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Pup Production at Scotian Shelf Grey Seal (*Halichoerus grypus*) Colonies in 2016

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Foreword

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

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ABSTRACT

To estimate grey seal (*Halichoerus grypus*) pup production, we conducted digital-photographic aerial surveys of breeding colonies on Sable Island and smaller islands along Atlantic coast of Nova Scotia in January 2016. A total of 74,889 pups was counted on the mosaic image from Sable Island. Given the high quality of the imagery, no correction to the count was applied for pups that could not be seen on the image. Small corrections were made for pups that were missed by the image reader (0.022) and for pup mortality (0.051) prior to the survey. To estimate the proportion of pups born at the time of the survey, a transition model was fit to the stages of known-age pups and the distribution of the pup stages collected weekly in the colony between December 14, 2015, and January 29, 2016. We estimated that 97% (SE=1%) of pups had been born by the time of the Sable Island survey. The estimated total pup production for Sable Island in 2016 was 83,600 with 95% confidence limits of 63,600 to 103,500. Pup production on Sable Island has continued to increase, but at a slower rate than it did in the late 1990s and early 2000s. Three digital-photographic aerial surveys were completed at Hay Island. Snow cover and the rocky shore of Hay Island made counting pups more challenging, but there was reasonable agreement between the multiple whole island counts (1,833, 2,002, 2,301). The model of the distribution of pupping was fit to the limited pup stage transect data available for these islands using the Sable Island pup stage durations. We estimated that 100% of pups had been born by the time Hay Island was surveyed by drone on January 28. The Sable correction for pre-survey mortality was also applied to the count. The estimated number of pups born on Hay Island was 2,500 with 95% confidence limits of 1,700 to 3,200. This is similar to pup counts in 2007 (2,600) and 2010 (2,500), suggesting that this breeding colony may have reached carrying capacity. A total of 1,849 pups was counted on four small islands (Round, Mud, Noddy and Flat) in the vicinity of Seal Island, southwest Nova Scotia. This was the first aerial photographic survey for these colonies. After applying corrections for mortality and the proportion of pups born, the total pup production estimate for the four islands in southwest Nova Scotia was 2,100 with 95% confidence limits of 1,800 to 2,400. This is about a 5-fold increase from visual counts from helicopter in 2010 (417). A helicopter survey of the coastline from Yarmouth to Cape Breton was used to obtain visual counts of pups born at other coastal Nova Scotian colonies. The total pups along the coast east of Halifax, not including Hay Island, has increased from 50 in 2010 to 78 in 2016. In total, 4,600 pups were produced by Coastal Nova Scotia breeding colonies, which accounts for 5.1% of the 88,200 pups born on the Scotian Shelf.

Production de nouveaux-nés dans les colonies de phoques gris (*Halichoerus grypus*) du plateau néo écossais en 2016

RÉSUMÉ

Pour estimer la production de jeunes phoques gris (*Halichoerus grypus*), nous avons mené des relevés aériens de photographies numériques des colonies de reproduction sur l'île de Sable et des îles plus petites le long de la côte atlantique de la Nouvelle-Écosse en janvier 2016. Au total, 74 889 jeunes phoques gris ont été dénombrés sur la mosaïque d'images de l'ile de Sable. Compte tenu de la qualité élevée des photographies, aucune correction sur le décompte n'a été appliquée aux jeunes phoques qui ne pouvaient pas être vus sur les photos. De petites corrections ont été faites pour les jeunes phoques ratés par le lecteur d'images (0,022) et pour la mortalité des jeunes phoques (0,051) avant le relevé. Pour estimer la proportion de phoques nés au moment du relevé, un modèle de transition a été adapté aux stades des jeunes phoques d'âge connu et la répartition des stades des jeunes phoques recueillis chaque semaine dans la colonie entre le 14 décembre 2015 et le 29 janvier 2016. Nous avons estimé que 97 % (SE = 1 %) des jeunes phoques étaient nés au moment du relevé sur l'île de Sable. La production totale estimée de jeunes phoques de l'île de Sable en 2016 était de 83 600 avec des limites de confiance à 95 % variant de 63 600 à 103 500. La production de jeunes phoques sur l'île de Sable a continué d'augmenter, mais à un rythme plus lent qu'à la fin des années 1990 et au début des années 2000. Trois relevés aériens de photographies numériques ont été réalisés à l'île Hay. La couverture de neige et la côte rocheuse de l'île Hay a rendu le décompte des jeunes phoques plus difficiles, mais il y avait un accord raisonnable entre les multiples décomptes de l'île (1 833, 2 002, 2 301). Le modèle de la distribution des jeunes phoques a été adapté aux données limitées des stades de jeunes phoques par transect disponibles pour ces îles en utilisant les durées des stades des jeunes phoques de l'île de Sable. Nous avons estimé que 100 % des jeunes phoques étaient nés au moment du relevé de l'île Hay à l'aide d'un drone le 28 janvier. La correction utilisée pour l'île de Sable pour la mortalité avant le relevé a également été appliquée au décompte. Le nombre estimé de phoques nés à l'ile Hay était de 2 500 avec des limites de confiance à 95 % variant de 1 700 à 3 200. Ce décompte est similaire aux décomptes de jeunes phoques obtenus en 2007 (2 600) et 2010 (2 500), ce qui suggère que cette colonie de reproduction pourrait avoir atteint sa capacité de support. Au total, 1 489 jeunes phoques ont été dénombrés sur quatre petites îles (Round, Mud, Noddy et Flat) à proximité de l'île Seal, au sud-ouest de la Nouvelle-Écosse. C'était le premier relevé photographique aérien pour ces colonies. Après avoir appliqué des corrections pour la mortalité et la proportion de jeunes phoques nés durant le relevé, l'estimation totale de la production de jeunes phoques pour les quatre îles du sud-ouest de la Nouvelle-Écosse s'élève à 2 100 avec des limites de confiance à 95 % de 1 800 à 2 400. Il s'agit d'une augmentation d'environ 5 fois par rapport aux relevés visuels faits à partir d'un hélicoptère en 2010 (417). Un relevé à l'aide d'un hélicoptère le long du littoral entre Yarmouth et le Cap-Breton a été utilisé pour obtenir des dénombrements visuels des jeunes phoques nés dans d'autres colonies côtières de la Nouvelle-Écosse. Le nombre total de jeunes phoques le long de la côte à l'est de Halifax, en excluant l'île Hay, est passé de 50 en 2010 à 78 en 2016. Au total, 4 600 jeunes phoques ont été produits dans des colonies de reproduction côtières de la Nouvelle-Écosse, ce qui représente 5,1 % des 88 200 jeunes phoques nés sur le plateau néo-écossais.

INTRODUCTION

There are few pinniped populations with time series of population estimates that are sufficiently long to illustrate long-term dynamics. One of the longest series of estimates of pinniped pup production comes from Sable Island, Nova Scotia. Since 1962, the number of grey seal (*Halichoerus grypus*) pups born on Sable Island has increased exponentially (Bowen et al. 2003; 2007; 2011). The other major grey seal breeding colony in the northwest Atlantic is located on the sea ice and small islands in the southern Gulf of St. Lawrence. In addition to these large colonies, there are a number of small grey seal breeding colonies on near-shore islands along the Atlantic Coast of Nova Scotia and in the Gulf of Maine, some of which have been established more recently and have increased rapidly (Mansfield and Beck 1977; Hammill et al. 1998). In Canada, three management units are recognized based on the location of breeding colonies: Gulf of St. Lawrence (GSL), Coastal Nova Scotia (CNS) and Sable Island.

Grey seals are iteroparous capital breeders that haul out on land or sea-ice to pup. There is variation among colonies and, over time, in the temporal distribution of pupping. In the northwest Atlantic, pupping occurs in the winter from early December to mid-February. Female grey seals mature between four and roughly 12 years of age, and reproduce into their 30s (Bowen et al. 2006, den Heyer et al. 2014). Throughout, lactation 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). Weaning is abrupt, with adult females leaving the colony and returning to sea. The weaned pups undergo a post-weaning fast of several weeks before going to sea on their first foraging trip (Noren et al. 2008).

Here we report on the 2016 aerial-photographic surveys of grey seal pup production at Sable Island and the islands along the Atlantic coast of Nova Scotia, including Hay Island off Cape Breton and four small islands in southwest Nova Scotia.

METHODS

Pup production was estimated from counts of live pups from aerial photographs of breeding colonies on Sable, Hay, Round, Noddy, Mud and Flat Islands (Table 2; Figure 1). In addition to the fixed-wing photographic surveys, drone aerial photography was available for Hay Island (Hammill et al. 2017). Pup production on the eastern shore (between Halifax and Hay Island, Figure 1) and in the Bras D'Or lakes was estimated from visual counts during a coast-wide helicopter survey.

COAST-WIDE HELICOPTER SURVEY

The Nova Scotia coastline was surveyed by helicopter between Halifax (44.67N, 63.61W) and Yarmouth, Nova Scotia (43.84N, 66.12W) on January 17th and 21st, and between White and Hay Islands on January 21st, 23rd and 28th. Visual counts for each colony located were conducted by two observers seated on the left side of the aircraft. Pups were counted by each observer as the aircraft slowly circled the colony at a distance of 30 m from the colony and at a speed of approximately 20 knots and an altitude of 60 m. After the survey had been completed, an average of the two counts was recorded. Each colony was only counted once on a given date. One new colony was identified at Red Island (45.80N, 60.75W).

DIGITAL PHOTOGRAPHIC SURVEYS BY PLANE

The aerial surveys of Sable, Hay, Round, Mud, Noddy, and Flat Islands were completed at an altitude of approximately 308 m (1,000 ft), in a fixed-wing aircraft provided and operated by The

Airborne Sensing Corporation. A Microsoft Vexcel UCX camera with motion compensation camera housing and integrated with in-flight GPS was used to provide 3 cm ground resolution. Each island, or set of islands, was completed as a one sortie mission 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 was used for all fixed-wing aerial photography.

