	31	189	760	102	90	1,172
1/7/2021	2	13	50	218	111	91	483
1/12/2021	6	8	41	569	503	380	1,501
1/13/2021	8	21	105	829	535	425	1,915
1/19/2021	3	2	11	120	160	355	648
1/20/2021	11	7	51	441	394	1,644	2,537
1/26/2021	8	0	10	177	150	1,497	1,834
1/27/2021	6	0	10	136	141	983	1,270
Amet Island							
1/5/2021	1	0	7	22	0	0	29
1/12/2021	1	0	15	67	6	0	88
1/19/2021	1	0	4	41	28	10	83
Brion Island							
1/11/2021	1	62	415	1,010	83	21	1591
1/15/2021	1	30	467	1,249	203	93	2,042
1/18/2021	1	19	285	1,726	439	473	2,942
1/20/2021	1	8	151	1,054	345	431	1,989
2/1/2021	1	7	68	212	245	880	1,412
Henry Island							
1/5/2021	1	22	258	84	0	0	364
1/13/2021	1	17	379	232	6	1	635
1/20/2021	1	14	159	490	110	32	805
1/22/2021	1	1	191	665	148	123	1,128
2/1/2021	1	4	36	283	181	531	1,035

Colony Date	No Surveys	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Total
2/9/2021	1	0	6	85	34	303	428
Pictou Island							
1/5/2021	1	43	450	13	1	0	507
1/12/2021	1	29	650	232	1	0	912
1/19/2021	1	58	681	643	46	14	1,442
1/21/2021	1	39	1,314	1,338	141	61	2,893
1/23/2021	1	52	393	923	224	68	1,660
2/1/2021	1	22	530	821	242	377	1,992
2/9/2021	1	1	66	468	184	523	1,242
Saddle-Purdy							
1/5/2021	1	54	202	2	0	0	258
1/12/2021	1	36	453	360	4	0	853
1/19/2021	2	46	593	953	57	23	1,672
1/23/2021	1	31	318	508	95	58	1,010
1/29/2021	1	0	154	818	216	326	1,514
Hay-Scatarie							
1/11/2021	1	2	166	345	22	14	549
1/13/2021	1	0	31	31	1	0	63
1/16/2021	2	4	162	444	153	113	876
1/22/2021	2	2	81	466	216	497	1,262
2/9/2021	2	0	2	46	33	289	370
Mud-Round-Noddy-Flat							
12/20/2020	8	31	107	31	0	0	169
1/9/2021	7	19	72	494	30	83	698
1/13/2021	9	0	21	98	95	261	475
1/27/2021	4	0	3	22	23	424	472

Table 4. Reader and consensus pup counts from 30 transects from digital images from the Sable Island survey on January 11 and Brion Island on January 13.

	Sable Island				Brion Island			
Transect	**Count**	**Consensus Count**	**Difference**	**Difference %**	**Count**	**Consensus count**	**Difference**	**Difference %**
1	1	1	0	0.00	2	2	0	0.00
2	14	15	-1	-6.67	43	42	1	2.38
3	41	42	-1	-2.38	85	85	0	0.00
4	5	5	0	0.00	79	78	1	1.28
5	87	87	0	0.00	81	81	0	0.00
6	50	51	-1	-1.96	48	49	-1	-2.04
7	98	98	0	0.00	14	15	-1	-6.67
8	77	77	0	0.00	8	8	0	0.00
9	60	59	1	1.69	38	38	0	0.00
10	64	64	0	0.00	52	52	0	0.00
11	237	237	0	0.00	68	68	0	0.00
12	75	74	1	1.35	103	105	-2	-1.90
13	142	142	0	0.00	95	96	-1	-1.04
14	158	158	0	0.00	91	90	1	1.11
15	181	181	0	0.00	66	67	-1	-1.49
16	130	132	-2	-1.52	77	78	-1	-1.28
17	175	175	0	0.00	103	106	-3	-2.83
18	266	264	2	0.76	104	104	0	0.00
19	27	27	0	0.00	122	121	1	0.83
20	156	159	-3	-1.89	99	100	-1	-1.00
21	102	103	-1	-0.97	86	86	0	0.00
22	258	259	-1	-0.39	98	98	0	0.00
23	176	176	0	0.00	72	71	1	1.41
24	56	57	-1	-1.75	38	40	-2	-5.00
25	36	36	0	0.00	223	225	-2	-0.89
26	128	130	-2	-1.54	115	114	1	0.88
27	105	106	-1	-0.94	119	119	0	0.00
28	132	133	-1	-0.75	138	137	1	0.73
29	203	204	-1	-0.49	105	102	3	2.94
30	230	231	-1	-0.43	2	2	0	0.00
Mean (SE)				**-0.6 (0.27)**				**-0.42 (0.36)**

Table 5. Total count of pups from imagery of mortality plots on Sable Island, and the number of pups that died in the plots, as well as percentage that died before imagery taken by plot and the mean and standard deviation (STD) of the percent of pup that died by year. Blank cells have no value.

Year	Location	Total count	Dead count	Percent	Mean	STD
2021	South Beach, east Dead Horse Pass	50	1	0.02	-	-
	A-frame	54	5	0.09	-	-
	Little Italy	97	11	0.11	-	-
	Boness Cove	136	3	0.02	-	-
	No. 4 East	155	11	0.07	-	-
	Legal Crossing, Central	113	2	0.02	-	-
	Blowout	75	1	0.01	-	-
	North Beach, East Light Dune	70	2	0.03	0.05	0.037
2016	North Beach, East Light Dune	76	1	0.01	-	-
	No. 4 West	57	0	0.00	-	-
	Beck’s Cove	64	4	0.06	-	-
	Legal Crossing, Inland, North	93	2	0.02	-	-
	Blowout	88	7	0.08	-	-
	Deadhorse Pass, South	107	8	0.07	-	-
	A-Frame, Inland, North	102	8	0.08	-	-
	Little Italy, Inland	107	7	0.07	-	-
	Tern Colony	112	6	0.05	-	-
	West of BIO, North	232	13	0.06	0.05	0.027
2010	East Light Dune	1,109	35	0.03	-	-
	Legal Crossing	1,433	41	0.03	-	-
	CWS - Tern Colony	496	11	0.02	-	-
	Blowout	1,922	36	0.02	-	-
	SouthBeach (to Beck's Cove)	638	33	0.05	-	-
	No. 4 West	1,216	32	0.03	-	-
	Bald Dune Cove	721	16	0.02	-	-
	East Light Cut	507	11	0.02	0.03	0.010
2007	Beck's Cove	167	5	0.03	-	-
	Blowout	1,268	33	0.03	-	-
	CWS	549	16	0.03	-	-
	East Light, north beach	1,082	49	0.05	-	-
	East Light cut, N	238	4	0.02	-	-
	Lakeshore	1,395	44	0.03	-	-
	Legal Crossing, E	1,392	21	0.02	-	-
	No. 4 West	239	13	0.05	-	-
	No. 4	311	11	0.04	0.03	0.012

Table 6. Estimates of stage durations from daily records Grey Seal pups followed from birth to Stage 5 in 1997 (n = 47), 2007 (n = 52), 2010 (n = 54), 2021 (n = 47). Data were fit with a gamma distribution. Density function for gamma is $\rho(\rho t)^{\kappa-1}\exp(-\rho t)$.

