OCCURRENCE PATTERNS AND SOCIAL BEHAVIORS OF HUMPBACK WHALES *(Megaptera novaeangliae)* WINTERING OFF PUERTO RICO, USA

A Dissertation

by

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ABSTRACT

Occurrence patterns and social behaviors of North Atlantic humpback whales *(Megaptera novaeangliae*) (NAHW) wintering off Puerto Rico were investigated to examine the relationship of this area to the aggregation wintering off the Dominican Republic. I described winter occurrence, movement and association patterns, and the relationship of group associations with bathymetric features in Mona Passage, immediately west of Puerto Rico. Data were collected from boat, land, and aerial surveys from 2011 to 2014. Acoustic data were collected with hydrophones deployed from a small vessel and units mounted to the sea floor, to determine the presence of singers (males). Photo-identification of individuals was used to describe intermixing of whales between higher latitudes and the study area. Social behaviors were described between intra- and inter-specific associations.

A pilot study was conducted January-March 2011 from land platforms using scan sampling. In 2012, boat-based data collection and aerial reconnaissance were added. A total of 240.9 hours vessel, 13.0 hours aerial, and 303.6 hours land observations were conducted over 165 days. One hundred ninety-seven groups of humpback whales were observed with N = 331 individuals: 91 (46.2%) singletons, 67 (34%) dyads, 17 (8.6%) mother-calf pairs, 8 (4.1%) in competitive breeding groups, 8 (4.1%) mother-calf-escort groups, and 6 (3.1%) mixed-species associations. Group associations were not random. A multinomial linear regression model supported group composition and behaviors were correlated with “hotspots” associated with four bathymetric features. Dyads and surface active groups were dispersed among features in deeper water. Singletons were observed further from a shelf edge, while singing males were closely associated with a shelf edge. Mother-calf pairs occurred nearshore in shallow water moving offshore when accompanied by an escort. Identification photos matched against the NAHW catalog indicated movement between most feeding grounds and throughout the West Indies. It is important to continue and expand this study in Puerto Rico to monitor long-term population changes, and as a means of predicting where human activity overlaps with NAHW occurrence, especially due to possible U.S. delisting of NAHW as endangered.

For Nicole, Bradford, Sarah, Noelle, Beau, Daegan, Harmony,

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NOMENCLATURE

AIC	Akaike Information Criterion
BDS	Bajo de Sico
BL	body length(s)
CCS	Center for Coastal Studies
COA	College of the Atlantic
DNA	deoxyribonucleic acid
DSG	Digital Spectrogram
ESA	Endangered Species Act
GIS	Geographic information System
GPS	Global Positioning System
h	hour(s)
Ha	alternative hypothesis
H_0	null hypothesis
IUCN	International Union for the Conservation of Nature
IWC	International Whaling Commission
KDE	kernel density estimate(s)
km	kilometer(s)
km^2	square kilometer(s)
kt	knot(s)
m	meter(s)
MCERC	Marine and Coastal Ecology Research Center
M-C	mother-calf pair
M-C-E	mother-calf-escort
MICS	Mingan Island Cetacean Study
min	minute(s)
mm	millimeter(s)
MMPA	Marine Mammal Protection Act

MoNAH	More of the North Atlantic Humpback
MSA	mixed-species association(s)
MUN	Memorial University of Newfoundland
NAHW	North Atlantic Humpback Whale(s)
NAHWC	North Atlantic Humpback Whale Catalog
nm	nautical mile(s)
NMFS	National Marine Fisheries Service
OMMAG	Observatoire des Mammifères Marins de l'Archipel Guadeloupéen or Marine Mammal Guadeloupean Archipelago Observatory
PAM	passive acoustic monitoring
PVC	polyvinyl chloride
SAG	surface active group
SPKS	sightings per km surveyed
USA	United States of America
USVI	United States Virgin Islands
YoNAH	Years of the North Atlantic Humpback

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CHAPTER I
INTRODUCTION AND LITERATURE REVIEW

Humpback whales *(Megaptera novaeangliae)* are medium sized whales of the family Balaenopteridae. At maturity, they can reach up to 16 – 18 meters (m) in length, and weigh approximately 40,000 kilograms (Johnson and Wolman 1984; Clapham and Mead 1999; Clapham 2009). They are easily identified by the large pectoral flippers ideal for maneuvering in the water column, a useful feature for foraging with bubble nets (Johnson and Wolman 1984) and maneuverability in competitive breeding groups (Sousa-Lima and Groch 2010). They often exhibit energetic surface behaviors, including lobtailing, flipper-slapping, and breaching (refer to Appendix B, Glossary for definitions of behaviors). Life expectancy of humpback whales is at least 45 years (Clapham and Mead 1999). Whaling is likely to have removed many mature animals from populations, creating a challenge for estimating maximum size and age of adults. Advancement in aging analyses from various tissues is increasing our understanding of the life span of humpback whales (Polanowski *et al.* 2014). Sexual maturity is attained between five and 12 years of age (Chittleborough 1955a, b; Clapham 1992). Females enter estrus during migration to winter habitats and are physiologically able to produce a calf yearly; however, three years (or more) between calves appears to be typical (Chittleborough 1958, 1965; Clapham 1996). Gestation is 11-12 months, with parturition occurring as females return to the winter habitats the following year (Chittleborough 1958, 1965; Nishiwaki 1959; Clapham 1996; Craig and Herman 2000). It is possible that some females enter postpartum estrus, particularly after a gestation fails to produce a viable calf (Chittleborough 1958, Tyack and Whitehead 1983). There is sparse evidence that humpback whales are capable of producing twin embryos, and there is no evidence that twins survive to parturition (Chittleborough 1955a). Calves are weaned after approximately one year with gradual separation occurring during their first season on the feeding grounds, and weaning is completed as mother and calf separate prior to (or during) the subsequent migration back to winter habitats (Clapham and Mayo 1990). It is these physical characteristics, behaviors, and the fact that they often occur nearshore that make humpback whales attractive to ecotourism worldwide.

Much anecdotal and scientific information about large whales, including the North Atlantic humpback whales (NAHW), came from data collection aboard whaling ships. Animals harvested and promptly prepared for market provided an opportunity to obtain tissue samples for gross and histological examination (Chittleborough 1958). Systematic investigations are relatively recent, with few papers published in the 1950's and most appearing after the early 1980's. In the 1950's and 1960's, Chittleborough (1955a, b, 1958, 1959, 1965) described growth and reproductive history of humpback whales based on histological investigations of numerous harvested animals. Considerable effort to survey humpback whale populations in the North Atlantic began in the 1980's (Mattila 1984; Mattila *et al*.1994; Clapham and Mayo1990; Clapham 1992; Stevick *et al.* 2001, 2003a).

