NOAA Technical Memorandum NMFS-NE-251

Trends and Patterns of Seal Abundance at Haul-out Sites in a Gray Seal Recolonization Zone

US DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service
Northeast Fisheries Science Center
Woods Hole, Massachusetts
March 2019

NOAA Technical Memorandum NMFS-NE-251

This series represents a secondary level of scientific publishing. All issues employ thorough internal scientific review; some issues employ external scientific review. Reviews are transparent collegial reviews, not anonymous peer reviews. All issues may be cited in formal scientific communications.

Trends and Patterns of Seal Abundance at Haul-out Sites in a Gray Seal Recolonization Zone

Richard M. Pace[1], Elizabeth Josephson[2], Stephanie A. Wood[2], Kimberly Murray[1], and Gordon Waring (retired)[1]

[1]*Northeast Fisheries Science Center, 166 Water Street, Woods, MA 02543-1026,*
[2]*Integrated Statistics, 16 Sumner Street, Woods Hole, MA 02543*

US DEPARTMENT OF COMMERCE
Wilbur Ross, Secretary
National Oceanic and Atmospheric Administration
Timothy Gallaudet, Under Secretary
National Marine Fisheries Service
Chris Oliver, Assistant Administrator for Fisheries
Northeast Fisheries Science Center
Woods Hole, Massachusetts

March 2019

Editorial Notes

Information Quality Act Compliance: In accordance with section 515 of Public Law 106-554, the Northeast Fisheries Science Center completed both technical and policy reviews for this report. These predissemination reviews are on file at the NEFSC Editorial Office.

Species Names: The NEFSC Editorial Office's policy on the use of species names in all technical communications is generally to follow the American Fisheries Society's lists of scientific and common names for fishes, mollusks, and decapod crustaceans and to follow the Society for Marine Mammalogy's guidance on scientific and common names for marine mammals. Exceptions to this policy occur when there are subsequent compelling revisions in the classifications of species, resulting in changes in the names of species.

Statistical Terms: The NEFSC Editorial Office's policy on the use of statistical terms in all technical communications is generally to follow the International Standards Organization's handbook of statistical methods.

Internet Availability: This issue of the NOAA Technical Memorandum NMFS-NE series is being as a paper and Web document in HTML (and thus searchable) and PDF formats and can be accessed at: http://www.nefsc.noaa.gov/nefsc/publications/.

TABLE OF CONTENTS

LIST OF FIGURES

ABSTRACT

Gray (*Halichoerus grypus*) and harbor seals (*Phoca vitulina*) were greatly reduced in numbers along maritime Canada and nearly extirpated from waters along the US Atlantic Coast by the mid1900s. Harbor seals were first to show substantial increases in US Atlantic waters. Expanding from a rapidly rebuilding residual population off Atlantic Canada, gray seals are recolonizing areas of southern New England. Although their abundance appears to vary seasonally, the presence of large numbers of gray seals raises questions about the potential for competitive exclusion of smaller harbor seals as well as public concern over resource conflicts. We counted gray and harbor seals hauled out on frequently used sites near the southern edge of a gray seal recolonization zone, primarily near Cape Cod, Massachusetts. Counts were made during periodic aerial surveys conducted during 2005-2015 to measure seal occupancy at haul outs and to gauge trends in abundance during that time period. We also used statistical models to characterize this variation. In particular, we characterized the annual cycle of gray seal abundance at haul outs with an expanding sinusoidal function and fit annually varying growth functions from year start to peak abundance to characterize the pattern of peak abundance change among years, relying on empirical Bayes methods to estimate parameters. We limited models of harbor seal counts to testing for change in the upward trend in peak counts. Gray seal peak abundance at haul outs occurred between 15 April and 13 May, and total abundance across surveyed sites increased from 10,847 in 2005 to 23,579 in 2015. Although peak abundance of gray seals in the study area more than doubled during our study, the rate of growth declined over time. Concomitant with increasing gray seal presence at haul outs, peak numbers of hauled out harbor seals detected in the study area increased for about half of the study period and then declined. Our study documents the fluctuating but increasing abundance of gray seals on haul-out sites at the edge of a gray seal recolonization zone during 2005-2015, and we provide further evidence that increasing gray seal populations may reduce use of the region by harbor seals. We did not measure total seal abundance in the region. Our work demonstrated that, despite a lack of knowledge about true availability and therefore total abundance, repeated surveys of haul outs can be informative about trends in seal abundance.

Keywords: abundance trend; *Halichoerus grypus;* gray seal; harbor seal; Northwest Atlantic; *Phoca vitulina*

INTRODUCTION

Gray (*Halichoerus grypus*) and harbor seals (*Phoca vitulina*) were historically distributed along the northeast coast of the United States (US) and Canada (CAN) through the 17th century. Harbor and gray seals were considered a nuisance to commercial fishing and nearly extirpated by the mid1900s via local and state bounty systems; some of which lasted well into the 20^{th} century (Andrews and Mott 1967; Lelli et al. 2009). Since bounties ended, both species have recolonized parts of their former range (Gilbert et al. 2005; Wood et al. 2011). This area includes former pupping colonies of gray seals on islands off of the Northeastern United States, where breeding and pupping were first observed again in the late 1980s (Rough 1991) and have steadily increased in size (Rough 1991, 1992, 1993, 1995; Wood et al. 2011). The Canadian gray seal population off Nova Scotia has increased substantially since the 1960s (Hammill et al. 1998; Bowen et al. 2003b, 2007). Seals with tags and brands indicating they were born on Sable Island (CAN) have been observed at US sites (Wood et al. 2011). Genetic analyses of gray seals born at sites throughout the northwest Atlantic demonstrated little genetic differentiation among these sites (Wood et al. 2011), and thus, the Canadian population has served as a source for the recovering US population. The majority of the US Atlantic harbor seal population is found along the Maine coast, with a subset of animals moving south to Cape Cod (MA) to winter during September to May (Barlas 1999; Gilbert et al. 2005; Payne and Selzer 1989). Harbor seal pup monitoring along the Maine coast since the 1980s showed this population increasing (Gilbert et al. 2005). Little is known about harbor seal movement between Canadian and US sites.

Coastal communities and conservationists have become embroiled in a debate about the apparent rapid recolonization and continued population growth of gray seals now inhabiting the waters off Cape Cod and the perceived impacts of seals on natural and recreational resources. Perceived impacts of a burgeoning gray seal population include consumption of commercial and recreational fish stocks, entanglement in commercial fishing gear, displacement of harbor seals, decreased water quality, and attraction of white sharks (*Carcharodon carcharias*), a seal predator, with resulting concerns regarding shark attacks and potential beach closures. What the debate lacks is adequate scientific basis to characterize these perceived impacts, particularly the lack of documentation of population numbers and haul-out use patterns that might better characterize trends in seal abundance.

Listed among the effects of a burgeoning gray seal population is the potential for displacement of harbor seals whether from physical interference at particular haul-out sites or from the general vicinity through competitive exclusion. Herreman et al. (2009) concluded that competition, primarily with a rapidly growing Stellar sea lion (*Eumetopias jubatus*) population, supported a competitive exclusion hypothesis to explain a decline in harbor seals in Prince William Sound and Glacier Bay. Physical displacement of harbor seals by gray seals is possible owing to the much larger size of gray seals, and predation of harbor seals by gray seals has been recorded in at least one area of sympatry (van Neer et al. 2015). The storied rapid growth of the population of gray seals that use Sable Island off Nova Scotia for pupping has been implicated along with shark predation as the primary drivers leading to declining harbor seal use and pupping of the area (Bowen et al 2003a). Conservation mandates within the United States call for regular assessments of the status marine mammal populations. In instances of declines in abundance, it is important to document principal causes driving change to properly target management efforts.

