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Contrasting trends in gray seal (*Halichoerus grypus*) pup production throughout the increasing northwest Atlantic metapopulation

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Abstract

The northwest Atlantic subspecies of gray seal (*Halicheorus grypus grypus*) has been increasing for more than a half century and has reestablished breeding colonies in Canadian and US waters. In 2016, visual, oblique, and vertical large-format digital photographic surveys were conducted at all known breeding colonies in the northwest Atlantic. Total pup production in the northwest Atlantic was estimated to be 109,000 (*SE* = 17,500) pups. At 87,500 (*SE* = 15,100) pups, Sable Island accounts for 80% of total pup production. Regional differences in pup production trends are evident. Pup production in the Gulf of St. Lawrence and along the eastern shore of Nova Scotia has been relatively stable. Since 2004, the rate of increase in pup production at Sable Island has slowed to about 5%–7% per year, while the newer colonies in southwest Nova Scotia and the northeastern United States are increasing rapidly. In 2016, the Muskeget Island (MA) breeding colony produced 3,900 (*SE* = 200) pups, making it the third largest breeding colony in the northwest Atlantic. This southward shift in production may reflect climate-mediated changes in population growth as well as reestablishment of colonies throughout the former range associated with increased protection.

KEYWORDS
Canada, gray seal, *Halichoerus grypus*, metapopulation, pup production, regional trends, United States

1 | INTRODUCTION

Species or metapopulations with broad geographic distributions are likely to face different environmental conditions which in turn may result in differing productivity and demographic trends (Andrewartha & Birch, 1960; Baker & Thompson, 2007; Street et al., 2015). Gray seal breeding colonies in the northwest Atlantic currently range over a

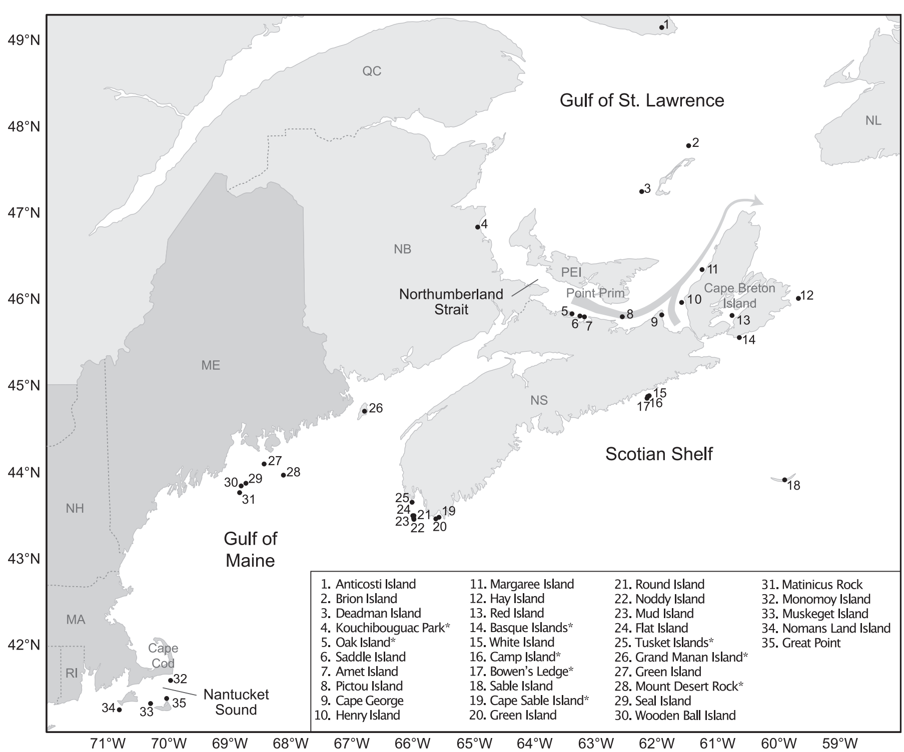

FIGURE 1 Map of gray seal breeding sites in Canada (light gray) and the United States (dark gray). Breeding colonies that are no longer used are indicated by an asterisk (*) in the legend. Ice flow in Northumberland Strait is indicated. Canada: NB = New Brunswick; NL = Newfoundland and Labrador; NS = Nova Scotia; PEI = Prince Edward Island; PQ = Quebec. United States: MA = Massachusetts; ME = Maine; NH = New Hampshire; RI = Rhode Island.

north–south distance of some 1,400 km encompassing six ecosystems (Figure 1; Frank et al., 2006). Females from these breeding colonies forage in ecosystems whose structure and functioning have shown differing temporal and spatial variability at decadal timescales (Shackell et al., 2012). Over this broad geographic range, the northwest Atlantic population has grown rapidly for more than half a century, largely accounted for by the rapid and persistent growth in pup production at Sable Island (Bowen et al., 2003, 2007, 2011; den Heyer et al., 2017). New breeding colonies have also been established throughout the species' range both in Canada and the northeastern United States while some breeding colonies have been lost (Mansfield & Beck, 1977; Wood et al., 2011, 2019). Gray seals disperse broadly throughout the continental shelf of the northwest Atlantic providing an opportunity for adults to move among breeding colonies (Breed et al., 2009; Harvey et al., 2008; Laviguer & Hammill, 1993; Stobo et al., 1990). Given these characteristics, the dynamics of gray seals in the northwest Atlantic can be usefully regarded as a metapopulation (Hanski, 1998).

Although many pinniped species have widespread and well-known breeding distributions (Forcada, 2018), there are few populations for which the time series of estimates of the number of pups born (pup production) is sufficiently long and frequent to investigate long-term dynamics. For example, pup production estimates at gray seal (*Halichoerus grypus macrorhynchus*) colonies around Scotland began in 1984 (Russell et al., 2019). Regular estimates of pup production of northern fur seals (*Callorhinus ursinus*) at rookeries on St. Paul Island and St. Georges Island in the Pribilof Islands are available since 1974 (Allen & Angliss, 2014). Counts of the number of pupping female southern elephant seals (*Mirounga leonina)* are available for 49 of 65 years on the main Isthmus study area of Macquarie Island from 1949 to 2015 (Hindell et al., 2017). One of the longest series is for breeding colonies of gray seals the northwest Atlantic (spp. *grypus*). Here, gray seals breed on ice and small islands in the southern Gulf of St. Lawrence, near-shore islands along coastal Nova Scotia, offshore at Sable Island, Nova Scotia, and at more recently recolonized coastal locations in northeastern United States (Figure 1). Pup production in the Gulf of St. Lawrence, along coastal Nova Scotia and at Sable Island has been estimated intermittently since the 1960s (Bowen et al., 2003, 2007, 2011; den Heyer et al., 2017; Hammill et al., 1998, 2007; Hammill, Gosselin, et al., 2017). Colonies in northeastern United States are some of the most recently established (1980s) and have been monitored periodically (Waring et al., 2016; Wood et al., 2011, 2019).

