Examining Space Use of Foraging Gray Seals (*Halichoerus grypus*) off the New England Coast

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List of Acronyms

AIC - Akaike's information criterion
CI – Confidence Interval
CMIP – Coupled Model Intercomparison Project
DE – Deviance Explained
DFO – Fisheries and Oceans Canada
GAM – Generalized Additive Model
GODAE – U.S. Global Ocean Data Assimilation Experiment
GOM – Gulf of Maine
GPS – Global Positioning System
HYCOM - Hybrid Coordinate Ocean Model
MA – Massachusetts
MGET – Marine Geospatial Ecology Tool
MMPA – Marine Mammal Protection Act
NEFSC – Northeast Fisheries Science Center
NMFS – National Marine Fisheries Service
NOAA – National Oceanic and Atmospheric Administration
PBR – Potential Biological Removal
PPA – Potential Path Area
PPV – Potential Path Volume
PSU – Practical Salinity Unit
RSD – Relative Standard Deviation
SD – Standard Deviation
STP – Space Time Prism
STC – Space Time Cube
TNC – The Nature Conservancy

Executive Summary

The Gray seal (*Halichoerus grypus*) is a highly migratory large phocid species occurring in the waters of the Northeast Atlantic Ocean. After severe depletion during the 19th and 20th century, this species has recolonized southerly US habitats around the Gulf of Maine (GOM) and Cape Cod, resulting in increasing conflict with commercial fisheries that overlap with seal foraging grounds. With uncertainty surrounding gray seal population dynamics as well as methodologies for the management of this ecologically important protected predator, there is an incentive to expand knowledge of gray seal feeding ecology and diet to better understand interactions between this species and economically profitable fishing sectors.

Gray seals demonstrate central place movement behavior wherein they alternate between large aggregations at terrestrial haul out sites and at-sea foraging trips. Seal foraging efforts show distinct season differences and diet composition differs noticeably between sex, with females targeting nearshore foraging patches and males traveling greater distances to offshore areas. Foraging efforts during the summertime are limited by predation pressure from white sharks, which are known to target seals entering and exiting the water at haulout sites. Feeding during the summertime is therefore characterized by shorter efforts that display uniformity between individuals while fall and winter feeding involves more prolonged at-sea efforts. Seals primarily target demersal fish species during foraging, with diet composition shifting seasonally to reflect changes to foraging patterns. While the species displays some degree of foraging plasticity, communities of the western North Atlantic commonly consume Atlantic cod (*Gadus morhua*). Research reveals this economically valuable species is routinely one of the top four species consumed for both males and females.

This study investigates gray seal foraging behavior off the coast of Cape Cod and throughout the GOM. Examining data from 4 tagged individuals, this analysis implements a potential path volume (PPV) methodology (Demšar and Long, 2019), to estimate space use in order to assess the effect of sex and season on seal foraging volume. Additionally, this analysis implements a generalized additive model (GAM) to predict species distribution and habitat suitability for a commercially important gray seal prey item, Atlantic cod, to determine potential spatial overlap between commercial fisheries and foraging seals.

Results from PPV analysis shows highly variable space use by foraging seals, with greater overall volumetric range during the Spring/Summer months. Mean PPV was larger

among male samples than females, with relatively high variability among female dive data. Overlap between foraging seals and predicted higher quality cod habitat varies by season. During the Springtime, areas of high probability of the presence of cod are patchily dispersed in gray seal foraging habitat. During the Fall/Winter however, higher quality cod habitat is more concentrated along the coastline north of Cape Cod, with seal foraging efforts concentrated in southeastern areas off the coast. Overlap between suitable cod habitat and foraging seals is therefore more probable during the Spring/Summer months.

The methodologies used in this study to assess overlap between commercially valuable fish species and foraging gray seals have the potential to act as a useful tool for managers and fishers moving forward. Additionally, these methods avoid some of the limitations associated with traditional foraging/diet composition studies. Together with more traditional diet analyses, species distribution modeling and range overlap analysis have the potential to create a more wholistic picture of seal foraging ecology off the New England coast.

Additionally, seal PPV is a useful metric to consider when evaluating trends in foraging ecology of this species. Although certain limitations exist for volumetric space use analysis, PPV can shed light on intricacies of seasonality and sex differentiation of foraging as well as modulation of behavior in response to predation pressure. Finally, the combination of the two methodologies implemented in this paper might help shed light on recovery of vulnerable cod stocks. In their diminished capacity, cod, which occupy a similar trophic niche to gray seals, pose little competitive threat to the robust seal population, which continues to exploit resources shared with not only cod, but also commercial fishermen. A more thorough understanding of gray seal foraging space use and associated take of primary prey items might therefore enable managers to better assess how seal feeding behavior directly impacts recovery of cod stocks.

Introduction

Gray Seals in the North Atlantic

The gray seal (*Halichoerus grypus*) is a highly migratory large phocid species occurring in the waters of the North Atlantic Ocean. During the 19th and 20th century, the species was culled heavily throughout Massachusetts (MA) and Maine (ME) (Lelli et al., 2009). It has been estimated that between 72,000 to 135,000 individuals may have been culled during this time, resulting in significant depletion of the regional population (Lelli et al., 2009). However, as a result of protections established by the Marine Mammal Protection Act (MMPA) of 1972 (16 U.S.C. §§ 1361 et seq.), gray seal populations have continued to reestablish throughout historical ranges, restoring ecological linkages in and around the western North Atlantic (den Heyer et al., 2020; Wood et al., 2020; Moxley et al., 2017; Skomal et al., 2017). More recently, gray seals have increasingly recolonized southerly US habitat areas, including the reestablishment of historic breeding colonies at Muskeget and Monomoy Islands in MA (Figure 1b) (Wood et al., 2020; den Heyer et al., 2020). Studies including pup counts, beach counts and population abundance modeling indicate continued growth at these breeding colonies (Wood et al., 2020; den Heyer et al. 2020; Punt et al., 2020; Moxley et al., 2017). However, there is a lack of consensus over growth rate estimations with rate of increase (R_{max}) calculations ranging from 5% to 26.3% per year (Punt et al., 2020; Wood et al., 2020; den Heyer et al, 2020). Currently, federal management efforts are implementing a 12% R_{max} for calculations of annual potential biological removal (PBR) (Hayes et al., 2019). Uncertainty surrounding gray seal population dynamics and the implementation of R_{max} values into management efforts has come under scrutiny from the recreational and commercial fishing sectors of New England, which are both impacted by gray seal population growth and dispersal (Nichols et al., 2011; Gruber, 2014).

Fishing is an economically valuable industry for Northern Atlantic coastal states with commercial fisheries landing upwards of 550 million pounds of fish products per year, generating almost $1.2 billion in New England alone (NMFS, 2020). Commercial and recreational fishers associate catch reduction and damaged gear with the increase in abundance of gray seals in the North Atlantic (Nichols et al., 2011; Rafferty et al., 2012; Gruber, 2014). Since protections under the MMPA leading to reestablishment of robust population numbers, gray seals have been increasingly caught as bycatch in commercial fisheries of the Northeast United States (Johnston et al., 2014). Interactions with fishing gear can often result in seal

mortality and damage to gear, incurring significant costs to fishers as well as having larger implications for incidental take authorizations under the MMPA (Nichols et al., 2011; Gruber, 2014; Office of Protected Resources, 2020). There is little evidence for a direct correlation between catch reduction and increase in seal abundance and few indicators that gray seal prey specifically on commercially and recreationally valuable species (Lerner et al., 2018; Bowen and Harrison, 1994). Previous analyses suggest that some portion of gray seals' diet may be derived from commercially important species such as Atlantic cod (*Gadus morhua*) (Ampela, 2009; Bowen and Harrison, 1994; Flanders et al., 2020). With costs incurred through gear damage and losses in catch attributed to gray seal populations, there are clear incentives to expand knowledge of gray seal feeding ecology, diet and foraging behavior to better understand interactions between this species and economically profitable fishing sectors.

Gray Seal Foraging Ecology

Gray seals demonstrate central place movement behavior wherein they alternate between large aggregations at terrestrial haul out sites and at-sea foraging trips (Reynolds et al., 1999; Breed et al. 2009). Adult seals generally breed in the winter (December through February), undergo annual molt on land between May and June (Breed et al., 2009) and then spend the rest of the year foraging (Hernandez et al., 2019). Gray seals exhibit differences in temporal and spatial habitat use between sexes, reflected in dissimilarities in foraging behavior and diet composition (Breed et al., 2006; Beck et al., 2007). Directly prior to and after breeding, male grey seals forage primarily in deep water areas while females use shallower regions closer to shore (Breed et al., 2006). These timeframes are characterized by distinct differences in diet composition before and after reproductive phases, with female seals foraging on higher quality nearshore fish species and males targeting deeper water demersal fishes (Breed et al., 2006; Beck et al. 2007). Studies outlining sex-based differences in foraging behavior suggest that male and female gray seals react differently to both seasonal prey availability and the energetic cost of reproduction (Breed et al., 2009; Beck et al., 2007) and regulate temporal duration and spatial distribution of foraging depending on energetic needs.

Additionally, gray seals exhibit pronounced seasonal trends in timing and duration of foraging, with longer and more spatially dispersed trips occurring during the winter and shorter near-shore trips dominating summer patterns (Moxley et al., 2020; Cronin et al., 2012; Breed et al., 2009). Winter foraging trips require more travel time to high quality prey patches (Olsson et

al., 2008; Breed et al., 2009) with deeper dives on average and more widely dispersed foraging locations. Studies in foraging patterns suggest summertime depletion of near-shore, high quality foraging patches and, consequently, more significant food/energy tradeoffs incurred by prolonged foraging trips during the winter (Breed et al., 2009). Gray seals foraging off the coast of Cape Cod, MA exhibit distinct seasonal change in trip patterns, expanding both spatial range and temporal duration of foraging trips during the winter (Moxley et al., 2020). Individual seal foraging habitat during colder months is significantly larger than warm weather foraging, with more pronounced differences in foraging patterns between individuals tagged from Cape Cod colonies (Moxley et al., 2020; Breed et al., 2009).

Conversely, gray seal foraging trips in the summer are characterized by smaller, near-shore overlapping foraging area with shorter foraging trips and more uniform nocturnal foraging efforts between individuals (Moxley et al., 2020; Cronin et al., 2012). Off the coast of Cape Cod, seals will depart haul out sites at or just after sunset, returning just before dawn, during nocturnal darkness (Moxley et al., 2020). Studies have connected uniformity in summertime foraging efforts between individuals from the same haul out sites to pressure from white sharks (*Carcharodon carcharias*), which are broadly distributed in the North Atlantic during summer months (Skomal et al, 2017; Curtis et al., 2014). While white sharks were significantly depleted during the first half of the 20th century, the western North Atlantic population has been rebounding since the 1990's as a result of conservation measures (Curtis et al., 2014). With the expansion of the gray seal population, white shark communities have continued to reestablish their role as a top trophic predator in the region (Paine, 1980), and have increasingly begun to occupy nearshore areas around seal colonies (Skomal et al., 2012). White sharks have been known to congregate and patrol around seal haul outs during the summer months, taking advantage the bottleneck of seals entering and exiting the water for foraging trips and targeting prey with increased frequency during dawn and dusk (Skomal et al., 2012; Fallows et al., 2016; Martin et al., 2005). Seals respond by limiting distance and duration of foraging trips, departing from haul out areas in packs so as to reduce the risk of predation (Moxley et al., 2020). The level of risk varies with foraging site distance from the central haul as well as timing of departure and return to haul out sites (Olsson et al., 2008; Hugie and Dill, 1994), and subsequent food-safety tradeoffs can account for pronounced uniformity between individuals foraging during the summer months (Brown & Kotler, 2004; Moxley et al, 2020). Seasonal and sex-based trends in

foraging are both a result of and cause for finer scale trends seen in the diet composition of grey seals in the western North Atlantic.

