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ABSTRACT

E PLURIBUS UNUM: WHAT INDIVIDUAL WHALES CAN TELL US ABOUT ENIGMATIC SPECIES' DISTRIBUTION AND SOCIAL ORGANIZATION

**by
Tanya Marie Lubansky**

Large whales have historically been difficult to study and many aspects of their ecology remain unknown especially at the long-term population level. The ability to identify individual whales based on natural markings provides the opportunity to track individuals over time and space; this data may offer more insight into the ecology of whales than previously imagined. This study demonstrates use of photo-identification data to model both social structure and habitat selection, minimizing the need for invasive research and greatly increasing the sample size used in such endeavors. A conditional logistic model is written for a 20-year sightings dataset on humpback whales collected by Allied Whale research trips and on the Bar Harbor Whale Watch Company vessels, examining choice of individuals over a given landscape and incorporating the cost of movement. Habitat choices are represented by static and remotely sensed variables including bathymetry, distance from shore, and sea surface temperature. Results show significant active decisions of whales to move towards specific hotspots ~23km offshore of intermediate depth. These models are validated by systematic boat surveys conducted during two field seasons. Sightings data are also applied to social networking analyses. Association indices are calculated for each dyad of whales and preferred association is tested for through a valid Markov chain of permutations. Network structure is delineated through optimal modularity clustering producing visualizations of communities. Significant preferred companionship is seen between 94 dyads and individuals are separated into

nine communities. Community structure is not entirely stable and shifts over time. Lastly, movement behavior and social structure between the whales in the northern Gulf of Maine are compared to that of the whales in the southern Gulf of Maine. The analyses listed above are run on a 26-year dataset provided by Provincetown Center for Coastal Studies on humpback whales on Stellwagen Bank. Differences are seen between northern and southern whales in use of habitat and degree of sociality. Whales in the southern aggregation are more gregarious, but have a lesser degree of long-term community structure. By applying new analytic tools to long-term observations, this research provides insights into humpback whale social behavior and ecology that should inform marine management strategies in the region.

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ENIGMATIC SPECIES' DISTRIBUTION AND SOCIAL ORGANIZATION**

**by
Tanya Marie Lubansky**

**A Dissertation
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APPROVAL PAGE

**E PLURIBUS UNUM: WHAT INDIVIDUAL WHALES CAN TELL US ABOUT
ENIGMATIC SPECIES' DISTRIBUTION AND SOCIAL ORGANIZATION**

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“I dedicate this thesis to both of my parents who have provided me with unconditional love and support through all of my life. My father, Kenneth, who has always encouraged and pushed me to pursue my passions even when different from his own. And my mother, Deena, who is the sweetest woman I know. Without my parents I would not be who I am and where I am in life today. “

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CHAPTER 1

INTRODUCTION

1.1 The Individual

Establishment of generalities and rules in the field of ecology is important for management; in order to conserve animals, some general patterns must be able to be predicted. However, ecosystems are complex and continually changing. Thus controversy exists on whether any generalities can ever actually be made. In the past two decades, there has been a push for individual-based modeling to elucidate population dynamics (Judson 1994; Lomnicki 1999; DeAngelis and Mooij 2005). By modeling individual behavior, one can exclude many unrealistic assumptions and account for individual variation while producing a more complex understanding of population level processes (Sutherland et al. 1996, Bolnick et al. 2003). Observations of individual behavior have provided framework on animal movement and optimal foraging (Mueller and Fagan 2008; Nathan et al. 2008; Hancock and Millneur-Gilland 2006). Advances on understanding the role of social learning in community function have also been discovered through observing individuals (Mueller et al. 2013)

Many species are difficult to study at the population level with remote or widely-spread distributions. Some are even impossible to observe for more than a small fraction of time (Mate et al. 1999; Brown et al. 2013). When data are scarce, modeling patterns of individuals proves beneficial. Data on individuals may be collected through a variety of means including direct observations and satellite tagging. Marine organisms are often the most difficult animals to observe with remote offshore habitat. Marine mammals, such as

cetaceans, do spend time at the surface but are often difficult to observe for long periods of time. While standardized surveys give estimates of abundance and occurrence, a more fine-scale understanding of habitat use and social behavior is more difficult to achieve. Studies on individual whales to elucidate larger patterns have been long been seen as important. Historically, knowledge was gained through use of a Discovery tag that was implanted into an animal and recovered at the death of that individual. These tags provided some limited understanding on movement patterns of individuals by documenting two locations of that particular whale. With increases in technology, much more interesting information has been collected through application of telemetry devices ranging from small location loggers to larger tags equipped with hydrophones and accelerometers (Mate et al. 2007). Tracking of individuals is also possible through examination of collected genetic samples (Rosenbaum et al. 2004; Pomilla and Rosenbaum 2005). Another useful and less invasive method to track individual behavior of cetaceans is the identification of individual markings, which can essentially be seen as a natural tag. Many species exhibit individual variation in physical traits or noticeable scarring. If photographed, an individual can be cataloged and future sightings later compared. This particular method has provided much knowledge on annual migration patterns, long-distance movements, and site fidelity (e.g., Stevick et al. 2006).

As it is one of the more surface-active cetaceans, the humpback whale (*Megaptera novaeangliae*) has been well studied since the 1970's. However, there are still unknowns regarding fine scale movement preferences and sociality. The primary objective of this thesis is to use the behavior of individual humpback whales within feeding grounds in the Gulf of Maine to determine population level patterns of ecology.

1.2 Study Location- the Gulf of Maine

The Gulf of Maine (GOM) is one of the most productive and well-studied oceanic regions in the United States (Carlton 2003). Often referred to as a “sea within a sea,” this region has historically been important culturally, economically, and scientifically. It still maintains some of the largest fisheries in the United States and supports a wealth of biodiversity associated with seasonal peaks in productivity. The spatial and temporal variation of life within the waters is largely driven by its unique physical properties and processes. The GOM region acquired its current shape and bathymetry from a series of geomorphologic processes spanning millions of years. Following periods of tectonic uplift and erosion, the entire area was covered by the Laurentide glaciation; during glacial retreat the GOM basin was deeply carved and sculpted (Uchupi and Bolmer 2008). The modern-day Gulf of Maine is now a 90,700 km² sea off the coast of New England with a bathymetry characterized as numerous basins separated by high banks and ridges (Townsend et al. 2004). A mosaic of oceanographic processes interact with this bathymetry to create a geologically rich environment that promotes life. Cold, nutrient rich waters flow from northern currents and are circulated throughout the region by tidal fluxes and influences from the bathymetry. Seasonal and interannual fluctuations of sea surface temperature (SST) are seen with average highs during the summer and lows during the winter (Balch et al. 2002). On a more local scale, annual fluctuations in SST vary with the underlying topography (Friedland and Hare 2007). The vertical upwelling of nutrients is amplified by tidal forces and seasonal convective mixing supporting seasonal blooms of phytoplankton, which attracts higher levels of biodiversity (including fish, seabirds, and marine mammals).

This study is focused primarily within a specific region in the northern GOM offshore of Bar Harbor, ME. This region is characterized by a complex series of underwater ridges and supports a seasonal population of humpback whales. From approximately June-October, individual humpback whales travel between three distinct “hotspots” within the study area. Chapter 3 also includes data from Stellwagen Bank Marine Sanctuary in the southern GOM. In this region, there is a longer seasonal timeframe of humpback whale sightings and a greater number of individual whales seen each year.

1.3 Humpback Whale Background

1.3.1 Biology

1.3.1.1 Taxonomy and Physiology. The humpback whale is classified under the order *Cetacea* and the suborder *Mysticeti*. The mysticetes are more commonly known as baleen whales, set apart from the toothed whales of suborder *Odontoceti*. Mysticetes evolved from cetaceans with teeth under selection pressures to take in vast quantities of prey rather than a single prey item; they use their baleen to filter organisms from water. Humpback whales further belong to the family *Balaenopteridae* known as the rorqual whales. The defining characteristic of this group is the presence of ventral grooves that enable throat expansion for gulp feeding. Humpbacks whales are easily distinguished from other rorquals by their dark stocky body and long pectoral flippers and are the only surviving member of their genus *Megaptera*. They are moderately large in size, averaging 13-15m in length with a record of 18m (Chittleborough 1965; Winn and Reichley 1985). Females are on average larger in body size than males (Lockyer 1984). Like all baleen

whales, humpback individuals in the northern hemisphere are smaller in size on average than those in the southern hemisphere which may signify differences in the duration of respective fasting periods.

1.3.1.2 Life History. Both male and female humpback whales reach sexual maturity at the age of 5-7 years, though evidence suggests some regions may have slower maturation rates than others (Clapham 1992; Gabrielle et al. 2007). Calves are born in low-latitude breeding grounds following an 11-12 month gestation period and are weaned from lactation after 6-10 months. By the end of their first year, calves typically achieve independence with permanent separation from their mother (Clapham and Mayo 1990). Because of the long gestation period, females cannot have more than one calf per year. The estimated mean birth interval for North Atlantic humpback whales is 2.38 years (Barlow and Clapham 1997). Intervals in southeastern Alaska have been estimated at 2.78 years and 1.72 years in Hawaii (Baker et al. 1987). Females may however become pregnant immediately following calving and some females have been reported with a birth interval of only 1 year (Clapham and Mayo 1987; Chittleborough 1958). It has been suggested that females with longer birth intervals may be more likely to produce male calves; however this has yet to be fully documented (Wiley and Clapham 1993).

Like many large mammals, humpback whales have a long life span and adults have a high rate of survivorship (Caughley 1966). The life expectancy of whales is difficult to measure and dispute remains regarding maximum age of a humpback. The most quantitative data regarding age has come from whaling biologists who would examine a laminar ear plug of dead whales. From this data the maximum age of a humpback whale was 48 years but this is likely biased due to gunner selectivity (Chittleborough 1965).

More data on age of animals may be acquired from naturally stranded animals; however this provides a low sample size and potential bias as well (Stevick 1999). The survival rate for an adult humpback whale has been estimated at both 0.951 and 0.96 (Buckland 1990; Barlow and Clapham 1997). Mortality of calves and juveniles is considered to be slightly higher and may vary depending on geographic region (Gabriele et al. 2001; Rosenbaum et al. 2002). The causes of natural mortality of large whales are also difficult to estimate. Because of their large body size, natural predators are few. However it has been suggested the predation pressure of killer whales may have originally driven the need for long distance migration to breed (Corkeron and Connor 1999). Both killer whales and false killer whales have been known to take marine mammals as prey (Silber et al. 1990; Florez-Gonzalez et al. 1994; Baird and Whitehead 2000; Ford et al. 2005). The impact of this predation is unknown and highly debated. Through analysis of fluke photographs, Clapham (2001) determined that killer whale predation on humpback whales in the North Atlantic was negligible and that most killer whale rate scars were acquired by calves during their first migration. Mehta et al. (2007) agreed with this finding, suggesting that adult baleen whales do not make up an important part of the killer whale diet. However, the threat posed by killer whale predation on humpback whales may vary geographically depending on differential prey selection (McCordic et al. 2013). Parasitism has also been thought to potentially effect large whales (Felix et al. 2006). External parasites include the whale louse and barnacle, neither of which would likely impact survivorship (Matthews 1978; Rowntree 1996). Little is known on the effect of endoparasitism in humpback whales (Clapham 2000). There has been one documented case of mortality where 14 humpback whales were fatally infected by a

dinoflagellate neurotoxin (Geraci et al. 1987). Unusual mortality events were also seen in North Atlantic humpback whales in both 2003 and 2006 but causes remain unknown (Robbins 2007).

1.3.2 Ecology

1.3.2.1 Movement Patterns. Movement of an animal reflects a complex result of competing demands and motivations. The habitat of cetaceans is dynamic and essentially free of barriers providing the opportunity for lots of movement. Movement patterns of the humpback whale have been well studied for many years as much of their distribution is relatively coastal. First understanding of these patterns was developed through whaling stations and fisheries (Matthews 1938; Dawbin 1966). A more thorough understanding has been developed through the development of techniques such as photo-identification of natural markings. Individual humpback whales can be identified by distinct markings on the ventral side of their fluke (Katona et al. 1979; Katona and Beard 1990). In the North Atlantic, a catalog of flukes has been maintained since the 1970's and now consists of almost 10,000 individuals. Re-sightings of known individuals have contributed greatly to current knowledge. Deployment of telemetry tags and genetic sampling has even further helped define generalities in spatial use (Mate 2007; Palsboll et al. 1997). Methods are discussed in more detail below.

The movement behaviors of migratory large whales can be broadly categorized by three scales: large-scale (1000's of kilometers), meso-scale (10-100's of kilometers), and fine-scale (0-10 kilometers). Movement decisions at each of those scales are likely driven by different needs (Kenney et al. 2001). Large directed basin-scale movements occur during seasonal migration. Each year, the humpback whale undergoes one of the most

extensive migrations known to mammals sometimes covering over 8,000 km (e.g., Stone et al. 1990; Rasmussen et al. 2007). This migration represents movement between high latitude foraging areas and low-latitude breeding sites. Time spent in high-latitude waters is correlated with seasonal productivity of those regions. Reasons for such long distance migration from those productive sites to reproduce are still only speculated but include predator evasion, temperature tolerance of calves, and cultural holdovers that may no longer be relevant (Corkeron and Connor 1999). The timing of these long-distance migrations are segregated by both sex and age, with pregnant females arriving first to breeding locations (Chittleborough 1965; Dawbin 1966). It has been suggested that some individuals do not make the long migrations each year but remain in feeding sites year round (Brown et al. 1995). Calves make their first migration to a foraging site with their mother and continually return to the same location each subsequent year; individuals have proven to show a high degree of site fidelity to specific regions (Clapham and Mayo 1987; Weinrich et al. 1993; Stevick et al. 2003b). In the North Atlantic Ocean, populations are spatially structured into four general feeding aggregations: the Gulf of Maine, eastern Canada, Western Greenland, and eastern North Atlantic. Individuals from each aggregation migrate to breeding sites in the West Indies; however, specific feeding and breeding sites are not necessarily correlated (Clapham 1999). Evidence suggests the timing of migrations from each specific feeding location may segregate breeding opportunities temporally (Stevick et al. 2003b). Geographic site fidelity has shown influence on genetic makeup of local populations (Palsboll et al. 2001; Weinrich et al. 2006).

At a more regional meso-scale, occasional movements of individual humpback

whales have been seen between feeding aggregations within a season (Katona and Beard 1990; Calambokidis et al. 1996). This may be related to interannual shifts in prey availability. Stevick et al. (2006) correlated rates of individual exchange between the Gulf of Maine and eastern Canada feeding aggregations with abundances of preferred prey. Distribution shifts were also observed in Norway following a crash in capelin stocks (Christensen et al. 1992). A smaller-scale site fidelity of individuals within the large general feeding aggregations has also been seen; movement of individuals between these foraging sites is common. In Western Greenland, rates of exchange between specific sites may actually be decreasing, suggesting even stronger site fidelity at a smaller scale (Larsen and Hammond 2004).

Within a specific region of a foraging location, movement of individuals is likely in response to local patch density of prey. Less is known about these small fine-scale movement events but recent advances in tagging technology have begun describing these decisions. The three-dimensional movements of humpback whales in response to fish shoals have been documented demonstrating diel patterns in diving depths and higher turning angles in regions of dense prey (Friedelaender et al. 2009; Hazen et al. 2009). Variation in movement patterns of individual whales has been suggested; some individuals may leave a specific feeding area and undertake a more large-scale movement event (Kennedy et al. 2014).

1.3.2.2 Foraging Patterns. Humpback whales are active predators and require significant intake of energy during the feeding season to sustain through a migration fast. As humpbacks are baleen whales with morphology selected towards consuming vast quantities of small prey at once, foraging behaviors reflect the need to exploit dense

patches of prey (Simila and Ugarte 1993; Piatt and Metheven 1992; Friedlaender et al. 2006; Witteveen et al. 2009). They are generalists and consume a variety of species mostly consisting of euphausiids and small schooling fish; specific behaviors such as bubble nets and clouds are utilized to consume certain types of prey (e.g., Jurasz and Jurasz 1979; Weinrich et al. 1992). These behaviors are likely acquired through cultural transmission (Weinrich et al. 2006; Allen et al. 2013). Specific preferences for certain prey are seen to vary geographically. Within the Gulf of Maine, while euphausiids have been documented as a source of prey (Paquet et al. 1997) diet is thought to be largely consisting of small schooling fish (Hain et al. 1995; Weinrich et al. 1997, Kenney et al. 1997). In the northern Gulf of Maine, Atlantic herring (*Clupea harengus*) is believed to be the preferred fish (Paquet et al. 1997; Weinrich et al. 1997). Sand lance (*Ammodytes* spp.) is documented as the main source of prey for humpback whales in the southern Gulf (Payne et al. 1990; Weinrich et al. 1992; Hain et al. 1995). Spatial distribution over foraging areas likely reflects preferences of these species but much remains unknown on small-scale movement patterns.

1.3.2.3 Social Structure. Unlike odontocetes, baleen whales are quite solitary; however sociality still remains an important factor of life history. The social structure of humpback whales is two-fold in nature with different motivations for interaction during the breeding and feeding seasons. During the breeding season, affiliations are based on the motivation to reproduce. Humpback whales are polygynous and polyandrous; no long-term bonds are demonstrated in mating. In breeding sites, competitive groups are formed composed of several males and one single female (Tyack and Whitehead 1983; Clapham 1992). The closest male associating with the female is known as the principal

escort and defends his position against the other competing males. These competitive groups can last for several hours with individuals remaining in association for the duration of that time. Competition can be quite violent and has even thought to result in death (Pack et al. 1998). During the breeding season, female interactions are minimal and females are even thought to avoid each other (Clapham 2000; Baker et al. 1987). Obviously, strong affiliations exist between mother and calf pairs. For 10-12 months after birth, a calf will remain in the association of its mother migrating as a pair to the higher latitude feeding grounds. After weaning, a mother and calf are broken and preferential associations are not seen again.

Social affiliations are not as obvious and well delineated during the summer feeding months. As group foraging is not as beneficial when consuming vast amounts of prey, humpback whales do not often form large pods. On occasion, cooperative group feeding does occur likely to condense patches of prey (Whitehead 1983; Weinrich and Kuhlberg 1991; Clapham 1993). Humpback whale societies on feeding grounds are generally described as “fission-fusion,” composed of small and unstable groups. Individuals may remain together for short periods of time from several hours to multiple days. However, long term bonds have rarely been observed. Ramp (2010) recently demonstrated long term affiliations between non-lactating females in the Gulf of St Lawrence through social networking techniques. Similar evaluations have not been investigated in populations in the Gulf of Maine.

1.3.3 Population Status and Conservation

Stocks of North Atlantic humpback whales were severely reduced by the whaling industry (Reeve et al. 2002; Tonnessen and Johnsen 1982). With a comparably coastal

distribution, humpbacks were one of the first species to be hunted to commercial extinction (Clapham 1999; Clapham et al. 1997). Although there are no concrete time series data, it is believed that at least 2000 humpback whales were taken by non-mechanical early whaling and 5000 taken by modern whaling by 1910 (Smith and Reeves 2003). Since the end of commercial whaling, populations in the North Atlantic have been thought to be consistently increasing though estimates vary and are uncertain due to lack of historical baselines (Best 1993; Paterson et al. 1994; Clapham et al. 1999). Stevick et al. (2003a) estimated the North Atlantic population to include approximately 11570 individual whales. In 1997, Barlow and Clapham estimated a 6.5% annual rate of increase. The humpback whale is still federally listed in the United States as an Endangered Species. It is also considered “vulnerable” to extinction by the World Conservation Union.

Although protected from commercial harvest, humpback whales remain threatened by multiple anthropogenic factors. As human use of the oceans continues to increase, the indirect effects of activities such as fishing and boating on whales have become more pronounced. Robbins and Mattila (2001) calculated based on scarring patterns that over half of the humpback whales in the Gulf of Maine have experienced entanglements in fishing gear. Lines usually become wrapped around the caudal peduncle and slowly but increasingly impact the fitness of that individual over time, reducing ability for movement and digging into the flesh. Ship strikes also pose a significant threat to humpbacks due to their coastal distribution. At least 3 North Atlantic humpback whales are killed each year by anthropogenic activity (Waring et al. 2003). While concrete understanding of the impact on the population level does not exist, some believe human

activities may be affecting recovery in certain areas (Volgenau et al. 1995). Whales are also affected by increase in underwater noise and potentially by the increase in whale-watching activity.

1.4 Methods Used to Study Cetaceans

With the increase in indirect anthropogenic threat, knowledge on distributions and behaviors of cetaceans has become increasingly important. However, as mentioned above, thorough understanding of the ecology of offshore animals who spend considerable time under water is difficult to achieve. Methods used to retrieve information have steadily evolved in response to increases in technology and computational capacity.

The earliest endeavors to understand whale biology and movement used data from whaling operations. Researchers allowed on whaling vessels could collect information on size, anatomy, and geographic locations of taken whales. Many distinctly numbered Discovery tags were also shot and implanted into whales, which could then be recovered when the whale was killed (Mate et al. 2007). These tags provided early understanding of movement and range as the scientist would know where the whale was geographically located at time of tagging and then at time of death. Following the moratorium on commercial whaling, methods of study shifted to less invasive approaches. To understand general ranges or seasonal occurrences, both systematic and opportunistic surveys can be utilized. Most surveys now use a distance sampling approach where at each sighting observers record location of the vessel, approximate distance of animals from the vessel, and radial angle of animals from the vessel (Buckland et al. 2001). With this data, one can estimate abundances by assuming that with increasing distance from the boat an

animal is decreasingly likely to be seen by an observer and calculating an estimate for individual animals not seen. Habitat models can also be built from survey data by analyzing where animals are seen and where they are not seen.

