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ARTICLE

A retrospective socio-ecological analysis of seal strandings in the Gulf of Maine

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Abstract

Over the past several decades, the Gulf of Maine has experienced significant socio-ecological change. Coastlines have become more densely populated and developed, rapid and dramatic climate change has affected coastal ocean environments, and seal populations have grown as a result of federal protections. Long-term data sets from marine mammal stranding networks represent a valuable resource for investigating indicator species for coastal ocean health during this period of change. 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, we tested for spatiotemporal correlations between stranding density and human population density, size of and proximity to seal haul-outs, sea surface temperature, North Atlantic Oscillation, snowfall, and sea ice extent. We found that in the Gulf of Maine proximity to coastal human population centers and large seal haul-outs are the greatest drivers of reported seal stranding density. Environmental factors played an important role only for harp seals, which do not breed in the study area, although recent shifts in the environmental seascape have the potential to affect all seal species in the Gulf of Maine.

KEYWORDS

gray seal, harbor seal, harp seal, marine mammal stranding, North Atlantic Oscillation, sea surface temperature

1 | INTRODUCTION

Pinniped abundance, distribution, and population health are influenced by a variety of environmental and anthropogenic factors. However, accurately describing the role of these factors through field research programs can be difficult, costly, and time consuming. Long-term data collected by marine mammal stranding response programs can instead be leveraged to improve our understanding of pinniped biology, ecology, and health. Studies of marine mammal strandings can illuminate the causes of morbidity and mortality (Greig et al., 2005; Sepúlveda et al., 2020). Stranding data can also provide insights into marine mammal life history, demography, abundance, and distribution (Early, 1997; Esquible & Atkinson, 2019; Pyenson, 2011). Because marine mammals are recognized as indicator species for ocean health (Gulland, 1999), such studies can serve to identify potential conservation concerns in coastal environments.

In the United States, a national network of organizations authorized by the Marine Mammal Health and Stranding Response Program of the National Oceanic and Atmospheric Administration (NOAA) is responsible for responding to and collecting data from live and dead stranded marine mammals (Becker et al., 1994). Live marine mammals are considered stranded when they are unable to return to the water or their natural habitat, and/or in apparent need of medical assistance. Marine mammals can strand singly or in groups, and large-scale mortality events with elevated numbers of strandings occurring in a given time period or geographic region are termed Unusual Mortality Events (UMEs).

The Gulf of Maine, a region which has experienced significant socio-ecological change in the last several decades, has been the site of several recent and ongoing marine mammal UMEs, attributed to both infectious disease and human interaction (Anthony et al., 2012; Siembieda et al., 2017). This biogeographically distinct body of water located in the Northwest Atlantic Ocean has over 4,000 km of coastline. The southern half of this region is characterized by sandy coastline and substantial human development, whereas the northeastern half is primarily rocky shoreline and considerably more rural and less accessible. Topographical features, temperature gradients, and ocean currents in the region create environments that are biologically rich and that support productive commercial fisheries and a diverse marine mammal community. A network currently comprised of 14 organizations responds to strandings of pinnipeds, cetaceans, and sea turtles in the Gulf of Maine.

Recent changes in the Gulf of Maine ecosystem have been driven by socio-ecological stressors, including exploitation of its natural resources and rapid climate change. Sea surface temperature (SST) in the Gulf of Maine is increasing at one of the fastest rates globally (Pershing et al., 2015), with the summer season being extended by as much as 2 days per year over the last 30 years (Thomas et al., 2017). Also, extent of sea ice in the neighboring Gulf of St. Lawrence has decreased significantly in recent decades (Ruest et al., 2015). Simultaneously, tourism in the region has increased, particularly in the summer months (Maine Office of Tourism, 2020), bringing waves of people to a coastal landscape that is already strained by multiple competing uses, including commercial fisheries, coastal development, ecotourism, and, most recently, marine renewable energy.

Four pinniped species use the Gulf of Maine habitat: harbor (*Phoca vitulina*), gray (*Halichoerus grypus*), harp (*Phoca groenlandicus*), and hooded (*Cystophora cristata*) seals. Harbor seals, the most abundant pinniped species in the Gulf of Maine, inhabit the coastal waters of Eastern Canada and Maine year-round, with the highest numbers observed in spring and summer, during and following their pupping season (Katona et al., 1993). Harbor seals pup on rocky ledges along the coast of Maine with the highest abundance around Penobscot Bay in mid-coast Maine (Gilbert et al., 2005). Gray seals, which are also present year-round, breed in the Gulf of Maine from mid-December to early February, with the largest pupping sites located around Cape Cod, Massachusetts, and smaller sites located on islands off mid-coast Maine (Wood et al., 2020). Harp seals do not breed in the Gulf of Maine, but visit there seasonally, typically during the winter months when aggregations of harp seals breed on pack ice in the Gulf of St. Lawrence and off Labrador in Canada (Katona et al., 1993). Hooded seals, which also breed on pack ice in the Gulf of St. Lawrence and off Newfoundland and Labrador in Canada (Katona et al., 1993) and do not breed in the Gulf of Maine, are infrequently sighted in this region, and are therefore excluded from the present study.

Seals in the Gulf of Maine exhibit a generally shared population history of depletion due to human activities, subsequent regulatory protection, and recent population growth (Hammill et al., 2015; Sigourney et al., 2021; Wood et al., 2020). Historically abundant seal populations were targeted by both commercial hunting and bounty programs in the 1800s and early 1900s (Lelli et al., 2009). Following the implementation of federal protections, harbor seals were the first seal species to recover in the Gulf of Maine, growing at a rate of 6.6% from the 1980s until the early 2000s, when their growth rate slowed to near zero (Gilbert et al., 2005; Sigourney et al., 2021). At present, the abundance of harbor seals in the Gulf of Maine is estimated to be 61,336 (*CV* = 0.08) individuals (Sigourney et al., 2021). In contrast, the gray seal population, which was essentially absent due to extirpation from US waters from the 1970s until the early 1990s, continues to grow at a rapid rate of up to 26.3% at some pupping sites (Wood et al., 2020). Their abundance in the Gulf of Maine is currently estimated to be 27,131 (*CV* = 0.22) individuals (Hayes et al., 2020). There is no current estimate of harp seal abundance in US waters, though the Northwest Atlantic stock, which breeds in Atlantic Canada and is the source of visitors to the Gulf of Maine, is currently estimated to be approximately 7.4 million individuals (Hayes et al., 2020). Similar to the harbor seals, harp seals in this region experienced rapid population growth from a minimum of 1.1 million individuals in the early 1970s to their maximum in 2008 and since then have experienced little population growth (Hammill et al., 2015). Following recovery of the Canadian breeding grounds, harp seal sightings and strandings in US waters have been relatively common since the mid-1990s (Soulen et al., 2013; Stevick & Fernald, 1998).