Gray Seal Diet Composition and Prey Preference

Gray seals target primarily demersal fishes during foraging (Beck et al. 2007, Breed et al. 2009) and, while the species displays some degree of foraging plasticity (Flanders et al., 2020; Spencer et al, 2017), there are several fishes, including hake, sand lance and Atlantic Cod (referred to henceforth as cod), that are particularly common diet items (Flanders et al., 2020; Beck et al. 2007; Ampela, 2009; Bowen and Harrison,1994). Although studies have shown diet composition to vary depending on opportunistic foraging that fluctuates with season, prey availability and geographical region (Ampela and Ferland, 2006; Bowen et al., 1993; Thompson et al., 1991; Prime and Hammond, 1990), others have noted that a degree of consistency in habitat use and associated foraging behavior occurs within some gray seal communities (Hernandez et al, 2019). Comparisons in diet composition have revealed individual specialization within populations (Araújo et al., 2011), reflecting difference in foraging tendencies between male and female groups as well as seasonal shifts in diet (Flanders et al., 2020; Hernendez et al., 2019; Ampela, 2009; Tucker et al., 2007). For gray seal communities of the western North Atlantic, cod is commonly one of the top four species consumed for both males and females (Bowen and Harrison, 1994; Ampela, 2009; Flanders et al., 2020). Studies have shown that rate of consumption of this benthopelagic fish species varies by sex and season (Ampela and Ferland 2006; Beck et al., 2007), with a significant increase in cod consumption during winter months mirroring the shift in foraging behavior from on-shore to offshore habitats (Ampela, 2009; Bowen et al., 1993). Given the proclivity of seals towards the commercially valuable cod species and the intricate foraging dynamics displayed by Cape Cod based populations, including food-safety tradeoffs incurred by foraging during summertime white shark season, there is a need for a more in depth understanding of prey item distribution and trends in foraging behavior to better understand the true impact of the gray seal community on the commercial fishing sector in the western North Atlantic.

Research Objectives

The objective of this study is to assess the foraging behavior of gray seals off the coast of MA as a method for exploring the relationship between this species and commercial the fishing

sector. Specifically, this analysis will examine spatial overlap between foraging gray seals and Atlantic cod, which is used as a proxy species for commercially valuable fishes, to determine potential areas of conflict between foraging seals and commercial fishing effort. Cod are used as a proxy in this study due to their historical and cultural significance in New England, commercial popularity, and status as a conservation concern (Rose, 2007). To predict the spatial distribution of Atlantic cod in areas off the MA coast this study implements a generalized additive model (GAM) to model species distribution and ultimately create a habitat prediction raster and assess overlap with seal foraging behavior using 2-dimensional seal tracking data. The species distribution model also provides valuable insight on variables that influence cod distribution and abundance. Additionally, this analysis aims to shed further light on the foraging ecology of gray seals by the estimation 3-dimensional space use during foraging efforts. This analysis implements a potential path volume (PPV) calculation (Demšar and Long, 2019) to assess the influence of sex and season on foraging behavior. Space use is a useful metric for assessing movement through the coastal marine habitat, and can potentially provide insight on the frequency of interactions between foraging seals and fishers in addition to shedding light on the influence of white shark predation pressure on seal space use. Finally, this analysis identifies some management implications of seal-cod overlap and consider how commercially valuable species distribution might impact gray seal conservation moving forward.

Methods
Study Area
This study examines prey distribution and seal foraging behavior off the coast of Cape Cod, MA and northward into the Gulf of Maine (GOM) (40-44° N, out to -60° W). The analyses focus primarily on nearshore foraging habitats around Nantucket Shoals and into Little Georges Bank (Figure 1a) however seal tracking data reveals longer foraging trips into the Gulf of Maine and out towards the continental shelf break which will also be addressed. The GOM, noted for colder waters, is located in the lee of North America and is isolated from the warm waters of the Atlantic by shoals of offshore banks (Brooks, 1985). The Gulf is deepest at the Georges Basin (397 m) and the bottom topography defines two other shallower basins (Jordan and Wilkinson). Temperature trends in the Gulf are defined by cyclonic circulation, which plays a large part in fluctuating temperature stratification throughout the area (Xue et al., 1999). The complex topography and variation in benthic sediment types result in a wide range of benthic habitats

throughout the Gulf making this an ecologically important habitat for many foraging marine mammals.

Figure 1. (a) Gulf of Maine study area including oceanographic features (from Townsend et al., 2015); (b) depicts Muskeget and Monomoy Islands, both of which are gray seal colony sites.

Modeling Prey Species Distribution
Data

This analysis assesses Atlantic cod catch data from the northwest Atlantic continental shelf, stretching from the northern GOM to the northern coast of North Carolina (35-44°N). The continental shelf is composed of a wide range of benthic habitats including numerous combinations of sediment grain size and seabed form (Greene et al., 2010). Various depths and

substrate types are home to different benthic macroinvertebrates and demersal fishes and the presence of Atlantic cod depends largely on a combination of depth, temperature, salinity and bottom type (Greene et al., 2010).

Prey habitat suitability modeling uses data from the OceanAdapt portal. OceanAdapt is a collaboration between Pinsky Lab of Rutgers University, the National Marine Fisheries Service (NMFS), and Fisheries and Oceans Canada (DFO) and includes a database of coastal surveys in North America from 1968 to 2011 (Pinsky et al., 2013). These data encompass 60,394 bottom-trawl samples covering ~3.3 million km^2 across nine regions of the continental shelf, providing distribution data on almost 300 fish species (Pinsky et al., 2013). In the Northeast United states, NOAA's Northeast Fisheries Science Center (NEFSC) conducts the seasonal data collection from Cape Hatteras, North Carolina up to the Canadian border (Azarovitz, 1981). Trawls are conducted during the Spring (March, April, May) and Fall (September, October, November), and provide data on biomass when a species is presence as well as notation of a species' absence. This survey uses a stratified random sample methodology and all fish caught are weighed, and counted. These sampling efforts employ a 12 mm mesh liner in trawl gear to retain smaller and juvenile fishes (Azarovitz, 1981). All of the data used are publicly available from the OceanAdapt website (https://oceanadapt.rutgers.edu/) which calibrates catch data depending on vessels used for sampling. Ocean temperature, salinity and depth information for model development is included in fish abundance data recorded from in situ measurements taken during sampling. Other benthic environmental data for each cod data point was sourced from the Nature Conservancy's (TNC) Northwest Atlantic Ecoregional Assessment and includes sediment grain size and benthic habitat classification data (Greene et al., 2010). Sediment size is broken down into 6 separate categories based on range in grain size. Benthic habitat classification data is a combination of depth, slope and seabed position, for example "shallow depression" is an area at a depth of 31-44 meters with a .05% maximum slope (Greene et al., 2010). There are 18 different benthic habitat categories included in this classification.

Generalized Additive Model (GAM) Development

Cod presence/absence data was downloaded from the Ocean's Adapt website (described above). Presence/absence is a binomial variable that indicates presence of the species (1) or absence of the species (0) in a given trawl effort. Methodologies for statistical modeling used

here incorporated data cleaning protocol following Roberts et al., 2020, which included separation of data by season (Spring and Fall), and implemented a generalized additive model (GAM) to model the influence of environmental predictor variables on cod presence/absence. GAMS are a semiparametric extension of generalized linear models (GLMs) and are implemented to fit nonlinear relationships between response and predictor variables (hereafter covariates), such as those commonly observed in fish communities (Wood, 2011; Roberts et al., 2020). Methods for binomial GAM modeling were modeled after Bacheler et al., 2018. This analysis developed two models, a binomial GAM that predicted cod presence or absence in the Fall and the same for the Spring. Models were separated by season to adjust for sampling patterns as well as seasonal migratory patterns of Atlantic cod (Campana et al., 1999). This analysis examined the influence of six covariates on cod presence/absence including bottom and surface temperature (°C), sediment size (mm), bottom and surface salinity (PSU), and benthic habitat classification (Greene et al., 2010). Climatological covariates, including temperature and salinity, are an effective way to capture long term variability in the state of the environment surrounding a focal species' location, and seasonal means (Spring and Fall in the case of this study) can help capture interannual variability which is particularly important for the highly seasonally variable Gulf of Maine (Mannocci et al., 2017). In both models, all covariates were continuous except for sediment size and benthic habitat classification. This model assumed the binary presence or absence of cod follows the Bernoulli distribution wherein the discrete probability distribution of random binary variable being present is given the value 1 with a probability π and the probability of absence is given a value 0 with the probability of $1 - \pi$. To that end, the probability of presence for Spring and Fall, respectively, as modeled by this analysis is denoted by:

$$\text{logit}(\pi) = \alpha + s_1 \text{ (surface salinity)} + s_2 \text{ (bottom salinity)} + s_3 \text{ (surface temp)} + s_4 \text{ (bottom temp)} + f_1(\text{benthic habitat}) + f_2(\text{sediment type})$$

where α is the model intercept, f is a categorical function, s is a smoothed spline function and α is the model intercept.

Covariates were included in the final GAM based on comparisons between various reduced model iterations, each with a different variable removed. This analysis compared

different model iterations using the Akaike's information criterion (AIC) (Burnham and Anderson, 2002), which assigns each model using a unique combination of covariates an AIC score, with the lowest relative score indicating the model with the best fit. The AIC is an estimate of the predicted difference between the fitted model and the measured covariates associated with the observed data, and is meant to find the most parsimonious model with the highest explained deviance between the fitted model and the observed data (Hastie and Tibshirani, 1990). The model that explained the most deviance with the fewest number of covariates as indicated by the lowest AIC score was chosen for habitat prediction. AIC was first calculated for the full model (using all covariates) with all subsequent model iterations, each one dropping one variable, compared to this baseline. Relative AIC scores were calculated by subtracting the AIC of the given model from the baseline model (ΔAIC). Deviance explained was also recorded for each model iteration (% DE). All GAM calculations were performed in RStudio (version 1.2.5022) using the mgcv library (Wood, 2011; https://www.rdocumentation.org/packages/mgcv/versions/1.8-34).