Gray seals are iteroparous, capital breeders that give birth to a single offspring on sea-ice or land (Baker et al., 1995; Bowen et al., 2006; Iverson et al., 1993). Females mature between four and roughly 12 years of age and reproduce into their 30s (Bowen et al., 2006; den Heyer et al., 2014; Hammill & Gosselin, 1995). Females attend their pup throughout a 16- to 18-day lactation period (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 postweaning fast of several weeks before going to sea on their first foraging trip (Noren et al., 2008).

The growth and recolonization of the northwest Atlantic gray seal metapopulation has provided an opportunity to examine temporal and spatial trends in dynamics over almost a half century. Here we estimate pup production at gray seal breeding colonies throughout their range in 2016. We also review the establishment of new breeding colonies and compare regional trends in pup production for the western Atlantic subspecies.

2 | METHODS

In 2016, live pups were counted at all known gray seal breeding colonies in the northwest Atlantic by one of three methods: (1) vertical photographs from an unoccupied aircraft system (UAS) or with a large-format camera mounted in a purpose modified aircraft, (2) oblique photographs from a helicopter, or (3) aerial visual counts (Table 1). At the Canadian colonies where counts from different platforms were available, the counts from vertical photographs with higher quality imagery were used (Hammill, Dale, et al., 2017; Johnston et al., 2017). For the US breeding colonies, only counts from images taken on NOAA Twin Otter surveys are reported here to provide consistent estimates across US colonies.

TABLE 1 Count of live pups from aerial surveys and counts adjusted for the distribution of births and mortality before the day of the photographic surveys.

Colony	Survey date	Method	Pups	Pups *SE*	Adjusted count	Adjusted *SE*	Total	Total *SE*
Sable								
Sable Island (NS)	January 12, 2016	vertical photo - AS plane	74,899		87,485	13,560		
Sable Total							87,500	15,100
Gulf of St. Lawrence (GSL)								
Saddle Island (NS)	January 25, 2016	vertical photo - UAS	2,370	46.0	2,484	76		
Pictou Island (NS)	January 15, 2016	vertical photo - AS plane	2,095	0.7	4,285	1,694		
Brion Island (PQ)	February 2, 2016	visual - Bell 429 + reported harvest	1,498					
Henry Island (NS)	February 1, 2016	oblique photo - Bell 429	748	25.7	793	44		
Deadman Island (PQ)	February 2, 2016	visual - Bell 429	90					
Anticosti Island (PQ)	January 25, 2016	visual - Surveillance	40					
Margaree Island (NS)	January 16. 2016	visual - Surveillance	16					
Amet Island (NS)	January 21, 2016	visual - Bell 429	123					
Cape George (NS)	February 1, 2016	visual - Bell 429	4					
Point Prim (Ice, NS/PEI)	January 28, 2016	visual - Bell 429	500					
GSL Total							9,800	2,000
Eastern Nova Scotia (ENS)								
Hay Island (NS)	January 12, 2016	vertical photo - AS Plane	1,833		2,641	520		
Red Island (NS)	January23, 2016	visual - Bell 429	41					
White Island (NS)	January 28, 2016	visual - Bell 429	37					
ENS Total							2,700	600
Gulf of Maine, Canada (GOM CAN)								
Mud, Round, Noddy, Flat Islands (NS)	January 8, 2016	vertical photo - AS Plane	1,849		2,105	164		
GOM CAN Total							2,100	200
Gulf of Maine, USA (GOM USA)								
Seal Island (ME)	January 17, 2016	vertical photo - NOAA TO	1,043	13.8				

TABLE 1 (Continued)

Colony	Survey date	Method	Pups	Pups *SE*	Adjusted count	Adjusted *SE*	Total	Total *SE*
Wooden Ball Island (ME)	January 17, 2016	vertical photo - NOAA TO	284					
Matinicus Rock (ME)	January 17, 2016	vertical photo - NOAA TO	193					
Green Island (ME)	January 17, 2016	vertical photo - NOAA TO	34					
GOM USA Total							1,600	10
Nantucket Sound (NS)								
Muskeget Island (MA)	January 15, 2016	vertical photo - NOAA TO	3,787	0.4	3,945	38		
Monomoy Island (MA)	January 15, 2016	vertical photo - NOAA TO	935	2.1				
Nomans Land Island (MA)	January 15, 2016	vertical photo - NOAA TO	32	4.2				
NS Total							4,900	200
Total							109,000	17,500

Note. Total counts and standard errors (*SE*) reported to the nearest 100 seals. AS Plane = Airborne Sensing plane; UAS = unoccupied aircraft systems; Bell 429 = Bell 429 Helicopter; Surveillance = King Air Surveillance plane; NOAA TO = NOAA Twin Otter.

2.1 | Vertical photographs

For the largest breeding colonies in Canada (Sable Island, Hay Island, and Pictou Island), as well as islands in southwest Nova Scotia (Round, Noddy, Mud, and Flat Islands), pup production was estimated from large-format aerial photographs taken by a fixed-wing aircraft operated by The Airborne Sensing Corporation. A Microsoft Vexcel UCX camera with motion compensation camera housing integrated with in-flight GPS was used to provide 3 cm ground resolution imagery. At Sable Island, Hay Island, and the group of islands in southwest Nova Scotia, the survey was conducted at an altitude of approximately 308 m (1,000 ft). At Pictou Island the survey was flown at an altitude of 420 m. Complete coverage of the breeding colonies was achieved by flying a series of parallel transects with 60% forward and 20% lateral overlap among adjacent photographs. The surveys at each of the breeding colonies were completed in a single flight to minimize error introduced by the movement of seals between areas covered by adjacent photographs. A digital surface model was used to orthorectify adjacent images using INPHO OrthoMaster software. All orthorectified photographs were projected in UTM Zone 20. During the seam editing, the mosaic seams were adjusted so that entire animals appeared on just one side of the seam. Original photos were used to confirm counts in areas where the mosaic tile was unclear. Identified pups were marked on an ArcGIS (ESRI ArcView 10.2.2) layer to avoid double counting. For the Sable Island survey, the photographic mosaic was broken into 600 m × 600 m tiles for ease of analysis, but as above care was taken to ensure pups appeared in only one tile. All the images from these surveys were counted by a single reader.

