A PELAGIC PARADOX: THE ECOLOGY OF A TOP PREDATOR IN AN OCEANIC DESERT

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This dissertation is dedicated to my grandfather, Sam Wong, who travelled across the Pacific Ocean many times so that his family would have a better life. And to my grandmother, who was left behind.

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ABSTRACT

Sperm whales (*Physeter macrocephalus*) are widely distributed in all oceans, but principally found in areas of high primary productivity. Historically, they were whaled extensively in the Sargasso Sea and recent surveys have also found large numbers there. However, the Sargasso Sea is an oceanic gyre considered to be low in productivity. This dissertation explores the paradox of a high abundance of large top predators in a body of water once described as an "oceanic desert". First, I compared the diet of sperm whales in the Sargasso Sea to those off Dominica, in the eastern Caribbean. Results suggested differences in trophic ecology between these two areas, with sperm whales in the Sargasso Sea feeding at a higher trophic level. Second, I examined the spatial and temporal distribution of sperm whales in the Sargasso Sea in relation to environmental variables using acoustic surveys and autonomous recording devices. Sperm whale prevalence around Kelvin seamount, part of the New England Seamount Chain, was higher in the spring compared to the winter. Habitat modeling results suggest that the mesoscale activity associated with the Gulf Stream plays an important role in sperm whale occurrence in this area, likely due to the enhancement of primary productivity in this region. Finally, I estimated the current density of sperm whales in the northwestern Sargasso Sea and compared their present distribution to their distribution during the open-boat whaling era (1775-1921). Sperm whale density in the northern Sargasso Sea is one of the highest found globally, showing that this region remains a hotspot for sperm whales. The area where sperm whale detections per unit effort is presently the highest showed little overlap with areas where whales were hunted historically. Whalers all but ignored this region except when transiting to other whaling grounds, perhaps a result of fixed whaling patterns due to the conservative use of knowledge at that time. My dissertation highlights patterns and processes that help to explain the presence and abundance of sperm whales in the Sargasso Sea and demonstrates the importance of western boundary currents, such as the Gulf Stream, to the distribution of marine top predators.

LIST OF ABBREVIATIONS USED

AIC	Akaike Information Criterion
chl-*a*	Chlorophyll-*a* concentration
EKE	Eddy Kinetic Energy
FAO	Food and Agriculture Organization
FGS	Faculty of Graduate Studies
GAM	Generalized Additive Model
GEE	Generalized Estimating Equations
GIS	Geographic Information System
GLM	Generalized Linear Model
IDW	Inverse Distance Weighted
IUCN	International Union for Conservation of Nature
IWC	International Whaling Commission
km	kilometer
m	metre
NGDC	National Geophysical Data Centre
QIC	Quasi-likelihood under the Independence model Criterion
SD	Seamount Distance
SSHA	Sea Surface Height Anomaly
SST	Sea Surface Temperature
UTC	Coordinated Universal Time
wk	week
WWF	World Wildlife Fund

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My parents fostered in me a great love of the outdoors by taking us hiking, camping, canoeing and skiing across the country. Being from Southern Ontario, my exposure to bodies of water consisted mainly of lakes, rivers and catching crayfish in the nearby creeks with my brother. It was our first family trip to British Columbia where my passion for the ocean began. On a misty, rainy day, we went whale watching on a small boat and after many long hours, encountered my first whale: a Pacific gray whale. That moment is forever engrained in my head, as is the very wet, rough ride home that caused half my family to be seasick. I'd like to thank my parents for showing an impressionable girl that underwater world, which ultimately lead me towards a life filled with rough seas.

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CHAPTER 1
INTRODUCTION

It is estimated that oceans cover 71% of our planet and make up about 90-99% of liveable space on earth (Angel 1993, Vega and Wiens 2012). However we know so little about the marine environment in which an estimated 91% of existing species in the ocean have yet to be identified (Mora et al. 2011). Although we have much to learn about the marine environment, we have been, and continue to be, very good at exploiting it. Historically, human exploitation of marine resources has lead to the extinctions of species such as the Great auk (*Pinguinus impennis*) (Bengtson 1984) and the Steller sea cow (*Hydrodamalis gigas*) (Turvey and Risley 2006) and the extirpation of species such as the North Atlantic gray whale (*Eschrichtius robustus*) (Bryant 1995, Mead and Mitchell 1984). Presently, the populations of marine top predators are declining at an alarming rate due to factors such as over-fishing (Myers et al. 2007, Myers and Worm 2003, Schindler et al. 2002). The effects of climate change are also causing population declines of marine top predators (Hyrenbach and Veit 2003, Veit 1997). These widespread population declines of marine top predators can have extensive cascading effects on the ecosystem (Estes et al. 2011, Myers et al. 2007).

Marine top predators are effective bio-indicators (Furness and Camphuysen 1997) and studying their distribution provides a better understanding of not only their prey populations, but also the health and status of marine ecosystems (Ballance 2007, Furness and Camphuysen 1997, Moore et al. 2008, Piatt et al. 2007, Sydeman et al. 2006). Marine top predators can be used to monitor changes in the integrity of marine ecosystems (Boyd et al. 2006) and provide insight into the effects of climate change in our oceans (Hazan et al. 2012, Wassmann et al. 2011). Studying the habitat use of marine top predators can inform conservation and management practices through the identification of marine “hotspots” (Block et al. 2011, Kaschner et al. 2011, Sydeman et al. 2006, Worm et al. 2003) that can ultimately lead to the identification, delineation, and establishment of sites for marine protected areas (Embling et al. 2010, Hooker et al. 2011, Ronconi et al. in press). Recently, the need for marine protected areas in *pelagic* systems has been recognized (Game et al. 2009, Hislop 2007), highlighting the importance of understanding the spatial and temporal distribution of marine top predators in the open ocean (Hyrenbach et al. 2000, Louzao et al. 2011).

The spatial and temporal distribution of organisms is non-random and animals select habitats through a series of hierarchal behavioural processes which maximize their survival and fitness (Block and Brennan 1993, Hutto 1985). The way in which species use a set of physical environmental factors to meet life requirements, such as feeding, reproduction, and rearing of young, is called habitat use (Block and Brennan 1993, Jones 2001). Terrestrial and marine processes operate on different spatial and temporal scales (Steele 1985, Steele 1991) and studying habitat selection in the marine ecosystem can be difficult due to its highly dynamic nature. Oceanic processes vary over temporal scales ranging from seconds to centuries and range spatially from millimetres to thousands of kilometres (Halley 2005) and the importance of taking spatial scale into account in studies of marine ecosystems is well documented (Jaquet 1996, Piatt 1990, Pinaud and Weimerskirch 2007, Schneider 2001).

Habitat-predator associations at large scales (10s to 100s km) can occur over ocean basins and are influenced by water masses, while habitat-predator associations at meso-scales (1s to 10s km) can occur at distinct physical features like fronts and eddies (Hunt et al. 1999). Finally, habitat-predator associations at fine scales (m to 10s m) can occur where prey are concentrated (Hunt et al. 1999). The relationship between temporal and spatial associations of predators and their prey will depend on whether physical processes aggregate prey directly, or result in enhanced primary production which, indirectly, results in higher abundance of prey (Hunt et al. 1999). The former case results in relationships at small spatial and temporal scales (Hunt et al. 1998, Piatt 1990), while the latter case results in relationships at larger scales that can span for 100s of kilometres and over several months (Jaquet and Whitehead 1996, Pirotta et al. 2011). Some physical processes, such as upwelling events associated with eastern boundary currents and shelf edges, result in predictable food patches and habitat associations that exist over large spatial and temporal scales (Weimerskirch 2007).

1.1 STUDY SPECIES – THE SPERM WHALE

My study species, the sperm whale (*Physeter macrocephalus*), is an important marine predator. Using Lockyer (1981)'s consumption rates and a population size of 361 400 animals (Whitehead 2002), Whitehead (2003) estimated that sperm whales consume about 100 Mt/yr (Whitehead 2003), which is comparable to the total annual catch of human marine fisheries over the last five years (~90 Mt/yr between 2006-2011; (FAO 2012)). Although global populations are not presently experiencing decline (Taylor et al. 2008), sperm whales were hunted extensively from the 18th to the last part of the 20th century (Bannister et al. 2008, Smith et al. 2012, Starbuck 1878) and recent population estimates indicate that their populations are currently only 32% of the pre-whaling level (Whitehead 2002). Sperm whales feed mainly on meso- and bathy-pelagic cephalopod species, and some fish (Kawakami 1980), for which they regularly dive to 800m, although dives to 2000m have been recorded (Whitehead 2003). Deep foraging dives make up 62% of a sperm whale's life (Whitehead 2003). Sperm whales are rarely found in waters above the continental shelves, preferring waters deeper than 1000m (Caldwell et al. 1966). Thus, the sperm whale is a creature of the deep ocean.

The diversity of cephalopods encompassing sperm whale diet include: the small chiroteuthids (<100g), the medium-sized and weakly-muscled histioteuthids, the ferocious Humboldt squid (*Dosidicus gigas*) and the giant architeuthids (400 kg) (Clarke et al. 1993, Smith and Whitehead 2000, Whitehead 2003). However, except for a few species (e.g. Humboldt squid), there is little overlap between sperm whale diet and human fisheries and very little is known about the cephalopod species upon which they prey. In fact, some of what we do know about these cephalopod species comes from sperm whales themselves (Clarke 1980, Clarke 1987). Studying the foraging ecology of these deep divers can provide insight into the deep water community of their prey and provide insight into their pelagic, deep-water habitat.

Watwood et al (2006) suggested that the success of sperm whales as predators can be attributed, in part, to their long-range echolocation. Sperm whales are equipped with one of the most powerful sonars in the world (Møhl et al. 2000), used predominately for finding prey. Their vocalizations consist of a series of clicks, which are produced in their nasal complex (Whitehead 2003) with most energy between 5 and 25 khz (Madsen et al. 2002b). These clicks are used primarily in echolocation and communication and are arranged in various patterns: usual clicks, slow clicks, creaks and codas. Usual clicks are thought to function primarily in searching echolocation and are a long train of regularly spaced clicks (0.5s-1.0s) that can last for several minutes (Jaquet et al. 2001, Madsen et al. 2002a, Whitehead and Weilgart 1990). Creaks made at depth are thought to occur when whales are homing in on prey (Whitehead 2003). One important component of this sonar system is the spermaceti organ, which contains spermaceti oil (Møhl 2001), however, during the 18th century, the value of spermaceti oil for use in candle-making and lubricant for delicate machinery (Proulx 1986), resulted in an extensive commercial hunt that lasted for a century (Starbuck 1878).

Sperm whales are one of the most widely distributed cetaceans in the world, found in all oceans from the equator to the pack ice of both poles (Rice 1989). Females and their offspring are found in the warmer waters of the tropics and sub-tropics (approximately between 40^{o}S and 40^{o}N in the Atlantic) while males also use higher latitudes, up to the polar waters (Rice 1989). Females form long-lasting associations, but males leave their natal group at about age ten and move to cooler waters, forming labile “bachelor” schools (Best 1979). Mature males periodically return to tropical waters to mate, though not much is known about this migration (Best 1979). Much of what we know about the habitat use of sperm whales comes from partially enclosed bodies of water, such as the Gulf of Mexico (Biggs et al. 2006, Davis et al. 2002, Scott-Hayward 2006), the Sea of Cortez (Jaquet and Gendron 2002), and the Mediterranean (Gannier et al. 2002, Gannier and Praca 2007, Pirotta et al. 2011, Praca et al. 2009), or pelagic island systems such as the Galapagos (Smith and Whitehead 1993, Whitehead 1996, Whitehead et al. 1989). Some research in the South Pacific has provided insight into the what drives sperm whale distribution in the open ocean (Jaquet and Whitehead 1996, Jaquet and Whitehead 1999), however with the exception of limited work by Waring and colleagues (Waring et al. 1993, Waring et al. 2001), virtually nothing is known about the temporal or spatial distribution in the pelagic waters of the Atlantic Ocean.

1.2 THE NORTH ATLANTIC OCEAN AND THE SARGASSO SEA

The Atlantic Ocean derives its name from the Greek god, Atlas. The open-boat sperm whale hunt began in the North Atlantic Ocean in the early 18th century and lasted until the end of modern whaling in the first part of the 20th century (Bannister et al. 2008, Starbuck 1878). Whalers focused their whaling efforts in distinct areas, called "grounds" and some of these grounds were hunted over a century (Bannister et al. 2008, Starbuck 1878). One part of the North Atlantic where sperm whales were consistently hunted is the Sargasso Sea (Bannister et al. 2008, Townsend 1935).

The Sargasso Sea (Figure 1.1) lies in the middle of the North Atlantic (between the parallels 20° and 35° N and the meridians 30° and 70° W) and is an oceanic gyre bounded by ocean currents of the Gulf Stream to its west, the North Atlantic Current to its north, the Canary Current to its east and the North Atlantic Equatorial Current to its south. The warm, clear waters of the Sargasso Sea were described as some of the poorest on earth (Blackburn 1981) and traditionally regarded as lifeless, save for the presence of masses of *Sargassum* seaweed, and their dependent fauna. However, this view is currently being debated, with researchers demonstrating that primary productivity in the Sargasso Sea is higher than previously assumed (McGillicuddy and Robinson 1997, McGillicuddy et al. 1998, Oschlies and Garçon 1998). My study area within the Sargasso Sea (Figure 1.1) is defined as waters deeper than 1000m and north of 23.5^0N and west of 50^0W. This area encompasses prominent bathymetric features such as the New England Seamount Chain and the island of Bermuda and is also bounded by a western boundary current: the Gulf Stream.

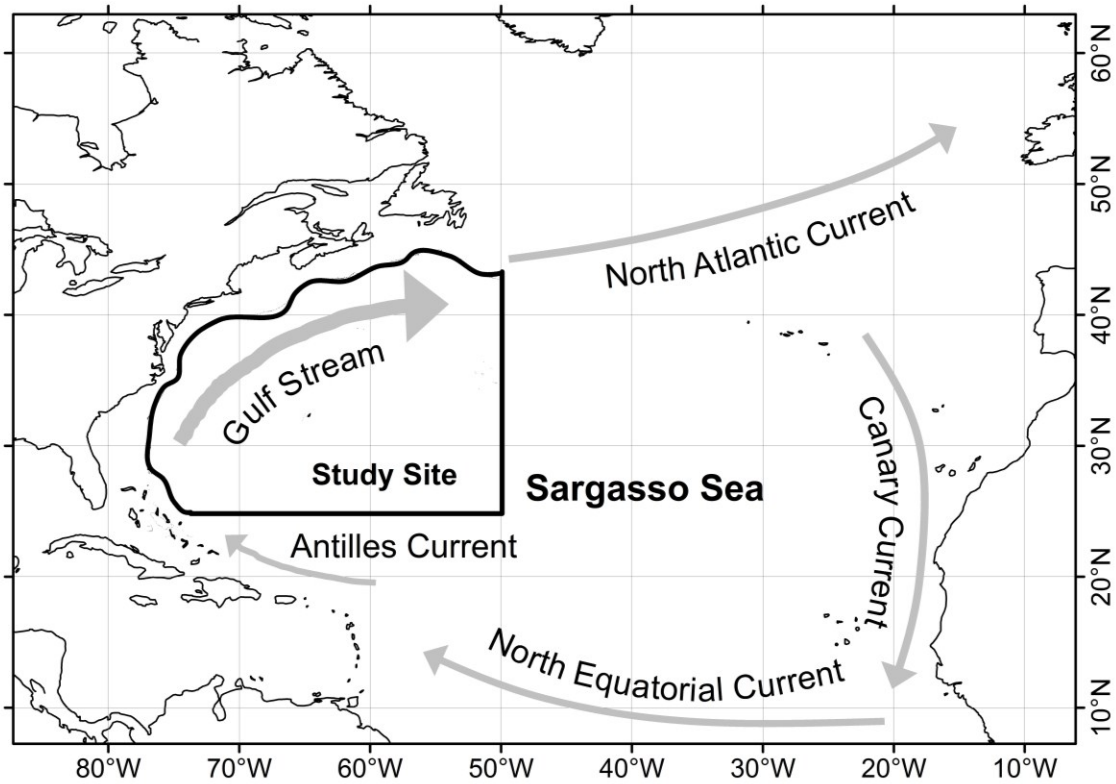

Figure 1.1 Map showing the location of the Sargasso Sea with surrounding currents. The study site is outlined in black.

The North Atlantic Ocean's bathymetry is characterized by the Mid-Atlantic Ridge, an underwater mountain range 3000 m from the seafloor, which separates the North American Plate from the Eurasian Plate in the North Atlantic Ocean. Thousands of seamounts and knolls, many associated with the Mid-Atlantic Ridge, riddle the ocean floor (Yesson et al. 2011). Seamounts are undersea mountains that rise steeply from the sea floor to below sea level and are known to influence oceanographic processes (as reviewed in Rogers, 1994). Seamounts, like other prominent topographic features, result in increased turbulence, mixing and mesoscale eddies, which transport nutrients into the euphotic zone, thereby increasing local production (Oschlies and Garcon 1998, Wolanski and Hamner 1988). Top ocean predator (e.g. large tuna, billfishes, sharks) diversity peaked near promiment topographic features, such as the seamounts in Hawaii and South East Australia (Worm et al. 2003). Worm et al. (2003) stressed the importance of prominent topographic features in food stressed areas, such as the open ocean.

The Gulf Stream is characterized by its warm, fast, narrow and deep flow (Loder et al. 1998, Mann and Lazier 1996, Tolmazin 1985). Mesoscale activity associated with the Gulf Stream, such as cold-core rings, eddies and meanders, increases primary and productivity in this area (Fuglister 1972, The Ring Group 1981, Orner et al. 1978) and may also influence the occurrence of marine top predators. For example, Podesta et al. (1993) found higher swordfish (*Xiphius gladius*) catch rates in the vicinity of fronts associated with the Gulf Stream. Seabird densities have also been related to cold-core filaments of Gulf Stream eddies and rings and Gulf Stream fronts (Haney 1985, Haney 1986a, Haney 1986b, Haney and McGillivary 1985).

Some of the processes and other mechanisms that drive other marine top predator distribution in this area may explain the paradox of many sperm whales - presently and historically - in an “unproductive” ocean: the Sargasso Sea. Studying the habitat use of sperm whales in the Sargasso Sea would provide us with a better understanding of factors that drive sperm whale distribution in the open ocean.

1.3 THESIS OUTLINE

The goal of this thesis is to examine habitat selection of sperm whales over a broad range of both temporal and spatial scales, to better understand how this top marine predator uses the open ocean. At a large scale, I will examine how sperm whales use the northwestern part of the Sargasso Sea, at a mesoscale, how they use a specific area within the Sargasso (the New England Seamount Chain) and at a fine scale, I will examine their diet. This thesis also examines sperm whale habitat use over different temporal scales including diet and foraging success over hours and days, seasonal use of the Sargasso Sea, and use of the Sargasso Sea over many years and centuries. The overall objective of my thesis is to provide an answer to the riddle of how a dense population of large, warm-blooded top predators can exist in an apparently “lifeless ocean”.

Chapter 2: This chapter examines the fine scale habitat use of sperm whales by investigating the diet of sperm whales in the Sargasso Sea and comparing it to that in the Caribbean using several approaches.

Chapter 3: In this chapter, I investigate the mesoscale habitat use of sperm whales in the northwestern part of the Sargasso Sea. I examined the temporal occurrence of sperm whales over the New England Seamount Chain in relation to oceanographic variables.

Chapter 4: This chapter examines the habitat use of sperm whales over a large spatial scale: the northwestern part of the Sargasso Sea. The objectives of this chapter are to identify predictors of sperm whale abundance and examine the relationship between environmental variables, movement and foraging success.

Chapter 5: In this final data chapter, sperm whale distribution is compared over large temporal scales: the contemporary distribution that spans decades (1993-2010) and the historical distribution that spans centuries (1775-1921). I also estimate the current density of sperm whales in the northwestern part of the Sargasso Sea.

Chapter 6: My thesis concludes with a discussion of the overall findings of my data chapters in the broad, overall context of what we know about marine top predator distribution in the open ocean and how my research may contribute to areas where information is lacking.

CHAPTER 2
SPATIO-TEMPORAL VARIABILITY OF SPERM WHALE (*PHYSETER MACROCEPHALUS*) DIET IN THE WESTERN NORTH ATLANTIC: EVIDENCE FROM STABLE ISOTOPES AND HARD-PART ANALYSIS

The work presented in Chapter 2 was submitted for publication:
Wong, S.N.P., V.L Yaroshewski*, H. Whitehead. Spatio-temporal variability of sperm whale (*Physeter macrocephalus*) diet in the western North Atlantic: evidence from stable isotopes and hard-part analysis. Marine Biology. Manuscript No: MABI-D-12-00487.
* V. Yaroshewski was responsible for the mtDNA barcoding portion of this paper.

2.1 INTRODUCTION

Large marine predators play a vital role as top consumers in marine ecosystems, yet their numbers have generally declined over the last several decades (Tremblay-Boyer et al. 2011). This has consequences for the lower trophic levels on which they prey (Myers and Worm 2003). Marine predators can be used as indicator species (Boyd and Murray 2001) and studying the trophic interactions and movements of marine predators in coastal and open-ocean ecosystems can identify critical habitat in these areas (Block et al. 2011).

Sperm whales are important mammalian predators in the ocean. The yearly biomass that the world population of sperm whales consumes is comparable to the total annual catch of all human marine fisheries (Whitehead 2003). Sperm whales feed mainly on meso- and bathy-pelagic cephalopod species and studying the foraging ecology of these deep divers can provide insight into the deep water community of their prey.

Studying the diet of sperm whales and other marine organisms is challenging because it is not generally possible to directly observe prey consumption. Much of what is known about sperm whale diet comes from analysis of stomach contents of stranded animals

(Evans and Hindell 2004) or those caught for commercial whaling (Clarke and MacLeod 1976, Clarke et al. 1976, Clarke and Roeleveld 1998). More recently, squid beaks collected from fecal samples of free-ranging sperm whales have been used to determine diet (Smith and Whitehead 2000). Analyses of stomach contents or fecal samples both present biases, which include: differential defecation or vomiting of beaks, failure to ingest the head, instances where collected beaks are the prey of the sperm whale's prey and in the case of fecal sample collection, the fact that large beaks sink faster and may be missed (Clarke et al. 1980, Clarke et al. 1988, Smith and Whitehead 2000, Clarke and Paliza 2001). Such biases will affect the overall assessment of sperm whale diets, perhaps making it difficult to compare across regions.

Molecular methods, such as mitochondrial DNA sequencing of soft cephalopod tissue found in association with feeding sperm whale groups is another tool that can be used to study sperm whale diet. However, only a relatively small number of cephalopod species have been sequenced at the mitochondrial cytochrome c oxidase (COI) locus (about 30% of known species) (Strugnell and Lindgren 2007), the region used to match samples to Genebank and BoLD databases. The level of accuracy to which this gene locus can be used to identify an unknown specimen is under debate and may depend on the family of cephalopods to which the query specimen belongs. Therefore, some caution must be taken when attempting to assign an unidentified cephalopod specimen to a sequence within the GenBank or BoLD search databases. Furthermore, the distribution of specimens recovered near feeding sperm whales may not well reflect their dietary intake.

The use of stable isotope analysis provides another method to examine the feeding ecology of sperm whales. Stable isotope signatures of predators reflect the isotopic composition of their assimilated prey, thus providing dietary information integrated over longer time scales than stomach contents or fecal samples (Deniro and Epstein 1978, Deniro and Epstein 1981, Hobson et al. 1994). Based on studies on the epidermal turnover rate of other odontocetes, Ruiz-Cooley et al. (2004) suggested that the turnover rate of sperm whale skin is at least 75 days, so the isotopic composition of skin reflects an average of the prey composition over this time scale. More specifically, $\delta^{15}N$ isotopes are used to indicate trophic position (Deniro and Epstein 1981) and in marine systems, δC13 reflects the relative primary productivity of an area (Newsome et al. 2010), with higher δC values in more productive, near-shore regions compared to more oligotrophic, pelagic systems (Hobson 1999). Baseline isotope signatures also differ among geographic regions and may enable inference related to movement patterns using ‘isoscapes’ (Graham et al. 2010, Jaeger et al. 2010). Stable isotope analysis has been used to examine the trophic ecology of sperm whales in the Pacific (Ruiz-Cooley et al. 2004, Marcoux et al. 2007) and the Gulf of Mexico (Ruiz-Cooley et al. 2010) using sloughed skin of focal sperm whales, as well as cephalopod beaks and soft tissue (e.g tentacles).

We studied sperm whale diets in two portions of the western North Atlantic: the Sargasso Sea and the eastern Caribbean Sea. The Sargasso Sea is a sub-tropical gyre which is bounded by ocean currents. In the past, the waters of the Sargasso Sea have been described as some of the “poorest on earth” (Blackburn 1981). However, mesoscale eddies, rings, and meanders associated with the Gulf Stream lead to increased productivity in the nutrient-poor waters of the Sargasso (Orner et al. 1978; Yoder et al. 1981). Large numbers of sperm whales (groups of adult females and immatures) are found in the Sargasso Sea, especially in the more energetic northwest portion (Chapter 5). It is not known which prey species are consumed by sperm whales in the Sargasso Sea, since beaks are rarely found in fecal samples compared to other areas in the Pacific and western North Atlantic Oceans. The movement of individuals in this area is also unknown, with no matches to photo-identification catalogues in other areas of the Atlantic. Sperm whales are also found in other parts of the western North Atlantic, such as the Eastern Caribbean Sea (Gero et al. 2007). Islands in the Lesser Antilles, such as Dominica, experience increased productivity on the Caribbean side as a result of downstream turbulence (Ingham and Mahnken 1966) and the “island mass” effect (Doty and Oguri 1956, Sander 1981). Comparing the feeding ecology of sperm whales between these two areas may shed insight into how two very different ecosystems can support substantial numbers of sperm whales.

The objectives of our study was to compare the foraging ecology of sperm whales in the Sargasso Sea and Dominica using stable isotope analysis, hard-part analysis and mitochondrial sequence analysis to assess diet. This study will provide a broader understanding of the feeding ecology of this important predator in the Atlantic Ocean and also shed insight into the cephalopod community in a remote and poorly studied area, the Sargasso Sea.

2.2 METHODS

2.2.1 Data Collection

Studies were conducted from a 12m sailing vessel or a 5m motor vessel during May and June in the Sargasso Sea, 2004-2007, and between January and May off Dominica in 2005, 2007-2009 (Figure 2.1). Research within the Sargasso Sea occurred east and south of the Gulf Stream in warm waters deeper than 1000m (bounded by latitudes 40^0N and 30^0N and longitudes 57^0W and 71^0W). Groups of whales (composed of adult females, immatures and calves) were tracked using a directional hydrophone. The size of each group was not determined for this study, but average group size in the Sargasso is 12.0 ± SD 6.6 and in Dominica is 6.6 ± SD 0.5 (Gero et al. 2009).

Individuals were identified using photo identification of flukes at the beginning of deep dives. After each observed dive, the vessel immediately approached the dive site. Within one minute from the time the whale dove, a dip net was used to collect squid beaks from fecal samples (if present). Beak rate (total number of beaks collected divided by the total number of defecations observed) was also calculated for each study site. Naturally-sloughed whale skin samples were collected while closely following focal animals. If skin samples were not from individuals that could be photographically identified, we used samples from the same group on different days. When that was not possible, we used samples on the same day from different encounters (to minimize the chance of re-sampling the same individual). While every pre-caution was taken to minimize sampling skin from the same individual, all fecal samples were used, regardless if multiple samples came from the same individual. Since sperm whales are highly sexually dimorphic (Rice 1989), mature males are easy to identify in the field. Samples from mature males (occasionally encountered) were not included since their stable isotope signatures would reflect the high latitudes where they are found (Rice 1989). Calves were not included in the analysis because they were assumed to be nursing, which results in nitrogen enrichment between mother and offspring (Hobson et al. 1987, Valenzuela et al. 2010). Soft tissue of cephalopods (eg. pieces of tentacle or mantle) found in proximity to sperm whale groups was also collected opportunistically. Samples were stored in 70% ethanol except for five whale skin samples that were stored in a dimethyl sulfoxide (DMSO) solution.

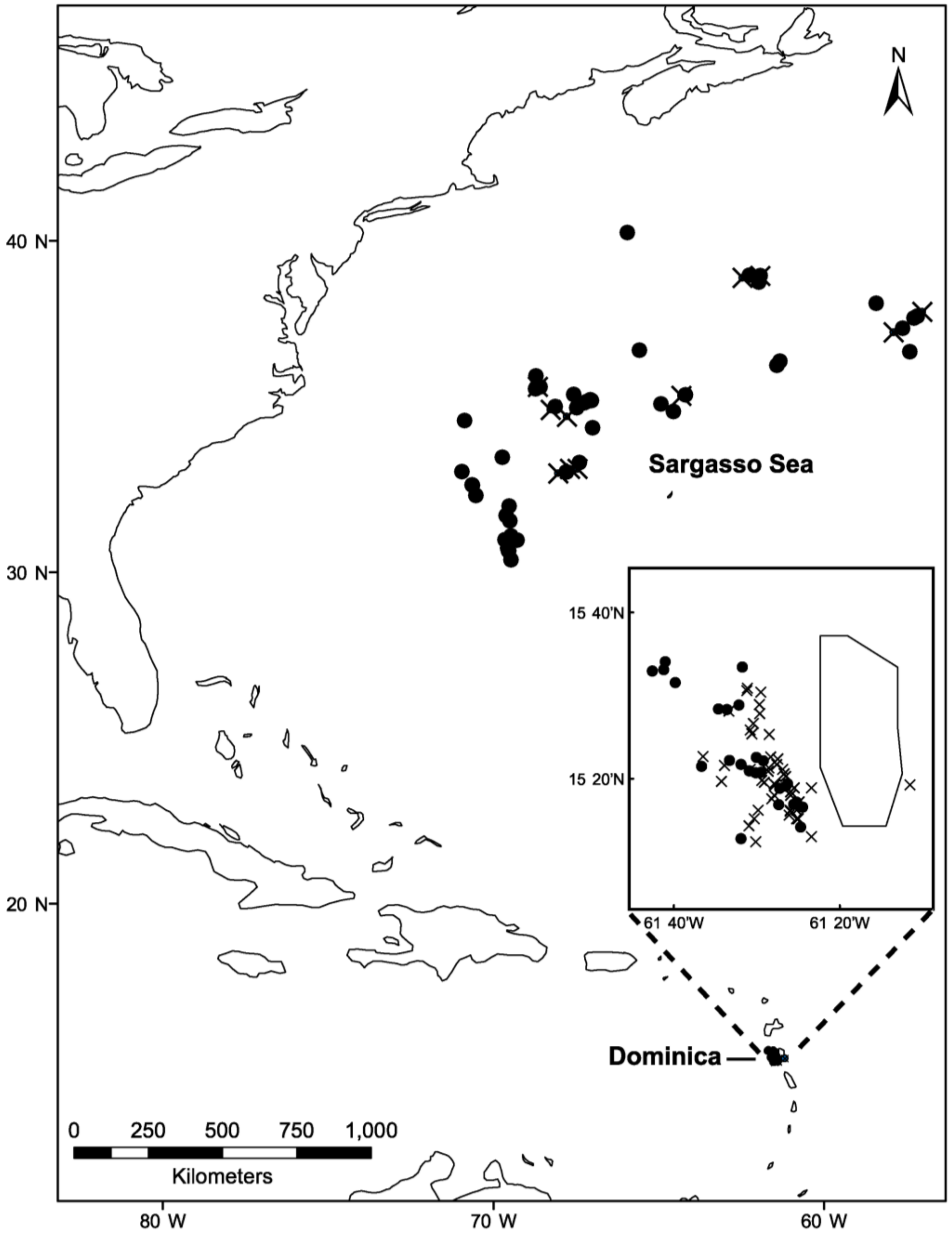

Figure 2.1 Map of study area showing locations of collected samples in the Sargasso Sea and off Dominica. ● represents whale skin samples collected. X represents prey samples collected (beaks from fecal samples and soft tissue from squid).

2.2.2 Hardpart Analysis

The cephalopod beaks collected in the fecal samples were cleaned with ethanol. Only the lower beaks were used for identification because an appropriate set of keys has not been developed for the upper beaks. The lower beaks were identified to genus according to the keys developed by Clarke (1986), although sometimes beaks could only be identified to family. Updated photographs and descriptions by Young and Vecchione (2004) were also used, and a reference collection of beaks identified to genus for a previous study (Smith and Whitehead 2000) was also used to aid identification. The lower beak rostral length (LRL) is a standard beak measurement made from the rostral tip to the corner of the jaw angle and was measured using a Wild Heerbrugg microscope with a reticulated eyepiece (accurate to the nearest 0.16mm). Where possible, the LRL measurements of the cephalopod beaks, r, were used to estimate wet weight (g), W, and mantle length (mm), l, of the squid using regression equations for *Histioteuthis* spp., *Chiroteuthis*, *Mastigoteuthis* and *Brachioteuthis* from Clarke (Clarke 1986).