Habitat Prediction Raster

Habitat prediction rasters were generated from the GAM developed from methods outlined in the previous section. Rasters are a matrix of cells organized into a grid where each cell is assigned information about a given variable, such as temperature or salinity. Raster data for benthic habitat and benthic sediment type (referenced above) were sourced from the Nature Conservancy's Conservation Gateway portal (https://www.conservationgateway.org/Pages/default.aspx). Climatological data, including surface temperature/salinity and bottom temperature/salinity, was found through the Hybrid Coordinate Ocean Model (HYCOM). HYCOM is a hydrodynamic ocean circulation model that predicts oceanographic conditions such as temperature, salinity, and sea surface elevation and is part of the U.S. Global Ocean Data Assimilation Experiment (GODAE) (https://www.hycom.org/). HYCOM data was accessed using Google Earth Engine (https://earthengine.google.com/) and the Marine Geospatial Ecology Tool (MGET) (Roberts et al., 2010). HYCOM climatological data was filtered to fit seal tracking data timeframe (June of 2013 through February of 2014) and split into Spring and Fall periods to reflect individual Spring and Fall GAMs. Spring and Fall periods were determined by trawl data collection times

(to reflect the data used to develop the models) which occurred during March, April and May for Springtime surveys and September, October and November for Fall surveys. To generate temperature and salinity rasters, HYCOM data was filtered into Spring and Fall then averaged over the timespan of seal tracking data collection. Data was processed in ArcGIS Pro to set uniform extent and cell size. Rasters were subsequently stacked in RStudio (version 1.2.5022) to create the final layer which included attributes for all covariates needed for habitat prediction based on model results (benthic habitat, sediment, surface and bottom temperature, surface and bottom salinity). The final GAM for each season was used to predict habitat probability for each stack, Spring and Fall, which was converted to display probability values indicating the chance of finding cod at any given pixel on a scale from 0 (lowest) to 1 (highest). Finally, this analysis visually compared 2-dimensional seal tracking data with the predicted cod habitat surface to assess overlap between cod distribution and seal foraging efforts during tracking periods.

3-Dimensional Foraging Range Estimation
Data

This analysis uses data for foraging range calculations from a study on daily and seasonal movements of Cape Cod gray seals by Moxley et al., 2020 with permission from the authors. A full description of the data can be found in Moxley et al., 2020 but elements pertinent to the methodology of these analysese are summarized below. The data consists of GPS trajectories of 8 individual gray seals tagged with GPS/GSMR telemetry tags (Global System for Mobile Communications/General Packet 145 Radio System, SMRU Instrumentation; www.smru.st-andrews.ac.uk/ Instrumentation/ Overview/; 10 cm x17 cm x 4 cm, 370 g in air) (Moxley et al., 2020). Tags were deployed for 2-9 months in 2013 on 4 males (3 aged 3-7 years old, 1 juvenile) and 4 females (4-12 years old). Two individuals included in these analyses do not have complete datasets due to a tag malfunction (tag number 656) and a shark kill (tag number 373). Seals were live caught with a beach seine at a tidal sandbar in Chatham Harbor, MA (41.67° N, 69.95° W).

Data Manipulation and Formatting.

Data was manipulated to fit formatting requirements for the potential path volume calculations from Demšar and Long, 2019 using tidyverse packages (https://www.tidyverse.org/) in Rstudio (version 1.2.5022). Data was projected into UTM 19N (WGS 84) coordinates and a center point was interpolated between each pair of dive-start longitude (lon)/ latitude (lat) and dive-end lon/lat. The results of data formatting, including x (interpolated longitude), y

(interpolated latitude), y (max dive depth), and t (time from t=0 in seconds) variables, were used for PPV calculations.

Foraging trips were identified using criteria from Moxley et al., 2020 and were considered independent when the wet/dry sensor on the tag was continuously dry for a minimum of ten minutes (Moxley et al., 2020). Trips were assigned a trajectory identification numbers (TrajID) based on a 24-hour foraging period measured on a noon to noon cycle in order to capture crepuscular and nocturnal feeding habits. Analyses avoided use of the midnight to midnight 24-hour cycle to ensure continuous foraging trip data rather than establishing an arbitrary midnight stop point to nighttime foraging activity. An independent time index was assigned for each unique TrajID for each individual seal, starting with the first dive of the 24-hour cycle at t=0 and counting up in seconds based on all subsequent trip start times. At the end of each 24-hour foraging cycle, the next series of dives were assigned the subsequent TrajID number. Thus, each individual seal had its own TrajID = 1 (first day of diving after being tagged) with the total number of unique TrajIDs varying depending on number of days of active diving. Each TrajID for each seal was analyzed independently for PPV in order to gain understanding of variation in volume with regard to sex and season.

Data was further subset to meet time and computational constraints that arose during analysis. Due to the memory intensive nature of the PPV calculation, this analysis was performed with a random stratified sample of the total dataset, including 15 random dive days from 4 individuals from each of the two season categories (Spring/Summer and Fall/Winter). These 120 dives were treated as a representative sample of the entire cohort in the effort to limit computational requirements. Dives were included in the Spring/Summer season if they occurred between June and the end of September while those falling between October and February were included in the Fall/Winter season.

Potential Path Volume Calculation

Foraging range was estimated using the wildlifeTG package (accessed at https://github.com/jedalong/wildlifeTG), which is an adaptation of the complete PPV algorithm from Demšar and Long, 2019. The process for these calculations is outlined as follows (adapted from Demšar and Long, 2019): (1) generalize a 2-D Potential Path Area, a metric used for estimating animal home ranges (Long and Nelson, 2012) into three geographic dimensions. The PPA, a projection of a Space-Time Prism (STP) which is a volumetric representation of all

possible paths between two observed points whose size and orientation within a Space-Time-Cube (STC) depends on the speed and movement between the two positions, is an ellipse built around a given trajectory. Long and Nelson (2012) suggest that the summation of PPVs calculated from a given trajectory can act as a geometric delineator of animal range (Long and Nelson, 2012). (2) The algorithm converts PPA into an ellipsoid, now the PPV, which is a projection of the four-dimensional (x,y,z,t) accessibility volume between two positions. (3) The PPV is calculated for all segments of the given trajectory (in this case, each individual dive performed during the 24-hour foraging cycle) and all PPVs are united to form an accessibility volume in three-dimensional geographic space. This volume represents the outer boundary of all movement within the given TrajID group and indicates the limits of space use in three geographical dimensions. The wildlife TG package requires delineation of maximum velocity of a given trajectory group (V_{max}) as well as resolution of the final PPV calculation (established by voxel, a 3-dimensional pixel, size). V_{max} and voxel size were determined using calculations from the original algorithm used in Demšar and Long, 2019 (see WildlifeTG Github repository for a full version of PPV code). The V_{max} parameter was calculated for each TrajID and was therefore unique depending on the individual and the day. Voxel size, however, was held constant throughout all PPV calculations to maintain consistent resolution of the final PPV product and was determined using the dive record with the largest spatial extent in the total dataset. Finally, this analysis included calculation of basic summary statistics for PPV and V_{max} for each individual by season as well as for the stratified sample cohort grouped by sex. Correlation between season/sex and PPV/V_{max} was tested using a two-sided T-test. Normality of data distribution was determined using a Shapiro-Wilk test. Difference in data distribution between Spring/Summer and Fall/Winter periods, as well as between male and female dive data, was determined using a Wilcox rank sum test.
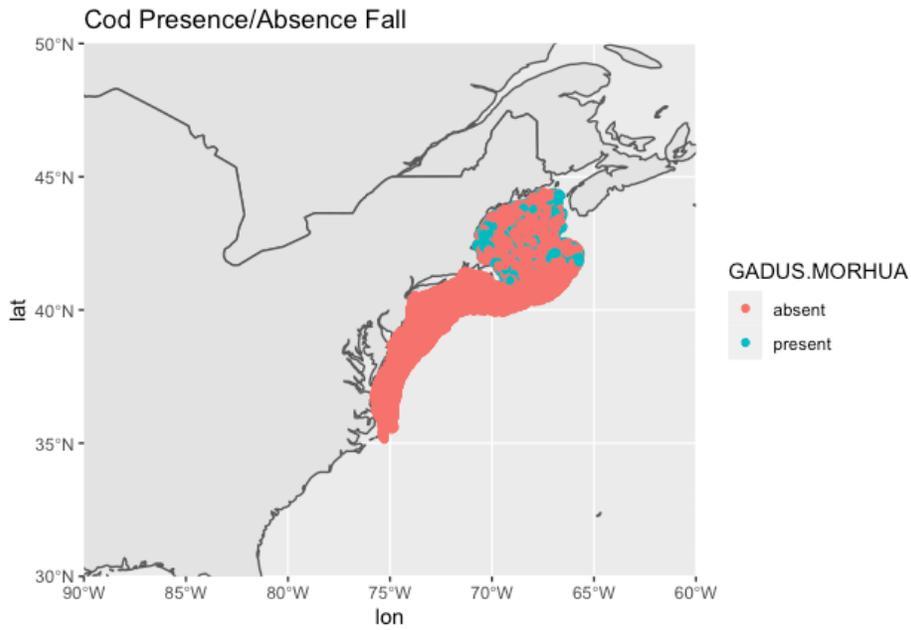
Results
Atlantic Cod Species Distribution Modeling and Overlap with Foraging Ranges
Species Distribution GAM Results

Cod were present in concentrated patches around the Gulf of Maine (Figure 2) at times found in nearshore trawling efforts but extending into sampling efforts closer to the continental shelf. Cod were present in 17% of trawls performed during the Fall and 27% of trawls performed during the Spring. The best Spring binomial GAM relating the presence or absence of cod included all six covariates and explained 28.3% of the deviance (Table 1a). The second-best model (excluding surface temperature) had a ΔAIC of 5.86, with other model iterations with considerably higher ΔAIC (Table 1a). The best Fall binomial GAM included all six covariates and explained 42.9% of the deviance (Table 1b). The second-best iteration of the Fall GAM (excluding surface salinity) had a ΔAIC 11.044 with all other iterations having considerably higher ΔAIC values (Table 1b). Both Fall and Spring final models, therefore, included all covariates. The final model for Spring species distribution GAM, all covariates were statistically significant predictors for cod presence/absence, with surface temperature having the lowest alpha level (0.01) yet still qualifying as a significant predictor. For Fall modeling, surface salinity had the highest alpha level (0.05) yet, along with all other covariates, was a statistically significant predictor of cod presence. Higher alpha levels among surface climatological covariates aligns with cod life history. Because this species is largely demersal, foraging and migrating along the benthos, it is reasonable that surface covariates would not have as significant an impact on presence/absence of the species as bottom covariates.
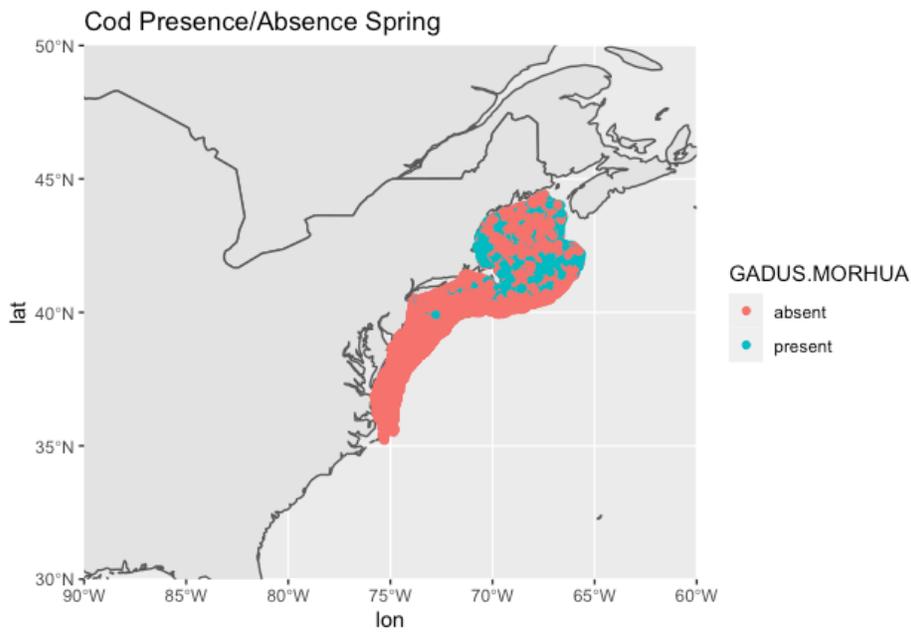
a.

b.