Broad surveys do not provide more fine-scale data and many generations of tags have been developed to get tracklines of individual whales over a landscape. With tagging, the challenge is to develop a tag that contains technology to retrieve the data you want, but is small enough to minimize impact on the whale and strong enough to remain attached for a desired duration of time. Early tags were conventional radio (VHF and HF), first implanted subdermally into a whale with a modified shotgun (Watkins and Schevill 1975). Handheld poles were also used to attach VHF tags to the body of whales (Mate and Harvey 1984). However, to get data from VHF tags the researcher must stay with a receiver within range of the antenna on the tagged whale. This would involve either following the whale in a vessel or only receiving position updates when the whale traveled by the receiver on shore. Thus, more recent studies have shifted to using ARGOS tags, where positions are collected and transmitted from satellites. Early satellite tags were quite large in size and difficult to attach to a large whale that could not be constrained. Eventually, technology advances produced smaller tag sizes allowing for projectile deployment and eventually tags that could be implanted beneath the skin of the whale. These tags can stay on the whale for hundreds of days; a recent study had a tag stay on a blue whale for 620 days (Mate et al. 2011). However, data is only locational. Larger tags like the DTAG can also track depth and body orientation of the animal (pitch, roll, and heading) as well as sound (Johnson and Tyack 2003). These tags are deployed with a long pole that can slap it onto the targeted animal and are attached via suction cup.

Custom software called TrackPlot can then provide 3-D visualizations of the whale's movements under the water (Ware et al. 2006).

Whales can also be monitored and studied with use of molecular techniques. Samples can be collected most easily from stranded or dead whales ashore. However, skin and blubber can be collected from free-ranging whales with biopsy sampling techniques (e.g., Palsboll et al. 1997). This is usually collected with the use of a crossbow with an arrow fitted with a barbed hollow tip and flotation device. From a small boat, the arrow is shot at the body of a whale, pings off, and floats at the surface of the water for retrieval. This sample can then be analyzed to assess diet (via stable isotopes or fatty acid signature analysis), heredity and sex of individuals, genetic variation of populations, etc. Molecular techniques have led to understanding of population stocks, whale distributions, social behavior, and strange movements (Rosenbaum et al. 2004).

A more simple way to identify and track movements of individual whales is to photograph natural markings. Many species of cetacean have distinct characteristics that are permanent enough to be used to identify an individual repeatedly over time. In the early 1970's, it was discovered that humpback whales possess individually unique black and white markings on the ventral side of their fluke (Katona and Whitehead 1981). Humpbacks typically raise their flukes out of the water when making a sounding dive, which allows researchers to photograph the markings. Individuals are often re-sighted in different locations and over various timeframes providing a natural understanding of movement. Several organizations have collected many images to create long-term catalogs of individuals within a given area. Allied Whale of College of the Atlantic in Bar Harbor, ME curates the North Atlantic Humpback Whale Catalog, which currently

contains 8000 individuals from all regions of the North Atlantic (from Gulf of Maine to Europe).

1.5 Thesis Objectives

Although widely studied, much is still unknown about movement patterns and social structure of the humpback whale. This thesis was designed to advance the limited baseline of knowledge on this population through exploration of individual behavior and to present quantitative techniques that could be used on many already existing cetacean datasets.

While large processes like the migration of humpback whales are well documented, less has been quantified on smaller scale movements. An individual is likely to return to the same feeding ground each year. However, once that individual has arrived to that general region, it has the choice of where to move around that area, how often to associate with other whales, and what individual whales to associate with. Throughout a season individuals seem to move quite a bit over the landscape, likely in search of prey. Pairs and groups are also seen to form and split. There may be a pattern and predictability in these behaviors that have not yet been elucidated. From personal observations, over a given season whales seem to move back and forth between distinct hotspots that are similar each year. These hotspots in whale density are most likely associated with peaks in productivity at those times. But what makes a whale decide to leave a given hotspot in search for another? These movements may be dependent on both transient and stable oceanographic features but may also be dependent on the movement of conspecifics. I think there is likely a more structured social network between individuals of whales within a region than is currently understood. From previous and un-quantified

observations, it appears to me that the common males of the study area tend to associate with each other each year. As no competition over feeding has been observed in humpback whales, they are either cooperating to feed under the water (little surface feeding is observed in this region) or have preferred companionships.

Many similar questions exist for whales in other regions but have not been addressed due to limitations of data. My research is focused on using photo-identification of natural markings as the main source of data, and I hope that the methods used in my thesis will be utilized by other organizations to address their questions in a logistically feasible way. These methods are useful in comparison to other techniques of data collection for several reasons. First, while boat surveys provide general ideas of whale distribution and can be used to create habitat models, these models represent a snapshot of time for whales in given locations. Whales seen in certain locations are correlated to the oceanographic features represented in those areas. By identifying individuals over time, you can actually look at active movements of individuals towards specific locations. If a whale is sighted in one area and then re-sighted in another area, it can be understood that the individual chose to move within that time period towards certain features. In a way, this method is similar to data provided by satellite tagging. However, there are many factors that make tagging not a feasible option for many organizations to study whales. For instance, tags are expensive. The cost of a single tag can be \$3700 (Mate 2011). Because of that expense only a certain number of tags can be used dependent on the budget of a project providing a small sample size. As there can be a degree of individuality in movement (Ford et al. 2012), a small number of tagged individuals may not be representative of the population. Lastly, the behavioral and/or physiological

responses of whales to tags are still unknown (Mate 2011).

In contrast, photo-identification data sets that already exist span many years and represent behavior patterns of many individuals. This minimizes cost while greatly increasing potential sample sizes. The methods used to collect photo-identification data are also much less invasive than any form of tagging. With my thesis, I demonstrate use of photo-identification data over three chapters looking first at the sociality and movement of whales within my study area and then expanding to compare these structures to whales from a different feeding aggregation. Clear and brief objectives of each chapter are outlined below.

Part I examines the sociality of humpback whales on feeding grounds in the northern Gulf of Maine through analysis of association patterns of known individual whales. In doing this, I elucidate relationships and create a social network of whales to provide one of the first such association analyses on this species and the first within this feeding aggregation. This study will provide important insight into the conflicting reports of humpback whale social structure during summer months.

Part II aims to analyze fine scale distribution patterns of humpback whales in the northern Gulf of Maine to further the understanding of seasonal fluctuations and hotspots in density. My methods present a novel use of photo-identification of individuals to demonstrate movement decisions leading to a predictive habitat model. Outcomes of this model will be compared to a more traditional model based on systematic transect surveys that were run offshore of Mount Desert Island during the field seasons of 2010-2013.

Part III examines differences in social structure and habitat selection between northern and southern GOM humpback whale feeding sub-regions. This study will

document the variability that may exist within the same species over different geographic areas to highlight the need for site-specific knowledge when developing management plans.

1.6 Data Collection and Effort

Data used in this thesis were collected by both myself and other researchers at Allied Whale of College of the Atlantic. Photo-identification data collection has been ongoing at Allied Whale since the 1970s but a more standardized regime began in 1995. I personally joined the effort as a research assistant in 2008. During that season, I collected data on a full-time basis, working as both a deckhand on the whale watch and a researcher. As researcher, I recorded data on every whale sighted, took photographs of each animal, and sorted/edited all images in the office. In 2010, I became the coordinator of Allied Whale systemized research transects, implementing data collection methodology, scheduling boat trips, and participating in all resulting field efforts. In 2011, I also began organizing the research program with the Bar Harbor Whale Watch Company. Every year, I serve as the interface between the Whale Watch and Allied Whale; I select research assistants, train them in photo-identification techniques, oversee field season data collection, edit and standardize all data entry, and maintain all equipment. In addition, I coordinate shore-based logistics, help plan and enact student projects at, assist in boat trips to, and maintain equipment for our offshore research station at Mount Desert Rock.

CHAPTER 2

SOCIAL NETWORKING IN HUMPBACK WHALES ON FEEDINGS GROUNDS

2.1 Background

Knowledge on the social structure of animals is critical to understanding both population biology and behavioral ecology. Many important aspects of life are influenced by society; social ties with other conspecifics may affect fitness, cultural transmission of information, genetic makeup, spatial distribution, and methods of exploiting resources (Wilson, 1975; Krutzen et al. 2003; McComb et al. 2003; Connor et al. 1998). There are varying definitions of social structure, which loosely center around how individuals in spatiotemporal proximity interact with each other (Whitehead 2010). Hinde (1975) built a now widely used framework to describe this structure as simple interactions and more complex relationships building to a hierarchal society. Methods of analyzing societies vary based on the type of organism and the ease or difficulty with which data can be collected. In vertebrate populations, experimentation is often impossible making simple hypothesis testing quite difficult; thus, many have turn to a more descriptive approach of analyzing associations and affiliations. Although the importance of social networks has been suggested for a long time (Wilson 1975), they have only recently gained prominence in the field of behavioral ecology (Krause 2007). Social networks consist of nodes representing individual animals with edges representing the relationship between a dyad, or pair of individuals (Croft et al. 2007). Essentially, a network can capture the complexity of a social structure by illuminating who is connected to who and further, how strong those connections are.

Understanding of the social structure of cetaceans is quite limited, as detailed long-term data is difficult to acquire. Within the past decade, much attention has been placed on elucidating these social organizations as it is thought to be an important part of their ecology, specifically in transmission of information (Whitehead; Connor; Baird). However, most studies have been focused on odontocetes, which often form large stable groups and spend time at the surface (Mann 2000). What has been particularly helpful in these studies has been the ability to identify individuals within a cetacean population (Whitehead 1995). Identification of individuals through photographic surveys is a noninvasive and logistically feasible technique to study these wide-ranging animals (Wursig & Jefferson 1977). Networks have been used to demonstrate patterns of social interactions in odontocetes, including bottlenose dolphins (Lusseau et al. 2005), sperm whales (Christal and Whitehead 2001), and killer whales (Baird and Whitehead 2000). This information has been useful in understanding spatial population structuring and cultural transmission, leading to proposed differences in management (Baird and Whitehead 2000; Foote et al. 2010, Whitehead and Rendell 2004; Wilson et al. 2004).

Even less is known about the social structure of mysticetes, or baleen whales. These animals are often more difficult to study because their offshore distributions, more solitary nature, and vast annual migrations between feeding and breeding locations. However, most of these species are still classified as endangered and face continually increasing anthropogenic threats, making the understanding of their biology more critical (Clapham 1999). Most social studies on baleen whales have been done when on their breeding grounds (Matilla et al. 1987; Clapham et al. 1992; Rosenbaum et al. 1997; Erts

and Rosenbaum 2003); however, the behavioral and environmental constraints of feeding grounds are likely to cause very different social organization during the summer months.

The North Atlantic humpback whale (*Megaptera noveangliae*) makes extensive migrations each year to arrive at summer foraging sites. Until recently, it has been assumed that humpback whale societies on feeding grounds are “fission-fusion”, mostly made of short unstable associations and that these short associations may be driven by kinship (Clapham 2000, Weinrich et al. 2006). However, re-associations of specific pairs have been observed over multiple years (Weinrich 1991) Further, Ramp et al. (2010) demonstrated that humpback societies on feeding grounds may be more complex than expected with some non-related, non-lactating females forming stable associations lasting up to six years. The mechanisms driving these associations are still unclear. In a very recent paper, Allen et al. (2013) quantified a network based cultural transmission of a new feeding behavior in possible response to shifts in prey species, stressing the importance of social interactions between individuals.

2.1.1 Objectives

In this section I examine the sociality of humpback whales on feeding grounds in the northern Gulf of Maine through analysis of association patterns of known individual whales. In doing this, I elucidate relationships and create a social network of whales providing one of the first such association analyses on this species and the first within this feeding aggregation. This study provides important insight into the conflicting reports of humpback whale social structure during summer months.

2.2 Methods

My dataset consists of sightings that have been recorded from both systematic research and opportunistic whale watch vessels from Allied Whale and the Bar Harbor Whale Watch Company. The data spans approximately 25 years and most sightings are located within and around the Schoodic Ridges of the Gulf of Maine, located offshore Mount Desert Island, ME. Data collected from whale watch vessels were recorded by trained observers and contain locational information, photo identification of each individual, behavioral observations, and noted associations between individuals. An association is defined as animals that are spatially within two body lengths of each other and diving/surfacing in synchrony (Weinrich and Kuhlberg 1991; Clapham 1993). Each individual whale has been identified by markings on the ventral of the fluke and matched to the North Atlantic Humpback Whale Catalog (NAHWC) housed at Allied Whale. In addition, the sex and approximate age is known for some of the whales within the catalog based on either skin biopsy results or having been seen with a calf.

For animals that are difficult to observe (like offshore, deep-diving whales), it is commonplace to record associations rather than interactions (Whitehead 2008). Association matrices were constructed composed of all individuals sighted during the entire study; for each noted association, individuals were either assigned a one (that individual was present in group) or a zero (that individual was not present in group). Association matrices were also constructed for each year to compare seasons.

Association indices were then calculated to estimate the proportion of time that each dyad spent together. A variety of association matrices exist with different degrees of assumptions. The simplest is a ratio: number of sightings where a dyad was associated

divided by the number of sightings where at least one of the pair was identified (Ginsberg and Young 1992). However, because not every individual can be identified in every sighting due to behavioral or logistical difficulties, we used the Half-Weight Index as shown below (Cairns and Schwager 1987; Bejder et al. 1998).

$$(2.1) \quad HWI = \frac{x}{(x + y_{ab} + 0.5(y_a + y_b))}$$

where x is the number of times both individual a and individual b are seen together, y_a and y_b represent when either individual a/b were seen alone, and y_{ab} where each individual was seen at the same time separately. Use of this index also allows for comparison to other cetacean studies as many refer to this index (e.g., Bejder et al. 1998, Ramp et al. 2010).

Next, I tested the randomness of the associations by applying permutations to the matrices to create null models. Essentially, these permutations look for preferred or avoided companionships between individuals. Bejder et al. (1998) demonstrated use of a routine developed by Manly (1995) to create alternative datasets. This method takes the existing matrices and performs a series of flips, where the 1s and 0s from a randomly selected row and column are switched, preserving the original dimensions of the matrix. I used this method with the extensions of Whitehead (1999) to remove demographic effects and Krause (2009), which preserves a valid Markov chain. Enough flips were repeated to create a randomized dataset and 1000 permuted matrices were subsequently constructed. Association indices of the actual data were then compared to the indices of the permuted data and z-scores were calculated to demonstrate significance. Degree centrality and

eigenvector centrality were then calculated to identify the range of sociality among the individuals (i.e. explore if certain individuals are more “popular” than others) (e.g., Lusseau et al. 2008).

Social networks were built to assess community structure. Visual representations were built displaying vertices (individual whales) and edges (connections between whales). Local communities were detected through a clustering algorithm using the method of optimal modularity. In this technique, divisions are placed between communities where fewer than expected edges are found (Newman 2006). Communities were delineated for each season and turnover between seasons was also examined.

Lastly, the scales in temporal strength of relationships were assessed using lagged association rates (LAR) described by Whitehead (1995; 2008). This technique estimates the probability of the association between a dyad a specified time lag (τ) after a previous association. The LAR $g(\tau)$ will be one if a dyad is always still associated after τ time units and zero if dyads split and never reform during that time. The null association rates are shown as

$$(2.2) \quad g(\tau) = \frac{n}{N}$$

where n is the total number of associations and N shows pairs of sampling periods τ time units apart. These values represent the expected lagged associations if whales were to randomly associate. Both rates were standardized by dividing by the number of associates within that sampling period as not all associates of an individual could have been identified. The precision was estimated using jackknife procedures. The standardized lagged association rates (SLAR) $g'(\tau)$ were plotted over time and compared to rates

estimated from the null models previously created through permutations. This allowed to observe how relationships changed over time. This procedure was carried out at various time scales. First, analyses were run on the complete whale data to observe relationships on the long term. To observe more short-term temporal dynamics, analyses were run within one season and between three consecutive seasons.

2.3 Results

2.3.1 Groups and Dyads

Over the entire study period, 152 individual whales were sighted and matched. 52 of those individuals were only seen once but most were sighted repeatedly between and within seasons, with the maximum number of re-sightings being 417. Group sizes were small, with a majority of the individuals being sighted alone (see Table 2.1). Those traveling with companions were most frequently seen in pairs and the largest group observed was 10 individuals (this group was observed cooperatively bubble net feeding).

Figure 2.1 shows the simple connections between individual whales. Most whales were at some point seen in association with another whale. Half-weight indices between dyads ranged from 0.01-0.6 (see Figure 2.2). A majority of the dyads had a half-weight index of values less than 0.2. The mean HWI was 0.039 (SD=0.07). The highest mean was seen in female-female associations (0.1, SD=0.1) and the lowest between males (0.01, SD=0.02). All calves had an association index of 1 with mothers. Calves were removed from subsequent analyses.

Table 2.1 Summary of Group Sightings Data

Group Size	Number of Groups	Percent of total
1	1299	66.86%
2	449	23.11%
3	133	6.85%
4	33	1.70%
5	9	0.46%
6	6	0.31%
7	9	0.46%
8	4	0.21%
10	1	0.05%
Total Groups	1943	

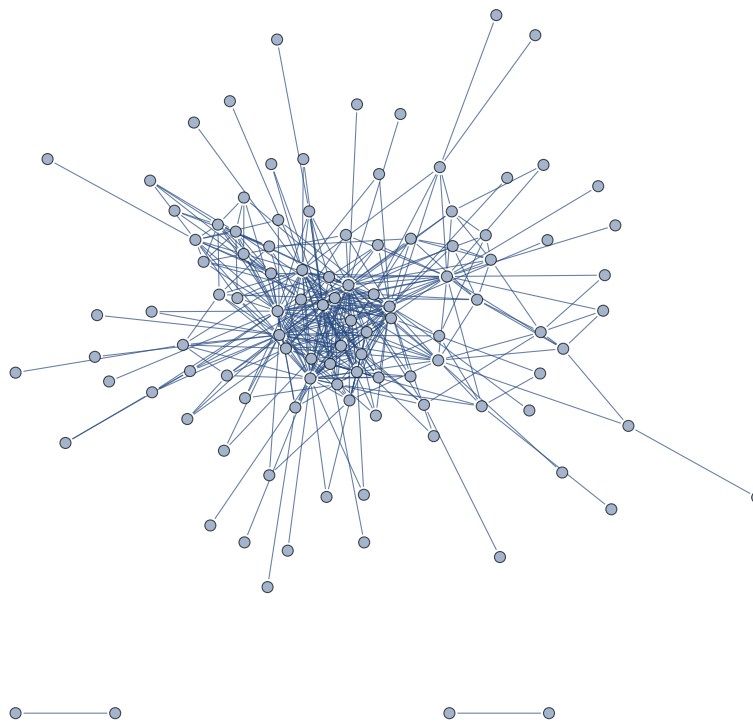


Figure 2.1. Simple network of connections between individual humpback whales throughout all seasons. Each node is an individual whale and each line represents an association between pairs. This network is unweighted.

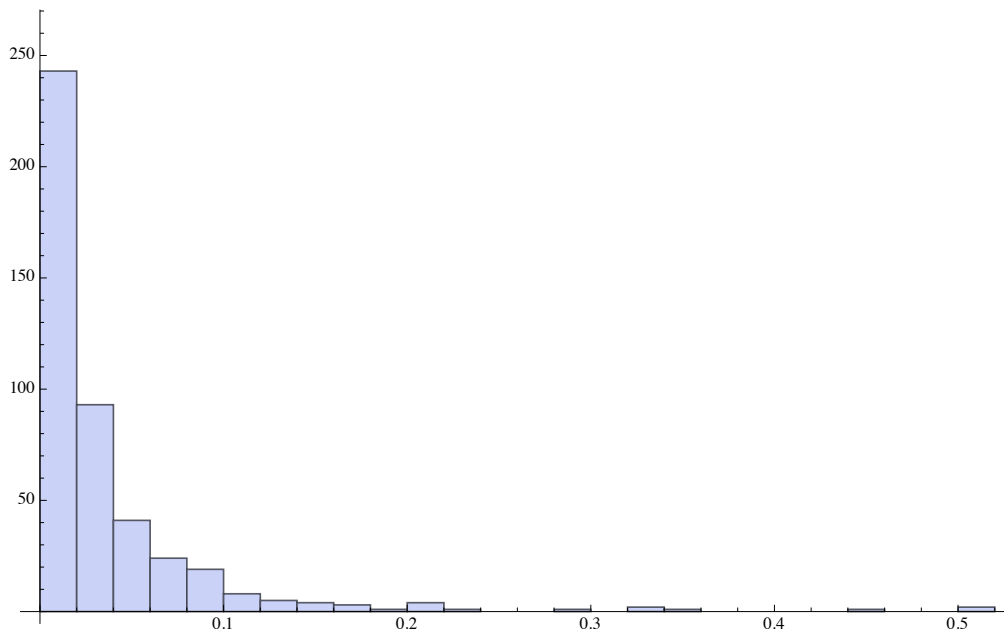


Figure 2.2 Frequencies of HWI values observed between dyads. HWI values range from 0-1.

2.3.2 Preferred associations

Null models were created to test for preferred or avoided associations. To achieve randomization of the association matrices, we first performed 10,000 “flips” of {0,1} pairs; this created a randomized matrix of the same structure and composed of the same individuals as the original data. 999 subsequent random matrices were created each separated by 10 additional flips of {0,1} pairs, resulting in a set of 1000 random association matrices.

Evidence was found for preferred companionship between individual humpback whales. 94 positive significant associations were found between dyads (z -scores > 1.96). 11 negative significant associations were also found (z -scores < -1.96). The majority of the significant associations were found between individuals of unknown sex; 29 preferred companionships were F-F, 17 were M-M, and 47 were M-F.

2.3.3 Network measures

Using positive z -scores from the null model as weights of association, the resulting network showed nine local communities mostly composed of individuals of both sex (Figure 2.3) The largest community was connected at least loosely to every other community and strongly to two other of the larger communities. Individuals within the network showed differences in sociality within the larger network. Degree centrality ranged from 0-35. Figure 2.4 shows a network with nodes weighted by the number of connections. Most individuals had a low degree centrality while several had a very high value. The four whales with highest degree centrality were older males. Degree centrality and eigenvector centrality were correlated; most individuals with many connections were connected to other well-connected individuals. There were a few outliers; e.g., a male

whale (Sword) had high degree centrality but one of the lowest values for eigenvector centrality. The network on a whole showed a relatively low centralization (0.265). Average path length was 6.02 and the density was 0.095.