NAHW have a seasonal distribution that varies between cold (higher latitude) waters during foraging and warmer (lower latitude) waters for calving and breeding (Clapham and Mayo 1987; Mattila *et al.* 1989; Corkeron and Connor 1999; Charif *et al.* 2001; Robbins *et al.* 2001; Barco *et al.* 2002; Clapham and Zerbini 2015) (Figure 1). In 1984, 2,200 animals were identified from the NAHW stock (Martin *et al*. 1984), whose summer habitats include the Gulf of Maine, Gulf of St. Lawrence, Newfoundland/Labrador, Greenland, Iceland, and Norway (Waring *et al.* 2014) (Figure 1), with the number of males and females nearly equal (Palsbøll *et al.* 1997). The Years of the North Atlantic Humpbacks (YoNAH) project during 1992 - 1993 estimated the overall NAHW stock at 11,570 animals (Palsbøll *et al.* 1997; Stevick *et al.* 2003a; Waring *et al.* 2014). Individuals of populations in the North Atlantic Ocean and South Atlantic Ocean migrate during their respective northern and southern winters; although their habitats overlap geographically they do not occupy the tropics simultaneously, and are considered reproductively isolated (Johnson and Wolman 1984; Roman and Palumbi

2003). The YoNAH and More of the North Atlantic Humpbacks (MoNAH) surveys conducted during winter months 2004-2005 counted almost two males for every female on the breeding grounds (areas on the winter habitats where competitive breeding aggregations [also known as “Surface Active Groups” or “SAG”] are formed) (Brown *et al.* 1995; Palsbøll *et al.* 1997; Waring *et al.* 2014). The disparity between the number of females and males in lower latitudes appears to reflect non-breeding (often termed "resting") and subadult females remaining in higher latitudes, and may include females occupying smaller nursery areas on the winter breeding/calving grounds throughout the West Indies (Mattila and Clapham 1989; Mattila *et al.* 1994), or it may be that males spend more time on the breeding grounds and females migrate regardless of their reproductive status (Mattila *et al.* 2001).

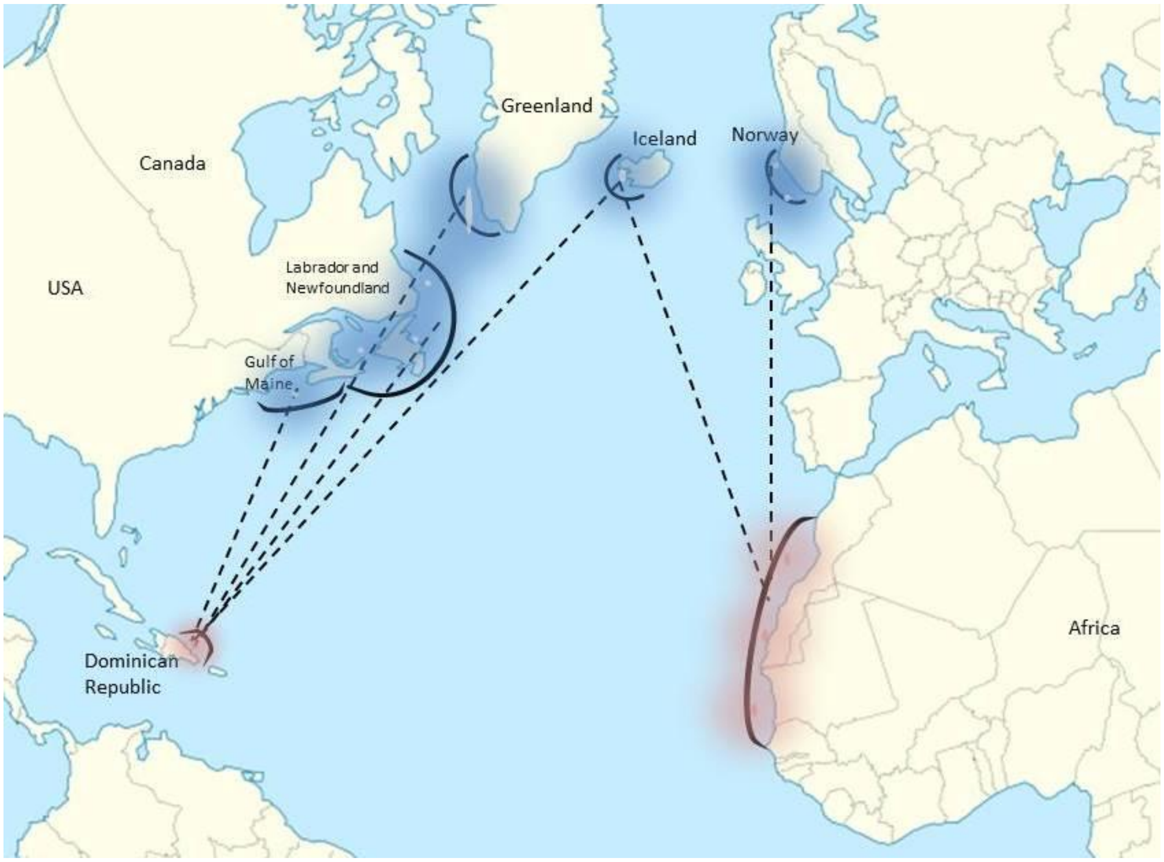

Figure 1. Migration patterns of humpback whales in the North Atlantic Ocean. Dotted lines are not representations of the actual migration routes, which remain unknown. Blue indicates the area of summer feeding grounds and pink indicates winter grounds. Feeding grounds (blue shaded areas) include the Gulf of Maine, areas off Newfoundland and Labrador, Canada (including the Gulf of St. Lawrence), Greenland, Iceland and Norway. Winter (breeding and calving) grounds (pink shaded areas) include the West Indies and Cape Verde Islands.

Because NAHW fast in winter habitats, the accumulation and storing of energy in the form of blubber to meet the high-energy demands of breeding and lactation must happen in summer. The summer feeding grounds consist of productive waters where food resources are concentrated (Johnson and Wolman 1984). Sand lance (*Ammodyte* spp.), euphausiids (krill), capelin (*Mallotus villosus),* and herring (*Clupea harengus*) are primary prey species of NAHW (Johnson and Wolman 1984).