Figure 2. Atlantic Cod presence absence for the (a) Fall; and (b) Spring seasons during NMFS scientific trawl data collection.

Table 1. Model parameters for the generalized additive models for the presence of Atlantic cod in Spring (a) and Fall (b) NMFS independent survey trawls. AIC denotes Akaike information criterion, which is used, along with % deviance explained, to indicate goodness of fit of the model iteration. Degrees of freedom are shown for factor (f) terms, and estimated degrees of freedom are shown for smoothed terms (s). Ex denotes that the covariate was excluded from that iteration of the model. Temp = temperature and SBF depth = benthic habitat classification. *** denotes alpha level of 0, ** is 0.001, * is 0.01 and . is 0.05. Both categorical variables are given the highest alpha level designated for any of the given levels of that variable.

a.

Spring Modeling								
Model	ΔAIC	% Deviance Explained	s(bottom temp)	s(surface temp)	f(sediment)	s(bottom salinity)	s(surface salinity)	f(SBF Depth)
All Variables	0	28.3	6.043***	2.395*	5***	5.979***	5.17***	17***
Minus Bottom Temp	65.989	27.4	ex	2.953	5***	8.673***	4.978***	17***
Minus Surface Temp	5.682	28.1	6.038***	ex	5***	6.004***	4.864***	17***
Minus Sediment	310.791	24.2	6.094***	4.323*	ex	5.407***	5.646***	17***
Minus Bottom Salinity	79.883	27.2	6.149***	4.462**	5***	ex	5.74***	17***
Minus Surface Salinity	87.562	27.4	6.29***	5.439*	5***	6.101***	ex	17***
Minus SBF Depth	224.28	25	6.331***	2.451**	5***	6.191***	5.064***	ex

b.

Fall Modeling								
Model	ΔAIC	% Deviance Explained	s(bottemp)	s(surftemp)	f(sediment)	s(botsalin)	s(surfsalin)	f(SBF Depth)
All Variables	0	42.9	3.01***	8.786***	5***	5.689***	3.999 .	17***
Minus Bottom Temp	175.924	39.8	ex	8.795***	5***	6.518***	3.231***	17***
Minus Surface Temp	245.913	38.4	2.967***	ex	5***	6.049***	3.839**	17***
Minus Sediment	235.471	38.7	3.405***	7.77***	ex	6.171***	4.289*	17***
Minus Bottom Salinity	82.085	41.1	3.62***	7.634***	5***	ex	1***	17**
Minus Surface Salinity	11.044	42.5	3.117***	7.712***	5***	5.553***	ex	17**
Minus SBF Depth	76.614	40.9	3.036***	7.694***	5***	5.774***	3.47 .	ex

Covariate effects for the best binomial GAM varied between Spring and Fall models (Figures 3 and 4 respectively). During the Spring, the GAM reveals a noticeably increased probability of finding cod at low bottom temperatures (below 10°C) with a relatively close association between bottom temperature and presence of cod indicated by the narrow 95% confidence interval dashed line (Figure 3d). Cod probability increases at surface temperatures above 10°C, although with a growing confidence interval indicating a reduction of close association (Figure 3c). The probability of the presence of cod is not closely related to surface salinity (Figure 3a), but peaks at around 33 PSU bottom salinity and grows as salinity gets higher but with a growing confidence interval (Figure 3b). Increased probability of finding cod during

the Fall is similarly associated with lower bottom temperatures and is higher between 10-15°C bottom temperature but decreases again as temperature rises above ~17°C (Figure 4b). Surface temperature is not as closely related with the presence of cod in the Fall, with probability increasing at higher temperatures but with a greater confidence interval (Figure 4a). Presence of cod is significantly higher at low surface salinity in contrast to Spring modeling (Figure 4c). However, based on the width of the 95% confidence intervals (CI), the relationship between surface salinity and presence probability are not as strong as other covariates. During the Fall, the probability of finding cod has a peak at bottom salinities of around 32 PSU (Figure 4d). Model results indicate that sediment size has a stronger relationship with cod presence during the Spring than the Fall (Figures 3e and 4e, respectively), yet in both cases there is an increase in probability at the largest sediment size. Finally, relationships between presence of cod and benthic habitat type are hard to identify for both Spring and Fall (Figures 3f and 4f, respectively). Covariate plots indicate a slight association between the presence of cod and deeper depths as well as steeper slopes, but the latter shows a noticeable increase in CI reflecting a weaker relationship.
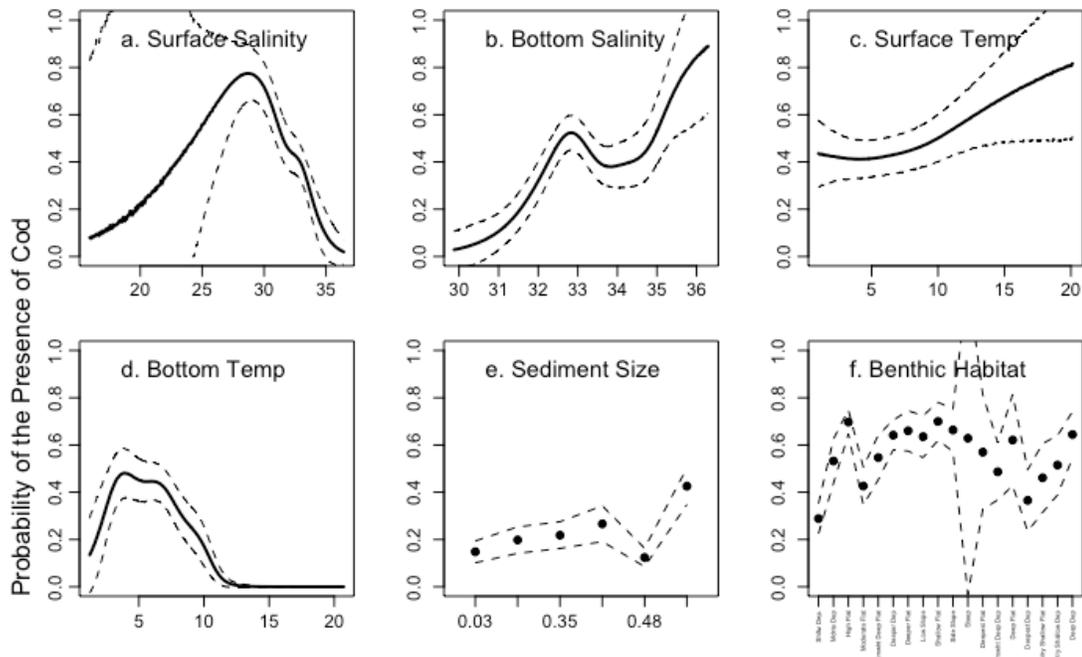

Figure 3. Predicted probability of cod presence during Spring trawls as a function of surface (a) and bottom (b) salinity (PSU), surface (c) and bottom (d) temperature (°C), sediment size (e) and benthic habitat classification (f). Benthic habitat classification includes: "Shallow Depression", "Moderate Depression", "High Flat", "Moderate Flat", "Somewhat Deep Flat", "Deeper Depression", "Deeper Flat", "Low Slope", "Shallow Flat", "Side Slope", "Steep", "Deepest Flat", "Somewhat Deep Depression", "Deep Flat", "Deepest Depression", "Very Shallow Flat", "Very Shallow Depression", "Deep Depression". Solid lines indicate probability of catching cod and dashed lines represent 95% confidence intervals.
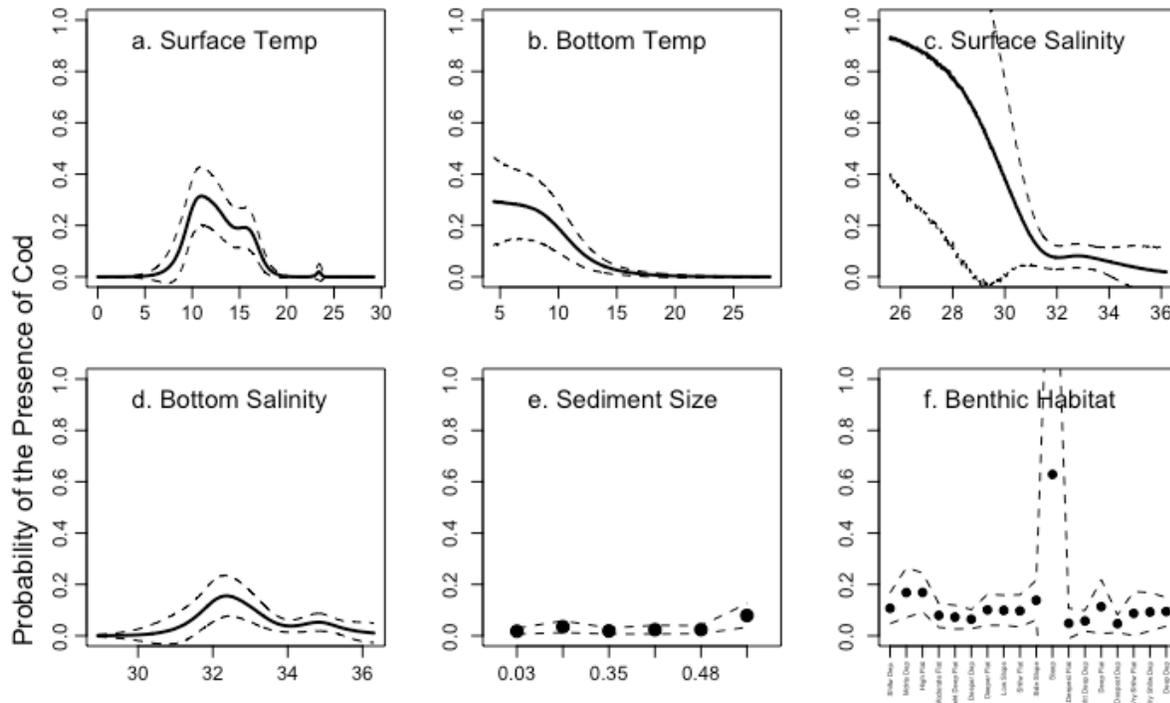
Figure 4. Predicted probability of catching cod during Fall trawls as a function of surface (a) and bottom (b) salinity (PSU), surface (c) and bottom (d) temperature (°C), sediment size (e) and benthic habitat classification (f). Benthic habitat classification includes: "Shallow Depression", "Moderate Depression", "High Flat", "Moderate Flat", "Somewhat Deep Flat", "Deeper Depression", "Deeper Flat", "Low Slope", "Shallow Flat", "Side Slope", "Steep", "Deepest Flat", "Somewhat Deep Depression", "Deep Flat", "Deepest Depression", "Very Shallow Flat", "Very Shallow Depression", "Deep Depression". Solid lines indicate probability of cod presence and dashed lines represent 95% confidence intervals.
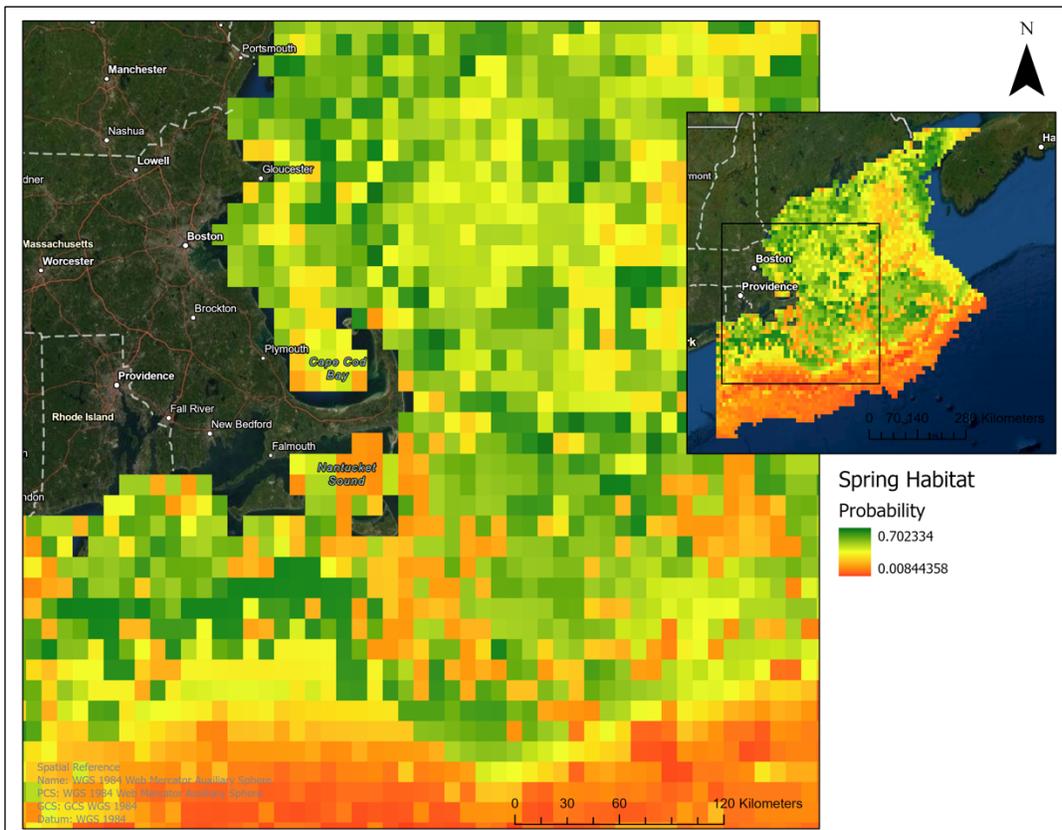
Habitat Raster and Seal Foraging