2.2.3 DNA Sequencing

For the cephalopod tissue collected opportunistically, regular identification using keys was not performed because these tissue samples did not have enough distinguishing features to identify the genus of cephalopod. However, total DNA was extracted according to the "Glassmilk" protocol outlined in Elphinstone et al. (2003). A 648 base pair fragment of the mitochondrial cytochrome *c* oxidase subunit I (COI) gene was amplified using Polymerase Chain Reaction (PCR). The forward and reverse primers used were the universal COI primers listed in Folmer et al. (1994):

LCO1490 - 5' - GGT CAA CAA ATC ATA AAG ATA TTG G - 3'
HCO2198 - 5' - TAA ACT TCA GGG TGA CCA AAA AAT CA - 3'

The purified PCR product was sequenced, after which the raw sequences were verified and corrected by eye, and aligned with the program BioEdit 7.0.9 (Hall 1999). These COI sequences from the unidentified specimens (the query sequences) were submitted to the online search database within Barcode of Life (BoLD) and GenBank, to compare sequences to attempt to identify the species of the unknown tissue samples. Within BoLD, the highest search criteria were used first (the unknown sequence was compared to verified and referenced sequences), and only if a match was not found were the less-constrained options chosen. A successful species "match" was defined as a sequence return of 98-100% identity match with a subject sequence based on the percent coverage or overlap, as well the number of common bases relative to the total sequence length and number of inserts when the query sequence was aligned with the subject sequence. Numerous examples in the literature demonstrated that intra-specific divergences were rarely found to be above 2%, and generally less than 1% (Avise 2000, Hebert et al. 2004, Roe and Sperling 2007). Indeed, a study examining COI sequence divergence in 13,320 congeneric species pairs from 11 different phyla reported that 98% of the species pairs showed greater than 2% sequence divergence (Hebert et al. 2003). We assumed that intra-specific sequence divergences in cephalopods would be similar. Rates of evolution for mitochondrial DNA tend to be elevated in molluscs, but COI does not behave the same for all cephalopod sequences (the rates of evolution are not consistent) (Strugnell and Lindgren 2007 and references therein). For example, mean sequence divergence in COI was found to be 2.3% in Decapodiformes and 5.9% in Octopodiformes (Carlini and Graves 1999). Also, Sinclair et al. (2007) observed 2.96% COI sequence divergence across geographically isolated populations of *Nautilus* in the Great Barrier Reef and Coral Sea, while as much as 10% COI sequence divergence was reported in populations of the same species of *Euprymna* (Strugnell and Lindgren 2007). However, it was indicated that molluscs showed a mean sequence divergence value of 11.1% (over all species pairs), and about 80% of the congeneric species pairs showed greater than 8% COI sequences divergence (Hebert et al. 2003). Therefore, we also assumed that a query sequence return of 90% or greater in terms of identity match/sequence overlap to a subject sequence within the two databases signified a positive identification within family or genera. Caution must be taken, however, given that in BoLD, only about 30% of *known* cephalopod species have been sequenced at the COI gene, and of these only 8 species have sequences from at least 5 individuals (Strugnell and Lindgren 2007).

2.2.4 Stable Isotope Analysis

Samples were prepared following techniques used in other studies of marine mammals (Marcoux et al. 2007) and cephalopods (Cherel and Hobson 2005). The lower wing from the beaks was used for isotope analysis. The lower wing encompasses the most recent growth and thus reflects the most recent diet of the individual (Cherel and Hobson 2005, Cherel et al. 2009a). All samples were dried at 60^0F for 24 hours. The five skin samples stored in DMSO solution were soaked and rinsed twice in distilled water before being dried; this technique results in no significant difference in carbon and nitrogen signatures between samples stored in DMSO solution and ethanol after lipids are extracted (Hobson et al. 1997, Todd et al. 1997, Marcoux et al. 2007). Lipids were extracted from skin and cephalopod tissue by soaking samples in a 2:1 solution of chloroform and methanol. Samples were re-dried and then ground into a homogenous mixture. It was not possible to grind the beak samples. Instead these were cut into very small pieces. Subsamples (~0.25 mg) of each were analyzed for stable isotope signatures of carbon (δ^{13}C) and nitrogen (δ^{15}N). Isotope ratios were measured using a Delta Plus continuous flow stable isotope ratio mass spectrometer (Thermo Finnigan / Bremen-Germany) coupled to a Carlo Erba elemental analyzer (CHNS-O EA1108).

Stable isotope ratios are expressed in δ notation as parts per thousand (‰) deviation from standard material (Peedee Belemnite rock for ^{13}C and atmospheric air for ^{15}N), according to the following equation:

$$\delta X = [(R_{\text{sample}} / R_{\text{standard}}) - 1] \times 1000$$

where X is ^{13}C or ^{15}N and R is the corresponding ratio ^{13}C/^{12}C or ^{15}N/^{14}N. Samples were run with standards interspersed every 8 samples and results were corrected to these standards. Ammonium sulphate (IAEA-N1 and IAEA-N2) were used as standards for nitrogen and carbon standards were IAEA-CH6 (sugar), EIL-72 (cellulose) and EIL-32 (graphite). The error for standard material is ± 0.2 ‰ for carbon and ± 0.3‰ for nitrogen.

2.2.5 Data Analysis

To examine the variability in stable isotope signatures of sperm whale skin in the Sargasso Sea and Dominica, a generalized linear model with an identity link function was used to examine the relationship between δ^{15}N and δ^{13}C signatures and the following variables: location (Sargasso versus Dominica), year (nested within location) and group (nested within location). We did not determine the sex of skin samples and thus all samples (adult females and immature males and females) were grouped together in the analysis. Ruiz-Cooley (2004) found no difference in isotope signatures between adult females and immature males. Statistical analysis was performed on the two different types of prey tissue (beaks and soft tissue) separately. A generalized linear model with an identity link function was again used to examine the relationship between δ^{15}N and δ^{13}C signatures of beaks and the following variables: location (Sargasso versus Dominica), genus/family, and size (LRL). *t*-tests were used to compare mean δ^{15}N and δ^{13}C values for sperm whale and squid soft tissues between the Sargasso Sea and Dominica.

2.3 RESULTS

2.3.1 Hardpart Analysis

A total of 71 lower beaks (6 from Sargasso Sea, 65 from Dominica) were collected over four field seasons in both study sites, of which all but 2 could be identified to genus. Over four field seasons, the total number of beaks collected per observed defecation (beak rate) was lower in the Sargasso Sea (mean = 0.09 ± 0.08, total number of defecations = 91) compared to Dominica (mean = 0.26 ± 0.26, total number of defecations = 295), but this difference was not significant (*t*-test, $t_6 = 1.205$, $p = 0.273$). The beaks collected from sperm whales off Dominica comprised 7 genera, where *Histioteuthis* spp. were most frequent (percent occurrence = 80.0%) followed by *Discoteuthis* (10.1%) (Table 2.1). Two genera were identified from the Sargasso Sea samples, with *Histioteuthis* spp. being most common (66.7%) (Table 2.1). The smallest cephalopods in the diet of sperm whales in the Sargasso Sea and off Dominica were of the genus *Chiroteuthis* (LRL = 3.4mm from Sargasso Sea, 4.1 ± 1.3mm from Dominica). There was no significant difference in *Histioteuthis* beak size for samples collected in the Sargasso Sea (LRL = 5.2 ± 0.4mm) and Dominica (LRL = 5.1 ± 0.7mm; t-test, $t_{54} = -0.324$, $p = 0.747$). Beaks from the genus *Discoteuthis* (LRL = 5.4 ± 0.8mm), *Mastigoteuthis* (LRL = 6.6 ±0.5mm) and *Octopoteuthis* (LRL = 9.1mm) were only collected from Dominica (Table 2.1).

Overall, there were no significant or obvious differences in the species composition or sizes of the beaks collected from sperm whale faeces in the two locations, though sample size for the Sargasso is very small, thus reducing power.

Table 2.1 Summary of beaks collected from fecal samples of free ranging sperm whales in the Sargasso Sea and off Dominica Island in the Caribbean. Lower rostral length (mm) (LRL) was used to estimate mantle length (mm) and wet weight (g) according to Clarke (1986).

Sargasso Sea

Genus/Family	n	%	LRL (mm) mean ± SD	LRL Range (mm)	Mantle length (mm) mean ± SD	Wet weight (g) mean ± SD
Histioteuthis	4	66.7	5.2 ± 0.4	4.8 - 5.7	101.1 ± 8.5	219.8 ± 38.1
Chiroteuthis	1	16.7	3.4	--	95.6	22.1
Unknown	1	16.7	4.8	--	--	--

Dominica

Genus/Family	n	%	LRL (mm) mean ± SD	LRL Range (mm)	Mantle length (mm) mean ± SD	Wet weight (g) mean ± SD
Histioteuthis	52	80.0	5.1 ± 0.7	2.8 - 6.6	98.6 ± 14.8	213.1 ± 64.3
Discoteuthis	7	10.8	5.4 ± 0.8	4.6 - 6.9	--	--
Chiroteuthis	2	3.1	4.1 ± 1.3	3.2 - 5.0	111.7 ± 31.2	39.4 ± 20.1
Mastigoteuthis	2	3.1	6.6 ± 0.5	6.3 - 7.0	191.3 ± 13.5	282.2 ± 56.4
Octopoteuthis	1	1.5	9.1	--	157.3	193.8
Unknown	1	1.5	--	--	--	--

2.3.2 DNA Sequencing

A total of 20 cephalopod tissue samples (6 from the Sargasso Sea and 14 from Dominica) were sequenced at the mitochondrial COI gene. Of these, only three of the unknown specimen sequences had confident taxonomic identification to species when compared to known sequences within the search databases of GenBank and BoLD (Table 2.2). Two of these samples, which were collected in the Sargasso Sea, were matched to *Architeuthis dux* (100% in BoLD and GenBank) and *Cycloteuthis sirventi* (99.85% in BoLD and 99% in GenBank). The third sample, collected from Dominica, was identified as *Histioteuthis* *hoylei* (98.62% match in BoLD and 98% match in GenBank). However, this species is restricted to the Pacific and Indian oceans. Recently, *H. hoylei* was reclassified and the Atlantic form is now called *H. arcturi* (Integrated Taxonomic Information System, 2011). Therefore, it is believed that this third specimen was likely *H. arcturi*.

From the other attempts to match the query sequences within the search databases, three further samples were identified to family with relative confidence (Table 2.2). Two of these tissue samples were from the Sargasso Sea and were likely from the family Lepidoteuthidae (92.51% in BoLD and 92% in GenBank for *Lepidoteuthis grimaldii*). These two samples were likely *Lepidoteuthis gramaldii* as this is the only species belonging to the Lepidoteuthidae family. The third sample, from Dominica, was likely from the family Onychoteuthidae (89.61% in BoLD and 89% in GenBank for *Onychoteuthis borealijaponica*). Thus, there were no overlaps in species or family between the soft cephalopod tissues collected in the Sargasso Sea or Dominica. Finally, while most of the other query sequences could not be identified, twelve of these had very similar sequences (those most closely matched to *Ancistrocheirus* spp. and *Gonatopsis* spp. with about 84%) (Table 2.2). Furthermore, there was a mean sequence divergence of 0.76% (with a range of 1 to 12 base positions differing) between all pairs of individuals, suggesting that these individuals were the same species, likely one which has not yet been described in GenBank or BoLD.

Table 2.2 The top taxonomic identification matches of the unknown diet tissue samples to known species from within the BoLD and GenBank search databases. The top match species name and percent similarity of the query sequence to the database specimen sequence is presented. The sequence accession number is also given for the specimen sequences from GenBank.

Query Sample Name	**Search Database**	**Top Identification Match**	**% Similarity**	**GenBank Accession No.**
BSH3	BoLD	*Lepidoteuthis grimaldii*	92.66	
	GenBank	*Lepidoteuthis grimaldii*	92	AF000049
DHS24	BoLD	*Gonatopsis japonicus*	84.62	
	GenBank	*Ancistrocheirus lesueuri*	84	GU220397
DSH23	BoLD	*Gonatopsis japonicus*	84.76	
	GenBank	*Ancistrocheirus lesueuri*	84	GU220397
DSH35A	BoLD	*Gonatopsis japonicus*	87.91	
	GenBank	*Notonykia sp.*	88	EU735378
DSH48	BoLD	*Gonatopsis japonicus*	84.41	
	GenBank	*Ancistrocheirus lesueuri*	84	GU220397
Sarg07_01	BoLD	*Architeuthis dux*	100	
	GenBank	*Architeuthis dux*	100	JF710644
Sarg07_02	BoLD	*Cycloteuthis sirventi*	99.85	
	GenBank	*Cycloteuthis sirventi*	99	AF000036
Sarg07_03	BoLD	*Gonatopsis japonicus*	84.37	
	GenBank	*Ancistrocheirus lesueuri*	83	GU220397
Sarg07_04	BoLD	*Gonatopsis japonicus*	84.21	
	GenBank	*Ancistrocheirus lesueuri*	84	GU220397
Sarg07-Squid02	BoLD	*Lepidoteuthis grimaldii*	92.51	
	GenBank	*Lepidoteuthis grimaldii*	92	AF000049
DSH08-02	BoLD	*Histioteuthis hoylei*	98.62	
	GenBank	*Histioteuthis hoylei*	98	AF000045
DSH08-13A	BoLD	*Onychoteuthis borealijaponica*	89.61	
	GenBank	*Onychoteuthis borealijaponica*	89	AB264120
DSH08-17	BoLD	*Gonatopsis japonicus*	84.28	
	GenBank	*Ancistrocheirus lesueuri*	83	GU220397
DSH08-18	BoLD	*Gonatopsis japonicus*	84.25	
	GenBank	*Ancistrocheirus lesueuri*	84	GU220397
DSH08-21A	BoLD	*Gonatopsis japonicus*	84.25	
	GenBank	*Ancistrocheirus lesueuri*	84	GU220397
DSH08-27A	BoLD	*Gonatopsis japonicus*	84.62	
	GenBank	*Ancistrocheirus lesueuri*	84	GU220397
DSH08-31A	BoLD	*Gonatopsis japonicus*	84.62	
	GenBank	*Ancistrocheirus lesueuri*	84	GU220397
D09-SH02	BoLD	*Moroteuthis lonnbergii*	88.33	
	GenBank	*Moroteuthis robusta*	88	GU112107
D09-SH04	BoLD	*Gonatopsis japonicus*	84.47	
	GenBank	*Ancistrocheirus lesueuri*	83	GU220397
D09-SH07A	BoLD	*Gonatopsis japonicus*	84.5	
	GenBank	*Gonatus pyros*	83	GU072735

2.3.3 Stable Isotopes

2.3.3.1 Sperm whales

A total of 73 skin samples (47 Sargasso Sea, 26 Dominica) were analyzed, representing a total of 36 groups (22 Sargasso Sea, 14 Dominica). The model examining the relationship between δ^{15}N values and location, year and group was significantly better than the intercept-only model (Likelihood-ratio test: $X^2_{37} = 141.71$, $p < 0.001$). The δ^{15}N signatures were significantly affected by location ($X^2_1 = 36.74$, $p < 0.001$) and group ($X^2_{31} = 166.52$, $p < 0.001$) but not year ($X^2_3 = 5.51$, $p = 0.138$). Further investigation into the effect of location on δ^{15}N signatures showed Sargasso Sea animals had significantly higher δ^{15}N signatures (13.2 ± SD 1.0‰) than Dominica animals (11.3 ± SD 0.5‰; t-test, $t_{71} = 8.72$, $p < 0.001$; Figure 2.2). This represents a difference of 1.9‰. There was no relationship found between δ^{15}N signatures and longitude ($r^2 = 0.032$, N = 46, $p = 0.231$). There was a significant positive relationship between δ^{15}N signatures and latitude within the Sargasso Sea ($r^2 = 0.226$, N = 46, $p = 0.001$); however, this relationship was driven by five individuals in the same group, which had the five lowest δ^{15}N of the Sargasso Sea animals. When these individuals were excluded from the analysis, no relationship was found between δ^{15}N signatures and latitude ($r^2 = 0.030$, N = 41, $p = 0.276$).

The model examining the relationship between δ^{13}C values and location, year and group was significantly better than the intercept-only model (Likelihood-ratio test: $X^2_{37} = 233.93$, $p < 0.001$). The δ^{13}C signatures were significantly affected by location ($X^2_1 = 75.04$, $p < 0.001$), group ($X^2_{31} = 440.44$, $p < 0.001$) and year ($X^2_3 = 30.13$, $p < 0.001$). Sargasso Sea animals had significantly lower δ^{13}C signatures (-16.5 ± SD 0.43‰) than Dominica animals (-15.3 ± SD 0.34‰; t-test, $t_{71} = -12.63$, $p < 0.001$; Figure 2.2). To further investigate the effects of year on δ^{13}C signatures, we examined the relationship between δ^{13}C signatures and year for each study site using an ANOVA. Despite a year effect in our model, there was no significant difference in δ^{13}C among years for the Sargasso Sea ($F_{3,43} = 1.453$, $p = 0.241$) or Dominica ($F_{3,22} = 2.024$, $p = 0.140$).

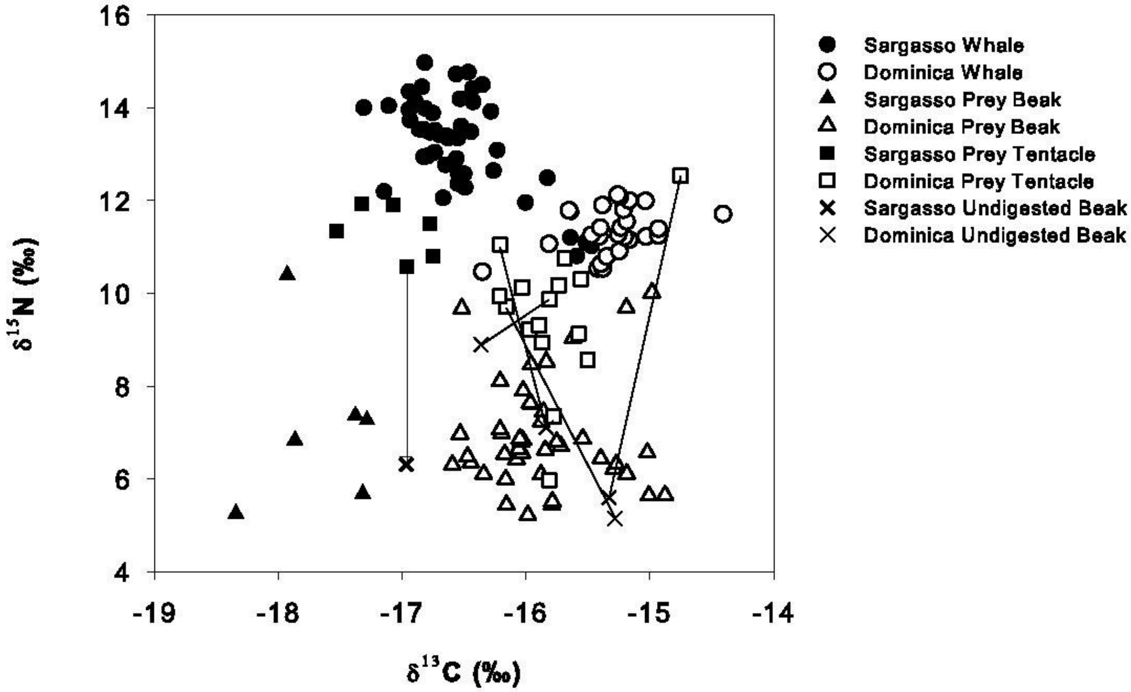

Figure 2.2 Individual δ^{15}N and δ^{13}C signatures for sperm whales (skin), their prey (cephalopod soft tissue and lower beaks) and undigested lower beaks (beaks attached to the cephalopod soft tissue) in the Sargasso Sea (2004-2007) and off Dominica Island (2005, 2007-2009). The undigested beaks are joined to their respective cephalopod soft tissue with a line.

2.3.3.2 Prey

Stable isotope analyses were performed on beaks collected from fecal samples (Table 2.3, Figure 2.2). There was no significant effect of location ($F_{1,41} = 0.215$, $p = 0.645$) or size ($F_{1,41} = 1.615$, $p = 0.211$) on δ^{15}N values of squid beaks, but there was a significant effect of genus ($F_{1,41} = 4.946$, $p = 0.001$). Size did not have a significant effect on δ^{13}C values of squid beaks ($F_{1,41} = 0.615$, $p = 0.437$), but there was a significant effect of location ($F_{1,41} = 126.681$, $p < 0.001$) and genus ($F_{5,41} = 8.111$, $p < 0.001$). The δ^{15}N values for beaks collected from fecal samples ranged from 5.6‰ to 10.4‰, with beaks from the genus *Chiroteuthis* being the most enriched ($\delta^{15}N = 9.5 \pm$ SD 1.0‰) and *Octopoteuthis* being the least ($\delta^{15}N = 5.6$‰) (Table 2.3). However, stable isotope analysis was performed on the lateral wall of the *Octopoteuthis* sample because analysis on the wing resulted in error and that sample was lost. Signatures of the lateral wall reflect dietary components earlier in life while the wing reflects the most recent diet (Cherel and Hobson 2005). Thus, this signature did not reflect the diet of the specimen when it was consumed by the sperm whale. The δ^{13}C values for beaks ranged from -17.9‰ to -14.9‰ with *Chiroteuthis* having the lowest δ^{13}C signatures (δ^{13}C = -16.8 ± SD 1.1‰) (Table 2.3). There was no significant difference between δ^{15}N values of *Histioteuthis* beaks collected in the Sargasso (6.8 ± SD 0.8‰) or Dominica (6.7 ± SD 0.8‰; t-test: t_{32} = 0.195, p = 0.846), but δ^{13}C values of beaks were significantly lower in the Sargasso (-17.5 ± SD 0.3‰) compared to Dominica (-16.1 ± SD 0.2‰; t-test: t_{32} = -11.090, p < 0.001). The difference in δ^{15}N between sperm whale signatures and signatures of beaks collected from fecal samples was 6.4‰ for Sargasso sperm whales and 4.6‰ for Dominica whales.

Table 2.3 Summary of isotope signatures of δ^{15}N and δ^{13}C of cephalopod beaks collected from the fecal samples of free-ranging sperm whales in the Sargasso Sea and Dominica.

Genus/family	Location	n	**δ^{15}N mean ± SD (‰)**	**Range of δ^{15}N (‰)**	**δ^{13}C mean ± SD (‰)**	**Range of δ^{13}C (‰)**
Histioteuthis	Sargasso	30	6.8 ± 0.8	5.7 to 7.4	-17.5 ± 0.3	-17.9 to -17.3
	Dominica	4	6.7 ± 0.8	5.2 to 8.5	-16.1 ± 0.2	-16.6 to -15.7
Chiroteuthis	Sargasso	1	10.4	--	-17.9	--
	Dominica	2	9.1 ± 0.8	8.5 to 9.7	-16.2 ± 0.5	-16.5 to -15.8
Discoteuthis	Dominica	7	6.8 ± 1.4	5.7 to 9.7	-15.3 ± 0.2	-15.6 to -14.9
Mastigoteuthis	Dominica	2	7.8 ± 1.8	6.6 to 9.0	-15.3 ± 0.4	-15.6 to -15.0
Octopoteuthis	Dominica	1	5.6*	--	-15.0*	--
Onychoteuthidae[¥]	Sargasso	1	6.3	--	-17.0	--
Onykia[¥]	Dominica	1	8.9	--	-16.4	--
Brachioteuthis[¥]	Dominica	1	5.1	--	-15.3	

* stable isotope analysis was performed on the lateral wall because analysis on the wing resulted in error and that sample was lost. Signatures of the lateral wall reflects dietary components earlier in life (Cherel and Hobson 2005) while the wing reflects the most recent diet. Thus, this signature does not reflect the diet of the specimen when it was consumed by the sperm whale.

[¥] Undigested beaks that were collected from the soft tissue of squid pieces found near groups of sperm whales

Cephalopod tentacles collected in the Sargasso Sea had significantly higher δ^{15}N values (11.3 ± SD 0.6‰) than samples collected in Dominica (9.6‰ ± SD 1.5‰; t-test: t_{20} = 2.814, p = 0.11) and Sargasso Sea cephalopod tentacle samples were significantly lower in δ^{13}C values (-17.1 ± SD 0.3‰) than Dominica (-15.8 ± SD 0.4‰; t-test: t_{20} = -7.815, p >0.001). Comparisons between isotopic signatures of tentacles and beaks from both locations showed a greater difference of δ^{15}N in the Sargasso (4.5‰) compared to

Dominica (2.9‰) (Figure 2.2). The trophic enrichment between sperm whales and tentacles was 1.9‰ for Sargasso whales and 1.7‰ for Dominica whales. The isotopic signatures of the tentacles with matches to species from the DNA sequencing were as follows: *Architeuthis dux* (Sargasso): δ^{15}N = 10.8‰, δ^{13}C = -16.8‰, *Cycloteuthis sirventi* (Sargasso): δ^{15}N = 11.5‰, δ^{13}C = -16.8‰ and *Histioteuthis arcturi* (Dominica)*:* δ^{15}N = 9.6‰, δ^{13}C= -16.9‰. The isotopic signatures of the tentacles with likely matches to family from the DNA sequencing were as follows: Lepidoteuthidae (both Sargasso): δ^{15}N = 11.9 ± 0.0‰, δ^{13}C = -17.2 ± 0.1‰, and Onychoteuthidae (Dominica): δ^{15}N = 9.7‰, δ^{13}C = -16.2‰.

Five tentacle samples still had a lower beak attached. Comparisons between isotopic signatures showed that tentacles were enriched in δ^{15}N from 1.0 to 6.9‰ compared to beaks, but the difference in δ^{13}C between tentacles and beaks varied (-0.88 to 0.58‰) (Table 2.4).

Table 2.4 Comparison of isotopic signatures δ^{15}N and δ^{13}C between the tentacle and beak of the five individual cephalopods.

Genus/Family	**Tissue type**	**δ^{15}N (‰)**	**Difference in δ^{15}N (‰)**	**δ^{13}C (‰)**	**Difference in δ^{13}C (‰)**
Onychoteuthidae	tentacle	10.6	4.3	-17.0	0
	beak	6.3		-17.0	
Histioteuthis	tentacle	11.0	3.9	-16.2	-0.4
	beak	7.1		-15.8	
Brachioteuthis	tentacle	9.7	4.5	-16.2	-0.9
	beak	5.2		-15.3	
Onykia	tentacle	9.9	1.0	-15.8	0.6
	beak	8.9		-16.4	
Unknown	tentacle	12.5	6.9*	-14.8	0.5
	beak	5.6		-15.3	
Mean Difference			**4.1**		**0.0**

*stable isotope analysis was performed on the lateral wall

2.4 DISCUSSION

2.4.1 Global comparisons of sperm whale diet

We used hard-part analysis and stable isotope analysis, complemented by mtDNA barcoding of cephalopod tissue to examine the diet of sperm whales in the western North Atlantic. Hard-part analysis indicated that *Histioteuthis* was the most frequently observed cephalopod genus in the fecal samples of sperm whales in the Sargasso Sea and Dominica, although very few beaks were collected from whales in the Sargasso Sea. The mtDNA barcoding of cephalopod tissue also suggests that *Histioteuthis* spp. form part of the diet of sperm whales off Dominica. These results are consistent with a study by Smith and Whitehead (2000), who found that the sperm whale diet in the Pacific, near the Galapagos Islands, primarily consisted of *Histioteuthis* spp. using hard-part analysis of fecal samples. Other sperm whale dietary studies using hard-part analysis from stranded animals or from commercially harvested animals found that *Histioteuthis* spp. were the most common cephalopod species by frequency of occurrence in both the Pacific (Clarke et al. 1976, Clarke and Roper 1998, Evans and Hindell 2004) and the Atlantic oceans (Clarke and MacLeod 1976, Clarke et al. 1993, Clarke and Pascoe 1997). However, mtDNA sequencing suggests that whales in the Sargasso Sea might be feeding, in part, on larger, higher trophic level squid such as *Architeuthis*. This is further supported by the lack of beaks collected: either beaks of these larger species aren't ingested or chances of collecting them are lower since far fewer large squid would need to consumed compared to the numerous numbers of smaller (ie *Histioteuthis*) squid. It has been suggested the prominence of *Histioteuthis* beaks is a result of 'prey of prey', when undigested beaks of smaller *Histioteuthis* squid may be found in the stomachs of other larger squid (Clarke et al. 1988, Clarke and Paliza 2001). The fact that the cephalopod species collected near groups of whales in the Sargasso Sea, as identified through mtDNA barcoding of soft tissues, were not represented in the hard-part analysis supports this "prey of prey" theory.

Beak size range (LRL) and mean estimated wet weight of the *Histioteuthis* collected in the Sargasso (LRL = 4.8-5.7mm, wet weight = 219.8g) and Dominica (LRL = 2.8-6.6mm, wet weight = 213.1g) are smaller than samples of *Histioteuthis hoylei* collected from fecal samples of sperm whales off the Galapagos (LRL = 5.0-8.0mm, mean wet weight = 351g) (Smith and Whitehead 2000) and from the stomach contents of whales harvested off Peru and Chile (LRL = 5.0-13.0mm, wet weight = 1145g) (Clarke et al. 1976). The smaller size could be explained by differences in species. The hard-part analysis of the fecal samples would suggest that sperm whales in the Sargasso Sea and Dominica feed mainly on small squid (mantle lengths around 10cm) (Table 2.1). However, it is likely that these small squid make up only a small part of the diet of whales in the Sargasso Sea, as stable isotope and mtDNA sequencing results suggest, or are 'prey of prey' (as suggested above). By contrast, all evidence suggests that whales in Dominica are feeding predominantly on these small squid, which are likely schooling, and large numbers would need to be consumed. These differences highlight the biases associated with sample collection and method of analysis.

Comparisons of stable isotope analysis of sperm whale skin between this study and other regions (Table 2.5), show similarities in isotope signatures within but not between ocean basins. δ^{15}N signatures from the two locations in the western North Atlantic (this study) were similar to those found in the Gulf of Mexico (12.3‰; Ruiz-Cooley and Engelhaupt 2010). However, δ^{15}N signatures of sperm whales in the Pacific Ocean were generally much higher, such as in Chile (21.1‰; Marcoux et al. 2007) and the Gulf of California (19.6‰; Ruiz-Cooley et al. 2004) (Table 2.5). The differences in δ^{15}N values between the Atlantic and Pacific oceans are a reflection of differences in the predominant nitrogen cycling regime, which influences baseline δ^{15}N signatures in the marine food web (Wada and Hattori 1991, Wallace et al. 2006) and ultimately different species compositions (e.g. the occurrence of *D. gigas* in the Pacific but not the Atlantic).

Table 2.5 Isotopic signatures (δ^{15}N and δ^{13}C) of sperm whales (*Physeter macrocephalus*) in the literature compared to this study.

Location	Tissue type	δ^{15}N mean (‰)	δ^{13}C mean (‰)	Study
Sargasso	Sloughed skin	13.2	-16.5	This study
Dominica	Sloughed skin	11.3	-15.3	This study
Gulf of Mexico	Skin (sloughed & biopsy)	12.3	-16.6	(Ruiz-Cooley and Engelhaupt 2010)
Chile	Sloughed skin	21.1	-16.0[a]	(Marcoux et al. 2007)
Galapagos	Sloughed skin	13.9	-16.0[a]	(Marcoux et al. 2007)
Gulf of	Sloughed skin	19.6	-13.8	(Ruiz-Cooley et al. 2004)

[a] mean δ^{13}C (‰) for all Pacific (Galapagos and Chile)

2.4.2 Comparisons of sperm whale diet in the Sargasso and Caribbean

While the hard-part analysis suggested that the diet of sperm whales in the Sargasso Sea was similar to those found off Dominica, the stable isotope analysis suggested that sperm whales in the Sargasso Sea may have a somewhat different trophic ecology than Dominica whales. The difference in mean δ^{15}N values of sperm whale skin between Sargasso Sea and Dominica was 1.9‰ higher for sperm whales in the Sargasso Sea. Mean enrichment of δ^{15}N for one trophic level is between 2.3-3.4‰ (Deniro and Epstein 1981, McCutchan et al. 2003), which is higher than the difference we observed between whales in the Sargasso Sea and Dominica. However, Cherel and Hobson (2005) considered 1.9‰ to be representative of about half a trophic level in cephalopod species, suggesting some of the diet of sperm whales in the Sargasso Sea may include higher trophic level squid. This theory is supported by the fact that δ^{15}N values for cephalopod tentacles collected from the Sargasso Sea were 1.7‰ higher than tentacles from Dominica, although our stable isotope results on the tentacles should be interpreted with caution given the low sample size. The identification of *Architeuthis dux*, the large giant squid, as potential prey of sperm whales in the Sargasso Sea is also an indication that higher trophic level cephalopods contribute to the diet of whales in this region.

Another explanation for the higher δ^{15}N values in the Sargasso Sea is inherent differences in habitat. Broadly, δ^{15}N in the ocean tends to decrease with increasing latitude (Wada and Hattori 1991). Takai et al. (2000) found that δ^{15}N and δ^{13}C values were lower in squid muscle from higher latitudes than lower latitudes. However, within the western North Atlantic, the pattern may be more complex. δ^{15}N values of zooplankton is very low in the southern Sargasso Sea and Caribbean (0-2‰), but the waters of the northwest Sargasso are likely influenced by the more enriched δ^{15}N values of the Gulf Stream (5.5 – 6‰) (Graham et al. 2010). This pattern may explain why δ^{15}N values of sperm whales off Dominica were significantly lower than sperm whales in the Sargasso Sea. Our data within the Sargasso Sea found no relationship between δ^{15}N and latitude once the group with overlapping isotopic signatures to Dominica was removed. However, we know very little about the movement patterns of sperm whales in the Sargasso Sea. If individuals in this area are wide-ranging and feeding across habitats of varying δ^{15}N values, their diet may not reflect the above pattern.

In contrast, sperm whales in the Sargasso Sea had lower δ^{13}C values than Dominica whales, although the difference was small (~1.2‰). This difference in δ^{13}C values was also reflected in the δ^{13}C signatures of the prey samples. δ^{13}C signatures are typically found to be higher in coastal marine ecosystems, such as off Dominica, in comparison with offshore pelagic ecosystems such as the Sargasso Sea (Deniro and Epstein 1978, Goericke and Fry 1994, Hobson et al. 1994). Although the waters off Dominica where sperm whales were sampled cannot be strictly classified as coastal, these waters experience increased productivity due to downstream turbulence (Ingham and Mahnken 1966) and the 'island mass' effect (Doty and Oguri 1956, Sander 1981). Areas of high productivity have higher δ^{13}C values than less productive regions (Graham et al. 2010). The difference in δ^{13}C between consumer and diet is generally very low, no more than 1‰ (Deniro and Epstein 1978; McCutchan et al. 2003). There was only a 0.5‰ difference in mean δ^{13}C values between sperm whales in Dominica and the tentacles and beaks collected there. Sperm whales in the Sargasso Sea had mean δ^{13}C values 0.6‰ higher than mean tentacle values and 1.1‰ higher than mean beak values.