Although both gray and harbor seals tend to aggregate and show some seasonal fidelity to beaches and ledges where they can haul out when not foraging, gray seal abundance at such sites can be orders of magnitude larger than harbor seals. Gray and harbor seals often overlap in space and time along the Northeast US Coast. At some sites they can be observed hauled out in close proximity, but at other sites gray seals appear to have displaced harbor seals from areas that they formerly used. For example, surveys of Monomoy Island (MA) 1983 to 1987 documented a minimum of 1,000 harbor seals there annually (Payne and Selzer 1989) while surveys from 1998-1999 (Barlas 1999) and 2005-2015 found few to no harbor seals.

Seals present at haul-out sites during any brief period, such as during a survey, represent an unknown fraction of animals. Individual seals haul out based on physiological or environmental cues occurring simultaneously on daily and seasonal time scales. In particular, both species will spend more time hauled out during pupping and molting periods, which are strongly seasonally driven (Anderson et al. 1975; Gilbert et al. 2005). Pupping seasons in the northwest Atlantic are December to February and May to June for gray and harbor seals, respectively (Gilbert et al. 2005; Bowen et al. 2003, 2007). During the pupping season, gray seal adults of both sexes are hauled out at sites for up to 5 weeks (Anderson and Harwood 1985). Harbor seals haul out more often during the pupping season (especially mother/pup pairs), and their daily haul-out behavior is tidally driven and heavily influenced by weather (Gilbert et al. 2005; Skinner 2006). Animals haul out in higher proportions and for longer periods of time during their annual molting period (Boulva and McLaren 1979; Leeney et al. 2010; Reder et al 2003; Reeves et al. 1992). Gray seals in the northwest Atlantic molt annually from March through June (Katona et al. 1983; Stobo et al. 1990; Bowen and Siniff 1999; Beck et al. 2000), while harbor seals molt in July-August (Katona et al. 1983).

Outside of molting and pupping seasons, time spent hauled out is reduced and more variable. Both gray and harbor seals also spend time resting at sea (Russell et al 2015), reducing their need to haul out for rest. Yochem et al. (1987) found an average of 41% of radio-tagged seals hauled out each day. Russell et al. (2015) reported probabilities of resting on land, and therefore being available to aerial survey observations, at 0.18-0.38 and 0.10-0.33 for gray and harbor seals, respectively, which is quite small when compared to an availability rate of 0.60 estimated for harbor seals during the molting season in California (Lowry et al. 2008). Distances traveled from haul-out sites, and therefore time at sea, vary between the 2 species as well. For instance, tagged gray seals traveled as far as 258.8 km from Sable Island (Austin et al. 2004), and 2,100 km from sites in the UK (McConnell et al. 1999). Satellite tagged harbor seals have exhibited shorter trips (<50km), though individual seals have been observed traveling 100s of km from haul-out sites (McConnell et al. 1999; Lowry et al. 2001; Sharples et al. 2012). Harbor seals' movements also vary by month (Lowry et al. 2001). Certainly time at sea and movement of individuals among sites reduce an individual seal's availability to be counted at any particular haul-out site and likely influence public perception about total abundance. Regardless of the downward bias that counts of hauled-out seals represent relative to total abundance, if seasonal seal availability is consistent among years, the visible fraction of seals available to be surveyed can be characterized through time to depict trends in the population. In addition, it is this visible fraction that influences public perception and therefore warrants a characterization through time.

To test the idea that regular surveys could be used to characterize seasonal and interannual abundance patterns, we used counts of seals hauled out on frequently used sites surrounding Cape Cod that were made during periodic aerial surveys conducted during 2005-2015 to characterize changes in abundance. We were particularly interested whether or not this simple approach would allow us to discern trends in abundance in a part of the gray seal range currently under rapid recolonization.

METHODS

Twenty-four locales, centered around Cape Cod and nearby islands of coastal Massachusetts, were identified as potential areas where seals might haul out (Figure 1). Haul-out sites were over flown using either a de Havilland Twin Otter (2005-2011) or Cessna Skymaster (2014-2015), and a series of spatially overlapping oblique photographs were taken to ensure complete coverage of the site. Surveys were flown at 230 m with a ground speed of approximately 185 km/h to maintain consistency with previous surveys (Scott and Gilbert 1982; CETAP 1982). The survey team usually consisted of a pilot, copilot, and an observer, but in some cases an additional recorder was present. Dates of surveys varied among years depending on aircraft availability, weather, and budget. All haul-out sites were observed during every survey, but photographs were only taken when seals were present, and the data analyzed herein excluded gray seal pupping seasons.

Digital images were organized to account for overlap and avoid double counting animals. Seals were assigned to species (gray seal, harbor seal, unknown harbor or gray, and other, such as the occasional harp seal); scanned for entanglements, tags, brands and other individually-identifiable markings; and counted using a paint-dot technique with standard image processing software (Corel PaintShop Pro Photo X2®). Most images were counted by a single individual, and a subset of those counted by others was crosschecked for consistency with the primary counter.

Analysis

We were interested in characterizing both within year and among year trends in abundance at haul outs within the study area. To examine area-specific occupancy, we pooled nearby sites into 10 focal areas (Figure 1). We then arrayed counts as an area by time heat map to coarsely depict dynamics in hauled out numbers among areas. To avoid issues of heterogeneity in periodic use of geographically close areas and because our interest was on overall abundance for the region, we used the summed counts across all haul outs as data for additional analysis. Because all haul-out sites were photographed on the same day during any survey, there was an extremely low chance of double counting seals.

We fitted mathematical models to seal count data to characterize their variation and used empirical Bayes methods to estimate model parameters. Estimation was completed using Markov Chain Monte Carlo (MCMC) simulation implemented in JAGS 4.0 (Plummer 2015) by using the package R2jags in the R statistical computing environment (R Core Team 2013). First, we used a periodically varying function fit to seal count data to characterize the complete time series of counts. The model took the form:

$$Y[i] = (\gamma + \beta * rTime[i]) * \left(1 + \alpha * sin((rTime[i] - \mu)/\tau)\right) \qquad (1)$$

where γ, β, α, and μ were parameters to be estimated. The value for τ was fixed a $1/(2*\pi)$ to represent an annual cycle. Values $Y[i]$ and $rTime[i]$ are the summed counts and time expressed as years (including fractions) since 1 January 2004 for the *ith* survey, respectively. The model was fit assuming observed counts were Poisson random variables with means $\lambda[i]$ and using an MCMC procedure with minimally informative priors: γ~uniform(1000,40000), β~uniform(100,1000), α~uniform(0,5), μ~uniform(0,12).

Because we were interested in possible trends in peak use of haul outs among years, we also fitted a hierarchical model to gray seal counts conducted during day of year (DOY) 0-150, a period that captured the highest observed counts of gray seals. These models use Richards' growth function (Richards 1959) to characterize the change in abundance within a year, while constraining trends among year minima and maxima to linear and power functional forms, respectively. That is, we modeled the log of seal counts by using the following relationships:

$$Y[j,k] \sim dpois(\lambda[j,k])$$

$$\log(\lambda[j,k]) = \delta[j] + (\gamma[j]-\delta[j])/(1 + \xi[j] * \exp(\beta[j]*(\tau[j]-DOY[j,k])))(1/\xi[j])$$

$$\delta[j] = a + b * yearct[j]$$

$$\gamma[j] = m + n * yearct[j]^p$$

where *Y[j,k]* and *DOY[j,k]* are respectively the counts and Day of Year for the jth year and kth occasion of a survey within the *jth* year; *ξ[j]*, *β[j]*, *τ[j]* are year-specific shape parameters associated with Richard's growth function; *δ[j]* are the annual minima fit by a linear function with parameters a and b; and *γ[j]* are

a~normal(0,0.01), the common intercept for min

b~normal(0,0.01), the common slope for D, the lower asymptote

m~normal(0,0.01), the common intercept for G, the upper asymptote

n~normal(0,0.01), the common slope for G, the upper asymptote

p~uniform(0,1), the common power for G, the upper asymptote

ξ[j] ~uniform(0.01,10), priors for unique H values among Years

β[j] ~normal(0,0.01), prior on values among unique B Years

τ[j] ~normal(0,0.01)

and normal distributions were specified by using precision = 1/standard deviation. In both simulations, we provided random starting points from within the range of priors, used an adaptation + burn-in sample of 5,000 iterations, and a final sample size of 10,000 iterations for estimation.

