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Black Scoter (*Melanitta americana*) Winter Habitat Use and Movement Patterns Along the Atlantic Coast of the United States

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BLACK SCOTER (*MELANITTA AMERICANA*) WINTER HABITAT USE AND
MOVEMENT PATTERNS ALONG THE ATLANTIC COAST OF
THE UNITED STATES

A Thesis
Presented to
the Graduate School of
Clemson University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science
Wildlife and Fisheries Biology

by
Hannah Plumpton
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Accepted by:
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ABSTRACT

While the Atlantic coast of the United States and Canada is a major wintering area for sea ducks, habitat use and movement patterns of sea ducks, such as the black scoter (*Melanitta americana*), are vastly unknown and understudied. The lack of information in conjunction with a rise in human activity in and near the Atlantic Ocean has led to an increased effort for the conservation and management of sea ducks, while minimizing human conflicts. The objectives of my study were to 1) identify variables that had the most influence on black scoter distribution in the Atlantic Ocean along the southeastern coast of the United States and 2) investigate the winter movement patterns of black scoters in the Atlantic Ocean by quantifying the number of wintering sites, arrival and departure dates to and from the wintering grounds, days at a wintering site, area of a wintering site, distance between wintering site, and test if winter movement patterns varied by sex or geography.

To identify the variables that were the most influential on black scoter distribution along the southeastern coast of the United States, I used aerial survey data from 2009 to 2012 provided by the United States Fish and Wildlife Service. I ran a Least Absolute Shrinkage and Selection Operator (LASSO) with broad and fine scale oceanographic and weather variables. The oceanographic variables of bathymetry, ocean floor slope, and distance to shore were found to have the greatest association with the distribution of black scoter. Additionally, my results suggest that oceanographic variables have a stronger relationship with black scoter distribution than weather variables.

To quantify winter movement patterns of black scoters, I used satellite telemetry data from 2009 to 2012 that was provided by the Sea Duck Joint Venture. I used Mann-Whitney *U*-tests to quantify the differentiation between sex and geography. While there was no difference between sexes, average wintering site area and distance between wintering sites differed by geographic region. Southern wintering sites were larger and farther apart than northern wintering sites. These results suggest that black scoter habitat use and movement patterns vary regionally. My results enable managers to focus sampling effort for black scoter abundance and distribution along the Atlantic coast. Habitat characteristics for black scoters identified in my study area should be carefully considered when planning anthropogenic activities along the southeast coast of the United States, such as offshore energy development.

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CHAPTER ONE

INTRODUCTION

Ecological and behavioral physiological phases of the annual life cycle of wildlife can influence individual- and population-level processes during subsequent phases (e.g., carry-over effects; Harrison et al. 2011, Marra et al. 2015). These carry-over may impact ecological and evolutionary processes in birds (Ebbinge and Spaans 1995, Baker et al. 2004, Norris et al. 2004, Saino et al. 2004, Gunnarsson et al. 2006, Sorensen et al. 2009, Sedinger and Alisauskas 2014). While research on birds is primarily conducted on the breeding grounds, migratory birds spend the majority of their annual life cycle off the breeding grounds (Marra et al. 2015). Poor quality habitat and a scarcity of resources during the wintering period and spring migration can decrease chances of survival and lower body condition for the subsequent phases of the annual cycle (Heitmeyer and Fredrickson 1981, Kaminski and Gluesing 1987, Ebbinge and Spaans 1995, Gunnarsson et al. 2006, Martin and Wiebe 2004, Studds and Marra 2007, Osnas et al. 2016, Rushing et al. 2017).

Availability of quality non-breeding habitats may influence population dynamics (Scott 1998, Harrison et al. 2011, Marra et al. 2015). The quality and quantity of habitats and associated resources during the non-breeding season may be important limiting factors for waterfowl (Lack 1966, Fretwell 1972). Poor winter habitat conditions have been associated with large mortality events (Camphuysen et al. 2002), decreased reproductive success (Nichols et al. 1983, Kaminski and Gluesing 1987, Raveling and Heitmeyer 1989, Oosterhuis and Dijk 2002, Guillemain et al. 2008), and decreased

population growth rates (Petersen and Douglas 2004, Saino et al. 2004, Sorensen et al. 2009).

Sea duck (tribe *Mergini*) distribution within the wintering range may be based on a variety of site-specific factors including local environmental conditions, food availability, predation risk, site fidelity, and human activity (Greenwood 1980, Guillemette et al. 1993, Madsen and Fox 1995, Lewis et al. 2008, Loring et al. 2014, Beuth et al. 2017). Sea ducks spend winters on large bodies of water, such as the Great Lakes and oceans, which are complex and difficult to study due to their dynamic nature, making it challenging to quantify habitat quality for sea ducks during the non-breeding season. While the Atlantic coast of the United States and Canada is a major wintering area for sea ducks, movement patterns and habitat use of sea ducks is mostly unknown and understudied (Kaplan 2011, Jodice et al. 2013, Boyd et al. 2015).

The 15 species of sea ducks are the least studied group of waterfowl in North America (Sea Duck Joint Venture 2014, Boyd et al. 2015). Very little is known about their life history traits, habitat preferences, and movement (Zipkin et al. 2010, Sea Duck Joint Venture 2014). As recently as 1999, basic biological information was lacking or non-existent for most sea ducks, as they inhabit remote, hard to access locations (Sea Duck Joint Venture 2014). Sea ducks breed in the tundra and boreal forest in the arctic and winter on large bodies of waters, such as the Great Lakes and the oceans. In the early 1990s, sea duck populations were declining with unknown causes (Caithamer et al. 2000, Sea Duck Joint Venture 2014). In 1999, the North American Waterfowl Management Plan (NAWMP) Plan Committee endorsed the Sea Duck Joint Venture (SDJV) to focus

on filling information gaps to improve the management and conservation of sea ducks in North America (Sea Duck Joint Venture 2014). In the first 10 years of the SDJV's existence, most of the studies on sea ducks were done on populations in the Pacific and Arctic regions of North America with comparatively little work done in the Atlantic flyway. Recently, there has been an increased focus to learn more about sea duck breeding habitat and success, migration timing and routes, and non-breeding habitat in the Atlantic flyway (Sea Duck Joint Venture 2015).

Five of 12 species of sea ducks that winter along the Atlantic coast are considered high priority due to historical or current population decline, habitat limitations, and concern about the impact of harvest (Sea Duck Joint Venture 2014). The five species are the long-tailed duck (*Clangula hyemalis*), American common eider (*Somateria mollissima*), black scoter (*Melanitta americana*), surf scoter (*M. perspicillata*) and white-winged scoter (*M. fusca*). Of these species, black scoters were found in high densities along the southern half of the Atlantic coast and had the most annual variation in their wintering distribution (Silverman et al. 2013). While there are no reliable data to estimate the long-term trends of the Atlantic black scoter population (Bowman et al 2015), the black scoter is listed on the International Union for Conservation of Nature and Natural Resources (IUCN) Red List of Threatened Species as "Near Threatened." (BirdLife International 2013). A species is "Near Threatened" when it does not qualify for "Endangered" or "Vulnerable" currently, but is likely to qualify for a threatened category possibly in the future. The "Near Threatened" category was assigned due to the current

decreasing population trend related to a variety of mixed evidence suggesting a moderately rapid decline (BirdLife International 2013).

There has been an increase in human activity in the Atlantic Ocean in the past several years (Silverman et al. 2013), but it remains unknown how anthropogenic activity might affect sea duck wintering distributions. These activities range from coastal development, aquaculture, shipping, sand mining, and energy production. The potential development of wind farms in off-shore areas in the Atlantic Ocean could lead to the possible displacement of black scoters due to loss of habitat and collisions with structures. Proposed wind energy development along the Atlantic coast that occurs in core black scoter wintering area increases potential to displace black scoters and decrease resources necessary to maintain physiological body condition (Studds and Marra 2007, Rushing et al. 2017).

Understanding wildlife population distribution and population dynamics as it relates to habitat use promotes effective conservation planning, minimizing human conflicts, and better survey planning for future monitoring programs (Newbold and Eadie 2004, Rushing et al. 2017). The objective of this study is to increase knowledge on the wintering habitat use and movement patterns of black scoters along the Atlantic coast of the United States and provide new insight into black scoter conservation and management.

CHAPTER TWO

BLACK SCOTER HABITAT USE ALONG THE SOUTHEASTERN COAST OF THE UNITED STATES

Introduction

Different phases of the annual life cycle can influence individual- and population-level processes during ensuing phases (e.g., carry-over effects; Harrison et al. 2011, Marra et al. 2015). These carry-over effects can strongly impact both ecological and evolutionary processes in birds (Ebbinge and Spaans 1995, Norris et al. 2004, Sorensen et al. 2009). While avian research is primarily conducted on the breeding grounds, migratory birds spend the majority of their annual life cycle off the breeding grounds (Marra et al. 2015). Poor quality habitat and variable resources during the wintering period and migration can decrease chances of survival and lower body condition for the subsequent phases of the annual cycle (Gunnarsson et al. 2006, Studds and Marra 2007, Rushing et al. 2017).

The quality and quantity of habitats and resources during the non-breeding season may be important limiting factors for waterfowl (Lack 1966, Fretwell 1972, Sedinger and Alisauskas 2014), and can have a detrimental effect on population dynamics (Alisauskas and Ankney 1992, Scott 1998, Martin and Wiebe 2004). Poor winter habitat conditions have been associated with large mortality events (Camphuysen et al. 2002), decreased reproductive success (Nichols et al. 1983, Oosterhuis and Dijk 2002, Guillemain et al. 2008), and decreased population growth rate (Petersen and Douglas 2004, Saino et al. 2004, Sorensen et al. 2009). Despite the importance of high quality wintering habitat,

there is limited information on winter habitat preference and use for sea ducks, particularly along the Atlantic coast of the United States (Kaplan 2011, Jodice et al. 2013, Boyd et al. 2015, Sea Duck Joint Venture, 2015).

Avian distribution results from the selection of habitats at multiple scales (Fretwell and Lucas 1970, Wiens 1985, Cunningham and Johnson 2016). Greater abundance of birds may indicate areas of higher quality habitat across a species' distribution (Einarsson 1988). Sea duck distribution within the wintering range may be based on a variety of factors including local environmental conditions (Loring et al. 2014, Beuth et al. 2017), food availability (Guillemette et al. 1993, Lewis et al. 2008), predation risk, site fidelity (Greenwood 1980), and human activity (Madsen and Fox 1995). Sea ducks winter on large bodies of water, such as the Great Lakes and oceans, which are complex and difficult to study due to their dynamic nature, making it challenging to quantify habitat quality for sea ducks during the non-breeding season. Therefore, because these dynamic systems are challenging to study using the environmental data currently available, quantitative methods are needed to analyze data with few observations and variables with small effects.

In an effort to quantify the abundance and wintering distribution of sea duck populations along the Atlantic coast, the U.S. Fish and Wildlife Service (USFWS) initiated the Atlantic Coast Wintering Sea Duck survey in 2008 and conducted aerial surveys from 2008 to 2012 along the Atlantic coast of the United States (Silverman et al. 2013). These surveys focused primarily on five species of concern due to current population declines, potential harvest implications, or habitat limitations (Sea Duck Joint

Venture 2014). The species surveyed were the common eider (*Somateria mollissima*), long-tailed duck (*Clangula hyemalis*) surf scoter (*Melanitta perspicillata*) white-winged scoter (*Melanitta fusca*) and the black scoter (*Melanitta americana*). Preliminary analyses from those aerial surveys indicated that black scoters had not only the largest range of the sea ducks surveyed, but also had the most variability in their inter-annual distribution (Silverman et al. 2013). A better understanding of the factors that are driving this inter-annual distribution will help improve future survey design.

Black scoter distribution can be influenced on a fine (< 2 km) and broad scale by oceanographic and weather conditions (Zipkin et al. 2010). Distance to shore and water depth effect black scoter winter distribution (Loring et al. 2014), as well as the North Atlantic Oscillation (Zipkin et al. 2010). In addition to oceanographic and weather variables, the wintering distribution of black scoters could be affected by a variety of anthropogenic sources, such as off-shore wind energy development, coastal development, aquaculture, shipping, sand mining, and energy production. It remains unknown how anthropogenic activity might affect sea duck wintering distributions (Silverman et al. 2013, Sea Duck Joint Venture 2015). The potential development of wind farms in off-shore areas in the Atlantic Ocean could lead to the possible displacement of black scoters due to loss of habitat and collisions with structures. In Europe, sea duck density was affected due to sea ducks avoiding areas with wind turbines in shallow water (Larsen and Guillemette 2007, Langston 2013). In New England, Loring et al. (2014) found that large core use areas for black scoters in near shore areas were surrounding the federal lease block for off-shore wind energy that could cause barrier effects and increase the

susceptibility to collisions (Fox et al. 2006, Langston 2013). Identifying key environmental factors could help identify near-shore and off-shore areas of the Atlantic coast where wind power facilities and other developments would have the least impact on black scoters (Silverman et al. 2013, Sea Duck Joint Venture 2015). The objective of this study was to identify environmental covariates that explained the most variation black scoter distribution along the Atlantic Coast of the Southeastern United States. Understanding what factors correlate black scoter habitat use can help to minimize human conflict, improve survey design, and increase knowledge for black scoter conservation and management.

Methods

Survey Design

The U.S. Fish and Wildlife Service conducted aerial off-shore winter surveys from 2009 to 2012. From 2009 to 2011, pilots flew from the North Carolina-Virginia border (36°55' N) U.S.-Canada border to Jacksonville, Florida (30°21' N) in February. In February 2012, pilots flew from the South Carolina-North Carolina border (33°75' N) to the Florida-Georgia border (30°70' N). Surveys consisted of east-west transects spaced at 5 nautical mile (nm) intervals of latitude (2.5 nm in 2012). Transect length was the longer of the two following distances: 14.8 km or the distance to the 16-m depth boundary starting from the coastline and heading east. Twelve 2-person crews (pilot-observer and observer) conducted the surveys using USFWS fixed-winged aircrafts flown at ca. 70 m and 204 km/h. The pilot-observer and observer counted all sea ducks within 250 m of

their side of the aircraft (Figure 1). More details about the survey methodology are described in Silverman et al. (2013).

In order to account for unoccupied areas in the survey, I subset the transects flown by USFWS during the aerial surveys into grid cells that were 1000 m long and 550 m wide (275 m on each side of the transect) using the packages Dspat (Johnson et al. 2014), GISTools (Brunsdon and Chen 2014), and spatstat (Baddeley et al. 2017) in program R (v. 3.4.0; R Development Core Team 2017). I used a width of 550 meters to encompass the area surveyed plus an additional 25 meters to each side of the surveyed area to account for possible global positioning system (GPS) error. I summed the number of black scoters observed in each grid cell as the response variable, ranging from zero to the maximum count value. To calculate the value for each environmental covariate of interest (below), I either used the center of the grid cell (for distance to shore) or calculated the mean of a given variable for each grid cell using the raster package (Hijmans et al. 2016).