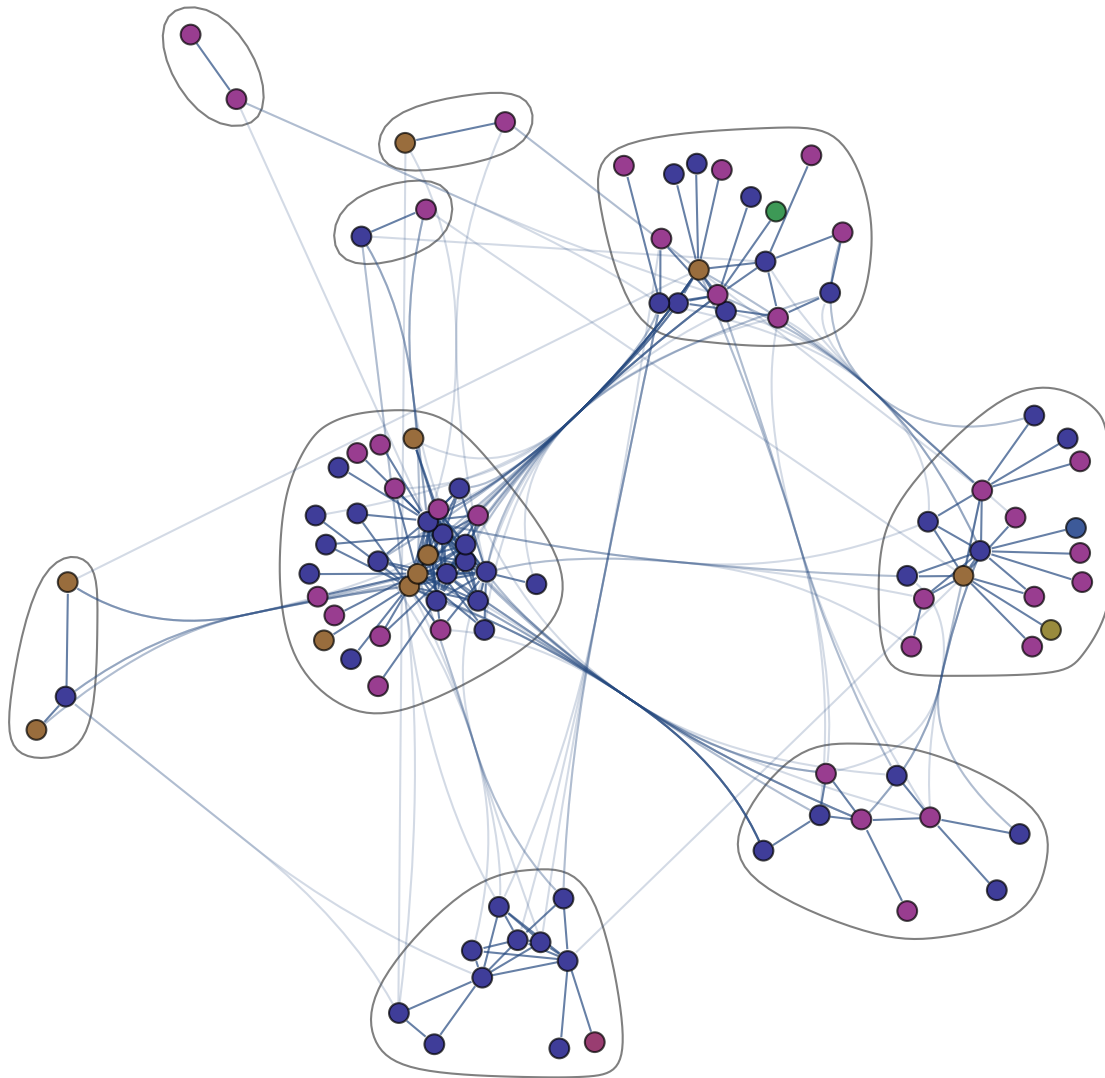


Figure 2.3. Community network weighted by z-scores from null model comparison and clustered through optimal modularity. Nodes are colored by sex (purple-unknown, pink-female, gold-male).

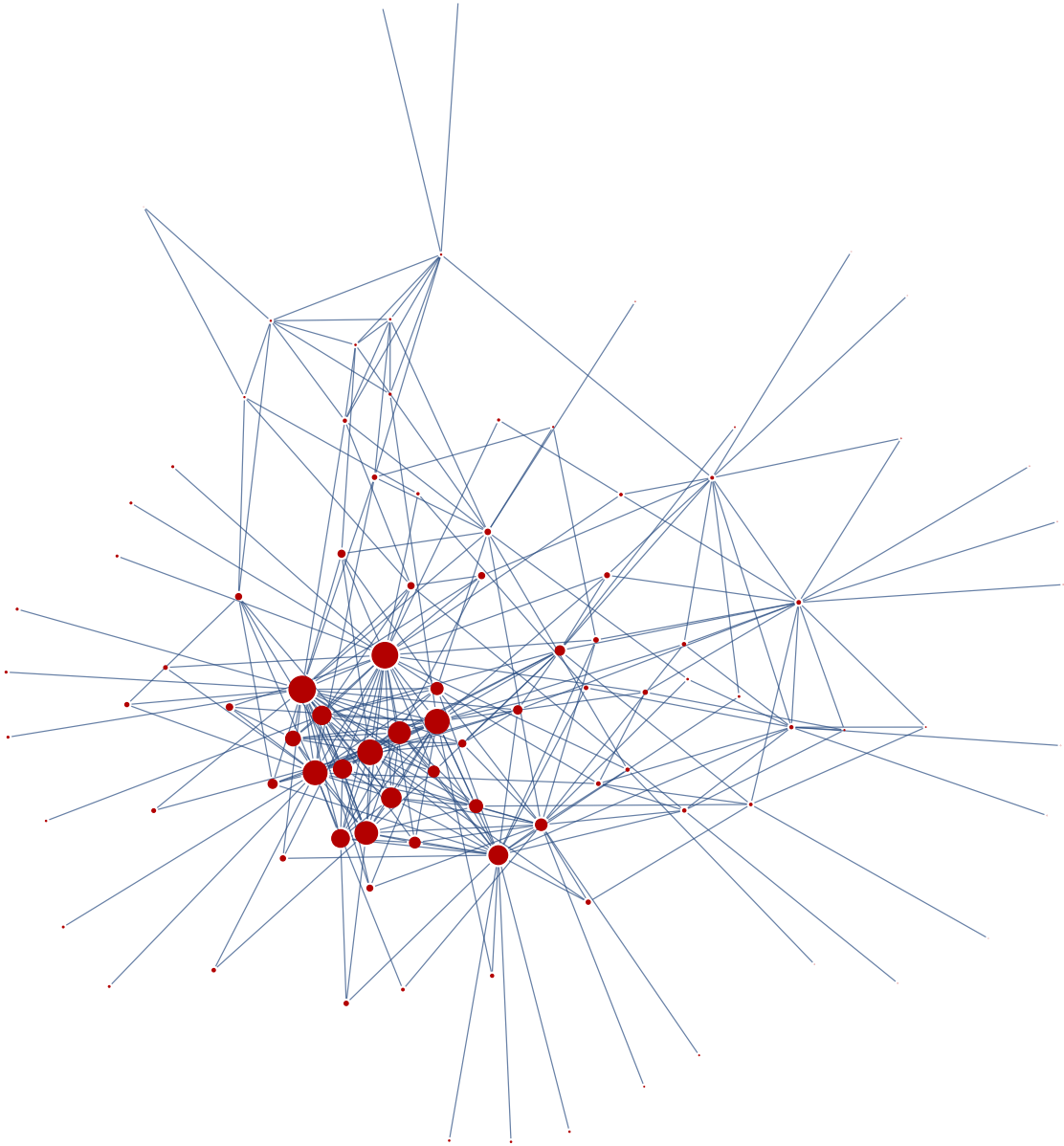


Figure 2.4. Network with nodes weighted by degree centrality. Larger nodes have more connections, smaller less.

2.3.4 Communities over time

Community structure and make-up did shift over time. Different individuals were seen in different years, though some were present throughout the entire time period. Many of the

individuals who were frequently sighted were grouped into the same local community but there were exceptions. Some individuals were seen almost every year but did not have preferred association with each other. Average half-weight indices between dyads showed some variation though values never exceeded 0.2 (Figure 2.5). Centralization also changed from year to year with a peak in 2002 (coinciding with the lowest mean HWI).

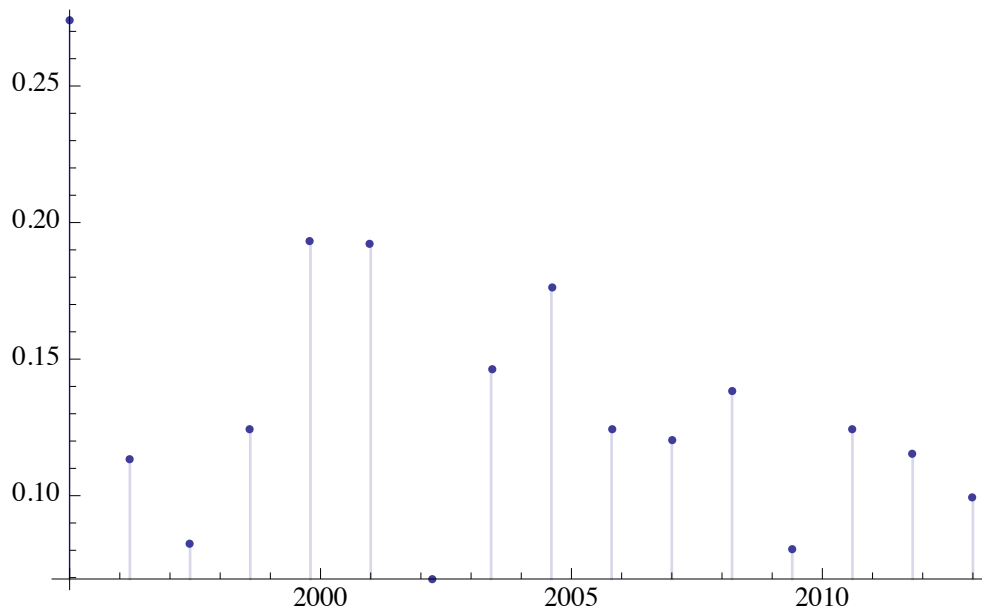


Figure 2.5. Mean HWI over time.

When partitioned, comparisons to null models and clustering produced a different number of local communities for each season. Figure 2.6 shows a community transition plot over nine years based on positive Z - scores. Each column of nodes represents a different year; the size of nodes is dependent on the size of the grouped community (i.e., big circle = community composed of many individuals). The edges between nodes essentially represent the movement of individuals from one community into another

between years. They are weighted by the "destination fraction"- or how large a fraction of individuals moves into a community the following year. A degree of inter-annual stability was seen, depicted by the large bars moving between communities from year to year.

2.3.5 Associations over time

The estimated values for SLARs demonstrated differences in temporal association strength at different time scales. Figure 2.7 depicts the long-term patterns in associations as seen with all of the data; time lags were in years. After the first year, the SLAR dropped to 0.053 showing that many dyads had disbanded but some did persist. With each subsequent time lag, the SLAR decreased but did remain above the random rates. The SLARs were also investigated at an intermediate scale to look at association persistence over several seasons. Figure 2.8 provides an example analyzing the most recent two years. An initial peak shows rates >0.25 suggesting a higher rate of persistence. After several days, the rates drop off considerably and then stabilize closer to the exhibited long-term rates. A spiked increase did appear at a time lag of approximately 350 days. The sustained rate of the second season was slightly higher than the first, suggesting inter-annual variation in persistence. Lastly, Figure 2.9 shows the change in SLAR over one season with time lag of days. In general, the rates decrease with time lags. However, near the end of the season, the observed rates actually meet the random rates suggesting the general dissolution of groups within that one year.

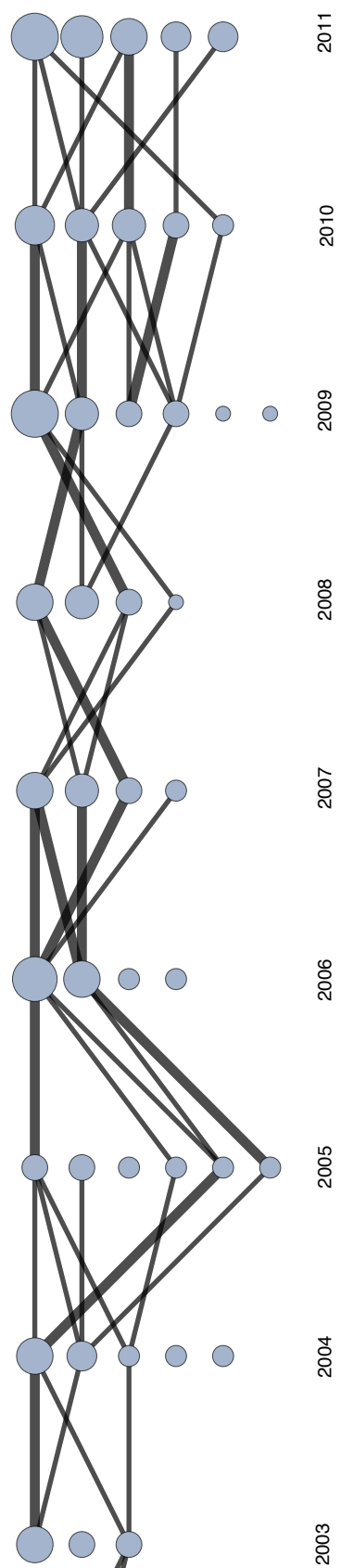


Figure 2.6. Community transition plot. This plot demonstrates the transfer of individual members between communities over time from 2003-2011. Within a year, each node represents a separate community (divided by optimal modularity). The nodes are sized and ordered by the actual size of the community with largest communities on top. Gray lines in between years represent the fraction of individuals that move from one community to another over time; the size of the line is weighted by the size of the fraction. Large straight lines denote community persistence between the years.

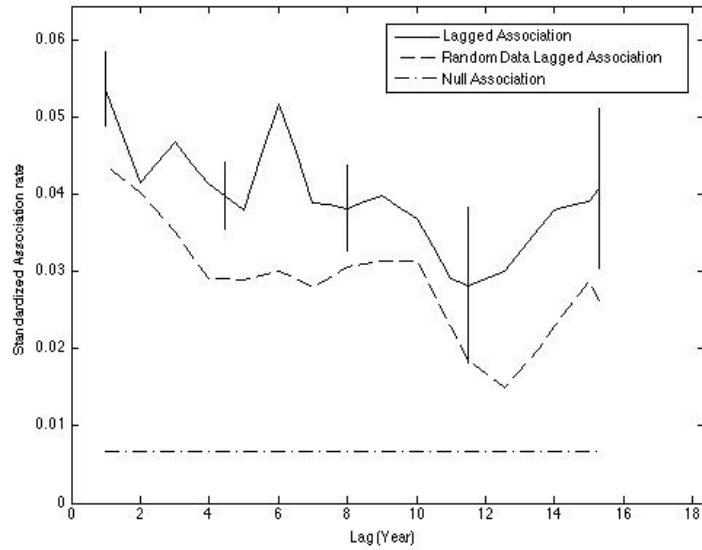


Figure 2.7. Standardized lagged association rates for all of the data with time lags of years. The solid line represents the actual data from communities; the dashed line shows the rates calculated from a randomized model. The bottom dotted line is the null association. Vertical bars represent jackknife estimates of precision.

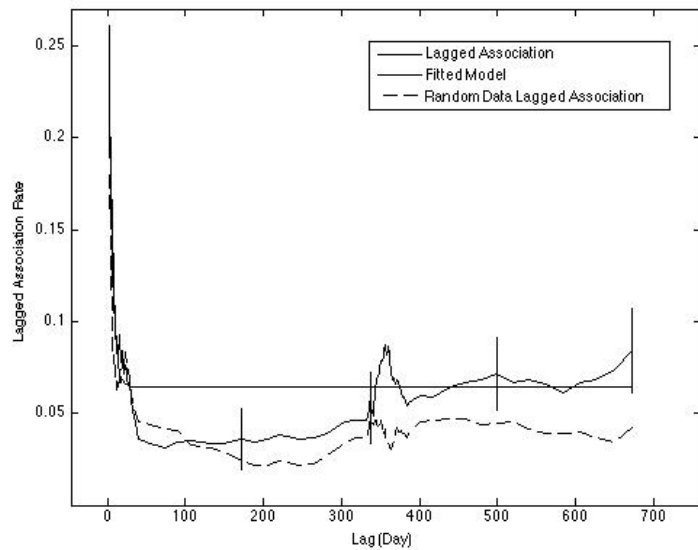


Figure 2.8. Standardized lagged association rates for a subset of data (2011-2012). Time lag is in days. The narrow solid line represents rates calculated from the data, the dashed from the randomized model. The bolded line is a model fit representing casual acquaintances + close companions. Vertical bars are jackknife estimates of precision.

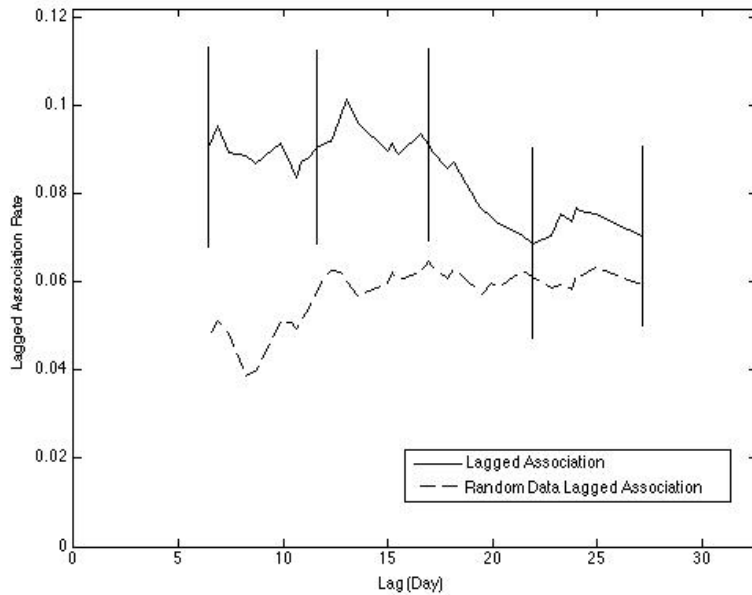


Figure 2.9. Standardized lagged association rates within one season. The solid line shows the rates estimated for the actual data; the dashed line is the randomized model. Vertical bars are jackknife estimates of precision.

2.4 Discussion

Group living develops in animals if there are benefits to fitness (Alexander 1974); the direct benefit may be multi-faceted and difficult to identify or explain. With cetaceans, the most obvious benefits of affiliative social behavior are defense from predators in an open environment devoid of refuge, increased potential of mating, group care of offspring, and cooperative foraging (Connor 2000). Humpback whales on feeding grounds in the Gulf of Maine receive little threat from predation. The only documented predators of humpbacks are killer whales (*Orcinus orca*). While many individuals exhibit rake scars on their flukes from past attacks, sightings of killer whales within the Gulf are rare (Mehta et al. 2007). Thus, predation pressure likely does not influence the observed social structure during the feeding season. In low-latitude breeding areas, the primary

resource for a humpback individual is access to a potential mate; during that season, associations are formed to benefit chance of reproduction. Ramp et al. (2010) suggested that humpback whales become increasingly likely to associate at the end of the feeding season in preparation for migration to breeding areas. At this time, pairings may represent reproductive incentives. However, throughout the rest of the season, the most likely explanation for grouped behavior is an increase in foraging success- potentially aiding in capture of schooling fish or in assisting in the tracking of prey patches. Many surface active behaviors are seen during the summer in this area (breaching, pectoral flipper slapping, etc.). It is unclear if this is a potentially a method of communication with other conspecifics. In some other regions, large group cooperative foraging (>10 individuals) is seen often (e.g., Glacier Bay Alaska). The smaller average group sizes seen in my study likely reflect differences in prey choice or in prey distribution. During this study, there was one large cooperative foraging event composed of frequently sighted individuals. Thus, these individuals do have “knowledge” of this type of foraging strategy but choose to most often associate in pairs and trios.

Few publications have sought to quantify social structure of humpback whales on feeding grounds; this structure has most often been described as a loose fission-fusion grouping of animals (Clapham 1999; Connor 2000). Recently, non-random associations between non-lactating females were demonstrated in the Gulf of St. Lawrence suggesting that there may be more stability in structure than previously assumed (Ramp et al. 2010). My results support this notion for a more stable structuring of communities on the feeding ground than previously thought. My data show many pairings between individuals that are significantly non-random, meaning that individuals choose whom

they associate with. While values of HWI were quite low in comparison to strong odontocete societies (e.g., bottlenose dolphin male alliances that rarely separate), the nonrandom significance supports companion choice in the humpback whales. While individuals are likely to often be also sighted alone and groups will split and reform, there is a pattern to which individuals will associate. Similar to Ramp et al. (2010), the strongest associations as demonstrated by HWI in my data were seen between females. However, many significant relationships were also seen between sexes and between males. Interestingly, the most well-connected and “popular” individuals were all males. This suggests that males on feeding grounds may not have as strong fidelity to each other but there may be value in having many associates and being a part of a local community. This is in contrast to previous thought on male associations. While these males are the most “popular” within the network, the overall network structure exhibits low centralization, meaning that influence or prestige is spread among individuals and not placed strongly within only one. In addition, the average shortest path length quite high, denoting a considerable distance between individuals. It may be important in the future to link the social behavior of these individual whales to their demonstrated movements. Some of these associations could be the product of overlapping spatial preferences or similar ranging behaviors. For instance, the well-connected whales may be those that travel over the widest range of landscape.

Analyses of the temporal component of associations did show that some relationships persist throughout years. While the probability that those dyads would be seen together on the long-term was low, they were still above random suggesting some stability in the bonds between individuals. On a smaller time-scale, my results also

suggest loose persistence of bonds within and between seasons. Initial association rates are relatively high after the first time lag demonstrating that if individuals are seen together one day, they are likely to still be together the next day. Unlike Ramp (2010), my data did not show an increase in association rates directly before migration; rather group disbanding at the end of the season. But the peak in the SLAR after a time lag of 350 days suggests those same groups may reform on the feeding area during the following year.

This study also demonstrates the first evidence for divisible local communities within a humpback whale social network based on association strengths. It has been long understood that individuals primarily make annual returns to the specific feeding ground they were brought to as calves. However, smaller-scale fidelity within that feeding group has not been documented. These communities do not stay the same inter-annually; however, some stability is seen in the clustering each year. In this, I see a fission-fusion society with annual interchange but with a core set of individual preferences in companionship.