Images from the NOAA Twin Otter belly-mounted camera were used to count live pups at seven colonies along the northeastern US coastline: Muskeget Island, Monomoy Island, and Nomans Land Island in Massachusetts, and Green Island, Seal Island, Matinicus Rock, and Wooden Ball in Maine. The camera system contained three Canon Mark III 5D cameras with Zeiss 85 mm prime lenses configured in a port-center-starboard configuration. Images were obtained in 2-s intervals and had roughly 60% horizontal overlap and 20% side overlap. The survey was flown at 229 m altitude with an image ground resolution of approximately 1 cm. For each colony, the images were stitched together using Microsoft Image Composite Editor (v. 1.4.4). Overlap between the composites was determined by visual inspection. These images were viewed and counted in Adobe Photoshop (v. 2015.5). The count tool was used to mark and tally live pups. The survey was counted by two independent readers for Muskeget, Monomoy, Nomans Land, and Seal Islands. The remaining colonies were counted by one reader.

A total survey of Saddle Island in the Gulf of St. Lawrence was completed using a small UAS (senseFly eBee; Hamill, Dale, et al., 2017). Photographs were taken with a Canon S110 RGB (3 cm ground resolution). The UAS was programmed to fly at an altitude of between 75 and 100 m with overlapping transects to allow a complete mosaic of the Island. Individual photos overlapped ~75% on both axes. The UAS imagery was stitched together using Pix4Dmapper to create mosaics and terrain models. Live pups were counted in ESRI ArcView (v. 9.3) and recorded by a single reader in an ArcGIS layer to avoid double counting.

2.2 | Oblique photos

At Henry Island, oblique photographs were taken from a Bell 429 twin engine helicopter. Photographs were taken with a 36.3 megapixel digital SLR Nikon D800 camera with a 35 mm lens (Zeiss, Distagon T* 2/35). The aircraft flew at an altitude of 60 m above ground and a horizontal distance of 30 m from the colony. This resulted in a resolution of 5 cm. Two readers read the imagery.

2.3 | Visual counts

To estimate pup production at smaller islands along the Canadian coastline (Oak, Amet, Deadman, Brion, and Red Islands), visual surveys were flown in a Bell 429 twin engine helicopter at an altitude of 60 m and about 30 m away from the colony. Two observers were seated on the left side of the aircraft, one in the front, the second in the back. Pups were counted by each observer as the aircraft slowly circled the colony at a speed of approximately 20 knots. After the survey had been completed, an average of the two counts was recorded. At Brion Island, there was a small harvest of pups prior to the survey. The total pup production at Brion Island includes reported harvests. Estimates of the number of pups born on Anticosti Island and Margaree Island were based on counts by a single observer flying in a King Air surveillance plane operated by the Conservation and Protection Branch within Fisheries and Oceans Canada.

There was little ice present in the southern Gulf of St. Lawrence in 2016. A small group of gray seals was observed on the ice in Northumberland Strait near Point Prim, Prince Edward Island, on January 28, but counts could not be completed before the ice shifted. The total pup production on this ice was estimated to be about 500 pups.

2.4 | New colonies

To locate new colonies on the Atlantic coast of Nova Scotia, a helicopter was flown between Halifax (44.67°N, 63.61°W) and Yarmouth, Nova Scotia (43.84°N, 66.12°W) on January 17 and 21, and between White Island (44.89°N, 62.14°W) and Hay Island (46.02°N, 59.69°W) on January 21, 23, and 28. Locations where pupping has previously occurred in the Northumberland Strait and around Cape Breton Island (Figure 1) were searched several times during January and February. A King Air surveillance plane completed surveys along the south and west coasts of Newfoundland in late January, but no gray seals were seen. In USA waters there was no comprehensive effort to identify new colonies. Given the high human population density along the coast of Massachusetts and New York, it is unlikely that new colonies would not have been identified. However, along the coast of Maine, there are many small islands that could provide breeding habitat.

2.5 | Estimation of total pup production

The estimation of pup production from live counts follows the approach given in Bowen et al. (1987), Myers and Bowen (1989), and Bowen et al. (2003, 2007). Total pup production (N) was estimated as follows:

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

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). Due to logistic constraints, not all corrections were available for all sites. At larger colonies (i.e., Sable Island, Pictou Island, Muskeget), stage composition surveys were completed to fit the birth distribution model to adjust the count for the proportion of pups born prior to the survey. Sable Island is the largest breeding colony and is readily accessible by researchers housed on the island. This allows for the daily collection of data during the breeding season to estimate pup stage duration and pup mortality on the breeding colony.

2.6 | Correction for missed pups

Pups can be misidentified during counting because of poor image quality or reader interpretation. For vertical photographic surveys on Sable Island, Hay Island, and the group of islands in southwest Nova Scotia, we estimated corrections for image quality and the reader variability. On Sable, the proportion of live pups that were photographed but not detected on the digital imagery was determined by comparing pups counted on the digital images of ground-truth plots to the number of pups counted in those plots by observers on the ground. In total, 21 ground-truth plots have been completed for vertical digital photogpraphic surveys of Sable Island (2016 n = 5; 2010 n = 6; 2007 n = 10). The plots were widely distributed throughout the colony, and each plot contained roughly 50 pups. Two or three researchers on the ground counted pups independently as close as possible to the time the survey aircraft was overhead. Three readers counted live pups on the aerial photographs of the five ground-truth plots independently and then reviewed the counts together to establish a consensus reference count for each ground-truth plot.

For Sable Island, Hay Island, and the group of islands in southwest Nova Scotia, one reader identified all live pups on the digital images in 2016. To check for bias or variation in the counting over the course of reading, three experienced readers counted each of 30 randomly selected areas on photographs with approximately 100 pups in each area. The differences between the reader and consensus count were plotted against the date of counting to test for systematic bias in the reader accuracy over the course of the counting.