A digital surface model (DSM) of all islands was used to orthorectify adjacent images using INPHO OrthoMaster software. The DSMs of all islands was down sampled to 5 m, except Hay Island which is at higher resolution of 6 cm. All orthorectified photographs were projected in UTM Zone 20. The mosaic for each location was broken into 600 m X 600 m tiles for ease of analysis. Live pups were counted in ESRI ArcMap 10.2.2 from the mosaic of tiles. A 60 m X 60 m grid was overlaid on the tiles to facilitate systematic counting. The locations of live grey seal pups were marked in a single ArcGIS layer to avoid double counting. Original photos were used to confirm counts in areas where the mosaic tile was unclear.

DIGITAL SURVEYS BY DRONE

Hay Island was also surveyed using a small UAV (senseFly eBee) equipped with a Canon S110 RGB on January 28. The UAV was programmed to fly between 75 and 100 m above ground level and photograph the island with 75% forward and lateral overlaps among adjacent images. The UAV imagery was stitched together using Pix4Dmapper to provide an island mosaic (see Hammill et al. 2017 for details). Live pups were counted in ESRI ArcView 9.3 from the mosaic. The locations of live grey seal pups were marked in a single ArcGIS layer to avoid double counting.

CORRECTION FOR MISSED PUPS

The proportion of live pups that were photographed but not detected on the photographs was determined by comparing pups counted in photographed ground plots to the number of pups counted by observers on the ground. In each of five rectangular ground plots (Figure 2), the corners were demarcated with red vinyl fabric enabling them to be located on the colour imagery. The plots were widely distributed throughout the colony and each plot contained roughly 50 pups. Two researchers on the ground counted pups independently as close as possible to the time the survey aircraft was overhead. Differences between observers were resolved before going to the next plot. Three readers counted live pups on the aerial photographs of the five ground truth plots independently, and they reviewed the counts together to establish a consensus reference count for each ground truth plot.

One reader read all photographs. To correct for bias in counting accuracy over time, 30 randomly selected areas with approximately 100 seals were counted by three readers to establish reference consensus pup counts. The difference between reader and consensus count were plotted against the date of counting.

PUP MORTALITY RATE

A portion of pups born on the breeding colony die before the aerial survey is flown. These animals 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. The proportion of pups that died prior to the aerial census was estimated at 10 locations throughout the colony (Figure 2). 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, 2015, and January 12, 2016.

TEMPORAL DISTRIBUTION OF BIRTHS

The temporal distribution of births was estimated from a transition model of known-age pups and the change over time in the proportion of each developmental stage in the population (Myers and Bowen 1989; Bowen et al. 2007). Grey seal pups are classified into five developmental stages based on pelage colour and body shape (Table 1; Radford et al. 1978; Kovacs and Lavigne 1986; Bowen et al. 2003). As done previously, the mean and variance of the duration (days) for stages 1 to 4 was estimated by fitting the transition model assuming a gamma distribution for each stage. Stage 5 is an absorbing stage. We used all known-age pup stage data from 1997, 2007 and 2010 to estimate duration of the 5 pup stages (Appendix 1).

To estimate how the proportion in each developmental stage changed over time, we recorded pup stages along transects through the colony each week over the course of the breeding season at 13 widely distributed areas (different from the ground plots referred to above; Figure 2) on Sable Island (Appendix 2). Pup stage surveys were also completed on two occasions on Hay Island and southwest Nova Scotia (Noddy, Round, Flat, and Mud Islands).

We considered two probability distributions, Gamma and Weibull, to model the distribution of pups born over time. In all parameterizations, ρ is the scale parameter and $K$is the shape parameter. We selected the model with the lowest Akaike's Information Criterion (AIC).

The date of first birth for Sable Island was estimated to be December 3, 2015 based on the oldest pups seen in the first days of the field program. We used the same date of first birth for all of the colonies.

PUP PRODUCTION ESTIMATES

The estimation of pup production follows the approach given in Bowen et al. (1987), Myers and Bowen (1989) and Bowen et al. (2003, 2007, and 2011). As there is no longer a distinct separation of west and east colonies, we fit one distribution model to the Sable Island colony. The number of pups born prior to the aerial survey is based on counts of live pups photographed. This number is then corrected for the fractions of live pups not detected on the imagery, pups that had died prior to the survey, and pups that were born after the survey was conducted.

Total pup production (*N*) was estimated as follows:

$$N = \left(\frac{count \bullet g}{(1-d) \bullet p}\right)$$

where *count* is the count 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 up to the day of the photographic 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).

RESULTS

SABLE ISLAND

Eighteen transects were flown over Sable Island on January 12, 2016, between 10:07 and 12:25 PM (Eastern Standard Time) resulting in 1,306 photographs and complete coverage of the colony. Image quality was high for most of the island (Figure 3a), although intermittent cloud cover resulted in high contrast and long shadows in some images. There were also several areas in overlap between flight lines where the merged images had 'ghost' or translucent seals. In total, 75 'ghost' seals were verified with the original photographs. A total of 74,899 pups was counted (Figure 2, Table 9).

A comparison of pup counts by ground observers and those from photographs indicated close correspondence in 3 of 5 locations (Table 3). The largest differences occurred in two ground truth plots on the east end of the island (Blow Out and CWS). In both cases seal density along the edges of these plots may have contributed to differences between the ground observations and the photographs. In the area called the Blow Out, the northern boundary, which crossed through a dense patch of pups at the bottom of a bowl, may have been interpreted differently by the ground observers than by the readers of the aerial images. The CWS plot was on the edge of the beach where pup density was high and the field team was working. We believe that in the hour and half between the ground count and the photograph, work activities could have redistributed the pups.

We also compared pup counts on 30 reference plots of the imagery compared to counts over time to test for bias in the ability of the reader to identify pups. The counts on the west spit, the earliest area read by the reader, were much higher than the consensus count (Table 4). A high number of juvenile seals in the area were identified by the inexperienced reader as pups. The reader recounted the entire west spit and the area called the West Washover, where juveniles are common. The second count for these areas was used for the total pup count and also used to assess the proportion of missed seals. After recounting, there was no trend over time in the difference between the reader and consensus counts (Figure 5), but the percentage of pups in the reader count was 2.21% (SE=0.67) less than the consensus count.

Ten 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 5.05% (SE=1.28) (Table 5).

Stage duration and staging transects

Stage duration was estimated from 153 seals that were staged daily from birth to stage 5 in the winter field seasons of 1997, 2007 and 2010 (Figure 6). Common shape (five parameters) and separate shape (eight parameters) gamma models were fit to the pup stage durations for stages 1 to 4. Model results from the gamma distribution are described in Table 6.

The developmental stage of 15,345 pups was recorded along ground transects in the 13 regions widely distributed throughout the colony over a 47 day period from December 14, 2015, to January 29, 2016 (Figure 7, Appendix 1). Two models were fitted to estimate the distribution of births over time and from that, the proportion of pups born by January 12, 2016 (Table 7). Date of the first birth was estimated as December 3, 2015, based on the oldest stage pups (Stage 3) observed on Sable Island when the field team arrived. These dates were used to define the limit of the left tail of the modelled distributions. All models fit reasonably well but, based on the AIC criteria, the Weibull model provided the best fit (Table 7).

Estimated pup production for the Sable Island colony was 83,600 (rounded to nearest hundred) with 95% confidence limits of 60,600 and 103,500 (based on log-normal distribution) (Table 9). The current estimate of pup production is below the exponential growth curve fit to the data from 1976 to 1997 (Figure 8). This is the fourth consecutive survey in which the residuals of the estimated rate of increase are negative, providing additional evidence for a decrease in the rate of growth in pup production.

EASTERN SHORE

The helicopter survey along the eastern shore of Nova Scotia identified two colonies (Table 2). A total of 78 pups were counted from the helicopter for breeding colonies on White Island (n=37) and Red Island (n=41).

In 2016, Hay Island was surveyed on January 12th and 15th by plane, and by drone on January 28. To estimate the distribution of births, the developmental stage of 2,025 pups was recorded along three transects, covering the Island, conducted on separate days between January 21 and January 28, 2016 (Appendix 2). Data from Sable Island were used to estimate the duration of each stage and the date of first birth (December 3, 2015). Two models were fitted to estimate the distribution of births over time and from that, the proportion of pups born by January 12, 15 and 28, respectively. Both models provide similar estimates of the proportion of pups born prior to the photographic surveys (Table 8), and the AICs provide basis of selection of preferred model (Table 7).

A total of 1,833 pups was counted on the January 12 mosaic image of Hay Island, and 2,002 pups on the January 15th image by the same experienced reader (Table 2). Once corrected for proportion born (Table 8), the two estimates differ by less than 5 pups. As Hay Island had the same high quality imagery as that of Sable Island, and it was counted by the same reader, the same correction for missed pups was applied. Some pre-weaning mortality undoubtedly occurred on Hay Island. We used the Sable Island estimates, based on data collected up until January 12th, to account for pup mortality. Using either the January 12, total pup production was estimated to be 2,470 (rounded) with 95% confidence limits of 1,700 and 3,200 (Table 9). This is similar to the count of 2,327 pups from the drone photographic survey on January 28th, for which correction factors for missed pups, pup mortality and proportion born are less certain.