It is unknown if migration from summer habitats is driven by predation pressure from killer whales (*Orcinus orca*), if warmer waters allow fasting cows (mothers) to nurse lean neonates (calves) and maximize the accumulation of blubber in preparation for the migration to feeding grounds, or if there is another reason NAHW undertake the long, seasonal migration (Corkeron and Connor 1999; Clapham 2001; Cartwright and Sullivan 2009b). Newborn humpback whale calves arrive on the summer feeding grounds with evidence of attacks from killer whales, including rake marks consistent with killer whale dentition (Figures 2 and 3) (Clapham 2001; Mehta *et al.* 2007; Steiger *et al.* 2008), but it is unknown what percentage of calves succumb to predation during the northern migration.

Figure 2. Humpback whale ventral side of flukes with scarring demonstrating the unique identification marks of each individual. Marine and Coastal Ecology Research Center (MCERC) catalog #98, photograph taken 17 April 2014 by Mithriel M. MacKay under National Marine Fisheries Permit #15682.

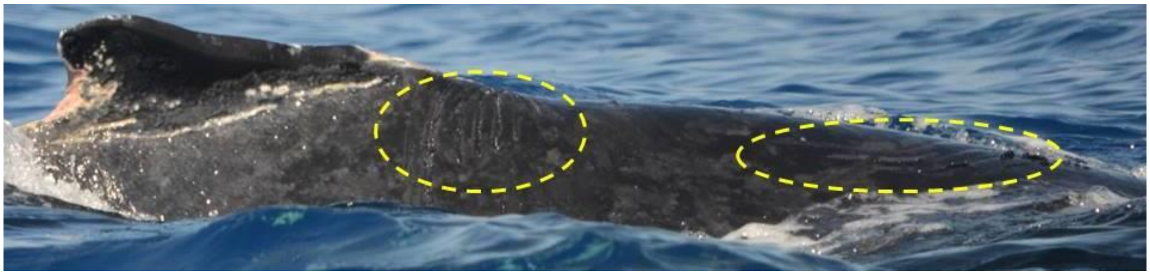

Figure 3. Natural marking including injury are used to identify individual whales. Photo of a humpback whale calf born winter 2014 and sighted by our research team with significant injuries consistent with an attack by killer whales. The yellow circles highlight fresh rake marks. Marine and Coastal Ecology Research Center (MCERC) catalog #96, photograph taken 26 March 2014 by Mithriel M. MacKay under National Marine Fisheries Permit #15682.

The ventral side of humpback whale flukes (tail) has unique coloration (pigment patterns) enabling identification of individuals. Additional scarring facilitates identification of individuals, such as the tearing at the central notch of the fluke pictured in Figure 2. Physical characteristics used to identify humpback whale individuals allow a mechanism for investigating details of occurrence patterns and sociality (Katona and Whitehead 1981). Images of individuals' distinct natural markings allow photo-identification catalogs to be established for referencing data recorded on individual animals (Katona and Whitehead 1981). The repository for fluke identification photographs for NAHW is curated by Allied Whale, College of the Atlantic (COA), Bar Harbor, Maine, USA, making it possible for collaboration between investigators studying NAHW on feeding grounds and the winter breeding/nursery areas.

In the early 1970's, winter habitats of humpback whales in the North Atlantic were described in the Greater Antilles (Winn and Winn 1978; Mattila and Clapham 1989; Katona and Beard 1990; Mehta *et al.* 2007). Areas with the highest density of NAHW in winter are Samaná Bay, and Silver and Navidad Banks off the Dominican Republic (Balcomb and Nichols 1982; Whitehead and Moore 1982; Mattila *et al.* 1989, 1994; Betancourt *et al.* 2012; Waring *et al.* 2014) and likely include smaller secondary areas throughout the West Indies from Puerto Rico to Venezuela (Winn *et al.* 1975; Levenson and Leapley 1978; Martin *et al.* 1984; Price 1985; Mattila and Clapham 1989).

Mother-calf (M-C) pairs appear to have a bias towards nearshore areas with a depth of 20 m or less, while mature males prefer deeper waters (Whitehead and Moore 1982; Mattila and Clapham 1989; Oviedo and Solis 2008). There is speculation that some nearshore habitats are occupied by mothers with calves because they provide warm waters and protection from high-energy wave action, decreasing energy demands on fasting cows and calves. Mother-calf pairs in relatively shallow nursery habitats may also avoid harassment from adult males seeking breeding opportunities (Perkins *et al.* 1982; Clapham 1992; Sanders *et al.* 2005; Craig *et al.* 2014; Clapham and Zerbini 2015).

Social occurrence patterns differ between the feeding grounds and the breeding grounds. NAHW may occur as singletons, M-C pairs, mother-calf with an escort (mother-calf-escort [M-C-E]), SAG, and group associations (individuals remain together for some length of time behaving in a similar or coordinated manner) for the purpose of foraging. The current understanding of NAHW social patterns includes associations of short duration in all habitats (minutes [min] to hours [h]), with the exception of M-C pairs (Clapham 1992). Foraging associations, including the number of individuals and duration of cooperative behaviors, are driven by the availability of prey species, and this leads to a variety of feeding strategies (Holt 1984; Friedlaender *et al*. 2009). Research being conducted on feeding grounds continues to redirect our interpretation of humpback whale associations, and it appears there are long-term associations of individuals foraging together over multiple seasons (Weinrich and Kuhlberg 1991; Weinrich 1991; Weinrich *et al.* 2006; Ramp *et al.* 2010; Allen *et al.* 2013).

Humpback whales have a multi-mate mating system, although it is unclear if breeding groups represent polygyny or polygynandry. Surface active groups are fast moving, energetic competitive groups that form when a focal female is pursued by a group of males (Tyack and Whitehead 1982; Clapham 1996; Clark and Clapham 2004, Darling *et al.* 2006). A primary escort (male) contends for the most advantageous breeding position near the focal female by “out chasing” and battling other adult males in pursuit of a chance to breed (see photo of competing individuals within a SAG in Appendix A). Females escorted by an adult male attract other males into SAG (Mattila *et* *al.* 1989; Clapham 1996; Darling *et al*. 2006) of energetic aggregations that tend to be of short duration, lasting from minutes to a few hours (Tyack and Whitehead 1983; Clapham *et al.* 1992; Mercado *et al.* 2003). Because intromission has not been observed between humpback whales, it is not possible to determine if competitors successfully mate with the focal female, although this seems likely given the investment of competitors. Calves may be found with mothers in SAG (a significant energetically demanding situation for lactating females and calves) (Lockyer 2007). There is evidence to support cooperation between males entering into competitive groups in whales wintering off Hawai'i (Darling *et al.* 2006). SAG disassociate and males seek other breeding opportunities; however, the number and frequency of individuals joining in SAG are unknown.