2.7 | Correction for pup mortality

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. On Sable Island in 2016, the proportion of pups that died prior to the aerial census was estimated at 10 locations throughout the colony. GPS locations of the vertices of the chosen areas were recorded so they could be plotted on the photographs. The areas chosen encompassed areas of high pup abundance with the polygon boundaries located in areas of low abundance using natural features such as dune edges. The total pup count in these polygons was compared to the number of dead pups collected from the same areas. Surveys for dead pups occurred roughly every three days between December 20, 2015, and January 12, 2016.

2.8 | Temporal birth distribution

As the breeding season for gray seals in the northwest Atlantic spans 6–8 weeks at individual colonies and varies geographically and interannually, it is necessary to correct the pup production estimate for the number of pups born after the pup count is completed. At the larger colonies where it was possible to conduct multiple pup-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 survey (Bowen et al., 1987, 2003, 2007; Myers & Bowen, 1989; Reed & Ashford, 1968). The distribution of births is estimated from stage duration and the change over time in the proportion of each developmental stage on the breeding colony. Gray seal pups are classified into five developmental stages based on pelage color and body shape (Bowen et al., 2003; Kovacs & Lavigne, 1986; Radford et al., 1978).

To inform the model of pup birth distribution, stage duration was estimated from seals that were staged daily from stage 1 (newborn) to stage 5. The mean and variance of the duration (days) for stages 1 to 4 was estimated by fitting the semi-Markov transition model with a gamma distribution for stage duration. Stage duration is not estimated for Stage 5, which is an absorbing stage (i.e., the end stage). 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:

$$m_j(t) = \int_0^{\infty} m_{j-1}(t-\tau)\varphi_{j-1}(\tau)d\tau \qquad j = 1\ldots,k \tag{2}$$

The proportion of pups that will be observed in stage j at time t, $n_j(t)$, is

$$n_j(t) = \int_0^\infty m_j(t-\tau)\left[1-\int_0^\tau \varphi_j(s)ds\right]d\tau \quad (3)$$

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.

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. We selected the model with the lowest Akaike's information criterion (AIC). Variance of the parameters and proportion born was estimated with a jackknife of stage transects.

Based on the pelage stage of oldest pups seen in the first days of the Sable Island field program (December 10, 2015), we estimated the start of the breeding season (the date of first birth) to be December 3, 2015. To fit the birth distribution models for Muskeget Island, the southwest Nova Scotia islands (Noddy, Round, Flat, and Mud Islands), and Hay Island we used December 10, 2015 as date of first birth. For colonies in Gulf of St. Lawrence, based on the staging transect data, the breeding season is estimated to start on December 30, 2015.

On Sable Island, we recorded pup stages along ground-observed transects through the colony weekly (n = 6) over the course of the breeding season at 13 widely distributed areas. Estimates of the temporal distribution of births were obtained from Hay Island, the southwest Nova Scotia islands, Saddle Island, Amet Island, Pictou Island, and Henry Island with visual surveys from the Bell 429 helicopter on three occasions. For Muskeget Island, the largest US colony, pup staging was assessed from digital images obtained by an APH-22 hexacopter, designed and constructed by Aerial Imaging Solutions, Old Lyme, Connecticut. The APH-22 was flown with an Olympus E-PM2 camera with 25 mm lens set to continually take still images at 2-s intervals. Mission planning was conducted using Mikrokopter's MikroKopter-Tool (v2 10c) software.

For regional trends for Sable and the Gulf of St. Lawrence, the smoothed line was fit using local polynomial regression (loess function, degree = 2). In Gulf of Maine and eastern Nova Scotia, the regional trend is a line between total of counts for all breeding colonies. All data analysis was completed using R (R Core Team, 2019).

3 | RESULTS

3.1 | Correction for missed pups

Comparison of ground counts with counts from digital imagery at Sable Island revealed that more pups were generally detected in the imagery than were counted on the ground, but the difference was small (mean difference = 0.62 pups, SE = 0.77). This was likely due to movement of pups situated on or near edges of ground plots. Thus, no correction for missed pups was warranted for the large-format photographs. For Sable Island large-format photographs, the comparison between the reader's counts and the consensus counts indicated that the reader's counts were on average 2.2% (SE = 0.67) lower than the consensus counts and that there was no trend with date of counting or reader experience. For Sable Island, Hay Island, and the group of colonies in southwest Nova Scotia with large-format photographs and the same reader, we applied this value as the correction for pups missed by the reader (g, see Equation 1).

3.2 | Correction for pup mortality

Pup mortality on the breeding colony prior to the aerial survey has been estimated on Sable Island in 2007, 2010, and 2016 (Bowen et al., 2007, 2011; den Heyer et al., 2017). Based on the counts of total pups from the digital imagery at the mortality sites in all three years, the mean percentage of pups that died prior to the aerial survey, *d*, was 4% (*SE* = 1%). The correction for pup mortality estimated on Sable Island was applied to the larger breeding colonies for which we estimated birth temporal distribution.

3.3 | Temporal distribution of births

Stage duration was estimated from 153 seals that were staged daily from stage 1 (newborn) to stage 5 at the Sable Island colony in 1997, 2007, and 2010. The separate shape model had lowest AIC (Table 2) and the estimated mean and variance of stage duration from that model was used in birth distribution models (Table 3). Visual inspection of

TABLE 2 Estimates of gamma shape and rate parameters and mean and variance (Var) for stage duration in days from model fit to daily records of pups followed from birth to Stage 5.

Stage	Description	Shape	Rate	Mean (days)	Var
1	newborn, wet, weak, yellowish (possibly), neck visible	13.71	4.29	3.2	0.8
2	tubular shape; body trunk width equals shoulder width, neck visible	17.90	4.89	3.7	0.8
3	body trunk is wider than the shoulders, neck not visible, no sign of molting	25.21	2.13	11.9	5.6
4	molting evident, flippers and nose not included in this criterion	9.01	1.61	5.6	3.5
5	completely molted (≥95% molted)				

TABLE 3 Comparison of gamma and Weibull pup distribution models fit to staging transects data from each colony. Both models had shape and rate parameters. Density function for gamma is $\rho(\rho t)^{\kappa-1}\exp(-\rho t)$ and Weibull is $\kappa\rho(\rho t)^{\kappa-1}\exp[-(\rho t)^{\kappa}]$, where ρ = rate, κ = shape. Best fitting model in bold.