SOUTHWEST SHORE

Breeding colonies of grey seals were found on four small islands (Round, Mud, Noddy and Flat) near Seal Island (43.24N, 66.00W) off southwest Nova Scotia (Figure 1). A total of 1,849 pups was counted on photographs from the aerial survey of these islands on January 8 (Table 2). To estimate the distribution of births, the developmental stage of 727 pups was recorded along five ground transects covering the Islands on separate days between January 17th and January 21st, 2016. Again, the imagery for southwest Nova Scotia islands was of the same high quality as that of Sable Island and counted by the same reader, therefore the same correction for missed pups seemed warranted. We also used the pre-weaning survey mortality estimates for Sable Island to correct the counts from the southwest Nova Scotia islands. Total production was estimated to be 2,090 (rounded) with 95% confidence limits of 1,800 and 2,400 (Table 9).

DISCUSSION

In comparison to the Sable Island breeding colony, a relatively small number of pups are born on islands along the southwest and eastern coast of Nova Scotia (Table 9). No pups were observed at Bowen's Ledge or the Basque Islands off of southern Cape Breton, which have historically had grey seal breeding colonies (Figure 9). New colonies were discovered on Hay

Island in 1993, and Noddy and Flat Islands on the southwestern shore of Nova Scotia (Hammill et al. 2007). Another new colony was found on Red Island in the Bras D'Or lakes in 2015, and here we report 41 pups in 2016.

The estimated 2016 pup production on Hay Island is not significantly different from 3 previous pup production estimates (Figure 10). The relative stability of these estimates, and the extensive distribution of pups on the island (Figure 4b), provides evidence that the island is unlikely to support a larger breeding colony.

The first breeding colony in southwest Nova Scotia was identified in 1993. By 2010, the southwest Nova Scotia breeding colonies expanded from Noddy and Flat Islands to Round and Mud, two adjacent islands (Figure 4a). Given their size, the smaller islands (Round and Noddy) are unlikely to support many more pups. However, there appears to be more breeding habitat available on the other islands. The 2016 estimated pup production in southwestern Nova Scotia is 2,100. The total number of pups counted in this, the first aerial photographic survey of these islands, is about five times the number of pups estimated from the helicopter based observers in 2010 (417, Figure 10). Although the 2010 helicopter based estimate was likely an underestimate (Hammill et al. 2017), the increase of more than a thousand pups in southwestern Nova Scotia must reflect immigration from other colonies.

Overall pup production on the eastern coast of Nova Scotia increased since 2010, with the southwestern Nova Scotia islands producing nearly half the pups born on coastal islands.

SOURCES OF ERROR IN ESTIMATED PUP PRODUCTION

Pup counts from the imagery must be corrected for several factors to estimate total pup production. First, as found in previous surveys, some live pups may be missed on the photographs resulting in an underestimate of total count. Here, we found the counts on the ground to be more uncertain than counts from the high resolution digital photos. The discrepancies between the ground counts and the photograph counts were the greatest observed in last 3 digital aerial-photographic surveys. However, we had fewer, smaller, and less well defined, ground truth plots in 2016 than in 2007 and 2010. As the photographs are of the same high resolution as 2007 and 2010, we are confident that no correction for missed pups based on ground truth plots is necessary. However, comparison of reader counts in a randomly selected set of validation plots indicated a small, but detectable bias in the reader count compared to the consensus count, and a correction factor was applied. This detection bias was not observed in 2010 aerial survey, and the addition of the correction factor results in increased uncertainty in the 2016 pup production estimate (see Figure 8 error bars). Second, pups that died before the aerial survey was conducted are unlikely to have been counted. The reader was instructed not to count obviously dead pups and on Sable Island, drifting sand and snow quickly cover dead pups making a portion of them invisible. To get an estimate of total number of pups born for the population model, we applied a correction for pup mortality. Both of these corrections were estimated on the Sable Island breeding colony and applied to the other colonies, where they may be less appropriate because of differences in the timing of the survey relative to pupping and pup mortality. However, as the reader was instructed not to count dead pups, and snow cover could be a factor on some coastal colonies, it was decided that this correction should be applied.

As in the past, we also scaled the count from the imagery to estimate total pup production over the breeding season by estimating the proportion of pups born on the date we flew the survey. To minimize the impact of this correction we attempt to fly the survey after peak pupping, but before pups begin to enter the water. For Sable, we have data on pup stage duration from three years and survey estimates of the proportion of pups in each stage throughout the 2016

breeding season. Also, we incorporate all pup observations on the colony in the early part of the field season to estimate first birth. For the other smaller coastal colonies, we have to assume that pup stage duration is the same as it is on Sable as it is not possible to complete daily sightings of known-age pups. For these colonies, we also have fewer stage distribution surveys, a less reliable estimate of first birth date in the colony, and less confidence in the birth distribution model assumption that stage 5 is an absorbing stage (i.e. no departure of weaned pups from colony). This contributes to greater uncertainty in the estimate of the proportion of pups born on the coastal islands, which currently is not captured in the variance of the estimate. The impact of these uncertainties could be explored with sensitivity analysis and expanded data collection, but any bias in the estimate of pup production on the small colonies will have very little impact of total pup production as roughly 95% of the pup production on Scotian Shelf is born on Sable Island.

TREND IN PUP PRODUCTION

Grey seal pup production on Sable Island (Figure 8, Appendix 3) and coastal Nova Scotia (Appendix 4) continues to increase. For nearly four decades (1962-1997), pup production on Sable Island increased exponentially at near the maximum intrinsic rate (Figure 8, Bowen et al. 2003). Since 1997, the rate of increase has been slower supporting the hypothesis that density-dependent changes in vital rates may be limiting population growth (Bowen et al. 2007, Bowen et al. 2011). Two density-dependent factors that may limit the population are competition for breeding habitat and food. While some of the colonies on small islands in coastal Nova Scotia (e.g., Hay Island) appear to be approaching or have reached carrying capacity with respect to breeding habitat, there is unused breeding habitat available on Sable Island. There are also many uninhabited islands along the coast that could support grey seal breeding colonies. For example, we identified a new colony on a small island in the Bras D'Or lakes (Red Island). There has also been a rapid increase in pup production in southwest Nova Scotia (Figure 10). In 2016, grey seal pup production in US breeding colonies in the Gulf of Maine was estimated by aerial survey to be more than 6,000 pups (Hayes et al., NOAA, unpublished data), up from the minimum estimate of 2,620 pups born in US breeding colonies in 2008 (Wood LaFond 2009). The rapid increase in grey seals breeding in the Gulf of Maine suggests that neither food nor breeding habitat is currently limiting population growth.

Given the availability of breeding habitat, food is more likely to limit the overall grey seal population size than habitat. At-sea competition for food resources could limit population growth by impacting survival and reproductive success. For the Sable breeding colony, which accounts for 95% of the pup production on the Scotian Shelf, we have estimates of juvenile and adult survival and reproductive rates from more than 40 years of mark-resighting (den Heyer et al. 2014, den Heyer and Bowen 2017). These estimates find no evidence of changes in adult survival or reproductive rates, and suggest that reduced rate of increase in pup production is mainly caused by lower juvenile survival.

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TABLES

Table 1. Developmental stages for grey seal pups.

Stage	Description
1	new born, 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 molting
4	molting evident, flippers and nose not included in this criterion
5	completely molted (>= 95% moulted)

Table 2. Total count of pups from aerial survey imagery and visual helicopter surveys on Atlantic coastline of Nova Scotia.

Location	Lat Degree N	Lon Degree W	Method	Date	Count
Sable Island	*43.9320*	*59.9115*	Plane	Jan 12	74889
Eastern Shore					
Hay Island	*46.0225*	*59.6857*	Plane	Jan 12	1833
			Plane	Jan 15	2002
			Drone	Jan 28	2327
White Island	*44.8872*	*62.1364*	Helicopter	Jan 28	37
Bowen's Ledge	*44.8685*	*62.1653*	Helicopter	-	0
Red Island	*45.8050*	*60.7710*	Helicopter	Jan 23	40, 41
Total Eastern Shore			Helicopter/Drone	Jan 28	2388
Southwest Shore					
Flat Island	*43.5087*	*66.0040*	Plane	Jan 8	71
			Helicopter	Jan 21	52
Mud Island	*43.4810*	*65.9884*	Plane	Jan 8	858
			Helicopter	Jan 21	331, 648
Noddy Island	*43.4655*	*65.9861*	Plane	Jan 8	382
			Helicopter	Jan 21	348
Round Island	*43.5074*	*65.9846*	Plane	Jan 8	538
			Helicopter	Jan 21	202, 345
Total Southwest Shore			Plane	Jan 8	1849

Table 3. Number of grey seal pups counted on five ground plots and from digital imagery of those plots on January 12, 2016.

Location	Photo	Ground	Ground count	Consensus count	Difference	%
CWS	10:58	10:20	42	49	7	14.29
East Washover	10:57	10:20	55	56	1	1.79
Blow Out	11:03	10:20	78	67	-11	-16.42
East of BIO	11:44	10:35	36	35	-1	-2.86
West of BIO	10:30	10:35	69	66	-3	-4.55
Mean (SE)						-1.55 (4.97)

Table 4. Number of grey seal pups counted on 30 digital image plots from the January 12, 2016 Sable survey. The West Spit was recounted and the second count used for population estimate.

