Ecology of Beaked Whales and Sperm Whales in the Western North Atlantic Ocean: Insights from Passive Acoustic Monitoring

by

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University Program in Ecology
Duke University

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Dissertation submitted in partial fulfillment of
the requirements for the degree of
Doctor of Philosophy in the University Program in Ecology
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ABSTRACT

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Abstract

Beaked whales (family Ziphiidae) and sperm whales (*Physeter macrocephalus*) are apex marine predators found throughout the world's deep oceans. These species are challenging to observe, and little is known about fundamental aspects of their ecology, including their spatiotemporal distributions and habitat use. Passive acoustic monitoring (PAM), can be used to detect their echolocation clicks during foraging dives, thereby providing an indication of species presence. My dissertation investigates the distribution, seasonal occurrence, and diel variability in acoustic detections of beaked whales and sperm whales in the western North Atlantic Ocean, using multi-year passive acoustic recordings collected along the continental slope between Florida and Nova Scotia. First, I describe spatiotemporal patterns in detections of beaked whale echolocation clicks from five beaked whale species and one signal type of unknown origin. At least two beaked whale click types were detected at each recording site, and detections occurred year-round, with site-specific variation in relative species occurrence. Notably, Cuvier's beaked whales (*Ziphius cavirostris*) were regularly detected in a region where they have not been commonly observed, and potential habitat partitioning among Cuvier's and Gervais' (*Mesoplodon europaeus*) beaked whales was apparent within their overlapping ranges. To examine the potential effects of using duty-cycled recording schedules on the detection of beaked whale clicks, I performed a subsampling experiment, and found that short, frequent listening periods were most effective for assessing daily presence of beaked whales. Furthermore, subsampling at low duty cycles led to consistently greater underestimation of *Mesoplodon* species than either Cuvier’s beaked whales or northern bottlenose whales (*Hyperoodon ampullatus*), leading to a potential bias in estimation of relative species occurrence. Next, I examine the occurrence of sperm whale echolocation clicks, which were recorded commonly between southern New England and North Carolina, but infrequently off the coast of Florida. In the northern half of the study region, I observed distinct seasonal patterns in the daily prevalence of sperm whale clicks, with a winter peak in occurrence off Cape Hatteras, North Carolina, followed by an increase later in the spring at sites further north, suggesting a shift in sperm whale concentrations which may relate to enhanced productivity occurring at higher latitudes in the spring. Finally, I explore the variability in daily detection rates of beaked whales and sperm whales in relation to dynamic oceanographic conditions off the Mid-Atlantic coast. Detection rates did not appear to correlate with temporal environmental variability, and persistent habitat features may be more important in predicting the occurrence of these species. Together, my dissertation provides substantial baseline information on the spatiotemporal occurrence of beaked and sperm whales in the western North Atlantic Ocean, highlighting the diversity within this guild of deep-diving odontocetes and demonstrating the use of PAM to provide species-specific insight into their ecology.

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General Introduction

Using passive acoustic monitoring to study cetacean ecology

Cetaceans use acoustic signals for communication, foraging, and spatial orientation, exploiting the efficient transmission of sound underwater to interact with their environment. Passive acoustic monitoring (PAM) can be used to detect, identify, and track species occurrence, by placing sensors underwater to listen for the sounds these animals produce. PAM may be conducted using a variety of different methods, including towed hydrophone arrays (e.g., Leaper et al. 2000, Barlow and Taylor 2005), autonomous gliders (e.g., Klinck et al. 2012, Baumgartner et al. 2013), bottom-mounted archival instruments (Mellinger et al. 2007, Sousa-Lima et al. 2013), and cabled seafloor arrays (e.g., Stafford et al. 1998). These different applications provide opportunities to assess the occurrence of cetacean species across multiple spatial and temporal scales (Van Parijs et al. 2009). A significant benefit of PAM is the ability to operate independently of daylight and weather conditions, as well as in regions that are remote or inhospitable to researchers (Van Opzeeland et al. 2013). Studies utilizing PAM for a variety of cetacean taxa have repeatedly revealed higher levels of occurrence than estimated from visual observations, demonstrating the value of listening underwater for animals that spend most of their lives submerged (e.g., Verfuß et al. 2007, Rayment et al. 2011, Yack et al. 2013, Baumann-Pickering et al. 2014).

Passive acoustic monitoring has some inherent limitations, particularly the requirement that, in order to be detected, animals be actively producing sounds. The ability to detect the presence of a species depends to a large degree on the species' acoustic behavior and vocal rates; highly vocal species are more easily detected than those that call infrequently. The spatial extent monitored is determined by the configuration of sensors and the range at which calls can be detected. Detection ranges are influenced by sound propagation conditions and the acoustic characteristics of calls, and vary widely from 100s of kilometers for loud, low-frequency baleen whale song (e.g., Stafford et al. 1998) to 100s of meters or less for high-frequency echolocation clicks (e.g., DeRuiter et al. 2010). The ability to identify calls using acoustic recordings collected without associated visual observations depends on the taxonomic group: some call types can be classified to species, including many baleen whale calls (e.g., Payne and McVay 1971, Clark 1982, Watkins et al. 1987, Parks and Tyack 2005, Rankin and Barlow 2005, Baumgartner et al. 2008) and some odontocete echolocation signals (e.g., Backus and Schevill 1966, Schevill et al. 1969, Soldevilla et al. 2008, Baumann-Pickering et al. 2013). Other call types remain difficult to identify below the family or genus level, such as many delphinid whistles (Oswald et al. 2003). Even for species with distinctive calls and well-known acoustic repertoires, PAM typically does not provide information on the sex, age, or number of individuals present (with some exceptions, e.g., Marques et al. 2009).

Despite these limitations, PAM can be used to obtain information on species occurrence that complements data from other sources, such as visual surveys (Brookes et al. 2013, Thompson et al. 2014). Visual shipboard and aerial surveys provide a snapshot of species occurrence across the survey area, while long-term PAM using fixed, bottom-mounted sensors allows data to be collected on species occurrence at high temporal resolutions over long periods of time. Furthermore, these data can be obtained at lower cost than visual surveys that require extended periods of ship time (Mellinger et al. 2007). This approach is particularly useful for assessing broad-scale movements and seasonal distribution patterns of wide-ranging or migratory species (e.g., Samaran et al. 2013, Risch et al. 2014), and for describing the year-round presence and relative occurrence of species within specific regions of interest (e.g., Soldevilla et al. 2010, Morano et al. 2012). For deep-diving and cryptic cetacean species that live far offshore and are rarely visible at the surface, PAM offers a unique means of addressing existing gaps in knowledge regarding their spatial distribution, seasonal occurrence, and habitat preferences, which is the focus of this dissertation.

Ecology and acoustic behavior of study species

Beaked Whales

Beaked whales are odontocete cetaceans belonging to the family Ziphiidae, which includes at least 22 species, representing nearly a quarter of all cetacean species

(Committee on Taxonomy 2016). This family is one of the most poorly known mammalian taxa, and at least three new beaked whale species have been recognized in the past two decades, underscoring how much we have yet to learn about this cryptic group of mammals (Dalebout et al. 2002, 2014, van Helden et al. 2002).

Beaked whales are widely distributed in both hemispheres, in the deep waters of all ocean basins (MacLeod et al. 2006). Past efforts to assess habitat preferences of beaked whales have suggested that these species are often associated with topographic features such as canyons (Hooker et al. 1999, Wimmer and Whitehead 2004), seamounts (Johnston et al. 2008, McDonald et al. 2009), and continental slopes (Waring et al. 2001, MacLeod and Zuur 2005, Moulins et al. 2007). Broad-scale surveys in the eastern tropical Pacific revealed that beaked whales also inhabit regions over the abyssal plains, but the extent to which they utilize this deep ocean habitat remains largely unknown (Ferguson et al. 2006).

Most information on the diet of beaked whales comes from analyses of the stomach contents of stranded beaked whales, which indicate that they consume a variety of deep-sea prey, primarily cephalopods and fish that live close to the seafloor (MacLeod et al. 2003). There are few detailed descriptions of diving and foraging behavior for most beaked whale species, but studies involving the deployment of multi-sensor animal-borne tags on Cuvier's (*Ziphius cavirostris*) and Blainville's (*Mesoplodon densirostris*) beaked whales have revealed extraordinary diving capabilities (Tyack et al. 2006b).

Individuals of these species typically perform a single long, deep foraging dive to more than 800 m in depth, followed by a series of shallow dives to depths less than 400 m (Baird et al. 2006, Tyack et al. 2006b). These deep foraging dives can last up to two hours in duration, and surface intervals may be as short as a few minutes (Schorr et al. 2014). Similar deep-diving behavior has been observed in northern bottlenose whales (*Hyperoodon ampullatus*) (Hooker and Baird 1999), and is likely to be characteristic of most or all beaked whale species.

The acoustic repertoires of most beaked whale species are not well described, but appear to consist primarily of echolocation signals. Beaked whales produce consistent echolocation clicks throughout the foraging portion of their deep dives (Johnson et al. 2004, Madsen et al. 2005, Tyack et al. 2006a). Clicks produced at regular intervals are interspersed with series of rapid pulses, termed "buzzes", which are believed to represent prey capture attempts (Johnson et al. 2004). Beaked whale echolocation clicks can be distinguished from clicks produced by other odontocetes by their longer pulse duration, longer inter-click-interval, and narrower frequency bandwidth, as well as characteristic frequency upsweeps (Baumann-Pickering et al. 2013). In addition to sharing these common characteristics that differ from the clicks produced by other odontocetes, beaked whale clicks also exhibit species-specific spectral and temporal characteristics, allowing click types to be classified to species in many cases (Baumann-Pickering et al. 2013).

Six beaked whale species inhabit the North Atlantic Ocean: the northern bottlenose whale, Cuvier's beaked whale, Sowerby's beaked whale (*M. bidens*), Blainville's beaked whale, Gervais' beaked whale (*M. europaeus*), and True's beaked whale (*M. mirus*). Very little is known about the abundance of these species, and information on population size is available only for Cuvier's beaked whales and an isolated population of northern bottlenose whales inhabiting the Gully, an undersea canyon along the Scotian Shelf. Cetacean abundance surveys conducted along the continental margin of the United States yielded an estimate of the abundance of Cuvier's beaked whales of 6,532 (CV=0.32) (Waring et al. 2014). However, this estimate has not been corrected for availability bias, the time that whales are unavailable to be sighted at the surface during dives, and thus is negatively biased to a signficant degree (Barlow 2015). The Scotian Shelf population of northern bottlenose whales in the Gully is estimated to contain 163 individuals (95% CI 119-214) (Fisheries and Oceans Canada 2016). No abundance estimates are available for Blainville's, Gervais', True's, and Sowerby's beaked whales, and virtually nothing is known about the population structure of any of these beaked whale species.

Sperm Whales

The sperm whale is the largest odontocete, and is found throughout the world's oceans from the equator to the polar ice edges (Rice 1989a). Globally, sperm whales once numbered over one million individuals, but sustained commercial whaling occurring from the 18th to mid-20th centuries reduced their numbers to approximately 360,000 (Whitehead 2002). Despite this reduction in abundance, sperm whales remain an ecologically important marine predator, occupying a relatively unique niche, and consuming as much as 100 megatons of biomass annually (Whitehead 2003).

Sperm whales are highly social animals, living in complex, multi-level societies (Whitehead 2003). Females form stable, matrilineal social units comprised of closely-related adult females and their calves (Whitehead et al. 1991). Males generally depart from their natal groups between the ages of 3 and 15 to form loose associations with other young males (Whitehead 2003). As they approach maturity, males become more solitary and geographically separated from female groups, roaming to higher latitudes to forage and periodically returning to tropical and sub-tropical regions to search for mates (Perry et al. 1999). Females are generally found in tropical to temperate waters year round. Sperm whales are highly sexually dimorphic, with adult females reaching lengths of 11 m and weighing up to 15 tons, in contrast to mature males, which may reach more than 15 m long and weigh up to 45 tons (Whitehead 2003).

Both male and female sperm whales perform deep dives to forage on meso- and bathypelagic cephalopods and some fish (Kawakami 1980). The composition of sperm whale diets varies by region, and they are known to consume a diverse array of cephalopod species belonging to least 17 different families, with a large portion of their diet consisting of medium to large squids with mantle lengths of 0.2 m to more than 1.0 m (Kawakami 1980, Rice 1989a, Whitehead 2003). The typical diving behavior of foraging sperm whales consists of 30-50 minute dives followed by 7-10 minute surface intervals (Papastavrou et al. 1989, Jaquet et al. 2000, Amano and Yoshioka 2003, Watwood et al. 2006). Average maximum dive depths are generally between 400 and 900 m and vary by region; some dives exceeding 1000 m in depth have also been reported (Watwood et al. 2006). Sperm whales are estimated to spend more than 60% of their lifetime at depth (Whitehead 2003).

Acoustic signals are an essential component of the foraging success of sperm whales. Their enormous nasal complex functions as a powerful biosonar system, and the impulsive, broadband echolocation clicks emitted by sperm whales have the highest recorded source levels of any biological sound (Backus and Schevill 1966, Norris and Harvey 1972, Møhl et al. 2000, Madsen et al. 2002a, Watwood et al. 2006). Echolocation clicks are regularly produced by both males and females throughout foraging dives at depths greater than approximately 200 m (Watwood et al. 2006). In addition to regular echolocation clicks, sperm whales produce several other click types including creaks, codas, and slow clicks (Watkins and Schevill 1977, Weilgart and Whitehead 1988, Jaquet et al. 2001, Miller et al. 2004). These click types differ in their acoustic characteristics including frequency range, energy content, duration, and inter-click-interval, as well as in behavioral context. The acoustic behavior of sperm whales provides a convenient window into their behavior and ecology, and has contributed significantly to our understanding of the species.

Study region: Western North Atlantic Ocean

The geographic scope of my study encompasses the continental slope off the east coast of North America, spanning latitudes from approximately 30° N off the coast of Florida to nearly 44° N along the edge of the Scotian Shelf. The continental shelf edge and slope in this region is an important habitat for beaked whales and sperm whales (Waring et al. 2001, Roberts et al. 2016a). Male sperm whales sometimes venture onto the continental shelf (Whitehead et al. 1992, Scott and Sadove 1997), but females and juveniles are typically encountered only in deeper waters. Beaked whales are restricted entirely to waters greater than 500 m depth. The distribution of these species in pelagic waters over the abyssal plain is largely unknown, as very little visual survey effort is routinely conducted beyond the shelf break and slope. Some beaked whales forage at or near the seafloor (Baird et al. 2016), and the continental slope may be a preferred foraging habitat (Gannier and Epinat 2008).

In addition to the potential ecological importance of the continental slope for deep-diving odontocetes, this region provides a practical setting in which to employ passive acoustic monitoring to listen for these species. Bottom-mounted recording instruments are typically constrained by depth limitations, and deploying these recorders on the continental slope allows hydrophones to be positioned close to the depths where sperm whales and beaked whales forage, without exceeding the limitations of these instruments.

In this dissertation, I analyzed passive acoustic recordings from six monitoring sites located along the continental slope between Florida and Nova Scotia (see Chaper 1, Fig. 1). These recordings were collected between 2011 and 2015, as part of several different passive acoustic monitoring programs. Most recording sites were located at depths between 800-1000 m, with the northernmost site at approximately 1500 m. When possible, the depth of the recording sites was kept consistent, but bathymetric features varied across sites and regions. The southernmost site, located off Jacksonville, Florida, was situated inshore of the Blake Plateau, a broad region of intermediate depth and relatively smooth bathymetry extending approximately 375 km offshore. Further north, the continental shelf becomes much narrower and the slope steeper. At the recording site in Onslow Bay, North Carolina, the continental slope is relatively smooth, but becomes more rugged off Cape Hatteras. The recording site at Norfolk Canyon, Virginia, was located approximately 15 km north of Norfolk Canyon and 25 km south of Washington Canyon, in a region with considerable bathymetric relief. Similarly, the Georges Bank recording site was located in a region with prominent variation in bathymetric features, including numerous canyons that transect the shelf break and slope. Finally, the northernmost recording site was located in the mouth of the Gully, a large undersea canyon along the Scotian Shelf. This canyon is known to be a biologically important area for many cetacean species, including beaked whales and sperm whales (Hooker et al. 1999, Moors-Murphy 2014).

Research Objectives

The overall objective of my dissertation was to employ passive acoustic monitoring at a broad geographic scale to study spatiotemporal patterns in the occurrence of beaked whales and sperm whales in the western North Atlantic Ocean, with the aim of providing new insight into the distribution, seasonality, diel behavior, and habitat utilization of these species. In Chapter 1, I describe spatial, seasonal, and diel patterns in the occurrence of beaked whale species across the six passive acoustic monitoring sites described above, using spectral and temporal characteristics of detected echolocation clicks to classify beaked whale clicks to the species level. Acoustic data from three of the six monitoring sites were collected using duty-cycled recording schedules, which may lead to the underestimation of species presence. Therefore, in Chapter 2, I investigate the effects of duty-cycled recording schedules on assessing the daily presence of beaked whale clicks. Using a subset of continuous recordings from three study sites, I present a subsampling experiment which explores potential biases in the detection rates of beaked whale species using various duty cycles. In Chapter 3, I shift my focus to sperm whales, and provide an overview of the spatiotemporal occurrence of sperm whales off the east coast of the U.S, with a particular aim of identifying seasonal shifts in distribution occurring in this region. Finally, in Chapter 4, I explore the habitat preferences of foraging beaked whales and sperm whales in an oceanographically dynamic region off the Mid-Atlantic coast, using environmental variables derived from an ocean circulation model to investigate whether these species target the Gulf Stream frontal edge while foraging.

Each chapter in this dissertation is intended to be publishable as a stand-alone paper, and there is consequently some repetition in the background information and methods described herein. Versions of chapters 1 and 2 have been published in the *Canadian Journal of Fisheries and Aquatic Sciences* and the *Journal of the Acoustical Society of America*, respectively, and a version of Chapter 3 is presently under review. These chapters are included in my dissertation with acknowledgement to the co-authors of each study, who contributed data, analysis tools, and helpful comments on earlier drafts of each manuscript.

Chapter 1: Using passive acoustic monitoring to document the distribution of beaked whale species in the western North Atlantic Ocean[1]

Introduction

Efforts to develop conservation strategies for elusive, rarely observed animals are often impeded by insufficient data and a limited understanding of species' biology and ecology. Beaked whales (family Ziphiidae) comprise one of the most species-rich families within the order Cetacea, with 22 described species (Committee on Taxonomy 2016), yet are among the most poorly understood large mammals on earth. This critical lack of information on the abundance, distribution, habitat preferences, and population structure of beaked whale species around the world is particularly concerning in light of the documented sensitivity of some beaked whales to certain types of anthropogenic noise (Cox et al. 2006, Weilgart 2007). In recent decades, a number of mass strandings of beaked whales have been linked to human-generated noise, specifically mid-frequency active military sonar (D'Amico et al. 2009, Filadelfo et al. 2009). These events have raised concerns about the acute effects of anthropogenic noise on beaked whales (e.g., Parsons et al. 2008), and prompted substantial research into behavioral responses to various

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noise stimuli (Tyack et al. 2011, Pirotta et al. 2012, DeRuiter et al. 2013, Moretti et al. 2014). As this work begins to shed light on species-specific responses to acoustic disturbance, there is a fundamental need to improve baseline information on the spatiotemporal occurrence of beaked whale species, particularly in regions where potentially harmful noise exposures are likely to occur (Weilgart 2007).

Traditional survey methods based on direct visual observation can be ineffective for assessing the abundance and distribution of rare or elusive species, particularly in remote or inaccessible habitats and across broad geographic regions (Thompson 2004). Among cetaceans, beaked whales present a particular observational challenge. Distributed throughout the world's oceans, they primarily inhabit deep waters along and beyond continental shelf edges, and perform lengthy foraging dives to prey on deep-water squid and fish (Mead 2009). These dives can last more than an hour and exceed 1000 m in depth, while surfacing intervals may be as short as a few minutes (e.g., Baird et al., 2006; Tyack et al., 2006). Due to their offshore habitat and deep-diving behavior, beaked whales are notoriously difficult to observe from ships and aircraft, and sighting rates are often further constrained by weather and sea state. Barlow (2015) estimated that the probability of sighting beaked whales along a transect line during standard vessel-based surveys declines exponentially with increasing sea state, and may be lower than 0.2 in the conditions most commonly encountered offshore. Even in good survey conditions, the cryptic surface behavior and similar morphology of species, particularly in the genus *Mesoplodon*, make it difficult to identify animals to the species level (MacLeod et al. 2006, Pitman 2009). In most species, the position of erupted teeth in adult males can be used as an identifying characteristic, but females and younger individuals lack this distinguishing feature. As a result, many beaked whale sightings are reported only to the genus or family level. The scarcity of beaked whale observations with confirmed species identifications has commonly led to the aggregation of data by genus, family, or larger ecological guild to increase statistical power in habitat modeling analyses (Waring et al. 2001, Davis et al. 2002, Ferguson et al. 2006, Roberts et al. 2016a) and abundance estimation (Waring et al. 2014). However, there is evidence that beaked whales occupy ecological niches that are distinct from other deep-diving odontocetes, and that individual beaked whale species exhibit fine-scale habitat partitioning within overlapping ranges (Schick et al. 2011).

Understanding the basic ecology and distribution of individual species is an important step toward effectively managing their populations and mitigating the effects of anthropogenic disturbance. Passive acoustic monitoring (PAM) with autonomous, seafloor-mounted recording instruments is uniquely suited to gathering species-specific information on beaked whales over long time scales. Like other odontocetes, beaked whales use echolocation to find prey in the deep ocean environment, and studies employing acoustic recording tags on beaked whales have revealed that they consistently produce echolocation clicks while performing deep foraging dives, typically throughout much of the dive duration (e.g., Tyack et al. 2006). Many beaked whale species produce stereotypical echolocation clicks with unique temporal and spectral characteristics, and recent studies have made important progress in describing and attributing these click types to species (Baumann-Pickering et al. 2013). These advances, combined with innovations in recording technology that allow the collection of broadband acoustic recordings over long deployment periods, have facilitated use of PAM to effectively study the spatiotemporal occurrence of beaked whale species (e.g., Baumann-Pickering et al. 2014). PAM systems are not dependent on weather conditions and are a particularly useful method for monitoring remote regions and obtaining year-round data on species presence.

In the western North Atlantic, there are growing concerns about the effects of anthropogenic ocean noise on cetaceans, including noise generated by heavy shipping traffic along the eastern seaboard of the United States and Canada, naval training exercises employing mid- and high-frequency active sonar and explosives, and the exploration and development of offshore energy resources involving the use of seismic airguns. Six beaked whale species in three genera are known to inhabit this region: Cuvier's beaked whale (*Ziphius cavirostris*), the northern bottlenose whale (*Hyperoodon ampullatus*), Sowerby's beaked whale (*Mesoplodon bidens*), Blainville's beaked whale (*M. densirostris*), Gervais' beaked whale (*M. europaeus*), and True's beaked whale (*M. mirus*). The geographic ranges of these species have been described in a preliminary manner, based substantially on stranding records (Macleod 2000, MacLeod et al. 2006), but their distribution and seasonality remain poorly understood, particularly for species in the genus *Mesoplodon*.

In this chapter, I use multi-year PAM to describe spatiotemporal patterns in beaked whale species occurrence along the continental slope in the western North Atlantic. My objectives are to expand knowledge of the distribution of beaked whale species along the shelf edge and to generate baseline data on year-round species occurrence to inform future monitoring and mitigation efforts in this region.

Methods

Acoustic Data Collection

I collected high-frequency passive acoustic recordings between August 2011 and May 2015 at six sites in the western North Atlantic Ocean (Table 1, Fig. 1). The study region extended from Florida, USA to Nova Scotia, Canada with recording sites located at depths ranging from 800 to 1800 m. All sites were situated along the continental slope, with the northernmost site located inside the Gully, a large undersea canyon at the eastern edge of the Scotian Shelf. At each site, we deployed either a High-frequency Acoustic Recording Package (HARP; Wiggins & Hildebrand 2007) or an Autonomous Multi-channel Acoustic Recorder (AMAR; JASCO Applied Sciences) to collect passive acoustic recordings. Both instruments were autonomous, bottom-mounted, archival systems that included an omni-directional hydrophone suspended approximately 12-55 m above the seafloor and on-board electronics and hard drives for data storage. Each HARP was equipped with an ITC-1042 (International Transducer Corporation, Santa Barbara, CA) sensor with a flat (± 2 dB) sensitivity of -200 dB re V/μPa from 10 Hz to 100 kHz, connected to a custom-built preamplifier board and bandpass filter (Wiggins and Hildebrand 2007). The calibrated system response was corrected for during analysis. Each AMAR was equipped with a GeoSpectrum M8 hydrophone with a nominal frequency response of -164 dB re V/μPa from 20 Hz to 170 kHz. The data included in this paper were collected under the auspices of multiple long-term PAM projects with varying research objectives; as a result, there was variation in the sampling rates and recording schedules used, as well as the timing and duration of instrument deployments (Table 1). Most of the recordings were collected at sampling rates of 200 kHz and above, providing a recording bandwidth of at least 10 Hz – 100 kHz, sufficient for detecting all known beaked whale signal types, which have peak frequencies between 16 kHz and approximately 70 kHz. The only exception was the first year of recordings from the Mid-Gully site, which were collected at a sampling rate of 128 kHz, adequate for detecting all but one beaked whale signal type, which is higher in frequency with energy mainly between 65-70 kHz. This click type is attributed to Sowerby's beaked whale, and was not included in my analysis of the first year of recordings from the Mid-Gully site. During each HARP deployment, recordings were made either continuously or on a 50% duty cycle, while the AMARs were programmed to record at lower duty cycles due to limitations in data storage capacity (see Table 1 for details on each duty-cycled recording schedule). I analyzed all recording days in which data were available across a full 24-hour period, and excluded partial recording days at the start and end of each deployment.

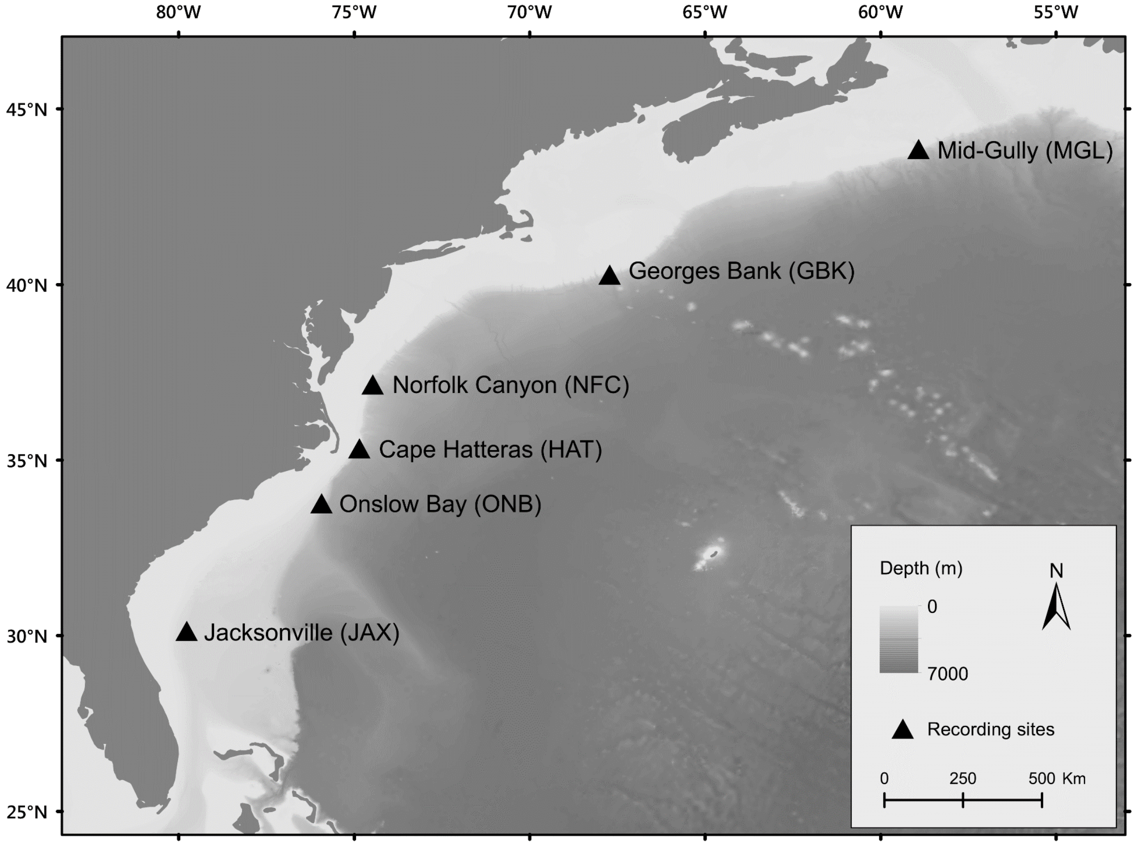

Figure 1: Locations of passive acoustic recording sites along the continental slope in the western North Atlantic Ocean. Bathymetry data source: General Bathymetric Chart of the Oceans, http://www.gebco.net

Table 1: Summary of passive acoustic monitoring effort along the continental slope in the western North Atlantic between 2011 and 2015.