While evidence for social structure and significant relationships between individuals is seen in this data, there are some limitations and assumptions mostly due to the opportunistic nature of the data collection. Though expensive and logistically difficult, there is a need for long-term focal animal follows and a wider spatial-temporal coverage. More concrete understanding might also be achieved if the sex and age of each sighted individual were known. While the overall mean HWI of individuals of unknown sex was low, knowing the sex of individuals would be helpful in interpreting the composition of the local communities. In addition, the definition of association used in

this study (whales traveling in synchrony within two body lengths) is commonly used in cetacean research but may have limitations. It is assumed that whales are only interacting if in close proximity; however, whales may potentially be in communication with each other long distances through transmission of low-frequency sounds (Tyack 2000; Au et al. 2006). In an acoustic playback study, humpback whales were thought to have responded to sounds 10 km away (Tyack and Whitehead 1983). If whales are actually communicating with other individuals within a large radius of many kilometers, the associations in this study are likely only a subset of a larger network of interactions. This broader social network may be all but impossible to quantify but the implications need to be realized in interpretation of this data.

The social analyses of this study support the hypothesis that bonds between humpback whale individuals during the feeding months appear to be stronger and more stable than originally thought. The purposes of these bonds remain unknown and may likely be a complex product of many factors including fitness benefit and possibly culture. As Allen et al. (2013) demonstrated, socially connected individuals may transfer valuable information between each other. Whales are long-lived and intelligent; knowledge gained through sociality may generate fitness benefits that are not easily observed during a study period.

CHAPTER 3

USING MOVEMENT DECISIONS OF INDIVIDUAL WHALES TO MODEL HABITAT SELECTION

3.1 Background

Quantifying the movement patterns of animals is critical to the understanding of life history and thus important to their conservation (Skellam, 1951; Nathan et al. 2008; Cagnacci et al. 2010). Identification of factors that determine where an animal is located spatially and what drives movement around that area greatly aids the development of effective management plans. Ideally, organisms occupy locations where their daily resource needs may be met (Burt 1943; Roever et al. 2013); the ability to move provides an organism with the ability to utilize their environment and choose their habitat. Habitat selection has long been studied by ecologists and is thought to be a product of many things including resource availability, community dynamics, and social structure (Gaillard et al. 2010). As it is a complex result of competing demands and motivations, the quantification of habitat selection is equally complex. The result is often a statistical comparison of habitat that is available versus habitat that is used by organisms. The method in doing this can be approached in many different ways but usually involves some form of spatial modeling based on animal locations. Two main types have been recognized. One is a presence-only design drawing comparisons between used and unused locations (e.g., Calenge and Basille 2008); a second is actually testing for selection, which can be defined as choice of habitat being disproportionate to its availability (Manly et al. 2002; McLoughlin et al. 2009). Both face the problem of needing to incorporate a spatial-temporal scale and the accessibility of resources (Beyer et al. 2010). One approach to representing resource accessibility is to use a movement

model that can weight the resources by an estimate of that accessibility (Hjermann 2000; Fieberg et al. 2010). Resource selection functions (RSFs) that examine the probability of an animal in choosing a particular resource have become commonly used in habitat selection (Roever et al. 2013).

Marine organisms provide additional challenges in that they are difficult to observe for long periods of time and are often wide-ranging with few barriers to their movement (Palumbi 2003; Rasmussen et al. 2007; Shillinger et al. 2008). Habitat modeling of cetaceans has become important due to increased anthropogenic threats to populations triggering the design of Marine Protected Areas. Current models typically are developed by either line-transect surveys fit with generalized linear models or generalized additive models to correlate sighted distributions with oceanographic variables (MacLeod et al. 2004; Redfern et al. 2006; Marubini et al. 2009; Embling et al. 2010). Other models are developed by analyzing individual movement patterns through GPS data loggers tagged on individual whales (Baumgartner and Mate 2005; Friedlander et al. 2006; Irvine et al. 2014). While tagging provides great insight into fine-scale movements, there are many limitations in this data such as low sample size, cost, and difficulty in acquiring permits (Redfern et al. 2006; Hebblewhite and Haydon 2010).

Essentially, habitat selection of baleen whales in foraging grounds is dependent on large-scale movements (long migration), meso-scale movements (search for hotspots), and small-scale movements (actual foraging) (Kenney et al. 2001; Hazen et al. 2009). Much is still unknown about fine-scale movement patterns within feeding grounds and many recent studies have been dedicated to gaining more insight on this in hopes to more accurately predict seasonal distributions (Friedlaender et al. 2009; Pendleton et al. 2009;

Pershing et al. 2009). The North Atlantic humpback whale makes incredible seasonal migrations from low latitude breeding grounds to high-latitude feeding sites. They are known for their site fidelity in feeding aggregations and this is thought to be a process of matrilineal information transfer (Weinrich et al. 2006). In the northern Gulf of Maine near Mount Desert Rock, humpback whales typically arrive in mid June and stay through September. Historical observations by whale watches and fishermen have suggested inter and intra-annual locational shifts in the areas of high whale concentrations. Each year, sightings are scattered across the region but focused around three distinct “hotspots”. However, much of these assumptions are biased due to the opportunistic nature of the observations. Many questions arise from the data. Why do the hotspots change over the years? Are there predictable patterns in movements around the area? It is assumed that the movement of whales is linked to prey density as energetic studies suggest that most cetaceans need daily food intake (Lockyer 1981; Kenney et al. 1985). However, given a patchy distribution of resources, whales are presented with a series of decisions to make in regards to movement.

3.1.1 Objectives

Chapter 3 analyzed fine scale distribution patterns of humpback whales in the northern Gulf of Maine to further the understanding of seasonal fluctuations and hotspots in density. The methods present a novel use of photo-identification of individuals to demonstrate movement decisions leading to a predictive habitat model. In addition, there is little information on scales of perception of whales. Landscapes were smoothed to assess appropriate variation in spatial contexts. Systematic transect surveys were also run to compare seasonal densities to model predictions.

3.2 Methods

3.2.1 Data

Data consisted of sightings from both opportunistic whale watches and systematic transects. The opportunistic sightings are from a long-term dataset collected on vessels of the Bar Harbor Whale Watch Company. As described in Chapter 2, on each trip, a researcher from Allied Whale collects data on each sighting that includes positions, group sizes, observed behavior, and photo identification. Chapter 1 discussed methods of photo-identification; individual whales were distinguished by markings on the ventral side of the fluke and compared to the North Atlantic Humpback Whale Catalog (NAWHC). In addition, distance sampling surveys were held during two field seasons. These surveys were run on a 26' research vessel and allowed for the expansion of effort beyond the typical movement range of the local whale watch vessels and examination of the density of whales in alternative locations. Transect lines were designed using Distance software and consisted of equal-spaced zig-zag lines placed in three designated study areas, each containing a historic hotspot. A chart of the study areas and current survey lines can be seen in Figure 3.1.

Surveys were run using distance sampling techniques (Buckland et al. 2000). The vessel traveled along the predetermined lines at a speed of 12 knots. On each survey, two observers located on either side of the boat called out all sightings of marine mammals, including data on species, group size, estimated distance from ship, and radial angles. A third person served as a recorder and gave a GPS time stamp for each sighting using Logger software. To eliminate visual bias dependent on sighting conditions, transects were only run on days with high visibility and wave height under three feet.

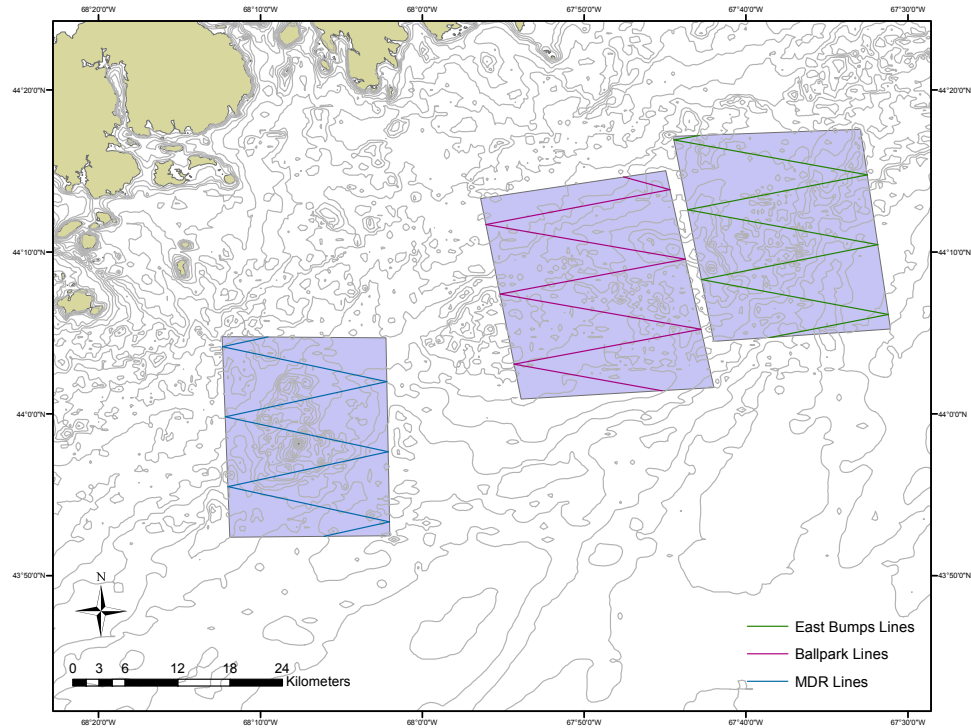


Figure 3.1 Transect lines covering whale feeding grounds.

3.2.2 Analyses

3.2.2.1 Movement Models. The opportunistic sightings dataset was partitioned first by individual whale, then by the year of sighting. Sets of sightings were then extracted where the same whale was seen on consecutive days. Consequently, the resulting dataset consisted of 733 pairs of locations (a start point and end point for one day movements of an individual) with dates ranging from 1993-2013.

Ocean habitats have very few barriers for movement, but a study area was designated based on historical observations and tracklines of whale watch vessels (Figure 3.2). Only sightings within the study area were used for analysis and animals outside were assumed to be heading towards a different feeding aggregation. Rasters for the

study area were created to represent landscape variables. Bathymetry data was obtained from USGS (<http://coastalmap.marine.usgs.gov/GISdata/regional/eastcoast/gome/bathymetry/contours/gom15ctr/gom15ctr.zip>, accessed on September 15, 2011) and converted to a raster in Esri ArcGIS v.10. An array to represent distance to shore was created from the bathymetry raster in Mathematica v.9. Squared versions of both bathymetry and slope were created; this allowed for non-linear interaction of preferences (e.g., Johnson and Gillingham 2005, Mashintonio et al. 2014). Bathymetry and distance from shore layers were standardized to have zero mean and unit standard deviation. Sea surface temperature data was extracted from MODIS Aqua satellite imagery in daily composites and converted to raster within Mathematica; this data was only available from 2002-2013. Last, a binary valid array for movements was created to remove areas to which it is not possible for whales to travel (i.e. land). All rasters had a cell size of 300 m by 300 m.

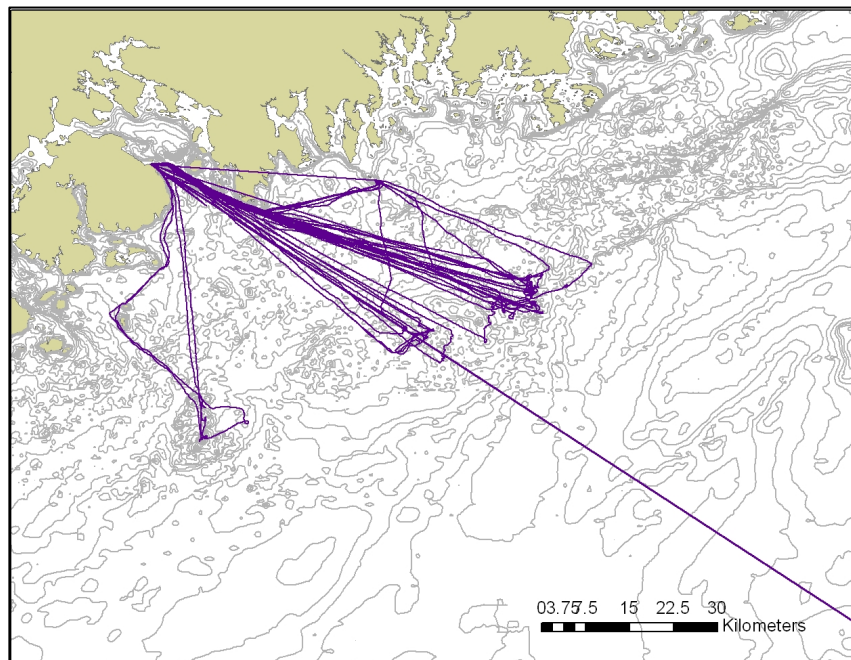


Figure 3.2 Subset of tracklines from the 2011 whale watch season.

Generalized additive models (GAMs) have most often used in marine mammal habitat selection studies (e.g., Embling et al. 2010; Anderwald et al. 2012). These models relate the response variables of locations to smoothed linear combinations of explanatory variables (Guisan et al. 2002). In this study, a conditional logistic model was applied to the sets of short-term movements; this model was originally developed for economic purposes to model consumer choice (McFadden 1984). Conditional logit allows for the examination of choice over a given landscape and the incorporation of cost of movement (e.g., Duchesne et al. 2010).

For each movement event i , every potential destination cell within the landscape has a vector of k predictor values x_j that represent landscape features as well as a distance value from the current location to that cell. The chosen cell y_i is represented as a binary response and given a value of one; a random subset of other available cells are assigned a value of zero. The probability p_j that an animal will choose a cell j within the available landscape as its next location is modeled as

$$P_i = \frac{e^{X_i\beta}}{\sum e^{X_i\beta}} \quad (3.1)$$

where β is a k by 1 vector of parameters to be estimated and X_i is the matrix of variables for all of the choices available for that event. With d_{ij} as the binary response vector, log-likelihood of the movement is

$$\mathcal{L}_i = \sum_{j \in C_i} d_{ij} \ln P(y_i = j) \quad (3.2)$$

The log-likelihood was maximized using a quasi-Newton algorithm and Akaike information criterion (AIC) was used for model selection. The model AIC values were then converted to model weights that sum to one and importance values were calculated for each parameter by summing the weights of the models in which that parameter appeared.

In this case, the events are the movements of whales in one day in relation to external variables. Pixels within a surrounding radius from the start point of the whale were analyzed for probability of selection. How large of a radius to include in a model depends on the movement capability of the animal during the time frame in question. Data was restricted to a radius of 20 pixels or six km, which retained 80% of the movement events. Movements larger within that time frame may represent a different kind of movement (i.e., searching for new feeding ground instead of movement within the feeding ground). The model again attempts to best match the probabilities to the actual response.

In the original model, the only variables included were distance from starting location, depth, slope, and distance from shore. These variables were constant and could be applied to all years that the dataset spanned. Data was truncated to the time period of 2002-2013 and a separate model was created with the dynamic variable of sea surface temperature. For this model, there were 468 movement events.

The variables of distance from shore and SST are intrinsically smoothed; bathymetry was the only variable smoothed within this study. Smoothing was done following techniques described by Mashintonio et al. (2014). The values of ocean depth were smoothed in an increasing radius from 0 to 40 pixels (the maximum representing

twice the size of the neighbor radius used for the model). Three models were fit at each radius: one using only the distance from the current location, one with the distance and smoothed depth at that radius, and the last also including the smoothed depth squared. The AIC was calculated for each model at each radius and the most appropriate scale was chosen by the lowest AIC.

A final model was run with the optimal smoothing scale. Landscape-wide habitat maps were created weighting the neighborhood pixels with model parameters.

3.2.2.2 Transect Data. Kernel densities were estimated from survey sightings for 2011 and 2013 using ArcGIS v.10. This function smooths a radius surrounding the point locations based on a quadratic formula where the greatest value is found in the center of the radius (the sighting location) and totals are calculated for intersecting radius cells. Density maps were also created using sightings of both humpback and fin whales.

3.2.2.3 Other Species. Movements of whales might not be solely dependent on environmental features but may also be affected by interactions with other animals. To investigate interspecific interactions, a permutation analysis was performed to see if humpback and fin whales (*Balaenoptera physalus*) tended to avoid each other or associate. A list was created of sightings data where more than one species were found on the same day. On each date, minimum distances between inter-species sightings were extracted (e.g., Figure 3.3). A model was then created to randomly assemble the actual sightings coordinates into date lists. These lists were partitioned to account for the proportion of sightings for each species on a given date in the actual data. From the randomized list, minimum distances were calculated. This process was repeated for 9999

iterations and the actual mean distance compared to the randomized model mean distance.

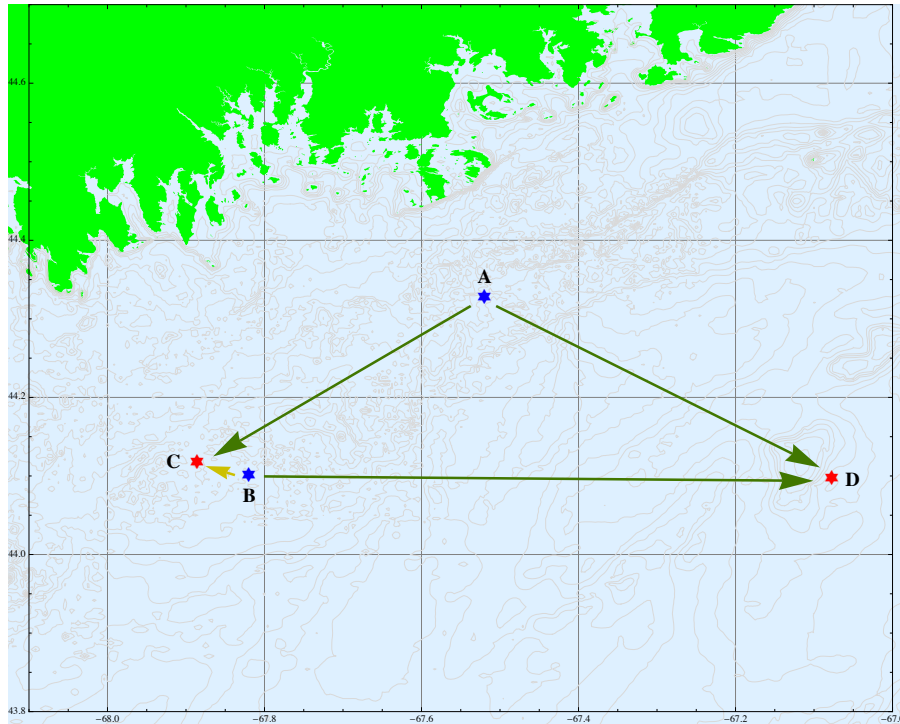


Figure 3.3 Example of interspecies distance measurements. Points A and B represent humpback whale sightings, while C and D represent fin whales sighted on that same day. The linear distance between B and C was selected as the minimum distance between the two species on that day.

3.3 Results

3.3.1 Movement Models

The optimal smoothing scale found for the bathymetry data was two pixels or 600 meters (Figure 3.4). The smoothed bathymetry layer is displayed in Figure 3.5. In early runs of the model, cost of movement (represented by distance from the current location) was always present as an important predictor; in subsequent models, cost was fixed so that it would automatically be included in every arrangement of variables. In early models, a

squared version of distance to shore was not included. This greatly limited the predictive value of the variable as whales were essentially forced to either like the shore or avoid the shore. Later models included the squared version, which actually decreased the importance of bathymetry as will be described below.

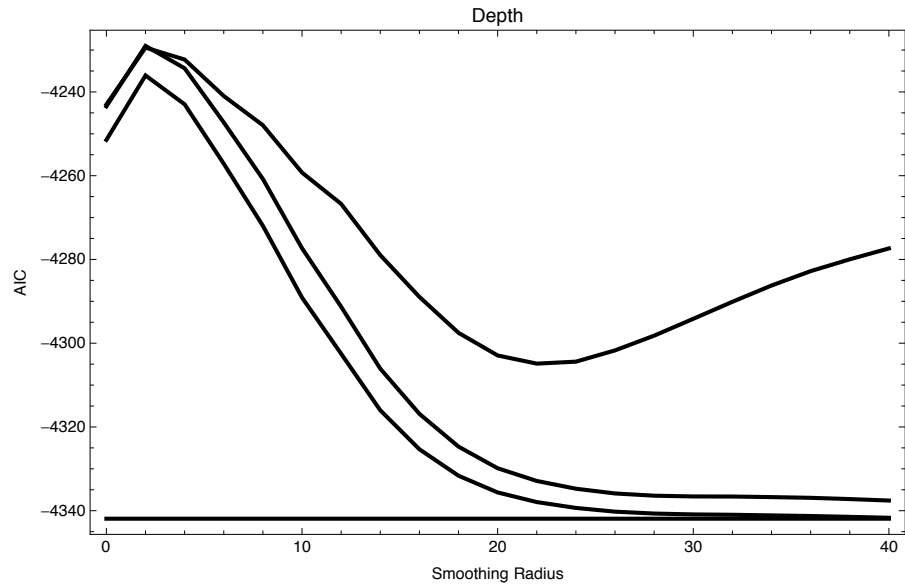


Figure 3.4 AIC values of models fit with the bathymetry raster smoothed at radii of 0 to 40 pixels. The bottom straight line represents the model fit with just distance from current location and the top lines show the models fit with depth and depth.²

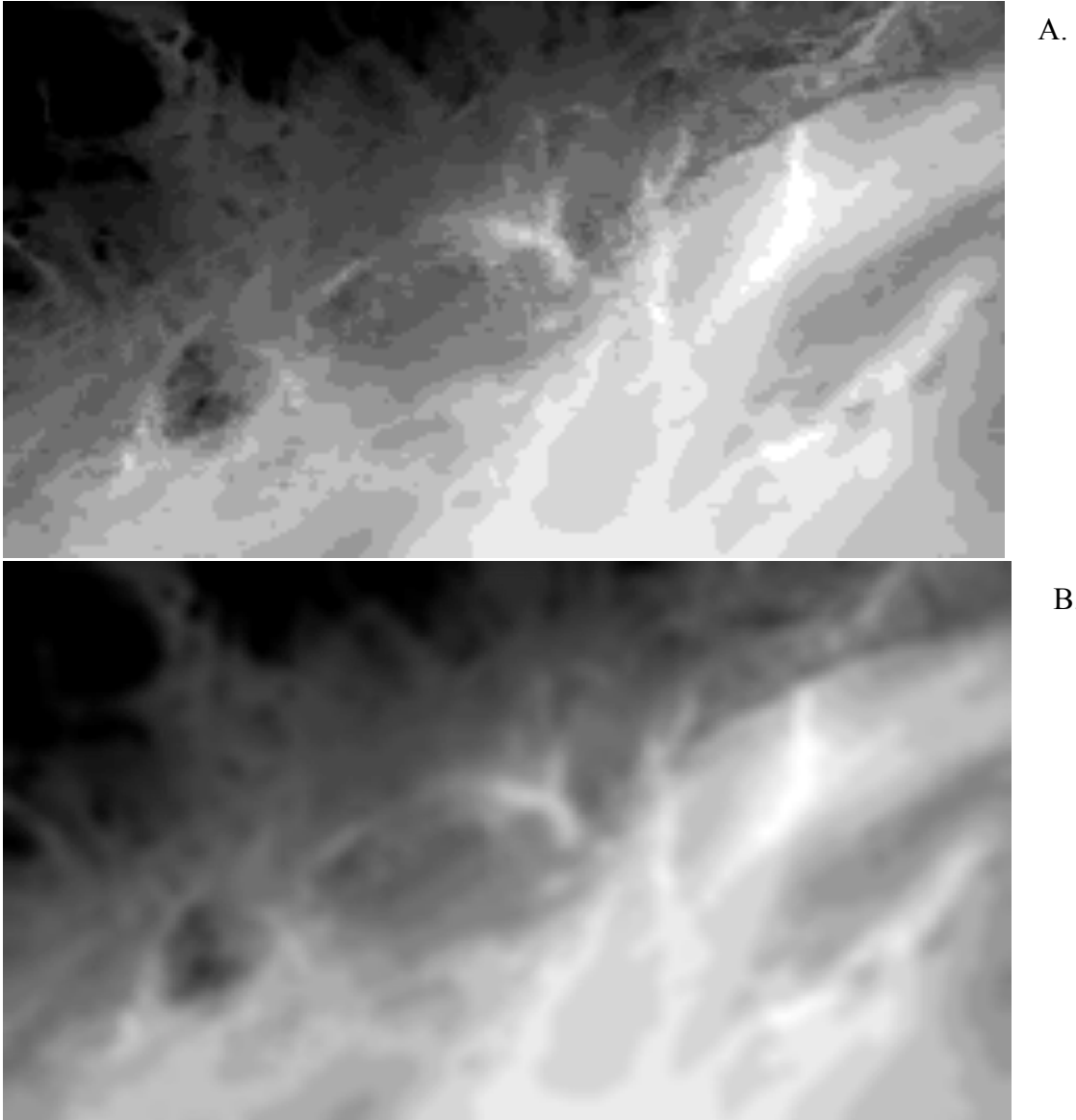


Figure 3.5. Original bathymetry raster (A.) and smoothed at a radius of two pixels (B.)