Plot	Consensus Count	Count	Date Counted	Difference	Percentage difference
1	87	109	May 4	12	
		91	June 19	4	4.60%
2	91	90	May 9	-1	-1.10%
3	96	92	May 10	-4	-4.17%
4	82	78	May 13	-4	-4.88%
5	112	97	May 17	-5	-4.46%
6	114	110	May 24	-4	-3.51%
7	91	91	May 27	0	0.00%
8	104	104	May 30	-1	-0.96%
9	93	95	June 1	2	2.15%
10	107	107	June 1	0	0.00%
11	95	92	June 6	-3	-3.16%
12	36	59	May 4	13	
			June 19	-3	-8.33%

Plot	Consensus Count	Count	Date Counted	Difference	Percentage difference
13	85	84	May 5	-1	-1.18%
14	76	76	May 5	0	0.00%
15	117	114	May 10	-3	-2.56%
16	65	55	May 12	-10	-15.38%
17	107	108	May 12	1	0.93%
18	84	83	May 16	-1	-1.19%
19	86	85	May 17	-1	-1.16%
20	70	67	May 17	-3	-4.29%
21	104	106	May 17	2	1.92%
22	95	93	May 18	-2	-2.11%
23	102	99	May 24	-3	-2.94%
24	81	82	May 25	1	1.23%
25	94	90	May 26	-4	-4.26%
26	132	127	May 30	-5	-3.79%
27	40	40	May 30	0	0.00%
28	58	58	June 1	0	0.00%
29	76	72	June 7	-4	-5.26%
30	116	113	June 6	-3	-2.59%
Mean (SE)					-2.21% (0.67)

Table 5. Percentage of pups that died up to 12 January, 2016, at 10 sites on Sable Island.

Area	Live Pups from Imagery	Dead Pup Count	Percentage
North Beach, East Light Dune	76	1	1.32%
No. 4 West	57	0	0.00%
Beck's Cove	64	4	6.25%
Legal Crossing, Inland, North	93	2	2.15%
Blowout	88	7	7.95%
Deadhorse Pass, South	107	8	7.48%
A-Frame, Inland, North	102	8	7.84%
Little Italy, Inland	107	7	6.54%
Tern Colony	112	6	5.36%
West of BIO, North	232	13	5.60%
Mean (SE)			5.05% (1.28)

Table 6. Estimates of stage durations, assuming gamma distribution, from daily records of Sable Island pups followed from birth to stage 5 in 1997 (n=47), 2007 (n=52), and 2010 (n=54), combined. Model and data updated from Bowen et al. 2011.

	Common Shape				Separate Shape			
Stage	Shape	Rate	Mean (d)	Variance	Shape	Rate	Mean (d)	Variance
1	18.78	5.82	3.22	0.55	13.71	4.29	3.20	0.75
2	18.78	5.12	3.67	0.72	17.90	4.89	3.66	0.75
3	18.78	1.59	11.79	7.40	25.21	2.13	11.85	5.57
4	18.78	3.33	5.64	1.69	9.01	1.61	5.58	3.46

Table 7. Comparison of Gamma and Weibull pup distribution models fit to staging transects data from each colony. Both models had two parameters. For all colonies, the preferred model is the Weibull (in bold).

Colony	Model	Shape	Rate	AIC
Sable Whole	Gamma	4.90 (0.43)	0.2 (0.02)	-36200
	Weibull	**2.78 (0.11)**	**25.83 (0.66)**	**-36184**
Hay Island	Gamma	15.24 (0.75)	0.46 (0.01)	-5200
	Weibull	**4.15 (0.23)**	**35.70 (0.89)**	**-5200**
SWNS	Gamma	5.62 (4.05)	0.27 (0.18)	-1607
	Weibull	**2.56 (0.53)**	**23.14 (0.84)**	**-1591**

Distribution	Density Function	Number of Parameters
Gamma	$\rho(\rho t)^{k-1}\exp(-\rho t)$	2
Weibull	$k\rho(\rho t)^{k-1}\exp[-(\rho t)^{k}]$	2

ρ=scale, κ=shape parameter

Table 8. Estimates of the proportion of pups born based on the 2 models and the date of first birth (Dec 3, 2015). Jackknife standard error is in parentheses. The bolded cells are from AIC selected model.

		Proportion Born	
Colony	**Date**	Gamma	Weibull
Sable	Jan 12	0.91 (0.02)	**0.97 (0.01)**
Hay	Jan 12	0.80 (0.02)	**0.80 (0.04)**
Hay	Jan 15	0.88 (0.01)	0.89 (0.03)
Hay	Jan 28	0.99 (0)	1.00 (0)
SWNS	Jan 8	0.94 (0.03)	**0.96 (0.02)**

Table 9. Estimate of grey seal pup production on Sable, Hay and Southwest Nova Scotia (SWNS) islands in 2016 with SE in parentheses.

Count	**Sable**	**Hay Island**	**SWNS**
Pup counts	74,899	1,833	1,849
Proportion of pups missed	0.022 (0.0067)	0.022 (0.0067)	0.022 (0.0067)
Dead pup correction	0.051 (0.0128)	0.051 (0.0128)	0.051 (0.0128)
Proportion born	0.965 (0.0108)	0.799 (0.0420)	0.955 (0.0191)
N	83,594 (10,170)	2,471 (380)	2,085 (156)
95% CI	63,600-103,528	1,725-3,217	1,778-2,392

FIGURES

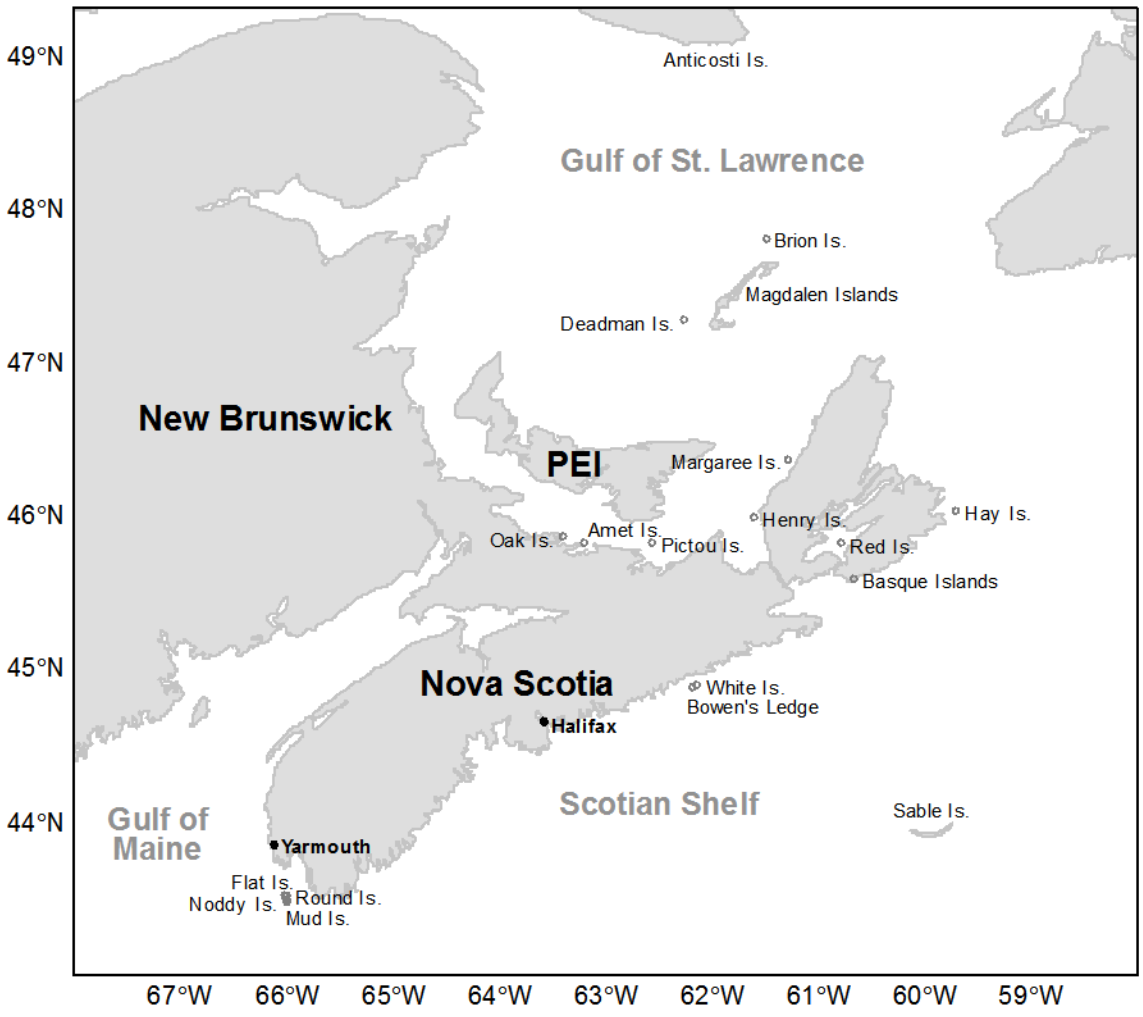


Figure 1. Map of historic and current land-based grey seal breeding colonies (open circles).