Site	Location	Instrument type[a]	Depth (m)	Recording dates	Number of recording days	Duty cycle[b] (mm:ss) (%)	Sampling rate (kHz)
Mid-Gully (MGL)	43.87N, 58.92W	AMAR	1780	10/12/12 - 4/10/13	179	2:00/15:00 (13%)	128
			1580	5/8/13 - 9/25/13	140	2:00/15:00 (13%)	128
			1525	11/15/13 - 4/6/14	141	2:10/20:00 (11%)	375
			1615	5/3/14 - 9/26/14	145	2:10/20:00 (11%)	375
Georges Bank (GBK)	40.29N, 67.72W	AMAR	800	7/27/14 - 5/26/15	304	2:40/30:00 (9%)	250
Norfolk Canyon (NFC)	37.16N, 74.47W	HARP	980	6/20/14 - 4/4/15	289	Continuous (100%)	200
Cape Hatteras (HAT)	35.34N, 74.85W	HARP	950	3/16/12 - 4/10/12	26	Continuous (100%)	200
			970	10/10/12 - 4/30/13	203	Continuous (100%)	200
			970	5/30/13 - 3/14/14	289	Continuous (100%)	200
			850	5/9/14 - 12/10/14	216	Continuous (100%)	200
Onslow Bay (ONB)	33.78N, 75.93W	HARP	950	8/19/11 - 11/30/11	104	5:00/10:00 (50%)	200
			915	7/14/12 - 10/1/12	80	5:00/10:00 (50%)	200
			850	10/25/12 - 6/29/13	248	5:00/10:00 (50%)	200
Jacksonville (JAX)	30.15N, 79.77W	HARP	800	8/24/14 - 5/28/15	278	Continuous (100%)	200

Detection and classification of beaked whale signals

To detect and classify beaked whale echolocation signals, I used a multi-step approach based on the methods described in Baumann-Pickering et al. (2013). I performed all signal processing using the custom software program *Triton* (Wiggins and Hildebrand 2007) and custom-written MATLAB (Mathworks, Inc., Natick, MA) routines. First, I applied an automated detection algorithm to identify and extract individual echolocation clicks within each dataset (see Roch et al. 2015; Soldevilla et al. 2008). Next, I applied a band-pass filter to each extracted signal, calculated spectra using 2.56 ms of Hann-windowed data centered on the click, and measured signal parameters including: peak and center frequencies, bandwidth, duration, signal-to-noise ratio, and inter-click-interval (ICI) between consecutive detections (Baumann-Pickering et al. 2013). To separate beaked whale clicks from other odontocete clicks, I applied a set of criteria based on spectral and temporal characteristics. Compared to echolocation clicks produced by other odontocetes, beaked whale echolocation clicks produced during the search phase of foraging dives are typically characterized by longer durations, consistent ICIs, and a frequency upsweep (Baumann-Pickering et al. 2013). I considered detected clicks to be potential beaked whale signals if they exhibited peak and center frequencies above thresholds of at least 32 and 25 kHz, respectively, durations of at least 0.355 ms, and frequency upsweeps with a sweep rate of at least 23 kHz/ms (as in Baumann-Pickering et al. 2016). I then applied a set of duration-based criteria, requiring the waveform envelope of each click to increase over the first 0.1 ms and to remain above a 50% energy threshold for a duration of at least 0.1 ms for the click to be considered a potential beaked whale click. Detection criteria were applied in a consistent manner across all datasets, except for the peak and center frequency thresholds, which I reduced to 23 kHz during analysis of the Mid-Gully recordings to ensure optimal detection of northern bottlenose whale clicks, which are lower in frequency than the other beaked whale signals recorded. While there are few existing records of northern bottlenose whales south of the Scotian Shelf (Wimmer and Whitehead 2004), I acknowledge that the frequency thresholds I initially applied may have resulted in the omission of northern bottlenose whale clicks by the detection system at the other recording sites, and I address this possibility in my discussion of the results.

For datasets comprised of continuous recordings, I grouped all potential beaked whale clicks into detection events based on the timing of their occurrence, defining a detection event as all potential beaked whale clicks separated by a gap of no more than 5 minutes between consecutive detections. In the case of duty-cycled recordings, I defined a detection event as all potential beaked whale clicks occurring within a single data file corresponding to the 2-5 minute “on” period of the recording cycle. For each detection event, I reviewed summary figures displaying histograms of peak frequency and ICI, a concatenated spectrogram of all clicks in the event, and a plot of mean click spectra overlaid on spectral templates of known beaked whale echolocation signal types (*sensu*

Baumann-Pickering et al. 2013). After examining these figures and browsing waveforms and spectrograms of individual clicks, I assigned one or more species classifications to each detection event, or marked the event as a false detection. All detection events that did not have clear, unambiguous characteristics of beaked whale clicks were marked as false detections likely produced by other odontocetes, and these detections were excluded from the analysis. Among the remaining detection events, most consisted of clicks produced by a single beaked whale species; however, overlapping detections of multiple beaked whale species also occurred and were identified as such.

This multistep detection process has been extensively evaluated in previous studies and the rate of missed detections estimated to be approximately 5% (Baumann-Pickering et al. 2016). I spot-checked the detection results for each of my datasets by visually examining long-term spectral averages (LTSAs; Wiggins & Hildebrand 2007) and spectrograms. I noted a few instances where the automated detection process failed to detect visible beaked whale clicks in the presence of strong background noise; however, beaked whale clicks that were not initially apparent during visual examination of LTSAs were also detected by the automated system, notably when they occurred amid intense bouts of echolocation from other odontocetes, a common occurrence at some of our recording sites. I was therefore not able to precisely characterize detector performance, but considered the automated detection method comparable to or slightly better than manual analysis of LTSAs for estimating hourly and daily presence of beaked whale clicks, based on substantive qualitative comparisons of my detection results with LTSAs and spectrograms. Since the final step of this process involved manual review and classification of each detected event, I was able to largely eliminate false detections of non-beaked whale clicks. Detections of unidentified or poorly known click types were reviewed by additional co-authors to assist in making a classification decision (SBP, HMM, DMC). I took a conservative approach to this analysis, excluding all detection events that could not be confidently identified to the level of species or recognized signal type, and my results should therefore be considered a minimum estimate of the presence of each beaked whale species or signal type at each recording site.

Analysis of spatial and temporal patterns

To examine spatial patterns in beaked whale acoustic presence across recording sites, I binned the manually classified beaked whale click events into daily presence or absence of each species. I compared species occurrence across sites by expressing the number of days each species was detected at each site as a percent of the number of recording days available. In addition, I compared the relative occurrence of species within each site by determining the percent of total daily beaked whale detections at each site attributed to each species. I performed these comparisons at the level of daily presence rather than on finer temporal scales to reduce potential bias in detection rates that may result from comparing data collected using different duty-cycled recording schedules. In Chapter 2, I present a detailed analysis of the effects of using duty-cycled recording schedules to detect different beaked whale species, and I discuss these potential biases in the results presented here.

To examine temporal patterns across months and years within each recording site, I binned detections of each beaked whale species into hourly presence and calculated the percent of hours per week with detections. For duty-cycled data, hourly presence was determined based on the recording periods that occurred within each hour of the day. For time periods with more than one year of data available, I also calculated the mean percent of hours with detections for each week of the year, averaged across all monitoring years, and plotted the mean along with the minimum and maximum values to illustrate the range of inter-annual variation. To examine temporal patterns on diel time scales, I plotted counts of species presence in each hour of the day, pooled across all recording days at each site. To compare hourly presence between day and night light regimes, I divided each calendar day into night and day diel periods based on local sunrise and sunset times. I calculated the proportion of hours within each diel period with detections of each species, to account for variation in the length of diel periods across different latitudes and seasons, and used a non-parametric Mann-Whitney *U* test to test for differences in beaked whale presence during day and night. I performed this test for each species at each site, as well as for each species pooled across all sites with detections. I additionally examined plots of the percent of diel period hours per week with detections to identify any seasonal changes in diel behavior that were not apparent when data were pooled across all recording days.

Results

Beaked whale echolocation signals

I identified six different beaked whale click types within the recordings (Fig. 2). Four of these were consistent with signals produced by northern bottlenose whales (Fig. 2A) (Wahlberg et al. 2011), Cuvier's beaked whales (Fig. 2B) (Zimmer et al. 2005a), Blainville's beaked whales (Fig. 2C) (Johnson et al. 2004), and Gervais' beaked whales (Fig. 2D) (Gillespie et al. 2009). The remaining two click types did not closely match any beaked whale signals previously described in the literature. However, I posit that one of these unknown click types is produced by Sowerby's beaked whale (Fig. 2E), based on similarities in frequency content and inter-click-interval (ICI) to a small sample of high-frequency clicks recorded in a visually-confirmed encounter with Sowerby's beaked whales by Cholewiak et al. (2013). This presumed species identification is further supported by the geographic occurrence of the click type, which matches the described range of the species (MacLeod et al. 2006, Waring et al. 2015). In particular, these clicks were frequently detected in the Gully, where Sowerby's beaked whales and northern bottlenose whales are the only Ziphiid species known to occur regularly (Whitehead

2013). I thus refer to this click type as Sowerby's beaked whale throughout this paper. The second unidentified click type had a similar spectral shape to clicks produced by Blainville's beaked whales, but was higher in frequency, with a peak frequency around 38 kHz (Fig. 2F). These click events were also differentiated from typical Blainville's beaked whale clicks by shorter click durations and slightly longer ICIs. I refer to this click type as "BW38" and the species remains unknown.

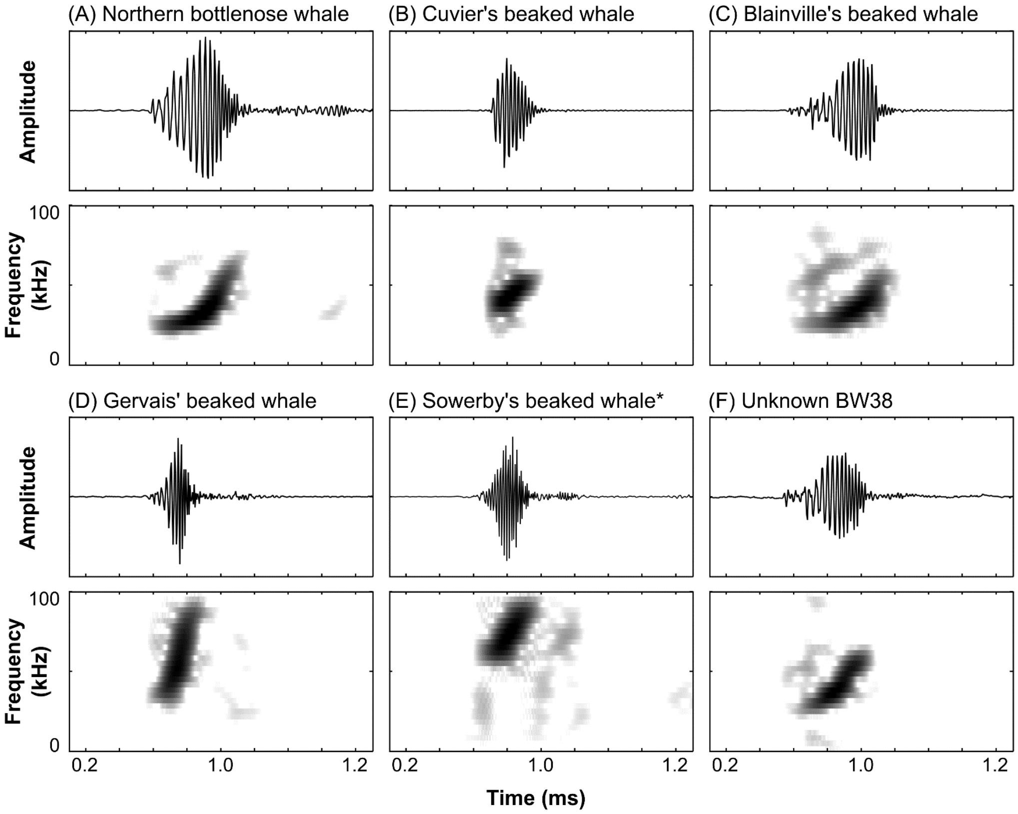

Figure 2: Example waveforms (upper panels) and spectrograms (lower panels) of each beaked whale click type recorded in this study. Spectrograms were calculated using a Hann window, 60 pt FFT, and 98% overlap. *Sowerby's beaked whale clicks are labeled as such based on a posited species identification of this click type.

Spatial patterns

I analyzed 2,642 days of recordings, and detected beaked whale signals at all six recording sites. Two to four different click types were present at each site, and I observed considerable variation in relative species occurrence across the study region. Fig. 3 shows the daily presence of each species at each site as a percentage of the number of recording days; Fig. 4 shows the daily presence of each species as a percentage of all beaked whale detection days at each site.

The highest levels of beaked whale presence occurred at the Mid-Gully (MGL) site, even though the recordings at this site were collected at relatively low duty cycles (see Table 1 for details). Two beaked whale species were nearly always present at this location: northern bottlenose whales, detected on all 605 recording days, and Sowerby's beaked whales, detected on 95% of the 286 days with high-frequency data. Data for the remaining 319 days at MGL were collected at a sampling rate of 128 kHz, providing insufficient recording bandwidth to reliably detect the higher-frequency Sowerby's beaked whale clicks. Cuvier's beaked whales were present less frequently at MGL, and were detected on 26% of the 605 recording days, although their daily presence may be underestimated as a result of the duty-cycled recordings, which are likely to have greater effects on the assessment of daily presence of rarely detected species (see Chapter 2).

The Georges Bank (GBK) and Norfolk Canyon (NFC) sites were characterized by lower overall beaked whale presence, with no species detected across a majority of recording days. At GBK, Sowerby's and Cuvier's beaked whales were detected on 15% and 13% percent of the 304 recording days, respectively, and Gervais' beaked whales were detected only once. Based on analyses presented in Chapter 2, it is likely that these results significantly underestimate daily presence, particularly of the *Mesoplodon* species, since data at this site were collected using a low duty cycle (less than 10% recording time; see Table 1). At NFC, recordings were made continuously, and Sowerby's, Cuvier's, and Gervais' beaked whales were detected on 36%, 20%, and 15% of the 289 recording days, respectively.

In contrast, beaked whale detections at both the Cape Hatteras (HAT) and Onslow Bay (ONB) sites were dominated by a single species present on nearly all recording days. At HAT, Cuvier's beaked whales were detected on 96% of the 734 recording days, with Gervais' beaked whales detected on 35% of days, Blainville's beaked whales on 1% of days, and a single detection of Sowerby's beaked whales (0.14% of days). At ONB, Gervais' beaked whales were detected on 97% of the 432 recording days, together with infrequent detections of Cuvier's (6% of days) and Blainville's (5% of days) beaked whales and the unknown BW38 click type (1.4% of days). Recordings at ONB employed a 50% duty cycle (5 minutes of recording time per 10 minute cycle period), and beaked whale daily presence may therefore be slightly underestimated.

However, this duty cycle is unlikely to have significantly reduced the daily detection rates of either Gervais' or Cuvier's beaked whales at this site, since Gervais' clicks were commonly present throughout multiple hours of the days, and Cuvier's clicks are usually detected for more than 5 minutes at a time (see Chapter 2). Finally, I found the lowest overall beaked whale presence at the Jacksonville (JAX) recording site, where Gervais' and Blainville's beaked whales were detected on only four (1.4%) and two (0.7%) of the 278 recording days, respectively.

I observed substantial overlap among species' ranges, as well as apparent latitudinal gradients in the relative occurrence of some species across the study region (Figs. 3 and 4). Northern bottlenose whales and Sowerby's beaked whales exhibited the most boreal distributions, with detections of northern bottlenose whales occurring only at the Mid-Gully site, and detections of Sowerby's beaked whales extending from the Mid-Gully as far south as Norfolk Canyon, with a single detection at Cape Hatteras. Cuvier's and Gervais' beaked whales occupied the broadest latitudinal ranges within the study region, with Cuvier's beaked whales exhibiting a more northerly distribution (MGL to ONB) and Gervais' a more southerly distribution (GBK to JAX). The ranges of these two species overlapped substantially and both species occurred at four of the six recording sites, but they exhibited strongly contrasting levels of occurrence at the Cape Hatteras and Onslow Bay recording sites off North Carolina (Figs. 3 and 4). Blainville's beaked whales appeared to be restricted to the southern portion of the study region

(HAT to JAX), and were not commonly detected at any recording site. Finally, the unknown BW38 click type was detected only at Onslow Bay.

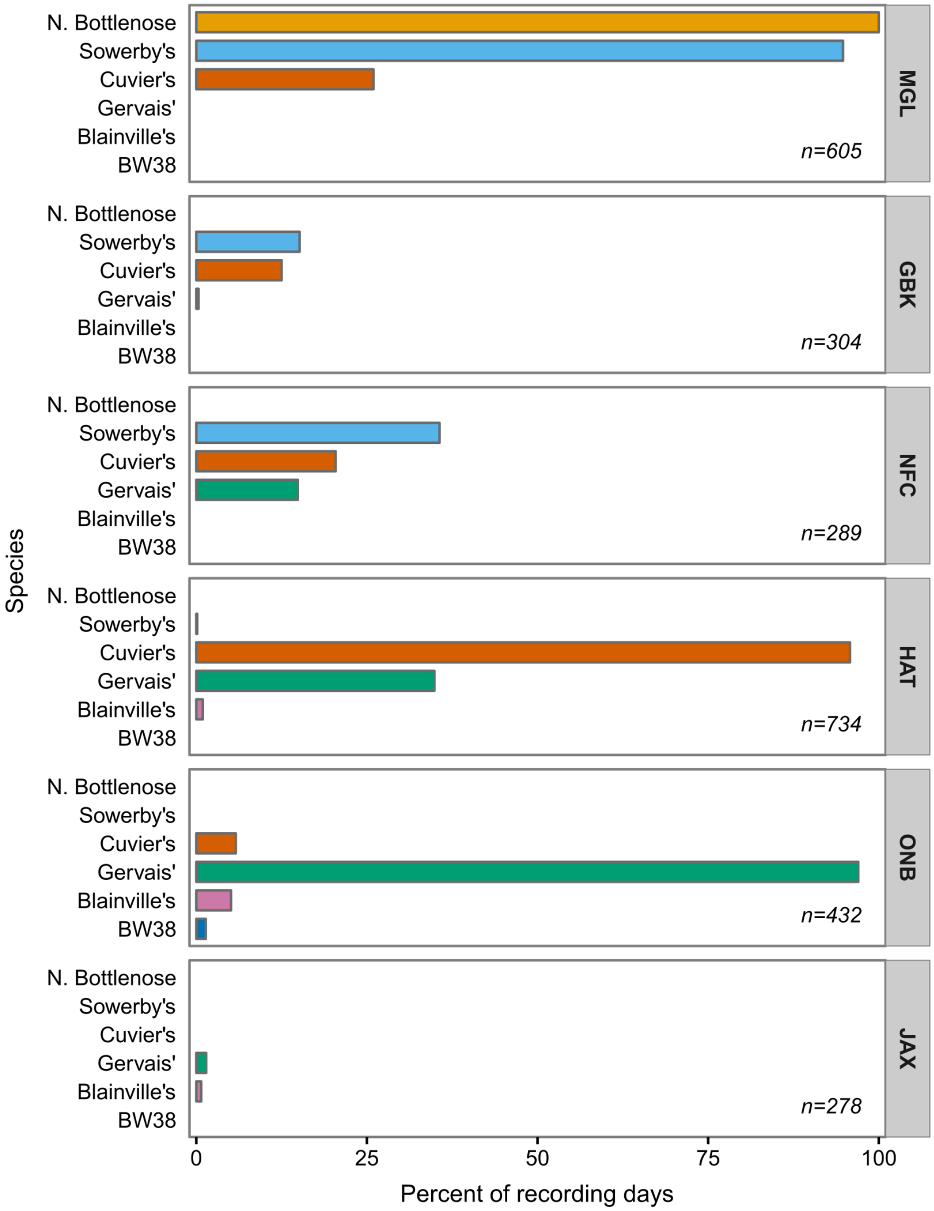

Figure 3: Percentage of total recording days (*n*) at each site with detections of each beaked whale species. Recording sites are shown from north (top) to south (bottom): Mid-Gully (MGL), Georges Bank (GBK), Norfolk Canyon (NFC), Cape Hatteras (HAT), Onslow Bay (ONB), and Jacksonville (JAX).

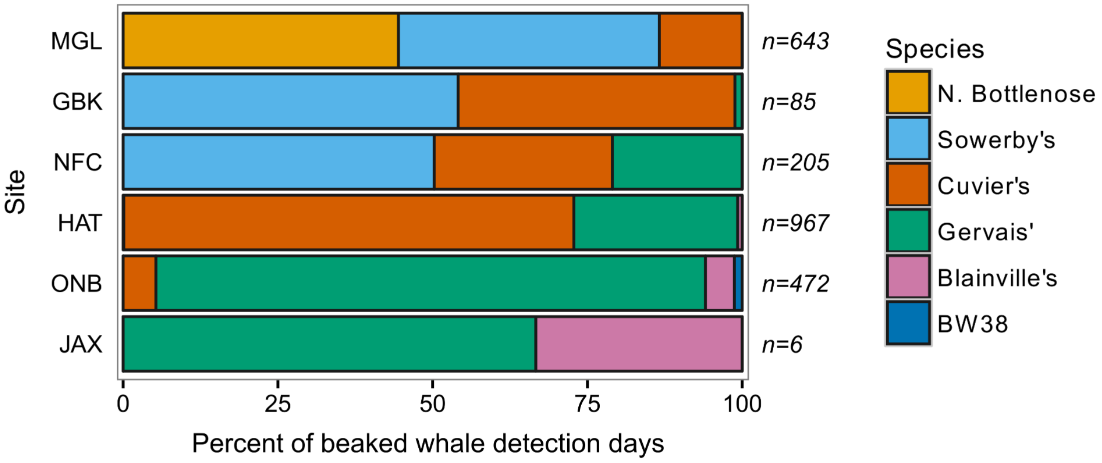

Figure 4: Percentage of total beaked whale detection days (*n*) at each site attributed to each species. Recording sites are shown from north (top) to south (bottom): Mid-Gully (MGL), Georges Bank (GBK), Norfolk Canyon (NFC), Cape Hatteras (HAT), Onslow Bay (ONB), and Jacksonville (JAX). At MGL, the relative percentages shown are based only on detection days with a sufficient sample rate to detect all beaked whale click types.

Seasonal and diel patterns

Data were available across multiple years at the Mid-Gully, Cape Hatteras, and Onslow Bay sites, with some gaps in monitoring coverage between successive recorder deployments. At each of the remaining sites, data were available from a single deployment spanning approximately 10 months. None of the species recorded exhibited strong evidence of seasonality, and relative species occurrence within each site was generally consistent over time, i.e. the species with the highest weekly occurrence typically remained highest throughout the recording periods (Fig. 5).

The only seasonal pattern that I observed consistently across multiple years occurred at the Mid-Gully recording site, where there was a brief decrease in northern bottlenose whale detections during July in both consecutive monitoring years (Figs. 5 & 6). In 2014, when high-frequency recordings were available, I observed an increase in Sowerby's beaked whale detections starting in June and continuing through August. Cuvier's beaked whales were detected at low levels throughout the year.

Data at the Georges Bank, Norfolk Canyon, and Jacksonville sites consisted of only a single year of monitoring, which limited my ability to draw inferences regarding temporal patterns on seasonal scales. On average, Sowerby's, Cuvier's, and Gervais' beaked whales were each detected in less than 1% of hours per week at Georges Bank and less than 3% of hours per week at Norfolk Canyon. At Jacksonville, there were sporadic detections of Gervais' beaked whales only in February, April, and May, and Blainville's beaked whales only in November and December. In Figs. 5 and 6 I use a reduced y-axis scale to show the temporal occurrence of beaked whales at these three sites. Again, it is important to note that the Georges Bank recordings were collected at a low duty cycle and hourly presence is likely significantly underestimated.

At Cape Hatteras, beaked whale presence was fairly consistent throughout the year, characterized by detections of Cuvier's beaked whales in a mean of 33% (± 14%) of hours per week, and detections of Gervais' beaked whales in a mean of 3.8% (± 4.6%) of hours per week. No clear seasonal patterns were apparent in the mean detection rates per week of the year (Fig. 6). At Onslow Bay, the mean detection rate of Gervais' beaked whales was 41% (± 19%) of hours per week, and appeared to be slightly higher during the months of September to March and lower from April to August, though for most time periods I lacked replicate years of monitoring at this site (Fig. 6). Sporadic detections of Cuvier's, Blainville's, and BW38 signals also occurred throughout the year.

For most species and sites, I detected similar rates of hourly presence across day and night diel periods, and did not observe distinct diel patterning (Appendix A, Figs. A13 and A14). Significantly higher daytime presence occurred only for Sowerby's beaked whales at Georges Bank (Mann-Whitney *U* test, W=1669.5, $p=3.12 \times 10^{-4}$) and Gervais' beaked whales at Cape Hatteras (Mann-Whitney *U* test, W=37812, $p=0.039$), but sample sizes were limited, especially in the former case, and more data are needed to assess the biological significance of these patterns. At the Mid-Gully site, northern bottlenose whales exhibited significantly higher nighttime presence (Mann-Whitney *U* test, W=152230, $p=2.46 \times 10^{-7}$), and this result appeared to be driven mainly by seasonal differences in day and night detection rates occurring from February through April in both consecutive years of monitoring, with no discernible diel patterning throughout the rest of the year (Appendix A, Fig. A15).

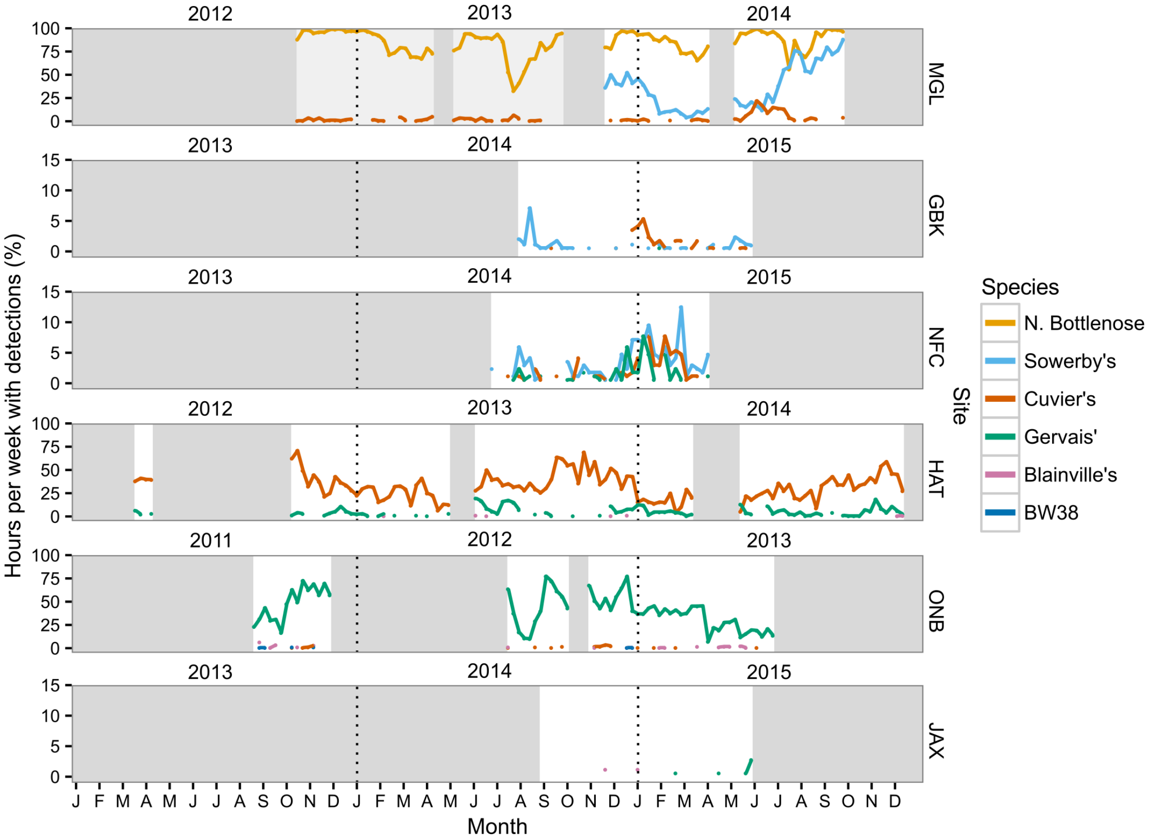

Figure 5: Percentage of hours per week with beaked whale detections at each recording site across all monitoring periods. Note that y-axis scales differ. Zero values are not plotted to distinguish between absence and low levels of presence. Years are indicated above each panel and separated by dotted lines. Dark gray shading indicates periods with no recording effort, light gray shading (top panel) indicates periods with data collected at a sampling rate insufficient for detecting Sowerby's beaked whale clicks.

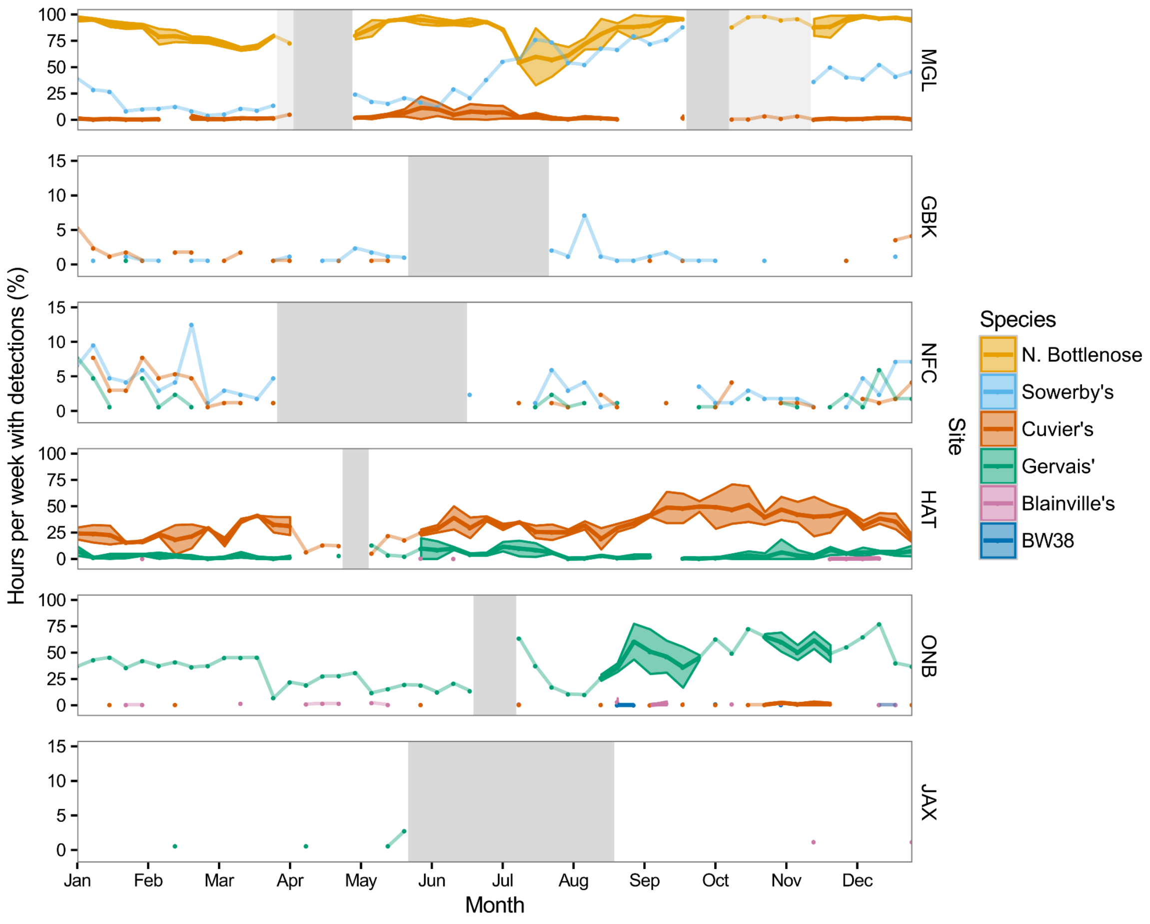

Figure 6: Mean percentage of hours per week of the year with beaked whale detections, averaged across all years with data. Thin studded lines indicate weekly detection rates during time periods with one year of data; bold lines indicate mean values during time periods with 2-3 years of data, and shaded ribbons show the range of values from minimum to maximum across years. Note that y-axis scales differ. Zero values are not plotted to distinguish between absence and low levels of presence. Dark gray shading indicates periods with no recording effort, light gray shading (top panel) indicates periods with data collected at a sampling rate insufficient for detecting Sowerby's beaked whale clicks.

