UNIVERSITY OF CALIFORNIA, SAN DIEGO

Deep-Diving Cetaceans of the Gulf of Mexico: Acoustic Ecology and Response to Natural and Anthropogenic Forces Including the Deepwater Horizon Oil Spill

A dissertation submitted in partial satisfaction of the
requirements for the degree
Doctor of Philosophy

in

Oceanography

by

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The dissertation of Karlina Paul Merkens is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

Chair

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2013

DEDICATION

To Lillian Irene, my inspiration, motivation, and the apple of my eye.

And to Michael, today, tomorrow, and forever.

EPIGRAPH

I must go down to the seas again, to the lonely sea and the sky,
And all I ask is a tall ship and a star to steer her by,
And the wheel's kick and the wind's song and the white sail's shaking,
And a grey mist on the sea's face, and a grey dawn breaking.

I must go down to the seas again, for the call of the running tide
Is a wild call and a clear call that may not be denied;
And all I ask is a windy day with the white clouds flying,
And the flung spray and the blown spume, and the sea-gulls crying.

I must go down to the seas again, to the vagrant gypsy life,
To the gull's way and the whale's way, where the wind's like a whetted knife;
And all I ask is a merry yarn from a laughing fellow-rover,
And quiet sleep and a sweet dream when the long trick's over.

— *Sea Fever, John Masefield*

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PUBLICATIONS

Journal Articles

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1. Merkens, K., McDonald, M.A., Baumann- Pickering, S., Frasier, K.E., Wiggins, S.M., Hildebrand, J.A. 2013. Deep-diving cetaceans and the Deepwater Horizon oil spill. Acoustical Society of America Meeting, San Francisco, CA. Oral Presentation.
2. Merkens, K., Frasier, K.E., McDonald, M.A., Bassett, H. R., Sirovic, A., Baumann- Pickering, S., Wiggins, S.M., Hildebrand, J.A. 2011. Monitoring of Cetaceans During and After the Deepwater Horizon Oil Spill Using Passive Acoustics. 19th Biennial Conference on the Biology of Marine Mammals, Tampa, FL. Oral Presentation.
3. Merkens, K., McDonald, M.A., Baumann-Pickering, S., Frasier, K., Wiggins, S.M., Hildebrand, J.A. 2011.Passive acoustic monitoring of sperm whales during and after the Deepwater Horizon oil spill. Acoustical Society of America Meeting, San Diego, CA. Oral Presentation.
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ABSTRACT OF THE DISSERTATION

Deep-Diving Cetaceans of the Gulf of Mexico: Acoustic Ecology and Response to Natural and Anthropogenic Forces Including the Deepwater Horizon Oil Spill

by

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Doctor of Philosophy in Oceanography

University of California, San Diego, 2013

John Hildebrand, Chair

Characterization of the spatiotemporal patterns of marine mammal populations is challenging yet critical for understanding their role in the ecosystem and how they are affected by ecological disturbance, such as anthropogenic activity. Gathering information about deep-diving cetaceans is particularly difficult because they spend so much of their lives well below the ocean's surface, however they can be detected using passive acoustic monitoring.

The Gulf of Mexico is home to at least six species of deep-diving cetaceans, and we recorded signals from *Ziphius cavirostris, Mesoplodon europaeus, M. densirostris, Physeter macrocephalus* and *Kogia* spp., as well as an unknown beaked whale-like signal. Using seafloor High Frequency Acoustic Recording Packages (HARPs) we monitored nearly-continuously at three deep-water sites (>900m depth) using a 200 kHz sampling rate, from May 2010 until February 2012, accumulating more than 1350 cumulative days of data.

Here I describe the species present, their detection trends over time and their relationships with the environment, including the Deepwater Horizon oil spill. This major environmental event took place in the northern Gulf of Mexico for roughly three months in the summer of 2010, and released approximately 210 billion gallons of oil and unmeasured amounts of natural gas mixed with chemical dispersants into the deep water along the continental slope.

The number of detections for each species fluctuated across sites on diel and seasonal time scales. Beaked whales were detected at a remarkably high rate at one site. Sperm whales were detected almost daily at another site. *Kogia* spp., which are very difficult to monitor visually, were easily detected acoustically and were present at all three sites.

I used mathematical models to relate acoustic detections of the different species to their environment. The models included both natural and anthropogenic factors, with data collected both in situ and remotely. Most models include mean sea surface temperature, indicating the importance of seasonal variations and the resulting ecological fluctuations. The results vary by species and location, and help us understand the ecology of these rare species as well as the potential impact of the oil spill on the region.

Chapter 1

Introduction

1.1 Cetaceans

The Cetacea, whales, dolphins and porpoises, are essential in their ecosystem because they are at the top of their food chain, therefore it is essential for us to study them so that we can assess ecosystem function and reduce negative anthropogenic impact on the environment. But this goal leads to many challenges and questions. How can we study animals that are so often below the surface of the water? How can we learn more about their habits, behavior and preferred habitats? Where are they and why are they there?

Cetaceans are found in all the Earth's marine environments, and have been described and studied for centuries. Much of our early understanding of these animals came from stranded individuals or those that were killed for human consumption (e.g. Beale 1839). Only in the last few decades have humans studied cetaceans without an interest in killing them, and we have quickly learned how little we know. With only other cetaceans and humans as their predators, whales are at the top of their food chain, whether they prefer vertebrate or invertebrate prey, and from that position they have a large effect on the the entire ecosystem. In some cases their ecosystem stretches across entire ocean basins, so the importance of an individual can be very large. To better understand our world, and the effect humans have on it, it is essential for us to better understand cetaceans.

Spending much of their time below the sea surface, these animals live in an environment that is inhospitable to humans. Therefore it is very difficult for us to observe them using our eyes, which is our preferred method of observation. Additionally, most marine mammals are active at all hours of the day, and therefore if we rely solely on vision we will not able to observe them at all for half of their lives (night time).

1.2 Deep-Diving Cetaceans

Deep-diving cetaceans are an extreme example of this situation. They live in very deep water, spending the vast majority of their lives not only below the water's surface, but also at great depths. The pressure and darkness are intense in this environment, yet these animals are adapted to these conditions. They do come to the surface, but for many species this happens only once per hour, and it is for a remarkably brief period. In a few minutes they replenish their oxygen stores and return to their home in the depths.

Fortunately for researchers cetaceans make and use sound, and deep-diving cetaceans are particularly reliant on sound because it is the only way for them to navigate and hunt in near total darkness. They make sounds for much of the time while diving, and therefore we can detect their presence in the area by "listening" for them. They make signals for echolocation that are easily detected using modern recording equipment, and despite the relatively limited auditory range of humans we can monitor for cetacean signals by looking at visual representations of the sounds.

Deep-diving cetaceans, such as beaked and sperm whales, have been insulated from the effects of human activities for thousands of years by generally living far from land, but as we have reached farther and deeper into the ocean in the last three centuries these poorly understood species have been increasingly impacted. Historically the major threat to sperm whales was whaling, which began on a large scale in the 18th century and reached a peak in the mid 20th century. Sperm whales are still harvested in the North Pacific, but current and future threats to all cetaceans are more widespread and chronic, including noise and chemical pollution, ship strikes, interactions with the fishing industry, climate change effects on habitat and prey, and more (Evans 2002, Northridge 2002, Reijnders and Aguilar 2002, Würsig and Richardson 2002, Fernandez et al. 2005, Carrillo and Ritter 2008).

In general if we define the category of deep-diving cetaceans to include all species that regularly dive below 500 meters, it contains at least 15 species. Of these, the sperm whale (*Physeter macrocephalus*) is the largest, with adult males being up to 18.3 meters long, while the dwarf sperm whale (*Kogia sima*) is the smallest, with adult males being 2.7 meters long. This wide range in size translates to a wide range in life-history and biology, however there are many similarities among these diverse species. For example, many of these species travel in small groups (2-10 individuals) and feed primarily on cephalopods. They are long-lived (10-100 years), bearing only one offspring at a time (Whitehead 2002b).

I will focus on three cetacean groups: sperm whales, pygmy and dwarf sperm whales (*Kogia breviceps* and *K. sima*), and selected beaked whales (family Ziphiidae). These groups were selected because of their similar ecology, because we have information on their acoustic signals (albeit limited in some cases), and because they are visually and acoustically detected in the Gulf of Mexico. We know more about some species than others. Sperm whale biology and distribution has been studied for centuries because of their desirability in both the wooden-boat and modern commercial whaling programs (Whitehead 2002b). However, sperm whale ecology and long-term population trends are less well understood, and their populations worldwide were so depleted by whaling that what we observe currently may not resemble pre-whaling conditions (Whitehead 2003). Additionally, sperm whale harvest is still ongoing, making continued research critical for facilitating appropriate management now and in the future.

Sperm whales are large and they can live for more than 70 years in cooperative groups, and are found in all oceans (Whitehead 2002b, Jefferson et al. 2008). Population estimates vary widely between 200,000 and 1,500,000 sperm whales worldwide (Whitehead 2002a, b). While females remain in social groups within a home range with a roughly 500 kilometer radius throughout their lives, males separate as adults, primarily living independently at higher latitudes (Würsig et al. 2000, Whitehead 2002b, Jefferson et al. 2008). As with the other deep-diving species, they feed on a variety of deep-living squids, of which the exact species composition varies by prey availability (Whitehead 2002b).

In contrast to the well-studied sperm whales, much of what we know about *Kogia* spp. and beaked whales comes from examination of stranded animals or studies in unusual locations where they are found close to shore (e.g. Johnson et al. 2004). Both groups are highly elusive, being entirely pelagic, having faint-to-invisible blows and showing only a low profile while at the water's surface (Mead 2002, Pitman 2002, Jefferson et al. 2008). *Kogia* spp. are distributed worldwide in temperate and tropical waters, although much of their range is questionable because it has been identified only by strandings (Willis and Baird 1998, Jefferson et al. 2008). They are small, being only about three meters in length, they live in small groups of less than 10 individuals, and the only analysis of age, which took place off the coast of South Africa, noted that they live relatively short lives of approximately 23 years (Jefferson et al. 2008). Based on gut content and isotope analysis it appears that the two species may feed at different depths on slightly different prey, which could affect their distribution, interactions with humans, and acoustics (Willis and Baird 1998, Barros et al. 1998). Visual differentiation of the two *Kogia* species is very difficult (Willis and Baird 1998, Jefferson et al. 2008), and very little is known about the differences in their ecology or acoustic behavior. Additional details of biology and ecology are lacking.

For most beaked whale species individual and population biology is relatively unknown, but is probably diverse across the different species. In general they are medium sized, being 4-13 meters in length. They tend to live in small groups of only one to six animals (Pitman 2002, Jefferson et al. 2008). The size of their home ranges or migrations is generally unknown (Pitman 2002) because of limited tagging studies (e.g. Johnson et al. 2004, Tyack et al. 2011) and because photo identification of *Mesoplodon* species ($n = 14$) is difficult; however, recent results suggest the short-term movements of some species are on the order of 25 square kilometers (Hooker et al. 2002). They often cannot be distinguished except by the teeth of adult males, and they do not raise flukes when diving (Aguilar Soto et al. 2007, Jefferson et al. 2008). In the Gulf of Mexico the known species are Gervais' (*Mesoplodon europaeus*), Cuvier's (*Ziphius cavirostris*), Blainville's (*Mesoplodon densirostris*) and Sowerby's (*Mesoplodon bidens*) beaked whales based on sightings and strandings (Würsig et al. 2000, Jefferson et al. 2008). The acoustic signals of three of these species (*M. europaeus, Z. cavirostris*, and *M. desirostris*) have been described in the literature and are classifiable based on these signals (Zimmer et al. 2005, Johnson et al. 2006, Gillespie et al. 2009).

Characterization of the spatiotemporal patterns of these animals is critical, not only for understanding their role in the ecosystem, but also how that role changes in the face of disturbance. We currently do not know how deep-diving cetaceans respond to disturbance events, which greatly limits our ability to understand the effects of anthropogenic disturbance and to predict how future disturbances will impact these species. The Gulf of Mexico provides a unique region for studying the effects of disturbance on deep-diving whales because it is possible to monitor their behavior, and we can characterize their response to a recent, human-induced disaster, the Deepwater Horizon (DH) oil spill.

Study and management of deep-diving cetaceans is a challenging task because these animals spend so much of their lives well below the ocean's surface, feeding at great depths for long durations. Sperm whales, for example, can dive for well over an hour to depths greater than 1,000 meters (Whitehead 2003, Watkins et al. 1993). While some deep-diving whales are internationally listed as threatened or endangered, many others have been studied so little that they are listed as "Data Deficient" (IUCN 2010), and new species are still being discovered (e.g. Dalebout et al. 2002). However, many deep-diving cetaceans are very active acoustically (Whitehead 2002b, Johnson et al. 2004, Madsen et al. 2005a), therefore we can monitor their presence and identify aspects of their behavior even in their dark, high-pressure environment by using passive acoustic monitoring (Whitehead and Weilgart 1990, Madsen et al. 2005b, Barlow et al. 2006, Aguilar Soto et al. 2008, Zimmer et al. 2008). Employing autonomous recording devices can also be economical because instruments can collect data for long durations without human input (Wiggins and Hildebrand 2007). And in the case of some species (e.g. sperm whales) the animals can often be detected acoustically at much greater distances than they can be detected visually (Madsen et al. 2002).

1.3 The Gulf of Mexico

The data presented here were collected in the semitropical Gulf of Mexico, where the circulation is primarily driven by the "Loop Current" flowing in from the Caribbean Sea and out through the Florida Straits between Florida and Cuba (Figure 1.1). Eddies, or "warm core rings" periodically form from this current and move to the west, eventually dissipating in the "Eddy Graveyard" along the coast of Texas and Mexico. "Cold core rings" also form periodically in the eastern Gulf and can remain in position for many months (e.g. Alvera-Azcarate et al. 2009). The other major oceanographic factor in this basin is the massive influx of fresh water and nutrients from the Mississippi River, which drains approximately 6,000,000 square kilometers of land (part of 31 US states and two Canadian provinces) and introduces approximately 500 trillion liters of fresh water per year into the Gulf (Würsig et al. 2000, National Park Service 2010). These conditions create high productivity in the Gulf of Mexico, particularly near the mouth of the Mississippi River, which is a region commonly exploited by both cetaceans and humans (Davis et al. 1998, O'Hern & Biggs 2009, Wilkinson et al. 2009). This high productivity has also lead to the annual presence of a hypoxic zone that is contained on the continental shelf to the west of the Mississippi River delta (Rabalais et al. 2002). It is not likely that this phenomena would have affected the deeper waters of the Gulf, and it has been shown that the areal coverage of this zone was not increased by the DH oil spill (Rabalais 2011).

The Gulf of Mexico is very heavily impacted by human activities other than the petroleum exploration and extraction that lead to the DH oil spill, with a significant amount of shipping throughout the Gulf, as well as intense fishing near the coasts, particularly bottom trawling for shrimp (Wilkinson et al. 2009). Due to factors such as significant development along the coastlines, the petroleum

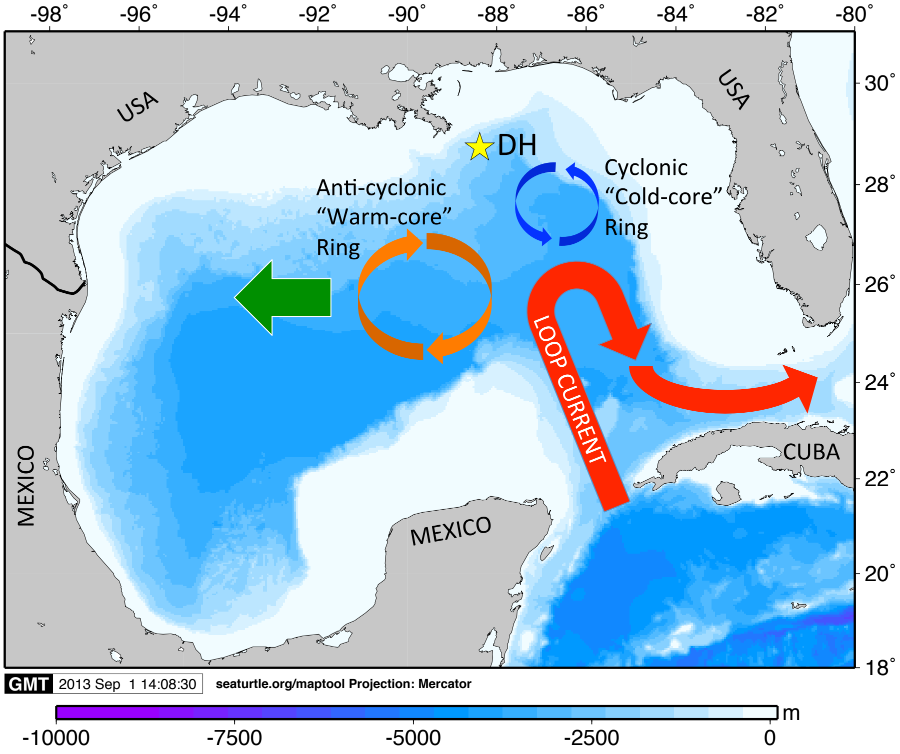


Figure 1.1: Basic bathymetry and surface circulation in the Gulf of Mexico showing the Loop Current (red), a "warm-core ring" (orange) and a "cold-core ring" (blue) as well as the site of the Deepwater Horizon oil rig (yellow star). General westward movement of "warm-core rings" indicated by green arrow.

and natural gas industries, and the slow circulation in the basin, coastal and shelf areas of the Gulf of Mexico have very high chemical pollution levels, and also high ambient noise, which is related to boat traffic and other human activities (Hildebrand 2009).

1.4 The Deepwater Horizon Oil Spill

Called one of the worst environmental disaster of the century, the Deepwater Horizon (DH) oil spill lasted for 87 days and spewed approximately 780,000 cubic meters (210,000,000 US gallons) of crude oil into the Mississippi Canyon region of the northern Gulf of Mexico (National Commission on the BP Deepwater Horizon Oil Spill and Offshore Drilling 2011) (Figure 1.2). The spill began when a methane gas explosion occurred on the Deepwater Horizon drilling rig, which was nearing the end of the initial drilling process to tap the Macondo well. Eleven workers have been presumed dead from the explosion and subsequent fire, and the rig eventually sank to the seafloor, leaving oil gushing from the broken riser pipe at approximately 1600 meters depth (National Commission on the BP Deepwater Horizon Oil Spill and Offshore Drilling 2011). The total volume of oil and natural gas that was released into the water has been heavily debated, and the exact numbers will likely never be known because of the difficulty in estimating the flow rate at the extreme depth of the wellhead. In addition to the oil and gas that leaked, 7000 cubic meters (1.84 million US gallons) of Corexit dispersants were added to the spill area, either injected at depth or spread over the sea surface (National Commission on the BP Deepwater Horizon Oil Spill and Offshore Drilling 2010). It has since been shown that the toxicity of the combination of oil and Corexit 9500A increases by 52 fold (Rico-Martinez et al. 2013). The effect of depth on the oil, on the Corexit and on the combination of the two substances is unknown, however a deep plume of oil was detected at approximately 1175 meters depth, and the addition of the chemical dispersants at depth has increased the amount of hydrocarbons below the sea surface (Spier et al. 2013). This is particularly significant when studying populations of deep-diving cetaceans because they were

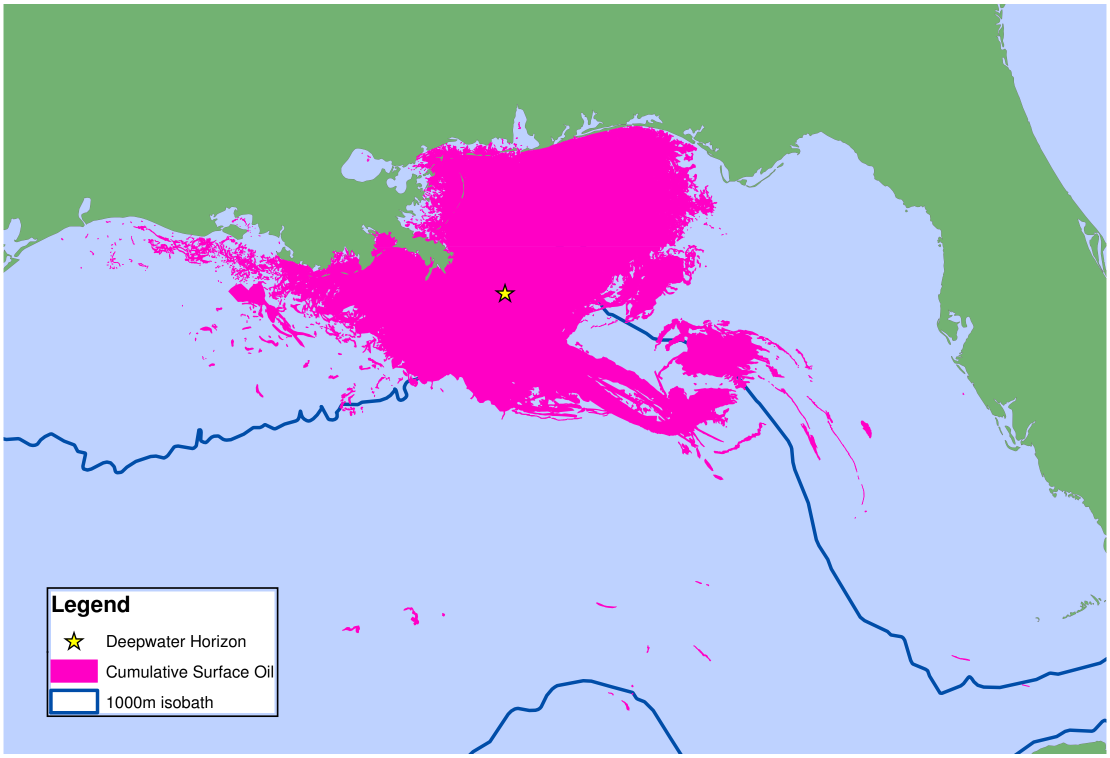


Figure 1.2: Cumulative surface oil (magenta) from Deepwater Horizon (yellow star) oil spill. Thick blue line indicates 1000 meter isobath.

not only exposed to hydrocarbons that collected on the surface and evaporated into the air, but they also regularly swim through, and feed in, deep-water habitat that was contaminated with the highly toxic combination of oil and chemical dispersants. Only a fraction of the oil and gas that spilled in the Gulf were recovered, the rest remaining in the environment, for example settling out onto the sediments in deep water (e.g. Lubchenco et al. 2010, Montagna et al. 2013). The long-term impact of the spill on the Gulf of Mexico ecosystem will take decades to understand, but in the short term I am able to use passive acoustics to confirm the direct exposure of deep-diving cetaceans to the spill and to model the relationships between cetacean detections and their habitat, including the oil spill.

1.5 Data Collection and Analysis Overview

The data used for this research were primarily collected using High-frequency Acoustic Recording Packages (HARPs)(Wiggins and Hildebrand 2007). These autonomous instruments record long-duration, wide bandwidth (10 Hz-100 kHz), continuous acoustic data, which allows for detection of all deep-diving cetaceans, including the high frequency clicks of *Kogia* spp. These long-duration data were processed using human analysts and by automated methods, both of which can efficiently distill terabytes of data into a manageable list of detections of the target species. Further analysis of the specific detections was then performed using standard statistical methods and additional automated routines. There are three deep-water HARP sites in the Gulf of Mexico (Figure 1.3), selected because of the local oceanography to include one site close to the DH wellhead (Mississippi Canyon), and two sites ideal for detection of deep-diving species and not exposed to oil (Green Canyon and Dry Tortugas).

The relationships between the acoustic detections and the animals' habitat at these sites were explored using mathematical models, including Generalized Additive Models (GAMs) and Zero-inflated Negative Binomial Generalized Linear Models (ZINB). Most often environmental or habitat models are generated using spatially diverse data from one or a few points in time. In contrast, the data presented used in these models are from a single location, but because of the dynamic, fluid nature of the ocean environment, the "habitat" characteristics at a single point will change over time as different water masses move past the HARPs.

1.6 Summary

My objective is to use passive acoustics to address the following question: What are the spatiotemporal patterns of deep-diving cetaceans in the Gulf of Mexico, and how are they influenced by natural and anthropogenic factors?

This dissertation presents research into the ecology of deep-diving cetaceans in the Gulf of Mexico with particular focus on the response to environmental conditions, including the disturbance caused by the Deepwater Horizon oil spill.

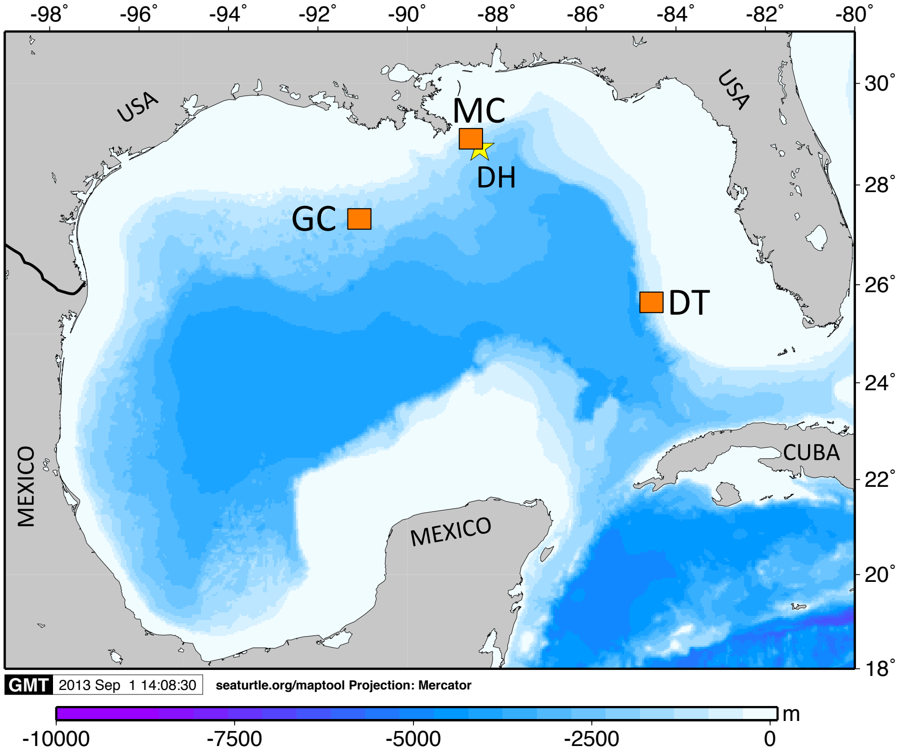


Figure 1.3: Locations of deep water HARPs in the Gulf of Mexico. Orange boxes indicate HARPs, yellow star indicates approximate site of Deepwater Horizon (DH) oil rig. HARPs are named according to location, from left to right: Green Canyon (GC), Mississippi Canyon (MC) and Dry Tortugas (DT).

Chapter 2 describes the data collection and analysis, preliminary data exploration and statistical methods. The remaining three chapters are divided by species group, with Chapter 3 focusing on the analysis of sperm whale detections, Chapter 4 focusing on three beaked whale species, and Chapter 5 focusing on the detections of *Kogia* spp. In general:

1. there are remarkable spatial and temporal patterns in the acoustic detections of deep-diving cetaceans in the Gulf of Mexico, and
2. patterns in the acoustic behavior of these species are related to environmental and anthropogenic factors, including the effects of the DH oil spill, showing the impact that this event had on these species.

Chapter 2

Data Acquisition and Processing

The data for the following chapters has been gathered and processed using similar methods. Therefore the data acquisition, processing and exploration are presented here. Details and results that are specific to each species group will be presented in later chapters.

2.1 Acoustic Data

2.1.1 Instrumentation and Sites

The core of the data for this research is passive acoustic recordings from deep waters in the Gulf of Mexico. Data recording began on May 16, 2010 after the Deepwater Horizon oil spill began April 26, 2010, and has continued since. The time series analyzed here extend through February 2012. These data were collected using High-frequency Acoustic Recording Packages (HARPs, Figure 2.1) (Wiggins and Hildebrand 2007).

These instruments have been shown to be effective for monitoring deep-diving cetaceans, and have been used for habitat modeling of other cetacean species (e.g. Baumann-Pickering et al. 2010, Soldevilla et al. 2010). HARPs comprise a base unit that rests on the seafloor when attached to ballast weights, with pressure cases containing a data logger and battery pack sufficient for many months. The data logger has a low-drift clock and hard drive storage for up to five terabytes of

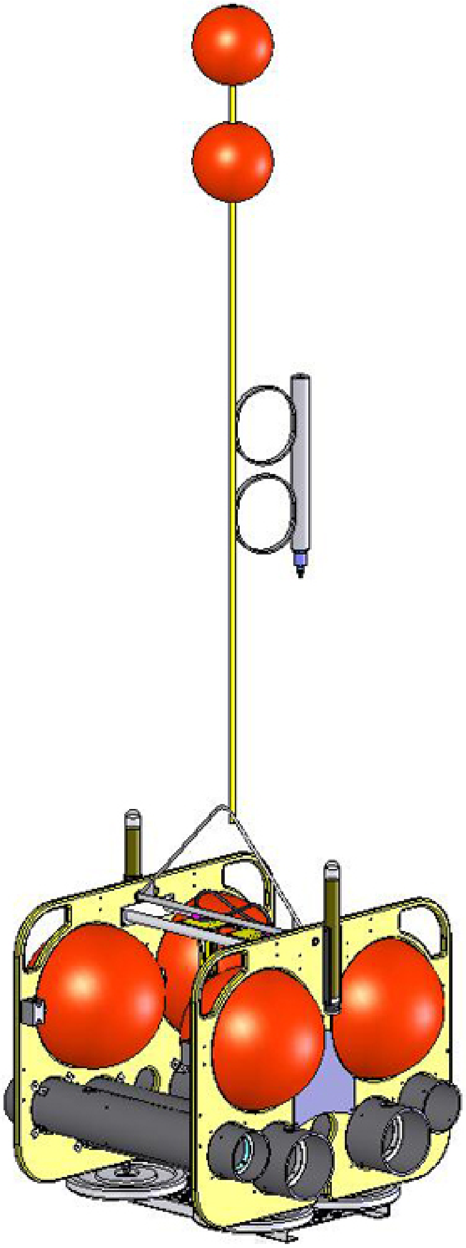


Figure 2.1: Schematic of High Frequency Acoustic Recording Package (HARP) used for data acquisition in the Gulf of Mexico. Base unit is roughly one meter on all sides, and the hydrophone is suspended approximately 10 meters above the seafloor.

acoustic data. The hydrophone is suspended about 10 meters off the seafloor and isolated to reduce flow noise.

HARPs were deployed at three deep-water locations in the Gulf of Mexico (Figure 1.3). The locations were selected to include:

1. a site close to the Deepwater Horizon (DH) wellhead, to monitor cetacean activity near the center of the spill (Mississippi Canyon, MC),
2. a site to the west of the wellhead, beyond the early extent of the oil, in case oil moved toward the west (Green Canyon, GC), and
3. a site to the southeast of the wellhead, downstream of the Loop Current, in case oil was entrained in the Loop Current (Dry Tortugas, DT).

At each site an instrument recorded continuously at 200 kHz (100 kHz Nyquist), with each deployment lasting on average 111 days (roughly 3.7 months). The gap between deployments varied from a few hours to a few weeks. Here we include data from 13 deployments, totaling 47.6 terabytes of data. Details of the characteristics of these sites, which were named according to location, and the data collected are presented in Table 2.1, mapped in Figure 1.3 and illustrated as a timeline of effort in Figure 2.2. HARPs were deployed at two additional locations in the Gulf of Mexico (for a total of five), however because they were in depths of less than 270 meters there were only a few detections of sperm whales at the deeper of the two shallow sites. Therefore they are not included in this analysis.

Table 2.1: Details about deep-water HARP deployments in the Gulf of Mexico

Site	Latitude (North)	Longitude (West)	Depth (m)	Cumulative Recording (days)
Mississippi Cyn. (MC)	28.85	88.48	980	560
Green Cyn.(GC)	27.56	91.17	1100	460
Dry Tortugas (DT)	25.77	84.70	1350	340

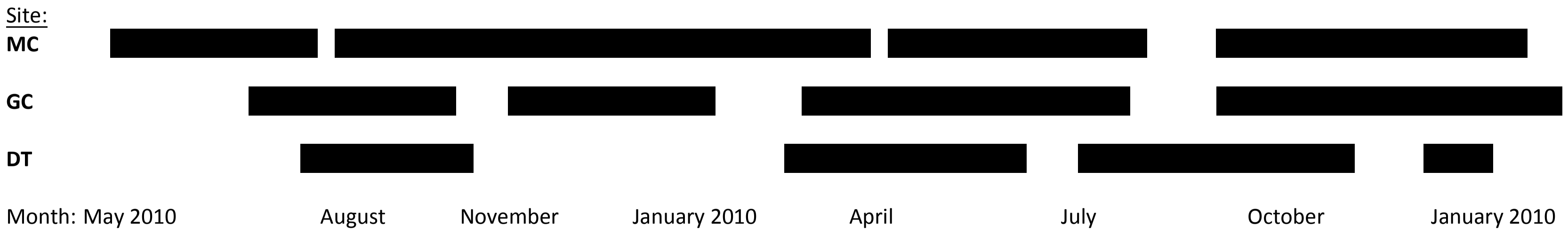


Figure 2.2: Effort of recording at deepwater HARP sites in the Gulf of Mexico

2.1.2 Analysis of Recordings

Recordings in wav format are averaged to generate long term spectral averages (LTSAs)(Wiggins 2003), which are manually inspected in 0.5 or 1 hour segments. Manual analysis was conducted by a trained analyst using customized MATLAB routines (Mathworks, Natick, MA) who visually examined LTSAs. An example LTSA is given in Figure 2.3, and the detailed characteristics of each species' signals are presented in the following chapters. Individual detections were defined as a series of multiple echolocation clicks, and a new detection was begun when clicks were separated by at least 30 minutes. During acoustic events that completely masked the cetacean signals, such as a close passage of a vessel, the detection was marked as ended. In the case of beaked whales, masking by Delphinids was possible, however extra care was taken to scan sections of high amplitude Delphinid detections to avoid missing beaked wales. Masking of *Kogia* spp. signals was unlikely given their high frequencies, which are above most other signals in this region.

Settings for brightness, contrast and other visualization parameters were kept constant for each species at each site to allow comparisons across all deployments. The start of a detection was marked when clicks were identified in the LTSA. The end of a detection was marked at the last click when at least 30 minutes with no clicks followed. These detections were logged using a graphical user interface, which produced spreadsheets for further analysis. The total number of 5-minute "bins" (non-overlapping time segments of 5-minutes each, starting from the beginning of each deployment) containing clicks was counted. These 5-minute bins were then combined to produce total number of 5-minute bins per time period, with the time period duration varying by site and species, as described below. This metric of 5-minute bin counting was selected because it provides more information than simple presence/absence per time period, but avoids contamination of false-positives, which can be problematic when counting individual clicks. For example, when a large group of animals is moving past the HARP, the duration of presence (i.e. the total number of 5-minute bins) will be greater than when a smaller group or individual is present, and similarly when animals remain in a region for a

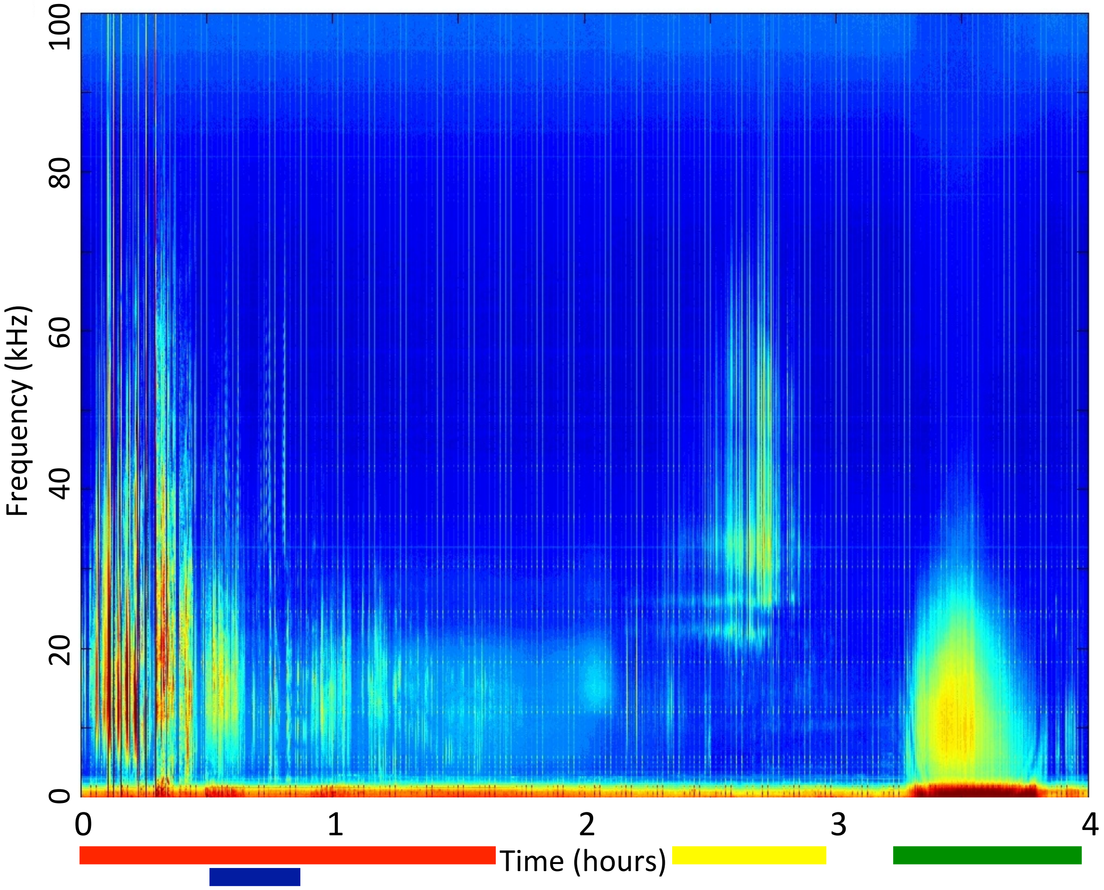


Figure 2.3: Example of a Long Term Spectral Average of Gulf of Mexico HARP data containing sperm whale (red bar, 4-80 kHz), beaked whale (blue bar, 30-80 kHz) and dolphin (yellow bar, 20-80 kHz) pulses and a close approach by a vessel (green bar, 0-40 kHz)

longer time period there will be a larger number of 5-minute bins with detections. Thus, we acquire a relative measure of how suitable each area is for each species. The time-series of detections for each species by site is presented in the following chapters.

The time periods used for data analysis were selected individually for each site to reduce autocorrelation among samples. To measure autocorrelation the 5-minute bins were grouped according to 1 and 5-day time periods, and the autocorrelation function was plotted using the *acf* function in R (version 2.14.1, The R Foundation for Statistical Computing 2011). Examination of these plots allowed identification of the time period (in number of days) that was required to reduce autocorrelation, and data were binned into either 1-day, 4-day or 5-day time periods (Table 2.2). Only complete time periods were included (i.e. any time period without complete effort was excluded from further analysis).

For the purposes of this study the exact detection range is not necessary, however preliminary analysis of acoustic propagation at each of the three sites has been conducted using the C-version of the Range-dependent Acoustic Model (Kaitlin Frasier, unpublished data, following methods of Helble et al. 2013). The site-specific differences are minimal and should not have notable impact on the analyses presented here, particularly for the beaked whales and *Kogia* spp., whose signals are at frequencies where attenuation dominates over effects of bathymetry. The effects of seasonal changes of propagation were also examined, and based on modeled sound speed profiles from the Generalized Digital Environment Model v 3.0. Despite a strong increase in surface temperatures in the summer, the temperature below approximately 200m remains relatively constant all year, therefore the propagation and detection of the echolocations signals from deep-diving cetaceans is not likely to change significantly over the course of the year (K. Frasier, unpublished data).

Table 2.2: Summary of the time-period selected to bin detections for each species at each site in order to limit autocorrelation in model residuals.

