

## ABSTRACT

FOLEY, HEATHER JAMIE. Spatial Ecology and Movement Patterns of Deep-Diving Odontocetes in the Western North Atlantic Ocean. (Under the direction of Dr. Krishna Pacifici).

Short-finned pilot whales (*Globicephala macrorhynchus*) and Cuvier's beaked whales (*Ziphius cavirostris*) are deep-diving odontocetes with broad distributions, and are of conservation concern given their history of increased injury and mortality resulting from direct interactions with fisheries and mass strandings resulting from mid-frequency active sonar. In the western North Atlantic, basic information on the spatiotemporal distribution, movement patterns, habitat preferences, home ranges, and residency of these highly mobile species are still unknown. To address this gap in knowledge, satellite telemetry tags were deployed on both species offshore of Cape Hatteras, North Carolina, and Jacksonville, Florida from 2014 – 2017. Tags durations varied by individual and species, with statistically analyzed portions ranging up to 151 days. While movements away from Cape Hatteras were small for Cuvier's beaked whales, short-finned pilot whales demonstrated long-distance movements, ranging from Florida to Georges Bank and eastward to the New England seamounts. Home ranges and core areas of high use were generated at the individual and population level via kernel density estimation, with short-finned pilot whales demonstrating wide-spanning home ranges and high individual variability in core use areas. Cuvier's beaked whales exhibited small, overlapping core use areas highly concentrated offshore of Cape Hatteras. Net squared displacement analyses suggest that Cuvier's beaked whales tagged belong to a resident population. Short-finned pilot whales were variable in their movement tactics, with individuals falling into several different strategies, including nomadic, dispersal, and home range behavior. Using a behavioral switching state-space

model to differentiate between area-restricted search (ARS) and transit behavior over a six-hour time step, generalized linear mixed models were run to evaluate several potential environmental drivers of behavior. ARS behavior was the dominant behavior in Cuvier's beaked whales, with the majority of tagged animals never exhibiting transit behavior. Individual short-finned pilot whales differed in their movement and behavior patterns, with two main movement modes observed. Many animals remained closely associated with the continental shelf break throughout their tag deployment, while others moved into offshore waters. However, some animals switched between patterns. ARS was observed nearly exclusively within 10 kilometers of the continental shelf break in short-finned pilot whales, while transit behavior was exhibited throughout their range, both along the continental shelf break and in pelagic waters. In addition, habitat preferences and behavior varied by tagging site in short-finned pilot whales. Despite long distances travelled by short-finned pilot whales, many individuals returned to Cape Hatteras, demonstrating some level of site fidelity. The strongest environmental drivers of transit behavior in Cuvier's beaked whales were distance from the continental shelf break and latitude, while distance to shelf break and slope best described the variability in short-finned pilot whale behavior. This work highlights the advantages of using satellite telemetry in pelagic marine predators to investigate movement and spatial use patterns in highly mobile species that are otherwise difficult to study over broad spatiotemporal scales. The spatial ecology of deep-diving odontocetes in the western North Atlantic investigated here can benefit management and conservation of these species vulnerable to anthropogenic and natural threats in the rapidly changing marine environment.

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Spatial Ecology and Movement Patterns of Deep-Diving Odontocetes  
in the western North Atlantic

by  
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## DEDICATION

This thesis is dedicated to my family, in particular my late grandmother, Gertrude Foley, who always encouraged education and independence above all things. My parents, both teachers, instilled a passionate desire for life-long learning and self-betterment that lead me to pursue my master's degree. My sister was a wonderful exemplar for successfully completing a graduate program while working full-time, and more importantly, enjoying life while doing so. Noah and Hannah, you always kept me smiling through frustrating times.

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## **BIOGRAPHY**

Heather Jamie Foley was born and raised in Coon Rapids, Minnesota. She followed her childhood dream to study marine biology and work with marine mammals to Boston University, where she received a dual Bachelor of Arts degree in Biology with a specialization in Marine Science and German Language and Literature in 2003. She then began her career of spatial analyses working at the Massachusetts Natural Heritage and Endangered Species Program for five years. An internship with the New England Aquarium's North Atlantic Right Whale Research Project in 2007 in the Bay of Fundy was her first exposure to cetacean fieldwork, and she never looked back, since travelling to every ocean basin researching marine mammal conservation throughout the world. In 2009, she relocated to Fernandina Beach, Florida to begin her current employment with Duke University. A move to the Duke University Marine Lab in Beaufort, North Carolina in 2011 and a desire for strengthening her skill set along with investigating her study species further prompted her to begin taking graduate courses while continuing her professional career at DUML. She enrolled at North Carolina State University in 2016, and is grateful to everyone who helped form her path.

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## LIST OF ABBREVIATIONS

AIC:	Akaike Information Criterion
Argos:	Advanced Research and Global Observation Satellite
ARS:	Area-Restricted Search
CEE:	Controlled Exposure Experiment
CRM:	Coastal Relief Model
EEZ:	Exclusive Economic Zone
GEBCO:	General Bathymetric Chart of the Oceans
GHRSSST:	Group for High Resolution Sea Surface Temperature
GLMM:	generalized linear mixed model
hr:	hour(s)
hSSSM:	hierarchical switching state-space model
KDE:	kernel density estimation
km:	kilometer(s)
LC:	Location Class
LIMPET:	Low-Impact Minimally-Percutaneous External-electronics Transmitter
m:	meter(s)
MAB:	Mid-Atlantic Bight
MCMC:	Markov Chain Monte Carlo
MFA:	mid frequency active
MGET:	Marine Geospatial Ecology Tools
MMPA:	Marine Mammal Protection Act
min:	minute(s)
nm:	nautical miles
NCEI:	National Center for Environmental Information
NMFS:	National Marine Fisheries Service
NOAA:	National Oceanic and Atmospheric Administration
NSD:	net squared displacement
OSCAR:	Ocean Surface Current Analysis Real-time
photo-id:	photo-identification
SAB:	South-Atlantic Bight
SPOT:	Smart Position and Temperature
SSM:	state-space model
SSSM:	switching state-space model
SST:	sea surface temperature
UD:	utilization distribution
U.S.:	United States
VIF:	variance inflation factor

## GENERAL INTRODUCTION

Under the United States (U.S.) Marine Mammal Protection Act (MMPA) of 1972, all marine mammal species are federally protected, and the U.S. National Marine Fisheries Service (NMFS) is the agency charged with gaining information on these species through population censuses and health assessments, in addition to working to prevent and mitigate anthropogenic mortality and serious injury to populations. Cetaceans are managed at the stock level, which, as defined by the MMPA, refers to “a group of marine mammals of the same species or smaller taxa in a common spatial arrangement, that interbreed when mature” (MMPA, 1972). In order to effectively manage and conserve cetacean species, both under federal mandates and an ever-changing environment impacted by a variety of anthropogenic threats, such as increased ocean noise (Nowacek et al. 2007), interactions with fisheries (Read et al. 2006), and climate change (Simmonds and Isaac 2007; Whitehead et al. 2008; Costa, Hüeckstädt, et al. 2010), obtaining a thorough understanding of species’ abundance, distribution, ecology, and behavior is necessary.

Spatial ecology can help address these biological parameters and define the scale(s) at which they are significant. The home range of an individual is the area in which the species regularly moves, including habitats that animals frequently use for breeding, foraging, resting and socializing (Burt 1943; Worton 1987). Defining home ranges for all cetacean species is vital to understand where these protected animals move and the habitats they utilize. Habitat selection is motivated by the need to forage, reproduce, and avoid predators, and can directly influence behavior, long-term fitness, and survival of animals (Hooker et al. 2002). Studies analyzing spatial and habitat use at individual and population levels can begin to define

social groups, populations, or stocks within a cetacean species, information necessary for proper management. Continuing to understand and refine the spatiotemporal scales at which these protected species operate is another important factor in spatial ecology studies (Redfern et al. 2006; McGarigal et al. 2016).

Many analytical methodologies, including habitat models (Embling et al. 2010), utilization distributions (Sveegaard et al. 2011), state-space models (Jonsen et al. 2007), and first passage time (Fauchald and Tveraa 2003), can pinpoint areas of particularly high density of species occurrence or detect foraging habitat. Combined with information on the environmental and social drivers defining these high-use areas, ‘hotspots’ can be used to identify priority regions for conservation. Additionally, the overlap of species’ preferred habitats and spatially explicit anthropogenic threats can be ascertained, such as bycatch from interactions with the U.S. Atlantic pelagic longline fishery (Thorne et al., in review), and subsequently used in mitigation strategies.

While the spatial ecology of many terrestrial species has been extensively studied (Kays et al. 2015), acquiring habitat use information for highly mobile marine mammal species, particularly those who inhabit pelagic waters, can be more of a challenge (Hussey et al. 2015). Habitat modeling, often used in terrestrial systems to identify important features and foraging areas for a species, presents a unique set of challenges in cetaceans, including the inherently patchy and three-dimensional nature of the marine environment, paucity of informed knowledge on prey species, short surface durations, as well as the complex social structure of many odontocetes (Redfern et al. 2006). Though marine predator distributions and movements are often correlated with the location and abundance of their prey, *in situ*

measurements of prey abundance are rarely obtainable in broad-scale, pelagic marine environments (Palacios et al. 2014). Therefore, physical oceanographic data, including remotely sensed data, such as bathymetric depth or sea surface temperature (SST), often serve as proxies for prey (Redfern et al. 2006). Currently, abundance estimates for cetacean species along the U.S. eastern seaboard are generated from non-comprehensive line-transect surveys, which are generally conducted solely during the summer season, covering only small or disjointed portions of many species' entire range, methods not greatly suited for habitat modeling or stock assessments (Mullin and Fulling 2003; Waring et al. 2014; Waring et al. 2016).

Over the past two decades, the development of many bio-logging instruments, such as digital acoustic tags (Johnson and Tyack 2003; Madsen et al. 2013) and satellite telemetry tags has helped revolutionize foraging and spatial ecology studies in highly mobile pelagic marine species (Block et al. 2011; Hazen et al. 2012; Hussey et al. 2015; Hays et al. 2016). Satellite telemetry is particularly useful for animals that are not often encountered and for species that cover large spatial scales (Block et al. 1998; Priede and Miller 2009). While mark-recapture studies can provide a coarse scale at which to define long-term movement patterns of widely-distributed offshore marine species, satellite tags refine these parameters at much finer scales and over longer study periods, all the while substantially reducing the level of research effort and funding required to reach remote locations (Hussey et al. 2015). Information on an animal's physical movements and location across both space and time, which was previously impossible if an individual was not directly observable from a vessel, is now obtainable. However, whether it be measured *in situ* or sensed remotely, obtaining

biologically relevant environmental data at scales similar to those at which the animal moves can still prove to be a challenge today (Bestley et al. 2012). Nonetheless, the drivers of animal movement across time and space can be determined when animal positions are linked with environmental covariates, allowing for greater ecological inferences. Satellite tags have been used to study several aspects of cetacean spatial use including habitat selection, migration patterns, and foraging and dive behavior (Bailey et al. 2010; Kennedy, Zerbini, Vásquez, et al. 2014; Bestley et al. 2016). While a small number of cetacean species have been studied in the western North Atlantic using satellite telemetry (Nawojchik and Etal 2003; Mate et al. 2005; Wells et al. 2013), no dedicated satellite-tagging studies of short-finned pilot whales (*Globicephala macrorhynchus*) or Cuvier's beaked whales (*Ziphius cavirostris*) have been conducted on free-ranging animals along the U.S. eastern seaboard to date.

In this thesis, I investigate habitat use and behavior as they relate to movement patterns of offshore odontocetes. Additionally, I aim to establish an essential baseline on the spatial ecology of both short-finned pilot whales and Cuvier's beaked whales, species of particular conservation concern, given their history of mass strandings and interactions with fisheries (Read et al. 2006; D'Amico et al. 2009; Tyack et al. 2011; DeRuiter et al. 2013). Describing where, when, how, and why these species move through their environments will help fill a knowledge void in these highly mobile offshore species, the ranges of which are still unclear. Understanding the factors that influence both habitat selection and behaviors of these species can aid in their management and conservation, and potential behavioral responses from future anthropogenic effects can be better identified, predicted, and mitigated.

I will evaluate the movement patterns, habitat use, and behavioral drivers from satellite telemetry positions of each species separately. My first chapter will focus on short-finned pilot whales and the second on Cuvier's beaked whales.

## **CHAPTER 1 – MOVEMENT ECOLOGY OF SHORT-FINNED PILOT WHALES (*GLOBICEPHALA MACRORHYNCHUS*) IN THE WESTERN NORTH ATLANTIC**

### **Abstract**

The short-finned pilot whale (*Globicephala macrorhynchus*) is a wide-ranging species found in tropical and subtropical waters that is susceptible to injury and mortality due to direct interactions with longline fisheries and mass strandings. Here, I integrate satellite telemetry data and oceanographic variables to summarize movement patterns, space use, and behavior drivers of 58 individual pilot whales fitted with satellite tags offshore of Cape Hatteras, North Carolina and Jacksonville, Florida from 2014 to 2017. To interpolate locations and estimate whether an animal's behavioral state was area-restricted search (ARS) or transit, I employed a hierarchical switching state-space model (hSSSM). Kernel density estimation (KDE) was used to create utilization distributions and identify high use areas of the species, which were generally close to the continental shelf break. I ran generalized linear mixed models (GLMMs) accounting for random variation between both individual whales and tagging site, examining several oceanographic predictor variables. Most (63%) locations were classified as foraging behavior, with an increased likelihood of transit at locations of low bathymetric slope and increased distance from the shelf. However, habitat selection and distribution of behaviors varied between tagging sites. Despite wide individual variability in home range areas, core use sizes, displacement from and periodicity of return to the Cape Hatteras area across the sample size, short-finned pilot whales do show some degree of philopatry to the Cape Hatteras study area. This work identifying high-use foraging areas can

better inform effective conservation and management of this species vulnerable to anthropogenic and natural threats.

## **Introduction**

Pilot whales are highly social members of the family Delphinidae that live worldwide in tropical and temperate waters of the continental shelf break and associated slope (Amos et al. 1993; Quick et al. 2017). They are sexually dimorphic animals known to feed on mesopelagic squid during foraging dive bouts to depths of 800 m (Sakai et al. 2011; Visser et al. 2014). Two species (short-finned and long-finned; *Globicephala melas*) of pilot whales exist, and both live in stable matrilineal groups and form both short-term (hours to days) and long-term (years) associations with other individuals (Ottensmeyer and Whitehead 2003; Visser et al. 2014). Pilot whales in the western North Atlantic are known to inhabit areas of high relief, such as submarine canyons, and tend to associate with the Gulf Stream wall and its associated thermal fronts (Waring et al. 2016). Though recent information on the species' seasonal distribution is deficient, Payne and Heinemann (1993) found pilot whales to be distributed along the U.S. eastern seaboard's continental shelf break in winter and early spring, with animals moving further north to waters in Georges Bank and the Gulf of Maine in late spring and tending to reside there through late fall.

Although both species of pilot whales are frequently observed throughout their ranges, which are known to overlap in some areas of the western North Atlantic (Waring et al. 2016), basic species-specific information on their distribution and movement patterns are still lacking. This is due in part to the inability to readily distinguish between the two species

at sea (Rone and Pace 2012; Waring et al. 2016). Additionally, as the offshore regions used by these species can be difficult and costly to access, most pilot whale habitat use information acquired to date has been generated through disjointed shipboard and aerial surveys conducted solely in summer months. These seasonal surveys do not allow for full inferences across the broad spatiotemporal scales at which these animals operate (Thorne et al. 2017). Currently, distribution, abundance, and stock structure estimates for pilot whales in the western North Atlantic are generated from visual line-transect surveys and genetic sampling. However, the last set of surveys to cover the entire geographic range of pilot whales in U.S. Atlantic waters occurred in 2011, and as such, updated distribution information is needed both for informed abundance estimates and for effective management of the species, which is vulnerable to mass strandings and increased serious injury and mortality due to interactions with the U.S. Atlantic pelagic longline fishery (Garrison 1992).

In addition to the spatially-explicit threat of bycatch, distributional shifts may occur in cetacean ranges due to anthropogenic disturbances such as controlled-exposure experiments (CEEs), mid-frequency active (MFA) sonar, or seismic surveys (Gordon et al. 2003; Gomez et al. 2016). Furthermore, long-term alterations to the marine environment due to climate change may have a direct impact on species' movement patterns and spatial use. In order to effectively assess current threats to the species and inform management, species-specific information on short-finned pilot whale's distribution and movement patterns is necessary over several temporal scales.

Long-term residency patterns and social structure of short-finned pilot whales offshore of Cape Hatteras, North Carolina have been studied since 2006 using photo-

identification methods. Several pairs, trios, and groups of four short-finned pilot whales have been observed together both intra- and inter-annually, in addition to over 30% of the unique, distinct individuals (339 of 1,149) being re-sighted in the area on up to seven separate occasions spanning up to ten years between first and last sightings (D. Waples, pers. comm.), demonstrating strong site fidelity and some level of long-term philopatry to the Cape Hatteras area. In addition, fine-scale, short-term diving and foraging ecology of the species has been evaluated using digital acoustic tags deployed for up to 24 hours on animals offshore of Cape Hatteras (Quick et al. 2017). However, these methodologies are limited to a single site and the spatiotemporal distributions and movement patterns of short-finned pilot whales over medium-term (weeks to months) temporal scales are still poorly understood. In order properly to define home ranges, core areas of high use, and evaluate individual variability of spatial use patterns of the species, work to fill the knowledge gap on these broad-scale movements is necessary.

Satellite telemetry offers several benefits over photo-identification and digital acoustic tags, including an increase in both spatial and temporal resolution while also allowing for inference on how distributions may change over time relative to the environment (Irvine et al. 2014; Abecassis et al. 2015). In addition, important habitats and high use areas can be identified at the individual and population level and compared with spatially explicit threats, such as bycatch, allowing for more effective management and conservation of the species.

Satellite-linked recorders were previously deployed on short-finned pilot whales in the western North Atlantic to investigate the movements of two individuals that were

released after stranding in Florida in 2011. Telemetry tracked them from the Florida Keys northward through the Blake Plateau, offshore of the east coast of Florida and south, east of the Bahamas, to the Dominican Republic and Cuba before transmissions ceased after 67 days, demonstrating the large spatial scale at which the species is believed to operate (Wells et al. 2013). Animals often moved with prevailing currents, and demonstrated average daily horizontal rates ranging from 2 – 7 km/hr, with highest rates traveled in waters <1,000 m. Mean daily water depths ranged from 639 – 2,795 m with SSTs ranging from 25° – 29° C (Wells et al. 2013).

The aim of the current chapter is to summarize movement patterns, home range dynamics, and spatial use of short-finned pilot whales using satellite telemetry. In addition, I will examine the relationship between species' behavior and oceanographic variables. Preliminary work generated from this telemetry study demonstrates that short-finned pilot whales show a strong affinity for the continental shelf break (200 m isobath) and its associated canyons. Some animals moved into offshore waters, closely affiliated with meanders and eddies associated with the Gulf Stream frontal system. However, area-restricted search (ARS) behavior, as determined from first passage time analyses, was highly concentrated along the shelf break and submarine canyons of the Mid-Atlantic Bight (MAB). I hypothesize high use areas for short-finned pilot whales will be concentrated along the continental shelf break, and the distribution of behavioral states of the species will be non-random, with more transit behavior than ARS in pelagic waters. In addition, I hypothesize that individual short-finned pilot whales will exhibit wide variation in displacement from the Cape Hatteras area and time to return, with pelagic individuals returning to the region less

frequently while shelf-break associated animals will demonstrate lower net displacements and shorter time away from the area, resulting in smaller home ranges for those animals.

## **Methods**

### *Study Area*

The outer continental shelf and steep slope waters offshore of Cape Hatteras define the study area (Figure 1.1). The continental shelf at Cape Hatteras is quite narrow, with bathymetry differences of over 1,200 m in less than 10 cross-shelf kilometers. The shelf expands both to the north and south, forming the Mid-Atlantic Bight and the South Atlantic Bight (SAB), respectively (Mullin and Fulling 2003). The dominant oceanographic feature in the area is the Gulf Stream, the North Atlantic ocean's largest frontal system (Chambault et al. 2017). The region of particular focus is named 'The Point', an area of many square kilometers approximately 35 nautical miles offshore, where the Gulf Stream Front flows northward into the study area and separates from the continental shelf, shifting to the northeast into oceanic waters. Many deep-diving cetacean species are known to inhabit The Point, including Cuvier's beaked whales (*Ziphius cavirostris*) and short-finned pilot whales (Waring et al. 2001; Mullin and Fulling 2003; Roberts et al. 2016).

### *Spatial Use*

#### Tagging and Tracking

Satellite tags of the Low Impact Minimally Percutaneous External-electronics Transmitter (LIMPET) configuration (Andrews et al. 2008; Baird et al. 2010; Baird et al. 2011) were remotely deployed using a pneumatic projector from a 9.1 m rigid-hulled boat.

Tags were attached with two 6.8-centimeter titanium darts with backward-facing petals into the dorsal fin or base thereof of 58 short-finned pilot whales off of Cape Hatteras, North Carolina and Jacksonville, Florida, between 2014 and 2017. In addition to the study site offshore of North Carolina described above, four satellite tags were opportunistically deployed on short-finned pilot whales approximately 75 nm offshore of Jacksonville, Florida, in June 2016 (Figure 1.1). The continental shelf and slope water habitat throughout the SAB differs drastically from that of the MAB, with >250 km separating the 200 m and 1,500 m isobaths offshore of Florida, and deeper waters (>1,000 m) not occurring until approximately 400 km from shore (Figure 1.1).

The majority of the tags deployed (n=35) were Smart Position and Temperature (SPOT5 & 6; Wildlife Computers, Redmond, WA) tags, which transmit only the surface location of the animals. Other animals (n=22) were equipped with Mk10-A SPLASH satellite-linked depth-recording tags from which both position and compressed data of dive records are transmitted. One location-depth SPLASH 10F prototype tag, which includes the capability to receive Fastloc-GPS positions, was also deployed. All three tag types transmit data to Advanced Research and Global Observation Satellite (Argos) receivers on polar-orbiting satellites. Tags were scheduled to transmit on a year and tag-specific regimen with SPOT5 tags deployed during 2014 - 2016 transmitting daily for the first 60 days of deployment, every third day for the subsequent 21 days, followed by every fifth day for the remainder of the deployment. SPOT6 tags put out in 2016 recorded daily transmissions, with the number of transmission hours per day being reduced after 60 and 105 days. Pilot whales with 2014 Mk10-A location-depth tags transmitted daily for 20 days, every third day for a

30-day span, followed by every ninth day for the remainder of the duration, while 2015 and 2016 dive tags transmitted daily for 20 days, every third day for the subsequent 12 days, followed by every ninth day. Based on local satellite coverage, 2014-2016 tags were programmed to transmit from 10-17 hours per day, based on tag type. All tags deployed in 2017 on short-finned pilot whales were scheduled to transmit for 17 hours per day, with no duty cycle employed.

Argos positions are assigned a location quality class (3, 2, 1, 0, A, B, and Z) based on the timing and number of transmissions received during a satellite pass (Irvine et al. 2014; McClintock et al. 2015). Numbered location classes have estimated error radii of <250 m for class 3, <500 m for class 2, <1,500 m for class 1, and >1,500 m for class 0 (Vincent et al. 2002), while lettered location classes (A and B) do not have an estimated level of error. Location class Z positions, considered invalid by Argos, were not included in analyses.

#### Location Filtering and Behavioral State Estimation

Turchin (1991) proposed that both movement patterns and behaviors in animals would change as a result of differences in habitat or prey density. Area-restricted search (ARS) behavior is associated with greater turning frequencies and angles and low persistence between locations. Conversely, animals that are transiting through areas, presumably due to insufficient prey densities or unsuitable habitat, tend to exhibit higher travel rates and smaller turning angles between locations.

Switching state-space models (SSSMs) are one method to estimate the behavior of animals. They simultaneously generate the ‘true’ track of the animal from the unfiltered,

error-prone positional data, in addition to calculating movement parameters based on the process model that allows movement parameters to vary between two distinct behaviors (Jonsen et al. 2005; Jonsen et al. 2013; Jonsen 2016). Combinations of turning angle and move persistence between positions determine the behavioral state classification at each estimated location.

A hierarchical switching state-space model (hSSSM), which employs joint estimation over multiple individual tracks, can improve behavioral state estimation and movement parameter accuracy. Regularized tracks for every individual at a chosen time-step are generated in addition to an estimated behavioral state ( $b_t$ ). Hierarchical SSSMs also provide greater insight into population-level movements, allowing improved understanding of population dynamics (Jonsen 2016).