Habitat Variables

Because distributions of sea ducks appear to respond to a combination of local habitat conditions and broad-scale weather patterns (Zipkin et al. 2010), I considered the following oceanic environmental variables in my analysis. A broad-scale variable, I considered was marine ecoregion and the fine-scale variables were distance to shore, bathymetry, ocean floor slope, and ocean floor substrate. Marine ecoregions are regions of relatively similar benthic and shelf pelagic (neritic) species composition and are clearly distinct from adjacent systems as a result of several variables including temperature regimes, currents, bathymetry, and sediments (Spalding et al. 2007). The

three ecoregions included in this study were Virginian, Carolinian, and Floridian.

Distance to shore is a fine-scale factor that may have a substantial impact on black scoter distribution. Black scoters in New England and Newfoundland primarily use subtidal (<20 m from shore) or near-shore habitats (<5km from shore; Goudie and Ankney 1988, Loring et al. 2014). Bathymetry, or water depth, also may affect black scoter distribution; black scoters primarily use water depths averaging 13-15 m in New England (Loring et al. 2014), but it is not known what water depth black scoters use along the southeastern coast of the United States. The slope of the ocean floor may influence black scoter distribution (Zipkin et al. 2010, Silverman et al. 2013), but given the variable nature of ocean-floor topography along the Southern Coast relative to the Northern Coast, it is unclear how slope will influence black scoters along the southeastern coast of the United States.

In addition to oceanographic variables, I also considered weather variables that could affect black scoter distribution. A broad-scale variable I considered was North Atlantic Oscillation (NAO) and the fine-scale variables were average wind speed and average time between waves. The NAO index is a broad-scale weather pattern that can affect black scoter distribution (Zipkin et al. 2010). The NAO index is based off the difference in air pressure at the surface sea-level between the semi-permanent low near southwest Iceland and the semi-permanent high over Gibraltar (Hurrell 1995, Hurrell et al. 2003). Positive phase NAO tends to be associated with above-normal temperatures and above-average precipitation along the eastern coast of the United States, while negative phase NAO tends to be associated with below-normal temperature and below-

normal precipitation along the eastern United States. Many influential fine-scale weather variables in terrestrial habitats (i.e. precipitation, air temperature) can have little influence in marine systems. Average wind speed (meters/sec) and average wave period (time between wave crests or troughs, sec) are fine-scale weather variables believed to more relevant variables in marine systems (Palm et al. 2013).

I acquired the following four data sets to assess possible effects of ocean environmental variables on black scoter wintering distribution. I obtained bathymetric data from the National Oceanic and Atmospheric Administration's (NOAA) National Geophysical Data, ETOPO1 Global Relief Model (Amante and Eakins 2009). I calculated ocean floor slope (degrees) by using the bathymetry data (Amante and Eakins 2009), and finding the difference of the values between neighboring cells (Table 1). I calculated distance to shore by finding the Euclidean distance between the center of the grid cell and the nearest shoreline. I obtained shoreline shapefile from NOAA's National Centers for Environmental Information Global Self-consistent, Hierarchical, High-resolution Geography Database (GSSH), version 2.3.6, using the intermediate resolution (i) and the boundary between land and ocean (L1; Wessel & Smith 1996). I obtained the ocean floor substrate data from NOAA's Office of Coastal Management Digital Coast, Atlantic Seafloor Sediment Continental Margin Mapping (CONMAP; Poppe et al. 2014). I acquired the shapefile for the marine ecoregions of the world (MEOW; Spalding et al. 2007) from the World Wildlife Fund (WWF).

I acquired the following three data sets to determine the effects of weather on black scoter wintering distribution. I obtained monthly values for NAO from the Climatic

Research Unit, University of East Anglia, Norwich, UK

(<https://crudata.uea.ac.uk/cru/data/nao/>). I obtained daily values of average wind speed for the corresponding dates of the aerial surveys for all grid cells from NOAA's National Data Buoy Center. I then averaged the daily wind speed of survey dates for each grid cell to calculate the average wind speed. I acquired data from 20 buoys located along the southeastern U.S. coast from the Virginia coast (37°60' N) to the Florida-Georgia border (30°70' N). I calculated the average wind speed across this region by using inverse distance interpolation over the latitude range of 28° to 39° N and over the longitude range of -82° to -72° N with the gstat package (Pebesma and Graeler 2017). Inverse distance interpolation is when cell values are predicted based on their distance from known cell values. Cells that are closer to known values will be more influential than points further away. The power value determines the influence distance from the known values, with a higher power value the distance influenced by the known values increases. I used a power value of 2 to calculate the average wind speed along the southeastern coast of the United States between the buoys. I obtained daily values of average wave period for the corresponding dates of the aerial surveys for all grid cells from the NOAA's National Data Buoy Center. I then averaged the daily average wave period of survey dates for each grid cell to calculate the average wave period. I acquired data from nine buoys located along the southeastern U.S. coast from the Chesapeake Bay (36°91' N) to the Georgia border (31°40' N). I calculated the daily wave period across this region by using inverse distance interpolation over the latitude range of 28° to 39° N and over the longitude range of -82° to -72° N with the gstat package (Pebesma and Graeler 2017). I used a power

value of 2 to calculate the average time between waves (sec) along the southeastern coast of the United States between the buoys (Table 1).

Model Fitting

I used the least absolute shrinkage and selection operator (LASSO; Tibshirani 1996) to determine environmental variables that best predicted black scoter wintering distribution along the southern Atlantic coast of the United States. The lasso regression is a penalized estimation method that reduces (i.e. shrinks) non-significant variables to zero, keeping only variables important to the model at a user-specified cutoff value (Tibshirani 1996, Hastie et al. 2015). While the cutoff value (lambda) can influence inference of the results, there are cutoffs that are commonly applied and therefore provide some level of standardization to the lasso process. The minimum lambda cutoff value is the log value of lambda that best minimizes the mean square error estimate by ten-fold cross-validation. When the minimum lambda cutoff is used, the variables remaining form the “best predicting model in cross-validation.” The minimum lambda cutoff also yields the model with the most parameters relative to the other cutoff values. Alternatively, the one standard error of lambda cutoff value is where the mean square error is within one standard error of the minimum error of lambda leaving the “simplest model whose accuracy is comparable with the best model (i.e. minimum error of lambda)” (Breiman et al. 1984, Hastie et al. 2015). The one standard error of lambda yields the most reduced model. I ran the lasso with a Poisson regression, using the glmnet package (Friedman et al. 2017) and with four cutoff values: 1) minimum lambda, 2) one standard error of lambda, 3) $\frac{1}{4}$ lambda, the value between the minimum lambda and the one standard error

of lambda and 4) $\frac{1}{2}$ lambda, the lambda value halfway between the minimum lambda and the one standard error of lambda. I considered four cutoff values to assist in identifying the most parsimonious model. I included the cutoff values of $\frac{1}{4}$ lambda and $\frac{1}{2}$ lambda to determine which variables may be of secondary importance to the model relative to the most important variables identified at one standard error of lambda. There is currently no consensus on a statistically valid method to calculate standard error of beta estimates for lasso regressions (Friedman et al. 2010, Kyung et al. 2010, Lockhart et al. 2014, Goeman et al. 2016), therefore I used a Poisson generalized linear model (GLM) with the coefficients remaining at $\frac{1}{2}$ lambda and $\frac{1}{4}$ lambda to calculate standard errors of regression coefficients.

I included nine independent variables in the model of black scoter distribution. There was no collinearity between variables and all variables were standardized to a mean value of zero and a standard deviation of 1. The six oceanographic variables evaluated were: bathymetry (m), ocean floor slope (degrees), distance to shore (Euclidean), ocean floor substrate, marine ecoregion, and survey year. I evaluated the following three weather variables: North Atlantic Oscillation (NAO), average wind speed, and average time between waves (Table 1). I also examined the quadratic terms for bathymetry, average wind speed, and distance to shore to see if black scoter abundance has a non-linear relationship with those variables, e.g., indicating a peak point of water depth for abundance. I included three interactive terms: bathymetry and distance to shore, NAO and bathymetry, and NAO and distance to shore. I incorporated the three interactive terms to see if fine-scale oceanographic variables were influenced by a broad-

scale weather variable. I choose these variables because Zipkin et al. (2010) observed that scoter species were observed in higher abundances in the nearshore (closer to shore) during cold, snowy winters (negative phase NAO).

Results

Over the four survey years, there was a total 16,733 grid cells, of which 509 had ≥ 1 black scoter. The number of black scoter surveyed varied annually and spatially (Fig. 1, Table 2). The lasso regression of black scoter abundance at the minimum lambda cutoff value retained all the variables, while the lasso regression at the one standard error of lambda cutoff value did not retained any variables (Table 3). The lasso at the $\frac{1}{4}$ lambda cutoff value retained eight variables: ecoregion, bathymetry, quadratic bathymetry, distance to shore, survey year, ocean floor slope, average time between waves, and average wind speed. The lasso regression at the $\frac{1}{2}$ lambda cutoff value retained three variables: bathymetry, distance to shore, and ocean floor slope (Table 3).

There were three ocean environmental variables that remained after the lasso regression at the $\frac{1}{2}$ lambda cutoff value. Bathymetry had a positive relationship with black scoter abundance and increased as water depth decreased (Fig. 2). Distance to shore had a negative relationship with black scoter abundance (Fig. 3). Ocean floor slope had a positive relationship with black scoter abundance (Fig 4). No weather variables remained in the lasso regression with a cutoff value of $\frac{1}{2}$ lambda.

There were five oceanographic variables and two weather variables that remained after the lasso regression at the cutoff value of $\frac{1}{4}$ lambda. The quadratic effect of

bathymetry indicated that black scoter abundance was the lowest at 22 m depth (Fig 5). The Virginian ecoregion and had a smaller black scoter abundance than the other two ecoregions (Table 3). The 2010 survey year had a positive relationship with black scoter abundance. The average wind speed had a negative relationship with black scoter abundance (Fig 6, Table 3). Average time between waves also had a negative relationship with black scoter abundance (Fig 7, Table 3).

Discussion

Few studies have examined sea duck habitat use along the Atlantic coast of North America, especially in the southeastern United States (Kaplan et al. 2011, Jodice et al. 2013, Bowman et al. 2015). My study shows that from North Carolina to the northern coast of Florida black scoter distribution is related to a combination of fine-scale habitat and weather conditions (Zipkin et al. 2010). Additionally, it reveals that the ocean environmental variables may have a stronger influence on black scoter distribution than weather variables.

Of the habitat characteristics used in my model for black scoter abundance along the southeastern coast of the United States, the most influential were bathymetry, distance to shore, and ocean floor slope. There was a negative relationship between abundance of black scoters and bathymetry. The average water depth that the black scoters selected in this study was ca. 6 meters, almost half the depth compared to habitats used by black scoters in New England (13 – 15 m, Loring et al. 2014). While the same water depths are available along the southeastern coast of the United States, they are located farther from

the nearest shoreline, indicating the importance of other environmental conditions in addition to bathymetry. Black scoters are not the only sea duck that show this regional variance in the relationship with bathymetry. Common eiders in southern New England were found in areas with an average depth of ca.15 m (Beuth et al. 2017), yet in the Gulf of St. Lawrence common eiders strongly selected shallow water depths 0-6 m where prey densities were the highest (Guillemette et al. 1993). Although black scoters can dive at depths exceeding 20m (Nilsson 1972), black scoters may occur in shallower water depth along the southeast coast because their primary food source, bivalves, could occur there in high densities.

The second habitat characteristic that is important to black scoter distribution in the southeastern region is distance to shore. The average distance to shore for black scoters in this study was 9.05 km, which was farther than black scoters in New England that used the nearshore (<5 km) and subtidal habitats (<20 m; Loring et al. 2014). The nearshore and subtidal habitats along the southeastern coast were available to black scoters but were mostly not used. The local topography could be the reason why black scoters that are located along the New England coastline and along the southeastern coastline are at different distances from shore. The water depth off the New England coast increases quickly over a relatively short distance, whereas the water depth off the southeastern coast increases slowly over a relatively long distance. The rapid increase in water depth restricts the area available to black scoters for diving and foraging.

Another habitat characteristic that is important to black scoter distribution is slope of the ocean floor. In this study there was a positive relationship with ocean floor slope

and black scoter abundance. However, although there is a positive relationship with ocean floor slope, the average slope that black scoters were seen at was only 0.05 degrees. Black scoter abundance and the slope of the ocean floor possibly reflects the associations with their preferred prey and substrate. Black scoters have been noted to prefer the flat topography predominantly found on the South Atlantic Bight (Zipkin et al. 2010, Silverman et al. 2013) over sandy substrates (Stott and Olson 1973; Loring et al. 2013) which is supported by the results from this study. In comparison, common eiders in southern New England preferred areas with a steeper topography over shallow reefs possessing an average slope of 0.7 degrees (Guillemette et al. 1993, Beuth et al. 2017). The differences in slope of the ocean floor however slight are important to black scoters and other sea ducks.

In this study, the oceanographic variables had more influence on black scoter distribution than weather variables. The quadratic bathymetry, average wind speed, average time between waves, the Virginian ecoregion and the 2010 survey year were variables influential to the model but were less important than the three afore mentioned variables. Black scoter abundance was the lowest at about 22 m water depth when bathymetry in the quadratic form black scoter abundance slightly increased at water depths greater than 22 meters. The abundance of black scoters may have decreased at water depths of 22 m because the benthic community at 22 m has little desirable prey species for black scoters. Black scoter abundance had a negative relationship with both average wind speed and average time between waves. Increased wind speed may have resulted in undesirable conditions that raised energetic demands and resulted in increased

feeding for black scoters (Paulus 1984, Lovvorn 1996). Diving is energetically expensive (de Leeuw 1996), and negative environmental conditions could require large energy expenditures for black scoters. Therefore, black scoters could have moved to areas of more favorable conditions (i.e., less wind) to conserve more energy (Pelletier et al. 2008). Black scoter abundance was lower in the Virginian ecoregion compared to the Carolinian ecoregion. A possible reason for this is that in the Virginian ecoregion, with the exception of Pamlico Sound, the water depth increases rapidly in a relatively short distance from the shoreline. The Carolinian ecoregion includes the South Atlantic Bight where the water depth increases relatively little over a longer distance. The rapid increase in water depth in the Virginian ecoregion limits the area that black scoters are capable of diving and obtaining food resources. The 2010 survey year differed in comparison to the other survey years. In 2010, one unusual and extremely large flock of black scoters was observed, off the coast of South Carolina, which was not seen in the other survey years. While survey year does not explain black scoter abundance spatially it does explain the variance in the data temporally. A wide range of oceanographic and weather variables were examined in this study but one common marine variable that I did not include was sea surface temperature. Sea surface temperature is a variable that is frequently important for understanding seabird distribution, but does not appear to affect black scoters and therefore I chose to omit it (Zipkin et al. 2010, Flanders et al. 2015).