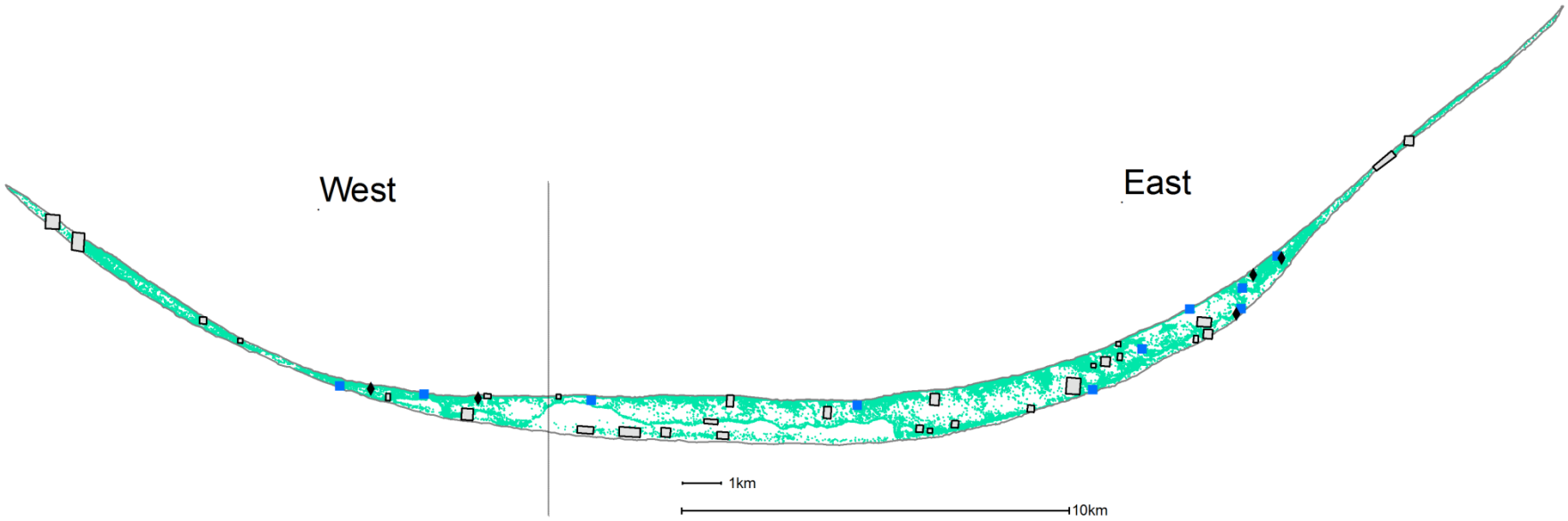
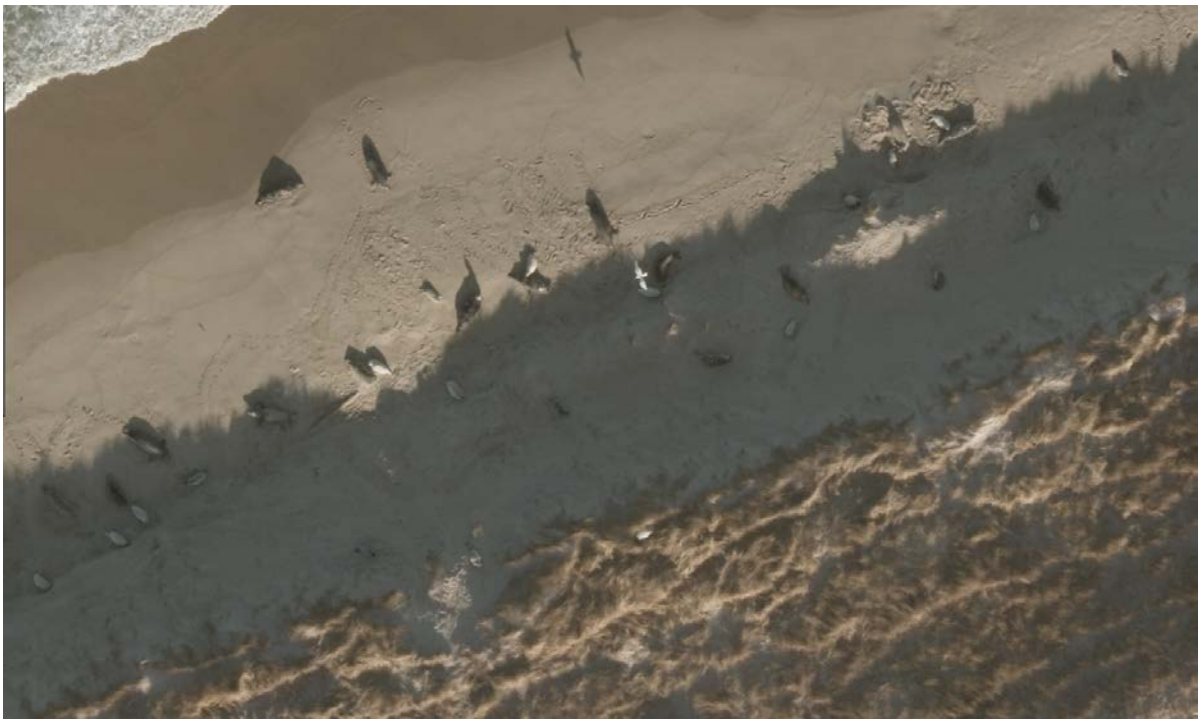


Figure 2. Map of the distribution of grey seal pups on Sable Island (green dots) and the location of mortality plots (blue squares), ground truth plots (black diamonds) and validation plots (black boxes).The horizontal line represents the east and west colony divide used in previous assessments.

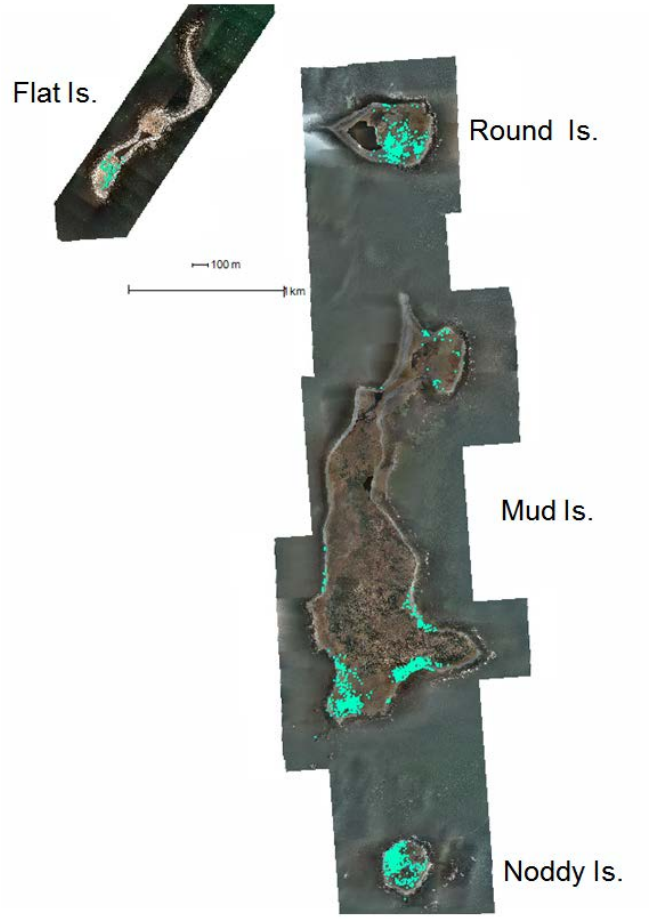
a)



b)

Figure 3. Example of digital imagery from (a) Sable Island and (b) Hay Island. Scale 1:125

a)



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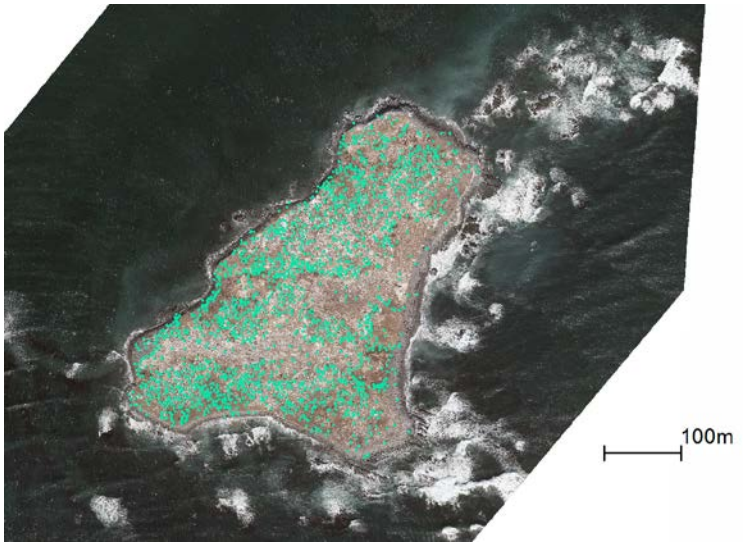

Figure 4. Distribution of pupping (green dots) on (a) Southwest Nova Scotia Islands (scale 1:25,000) and (b) Hay Island (1:3000) in January 2016.

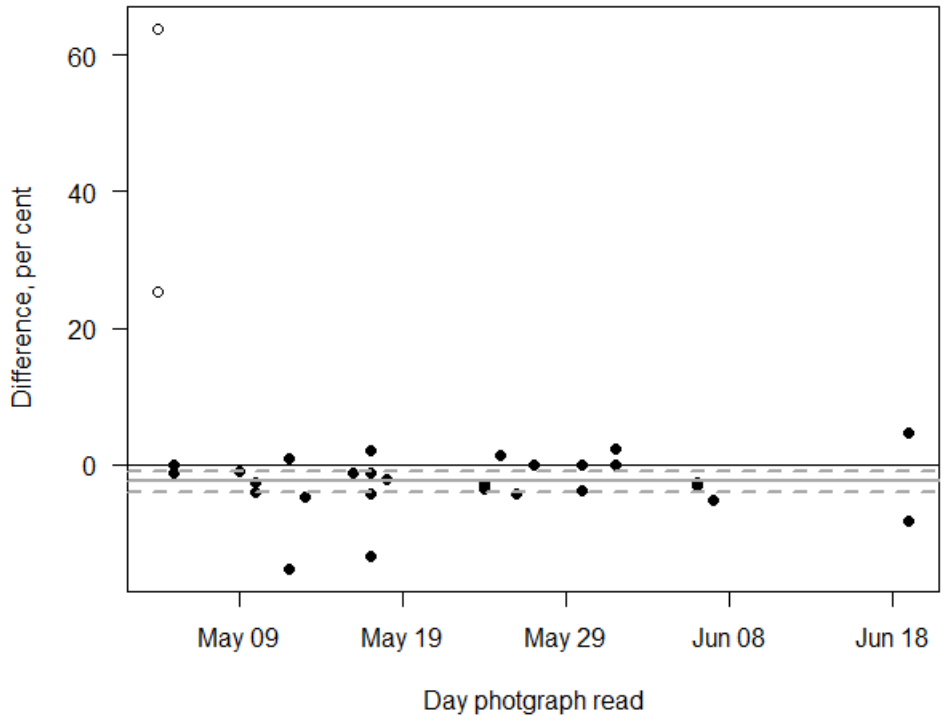

Figure 5. Comparison of the difference between reader pup count and the consensus pup count on validation plots, plotted by date counted by the reader. The solid horizontal line is the origin, the light grey line is mean and 95% confidence intervals are indicated by dashed line. Open circles were recounted by reader and not included in the overall average.

