SPATIAL ECOLOGY OF THE NORTH ATLANTIC RIGHT WHALE (*EUBALAENA GLACIALIS*)

by

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University Program in Ecology
Duke University

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Dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Environment in the Graduate School of Duke University

2008
ABSTRACT

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Despite decades of protection, the endangered North Atlantic right whale (Eubalaena glacialis) has failed to recover, primarily due to interactions with fishing gear and ship strikes. Right whales range along the U.S. east coast, foraging year round in the Gulf of Maine while a subset of the population travels to the South Atlantic Bight each year to calve. The habitat requirements of the right whale are poorly understood. I investigated the relationship between the distribution of right whales and physical oceanographic conditions in an effort to create predictive models of essential right whale habitats. Additionally, the distribution of right and humpback whales (Megaptera novaeangliae) relative to fixed fishing gear was examined to assess spatio-temporal overlap. Habitat preferences were assessed using aerial survey data of whale locations and a range of topological and satellite derived physical parameters including bathymetry, sediment type, sea surface temperature, thermal gradients and surface roughness. A suite of non-parametric quantitative techniques including Mantel tests, log likelihood functions, Generalized Additive Models, Spearman Rank Correlations and the Williamson’s spatial overlap index were used to assess relationships between whales and habitat variables. Our findings indicate that suitable calving habitat along the east coast may extend much farther to the north than is currently recognized. Our model correctly identified several well documented current and historic calving grounds in the eastern Atlantic but failed to fully identify a heavily used calving area off Argentina, which is
characterized by lower surface water temperatures than the other calving regions. In the
Gulf of Maine, right whale distribution was correlated primarily with sea surface
temperature, sediment type and bathymetry. Predictive models offered insights into right
whale habitat preferences for foraging but failed to wholly capture the physical factors
underlying right whale distribution. I found the relative density of right and humpback
whales and fixed fishing gear in the Gulf of Maine to be negatively correlated in most
seasons and areas. These findings demonstrate that the regular co-occurrence of high
densities of whales and gear is not a prerequisite for entanglement. Prohibiting entangling
lines in areas where whales are known to forage could substantively reduce
entanglement.
Dedication

To my parents, for taking me to the ocean to play.
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Acknowledgements

This dissertation has been a major project for me and is the culmination of years of work. I well realize that my task would have been impossible were it not for the help and assistance I have received along the way from many people.

First of all I would like to thank my advisor, Andy Read. Andy allowed me tremendous leeway as I scoped out my research and has treated me like a colleague throughout my time at the Duke Marine Lab. His confidence in my ability to tackle difficult challenges and his gentle nudging at some critical moments are much appreciated. I look forward to continued collaboration with Andy on new projects in the future.

I also thank each of my committee members for agreeing to serve on my committee and for helping me in various ways over the years. Pat Halpin encouraged me to reach out beyond my ‘comfort zone’ and utilize new and sophisticated modeling techniques to analyze data. His vision of how I could use cutting edge geospatial analysis in my research was critical for my work. Larry Crowder helped me as I began to formulate my research plan and played a devil’s advocate role that allowed me focus on the issues that were most important. His lunchtime chats have been a source of friendship and support. Phil Clapham encouraged me early on as I considered whether to pursue my PhD and his research on large whales around the world has been a continuing source of knowledge and inspiration.
Of course, I am indebted to all those from whom I was able to gather the essential
data that forms the basis for my analyses. I would like to thank the Right Whale
Consortium, Tim Cole, Nathalie Jacquet, Bill McLellan and Bob Kenny for the use of
their data. A special thanks goes out to the numerous field personnel who spent countless
hours documenting right whale distribution. I would like to recognize the ultimate
sacrifice made by Emily Agro, Michael Newcomer, Tom Hinds and Jackie Ciano who
perished in the tragic crash of a survey plane off the coast of Florida in 2003 while
collecting data. My research directly benefited from their efforts and I am immensely
appreciative of that.

There are many colleagues at the Duke Marine Lab to whom I owe my gratitude
for their help along the long road to completion of this document. Danielle Waples,
heroine of the Read Lab, has made a huge difference with her seemingly endless patience
as I constantly begged for help with one thing or another. Lucie Hazen’s impressive
knowledge base and attention to detail ensured that my projects stayed on track. The
talented office staff at DUML, including Patty Nolin, Linda Nichols and Nancy Morgans,
worked hard to help me juggle the many administrative details associated with my
dissertation. And I will always appreciate Sophie Turnage holding my mail for me in the
few intervening years when I was not at the lab.

Song Qian provided me with help on the most complicated code in my models
and his guidance was invaluable to my work. Jason Roberts also deserves an enormous
thank you for his work in getting several elements of my satellite data organized.
During my time working at the National Marine Fisheries I was very fortunate to have worked with many wonderful colleagues. In particular, I am greatly indebted to Donna Wieting for her belief in me and her continuing support and encouragement while I was at Duke.

I also want to thank Charlotte Gray, Carrie Selberg and Keith Arnold, my MEM friends and former DC housemates, for their friendship, constant encouragement and willingness to listen when I needed to test out an idea or just needed to someone to talk to. Kristen Hart - my wonderful housemate in Beaufort and friend helped keep me sane me in my early years of the PhD process.

In addition, I am grateful to my labmates – past and present – who provided advice and friendship as needed. My thanks to those who have shown me it can be done and helped me along the way - Heather Koopman, Damon Gannon, Tara Cox, Caterina D’Agrosa, Dave Johnson, Andrew Westgate, Ari Friedlaender, Vicky Thayer, Lesley Thorne, Lynne Williams and Wendy Dow and Leigh Torres, whose dog Mango was Piper’s canine partner-in-crime at the lab. My thanks especially go to Kim Urian for her help and encouragement over the years and for her endless enthusiasm. My special gratitude goes to Catherine McClellan for her help and encouragement in recent months. She has been a kindred spirit who understands the unique joys and unimaginable frustrations of working in the vexing world of “cutting edge” geospatial mega-models.

I am very thankful for the friendship of Kelly Stewart and Jeremy who have been incredibly supportive and eternally upbeat. In particular, I am grateful for the times they
helped me care for my best canine friend, Piper, during my many absences from Beaufort. Thanks to Lucie and Elliot Hazen who have been the best of neighbors and friends. Lucy’s gifts of homemade goodies kept me going in the last few weeks.

My final and heartiest thank you goes to my family. I thank my Mom and Dad and sister for always loving and supporting me even when I wasn’t sure about myself. Throughout my life they have always made me feel that I could accomplish anything I set out to do. I also give a special thanks to my dog, and permanent office mate, Piper, who was quite literally there for me at all times.
Introduction

During the past decade, ecologists have initiated an intense effort to identify and model habitat preferences and distribution patterns of marine species (Guisan & Zimmermann 2000). Understanding how a species interacts with its environment is a central tenet of ecology and with the availability of affordable, fast computing power, it is now possible to describe complex ecological interactions in a quantitative manner (Guisan & Thuiller 2005). The marine environment presents a unique challenge to researchers, because, unlike terrestrial systems, the ocean’s dynamic motion generates a continuously shifting, multidimensional habitat. The ephemeral nature of marine systems creates the spatial and temporal heterogeneity that drives ecological interactions, influencing the movements and behavior of many marine animals. This variation also challenges ecologists who wish to describe this complex environment. Only through a rigorous assessment of patterns of distribution can I develop analytical models of a species habitat use and suggest functional relationships that may influence habitat choice (Austin 2002).

Mysticetes make an especially interesting subject for the study of habitat selection due to their extreme mobility and relatively tight trophic linkages. Whales respond to the environment over an enormous range of scales. Individuals migrate through entire ocean basins (Knowlton et al. 1992, Jacobsen et al. 2004), yet respond precisely to the distribution of prey on foraging grounds (Watkins & Schevill 1979, Mayo & Marx 1990).
Despite great interest in the ecology of these iconic animals, there have been relatively few quantitative studies of their patterns of habitat use and selection.

Heavily exploited by coastal hunters since the fourteenth century, the North Atlantic right whale (*Eubalaena glacialis*) population is estimated at approximately 350 individuals (Kraus *et al.* 2001). Many catches were made prior to the establishment of written records, so it is difficult to estimate the pre-exploitation population size. Reeves *et al.* (2007) used catch records to suggest an original population of between 3,000 – 11,000 individuals. The U.S. Right Whale Recovery Plan relies on Gaskin (1991) for its estimate of 10,000 individuals. The long tradition of right whale exploitation on both sides of the Atlantic has relied on the whales’ slow movements, prolonged surface time when feeding and penchant for coastal habitats. It is also possible that the population has cycled through several periods of exploitation and subsequent recovery, as evidenced by cyclic effort in coastal whaling for right whales along the U.S. coast from the mid 17th century through the beginning of the 20th century (Best 2001).

Despite half a century of protection, the North Atlantic right whale remains critically endangered (Clapham *et al.* 1999, Kraus *et al.* 2005). The population has a declining survival probability, most notable among reproductively active females, which has resulted in a negative population growth rate ($\lambda < 1$) since 1992 (Fujiwara & Caswell 2001). The status of the right whale remains tenuous as a result of past historical exploitation and current removals through by-catch and ship strikes. Entanglement in fishing gear and collisions with ships are now the primary factors contributing to the species’ failure to recover (Knowlton & Kraus 2001). These threats persist throughout the
species’ range and have proven cumbersome to manage (Johnson et al. 2007, Knowlton & Brown 2007). Mortalities from entanglement and ship strikes occur infrequently, but each event contributes significantly to the species’ risk of extinction because of the very small population size. Unless current mortality levels are reduced, right whales are expected to become extinct within the next 250 years (Fujiwara & Caswell 2001).

Historically, right whales ranged across the North Atlantic basin from Norway to the Canadian Maritimes and Senegal to Florida (Reeves et al. 2007). Today, most of the remaining right whales are found in the western North Atlantic with the eastern population estimated to be only in the tens of animals (Best 2001). In spring and summer whales forage in the Gulf of Maine and on the Scotian Shelf. A subset of the population, including pregnant females and some juveniles, migrate to the South Atlantic Bight in winter, while the remainder of the population remains in or near the Gulf of Maine (Kraus et al. 1986, Cole et al. 2007). A handful of right whales have been sighted off Greenland (Knowlton et al. 1992) and Norway (Jacobsen et al. 2004), but the motivation for and frequency of these trans-Atlantic crossings remains unknown.

My work focuses on evaluating the habitat choices, and underlying ecological needs, of right whales by assessing their patterns of distribution. The underlying premise of my work is that the observed distribution patterns of right whales provide insight into their requirements for foraging and calving. An examination of the physical characteristics of areas used frequently by right whales may reveal the importance of various aspects of habitat to the survival of these highly endangered animals. My work also addresses the spatial pattern of threats by examining the co-occurrence of whales and
fishing gear in time and space. Knowledge of where and when whales are likely to encounter harm will improve efforts to reduce these risks and assist in the recovery of this population.

My first chapter details the association of right whales and habitat parameters on their calving grounds. Until recently, little attention has been paid to the habitat conditions at calving grounds since whales tend to fast while at calving areas. Most research has focused on habitat characteristics linked to foraging. This assessment explicitly details habitat conditions associated with mother/calf pairs on calving grounds and includes the development of a predictive model of optimal calving habitat based on the whales’ patterns of habitat use. As a complement to the first investigation, the second chapter identifies relationships between right whale distribution and oceanographic parameters in the Gulf of Maine. Whales primarily feed while in the Gulf so optimal habitat is closely tied to conditions associated prey aggregation and enhancement. Building on previous work (Mayo & Marx 1990, Kenney et al. 2001, Baumgartner et al. 2003a, Baumgartner et al. 2003b, Baumgartner & Mate 2003, 2005, Jiang et al. 2007), I developed a predictive model of likely foraging habitat based on habitat characteristics linked to right whales’ primary prey, late stage Calanus finmarchicus. The final chapter takes an applied approach to distribution analysis by detailing the relationship between right and humpback whales (Megaptera novaeangliae) and fixed fishing gear in the Gulf of Maine. Entanglement remains a pervasive problem for both endangered whales but little is known about where and when interactions occur. My analysis indicates areas and
seasons where encounters with gear are more likely and discusses broader trends of gear distribution.
Chapter 1: Predictive Modeling of Right Whale (*Eubalaena glacialis*) Calving Habitat in the Atlantic Ocean
Introduction

Each winter, a portion of the North Atlantic right whale (*Eubalaena glacialis*) population migrates from feeding grounds off New England and eastern Canada to a well documented calving area along the South Atlantic Bight (Winn et al. 1986, Kraus 1993). This region is the only known calving site for right whales in the North Atlantic. Females give birth between December and March before returning to the northeast in the late winter or early spring (Kraus et al. 1986). Most of the whales traveling to the calving ground are pregnant females but the migration includes some juveniles, non-reproductive females and, more rarely, adult males (Kraus et al. 1986).

Observations from the South Atlantic Bight (SAB) calving ground (Kraus et al. 1986, Kraus 1993, Knowlton et al. 1994) and calving grounds of Southern right whales (*Eubalaena australis*) (Payne 1986, Best 2000, de Oliveira Santos et al. 2001, Elwen & Best 2004c) indicate marked similarities among right whale calving habitats. Each of these habitats is calmer, warmer and shallower than the respective foraging grounds. Similar characteristics describe the calving grounds of gray whales (*Eschrichtius robustus*) along Mexico’s Baja Peninsula (Norris et al. 1977, Jones & Swartz 1984, Pacheco 1998, Urbán et al. 2003) and humpback whale (*Megaptera novaeangliae*) calving grounds in the Hawaiian Islands (Smultea 1994, Craig & Herman 2000, Johnston et al. 2007), Dominican Republic (Whitehead & Moore 1982) and Madagascar (Ersts & Rosenbaum 2003). The similarities amongst the calving grounds of these baleen whales
suggest that physical habitat characteristics are broadly important for successful 
reproduction.

Given these similarities, many researchers have speculated that calving habitat 
offers specific reproductive benefits that enhance calf survival and growth (Thomas & 
whales rarely feed while on calving grounds, so prey resources are unlikely to influence 
habitat choice (Thomas & Taber 1984, Best & Schell 1996, Tormosov et al. 1998). The 
shallow topography of calving areas may offer protection from predation (Wursig & 
Wursig 1980, Thomas & Taber 1984), discourage mating attempts by aggressive males 
(Smultea 1994) or act as a structural boundary for neonates acquiring basic motor skills 
(Storro-Patterson & Kipping 1977, Taber & Thomas 1982). Calm areas may be 
especially advantageous for neonates given their high surfacing frequency (Thomas & 
Taber 1984), limited buoyancy and poor swimming abilities (Taber & Thomas 1982, 
Thomas & Taber 1984, Elwen & Best 2004b). Finally, the relatively warm temperatures 
of most calving areas may optimize energy reserves (Brodie 1975, Taber & Thomas 

Here I report on an assessment of topological and physical conditions associated 
with the presence of right whale calves in the South Atlantic Bight and describe the 
development of a predictive model of calving habitat. The habitat variables I chose were 
based on their ubiquity across calving grounds and their presumed benefits to mothers 
and calves. I evaluated the importance of water depth, sea surface temperature and 
surface roughness to the distribution of calves over a six-year period (2000 – 2005) using
Mantel tests and Bayesian probability density functions. I tested the hypothesis that right whale mothers with newborn calves use shallow, calm, temperate waters because these conditions provide a fitness advantage to the calves. Additionally, I sought to confirm Keller et al’s (2006) finding from earlier data (1991-1998) that right whale mothers prefer relatively moderate (12°C – 21°C) rather than warm (> 21°C) surface waters on the calving grounds due to thermal limitations. I also report on the applicability of our predictive habitat models to calving areas in the South Atlantic and historic winter whaling grounds in the North Atlantic. Lastly, I attempted to explicitly identify previously undocumented calving habitats.

In other publications, terminology such as “calving ground”, “nursery ground” and “breeding ground” are used interchangeably or to different ends. This may be due to regional or academic differences in accepted norms of vocabulary. To alleviate such confusion, for this work, I explicitly define a “calving ground” as an area where parturition is known or suspected to occur regularly in season; a “breeding ground” as an area where whales are known or suspected to mate, which may or may not overlap with a calving ground, and a “nursery ground” as an area where parturition does not occur but where young calves (< 1 year) are frequently present.
Methods

Study Area

The SAB is a wide, shallow embayment along the southeastern U.S. extending approximately from Cape Hatteras, NC to Palm Beach, FL. The continental shelf along the SAB varies from 4 to 140km in width and acts as a barrier to the Gulf Stream on the western edge. Winter surface temperatures range from 8°C to 25°C. Pulses of warm water frequently move shoreward as the result of Gulf Stream meanders, but a steady tongue of colder water persists directly adjacent to shore in winter (Stegmann & Yoder 1996). The presence of this colder water was noted by Keller et al (2006) as an important determinant of right whale distribution during winter. The gently sloping topography is characterized by soft sediment interspersed with hard bottom areas which provide important habitat for a variety of fish species. Heavy vessel traffic is common around ports and active fisheries occur throughout the Bight.