Given the inherent error associated with Argos positions (Vincent et al. 2002; Costa, Robinson, et al. 2010) and large geographic range covered by short-finned pilot whales, a hSSSM was used to generate both estimated locations of each animal and inferred behavioral state: ARS or transit (Patterson et al. 2008; Breed et al. 2009; Beyer et al. 2013; Beatty et al. 2016). Often exhibited when an animal encounters areas of high prey density, ARS is typically inferred as foraging in cetaceans, but could also include breeding or resting behaviors (Schick et al. 2008; Bailey et al. 2010; Kennedy, Zerbini, Rone, et al. 2014). Based on the average number of telemetry locations per day across all tagged short-finned pilot whales ( $n=9$ ), a 6-hr time step was chosen, and locations at each time step were estimated for 53 individual tags of suitable duration. As error in hSSSM positional estimates increases rapidly with extended gaps in raw data (Bailey et al. 2008), all raw Argos positions following

transmission gaps greater than three days were excluded from analyses, as well as any tags of duration shorter than 2 days or which generated <20 total positions (Jonsen 2016). In addition, one individual (GmTag182) was excluded from statistical analyses due to its proximity (<50 km) to a controlled exposure experiment (CEE) in the Cape Hatteras region on 12 September 2017. In this study, MFA sonar was played to animals equipped with satellite tags in order to assess their response to anthropogenic noise. Other tags active on the date of the CEE were >300 km from the sound source of the experiment, and as such, were not considered focal animals potentially affected by the acoustic experiment, and were included in the broad-scale movement analyses presented here. The hSSSM was run using the ‘bsam’ package (Jonsen et al. 2005; Jonsen 2016) in R statistical software v.3.4.3. (R Core Team 2017). Two chains of 40,000 iterations were run with an initial burn of 30,000. To reduce within chain sample autocorrelation every 10<sup>th</sup> sample was retained for 1,000 final posterior samples used in each chain (Jonsen 2016). Model convergence was visually assessed using trace and autocorrelation plots, as well as the Gelman-Rubin scale reduction factor ( $\hat{r}$ ).

### Home Range Estimation

In order to identify specific areas and habitats highly utilized by short-finned pilot whales throughout their distributions, home range and core use areas were produced using the hSSSM-estimated locations. Utilization distributions (UDs) were generated through kernel density estimation (KDE) using a bivariate plug-in bandwidth matrix as the smoothing parameter (Duong and Hazelton, 2003; Duong and Hazelton, 2005; Duong, 2007). The plug-

in method allows for separate bandwidths in the x and y directions and identifies high use areas well, even with dependent telemetry data (Hall et al. 1995; Jones et al. 1996; Walter et al. 2015). Core use areas, which represent particularly high-use regions of each animal's UD (Johnston et al. 2005; Acuña-Marrero et al. 2017) were defined as the 50% probability contour from the resulting UD, while home range was designated as the 95% probability contour. After projecting locations to the Albers Equal Area projection, home range and core use areas along with their associated isopleths were generated for individual animals and across the entire sample size in R using the 'ks' package (Duong 2007). Linear regression was used to evaluate the relationship between the proportion of ARS behavior exhibited by each individual and the areal size of both individual home range and core use areas.

### Movement Patterns

Net squared displacement (NSD), the Euclidean distance between an animal's initial and subsequent locations over time, has been used both in marine and terrestrial systems to evaluate movement patterns of individual animals (Bunnefeld et al. 2011; Papworth et al. 2012; Harrison, 2012). Animal movements lie on a continuum between nomadism, in which an animal never remains in the same place for long periods, and sedentarism, where an animal is spatially constrained within a home range (Börger and Fryxell 2012). The two other over-arching movement tactics are dispersal and migration. Specific movement patterns are classified to individuals by fitting an animal's NSD curve to a series of potential non-linear mixed movement models unique to each tactic, linking theoretical expectations in variation to observed NSD (Singh et al. 2012; Couriot et al. 2018). Home range, or residency models,

have either a constant NSD or one that asymptotes following a linear increase. Nomadism is denoted by a continuous, linear increase in NSD over time, while migration models show seasonal departures and return to an initial location, following a plateau. Dispersing animals demonstrate departure from an animal's initial location followed by a plateau, but fail to return (Börger and Fryxell 2012). To determine the movement tactics of individual short-finned pilot whales, NSD was calculated in R, and candidate movement models were run using 'nlme' package (Pinheiro et al. 2017). The best fitting model and its associated movement pattern category for each individual was assigned using concordance criterion values, with the largest value corresponding to the most appropriate tactic. Random effects were included in models to account for individual variability, in addition to sparse or unbalanced data, but see Börger and Fryxell (2012) for additional detail on model structure and selection.

#### *Describing Variability in Short-finned Pilot Whale Behavior*

One documented reaction of odontocetes exposed to anthropogenic noise in the marine environment is the cessation of foraging and directed movement away from the source of acoustic disturbance (Tyack et al. 2011; DeRuiter et al. 2013). As short-finned pilot whales could demonstrate similar reactions in response to MFA sonar or CEEs, determining an animal's propensity to cease foraging and engage in transit behavior may help assess and mitigate potential behavioral responses to future disturbances. By using the estimated behavioral state as a response variable in a multivariate model including potential predictor variables, we can determine the external drivers of short-finned pilot whale behavior.

While using hSSSMs to estimate locations on a regular time scale ameliorates the degree of temporal autocorrelation in telemetry data, positions are still spatially autocorrelated within individuals. As such, standard linear regression models are not well suited for this data set, and a statistical model in which the assumption of independence is relaxed or a correlation structure is included, such as a generalized linear mixed model (GLMM), is necessary. These models combine generalized linear models and mixed effect models, allowing for both fixed and random predictor variables, which can help account for spatial dependencies within individuals as well as variability between tagged whales (Guisan et al. 2002; Gillies et al. 2006; Hebblewhite and Merrill 2008; Bolker et al. 2009; Koper and Manseau 2009).

To examine the relationship between short-finned pilot whales behavior and potential environmental predictors, GLMMs were run using behavioral state as a binary response variable (presence of transit behavior or lack thereof) with several environmental covariates as predictor variables. Potential fixed effects included depth, bathymetric slope, distance to shelf break, distance to canyon, SST, and surface current, as well as month and year to analyze any potential seasonal effects on behavior. Individual pilot whale and tagging site (North Carolina or Florida) were chosen as random effects.

Whenever possible, 3 arc-second coastal relief models (Northeast Atlantic, Southeast Atlantic, and Florida) from the National Oceanic and Atmospheric Administration's (NOAA) National Center for Environmental Information (NCEI) were used to extract depth at each location. For offshore areas not included in NCEI's coastal models, 30 arc-second data from the General Bathymetric Chart of the Oceans (GEBCO) 2014 global bathymetry grid were

used ([www.gebco.net](http://www.gebco.net)). Slope and the 200 m contour, which served as a proxy for the continental shelf break, were generated from the GEBCO raster. Distance to both the shelf break and the closest major canyon of the U.S. Atlantic coast was calculated using ArcGIS for each position. Major canyons were identified using a shapefile generated by The Nature Conservancy and housed on the Mid-Atlantic Ocean Data Portal (<http://portal.midatlanticocean.org/>). Daily mean SST values were interpolated from the Group for High Resolution Sea Surface Temperature (GHR SST) grids with a 1 km resolution using Duke University's Marine Geospatial Ecology Tools (MGET; Roberts 2010). Surface currents, represented as the absolute magnitude of velocity (m/s), were extracted from NOAA's Ocean Surface Current Analysis Real-time (OSCAR) data set at 5-day, 0.33° resolution using MGET, estimating ocean currents from sea surface height altimeters, surface vector wind scatterometers, and sea surface temperature sensors (Bonjean and Lagerloef 2002).

Collinearity of covariates were assessed using Pearson and Spearman correlation coefficients  $<0.6$  and variance inflation factors (VIFs)  $<3$  (Zuur et al. 2009). To aid in model convergence, SST was centered and scaled to its mean, while slope, OSCAR current velocity, shelf break distance, and distance to canyons were scaled (Bolker et al. 2009). Due to sparse data sets over all levels of the categorical descriptor variables of month and year, no interaction terms were evaluated.

Models were run in the 'lme4' package in R, where maximum likelihood estimates and confidence intervals are estimated through Laplace approximation (Bates et al. 2015). Given a skew in response variable, with more ARS positions than transit, a complementary

log log (cloglog) link was used (Zuur et al. 2009). The dredge function within the R package ‘MuMIn’ (Barton 2018) was used to find the most parsimonious combination of covariates, and model selection utilized second-order Akaike information criterion (AICc; Mazerolle 2016, Akaike, 1973) in the ‘AICcmodavg’ R package and ‘MuMIn’.

## **Results**

### *Spatial Use*

Short-finned pilot whales tagged in this study ranged widely throughout the western North Atlantic with locations spanning from the southern portion of Florida north to Georges Bank and eastward to the New England seamounts, with at least one individual travelling outside the U.S. Exclusive Economic Zone (EEZ) into Canadian waters (Figure 1.2). Animals tagged off Jacksonville, Florida (n=4) spanned throughout the Blake Plateau (Figure 1.2). Two main movement modes were clear throughout the animals tagged off North Carolina, with the majority of tagged individuals demonstrated a strong affinity to the continental shelf break throughout their entire tag duration, while a subset of individuals moved offshore into more pelagic waters (Figure 1.2). However, some animals did switch between the two patterns, returning to the continental shelf break and slope waters after time in more pelagic waters or moving offshore after time spent along the shelf. As described in Thorne et al. (2017), the canyons of the MAB were hotspots of location density for short-finned pilot whales, with several individuals spending several days to weeks within canyon habitat.

Tag duration ranged up to 249 days, with an average of 60 days and a median of 38 days, though analyzed tag durations averaged 45 days (median = 32), with the longest duration of 152 days (Table 1.1). Data spanned all months from May through January, with no positions in February, March, or April included in analyses. Animals traveled up to 6,182 km throughout the analyzed tag durations as calculated by the sum of minimum great circle distances between successive locations, with a median cumulative distance traveled of 1,720 km (mean = 1,952; Table 1.1). It should be noted that individual travel distances are a vast underestimate, both as straight-line distances between points calculated do not represent the actual course taken, and many of the Argos positions acquired during duty-cycling of tags were excluded from analyses. The median depth at locations was 783 m (mean = 1,083 m, maximum = 5,193 m). Median distance to the continental shelf break was 3.8 km (mean = 33.2). Slopes ranged from 0° to 21°, with an average value of 5.7° (median = 6.0°). Sea surface temperatures varied by season and location and spanned 15.0°C to 31.4°C (median = 24.8°C). The absolute magnitude of OSCAR ocean current velocity ranged from 0.02 m/s to 1.65 m/s, with a median value of 0.37 m/s (mean = 0.46 m/s).

Habitat use varied between the tagging sites of Florida and North Carolina, particularly in bathymetric variables. Animals tagged off Florida demonstrated deeper median depths, as well as higher median SST, current velocity, distance to shelf break, and distance to canyons. Despite offshore habitats being utilized by short-finned pilot whales (Figure 1.1), animals tagged off North Carolina maintained a strong affinity for the continental shelf break, with a median distance to the shelf break of 3.6 km, while Florida animals demonstrated a median shelf break distance of 61.7 km. For animals tagged in North

Carolina, 61% of positions were within 5 km of the 200 m isobath, and 80% of positions were <10 km from the shelf break. Only three individual positions (0.6%) were within 10 km of the 200 m isobath for animals tagged off Florida.

### *Location Filtering and Behavioral State Estimation*

The hierarchical switching state-space model, which was run across all short-finned pilot whale tracks of suitable length (n=53), estimates behavioral state as both a binary variable and a continuous ‘b-value’ ranging from 1 to 2, which is generated from the posterior means of the Markov Chain Monte Carlo (MCMC) samples. Cutoffs of 1.25 and 1.75 were used, with ARS being designated as those locations with b-values  $\geq 1.75$ , and transit behaviors  $\leq 1.25$  (Jonsen et al. 2007; Bailey et al. 2012; Kennedy, Zerbini, Rone, et al. 2014; Acuña-Marrero et al. 2017). Behavioral state values falling between these cutoffs were considered to be uncertain. The hSSSM estimated 63% of the 10,200 predicted locations to be ARS behavior ( $b_t \geq 1.75$ ), with 20% of points deemed transit behavior ( $b_t \leq 1.25$ ), and 17% undetermined (Figure 1.3). The median  $b_t$  value across the sample size was 1.89 (mean = 1.69), indicating the animals were foraging more often than exhibiting transit behaviors. ARS behavior was incredibly dominant in positions close to the continental shelf break (Figure 1.4) with over 79% of locations within 5 km of the continental shelf break associated with ARS and only 10% of ARS positions occurring >10 km from the shelf. Conversely, transit behavior was observed throughout the geographic range of the short-finned pilot whales (Figure 1.5). Individual animals exhibited wide variability in the proportion of time spent in ARS throughout their tag’s duration, ranging from 0.02 to 1.0, with a median ARS

proportion of 0.70 (mean = 0.63; Table 1.1). Clear differences in the distribution of behavioral state values were apparent between animals tagged in North Carolina and those tagged in Florida. Animals tagged off Jacksonville spent more time (0.60) in transit mode with a median b-value of 1.1 compared to animals tagged off Cape Hatteras, who had a transit proportion of 0.18 and a median b-value of 1.9 (Figure 1.6). Similarly, whales tagged off Jacksonville had lower proportions of time spent in ARS (individual proportion range 0.14 – 0.32) than those tagged in the MAB (Table 1.1).

### *Home Range Estimation*

Kernel density estimation generated a population-level home range (95% isopleth) of 223,982 km<sup>2</sup> and a core use area (50% isopleth) of 5,290 km<sup>2</sup> across all years and individuals. The home range area for the tagged individuals spanned north to south along the continental shelf break and associated slope waters, including offshore waters east to the New England Seamounts, as well as Blake Plateau waters offshore of Florida (Figure 1.7). The population-level core use area, however, was concentrated solely along the continental shelf break offshore of North Carolina and Virginia, including Norfolk, Washington, and Wilmington Canyons (Figure 1.7). Individual core use areas widely varied from 72 to 54,922 km<sup>2</sup> (mean = 4,836 km<sup>2</sup>), while individual home range areas spanned from 272 to 243,220 km<sup>2</sup> (mean = 24,961 km<sup>2</sup>; Table 1.1). Linear regression showed a significant negative relationship exists between both the individual core use ( $p = 3.9e-10$ ,  $R^2 = 0.54$ ) and home range areas ( $p = 5.0e-12$ ,  $R^2 = 0.61$ ) and the proportion of ARS in each track's duration, with a higher ARS proportions resulting in smaller core use and home range sizes. Individual core use areas

were projected in ArcMap 10.5, and showed a large degree of overlap between tagged animals, particularly near the tagging site and northward along the continental shelf break (Figure 1.8).

### *Movement Patterns*

Maximum net displacement for each individual, calculated as the maximum value of the square root of each animal's NSD over time, ranged from 20.8 km to 1,197 km (Table 1.1). While distances from tagging location varied considerably throughout tag deployments across the sample size (Figure 1.9), many individuals frequently returned to their initial locations in both Cape Hatteras and Jacksonville, despite large displacements (Figures 1.10 – 1.11).

Concordance criterion for the suite of potential movement pattern models demonstrated short-finned pilot whales to be widely variable in their movement tactics over both space and time. Some (60%) animals were designated as dispersers, with 15% nomadic, 11% migratory, 11% resident, and a single individual for which the null model best fit the dataset. Several migratory models failed to converge for many individual short-finned pilot whales, likely due to relatively short tracking durations (Appendix A).

### *Describing Variability in Short-finned Pilot Whale Behavior*

Several covariates were excluded from models based on correlation coefficients  $>0.6$ . As longitude was found to be collinear with latitude, depth, and distance to shelf break, it was eliminated as a predictor variable. Similarly, latitude was collinear with distance to

canyon, and not evaluated. Depth and distance to shelf break were also found to be highly collinear (Pearson coefficient 0.88), and depth was removed from potential model sets.

To evaluate how behavioral state is influenced by the environmental covariates, a suite of 28 potential models was run. Models excluded any positions at which the behavioral state was estimated to be uncertain. The most parsimonious model included shelf break distance, slope, current velocity, canyon distance, sea surface temperature, and month as significant fixed effects (Table 1.2). Slope demonstrated the strongest level of statistical significance, followed by distance to the continental shelf break, surface current velocity, canyon distance, sea surface temperature, and month (Table 1.3). Parameter estimates indicate that transit behavior is most likely to occur further from the shelf break at higher sea surface temperatures in the months of June, July, and September. Additionally, transit behavior is more prevalent as surface currents, slope and distance to canyon decrease. Both whale id and tagging site were set as random effects in the ‘best’ model. Intercepts for tagging locations resulted in opposite signs, showing the differences in behaviors between the two sites (Table 1.4). Conditional level coefficients for individual whales varied widely across the sample size (Table 1.5). Whales that spent the majority of their tag deployment in pelagic waters away from the continental shelf break showed more positive coefficient estimates (Figure 1.12), demonstrating those animals were more likely to exhibit transit behavior than those who remained close to the shelf break during their tag’s duration.

## **Discussion**

This project presents much of the first information on medium-term and long-distance movements of short-finned pilot whales in the western North Atlantic, other than those obtained from stranded individuals (Wells et al. 2013). Short-finned pilot whales tagged in this study exhibit a broad distribution from Georges Bank in the north to southern Florida, and results demonstrate individuals are capable of long distance movements with substantial home ranges along the continental slope and extending out into oceanic waters. A switching state-space model approach reliably estimated animal locations and distinguished between two behavioral states, with area-restricted search behavior dominant in areas close to the continental shelf break. These results are not surprising, given the MAB shelf system is one of the most productive in the world (Ryan et al. 1999). Similar results were reported in humpback whales and hooded seals, and were also attributed to areas of increased upwelling, high productivity, and consistent prey aggregations (Kennedy, Zerbini, Rone, et al. 2014; Garrigue et al. 2015; Vacquie-Garcia et al. 2017).

Though our methodologies differed, our results align well with those of Thorne et al. (2017), confirming the continental shelf break and its associated canyons and slope region to be important foraging habitat for short-finned pilot whales, with the majority of ARS behavior exhibited in waters <1,000 m. A recent study of over 50 marine vertebrates, including short-finned pilot whales, found a ‘remarkable convergence’ in patterns across taxa, with habitat type directly influencing movement. Nearly all taxa demonstrated more directed, linear movements (i.e. transit behavior) with increasing distance from shore, while more complex movements (i.e. ARS) were demonstrated closer to land, likely related to the

homogeneity levels of onshore and offshore habitats and associated prey (Sequeira et al. 2018). This study suggests offshore animals use more dynamic, ephemeral oceanographic features, such as currents, fronts, and eddies as their movement and foraging cues, while shelf animals experience a wider variety of resources and threats contributing to the additional complexity of their movements.

While the continental shelf break has been established as a reliable prey source for short-finned pilot whales, still unexplained is what specifically drives animals to depart the slope areas and move into pelagic waters. Seamounts have been proposed as important offshore habitat for humpback whales (Garrigue et al. 2015), and may serve as a destination for individuals that depart Cape Hatteras. A more likely explanation, however, is that both persistent and ephemeral mesoscale fronts and eddies, which can form pelagic foraging areas for mobile marine vertebrates (Davis et al. 2002; Scales et al. 2014; Cotté et al. 2015), are driving the species into deeper, oceanic waters. Animals utilizing offshore areas as an alternative foraging area could also benefit from reduced intraspecific and interspecific competition occurring in the Cape Hatteras region (Campagna et al. 2006).

Despite wide individual variability in movement patterns and net displacement, nearly all individuals tagged returned to the Cape Hatteras area during their tag deployment, indicating some degree of philopatry. Additionally, core use areas for the majority of individuals are focused near Cape Hatteras along the continental shelf break. Photo-identification work of short-finned pilot whales in the area also suggests some degree of long-term residency to the Cape Hatteras study area, although animals return to the area with

variable periodicity. Altogether, our results indicate the importance of the Cape Hatteras region to the species.

Philopatric behavior was observed in tiger sharks at the Galapagos Marine Reserve, and was attributed to the presence of a predictable prey source in addition to suitable habitat driving the animals to return (Acuña-Marrero et al. 2017). Ultimately, prey availability drives a predator's distribution, and future work could aim to tease apart what specific features make Cape Hatteras unique to drive the philopatry of short-finned pilot whales, despite the availability of similar habitats and prey species in other areas. However, it is likely that the amalgamation of waters from the Labrador Current and the Gulf Stream Front in the area create smaller fine- and meso-scale activity and eddies (Skov et al. 2008; Bailleul et al. 2010), allowing for strong, persistent prey aggregations to which short-finned pilot whales are attracted. An alternate hypothesis to explain residency of adult female tiger sharks in the Galapagos was breeding site availability (Acuña-Marrero et al. 2017), which may also be possible in the Cape Hatteras area. However, while short-finned pilot whales travel in stable matrilineal groups, gestation and calving cycles of the species in the region are poorly understood, despite young-of-year calves being consistently observed in the area.

Home range analyses indicate great variability in individual core use areas, which may be due in part to unique foraging strategies employed by individual whales (Irvine et al. 2014; Kennedy, Zerbini, Rone, et al. 2014). Irvine et al. (2014) proposed that blue whales with larger home ranges may choose to depart areas of marginal productivity in search of novel prey sources, while individuals with smaller home ranges choose to remain in marginally productive, albeit established, foraging areas. He also acknowledges that prey

preference may drive individual foraging strategies. Individual variation in foraging has been documented in several species of marine predators, and is proposed to reduce competition within a species (McHuron et al. 2018). Short-finned pilot whales likely feed on a variety of prey species (M. Bowers 2016 Unpublished PhD Thesis, Duke University), which may explain the high variability in their movement patterns.

In addition to broad-scale movement patterns and habitat preferences, behavior and important drivers thereof were able to be quantified in this study using generalized linear mixed models. The most important predictors of behavioral state in short-finned pilot whales were slope and distance to shelf break, with increased transit behavior in areas of low slope and increased distance from the 200 m isobath, results which align well with recent work (Sequeira et al. 2018). As steep slope areas are often characterized by increased upwelling and associated prey aggregation (Pace et al. 2018), it is intuitive that ARS behavior would be dominant in such locations. Interestingly, parameter estimates from the most parsimonious model indicate increased transit behavior at locations closer to the major Mid-Atlantic submarine canyons than further, despite much of the transit behavior in the data set estimated in pelagic waters at increased distances from any canyon. One hypothesis for this counter-intuitive result is that as short-finned pilot whales move north and south along the continental shelf break, they may increase their rates of travel and path persistence, behaviors characteristic of transit, while moving between canyons, indicating increased transit behavior as they approach a canyon, within which they may engage in ARS behavior. Furthermore, past cetacean research along the continental shelf break of the northeast U.S. has found that despite the shelf edge being heavily utilized by a variety of species, cetacean biomass within

canyon areas was significantly lower than the surrounding shelf break region (Kenney and Winn 1987).

The GLMMs presented here, while accounting for some degree of the variability in behavior within the population, are likely still missing several important drivers or processes that would fully describe short-finned pilot whales behavior. Most importantly, a single variable used as a proxy for prey abundance is lacking. Marine megafauna are known to congregate in response to increased availability of prey (Laidre et al. 2004), but the poorly understood diet of short-finned pilot whales, combined with the complexity of marine predator interactions with prey that is often patchily distributed over both space and time precludes such a straight-forward metric (Mintzer et al. 2008; Abecassis et al. 2015). Beyond prey, several additional remotely sensed environmental covariates might offer added explanatory power to the models. However, given the broad spatiotemporal scales of this multi-season and multi-year study, proper spatiotemporal coverage was not available for all desired covariates. For example, chlorophyll levels, recorded at enhanced levels along the shelf break of the MAB annually from mid-April to late June (Ryan et al. 1999), which could describe the productivity within the area, as well as potential seasonal influences on movement, were not available for all positions at any scale finer than annually, and as such, excluded from analyses.

Similarly, the spatiotemporal resolution of the covariates used in the study may not align with the scales of behavior and habitat selection in short-finned pilot whales. The hSSSM and GLMMs in this work estimate behavior over 6-hr time-steps, for which 5-day, 8-day, or monthly environmental covariate composites gathered over coarse spatial scales may

lead to inaccuracy in predictions of environmental covariates as well as introduce bias into the models (Scales, Hazen, et al. 2017). Additionally, a 6-hr time step may not best encapsulate behavioral switches within the operating scale of individual short-finned pilot whales. Animals could exhibit behavioral switches within that period, which would be lost in the data. However, foraging bouts for a subset of satellite-tagged short-finned pilot whales offshore of Cape Hatteras averaged 2.94 hours, and ranged up to 14 hours (M. Bowers 2016 Unpublished PhD Thesis, Duke University). The choice of a 6-hr time step was therefore driven by this information, as well as the raw Argos data resolution.

Beyond the potential environmental drivers of short-finned pilot whale behavior, sociality could also play an important role in individual behavior. Social creatures, such as pilot whales, can influence and thereby be influenced by the other animals with which they interact (Visser et al. 2014). As such, spatial and habitat use may be specific to and vary by social group. Long-finned pilot whales in Norway demonstrated a social foraging strategy, in which individual foraging decisions were influenced by the social group in which the animal lives (Marshall et al. 2012). Specifically, individual social groups synchronized their foraging bouts, further demonstrating the importance of accounting for population-level drivers in the description of short-finned pilot whale behavior. Integrating social structure as an explanatory variable could likely aid in fully describing the behavior of these animals.