Year	Stage	CS Shape	CS Rate	CS Mean	CS Var	SS Shape	SS Rate	SS Mean	SS Var
2021	1	12.8629	4.3417	3.0	0.68	315.5848	105.7674	3.0	0.03
	2	12.8629	2.8919	4.5	1.54	63.1787	13.6630	4.6	0.34
	3	12.8629	1.3137	9.8	7.45	7.5275	0.7851	9.6	12.21
	4	12.8629	1.1155	11.5	10.34	2.1506	0.1017	21.2	208.06
2010	1	21.4900	7.6832	2.8	0.36	11.1749	4.0291	2.8	0.69
	2	21.4900	5.4825	3.9	0.71	88.5218	22.5274	3.9	0.17
	3	21.4900	1.6420	13.1	7.97	31.7103	2.4206	13.1	5.41
	4	21.4900	4.7485	4.5	0.95	3.7174	0.8260	4.5	5.45
2007	1	25.1543	8.4940	3.0	0.35	30.9494	10.4025	3.0	0.29
	2	25.1543	8.2674	3.0	0.37	57.3105	18.7403	3.1	0.16
	3	25.1543	2.1113	11.9	5.64	25.9406	2.1906	11.8	5.41
	4	25.1543	4.7648	5.3	1.11	8.9467	1.6816	5.3	3.16
1997	1	21.1999	5.4541	3.9	0.71	22.0426	5.6670	3.9	0.69
	2	21.1999	5.2657	4.0	0.76	23.4430	5.8169	4.0	0.69
	3	21.1999	2.0168	10.5	5.21	19.7099	1.8781	10.5	5.59
	4	21.1999	3.0093	7.0	2.34	24.2914	3.4408	7.1	2.05
1997 –2010	1	18.7782	5.8232	3.2	0.55	13.7142	4.2873	3.2	0.75
	2	18.7782	5.1209	3.7	0.72	17.8973	4.8861	3.7	0.75
	3	18.7782	1.5926	11.8	7.4	25.2143	2.1281	11.9	5.57
	4	18.7782	3.3292	5.6	1.69	9.0058	1.6134	5.6	3.46
All	1	16.9384	5.3599	3.2	0.59	15.8732	5.0320	3.2	0.63
	2	16.9384	4.4033	3.9	0.87	19.8932	5.1591	3.9	0.75
	3	16.9384	1.4958	11.3	7.57	17.7055	1.5648	11.3	7.23
	4	16.9384	2.6311	6.4	2.45	11.6960	1.8140	6.5	3.55

Table 7. Comparison of gamma and Weibull Myers birth distribution models fitted to staging transects data from each colony. Both models had shape (κ) and rate (ρ) parameters. Density function for gamma is $\rho(\rho t)^{\kappa-1}\exp(-\rho t)$ *and Weibull is* $\kappa\rho(\rho t)^{\kappa-1}\exp[-(\rho t)^{\kappa}]$*. Best fitting model in bold.*

Colony	Model	Shape	Shape SE	Rate	Rate SE	AIC
Sable Island	Gamma	4.9377	0.3749	0.2546	0.0179	-44,005.5
	Weibull	**2.4723**	**0.1183**	**21.4875**	**0.3528**	**-44,159.9**
Brion Island	**Gamma**	**1.8216**	**0.181**	**0.1297**	**0.0179**	**-23,554.3**
	Weibull	1.5216	0.163	14.4981	1.1095	-23,468.6
Henry Island	**Gamma**	**3.3842**	**0.6662**	**0.1924**	**0.041**	**-10,045.2**
	Weibull	2.1028	0.2193	19.0577	0.6789	-10,032.5
Pictou Island	Gamma	6.8694	1.2327	0.2175	0.058	-26,933.7
	Weibull	**3.3749**	**0.229**	**32.8702**	**2.3271**	**-27,033.2**
Saddle-Purdy	**Gamma**	**4.9003**	**0.7259**	**0.2326**	**0.0443**	**-12,490.2**
	Weibull	2.8095	0.2659	21.9288	1.2701	-12,422.8
Hay-Scatarie	**Gamma**	**2.9802**	**0.55**	**0.1581**	**0.0286**	**-7,449.49**
	Weibull	1.9401	0.2222	20.2351	2.1513	-7,435.43
Mud-Round-	**Gamma**	**1.5723**	**0.4437**	**0.1263**	**0.0337**	**-3,666.53**
Noddy-Flat	Weibull	1.408	0.2618	13.1044	1.3887	-3,644.22

Table 8. Count of live pups from aerial survey, the estimated proportion (Prop) born and variances (Prop Var) and counts adjusted (Adj Count) for the distribution of births, missed pups and mortality before the day of the photographic surveys based on Myers (MBD) and Bayesian birth distribution models, with standard error (SE), and lower (LL) and upper (UL) 95% confidence limits. The deviation in the count (Dev Count) in absolute numbers and percentage are also presented. The estimates from the maximum count are in bold.