Discussion

The results of this study provide a new perspective on the occurrence and distribution of beaked whale species along the western North Atlantic shelf break. Despite their oft-cited status as “rare and elusive” species, beaked whales were acoustically detected regularly throughout most of the study region, suggesting that low sighting rates in traditional visual surveys reflect inherent difficulties in observing beaked whales at sea rather than their rarity of occurrence within the region. In fact, beaked whales were a common component of the acoustic record at most of the sites I sampled.

I recorded clicks produced by four of the six beaked whale species known to inhabit the North Atlantic, as well as a click type likely produced by Sowerby’s beaked whales. This posited species identification remains to be conclusively confirmed with additional field recordings or animal-borne acoustic tags, but represents an important new finding, since these clicks were regularly recorded at several sites and may provide new insight into the occurrence of Sowerby’s beaked whales. The only North Atlantic beaked whale species apparently absent from the recordings was True’s beaked whale (*M. mirus*), an enigmatic species known primarily from stranded specimens. In the western North Atlantic, True’s beaked whales have stranded between Newfoundland and Florida (Macleod 2000, Pitman 2009), and historically there have been few documented sightings at sea. During shipboard surveys conducted by the Northeast

Fisheries Science Center in the summer of 2016 (NEFSC, unpublished data), several potential groups of True's beaked whales were identified at sea and concurrent acoustic recordings were collected during these encounters, but quantitative analyses have not yet been conducted and at present there are no available descriptions of True's beaked whale echolocation signals. I recorded one unidentified beaked whale click type at Onslow Bay, referred to as BW38, but there is currently no evidence linking this signal type to True's beaked whales, and more recordings are needed before I can reasonably speculate on which species produces the BW38 click type.

My results revealed considerable spatial variation in beaked whale species' presence among recording sites. These patterns are largely consistent with prior knowledge of the latitudinal ranges of beaked whale species (MacLeod et al. 2006), but also offer new insights into species-specific habitat use which merit further examination. The low but consistent acoustic presence of Cuvier's beaked whales in the Gully was surprising, as this species has rarely been encountered along the Scotian Shelf despite several decades of survey effort (Whitehead 2013). MacLeod et al. (2003) hypothesized that Cuvier's beaked whales and northern bottlenose whales compete for similar prey and therefore do not occur sympatrically; in contrast, my results indicate that there is some degree of geographic overlap among these two species. The Gully is critical habitat for a small, highly resident population of northern bottlenose whales known to occupy the canyon and surrounding areas year-round (Fisheries and Oceans Canada 2016), and became a federal marine protected area (MPA) in 2004 (DFO 2004). Whitehead (2013) documented a significant increase in the abundance of Sowerby's beaked whales in the Gully between 1998 and 2011, which he suggested might have been related to changes in the ecology of the Scotian Shelf ecosystem (Frank et al. 2011), or to the reduction in human activities in the Gully region after MPA protections were implemented, including a decrease in anthropogenic noise. It is possible that the presence of Cuvier's beaked whales in the Gully throughout the 2012-2014 monitoring period represents a similar, recent trend toward increasing use of this habitat by a species that was not historically present. A confirmed sighting of Cuvier's beaked whales during the summer of 2015 represents the first known visual record of this species inside the Gully (H. Whitehead, unpublished data).

I report northern bottlenose whale detections only at the Mid-Gully recording site, but acknowledge the possibility that northern bottlenose whales were present and not detected at my other recording sites, since the detection criteria were not adjusted to optimally detect the lower-frequency clicks of this species in all datasets. However, northern bottlenose whales have very rarely been sighted south of the Scotian Shelf, with the southernmost sighting occurring east of New Jersey during the 1980s (Reeves et al. 1993, Wimmer and Whitehead 2004). The geographic range of this species is better known than many of the other Atlantic beaked whale species, since they are easier to observe and identify at sea due to their larger size and tendency to approach vessels

(Barlow et al. 2006). It is highly unlikely that northern bottlenose whales occur at any recording site south of Georges Bank, where the low duty cycle limited my ability to record rare events regardless of the click detection parameters used. Nevertheless, I note that my description of the occurrence of this species within our study region may be incomplete and recommend that future recordings collected off the northeastern U.S. be analyzed for northern bottlenose whale clicks.

To the south along the U.S. east coast, I observed remarkably different levels of presence of Cuvier's and Gervais' beaked whales at the Cape Hatteras and Onslow Bay recording sites, located just 200 km apart at similar depths along the continental slope, and this pattern remained consistent across multiple years of monitoring. The degree to which this apparent habitat partitioning may relate to foraging preferences and the distributions of prey resources is uncertain, as the diets of both species are poorly known (MacLeod et al. 2003). Cape Hatteras is considered an important biogeographic boundary due to the convergence of distinct water masses, which may affect the assemblages of demersal squid and fish species present north and south of this boundary (e.g., Briggs and Bowen, 2012; Pappalardo et al., 2015). Further data on the diets of individual beaked whale species as well as the ecology of their prey could help shed light on the patterns observed; for now, I simply note that there is clear spatial patterning in the use of slope habitats at similar depth strata by co-occurring beaked whale species.

The dearth of beaked whale detections at the Jacksonville recording site is likely related to the bathymetry of the continental margin off the southeastern U.S. The area beyond the continental shelf is characterized by the Blake Plateau, a relatively flat region of intermediate depth (500-1000 m) that extends 375 km offshore before steeply dropping off to the deep ocean basin. Beaked whales are often associated with complex topography including steep shelf edges and canyons (Waring et al. 2001, MacLeod and Zuur 2005), and I hypothesize that higher beaked whale presence likely occurs along the outer edge of the Blake Plateau, where oceanographic and bathymetric characteristics are more similar to continental slope environments further north. The Blake Plateau extends almost to the edge of the U.S. EEZ and little survey effort has been conducted near the outer edge, but habitat modeling performed by Roberts et al. (2016) also predicted higher beaked whale abundance along this outer slope than along the continental shelf break further inshore.

Previously, most data on beaked whale occurrence in the northwest Atlantic has come from shipboard and aerial surveys conducted primarily during the spring and summer months, when weather conditions are most favorable for survey effort, and in many areas there is little to no information on species occurrence during other times of year (Waring et al. 2014). In the present study, I did not find strong seasonal variation in beaked whale occurrence at most recording sites, and species were generally present at similar levels year-round, which I believe is an important finding given the difficulty of conducting visual surveys outside the spring and summer months. Temporal coverage was limited to a single year or included substantial gaps at several of the monitoring sites, and data from additional years may be necessary to reveal subtler seasonal or inter-annual trends. However, results from large-scale PAM in the North Pacific demonstrated a similar lack of temporal patterning in the detection of beaked whale acoustic signals (Baumann-Pickering et al. 2014), and coordinated seasonal movements have not been documented in any beaked whale species. Studies utilizing photographic identification or animal-borne satellite telemetry tags have revealed a high degree of site fidelity within some beaked whale populations, including Cuvier's and Blainville's beaked whales in Hawai'i (McSweeney et al. 2007, Schorr et al. 2010), Blainville's beaked whales in the Bahamas (Claridge 2013), and northern bottlenose whales in Nova Scotia (Hooker et al. 2002, Wimmer and Whitehead 2004). Preliminary results from ongoing research off Cape Hatteras, North Carolina have suggested a similar pattern for Cuvier's beaked whales at this site, with satellite-tagged individuals remaining within a small core area along the continental slope for weeks or months at a time (Baird et al. 2016). The consistent year-round acoustic presence I documented provides further evidence that Cuvier's beaked whales are highly resident at this location.

The absence of clear diel patterning in the hourly acoustic presence of beaked whale echolocation signals at most recording sites suggests that the species recorded generally perform foraging dives throughout the day and night in these areas. Diel pattern analyses were based only on hourly acoustic presence within day and night diel periods, and do not provide a detailed comparison of relative foraging effort across all hours of the day, which would require analysis at a finer temporal scale or the use of a different metric, such as click rates. Previous studies examining the diving behavior of Cuvier's and Blainville's beaked whales found that individuals of these species performed deep foraging dives at similar rates during night and day (Baird et al. 2008, Schorr et al. 2014). Little is known about the foraging behavior or diving patterns of Gervais' and Sowerby's beaked whales. Moors (2012) found evidence of higher nighttime click rates and seasonal variation in the diel behavior of northern bottlenose whales, similar to our results for this species, but it is unknown whether these patterns are driven by prey availability, predator avoidance, social behavior, or some combination of factors.

There are several sources of uncertainty that are important to consider when interpreting the results of this study. Firstly, the range over which beaked whale clicks are detected may vary between recording sites, due to differences in hydrophone depth and instrument sensitivity. In general, detection ranges for beaked whale clicks are expected to be fairly small due to the rapid attenuation of high frequency sound (Zimmer et al. 2008, Kuš̈el et al. 2011). Hildebrand et al. (2015) estimated that beaked whale clicks are detected with certainty only within a few hundred meters of a bottom-mounted HARP, with a maximum detection range of no more than 3.5 kilometers for on-axis clicks directed at the hydrophone. While these ranges were found to be invariant across monitoring sites, my study included a broader range of depths and two instrument types with different sensitivities, which may result in greater variation in site-specific detection ranges. Secondly, the effects of species-specific behavior on detection rates of beaked whales on bottom-mounted recorders are largely unknown. Quantitative estimates of the probability of detecting each species at each recording site would require detailed information on the acoustic behavior of each species during foraging dives, including source levels and directionality of clicks as well as rates of click production and patterns of movement during dives (see Hildebrand et al. 2015). For most beaked whale species this information does not exist, or is available only from a small number of individuals sampled at specific locations. I caution that these results should only be interpreted as the amount of time one or more individuals of a species were present and acoustically active at a site, and do not necessarily provide an indication of relative abundance, since we do not know the number of individuals present. Lastly, I classified beaked whale clicks based on existing information on click types and acoustic behavior. Prior studies have shown that many beaked whale species produce a stereotyped echolocation signal type that is stable across geographic regions (Baumann-Pickering et al. 2014). However, I acknowledge that scientific understanding of the acoustic behavior of most beaked whale species is far from complete, particularly for True’s, Sowerby’s, and Gervais’ beaked whales in the Atlantic Ocean. Collecting additional data on the acoustic behavior of these species may allow further insight to be gained from PAM data in the future.

While there are many remaining gaps in scientific knowledge of beaked whale ecology, passive acoustic monitoring is a useful method for obtaining species-specific presence data, and can be a valuable tool for identifying important beaked whale habitats. Although passive acoustic methods do not allow detection of silent animals, numerous studies have shown that echolocation is a consistent feature of deep foraging dives performed by Cuvier's (Johnson et al. 2004, Tyack et al. 2006b) and Blainville's (Johnson et al. 2004, 2006, Madsen et al. 2005, 2013, Tyack et al. 2006b, Arranz et al. 2011) beaked whales, and it is reasonable to assume that echolocation is an essential aspect of foraging for all beaked whale species. Acoustic detections on bottom-mounted recorders can therefore be considered a proxy for foraging activity, providing insight into species' ecology. I suggest that, in addition to the Gully, which is known critical habitat for beaked whales, the Cape Hatteras and Onslow Bay monitoring sites in this study should also be considered important beaked whale habitats, with at least one species present in these areas on more than 95% of days throughout the year. By contrast, the Jacksonville recording site appears to be an area infrequently visited by foraging beaked whales, which is an important result due to the potential for future acoustic disturbance at this site. Installation of a new Undersea Warfare Training Range by the U.S. Navy is currently underway just inshore of the recording site, and the collection of baseline data on species occurrence before this range becomes operational is critical to assess potential effects of increased human activity and sonar use in this region. While these effects may extend beyond the range over which beaked whale clicks were detected on the HARP, my results provide an initial baseline for this site and support previous research suggesting that the inner continental slope and Blake Plateau region may not provide quality foraging habitat for beaked whales (Roberts et al. 2016a).

In summary, this study revealed year-round presence of multiple beaked whale species along the western North Atlantic continental slope, including nearly continuous beaked whale presence at three of the six monitoring sites. These results provide insight into variation in the relative occurrence of beaked whale species, and help advance our limited understanding of the distribution of species in the genus *Mesoplodon*. I observed distinct differences in habitat use among species throughout the study region, and reiterate the importance of improving species-specific information on the ecology, distribution, and habitat preferences of beaked whales, particularly when considering the potential effects of anthropogenic noise. Assessment of population-level effects of anthropogenic disturbance is challenging for any cetacean species, and particularly problematic for beaked whales, due to the low encounter rates during visual surveys (Taylor et al. 2007). Here, I did not attempt to estimate species' abundance, although methods are being developed to use passive acoustic data for that purpose (Marques et al. 2009, Hildebrand et al. 2015). Instead, I demonstrate the utility of PAM to estimate baseline levels of occurrence of beaked whale species across broad spatial scales and at high temporal resolutions, facilitating the detection of changes in distributions and habitat use over time. Critically, and unlike the results of many visual surveys, my results are species-specific, improving the information available to managers for assessing and mitigating potential threats to these species.

Chapter 2: Effects of duty-cycled passive acoustic recordings on detecting the presence of beaked whales in the northwest Atlantic[1]

Introduction

Passive acoustic monitoring (PAM) with autonomous recording instruments is a common technique used to study patterns of cetacean occurrence. Over the past several decades, this method has been applied most extensively to record low-frequency vocalizations from baleen whales, and is particularly valuable for monitoring remote locations and detecting rare or elusive species infrequently encountered at sea (e.g., Mellinger et al., 2007; Sousa-Lima et al., 2013). Recent technological improvements in the performance of autonomous recorders have led to the increasing use of PAM to detect higher frequency signals, including odontocete echolocation (Sousa-Lima et al. 2013). This approach has particular value for studying beaked whales (family Ziphiidae), which are among the most difficult cetacean species to observe due to their offshore distributions and deep-diving behavior. Detection of beaked whale echolocation signals using autonomous, seafloor-mounted recorders offers unique insight into the occurrence and foraging activity of these species, especially over long time scales and in poorly-surveyed regions (e.g., Baumann-Pickering et al. 2014).

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Most beaked whale species produce frequency-modulated upswept pulse signals with center frequencies ranging from approximately 20 kHz to nearly 70 kHz (Baumann-Pickering et al. 2013). Detection of these signals in passive acoustic recordings requires the use of high sampling rates (>100 kHz), which quickly leads to the accumulation of many terabytes of acoustic data over weeks or months of monitoring. Despite rapid advances in recording technology, data storage capacity remains the primary limiting factor in deployment durations of autonomous recording instruments, particularly at such high sampling rates (Sousa-Lima et al. 2013). Recorder deployment and recovery is both costly and logistically challenging, so the collection of high-frequency data for prolonged periods often involves a reduced recording schedule, employing a duty cycle to extend the duration of each deployment (e.g., Au et al. 2013). Using this approach, recordings are made for a specified time period at a regularly repeating interval, alternating with a non-recording period to reduce the amount of data collected per day and extend the overall monitoring period.

Recording schedules are often chosen based primarily on practical considerations, such as the specifications of the recording instrument, the required sampling rate, and the desired deployment duration, rather than detailed prior knowledge of the target species' acoustic behavior and detectability. However, it is important to consider any biases that may be introduced by using a reduced recording schedule (Thomisch et al. 2015). If the duty cycle listening period and recording interval are not appropriately matched to the duration and timing of acoustic events of interest, potential detections may be missed and species occurrence underestimated (Miksis-Olds et al. 2010, Sousa-Lima et al. 2013, Thomisch et al. 2015).

These considerations are rarely addressed in PAM studies, and may be especially important when using PAM to establish baseline information on the spatial and temporal occurrence of beaked whales, because underlying patterns in the relative occurrence and acoustic behavior of these species in most regions are poorly known. In this chapter I examine the potential effects of duty cycles on the assessment of daily presence of beaked whale echolocation signals in passive acoustic recordings, using datasets from three locations in the northwest Atlantic as case studies.

Methods

Data collection

Continuous passive acoustic recordings were collected at three locations along the continental shelf slope in the northwest Atlantic. In the mid-Atlantic region off the U.S. east coast, recordings were made offshore of Cape Hatteras, North Carolina (35° 20′ N, 74° 51′ W) from 30 May 2013 to 14 March 2014 (289 days) and near Norfolk Canyon, Virginia (37° 10′ N, 74° 28′ W) from 20 June 2014 to 4 April 2015 (289 days). At both sites, a High-frequency Acoustic Recording Package (HARP; Wiggins and Hildebrand 2007) was deployed at a depth of approximately 975 m, programmed to record continuously at a 200 kHz sampling rate. Along the Scotian Shelf off eastern Canada, recordings were made in the Gully, a prominent undersea canyon (42° 57’N, 58° 60’W) from 17 March 2010 to 25 March 2010 (8 days). At this site, an Autonomous Multichannel Acoustic Recorder (AMAR; JASCO Applied Sciences) was deployed at a depth of 1150 m, programmed to record continuously at a 384 kHz sampling rate.

Beaked whale detection & classification

Beaked whale echolocation signals were detected using a multistep process following the methods described in Baumann-Pickering et al. (2013). First, an automated detection algorithm was run through each full acoustic dataset to find echolocation clicks (Soldevilla et al. 2008). To discriminate between delphinid and beaked whale clicks, criteria based on spectral and temporal characteristics were applied (see Baumann-Pickering et al., 2013 for details). Clicks with peak and center frequencies of at least 32 and 25 kHz, respectively, durations of at least 355 μs, and frequency-modulated upsweeps with a sweep rate of at least 23 kHz/ms were considered potential beaked whale signals. The peak and center frequency thresholds were reduced to 23 kHz for the Gully dataset to detect clicks of northern bottlenose whales, *Hyperoodon ampullatus*. Due to a high level of false detections of non-beaked whale clicks after this initial discrimination step, an additional set of criteria was applied, requiring the waveform envelope of each click to increase over the first 0.1 ms and to remain above a 50% energy threshold for a duration of at least 0.1 ms. Clicks not meeting the criteria were removed from the analysis. The remaining clicks were grouped into detection events, defined as all consecutive beaked whale click trains separated by no more than 5 minutes. In a final classification step, each detected event was manually reviewed and assigned a species classification. Remaining false detections of non-beaked whale click events were removed from the analysis.

Subsampling analyses

To investigate the effects of using duty-cycled recordings to assess the daily presence of beaked whale echolocation signals, days with beaked whale detections in the continuous acoustic datasets were subsampled to simulate data collected at reduced recording schedules. Each recording schedule was defined by a duty cycle, representing the percent of time listening, and a cycle period duration in minutes, indicating the time between the start of one listening phase and the start of the next, repeated continuously throughout each day. Duty cycles of 50%, 25%, and 10% and cycle periods of 10, 20, 30, and 60 minutes were analyzed, for a total of 12 different recording schedules (Table 2).

Table 2: Recording schedules used for subsampling beaked whale detections. Each recording schedule is given as the number of minutes of listening time within each cycle period; cycle periods repeat continuously throughout each day.

	Cycle Period (minutes)			
Duty Cycle (%)	**10**	**20**	**30**	**60**
50	5 min	10 min	15 min	30 min
25	3 min[a]	5 min	8 min[a]	15 min
10	1 min	2 min	3 min	6 min

[a] Rounded up to the nearest full minute

To calculate a mean proportion of days ($\mathbf{P_d}$) for which daily presence was correctly assessed using each recording schedule, repeated subsampling was performed over each possible independent position of the duty cycle listening phase within the cycle period. For example, with a 50% duty cycle and 10 minute cycle period, there are two possible independent, non-overlapping positions for the 5-minute listening phase: 00:00-05:00 or 05:00-10:00. For each day i and listening phase position j, presence ($\boldsymbol{d}=1$) or absence ($\boldsymbol{d}=0$) of beaked whale detections in the subsampled data was determined, with presence defined as at least one detection event occurring within or overlapping with a listening phase. To calculate the mean proportion of days correctly assessed for beaked whale acoustic presence with a given recording schedule, the proportion of days with presence out of all $\boldsymbol{n}$ days with detections was averaged across all $\boldsymbol{p}$ listening phase positions:

$$\overline{\boldsymbol{P_d}} = \frac{\boldsymbol{1}}{\boldsymbol{np}}\sum_{\boldsymbol{j=1}}^{\boldsymbol{p}}\sum_{\boldsymbol{i=1}}^{\boldsymbol{n}} \boldsymbol{d_{i,j}} \tag{1}$$

The standard deviation for each recording schedule was calculated across the $\boldsymbol{p}$ independent listening phase positions. The subsampling calculation in Eq. (1) was repeated with all 12 recording schedules for each beaked whale species in each dataset.

Results

Description of acoustic datasets

Five distinct beaked whale click types were identified within the recordings. Four of these have been previously attributed to specific species: Cuvier's (*Ziphius cavirostris*), Gervais' (*Mesoplodon europaeus*) and Blainville's (*M. densirostris*) beaked whales and northern bottlenose whales (e.g., Johnson et al. 2004, Zimmer et al. 2005a, Gillespie et al. 2009, Wahlberg et al. 2011). The fifth click type is likely produced by Sowerby's beaked whales (*M. bidens*), based on similarities to clicks recorded in the presence of this species by Cholewiak et al. (2013) and known occurrence of Sowerby's beaked whales at the locations where this click type was recorded (Whitehead 2013, Waring et al. 2015). For simplicity, these clicks will be referred to as Sowerby's beaked whales throughout this paper. Table 3 provides a summary of the occurrence of each species within each full dataset. Multiple beaked whale species were detected at each recording site, with markedly different patterns in relative species occurrence among sites. The highest detection rates occurred at Cape Hatteras where Cuvier's beaked whales were detected most frequently. At Norfolk Canyon there were fewer beaked whale detections overall, and similar levels of occurrence of Sowerby's, Cuvier's, and Gervais' beaked whales. The Gully dataset, represented by a much smaller sample of recording days, contained detections of northern bottlenose whales and Sowerby's beaked whales at similar daily levels, but with more detections per day and longer detection durations for northern bottlenose whales.

Table 3: Summary of beaked whale detections in the continuous acoustic datasets analyzed. Mean number of detections per day was calculated across all *n* days with at least one detection. The number of detected events per day and the detection duration are reported as the mean ± standard deviation.

Site	Species	Number of days detected (*n*)	Percent of days detected	Mean number of detections per day	Mean detection duration (min)
Cape Hatteras	*Z. cavirostris*	272	94	11.8 (± 7.3)	7.3 (± 7.5)
	M. europaeus	120	42	3.3 (± 2.8)	5.5 (± 5.5)
(N=289 days)	*M. densirostris*	4	1	1.8 (± 0.5)	3.2 (± 3.0)
Norfolk Canyon	*Z. cavirostris*	59	20	2.0 (± 1.5)	7.6 (± 6.5)
	M. europaeus	43	15	1.9 (± 1.1)	6.0 (± 5.0)
(N=289 days)	*M. bidens*	103	36	1.9 (± 1.3)	4.7 (± 3.8)
The Gully	*H. ampullatus*	6	75	7.0 (± 2.3)	22.3 (± 17.9)
(N=8 days)	*M. bidens*	7	88	3.0 (± 2.2)	6.6 (± 3.7)

Subsampling comparisons

The effects of different recording schedules were compared by estimating the mean proportion of days correctly assessed for acoustic presence of each beaked whale species within each dataset. For all species at all sites, higher duty cycles (greater percent of time listening) resulted in higher proportions of days with a correct assessment (Fig. 7). Within a given duty cycle, shorter cycle periods consistently resulted in more days with a correct assessment. The effect of cycle period duration was most pronounced at the lowest duty cycles. For all but the most commonly detected species (Fig. 7A and 7G), a 10% duty cycle with a 60 minute cycle period resulted in correct assessment of presence in approximately 30%-60% of days, while the same duty cycle with a 10 minute cycle period resulted in correct assessment of presence in approximately 60%-95% of days (Fig. 7B-7F, 7H).

The degree to which daily presence was underestimated by subsampling varied among species and datasets. Subsampling had the largest effect on the probability of correctly assessing the daily presence of rarely detected species, and little to no effect on very commonly detected species, even at the lowest duty cycles. To investigate how low duty cycles differentially affected the assessment of presence among species within each dataset, a one-way analysis of variance (ANOVA) was used to examine differences in the mean proportion of days correctly assessed for each species after subsampling with a 10% duty cycle and a cycle period duration of 10, 20, 30, or 60 minutes. At Cape

Hatteras, there was significant variation among species in the mean proportion of days correctly assessed using any cycle period duration (ANOVA, all *p*-values <0.05). Post-hoc Tukey HSD tests indicated that the proportion of days correctly assessed was significantly higher for Cuvier's beaked whales than either Gervais' or Blainville's beaked whales, and higher for Gervais' than Blainville's beaked whales at the α=0.05 level. At Norfolk Canyon, there was significant variation among species for cycle period durations of 10, 20, and 30 minutes (ANOVA, all *p*-values <0.05). Here, the proportion of days correctly assessed was significantly higher for Cuvier's than either Sowerby's or Gervais' beaked whales at the α=0.05 level, while assessment of presence of the two *Mesoplodon* species did not differ significantly. At the Gully site, the proportion of days correctly assessed was significantly higher for northern bottlenose whales than Sowerby's beaked whales across all cycle period durations (Welch's t-test, *p*-values <0.05).

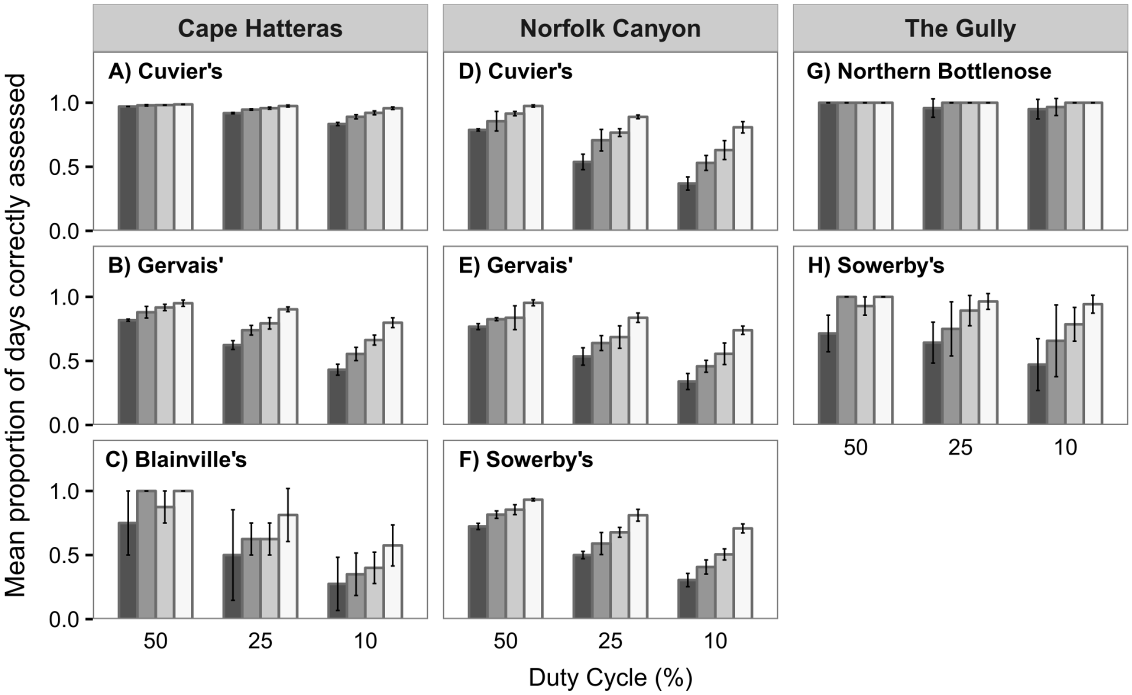

Figure 7: Comparison of the mean proportion of days correctly assessed for beaked whale acoustic presence after subsampling. Error bars indicate standard deviation. Groups of bars represent duty cycle (% of time listening), and the individual bars in each group represent cycle periods of 60, 30, 20, and 10 minutes, from left (dark gray) to right (light gray).

Discussion

Predictably, any reduction in recording effort over a given monitoring period will lead to underestimation of species presence, except for those that are continuously present and acoustically active (Riera et al. 2013, Thomisch et al. 2015). The results presented here demonstrate that frequent, short listening periods provide a more accurate assessment of daily presence than longer, less frequent periods, even when the overall amount of recording effort is lower. Unlike many other marine mammal species, which may be detected over long distances for hours at a time, beaked whale clicks are only detected over relatively short ranges and durations, while the animal is foraging in close proximity to the recorder (Hildebrand et al. 2015). Consequently, many beaked whale detections are likely to be missed if recordings are collected on a schedule where the cycle period duration greatly exceeds the average duration of detection events, which may be as short as a few minutes.