The final model was run first with the larger set of movements and all landscapes excepting SST (cost, bathymetry, bathymetry², distance to shore, and distance to shore²). The most parsimonious model included all variables except bathymetry² (Table 3.1). With minimal gain in AIC, the second best model did include all variables but was the only model in the top ten with that feature. Every other model excluded at least one of the variables. Cost had a negative effect on location choice, as expected. With the exception

of bathymetry², all variables had very high importance (Table 3.2). When parameter weights were used to create a landscape quality map (Figure 3.6), several patches of quality habitat were delineated. End points of movement events were mostly found in areas rated as high quality but there were some exceptions, indicating that other factors may be needed to explain the movements. In addition, some areas rated as high quality were not selected during any movements. Ocean depth and distance from shore variables were found to be highly correlated ($\rho = 0.86$) and they likely have a strong interaction with the model fitting, demonstrated by most models containing one or the other. If weighted parameters are applied separately to create a landscape map, results for quality habitat appear much different. On its own, the map for optimum depth is misleading; the best habitat appears to be land with a strong gradient leading offshore (Figure 3.7). In contrast, a map weighted only by distance from shore parameters depicts a narrow band of quality habitat (Figure 3.8). This dynamic suggests that distance from shore is the stronger predicting variable; whales prefer a narrow range of water offshore and within that band, shallower areas. The optimum distance for whales was calculated to be approximately 23.85 km from shore.

Table 3.1. Top Ten Models in Base Fitting

AIC	Cost	Bathymetry	Bathymetry ²	Distance to Shore	Distance to Shore ²
4012.54	-0.17	-1.66	-	-2.85	-8.41
4014.29	-0.17	-1.68	-0.13	-2.84	-8.35
4059.7	-0.18	-1.9	-	-	-4.51
4060.89	-0.18	-1.94	-0.23	-	-4.42
4144.99	-0.18	-	-	-3.5	-8.3
4146.98	-0.18	-	0.02	-3.5	-8.31
4155.4	-0.19	-1.89	-0.77	0.72	-
4162.55	-0.19	-1.75	-	0.8	-
4162.78	-0.19	-1.74	-0.86	-	-
4172.16	-0.2	-1.56	-	-	-

Table 3.2 Importance of Parameters in Base Model

	Importance	Value
Cost	1	-0.171024
Bathymetry	1	-1.66279
Bathymetry ₂	0.294821	-0.129346
Distance to Shore	1	-2.84482
Distance to Shore ₂	1	-8.38861

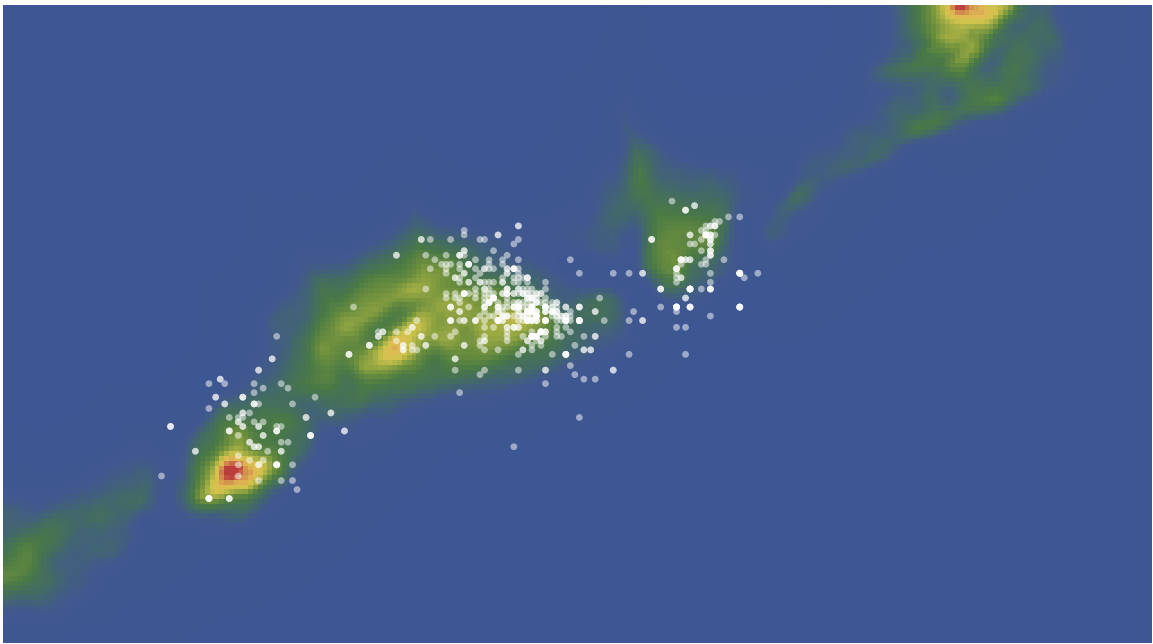


Figure 3.6 Landscape habitat rated by parameter weights. White points represent end location of movement events.

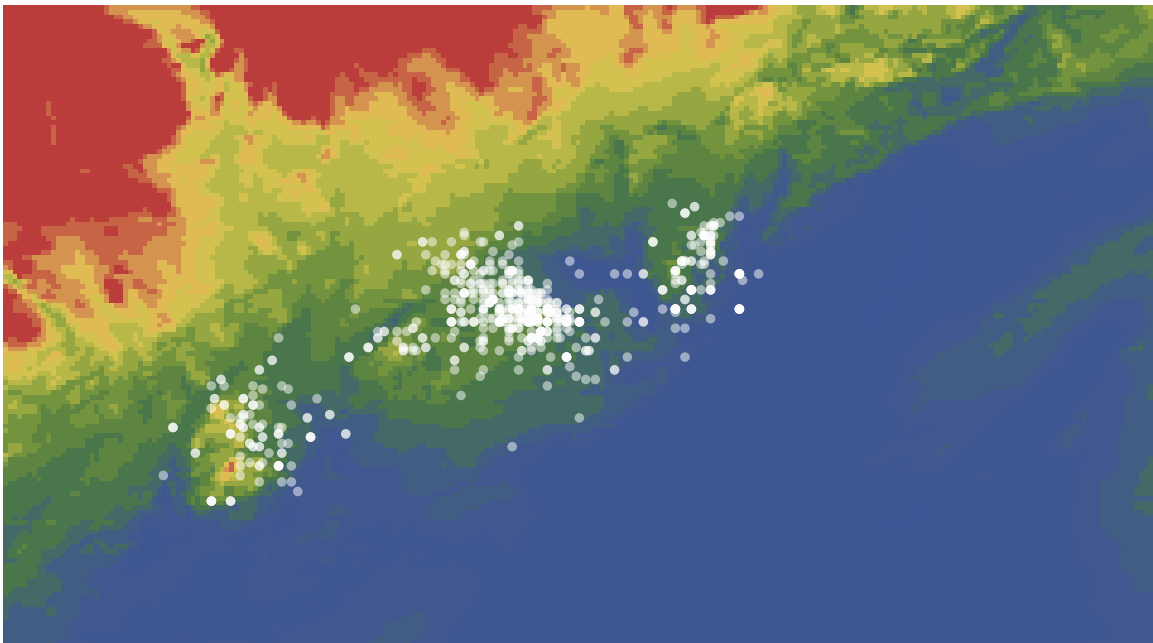


Figure 3.7 Landscape weighted only by the parameter weight of depth. White points represent end location of movement events.

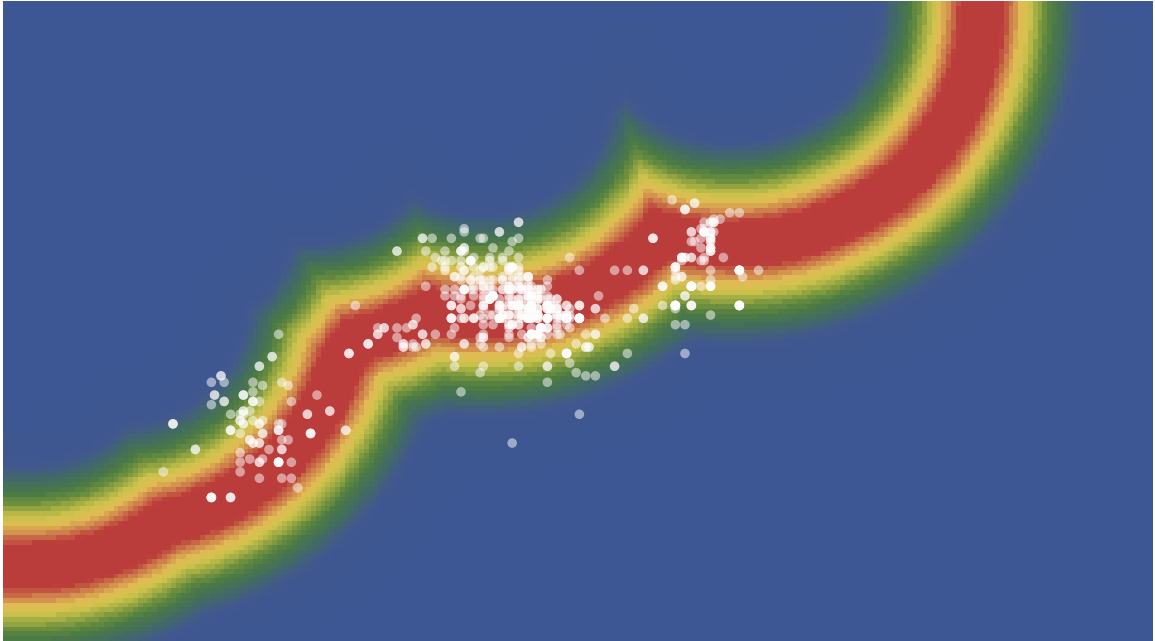


Figure 3.8 Landscape weighted only by the parameter weight of distance from shore. White points represent end location of movement events.

With the addition of SST as a parameter, the contracted dataset of movements were fit well by models. The model with the lowest AIC included all variables except SST and all variables were included in the second best model (Table 3.3). With this fitting, bathymetry was included in all top models. As in the previous base fitting, distance from the original location, bathymetry, and distance from shore held the greatest importance the whale movements (Table 3.4). While included in several of the best models, SST actually had the least importance as a parameter. However, its addition seemed to increase the importance of bathymetry². If landscape maps were recreated depicting best areas of depth and distance, a wider range of water is labeled as good quality (Figure 3.9). When separated by single variables, the map for distance from shore looks similar as seen above (Figure 3.10) but the map for bathymetry shows a preference now for

intermediate depth (Figure 3.11).

Table 3.3 Top Ten Models Fit with Small Sightings Dataset and with SST as an Additional Variable

AIC	Cost	Bathymetry	Bathymetry ²	Distance to Shore	Distance to Shore ²	SST
2509.35	-0.17	-3.08	-1.41	-4.61	-7.45	-
2511.34	-0.17	-3.08	-1.42	-4.69	-7.51	0.03
2518.19	-0.17	-2.03	-	-4.78	-7.92	-
2520.19	-0.17	-2.04	-	-4.75	-7.92	-0.03
2539.56	-0.18	-3.23	-1.52	-	-3.23	-1.36
2549.41	-0.18	-2.08	-	-	-3.6	-1.46
2553.53	-0.18	-3.58	-1.73	-	-2.17	-
2566.19	-0.19	-2.25	-	-	-2.53	-
2580.72	-0.19	-3.69	-2.16	1.22	-	-0.88
2583.66	-0.19	-3.86	-2.31	0.53	-	-

Table 3.4 Importance of Parameters of Model Fit with Small Dataset and SST as an Additional Variable

	Importance	Value
Cost	1	-0.169821
Bathymetry	1	-3.06479
Bathymetry ²	0.98811	-1.41392
Distance to Shore	1	-4.6329
Distance to Shore ²	1	-7.46843
SST	0.26999	0.0340594

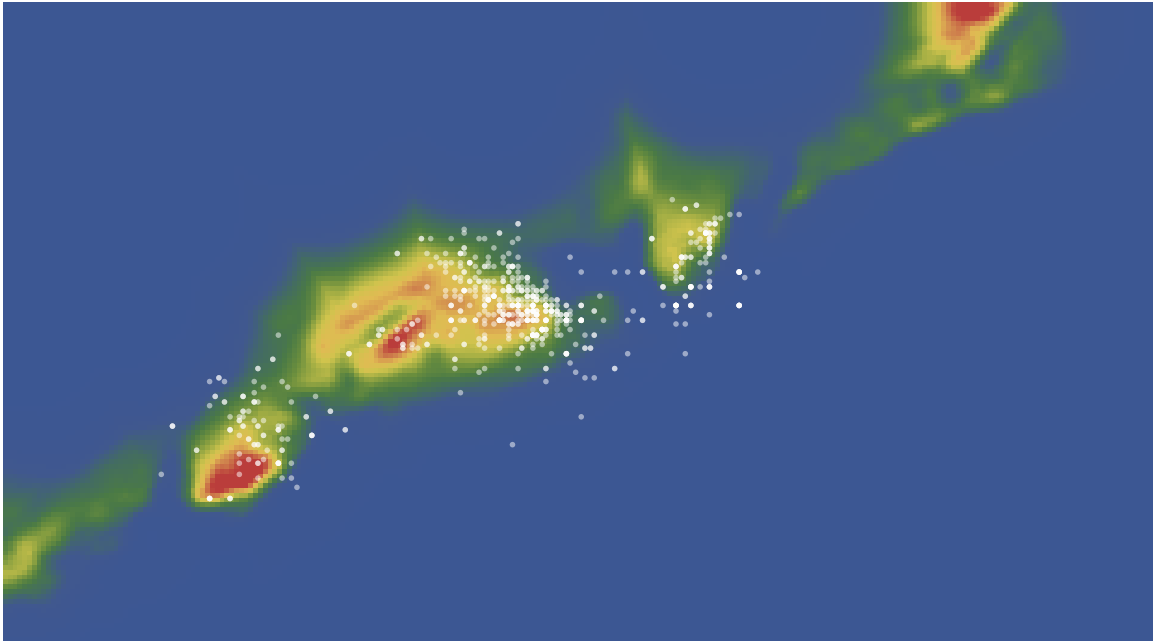


Figure 3.9 Landscape map weighted for habitat quality by parameters for combined depth and distance from shore as fit by the model including SST.

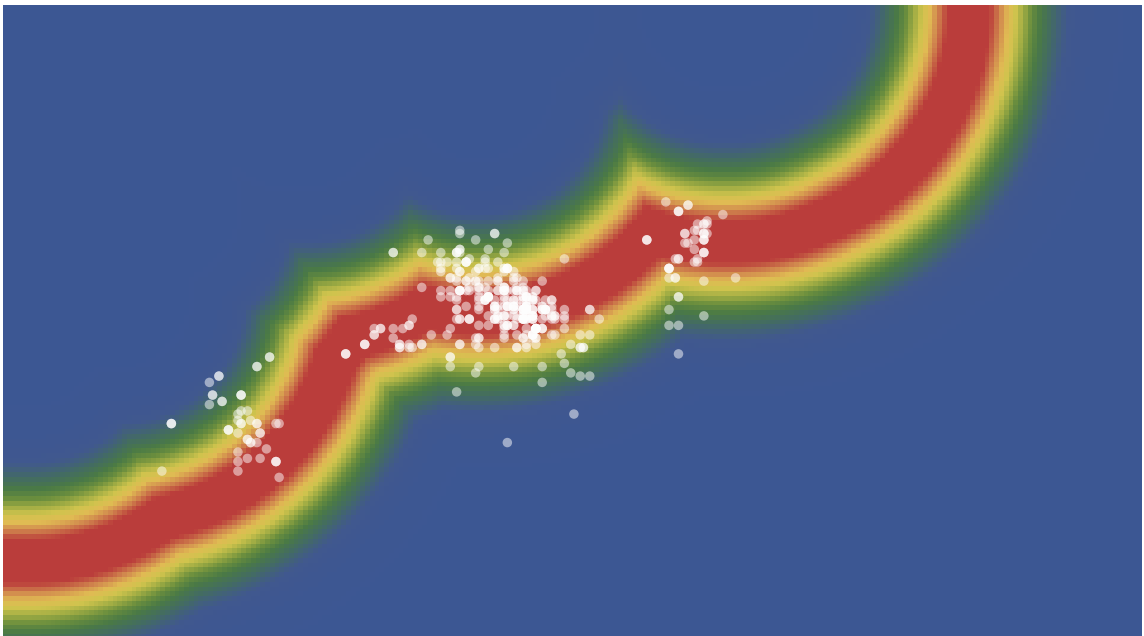


Figure 3.10 Landscape weighted by only the parameter for distance from shore as fit by the model including SST.

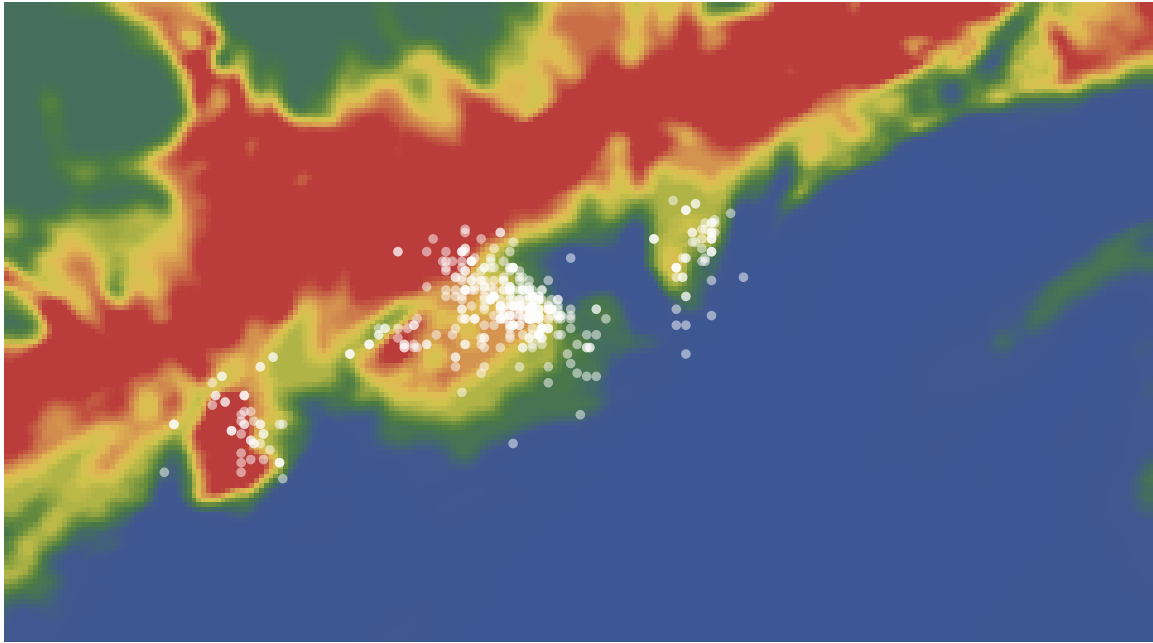


Figure 3.11 Landscape weighted by only the parameter for depth as fit by the model including SST.