Data from Aerial Surveys

As part of the Southeast Early Warning System (EWS) for mariners, aerial surveys of the calving ground were conducted by 3 different organizations (the New England Aquarium, Wildlife Trust and Florida Fish and Wildlife Research Institute) between January 2000 and March 2005. The EWS surveys were conducted from fixed wing aircraft following the same protocols. Each aircraft traveled at a speed of approximately 100 knots and an altitude of 750 feet with two observers and one data
recorder aboard each plane. Surveys were flown on all good weather days each winter between December 1 and March 31.

The aerial surveys were designed to warn mariners of whales in the vicinity and to collect photographs of individual animals. Survey effort was biased towards searching the federally designated Southeast Right Whale Critical Habitat zone (National Marine Fisheries Service 1994), although the distribution of whales extends outside this area. Some flights were conducted both offshore and to the north of the Critical Habitat zone. The spatial extent of search effort varied over time, with the most surveys conducted between Savannah, GA and Cape Canaveral, FL. These surveys were not designed for habitat analysis and, as such, flights were concentrated in areas where whales were known or expected to be present, with little effort dedicated to a broader geographical region. From historical records (Reeves 2001) and earlier Bureau of Land Management and Southeast Fisheries Science Center surveys (Read et al. 2008), right whales rarely occur offshore (> 40km) in the southeast. Nonetheless, the limited geographic extent of the surveys restricted our biogeographic analyses to these areas.

The surveys did not follow formal line transect protocols. Instead, predetermined tracklines were used to ensure a consistent search area in most surveys. At each right whale sighting the plane departed from the trackline to circle the individual(s) and obtain an accurate location and count, along with photographs for individual identification. Positions were recorded using a GPS (Global Positioning System) at frequent intervals along each trackline to document effort. While underway, Beaufort Sea State, weather, visibility and the location and details of each whale sighting were recorded.
A filter was employed to account for the “circling” that occurred when whales were located. The filter was applied to all survey effort and any instance in which the plane left the trackline and made more than 2 circles within a 2km range was removed. In addition, I removed from analysis the few portions of the survey data with a Beaufort Sea State greater than 3. To account for differential survey effort along the coast I overlaid the entire search area with a 5km analysis grid and for each month calculated the length of trackline in each analysis cell. This became the measure of search effort expended per analysis unit.

I used separate data sets to evaluate model performance. These validation data sets included earlier EWS surveys (1996-1999) and surveys from the University of North Carolina Wilmington (2001-2002) that partly overlapped with the original data set but also extended to the north of the EWS surveys. The same flight and data recording protocols were used for these surveys and all data were processed using the procedures described above.

**Environmental Data**

I acquired physical data from several sources and custom processed these observations to meet the needs of our analysis. I used ArcGIS Desktop 9.2 (ESRI, Redlands, CA), Python, S-Plus and R software packages to conduct data processing and analysis. I used the Albers Equal Area Conic projection for local data processing in the Southeastern US and Mollweide for ocean-wide analysis. I derived bathymetric data from S2004 one-arc-minute global bathymetry (unpublished data, W. Smith). The product is an
unpublished but verified (Marks & Smith 2006) amalgamation of Smith and Sandwell (1997) and the General Bathymetric Charts of the Ocean from the British Oceanographic Data Center. This data set provides the highest resolution global coverage currently available. As a complement to these data, I used the Global Self-Consistent, Hierarchical, High-resolution Shoreline (GSHHS) data set which also offers global coverage (Wessel & Smith 1996).

For ocean temperature, I used Advanced Very High Resolution Radiometer (AVHRR) Version 5 sea surface temperature (SST) imagery obtained from the National Oceanic and Atmospheric Administration’s National Oceanographic Data Center. This latest version of the AVHRR data has an accuracy of 0.3°C and a resolution of 4.6 km making it one of the highest resolution dataset available with a global extent. To ensure that clouds were eliminated from the data, only pixels with an image quality level > 3 were included in the data processing (Kilpatrick et al. 2001). I calculated monthly averages for each of the 23 months examined. In some months, due to extreme winter cloudiness, it was necessary to interpolate (via kriging) cell values to fill in missing data gaps although, in most coastal areas, data gaps were small and fell directly adjacent to quality data.

I obtained sea surface roughness data from the NASA Scatterometer Climate Record Pathfinder project through Brigham Young University’s Microwave Earth Remote Sensing Laboratory. I used enhanced resolution backscatter images from the QuikScat instrument for our analysis (Long & Hicks 2005). Normalized radar backscatter (sigma-0) is a measure of wind-driven surface roughness over the ocean. This is an
excellent measure of surface choppiness although, because roughness is primarily a measure of the amplitude and extent of wind-induced capillary and gravity waves, in calm conditions the scatterometer may fail to detect swell propagating from a distant source. Level 1b backscatter data is commonly used to examine sea ice extent or climate variation, but its applicability as a direct measure of surface conditions also proved an excellent fit for this novel use.

Because my analysis employed a monthly timeframe, I focused on optimizing spatial and not temporal resolution. As a result, all available satellite passes were aggregated and higher resolution “slice-based” backscatter images were chosen over “egg-based” images despite increased noise in the data from any individual pass. Slice images have a pixel resolution of 2.225km and an effective resolution of approximately 5km. For each month in our analysis I calculated the average normalized backscatter value.

In most areas, backscatter imagery is contaminated at the land/sea interface due to much larger sigma-0 values over land in comparison to ocean. To resolve this problem, I removed contaminated data within this interface and used values from adjacent offshore pixels as a proxy for inshore conditions. The extent of the interface was determined by examining trends in pixel deviation perpendicular from shore. All pixels within 12km of the coast were substituted with values from the nearest high quality cells. An interpolation was not performed, but rather inshore conditions were presumed to be best represented by adjacent uncontaminated cells.
A large portion of right whale calf sightings (40%) fell within 12 km of shore, so I consulted data from several moored buoys in the region to investigate whether my assumption of the continuity of surface roughness for inshore waters was valid. Fifteen year climatologies from stations (SAUF1 and FBIS1) within 100m of the coast registered average winter wind speeds between 8.1-9.3 knots and 9.2-9.6 knots respectively (NOAA's National Data Buoy Center). Two additional buoy stations, one 29km (41008) and another 35km (41009) offshore registered average winter wind speeds between 10.1-11.2 knots and 12.4-13.1 knots respectively. A fifth buoy, 60 km offshore (41004), registered average winter speeds between 13.2-14.7 knots. Given these long term trends in actual winter nearshore winds for the South Atlantic Bight it appears that there is likely only minor variation within 12km of shore. Nevertheless, it is possible that these data underestimates the calmness of the nearshore environment.

**Analytical Methods**

**Temporal and Spatial Framework**

According to Best (2000), females with calves remain on South African calving grounds an average of 59 ± 3.9 days. In the western North Atlantic the calving season spans approximately 4 months (December - March) and for most analyses I used monthly data aggregated over all 6 years (5 years for December). I used a 5km² sampling unit for most analyses, due to resolution constraints of the satellite data. This sampling unit is appropriate for calving habitat, because individuals likely select habitat at a coarser grain
than the highly discrete oceanographic features used in foraging areas. Any sampling unit with less than 10km of flight tracks in any given month was eliminated from the analysis due to insufficient search effort. As a result, 4 calf sightings were removed from the analysis. Additionally, 3 further sightings were excluded because their position estimates fell landward of the coastal interface. I limited my analysis to areas seaward of barrier islands and did not include estuarine or river environments.

**Assessment of Population Differences**

Our analyses included only sightings of mother/calf pairs so that I could focus on core habitat characteristics explicitly sought by calving females. In the Southern Hemisphere mother/calf pairs inhabit shallower, more near-shore areas relative to other whales on the calving grounds (Payne 1986, Best 2000, Elwen & Best 2004c). To investigate whether other whales were associated with different habitat conditions than those used by mother/calf pairs, I performed a Wilcoxon rank-sum test on pooled data from both groups.

**Assessment of Habitat Variables**

Following Schick and Urban (2000), I performed Mantel tests in S-Plus (Insightful Corp.) to evaluate the association of mother/calf pairs with habitat conditions. Mantel tests are non-parametric, partial regression techniques based on dissimilarity matrices (Mantel 1967). The tests assess the degree of correlation between sightings and habitat variables, while taking into account the autocorrelation of these variables and inter-correlation among other variables. This technique explicitly considers space as a
predictor variable, evaluating whether spatially structured parameters that are not included in the analysis influence whale distribution. Mantel tests assume a linear relationship between predictor and response variables; this may be an unrealistic assumption for some species/environment interactions.

I performed separate tests for all years of data aggregated by month (December, January, February and March) and made comparisons among months. I used sightings of mother/calf pairs to represent the presence of whales and derived absences from an equal number of random positions distributed relative to survey effort. I performed simple Mantel tests, evaluating the relationship between the dependent variables and all environmental variables, as well as pure partial Mantel tests to investigate any correlations with each environmental variable separately. Significance testing was conducted via permutation procedures because the structure of the dissimilarity matrix is not independent.

**Models of Calving Habitat**

To create a model of preferred calving habitat, I used a “presence-only” format based solely on the conditions where mother/calf pairs were sighted. I chose this technique because of the very small population of right whales along the U.S. east coast and the limited spatial extent of the aerial surveys. As a remnant population, North Atlantic right whales are not in ecological equilibrium with their environment and thus may not be distributed across all regions of suitable habitat. In fact, the population may be considered “dispersal limited,” due to their inability to occupy all quality habitats.
available to them (Pulliam 2000). Ecological equilibrium is a common assumption in species distribution models (Guisan & Theurillat 2000, Guisan & Thuiller 2005) but this assumption is not reasonable for this population. If habitat conditions associated with whale absence are incorporated into a model as “unsuitable”, the outcome may be biased away from suitable habitat due to limited species dispersal.

I calculated the relative density of calf sightings over each 5km$^2$ sampling unit and measured the habitat conditions where whales were sighted. Based on these samples, I used a Bayesian methodology to estimate non-parametric probability density functions (PDFs) for each of the 3 variables (SST, surface roughness and depth) for each cumulative month. Mode coefficients from the PDFs provided the parameters for a log likelihood function to calculate a likelihood surface of calving habitat (Equation1).

$$
\text{Equation 1}
$$

$$
\Pr(\text{habitat}) = \left[ \left( \mu_{\text{depth}} \right)_{\text{depth}} - \log \gamma(\mu_{\text{depth}}) - e^{x_{\text{depth}}} - (\mu_{\text{depth}} + 1) \ln x_{\text{depth}} \right] + \left[ \left( \mu_{\text{sst}} \right)_{\text{sst}} - \log \gamma(\mu_{\text{sst}}) - e^{x_{\text{sst}}} - (\mu_{\text{sst}} + 1) \ln x_{\text{sst}} \right] + \left[ \left( \mu_{\text{rough}} \right)_{\text{rough}} - \log \gamma(\mu_{\text{rough}}) - e^{x_{\text{rough}}} - (\mu_{\text{rough}} + 1) \ln x_{\text{rough}} \right]
$$

The function was applied to all coastal areas and many offshore portions of the Atlantic Ocean to ensure that the broadest possible region was evaluated. Surface roughness data were not available for the mid-ocean environment so this zone was not evaluated. In the Southern Hemisphere, the timing of the austral calving season complicated comparisons. To account for this temporal shift, the model was applied instead to the primary calving months in the Southern Hemisphere (Best 1994), July-October. This non-parametric method was particularly well suited for my data, as it
requires no presumption of data independence. Bayesian PDFs were calculated in WinBugs (from the Bayesian Sampling Using Gibbs Sampling BUGS project) with likelihood functions calculated using R and ArcGIS.

I used Receiver Operator Characteristic (ROC) curves to assess model accuracy and establish optimal habitat thresholds (Figure 1). The ROC curve is an illustration of the relationship between the proportion of true positives and false positives over a range of different threshold probabilities, derived from samples of a predictive surface. The optimal threshold value optimizes errors of omission and errors of commission; I used this threshold to delineate predicted calving habitat from non-calving habitat. The Area Under the Curve (AUC) is a non-parametric statistic derived from the ROC curve. Usually, the AUC represents the overall discrimination capacity of the model and is frequently used as a measure of overall model performance. In this case, my AUC values are artificially low, due to a higher rate of commission errors (instances where whales were predicted to be present but documented as absent) (Lobo et al. 2008). As discussed above, this is because whales cannot occupy all available habitats due to their very small population size. I report AUC values with this caveat.
Figure 1: Confusion matrix illustrating inputs for assessing model accuracy and diagram of a Receiver Operator Characteristic (ROC) curve depicting the optimized threshold value and area under the curve (AUC).

I calculated separate ROC curves for each of the 4 models. I sampled the value of each predictive surface using the cumulative monthly sightings of mother/calf pairs and an equal number of random positions. The same sightings data used to create the models were employed to calculate the ROC curves to ensure that habitat threshold (cutoff) values were based on the largest number of samples possible. Random positions were distributed proportionately to survey effort to account for the differential effort across the spatial extent of the survey zone. In expectation of a high rate of commission errors I chose to calculate a second set of ROC curves using random points distributed equally across the spatial extent of the search area. This allowed me to investigate the effect of intensive, localized survey effort on the performance and specificity of the model.

In addition to the ROC curves, I made further assessments of model performance. I employed validation data sets that were spatially and temporally distinct from those employed for model development to sample the predictive surface for each of the four models. I used random points distributed relative to survey effort for comparison and
calculated confusion matrices for each model, based on the thresholds determined by the ROC curves. Using the same procedures, we used sightings of adult whales from the original data to evaluate the models’ performance with respect to non-calf sightings. I report on the total model accuracy and sensitivity of the models to each data set.

I derived a final, single model of optimal calving habitat by combining all four monthly models. This resulted in a combined model delineated by the number of months (1-4) a given area was selected as optimal calving habitat. This provided not only a spatial depiction of calving habitat but also a measure of temporal continuity. I used both the model data and validation data sets to calculate the rate of true positives for each data set to evaluate the ability of the combined models to predict calf presence.

To focus the model on the most robust habitat areas, I removed a small number of “outlier” cells with less than 30km of continuous predicted habitat. This cutoff was chosen to reflect a minimum size of habitat right whales are known to frequent for extended periods (Thomas & Taber 1984, Best 2000). An area was considered continuous as long as no two predicted habitat cells fell more than 5km apart. This spatial editing was designed to remove sparse “sprinkles” of predicted habitat and highlight continuous habitat areas more ecologically relevant for calving. In total, 4.3% of predicted habitat cells were removed.

This final model was applied to the entire North Atlantic and I report here on the spatial extent and temporal continuity of the predicted calving habitat for right whales throughout this range. The applicability of the habitat models to historic calving areas in the Eastern Atlantic was assessed qualitatively, as there are no documented sightings of
mothers and calves nor dedicated survey effort from this area. Historically, whalers targeted right whales at two sites in the Eastern North Atlantic: the Bay of Biscay off Spain and Cintra Bay off Western Sahara (Aguilar 1986, Reeves & Mitchell 1990, Reeves 2001). These whaling grounds were exploited primarily during winter months; in Cintra Bay calves were harvested, suggesting the area was a calving or nursery ground. I used the extent of whaling settlements identified along the Spanish coast (Aguilar 1986) as a proxy for the extent of whaling activity in the Bay of Biscay and the distribution of whaling activities described in Reeves and Mitchell (1986) to describe the grounds off Cintra Bay. Additionally, I consulted Clark (1887), who reported a possible whaling ground just to the south of Cintra Bay. I describe here the overlap of modeled habitat areas with these known whaling grounds.

The timing of right whale parturition in the southern hemisphere differs from that in the northern hemisphere. In addition, the right whales found in the South Atlantic are a distinct species (Eubalaena australis). Thus, I consider my assessments of calving habitat in the South Atlantic to be exploratory in nature. I undertook a qualitative comparison of the results of my predictive habitat model, based on published descriptions of several South Atlantic calving grounds. The Southern right whale remains endangered, but more than 10,000 individuals exist (Best 2001). Calving grounds along the coasts of South Africa and Argentina have been extensively surveyed over many years and additional calving areas in Brazil have been partially investigated.
Result

Analysis of Right Whale Habitat

Between January 2000 and March 2005, 633 sightings of right whale mother/calf pairs were recorded in the study area. Sightings were concentrated along the Florida/Georgia boarder although this was also the site of the most intensive survey effort (Figure 2). Extensive aerial survey effort occurred along the coast between Cape Canaveral, FL and the Georgia/South Carolina border. Only 117 right whales calves were born during this period (Kraus et al. 2007) meaning that many mother/calf pairs were sighted repeatedly.

Figure 2: (a) Sightings of right whale mother/calf pairs and associated (b) aerial survey search effort indicated by kilometers of trackline flown along the South Atlantic Bight between January 2000 and March 2005.
Sightings of right whale mothers and calves occurred within a narrow range of physical parameters (Figure 3). Mean depth of these sightings varied from 13.8m ± 0.6 in March to 15.5m ± 0.6 in January. Mean SST varied from 14.2°C ± 0.4 in February to 17.7°C ± 0.3 in December. Mean surface roughness varied from -24.8dB ± 0.4 in March to -23.3dB ± 0.5 in February. Higher backscatter values (e.g. -25) reflect a calmer surface, while lower values (e.g. -20) indicate rougher, choppier conditions. Thus, compared to available conditions throughout the study area, mother/calf pairs occurred in shallower, cooler waters during all months. In December and January most pairs were located in waters calmer than the rest of the study area, but the range of preferred values widened in February/March and whales occupied rougher surface waters, especially in March (Figure 3).