Finally, we modeled the time series of maximum spring harbor seal counts by using a broken stick or segmented regression model. That is, we allowed the maximum count for each year to vary linearly through time with a potential of two different slopes that change at some unknown time during the study period as in:

$$Max(count)[j] \sim dpois(\lambda[j])$$
$$\log(\lambda[j]) = \alpha + (\beta1 *\xi[j] + \beta2*(1-\xi[j])) *(YEAR[j]- Year.change)$$

where, a is the intercept, β_1 and β_2 are slopes, ξ[j] is an indicator variable with value of 1 if YEAR[j] < Year.change and 0 otherwise, and Year.change is the point where the slope changes.

Parameters were estimated by using an MCMC procedure with minimally informative priors: α ~normal(0,0.01), Year.change~uniform(2,10), β1 ~normal(0,0.01), β2 ~normal(0,0.01).

In all cases we used 3 chains and computed the Gelman-Rubin convergence statistic, which was <1.1 for all model parameters, to determine when the algorithms had converged (Gelman and Rubin 1992).

RESULTS

We conducted 78 surveys during 2005-2015 including 7, 7, 8, 9, 9, 7, 6, 0, 0, 13, and 12 in each year respectively. We counted seals on a total of 21,996 photos. Of these, 83% were counted by a single primary counter. Of the photographs counted by others, 814 (22%) were double counted to ensure consistency with the primary counter. Seal occupancy and abundance varied considerably among sites and across time and space (Figure 2). The general appearance of heat plots for both species indicated the following patterns in numbers of seals hauled out: (1) strong seasonal patterns of abundance existed among most areas; (2) a few areas dominated the abundance patterns, and the most highly used areas differed between species; (3) highest gray seal abundances at the areas of greatest use were an order of magnitude higher than harbor seal abundances in their areas of greatest use; and (4) relative overall abundance trends were apparent in both species, with gray seals increasing and harbor seals decreasing during the study period.

Gray Seals

Highest cumulative counts among haul-out sites were observed between 15 April and 13 May and increased from 10,847 in 2005 to 23,579 in 2015. Two separate models of count data were useful in characterizing variation in counts within and among years. The complete time series of cumulative counts generally followed a cyclical pattern that was moderately well characterized with an expanding periodic regression (Figure 3). However, that model only weakly captured the growth in peak numbers through time. An alternative model primarily used to characterize the early seasonal growth in abundance to a peak while searching for evidence of interannual population growth had good convergence properties for all estimated parameters. Despite having only a few surveys per year, the evidence seemed strong that early abundance at haul outs was low and rose quite quickly to an apparent peak (Figure 4) that likely coincided with adult molt. Further, observed peaks seemed to support the idea that abundance increased dramatically during the study period, albeit at an ever decreasing rate (Figure 4). From 2005-2010 growth averaged roughly 5%, whereas from 2010-2015, peak abundance increased at an average of 2% per year.

Harbor Seals

We had intended to characterize variation in seal counts for both species in a similar manner, that is to say with a mathematical model, but harbor seal counts lacked some of the consistency over time found in gray seal counts (Figure 5). In particular, data from 2005 were inconsistent with the 8 other years in that the maximum count occurred in the fall rather than spring. That particular inconsistency rendered a mathematical summary more tenuous than for gray seals. Other known factors made our harbor seal counts somewhat less patterned than the gray seal counts. Human disturbance at a well-used harbor seal haul-out area almost surely influenced a low count during our second survey in 2010 (Figure 5a). Despite these complications, inspection of annual counts revealed that peak numbers of harbor seals were observed at approximately the same time each year (between DOY 80 and 100). Further, the observed maximum counts progressively increased from 1,978 to 3,778 during 2005-2009 and progressively declined in the 4 surveys after 2009 to the smallest peak abundance of 1,435 among all years observed in 2015.

DISCUSSION

Strong and directional population dynamics were observed for 2 species of seals in New England during 2005-2015. The abundance of seals in the area and the fraction likely to be hauled out on any given day are 2 highly variable processes simultaneously influencing the summed counts of seals present at study area haul outs. However, the underlying dynamics were evident from our aerial surveys. For Cape Cod waters, the seasonal abundance of seals varies as the composition of seasonal migrants and possible year-round resident animals changes. Seals found in the study area also spend time in the waters off Nova Scotia, using areas in between to forage (Breed et al. 2006). During the pupping season, both male and female adult gray seals on Muskeget Island, MA, have been observed with brands indicating they had been born on Sable Island, Canada (Rough 1991, 1992, 1993, 1995; Wood et al. 2011), evidence that dispersal from Canada has played a role in the reestablishment of US pupping sites. This finding has been corroborated by genetic evidence; mitochondrial and microsatellite genetic analyses comparing gray seal pups born in the Gulf of St. Lawrence (CAN), Sable Island (CAN), Green Island (ME, USA) and Muskeget Island (MA, USA) showed no detectable population structure among these sites, indicating that both male and female seals are moving between these pupping sites (Wood et al. 2011).

Despite the many factors that tend to influence harbor seal use of haul outs (Cowles et al. 2013), environmental influences did not seem to obscure the major patterns of harbor seal abundance in our study area. That is, most harbor seals in our study area appear to be winter-only residents and likely go north to the many rocky ledges of Maine and Maritime Canada by late spring. This tread is in keeping with our observations from a small but informative telemetry study that included several animals tagged from monitored, haul-out areas (Waring et al. 2006). More surprising was the evidence from our data that the peak numbers available to be counted within our area declined toward the end of our study to less than half of the peak observed in 2009. Although not definitive evidence for a real decline in total abundance of harbor seals overwintering in this region, this observed decline agrees with the findings of Johnston et al. (2015) who found evidence that the numbers of by-caught harbor seals were on the decline in southern New England while gray seal by-caught numbers were increasing. Similar trend relationships between sympatric gray and harbor seal colonies have been observed in Canada (Bowen et al. 2003a) and Great Britain (Jones et al. 2015).

We demonstrated an increase in the minimum number of observed gray seals using haul-out sites around Cape Cod waters; however, this trend is increasing at a slower rate compared to a decade ago. This trend is similar to that observed on Sable Island off Nova Scotia, Canada, where the population size, estimated from a pup production model, increased at an exponential rate from 1962-1997 (Bowen et al. 2003b) but has since slowed (Bowen et al. 2011, 2007; den Heyer et al. 2014). The slowing of gray seal population growth in Canada has prompted investigation into density-dependent changes in vital rates as the population likely experiences resource limitations (Hammill et al. 2014, den Heyer et al. 2014). The number of pups born within our study appears to still be on the increase (Hayes et al. 2018).

Abundance levels reported here represent a minimum population estimate because we have made no assumptions about fractions of local populations being hauled out during our surveys.