As might be expected, frequent strandings of harbor, gray, and harp seals along the Gulf of Maine coastline are associated with frequent sightings of these species in this region (Figure

1). Previous analyses have reported over 3,500 strandings of these three seal species along the coast of Maine from 2007 to 2019, with harbor seals representing over 70% of the strandings each year (Newcomb et al., 2021). Similarly, a prior analysis of harp seal strandings reports over 3,000 strandings from 1991 to 2010 along the eastern coast of the US (Soulen et al., 2013). Prior analyses have investigated an isolated set of factors affecting seal stranding rates, including human interaction (Newcomb et al., 2021), sea ice extent (Soulen et al., 2013), human population density, and shoreline characteristics (Harris & Gupta, 2006). Some analyses have also reported significant trends in stranding rates, including an increase in the annual number of gray seal, but not harbor seal, strandings reported in southern New England from 1990 to 2012 (Johnston et al., 2015), and an increase in the reports of seal strandings with human interaction in Maine from 2007 to 2019 (Newcomb et al., 2021). These recent trends in seal strandings, along with recorded shifts in ocean temperature and seasonal phenology (Pershing et al., 2015; Thomas et al., 2017), may be concerning indicators for Gulf of Maine ecosystem health. In this study, we therefore expand upon our prior analysis of seal strandings with human interaction in Maine (Newcomb et al., 2021), to conduct a comprehensive analysis of all harbor, gray, and harp seal strandings throughout the Gulf of Maine that aims to identify environmental correlates of stranding density.

To fully understand when, where, and why marine mammals strand, it is critical to consider the interconnectedness between anthropogenic and environmental factors. Data collected from stranded marine mammals in the US and elsewhere suggest that stranding densities can be predicted, in part, by environmental factors, including SST (for some cetacean species; Ijsseldijk et al., 2018; MacLeod et al., 2005; Warlick et al., 2022), sea ice extent (for harp seal; Soulen et al., 2013), and the North Atlantic Oscillation (NAO) (for hooded seal and both resident and migratory cetaceans; Truchon et al., 2013). However, numerous studies have also found that variation in stranding frequency and distribution can be attributed to variable reporting effort; where more humans are present, there is an increased likelihood that a marine mammal will be observed and reported (Harris & Gupta, 2006; Olson et al., 2020). Here, we used generalized additive mixed models (GAMMs) to analyze harbor, harp, and gray seal stranding records in the Gulf of Maine from 2002 to 2017. With our analysis, we aimed to better understand how anthropogenic and environmental factors, specifically human population size, proximity to seal haul-outs, SST, NAO, snowfall, and sea ice extent, influence seal stranding patterns.

2 | METHODS

2.1 | Stranding data

Stranding data for this study were provided on request from the US Marine Mammal Health and Stranding Response Program's National Stranding Database on August 28, 2018. These data had been collected by multiple stranding response organizations: (from north to south) Allied Whale of the College of the Atlantic, Maine Department of Marine Resources, Marine Mammals of Maine, University of New England, Marine Animal Lifeline, Seacoast Science Center, New England Aquarium, and the International Fund for Animal Welfare. Stranding response activities performed by these organizations spanned, collectively, the entire Gulf of Maine coastline throughout the study period, though stranding response effort and protocols may have varied geographically and temporally, due to variable funding levels, public awareness, and organizational differences.

We analyzed strandings of harbor, harp, and gray seals from 2002 to 2017 in Maine, New Hampshire, and Massachusetts. The data collected for each reported stranding include date, location, species, and age class. Other data such as morphology (length and weight), condition (e.g., sick, injured, abandoned, out of habitat, etc.), and evidence of human interaction are also often collected during stranding response, but are not a focus of the current study. The types of human interaction observed among stranded pinnipeds in Maine during the study period have been previously analyzed (Newcomb et al., 2021). We excluded from our study any reports that lacked sufficient detail and were not confirmed by a trained responder. Furthermore, any stranding listed with a carcass condition of "mummified" was not included, because of the magnitude of uncertainty surrounding the time and location of death given the level of decomposition. The records that remained included confirmed reports of live stranded seals, as well as dead seals that were deemed to be freshly dead or of moderate or advanced decomposition stage.

2.2 | Study design

We first conducted hierarchical quality assessment/quality control on the location information associated with the records, as these data were 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 used to plot all points on a map using ArcGIS or Google Earth, and the maps were visually inspected for outliers, such as points that were too far from the coast or located outside of the Gulf of Maine. Outliers were removed from our analysis. After visual outlier analysis, we further inspected a random 10% of the records from each species per year to ensure the coordinates matched the description of the stranding location.

Following quality assessment/quality control, we created subsets of the data by species, and if the sample size was sufficiently large, by age class, to reflect known differences in natural history. The five age classes present in our data are: pup (includes dependent animals that are still nursing and animals within a few months of weaning); yearling (animals postweaning and ≤2 years); subadult (>2 years old but not yet mature); adult (sexually mature); and unknown. Age class is typically determined by marine mammal stranding responders via visual inspection of the animal or photographs, using information such as teeth and length/age relationships, as well as inspection of reproductive organs when an animal is necropsied. For seals with a known pupping season, time of year is important in distinguishing pups from yearlings.

We report here on analyses of four data sets: harp seals (all age classes), gray seals (all age classes), harbor seal adults, and harbor seal pups. The choice to split harbor seals into two models excluded harbor seal yearlings and subadults, which represent a small proportion (<15%) of the data set but allowed us to investigate different patterns between pups and adults, which had sufficient sample sizes to do so for this species. Sample size limitations precluded subdividing the gray and harp seal data sets by age class.