Results from cod habitat suitability prediction raster shows a definitive difference in cod distribution between Spring and Fall time periods. Figures 5a and 6a show Spring and Fall habitat prediction rasters, with the green values indicating a higher probability of the presence of cod (1 being 100% probability) and a reduction in probability with warmer colors (red being a probability of .008). In this case, suitable cod habitat is associated with yellow to green values (ratings above ~.5 or 50% probability) while less suitable habitat is indicated with warmer colors (ratings below ~.5). During the Spring season areas of higher suitability are somewhat concentrated nearshore relative to regions closer to the continental shelf (Figure 5a). Springtime suitable habitat, however, is more scattered throughout the Gulf of Maine and, compared to Fall habitat distribution, does not display any noticeable spatial distribution trend. This agrees with results from NMFS trawling efforts, which produced more cod present throughout the Gulf as compared to Fall sampling efforts (Figure 2b). During the Spring, onshore areas closest to Cape

Cod and Nantucket are characterized by patches of darker green interspersed with yellow and orange, indicating isolated patches of higher quality habitat intermixed with those of lower quality. Conversely, the spatial prediction of suitable habitat during the Fall season displays more noticeable spatial trends (Figure 6a). Areas of higher quality habitat are still more closely associated with nearshore areas but mirror the thermal trends occurring as a result of influence from Georges Bank and Nantucket Shoals (Brooks, 1985). These results somewhat reflect NMFS sampling efforts in the Fall, which produced more concentrated presence of cod in nearshore patches (Figure 2a). In the Fall, higher quality habitat is more densely grouped around the north eastern side of Cape Cod and continues to track the coastline up into the Gulf of Maine while lower quality habitat is predominant around the areas to the south east of Cape Cod, including the coastline around Nantucket and Martha's Vineyard.

A visual comparison of the distribution of high-quality cod habitat and seal foraging behavior reveals varying degrees of overlap between Spring and Fall seasons. During the Spring time, seal foraging behavior is more concentrated nearshore, with the exception of one outlier that shows a far-reaching offshore effort (Figure 5b) These nearshore efforts seem to be concentrated on the northeastern side of Cape Cod and Nantucket, specifically the area between the two. While these nearshore foraging efforts undoubtedly overlap with patches of high-quality cod habitat, it is difficult to determine whether foraging seals are targeting cod in these areas or are merely habitually limiting Springtime foraging, particularly given predation pressure from white sharks. During the Fall, foraging efforts expand slightly, with individuals increasing their foraging territory to areas further offshore to the south of Nantucket (Figure 6b). During this time period foraging seals seem to overlap more frequently with areas of low cod habitat suitability, indicating that foraging individuals are not necessarily targeting areas where cod are more likely to exist.

a.

b.

Figure 5. (a) Habitat suitability rasters for Atlantic cod during the Spring season. Habitat prediction surface shows probability of the presence of cod from 0 (lowest) to 1 (highest) with green values indicating areas of relatively high probability of encountering cod. (b) Spring 2-dimensional tracking data for gray seals during the same timeframe.

a.

b.

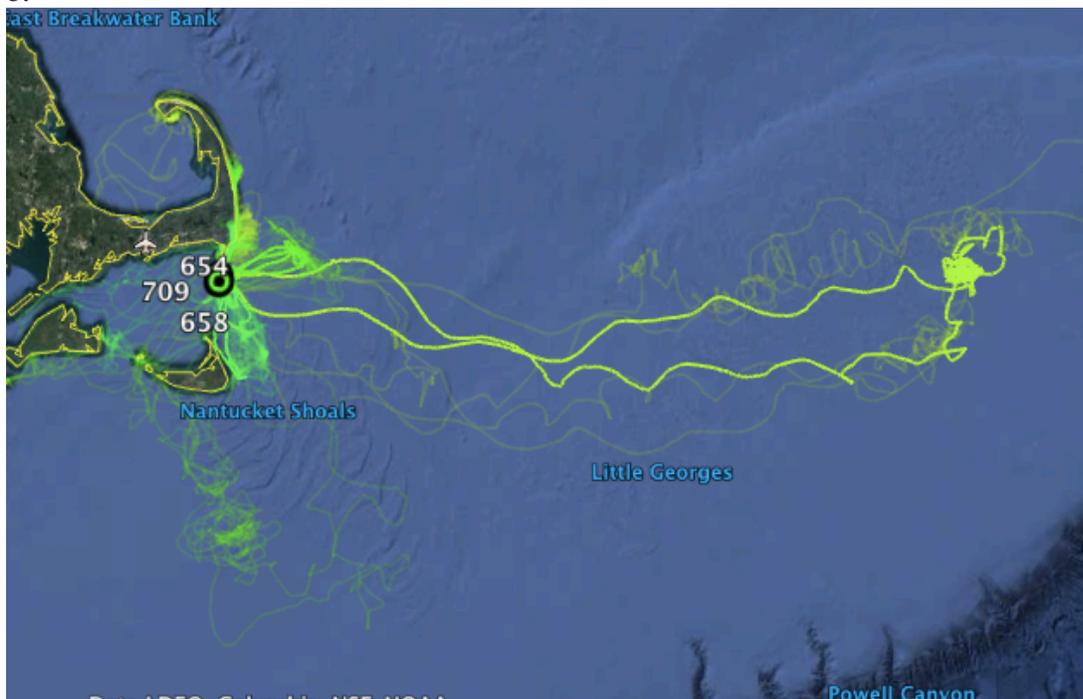
Figure 6. (a) Habitat suitability rasters for Atlantic cod during the Fall. Habitat prediction surface shows probability of the presence of cod from 0 (lowest) to 1 (highest) with green values indicating areas of relatively high probability of encountering cod. (b) 2-dimensional tracking data for gray seals during the same timeframe.

Potential Path Volume
PPV Based on Season

Overall space use (estimated by PPV in km^3) by season for the four-individual cohort subsampled for this analysis is summarized in Table 2. Potential path volume for foraging seals was larger during the Spring/Summer months than for the Fall/Winter months, but both cases show large standard deviations indicating variability in the data, the absence of grouping around the mean and a non-normal distribution. Median volume of foraging space use in Fall/Winter was 661.628 (km^3) while median for Spring/Summer space use was 21051.15 (km^3) (Table 2). This indicated that overall volumetric data from the Fall/Winter has a middle value lower than that of Spring/Summer foraging, suggesting that Spring/Summer range of volumetric values are higher than that of the Fall/Winter. More specifically, results outlining the impact of season on foraging space use broken down by individual are shown in Figure 7. Consistent with overall cohort values, this figure demonstrates similar greater mean volume in Spring/Summer foraging efforts yet high variability both between and among individuals' foraging efforts. Mean values between individuals vary widely, exemplified by the significantly larger mean Spring/Summer value demonstrated by individual 652 when compared to Spring/Summer mean values of other individuals in the cohort. Larger Spring/Summer foraging space use is further reflected in median values of the cohort, with three out of the four individuals showing a larger median foraging volume in the Spring/Summer (Table 3). Overall, relative standard deviation (RSD) was similar among all individuals for both seasonal periods, suggesting comparable degrees of variability in foraging efforts year-round. The individual with the greatest RSD during both seasonal periods, however, was tag number 658, indicating that this animal exhibited the highest overall variation in foraging behavior, potentially reflecting routine foraging movement both on and offshore.

A two sided T- test showed significant difference between foraging path volume of Spring/Summer versus Fall/Winter foraging (t(61) = 2.2062, p = .031), with Spring/Summer mean values greater on average than Fall/Winter, however results from the Shapiro-Wilk normality test indicated that data did not show a normal distribution (with $p_{Spring/Summer}$ and $p_{Fall/Winter}$ < 0.001). Considering results from the Shapiro-Wilk test, data was log transformed in the effort to achieve normal distribution. Results from a two sided T-test on log transformed data also indicated significant difference between mean foraging path volume of Spring/Summer versus Fall/Winter foraging (t(117) = 4.43, p = <0.001), with Spring/Summer mean volume

values larger than Fall/Winter, however only the log transformed Fall/Winter data met criteria for normal distribution under the Shapiro-Wilk test ($p_{Fall/Winter} > .66$ and $p_{Spring/Summer} < .05$). Analysis therefore incorporated a non-parametric test to assess whether there was a significant difference in data distribution using the Wilcox rank sum test. Results indicate that the distribution of Spring/Summer and Fall/Winter foraging efforts are significantly different ($p < 0.001$), although further analysis is required to interpret finer scale differences.

Table 2. Summary statistics of PPV for Spring and Fall season foraging trips of gray seals (N=60 for Spring and Fall, respectively). SD = standard deviation.

