



Rates of increase in gray seal (*Halichoerus grypus atlantica*) pupping at recolonized sites in the United States, 1988–2019

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Gray seals were historically distributed along the northeastern coast of the United States, but bounties and lack of protection reduced numbers and they were rarely observed for most of the 20th century. Once protections were enacted, the population started to rebound. Here, we describe the recolonization and recovery of gray seals in the United States, focusing on the re-establishment of pupping sites. We fit individual generalized linear models to various time series (1988–2019) to estimate rates of increase in observed pup counts at four of the more data-rich sites. Annual rate of increase at individual sites ranged from -0.2% (95% CI: -2.3 – 1.9%) to 26.3% (95% CI: 21.6 – 31.4%). The increase in sites and number of pups born in the United States is driven by population growth and immigration from Canadian colonies and is part of a larger recovery of the Northwest Atlantic population. Wildlife protection, a healthy source population, habitat availability, and species traits that allow for dispersal and high productivity were all important factors in this recovery.

Key words: conservation, generalized linear models, *Halichoerus grypus*, population recovery, rates of increase, recolonization

The ability for a depleted population to naturally recolonize historical habitat varies. In general, the way in which a population expands its range depends on three factors: the propensity of individuals to disperse, the potential population growth and life history traits of the species, and environmental conditions (e.g., habitat availability and quality—Lubina and Levin 1988). Favorable conditions in all three of these factors, and the existence of a source population in Canada, have enabled gray seals (*Halichoerus grypus atlantica*) to reestablish pupping colonies in the northeastern United States after regional extirpation.

Gray seals are a large, sexually dimorphic, highly philopatric species whose range is restricted to the North Atlantic (Davies 1957; Twiss et al. 1994; Pomeroy et al. 2000). There are two recognized subspecies, one in the Baltic Sea (*Halichoerus grypus grypus*) and the other in the North Atlantic (*H. g. atlantica*—Olsen et al. 2016). Within the North Atlantic, they are further divided into two populations, the Northeast Atlantic population and Northwest Atlantic population, based on cranial differences (Rice 1998) and mtDNA studies (Boskovic et al. 1996).

Gray seals were historically distributed along the northeastern coast of the United States as evidenced by

extensive archaeological records found at sites from New Haven, Connecticut to Machias Bay, Maine, which have been dated to approximately 2500 BCE–1600 CE (Eaton 1898; Waters 1967; Ritchie 1969; Robinson 1985; Spiess and Lewis 2001; Fig. 1). In 1792, a Nantucket, Massachusetts, resident wrote of a “bounty of gray seals” on Muskeget Island (Weatherbee et al. 1972).

State seal bounty systems targeting both harbor (*Phoca vitulina vitulina*) and gray seals existed in Maine (1895–1905) and Massachusetts (1888–1908 and 1919–1962), with additional hunting not recorded in bounty statistics (Lelli et al. 2009). This hunting pressure depleted the population, and they were extirpated from the United States during the early to mid-20th century (Andrews and Mott 1967; Lelli et al. 2009). The decline in the United States was part of a larger decline throughout the Northwest Atlantic. By the mid- to late 1800s, gray seals were rare in Canada and remained so until the mid-1900s (Lavigne and Hammill 1993). In 1966, the Canadian (Gulf of St. Lawrence and Sable Island) population was roughly estimated to be 5,600