Site	Species	Time period (days)
MC	*P. macrocephalus*	4
MC	*Z. cavirostris*	1
MC	*M. densirostris*	1
MC	Unknown beaked whale	1
MC	*Kogia spp.*	1
GC	*P. macrocephalus*	4
GC	*Z. cavirostris*	1
GC	*M. densirostris*	1
GC	Unknown beaked whale	1
GC	*Kogia spp.*	1
DT	*P. macrocephalus*	1
DT	*Z. cavirostris*	5
DT	*M. densirostris*	4
DT	Unknown beaked whale	1
DT	*Kogia spp.*	1

2.2 Environmental Data

2.2.1 Data From HARPs

Data that were collected to describe the environment came from a variety of sources. A count of close boat approaches per time period and a time series of ambient noise levels at two frequencies were obtained directly from the HARP recordings. Previous studies have shown a response by cetaceans to the presence of boats, and the number of vessels acting in response to the DH oil spill was much greater than typical for the area (Figure 2.4), therefore close approaches of boats to the HARPs were counted by manual analysis of the LTSAs. For this metric only boats that produced notable energy at frequencies above 1 kHz, such as those shown in Figure 2.5, were counted (i.e. we were not concerned about distant shipping noise for this analysis). At MC the vessel signals were logged with a minimum peak signal-to-noise ratio (SNR) of 3 dB (relative to the background noise in a one hour window) at 10 kHz. Background noise levels are much lower at GC and DT, so at those sites vessel signals were logged with a minimum peak

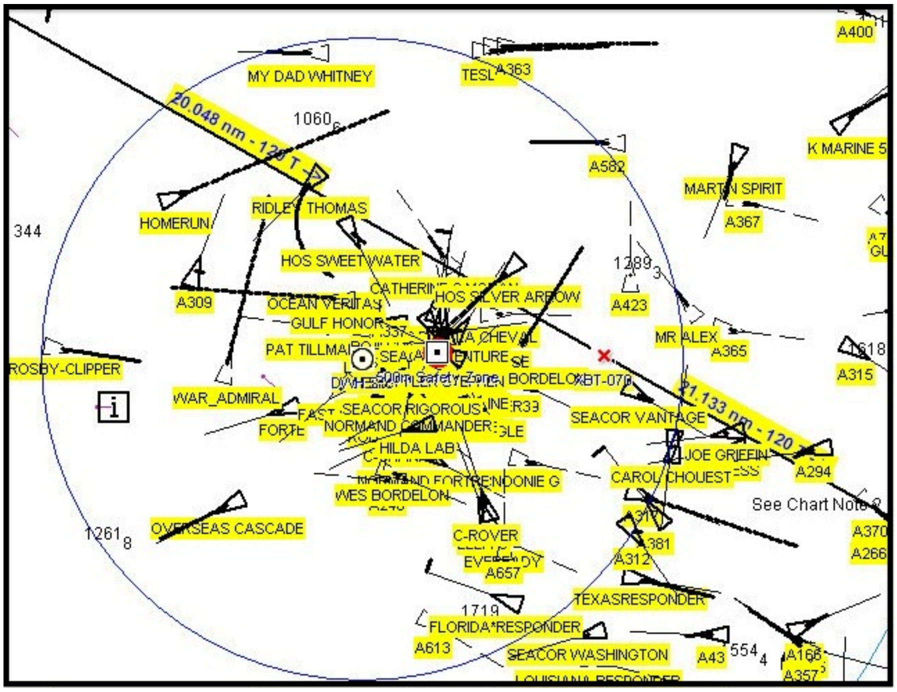


Figure 2.4: Example screen capture from navigational computer from on board a vessel near the DH wellhead during the spill response illustratiing the large number of vessels in the area. Blue circle is 5 nautical mile radius from wellhead.

SNR of 6 dB (relative to the background noise in a one hour window) at 10 kHz. Background noise levels do change, however, so masking by animals (e.g. echolocating dolphins) or environmental conditions (e.g. rain) might occur. Each passage of a boat was counted as a single event, and summed per time period (Figure 2.6).

Ambient noise was measured in the LTSAs by taking a sample measurement every 5 seconds for 55 out of every 75 seconds, and then averaging all the sample measurements per day to produce a time series. Measurements were taken at two different frequencies: 40 Hz and 1 kHz. 40 Hz was selected because this frequency band is dominated by distant ship traffic and, more significantly in the Gulf of Mexico, by pulses from air-guns for seismic testing. The time series of noise in the 40 Hz band at site GC, for example, includes numerous peaks and troughs (Figure 2.7), all of which were manually checked by examining the spectrograms of the data (Figure 2.8) and all proved to be due to either an increase or decrease in air-gun pulses. Note the overall increase in noise during the later half of the

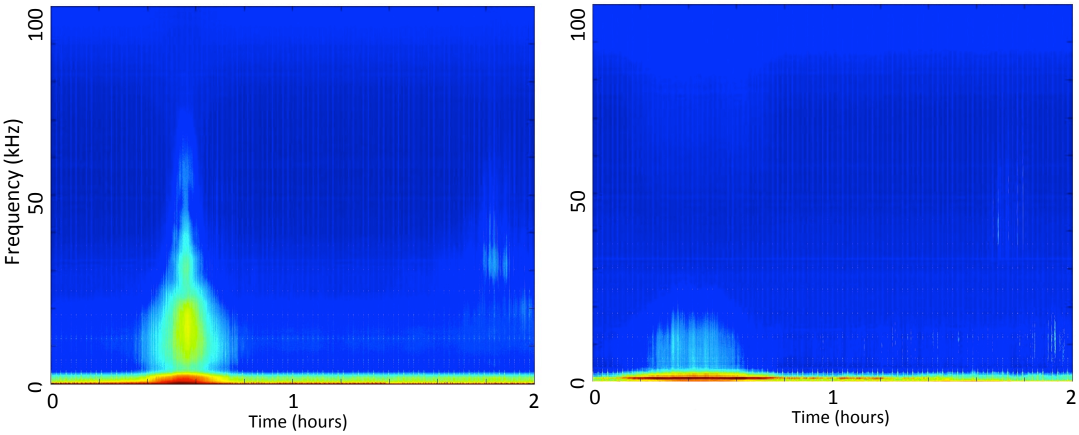


Figure 2.5: Example of individual vessel detections in Long Term Spectral Averages. Left: closer/higher energy vessel passing from 0.35-0.8 hours. Right: farther/lower energy vessel passing from 0.1-1.2 hours.

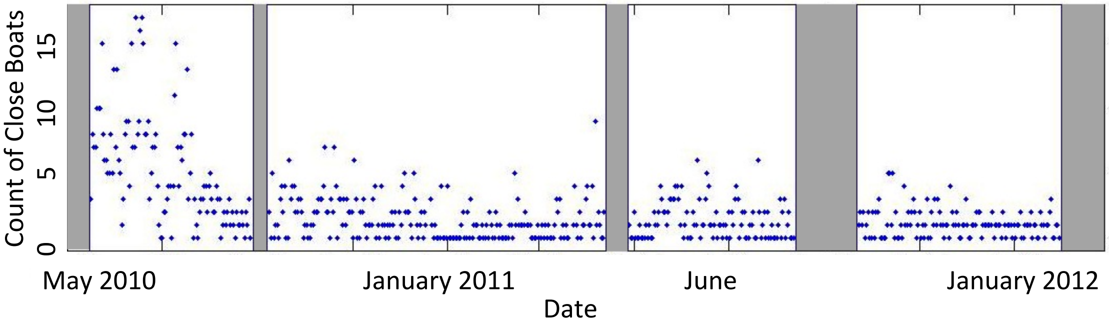


Figure 2.6: Time series of number of close vessel approaches per day as detected in the HARP data at MC. Note the high number of boats during the first part of the time series, corresponding to the DH oil spill response.

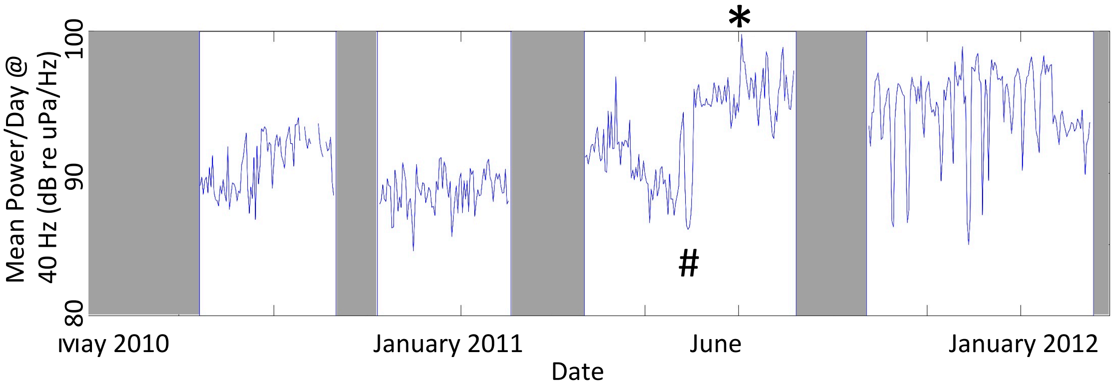


Figure 2.7: Timeseries of ambient noise at 40Hz at GC. Daily averages. (*) and (#) correspond to LTSA examples in figure 2.8, top and bottom, respectively. (#) corresponded to Memorial Day holiday weekend. Gray indicates no recording effort.

time series, which may have had an impact on the habitat modeling process. 1 kHz was selected because this frequency is lower than most signals generated by sperm whales, but will be dominated by noise from wind and nearby boats.

2.2.2 Data from Satellites and Other Sources

To represent temporal changes, such as fluctuations in the duration of daylight and associated biological processes, temporal variables have been included: mean sea surface temperature (SST), Date, Day of Year (Julian Day), 4-day Block, Month, and Season. The 4-day block was calculated from the start of the year, which resulted in 91 4-day blocks per year. There is one additional day per year (in non-leap years), which was added to the last block of the year. In the habitat models a cyclic smooth was applied to Day of Year, Block, and Month. As such, the last day of the year (#365) will be smoothly connected with the first (#1). This is appropriate because of the cyclic nature of annual processes and the relatively arbitrary nature of the start/end of the human-defined time-periods. In the model generation and selection process mean SST was included as the initial "temporal" parameter because it varies predictably with the time of the year and because it is more biologically interpretable than the other parameters. After a best model was selected (see below), the additional temporal parameters (Date, Day-of-Year, Block and Month) were added individually and the AICc was used to select the

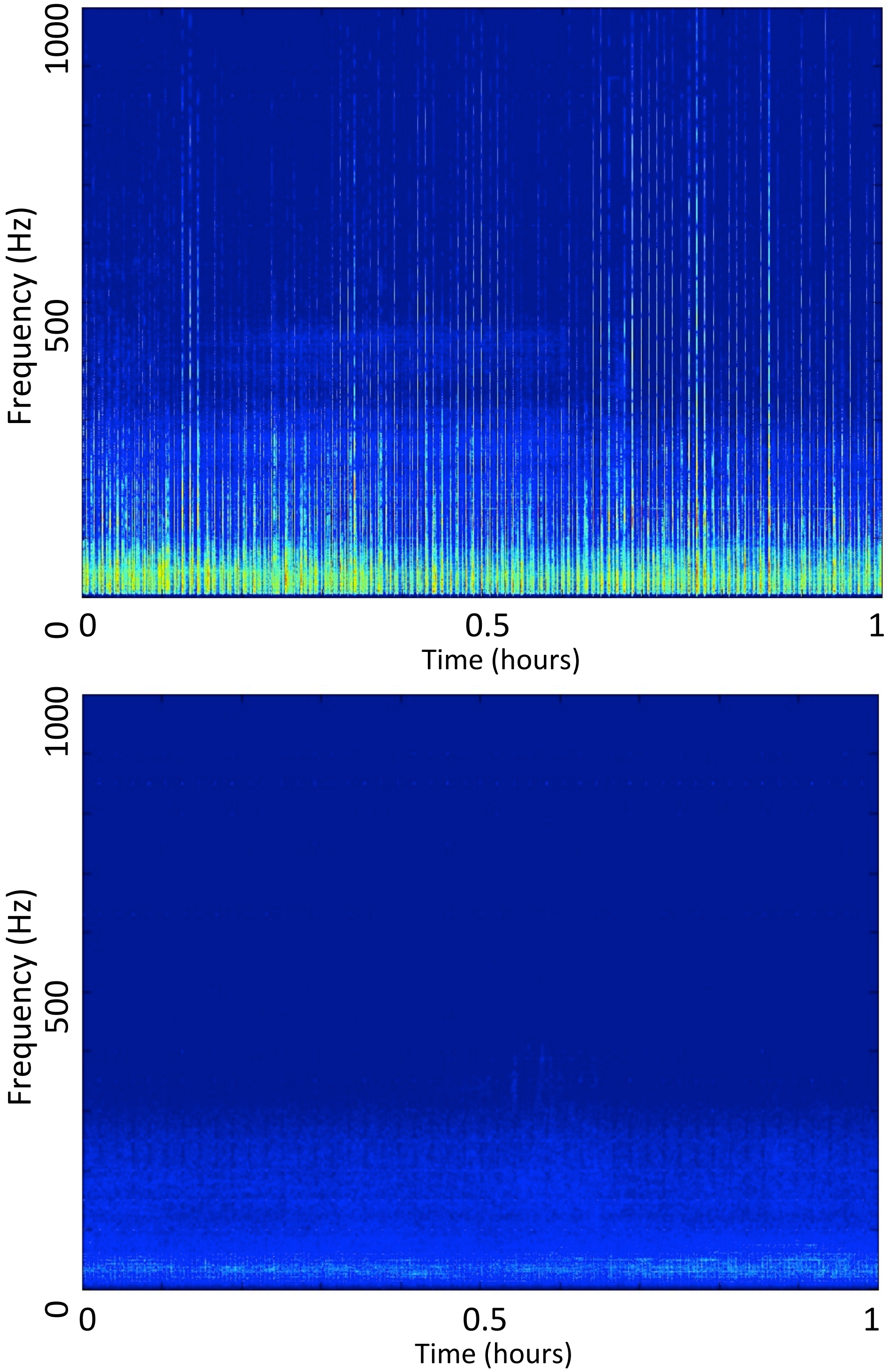


Figure 2.8: Example spectrograms of 1 hour window with exceptionally high intensity airgun signals (top) and no airgun signals (bottom). Top image corresponds to (*) maximum on figure 2.7 while bottom corresponds to (#) minimum on that same figure. Minimum (#) corresponded to the Memorial Day holiday weekend.

best model. If mean SST was selected in the best model, the addition of Date was tested, however the other three temporal parameters are highly collinear with mean SST, and therefore were not included. If mean SST was not included in the best model, then the addition of all four temporal parameters were tested.

In much of the biological world there are strong relationships with lunar cycles, and cetaceans are no exception (e.g. Wright 2005). A metric of lunar illumination has been included to represent this cycle (U.S. Naval Observatory, `http://aa.usno.navy.mil/data/docs/MoonFraction.php`). This does not take cloud-cover into account, because no reliable metric of cloud cover could be located for this specific area.

Because of the importance of the Mississippi river outflow on the ecosystem of the Gulf of Mexico, the flow rate at the base of the river has also been included. The daily discharge is measured at Tarbert Landing, LA by the US Army Corps of Engineers (`http://www2.mvn.usace.army.mil/cgi-bin/wcmanual.pl?01100`). This flow is related to many factors, including surface salinity, temperature, amount of particulates and amount of chemical pollution (particularly fertilizer and pesticides from farm production). The effect of the Mississippi river is not likely to influence the environment at sites GC and DT, and therefore has only been included in the models for site MC.

A wide variety of oceanographic data are available from satellite measurements, and for these models we have included merged SST, sea surface height anomaly (SSHA), wind speed (WIND), and chlorophyll a concentration (CHLA). All data were selected because they have been shown to be significant for marine mammals in other habitat modeling studies. Additionally, we required data that were available on a daily timescale, and were available for the region directly over and around all three HARP sites, which eliminated some data sets that are not available at this frequency.

SST data are a merged product, combining data from multiple satellites as well as modeled interpolation to eliminate gaps in data. The spatial resolution is 0.011 degree. These were available at `http://mur.jpl.nasa.gov/`. The SSHA data are also merged from multiple satellites, and are processed by the CCAR group at University of Colorado (`http://eddy.colorado.edu/ccar/ssh/hist_gom_grid_viewer`). The data used in these analyses is generated on a 0.25 degree pixel size, and the reference height for calculations of anomaly is specific for the Gulf of Mexico. A third blended satellite product is WIND, available via `http://www.ncdc.noaa.gov/oa/rsad/air-sea/seawinds.html`. They are at 0.25 degree spatial resolution.

CHLA data came from the GlobColour project (`http://www.globcolour.info/`). Quality-screening identified many suspiciously high values for sites MC and DT. This is likely due to signal contamination from high levels of particulates from Mississippi River outflow, the presence of surface oil during the period of the DH oil spill, or other factors that influence the color of the sea surface. Additionally, there are significant data gaps because of cloud cover. Therefore, this parameter was not included in final analysis.

All satellite data were processed using either MATLAB (SSHA, WIND) or Windows Image Manager (SST, CHLA; WIM/WAM, Mati Kahru, SIO). For all of these the mean and standard deviation per time period were included as potential model parameters. Mean and standard deviation of SSHA in 4 pixels around the HARP was measured, corresponding to an area of roughly 26 km^2. CHLA mean and standard deviation was measured on a scale of nine pixels. SST mean and standard deviation was measured in a 15 km radius circle centered on the HARPs. The standard deviaton of each parameter was included to look for regions of high gradients, such as might be found along the edges of oceanographic features like fronts and eddies or rings.

An additional parameter was derived from images of SST: distance to fronts. This required multiple steps of processing, beginning with Single Image Edge Detection (SIED) with a fixed window size of 32 by Wim/Wam (Figure 2.9). The output of the "wam_edge" program was formatted and processed using arcGIS (ESRI) and Python to measure the distance from each HARP location to the nearest point in a front. Images were projected using the USA contiguous equidistant conic projection. The nearest front was measured for every day. For longer time periods the average nearest distance for that time period was

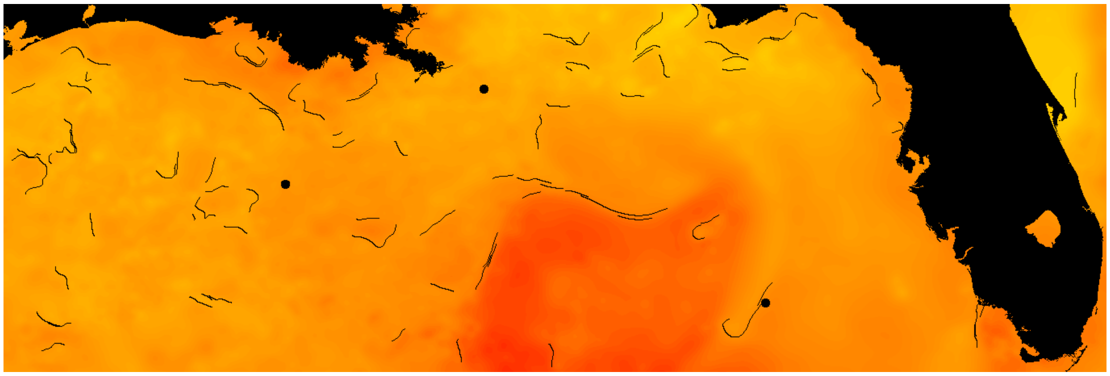


Figure 2.9: Example of Single Image Edge Detection analysis of SST from 16 May 2010. Black lines are locations of thermal fronts. Black circles indicate locations of HARPs. The distance from each HARP to the nearest point in the nearest front was included in habitat models.

calculated.

Anthropogenic data were also included, particularly relating to the DWH oil spill. These data are only available to Natural Resource Damage Assessment responders via the Environmental Response Management Application website (`http://gomex.erma.noaa.gov/erma.html`). Two oil metrics were gathered, both based on data generated by WEST Inc. (Cheyenne, WY) for the Natural Resources Damage Assessment (NRDA) response effort. First, the total area of surface oil in the entire region was measured using arcGIS. Second, presence or absence of surface oil in a 30 square kilometer box centered on the HARP was recorded. Also, two metrics of aerially-spread dispersant chemicals were included. First, the total gallons of dispersant spread in the entire region was recorded, as reported by BP for the NRDA response effort. Second, the presence or absence of aerially-spread chemicals in the same 30 square kilometer box centered on the HARP was included.

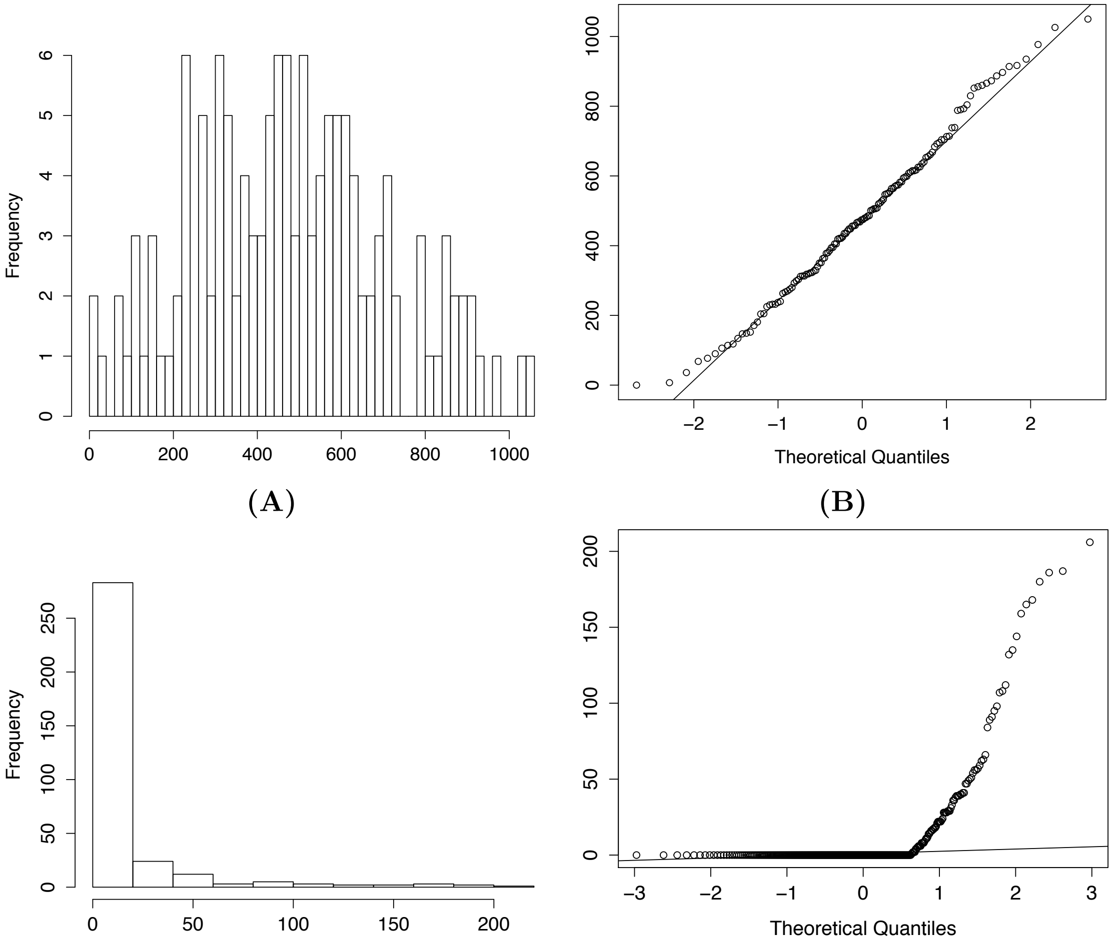
Because of the extreme anthropogenic activity during the DH oil spill we were particularly interested in metrics of human activity. Therefore we hoped to get information about the number of boats present on a regional scale, beyond what was easily identifiable in the HARP data (subsection 2.2.1). A potential source of information about vessels in the region was archived Automatic Information System (AIS) data (example in Figure 2.4). These identification signals, are normally required from all large vessels and were required from many boats involved in the DH spill response. Transmissions include a variety of information about boat, such as ship ID number, speed, heading, and more. The encoded messages can be detected and archived on computers within transmission range. Unfortunately the coverage area of the archived data, and the quality of the timestamps generated by the archive computers, were unknown, making these data unusable.

There is a conspicuous lack of parameters relating directly to the primarily prey of deep-diving cetaceans: deep-living squid. It is likely that most patterns in movement of all of these deep-diving cetacean species are related to their search for food, and therefore a metric of abundance of prey should certainly be included in the best habitat model. Unfortunately there are no time series data that relate to squid or the deep-scattering layer in general for the Gulf of Mexico. There have been a handful of assessment cruises, however these span no more than three weeks at a time, and all are separated by at least one year, so while they provide essential information about the species of deep squid and fish that can be found in the Gulf, they are not applicable to the analyses presented here.

2.3 Data Exploration

Initial data exploration was conducted to identify trends and correlations in both the explanatory and predictor variables. The modeling methods did not require the explanatory variables to be normally distributed, however the approximate level of zero-inflation, relative to a normal distribution, was assessed to determine which method would be most appropriate. Histograms and Q-Q plots of the response variables were generated to identify which site/species combinations were zero-inflated (example in Figure 2.10).

Some explanatory variables were included as factors: month, season, presence of surface oil and presence of aerial dispersants. The cetacean detections were related to these parameters using boxplots to help identify uneven coverage and heterogeneity across factor categories.



(A) **(B)**

(C) **(D)**

Figure 2.10: Examples of diagnostic plots from two sites where the number of detections were roughly normally distributed (MC, subfigures A and B) and highly zero-inflated (DT, subfigures C and D). Examination of these plots assisted in selecting the most appropriate analysis method. To be considered normal the data in the histograms (subfigures A and C) the data should follow a bell-shaped curve, and in the Q-Q plot (subfigures B andD) the points should lie along the solid line.

Cleveland dot plots were used to identify outliers by plotting the data in sequence (Figure 2.11). A handful of potential outliers were identified, and transformations were applied to the distance to fronts (DISF), surface area of oil (OARE) and gallons of aerial dispersant (DGAL) parameters to limit the effect of those extreme values. With the power of computer-automated modeling, it was possible to generate models with transformed or un-transformed data, and to then use model selection methods to identify which form of the parameter produced the best model.

Correlations between parameters can confuse modeling results, therefore collinear parameters need to be identified before modeling. The correlation among all parameters was tested using the *cor* function in R. A threshold of 0.5 was set to identify correlations that should be avoided. Additionally pairsplots were generated for all parameters to allow for visual examination of relationships (see example in Figure 2.12). All collinearities were recorded, and avoided when generating formulas for modeling by only allowing models with one parameter or the other to be selected.

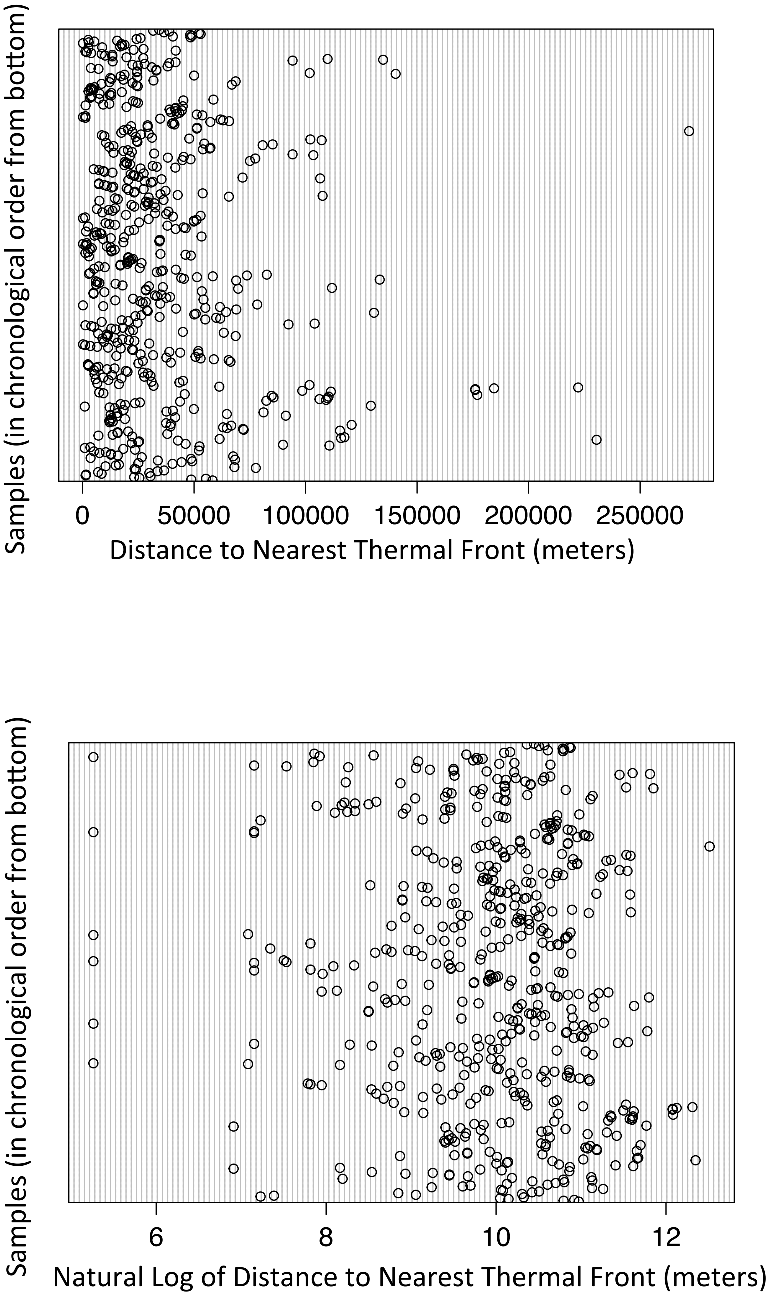


Figure 2.11: Cleveland dot plots of example explanatory data set (distance to nearest thermal front). Top subfigure shows untransformed data with potential outliers that could make models perform poorly. Bottom shows the same data set with a natural log transformation, applied to reduce the effect of the outliers.

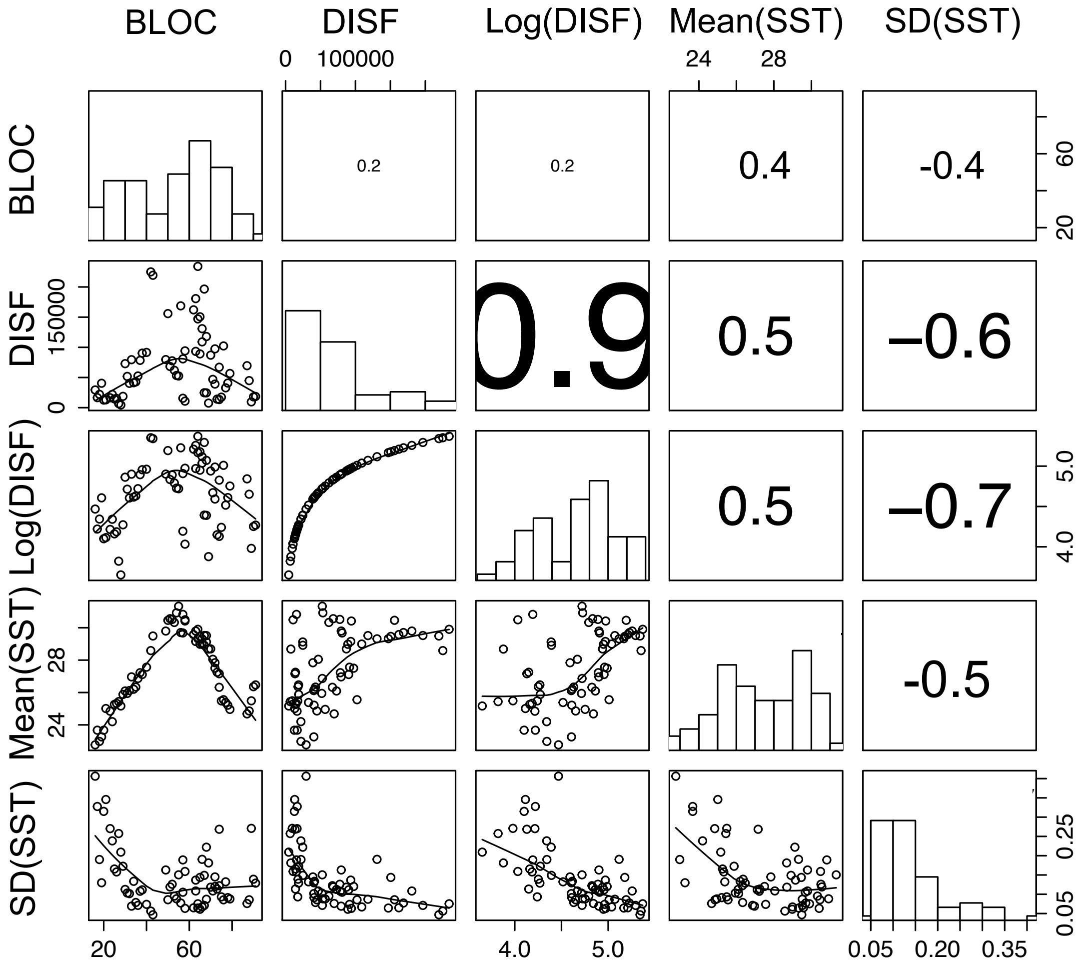


Figure 2.12: Pairs-plot example of a subset of environmental parameters for models at DT, generated to aid in identification of correlations between parameters and normality of parameter distribution. Values of correlation are plotted above the diagonal, with size of font relative to amount of correlation. Histograms of the data are along the diagonal. The relationship against all other parameters (with a smooth line to highlight trend) are plotted below the diagonal. Parameters in order from left to right (and top to bottom): 4-day block of the year (BLOC), distance to the nearest thermal front (DISF), log of the distance to the nearest thermal front (log(DISF)), mean sea surface temperature (mean(SST)), and standard deviation of the sea surface temperature (SD(SST)).

2.4 Trend Analysis

All statistical tests were conducted using $p < 0.05$ unless otherwise noted.

2.4.1 Seasonal and Oil-spill related trends

Exploratory analysis suggested a seasonal pattern in the detections for some of the species at some of the sites. For detections of sperm whales at MC the detections were roughly normally distributed, and the variance for data from each season was shown to be similar using the Brown-Forsythe test (*levene.test* in R library *lawstat*, median), therefore an analysis of variance (anova) was computed to check for seasonal differences, and a Tukey test was then used to identify which seasons were different. The detections at the other sites and of the other species were not normally distributed, and therefore the non-parametric Kruskall-Wallis test was used to identify differences among seasons, followed by a post-hoc Mann-Whitney test to identify the seasons that were different. Only approximate p-values are possible using these non-parametric methods because of the presence of tied data.

The short-term impact of the oil spill was of particular interest, and I used multiple methods to compare the period of the oil spill to other periods. This study spans two summer seasons. The first was during 2010, when extensive oil was present at the surface from the DH oil spill and the intense spill response activities were underway near the wellhead. The second was during 2011 when there was no oil at the surface confirmed to be from the DH wellhead and no known unusual activity near the wellhead. This allows us to directly compare the two summers. This was done using the non-parametric Mann-Whitney U test, which was selected because the data do not meet the assumptions of the parametric t-test.

This method was also used to compare the period of the oil spill with the period directly following. There were numerous possible acute effects of the oil spill on the cetacean community, including direct exposure to the oil, direct exposure to the dispersants (and the combination of the two, which has been shown to be more toxic than either alone) (Montagna et al. 2013), acute impacts on the food chain, and impacts of an increased number of boats and general human activity in the region. Although the oil stopped flowing from the wellhead on July 15, 2010, there was increased human activity in the region for a number of months following, therefore the "end" of the acute oil spill impacts is not clearly defined.

Given this, we compared the mean detections before and after a set of “breakpoints”: July 15 (MC only), August 1, August 15, September 1, September 15, October 1, October 15 and November 1. The number of days from the start of recording to the breakpoint was calculated, and the same number of days after the breakpoint was used for the second period. For example, at site MC the first full day of recording was May 16, with 91 days to the breakpoint at August 15, and the second period spanning 91 days from August 15 until November 13. This analysis was only performed for data from MC and GC because data collection at DT did not begin until August 9, and there was a gap between deployments leaving no data between October 26, 2010 and March 4, 2011.

In addition to comparing the mean detections before and after the breakpoints, I explored whether the general trend in number of detections was similar in the two periods. This was done by creating linear models of the detections that included as explanatory variables the day since the start of the period (either since the start of recording, or since the breakpoint), and an interaction term between the day since start of period and whether the detection belonged to the period before or after the breakpoint. The p-value of the interaction term indicates whether the trends of the two periods are different.

2.4.2 Diel patterns

In addition to the animals’ relationships with their environment and human activity, we examined the diel activity patterns of the different species. Detections were binned according to hour of the day. For each species at each site the hourly detections were further binned according to day vs. night and crepuscular (dawn and dusk) vs. not crepuscular groups. The hours to be included in the daytime period were determined by examining the time of sunrise and sunset throughout the year. During 2010 and 2011 sunrise took place between 0550 and 0750 local time, and sunset takes place between 1750 and 2000. Therefore in this analysis the daytime period extends from 0700 until 1900. Similarly the crepuscular (dawn/dusk) periods were identified as spanning two hours before and after the average sunrise and sunset, therefore from 0500-0900 and 1700-2100.

Detection of differences was carried out by use of an exact binomial test (*binom.test* in R library *stats*) where success was classified as being a daytime detection for the diurnal/nocturnal comparison or a crepuscular detection for the crepuscular/not crepuscular comparison. The sample estimate of the probability of success was used to identify whether a significantly different rate of detection was due to a diel pattern of behavior. For example, the unknown beaked whale signal had zero probability of success in the day/night test, indicating that there was no chance of "success", meaning totally nocturnal behavior.

2.5 Habitat Modeling

2.5.1 Generalized Additive Models (GAMs)

Generalized Additive Models (GAMs) provide an appropriate framework for analysis of the relationships between detections of deep-diving whales and their habitat because the relationships are expected to be non-linear (Hastie and Tibshirani 1990). GAMs are an extension of the generalized linear model (GLM) that allow non-normal response variables and linear combinations of nonparametric forms of predictor variables, such as smoothing splines. Within the GAM framework, represented by:

$$g(E(Y)) = \beta_0 + f_1(x_1) + f_2(x_2) + ... + f_m(x_m) \tag{2.1}$$

where E(Y) are the estimates of the response variable (in this case cetacean detections), and g is the link function. The f_m functions can be parametric or non-parametric, such as thin-plate smoothing splines, and are combined linearly. Because of the flexibility allowed by the non-parametric functions, interpretation

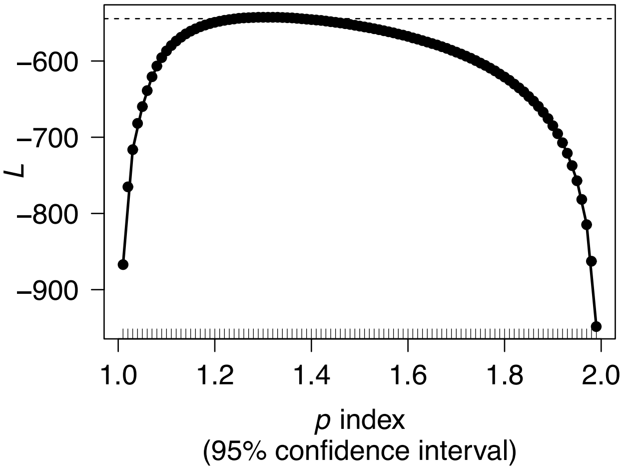


Figure 2.13: Example of plot output by the tweedie.profile function to estimate the maximum likelihood value of power (p) for use in the Tweedie distribution for detections of Gervais' beaked whale at GC.

of results can be less straightforward than with linear polynomial models.

The data were separated into those that were clearly zero-inflated, and those that were not. The data that were not zero-inflated were modeled using the *mgcv* package in R (CRAN), which allows for automated estimation of the smooths of explanatory variables. A thin-plate spline with shrinkage was used for most variables, which allows the estimated degrees of freedom to go to zero, effectively removing the parameter from the model.

Despite not being heavily zero-inflated, these data are still over-dispersed, as determined by examination of Q-Q and deviance residuals vs. fitted values plots and histograms of the residuals. Given these results a Tweedie distribution with a log link was used in the models (Tweedie 1984). This distribution family is very flexible and allows for over-dispersion. The spread of the distribution is related to the power (p), and identifying the ideal p was carried out using the *tweedie.profile* function (library *Tweedie*). This function performs maximum likelihood estimation of p. It also generates plots to assist in the visualization of the point identification (example Figure 2.13).

Given the various collinearities that were present for the different species/site combinations, an automated process was carried out to generate all possible functions that avoided collinearities. These functions (generally numbering around 4000) were iteratively processed, and Akaike's Information Criteria corrected for small sample size (AICc) was calculated for each. The model with the lowest AICc was selected as the best model, however all models within two AICc units of the best were examined, and if a simpler version of the lowest AICc model was included, that was used as the best model.

After a best model was selected, the model was validated by examining output plots, including plots of:

1. a histogram of the residuals,
2. the Q-Q probabilities of the residuals,
3. the original response variable vs. the fitted values, and
4. the residuals vs. each possible predictor variable.

Model results are tabulated in the chapters below, and plots of the relationship between the parameter and the response variable were generated for qualitative evaluation.

2.5.2 Zero-inflated Negative Binomial (ZINB) Generalized Linear Models

As is often the case with ecological data, most of the sets of detections of these deep-diving cetaceans were highly zero-inflated. Having too many zeros makes these data not fit well with standard families of distributions for modeling, even those that can handle over-dispersion, leading to exploration of other methods. For the data modeled using 1-day bins in Table 2.2 a Zero-Inflated GLM using a Negative Binomial distribution (ZINB) was used, which follows a 2-step modeling process. In the first step a model using a binomial distribution and logit link addresses the "zeros" (presence/absence). In the second step the positive count data are modeled using a negative binomial distribution and log link function.

The negative binomial distribution was chosen over a Poisson distribution (the most common choice for count data) because the data were over-dispersed even after most of the zeros were removed. This process allowed for count data to be zero because it is possible to have “good” zero counts (for example, when the habitat is good, but the animals are not there).

The function *zeroinfl* (library *pscl*) was used as the base for the models. This function, however, does not allow for smooths of the predictor variables, which is required for GAMs. Given that most of the parameters in test models were smoothed with 1-2 degrees of freedom, we decided to use only parametric forms of the predictor variables, including linear, second and third degree polynomials.

Even when avoiding collinearities, and excluding all temporal parameters (Date, Day of Year/Block, Month), the total number of possible models when considering all combinations of both the zeros and the counts components was so high that there was not sufficient time to run every model (e.g. this would have taken over a year on one computer for one set of data). Therefore two sets of models were generated: one with all possible combinations of parameters in the counts model and a null model for the zeros and another with all possible combinations in the zeros model, and null model for the counts. Both sets of models were fit, and the models with the lowest AICc value from each set was selected and combined. As with the non-zero-inflated models, all candidate models within two AICc units were examined and are included in the discussion.