Volume by Season (km^3)

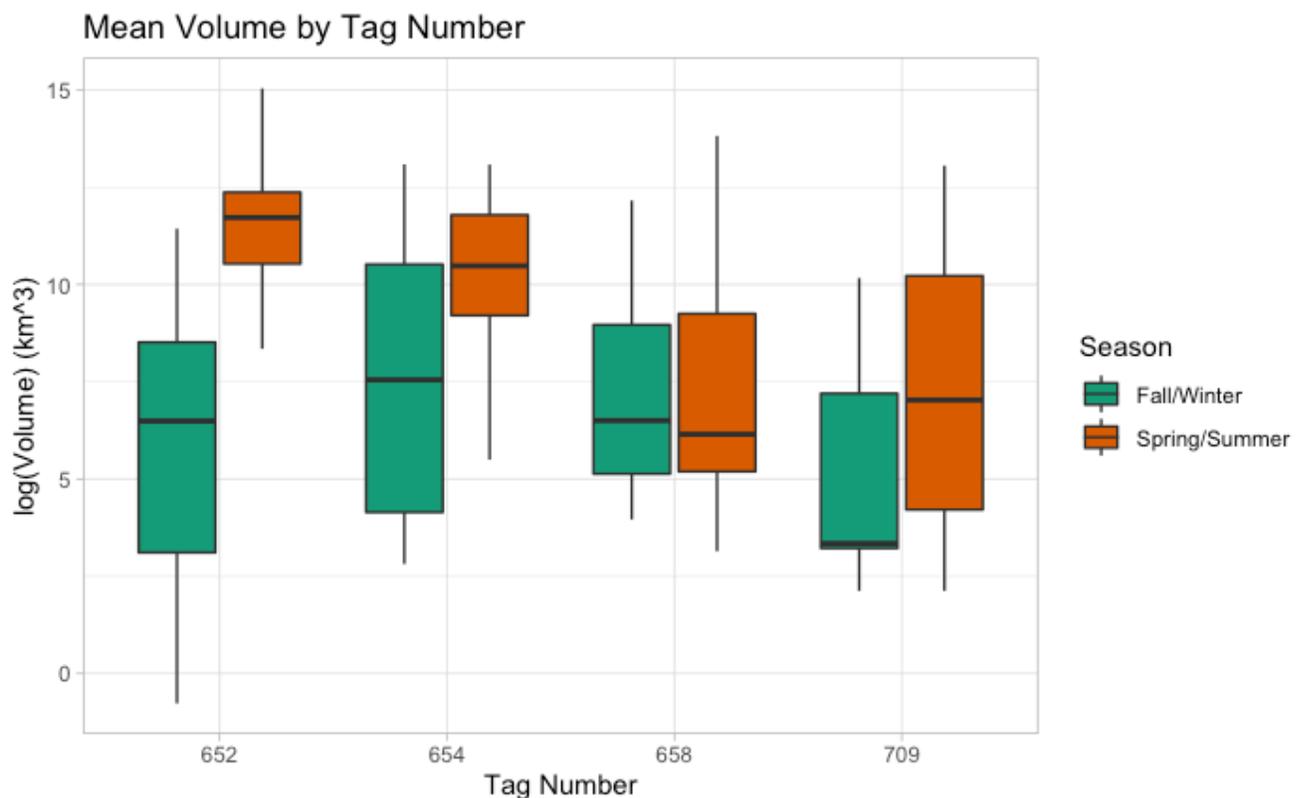| Season	min	max	mean	sd	median
Fall/Winter	0.4634878	483321.8	26086.72	79518.86	661.6288
Spring/Summer	8.3427805	3404008.8	188913.07	566138.31	21051.1504

Figure 7. Log of PPVs by tag number for Spring and Fall foraging efforts shows greater mean path volume during Spring/Summer foraging with high overall variability among all individuals during both seasons.

Table 3. Summary statistics of PPV for Spring and Fall season foraging trips of gray seals separated by individual tag number (N=15 for Spring and Fall, respectively for each individual). Relative standard deviation (RSD) of mean PPV shows comparable levels of variability across all individuals and both seasons. SD = standard deviation.

Volume by Season (km^3)

TagNumber	Season	min	max	mean	sd	median	RSD
652	Fall/Winter	0.4634878	92459.33	10038.219	24003.984	658.15269	239.1259
652	Spring/Summer	4216.8120000	3404008.81	510266.185	1045952.516	122996.70000	204.9817
654	Fall/Winter	16.6855611	483321.84	71534.952	143152.789	1897.98300	200.1159
654	Spring/Summer	243.7945871	480463.00	113453.961	157581.239	35530.51000	138.8944
658	Fall/Winter	52.3741223	190897.65	19595.461	49296.383	665.10500	251.5704
658	Spring/Summer	23.1743904	1003935.00	83015.549	258195.885	468.58617	311.0211
709	Fall/Winter	8.3427805	26039.21	3178.229	7243.453	28.27276	227.9085
709	Spring/Summer	8.3427805	468303.90	48916.599	124333.618	1128.59281	254.1747

Results for maximum velocity between seasons is summarized in Table 4. While the mean for Fall/Winter foraging was higher than for Spring/Summer, high standard deviation in both instances indicate variability within maximum velocity data. Mean maximum velocity did not show definitive seasonal trends, with two individuals (658 and 709) showing higher mean V_{max} during Fall/Winter and two individuals (654 and 652) showing higher mean V_{max} during Spring/Summer foraging (Figure 8). Generally, RSD was higher during in Fall/Winter periods (Table 5), with the exception of individual 658, potentially reflecting sporadic feeding efforts by this animal. Individual 709 had the highest RSD for both seasonal periods. Anecdotally, this individual's movements were generally abnormal due in large part to habituation towards feeding at a fish landing dock in the area. This uncharacteristic foraging behavior may be the source of observed variability of the seals movements and explain higher RSD in the case of maximum foraging velocity.

Table 4. Summary statistics of maximum velocity (V_{max}) for Spring and Fall season foraging trips of gray seals (N=60 for Spring and Fall, respectively). RSD = relative standard deviation. SD = standard deviation.

Vmax by Season (m/s)

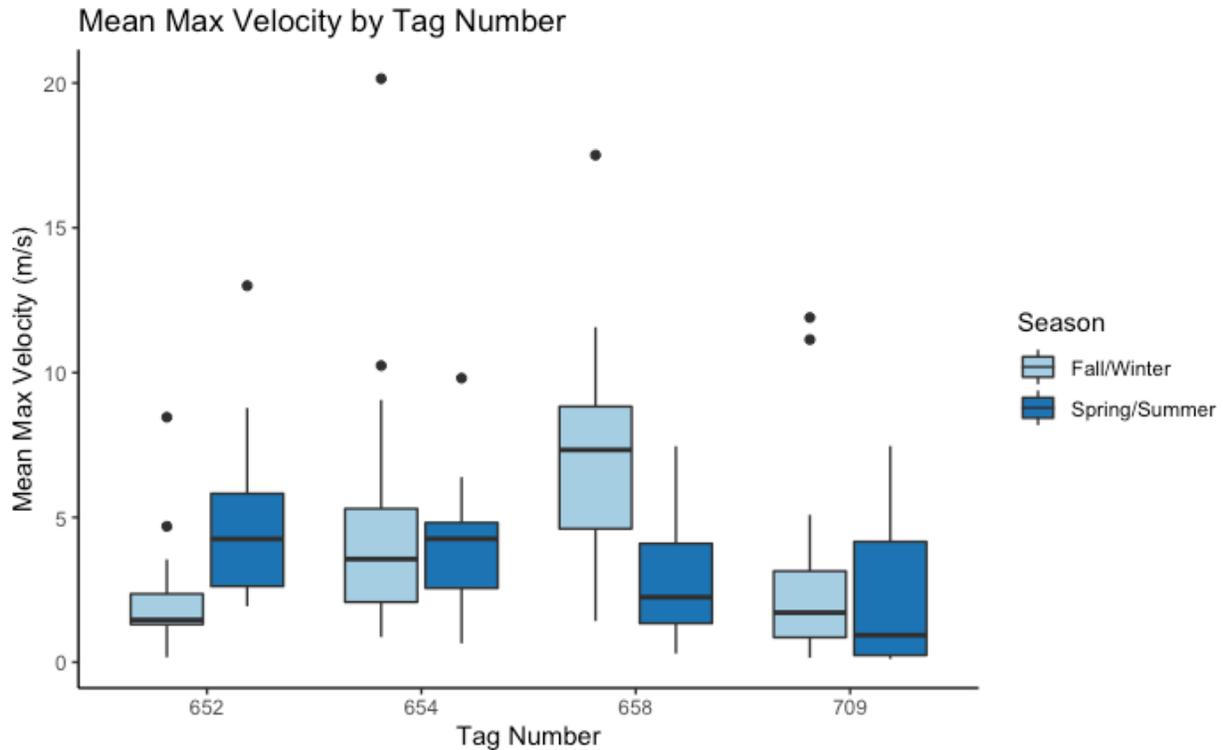| Season	min	max	mean	sd	median
Fall/Winter	0.153	20.15	4.369883	4.208380	2.8225
Spring/Summer	0.110	13.00	3.472700	2.578888	2.9700

Figure 8. Mean maximum velocity (V_{max}) by tag number for Spring and Fall foraging efforts. Greater mean V_{max} was split between individuals, with 652 and 654 exhibiting higher mean V_{max} during Spring/Summer months and 658 and 709 showing higher V_{max} during Fall/Winter months.

Table 5. Summary statistics of V_{max} for Spring and Fall season foraging trips of gray seals separated by individual tag number (N=15 for Spring and Fall, respectively for each individual). Relative standard deviation (RSD) of mean PPV shows higher overall variability during the Fall/Winter with the exception of individual 658. SD = standard deviation.

Vmax by Season (m/s)

TagNumber	Season	min	max	mean	sd	median	RSD
652	Fall/Winter	0.166	8.460	2.193733	2.097732	1.460	95.62385
652	Spring/Summer	1.930	13.000	4.900867	2.937739	4.255	59.94325
654	Fall/Winter	0.866	20.150	4.983267	4.978025	3.560	99.89481
654	Spring/Summer	0.650	9.809	4.002400	2.314354	4.260	57.82417
658	Fall/Winter	1.420	17.510	7.201533	4.032520	7.330	55.99530
658	Spring/Summer	0.296	7.460	2.815067	1.983795	2.245	70.47064
709	Fall/Winter	0.153	11.900	3.101000	3.660804	1.710	118.05238
709	Spring/Summer	0.110	7.466	2.172467	2.311945	0.930	106.42027

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PPV Based on Sex

An assessment of the relationship between space use and sex was less conclusive given the random nature of the stratified sample, which included 3 females and 1 male out of the total cohort, resulting in not only fewer samples from male foraging efforts than female but also lower

overall diversity of samples. Results from an analysis of sex and foraging volume are summarized in Table 6, with a visual of mean volume and standard error shown in Figure 9. Median volume of foraging effort was larger for males (15,595.440 km^3) than females (1,395.562 km^3) based on the sample for the singular male (N = 30) and the three females (N = 90). A T-test of difference in mean volume between male and female foraging efforts revealed a non-significant difference between the two (p = 0.72), and results from the Shapiro-Wilk normality test for datasets of both sexes showed non-normal distribution for both (p$_{Male}$ and p$_{Female}$ < 0.001). Log transformation of data by sex produced a normal distribution for both male and female datasets based on results from the Shapiro-Wilk test (p$_{Male}$ > 0.05 and p$_{Female}$ > 0.30). A T-test using these data showed significant difference between foraging volume of the two groups (t(57) = 2.366, p = 0.02), with male mean foraging volume larger than female mean foraging volume which corresponds with the comparison of median foraging volumes between the two sexes (Table 6). While these results indicate significant difference in foraging volume based on sex, with median PPV larger among males than females, the implications of only a single individual included in the male dataset should be considered and will have undoubtedly impacted analyses particularly with regards to observed variability, requiring further steps in the interpretation of sex on foraging volume.

