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HARP, HARBOR AND GRAY SEAL STRANDINGS IN THE GULF OF MAINE:

A RETROSPECTIVE SOCIO-ECOLOGICAL ANALYSIS

By

Holland Haverkamp

B.A. Brooks Institute of Photography, 2005

A THESIS

Submitted in Partial Fulfillment of the

Requirements for the Degree of

Master of Science

(in Ecology and Environmental Sciences)

The Graduate School

The University of Maine

August 2020

Advisory Committee:

Kristina Cammen, Assistant Professor of Marine Sciences, Advisor

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Thesis Advisor: Dr. Kristina Cammen

An Abstract of the Thesis Presented
in Partial Fulfillment of the Requirements for the
Master of Science
(in Ecology and Environmental Sciences)
August 2020

Over the past several decades, the Gulf of Maine (GOM) has experienced significant socio-ecological change. Extreme climatic variation increases in human population, and visitation of coastal areas have significantly impacted coastal ocean health and redefined multispecies ecologies. While pinniped populations in the Northeast United States have generally grown following federal protection, they have also experienced multiple mortality events over the past two decades. Long-term datasets from marine mammal stranding networks represent a valuable resource for investigating trends in marine mammal health during this period of change. Here, I evaluated potential drivers of marine mammal strandings using data collected from stranded harbor (*Phoca vitulina*), harp (*Pagophilus groenlandicus*) and gray (*Halichoerus grypus*) seals from 2002 to 2017 in Massachusetts, New Hampshire and Maine. I tested for spatio-temporal correlations between stranding density and potential social (e.g., population density) and environmental (e.g., sea surface temperature, North Atlantic Oscillation, snowfall and sea ice extent) factors. Our models reveal significant effects of location and human population density on stranding rates across species—signifying that, even after correcting for reporting effort, pinnipeds are more likely to strand near more densely populated human epicenters in the GOM—as well as species-

specific relationships with some environmental factors. These analyses increase our understanding of the circumstances that lead pinnipeds to strand in the Gulf of Maine and provide context within which these species may serve as sentinels of coastal ocean health.

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INTRODUCTION

Pinniped abundance and distribution are influenced by a variety of human-related and environmental factors; however, accurately describing these trends can be difficult, costly and time consuming as these species spend much of their time at sea (Meager & Sumpton, 2016). Long-term data collected by marine mammal stranding response programs can be leveraged to help address these knowledge gaps. Stranding data can offer demographic (Mannocci et al., 2012) and species diversity information (Pyenson, 2011) that is often lacking in landscape ecology studies¹, thereby enriching our understanding of both species abundance and distribution as they vary over time and space. Spatio-temporal patterns of strandings can also provide valuable insight into the varied and interacting factors that influence when, where and why marine mammals strand.

This type of information can be valuable to agencies involved in marine mammal management and conservation, as a means to anticipate shifts in marine mammal populations (Laidre et al., 2015), whether driven by human causes, environmental change, or a combination of the two. Climate change related range shifts have been observed in many marine mammal populations (Clarke et al., 2013; Hamilton, Lydersen, Ims, & Kovacs, 2015; Ijsseldijk et al., 2018), and it is predicted that as the climate progressively changes, these influences will be more widespread. Marine mammals are widely recognized as indicator species for ocean—and therefore global—health (Simeone, Gulland, Norris, & Rowles, 2015). They are considered sentinel organisms because they have long life spans, feed at high trophic levels, have extensive

¹ Studies in landscape ecology focus on the patterns and interactions between ecosystems within a region of interest, as opposed to individual species or ecological processes.

fat stores and they accumulate anthropogenic toxins (Reddy, Dierauf, & Gulland, 2001). They are also conspicuous (generally), and hold charismatic value to humans; therefore, they are more likely to be observed (Bossart, 2011). As climate-induced changes to environmental health continue, the potentially negative effects on marine mammals, such as epizootic disease outbreaks, can serve as bellwethers for not only ocean health, but also human health (Bossart, 2011).

Previous studies have found that stranding densities can be predicted in part by environmental and ecological factors. Studies of stranded pinnipeds, as well as cetaceans, have found correlations of stranding density with oceanic conditions, such as sea surface temperature (Ijsseldijk et al., 2018; Macleod et al., 2005), sea ice extent (Johnston, Bowers, Friedlaender, & Lavigne, 2012; Soulen, Cammen, Schultz, & Johnston, 2013), El Niño and La Niña (Colegrove, Greig, & Gulland, 2005; Hanni, Long, Jones, Pyle, & Morgan, 1997), and the North Atlantic Oscillation (Pierce, Santos, Smeenk, Saveliev, & Zuur, 2007; Truchon et al., 2013). Prado et al. (2016) found that strandings along the east coast of South America were strongly correlated with seasonality, and they theorized this was an indirect result of fishing effort impacting cetaceans and post-reproductive dispersal among otariids. However, numerous studies have also found that variation in stranding frequency and distributions can at least partially be explained by reporting effort, as this can vary between years and response agencies (Gulland & Hall, 2007; Papastavrou, Leaper, & Lavigne, 2017; Savenkoff et al., 2007).

Although several studies have used strandings data to analyze abundance and distribution of seals in the US Gulf of Maine (Harris & Gupta, 2006; McAlpine, Donald F., Stevick, Peter T., Murison, 1999; Soulen et al., 2013; Stevick & Fernald, 1998), few have looked at the

interconnectedness between anthropogenic and environmental factors influencing when and where seals strand. Here, I use generalized additive mixed models (GAMMs) to analyze the harbor (*Phoca vitulina*), harp (*Phoca groenlandica*) and gray seal (*Halichoerus grypus*) stranding record in the Gulf of Maine from 2002-2017 to better understand how anthropogenic and environmental factors, specifically human population, sea surface temperature, the North Atlantic Oscillation, snowfall and sea ice extent in the Gulf of St. Lawrence, influence seal stranding patterns. Our findings, that pinniped strandings in the Northwest Atlantic are observed most frequently at human population epicenters, independent of reporting effect, and that sea surface temperature and the North Atlantic Oscillation may have some predictive power, provide insights that are relevant to marine mammal policy.

Study area and species

Bordered by Cape Cod, Massachusetts to the south and Nova Scotia, Canada to the north, the Gulf of Maine (GOM) is a biogeographically distinct province (Byrd et al., 2014). Topographical features, temperature gradients, and ocean currents that limit recruitment and affect mortality define marine biogeographic boundaries that are known to have long-term influences on phylogeography and species diversity within their environments (Wares, Gaines, & Cunningham, 2001). These environmental discontinuities can have long term impacts on the ecological landscape. In the Gulf of Maine, Georges Bank, the Scotian Shelf and the Eastern Maine Coastal Current create environments that are biologically rich, creating what have been, historically, productive fishing grounds for marine mammals and humans alike.

Concomitant to the long-term effects of these biogeographic features are the relatively recent—but potentially highly impactful—effects of socio-ecological stressors, such as

anthropogenic climate change, which also influence the ecology in the Gulf of Maine. Sea surface temperature (SST) in the Gulf of Maine is increasing at one of the fastest rates globally (Pershing et al., 2016), and alteration of SST phenology has extended the summer season by as much as two days per year over the last thirty years (Thomas et al., 2017). Extent of sea ice in the Gulf of St. Lawrence has decreased significantly over the last several decades (Ruest et al., 2015), directly affecting the ecological landscape in the Gulf of Maine through shifts in the timing of seasonal migrations. The North Atlantic Oscillation (NAO), which has been shown as a driver of a rapidly changing climate (Delworth et al., 2016), has undergone marked variability over the last 4 decades (Li, Sun, & Jin, 2013). Simultaneously, tourism in the region has continuously increased, particularly in the summer months, bringing waves of people to already contested coastal landscapes, where a legacy of fisheries and other maritime industries are in a state of flux.

This region, which comprises over 4,000 kilometers of coastline, including inlets and islands, encompasses all breeding habitats of harbor and gray seals in US Atlantic waters (Figure 1). The southeastern half of this region is made up of sandy coastline and substantial human development, whereas the northeastern half consists of mostly rocky shores and is considerably more rural. Dense human population centers include Boston, Massachusetts and Portland, Maine. Active maritime industries and tourism dominate much of the coastal landscape, as well as the nearshore waters. Both fisheries and tourism experience strong seasonal trends. For example, Acadia National Park (in Downeast Maine) brings in over 2.5 million visitors per year, predominantly in the summer months. Cape Cod, Massachusetts experiences similar trends. In addition to impacting the potential levels of reporting by the

public, these strong fluctuations in the phenology of human activity in these environments directly influence the local ecology, including the local pinniped populations.