It has also been established that behavioral switches in individuals are not driven solely by external forces, but also are initiated by internal drivers within each individual (Bestley et al. 2012). Though difficult to quantify in pelagic cetaceans, future models could include covariates such as life stage, body condition, or metabolic rate to help describe the

individual variability in behavior. Furthermore, behaviors and space use of animals could be attributed to memory and experience, in addition to site fidelity of specific subpopulations (Laidre et al. 2004; Acuña-Marrero et al. 2017).

The hierarchical switching state-space model itself presents a few caveats. The first is in the behavioral state estimation, which utilizes a first-difference correlated random walk as the process model. Autocorrelation in turning angle and rate between raw Argos points are used, in part, to estimate the behavioral state. However, the model does not take ocean current into account. The velocity over ground calculated for each successive location in the hSSSM is attributed to only the speed of the animal, when the velocity of the current is also an important component of the rate between locations (Gaspar et al. 2006). Jonsen and colleagues (2007) acknowledge that the model may incorrectly classify behaviors in the presence of strong ocean currents, particularly when switches in behavior result from advection as opposed to active behavior. Southern elephant seals' horizontal movements were found to not be independent of surface currents; rather, they foraged more intensely in areas of increased horizontal drift, allocating increased energy to diving and prey capture over search for additional resources (Della Penna et al. 2015). Despite remotely sensed surface currents included in this study as predictor variable, currents would ideally be considered within the behavioral state estimation of the hSSSM. Additionally, currents at the depths of the animals, rather than the water's surface, would be ideal. Gaspar and colleagues (2006) found that animals that do not dive as deep in the water column were more affected by surface currents. Taken together, behaviors estimated as transit in this study may in fact be foraging behavior (or vice versa) masked by the strong Gulf Stream current through which

the tagged animals regularly travelled. The strong differences in distributions of behavioral state values between North Carolina-tagged and Florida-tagged animals may also be due in part to this phenomenon, where Florida animals, which are in a shallower environment, are being strongly advected to the northeast with the Gulf Stream current. Still unexplained, however, is what drives the animals off Florida to depart the strong northeasterly current, which may assist their transit to more productive feeding areas to the north by lowering the metabolic costs of horizontal travel (Sleeman et al. 2010), and turn back south, as animals did on several occasions. North Carolina individuals, generally utilizing deeper waters offshore of Cape Hatteras and frequently diving to the ocean floor to forage (Quick et al. 2017) may not be as directly influenced by currents, though the Gulf Stream Front inevitably plays a role in their movement patterns, particularly in those animals who travel into pelagic waters. Further work is necessary in order to determine if animals utilizing offshore areas are engaging in active locomotion or more passive drifting, assisted by currents.

In addition to ARS being potentially masked as transit behavior through the hSSSM, it should also be recognized that ARS does not only denote foraging behavior. Additional behaviors, such as socializing, breeding, and resting, in which short-finned pilot whales may often engage, would be included as ARS within the hSSSM output (Bailey et al. 2010). However, regardless of what activities constitute ARS, very little area-restricted search behavior was estimated in pelagic waters, which begs the question whether short-finned pilot whales are actively foraging while offshore. Integration of dive behavior from the Mk-10A tags could begin to inform this question and ground-truth behaviors estimated from the hSSSM.

Due to the duty cycling of tags deployed in early years, seasonality could not be fully analyzed in short-finned pilot whales. In addition, relatively short tag durations limit the extent of our ecological inferences over greater spatiotemporal scales. In order to evaluate any potential annual or seasonal cycles present in movement or spatial use patterns at the seasonal level, a more robust data set, particularly focused on a greater sample size in winter months, is necessary. Additionally, to ameliorate potential bias to the tagging location, deployment of tags should occur in different sites, and ideally, at different times throughout the year along the continental shelf break in order to see how core use, home range, and spatial use patterns differ.

Net squared displacement and its associated migration pattern analyses through non-linear mixed models were not particularly well suited to classify this highly variable species. Unfortunately, the individual differences in movement over several spatiotemporal scales of short-finned pilot whales did not allow definitive population-level inferences on their movement and migration patterns to be made. Furthermore, as the migration models have starting parameters based on annual migrations, the variable periodicity of animals departing and returning to the Cape Hatteras area made model fit impossible. However, it is clear that different pilot whales within the population exhibited a variety of movement patterns including nomadism, dispersal, and home range patterns, which often varied with time, consistent with findings from Singh et al. (2012). Despite the finding that NSD models were generally applicable to marine predators (Harrison, 2012), the average tag duration in short-finned pilot whales precluded a full comparison on these models based on annual migrations.

Tags of longer duration might aid in both model convergence and migration pattern classification for short-finned pilot whales.

Despite all of the limitations involved with this study, the knowledge gap on baseline spatial use and habitat preferences of short-finned pilot whales in the western North Atlantic has been filled. In order to glean metrics and results sufficient for management, however, inferences beyond the individual animal level are necessary, particularly given the social nature of short-finned pilot whales. An incredible amount of individual variability within short-finned pilot whale movements, home ranges, displacements, and behavior was observed in this work. As such, population-level metrics are difficult to quantify, though a robust sample size begins to improve the ability to do so.

Many interesting differences between animals tagged off Florida and those tagged in the MAB emerged through this work. Florida animals are selecting for deeper waters on average, despite a more gradual continental slope within the study site (Figure 1.1). In addition, animals moving through the SAB are rarely engaging in ARS behavior, despite the fact that some of these behaviors may be masked through the hSSSM, as described above. Furthermore, these animals are of considerable distance from the continental shelf break and its associated canyons, areas known to aggregate prey for short-finned pilot whales (Thorne et al. 2017). Taken together, one hypothesis for these differences in behavior is that short-finned pilot whales in the western North Atlantic may be exhibiting habitat or location-specific foraging strategies to maximize their fitness.

There is no shortage of future work that can be done to complement this study. Integrating dive data from Mk-10A tags would be a natural next step, to both ground-truth

hSSSM output, as well as helping to define how animals who utilize pelagic waters are selecting for their habitat, and what drives them to return to Cape Hatteras or the shelf break. Additionally, comparing across all temporal scales for which data is available by amalgamating fine-scale digital acoustic tag movement in addition to the long-term residency patterns from photo-identification would help to more fully understand the drivers of movement in this highly variable species. For example, diel patterns in short-finned pilot whale foraging behavior offshore of Cape Hatteras have been analyzed using digital acoustic tags over a limited temporal scale (M. Bowers 2016 Unpublished PhD Thesis, Duke University). Integrating dive behavior over both tag types could produce a robust data set capable of population-level inferences across several spatiotemporal scales. Significant sex and size differences have been documented in marine species for both home range size and foraging behavior (M. Bowers 2016 Unpublished PhD Thesis, Duke University). Though sex and age-class can be difficult to ascertain in some short-finned pilot whales, photographs and biopsies of tagged animals could be used to begin to identify habitat and spatial use differences between males, females, juvenile, and adult individuals.

Understanding movement patterns is crucial to assessing habitat use, and knowledge of both are needed in the development of efficient conservation management strategies. As both direct and indirect threats to cetacean populations increase in the world's oceans due to fisheries bycatch, changes in the marine environment stemming from climate change, and increased anthropogenic noise from sources such as MFA sonar and seismic air guns, animals such as short-finned pilot whales may be driven from their preferred habitat. As such, shifts in species distributions may occur. This work provides a necessary baseline from

which to assess and mitigate potential impacts on short-finned pilot whales to these threats. A continued knowledge of the species is vital to protect and manage populations worldwide.

## Tables

Table 1.1. Summary of short-finned pilot whale satellite tag deployments, including tag id, tag type, deployment date and site, full and analyzed tag duration, number of post hierarchical switching state-space model (hSSSM) positions, proportion of track within area-restricted search (ARS) behavior, total distance traveled, core use area, home range area, and maximum net displacement. Tags denoted with an asterisk were not included in analyses.

Tag ID	Tag Type	Deploy Date	Deploy Site	Full Tag Duration (days)	Analyzed Tag Duration (days)	Post hSSSM locns	ARS Prop.	Total Distance traveled (km)	Core Use (50% isopleth) Area (km <sup>2</sup> )	Home Range (95% isopleth) Area (km <sup>2</sup> )	Max. Net Disp. (km <sup>2</sup> )
GmTag084*	SPOT5	5/14/2014	NC	0.3							
GmTag085	MK10-A	5/14/2014	NC	37.5	14.7	59	0.97	361.5	72.2	272.4	20.8
GmTag086	SPOT5	5/14/2014	NC	78.6	78.6	315	0.65	3135.6	533.2	4483.8	329.7
GmTag087	SPOT5	5/18/2014	NC	193.8	78.9	316	0.48	3373.0	3696.1	42660.0	759.2
GmTag088	SPOT5	6/7/2014	NC	103.3	78.9	316	0.21	4576.1	28778.9	127447.5	1179.9
GmTag090	SPOT5	6/8/2014	NC	54.3	54.3	218	0.58	2122.6	1023.3	8092.4	387.9
GmTag092	SPOT5	6/11/2014	NC	48.9	48.9	196	0.70	1859.6	1620.0	8240.8	310.5
GmTag093	MK10-A	6/11/2014	NC	17.9	17.9	72	0.76	703.4	237.7	1470.6	145.4
GmTag094	SPOT5	6/11/2014	NC	83.7	78.7	315	0.70	2244.8	1342.2	7996.7	474.8
GmTag095	SPOT5	6/11/2014	NC	83.6	78.8	316	0.78	2260.0	927.6	7345.3	434.3
GmTag096*	SPOT5	9/11/2014	NC	1.3							
GmTag097	SPOT5	9/11/2014	NC	31.6	31.6	127	1.00	757.4	90.6	548.8	46.4
GmTag098	Mk10-A	9/11/2014	NC	27.9	27.9	112	0.70	908.0	586.0	3095.6	227.3
GmTag099	SPOT5	9/11/2014	NC	63.5	63.5	255	0.91	1894.9	446.2	2467.6	207.6
GmTag100	Mk10-A	9/11/2014	NC	25.0	25.0	100	0.68	813.3	455.8	2552.3	223.8
GmTag101	SPOT5	9/13/2014	NC	32.2	32.2	129	0.85	1116.4	232.2	1856.0	187.3

Table 1.1 (continued).

Tag ID	Tag Type	Deploy Date	Deploy Site	Full Tag Duration (days)	Analyzed Tag Duration (days)	Post hSSSM locns	ARS Prop.	Total Distance traveled (km)	Core Use (50% isopleth) Area (km <sup>2</sup> )	Home Range (95% isopleth) Area (km <sup>2</sup> )	Max. Net Disp. (km <sup>2</sup> )
GmTag102	SPOT5	9/13/2014	NC	9.4	9.4	38	0.68	323.6	75.1	739.9	152.8
GmTag103	SPOT5	9/13/2014	NC	113.3	79.1	317	0.79	2666.1	409.9	3664.5	122.2
GmTag122	SPOT5	5/16/2015	NC	58.0	58.0	233	0.76	2082.5	198.8	3210.3	334.8
GmTag123	Mk10-A	5/16/2015	NC	13.7	13.7	55	0.65	511.8	526.4	1848.3	159.3
GmTag124	SPOT5	5/16/2015	NC	60.8	60.8	244	0.66	2028.4	811.5	15557.2	341.4
GmTag125	SPOT5	5/19/2015	NC	139.2	78.6	315	0.89	1951.7	374.3	2418.2	206.2
GmTag126	SPOT5	5/19/2015	NC	44.6	44.6	179	0.58	1720.4	2080.1	12456.9	530.4
GmTag127	Mk10-A	5/19/2015	NC	30.7	30.7	123	0.88	730.0	224.7	1231.9	162.5
GmTag128	SPOT5	6/16/2015	NC	38.6	38.6	155	0.79	1232.5	191.9	1313.3	163.7
GmTag129	SPOT5	6/16/2015	NC	8.8	8.8	36	0.81	321.6	407.0	1757.9	163.8
GmTag130	SPOT5	6/16/2015	NC	198.5	78.7	315	0.80	1925.1	422.7	5181.5	485.5
GmTag131	SPOT5	6/16/2015	NC	94.1	79.1	317	0.08	5872.1	52032.5	217977.8	1197.1
GmTag134	SPOT5	10/15/2015	NC	57.2	57.2	229	0.84	1635.5	158.2	2313.3	193.1
GmTag135	Mk10-A	10/15/2015	NC	30.9	30.9	124	0.70	1088.9	462.3	3339.5	189.9
GmTag136	SPOT5	10/16/2015	NC	149.0	79.3	318	0.96	1569.2	132.9	1116.7	171.4
GmTag137	SPOT5	10/20/2015	NC	154.4	79.3	318	0.52	3359.5	803.4	5556.8	317.3
GmTag138	Mk10-A	10/20/2015	NC	24.5	24.5	99	0.32	1068.9	1258.3	11039.4	264.4
GmTag139	SPOT5	10/20/2015	NC	64.1	64.1	257	0.02	6182.0	54922.0	243220.2	1191.3
GmTag140*	SPOT5	10/20/2015	NC	10.6							
GmTag141	SPOT5	10/20/2015	NC	34.2	34.2	137	0.46	1694.3	1990.2	11768.3	195.1
GmTag142	SPOT5	10/21/2015	NC	349.0	79.3	318	0.77	2309.8	311.3	5572.0	297.3

Table 1.1 (continued).

Tag ID	Tag Type	Deploy Date	Deploy Site	Full Tag Duration (days)	Analyzed Tag Duration (days)	Post hSSSM locns	ARS Prop.	Total Distance traveled (km)	Core Use (50% isopleth) Area (km <sup>2</sup> )	Home Range (95% isopleth) Area (km <sup>2</sup> )	Max. Net Disp. (km <sup>2</sup> )
GmTag157	SPOT6	5/25/2016	NC	131.8	131.8	528	0.64	3836.3	2517.3	15096.8	623.9
GmTag158	SPOT5	5/25/2016	NC	150.4	80.3	322	0.75	2665.9	1062.0	5520.4	329.3
GmTag159	GPS	5/26/2016	NC	24.5	24.5	99	0.34	1894.3	9426.3	67336.2	658.0
GmTag160	SPOT6	5/26/2016	NC	156.7	151.7	607	0.72	4987.9	1064.7	9813.7	433.4
GmTag161	SPOT6	5/27/2016	NC	24.4	24.4	98	0.68	1007.3	199.7	3413.1	266.5
GmTag162	SPOT6	6/1/2016	FL	40.2	40.2	161	0.25	2810.7	8243.6	40757.0	303.7
GmTag163	Mk10-A	6/1/2016	FL	38.8	30.0	121	0.21	1850.3	6932.0	36512.2	222.7
GmTag164	SPOT6	6/2/2016	FL	47.2	47.2	189	0.14	4143.4	24287.3	90630.9	308.3
GmTag165	Mk10-A	6/2/2016	FL	26.9	16.2	65	0.32	1299.4	7948.3	30804.5	263.7
GmTag172	Mk10-A	5/10/2017	NC	32.8	32.8	132	0.88	1294.3	388.8	1686.7	164.9
GmTag173	Mk10-A	5/11/2017	NC	23.8	23.8	96	0.82	798.0	361.7	1800.0	172.6
GmTag174	Mk10-A	5/11/2017	NC	31.4	31.4	126	0.86	1104.0	285.6	1461.3	119.1
GmTag175	Mk10-A	5/16/2017	NC	25.6	25.6	103	0.91	616.7	187.4	1487.0	166.3
GmTag176	Mk10-A	5/16/2017	NC	13.0	13.0	52	0.85	377.4	130.9	1125.5	151.2
GmTag177	Mk10-A	5/17/2017	NC	28.3	28.3	114	0.83	971.3	276.8	1316.0	147.3
GmTag178	Mk10-A	5/17/2017	NC	18.7	18.7	75	0.47	1097.4	1592.0	20547.7	328.9
GmTag179*	Mk10-A	5/17/2017	NC	0.3							
GmTag180	Mk10-A	5/17/2017	NC	32.7	21.3	86	0.53	1068.2	1610.0	18356.1	324.7
GmTag181	Mk10-A	8/20/2017	NC	30.9	30.9	124	0.10	2376.3	12512.8	87157.0	878.4
GmTag182*	Mk10-A	8/20/2017	NC	29.5							
GmTag183	Mk10-A	8/20/2017	NC	32.2	32.2	129	0.15	2902.8	19487.8	118300.3	748.8

Table 1.2. Summary of best-fitting model with parameters, coefficient estimates, standard errors, and p-values for each fixed effect. Bold face denotes statistical significance ( $p < 0.05$ ).

	Estimate	Standard Error	Z statistic	p value
Intercept	-0.766	1.091	-0.702	0.483
<b>Distance to Shelf Break</b>	<b>0.394</b>	<b>0.042</b>	<b>9.459</b>	<b>3.10E-21</b>
<b>Slope</b>	<b>-0.600</b>	<b>0.041</b>	<b>-14.543</b>	<b>6.45E-48</b>
<b>Sea Surface Temperature</b>	<b>0.154</b>	<b>0.055</b>	<b>2.793</b>	<b>0.005</b>
<b>Surface current velocity</b>	<b>-0.262</b>	<b>0.038</b>	<b>-6.923</b>	<b>4.43E-12</b>
<b>Distance to Canyon</b>	<b>-0.432</b>	<b>0.074</b>	<b>-5.852</b>	<b>4.85E-09</b>
May	-0.139	0.415	-0.336	0.737
June	0.004	0.398	0.009	0.993
July	0.029	0.398	0.072	0.943
August	-0.191	0.401	-0.477	0.634
September	0.070	0.392	0.179	0.858
October	-0.287	0.317	-0.905	0.366
November	-0.617	0.303	-2.039	0.041
December	-0.698	0.310	-2.251	0.024

Table 1.3. ANOVA results from best-fitting model, showing statistical significance of each covariate.

	Chisq	Df	Pr(>Chisq)
<b>Month</b>	<b>20.790</b>	<b>8</b>	<b>0.008</b>
<b>Distance to Shelf Break</b>	<b>89.479</b>	<b>1</b>	<b>3.10E-21</b>
<b>Slope</b>	<b>211.506</b>	<b>1</b>	<b>6.45E-48</b>
<b>Sea Surface Temperature</b>	<b>7.800</b>	<b>1</b>	<b>0.005</b>
<b>Surface current velocity</b>	<b>47.924</b>	<b>1</b>	<b>4.43E-12</b>
<b>Distance to Canyon</b>	<b>34.249</b>	<b>1</b>	<b>4.85E-09</b>

Table 1.4. Intercept coefficient estimates for random effect site from best-fitting model.

Site	Intercept	Standard Error
Florida	0.497	0.584
North Carolina	-1.972	0.191

Table 1.5. Intercept coefficient estimates for random effect id from best-fitting model.

id	Intercept	Standard Error
GmTag085	-2.259	0.828
GmTag086	-0.585	0.252
GmTag087	0.124	0.222
GmTag088	0.223	0.207
GmTag090	-0.503	0.267
GmTag092	-1.036	0.283
GmTag093	-0.775	0.384
GmTag094	-1.085	0.272
GmTag095	-1.682	0.294
GmTag097	-2.821	0.751
GmTag098	-0.559	0.349
GmTag099	-2.629	0.490
GmTag100	-0.677	0.388
GmTag101	-1.473	0.396
GmTag102	-0.366	0.502
GmTag103	-1.414	0.341
GmTag122	-0.511	0.264
GmTag123	-0.534	0.502
GmTag124	-0.341	0.237
GmTag125	-2.660	0.400
GmTag126	-0.429	0.269
GmTag127	-1.671	0.473
GmTag128	-1.165	0.354
GmTag129	-0.920	0.492
GmTag130	-1.860	0.289
GmTag131	0.596	0.208
GmTag134	-0.124	0.294
GmTag135	0.249	0.312
GmTag136	-2.015	0.507
GmTag137	1.092	0.220
GmTag138	0.660	0.291
GmTag139	2.112	0.230
GmTag141	0.890	0.242
GmTag142	-0.117	0.256
GmTag157	-0.890	0.220
GmTag158	-2.313	0.371

Table 1.5 (continued).

id	Intercept	Standard Error
GmTag159	0.704	0.243
GmTag160	-1.213	0.236
GmTag161	0.114	0.285
GmTag162	-0.594	0.590
GmTag163	-0.507	0.594
GmTag164	-0.111	0.590
GmTag165	-0.666	0.598
GmTag172	-2.187	0.560
GmTag173	-2.724	0.764
GmTag174	-2.787	0.755
GmTag175	-2.294	0.649
GmTag176	-2.026	0.868
GmTag177	-1.589	0.442
GmTag178	0.199	0.286
GmTag180	0.186	0.276
GmTag181	1.714	0.250
GmTag183	0.711	0.229

## Figures

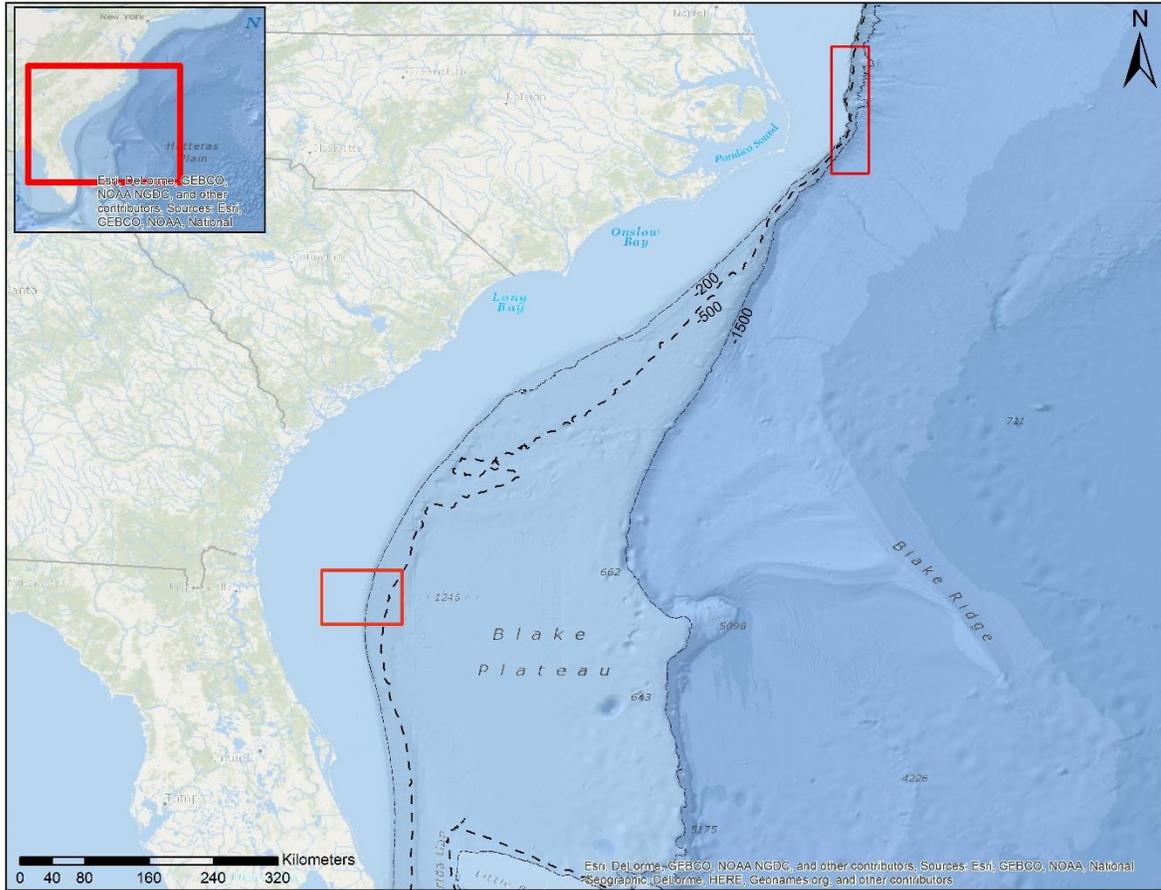


Figure 1.1. Plot of the study sites offshore of Cape Hatteras, North Carolina, and Jacksonville, Florida with the 200 m, 500 m, and 1,500 m isobaths represented by dashed lines.