Associations between other species of cetaceans and humpback whales have been noted (Brownell 1964; Glockner-Ferrari and Ferrari 1985; Ciano and Jørgensen 2000; Steiger *et al.* 2008; Deakos *et al.* 2010; Smultea and Bacon 2012, 2013). Examples of these "mixed-species associations" (MSA) include humpback whales observed interacting with dolphins (Glockner-Ferrari and Ferrari 1985; Deakos *et al.* 2010) and following killer whales killing a gray whale (*Eschrichtius robustus*) calf near Monterey, California on 3 May 2012 (A. Schulman-Janiger, American Cetacean Society, 24 January 2015, personal communication). The reason for MSA is unknown but likely includes coincidence (concurrent feeding opportunities), play (observed in groups with humpback whales and dolphins), and aggression (killer whale predation and pilot whale harassment, for example).

Male humpback whales sing during the winter breeding and calving season (Winn and Winn 1978; Mattila *et al.* 1987; Clapham 1996; Darling *et al.* 2006; Stimpert *et al.* 2012; Vu *et al.* 2012; Herman *et al.* 2013), most likely for working out relationships for access to estrous females (Payne and McVay 1971; Tyack 1981; Darling *et al.* 1983; Darling *et.al* 2006). Published research on humpback whale song has concluded that song plays a significant role in relationships on the breeding grounds (Payne and McVay 1971; Winn and Winn 1978; Tyack 1981; Darling *et al.* 2006), and that the complexity and differences in the song could be accounted for by female choice (Craig and Herman 2000; Craig *et al.* 2002; Pack *et al.* 2009). Songs, which can be broken down into a repertoire of vocalizations, are unique to populations occupying a single ocean (Winn *et al.* 1981). At least some research has suggested that song plays an active role in sorting relationships among males (Tyack and Whitehead 1983; Baker and Herman 1984; Helwig *et al.* 1992; Medrano *et al.* 1994; Frankel *et al.* 1995; Clapham 1996; Darling *et al.* 2006). Singing may be advertising to potential mates, or signaling other male rivals and allies (Payne and McVay 1971; Tyack 1981; Darling *et al.* 1983, 2006) ,although the exact role and function of the song is unknown. There has been speculation that singing, in addition to being for reproductive purposes, may also be a means of gathering information about the physical structures of the immediate underwater area (Mercado and Frazer 1999; Mercado *et al.* 2003). There is some consensus that the song serves more than one purpose in social interactions (Winn and Winn 1978; Tyack 1981; Baker and Herman 1984; Clapham 1996; Frazer and Mercado 2000; Darling and Bérubé 2001; Herman *et al.* 2013),. Whether male humpback whales sing to work out social relationships among males or to advertise fitness to females is still debated (Darling and Bérubé 2001; Darling *et al.* 2006) and unraveling the meaning(s) of these vocalizations will take considerable research effort.

Humpback whales have been killed by humans since at least the 17th Century, but were not decimated until modern factory whaling in the 20th Century (Reeves *et al*. 2001; Clapham and Zerbini 2015). The International Whaling Commission (IWC) issued protection from harvest in 1966 (Stevick *et al.* 2003a; Ruegg *et al.* 2013). The Marine Mammal Protection Act (MMPA) (1972) and Endangered Species Act (ESA) (1973) in the United States facilitate the on-going recovery of NAHW. The International Union for the Conservation of Nature (IUCN) Red List includes NAHW as “endangered” in 1986, “vulnerable” in 1990, and currently as a species of “least concern”. NAHW remain “endangered” under the USA ESA listing and are currently being considered for delisting (79 FR 36281; Bettridge *et al.* 2015). The NAHW stock has made a remarkable recovery, and this may be largely attributed to the moratorium on whaling, few predators, and the ability to shift prey species with availability and abundance (Gerber *et al.* 2000; Stevick *et al.* 2003a). The latest population size estimate for the North Atlantic (U.S. Atlantic and Gulf of Mexico Marine Mammal Stock Assessments - 2013, Waring *et al.* 2014) resulted from the YoNAH and MoNAH surveys, and there has not been adequate sampling since 1992 and 1993 for an ocean-scale estimate. The recovery rate of the NAHW stock has been estimated between 3% and 6.5% per annum (Barlow and Clapham 1997; Stevick *et al.* 2003a).

Because the continued recovery of NAHW is dependent upon preservation of their feeding, breeding, and nursery habitats, identifying and managing these critical areas may lead to recovery to pre-whaling abundance (National Marine Fisheries Service [NMFS]1991). Critical habitats are defined as, "portions of a cetacean distribution range that have a key particular value for day to day survival and maintaining a healthy population growth" (Oviedo and Solis 2008), and this range for NAHW likely includes a large aggregation where thousands of individuals converge each winter, and smaller aggregations occur throughout the West Indies. At least 85% of the NAHW population converges on Silver Bank, Dominican Republic (Winn *et al.* 1975). Examination of whaling records (Mitchell and Reeves 1983; Mattila *et al.* 1994) indicates that this represents a shift of humpback whale occurrence patterns from the southeastern Caribbean in the 19th Century.

The broad goal of this dissertation is to begin to understand occurrence patterns and social behaviors of NAHW off Puerto Rico, with comparisons to the large, wintering aggregation off the Dominican Republic. The area off Puerto Rico's west coast has indications of representing critical habitats for NAHW, supported by the presence of singers, M-C pairs, and competitive breeding groups (Mattila 1984; Martin *et al.* 1984; Mattila and Clapham 1989). Individuals seeking breeding opportunities are likely to have a higher chance at participating in SAG in the Dominican Republic rather than low-density areas (Clapham 1996); however, singers have been detected past the Dominican Republic in Mona Passage. If numbers of receptive females are the sole consideration for males migrating to the winter habitats, and the chance of encountering a female in estrus is greatly reduced in Mona Passage, perhaps there is another reason for occupying this area. As the population recovers from whaling, small areas away from the primary aggregation may serve as a refuge for M-C pairs, indicated by an increase in their presence throughout the West Indies. Determining when NAHW occupy Mona Passage, how long they stay in that area, which areas they originate from in the higher latitudes, and association patterns (development of social and reproductive groups) have the potential to lay the foundation for an understanding of the importance of this area and providing marine managers with current information.