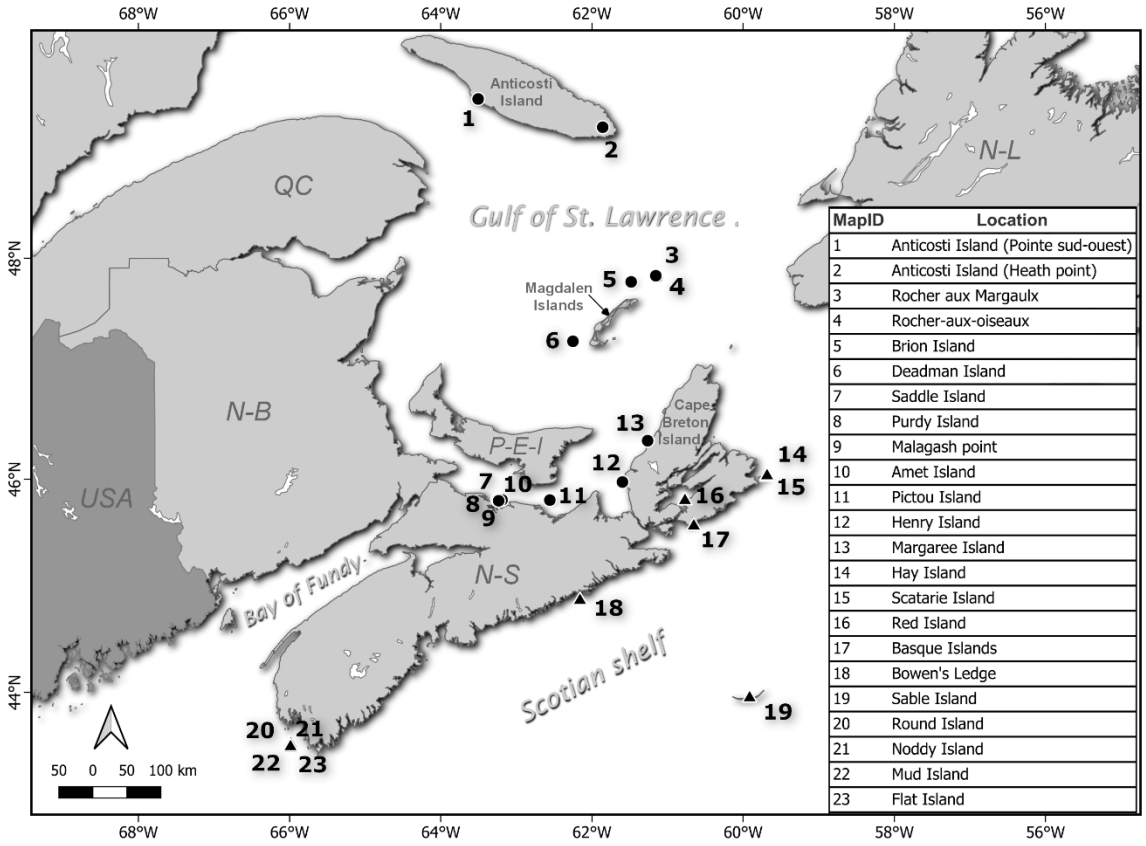
Survey Date	Count	Meyers Birth Distribution						Bayesian							
		Prop	Prop Var	Adj Count	Adj Count SE	Adj Count LL	Adj Count UL	Prop	Prop Var	Adj Count	Adj Count SE	Adj Count LL	Adj Count UL	Dev Count	Dev Count %
Sable Island															
1/11/2021	**72,209**	**0.987**	**0.001**	**76,587**	**2,933**	**70,838**	**82,337**	**0.991**	**0.000**	**76,367**	**1,550**	**73,329**	**79,405**	**220**	**0.3**
Brion Island															
1/13/2021	4,987	0.849	0.004	6,141	452	5,255	7,026	0.939	0.000	5,563	165	5,240	5,886	578	9.4
1/15/2021	**5,151**	**0.877**	**0.003**	**6,137**	**405**	**5,344**	**6,930**	**0.956**	**0.000**	**5,635**	**153**	**5,336**	**5,935**	**502**	**8.2**
1/20/2021	4,350	0.928	0.002	4,899	244	4,422	5,377	0.982	0.000	4,633	113	4,410	4,855	266	5.4
Henry Island															
1/5/2021	395	0.460	0.004	898	125	653	1,143	0.648	0.010	646	104	443	849	252	28.1
1/13/2021	1,218	0.756	0.005	1,683	166	1,359	2,008	0.880	0.002	1,456	83	1,294	1,618	227	13.5
1/20/2021	1,397	0.895	0.004	1,632	124	1,388	1,876	0.958	0.000	1,528	47	1,436	1,620	104	6.4
1/22/2021	**1,447**	**0.918**	**0.003**	**1,647**	**112**	**1,427**	**1,867**	**0.969**	**0.000**	**1,563**	**44**	**1,478**	**1,649**	**84**	**5.1**
Pictou Island															
1/16/2021	2,792	0.560	0.061	5,213	2,308	689	9,737	0.858	0.002	3,434	212	3,019	3,849	1,779	34.1
1/21/2021	3,452	0.743	0.064	4,855	1,662	1,598	8,113	0.921	0.001	3,939	156	3,633	4,244	916	18.9
1/23/2021	**3,604**	**0.804**	**0.055**	**4,684**	**1,375**	**1,989**	**7,378**	**0.938**	**0.001**	**4,032**	**139**	**3,760**	**4,304**	**652**	**13.9**
Saddle Island															
1/13/2021	1,750	0.636	0.018	2,877	618	1,666	4,087	0.823	0.003	2,247	166	1,921	2,572	630	21.9
1/16/2021	2,530	0.736	0.019	3,593	670	2,279	4,907	0.889	0.002	2,996	151	2,700	3,291	597	16.6
1/19/2021	2,873	0.814	0.016	3,687	581	2,549	4,825	0.933	0.001	3,236	120	3,001	3,470	451	12.2
1/23/2021	**3,155**	**0.889**	**0.011**	**3,711**	**447**	**2,835**	**4,587**	**0.966**	**0.000**	**3,422**	**97**	**3,231**	**3,613**	**289**	**7.8**
Hay Island															
1/11/2021	1,619	0.821	0.023	2,065	386	1,309	2,821	0.949	0.001	1,792	63	1,668	1,916	273	13.2
1/11/2021	1,614	0.821	0.023	2,058	384	1,305	2,812	0.949	0.001	1,786	63	1,662	1,910	272	13.2
1/13/2021	**1,705**	**0.855**	**0.019**	**2,089**	**338**	**1,427**	**2,752**	**0.966**	**0.000**	**1,852**	**56**	**1,742**	**1,963**	**237**	**11.3**

Survey Date	Count	Meyers Birth Distribution						Bayesian							
		Prop	Prop Var	Adj Count	Adj Count SE	Adj Count LL	Adj Count UL	Prop	Prop Var	Adj Count	Adj Count SE	Adj Count LL	Adj Count UL	Dev Count	Dev Count %
1/16/2021	1,702	0.895	0.013	1,992	259	1,484	2,500	0.982	0.000	1,817	48	1,723	1,911	175	8.8
1/22/2021	1,637	0.946	0.006	1,812	150	1,517	2,106	0.995	0.000	1,722	41	1,641	1,803	90	5.0
Scatarie Island															
1/13/2021	70	0.855	0.019	86	14	59	113	0.966	0.000	76	2	72	81	10	11.6
1/16/2021	107	0.895	0.013	125	16	93	157	0.982	0.000	114	3	108	120	11	8.6
1/22/2021	**121**	**0.946**	**0.006**	**134**	**11**	**112**	**156**	**0.995**	**0.000**	**127**	**3**	**121**	**133**	**7**	**5.0**
Mud Island															
1/16/2021	**1,456**	**0.972**	**0.006**	**1,569**	**129**	**1,316**	**1,822**	**0.991**	**0.000**	**1,539**	**33**	**1,475**	**1,603**	**30**	**1.9**
Noddy Island															
1/16/2021	**184**	**0.972**	**0.006**	**198**	**16**	**166**	**230**	**0.991**	**0.000**	**195**	**4**	**186**	**203**	**3**	**1.8**
Round Island															
1/16/2021	**560**	**0.972**	**0.006**	**603**	**50**	**506**	**701**	**0.991**	**0.000**	**592**	**13**	**567**	**617**	**11**	**1.8**
Flat Island															
1/16/2021	**46**	**0.972**	**0.006**	**50**	**4**	**42**	**58**	**0.991**	**0.000**	**49**	**1**	**47**	**51**	**1**	**2.7**
Total Max Count	**89,638**	**-**	**-**	**97,409**	**-**	**86,002**	**108,818**	**-**	**-**	**95,373**	**-**	**91,272**	**99,476**	**2,036**	**2.1**

Table 9. Count and standard deviation (SD) of the number of live pups from aerial survey and counts adjusted for the distribution of births and mortality before the day of the photographic surveys. Total counts and standard errors (SE) reported to the nearest 100 seals. Gulf = Gulf of St. Lawrence; CNS = Coastal Nova Scotia. Dash indicates that there is no estimate.