We sought only to characterize the variability in observed seal presence at haul outs to understand trends in minimum abundance in southeastern Massachusetts and to inform future attempts at estimating seal abundance in the region. Other studies have quantified the percentage of time gray and harbor seals spend hauled out in order to adjust survey counts to account for animals not available to be seen at the time of the survey (Gilbert et al. 2005; Huber et al. 2001; Lonergan et al. 2011; Skinner 2006). These studies have reported adjustment range factors of 1.53 to 2.54, but these adjustments are not appropriate to use with our survey counts because haul-out behaviors are influenced by site-specific environmental conditions and seasonally varying physiological drives as well as age and sex structures within a population (Russell et al. 2015). Thus, a single multiplier will not work for a multiseasonal survey. Future studies may want to estimate detection rates of seals to calculate animal use days within the area which might be coupled with telemetry studies to elucidate the distribution of hauled out seals in principal foraging areas. This information, coupled with foraging data might help to better inform the public debate concerning gray seal influence on the region’s food web. Until that work is completed, we believe that the frequent resurvey of haul outs provides useful information about trends in seal presence in the region.

ACKNOWLEDGEMENTS

The work of the aerial survey team at the Center for Coastal Studies, Provincetown MA, including L. Sette, and the Northeast Fisheries Science Center aerial crew was essential in collecting the data analyzed herein. This work was conducted under NOAA permits #17670, 775-1875, and 775-1600, as well as scientific research and collecting permits from the Cape Cod National Seashore for flights over the National Seashore and special use permits from the US Fish and Wildlife Service (USFWS) National Refuge Wildlife (NWR) System for flights over Monomoy NWR, Nomans NWR, and Nantucket NWR. We thank M. Hammill, S. Hayes, and M. Simpkins who suggested improvements to the manuscript.

REFERENCES CITED

Anderson SS, Burton RW, Summers CF. 1975. Behaviour of grey seals (*Halichoerus grypus*) during a breeding season at North Rona. J Zool, Lond. 177:179-195.

Anderson SS, Harwood J. 1985. Time budgets and topography: how energy reserves and terrain determine the breeding behaviour of grey seals. Anim Behav 33:1343-348.

Andrews JC, Mott PR. 1967. Seals at Nantucket, Massachusetts. J Mammal. 48(4):657-658. doi:10.2307/1377597

Austin D, Bowen WD, McMillan JI. 2004. Intraspecific variation in movement patterns: modeling individual behaviour in a large marine predator. Oikos 105(1):15–30.

Barlas ME. 1999. The distribution and abundance of harbor seals (*Phoca vitulina concolor*) and gray seals (*Halichoerus grypus*) in southern New England winter 1998–summer 1999. MA thesis. Boston University, Boston, MA.

Beck CA, Bowen WD, Iverson SJ. 2000. Seasonal changes in buoyancy and diving behaviour of adult grey seals. J. Exp. Biol. 203(15):2323–2330.

Boulva J, McLaren IA. 1979. Biology of the harbor seal, *Phoca vitulina*, in eastern Canada Bull Fish Res Bd Can 200:32.

Bowen WD, den Heyer C, McMillan JI, Hammill MO. 2011. Pup production at Scotian Shelf grey seal (*Halichoerus grypus*) colonies in 2010. Canadian Science Advisory Secretariat (CSAS) Res. Doc. 2011/066.

Bowen WD, Ellis SL, Iverson SJ, Boness DJ. 2003a. Maternal and newborn life-history traits during periods of contrasting population trends: implications for explaining the decline of harbor seals (*Phoca vetulina*) on Sable Island. J Zool. 261:155-163.

Bowen WD, McMillan JI, Mohn R. 2003b. Sustained exponential population growth of grey seals at Sable Island. ICES J Mar Sci 60:1265–1374. doi:10.1016/S1054-3139(03)00147-4

Bowen WD, McMillan JI, Blanchard W. 2007. Reduced population growth of gray seals at Sable Island: Evidence from pup production and age of primiparity. Mar Mamm Sci 23(1):48–64. doi: 10.1111/j.1748-7692.2006.00085.x

Bowen WD, Siniff DB. 1999. Distribution, population biology, and feeding ecology of marine mammals. In: Bowen WD, Siniff DB, Reynolds JE, Rommel SA, editors. Biology of Marine Mammals. Smithsonian Institution Press, Washington, DC. p 423–484

Breed G, Bowen WD, McMillan JI, Leonard ML. 2006. Sexual segregation of seasonal foraging habitats in a non-migratory marine mammal. Proc R Soc B Biol Sci 273: 2319–2326.

CETAP 1982. A characterization of marine mammals and turtles in the mid- and North Atlantic areas of the US outer continental shelf, final report, Cetacean and Turtle Assessment

Program, University of Rhode Island, Contract AA551-CT8-48, Bureau of Land Management, Washington, DC.

Cowles JD, Henson SM, Hayward JL, Chacko MW. 2013. A method for predicting harbor seal (*Phoca vitulina*) haulout and monitoring long-term population trends without telemetry. Natural Resource Modeling 26:605-627.

den Heyer CE, Bowen WD, McMillan JI. 2014. Long-term changes in grey seal vital rates at Sable Island estimated from POPAN mark-resighting analysis of branded seals. Canadian Science Advisory Secretariat (CSAS) Res. Doc. 2013/021.

Gelman A, Rubin DB. 1992. Inference from iterative simulation using multiple sequences. Statist Sci 7:457–472.

Gilbert JR, Waring GT, Wynne KM, Guldager N. 2005. Changes in abundance of harbor seals in Maine, 1981–2001. Mar Mamm Sci 21(3):519–535.

Hammill MO, den Heyer CE, Bowen WD. 2014. Grey seal population trends in Canadian waters, 1960–2014. Canadian Science Advisory Secretariat (CSAS) Res. Doc. 2014/037.

Hammill MO, Stenson GB, Myers RA, Stobo WT. 1998. Pup production and population trends of the grey seal (*Halichoerus grypus*) in the Gulf of St Lawrence. Can J Fish Aquat Sci. 55:423-430.

Hayes SA, Josephson E, Maze-Foley K, Rosel PE, Byrd B, Chavez-Rosales S, Col TVN, Engleby L, Garrison LP, Hatch J, Henry A, Horstman SC, Litz J, Lyssikatos MC, Mullin KD, Orphanides C, Pace RM, Palka DL, Soldevilla M, Wenzel FW. 2018. TM 245 US Atlantic and Gulf of Mexico Marine Mammal Stock Assessments - 2017. NOAA Tech Memo NMFS NE-245; 371 p

Herreman JK, Blundell GM, Merav B-D. 2009. Evidence of bottom-up control of diet driven by top-down process in a declining harbor seal *Phoca vitulina richardsi* population. Mar Ecol Prog Ser 374:287-300.

Huber HR, Jeffries SJ, Brown RF, DeLong RL, VanBlaricom GR. 2001. Correcting aerial survey counts of harbor seals (*Phoca vitulina richardsi*) in Washington and Oregon. Mar Mamm Sci 17(2):276–293.Johnston DW, Frungillo J, Smith A, Moore K, Sharp B, Schuh J, Read AJ. 2015. Trends in stranding and by-catch rates of gray and harbor seals along the northeastern coast of the United States: Evidence of divergence in the abundance of two sympatric phocid species? PLoS ONE 10(7): e0131660. doi:10.1371/journal.pone.0131660

Jones EL, McConnell BJ, Smout S, Hammond PS, Duck CD, Morris CD, Thompson D, Russell DJF, Vincent C, Cronin M, Sharples RJ, Matthiopoulos J. 2015. Patterns of space use in sympatric marine colonial predators reveal scales of spatial partitioning. Mar Ecol Prog Ser 534:235-249.

Katona SK, Rough V, Richardson DT. 1983. A field guide to the whales, porpoises and seals of the Gulf of Maine and Eastern Canada - Cape Cod to Newfoundland. Smithsonian, Washington, DC.