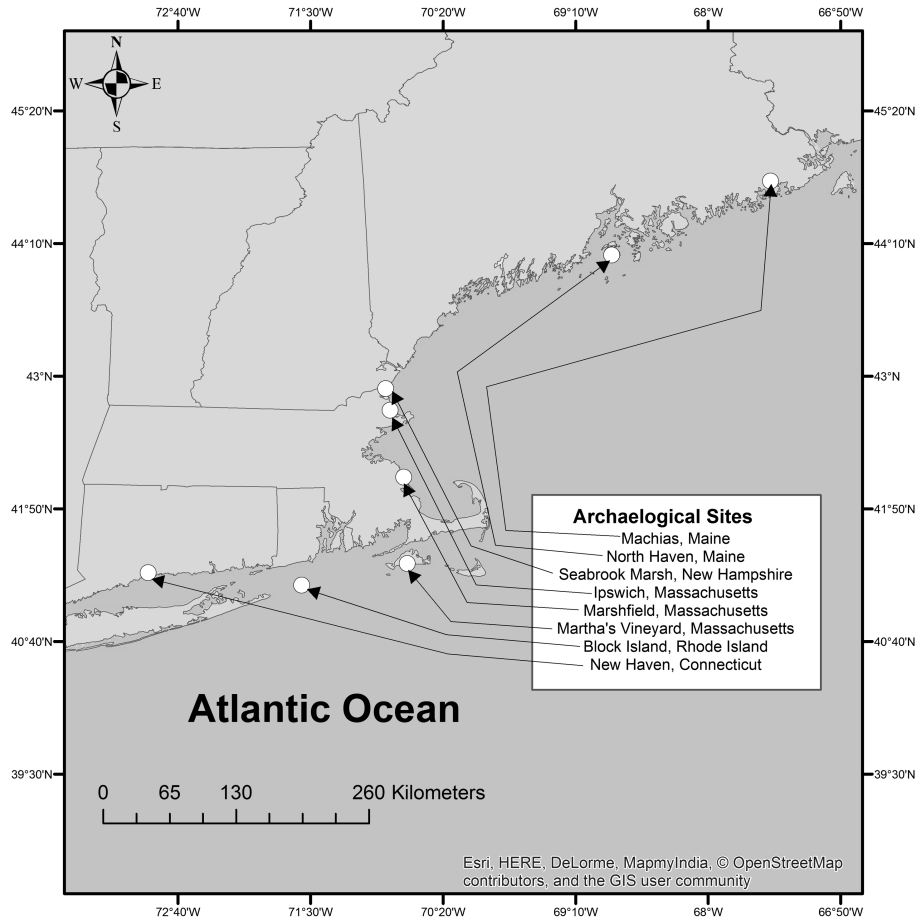


Fig. 1.—Archaeological sites containing gray seal (*Halichoerus grypus atlantica*) remains in the United States, 2500 BCE–1600 CE.

gray seals, with more seals occurring in the Gulf of St. Lawrence (Mansfield 1966).

Legal protection was key in gray seal recovery in the United States. The state of Massachusetts enacted a law to protect gray seals in 1965, and the federal government passed the U.S. Marine Mammal Protection Act (MMPA) in 1972. Under the MMPA, it is illegal to harass, hunt, capture, collect, or kill any marine mammal, or attempt any of these actions (50 CFR 216.3). The goal of the MMPA is to maintain marine mammal populations at a level between the population's maximum net productivity and carrying capacity (otherwise referred to as the "optimal sustainable population"). Determining whether the size of a population is within this range requires substantial data not available for most species (Gerrodette and DeMaster 1990); however, increasing trends in abundance in a population have been used as an indicator of recovery (Magera et al. 2013).

Prior to the passage of the MMPA in the United States, the Canadian gray seal population started to recover. Gray seals at Canadian sites have increased from the 1970s to the present time (Bowen et al. 2003, 2007, 2011; den Heyer et al. 2017). By nature of its remote location, the Sable Island seals have been protected from hunting, and in 2013, the island became a National Park under Parks Canada. Most notable is the > 30 years of exponential growth, at an annual rate of increase of 12.8%, on Sable Island (Bowen et al. 2003). This recovery

is due in part to the life history traits of the gray seal compared to other large, long-lived mammal species. These include early age at first reproduction for females (4–5 years—Bowen et al. 2006), long life span (up to 34 years or longer), and annual reproductive events for most adult females (Zwanenburg and Bowen 1990).