Assessment of the daily presence of beaked whales in subsampled recordings was strongly influenced by the underlying levels of acoustic activity of each species, which differed among locations. As beaked whale occurrence is spatially variable (e.g., Baumann-Pickering et al., 2014), it is not possible to generate a broadly applicable correction factor for beaked whale presence in duty-cycled recordings collected at other locations. Nevertheless, it is worth noting that a consistent pattern was observed among species. At low duty cycles (10% listening time) the daily presence of *Mesoplodon* species was underestimated to a significantly greater degree than either Cuvier's beaked whales or northern bottlenose whales, across all three datasets examined. This result may be explained in part by the high numbers of detections per day of Cuvier's beaked whales and northern bottlenose whales at Cape Hatteras and the Gully, respectively, but the same pattern was found at Norfolk Canyon, where Cuvier's beaked whales did not occur more frequently than the other species (Table 3).

Cuvier's beaked whales and northern bottlenose whales exhibited longer mean detection durations than *Mesoplodon* species. This could reflect greater numbers of individuals present, behavioral differences in dive depths and movement patterns of foraging animals, and/or acoustic characteristics of echolocation signals, such as frequency content, source level, and beam width (Tyack et al. 2006a, Zimmer et al. 2008, Shaffer et al. 2013). The foraging and acoustic behavior of Cuvier's and Blainville's beaked whales have been reasonably well-studied (e.g., Baird et al., 2006; Johnson et al., 2008; Tyack et al., 2006b), but there is little to no information available for many other beaked whale species, including Gervais' and Sowerby's beaked whales. Further data obtained from tagging studies may shed light on differences in acoustic detectability and help inform PAM efforts for these species.

Ultimately, recording schedules must be chosen to balance the scope and goals of the study with the capabilities of the recording system (Thomisch et al. 2015). As technology continues to improve and data storage becomes less expensive, it is becoming feasible to collect continuous recordings over long deployment periods, even at high sampling rates. In cases where continuous monitoring is not practicable, a recording schedule based on short, frequent listening periods is recommended as the best choice for detecting beaked whales. However, it should not be assumed that all species will be equally under-sampled at the level of daily presence, as low duty cycles can lead to biased estimation of relative species occurrence. Whenever possible, duty-cycled recordings should be validated against continuous data collected within the same or similar regions where the same species of interest are detected. At a minimum, it is necessary to carefully consider the inferences drawn from duty-cycled recordings, particularly where these recordings provide the only available information on the relative occurrence of beaked whales and other poorly-known species.

Chapter 3: Spatial and seasonal patterns in acoustic detections of sperm whales (*Physeter macrocephalus*) along the continental slope in the western North Atlantic Ocean[1]

Introduction

The seasonal distributions of many pelagic cetacean species are poorly known, owing to their highly mobile lifestyle and the vast extent of their oceanic habitat, which makes habitat-scale observations exceedingly difficult. Shipboard and aerial surveys for cetaceans are typically costly, labor-intensive, and dependent on weather conditions, and these practical limitations create a tradeoff between surveying broad spatial areas and obtaining repeated observations over time within the same region. Consequently, assessing spatiotemporal patterns in cetacean occurrence remains a challenge, especially for species that range across ocean basins.

Sperm whales (*Physeter macrocephalus*) are among the most widely distributed mammalian species on earth, found throughout the world's oceans from the equator to the polar ice edges (Rice 1989b), with individual home ranges that can span more than 1,000 km in diameter (Whitehead 2003). The global distribution of this species has held particular significance to humans for nearly three centuries, as sperm whales were an

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important target for the whaling industry in the 18th and 19th centuries, beginning in the Atlantic Ocean and later expanding throughout the world. Sperm whales were targeted again by modern whalers in the mid-20th century, with catch rates peaking in the 1960s prior to an international moratorium on commercial whaling which took effect in 1985 (Best 1983). Whitehead (2002) estimated that the global abundance of sperm whales was reduced to 30% of their pre-whaling numbers as a result of human exploitation.

Charts compiled from whaling logbooks provide some of the earliest information on the spatial and temporal distributions of sperm whales, and document the presence of “grounds” or areas of relatively high density in each ocean basin (Townsend 1935). In the western North Atlantic, sperm whales were hunted off the entire east coast of the United States, with a particular emphasis on the “Charleston Ground” located southeast of Cape Hatteras, North Carolina and some historical references to the “Hatteras Ground,” located closer to the cape (Goode 1884, Townsend 1935, Smith et al. 2012). Concentrations of sperm whales were observed east of the U.S. coast between Cape Hatteras and the Bahamas, particularly between February and May (Tomilin 1957). Today, sperm whales inhabiting the western North Atlantic are mainly encountered along the edge of the continental shelf and offshore, particularly near submarine canyons and seamounts (Waring et al. 2001, Wong and Whitehead 2014). A seasonal latitudinal shift in sperm whale densities has been suggested to occur in this region, with greater concentrations found east and northeast of Cape Hatteras during the winter months followed by a northward expansion to the shelf break along the mid-Atlantic Bight, Georges Bank, and southern New England during the spring and summer (Perry et al. 1999, Waring et al. 2014). A recent effort to create spatially and temporally explicit models of sperm whale density throughout the U.S. east coast region by Roberts et al. (2016) provided support for this pattern, but the authors noted that survey data from non-summer periods were scarce, limiting their ability to effectively model seasonal changes (see also Roberts et al. 2016b). Most information on sperm whale occurrence and abundance in U.S. waters in the past few decades has come from dedicated shipboard and aerial visual surveys conducted over the continental shelf and along the shelf break and slope regions during spring and summer months, when weather conditions are most favorable for visual observation.

To overcome this seasonal bias in cetacean occurrence data, passive acoustic monitoring is increasingly being used to obtain continuous records of species presence throughout the year, especially in remote offshore regions that are difficult to access, particularly during the winter. Recently, broad-scale passive acoustic monitoring with fixed recorders has been effectively used to describe seasonal migration patterns of baleen whale species (Risch et al. 2014, Thomisch et al. 2016) as well as spatiotemporal distributions of odontocetes, such as beaked whales, at locations distributed across an ocean basin (Baumann-Pickering et al. 2014).

Sperm whales are highly vocal, producing several types of impulsive broadband signals that fulfill both sensory and communicative functions. The most commonly produced sperm whale sounds are echolocation clicks, often referred to as “regular” or “usual” clicks. These powerful, highly directional clicks are typically produced at evenly spaced intervals of 0.2-2.0 s throughout foraging dives (Wahlberg 2002, Watwood et al. 2006), and contain energy predominantly at frequencies between 5-15 kHz (Madsen et al. 2002a, Møhl et al. 2003, Zimmer et al. 2005b). During foraging dives, trains of regular clicks are punctuated by “creaks” (also called buzzes), consisting of short bursts of clicks with a higher repetition rate, which are believed to occur during prey capture attempts as the whale closes in on prey (Miller et al. 2004). Sperm whales also emit clicks associated with social behavior, including “codas”, which are patterned series of clicks most commonly recorded among female groups (Watkins and Schevill 1977, Weilgart and Whitehead 1993), and “slow clicks” or “clangs,” which are produced by mature males and characterized by lower frequency content, longer inter-click-intervals (> 2 s), and a distinctive ringing tone that makes them audibly distinct from regular clicks (Weilgart and Whitehead 1988).

Since the first descriptions of sperm whale calls by Backus and Scheville (1966), vessel-based acoustic surveys have played an important role in the study of this species. Real-time passive acoustic monitoring allows researchers to detect and track vocalizing animals during the long periods when they are not visible at the surface, thus providing a window into foraging behaviors and social interactions. Despite longstanding scientific interest in the acoustic behavior of sperm whales and the widespread use of acoustic methods to assist in locating, tracking, and counting these whales (e.g., Wahlberg 2002, Barlow and Taylor 2005), only a few published studies have employed fixed, bottom-mounted acoustic recorders to examine the seasonal presence and foraging activity of sperm whales across broad spatial scales and/or multiple seasons or years (Mellinger et al. 2004, Wong and Whitehead 2014). In this chapter, I describe seasonal patterns in acoustic detections of sperm whales along a portion of the continental slope in the western North Atlantic. I analyzed passive acoustic recordings collected between Florida and New England to provide new baseline information on year-round sperm whale presence in this region, and determine whether there is evidence of seasonal shifts in the relative occurrence of sperm whales across recording sites.

Methods

Data Collection

I collected passive acoustic recordings at five sites along the continental slope in the western North Atlantic Ocean between August 2011 and May 2015 (Fig. 8, Table 4). All recording sites were located at depths between 800 and 970 m. Temporal coverage varied among sites, due to evolving data collection objectives and occasional instrument failures that occurred over the course of the study. The total recording effort consisted of a single 10-month deployment at each of the Georges Bank, Norfolk Canyon, and Jacksonville sites, and multiple deployments conducted across 2-3 years at the Cape Hatteras and Onslow Bay sites (Table 4). I used two types of autonomous, bottom-mounted recording devices to collect passive acoustic recordings: High-frequency Acoustic Recording Packages (HARPs; Wiggins and Hildebrand 2007) and an Autonomous Multi-channel Acoustic Recorder (AMAR; JASCO Applied Sciences). HARPs were programmed to collect recordings at a sampling rate of 200 kHz, either continuously (Jacksonville, Cape Hatteras, and Norfolk Canyon sites) or on a duty-cycled schedule of 5 minutes of recording time repeating every 10 minutes (Onslow Bay site). The AMAR, deployed at the Georges Bank site, sampled at 250 kHz on a duty cycle of 2 minutes and 40 seconds repeating every 30 minutes. This recording schedule was used to maximize the deployment duration, given the data storage capacity of the device. After retrieval of each instrument, I analyzed all recording days that included a full 24 hours of data, excluding the first and last day of each deployment which had only partial recording coverage.

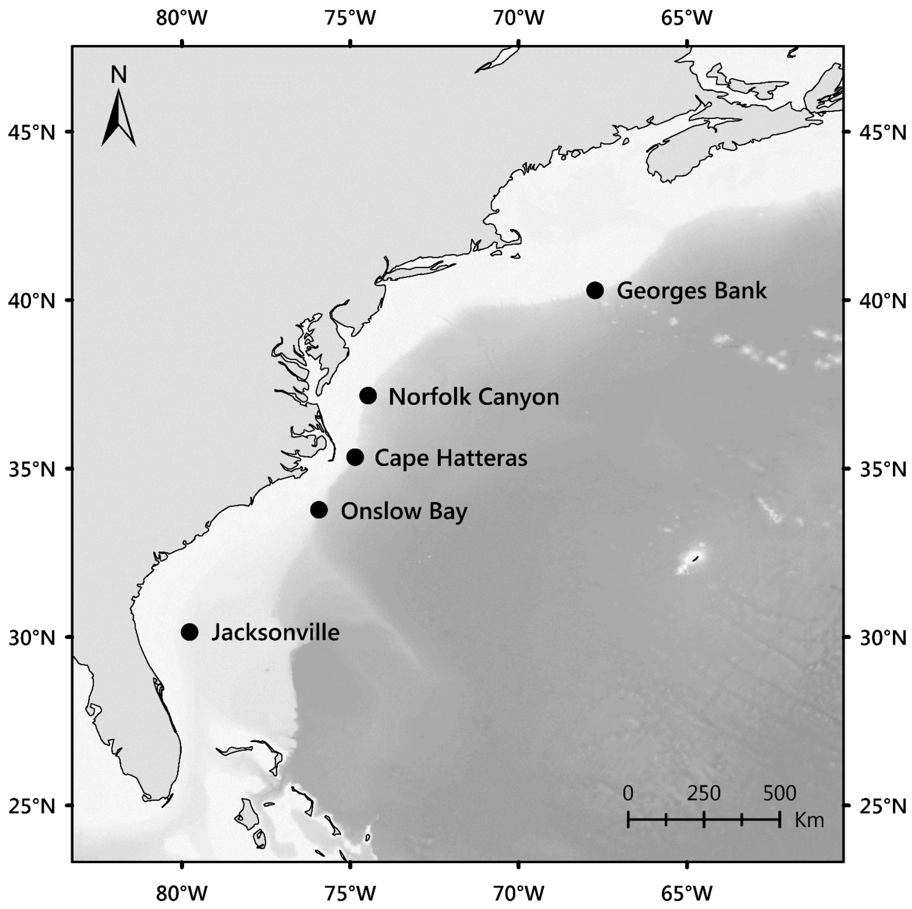


Figure 8: Map of passive acoustic recording sites off the east coast of North America in the western North Atlantic Ocean

Table 4: Summary of passive acoustic monitoring effort along the western North Atlantic continental slope between 2011 and 2015. Recorder type specifies either an Autonomous Multi-channel Acoustic Recorder (AMAR) or High-frequency Acoustic Recording Package (HARP). Duty cycles are defined as the duration of the recording period/cycle period (interval between the start of one recording period and the start of the next).

Site	Location	Depth (m)	Recording dates	Recording days	Recorder type	Duty cycle (mm:ss)	Sampling rate (kHz)
Georges Bank	40.29N, 67.72W	800	7/27/14-5/26/15	304	AMAR	2:40/30:00	250
Norfolk Canyon	37.16N, 74.47W	980	6/20/14-4/4/15	289	HARP	Continuous	200
Cape Hatteras	35.34N, 74.85W	950 970 970 850	3/16/12-4/10/12 10/10/12-4/30/13 5/30/13-3/14/14 5/9/14-12/10/14	734	HARP	Continuous	200
Onslow Bay	33.78N, 75.93W	950 915 850	8/19/11-11/30/11 7/14/12-10/1/12 10/25/12-6/29/13	432	HARP	5:00/10:00	200
Jacksonville	30.15N, 79.77W	806	8/24/14-5/28/15	278	HARP	Continuous	200

Acoustic Data Analysis

I manually screened the acoustic recordings for sperm whale signals using long-term spectral averages (LTSAs), which provide a compressed spectrogram view allowing efficient visual examination of long datasets (Wiggins and Hildebrand 2007). I used the custom software program *Triton* (Scripps Whale Acoustic Lab, Scripps Institution of Oceanography, La Jolla, CA) developed in MATLAB (The Mathworks, Inc., Natick, MA) to compute LTSAs with a time and frequency resolution of 5 s and 100 Hz, respectively. For analysis, I viewed 0.5 to 1 h LTSA segments across a frequency range of 0-30 kHz, and marked the hourly presence or absence of sperm whale echolocation clicks, which were visible and distinguishable from background noise and signals from other species (Fig. 9). During periods with higher background noise or many overlapping delphinid vocalizations, I verified the presence of sperm whale clicks by visually examining spectrograms (FFT 1024, 0.5 overlap) with a 10 s time window and 0-30 kHz frequency range and listening to sections of interest.

In addition to regular (echolocation) clicks, I occasionally observed slow clicks, codas, and creaks in the recordings; however, only regular clicks were consistently identifiable in the LTSAs, and were present far more frequently than any other sperm whale click type. For this analysis, therefore, I chose to focus solely on regular clicks, which are produced by both sexes and all age classes of sperm whales with the exception of young calves, and thus provide a reliable indication of sperm whale presence and foraging activity (Whitehead 2003).

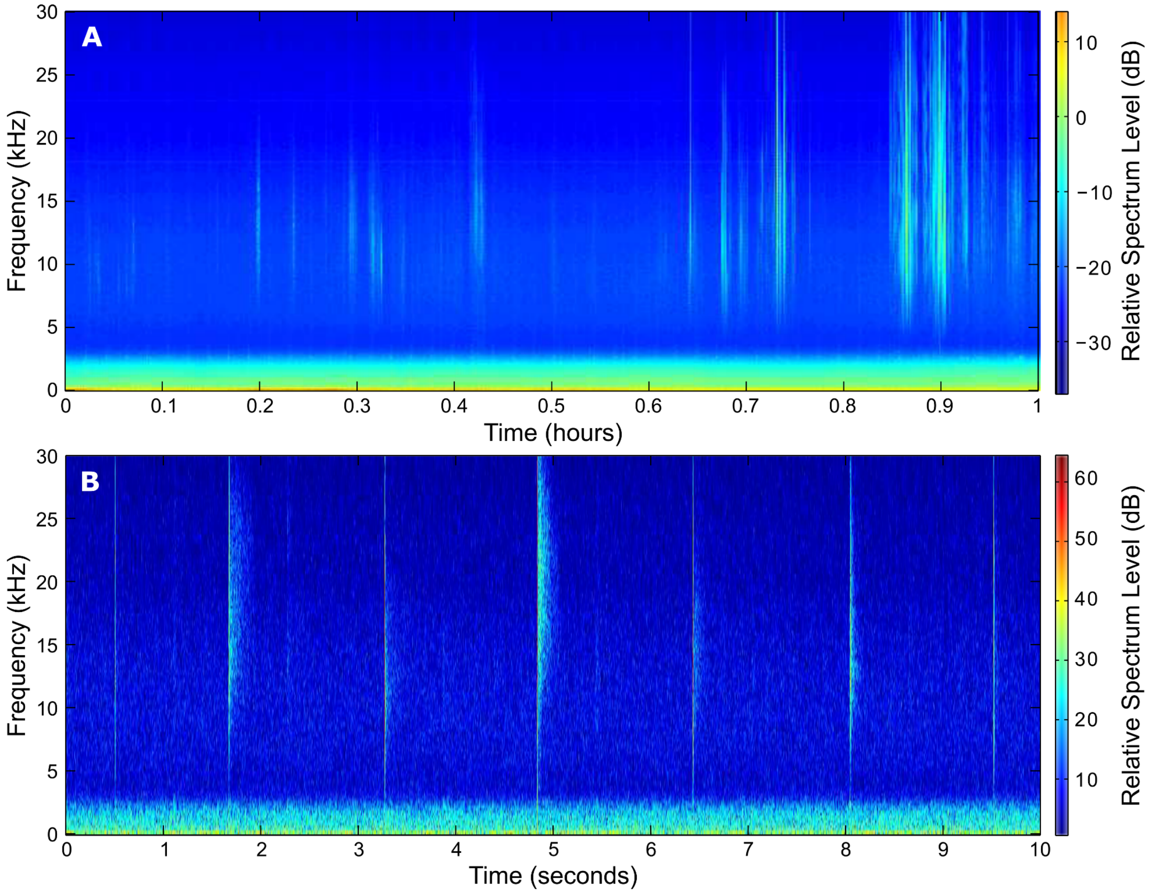


Figure 9: Example (A) 1-hr long-term spectral average (LTSA) and (B) 10-s spectrogram containing sperm whale regular clicks

Effects of duty-cycled recording schedules

Recordings at the Georges Bank and Onslow Bay sites were collected using duty-cycled recording schedules, potentially leading to the underestimation of sperm whale acoustic presence. To estimate the probability of correctly assessing the hourly and daily presence of sperm whale clicks in the duty-cycled recordings, I performed a subsampling experiment using continuous HARP recordings from the Norfolk Canyon, Cape Hatteras, and Jacksonville sites. I randomly selected 100 recording days in which sperm whale signals were present, containing a total of 903 hours with click detections, and then subsampled these data based on the two duty-cycled recording schedules: 5 min per 10 min cycle period or 3 min per 30 min cycle period, repeating continuously throughout each day. For each recording schedule I performed repeated subsampling, shifting the position of the recording period through the cycle period in one-minute increments, and determining the presence or absence of clicks on an hourly and daily basis with each subsampling permutation (10 or 30 possible permutations depending on the recording schedule). Detection probabilities for each hour and day were calculated as the proportion of permutations which resulted in a correct assessment of presence. Finally, I calculated the mean and standard deviation of the hourly and daily detection probabilities for each recording schedule across all sampled hours and days (Table 5).

Table 5: Results of subsampling a randomly selected subset of continuous recordings to estimate the mean probability (± standard deviation) of correctly assessing daily and hourly presence of sperm whale clicks with each duty-cycled recording schedule. Duty cycles are specified by the number of minutes of recording time/cycle period and the percent of time recordings were made.

	Duty cycle	
	5/10 (50%)	**3/30 (10%)**
Daily *n = 100*	0.99 (± 0.07)	0.92 (± 0.20)
Hourly *n = 903*	0.92 (± 0.16)	0.58 (± 0.33)

Statistical Analysis

To examine seasonal patterns in sperm whale acoustic presence at each recording site, I used the number of hours per day with clicks, expressed as a proportion, to compare the relative presence of foraging sperm whales across seasons, defined as winter (January-March), spring (April-June), summer (July-September) and fall (October-December). For each site, I fit a binomial generalized linear model (GLM) with season as a categorical explanatory variable, and used a generalized estimating equation (GEE) approach to account for temporal autocorrelation in the model residuals (Liang and Zeger 1986). GLMs assume independence among model residuals, but the GEE method explicitly models the correlation within specified 'blocks' of data, assuming independence between blocks, to produce robust standard errors and p-values (e.g., Panigada et al. 2008, Bailey et al. 2013, Pirotta et al. 2014). Here, I used an autoregressive (AR1) correlation structure to model the temporal dependence within blocks, since the dependence is expected to decay with time. The extent of residual autocorrelation varied among recording sites, so for each site I chose a block size of 5, 20, or 30 days based on examination of autocorrelation function (ACF) plots of the GLM residuals. Blocks were defined based on contiguous recording days. Seasonal recording effort varied among sites, with data available from 2-3 years per season at Cape Hatteras, 1-2 years per season at Onslow Bay, and a single year at Georges Bank, Norfolk Canyon, and Jacksonville. Because I lacked full seasonal coverage across replicate years of monitoring at most of the recording sites, I did not attempt to assess inter-annual variation by including an interaction between season and year. Instead, data from all years with recording effort were pooled by season within each site (Table 6). At Norfolk Canyon, only 15 days of recording effort took place during the spring, and I therefore omitted spring in the seasonal model for this site. I fit models using the 'geeglm' function in the *geepack* library in R (Halekoh et al. 2006), and performed post-hoc pairwise comparisons using the least-squares means ('lsmeans') function in the *lsmeans* library (Lenth 2016) to evaluate differences among seasons.

Table 6: Seasonal recording effort across sites, specified by the number of recording days per season at each recording site, pooled across all years.

Site	**Season**			
	Winter (Jan-Mar)	Spring (Apr-Jun)	Summer (Jul-Sep)	Fall (Oct-Dec)
Georges Bank (2014-2015)	90	56	66	92
Norfolk Canyon (2014-2015)	90	15	92	92
Cape Hatteras (2012-2014)	179	125	184	246
Onslow Bay (2011-2013)	90	90	122	130
Jacksonville (2014-2015)	90	58	38	92

To illustrate diel patterns in sperm whale acoustic presence across time of day at each recording site, I plotted counts of hourly click presence for each hour of the day, summed across all recording days. To compare the relative hourly presence of clicks between day and night at each recording site, I determined local sunrise and sunset times for each calendar day with recording effort, based on data from the U.S. Naval Observatory website (http://aa.usno.navy.mil). I defined day and night diel periods as the hours between sunrise and sunset and the hours between sunset and sunrise, respectively. The hour encompassing each sunrise and sunset time was assigned to the diel period containing the majority of that hour. For each recording day, I calculated the number of hours with sperm whale detections as a percentage of the total number of hours in each diel period, to account for variation in the length of diel periods across latitudes and seasons. To test for differences in acoustic presence between day and night diel periods at each site, I used a non-parametric Mann-Whitney *U* test, including only days with sperm whale detections present.

Results

I analyzed more than 48,000 hours of passive acoustic recordings collected across the five study sites, with the highest recording effort at the Cape Hatteras and Onslow Bay sites (Table 7). Sperm whale clicks were detected at all sites, in 54% of all recording days and 16.5% of all recording hours. Evaluation of the duty-cycled recording schedules employed at Onslow Bay and Georges Bank indicated that daily presence was not substantially underestimated in the duty-cycled data, with a greater than 90% probability of correctly assessing presence (Table 5). Therefore, daily acoustic presence provided a consistent metric to compare the relative occurrence of sperm whales across recording sites. Hourly presence was substantially underestimated by the lower duty-cycled recording schedule employed at Georges Bank, with a 58% (± 33%) mean probability of correctly assessing hourly presence (Table 5).

At the level of daily presence, sperm whales were present most frequently at Georges Bank, where clicks were detected on 77% of recording days. Sperm whale clicks were present in 59%, 65%, and 49% of recording days at Norfolk Canyon, Cape Hatteras, and Onslow Bay, respectively. At Jacksonville there were notably few sperm whale detections, with clicks present on just 4% of recording days. Hourly presence followed the same trend across recording sites, except that hourly presence was slightly lower at Georges Bank (21% of recording hours) than at Cape Hatteras (23% of recording hours), likely due to substantial underestimation of hourly presence in the duty-cycled recordings collected at Georges Bank.

Table 7: Summary of sperm whale regular click detections across recording sites: Georges Bank (GBK), Norfolk Canyon (NFC), Cape Hatteras (HAT), Onslow Bay (ONB), and Jacksonville (JAX).

	GBK	NFC	HAT	ONB	JAX	Total
Number of recording days	304	289	734	432	278	2,037
Days with click detections	233	170	474	212	11	1,100
Days with click detections (%)	77	59	65	49	4	54
Number of recording hours	7,296	6,936	17,616	10,368	6,672	48,888
Hours with click detections	1,522	1,095	4,071	1,338	42	8,068
Hours with click detections (%)	21	16	23	13	0.6	16.5

Sperm whale clicks were detected in all seasons of the year at each recording site, with considerable temporal variability in the number of hours per day with detections (Fig. 10). There were clear seasonal patterns in sperm whale occurrence at Georges Bank, Norfolk Canyon, and Cape Hatteras, and weaker evidence of seasonality at Onslow Bay (Fig. 11). GEE-GLM models revealed significant effects of season on sperm whale occurrence at all sites except for Jacksonville, where there were very few sperm whale detections. At Georges Bank, sperm whale occurrence was significantly higher during spring than any other season, with no clear differences among winter, summer, and fall (Table 8; Fig. 11). The available data from Norfolk Canyon suggested a similar pattern at this site, but I did not include spring in my statistical comparison of seasons at this site, due to the small sample size of recording days collected during spring. I found significantly lower sperm whale occurrence in fall than either winter or summer at

Norfolk Canyon (Table 8; Fig. 11). Cape Hatteras exhibited the most distinct seasonal pattern of any recording site, with significantly higher sperm whale occurrence during the winter than any other season (Table 8; Fig. 11). Sperm whale clicks were present at intermediate levels during the spring and summer seasons, and at consistently low levels during the fall, and this pattern appeared to be similar across multiple years of monitoring (Fig. 10). The winter peak in sperm whale occurrence that I observed at Cape Hatteras was not present just to the south in Onslow Bay, where sperm whale click presence was higher during spring than winter (Table 8), but otherwise not strongly seasonal (Fig. 11). At Jacksonville, sperm whale clicks were present only sporadically throughout the year, and sample sizes were too small to determine any effect of season.

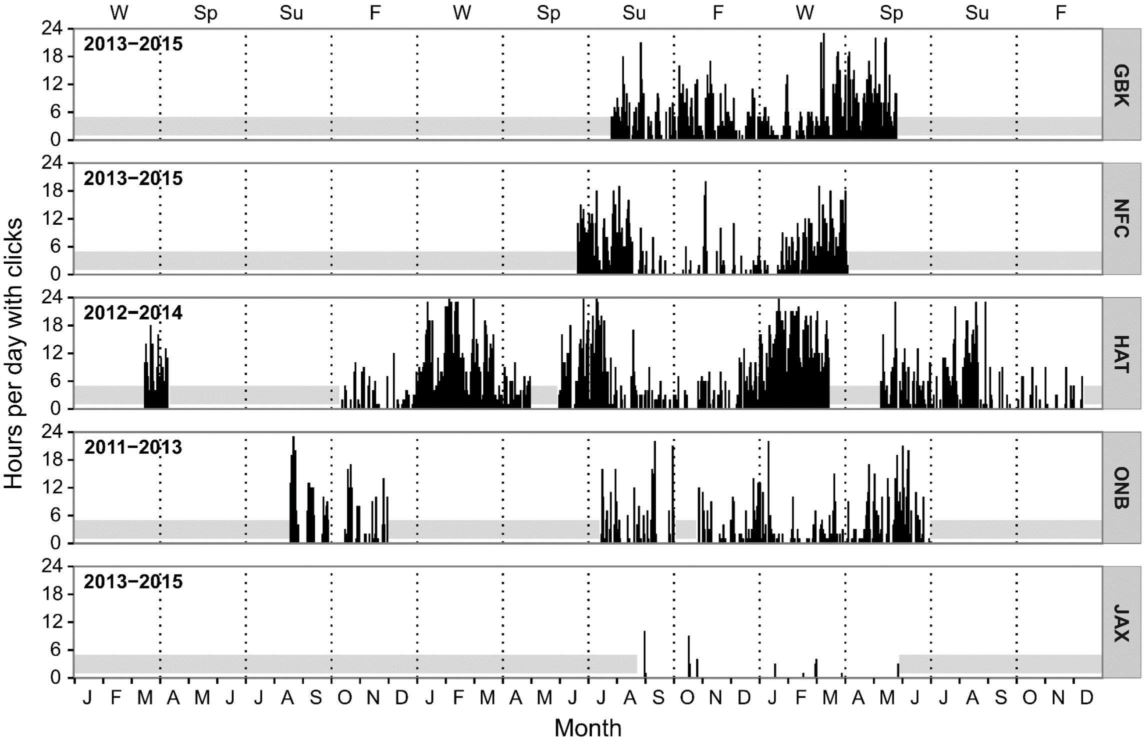


Figure 10: Temporal occurrence of sperm whale regular clicks across all recording periods at the Georges Bank (GBK), Norfolk Canyon (NFC), Cape Hatteras (HAT), Onslow Bay (ONB), and Jacksonville (JAX) recording sites. Gray bars indicate periods with no recording effort. Years are specified on each panel; seasons are indicated on top axis and delineated by dotted lines.