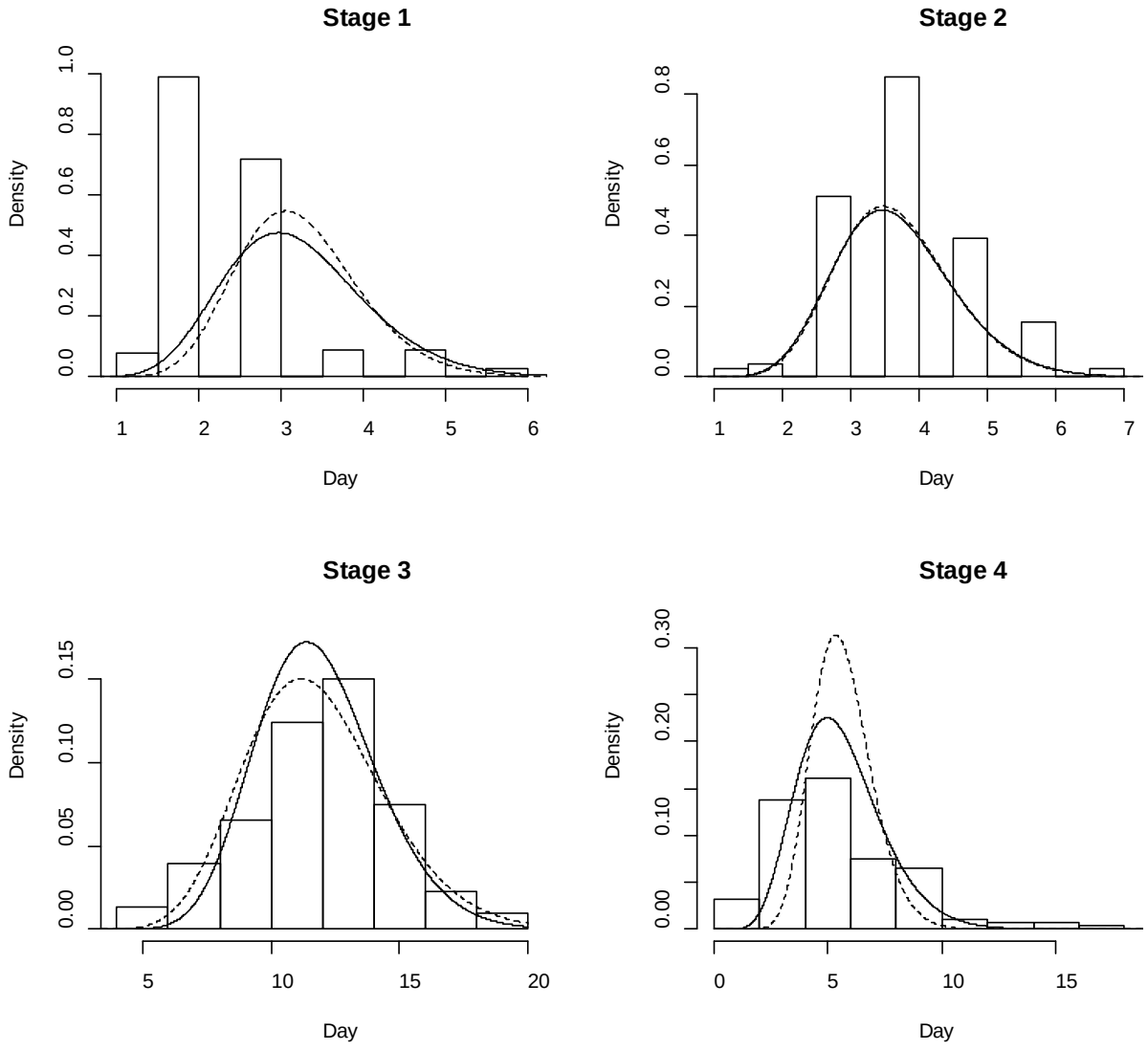

Figure 6. Fit of gamma model to pup stage duration from known aged pups assessed in 1997, 2007 and 2010 (n=153). The solid line is a common shape model and the dashed line has a separate shape for each stage.

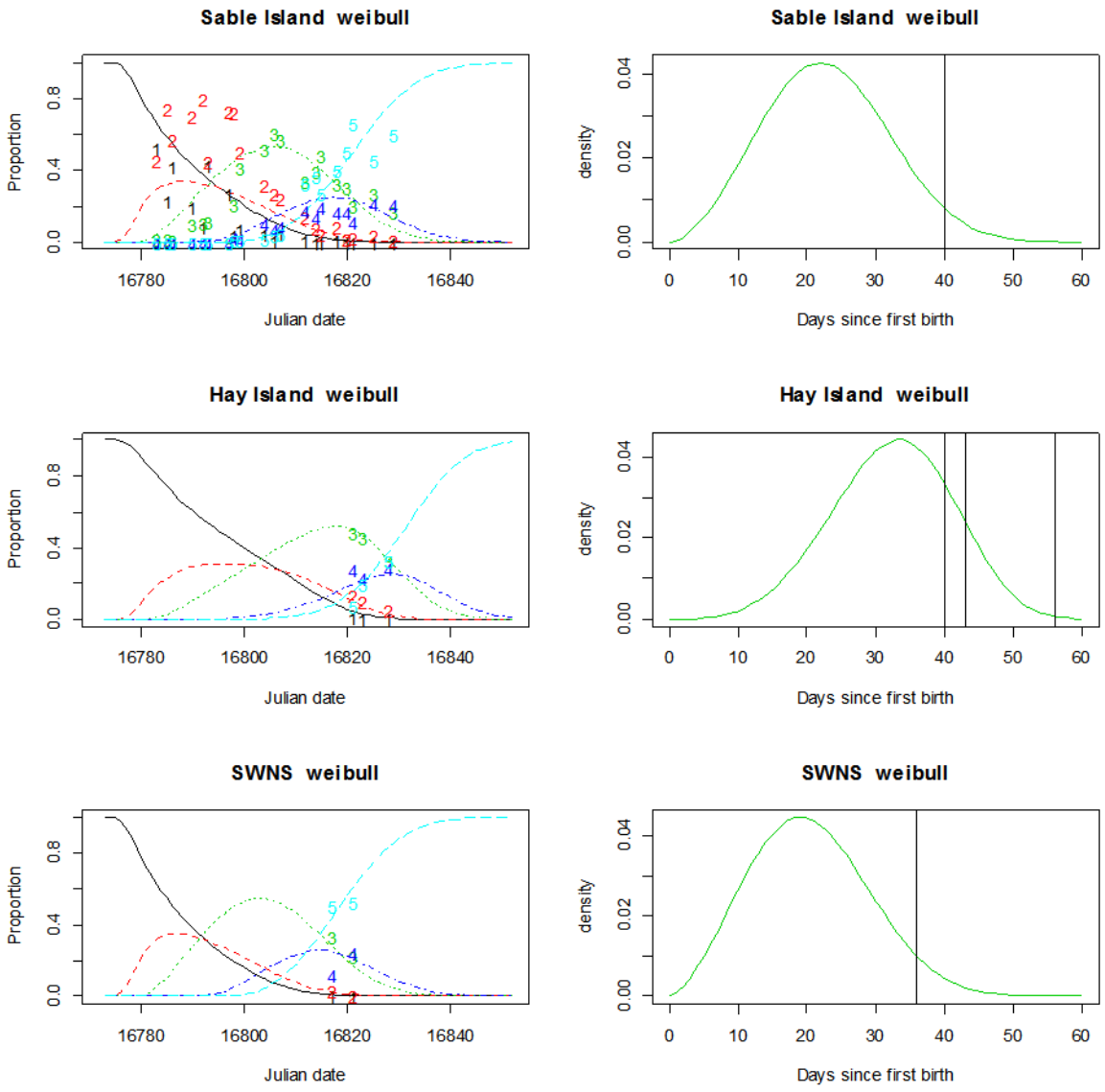

Figure 7. Fit of pupping distribution models to the transect data and the plot of pupping distributions with vertical bars indicating the day of the count. For all models the day of first birth is assumed to be Dec 3, 2015.