After selecting one combination model, each of the temporal parameters (that had been excluded up to this point) was added in turn and the AICc computed for comparison. If addition of the parameter improved the AICc by at least two, then the parameter was added to the model and one further selection step was initiated. In each case at most one of the three possible temporal parameters improved the model, therefore we were not required to select between temporal parameters. The final step involved using a "drop one" approach to iteratively remove one parameter at a time from the model, checking AICc after each removal, and selecting the model with the lowest AICc as the new best model, repeating the "drop one" process until the AICc could not be improved by dropping any parameters. This final model was run and output plots examined for validation, as in subsection 2.5.1 above.

In general, both GAM and ZINB models were used to compare the temporal patterns of whale detections to natural and anthropogenic factors, and has been compared across control and experimental sites.

2.6 Summary

Ecological constraints required that each species be considered separately, and each site be considered separately. This resulted in analysis of 15 unique data sets. Given this relatively large number of analyses, data exploration was critical in assessing the quality of data and identifying errors and collinearities. Unique features of each species' data set influenced data processing, therefore details of data processing that are species-specific are included in subsequent chapters as appropriate.

Chapter 3

Sperm whale ecology and habitat modeling

3.1 Abstract

Sperm whales (*Physeter macrocephalus*) in the Gulf of Mexico are considered a separate population from those in the Atlantic, and comprise males and females, young and adult. They are found throughout the Gulf, but are generally concentrated along the 1000 meter isobath, particularly in the northern Gulf. Using passive acoustic data from seafloor-mounted High-frequency Acoustic Recording Packages I monitored for presence at three sites deeper than 980 meters. The time series show nearly constant presence at Mississippi Canyon (MC), frequent presence with occasional periods of high detection at Green Canyon (GC), and occasional presence at Dry Tortugas (DT). Analysis of diel patterns revealed that sperm whale at MC were nocturnal and anti-crepuscular while at GC the were diurnal and no significant diel trend was found at DT. Despite being statistically significant these patterns may not be biologically important. At MC sperm whales were detected significantly more frequently in the fall than in other seasons ($p < 0.05$), while at DT they were detected less often in fall than in all the other seasons. At MC the detection rate during the Deepwater Horizon oil spill and response increased from a low at the start of recording in May 2010, but was

heavily influenced by high detection rates during early October 2010. During the same period the number of detections at GC decreased after the start of recording (July 2010), but was heavily influenced by a period of high detections during mid-November 2010. The relationships with environmental parameters were examined using Generalized Additive and Zero-inflated Generalized Linear models, and at all three sites the sea surface temperature, sea surface height anomaly, wind speed and distance to the closest front were included in the best models. The total area of surface oiling was included in the best model at MC. These models explained 8 - 30% of the deviance. In general the results show that there are seasonal patterns in the movements of sperm whales in the northern Gulf of Mexico, and there may be diel patterns of behavior. Also, sperm whales are shown to respond to changes in their environment, favoring more dynamic regions such as areas close to fronts or the edges of mesoscale oceanographic features.

3.2 Introduction to Sperm Whales

3.2.1 General Biology and Distribution

Sperm whales (*Physeter macrocephalus*) are the largest of the toothed whales, and are found in all of the world's oceans from the equator to the ice edge (Figure 3.1). They are a sexually dimorphic species, with females growing up to 12 meters in length and males over 18 meters and weighing up to 57,000 kilograms (Jefferson et al. 2008). Their primary prey consists of a variety of cephalopod species as well as fish and other invertebrates that are swallowed whole via suction feeding (Werth 2004). Individuals can live to be at least 70 years old, possibly much older (Jefferson et al. 2008). Females have one calf every 5 years, leading to fairly low fecundity (Whitehead 2002b).

3.2.2 Social Structure and Behavior

Globally sperm whales are organized into regional groups, with relatively little mixing between regions (Mesnick et al. 2011). They have a polygynous social

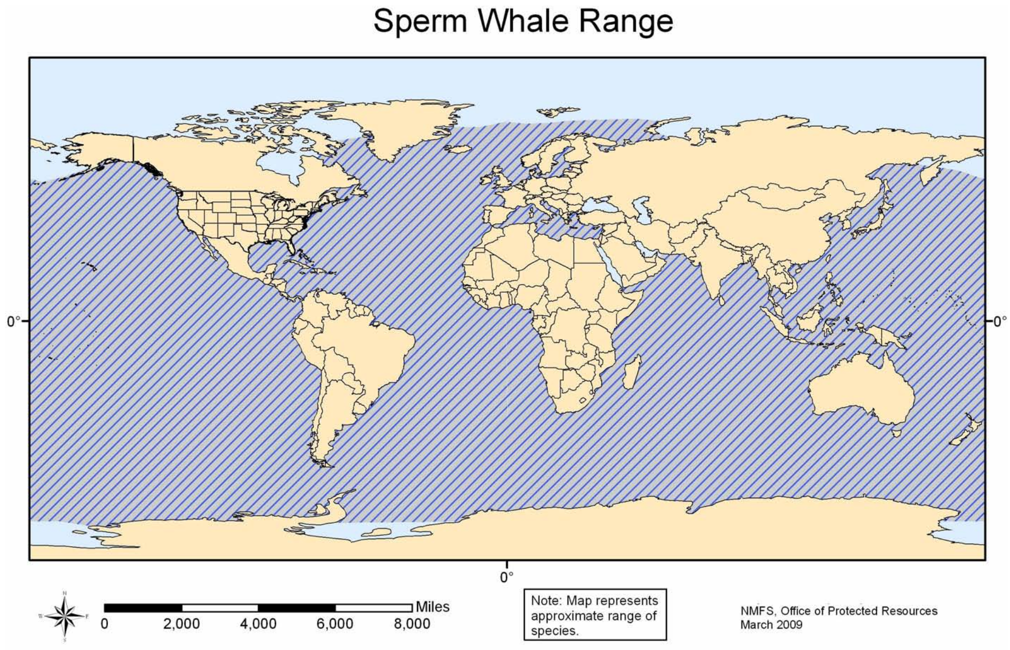


Figure 3.1: Global distribution of sperm whales. Note that females and young animals remain closer to the equator (generally below 40 degrees north and south) and adult males extend further poleward. (courtesy of NOAA/NMFS, http://www.nmfs.noaa.gov/)

structure in which young animals and females maintain long-term associations in groups of 10-30 or more (Whitehead 2002b). As young males mature they leave their maternal groups and join “bachelor pods” with other males, traveling together for many years before separating from the group. Older lone males often travel to very high latitudes to feed, but return to lower latitudes periodically to mate with females who tend to stay below approximately 40 degrees latitude (Whitehead 2002b). A single male generally stays with a group of females for a short period of time (Jefferson et al. 2008). The groups, whether primarily females or males, tend to stay together for long periods, probably months to years, and feed in a semi-synchronized, possibly co-operative way (Mate and Urban 2010). They have displayed extreme group loyalty, particularly when attacked by killer whales (*Orcinus orca*) that can fatally wound an entire group of sperm whales (Pitman et al. 2001). While feeding they travel approximately four kilometers per hour, gradually moving through an area (Whitehead 2003).

Sperm whale behavior alternates between socializing and feeding

(Whitehead 2002b). Socializing involves gathering at the sea surface for periods of hours to days and the duration and particular behaviors exhibited can be highly flexible. In addition to logging (lying nearly motionless at the surface), sperm whales are often seen to spyhop (raise the head above the water, apparently to look more clearly at objects in the air) and breach. They often raise their flukes when beginning a dive. Feeding, on the other hand, is fairly stereotyped, although the exact behaviors are generally unknown because visual observation is not typically possible at depth. All sperm whales are deep-divers, with the typical feeding dive lasting around 45 minutes and going to depths of several 100s of meters, depending on the local bathymetry (Jefferson et al. 2008). Groups can spread out over a kilometer or more when feeding (Jefferson et al. 2008), but have shown coordinated behavior despite separation (Mate and Urban 2010). In order to utilize such great depths sperm whales use echolocation to coordinate movements and hunting (Whitehead 2002b, Jefferson et al. 2008).

3.2.3 Temporal Patterns

Sperm whale temporal patterns have been described in a handful of locations (e.g. Norway, New Zealand, Galapagos, Alaska) using various techniques (e.g. whaling records, acoustic and visual observation, tags) (Townsend 1935 in Jaquet 1996, Nishiwaki et al. 1966 in Jaquet 1996, and Oshumi and Masaki 1977 in Jaquet 1996, Christensen et al. 1992, Whitehead 1996, Childerhouse et al. 1995, Jaquet et al. 2001, Mellinger et al. 2004, Read et al. 2010). In general there is little consensus on universal trends over any time period (daily to interannually) (Whitehead 2003). In the Gulf of Mexico I expect to find patterns in both diel and seasonal trends. On a diel basis I hypothesize that there is a decrease in sperm whale activity during crepuscular periods, similar to what was observed by Miller et al. in the northern Gulf (in Jochens et al. 2008).

Seasonally I anticipate that there will be increased detections in one period of the year because sperm whales in the Gulf are known to have fairly large home ranges that often overlap MC and sometimes GC and DT. However, without data on fluctuations in their prey species or other possible driving forces, the exact trends cannot be predicted. Additionally I expect that there was a decreased presence of sperm whales at MC in the summer and fall of 2010, during the DH oil spill and response activities. Comparison of the published trends to my findings from the Gulf of Mexico will help to illustrate differences and similarities between sperm whale populations, and may help clarify the response of these whales to the DH oil spill by highlighting any changes in the spill and post-spill periods.

3.2.4 Habitat Preferences

The habitat preferences of sperm whales have been the subject of investigation for over 200 years because of their importance to commercial whaling, but, as with temporal patterns, there is little consensus on the details. Globally they show preference for continental slopes, particularly along the 1000 meter isobath, but are also found in deeper waters and the middle of gyres (Waring et al. 2001). Conflicting results have been produced in a variety of studies over the past 40 years. For example, sperm whales prefer both upwelling and downwelling regions, higher and lower sea surface temperatures, and habitat on the continental slope as well as in the deep waters far from continents or islands (Jaquet 1996). These apparently contradictory findings may be the result of analyses on varying temporal and spatial scales (Jaquet 1996). The observed differences could also be the result of population- or pod-level differences, as observed by Whitehead and Rendell (2004). In the Gulf of Mexico sperm whales have been shown to prefer habitat that is along the shelf break, in areas of high productivity, generally close to the Mississippi River delta and the canyons in the northeast (Davis et al. 2002, Read et al. 2010). I hypothesize that the results from this analysis will confirm these findings by showing that sea surface height anomaly and the distance to thermal fronts are the most important habitat parameters for sperm whales at all three sites. Additionally I expect that sperm whales will be detected more often at MC, an area that is known sperm whale habitat.

3.2.5 Acoustics

Sounds are used for a variety of functions, including echolocation and communication. They produce a number of different sounds, often different arrangements of single pulses, or clicks, but the most common is the "usual click", which lasts 2-24 milliseconds and has energy between 1 and 15 kHz (Frankel 2002). Usual clicks are generated at roughly 1-2 per second for much of a feeding dive (Watwood et al. 2006). At the beginning and end of each dive as well as during the period when they are at the surface between dives their echolocations are much more sporadic or absent. The usual click is the signal we have focused on. Because they are large animals their usual clicks are high amplitude and can be detected by an acoustic sensor for many kilometers. As mentioned in Chapter 1, the acoustic propagation at each site was fairly similar, allowing for comparison of the results across sites.

3.3 Sperm-Whale Specific Methods

The manual analysis of the acoustic data was conducted by examining 1-hour windows of the Long-Term Spectra Averages with a bandwidth of 100 Hz-30 kHz because of the frequency content t. The 1-hour windows were overlapped by 0.5 hours to reduce the chance of missing a signal. The remainder of the data processing and analysis is consistent across species and described in Chapter 2 above.

3.4 Results of Exploratory Analysis

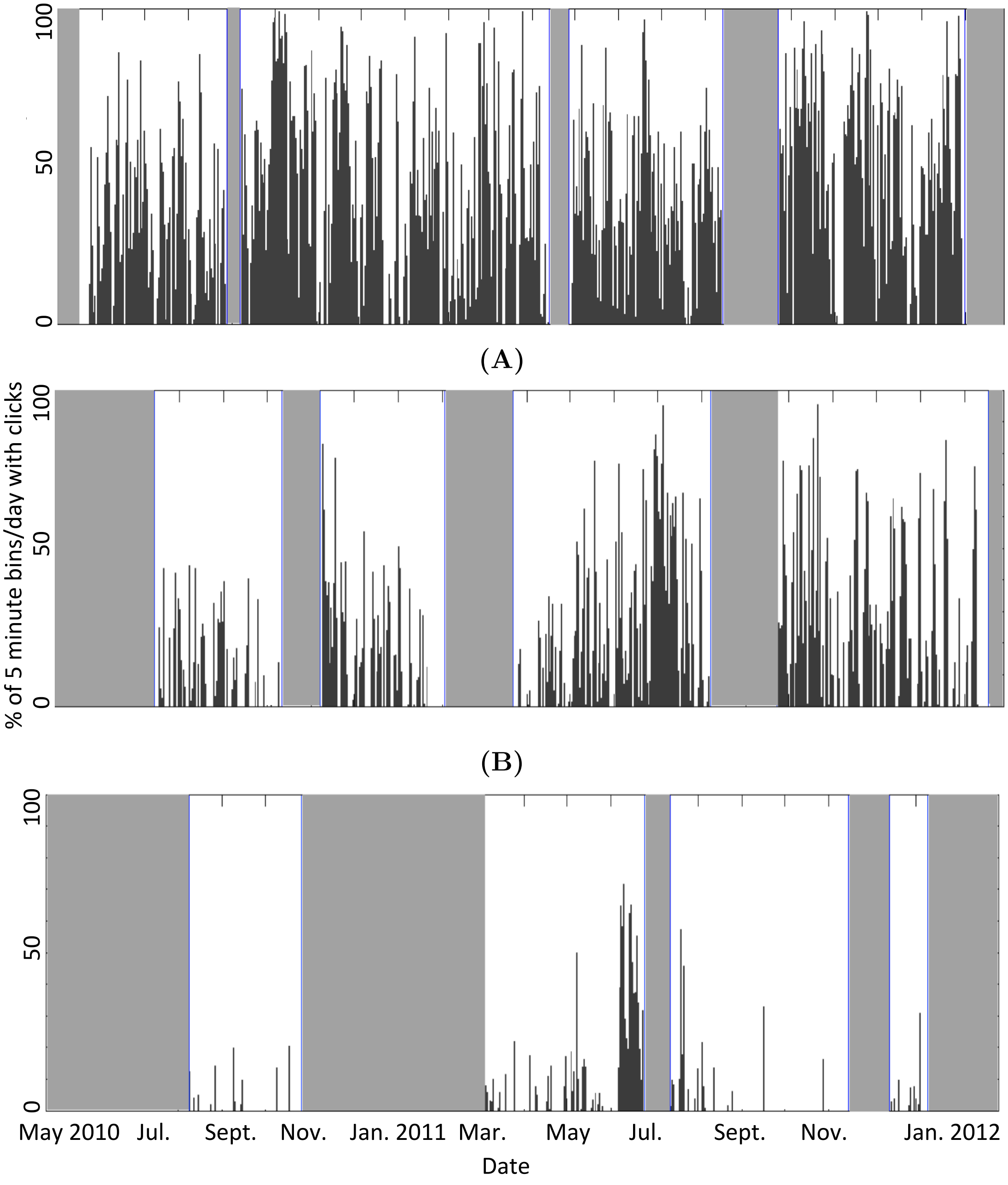
The time series of sperm whale detections at all three sites are shown in Figure 3.2. Note the difference between the overall detection rates, with DT being much lower than the other two sites and GC being moderate between MC and DT. At MC there is a period of remarkably high detections in early October 2010, which is important in the analysis of temporal trends relating to the oil spill (subsection 3.5.2 below). There are also pulses in detections at GC and DT that are worth noting. At GC the increase is in July 2011, and at DT the period of increased detections is June 2011. These patterns of detections support the hypothesis that sperm whales are not detected equally at all three sites but are more often encountered at MC.

As described in Chapter 2 above, exploratory analysis of sperm whale detections indicated that there was autocorrelation between detections at MC and at GC, and therefore these data were binned into 4-day time periods for subsequent analyses. Because there was not even sampling effort throughout the year (e.g. spring was only covered once while the other seasons were covered twice, and there were gaps in effort between some deployments), changes in the number of detections per season could only be examined at MC where the sample size was sufficient.

Additionally, histograms and Q-Q plots showed that the detection data were highly zero-inflated at DT, slightly zero-inflated at GC, and overdispersed at MC (see Figure 2.10). This led to using a GAM with a Tweedie distribution for GC and MC and a zero-inflated GLM with a negative binomial distribution for the count data for DT. The number of detections and the presence of zeros is tabulated below (Table 3.1).

Table 3.1: Parameters indicating whether data set was zero-inflated.

Site	Time-period length	# time-periods with detections	% of time periods with 0
MC	4-days	135	0.74
GC	4-days	102	6.42
DT	1-day	90	73.53



(A)

(B)

(C)

Figure 3.2: Time series of sperm whale detections as % of 5-minute bins per day at MC (A), GC (B) and DT (C). Gray indicates no recording effort.

3.5 Results and Discussion of Trend Analysis

All tests were conducted using $p < 0.05$ unless otherwise noted.

3.5.1 Diel patterns

Past research on sperm whale diel behavior has produced varying results, perhaps based on regional, population-level differences, therefore it was unclear what diel patterns, if any, would be present in the HARP recordings from the Gulf of Mexico (Whitehead 2003, Aoki et al. 2007, Pastavartou et al. 1989, Davis et al. 2007, Hodge 2011, Barlow and Taylor 2005). Diel patterns in sperm whale detections were different at each of the three sites and are described in Table 3.2 and Figure 3.3.

At DT there was no significant diel pattern, however this data set was the smallest of the three, and if a diel pattern were subtle it may not be detectible with this number of samples. Additionally, the whales at this location are suspected to be predominantly single males traveling through the area, and are therefore likely to exhibit different behavior from the groups of females and young males that are most commonly found near MC and GC. Previous studies from other regions have similarly not identified any diel patterns in feeding behavior (Whitehead 2003), so although this was not the hypothesized pattern, it was not unexpected.

The daytime foraging pattern observed at GC is similar to what was found in a smaller set of HARP data from the coast of North Carolina (Hodge 2011). As with DT these results do not support my hypothesis, but are not unexpected.

At MC nocturnal and anti-crepuscular patterns were statistically significant, however they are so small that they are difficult to identify in subfigure 3.3 (A), despite the large sample size, and may not be biologically significant.

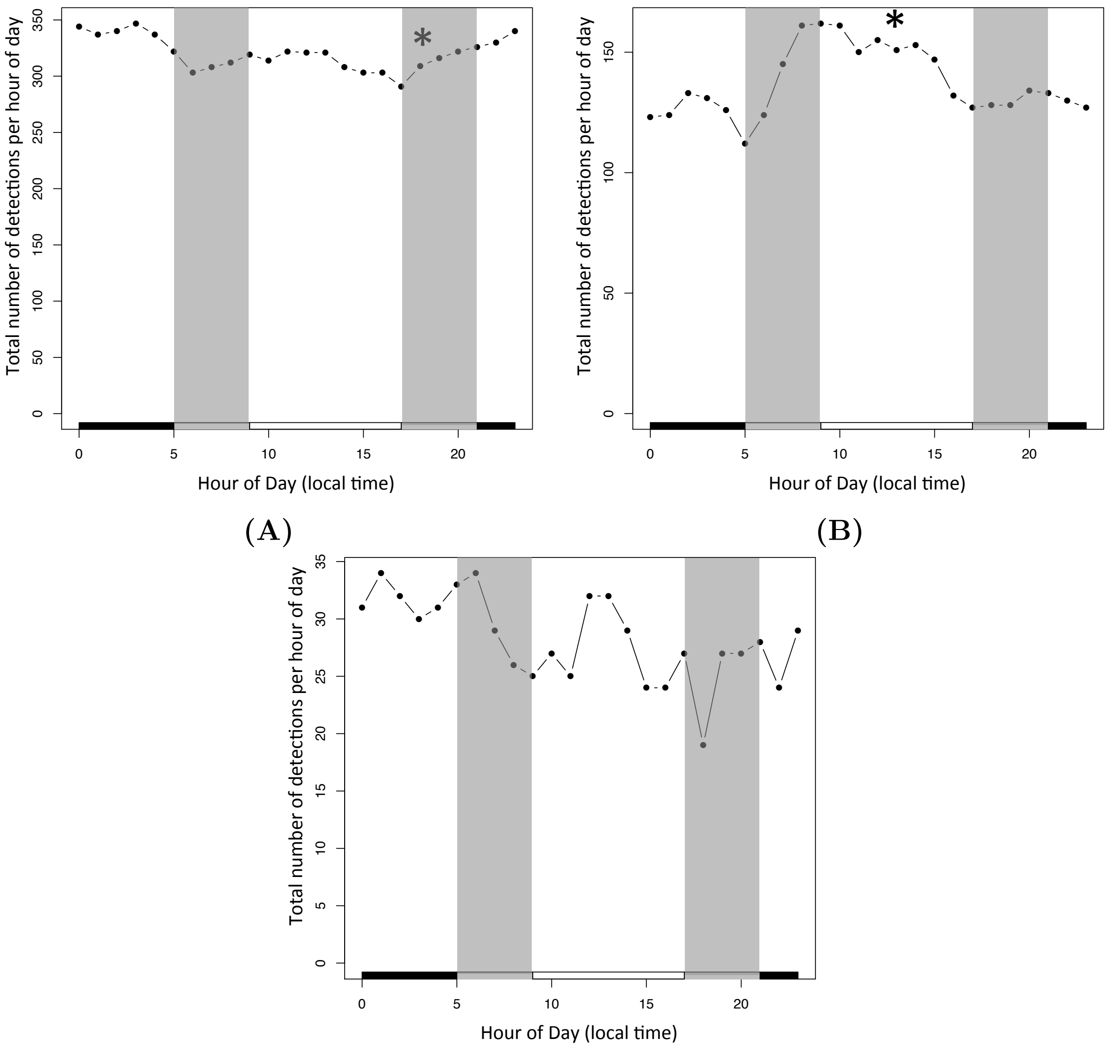
It is unclear why there would be different patterns at GC and MC, however these may relate to differences in prey availability at the two sites. For example, differences in prey were posited by Aoki et al. (2007) to cause different diel behaviors of sperm whales at two otherwise similar locations southeast of Japan. It is also known from tagging studies that at least some individuals tend to move

Table 3.2: Diel patterns of sperm whales by site. (-) indicates no significant pattern in that category.

Site	MC	GC	DT
Total # 5-min bins	7695	3297	679
Day/Night p-values	Nocturnal 0.008	Diurnal <0.0001	- 0.125
Dawn/Dusk p-values	Anti-Crepuscular 0.047	- 0.145	- 0.775

from their core area near MC toward the west where they linger near the Texas coast before returning to the area around MC (Mate et al. in Jochens et al. 2008). Therefore the GC HARP may be along the transit corridor, and the behavior exhibited by animals in transit is likely to be different from that of animals within their core range (Whitehead 2003).

The results from MC do support my hypothesis that sperm whales are less active during crepuscular periods, however the conflicting results from all three sites show that diel patterns may not be straight-forward for sperm whales in the Gulf of Mexico. I note that with HARP data it is not possible to discriminate between behavioral changes, as described above, and movement patterns that might take sperm whales away from the HARPs on a daily basis.



(A) **(B)**

(C)

Figure 3.3: Detections of sperm whales per hour of the day (local time) at MC, GC (B) and DT (C). Color bar at bottom indicates day (white) and night (black) while vertical boxes indicate crepuscular (gray) periods. Note nocturnal, anti-crepuscular activity at MC (A)(*) and diurnal activity at GC (B)(*). Although these patterns are significant, the change is very small and may not be biologically significant.

3.5.2 Seasonal trends

Sperm whale detections were tested for seasonal differences (see subsection 2.4.2 for methods), and the results varied by site. At GC there were no significant seasonal trends. At MC there were significantly more detections in the fall months (September, October, November) than in any of the other three seasons (Figure 3.4). In contrast, there were significantly fewer detections in the fall months than during all other seasons at DT.

The decreased detections in fall at MC suggest a seasonal pattern of movement, perhaps related to changes in abundance of prey. Similar seasonal movement around the Gulf of Mexico has been shown in a previous study (Jochens et al. 2008). Sperm whales in the MC region were equipped with satellite tags, and their movements indicated that their "core area" (where they spend 50% of their time) was localized near MC. The "home range" (where they spend 95% of their time) extends west along the continental slope spanning the depths from approximately 300-2000m. These animals often moved great distances in spring and fall months (Jochens et al. 2008), although these unpredictable movements, would not be considered a migration. Therefore, if the HARP at MC is on the edge of their core area the sperm whales in this region might be more likely to pass near to the HARP when they are undergoing a long-distance move to another part of their core area or home range.

Such movements might be motivated by changes in prey distribution. The annual cycle of biological productivity in the Gulf of Mexico is fairly strong, with peaks in chlorophyll-a concentration in the fall and winter as the mixed layer depth shoals. This annual cycle of surface productivity may translate to an annual pulse in squid abundance. Although very little is known about the lag time between primary productivity at the surface and increased abundance of deep-living squids, a period on the order of four to six months is reasonable (Vinogradov 1981 in Jaquet 1996). Alternatively, squid are known to make seasonal migrations related to spawning activity, and although little is known about the patterns of squid in the Gulf of Mexico or of deep-living squid, it is possible that some aggregation of squid in the region of the MC HARP might lead to a periodic increase of sperm whales at this location.

The opposite pattern, with sperm whales less abundant at DT in the fall, could be related to the conditions at MC. A phenomenon like an increase in abundance of prey that concentrates sperm whales at MC may draw animals away from the DT region.

It is also believed that the sperm whales at DT are more likely to be moving in and out of the Gulf, not "resident" like the animals at MC. Therefore this may simply be a time of year when these animals are not moving.

The area close to GC is not as heavily influenced by the seasonal patterns of the Mississippi River, and is also outside of the known core area of the sperm whales that were tagged near MC (Jochens et al. 2008), therefore a lack of seasonal trend is not unexpected.

My hypothesis that there would be a seasonal peak in sperm whale detections was supported by the results from MC, but not DT or GC. The opposite trend being observed at MC and DT is confusing, however the small sample size at DT means the trends at this site are highly susceptible to the influence of a few data points, and should be treated with caution.

It is unlikely that seasonal differences in acoustic propagation had much effect on detection rates because the sperm whales generally dive below the stratified surface layers on foraging dives, which is primarily when we detect them.

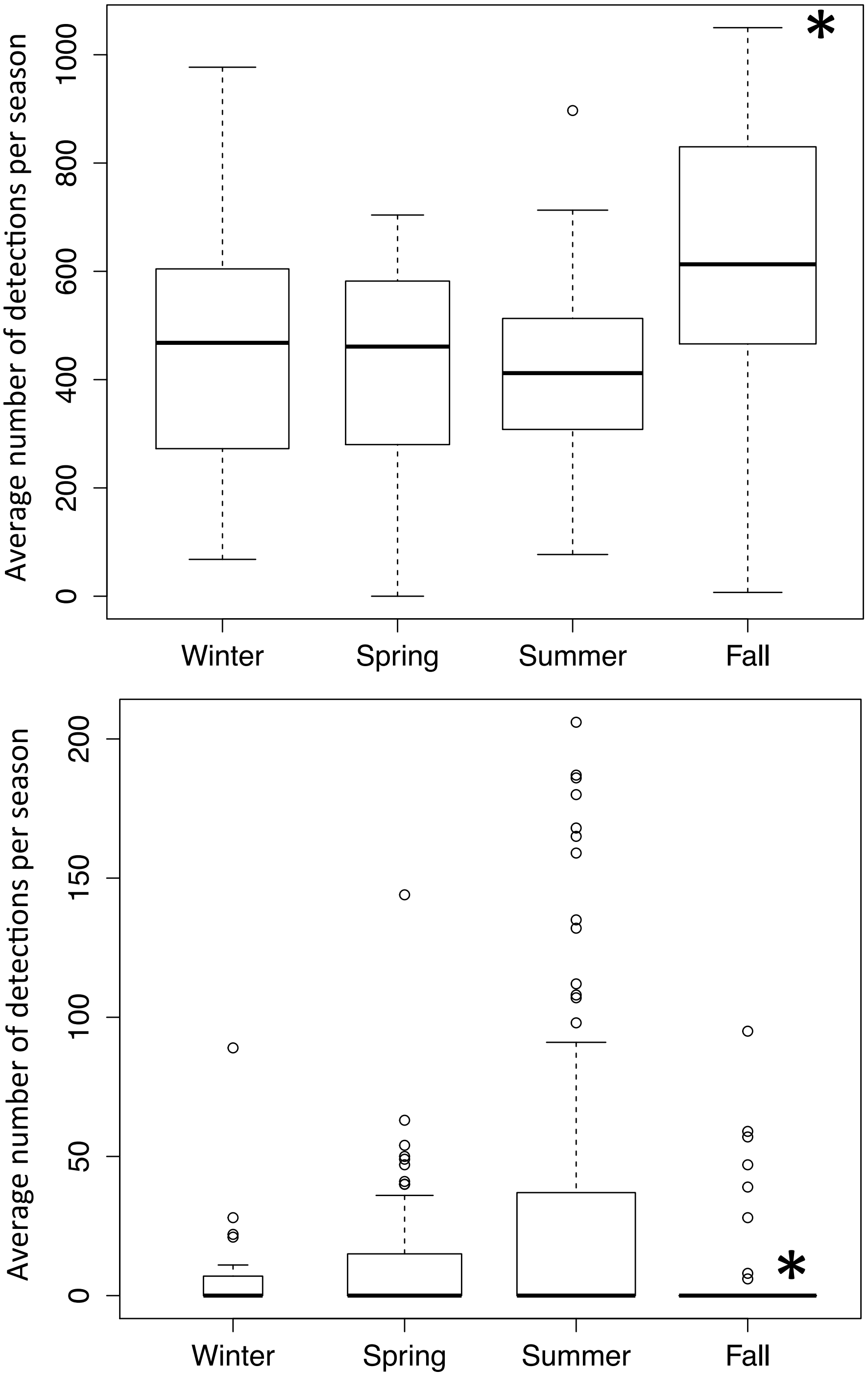


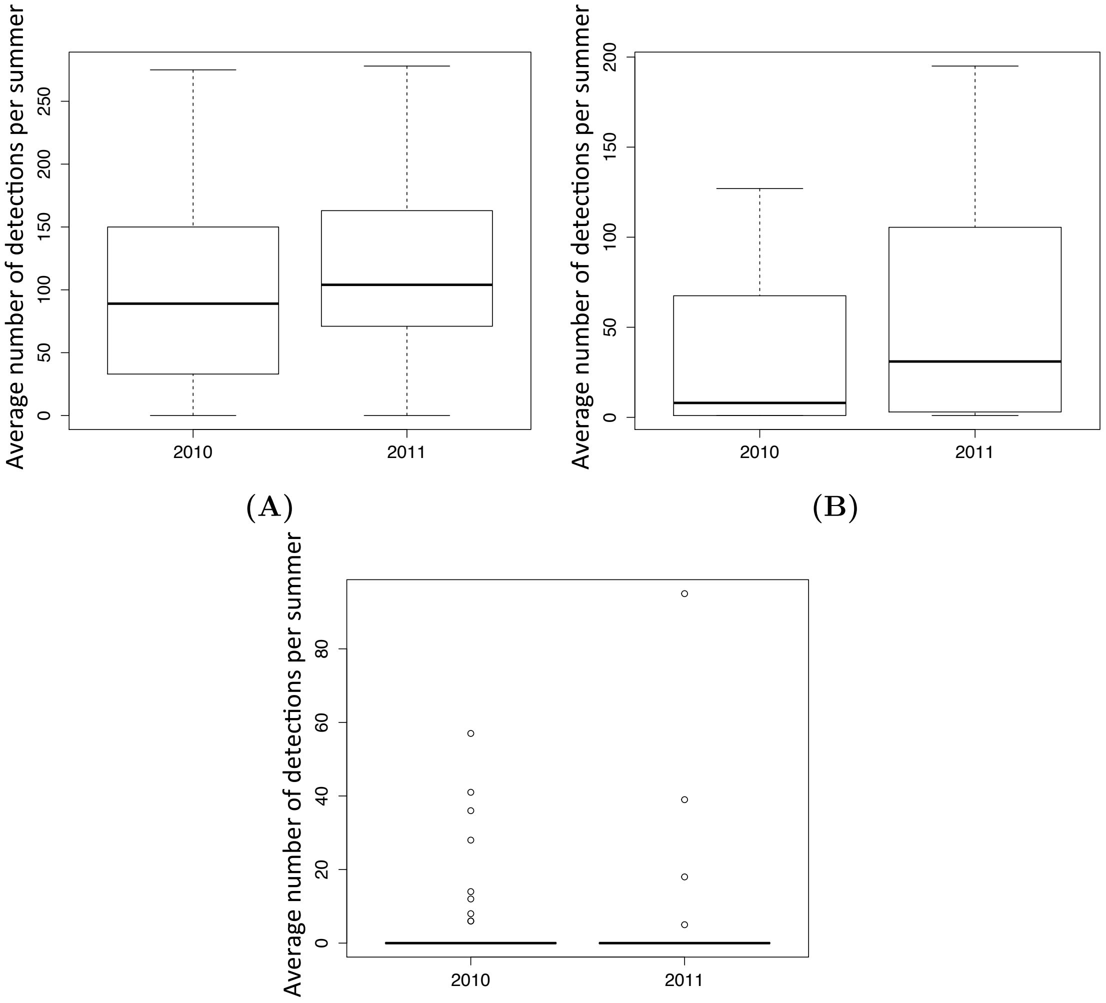
Figure 3.4: Box plot of sperm whale detections per season at MC (top)and DT (bottom). Top and bottom of boxes are at 75th and 25th percentiles; whiskers extend to 1.5 times the interquartile range. At MC mean detections in fall (*) were significantly ($p < 0.05$) higher than in all other seasons whereas at DT mean detections in fall (*) were significantly lower than in all other seasons.

3.5.3 Oil-spill related trends

There were no significant differences between the mean detections of sperm whales at each site in the summer of 2010 (during the DH oil spill) and the same days in the summer of 2011 (Figure 3.5). This suggests that sperm whales did not relocate during the summer of the oil spill to avoid the oil or related anthropogenic activities, in which case the mean number of detections in both summers would be consistent with previous years. Alternatively, the sperm whales may have avoided the areas during both summers, in which case an increase in the number of detections in future years would be expected. Given that there was no direct impact of the oil spill on the the areas of GC and DT, it is possible that the explanation for why there was no change could be different for each of the sites (e.g. at GC and DT there might have been no impact, hence no change, while at MC there was continued avoidance in both summers, hence no change).

Similar tests were conducted to compare detections during the period of the spill and the subsequent months. In this case I looked at both the mean and the slope of the data before and after various breakpoints at MC and GC, and the results are tabulated below (Table 3.3). Example plots of the slopes before and after a set of breakpoints is shown in Figure 3.6. At MC there was a pulse of sperm whale detections in early October 2010 (see Figure 3.2), which had a strong influence on the mean and slope comparisons. Depending on whether this pulse was found in the period before or after the breakpoint the slope of the after period changed drastically. Although the slope before the breakpoint was always positive, indicating an increase in sperm whale presence over time, the slope after the breakpoint changed from negative to positive depending on whether the October pulse was included in the time period or not. Therefore the comparison of means and slopes during these time periods at MC is primarily an exploration of this pulse of detections and not much can be learned about the short term effects of the oil spill, unless a connection between this October pulse and the oil spill can be made.

At GC there was a gap in effort between October 11 and November 8, which reduces the sample size for the period after the September 15-November 1



(A) **(B)**

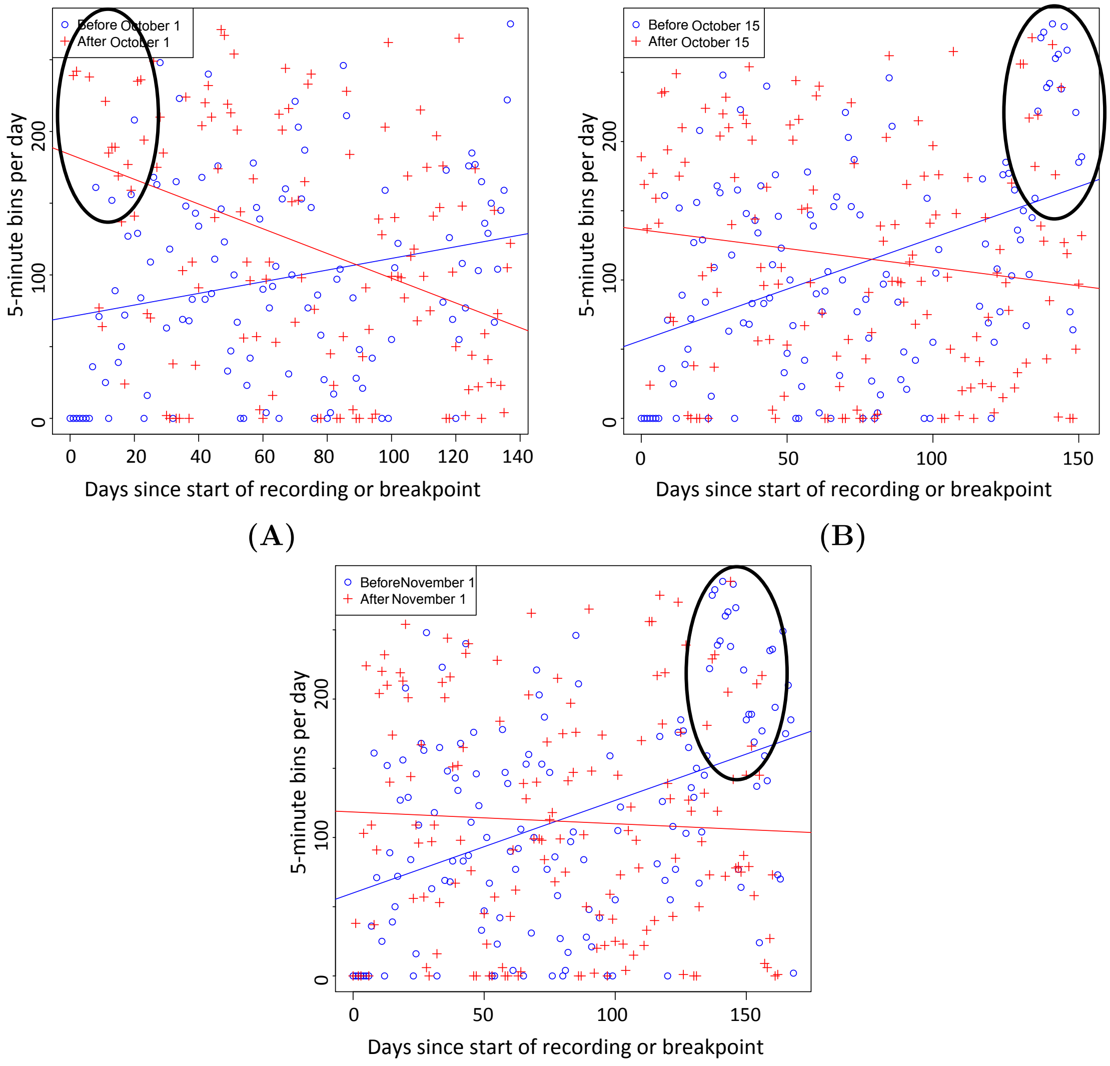
(C)

Figure 3.5: Box plots of sperm whale detections in the summer of 2010 and 2011at MC (A), GC (B) and DT (C). Top and bottom of boxes are at 75th and 25th percentiles; whiskers extend to 1.5 times the interquartile range. There is no significant difference between the two years at any site. Note: at DT the mean is zero in both years because there are so few detections.

breakpoints, and there was a pulse of increased detections in early/mid November, which has a strong effect on the periods that span that time. Because of these features, one cannot draw conclusions about what effects the oil spill might have had at this location. Despite the suggestion of decreased detections during June of 2010 based on qualitative examination of the time series (Figure 3.2) my hypothesis of a reduced presence of sperm whales during the summer and fall of 2010 was not supported.

Table 3.3: Comparison of means and slopes for sperm whale detections before and after breakpoints separating period of oil spill from post-oil spill at MC and GC. (+) indicates a significantly higher mean after the breakpoint, (-) indicates a significantly lower mean after the breakpoint, (same) indicates no difference between periods ($p < 0.05$). When the differences in slopes was significant the value of the slope is included in the table. The slope before the breakpoints at MC is always positive. Data collection at GC did not begin until July 15.

Breakpoint	Jul 15	Aug 01	Aug 15	Sep 01	Sep 15	Oct 01	Oct 15	Nov 01
MC:								
mean after	same	+	+	+	+	+	same	same
slope before	same	0.84	same	same	0.12	0.41	0.74	0.67
slope after	same	2.21	same	same	-0.82	-0.86	-0.27	-0.08
GC:								
mean after	NA	same	same	-	same	same	+	same
slope before	NA	same	same	same	-0.09	same	-0.26	-0.27
slope after	NA	same	same	same	1.85	same	-1.18	-1.10



(A) **(B)**

(C)

Figure 3.6: Example plots showing different slopes before and after breakpoints. Lines are a linear fit to the data points for each period. Note the pulse of detections in early October (black oval) that moves from one period to the other as the breakpoint shifts. This pulse was also visible in the time series of detections (Figure 3.2), and greatly influences the strength of the slope for the period including the pulse, although it does not change the overall relationship between the two slopes.