Interpretation of δ^{15}N signatures of predators (whales) relative to signatures of their prey (squid) requires information on δ^{15}N enrichment between predator and prey tissues. Although δ^{15}N enrichment between trophic levels is typically ~3.0‰, fractionation values (difference in δ^{15}N between predator and specific prey items consumed) observed in nature can differ among predators (e.g. birds vs. mammals) and tissue types (e.g. muscle vs. chitin) (Kelly 2000). Fractionation values between sperm whale skin and prey (muscle and beaks) are sparse. δ^{15}N enrichment values between whale skin and cephalopod muscle tissue range from 2.7‰ for large *D. gigas,* 4.3‰ for Histioteuthids and Ommastrephidae, and 5.0‰ for small *D. gigas* (Ruiz-Cooley et al. 2004, Ruiz-Cooley and Engelhaupt 2010). Comparisons between whale skin and *Histioteuthis* beaks showed δ^{15}N enrichment of 3.3‰ off Chile and 4.3‰ in the Galapagos (Marcoux et al. 2007). These fractionation values can act as a guide for the interpretation of δ^{15}N differences observed between whales and their prey in the Sargasso (6.4‰ and 1.9‰ relative to sampled beaks and tentacles, respectively) and Dominica (4.6‰ and 1.7‰ relative to sampled beaks and tentacles, respectively). It is likely that the beaks collected from the fecal samples of Dominica sperm whales represent the majority of their diet quite well. However, the larger difference in δ^{15}N in the Sargasso between sperm whales and beaks (6.4‰) suggests that these whales were feeding mainly on different species than the species of beaks collected. This theory is supported by the mtDNA barcoding results of the cephalopod tissue, whereby the species of cephalopod tissue in the Sargasso Sea did not match the identified beaks. The beaks collected could be the prey of their prey (a bias suggested by (Clarke and Paliza 2001)), or may have only constituted a small portion of their diet. If Sargasso Sperm whales were indeed feeding at higher trophic levels (i.e. larger squid) than Dominica animals, this would explain the lower rates of beak collection in the Sargasso due to faster sinking rates of large sized beaks, as well as differential digestion rates, differences in rates of discarding the heads of the squids and selective vomiting of tissue or beak types/sizes.

As mentioned previously, the proportion of lower beaks collected per observed defecation in the Sargasso Sea was lower (mean 0.09) than off Dominica (0.26), although the difference was not significant. However, both rates were much lower than those recorded in other regions, such as off the Galapagos, in the South Pacific Ocean (five field seasons, mean = 1.10 ± 0.60, total number of defecations = 172). The high variability in defecation rate might be a reflection in the variability amongst individuals.

However, hard-part analysis alone may miss larger, higher trophic level cephalopods. Simply relying on hard-part analysis of fecal samples to examine diet of sperm whales here would result in a biased, incomplete picture of the foraging ecology for sperm whales in the Sargasso Sea. Stable isotope analysis provides integrated dietary information over a longer period of time, at least up to 75 days (Ruiz-Cooley et al. 2004). However, it is not possible to elucidate dietary composition from stable isotope analysis with a limited and incomplete prey dataset, as is the case for the Sargasso Sea. Mitochondrial DNA barcoding of cephalopod tissues can improve our understanding of the prey base in this and other regions. Our study demonstrates the importance of integrating multiple techniques, such as stable isotope analysis, hard-part analysis and mtDNA barcoding to examine the diet of sperm whales. This multi-tool approach has been proven valuable by researchers studying other marine predators such as seabirds (Bearhop et al. 2001) and seals (Burns et al. 1998).

Finally, the overlapping isotope signatures of one group sampled in the Sargasso Sea and the sperm whales off Dominica suggests that their diets, and by extension their ranges, were likely overlapping during some portions of the year (Figure 2.2). Isotopic signatures have proven useful in understanding movement patterns and ecological niches of marine organisms because different areas of the ocean have unique isotopic signatures (Wallace et al. 2006, Graham et al. 2010). Little is known about the movement patterns of sperm whales in the Sargasso Sea and whether they remain there year-round. To date, there have been no matches (using photo identification of flukes) between sperm whales photographed in the Sargasso Sea and sperm whales found in other areas of the Atlantic Ocean, such as the Gulf of Mexico, off Dominica or off the Azores. However, our data suggest that this one group sampled in the Sargasso Sea likely spends a significant amount of time in habitats similar to Dominica.

2.4.3 Insights into the cephalopod community in the western North Atlantic

Cephalopods are important prey items for cetaceans (Clarke 1996) and many other top predators (Croxall and Prince 1996, Klages 1996). Our capacity to study the feeding ecology of these predators relies on our ability to properly identify hard-parts to species or genus and to interpret the stable isotope data, and ultimately requires an understanding of the cephalopod community in the study area. Very limited information exists on the cephalopod community in the Sargasso Sea, thus, our results contribute to the overall understanding of cephalopods in this region.

The limited number of cephalopod soft tissue samples from our study that could be identified to species or family provides some insight into the possible species consumed by sperm whales in this region. *Architeuthis dux* is a large, wide ranging cephalopod (Guerra et al. 2011) that occupies the upper trophic level in cephalopod communities (Cherel et al. 2009b, Guerra et al. 2010). Of our 23 soft tissue samples, *Architeuthis dux* had the seventh highest δ^{15}N value (10.8‰). The highest incidences of *Architeuthis* records occur where the abyssal depth plains meet shallower continental shelves and include areas of deep canyons and channels (Guerra et al. 2011). These are areas of high productivity. Our sample was collected in the northern part of the Sargasso Sea (38.94^{0}N, - 61.93^{0}W), where eddies associated with the Gulf Stream would lead to increased productivity. The family Lepidoteuthidae also seems to be an upper trophic level predator: two collected tissue samples had the second and third highest δ^{15}N values (both 11.9‰) of all the soft tissue samples. One of these samples was collected in the northern part of the Sargasso Sea (37.25^{0}N, -57.90^{0}W), while the other was collected further southwest (35.33^{0}N, -64.32^{0}W). Lepidoteuthidae is described as a large squid with a mantle length reaching nearly 100cm (Young and Vecchione 2009). Very little is known about *Cycloteuthis sirventi*, however it has the fifth highest δ^{15}N value (11.5‰) suggesting it is also a top predator within the cephalopod community. Of the cephalopods from the Sargasso Sea that could be identified through DNA sequencing, it was collected the furthest south (33.12^{0}N, -67.46^{0}W).

The trophic ecology of *Architeuthis* and *Cycloteuthis* contrasts greatly with that of *Histioteuthis* spp., beaks of which were most frequently observed in the fecal samples from both regions. *Histioteuthis* spp. are weakly muscled and moderately sized (Voss et al. 1992) and occupy lower trophic levels within cephalopod communities (Cherel et al. 2009b). In contrast, a small number of beaks from *Chiroteuthis* spp. were also found in the fecal samples of sperm whales from both regions. These beaks had the highest δ^{15}N values of all beaks, despite being the smallest. *Chiroteuthis* spp. occupied the highest trophic level of deep-sea cephalopods in the Southern Ocean, with the second highest δ^{15}N value (Cherel et al. 2009b). Due to their small size, *Chiroteuthis* sp. beaks might be missed when collecting fecal samples (Smith and Whitehead 2000) and might contribute to a larger portion of the diet in both regions than the hard-part analysis suggests.

Since our prey samples consisted of both cephalopod beaks and soft tissue, an understanding of how isotopic signatures differ between the two tissue types is important in the interpretation of our data. Different metabolic pathways exist between protein and chitin structures, and chitin is depleted in nitrogen relative to diet (Schimmelmann and DeNiro 1988). Since cephalopod beaks are composed of structural molecules like chitin (Hunt and Nixon 1981, Miserez et al. 2008) we would expect to see lower δ^{15}N values in cephalopod beaks compared to muscle. Studies comparing δ^{15}N signatures of cephalopod muscle and respective lower beaks found an enrichment in the muscle of 3 - 4 ‰ (Cherel and Hobson 2005) and 3.9 – 6.1‰ (Hobson and Cherel 2006). Furthermore, Ruiz-Cooley et al. (2006) found a 4.0‰ enrichment for *Dosidicus gigas* while Cherel et al. (2009a) found a 2.5 to 3.5‰ enrichment, suggesting a correction factor should be applied before comparing δ^{15}N values of hard tissue to those from other tissue. Cherel et al. (2009b) added a value of 3.0‰ to their δ^{15}N values of lower beaks. The low end of our range of enrichment between soft tissue and beaks (1.0 to 6.9‰), is lower than the above values. The limited sample sizes from this study precluded confident usage of correction factors for beak signatures from the Sargasso Sea or Dominica.

2.5 SUMMARY

Hard-part analysis of fecal samples from free-ranging sperm whales in the Sargasso Sea and off Dominica Island suggests that *Histioteuthis* species dominate the diet of sperm whales in both locations. However, stable isotope analysis revealed that sperm whales in the Sargasso Sea may be feeding, in part, on higher trophic level cephalopods compared to sperm whales off Dominica. mtDNA sequencing also suggested the sperm whales in the Sargasso Sea are feeding on larger, higher trophic level squid. Given the low number of lower beaks collected from whales in the Sargasso Sea and biases associated with hard-part analysis, this study demonstrates the value of using a multi-tool approach to study the diet of large whales. Results of the stable isotope analysis also identified dietary overlap between some individuals of the Sargasso with all individuals of Dominica, suggesting connectivity between these populations. Given the time-lag in epidermal turnover rates, stable isotope analysis of skin tissues could prove useful in determining movement patterns and connectivity among populations of sperm whales throughout the North Atlantic Ocean. Our study provides the only information on the feeding ecology of sperm whales in an infrequently studied area, the Sargasso Sea, and also provides insight into the cephalopod community of this region.

CHAPTER 3

SEASONAL OCCURRENCE OF SPERM WHALES (*PHYSETER MACROCEPHALUS*) AROUND KELVIN SEAMOUNT IN THE SARGASSO SEA IN RELATION TO OCEANOGRAPHIC PROCESSES

3.1 INTRODUCTION

Top predators can be used as indicators of not only the health and status of marine ecosystems but also changes in the integrity of that ecosystem (Boyd et al. 2006, Furness and Camphuysen 1997, Piatt et al. 2007). Studies on the spatial and temporal distribution of marine predators can be used to identify biologically diverse “hotspots” and inform management and conservation (Sydeman et al. 2006, Worm et al. 2003). Identifying the oceanographic processes driving the distribution and abundance of marine predators leads to a better understanding of this fluid and dynamic habitat. Species richness and abundance can be explained by sea surface temperature (Worm et al. 2005), primary productivity (Whitehead et al. 2010) and prominent bathymetric features such as seamounts, islands and slope (Morato et al. 2010, Morato et al. 2008, Worm et al. 2003). The distribution and abundance of top marine predators are also associated with areas of increased productivity due to mesoscale activity, such as fronts (Haney 1986, Podesta et al. 1993), which aggregate prey (Olson et al. 1994, Schneider 1990), and cyclonic eddies, as indicated by negative sea surface height anomalies (SSHA) (Teo and Block 2010), which can lead to increased primary and secondary productivity (Yoder 1985). Oceanic processes associated with major currents, such as upwellings, also aggregate top predators (Block et al. 2011).

Sperm whales (*Physeter macrocephalus*) are one of the most widely distributed cetaceans in the world, found in all oceans from the equator to the pack ice of both poles (Rice 1989). They are an important oceanic predator (Whitehead 2003), feeding mainly on meso- and bathypelagic cephalopods, especially those in the Octopoteuthidae and Histioteuthidae families (Kawakami 1980). Despite their wide distribution, sperm whales are clumped geographically. Previous research has found that sperm whale distribution is associated with areas of high primary or secondary productivity (Gulland 1974, Jaquet and Whitehead 1996, Jaquet et al. 1996) and topographic features, such as depth and slope (Pirotta et al. 2011). Sperm whales were associated with warm-core rings off the Gulf Stream (Griffin 1999, Waring et al. 1993), cyclonic eddies in the Gulf of Mexico (Ortega-Ortiz and Mate 2006), frontal zones (Gannier and Praca 2007) and negative SSHA (Biggs et al. 2006) in the Mediterranean Sea.

Recent surveys (Chapter 5) have found large numbers of sperm whales in the Sargasso Sea and historically, this area supported a lucrative whaling industry for sperm whales (Smith et al. 2012, Townsend 1935). The Sargasso Sea lies in the middle of the North Atlantic and is bordered by ocean currents, such as the Gulf Stream to its west. The warm, clear waters of the Sargasso Sea were described as some of the poorest on earth (Blackburn et al. 1970), however, the northern part of the Sargasso Sea experiences increased productivity due to the presence of eddies, rings and meanders associated with the Gulf Stream (McGillicuddy et al. 1998, Ortner et al. 1978). Oceanic fronts, currents and bathymetry are some factors influencing the distribution and abundance of squid (Bakun and Csirke 1998, O'Dor 1992). Thus, eddies, fronts, meanders, and cold-core rings associated with the Gulf Stream may influence the occurrence of sperm whales in this area.

Prominent bathymetric features are also found in the Sargasso Sea, such as the New England Seamount Chain, whose major peaks rise as much as 4,000m above the abyssal plain (Fig. 1). Nutrients are transported into the euphotic zone, thereby increasing local production as a result of increased turbulence, mixing and mesoscale eddies associated with seamounts (Oschlies and Garcon 1998, Wolanski and Hamner 1988). Several studies have shown an association of marine predators with seamounts, such as large tuna, billfishes and sharks (Morato et al. 2008, Worm et al. 2003), common dolphins (*Delphinus delphis*), Cory's shearwaters (*Calonectris diomedea*) (Morato et al. 2008) and beaked whales (Johnston et al. 2008), but examination of sperm whale association with seamounts found no such association (Morato et al. 2008).

Much of what is known about factors driving sperm whale distribution is the result of research conducted in water bodies partially enclosed by land, such as gulfs or seas (Gannier and Praca 2007, Jaquet and Gendron 2002, Pirotta et al. 2011, Praca et al. 2009) or in pelagic systems near islands (Morato et al. 2008). With the exception of sperm whale research conducted in the Pacific Ocean (Jaquet and Whitehead 1996, Jaquet and Whitehead 1999), and some offshore work in the Atlantic Ocean (Waring et al. 1993), very little is known about how oceanographic variables influence the distribution of sperm whales in the open ocean and whether their distribution varies seasonally.

As a result of extreme weather conditions (hurricanes in the summer, followed by winter storms), it is difficult to conduct small vessel-based surveys in the Sargasso Sea outside of the spring season and ship-based marine mammal surveys for this region does not exist. Thus seasonal variability of sperm whale occurrence in this area is unknown. Autonomous recording devices can overcome the difficulties of weather and remoteness and provide the opportunity to examine the prevalence of sperm whales in this little-studied area throughout the year. These devices have been used successfully to monitor the abundance and habitat use of other marine mammals elsewhere (Soldevilla et al. 2011). Although the depth of this area (over 5,000m) makes it difficult to survey using submersible recording devices, Kelvin Seamount, part of the New England Seamount Chain, provides a perfect platform on which to deploy an autonomous recording unit. Since the New England Seamount chain strongly influences the trajectory of the Gulf Stream (Richardson 1981), deployment on Kelvin Seamount provides an opportunity to examine whether this interaction plays an important role in the distribution and abundance of sperm whales in the Sargasso Sea. My objective was to examine the seasonal occurrence of sperm whales over Kelvin Seamount and relate their prevalence to oceanographic conditions.

3.2 METHODS

3.2.1 Data Collection and Preparation

An autonomous acoustic recording device (Cornell Bioacoustics Research Program, Ithaca, NY) hereafter referred to as a "pop-up", was deployed on Kelvin Seamount (approx: 38^0 48'N; 64^0 05'W; Figure 3.1) four times between May 2006 and June 2007 (1st deployment: May 11-June 2 2006, 2nd: June 2-21, 2006, 3rd: November 2 2006-May 5 2007, 4th: May 5-June 20 2007). Due to logistical constraints and severe weather, it was not possible to deploy the pop-up for a second winter deployment (November to May) or from July to November therefore, temporal variability could only be examined from November to June. The pop-ups recorded for two minutes every hour at frequencies up to 5khz (first and second deployment), 10khz (third deployment) or 25khz (fourth deployment). All recordings covered the range of sperm whale vocalizations (Madsen et al. 2002).

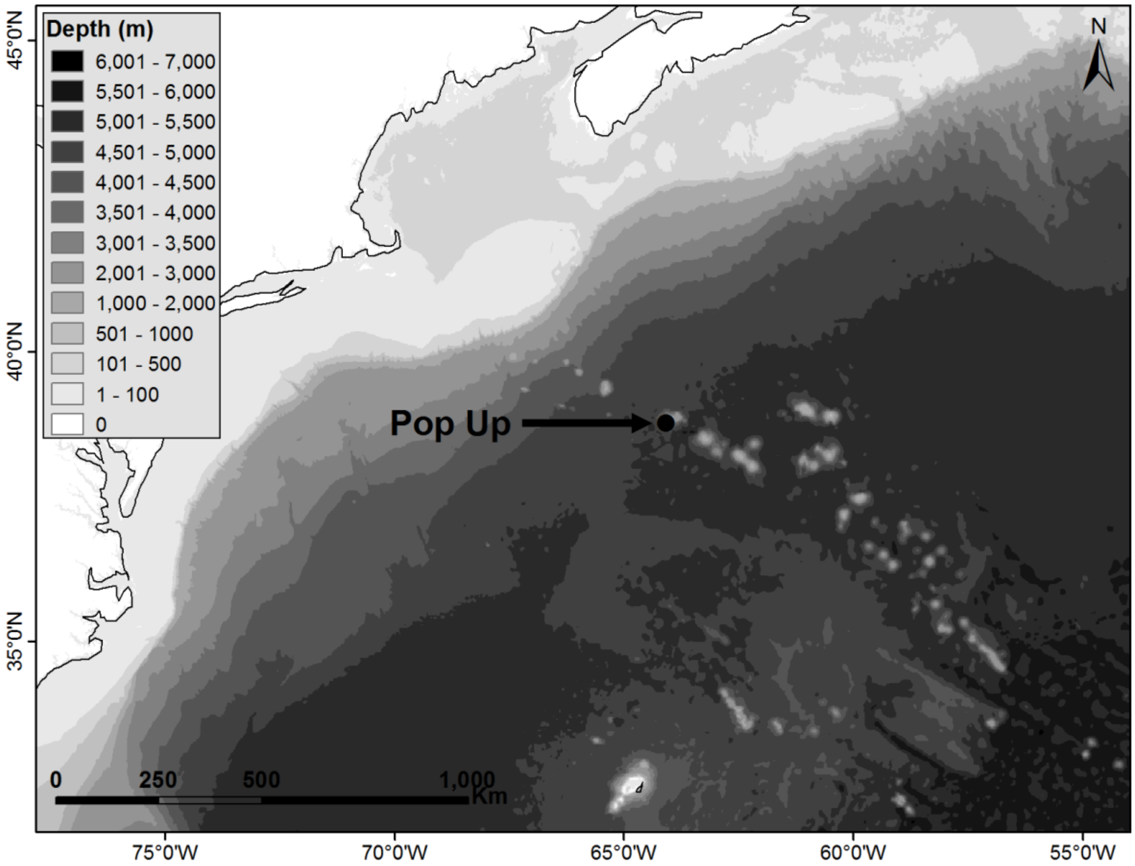

Figure 3.1 Study area location showing the New England Seamount Chain and Kelvin seamount in the western North Atlantic Ocean, where an autonomous acoustic recording device (pop-up) was deployed to examine seasonal sperm whale prevalence in this area.

Weekly composite chlorophyll-*a* concentration (as a proxy for primary productivity) and sea surface temperature (SST) data were downloaded from Aqua-MODIS satellite images (http://oceancolor.gsfc.nasa.gov/) for the period of study. Aqua-MODIS images provide chlorophyll-*a* concentrations in mg·m^{-3} and SST in degrees Celsius at a resolution of 4 x 4 km pixels. Chlorophyll-*a* and SST images were imported into a Geographic Information System (Idrisi Andes Edition). Sea surface height anomaly (SSHA) and geostrophic velocity anomaly data were downloaded from Aviso's global sea surface height products (http://www.aviso.oceanobs.com/en/data/products/sea-surface-height-products/global/index.html) at a resolution of 28.7 x 28.7km. These data were derived from merged satellite altimetry measurements of four altimeters (Jason-1, ENVISAT/ERS, GEosat Follow-On and Topex/Poseidon interlased). Eddy kinetic energy (EKE) is a measure of turbulence and flow of a region and can be used to identify where mesocale eddies and meanders are common and also identify the presence of major currents, such as the Gulf Stream (Teo and Block 2010). EKE was calculated using the following formula:

$$\mathbf{EKE=1/2\ X\ (u'^2+v'^2)}$$

where u and v are zonal and meridian geostrophic currents components, respectively and EKE is a deviation from the mean.

The location of the pop-up was digitized and a "real time" value for chlorophyll-*a* concentration, SST, SSHA and EKE was calculated for that pixel. SST slope (as an indicator the presence of fronts) was also calculated for that pixel using the Idrisi SURFACE function which determines the slope of a cell based on the cell value and the values of the immediate neighbouring cells (Rook's case procedure) (Eastman 2006). To investigate regional oceanographic conditions at multiple scales and to reduce the amount of missing chlorophyll-*a* and SST data due to cloud cover, the following values were calculated for quadrants 12x12 km, 20x20 km, 36x36 km, 68x68 km, 132x132 km and 260x260 km centered around the pop-up: mean chlorophyll-*a* concentration, mean SST, mean SST slope and standard deviation of SST (as a measure of ocean temperature variability). A temporal lag between sperm whale occurrence and SST and chlorophyll-*a* concentration is expected, given the time needed for primary productivity to transfer to top predators (Croll et al. 2005, Jaquet 1996). Thus, the values of chlorophyll-*a* concentration and SST were also calculated for one to eight weeks previously.

3.2.2 Analysis

Pop-up recordings were converted to AIFF files and analyzed using Raven Pro 1.3 (Bioacoustics Research Program, Cornell Lab of Ornithology). Each two-minute recording was examined acoustically and visually (using the spectrogram) for the presence of sperm whale clicks. These clicks are used primarily in echolocation and communication and are arranged in various patterns: usual clicks, slow clicks, creaks and codas. The majority of clicks detected were usual clicks, which are thought to function primarily in searching echolocation and are a long train of regularly spaced clicks (0.5s-1.0s) that can last for several minutes (Jaquet et al. 2001, Madsen et al. 2002, Whitehead and Weilgart 1990).

To examine the seasonal occurrence of sperm whales around Kelvin Seamount, I calculated a weekly proportion of sperm whales detected (number of two-minute hourly recordings where clicks were detected) for each month. I used Kruskal-Wallis test to compare the proportion of sperm whales detected among months using weekly proportion of sperm whales detected as the unit of analysis. Months were grouped into two seasons: spring (April-June) and winter (November-March) and the mean proportion of sperm detected for winter and spring were compared using a Mann-Whitney U Test.

I modeled the response variable (weekly proportion of sperm whales detected) using a Generalized Linear Model (McCullagh and Nelder 1989) in R. Proportional data was modeled with a binomial distribution and logit link function (Lewis 2004). The model included the following variables: month (treated as a factor), chlorophyll-*a* concentration, SST, SST slope, SST standard deviation, SSHA and EKE. Including all the chlorophyll-*a* and SST-related covariates at the different spatial scales (quadrant size) and temporal scales (lags) would have resulted in instability due to the collinearity between the variables. Therefore, an ad hoc procedure was performed to select the most appropriate spatial and temporal (lag) scales to use in the final model. First, I ran correlations tests on the different spatial scales for chlorophyll-*a* and SST, to identify whether they were correlated and if it was appropriate to use the scale at which contained the least missing data. Due to the small sample size, second-order Akaike's Information Criterion (AICc) approach was used to evaluate the covariates at different temporal lags (Burnham and Anderson 2002). To determine which temporal lag to use in the final model, I ran models (GLM) containing the covariate at each temporal lag and used the lag with the lowest AICc score in the final model. Once the appropriate spatial and temporal scales were selected, a full model was fitted. I used a manual backward stepwise approach. At each step, a series of reduced models (containing all variables but one) were fitted and the model with the lowest AICc score was used in the following step. This procedure was continued until removal of any variable caused the AICc score to increase.

3.3 RESULTS

A total of 6,505 hourly, 2-minute recordings from May 11 to June 21, 2006 and November 2, 2006 to June 20, 2007 were examined. Mean weekly proportion of sperm whales heard was significantly higher in spring (mean ± SD = 0.51 ± 0.21) compared to winter (mean ± SD = 0.16 ± 0.08) (Mann-Whitney U Test: $n_1 = 17$, $n_2 = 20$, $U = 20.000$ z = -4.572, p <0.001) (Figure 3.2). There were strong differences in proportion of sperm whales heard among months (Figure 3.3; Kruskal-Wallis H(7) = 23.407, p = 0.001). The proportion of sperm whales heard in May and June appear to be significantly higher than the winter months of November to March (Figure 3.3).

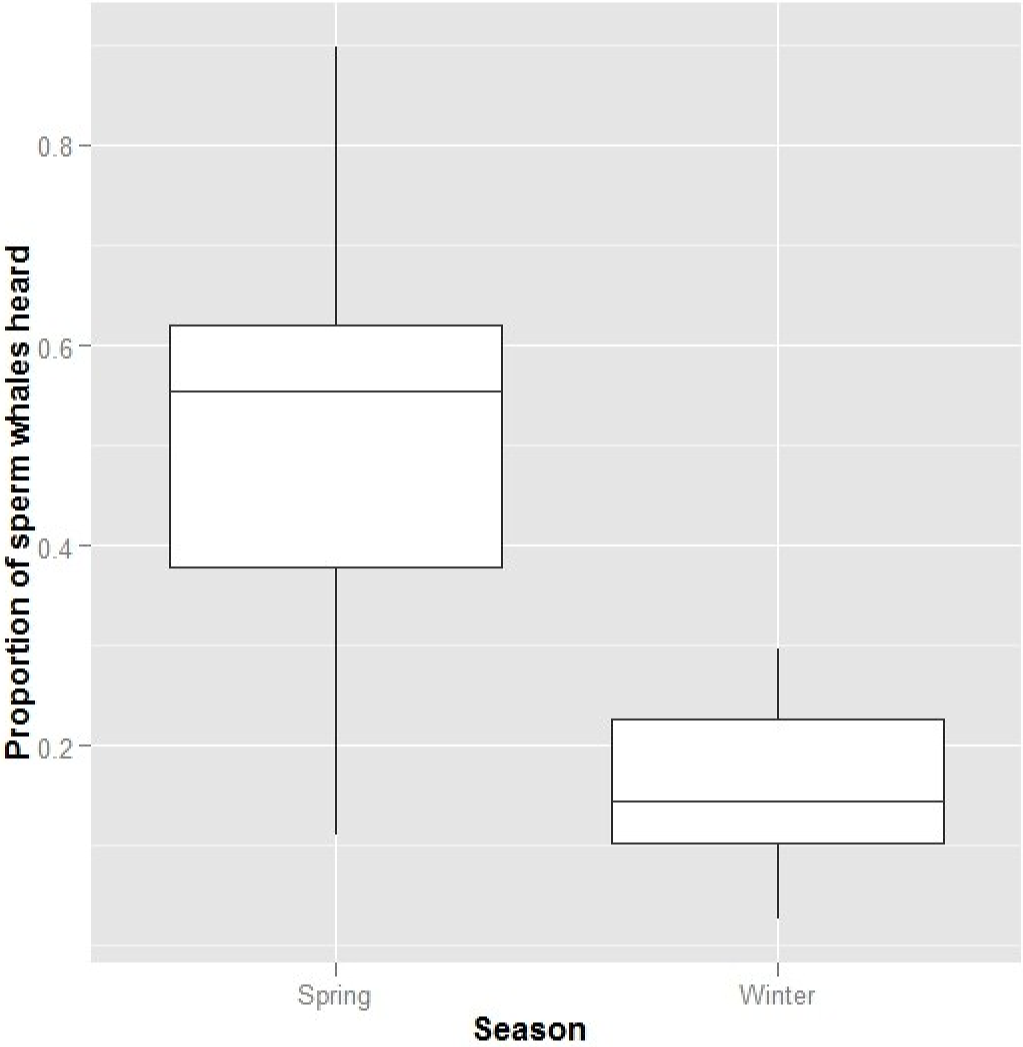

Figure 3.2 Seasonal proportion of sperm whales heard (mean ± SE) during 2-minute recordings from an autonomous recording device deployed on Kelvin Seamount (approx: 38^0 48'N; 64^0 05'W) from May-June 2006 and November 2006 to June 2007. Weekly proportion of sperm whales heard was the unit of analysis, spring = April to June, winter = November to March.

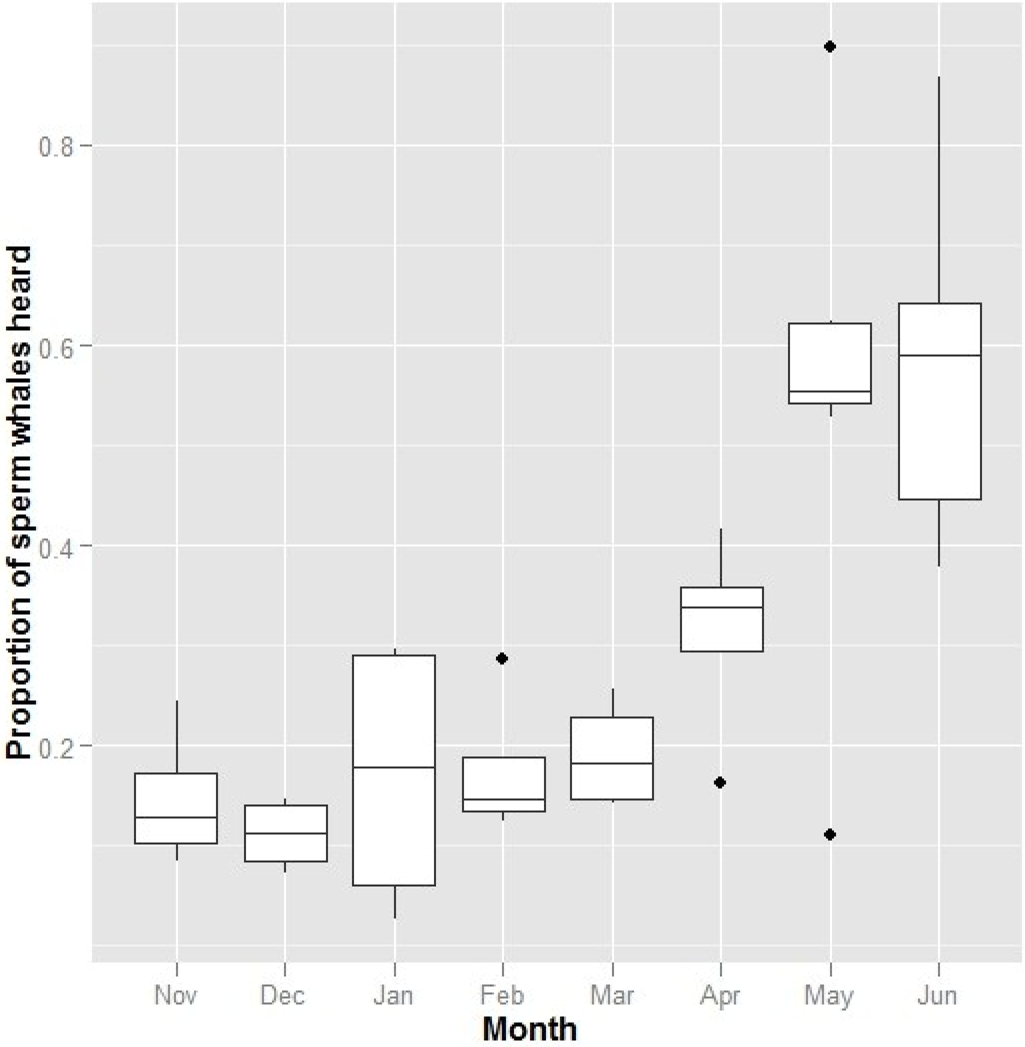

Figure 3.3 Monthly proportion of sperm whales heard (mean ± SE) from an autonomous recording device deployed on Kelvin Seamount (approx: 38^0 48'N; 64^0 05'W) from May-June 2006 and November 2006 to June 2007. Proportion of sperm whales detected is the weekly proportion of two-minute hourly recordings where sperm whale clicks were detected.

Pop-up recordings produced 36 weeks of data, which were linked to satellite derived oceanographic data. Due to poor satellite coverage, chlorophyll-*a* data could not be obtained for four weeks (May 17-23, 2006, January 25-February 1, 2007, March 6-13, 2007, March 14-21, 2007). These weeks were excluded from the analysis, resulting in a sample size of 33 weeks. The chlorophyll-*a* concentration in the cell where the pop-up was located and averaged over 12x12 km, 20x20 km, 36x36 km and 68x68 km, was not always possible due to poor satellite coverage. However, mean chlorophyll-*a* concentration at these scales were strongly correlated with values at 132x132 km (in cell: $r^2 = 0.782$, n = 23, $p < 0.001$; mean at 12 km: $r^2 = 0.804$, n = 23, $p <0.001$; mean at 20 km: $r^2 = 0.841$, n = 23, $p <0.001$; mean at 36 km: $r^2 = 0.896$, n = 23, $p <0.001$; mean at 68 km: $r^2 = 0.967$, n = 23, $p < 0.001$). This was also true for mean SST (in cell: $r^2 = 0.938$, n = 34, $p < 0.001$; mean at 12 km: $r^2 = 0.945$, n = 34, $p <0.001$; mean at 20 km: $r^2 = 0.963$, n = 34, $p <0.001$; mean at 36 km: $r^2 = 0.968$, n = 34, $p <0.001$; mean at 68 km: $r^2 = 0.990$, n = 34, $p < 0.001$). Thus, values for chlorophyll-*a* concentration, SST, SST standard deviation and SST slope at the 132x132 km scale were included in the model to retain the maximum sample size of 33 weeks. This scale is roughly 66 km away from the pop-up location and is about the distance a sperm whale could cover in a day (Whitehead 2003).

The ad hoc procedure evaluating the different temporal lags for chlorophyll-*a* and the SST covariates resulted in the following temporal lags with the lowest AICc score: chlorophyll-*a* concentration at a 4 week lag, SST at an 8 week lag, SST slope at a 2 week lag and SST SD in real time. Therefore, the final Generalized Linear model included month (as a factor) and the following covariates: mean chlorophyll-*a* concentration 4 week lag, SST 8 week lag, SST slope 2 week lag, SST standard deviation in real-time, SSHA and EKE. The final model, after variable selection using AICc scores, retained month, chlorophyll-*a* at a 4 week lag and EKE as the best predictors to explain the weekly proportion of sperm whales heard. There was a significant positive relationship between proportion of sperm whales heard and chlorophyll-*a* concentration 4 week lag (Spearmans correlation: $r_s = 0.682$, n = 17, $p = 0.003$) (Figure 3.4) and proportion of sperm whales heard and EKE (Spearmans correlation: $r_s = 0.578$, n = 17, $p = 0.015$) (Figure 3.5).