Location	Method	Date	Count	Count SD	Adj Count	Adj Count SE	Total	Total SE
Sable Island	Plane - Large size aerial photography	1/11/2021	72,209	-	76,587	2,933	76,600	2,900
Gulf								
Brion Island	Plane - Large size aerial photography	1/15/2021	5,151	-	6,137	405	-	-
Saddle Island	Helicopter - Pod camera	1/23/2021	3,155	-	3,711	447	-	-
Pictou Island	Plane - Large size aerial photography	1/23/2021	3,604	-	4,684	1,375	-	-
Henry Island	Helicopter - Pod camera	1/22/2021	1,447	-	1,647	112	-	-
Purdy Island	Helicopter - Pod camera	1/29/2021	169	-	186	14	-	-
Anticosti Island - Pointe Sud-ouest	Plane C&P	1/12/2021	165	6.2	-	-	-	-
Deadman Island	Plane C&P	1/23/2021	132	2.7	-	-	-	-
Rocher aux Oiseaux	Plane C&P	1/27/2021	87	3.3	-	-	-	-
Margaree Island	Plane C&P	1/5/2021	39	0.5	-	-	-	-
Rocher aux Margaulx	Plane C&P	1/23/2021	13	0.5	-	-	-	-
Amet Island	Helicopter - Pod camera	1/23/2021	98	-	-	-	-	-
Anticosti Island - Heath Point	Plane C&P	1/11/2021	9	-	-	-	-	-
Gulf Total			-	-	-	-	16,900	2,400
CNS								
Hay Island	Helicopter - Pod camera	1/13/2021	1,705	-	2,089	338	-	-
Mud Island	Plane - Large size aerial photography	1/16/2021	1,456	-	1,569	129	-	-
Round Island	Plane - Large size aerial photography	1/16/2021	560	-	603	50	-	-
Noddy Island	Plane - Large size aerial photography	1/16/2021	184	-	198	16	-	-
Scatarie Island	Helicopter - Pod camera	1/22/2021	121	-	134	11	-	-
Red Island	Helicopter - Visual	1/16/2021	46	-	50	4	-	-
Flat Island	Plane - Large size aerial photography	1/16/2021	46	-	50	4	-	-
Basque Island	Helicopter - Visual Staging	1/13/2021	8	-	-	-	-	-
Bowen's Ledge	Helicopter - Pod camera	1/16/2021	2	-	-	-	-	-
CNS Total			-	-	-	-	4,700	550
TOTAL			90,426	-	-	-	98,200	5,800

FIGURES



MapID	Location
1	Anticosti Island (Pointe sud-ouest)
2	Anticosti Island (Heath point)
3	Rocher aux Margaulx
4	Rocher-aux-oiseaux
5	Brion Island
6	Deadman Island
7	Saddle Island
8	Purdy Island
9	Malagash point
10	Amet Island
11	Pictou Island
12	Henry Island
13	Margaree Island
14	Hay Island
15	Scatarie Island
16	Red Island
17	Basque Islands
18	Bowen's Ledge
19	Sable Island
20	Round Island
21	Noddy Island
22	Mud Island
23	Flat Island

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.

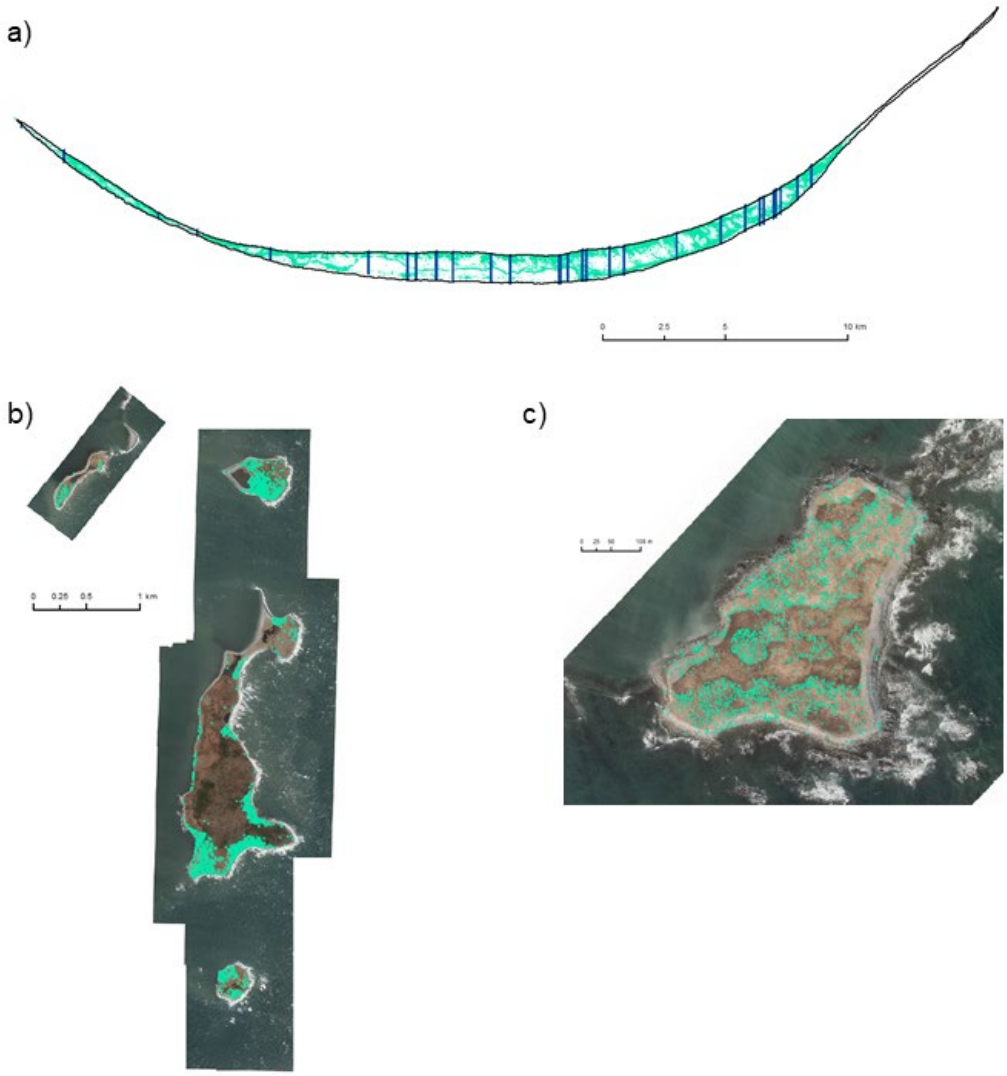


Figure 2. Distribution of Grey Seal pups on (a) Sable Island (green dots) and validation count transects (blue lines), (b) Southwest Nova Scotia Islands and (c) Hay Island.