3.6 Results and Discussion of GAMs and ZINB models

For data from MC and GC, analysis of relationships with environmental parameters was carried out using GAMs while detections at DT were so sparse that a ZINB GLM was used instead (for details of methods, see section 2.5). The results of model selection for the sperm whale detections are presented in Table 3.4. Because the response variable is periods of time with echolocation clicks, and these clicks are generated primarily during foraging dives, these models probably relate most closely to aspects of foraging ecology such as processes that increase prey populations or density. Although these models are based on analysis of conditions at a single location, because of the dynamic, fluid nature of the ocean environment, the habitat characteristics at a single point will change over time as different water masses move past the HARPs. This allows us to assess the relationship of animal detections with different environmental conditions without needing to sample across a large amount of space.

Table 3.4: Parameters for habitat models of sperm whales. (s) indicates a smooth function in the GAM, with estimated degrees of freedom in parentheses; (L) indicates a linear function, (p) indicates a polynomial, with order in parentheses.

Site	MC	GC	DT
Model Type	GAM	GAM	Zero-inflated GLM
Tweedie p-parameter	1.33	1.48	NA
Selected model parameters	L(mean(SST)) + s(mean(SSHA),1.23) + L(log(DISF)) + L(mean(WIND)) + s(log(OARE),1.84)	s(Date,1.44) + L(mean(SST)) + s(SD(SSHA),1.48) + L(NOIS01) + s(NOIS40,2.1)	counts: p(SD(SST),3) + p(mean(SSHA),2) zeros: p(SD(SST),3) + p(mean(WIND),2) + L(BOAT) + L(NOIS40)
% Deviance explained	19.7	30.1	8.64

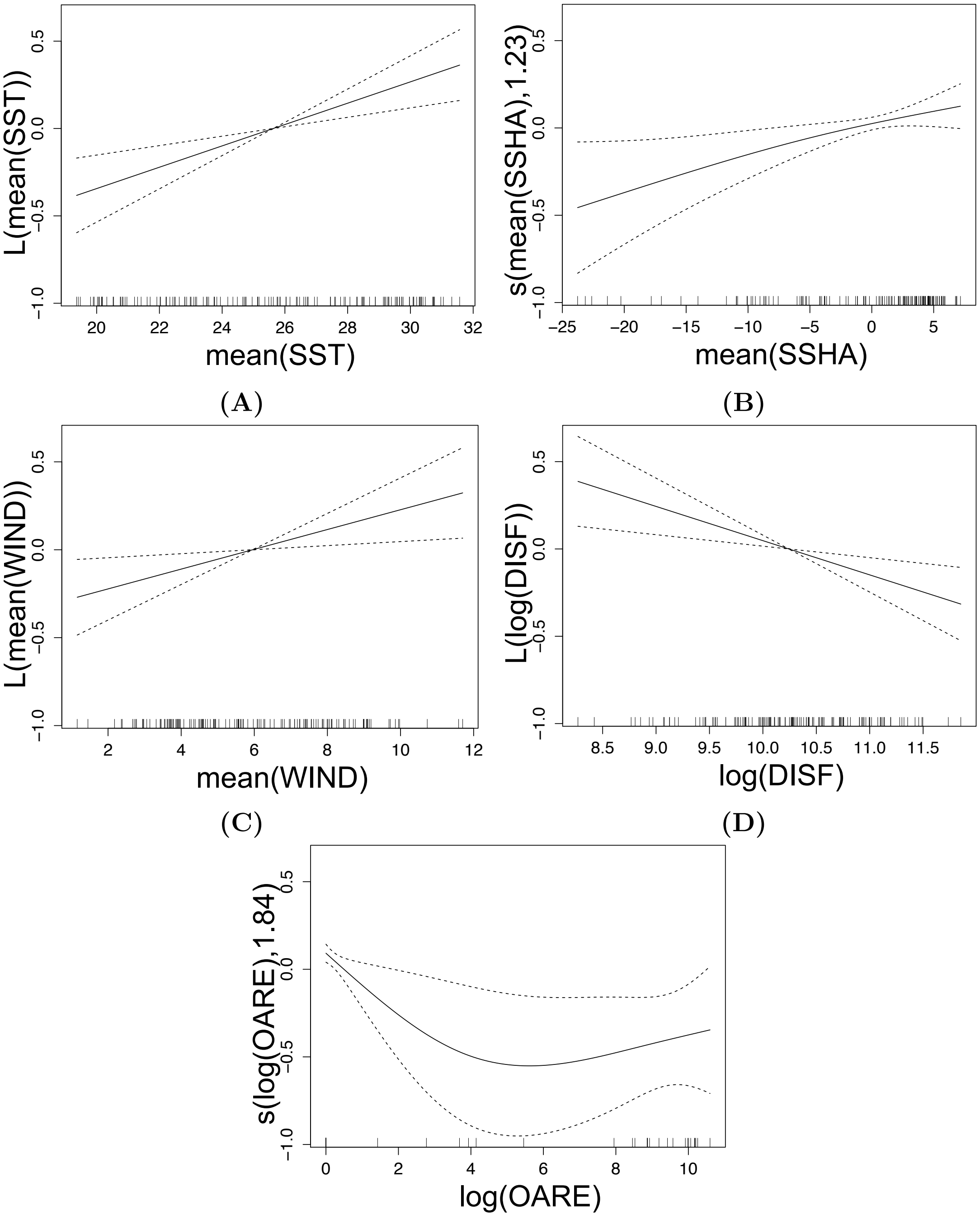
3.6.1 Sperm whales at Mississippi Canyon

The relationships between the smooths of the explanatory variables and sperm whale detections at MC are depicted in Figure 3.7, and the same vertical axis scale has been used in each of the subfigures to allow for comparison of the importance of the variable through comparison of the scale of the slope. From this it is clear that all five parameters in this model have similar strength.

Sperm whale detections were positively related to a linear fit of mean(SST) (subfigure 3.7 (A)), indicating that there were more detections in warmer (summer and early fall) periods when SST is warmer throughout the region. This trend is confirmed by the analysis of differences in means per season described above (subsection 3.5.2), which showed significantly more detections in the fall. This seasonal pattern is likely related to the movement of sperm whales around or in and out of the vicinity of MC. See section 3.5.2 for details.

An increased mean(SST) might also relate to the presence of warm core rings passing near to the HARP, which cause short-term elevation of SST. These mesoscale features are eddies from the Loop Current that break off and move toward the west, often passing close to MC and GC. With the center of the ring being warmer than surrounding waters, it leaves a measurable signal as it drifts past. If sperm whales were present in increasing numbers near or in these features then their presence ought to increase with increased SST. Past research has shown that sperm whales were not likely to be located inside such rings, but do tend to be found in higher numbers on the periphery (Waring 1993, Griffin 1999, Biggs 2000, Baumgartner et al. 2001).

There is a nearly linear relationship between sperm whale detections and mean(SSHA) at MC, with a positive trend indicating an increase in detections when mean(SSHA) is higher (subfigure 3.7(B)). Like mean(SST), the mean(SSHA) at MC is also related to seasonal variability, so the extreme low values of mean(SSHA) occur in the spring/early summer. This pattern is inversely related to the rate of freshwater discharge from the Mississippi River (MSRD), such that low mean(SSHA) corresponds to high MSRD, with a slight time lag. This relationship may be caused by the physical interaction of the fresh river water



(A) **(B)**

(C) **(D)**

(E)

Figure 3.7: Modeled partial fits of habitat parameters included in best model of sperm whale detections at MC. (s) indicates a smooth function in the GAM, with estimated degrees of freedom (edf) in parentheses; (L) indicates a linear function. Rug plot along bottom indicates location of detections. (A) mean sea surface temperature, (B) mean sea surface height anomaly, (C) mean wind speed, (D) log of distance to nearest front, (D) log of area of surface oil.

with the higher salinity seawater in the Gulf, but the exact mechanism is unknown (Bruce Cornuelle, personal communication). Sperm whales may actively avoid the MC area during times of low mean(SSHA)/high MSRD if, for example, the influx of large amounts of Mississippi River water has a negative impact on their prey. However, the majority of measurements occur during periods of moderate mean(SSHA), and the error bars are fairly wide at extremely low and extremely high mean(SSHA), therefore the relationship may be close to zero.

Mean wind speed (WIND) was also selected as an important parameter, and the figure illustrates the positive linear relationship (subfigure 3.7(C)). Globally wind speed is related to biological activity because higher wind speeds generate increased mixing of the surface waters, leading to increased nutrient flux to the surface. This can produce an increase in primary productivity, which in turn results in increased abundance at higher trophic levels. This series of connections was shown by Croll et al. (2005), who examined wind-driven upwelling in relation to marine mammal presence on the California coast. In the Gulf of Mexico increased winds can produce surface mixing as well as wind-driven upwelling (Weisberg et al. 2000). There is likely a lag between increased wind and increased primary productivity, and an additional delay between increased primary productivity and increased sperm whale prey abundance. Therefore introducing a lag between the wind speed and sperm whale detections might produce a stronger relationship, but the identifying appropriate length of time for such a lag would be highly speculative.

Relatedly, although hurricanes do locally increase windspeed, there were no major storms that passed close enough to any of the deep HARP sites to be notable in this time series. It is also noteworthy that the positive trend indicates it is not likely that there was masking of sperm whales by low levels of wind.

Distance to the nearest front (DISF) was also selected as an important variable, and the relationship between MC sperm whale detections and DISF was linear and negative (subfigure 3.7(D)). Because there are a few extremely high values that produced non-homogeneous residuals, both natural-log transformed and untransformed DISF data were tested in the model, and the AICcs were within

0.02. Therefore the transformed data were selected because the residuals were more homogeneous. Sperm whales have been shown to concentrate around mesoscale features, such as fronts and eddies (Waring 1993, Davis 1998, Griffin 1999, Biggs 2000, Baumgartner et al. 2001), therefore, it is logical that a farther distance to the nearest front should correspond to fewer sperm whale detections.

The final parameter included in the model was the total area of surface oil from the DH oil spill (OARE, subfigure 3.7(E)). As with DISF this variable was also natural-log transformed to limit the effects of a few extreme values. The downward trend in the figure indicates that there were more detections of sperm whales when there was no surface oil. The oil spill took place during the first few months of this time series ($n(\text{days} > 0\ ) = 25$, $n(\text{days} = 0) = 111$), therefore the majority of measurements of log(OARE) are zero, hence the narrow confidence interval near where log(OARE) equals zero. The wide error bars at high values of log(OARE) are caused by the small number of samples at high values. The low number of detections during the period of the oil spill (especially zero detections in the first six days of the time series) suggests some avoidance of the area close to the DH wellhead, but not for the entire duration of the spill. There have been no previous studies of sperm whales and oil spills, however research on killer whales (*Orcinus orca*) impacted by the Exxon Valdez oil spill indicated no notable avoidance of the oil contaminated region, which resulted in acute exposure to oil and likely lead to the death of multiple individuals and the expected extinction of two local groups (Matkin et al. 2008). It remains unknown how many sperm whales were directly exposed to the oil from the DH spill, particularly as oil that did not rise to the surface has continued to be difficult to assess but potentially abundant, and may have already had significant negative impacts on the local ecosystem (Montagna et al. 2013), particularly deep-diving species that are regularly surrounded by the deep oil.

Despite the relatively wide error bars (dashed lines), all of the trends observed in the best fit (solid line) are still likely to have been observed. In general all of the relationships are probably linked to the presence of sperm whale prey near the HARP, however, as noted above, there is no direct measure of deep squid abundance available, therefore the number of links between these physical parameters and sperm whale abundance is greater. This is reflected in the overall poor fit of the best model to the data, explaining less than 20% of the deviance (note the narrow span of the y-axis in all subfigures of Figure 3.7). Although this is a fairly good fit relative to the fits of models for sperm whales from other regions (e.g. Becker et al. 2010), it is still low. However, it may be improved with a longer time series of sperm whale detections. These results support the hypothesis that sea surface height anomaly and the distance to fronts are important in preferred sperm whale habitat.

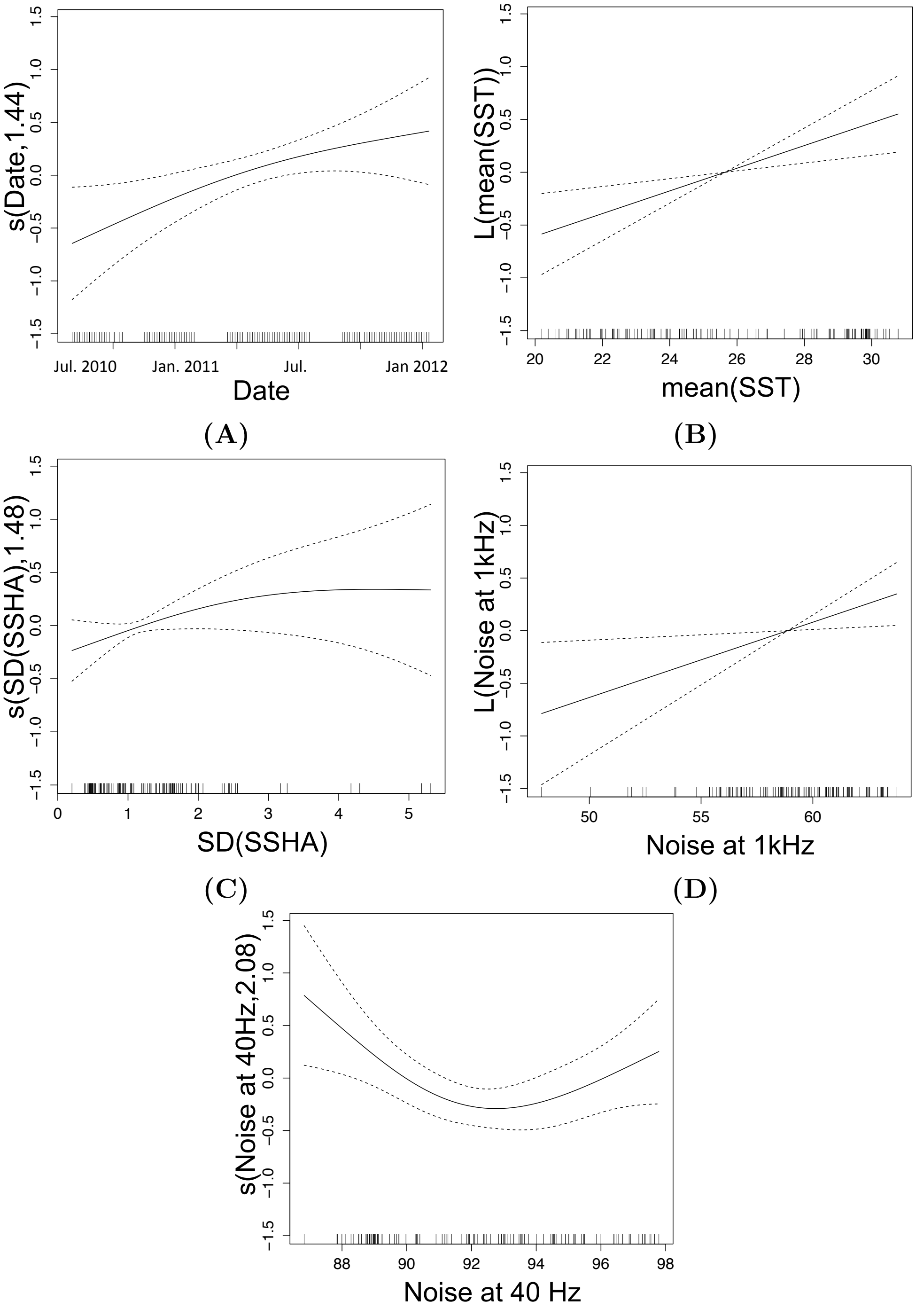
3.6.2 Sperm whales at Green Canyon

A similar suite of five explanatory variables was selected for sperm whales at GC: date, mean(SST), SSHA, noise at 1 kHz, and noise at 40 Hz (Figure 3.8). All partial fits are plotted on the same scale on the y-axis for comparison, and all have similar strength in the best fit model.

The linear relationship with mean(SST) indicates an increase in the number of detections in the warm (summer and fall) months (subfigure 3.8(B)). Because the mean(SST) goes up and down on an annual cycle this trend indicates that there are more sperm whales at one time of the year, which is suggested by box plots of the data. Unfortunately the uneven effort across the seasons in this data set precludes statistical comparison of the means until more data have been collected.

Another parameter related to temporal trends was also included in the final model: Date (subfigure 3.8(A)). This is essentially a measurement of the number of days since the start of recording at this site. There is an overall increasing trend, which can also be seen in the time series of the detections (Figure 3.2). In the time series a large pulse of detections is clearly seen in the mid-summer of 2011 and generally high levels of detections are maintained until the end of the data set. A longer time series may significantly change this relationship between detections and date.

Sperm whale detections at GC have a positive relationship to SD(SSHA) (subfigure 3.8(C)). This metric is related to the local presence of mesoscale features,



(A)

(B)

(C)

(D)

(E)

Figure 3.8: Modeled partial fits of habitat parameters included in best model of sperm whale detections at GC. (s) indicates a smooth function in the GAM, with estimated degrees of freedom in parentheses; (L) indicates a linear function. Rug plot along bottom indicates location of detections. (A) date, (B) mean sea surface temperature, (C) standard deviation of sea surface height anomaly, (D) noise at 1 kHz, (E) noise at 40 Hz.

the edges of which are characterized by a strong change SSHA. This association between sperm whales and the edges of features such as fronts or warm-core and cold-core rings has been shown in other studies from the Gulf of Mexico and Atlantic (Waring 1993, Griffin 1999, Rankin 1999, Biggs 2000, Baumgartner et al. 2001). This relationship may be due to the eddies' capacity to locally concentrate sperm whale food. The wide error bars (dotted lines) at the higher values are due to a small number of samples at values above three (corresponding to the rare occurrence when a front or eddy edge passed directly over the HARP). Due to those large error bars the positive trend is questionable, however eliminating the extreme values above 3 produces much narrower error bars and confirms the positive trend.

The ambient noise at 1 kHz is linearly related to sperm whale detections (subfigure 3.8(D)). This noise metric is almost entirely a measurement of wind speed, which dominates the ambient noise above 200 Hz (Wenz 1962), and it has been shown in other regions that an increase in windspeed correlates with a linear increase in ambient noise (Roth et al. 2012). Thus the measurements of mean noise at 1 kHz are an *in situ* measurement of windspeed. As discussed above, an increase in wind speed likely corresponds to an increase in upwelling andor mixing, primary productivity and ultimately more prey available for sperm whales. This may explain the positive relationship between noise at 1 kHz in the HARP data and the detection of sperm whales. The confidence intervals at low levels are wide due to the small sample size below 55 dB, however the slope remains positive within the extremes of the confidence interval.

Ambient noise at 40Hz is the final parameter that was selected for the best model (subfigure 3.8(E)). This parameter is directly related to the amount of seismic testing with air guns in the vicinity. The signals from air guns are especially prevalent at GC, and the later half of the time series was marked by fairly constant seismic testing activity, as evidenced by overall higher levels of noise in this frequency band (see Figures 2.7 and 2.8). The relationship between noise at 40Hz, and sperm whale detections is "U" shaped, with a minimum around 93 dB. Although there is conflicting evidence on whether sperm whales do not respond to seismic testing or actively avoid it (Mate et al. 1994, Rankin 1999, Davis et al. 2000, Madsen and Mohl 2000, Madsen et al. 2002, Stone and Tasker 2006, Jochens et al. 2008, Wier 2008, Miller et al. 2009, Moulton and Holst 2010), it seems unlikely that they should be attracted to these noise sources (as indicated by the increase in detections as the noise level rises above 93 dB). However, there is a clear increase in sperm whale detections toward the end of the time series which coincides with the phase of increased noise (see Figure 3.2), therefore the relationship is not due to anomaly in the data. This relationship should be treated with caution however, because given the fairly-wide error bars it is possible that a simple negative linear relationship exists instead of the complicated "U" shape, which would agree better with results of previous studies. A longer time series may provide more clarity on this relationship.

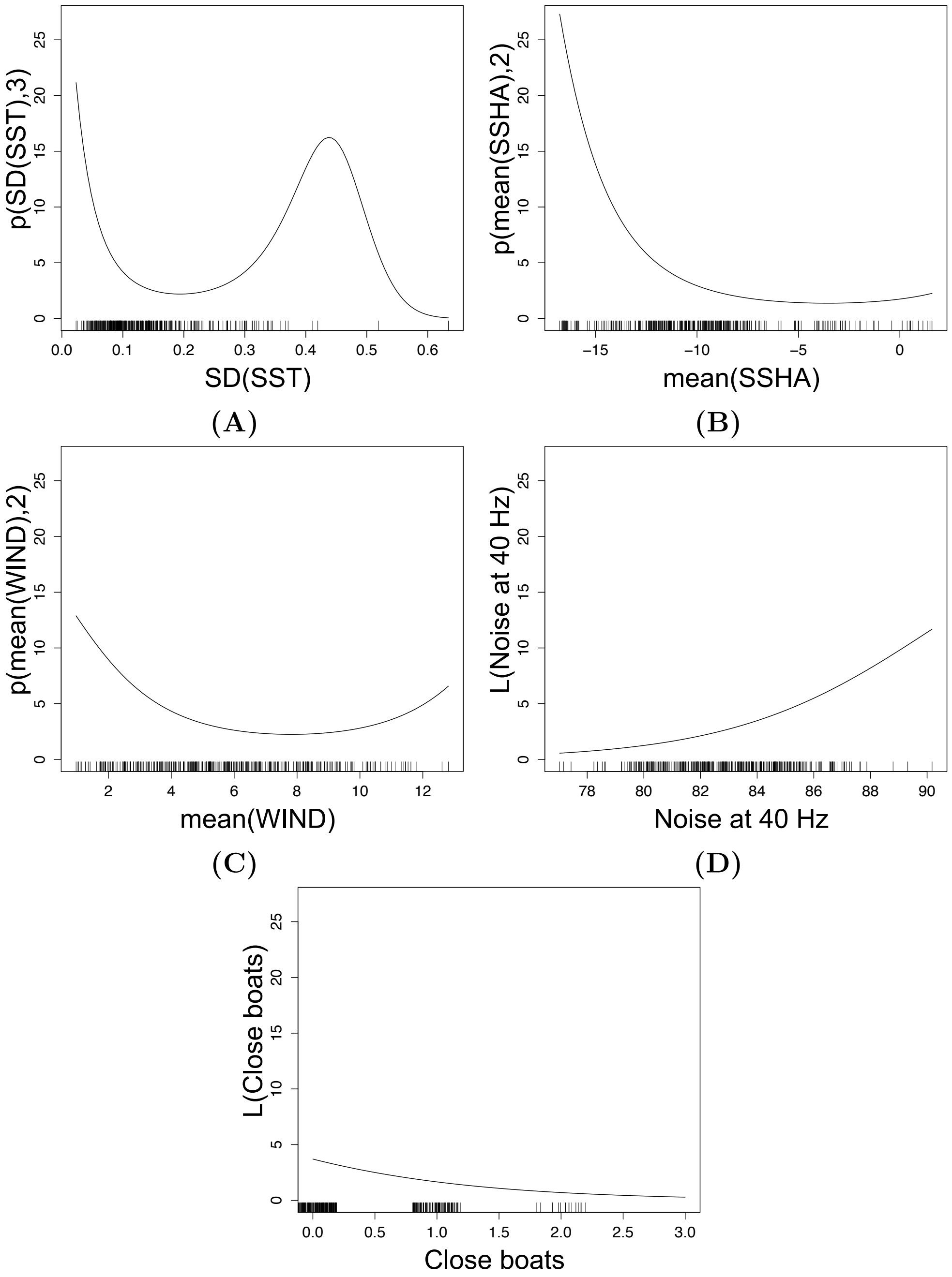
In summary the best model for sperm whale detections at GC included variables related to seasonal patterns, proximity to mesoscale oceanographic features, general biological productivity and human activity. This model explained 30.1% of the deviance, which is remarkably good for a sperm whale model, particularly without spatial coverage that could include depth or seafloor slope as parameters, which are almost always significant in other models (e.g. Waring 1993, Jaquet 1996, Davis 1998, Griffin 1999, Baumgartner 2001, Waring 2001, Davis et al. 2002, de Stephanis 2008, Skov 2008, Praca 2009, Pirotta et al. 2011). These results do support my hypothesis that sea surface surface height is an important parameter defining sperm whale habitat, however distance to thermal fronts was not included as anticipated.

3.6.3 Sperm whales at Dry Tortugas

The detections of sperm whales at DT were notably different from those at the other two sites, being fairly infrequent with the exception of one large pulse in June 2011 (see Figure 3.2). As shown in Table 3.1 over 73% of days monitored included 0 detections. This zero-inflation was too great to be accounted for by using specialized distributions that can accommodate over-dispersion (e.g. negative binomial or Tweedie) in a GAM, therefore a two-step zero-inflated GLM method with a negative binomial distribution (ZINB) was required (see subsection 2.5.1 for details). The first step models the presence and absence "zeros" model (binomial with logit link), while the second step models the positive "count" data (negative binomial with log link). The "count" model does allow for zeros, which is appropriate given that animals may not be present even if the conditions are good (e.g. the conditions might be better elsewhere). The best model combination for sperm whales at DT included five parameters for the zeros and two parameters for the count data (see Table 3.4). The modeled partial fits are plotted in Figure 3.9. Note that confidence intervals were not estimated, however rug plots indicate distribution of measurements, with narrower error bars expected in sections having more samples.

A third degree polynomial fit to SD(SST) was selected in the final model, and the plot of the partial fit (Figure 3.9 (A)) illustrates a general decreasing trend with a local maximum around 0.45. This large peak is likely due to the highest values in SD(SST) coinciding with a few days of high detections, and because of the small sample size overall these few days have an exceptionally large effect on the overall trend. The overall negative relationship indicates a preference for more changeable water temperatures, suggesting higher presence when mesoscale oceanographic features, such as eddies or fronts, are near the HARP. This preference is similar to what was found at MC and GC, discussed above, and is important for both the counts and the zeros components of the model.

Mean(SSHA) was fit using a second degree polynomial, and the partial fit plot (Figure 3.9 (B)) shows an "L" shaped curve. This parameter was only selected



(A) **(B)**

(C) **(D)**

(E)

Figure 3.9: Modeled partial fits of habitat parameters included in best model of sperm whale detections at DT. (p) indicates a polynomial function in the GLM, with degree in parentheses; (L) indicates a linear function. Confidence intervals not estimated using ZINB method. (A) standard deviation of sea surface temperature, (B) mean sea surface height anomaly, (C) mean of wind speed, (D) noise at 40Hz, (E) count of close boats. Noise has been included to show multiple measurements at the same value.

for the counts model, indicating that the SSHA is related to how many, or for how long, sperm whales are present, not whether they are present or absent. At DT the SSHA is directly related to two phenomena: the meanderings of the Loop Current closer to and farther from the HARP and the presence of cold-core rings. Both the Loop Current and cold-core rings may bring with them nutrient rich waters, either entrained from the Mississippi River outflow region or from localized upwelling in the ring. This transport of highly productive waters, and the prey that develop in those conditions, could attract sperm whales to the feature. Semi-permanent cold-core eddies periodically form in the northeast Gulf and can either move west (often in parallel with a warm-core ring) or south with the Loop Current (Biggs et al. 1997). The high pulse of detections in June 2011 coincides with the presence of a cold-core ring (exceptionally low SSHA) moving southeast through the DT area, as depicted in Figure 3.10.

A second degree polynomial was also selected for the relationship with mean windspeed, which shows a "U" shaped curve with a minimum around eight meters per second (Figure 3.9 (C)). This parameter, and the two following, were only selected for the zeros model, indicating they are important for determining the presence or absence of sperm whales at DT, and not particularly important for determining how many or for how long sperm whales are there. Increased wind speed likely correlates to increased upwelling in this area, leading to increases in primary productivity, and ultimately to increased prey for these top predators, as described in section 3.6.1 above. The non-linear relationship between mean wind speed and sperm whale detections may be due to a temporal lag between a period of increased wind and the ecological impacts at DT.

The increasing trend in the relationship with noise at 40 Hz is surprising because noise in this band is heavily influenced by seismic air gun pulses as well as the presence of ships (Figure 3.9 (D)), and one would not expect whales to prefer areas with large amounts of such noise. However, there is only one day out of the entire time series when the noise levels indicate close air guns, otherwise the air gun signals are fairly distant. Note that the majority of measurements occur during the mid-range values of noise, therefore the measurements at either end

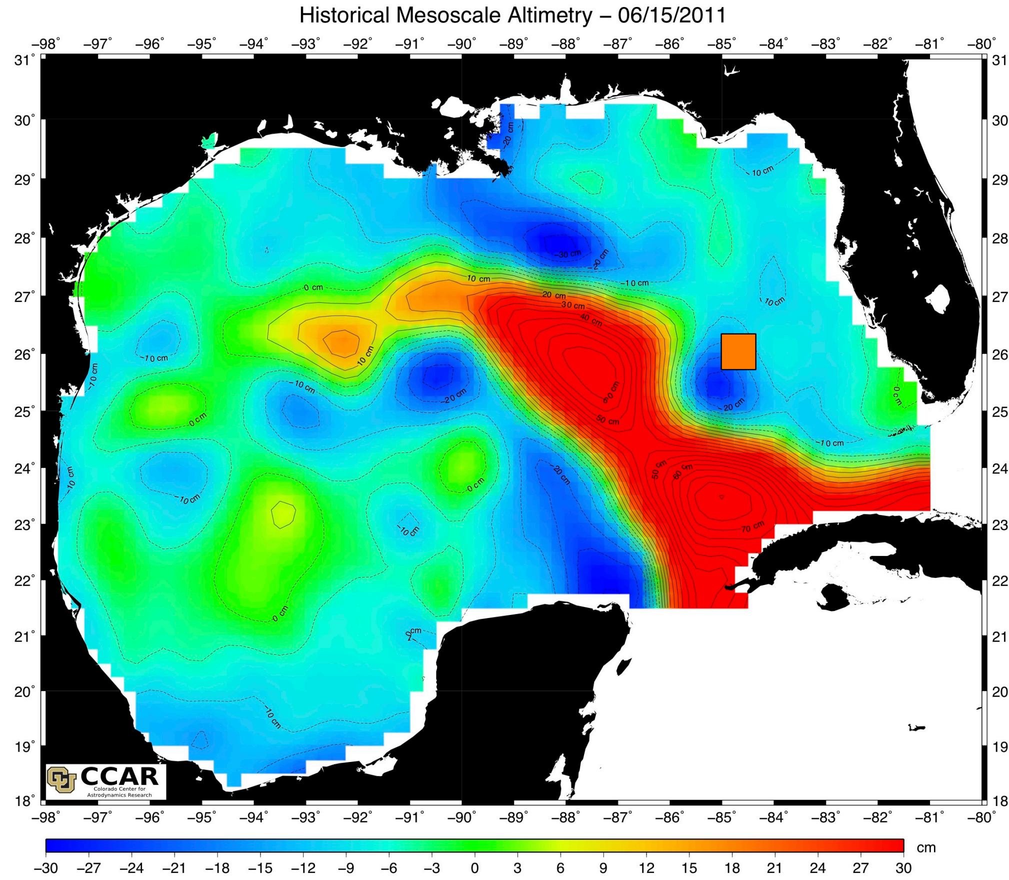


Figure 3.10: Map of sea surface height anomaly for June 15, 2011. Color scale indicates SSHA in cm, doted lines at 10 cm contours. Note the extremely low values indicating a cold-core eddy near HARP at DT (orange square, not to scale).

may have an disproportionately large effect on the overall trend.

The final parameter included in the zeros model is the count of ships passing close to the HARP, and a slightly negative relationships is seen in Figure 3.9 (E). Note, however, that the scale on the x-axis only goes from zero to three, and there was only one day with three boats, which happened to have zero sperm whale detections. The vast majority of days had 0 ships because this location is not in a shipping channel or close to a busy port area. Behavioral response by sperm whales to whale-watching boats has been shown (Gordon et al. 1992), although some whales may become habituated to frequent boat traffic. The importance of the number of close boats in this model is not surprising, however the small number of non-zero measurements does suggest that the relationship may be questionable.

As with GC these results support my hypothesis that sea surface height is important for sperm whale habitat, but that distance to the nearest thermal front is not as important as expected.

3.7 Summary

My hypotheses for the sperm whale analysis were both supported and falsified by they results presented above, depending on the site. The time series of detections of sperm whales was quite different at the three sites, as predicted. At MC animals were present nearly constantly, while at GC they were detected less often, and at DT the number of detections at was remarkably smaller than at the other two sites. This supports the current understanding of sperm whale distribution in the Gulf of Mexico, with more animals consistently found along the northern continental slope.

Analysis of diel trends revealed the anticipated anti-crepuscular pattern at one site (MC), but not at the other two. Additionally the detections at MC supported an unexpected nocturnal foraging behavioral pattern while at GC they supported a unexpected diurnal pattern. Seasonally an increase of detections in one season was hypothesized and this was observed at MC, but not at GC. A slightly different pattern was seen at DT with a drop in detections in one season (winter).

These complicated results agree with global knowledge of the unpredictable nature of sperm whale temporal patterns that vary depending on location, and show that sperm whales in the Gulf of Mexico do not have clear, consistent diel or seasonal patterns.

The response of sperm whales to the DH oil spill remains unclear, but the combined results of multiple analyses suggest that there were fewer animals echolocating near the center of the spill while oil was being released. Examination of the time series of detections at MC suggested that there was a decrease in detections during the beginning of the spill, a comparison of the number of detections in the summer of 2010 and 2011 showed no significant difference. Also, the number and rate of detections for different time periods during and directly after the DH oil spill were highly influenced by anomalous periods of high numbers of detections and gaps in the data, making it difficult to identify meaningful trends. In contrast, the amount of oil at the surface of the water was included in the best fit habitat model for MC. Within the framework of the habitat model the confounding factors like seasonality and gaps in the time series should have been accounted for, lending greater strength to the conclusion that there were fewer sperm whales present at MC during the DH oil spill. Over the extent of this data set, however there does not appear to be a long-term trend following the spill as shown by the absence of date as an important parameter for the best habitat model at MC.

My hypotheses about model parameters were partially supported. The best habitat models at all three sites included mean and SD(SST), mean and SD(SSHA) and wind speed, indicating the importance of seasonality and the presence of mesoscale oceanographic features. These results are similar overall to what has been found in other studies and as hypothesized. However, the distance to thermal fronts was not included in the models at GC or DT, which falsifying my hypothesis of the importance of this parameter. In general these results suggest that sperm whales in the Gulf of Mexico may move in relation to conditions that are measurable at the sea surface. In particular there appears to be a fairly strong seasonal movement pattern that could be migration-like, with animals rotating through different preferred habitats at different times of the year. I also showed that mesoscale oceanographic features are important for smaller-scale movement patterns, which supports the results of previous studies based on sightings of sperm whales in this region.

Taken together these results on the diel, seasonal and habitat-related activities of sperm whales in the Gulf of Mexico reinforce the complicated patterns, or complete lack of patterns, that have been observed in previous studies of sperm whales around the world. A longer time series may produce more reliable results, particularly as data from additional years that do not include an oil spill are available for analysis.

Chapter 3 in part, is currently being prepared for submission for publication. Merkens, Karlina; Frasier, Kaitlin; Wiggins, Sean; Hildebrand, John. “Sperm whale ecology and habitat modeling in the Gulf of Mexico”. The dissertation author was the primary investigator and author of this material.

Chapter 4

Beaked whale ecology and habitat modeling

4.1 Abstract

In the Gulf of Mexico there are records of four species of beaked whales: Cuvier's (*Ziphius cavirostris*), Gervais' (*Mesoplodon europaeus*), Blainville's (*M. densirostris*) and Sowerby's beaked whales (*M. bidens*, considered extralimital). Passive acoustic monitoring from May 2010 to February 2012 using High-frequency Acoustic Recording Packages (HARPs) at three sites deeper than 900 meters revealed frequent detections of Cuvier's and Gervais' and rare detections of Blainville's, as well as occasional detections of a beaked-whale like signal that does not match with any known species. This unknown signal is very similar to an unknown signal from the Pacific ocean. The detections of Cuvier's and Gervais' are remarkably high at one site (Dry Tortugas). Analysis of diel patterns reveals generally nocturnal activity, particularly for the unknown signal, which is only detected at night. This increases the similarity to unknown signal in the Pacific ocean, which is also detected more often at night. Seasonal differences were identified, with significantly more detections during the cooler months for both Cuvier's and Gervais' at two sites (Mississippi Canyon and Green Canyon). Comparison of means and rates of detections at multiple time periods to test the acute impacts of the Deepwater Horizon (DH) oil spill suggest minimal effects in the short time frame, primarily because of the small number of detections, and resulting sensitivity to extreme values. Modeling of the relationships with environmental parameters using Generalized Additive and Zero-inflated Generalized Linear models, and including anthropogenic activity relating to the DH oil spill, indicates the importance of sea surface temperature (and the related seasonal variations) and sea surface height to the preferred habitat of these species. Functional relationships varied by species and site. The total area of surface oiling was included in the best model at MC for both Cuvier's and Gervais' beaked whales. These results give greater insight into the behavior and ecology of beaked whales in the Gulf of Mexico.

4.2 Introduction

4.2.1 General Biology, Behavior, Social Structure and Distribution

The family Ziphiidae comprises the beaked whales, which is a diverse group of odontocetes that are relatively poorly understood. As a group they are deep-diving, suction-feeding teuthivores who are most often found along continental slopes and in deep water (Pitman 2002). The group includes at least 21 species, many of which are only known from a few specimens, and some of which have never been seen alive (Jefferson et al. 2008).

For most beaked whale species the individual and population biology is effectively unknown, but is probably diverse across the different species. All beaked whales are exceptionally difficult to study, being highly elusive and entirely pelagic, having faint-to-invisible blows, showing only a low profile while at the water's surface, and not raising flukes when diving (Mead 2002, Pitman 2002, Aguilar de Soto et al. 2008, Jefferson et al. 2008). The different species often cannot be distinguished except by the teeth of adult males, which makes photo identification difficult. In general they are medium sized (4-13 m in length) and sexually dimorphic, with females being larger and males having unique dentition that aids in species identification. They tend to live in small groups of one to six animals (Pitman 2002, Jefferson et al. 2008). The size of their home ranges or migrations is generally unknown (Pitman 2002), but a handful of tagging studies have begun to shed light on this issue, suggesting movements on the order of tens of kilometers every few days (e.g. Hooker et al. 2002, Tyack et al. 2011). They are known for their extreme diving behavior, spending the majority of their time well below the water's surface, and regularly diving for more than 30 minutes to depths of a thousand of meters (Pitman 2002).

In the Gulf of Mexico there have been confirmed sightings or strandings of Cuvier's (*Ziphius cavirostris*), Gervais' (*Mesoplodon europaeus*), Blainville's (*M. densirostris*) and Sowerby's (*M. bidens,*) beaked whales (Würsig et al. 2000, Jefferson et al. 2008). The global distributions of the three species most commonly detected on the HARPs in the Gulf of Mexico are presented in Figure 4.1. The single record of Sowerby's beaked whale is from an animal that stranded, and it is considered to be an extralimital occurrence of this usually North Atlantic species. We have no recordings that match the known signal of Sowerby's beaked whale, therefore this species will not be considered in this analysis. Based on analysis of HARP data from other regions (Baumann-Pickering et al. 2012), from assessments of beaked whales in the Gulf of Mexico (Mullin and Fulling 2004), and from studies of sperm whales in the Gulf of Mexico (e.g. Davis et al. 2002, Jochens et al. 2008), a species with similar prey and habitat preferences, I anticipate finding more beaked whales at GC and MC than at DT, and fewer detections than sperm whales (e.g. at a rate of approximately one per week).