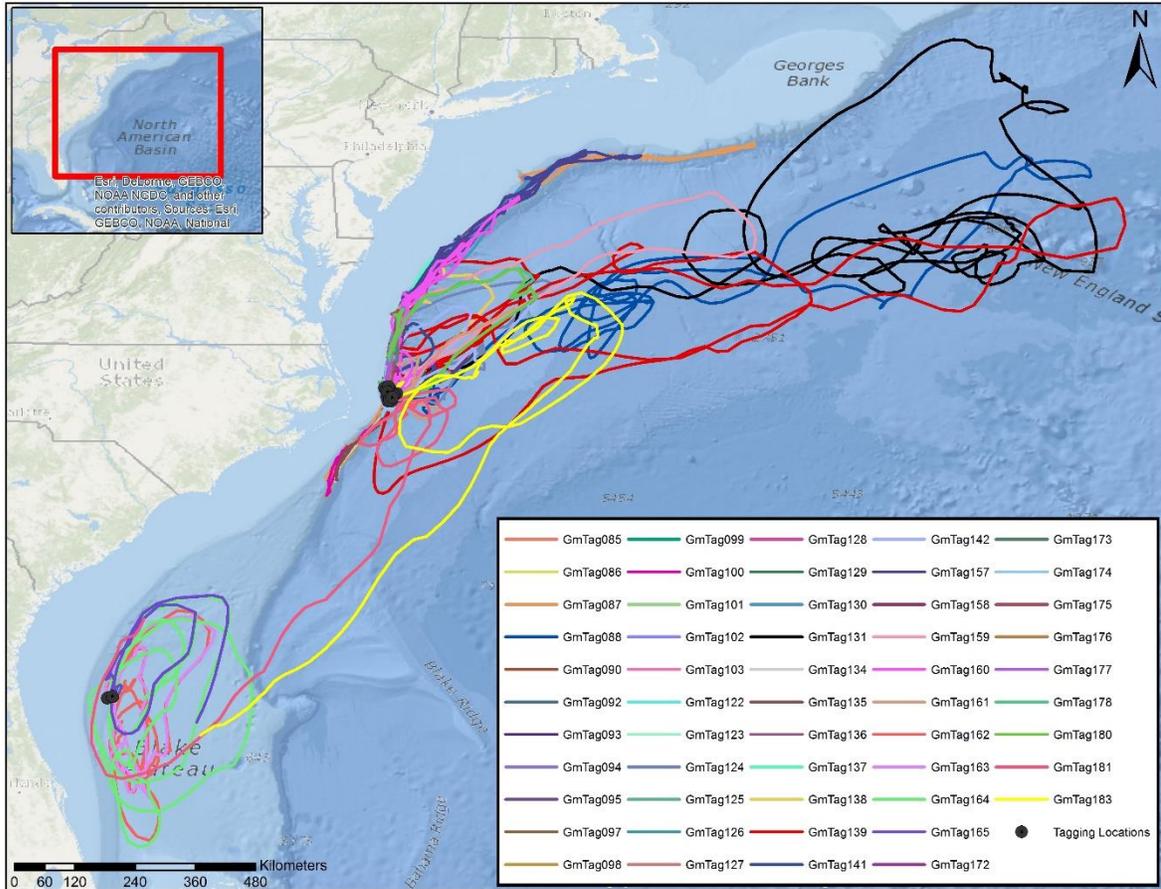


Figure 1.2. Map of individual tracks of short-finned pilot whales (n=53) re-sampled to a 6-hr time step via a hierarchical switching state-space model. Tagging locations are represented with black circles.

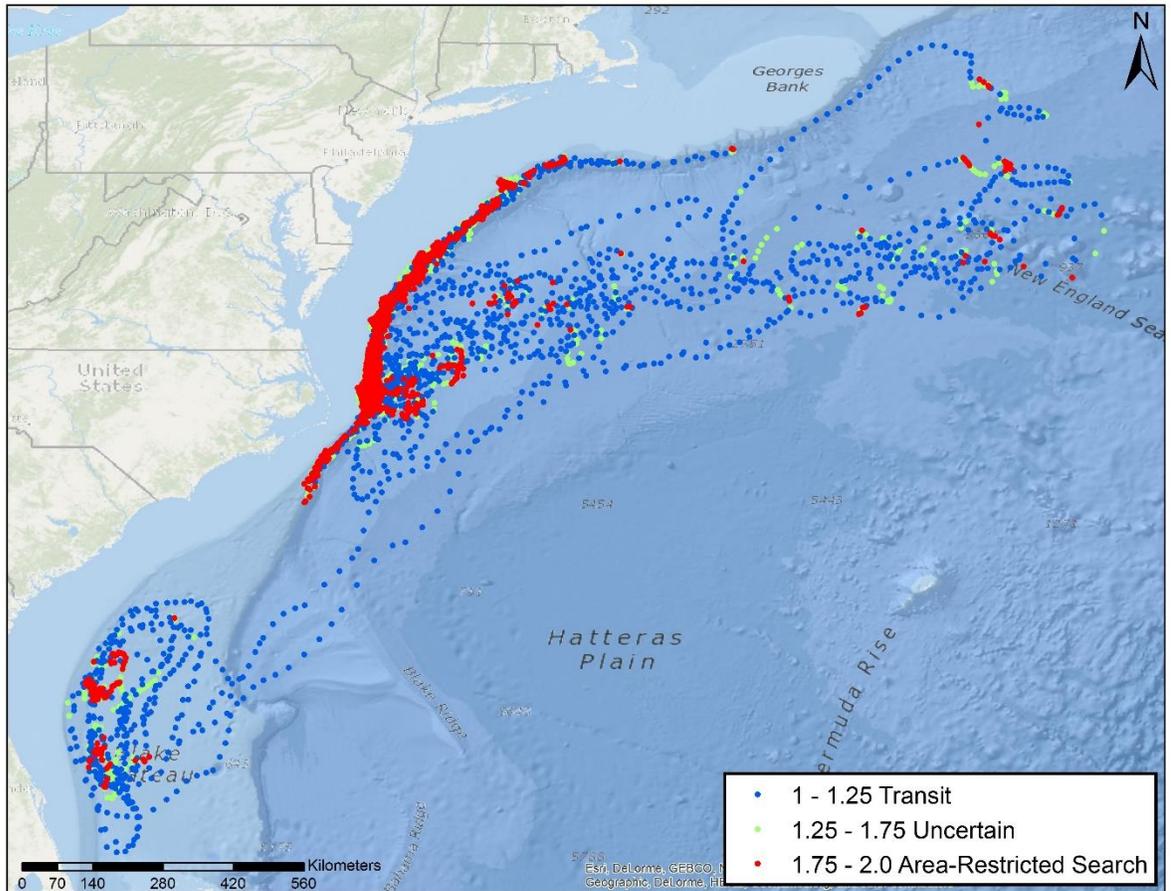


Figure 1.3. Map of behavioral states estimated from a hierarchical switching state-space model ranging from 1-2 of short-finned pilot whales (n=53). Red indicates area-restricted search behavior, blue shows transit behavior, and green shows uncertain values.

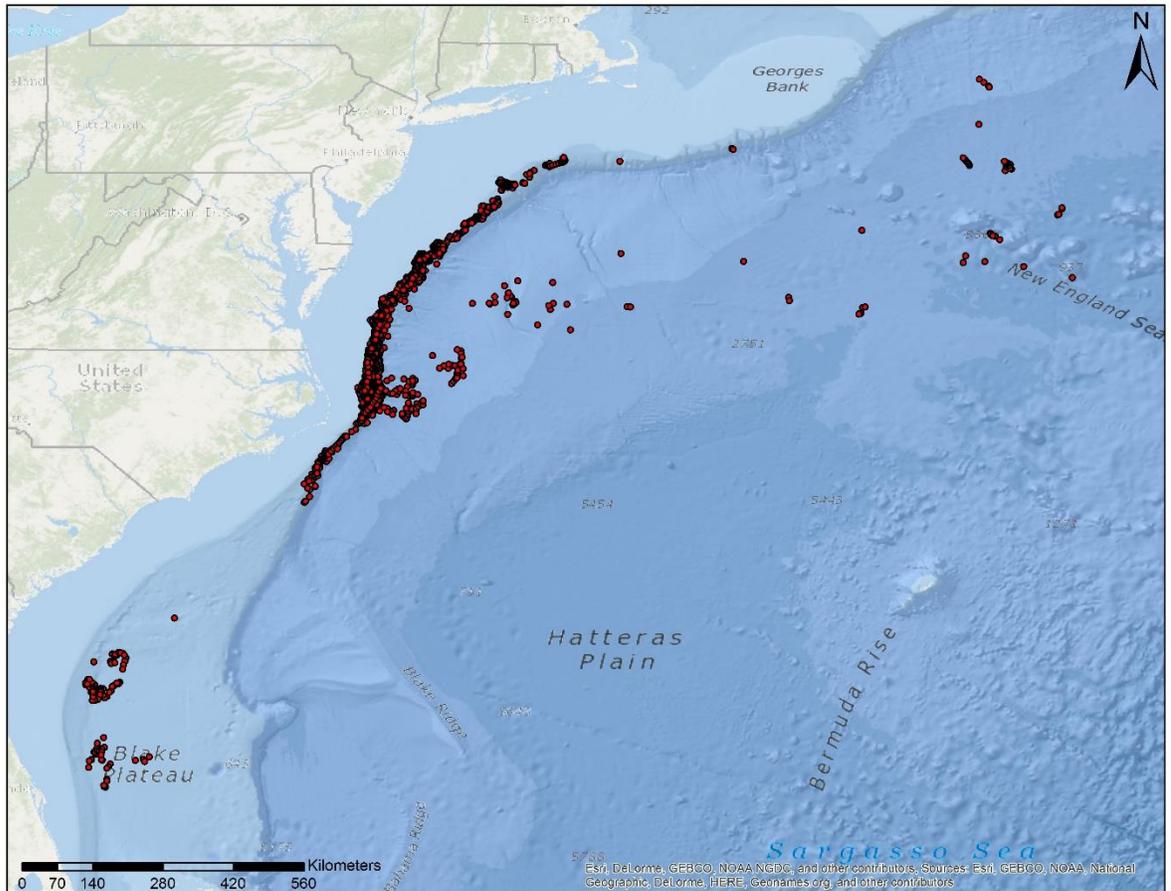


Figure 1.4. Map of area-restricted search ( $b_t \geq 1.75$ ) behavioral state locations estimated from a hierarchical switching state-space model of short-finned pilot whales ( $n=53$ ).

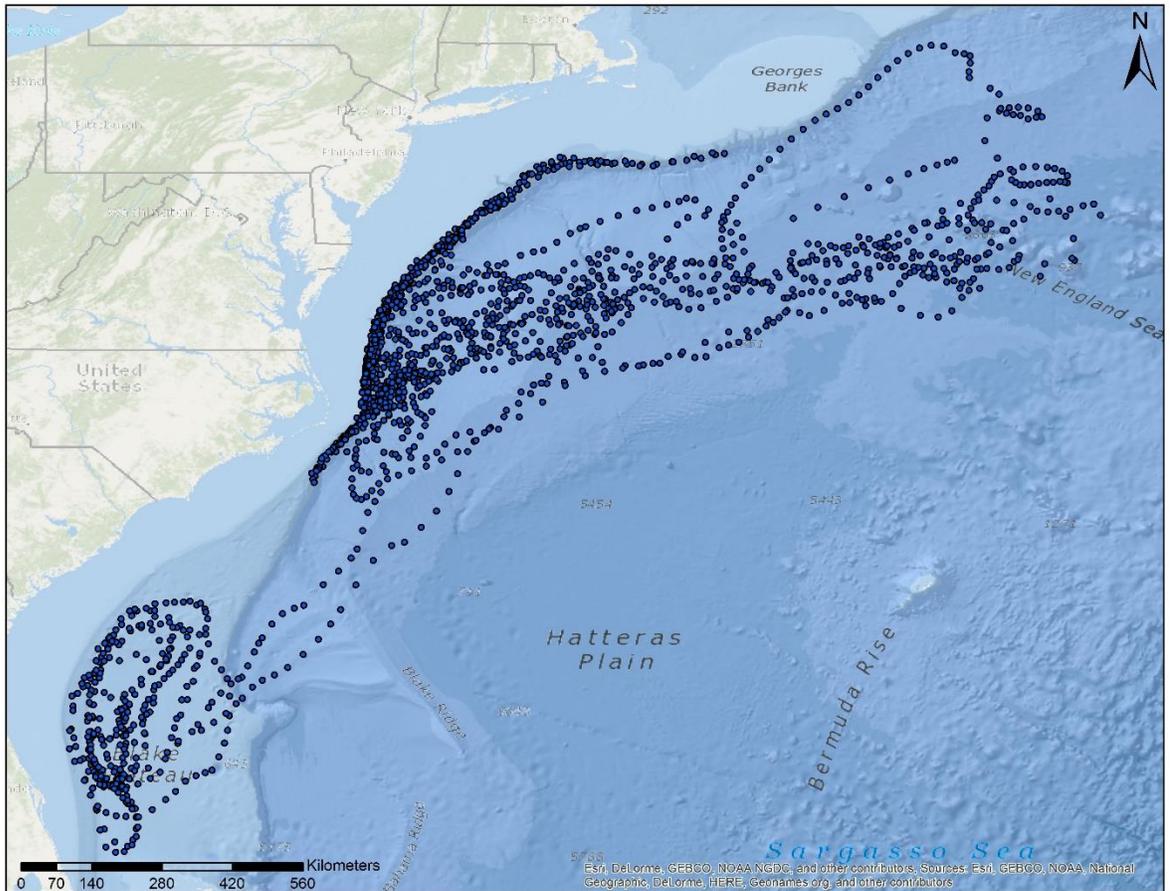


Figure 1.5. Map of transit ( $b_t \leq 1.25$ ) behavioral state locations estimated from a hierarchical switching state-space model of short-finned pilot whales ( $n=53$ ).

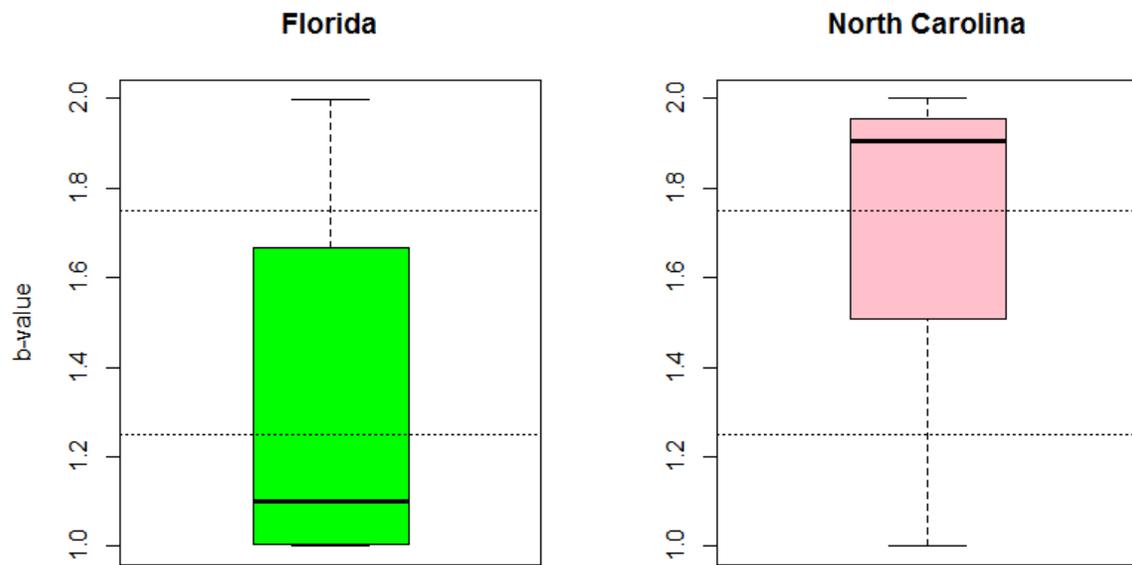


Figure 1.6. Distributions of behavioral state (b-value) for short-finned pilot whales tagged in Florida (green, n=4) and North Carolina (pink, n=49). Dashed lines indicate cutoff points for transit behavior (b-value  $\leq 1.25$ ) and area-restricted search behavior (b-value  $\geq 1.75$ ).

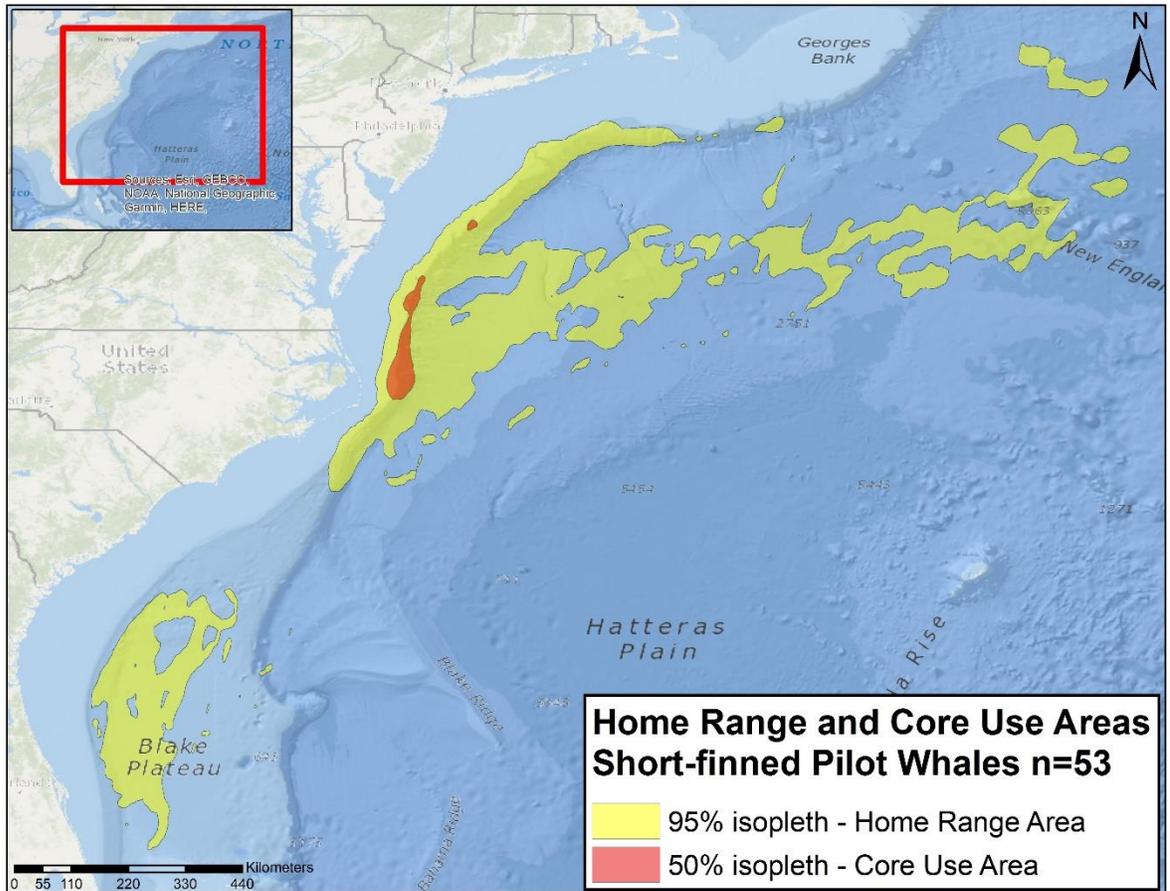


Figure 1.7. Map of home range area (yellow) and core use area (red) for satellite-tagged short-finned pilot whales (n=53) generated from kernel density estimation using the plug-in bandwidth estimator.

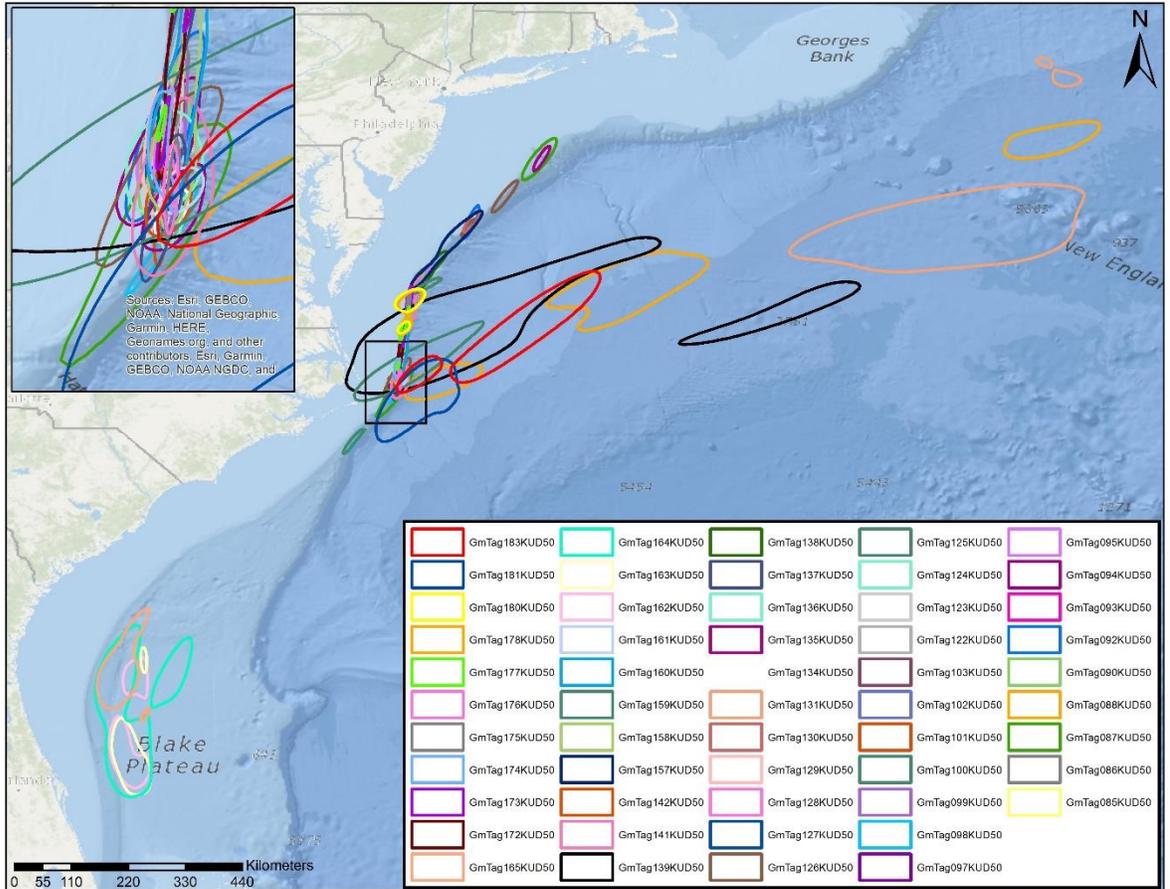


Figure 1.8. Map of individual short-finned pilot whale core use areas (50% isopleth; n=53). Inset map denoted by black rectangle.

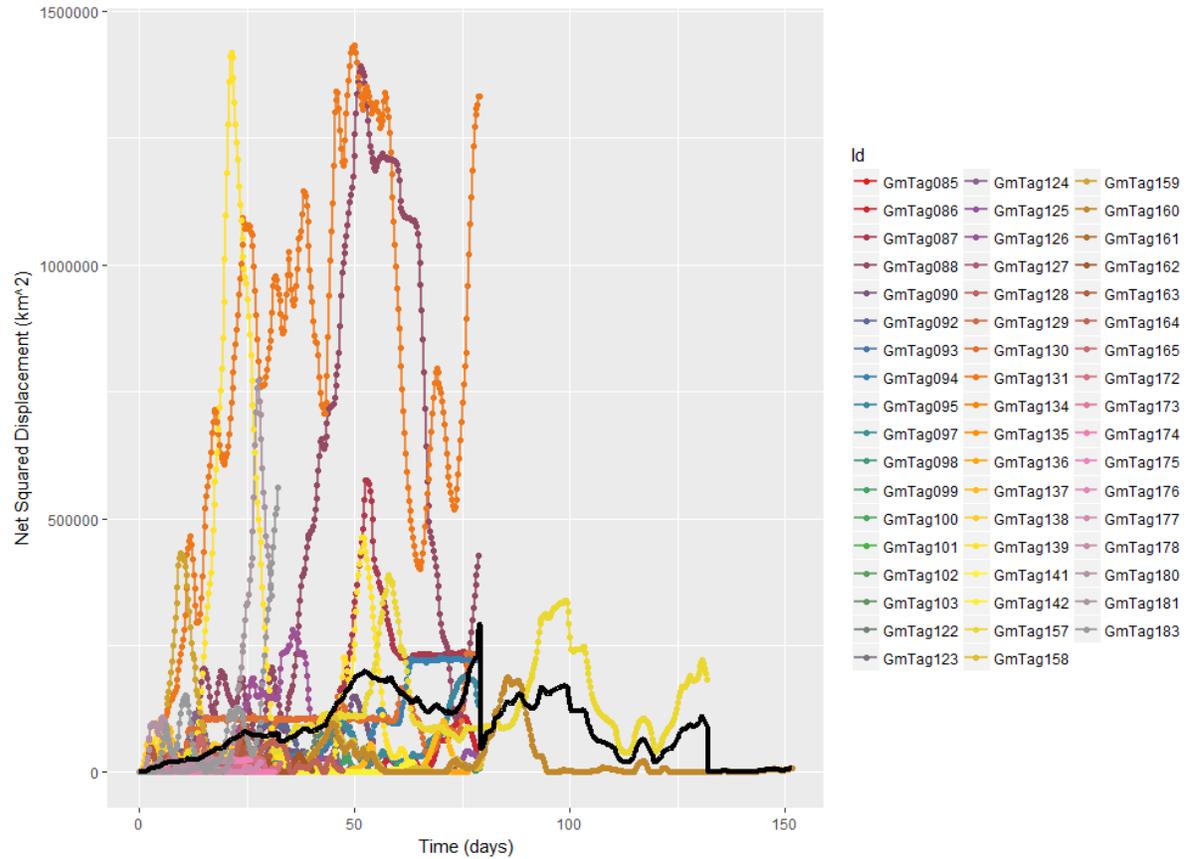


Figure 1.9. Net squared displacement (km<sup>2</sup>) over tag duration (days) for satellite-tagged short-finned pilot whales (n=53). Population mean line represented by solid black line. Highest peak represents the maximum displacement, where values close to zero represent a return to an individual's initial location.