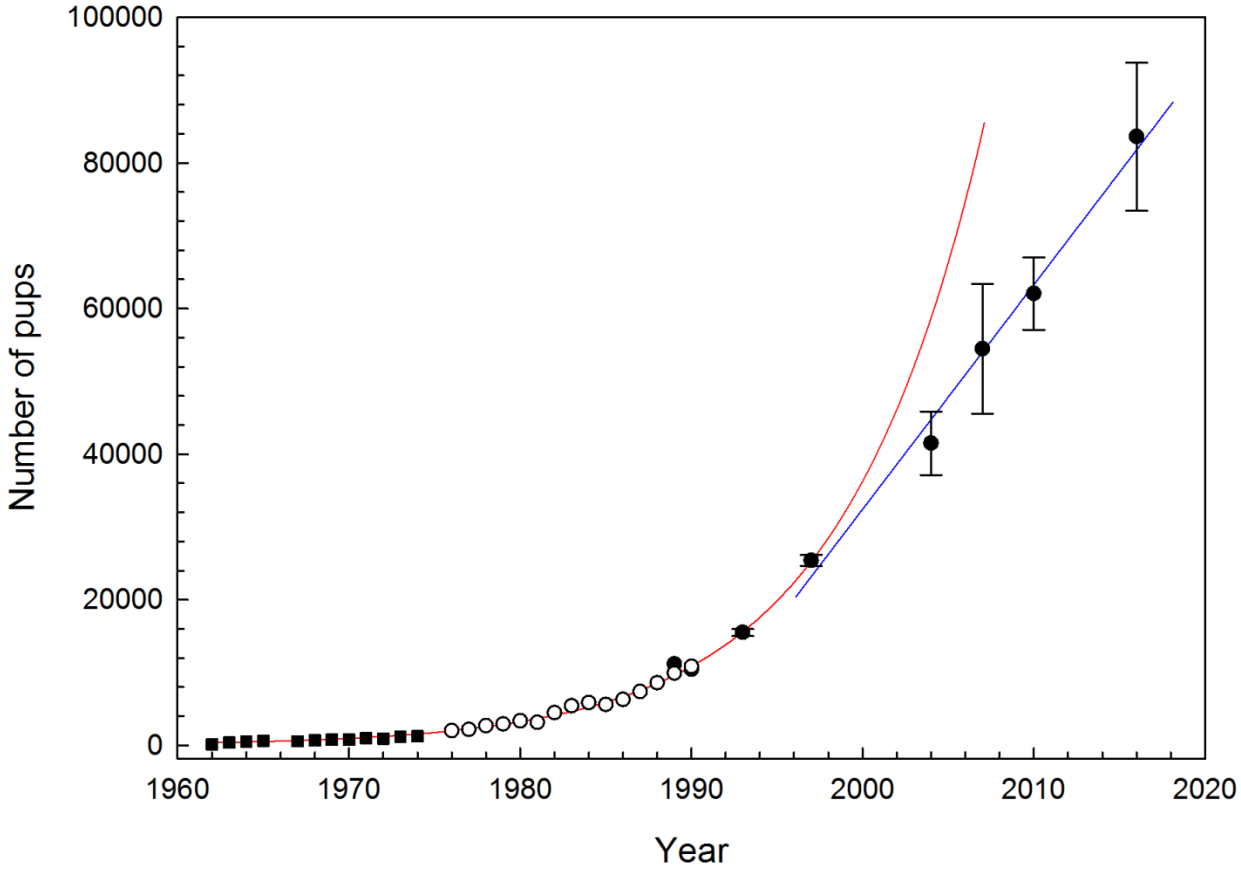

Figure 8. Trend in grey seal pup production on Sable Island, 1962 to 2016, based on incomplete tagging (1962-1974), complete cohort tagging (1976-1990) and aerial photographic surveys (1989-2016). Error bars are SE. The red line represents an exponential curve fit to the 1976 to 1997 estimates. The blue line represents a linear regression fit to the 1997 to 2016 estimates.

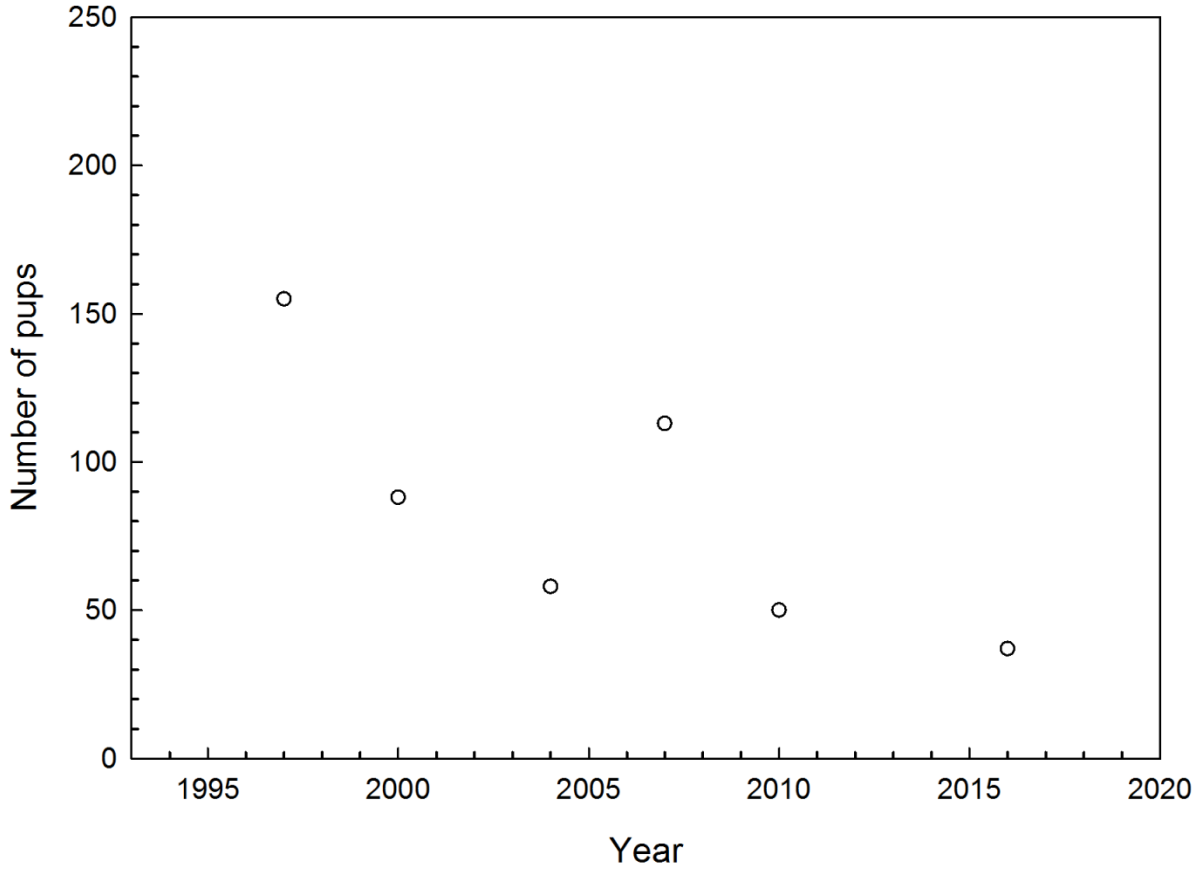

Figure 9. Trend in grey seal pup production for coastal Nova Scotia colonies on White Island and Bowen's Ledge based on aerial survey counts. Counts are uncorrected.

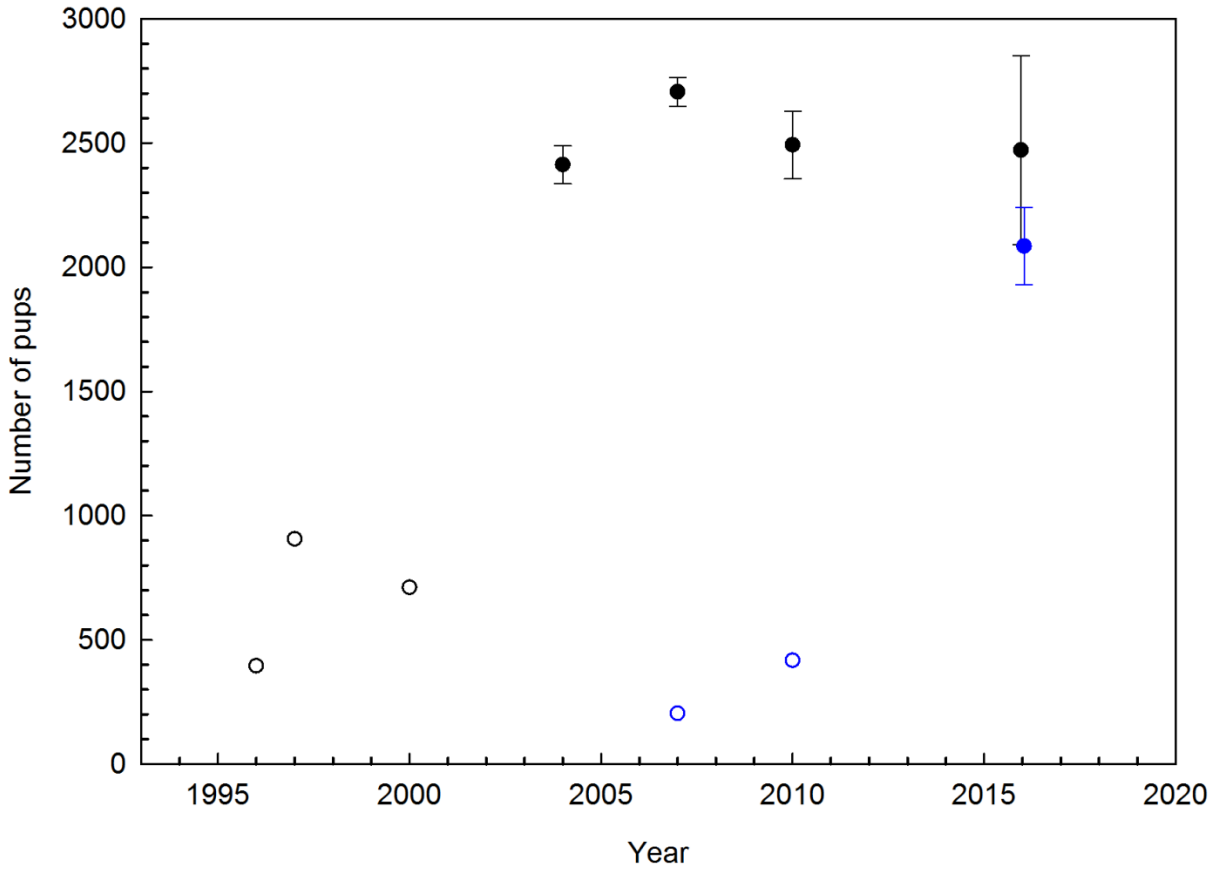

Figure 10. Trends in grey seal pup production for coastal Nova Scotia colonies located on Hay Island (black) and Flat, Mud, Round and Noddy Islands combined (SWNS; blue) based on aerial survey counts. Open circles are uncorrected counts, closed circles are corrected counts. Error bars are SE.