Table 1: Mean (± 1 SE) physical and topographic conditions associated with sightings of right whale mother/calf pairs and non-calf associated sightings during 2000 – 2005 winter aerial surveys.

<table>
<thead>
<tr>
<th>Variable</th>
<th>Mother/Calf Pairs</th>
<th>Non-Calf Associated Sightings</th>
<th>Z-values</th>
<th>P-values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Surface Roughness (dB)</td>
<td>-25.021 ± 0.024</td>
<td>-24.853 ± 0.029</td>
<td>-4.348</td>
<td>&lt; 0.001</td>
</tr>
<tr>
<td>Surface Temperature (°C)</td>
<td>16.423 ± 0.084</td>
<td>16.75 ± 0.086</td>
<td>2.6105</td>
<td>0.009</td>
</tr>
<tr>
<td>Distance from Shore (km)</td>
<td>16.636 ± 0.397</td>
<td>16.634 ± 0.451</td>
<td>-0.618</td>
<td>0.537</td>
</tr>
<tr>
<td>Depth (m)</td>
<td>15.47 ± 0.184</td>
<td>15.50 ± 0.173</td>
<td>0.170</td>
<td>0.865</td>
</tr>
<tr>
<td>Slope (°)</td>
<td>0.17 ± 0.006</td>
<td>0.168 ± 0.006</td>
<td>-0.068</td>
<td>0.946</td>
</tr>
<tr>
<td>Sightings (n)</td>
<td>633</td>
<td>589</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

During the 2000-2005 survey period 589 sightings were made in which calves were not present. The habitat used by these whales differed from that used by mothers and calves with respect to surface roughness and SST (Table 1). Mother/calf pairs
occurred in significantly calmer and colder water, but the difference in actual values of these parameters was small and may not have been ecologically relevant. There was no statistical difference in the mean depth, slope or distance from shore for these two groups.

Simple Mantel tests demonstrated a significant association between the distribution of mothers and calves and combined habitat variables in each month (Table 2). Individual variables demonstrated different influences on whale distribution depending upon the month, although all three parameters were repeatedly correlated with the distribution of mothers and calves. SST and surface roughness were correlated with sightings in December (Mantel r = 0.0825, p < 0.001, Mantel r = 0.256, p < 0.001) and January (Mantel r = 0.0194, p < 0.001, Mantel r = 0.0191, p < 0.001), while depth was correlated with sightings in February (Mantel r = 0.0184, p < 0.001). Depth (Mantel r = 0.0110, p = 0.026) and SST (Mantel r = 0.0117, p = 0.025) were correlated with sightings in March. By far, the strongest signal occurred in December, when mothers and calves demonstrated a strong preference for calmer waters (Mantel r = 0.256, p < 0.001). In December, January and March no other spatially structured variable was correlated with the distribution of female right whales and their calves. It is notable that the distribution of whales in February was correlated with some unknown, spatially structured feature. Thus, the three variables I examined may not fully capture the effects of habitat features on the distribution of right whale mother/calf pairs in February.
Figure 3: Box-plots of habitat conditions associated with the search area and mother/calf sightings for each cumulative month. Plots illustrate median and 25-75% quartile values with 5 and 95 percentile outliers indicated by dots.
Figure 4: Predicted optimal calving habitat by month. Colored areas indicate optimal habitat selected for each month. Red areas indicate the strongest probability of habitat while blue indicates a lower probability.
Table 2: Mantel r-coefficients and p-values for tests between dissimilarity matrices, depth (m), SST (°C) and surface roughness (dB) with presence/absence of mother/calf pairs for each cumulative month. Environment: correlation of combined environment variables with mother/calf distribution; Depth: pure partial test showing correlation between depth and mother/calf distribution; SST: pure partial test showing correlation between SST and mother/calf distribution; Roughness: pure partial test showing correlation between surface roughness and mother/calf distribution; Space: pure partial test showing correlation between unknown spatially structure variables and mother/calf distribution.

<table>
<thead>
<tr>
<th>Mantel Test</th>
<th>December</th>
<th>January</th>
<th>February</th>
<th>March</th>
</tr>
</thead>
<tbody>
<tr>
<td>Environment</td>
<td>0.1167</td>
<td>0.0215</td>
<td>0.0179</td>
<td>0.0217</td>
</tr>
<tr>
<td></td>
<td>p &lt; 0.001</td>
<td>p &lt; 0.001</td>
<td>p = 0.002</td>
<td>p = 0.005</td>
</tr>
<tr>
<td>Depth</td>
<td>0.0499</td>
<td>0.0002</td>
<td>0.0184</td>
<td>0.0110</td>
</tr>
<tr>
<td></td>
<td>p = 1</td>
<td>p = 0.368</td>
<td>p &lt; 0.001</td>
<td>p = 0.026</td>
</tr>
<tr>
<td>SST</td>
<td>0.0825</td>
<td>0.0194</td>
<td>-0.0100</td>
<td>0.0117</td>
</tr>
<tr>
<td></td>
<td>p &lt; 0.001</td>
<td>p &lt; 0.001</td>
<td>p = 1</td>
<td>p = 0.025</td>
</tr>
<tr>
<td>Roughness</td>
<td>0.2560</td>
<td>0.0191</td>
<td>-0.0016</td>
<td>-0.0060</td>
</tr>
<tr>
<td></td>
<td>p &lt; 0.001</td>
<td>p &lt; 0.001</td>
<td>p = 0.848</td>
<td>p = 0.953</td>
</tr>
<tr>
<td>Space</td>
<td>-0.0368</td>
<td>-0.0066</td>
<td>0.0107</td>
<td>-0.0060</td>
</tr>
<tr>
<td></td>
<td>p = 1</td>
<td>p = 0.998</td>
<td>p = 0.002</td>
<td>p = 0.964</td>
</tr>
</tbody>
</table>

Models of Calving Habitat

Nearshore waters in mid-latitude areas offered the most favorable calving habitat (Figure 4) along the SAB. The models predicted that coastal areas within 40-50km of shore between Cape Lookout, NC and Daytona Beach, FL form the core calving habitat, although some sparse habitat was identified as far north as Virginia Beach, VA and as far south as Port St. Lucie, FL. The models exhibited the highest level of agreement between Daytona Beach, FL and Cape Fear, NC with most of this region selected as calving habitat by three or more of the models.
Based on ROC curves, the December model demonstrated the highest performance (AUC = 0.81) with January and March performing moderately well (AUC = 0.68 and 0.66, respectively) and February with the worst performance (AUC = 0.55). For perspective, an AUC value of 0.5 indicates that a model performed no better than a coin toss in distinguishing habitat from non-habitat. Despite the range of AUC values, all models had consistently high true positive rates (December = 0.82, January = 0.84, February = 0.80, March = 0.81) meaning the models correctly identified mother/calf pairs occurring within optimal habitat 80-84% of the time. In contrast, the false positive rate showed much greater variability (December = 0.29, January = 0.52, February = 0.64, March = 0.51).

Table 3: Model performance parameters derived from Receiver Operator Characteristic (ROC) curves for each of the 4 monthly models. AUC: Area Under the Curve; Sensitivity: true positive rate (whale sightings correctly predicted as occurring within optimal habitat); Specificity: false positive rate (positions where whales were absent but predicted as occurring within optimal habitat) Data tested included all sightings of mother/calf pairs between 2000-2005 seasons and a.) random (control) points distributed relative to total search effort or b.) control points distributed randomly across the spatial extent of the aerial survey search area.

<table>
<thead>
<tr>
<th></th>
<th>December</th>
<th>January</th>
<th>February</th>
<th>March</th>
</tr>
</thead>
<tbody>
<tr>
<td>AUC</td>
<td>0.81</td>
<td>0.68</td>
<td>0.55</td>
<td>0.66</td>
</tr>
<tr>
<td>Threshold</td>
<td>-7.4015</td>
<td>-8.0803</td>
<td>-8.1723</td>
<td>-7.2130</td>
</tr>
<tr>
<td>Sensitivity</td>
<td>0.82</td>
<td>0.84</td>
<td>0.80</td>
<td>0.81</td>
</tr>
<tr>
<td>Specificity</td>
<td>0.29</td>
<td>0.52</td>
<td>0.64</td>
<td>0.51</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>December</th>
<th>January</th>
<th>February</th>
<th>March</th>
</tr>
</thead>
<tbody>
<tr>
<td>AUC</td>
<td>0.80</td>
<td>0.67</td>
<td>0.69</td>
<td>0.74</td>
</tr>
<tr>
<td>Sensitivity</td>
<td>0.81</td>
<td>0.85</td>
<td>0.84</td>
<td>0.80</td>
</tr>
<tr>
<td>Specificity</td>
<td>0.29</td>
<td>0.52</td>
<td>0.46</td>
<td>0.37</td>
</tr>
</tbody>
</table>

As discussed earlier, I expected an elevated false positive rate (errors of commission) due to the design and extent of aerial surveys. Based on the results of the
model assessments, I calculated that 49.6% of the spatial extent surveyed fell within the
collective predicted habitat and 66.0% of total effort (km of trackline flown) fell within
the same area. This indicates that the optimal habitat area was heavily oversampled
(consistent with the intent of this monitoring effort). Results from the comparison ROC
curves (Table 3), calculated using random absence points, rather than distributing these
points relative to the distribution of survey effort, demonstrated lower false positive rates
and correspondingly higher AUC values for February (AUC = 0.69, Specificity = 0.46)
and March (AUC = 0.74, Specificity = 0.37). There were only minor differences in the
AUC values for these two sampling approaches in December and January.

The different sampling structure did not result in fundamentally different
threshold values for any of the models. There was no change in threshold values in
December or January and the differences were minimal (> 0.02) for March and February.
So, despite oversampling within the area of optimal habitat, the models were able to
robustly distinguish between optimal and sub-optimal habitat.

Model evaluation using sightings data from earlier years (1996-1999)
demonstrated that the models correctly predicted calving habitat outside the temporal
range of data used for model creation. Most sightings (0.80, n=15) occurred within the
predicted habitat for the December model, 0.77 (n=74) for January, 0.73 (n=48) for
February and 0.78 (n=9) for March. Total model accuracy was lower in each month
(December = 0.67, January = 0.60, February = 0.66 and March = 0.61). The February
model was also evaluated with the surveys conducted in the northern SAB by the
University of North Carolina at Wilmington (UNCW); a lack of survey effort prevented
evaluation of the other monthly models. Sightings made by the UNCW team occurred in predicted habitat at a rate of 0.80 (n=10) with a total model accuracy of 0.80.

A combined habitat model summarizing all four monthly components was used to investigate the sensitivity of the models as a whole. This combined model is the best representation of calving habitat both in time and space (Figure 5) and indicates that core calving habitat extends from Daytona Beach, FL to North Carolina, extending well to the north of the current Southeast Critical Habitat zone. Sightings of right whale mothers and calves occurred in predicted habitat at the highest rates in areas with the most temporally consistent habitat (Table 4). My measure of temporal continuity is the number of models which identify any given area as habitat. Overall, 86.8% of the 2000-2005 mother/calf sightings, 86.8% of the 1999-1996 mother/calf sightings, 90% of the UNCW mother/calf sightings and 88.0% of non-calf sightings occurred within habitat areas identified by one or more models.

Table 4: Rate of whale sightings occurring within the combined predicted habitat, delineated by month.

<table>
<thead>
<tr>
<th></th>
<th>Number of models (months) that identified an area as habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Not predicted</td>
</tr>
<tr>
<td>Mother/calf sightings (2000-2005) n=647</td>
<td>0.127</td>
</tr>
<tr>
<td>Mother/calf sightings (1996-1999) n=146</td>
<td>0.15</td>
</tr>
<tr>
<td>Mother/calf sightings (UNCW data) n=10</td>
<td>0.10</td>
</tr>
<tr>
<td>Non-calf sightings (2000-2005) n=609</td>
<td>0.118</td>
</tr>
</tbody>
</table>

Application of the edited, combined habitat model to the remainder of the Atlantic revealed several areas with optimal calving habitat for right whales. In the Western North
Atlantic, the model identified no calving habitat south of 22º N or north of 36º N. The model predicted a broad region of suitable habitat along the entire northern coast of the Gulf of Mexico stretching from the Florida to Mexico (Figure 6a). Large portions of this habitat area were selected by all four models, indicating strong temporal continuity.

In the eastern North Atlantic, the model predicted calving habitat from Spain to Senegal between 44º N and 14º N. In the Bay of Biscay, the model identified three discrete habitat areas along the northern Spanish coast that include historic coastal whaling villages (Aguilar 1986), where right whales are known to have been hunted from the 1100s to the 1700s (Figure 6b). Interestingly, none of these habitat areas were selected by all four models, indicating that the region is suitable only during certain months. Other, sparser areas of habitat were identified along the west coast of Portugal and a more discrete area along the Gulf of Cadiz. Along West Africa a thin strip of calving habitat was predicted along most of the Moroccan and northern Western Saharan coast. There are no published records of whaling for right whales in the Gulf of Cadiz or off Morocco.

Off southern Western Sahara, the model predicted an area of calving habitat which overlaps with the known historic calving area off Cintra (16.25ºE, 23.00ºS) and Gorrei Bays (Figure 7) (Reeves & Mitchell 1986). Additional calving habitat was predicted along the Mauritanian and Senegalese coasts. This region was identified by A.H. Clark (1887) as a right whale hunting ground, but no additional sources could be found to confirm this assertion.
Figure 5: Combined habitat model for the Southeastern U.S. coast showing extent of the current federally designated critical habitat area for right whales.
In South Africa, the model predicted a narrow strip of broken calving habitat running the length of the coast from Tiger Bay in Angola (11.78°E, 16.67°S) to Algoa Bay (25.94°E, 33.85°S). Two areas, one along the southern Angolan and northern Namibian coasts (Figure 9) and the second along the southern South African coast (Figure 8) stand out as temporally robust calving habitat. Much of the predicted habitat along the South African coast overlaps with a well documented right whale calving ground (Best 2000). Most of the predicted area was selected in all four months, but the model did not predict the entire spatial extent of the calving ground. The predicted habitat to the north, along the Angolan and Namibian coasts overlaps with a region that has not been well surveyed and thus there is little information about right whales in this area. Historic accounts indicate that right whales were taken within the region at Tiger Bay in Angola and Rocky Point in Namibia (Lacroix 1968) and there are modern unconfirmed accounts of sightings in the region (Roux et al. 2001).

Along the South American coast the model predicted non-continuous calving habitat (Figure 10) from Blanca Bay in Argentina (62.00°W, 40.00°S) up to Sao Paulo, Brazil (46.25°W, 24.00°S). The most robust habitat areas, both spatially and temporally, fell between Samborombon Bay and Cape Santa Marta Grande, Brazil. This region of the coast has not been well surveyed and little information is available with which to compare my model findings. Notably, the model failed to predict a well documented calving area (Payne 1986, Rowntree et al. 2001) off Peninsula Valdes (63.83°W, 42.51°S), Argentina, but did capture known right whale habitat (Groch et al. 2005) between Cape Santa Marta Grade and Rio de Janeiro, Brazil.
Figure 6: Predicted right whale calving habitat for the Gulf of Mexico and the Bay of Biscay
Figure 7: Predicted right whale calving habitat along the northwest African coast.
Figure 8: Predicted right whale calving habitat along the South African coast.

- **Zone with the highest proportion of mother/calf pairs (Best, 2000)**
- **Full extent of regularly surveyed winter calving grounds (Best, 2000)**

Combined Predicted Habitat:
- Blue = area selected by 1 model
- Yellow = area selected by 3 models
- Green = area selected by 2 models
- Red = area selected by all models

SOUTH AFRICA

- Algoa Bay
- Plettenberg Bay
- Cape Agulhas
- De Hoop and St. Sebastian Bay
- Cape Columbine
- Western Cape
- Atlantic Ocean
- Indian Ocean

Full extent of regularly surveyed winter calving grounds (Best, 2000)
Figure 9: Predicted right whale calving habitat along the southwest Africa coast.
Limited surveys show right whales along the coast.

Center of historic shore based whaling (Ellis, 1969)

Well documented right whale calving ground

Combined Predicted Habitat

- Blue = area selected by 1 model
- Yellow = area selected by 3 models
- Green = area selected by 2 models
- Red = area selected by all models

Figure 10: Predicted right whale calving habitat along the east coast of South America.
Discussion

The distribution of female right whales and their calves along the South Atlantic Bight is correlated with depth, SST and surface roughness, although the importance of each variable differs from month to month. Predictive models of the whales’ habitat preferences accurately captured the distribution of a large proportion (> 85%) of right whale sightings in the SAB. The accuracy of the predictive models supports the hypothesis that adult female whales seek out these conditions to give birth and rear their calves. This finding is further supported by the overlap of modeled habitat with historic calving grounds and some (but not all) modern calving areas in other parts of the Atlantic, suggesting that this suite of habitat characteristics is broadly important for right whales.