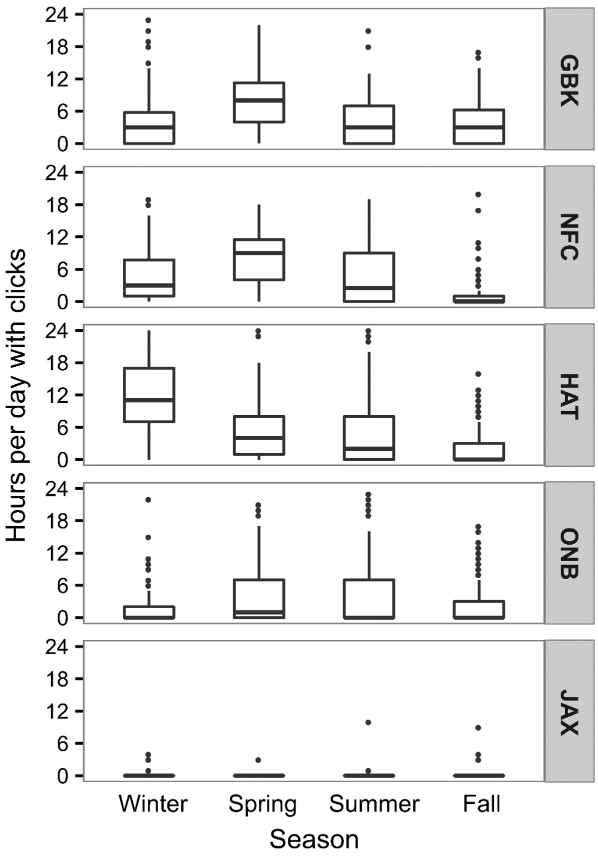


Figure 11: Seasonal occurrence of sperm whale clicks at the Georges Bank (GBK), Norfolk Canyon (NFC), Cape Hatteras (HAT), Onslow Bay (ONB), and Jacksonville (JAX) recording sites, pooled across all years with recordings. Boxplots show the median and first and third quartiles, with whiskers extending to 1.5 times the inter-quartile range, and points represent data beyond this range.

Table 8: Results of least-squares means pairwise comparisons among seasons based on GEE-GLM models of sperm whale occurrence at each recording site. Parameter estimates on the link scale are shown above the diagonal and p-values below, with bold font indicating p-values <0.05.

Georges Bank	Winter	Spring	Summer	Fall
Winter	-	-1.0074	-0.1024	0.0265
Spring	**0.0041**	-	0.9051	1.0339
Summer	0.9936	**0.0153**	-	0.1288
Fall	0.9998	**<0.0001**	0.9761	-

Norfolk Canyon	Winter	Spring	Summer	Fall
Winter	-	-	-0.0779	1.2596
Spring	-	-	-	-
Summer	0.9864	-	-	1.3375
Fall	**0.0085**	-	**0.0053**	-

Cape Hatteras	Winter	Spring	Summer	Fall
Winter	-	0.99	1.198	1.985
Spring	**<0.0001**	-	0.207	0.995
Summer	**0.0157**	0.9241	-	0.787
Fall	**<0.0001**	**0.0006**	0.1736	-

Onslow Bay	Winter	Spring	Summer	Fall
Winter	-	-0.8241	-0.8117	-0.2998
Spring	**0.0298**	-	0.0124	0.5243
Summer	0.0709	1.000	-	0.5118
Fall	0.7632	0.2513	0.367	-

Sperm whale regular clicks were recorded in all hours of the day, and I did not observe noteworthy patterns in click presence by time of day at any recording site (Fig. 12a). Comparison of hourly presence between day and night diel periods (Fig. 12b) resulted in a significant difference only at the Georges Bank site, where the median percent of hours with clicks per diel period was greater during the day (27%) than during the night (18%) (Mann-Whitney *U*, U=31706, p=0.00049). This result was statistically significant, but it is not clear whether this pattern has particular biological significance, because sperm whale foraging clicks were detected frequently in all hours of the day at this site, as shown in Fig. 12a.

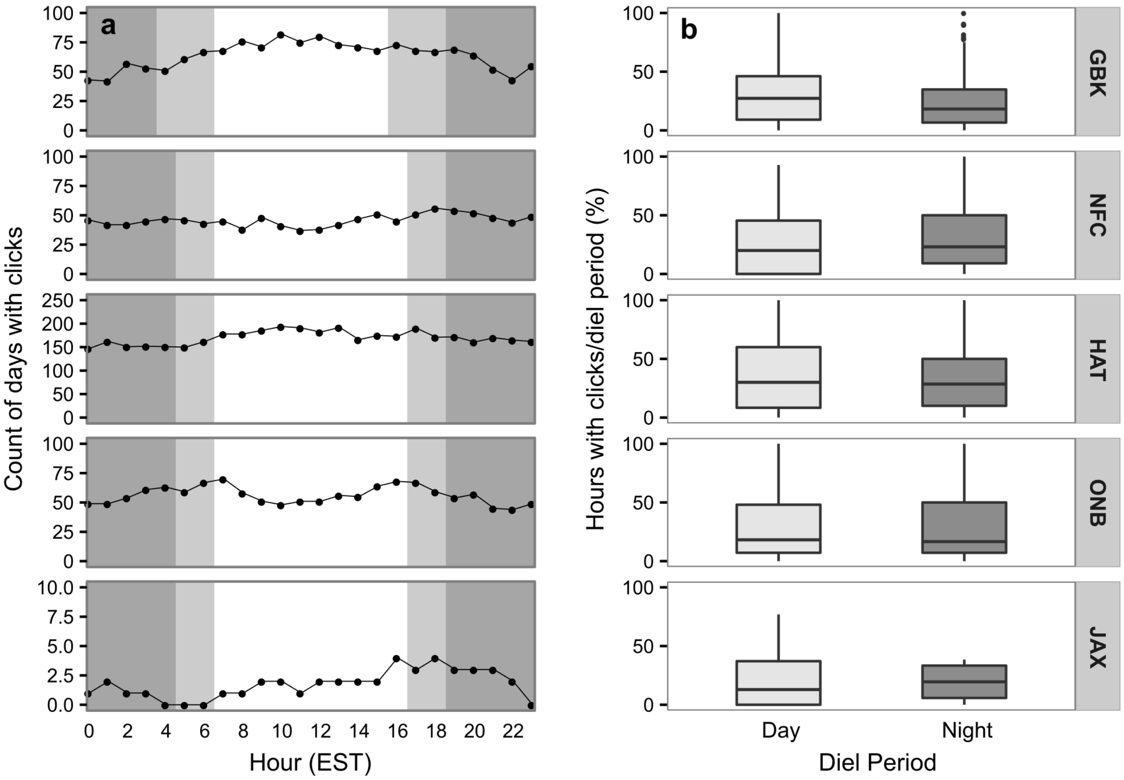


Figure 12: Diel patterns in sperm whale click detections across the Georges Bank (GBK), Norfolk Canyon (NFC), Cape Hatteras (HAT), Onslow Bay (ONB), and Jacksonville (JAX) recording sites, shown as (a) count of the total number of days with clicks present in each hour of the day, with dark gray shading indicating nighttime hours, white background indicating daytime hours, and light gray shading indicating hours that were classified as either night or day depending on the time of year, and (b) the percent of hours per diel period with sperm whale clicks, with boxplots showing the median and first and third quartiles, whiskers extending to 1.5 times the inter-quartile range, and points representing data beyond this range.

Discussion

This study represents the first broad-scale passive acoustic monitoring effort for sperm whales in the Atlantic Ocean, incorporating data from multiple sites and seasons. I detected sperm whale regular clicks year-round along the continental slope between

North Carolina and New England, and observed both spatial and seasonal variation in relative occurrence. Sperm whales were commonly present at all but the southernmost recording site, with the highest daily presence recorded along Georges Bank off southern New England, as well as in the mid-Atlantic region off Cape Hatteras, North Carolina. Both of these areas have been noted as seasonally important habitats for sperm whales in the western North Atlantic (Waring et al. 2014). The "Hatteras Ground" was recognized as an important habitat for sperm whales prior to the 20th century (Goode 1884). The Cape Hatteras slope area is characterized by a dynamic convergence of water masses that act to enhance biological productivity in the region, supporting a high density and diversity of cetacean species (Roberts et al. 2016a). In contrast to the northern portion of the study area, there were very few sperm whale clicks recorded off Jacksonville, Florida. This recording site was located on the continental slope at a comparable depth to the other sites in the study, but the bathymetry of the continental margin off the coast of Florida differs from that of the northern sites. Off Florida, the slope descends only to approximately 800-1000 m depth before flattening out into the Blake Plateau, which extends 375 km offshore before dropping off steeply to the abyssal plain. In contrast to the deeper slope waters further north, this area of intermediate depth over the Blake Plateau may not represent high-quality habitat for sperm whales.

The seasonal patterns I observed at the Georges Bank, Norfolk Canyon, and Cape Hatteras study sites are generally consistent with the seasonal shift in sperm whale concentrations previously described in the western North Atlantic (Perry et al. 1999, Waring et al. 2014). At Cape Hatteras, sperm whale click occurrence peaked during the winter months, when higher concentrations of sperm whales are expected in this region (Perry et al. 1999). Clicks were present at intermediate levels during the spring and early summer, and at consistently low levels during the late summer and fall, when most sperm whales are likely foraging at higher latitudes and in the continental shelf waters off New England (Waring et al. 2014). North of Cape Hatteras, the seasonal peak in sperm whale click occurrence appeared later in the year, with a particularly notable increase during spring at Georges Bank. Wong and Whitehead (2014) reported a similar higher prevalence of sperm whale clicks during the spring at Kelvin Seamount, part of the New England seamount chain extending southeast from Georges Bank, and it is likely that these seamounts represent an important seasonal foraging habitat for sperm whales. South of Cape Hatteras, seasonal patterns in sperm whale occurrence were less apparent in the data. Density maps produced by Roberts et al. (2016b) indicate lower sperm whale abundance along the continental slope off the southeastern U.S., and suggest a more offshore distribution in this region.

The seasonal distribution of sperm whales is likely driven to a large degree by the pursuit of foraging opportunities, which may vary across different spatial and temporal scales (Jaquet and Whitehead 1996). In the Pacific, sperm whale distributions are broadly associated with regions of higher primary productivity, though these relationships are often difficult to discern due to the spatial and temporal lags between increased primary productivity and enhanced foraging opportunities for upper trophic level predators (Jaquet and Whitehead 1996, Jaquet et al. 1996). On smaller scales, sperm whales have been found to associate with distinct oceanographic features such as sea-surface temperature fronts (e.g., Gannier and Praca 2006) and eddies (e.g., Biggs et al. 2000) which may aggregate prey. The prominent oceanographic feature in our study region is the powerful Gulf Stream, flowing north and northeastward just beyond the shelf break. Sperm whales are often encountered near Gulf Stream eddies, particularly where these features interact with bathymetric features of the shelf edge (Waring et al. 1993, Griffin 1999) or seamounts (Wong and Whitehead 2014). However, these oceanographic relationships are still poorly understood, and knowledge of prey distributions in this region is extremely limited.

The spatial inferences drawn from this study are broad by necessity, because data were collected with a single recording device at each site, separated by distances of up to 700 km. Sperm whale distributions are typically patchy, and although the patterns I observed are largely consistent with expected latitudinal trends, they likely reflect characteristics of the individual recording sites as well as broader trends. An approximate detection range of 16 km has been estimated for sperm whale regular clicks at depth (Madsen et al. 2002b), so each of my recording sites should be considered an individual point sample. Detection range may vary due to sound propagation conditions, ambient noise levels, and click characteristics, including source level, directionality, and orientation of the animal relative to the receiver. A full analysis of the site-specific detection range and temporal variation in the detection probability of sperm whale clicks was beyond the scope of this study. Thus, the hourly presence reported here should be considered a minimum estimate of the amount of time one or more sperm whales were present at the location of each recorder. Using hourly time bins reduced some of the variability in click detection because it increased the chances of recording at least a few on-axis clicks over the duration of a foraging dive. Additionally, all recordings were collected at high sampling rates, encompassing the full frequency spectrum of sperm whale clicks. Ambient noise is usually loudest at low frequencies, so the availability of broadband data improved the visibility of clicks.

The use of GEE-GLM models allowed for a robust comparison of the relative occurrence of sperm whale clicks across seasons, despite the presence of temporal autocorrelation, which reduces the validity of many commonly-used statistical tests that rely on the assumption of independence in the response variable. The seasonal comparisons I performed provide a broad overview of seasonality in sperm whale occurrence based on the available recordings, and do not account for temporal variation occurring at finer time scales within seasons. Collecting additional years of recordings, particularly at the Georges Bank and Norfolk Canyon sites, and reducing the gaps between successive deployments would improve our ability to describe and predict seasonal patterns and to detect inter-annual trends in sperm whale occurrence. The use of duty-cycled recording schedules at the Georges Bank and Onslow Bay recording sites likely resulted in some underestimation of hourly presence of sperm whales at these sites, particularly at Georges Bank where data were collected only 10% of the time. This reduction in temporal resolution could make seasonal patterns more difficult to detect, but should not create bias in the patterns I observed, because recording effort was consistent across all recording days within a site, and seasonality was assessed separately at each site.

I recorded sperm whale regular clicks across all hours of the day, and did not find strong diel patterns in relative presence at any recording site. At Georges Bank, click presence was slightly higher during daylight hours, but the biological significance of this pattern is difficult to discern without further information on the diving behavior and movements of the whales that were present. Diel foraging patterns are common in some odontocete species (e.g., Norris & Dohl 1980, Carlstrom 2005, Soldevilla et al. 2010), but have been observed inconsistently in sperm whales (e.g., Aoki et al. 2007, Davis et al. 2007), indicating that the foraging behavior of this species may depend on local environmental characteristics and prey behavior. Diel patterns in sperm whale click detections were found in two previous passive acoustic monitoring studies conducted within my study region over shorter time periods and at shallower depths. Hodge et al. (2013) observed a clear nocturnal pattern in sperm whale click detections on a recorder deployed near the 200 m depth contour in Onslow Bay, North Carolina, during summer 2008. Oswald et al. (2012) found a similar pattern on an array of recorders deployed at approximately 180 m depth in Jacksonville, Florida, during fall 2009. In the present study, I found no evidence of a nocturnal pattern in sperm whale acoustic presence at either the Onslow Bay or Jacksonville recording sites, both of which were located beyond the shelf break at depths greater than 800 m, suggesting that the patterns previously observed at the shallower recording sites may have been a result of the movement of individuals onto the shelf at night.

In addition to foraging opportunities, social factors may play a role in determining the spatiotemporal distribution of sperm whales recorded in this study. Males and females exhibit distinct social behaviors and inhabit different geographic ranges throughout their adult lives. Females and juveniles live in family groups and occupy tropical to temperate waters year-round, while mature males are often solitary and forage at higher latitudes during the summer (Whitehead 2003). Details on the social behavior of sperm whales in the western North Atlantic are scarce, but it is likely that I recorded both female-calf groups and solitary males in this study, because their estimated ranges overlap throughout our study region (Perry et al. 1999). Lone individuals and groups of sperm whales with calves have been observed during shipboard and aerial surveys conducted along the continental shelf break and slope in southern New England and off the Mid-Atlantic coast (unpublished data).

Quantifying the occurrence of different sperm whale click types could provide some insight into the demographics and social context of animals present. Slow clicks are produced only by mature males (Weilgart and Whitehead 1988), while codas are most frequently recorded among female groups (Whitehead and Weilgart 1991, Marcoux et al. 2006), and the presence of different coda types can provide information on clan identity (Rendell and Whitehead 2003, Gero et al. 2016). Here, I did not analyze the recordings for slow clicks and codas, because these click types were difficult to visually distinguish in the LTSAs, due to their energy content at lower frequencies which coincided with higher levels of ambient noise, and to the lower source levels of coda clicks (Madsen et al. 2002a). A thorough analysis of these click types would require a detailed manual examination of the recordings using spectrograms, which was not feasible with the 5.5 years of data collected in this study. Furthermore, codas are most often recorded when animals are observed socializing near the surface rather than during deep dives (Whitehead and Weilgart 1991), and it is not known how well these signals propagate to bottom-mounted recorders deployed in deep water. Investigating the detectability of codas on hydrophones located at depth and developing efficient methods to detect and classify sperm whale codas and slow clicks within large acoustic datasets would be useful objectives for future studies.

In this chapter, I have demonstrated the use of broad-scale passive acoustic monitoring to assess spatial and temporal patterns in sperm whale occurrence. The spatiotemporal distribution of sperm whales in the western North Atlantic and elsewhere around the world has been shaped in significant and complex ways by the long history of human exploitation of the species, which dramatically reduced their populations. To date, there is little evidence that sperm whale populations have recovered since the cessation of large-scale commercial whaling more than 30 years ago (Carroll et al. 2014, Gero and Whitehead 2016), and the species is internationally listed as vulnerable on the IUCN Red List of Threatened Species. Understanding the contemporary seasonal distribution of sperm whales has important implications for management and conservation, as they still face a wide range of human-caused stressors, including entanglement in fishing gear, ship strikes, and exposure to anthropogenic noise (e.g., Laist et al. 2001, Moore & van der Hoop 2012, Isojunno et al. 2016). Passive acoustic monitoring is a valuable non-invasive tool for obtaining consistent year-round information on sperm whale occurrence and gaining insight into seasonal movement patterns. My results provide a comprehensive year-round baseline on the occurrence of this species at multiple recording sites in the western North Atlantic Ocean, and suggest a seasonal shift in sperm whale occurrence particularly north of Cape Hatteras. To improve the utility of these results, I recommend continued passive acoustic monitoring across multiple years at the same study sites, with an effort to minimize the gaps in recording time between successive instrument deployments. Additionally, the integration of seasonal occurrence data obtained from passive acoustic monitoring with broader spatial data collected through visual surveys as well as fine-scale behavioral data will help to create a richer understanding of the ecology of sperm whales.

Chapter 4: Do foraging beaked whales and sperm whales target the Gulf Stream frontal edge? Using passive acoustic monitoring to explore habitat associations

Introduction

Marine environments are characterized by dynamic physical processes, resulting in resource distributions that vary across space and time. This environmental heterogeneity is reflected in the distribution patterns of wide-ranging marine predators, which seek out prey patches in a vast oceanic habitat (Forney 2000, Redfern et al. 2006). On an ocean-basin scale, the distribution patterns of these predators are influenced by latitude, bathymetry, and the locations of large water masses and currents (Worm et al. 2003). At smaller spatial scales (10s to 100s of kilometers), dynamic oceanographic features influence the distributions of predators, including fronts, eddies, and upwelling zones, which occur on various temporal scales (Redfern et al. 2006). Some of these features are static and highly persistent across seasons and years, while others are more ephemeral, and fluctuate in strength and position (Belkin et al. 2009). Exploring how marine predators respond to environmental variability across various temporal scales can improve our understanding of the fundamental ecology of these species (Mannocci et al. 2014, Scales et al. 2017).

Oceanic fronts occur at the interface between water masses with distinct properties, and are manifested by strong horizontal gradients in physical characteristics, such as temperature, salinity, density, or ocean color (Belkin et al. 2009). These discontinuities provide ecologically significant structure in ocean ecosystems, and are often areas with high biodiversity and biomass relative to surrounding waters (Le Fevre 1986, Olson et al. 1994, Belkin et al. 2009, Scales et al. 2014b). Convergence and vertical mixing at fronts enhances nutrient retention and increases primary productivity (Olson et al. 1994). This productivity, coupled with aggregation of zooplankton and advection of organisms to convergence zones (Franks 1992, Olson et al. 1994) creates high-quality foraging habitat for consumers and, in turn, apex predators (Bost et al. 2009, Scales et al. 2014b). The mechanisms of bio-aggregation along fronts vary across systems and the links between prey dynamics and physical processes are poorly understood. However, fronts are recognized as preferred foraging habitats for upper-trophic level predators, including large migratory fishes, seabirds, and marine mammals (Royer et al. 2004, Bost et al. 2009, Scales et al. 2014a, 2014b).

Many studies investigating the importance of fronts for marine predators have focused on large oceanic fronts occurring in offshore regions (e.g., Bost et al. 2009) and less effort has been made to study the effects of these features in shelf-break and slope regions, where bathymetry may also have an important influence on prey availability. In the western North Atlantic Ocean, a persistent front occurs offshore of Cape Hatteras, North Carolina, where the powerful Gulf Stream current separates from the continental margin and turns eastward toward the deep ocean. The warm, salty waters of the Gulf

Stream collide with cooler shelf waters from the Mid-Atlantic Bight and the southward-flowing Labrador Current, creating a sharp along-shelf front along the northwestern edge of the Gulf Stream. In the vicinity of Cape Hatteras, the path of the Gulf Stream is relatively constrained along the narrow continental shelf and steep slope, and typically does not undergo large fluctuations (Miller 1994, Savidge 2004). North and east of Cape Hatteras, meanders develop and increase in amplitude and period as they propagate downstream (Tracey and Watts 1986, Savidge 2004).

The Cape Hatteras shelf break and slope is characterized by high productivity and biodiversity and supports an unusually rich assemblage of cetacean species (Halpin et al. 2009). Sperm whales (*Physeter macrocephalus*) and several species of beaked whales (family Ziphiidae) inhabit this region. Previous studies have suggested that oceanographic features such as fronts and eddies create important foraging habitat for sperm whales (e.g., Griffin 1999, Biggs et al. 2000, Gannier and Praca 2006), which prey on mesopelagic and bathypelagic cephalopods, supplemented by fish and other deep-water organisms (Rice 1989a, Clarke et al. 1993, Santos et al. 2002). Beaked whales are generally believed to forage on similar prey types (Santos et al. 2001, MacLeod et al. 2003), although little information is available on their diets. The ecology and distribution of deep-sea cephalopods in the western North Atlantic are largely unknown, but large current systems can play an important role in the recruitment and abundance of squids (Coelho 1985, O'Dor 1992). In the absence of prey data, examining proxy relationships between predators and environmental characteristics may provide insight into the foraging habitats of these predators (Torres et al. 2008).

An understanding of how sperm whales and beaked whales associate with dynamic oceanographic features over time requires information on species occurrence and contemporaneous environmental conditions at sufficient temporal resolutions. Most previous efforts to understand the environmental drivers of the distribution of these species have relied on observations made during ship and aerial line-transect surveys. However, such observations are typically poorly suited to assess fine-scale *temporal* variability, and thus research efforts have focused on modeling habitat preferences using *spatial* variation in environmental conditions measured at the time surveys are conducted (e.g., Hamazaki 2002, Ferguson et al. 2006) or by using temporally-averaged environmental data fields (e.g., Kaschner et al. 2006, Mannocci et al. 2014).

However, odontocete cetaceans employ echolocation while foraging, enabling the use of passive acoustic monitoring (PAM) to collect time-series data on species occurrence and foraging activity at fixed locations. Long-term PAM conducted at high temporal resolutions offers the opportunity to examine patterns in habitat use in relation to local environmental variability at various temporal scales (Soldevilla et al. 2011, Pirotta et al. 2014, Wong and Whitehead 2014, Cox et al. 2016). When *in situ* environmental measurements are not available, remotely-sensed variables, such as sea surface temperature are typically derived from satellites. Such data are frequently incomplete, however, due to cloud cover, and some degree of spatial and temporal averaging is required to deal with missing data (e.g. multi-day composite images and/or spatial interpolation across cloud-masked areas). Alternatively, habitat variables may be derived from ocean circulation models with frequent time-steps, allowing environmental variability to be estimated at higher temporal resolution (Redfern et al. 2006, Becker et al. 2016, Scales et al. 2017).

The aim of the present chapter is to explore temporal patterns in sperm whale and beaked whale foraging activity off the Mid-Atlantic coast in relation to dynamic physical oceanography, primarily the influence of the Gulf Stream frontal edge along the continental slope. I chose two passive acoustic monitoring sites for comparison: Cape Hatteras, located within the average path of the Gulf Stream and close to the strong, persistent along-shelf front, and Norfolk Canyon, located north and west of the Gulf Stream but periodically influenced by eddies and jets formed by Gulf Stream meanders. At each site, I used daily detection rates of echolocation clicks from sperm whales and commonly detected beaked whale species to examine the relationship between the foraging activity of these species with oceanographic variables sourced from a regional ocean circulation model. Specifically, I sought to address whether the presence of fronts at or near the monitoring sites was correlated with increased presence and foraging activity of these top predators.

Methods

Passive Acoustic Monitoring

I collected passive acoustic recordings using autonomous, bottom-mounted high-frequency acoustic recording packages (HARPs; Wiggins and Hildebrand 2007) deployed on the continental slope off Cape Hatteras, North Carolina (35.34° N, 74.85° W) and near Norfolk Canyon off Virginia (37.16° N, 74.47° W) (Fig. 13). Each HARP was moored at a bottom depth of approximately 900 m, with the hydrophone suspended 10-12 m above the seafloor, and programmed to record continuously at a sampling rate of 200 kHz. At Cape Hatteras, recordings were made for a total of 734 recording days during four deployment periods: 16 March 2012 – 10 April 2012 (26 days), 10 October 2012 – 30 April 2013 (203 days), 30 May 2013 – 14 March 2014 (289 days), and 9 May 2014 – 10 December 2014 (216 days). At Norfolk Canyon, recordings were made during a single deployment period from 20 June 2014 – 5 April 2015 (289 days).

Acoustic recordings were processed in MATLAB (The Mathworks, Inc., Natick, MA) using the *Triton* software (Scripps Whale Acoustic Lab, Scripps Institution of Oceanography, La Jolla, CA) and custom MATLAB routines. Using *Triton*, I computed long-term spectral averages (LTSAs; Wiggins and Hildebrand 2007) to allow visual review of the recordings. To detect beaked whale echolocation clicks, I used a multi-step detection/classification process combining automated click detection with manual review and classification of detections to the species level, as described in detail in

Chapter 1. To detect sperm whale echolocation clicks, I visually examined LTSAs and logged the presence of clicks on an hourly basis, as described in Chapter 3. I used the number of hours per day with echolocation signals present as a metric of species presence at each site. In this chapter, I focused on the occurrence of sperm whales and Cuvier's beaked whales (*Ziphius cavirostris*) at Cape Hatteras, and sperm whales, Cuvier's beaked whales, and Sowerby's beaked whales (*Mesoplodon bidens*) at Norfolk Canyon.

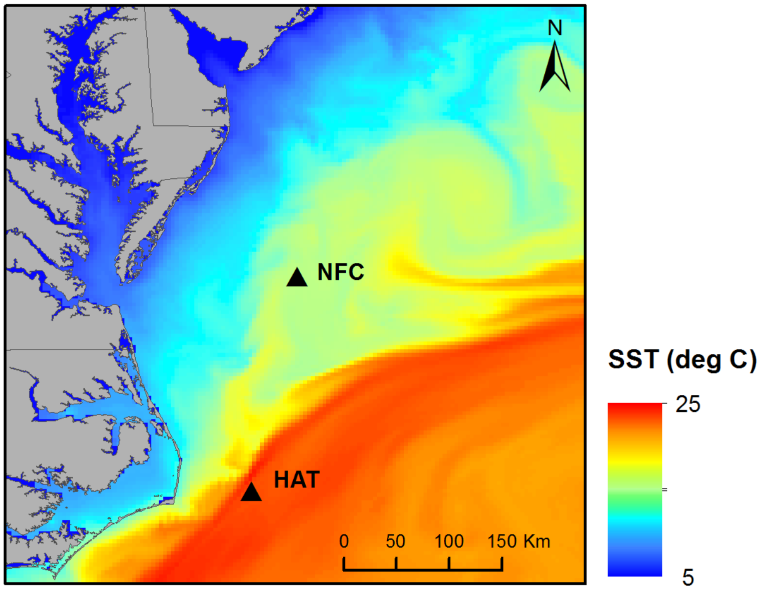


Figure 13: Map of Cape Hatteras (HAT) and Norfolk Canyon (NFC) recording sites with daily mean sea surface temperature (SST) for January 1, 2014, sourced from the regional Navy Coastal Ocean Model.

Environmental Covariates

I obtained oceanographic variables from the Naval Oceanographic Office Regional Navy Coastal Ocean Model (NCOM; https://www.ncdc.noaa.gov/data-access/model-data/model-datasets/navoceano-ncom-reg) for the U.S. East Coast Region. Output from the regional NCOM is available from 2009 to present, at a time step of 3 hours, and contains 40 terrain-following depth layers. The horizontal resolution of the model was 1/36 degree prior to April 5, 2013 and 1/30 degree after this date. I downloaded surface layer temperature, salinity, and velocity variables across a 5° by 5° area centered on each recording site, for every year in which passive acoustic monitoring effort occurred (2012-2014 at Cape Hatteras; 2014-2015 at Norfolk Canyon). To perform all analyses at a consistent spatial resolution, I applied a linear interpolation to the model output prior to the April 2013 resolution change, and resampled each variable on the 1/30 degree grid corresponding to the later model output, resulting in a horizontal resolution of approximately 3 km.

To characterize the environment at each HARP site on a daily scale, I created a set of environmental covariates derived from the surface temperature and salinity fields. Daily mean values of sea surface temperature (SST) and surface salinity provide an indication of the the presence of Gulf Stream water or slope water; SST also undergoes seasonal warming. Initially, I examined daily mean SST and salinity at three spatial scales: 1 pixel corresponding to the HARP site, a 10 x 10 pixel area centered on the

HARP site (approximately 30 x 30 km), and a 20 x 20 pixel area centered on the HARP site (approximately 60 x 60 km). Each variable was highly correlated across all three scales (Pearson correlation > 0.75), so I chose the 10 x 10 pixel scale to encompass the area over which sperm whale clicks may be detected; the maximum detection range of sperm whale clicks at depth has been estimated to be 16 km from the recorder (Madsen et al. 2002b). As a proxy for the presence of fronts in the vicinity of each HARP site, I calculated the standard deviation in SST and salinity in the spatial domain across the same 10 x 10 pixel region. Temperature and salinity fronts are expected to co-occur (Belkin et al. 2009), but SST reflects surface warming during the summer which may obscure temperature differences between water masses. By contrast, surface salinity does not undergo a strong seasonal change and the salinity gradients between water masses remain similar throughout the year.