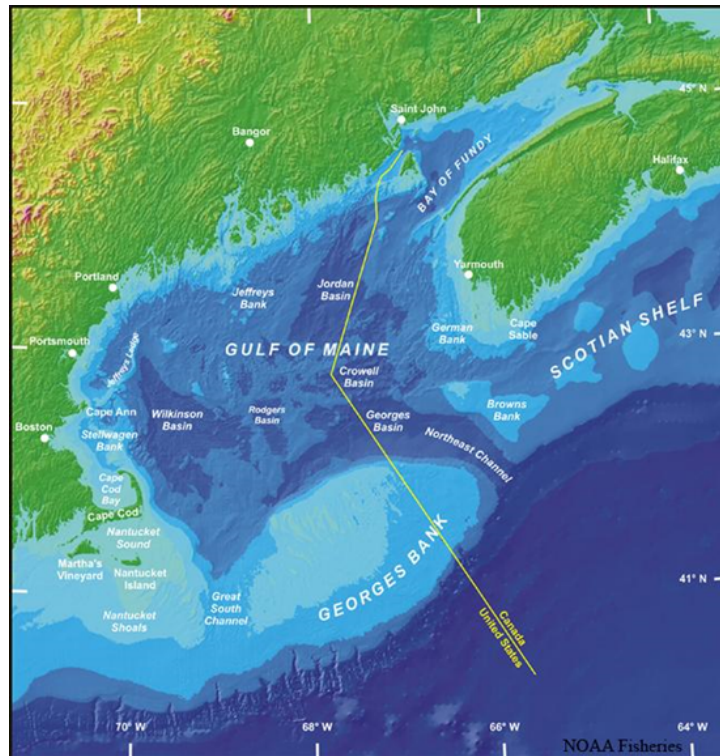


Figure 1. Map of the Gulf of Maine, including border between US and CA.

Harbor seals

Harbor seals, the most abundant pinniped species in the GOM, inhabit the coastal waters of Eastern Canada and Maine year-round, but their numbers generally increase from spring through autumn when thousands migrate to the Northeastern US (Katona, Richardson, & Rough, 1993). It is during this time, from mid-April to mid-June, when adult females seek out protected areas to give birth to their pups. As autumn approaches, the seals migrate south to the Cape Cod region, with hundreds to thousands going as far as North Carolina. This migration then reverses in spring, and the harbor seals come back to Maine, New Hampshire and Eastern Canada to spend the summer. During the late 1800's and well into the 1900's, harbor—as well as gray—seal bounties caused the populations to be severely depleted, and even extirpated in

several localities. Lelli, Harris and Aboueissa (2009) estimate that roughly 40,000 seal bounties were collected during the late 19th and early 20th centuries. It was not until after these bounties were lifted, and the US Marine Mammal Protection Act (MMPA) was passed, that these populations rebounded (Roman et al., 2013).

harbor seal abundance in Maine increased by 5.5% year⁻¹ after the passage of the MMPA, with the majority of that increase being pups, which increased from 6.4% of the population in 1981 to 24.4% of the population in 2001 (Gilbert, Waring, Wynne, & Guldager, 2005). As abundance has increased, so have the number of ledges used during pupping season,

signifying an expansion of distribution during the summer months. More recent population estimates suggest a leveling off or potential reversal of population growth trends from the prior decades. Estimates from an aerial survey conducted in 2012 suggested a decrease in seals from 99,340 in 2001 to 75,834 in 2012 (Waring, DiGiovanni Jr., Josephson, Wood, & Gilbert, 2015). However, variation in methods between the 2001 and 2012 surveys and the lack of more recent data (estimates from an aerial survey conducted in 2018 are pending) have led to uncertainty around the current harbor seal population status.

Gray seals

Gray seals have a more northern distribution than that of the harbor seals, occurring from Nantucket Sound, Massachusetts, as far north as northern Labrador, Canada (Katona et al., 1993). The western Atlantic stock breeds in eastern Canada and the northeastern United States from mid-December to early February. For much of the 20th century, gray seals were nearly extirpated from US waters, largely due to a lack of protection and aggressive bounties (Wood, Murray, Josephson, & Gilbert, 2020). Similarly, in Eastern Canada, gray seal populations

declined to fewer than 10,000 beginning in the late 1800's and persisting until the 1960's (Lavigne & Hammill, 1993). More recently, since the cessation of bounties and implementation of federal protection in US waters, gray seal populations across the Northwest Atlantic have experienced population growth. The population in Eastern Canada reached an estimated size of nearly half a million individuals in 2011, and gray seal populations have grown substantially in abundance in the Gulf of Maine (Hayes, Josephson, Maze-Foley, & Rosel, 2017). In Maine, haul out sites which were once dominated by harbor seals are now shared with gray seals (Gilbert et al., 2005). Prior to 1993, no gray seals were observed in aerial surveys conducted during harbor seal pupping season, but nearly 2,000 were observed in a 2001 survey.

This shift in species composition has been even more dramatic on Sable Island, Canada, 150 miles off the coast of Nova Scotia. Here, gray seals populations have increased dramatically, and harbor seals have declined to become virtually absent from the colony. Sharks represent a source of natural mortality in this region, specifically on the smaller harbor seals; and the rate of shark-induced mortality increased concomitantly with the decrease in harbor seal abundance during the 1990's (Lucas & Stobo, 2000). However, shark induced-mortality alone is not enough to explain the decrease in harbor seals in Eastern Canada. It is feasible that interspecific competition with gray seals (Hall & Kershaw, 2012; Johnston et al., 2015), which have overlapping diets, could have caused the harbor seals to decline (Pace et al., 2019; Bowen & McMillan, 2003). There is evidence that dispersal of gray seals from Sable Island has played a role in the reestablishment of US pupping sites (Pace et al., 2019), and similar instances of harbor seals being displaced by gray seals at beaches and ledges have been observed in the

Northeast US (Pace et al., 2019). However, the increasing trend of gray seals in Sable Island, as well as that in Cape Cod, Massachusetts, has slowed compared to a decade ago (M. O. Hammill, Heyer, Bowen, & Lang, 2017).

Harp seals

The northwest Atlantic harp seal has a complex migration and reproductive cycle. During winter, they breed on pack ice in the Gulf of St. Lawrence and off Labrador, in Canada. As the ice retreats in late spring, the seals advance northwards, arriving in Baffin Island and southern Greenland (Katona et al., 1993). After summer, harp seals then head south again, ahead of the advancing ice. Although it is beyond the range of the larger colonies, individual seals do stray into the Gulf of Maine, and occasionally as far south as Virginia. This population has been commercially harvested since the 1700's (Sergeant, 1991), and concerns over its future was one of the factors that contributed to the adoption of the MMPA (Hammill et al., 2015). The MMPA, combined with a ban on the import of pelts and hunting quotas in Canada (Katona et al., 1993), as well as a shift in policy and attitudes in Canada, caused their population to rise from a low of 1.1 million in the early 1970's to over 7 million in the last decade (Mike O. Hammill et al., 2015). Before 1994, there were no confirmed harp seal sightings in the Gulf of Maine; however, since then, sightings have consistently increased, possibly as a result of range expansion or changing oceanographic conditions (Stevick & Fernald, 1998). It has been shown that harp seals, particularly yearlings, strand more frequently during years of decreased ice cover (Soulen et al., 2013). With sea ice generally breaking up earlier in the year as the global climate warms, pagophilic seals will increasingly spend more time at sea, and it is probable that they will be more frequent visitors to the Gulf of Maine.