Observations of branded or tagged seals born at Canadian pupping sites demonstrate that immigration has been an important part of U.S. gray seal recovery (Rough 2000; Breed et al. 2009; Wood et al. 2011; Cammen et al. 2018a, 2018b). Wood LaFond (2009) documented that many of the first breeding females on Muskeget and Monomoy Islands had been born on Sable Island. Subsequent satellite tagging projects demonstrated the ability of gray seals to disperse widely, including observations of animals from Sable Island and the Gulf of St. Lawrence moving into U.S. waters as far south as Muskeget Island (Breed et al. 2009; M. O. Hammill, Department of Fisheries and Oceans, pers. comm.). Additionally, genetic analyses comparing pups born in the Gulf of St. Lawrence, Sable Island, Muskeget Island, and Green Island found enough individuals are moving between pupping sites that no population structure was detected (Wood et al. 2011; Cammen et al. 2018a, 2018b). This capacity for gray seals to disperse widely has contributed to their recovery in the Northwest Atlantic.

The pupping season is an ideal time for surveying seals as their locations are predictable in time and space, and hauled-out individuals are visibly available to be counted. Given pupping sites are often offshore islands or distributed along remote coastlines, aerial surveys are an efficient way to survey them. The data collected via aerial surveys of gray seal pupping sites can be used to simply document location and raw numbers or can be combined with other information (e.g., ground surveys to collect pup age and mortality data) to model pup production or total population size. Multiple surveys are required over the length of the pupping season to model total pup production (Bowen et al. 2003, 2007, 2011; Duck and Thomas 2007; Wood et al. 2007; Brasseur et al. 2014; den Heyer et al. 2017).

In the Northwest Atlantic, gray seal pups are born from December to February over approximately a 6-week period with some pups being born, weaned, and leaving the site before others are born (Bowen et al. 2003, 2007). The counts we present here were collected during the pupping season in the U.S. segment of the Northwest Atlantic population. In this paper, we document the history of gray seal recolonization at U.S. pupping sites and use these ground and aerial surveys to report rates of increase in minimum pup counts over time at different sites from 1988 to 2019.

MATERIALS AND METHODS

Surveys.—Land-based surveys were initiated on Muskeget Island in 1988 and Monomoy Island in 1990 and transitioned to aerial surveys in 1994 (Rough 1995; Wood LaFond 2009). Aerial surveys began in Maine in 1994 (Wood LaFond 2009). These surveys were conducted in one of three small plane models from 1994 to 2019 (e.g., Cessna 252, Cessna Skymaster, de Havilland Canada Twin Otter). Survey altitude ranged from 180 to 230 m depending on platform (the Cessnas flew at 180 m while the de Havilland flew at 230 m). The on-ground sampling distance for surveys flown at the higher altitude of 230 m was approximately 1 cm/pixel (Johnston et al. 2017), which is more than enough resolution to identify seals. These surveys targeted known and suspected pupping sites in Massachusetts and Maine (Fig. 2). Pupping sites were surveyed 1–5 times during the pupping season (mid-December to early February) annually depending on weather and funding. For the 1994–2015 and 2019 surveys, sites were photographed obliquely from the side window of the plane. Surveys conducted 1994–2004 used a 35 mm camera with a 300 mm lens and 400-speed color slide film, and in 2005, slide film was replaced with digital images (Rough 1995; Wood LaFond 2009). In 2016, a belly-mounted camera system, using three Canon Mark III 5D cameras with Zeiss 85 mm prime lenses configured in a port-center-starboard configuration, was used (Johnston et al. 2017). In 2018, a ground-based survey at Great Point documented the ninth U.S. pupping site.

Image processing.—Images were assessed for overlap both within and among transects. Finding overlap among transects was especially challenging for surveys with many transects or when the island was approached from multiple

directions. Prior to the shift to digital images, slide images were projected onto a white board for counting. For the digital images, when enough image overlap existed, stitching software (Microsoft Image Composite Editor v. 1.4.4—64 bit; Microsoft Corporation, Redmond, Washington) was used to create composite digital images that were used to visualize island coverage and overlap in the aerial images. Seals in the images were counted using a paint-dot technique with standard image processing software (either Adobe Photoshop v. 2015.5; Adobe, San Jose, California; or Paint Shop Pro Photo X2; Corel Corporation, Ottawa, Ontario, Canada; or GIMP; <https://www.gimp.org>). For Muskeget and Monomoy surveys in 1994–1999, the images were counted twice by the same person (Rough 1995, 2000). For Muskeget (2001–2008 and 2016), Seal (2000–2008 and 2016), and Green (1994–2008), two trained observers independently counted pups. These counts were compared and when possible, differences were rectified by jointly reviewing the slides; an average of the two total counts was taken when differences remained. For the remaining sites, the images were counted once with two scientists jointly reviewing images to be used for counts, areas of overlap, and pups in question.