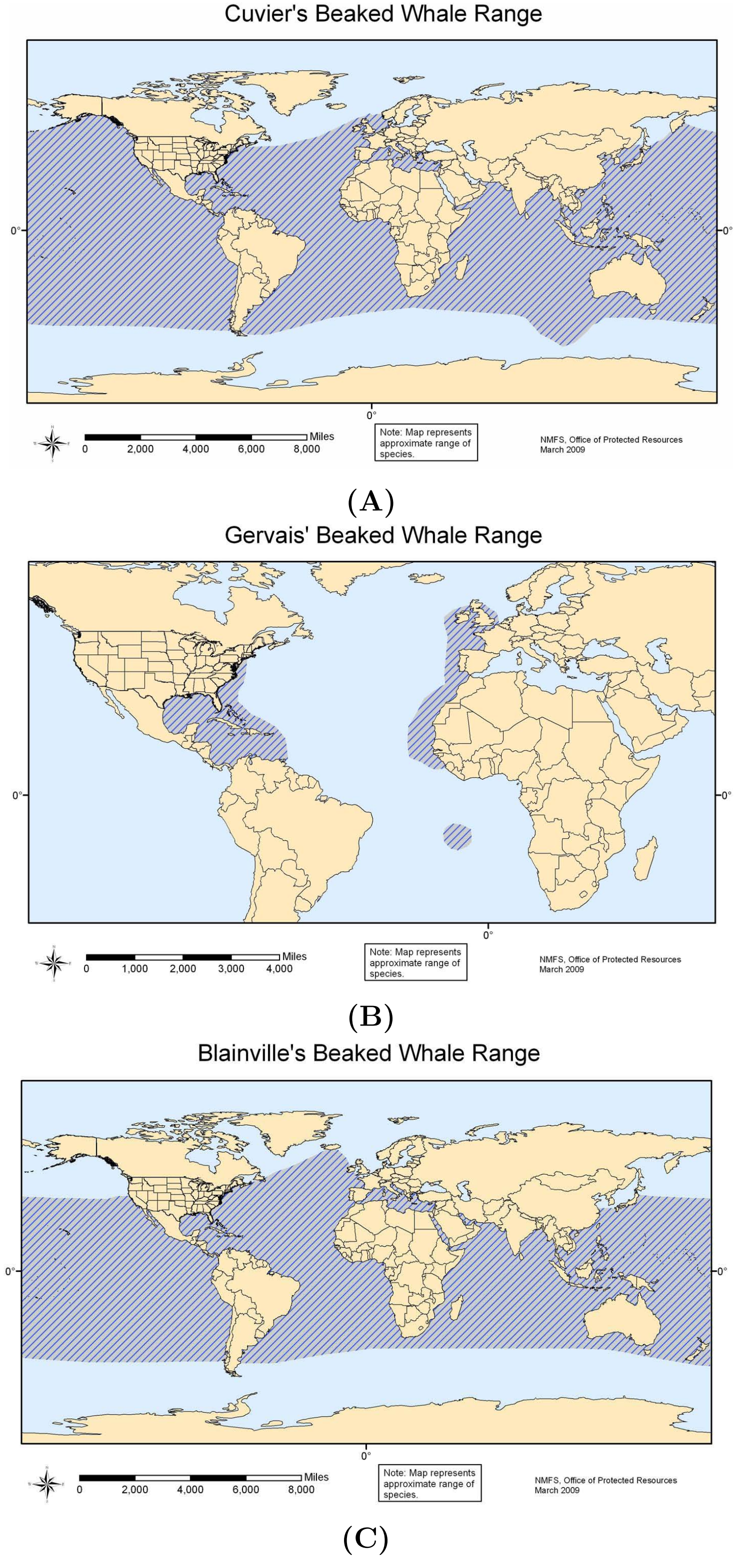


Figure 4.1: Global distribution of (A) Cuvier's, (B) Gervais, and (C) Blainville's beaked whales. (courtesy of NOAA-NMFS, http://www.nmfs.noaa.gov/)

4.2.2 Temporal Patterns

Diel and seasonal patterns of beaked whales have been examined in a few instances globally, and generally indicate little or no trend. Increased nocturnal behavior has been found for some species in some locations (Au et al. 2013, McDonald et al. 2009), although another study found similar dive rates between day and night (Baird et al. 2008). Based on these results from previous studies I hypothesize that there will be no diel patterns for Cuvier's or Gervais' beaked whale, but that BWG, perhaps being similar to the unknown beaked whale from the Pacific ocean, will be entirely nocturnal.

Seasonal patterns of beaked whale presence have previously been reported a handful of times, although most studies have been based on sightings or strandings, both of which can be heavily biased by seasonal differences in weather and oceanographic conditions. Additionally most studies that report on seasonal trends are based on so few detections that presence or absence is all that can be assessed, not relative abundance in any season (Miggnucci-Giannoni 1998, McSweeney et al. 2007, Baird et al. 2013). A few researchers have been able to assess changes in seasonal abundance of sightings, strandings or acoustic detections, and the results are conflicting based on region or species (Smith 2010, MacLeod et al. 2004, Baumann-Pickering et al. 2012). Such inconsistent results lead me to expect that in the Gulf of Mexico all three beaked whale species will demonstrate no significant pattern in seasonal detections, except for a decrease in detections during the summer and fall of 2010 while the DH oil spill and response was underway.

4.2.3 Habitat Preferences

Beaked whales as a group generally occur in deep water along continental slopes or around islands with steep bathymetry (Pitman 2002), and relatively little is known about the particular preferences of individual species. Given other similarities to sperm whales (e.g. deep-diving behavior, prey preferences, etc.) it seems reasonable to hypothesize that the habitat preferences of beaked whales will be similar. Therefore I predict that features related to proximity to mesoscale oceanographic features, such as sea surface height anomaly and the distance to thermal fronts, will be most important in the best fit models for all beaked whale species tested.

4.2.4 Acoustics

The acoustic signals of the three species for which we have recordings (Cuvier's, Gervais' and Blainville's) have been described in the literature and the species are classifiable based on these signals (Zimmer et al. 2005, Johnson et al. 2006, Gillespie et al. 2009). In general the signals are frequency modulated pulses with a peak frequency around 40 kHz, pulse duration of 450-580 microseconds, and inter-pulse-interval of 275-340 milliseconds (Baumann-Pickering et al. 2013). Additionally we have detections of a signal that is similar to beaked whales, however it does not match with any of the four species that are known to be present in the Gulf. These signals are very similar to a signal that has been recorded in the Pacific ocean, which also has not been confirmed to species (McDonald et al. 2009, Johnston et al. 2008, Baumann-Pickering et al. 2013). For the sake of this analysis we consider this signal to be from a separate beaked whale species, and it has been temporarily called the unknown Beaked Whale from the Gulf of Mexico (BWG).

As mentioned in section 2.1.2, the acoustic propagation at each site was similar, allowing for comparison of the results across sites. This is particularly true for beaked whale signals, which attenuate over fairly short distances (e.g. less than five kilometers), and are therefore not subject to the effects of bathymetry on long-range propagation.

4.3 Beaked Whale Specific Methods

Manual analysis of the acoustic data to identify beaked whale signals required the analyst to scan 1-hour windows of long-term spectra averages (LTSAs) between 10 and 100 kHz. Each window was moved forward by 0.5 hours to ensure detection of signals, particularly the BWG signals, which were often in bouts shorter than five minutes. Each detection consisted of the pulses that were not separated by more than 30 minutes. Detections were provisionally classified to species by close examination of a random selection of individual pulses.

In a second step the detection start and stop times were used to guide an automated detector through the data. This detector, developed by M. Roch and S. Baumann-Pickering, identifies pulses using the Teager energy operator (Kaiser 1990), and measures and stores a variety of information about each pulse, such as inter-pulse-interval, pulse duration, median frequency, etc. (e.g. Baumann-Pickering et al. 2013). The spectral information of the pulse is also stored, and a series of images was generated to assist species identification, including spectrograms of each click in the detection sorted by peak frequency and concatenated, the mean spectra for the detection, and histograms of inter-pulse-interval and peak frequency. Detection events with pulses that were too few in number or too low in amplitude for classification were discarded.

4.4 Results of Exploratory Analysis

The detection rates of the four beaked whale species vary greatly between sites. The time series of detections of the three most commonly detected beaked whale species at all three sites are shown in Figures 4.2, 4.3 and 4.4. For Cuvier's beaked whale there appears to be a seasonal pattern at MC and GC, with higher numbers of detections during the winter months and fewer or no detections during the summer. Detections for Gervais' beaked whale do not show any clear trend over time, however there is an increased level of detections during September and October 2010 that may impact the analysis of trends associated with the oil spill. There is no clear trend in detections over time for the unknown signal BWG. Details are recorded in Table 4.1 and further analysis of seasonal patterns is addressed in subsection 4.5.2. Blainville's beaked whales were only detected at site GC, and there were too few detections for further analysis at this time.

In general it is clear that there was an unexpected abundance of Gervais' and Cuvier's beaked whale detections at DT, which is entirely opposite from the hypothesized distribution pattern. Additionally Gervais' beaked whale was detected much more frequently at all three sites than expected, with detections occurring on average every other day or more often at MC and GC, and nearly every day at DT. Cuvier's beaked whale is also detected more frequently than expected at DT, but a more sporadic pattern is observed at MC and GC, similar to the hypothesized detection rate of once per week.

As described in subsection 2.1.2 a 4-day time period was initially used for Gervais' and Cuvier's beaked whale detections at DT, however initial modeling showed that autocorrelation was still problematic in the model residuals for Cuvier's beaked whale detections. Therefore, a time period of five days was used for this species at this site to eliminate autocorrelation in the residuals.

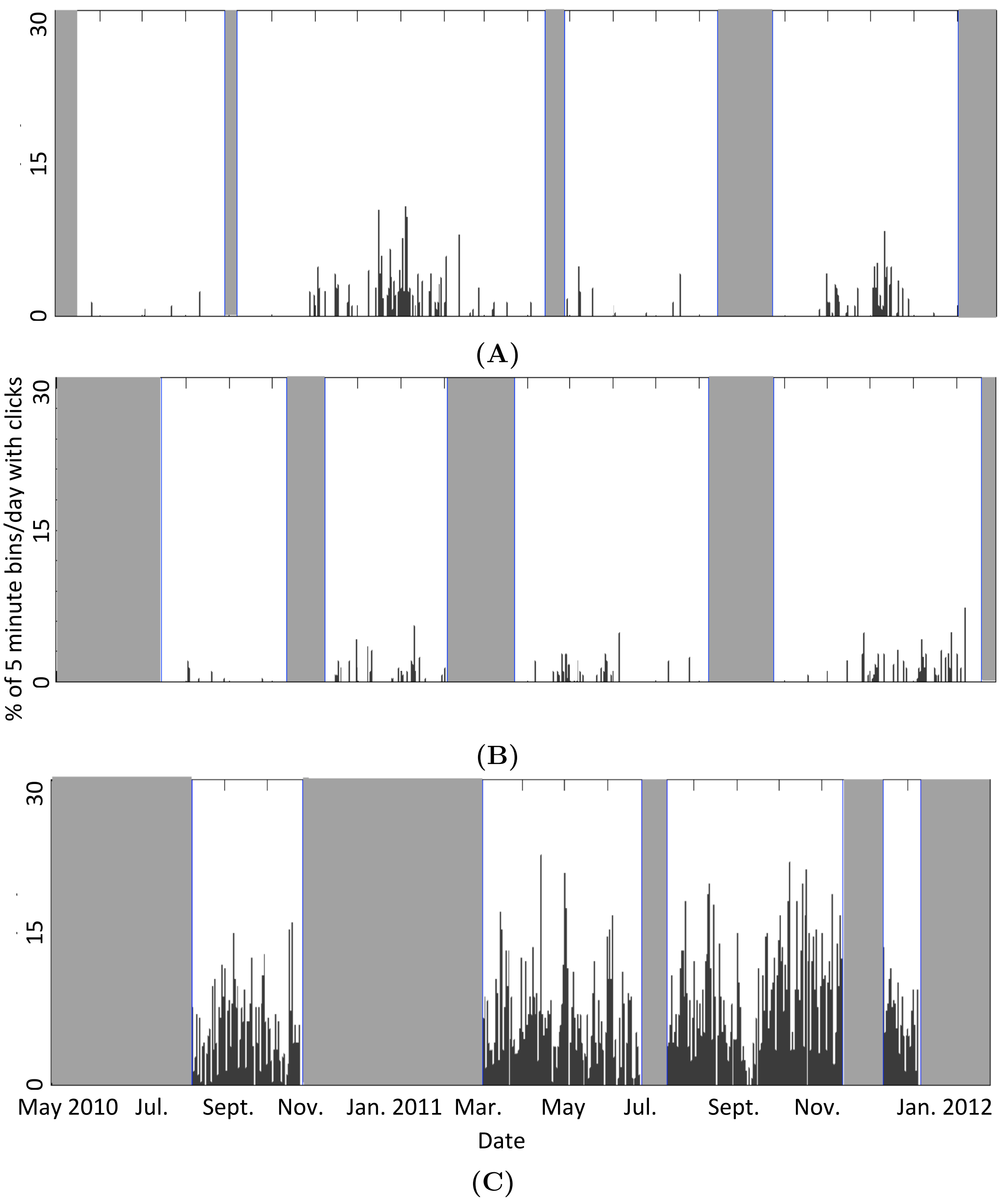


Figure 4.2: Time series of Cuvier's beaked whale detections as % of 5-minute bins per day at MC(A), GC (B) and DT(C). Gray indicates no recording effort. Same vertical scale as Figures 4.3 and 4.4 to allow comparison of detection rates.

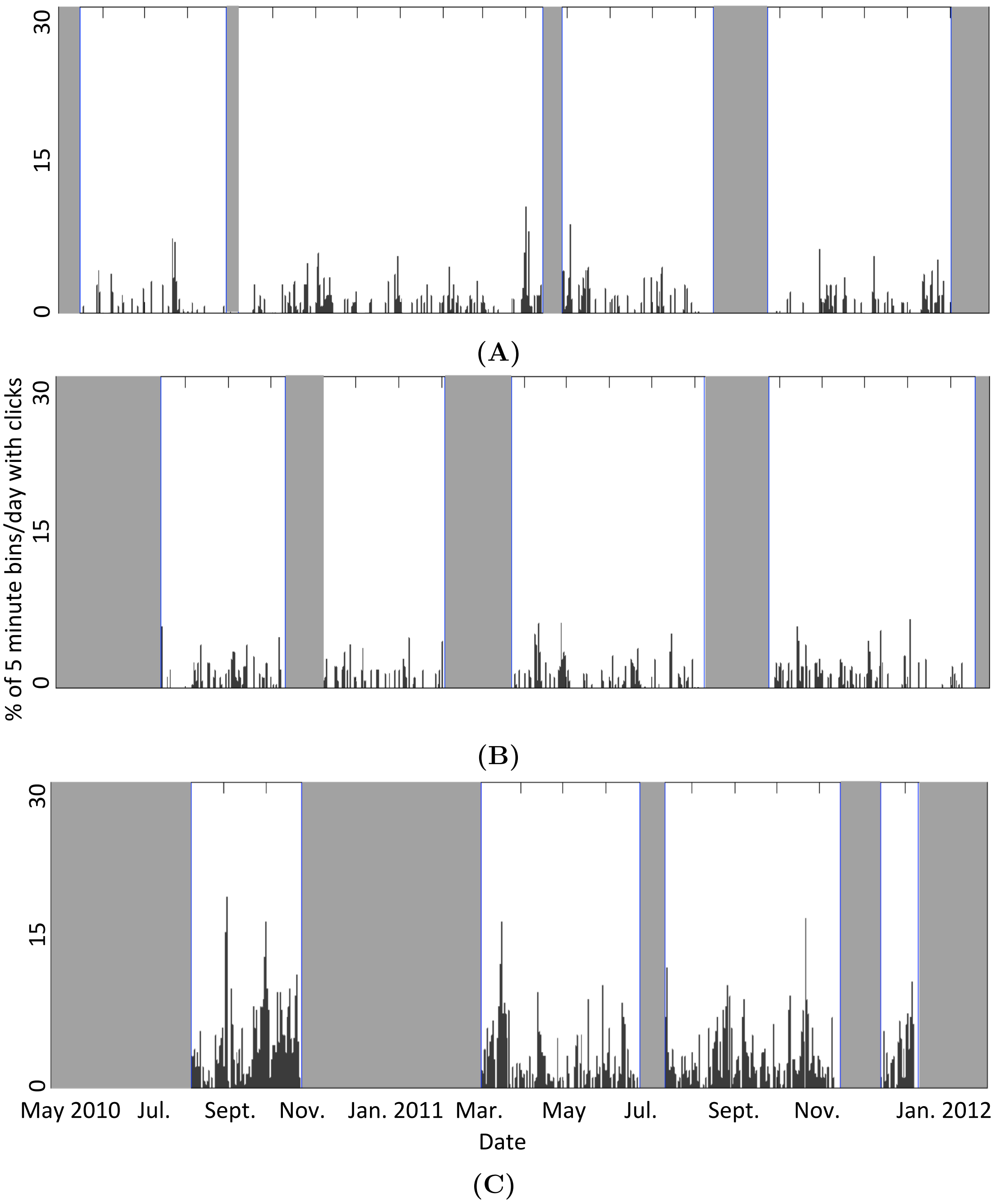


Figure 4.3: Time series of Gervais' beaked whales detections as % of 5-minute bins per day at MC(A), GC (B) and DT(C). Gray indicates no recording effort. Same vertical scale as Figures 4.2 and 4.4 to allow comparison of detection rates.

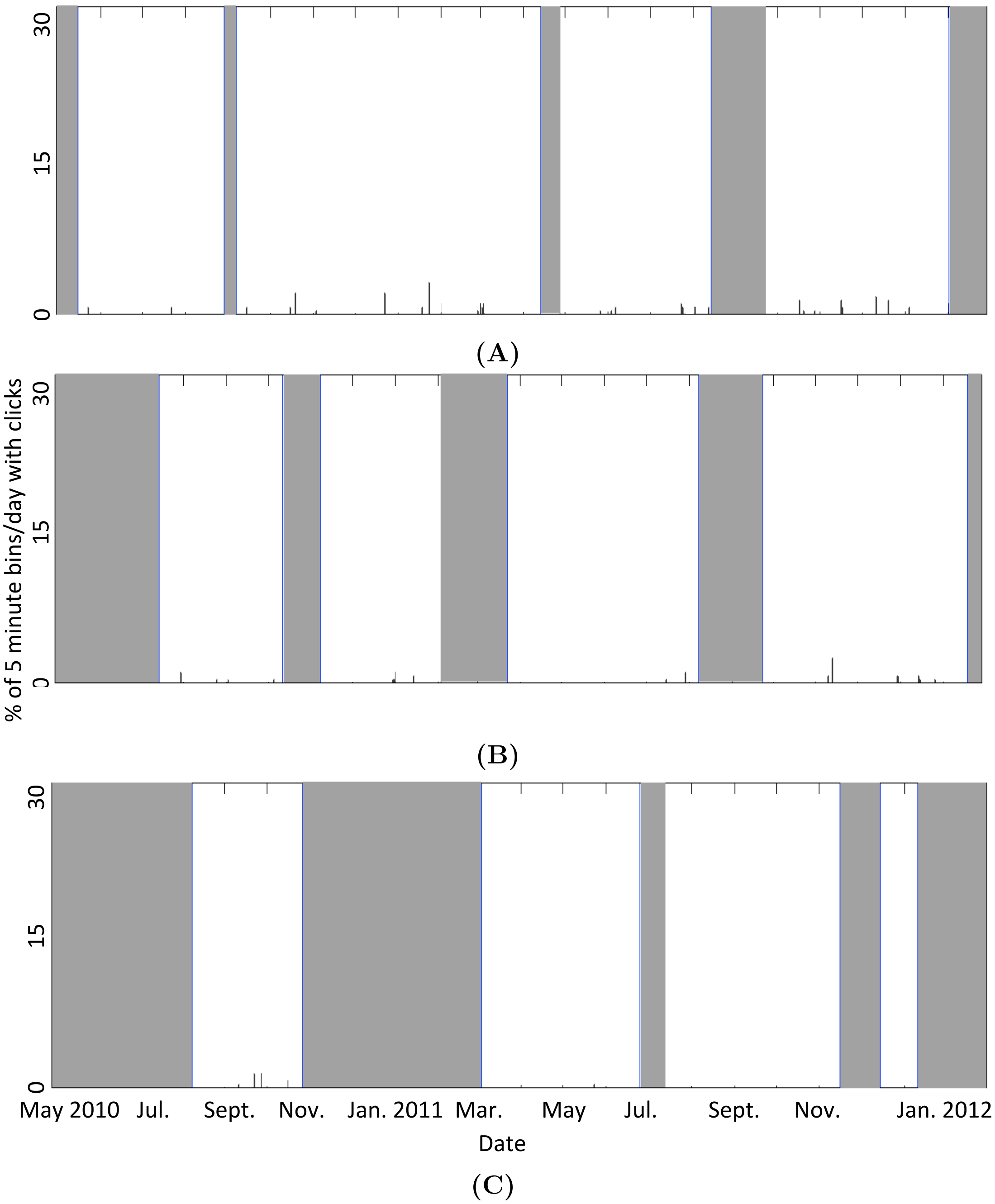


Figure 4.4: Time series of the unknown beaked whale signal BWG detections as % of 5-minute bins per day at MC(A), GC (B) and DT(C). Gray indicates no recording effort. Same vertical scale as Figures 4.2 and 4.3 to allow comparison of detection rates.

Table 4.1: Parameters indicating whether data set was zero-inflated.

Species-site	Time-period length	# time-periods with detections	% of time periods with 0
Zc-MC	1-days	94	82.7
Zc-GC	1-days	86	80.8
Zc-DT	5-day	84	0
Me-MC	1-days	205	62.3
Me-GC	1-days	184	58.9
Me-DT	4-day	84	0
BWG-MC	1-days	27	95.0
BWG-GC	1-days	15	96.7
BWG-DT	1-day	4	98.8

4.5 Results and Discussion of Trend Analysis

All tests were conducted using $p < 0.05$ unless otherwise noted.

4.5.1 Diel patterns

Detections of all three beaked whale species were tested for daily patterns (Tables 4.2, 4.3 and 4.4 and Figures 4.5, 4.6 and 4.7). Cuvier's beaked whales exhibited no diel patterns at GC and DT, but were detected more often at night at MC ($p < 0.001$). Gervais' detections were nocturnal at MC and DT and anti-crepuscular at MC and GC. BWG signals were nocturnal at MC and GC ($p < 0.001$), and anti-crepuscular at MC but crepuscular at DT. These complicated results do not clearly support or falsify the hypotheses that there would be no significant patterns for Cuvier's and Gervais' and nocturnal behavior for BWG.

Odontocetes in general often show differences in behavior between day and night, usually related to changes in foraging (Heithaus and Dill 2002). For surface-living species, including most dolphins, studies have shown behavior patterns that match the daily vertical migration of their prey. For example, when feeding during the daytime cetaceans may dive deeper to get to their prey, and often do more of their feeding at night when their prey comes closer to the surface (e.g. Benoit-Bird et al. 2003, Baird et al. 2005, Henderson 2010, Soldevilla 2010, Hodge 2011). Beaked whales, being deep-diving cetaceans, are likely to have different patterns because their prey do not come all the way to the surface at any time. However, many squids, including some deep-living species, do undergo daily vertical migration, moving to shallower depths at night (Watanabe 2006).

Table 4.2: Diel patterns of Cuvier's beaked whales by site. (-) indicates no significant pattern in that category.

Site	MC	GC	DT
Total # 5-min bins	810	455	6984
Day/Night p-values	Nocturnal <0.001	- 0.453	- 0.573
Crepuscular p-values	- 0.737	- 0.066	- 0.072

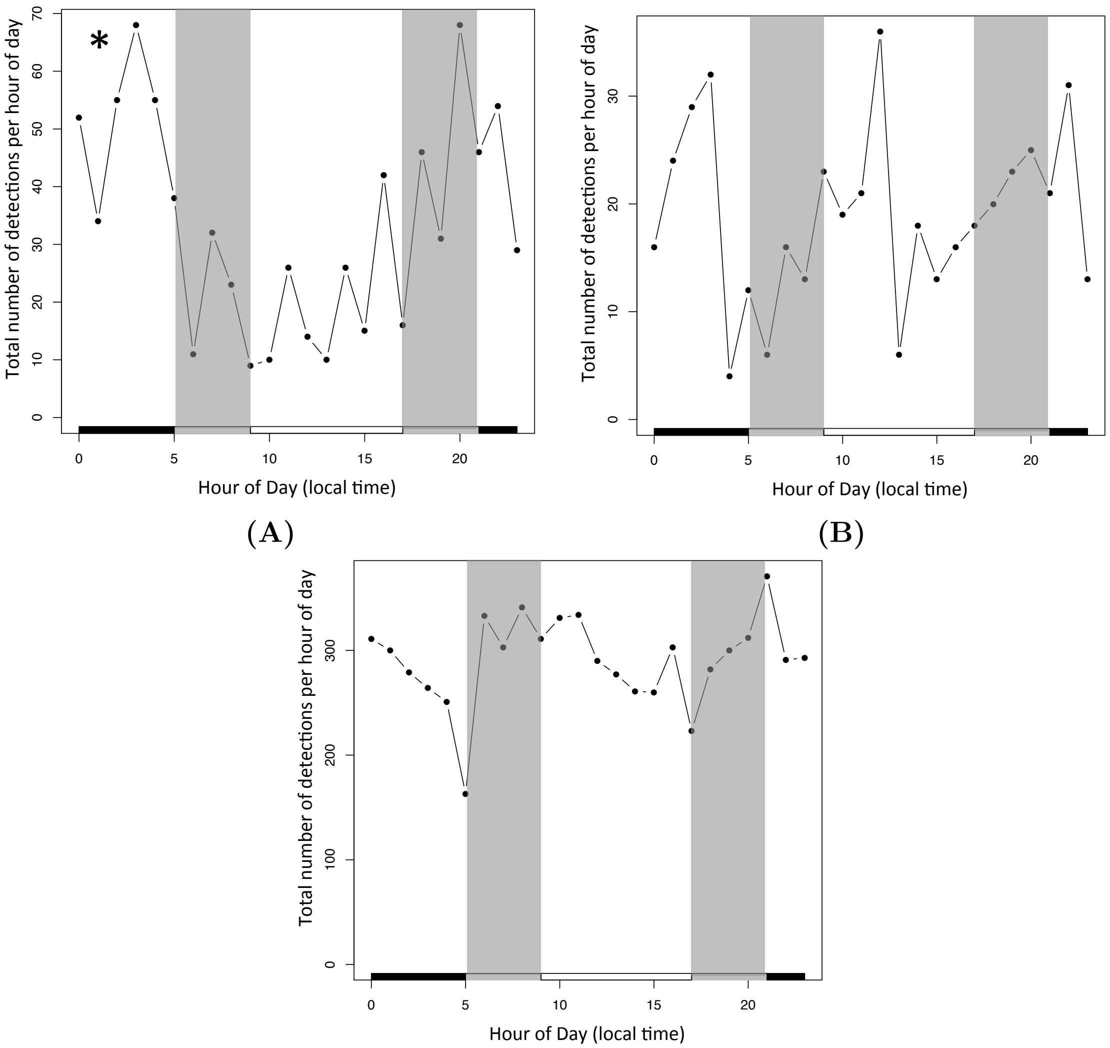
Table 4.3: Diel patterns of Gervais' beaked whales by site. (-) indicates no significant pattern in that category.

Site	MC	GC	DT
Total # 5-min bins	1217	1044	3142
Day/Night p-values	Nocturnal 0.039	- 0.337	Nocturnal 0.0257
Crepuscular p-values	Anti-crepuscular 0.012	Anti-crepuscular <0.001	- 0.233

Table 4.4: Diel patterns of BWG signal by site. (-) indicates no significant pattern in that category.

Site	MC	GC	DT
Total # 5-min bins	810	455	6984
Day/Night p-values	Nocturnal <0.001	Nocturnal <0.001	- 0.388
Crepuscular p-values	Anti-crepuscular 0.002	- 0.355	Crepuscular 0.004

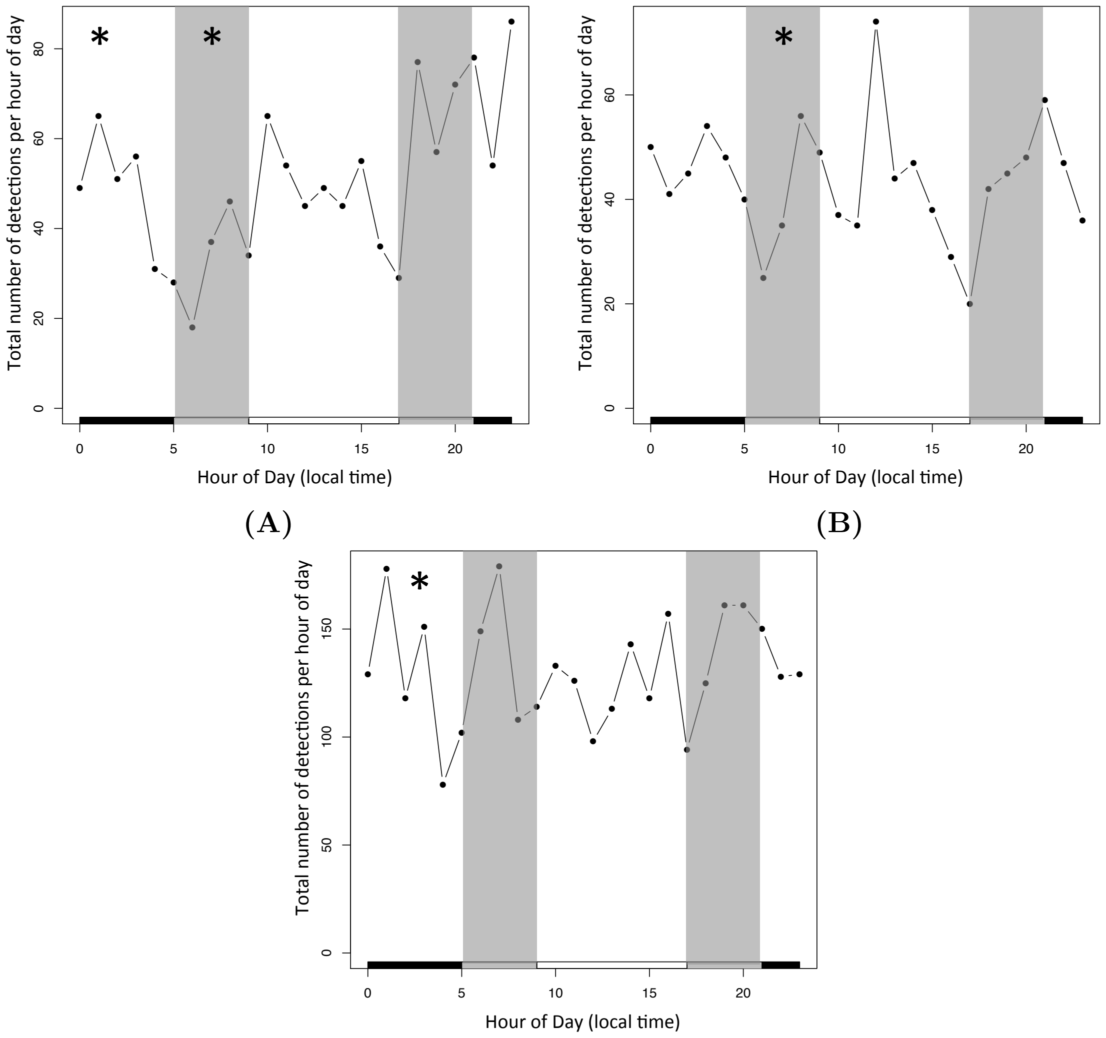
The diel activity of beaked whales have only been examined a few times, and the patterns are often not clear. For example, Schorr et al. (2010) looked at behavior of Blainville's beaked whales around Hawaii, and found that there was a significant difference in median dive depth between the day and the night, however the difference was small enough that there was likely no biological significance. Au et al. (2013) also looked at beaked whales in the main Hawaiian islands and found that more foraging took place at night, although the authors did not identify signals to species level.



(A) (B)

(C)

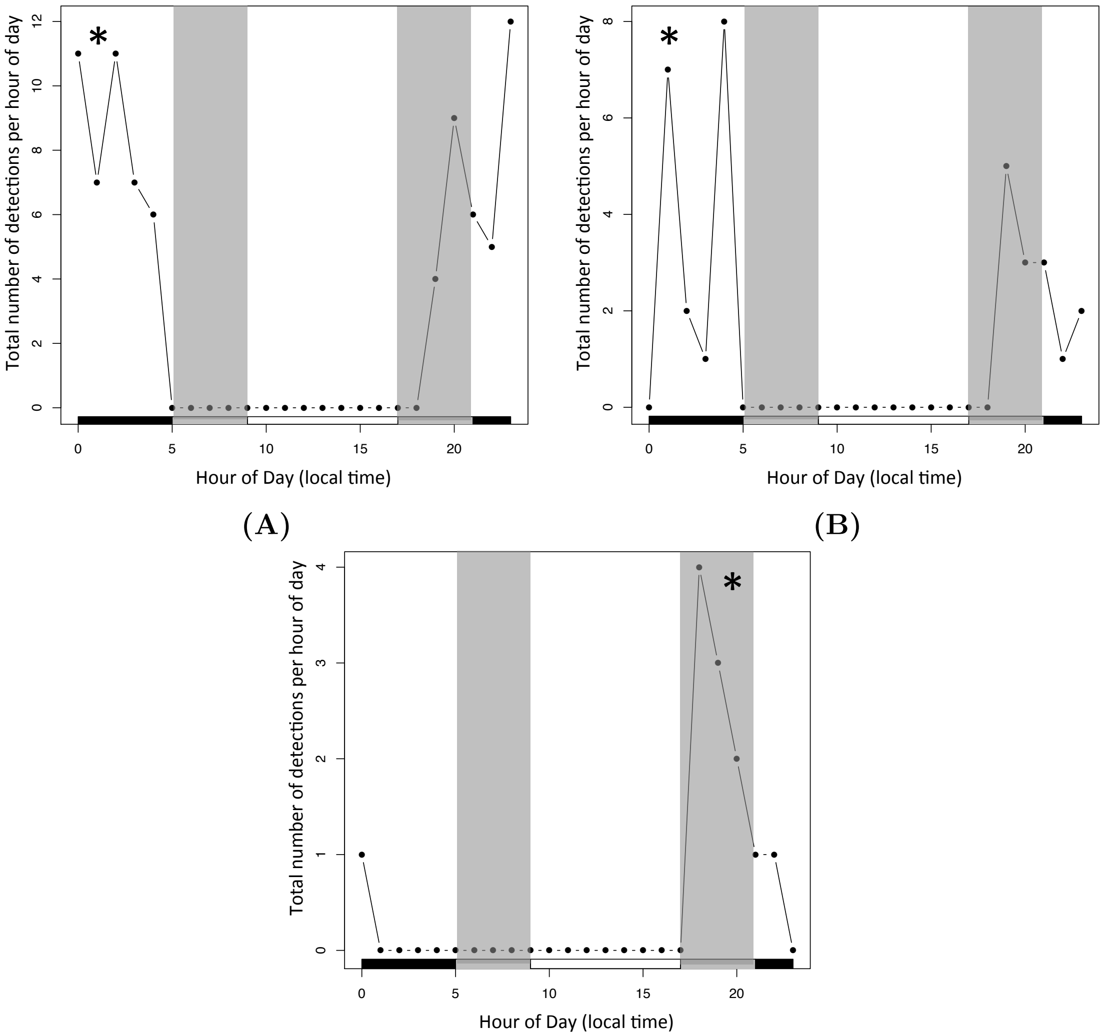
Figure 4.5: Detections of Cuvier's beaked whales per hour of the day (local time) at MC (A), GC (B), and DT (C). Color bar at bottom indicates day (white) and night (black) while vertical boxes indicate crepuscular (gray) periods. Note significant nocturnal activity at MC (A)(*).



(A) **(B)**

(C)

Figure 4.6: Detections of beaked whales per hour of the day (local time) for Gervais' beaked whales at MC (A), GC (B), and DT (C). Color bar at bottom indicates day (white) and night (black) while vertical boxes indicate crepuscular (gray) periods. Note significant nocturnal and anti-crepuscular activity at MC (A), anti-crepuscular activity at GC (B) and nocturnal activity at DT (C).



(A)

(B)

(C)

Figure 4.7: Detections of beaked whales per hour of the day (local time) for BWG (at MC (A), GC (B), and DT (C). Color bar at bottom indicates day (white) and night (black) while vertical boxes indicate crepuscular (gray) periods. Note significant nocturnal activity of the BWG signal at MC (A) and GC (B), and crepuscular activity at DT (C).

The differences in diel detection patterns between Gulf of Mexico HARP sites for Cuvier's beaked whales could be related to differences in the behavior of the prey species at those sites, or there could be other explanations. For example, Baird et al. (2008) used time-depth tags to identify behavioral differences for Cuvier's beaked whales between day and night, with more time spent at depth and more bounce dives performed in the daytime. The authors suggest this may relate to predator avoidance. Such differences in diving behavior may produce differences in acoustic behavior, particularly the duration of each encounter, which could be monitored using HARPs. The total duration of encounters and other details of acoustic patterns during night and day were not examined for this analysis.

This is the first analysis of Gervais' beaked whales' diel behavior because sightings and recordings of this species are very rare and monitoring for longer than a few hours has not been possible (Gillespie et al. 2009). As with Cuvier's beaked whales the increased nocturnal acoustic activity is most likely due to changes in behavior related to changes in prey location in the water column.

The nocturnal behavior of BWG is also likely related to foraging activity, which might increase at night as their prey moves toward the surface. Another possibility is that this species makes daily movements on and off the continental slope making them undetectable during the day when they are offshore. This extreme nocturnal pattern matches what was observed for another unknown species detected at multiple sites in the Pacific Ocean that has a very similar acoustic signal (McDonald et al. 2009, Baumann-Pickering et al. 2013), offering additional evidence that these two signal types might come from the same or similar species.

The conflicting results for BWG, which was crepuscular at DT and anti-crepuscular at MC, are likely due to the very small sample size of the DT dataset (12 observations) and the complete lack of detections during daytime hours at either site. In this case nine detections happened to occur around sunset, therefore the detections were classified as crepuscular, but a slight shift in how twilight and night were classified would shift them into the night category, making DT match with MC and GC by having nocturnal detections, not crepuscular. A larger sample size would clarify this relationship.

4.5.2 Seasonal trends

Beaked whale detections were tested for seasonal differences using non-parametric tests, and the patterns varied by species and site. There were no significant patterns for BWG at any site, probably due to the small number of detections.

For Cuvier's beaked whales there was no seasonal pattern at DT, but at MC there were significantly more detections in the winter (December, January, February) than in any of the other seasons, and there were more detections in the fall (September, October, November) than in the summer (June, July, August) (Figure 4.8 top). This increase in fall is likely due to the higher level of detections in November, which continued through the winter. Such a seasonal increase in the colder months is similar to the increase in sperm whale detections at this site during the fall, although shifted slightly later in the year.

A similar pattern was seen at GC, where the number of detections was significantly higher in winter and in spring than in summer or fall (Figure 4.8 bottom). Although there were relatively few detections in total, there were almost no detections in the summer and fall. Combined with the patterns at MC, this could suggest a general westward movement of Cuvier's beaked whales over the course of the cooler months. In general, there was an increase of Cuvier's beaked whale detections in the cooler (end of fall, winter, spring) months at the northern sites. This trend may indicate regular, seasonal movements of this species.

Seasonal patterns were also detected for Gervais' beaked whales at MC and GC, but not at DT (Figure 4.9). At MC there were significantly more detections in the spring months (March, April, May) than in the summer (June, July, August). However this only includes one partial spring (missing one week of March and two weeks of April), so the biological significance of this relationship is unclear and will not be discussed further. The mean number of detections for Gervais' beaked whales at GC was significantly higher in fall than in winter. This pattern is different from what was seen for Cuvier's beaked whales at MC and GC where the highest number of detections was in the winter. This suggests different annual cycles of movement between the two species, perhaps due to different prey preferences or

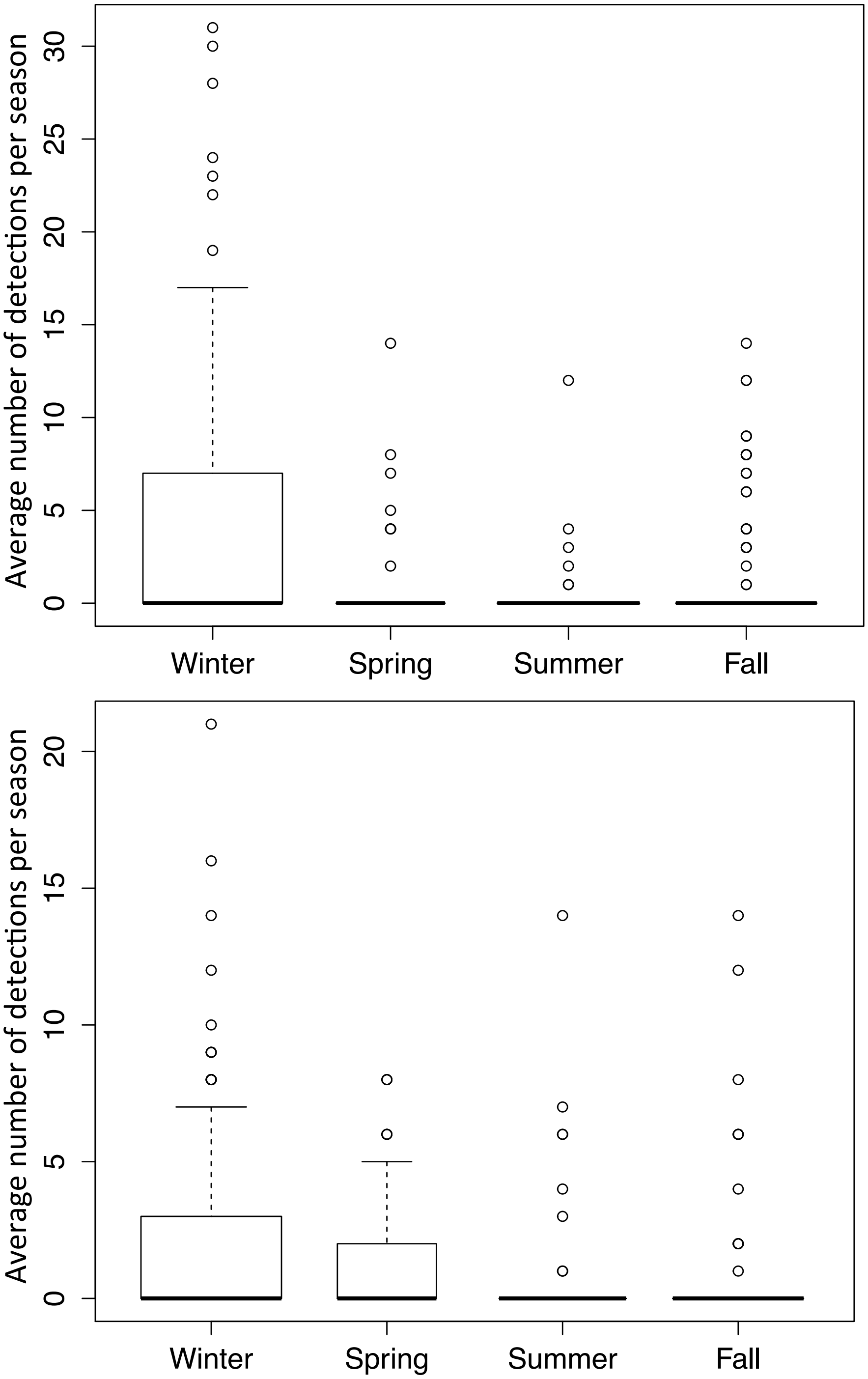


Figure 4.8: Box plot of Cuvier's beaked whale detections per season at MC (top) and GC (bottom). Top and bottom of boxes are at 75th and 25th percentiles; whiskers extend to 1.5 times the interquartile range. At MC the mean number of detections in winter was significantly ($p < 0.05$) higher than in all other seasons, and the mean number of detections in fall was significantly higher than in summer. At GC there were significantly more detections in winter than in summer of fall and also more in spring than in summer or fall.