Colony	Model	Shape	Shape *SE*	Rate	Rate *SE*	Proportion	Proportion *SE*	AIC
Sable	**gamma**	**4.936**	**0.425**	**0.203**	**0.021**	**0.912**	**0.017**	**−36,165.20**
	Weibull	2.789	0.108	25.867	0.658	0.966	0.011	−36,158.20
Pictou	**gamma**	**5.816**	**2.371**	**0.346**	**0.174**	**0.509**	**0.094**	**−5,743.88**
	Weibull	2.876	0.612	18.044	1.856	0.507	0.091	−5,682.08
Henry	**gamma**	**3.544**	**0.459**	**0.253**	**0.056**	**0.983**	**0.012**	**−1,654.84**
	Weibull	2.209	0.316	15.083	1.194	0.998	0.004	−1,647.60
Saddle	**gamma**	**7.404**	**5.174**	**0.614**	**0.358**	**0.994**	**0.005**	**−1,803.60**
	Weibull	3.207	0.787	13.520	1.098	1.000	0.001	−1,739.490
Hay	**gamma**	**25.055**	**12.866**	**0.701**	**0.315**	**0.739**	**0.069**	**−10,554.90**
	Weibull	5.520	1.635	38.401	2.643	0.714	0.095	−10,479.40
SWNS	**gamma**	**5.619**	**3.978**	**0.265**	**0.173**	**0.935**	**0.031**	**−1,607.04**
	Weibull	2.566	0.526	23.180	0.834	0.955	0.019	−1,590.43
Muskeget	gamma	19.666	4.957	0.836	0.290	0.999	0.001	−2,404.98
	Weibull	**4.784**	**0.592**	**25.500**	**2.491**	**1.000**	**0.000**	**−2,439.28**

the fit of the stage duration models (Figure S1) and distribution of birth models to the survey transects (Figure S2) show that the models fit the data reasonably well.

3.4 | Pup production in 2016

Total pup production (109,000 *SE* = 17,500) of the northwest Atlantic subspecies was determined by summing the individual colony estimates in each region and then adding these regional estimates (Table 1, Figure 1). Standard errors are not available for all colonies and therefore the reported standard error of the estimated total production may not fully reflect the uncertainty around that estimate. However, the underestimate of uncertainty should be small as colonies lacking a standard error estimate accounted for <2% of the total pup production.

3.5 | Gulf of St. Lawrence

Based on repeated surveys by air, no new coastal colonies were found in the Gulf of St. Lawrence. Further, no pups were observed at sites that had been used in previous years along the shoreline of the Kouchibouguac National Park or at Oak Island. In 2016 ice cover was among the lowest ever recorded during the gray seal breeding season. Nevertheless, approximately 500 pups were observed along the edge of drifting pack ice near Point Prim, Prince Edward Island. Pups were observed at Saddle, Pictou, Henry, Margaree, Deadman (Île de corp morts), Brion, and Anticosti Islands.

The correction to account for pups born after the survey was large for Pictou Island, as we estimate that at the time of survey only 50.9% (*SE* = 9.4) of the pups were born, while the correction was negligible for Saddle and Henry Islands with 99.4% (*SE* = 0.5), and 98.3% (*SE* = 1.2) of pups born prior to the survey (Table 3, Figure S2). Total estimated gray seal pup production in the Gulf was 9,800 (*SE* = 2,000) pups (Table 1).

3.6 | Sable Island

Eighteen transects flown over Sable Island on January 12, 2016, resulted in high quality imagery (Figure 2a), although intermittent cloud cover resulted in high contrast and long shadows in some images. Translucent or "ghost" seals were observed on the mosaic image in several locations. In total, 75 ghost seals were verified using the original photographs. A total of 74,899 pups was counted (Table 1).

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 (Table S1). Based on the AIC criteria, the gamma model of birth distribution provided the best fit and estimated that 91.2% (*SE* = 1.7) of pups had been born by the time of the photographic survey (Table 3, Figure S2). The estimated pup production for the Sable Island colony was 87,500 (*SE* = 15,100; Table 1).

3.7 | Eastern Nova Scotia

A total of 1,833 pups was counted on Hay Island on January 12 (Table 1). To estimate the distribution of births, the developmental stages of 2,025 pups were recorded along three ground transects covering the Island between January 21 and January 28, 2016 (Table S1). The gamma model of birth distribution had the lowest AIC and estimated that 73.9 percent (SE = 6.9) of pups had been born by the time of the photographic survey (Table 3, Figure S2). Based on the January 12 aerial survey, and applying Sable Island estimates of pups missed

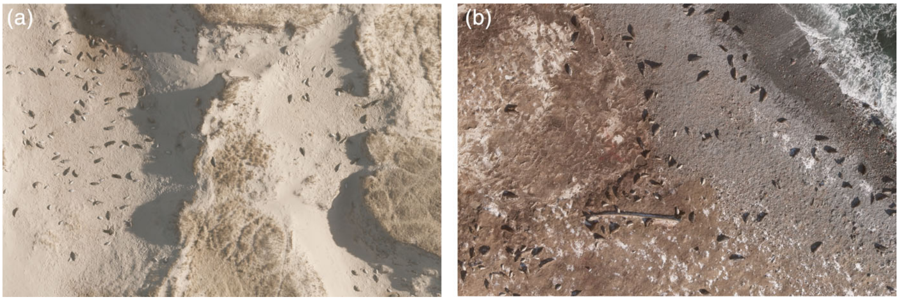

FIGURE 2 Examples of digital imagery from (a) Sable Island and (b) Hay Island.

and pup mortality prior to the survey, total production on Hay Island was estimated to be 2,700 (*SE* = 600; Table 1).

The helicopter survey along the eastern shore of Nova Scotia provided pup counts for two colonies; White Island (37 pups) and a new colony first identified in 2015 at Red Island in Bras D'Or Lakes (41 pups). No other new colonies were found along the coast of Nova Scotia, and some areas which have historically supported colonies, such as Bowen's Ledge (Figure 1), had no pups in 2016.