Stranding data

In the United States, a national marine mammal stranding network was formed in 1992 as part of the reauthorization of the US Marine Mammal Protection Act (MMPA). This Act broadly aims to maintain marine mammal stocks as functional elements in the ecosystem. Towards this aim, the Marine Mammal Health and Stranding Response Program was created to collect and disseminate data, correlate the health of marine mammals with environmental parameters, and coordinate an effective response to unusual mortality events² (Hofman, 1987; Simeone et al., 2015). In application, a major responsibility of this program is to respond to stranded marine mammals. Under section 401(3) of the US MMPA, marine mammals are considered stranded either when they are dead, or when they are alive and: a) unable to return to the water, b) in apparent need of medical assistance, and/or c) unable to return to their habitat. This policy, by prohibiting any incidental takes (“takes” are defined as: to harass, hunt, capture, or kill, or attempt to harass, hunt, capture, or kill any marine mammal) of marine mammals, is among the most sweeping environmental policies in modern American history, and resulted in significant increases in many marine mammal populations—including harbor, harp and gray seals (Roman et al., 2013). In this study, I aggregated and analyzed the stranding data of harbor, harp and gray seals in Maine, Massachusetts and New Hampshire from 2002-2017, to better understand a) their abundance and distribution over the study period and b) what, if any, environmental and social variables effected where and when strandings were observed.

² An Unusual Mortality Event (UME) is defined under the Marine Mammal Protection Act” as a stranding **event** that is unexpected, involves a significant die-off of any marine mammal population, and demands immediate response.”

METHODS

Stranding data for this study were extracted by request from the Marine Mammal Health and Stranding Response Program's National Stranding Database which includes contributions from 11 organizations in Maine, New Hampshire and Massachusetts. Contributing organizations included (from north to south) the College of the Atlantic's Allied Whale, National Marine Fisheries Service, Maine Department of Marine Resources, Marine Mammals of Maine, University of New England Marine Animal Rehabilitation Center, Marine Animal Lifeline, Seacoast Science Center, New England Aquarium, National Aquarium in Baltimore, International Fund for Animal Welfare, Riverhead Foundation, and the National Aquarium in Baltimore. Contact details for these organizations can be found in Appendix A.

The data that these stranding networks collect varies in both complexity and detail, the most basic being "Level-A Data", a benchmark that is minimally collected for all stranding events. Level-A data include date, species, morphology, health/condition, physical evidence of 'human interaction' and location of stranding. These data detail, to whatever extent possible, the circumstances surrounding the marine mammal stranding. In this study, we analyzed 9,165 records of Level-A data from harbor, harp and gray seal strandings that occurred from 2002 to 2017. Although previous studies have utilized this type of data, this is, to my knowledge, the most extensive analysis of marine mammal stranding data in the Gulf of Maine region to date.

I conducted a hierarchical quality assessment/quality control analysis on the location information associated with the records, as this information was critical to our spatial analysis. Location information for strandings is recorded by town and county name, as well as with latitude and longitude coordinates. These coordinates were first used to plot all points on a

map using ArcGIS or Google Earth. This allowed for a visual inspection of outliers, such as points that were too far from the coast or located outside of the Gulf of Maine. The outliers (n = 121; 1.4% of all strandings) were removed from our analysis. After visual analysis, I then further inspected a random 10% of the records from each species to ensure the coordinates matched the locality information provided. Of the records randomly sampled, fewer than 7% had errors in latitude and longitude coordinates.

When a stranding event is entered into the National Database, an associated confidence code: low, medium, high or unconfirmed, is chosen based on how confident the reporter is in the information provided. Observations with unconfirmed confidence codes (n = 621) were not included in this analysis. Furthermore, any stranding listed with a body condition of 'mummified' (n = 170) was not included, because the temporal scale of the analysis might not accurately reflect the time of death of that seal given its advanced level of decomposition. Finally, a small sample of harp seal strandings from Massachusetts (n = 33) were not included in the analysis because they were sourced as part of another study reported by a scientist carrying out a study on Nantucket Island, rather than by reports to the stranding networks listed above. After these steps, our final dataset consisted of 8,220 observations.

Study Design

The data were aggregated into 5 separate datasets for analysis: harbor seal adults, harbor seal pups, harp seal yearlings, all age classes (AAC) of harp seals and all gray seals. These distinctions were made to better reflect the natural history of each species and age class, with an aim at understanding how and when they strand, as well as how the circumstances of their stranding are affected by social and environmental factors. Harp seals, for example, have very

different seasonal and temporal migratory patterns than harbor seals, and therefore utilize the Gulf of Maine in different seasons and in different areas than harbor seals do. Additionally, these distinctions in datasets were made based on available sample sizes. Gray seals, for example, could not be parsed into separate datasets based on age class because there were too few strandings.

My study area was parsed into 0.2° grids (Figure 2). Although a variety of grid sizes were initially explored (0.05° , 0.1° , 0.4°), this size was ultimately used based on knowledge of the daily behavior of the pinniped species focused on in this study, and the relative size of the inlets, bays and islands along the coastal region in our study area. All analyses were completed at a seasonal time scale where Winter included December, January and February; Spring included March, April and May; Summer included June, July and August; and finally, Fall included September, October and November. From 2002 to 2017 in total, our analysis included 64 seasons for which a seal stranding could be observed in any particular grid box. Grid boxes were only included in the models if there was at least one stranding of that particular species/age class in any given season over the 16-year time period; therefore, the number and location of boxes differ between models. For example, when modelling gray seals, if a certain grid box had 2 records of strandings in Spring 2004, but no other strandings in that grid box over the 16-year study period, then it would receive a 2 for that box in Spring 2004, and 63 0's for the rest of the seasons in that box. Alternatively, if a grid box had no recorded strandings over the 16-year period it was excluded from the model altogether.

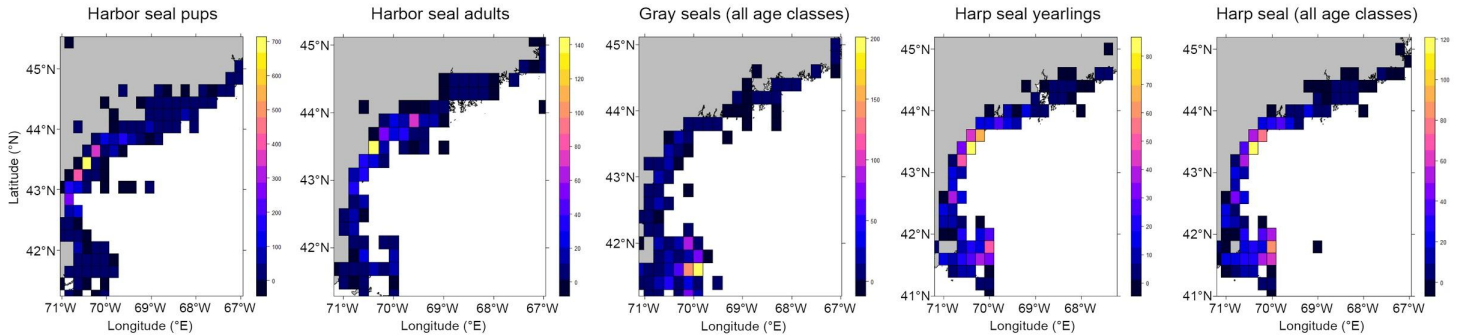


Figure 2. Maps portraying stranding density of five pinniped species/age classes. Study region is in the Gulf of Maine from 2002-2017. Grid size is 0.2°.

Explanatory Variables

Based on a combination of ecological relevance and data availability, covariate exploration yielded inclusion of the following in my analyses: human population density, NAO, SST, previous season SST, snowfall and sea ice extent (Table 1). Latitude and longitude were also included as covariates, and year as a random effect. Variance inflation factors were calculated for all covariates and indicated that correlations between covariates were not a cause of concern, with the exception of longitude and human population, which had a threshold greater than 3 (Zuur, Leno & Elphick, 2010). For this reason, longitude was not included in the models and, instead, human population and latitude were included as an interacting term.

Table 2.1. Explanatory variables. Environmental and social variables utilized in generalized additive mixed models, their source, raw geographic range and raw temporal scale.