Leene, RH, Broderick AC, Mills C, Sayer S, Witt MJ, Godley BJ. 2010. Abundance, distribution and haul-out behavior of grey seals (*Halichaerus grypus*) in Cornwall and the Isles of Scilly, UK. J. Mar. Bio. Assoc. of the UK 90:1033-1040.

Lelli B, Harris DE, Aboueissa AEM. 2009. Seal bounties in Maine and Massachusetts, 1888 to 1962. Northeast Nat 16(2):239–254.

Lonergan M, Duck CD, Thompson D, Moss S, McConnell B. 2011. British grey seal (*Halichoerus grypus)* abundance in 2008: an assessment based on aerial counts and satellite telemetry. ICES J Mar Sci 68:2201–2209.

Lowry MS, Caretta JS, Forney KA. 2008. Pacific harbor seal census in California during May-July 2002 and 2004. California Fish and Game 94(4):180-193.

Lowry LF, Frost KJ, Hoep JM, Delong RA. 2001. Movements of satellite-tagged subadult and adult harbor seals in Prince William Sound, Alaska Mar Mamm Sci 17(4):835–861.

McConnell BJ, Fedak MA, Lovell P, Hammond PS. 1999. Movements and foraging areas of grey seals in the North Sea. J. Appl Ecol 36:573-590.

Payne PM, Selzer LA. 1989. The distribution, abundance and selected prey of the harbor seal, Phoca vitulina concolor, in southern New England Mar Mamm Sci 5(2):173–192.

Plummer M. 2015. JAGS version 3.4.0 user manual. https://sourceforge.net/projects/mcmc-jags/files/Manuals/4.x/jags_user_manual.pdf. Accessed 25 October 2015.

R Core Team. 2013. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from http://www.r-project.org/.

Reder S, Lydersen C, Arnold W, Kovacs KM. 2003. Haulout behaviour of High Arctic harbour seals (*Phoca vitulina vitulina*) in Svalbard, Norway. Polar Biol 27:6–16.

Reeves RR, Stewart BS, Leatherwood S. 1992. Harbor seal *Phoca vitulina*. In: The Sierra Club Handbook of Seals and Sirenians, Sierra Club Books, San Francisco. p. 130–142.

Richards FJ. 1959. A flexible growth function for empirical use. Journal of Experimental Botany 10 (2):290–300. doi:10.1093/jxb/10.2.29

Rough V. 1991. Gray seal pupping at Monomoy National Wildlife Refuge, winter 1991. 9 pp. https://www.nefsc.noaa.gov/psb/psbPublications.html

Rough V. 1992. Muskeget gray seals, winter and spring, 1992. 13 pp. https://www.nefsc.noaa.gov/psb/psbPublications.html

Rough V. 1993. Muskeget gray seals, winter and spring, 1993. 18pp. https://www.nefsc.noaa.gov/psb/psbPublications.html

Rough V. 1995. Gray seals in Nantucket Sound, Massachusetts, winter and spring, 1994. Final Report to the Marine Mammal Commission, Silver Spring, MD. 30 pp. https://www.nefsc.noaa.gov/psb/psbPublications.html.

Russell DJF, McClintock BT, Matthiopoulous J, Thompson PM, Thompson D, Hammond PS, Jones EL, MacKenzie ML, Moss S, McConnell BJ. 2015. Intrinsic and extrinsic drivers of activity budgets in sympatric grey and harbour seals. Oikos 124(11):1462–1472. doi: 10.1111/oik.01810.

Scott GP, Gilbert JR. 1982. Problems and progress in the US BLM-sponsored CETAP surveys. Reports of the International Whaling Commission 32.

Sharples RJ, Moss SE, Patterson TA, Hammond PS. 2012. Spatial Variation in Foraging Behaviour of a Marine Top Predator (*Phoca vitulina*) Determined by a Large-Scale Satellite Tagging Program. PLoS ONE 7(5): e37216. https://doi.org/10.1371/journal.pone.0037216

Skinner JP. 2006. Physical and behavioral development of nursing harbor seal (*Phoca vitulina*) pups in Maine. MS thesis. The University of Maine, Orono, ME.

Stobo WT, Beck B, Horne JK. 1990. Seasonal movements of grey seals (*Halichoerus grypus*) in the northwest Atlantic. In: Bowen WD. Editor. Population biology of sealworm (*Pseudoterranova decipiens*) in relation to its intermediate and seal hosts. Can Bull Fish Aquat Sci 222.

Waring GT, Gilbert JR, Lofton J, Cabana N. 2006.Short-term movements of radio-tagged harbor seals in New England. Northeastern Nat 13:1-14.

Wood SA, Frasier TR, McLeod BA, Gilbert JR, White BN, Bowen WD, Hammill MO, Waring GT, Brault S. 2011. The genetics of recolonization: an analysis of the stock structure of grey seals (*Halichoerus grypus*) in the northwest Atlantic Can J Zool 89:490–497.

Yochem PK, Stewart BS, DeLong RL, DeMaster DP. 1987. Diel haul-out patterns and site fidelity of harbor seals (*Phoca vitulina richardsi*) on San Miguel Island, California, in autumn. Mar Mamm Sci 3(4):323–332.

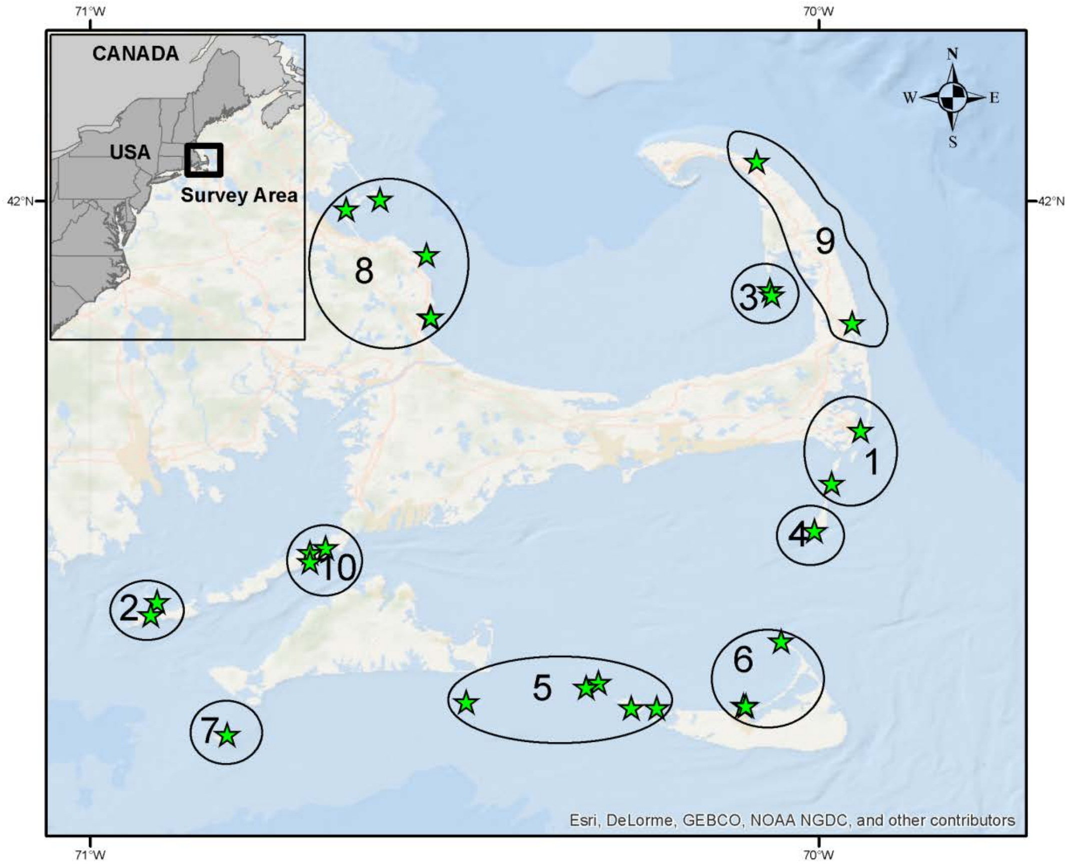


Figure 1. General locations of haul out sites in our study area. Also depicted are boundaries for 10 area groups pooled to examine occupancy: (1) Chatham; (2) Cuttyhunk; (3) Cape Cod National Seashore, Jeremy Point; (4) Monomoy; (5) Muskeget; (6) Nantucket; (7) Nomans; (8) Plymouth; (9) Cape Cod National Seashore, Atlantic coast ("Seashore"); and (10) Woods Hole.