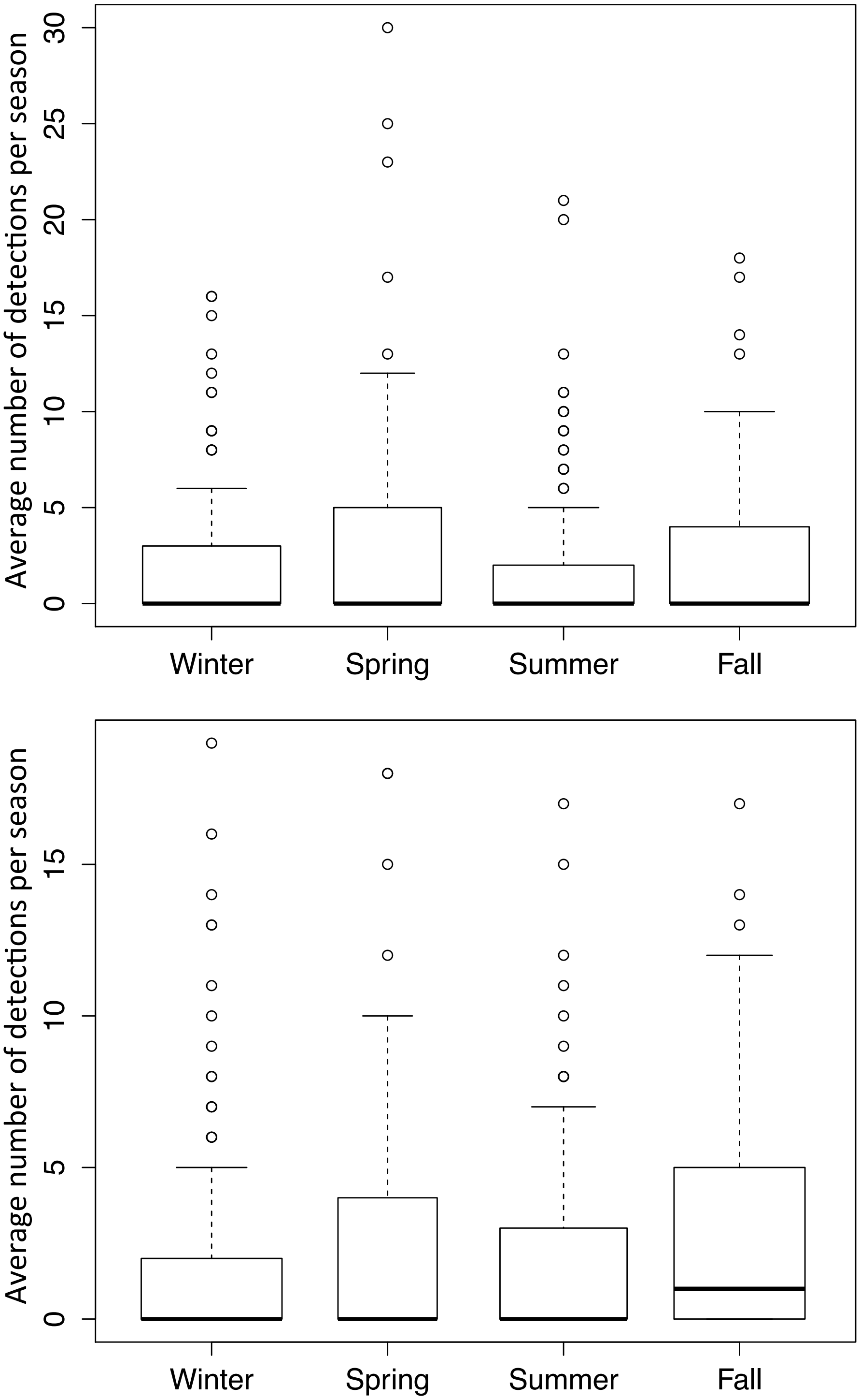


Figure 4.9: Box plot of Gervais' beaked whale detections per season at MC (top) and GC (bottom). Top and bottom of boxes are at 75th and 25th percentiles; whiskers extend to 1.5 times the interquartile range. At MC the mean number of detections in spring was significantly ($p < 0.05$) higher than in summer. At GC there were significantly more detections in winter than in fall.

other mechanisms that act to limit competition between the species.

Taken together the results of the analysis of Cuvier's and Gervais' seasonal trends do not support the hypothesis that there are no seasonal trends for beaked whales in the Gulf of Mexico, however the small number of seasons in the data set make the results less convincing. It is unlikely that seasonal differences in acoustic propagation have much effect on detection rates because their foraging dives, when they are detected on the HARPs, generally go well below the stratified surface layers.

There have only been a few previous investigations of seasonal trends of beaked whales. In general it is difficult to gather sufficient data for such analyses, primarily because of the challenges in detecting beaked whales visually, especially in rough weather. This can produce a bias in results due to poor visibility conditions being most common in the winter. Additionally, beaked whales are often found far from shore, therefore requiring significant effort to bring observers to their habitat, making long-term studies prohibitively expensive. The studies that have reported on seasonal presence of beaked whales usually rely on small samples of sighting data or records of stranded animals. Most analyses have shown no notable seasonal pattern. In one study in the Hawaiian islands and another in the Caribbean Sea Cuvier's beaked whales were sighted in all seasons of the year, but there were too few sightings overall to examine significance of seasonal variations (Miggnucci-Giannoni 1998, McSweeey et al. 2007, Baird et al. 2013).

With a larger data set and increased precision, Smith (2010) looked at sightings of Cuvier's beaked whales from ships of opportunities (regional ferries) and strandings in the Bay of Biscay, and found year-round presence throughout the region, but a northward shift in the summer months. This is similar to a pattern seen in the North Atlantic by MacLeod et al. (2004) who found that two beaked whale species, northern bottlenose whales (*Hyperoodon ampullatus*) and Cuvier's beaked whales, stranded more frequently in August-October and in November-July respectively. The authors suggested that this indicates a seasonal movement in and out of the region, perhaps as a mechanism to reduce competition between the two species. In the eastern North Pacific a year-round presence of

Cuvier's beaked whales was found based on strandings, but the sample size was too small for testing of seasonal variations (Mitchell 1968). It is important to keep in mind that inference based on strandings can be problematic because any seasonal difference in stranding rates may be due not to increased abundance, but to other factors. For example, there may be seasonal effects on the likelihood that a stranded animal reaches the shore or a change in the environment (e.g. storm frequency or alterations in currents) that causes more strandings to take place or to be recorded regardless of whether there is actually an increase in the number of animals in the region.

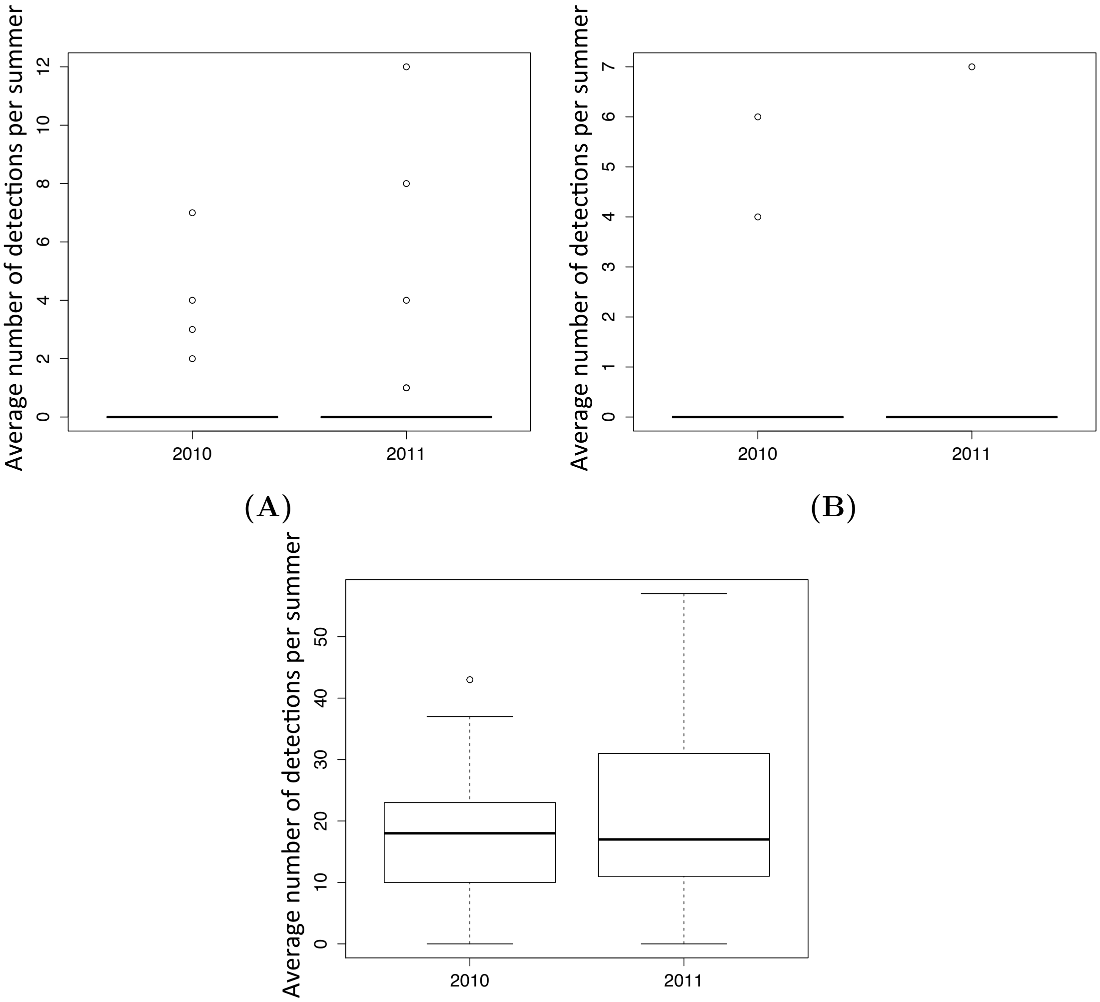
Baumann-Pickering et al. (2012) assessed seasonal patterns of detections of 11 beaked whale species in long-term acoustic data sets from multiple sites in the North Pacific. The authors found no strong seasonal pattern for most species, but some of the species were detected more frequently in one season in certain years or at certain sites. For example, at two sites in southern California there were more detections of Cuvier's beaked whale in the summer months, except one year when they were more common in the winter. Patterns like this lead Hildebrand et al. (2012) to suggest that instead of beaked whales exhibiting strong seasonal migrations, "local effects on prey abundance and preferred habitat structures likely drive most of their presence at a site."

The mild seasonal patterns detected in the Gulf of Mexico are similar to those seen for these species in other regions, being subtle and varying by site. The lack of any seasonal pattern at DT suggests that there might be a north-south movement, with Cuvier's and Gervais' beaked whales always being present toward the south (i.e. at DT), but expanding toward the north in the cooler months where they are detected at MC and GC. Two other possibilities are that these species undergo seasonal movements in an east-west or an onshore-offshore direction in the northern Gulf. All three of these movement patterns would result in seasonal differences in the ability to detect the animals, either because of their actually moving away from the HARPs, or by being less detectable because of changes in the acoustic propagation as they move to different areas around the instruments.

Researchers often attribute seasonal patterns in cetacean movement to changes in prey. Another option is that movements are related to social activities, such as breeding or calving. Both of these ultimate forces cannot be tested with the data that are currently available, but further study, such as measurements of local prey concentrations and observations of social behavior patterns, could clarify the cause of seasonal movements. If changes in prey are the major driving force, this would suggest that there is an annual cycle in prey abundance. Given that there is an annual wintertime peak in primary productivity in the Gulf of Mexico, and that other studies have shown that there is a multi-month lag between increased primary productivity and increased cetacean prey such as krill (e.g. Croll et al. 2005), it seems possible that there is a full year lag time between the increase in primary productivity and an increase in squid.

4.5.3 Oil-spill related trends

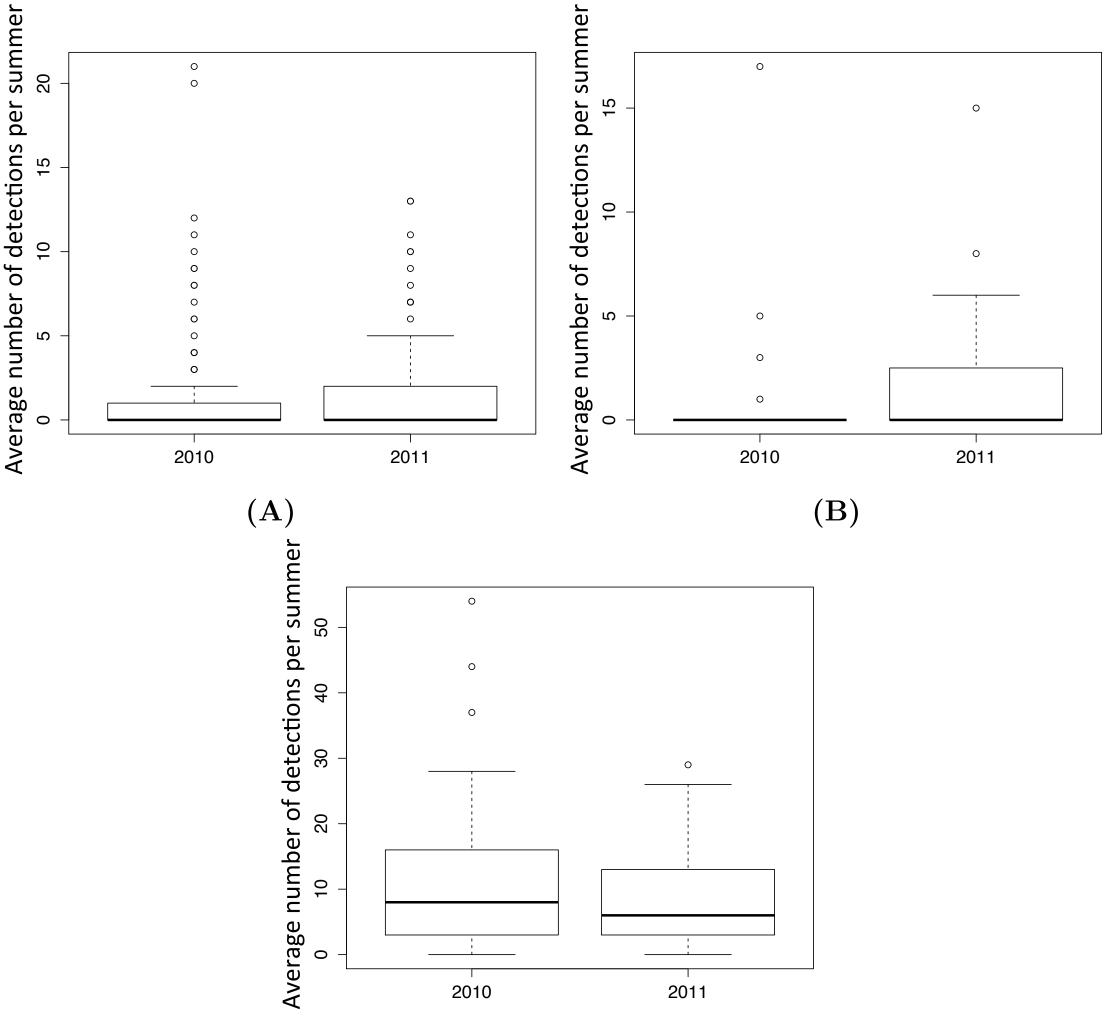
Detections of the three species during the summer of 2010, while the oil spill was underway, and the summer of 2011, one year after the spill, were compared with the same days of the year included in both samples. The only significant difference was for BWG at DT, which showed that there were more detections in 2010 than 2011, however the extremely small sample size of non-zero measurements (2010: $n = 3$, 2011: $n = 0$) makes this result questionable (Figures 4.10, 4.11 and 4.12).



(A) **(B)**

(C)

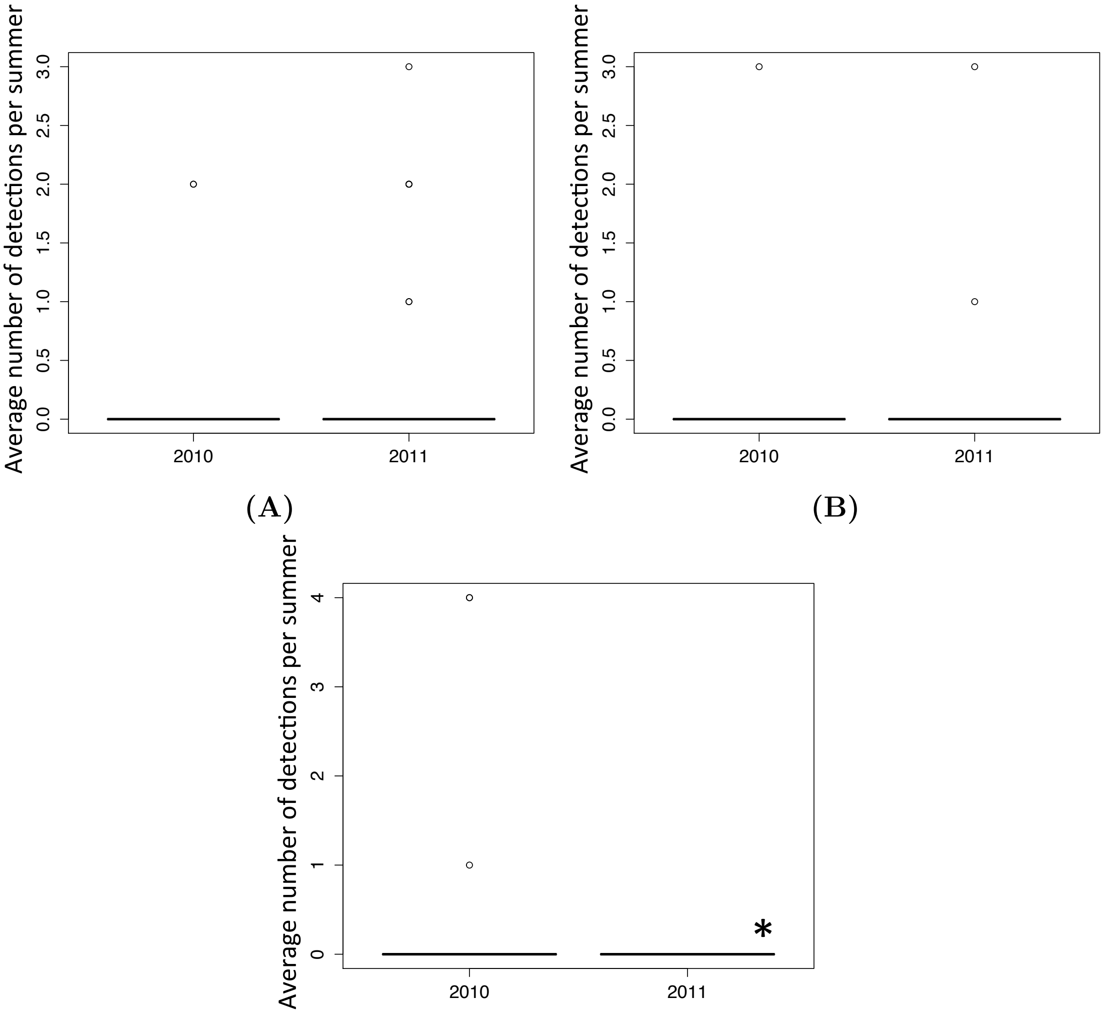
Figure 4.10: Box plots of Cuvier's beaked whale detections in the summers of 2010 and 2011 at MC (A), GC (B) and DT (C). Top and bottom of boxes are at 75th and 25th percentiles; whiskers extend to 1.5 times the interquartile range. There is no significant difference between the two years at any site. Note: at MC and GC the mean is zero in both years because there are so few detections.



(A) **(B)**

(C)

Figure 4.11: Box plots of Gervais' beaked whale detections in the summers of 2010 and 2011 at MC (A), GC (B) and DT (C). Top and bottom of boxes are at 75th and 25th percentiles; whiskers extend to 1.5 times the interquartile range. There is no significant difference between the two years at any site.



(A) (B)

(C)

Figure 4.12: Box plots of the detections of the unknown beaked whale (BWG) signal in the summers of 2010 and 2011 at MC (A), GC (B) and DT (C). Top and bottom of boxes are at 75th and 25th percentiles; whiskers extend to 1.5 times the interquartile range. There is a significant difference between the two years at DT (*), however the sample size of non-zero measurements is extremely small (2010: n = 3, 2011: n = 0), making this result questionable. Note: at al sites the mean is zero in both years because there are so few detections.

Results of testing of means and slopes during the period of the spill and the subsequent months, separated by various breakpoints, at sites MC and GC are tabulated below (Tables 4.5 and 4.6). No significant differences were detected for BWG, likely because the sample size was extremely small, therefore no table is included.

Table 4.5: Comparison of means and slopes for Cuvier's beaked whale detections before and after breakpoints separating period of oil spill from post-oil spill at MC and GC. (+) indicates a significantly higher mean after the breakpoint, (same) indicates no difference between periods ($p < 0.05$). When the difference between slopes was significant the value of the slope is included in the table. Data collection at GC did not begin until July 15. Note: very small sample size at both sites.

Breakpoint	Jul 15	Aug 1	Aug 15	Sep 1	Sep 15	Oct 1	Oct 15	Nov 1
MC:								
mean after	same	same	same	+	+	+	same	+
slope before	same	same	0	0	0	0	same	0
slope after	same	same	0.03	0.05	0.09	0.04	same	-0.03
GC:								
mean after	NA	same	same	same	same	+	+	+
slope before	NA	0	same	same	same	0	same	same
slope after	NA	-0.16	same	same	same	0.03	same	same

Table 4.6: Comparison of means and slopes for Gervais' beaked whale detections before and after breakpoints separating period of oil spill from post-oil spill at MC and GC. (+) indicates a significantly higher mean after the breakpoint, (-) indicates a significantly lower mean after the breakpoint, (same) indicates no difference between periods ($p < 0.05$). When the difference in slopes was significant the value of the slope is included in the table. Data collection at GC did not begin until July 15.

Breakpoint	Jul 15	Aug 1	Aug 15	Sep 1	Sep 15	Oct 1	Oct 15	Nov 1
MC:								
mean after	same	-	+	+	+	+	+	+
slope before	0	same	0	same	same	same	same	same
slope after	-0.9	same	0.08	same	same	same	same	same
GC:								
mean after	NA	same	+	same	same	same	same	same
slope before	NA	-0.39	same	same	same	same	same	same
slope after	NA	0.21	same	same	same	same	same	same

For Cuvier's beaked whales the sample size before the breakpoints at site MC was at most four non-zero measurements, and at GC was at most six non-zero measurements, so despite the statistical significance of the results, the differences in slopes may not be biologically significant. At MC there is an increase of detections during the winter (November - February) of 2010/2011, which appears to be repeated in the winter of 2011/2012 (see Figure 4.2). This potentially season-related increase in detections influences the trends of the post-breakpoint data set, but may or may not be related to the impact of the DH oil spill. Additional data will help to confirm whether this seasonal pattern is ongoing. At GC there also may be a seasonal pattern with low detection rates during the summer/early fall months, which influences the slope for the October 1 breakpoint because the beginning of that time period includes only zeros but the number of detections increases from there.

For Gervais' beaked whale the gap between deployments at the end of August had a notable impact on the overall trends of detections of the two periods when that gap fell at the end of one time period (July 15 breakpoint) or the beginning of the other (August 15 breakpoint). The influence of this gap was not seen in the sperm whale data set because of the higher number of samples, and in the case of Cuvier's beaked whale the number of samples was too low for the gap to be important. At GC the non-zero sample size of Gervais' detections for analysis of the August 1 breakpoint was small, so the significant difference in slopes there is heavily impacted by the few positive measurements.

In general there were so few detections of beaked whales at MC and GC during the period of the DH oil spill and in the following summer that the results do not provide a reliable indication of the possible impacts of the spill, and although there are statistically significant results, they should be treated with caution and not assumed to either support or falsify the original hypothesis of decreased detections during the spill.

4.6 Results and Discussion of GAMs and ZINB models

Modeling of each species of beaked whale at each site had to be treated separately because of variations in data quality and quantity. At MC and GC the data for Cuvier's and Gervais' beaked whales were strongly zero-inflated, and were therefore modeled using the ZINB process. However, both species were detected frequently at DT, therefore they were modeled using a standard GAM procedure. The unknown beaked whale-like signal (BWG) was detected too infrequently for habitat modeling at any site (for details of zero inflation see Table 4.1). Because the response variable was periods of time with echolocation clicks, which were generated primarily during foraging dives, these models are likely to address aspects of foraging ecology such as processes that increase prey population abundance or density. Although these models are based on analysis of conditions at a single location, because of the dynamic, fluid nature of the ocean environment the "habitat" characteristics at a single point will change over time as different water masses move past the HARPs. This allows us to assess the relationships with varying environmental conditions without needing to sample across a large space. In general the results support the hypothesis that sea surface height anomaly (SSHA) is an important parameter for identifying beaked whale habitat, suggesting that beaked whales are more likely to be found in association with mesoscale features such as warm and cold-core rings. The distance to the nearest thermal front, however, was only included in one out of six of the best fit models, and is therefore not as likely to be a defining feature of beaked whale habitat.

4.6.1 Cuvier's Beaked Whales

Cuvier's beaked whale detections were modeled using a GAM at DT and a ZINB GLM at MC and GC (for details of methods, see section 2.5). Model details are tabulated in Table 4.7.

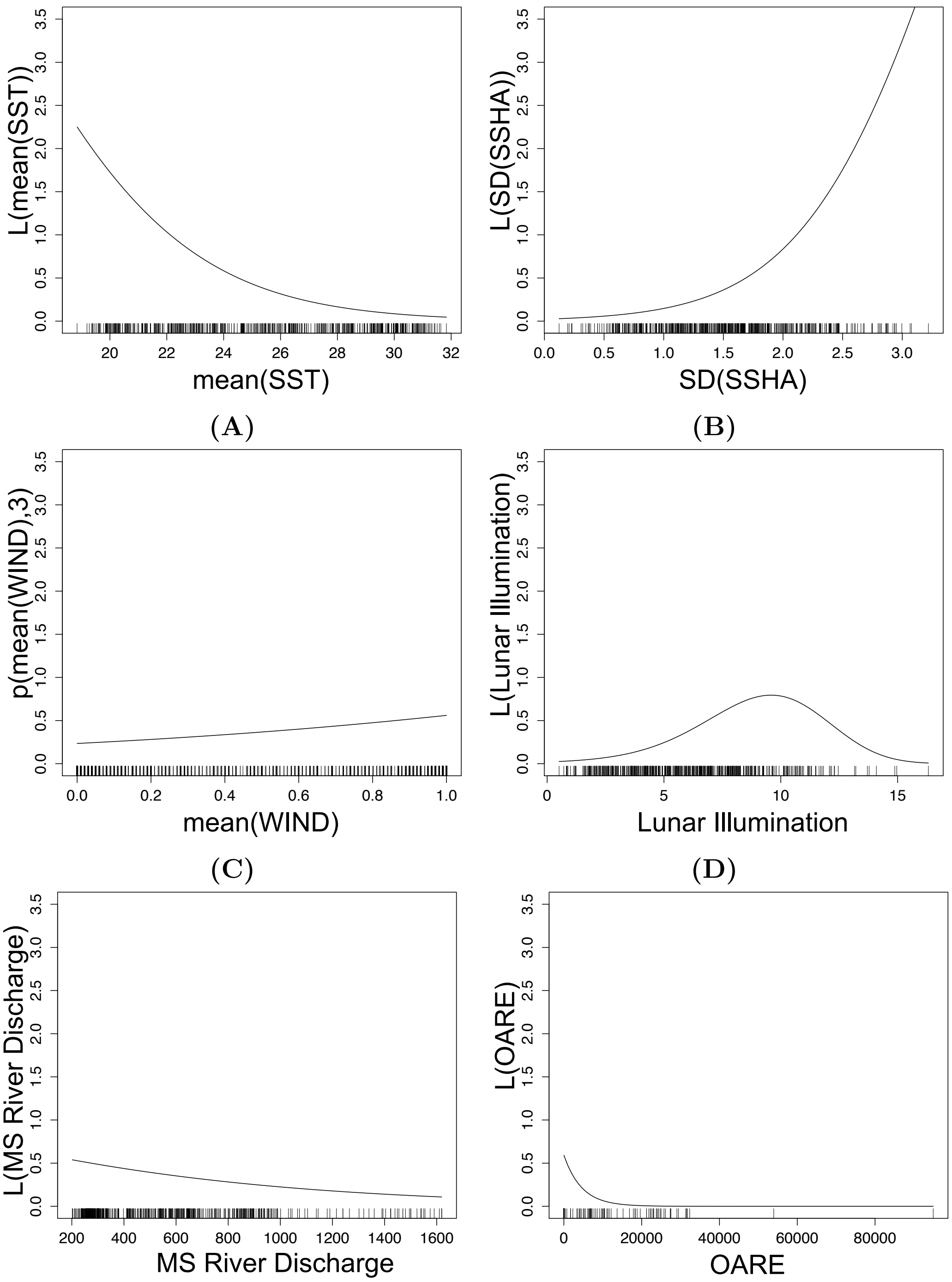
Table 4.7: Parameters for habitat models of Cuvier's beaked whales. (s) indicates a smooth function in the GAM, with estimated degrees of freedom in parentheses; (L) indicates a linear function, (p) indicates a polynomial, with power in parentheses.

Site	MC	GC	DT
R library/ function	pscl/zeroinfl	pscl/zeroinfl	mgcv/gam
Tweedie p-parameter	NA	NA	1.11
Selected model parameters	counts: L(mean(SST)) + L(SD(SSHA) + p(mean(WIND),3) + L(OARE) zeros: L(mean(SST)) + L(SD(SSHA)) + p(mean(WIND),3) + L(LUIL) + L(MSRD)	counts: L(mean(SST)) + L(mean(SSHA)) + p(NOIS40Hz,3) zeros: L(mean(SST)n) + L(mean(SSHA)) + p(NOIS1kHz,2)	s(mean(SST),2.77) + s(mean(SSHA),2.11) + s(SD(SSHA),2.62) + s(SD(SST),3) + L(mean(WIND)) + L(NOIS40Hz)
% Deviance explained	16.9	7.36	43.7

Cuvier's beaked whales at MC

At MC a ZINB model was used because of the high percentage of zeros in the data (82.7%), and the final models (zeros and counts) included seven parameters. The partial fits of those parameters are shown in Figure 4.13. The downward trend in the relationship with mean sea surface temperature (mean(SST)) (subfigure 4.13(A)) indicates a preference for cooler temperatures, which are generally encountered during the late fall and winter in the Gulf of Mexico. This finding corresponds to the seasonal trend of increased detections in the fall and winter months (see subsection 4.5.2). The inclusion of mean(SST) in the model should remove much of the variability due to seasonal fluctuations in other parameters. As described in the subsection on seasonal trends (4.5.2), there have been a few prior studies of beaked whale seasonality, which suggest that regular seasonal movements may be possible for this species.

In subfigure 4.13 (B) the partial fit of the standard deviation of sea surface height anomaly (SD(SSHA)) follows an increasing trend, which suggests that these



(A) **(B)**

(C) **(D)**

(E) **(F)**

Figure 4.13: Modeled partial fits of environmental parameters included in best model of Cuvier's beaked whale detections at MC. (p) indicates a polynomial function in the GLM, with degree in parentheses; (L) indicates a linear function. Error bars not estimated using ZINB method. (A) mean of sea surface temperature (SST), (B) standard deviation of sea surface height anomaly (SSHA), (C) mean of wind speed (WIND), (D) lunar illumination, (E) Mississippi River outflow and (F) area of surface oil (OARE).

animals prefer to be located in regions of high SSHA variability. These conditions would be found along the edges of currents and mesoscale features like eddies or warm-core rings. A previous study in the Gulf of Mexico found that "squid-eaters" (including beaked whales, *Kogia* spp. and an assortment of Delphinids) were often found in the periphery of anti-cyclonic, warm-core features (Davis et al. 2002). The biological significance of this parameter relates in general to the physical concentration of prey in the center or around the edges of oceanographic features with a measurable SSHA signature. No other previous studies of beaked whale habitat have included SSHA, but the inclusion of this parameter in this model, and in the models for this species at GC and DT, indicates that it is an important characteristic of Cuvier's beaked whale habitat and should be taken into account in future analyses.

Four other parameters were included in the best fit model, however the relative importance of these was small compared to the first two parameters, as illustrated by the strength of the partial fit curves in 4.13 (C-F). The partial fit of mean wind speed (WIND) shows an increase with a peak around nine meters per second followed by a decrease at higher speeds (Figure 4.13(C)). This trend is very different from what was seen for sperm whales at DT and MC where WIND was also included in the best fit model. Although windspeeds are related to upwelling, primary productivity and ultimately populations of deep-diving cetacean prey, the variability in the modeled partial fits indicates that the relationships are complicated and not easily modeled. Another parameter of lesser importance was lunar illumination (D), which shows a mild positive trend, suggesting an increase of foraging activity during the full moon. Such trends have been suggested in visually hunting odontocetes, which suggests that this species might hunt visually when the conditions are right (e.g. Benoit-Bird et al. 2009). Mississippi River discharge (E) also has a mild relationship, with the negative slope indicating a potential decrease in detections during periods of high river flow, which is generally in the spring and early summer. This reinforces the seasonal patterns of decreased detections during the spring and summer relative to the fall and winter, described in subsection 4.5.2.

The final parameter, a measure of total surface area of oil from the DH spill for the entire northern Gulf (OARE, subfigure 4.13 (F)), shows a rapid decline for all positive values, indicating a preference for the no-oil period. It is important to note that the majority of detections occurred during the no-oil period, when OARE is zero. However, the scale of this parameter is also very small, suggesting that the effect of the surface oil on the presence or abundance of Cuvier's beaked whale at MC, or the ability to assess that effect with the given data set, is limited.

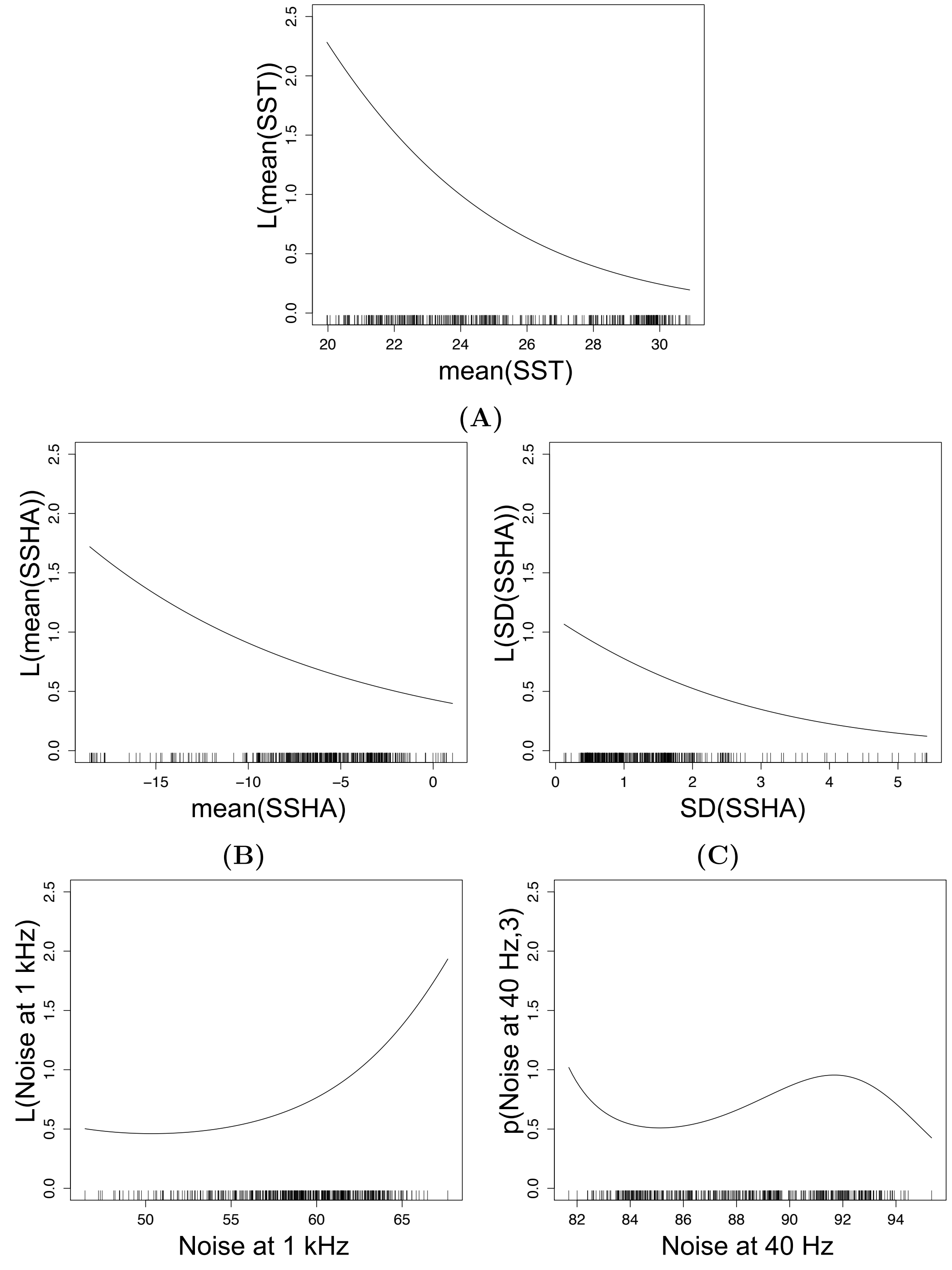
In general this model for Cuvier's beaked whales at MC does explain a relatively large percentage of the deviance (16.9%) relative to models from other studies (e.g. Becker et al. 2010), hsowever the importance of four of the included parameters is minimal as determined by comparison of the scale of the partial fits. Most previous studies have often found a relationship with mean(SST), and these results also support the importance of SST, but also show the significance of SSHA when assessing potential beaked whale habitat.

Cuvier's beaked whales at GC

The best ZINB models for Cuvier's at site GC (zeros and counts) included five parameters (see Table 4.7). The plots of the partial fits to those parameters are shown in Figure 4.14, and begin with the linear fit of mean(SST) (A). Similar to MC there was a negative trend, indicating a preference for cooler water. As was the case at MC, this reinforces the findings of the seasonal analysis (subsection 4.5.2), where it was shown that there were significantly more detections in the cooler months (fall and winter).

There was also a negative slope in the relationship with mean(SSHA)(B), which suggests a preference for waters with a lower sea surface height, such as the centers of cold-core rings. A similar negative slope was seen for SD(SSHA)(C), which is opposite of what was seen at MC above.

Subfigure (D) shows the positive relationship with noise at 1 kHz. This parameter is directly related to windspeed, therefore these results may indicate a preference for windier environments. However, as was shown with the model results for Cuvier's at MC and sperm whales at MC and DT, the connection between deep-diving cetacean detections and 1 kHz noise or windspeed is complicated, and the



(A)

(B) **(C)**

(D) **(E)**

Figure 4.14: Modeled partial fits of environmental parameters included in best model of Cuvier's beaked whale detections at GC. (p) indicates a polynomial function in the GLM, with degree in parentheses; (L) indicates a linear function. Error bars not estimated using ZINB method. (A) mean of sea surface temperature (SST), (B) mean of sea surface height anomaly (SSHA), (C) standard deviation of SSHA, (D) noise at 1 kHz, (E) noise at 40 Hz.

varied partial fit curves make interpretation of this relationship difficult.