Elwen and Best (2004a, 2004b) conducted an extensive investigation of right whale calving habitat along the southern South African coast and discovered that whales in this area preferred shallow, sheltered habitats that offered protection from wind and swell. No obvious reproductive advantage was associated with these habitat characteristics, although the data were pooled into sampling bins that may have masked important variation (Elwen & Best 2004c). Unfortunately, their analysis failed to consider water temperature as a habitat variable influencing distribution. Elwen and Best (2004a, 2004b) also found right whales on calving grounds preferred soft bottom habitats with gentle slopes. Substrate and slope were not considered in the present analysis. Right whales occupy such shallow areas that by default they occur in areas with a gentle slope. In the SAB, slope did not vary enough to make it a meaningful parameter in the models.
Substrate was not considered because of a lack of suitable data for the broader Atlantic Ocean and because available substrate data for the SAB showed little variation.

**South Atlantic Bight Habitat**

The combined model predicts an area of core calving habitat along the SAB that is much more extensive than recognized by current management measures. As expected, the predicted calving habitat falls close to shore with no area of predicted habitat further than 60km offshore. Most notably, the predicted habitat extends much farther to the north, to North Carolina. The current Southeast Critical Habitat zone extends only to Sea Island, Georgia, far to the south of the northern limit of the predicted habitat. This finding may have important implications for the future conservation of right whales in this region.

The ontogeny of calf behavior throughout the season is reflected in the habitat associations and model performance across months. In December, most (if not all) calves are in their first weeks of life. By March, the calf population is likely more mixed, with both neonates and older calves present. The particularly strong performance of the December model is consistent with the homogeneity of newborn calves early in the season. Additionally, the trend toward mother/calf pairs occupying the calmest waters in December and rougher water in March is presumably related to the higher number of more mature calves in March.

Of the few sightings “missed” by the model (meaning they were incorrectly classified as occurring outside optimal calving habitat), most occurred in close proximity
to the coast just to the north of Cape Canaveral, FL. The failure of the models to identify this small sliver of habitat is due to the resolution constraints of the analysis. High resolution Coastwatch AVHRR data indicates the presence of a narrow tongue of cold water (< 20°C) along this stretch of coast between January and March. I was unable to detect this small area of cold water because of the resolution (4.6km) of the SST data.

Scientists have been aware for some time that mother/calf pairs are using habitat outside the core aerial survey zone (Cape Canaveral, FL to Savannah, GA) in the SAB. Between 1999 and 2007, eight calves were sighted on the Gulf of Maine foraging grounds but were not detected on winter surveys of the calving ground or the Mid-Atlantic corridor (Melissa Patrician, WHOI, personal communication, 10/18/07). In 2007, an additional calf was sighted in the Mid-Atlantic that had not been sighted on the calving ground. These individuals make up a small percentage (5.6%) of the 162 calves born during this period, but these observations demonstrate that some parturition occurs outside the EWS survey area. The combined habitat model predicts that it would be feasible for a mother/calf pair to spend the entire calving season between Savannah, GA and Hatteras, NC and remain within suitable calving habitat.

Historic records provide some clues to the distribution of right whales along the SAB, although the population was so depleted by intensive whaling in northern waters that by 1730 few commercial whaling operations targeted right whales (Reeves et al. 2004). Right whales were taken in small numbers during the winter from North Carolina to Florida. A small, shore-based fishery took place during the 1700s and 1800s between Cape Hatteras, NC and Bear Inlet, NC with most effort occurring at Cape Lookout (Clark
1887, Earll 1887b, Reeves & Mitchell 1988, Simpson & Simpson 1990). This is particularly interesting because the topography at Cape Fear, Cape Lookout and Cape Hatteras result in localized “bumps” of predicted habitat that have a higher temporal consistency than the adjacent bays. Additionally, the predicted calving habitat is very close to shore north of Long Bay. It is curious to note that, despite the well documented calving habitat along the coast of Florida, there are no records of a shore-based fishery, except for a limited pre-colonial hunt, is in this region (Reeves & Mitchell 1988).

Records from the late 1800s show that a limited number of pelagic whalers visited northern Florida, Georgia and South Carolina waters during the winter months to hunt right whales (Clark 1887, Reeves & Mitchell 1986). One record from 1878 indicates that the whaling off Georgia and South Carolina was “more plenty” than in the past (Earll 1887a). Another account explicitly notes that the whaling ground could be found “on a bar about 4 miles from shore” between Brunswick, GA and Port Royal, SC (Clark 1887). Remarkably, predicted habitat between Brunswick and Port Royal begins, on average, 3.9 miles from shore.

**Water Temperature and Thermal Limitations**

Shallow areas occur over the entire continental shelf along the SAB, but during winter, the only areas offering the calm waters preferred by mother/calf pairs occur south of Virginia Beach, VA. This requirement for calm water appears to be the factor limiting the northern extent of the calving ground. Predicted calving habitat occurs in the coldest SST available within these calm waters.
Keller et al. (2006) found that whale sightings from earlier surveys (1991-1998) on the calving ground were associated with cool SST (mean = 14.3°C) and suggested that the distribution of right whales may be limited by warm water. Females with calves remain longer at calving grounds than other individuals (Jones & Swartz 1984, Rowntree et al. 2001) and thus must be able to tolerate these habitat conditions for an extended period of time. Kenney (2007) found that of 5000 sightings from the North Atlantic Right Whale Consortium for which concurrent surface temperature data were available none occurred in water greater than 21.8°C.

Right whales possess thick blubber and lack a dorsal fin making them better adapted for cold, icy environments than the balmy waters of Florida. Angell (2006) found North Atlantic right whales had a mean blubber thickness of 12.2cm (range 8 - 22cm) and Southern right whales had a mean thickness of 16.1cm (range 5 - 26cm). The blubber of near pregnant females was thicker than that of females in late lactation or nulliparious females (Angell 2006). The thick blubber of parturient females may pose a thermal constraint. Calves are unlikely to face such constraints; blubber from newborn calves in South Africa averaged 5cm in thickness (Reeb et al. 2007). The extreme thickness of right whale blubber, designed to retain heat and store energy, may impede the ability of these animals to inhabit warm waters. Female humpback whales, with blubber thicknesses of 8-11cm (Mason Weinrich, personal communication, 3/17/08) also calve in shallow and calm waters but farther to the south, in the Caribbean (Whitehead & Moore 1982) where winter SST values exceed 24°C.
Other Factors Influencing Right Whale Distribution

One important consideration not included in these models is predation risk. Killer whales (*Orcinus orca*) are known to prey on large whales, with a particular focus on young individuals (Scammon 1874, Jefferson et al. 1991, Pitman et al. 2001, Ford et al. 2005, Melnikov & Zagrebin 2005). Corkeron and Conner (1999) suggested that predation pressure from killer whales is the impetus for the migration of baleen whales to low latitude waters, where killer whales are less common. Clapham (2001) argued against this hypothesis, suggesting that whale migration was driven by energy conservation in warmer waters and noting that calves were indeed preyed on by killer whales on low latitude calving grounds. Mehta (2007) supported Clapham, by pointing out that most killer whale predation on whales focuses on calves either at calving grounds or during the northward migration, based on patterns of scar acquisition by humpback whales.

Killer whale distribution in the Atlantic can best be described as cosmopolitan and poorly understood. Both historic and recent sightings have occurred in right whale calving habitat, including the SAB, at Peninsula Valdes and historically (at least) at Cintra Bay (Katona et al. 1988, Mitchell & Reeves 1988, Reeves & Mitchell. 1988). Killer whales have been observed harassing or attacking right whales (Omura 1958, Cummings et al. 1971, Cummings et al. 1972, Jefferson et al. 1991, Reeves et al. 2006) in both the Pacific and the Atlantic Oceans.

No killer whales were observed during the aerial surveys of the SAB calving ground, but 9% of North Atlantic right whales (for which appropriate photographs were available) bear scars from killer whale interactions (Kraus 1990). Evaluating predation
risk, either real or anticipated, is extremely difficult given the rarity of right whales and
the transient nature of mammal-eating killer whales. Also, the experience of a single
failed attack or aggressive posturing may be enough to influence the distribution or
behavior of a large whale for years afterward, regardless of actual risk (Wirsing et al.
2008).

It is feasible that the shallow nature of calving grounds offer right whale calves
some protection from predators. Several accounts of attacks indicate that whales will seek
shallow water as a means of escape from killer whale attacks. Off Peninsula Valdes, two
right whales were observed moving into “very shallow water” following a killer whale
attack and subsequent vigorous defense by the whales (Cummings et al. 1971). Ford et al.
(2005) described killer whale attacks on minke whales in which the killer whales grasped
a whale’s pectoral fin and dragged it into deeper water, and another instance in which a
minke whale beached itself to escape. Andrews (1914) indicates that gray whales along
the California coast would “head for shore and slide in as close as possible to the beach
where sometimes the Killers will not follow them”. Shallow water habitats may offer
some protection by eliminating the possibility of attack from below or from shoreward.
Additionally, shallow water limits the maneuverability of the predator. Retreat into
shallow water and subsequent defense of a calf would be consistent with the fight
response Ford and Reeves (2007) attribute to right whales. It may also explain why
mother/calf pairs remain close to shore, in shallow water, during their migration back to
foraging grounds.
Site fidelity is also likely to play an important role in the distribution of parturient whales along the SAB. For example, Best (2000) found that more than 90% of calves born on the South African coast return to this area to bear their first calf. Most (72%) experienced mothers in South Africa were sighted within 90km of the area where they were sighted with their first calf. Rowntree (2001) identified a similar pattern off Argentina, where more than half of the experienced mothers were re-sighted on the calving grounds at Peninsula Valdes in subsequent years. As part of the EWS surveys, photographs of individual whales are taken for identification and could be used to assess site fidelity in the SAB in the future.

**Predicted Calving Habitat in the North Atlantic**

The model identified an extensive band of calving habitat stretching across the northern Gulf of Mexico but over the past century only a handful of right whales, including a single calf, have been documented in the Gulf (Moore & Clark 1963, Schmidly et al. 1972, Mead 1986). In addition, only one unsubstantiated historical reference is made to right whales in the Gulf (Clark 1887). The failure of right whales to use an apparently suitable habitat may be due to the thermal barrier a whale would need to pass through in order to reach the Gulf of Mexico. The model did not identify any optimal calving habitat between Cape Canaveral, FL on the Atlantic coast and Naples, FL on the Gulf coast. If a whale were to travel to the Gulf of Mexico using the coldest route possible it would still have to cross the Gulf Stream traveling through waters with an average SST between 23°C and 25°C. These temperatures, as discussed earlier, may be
too warm to be tolerated by most right whales. Thus, while the Gulf of Mexico may physically offer calving habitat it may not be functionally accessible to most right whales.

In the Bay of Biscay, the model identified several patches of habitat proximate to historic whaling villages along the Spanish coast (Aguilar 1986). The predicted habitat in this region is limited by the availability of shallow water and the colder surface temperatures in winter in comparison to the SAB calving ground. Average SST values for the southern Bay of Biscay are 13°C-15°C in December, 12°C -14°C in January, 12°C - 13°C in February and 12°C -13°C in March. This range of temperatures lies just at or below the preferences of right whales in the SAB. However, if the temperature preferences in the SAB are guided at least partially by the availability of cold water in calm areas, as suggested above, it is reasonable to assume that the models may be too conservative in assessing the range of colder temperatures that right whales use for calving. However, the extent of the calving ground is still restricted by the availability of shallow water.

In the past 50 years, only six right whale sightings have been documented in the eastern North Atlantic during the winter months. These sightings occurred off Madeira, the Canary Islands, Portugal and one, more than 100km off the northeast coast of Spain (International Whaling Commission 2000). No sightings occurred in areas known as historic right whaling grounds although two right whales were taken during the winter off Madeira in 1959 and 1967 (Brown 1986).

Along southern Spain, Morocco and northern Western Sahara a thin strip of non-continuous habitat was identified in a region with no historical records of right whales
(Aguilar & Borrell 2007). To the south, a more robust habitat area was identified in the historic calving grounds at Cintra and Gorrei Bays. This habitat area is much broader than the extent of the whaling grounds described by Reeves and Mitchell (1986), although this may be due to limited historical documentation of the whaling ground. The lack of historical corroboration for the “Morocco” strip may indicate a limitation of the model or it may highlight a previously unrecognized right whale habitat. Another possibility is that there is a more preferable habitat nearby. Unused or less preferred habitat may occur due to an abundance of better (temporally consistent and spatially broad and continuous) habitat in a region.

**Predicted Calving Habitat in the South Atlantic**

The extent of the predicted habitat along the southwest African coast was limited by depth along the entire length of the coast. There are few areas in this region with broad stretches of shallow water and thus calving habitat occurs along the coast in a narrow strip (width < 3km). The narrowness of the habitat is confirmed by the distribution of whales along the coast. Between 1971 and 1987, all mother/calf pairs sighted along the South African coast were found within 0.93 km of shore (Best 1990). The habitat is also bounded by high average SST values just north of the Angolan boarder and to the east of Algoa Bay. In South Africa, the general western movement of whales over the course of the season and the increasing density of whales in western bays (Best 2000) may be the result of increasing surface temperatures that permeate nearshore areas from east to west during the season. Historic accounts of whaling off Delagoa Bay, Mozambique
(Townsend 1935, Richards & Du Pasquier 1989) and modern reports of right whales off Madagascar (Rosenbaum et al. 2001) are surprising given the high temperatures (>21.5°C) in these regions throughout the winter. The model predicted no calving habitat east of Algoa Bay, due to high surface temperatures. The model identified calving habitat in four of the five South African bays where historic shore-based whaling operations took place, but did not identify any habitat near Durban where several modern (1900s) whaling stations operated (Best & Ross 1986). Colder temperatures along the eastern South African and Namibian coasts (< 14°C) account for the patchiness and briefer temporal extent (1-2 months) of the predicted habitat in this region, although again, temperatures colder than those chosen by North Atlantic right whales may be acceptable to Southern right whales.

Average surface roughness values indicate that most of the coast is moderately calm (i.e. > 23dB) during winter but the surface becomes notably rougher just to the east of Algoa Bay and between Cape Columbine and Cape Agulhas. Cape Agulhas is regarded as a demarcation line between calving habitat to the east in calm De Hoop and St. Sebastian Bays and a breeding area to the west in rougher Walker Bay (Elwen & Best 2004b). Offshore swell is common along the coast and I noted that in several bays predicted habitat occurred mostly on the western side. This concurs with Elwen and Best’s (2004b) findings that mother/calf pairs cluster in portions of the bays with the greatest protection from swell and wind.

Optimal calving habitat was identified along the entire coast of Namibia but south of Rocky Point calving habitat becomes less continuous and optimal conditions
only occur in September due to the cold water temperatures (< 13°C) along the coast. Of the 18 confirmed and 19 probable right whale sightings along the Namibian coast between 1971-1999 all occurred within 3km of shore (Roux et al. 2001), which is consistent with the thin strip of habitat identified along the coast. The predicted habitat co-occurs along areas known for historic right whale takes but the predicted habitat is more pronounced temporally between Tiger Bay and Rocky Point. It is possible that this northern area was and/or is a primary calving ground and the southern part of the coast a migratory route. Lacroix (1968) notes that between June and September whalers located right whales in bays all along the Namibian coast up to Tiger Bay while Richards and Du Pasquier (1989) highlight Walvis Bay as a popular spot for right whales. As discussed earlier, the colder waters along the southern Namibian coast may fall within the preferences of the Southern right whale. In general, the distribution of right whales along this coast both historically and today is not well documented and prevents a full comparison with our model.

The accuracy of the model along the African coast was somewhat compromised by the width of the calving habitat relative to the resolution of our data. Satellite-based measurements often falter at the coastal interface and this can be especially pronounced in areas with steep topography such as the high cliffs along the South African coast. As a result, the model may have failed to fully identify narrow patches of suitable habitat directly against the shoreline. However, these gaps do not diminish the overall trend of clear overlap between predicted habitat and known right whale calving areas.
Predicted calving habitat along the coasts of Argentina, Uruguay and Brazil was strongly influenced by water temperature. A dramatic temperature gradient exists between northern Argentina and Southern Brazil in winter, with surface waters increasing from approximately 10°C to over 20°C within this zone. The entire predicted habitat fell within this gradient. The most robust habitat areas occurred off Uruguay and southern Brazil and fell into 2 distinct types. One part, mostly along Uruguay, was temporally limited (selected over 1-2 months) but spatially broad, with one section 150km wide. The other area, along the Brazilian states of Rio Grande Do Sul and Santa Catarina, was much narrower but more temporarily robust.

Both historic and modern day records of right whales from this area are incomplete, challenging our ability to draw comparisons with our model predictions. Townsend (1935) identified an area from northern Argentina to southern Brazil as a whaling ground, although these offshore catches are curious given the right whale’s penchant for shallow habitat on calving grounds. Castello and Pinedo (1979) indicate that, historically, right whales occurred primarily between 36ºS and 48ºS although they give no source for this broad statement. Right whales were known to calve in the bays of Santa Catarina and Rio Grande do Sul and seven shore-based whaling stations operated at various times along the Santa Catarina coast between 1740 and 1864 (Ellis 1969). Illegal takes occurred along Santa Catarina up until 1973 and included 26 right whales taken between 1956 and 1959 (Castello & Pinedo 1979, de Oliveira Santos et al. 2001). A modern day assessment of right whales along Rio Grande do Sul recorded 23 stranding and 12 sightings of mother/calf pairs between 1977 and 1986 (Greig et al. 2001). Santa
Caterina to the north is widely considered the primary calving area in Brazilian waters and recent survey effort has identified an increasing number of right whales in this region (Groch et al. 2005). The recent and historic presence of right whales along the Santa Catarina and Rio Grande do Sul coasts coincides with the more northern, temporally consistent strip of predicted habitat.