APPENDICES

Appendix 1. The count of the number of pups observed on Sable Island in each developmental stage on each day. Day 1 is the birth day of an individual pup.

Day	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5
1	153	0	0	0	0
2	147	6	0	0	0
3	71	61	0	0	0
4	16	137	0	0	0
5	9	144	0	0	0
6	2	133	18	0	0
7	0	79	74	0	0
8	0	42	111	0	0
9	0	20	133	0	0
10	0	6	147	0	0
11	0	0	153	0	0
12	0	0	152	1	0
13	0	0	152	1	0
14	0	0	150	3	0
15	0	0	147	6	0
16	0	0	140	13	0
17	0	0	135	18	0
18	0	0	115	38	0
19	0	0	94	57	1
20	0	0	66	76	8
21	0	0	47	87	13
22	0	0	26	102	20
23	0	0	17	103	31

Day	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5
24	0	0	7	98	44
25	0	0	3	83	61
26	0	0	1	67	77
27	0	0	1	52	92
28	0	0	1	43	99
29	0	0	0	24	119
30	0	0	0	15	124
31	0	0	0	8	133
32	0	0	0	2	120
33	0	0	0	1	121
34	0	0	0	0	99
35	0	0	0	0	95
36	0	0	0	0	80
37	0	0	0	0	47
38	0	0	0	0	47
39	0	0	0	0	25
40	0	0	0	0	6

Appendix 2. Development stage of pups recorded on transects from southwest Nova Scotia Islands (SWNS; Noddy, Round, Flat and Mud), Eastern Nova Scotia Islands (ENS; Hay, Red and White) and on Sable Island. Pup staging data were recorded on the ground, from helicopter by experienced observers or from photographs taken by hand held cameras or drones. The Red and White Island transects from ENS were not included in the model.

Colony	Location	Date	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Method
SWNS	Noddy	1/17/2016	1	10	94	33	141	ground
SWNS	Noddy	1/21/2016	0	1	23	27	60	helicopter
SWNS	Round	1/21/2016	0	1	22	37	66	helicopter
SWNS	Flat	1/21/2016	0	0	19	5	4	helicopter
SWNS	Mud	1/21/2016	0	0	37	40	106	helicopter
ENS	Hay	1/21/2016	1	9	32	18	5	helicopter
ENS	Hay	1/23/2016	2	27	120	60	52	hand camera
ENS	Hay	1/28/2016	5	95	560	479	560	ground
ENS	Hay	1/28/2016	0	140	1418	593	159	drone flight
ENS	Red	1/23/2016	0	4	33	3	1	helicopter
ENS	White	1/28/2016	0	3	15	6	5	ground
Sable	1	12/14/2015	38	32	0	0	0	ground
Sable	1	12/21/2015	27	153	22	1	0	ground
Sable	1	12/29/2015	7	167	32	9	1	ground
Sable	1	1/4/2016	11	40	114	39	5	ground
Sable	1	1/12/2016	1	23	74	25	100	ground
Sable	1	1/18/2016	0	24	68	35	77	ground
Sable	2	12/14/2015	104	90	4	0	0	ground
Sable	2	12/21/2015	27	154	28	0	0	ground
Sable	2	12/29/2015	7	136	56	2	2	ground
Sable	2	1/4/2016	9	60	110	24	4	ground
Sable	2	1/12/2016	2	34	69	44	57	ground

Colony	Location	Date	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Method
Sable	2	1/18/2016	4	19	73	25	107	ground
Sable	3	12/16/2015	55	140	2	0	0	ground
Sable	3	12/23/2015	16	163	20	0	0	ground
Sable	3	12/30/2015	11	149	49	4	2	ground
Sable	3	1/6/2016	2	51	121	21	16	ground
Sable	3	1/14/2016	0	9	74	30	96	ground
Sable	3	1/20/2016	0	5	57	29	115	ground
Sable	4	12/16/2015	43	187	7	0	0	ground
Sable	4	12/23/2015	22	185	28	2	0	ground
Sable	4	12/30/2015	9	161	54	2	1	ground
Sable	4	1/6/2016	2	71	149	9	0	ground
Sable	4	1/14/2016	0	22	106	33	70	ground
Sable	4	1/20/2016	0	2	70	41	88	ground
Sable	10	12/17/2015	36	52	0	0	0	ground
Sable	10	12/24/2015	91	66	6	0	0	ground
Sable	10	12/30/2015	22	70	92	0	0	ground
Sable	10	1/7/2016	16	55	144	14	5	ground
Sable	10	1/15/2016	1	6	116	56	40	ground
Sable	10	1/25/2016	2	4	35	74	90	ground
Sable	11	12/17/2015	37	83	0	0	0	ground
Sable	11	12/24/2015	34	154	30	0	0	ground
Sable	11	12/30/2015	5	150	69	6	0	ground
Sable	11	1/7/2016	3	37	145	24	7	ground
Sable	11	1/14/2016	0	24	74	29	85	ground

Colony	Location	Date	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Method
Sable	11	1/21/2016	0	8	50	22	118	ground
Sable	12	12/17/2015	28	112	1	0	0	ground
Sable	12	12/24/2015	34	171	14	0	0	ground
Sable	12	12/30/2015	5	141	48	6	7	ground
Sable	12	1/7/2016	1	29	133	41	23	ground
Sable	12	1/14/2016	4	9	80	28	62	ground
Sable	12	1/21/2016	0	2	32	25	153	ground
Sable	13	12/21/2015	50	69	1	0	0	ground
Sable	13	12/28/2015	52	140	0	0	0	ground
Sable	13	1/4/2016	7	103	109	3	2	ground
Sable	13	1/12/2016	3	36	90	49	61	ground
Sable	13	1/18/2016	0	17	69	52	80	ground
Sable	13	1/29/2016	1	3	35	44	126	ground
Sable	5	12/17/2015	31	53	2	0	0	ground
Sable	5	12/24/2015	134	53	9	0	0	ground
Sable	5	12/30/2015	29	96	106	0	0	ground
Sable	5	1/7/2016	12	83	130	7	2	ground
Sable	5	1/15/2016	0	11	94	42	76	ground
Sable	5	1/25/2016	0	5	29	72	83	ground
Sable	6	12/17/2015	8	2	0	0	0	ground
Sable	6	12/24/2015	122	74	26	0	0	ground
Sable	6	12/30/2015	21	67	112	2	1	ground
Sable	6	1/7/2016	10	55	142	10	2	ground
Sable	6	1/15/2016	0	11	118	43	41	ground

Colony	Location	Date	Stage 1	Stage 2	Stage 3	Stage 4	Stage 5	Method
Sable	6	1/25/2016	1	10	82	24	93	ground
Sable	7	12/17/2015	40	43	1	0	0	ground
Sable	7	12/24/2015	83	53	33	0	0	ground
Sable	7	12/30/2015	8	72	110	0	0	ground
Sable	7	1/7/2016	10	67	115	19	9	ground
Sable	7	1/15/2016	0	18	120	36	40	ground
Sable	7	1/25/2016	0	9	71	30	96	ground
Sable	8	12/17/2015	62	54	1	0	0	ground
Sable	8	12/24/2015	101	59	27	0	0	ground
Sable	8	12/30/2015	17	78	104	5	1	ground
Sable	8	1/7/2016	13	78	116	27	22	ground
Sable	8	1/15/2016	1	10	100	36	72	ground
Sable	8	1/25/2016	2	15	81	44	70	ground
Sable	9	12/17/2015	89	51	1	0	0	ground
Sable	9	12/24/2015	78	67	35	0	0	ground
Sable	9	12/30/2015	17	56	114	6	1	ground
Sable	9	1/7/2016	10	52	123	14	20	ground
Sable	9	1/15/2016	1	7	85	39	83	ground
Sable	9	1/25/2016	0	7	44	34	139	ground

Appendix 3. Grey seal pup production on Sable Island, 1962 to 2016, based on incomplete tagging (1962-1974), complete cohort tagging (1976-1990) and aerial photographic surveys (1989-2016). Values in parentheses are SE.

Year	Number of pups
1962	134
1963	400
1964	550
1965	660
1967	580
1968	700
1969	800
1970	800
1971	1000
1972	950
1973	1200
1974	1250
1976	2000
1977	2181
1978	2687
1979	2933
1980	3344
1981	3143
1982	4489
1983	5435
1984	5856
1985	5606
1986	6301
1987	7391
1988	8593
1989	9906[1], 11168[2]
1990	10838[1], 10457[2]
1993	15500 (463)
1997	25400 (750)
2004	41500 (4381)
2007	54482 (8909)
2010	62054 (4973)
2016	83594 (10170)

[1] complete tagging
[2] aerial survey

Appendix 4. Grey seal pup production on for coastal Nova Scotia colonies located on Hay Island, White Island and Bowen's Ledge and on Flat, Mud, Round and Noddy Islands combined (SWNS) based on aerial survey counts. Values in italics are corrected counts. Values in parentheses are SE.

Colony	Year	Number of pups
Hay Island	1996	395
	1997	906
	2000	711
	2004	*2413 (76)*
	2007	*2706 (57)*
	2010	*2492 (136)*
	2016	*2471 (380)*
White Island/Bowen's Ledge	1997	155
	2000	88
	2004	58
	2007	113
	2010	50
	2016	37
SWNS	2007	204
	2010	417
	2016	*2085 (156)*