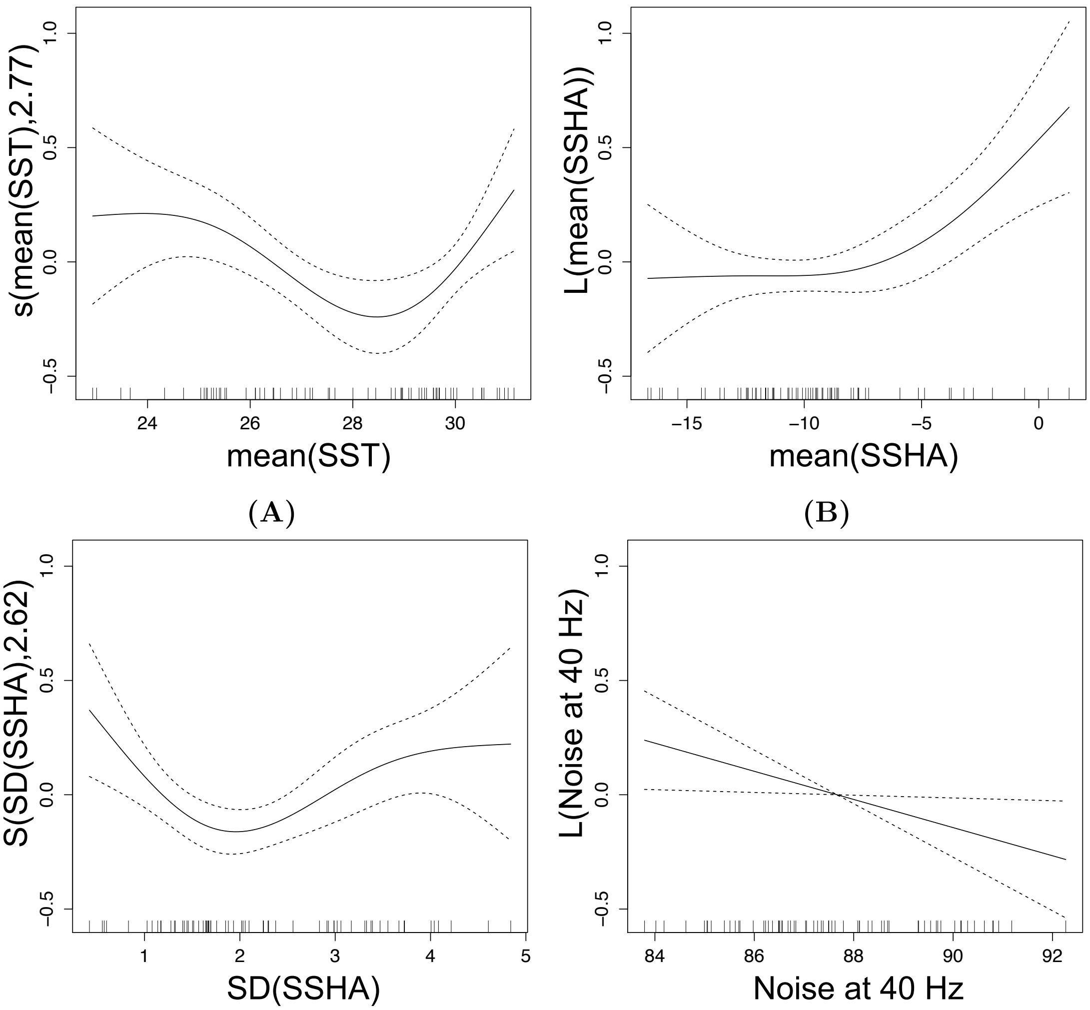
The final parameter included in this best fit model was noise at 40 Hz (E), which is primarily a metric for seismic air-gun pulses, and it is highly variable over time at GC (see Figure 2.7). Subfigure 4.14 (E) shows a sideways “S” shaped polynomial fit, with a decrease until about 85 dB, followed by an increase until about 92 dB, and then another decrease. This complicated relationship is unexpected, and difficult to interpret because there is no clear biological explanation for why beaked whales might prefer a specific mid-range of noise levels at this frequency.

Overall the relative importance of these five parameters was similar, based on qualitative comparison of the scope of the curves shown in Figure 4.14. This contrasts with the results from MC where two parameters (mean(SST) and SD(SSHA)) were more important to the model than the other four parameters. However, this model explains only 7.36% of the deviance from the null model, so the overall predictive power is low.

Cuvier’s beaked whales at DT

When the detections of Cuvier’s beaked whale at DT were binned by five days to avoid autocorrelation, there was at least one detection in every bin, so a standard GAM method could be used. The plots of the partial fits from the best model, which included four parameters, are shown in Figure 4.15.

Like the other two sites the model for Cuvier’s beaked whale detections at DT also included mean(SST) (A), but the shape of the smooth was different from the relationship observed at the other two sites, having a “U” shape, with a minimum around 28.5 degrees. The low point does occur when there were only a few detections, so a larger sample size, with better coverage across the seasons, might change the shape. Considering the width of the error bars it is possible that there is little or no relationship between the Cuvier’s detections at DT and mean(SST). The deviance explained by this model (43.7%) was much higher than the models from the other two sites, so the relationship shown here may be closer to the truth.



(A) **(B)**

(C) **(D)**

Figure 4.15: Modeled partial fits of environmental parameters included in best model of Cuvier's beaked whale detections at DT. (s) indicates a smooth function in the GAM, with estimated degrees of freedom (edf) in parentheses; (L) indicates a linear function. Rug plot along bottom indicates location of detections. (A) mean sea surface temperature, (B) mean sea surface height anomaly, (C) standard deviation of sea surface height anomaly, (D) noise at 40 Hz.

Figure 4.15 (B) shows the smooth of mean(SSHA), which is nearly horizontal up to -8, and then increases at larger values. The majority of data points are in the horizontal region, but the error bars are fairly consistent up to the highest values, confirming that this is a good fit to these data. The trend suggests some preference for areas of higher SSHA, such as near and in the Loop Current. SD(SSHA) was also included in the best model, which shows a "U" shaped smooth in subfigure (C), with a minimum around two centimeters. This indicates a preference for areas with low variability in SSHA, such as might be found farther from mesoscale features such as eddies or the edge of the loop current. However, the flaring in the error bars at the right end of the figure, due to the small number of points at the extreme, shows that the strength of the trend may be weak.

The final parameter included in the best model was the metric of noise at 40 Hz (E). The negative linear relationship to Cuvier's detections, suggests avoidance of seismic air-gun pulses.

4.6.2 Gervais' beaked whales

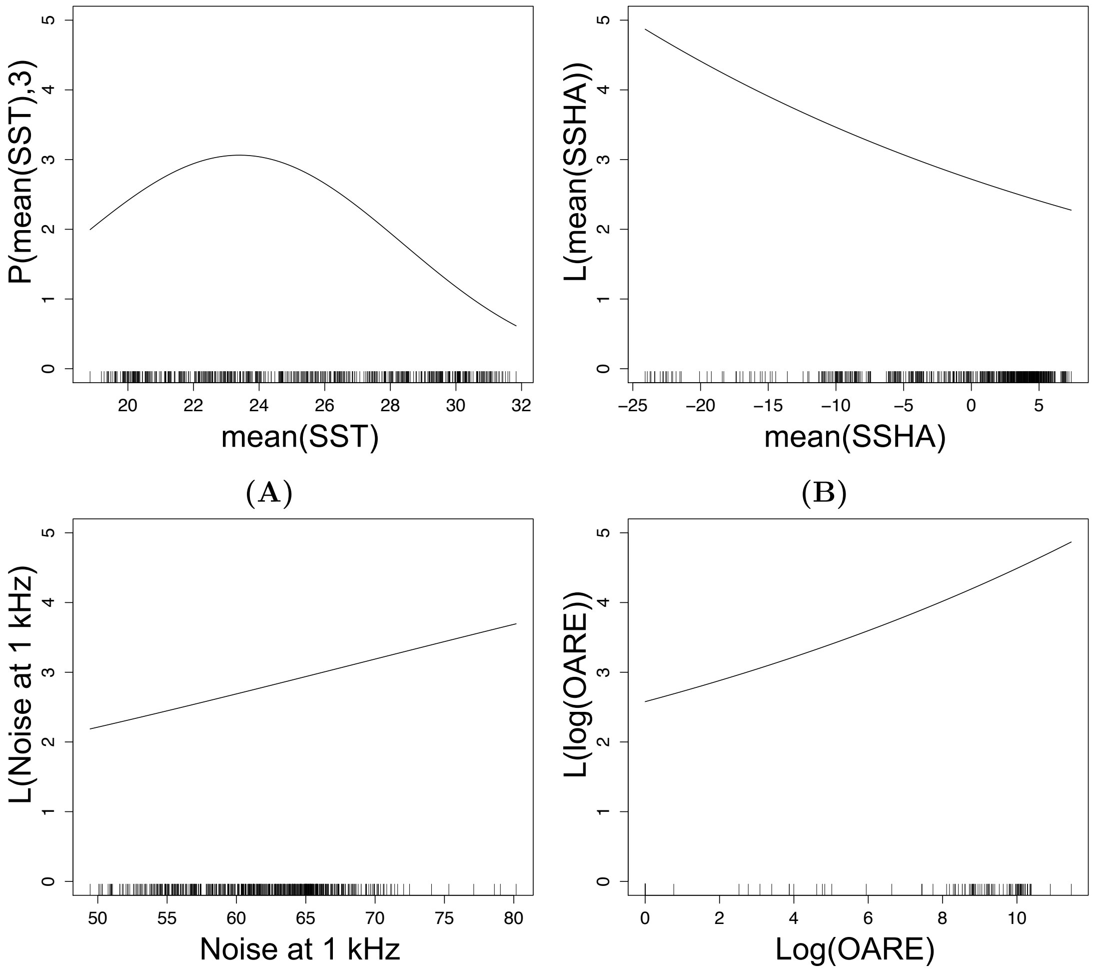
The habitat models for Gervais' beaked whale are presented according to site below (Table 4.8). As for Cuvier's beaked whale a GAM was used for detections from DT while a ZINB model was used for detections from MC and GC.

Table 4.8: Parameters for habitat models of Gervais' beaked whales. (s) indicates a smooth function in the GAM, with estimated degrees of freedom in parentheses; (L) indicates a linear function, (p) indicates a polynomial, with power in parentheses.

Site	MC	GC	DT
Model Type	Zero-inflated GLM	Zero-inflated GLM	GAM
Tweedie p-parameter	NA	NA	2
Selected model parameters	counts: p(mean(SST),2) +L(mean(SSHA)) + L(log(OARE)) zeros: p(mean(SST),2) + L(NOIS1kHz)	counts: L(DISF) zeros: L(mean(SST)) + L(SD(SSHA)) + p(NOIS40Hz,3) + p(NOIS1kHz,2)	s(Date,1.71) + L(mean(SST)) + s(SD(SST),1.42) + s(BOAT,1.99)
% Deviance explained	1.46	1.8	23.5

Gervais' beaked whales at MC

The best model selected for Gervais' beaked whale detections at MC included four parameters, which are illustrated in Figure 4.16. Models for Gervais' at all three sites included mean(SST) as a parameter (A). At MC the relationship was via a third degree polynomial, and the partial fit shows an inverted "U" shape with a peak around 24 degrees, indicating a preference for water temperatures close to that value. This most likely relates to seasonal patterns, with increased detections during early spring and late fall when temperatures around 24 degrees are most common. In the seasonal analysis (subsection 4.5.2) there were significantly more detections in spring than in summer, however the results were questionable because of the patchy coverage in spring. A longer time series may help clarify this relationship.



(A) **(B)**

(C) **(D)**

Figure 4.16: Modeled partial fits of environmental parameters included in best model of Gervais' beaked whale detections at MC. (p) indicates a polynomial function in the GLM, with degree in parentheses; (L) indicates a linear function. Error bars not estimated using ZINB method. (A) mean sea surface temperature (SST), (B) mean sea surface height anomaly (SSHA), (C) noise at 1 kHz, (D) natural log of oil surface area (OARE).

The mean(SSHA) was also selected for the best model, and it has a monotonic negative relationship with Gervais' detections, as shown in subfigure (B). This suggests a preference for regions of low SSHA, such as the interior or cold core rings. These results are similar to those from Davis et al. (2002), who found "squid-eaters" (including beaked whales, *Kogia* spp. and an assortment of Delphinids) more often outside of anti-cyclonic, warm-core features.

The last two parameters, noise at 1 kHz and the natural log of OARE both have linear increasing relationships with Gervais' at MC (C and D). The positive trend of noise at 1 kHz, which is a proxy for windspeed, was similar to what was found for Cuvier's beaked whale at GC and for sperm whales at MC and GC, suggesting an overall preference of deep-diving cetaceans for regions with increased wind. Biologically this trend could be due to regional increases in productivity and prey abundance due to increased wind and upwelling. However, the numerous links in this chain lead to difficulty in clear interpretation of the results, and is likely the cause of the conflicting, complicated trends seen for this parameter for sperm whales at DT and Cuvier's beaked whale at MC.

The positive relationship with log(OARE), which would indicate a preference for habitat with higher levels of surface oil, was not expected. There were no clear indications of an increase in detections during the period of the oil spill (see Figure 4.3 (A)), however, there was a fairly large gap in the data during the fall of 2011, which may have an influence on this result. Also, note that overall this model explained only 1.46% of the deviance, so even though it was selected as the best model out of all the options, it is still not a model with much predictive power, and all results should be treated with caution.

Gervais' beaked whales at GC

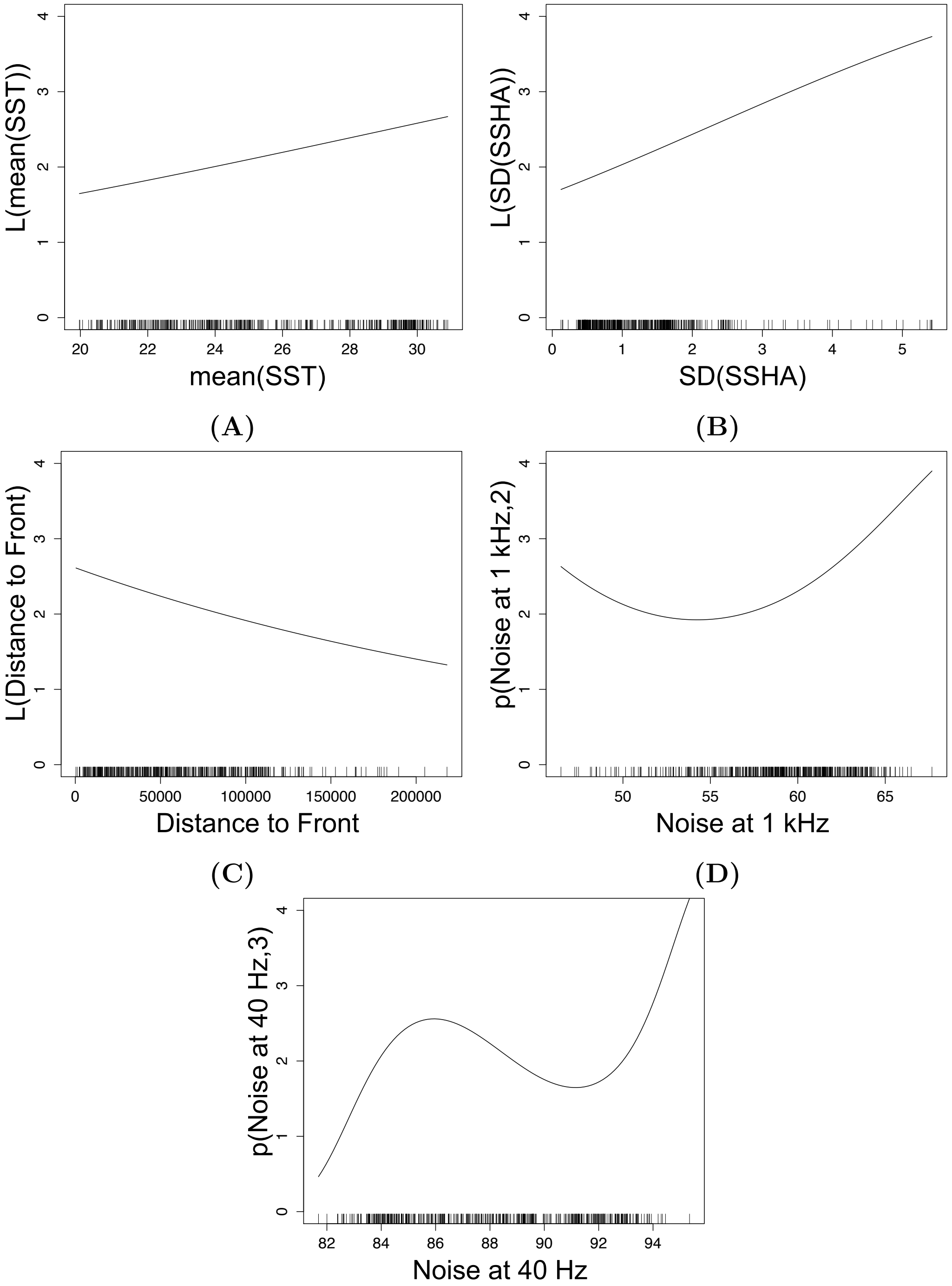
The ZINB modeling for Gervais' detections at GC produced a best fit model with five predictor variables, as seen in Figure 4.17. As with all of the other beaked whale models mean(SST) (subfigure (A)) was included, however in this case the trend was opposite of what has been seen before. The positive linear slope indicates a preference for warmer temperatures, which would correspond to higher detections during the summer months, but such a trend was not shown in the seasonal trend analysis (see subsection 4.5.2). These conflicting results suggest that the seasonal patterns of Gervais' beaked whales at GC are complicated or not easily assessed with the current data set.

The SD(SSHA) also showed a positive relationship (subfigure (B)), suggesting Gervais' beaked whales at GC prefer habitat with highly variable SSHA, such as along the edges of mesoscale features like warm or cold core rings that might concentrate their prey. A similar pattern was seen for Cuvier's beaked whale at MC (subfigure 4.13), and was expected based on previous studies of other deep-diving cetaceans (e.g. Waring 1993, Griffin 1999, Rankin 1999, Biggs 2000, Baumgartner et al. 2001, Davis et al. 2002).

The third parameter, distance to the nearest front (C), also supports the expected finding that Gervais' beaked whales are more likely to be found in areas of dynamic habitat. In this case the positive linear fit suggests that animals are more likely to be found close to thermal fronts, and is similar to the trend seen for sperm whales at MC (subfigure 3.7).

Noise at 1 kHz is the fourth parameter, and the partial fit shows a "U" shaped trend with a minimum around 55 dB (Figure 4.17 (D)). This parameter is directly correlated with wind speed, indicating a preference against intermediate wind speeds, however the chain between wind speed and increased cetacean prey is so long that the actual relationship is difficult to interpret, despite this parameter being included in this best fit model.

A third degree polynomial of noise at 40 Hz was selected as the final parameter, and the "S" shaped relationship is shown in subfigure (E). There is a local maximum around 86 dB and a local minimum around 92 dB with higher



(A) **(B)**

(C) **(D)**

(E)

Figure 4.17: Modeled partial fits of environmental parameters included in best model of Gervais' beaked whale detections at GC. (p) indicates a polynomial function in the GLM, with degree in parentheses; (L) indicates a linear function. Error bars not estimated using ZINB method. (A) mean sea surface temperature (SST), (B) standard deviation of sea surface height anomaly (SSHA), (C) distance to the nearest front, (D) noise at 1 kHz, (E) noise at 40 Hz.

detection rates corresponding to higher noise measurements above 92 dB. As a metric primarily driven by seismic air gun activity, the trends at the extrema are likely due to the polynomial fit, which will extend to infinity in each direction when not limited. These trends and should not be taken to indicate that Gervais' beaked whales prefer regions with very high noise at 40 Hz, and a larger data set may reduce the complicated nature of this relationship.

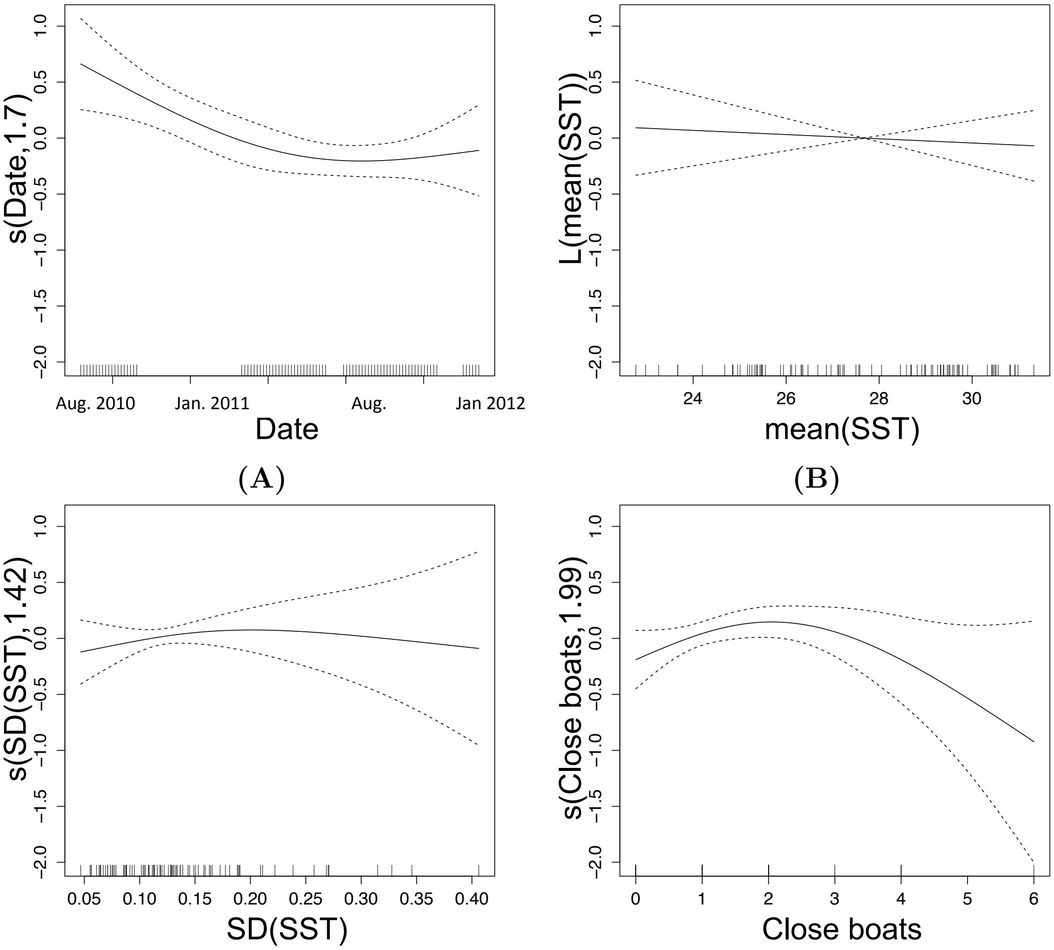
Similar to the model of Gervais' beaked whales at MC, this model for the habitat at GC explained only 1.8% of the deviance, so even though it was selected as the best model out of all the options, it still does not have much predictive power.

Gervais' beaked whales at DT

The final habitat model for beaked whales relates detections of Gervais' beaked whales to the habitat at DT. As in Cuvier's above (subsection 4.6.1) there were enough detections of Gervais' at DT that when the data were binned there was at least one detection in each bin, allowing the use of a GAM instead of a zero-inflated model. The best model included four parameters, the smooths of which are shown in Figure 4.18. The first parameter was the date, which is essentially a metric for trends since the start of recording. The general decrease, as seen in subfigure (A), indicates a decrease in detections over time, which may be due to the higher number of detections during the first half of the time series, as seen in Figure 4.3 (C). This is the only site/species combination to suggest a long-term trend in the number of detections over time. A longer time series will help confirm whether this trend is ongoing or simply an artifact from these two years of data.

The best model for Gervais' at DT also included mean(SST) (B), and the best fit line is a negative trend, indicating a preference for cooler waters, which are generally found in the fall and winter months. However, the error bars (dotted lines) suggest that the relationship could either be positive or negative, which corroborates the finding that there was no clear seasonal trend in detections (see subsection 4.5.2).

The variability in the SST, as measured by the SD(SST) was also important



(A) **(B)**

(C) **(D)**

Figure 4.18: Modeled partial fits of environmental parameters included in best model of Gervais' beaked whale detections at DT. (s) indicates a smooth function in the GAM, with estimated degrees of freedom (edf) in parentheses; (L) indicates a linear function. Rug plot along bottom indicates location of detections. (A) date, (B) mean sea surface temperature, (C) mean sea surface temperature, (D) count of close boats.

for the model and subfigure 4.18 (C) shows the generally increasing trend with a possible decrease at higher values. The confidence interval is significantly flared at the extreme values, which suggests that a monotonically increasing or decreasing trend is possible, or even no trend at all. This parameter relates to the proximity of areas of steep gradient in SST, which is most common at frontal zones, so the unclear relationship between Gervais' detections and SD(SST) suggests a complicated relationship between this species and variability in SST.

The final parameter in this model is the count of close boats, and the smooth is an upside-down "U" with a peak around two. Note that there is only one measurement at six, which may have disproportionally large influence on the overall pattern, and that the flare in error bars (dotted lines) at high values allow for a completely horizontal trend, with no relationship between boats and Gervais' detections. As beaked whales are generally known to be elusive, avoiding contact with boats (Pitman 2002), it could be expected that there would be fewer detections on days when there was a high number of ships in the area. A longer time series, however, may be needed to more thoroughly explore this relationship.

This model performed much better than the models for the other two sites, explaining 23.5% of the deviance, however it is still only a moderate fit.

4.7 Summary

My hypotheses for beaked whales as a group were generally supported, with a few exceptions. I expected to find more detections of all beaked whale species at MC and GC, however the overall number of detections for Cuvier's and Gervais' beaked whales at DT was remarkably high. The detection rate for BWG was consistently low, but higher at MC than at the other two sites. I also anticipated detecting beaked whales less frequently than sperm whales, but both Cuvier's and Gervais' beaked whales were detected at DT on an almost daily basis. In general these results indicate that there may be more beaked whales in the Gulf of Mexico than currently estimated based on visual sighting surveys.

The diel patterns for all three species were complicated by differences between the three sites. While the hypothesis that BWG would be nocturnal was supported, the other two species did show diel patterns, being nocturnal at some locations and not at others. These results are similar to what has been seen at other locations globally, where most species of beaked whales do not have a consistent diel pattern, but instead seem to be influenced by local conditions.

I anticipated finding no clear seasonal trend for any of the three beaked whale species, which was shown to be the case with BWG. However there was an increase in detections during the cooler months for Cuvier's and Gervais' beaked whales at the northern two sites, suggesting the possibility of regular movements of these species, either north-south or east-west. Such seasonal movements have been detected for beaked whales at a few other locations globally.

As with the sperm whales, the response of the beaked whale species to the DH oil spill remains unclear, but overall there appears to have been minimal effect in the short term. Although I hypothesized finding fewer detections of beaked whales at MC during the DH oil spill, testing for differences between the summers of 2010 and 2011 and for periods during and immediately after the oil spill showed no little-to-no relationship. Also, any trends that were statistically significant were heavily influenced by extreme values and gaps in data because of the small sample size for all three species, and therefore should be treated with caution. The oil spill did have a negative effect on Cuvier's beaked whales, as shown by the inclusion of the amount of surface oil in the best fit habitat model. For Gervais' beaked whale, however, the opposite relationship was shown, which was unexpected by may have been heavily influenced by a gap in the time series. A long-term trend that could relate to was found for Gervais' beaked whales at DT, which were detected less frequently over time as shown by the inclusion of the date parameter in the best fit model. No long term trends were seen for the other species or sites, indicating that either there is no trend or that it is not detectable in the given data set.

I hypothesized that sea surface height anomaly (SSHA) and the distance to thermal fronts would be important parameters to identify beaked whale habitat, but this was only partially supported. Both the mean and the standard deviation of SSHA were important for both Cuvier's and Gervais', but the distance to thermal fronts was only included in one of the best fit models (for Gervais' at GC), suggesting that beaked whales are not generally associated with thermal fronts. In general the best habitat models for Cuvier's and Gervais' at all sites indicated the importance of sea surface temperature (and the related seasonal variations), and SSHA, although the functional relationships varied by species and site, with no clear generalization possible.

Overall the results presented above are similar to what has been found in other studies of beaked whale behavior and habitat, showing little diel or seasonal pattern for most species and perhaps loose associations with mesoscale oceanographic features. Future studies would hopefully be able to include metrics of beaked whale prey abundance and location, and a longer time series from the northern Gulf of Mexico may show long-term response patterns to the DH spill.

Chapter 4 in part, is currently being prepared for submission for publication. Merkens, Karlina; Baumann-Pickering, Simone; McDonald, Mark; Frasier, Kaitlin; Wiggins, Sean; Hildebrand, John. "Beaked Whale ecology and habitat modeling in the Gulf of Mexico". The dissertation author was the primary investigator and author of this material.

Chapter 5

Kogia spp. ecology and habitat modeling

5.1 Abstract

Dwarf and pygmy sperm whales (*Kogia sima* and *K. breviceps*) in the Gulf of Mexico are frequently encountered through strandings, however very little is known about normal, healthy individuals. They are known to be deep-diving species based on gut content analysis from other regions. The acoustic signals of both species peak around 120 kHz, putting them out of range of many recording devices. Using passive acoustic data from seafloor-mounted High-frequency Acoustic Recording Packages we monitored for *Kogia* spp. presence at three sites deeper than 900m by detecting the low-frequency component of the clicks. The two species cannot be distinguished acoustically based on these data, therefore the results presented are for both species combined. *Kogia* spp. were detected at all three sites, with fewer detections at Dry Tortugas (DT) than at the other two locations. Analysis of diel detection patterns showed crepuscular and nocturnal behavior at Mississippi Canyon (MC). Significant seasonal patterns were detected at MC and Green Canyon (GC), with fewer detections in the cooler months at both sites. There were significantly more detections in the summer of 2011 compared to 2010 ($p < 0.0001$) at Mississippi Canyon (MC),

the site close to the Deepwater Horizon (DH) oil spill. Also at MC there were no changes in detections over the months during and immediately after the DH oil spill, whereas the possible seasonal pattern at GC impacted the number and rate of detections when comparing the period of the oil spill with the subsequent months. The relationships with environmental parameters were examined using Generalized Additive and Zero-inflated Generalized Linear models. Both sea surface temperature and sea surface height were selected for the best models at two out of three sites. The total area of surface oiling was included in the best model at MC, highlighting possible effects of the DH oil spill on these species. These results further our understanding of the behavior and ecology of sperm whales in the Gulf of Mexico.

5.2 Introduction to *Kogia* spp.

5.2.1 General Biology

The family Kogiidae comprises two species, the dwarf sperm whale (*Kogia sima*) and the pygmy sperm whale (*K. breviceps*), and for the sake of this analysis the two species are grouped together and will be referred to collectively as *Kogia* spp. Individuals of the *Kogia* spp. are rarely seen at sea because they are highly elusive and entirely pelagic, having faint-to-invisible blows and showing only a low profile while at the water's surface (McAlpine 2002, Jefferson et al. 2008). Therefore, much of what is known about them is derived from investigations of stranded individuals.

Most closely related to the sperm whale (*P. macrocephalus*), the *Kogia* spp. are both much smaller than their large relatives, being 3.8 meters or less and 450 kilograms or less (McAlpine 2002). *Kogia sima* is generally smaller than *K. breviceps*. Both are primarily suction feeding teuthivores, but stomach contents have shown consumption of crustaceans and fish.

It has been suggested that they are rare, however there is not enough information to classify them (McAlpine 2002, IUCN 2010). Visual differentiation of the two *Kogia* species is very difficult, even with stranded animals (Willis and

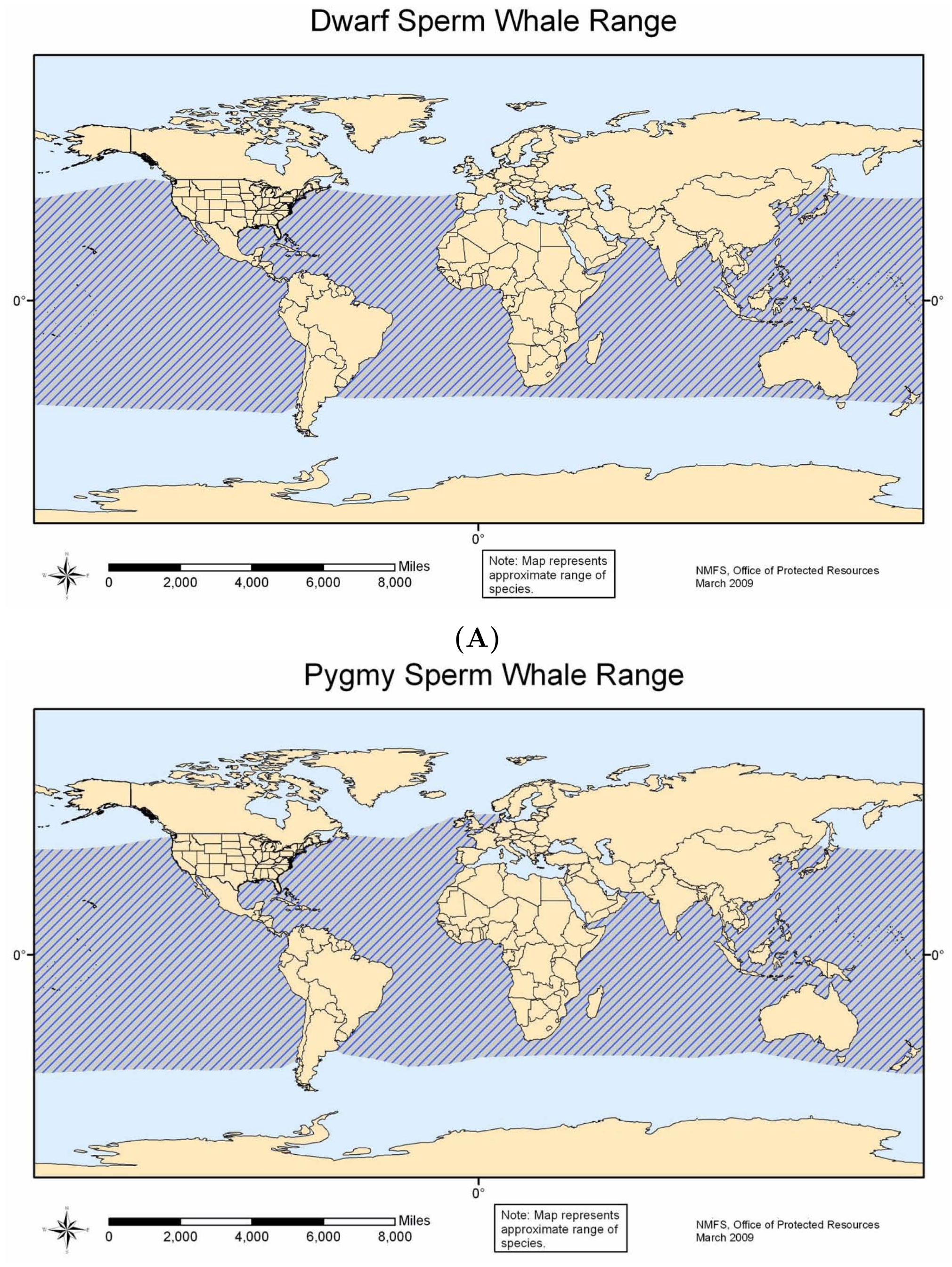
Baird 1998, Jefferson et al. 2008). The only analysis of age, which took place off the coast of South Africa, noted that they live relatively short lives of approximately 23 years (Plön 2004, Jefferson et al. 2008).

5.2.2 Distribution, Habitat Preferences, Behavior and Temporal Patterns

The *Kogia* spp. are widely distributed in tropical and temperate waters worldwide (Figure 5.1), although much of their distribution has been inferred from stranding records (Willis and Baird 1998, Würsig et al. 2000, Jefferson et al. 2008, Waring et al. 2009). Across their range they are likely located along the continental shelf and slope and occasionally over the abyssal plain (e.g. Fiedler et al. 1990, Baird et al. 1996, Jackson et al. 2004, Baird 2005). Given the bathymetric similarities at the three HARP sites it is predicted that *Kogia* spp. will be detected equally at all three sites.

Based on gut content and isotope analysis it appears that the two species may feed at different depths on slightly different prey, with *K. sima*, feeding in shallower water than *K. breviceps* (Willis and Baird 1998, Barros et al. 1998). These slight differences could affect their distribution, interactions with humans, and acoustics. Otherwise their habitat preferences are entirely unknown. Based on presumed ecological similarities with the other deep-diving cetaceans, I hypothesize that the *Kogia* spp. will be found more often in regions of dynamic oceanography, such as around the edges of fronts and mesoscale features. This association will be shown through selection of SSHA or the standard deviation of SSHA and the distance to the nearest thermal front in the best fit models.

Little is known of *Kogia* spp. behavior or social activites, although they are most often seen in groups of fewer than 10 individuals, and appear to associate with animals of different ages and sexes. When they are seen they often lie motionless at the surface (Jefferson et al. 2008). Although some other species of odontocetes are known to have increased feeding activity at night (Heithaus and Dill 2002), the behavior of other deep-diving cetaceans often shows no diel pattern (e.g. Whitehead 2003, Schorr et al 2010), and the only previous study



(A)

(B)

Figure 5.1: Global distribution of dwarf sperm whale (*K. sima*, top) and pygmy sperm whale (*K. breviceps*, bottom). (courtesy of NOAA/NMFS, http://www.nmfs.noaa.gov/)

of *Kogia* spp. diel behavior showed no clear patterns (Hodge 2011). Therefore, I hypothesize that detections of *Kogia* spp. in the Gulf of Mexico will show no diel patterns.

Studies of strandings of *Kogia* spp. have occasionally addressed possible seasonal patterns in *Kogia*, and at higher latitudes the data suggested seasonal movements (Sylvestre 1988, Kemper and Ling 1991, Santos et al. 2006). In the Gulf of Mexico, however, there appears to be no seasonal pattern in strandings (Gunter et al. 1955, Caldwell et al. 1960, Delgado-Estrella and Vasquez 1998, Hansen at al. in Davis and Fargion eds. 1996), which leads me to predict that the HARP data will include no significant pattern in seasonal detections for *Kogia* spp., except for a decrease in detections during the summer and fall of 2010 while the DH oil spill and response was underway.

5.2.3 Acoustics

The acoustics of *Kogia* spp. have only recently begun to be understood, which is primarily because their signals are at such high frequencies that the technology to make recordings did not exist until the last few decades. There have been only a few published studies addressing the sounds and acoustic anatomy of *Kogia* spp., all from animals that were stranded and recorded on land or while in captivity for rehabilitation (Caldwell et al. 1966, Karol et al. 1978, Caldwell and Caldwell 1987 in Marten 2000, Thomas et al. 1990, Caldwell and Caldwell 1991, Goold and Clarke 2000, Marten 2000, Clarke 2003, Madsen et al. 2005a). It is known that the clicks of *K. breviceps*, presumably used for echolocation, last on average 119 microseconds (+/- 19 mircoseconds); they have an apparent source level of 175 dB//re 1 μPa (pp), and Inter-click-intervals (ICI) varying between 40-70 milliseconds (Marten 2000, Madsen et al. 2005a). These clicks are also very high frequency, ranging from 60-200 kHz with a peak around 125kHz (Marten 2000, Madsen et al. 2005a). Madsen et al. (2005a) hypothesized that these high frequency clicks may have resulted from convergent evolution in a number of small cetacean species to take advantage of a low noise window that exists in the oceans at 100 kHz. There are no published records of the acoustic signals of *K.*

sima, however one encounter with wild animals confirm that the characteristics are similar (V. Janik, unpublished data). The shape of their highly asymmetrical skull is likely related to generation of acoustic signals (McAlpine 2002).

As mentioned in Chapter 2, the acoustic propagation at each site was similar, allowing for comparison of the results across sites. This is particularly true for *Kogia* spp. signals, which attenuate very rapidly, resulting in a detection range less than one kilometer.

5.3 *Kogia* Specific Methods

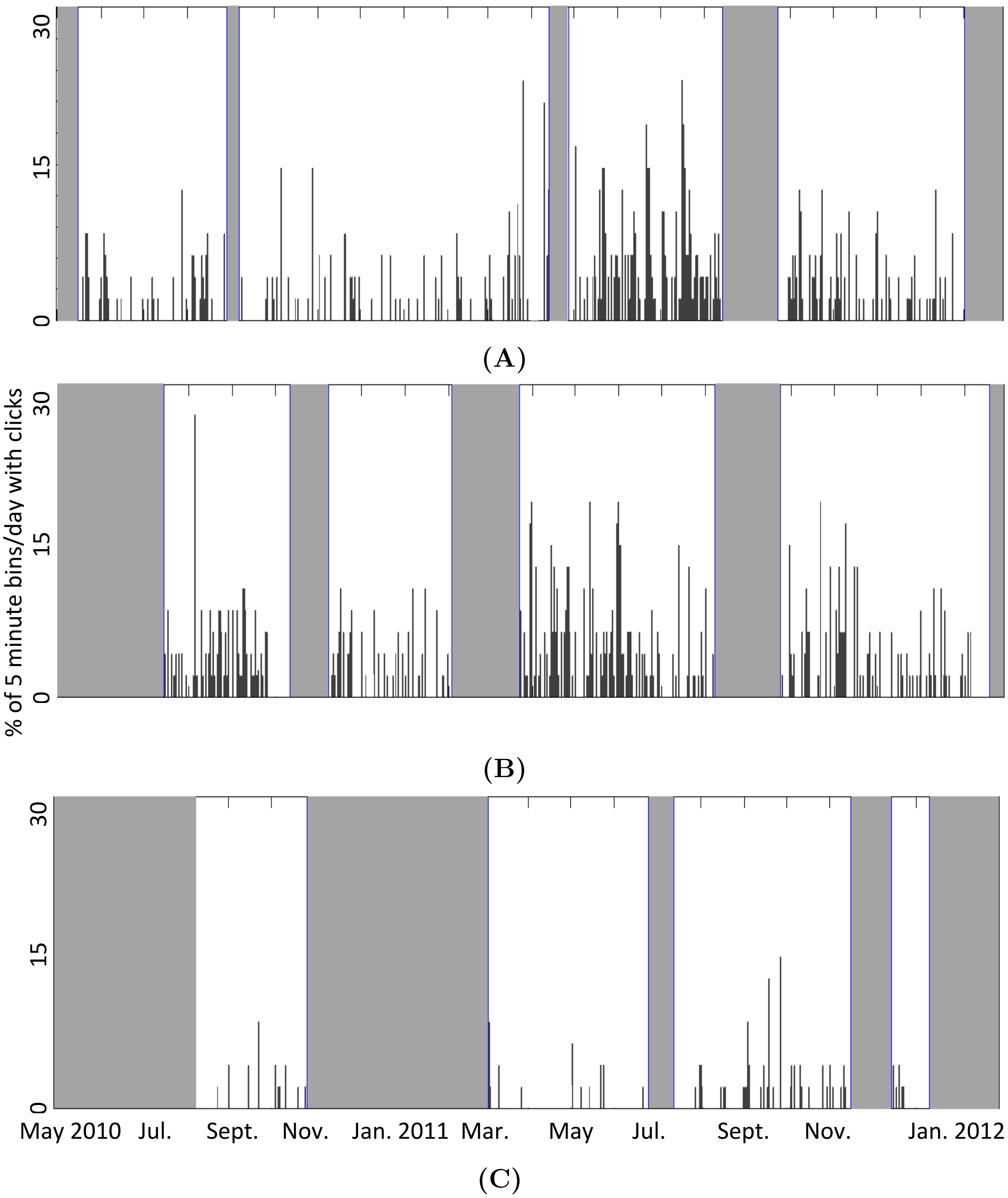
With the lower frequency components of *Kogia* spp. signals reaching as low as 80 kHz, they can be detected in the 100 kHz Nyquist HARP data. This information is sufficient for the purpose of a first assessment of presence and temporal behavioral trends. We did deploy an instrument sampling at at 320 kHz, which recorded four encounters with *Kogia* spp. in approximately 40 hours. Of those, only one would have been detected on the 200 kHz instrument. Based on this initial comparison we are likely missing many detections of *Kogia* spp. when the animals are not close enough to the HARP for the lower frequency energy to be detected. Because of the high frequencies of these species' signals and the short duration of encounters, visual analysis of the acoustic data was conducted by examining a 30 minute Long-Term Spectral Average (LTSA), with a 15 minute overlap to reduce the chance of missing a detection because of screen resolution. Frequencies from 70 to 100 kHz were examined, which is above most of the energy from most other sources in the Gulf of Mexico, thus masking is not a concern. Automated methods were not used because the ease and rapidity of manually detection made automation unnecessary

5.4 Results of Exploratory Analysis

The time series of the *Kogia* spp. detections at all three sites are shown in Figure 5.2. These data suggest seasonal cycles at both GC and DT (subfigures 5.2 (B) and (C)), with DT having increased detections during the fall (September - November), and GC having decreased detections in the winter (December - February). In comparison, data from MC did not suggest a seasonal pattern (A), but there were more detections during the summer of 2011 than during any other period. Detections of *Kogia* spp. were zero-inflated at all sites (Table 5.1), however there were more detections at MC and GC than at DT, which is different from the expected pattern of similar detection rates at all sites.