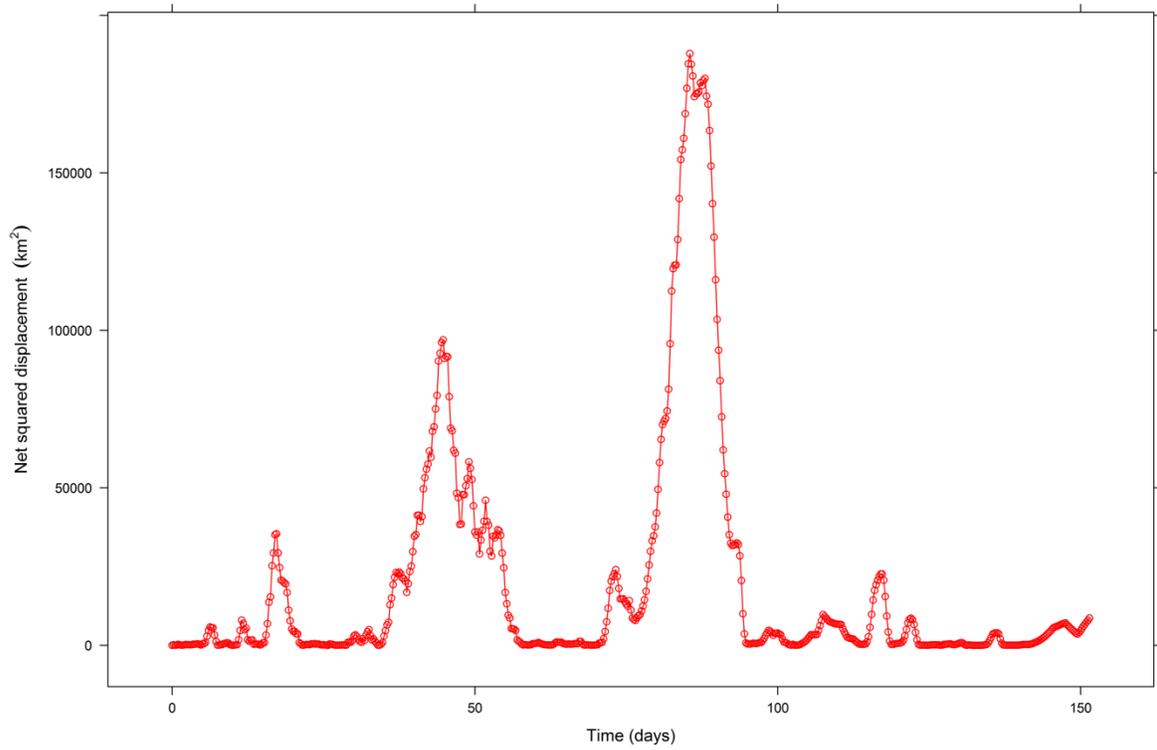


Figure 1.10. Net squared displacement (km<sup>2</sup>) over tag duration (days) for GmTag160. Highest peak represents the maximum displacement, where values close to zero represent a return to its initial location.

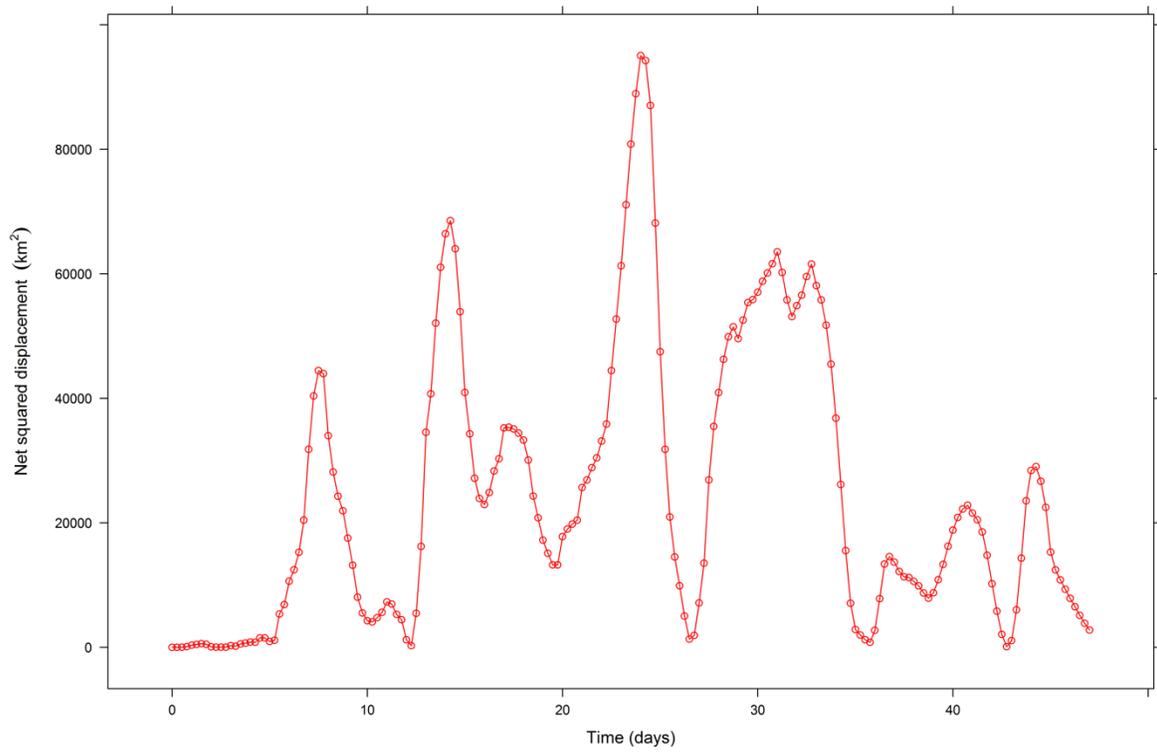


Figure 1.11. Net squared displacement (km<sup>2</sup>) over tag duration for GmTag164. Highest peak represents the maximum displacement, where values close to zero represent a return to its initial location.

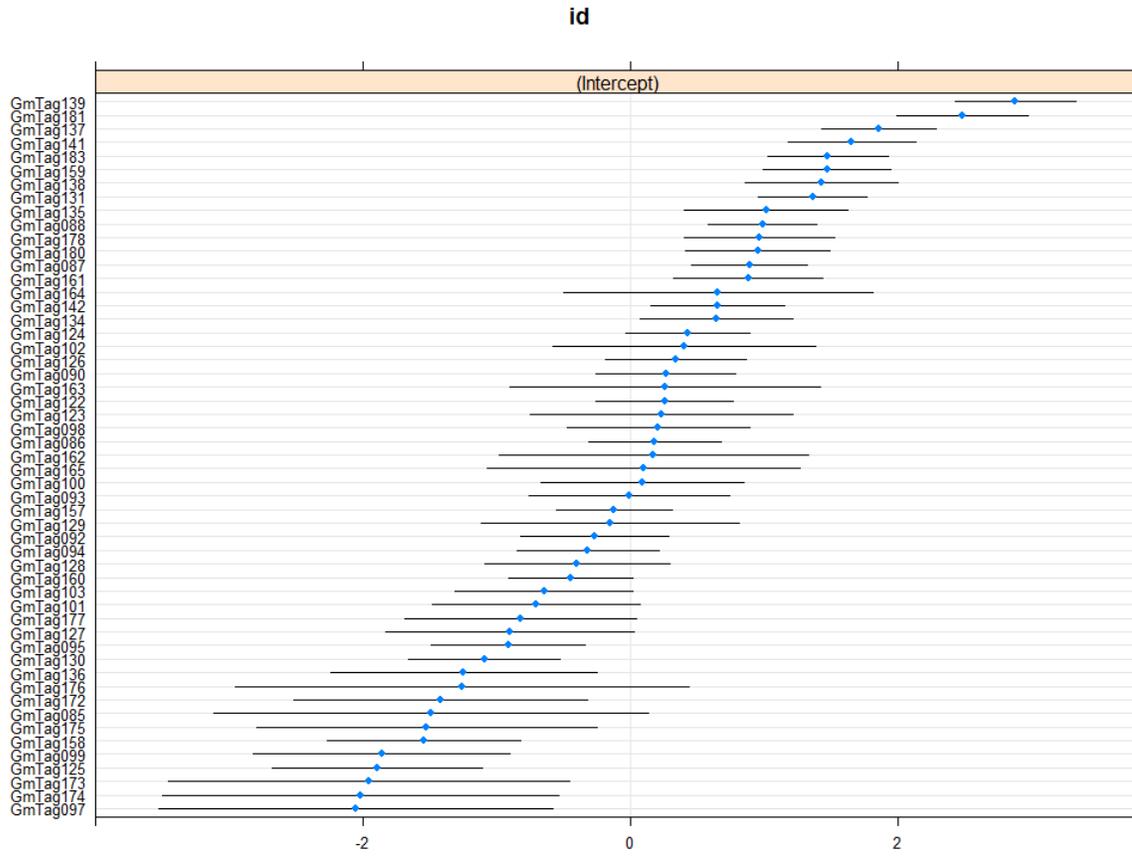


Figure 1.12. Intercepts and standard errors for the random effect of individual short-finned pilot whale.

## CHAPTER 2 – RESIDENCY AND MOVEMENT PATTERNS OF CUVIER’S BEAKED WHALES (*ZIPHIUS CAVIROSTRIS*) OFFSHORE OF CAPE HATTERAS, NORTH CAROLINA

### Abstract

Cuvier’s beaked whales (*Ziphius cavirostris*) are a wide-ranging, deep-diving species particularly sensitive to anthropogenic noise. Though current assessments define one stock for the western North Atlantic, knowledge on the residency patterns, stock structure, and predicted distributions of the species throughout the area is currently lacking. This work estimates movement, space use, site fidelity and behavior patterns of 20 individuals fitted with satellite telemetry tags offshore of Cape Hatteras, North Carolina from 2014 to 2017. A hierarchical switching state-space model (hSSSM) approach was utilized to filter locations and estimate between two behavioral states: area-restricted search (ARS) and transit. Kernel density estimation was employed to identify high use areas of the species, and net squared displacement analyses were used to determine the residency of the population to the Cape Hatteras area. The vast majority (96%) of locations were classified as foraging behavior, particularly in waters close to the continental shelf break. Generalized linear mixed effect models were run accounting for random variation among individuals to investigate the potential influence of physical oceanographic features (depth, bathymetric slope, distance to shelf break, sea surface temperature, and latitude) on behavioral state. Transit behavior, which was generally estimated when individuals departed from the study area, was most strongly predicted by positions of higher latitude and increased distance from the continental shelf break. Overall, this research suggests a localized, resident population of Cuvier’s

beaked whales offshore of Cape Hatteras with a small, defined core use foraging area and little displacement from the study site, though animals do depart and return to the area with variable frequency. These movement and spatial use patterns of Cuvier's beaked whales can better inform future conservation and management of this species which is vulnerable to disturbances and distribution shifts stemming from several anthropogenic noise sources, such as mid frequency active sonar or seismic exploration.

## **Introduction**

Cuvier's beaked whales (*Ziphius cavirostris*) are deep-diving odontocetes belonging to the family Ziphiidae. Though not well-studied or understood, they are a cosmopolitan beaked whale species known to use deep shelf edge and continental slope waters, with a significantly higher average sighting rate in submarine canyon habitat (Waring et al. 2001; Tyack et al. 2006). The species is the deepest-diving air-breathing vertebrate, with recorded dive depths up to 3,567 m over two hours of in duration (J. Shearer, in prep; Schorr et al. 2014). Typically an animal will demonstrate a long, deep foraging dive to depths over 800 m, followed by a series of shorter-duration 'bounce dives' to depths <400 m (Baird et al. 2006; Tyack et al. 2006). Cuvier's beaked whales primarily feed on meso- and benthic-pelagic cephalopods, in addition to some fish and small crustacean species (Waring et al. 2001), and it is believed that fixed bathymetric features including canyons, shelf edges, and seamounts serve to concentrate and/or aggregate prey and influence the distribution of Cuvier's beaked whales (Moulins et al. 2007; Moors-Murphy 2014). It is also proposed that the species

maintains strong associations with warm-core rings and other ephemeral features affiliated with the Gulf Stream, leading to high abundances in these areas (Waring et al. 2016).

The species is of high conservation concern as a result of their response to naval mid-frequency active (MFA) sonar activities, which has been known to elucidate mass strandings (Cox et al. 2006; D'Amico et al. 2009; Tyack et al. 2011; DeRuiter et al. 2013). Behavioral response studies conducted using controlled exposure experiments (CEEs) in the Bahamas, Norway, and southern California have demonstrated the species' particular vulnerability and sensitivity to acoustic disturbances (Southall et al. 2016), with focal individuals reacting strongly to simulated sonar by moving away from the source of acoustic disturbance and interrupting foraging, both behaviors that could result in a significant fitness cost to the animal (Tyack et al. 2011; DeRuiter et al. 2013).

Studies in several locations including the Ligurian Sea, the island of Hawaii, and southern California have demonstrated high degrees of site fidelity in Cuvier's beaked whale populations (McSweeney et al. 2007; Falcone et al. 2017). NMFS currently recognizes a single stock for the species for the western North Atlantic (Waring et al. 2016). However, the continental slope waters offshore of Cape Hatteras, North Carolina appear to be particularly important habitat for Cuvier's beaked whales with long-term site fidelity occurring both within and between seasons and years (Forney et al. 2017). Recent literature has demonstrated year-round presence of the species in this area, with substantially fewer visual and acoustic detections in both Norfolk Canyon to the north and Onslow Bay to the south (Stanistreet et al. 2017; McLellan et al. 2018).

The western North Atlantic is an area of growing concern for increased ocean noise on cetaceans (Stanistreet et al. 2017). Heavy shipping traffic along the U.S. eastern seaboard, naval exercises using MFA sonar, and the recent potential for offshore energy exploration surveys employing seismic air guns are all potential anthropogenic disturbances to local species (Schick et al. 2011). Given the established presence of Cuvier's beaked whales offshore of Cape Hatteras, as well as the species' particular sensitivity to anthropogenic noise, a better understanding of the baseline movement and spatial use patterns of Cuvier's beaked whales, particularly in areas where potential acoustic disturbances are likely, is vital (Weilgart 2007; Coomber et al. 2016; Forney et al. 2017). Traditional residency analyses in cetaceans often utilize mark-recapture methods based on photo-identification. However, due to the cryptic nature of this deep-diving odontocete that spends very little time at the ocean's surface, such methodology is not particularly well suited for the species. The use of bio-logging instruments, such as satellite telemetry tags, permits long-term tracking of elusive animals over weeks and months, allowing both movement and residency patterns to be analyzed at a finer scale in highly mobile, pelagic species (Hussey et al. 2015; Hays et al. 2016).

Describing how environmental factors influence individual animal movement can begin to shed light on the potential responsiveness of a population to future change, an overarching goal of animal ecology (Bestley et al. 2012). As movement can directly influence both the distribution of animals and ecological processes such as habitat selection and home range dynamics, a more complete understanding of Cuvier's beaked whales' movement ecology in the northwest Atlantic could help define the potential behavioral

responses of the species to both CEEs and MFA sonar, further helping to establish and define management and mitigation strategies for any potential acoustic disturbances to the species across their range.

In this chapter, I summarize the spatial ecology of Cuvier's beaked whales in the Cape Hatteras area and identify the drivers of behavior, including potential departure from the area, using data from 20 individuals satellite-tagged between 2014 and 2017. The ultimate objective is to quantitatively determine the geographic range and residency of the population using telemetry data. An additional aim of this study is to identify what environmental factors may drive Cuvier's beaked whales to cease foraging behavior and cause them to depart the Cape Hatteras area, as well as the periodicity at which they might return. Based on Cuvier's beaked whale work in other areas (McSweeney et al. 2007; DeRuiter et al. 2013; Falcone et al. 2017), as well as recent studies within the Cape Hatteras outer continental slope waters, I hypothesize that Cuvier's beaked whales will demonstrate high site fidelity to the area with small home range sizes. Individuals will display little variation in spatial use patterns, with depth most significantly driving habitat selection and movement patterns.

## **Methods**

### *Study area*

The study area includes the outer continental shelf and steep slope waters offshore of Cape Hatteras, North Carolina, United States (Figure 2.1). The very narrow continental shelf at Cape Hatteras, where depth increases from 200 m to over 1,500 m in less than 10 km

longitudinally, expands to both the north and south, forming the Mid-Atlantic Bight (MAB) and the South-Atlantic Bight (SAB), respectively (Mullin and Fulling 2003). The Gulf Stream is the dominant oceanographic feature in the area, forming the North Atlantic's largest frontal system (Chambault et al. 2017). The region of particular focus is 'The Point', an area of many square kilometers approximately 35 nm offshore, where the Gulf Stream Front flows into the study area from the southwest and peels off from the continental shelf, shifting to the northeast into pelagic waters (Forney et al. 2017). As the Cape Hatteras shelf and slope waters are an area of overlapping range for many northern, temperate cetacean species inhabiting the cooler Labrador Current along with subtropical species associated with warmer, saltier Gulf Stream waters, surveys were focused in this region to improve sighting opportunities of deep-diving cetacean species known to densely inhabit the region, including Cuvier's beaked whales (Waring et al. 2001; Mullin and Fulling 2003; Roberts et al. 2016).

### *Spatial Use*

#### Tagging and Tracking

Satellite tags of the Low Impact Minimally Percutaneous External-electronics Transmitter (LIMPET) configuration (Andrews et al. 2008; Baird et al. 2010; Baird et al. 2011) were remotely deployed using a pneumatic rifle from a 9.1 m rigid-hulled boat into either the dorsal fin or the base thereof of 20 Cuvier's beaked whales off of Cape Hatteras, North Carolina between 2014 and 2017. As described in Thorne et al. (2017), the tags were attached to the animal with two titanium darts with backward facing petals. The majority of the tags deployed (n=16) were Mk10-A SPLASH satellite-linked depth-recording tags from

which both position and compressed data of dive records are transmitted (Wildlife Computers, Redmond, WA). Other animals (n=4) were equipped with Smart Position and Temperature (SPOT5 & 6) tags, which transmit only the surface location of the animals. Both tag types transmit location estimates to Advanced Research and Global Observation Satellite (Argos) receivers on polar-orbiting satellites. In order to increase both the spatial and temporal scales at which data were able to be collected, tags were scheduled to transmit on a year and tag-specific regimen with position-only SPOT tags deployed from 2014-2015 transmitting daily for 80 days, followed by every second day for 10 days, and every fifth day until the tag ceased. SPOT tags in 2016 transmitted daily, with the number of transmitting hours being reduced at 80 and 105 days. Dive tags on 2014 Cuvier's beaked whales transmitted daily for 28 days, and every second day for the remainder of the tag, while tags deployed in 2015 and 2016 transmitted every day for 25 days, then every other day for 8 days, followed by every third day for the remainder of the tag. Based on local satellite coverage, 2014-2016 tags were programmed to transmit from 18-20 hours per day, based on tag type. All tags deployed in 2017 transmitted for 21 hours daily, with no duty-cycle employed.

All positions are assigned an estimated accuracy location class (LC) based on the timing and number of transmissions received during a satellite pass (Irvine et al. 2014). Numbered LCs (0-3) have designated error radii of >1,500 m, 500-1,500 m, 250-500 m, and <250 m respectively (Vincent et al. 2002), while lettered LCs (A and B) do not have an estimated level of error. Location class Z positions are considered invalid by Argos, and were not included in analyses.

### Location Filtering and Behavioral State Estimation

Jonsen and colleagues (Jonsen et al. 2003; Jonsen et al. 2005; Jonsen et al. 2007; Bestley et al. 2012) proposed modelling animal movement and associated behaviors using a state-space framework. State-space models (SSMs) allow both the uncertainty in the Argos positional information and the movement dynamics to be separately accounted for during estimation through two stochastic models (Silva et al. 2014). Two separate first-difference correlated random walks are used in the process model (transition equation) of a switching state-space model (SSSM), which allow parameters to vary between two distinct behaviors states while also estimating the animal's location. The two states are defined by individual combinations of both the mean turning angle and move persistence of the animal. In addition, an observation model uses the unobserved states estimated by the process model while incorporating the Argos location error structure to the observed data (Silva et al. 2014).

Hierarchical, or joint estimation over multiple individuals, can vastly improve behavioral state estimation and improve accuracy of movement parameters by borrowing strengths across all individual animal tracks (Jonsen 2016), and is particularly suited to data with large location error relative to the scale of movement. The hierarchical form assumes that as animals within a population have some fundamentally similar movement behaviors, model parameters can be shared across multiple individuals. In addition, population-level movements can better be assessed through hierarchical SSSM, allowing improved understanding of population dynamics (Jonsen 2016).

Given the varying duty cycles employed in this study, the irregular intervals of collected locations, and the considerable error structure associated with Argos locations, a

hierarchical Bayesian switching state-space model (hSSSM) was employed to both estimate the locations of the animal along with distinguishing between two behavioral states: area-restricted search (ARS) and transit. ARS, which is typically inferred as foraging behavior in cetaceans, but could also include behaviors such as breeding or resting (Bailey et al. 2010), is associated with frequent course reversals and relatively slow movements, while transit has higher rates of movement and increased persistence between locations (Jonsen 2016).

After removing all points with duplicate timestamps, the hSSSM was run using the JAGS software within the R package ‘bsam’ (Jonsen 2016) to estimate position and behavioral state at regular 6-hour time intervals across all individuals. Tags generated an average of six positions per day. After a burn in of 30,000 samples, 10,000 MCMC samples in each of two chains were generated. Every 10<sup>th</sup> sample was retained to reduce within chain sample autocorrelation (Jonsen 2016), for 2,000 final posterior samples used to calculate model parameters and estimated locations. Model convergence was assessed visually using trace and autocorrelation plots, as well as the Gelman-Rubin scale reduction factor ( $\hat{r}$ ), generated through the ‘bsam’ package (Jonsen 2016).

### Home Range Estimation

To generate individual and population-level home range and core use areas from the hSSSM output, utilization distributions (UDs) were generated for all individuals using kernel density estimation (KDE). Core use areas were calculated to represent particularly high use areas within each individual’s UD (Johnston et al. 2005; Hauser et al. 2014). Though home range estimation can be sensitive to auto-correlated data, serial independence of observations

is not required (De Solla et al. 1999). Instead, maximizing the number of observations while using regularly spaced time intervals, such as those generated from the hSSSM, lead to more precise and accurate KDE results (De Solla et al. 1999; Fieberg 2007). After the hSSSM-estimated locations were projected to the Albers Equal Area projection, core use (50% probability contour) and home range (95% probability contour) areas and associated isopleths were generated in the R package 'ks' using the bivariate plug-in bandwidth matrix as the smoothing parameter (Duong and Hazelton, 2003; Duong and Hazelton, 2005; Duong, 2007). The plug-in bandwidth is a 'second-generation' kernel density estimator allowing for separate bandwidths in the x and y directions that performs well at identifying high use areas, even with dependent telemetry data (Hall et al. 1995; Jones et al. 1996; Walter et al. 2015).

### Movement Patterns

Bunnefeld and colleagues (Bunnefeld et al. 2011; Papworth et al. 2012) demonstrated the scale-independent, model-driven measurement of net squared displacement (NSD) as a method to distinguish between a variety of potential animal movement patterns, such as migration, dispersal, nomadism and home range (i.e. resident) individuals within a population. Straight-line distances between the initial location of an animal and its subsequent locations are calculated and squared, and the resulting curves plotted against time. The curves are then fit to a suite of non-linear least squares movement models, each function unique to a movement type, and Akaike Information Criterion (AIC) values are used to classify an individual's movement pattern (Bunnefeld et al. 2011). Resident animals, who do not demonstrate large changes in NSD over time and whose movement is generally

limited to a stable home range, are best described with an intercept model, with a resulting asymptotic form of the NSD curve (Börger et al. 2008; Bunnefeld et al. 2011). Nomadic behavior, in which an animal never remains in one place for long periods, demonstrates a NSD curve that increases linearly over time. Dispersal animals demonstrate departures from their initial locations, while migratory individuals depart and return seasonally. To test the hypothesis that Cuvier's beaked whales offshore of Cape Hatteras, North Carolina are a resident population, I calculated NSD and ran a candidate set of movement pattern models for all individual tag deployments with more than 100 relocations, or approximately 25 days of tag duration, adapting R code from Papworth and colleagues (2012).