Variable	Source	Scale and Resolution (Raw Data)	
		Geographic	Temporal
<i>Environmental</i>			
Sea surface temperature	Satellite Oceanography Data Laboratory, University of Maine	1.1 kilometer	Daily
Sea Ice Cover	NASA Sea Ice Concentrations - Nimbus-7 SMMR and DMSP SSM/I-SSMIS Passive Microwave Data algorithms	Gulf of St Lawrence	Monthly
NAO Index	NOAA Climate Prediction Center	North Atlantic	Monthly
Snowfall	Northeast Regional Climate Center, Cornell University	Variable locations	Daily
<i>Social</i>			
Human population density	US Census Bureau	Coastal towns of ME, NH, MA	Annual

Human population data were procured from the US Census Department, and aggregated by year and by town for all towns that contained at least one stranding over the time series. After correcting town names that were duplicates of each other in the stranding database, but with minor disparities (e.g., Addison vs. Addison Town), there were 253 towns in Maine, 155 in Massachusetts, and 49 in New Hampshire, for a cumulative total of 457 towns in our dataset. Final values used in analysis were the sum of census counts for all towns in a given year in a particular grid box. Where values were missing because a grid box did not contain any towns, an average of nearest neighbor values was used. Nearest neighbors in this case refers to any grid box surrounding the grid box with a missing value, or approximately a circle with a radius of 29km. Population values were converted to a log scale for analyses, to correct for skewness created by large values, such as in Boston, Massachusetts or Portland, Maine.

I utilized NAO index data from the National Oceanic and Atmospheric Administration (NOAA), Climate Prediction Center (“Daily North Atlantic Oscillation Index,” 2002). The NAO index is a measure of the sea-level pressure difference in the North Atlantic Ocean between the Subtropical High and the Subpolar Low. A negative NAO pressure value, which represents relatively small differences between these two pressure gradients, is typically conducive of colder, wetter winters in the Northeast US. This index serves as a proxy for climatic variability over the entirety of the North Atlantic Ocean, and several studies have found significant correlations between it and marine mammal strandings (Evans et al., 2005; Truchon et al., 2013). Furthermore, this cyclical climatic variation has been linked with recruitment of multiple pagophilic seal species (Ferguson, Stirling, & McLoughlin, 2005; Friedlaender, Johnston, Fink, & Lavigne, 2006), positioning it as an important explanatory variable for this study. The standardized anomalies are calculated and collected by NOAA Fisheries, and therefore no further manipulation of the raw data were required for our analysis other than to convert the monthly values into seasonal averages.

NOAA satellite SST data were received, processed and provided by Dr. A. Thomas, Satellite Oceanography Data Lab, University of Maine. Observations were made daily at a spatial scale of 1.1km, and converted into seasonal anomalies to coincide with our study parameters. Nearest neighbors (average of all data points contiguous to the missing value) and nearest-neighbors’ neighbors (average of data points abutting nearest neighbors) were used to fill in missing values, when possible (e.g., missing due to cloud cover). Grid boxes for which SST could not be imputed in this fashion (~1% of grid boxes for the harbor seal pup and adult models) were excluded from the analysis so that sample sizes were equal across all models and

AIC values were comparable. Using a cross correlation function, I identified that the strongest correlation between SST and stranding density in our dataset occurred at a 4-month lag; that is, the probability of a stranding being observed as a function of SST was most affected by values four months before that stranding. For that reason, SST for the season before the observed stranding (“prev SST”) was also included in our models. SST has been correlated with frequency of marine mammal stranding in all parts of the globe and across most marine mammal taxa (Forcada, Trathan, Reid, & Murphy, 2005; Ijsseldijk et al., 2018; Macleod et al., 2005; Truchon et al., 2013).

It has been shown that pagophilic seals occasionally consume snow, presumably for the sake of hydration (Schots, Bue, & Nordøy, 2017), when other forms of freshwater are scarce—potentially situating snow as a limiting resource during harp seal migration. Snowfall data were collected by the Northeast Regional Climate Center of Cornell University. From raw daily snowfall values, I calculated cumulative monthly values in each grid box. In the event a grid box did not have a snowfall value, nearest neighbors and nearest-neighbors’ neighbors were used, as described above. These monthly cumulative totals of snowfall were then converted into monthly anomalies. The three-monthly anomalies in a given season were then averaged to create one seasonal value per grid box.

Hammill et al. (2015) found that poor sea ice conditions result in increased harp seal pup mortality, particularly if a threshold level of 60% decline in sea ice cover is met. Sea ice coverage data used in this study were produced by the US National Sea Ice Data Center in Boulder, Colorado. Given the seasonality of harp seal breeding, pupping and southern migration, only values during the winter and spring were utilized. The sea ice coverage values

were derived from the Defense Meteorological Satellite Program's Special Sensor Microwave Imagers (satellites F8, F11, and F13) for 2002 through 2007 and Special Sensor Microwave Imager Sounder (satellites F16, F17 and F18) for 2008 through 2017. Monthly mean values were used to create seasonal averages, resulting in a single value for 'winter' and a single value for 'spring' which were used in the harp seal models, regardless of which grid box a stranding was observed in.

Model Description

Generalized Additive Mixed Models (GAMMs) were used to analyze the relationship between the frequency of strandings in a grid box (with no observations being a '0', a single stranding in one grid box in one season being a '1', and so on) in a season and the explanatory variables using a tweedie distribution model. A tweedie model was utilized due to its ability to handle a substantial number of 0's in the data (Tweedie, 1984), as is the case in this study since observed strandings can be scarce, particularly in more rural areas or outside of the seals' migratory seasons. GAMMs are a useful tool here because they combine the use of linear mixed models, which incorporate random effects, and generalized linear models, which can handle non-normal data (Bolker et al., 2009). Additionally, this function allows for cross validation, which automatically determines the optimal amount of smoothing, capturing important patterns in the data (Zuur et al., 2009). The full GAMM, evaluated independently for each of five models—harbor seal adults, harbor seal pups, harp seal yearlings, harp seal AAC, and gray seals—included the variables latitude, season, human population, human population:latitude, SST for the current and previous seasons, NAO, and a random effect for year. To account for the time they spend in the GOM (either due to migration patterns or pupping season), harp seal

models (for yearling and all age classes) and harbor seal pup models were limited to two seasons—winter and spring for harp seals, and spring and summer for harbor seal pups. The harp seal models (yearlings and AAC) also incorporated the variables snowfall and sea ice extent. Human population and latitude were included in all models as control variables. Human population in particular was used as a correction term for sighting probability (i.e., observation effort). All modeling was completed using the ‘mgcv’ package in R Studio version 1.2.5 (R Development Core Team 3.0.1., 2013).

‘Year’ was treated as a random effect to account for the effects of episodic or sporadic events that could not be included in our model, such as unusual mortality events (UMEs). 2006, for instance, had nearly three times greater strandings than the average of all years over the study period. During this time, NOAA Fisheries had declared an UME for pinnipeds between Virginia and Maine; in total, an estimated 800 pinnipeds were identified as part of this UME. A similar UME occurred in 2011, affecting 784 pinnipeds in Maine, New Hampshire and Massachusetts. Infectious disease was determined to be the cause in both of these cases.

Modelling within each of the five datasets was done in a stepwise fashion, beginning with a base model (human population:latitude, human population, latitude and year), and then incrementally adding the remaining explanatory variables one at a time and cumulatively until all combinations had been explored. “Deviance explained” (analogous to variance in a linear regression), adjusted R^2 , and Akaike Information Criterion (AIC) scores were calculated. Smoother estimates for the selected covariates were plotted. When the slopes were positive, the covariates were related positively to the dependent variables, suggesting that an increase in the explanatory variable correlates with an increase in stranding density.

RESULTS

From 2002 to 2017, local marine mammal stranding response networks identified and recorded 9,165 stranded harbor, harp and gray seals in the Gulf of Maine between Massachusetts and Maine. Of these 9,165 records, 8,220 were considered viable for this study following the quality control/quality assessment procedures described above. The majority (69.0%) of stranded pinnipeds in our study area were harbor seals (Table 2). The most commonly stranded age class per species were pups (66.0%) for harbor seals, yearlings (69.8%) for harp seals, and adults (31.1%) for gray seals. Males stranded more frequently than females in all species, particularly with the harp seals, where 47.9% were males, 27.4% were females, and 24.8% could not be identified.

Table 3.1. Number, sex, and age class of harbor, harp and gray seal strandings. Study area is Maine, New Hampshire and Massachusetts from 2002 to 2017 (N=8,220).