Table 6. Summary statistics for PPV of male and female gray seal foraging trips (N=90 for females and N=30 for males). SD = standard deviation, RSD = relative standard deviation. Median male PPV is larger than female, suggesting overall larger distribution of PPV in male foraging efforts.

Volume by Sex (km^3)

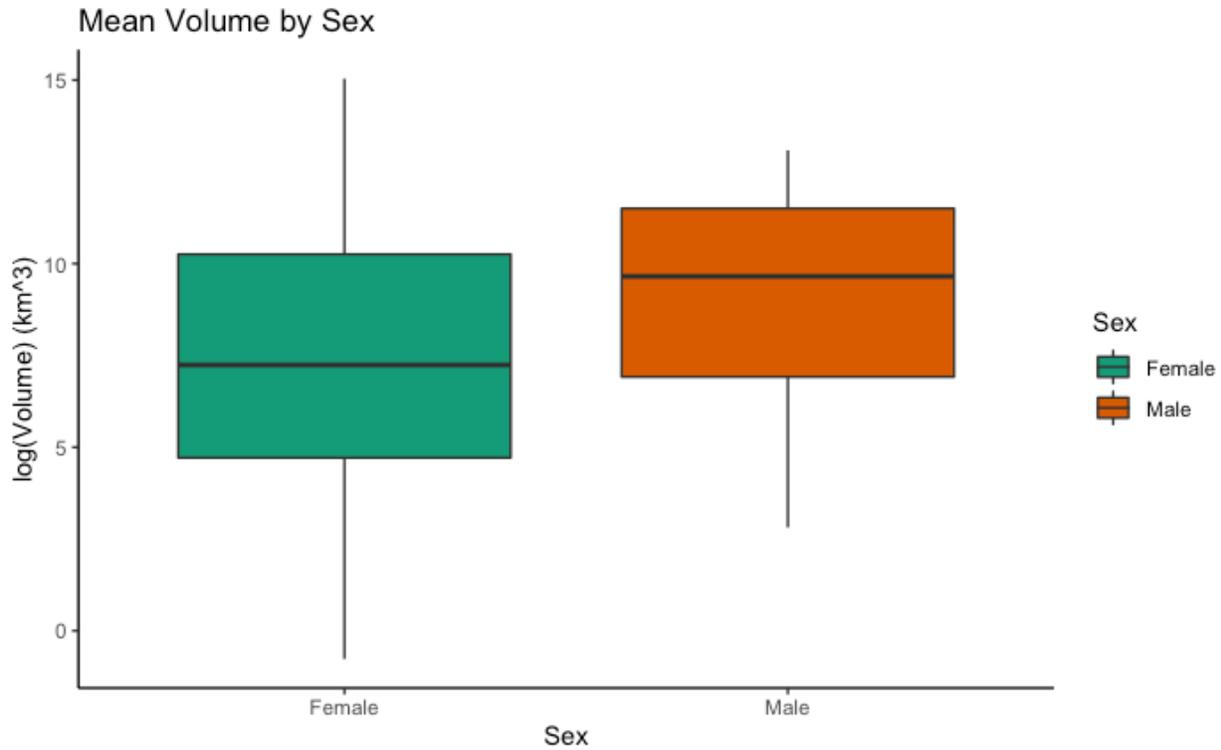| Sex	min	max	mean	sd	median	RSD
Female	0.4634878	3404008.8	112501.71	467144.8	1395.562	415.2335
Male	16.6855611	483321.8	92494.46	149449.9	15595.440	161.5772

Figure 9. Log of PPVs for female (N = 90) and male (N=30) gray seals, showing a greater mean PPV among male samples and higher degree of variability in female volumes relative to male.

Results from a comparison of V_{max} between males are females are summarized in Table 7 and indicate that both mean and median V_{max} among females was lower than males. Mean V_{max} (Table 7) and foraging volume (Table 6) among males appear to be less variable than females, with a lower RSD for the male volumes than female volumes, likely owing to a level of diversity in the female sample that is not mirrored in the male sample which is likely the primary cause for a larger number of outlier data points in the female dataset (Figure 10). Further analysis is therefore required for more conclusive trends between sex and V_{max}/foraging volume.

Table 7. Summary statistics of V_{max} for Spring and Fall season foraging trips of gray seals (N=90 for females and N=30 for males). SD = standard deviation, RSD = relative standard deviation.

Vmax by Sex (m/s)

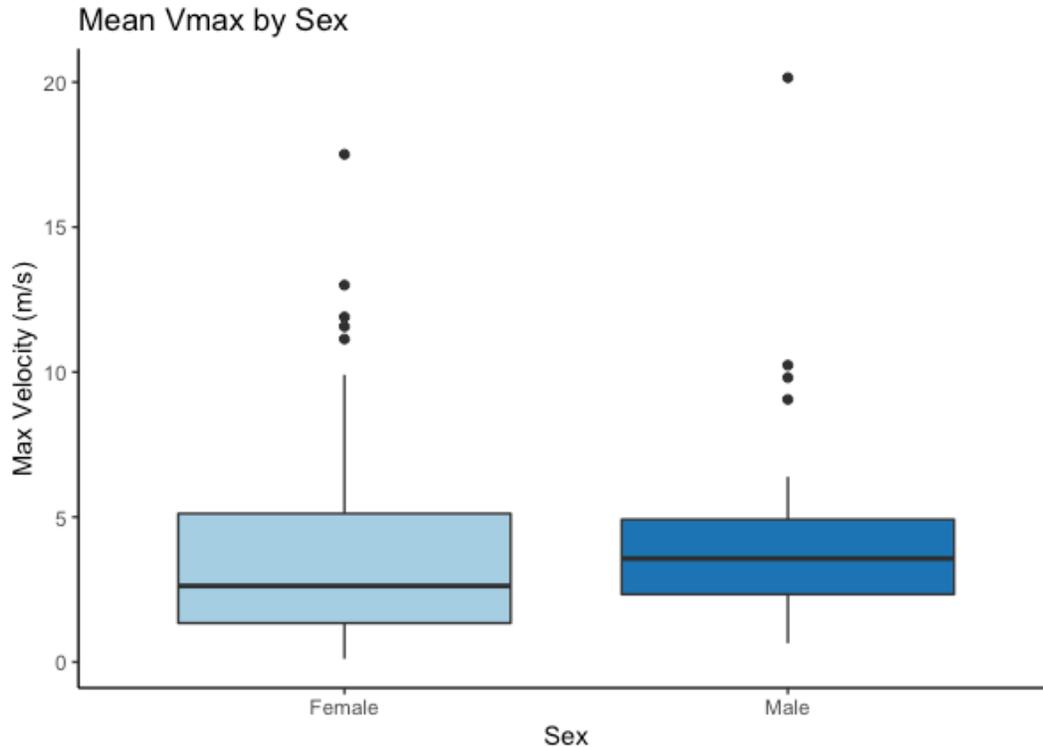| Sex	min	max	mean	sd	median	RSD
Female	0.11	17.51	3.730778	3.384125	2.625	90.70830
Male	0.65	20.15	4.492833	3.846778	3.570	85.62031

Figure 10. Mean V_{max} for female (N = 90) and male (N=30) gray seals, showing a greater mean V_{max} among male samples and higher degree of variability in female V_{max} relative to male.

Discussion

Fish/Seal Overlap and Methodological Considerations

This analysis presents a method for assessing overlap between foraging seals and commercially valuable fish species. Results from cod spatial habitat prediction combined with tracking data from seal foraging efforts presents a compelling addition to previous seal foraging ecology assessments. Historically, gray seal diet and foraging behavior has been largely evaluated using fecal/stomach contents hard parts analysis (e.g. Prime and Hammond, 1990) or fecal DNA sequencing (e.g. Flanders et al., 2020), which can provide insight into diet composition but might be limited by sample availability. Many of these samples are acquired opportunistically from haulout areas or specimens caught as by-catch, which can impact the degree of accuracy with which samples represent trends in population diet overall. The intricacies of gray seal foraging ecology have been further elucidated by the adaptation of stable isotope analysis (e.g. Hernandez et al., 2019 and Tucker et al., 2007), providing additional insight into seasonal and individual variability in foraging niches. These methods rely on samples taken from fur, skin or blood samples, which are sometimes difficult to obtain and require costly equipment and considerable effort. Additionally, methodologies for hard parts

analysis, fecal DNA analysis and stable isotope analysis require laboratory space and specialized equipment as well as the availability of laboratory technicians to process samples. Species distribution modeling and development of a habitat prediction raster, on the other hand, is more accessible, with modeling conducted on a computer using R software and data that is frequently available from historic fieldwork and preexisting databases, such as OceanAdapt. Using spatial overlap as an assessment of seal foraging ecology reduces some of the uncertainty introduced by sampling for fecal specimens and may limit costs associated with tissue sample extraction for stable isotope analysis in addition to avoiding laboratory processing costs.

Modeling habitat of primary prey items not only circumnavigates limitations of traditional diet analyses, but also presents opportunities for expansion of gray seal foraging ecology assessments. While not performed in this analysis, modeling potential prey habitat into the future is now possible using a similar methodology outlined here but replacing historic climatological data with that of models such as the World Climate Research Programme's Coupled Model Intercomparison Project (CMIP) (https://www.wcrp-climate.org/wgcm-cmip) which provides projections of climatological shifts into the future (e.g. Nye et al., 2009). By implementing future climatological predictions in model development, it would be possible to determine how prey distribution might shift moving forward and potential implications for interactions between fishing effort and foraging animals. These interactions are often detrimental to fishers and seals alike, with animals caught, and many times killed, as bycatch in fishing gear as well as costs sustained by the fisher resulting from depredation and gear damage (Nichols et al., 2011; Gruber, 2014). Although managers, including NFMS and New England States agencies, are still working to fully understand the nature of interactions between foraging gray seals and fishers, preemptive management techniques aimed at mitigating negative interactions between the two would be beneficial to an already contentious management space. Assessments of commercially valuable prey distribution, including future projections and current distribution probability surfaces, have the potential to act as a tool for fishers. With the ability to determine areas of high prey habitat suitability that simultaneously experience significant seal foraging traffic, fishers might be able to preemptively avoid potential areas of high seal foraging activity, thereby limiting detrimental interactions between fishing efforts and foraging seals and mitigating conflict between the fishing and conservation sectors.

While there are several benefits to the implementation of statistical modeling of species distribution of seal prey items, it is important to note that the type of spatial evaluation presented in this analysis is somewhat limited in determining finer scale elements of seal diet, such as compositional breakdown by species. Instead, habitat modeling is more suited for understanding broad scale trends in foraging ecology. Additionally, while a habitat raster is useful for determining potential spatial distribution of a target species, it is by no means certain that the target species will be present in habitat with a high predicted probability of occurrence. Although the habitat modeling performed in this study is a good starting point for determining potential overlap between foraging seals and commercially important species, the models included here did not consider cod biomass, but only presence/absence, as a response variable. Moving forward, therefore, it would be important to expand modeling efforts to consider biomass of target prey items when present to more fully understand how foraging seals might interact with not only these prey items, but also fishing efforts targeting the same species. The addition of biomass of a species when present might provide a clearer indication of whether a foraging seal, or indeed a fisher, would expend energy to visit a prey patch based on quality of the patch, with areas of high biomass likely being more frequently visited by both seal and fisher. Despite these limitations, however, suitable habitat for targeted prey items is a useful metric to consider when evaluating seal foraging ecology and spatial overlap with fishing effort. Combined with finer scale analyses of diet composition using hard parts/DNA and isotopic niche analysis, these methodologies can work together to create a more wholistic impression of seal foraging ecology in areas where overlap with commercially important fisheries are likely to occur.