Notably the model failed to detect the well documented Peninsula Valdes calving area in Argentina. The main reason for this discrepancy appears to be water temperature. Average surface temperatures around the Peninsula are 10°C-12°C in July, 9.2°C -11°C in August, 9.2°C -11°C in September and 10°C -12°C in October. These temperatures fall below the temperature preferences for right whales in the northwest Atlantic and thus are underrepresented in the model. However, these lower temperatures may fall within the range preferred by Southern right whales. In all other respects (depth and surface roughness) the coast of the Peninsula offers the same habitat as the SAB habitat.
Chapter 2: Predictive Modeling of North Atlantic Right Whale (Eubalaena glacialis) Habitat Preferences in the Gulf of Maine
Introduction

The Gulf of Maine and eastern Scotian Shelf are the primary foraging areas for the endangered North Atlantic right whale (*Eubalaena glacialis*) (Gaskin 1991, Kenney et al. 2001). Right whales inhabit the Gulf year round and are known to forage in large aggregations, especially during spring. Foraging occurs in both nearshore and offshore waters. Numerous studies have confirmed a significant association between right whales and high zooplankton densities (Murison & Gaskin 1989, Mayo & Marx 1990, Beardsley et al. 1996, Baumgartner et al. 2003a). In particular, right whales target the copepod, *Calanus finmarchicus*, which is ubiquitous throughout the Gulf and forms the backbone of the food web (Watkins & Schevill 1976, Murison & Gaskin 1989, Mayo & Marx 1990, Kenney & Wishner 1995, Wishner et al. 1995, Baumgartner et al. 2003a, Baumgartner et al. 2003b, Baumgartner & Mate 2003).

In late winter and early spring right whales occur primarily in and around Cape Cod Bay. While in the Bay, right whales are known to feed on *C. finmarchicus* but have also been observed feeding on *Pseudocalanus sp.*, Euphausids and *Centropages sp.* (Watkins & Schevill 1976, Mayo & Marx 1990). This is one of the only areas where right whales are observed foraging on prey other than *C. finmarchicus*. During spring, right whales move out of the Bay and into the Great South Channel where they congregate in high densities for the remainder of the spring and early summer. In 1992, right whales were notable absent from the Great South Channel but this was considered an anomalous event (Kenney 2001).
In spring and early summer, right whales are known to feed both at the surface and at depth, in response to the vertical movements of *C. finmarchicus* patches (Mayo & Marx 1990, Wishner et al. 1995). As the summer progresses, however, *C. finmarchicus* attains its final copepodite developmental stage (C5) and settles into deeper waters to enter diapause (Baumgartner et al. 2007). As this transition occurs, right whales move north to Grand Manan and Roseway Basins to feed more exclusively on these dense aggregations of C5 copepods in deeper waters, often bypassing less lipid rich copepodite stages in shallower water (Baumgartner et al. 2003b).

Right whales are continuous feeders, swimming open-mouthed, allowing prey to stream into their long, fine baleen (Mayo & Marx 1990). Unlike humpback whales (*Megaptera novaeangliae*), which also forage in the Gulf of Maine, right whales do not aggregate prey via foraging behaviors (e.g. bubble netting). Instead, they rely entirely on oceanographic processes to aggregate their prey. Given the tight association between right whales and *C. finmarchicus*, the habitat preferred by right whales is likely analogous to the physical conditions which aggregate *C. finmarchicus*. The bio-physical parameters that contribute to aggregations of *C. finmarchicus* are only partially understood and vary by area, season and copepodite development stage.

Some basic habitat parameters may offer clues to the processes which aggregate *C. finmarchicus*. *C. finmarchicus* is known to aggregate or become entrained in deeper basins during the late summer and fall (Sameoto & Herman 1990) and in the Great South Channel the depth gradient contributes to a strong thermal front known to aggregate *C. finmarchicus*. Sedimentation can serve as an indicator of energy in the benthic
environment. High energy environments, with strong currents are characterized by larger and more heterogeneous substrates while low energy environments are characterized by fine sediments (Pinet 1992). Deep areas with flat slopes and fine sediments reflect low energy environments (such as a deep basin) where *C. finmarchicus* in diapause can settle or become entrained.

![Map of the Gulf of Maine highlighting relevant topological features.](image-url)
Satellite derived SST and SST fronts are directly linked with surface aggregations of *C. finmarchicus* (Brown & Winn 1989). Kenney et al (2001) suggested that right whales may use temperature cues as a means of locating prey. During spring in the Great South Channel, a persistent tidal mixing front separates well mixed, colder water to the south from thermally stratified warm water to the north (Chen et al. 1995). This front is used by right whales for foraging and is associated with extremely high densities of *C. finmarchicus*. In contrast, Baumgartner et al (2003b) found no association between right whales and thermal fronts or SST in the Grand Manan Basin but this might be expected of whales foraging at depth.

In this chapter, I report on an assessment of topological and physical conditions associated with right whales in the Gulf of Maine and describe the development of a predictive model of foraging habitat. Habitat variables were chosen based on their suspected ecological linkage to *C. finmarchicus* aggregation or entrainment. Variable selection was limited to readily available data. A principal goal of this project was to investigate our ability to identify optimal right whale foraging habitat without the use of *in situ* measurements. I evaluated the significance of water depth, topological gradients, sediment type, sea surface temperature (SST) and sea surface frontal boundaries to the spatial variability of whales over a five year period (2002 – 2006). Assessments were made using Mantel tests and Generalized Additive Models. I hypothesized that right whale distribution would be closely associated with SST and SST fronts in winter and spring when whales forage at the surface and in mid-depths while topography and benthic
characteristics would play a greater role in distribution during summer and fall when near bottom foraging is more common.

Methods

Study Area

The Gulf of Maine (Figure 11) is a large embayment bordered on its eastern margin by submarine banks which partly enclose the Gulf from the greater Atlantic. The largest tides in the world occur in the Gulf and the strong currents produced by these tides keep the water column well mixed in most areas, enhancing productivity. Within in Gulf, topography is varied with shallow (< 40m) banks and protrusions such as Jeffrey’s Ledge as well as deep basins (>200 meters) including Wilkinson, Jordan, Grand Manan, Roseway and Georges Basins. The strong currents and varied topography of the Gulf create a heterogeneous and highly complex habitat.

Whale Sighting Data from Aerial Surveys

As part of the broader Right Whale Sighting Advisory System, aerial surveys were conducted in the Gulf of Maine by the NOAA Northeast Fisheries Science Center (NEFSC) and the Provincetown Center for Coastal Studies (PCCS) between 2002 and 2006. The NEFSC surveys were flown across the Gulf north of 40.35°N between the U.S. coast and the Hague Line, which delineates U.S. and Canadian waters. PCCS flew surveys exclusively over nearshore waters in Cape Cod Bay and to the east of Cape Cod. The surveys were conducted from fixed wing aircraft following the same protocols. Each
aircraft traveled at a speed of approximately 100 knots and an altitude of 750 feet with
two observers and one data recorder aboard each plane.

NESFC surveys were conducted year round, dependent on weather. The surveys fell into three categories: broad-scale flights, set trackline flights and management directed flights. For the broad-scale surveys, a stratified random design was employed (Cole et al. 2007). U.S. waters north of 40.35°N were divided up into 16 blocks, each containing 20 tracklines spaced 1.85km apart. Two to three blocks were surveyed during one flight with individual tracklines randomly selected from within each block. The NEFSC surveys were not specifically designed for habitat analysis per se, but search effort occurred in regions including those where no right whales were expected allowing for a broad biogeographic analysis.

In addition to these flights, NESFC surveys were also conducted, on occasion, along pre-determined sets of tracklines over the Great South Channel and the mid-Gulf region. These flights, while not conducted using a randomized design, were flown without prior knowledge of whale presence and followed a set trackline. These surveys were included in the analysis. The NEFSC also flew a limited number of “management directed” flights. These surveys were launched primarily with prior knowledge of a right whale’s location and were used as a validation dataset, not in model development.

PCCS surveys took place mostly between January and mid-May and flew in areas where right whales were known or expected to be present. These surveys followed a set of predetermined tracklines (2.75 km apart) over Cape Cod Bay and along the eastern shore of the Cape. On occasion, flights were conducted outside the standard tracklines,
often in response to a lack of sightings in Cape Cod Bay. These flights did not follow the standard tracklines and may have included prior knowledge that right whales were in an alternate location, so they were used only as validation data.

The aerial surveys were designed to warn mariners of right whales in the vicinity and to collect photographs of individual animals, so they did not follow formal line transect protocols. At each right whale sighting the plane departed from the trackline to circle individual(s) and obtain an accurate location and count, along with photographs for individual identification. Due to safety concerns the NEFSC flights did not break track for right whales while in Cape Cod Bay when PCCS was conducting surveys.

Positions were recorded using a GPS (Global Positioning System) at frequent intervals along each trackline to document effort. While underway, Beaufort sea state, weather, visibility and the location and details of each whale sighting were recorded. The NESFC surveys explicitly documented the excessive “circling” that occurred when right whales were sighted as off effort and these periods were not included in this analysis. To ensure that the PCCS data conformed to this standard, a filter was applied to the PCCS survey effort data. All instances where the plane left the trackline and made more than 2 circles within a 2km range were removed. Removing the excessive circling prevented bias in the calculation of survey effort since no actual sightings effort was ongoing while individual whales were photographed.

Approximately 15 % of survey effort was conducted in Beaufort sea states > 3. Vessel surveys focusing on smaller cetaceans have documented significant differences in sightings rates relative to Beaufort sea state (Palka 1995). I found no significant
difference in sighting rates for right whales (p=0.707) in Beaufort sea states 0 to 5. As a result, all surveys conducted during Beaufort sea state conditions < 6 were included in the analysis. I removed the very few portions (< 0.1%) of the survey data with a Beaufort sea state > 6.

In addition to these recent surveys, right whale sightings from the Cetacean and Turtle Assessment Program (1979-1982) were used to assess the ability of the models to predict right whale habitat use over time (CETAP 1982). Both ship based and aerial surveys were conducted year round along the eastern seaboard. These data provide an excellent resource for model validation because the surveys were not explicitly designed to target right whales. In keeping with the other data only surveys conducted in Beaufort sea states < 6 were included in the analysis.

Environmental Data

Topological data were custom processed to meet the needs of the analysis. I derived bathymetric data (depth and depth gradient) from a combination of the National Geophysical Data Center coastal relief data and U.S. Geological Survey Gulf of Maine bathymetry (Divins & Metzger, Roworth & Signell 1998). This is the highest resolution data available for the Gulf and allowed for the extraction of accurate depth gradients. I used the Global Self-Consistent, Hierarchical, High-resolution Shoreline (GSHHS) data for shoreline delineation (Wessel & Smith 1996). The accuracy of this shoreline dataset was especially important because of the high number of whale sightings close to shore.
Sediment type was derived from a collection of U.S Geological Survey sediment samples from the Gulf of Maine (Poppe et al. 2003, Poppe et al. 2005). These observations were divided into 10 sediment types (clay, clay mix, silt, silt mix, sand mix, sand, gravel sediment, gravel, cobble/boulders and bedrock), with each assigned a numerical value from 1-10 in order of increasing dominant grain size. The values do not directly correspond to actual grain size but are used as an index. The dominant sediment type for every 100m was identified and gaps were substituted with values from the nearest cells with data. An interpolation was not performed, but rather areas without data were presumed to be best represented by adjacent areas with sampled data.

For ocean temperature, I used Advanced Very High Resolution Radiometer (AVHRR) Version 5 sea surface temperature (SST) imagery obtained from the National Oceanic and Atmospheric Administration’s National Oceanographic Data Center. This latest version of the AVHRR data has an accuracy of 0.3°C and a resolution of 4.6 km. To ensure that clouds were eliminated from the data, only pixels with an image quality level > 3 were included in the data processing (Kilpatrick et al. 2001). Data were averaged cumulatively over all years for each respective temporal analysis unit. In some months, due to extreme winter cloudiness, it was necessary to interpolate (via kriging) cell values to fill in missing data gaps although, in most coastal areas, data gaps were small and fell directly adjacent to quality data.

Surface thermal fronts were extracted from daily AVHRR data following Cayula and Cornillon (1995). For each grid cell I calculated the number of SST fronts which occurred in a given cell during the temporal analysis unit (month or season) and assessed
the number of days the grid cell was also cloud free (i.e available for assessment). I then derived an index of frontal activity equal to the number of days a SST front was present divided by the number of cloud free days for that cell. This correction was necessary to account for differences in cloudiness and prevent biased measurements.

**Analytical Methods**

**Temporal and Spatial Framework**

I chose to use temporal units for analysis based on a combination of data availability and seasonal differences in distribution. My units of temporal analysis included winter (January and February), March, April, May, June, summer (July, August and September) and fall (October, November and December). In summer, fall and winter a lack of sightings required that I amalgamate data by seasonal timeframe. Right whales frequently occur in discrete habitats over 2-4 month time periods so the use of a seasonal time frame for analysis is reasonable.

I used a 5km² effort sampling unit, due to resolution constraints of the satellite data. Any sampling unit with less than 5km of flight tracks in any given month was eliminated from the analysis due to insufficient search effort. No sightings were removed from analysis do to a lack of search effort. Individual sightings locations were used for all statistical analyses.
Assessment of Habitat Variables

Following Schick and Urban (2000), I performed Mantel tests in S-Plus (Insightful Corp.) to evaluate the association of whales with habitat conditions. Mantel tests are non-parametric, partial regression techniques based on dissimilarity matrices (Mantel 1967). The tests assess the degree of correlation between sightings and habitat variables, while taking into account the autocorrelation of these variables and inter-correlation among other variables. This technique explicitly considers space as a predictor variable, evaluating whether spatially structured parameters that are not included in the analysis influence whale distribution. Mantel tests assume a linear relationship between predictor and response variables; this may be an unrealistic assumption for some species/environment interactions.

I performed separate tests for each temporal sampling unit. I used sightings of whales to represent whale presence and derived absences from an equal number of random positions distributed relative to survey effort. I performed simple Mantel tests, evaluating the relationship between the dependent variables and all environmental variables, as well as pure partial Mantel tests to investigate any correlations with each environmental variable separately. Significance testing was conducted via permutation procedures because the structure of the dissimilarity matrix is not independent.

Models of Foraging Habitat

Models of foraging habitat were derived from Generalized Additive Models (GAMs). Like Mantel tests, GAMs are a non-parametric partial regression technique but
in an additive model the predictor is specified by the sum of smoothing spline functions of some or all of the covariates (Hastie & Tibshirani 1987). GAMs allow for the estimation of non-linear relationships, which is especially useful for modeling ecological interactions (Austin 2002). This characteristic makes GAMs well suited for assessing cetacean relationships with the environment (Forney 1999, Sinclair et al. 2005).

I performed separate tests for each temporal sampling unit using a stepwise GAM and backward selection. Akaike’s Information Criterion (AIC) was employed to guide optimal variable selection. GAMs are prone to overfit data and produce inflated p-values (Guisan et al. 2002) thus only variables with a p-value < 0.01 were included in the final models. As with the Mantel tests, I used sightings of whales to represent whale presence and derived absences from an equal number of random positions distributed relative to survey effort.

Model parameters were derived for each variable from the GAM outputs. I identified the ranges of each significant variable which had a positive influence on whale presence but did not consider the strength of this influence in our final models. The outputs for all variables in a given model were then combined to produce a single assessment of predicted foraging habitat for each month or season.

Model Validation

I employed three sets of data to test the performance of the right whale foraging habitat model. Data included the right whale sightings used to build the model, sightings from the concurrent directed survey flights and older sightings from CETAP surveys
collected between 1979 and 1982. Both the directed survey fights and the CETAP data also included areas that were spatially distinct from the data used for model development. Right whale sightings and an equal number of random points distributed relative to survey effort were tested against the predicted habitat for each month or season. I calculated confusion matrices for each model and set of data. Overall model performance was assessed using the true skill statistic (TSS) (Figure 12). TSS ranges from 1 to -1 with increasing positive numbers indicating a high degree of model accuracy and discrimination. The statistic accounts for both model sensitivity and model specificity and is applicable to binomial models (Allouche et al. 2006). Furthermore, the TSS is not influenced by the size of the validation data set.

<table>
<thead>
<tr>
<th>Predicted Habitat</th>
<th>Recorded Present</th>
<th>Recorded Absent</th>
</tr>
</thead>
<tbody>
<tr>
<td>Predicted No Habitat</td>
<td>A: True Positive Fraction</td>
<td>B: False Positive Fraction</td>
</tr>
<tr>
<td></td>
<td>C: False Negative Fraction</td>
<td>D: True Negative Fraction</td>
</tr>
</tbody>
</table>

true skill statistic = \( \frac{A}{A+C} + \frac{D}{B=D} - 1 \)

Figure 12: Confusion matrix illustrating inputs for assessing model accuracy and equation for the true skill statistic (TSS). A: whales sighted and habitat predicted, B: whales not sighted and habitat predicted, C: whales sighted and habitat not predicted, D: whales not sighted and habitat not predicted
Results

Gulf of Maine Habitat

Between 2002 and 2006, 3647 right whale sightings were recorded by aerial survey teams in the Gulf of Maine (Figure 13). Given the small population of right whales, many of these observations were re-sightings of the same individuals. The whales followed consistent patterns of distribution between years with most sightings occurring in Cape Cod Bay during winter and early spring and in the Great South Channel in spring. These areas were also the focus of the most intensive survey effort. Even accounting for search effort, extremely high densities of whales were recorded including one group of sightings in July of 2005 which had 100 whales (almost one-third of the entire right whale population).