Species	Total strandings		Sex (%/Species)			Age Class (%/Species)				
	(n)	(%)	Male	Female	Unk. sex	Pup	Yearling	Subadult	Adult	Unk. age
Harbor seal	5,666	69.0	32.2	30.5	38.2	66.0	9.4	4.7	15.1	4.8
Harp seal	1,277	15.5	47.9	27.4	24.8	1.2	69.8	10.8	8.5	9.7
Gray seal	1,277	15.5	41.6	32.3	26.2	24.1	17.1	20.8	31.1	9.9

The frequency of gray seal strandings increased significantly over the study period, from 17 in 2002 to 168 in 2017, whereas the frequency of harp seal strandings decreased significantly, from 89 in 2002 to 36 in 2017 (Figure 3). Harbor seal stranding frequency was relatively flat over the 16-year period, with the exception of in 2004-2006 and 2011 when a

disproportionately high amount stranded due to UME's, which were declared in 2—6 and 2011. Harp seals also saw a spike in strandings around that time, in 2004, and saw a general decline in stranding frequency over the stranding period.

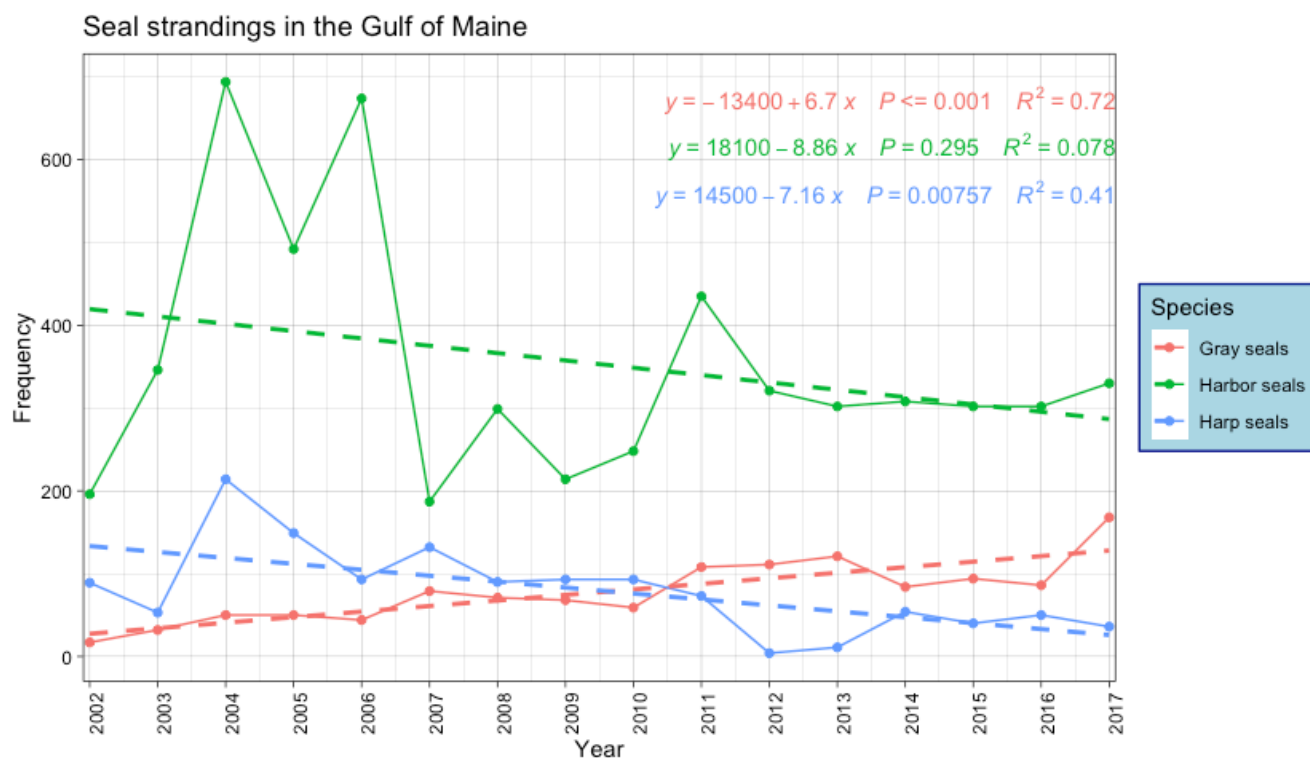


Figure 3. Annual strandings of 3 species of seals in the Gulf of Maine from 2002 to 2017. Dashed lines represent the linear trend for each species.

Final models explained 29.4% to 47.3% of the total deviance in stranding density, with gray seal models explaining the least and harp seal AAC models explaining the most (Table 3). The majority of this explained deviance could be attributed to the four parameters included in the base model for all species and age classes examined here. Total deviance explained in base models, which include human population, latitude, human population:latitude, and year, ranged from a low of 29.4% in the gray seal model to a high of 45.8% in the harp seal AAC model. Year, and the interaction between human population and latitude, were statistically

significant predictor variables in all models. When modeled with the random effect year alone, deviance explained and adjusted R^2 were much lower than the base model, ranging from 2.69% explained in the harbor seal pup model, to 15.4% in the harp seal yearling model.

Table 3.2. Generalized Additive Mixed Model statistics for all models (harbor seal pups, harbor seal adults, gray seals, harp seal yearlings and harp seal all age classes [AAC]). Models included human population density (pop), latitude (lat), the interaction of human population density and latitude (pop:lat), sea surface temperature (sst), sea surface temperature for the previous season (prev sst), North Atlantic Oscillation (nao), snowfall (snow), and sea ice extent in the Gulf of St. Lawrence (ice). Akaike Information Criterion (AIC) scores are presented as differences from the lowest score within each category. Asterisks denote statistical significance ($^{\dagger}<0.1$, $^*<0.05$, $^{**}<0.01$, $^{***}<0.001$). Sample size (n) for each model is the product of the number of grid boxes and number of seasons.

Model	Adjusted R^2	Deviance %	Δ AIC
Harbor seal - pup, n = 4464			
pop:lat ^{***} , pop, lat, year ^{***}	0.178	33.2	269.166
pop:lat ^{***} , pop, lat, sst ^{**} , year ^{***}	0.299	39.7	2.873
pop:lat ^{***} , pop, lat, prev sst ^{**} , year ^{***}	0.299	39.7	3.129
pop:lat ^{***} , pop, lat, nao ^{**} , year ^{***}	0.214	35.0	202.521
pop:lat ^{***} , pop, lat, nao [*] , sst ^{**} , year ^{***}	0.302	39.9	1.242
pop:lat ^{***} , pop, lat, nao [*] , prev sst [*] , year ^{***}	0.302	39.9	0
Harbor seal - adult, n = 4864			
pop:lat ^{***} , pop, lat [*] , year ^{***}	0.140	32.5	3092.914
pop:lat ^{***} , pop, lat [*] , sst ^{**} , year ^{***}	0.266	39.7	14.882
pop:lat ^{***} , pop, lat [†] , prev sst ^{**} , year ^{***}	0.276	39.6	36.574
pop:lat ^{***} , pop, lat [†] , nao ^{***} , year ^{***}	0.168	34.2	2240.95
pop:lat ^{***} , pop, lat [*] , nao, sst ^{**} , year ^{***}	0.266	39.7	10.47
pop:lat ^{***} , pop, lat [†] , nao [*] , prev sst ^{**} , year ^{***}	0.283	39.8	0
Gray seal, n = 4992			
pop:lat ^{***} , pop, lat, year ^{***}	0.157	29.4	0
pop:lat ^{***} , pop, lat, sst [*] , year ^{***}	0.262	37.6	3715.675
pop:lat ^{***} , pop, lat, prev sst ^{**} , year ^{***}	0.266	37.6	3733.675
pop:lat ^{***} , pop, lat, nao, year ^{***}	0.254	37.3	3592.475
pop:lat ^{***} , pop, lat, nao, sst ^{**} , year ^{***}	0.260	37.6	3740.135
pop:lat ^{***} , pop, lat, nao, prev sst ^{**} , year ^{***}	0.265	37.6	3740.855
Harp seal - yearling, n = 2304			
pop:lat ^{***} , pop [*] , lat [*] , year ^{***}	0.362	43.9	0

pop:lat***, pop*, lat*, sst*, year***	0.368	44.2	90.998
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Table 3.2 continued