To select surveys for the analysis, we retained only those surveys conducted during peak pupping on the colony and that had full coverage of the colony and good image quality. We considered peak pupping to be between 5 January and 5 February, based on the breeding phenology at Muskeget. Therefore, of the 110 surveys considered for model inclusion, 15 were removed due to poor image quality or site coverage, and three were removed because they were outside of the peak pupping window.

Description of pupping colonies.—A total of nine pupping sites have been identified along approximately 600 km of coastline in the Northeast United States (Table 1; Fig. 2). The Massachusetts sites (Great Point, Monomoy Island, Muskeget Island, and Nomans Land Island) are characterized by low-lying, sandy beaches with dunes and beach grass, whereas the Maine sites (Green Island, Matinicus Rock, Mount Desert Rock, Seal Island, and Wooden Ball Island) are islands with large rocky outcroppings and shallow soil covering some areas. In addition to varying habitat, the sites also range in size from 0.03 km² (Green Island) to 30.77 km² (Monomoy Island). While most of the sites are offshore islands, Monomoy Island has periodically been connected to the mainland. The well-established sites (e.g., Muskeget, Seal, Green Islands) tend to only have adult males, adult females, and pups on them during the pupping season, whereas juveniles and nonbreeding adults can also be observed on the more recently recolonized sites (e.g., Nomans Land Island, Great Point). Pupping began at different times during 1988 to 2019 and was first documented on Muskeget in 1988 (Wood LaFond 2009).

Statistical analysis.—For four of the more data-rich sites (Muskeget, Monomoy, Seal, Green), we fit separate generalized linear models (GLMs) with a Poisson distribution and log link to the number of pups born over time at each of the sites. Our response in the model was the maximum number of pups