Simple Mantel tests demonstrated a significant association between the distribution of whales and combined habitat variables in each season/month except winter (Table 5). Individual variables demonstrated a variety of influences on whale distribution with no clear trend. In winter, slope and sediment were correlated with whale sightings (Mantel r = 0.007, p = 0.016, Mantel r = 0.048, p < 0.001). In March, slope was the only parameter correlated with whale presence (Mantel r = 0.002, p < 0.012). In April and May, sediment was identically correlated with whales (Mantel r = 0.012, p < 0.001). SST was associated with whales in April and SST gradients associated with whales in May. During June, only depth was correlated with whale presence (Mantel r = 0.012, p < 0.001). Sediment was again associated with whales in summer and fall (Mantel r = 0.042,
p = 0.002, Mantel r = 0.230, p < 0.001) and in fall the correlation was the strongest of any assessed. In summer, SST fronts were also associated with whales (Mantel r = 0.017, p = 0.038) and in fall SST was correlated with whale presence (Mantel r = 0.026, p = 0.005). Notably, the distribution of whales in all months and seasons was correlated with some unknown, spatially structured feature. Thus, the parameters examined here may not fully capture the effects of habitat features on the spatial distribution of right whales.

Table 5: Mantel r-coefficients and p-values for tests between dissimilarity matrices, depth (m), Slope, Sediment size, SST (°C) and SST with presence/absence of whales for each cumulative time period. Environment: correlation of combined environment variables with whale distribution; Depth: pure partial test showing correlation between depth and whale distribution; Slope: pure partial test showing correlation between bottom slope and whale distribution; Sediment: pure partial test showing correlation between sediment grain size and whale distribution; SST: pure partial test showing correlation between SST and whale distribution; SST Fronts: pure partial test showing correlation between frequency of SST fronts and whale distribution; Space: pure partial test showing correlation between unknown spatially structure variables and whale distribution.

<table>
<thead>
<tr>
<th>Mantel Test</th>
<th>March n = 226</th>
<th>April n = 402</th>
<th>May n = 380</th>
<th>June n = 377</th>
<th>Summer n = 69</th>
<th>Fall n = 66</th>
<th>Winter n = 113</th>
</tr>
</thead>
<tbody>
<tr>
<td>Environment</td>
<td>0.009</td>
<td>0.007</td>
<td>0.020</td>
<td>0.029</td>
<td>0.043</td>
<td>0.048</td>
<td>0.005</td>
</tr>
<tr>
<td></td>
<td>p &lt; 0.001</td>
<td>p &lt; 0.001</td>
<td>p &lt; 0.001</td>
<td>p &lt; 0.001</td>
<td>p &lt; 0.001</td>
<td>p &lt; 0.001</td>
<td>p = 0.099</td>
</tr>
<tr>
<td>Depth (m)</td>
<td>-0.004</td>
<td>-0.008</td>
<td>0.008</td>
<td>0.012</td>
<td>-0.038</td>
<td>-0.038</td>
<td>-0.018</td>
</tr>
<tr>
<td></td>
<td>p = 1</td>
<td>p = 1</td>
<td>p &lt; 0.001</td>
<td>p &lt; 0.001</td>
<td>p = 1</td>
<td>p = 1</td>
<td>p = 1</td>
</tr>
<tr>
<td>Slope</td>
<td>0.002</td>
<td>-0.005</td>
<td>-0.020</td>
<td>-0.019</td>
<td>0.010</td>
<td>0.010</td>
<td>0.007</td>
</tr>
<tr>
<td></td>
<td>p = 0.012</td>
<td>p = 1</td>
<td>p = 1</td>
<td>p = 1</td>
<td>p = 0.084</td>
<td>p = 0.016</td>
<td>p = 0.016</td>
</tr>
<tr>
<td>Sediment</td>
<td>0.004</td>
<td>0.012</td>
<td>0.012</td>
<td>-0.013</td>
<td>0.042</td>
<td>0.230</td>
<td>0.048</td>
</tr>
<tr>
<td></td>
<td>p = 0.073</td>
<td>p &lt; 0.001</td>
<td>p &lt; 0.001</td>
<td>p = 1</td>
<td>p = 0.002</td>
<td>p &lt; 0.001</td>
<td>p &lt; 0.001</td>
</tr>
<tr>
<td>SST</td>
<td>0.004</td>
<td>0.004</td>
<td>-0.057</td>
<td>-0.010</td>
<td>0.026</td>
<td>0.002</td>
<td>0.002</td>
</tr>
<tr>
<td></td>
<td>p = 0.056</td>
<td>p = 0.007</td>
<td>p = 1</td>
<td>p = 1</td>
<td>p = 0.005</td>
<td>p = 0.017</td>
<td>p = 0.177</td>
</tr>
<tr>
<td>SST Fronts</td>
<td>-0.003</td>
<td>-0.006</td>
<td>0.031</td>
<td>-0.009</td>
<td>0.017</td>
<td>-0.019</td>
<td>-0.002</td>
</tr>
<tr>
<td></td>
<td>p = 1</td>
<td>p = 1</td>
<td>p &lt; 0.001</td>
<td>p = 1</td>
<td>p = 0.038</td>
<td>p = 1</td>
<td>p = 0.957</td>
</tr>
<tr>
<td>Space</td>
<td>0.029</td>
<td>0.056</td>
<td>0.143</td>
<td>0.098</td>
<td>0.103</td>
<td>0.029</td>
<td>0.017</td>
</tr>
<tr>
<td></td>
<td>p &lt; 0.001</td>
<td>p &lt; 0.001</td>
<td>p &lt; 0.001</td>
<td>p &lt; 0.001</td>
<td>p &lt; 0.001</td>
<td>p &lt; 0.001</td>
<td>p &lt; 0.001</td>
</tr>
</tbody>
</table>
Figure 13: Right whale sightings in the Gulf of Maine by cumulative season or month (2002-2006). Larger dots indicate higher numbers of whales sighted. The 100m isobaths is depicted.
Habitat Models

Predicted right whale habitat varied greatly between months/seasons (Figure 14). The summer and fall models demonstrated the best fit with the greatest proportion of model deviance explained by the habitat parameters (\(r^2 = 0.56\) and \(r^2 = 0.43\)) (Table 6). In contrast, the models for March and April demonstrated poor fit with \(r^2\) values of only 0.11 and 0.10 respectively. The May and June models were moderately well fit and both had an \(r^2\) of 0.38.

Model accuracy was equally varied when compared with the sightings used to create the models. A high proportion of right whale sightings occurred within predicted habitat during summer (0.95, n=69) and fall (0.92, n=66). The models for May and March also correctly predicted sightings as occurring in modeled habitat most of the time (0.67, n = 380, 0.67, n = 226). The winter, April and June models correctly predicted less than half of right whale sightings, demonstrating poor predictive ability.

TSS performance scores reflected the GAM results. When using the original sightings data for assessment, the summer and fall models had the best scores (TSS = 0.6377 and 0.6818) followed by May with a score of 0.5526. The remainder of the models had TSS scores below 0.3 indicating particularly poor performance especially because the sightings used for assessment were the same as those used to build the models. The TTS scores for the directed survey data were generally poor with the winter model receiving the highest score of 0.50. Performance scores for the CETAP data were also fairly low although the fall and May models returned the highest scores at 0.4444 and 0.4803 respectively.
Table 6: Results of generalized additive models and model performance assessment. Month/Season indicates temporal sampling unit; GAM indicates parameters chosen for inclusion in the model via stepwise GAM with the associated p-value; $r^2$ represents the deviance explained by the model; TSS original, performance statistic for the model calculated using the survey data which built the model; TSS directed, performance statistic for the model calculated using the directed survey data; TSS CETAP, performance statistic for the model calculated using the CETAP data;

<table>
<thead>
<tr>
<th>Month /Season</th>
<th>GAM (parameters)</th>
<th>p-value</th>
<th>r^2</th>
<th>TSS (original)</th>
<th>TSS (directed)</th>
<th>TSS (CETAP)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter</td>
<td>s(sediment)</td>
<td>&lt; 0.001</td>
<td>0.21</td>
<td>0.2655</td>
<td>0.5000</td>
<td>N/A</td>
</tr>
<tr>
<td></td>
<td>s(SST)</td>
<td>&lt; 0.001</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>s(depth)</td>
<td>0.002</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>March</td>
<td>s(depth)</td>
<td>&lt; 0.001</td>
<td>0.11</td>
<td>0.2743</td>
<td>0.1912</td>
<td>0.2091</td>
</tr>
<tr>
<td></td>
<td>s(sediment)</td>
<td>&lt; 0.001</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>s(sst fronts)</td>
<td>0.005</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>April</td>
<td>s(slope)</td>
<td>0.017</td>
<td>0.10</td>
<td>0.2425</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>s(sediment)</td>
<td>0.005</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>s(SST)</td>
<td>&lt; 0.001</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>May</td>
<td>s(depth)</td>
<td>&lt; 0.001</td>
<td>0.38</td>
<td>0.5526</td>
<td>0.3060</td>
<td>0.4803</td>
</tr>
<tr>
<td></td>
<td>s(sediment)</td>
<td>&lt; 0.001</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>s(SST)</td>
<td>&lt; 0.001</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>June</td>
<td>s(depth)</td>
<td>&lt; 0.001</td>
<td>0.38</td>
<td>0.2918</td>
<td>0</td>
<td>0.1333</td>
</tr>
<tr>
<td></td>
<td>s(sediment)</td>
<td>0.002</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>s(SST)</td>
<td>&lt; 0.001</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Summer</td>
<td>s(depth)</td>
<td>&lt; 0.001</td>
<td>0.56</td>
<td>0.6377</td>
<td>0.3895</td>
<td>0.3774</td>
</tr>
<tr>
<td></td>
<td>s(SST)</td>
<td>&lt; 0.001</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Fall</td>
<td>s(SST)</td>
<td>&lt; 0.001</td>
<td>0.43</td>
<td>0.6818</td>
<td>-0.2264</td>
<td>0.4444</td>
</tr>
</tbody>
</table>
Figure 14: Predicted right whale foraging habitat in the Gulf of Maine by month or season. Blue regions indicate predicted habitat as identified by GAMs. The 100m isobaths is depicted.
Discussion

The distribution of right whales within the Gulf of Maine is correlated with depth, slope, sediment, SST and SST fronts to differing degrees throughout the year. However, Mantel tests indicate that other spatially structured parameters have a significant influence over whale distribution. This suggests that the analysis conducted here failed to capture a significant physical parameter(s) influencing right whale presence in all months of the year.

Predictive models of the whales’ habitat preferences in fall and summer accurately captured the distribution of a large proportion of right whale sightings in the Gulf (0.95 and 0.92) and successfully identified known foraging habitats outside the survey areas (Grand Manan and Roseway Basin). In general, habitat models from other months did not perform well although the habitat model for the month of May demonstrated moderate performance, correctly identifying 67% of sightings as occurring in foraging habitat.

The mixed results of the predictive models do not support the hypotheses that right whale distribution is associated with SST and SST fronts in winter and spring and that topography and benthic characteristics influence distribution during summer and fall. In fact, these findings suggest that the opposite is true. Sediment type was repeatedly associated with whale presence in both Mantel tests and GAMs especially in the spring months. This is somewhat unexpected since *C. finmarchicus* aggregations are known to be associated with surface frontal activity in spring.
The predictive models for May and June selected a fairly restricted range of habitat but the other models were quite broad, identifying foraging habitat in areas unlikely to offer conditions suitable for feeding. Additionally, the characteristics of the best models offer little ecological insight. For example, in fall, whales were highly associated with surface temperatures between 9.5 and 10.5ºC and in summer whales were associated with depths > 120m, gravelly sediments and surface temperatures between 12.2 and 13.2 ºC. This indicates that while the models have some predictive capacity they may not be ecologically relevant or meaningful. The variables I selected may not be associated with features that aggregate suitable prey or I may have analyzed them at spatial or temporal scales inappropriate to the relationships I was trying to assess.

I used a SST front detection algorithm (Cayula & Cornillon 1995) specifically designed to extract both weak and strong temperature gradient. This analysis considered the persistence of frontal features but differences in gradient strength were not taken into account. It is possible that strong gradients, such as the tidal mixing front in the Great South Channel, are disproportionally associated with zooplankton aggregation. Thermal gradients were ubiquitous throughout the Gulf in all seasons except winter. The failure to incorporate frontal strength into our models may explain the lack of association identified between whales and SST fronts in our GAMs.

Winter habitat appears especially complex due to the existence of two clusters of sightings in very different habitats. Right whales were sighted in considerable numbers both in Cape Cod Bay and in the central Gulf. This bimodal distribution may represent two different winter foraging strategies. Whales in Cape Cod Bay may exploit easily
accessible surface prey even if the prey quality (e.g. *Pseudocalanus*) is low, while whales in the central Gulf may target energy rich *C. finmarchicus* in less assessable deep water. If true, the presence of two alternative strategies obfuscates a single model of optimal foraging habitat for the winter.

Unlike calving grounds where whales may seek out a set of habitat conditions over an extended period of time, foraging grounds are highly heterogeneous. It is this heterogeneity which aggregates prey at fine scales and attracts right whales. Foraging habitat is not a continuous area but rather a group of discrete ephemeral sites. Traveling between patches may obscure the identification of foraging areas because habitat conditions associated with individuals moving between foraging spots is included in the models.

Finally, factors other than feeding may influence whale distribution in the Gulf of Maine. Right whales are known to exhibit social and mating behaviors on the foraging grounds (Kraus & Hatch 2001). If social and reproductive behavior takes place in proximity to optimal foraging sites, these activities may have little impact on distribution models. However, if these activities encourage distribution away from optimal feeding areas as Baumgartner and Mate (2005) tentatively suggest, these behaviors may diminish the usefulness of predictive foraging models.
Chapter 3: Spatial and Temporal Overlap of Fixed Fishing Gear with North Atlantic Right Whales (*Eubalaena glacialis*) and Humpback Whales (*Megaptera novaeangliae*) in the Gulf of Maine
**Introduction**

The bycatch of marine mammals incidental to fishing operations is a serious global conservation problem (Read et al. 2006). In the western North Atlantic, entanglement in fishing gear is a significant source of anthropogenetic mortality and serious injury for two species of endangered whales: the North Atlantic right whale (*Eubalaena glacialis*) and the humpback whale (*Megaptera novaeangliae*). Fixed fishing gear, including pot/trap gear and anchored (sink) gillnet, is implicated in 89% of identifiable entanglements although other gear, including anchor lines, Danish seines and aquaculture nets also entangle whales (Johnson et al. 2005). Whales may carry off gear once entangled, so the mechanism and circumstances surrounding entanglement remain poorly understood and researchers rarely are able to determine where or when interactions occur (Johnson et al. 2007).

Analyses of entanglement scars on humpback and right whales demonstrate extremely high rates of gear interaction. Knowlton et al (2005) found that 76% of the right whale population bear scars from gear interactions, with many individuals displaying multiple scars from separate entanglement events. Robbins and Mattila (2000) found that approximately half (48%-65%) of humpback whales photographed between 1997 and 1999 bore scars from gear interactions. Most right whale entanglements involve pot/trap gear while humpback entanglements are more evenly divided between pot/trap gear and gillnets (Johnson et al. 2005). The prevalence of live whales with scars indicates that most entanglements result in a whale successfully shedding gear, however, the
severity of abrasion required to leave a lasting scar suggests considerable injury (Woodward et al. 2006).

Mortalities and serious injuries resulting from gear interactions are underreported (Knowlton & Kraus 2001). Severe entanglements can lead to reduced food consumption and ultimately emaciation, so when a whales dies its carcass may sink and go undetected. Between 2001 and 2005, 24 confirmed right whale entanglements, resulting in three mortalities and four serious injuries, were documented (Nelson et al. 2007). During this same period, 70 humpback entanglements resulting in eight mortalities and six serious injuries were also recorded (Nelson et al. 2007).