Strandings were aggregated temporally by season and spatially by assignment to a 0.2° × 0.2° (~22 × 16 km) grid box. This grid box size was deemed appropriate given the relative size of the inlets and islands along the coastal region in our study area and the spatial resolution of our model covariates. A prior study of harp seal strandings in the Gulf of Maine that compared 5 km and 10 km spatial resolution found that the 5 km grid boxes were only more informative for predictor variables that varied over short distances along the coast (Harris & Gupta, 2006), which is not expected for the variables included in our model (Table 1). Furthermore, the typical recorded daily distances traveled by adult and weaned juvenile gray seals in our region exceed our grid box size (Moxley et al., 2020; Murray et al., 2021), suggesting smaller grid boxes could be poor reflections of the seasonal trends in stranding density we aim to model. Published movement data are unavailable for the other seal species in the Gulf of Maine, but our unpublished data from satellite tagging of live capture and rehabilitated harbor seals are consistent with long-distance movement potential. A study of harbor seal movement patterns on the West coast previously reported that daily distances were shorter for wild weaned seals (M = 3.2 km ± 2.0 SD) than rehabilitated seals (M = 6.1 km ± 3.0 SD), but still found that cumulative monthly distances traveled for both groups of seals (range: 52.9–429.3 km) exceeded our grid box size (Gaydos et al., 2012), consistent with its relevance at the seasonal scale we use in our study.

Seasons were defined as winter from December through February; spring from March through May; summer from June through August; and fall from September through November. To account for seasonal patterns of habitat use in the Gulf of Maine, the harp seal model included only winter and spring, and the harbor seal pup model excluded winter, while all other models included all four seasons. Harp seals are rarely observed in the Gulf of Maine during summer and fall. Harbor seal pups are born in late spring and early summer, and would therefore be several months postweaning by winter and considered "yearlings" by our age class definitions. Grid boxes were excluded from the analyses if no strandings of a particular species/age class were observed over the 16-year period; therefore, the number and location of grid boxes differ between models.

2.3 | Analyses

Generalized additive mixed models (GAMMs) were used to analyze the relationship between explanatory variables and the seasonal frequency of strandings in a grid box (stranding density) using a Tweedie distribution model to account for a substantial number of zeroes in the data. All modeling was completed using the "mgcv" package (version 1.2-5) in R (Wood, 2011). For all species, models with ecological and environmental explanatory variables were compared with a base model that included stranding date (season and year) and stranding location (latitude or longitude). Year was included as a random effect to account for variation among years. Every combination of explanatory variables was explored, from the base model with a single additional explanatory variable to a full model with all variables included. The Akaike information criterion (AIC) was used to evaluate the relative fit of each model.

Based on a combination of ecological relevance and data availability, we included the following explanatory variables in our spatiotemporal analyses: human population density, size of and proximity to seal haul-outs, NAO, SST, snowfall, and sea ice extent (Table 1). The latter two were included only in analyses of harp seal strandings. For models with human and seal density, we also tested the addition of an interaction term between these two variables. Variance inflation factors indicated little to no correlation between covariates, with the exception of latitude in the harp seal model and longitude in the gray and harbor seal models. Latitude and longitude were found to be correlated with each other and with human population and seal population. For this reason, only one measure of stranding location, latitude (harp) or longitude (harbor and gray), was included in each model.

Human population density can affect stranding density, either as a result of human interaction (e.g., Goldstein et al., 1999) or as a proxy of observation effort resulting in the likelihood of strandings being reported (e.g., Olson et al., 2020). To assess this relationship within our data set, human population data were procured from the US Census Bureau and aggregated by year and by town for all towns that contained at least one stranding over the time series (n = 457). Annual census counts were summed for all towns within each grid box. Human population values were converted to a log scale for analyses.

Spatial and temporal trends in seal abundance in the Gulf of Maine are also likely to affect seal stranding density. To evaluate this factor, we included a weighted proxy of annual local seal abundance, based on distance from and relative size of local pupping sites, in the models for gray and harbor seals.

This variable was not included for harp seals, which do not breed or haul out in aggregations in the Gulf of Maine. Each harbor and gray seal grid box was assigned a value calculated as the sum of respective seal counts at each major colony in the study region times the inverse of the distance from the colony to the respective grid box. Distance was calculated as the shortest path not crossing land using the *gridDistance* function of the "raster" package in R (Hijmans, 2022), implemented on a 100 × 100 blocked raster layer created from a Gulf of Maine shapefile. Seal abundance values were converted to a log scale for analyses.

Annual observed gray seal pup counts were included from breeding colonies that have been consistently surveyed throughout the study period (Massachusetts: Muskeget and Monomoy Islands; Maine: Green and Seal Islands) (Wood et al., 2020). When pup counts were not available for a colony in a given year, the value was inferred from a prior survey count using site-specific annual rates of increase. Harbor seal pupping is more widely distributed along the coast of Maine, and data from prior aerial surveys have been aggregated by geographically defined bay units that include multiple ledges with observed pupping (Gilbert et al., 2005; Sigourney et al., 2021; Waring et al., 2015). Annual counts of harbor seals are not available throughout the study period, so we estimated annual abundance from pup (for harbor seal pup model) and nonpup (for harbor seal adult model) Bayesian models that were parameterized using data from surveys in 1993, 1997, 2001, 2012, and 2018 (Sigourney et al., 2021).

The North Atlantic Oscillation 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 (e.g., Truchon et al., 2013) and recruitment (Johnston et al., 2005). To assess the effect of the NAO on stranding frequency in the Gulf of Maine, we utilized NAO index data from the NOAA Climate Prediction Center. The NAO index is reported as a standardized anomaly, which we converted from monthly values into seasonal averages. 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 value, which represents relatively small differences between these two pressure gradients, is typically conducive of colder, wetter winters in the Northeast US, but less sea ice on harp seal breeding grounds in Canada. A positive NAO value is typically associated with more sea ice in Canada and milder winters in the Northeast US.

Warming waters have previously been correlated with shifts in marine mammal distribution as assessed through the stranding record and attributed to the effects of climate change on habitat suitability and prey availability (Ijsseldijk et al., 2018; MacLeod et al., 2005; Truchon et al., 2013). We assessed the impact of SST on seal stranding density using daily NOAA SST data acquired from the NOAA Earth System Research Laboratory (hhtp://www.esrl.noaa.gov/psd/). Daily observations were converted into seasonal anomalies to coincide with our study parameters. Using a cross correlation function (CCF), we identified that the strongest correlation between SST and seal stranding density occurred at a 4-month lag, so we included SST for the season prior to the observed stranding in our final models.