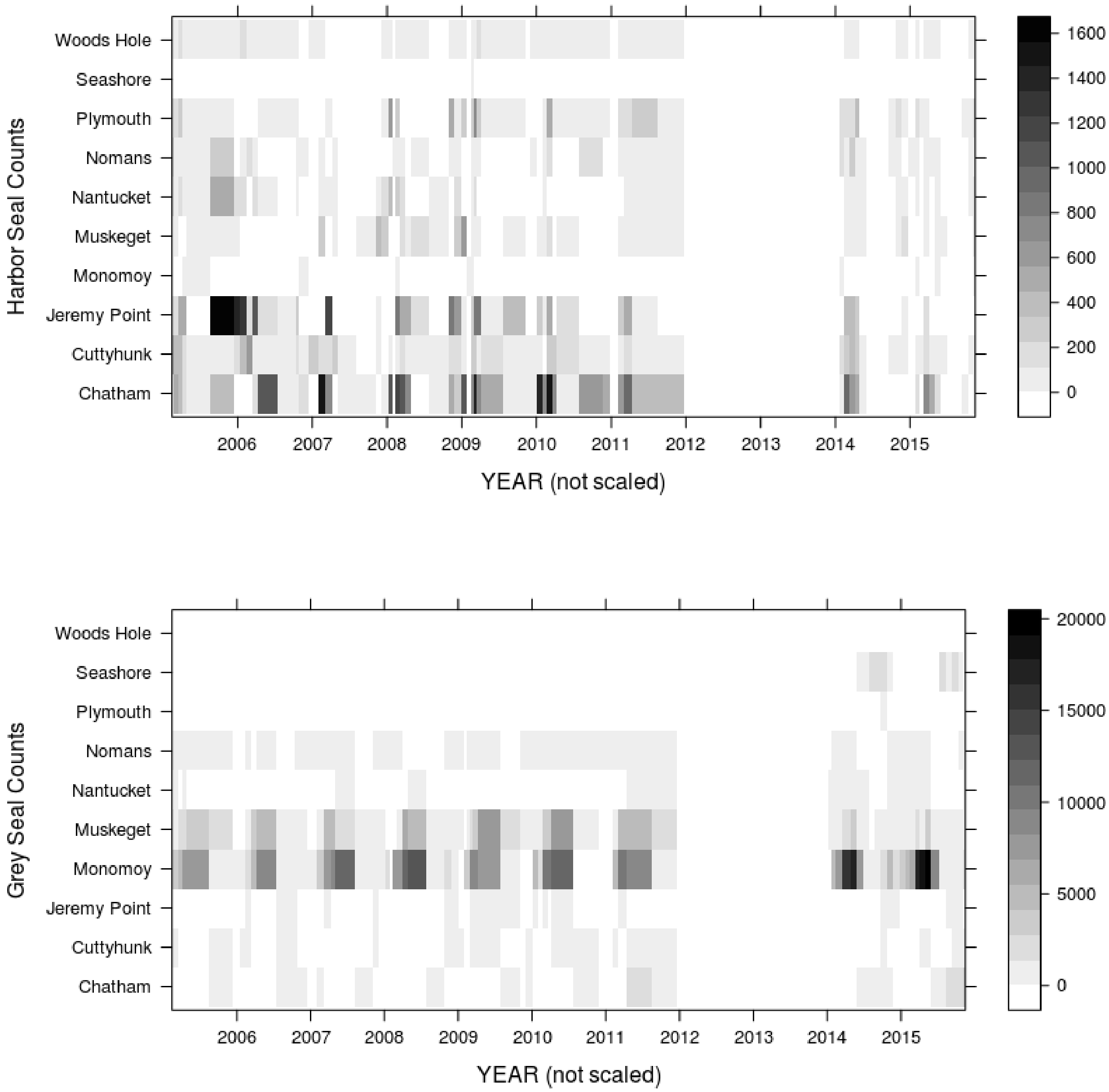


Figure 2. Species specific heat maps of counts of harbor (*Phoca vitulina*) (a) and gray seals (*Halichoerus grypus*) (b) observed during 2005-2015 at 10 areas in southern New England (see Figure 1). Note that length of a grid square along the x-axis differs among years and represents the time between surveys. Also note that Y-axes and color schemes differ between species.

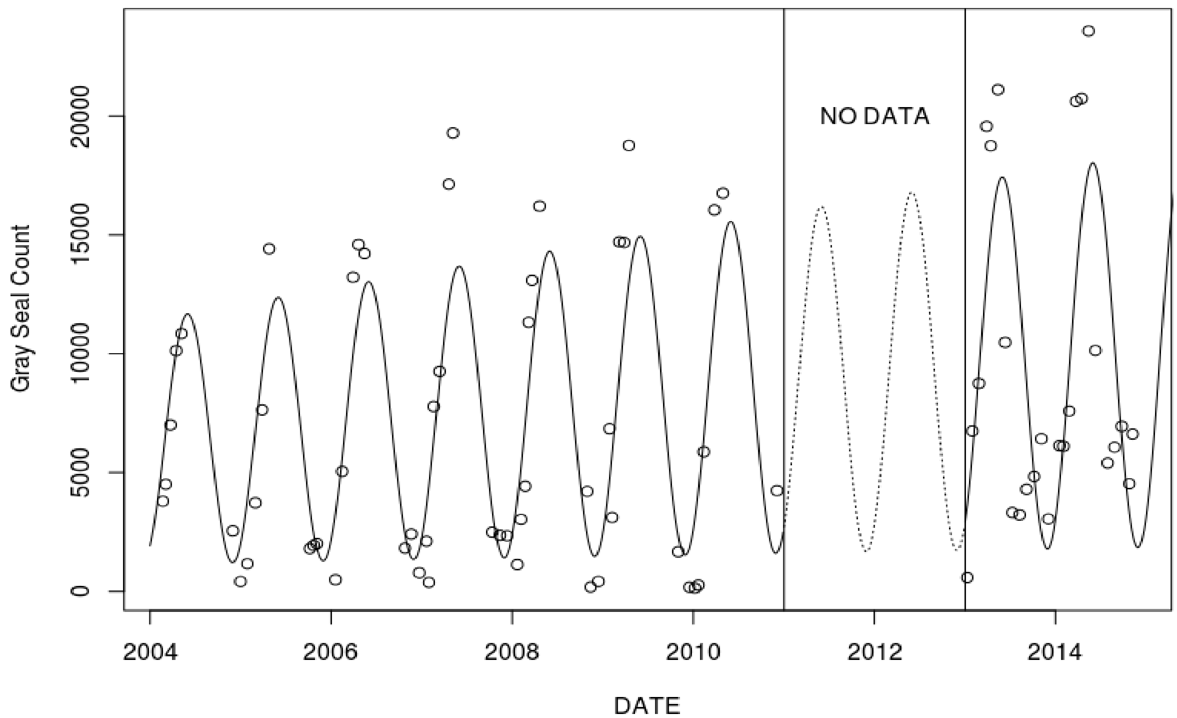
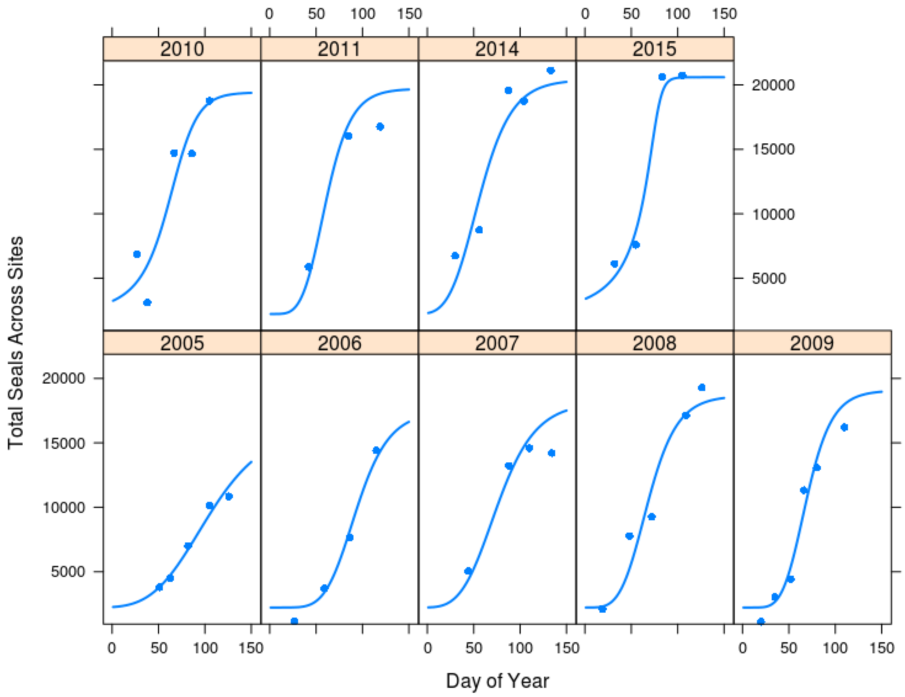