Conditions occurring during one phase of the annual cycle often continue to affect individuals and populations during ensuing phases (Marra et al. 2015). Poor quality habitat and a shortage of available resources during the wintering period can limit the

amount of fat reserves for scoters preceding migration (Studds and Marra 2007). The lack of fat reserves increases their vulnerability to the harsh conditions that are faced during migration (Alisauskas and Ankney 1992, Ebbinge and Spaans 1995, Guillemain et al. 2008). Abiotic conditions encountered on the wintering grounds may affect black scoter population dynamics thru the indirect effects of dispersal decision, spring migration, and reproductive success (Scott 1998, Martin and Wiebe 2004). Black scoters breed in the arctic and experience more variation in environmental conditions (i.e. wind, temperature, precipitation, etc.) on the breeding grounds than birds that breed at lower latitudes (Martin and Wiebe 2004), which can be exacerbated by arriving from the wintering grounds in poor condition (Fretwell 1972, Alisauskas and Ankney 1992). In response to the growing interest in off-shore wind energy development, it is important to identify areas of high quality habitat for black scoters. Minimizing the degradation and destruction of wintering habitat will help to alleviate negative impacts on black scoter population dynamics, both directly and indirectly.

The lasso regression is a developing area of research in the field of ecology, but provides an alternate method to examining variable selection. Lasso regression focuses on variable selection rather than model selection to reduce overfitting of models. A common method of model selection is ranking models by Akaike's Information Criterion (AIC; Burnham and Anderson 2002). While this is a useful method, it focuses on the best candidate model to explain the data rather than which variables have the most impact on the data. In comparison, lasso regression shrinks coefficients towards zero leaving only the variables that profoundly contribute to the model (Tibshirani 1996). While AIC

model selection relies on creating a set of candidate models based on hypotheses, lasso regression is a good alternate method to use when there are no a priori predictions, as was the case in this study. Lasso, and other shrinkage models used when there are few observations, have been shown to produce models with smaller mean squared prediction error (Dahlgren 2010). Shrinkage models have also been shown in simulations to outperform subset models, when scenarios had few observations and many variables with small effects (Tibshirani 1996, Ribbing et al. 2007). Lasso and other shrinkage models are similar to subset models but are more continuous and are not as affected from high variability (Hastie et al. 2009). Lasso is another method to consider applying for variable selection, especially when there are few observations and several variables being examined, which is often the case with ecological data.

Local ocean environmental variables as well as weather variables are important to understanding black scoter distribution. My results also show the importance of oceanographic variables, both on a local and regional scale. The identification of key habitat variables provides valuable insight into black scoter wintering distribution and habitat use. Identifying the areas of high quality wintering habitat and resources enables the protection of those areas through preservation and minimizing human conflicts. Understanding wildlife population distribution and population dynamics as it relates to habitat use allows for more effective conservation planning, minimizing human conflicts, and better survey planning for future monitoring programs (Newbold and Eadie 2004, Rushing et al. 2017).

Management Implications

Black scoters along the southeastern coast of the United States were located an average of 9 km from the nearest shoreline where water depths were <6 m and at areas with a slight slope (0.05 degrees, Table 4). Managers interested in protecting wintering habitat for black scoters in the southeast should prioritize areas that are shallow (<15m deep), close to shore (<15 km from land) and have a slight slope (<1 degrees). My results enable managers to focus sampling effort for black scoter abundance and distribution along the southeastern coast. Habitat characteristics for black scoters identified in my study area should be carefully considered when planning anthropogenic activities along the southeast coast of the United States, such as offshore energy development.

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TABLES

Table 1: The eight covariates examined in relation to black scoter abundance along the southeastern coast of the United States during the winters from 2009 to 2012, the covariates' spatial scale or resolution and the source of variable.

Variable	Spatial Scale/Resolution	Source
Bathymetry (water depth)	WGS 84 1 arc-minute (cell size)	NOAA National Centers for Environmental Information (Amante and Eakins 2009)
Wind Speed	Inverse distance weights between 20 buoys	NOAA National Data Buoy Center
Average Wave Period	Inverse distance weights between 9 buoys	NOAA National Data Buoy Center
North Atlantic Oscillation	Monthly Value, Feb 2009 to Feb 2012	Climatic Research Unit, University of East Anglia, Norwich, UK
Ocean Substrate	0.00001 lat/long resolution vector data, shapefile NAD 83	NOAA Office of Coastal Management Digital Coast Atlantic Seafloor Sediment (CONMAP) data (provider USGS)
Distance to Shore	Euclidean distance between black scoter location and edge of the Atlantic coastline	NOAA National Centers for Environmental Information GSHHG data (shoreline data)
Ocean Bottom Slope	Calculated from bathymetry layer, difference of the values between neighboring cells	NOAA National Centers for Environmental Information ETOPO1 data
Marine Ecoregion		World Wildlife Fund (Sprawling et al 2007)

Table 2: The mean, minimum, and maximum count of black scoters observed and the number of grid cells where black scoter abundance was ≤ 1 during each survey year in a given cell among all surveyed cells, during the winters from 2009 to 2012 along the southeastern coast of the United States.

Survey Year	Mean	Minimum	Maximum	No. of Occupied Cells
2009	39.75	1	475	80
2010	100.40	1	9,080	157
2011	66.63	1	2,910	164
2012	93.94	1	2,900	108

Table 3: Black scoter abundance along the southeastern coast of the United States during the winters from 2009 to 2012 response to the significant variables for black scoter distribution. The lasso beta values for the cutoff value halfway between the one standard error of lambda and the minimum lambda ($\frac{1}{2}$ lambda) and the cutoff value $\frac{1}{4}$ between the minimum lambda and the one standard error of lambda ($\frac{1}{4}$ lambda) were calculated using the lasso regression. The standard error values for the cutoff value $\frac{1}{2}$ lambda and $\frac{1}{4}$ lambda were calculated using generalized linear models.

Minimum Lambda (s=0.007)	$\frac{1}{4}$ Lambda (s=0.484)	Beta	Standard Error	$\frac{1}{2}$ Lambda (s=0.968)	Beta	Standard Error	One Standard Error of Lambda (s=1.944)
Intercept	Intercept	0.577	0.023	Intercept	0.768	0.008	No Variables Retained
Bathymetry	Bathymetry	0.898	0.037	Bathymetry	0.344	0.006	
Distance to Shore	Distance to Shore	-0.548	0.009	Distance to Shore	-0.252	0.009	
Ocean Floor Slope	Ocean Floor Slope	0.164	0.004	Ocean Floor Slope	0.021	0.003	
Quadratic Bathymetry	Quadratic Bathymetry	-0.440	0.024				
Wind Speed	Wind Speed	-0.237	0.009				
Time Between Waves	Time Between Waves	-0.164	0.014				
Quadratic Wind Speed	Survey Year 2010	0.341	0.020				
Quadratic Distance to Shore	Virginian Ecoregion	-0.145	0.022				
Virginian Ecoregion							

Floridian
Ecoregion

Survey
Year 2010

Survey
Year 2011

Survey
Year 2012

Sediment
(sand)

Sediment
(gravel-
sand)

Sediment
(clay-
silt/sand)

Sediment
(sand/silt/
clay)

NAO x
Distance to
Shore

Distance to
Shore x
Bathymetry

NAO x
Bathymetry

Table 4: The mean (standard error, minimum, and maximum of each variable for the grid cells that had black scoters abundance greater than zero (n = 509) during the winters from 2009 to 2012 along the southeastern coast of the United States.

Variable	Mean (SE)	Minimum	Maximum
North Atlantic Oscillation	-0.264 (0.12)	-3.924	2.791
Bathymetry (meters)	-5.612 (0.14)	-24.000	0.0
Slope (degrees)	0.054 (0.002)	0.0	0.327
Distance to Shore (km)	9.051 (0.56)	0.023	40.508
Average Wind Speed (m/s)	5.106 (0.04)	2.562	6.918
Average Time between waves (sec)	5.063 (0.02)	4.293	5.943

FIGURES

Figure 1: The distribution and flock size of black scoters by year along the southeastern coast of the United States during the winters from 2009 to 2012.

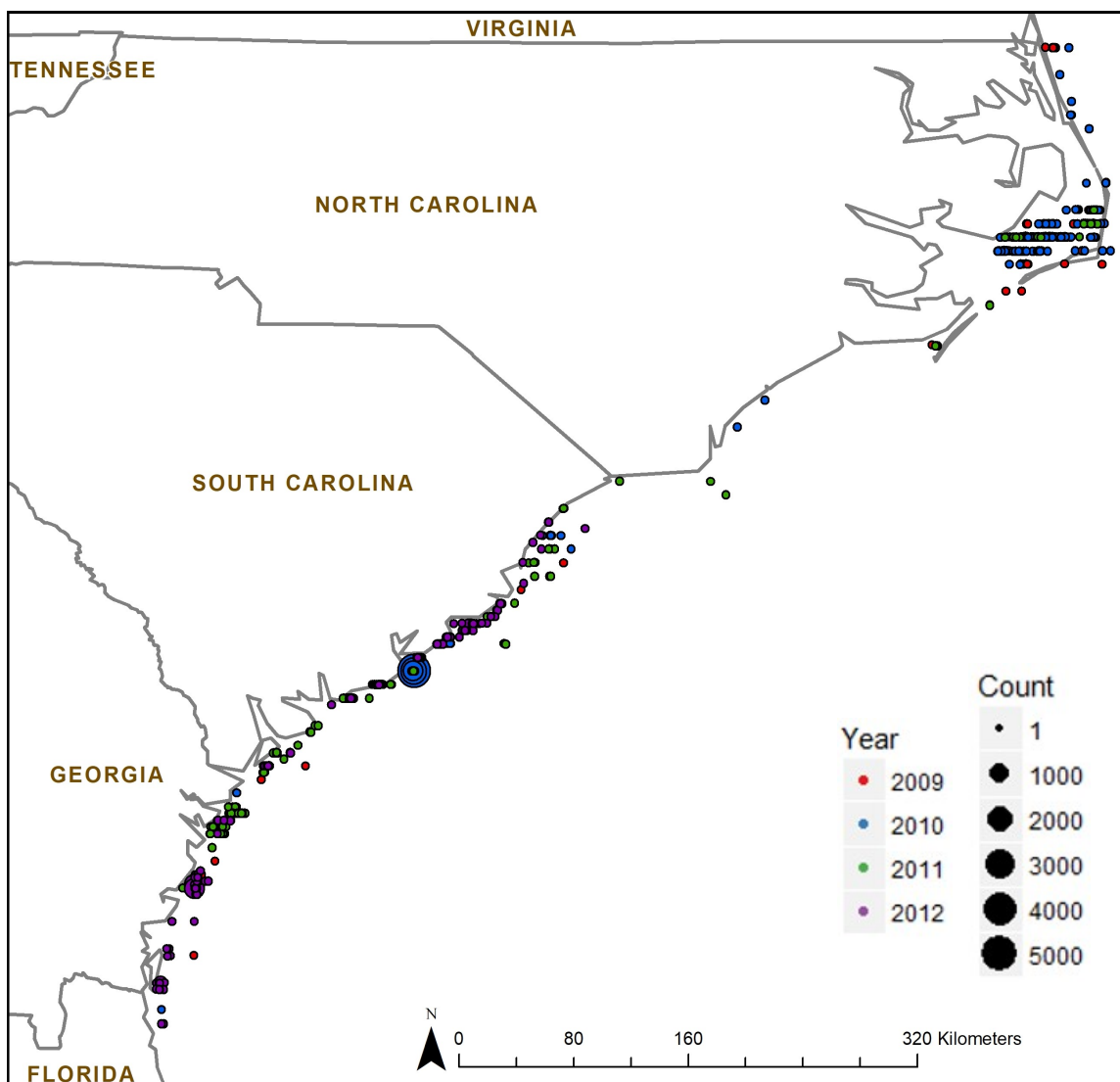


Figure 2: Black scoter abundance in response to bathymetry along the southeastern coast of the United States during the winters from 2009 to 2012 at the lasso cutoff value $\frac{1}{2}$ between minimum lambda and one standard error of lambda.

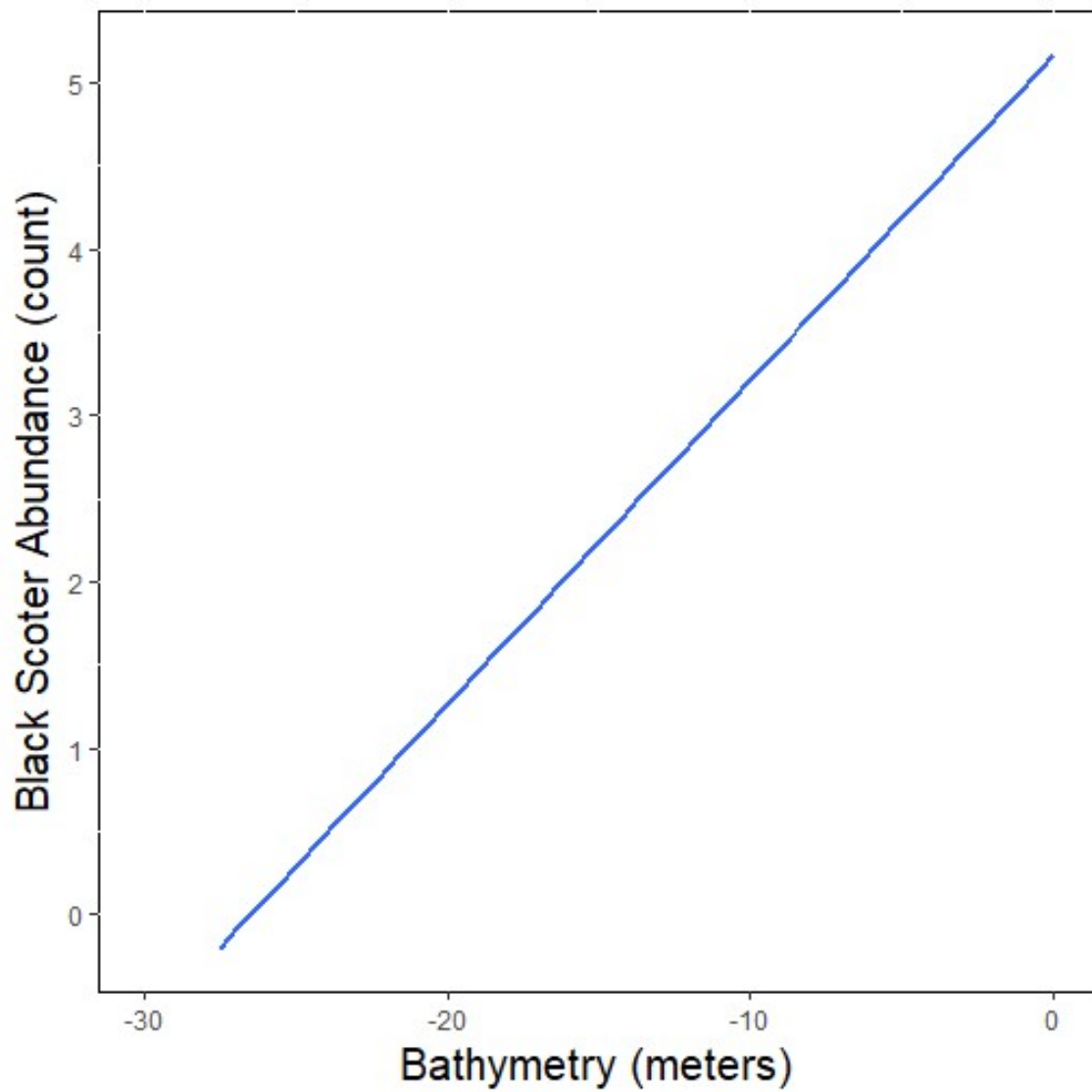


Figure 3: Black scoter abundance in response to distance to shore along the southeastern coast of the United States during the winters from 2009 to 2012 at the lasso cutoff value $\frac{1}{2}$ between minimum lambda and one standard error of lambda.