3.8 | Gulf of Maine (Canada)

Breeding colonies of gray seals were found on only four small islands (Round, Mud, Noddy, and Flat) off southwest Nova Scotia (Figure 1). A total of 1,849 pups was counted on these islands on January 8 (Table 1). The developmental stage of 727 pups was recorded along ground transects on January 17 and 21, 2016 (Table S1). As above, the gamma was the best fit to the data and estimated that 93.5% (*SE* = 3.1) of pups had been born by the time of the photographic survey (Table 3, Figure S2). Applying Sable Island estimates of pups missed and pup mortality prior to the survey, total production was estimated to be 2,100 (*SE* = 200) (Table 1).

3.9 | Gulf of Maine (USA) and Nantucket Sound

At the largest colony, Muskeget Island, 3,787 (*SE* = 0.35) live pups were counted from aerial photographs taken on January 15 (Hayes et al., 2017). The developmental stage of 764 pups was recorded from digital photographs on January 7, 15, and 20, 2016 (Table S1). The Weibull model was the best fit to the data indicating that all the pups (100%, *SE* = 0) had been born by the time of the photographic survey (Table 3, Figure S2). Applying the Sable correction for pup mortality prior to the survey, the estimated production was 4,900 (*SE* = 200) for the colonies in Massachusetts and 1,600 (*SE* = 14) for the colonies in Maine for a grand total of 6,500 (*SE* = 200) for the US breeding colonies. Notably, Mt. Desert Rock was not surveyed in 2016, although it has been checked opportunistically over the years. In January 2004, 2012, and 2014 only one pup was seen in each of the surveys of Mt. Desert Rock, and in 2019 no pups were observed (Wood et al., 2019).

4 | DISCUSSION

Pup production surveys were carried out at all known gray seal breeding colonies in both Canada and the United States in 2016. The results of those surveys show that the northwest Atlantic subspecies continues to increase and that there are marked regional differences in the current contribution to pup production. Sable Island became the largest breeding colony in northwest Atlantic in the 1980s and continues to grow. Currently, Sable Island accounts for about 80% of total pup production in the northwest Atlantic. The second largest breeding colony in 2016 was in the southern Gulf of St. Lawrence on Pictou Island and the third largest colony was Muskeget Island off the coast of Massachusetts.

Several different methods are used to estimate the number of pups born at breeding colonies, partly because of the dramatically different sizes of the colonies throughout the range. To assess the spatial distribution of pupping in 2016, we apply bias corrections for pups born after the survey or missed because of mortality prior to the survey, to the pup counts for most of the large colonies. Estimates of pup production based on visual counts or oblique photography during a single survey, when not corrected for proportion of pups born, mortality, or detection, will almost certainly underestimate total pup production and do not provide a measure of uncertainty; however, pup production at colonies where these methods were used accounted for only 2% of the estimated total production. Visual counts and oblique photography are practical and cost-effective ways to estimate production at small colonies (<500 pups). Nevertheless, they tend to be negatively biased when the visual observers are overwhelmed, or pups are hidden from view. Expanding the use of the large format vertical photography and increasing the use of drones could increase the precision and accuracy of estimates at small colonies (Johnston et al., 2017) and help to correct for the pups born after the survey is completed.

4.1 | Regional trends

The northwest Atlantic subspecies of the gray seal was severely depleted by seal culling programs in the United States during the late 1800s (Lelli & Harris, 2006; Wood et al., 2019). In Canada, commercial harvesting in the 1800s led to significant reductions in the population and gray seals were considered uncommon or rare well into the middle of the last century (Fisher, 1950; Lavigueur & Hammill, 1993). Government culling programs undertaken briefly in the 1940s and again from the late 1960s through the middle 1980s hampered recovery (Bowen & Lidgard, 2013; Lavigueur & Hammill, 1993). The effect of these control programs was to extirpate breeding colonies in both the United States and Canada, except for small colonies on Sable Island, coastal islands in eastern Nova Scotia, and pack ice in the southern Gulf of St. Lawrence. Despite continued control efforts, gray seals began to increase in the early 1960s in both the Gulf of St. Lawrence and on Sable Island (Figure 3). Associated with, and perhaps a direct result of this increase, new breeding colonies have been established throughout the range of the metapopulation (Table 4). The establishment of new breeding colonies has been observed in other increasing pinniped metapopulations such as the eastern population of Steller sea lions, *Eumetopias jubatus*, (National Marine Fisheries Service [NMFS], 2013), gray seals in the United Kingdom and North Sea (Abt & Engler, 2009; Harrison et al., 2006; Russell et al., 2019; Thomas et al., 2019), and Hawaiian monk seals, *Neomonachus schauinslandi*, in the main islands (Baker et al., 2011).

In the Gulf of St. Lawrence pup production increased from the mid-1960s through the mid-1990s, although the estimates are sometimes imprecise (Figure 3b). Except for two low estimates in 1997 and 2000, pup production in the Gulf of St. Lawrence appears to have been relatively stable since 2004. Over this same period, there has been a shift in the proportion of pupping that occurred on ice, down from almost 100% in 1996 to just 1% in 2016 (Hammill, Gosselin, et al., 2017). Given the reduced ice cover in recent years, a shift to land breeding is not unexpected. In the Baltic sea, where ice cover has also become less frequent, gray seals have shifted to pupping on land (Jüssi et al., 2008).

At Sable Island, the largest colony, pup production has increased since the early 1960s, and continues to increase though 2016 (Figure 3a). However, the current estimate of pup production increase is well below the 13% annual exponential growth estimated during the period 1976 to 1997 (Bowen et al., 2003, 2007). Since 2007, the rate of increase has slowed to about 5 to 7% per annum.