Research Objectives

This dissertation represents the beginning of a long-term systematic investigation of occurrence patterns and social behaviors of NAHW wintering off Puerto Rico. Recovery from whaling is promising if management strategy, policies, and regulations continue to protect this species from anthropogenic activities such as whaling, chemical contaminants, and ship strikes. The majority of effort of humpback whale research in the North Atlantic has been conducted on the feeding grounds and the largest aggregation of wintering individuals off the Dominican Republic. It is possible to begin to understand the importance of small secondary habitats by answering some fundamental questions to indicate how future research effort should be directed. The following objectives are the premise for this current study of wintering NAHW:

1) Examine timing of occurrence patterns and behaviors of humpback whales arriving off Puerto Rico over multiple years;

2) Define habitat use in the study area with consideration for differences between age, sex, and reproductive status;

3) Examine the social behaviors of humpbacks, including association patterns, in the study area; and,

4) Investigate the possibility of a relationship between bathymetric features off Puerto Rico and movement patterns and behaviors of humpback whales.

Overview of Chapters

Chapter I contains background information to facilitate an understanding of the purpose and value of current research effort. The introduction is not an attempt at a comprehensive review of the literature, but rather to orient the reader to this study. In addition to providing a review of the literature, this chapter provides a broad overview of research objectives. Chapters II, III, and IV examine specific questions designed to understand the importance of the study area. Chapter II examines the occurrence patterns, with consideration for clustering near bathymetric features, of humpback whales migrating to waters off Puerto Rico. Acoustic, sighting, and bathymetry data collected during four field years were analyzed to determine occurrence patterns within and between years. This chapter is the foundation for continued research effort with an aim at understanding the use of a smaller secondary habitat during winter. Chapter III is a study of movement patterns of humpback whales sighted off the west coast of Puerto Rico and feeding grounds or breeding grounds. The North Atlantic humpback whale catalog (NAHWC) is utilized to determine where individuals have been sighted by other investigators and to obtain an indication of the connection of Mona Passage to humpback whale habitats in the North Atlantic. Chapter IV examines association patterns of humpback whales, including intra- and inter-species interactions within and between years. Behaviors by group-type are examined as an indicator for length of time NAHW may remain in the study area. Chapter V summarizes the results of this research, with suggestions of future research questions.

Importance of Research/Justification

The discovery that individuals can be identified using natural markings has advanced the study of humpback whales (Katona *et al.* 1979; Katona and Whitehead 1981; Kaufman *et al.* 1990). Identification of individuals has facilitated a greater understanding of social organization, migration destinations, population dynamics in winter areas, and foraging behaviors. With the exception of incidental recordings of NAHW singers by fisheries biologists and an investigation of humpback whale vocalizations as they pertain to physical characteristics of this area (Mercado *et al.* 2007), it has been over a decade since humpback whale research has been conducted off Puerto Rico (Balcomb and Nichols 1982; Sanders *et al*. 2005) and almost three decades since the last investigation was conducted over multiple seasons. Research efforts by Swartz *et al.* (2002) were limited to detection of individuals by acoustics and line-transect surveys around Puerto Rico. Behaviors were not included in Swartz's research off Puerto Rico, and were last examined during the work by David Mattila and Phillip Clapham in the early 1980's and during the YoNAH and MoNAH surveys (Mattila 1984; Mattila *et al.* 1989, 1994; Clapham *et al.* 1992; Clapham and Mattila 1993).

Rincón, Puerto Rico, includes areas that are shallow, warm, and protected from high-energy wave action. The physical characteristics of this area fit the needs of humpback whale mothers nursing calves. The opportunity for breeding is likely to be low, as indications from incidental passive acoustic monitoring (PAM) from fisheries biologists hints at a lower density of singers than off the Dominican Republic. If we accept the assertion that nearshore areas with fewer energetic demands are likely to benefit mothers with neonates (Perkins *et al.* 1982; Clapham 1992; Sanders *et al.* 2005; Craig *et al.* 2014; Clapham and Zerbini 2015), then it is logical that female humpback whales have a bias for this shallow nearshore nursery area in calving years, and migrate to more populated habitats during breeding years. Additionally, identifying which discrete feeding ground individual humpback whales started their migration may aid in clarifying the potential impact to any single winter habitat. For example, if a majority of individuals migrated from a single feeding ground to a single winter habitat, any negative (or positive) impact to their winter habitat is likely to be of greater magnitude than if the aggregation is a mix of individuals from several feeding grounds.

There are challenges inherent in the study of a subset of a population of an endangered species on a small habitat where a low-density aggregation is expected. Obtaining a robust data set requires a large number of effort hours compared to a densely populated area. This research design includes *ad libitum* data collection methods that are valuable for descriptive research where foundation work is being collected (Mann 1999). There are also advantages to studying low-density areas that cannot be easily found in densely populated areas. The low-density area allows an observer to examine behaviors of individuals that may be difficult to understand in the midst of several thousand humpback whales. There is potential to collect data that may otherwise be masked by large numbers of individuals transiting within a study area. For example, it is possible to identify a singer and record that individual's vocalizations with a high degree of confidence that the audio capture can be attributed to a particular (perhaps photographically identified) whale. This long-term study was designed to answer some fundamental questions and establish a robust foundation for future research (including an open-ended extension of this project) as the number of individuals increase throughout the North Atlantic, including Puerto Rico.

CHAPTER II

NORTH ATLANTIC HUMPBACK WHALE (*Megaptera novaeangliae*) OCCURRENCE PATTERNS ASSOCIATED WITH BATHYMETRY DEFINE FOUR "HOTSPOTS" OFF WESTERN PUERTO RICO, USA

Introduction

NAHW migrate from feeding grounds in higher latitudes to breeding and calving grounds in lower latitudes (Clapham and Mayo 1987; Mattila *et al.* 1989; Corkeron and Connor 1999; Charif *et al.* 2001; Robbins *et al.* 2001; Barco *et al.* 2002; Clapham and Zerbini 2015) (Chapter 1, Figure 1). Silver Bank, Dominican Republic, is the location of the main aggregation of NAHW, with smaller aggregations on Navidad Bank and in Samaná Bay. Some NAHW migrate past the large aggregation off the Dominican Republic to waters around Puerto Rico and the Lesser Antilles. It is not known whether the smaller areas throughout the Caribbean Sea are populated as an "overflow" from the larger aggregation, if they are remnants of what was once a densely populated area larger than the seasonal aggregation off the Dominican Republic prior to whaling, or if the islands serve another important function in humpback whale life history. The latter would indicate that the area off Puerto Rico is a critical habitat (Oviedo and Solis 2008). The limited information describing seasonal occurrence patterns of NAHW wintering off Puerto Rico is from log books of whaling ships and the sparse surveys of cetaceans that have been conducted in this area (Mattila *et al.* 1989; Palsbøll *et al.* 1997; Mignucci-Giannoni 1998; Stevick *et al.* 1998, 1999, 2003a; Swartz *et al.* 2002). A multiyear study over consecutive seasons, and most winter months, had not been conducted before my work apart from the main aggregation. This study provides current information regarding the relationship of smaller secondary areas to the large aggregation in the area occupied by thousands of humpback whales off the Dominican Republic.