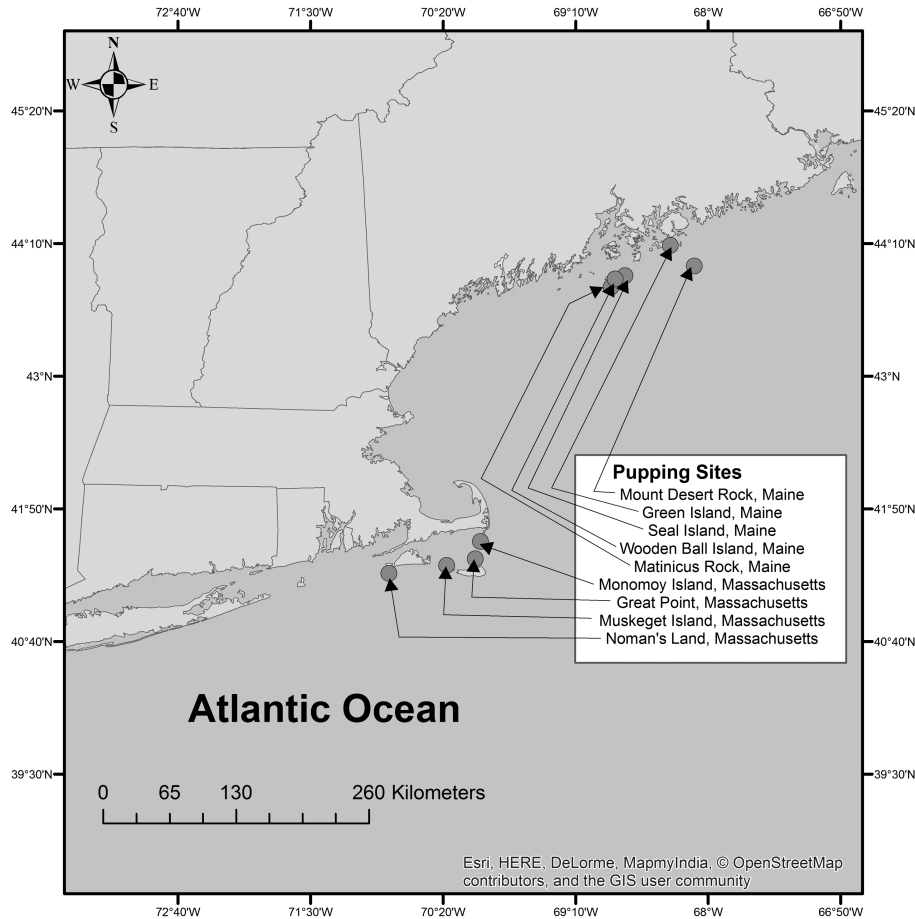


Fig. 2.—Gray seal (*Halichoerus grypus atlantica*) pupping sites in the United States, 1988–2019.

Table 1.—Characteristics of gray seal (*Halichoerus grypus atlantica*) pupping sites in the United States.

Site	Location	Size (km ²)	Terrain	First documented pupping
Great Point	41°23'19"N/70°02'45"W	0.08	Sand	2018
Green Island	44°09'34"N/68°20'03"W	0.03	Rock	1994
Matinicus Rock	43°47'08"N/68°51'11"W	0.11	Rock	2011
Monomoy Island	41°35'24"N/69°59'25"W	30.77	Sand	1990
Mount Desert Rock	43°58'07"N/68°07'42"W	0.10	Rock	2004
Muskeget Island	41°20'15"N/70°18'18"W	1.18	Sand	1988
Nomans Land	41°15'20"N/70°48'58"W	2.54	Sand	2011
Seal Island	43°53'15"N/68°44'25"W	0.26	Rock	2000
Wooden Ball Island	43°51'16"N/68°49'06"W	0.68	Rock	2012

(*Y*) on the colony in a given year (*t*), which represented a minimum count of total pup production. We fit the GLM with a quasi-Poisson family because the variance of the counts was much greater than the mean assumed by the Poisson family. The expected value of *Y* is:

$$E(Y) = \mu = e^{\alpha + rt}$$

where μ = the mean number of pups born in year *t*; *r* = mean rate of increase in number of pups born; α = constant intercept term. and

$$Var(Y) = \rho E(Y)$$

where ρ = the dispersion parameter.

We did not estimate rates of increase for Great Point, Matinicus, Mt. Desert Rock, Nomans Land, or Wooden Ball due to their recent establishment and limited data.

RESULTS

Surveys.—The early ground counts and aerial survey images produced raw pup counts for the single day on which the surveys were conducted (Table 2). There was a steady increase in the number of pups born at most sites over the study period. However, pupping was sporadic at Monomoy from 1990 to 2008. In 2009, a minimum of 68 pups were counted, 10 years

Table 2.—Minimum counts of gray seal (*Halichoerus grypus atlantica*) pups observed from 1988 to 2019 at United States sites. * indicates site not surveyed; ** indicates the counts were removed due to poor image quality/coverage, *** indicates the counts were removed due to survey date. Great Point, Matinicus Rock, Mt. Desert Rock, Nomans Land, and Wooden Ball are pupping sites that were not included in the trend analysis.