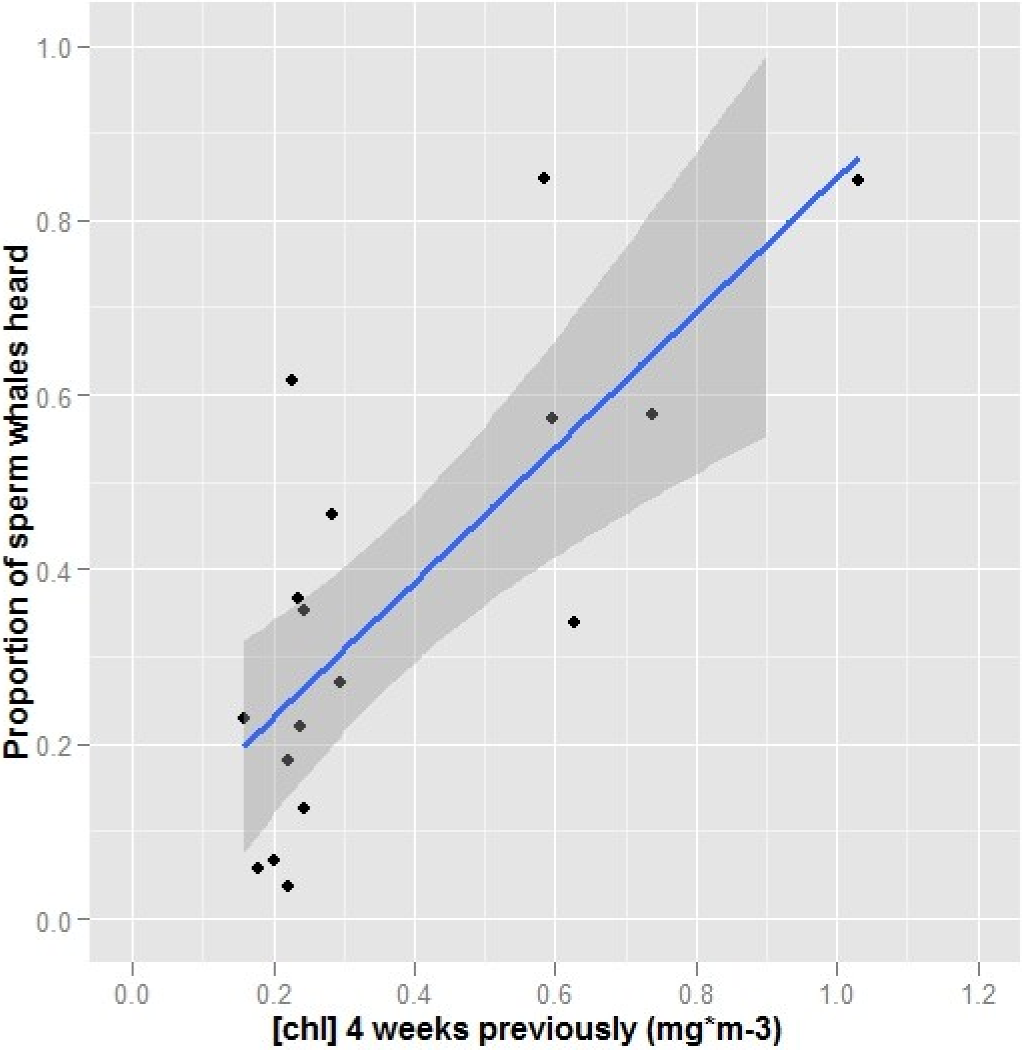

Figure 3.4 Relationship between mean proportion of sperm whales detected and mean chlorophyll-*a* concentration (mg·m^{-3}) in an area 66 km from pop-up (deployed on Kelvin Seamount). Proportion of sperm whales detected is the weekly proportion of two-minute hourly recordings where sperm whale clicks were detected.

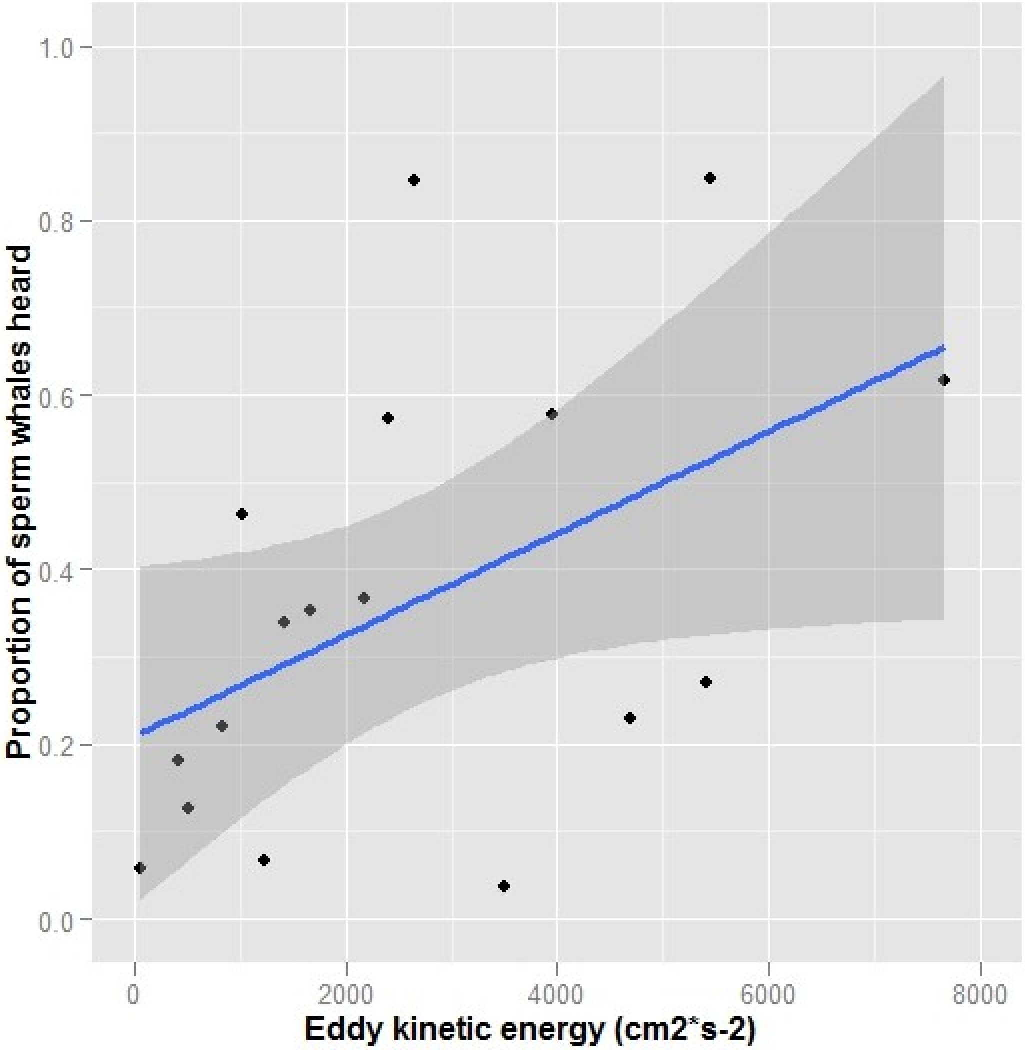

Figure 3.5 Relationship between mean proportion of sperm whales detected and eddy kinetic energy ($cm^2 \cdot s^{-2}$) around the pop-up (deployed on Kelvin seamount). Proportion of sperm whales detected is the weekly proportion of two-minute hourly recordings where sperm whale clicks were detected.

3.4 DISCUSSION

This is the first study to examine the contemporary temporal variability of sperm whale occurrence in the western North Atlantic Ocean. The occurrence of sperm whales around Kelvin Seamount is variable from November to April, with greater numbers occurring in the spring (April to June: 51%) compared to the winter months (November to March: 16%) (Figure 3.2). Similarly, from 1780 to 1920, commercial whaling ships sighted sperm whales in the northwest portion of the Sargasso Sea more frequently in the spring and summer months than the winter months, with very low sightings from December to February (see figures in Smith et al. (2012)). I was not able to examine summer occurrence of sperm whales in this area since pop-ups were not deployed between July and October.

Few studies have examined the seasonal variability of sperm whale distribution and what factors might be driving seasonal occurrence. In the Gulf of California, sperm whales remain in the same areas throughout the season, but change their aggregative behaviour, reflecting changes in prey availability (Jaquet and Gendron 2002). However, seasonal variability in the distribution of male sperm whales off South Island, New Zealand, exists: whales are more limited to deep canyons in the summer, but more evenly distributed in the winter, possibly due to changes in prey (Jaquet et al. 2000). That sperm whales were heard so frequently during the spring around Kelvin Seamount suggests that food availability in this area is quite high during this time.

Since it was not possible to measure the relationship between sperm whales and their prey directly, we used environmental parameters as proxies for prey availability to provide insight into the large difference in temporal distribution between spring and winter months. In this study, month, chlorophyll-*a* concentration four weeks previously and eddy kinetic energy best explained the variation in sperm whale occurrence, using an AICc approach. Previous studies examining the relationship between odontocetes and chlorophyll-*a* concentration have also found temporal lags of 4 weeks (Soldevilla et al. 2011). Our finding that primary production is a predictor variable for sperm whale occurrence is consistent with other studies in the Pacific (Jaquet and Whitehead 1996) and the Mediterranean Sea (Praca et al. 2009). Although, it's been demonstrated the correlations between physical gradients such as chl-*a* concentration is higher at mid-trophic level communities than high-trophic level communities (Renner et al. 2012).

There was a significant, positive relationship between the proportion of sperm whales heard and chlorophyll-*a* concentration four weeks previously (Figure 3.4) and EKE (Figure 3.5). Areas with high EKE indicate high variability and are defined by increased turbulence associated with eddies, fronts and Gulf Stream meanders Stammer and Wunsch 1999; Venaille et al. 2011). These turbulent and/or boundary areas may attract and concentrate a wide range of prey and associated predators. Mesoscale activity can lead to important hotspots for enhanced phytoplankton activity (Falkowski et al. 1991, McGillicuddy et al. 1998) and fronts are important oceanographic features that aggregate prey and marine megafauna (Bost et al. 2009, Olson et al. 1994, Raymond et al. 2010, Schneider 1990). Indeed, the distribution of some squid species is influenced by EKE (Chen et al. 2011). Consequently, sperm whales may also be attracted to these productive habitats as a result of the increased probability of finding prey. For example, aggregations of sperm whales in the northwestern Mediterranean Sea coincide with the presence of SST fronts (Gannier and Praca 2007). Gulf Stream mesoscale eddies also influence the distribution of other top predators. For example, higher swordfish (*Xiphius gladius*) catch rates are found in the vicinity of thermal fronts (Podesta et al. 1993), tuna species aggregate in frontal systems (Laurs et al. 1984), seabird densities at eddies are much higher at thermal fronts than in adjacent shelf and Gulf Stream waters (Haney 1986a) and black-capped petrels (*Pterodrom hasitata*) appear to have an affinity for the inshore frontal boundary of the Gulf Stream (Haney 1987b).

Although the diet of sperm whales in the Sargasso Sea is not known, some research indicates that it includes the giant squid (*Architeuthis dux*), *Cycloteuthis sirventi* and *Histioteuthis* spp. (Chapter 2). Very little is known about the deep-water squid species in this area, however, the Gulf Stream plays an important role in some other well-known squid species. For example, short-finned squid (*Illex illecebrosus*) use the Gulf Stream to facilitate their migration (Bakun and Csirke 1998, Mann and Lazier 2006, O'Dor and

Coelho 1993). Bakun and Csirke (1998) proposed that adults spawn at the northern edge of the Gulf Stream and egg masses, hatchlings and paralarvae drift north in the warm waters of the Gulf Stream (O'Dor and Coelho 1993). The increased productivity as a result of Gulf Stream meanders and eddies, combined with the seasonal life cycles of cephalopods likely plays an important role in the prey of sperm whales in this area.

There is evidence that a seasonal cycle exists for the Gulf Stream position, with more northerly locations in the summer/fall and more southerly locations in the winter/spring (Tracey and Watts 1986). This corresponds to transport, which is lower in the summer/fall and higher in the winter/spring (Tracey and Watts 1986). Examining the relationship between sea surface temperature in real time and month suggests that the Gulf Stream is further south in parts of the winter, since temperatures over the seamount are cool (~16^0C) (Figure 3.6). If mesoscale eddies are driving sperm whale distribution, then the fact that mesoscale variability is less in the winter might explain the corresponding lower sperm whale occurrence at this time of year. Winter movements of sperm whales in the Sargasso Sea are not known, and these pop-up recordings provide the first and only available data on sperm whale occurrence in the Sargasso Sea during this time of year.

While it is clear that the Gulf Stream influence contributes to the large proportion of sperm whales in this area during the spring, the seamount chain itself may also play an important role in sperm whale distribution in the region. Worm et al. (2003) stressed the importance of prominent topographic features in food stressed areas, such as the open ocean. Skov et al. (2008) found that sperm whales had higher affinities to cross-seamount or cross-frontal structures along the mid-Atlantic Ridge. Although Morato et al. (2008) found common dolphins were sighted significantly higher in the vicinity of the Azores seamounts, they found no association between sperm whales and seamounts. The lack of a difference in sperm whale abundance with proximity to seamounts may be due to the spatial scale examined in their study, which was 0 to 100 km from the nearest seamount. The distance at which seamounts-associated processes drive sperm whale abundance may be greater than 100 km. Sperm whales were one of the most frequently encountered marine mammal during their surveys of the Azores archipelago, suggesting this area is important sperm whale habitat. Finally, Richardson (1981) examined how the New England Seamounts influenced the Gulf Stream trajectory. He found large-amplitude meanders beginning at the New England Seamount Chain and small, localized eddies at individual seamounts. Thus, the interaction between the Gulf Stream and the New England Seamount Chain may also influence sperm whales in this region.

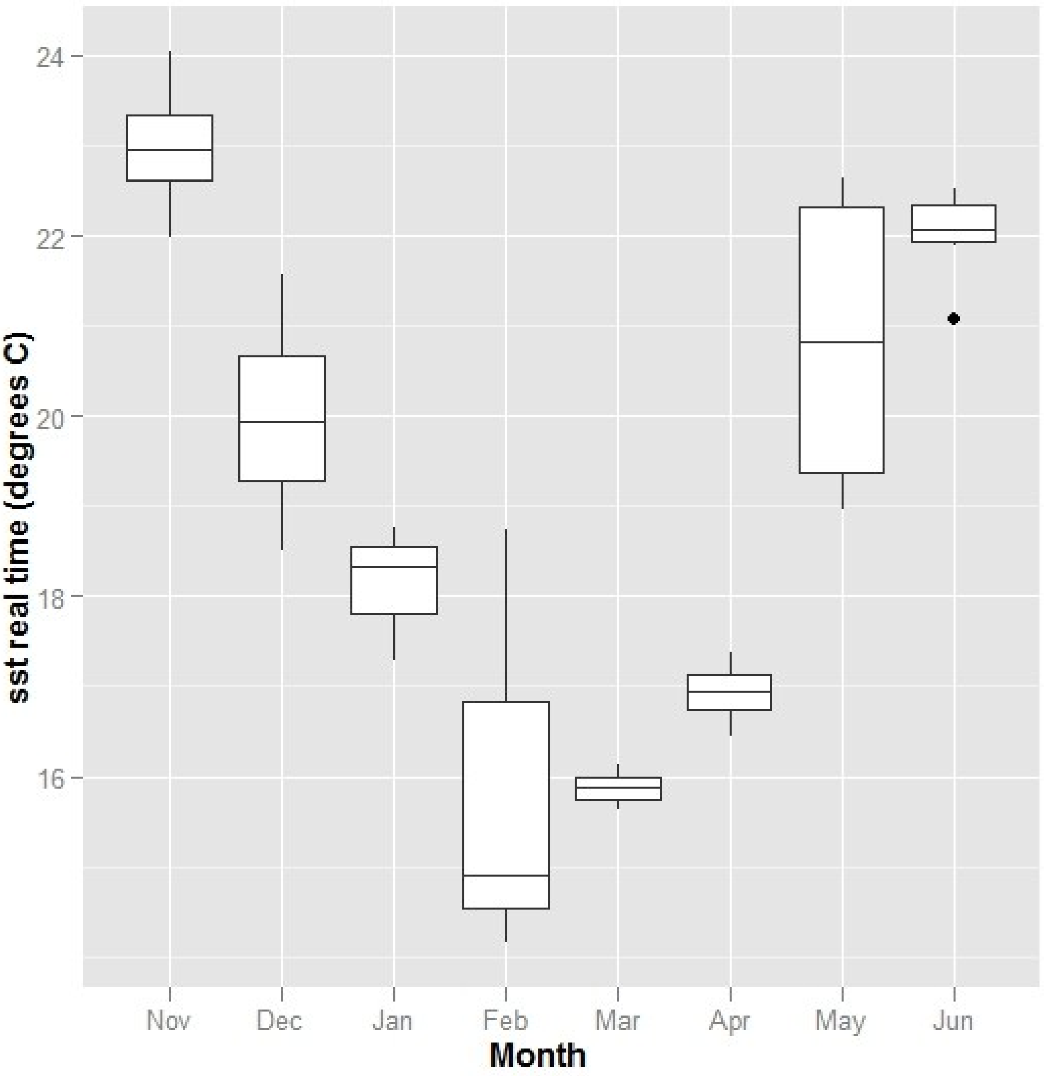

Figure 3.6 Mean weekly sea surface temperature (in real time) (mean ± SE) over Kelvin Seamount (approx: 38^0 48’N; 64^0 05’W) from May-June 2006 and November 2006 to June 2007.

3.5 SUMMARY

Overall, I found strong seasonal variability in sperm whale occurrence around Kelvin Seamount in the Sargasso Sea between November and June, with sperm whale occurrence being significantly higher in the spring (51%) than the winter (16%). Month, chlorophyll-*a* concentration with a four week temporal lag and eddy kinetic energy can best explain this pattern. Regional oceanographic conditions around the New England Seamount Chain and seasonal changes in mesoscale variability are likely driving the temporal distribution of sperm whales in this region. It appears that the effects of the Gulf Stream are important to sperm whale distribution in this region.

CHAPTER 4

DISTRIBUTION OF SPERM WHALES (*PHYSETER MACROCEPHALUS*) IN THE SARGASSO SEA.

4.1 INTRODUCTION

Habitat is an important concept in ecology. Habitat use is influenced by a number of factors such as food, shelter, and breeding habitat, and may be constrained by morphology and physiology (Hilden 1965). Identifying the habitats of top predators in pelagic systems can lead to the identification of "hotspots" that can ultimately inform conservation and management practices (Sydeman et al. 2006, Worm et al. 2003). Identifying the metrics leading to increased foraging success of top predators can result in a better understanding of the biological and physical oceanographic processes that drive ecosystem productivity and their prey (Robinson et al. 2012). The distribution of top predators is best explained by the distribution and abundance of their prey (Ainley et al. 2009; Friedlaender et al. 2006; Piatt et al. 1989; Renner et al. 2012). However, it is often difficult, if not impossible to measure prey abundance and thus, environmental factors are often used as proxies for prey distribution (Ainley et al 2005). Species richness and abundance of marine top predators can sometimes be explained by sea surface temperature (Whitehead et al. 2010, Worm et al. 2005), primary productivity (Praca et al. 2009) and prominent bathymetric features such as seamounts, islands and slope (Morato et al. 2010, Worm et al. 2003). The distribution and abundance of marine top predators is also associated with mesoscale activity such as fronts (Haney 1986a, Podesta et al. 1993) and cyclonic eddies, (as indicated by negative sea surface height anomalies) (Teo and Block 2010), which lead to areas of increased productivity.

Sperm whales (*Physeter macrocephalus*) are a top oceanic predator (Whitehead 2003), feeding mainly on meso- and bathy-pelagic cephalopod species (Kawakami 1980). They are widely distributed in all oceans (Rice 1989), yet they are clumped geographically.

Early whalers recognized their uneven distribution and focused their activity in areas colloquially referred to as “whaling grounds” (Bannister et al. 2008, Maury 1852, Townsend 1935). These “grounds” are generally associated with areas of high primary or secondary productivity (Gulland 1974, Jaquet and Whitehead 1996, Jaquet et al. 1996). Measure the abundance and distribution of the cephalopod prey is difficult, if not impossible. However, previous research has found that sperm whale distribution or density is associated with topographic features, such as depth and slope (Pirotta et al. 2011), areas of upwelling (Caldwell et al. 1966, Drury and Smith 1968, Gulland 1974), areas of downwelling (Berzin 1971, Best 1979, Gaskin 1973, Ivanshin 1978), thermal fronts (Gannier et al. 2002, Gannier and Praca 2007), warm-core rings (Griffin 1999, Waring et al. 1993), cyclonic eddies (Ortega-Ortiz & Mate 2006), higher than average chlorophyll concentration (Biggs et al. 2006), negative sea surface height anamolies (Biggs et al. 2006) and low sea surface temperature (Ramirez and Urquizo 1985, Whitehead et al. 1989). Foraging success of sperm whales has been related to low sea surface temperatures (Smith and Whitehead 1993, Whitehead et al. 1989) and areas of upwelling (Rendell et al. 2004).

Historically, the Sargasso Sea, an oceanic gyre bounded by currents in the North Atlantic Ocean, supported a lucrative whaling industry for sperm whales (Bannister et al. 2008, Smith et al. 2012) and recent surveys have found large numbers of sperm whales in the northern part (Chapter 5). However, in comparison to other regions where sperm whales were found in great numbers, such as the equatorial current (Townsend 1935), the Sargasso Sea is low in productivity (Blackburn 1981). How this area is able to support such large numbers of sperm whales presently and historically is unclear.

The northern part of the Sargasso Sea experiences enhanced primary productivity as a result of the mesoscale activity associated with the Stream influence and winter mixing (McGillicuddy and Robinson 1997, McGillicuddy et al. 1998, Ortner et al. 1978). Recent evidence suggests that this mesoscale activity associated and its interaction with seamounts may play a role in this area’s ability to support high densities of sperm whales (Chapter 3). Sperm whales in the Sargasso Sea are likely feeding on large cephalopods, such as the giant squid (*Architeuthis dux*), and their diet appears to differ from that in some others areas of the Atlantic, such as the Caribbean, in both species composition and trophic ecology (Chapter 2). Knowledge of the physical and biological oceanographic variables that influence sperm whale foraging success in this area would provide insight into the basis of sperm whale distribution in the Sargasso Sea.

With the exception of limited offshore work in the Atlantic Ocean (Waring et al. 1993) and sperm whale research conducted in the Pacific Ocean (Jaquet and Whitehead 1996, 1999), very little is known about how oceanographic variables influence the distribution of sperm whales in the open ocean. The objective of my study was to examine the spatial distribution, foraging success and movement patterns of sperm whales in the northwestern Sargasso Sea in relation to oceanographic and bathymetric variables. The Gulf Stream is a dominant feature in this area and in light of the evidence described above, that mesoscale activity associated with the Gulf Stream leads to enhanced productivity, I predicted that the Gulf Stream would influence sperm whale distribution in this area. Specifically, I predicted that sperm whale presence would be associated with areas with increased mesoscale activity (eg. eddies (Biggs et al. 2006)), higher levels of primary productivity (Jaquet 1996, Jaquet et al. 1996) and that the probability of sperm whale presence would increase with proximity to the Gulf Stream (i.e. higher latitudes and more westerly longitudes).

4.2 METHODS

4.2.1 Data Collection

Acoustic surveys of sperm whales were conducted in the western North Atlantic Ocean from 2004-2007 and 2010 (Figure 4.1, Table 4.1) from a 12 m auxiliary sailing vessel, and in 2008 (June 25-July 5) from a 32 m auxiliary sailing vessel, using a towed omni-directional hydrophone array. The study area was defined as waters deeper than 1000 m, west of 50^0W and north of 23.5^0N and hereby referred to as the Sargasso Sea. Every 30 minutes, we listened to the hydrophone for the presence of sperm whale clicks (hereby referred to as 'listens'), used primarily in echolocation and communication

(Whitehead 2003). The majority of clicks detected were usual clicks, which are a long train of regularly spaced clicks (0.5s-1.0s) that can last for several minutes and are thought to function primarily in searching echolocation (Jaquet et al. 2001, Madsen et al. 2002a, Whitehead and Weilgart 1990). These acoustic surveys provided presence and absence data used in habitat modeling below.

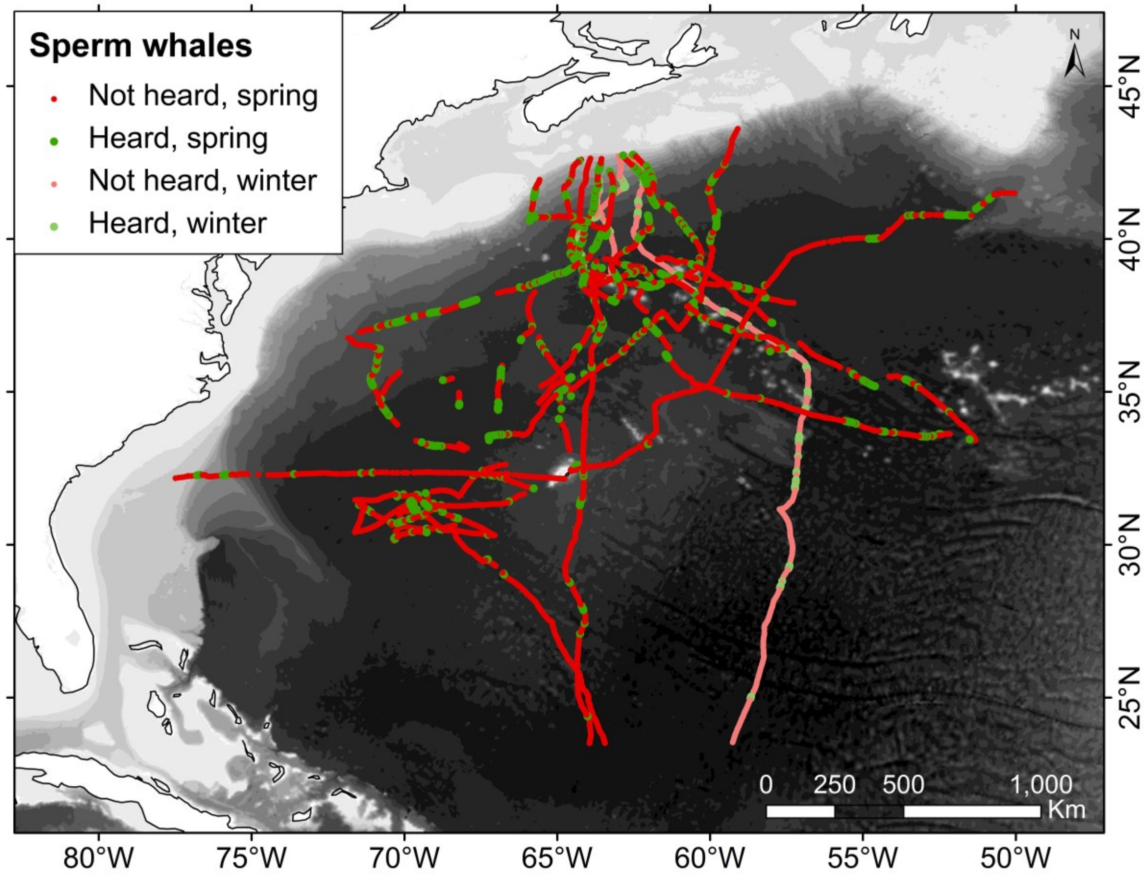

Figure 4.1 Distribution of sperm whale acoustic surveys from 2004 – 2008, 2010 during spring (April – July) and winter (November, February – March) in the Sargasso Sea. Points are plotted over a bathymetry map and each point represents a location where hydrophones were used to listen for the presence/absence of sperm whale clicks. Listens occurred every 30 minutes while vessels were in transit.

Table 4.1 Details of the acoustic surveys.

Year	**Start date**	**End date**	**Season**	**Total distance surveyed (km)**
2004	May 5	May 21	Spring	784
2004	June 4	June 14	Spring	624
2005	April 23	May 20	Spring	2,884
2005	May 31	June 22	Spring	1,853
2006	May 31	June 23	Spring	3,642
2006	October 31	November 4	Winter	932
2007	May 4	May 25	Spring	3,126
2007	June 7	June 25	Spring	2,753
2008	February 24	March 5	Winter	2,444
2008	June 25	July 5	Spring	3,013
2010	April 26	May 3	Spring	1,809
Total distance surveyed all surveys combined				**23,864**

Weather permitting (wind force ≤ 4 on the Beaufort scale), when sperm whale groups were detected, the survey was stopped and the groups (composed of adult females, immatures and calves) were followed acoustically (using a directional hydrophone) and visually for several hours or several days. We followed groups to collect information on fine-scale movement patterns of sperm whale groups and for indices of foraging success (defecation rate, explained below). The vessel's position was recorded every 10 minutes using a Global Positioning System (GPS). During daylight hours, individuals were followed closely (< 50m behind) and photographs of their flukes were taken. Immediately after each observed dive, the vessel approached the dive site (slick) and recorded whether the whale defecated (as indicated by a brown patch in the water). The vessel usually reached the slick within one minute of the dive, however researchers only recorded the presence or absence of defecation if they were confident defecation could be determined. Since deep-diving mammals usually shut down non-essential physiological systems at depth (Kooyman et al. 1981), it is believed that sperm whales almost always defecate at the surface (Jaquet and Whitehead 1999, Whitehead 2003).

4.2.2 Environmental Covariates

The variables used to examine habitat associations with sperm whale distribution were: depth, slope gradient, distance to seamount, chlorophyll-*a* concentration (chl-*a*) (as a proxy for primary productivity), sea surface temperature (SST), sea surface height anomaly (SSHA) and eddy kinetic energy (EKE) (Table 4.2). SSHA can be used to identify the presence of eddies, with negative values indicating the presence of cyclonic eddies (Teo and Block 2010). EKE is a measure of turbulence and flow of a region and can be used to identify where mesoscale eddies and meanders are common and also to mark the presence of major currents, such as the Gulf Stream (Teo and Block 2010).

Table 4.2 Environmental covariates used in the analysis and their spatial and temporal scale

Covariate	**Unit**	**Spatial scale**	**Temporal scale**	**Temporal lag**
Latitude	Decimal degrees		--	--
Longitude	Decimal degrees		--	--
Depth	m	1 arc-minute	--	--
Slope	Degrees	1 arc-minute	--	--
Distance to seamount	km (log)		--	--
SST	^{0}C	4 x 4 km	weekly	Real time (0wk) lagged up to 8 weeks previous
EKE	cm^2• s^{-2}	1/3^0 by 1/3^0	weekly	Real time (0wk)
SSHA	cm	1/3^0 by 1/3^0	weekly	Real time (0wk)
*Chl-*a*	mg•m^{-3}	4 x 4 km	weekly	Real time (0wk) lagged up to 8 weeks previous

* only used in final analysis.

Depth was acquired from the National Geophysical Data Center (NGDC)'s 1-arc minute Gridded Global Relief Data (ETOPO1) dataset (Amante and Eakins 2009) (http://www.ngdc.noaa.gov/mgg/gdas/gd_designagrid.html) and expressed as a negative value in metres. Slope gradient (hereafter referred to as 'slope'), defined as the maximum rate of change in depth within a given grid cell to that of its neighbouring cells and expressed as degrees of slope, was calculated using Geographic Information System (GIS) software (ArcMap). Distance to seamount (defined as underwater mountains that were no more than 2500 m below the surface, in an area where average depth was roughly 5000m) was expressed in degrees and calculated using GIS software (Idrisi).

Eight-day composite chl-*a* and SST data were downloaded from Aqua-MODIS satellite images (http://oceancolor.gsfc.nasa.gov/) for the period of study. Aqua-MODIS images provide chl-*a* in $mg \cdot m^{-3}$ and SST in degrees Celsius at a resolution of 4km x 4km. Chl-*a* and SST images were imported into Idrisi (Andes Edition). Cloud cover resulted in missing values for SST data and especially chl-*a* within the study area. Excluding weeks where data was missing would have significantly reduced my sample size and since I was interested in overall patterns, I decided to use interpolation techniques to estimate missing values. Following similar criteria used by Teo et al. (2010), I excluded all 8-day composites that had more than 50% missing values. For the remaining missing values, missing pixels were interpolated using nearest neighbour inverse distance weighted (IDW) interpolation in GIS (ArcMap) (Arnould and Kirkwood 2008). A temporal lag between sperm whale occurrence and SST and chl-*a* concentration is expected, given the time needed for primary productivity to transfer up to higher trophic levels (Croll et al. 2005, Jaquet and Whitehead 1996). Thus, in addition to real-time values (0wk), the lagged values for chl-*a* concentration and SST were also calculated for one (1wk) to eight weeks (8wk) previously.

SSHA and geostrophic velocity anomaly data were downloaded from Aviso's global sea surface height products (http://www.aviso.oceanobs.com/en/data/products/sea-surface-height-products/global/index.html) at a resolution of $1/3^0$ by $1/3^0$ on a Mercator grid. These data were derived from merged satellite altimetry measurements of four altimeters (Jason-1, ENVISAT/ERS, GEosat Follow-On and Topex/Poseidon interlased). EKE was calculated using the following formula:

$$\mathbf{EKE=1/2\ X\ (u'^2+v'^2)}$$

where u and v are zonal and meridian geostrophic currents components, respectively and EKE is a deviation from the mean.

4.2.3 Analysis

4.2.3.1 Foraging success and movement

Data collected during while following sperm whale group was used to examine foraging success and movement. Foraging success of sperm whales was evaluated using defecation rate (the proportion of fluke-ups made by whales within 50m of the boat that were accompanied by defecations), which has been used as an indicator of sperm whale feeding success in previous research (Smith and Whitehead 1993, Whitehead et al. 1989, Whitehead and Rendell 2004). For groups that were followed at least 12 consecutive hours, mean defecation rate over the entire encounter was calculated when 1) at least 15 slicks were checked (Jaquet et al. 1999) and 2) when at least 8 slicks were checked (to increase sample size). Daily defecation rate was also calculated for groups when at least 8 slicks were checked. To examine fine-scale movement of sperm whale groups, I also calculated the total distance travelled over 12 hours of daylight (7:00-19:00 local time, UTC-3), hereby referred to as the 12-hour displacement.