Puerto Rico is located at 18° North Latitude, 67° West Longitude, approximately 182 nm (338 km) southeast of Hispaniola. The largest island in the Puerto Rican Archipelago is approximately 60 km wide (north to south) and 173 km long (west to east). The Atlantic Ocean is north of Puerto Rico with the Caribbean Sea bordering the west, east, and south coasts. Mona Passage is an underwater canyon between the west coast of Puerto Rico and the island of Hispaniola with variable depths throughout the canyon, and includes smaller islands, with seamounts rising within 10 m of the surface. Mona Passage has varying slopes of 10 - 50 degrees extending from 20 - 30 km wide, 140 km long, and 2 - 3.5 km deep (Mondziel *et al.* 2010). The deepest part of the canyon is greater than 1,000 m and reefs and seamounts are scattered throughout the canyon, creating shallow areas. The west coast of Puerto Rico, extending into Mona Passage, has a coastal shelf extending approximately 0.5 km along the west coast at the closest point (Rincón) between Aguadilla (at the northwest tip) and Mayagüez (center of the west coast), where the coastal shelf extends out at its furthest point, 15 nm / 27 km surrounding the southwest corner of the island. The variation along the canyon provides relatively shallow areas as well as deep gorges (Schuchert 1936; Brink 2007; United States Geological Survey Simrad EM-1002 survey from National Oceanic and Atmospheric Administration ship *Nancy Foster*, 2007 survey) (Figure 4), facilitating a study of habitat preferences among humpback whales in the context of bathymetric features.

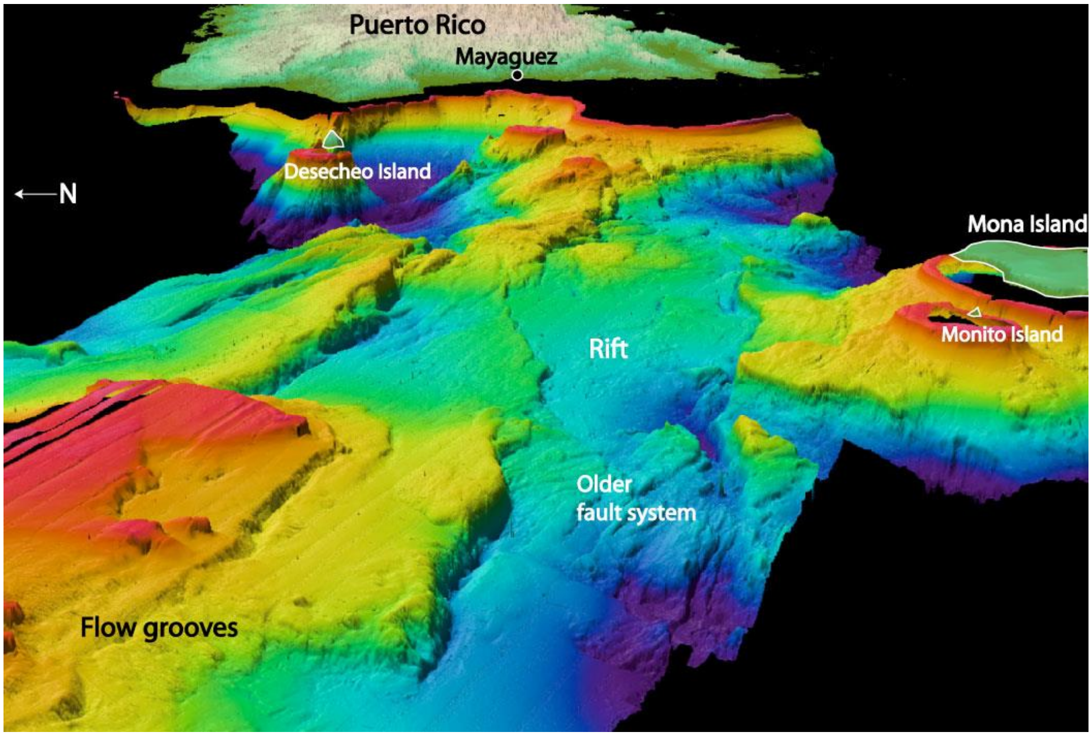

Figure 4. “Perspective” view of the bathymetry of the Mona Passage, looking eastward toward Puerto Rico. Depths indicated by color, from red (shallowest) to purple (deepest); black indicates sea floor not mapped during this study. Small islands are outlined in white to make them more visible. Photo and figure caption reprinted with permission. Accessed from http://soundwaves.usgs.gov/2007/05/ (Brink 2007).

Humpback whale mothers show a preference for nearshore areas where the waters are less than 20 m deep, leading to speculation that the energy demands in these areas are favorable for calves (Whitehead and Moore 1982; Félix and Haase 2001; Smultea 1994; Cartwright *et al.* 2012) and are consistent with the western coastline of Puerto Rico in Mona Passage. In addition to protection from the energy demands offshore, there has been speculation that M-C pairs have a bias for nearshore shallow areas, to avoid having a calf in highly energetically demanding SAG (Cartwright and Sullivan 2009b). Subtropical waters near the equator likely provide an environment favorable for lactating fasting females transferring a significant portion of their body weight to their calves (Lockyer 2007; Cartwright *et al.* 2012), although the reason for humpback whale migration is still the subject of debate (see Corkeron and Connor 1999;

Clapham 2001; Connor and Corkeron 2001 for a relevant discussion). In addition to preferences of M-C, dyads have been observed nearshore and breeding groups show a bias for deeper waters past the shelf break (Whitehead and Moore 1982; Mattila and Clapham 1989; Mignucci-Giannoni 1998; Félix and Haase 2001; Swartz *et al.* 2002; Frantzis *et al.* 2004; Felix and Haase 2005; Kaschner *et al.* 2006). It is unknown whether associations with bathymetric features and/or proximity to shoreline occur for NAHW in Mona Passage.