pop:lat***, pop, lat, prev sst**, year***	0.361	43.9	1.966
pop:lat***, pop', lat, nao***, year***	0.382	45	297.742
pop:lat***, pop', lat*, snow, year***	0.368	44.2	71.929
pop:lat***, pop*, lat*, ice, year***	0.368	43.9	15.128
pop:lat***, pop*, lat*, nao***, sst, year***	0.385	45.2	361.886
pop:lat***, pop*, lat*, nao***, sst, ice, year***	0.385	45.1	361.619
pop:lat***, pop', lat*, nao***, sst, snow, year***	0.385	45.3	432.527
pop:lat***, pop', lat*, nao*** sst, snow, ice, year***	0.384	45.3	429.599
pop:lat***, pop', lat*, nao***, snow, ice, year***	0.38	45.2	377.726
pop:lat***, pop', lat*, snow, ice, year***	0.367	44.1	71.798
pop:lat***, pop', lat*, sst*, snow, ice, year***	0.372	44.4	146.746
pop:lat***, pop', lat*, nao***, snow, ice, year***	0.38	45.2	377.726
pop:lat***, pop', lat*, prev sst, snow, ice, year***	0.366	44.2	81.209
pop:lat***, pop', lat*, nao***, prev sst, snow, ice, year***	0.38	45.2	380.506
Harp seal AAC, n = 2464			
pop:lat***, pop, lat**, year***	0.405	45.8	0
pop:lat***, pop, lat**, sst**, year***	0.412	46.1	105.721
pop:lat***, pop, lat, prev sst, year***	0.403	45.9	5.894
pop:lat***, pop, lat, nao***, year***	0.423	47.1	475.637
pop:lat***, pop, lat, snow, year***	0.408	46.1	117.457
pop:lat***, pop, lat**, ice, year***	0.404	45.9	8.4
pop:lat***, pop, lat**, nao***, sst, year***	0.424	47	448.873
pop:lat***, pop, lat**, snow, ice, year***	0.406	46	60.538
pop:lat***, pop, lat**, prev, snow, ice, year***	0.405	46	66.331
pop:lat***, pop, lat**, sst**, snow, ice, year***	0.413	46.3	169.354
pop:lat***, pop, lat*, nao***, sst, snow, ice, year***	0.423	47.3	555.619

Although the environmental variables often showed significant impacts on the probability of observing a stranded seal, their effect size was relatively small (Table 4). The environmental variables that increased the total deviance explained by the greatest amount

when added to the base model were SST and previous SST, which increased deviance by 6.5%, 7.2% and 8.2% in the harbor seal pup, harbor seal adult and gray seal models, respectively. These, along with NAO in the gray seal model, which increased total deviance explained by 7.9%, were the only environmental variables that were, perhaps, biologically relevant. However, NAO was not statistically significant in the gray seal models.

In the harbor seal pup model, both SST and previous SST predicted a doubling of stranding density, from 0.5 to 1.0 stranding per grid box per season, when temperatures increased from 0°C to 3°C warmer than the seasonal average (Figure 3). By contrast, the density of harbor seal adult strandings peaked at an SST anomaly of 0°C, and decreased three-fold (from 0.15 to 0.05 strandings per grid box per season) as the average seasonal SST increased or decreased by 3°C. When analyzing with SST for the previous season, the trend was similar but the peak was at 1.5°C, as well as when SST approached -3°C. Gray seals response to SST appeared minimal; from -3°C to 3°C, stranding density increased from 0.0 strandings to 0.03 strandings—a very small magnitude. With prev SST, stranding density increased from 10 strandings at -3°C to 15 strandings at 0°C, and then decreased again to 5 at 3°C.

Among the harp seal yearling and AAC models, the only environmental variable that explained more than 0.3% was NAO, at 1.1% and 1.3% respectively. The relationship between harp seal stranding density and NAO was bimodal: higher stranding densities were found at index values of -0.6 and 0.6 (Figure 3). Harbor seal pup and adult strandings were not correlated strongly with NAO; the deviance explained by those parameters was 1.8% and 1.7%, and the confidence intervals were relatively wide.

Table 3.3. R^2 (adjusted) and deviance explained for 5 species/age classes of observed pinniped strandings in the Gulf of Maine from 2002-2017. Base model includes human population:latitude, human population, latitude and year as explanatory variables. Additional explanatory variables equate to the base model plus that covariate alone. Deviance explained values in SST, previous SST, NAO, snowfall and sea ice extent columns are in addition to the value in the base model.

Species	Base model		SST		Previous SST		NAO		Snowfall		Sea ice extent	
	Dev %	Adj. R^2	Δ Dev %	Adj. R^2	Δ Dev %	Adj. R^2	Δ Dev %	Adj. R^2	Δ Dev %	Adj. R^2	Δ Dev %	Adj. R^2
Harbor seal pups	33.2	.178	6.5	.299	6.5	.299	1.8	.214	na	na	na	na
Harbor seal adults	32.5	.140	7.2	.266	7.1	.276	1.7	.168	na	na	na	na
Gray seals	29.4	.157	8.2	.262	8.2	.266	7.9	.254	na	na	na	na
Harp seal yearling	43.9	.362	0.3	.368	0.0	.361	1.1	.382	0.3	.368	0.0	.368
Harp seal AAC	45.8	.405	0.3	.412	0.1	.403	1.3	.423	0.3	.408	0.1	.404

The model that explained the greatest deviance in seal stranding densities was the harp seal AAC model that included human population, latitude, and their interaction, year, SST, NAO, snowfall and sea ice extent in the Gulf of St. Lawrence. However, at 47.3% deviance explained, this is only 0.2% more than that same model without sea surface temperature, snowfall and sea ice extent. Based on AIC scores alone, “best” models were as follows:

- Base model plus prev SST and NAO for harbor seal pups (AIC 8897) and adults (AIC 6999)
- Base model for gray seals (AIC 6540), harp seal yearlings (AIC 5624) and harp seal AAC (AIC 4163).

For the harbor seal models, the base model plus prev SST and NAO also explained the greatest deviance. In the gray seal models however, utilizing either SST, prev SST, NAO, or a

combination of them yielded an extra ~8% deviance explained and a ~0.11 increase in the adjusted R^2 value. Using AIC scores to choose the “best” model, despite having a lower effect size, is reflective of the optimal tradeoffs between bias and variance (Richards, 2005). Thus one should decide which model(s) is an oversimplification of the system, and which are too uncertain due to the additional parameters (Burhnam & Anderson, 2002). Importantly, Burhnam and Anderson (2002) note that this rationale of minimizing bias and variance is a statistical concept and not necessarily reflective of a biological [ecological] reality.

The highest density of strandings were observed across all models at the latitudes where human populations were high (Figure 3). The highest density of harbor seal pup and adult strandings occurred at a latitude of 43.5° , the location of Portland, Maine, when the population in a grid box was approximately 100,000 people. Gray seals also exhibited a narrow peak of high density strandings located further to the south at latitude 42° , in Cape Cod, Massachusetts, where the population in a grid box was about 10,000. Harp seals exhibited a bimodal distribution of peak stranding density, with a strong peak in the Portland, Maine region and a somewhat lesser peak in the Massachusetts region. They also exhibited a unique pattern of stranding density centered at latitude 43.5° , in which density was markedly high as population increased in a cone-like shape that became more broad and diffuse as population increased, signifying that at those higher population values latitude is not as strong a factor.