To examine the relationship between foraging success and group movement, Spearman coefficient of correlations were calculated between defecation rate (index of foraging success) and 12-hour displacement (daily and mean). Very little is known about the time lag between ingestion and excretion in sperm whales, but Smith and Whitehead (1993) suggest defecation rate likely reflects foraging success of the past 12 hours. Therefore, Spearman coefficient of correlations was calculated between daily 12-hour displacement and daily defecation rate 1 day later. To examine whether certain habitat variables might explain foraging success or movement, I also used Spearman coefficient of correlations to examine the relationship between foraging success and movement (defecation rate and 12-hour displacement) and the following variables (mean during the encounter): distance to seamount, depth, chl-*a*, SST, EKE and SSHA.

4.2.3.2 Habitat use

To examine the relationships between sperm whale distribution (presence/absence) and the environmental covariates described above, I used a binomial-based Generalized Additive Model (GAM) framework with a logit link function (Hastie and Tibshirani 1990, Wood 2006). My survey data suffers from spatial autocorrelation: the presence/absence of a sperm whale at one listen will be similar to the presence/absence of a sperm whale at the previous or following listen. GAM inference assumes independence between model residuals; an assumption that would be violated if all listens were used. Spatial autocorrelation in the data leads to the underestimation of standard errors of the model estimates, and can lead to predictors being identified as significant, when they are not (Lennon, 2000). One approach to reducing spatial autocorrelation is to subset data, however this approach results in discarding much of the data collected and reduces sample size. Instead, I used an approach recently introduced by Pirotta et al. (2011) that relaxes the independence assumption and models the correlation between residuals using Generalized Estimating Equations (GEEs) (Liang and Zeger 1986).

To account for autocorrelation, the listens from the acoustic surveys were grouped into blocks: independence of listens is assumed between blocks, but within blocks listens are allowed to be correlated. For the survey data, two types of blocks were assigned: "present" was defined as consecutive listens when sperm whale clicks were heard (this could be as few as one listen) and "absent" was defined as consecutive listens when sperm whale clicks were not heard (between "present" blocks). Since there could be long stretches (longer than 20 hours) when no sperm whale clicks were heard, I chose to divide the "absent" blocks (Scott-Hayward 2006). To determine how many listens (or hours) should constitute a block, I ran an autocorrelation function (acf) on legs that lasted longer than 24 hours. The acf on the residuals were found to be autocorrelated at 10 listens. Therefore, if blocks were greater than 10 listens apart, a new "absent" block was assigned.

To examine the relationship between sperm whale presence/absence and our covariates, I fit a bionomial-based GEE-GLM with a logit link function as in Pirotta et al. (2011) using the geepack library (Yan et al. 2010) in R (Team 2009). Following Pirotta et al. (2011), I used a working independence model since the underlying structure of dependence between residuals was not known (Pan 2001) and the correlation structure was defined by blocks. All covariates were considered as linear terms or as 1-dimensional smooth terms using the splines library in R (Team 2009) which builds cubic *B*-splines within the GEE-GLM, resulting in a GEE-GAM. Smooth terms had four degrees of freedom with one internal knot at the mean value of each variable (Pirotta et al. 2011). This is explained further below.

Including chl-*a* in the model would reduce the sample size considerably (by ~75%) due to the extent of missing data. I decided, for my initial model, to exclude chl-*a* and only included the following covariates: latitude, longitude, year, depth, slope, distance to seamount, SST, EKE and SSHA. I used a modified version of the Akaike Information Criterion (AIC) (Burnham and Anderson 2002) to select the best set of variables to retain in the final model: the quasi-likelihood under the independence model criterion (QIC; (Pan 2001)). QIC accounts for the fact GEEs are based on quasi-likelihood. To select the variables, I used a backward stepwise approach using QIC_u (Hardin and Hilbe 2003) using the yags library (Carey 2004) in R. However, before full model backward-stepwise could be preformed, a series of steps were required to reduce the number of candidate variables and simplify the data set. These steps are described below and in a flow chart (Figure 4.2).

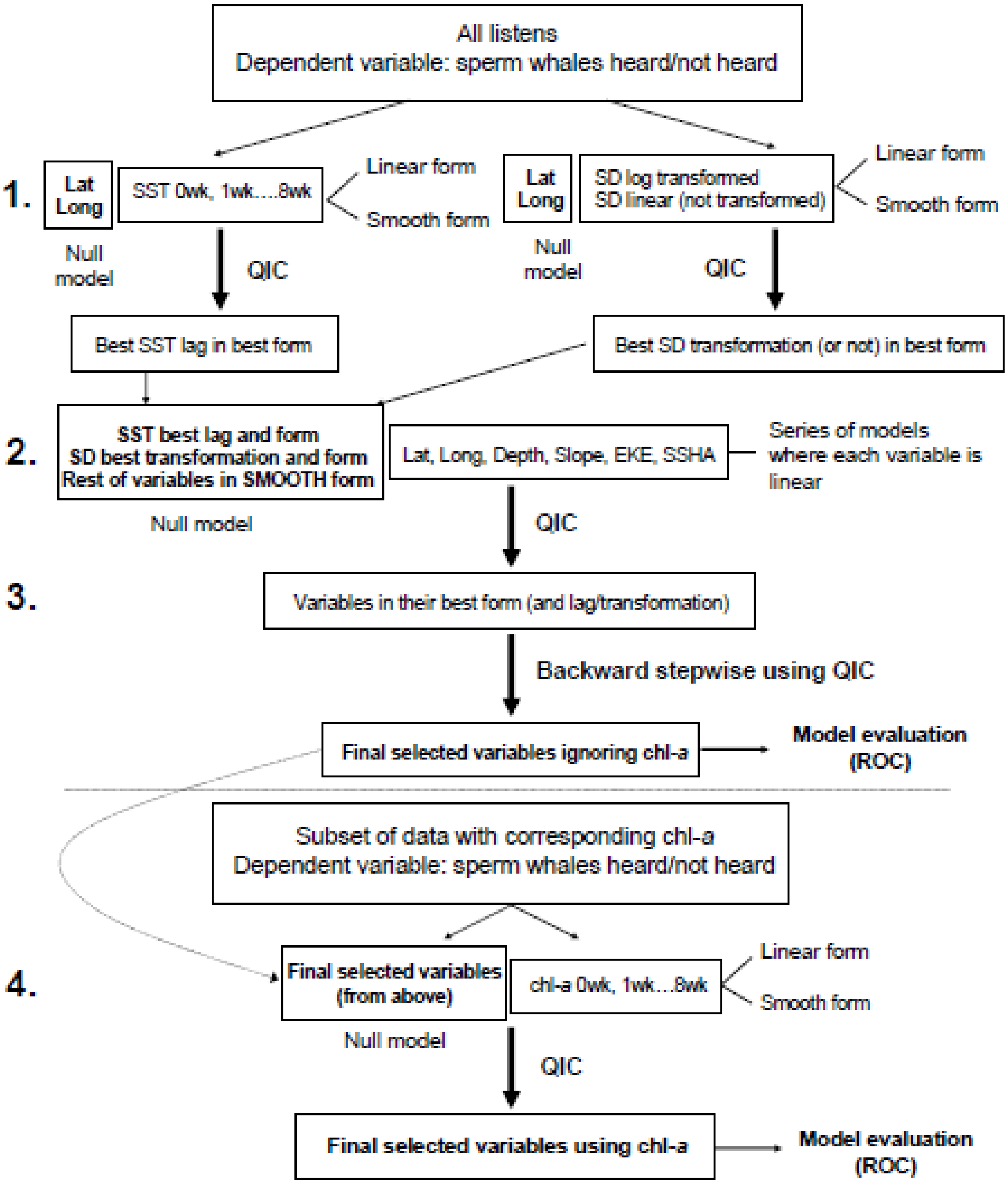

Figure 4.2 Flow chart illustrating the steps of the analysis examining the relationship between sperm whale presence and environmental covariates. Step 1: selection of the best form (linear or smooth) and lag (for SST) and transformation (SD). Step 2: selection of the best form (linear or smooth) for all remaining covariates. Step 3: selection of the best variables to explain sperm whale presence. Step 4: rerunning the models with a reduced data set to evaluate whether inclusion of chl-*a* improved the models. Chl-*a* = chlorophyll-*a* concentration, SST = sea surface temperature (0wk = real time, 1wk = 1 week previous, 8 wk = 8 weeks previous etc), SD = seamount distance, EKE = eddy kinetic energy, SSHA = sea surface height anomaly.

Including all the SST covariates at the different temporal scales would have resulted in instability due to the collinearity between the variables. Therefore, an ad hoc procedure was performed to select the most appropriate temporal scale (lag) and best form (linear or smooth) to use in the final model by comparing the QIC_u score of a null model (containing latitude and longitude) and a series of models containing SST at each temporal lag in both forms (linear or smooth) (Step 1 in Figure 4.2). I used the temporal lag (and form) with the lowest QIC_u score in the next step. I also used the same ad hoc procedure to select whether seamount distance should be included in the final model as log-transformed (or not), and the best form (linear or smooth) (Step 1 in Figure 4.2). At the end of Step 1, I had selected a) SST at best temporal lag and form, and b) SD in best transformation and form. I then considered all of the other covariates (including latitude and longitude) as linear or smooth form. This was done by creating a null model which contained: 1) SST in the best temporal lag and form, 2) SD in best transformation and form and finally 3) the remaining covariates as smooth form. This null model was then compared to a series of models in which each covariate was replaced in its linear form (Step 2, Figure 2.2). The QIC_u approach was used to select which form was best for each variable. Once the most appropriate temporal lag and form for each variable was selected (Step 1-2, Figure 4.2), a series of reduced models (containing all variables but one) were fitted and the model with the lowest QIC_u score was used in the following step. This procedure was continued until removal of any variable caused the QIC_u score to increase resulting in our final model (Step 3 in Figure 4.2). Since I was still interested in the effect of primary productivity (chl-*a*) on sperm whale distribution, I then reduced the dataset such that there were no missing chl-*a* values and compared the null model (which contained the final variables selected above, end of Step 3) to models which contained chl-*a* at different temporal scales (lag) and form (linear or smooth) using QIC_u to see if the addition of chl-*a* improved the model (Step 4 in Figure 4.2).

Partial residual plots were used to examine the relationship between the response variable and sperm whale presence (ggplot 2: Wickham 2009). Confusion matrices, which compare predicted and actual values, were used to evaluate the model performance. Confusion matrices require a cut-off probability value which identifies at what threshold a prediction is considered a presence or absence. To avoid biases resulting from an inappropriate cut-off value (Boyce et al. 2002), I followed the approach taken by Pirotta et al. (2011) and used a Receiver Operating Characteristic (ROC) curve (ROCR library in R; Sing et al. 2009). ROC curves plot the proportion of correctly classified presences (sensitivity) to the proportion of incorrectly classified presences (specificity) (Zweig and Campbell 1993). Each point on the ROC curve represents a sensitivity/specificity pair corresponding to the cut-off value. The best cut-off probability is the one that maximizes the balance between sensitivity and specificity. The area under the ROC curve (auc) is a measure of how well the model performed. A value of 0.5 indicates a model with no predictive power, a value of 1 indicates a perfect model and a value of 0.7 is considered "useful" (Boyce et al. 2002).

I also wanted to explore whether different parameters were influencing sperm whale distribution in the northern part of the Sargasso Sea compared to the southern part, especially as survey effort and detection rates were higher in the northern part of the Sargasso Sea (Figure 4.3). Maps of EKE suggest that north of about 35^0N, EKE is higher than south of this boundary (Ducet et al. 2000, Fratantoni 2001, Oschlies and Garçon 1998) and the density of sperm whales north of 35^0N (5.30 sperm whales per 1000 km^2) I nearly twice the density south of 35^0N (2.89 sperm whales per 1000 km^2) (Chapter 5). Therefore, I divided the study area into the northern section and southern section (delineated by the 35^0N latitudinal line) and ran the models on each section.

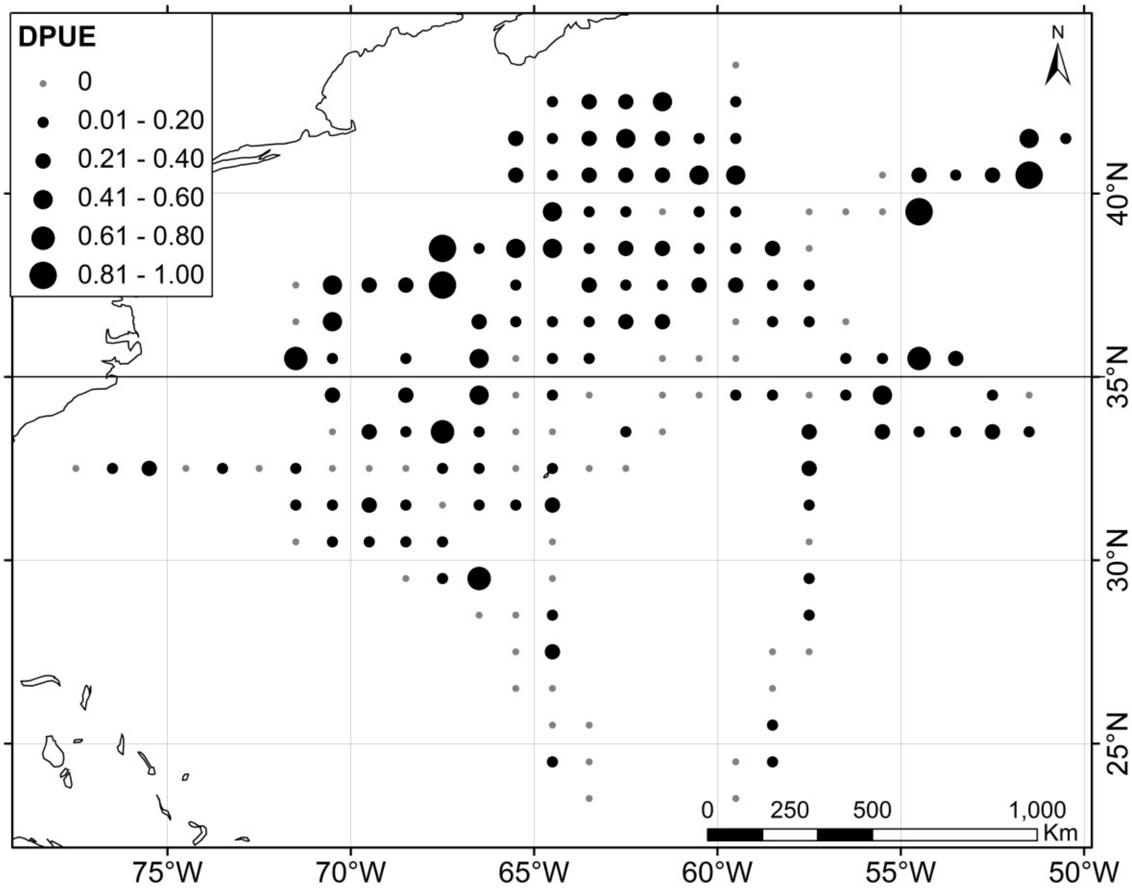

Figure 4.3 The detections of sperm whales per unit effort (DPUE) in 1 degree grid cells. Effort was defined as the number of listens per grid cell and detections were the number of listens when sperm whale clicks were heard.

4.3 RESULTS

A total distance of 23,864 km (4,374 listens) was surveyed across 6 years of study (Table 4.1) and sperm whales were heard 820 times (18.7% of listens). Most survey effort was during spring surveys (20,488 km and 3,771 listens) with a higher proportion of sperm whale detections (728 times heard, or 19.3% of listens) compared to winter surveys (3,376 km and 603 listens of which 92 were detections, or 15.3% of listens) (Figure 4.3). A total of 46 groups were tracked for periods of time ranging from 2 hours to 241 hours (mean = 30 hours) in duration.

4.3.1 Foraging Success and Movement

There was no significant correlation between defecation rate and 12-hour displacement when a minimum of 15 slicks were checked for a group (n = 9, r_s = -0.200, p = 0.606) or when at least 8 slicks were checked (n = 18, r_s = -0.131, p = 0.604). In addition, there was no significant correlation between daily defecation rate (with at least 8 slicks checked) and daily 12-hour displacement (n = 26, r_s = -0.007, p = 0.975) or between daily 12-hour displacement and the defecation rate one day following (n = 26, r_s = -0.007, p = 0.975). There was no significant correlation between either defecation rate or 12-hour displacement and any of the oceanographic and bathymetric variables except for a significant positive relationship between 12-hour displacement and EKE (n = 22, r_s = 0.486, p = 0.022) (Table 4.3).

Table 4.3 Spearman correlation coefficients between the index of foraging success (defecation rate: n = 22) and 12-hour displacement (n =22) and oceanographic and bathymetric variables. [chl-*a*] = chlorophyll-a concentration, SST = sea surface temperature, EKE = eddy kinetic energy, SSHA = sea surface height anomaly.

	Depth (m)	**Slope (deg)**	**Seamount distance (deg)**	**[chl-*a*] ($mg \cdot m^{-3}$)**	**SST (^0C)**	**EKE ($cm \cdot s^{-2}$)**	**SSHA (cm)**
Defecation rate	0.251	-0.411	0.234	-0.376	-0.102	-0.144	0.131
12-hour displacement	-0.099	0.241	-0.181	0.326	-0.111	**0.486***	-0.330

* = $p < 0.05$

4.3.2 Habitat Use

For the entire study area in the Sargasso Sea, SST at 0wk (smooth form) and non-transformed seamount distance (linear form) were the variables selected during the ad hoc procedure (Step 1, Figure 4.2). The remaining covariates in the model were linear form except depth (Step 2, Figure 4.2). The final model, after variable selection using QIC_u scores, retained latitude, longitude and SST at 0wk to explain the probability of detecting sperm whales (Table 4.4). The confusion matrix suggested the model correctly predicted 69% of the presences and 57% of the absences. The AUC was 0.66, which falls below the threshold of 0.7 that Boyce et al (2002) consider to be “useful”. The probability of detecting sperm whales increased with latitude (Figure 4.4a), longitude west (Figure 4.4b) and SST at 0wk up to about 23-24^{0}C (Figure 4.4c). I ran the same analysis using only surveys that were conducted during the spring (April – July) and the final model retained the same variables as above, but also included seamount distance (smooth form) with the probability of detecting sperm whales decreasing with seamount distance (Figure 4.4d). The AUC was 0.69 (Table 4.4).

Table 4.4 Model results examining the relationship between sperm whale occurrence and environmental parameters. AUC = area under the curve, Chl-*a* = chlorophyll-*a* concentration, SST = sea surface temperature, EKE = eddy kinetic energy, SSHA = sea surface height anomaly.

Model	**Variables selected (ignoring chl-*a*)**	**Cut-off probabilility value**	**% correctly predicted presences**	**% correctly predicted absences**	**AUC**	**Variables selected using chl-*a* data**	**Cut-off probability value**	**% correctly predicted presences**	**% correctly predicted absences**	**AUC**
Entire Sargasso	latitude, longitude, SST 0wk	0.188	69	57	0.66	latitude, longitude, SST 0wk, **chl-*a* 2wk**	0.213	83	69	0.81
Entire Sargasso Spring only	latitude, longitude, SST 0wk, seamount distance	0.204	67	63	0.69	latitude, longitude, SST 0wk, seamount distance, **chl-*a* 6wk**	0.279	70	75	0.81
Northern Sargasso (> 35^0N)	latitude, longitude, SST 0wk SSHA	0.288	44	76	0.64	latitude, longitude, SST 0wk, SSHA, **chl-*a* 6wk**	0.282	81	59	0.77
Southern Sargasso (< 35^0N)	latitude, longitude, year, seamount distance, EKE, SST 0wk	0.160	70	74	0.78	--	--	--	--	--

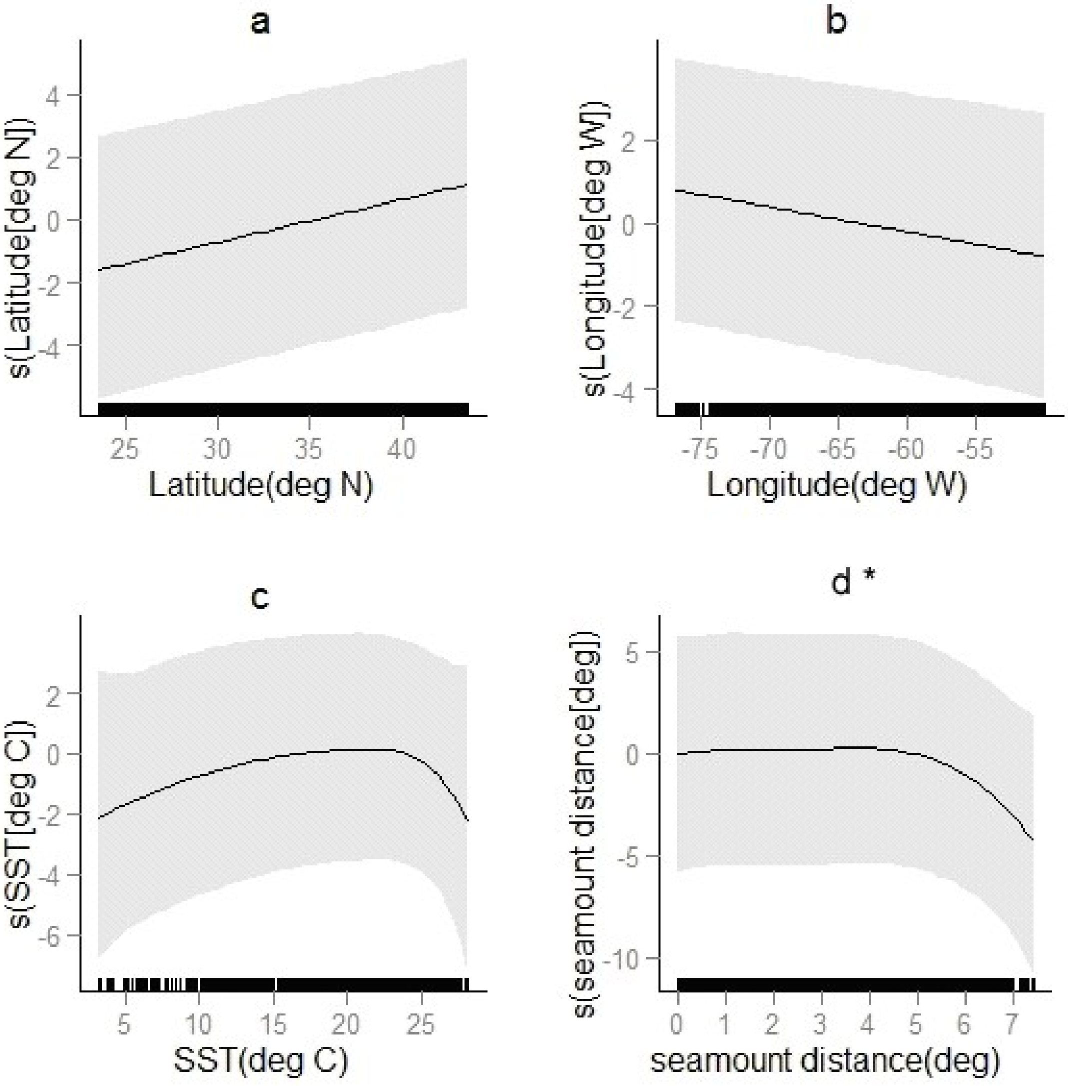

Figure 4.4 The relationship between sperm whale presence and the following predictors in the entire study area during all seasons: a) latitude, b), longitude and c) SST at 0wk. The relationship between sperm whale presence and seamount distance using spring data only is shown in d*. Shaded areas represent the 95% confidence intervals. A rug plot (vertical pars along the top edge of the horizontal axis) shows the actual distribution of the data.

The correlation matrix showed that SST at all temporal lags were significantly correlated (r_s ranging from 0.92 to 0.81), so I used SST at 0wk for the remaining models (north and south). For the northern Sargasso Sea (> 35^0N) the non-transformed seamount distance (linear form) was selected. The remaining covariates selected in the model were linear form except SST at 0wk and SSHA. The final model, after variable selection using QIC_u scores, retained latitude, longitude, SSHA and SST at 0wk (Table 4.4). The confusion matrix suggested the model correctly predicted only 44%% of the presences and 76% of the absences. The AUC was 0.64. In the northern Sargasso Sea, the probability of detecting sperm whales increased with latitude (Figure 4.5a) and decreased with longitude (Figure 4.5b). Probability of detecting sperm whales was highest when SSHA was negative (around -75 to -25cm) (Figure 4.5c) and increased with SST up to about 24^0C (Figure 4.5d).

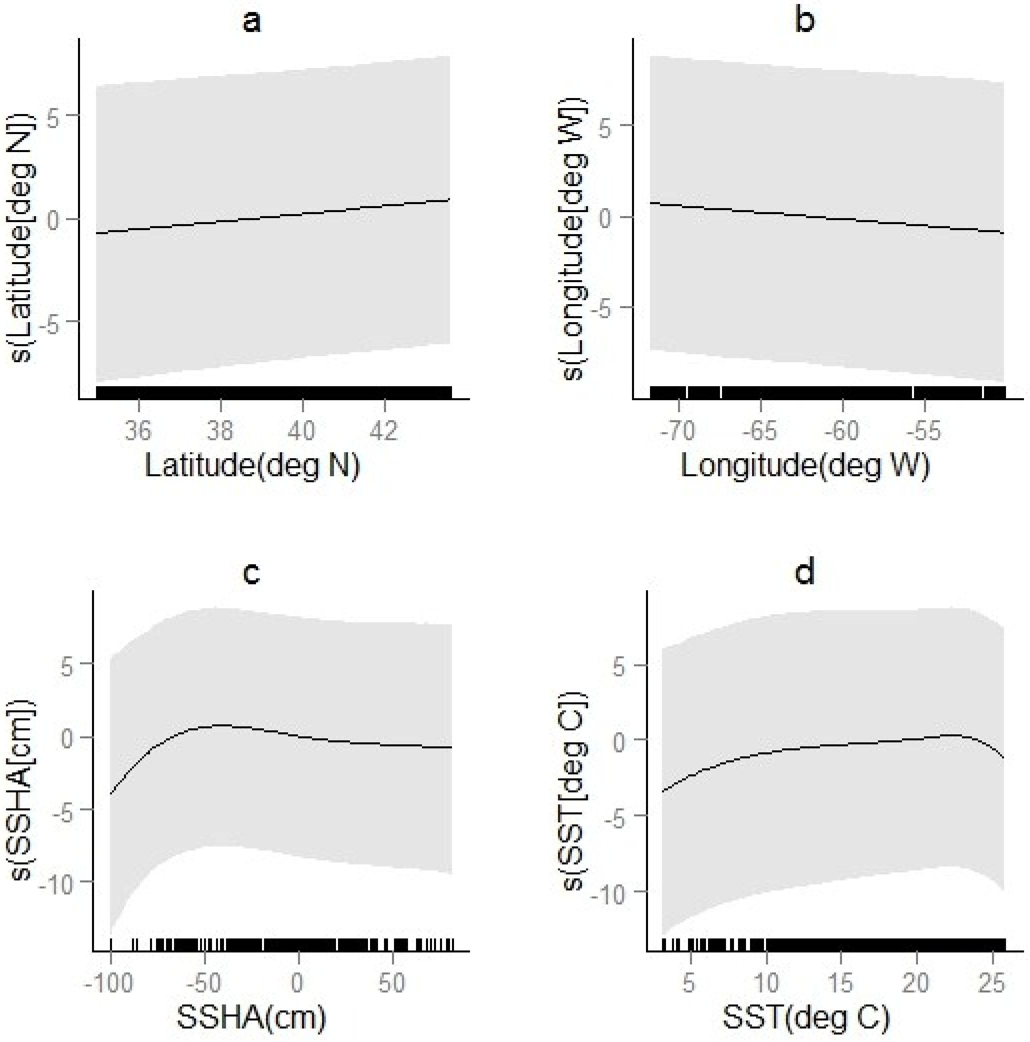

Figure 4.5 The relationship between sperm whale presence and the following predictors in the Northern part of the Sargasso Sea, (>35^{0}N) in all seasons: a) latitude, b) longitude, c) SSHA, and d) SST in real time. Shaded areas represent the 95% confidence intervals. A rug plot shows the actual distribution of the data.

For the Southern Sargasso Sea (>35^{0}N), the non-transformed seamount distance (smooth form) was selected. All remaining variables were selected as linear form except latitude, longitude, and SST at 0wk. The final model, after variable selection using QIC_u scores, retained latitude, longitude, year, distance to seamount, EKE and SST at 0wk (Table 4.4, Figure 4.6). The confusion matrix suggested the model correctly predicted 70% of the presences and 74% of the absences. The AUC was 0.78, considered “useful” (Boyce et al. 2002).

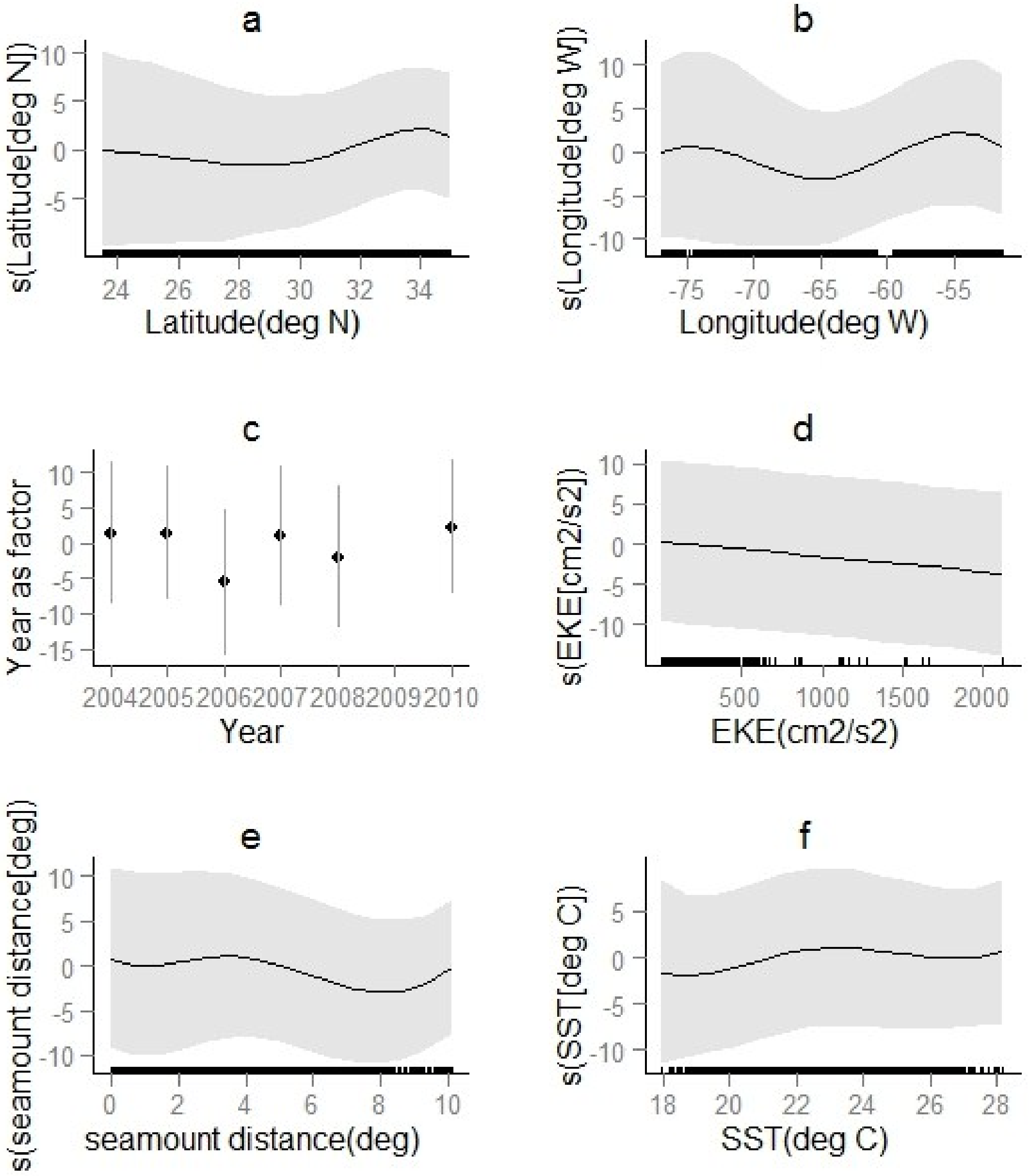

Figure 4.6 The relationship between sperm whale presence and the following predictors in the Southern part of the Sargasso Sea, (<35^0N) in all seasons: a) latitude, b), longitude and c) SST in real time. Shaded areas represent the 95% confidence intervals. A rug plot shows the actual distribution of the data.

To examine whether the addition of chlorophyll improved the models (selected above), I excluded data where chlorophyll was missing. For the entire study area, the dataset was reduced by over 75% to 1015 observations, of which 193 (19%) were detections. The addition of chl-*a* at a 2 wk lag (smooth form) improved the model (according to QIC_u

scores) (Table 4.4). The confusion matrix suggested the model correctly predicted 83% of the presences and 69% of the absences. The AUC was 0.81. The probably of detecting sperm whales increased with chl-*a* 2wk lag (Figure 4.7a) The relationship between sperm whale presence and our original variables (latitude, longitude and SST at 0wk) stayed the same, except the parameter estimate for latitude was much closer to zero (0.002) compared to prior to adding chlorophyll (0.136). For the spring Sargasso, the dataset was reduced to 887 observations (24% of original) of which 185 were detections (21%) and the addition of chl-*a* 6 week lag (smooth form) improved the model (Table 4.4, Figure 4.7b).

For the northern Sargasso, the dataset was reduced to 467 observations (20% of original data) of which 153 (33%) were detections. We compared the model using the variables selected by QIC (latitude, longitude, SSHA and SST at 0wk) and found the addition of chl-*a* 6 at a week lag (smooth form) improved the model (Table 4.4). The confusion matrix suggested the model correctly predicted 81% of the presences and 59% of the absences. The AUC was 0.77. Probability of detecting sperm whales increased with chl-*a* 6 wk lag (Figure 4.7c). We were not able to test whether adding chl-*a* improved our model for the southern Sargasso Sea, as reducing the data to exclude all missing chlorophyll values resulted in 547 observations (28% of original) but of those there were only 37 detections (less than 7%). Running the model on this dataset resulted in quasi-complete separation, which occurs when an outcome variable separates a predictor variable to a certain degree and is likely due to the low number of detections in this dataset. In this case, a maximum likelihood estimate does not exist, so the models could not be run.