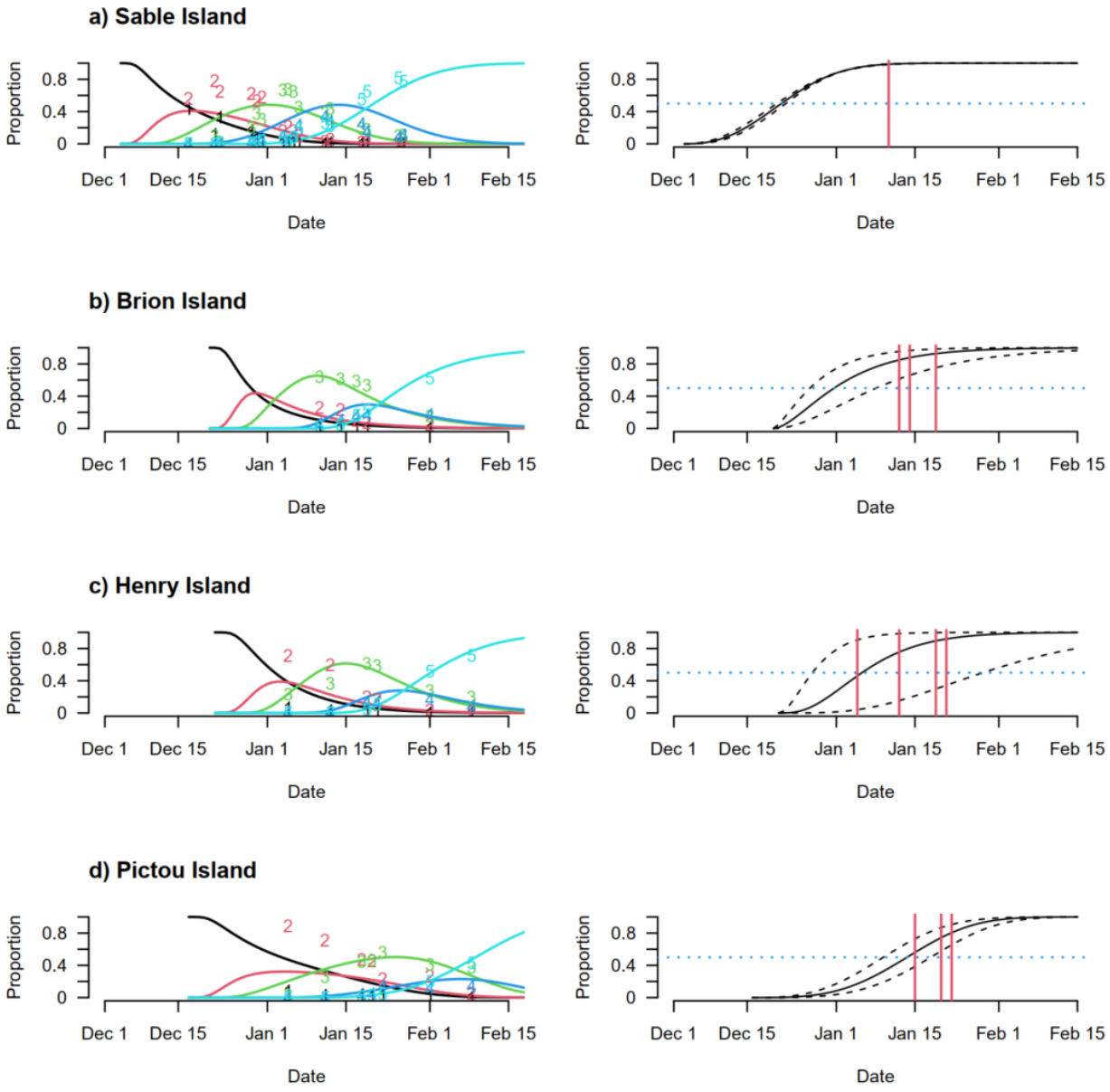


Figure 3.1. The left hand column indicates the fit of the MBD model to the stage composition survey data for each colony. The proportion of each stage is plotted, the number indicates the stage and the coloured line indicates the estimated proportion in that stage. The right hand column is the estimated cumulative distribution of births, where the horizontal red line indicates the day aerial surveys were flown, and the blue dotted horizontal line indicates when 50% of pups were born. Limits for the 95% confidence interval is plotted in dashed lines.

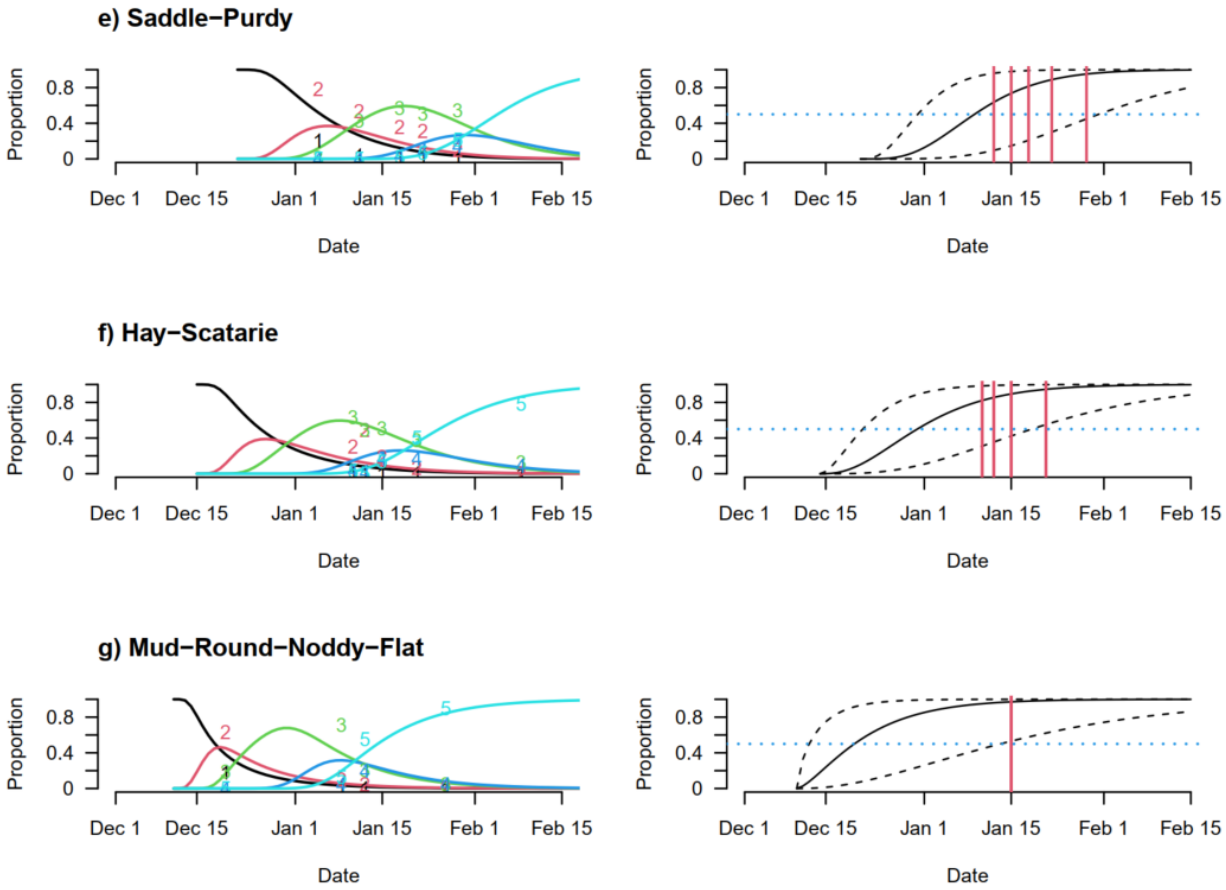


Figure 3.2. The left hand column indicates the fit of the MBD model to the stage composition survey data for each colony. The proportion of each stage is plotted, the number indicates the stage and the coloured line indicates the estimated proportion in that stage. The right hand column is the estimated cumulative distribution of births, where the horizontal red line indicates the day aerial surveys were flown, and the blue dotted horizontal line indicates when 50% of pups were born. Limits for the 95% confidence interval is plotted in dashed lines.