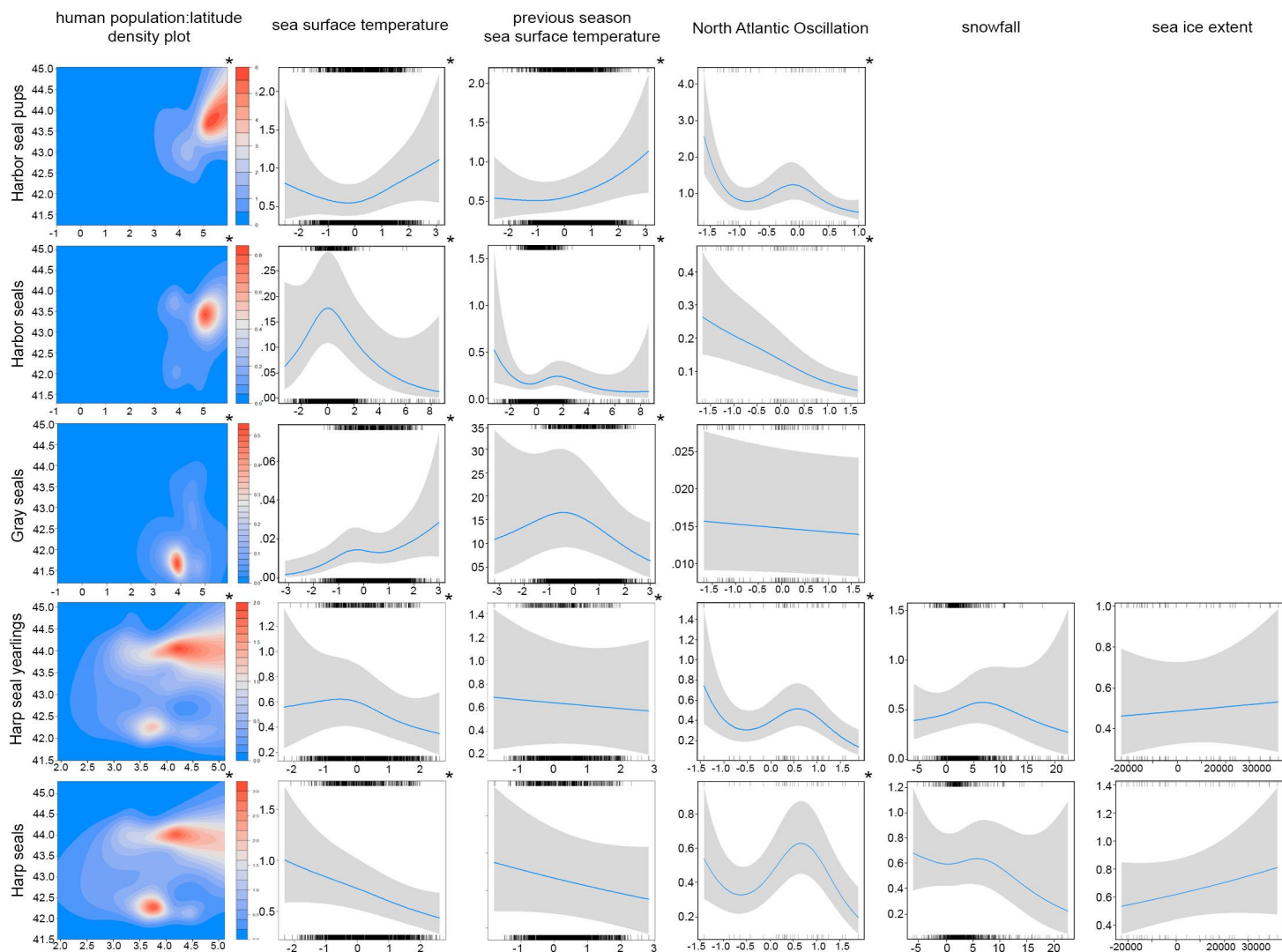


Figure 4. Density maps and smoother estimates of pinniped strandings and covariates. Density maps (left) are of the interaction between human population (log scale) and latitude of stranded pinnipeds. Smoother estimates (solid lines) are for the environmental predictors of sea surface temperature, North Atlantic Oscillation, snowfall and sea ice extent as obtained by generalized additive mixed models (GAMMs) for stranded pinnipeds. Each covariate smoother was chosen from the model that included the base model plus that individual covariate only. The approximate 95% confidence envelopes are indicated (gray shading). * in the top right corner of variables signify that they are statistically significant. Hash marks on bottom of plots represent observations with positive residuals, and those on the top are observations with negative residuals.

Snowfall and sea ice extent in the Gulf of St. Lawrence were only utilized in the harp seal AAC and harp seal yearling models. The harp seal AAC models generally exhibited a linear increase in expected strandings as sea ice extent increased, whereas the harp seal yearling

models were relatively flat (Figure 3). Both had large confidence intervals (CIs), in which 95% of the density in strandings was expected to occur (Nakagawa & Cuthill, 2007). In the harp seal yearling and harp seal AAC models, neither sea ice extent nor snowfall showed substantive predictive power on stranding density.

DISCUSSION

A tale of two species: seals and humans

This study utilized harbor, harp and gray seal strandings data to investigate spatial and temporal occurrence patterns in the Gulf of Maine over a 16-year period. It further identified potential links between stranding events and both anthropogenic and environmental conditions using GAMMs. Our results illustrate the influence of the interaction between human population density and latitude on stranded seal density. In all models, this relationship explained more than any other available explanatory variable, including SST, NAO, snowfall, and sea ice extent. Neither population nor latitude alone explained nearly as much variability as their combined interaction. From this interaction, I can infer that seals are not only stranding more frequently in specific geographic regions simply because of where they are, but because of how the landscape is being utilized by humans. I propose here two hypotheses as to why seals strand, or why stranded seals are more frequently observed, near more densely populated centers.

First, when more humans are present there is an increased likelihood that a stranded seal will be observed (reporting effect), simply because there are “more eyes on the beach.” This theory is consistent with our study findings, considering that observations of stranded seals were significantly higher in areas surrounding the urban centers of Portland, Maine and Cape Cod, Massachusetts and significantly lower in more rural areas, specifically in Eastern Maine. However, to help correct for this observer bias in data analysis, human population density was also included as an explanatory variable in all models. As a linear correction term, human population should correct for increased observation as it relates to higher population levels. Yet

still, the interacting term of human population and latitude was a significant predictor of seal strandings. If population alone had the same level of influence on stranding observations, the density plot in Figure 2 would have been a gradient with density increasing from left to right. Similarly, if latitude had the same level of influence, the density plots would have a gradient of more frequent strandings across all population values at those latitudes where strandings were most frequently observed.

A second hypothesis proposed here on the link between human population, latitude and observed seal strandings is that human activities are leading to, or at least influencing, when and where a seal strands. This interaction term signifies that there are more strandings on a per capita basis in specific areas. That is to say, if you are on the coast in one of the stranding hotspots, you are more likely to observe a stranded seal than if you go to the coast in an area where fewer strandings have been observed. This may seem obvious, but it is an important distinction—that there are not simply more people in more urbanized areas to observe stranded seals; there are, instead, a greater number of stranded seals to observe. This line of inquiry is well supported in both the academic literature (Barcenas-De la Cruz, DeRango, Johnson, & Simeone, 2017; Moore et al., 2013; Truchon, Measures, Brêthes, Albert, & Michaud, 2018) and in the Level-A datasheets created by the stranding response agencies. All Level-A datasheets include the presence/absence of Human Interaction (HI), and when present, these data include a HI Report. Evidence of HI was noted in the Level-A forms for 11.3% (n = 834) of stranded pinniped cases during the study period. Evidence of human interaction is noted only when the response team can reasonably assert that human activities were involved in the stranding, such as when interactions are observed or through physical evidence (i.e. fishing

gear, vessel wounds). This conservative approach to noting human interaction therefore likely underestimates the influence of humans on these seal populations, as there is often no evidence for an observer or professional marine mammal responder to say with certainty whether a marine mammal's stranding was human induced. This is further confounded when multiple factors lead to a seal's stranding, as is often the case (e.g. entanglement in debris leads to poor nutrition, etc.).

It is important to note that the influence of human population and latitude on pinniped strandings in the GOM represents a strong spatial signal in these two coastal regions (Portland, Maine and Cape Cod, Massachusetts). Although the generalizability of these results has not been tested, it is likely that similar findings may be discovered in other coastal human epicenters. The coastal regions of the Northeast US encompass a contested landscape between humans and non-humans. The built environment at the land-sea interface has altered any concept of what was once "pristine." The structure and function of marine ecosystems, as well as their ability to recover from anthropogenic and environmental perturbations, have been altered (Sherman, 2000), especially since colonization and industrialization. Recreation, tourism, resource use and industry have taken humans well beyond the confines of their terrestrial base and into the Gulf of Maine itself. Marine vessels (Vanderlaan & Taggart, 2007; Wilson et al., 2017), noise (Halliday, Insley, Hilliard, de Jong, & Pine, 2017; Koschinski et al., 2003), pollution (Kucklick et al., 1994; Reijnders, 1986; Swart et al., 1994), toxins and debris (Engler, 2012; Simmonds, 2017), and competition for prey (Matthiopoulos et al., 2008; Overholtz & Link, 2007; Read, 2008) are all recognized as potential contributors to declining marine mammal health. These waters, once dominated by marine mammals and other aquatic

organisms are now increasingly shared. In this new ecology, multiple species are inextricably entangled - influencing each other's health and wellbeing, restricting each other's survival and livability, and frequently redefining what it is to be resilient.