#### *Describing Variability in Cuvier's Beaked Whale Behavior*

To determine any potential environmental predictors of an animal ceasing foraging activity and departing the Cape Hatteras area, analogous to an animal switching from ARS behavior to transit, I used generalized linear mixed models (GLMMs.) These models combine generalized linear models and mixed effect models to allow both fixed and random predictor variables. GLMMs are robust and well suited to account for the spatial and temporal auto-correlation of repeated measures on single individuals inherent in telemetry data, as well as the random effects generated by the variability and unbalanced sampling of individuals (Guisan et al. 2002; Gillies et al. 2006; Hebblewhite and Merrill 2008; Bolker et al. 2009; Koper and Manseau 2009). The analyses here aim to describe how the binary response variable of behavior (ARS or transit) changes as a function of the predictor variables. The GLMM, in matrix notation, is given by:

$$\mathbf{y}=\mathbf{X}\boldsymbol{\beta}+\mathbf{Z}\boldsymbol{\gamma}+\boldsymbol{\varepsilon}$$

where  $\mathbf{y}$  is the  $(n \times 1)$  response vector;  $\mathbf{X}$  is a  $(n \times p)$  design matrix of the  $(p)$  fixed-effects predictor variables;  $\boldsymbol{\beta}$  is a  $(p \times 1)$  vector of the fixed-effects regression coefficients;  $\mathbf{Z}$  is the  $(n \times q)$  design matrix for the  $(q)$  random effects;  $\boldsymbol{\gamma}$  is a  $(q \times 1)$  vector of the random effects, and  $\boldsymbol{\varepsilon}$  is a  $(n \times 1)$  column vector of the errors, or unexplained variability within the model.

Both fixed and random effects combine to form the linear predictor:

$$\boldsymbol{\eta}=\mathbf{X}\boldsymbol{\beta}+\mathbf{Z}\boldsymbol{\gamma}$$

which is linked to the response variable via the link function. Positions estimated as uncertain ( $b_t > 1.25$  and  $< 1.75$ ) were not included in the analyses. As the response variable was binary, the binomial family was chosen, and given the skewed behavior data, with only 5% of included positions considered transit, a complementary log log (cloglog) link was used, rather than a logit or probit link, which are more suitable for approximately equal numbers of each binary response (Zuur et al. 2009). Possible fixed effects in this study included depth, slope, distance to shelf break, sea surface temperature, latitude, and longitude, as well as month and year to analyze whether any seasonal effects may be present in behavior.

Individual animal was set as a random effect. Due to limited data across levels of the categorical descriptor variables of month and year, no interaction terms were included.

Though characterizing the environment through which highly mobile marine species move can provide a unique challenge, particularly with animals who spend much time at depth (Bestley et al. 2012), several potential environmental predictors of behavioral state

were chosen as model covariates. The National Oceanic and Atmospheric Association's National Center for Environmental Information's (NCEI) 3 arc-second Southeast Atlantic U.S. Coastal Relief Model (CRM) was used to generate depth values whenever possible. For any areas not included in NCEI's CRM (<6% of locations in this study), 30 arc-second data from the General Bathymetric Chart of the Oceans (GEBCO) 2014 global bathymetry grid were used ([www.gebco.net](http://www.gebco.net)). The GEBCO bathymetric grid was also used to generate slope values and the 200 m isobath contour to serve as a proxy for the continental shelf break (Thorne et al. 2017). Group for High Resolution Sea Surface Temperature (GHRSSST) grids with a 1 km resolution were obtained using the NOAA Coastwatch tool Xtractomatic (<http://coastwatch.pfel.noaa.gov/xtracto/>). Daily mean values were calculated based on the confidence intervals of both latitude and longitude of each position derived from the hSSSM.

Covariates were analyzed for collinearity using correlation coefficients <0.6 and variance inflation factors (VIFs), and longitude was excluded from candidate models due to multicollinearity with latitude. Despite the bathymetric variables of depth and distance to shelf break being correlated (Pearson correlation 0.68), both were included in potential models given VIFs <3 for all potential covariates (Zuur et al. 2009). To help with model convergence, the continuous predictors of depth, SST, and latitude were both centered to their mean and scaled while distance to shelf break and slope were only scaled (Bolker et al. 2009). Models were run using the `glmer` command within the 'lme4' package in R, where maximum likelihood estimates and confidence intervals were estimated using Laplace approximation (Bates et al. 2015). The dredge function in the 'MuMIn' R package (Barton 2018) was used to find the most parsimonious combination of covariates, and model

selection was conducted using second-order Akaike information criterion (AICc; Mazerolle 2016, Akaike, 1973) in both the 'AICcmodavg' R package and 'MuMIn'.

## **Results**

### *Spatial Use*

Twenty Cuvier's beaked whales were satellite-tagged between May 2014 and May 2017, with tags ranging in duration from 2 to 93 days with an average length deployment of  $42 \pm 21$  days (Table 2.1). Animals remained in close association with the continental shelf and slope waters, ranging from Onslow Bay, North Carolina in the south to the Virginia/Maryland border to the north (Figure 2.2). Though a few individuals displayed sallies into more northern or southern waters, the majority of tagged individuals demonstrated fine (0 – 10s km) and meso-scale (10 – 100s km) movements over their tag duration, remaining near to the tagging location offshore of Cape Hatteras, with no animal venturing further than 272 km from its initial observed location (Table 2.1, Figure 2.2). Total travel distances per individual tag duration were calculated as great circle distances between the hSSSM-estimated locations, representing the absolute minimum distance traversed between locations, and ranged from 29 to 4,802 km across individuals. The median water depth at estimated surface locations was 1,590 m (mean = 1,524, range = 47 to 3,662 m). The median distance to the continental shelf break (200 m isobath) was 10 km (mean = 13.6 km), with a max distance from the shelf break of 165 km. Slope had a median value of  $4.9^\circ$ , an average of  $5.7^\circ$ , and a maximum of  $18.6^\circ$ . Sea surface temperature values at estimated locations ranged from  $16.1^\circ\text{C}$  to  $30.4^\circ\text{C}$ , with an average of  $26.2^\circ\text{C}$  (median =  $26.3^\circ\text{C}$ ).

### *Location Filtering and Behavioral State Estimation*

Within the hSSSM, the behavioral state at time  $t$  ( $b_t$ ) is estimated using the mean value from Markov Chain Monte Carlo (MCMC) samples, which provide a continuous value from 1 (transit) to 2 (ARS) (Bailey et al. 2010). Per many previous studies, behavioral state values of 1 - 1.25 were considered transit behavior, while 1.75 - 2.0 were classified as ARS. Values in between were considered uncertain (Jonsen et al. 2007; Bailey et al. 2012; Kennedy, Zerbini, Rone, et al. 2014; Acuña-Marrero et al. 2017).

The hSSSM generated 3,354 estimated locations across 20 individuals and clearly distinguished between transit (4.8% of locations) and area-restricted search (93.5%) behaviors, with 1.7% of points classified as uncertain (Figure 2.3). ARS behavior was dominant across most individuals, with the vast majority of animals remaining within that behavioral mode for the entirety of their tag's duration (Table 2.1). ARS behavior was more prevalent in locations close to the study site and continental shelf break (average distance to 200 m isobath = 11.3 km) (Figure 2.3), while transit behavior was generally predicted when animals departed from the study site, northward and eastward of the shelf break (average distance to 200 m isobath = 50.5 km).

### *Home Range Estimation*

Utilization distributions generated from kernel density estimation demonstrated a home range area for the population of all tagged individuals ranging from the Virginia/North Carolina border southward to Onslow Bay, North Carolina, straddling the continental shelf break. The core use area, or 50% isopleth as generated from KDE, across all years and

individuals (area = 583 km<sup>2</sup>) highlighted one high-use area for the population just eastward of the continental shelf break offshore of Cape Hatteras (Figure 2.4). The home range for the population was estimated from the 95% isopleth and had an area of 7,647 km<sup>2</sup> (Figure 2.4). Individual core use areas ranged from 22 to 872 km<sup>2</sup>, while individual home range areas spanned from 72 to 12,697 km<sup>2</sup> (Table 2.1). All individual core use areas were overlaid in ArcMap 10.5, and showed a large degree of overlap between tagged individuals (Figure 2.5).

### *Movement Patterns*

Net squared displacement was plotted over time for each individual, along with the population mean (Figure 2.6). In addition, tagged individuals' maximum net displacement from their initially estimated location was calculated as the maximum value of the square root of each NSD at every subsequent location. Maximum net displacement ranged from 14 km for the shortest-duration tag to 272 km for ZcTag057, which also had the largest core use and home range areas (Table 2.1). Though ZcTag057 demonstrated the maximum net displacement for the sample, its tag duration was one week longer than the sample size mean, demonstrating increased time of tag duration did not necessarily indicate further displacement from the Cape Hatteras survey area (Figure 2.7). Every individual with more than 100 estimated locations, to which NSD movement model analyses were restricted, returned to the Cape Hatteras area at some or many points during their tag's duration (see Figure 2.8). Potential movement pattern model fits demonstrated individual Cuvier's beaked whales to fall predominantly into the 'home range' or resident movement pattern. However, AIC values for three individuals (ZcTag041, ZcTag049, and ZcTag050) indicated a better fit

for the nomadic movement form. Migratory, mixed migratory, and dispersal movement models failed to converge for all individuals (Appendix B).

#### *Describing Variability in Cuvier's Beaked Whale Behavior*

Several candidate GLMMs failed to converge, likely due to a sparse, skewed behavior data set, and as such, seasonal variables (month and year) were excluded. All of the top six models based on AICc included distance to shelf break and latitude as fixed explanatory variables with individual whale as a random effect. The most parsimonious model in the candidate set also included slope as a descriptor variable, though it was the only covariate to not be classified as significant (Table 2.2). Latitude was determined to be the strongest predictor of behavioral state, followed by distance to the continental shelf break and slope (Table 2.2). Coefficients for the random effect of individual beaked whales were relatively consistent across most individuals, albeit with large standard errors (Table 2.3, Figure 2.10). However, animals who spent the majority of their tag deployment in pelagic waters away from the continental shelf break showed more positive coefficient estimates (Table 2.3), demonstrating those animals were more likely to exhibit transit behavior than those who remained close to the shelf break during their tag's duration. This was likely an artifact of the data, as those individuals exhibited more transit behavior than the rest of the sample size, creating less skew in the response variable.

## Discussion

Using satellite telemetry data and a hierarchical switching state-space model approach to analyze the movement of Cuvier's beaked whales offshore of Cape Hatteras, North Carolina has generated several important aspects of the spatial use, habitat preferences, behavior, and residency of the population. The estimated locations from the hSSSM demonstrate the small geographic range of the species along the outer continental slope waters of North Carolina. Individuals tend to prefer deep (>1,000 m) waters with high relief, warm SSTs, and small distances to the shelf break. Area-restricted search was the dominant behavior (96% of locations) inferred throughout the sample size, with transit behavior not occurring at any point in the tag duration of 75% (n=15) of the tagged individuals (Table 2.1).

Kernel density estimation identified a localized high use area for the species, in addition to highly overlapping core use areas between tagged individuals. Though Cuvier's beaked whales are known to frequent deep, slope waters (Waring et al. 2001), it is still relatively unclear what fine scale habitat characteristics of this small high use area offshore of Cape Hatteras attract the species. Similar degrees of relief and bathymetry are available to both the north and the south of the population's core use area, yet these regions are not as strongly selected. However, the confluence of the Gulf Stream and the Labrador Current, which can spatiotemporally vary, often occurs within or near the species' defined core use area, producing warm core rings and productive fronts and eddies with which the species is known to associate. These mesoscale features can aggregate prey, the ultimate determinant of marine mammal distributions (Laidre et al. 2004; Waring et al. 2016). Due to their ephemeral

and patchy nature, these oceanographic features and processes are incredibly difficult to identify and quantify over relevant spatiotemporal scales, even with the advancement of front-detecting algorithms applied to remotely-sensed data (Etnoyer et al. 2006). However, future work should seek to include the best proxies therefore.

It has been also been proposed that beaked whales may occupy distinct ecological niches, exhibiting fine-scale habitat partitioning within overlapping ranges of other odontocetes who share similar prey species, such as short-finned pilot whales and sperm whales (*Physeter macrocephalus*) (Schick et al. 2011). Cuvier's beaked whales within the area may have developed a specialized foraging strategy within a small high use area in order to maximize fitness and reduce interspecific competition, though despite recent studies, the foraging ecology of beaked whales in the western North Atlantic is still poorly understood, and additional study is necessary (MacLeod et al. 2003; West et al. 2017).

All migratory, mixed migratory, and dispersal pattern models failed to converge in the NSD analyses, possibly due to the data set of relatively short tag durations not supporting the complexity and functional forms of models based on annual animal movement patterns (Bunnefeld et al. 2011). However, as the non-linear models require and are quite sensitive to a chosen set of initial parameters based on the scale of an animal's movement, individual variability in movement and tag duration could have resulted in the choice of improper start values, even after much trial-and-error manipulation, which would also have led to non-convergence (Harrison, 2012). Results indicated most individuals fell under the originally hypothesized 'resident', or home range, movement pattern, with only three individuals demonstrating a better fit to the nomadic movement curve (Appendix B). However, this is

likely because each of these three tag's transmissions ceased when the animal was at its maximum NSD (e.g. Figure 2.9). As NSD should increase linearly with time for nomadic movement (Harrison, 2012), such individuals would have been misclassified. For example, ZcTag049 was the longest duration tag (Table 2.1), and remained clearly resident to the study area for nearly three months before departing the area just before tag failure (Figure 2.9). Model fit for ZcTag049, therefore, was more suited to a nomad than a resident. As every animal with more than 100 relocations returned to its initial location at some point during their tag duration, more transmission time would likely have allowed these individuals time to return to their core use areas, and would likely have categorized their movement patterns as resident/home range. Interestingly, some of the tagged animals never returned to their initial locations (ZcTag046 and ZcTag051). Despite constituting some of the shortest tag durations among the sample size (Table 2.1), it is conceivable these individuals were not members of the resident population and rather part of a separate oceanic population within the stock utilizing a portion of their range that spatially overlaps with that of the resident Cape Hatteras animals.

Animals are known to use smaller home ranges than expected from their observed mobility levels, particularly in predictable environments with high prey availability (Börger et al. 2008; Acuña-Marrero et al. 2017; Couriot et al. 2018). Despite an expansive species range for Cuvier's beaked whales throughout the entire western North Atlantic (Waring et al. 2016), the small and overlapping core use areas, along with low displacements and categorizations of individual movement patterns from NSD analyses for the tagged individuals indicate that animals offshore Cape Hatteras, North Carolina belong to a resident

population. This claim is further bolstered by recent literature demonstrating a year-round presence of Cuvier's beaked whales in the Cape Hatteras study area (Stanistreet et al. 2017; McLellan et al. 2018) as well as photo-identification analyses from the area that reveal a particularly high re-sighting rate for the species (18%) despite limited sample sizes. Over half of the individuals satellite-tagged in this study have been re-sighted within the Cape Hatteras area, and many other animals uniquely identified from photographs have been re-sighted inter-seasonally and inter-annually, with up to four years between sightings and as many as six re-sightings for one individual whale within the study site (D. Waples, pers. comm). Altogether, this body of work demonstrates the extreme site fidelity and residency of Cuvier's beaked whales to the continental slope waters offshore of Cape Hatteras across several spatiotemporal scales.

Despite the medium and long-term residency of Cuvier's beaked whales to the Cape Hatteras area, the periodicity at which animals depart and return to the area is incredibly variable between and within individuals and difficult to quantify. Some animals demonstrated only a few forays away from Cape Hatteras (Figure 2.7), while other individuals departed and returned to the area many times throughout their tag duration (Figure 2.8). Tyack and colleagues (2011) found that a satellite-tagged Cuvier's beaked whale in the Bahamas moved 'several tens of km' away from an area of a CEE, and took approximately three days to return, determined as a 'clear reaction to sonar'. Calculating such metrics for the Cape Hatteras individuals could help define typical behavior for the population from which potential behavioral responses could be assessed. However, further work is necessary in order to elucidate population-level patterns of departure from the area.

Generalized linear mixed models indicate that distance to shelf break and latitude are significant predictors of behavioral state in Cuvier's beaked whales with transit behavior more likely to occur at positions further from the continental shelf break and higher (more northerly) latitudes. Although model results match patterns observed in the hSSSM output, there are a few caveats. The response variable of behavior was incredibly skewed, with ARS dominant throughout the data set, which could have led to issues with model fit. Potential collinearity between depth and distance to shelf break variables might also have affected coefficient values and significance levels.

My hypotheses that depth would be the strongest predictor of behavioral state was incorrect, and in fact, distance to shelf break, latitude, and slope all exhibited higher levels of significance. However, static physical features, such as depth and slope may not be the best proxies for cetacean habitat at fine-scale use (Johnston et al. 2005). Instead, temporally dynamic covariates, such as mesoscale activity (upwelling, fronts, eddies, or currents), and their interactions with the physical features and processes that can aggregate resources may be more directly applicable for identifying fine-scale cetacean habitat (Briscoe et al. 2018).

Though animals don't respond to physical oceanographic variables such as slope directly, they are often used as proxies for prey distribution (Palacios et al. 2014). Prey abundance is an often absent, albeit desired, descriptor variable in cetacean studies, and would better help define the scale of movement patterns, as the scale at which Cuvier's beaked whales move likely corresponds to the scale at which their prey species are distributed. However, little is known about the abundance of meso- and benthic-pelagic squid and fish in the western North Atlantic or how they aggregate in relation to oceanographic

variables. To be used in future analyses, effective prey sampling would need to span several dimensions, geographic scales, and time spans, and is currently impossible.

Another potential descriptive variable that was unable to be included in this study is seasonality. Currently, on-the-water effort occurs only between late spring and early fall when weather is most conducive to offshore surveys. That limitation, along with the added caveat of medium-term tag duration in cetacean telemetry, particularly in this deep-diving species, precludes any telemetry data for Cuvier's beaked whales between January and April. In addition, a skew behavior data from May to December prevented seasonal variables from being included in the GLMMs. However, seasonal movements have not been previously documented in beaked whales (Stanistreet et al. 2017), and recent acoustic and visual studies in the region have detected Cuvier's beaked whales at similar levels year-round, with little to no seasonal variation (Stanistreet et al. 2017; McLellan et al. 2018). Nonetheless, future study could aim to expand effort to other times of the year in order to assess the year-round residency patterns and to further examine any potential for seasonal or inter-annual changes in movement patterns, spatial use, and behavior of the species.

Though GLMMs were utilized to identify significant drivers of behavior, they can also help to distinguish important habitats preferred by animals, information which can be beneficial in management of the species. However, selection of habitat can be difficult to determine in species or populations with high site fidelity (Laidre et al. 2004), as spatial constraints can limit the ability of animals to respond to their environment (Briscoe et al. 2018). As such, the scale of the movement of Cuvier's beaked whales relative to the spatiotemporal resolution of both the environmental variables (~1 km) and positional data (6-

hr) is another important aspect to consider. Tags generated an average of 6 positions per day, or every four hours. Meso- (10 - 100s km) and large-scale movements (100 - 1000s km) are more easily detected at such resolutions, but finer-scale movements (0 - 10s km) and behavioral switches within such timeframes may not be as easily discernible. Alternatively, the meso-scale, medium-term results presented here could be combined with both long-term residency patterns generated from photo-identification and fine-scale movement patterns from the use of digital acoustic tags (Quick et al. 2017). Amalgamating data over several spatial and temporal scales will help to define what is ultimately driving Cuvier's beaked whales' movement and behavior.

Integration of the dive behavior obtained from the Mk10-A SPLASH tags is a logical next step in order to more fully understand the movement patterns of these animals. Interpolating dive information across the predicted locations could begin to ground truth the behavioral state output. For example, ZcTag057, which exhibited the furthest net displacement and largest core use and home range areas, in addition to the highest proportion of its tag duration in transit behavior (Table 2.1, Figure 2.7), did not demonstrate any deep foraging dives during the time in which it had departed Cape Hatteras, helping to validate the hSSSM behavioral estimates (W. Cioffi, pers. comm.).

Population structure of the species is another important consideration of this work. Distributions, movement patterns, dive behavior, and foraging strategies may be sex, age class, or life-stage specific (Hauser et al. 2014; Acuña-Marrero et al. 2017; Vacquie-Garcia et al. 2017; Hückstädt et al. 2018; Briscoe et al. 2018). Though difficult to assess at sea (Coomber et al. 2016), sex and age class of Cuvier's beaked whales could be ascertained for

most individuals from photographs and used in further comparative studies. Genetic information obtained from biopsy samples could also be used to generate a defined knowledge of population structure of Cuvier's beaked whales which is currently lacking (Forney et al. 2017).

Information on the stock structure of Cuvier's beaked whales is vital in order to best manage and conserve the species, and is currently lacking. As there is one defined stock for the species spanning the entire western North Atlantic (Waring et al. 2016), several additional populations outside of Cape Hatteras must exist. We recognize the potential bias to the tagging location in this study, as all animals were instrumented within a few square kilometers (Figure 2.2). Identifying and describing other populations within the stock as it is currently defined would require tagging additional animals in new locations.

Effective conservation and management measures also rely on accurate descriptions of a species' space use and predictions of their distributions (Palacios et al. 2014; Winton et al. 2018). This study demonstrated the continental slope waters offshore of Cape Hatteras, North Carolina to be important foraging habitat for a Cuvier's beaked whale population. Analyses of how animal movement and behavior are influenced by environmental factors, such as my discovery that latitude and distance from shelf break were the strongest predictors of transit behavior, are vital to begin to understand and predict responsiveness to environmental change, including potential distribution shifts from anthropogenic noise (Gomez et al., 2016; Bestley et al., 2013). The two main disruptions to animal space use are dispersal and migration (Bunnefeld et al. 2011). Although the Cuvier's beaked whales in this study demonstrate small core use areas and very little propensity to either dispersal or

migration, MFA sonar and other acoustic disturbances such as ocean noise generated from seismic exploration may cause individuals or populations to be forced out of their stable home ranges, potentially modifying their distributions. This work represents the largest sample size of telemetry data from any Cuvier's beaked whale population in the world, and the movement ecology presented here is an important first step to better allow us to predict and assess any future behavioral or distributional shifts of species in response to both change the marine environment and anthropogenic disturbance.

## Tables

Table 2.1. Summary of Cuvier's beaked whale satellite tag deployments, including tag id, tag type, deployment date, tag duration, number of post hierarchical switching state-space model (hSSSM) positions, proportion of track within area-restricted search (ARS) behavior, total distance traveled, core use area, home range area, and maximum net displacement.

Tag ID	Tag Type	Deployment Date	Duration (days)	Post hSSSM locations	ARS Prop.	Total Distance traveled (km)	Core Use (50% isopleth) Area (km <sup>2</sup> )	Home Range (95% isopleth) Area (km <sup>2</sup> )	Maximum Net Displacement (km <sup>2</sup> )
ZcTag029	Mk10-A	5/13/2014	59.9	241	0.68	2480	823.8	7474.1	243.9
ZcTag030	Mk10-A	9/16/2014	40.4	156	1.0	656	109.8	624.6	46.55
ZcTag031	SPOT5	9/16/2014	35.6	130	0.88	817	800.6	3977.4	183.77
ZcTag038	Mk10-A	6/14/2015	56.4	223	1.0	1273	635.7	2511.4	98.53
ZcTag039	SPOT5	6/14/2015	39.4	157	1.0	611	140.0	591.3	39.24
ZcTag040	Mk10-A	6/14/2015	2.0	8	1.0	29	21.6	71.6	13.71
ZcTag041	Mk10-A	10/15/2015	34.3	138	1.0	686	181.0	812.0	42.46
ZcTag042	Mk10-A	10/21/2015	59.2	238	1.0	990	162.1	689.7	33.32
ZcTag043	SPOT5	10/21/2015	56.8	228	1.0	679	139.6	717.7	41.70
ZcTag046	Mk10-A	5/25/2016	16.1	61	1.0	223	87.8	304.9	24.02
ZcTag047	Mk10-A	5/25/2016	66.9	268	1.0	891	123.6	548.6	39.08
ZcTag048	Mk10-A	5/27/2016	36.4	146	1.0	478	71.0	347.9	25.14
ZcTag049	SPOT6	5/27/2016	92.8	368	0.96	1725	162.1	952.1	134.25
ZcTag050	Mk10-A	8/20/2016	30.4	122	1.0	584	147.7	1060.6	57.56
ZcTag051	Mk10-A	8/21/2016	11.4	46	0.72	426	557.8	3381.4	186.56
ZcTag054	Mk10-A	5/10/2017	18.1	72	1.0	345	218.3	770.9	72.79
ZcTag055	Mk10-A	5/10/2017	52.9	207	1.0	1236	354.0	1389.6	58.83
ZcTag056	Mk10-A	5/10/2017	47.9	191	1.0	1040	505.9	1737.7	54.30
ZcTag057	Mk10-A	5/16/2017	49.4	197	0.50	4802	872.2	12696.6	271.93
ZcTag058	Mk10-A	5/16/2017	39.1	157	1.0	764	142.2	816.0	45.18

Table 2.2. Summary of best-fitting model with coefficient estimates, standard errors, and p values for each fixed effect. Bold face denotes statistical significance ( $p < 0.05$ ).