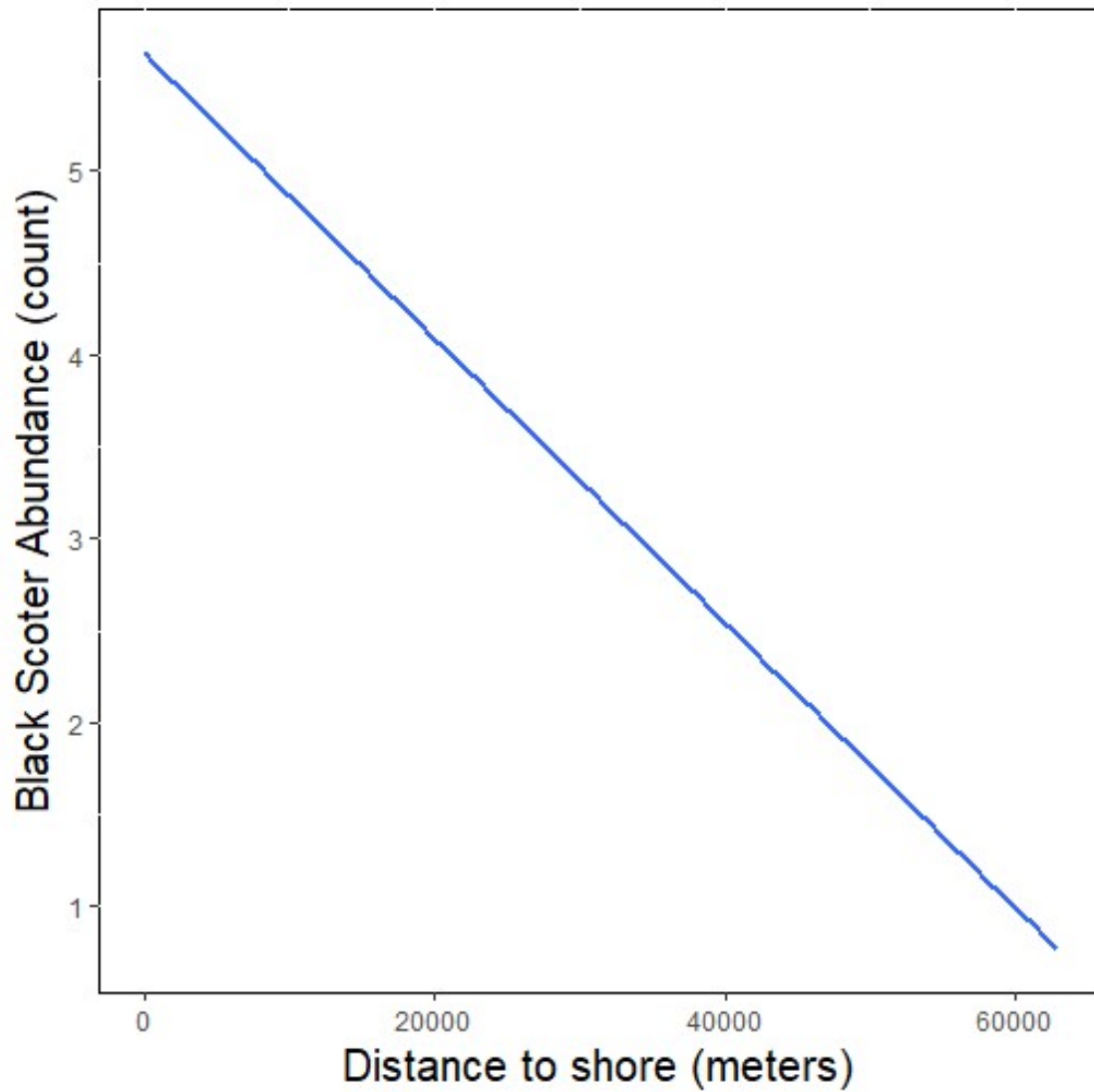


Figure 4: Black scoter abundance in response to ocean floor slope along the southeastern coast of the United States during the winters from 2009 to 2012 at the lasso cutoff value $\frac{1}{2}$ between minimum lambda and one standard error of lambda (scaled).

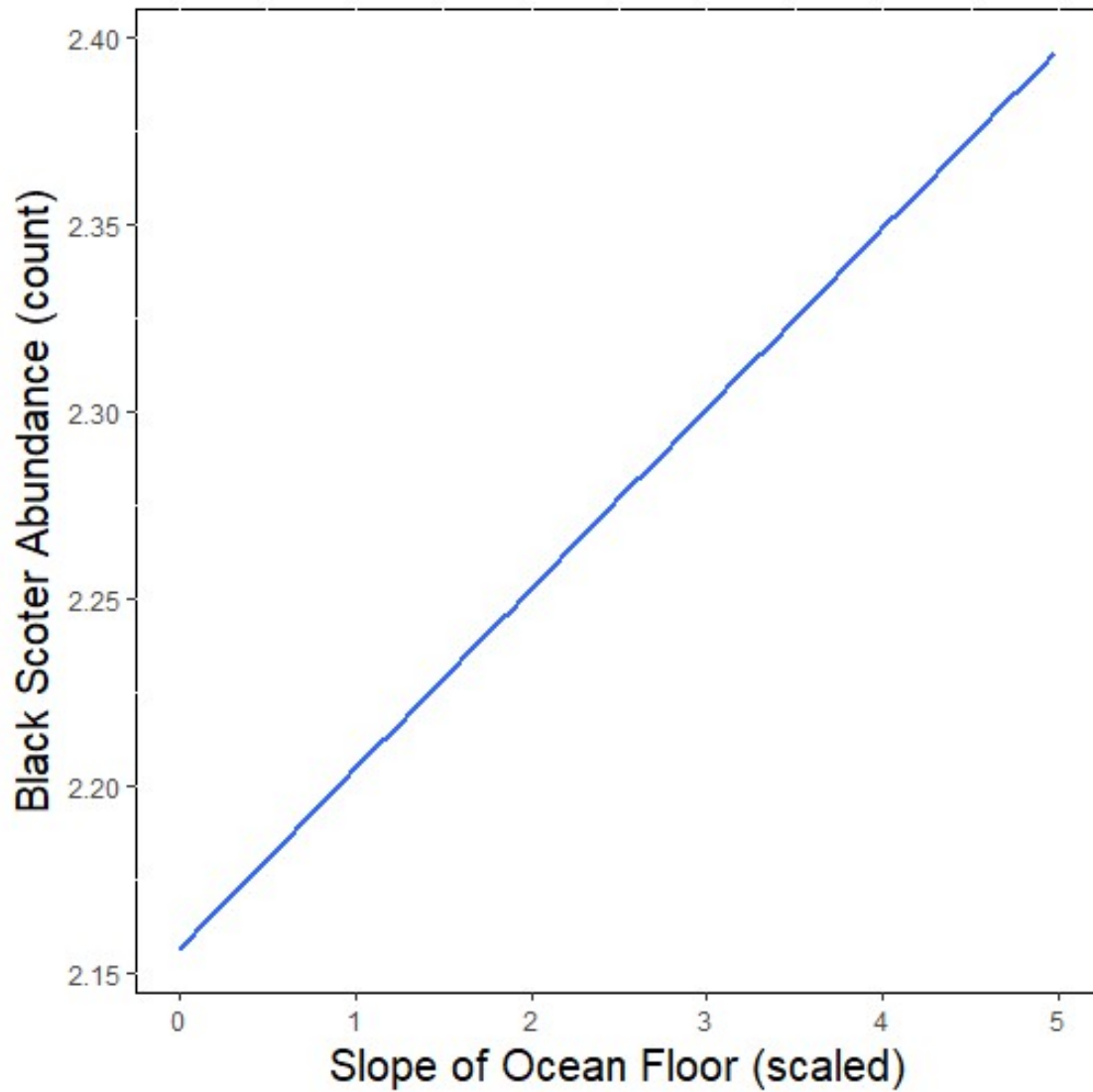


Figure 5: Black scoter abundance in response to the quadratic effect of bathymetry along the southeastern coast of the United States during the winters from 2009 to 2012 at the lasso cutoff value $\frac{1}{4}$ between minimum lambda and one standard error of lambda.

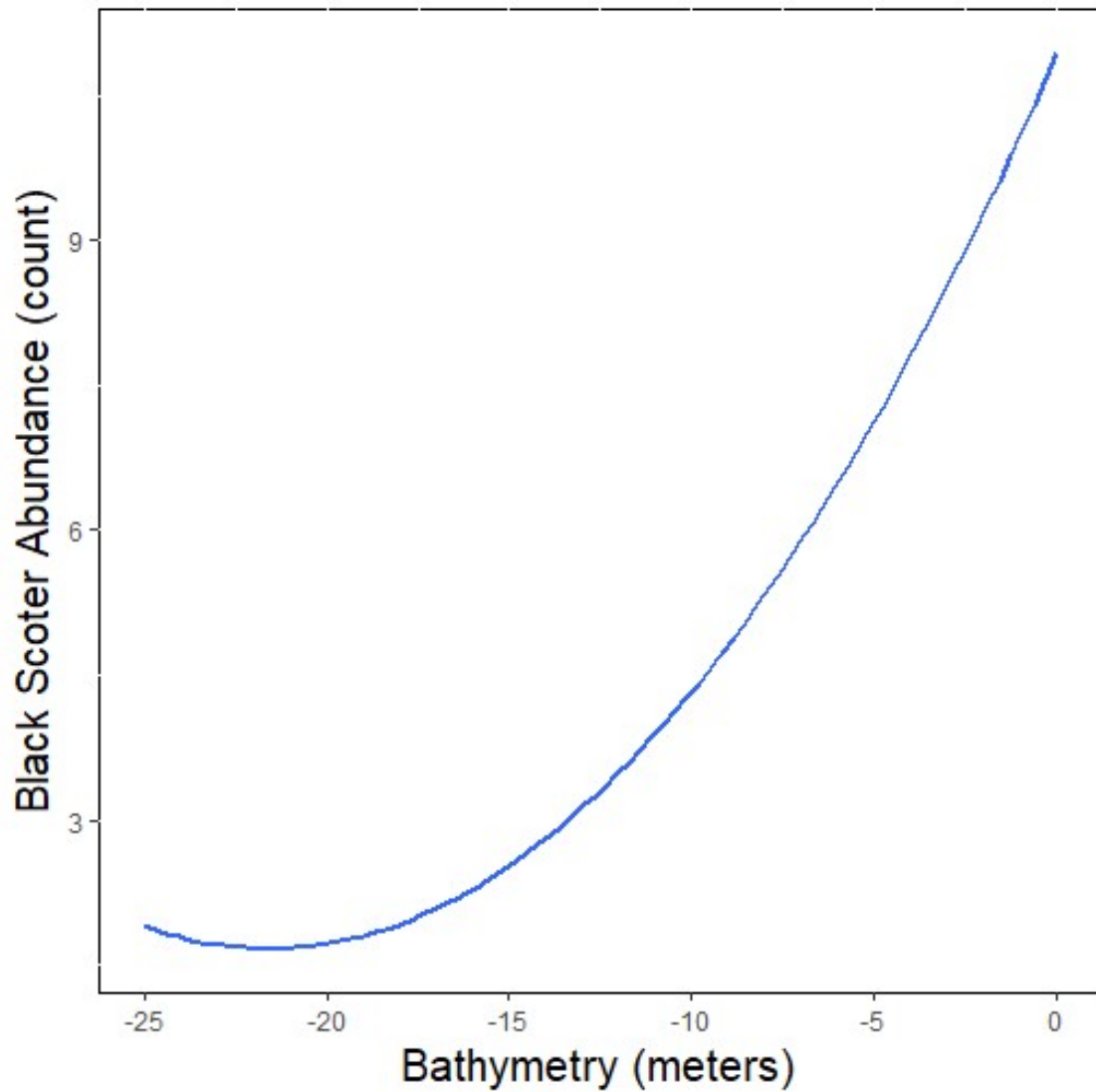


Figure 6: Black scoter abundance in response to average wind speed along the southeastern coast of the United States during the winters from 2009 to 2012 at the lasso cutoff value $\frac{1}{4}$ between minimum lambda and one standard error of lambda (scaled).