It has been shown that pagophilic seals occasionally consume snow, presumably for the sake of hydration (Gales & Renouf, 1993; Schots et al., 2017), when other forms of freshwater are scarce—potentially situating snow as a limiting resource during harp seal migration. We therefore assessed the impact of snowfall on harp seal stranding density using snowfall data collected by the Northeast Regional Climate Center of Cornell University. From raw daily snowfall values, we calculated cumulative monthly values in each grid box. These monthly cumulative totals of snowfall were then converted into monthly anomalies and seasonal averages.

Finally, sea ice extent is also an important factor determining juvenile survival, migration timing, and thus stranding rates of pagophilic seals, particularly yearlings (Soulen et al., 2013). Specifically, sea ice in the Gulf of St. Lawrence is an important pupping substrate for the harp seals that visit the Gulf of Maine (Katona et al., 1993). We assessed the impact of sea ice extent in the Gulf of St. Lawrence on harp seal stranding density using data from the US National Sea Ice Data Center in Boulder, Colorado. 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 for each year of our study.

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 for all explanatory variables, when possible. Grid boxes for which values could not be imputed in this fashion were excluded from the analysis so that sample sizes were equal across all models within a given data set and AIC values were comparable.

3 | RESULTS

From 2002 to 2017, a total of 8,545 stranded harbor, harp, and gray seals were reported along the US coastline of the Gulf of Maine (Figure 1). Following quality control/quality assessment procedures, 8,167 records were retained for our analysis. Of the 10% of records randomly sampled to check for agreement between geospatial coordinates and stranding location descriptions, fewer than 7% appeared to have errors in latitude and longitude coordinates.

The majority (68.9%) of stranded seals in our study area were harbor seals (Table 2). The most commonly stranded age classes per species were pups (66.1%) for harbor seals, yearlings (70.0%) for harp seals, and adults (32.0%) for gray seals. Males stranded more frequently than females, particularly among harp and gray seals, though sex was not identified for over a quarter of the strandings for each species. This trend was observed across both younger and older age classes for harp and gray seals.

The annual number of gray seal strandings increased over the study period, whereas harp seal strandings showed the opposite trend, declining particularly during the middle of our time period (Figure 2). The number of harbor seal strandings each year was relatively consistent during the 16-year study period, with the exception of peaks in 2004–2006 and 2011 during large-scale mortality events attributed to outbreaks of influenza A virus and phocine distemper virus (Anthony et al., 2012; Siembieda et al., 2017). A spike in strandings was also observed for harp seals in 2004.

The best (i.e., top five based on Akaike information criterion, AIC) models for each species and age class explained 28.2% to 38.0% of the total deviance in stranding density (Table 3). In all species and age classes, stranding location (latitude or longitude) and year were significant explanatory variables. Season was also a statistically significant explanatory variable in all models for harbor and gray seals, but not harp seals (Figure 3). Harbor seal strandings occurred most frequently in the summer, while gray seal strandings were common in both spring and summer seasons. Harp seals almost exclusively stranded in our study area during the winter and spring months, with no difference between the two seasons.

Harbor seal pup stranding density was best explained by models that included the effects of human population density, seal abundance, and the interaction of these two terms (Table 3). When the interaction term was present, the main effect of human population density became nonsignificant, though seal abundance remained a significant explanatory variable. The addition of SST and/or NAO to the model resulted in a slight drop in AIC, but little additional deviance explained.

Across seal species and age classes, our models were able to explain the least amount of deviance (minimum deviance explained = 28.2%) in harbor seal adult stranding density (Table 3). Though the addition of explanatory variables beyond the base model resulted in slight increases in the deviance explained, this came at a cost of higher AIC values, suggesting the base model was the best fit for the data. Of note compared to the harbor seal pup models, none of the top harbor seal adult models included seal abundance.

Local seal abundance was identified as the most important explanatory variable beyond the base model for gray seals, with the addition of SST or NAO resulting in little to no to increase in deviance explained (Table 3). Models that included human population density instead of seal abundance were a poorer fit to the data, and the addition of the interaction term of these two variables resulted in an increase in AIC compared to similar models without the interaction term.

Finally, all five of the top harp seal models included human population density and NAO, with no change in deviance explained through the addition of SST, ice extent, or snowfall

(Table 3).

For all species and age classes, the partial effect of human population density was significant when added to the base model. Higher seal stranding density was generally predicted as human population density increased (Figure 3). Peak density was observed for gray and harp seals in grid boxes with human population density of ~10,000; such human population sizes are observed in our study region around Cape Cod, Massachusetts (Figure 1). Harbor seal strandings peaked in grid boxes with ~100,000 people, which are located around Portland, Maine. The partial effect of seal abundance was also significant when added to the base model in all cases. For both gray and harbor seals, an increase in stranding density was predicted as seal abundance increased to its near maximum for the respective species (Figure 3). Exploration of the interaction between the two terms, human population density and seal abundance, revealed a bimodal distribution of stranding density, with peaks at human population density values of both ~10,000 and ~100,000 for harbor and gray seal models (Figure 4). The interaction plots further revealed that elevated stranding density was predicted across a range of seal abundance values at high human population density.

NAO, which was found to be a significant explanatory variable for harbor seal pups and harp seals, showed similar patterns in both species. Stranding densities were predicted generally to decrease as NAO became more positive or more negative around an index of 0, though the magnitude of this effect was much less for harbor seal pups than harp seals (Figure 3). For harp seals, peak stranding densities were predicted in mildly positive NAO years, with the number of strandings falling as the NAO index increased, which is associated with milder winters in the Northeast US but colder winters with more sea ice in northern Canada.

Among harbor seal pups and adults, stranding density was predicted to increase as SST increased above the seasonal average (Figure 3). Little to no significant effect of SST on stranding density was observed for gray and harp seals. Finally, the partial effects of snowfall and sea ice extent were only evaluated for harp seals, and neither covariate explained significant additional deviance in stranding density compared to the base model.

4 | DISCUSSION

This study used data from reported harbor, harp, and gray seal strandings to investigate spatial and temporal patterns in seal strandings over a 16-year period in the Gulf of Maine, at a time when the ecosystem experienced rapid environmental change, including rising ocean temperatures and extended summers. The temporal analysis revealed that the frequency of strandings among the three species trended differently across time. The spatiotemporal analysis identified potential links between stranding events, human population density, proximity to large seal haul-outs, and environmental conditions. We offer an interpretation of these findings that acknowledges the limitations of our data set, which could be biased by uneven sampling effort (see discussion of reporting effect below), as well as the limitations of our models, which only included some of the possible variables that could affect seal stranding density.