Figure 3. Expanding periodic fluctuation fit to counts of gray seals (*Halichoerus grypus*) observed during repeated surveys of areas in southern New England during 2005-2015.

(a)



(b)

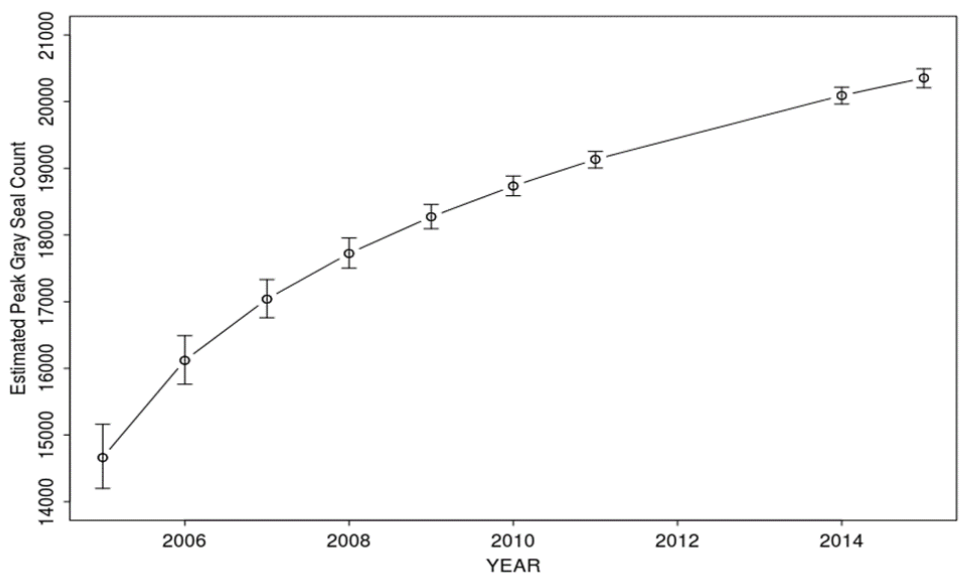
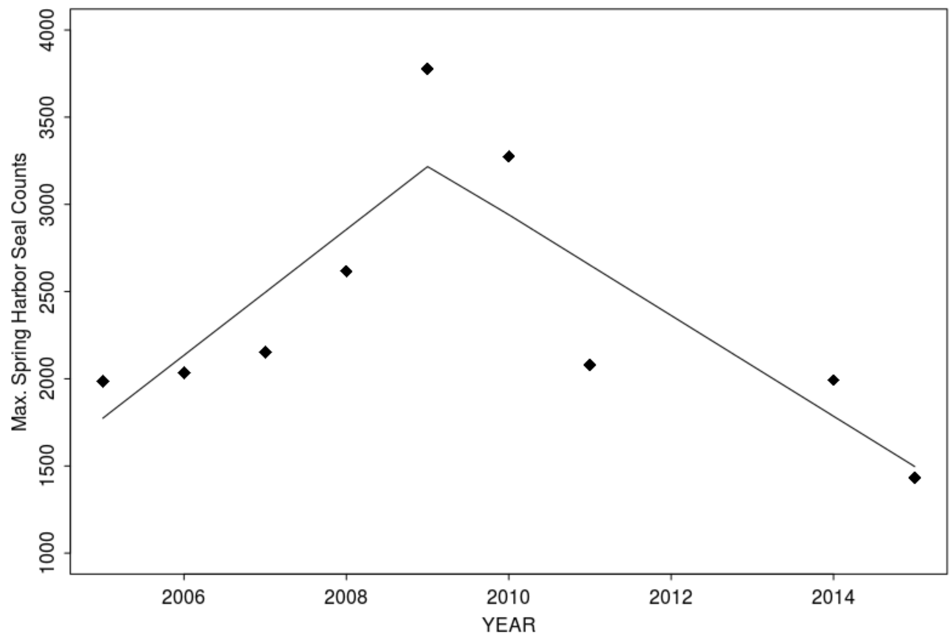


Figure 4. Observed counts and fitted growth functions (a) of the annual buildup of gray seals (*Halichoerus grypus*) using haul outs in areas in southern New England during 2005-2015. (b) A plot of estimated asymptotes to the growth curves, including 95% credible regions.

(a)



(b)

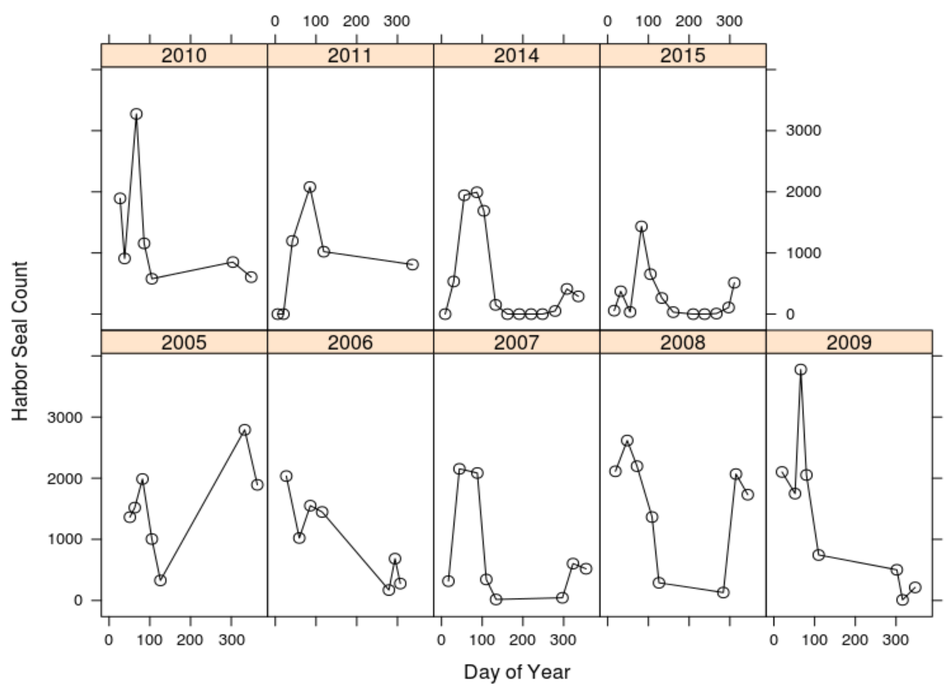


Figure 5. Observed counts of harbor seals (*Phoca vitulina*) during repeated surveys of areas in southern New England during 2005-2015. (a) Summed counts across haul-out sites for all surveys. (b) Peak counts together with fitted broken stick model to those data.