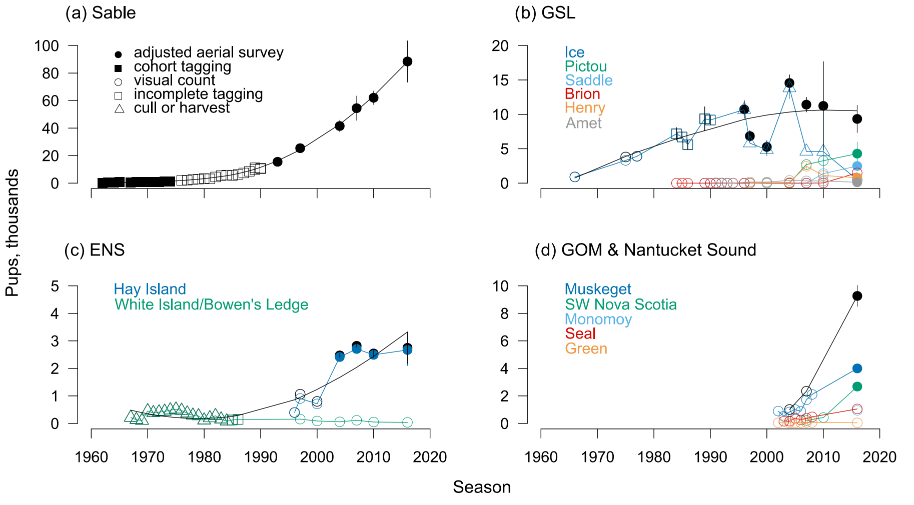

FIGURE 3 Regional trends in pup production throughout the range of the northwest Atlantic gray seal subspecies for (a) Sable Island, (b) Gulf of St. Lawrence (GSL), (c) Eastern Nova Scotia (ENS), and (d) Gulf of Maine (GOM) and Nantucket Sound. Totals for each region are plotted in black and the trends for largest breeding colonies are presented separately. Open circles are counts from the air or from photographs, filled circles are counts from aerial photography and adjusted for the distribution of births and pup mortality, open black squares are incomplete tagging, filled black squares are complete tagging, and open triangles are estimates from culls or harvests. The 2016 estimate for Seal Island is hidden behind the symbol for Monomoy.

Along coastal Nova Scotia, only a few pups were observed at Bowen's Ledge or the Basque Islands off southern Cape Breton (Table 4), which had gray seal breeding colonies that produced several hundred pups in the 1960s and early 1970s (Mansfield & Beck, 1977; Zwanenburg & Bowen, 1990). A new colony, discovered on Red Island in the Bras D'Or lakes in 2015, was used again in 2016. The largest colony along coastal Nova Scotia, Hay Island, was discovered in 1993. Pup production at this colony rose rapidly to 2004, but estimates have been relatively stable through 2016 (Figure 3c). The breeding colonies in southwest Nova Scotia were identified in 1993. By 2010, the breeding colonies in this area had expanded both in abundance and in the number of sites, from Noddy and Flat islands to Round and Mud, two adjacent islands. In the first large-format, aerial-photographic survey of these colonies, the estimated pup production in 2016 was 2,100 (Table 1), more than four times the number of pups estimated from helicopter-based counts in 2010 (417). Another new colony on Green Island (43°41.3′N, 66°08.5′W) near Yarmouth, Nova Scotia, Canada (Figure 1) was found in southwest Nova Scotia in 2018.

In northeastern United States, the three largest gray seal breeding colonies are Muskeget and Monomoy Islands in Massachusetts, and Seal Island in Maine. Since 2010, pupping has also been observed at Nomans Land Island in Massachusetts and Wooden Ball Island and Matinicus Rock in Maine (Hayes et al., 2017; Wood et al., 2019). The historic pupping site on Muskeget Island in Massachusetts was reestablished in 1988 while the breeding colonies established Green Island in the mid-1990s and Seal Island in 2000, may also have supported colonies historically (Mansfield & Beck, 1977; Wood et al., 2019). Pup production, particularly at colonies in Nantucket Sound, has been increasing rapidly (Wood et al., 2019).

The sustained rapid growth rate at new colonies suggests recruitment from the larger established breeding colonies. Gray seals have high site fidelity once they have recruited to a breeding colony, but young of the year show a wide dispersal (Lavigueur & Hammill, 1993; Mansfield & Beck, 1977; Stobo et al., 1990) that could contribute to movement of individuals among breeding colonies. Adult females, branded on Sable Island as young of the year, are known to have recruited to other breeding colonies in both Canada (Hay Island, southwest Nova Scotia) and the United States (Muskeget Island) and similarly adult females branded in the Gulf of St. Lawrence as young of the year have been

TABLE 4 History of gray seal breeding colonies in the northwest Atlantic population. Locations in Figure 1.

Breeding colony	First reported	Comment, last known use	Source
Sable Island (NS)	<1850		Gilpin, 1858
Gulf of St. Lawrence			
Ice - Northumberland Strait/St. Georges Bay	<1700	~500 pups on ice near Point Prim in 2016	Lavigueur & Hammill, 1993; Hammill, Gosselin, et al., 2017
Saddle Island (NS)	2010		Hammill, Gosselin, et al., 2017
Pictou Island (NS)	1997		Hammill et al., 2007
Brion Island (PQ)	2010		Hammill, Gosselin, et al., 2017
Henry Island (NS)	1997		Hammill et al., 2007
Deadman Island (PQ)	<1951		Mansfield & Beck, 1977
Anticosti Island (PQ)	2007		Hammill et al., 2007
Margaree Island (NS)	1997		this paper
Amet Island (NS)	~1950		Mansfield & Beck, 1977
Kouchibouguac Park (NB)	2007		Hammill et al., 2007
Oak Island (NS)	2007		Hammill et al., 2007
Eastern Nova Scotia			
Basque Islands	1962	Eroded, 20 pups last seen in 2016, none seen in 2018	Mansfield & Beck, 1977
Hay Island (NS)	1993		Hammill et al., 2007
Red Island (NS)	2015		this paper
Bowen's Ledge, Camp Island, White Island (NS)	1968	37 pups in 2016	Mansfield & Beck, 1977
Gulf of Maine (Canada)			
Tusket Islands, Cape Sable Island	<1700		Densy 1672, in Lavigueur & Hammill, 1993
Noddy Island, Flat Island (NS)	1993		Bowen et al., 2011
Mud Island, Round Island (NS)	2010		Bowen et al., 2011
Grand Manan Island	<1974		Mansfield & Beck, 1977
Green Island (NS)	2018	Pups first observed in 2018	this paper
Gulf of Maine (US)			
Seal Island (ME)	2000		Wood et al., 2019
Green Island (ME)	1994		Wood et al., 2019
Wooden Ball Island (ME)	2012		Wood et al., 2019
Matinicus Rock (ME)	2011		Wood et al., 2019
Mount Desert Rock (ME)	2004	Not surveyed in 2016, and no pups in 2019	Wood et al., 2019

(Continues)

TABLE 4 (Continued)

Breeding colony	First reported	Comment, last known use	Source
Nantucket Sound			
Muskeget Island (MA)	1988		Wood LaFond, 2009
Monomoy Island (MA)	1990		Wood et al., 2019
Nomans Land Island (MA)	2011		Wood et al., 2019
Great Point (MA)	2018	Pups first observed in 2018	Wood et al., 2019

Note. No entry in "Last known use" column indicates active site in 2016.