4.1 | Temporal analysis: Strandings reflect seal population trends

Over the course of our study period, we observed an increasing trend in gray seal strandings and a decline in harp seal strandings, while harbor seal strandings remained relatively constant when excluding years with disease outbreaks (e.g., phocine distemper virus in 2006 and influenza A virus in 2011; Anthony et al., 2012; Siembieda et al., 2017; Figure 2). The trends we observed for gray and harbor seal strandings match expectations associated with documented increases in gray seal populations in the region (Wood et al., 2020) and the lack of population growth for harbor seals during this time period (Sigourney et al., 2021). The trend observed for gray seals, but not harbor seals, is also consistent with a prior study of strandings in the southern part of our study region, which reported concurrent increases in gray seals and declines in harbor seals (Johnston et al., 2015). The observed decrease in harp seal strandings is in contrast to an increasing trend in annual harp seal strandings observed in the late 1990s (Harris et al., 2002), but consistent with a decrease in stranding rate, decoupled from the effects of ice cover, which was first noted during the late 2000s (Soulen et al., 2013). The start of this decline in harp seal strandings coincides with the leveling off of harp seal breeding population growth in Atlantic Canada (Hammill et al., 2015), and may also reflect shifting environmental conditions that alter harp seal distribution (Soulen et al., 2013). These environmental factors were further explored through spatiotemporal models.

4.2 | Ecological explanatory variables: When seals and humans interact

Our results highlight the influence of human population density and local seal abundance on seal stranding density. Human population density was present as a significant explanatory variable among the top five models for all species and age classes (Table 3). Distance to public beach access and human population proximity have been previously identified as significant factors influencing the density of reported pinniped strandings. Most studies report a positive association between strandings and human population density, primarily attributed to the reporting effect (Esquible & Atkinson, 2019; Olson et al., 2020). However, while Harris and Gupta (2006) found a positive association of harp seal stranding density and distance to public beach access in the Northeast US, they also found higher stranding density to be associated with lower human population density, and suggested that seals or human beachgoers who report stranded seals may avoid industrialized shorelines near population centers. We observed similarly low stranding frequencies in close proximity to Boston, Massachusetts, the most industrialized part of our Gulf of Maine coastline, but found hotspots of harbor seal strandings near Portland, the largest city in Maine. Gray seals had relatively high rates of stranding near Cape Cod, Massachusetts, which has a medium population density, but like the Portland region has greater public beach access and a large summer beach-going tourist population. Harp seal stranding density was also high near Portland and Cape Cod, though this species strands primarily during the tourist off-season. Consistent with expectations of the reporting effect, we found consistently lower stranding densities across species in more rural areas, specifically in Eastern Maine, where habitat type (rocky shores and beaches) also makes cryptic seals less visible.

The location of seal haul-out sites and breeding colonies can also affect stranding locations (Warlick et al., 2018). The variation we observed in human population sizes at which seal stranding density peaked among species can be largely explained by the proximity to major seal haul-out sites. In fact, for gray seals, seal abundance appeared to be a more important predictor of seal stranding density than human population density. The largest gray seal breeding colonies and haul-out sites in our study area are located near Cape Cod, while harbor seals breed and pup in Maine, and therefore are more frequently observed there. Harp seals do not breed or haul out in aggregate in the Gulf of Maine; they are typically observed individually and presumed to be resting only temporarily onshore between foraging trips.

The significance, or lack thereof, of the interaction term between human population density and our proxy of seal abundance varied among species. This interaction term appeared most important in explaining harbor seal pup stranding density and was not present in the top models for harbor seal adults or gray seals (Table 3). When the terms interacted, in areas of high human population density, high stranding rates were observed across a range of seal abundance values (Figure 4). This observation is suggestive of the reporting effect, which appears particularly important for harbor seal pups in our study region.

Beyond the reporting effect, human activities may also influence when and where a seal strands. While many indirect causes of strandings cannot be determined, stranding networks do record evidence of human interaction that can include entanglement in or ingestion of fishing gear or debris, hooking by commercial or recreational fishing gear, vessel trauma, gunshot, and harassment. A complementary analysis of human interaction cases in Maine from 2007 to 2019 found that these cases comprised approximately 15% of all seal strandings and that the frequency of human interaction increased over time. Seal-human interaction cases in Maine were typically associated with areas of dense human populations and were most commonly described as harassment (Newcomb et al., 2021).

4.3 | Environmental explanatory variables: Low local impact

Our models reported that many of the assessed environmental covariates were statistically significant ($p < .05$) explanatory variables of seal stranding density across species and age classes (Table 3). In fact, all but snowfall and sea ice extent were found to be significant explanatory variables in multiple models. Yet, further consideration of the model output reveals the partial effect size of the environmental covariates was relatively small and thus unlikely to be biologically relevant in most cases (Figure 3). The one notable exception is of harp seals and NAO, where the models suggest this environmental variable may play a biologically relevant role in influencing stranding rates. Uniquely, this case represents the single studied seal species that does not breed in the Gulf of Maine and an environmental variable evaluated at an annual, ocean-basin scale rather than the seasonal, local scale at which strandings and most other explanatory variables were measured.

There are several reasons why it is challenging to select and model the most relevant environmental covariates, and why these covariates often have low explanatory power in ecological modeling. Although marine mammal distributions may be influenced by oceanographic and environmental variables, such as those tested here, it is often believed that marine mammals do not respond directly to these factors (Palacios et al., 2013), and the indirect effects of these variables (such as their impact on marine mammals' prey) can be difficult to measure and model. Further complicating things is that, in marine ecosystems, predictor variables measured in the "present" are often a manifestation of the past, resulting in spatial and temporal mismatch and reduced explanatory power (Grémillet et al., 2008).

Both sea ice extent and NAO have been reported to be correlated with recruitment (Johnston et al., 2005) and strandings (Soulen et al., 2013; Truchon et al., 2013) of multiple species of seals, including harp seals, that require ice for successful molting, pupping, and nursing. Similar to these earlier studies, we found that harp seal stranding density declined as NAO became more positive (Figure 3). Though the negative correlation between strandings and NAO is typically attributed to greater sea ice extent on the breeding grounds during positive NAO years, we did not find any direct effect of sea ice extent on harp seal strandings in our data set. This incongruence may reflect a decoupling of the effect of sea ice extent on stranding rates in the Northeast US due to phenological shifts in harp seal breeding and migration timing, as initially suggested by Soulen et al. (2013). We also observed no significant partial effect of snowfall, despite observations from stranding networks that harp seals strand in poor health condition when the environment lacks snow, putatively because snow is a source of hydration when other forms of freshwater are scarce (Gales & Renouf, 1993; Schots et al., 2017). This apparent discrepancy may be due to a mismatch in timescale between the immediate effects of dehydration and the seasonal timescale of our analysis.