To quantify the distance to the nearest front from each HARP site, I applied a Canny edge detection algorithm (Canny 1986) to identify strong fronts in both surface temperature and salinity (see Castelao et al. 2006, Wall et al. 2008). The Canny edge detection process involves several steps: initially, the SST or salinity field is smoothed using a Gaussian filter, with the filter size determined by the chosen standard deviation, sigma. Gradient values are then computed for each pixel in each direction, and local maxima are identified. Finally, a double set of thresholds is applied, where pixels with gradient values higher than an upper threshold are selected as edges, and edges are traced perpendicular to the gradient direction, incorporating any adjacent pixels with gradient values above a lower threshold. The result is a thin (single pixel) trace of the position of a front (Appendix B, Fig B26). The choice of gradient threshold values determines which fronts are detected, so to assess the effects of varying thresholds, I created frontal maps using two different upper thresholds for both temperature and salinity (referred to as Th1 and Th2; see Table 9). In each case, lower thresholds were automatically set at 0.4 times the upper threshold. Following Scales et al. (2014a) I selected upper thresholds of 0.4 and 1.0 for SST gradients. For salinity gradients, I empirically selected upper threshold values of 0.1 and 0.2 after visual examination of surface salinity gradient maps. After creating front maps with each set of front detection thresholds, I calculated the daily mean distance between each HARP site and the nearest front pixel in kilometers. The distance to front metric sometimes resulted in large values (100 km or more), when no strong fronts were present in the nearby vicinity of the HARP, particularly when higher thresholds were applied during front detection. Fronts at these distances are unlikely to have a direct influence on species presence at the HARP site, so I additionally created binary categorical variables indicating the presence or absence of a front within 15 km of the HARP site, based on each set of front detection thresholds (Table 9).

Table 9: Covariates used to model species presence. Each front metric was calculated using two different gradient thresholds applied during edge detection (Th1 and Th2).

Covariate	Temporal Resolution	Spatial resolution	Form
Month of year	--	--	Categorical
Sea Surface Temperature (SST) (°C)	Daily mean	30 km x 30 km (10 x 10 pixels)	Continuous (B-spline)
Surface Salinity	Daily mean	30 km x 30 km (10 x 10 pixels)	Continuous (B-spline)
SST standard deviation (°C)	Daily mean	30 km x 30 km (10 x 10 pixels)	Continuous (B-spline)
Salinity standard deviation	Daily mean	30 km x 30 km (10 x 10 pixels)	Continuous (B-spline)
Distance to SST front *Th1 = 0.4* *Th2 = 1.0*	Daily mean	~ 3 km (1 pixel)	Continuous (B-spline)
Distance to salinity front *Th1 = 0.1* *Th2 = 0.2*	Daily mean	~ 3 km (1 pixel)	Continuous (B-spline)
Presence of SST front *Th1 = 0.4* *Th2 = 1.0*	Daily mean	15 km	Categorical (presence = 1, absence = 0)
Presence of salinity front *Th1 = 0.1* *Th2 = 0.2*	Daily mean	15 km	Categorical (presence = 1, absence = 0)

Statistical Modeling

To model the influence of the environmental covariates described above on species' detection rates, I used the proportion of hours per day with acoustic detections as the response variable for sperm whales and Cuvier's beaked whales at Cape Hatteras, and sperm whales at Norfolk Canyon. For Cuvier's and Sowerby's beaked whales at Norfolk Canyon, I instead used daily presence/absence of acoustic detections as a binary response variable, due to low detection rates of these species. I performed all analyses using a Generalized Additive Modelling (GAM) framework with a binomial error distribution and logit link function. GAMs allow for flexible, nonlinear relationships between response and predictor variables, and are commonly used to model cetacean species distributions and investigate habitat preferences (e.g., Forney 2000, Ferguson et al. 2006, Becker et al. 2010). I examined model residuals for temporal autocorrelation using autocorrelation function (ACF) plots, and used a Generalized Estimating Equation (GEE) approach to account for the observed autocorrelation, by defining blocks of time in which observations may be correlated (e.g., Panigada et al. 2008, Bailey et al. 2013, Pirotta et al. 2014). Due to the time series nature of the data, residual autocorrelation is expected to decay with time, and I therefore chose an autoregressive (AR1) structure to model the correlation within blocks. I selected a block size for each model based on the lag (number of consecutive days) at which residual correlation fell below the 95% confidence intervals around zero on each ACF plot (Appendix B, Figs. B27 & B28).

Models that did not show significant autocorrelation in residuals were fit as regular GAMs.

The environmental covariates included in this study (Table 9) represent different ways of measuring co-varying features of the environment and estimating the presence of oceanic fronts at the HARP sites. Consequently, these metrics are not independent and exhibit varying degrees of correlation. Including collinear predictors in the same model can result in instability and unreliable parameter estimates, so I tested each environmental covariate in separate stand-alone models (e.g., Cox et al. 2016). Each continuous covariate was modeled as a B-spline with 3 degrees of freedom, to allow for nonlinear relationships with the response variable while preventing unrealistic complexity (Forney 2000). Month was included as a categorical covariate in each model, to account for seasonal patterns that may not be driven by local environmental variability. I used a marginal F-test statistic to compare the addition of each environmental covariate to a model containing only month, based on the null hypothesis that the addition of the covariate would not improve model fit. I did not attempt to select a single ‘best’ model, but examined the effects of each covariate which significantly improved model fit over month alone, based on F-test p-values less than 0.05. To visualize the relationship between each significant covariate and the response, I created partial fit plots with 95% confidence intervals based on the GEE standard errors. I also examined plots of fitted vs. observed values to assess model fit.

Results

Cape Hatteras

At the Cape Hatteras recording site, detection rates of sperm whales ranged from 0 to 24 hours per day, with a seasonal peak in detections from January through March. Detection rates exhibited broad variation during June and July, followed by fewer detections and more days in which sperm whale clicks were absent from the recordings throughout the late summer and fall (Fig. 14). Detection rates of Cuvier's beaked whales ranged from 0 to 22 hours per day, with few zero values, indicating consistent daily presence of this species throughout the year. Detection rates of Cuvier's beaked whales appeared to be slightly higher in the late summer and fall, compared to the winter, but there was generally wide variation throughout the year and no clear evidence of seasonality (Fig. 2). The lower detection rates in April and May for both species are partially due to gaps in recording effort during this time.

The Cape Hatteras recording site was located within the usual path of the Gulf Stream (Fig. 13), which is reflected in the mean sea surface temperature and salinity values from the NCOM model output at this site (Fig. 15). Mean SST, salinity, and the spatial standard deviation of these variables at Cape Hatteras exhibited greater variability from November through April and less variation from June through October (Fig. 15). SST was correlated with month, and was, therefore, not assessed as a potential predictor of species occurrence. The distance to front metrics calculated using both sets of gradient thresholds for front detection showed the consistent presence of a strong temperature and salinity front approximately 10-20 km from the HARP site (Fig. 15).

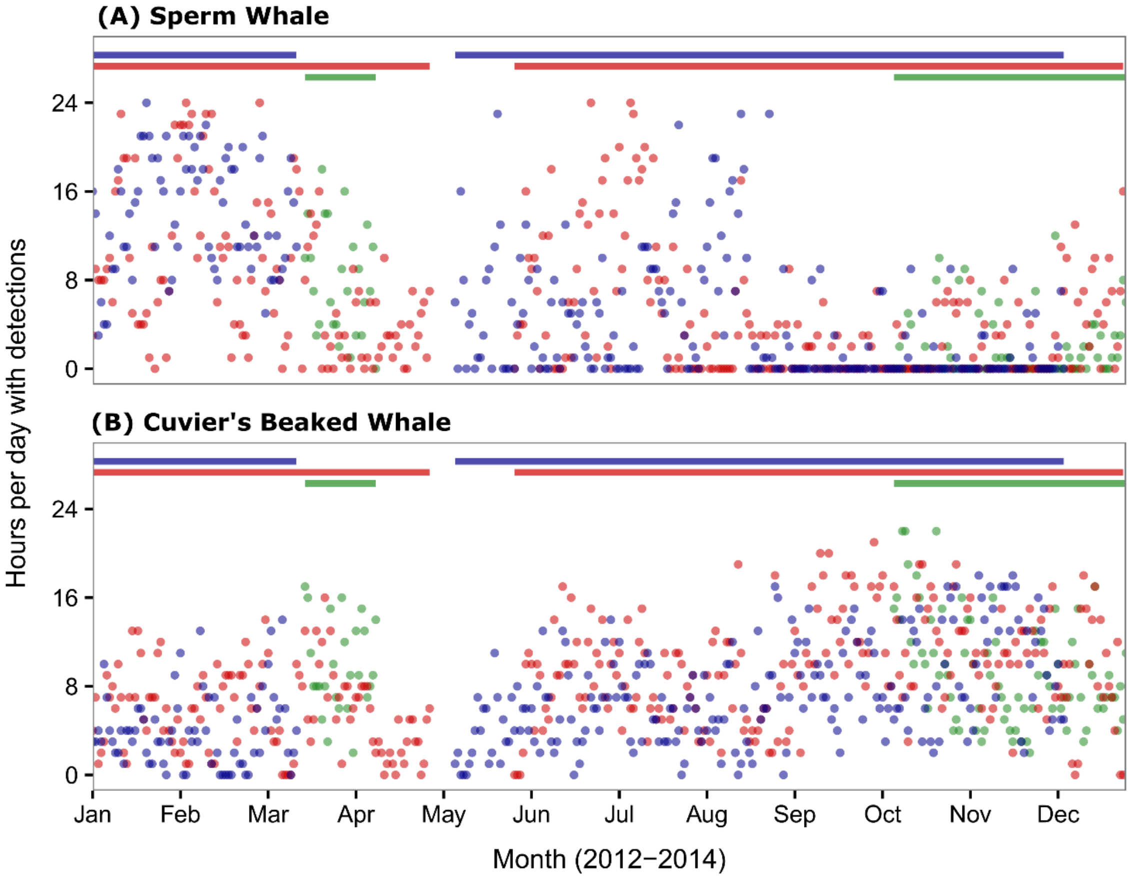


Figure 14: Daily detection rates of echolocation clicks from sperm whales (A) and Cuvier's beaked whales (B) at the Cape Hatteras monitoring site in 2012 (green points), 2013 (red points), and 2014 (blue points). Colored bars indicate periods with recording effort in each year.

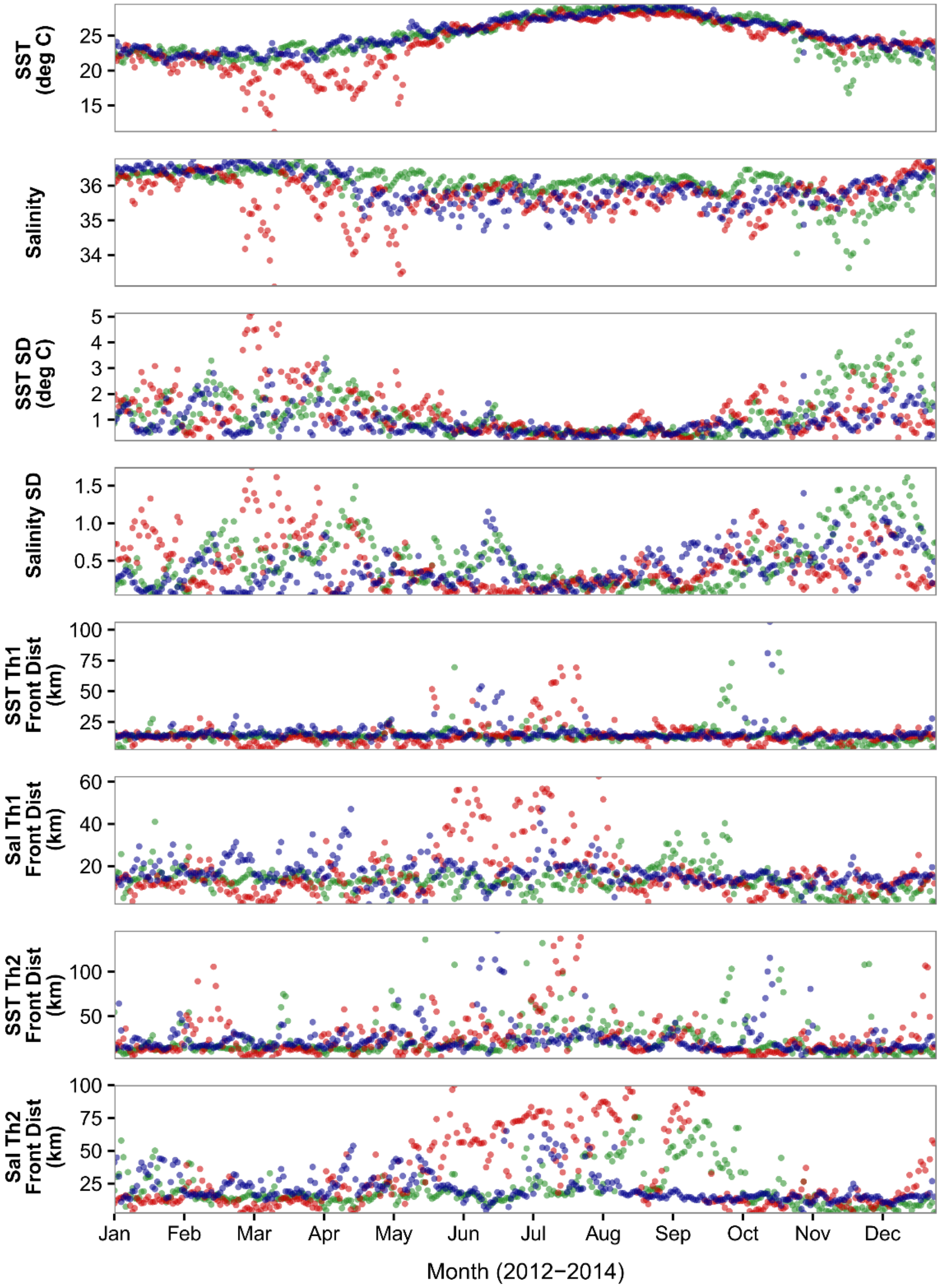


Figure 15: Daily mean values of each modeled oceanographic variable at the Cape Hatteras recording site in 2012 (green points), 2013 (red points), and 2014 (blue points).

Results of the GEE-GAM models suggested that sperm whale detection rates varied with salinity ($p<0.001$), salinity standard deviation ($p<0.001$), SST standard deviation ($p=0.002$), and distance to nearest salinity front, regardless of the gradient threshold used in front detection (Th1, $p=0.017$; Th2, $p<0.001$). Additionally, there was a negative relationship between sperm whale detection rates and the presence of a strong salinity front (detected using Th2) within 15 km of the HARP site ($p=0.006$). Partial fit plots showed sperm whale detection rates increasing with salinity over the usual range of measured salinity values, and decreasing with salinity standard deviation and SST standard deviation (Fig. 16). Sperm whale detection rates also increased with distance to nearest salinity front (using both Th1 and Th2), particularly for distances under approximately 30 km (Fig. 17). Likewise, the presence of a strong salinity front within 15 km of the HARP site corresponded with lower sperm whale detection rates (Fig. 17). Confidence intervals around these estimated relationships are fairly wide and they should be interpreted with caution, particularly where there is uneven representation of covariate data values, as shown by the rug plots in Figs. 16 and 17. Plots of observed vs. fitted values revealed considerable noise in model fit, with low observed detection rates generally under-predicted by the model and higher observed detection rates over-predicted (Appendix B, Figs. B29 & B30). Model fit estimated by R^2 values for each individual model was between 0.41-0.42, and the addition of the environmental covariates only slightly improved model fit over month alone ($R^2 = 0.39$).

Cuvier’s beaked whale detection rates varied with salinity ($p<0.001$), and SST standard deviation ($p<0.001$) and showed a positive relationship with the presence of a strong SST front (Th2; $p=0.024$) and the presence of a strong salinity front (Th2; $p=0.039$) within 15 km of the HARP site (Figs. 18 and 19). Plots of observed vs. fitted values indicated a poor model fit, with an estimated R^2 value of 0.22 for the model containing only month, and R^2 values of 0.22-0.25 for models with individual environmental covariates added (Appendix B, Fig B31). As was the case for sperm whales, confidence intervals around the estimated relationships shown in the partial fit plots are relatively wide, and most of the variation in daily detection rates is not well-explained by the covariates examined here.

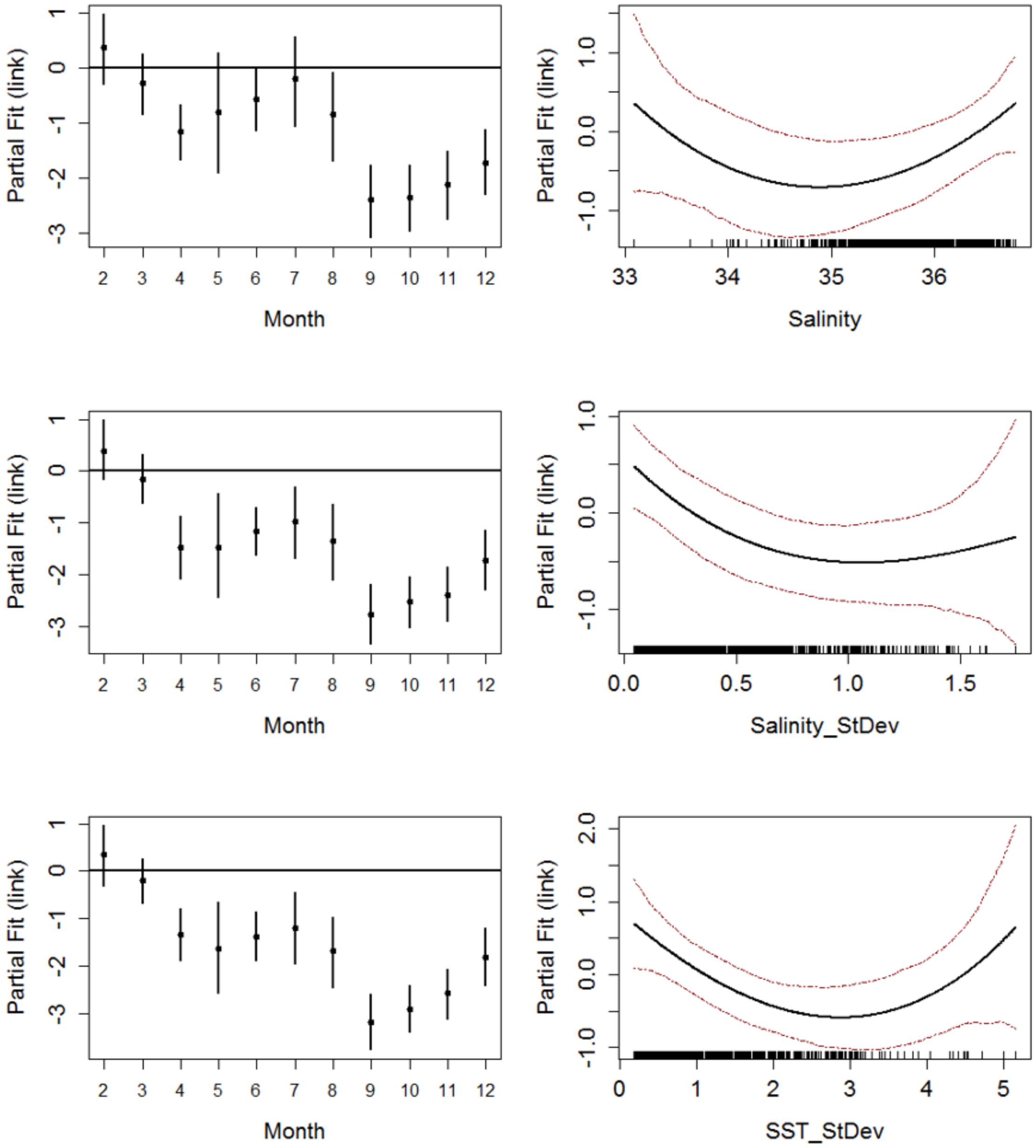


Figure 16: Partial fit plots showing the relationship between daily sperm whale detection rates at Cape Hatteras and each covariate in models containing month plus salinity (top), salinity standard deviation (middle) and SST standard deviation (bottom), on the scale of the logit link function. For continuous covariates, a rug plot with measured data values is shown along the bottom.

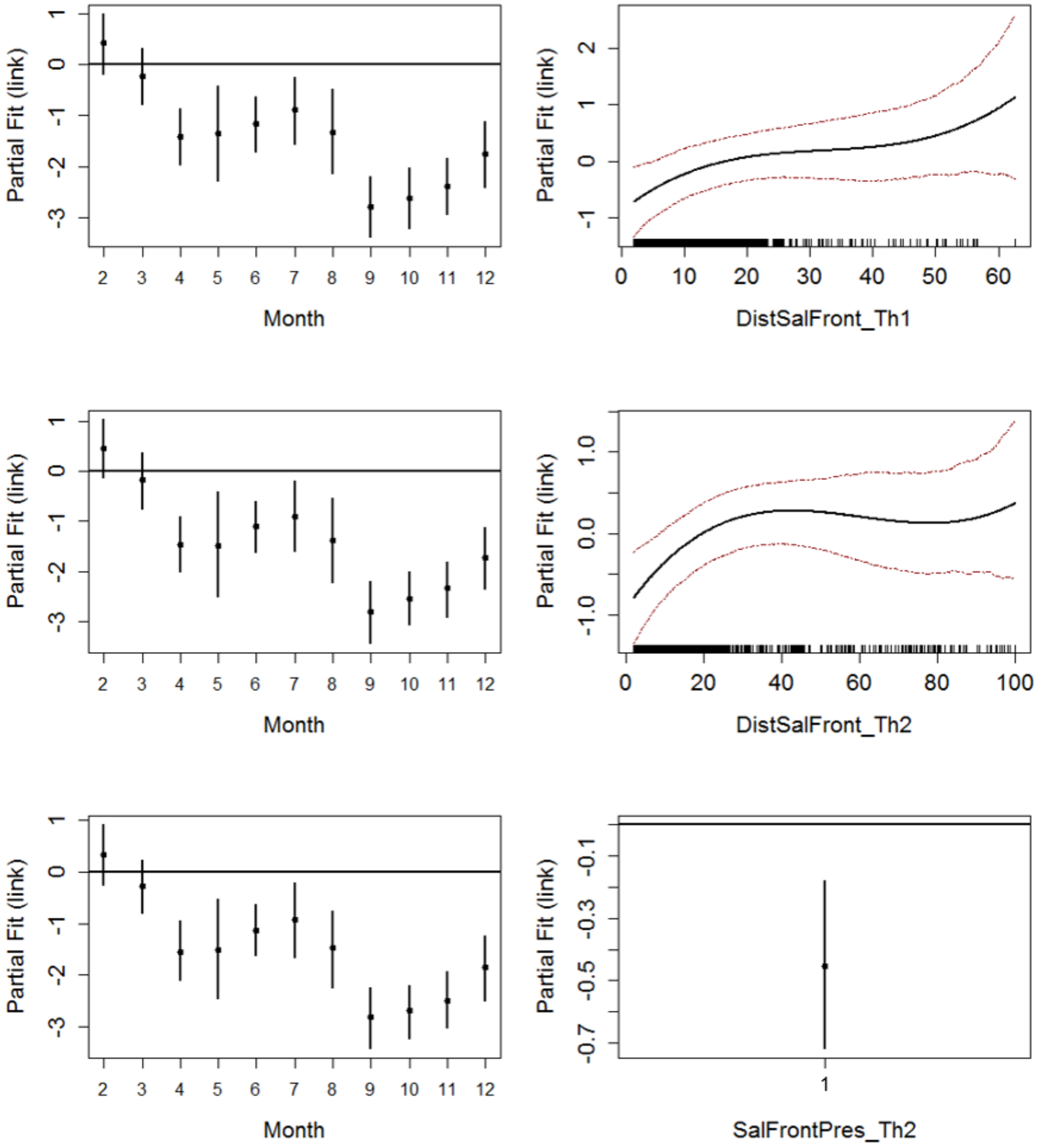


Figure 17: Partial fit plots showing the relationship between daily detection rates of sperm whales at Cape Hatteras and each covariate in models containing month plus distance to nearest salinity front detected using Th1 (top), distance to nearest salinity front detected using Th2 (middle) and presence of salinity front detected using Th2 (bottom), on the scale of the logit link function. For continuous covariates, a rug plot with measured data values is shown along the bottom of each plot.

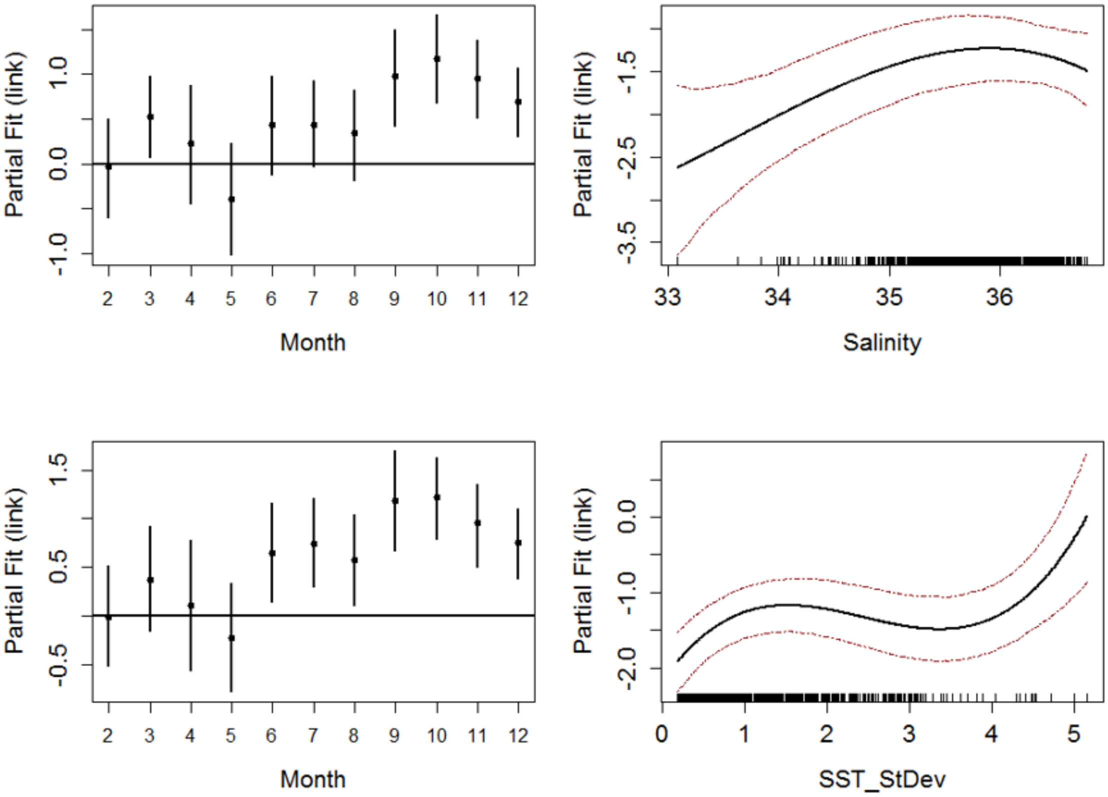


Figure 18: Partial fit plots showing the relationship between daily detection rates of Cuvier's beaked whales at Cape Hatteras and each covariate in models containing month plus salinity (top), and salinity SD (bottom), on the scale of the logit link function. For continuous covariates, a rug plot with measured data values is shown along the bottom of each plot.

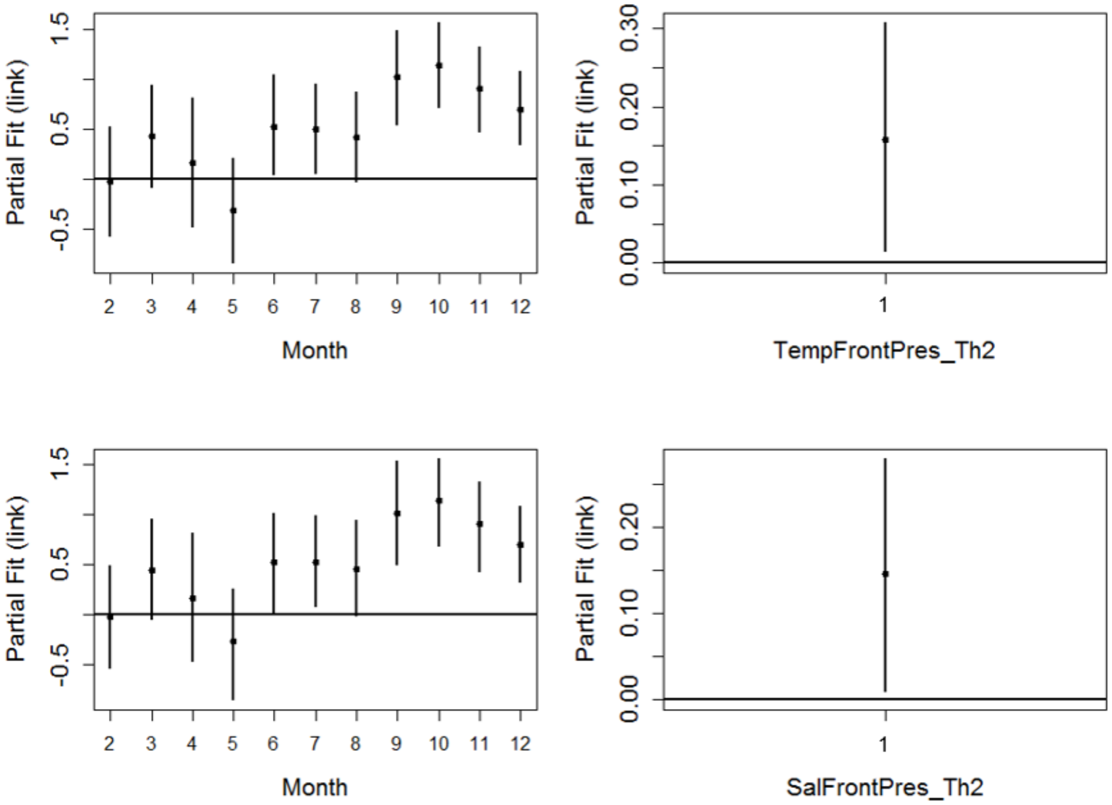


Figure 19: Partial fit plots showing the relationship between daily detection rates of Cuvier's beaked whales at Cape Hatteras and each covariate in models containing month plus the presence of an SST front detected using Th2 (top), and the presence of a salinity front detected using Th2 (bottom), on the scale of the logit link function.

Norfolk Canyon

Daily detection rates of sperm whales at Norfolk Canyon ranged from 0 to 22 hours per day, with wide variation in detection rates and relatively few days of absence in July and August 2014. Between September and January, detection rates were lower and daily presence was more sporadic, followed by an increase in detection rates from February until the recording period ended in April 2015 (Fig. 20). Cuvier's and Sowerby's beaked whales were detected less frequently, with detection rates ranging from 0 to 7 hours per day for each species, and the highest detection rates occurring in January and February 2015 (Fig. 20).