Year	Green	Great Point	Matinicus Rock	Monomoy	Mt. Desert Rock	Muskeget	Nomans Land	Seal	Wooden Ball
1988	*	*	*	*	*	5	*	*	*
1989	*	*	*	*	*	0	*	*	*
1990	*	*	*	9	*	*	*	*	*
1991	*	*	*	3	*	6	*	*	*
1992	*	*	*	0	*	12	*	*	*
1993	*	*	*	*	*	28	*	*	*
1994	39	*	*	1	*	57	*	0	*
1995	48	*	*	2	*	98	*	*	*
1996	**	*	*	6	*	162	*	*	*
1997	33	*	*	10	*	212	*	*	*
1998	**	*	*	***	*	333	*	*	*
1999	28	*	*	***	*	472	*	*	*
2000	33	*	*	***	*	633	*	77	*
2001	**	*	*	*	*	*	*	91	*
2002	34	*	*	0	*	883	*	147	*
2003	**	*	*	0	*	824	*	**	*
2004	26	*	*	4	1	**	*	150	*
2005	33	*	*	1	*	992	*	365	*
2006	43	*	*	8	*	868	*	239	*
2007	57	*	*	9	*	1,704	*	364	*
2008	59	*	*	2	*	2,095	*	466	*
2009	48	*	*	68	*	**	*	**	*
2010	51	*	*	154	*	1,841	*	**	*
2011	65	*	112	325	*	3,173	1	**	*
2012	41	*	**	**	1	2,831	8	**	*
2013	*	*	*	633	*	2,750	4	**	*
2014	30	*	201	507	1	3,073	16	**	*
2015	33	*	182	768	*	**	23	**	185
2016	34	*	193	935	*	3,787	32	1,043	284
2017	*	*	*	*	*	*	*	*	*
2018	*	11	*	*	*	*	*	*	*
2019	16	5	193	1,190	0	3,532	103	854	360

later, 1,190 were counted in 2019. Counts on Green remained relatively flat, with 39 pups observed in 1994 and 16 observed in 2019. Single pups were first observed on Nomans Land Island and Mt. Desert Rock in 2011 and 2004, respectively. The number of pups born on Nomans has increased while only single pups have been observed sporadically at Mt. Desert Rock. Eleven pups were counted on the ground at Great Point in 2018. For Matinicus Rock and Wooden Ball, over 100 pups were counted the first time they were surveyed (2011 and 2015, respectively); therefore, it is unknown when pupping began at these two sites. These sites will continue to be surveyed along with the longer established sites in future efforts.

Rates of increase.—The number of pups increased at a rate of 12.8%/year (95% CI: 10.9–14.9%) on Muskeget Island, 26.3%/year (95% CI: 21.6–31.4%) on Monomoy Island, 11.5%/year (95% CI: 8.5–14.7%) on Seal Island, and –0.2%/year (95% CI: –2.3–1.9%) on Green Island (Fig. 3; Table 3). With the exception of Green Island, rates of increase in the number of pups born at Muskeget, Monomoy, and Seal Island are increasing significantly.

DISCUSSION

After being effectively absent from U.S. waters for most of the 20th century, gray seals have recolonized historical habitat and

established multiple, growing pupping colonies. Three of the four sites modeled had mean rates of increase higher than 11%, with rates on Monomoy as high as 26%. Demographic analyses based on values in the literature suggest that rates of increase in closed gray seal populations cannot exceed 11% (Harding and Harkonen 1999). Our high rates of increase in minimum pup production suggests that immigration of seals from other areas has supplemented the breeding population in U.S. waters. Evidence of immigration is supported by field observations of branded and tagged pups of Canadian origin at U.S. sites, satellite tracking, and genetics studies (Rough 2000; Breed et al. 2009; Wood et al. 2011; Cammen et al. 2018a, 2018b). In addition to an increase in the numbers of pups at established U.S. sites, the number of sites has increased from one in 1988 to nine in 2019.

Sable Island accounts for more than 85% of Northwest Atlantic pup production (den Heyer et al. 2017) and appears to be an important source of animals colonizing U.S. sites based on resightings of branded animals. The Sable Island population grew exponentially from the early 1960s to 1997 (Bowen et al. 2003), but subsequent surveys have shown a slower growth rate (Bowen et al. 2007; den Heyer et al. 2014, 2017). An analysis of vital rates at Sable Island found that the estimated age of females at first birth has increased from 5.6 to 6.5 years, and