An investigation of humpback whale singers and their proximity to bathymetric features on winter habitats has not been undertaken, with the exception of some speculation that singers are ranging (Mercado *et al.* 2007, 2008) and may be using song for sonar (Frazer and Mercado 2000). Humpback whale anatomy is not consistent with the capability of producing and receiving sonar (Beamish 1978; Reidenberg and Laitman 2007; Adam *et al.* 2013); however, it is possible that the canyons and ledges give singers some acoustic advantage (Mercado and Frazer 1999; Frankel *et al*. 1995). Because of the proximity of Puerto Rico to the Dominican Republic, and because the bathymetry in Mona Passage along the west coast of Puerto Rico is consistent with habitats occupied by mothers and calves (Cartwright et al. 2012), it is anticipated that females will be found along Puerto Rico's west coast during calving years. Current data suggest reproductive behaviors for humpback whales include female choice (Cartwright and Sullivan 2009a; Pack *et al.* 2009), and I anticipate that site fidelity during breeding years will favor females selecting the high-density aggregation off the Dominican Republic. It is logical to expect that males looking for a breeding opportunity will be less likely to occupy areas with M-C pairs or few receptive females.

This study examines the occurrence patterns of NAHW, including temporal and spatial distribution, in Mona Passage. I investigated the relationship between individuals near coastlines, seamounts (submarine mountains with the summit below the surface), ridges (subsurface mountain ranges), shelves (projecting ridges), and ledges (reefs, ridges, or lines of rock) in Mona Passage where these physical features may provide an acoustic advantage to singing males. I predict that this area off Puerto Rico is occupied by M-C pairs and few singletons (not singing) each winter, with singers and breeding groups representing a very small percentage of humpback whale groups in the same area. The following null hypotheses were tested: 1) NAHW occurrence patterns are not seasonal and predictable during winter in Mona Passage, immediately off western Puerto Rico, with breeding groups and non-breeding groups equally represented, and 2) groups (M-C, M-C-E, singers, SAG, dyads) are not associated with bathymetric features. Alternative hypotheses are based on studies conducted on other NAHW winter habitats in the North Atlantic and Hawai'i. Alternative hypotheses are as follows: 1) NAHW migrate to Mona Passage each winter, with the number of group associations favoring non-breeding groups (M-C pairs), and 2) groups are more likely to be found associated with bathymetric features where M-C pairs are found in near coastal areas in depths 20 m or less, SAG are found offshore in deeper waters, and singers are near shelves where there may be an acoustic advantage.

Methods

A pilot study between January and April 2011 was designed to determine where to focus data collection from a small vessel and land for subsequent seasons. Cliffs overlooking the survey area were selected from where humpback whales had been sighted during previous surveys and where anecdotal information (fishermen, residents, fisheries biologists) indicated sightings of humpback whales in Mona Passage during previous winters. The west and southwest coasts were selected as a matter of practical feasibility and efficiency for a small team, with the aim of determining if humpback whales were close enough to shore to collect data from land. During the study, humpback whale sighting methods were conducted from shore, vessel (by visual and hydrophone listening aids), airplane, and stationary bottom mounted underwater listening devices.

Shore-based observations

Observations were conducted from shore-lining cliffs at four locations in 2011 (Rincón - El Faro; Cabo Rojo - El Faro; La Ventana, Guayanilla; and Punta Ballena, Guayanilla), two locations in 2012 (Puerto del Mar, Aguadilla; Rincón - El Faro), and a single platform in the 2013 and 2014 seasons (Rincón - El Faro) (Figure 5) to determine the optimum location for land surveys. The land station was reduced to one site when it became apparent that sighting humpback whales from a cliff would be possible from a single location. Rincón - El Faro has a viewing elevation of 11.6 m, which yielded a distance to horizon of 12.2 km and a 200 degree panoramic view. Data collection was attempted from a secondary site overlooking Aguadilla Bay in winter 2012 from a vantage of 72.0 m and a distance to horizon of 30.3 km. This site was not used since the end of winter 2012 when few humpback whales were sighted inside the bay and the distance was too far to see humpback whales outside of the bay.

My team consisted of observers using reticle binoculars and the unaided eye. A theodolite was used to collect horizontal and vertical angles to a group of humpback whales, then converted into GPS coordinates using the program *Mysticetus* (Entiat Inc., http://www.mysticetus.com). Two observers scanned an area of approximately 5 degrees (one binocular field of view) per minute for 20 min. At least one observer scanned the same area with unaided eye. To prevent eye fatigue, observers rotated between scanning with binoculars, theodolite data acquisition, scanning with unaided eye, and recording data. When a group of humpback whales was sighted, scanning was suspended and a focal follow was initiated until the humpback whale(s) were no longer sighted, or data collection on location, behavior, group composition, and size of group was deemed to be complete.

Boat-based observations

For boat surveys, I chartered a 32’ Eduardoño (Panga) boat with a Bimini top and dual outboard 175 horsepower - 2 stroke Yamaha motors for surveying offshore. Our team was comprised of an experienced captain dedicated to boat operations and 5 - 9 additional observers. Boat effort was concentrated in the mornings, preceding the effects of the trade winds, allowing for 4 - 6 h per day 1 - 3 days per week. Observation effort took place immediately after launching the boat and was terminated when the boat returned to the ramp. The south coast was surveyed in 2012, but I discontinued due to few sightings and in favor of west coast effort for subsequent years.

Boat observers were positioned and scanning commenced immediately after the boat launch, with 360 degree coverage. The team was equipped with reticle binoculars (Bushnell and Fujinon 7 X 50 mm), laser range finder (Bushnell yardage Pro 1000), Garmin 76x GPS, and BT (Bluetooth) 358 GPS units and mapping capability (Etopo1 Worldwide 1-arc minute bedrock topography, NOAA; Puerto Rico = 3 arc seconds) in real-time (*Mysticetus*, Microsoft Surface Pro computer tablet), Rite-In-Rain log book, and a handheld "weather station" (Minox Windwatch Pro 2). Beaufort sea state along the west coast and away from shore varied greatly from day to day; and the departure location, distance from shore surveyed, and area surveyed were largely dictated by weather. In general, Beaufort sea state above 4, swell over 4 feet (ft), and rain were criteria for terminating boat effort.

Near the beginning of a boat survey, if a humpback whale was not sighted before we reached a predetermined hydrophone enabled "listening point" (see below); we deployed a directional hydrophone from the boat to listen for singing NAHW. Listening points are locations outside of the bay where the boat was launched or a location where humpback whales singing had been detected multiple times on previous excursions. The boat was motored into the area near a singer, and we continued recording vocalizations and waited for the individual to surface to collect data; if humpback whale singing was not detected, the boat was moved to another predetermined listening point.