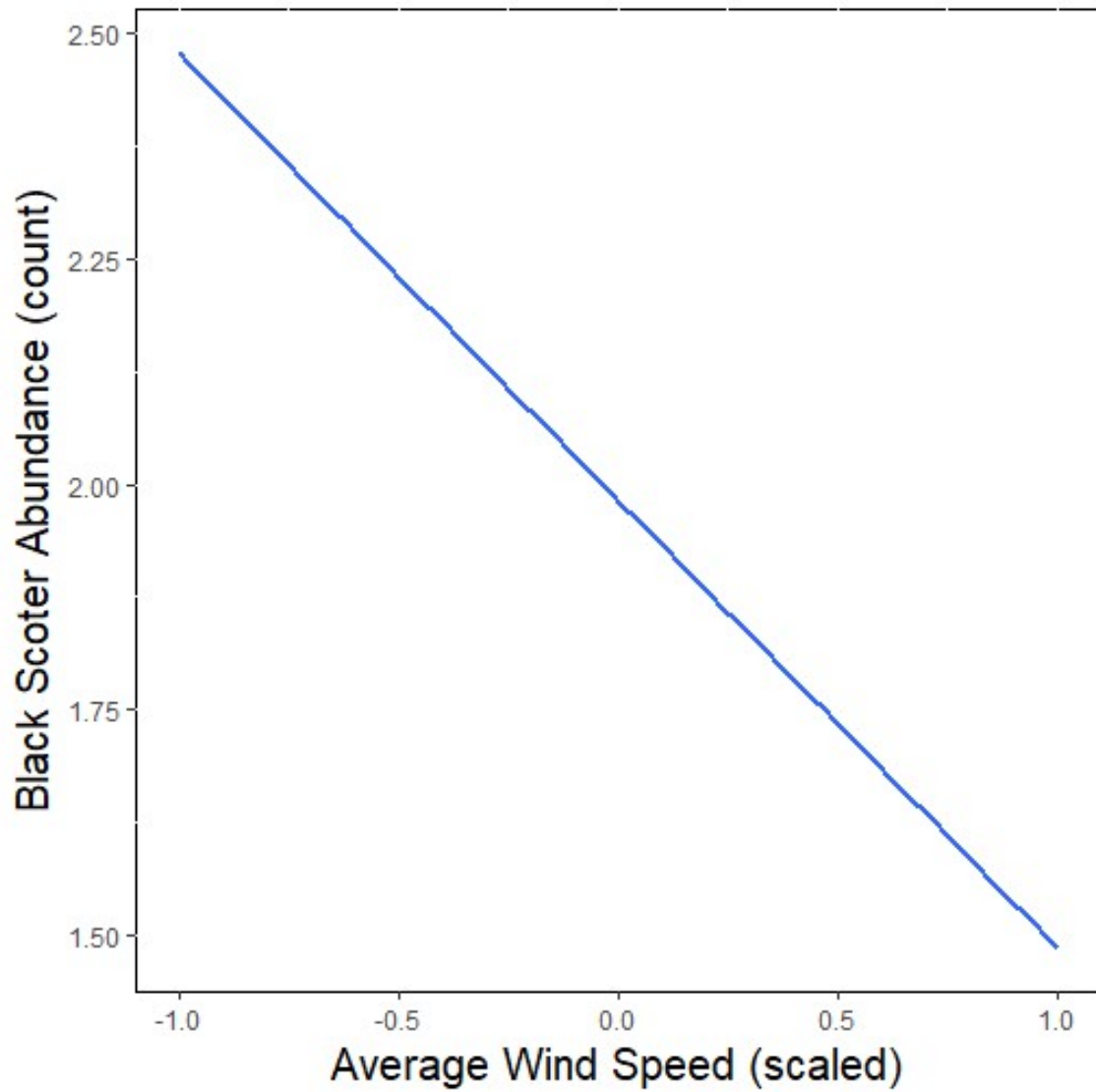
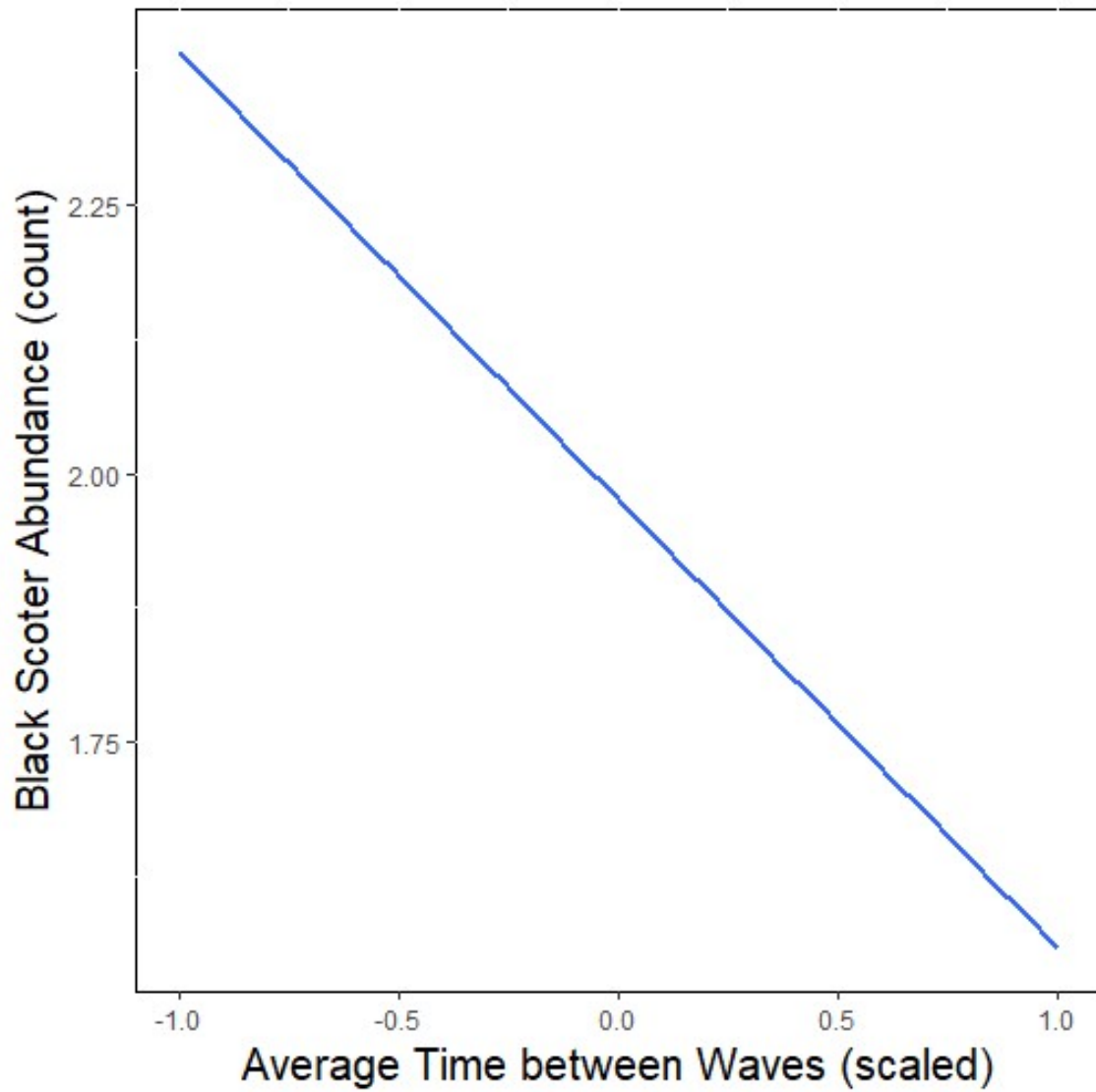


Figure 7: Black scoter abundance in response to average time between waves along the southeastern coast of the United States during the winters from 2009 to 2012 at the lasso cutoff value $\frac{1}{4}$ between minimum lambda and one standard error of lambda (scaled).



CHAPTER THREE

WINTER MOVEMENT OF BLACK SCOTERS IN THE ATLANTIC OCEAN, USA

Introduction

The availability of good quality non-breeding habitats affect population dynamics (Scott 1998, Harrison et al. 2011, Marra et al. 2015). Poor quality habitat and a scarcity of resources during the wintering period and spring migration can decrease chances of survival and lower body condition for the subsequent phases of the annual cycle (e.g. carry-over effects; Gunnarsson et al. 2006, Studds and Marra 2007, Rushing et al. 2017). These carry-over effects can strongly impact both ecological and evolutionary processes in birds (Ebbinge and Spaans 1995, Norris et al. 2004, Sorensen et al. 2009). While avian research is primarily conducted on the breeding grounds, migratory birds spend the majority of their annual life cycle off the breeding grounds (Marra et al. 2015). The quality and quantity of habitats and resources during the non-breeding season may be important limiting factors for waterfowl (Lack 1966, Fretwell 1972, Sedinger and Alisauskas 2014), and can have a detrimental effect on population dynamics (Alisauskas and Ankney 1992, Scott 1998, Martin and Wiebe 2004). Poor winter habitat conditions have been associated with large mortality events (Camphuysen et al. 2002), decreased reproductive success (Nichols et al. 1983, Oosterhuis and Dijk 2002, Guillemain et al. 2008), and decreased population growth rate (Petersen and Douglas 2004, Sorensen et al. 2009, Wilson et al. 2011). Information on winter habitat preference and use for sea ducks is needed to identify areas of good quality habitat, but that information is limited (Sea Duck Joint Venture, 2015).

Sea duck distribution within the wintering range may be based on a variety of factors including local environmental conditions (Loring et al. 2014, Beuth et al. 2017), food availability (Guillemette et al. 1993, Lewis et al. 2008), predation risk, site fidelity (Greenwood 1980), and human activity (Madsen and Fox 1995). Sea ducks spend the winters on large bodies of water, such as the Great Lakes and oceans, which are complex and difficult to study due to their dynamic nature, making it challenging to quantify habitat quality for sea ducks during the non-breeding season. Sea duck movements and site use in relation to environmental factors are vastly unknown and understudied along the Atlantic coast of the United States (Kaplan 2011, Jodice et al. 2013, Boyd et al. 2015), but may have carry-over effects throughout their annual cycle (Alisauskas and Ankney 1992, Scott 1998, Martin and Wiebe 2004).

Most North American sea duck research conducted during the non-breeding season is focused on portions of the population that winter in northern locations (off the coast of Alaska and British Columbia in the Pacific Ocean and off the coast of eastern Canada and New England in the Atlantic Ocean). Research on the southern wintering populations, those that winter along the Pacific coast of the continental United States and the Mid-Atlantic and southeastern coast of the United States, is limited. Northern and southern wintering sites have different tidal regimes, sediments, food resources, temperature regimes as well as ice conditions (Spalding et al. 2007, Boyd et al. 2015), which could influence the movement and distribution of sea ducks in different regions (Nilsson 1972, Stott and Olson 1973, Kirk et al. 2008, Schummer et al. 2008).

In addition to regional variation in geography, sea ducks encounter potential impacts from a variety of anthropogenic activities, but it is unknown how these activities might affect the wintering distribution of sea ducks (Silverman et al. 2013), or if these affects vary between northern and southern wintering sites. The potential development of wind farms in offshore areas in the Atlantic Ocean could lead to the possible displacement of black scoters due to loss of habitat and collisions with structures. In Europe, sea duck density decreased in response to sea ducks avoiding areas with wind turbines in shallow water (Larsen and Guillemette 2007, Langston 2013). In New England, Loring et al. (2014) found that large core use areas for black scoters in near shore areas were surrounding the federal lease block. The future wind turbines in the federal lease block could cause barrier effects and increase the susceptibility to collisions (Fox et al. 2006, Langston 2013). Proposed wind energy development along the Atlantic coast that occurs in core black scoter wintering sites has a higher potential to displace black scoters and increases the risk of reduced available resources (Studds and Marra 2007, Rushing et al. 2017). Understanding spatiotemporal dynamics of black scoters is important to recognize the potential impacts of future offshore energy development and additional anthropogenic activities.

In the early 1990s, it was noted that several sea duck populations were declining due to unknown causes (Caithamer et al. 2000, Sea Duck Joint Venture 2014). In response, there has been an increased effort to learn more about the life cycle of sea ducks in North America, particularly focusing on breeding habitat and reproductive success, migration timing and route, and non-breeding habitat. One of the sea duck

species declining and of high conservation concern is the black scoter (*Melanitta americana*, Sea Duck Joint Venture 2014). The black scoter is listed on the International Union for Conservation of Nature and Natural Resources (IUCN) Red List of Threatened Species as “Near Threatened” (BirdLife International 2013). Black scoters are long-lived sea ducks with delayed breeding that breed in Canada and winter off the coastlines of the United States (Sea Duck Joint Venture 2015). The Pacific black scoter population breeds in Alaska and winters off the southern Alaska and western coast of United States and Canada, while the Atlantic population of black scoters breeds in northern Canada and winters off the eastern coast of the United States. While there is considerable information known about the Pacific population of black scoters, there is very little information known about the Atlantic population of black scoters (Bordage and Savard 2011, Boyd et al. 2015, Sea Duck Joint Venture 2015). As anthropogenic activity along the Atlantic coast has risen, there has been an increased effort to learn more about the life cycle of black scoters in the Atlantic population. Knowledge of wintering habitat use and movement patterns for black scoters along the Atlantic coast is particularly limited (Bordage and Savard 2011, Bowman et al. 2015). However, the identification of limiting factors on the wintering grounds (e.g. Atlantic Ocean along the United States), even within the Atlantic population, may vary among wintering sites (i.e. core use areas) within the Atlantic.

To better understand wintering site use and movement patterns of black scoters during the non-breeding season, I analyzed locations of black scoters acquired via satellite telemetry scoters to 1) delineate arrival and departure dates to and from the

wintering grounds; 2) identify the number of sites used, area of each site, and duration of time spent at each site during the wintering period; 3) delineate the distance traveled between wintering sites; 4) quantify the differentiation of migration timing and site use between sex and geography; and 5) identify differences in habitat features for wintering sites by geographic location. The information from this study will increase the knowledge on wintering ecology of black scoters and provide new insight into black scoter conservation and management.

Methods

Chaleur Bay, New Brunswick/Quebec, Canada is a major spring stopover for migrating sea ducks, including black scoters (Sea Duck Joint Venture 2015). Sea Duck Joint Venture captured black scoters at this “bottleneck” location of the Atlantic Flyway to obtain representative sample of ducks using this travel corridor. Sea Duck Joint Venture used floating mist nests to capture 19 adult female black scoters in 2009 and 47 adult black scoters (19 females and 28 males) in 2010 (Sea Duck Joint Venture 2015). Each scoter was surgically implanted with a satellite telemetry transmitters (PTTs) in the abdominal cavity, following Korschgen et al. (1996). The PTTs weighed 38 - 50 grams and had a battery life of ≥ 750 hours. The duty-cycle of the transmitters in 2009 was 6 hours on and 72 hours off which resulted in an average battery life of 438 days. The duty-cycle of the transmitters in 2010 was 2 hours on and 72 hours off which resulted in an average battery life of 803 days (Sea Duck Joint Venture 2015). The telemetry data from the PTTs were collected via the Argos system of satellites, downloaded nightly and

archived, and filtered with the Douglas Argos Filter to remove redundant data and errant points (Douglas et al. 2012).

Data Formatting

To incorporate 2009 and 2010 data, I removed any points that occurred later than 2 hours after the first point recorded for each duty cycle, resulting in both years having points in a 2-hour window. The Douglas Argos Filter assigns a location class based on the quality (accuracy) of the location recorded. The location classes are: L3, L2, L1, L0, LA, LB, and LZ, listed from high to low accuracy. I removed points with location classes of L0, LA, LB, and LZ while retaining the location classes of L3, L2, and L1 with the possible location errors of ± 1 km, 5 km, and 10 km respectively (Douglas et al. 2012). Preliminary examination of the data indicated that using the location error associated with the L3, L2, and L1 location classes would not greatly affect the delineation of wintering sites, due to the size of the wintering sites relative to the possible location error. The data for each scoter was separated by year, with points occurring after 31 August and before 1 May of the following year. I excluded any points that were further west than the coast of Florida ($-81^{\circ}50'$ W) and further north than the US-Canada border ($44^{\circ}50'$ N) were excluded. One point, per bird per wintering season, was randomly selected per day to minimize spatial bias when comparing between birds and years. An individual was included in the calculations if there were ≥ 30 points for a given winter season (Seaman et al. 1999).