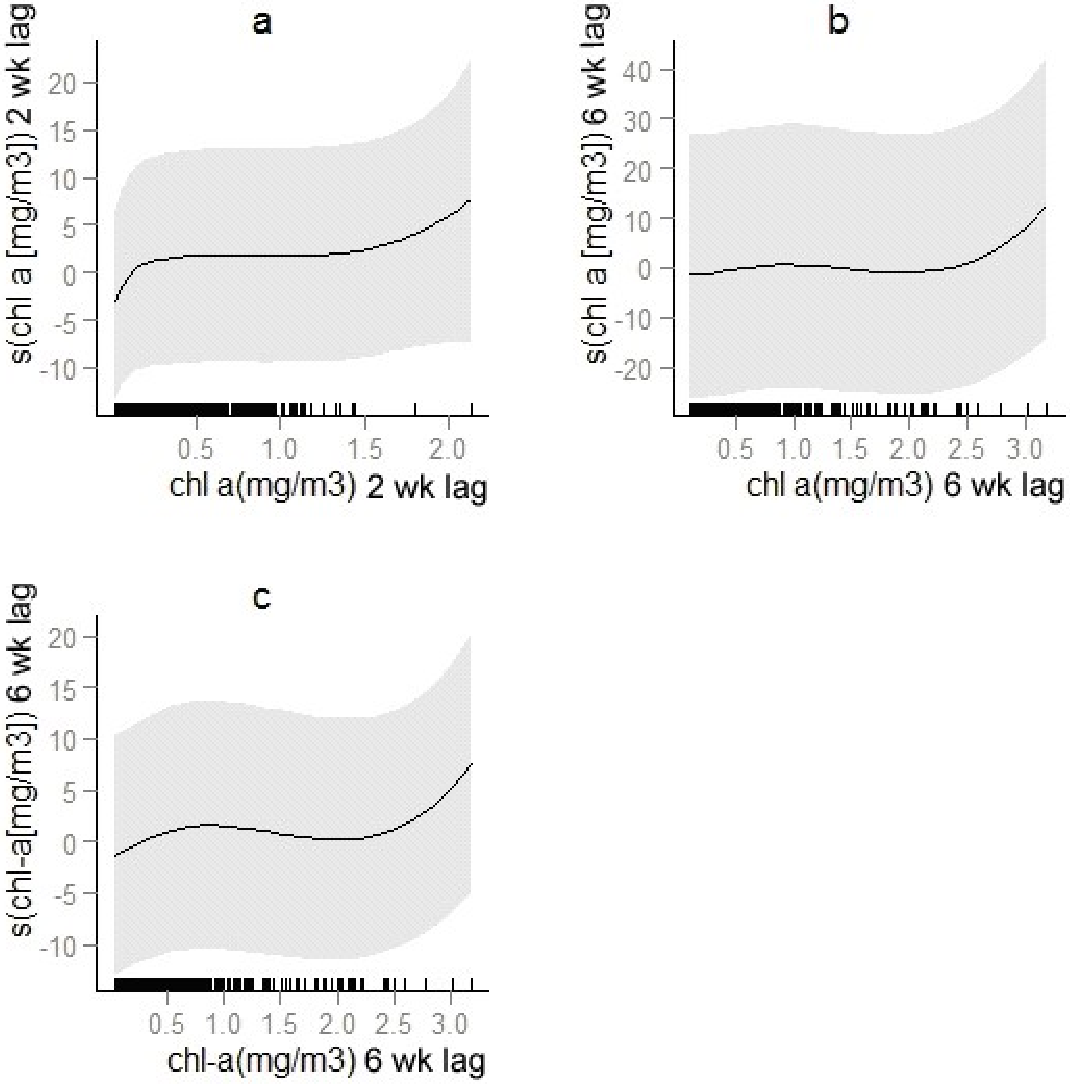

Figure 4.7 The relationship between sperm whale presence and chlorophyll *a* concentration for a) the Sargasso Sea during all seasons, b) the northern part of the Sargasso Sea (> 35^0N), and c) the Sargasso Sea during the spring only (April – July). A rug plot shows the actual distribution of the data.

4.4 DISCUSSION

4.4.1 Foraging Success and Movement

I used defecation rate as a proxy for foraging success and 12-hour displacement as a measure of movement, expecting that higher defecation rates and lower 12-hour displacements would suggest higher foraging success. Previous research in the Pacific Ocean found a significant, negative relationship between defecation rate and 12-hour displacement (Whitehead 1996). I found no significant relationship between defecation rate and 12-hour displacement, however, given the sample size (n = 9 and 18), I have no power to say whether there is a difference in trends between the Pacific and Atlantic.

No significant relationships between the index of foraging success or movement and environmental variables were found, except for a significant, positive relationship between 12-hour displacement and EKE ($n = 22$, $r_s = 0.486$, $p = 0.022$). EKE is a measure of mesoscale variability and higher values indicate where eddies and meanders are common (Teo and Block 2010). This may result in faster movement of the sperm whales (or more movement), so I would expect a higher 12-hour displacement with higher EKE. My inability to find a relationship between feeding success and environmental variables may be the result of spatial and/or temporal lags, as suggested by Jacket and Whitehead (1999) who found no significant relationships between foraging success and environmental variables. More likely, it is due to the small sample size.

4.4.2 Habitat Use

I examined the habitat use of sperm whale presence and different environmental covariates for our study area in the Sargasso Sea. The probability of detecting sperm whales increased with latitude in all the models (Figure 4.4a, Figure 4.5a, Figure 4.6a), and when using only the spring (April-July) survey data suggesting that sperm whales are more prevalent in the northern part of the Sargasso Sea. This is not surprising given that one of the highest density estimates of sperm whales globally is found in the northern (> 35^0N) Sargasso Sea (Chapter 5). The probability of detecting sperm whales in these models also increased with westerly longitude (Figure 4.4b, Figure 4.5b, Figure 4.6b), suggesting sperm whales occur more in the western part of the Sargasso Sea. Indeed the highest densities of sperm whales measured thus far are found off the US east coast, off the continental shelf (Whitehead 2002) and this area was whaled extensively during the open-boat whaling era (Bannister et al. 2008). Although previous research has found that sperm whale occurrence is inversely related to SST (Jaquet 1996, Pirotta et al. 2011, Ramirez and Urquizo 1985, Whitehead et al. 1989), my models for the entire Sargasso Sea (Figure 4.4c) and the northern Sargasso Sea (Figure 4.5c) found that higher temperatures (around 23-24^{0}C) have the highest probability of detection. The addition of chl-*a* (as a proxy for primary productivity) at varying time lags improved the models (albeit, with a much reduced dataset), suggesting that the probability of sperm whale detections was highest in areas with high primary productivity (Figure 4.7). Indeed, the parameter estimate for latitude in the model for the entire Sargasso Sea was nearly zero (0.002) when chl-*a* was added to the model, suggesting that chl-*a* was a more important predictor of sperm whale presence than latitude, and that the increased abundance of sperm whales in the northern Sargasso Sea may be linked to greater productivity. Mechanisms creating greater food availability for sperm whales in the northern Sargasso are not known but are likely linked to the presence of the Gulf Stream, the dominant physical oceanographic feature in this area.

4.4.3 The Importance of the Gulf Stream to Sperm Whale Distribution

The northwestern part of the Sargasso Sea, where the probability of detecting sperm whales is highest, is where mesoscale activity of the Gulf Stream increases primary productivity. Maximum Gulf Stream transport occurs around 65^{0}W and it is at this longitude where the current becomes unstable and develops large north-south oscillations (meanders) (Mann and Lazier 1996). Cold-core rings, which result in increased primary (The Ring Group 1981) and secondary (Ortner et al. 1978) productivity, are most frequently observed in the western Sargasso Sea, along a “corridor” 200 miles offshore of the Gulf Stream axis, between 28^{0}N and 36^{0}N and tend to drift south-westward (Parker 1971; Lai and Richardson 1977; Richardson 1983), which might explain why sperm whales are found in more westerly latitudes. That sperm whales are more likely to be present at higher temperatures may be a result of their proximity to the Gulf Stream, which has temperatures ranging from 25^{0}C – 28^{0}C (Mann and Lazier 1996) or rings and meanders associated with the Gulf Stream. Temperatures within the range of 22.5-24.5^{0}C, where probability of detecting sperm whales is highest, are found along the Gulf Stream (a width of roughly 100-150km) and in areas of eddies and meanders associated with the Gulf Stream in the northern part of the study area (Figure 4.8) and might explain why. Although these temperatures are also in lower latitudes where the models suggest that sperm whales are less likely to be detected (Figure 4.8), these temperatures occur in the uniformly warm waters expected in the tropics, where mesocale activity is less. Furthermore, any SST effects in the southern Sargasso Sea may be confounded by the many other variables interacting with sperm whale distribution here (Figure 4.5).

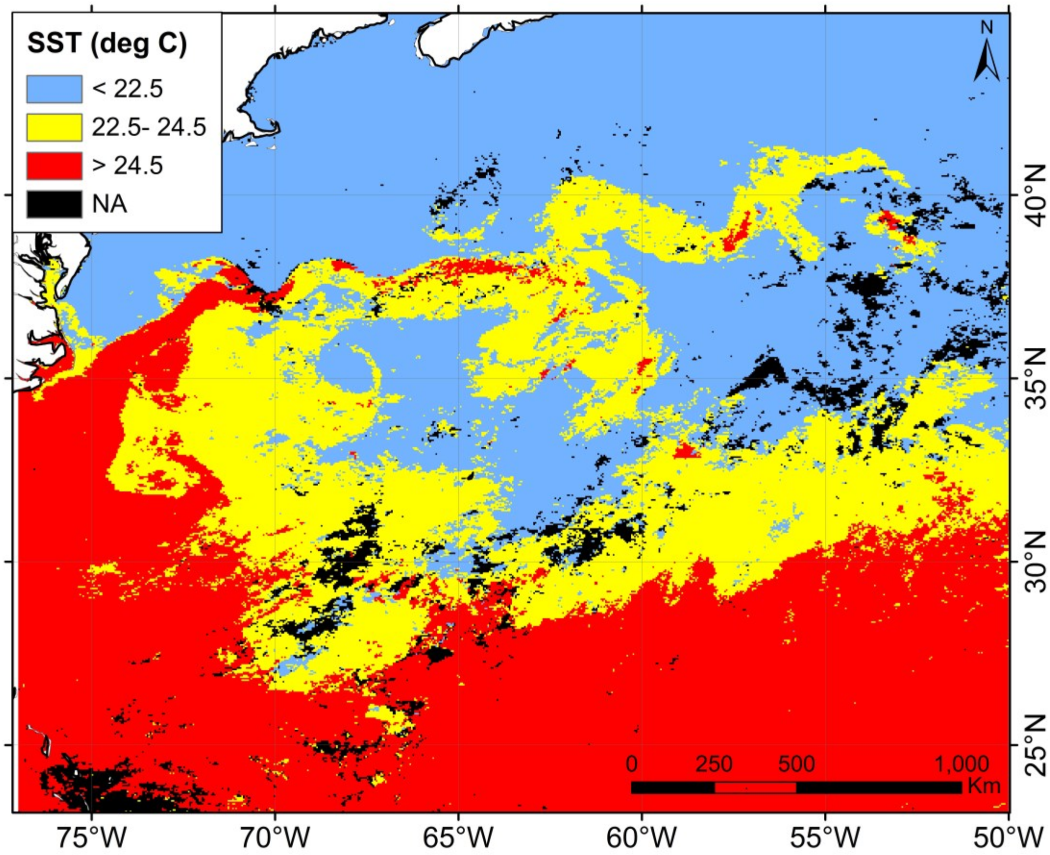

Figure 4.8 Distribution of sea surface temperatures (SST) from June 10-17, 2007, highlighting the range from 22.5-24.5^{0}C, which is the peak temperature range influencing sperm whale presence in the habitat models.

In the model for the northern Sargasso Sea, SSHA was also a predictor for sperm whale presence, with a greater probability of detection in areas of negative (-75 to -25cm) SSHA, an indication of cyclonic eddies (Teo and Block 2010). These cyclonic eddies are also associated with the Gulf Stream (Watts 1983) (Figure 4.9). Sperm whales in the Gulf of Mexico were most frequently encountered in areas with negative SSHA, likely because increased primary productivity associated with the cyclonic eddies resulted in richer feeding grounds (Biggs et al. 2006a) and other deep-diving predators forage near the edge of cyclonic eddies (Bailleul et al. 2010).

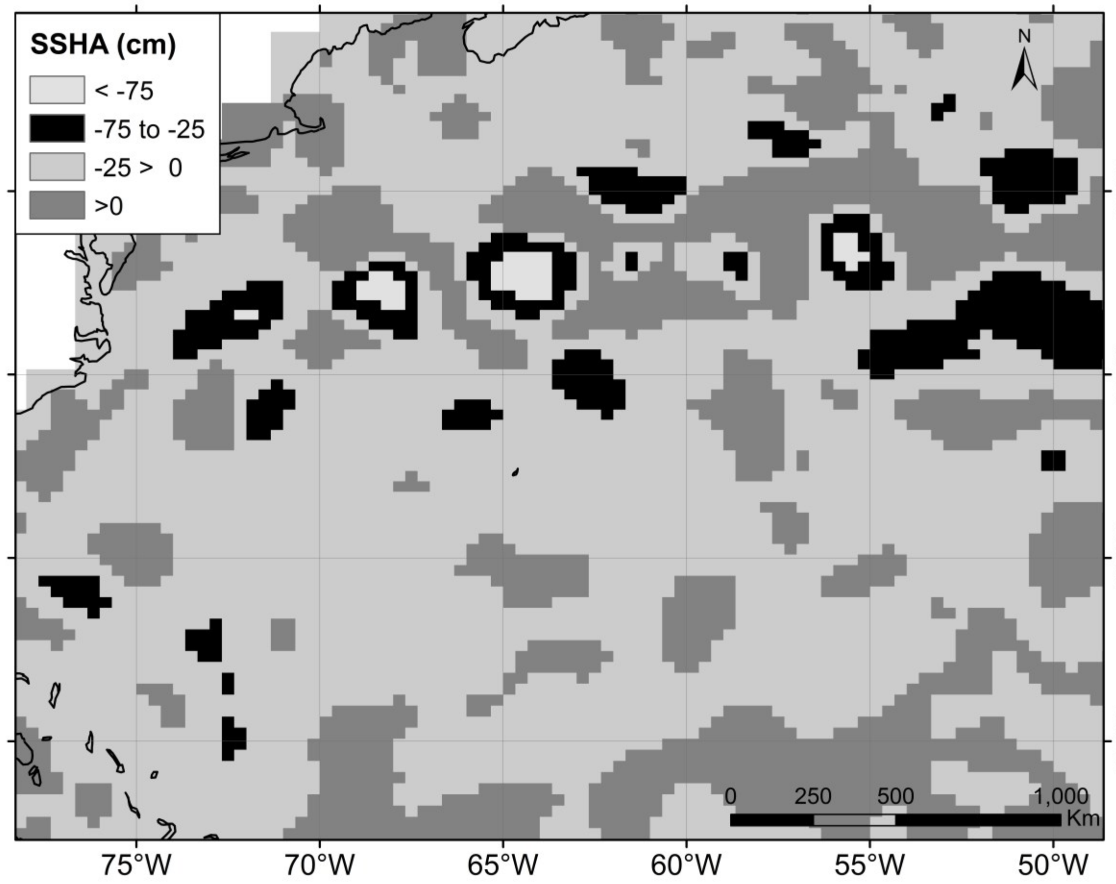

Figure 4.9 Sea surface height anomaly (SSHA) on May 16, 2006, highlighting the SSHA range from -75 to -25cm, which is the peak SSHA range influencing sperm whale presence in the habitat models for the northern Sargasso Sea (> 35^0N).

Finally, in the model that used only data collected in the spring, distance to seamount was also a predictor for sperm whale detection, with the probability of detection decreasing after about 4.5 degrees. Seamounts appear to be responsible for large meanders and semi-permanent rings of the Gulf Stream, and meanders often overlie the New England Seamount Chain (Richardson 1983), which is found in the northern part of our study area (running southeast from roughly 40^0 - 35^0N). The largest frequency of warm-core ring formation is seen near the New England Seamount Chain (Auer 1987). It thus appears that the Gulf Stream and its associated processes are likely influencing sperm whale presence in the northern part of the Sargasso Sea, possibly as a result of the Gulf Stream's influence on cephalopod distribution.

Deep-water cephalopods readily escape trawls and nets (Clarke 1977), and are difficult to study acoustically (Starr and Thorne 1998), so very little is known about cephalopods in this area. However, currents and eddies play an important role in the migration and life cycle of cephalopod species, especially the Gulf Stream (Bakun and Csirke 1998, Mann and Lazier 1996, O'Dor 1992) and Kuroshio current, a western boundary current in the North Pacific (Mann and Lazier 1996). Higher abundance and diversity of the early stages of cephalopods are found in the northern part of the Sargasso Sea (> 27^0N) (Diekmann and Piatkowski 2002) and the highest abundance of planktonic cephalopods is found in the vicinity of the Gulf Stream (Vecchione et al. 2001). Thus, while we know little about the distribution of sperm whale cephalopod prey in the Sargasso Sea, it appears that the Gulf Stream and associated mesoscale activity might influence cephalopod distribution in this area and thus, sperm whale distribution.

4.4.4 Model Evaluation

The AUC scores of the models that excluded chl-*a* data were all below the "useful" threshold of 0.7 (Boyce et al. 2002), however the consistency of latitude, longitude and SST being selected as variables in the final models suggests that these are indeed good predictors for sperm whale presence in the northwestern Sargasso Sea. The spring model (AUC = 0.69) performed a little better than the overall model (AUC = 0.66), suggesting that the limited winter data may be confusing the results of the overall model and that perhaps sperm whales are selecting slightly different habitats in the spring compared to the winter. There is evidence of seasonal variability of sperm whale occurrence around

Kelvin Seamount, part of the New England Seamount Chain (Chapter 3). When chl-*a* was considered in the models, AUC scores were higher (0.77 to 0.81). While these scores can't be directly compared because only a subset of data was used in the models that considered chl-*a*, the good model performance with the addition of chl-*a* suggests that primary productivity is an important predictor of sperm whale occurrence in this region.

The southern Sargasso Sea (< 35^0N) model performed well (AUC = 0.72) despite the exclusion of chl-*a* data. However, the number of the selected variables (latitude, longitude, year, EKE, distance to seamount and SST), the wide confidence intervals and the inability to clearly evaluate whether chl-*a* improved the model suggests that sperm whale presence in the southern Sargasso Sea might be driven by variables that were not include in the model. Sperm whales regularly dive up to 1000m for their prey (Whitehead 2003), so measures that better describe the deep water habitat which sperm whales inhabit might improve our ability to understand what drives sperm whale distribution in this area. For example, Jaquet and Whitehead (1996) found a positive correlation between sperm whale density and the intensity and thickness of the middle (50-300m) and deep (300-600m) scattering layers and there is evidence that sperm whales often dive through the deep scattering layer (Sarvas and Flemmin 1999, Wahlberg 2002). Furthermore, although I examined some variables on different temporal scales (lags: chl-*a* and SST), I used the smallest resolution for our environmental covariates and did not increase spatial scale. Other studies have shown that the relationship between sperm whale distribution and environmental covariates can only be seen at large spatial scales (Jaquet and Whitehead 1996) and that spatial scale should be taken into consideration (Jaquet 1996, Pirotta et al. 2011).

4.5 SUMMARY

The close association found between sperm whale presence and variables such as primary productivity (Praca et al. 2009), cool sea surface temperatures (Rendell et al. 2004) and bathymetry (Pirotta et al. 2011, Praca et al. 2009) were found in semi-enclosed waters such as the Gulf of Mexico or the Mediterranean, around islands (Galapagos, Azores) in the open ocean or in systems dominated by the highly productive eastern boundary currents (off Chile). Despite some limitations to the models and limitations in the data (e.g. the missing chl-*a* values due to cloud cover), this study is one of the few that have examined sperm whale distribution in the open ocean. The models found that the probability of sperm whale detections is highest in the northwestern part of the Sargasso Sea in areas with SST of 23-24^{0}C and high primary productivity. These results suggest that the Gulf Stream and its associated mesoscale activity is driving sperm whale distribution in this area.

CHAPTER 5

SPERM WHALE (*PHYSETER MACROCEPHALUS*) DISTRIBUTION AND DENSITY IN THE SARGASSO SEA: 1775-1921 AND 1993-2010

The work presented in Chapter 5 was done in collaboration with two other co-authors:

1) Julie Horrocks developed the Bayesian method for estimating densities and ran the analysis (after I had prepared the data).
2) Tim Smith provided the whaling data, which he also prepared for the analysis.

5.1 INTRODUCTION

Over-exploitation by humans dates back to prehistoric times and has not only resulted in depletion of resources, but has caused the extinction of some species, including: the moa (Dinornithiformes), the great auk (*Pinguinus impennis*), the passenger pigeon (*Ectopistes migratorius*) and the Steller's sea cow (*Hydrodamalis gigas*) (Bengtson 1984, Blockstein 2002, Greenway 1958, 2000, Turvey and Risley 2006). Marine ecosystems and biodiversity are being severely impacted by both modern and historic over-fishing (Jackson et al. 2001, Worm et al. 2006). Whaling is perhaps one of the most significant and spatially extensive examples of marine exploitation (Reeves and Smith 2006) and not only lead to major reductions of baleen whale populations, but was also responsible for the extirpation of the North Atlantic population of gray whales (*Eschrichtius robustus*) (Bryant 1995, Mead and Mitchell 1984).The full extent of the effects of whaling is not fully understood, however there have been attempts to estimate pre-whaling populations of some species to provide information on the recovery of populations (Roman and Palumbi 2003, Whitehead 2002).

Sperm whales (*Physeter macrocephalus*) are one of the most widely distributed marine mammals (Rice 1998), diving to great depths for their cephalopod prey (Whitehead 2003). The spermaceti organ is an important component of their sophisticated sonar system used to find prey (Møhl 2001), but the spermaceti was also coveted in the early

18th century for use in candle making and as the finest lubricant for delicate machinery (Proulx 1986), resulting in an extensive hunt from the 18th century to the first part of the 20th century. ‘Open-boat’ whaling for sperm whales, characterized by mother ship operations with whaleboats being hand- and sail-powered, began in 1712, peaked in 1840-1850 and continued into the early 20th century (Bannister et al. 2008, Proulx 1986, Reeves and Smith 2006). Modern whaling, characterized by cannon-fired harpoons and steam-powered ships, began at the end of the 19th century for sperm whales, but peaked in 1960-1970 (Bannister et al. 2008, Best 1983, Reeves and Smith 2006). ‘Open-boat’ whaling for sperm whales began in the North Atlantic, but activity moved to the Pacific and Indian Ocean just prior to the beginning of the 19th century. By the last half of the 19th century, much of the whaling in the Pacific and Indian Oceans was abandoned, although it continued throughout the Atlantic (Bannister et al. 2008, Reeves and Smith 2006). Modern whaling was extensive through almost all oceans except in the western North Atlantic where there was very little. Sperm whale catches were largely restricted to the 454 males taken by eastern Canadian whaling stations between 1904 and 1970 (Mitchell 1974).

The sustained ‘Open-boat’ sperm whale hunt in the North Atlantic suggests that sperm whales were abundant in this ocean basin. Whitehead (2002) estimated the density of whales to be 17.04 whales per 1000km^2 off the US east coast in 2000; globally the highest estimated sperm whale density of areas surveyed. Recent surveys in the northwest part of the Sargasso Sea, an oceanic gyre in the North Atlantic Ocean, have found large numbers of sperm whales, but density estimates have not been made and so it is not known how these compare to other areas where sperm whales are prevalent. Historically, whalers hunted in “whaling grounds”, a colloquial name for well-recognized whaling areas (Maury 1852, Townsend 1935). In the North Atlantic, 11 grounds have been identified (Bannister et al. 2008) and their use through the decades suggests that sperm whales were plentiful in these areas and might represent sperm whale “hotspots” during the whaling era. It is not known whether current sperm whale “hotspots” concur with historic whaling grounds, but an examination of contemporary and historic distributions should provide insight into the recovery of sperm whale populations (e.g. Hope and Whitehead 1991).

The objectives of our study were to estimate current sperm whale density in the Sargasso Sea and compare contemporary patterns of distribution with those from the whaling era. We also examined how use of whaling grounds in the North Atlantic changed seasonally and throughout the open-boat whaling era.

5.2 METHODS

5.2.1 Data Collection

Contemporary sperm whale density in the northwest Atlantic Ocean (west of 50^0W and north of 23.5^0N and hereby referred to as the Sargasso Sea) was estimated using acoustic surveys from 2004-2008 and 2010 during the spring and summer months (April to June) (Figure 5.1). Acoustic surveys were conducted from a 12 m auxiliary sailing vessel using a towed hydrophone array. In 2008 (June 25-July 5), a 32 m auxiliary sailing vessel was used. Every 30 minutes, we listened to the hydrophone for the presence of sperm whale clicks (hereby referred to as 'listens'). Sperm whale clicks are used primarily in echolocation and communication (Whitehead 2003). The majority of clicks detected were usual clicks, which are thought to function primarily in searching echolocation and are a long train of regularly spaced clicks (0.5s-1.0s) that can last for several minutes (Jaquet et al. 2001, Madsen et al. 2002, Whitehead and Weilgart 1990). The distance traveled between 30 minute listens was significantly larger in 2008 (7.99 km ± 2.73SD) than the years 2004-2007, 2010 (4.82 km ± 1.17 SD; t-test: $t_{4123} = 41.506$, $p < 0.001$), so survey data from 2008 was not used in any of the combined density estimates.

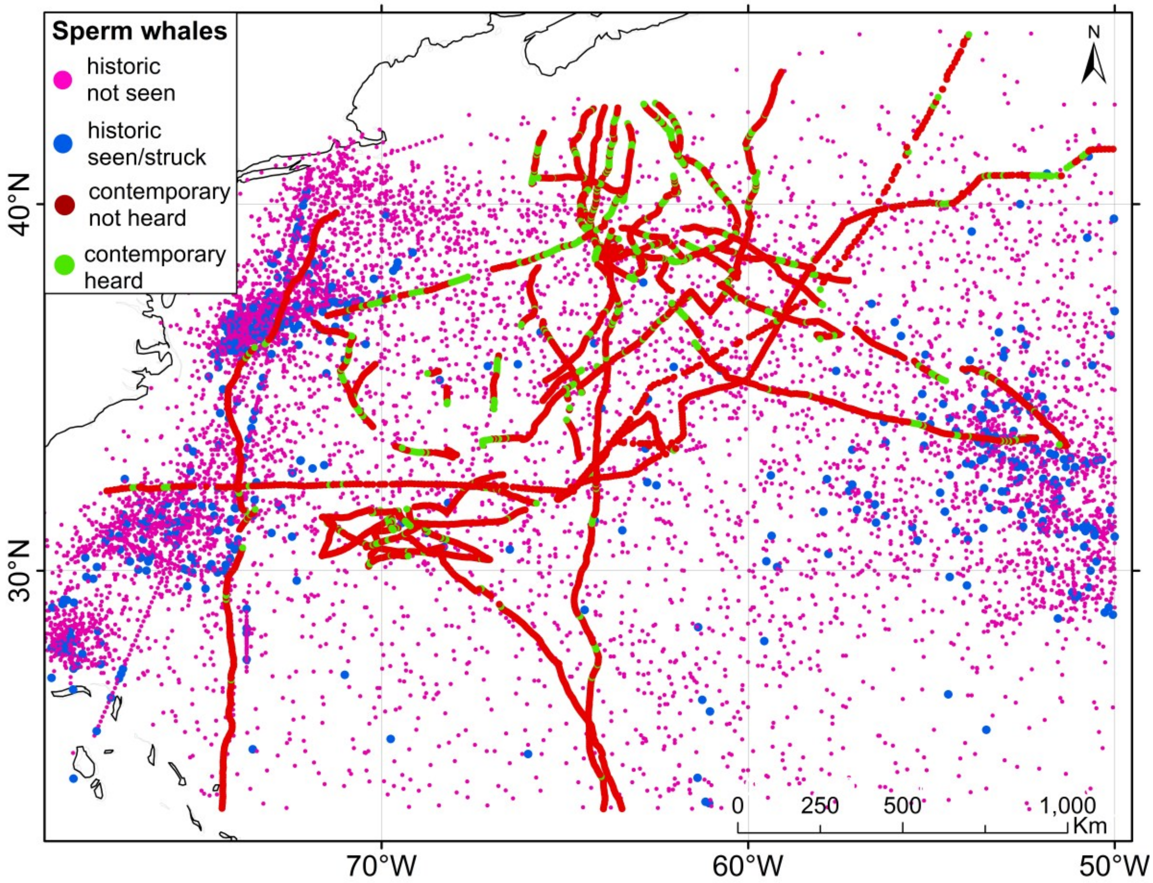

Figure 5.1 Map showing contemporary and historic sperm whale distribution of the study area and effort. Contemporary data is from acoustic surveys (1993, 1995, 2001, 2004-2008, 2010) where listens were conducted every 30 minutes for the presence of sperm whale clicks. Historic distribution is from the whaling logbooks (1775-1921) where the vessels position was plotted daily and if sperm whales were seen or struck. Transits not included in historic data.

Contemporary patterns of sperm whale distribution were determined from the surveys described above but also included surveys conducted in the winter (Table 5.1). To increase coverage, surveys conducted in 1993, 1995 (from the same 12 m auxiliary sailing vessel) and 2001 (from a 17-m auxiliary sailing vessel) were also included (Figure 5.1, Table 5.1). These surveys were conducted using the same methods described above, although listens were made every 20 minutes in 2001. The vessel used in 2001 was faster than the vessels used in other years, however, it should be noted that total distance traveled in 20 minutes (4.23 km ± 1.82) was significantly different from the distance between listens in all other years (5.15 km ± 1.55; t-test: $t_{5251} = 6.212$, $p < 0.001$).

Table 5.1 Details of contemporary surveys used in the analysis.

Year	**Start date**	**End date**	**Used in abundance estimate?**	**Used for distribution pattern?**	**Total distance surveyed (km)**
1993	May 25	June 2	No	Yes	1,849
1995	May 17	May 22	No	Yes	1,172
2001	May 17	May 22	No	Yes	929
2001	June 2	June 8	No	Yes	1,699
2004	May 5	May 21	Yes	Yes	784
2004	June 4	June 14	Yes	Yes	624
2005	April 23	May 20	Yes	Yes	2,884
2005	May 31	June 22	Yes	Yes	1,853
2006	May 31	June 23	Yes	Yes	3,642
2006	October 31	November 4	No	Yes	932
2007	May 4	May 25	Yes	Yes	3,126
2007	June 7	June 25	Yes	Yes	2,753
2008	February 24*	March 5	No	Yes	2,444
2008	June 25	July 5	No	Yes	3,013
2010	April 26	May 3	Yes	Yes	1,809
			Total distance surveyed (km)		**29,513**

* used to compare the maximum likelihood method (Horrocks et al. 2011) and the Bayesian method (Horrocks et al. in prep)

Historical distribution patterns of sperm whales were examined using data extracted from American whaling vessel logbooks (1775-1921) as described by Smith et al. (2012). These logbooks contain periodic entries (usually daily) of vessel location and encounters with whales (sighted and/or struck). To compare historical distribution to contemporary distribution, we limited the historic data to the study area, defined as north of 23.5^0N and west of 50^0W (Figure 5.1). However, to investigate how use of whaling grounds in the North Atlantic might have changed by season or through the decades, we used all data available north of 0^0 for the entire North Atlantic (Figure 5.2). The logbooks used were from vessels that were outbound from home ports in New England for whaling in the North Atlantic and other areas and vessels inbound at the end of voyages. Of these vessels, some were actively whaling in the study area or the North Atlantic in general, while others were primarily transiting the North Atlantic. To avoid including data from vessels that were primarily transiting, only segments of voyages that reported whales in the North Atlantic and those that spent more than three days in the study area were used.

Segments were defined by the origin of the voyage, when the vessel crossed or re-crossed the equator, and when there was a gap in whaling activity or uncertainty about vessel location.

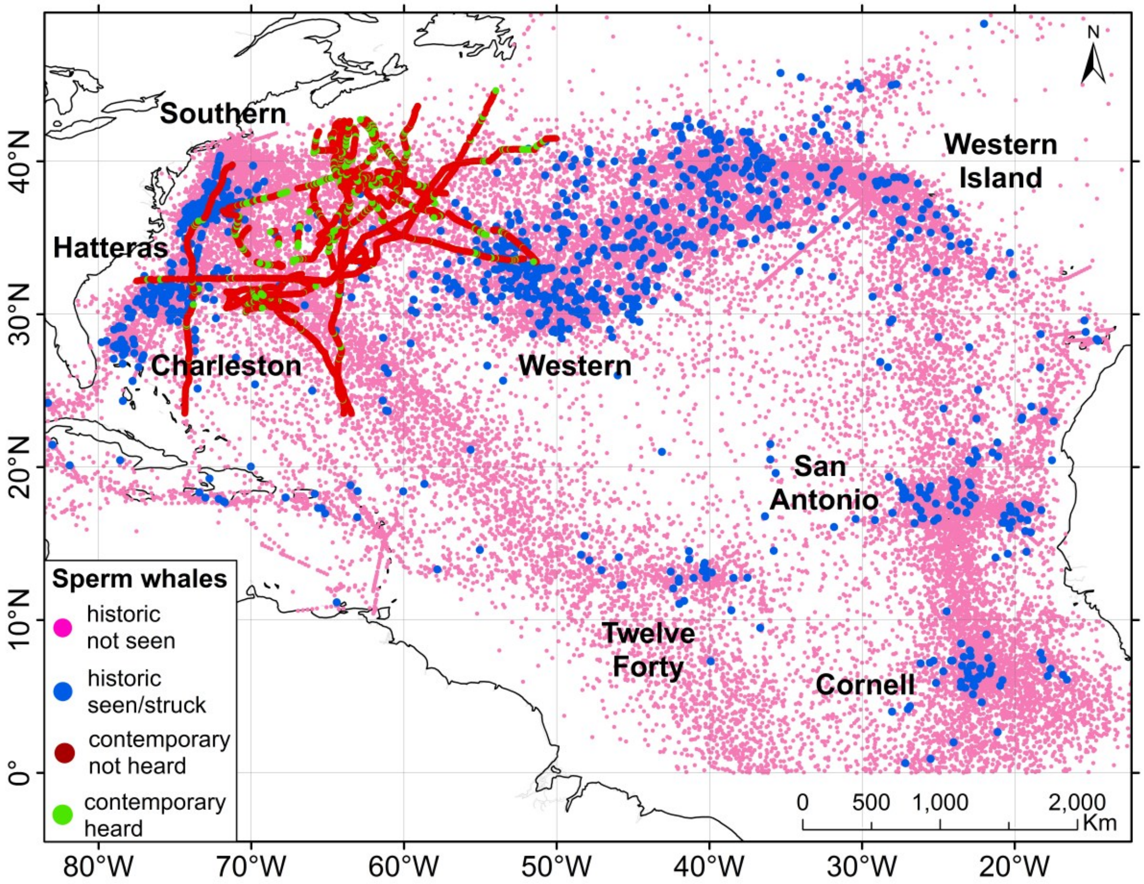

Figure 5.2 Map showing contemporary and historic sperm whale distribution of the entire North Atlantic and effort. Contemporary data is from acoustic surveys (1993, 1995, 2001, 2004-2008, 2010) where listens were conducted every 30 minutes for the presence of sperm whale clicks. Historic distribution is from the whaling logbooks (1774-1921) where the vessels position was plotted daily and if sperm whales were seen or struck. Transits are not included in historic data. The names of the whaling grounds are labelled.