A significant partial effect of SST on stranding density was observed for both harbor seal pups and adults (Figure 3), though this environmental variable contributed little to explaining the deviance observed in stranding density among the top models for either age class (Table 3). Changing water temperatures may have indirect effects on marine mammal distribution or health, and thus influence stranding rates by altering habitat suitability, including prey distribution and availability. Climate variability, including SST, has been shown to significantly affect pup production and survival in several other pinniped species worldwide (Forcada et al., 2005; Laake et al., 2018; McIntosh et al., 2012). In our study system, where the strongest correlation between seal stranding density and SST was observed at a 4-month lag, the modeled effect of SST on harbor seal pup strandings most likely reflects the effects experienced by the adult female during pregnancy. Future studies may be able to investigate this hypothesis, and others related to the impact of environmental factors on the health of stranded marine mammals, using data collected on body condition by stranding responders (Teman et al., 2022). These data were considered beyond the scope of the current study. In areas where

SST is linked to sea ice extent, researchers have also found SST to be a significant predictor of interannual variation in stranding rates for ice-breeding seals (Truchon et al., 2013). We likely did not observe this effect of SST on harp seal stranding rates in our study because the fine-scale spatiotemporal resolution of our SST data reflected local ecosystem dynamics, such as prey availability, rather than the dynamics of the harp seal breeding grounds.

4.4 | Conclusions

Marine mammal stranding data have the potential to provide highly valuable insights relevant to threats to individuals (e.g., entanglement), populations (e.g., epizootic disease outbreaks), and, as a study of indicator species for coastal ocean health, even ecosystems (e.g., climate change). Despite challenges associated with their opportunistic nature, strandings data provide a unique data set 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 that enables us to better understand how marine mammals are influenced by anthropogenic and environmental factors. As existing and emerging risks to marine mammals from a combination of environmental forcings and anthropogenic activities are realized, spatiotemporal models that account for the interaction of these factors are increasingly salient. This study indicates that in the Gulf of Maine proximity to coastal human population centers and large seal haul-outs are the greatest drivers in seal stranding density. Only for harp seals, which do not breed in the study area, do environmental factors play an important role in predicting stranding density, despite rapid and dramatic shifts in the environmental seascape in recent decades affecting all seals in the Gulf of Maine.

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DATA ACCESSIBILITY

The data sets analyzed during the current study are available by request from the US Marine Mammal Health and Stranding Response Program's National Stranding Database.

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TABLE 1 Explanatory variables utilized in generalized additive mixed models.

Variable	**Source**	**Scale and resolution (raw data)**		**Scale and resolution (model)**	
		Geographic	**Temporal**	**Geographic**[a]	**Temporal**
Human population density	US Census Bureau	Coastal towns of Maine, New Hampshire, and Massachusetts	Annual	Log_{10} (sum within 0.2° × 0.2° grid box)	Annual
Gray seal population density	Wood et al. (2020)	Muskeget, Monomoy, Seal, and Green Island colonies	Annual	Log_{10} (sum[abundance × (distance+1)$^{-1}$])	Annual
Harbor seal population density (pup and nonpup)	Sigourney et al. (2021)	21 bays in Maine	Annual	Log_{10} (sum[abundance × (distance+1)$^{-1}$])	Annual
Sea surface temperature (SST)	NOAA Earth System Research Laboratory	1.1 km	Daily	Average within 0.2° × 0.2° grid box	Previous season anomaly[b,c]
Sea ice cover	US National Sea Ice Data Center	Gulf of St. Lawrence	Monthly	Gulf of St. Lawrence (breeding grounds)	Seasonal average
North Atlantic Oscillation	NOAA Climate Prediction	North Atlantic	Monthly	Whole study area	Seasonal average

(NAO) Index	Center				
Snowfall	Northeast Regional Climate Center, Cornell University	Coastal towns of Maine, New Hampshire, and Massachusetts	Daily	Sum within 0.2° × 0.2° grid box	Seasonal average of cumulative monthly anomalies[c]

[a] 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.

[b] The average SST anomaly of the season prior to the stranding was used in our models to reflect a 4-month lag in the strongest correlation between SST and stranding density identified using a cross correlation function.

[c] Anomalies were calculated as deviations from the average across the study period, 2002 to 2017.

TABLE 2 Number, sex, and age class of harbor, harp, and gray seal strandings in Maine, New Hampshire, and Massachusetts from 2002 to 2017 (*N* = 8,167).

	Total strandings		Sex (%/species)			Age class (%/species)				
Species	**(*n*)**	**(%)**	**Male**	**Female**	**Unknown sex**	**Pup**	**Yearling**	**Subadult**	**Adult**	**Unknown age**
Harbor seal	5,650	68.9	32.2	30.5	37.3	66.1	9.4	4.7	15.1	4.6
Harp seal	1,275	15.5	47.9	27.4	24.7	1.2	70.0	10.8	8.6	9.5
Gray seal	1,242	15.6	42.6	33.2	24.2	22.3	17.6	18.2	32.0	9.9

TABLE 3 Top five generalized additive mixed models (GAMMs) predicting seal stranding density.