The Norfolk Canyon recording site was located in cooler waters outside the Gulf Stream, and seasonal warming in sea surface temperature was more pronounced at this site (Fig. 21). Both salinity and distance to weak temperature fronts (detected using Th1) also exhibited seasonal trends and were correlated with month, so I did not assess the effects of these covariates on species presence. The distance to front metrics exhibited wider variation and often larger distances than at Cape Hatteras, because the Norfolk Canyon site was located far from the Gulf Stream frontal edge (Fig. 21). The presence/absence metric for strong salinity fronts (detected using Th2) within 15 km of the HARP resulted in only two days in which a front was present, so I did not use this covariate to model species detection rates at Norfolk Canyon.

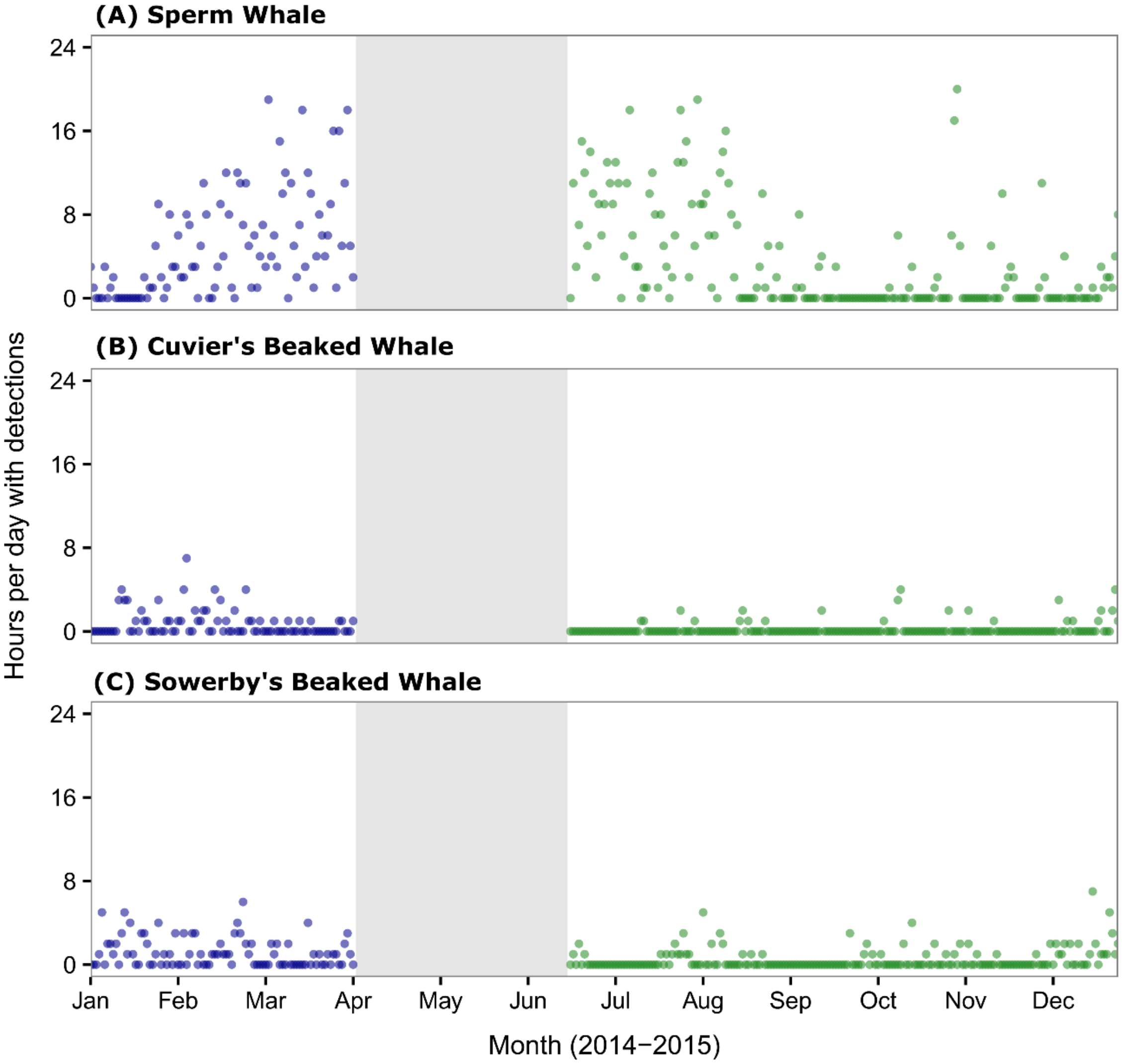


Figure 20: Daily detection rates of echolocation clicks from sperm whales (A), Cuvier's beaked whales (B), and Sowerby's beaked whales (C) at the Norfolk Canyon monitoring site in 2014 (green points) and 2014 (blue points). Gray shading indicates the portion of the year with no recording effort.

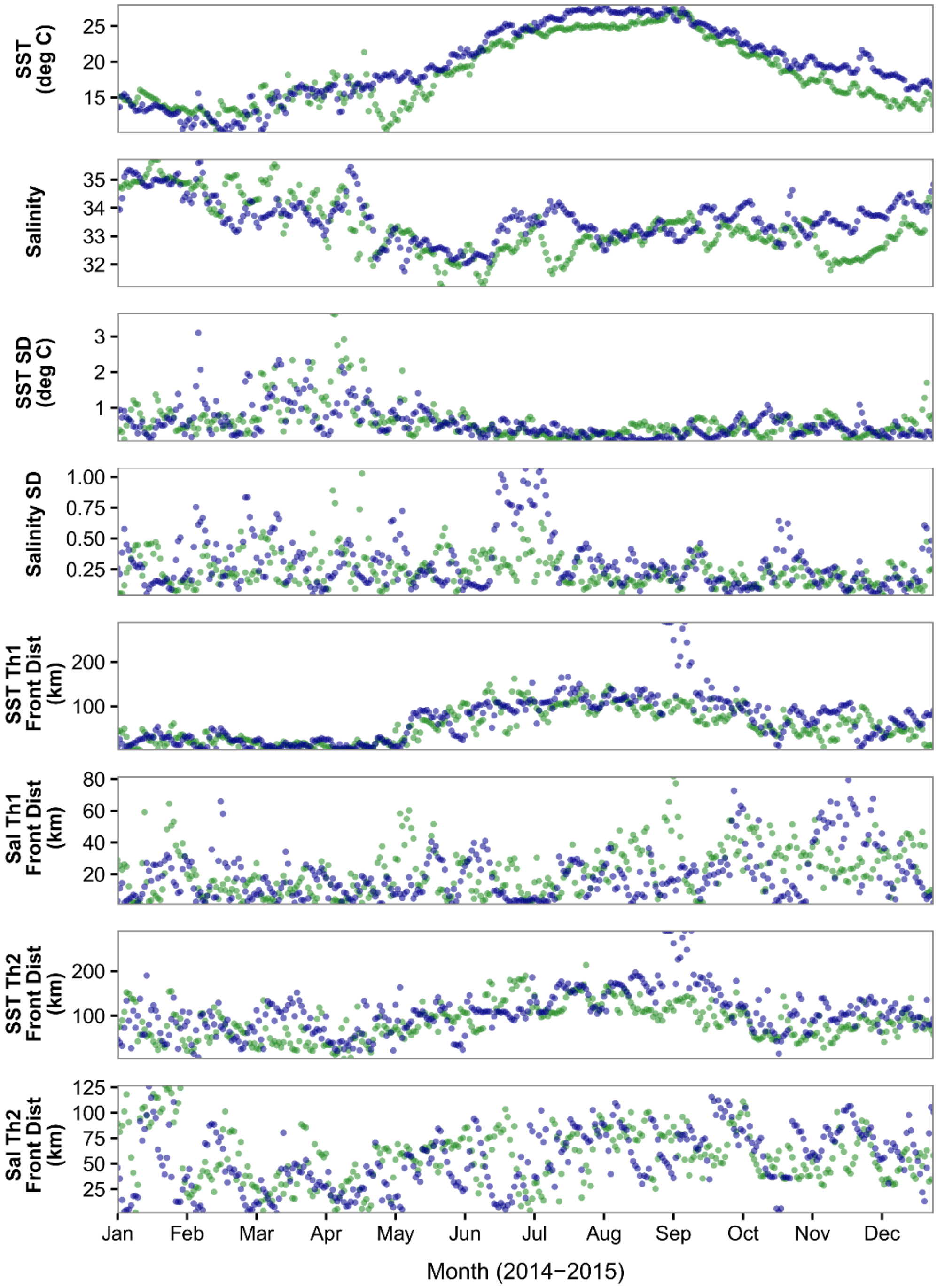


Figure 21: Daily mean values of each modeled oceanographic variable at the Norfolk Canyon recording site in 2014 (green points) and 2015 (blue points).

Model results indicated that daily detection rates of sperm whales at Norfolk Canyon varied with the spatial standard deviation of both SST (p=0.007) and salinity (p=0.008), and with the distance to the nearest salinity front using the weaker front detection threshold (Th1; p=0.036). Partial fit plots suggested similar relationships to those found at Cape Hatteras: sperm whale detection rates generally decreased with increasing standard deviation in SST and salinity, and increased with increasing distance to salinity fronts within approximately 30 km (Fig. 22). Again, confidence intervals were wide, particularly for the standard deviation metrics, and the range of covariate values represented was uneven, as shown by the rug plots in Fig. 22. Plots of observed vs. fitted values indicated that model fit was generally poor, with an estimated R^2 value of 0.33 for the model containing month alone, and 0.33-0.36 for models including an additional environmental covariate (Appendix B, Fig. B32). As with the results from Cape Hatteras, the addition of each environmental covariate only slightly improved model fit over month alone, and most of the variation explained by the model can be attributed to seasonal patterns.

Sample sizes were smaller for the beaked whale species at Norfolk Canyon, with Cuvier’s and Sowerby’s beaked whales detected on 59 and 103 recording days, respectively. Variation in daily detection rates was low, ranging from 0 to 7 hours per day, so I modeled the daily presence or absence of detections of these species as a binary response using a binomial-based GAM. GEE models were not necessary since there was no evidence of residual autocorrelation (Appendix B, Fig. B28). No significant relationships were found between beaked whale species presence and any of the environmental covariates tested.

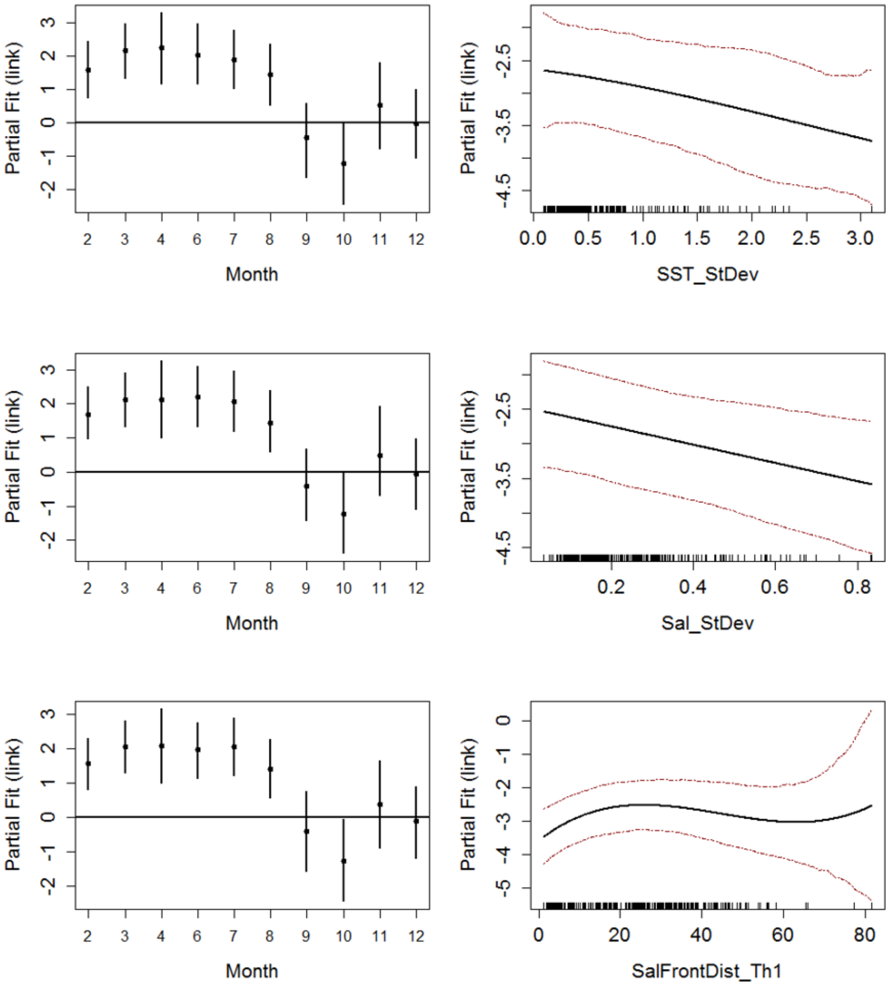


Figure 22: Partial fit plots showing the relationship between daily detection rates of sperm whales at Norfolk Canyon and each covariate in models containing month plus SST standard deviation (top), salinity standard deviation (middle), and distance to nearest salinity front detected using Th1, on the scale of the logit link function. For continuous covariates, a rug plot with measured data values is shown along the bottom.

Discussion

Detection rates of sperm whales at Cape Hatteras and Norfolk Canyon were not associated with the presence of sea surface temperature or salinity fronts; my results actually suggested the opposite pattern at both recording sites, with higher detection rates during periods of lower spatial standard deviation in SST and salinity and greater distance to the nearest front. For Cuvier’s beaked whales at Cape Hatteras, my results did indicate a positive association with front presence, but with a high degree of uncertainty. At Norfolk Canyon, sample sizes for the daily presence of Cuvier’s and Sowerby’s beaked whales were more limited, and I did not find significant associations between the presence of these species and any oceanographic variable examined.

At both sites, sperm whale detection rates exhibited clear seasonality (see Chapter 3), which made it difficult to disentangle seasonal patterns in species presence in the region from daily variation in foraging activity at each HARP site. A northward shift in sperm whale densities has been documented off the northeastern U.S. during the spring and summer (Perry et al. 1999, Waring et al. 2014, Roberts et al. 2016b). Male sperm whales, in particular, are wide-ranging, and their seasonal movements may be timed to take advantage of enhanced foraging conditions at higher latitudes in the North Atlantic. I attempted to account for these broader seasonal patterns by including month as a predictor variable in each model. However, there are multiple possible interpretations of zero values in the detection data, which reduces the power of this study to detect relationships between sperm whale foraging activity and local environmental variability. Local foraging conditions may be poor, and therefore foraging activity is low, or conditions may be good, but sperm whales are not present in the region because they are exploiting seasonal productivity occurring elsewhere during certain times of year.

Detection rates of Cuvier's beaked whales at Cape Hatteras had a more even distribution throughout the year and there were fewer days with no detections, providing a better case study for exploring potential responses to local environmental variability. Year-round acoustic detections suggest that Cuvier's beaked whales are resident in the area (see Chapter 1), and preliminary results from satellite telemetry studies have revealed that individuals typically remain within a small core area along the shelf slope off Cape Hatteras for weeks to months at a time (Forney et al. *in press*, Baird et al. 2016). Therefore, prey must be available to these beaked whales in this region year round. My results provided some support for the hypothesis that beaked whales forage near fronts: sea surface temperature and salinity fronts at the HARP site corresponded with increased beaked whale foraging activity. However, my ability to detect habitat preferences was limited by the relatively narrow range of environmental variability experienced at the Cape Hatteras site. The path of the Gulf Stream and position of the along-shelf front in this region are reasonably stable (Savidge 2004), and the distance to front metrics did not exhibit a great deal of variation. Adding a spatial dimension to this study by placing additional recorders at Cape Hatteras at different distances from the front would allow for a more informative comparison of Cuvier's beaked whale foraging activity in relation to the Gulf Stream frontal edge.

At both recording sites, only a small proportion of the variability in species detection rates was explained by the environmental covariates examined, which is not uncommon in studies using indirect proxy variables to characterize foraging habitat (Forney et al. 2012, Mannocci et al. 2014). The mechanistic links between physical features of the environment and the foraging behavior of marine predators are not well understood, and the oceanographic variables tested in this study may not effectively characterize biophysical conditions that are relevant to deep-diving marine predators. I restricted my analysis to surface temperature and salinity fields, to provide results that are comparable to previous studies which used remotely-sensed oceanographic data. However, the position of surface fronts may not correspond directly to ecological structure within the water column, and there may be spatial lags between surface features and concentrations of prey at depth, where sperm whales and beaked whales forage.

Little is known about how cetaceans perceive their environment and respond to environmental cues, and it is possible that sperm whales and beaked whales do not respond directly to environmental variability over short temporal scales, but instead rely on predictable foraging habitats. Seabirds are known to utilize mesoscale oceanic fronts that are consistent in space and time as preferred foraging regions (Bost et al. 2009, Scales et al. 2014a). Stable, persistent fronts are likely to support sustained productivity, attracting mid-trophic level consumers and creating foraging opportunities for top predators, whereas more ephemeral features may not have the same bio-aggregative effects. Some studies of odontocetes have revealed significant associations with dynamic habitat features on daily temporal scales (Pirotta et al. 2014, Cox et al. 2016); in other cases, species distributions were better predicted by longer-term average conditions, and including contemporaneous environmental variables did not improve the predictive capabilities of habitat models (Mannocci et al. 2014). The temporal scales at which marine predators identify and respond to environmental change remains a complex question, and the appropriate scale at which to study habitat selection may vary depending on the dynamics of the particular system (Scales et al. 2017).

This study represents an exploratory analysis of the temporal responses of deep-diving marine mammals to dynamic oceanographic features, based on passive acoustic monitoring at fixed locations. The absence of clear patterns is not particularly surprising given the data limitations and our relatively poor understanding of the linkages between physical oceanographic features and the foraging behavior of these species. It is also possible that bathymetric features have a greater influence than dynamic oceanography on habitat selection by sperm whales and beaked whales. Cuvier's beaked whales tagged with time-depth recorders at Cape Hatteras have been observed to dive to or close to the seafloor while foraging, and exhibit strong site fidelity to the slope region (Forney et al. *in press*., Baird et al. 2016). The continental slope and regions with variable bottom topography have been identified as important habitat for Cuvier's beaked whales in the Mediterranean Sea (Gannier and Epinat 2008). Sperm whales may be associated with canyons and seamounts (Waring et al. 2001, Wong and Whitehead 2014), and have been observed to forage along the edges of warm-core eddies where these features interact with slope waters (Griffin 1999). In this study, I did not have the appropriate spatial coverage to examine the effects of bathymetry or the interactions between bathymetry and oceanography on detection rates.

Passive acoustic monitoring does offer some advantages for investigating habitat selection by deep-diving odontocetes. Echolocation clicks are produced primarily during foraging dives, and acoustic detections consequently provide behavioral context which can lead to more informative studies of habitat selection (Roever et al. 2014). In addition, the ability to identify beaked whales to the species level provides the opportunity to examine the habitat preferences of individual species, which may be masked when beaked whales are studied as a single guild, which is often necessary with visual survey data due to limited sample sizes of sightings identified to the species level (Mannocci et al. 2014, Roberts et al. 2016a). I offer some suggestions to improve efforts to assess the habitat selection of these species using PAM data. Collecting acoustic data over additional years with full recording effort across seasons would allow an assessment of the predictive capabilities of models across independent years, which I was not able to do here. For sperm whales, including interaction terms between month and environmental covariates may help to better account for patterns occurring across multiple, nested temporal scales. Alternatively, it may be useful to examine habitat associations within a single season, when sperm whales are typically present in the area.

Finally, while the lack of environmental variability at the Cape Hatteras site made it difficult to model relationships between oceanographic conditions and species detection rates at this site, it is clear that the persistent Gulf Stream front is an important feature of the Cape Hatteras shelf/slope region. Bio-aggregation occurring at this convergence zone may play a role in the remarkably high density and diversity of marine predators in this region, and contribute to the difference in overall detection rates of sperm whales and beaked whales at the Cape Hatteras and Norfolk Canyon recording sites.

Conclusions

Few mammalian species are more challenging to observe and study than those inhabiting the depths of the pelagic oceans. Beaked whales (family Ziphiidae) and sperm whales (*Physeter macrocephalus*) have been aptly termed "surfacers" rather than divers, as they spend most of their lifetimes at depth (Ponganis 2015). Our understanding of the biology and ecology of these cryptic species is mostly limited to certain aspects of their behavior, morphology, and social systems (in the case of sperm whales), and very little is known about the range of oceanic habitats they occupy, or of the environmental influences that shape their spatiotemporal distributions.

In this dissertation, I used broad-scale passive acoustic monitoring (PAM) to provide new insight into the distribution and seasonal occurrence patterns of beaked whales and sperm whales in the western North Atlantic Ocean. This study represents the largest PAM research effort for odontocetes in the western North Atlantic to date, and provides the first year-round records of the occurrence of these species in many areas. My research highlights the importance of studying beaked whales at the species level, and demonstrates the efficacy of PAM to do so.

The continental margin off North America between Cape Hatteras and Nova Scotia is recognized as a key area for beaked whales, based on the frequent occurrence of beaked whales and high species diversity in the region (MacLeod and Mitchell 2005). My results in Chapter 1 provide general support for this view, and indicate that the continental slope provides important habitat for beaked whales as far south as Onslow Bay, North Carolina. Across the study region, I found broad overlap in the latitudinal ranges of beaked whale species, including a greater degree of spatial and temporal overlap among some species than previously observed. MacLeod (2005) hypothesized that beaked whale species in the Atlantic may be separated into guilds based on the preferred size of prey items consumed, and suggested that species within each prey-size guild are geographically segregated based on water temperature, thereby reducing competition for similar prey resources. However, the year-round sympatry of northern bottlenose whales (*Hyperoodon ampullatus*) and Cuvier's beaked whales (*Ziphius cavirostris*) in the Gully suggest that competitive exclusion does not prevent the co-occurrence of these species. A preliminary review of acoustic data collected elsewhere along the edge of the Scotian Shelf has revealed the presence of at least one *Mesoplodon* species not previously known to inhabit the region (Julien Delarue, personal communication). Together, these findings offer an important reminder that our understanding of beaked whale occurrence is far from complete, and the absence of sightings or stranding records of a beaked whale species within a given region does not preclude the presence of the species.

Previously, beaked whales were generally assumed to be widely distributed along continental margins (e.g., MacLeod and Mitchell 2005), and little information was available on fine-scale patterns of occurrence of individual species. However, beaked whale habitat use along the continental slope in the western North Atlantic now appears to be heterogeneous, and certain areas support resident, year-round concentrations of beaked whales. In other parts of the world, resident populations of beaked whale exhibit high levels of site fidelity (McSweeney et al. 2007, Schorr et al. 2010, Claridge 2013). The results of my dissertation, combined with recent satellite telemetry studies (Forney et al. *in press*., Baird et al. 2016), indicate that this is the case for Cuvier's beaked whales off Cape Hatteras. Perhaps more unexpectedly, I found similarly high and consistent levels of occurrence of Gervais' beaked whales (*Mesoplodon europaeus*) on the continental slope off Onslow Bay, North Carolina. This site was not previously recognized as an important habitat for beaked whales, and almost nothing is known about the ecology and behavior of this species. This spatial structuring of habitats within the overlapping ranges of beaked whale species underscores the need for a better understanding of beaked whale occurrence and ecology at the species level.

Sperm whales have received substantially more research attention than beaked whales, partly due to the long history of human exploitation of the species, as well as the fact that they are somewhat easier to observe. Sperm whales are larger, exhibit more visible surface behavior, and produce loud, distinctive echolocation clicks that may be detected at greater distances than beaked whale clicks. Dedicated studies of sperm whale populations over the past several decades have offered an intriguing view into their complex social systems (Whitehead 2003). Nevertheless, surprisingly little is known about the distribution and seasonal movements of sperm whales in many regions of the world, including the western North Atlantic. My results in Chapter 3 demonstrate that the occurrence of sperm whales in this region is more seasonally variable than that of beaked whales, reflecting the nomadic lifestyle and large home ranges of sperm whales. More data are necessary to investigate the inter-annual variability in seasonal occurrence patterns and to reveal how environmental conditions may influence these patterns.

The spatial and temporal scope of my study was determined largely by the availability of high-frequency passive acoustic recordings. Data collection efforts spanned several independent monitoring projects, resulting in a patchwork of available data which I combined to conduct a broad-scale analysis. Temporal coverage differed among sites, due to varying research goals and logistical constraints. Collecting more synoptic data across consecutive years at the same recording sites, with as few gaps as possible, will improve our ability to quantitatively assess seasonal and inter-annual patterns of species occurrence. High-frequency Acoustic Recording Packages (HARPs) currently have the capacity to collect continuous recordings at a sampling rate of 200 kHz for approximately 9.5 months. Improvements in the data storage capacity of these instruments, enabling them to record for a full year, should aid considerably in reducing the periods of missing data between successive deployments, which often occurred because the HARPs reached full capacity during the winter, when weather conditions prevented timely recovery and servicing of the instruments. Duty-cycled recording schedules can be used to extend deployment durations, but these datasets are more difficult to analyze and interpret, and often result in the underestimation of species occurrence. My results in Chapter 2 suggest that duty-cycled recordings may also contribute bias to estimates of relative species occurrence, and continuous recordings are preferable whenever possible.

Despite the variation in recording effort across sites, my pooled dataset represents the most comprehensive collection of high-frequency recordings from the western North Atlantic to date. The results presented in my dissertation provide a substantial baseline on species occurrence which may be used to develop further hypotheses regarding the distribution and habitat selection of these species. My recording sites spanned a broad range of latitudes and were characterized by variable bathymetric and oceanographic features, making it difficult to draw inferences about which specific environmental factors influenced the occurrence of species at each recording site. I did not find clear correlations between daily detection rates and dynamic oceanographic conditions based on temporal environmental variation alone (Chapter 4). However, a study deploying multiple recorders to address this question on a local scale could better assess the potential importance of persistent oceanographic features such as the Gulf Stream front, as well as bathymetric features such as the presence of undersea canyons. PAM methods using bottom-mounted recorders hold promise for moving beyond baseline monitoring and toward addressing specific, hypothesis-driven questions, but such work will require that data collection efforts are planned with these questions in mind.

Ultimately, PAM is a useful methodology for studying cetacean ecology, and offers some key advantages in the study of beaked whales and sperm whales, which I have noted above and elsewhere in this dissertation. But PAM is by no means a panacea, and a variety of survey and monitoring approaches need to be combined to understand the ecology and biology of these species. In practice, the spatial extent that can be monitored by autonomous, archival recorders will always be limited by cost and logistical considerations, including the nontrivial task of efficiently processing and analyzing very large quantities of acoustic data. The primary advantage of this method, however, is the unbiased seasonal coverage and high temporal resolution of the data, and in the case of beaked whales, the ability to obtain species-specific information. Further development of analytical methods and visualization tools to integrate multiple data types will improve our ability to model the habitat preferences, distribution, and population sizes of these and other marine species (Fujioka et al. 2014a, 2014b). For example, the temporal information obtained from PAM data may be used to validate the seasonal predictions of spatiotemporal distribution models created using spatial survey data (e.g., Roberts et al. 2016). As a first step, presenting the results of multi-platform surveys synoptically, rather than independently based on data type, may help to identify the ways in which these sources of information complement each other and the limitations and biases inherent in each method.

Finally, in addition to improving our understanding of the fundamental ecology of cetacean species, PAM data may be particularly valuable to inform conservation efforts for beaked whales. In recent decades, there has been increasing concern for beaked whales from a conservation perspective, following several mass strandings linked to anthropogenic sources of noise (Cox et al. 2006). As we seek to understand the behavioral responses of beaked whale species to acoustic disturbance (e.g., DeRuiter et al. 2013, Miller et al. 2015), we urgently need a basic understanding of where and when these species occur, to estimate the potential effects of such disturbance on beaked whale populations (Forney et al. *in press*). The results of my dissertation highlight key differences in the spatial and temporal distributions of beaked whale species along the continental slope, and it is important that we recognize the diversity that exists within this taxa. To this end, PAM will continue to play a key role in the study and conservation of these species.

Appendix A: Supplementary figures for Chapter 1

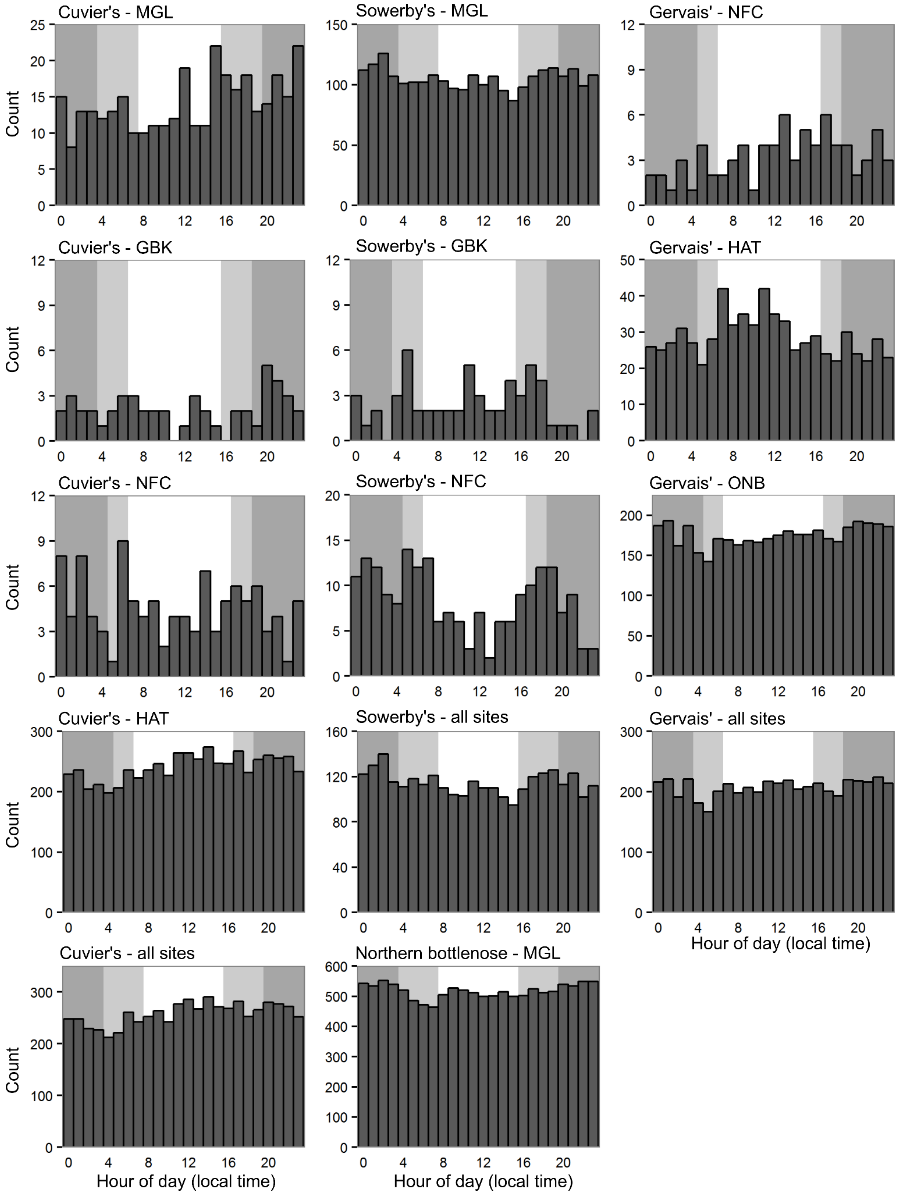


Figure A23: Count of hourly presence by hour of the day (local time) for each species and recording site with at least 50 detection hours. Dark gray shading indicates nighttime hours, light gray shading indicates hours that were either day or night depending on time of year, and white background indicates daylight hours, based on local sunrise and sunset times.