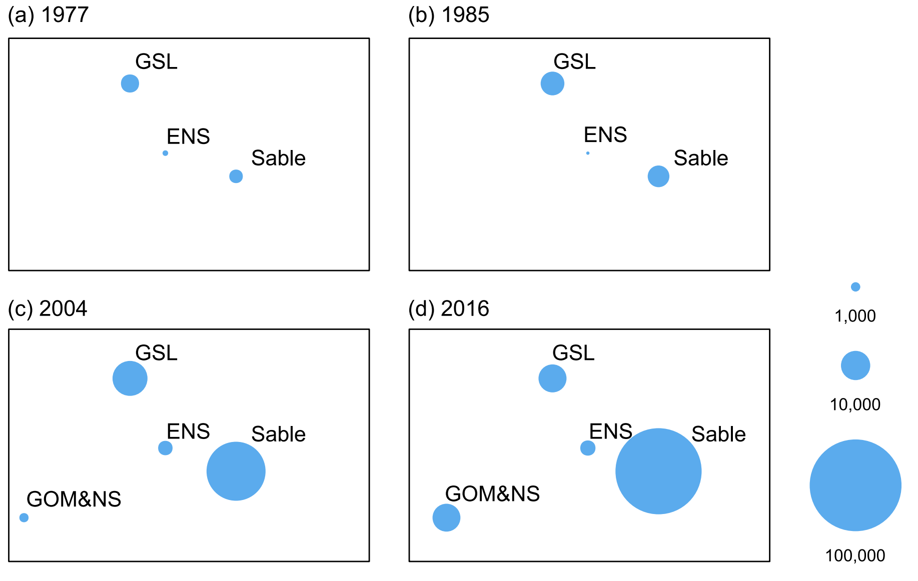

FIGURE 4 Plot of the relative size of breeding colonies in the Gulf of St. Lawrence (GSL), eastern Nova Scotia (ENS), Sable Island, and Gulf of Maine and Nantucket Sound (GOM&NS) in (a) 1977, (b) 1985, (c) 2004, and (d) 2016, when we have comprehensive estimates of pup production for northwest Atlantic metapopulation.

sighted on Sable Island, providing evidence of exchange among colonies. While the northwest Atlantic gray seals may have once been better described as a classical metapopulation with roughly evenly sized breeding colonies, the current large size of Sable Island breeding colony suggest a mainland-island structure (Harrison and Taylor, 1997). The continued efforts to individually mark gray seals provides opportunity for resighting surveys to estimate exchange of seals among the breeding colonies and incorporate metapopulation structure in population models.

In many respects the spatial and temporal trends in production in our study population are similar to those observed in the increasing eastern Atlantic gray seal subspecies (Abt & Engler, 2009; Harrison et al., 2006; Russel et al., 2019; Thomas et al., 2019). Although the number of pups throughout the United Kingdom has grown since the 1960s when records began, there is evidence that the rate of pup production is leveling off in all areas except the central and southern North Sea (Russel et al., 2019; Thomas et al., 2019). The numbers born in the Hebrides have changed little since 1992 and growth has been slowing in Orkney Islands since the late 1990s.

Over the past half century, pup production in the northwest Atlantic has shifted southward. In the 1960s, about 90% of production was in the Gulf of St. Lawrence with only 10% further south mainly at Sable Island (Figure 4). By

2016, there had been a complete reversal of the spatial distribution of production with more than 90% of production occurring south of the Gulf of St. Lawrence (80% on Sable Island, 5% coastal Nova Scotia, and 5% in northeastern US colonies). As is commonly observed in other taxa (Grandi et al., 2008; Swenson et al., 1998), some of the redistribution of pup production presumably is simply accounted for by the geographic expansion of breeding colonies associated with the rapid increase over the past half century. However, ecosystem changes may also play a role. For example, climate change is thought to underlie a northward movement of breeding in the eastern population of Stellar sea lions (NMFS, 2013). In the northwest Atlantic, six continental shelf or inland sea ecosystems are used by gray seals, all of which have undergone changes in recent decades. Shackell et al. (2012) compared responses to fishing pressure and climate across seven northwest Atlantic ecosystems and found a common pattern in biological indicators such as an increase in phytoplankton abundance, mid-trophic level biomass, a decline in predator groundfish body size and changes in fish species composition. These changes were associated with fishing indices and trends in the Atlantic Multidecadal Oscillation. We speculate that both the decline in predator fish and the increase in mid-trophic level species favored gray seals by reducing interspecific competition and increasing food availability.

The overall rate of increase in northwest Atlantic gray seals has slowed. Nevertheless, the establishment of new breeding colonies and the southward redistribution of pup production suggest that continued population increase can be expected. As gray seal populations continue to increase, we should expect this large marine predator to play an increasingly important role in continental shelf ecosystems.

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AUTHOR CONTRIBUTIONS

Cornelia den Heyer: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; supervision; validation; visualization; writing-original draft; writing-review and editing. **Don Bowen:** Conceptualization; formal analysis; funding acquisition; investigation; methodology; project administration; resources; supervision; writing-original draft; writing-review and editing. **Julian Dale:** Investigation; methodology; project administration; validation; writing-review and editing. **Jean-François Gosselin:** Data curation; investigation; methodology; project administration; supervision; writing-original draft. **Michael Hammill:** Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; project administration; resources; supervision; validation; writing-original draft; writing-review and editing. **David Johnston:** Investigation; methodology; project administration; resources; validation; writing-review and editing. **Shelley Lang:** Data curation; formal analysis; investigation; methodology; project administration; resources; validation; visualization; writing-original draft; writing-review and editing. **Kimberly Murray:** Conceptualization; data curation; funding acquisition; investigation; methodology; project administration; resources; supervision; validation; writing-original draft; writing-review and editing. **Garry Stenson:** Conceptualization; data curation; investigation; methodology; project administration; resources; supervision; writing-original draft; writing-review and editing. **Stephanie Wood:** Conceptualization; data curation; investigation; methodology; project administration; writing-original draft; writing-review and editing.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of this article.

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