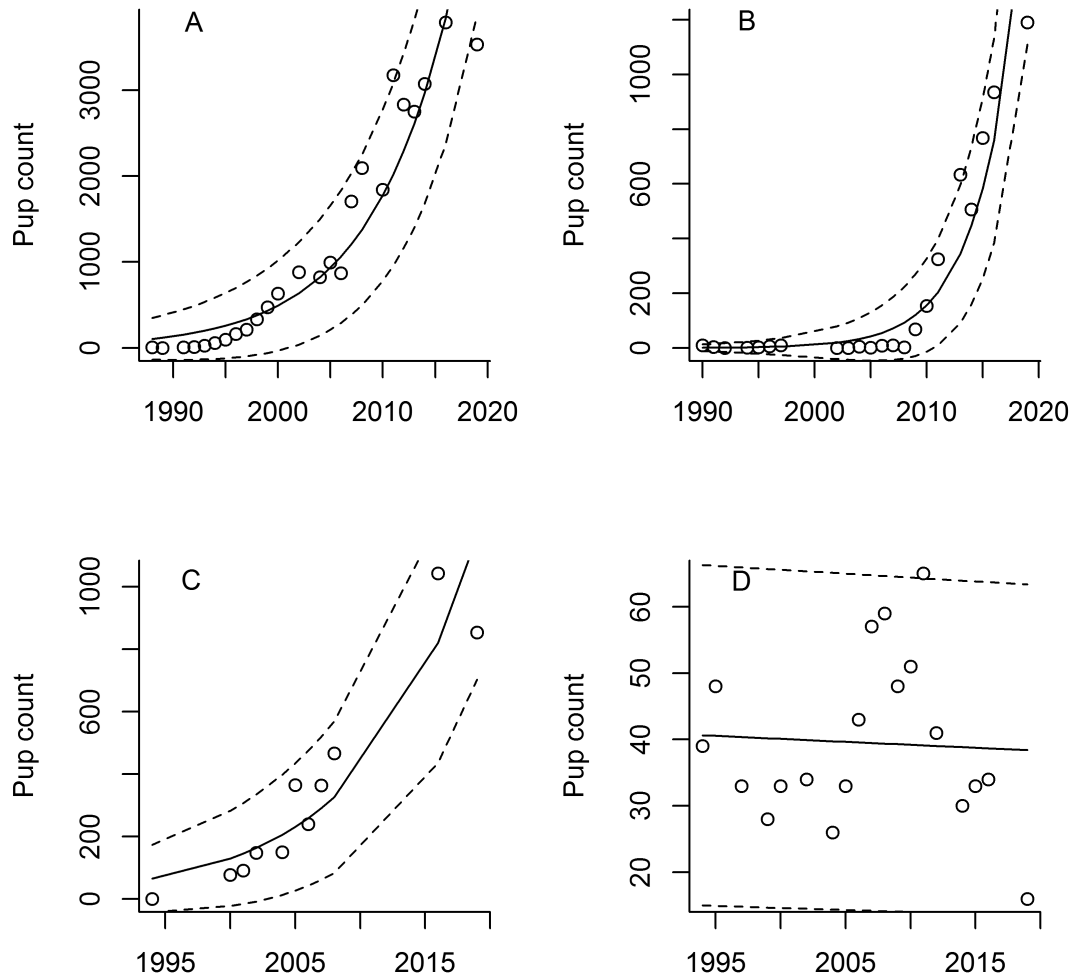


Fig. 3.—Estimated mean rates of increase (solid line) and 95% CIs (dashed lines) in number of gray seal (*Halichoerus grypus atlantica*) pups born at four United States pupping colonies at various times from 1988 to 2019. A = Muskeget Island, B = Monomoy Island, C = Seal Island, D = Green Island.

survival of juveniles has decreased from 0.74 to 0.33 (den Heyer et al. 2014). These changes in vital rates are indicative of a population that is near carrying capacity. If Sable Island is a major source population for the United States, changes in vital rates on Sable will likely impact the population dynamics at U.S. colonies, although this impact may be less at U.S. sites that are close to carrying capacity themselves.