3.3.2 Transect densities

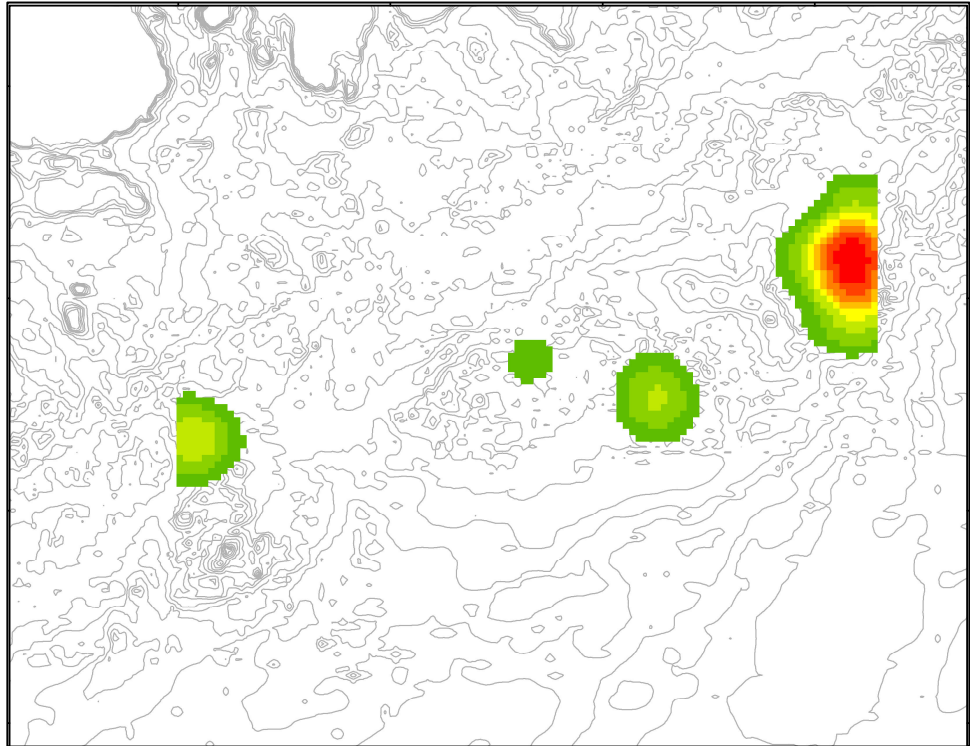
Systemized surveys were run as weather and crew permitted. In 2011, transects of the total study area were completed four times split over 12 days within the field season of June-October. Logistics in boats and crew complicated the surveys in 2012 and data was not considered comparable to the other years. In 2013, complete transects were achieved three times split over nine days covering June-October. Table 3.5 shows the number of baleen whale sightings during the two years. More animals of all species were seen in 2011 than in 2012. Core density areas shifted between the two study years (Figure 3.12). Higher densities were centered on regions predicted by the base model as high quality.

Table 3.5 Species Sightings from Boat-Based Surveys in 2011 and 2013

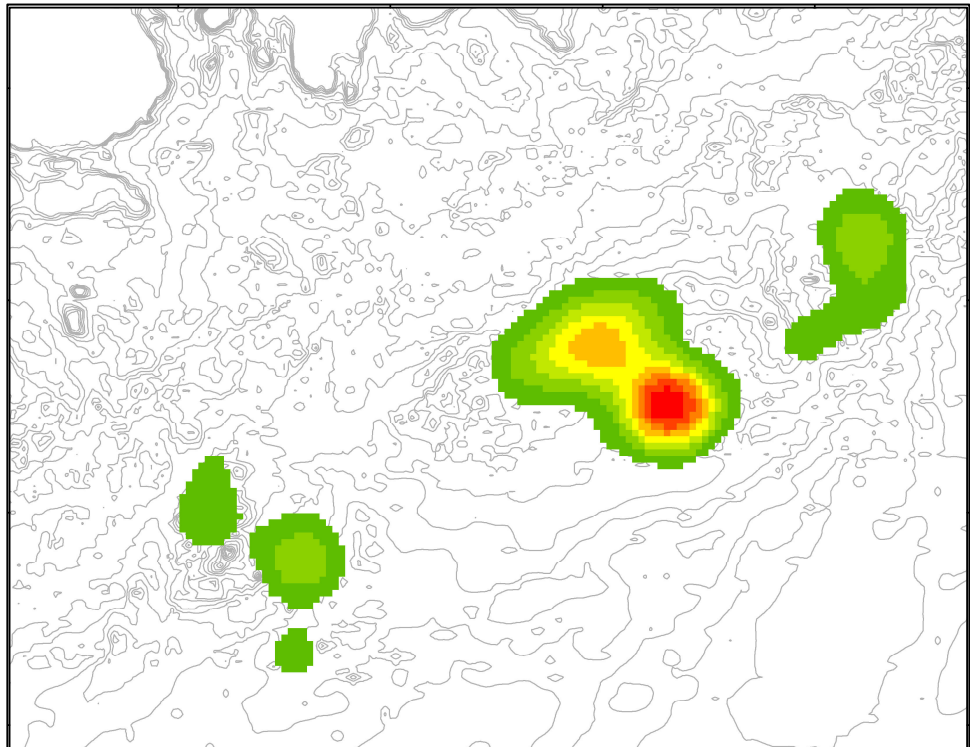
	2011	2013
Humpback	43	20
Fin	45	15
Minke	20	5
Right	0	2
Unidentified	25	6

3.3.3 Interspecific effects

There were 824 dates found where humpback and fin whales were sighted on the same day. The mean minimum distance (in km \pm SD) from the observed data (10.0873 ± 2.5638) was found to be significantly smaller than that calculated from a model predicted stochastically (15.1619 ± 0.8235); paired-sample t test; $p = 0.0001$). These results suggest that humpback and fin whales in this feeding ground tend to associate with one another more than would be expected by random.



A.



B.

Figure 3.12. Kernel densities of sightings in 2011 (A.) and 2013 (B.).

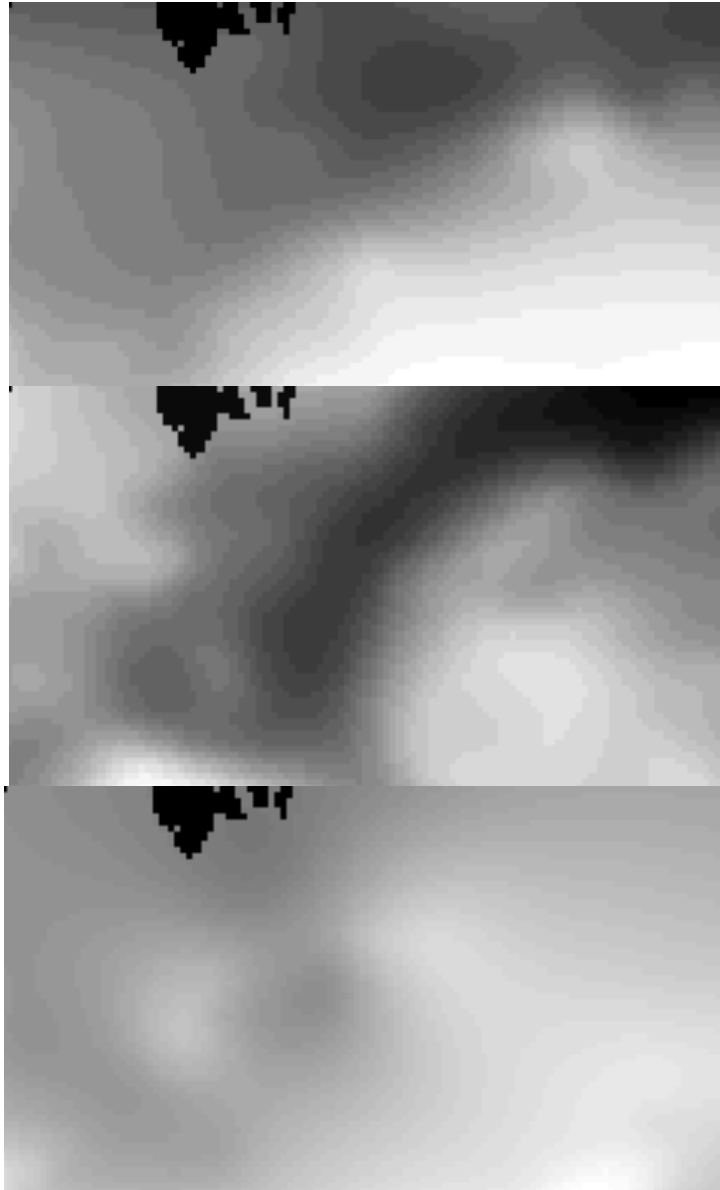


Figure 3.13 Examples of variation in SST data.

3.4 Discussion

This study demonstrated that photo-identification data can be used to study habitat selection in whales. Sample size and temporal range of existing datasets provided ample opportunity to elicit population level preferences from individual choice. The produced

models illustrated not only areas that whales were sighted in but also active movement of those whales toward specific locations.

Once arriving to this general region, it is assumed that whales are going to utilize the landscape in a way that maximizes their foraging efforts. Whales tended to stay close to their initial location; as expected, cost of travel greatly influenced the value of landscape parameters. Given the patchiness of resources in the ocean, it makes sense that an animal would not leave an area unless in search of a better patch. The predictive importance of water depth was also not surprising; the sea floor is one of the only static habitat features. While the areas near land are still quite deep and could be suitable habitat, the whales tended to avoid the shoreline. Appropriately sized aggregations of productivity that make foraging efficient are not likely found close in shore. It was surprising that distance offshore seemed to be the biggest predictor. The addition of SST to the model did not have as strong an effect as anticipated. Temperature of the water did actually show considerable variation on a daily and seasonal basis (e.g., Figure 3.13). Nearshore waters are often quite different in temperature from offshore, possibly explaining some of the preference in whales staying away from land. Dynamic variables such as SST are difficult to use in prediction of quality habitat in that these predicted regions would change temporally; an area that may be attractive for a whale on a particular day may not be as attractive next month.

Variation in SST may have attributed to the difference in density illustrated by the 2011 and 2013 transects. It may be that the more permanent features of distance from shore and depth constrain whales to these consistent areas shown in the quality maps but the inter and intra-seasonal shifts between those core regions are caused by the dynamics

of SST. The average SST within the Gulf of Maine has been experiencing dramatic changes due to global climate change, rising approximately .23 C. In fact, in the last ten years the Gulf of Maine temperatures have risen at a faster rate than 99.85% of the global waters (Pershing 2014). As temperatures continue to change, we may see differences each year in productivity and thus whale distributions.

Additional habitat variables are needed to biologically explain the movements of these whales within the foraging ground. Movements are likely representing a search for food and the end locations should represent areas of condensed prey. These are likely found in regions with upwelling of nutrients, which often happens when ocean currents interact with a complex seafloor. While depth was found to be a strong predictor in this study, the change in depth or slope may prove to be more relevant. The slope would represent that complexity that might cause the temporary blooms of life when the conditions are right which in turn attract whales. Similarly, it may be of use to incorporate SST fronts or gradients in the next stage of research.

Past studies have stressed the lack of understanding of the spatial scale on which whales are operating (e.g., Hazen et al. 2009). These methods provided one of the first looks at the scale of selection of humpback whales through smoothing. Both depth and slope had stronger predictive power when smoothed rather than at base resolution. Whales were shown to respond to depth at a relatively small scale and slope at a much larger scale. Allowing for different scales in the interacting variables improves understanding of these fine scale decisions made by individual whales and may help to better delineate quality habitats and protected areas.

Boat-based surveys demonstrated that this is a widely spaced population with

aggregations of individuals located in core areas. With this type of distribution, it becomes difficult to collect a high sample size of locational data, as encounter rate is quite low. In addition, each survey only provides a snapshot in time of distribution and sightings do not demonstrate active movement towards regions. However, the densities shown through the surveys did seem to coincide with areas predicted as suitable habitat. Thus predictive modeling of long-term photo identification data may provide a much more feasible and less logistically intensive way to quantify habitat. It must be noted though that bias may exist with this opportunistic data in that the points collected are only in those locations chosen by whale watch captains each day. In this particular whale watch company, on a given day, a captain will tend to return to an area where whales have recently been sighted. The boat will stop before arriving to those coordinates if whales are sighted en route. If the boat arrives to that area but no whales are found, the captain will then begin to search the landscape in a zig-zag pattern. By returning initially to known locations, there may self-selection of areas that are good for whales, which might in turn exaggerate the quality habitat predicted by the models. Also, whales that have moved to other locations might not be able to be photographed by the researcher.

The location data on the habitat quality map shows several end sightings falling within areas not considered suitable. It seems there are definitely factors not included in these models that may be of importance to humpback whales. Occurrences of other similar species like the fin whale did not seem to affect the humpbacks on this area. In fact, it seemed rather the opposite: that humpback and fin whales seemed to aggregate. This makes sense again given the probable patchy distribution of prey. It is also possible that social dynamics between the humpbacks may affect their individual movement

decisions. As demonstrated in Chapter 2, many individuals have significant relationships with other whales. It would be interesting to know if there is a progression in whale density, e.g., if whales tend to approach regions not because of habitat quality but because of communication with other individuals. Fine-scale data on prey distribution (e.g., acoustic backscattering of fish density) would also provide better insight into these small-scale movements within the feeding grounds.

CHAPTER 4

COMPARISON OF NORTHERN AND SOUTHERN GULF OF MAINE WHALE AGGREGATIONS

4.1 Background

As discussed in Chapters 2 and 3, there is a need for better understanding of social organization and critical habitat of baleen whales. As these animals have wide spatial ranges and the ability to travel long distances, it is of great importance to also extend analyses outside of one small geographic location. As mentioned earlier, North Atlantic humpback whales make long-distance migrations from low-latitude breeding sites to high-latitude feeding grounds. In the wide-ranging Years of the North Atlantic Humpback (YONAH) study, Stevick et al. (2006) recognized four distinct feeding aggregations of the NA humpback whale: the Gulf of Maine (GOM), eastern Canada, West Greenland, and the eastern North Atlantic. However, they also brought to attention the smaller scale site fidelity. Even within these broad aggregations, individual whales show preference to specific feeding sites at a quite local level. While travel rates between the large feeding aggregations are very low, there is a temporally varying degree of travel of individuals between their smaller scale preferred locations; this movement at the smaller scale is thought to be driven by possible shifts in prey abundance.

Most studies on the humpback whales in the GOM have been quite focused on one smaller sub-region within the feeding aggregation; the majority of these on Stellwagen Bank (e.g., Clapham 1993; Weinrich et al. 1997; Weinrich et al. 2006; Hazen et al. 2009). Though not quantified or published, differences have been observed in feeding behavior and seasonal densities of humpback whales between the southern and northern subregions, with higher group sizes and more surface active foraging seen in the

south. There is a great need to integrate data across multiple spatial-temporal scales (Redfern et al. 2006).

Social structure is influenced by factors such as population density and distribution or abundance of resources (Whitehead 2000). Lusseau et al. (2003) saw differences in the stability of social associations of bottlenose dolphins in areas with different environmental conditions. The primary prey of humpback whales in the southern GOM is thought to be sandlance (*Ammodytes americanus*) while in the northern GOM is a variety of euphausiids and herring (*Clupea harengus*) (Weinrich et al. 1992; Paquet et al 1997; Weinrich et al. 1997). The prey differentiation coupled with the higher concentration of whales could produce quite a different social organization as well as differences in habitat preference.

4.1.1 Objectives

This final chapter examines differences in social structure and habitat selection between northern and southern GOM humpback whale feeding sub-regions. This study aimed to document the variability that may exist within the same species over different geographic areas and highlight the need for site-specific knowledge when developing management plans.

4.2 Methods

4.2.1 Data

Data was obtained from the humpback whale program at Provincetown Center for Coastal Studies (PCCS). This dataset is similar in scope to the dataset from Allied Whale (AW) described in Chapters 2 and 3 in that it was collected both systematically and

opportunistically and that each sighting contains geographic coordinates, photographic identification of individuals, and group size. The records were collected by trained observers and associations were defined by the same metric as with AW. The sightings extend spatially in the southern GOM from Jeffreys Ledge, across Stellwagen Bank and to the Great South Channel to the southeast of Cape Cod and temporally from the 1979 to 2005. The study area was set as a rectangle with a buffer of 10 km surrounding the extent of the sightings. Figure 4.1 shows the spatial location of the southern study area in reference to the northern site analyzed in earlier chapters.

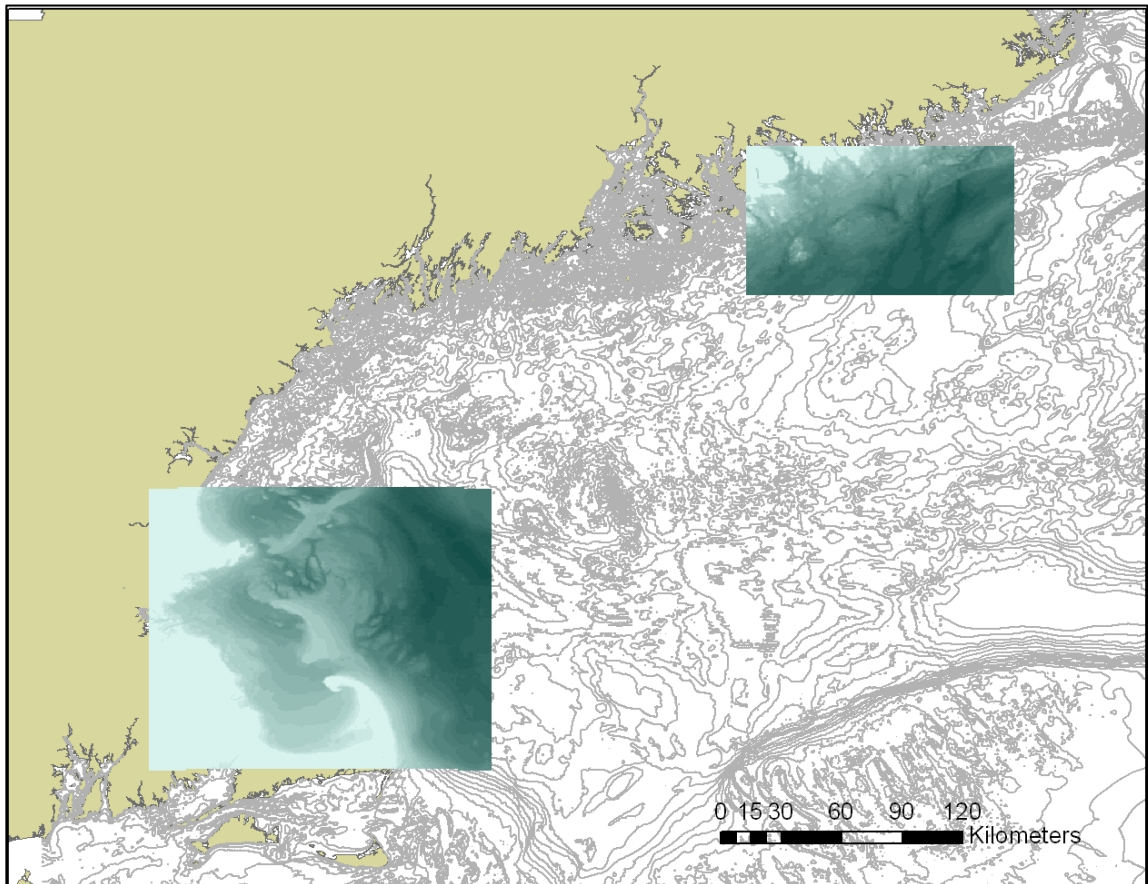


Figure 4.1 Study areas in reference to each other. The PCCS study area is located directly off the tip of Cape Cod and covers Stellwagen Bank National Marine Sanctuary.

Data on bathymetry were collected from the same source at the same resolution as the AW region in Chapter II (<http://coastalmap.marine.usgs.gov/GISdata/regional/eastcoast/gome/bathymetry/contours/gom15ctr/gom15ctr.zip>). The layer was clipped to the extent of the study region and converted to raster in ArcGIS. A raster image representing distance to shore was created within Mathematica. Squared versions were made of both depth and distance from shore. All landscapes were split into pixels 500 x 500 representing meters.

4.2.2 Social Structure

The social network analyses described in Chapter 2 were performed on the PCCS data and compared to results from analyses on AW data. Half-weight indices were calculated for each observed dyad. A null model was also created through permutations to test for preferred companionship. To compare the northern and southern social structures, I explored differences in observed group sizes in sightings, average number of associates, and association strengths (Whitehead 2000). Lastly, temporal strength of associations of the southern whales were tested using the standardized lagged association rates in SOCPROG v. 2.5 (Whitehead 2009). As data on sex of individual whales were more complete with the PCCS catalog, the temporal strength of relationships as related to sex was investigated in more detail. Separate permutation null models were created and lagged association rates were calculated for female-female, male-female, male-male relationships.

4.2.3 Habitat Selection

PCCS data was partitioned into consecutive day sightings of individual whales. Those short term movements were fit to the conditional logistic regression model described in Chapter 2. Environmental variables included were: bathymetry, distance from shore. The best model was chosen using AIC. A map of habitat quality was created with the weights of parameters. Outputs of this model were compared to the outputs from the AW data.

4.3 Results

4.3.1 Groups and Dyads

The dataset from PCCS was much more extensive than the AW sightings, containing 942 individual whales. Many individuals were sighted multiple times throughout the study; the maximum number of re-sights for an individual was 506, which was similar to the maximum number observed with the AW data. 178 individuals were only sighted once. Table 4.1 shows the recorded group sizes. Of 17605 sightings, 77% were single whales and the second most commonly seen size were pairs of individuals. Because of the large amount of data, subsequent analyses were limited to individuals who were sighted at least 20 times throughout the study period.

Half-weight indices were lower in range to those calculated for the AW data (Figure 4.2), spanning from 0 to 0.14. However, the mean HWI for the southern whales was significantly greater than the mean for the northern whales (Figure 4.3). These values were still relatively low suggesting flexibility in associations. Very little variation was seen in average HWI between sex classes (Figure 4.4), though the calculated indices were

much smaller than seen in AW data. This may be an artifact of a much larger sample size of sexed individuals.