Most entanglements are believed to occur along the U.S. eastern seaboard and the Canadian Maritime Provinces. The Gulf of Maine and Scotian Shelf are the primary foraging grounds for right (Winn et al. 1986) and humpback whales (Katona & Beard 1990, Clapham et al. 2003) and the site of several important fixed gear fisheries. In particular, lobster trap gear is ubiquitous throughout the Gulf of Maine with over 3 million traps fished annually (Steneck 2006). At present, in U.S. waters, the American lobster trap/pot fishery includes approximately 13,000 participants (72 FR 66048). The American Lobster (*Homarus americanus*) is by far the most valuable species landed in New England and accounts for 82% of fisheries revenue for the state of Maine and 12% for Massachusetts (National Marine Fisheries Service 2008). Gillnet fishing is also widespread in the Gulf but with far fewer participants due to increased regulation in recent years. The northeast multispecies fishery is the largest fishery employing sink gillnets and includes 341 permit holders (72 FR 66048).
Whales interact primarily with two portions of fishing gear; the buoy line connecting gear to a surface float and floating line which connects traps along the bottom or net panels to an anchor (Johnson et al. 2005). Lobstermen employ several different gear configurations depending on their location and the terrain they are fishing. In general, offshore lobstermen use strings of approximately 40 traps (1.6 - 1.8km long), while inshore lobstermen use a variety of configurations ranging from 1 trap per surface buoy to a string of 15-25 traps (personal communication, Erin Burke, 3/2/08). As a result of these differences, there is a higher ratio of surface buoys to traps inshore than offshore. In Massachusetts, 83% of lobster gear was deployed in nearshore (state) waters in 2005 (Dean et al. 2007). Gillnet fishermen use strings of 300 foot net panels configured in a single panel or in strings of up to 30 panels with the most common gillnets consisting of 5 to 12 panels. Based on a 1999 assessment, approximately 80% of New England gillnet fishermen operated in nearshore, state waters and 17% fished offshore (Bisack 2003).

I used a combination of self-reported lobster fishing data and independent aerial observations of gear distribution to evaluate the spatial and temporal overlap of fixed fishing gear and whales in the Gulf of Maine. I hypothesized that gear and whales are distributed non-uniformly relative to each other in the Gulf. Using a seasonal timeframe, I assessed whether overlap (if any) was correlated using Spearman’s rank correlation coefficients and the Williamson index of spatial overlap (Williamson et al. 1989). My aim was to identify regions with high proportions of both gear and whales and to highlight those areas with minimal spatio-temporal overlap.
Methods

Study Area

The Gulf of Maine is a large embayment bordered on its eastern margin by submarine banks which partly enclose the Gulf from the greater Atlantic. Within the Gulf are several deep basins (>200 meters) including Wilkinson Basin and Jordan Basin. Cold slope water enters the Gulf through the Northeast Channel and circulates in a counter clockwise motion. The mixture of shallow topography, enriched waters and coastal nutrient input generates exceptionally high productivity. Right and humpback whales take advantage of this bounty, foraging in high numbers especially during the spring and summer months although the whales are sighted year round. Fishermen also respond to this productivity. The greater Gulf of Maine region hosts some of the most valuable fisheries in the world.

Whale Sighting Data from Aerial Surveys

As part of the broader Right Whale Sighting Advisory System, aerial surveys were conducted in the Gulf of Maine by the NOAA Northeast Fisheries Science Center (NEFSC) and the Provincetown Center for Coastal Studies (PCCS) between 2002 and 2006. The NEFSC surveys were flown across the Gulf north of 40.35°N between the U.S. coast and the Hague line, which separates U.S. from Canadian waters. PCCS flew surveys exclusively over nearshore waters off Cape Cod, MA. The surveys were conducted from fixed wing aircraft following the same protocols. Each aircraft traveled at
a speed of approximately 100 knots and an altitude of 750 feet with two observers and one data recorder aboard each plane.

NESFC surveys were conducted year round, dependent on weather, and used a broad-scale stratified random design (Cole et al. 2007). U.S. waters north of 40.35°N were divided up into 16 blocks with each containing 20 tracklines spaced 1.85km apart. Two to three blocks were surveyed during one flight with individual tracklines randomly selected from within each block. The NEFSC surveys were not specifically designed for habitat analysis *per se*, but search effort occurred in regions including those where no right whales were expected allowing for a broad biogeographic analysis. Occasionally, additional, non-broad-scale flights were conducted for management purposes and sightings from these were also included. PCCS surveys took place between January and mid-May and flew in areas where right whales were known or expected to be present. These surveys mostly followed a set of predetermined tracklines (2.75 km apart) over Cape Cod Bay and along the eastern shore of the Cape.

Because the aerial surveys were designed to warn mariners of right whales in the vicinity and to collect photographs of individual animals, they did not follow formal line transect protocols. At each right whale sighting the plane departed from the trackline to circle individual(s) and obtain an accurate location and count, along with photographs for individual identification. Planes did not break track for humpback whales and all humpbacks sighting were documented from the trackline. For safety reasons the NEFSC flights did not break track for right whales while in Cape Cod Bay when PCCS was conducting surveys.
Positions were recorded using a GPS (Global Positioning System) at frequent intervals along each trackline to document effort. While underway, Beaufort Sea State, weather, visibility and the location and details of each whale sighting were recorded. The NESFC surveys explicitly documented the excessive “circling” that occurred when right whales were spotted as off effort time and it was not included in this analysis. To ensure that the PCCS data conformed to this standard, a filter was applied to the PCCS survey effort data. All instances where the plane left the trackline and made more than 2 circles within a 2km range were removed. Removing the excessive circling prevented bias in the calculation of relative whale densities since no actual sightings effort was ongoing while photographing individual whales.

All surveys conducted during Beaufort sea state conditions < 6 were included in our analysis. Boat based surveys focusing on smaller cetaceans have documented significant differences in sightings rates relative to Beaufort sea state (Palka 1995). I found no significant difference in sighting rates for either right whales (p=0.707) or humpback whales (p=0.455) during Beaufort sea states 0 to 5. I removed from analysis the very few portions of the survey data with a Beaufort sea state > 6.

**Gear Data from Aerial Surveys**

Surface buoys marking fixed fishing gear were documented in 2005 and 2006 during the NEFSC surveys. Fixed gear in the Gulf of Maine includes mostly pot/trap gear targeting lobster or sink gillnet targeting primarily groundfish, monkfish, skates and blue fish. Gear is marked at the surface by a combination of foam buoys and large poly balls
or “high-flyers” (multiple foam buoys with a spar). Sightings of surface buoys/balls were recorded from the trackline but it was seldom possible to identify the type of gear (gillnet or traps). In some instances, the gear was too dense for an accurate count or other sightings prevented an individual gear tally. In these situations, gear “fields” were documented as light, light-moderate, moderate, moderate-heavy and heavy. The start and end of each gear field was also recorded. Fields of gear occurred only in nearshore waters where fishing effort is most intense. A field of gear with fewer than 8-10 pieces of was considered light and more than 20 was considered heavy. I assigned a numerical value to each gear field category and the results of both individual gear sightings and gear field values were combined to create a total gear value for each analysis cell. The relative density of gear was then calculated for each analysis cell.

**State Lobster Fishing Effort Data**

Lobster fishing effort data were obtained from the States of Massachusetts and Rhode Island for the years 2002-2006. Lobstermen landing in either state are required to fill out annual reports detailing the location of fishing activity and (for Massachusetts) effort expended within predetermined reporting zones for each month of the year (Figure 15). Massachusetts conducts random audits of 150 permit holders each year to ensure accurate reporting. Small quantities of lobster are collected by trawl or by hand but these effort data were not included in our analysis.

This investigation was concerned with the amount of gear present in the water, rather than actual fishing effort (i.e. the number of times traps are hauled times the
number of traps), so I used a calculation of the maximum number of traps a lobstermen has in the water per season as a measure of gear. The State of Rhode Island does not calculate maximum traps for their lobsterman, so levels for Rhode Island lobstermen were estimated based on landings using the trap values from Massachusetts lobstermen operating in the same or adjacent statistical areas. Massachusetts is prohibited from releasing any data that describes or specifies the activity of three or fewer fishermen to protect confidentiality. As a result, for some statistical areas I know fishing activity took place but I do not have an exact value for the number of traps used.

The statistical reporting areas used by the States were established to standardize the collection of general fisheries data and had to be modified for the present analysis. The zones considered here include 15 nearshore areas around Massachusetts and Rhode Island and 11 offshore zones (Figure 15). Modifications were made to the official zones based on fishing regulations and the biology of the lobster. Areas 21, 24 and 25 extend into Canadian waters. I made the assumption that no lobstermen were engaged in illegal fishing in Canada and restricted those zones to the portions that fall within U.S. waters. Second, portions of zones 16, 17, 23 and 25 extend into waters deeper than 700m where lobsters cannot survive (Cooper & Uzmann 1971). To account for this habitat limitation, I considered only portions of zones in less than 700 meters of water. Third, zone 20 overlaps with the state waters of New Hampshire and Maine. I was unable to obtain spatio-temporal lobster fishing data from either state consistent with that of Massachusetts or Rhode Island so the territorial waters of these states were removed from analysis.
Data from Massachusetts waters captures the full extent of lobster gear in state waters; however, any lobstermen with an appropriate permit can fish offshore outside state waters. Data based solely on landings from Massachusetts and Rhode Island do not fully account for all lobster fishing effort in offshore areas. However, based on 2007 vessel permit statistics (National Marine Fisheries Service 2007), I found that of the 85 vessels (> 40ft) with a permit to fish in the offshore Lobster Management Area 3 (Atlantic States Marine Fisheries Commission 1997), 70% designate Massachusetts or Rhode Island as their primary port. While these data do not account for all lobster effort in the offshore areas it accounts for 70% of the vessels able to lobster offshore. Additionally, most of the offshore fishery is executed in proximity to Georges Bank. Massachusetts and Rhode Island host the closest major ports (New Bedford, MA or Point Judith, RI) to Georges Bank. In fact, the Atlantic States Marine Fisheries Commission (ASMFC), which manages the lobster fishery, uses the Massachusetts data as a proxy for Georges Bank fishing effort (Atlantic States Marine Fisheries Commission 2006).
Figure 15: Amended statistical reporting areas for the lobster fishery. Green indicates inshore zones and blue denotes offshore zones. The 100m depth contour is noted.

**Analysis Methods**

The co-occurrence of whales and fishing gear was assessed on a seasonal time frame in accordance with the seasonal nature of both fishing activity and whale movements in the Gulf. Data were pooled by season across all five years for the state
lobster data and over both years for the observed gear data. Overlap was also assessed for collective inshore and offshore areas over all years. Inshore areas were defined by the extent of state territorial waters, as this boundary also delineates state and federal fisheries regulations. The overlap of whales and gear was evaluated separately for each of the fishing gear data sets. I define the term “overlap” to mean areas where whales and gear were documented within the same analysis unit over the course of a season. This does not imply that gear and whales were sighted synoptically.

The spatial extent of the state reporting zones determined the spatial unit of analysis for this data. Any sampling unit with less than 20% of the total area surveyed during any given season was removed from the analysis because of insufficient search effort. For gear sightings collected during aerial surveys I employed an 8km\(^2\) sample unit. This cell size was chosen based on a combination of the sighting distance for surface buoys (up to 4km) and the length of trap and net strings which can reach nearly 2km in offshore waters. Only cells containing at least 8km of survey trackline in a season were included in the analysis.

To evaluate correlations with state reported lobster gear I used Williamson’s spatial overlap index (Williamson 1993) and Spearman rank correlation coefficients. The Williamson index was originally developed to investigate the overlap of predator and prey populations. Here I characterize the degree to which the correlation between whales and gear deviate from a random distribution (Equation 2). Values < 1 indicate less than expected overlap and values > 1 indicate greater than expected overlap. Significance values for the overlap index were calculated via permutation procedures with
randomizations run 5000 times (Garrison et al. 2000). Overlap indexes were calculated for each cumulative season and for pooled inshore and offshore data.

Equation 2: Williamson spatial overlap index. $O_{ij} = \text{overlap value}; z = \text{individual sample unit}; m = \text{number of samples}; N$ is the relative density of $i$, whales and $j$, gear.

\[ O_{ij} = \frac{\sum_{z} (N_{iz}N_{jz})^m}{\sum_{z} (N_{iz}) \times \sum_{z} (N_{jz})} \]

Spearman rank correlation is a non-parametric technique which relies on rank order to assess correlation. Values range from -1 to +1 with negative values indicating repulsion and positive values indicative of attraction. Coefficients were calculated for each cumulative season and for inshore/offshore areas. Only areas where either gear or whales were present were included in the analysis. To evaluate the correlation of whales and gear observed during aerial surveys I used only Spearman rank correlation coefficients. This technique was selected for the observed gear data due to the more subjective nature of the data.

Descriptive statistics were used to identify areas of particularly strong overlap or areas with a consistent lack of overlap. I identified two levels of overlap hotspots; level 1 “hotspots” were defined as areas where the top quartile of whale and gear density co-occurred and level 2 “hotspots” as areas where the top quartile of either whales or gear co-occurred in an area with whale or gear values greater than the median. Areas with no overlap, or “coldspots”, were also identified. Lastly, all incidences of overlap and no overlap were evaluated for temporal consistency.
**Results**

**Patterns of Whale Distribution**

Between 2002 and 2006, 3647 right whale and 3724 humpback whale sightings were recorded during aerial surveys in the Gulf of Maine (Figure 16). Many of these observations included re-sightings of the same individuals. Whales were sighted in the Gulf year-round but were most prevalent in spring (68% of right whale and 59% of humpback sightings). In the winter months, 54% of right whale sightings and 22% of humpback whale sightings occurred inshore but only 18% of survey effort was dedicated to nearshore areas. The high proportion of right whale sightings relative to survey effort demonstrated the whales’ strong preference for nearshore waters in winter. During spring, 18% of right whale observations and 10% of humpback whale observations occurred inshore with 23% of survey effort also taking place inshore. Little survey effort was dedicated to nearshore waters in summer (2%) and whale sightings reflected this with < 0.1% of right or humpback sightings observed inshore. During fall, 13% of survey effort was conducted inshore and 12% of humpback whale observations occurred inshore, but no right whales were seen in this area.

**Patterns of Gear Distribution**

Fixed fishing gear occurred throughout the Gulf during all seasons (Figures 17 and 18). Most notable was the high density of gear close to shore. During 2005 and 2006, 8.6% of survey effort occurred in state waters but 22% of fishing gear was sighted inshore. This trend was consistent over all seasons but most pronounced in summer when
9% of survey effort occurred nearshore but 28% of gear was sighted there. According to state data (Figure 18), maximum lobster trap densities reached a remarkable 294 traps / km² in Massachusetts waters during the summer. In most offshore areas trap density was very low with less than 1 trap / km². During the winter months there was a notable reduction in lobster trap density.

Figure 16: Distribution of right and humpback whales in the Gulf of Maine by cumulative season (2002-2006). Blue dots indicate humpback whale sightings and pink dots indicate right whale sightings.
Figure 17: Observations of fixed fishing gear in the Gulf of Maine (2005-2006). Larger dots indicate higher numbers of gear sightings.
Figure 18: Average cumulative seasonal density of lobster traps in Massachusetts and Rhode Island state waters and offshore areas as reported by lobstermen (2002-2006).
Overlap Assessment

Based on state data, overlap index values for right whales and lobster gear were significantly less than expected in winter and fall and showed no significant trend during spring, summer or for inshore/offshore areas (Table 7). For humpback whales, index values indicated less than expected overlap during winter, spring and summer but no significant trend in fall or for inshore/offshore areas. I found a significant negative correlation between right whales and lobster gear for all seasons and areas except spring (Table 8). However, the coefficients were moderately weak, ranging from -0.212 to -0.364. Humpback whales were negatively correlated with lobster gear in every season and in offshore areas. Correlation coefficients were strongest for humpback whales in spring and summer. Notably, both analyses indicated no significant correlation between right whales and gear during spring or between humpback whales and gear in inshore areas.

Table 7: Williamson's spatial overlap index for state reported lobster gear and right whales/humpbacks. Overlap assessed by cumulative (2002-2006) season and inshore/offshore region. Significant values are in bold type. P-values calculated via permutation procedures with 5000 replications.

<table>
<thead>
<tr>
<th></th>
<th>Right Whales</th>
<th>Humpback Whales</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter (n = 62)</td>
<td>0.267, p = 0.017</td>
<td>0.171, p = 0.018</td>
</tr>
<tr>
<td>Spring (n = 109)</td>
<td>0.515, p = 0.143</td>
<td>0.259, p &lt; 0.001</td>
</tr>
<tr>
<td>Summer (n = 69)</td>
<td>0.889, p = 0.806</td>
<td>0.153, p = 0.002</td>
</tr>
<tr>
<td>Fall (n = 99)</td>
<td>0.005, p = 0.002</td>
<td>1.462, p = 0.386</td>
</tr>
<tr>
<td>Inshore (n = 208)</td>
<td>0.693, p = 0.454</td>
<td>1.374, p = 0.412</td>
</tr>
<tr>
<td>Offshore (n = 118)</td>
<td>0.447, p = 0.064</td>
<td>0.630, p = 0.083</td>
</tr>
</tbody>
</table>
Table 8: Spearman’s rank correlation coefficients for state reported lobster gear and right whales/humpbacks. Overlap assessed by cumulative (2002-2006) season and inshore/offshore region. Significant values are in bold type.