Differences in rates of increase among the U.S. pupping colonies may be due to a combination of available space, immigration, the presence of predators, and proximity to other colonies. For instance, Monomoy Island exhibited the highest growth rate (26%) across all sites examined in the trend analysis. Pupping was sporadic on Monomoy until 2009, after which time pup numbers have been increasing (Rough 1995; Wood LaFond 2009; Puryear et al. 2016; Johnston et al. 2017). This may be the result of crowding in prime pup habitat on nearby Muskeget Island, or the fact that coyotes have been removed from the island to protect birds from 1998 through the present (U.S. Fish and Wildlife Service 2016; S. Koch, U.S. Fish and Wildlife Service, pers. comm.). Monomoy also has the largest land area compared to other sites, so space is unlikely to be a limiting factor

there. Unlike Monomoy, Muskeget may be more constrained by space but is buffered from predators due to its distance from the mainland and shallow shoals surrounding the island. In the early 1990s, pupping took place only on the east and north sides of Muskeget Island, yet over time mothers and pups have spread and in 2019 pupping took place around the entire circumference of the island, constraining future expansion. A similar expansion of pupping habitat used has been observed on Seal Island.

The slight decrease (-0.2%) on Green Island suggests that this site may have already been at carrying capacity when pupping was first documented in 1994. Compared to other pupping sites, Green is the smallest, so growth may be constrained by space limitations there.

Bonner (1989) attributed the increase in seals during the 20th century more to restoration of habitat (i.e., humans abandoned remote islands) than to protection or decreased hunting pressure. So, in addition to immigration from Canada, changing human land use in the recovery of U.S. pupping sites was a likely factor. Generally, island use by humans has declined at U.S. pupping sites since the mid-1900s. Changes have included a shift away from hunting and fishing (e.g.,

Table 3.—Estimated mean rate of increase (r) and 95% CIs in the number of gray seal (*Halichoerus grypus atlantica*) pups born at four United States pupping sites between 1988 and 2019.

Pupping site	r (%)	95% CI (%)	Years included
Muskeget Island	12.8	10.9–14.9	1988–2019
Monomoy Island	26.3	21.6–31.4	1990–2019
Seal Island	11.5	8.5–14.7	1994–2019
Green Island	–0.2	–2.3–1.9	1994–2019

Muskeget), the creation and management of lands as wild-life refuges (Nomans Land, Monomoy Island, Seal Island, Great Point, and Matinicus Rock), and the cessation of U.S. Naval bombing practice (Nomans Land and Seal islands). Seal and Nomans Land islands are closed to the public due to unexploded ordnance. Wooden Ball and Green islands are privately owned and uninhabited. The recovering gray seal population has benefited from the availability of these relatively uninhabited areas.

The gray seal pupping season occurs over a 6-week period so there is not a single day during the season when all pups are available for observation. The data presented here and used in the trend analysis are the minimum number of pups born and not total pup production, which would be higher. We restricted our dataset of single-day counts to include only those surveys that were conducted during the presumed peak pupping period and had sufficient coverage of pupping sites. However, we recognize that the “true” number of pups may have been higher each year if additional pups were born after a survey was conducted. We also assumed the breeding phenology at all pupping sites followed that of Muskeget, because we have the longest time series of data for Muskeget and in some years, multiple surveys per season to document when peak pupping occurs. Multiple surveys within a season are needed at other pupping sites to validate this assumption.

Many marine animal populations around the world are reported to be increasing as a result of a reduction of human impacts and habitat loss, combined with favorable life history and environmental conditions (Lotze et al. 2011). These conditions also contributed to gray seal recovery in the Netherlands (Brasseur et al. 2014) in a similar time frame to that at U.S. sites. For Muskeget Island, the oldest and largest pupping colony in the United States, we demonstrate an increase in gray seal pupping over a 30-year period, 45 years after implementation of the U.S. Marine Mammal Protection Act. Gray seal recolonization in the United States is a conservation success story and exemplifies the important combination that a healthy source population, dispersal propensity, protection from harassment or hunting, and the availability of habitat play in species recovery.

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