Harbor seal – pup, *n* = 4,560															**ΔAIC**	**% Deviance explained**
stranding density	base	+	human	+	seal**	+	(human × seal)***			+	NAO**			—	0.00	38.0
stranding density	base	+	human	+	seal**	+	(human × seal)***	+	SST	+	NAO**			—	0.22	38.0
stranding density	base	+	human	+	seal**	+	(human × seal)***	+	SST*					—	3.99	37.7
stranding density	base	+	human	+	seal**	+	(human × seal)***							—	6.01	37.7
stranding density	base	+	human**	+	seal**			+	SST*	+	NAO*			—	167.10	33.1
Harbor seal – adult, *n* = 4,864																
stranding density	base													—	0.00	28.2
stranding density	base									+	NAO			—	2.05	28.3
stranding density	base	+	human**											—	15.24	29.8
stranding density	base	+	human**							+	NAO			—	17.50	29.9
stranding density	base							+	SST**					—	17.97	28.9
Gray seal, *n* = 5,056																
stranding density	base			+	seal**									—	0.00	32.3
stranding density	base			+	seal**					+	NAO			—	2.45	32.3
stranding density	base			+	seal**			+	SST*					—	10.96	32.6
stranding density	base	+	human**											—	14.75	28.8
stranding density	base	+	human**					+	SST**					—	15.94	29.2
Harp seal, *n* = 2,464																
stranding density ~	base	+	human***		—		—			+	NAO***				0.00	37.9
stranding density ~	base	+	human***		—		—			+	NAO***	+	ice		1.32	37.9
stranding density ~	base	+	human***		—		—			+	NAO***	+	snow		1.78	37.9
stranding density ~	base	+	human***		—		—	+	SST	+	NAO***				2.04	37.9
stranding density ~	base	+	human***		—		—	+	SST	+	NAO***	+	ice		3.43	37.9

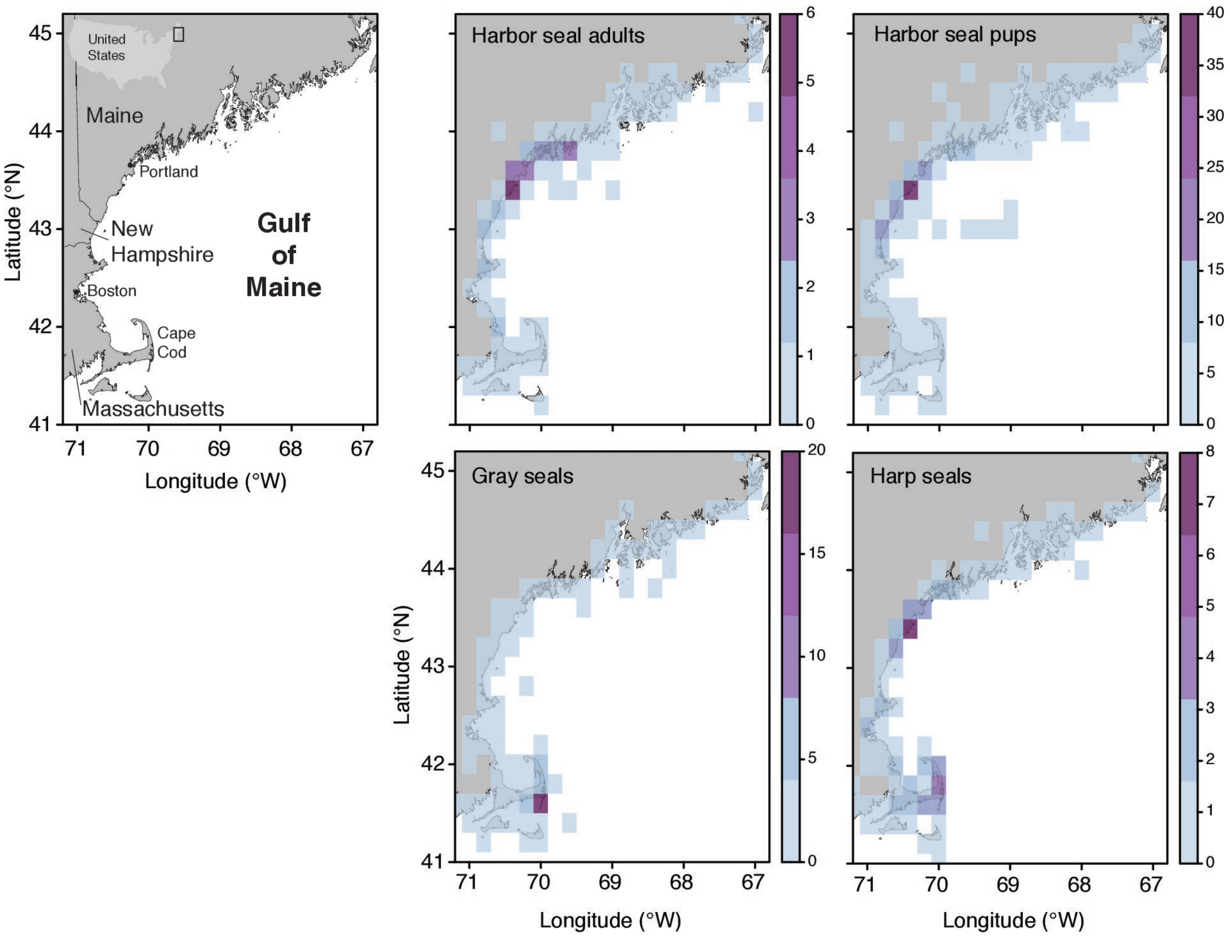
Note: Sample size (*n*) for each data set is the product of the number of grid boxes and number of seasons. The base for all models included latitude (harp seals) or longitude (harbor and gray seals), season, and year. Additional variables included human population density (log_{10} scale), a proxy for seal abundance (log_{10} scale) calculated as the product of size and inverse distance to regional breeding colonies and haul-out sites for the given species, sea surface temperature for the season prior to the stranding (SST), North Atlantic Oscillation (NAO), local snowfall (snow), and sea ice extent in the Gulf of St. Lawrence (ice). All noncategorical explanatory variables were included in the model as smooth terms; year was included as a random effect. – indicates that a given variable was not included in the model set evaluation for that category. Delta Akaike Information Criterion (ΔAIC) scores are presented as differences from the lowest score within each category. Symbols denote statistical significance of covariates (*$p < .05$, **$p < .01$, ***$p < .001$). All variables in the base model were significant ($p < .001$) except season in the harp seal models. Additional model statistics presented in Table S1.

FIGURE 1 Stranding density of harbor, gray, and harp seals in the Gulf of Maine. Color indicates the average number of individuals stranded per grid box over the study period, from 2002 to 2017. Grid size is 0.2° × 0.2°.

FIGURE 2 Annual number of strandings for harbor (black dots), harp (red triangles), and gray (blue squares) seals in the Gulf of Maine from 2002 to 2017. Gray shading indicates 95% confidence envelopes around fitted local polynomial regressions calculated using the "loess" function in the ggplot2 package in R.