Table 4.1 Frequencies of Observed Group Sizes

Group Size	Number of Groups	Percent of Total
1	13556	77.00%
2	3303	18.76%
3	582	3.31%
4	112	0.64%
5	35	0.20%
6	7	0.04%
7	5	0.03%
8	4	0.02%
9	1	0.01%
Total Groups	17605	

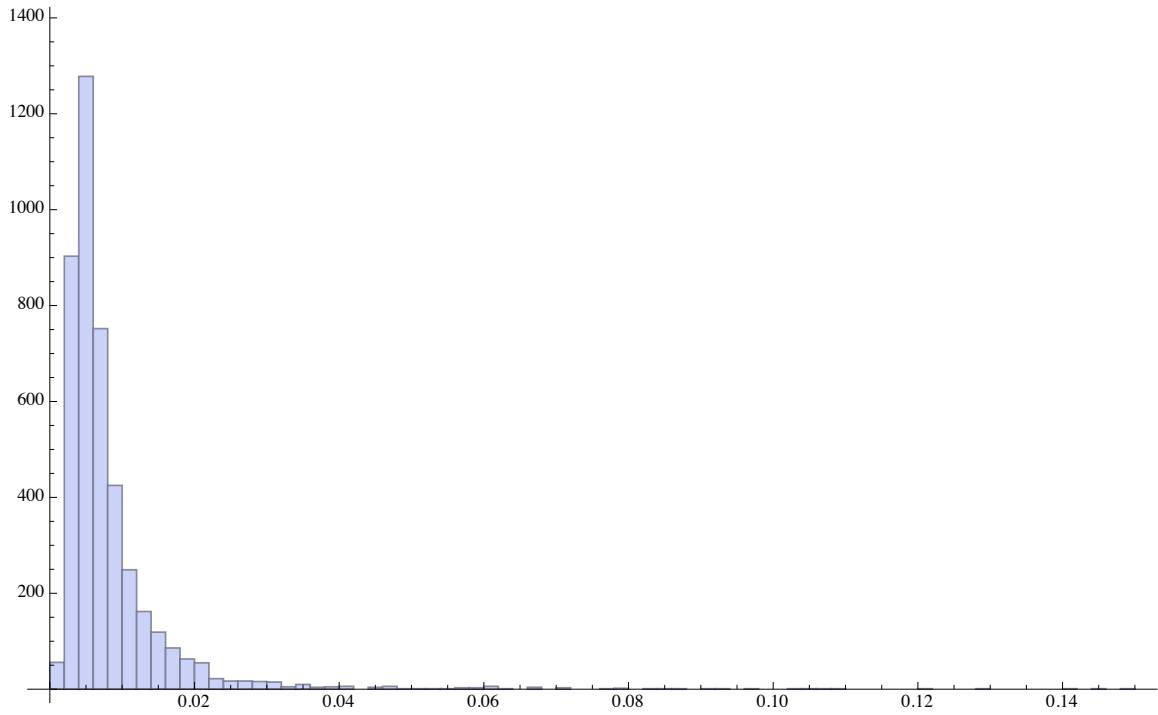


Figure 4.2 Frequencies of HWI values calculated between the PCCS dyads.

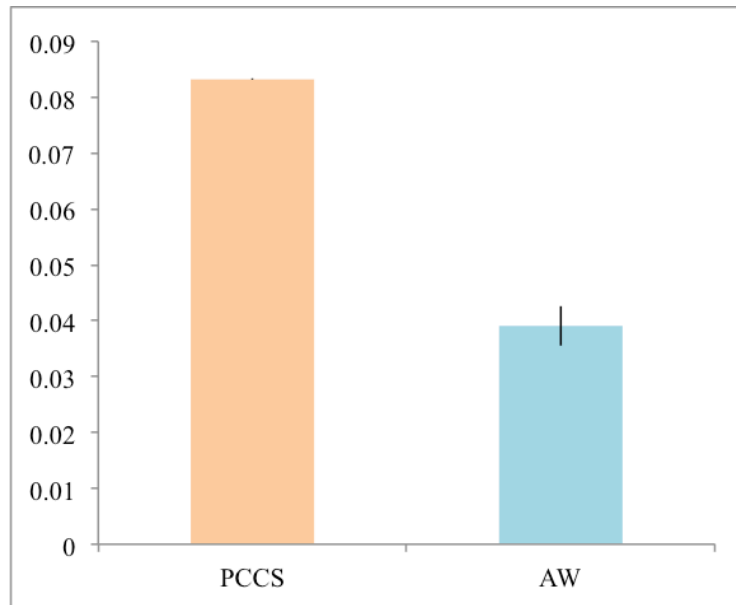


Figure 4.3 Mean HWI calculated for both PCCS and AW dyads. Black bars represent standard error.

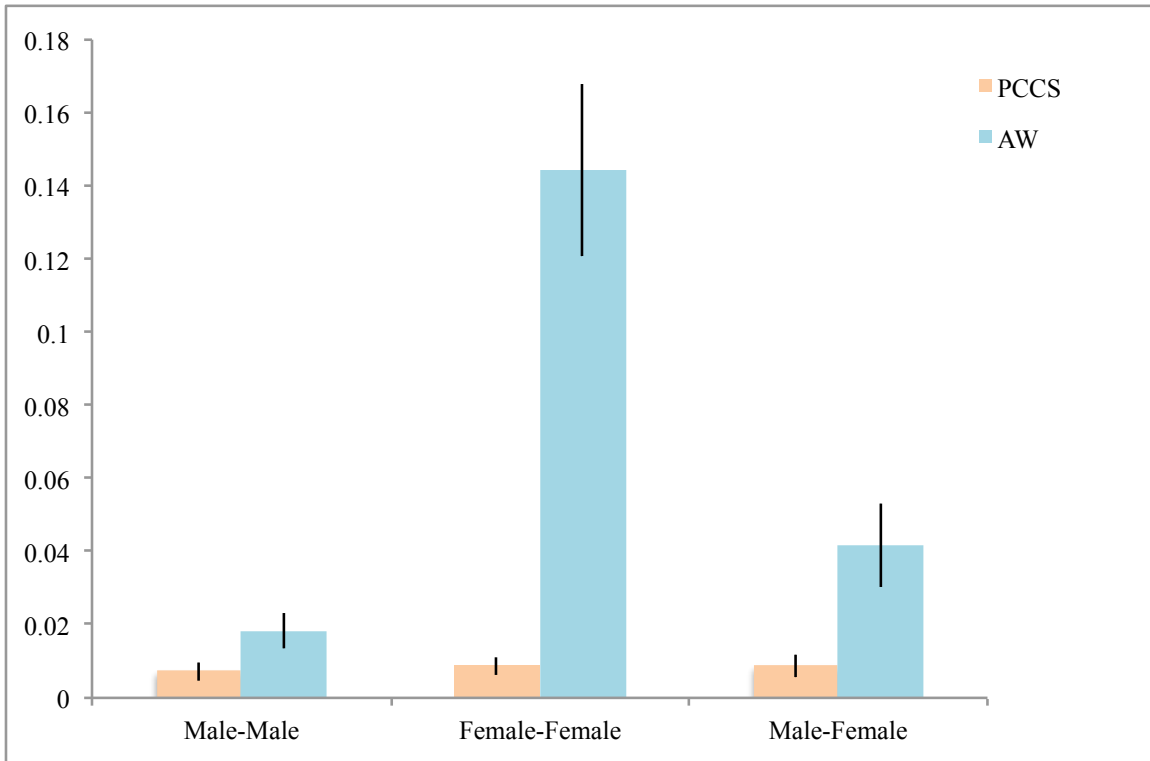


Figure 4.4 Mean HWI between sex classes for PCCS whales and AW whales. Black bars represent standard error.

4.3.2 Preferred Associations

Permutations produced null models using the flip method described in Chapter 2. Comparison of the actual data indices to the randomized datasets demonstrated significantly preferred relationships between dyads. Positive relationships were seen in 4317 dyads (z -values >1.96). Of those relationships, the greatest number was between males and females (1709). 1480 preferred companions were female-female and the least number of significant relationships were documented between males (493). This sample size of data was much greater but a similar pattern was shown as with the AW whales.

4.3.3 Network Measures

A simple network weighted by HWI with divisions calculated through optimal modularity is shown in Figure 4.5. This network showed several tightly clustered communities with strong ties to each other. A tier of outlying communities was attached to the strong central cluster. Several dyads, a triple, and a group of eight were not at all connected to the network. The network was greatly altered when weighted by significant relationships (demonstrated by positive z-scores from the null-model). This network (Figure 4.6) shows one very central and large community surrounded by a single tier of outlying communities. Outliers were loosely connected to each other and more strongly connected to central community. Communities were composed of members of both sexes.

Degree centrality in the PCCS whales ranged from 0 to 60, a much higher range than seen in AW whales. Eigenvector centrality was also higher, ranging up to 0.15. This suggests that more whales were well connected to well connected individuals. Average path length was 2.52; again lower than AW path length. Centralization of the network showed annual fluctuations ranging from 0 to 2.5. The average value of centralization was 0.13 which was lower than demonstrated by the AW network. This infers that less importance is held by individual whales in the PCCS community.

Null models were also created for each year. When networks were created on an annual basis weighted by the positive z-scores seen that season, there was more variety in clustering. Some networks were very closely knit where others showed greater division (see Figure 4.7 for examples). Average HWI values varied from year to year with a wider range of values than seen in the AW data. Figure 4.8 shows average HWI for both AW

and PCCS datasets in years where the studies overlapped. Some of the trends in rising or falling of mean index values were similar with both showing the highest values in the year 2000 (PCCS = 0.7, AW = 0.2). That year also corresponded with fewer individuals being sighted in general.

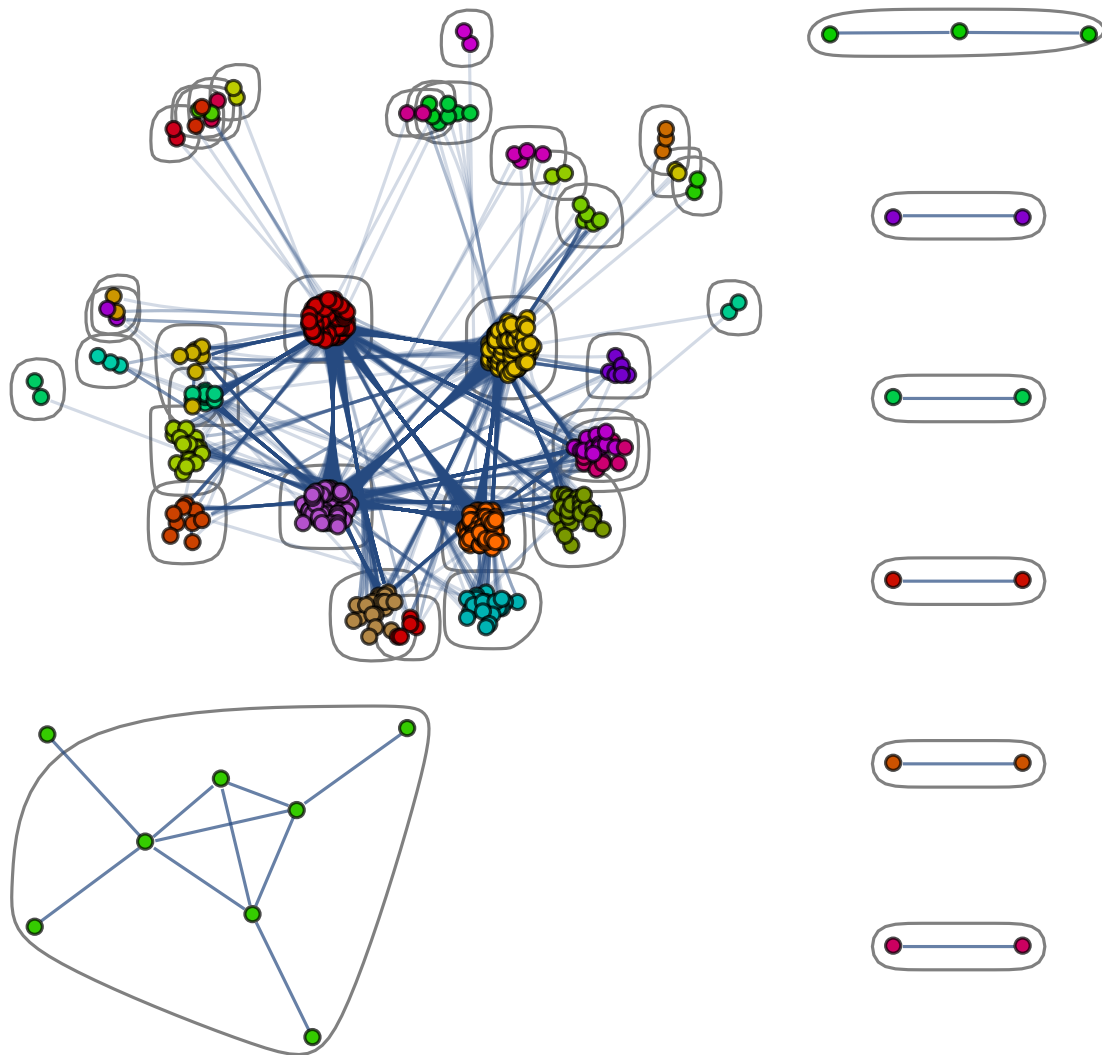


Figure 4.5 PCCS network weighted by HWI values.

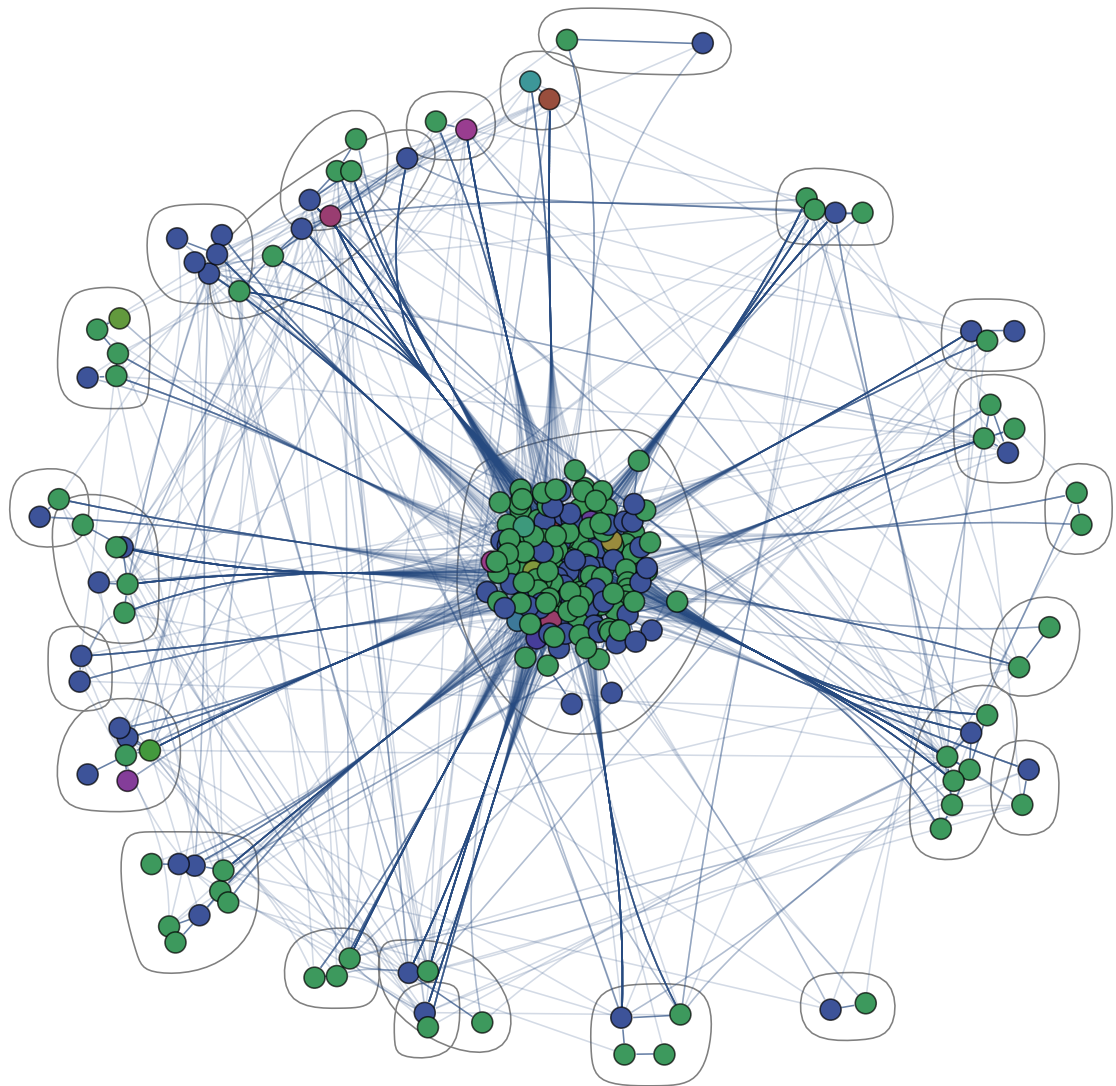


Figure 4.6 PCCS network weighted by positive z-scores. Green nodes are female individuals, blue nodes are males, and pink unknown sex.

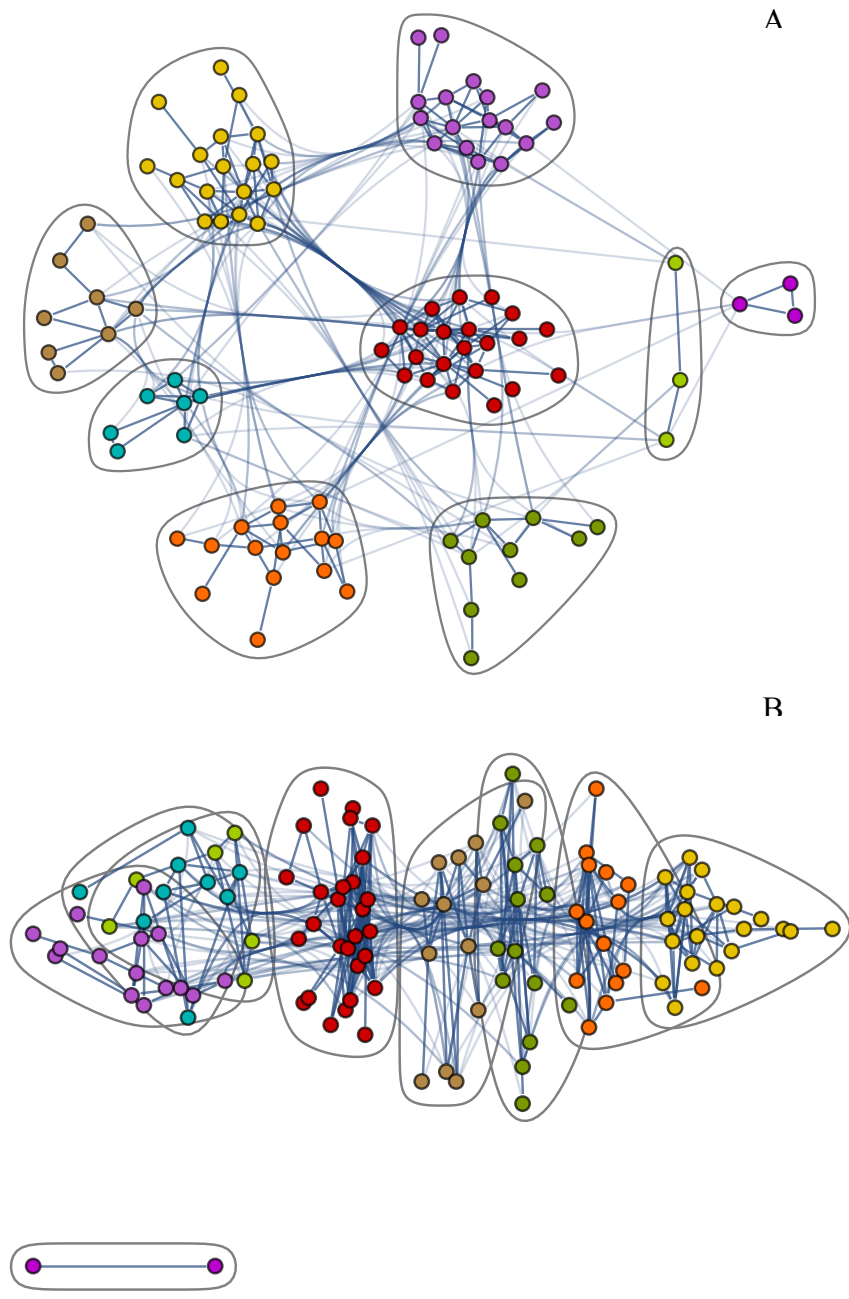


Figure 4.7 Examples of variation in annual community structure. A. shows a more divided network and B. a tightly clustered year.

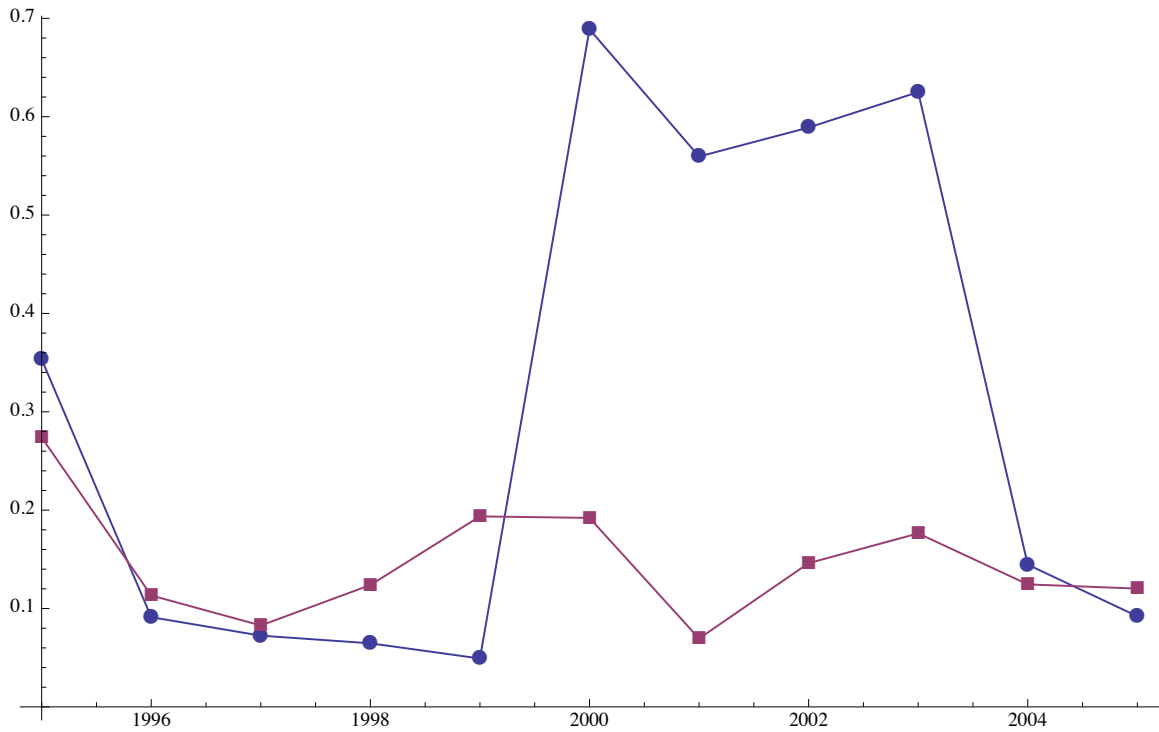


Figure 4.8 Annual mean HWI values over time. The blue line represents PCCS data and the pink represents AW.