<table>
<thead>
<tr>
<th>Season</th>
<th>Right Whales</th>
<th>n</th>
<th>Humpback Whales</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter</td>
<td>-0.317, p = 0.020</td>
<td>54</td>
<td>-0.323, p = 0.017</td>
<td>55</td>
</tr>
<tr>
<td>Spring</td>
<td>-0.189, p = 0.056</td>
<td>103</td>
<td>-0.597, p &lt; 0.001</td>
<td>103</td>
</tr>
<tr>
<td>Summer</td>
<td>-0.355, p = 0.003</td>
<td>68</td>
<td>-0.595, p &lt; 0.001</td>
<td>68</td>
</tr>
<tr>
<td>Fall</td>
<td>-0.364, p &lt; 0.001</td>
<td>92</td>
<td>-0.306, p = 0.003</td>
<td>95</td>
</tr>
<tr>
<td>Inshore</td>
<td>-0.212, p = 0.003</td>
<td>193</td>
<td>-0.051, p = 0.476</td>
<td>194</td>
</tr>
<tr>
<td>Offshore</td>
<td>-0.331, p &lt; 0.001</td>
<td>112</td>
<td>-0.243, p = 0.009</td>
<td>115</td>
</tr>
</tbody>
</table>

Based on gear observations from the entire Gulf, I found significant negative correlations between both whales and fixed gear during all seasons and in offshore and nearshore regions (Table 9). This provided strong evidence that areas with the densest gear host fewer whales and regions with the highest concentrations of whales have less gear. The strength of the correlations varied somewhat with the strongest correlation occurring in spring for both whales.

Table 9: Spearman’s rank correlation coefficients for fixed fishing gear and right whales/humpbacks observed during aerial surveys. Overlap assessed by cumulative (2005-2006) season and inshore/offshore region. Significant values are in bold type.

<table>
<thead>
<tr>
<th>Season</th>
<th>Right Whales</th>
<th>n</th>
<th>Humpback Whales</th>
<th>n</th>
</tr>
</thead>
<tbody>
<tr>
<td>Winter</td>
<td>-0.626, p &lt; 0.001</td>
<td>382</td>
<td>-0.352, p &lt; 0.001</td>
<td>335</td>
</tr>
<tr>
<td>Spring</td>
<td>-0.701, p &lt; 0.001</td>
<td>490</td>
<td>-0.710, p &lt; 0.001</td>
<td>507</td>
</tr>
<tr>
<td>Summer</td>
<td>-0.348, p &lt; 0.001</td>
<td>488</td>
<td>-0.645, p &lt; 0.001</td>
<td>588</td>
</tr>
<tr>
<td>Fall</td>
<td>-0.470, p &lt; 0.001</td>
<td>452</td>
<td>-0.517, p &lt; 0.001</td>
<td>468</td>
</tr>
<tr>
<td>Inshore</td>
<td>-0.570, p &lt; 0.001</td>
<td>395</td>
<td>-0.415, p &lt; 0.001</td>
<td>370</td>
</tr>
<tr>
<td>Offshore</td>
<td>-0.569, p &lt; 0.001</td>
<td>1421</td>
<td>-0.644, p &lt; 0.001</td>
<td>1543</td>
</tr>
</tbody>
</table>

Few whale/gear overlap hotspots were identified for either right or humpback whales and none demonstrated temporal consistency across all study years (Figures 19 and 20). Equally rare were areas of no gear/whale overlap. Several areas were identified as having no overlap but few exhibited temporal consistency with the exception of a
small area (#11) east of Nantucket. Overall, overlap varied considerably by whale species and season (Figures 22-29) with spring the most common season for co-occurrence.

The most notable area of high gear and whale overlap occurred in spring around Cape Cod. This coincidental distribution involved both right and humpback whales but was most pronounced for right whales. For humpback whales, overlap also occurred around Cape Cod in fall. Two additional hot spots (for both species) were identified off Cape Ann, MA in summer.

Based on the 2005-2006 aerial survey gear data, overlap of gear and whales was observed for both species in every season except for right whales in fall 2005 (Figure 21). The overlap of gear and whales was most evident in spring and summer along the Great South Channel and off Cape Cod. Overlap occurred in proximity to Jeffrey’s Ledge during fall for both species and in more sparse areas during fall and winter. In every season, whales were also observed in areas adjacent to cells with gear observations (Figures 30-33). Notably, of the 44 areas where right whales overlapped with gear during 2005 and 2006, 66% occurred (at least partially) within one of the two right whale critical habitat zones in Cape Cod Bay and the Great South Channel (National Marine Fisheries Service 1994). Of the 77 areas where humpback whales overlapped with gear, 46% also fell within the right whale critical habitat areas.
Figure 19: Overlap of right whales and lobster trap gear. Level 1 hotspots: areas where the top quartile of whale and gear values co-occurred; Level 2 hotspots: areas where the top quartile of either whales or gear co-occurred in an area with whale or gear values greater than the median; Coldspots: areas where whales and gear do not overlap. The legend indicates the number of years the area was identified as a hotspot or coldspot.
Figure 20: Overlap of humpback whales and lobster trap gear. Level 1 hotspots: areas where the top quartile of whale and gear values co-occurred; Level 2 hotspots: areas where the top quartile of either whales or gear co-occurred in an area with whale or gear values greater than the median; Coldspots: areas where whales and gear do not overlap. The legend indicates the number of years the area was identified as a hotspot or coldspot.
Figure 21: Areas of overlap identified between right and humpback whales and observed fixed fishing gear by cumulative season (2005 and 2006).
Discussion

The relative density of right and humpback whales and fixed fishing gear in the Gulf of Maine is negatively correlated in most seasons. Whales occur most frequently in areas where gear is less dense and conversely areas with dense gear have low densities of whales. At first, this appears counter-intuitive given the high proportion of whales bearing scars from entanglement. These findings demonstrate that the regular co-occurrence of high densities of whales and gear is not a prerequisite for entanglement. Rather, entanglement appears to be a far more diffuse problem.

The proliferation of lobster fisheries in the Gulf of Maine has resulted in an unprecedented saturation of gear, especially in nearshore waters. As a result, the concept of gear density is somewhat distorted. Even regions with relatively moderate densities of gear have a high number of potentially entangling lines. My analysis suggests that overlap with moderate, or even low, density gear is sufficient to facilitate entanglement.

Myers et al (2007) highlighted the overexploitation in the U.S. lobster fishery and argued that a substantial reduction in the number of traps fished would benefit both lobstermen and whales. If trap reductions were to occur, it is likely that regions with the highest numbers of traps would see the greatest reductions. These areas would include nearshore, state waters but likely not offshore regions. However, substantial trap reductions in these areas may offer little conservation benefit to whales since most whales occur outside areas with high densities of traps. My analysis indicates that reducing trap densities to more moderate levels may do little to prevent entanglement.

Myers et al (2007) also suggested limiting the duration of the lobster fishing season, as is
done in Canada. This measure, if adopted throughout the U.S. side of the Gulf of Maine, could have a substantial impact on entanglement, especially if lobster fishing were prohibited during spring.

Evaluation of individual level 1 and level 2 “hotspots” based on state data yielded several areas of pronounced overlap around Cape Cod, MA in spring and fall. Surprisingly, however, these hotspots lacked temporal consistency, due primarily to variation in whale density. This lack of consistency may be an artifact of the statistical zones used to delineate lobster fishing effort. The zones were established for general fisheries data collection and I found that frequently aggregations of whales in Cape Cod Bay and just offshore of Cape Cod (to the north and east) were arbitrarily split into different statistical zones. If whales in one year were more concentrated to the east or west the bulk of the whale density would fall into different bins thus reducing the temporal consistency of any one zone’s overlap rating.

Given the localized nature of the Cape Cod hotspots, spatio-temporal management (i.e. area closures for fixed gear) in this region could provide enhanced protection from entanglement for both species of whales. The entire Cape Cod Bay area and the state waters just to the north and east of Cape Cod should be considered one management unit to account for the variation in whale distribution between years. Despite variation in distribution, both right and humpback whales consistently use this nearshore region each year. Historic records reinforce the consistency of right whale distribution in this area over time. Harvest records dating back to the early 1600s
demonstrate the presence of right whales in Cape Cod Bay and in nearshore waters off Cape Cod in winter and spring (Reeves et al. 1999) as is common today.

My ability to detect overlap hotspots was partially compromised in one area. The proximity of statistical area 20 to the coasts of both Maine and New Hampshire means that I have underestimated the lobster fishing effort in this zone and I report my findings with this caveat. Area 20 contains a bathymetric feature called Jeffrey’s Ledge which is a known foraging area for large whales. Right whales overlapped with gear in this area during fall and humpback whales overlapped with gear in this region during every season except winter. Whales may overlap with lobster gear in Area 20 more frequently than indicated by my analysis.

A lack of information about the mechanism of entanglement prevents detailed analysis of the factors that contribute to entanglement events. However, available data suggest that whales are more likely to become entangled while foraging. Johnson et al (2005) found that 77% of right whale entanglements and 43% of humpback whale entanglements included gear attachment in the mouth. Large whales open their mouths almost exclusively for food consumption and as such, a sizable portion of entanglements must occur during feeding. Additionally, both humpback and right whales are known to forage in dense groups. Given the potentially heightened risk of entanglement during feeding the targeted protection of high density whale aggregations, irrespective of local gear density, is warranted.

The most dense and temporally consistent foraging aggregations of right whales occur in the Great South Channel during spring and early summer. This area is already
federally designated Critical Habitat for right whales. Based on the aerial observations, the highest proportion of gear/whale overlap was identified in this important foraging habitat during spring and summer. Eliminating entangling lines from the Critical Habitat area in spring and summer would provide a considerable conservation benefit to both right and humpback whales.

Additionally, the elimination of gear from the Cape Cod Bay right whale Critical Habitat area in winter and spring would also enhance protection for right whales. It is especially important to remove surface or buoy lines from this habitat since the majority of right whales surface feed in the Bay in winter and early spring (Mayo & Marx 1990). Finally, overlap was documented for both species just to the east of Jeffrey’s Ledge off the New Hampshire/Maine coast. This region is a foraging habitat for both right and humpback whales and fall foraging aggregations are well documented (Weinrich et al. 2000). Removing entangling lines from this area during the fall months would provide enhanced protection for both whale species.

Understanding where and when whales and gear co-occur does not provide a measure of entanglement risk, only an assessment of entanglement opportunity. Given the diffuse nature of whale/gear overlap, right and humpback whales are nearly always in some danger of entanglement in all areas of the Gulf throughout the year. Over the past decade the National Marine Fisheries Service has employed a combination of time/area fishery closures and area specific gear modifications aimed at addressing the entanglement problem. These efforts, so far, have failed to prevent new entanglements. The removal of entangling lines from the entire Gulf, year round, is the only option
which will eliminate entanglement risk to whales. However, strategic fishery management, prohibiting all entangling lines in areas where whales are known to aggregate and forage, could substantively reduce entanglement incidents.
Synthesis

The goal of this research was to evaluate ecological linkages between right whale distribution and the physical environment to gain insight into the whales’ habitat preferences. Additionally, I assessed the overlap of whales and fixed fishing gear in the Gulf of Maine. Understanding how a species interacts with its environment is a basic goal of ecology. This assessment is especially relevant given the critically endangered status of North Atlantic right whales.

I found that nearshore waters in mid-latitude areas offered the most favorable calving habitat (Figure 3) along the South Atlantic Bight. The models predicted that coastal areas within 40-50km of shore between Cape Lookout, NC and Daytona Beach, FL are core calving habitat. The models exhibited the highest level of agreement between Daytona Beach, FL and Cape Fear, NC with most of this region selected as calving habitat by three or more models. Calving habitat identified along the southeast coast proved very similar to both historic calving areas in the Northeastern Atlantic and to historic and current calving areas in several regions in the South Atlantic, with a few notable exceptions.

Habitat assessments in the Gulf of Maine did not yield such clear results but rather highlighted and reaffirmed the complex nature of foraging habitats. Right whale foraging habitat is closely tied to the suite of bio-physical factors that aggregate their primary prey, *C. finmarchicus*. I found that the distribution of right whales was positively associated with depth, depth gradient, SST, SST gradient and bottom sediments to
varying degrees throughout the year. Models of foraging habitat were most accurate in summer and fall when right whales forage primarily at depth. The results of the gear overlap analysis were more decisive. Whales are most prevalent in time and space where gear is least dense, and areas with dense gear are less frequented by whales.

The successes and failures of this work suggest that alternate methodology for habitat assessment should be more fully explored. Perhaps habitat can best be examined by subjectively choosing areas of high use and focusing efforts on fully examining every aspect of a small zone over a long time period. In doing so, we can assess conditions that are most appealing to the greatest number of individuals. Additional, we can evaluate conditions before whales arrive, while they use the habitat and document conditions after whales depart for other areas. This may provide insight into factors which trigger whales’ arrival and departure. Investigating mechanisms which prompt distributional changes may help us to identify thresholds of acceptable habitat. By focusing attention only on conditions when whales are present and not at the point of arrival and departure e may be missing out on an important piece of the habitat puzzle.

Some aspects of this research directly inform questions of whale management and conservation. The identification of a broad stretch of optimal calving habitat along the coasts of Georgia and South Carolina and southern North Carolina suggests that a reassessment of right whale critical habitat in the southeast may be in order. It is imperative that aerial surveys be continued and expanded in this region to fully document and evaluate the whales’ use of the area. The survival of newborn calves is critical to the
successful recovery of the North Atlantic right whale population and this assessment of their habitat should be taken into consideration in future management actions.

The tendency of right whales to aggregate, whether it is on calving grounds or in extremely dense aggregations in foraging areas, raises concerns about the vulnerability of this population to localized threats. A large number of whales can potentially be harmed at one time in a very discrete area. Every effort must be made to eliminate threats from the most high use areas.

Finally, the negative correlation of whales and fishing gear in the Gulf of Maine confirmed what many researchers have long realized about the problem of entanglement. The risk of entanglement is exceptionally diffuse. Entanglement persists even though high densities and whales and gear do not regularly co-occur in the Gulf of Maine. I did identify several areas where whale/gear overlap occurred. In these regions, strategic fishery management, prohibiting all entangling lines where whales are known to aggregate and forage, could substantively reduce entanglement incidents.
Appendix A: Humpback Whale Overlap with Lobster Gear

Figure 22: Winter distribution of humpback whales and lobster gear by statistical reporting area. Pink: whales and lobster gear present, Green: whales are present but gear not documented; Yellow: gear documented but no whales observed; Blue: no whales observed and no gear documented; White: not enough data to assess distribution.
Figure 23: Spring distribution of humpback whales and lobster gear by statistical reporting area. Pink: whales and lobster gear present, Green: whales are present but gear not documented; Yellow: gear documented but no whales observed; Blue: no whales observed and no gear documented; White: not enough data to assess distribution.
Legend:
- Pink: whales and lobster gear co-occur
- Green: whales present; no lobster gear
- Yellow: gear documented but no whales observed
- Blue: no whales observed and no gear documented
- White: not enough data to evaluate

Figure 24: Summer distribution of humpback whales and lobster gear by statistical reporting area. Pink: whales and lobster gear present, Green: whales are present but gear not documented; Yellow: gear documented but no whales observed; Blue: no whales observed and no gear documented; White: not enough data to asses distribution.
Legend:
- Pink: whales and lobster gear co-occur
- Green: whales present; no lobster gear
- Yellow: gear documented but no whales observed
- Blue: no whales observed and no gear documented
- White: not enough data to evaluate

Figure 25: Fall distribution of humpback whales and lobster gear by statistical reporting area. Pink: whales and lobster gear present, Green: whales are present but gear not documented; Yellow: gear documented but no whales observed; Blue: no whales observed and no gear documented; White: not enough data to assess distribution.
Appendix B: Right Whale Overlap with Lobster Gear

Figure 26: Winter distribution of right whales and lobster gear by statistical reporting area. Pink: whales and lobster gear present, Green: whales are present but gear not documented; Yellow: gear documented but no whales observed; Blue: no whales observed and no gear documented; White: not enough data to assess distribution.
Figure 27: Spring distribution of right whales and lobster gear by statistical reporting area. Pink: whales and lobster gear present, Green: whales are present but gear not documented; Yellow: gear documented but no whales observed; Blue: no whales observed and no gear documented; White: not enough data to assess distribution.
Figure 28: Summer distribution of right whales and lobster gear by statistical reporting area. Pink: whales and lobster gear present, Green: whales are present but gear not documented; Yellow: gear documented but no whales observed; Blue: no whales observed and no gear documented; White: not enough data to assess distribution.
Figure 29: Fall distribution of right whales and lobster gear by statistical reporting area. Pink: whales and lobster gear present, Green: whales are present but gear not documented; Yellow: gear documented but no whales observed; Blue: no whales observed and no gear documented; White: not enough data to assess distribution.
Appendix C: Right and Humpback Whale Overlap with Fixed Fishing Gear

Figure 30: Winter distribution of whales and fixed fishing gear in the Gulf of Maine (2005-2006). Pink: whales and fishing gear observed; Green: whales were observed but no gear observed; Blue: gear observed but no whales sighted; White = area searched over the entire season.
Figure 31: Spring distribution of whales and fixed fishing gear in the Gulf of Maine (2005-2006). Pink: whales and fishing gear observed; Green: whales were observed but no gear observed; Blue: gear observed but no whales sighted; White = area searched over the entire season.
Figure 32: Summer distribution of whales and fixed fishing gear in the Gulf of Maine (2005-2006). Pink: whales and fishing gear observed; Green: whales were observed but no gear observed; Blue: gear observed but no whales sighted; White = area searched over the entire season.
Figure 33: Fall distribution of whales and fixed fishing gear in the Gulf of Maine (2005-2006). Pink: whales and fishing gear observed; Green: whales were observed but no gear observed; Blue: gear observed but no whales sighted; White = area searched over the entire season.
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Peer Reviewed Publications