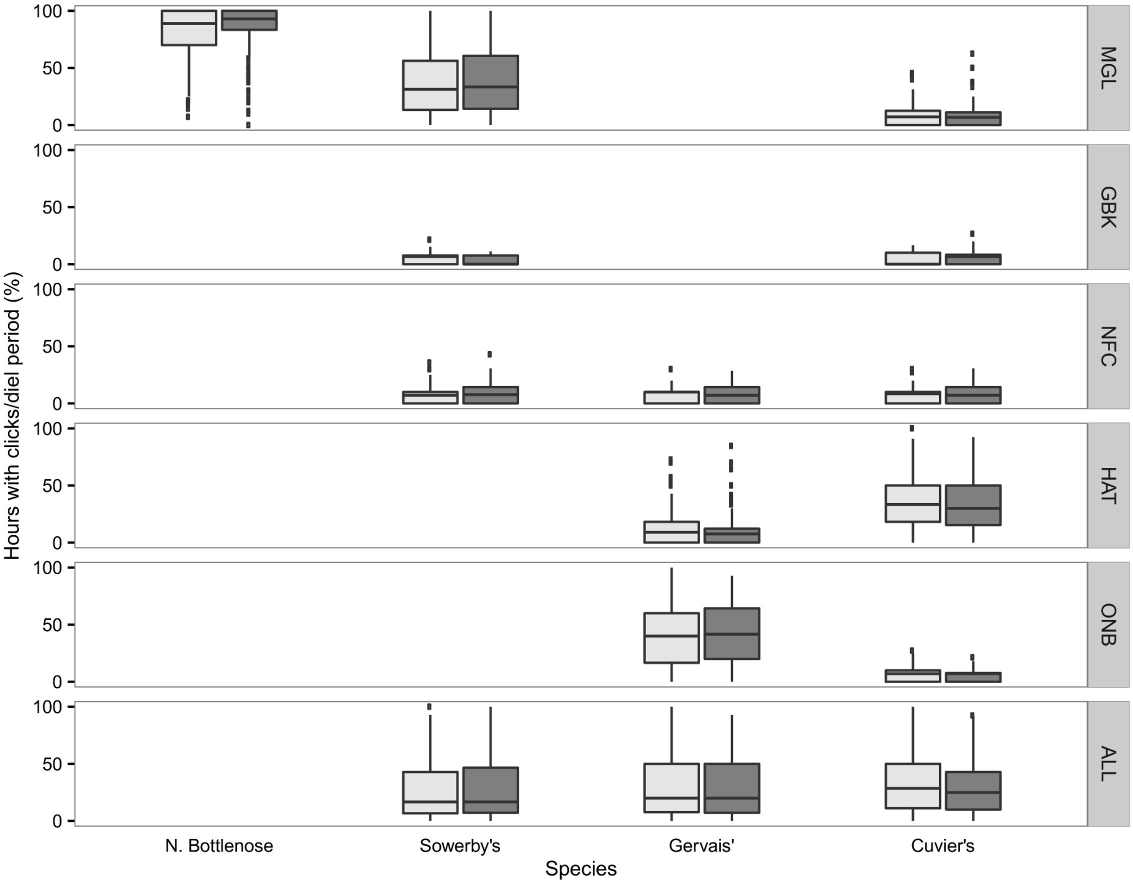


Figure A24: Boxplots of the percent of hours per diel period (light gray: day, dark gray: night) with detections of each beaked whale species, pooled across all recording days at each site. Comparisons are shown for each species/site with at least 50 total detection hours. The bottom panel consists of all detections of Sowerby's, Gervais', and Cuvier's pooled across all sites.

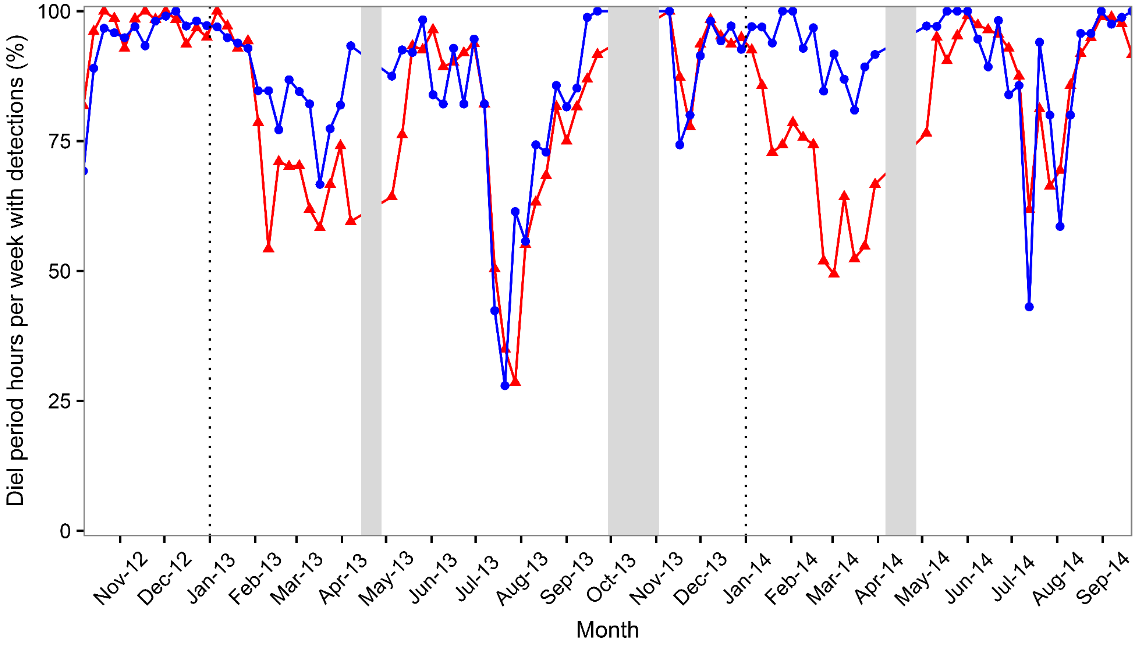


Figure A25: Percentage of diel period hours per week with detections during day (red triangles) and night (blue circles) diel periods for northern bottlenose whales at the Mid-Gully recording site from October 2012 to September 2014. Gray shading indicates time periods with no recording effort; dotted lines separate calendar years.

Appendix B: Supplementary figures for Chapter 4

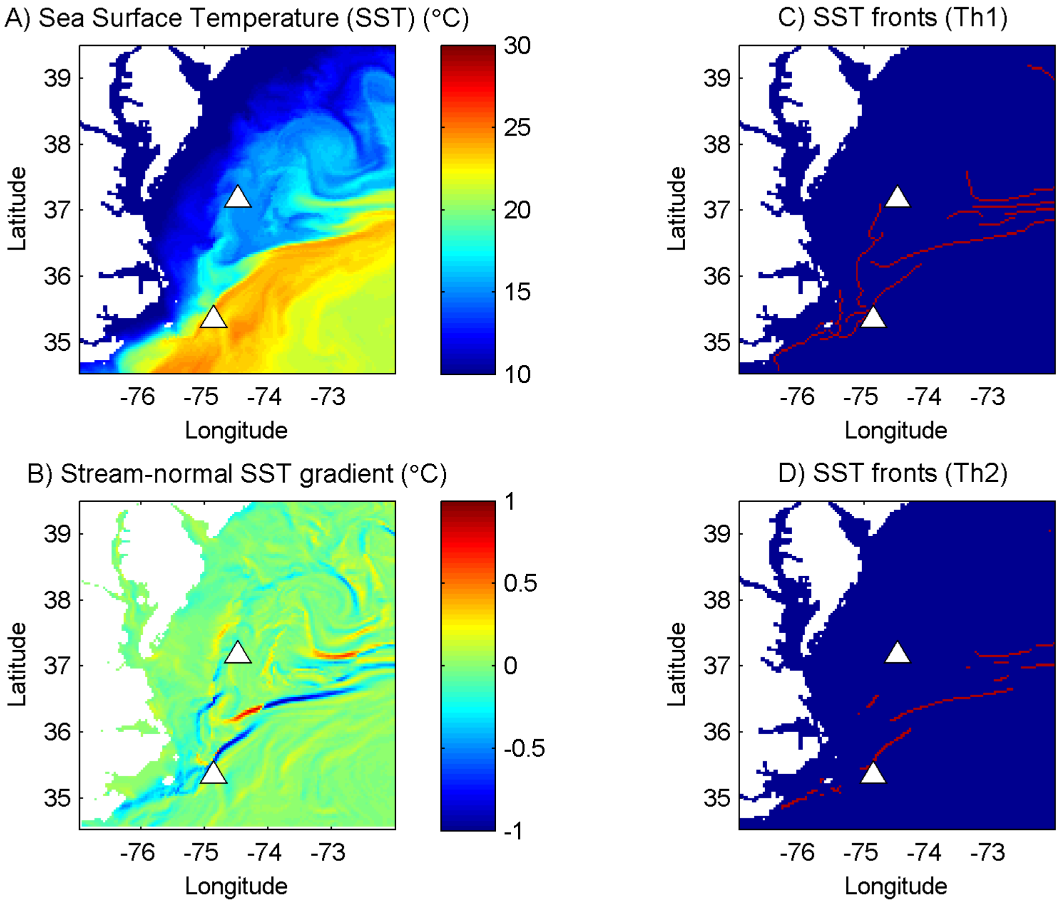


Figure B26: Example maps of sea surface temperature (SST) (A), SST gradient per pixel calculated in the direction normal to flow (B), and SST fronts detected using Th1 (0.4°C) (C), and Th2 (1.0 °C) (D). HARP sites are designated on each map by white triangles.

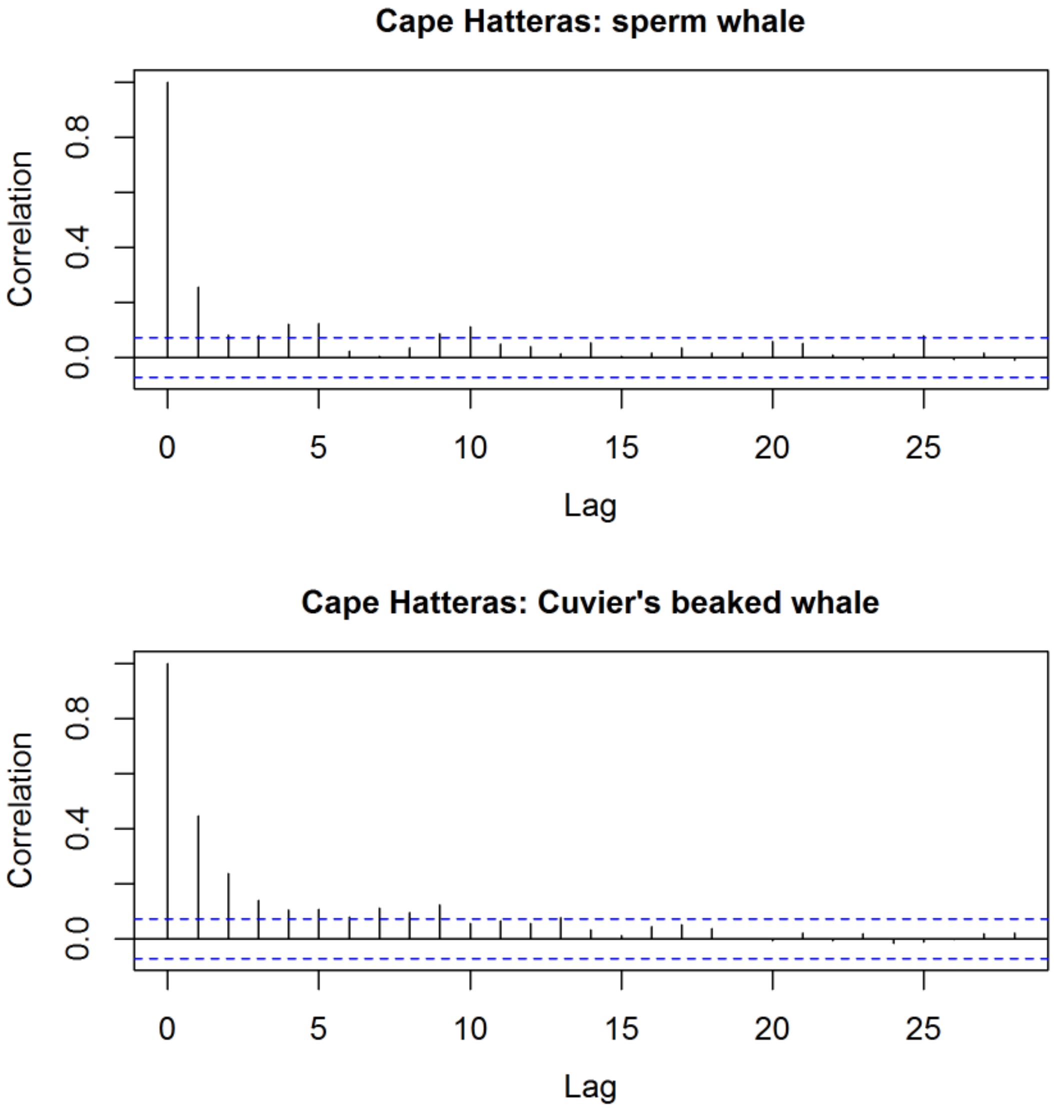


Figure B27: Autocorrelation function plots of Pearson's residuals from models of sperm whale detections (upper) and Cuvier's beaked whale detections (lower) at Cape Hatteras, including 95% confidence intervals around zero autocorrelation (blue dashed lines).

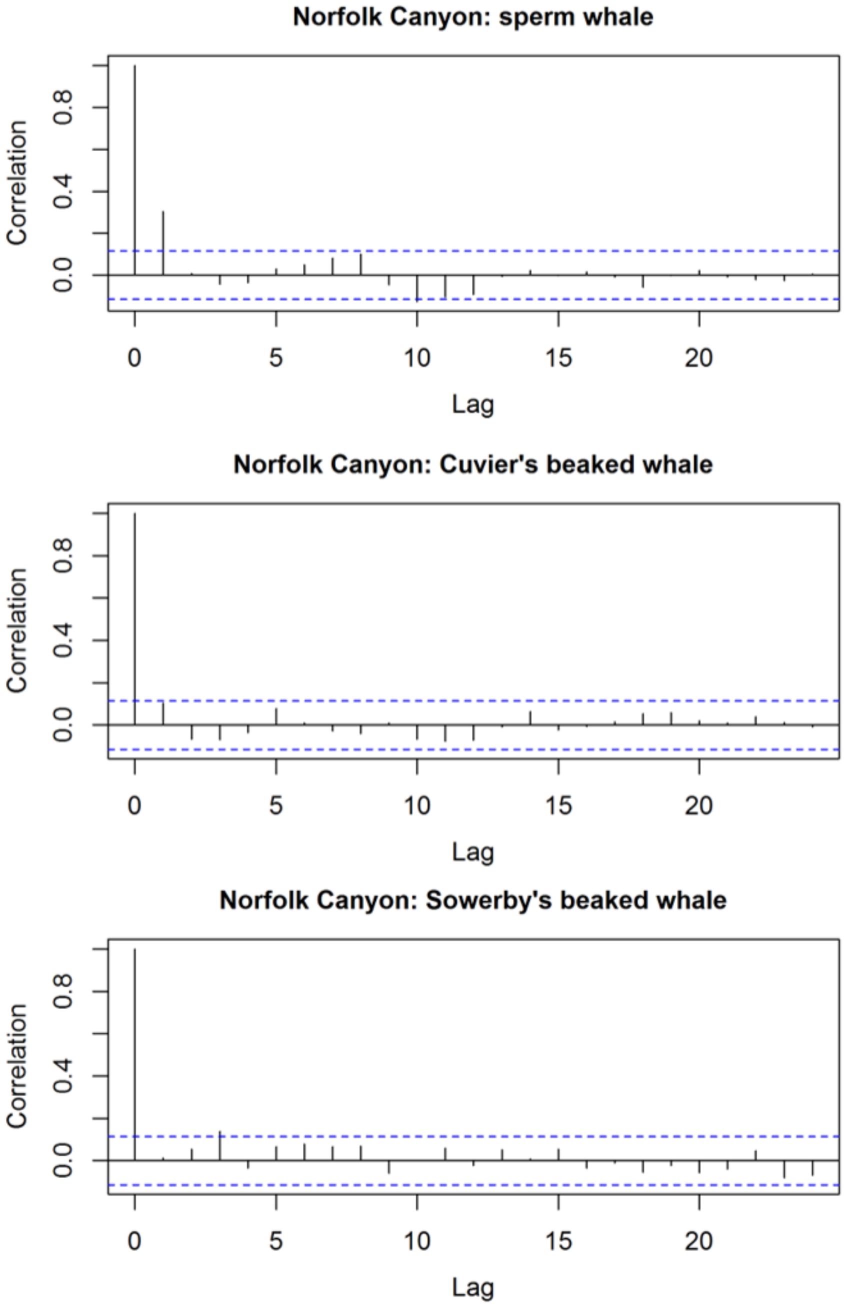
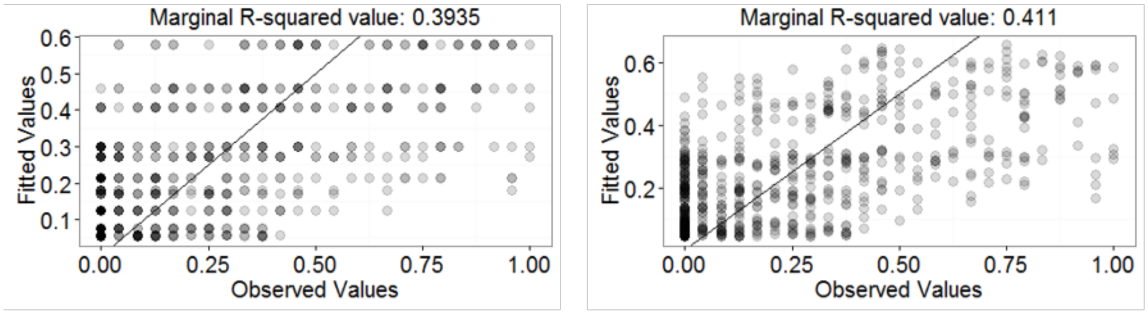
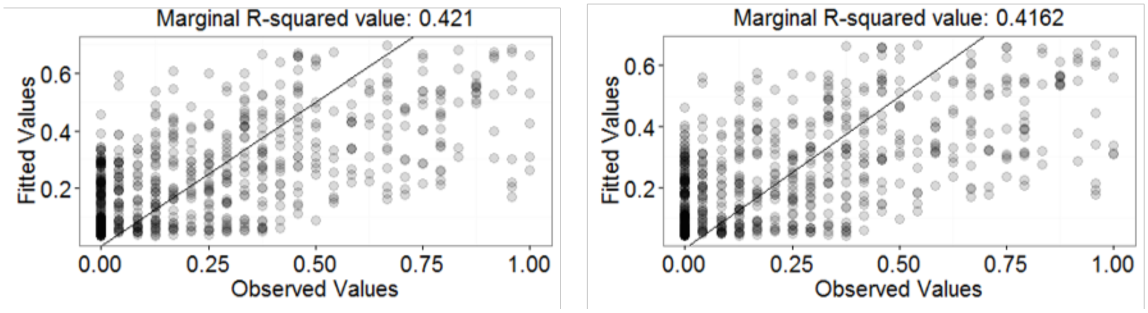


Figure B28: Autocorrelation function plots of Pearson's residuals from models of sperm whale detections (upper), Cuvier's beaked whale detections (middle), and Sowerby's beaked whale detections (lower) at Norfolk Canyon, including 95% confidence intervals around zero autocorrelation (blue dashed lines).



(A) Month

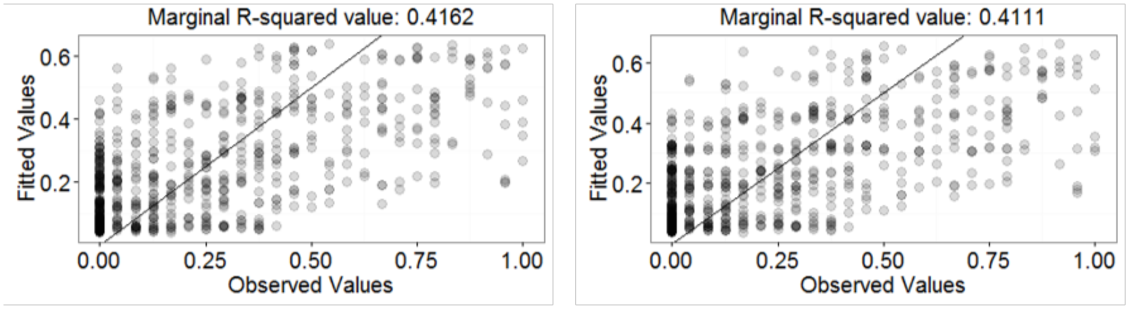
(B) Month + salinity



(C) Month + SST standard deviation

(D) Month + salinity standard deviation

Figure B29: Observed vs. fitted values for models of sperm whale detection rates at Cape Hatteras; diagonal line indicates perfect model fit.



(A) Month + distance to salinity front (Th1)

(B) Month + distance to salinity front (Th2)

(C) Month + presence of salinity front (Th2)

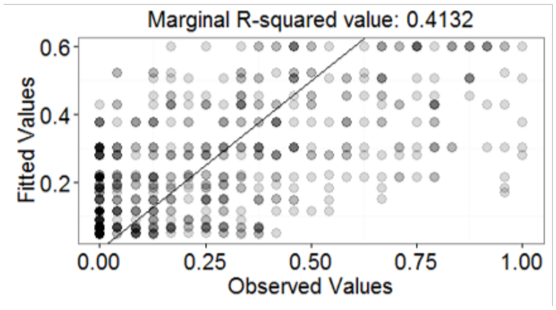
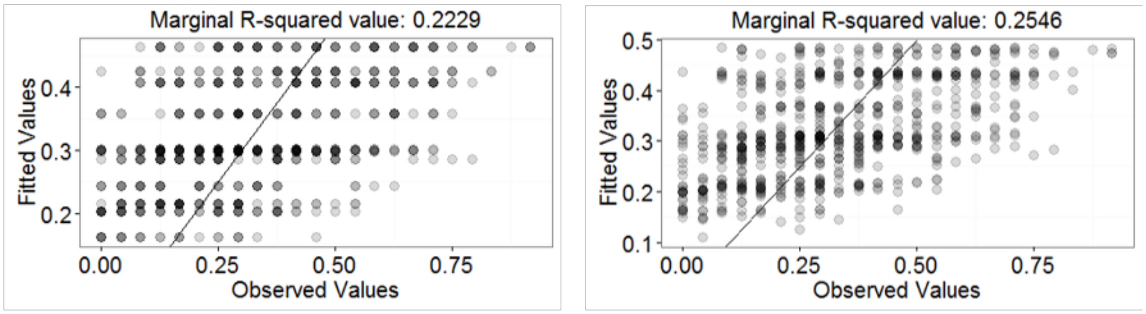
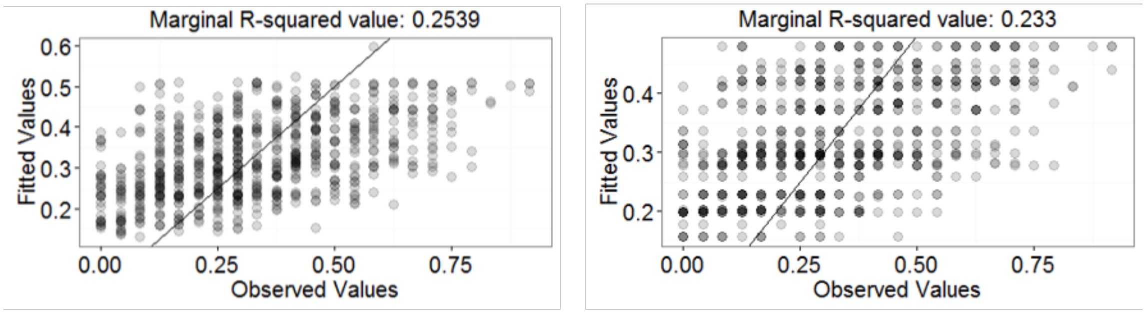


Figure B30: Observed vs. fitted values for models of sperm whale detection rates at Cape Hatteras; diagonal line indicates perfect model fit.


(A) Month

(B) Month + salinity


(C) Month + SST standard deviation

(D) Month + presence of SST front (Th2)

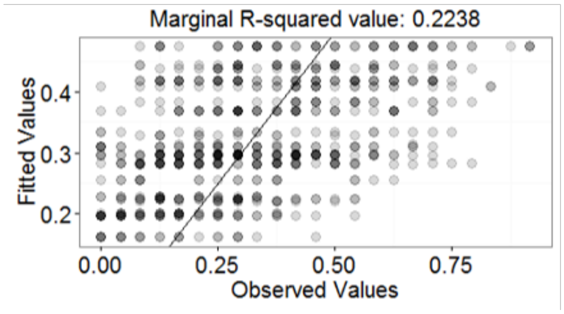
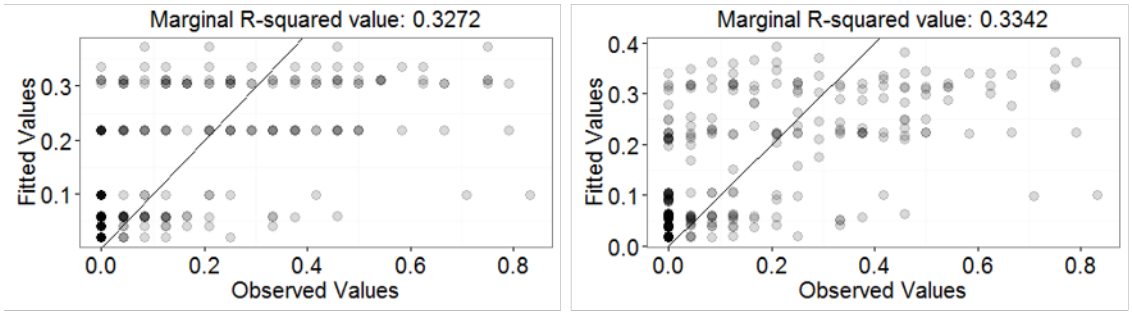
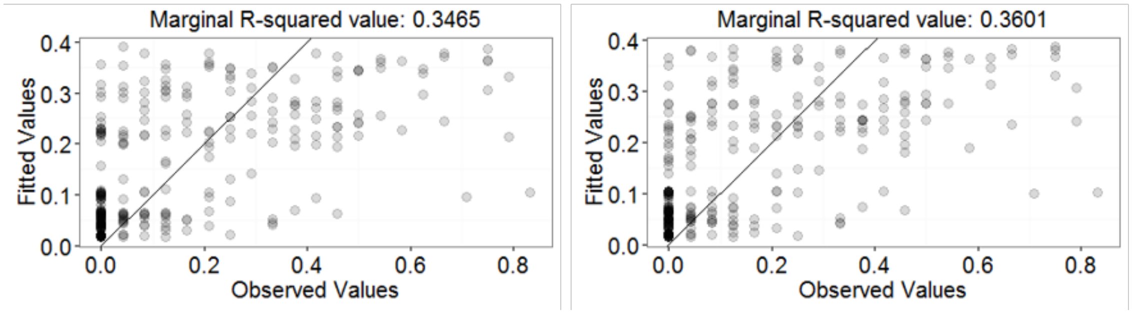

(C) Month + presence of salinity front (Th2)

Figure B31: Observed vs. fitted values for models of Cuvier's beaked whale detection rates at Cape Hatteras; diagonal line indicates perfect model fit.



(A) Month

(B) Month + SST standard deviation



(C) Month + salinity standard deviation

(D) Month + distance to salinity front (Th1)

Figure B32: Observed vs. fitted values for models of sperm whale detection rates at Norfolk Canyon; diagonal line indicates perfect model fit.

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Biography

Joy Elia Stanistreet was born on June 9, 1987 in Riparius, New York, USA. She was homeschooled through Oak Meadow School, then went on to attend the University of California Santa Cruz, graduating *summa cum laude* in June 2009 with a Bachelor of Science in Marine Biology. While attending UCSC, she received an Ernest F. Hollings Undergraduate Scholarship from the National Oceanic and Atmospheric Administration, which led to a summer internship position and post-graduate employment at the NOAA Northeast Fisheries Science Center in Woods Hole, Massachusetts. Stanistreet began her doctoral studies at Duke University in August 2011, and received a National Defense Science and Engineering Graduate Fellowship in 2012. She is a member of the Society for Marine Mammalogy and the Association for Women in Science, and has published three articles to date, which are listed below.

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