Wintering Sites and Arrival and Departure Dates

For each bird, the arrival date and departure date to the wintering grounds (i.e. Atlantic Ocean off the United States) was specified as the earliest and latest date recorded at the individual's first and last wintering site, respectively. The number of "core" wintering sites that were used annually for each scoter was determined by applying a 50% fixed kernel utilization distribution (UD; i.e. core habitat use) with the plug-in method for bandwidth selection using the "ks" package (Duong 2017) in Program R, version 3.4.0 (R Development Core Team 2017). Each polygon created after applying a 50% fixed kernel UD was delineated as a separate "wintering site." The first wintering site birds arrived on once they reached the wintering grounds was the "first wintering site," if a bird then moved to another wintering site that wintering site was referred to as the "second wintering site". A wintering site was used more than once if the scoter spent more than 14 days away from the wintering site and then returned to the wintering site. Fourteen consecutive days was chosen because it was deemed a long enough time period for a scoter to establish another wintering site before returning to the original wintering site (Phillips et al. 2006). Because a wintering site could be used multiple times, the "first period of time at a wintering site" was the time spent continuously at a wintering site before leaving the wintering site. The next time spent continuously at a wintering site was considered the "second period of time at a winter site", regardless of whether it was the previously used wintering site or a new wintering site.

Wintering Site Area and Distance between Wintering Sites

I removed non-available habitat (i.e., land) from the 50% home range area and calculated the area of each polygon using ArcMap 10.5.1 (ESRI 2011). The center of the polygons representing each wintering site was calculated by using the “Feature to Point” tool in ArcGIS. The distance traveled between the wintering sites was calculated by using the points representing the center of each wintering site and the “Point Distance” tool in ArcGIS (Figure 1). I calculated the average area of the wintering sites by averaging the size of all wintering sites for each bird annually. I calculated the average distance between wintering sites by averaging all of the distances between wintering sites for each bird annually.

Statistical Analyses

I used Mann-Whitney U-tests in R (Mann and Whitney 1947) to test differences between sex and geographic locations (northern or southern population) for 1) the arrival date to the wintering grounds, 2) the departure date from the wintering grounds, 3) average areal extent of each wintering site, and 4) average distance between the wintering sites. I defined wintering “geographic locations” as where a scoter spent the majority of its time on the wintering ground, and partitioned the Atlantic coast of North America into two regions. I defined the Chesapeake Bay and any location north as the “northern coast of the United States” and any location south of the Chesapeake Bay as the “southern coast of the United States.” I then assigned scoters to a region based on where they spent the most days. I assigned birds to either region by summing the total number of days spent between the northern (Chesapeake Bay and north) and southern (south of

Chesapeake Bay) coasts of the United States. For example, if a bird spent 20 days at a wintering site north of Chesapeake Bay and 42 days at a wintering site south of the Chesapeake Bay, I classified it to the southern region.

Habitat Use of Northern and Southern Wintering Sites

I examined the habitat features of the wintering sites based on their geographic location. I assigned each individual wintering site as defined above. I compared the bathymetry, ocean floor slope, distance to shore, ocean floor substrate, and marine ecoregion with a GLM with a binomial regression examining between northern wintering sites and southern sites. I additionally examined one post-hoc model, which contained the bathymetry, ocean floor slope, and distance to shore variables. To calculate the value for each covariate of interest for a wintering site, I either used the center of the wintering site (for distance to shore) or calculated the mean of a given variable for each wintering site using the raster package (Hijmans et al. 2016). I obtained bathymetric data from the National Oceanic and Atmospheric Administration's (NOAA) National Geophysical Data, ETOPO1 Global Relief Model (Amante and Eakins 2009). I calculated ocean floor slope by using the bathymetry data (Amante and Eakins 2009), and finding the difference of the values between neighboring cells. I calculated distance to shore by finding the Euclidean distance between the center of the wintering site and the shoreline. I obtained shoreline shapefile from NOAA's National Centers for Environmental Information Global Self-consistent, Hierarchical, High-resolution Geography Database (GSSH), version 2.3.6, using the intermediate resolution (i) and the boundary between land and ocean (L1; Wessel & Smith 1996). I obtained the ocean floor substrate data from

NOAA's Office of Coastal Management Digital Coast, Atlantic Seafloor Sediment Continental Margin Mapping (CONMAP; Poppe et al. 2014). I acquired the shapefile for the marine ecoregions of the world (MEOW; Spalding et al. 2007) from the World Wildlife Fund (WWF).

Results

Arrival and Departure Dates

There were 44 birds that provided data for a least one winter season with 18 birds providing data for more than one wintering season. The average arrival date to the first wintering site on the wintering grounds was 12 November (95% CI: ± 3.8 days, range = 6 September – 17 December). There was no difference in the arrival date between the sexes ($U = 665.0$, $P = 0.084$). There was no statistical difference in arrival date between the wintering geographic location ($U = 384.5$, $P = 0.222$; Fig 2). The average departure date from the final wintering site was 25 March (95% CI: ± 3.0 days, range = 22 January – 27 April). There was no statistical difference in the departure date between the sexes ($U = 518.0$, $P = 0.860$) or in the departure date between the geographic locations ($U = 517.0$, $P = 0.546$; Fig 3).

Wintering Sites

Black scoters used 1.8 (95% CI: 1.6 – 2.0) distinct wintering sites on average (one wintering site $n = 25$, two wintering sites $n = 27$, and three wintering sites $n = 14$; Fig 4). The mean number of days spent during the first period of time at a wintering site was 70.8 days (95% CI: 59.4 days – 82.3 days, range = 7 – 167 days). The mean number of

days spent during the second period of time at a winter site was 64.0 days (95% CI: 53.1 days – 75.0 days, range = 9– 119 days). The average number of days spent during the third period of time at a winter site was 41.4 days (95% CI: 26.4 days – 56.3 days, range = 7 – 115 days). In four winter seasons, black scoters used 3 separate wintering sites and used a previous site a second time. The mean number of days spent during the fourth period of time at a winter site was 27.0 days (95% CI: 8.1 days – 45.8 days, range = 14 – 51 days; Fig 5).

Distance between Wintering Sites

The average distance between the first wintering site and the second wintering site was 346.7 km (95% CI: 258.2 km – 435.1 km, $n = 41$, range = 45.2 – 1239.5 km). The average distance between the second duration of time at a wintering site and the third duration of time at a wintering site was 441.0 km (95% CI: 227.2 km – 6543.8 km, $n = 14$, range = 38.5 km – 1412.4 km). The average distance between the third duration of time at a wintering site and the fourth duration of time at a wintering site was 353.0 km (95% CI: 325.8 km – 380.2 km, $n = 4$, range = 321.7 – 388.7 km; Fig 6). There was no statistical difference in the average distance between wintering sites between sexes ($U = 178.0$, $P = 0.965$). There was a statistical difference in the average distance between wintering geographic locations ($U = 50.0$, $P = 0.004$; Fig 7).

Wintering Site Area

The average size of the first wintering site was 2,711.2 km² (95% CI: 1929.6 km² – 3492.9 km², $n = 66$). The smallest first wintering site was 28 km² and the largest first wintering site was 12,298 km². The average size of the second wintering site was 3,219.3

km² (95% CI: 2144.7 km² – 4293.9 km², n = 41), and the average size of the third wintering site was 2,029.6 km² (95% CI: 1188.4 km² – 2870.7 km², n = 14; Fig 8). There was no difference in the average wintering site area between the sexes ($U = 535.0$, $P = 0.974$). There was a statistical difference in the average wintering site area between wintering geography locations ($U = 125.5$, $P < 0.001$; Fig 9).

Habitat Use of Northern and Southern Wintering Sites

Northern wintering sites were located in deeper waters, closer to shore, and on steeper slopes compared to the southern wintering sites (Table 1). The global model failed to converge (standard error > 8,000 for ocean floor sediment and marine ecoregion), therefore a second model without the ocean floor sediment and marine ecoregion variables was created, post-hoc. In the second model, $P < 0.05$ for both bathymetry and ocean floor slope. Bathymetry was positively correlated to the wintering site's geographic location ($P = 0.005$), with deeper water depth in the northern wintering sites. Ocean floor slope was negatively correlated to wintering site's geographic location ($P < 0.001$), with steeper ocean floor slope in the northern wintering sites.

Discussion

Movement patterns of black scoters in the Atlantic during winter varies greatly among individuals and geographic locations along the coast. My results provide greater insight into black scoter movement on the wintering grounds. The results of this study indicate that while a few individuals arrived relatively early or late and departed relatively early or late from the wintering grounds, the majority of black scoters arrived

and departed within a two-week period. Moreover, my results suggest that there are differences in movement patterns and the wintering ecology of black scoters primarily located in northern locations compared to southern locations along the Atlantic Coast of the United States.

Arrival and departure dates to and from the wintering grounds differed greatly among individuals but this difference was not related to sex. The arrival date to the first wintering site ranged over four months (September to December). While there was a wide time period in the arrival date to the first wintering site, there was not a lot of variability. The small variability emphasizes that the peak arrival time for the scoters to reach their first wintering site is mid-November. Another sea duck, king eiders (*Somateria spectabilis*), also have a wide range in arrival dates to the wintering grounds (Oppel et al. 2008). There was also a four-month range (January to April) in the departure date for black scoters. Similar to the lack of variability with the arrival date, the departure date also had limited variation, highlighting that the departure date from the last wintering site, for the majority of the birds, is late-March.

The average time spent on the wintering grounds was about 4.5 months, similar to king eiders (Oppel et al. 2008) but less than harlequin ducks (*Histrionicus histrionicus*) (Iverson and Esler 2006). Black scoters may spend less time on the wintering grounds compared to other sea ducks because they have to migrate a longer distance to the breeding grounds than other sea ducks. The majority of black scoters that winter along the Atlantic coast breed in northern Manitoba, northern Saskatchewan, and southeast Northwest Territories, Canada (< 3,500 km; Sea Duck Joint Venture 2015). In

comparison, harlequin ducks spend almost a month and a half longer on the wintering grounds along the coast of Alaska before migrating to inland Alaska to breed ($> 1,000$ km; Robertson and Goudie 1999, Iverson and Esler 2006).

While some species of sea duck are relatively sedentary and remain at one wintering site (Robertson and Cooke 1999, Iverson and Esler 2006), other sea ducks are known to conduct extensive winter movements (Vaitkus 1999). My study supports the results found by Loring et al. (2014) that 1-3 wintering sites were used by black scoters along the Atlantic coast of the United States. Although black scoters were fairly sedentary, using up to a possible three wintering sites, they often made long-distance movements between these sites. It is likely that black scoters remained at a location until the food resources were depleted and chose to move to a habitat with greater prey abundance rather than remain and increase foraging effort (Kirk et al. 2007).

The average distance black scoters traveled between wintering sites on the Atlantic coast was more than double the distance traveled between wintering sites on the New England shelf (Loring et al. 2014). Similar to black scoters in the Atlantic Ocean, king eiders in the Bering Sea can move hundreds of kilometers between wintering sites (Oppel et al. 2008). This may be because black scoters and king eiders are less restrictive in their habitat requirements during winter and are able to move away from areas with less ideal conditions (Phillips et al. 2006). Although king eiders also traveled large distances between wintering sites like the black scoter, the distance traveled between wintering sites by black scoters was noticeably larger than that of most other sea ducks (Iverson and Esler 2006, Merkel et al. 2006). Black scoters might travel further along the

coast of the United States because resources, such as food, could be less concentrated due to variation in habitat features, resulting in the scoters moving further distances to find resources (Marzluff et al. 1997, Kirk et al. 2007). The concentration of resources may affect the distance between wintering sites and the area of the wintering site as well (Marzluff et al. 1997). The size of each wintering site range (i.e. core home ranges) widely varies for black scoters in the Atlantic. King eiders in the Bering Sea have an average winter home range (Oppel et al. 2008) over twice the average size of one wintering site of black scoters along the Atlantic coast of the United States. King eiders may have larger winter home ranges than black scoters due regional variance in ecological conditions such as ice conditions forcing king eiders to travel farther to find open water (Petersen and Douglas 2004). My results therefore suggest that the size of core home ranges for black scoter is larger compared to those reported for most other sea duck species (Iverson and Esler 2006, Merkel et al. 2006, Reed and Flint 2007, Kirk et al. 2008). The distribution of resources in the Atlantic, resulting from regional variation in habitat features, may result in black scoters having larger wintering sites than other sea ducks.

Habitat features associated with different benthic prey types and densities can greatly influence the movement and distribution of diving ducks, such as sea ducks (Nilsson 1972, Stott and Olson 1973, Kirk et al. 2008, Schummer et al. 2008). Regional variance in ecological conditions may vary not only by latitude but also by longitude. Different tidal regimes, sediments, temperature regimes as well as ice conditions could contribute to different prey dynamics on the west and east coasts of North America

(Spalding et al. 2007, Derksen et al. 2015). On the Pacific coast, black scoters use habitats characterized by gravel and cobble shores (Savard 1988, Savard 1989, Bordage and Savard 1995); however, black scoters are found in areas with a sandy ocean floor along the Atlantic coast of the United States (Stott and Olson 1973, Loring et al. 2013, Loring et al. 2014). Black scoters that wintered along the coast of New England traveled on average half the distance than black scoters wintering in both the Mid-Atlantic and New England regions (Chesapeake Bay and north; Loring et al. 2014), suggesting that food resources are more concentrated along the New England coast and become less concentrated towards the Chesapeake Bay.

There was no difference found between sex and the arrival date to the first wintering site, departure from the last wintering site, the average wintering site area, and the average distance between wintering sites. The lack of differentiation between males and female arrival date has been reported in other sea ducks (Merkel et al. 2006, Oppel et al. 2008, Loring et al. 2014). Several species of ducks form pair bonds during the fall and winter and travel together during migration, resulting in similar migration phenology between sexes (Rohwer and Anderson 1988). King eiders (Oppel et al. 2008), Steller's eiders, and harlequin ducks (Reed and Flint 2007) similarly did not differ in the size of the wintering range based on sex. A reason for the lack of variation in wintering range and distance between males and females is that they are similar in size and have comparable energetic costs (Bordage and Savard 2011). There was no difference in distance traveled for king eiders (Oppel et al. 2008) and common eiders (Merkel et al. 2006) for males and females. This may be the result because males and females largely

overlap in wintering locations and have similar experiences in acquiring resources.

Overall, there was no statistical difference between males and females black scoters in their ecology and movement on their wintering grounds on the Atlantic coast of the United States.