Seal Space Use: Implications for Conservation and Management

Trends in seal space use outlined in this study help expand on our understanding of seal movement during foraging periods, however results from the comparison of volumetric space use between Spring/Summer and Fall/Winter foraging periods contradict results from previous studies. Predation pressure from white sharks is known to limit seal foraging distribution in the warmer months as sharks congregate around haulout sites to target seals as they exit or enter the water (Skomal et al., 2012; Fallows et al., 2016; Martin et al., 2005). Risk of predation increases with foraging distance from the haulout site (Olsson et al., 2008; Hugie and Dill, 1994) and seals respond by limiting foraging movements to nearshore areas (Moxley et al., 2020). Seals therefore exhibit a noticeable expansion in range during the winter months as pressure from white sharks

dissipates (Moxley, 2016), implying a subsequent increase in space use during this time period. This analysis, however, revealed overall higher foraging volume among the Spring/Summer season, although results cannot be considered conclusive based on the complications with data distribution mentioned above. Despite uncertainty surrounding the extract nature of differences in foraging volume based on season, however, nonparametric test results indicate that overall foraging space use is significantly different between the two seasonal periods, although further study is required for a more thorough understanding of these differences.

Additionally, there is a greater overall variability in foraging patterns during colder months, potentially reflecting the longer and more widespread foraging efforts identified in previous studies of seal foraging ecology (Moxley et al., 2020). This analysis found variability in Fall/Winter foraging efforts to be higher among all individuals, reflecting an expansion of range into offshore habitats (Olsson et al., 2008; Breed et al., 2009). As a result of the depletion of nearshore prey patches during constricted summertime foraging, seals are required to make more prolonged foraging efforts (Breed et al., 2009), and exhibit an expansion of spatial range and temporal trip duration during the colder months (Moxley et al., 2020). Variability both between and among individuals' foraging efforts is therefore more pronounced, reflecting expansion of wintertime foraging range required to target more dispersed high-quality prey patches (Moxley et al., 2020; Breed et al., 2009). Yet while variability from Fall/Winter foraging volume is concurrent with past analyses, variability of Spring/Summer volume was still found to be greater than previous results would suggest. Presumably, the range limitations incurred by white shark presence, which studies have shown result in more pronounced overall uniformity between individuals foraging during the summer months (Brown & Kotler, 2004; Moxley et al, 2020), would significantly reduce overall variability of foraging volume during warmer months. Results from this analysis, however, show pronounced variability during this time period, albeit not to the degree of Fall/Winter foraging efforts, contrary to the expected trends in seasonal differences of mean volumetric space use.

This analysis was able to further illustrate trends in foraging behavior through assessment of the impact of sex on foraging space use. Median values of foraging volume based on sex revealed an overall larger space use among males, although results are compromised by implications of having only a single male represented in the dataset used for this analysis. Greater volumetric space use shown by the male individual, however, is concurrent with results

from past research. Historically, male and female seals have demonstrated divergent foraging responses to energetic costs of reproduction as well as seasonal prey availability, with males commonly targeting a greater proportion of deep-water demersal fish species (Breed et al., 2006; Beck et al. 2007; Breed et al., 2009). Conversely, females make up for energetic demands of reproduction by primarily targeting shallower prey patches located closer to shore (Breed et al., 2006). Results from this analysis echo sex-based foraging trends seen in past, with median foraging volumes of male efforts larger than female. However, it is important to note that variability in the volume of foraging effort among females was more pronounced, contrary to what was expected given larger range extent seen in males. This is undoubtedly caused by disparate cohort size among male and female samples, wherein dive data from three females were used compared to data from only one male. The increased variability seen in the female dataset reflects the inter-individual differences in foraging habits, which is not captured in the limited male sample.

Despite limitations of these analyses, an exploration of seal space use during foraging efforts is important in understanding seal foraging ecology more broadly. Seasonal volumetric space use can help shed light on range dynamics during commercially important fishing seasons, helping managers and fishers alike to anticipate potential interactions with this protected species. Furthermore, a more thorough understanding of seal space use might shed more light on the predator-prey dynamic between gray seals and white sharks. Pronounced trends in foraging behavior and space use might help elucidate how this species responds to food-safety tradeoffs during the summer months. A more contained foraging effort, which presumably would be reflected in a smaller overall foraging volume, would further support the argument for white shark predation pressure as a primary mechanism for limiting seal foraging range during the Spring/Summer. This, in turn, might have larger implications for managing interactions between commercial fishing efforts and foraging seals. Although white shark presence is inherently problematic for coastal recreation and communities that rely on tourism during the summer months, the range control inflicted by sharks has the potential to significantly limit interactions between fisheries. By restricting seal movement through the threat of predation, white sharks might act as natural conflict mitigation between commercial fishers and protected gray seals, simplifying the complicated conservation issue that management entities, such as NOAA, currently face with gray seal communities off the MA coast. While further study is required to

better assess trends in space use of foraging gray seals, an improved understanding of foraging behavior, and potential impacts of shark predation, might greatly benefit managers, coastal communities and fishers alike.

Finally, it's important to consider how a more holistic view of seal foraging distribution, and overlap with prime cod habitat, might shed light on recovery of cod stocks. The vulnerable cod population continues to confound management entities, which struggle to understand the inability of the species to recover despite concerted conservation efforts (Cook, 2019; NOAA Fisheries, 2021). With a long legacy in the New England area and particular commercial value (Rose, 2019), recovery of the cod fishery remains a critical conservation issue. Cod are a long-lived demersal species and act as a top predator in the bottom ocean community, feeding on many different fish species and invertebrates (NOAA Fisheries, 2021; Kindsvater and Palkovacs, 2017). As a top predator in deep water regions, cod occupy a similar ecological niche as gray seals who, as previously mentioned, also target demersal fish species during foraging efforts (Beck et al. 2007, Breed et al. 2009). Currently, overfishing has severe implications for cod's ecological niche, truncating age and size structure and inhibiting the species' role as a top predator (Kindsvater and Palkovacs, 2017). While cod stocks decline, gray seals populations continue to increase under protections of the MMPA (Wood et al., 2020). The diminished cod stock poses little competitive threat to the robust seal population, which exploits resources shared with not only cod, but also commercial fishermen. The issue of 'not enough fish in the sea' is a widespread one, but an expansion of knowledge of gray seal foraging efforts might provide valuable insight into issues currently plaguing recovering cod stocks and fishers alike. A more thorough understanding of gray seal foraging space use and associated take of commercially important primary prey items might enable managers to better assess how seal feeding behavior directly impacts recovery of cod stocks.

Conclusions

The dramatic and continued expansion of the southern New England grey seal population is an exceptional story of recovery from historically depleted populations. However, as gray seal communities continue to recolonize these areas, the increased presence of this mesopredator, and associated trophic implications (Paine, 1980), have become a source of contention for fishers and tourists, creating a unique conservation issue. Managers are faced with the question of navigating conservation of a booming protected marine mammal population while respecting the interests of

the commercial fishing sector, to whom gray seals are many times seen as a nuisance. These analyses outline two approaches for better understanding the foraging ecology of gray seals from two perspectives. The first, which includes implementation of species distribution modeling to understand interactions between foraging seals and commercially important fish species, aims to understand potential hot spots where both fishers and seals might hunt for target species. The second, which outlines the use of a potential path volume methodology to elucidate space use of foraging seals, is meant to further expand upon previous studies of gray seal foraging ecology off the coast of Cape Cod to help determine seasonal variation in foraging efforts and the potential mechanisms driving trends in seal space use. As managers continue to grapple with the conservation of gray seals in New England, these techniques offer valuable inside into movements of the species. While the methodologies outlined here are still in a nascent stage, together with traditional analyses of gray seal diet composition, a more thorough understanding of the intricacies of gray seal feeding ecology and associated implications for the surrounding ecosystems will help managers mitigate negative interactions between seals and humans into the future while fulfilling conservation requirements established by the MMPA.

Limitations and Further Study

When interpreting the results from these analyses it's important to consider some limitations of the methodologies outlined here. Firstly, the data used for constructing species distribution models, while comprehensive, did not produce a large percentage of cod caught in either Fall or Spring trawls. The presence/absence of cod in trawl sampling efforts might not be entirely representative of population distribution and future modeling efforts should include a more diverse dataset from both fishery independent and dependent sampling efforts (see Pauly et al., 2013 for the merits of fishery dependent and independent data collection). Additionally, the benthic habitat classification composite variable used in modeling makes it difficult to parse out individual impacts of slope/position/depth on cod presence/absence. Future modeling should therefore consider inclusion of these three variables as separate covariates. Next steps for modeling cod habitat should also include biomass as a response variable, to better predict abundance of the species when present as a useful metric for determining likelihood of seals/fishers targeting areas of cod presence given the assumption that both would be more compelled to harvest in areas of higher abundance. Further assessments of seal foraging and overlap would also depend on additional tracking data from seal communities, which can be

costly and labor intensive to collect. It should also be noted that NMFS trawl data is separated into Fall/Spring seasons, while seal foraging exhibits distinct trends between Summer and Winter foraging periods. The overlay of cod habitat in the Spring/Fall with foraging efforts of these corresponding periods might therefore not entirely capture trends seen in gray seal foraging behavior. Future expansion on this project should therefore include fishing data from the Winter/Summer seasons as well to accurately determine how seal foraging might respond to prey species distribution within corresponding time periods. Finally, it is a well-known fact that all modeling comes with its own limitations; in the words of George Box "all models are wrong, some are useful". It is important to always ground truth results with field research to understand the shortcomings of the statistical modeling process (for more on species distribution modeling see Mannocci et al., 2017).

Secondly, the adaptation of the PPV methodology for this analysis revealed several conceptual issues that bear further consideration. The computational requirements of this methodology are considerable and depend on thorough attention to certain variables, such as voxel size resolution and maximum velocity. To that end, the voxel size used in this analysis was held constant throughout PPV calculations among all individuals to maintain a consistent resolution. This number was derived from the individual seal with the largest foraging extent however it is important to note that some movements of this individual were uncharacteristically widespread and don't necessarily reflect traditional foraging tactics used by this species. Future implementation of this methodology should therefore include more in-depth contemplation of voxel size and consider limiting overall extent of cohort foraging to produce a realistic resolution and voxel size. Finally, the random stratified sample taken for this analysis produced results contrary to results seen in past studies on gray seal foraging behavior and what was originally hypothesized. As samples taken from the total cohort came from only 4 individuals and were limited in number (N = 15 for each individual for Spring/Summer and Fall/Winter respectively), the next steps in this methodology should be to expand calculation to the entire cohort and all dive days recorded for each individual in the hope that this might better align with historic foraging ecology research. Given these adjustments, the continued development of PPV methodology undoubtedly has the potential to provide a clearer, more accurate understanding of seal foraging space use.

Acknowledgments

Code Availability

Code used to run these analyses, perform statistical analyses and generate figures can be found at: https://github.com/bcanfields/Master-s-Project

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