FIGURE 3 Partial effects of human population density ($\log_{10}$ scale), seal abundance (estimated as the product of size and inverse distance to local seal haul-outs), sea surface temperature anomaly (°C), North Atlantic Oscillation, snowfall anomaly (in.), and sea ice extent (km^2) as obtained by generalized additive mixed models (GAMMs) of recorded seasonal stranding density for four species/age classes of seals in the Gulf of Maine from 2002 to 2017. Partial effects represent the additional deviance in stranding density that is explained when the specified variable is added to the base model (latitude/longitude, year, and season). Gray shading indicates 95% confidence envelopes. Symbols in the top left corner of the plots denote statistical significance of covariates (*$p < .05$, **$p < .01$, ***$p < .001$). Hash marks on the bottom of plots represent observations with negative residuals, and those on the top are observations with positive residuals.

FIGURE 4 Density maps showing of the interacting effect of human population density (log scale) and seal abundance on recorded seasonal stranding density for harbor and gray seals in the Gulf of Maine from 2002 to 2017. Seal abundance values are calculated for each species as described in the text to represent size of nearby colonies weighted by distance. Harp seals are not included because they do not breed or haul out in large aggregations in the Gulf of Maine so there are no abundance estimates available for this region.



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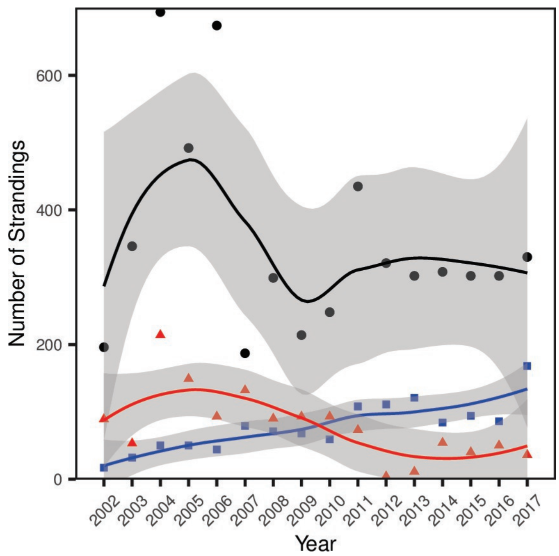

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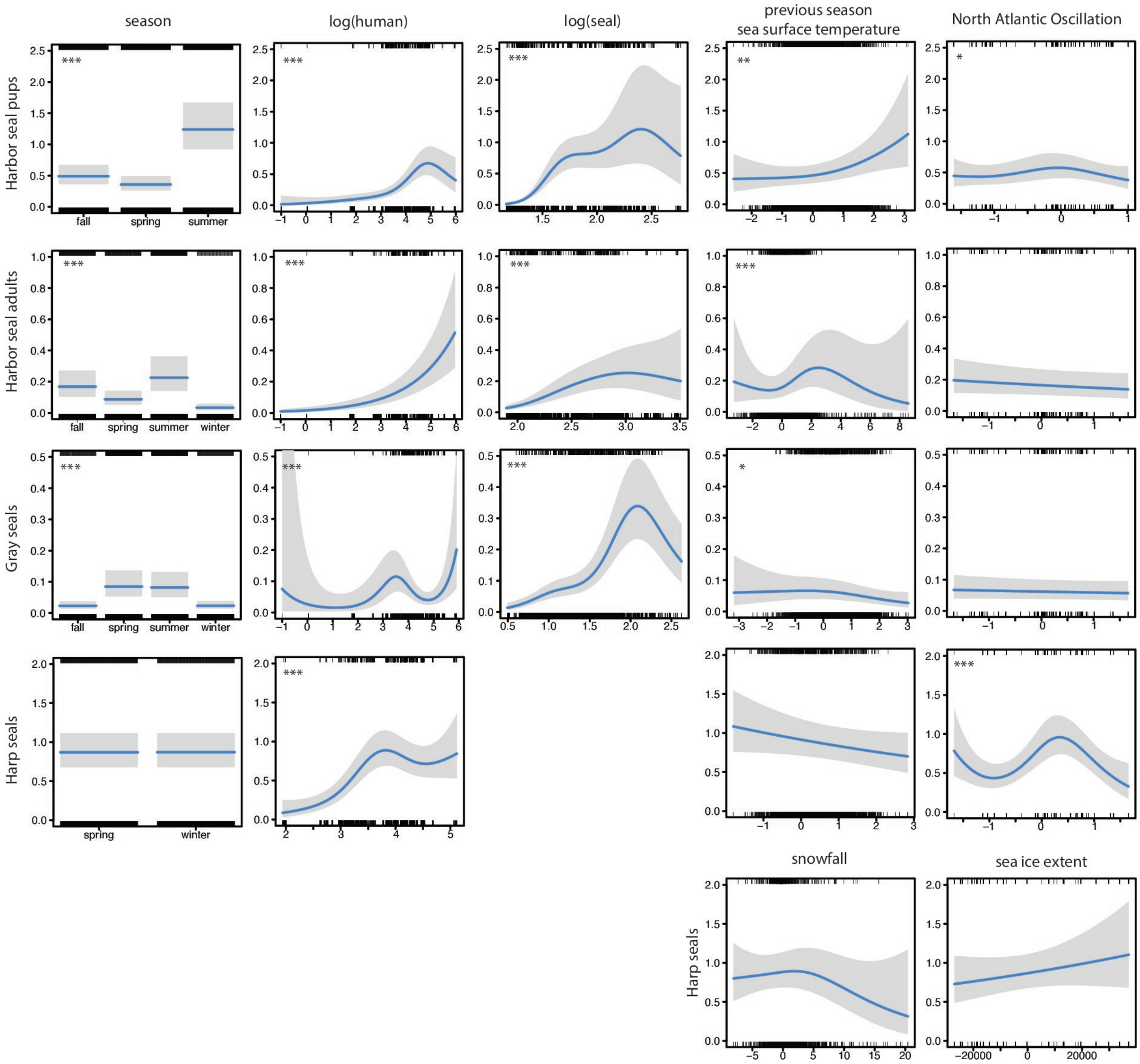

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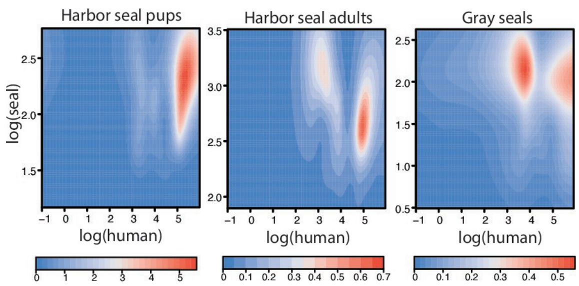

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