Publishing in *NOAA Technical Memorandum NMFS-NE*

Manuscript Qualification

This series represents a secondary level of scientific publishing in the National Marine Fisheries Service (NMFS). For all issues, the series employs thorough internal scientific review, but not necessarily external scientific review. For most issues, the series employs rigorous technical and copy editing. Manuscripts that may warrant a primary level of scientific publishing should be initially submitted to one of NMFS's primary series (*i.e., Fishery Bulletin, NOAA Professional Paper NMFS,* or *Marine Fisheries Review*).

Identical, or fundamentally identical, manuscripts should not be concurrently submitted to this and any other publication series. Manuscripts which have been rejected by any primary series strictly because of geographic or temporal limitations may be submitted to this series.

Manuscripts by Northeast Fisheries Science Center (NEFSC) authors will be published in this series upon approval by the NEFSC's Deputy Science & Research Director. Manuscripts by non-NEFSC authors may be published in this series if: 1) the manuscript serves the NEFSC's mission; 2) the manuscript meets the Deputy Science & Research Director's approval; and 3) the author arranges for the printing and binding funds to be transferred to the NEFSC's Research Communications Branch account from another federal account. For all manuscripts submitted by non-NEFSC authors and published in this series, the NEFSC will disavow all responsibility for the manuscripts' contents; authors must accept such responsibility.

The ethics of scientific research and scientific publishing are a serious matter. All manuscripts submitted to this series are expected to adhere -- at a minimum -- to the ethical guidelines contained in Chapter 2 ("Publication Policies and Practices") of the *Scientific Style and Format: the CSE Manual for Authors, Editors, and Publishers*, seventh edition (Reston VA: Council of Science Editors). Copies of the manual are available at virtually all scientific libraries.

Manuscript Preparation

Organization: Manuscripts must have an abstract, table of contents, and -- if applicable -- lists of tables, figures, and acronyms. As much as possible, use traditional scientific manuscript organization for sections: "Introduction," "Study Area," "Methods & Materials," "Results," "Discussion" and/or "Conclusions," "Acknowledgments," and "References Cited."

Style: All NEFSC publication and report series are obligated to conform to the style contained in the most recent edition of the *United States Government Printing Office Style Manual*. That style manual is silent on many aspects of scientific manuscripts. NEFSC publication and report series rely more on the *CSE Style Manual,* seventh edition.

For in-text citations, use the name-date system. A special effort should be made to ensure that the list of cited works contains all necessary bibliographic information. For abbreviating serial titles in such lists, use the guidance of the International Standards Organization; such guidance is easily accessed through the various Cambridge Scientific Abstracts' serials source lists (see *http://www.public.iastate.edu/~CYBERSTACKS/JAS.htm*). Personal communications must include date of contact and full name and mailing address of source.

For spelling of scientific and common names of fishes, mollusks, and decapod crustaceans from the United States and Canada, use *Special Publications* No. 29 (fishes), 26 (mollusks), and 17 (decapod crustaceans) of the American Fisheries Society (Bethesda MD). For spelling of scientific and common names of marine mammals, use *Special Publication* No. 4 of the Society for Marine Mammalogy (Lawrence KS). For spelling in general, use the most recent edition of *Webster's Third New International Dictionary of the English Language Unabridged* (Springfield MA: G. & C. Merriam).

Typing text, tables, and figure captions: Text, tables, and figure captions should be converted to Word. In general, keep text simple (*e.g.*, do not switch fonts and type sizes, do not use hard returns within paragraphs, do not indent except to begin paragraphs). Also, do not use an automatic footnoting function; all notes should be indicated in the text by simple numerical superscripts, and listed together in an "Endnotes" section prior to the "References Cited" section. Especially, do not use a graphics function for embedding tables and figures in text.

Tables should be prepared with a table formatting function. Each figure should be supplied in digital format (preferably GIF or JPG), unless there is no digital file of a given figure. Except under extraordinary circumstances, color will not be used in illustrations.

Manuscript Submission

Authors must submit separate digital files of the manuscript text, tables, and figures. The manuscript must have cleared NEFSC's online internal review system. Non-NEFSC authors who are not federal employees will be required to sign a "Release of Copyright" form.

Send all materials and address all correspondence to: Jarita A. Davis (Editor), Editorial Office, NMFS Northeast Fisheries Science Center, 166 Water Street, Woods Hole, MA 02543-1026.

Northeast Fisheries Science Center
Operations, Management & Information Division
Research Communications Branch
Editorial Office

National Marine Fisheries Service, NOAA
166 Water St.
Woods Hole, MA 02543-1026

MEDIA
MAIL

Publications and Reports of the Northeast Fisheries Science Center

The mission of NOAA's National Marine Fisheries Service (NMFS) is "stewardship of living marine resources for the benefit of the nation through their science-based conservation and management and promotion of the health of their environment." As the research arm of the NMFS's Northeast Region, the Northeast Fisheries Science Center (NEFSC) supports the NMFS mission by "conducting ecosystem-based research and assessments of living marine resources, with a focus on the Northeast Shelf, to promote the recovery and long-term sustainability of these resources and to generate social and economic opportunities and benefits from their use." Results of NEFSC research are largely reported in primary scientific media (*e.g.*, anonymously-peer-reviewed scientific journals). However, to assist itself in providing data, information, and advice to its constituents, the NEFSC occasionally releases its results in its own media. Currently, there are three such media:

NOAA Technical Memorandum NMFS-NE -- This series is issued irregularly. The series typically includes: data reports of long-term field or lab studies of important species or habitats; synthesis reports for important species or habitats; annual reports of overall assessment or monitoring programs; manuals describing program-wide surveying or experimental techniques; literature surveys of important species or habitat topics; proceedings and collected papers of scientific meetings; and indexed and/or annotated bibliographies. All issues receive internal scientific review and most issues receive technical and copy editing.

Northeast Fisheries Science Center Reference Document -- This series is issued irregularly. The series typically includes: data reports on field and lab studies; progress reports on experiments, monitoring, and assessments; background papers for, collected abstracts of, and/or summary reports of scientific meetings; and simple bibliographies. Issues receive internal scientific review, but no technical or copy editing.

Resource Survey Report (formerly *Fishermen's Report*) -- This information report is a quick-turnaround report on the distribution and relative abundance of selected living marine resources as derived from each of the NEFSC's periodic research vessel surveys of the Northeast's continental shelf. There is no scientific review, nor any technical or copy editing, of this report.

OBTAINING A COPY: To obtain a copy of a *NOAA Technical Memorandum NMFS-NE* or a *Northeast Fisheries Science Center Reference Document*, or to subscribe to the *Resource Survey Report*, either contact the NEFSC Editorial Office (166 Water St., Woods Hole, MA 02543-1026; 508-495-2228) or consult the NEFSC webpage on "Reports and Publications" (*http://www.nefsc.noaa.gov/nefsc/publications/*).