While there was no difference between males and female in temporal patterns of movement, there were some pronounced differences between black scoters a larger portion of the winter along the northern coast of the United States compared to the southern coast of the United States. Scoters that spent a higher portion of the winter along the southern coast had more than double the average wintering site area and traveled twice as far between wintering sites than the scoters that spent the majority of the winter along the northern coast. The concentration of resources could vary along the Atlantic coast resulting in the disparity of wintering site areas in different regions. An increase of prey variability and higher rates of prey depletion have been associated with higher home ranges (Tufto et al 1996, Marzluff et al. 1997, Ferguson et al. 1999).

Black scoters rarely used the same wintering site more than once. All of the wintering sites used more than once were used before the scoter moved further south and then the sites were used a second time as scoters moved back north. Black scoters may return to a winter site as they are preparing for spring migration because they are familiar with the resources available at the wintering site (Robertson and Cooke 1999). Oppel et al. (2008) found that half of king eiders in their study, returned to a more northerly wintering site after leaving it and traveling further south. Only in 4 winter seasons, black scoters spent several days moving between two wintering sites. Most of the scoters would

spend time at a wintering site and then move to another wintering site. In the four winter seasons, black scoters spent an extended period time at a wintering site and then would move to a new wintering site for a few days before returning to the previous wintering site for a few days. The scoter would spend a few days at each wintering site several times before the scoter chose to remain at the new wintering site.

The wintering sites use by black scoters varied by water depth, ocean floor slope, and distance to shore based on their geographic location. Wintering sites situated along the northern coast of the United States were located in deeper waters, closer to shore, and on steeper slopes compared to the wintering sites along the southern coast. The average water depth for northern wintering sites was 14 meters deeper than the southern wintering sites. The water depth for northern wintering sites in this study were deeper than what was found by Loring et al. (2014) for black scoters in southern New England. Common eiders in southern New England used on average a slightly deeper water depth than black scoters (Beuth et al. 2017) and in the Gulf of St. Lawrence they spent a large amount of time in shallow water (< 6 m, Guillemette et al. 1993). Although black scoters can dive at depths exceeding 20m (Nilsson 1972), black scoters might occur in shallower water depth along the southeastern coast than in New England because bivalves could occur in higher densities in shallower water than in New England (Guillemette et al. 1993). Black scoters may occur in shallower water depth along the southeast coast because their primary food source, bivalves, could occur there in high densities. Thus, bathymetry may be a surrogate for the bivalve distribution along the Atlantic coast of the United States

and why black scoters occur in shallower water depth along the southeastern coast than in New England.

The average ocean floor slope for northern wintering sites was steeper than the southern wintering sites. The slope of the ocean floor possibly reflects the associations with their preferred prey and substrate. In the southern portion of their wintering range, black scoters have been noted to prefer the flat topography predominantly found on the South Atlantic Bight (Zipkin et al. 2010, Silverman et al. 2013) over sandy substrates (Stott and Olson 1973; Loring et al. 2013) which is supported by the results from this study. In comparison, common eiders in southern New England preferred areas with a much steeper topography (Beuth et al. 2017).

The average distance to shore for northern wintering sites was slightly further than the results found by Loring et al. (2014). Common eiders wintering in southern New England, in comparison, are located much closer to shore than black scoters (Beuth et al. 2017). The average distance to shore for southern wintering sites was further from shore than the northern wintering sites by about 2.5 kilometers. Southern wintering sites might be further away from shore than northern wintering sites because water depth increases rapidly in a relatively short distance from shore in New England, where the water depth increases slowly as the distance from shore increases in the southeast.

Understanding wildlife population distribution and population dynamics as it relates to habitat selection allows for more effective conservation planning, minimizing human conflicts, and better survey planning for future monitoring programs (Newbold and Eadie 2004, Rushing et al. 2017). This study provides insight on the wintering

ecology and movement of black scoters along the Atlantic coast of the United States. Geography showed a decisive difference in the average wintering site area and distance between wintering sites. Habitat use of wintering sites for black scoters does vary geographically between northern and southern populations. Biotic or abiotic conditions encountered on the wintering grounds may be important to the black scoter population dynamics thru the indirect effects of dispersal decision, spring migration, and reproductive success (Scott 1998, Martin & Wiebe 2004). This information, coupled with other studies on black scoter wintering ecology and movement, allows for more effective conservation and management of this species, while minimizing human conflicts and for future monitoring programs.

Management Implications

The average arrival date to the first wintering site for black scoters was 12 November. The average departure date for black scoters from the last wintering site was 25 March. There was no difference in habitat use and movement between male and female black scoters. Wintering sites located along the northern coast of the United States (Chesapeake Bay and north) are smaller and closer to shore than wintering sites located along the southern coast of the United States (south of the Chesapeake Bay). Black scoter wintering sites along the northern coast of the United States are located closer to shore and in deeper waters with a steeper slopes than wintering sites along the southern coast of the United States.

My results increase the knowledge on black scoter wintering use and movement, information that was lacking. Managers interested in protecting wintering habitat for

black scoters along the Atlantic coast of the United States should consider that high quality habitat for black scoters varies geographically. High quality black scoter habitat in New England may not be high quality habitat in the southeast. My results enable managers to focus sampling effort for black scoter abundance and distribution along the Atlantic coast. Habitat characteristics for black scoters identified in my study area should be carefully considered when planning anthropogenic activities along the southeast coast of the United States, such as offshore energy development.

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TABLES

Table 1: The mean bathymetry (m), ocean floor slope (degrees), and distance to shore (km) and range for individual black scoter wintering sites obtained via satellite telemetry along the Atlantic coast of the United States from September 2009 to April by geography. Northern wintering sites are wintering sites that are located at the Chesapeake Bay and north. Southern wintering sites are wintering sites that are located south of the Chesapeake Bay.

Wintering Site	Bathymetry (m, range)	Ocean Floor Slope (degree, range)	Distance to Shore (km, range)
Northern (n = 92)	-22.22 (-125.00 – 1.00)	0.12 (0.04 – 0.47)	6.47 (0.02 – 18.42)
Southern (n = 46)	-7.91 (-13.99 – 0.00)	0.05 (0.02 – 0.08)	9.02 (0.005 – 25.99)

FIGURES

Figure 1: 50% fixed kernel density map for one black scoter (as an example) that was satellite tagged with a Platform Transmitting Terminal (PTT) during on wintering season along the Atlantic coast of the United States during the winter of 2010 – 11. The map identifies the number of wintering sites used during the wintering period, the area of each wintering site (km^2), and the distance between the wintering sites (km).

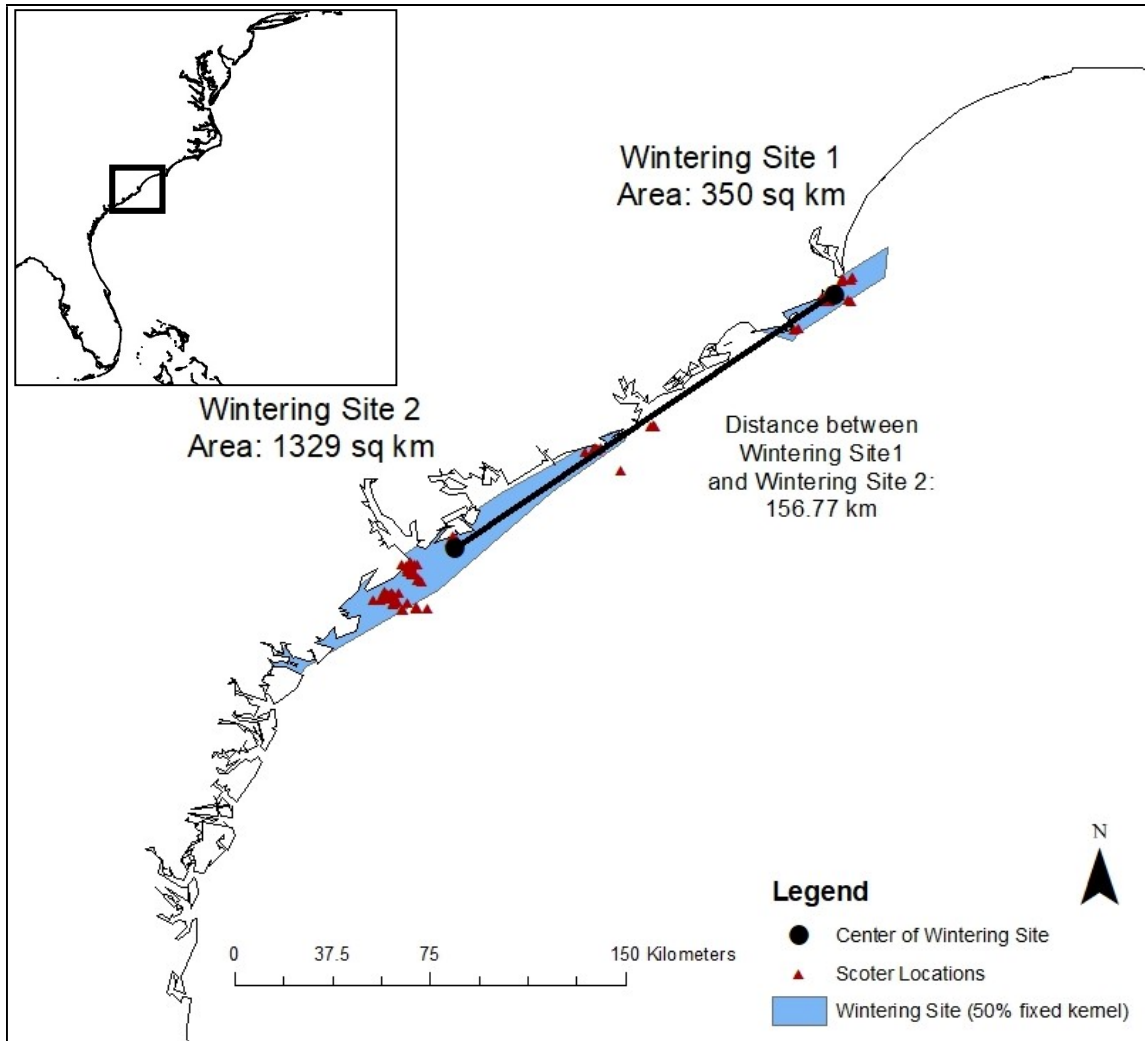


Figure 2: Violin plot showing the frequency (kernel density plot on its side), interquartile range, 95% confidence interval, and median (♦) of black scoter arrival dates to the first wintering site (Julian date) along the Atlantic coast of the United States from September 2009 to April 2012 by geographic location (the Chesapeake Bay and north or south of the Chesapeake Bay).

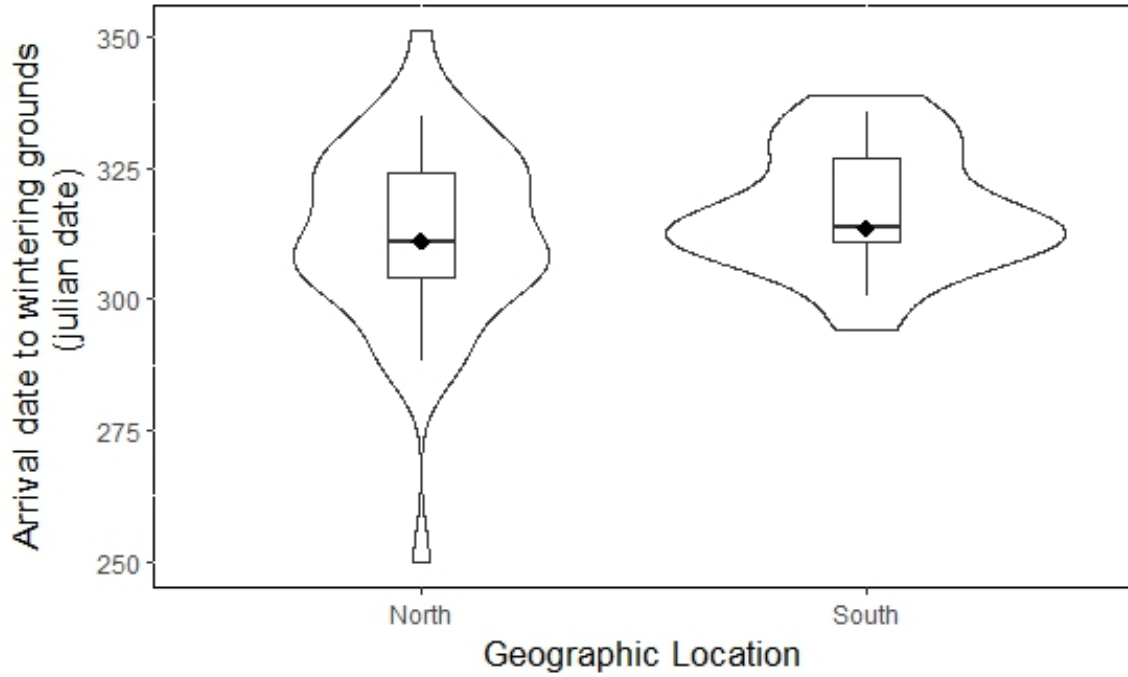


Figure 3: Violin plot showing the frequency (kernel density plot on its side), interquartile range, 95% confidence interval, and median (◆) of black scoter departure dates from the last wintering site (Julian date) along the Atlantic coast of the United States from September 2009 to April 2012 by geographic location (the Chesapeake Bay and north or south of the Chesapeake Bay).

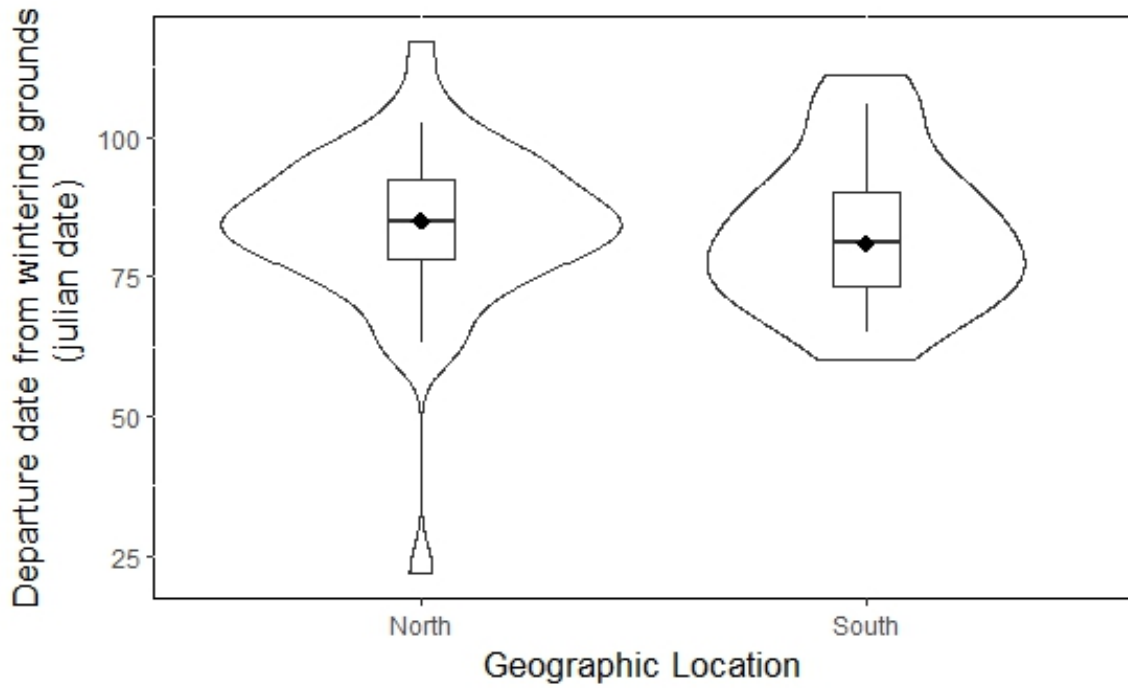


Figure 4: Number of distinct wintering sites (one wintering site $n = 25$, two wintering sites $n = 27$, and three wintering sites $n = 14$) used by black scoters that winter along the Atlantic coast of the United States during a wintering season from September 2009 to April 2012.