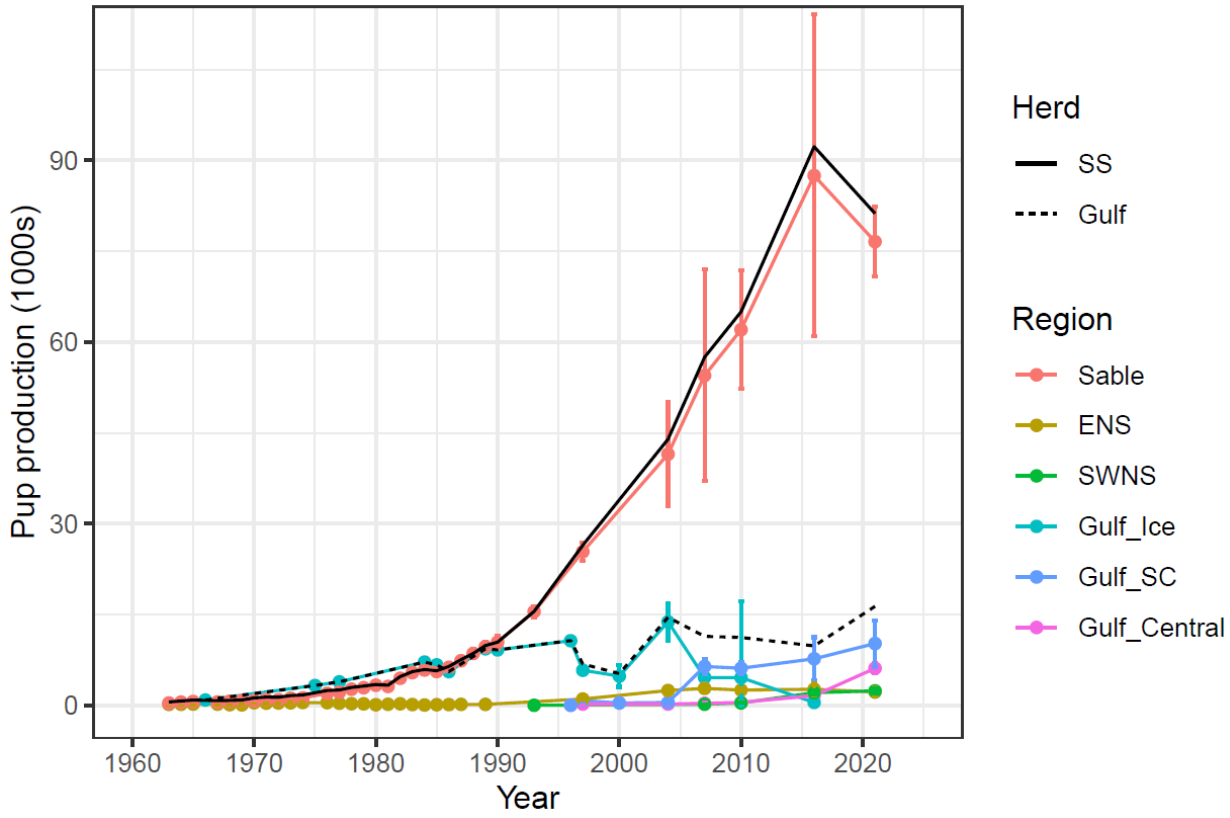


Figure 4. Regional trends in pup production throughout the Canadian range of Grey Seals. The black solid line is total production for Scotian Shelf (SS), and the dashed black line is for the Gulf of St. Lawrence (Gulf). Coloured lines indicate Sable Island (Sable), eastern Nova Scotian (ENS) and southwest Nova Scotia (SWNS) colonies, the colonies on the ice (Gulf_Ice), southern coast (Gulf_SC) and the central area (Gulf_Central) of the Gulf of St. Lawrence.

APPENDIX

Table A1. Number of transects flown and photographs taken for each colony.

Colony	Number of Transects	Number of Photos
Brion	14	437
Flat	2	26
Hay	2	19
Mud Round Noddy	5	202
Pictou	10	589
Sable	18	1,313
Saddle	2	28

Table A2. AIC table for models of stage duration fit with common shape (CS-Shape) and separate shape (SS-Shape) by winter season.

Year	CS-Shape	SS-Shape
2021	469.7769	433.2672
2010	613.4738	601.8626
2007	553.7588	549.3082
1997	634.9709	634.7939
1997_2010	1,984.947	1,974.154
All	**2,524.746**	**2,523.38**

Table A3. The number of pup developmental stage surveys completed on the ground or from helicopter by location.

Colony	No Surveys	No Pups	First Survey	Last Survey
Amet Island	3	200	1/5/2021	1/19/2021
Basque Island	1	8	1/13/2021	1/13/2021
Bowen's Ledge	1	2	1/16/2021	1/16/2021
Brion Island	5	9,976	1/11/2021	2/1/2021
Margaree Island	1	12	1/13/2021	1/13/2021
Deadman Island	1	23	1/15/2021	1/15/2021
Hay-Scatarie	8	3,120	1/11/2021	2/9/2021
Henry Island	6	4,395	1/5/2021	2/9/2021
Mud-Round-Noddy-Flat	28	1,814	12/20/2020	1/27/2021
Pictou Island	7	10,648	1/5/2021	2/9/2021
Red Island	3	153	1/13/2021	1/22/2021
Sable Island	98	19,574	12/17/2020	1/27/2021
Saddle-Purdy	6	5,307	1/5/2021	1/29/2021
Total	**168**	**55,232**	**12/17/2020**	**2/9/2021**

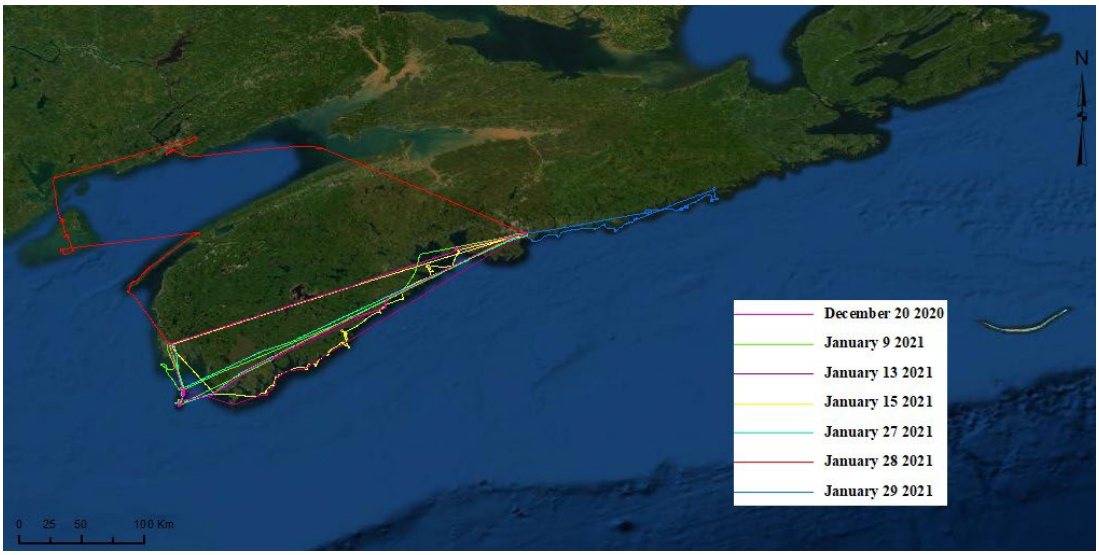


Figure A1. Directed Grey Seal reconnaissance surveys in winter of 2020–2021 (January 15, 28, 29) near and around known seal haul outs on the Atlantic coast of New Brunswick and Nova Scotia. Opportunistic (December 20, January 9, 13, 27) searches were completed along Nova Scotia coastline in transit to the breeding colonies in southwest Nova Scotia. The eastern coast of Nova Scotia, including Cape Breton Island and the Gulf of St. Lawrence, was searched during flights to established colonies.