	Estimate	Standard Error	Z statistic	P value
<b>Intercept</b>	<b>-13.479</b>	<b>2.781</b>	<b>-4.846</b>	<b>1.2571E-06</b>
<b>Distance to Shelf Break</b>	<b>0.858</b>	<b>0.248</b>	<b>3.458</b>	<b>0.000543</b>
<b>Latitude</b>	<b>2.135</b>	<b>0.251</b>	<b>8.489</b>	<b>2.09E-17</b>
Slope	-0.492	0.338	-1.453	0.146213

Table 2.3. Intercept coefficient estimates for random effect id from best-fitting model.

id	Intercept	Standard Error
ZcTag029	-3.1440	0.240
ZcTag030	-13.5716	10.524
ZcTag031	-0.9890	0.356
ZcTag038	-13.9833	8.959
ZcTag039	-13.4911	10.935
ZcTag040	-13.4809	10.991
ZcTag041	-13.5099	10.835
ZcTag042	-13.5035	10.869
ZcTag043	-13.5249	10.757
ZcTag046	-13.4900	10.941
ZcTag047	-13.5305	10.728
ZcTag048	-13.4943	10.918
ZcTag049	-13.6683	10.085
ZcTag050	-13.5154	10.806
ZcTag051	1.0435	0.399
ZcTag054	-13.4823	10.983
ZcTag055	-13.5249	10.757
ZcTag056	-13.5188	10.788
ZcTag057	-3.1963	0.228
ZcTag058	-13.5268	10.747

## Figures

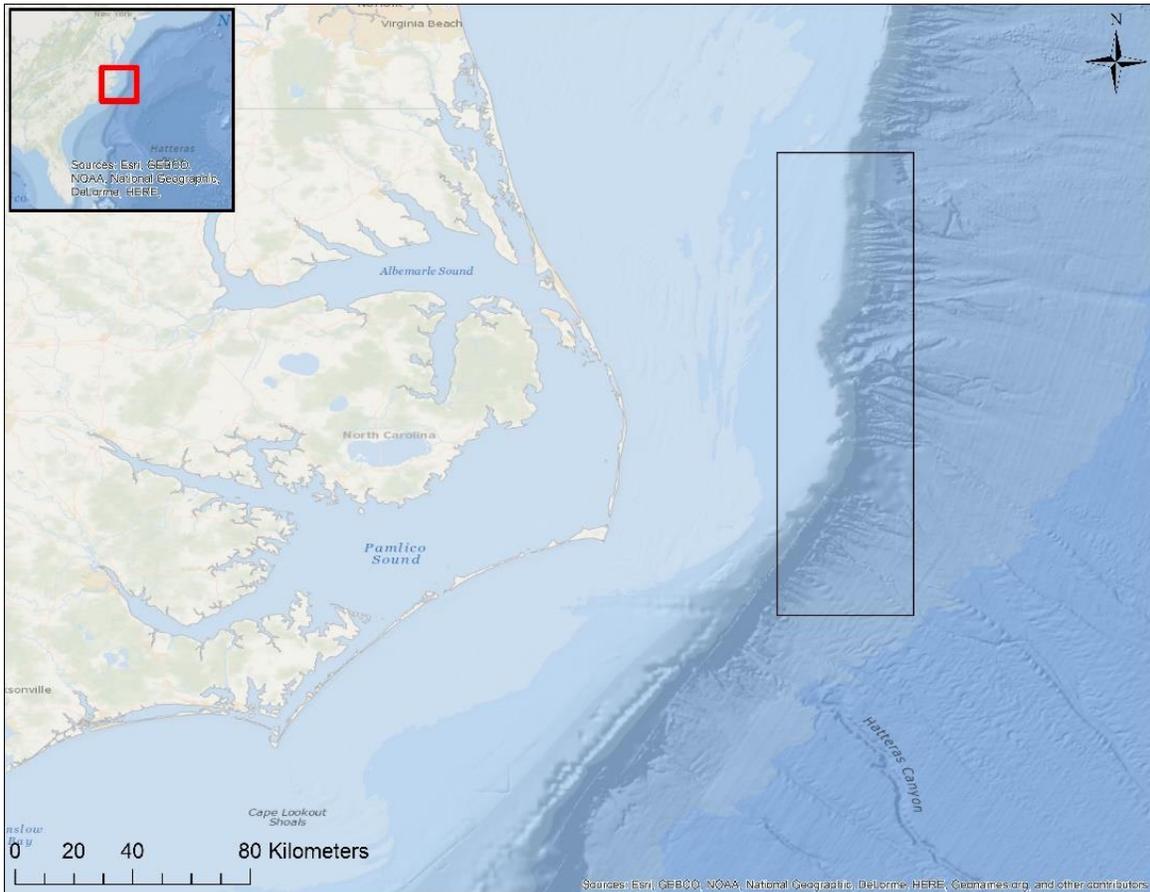


Figure 2.1. Plot of the study site, offshore of Cape Hatteras, North Carolina.

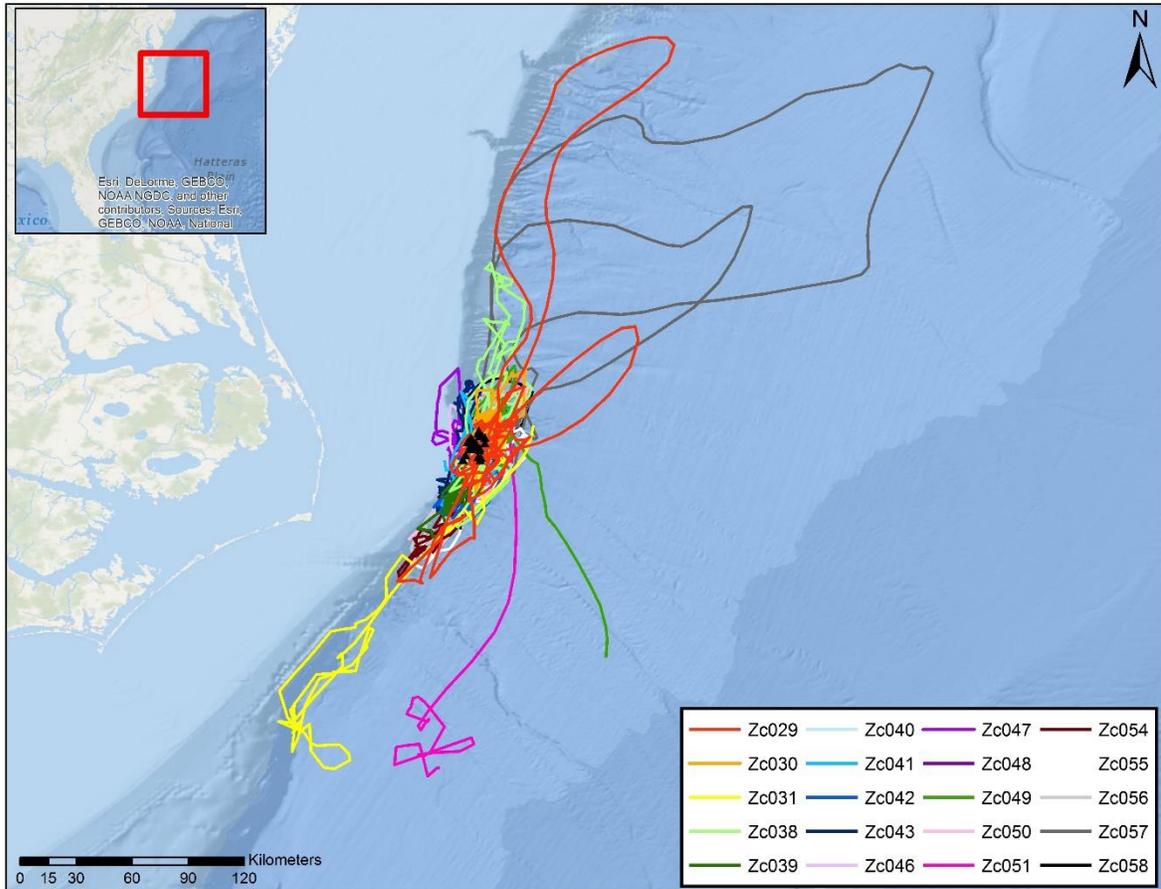


Figure 2.2. Map of individual tracks of Cuvier's beaked whales (n=20) re-sampled to a 6-hr time step via a hierarchical switching state-space model. Tagging locations represented with black triangles.

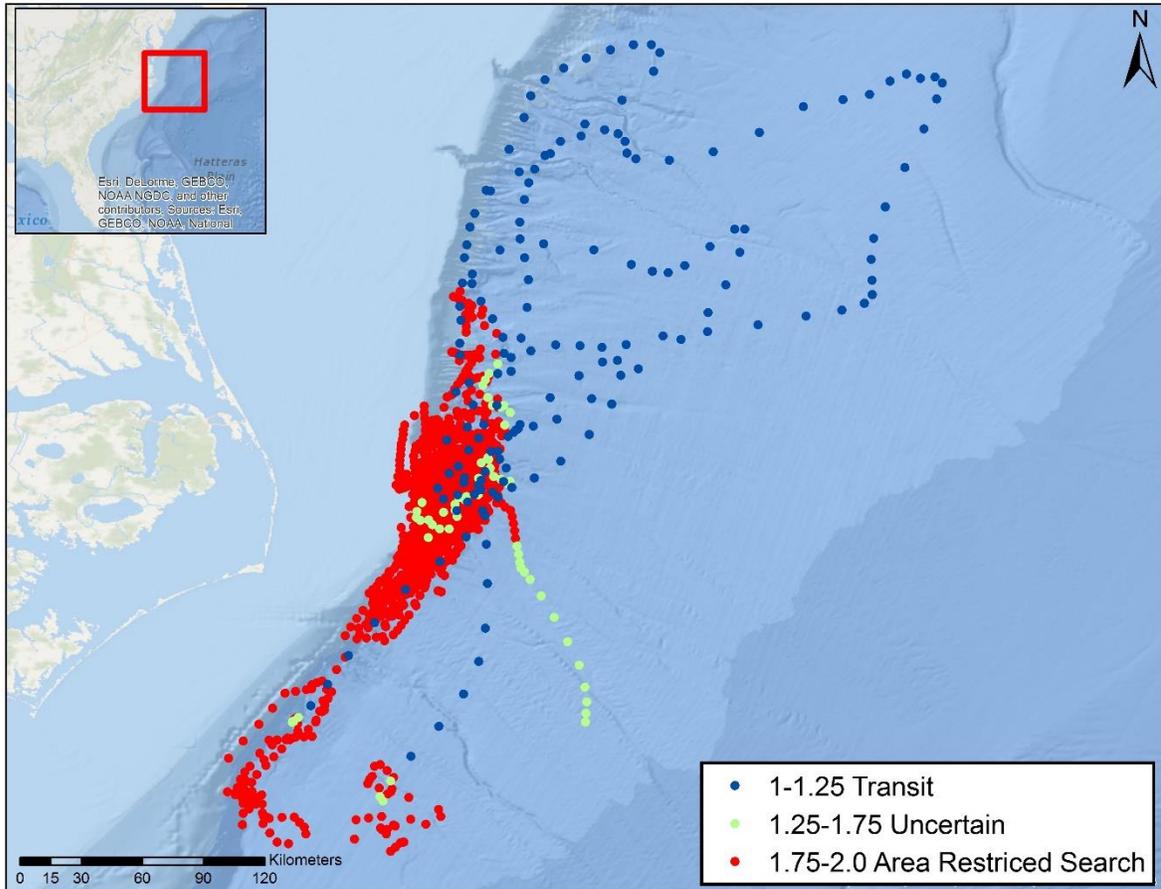


Figure 2.3. Map of behavioral states estimated from hierarchical switching state-space model ranging from 1-2 of Cuvier's beaked whales (n=20). Red indicates area-restricted search behavior, blue shows transit behavior, and green shows uncertain values.

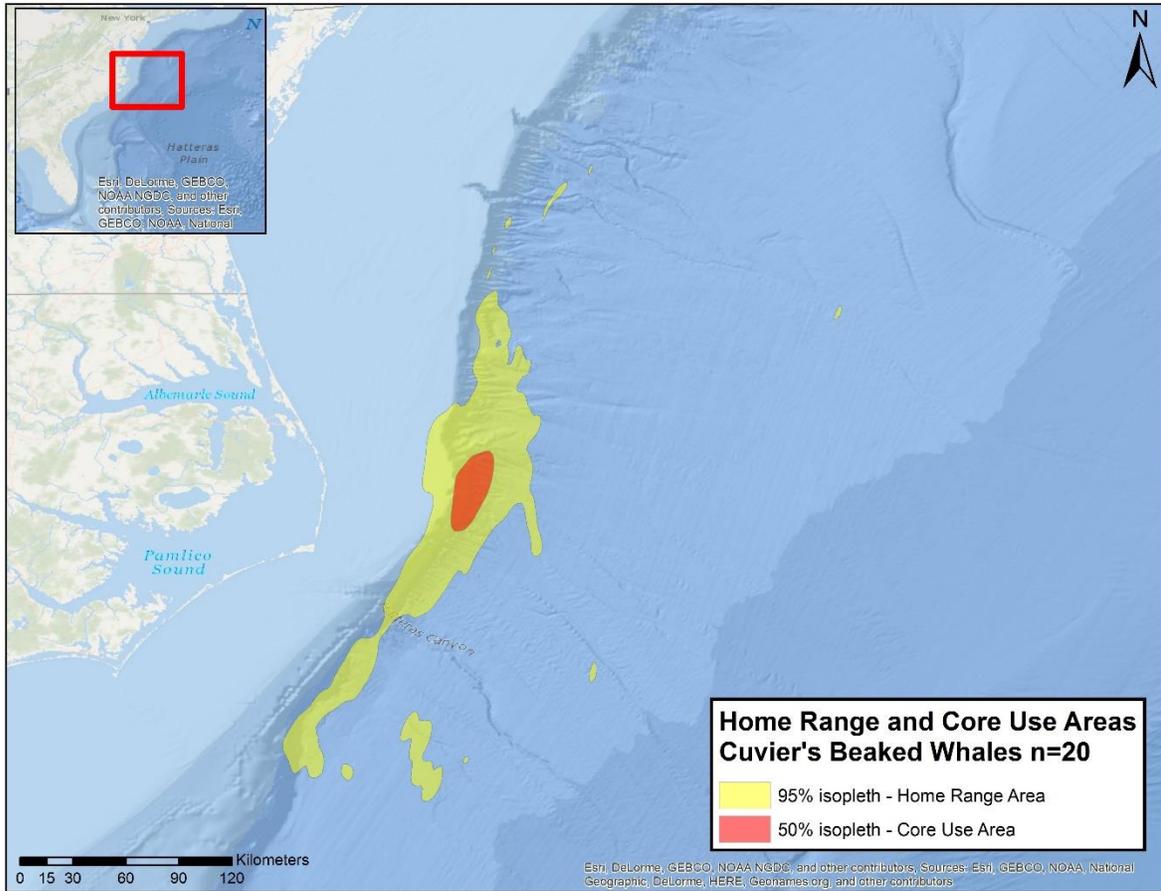


Figure 2.4. Map of home range area (yellow) and core use area (red) for satellite-tagged Cuvier's beaked whales (n=20) generated from kernel density estimation.

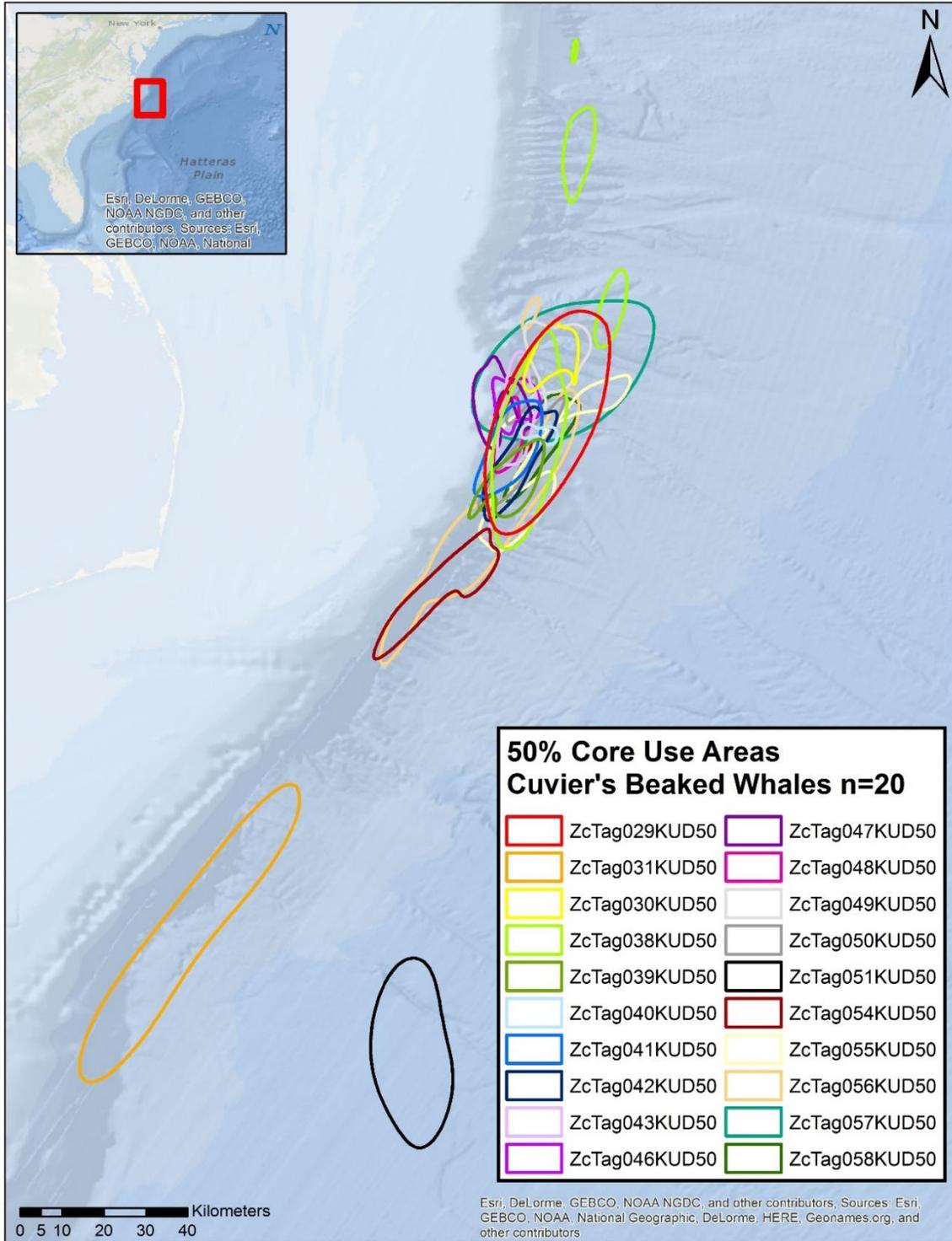


Figure 2.5. Map of individual Cuvier's beaked whales core use areas (n=20).

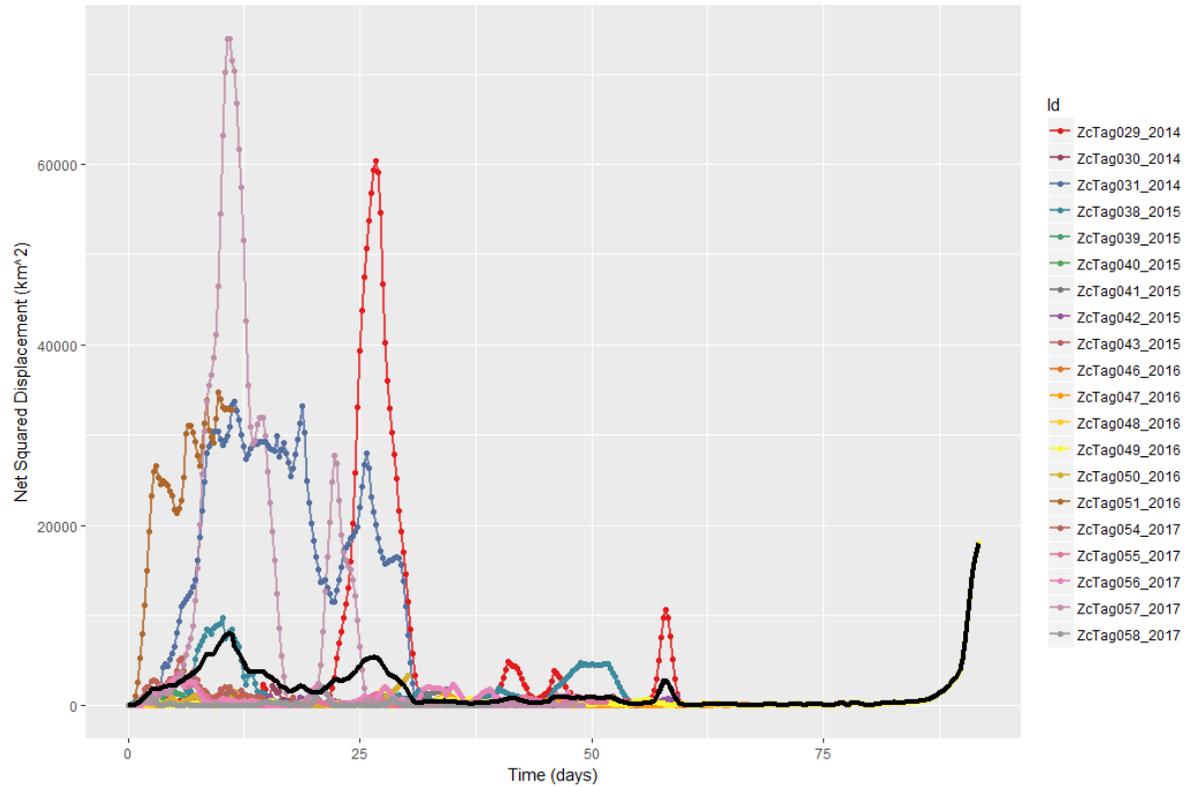


Figure 2.6. Net squared displacement (km<sup>2</sup>) over tag duration for satellite-tagged Cuvier's beaked whales (n=20). Population mean line represented by solid black line. Highest peak represents the maximum displacement, where values close to zero represent a return to an individual's initial location.

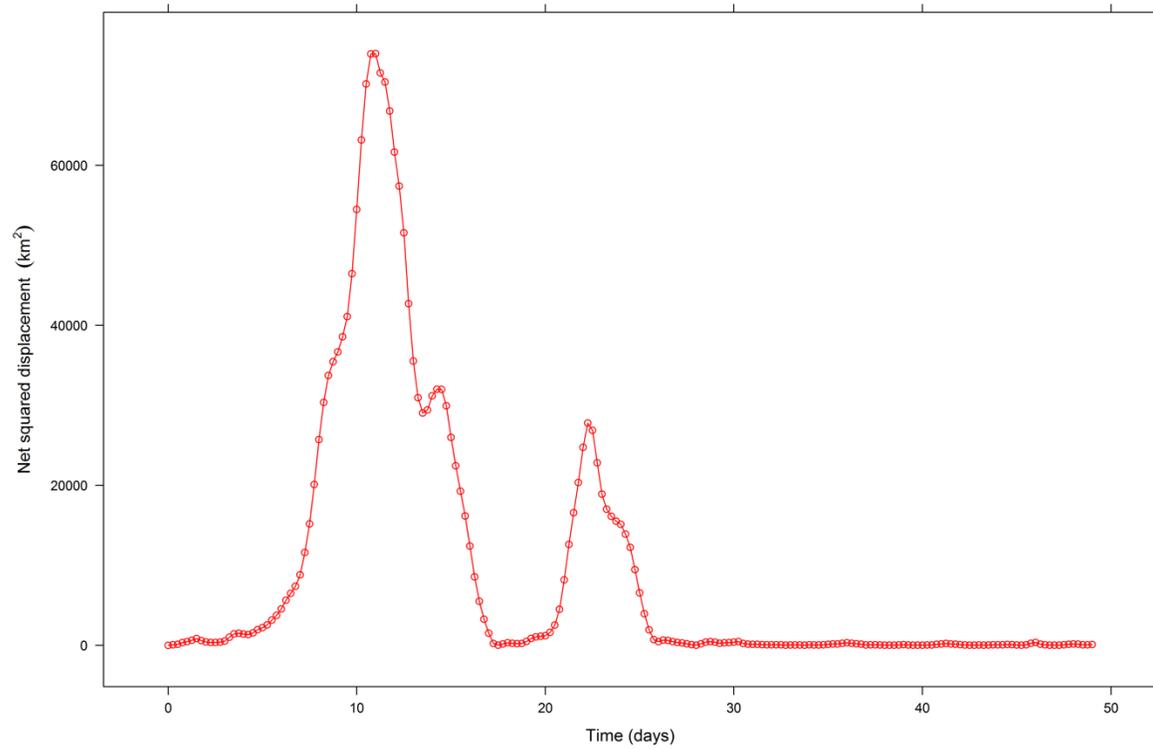


Figure 2.7. Net squared displacement (km<sup>2</sup>) over tag duration for ZcTag057. Highest peak represents the maximum displacement, where values close to zero represent a return to its initial location.