5.2.2 Data Analysis

To estimate density of sperm whale groups, we used a Bayesian model (Horrocks et al, in prep) which combines an approximate likelihood for the data with a prior distribution for the parameters, in order to generate a posterior distribution for the parameters. Here the parameters are density, probability of detection and range of detection. The data consists of a binary time series, summarized into counts of triplets of the form 000, 001, etc., representing triplets of consecutive listens, where a 1 indicates that whales were heard and a 0 indicates that no whales were heard. The approximate likelihood is similar to that developed in Horrocks et al. (2011) for estimating density from a single binary passive acoustic transect when the probability of detection and range of detection are unknown. It differs in that it conditions on the values of the first two listens (whether 0 or 1). Vague priors were used in the Bayesian model, all with precisions (1/variance) of 0.00001. For alpha (group density), we used a truncated normal prior restricted to be greater than 0, with mean 0.00035, while for mu (probability of detection) we used a truncated normal prior restricted to the interval (0,1), with mean 0.9. For r (radius of detection in km), we used a truncated normal prior with mean 9.5, restricted to be greater than a typical distance between listens (5.88 km). We compared the maximum likelihood method (Horrocks et al. 2011) and the Bayesian method (Horrocks et al., in prep) on the single winter transect (February 24-March 5, 2008: Table 5.1) analyzed in Horrocks et al. (2011), and found results to be similar (Table 5.2). Sensitivity analysis showed that these results were not sensitive to the chosen priors. For all further analyses, we used a modified version of the Bayesian model which combined data from multiple transects. Only transects that consisted of at least 10 consecutive listens that were at most 0.655 hours apart were included in the analysis. Data was from 2008 was omitted from the combined-years estimate as it was deemed unreliable due to the presence of many short transects.

Table 5.2 Comparison of density estimates of sperm whale groups per 1000 km^2 during one winter survey (February 24-March 5, 2008) using two different methods: maximum likelihood (ML) and Bayesian.

	ML Method	**Bayesian Method**
Density of sperm whale groups/1000km^2 (95% interval)*	0.36 (0.16, 0.74)	0.37 (0.13, 0.73)
Probably of detection (95% interval)*	0.90 (0.64, 1.00)	0.82 (0.53, 0.98)
Radius of detection (km) (95% interval)*	9.29 (6.95, 15.14)	10.7 (7.2, 18.7)

* For ML Method, 95% interval = 95% confidence interval, for Bayesian method, 95% interval = 95% credible interval

To compare contemporary and historical distribution of sperm whales, all contemporary surveys available were used (1993, 1995, 2001, 2004-2008, 2010). Despite evidence that sperm whale occurrence varies seasonally in the northern part of the Sargasso Sea (Chapter 3), we included all transects and logbook data regardless of season because we were most interested in broad, overall patterns of distribution. For the contemporary surveys, we calculated the total number of listens in each 1^0 by 1^0 grid cell as a measure of effort (Figure 5.3a) and the total number of listens where sperm whale clicks were heard (detections). For the historical data, we calculated the total number of days that whaling vessels were whaling in each 1^0 by 1^0 grid cell as a measure of effort (Figure 5.3b) and the total number of days when sperm whales were sighted and/or struck (detections). Detections per unit effort (DPUE) was calculated for each dataset for each grid cell.

For both datasets, effort across the study area was variable, ranging from 1 to 156 listens in a 1^0 by 1^0 grid cell for contemporary data, and 1 to 306 days in a 1^0 by 1^0 grid cell for historical data (Figure 5.3). Furthermore, the magnitude of effort between the two datasets did not overlap: where effort for the contemporary data was highest, it was the lowest for the historical data and vice versa. Since we were interested in comparing broad, overall distribution of sperm whales historically and currently, we decided to make the comparisons at decreasing grid cell size (increasing resolution) to investigate whether a consistent pattern emerged.

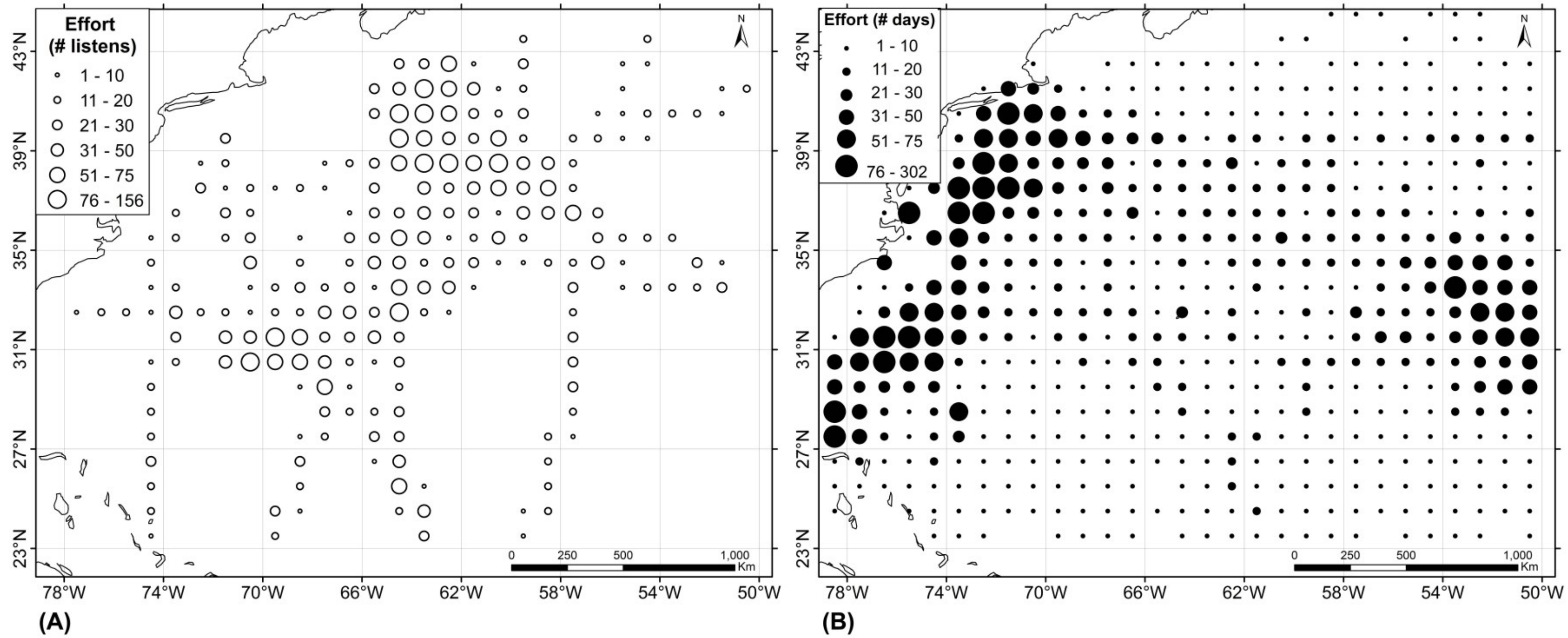

Figure 5.3 Comparisons of effort for contemporary data (A) and historical data (B). For contemporary surveys, effort was defined as the total number of listens per 1^0 by 1^0 grid cell. For historical data, effort was defined as the total number of days whaling boats were whaling in each 1^0 by 1^0 grid cell.

First, we divided the study area into north and south (using 35^0N as the boundary), and then divided the study area into four quadrants (northwest, northeast, southwest, southeast) using 35^0N and 64^0W as the boundaries. We chose the following grid cell sizes: 10^0 by 10^0, 6^0 by 6^0, 5^0 by 5^0, 4^0 by 4^0, 3^0 by 3^0, 2^0 by 2^0, and 1^0 by 1^0. For each grid cell (or quadrant) at each resolution, the total effort (listens for contemporary data, whaling days for historic data) and the total number of detections were calculated. To make the datasets more comparable, we calculated the following ratio for each grid cell: DPUE divided by the overall mean DPUE for that resolution. For each resolution, we calculated the “change” between historical and contemporary distribution defined as the the ratio of the historical data substracted from the ratio of the contemporary data. More negative values would suggest that DPUE was higher historically and more positive values would suggest DPUE is higher at present. Contemporary surveys were only conducted between November and June and previous work has shown that sperm whale occurrence can vary seasonally (Chapter 3). To determine whether it was appropriate to use the entire dataset for the logbooks (which covered the entire year) we also calculated DPUE and the ratios for the 10^0 by 10^0 grid cell resolution using only logbook data from November to June. We found that DPUE was nearly the same as using the entire dataset and the overall patterns were the same, so we included the entire logbook dataset, regardless of month.

To examine seasonal or decadal changes in use of whaling grounds in the North Atlantic, we plotted daily vessel location and whether sperm whales were seen and/or struck by season (spring =March to May, summer =June to August, autumn =September to November, winter = December to February) and by decade (beginning with 1775-1779 and ending with 1920-1921).

5.3 RESULTS

From 1993 to 2010, a total of 29,513 km (207 days) were surveyed in the Sargasso Sea (Figure 5.1, Table 5.1). Density estimates were made from 17,475 km (152 days) of these surveys. Based on the criteria for extracting data from the whaling logbooks, the historic dataset in our study area (north of 35^0N and west of 50^0W) used data from 287 segments in 231 voyage tracks. A total of 8,585 days of observation were included in our analysis, of which 538 included reports of one or more sperm whales sighted and/or struck. The historic dataset used to examine seasonal and decadal changes in whaling ground use for the entire North Atlantic used data from 311 segments in 231 voyage tracks. A total of 27,022 days of observation were used, of which 1,309 included reports of one or more sperm whales sighted and/or struck (Figure 5.2).

5.3.1 Density Estimates

The density of sperm whale groups per 1000 km^2 in the Sargasso Sea from April to July was estimated to be 0.36 (95% Bayesian credible interval (BCI): 0.27, 0.47) (Table 5.3). Using mean group size of 12.05 (SD = 6.56) animals in the Sargasso Sea (Gero et al. 2009), results in a density of 4.34 (95% CI: 2.54, 6.14) sperm whales per 1000 km^2. The probability of detection was 0.74 (95% BCI: 0.67, 0.80) and radius of detection was 17.5 (95% BCI 14.6, 21.2). Density of sperm whale groups per 1000 km^2 in the Sargasso Sea varied yearly, ranging from 0.50 (95% BCI: 0.33, 0.71) in 2007 to 0.11 (95% BCI: 0.02, 0.28) in 2008 (Table 5.3). The years with the highest radius of detection (2006 = 25.6 km (95% BCI: 14.6, 39.2), 2008 = 26.3 km (95% BCI: 13.4, 52.5)) also had the lowest probability of detection (2006 = 0.54 (95% BCI: 0.42, 0.67), 2008 = 0.53 (95% BCI: 0.30, 0.77)) (Table 5.3).

Table 5.3 Density estimates of sperm whale groups per 1000 km^2 by year using the Bayesian method. The estimates for combined transects includes spring (April – July) transects in 2005-2008 and 2010. BCI = 95% Bayesian credible interval. Total effort = total number of listens.

Year	**Total Effort**	**Total Detections**	**Density of sperm whale groups/1000km^2 (95% BCI)**	**Detection probability (95% BCI)**	**Radius of detection (km) (95% BCI)**
2004	272	55	0.40 (0.12, 0.87)	0.74 (0.52, 0.90)	18.8 (10.8, 34.6)
2005	928	89	0.30 (0.13, 0.51)	0.64 (0.45, 0.80)	15.3 (10.2, 4.9)
2006	655	128	0.23 (0.08, 0.51)	0.54 (0.42, 0.67)	25.6 (14.6, 39.2)
2007	1114	268	0.50 (0.33, 0.71)	0.84 (0.76, 0.91)	15.4 (12.6, 19.5)
2008*	317	25	0.11 (0.02, 0.28)	0.53 (0.30, 0.77)	26.3 (13.4, 52.5)
2010	328	29	0.41 (0.22, 0.99)	0.76 (0.59, 0.98)	11.8 (6.0, 13.4)
Combined (2004-2007, 2010)	3297	569	**0.36** **(0.27, 0.47)**	**0.74** **(0.67, 0.80)**	**17.5** **(14.6, 21.2)**

* Distance between listens used was 8 km in 2008 because a fast boat was used for the surveys.

Density of sperm whale groups per 1000 km^2 was higher north of 35^0N (0.44, 95% BCI: 0.31, 0.58) than south (0.24, 95% BCI: 0.11, 0.42), although this was not significant (t-test: $t_{3138} = 1.826$, $p = 0.067$) (Table 5.4). Using the same mean group size of 12.05 animals results in a density of 5.30 (95% CI: 3.00, 7.61) sperm whales per 1000 km^2 north of 35^0N and 2.89 (95% CI: 0.82, 4.96) sperm whales per 1000km^2 south of 35^0N. Density of sperm whale groups was higher west (0.42, 95% CI: 0.30, 0.56) of 64^0W than east (0.32, 95% CI: 0.19, 0.47), although this difference was not significant (t-test: $t_{3144} = 1.027$, $p = 0.305$) (Table 5.4). This results in 5.06 (95% CI: 2.85, 7.27) sperm whales per 1000 km^2 west of 64^0W and 3.86 (95% CI: 1.79, 5.92) sperm whales per 1000 km^2 east of 64^0W.

Table 5.4 Density estimates of sperm whale groups by region using the Bayesian method and spring (April-July) transects in 2005-2008 and 2010. In the study area, 35^0N separates 'North' and 'South'. 'East' and 'West' are separated by 64^0W. Total effort = total number of listens.

Region	**Density of sperm whale groups/1000km^2 (95% BCI)**	**Detection probability (95% BCI)**	**Radius of detection (km) (95% BCI)**	**Total Effort**	**Total detections**
North	0.72 (0.46, 1.07)	0.80 (0.68, 0.90)	11.5 (9.15, 14.6)	828	163
South	0.22 (0.02, 0.71)	0.55 (0.10, 0.95)	13.6 (6.23, 40.5)	320	7
East	0.32 (0.11, 0.60)	0.82 (0.61, 0.96)	13.0 (8.62, 23.4)	404	42
West	0.84 (0.46, 1.34)	0.77 (0.60, 0.91)	10.5 (7.90, 14.5)	518	91

5.3.2 Distribution

The DPUE for the northern section of the Sargasso Sea (north of 35^0N) was nearly 1.5 times higher than the mean DPUE for the contemporary data, and the southern section was nearly half the mean DPUE (Table 5.5). By contrast, the northern and southern sections of the Sargasso Sea had similar DPUE historically (Table 5.5). The same trend was observed for the contemporary distribution when divided into four quadrants: both the northwest and northeast quadrant were higher than the mean (1.61 and 1.24 respectively), while the southern quadrants were lower (southwest: 0.63, southeast: 0.52) (Table 5.6). The northwest quadrant was also higher than the overall mean (1.25) for the historic distribution (Table 5.6). However, in contrast to the contemporary distribution, the southeast quadrant was 1.29 times greater than the overall mean and the northeast quadrant was less than half the mean (Table 5.6). These were the quadrants with the largest difference (NE: 0.76, SE: -0.77), suggesting sperm whales are more prevalent in the northeast section at present, but they were more prevalent in the southeast historically (Table 5.6).

Table 5.5 Comparison between contemporary (1993-2010) and historic (1775-1921) sperm whale distribution in the northern and southern part of the western North Atlantic. The boundary between north and south was defined as 35^0N. For contemporary data, total effort = total number of listens and total detections = total number of listens when whales were heard. For historic data, total effort = number of days whaled and total detections = total number of days when a sperm whale was sighted and/or struck. DPUE = Detection per unit effort. Change is the ratio for contemporary distribution minus the ratio for historical distribution. More negative values indicates DPUE was higher historically, more positive values indicates DPUE is higher presently.

Location	Total effort	Total detections	DPUE	Mean DPUE	Ratio of DPUE: mean	Change
Contemporary						
North	2935	582	0.20	0.14 ± 0.077	1.38	0.42
South	2587	230	0.09		0.62	- 0.42
Historical						
North	3721	223	0.06	0.06 ± 0.003	0.96	--
South	4862	315	0.06		1.04	--

Table 5.6 Comparison between contemporary (1993-2010) and historic (1775-1921) sperm whale distribution in four quadrants of the western North Atlantic. The boundary between north and south was defined as 35^0N, the boundary between east and west was defined as -64^0W. For contemporary data, total effort = total number of listens and total detections = total number of listens when whales were heard. For historic data, total effort = number of days whaled and total detections = total number of days when a sperm whale was sighted and/or struck. DPUE = Detection per unit effort. Change is the ratio for contemporary distribution minus the ratio for historical distribution. More negative values indicates DPUE was higher historically, more positive values indicates DPUE is higher presently.

Quadrant	Total effort	Total detections	DPUE	Mean DPUE ± SD	Ratio of DPUE: mean	Change
Contemporary						
Northwest	818	194	0.24	0.15 ± 0.076	1.61	0.36
Northeast	2117	388	0.18		1.24	0.76
Southwest	1932	180	0.09		0.63	- 0.35
Southeast	655	50	0.08		0.52	- 0.77
Historical						
Northwest	2655	193	0.07	0.06 ± 0.022	1.25	--
Northeast	1066	30	0.03		0.48	--
Southwest	2763	157	0.06		0.98	--
Southeast	2099	158	0.08		1.29	--

Increasing the resolution to 10^0 by 10^0 grid cell size provides more detail to the contemporary and historic distribution differences in the southern and northern sections of the Sargasso Sea. Currently, the greatest DPUE is found in the mid northern section (midpoints 38^0N and 65^0W) (Table 5.7). This grid cell has the lowest DPUE historically and this is where the greatest difference occurs (1.40) (Table 5.7). Historically the eastern and western grids in the south were highest (Table 5.7).

Table 5.7 Comparison between contemporary (1993-2010) and historic (1775-1921) sperm whale distribution in the western North Atlantic as defined by 10^0 by 10^0 grid cells. For contemporary data, total effort = total number of listens and total detections = total number of listens when whales were heard. For historic data, total effort = number of days whaled and total detections = total number of days when a sperm whale was sighted and/or struck. DPUE = Detection per unit effort. Change is the ratio for contemporary distribution minus the ratio for historical distribution. More negative values indicates DPUE was higher historically, more positive values indicates DPUE is higher presently.

Lat midpt of cell (^{0}N)	**Long midpt of cell (^{0}W)**	**Total effort**	**Total detections**	**DPUE**	**Mean DPUE ± SD**	**Ratio of DPUE: mean**	**Change**
Contemporary							
38	-75	245	35	0.14	0.12 ± 0.050	1.17	-0.40
38	-65	2444	494	0.20		1.65	1.40
38	-55	897	132	0.15		1.20	0.05
28	-75	479	37	0.08		0.63	-0.62
28	-65	1244	98	0.08		0.64	0.21
28	-55	186	16	0.09		0.70	-0.64
Historical							
38	-75	2194	196	0.09	0.06 ± 0.030	1.57	--
38	-65	1274	18	0.01		0.25	--
38	-55	1265	83	0.07		1.15	--
28	-75	1860	133	0.07		1.26	--
28	-65	735	18	0.02		0.43	--
28	-55	1173	90	0.09		1.35	--

Decreasing the cell size further demonstrated that currently, sperm whale distribution is highest in the northern part of the Sargasso Sea, especially in the mid-northern section, while sperm whale distribution was highest in the far western and eastern sections of the Sargasso Sea historically. The greatest differences between contemporary and historical distribution also occurred in these areas: where DPUE is highest currently, is where it was lowest historically and vice versa (Figure 5.4).

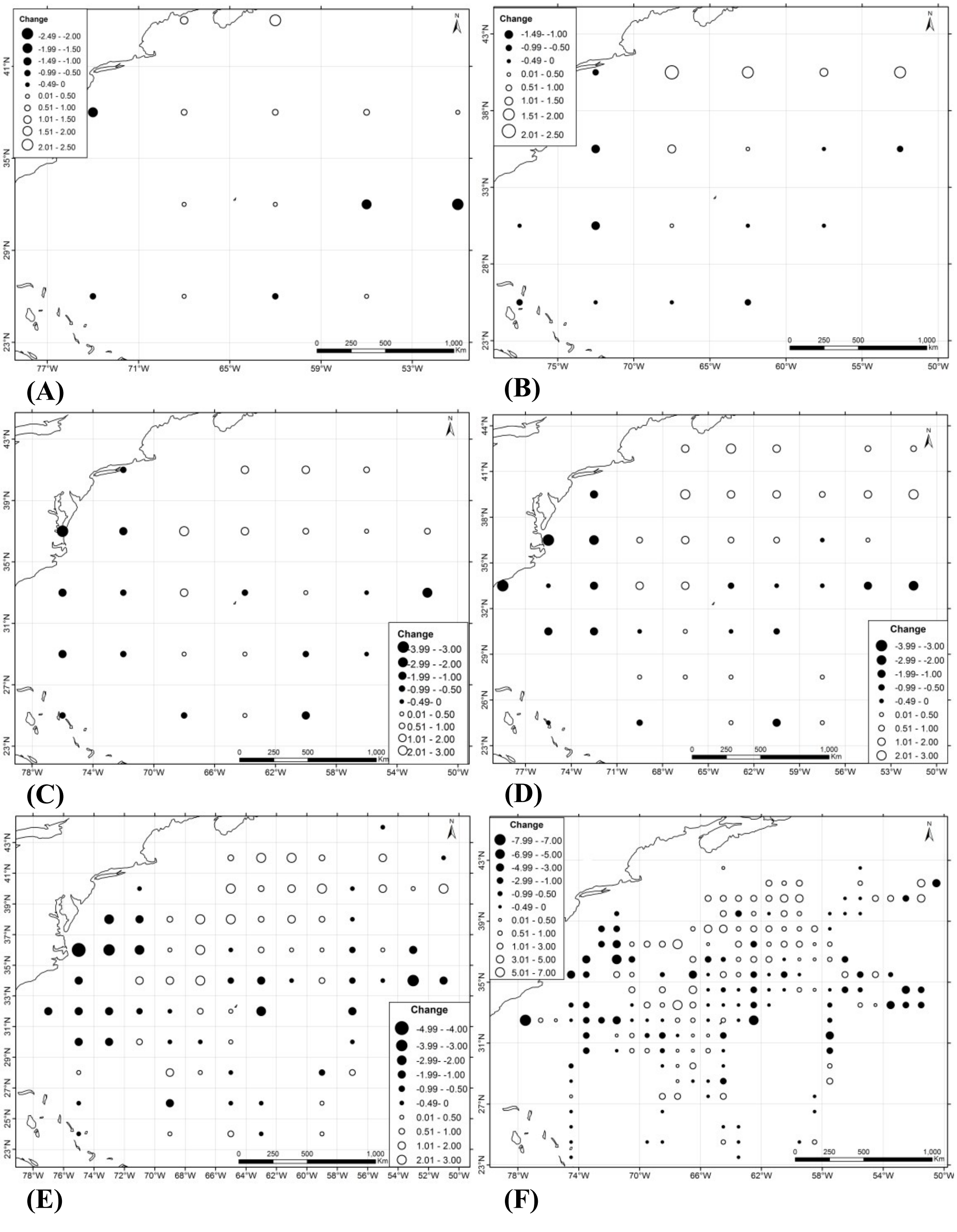

Figure 5.4 The change in the ratio of detection per unit effort (DPUE) per grid cell divided by the overall mean DPUE between contemporary and historical distribution. The change was calculated by subtracting the historical layer from the contemporary layer. The more negative values suggest a larger DPUE historically and more positive values suggest a larger DPUE currently. (A) 6^0 by 6^0 grid cell, (B) 5^0 by 5^0 grid cell, (C) 4^0 by 4^0 grid cell, (D) 3^0 by 3^0 grid cell, (E) 2^0 by 2^0 grid cell, (F) 1^0 by 1^0 grid cell.

Open-boat whaling in the North Atlantic used whaling grounds (as defined by Bannister et al. 2008) differently by season (Figure 5.5). In the spring (n = 6,470 whaling days), whaling was concentrated along the US east coast, in what has been defined as the Southern Ground (34^{0}N-41^{0}N, 60^{0}W-74^{0}W), the Hatteras Ground (29^{0}N-37^{0}N, 68^{0}W-76^{0}W), and the Charleston Grounds (a: 28^{0}N-33^{0}N, 67^{0}W-76^{0}W and b: 29^{0}N-32^{0}N, 74^{0}W-79^{0}W). Some whaling occurred in the Western Ground (27^{0}N-41^{0}N, 34^{0}W-58^{0}W), the Western Island Ground (= Azores: 35^{0}N-41^{0}N, 23^{0}W-34^{0}W), the San Antonio Ground (= Cape Verde: 14^{0}N-22^{0}N, 19^{0}W-29^{0}W) and the Twelve-Forty Ground (10^{0}N-17^{0}N, 35^{0}W-46^{0}W). Whaling in the summer (n = 10,222 whaling days) included the Southern, Charleston and Hatteras Grounds, but was also concentrated in the Western Ground and extended into the Western Island Ground (Azores). Autumn whaling (n = 6,929 whaling days) was similar to the summer, although less time was spent off the US east coast and more time was spent off the coast of West Africa: the San Antonio Ground and parts of the Cornell Ground (1^{0}N-9^{0}N, 18^{0}W-28^{0}W). Much less whaling occurred in the North Atlantic in the winter (n = 3,401 whaling days), when the weather would have been unfavourable, and was concentrated in small pockets in the Charleston, San Antonio and Cornell Grounds.

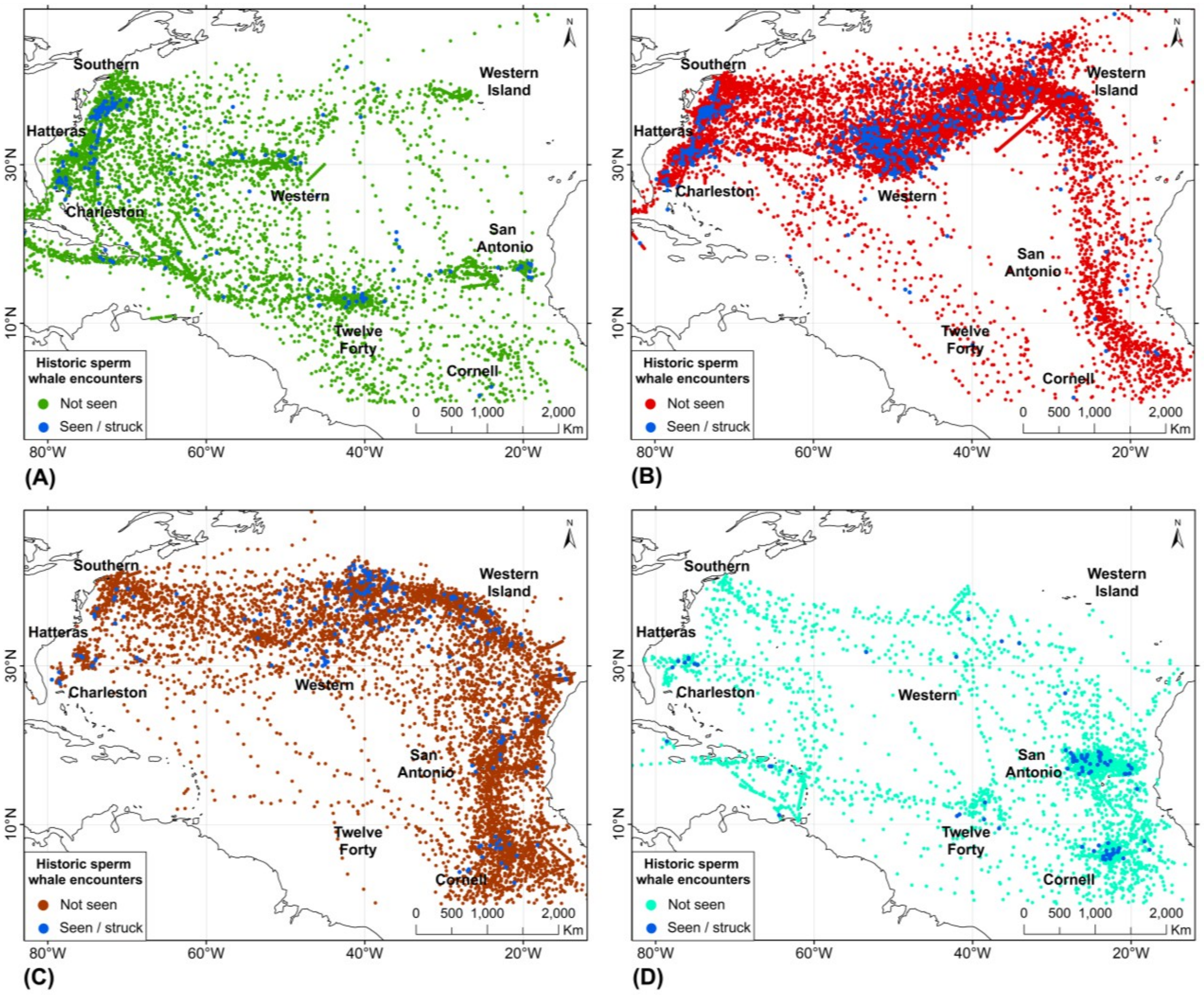

Figure 5.5 Seasonal use of whaling grounds from 1775-1921. (A) spring: March – May, (B) summer: June – August, (C) autumn: September – November, (D) winter: December - February

Figure 5.6 shows the decadal changes of whaling ground use from 1775 to 1921. From 1775 to 1809, whaling occurred off the US east coast, in the Caribbean and off West Africa, although data from the logbooks is thin for this time period (total number of whaling days in 1770-1779 = 259). By 1810, whalers began to cross the Atlantic using the Gulf Stream (total number of whaling days = 1,659). Open-boat whaling in the North Atlantic was most extensive from 1830 to 1870, which is reflected the amount of data in the logbooks for this time period (total number of whaling = 18,373). Southern, Charleston, Hatteras, Western and Western Island (Azores) Grounds were used extensively, as well as the San Antonio and Cornell Grounds off the coast of West Africa. Open-boat whaling began to decline after 1870 (total number of whaling days = 5,621), but the same grounds continued to be used. By 1900 (total number of whaling = 1,110), some whaling occurred in small pockets on established grounds such as the Southern, Western and San Antonio Grounds.

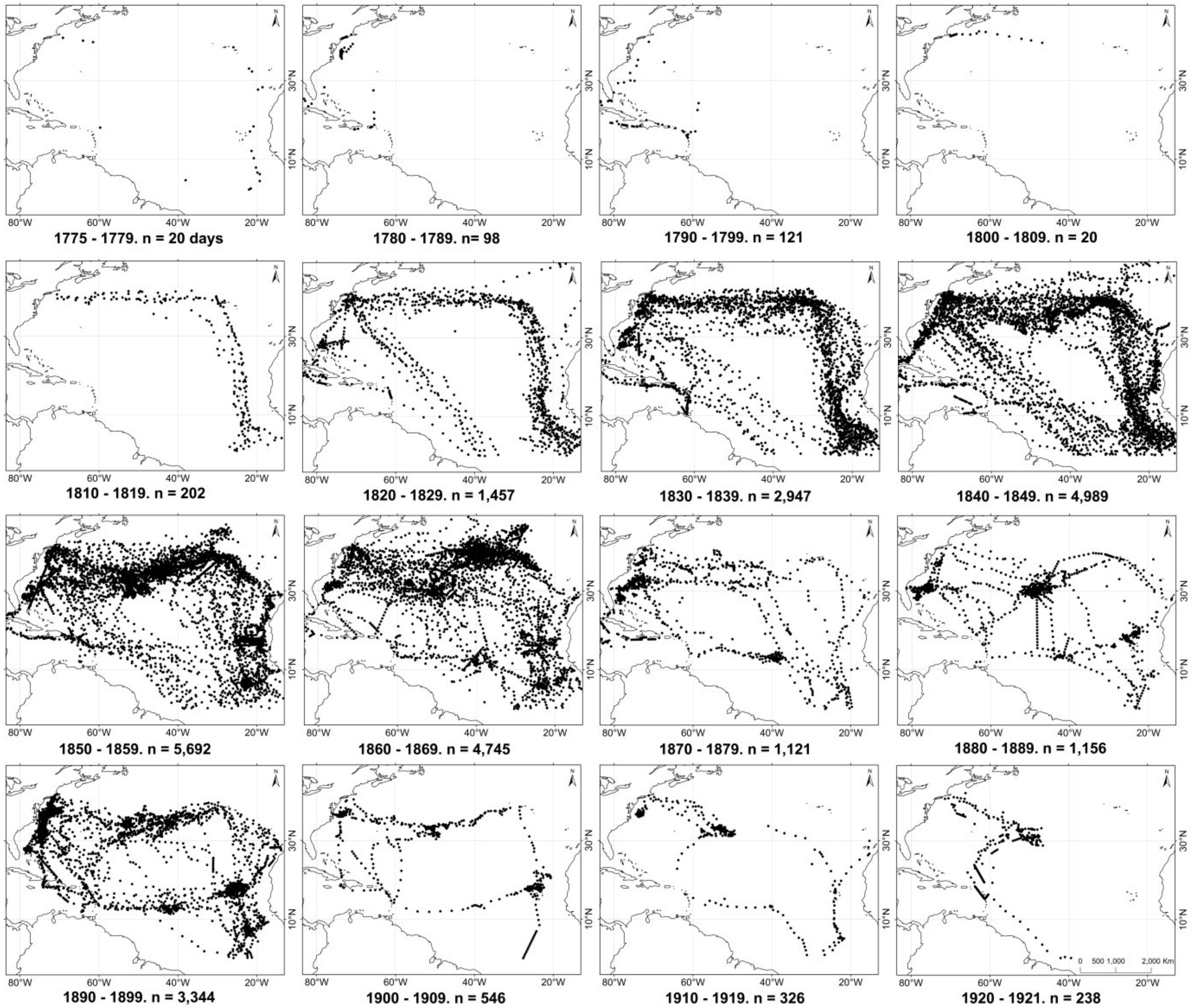

Figure 5.6 Decadal use of whaling grounds from 1775 to 1921

5.4 DISCUSSION

Using a Bayesian method for estimating the density of groups and a mean group size of 12 animals in the Sargasso Sea, we estimated the density of sperm whales per 1000 km^2 in this area to be 4.34. The density of sperm whales per 1000 km^2 in the northern section of the Sargasso Sea (north of 35^0N) was even higher (5.30). These density estimates are some of the highest for sperm whales globally (Table 5.8). It should be noted that data collection methods for estimating sperm whale density in Table 5.8 differed between regions (some were ship-based and visual and/or acoustic, others were aerial), as did the estimation method. However, our estimates and those estimated previously suggest that the density of sperm whales in the temperate North Atlantic is generally higher than other regions around the globe (North Pacific, Antarctic).