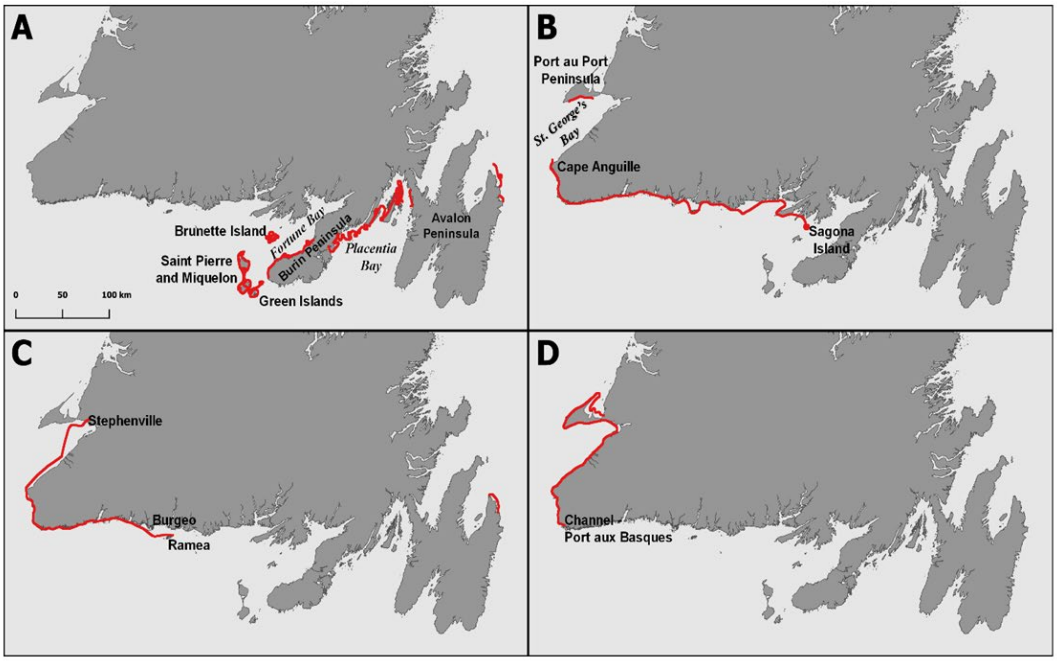


Figure A2. Opportunistic Grey Seal reconnaissance surveys along the Newfoundland coastline in winter of 2020–2021. The flight (red line) occurring on (A) January 14, (B) January 25, (C) February 5, and (D) February 10.

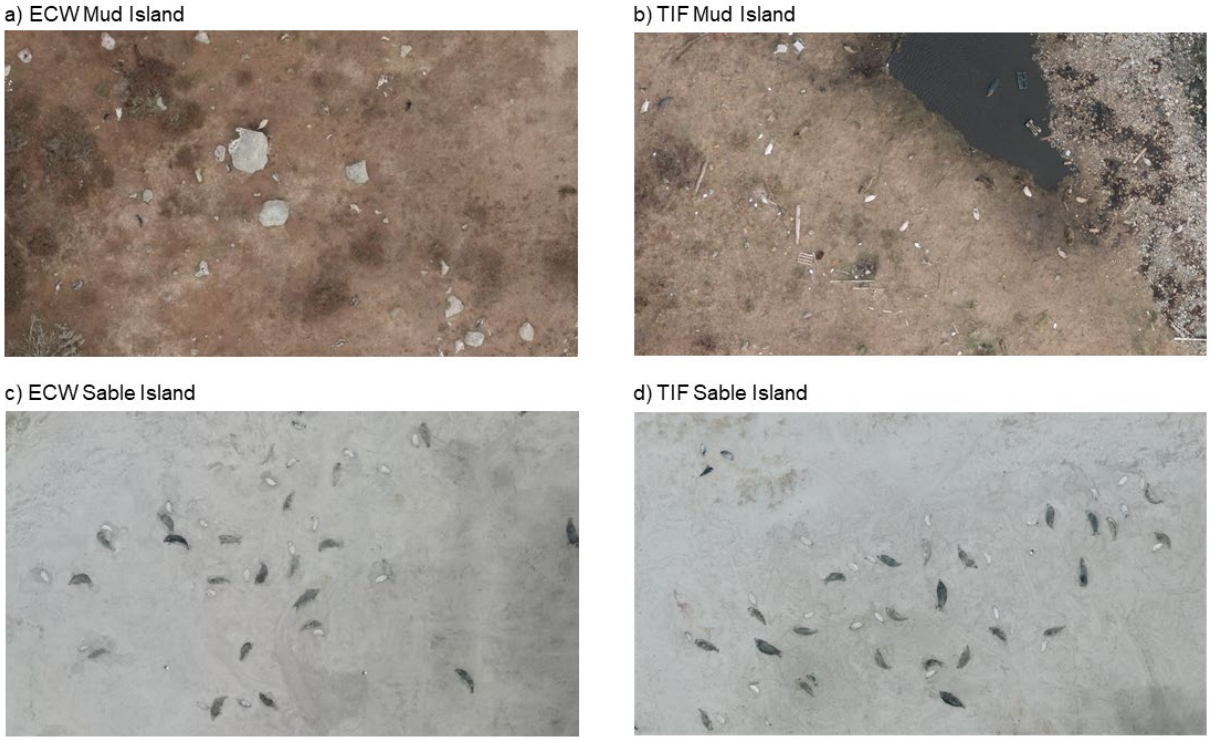


Figure A3. Example of digital aerial imagery from Mud Island (a,b) and Sable Island (c,d) in two different formats (.ECW and .TIF).