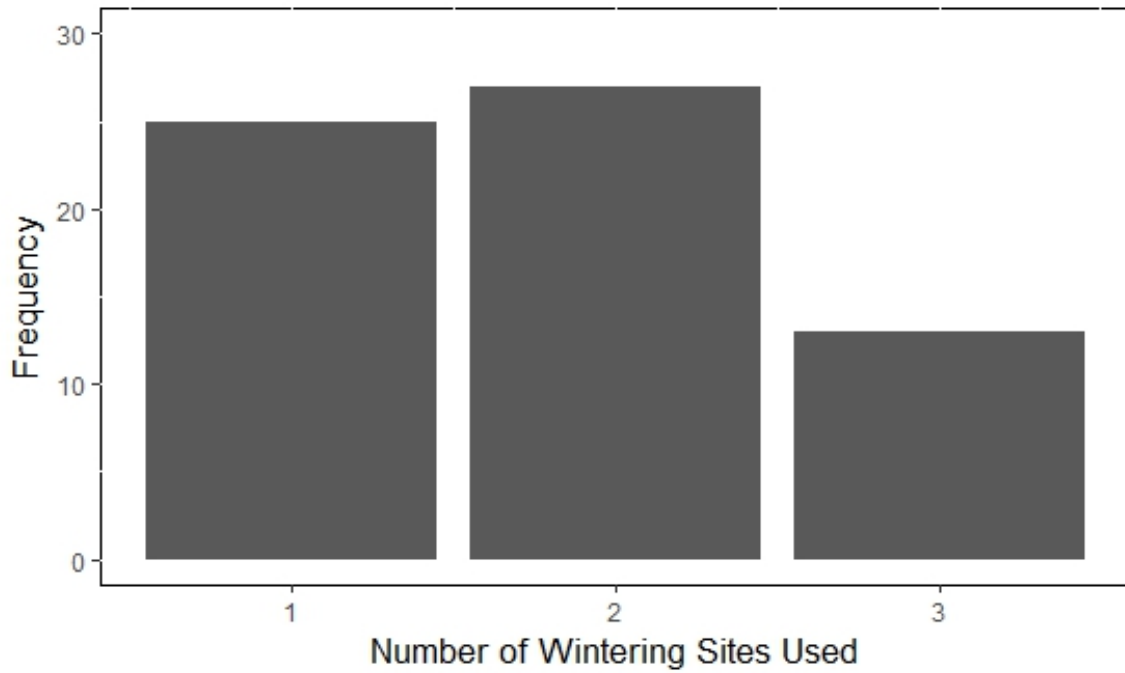


Figure 5: Box plot of days black scoters spent during each period of time (the period of time spent continuously at a wintering site before leaving the wintering site) at a wintering site along the Atlantic coast of the United States from September 2009 to April 2012.

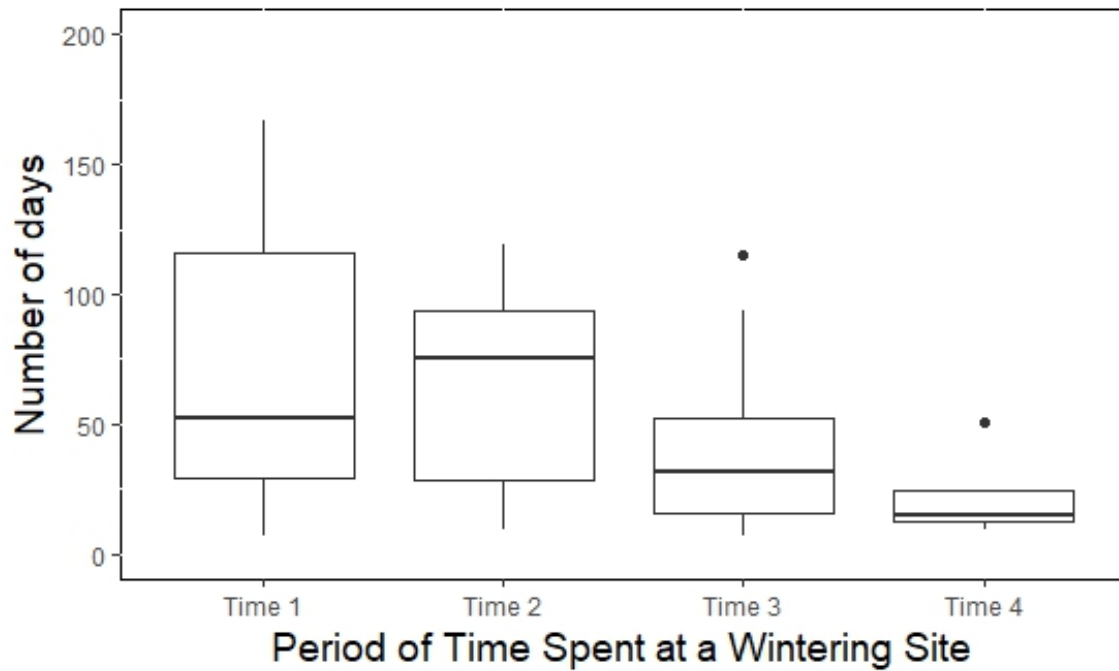


Figure 6: Box plot of distance between wintering sites (km) used by black scoters wintering along the Atlantic Coast of the United States from September 2009 to April 2012 (Site 1 – Site 2 n = 41, Site 2 – Site 3 n = 14, Site 3 – Site 4 n = 4).

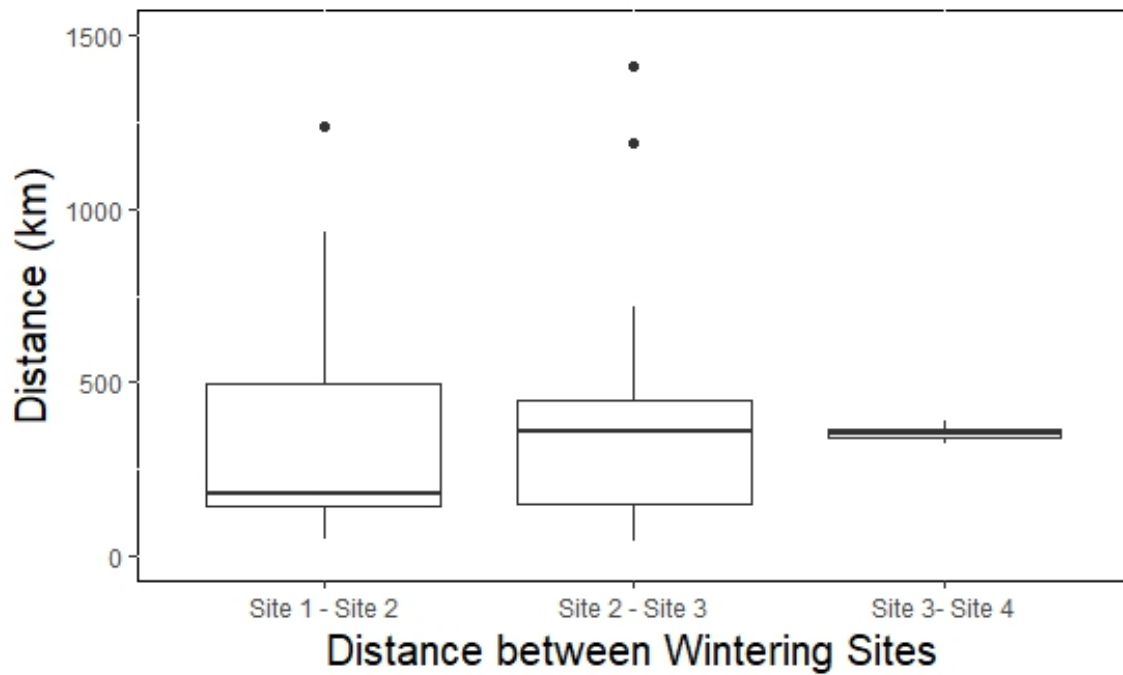


Figure 7: Violin plot showing the frequency (kernel density plot on its side), interquartile range, 95% confidence interval, and median (♦) of the average distance between wintering sites (km) used by black scoters wintering along the Atlantic coast of the United States by geographic location (the Chesapeake Bay and north or south of the Chesapeake Bay).

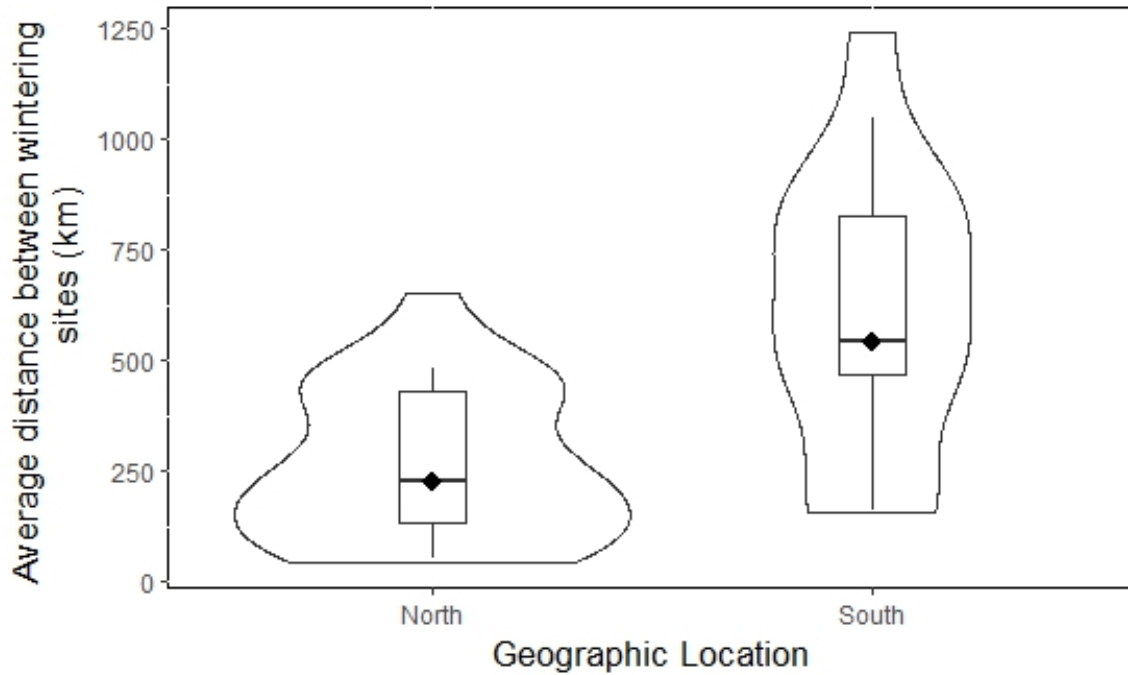


Figure 8: Box plot of the wintering sites (km^2) used by black scoters wintering along the Atlantic coast of the United States from September 2009 to April 2012.

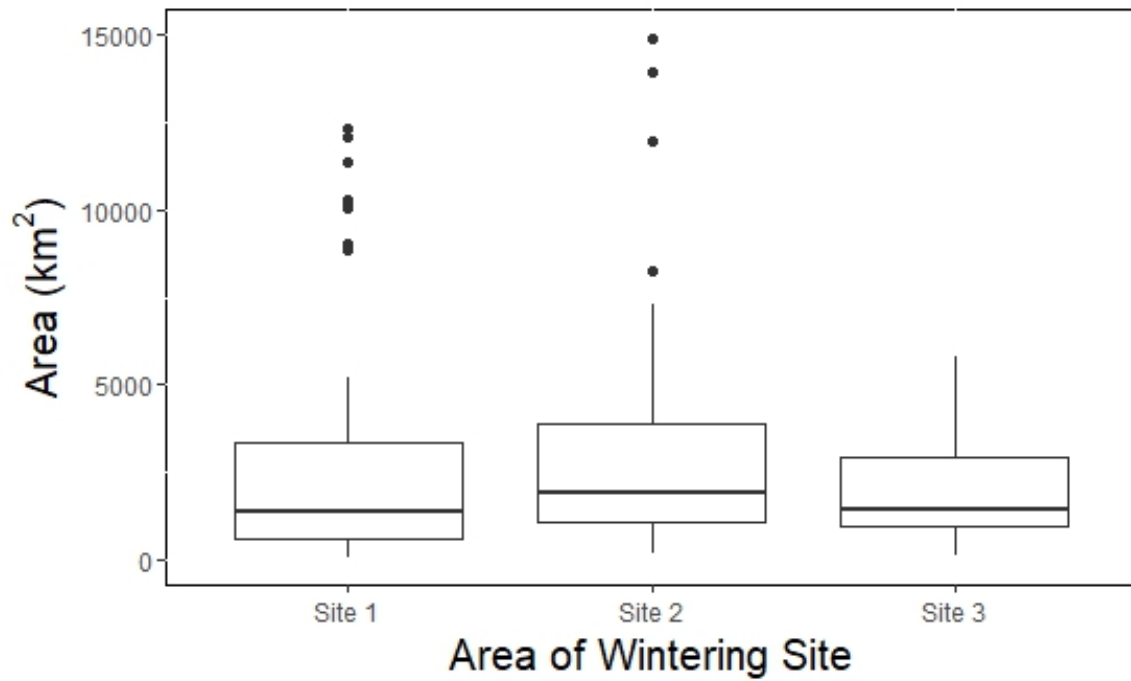


Figure 9: Violin plot showing the frequency (kernel density plot on its side), interquartile range, 95% confidence interval, and median (♦) of the average wintering site area (km^2) used by black scoters wintering along the Atlantic coast of the United States by geographic location (the Chesapeake Bay and north or south of the Chesapeake Bay).