Because of the large sample size, the community transition plots did not show as much relevance with the PCCS data. Nevertheless, some persistence between communities was seen interannually. Some years also had very different community composition with changes in the frequently sighted individuals (Figure 4.9).

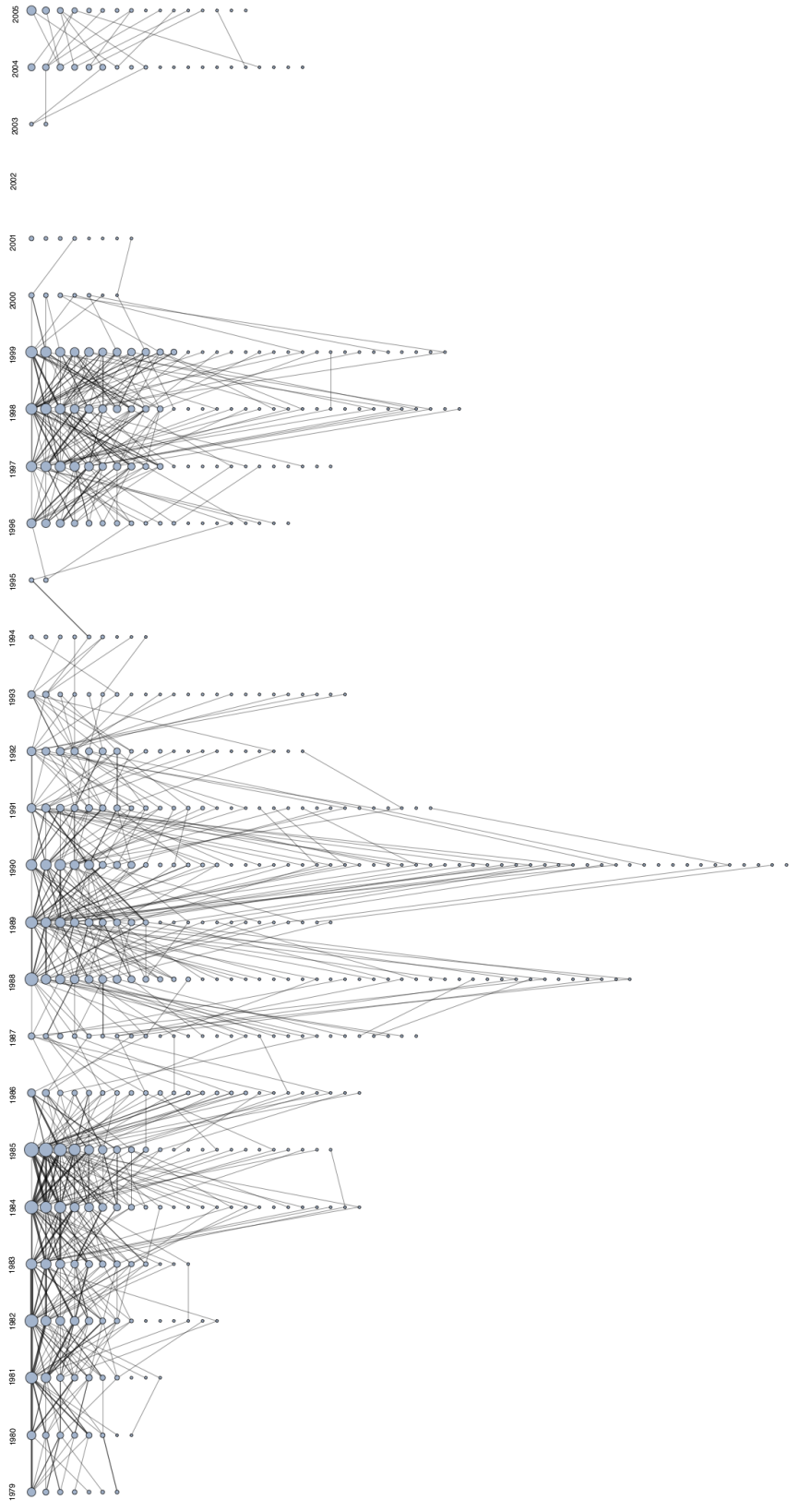


Figure 4.9 Community transition plot for PCCS data. The first column is 1979 and subsequent columns are the following years. Each node represents a community. The horizontal bars connecting the columns represent the fraction a community transferring into a different community the next year.

4.3.4 Temporal Associations

Standardized lagged association rates were calculated for the full extent of the PCCS data and then explored within several subsets. The temporal strength of AW relationships seemed stronger on whole than in PCCS whales. Figure 4.10 shows SLAR in time lags in years of all PCCS relationships. SLAR values were immediately lower than AW after the first year (0.011 compared with 0.058) and were never far above the random model. A smaller subset of data did show greater strength in relationships but also a steady disassociation over time (e.g., Figure 4.11). Analysis within one season actually suggested higher rates of association in PCCS whales than in AW whales, though with less precision (e.g., Figure 4.12). Data within 1997 showed a rapid disassociation followed by almost steady overall persistence at the end of the season.

When split by sex, there were some interesting patterns. While male-male relationships reform a few times during the first few seasons, eventually the associates fizzle out and stay below the random model (Figure 4.13). However, female-female associations seem to consistently reform with high peaks above the random (Figure 4.14). This suggests longer-term relationships between the individual female whales.

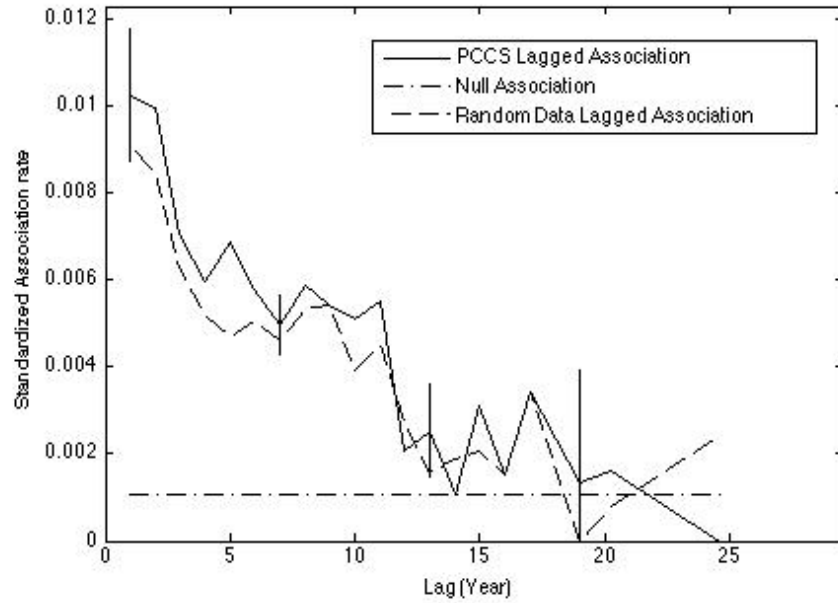


Figure 4.10 Standardized lagged association rates of the full extent of PCCS data. Time lags are set as years. Vertical bars represent precision estimates.

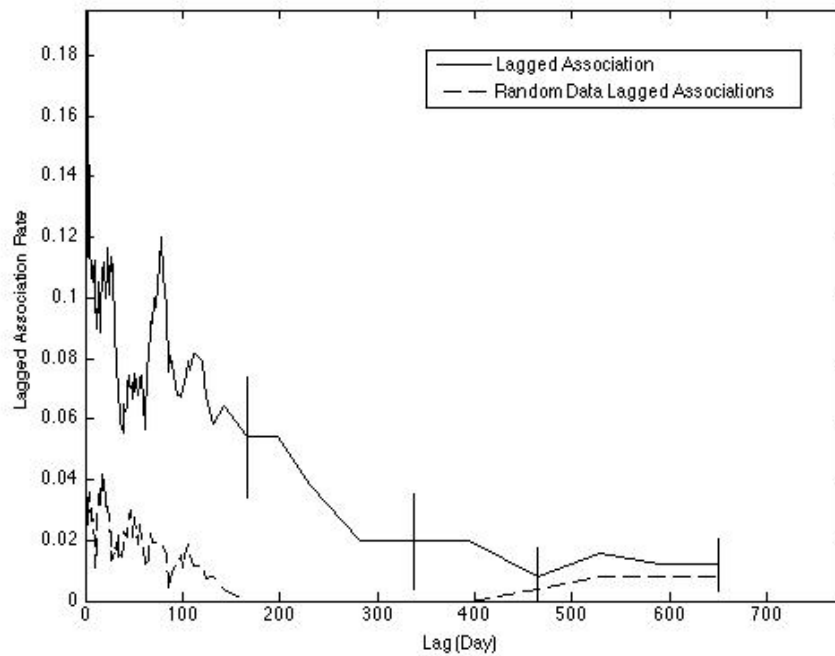


Figure 4.11 Standardized lagged association rates of PCCS data from 1998-2000, data truncated as example of relationships over multiple seasons. Time lags are in days. Vertical bars represent jackknife estimates of precision.

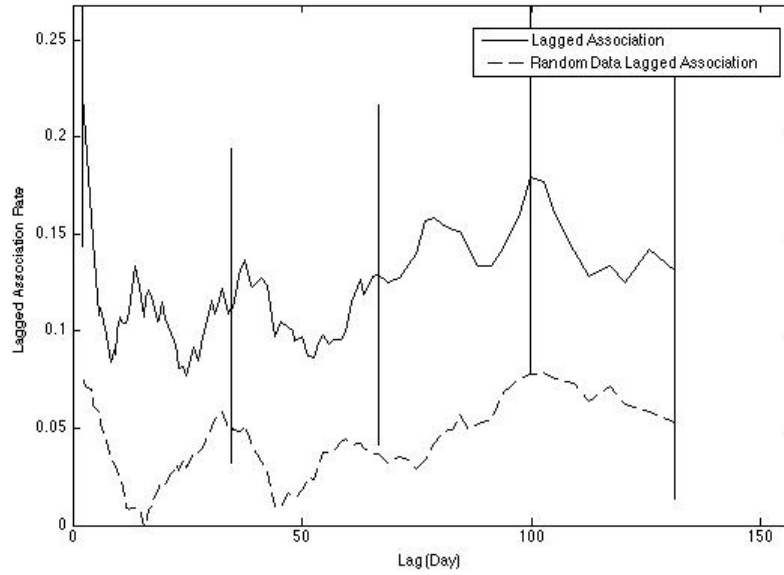


Figure 4.12 Standardized lagged association rates of PCCS data limited to 1997 as example of relationships over one season. Vertical bars represent jackknife estimates of precision.

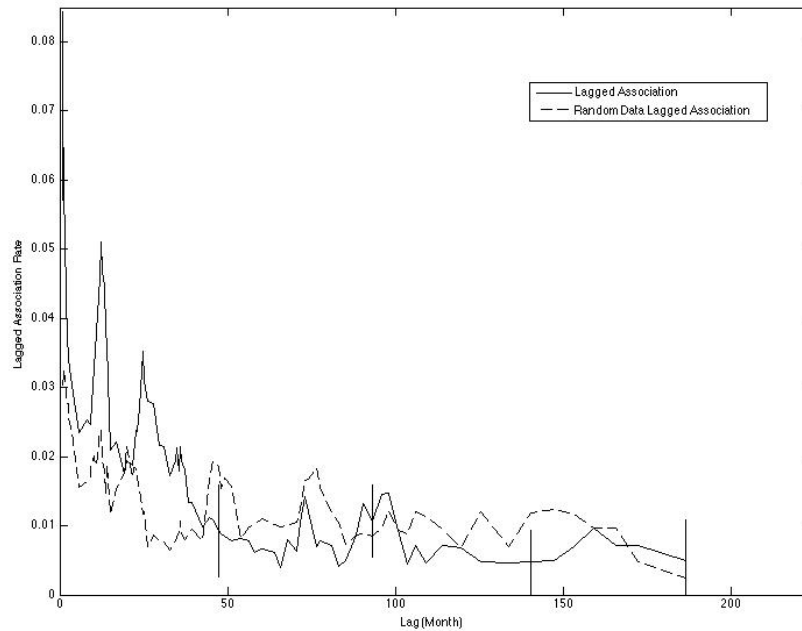


Figure 4.13 Standardized lagged association rates of male-male relationships of PCCS data. Vertical bars represent estimates of precision.

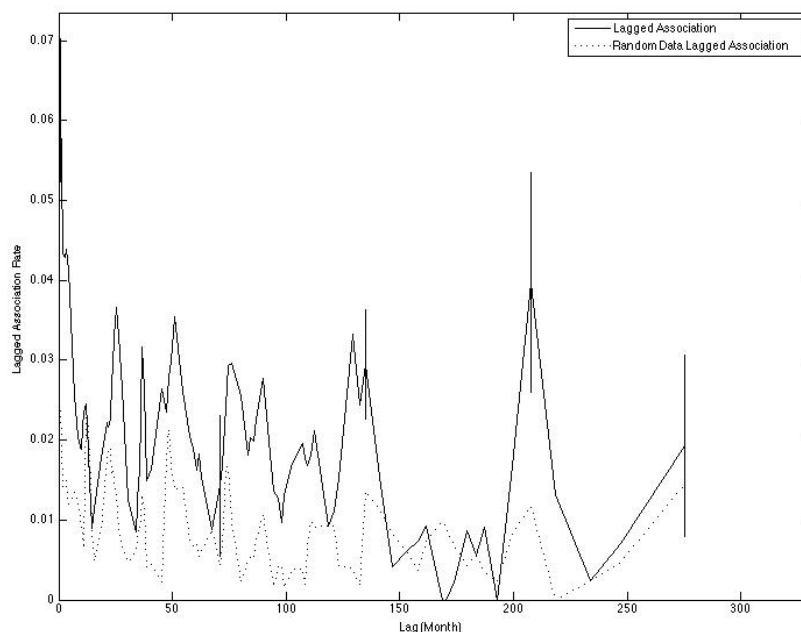


Figure 4.14 Standardized lagged association rates of female-female relationships within PCCS data. Vertical bars represent jackknife estimates of precision.

4.3.5 Habitat

There were 8644 one-day movement events in the PCCS dataset. Overall movement patterns were similar to the one-day events seen in the northern whales, categorized by mostly small-scale movements a several more long distance travels. The average daily movement was slightly larger for southern whales (6.63 km) than for northern whales (4.16 km). The longest distance was recorded as 62.09 km traveled over the course of one day. This may have been a mistake with data entry and individual identification or may have just been aberrant movement. Whale sightings in the south were also distributed over a wider study area than the original northern dataset.

Outputs from the conditional logistic regression model were similar to those seen with the AW whales. The best model with the lowest AIC included all variables (cost, bathymetry, bathymetry², distance from shore, and distance from shore²). All other

models dropped one or multiple variables (Table 4.2). There again was a correlation between water depth and distance from shore, though not quite as strong in this region as in Maine. All variables had high importance for the model (Table 4.3). A landscape-wide map of habitat quality is shown in Figure 4.15. End points are highly clustered in the red region near the tip of Cape Cod. A few scattered end points are also found in further away regions predicted as preferred habitat. The optimal distance from shore was found to be approximately 13.74 km, about 10 km closer to land than the northern whales.

Table 4.2 Best Models Fit by the Conditional Logistic Regression Analysis

AIC	Cost	Bathymetry	Bathymetry ²	Distance to Shore	Distance to Shore ²
57547.1	0	-2.52	-1.37	-0.55	-1.33
57656.5	0	-1.53	-	-0.58	-1.33
57668	0	-2.74	-1.45	-	-1
57788.8	0	-1.69	-	-	-0.99
58008.1	-0.01	-2.61	-1.44	-	-
58008.9	-0.01	-2.59	-1.44	-0.04	-
58129.5	-0.01	-1.51	-	-0.07	-
58130	-0.01	-1.53	-	-	-
58266.1	-0.01	-	0.99	-0.87	-1.34
58525.7	-0.01	-	-	-0.99	-1.37

Table 4.3 Parameter Importance and Value Predicted by Habitat Model

	Importance	Value
Cost	1	-0.00303663
Bathymetry	1	-2.52286
Bathymetry ²	1	-1.37233
Distance to Shore	1	-0.550745
Distance to Shore ²	1	-1.33275

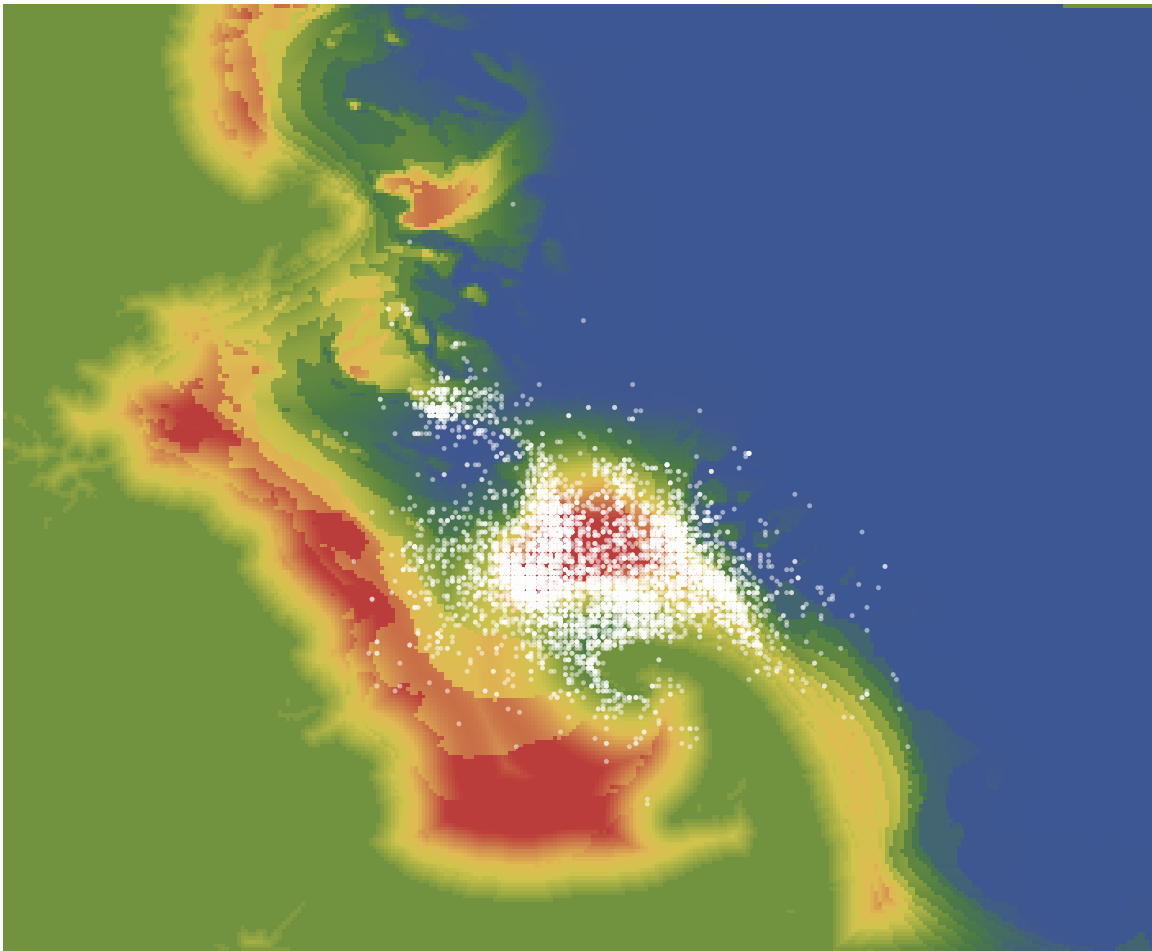


Figure 4.15 Habitat map with quality determined by parameter weights of conditional logistic model. White points are end locations of whale movement events.

4.4 Discussion

Whale populations or stocks are often difficult to manage because of their wide ranges yet often demonstrated small-scale site fidelities. Does one consider a population to be within an entire ocean basin or does it make more sense to manage the smallest discrete subsets? Decisions depend on the amount of variation seen between these subsets; however, variation can be difficult to understand without comparable studies in all regions. As whales are logistically complicated to study in general, standardized effort in data collection over wide regions is usually impossible. The use of photo-identification data over wide-regions has the potential to allow for needed comparisons. Tracking individuals over time and space provides a large set of data that is relatively uniform wherever it has been collected. This study allowed for the techniques developed and described in Chapters 2 and 3 to be expanded to a separate region and allowed for the comparison of results.

Analysis of the social structure of the southern GOM whales supported the findings described in Chapter 2. Overall trends of both communities were comparable. This was actually surprising; I predicted that the higher density of whales and number of whales seen per season in Massachusetts would create a much different society. However, both societies would be categorized by fission-fusion groups that form and disband throughout the season. Group sizes are typically small with a few exceptions. Within both regions, there is evidence for significant preferred companionship among individuals and the highest count of significant relationships were seen between males and females. Where the differences arise are in the finer details of the social structures. PCCS whales seemed more gregarious with higher average association indices, higher

numbers of individual connections, and stronger within season ties. On the other hand, the AW whales demonstrated stronger long-term relationships. The comparison here might be similar to relating humans in a city to humans in a rural town; the urban individuals have many more associates due to the higher density surrounding them and higher rates of encounters where the rural townsfolk may develop bonds that last a lifetime within the small pool of individuals available to them. These small differences in social behavior may also reflect differences in the distribution of prey.

The PCCS data allowed for the application of the conditional logistic regression model on a much larger sample size. General movements patterns within the feeding ground were similar to AW in which distinct hotspots were selected based on water depth and distance to shore. However, there was a difference in the optimal distance from shore selected by the PCCS whales. This suggests that parameters predicted for whales in one particular location may not necessarily be applicable for that same species world-wide. Fine-scale regional differences in habitat or prey choice may produce differences in movement decisions. Model selection might be greatly improved with the addition of more complex oceanographic variables that were not available for this study.

This work was the start of what will hopefully become a more widespread practice in the sharing of photo-identification data to make regional comparisons and thus acquire a higher level understanding of species dynamics.

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