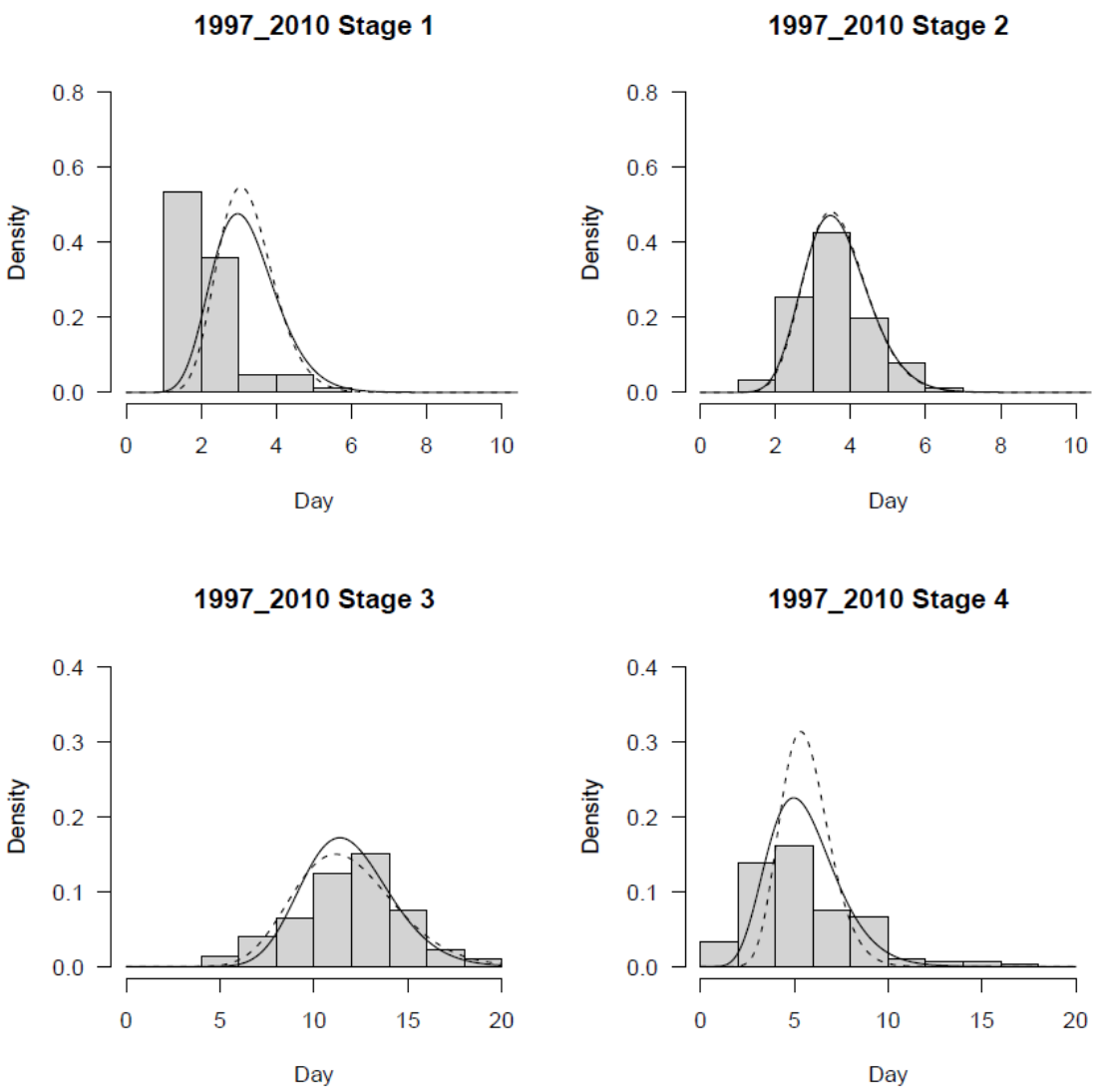


Figure A4. Density of pups in Stages 1 to 4 by days from daily follows on Sable Island in 1997–2010 (n = 153). The solid line is density distribution estimated from the common-shape MBD model and the dashed line is estimated from the separate-shape MBD model.

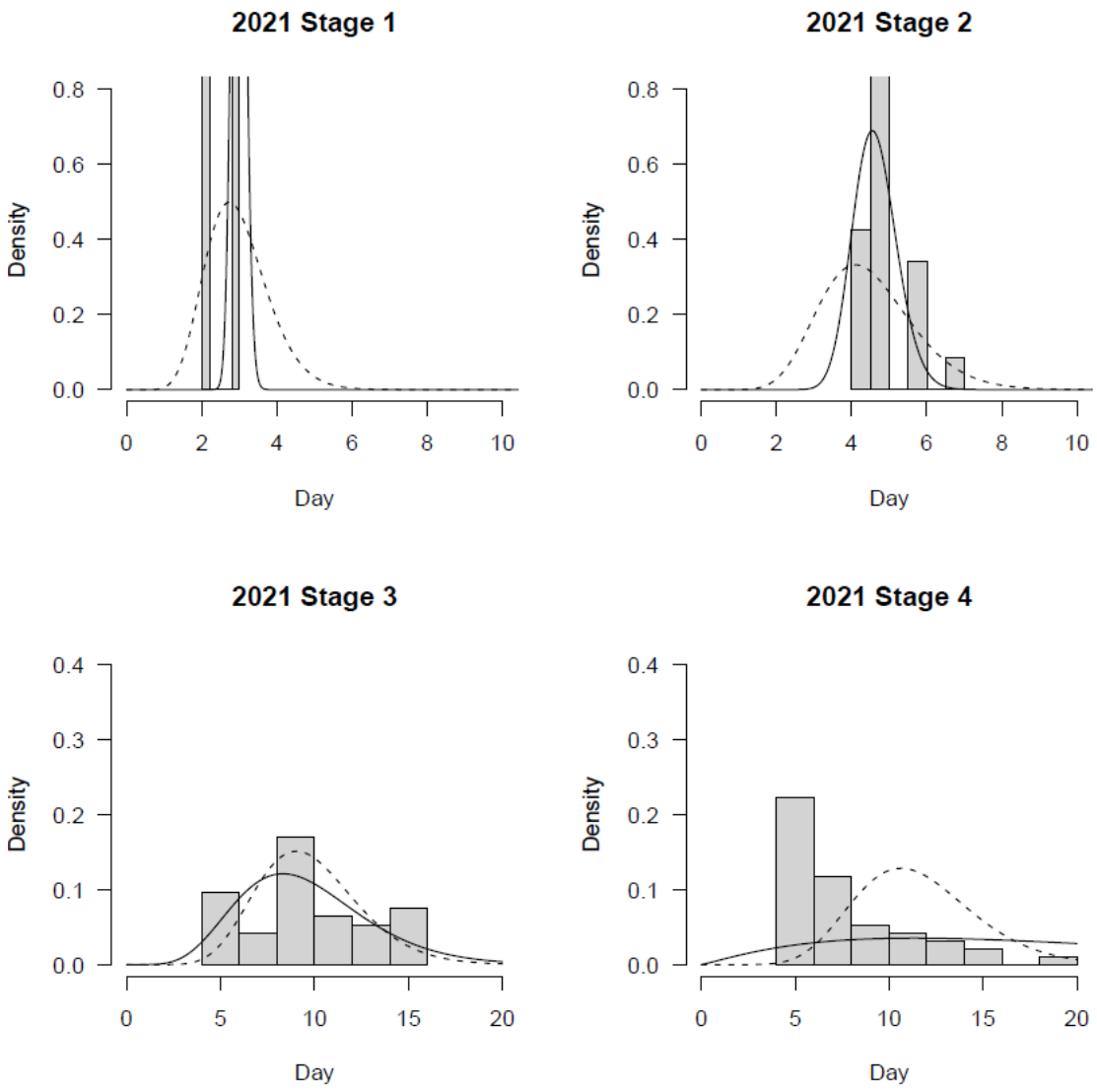


Figure A5. Density of pups in Stages 1 to 4 by days in the stage on Sable Island in 2021 (n = 47). The solid line is density distribution estimated from the common-shape MBD model, and the dashed line is estimated from the separate-shape MBD model.