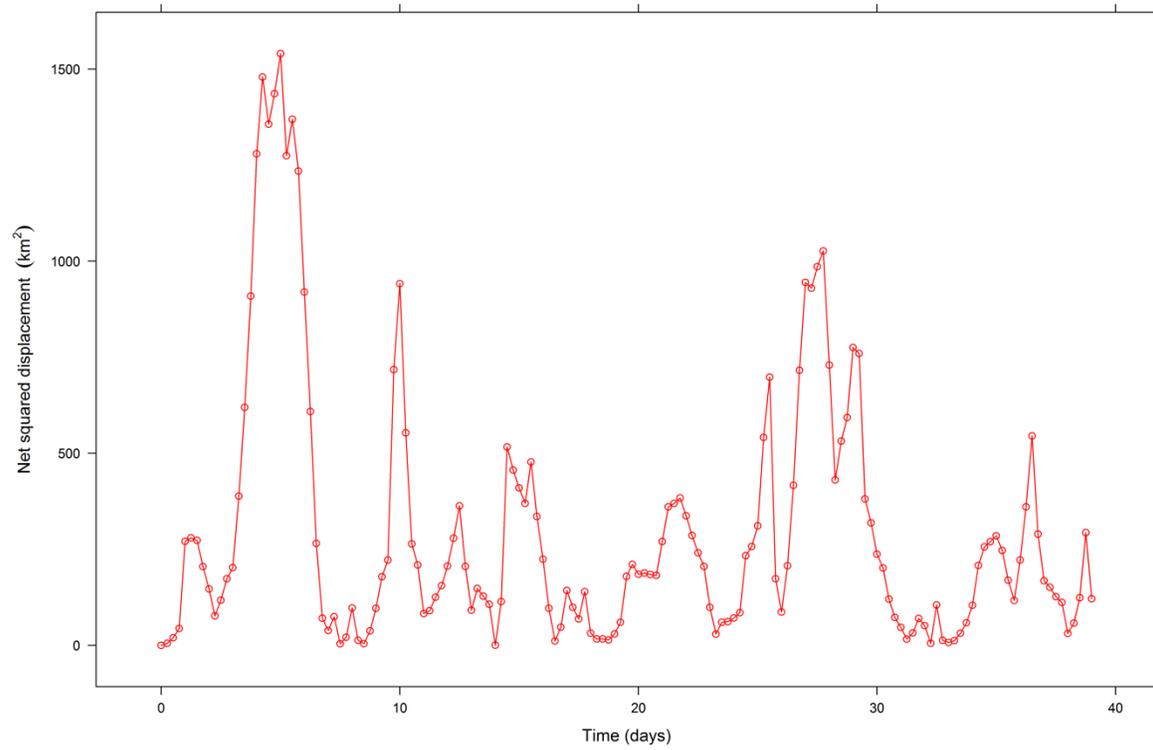


Figure 2.8. Net squared displacement (km<sup>2</sup>) over tag duration for ZcTag039. Highest peak represents the maximum displacement, where values close to zero represent a return to its initial location

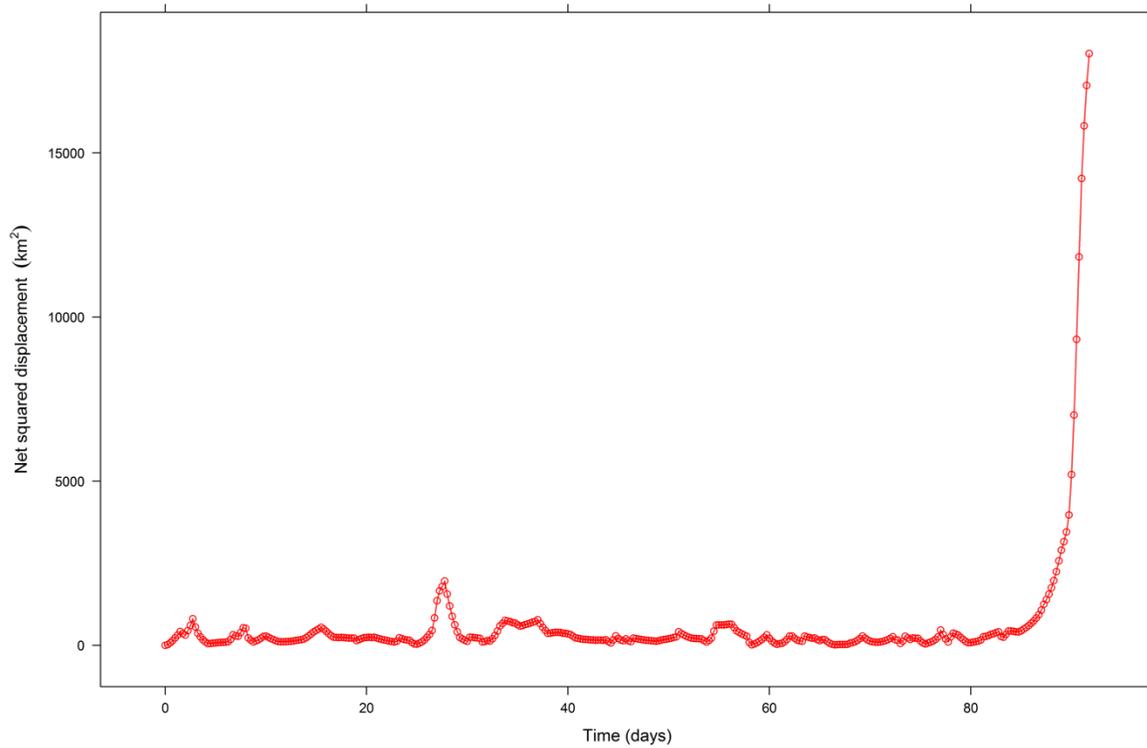


Figure 2.9. Net squared displacement (km<sup>2</sup>) over tag duration for ZcTag049. Highest peak represents the maximum displacement, where values close to zero represent a return to its initial location.

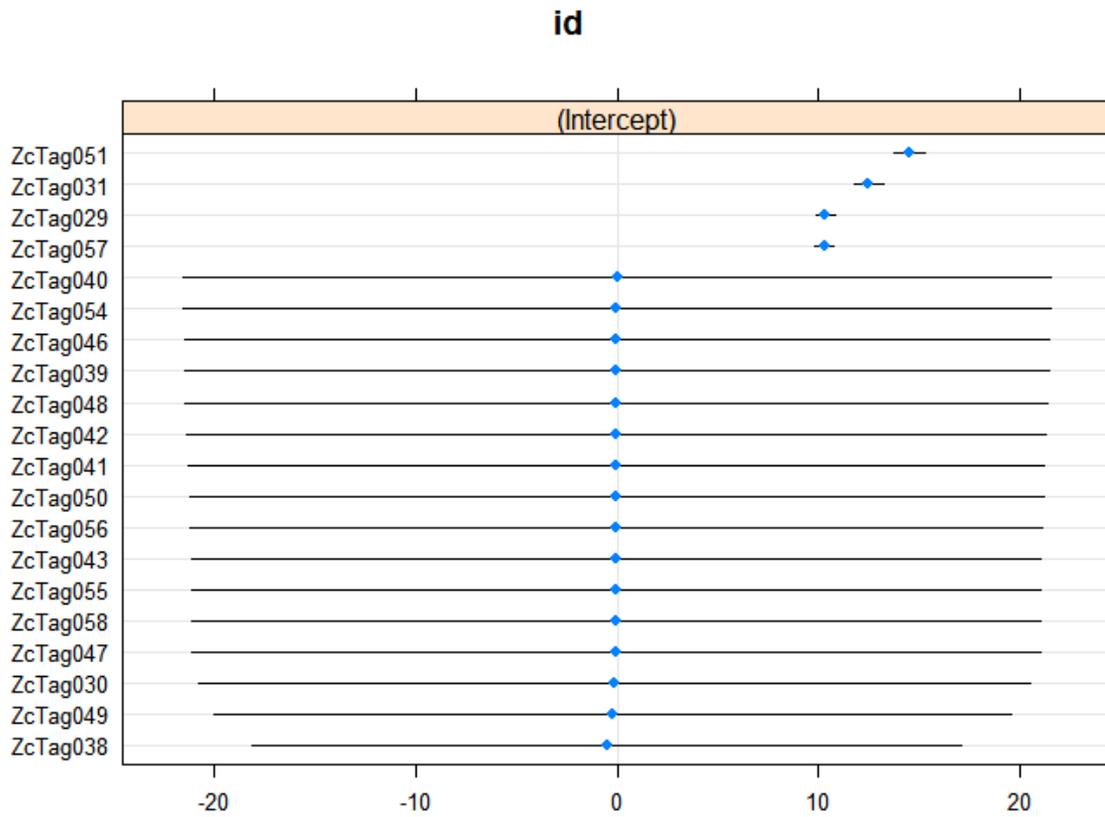


Figure 2.10. Intercepts and standard errors for the random effect of individual Cuvier's beaked whale.

## CONCLUSIONS

The analysis of movement data is one of a limited number of methodologies allowing inference on the complex social and biological processes driving animal behavior (Gurarie et al. 2016). In particular, the behavior of deep-diving, pelagic marine predators is difficult to study given the three-dimensional, patchy nature of the marine environment, the small amount of time animals spend at the water's surface, and the complex social structure of many such species (Redfern et al. 2006). In this work, satellite telemetry, which is a particularly advantageous method to study animals who inhabit remote, inaccessible areas (Kennedy, Zerbini, Rone, et al. 2014) allowed for the discovery of basic knowledge on the movement and behavioral ecology of deep-diving odontocetes in the western North Atlantic. Latitudinal ranges, habitat preferences, home ranges, residency patterns, and the environmental influences driving the spatiotemporal distributions and behavior of both short-finned pilot whales and Cuvier's beaked whales were estimated, our understanding of which was heretofore limited. This study represents one of the largest sample sizes of satellite telemetry tags deployed on these species anywhere in the world, and the first of such efforts on free-ranging animals in the western North Atlantic.

In chapter 1, an hSSSM performed well for the short-finned pilot whale data set, distinguishing between area-restricted search and transit behavior. ARS was found to occur more often than transit in the species (63% of locations), particularly in locations close to the continental shelf break. Kernel density estimation revealed the majority of individual core use areas to be concentrated in the Cape Hatteras study site or along the continental shelf break, which may be attributed to individual prey preferences or foraging strategies, as well

as other intrinsic factors such as size, sex, or experience. Habitat selection and distribution of behaviors varied between tagging sites, with animals tagged offshore of Jacksonville, Florida exhibiting more transit behavior in deeper depths further from the shelf break, which could also be explained by specialized foraging strategies based on location. Generalized linear mixed models accounting for random variation between both individual whales and tagging site found the most significant drivers of short-finned pilot whale transit behavior to be bathymetric slope and distance to shelf break, with increased likelihood of transit at locations of low slope and increased distance from the continental shelf, findings consistent with previous studies. Despite the substantial individual variability in displacement from and periodicity of return to the Cape Hatteras area, short-finned pilot whales do show some degree of philopatry to the Cape Hatteras study area, confirmed by long-term photo-identification studies. This work can better inform effective conservation and management of this species vulnerable to interactions with the U.S. Atlantic longline fishery.

Results from Chapter 2 found Cuvier's beaked whales to be resident to the Cape Hatteras slope waters, with small, overlapping core use areas and low displacement from the tagging site. Nearly all movements (94%) were classified as foraging, with many individuals never exhibiting transit behavior throughout the study. Variability in the behavior of Cuvier's beaked whales was best described by two predictor variables, with more transit observed at higher latitudes and increased distance from the shelf break. As the dynamic marine environment changes, continuing to increase in anthropogenic disturbances, including ocean noise and climate change, resident populations such as the Cuvier's beaked whales offshore of Cape Hatteras may not have the ability to relocate or shift their distributions accordingly.

As such, the results from this study can better inform future conservation and management of this species particularly sensitive to acoustic disturbances

Although both species presented in this thesis are highly mobile, sharing wide distributions spanning many oceans basins and prefer deep-water habitats, such as the continental shelf and slope waters and associated areas of high relief, this work demonstrates the species to use the Cape Hatteras area and associated habitats differently. Cuvier's beaked whales belong to a resident population, while short-finned pilot whales demonstrate long-distance movements throughout the western North Atlantic, in addition to some degree of site fidelity for the Cape Hatteras area. This pattern was consistent through several analyses conducted, such as home range estimation, as the population-level core use area for short-finned pilot whales was ten times as large as that for the resident Cuvier's beaked whale population. Ecological theory suggests that co-occurring species limit competition by occupying different locations or prey preferences (Hauser et al. 2014). Habitat partitioning and/or unique foraging strategies may be occurring between the species, with short-finned pilot whale targeting the continental shelf edge, and Cuvier's beaked whales occupying deeper, slope waters. Prolonged residency in specific areas should be associated with higher resources (Scales, Schorr, et al. 2017), and although both species may target similar prey, it may be possible that short-finned pilot whales have a broader foraging niche than Cuvier's beaked whales. Short-finned pilot whales may be capable of locating and capturing prey in a variety of shelf, slope, and pelagic habitats, while Cuvier's beaked whales may be more localized in their movement patterns due to predictable levels of specific prey species in the Cape Hatteras region. However, little is known about the diets or prey preferences of either

species in the western North Atlantic (MacLeod et al. 2003; Mintzer et al. 2008), and additional study would greatly aid future work.

Through this study, vital knowledge of the spatial use, movement patterns, habitat preferences and behavior of short-finned pilot whales and Cuvier's beaked whales in the western North Atlantic was acquired. Despite relatively short tag durations for each species, useful population-level inferences were generated, which can help to inform management and conservation measures. Ideally, the results of this medium-term movement and spatial use pattern study can be combined with data from fine-scale behavioral digital acoustic tags, as well as the long-term residency patterns generated from photo-identification methods that have been observed for both species in the region. Amalgamating over several temporal scales will help to ultimately define what is driving the animals to return to the area and work to protect the long-term viability of both species.

Additionally, future work could be focused on directly predicting how disturbances will affect cetacean populations. How would an individual short-finned pilot whale or Cuvier's beaked whale respond to a potential disturbance such as anthropogenic noise? Will they shift their home range area away from the disturbance? Will they forage less? Will they demonstrate more transit behavior? Work involving scenario planning could help better mitigate potential disturbances.

As the world's oceans change due to anthropogenic effects, cetaceans are likely to modify their distributions over both space and time as a response to potential disturbances, particularly MFA sonar (Gomez et al. 2016). Possessing a full understanding of the drivers of cetacean space use, both individual and environmental, outside of any specific disturbance,

will better allow us to predict and mitigate any behavioral changes, distribution shifts, or other potential detrimental effects to exposure threats in the future. Population and species-level extrapolations can also be useful in cross-species and regional comparisons and predictions, helping to generate measures to protect all marine mammals from exposure risks, aiding in the long-term conservation of populations worldwide.

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## APPENDICES

**Appendix A.** Concordance criterion values for potential movement models for each individual short-finned pilot whale.

id	CC1.HRA	CC1.HRB	CC1.Disp1	CC1.Disp2	CC1.Disp3	CC1.nomadA	CC1.nomadB	CC1.nomadC	CC1.nomadD	CC1.Null	CC1.Migr1	CC1.Migr2	best.CC1ID
GmTag085	0.004	0.006	0.004	0.049	0.004	0.003	0.000	0.004	0.002	0	1.11E-16	0	Dispmod2
GmTag086	0.182	0.180	0.181	0.233	0.771	0.415	0.132	0.780	0.045	0	4.44E-15	0	NomadC
GmTag087	0.380	0.515	0.391	0.893	0.647	0.629	0.289	0.402	0.154	0	-2.84E-14	0	Dispmod2
GmTag088	0.412	0.487	0.460	0.751	0.763	0.497	0.052	0.028	0.115	-2.22E-16	-2.80E-14	0	Dispmod3
GmTag090	0.345	0.381	0.394	0.632	0.768	0.562	0.333	0.379	0.093	0	-1.93E-14	0	Dispmod3
GmTag092	0.482	0.552	0.608	0.816	0.670	0.642	0.427	0.042	0.114	2.22E-16	-2.49E-14	0	Dispmod2
GmTag093	-0.086	-0.083	-0.173	-0.177	-0.101	-0.102	-0.007	0.000	0.003	1.11E-16	1.67E-15	0	NomadD
GmTag094	0.374	0.576	0.366	0.944	0.944	0.741	0.508	0.851	0.176	0	-2.40E-14	0	Dispmod2
GmTag095	0.355	0.430	0.375	0.564	0.815	0.634	0.411	0.796	0.112	2.22E-16	-1.38E-14	0	Dispmod3
GmTag097	0.060	0.108	0.080	0.159	0.046	0.037	0.002	0.490	0.008	0	-1.33E-15	0	NomadC
GmTag098	0.212	0.177	0.013	-0.112	-0.027	0.104	0.065	-0.002	0.062	0	-7.55E-15	0	HRmodA
GmTag099	0.183	0.164	0.203	0.224	0.296	0.287	0.021	0.287	0.042	-2.22E-16	1.03E-14	0	Dispmod3
GmTag100	0.403	0.353	0.201	-0.036	0.136	0.320	0.128	0.000	0.099	0	-2.15E-14	0	HRmodA
GmTag101	-0.054	-0.043	-0.164	-0.111	-0.201	-0.153	-0.016	-0.008	0.010	0	1.19E-14	0	NomadD
GmTag102	0.417	0.448	0.414	0.036	0.176	0.505	0.117	0.000	0.265	0	-4.00E-15	0	NomadA
GmTag103	0.007	0.006	-0.019	-0.028	0.431	0.058	0.001	0.130	0.012	0	2.44E-15	0	Dispmod3
GmTag122	0.142	0.139	0.185	0.281	0.175	0.205	0.093	0.040	0.025	0	-4.00E-15	0	Dispmod2
GmTag123	0.180	0.172	0.028	-0.024	0.029	0.141	0.066	0.000	0.124	2.22E-16	-2.00E-15	0	HRmodA
GmTag124	-0.112	-0.091	-0.119	-0.066	-0.087	-0.116	-0.127	-0.115	-0.006	0	4.00E-15	0	Migrmod1
GmTag125	0.162	0.151	0.204	0.265	0.479	0.229	0.034	0.377	0.024	0	1.14E-14	0	Dispmod3
GmTag126	0.615	0.676	0.769	0.894	0.668	0.723	0.384	0.007	0.170	0	-2.86E-14	0	Dispmod2
GmTag127	0.294	0.255	0.271	0.184	0.126	0.277	0.066	-0.002	0.096	-2.22E-16	-1.78E-14	0	HRmodA
GmTag128	0.153	0.128	0.198	0.258	0.129	0.181	0.022	0.006	0.058	0	-1.35E-14	0	Dispmod2
GmTag129	0.754	0.769	0.593	0.014	0.154	0.719	0.387	0.000	0.202	0	-1.11E-14	0	HRmodB
GmTag130	0.658	0.649	0.654	0.715	0.511	0.557	0.595	0.233	0.082	0	-2.22E-14	0	Dispmod2
GmTag131	0.695	0.689	0.755	0.771	0.750	0.516	0.026	0.068	0.225	0	-3.35E-14	0	Dispmod2
GmTag134	-0.083	-0.062	-0.085	-0.059	-0.170	-0.117	-0.017	-0.171	-0.014	1.11E-16	-6.22E-15	0	NullMod
GmTag135	-0.127	-0.091	-0.143	-0.087	-0.153	-0.190	-0.024	-0.004	-0.039	-2.22E-16	1.17E-14	0	Migrmod1
GmTag136	-0.017	-0.014	-0.016	-0.013	-0.063	-0.056	-0.003	-0.060	0.004	0	-6.00E-15	0	NomadD
GmTag137	-0.067	-0.059	-0.085	-0.088	0.034	-0.029	-0.023	0.046	-0.004	0	-4.44E-16	0	NomadC
GmTag138	0.210	0.212	0.340	0.375	0.266	0.265	0.229	0.000	0.028	1.11E-16	-2.11E-14	0	Dispmod2

Appendix A (continued).

id	CC1.HRA	CC1.HRB	CC1.Disp1	CC1.Disp2	CC1.Disp3	CC1.nomadA	CC1.nomadB	CC1.nomadC	CC1.nomadD	CC1.Null	CC1.Migr1	CC1.Migr2	best.CC1ID
GmTag139	0.008	0.062	0.000	0.145	-0.037	-0.068	-0.009	-0.035	-0.008	-2.22E-16	4.77E-15	0	Dispmod2
GmTag141	-0.239	-0.182	-0.244	-0.146	-0.222	-0.294	-0.072	-0.003	-0.043	0	2.84E-14	0	Migrmod1
GmTag142	0.024	0.024	0.008	0.010	0.822	0.131	0.022	0.549	0.007	1.11E-16	1.17E-14	0	Dispmod3
GmTag157	0.356	0.434	0.367	0.556	0.344	0.433	0.401	0.133	0.077	-2.22E-16	-9.55E-15	0	Dispmod2
GmTag158	0.176	0.167	0.222	0.291	0.048	0.163	0.067	-0.003	0.022	0	2.66E-15	0	Dispmod2
GmTag159	-0.040	0.018	-0.120	0.103	-0.050	-0.074	-0.011	0.000	-0.003	0	3.66E-15	0	Dispmod2
GmTag160	0.046	0.044	0.057	0.076	-0.001	-0.013	0.007	-0.143	0.003	1.11E-16	-2.22E-15	0	Dispmod2
GmTag161	0.192	0.164	0.312	0.788	0.217	0.286	0.075	0.003	0.074	-2.22E-16	-1.33E-14	0	Dispmod2
GmTag162	-0.014	-0.012	-0.011	0.046	-0.076	-0.045	-0.007	-0.005	0.005	2.22E-16	3.33E-15	0	Dispmod2
GmTag163	0.138	0.119	0.191	0.206	0.168	0.176	0.056	0.001	0.031	0	-1.55E-14	0	Dispmod2
GmTag164	0.199	0.176	0.187	0.289	-0.031	0.087	0.082	-0.016	0.027	0	-5.11E-15	0	Dispmod2
GmTag165	0.542	0.540	0.546	0.459	0.203	0.549	0.359	0.000	0.109	-2.22E-16	-2.13E-14	0	NomadA
GmTag172	0.513	0.479	0.630	0.702	0.532	0.584	0.084	0.009	0.166	-2.22E-16	-4.24E-14	0	Dispmod2
GmTag173	0.770	0.753	0.828	0.607	0.606	0.809	0.212	0.001	0.187	0	-5.06E-14	0	Dispmod1
GmTag174	-0.093	-0.089	-0.056	-0.001	-0.055	-0.061	-0.004	-0.010	-0.011	0	2.11E-15	0	Migrmod1
GmTag175	0.782	0.769	0.867	0.733	0.626	0.838	0.216	0.002	0.214	0	-5.13E-14	0	Dispmod1
GmTag176	0.455	0.479	0.524	0.170	0.226	0.500	0.119	0.000	0.226	0	-8.44E-15	0	Dispmod1
GmTag177	0.141	0.121	0.046	0.063	0.096	0.115	0.021	0.002	0.110	0	-7.33E-15	0	HRmodA
GmTag178	-0.231	-0.188	-0.237	-0.074	-0.125	-0.214	-0.233	0.000	-0.014	0	1.45E-14	0	Migrmod1
GmTag180	-0.263	-0.206	-0.250	-0.084	-0.156	-0.251	-0.293	0.000	-0.020	0	1.74E-14	0	Migrmod1
GmTag181	0.395	0.433	0.600	0.930	0.914	0.523	0.112	0.001	0.205	0	-1.38E-14	0	Dispmod2
GmTag183	0.372	0.419	0.496	0.861	0.898	0.490	0.165	0.002	0.143	1.11E-16	-1.55E-14	0	Dispmod3

**Appendix B.** Akaike Information Criterion (AIC) values for potential movement models for each individual Cuvier's beaked whale.

ID_YEAR	Locations	Migratory	Mixed Migratory	Dispersal	Home Range/ Resident	Nomadic
ZcTag029_2014	240	0	0	0	5201.544878	5212.620799
ZcTag030_2014	156	0	0	0	2237.659269	2258.959198
ZcTag031_2014	130	0	0	0	2785.130032	2837.161
ZcTag038_2015	223	0	0	0	4096.012992	4131.913563
ZcTag039_2015	157	0	0	0	2280.889412	2326.695956
ZcTag040_2015	8					
ZcTag041_2015	138	0	0	0	2039.792301	1997.286205
ZcTag042_2015	238	0	0	0	3185.488036	3230.140815
ZcTag043_2015	228	0	0	0	3342.814226	3389.686977
ZcTag046_2016	61					
ZcTag047_2016	268	0	0	0	3648.873489	3663.213268
ZcTag048_2016	146	0	0	0	1814.218309	1825.174226
ZcTag049_2016	368	0	0	0	6612.70581	6585.557419
ZcTag050_2016	122	0	0	0	1925.798505	1922.837635
ZcTag051_2016	46					
ZcTag054_2017	72					
ZcTag055_2017	207	0	0	0	3301.017401	3361.069189
ZcTag056_2017	191	0	0	0	3096.916051	3163.608048
ZcTag057_2017	197	0	0	0	4407.675333	4447.83487
ZcTag058_2017	157	0	0	0	2290.114623	2312.00571