Table 5.1: Parameters indicating whether data set was zero-inflated.

Site	Time-period length	# time-periods with detections	% of time periods with 0
MC	1-day	207	62.0
GC	1-day	213	52.5
DT	1-day	56	83.5



(A)

(B)

(C)

Figure 5.2: Time series of *Kogia* spp. detections as % of 5-minute bins per day at MC(A), GC (B) and DT(C). Gray indicates no recording effort.

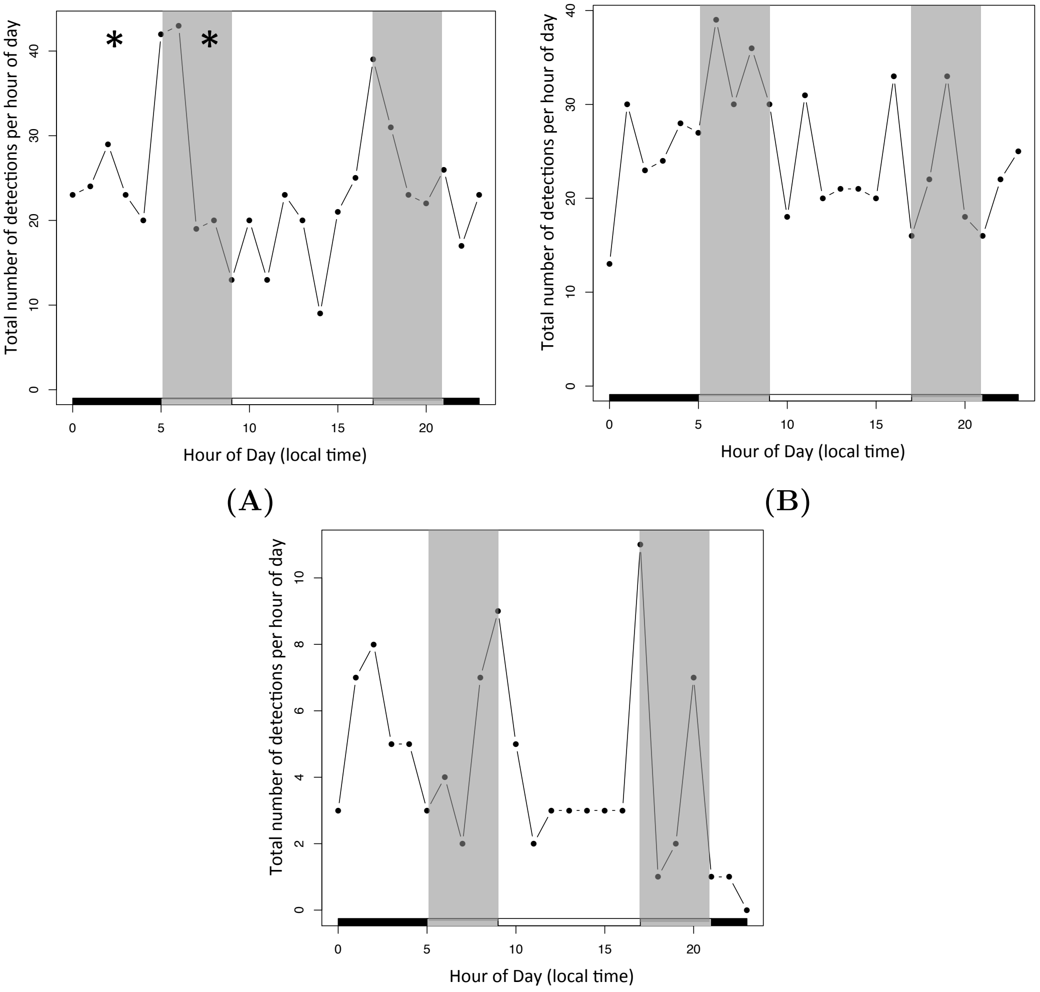
5.5 Results of Trend Analysis

All tests were conducted using $p < 0.05$ unless otherwise noted.

5.5.1 Diel patterns

Detections of *Kogia* spp. were tested for diel patterns, and only data from MC showed any significant results (Table 5.2). The crepuscular pattern is clearly visible in the histogram of the data (Figure 5.3), whereas it is likely that the significant increase in nocturnal detections is simply due to some of the crepuscular detections being included in the nighttime period when they occur shortly after sunset. These results falsify the hypothesis that there would be no diel pattern for *Kogia* spp. in the Gulf of Mexico, however because there are significant patterns at only one out of three sites the overall trend is not clear.

As with the other deep-diving cetaceans, diel patterns for *Kogia* spp. are likely to be related to cycles in foraging and feeding activity. Increased crepuscular detection may be due to increased feeding while their preferred prey shoals and sinks as part of daily vertical migration. Both *Kogia* species have been shown to be primarily squid-eaters (Staudinger et al. 2013), and squid are known to undergo daily migration like many other pelagic species (Watanabe 2006). Another related explanation for this increased number of detections during crepuscular periods is that *Kogia* spp. dive to deeper depths during these hours of the day. The high frequency signals generated by *Kogia* spp. attenuate quickly in the water, so the animals must be fairly close to the HARP to be detected (approximately less than 600 meters (M. McDonald, unpublished data)). At MC the HARP is moored at approximately 980 meters, so the animals would have to dive to at least 380 meters in order to be detected even if they are directly above the instrument and their acoustic pulses are aimed directly at the hydrophone. The *Kogia* spp. may be diving deeper during twilight, making their signals more likely to be detected, even if their feeding rates are constant throughout the day. Previous analysis of acoustic detections of *Kogia* spp. off the coast of North Carolina, USA showed no clear diel pattern (Hodge 2011).



(A)

(B)

(C)

Figure 5.3: Detections of *Kogia* spp. per hour of the day (local time) at MC(A), GC (B) and DT(C). Color bar at bottom of each plot indicates day (white), night (black) and crepuscular (gray) periods. Note significant nocturnal and crepuscular activity at MC (A).

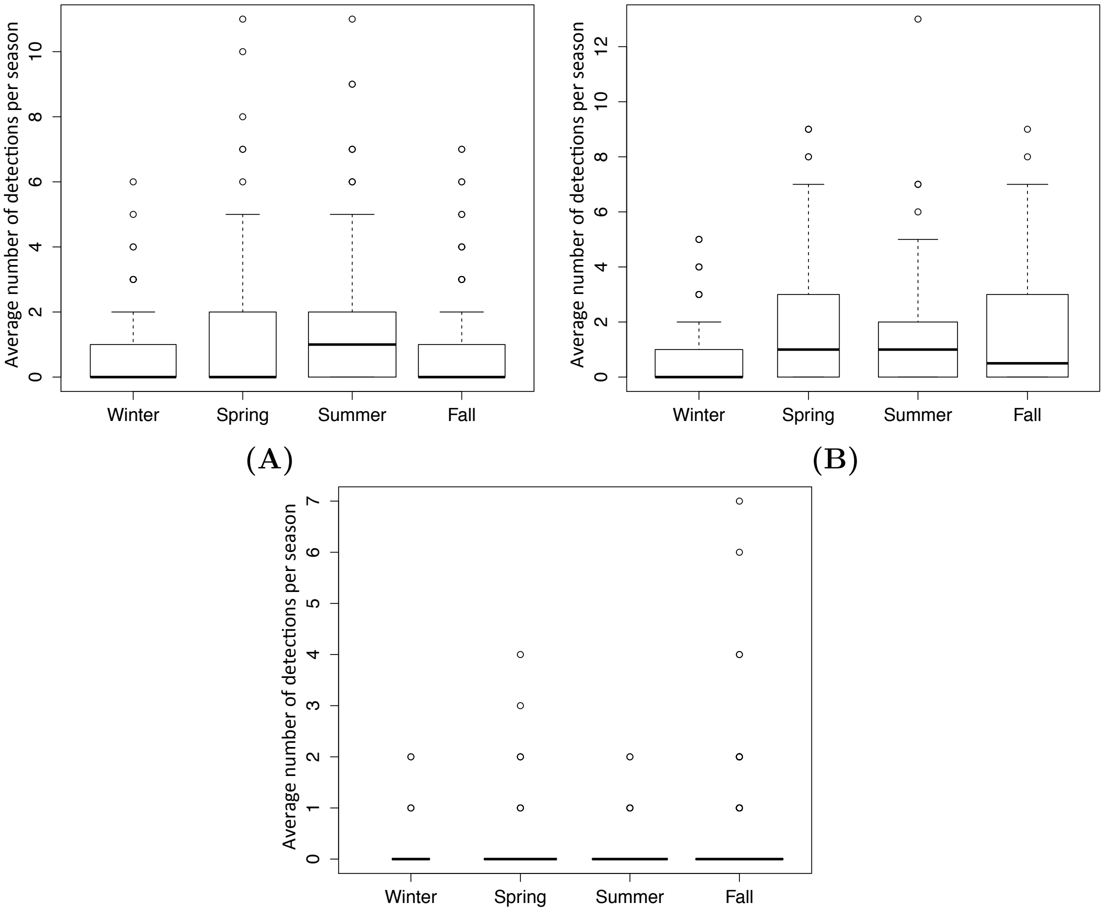
Table 5.2: Diel patterns of *Kogia* spp. signals by site. (-) indicates no significant pattern in that category.

Site	MC	GC	DT
Total # Detections (5-min bins)	568	596	98
Day/Night p-values	Nocturnal 0.010	- 1	- 0.614
Crepuscular p-values	Crepuscular <0.001	- 0.056	- 0.391

5.5.2 Seasonal trends

The average number of detections of *Kogia* spp. per season were compared, and significant differences were found at all three sites (Figure 5.4). At MC there were significantly more *Kogia* detections in the summer than the winter or the fall. This trend is heavily influenced by a large pulse of detections in the summer of 2011 and a low number of detections in January from both years. The pattern was similar at GC where there were fewer detections in the winter months than in all other seasons. At DT there were more detections in the fall than in the spring, but there was only one partial spring, so the biological significance of this trend is questionable and will not be discussed further. These results contradict the hypothesis that there would be no seasonal patterns for these two species in the Gulf of Mexico.

With one exception, the seasonality of *Kogia* spp. has only been examined previously by looking for general trends in stranding records. Although the data sets are often too small to show a statistically significant pattern, these records often suggest seasonality. Strandings that occurred only between June and December led Sylvestre (1988) to posit seasonal movements of *Kogia* spp. around New Caledonia. In southern Australia pygmy sperm whales (*K. breviceps*) stranded from April to October (Kemper and Ling 1991) while in the northeast Atlantic the same species stranded more in the autumn and winter (Santos et al. 2006). However, in the Gulf of Mexico *Kogia* spp. have stranded or been observed at sea in all seasons (Gunter et al. 1955, Caldwell et al. 1960, Delgado-Estrella and Vasquez 1998, Hansen at al. in Davis and Fargion 1996). In general it is assumed



(A) **(B)**

(C)

Figure 5.4: Box plot of *Kogia* spp. detections per season at at MC(A), GC (B) and DT (C). Top and bottom of boxes are at 75th and 25th percentiles; whiskers extend to 1.5 times the interquartile range. At MC the mean number of detections was significantly higher in the summer than in the fall or winter. At GC there were significantly fewer detections in winter than in all other seasons.

that the rate of stranding animals translates to the overall abundance of animals in the area, however there are a number of factors, such as coastal weather and changes in oceanographic features, that could increase the chance of strandings taking place or being discovered.

Using passive acoustics allows us to avoid many of the complications involved with assessing strandings, particularly because we are monitoring for living animals that are more likely to be normal and healthy than those found on shore. In a similar study Hodge (2011) detected *Kogia* spp. signals in all seasons in HARP data from the coast of North Carolina, USA. The large number of detections from the Gulf of Mexico HARP data (much larger than most stranding data sets) allows us to look not only at presence, but also at changes on a seasonal basis. It is unlikely that seasonal differences in acoustic propagation have much effect on detection rates because the *Kogia* spp. must dive to depths below the stratified surface layers before they are detected on the HARPs.

Fewer detections in the cooler months at both MC and GC suggest a seasonal movement into the northern Gulf in the summer. In general cetaceans make annual movements or migrations to take advantage of seasonally abundant prey and/or to avoid predation (Stern 2002). In the case of *Kogia* spp. it is likely that there is increased abundance of their squid prey in the northern Gulf of Mexico in the summer. Another possibility is that *Kogia* spp. move from the slope to deep water seasonally, although this pattern has not been reported in odontocetes. Researchers most often attribute seasonal patterns in cetacean movement to changes in prey. Another option is that movements are related to social activities, such as breeding or calving. Both of these ultimate forces cannot be tested with the data that are currently available, but further study, such as measurements of local prey concentrations and observations of social behavior patterns, could clarify the cause of seasonal movements.

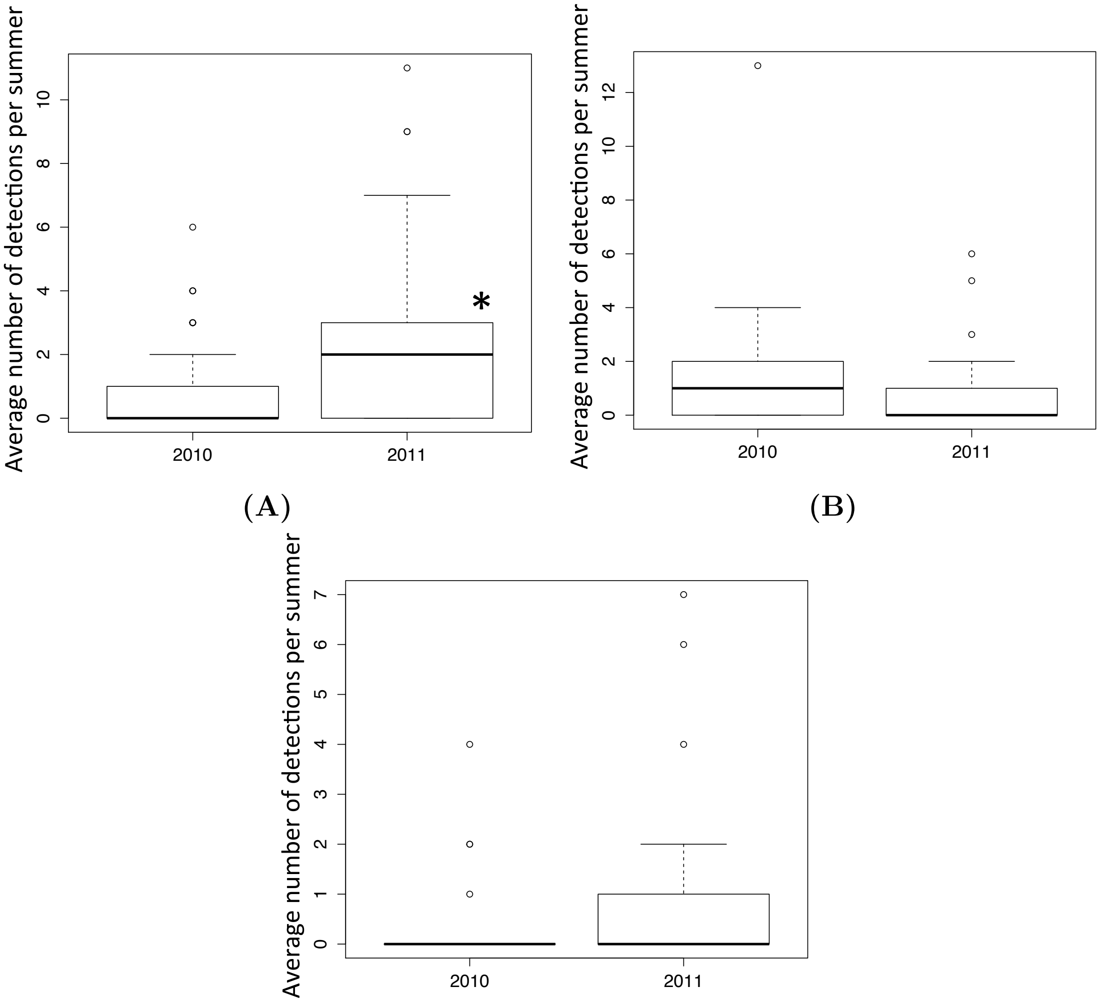
5.5.3 Oil-spill related trends

Comparing the mean detections of *Kogia* spp. at each site in the summer of 2010 (during spill) and the same days in the summer of 2011 showed that there was no significant difference between the two summers at GC and DT (Figure 5.5), however there was a highly significant difference at MC, which appears to be related to a consistently higher number of detections during the summer of 2011 (see Figure 5.2). This finding supports the hypothesis that there would be fewer detections while the DH oil spill was underway at MC.

Results of similar testing of means and slopes during the period of the spill and the subsequent months, separated by various breakpoints, at sites MC and GC are tabulated below (Table 5.3). The two periods were never significantly different at MC. However, there were significant differences between time periods at GC, which may be primarily due to the seasonal pattern at GC, with a decreased presence in the winter months. This caused lower means after the later breakpoints (October 1 - November 1), and decreased slope after the September 1 breakpoint.

Table 5.3: Comparison of means and slopes for sperm whale detections before and after breakpoints separating period of oil spill from post-oil spill at GC. There were no differences at MC. (+) indicates a significantly higher mean after the breakpoint, (-) indicates a significantly lower mean after the breakpoint, (same) indicates no difference between periods ($p < 0.05$). When the differences in slopes were significant the value of the slope is included in the table. Data collection at GC did not begin until July 15.

Breakpoint	Jul 15	Aug 1	Aug 15	Sep 1	Sep 15	Oct 1	Oct 15	Nov 1
GC: mean after	NA	same	+	same	same	-	-	-
slope before	NA	same	same	0.02	same	same	same	same
slope after	NA	same	same	-0.07	same	same	same	same



(A) **(B)**

(C)

Figure 5.5: Box plots of *Kogia* spp. detections in the summer of 2010 and 2011 at MC(A), GC (B) and DT(C). Top and bottom of boxes are at 75th and 25th percentiles; whiskers extend to 1.5 times the interquartile range. The difference in detections at MC (A) was highly significant ($p < 0.0001$).

5.6 Results and Discussion of ZINB models

All three *Kogia* spp. data sets were highly zero-inflated (see Table 5.1), therefore the ZINB modeling process was used to relate the detections to environmental parameters for all three sites. The details of the model formulas are included in Table 5.4. Because the response variable is periods of time with echolocation clicks, which are generated primarily during foraging dives, and because these animals are only likely to be deep enough to be detected by the HARPs while on foraging dives, these models probably address aspects of foraging ecology such as processes that increase prey populations or density. Although these models are based on analysis of conditions at a single location, because of the dynamic, fluid nature of the ocean environment, the "habitat" characteristics at a single point will change over time as different water masses move past the HARP. This allows us to assess the relationship with different environmental conditions without needing to sample across a large space.

In general the results do not support nor falsify the hypothesis that SSHA is an important parameter for identifying *Kogia* spp. habitat because mean(SSHA) is included only in the models at MC and the SD(SSHA) is only included in the zeros model for DT. Additionally the hypothesis that *Kogia* spp. associate with thermal fronts is falsified by these results because none of the best fit models included this parameter.

Table 5.4: Parameters for habitat models of *Kogia* spp., all models were Zero-inflated GLM. (L) indicates a linear function; (p) indicates a polynomial, with power in parentheses.

Site	MC	GC	DT
Selected model parameters	counts: L(mean(SSHA)) + p(LUIL,2) + L(OARE) zeros: L(mean(SSHA))	counts: p(mean(SST),2) + L(SD(SST)) + p(NOIS01kHz,3) zeros: p(DOYR,2)	counts: p(mean(SST),3) zeros: + L(SD(SST)) + L(SD(SSHA)) + L(mean(WIND))
% Deviance explained	4.98	2.73	11.92

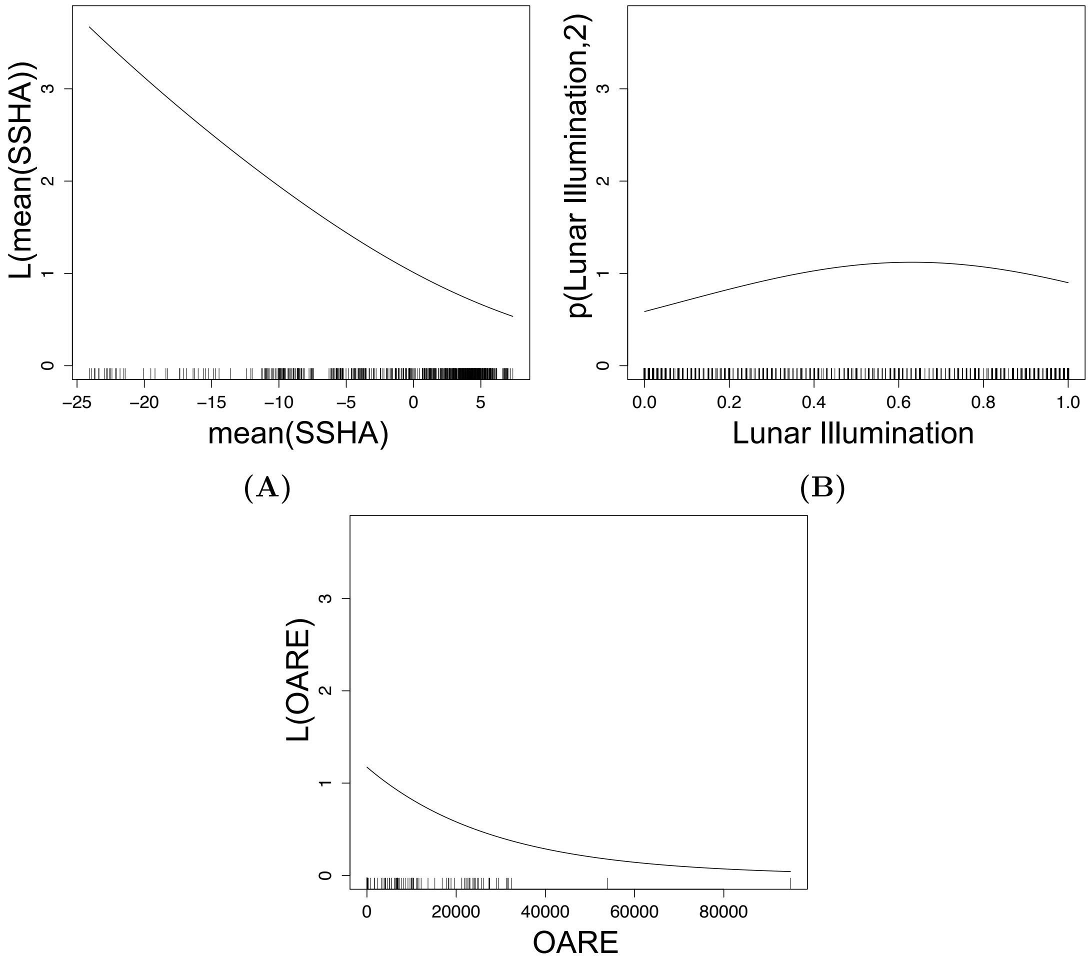
5.6.1 *Kogia* spp. at Mississippi Canyon

The best model for the *Kogia* spp. detections at MC included three parameters, and the plots of the partial fits are presented in Figure 5.6. The linear fit of mean(SSHA) exhibits a negative slope, indicating a preference for regions of lower SSHA, which occurs most in cold-core rings. This is similar to the findings of Davis et al. (2002) who found who found "squid-eaters" (including beaked whales, *Kogia* spp. and an assortment of Delphinids) more often away from anti-cyclonic, warm-core features. Additionally this is similar to the trends shown for other deep-diving species in the current analysis, including sperm whales at DT (Figure 3.9), Cuvier's beaked whales at GC (Figure 4.14) and Gervais beaked whales at MC (Figure 4.16).

The second parameter included in the best model was lunar illumination, and the figure (B) indicates an upside-down "U" shape with a peak around 0.6, suggesting increased activity at this location when roughly 60% of the moon is illuminated (mid-waxing and mid-waning). A relationship to the lunar cycle likely relates to nighttime foraging on the deep scattering layer. Increased lunar illumination (e.g. during the full moon) can have a dampening effect on the strength of the daily vertical migration such that prey species avoid predation at the surface by not moving as far up in the water column. Based on gut content analysis of stranded individuals *Kogia* spp. are presumed to feed predominantly at depths where lunar illumination would have relatively little impact (e.g. below 500 meters)(Willis and Baird 1998), however they may feed at shallower depths as well and could therefore be affected by the lunar cycle.

A negative linear relationship was found with the third parameter, a measure of total surface area of oil from the DH spill for the entire northern Gulf (OARE) (subfigure (C)). This trend of fewer detections when there was more surface oil present is similar to what was found for sperm whales (Figure 3.7) and Cuvier's beaked whales at MC (Figure 4.13), and indicates that *Kogia* spp. may have been avoiding the region of the DH oil spill.

Overall this model explained only 4.98% of deviance from the null model, therefore the conclusions should be considered tentative.



(A) **(B)**

(C)

Figure 5.6: Modeled partial fits of environmental parameters included in best model of *Kogia* spp. detections at MC. (p) indicates a polynomial function in the GLM, with degree in parentheses; (L) indicates a linear function. Error bars not estimated using ZINB method. (A) mean sea surface height anomaly (SSHA), (B) lunar illumination, (C) oil surface area (OARE).

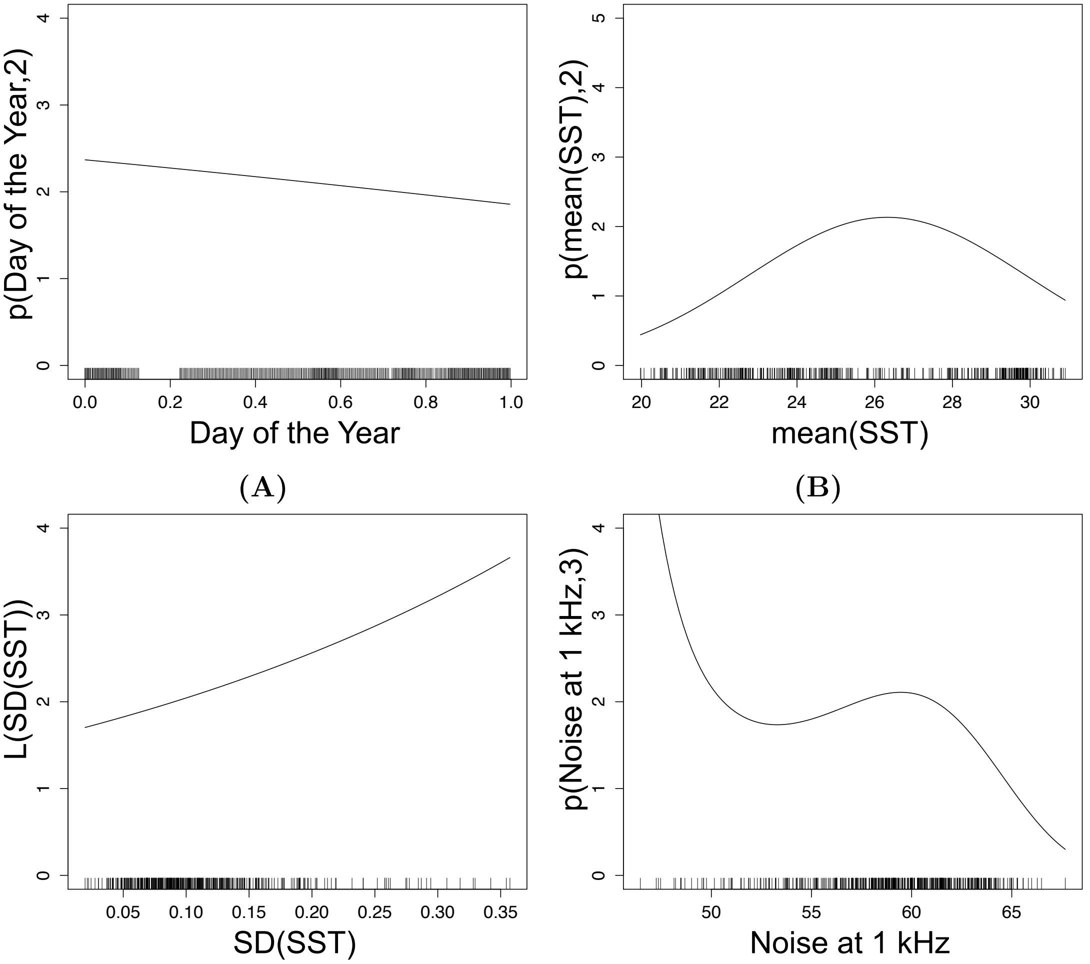
5.6.2 *Kogia* spp. at Green Canyon

Four environmental parameters were selected for the best model at GC, as shown in Figure 5.7. Day of the year (A) was included as the only parameter in the zeros model, indicating an annual cycle of presence and absence at this HARP site. This finding is reinforced by the analysis of seasonal trends that showed fewer detections in winter than in all other seasons (see subsection 5.5.2). A polynomial fit was selected, however the curve is effectively linear, and the magnitude of the slope is very mild, indicating a very small contribution by this parameter to the model overall.

In the counts model the mean(SST) (subfigure (B)) was included instead of day of the year to relate to a possible annual cycle. The partial fit to this parameter shows an upside-down "U" shape with a single peak around 26 degrees. This trend suggests a preference for mid-temperature surface waters as might be encountered during the spring and fall, and could be due to the period of increased detections in the late spring of 2011, visible in Figure 5.2 (B). Although the seasonal trend analysis did not show a significantly higher number of detections in the spring or fall months, this pattern may not have been measurable with the current time series.

The SD(SST) was also included in the best model, and the partial fit (C) shows a positive relationship with *Kogia* spp. detections, indicating a higher detections during periods of high variability in SST. This suggests a preference for dynamic areas like thermal fronts and the edges of warm-core rings. Baumgartner et al. (2001) also found that SD(SST) was an important characteristic of *Kogia* spp. habitat in the Gulf of Mexico, with more sightings in areas of high variability.

The final parameter to be included in the best fit model was the noise at 1 kHz, which was fit with a third degree polynomial. The partial fit shows a local minimum around 54 dB and a local maximum around 60 dB (subfigure 5.7 (D)). The extreme values at the lowest and highest measurements are likely related to the behavior of the polynomial tending toward infinity at the extremes more than the nature of the actual data. In general the majority of the curve (e.g. between 50 and 62 dB) is close to horizontal. Noise at 1 kHz is directly



(A) **(B)** **(C)** **(D)**

Figure 5.7: Modeled partial fits of environmental parameters included in best model of *Kogia* spp. detections at GC. (p) indicates a polynomial function in the GLM, with degree in parentheses; (L) indicates a linear function. Error bars not estimated using ZINB method. (A) day of year, (B) mean sea surface temperature, (C) standard deviation of sea surface temperature, (D) noise at 1 kHz.

related to wind speed, so this figure suggests that wind speed (and probably the resulting upwelling, biological productivity and increase in *Kogia* spp. prey) is an important parameter defining these species' preferred habitat. However, the complicated curve, and the similarly conflicting results from other species in the current study, make interpretation of the biological significance impossible at this time.

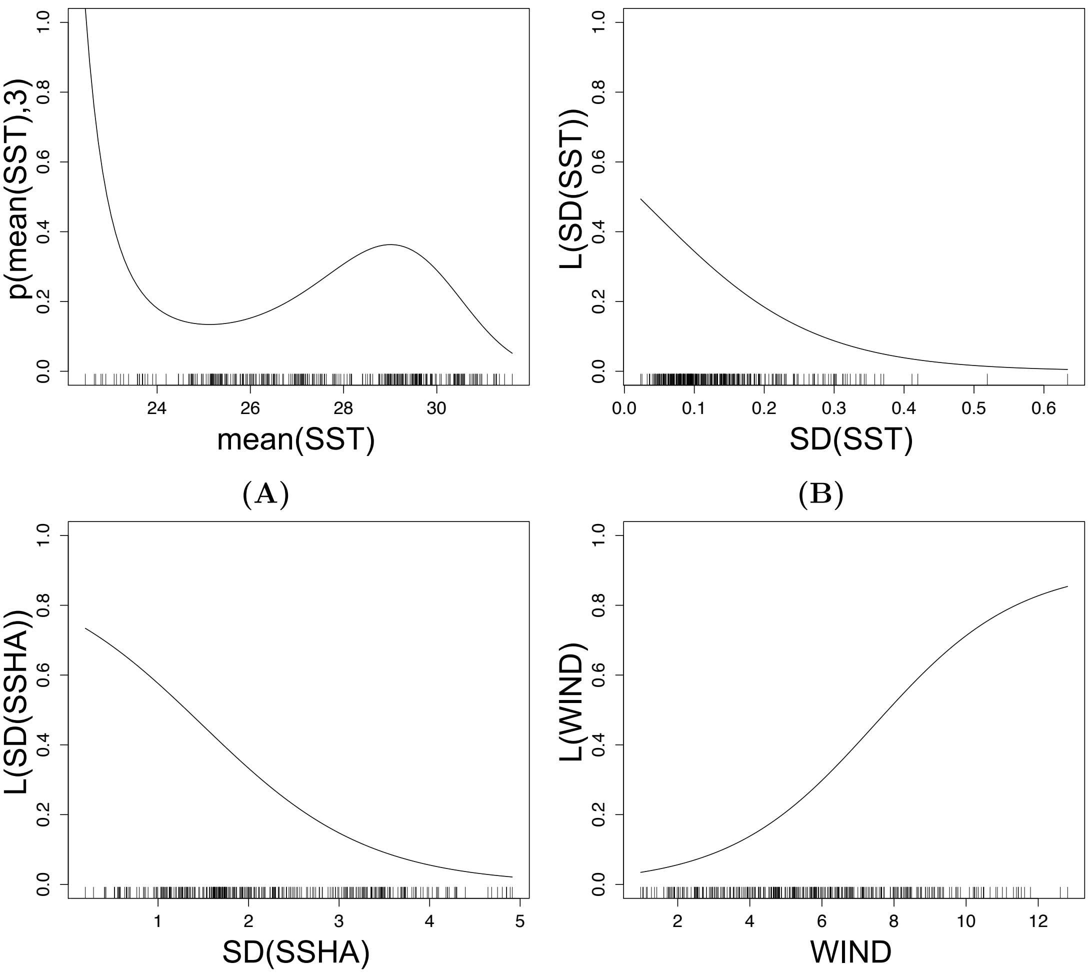
This best fit model explained only 2.73% of the deviance, so the results should be treated with caution.

5.6.3 *Kogia* spp. at Dry Tortugas

The final model is for *Kogia* spp. detections at DT, which are even fewer in number than those at the other two sites, with no more than 15 minutes including detections in any given day, and many days without detections. Four parameters were selected for the best models, as shown in Figure 5.8.

The polynomial fit to mean(SST) (A) produces a curve with a local minimum around 25 degrees and a local maximum around 29 degrees, suggesting a complex relationship with temperature (and hence seasonal) conditions. As has been seen before with third degree polynomial fits, the values at the extrema are likely to be more negative and more positive than the data might indicate. The seasonal analysis showed a statistically significant pattern with more detections in spring than in fall (subsection 5.5.2), however the uneven effort across the seasons leaves the biological significance of that result in doubt and does not help to clarify the complicated relationship indicated here.

The SD(SST) was also included in the best fit model, and the partial fit (B) shows a negative slope, unlike at GC, suggesting a preference for waters with low levels of thermal variability. This pattern is reinforced by the partial fit to SD(SSHA), which also showed a negative slope (C), indicating similar tendencies toward less dynamic conditions. These results are opposite from the findings for most of the other deep-diving cetaceans at all sites and previous studies (Baumgartner et al. 2001), and there is no clear indication of what might cause the differences.



(A) **(B)**

(C) **(D)**

Figure 5.8: Modeled partial fits of environmental parameters included in best model of *Kogia* spp. detections at DT. (p) indicates a polynomial function in the GLM, with degree in parentheses; (L) indicates a linear function. Error bars could not be estimated using ZINB method. (A) mean sea surface temperature (SST), (B) standard deviation of SST, (C) standard deviation of sea surface height anomaly (SSHA), (D) mean wind speed.

The final parameter to be included was mean windspeed, which was positively related to *Kogia* spp. detections (subfigure (D)), suggesting an increased number of detections during periods of higher wind speeds. In general wind speed is higher in the late fall and early winter months, and although the inclusion of the mean(SST) in the model should account for most of the seasonal variability, there may be some residual seasonal pattern, which is best modeled by including wind speed.

Overall this model explained 11.92% of the deviance, which is better than the other two models for *Kogia* spp., however these trends are difficult to interpret, being either very complicated or opposite from the trends seen at other sites and for other species. The unique oceanography at DT as compared to MC and GC may have a significant impact, and the population of *Kogia* spp. at this site may also be different enough to make the results at this site remarkably different fro the other two.

5.7 Summary

As with sperm whales and beaked whales I found that some of my hypotheses for *Kogia* spp. were supported while others were falsified when looking at all three sites. Although I expected to find that there were equal detection rates at all three sites, qualitative examination of the time series showed that there were fewer detections at DT than at the other two sites. In general it was remarkable that *Kogia* spp. were detected at all, and their regular appearance at all three sites suggests that these animals are found throughout the Gulf of Mexico in higher abundance than visual sighting surveys indicate.

Temporally I hypothesized that there would be no diel and no seasonal patterns in *Kogia* spp. detections based on the scant previous studies. Although there was the suggestion of a diel pattern at MC, the lack of significant trends at the other sites suggests that on the whole *Kogia* spp. in the Gulf of Mexico are not strongly diel. In contrast there were seasonal patterns, with fewer detections during winter at two out of the three sites (MC and GC). This finding suggests a seasonal north-south or east-west movement that might be similar to beaked whales, which could be addressed in future studies.

The response of *Kogia* spp. to the DH oil spill appears to be negative, with a significant increase in detections in the summer of 2011 compared to 2010 (p <0.0001) at MC. Also the inclusion of the area of surface oil as a parameter in the best fit habitat model at MC indicates a preference for the period without oil, particularly as other parameters in this model are likely to account for any seasonal differences. The comparison of detections during the oil spill to the period just following indicates that there was not significant difference in the short-term, however the seasonal nature of *Kogia* spp. presence at this site may obscure any patterns on the scale of a few months. Over the duration of this data set there was no measurable long-term trend that might indicate a slower response to the spill.

My hypotheses that sea surface temperature (SST) and the distance to the nearest thermal front would be the most important parameters defining *Kogia* spp. habitat were not supported. Although the mean and standard deviation of SST was included in the models for two sites, the relationships were not consistent across sites and SST was not included for the model at MC at all. These results indicate that this parameter is not as important as expected. Additionally the distance to the nearest front was never included in a model for these species. In general I found that although *Kogia* spp. could be detected by the HARPs, we may be missing enough detections that we cannot sufficiently capture the trends in presence and abundance at each site. Also we are lacking a habitat parameter that represents the prey of these deep-diving species, which would very likely improve the predictive capabilities of the models. Continued acoustic analysis of these elusive species, particularly with sampling higher frequencies to improve detection rates, and closer study of deep-diving cetacean prey will greatly enhance our understanding of the *Kogia* species.

Chapter 5 in part, is currently being prepared for submission for publication. Merkens, Karlina; McDonald, Mark; Frasier, Kaitlin; Wiggins, Sean; Hildebrand, John. "*Kogia* spp. ecology and habitat modeling in the Gulf of Mexico". The dissertation author was the primary investigator and author of this material.

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