Both the North Atlantic and North Pacific were heavily whaled, although open boat whaling began in the North Atlantic in the early 18th century and didn't move into the Pacific until the late 18th/early 19th century (Best 1983, Starbuck 1878). Similar numbers of sperm whales are estimated to have been killed in the North Atlantic and Pacific during the open-boat whaling era, with the North Pacific making up 23.8% of sperm whales killed and the North Atlantic 19.3% (Table 6 in Best 1983). However, many more sperm whales were killed in the North Pacific (283,000) than the North Atlantic (39,000) during the 20th century (see Table 9.5 in Smith et al. 2008), and most of these were taken in the eastern North Atlantic. It is therefore possible that sperm whales in the North Atlantic, and especially in the western North Atlantic, have had more time to recover from past whaling and might explain why densities are higher.

Table 5.8 Estimates of sperm whale density from visual ship-board (VS), acoustic ship-board (AS), passive acoustic (PA) and aerial (A) surveys.

Area	**Survey type**	**Density (whales/ 1000km^2)**	**Source**
US east coast	VS	17.04	National Marine Fisheries Service (2000)*
Northern Gulf of Mexico	VS	7.42	National Marine Fisheries Service (2010)**
Northern Sargasso Sea (N of 35^0N, W of 50^0W)	**AS**	**5.30**	**This study**
Northeast Atlantic	VS	4.90	Christensen et al. (1992)*
Sargasso Sea (N of 23.5^0N, W of 50^0W)	**AS**	**4.34**	**This study**
Eastern temperate North Pacific	VS-AS	3.0-4.2	(Barlow and Taylor 2005)
France and Spain (off continental shelf)	AS	3.60	(Swift et al. 2009)
Hawaii	VS	2.82	(Barlow 2006)
US west coast	VS	1.70	(Barlow and Forney 2007)
Faroe-Shetland Channel	AS	1.44	(Hastie et al. 2003)
Eastern tropical Pacific	VS	1.36	Wade and Gerrodette (1993)*
Western North Pacific	VS	1.16	Kato and Miyashita (2000)*
Iceland-Faeroes	VS	0.77	Gunlaugsson and Sigurjónsson (1990)*
East Antarctica (62^0S-66^0S, 80^0E-125^0E)	AS	0.50-0.73	(Gillespie 1997)
Antarctica (S of 60^0S)	VS	0.65	International Whaling Commission (2001)*
Ionian Sea (Mediterranean)	AS	0.23	(Lewis et al. 2007)
Scotia Sea, West Antarctic (50^0S-70^0S, 20^0W-70^0W	AS	0.19	(Leaper et al. 2000)
Bahamas	PA	0.16	(Ward et al. 2012)
South Georgia (40^0S-60^0S, 30^0W-60^0W)	AS	0.13	(Leaper et al. 2000)

* density estimates were corrected by Whitehead (2002).

** density estimates were corrected as in Whitehead (2002)

There is some evidence that the current distribution of some whale species is similar to the historical distribution. Hope and Whitehead (1991) found that sperm whale distribution off the Galápagos Islands was similar between 1830-1850 and 1985-1989. Recent surveys have found that the distribution of North Pacific right whales (*Eubalaena japonica*) coincides with some of their historic distribution, although their historic distribution was more expansive and included deeper water than recent surveys have found (although survey effort may partly explain this pattern) (Shelden et al. 2005). However, other studies have shown that contemporary distribution differs from historical distribution. Humpback whales *(Megaptera novaeangliae*) are at present, much more abundant off the Greater Antilles than the Lesser Antilles during the winter months, which was the opposite distribution pattern found during the whaling era (Swartz et al. 2003). In our study, although effort varied spatially within each dataset and differently in the two datasets (where contemporary data effort was highest, effort was lowest for historical data and vice versa), a clear pattern did emerge at all resolutions: where we currently detect the most sperm whales (north of 35^0N, roughly between 66^0 and 60^0W and hereby called the Northern Sargasso Hotspot), is not where the whaling grounds were located during the open-boat whaling.

Our contemporary dataset is insufficient to examine whether sperm whales currently occur at high densities in established whaling grounds, such as the Western, Southern, Hatteras, and Charleston Grounds, because our acoustic surveys did not traverse those areas substantially. However, sperm whale density estimates from surveys conducted off the US east coast (Service 2000), which include the area known as the Hatteras and Southern Grounds, are the highest globally (Whitehead 2002), suggesting this area remains a sperm whale “hotspot”. That whaling effort was low in an area where current sperm whale densities are high is an unexpected puzzle. We suggest several possible explanations: 1) sperm whales in that area were exploited in the early decades of open-boat whaling, but were decimated to such an extent that this area was no longer being used by the time we have data from the logbooks, 2) whales were not found in the current hotspot historically, 3) whales did occur in large numbers in this area historically, but whalers missed them or did not exploit them.

Whaling in the North Atlantic began in the early 18th century (about 1715) and expanded after 1750 when the demand for sperm oil for candles increased and peaked from 1771-1775 (Best 1983, Starbuck 1878). Data used in our analysis from the whaling logbooks did not begin until 1775, so if sperm whales were being exploited in the Northern Sargasso Hotspot, there is no record of it. On-board processing of oil did not begin until about 1760 (Proulx 1986), which may have restricted New England whalers to nearby waters (such as the Southern, Charleston and Hatteras Grounds) and would not have included the Northern Sargasso Hotspot. From the start of the American War of Independence in 1775 until 1783, whaling suffered a setback due to loss of vessels and restricted movement, but post war, whaling activity expanded (Best 1983). One would assume that if whales were being exploited in the Northern Sargasso Hotspot before the war that whalers would return to that area following the war. Although data from the logbooks is limited from 1780-1820 (total number of whaling days = 441) there is no evidence that whalers frequented that area then, or in later decades. Furthermore, sperm whale ranges in this region and elsewhere in the North Atlantic span up to the order of 500 km (Whitehead et al. 2012). Thus, we would not expect decimation over scales less than or comparable to this to have any permanent effects. This means the relative value of the Northern Sargasso Hotspot may not have changed much over the course of whaling even though the population was being reduced, and the whales were largely being killed elsewhere. Finally, other grounds such as the Southern, Charleston, Hatteras and Western Grounds were used for over a century (Bannister et al. 2008) and were heavily exploited when open-boat whaling was at its peak production from 1830 to 1850 (Bannister et al. 2008), yet these grounds continued to be used until the end of the open-boat whaling era. Finally, even if this area had previously been heavily exploited, there is no reason that sperm whales would have moved back into those areas given their wide ranges. Thus, it seems unlikely that in the early decades of open-boat whaling, when there was much less effort and smaller vessels, that the Northern Sargasso Hotspot would have been decimated.

It is impossible to say for certain whether whales frequented the current Northern Sargasso Hotspot two centuries past. However, by examining what makes this area good habitat for sperm whales currently, we can consider whether this was also true historically. Sperm whale distribution has been associated with areas of high primary and secondary productivity (Gulland 1974, Jaquet 1996, Jaquet and Whitehead 1996), areas of upwelling (Caldwell et al. 1966, Gulland 1974, Smith and Whitehead 1993) and downwelling (Best 1979, Gaskin 1973, Ivanshin 1978). Sperm whales have also been associated with thermal fronts, such as warm-core rings (Griffin 1999, Waring et al. 1993). The Gulf Stream is a prominent feature influencing the productivity and distribution of marine predators in the northern part of the Sargasso Sea. Primary and secondary productivity in the Sargasso Sea is increased by mesoscale features associated with the Gulf Stream, such as cold-core rings (The Ring Group 1981, Ortner et al. 1978, Wiebe et al. 1976) and meanders and cyclonic fronts that result in upwelling of cooler, more productive water (Lee and Brooks 1979, Yoder et al. 1981). Recent research suggests that sperm whale occurrence in this area can at least partially be explained by the processes associated with the Gulf Stream (Chapter 3 and 4). The Gulf Stream's existence has first discovered in 1513 and by 1519 it was so well known, that Spanish ships were using it to cross the Atlantic on their homeward bound sail to Spain (Stommel 1965). Although the Gulf Stream track can vary seasonally (Fuglister 1951, Stommel 1965, Tracey and Watts 1986), it is a permanent fixture and there is no evidence that processes associated with the Gulf Stream have changed drastically over the last two hundred year.

While processes associated with the Gulf Stream may influence the distribution of sperm whales, SST is also an important predictor of sperm whale occurrence in this area (Chapter 4). There is much evidence that ocean temperatures are warming as a result of climate change (Meehl et al. 2005; Wigley 2005) and this is also true in the Atlantic Ocean (Parilla et al. 2005). Increased SST can cause changes in the abundance, distribution and recruitment of cephalopods (Rodhouse 2010; Zeidberg and Robison 2007). Environmental change, such as ocean warming, is one factor contributing to the northern range expansion of Humboldt squid (*Dosidicus gigas*) in the North Pacific (Zeiberg and Robison 2007). Thus, there is a possibility that as a result of changes in SST, that cephalopod prey in the Northern Hotspot is more abundant than two hundred years ago. However, this would not explain why the Western Ground and Western Island Ground, at the same northern latitudes were hunted extensively during the historic whaling era.

If we assume that sperm whales were always found in the Northern Sargasso Hotspot, then did whalers miss seeing them because they did not spend much time in that area? Examining the transit data from the logbooks might provide some insight into whether whalers even traversed that area. A total of 5694 days of transit, from 176 segments of 136 voyages were plotted by heading for each season (spring = March to May, summer = June to August, autumn = September to November, winter = December to February) (Figure 5.7). Spring transits (n = 1990 whaling days) were dominated by ships returning to New England (mainly northwest heading). In the summer (n = 1285 whaling days), ships were returning to New England but also using the Gulf Stream (presumably) to cross the Atlantic. Ships were not returning to New England in autumn (n = 1309 whaling days), likely because this would be the time of year where hurricanes would have occurred, but most transits involved ships using the Gulf Stream to cross the Atlantic. In the winter (n = 1110 whaling days), some ships were crossing the Atlantic with the Gulf Stream and others were returning to New England.

Figure 5.7 illustrates that whalers were passing through the Northern Sargasso Hotspot. The development of the whaling fishery shows that one whaling ground was discovered after another (Best 1983) and that it was likely an exploratory process of discovery (T. Smith, pers comm.). Although they were in transit and perhaps not focused on finding whales, it is difficult to believe that none were sighted in this area. Furthermore, whalers would have passed through this area enroute to the Western Ground, which was whaled extensively. Indeed, there is evidence that the whalers were aware that sperm whales were found in this area. In a letter to Alphonsus le Roy regarding the Gulf Stream, Benjamin Franklin mentioned a Nantucket sea-captain that he knew who explained to him that Rhode-Island captains were well acquainted with the Gulf stream because "…in our pursuit of whales, which keep near the sides of it, but are not to be met with in it, we run down along the sides, and frequently cross it to change our side…" (Franklin 1786).

There is no reason to believe that sea and weather conditions in the Northern Sargasso Hotspot would be greatly different than in the Western Ground. If they were sighted, why did whalers not return to the area to further investigate, especially as yields on established grounds began to decrease?

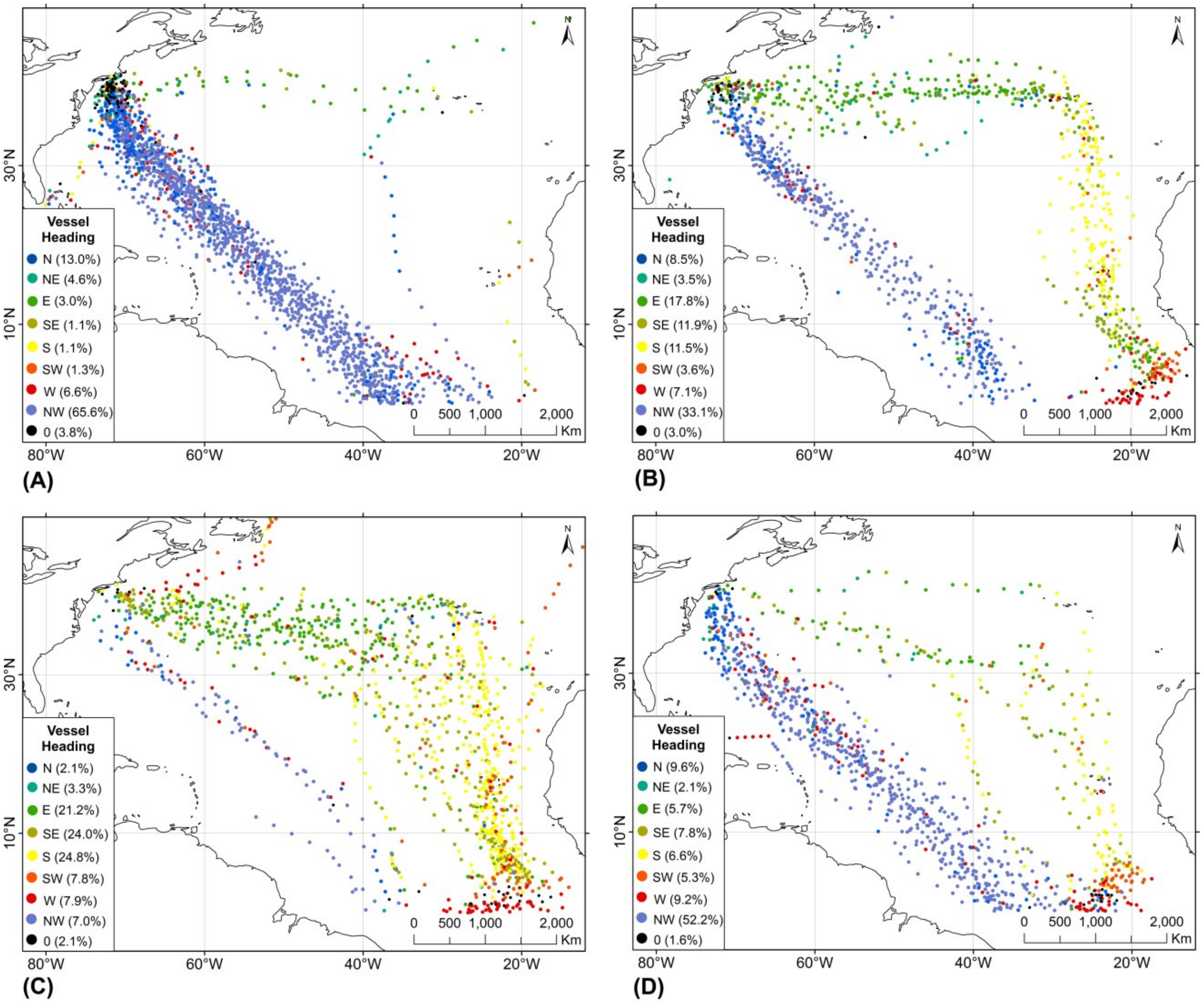

Figure 5.7 Transit headings of whaling vessels 1775-1921. (A) spring: March – May, (B) summer: June – August, (C) autumn: September – November, (D) winter: December - February

Except for the period between 1830-1835, American whalers on the Galápagos and western North Pacific grounds generally followed a pattern of leaving if yields appeared to be less than that obtained elsewhere, exploiting grounds so that yields were equal on all grounds (Whitehead and Hope 1991), thus is it puzzling why whalers in this area would not be interested in capitalizing on a newly discovered ground. If sperm whales existed in high numbers in the Northern Sargasso Hotspot, perhaps the reason they weren't exploited was because whalers (or the ship's owners) were stubbornly stuck in a pattern of what "they knew". It is well documented that American whalers exchanged information about catches and sightings (Tillman and Breiwick 1983), but perhaps the information was not always accurate. If it had already been established that in the North Atlantic, the Southern, Charleston, Hatteras and Western Grounds were areas to hunt whales, perhaps the whalers stubbornly returned to these grounds, or were told to return to them by the owners based on catch reports from other whalers just recently returned.

5.5 SUMMARY

The density of sperm whales occur in the northern Sargasso Sea is among the highest globally. Indeed, currently the area between 60^0 and 66^0W, north of 35^0N has the highest proportion of detections per unit effort compared to other areas in the Sargasso Sea. Yet, this area does not overlap with the historical whaling grounds and whalers spent little time whaling there, although they transited through the area enroute to other whaling grounds, such as the nearby Western Ground, especially in the summer and autumn. It could be that sperm whales did not frequent this area in the past and moved there more recently. Or perhaps they were always found in this area in high numbers, but for some reason, either because they were missed or due to stubborn whaling patterns, they were never exploited.

CHAPTER 6
CONCLUSION

I first set out on this research because I wanted to resolve the paradox of why there were so many sperm whales in the Sargasso Sea. Beginning at the end of the 18th century, sperm whales were hunted extensively in the Sargasso Sea for over a century (Bannister et al. 2008). Recent sperm whale density estimates off the US east coast are the highest globally (Whitehead 2002) and early fieldwork in the Sargasso Sea (beginning 2004) suggested that large number of sperm whales were found there (H. Whitehead, pers. comm). However, all previous studies of sperm whale habitat would point to the contrary. Sperm whale distribution is typically associated with high primary and secondary productivity (Gannier et al. 2002, Jaquet and Whitehead 1996, Praca et al. 2009). Yet the common belief was that the warm, clear waters of the Sargasso Sea were an oceanic desert (Blackburn 1981). Indeed, sailing around the Sargasso Sea, we encountered very limited marine life at the surface, save for *Sargassum* and its associated fauna, Portuguese Man O' War (*Physalia physalis*), a few Cory's shearwaters (*Calonectris diomedea*) and the occasional tropicbird (*Phaethon* spp.) or group of dolphins. However, in the midst of these blue waters, sperm whales were frequently encountered. The sperm whale is a very large, top-predator, raising suspicions that this was not the vast oceanic desert it was believed to be.

Our suspicions that sperm whale abundance was high in the Sargasso Sea were confirmed by density estimates from our acoustic survey data. The current sperm whale density in the Sargasso Sea is estimated to be 4.34 sperm whales/1000 km^2; one of the highest densities found globally (Chapter 5). In fact, the estimated density in the northern Sargasso Sea (5.30 sperm whales/1000 km^2) is the third-highest density of all estimates globally (Chapter 5). This high abundance of sperm whales in the Sargasso Sea is not just a recent phenomenon: the sperm whales in the Sargasso Sea supported an important whaling industry for much of a century (the 19th) during the open-boat whaling era (Bannister et al. 2008, Townsend 1935). So, despite not being an area known for its high productivity, the Sargasso Sea supports a high density, and biomass, of sperm whales.

My work has begun to unravel this pelagic paradox by demonstrating that physical processes associated with the Gulf Stream, which have been shown to increase productivity to this region (McGillicuddy and Robinson 1997, McGillicuddy et al. 1998, Ortner et al. 1978), influence the distribution of sperm whales in the northern part of the Sargasso Sea and can, in part, explain the large numbers found there currently, and in the past. However, large numbers of sperm whales were hunted extensively much further east than my study area (Bannister et al. 2008). This area would likely not be as influenced by mesoscale activity associated with the Gulf Stream and would thus likely be much lower in productivity. Why large numbers of sperm whales were, and may continue to be, found in this region, remains a paradox to be solved. This highlights how little we know about this deep-sea environment.

6.1 DEEP-WATER CEPHALOPOD COMMUNITIES

The deep-sea, which can be defined as open ocean and deep waters beyond the 200-mile Exclusive Economic Zones, makes up 50% of the Earth's surface and 64% of the world's oceans (Laffoley et al. 2011, WWF/IUCN 2001), yet we know very little about it (Gage and Tyler 1991). We are just beginning to understand the great diversity of this ecosystem, especially around seamounts and hydrothermic vents (Pitcher et al. 2007, Van Dover 2000). With the increased pressure from deep-sea fisheries, whose sustainability is questioned (Norse et al. 2012), efforts directed towards understanding and conserving this fragile ecosystem have gained momentum (Roberts 2002). Recently, there has been a push for the protection of the Sargasso Sea and the global recognition of its ecological significance and the threats it faces (Sargasso Sea Alliance: (Laffoley et al. 2011)). However, the Sargasso Sea encompasses a huge area and protection of its entirety is not feasible, therefore research is needed to identify habitat and hotspots most critical for protection.

One gap in our knowledge about the deep-sea concerns the cephalopod communities found there. Deep-water cephalopods easily escape trawls and nets (Clarke 1977) and they are difficult to study acoustically (Starr and Thorne 1998), thus very little is known about cephalopods in the Sargasso Sea. Sperm whales, however, are very good at capturing cephalopods so that a substantial part of what we know about these deep-sea species comes from sperm whales themselves (Clarke 1977, Clarke 1980). Examination of sperm whale diet in the Sargasso Sea, through the use of fecal samples, stable isotopes and mtDNA barcoding provided some insight into the deep-water cephalopod community in this region (Chapter 2). Stable isotope analysis suggested that there is a difference in the trophic ecology of sperm whales in the Sargasso Sea compared to sperm whales off Dominica, in the Caribbean: sperm whales in the Sargasso Sea had significantly higher δ^{15}N values (mean = 13.2‰) than Dominica (11.3‰). Hard part analysis suggested that *Histioteuthis*, a weakly muscled genus (Voss et al. 1992) occupying low trophic levels in the cephalopod community (Cherel et al. 2009), was the most frequently encountered genus in fecal samples from both regions. However mtDNA barcoding of cephalopod tissue collected in the Sargasso Sea near sperm whales groups were identified to *Architeuthis dux*, *Cycloteuthis sirventi* and the Lepidoteuthidae family, which are large cephalopods, occupying higher trophic levels (Guerra et al. 2011, Young and Vecchione 2009). It seems that sperm whales in the Sargasso Sea might be feeding on larger cephalopods, or cephalopods occupying higher trophic levels, than in other areas of the Atlantic. This may be the result of an underlying difference in trophic structure between the two regions. Miller et al. (2011) found that fish from highly productive marine systems foraged at lower trophic levels compared to fish in less productive systems. They suggested that nekton were feeding lower on the food web due to the higher abundance of lower trophic level prey within highly productive ecosystems. This pattern may be occurring in our study areas, whereby cephalopods in the Sargasso Sea (less productive) may be feeding on adjacent trophic levels (i.e. other cephalaopods) compared to cephalopods off Dominica (more productive) which might be feeding more predominantly on lower trophic level prey.

In an area where virtually nothing is known about the cephalopod community (M. Vecchione, pers. comm.), this study provides insight into the species that occur in the Sargasso Sea. Thus, I have demonstrated that there are many sperm whales in the Sargasso Sea and shed some insight into their diet but there remains the question: “why are they there?”

6.2 THE IMPORTANCE OF WESTERN BOUNDARY CURRENTS TO MARINE TOP PREDATORS

Open ocean circulation affects global patterns of primary productivity and sea surface temperature (Bakun 1996, Mann and Lazier 2006, Tolmazin 1985), which ultimately influence the distribution and abundance of marine organisms of all trophic levels from zooplankton (Rutherford et al. 1999) to top predators (Tittensor et al. 2010, Whitehead et al. 2010, Worm et al. 2005). Major surface currents are created by the drag of wind on the surface of the water (Mann and Lazier 2006). This wind-driven circulation results in subtropical gyres, like the Sargasso Sea, which are typically considered to be low in primary productivity (Blackburn 1981; Tolmazin 1985). However, the idea that the Sargasso Sea is an oceanic desert devoid of life is an old one and research over the past several decades has demonstrated that it is much more productive than previously thought, especially in the northwestern area due to rings, meanders, fronts and eddies associated with the Gulf Stream (Fuglister 1972, The Ring Group 1981, Loder et al. 1998, McGillicuddy and Robinson 1997, McGillicuddy et al. 1998, Oschlies 2002, Oschlies and Garcon 1998).

The mesoscale oceanographic activity associated with the Gulf Stream appears to influence sperm whale presence in this area (Chapter 3, 4). Sperm whale occurrence around the Kelvin Seamount, part of the New England Seamount Chain, was significantly higher in the spring (51%) compared to the winter (16%) and chlorophyll-*a* concentration (as an index of primary productivity) and eddy kinetic energy were predictors of sperm whale presence in this area (Chapter 3). In addition, the probability of sperm whale detection was highest in the northwestern part of the Sargasso Sea and with sea surface temperatures around 23-24^{0}C (Chapter 4). These results suggest that this western boundary current plays an important role in the distribution of sperm whales in the western North Atlantic. Likewise, other western boundary currents support high densities of whales - intense whaling also occurred off the coast of Japan in the 19th and 20th centuries (Bannister et al. 2008, Ohsumi 1980), where the Kuroshio Current, the western boundary current of the North Pacific, influences the productivity of this area (Kun and

Natarov 1970, Taniguchi and Kawamura 1970). Western boundary currents, therefore, may generally enhance sperm whale abundance. A great deal is known about the association of marine top predators and coastal upwelling regions created by eastern boundary currents (Becker and Beissinger 2003, Duffy 1983, Duffy 1989), but western boundary currents have received much less attention.

Coastal upwelling brings cold, nutrient-rich water into the eastern boundary currents, making them some of the most biologically productive areas of the ocean (Cushing 1971, Mann and Lazier 2006, Tolmazin 1985). Eastern boundary currents support abundant populations of many species of cetaceans (Ballance et al. 2006, Etnoyer et al. 2004, Weir 2010), seabirds (Abrams and Griffiths 1981, Duffy 1983, Duffy 1989, Jehl 1973) and large predatory fish, such as tuna, marlin and swordfish (Etnoyer et al. 2004, Fiedler and Bernard 1987, Laurs et al. 1984). By contrast, western boundary currents are warm, narrow, rapid and deep currents found on the western side of ocean basins at temperate latitudes and productivity at the core of the western boundary currents themselves is low (Longhurst 2007). With the exception of my research and the distribution of whaling effort in the Pacific, there is no evidence that western boundary currents support high densities of cetaceans. However, fronts associated with both the Kuroshio currents and the Gulf Stream appear to support large predator fish concentrations (Laurs et al. 1984, Podesta et al. 1993, Uda 1970, Ulanski 2008). Western boundary currents regions are also important foraging areas for some seabirds such as yellow-nosed albatross (*Thalassarche chlororhynchos*) (Pinaud and Weimerskirch 2005), sooty shearwaters (*Puffinus griseus*) (Shaffer et al. 2006), and short-tailed albatross (*Phoebastria albatrus*) (Suryan et al. 2006). Increased foraging opportunity results in high abundance of seabirds in Gulf Stream frontal eddies, rings and meanders (Haney 1986a, Haney 1986b, Haney 1987, Haney and McGillivary 1985). Western boundary currents also play an integral role in the life cycle of some marine top predators, which use the current for migration (e.g. Atlantic bluefin tuna, *Thunnus thynnus*: Block et al. 2011); whale sharks, *Rhinocodon typus*: Hsu et al. 2007), and in larval dispersal (e.g. swordfish, *Xiphius gladius*: Govoni et al. 2000).

Clearly, there is much evidence in the literature that western boundary currents support high numbers of some marine top predators, such as seabirds and large predatory fish, but there is little indication that western boundary currents are important for cetaceans, with the possible exception of sperm whales. Chapters 3 and 4 suggest that the Gulf Stream influences sperm whale distribution in the Sargasso Sea. This is not a recent observation: whalers from Nantucket discovered the large density of sperm whales in the western part of the Sargasso Sea over two hundred years ago.

6.3 HOW THE PAST SHAPED THE PRESENT

Open-boat whaling for sperm whales began in the western Atlantic with the accidental discovery of sperm whales off the US east coast when Nantucket whaler, Christopher Hussey, was blow out to sea while hunting for right whales (*Eubalaena glacialis*) (Bannister et al. 2008, Best 1983, Proulx 1986). These Nantucket whalers were in fact lucky that hotspots of sperm whales, (e.g. Charleston and Hatteras whaling grounds), were near to their island. While these grounds and others in the North Atlantic were exploited for over one hundred years, there does not appear to be much of a correlation between the areas where we presently find a high density of sperm whales (north of 35^0N and between $60\text{-}66^0$W) and the areas in which the whalers focused their efforts (Chapter 5). Possible explanations for this mismatch include the lack of discovery of the present hotspot by the whalers or a limitation on the use of new “grounds” due to conservative use of knowledge available at the time. Regardless, the western Sargasso Sea was hunted extensively, especially during the first half of the 19th century. Modern whaling began at the end of the 19th century, but sperm whale catches did not peak until 1960-1970 (Bannister et al. 2008, Best 1983, Reeves and Smith 2006). Modern whaling was extensive in all oceans, including the Kuroshio-influenced region off Japan (Ohsumi 1980), but little modern whaling occurred in the western North Atlantic (Mitchell 1974) or the North Atlantic in general (Jonsgård 1977). It appears that the open-boat whaling success in the western North Atlantic was all but forgotten. This had consequences for current populations found there. The highest densities of sperm whales are found in the western Atlantic (Chapter 5), likely due to the much longer period of recovery time post-whaling. But if the western North Atlantic was such a hotspot for sperm whales, why did so little modern whaling occur there?

The reprieve that sperm whales in the western Atlantic received during modern whaling can be traced to the history of modern whaling and the economy. By the end of the 19th century, catches by the American fleet of open-boat whalers had severely declined and there was little market for oil (Best 1983). Modern whaling began in Norway, through the development of steam-powered ships and high-powered deck cannons. This technology allowed the exploitation of the much faster rorqual whales, which were the first whales to be harvested and Norwegians initially dominated modern whaling (Davis et al. 1997, Tønnessen 1982). By the time the market for oil had revived and modern whaling practices had evolved, the American whaling industry was essentially non-existent: there was no capital to build new ships, nor experienced seaman (Davis et al. 1997). In many ways, modern whaling passed by the Americans as the country's interests turned to other commodities and ventures.

The few pelagic American vessels involved in modern whaling focused their efforts in the Pacific and Antarctic oceans and the only shore-based whaling stations were on the west coast (Reeves and Smith 2006). Similarly, the countries involved in modern whaling, including those of western Europe, Norway, Netherlands, Great Britain, Japan, the Soviet Union and South Africa targeted the North Pacific, Antarctic and to a lesser extent the South Pacific and South Atlantic (Reeves and Smith 2006). After the Second World War, the only stations remaining on the eastern seaboard were in eastern Canada, and few sperm whales were taken from them (Mitchell 1974).

Perhaps the reason modern whalers did not return to the western North Atlantic was due to the fact that those that knew best the whaling grounds in this area, were no longer taking part in the sperm whale hunt. By 1960, when catches of sperm whales peaked (Whitehead 2003), most of the open-boat whalers had passed away and their descendents had moved onto other things. Save for a few academics that might have read the Maury (1852) and Townsend (1935) whaling charts, few knew of the previously successful and lucrative whaling grounds in the western North Atlantic. The knowledge of sperm whale distribution in the North Atlantic essentially died with the end of the open-boat whaling era and those involved in the modern whaling hunt returned to the whaling grounds they knew best, in the Pacific, Indian and Antarctic Oceans. The sperm whales in the western North Atlantic were forgotten.

While it is impossible to say for sure why the western North Atlantic was largely spared from modern whaling, it is clear that sperm whales continue to occur in high numbers in this region. Their presence is strongly influenced by the mesoscale oceanographic activity of the Gulf Stream, which leads to increased productivity and results in good habitat for sperm whales.

6.4 FINAL REMARKS

The open ocean is a mysterious place that we are only just beginning to understand. It is distant and costly to conduct research there and weather conditions make work difficult, if not impossible, at times. What are the underlying processes that drive marine life? What makes good oceanic habitat for organisms? I have spent a lot of time at sea conducting surveys, both acoustic and visual, in the Atlantic, Pacific and Arctic Oceans. Many frantic hours recording detections or sightings are often interspersed with long hours (or days) of very few sightings, where the ocean looks like it will go on forever and is devoid of any life. Yet, suddenly, out of nowhere, a large group of marine animals will appear, sometimes multi-species aggregations. This always leads me to wonder "why are they ***here***?" On many of these surveys, I am in the company of physical and biological oceanographers, who understand the dynamics of these waters far better than I. Using a combination state-of-the-art instruments and nets, their goal is to try and understand these underlying processes and the complex oceanography of the area. And they are very good at it. Yet, when I sight a group of foraging sperm whales or shearwaters in the middle of the vast, blue waters, it is clear who the best oceanographers really are. Marine top predators can teach us an enormous amount about the open ocean ecosystem. We just need to pay attention.

Appendix 1
PUBLICATIONS

The work presented in Chapter 2 was submitted for publication:
Wong, S.N.P., V.L Yaroshewski, H. Whitehead. Spatio-temporal variability of sperm whale (*Physeter macrocephalus*) diet in the western North Atlantic: evidence from stable isotopes and hard-part analysis. Marine Biology. Manuscript Number: MABI-D-12-00487.

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