Environmental variables

Despite often being statistically significant ($p < 0.05$), many of the environmental variables used in this study are unlikely to be biologically relevant. A doctrine that statistical significance—the ability to reject our null hypothesis—has been given undue importance in the ecological sciences has begun to pervade science (Nakagawa & Cuthill, 2007). Instead, it is far more important to consider the strength of the relationships as indicated by the R^2 coefficients and the deviance explained (Martínez-Abraín, 2008). These statistical metrics are more appropriate for the determination of whether or not an explanatory variable is biologically relevant; and in the case of this study, the R^2 coefficients and the deviance explained were low for most environmental variables across models.

The strength of the anthropogenic factors on expected deviance in seal stranding density are so strong that they may, in part, be overshadowing any impact that the environmental variables have. Both sea ice extent in the Gulf of St. Lawrence (Johnston et al., 2012; Soulen et al., 2013; Truchon et al., 2013) and NAO (Ari S. Friedlaender, Johnston, & Halpin, 2010; Johnston et al., 2012; Truchon et al., 2013) have been correlated with pinniped strandings in other studies. At 7.9%, NAO is, perhaps, relevant in predicting gray seal strandings in our models; however, a very wide CI and higher AIC score (in relation to the other models) signify this may not, in fact, be biologically relevant. Harp seals require ice for successful molting, pupping, nursing and resting; thus a reduction in sea ice is potentially deleterious to

their general health and reproductive success. Yet, my models failed to find that either NAO or sea ice extent had any effect on stranding density. However, I would caution against straightforward thinking and linear causation in this case. Harp seals are adapted to cope with environmental variability and may be buffered against variations in climate (Friedlaender et al., 2010). It is also possible that a loss of sea ice has opened up feeding pathways and increased productivity, both of which could, potentially, benefit seals in the region. Further confounding the relationship, sea ice melting sooner might induce earlier harp seal migration, allowing them to migrate farther than they ever have in recorded history. It may be that they are indeed stranding more frequently as a result of these changing climatic conditions, but the data are masked to the constraints of our study area. Related to this, it is plausible that the high mobility inherent in pinnipeds may allow them to escape adverse environmental conditions by rapidly responding to the effects of climate change or other disturbances (Harwood, 2001) and escape the adverse impacts of a fragmented landscape (Debinski & Holt, 2000).

Harbor pup, harbor adult and gray seal models all reflected an effect of SST on stranding density; SST for the previous season had an even better fit within models than the current season, although only marginally. MacLeod et al. (2005) found that warming waters lead to a decline in cold water marine mammal species and an increase in warm water species. Although their study was limited to dolphins and porpoises, this hypothesis would be consistent with this study, as SST appears to be linked to harbor and gray seal strandings. It is also notable that harp seal stranding observations have decreased over the study period, in line with increased sea surface temperatures. Similarly, Ijsseldijk et al. (2018) contribute shifts in white-beaked dolphin distribution in the North Sea coast at least partially to anthropogenic climate change and its

concomitant effects (habitat suitability, prey distribution and prey availability). The effect of warming waters in the GOM on harbor and gray seal strandings cannot be analyzed in a vacuum, as these effects are inextricably linked with anthropogenic forcings, namely a changing climate – a reflection of a human population ruled by a global, capitalist market.

Although marine mammal distributions may be influenced by oceanographic and environmental variables, such as those utilized here, it is often believed that marine mammals do not respond to them directly (Palacios, Baumgartner, Laidre, & Gregr, 2014), if at all. Many factors: prey availability, socializing, site fidelity, interspecies competition, direct removal (i.e., sealing), bycatch, etc., all may be indirectly influenced by environmental conditions and phenomena. Thus, these variables can be difficult to measure and model. Further complicating things is that, in marine ecosystems, predictor variables measured in the ‘present’ are often the manifestation of the past (Olson, 2002), or perhaps situated in the present and multiple pasts, potentially resulting in spatial and temporal mismatch (Grémillet et al., 2008). All of these interactions will lead to reduced explanatory power.

Stranding data: a cautionary tale

Marine mammal stranding data have the potential to be highly valuable to aid in our understanding of threats to individuals (e.g., entanglement), populations (e.g., epizootic disease outbreaks), and ecosystems (e.g., climate changes). Yet, it is important to note that there are numerous challenges and potential issues with using strandings data for scientific research. The consistency of data can vary widely over time; it is opportunistic, making it vulnerable to reporting bias (Harris & Gupta, 2006). The coastline in the Northeastern US is extensive, and thus stranding networks rely substantially on public reporting and trained volunteers.

Additionally, it is not uncommon for stranding networks to change protocols over time, particularly as staff and volunteers change (Harris, Lelli, & Jakush, 2002), which can also lead to inconsistency, non-standardized protocols, and spatial or temporal gaps in reporting. “Carcass drift” can result in a carcass being discovered far away from where the original mortality event occurred (Peltier et al., 2014), if at all (Williams et al., 2011), creating ambiguity in both time and location, and sometimes cause of death. Finally, public reporting of animals on the beach may not be stranded at all, but could simply be resting, pupping or molting animals, leading to potential over-representation of observed strandings, particularly in populated areas. Despite these challenges, strandings provide a unique dataset that would otherwise be difficult and costly to collect. These data, when continuously collected—as is the case with the data used in this study—achieve high temporal and spatial resolution, yielding an invaluable resource to better understand the spatio-temporal patterns in marine mammal distribution and behavior, as well as how marine mammals are influenced by anthropogenic and environmental factors.

As existing and emerging risks to marine mammals from environmental forcing and anthropogenic activities are realized, conservation and management-driven spatio-temporal models that account for these factors are increasingly salient. This study indicates that, in the GOM, proximity to dense, coastal human population centers is the greatest driver in pinniped stranding density. SST is also biologically relevant in harbor seal pup and adult stranding patterns, as is SST and NAO for gray seals. Future studies might consider more creative approaches to both modeling and methodology, including the use of local wisdoms. As highly migratory species that cross biogeographical and political boundaries, no one stakeholder group alone can fully address their health. Considered together, scientific and traditional

ecological knowledge can bring fresh perspectives. Successful conservation will require communication across a diversity of stakeholders that directly engage with the species (e.g., local and regional governments, indigenous groups, non-governmental groups), as well as continued engagement by federal governments.

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APPENDIX

Appendix A. Marine mammal stranding response organizations

Organization	Address	Phone Number
College of the Atlantic's Allied Whale	105 Eden St, Bar Harbor, ME 04609	(207) 288-5644
National Marine Fisheries Service	130 Oak St, Ellsworth, ME 04605	(207) 664-0508
Maine Department of Marine Resources	32 Blossom Ln, Augusta, ME 04330	(207) 624-6550
Marine Mammals of Maine	P.O. Box 751, Bath, ME 04530	(207) 844-8718
University of New England Marine Animal Rehabilitation Center*	11 Hills Beach Rd, Biddeford, ME 04005	N/A
Marine Animal Lifeline*	New Hampshire	N/A
Seacoast Science Center	570 Ocean Boulevard Rye, NH 03870	(603) 997-9448
New England Aquarium	1 Central Wharf, Boston, MA 02110	(617) 973-5200
International Fund for Animal Welfare	290 Summer Street, Yarmouth Port, MA 02675	(202) 536 1900
Riverhead Foundation	467 E Main St, Riverhead, NY 11901	(631) 369-9840
National Aquarium in Baltimore	501 E Pratt St, Baltimore, MD 21202	(410) 576-3880

*No longer in operation

BIOGRAPHY OF THE AUTHOR

Holland Haverkamp has a professional background in filmmaking and photography, but has long been interested, concerned and passionate about the health of our planet's ecologies, both marine and terrestrial. He is guided by a notion that all life and non-life (should there be such a thing) are intertwined, never acting independently. Holland and his partner have six children, whom create a full and delightfully overwhelming life for them all. He is a candidate for the Master's degree in Ecology and Environmental Sciences from the University of Maine in August, 2020.