The hydrophone deployed from the boat was a model H2A-XLR (Aquarian Audio Products, Seattle, Washington) or similar handheld unit with 10 - 20 m of cable. Distance to the singer was estimated based on the volume of sound and marine conditions and confirmed when the whale surfaced. With experience, I was able to estimate the distance of whales singing with consideration for sea state. If the singer was estimated to be within detection range of our directional hydrophone, a custom-made directional hydrophone (modeled after Whitehead and Gordon 1986; Weilgart and Whitehead 1997; Whitehead *et al.* 1998; Douglas *et al.* 2005) was lowered into the water on a pole to determine the compass bearing to the singer. The directional hydrophone brought us closer to the location of the singer and the team waited for a whale to surface.

Once whales were either sighted with unaided eyes, binoculars, or aid of the hydrophone system, individual and group behaviors were recorded at each surfacing. A waypoint was marked with a GPS and mapped in real-time in the program *Mysticetus*. I attempted to photograph flukes, dorsal fins, and scars of all individuals in each group. High-resolution still shots were captured by 1-2 photographers with a digital single-lens reflex camera (Nikon D7000 with Sigma 50-500 mm and Nikor 55-300 mm lenses) fitted with a video camera (GoPro2 or Midland XTC 100). If whales approached our boat upon surfacing, underwater video cameras (GoPro2, GoPro Hero 3, Midland XTC 100) fastened to a PVC pole were lowered into the water in an attempt to capture fluke photos subsurface. Fluke photos were entered in iMatch5 and along with metadata that included date, time, and identification of all whales in the same group. Images of dorsal fins were obtained in addition to, or in lieu of, fluke photos whenever possible. An attempt to match all images in the local catalog was made to determine sighting history and record group composition. Photographs were compiled into a catalog and submitted to the repository for NAHW (Allied Whale Project, COA).

Boat effort was restricted by weather, including increased winds and swell most afternoons; however, coverage of the survey area over four seasons was sufficient to sight groups throughout Mona Passage, collecting data reflective of location and group behaviors (Figures 5 and 6). The result is an indication of occurrence patterns while minimizing the inherent bias in *ad libitum* survey methods. Methods did not include line-transects for several reasons. This study was not aimed at an abundance estimate that would require a systematic survey of the area of interest. Instead, our goal was to find whales in a low-density area and attempt to determine if they were transiting through Mona Passage and what purpose, if any, this area serves for wintering NAHW. Line-transects would have limited our ability to see whales over such a large area; therefore, modifications were made to the methods during the first two seasons to locate whales and maximize the number of sightings per distance transited through the survey area. Summary of effort (expressed as raw tracklines per 5 km^2 in Figure 6) is a reflection of the distance transited throughout the study area over the 4 years of this study, and provides a visual representation of a successful attempt to survey the study area while transiting between locations where whales were heard singing or groups were sighted from a distance.

Aerial observations

Aerial surveys were employed as a means of reconnaissance during times when humpback whales were particularly difficult to locate (when movement patterns shifted within and between years), sea state was favorable for aerial observations but not for boat and land observations, fishermen reported multiple sightings of NAHW in an offshore location, and to get a periodic overview of the study area. A Cessna Skyhawk II (high-wing, single engine) and pilot were chartered beginning in 2012. The plane has four seats accommodating the pilot, two observers (right wing and left wing), and a data recorder/observer. The duration of each aerial survey was between 1 and 2 h, which allowed for enough flight time to scan a majority of the study area with sufficient coverage to determine the location of NAHW in a single flight. The pilot was directed to maintain an altitude of at least 457 m (1,500 ft) over the survey area to avoid harassment (Würsig *et al.* 1985, 1989; Richardson *et al.* 1995). When a whale was sighted, the observer obtained a declination angle using a Suunto clinometer. The altitude and GPS location of the plane at the time of the sighting were entered into the database using a GlobalSat BT 358 GPS unit (live feed) in conjunction with *Mysticetus,* thereby creating a waypoint overlaying a bathymetric map of the area in real-time. Focal follows were not conducted from the air.

Boat effort and observations from land were impacted by the trade winds and accompanying increase in Beaufort sea state that occurred most afternoons, with some degree of variability between and within seasons. It became clear that data collection should largely be limited to morning hours (typically from first light to noon each day) and an attempt to distribute data collection over all daylight hours was abandoned during the 2012 season. In 2014, a single land platform, vessel surveys, and occasional aerial reconnaissance continued to be our standard operating procedure for data collection. Observations through the end of April 2014 are included in these analyses.

Acoustic data collection from stationary recording units

Digital Spectrogram (DSG) Long-Term Acoustic Recorders (Loggerhead Instruments Inc., Sarasota, Florida, USA) were mounted to the sea floor in Mona Passage in December 2006 by fisheries biologists from University of Puerto Rico, Isla Mayagüez, Lajas, Puerto Rico. Additional DSG were placed in 2011, effectively monitoring the area between Puerto Rico’s east coast and St. Thomas (United States Virgin Islands [USVI]) for humpback whale singers (map is excluded to preserve confidentiality of DSG placement for fisheries recovery effort). The hydrophones were deployed for fisheries data each season ahead of the humpback whales' arrival in the area, and recordings continued well after humpback whales left the area. Ishmael Acoustic Software (www.bioacoustics.us/ishmael.html;Cooperative Institute for Marine Resources Studies, Oregon State University, Dr. David K. Mellinger) was used to analyze the data from the DSG (as well as from boat-deployed hydrophones). Data were scanned visually for the presence of NAHW song that would indicate presence of males. Acoustic capture files were loaded into the software and spectrograms were displayed. When NAHW vocalizations were detected, the file number was noted on an Excel spreadsheet.

Mapping and statistics

Geographic Information System (GIS) mapping technology was used to analyze sightings per km surveyed (SPKS) and kernel density estimate (KDE) with respect to bathymetry. Maps were generated using existing datasets from the National Centers for Environmental Information (http://ngdc.noaa.gov; gridded data = 3 arc seconds). Kernel density estimators were derived using standard methods. KDE calculates the density of points within a specified neighborhood around each point. Within KDE, a defined, smooth and optimally bound function (the kernel) is employed to spread values across an area. Within the data set SPKS were calculated. This metric is derived by a summation of sightings divided by the summation of distances surveyed (sightings / km). These values were then included in grid cells. In this study SPKS is defined by sightings in each 5 km^2 block (Figure 6) surveyed between 2012 and 2014 by boat. SPKS creates a visual representation of relative density observed throughout the study area, however; it is important to note that in the absence of line-transect survey patterns this is not an accurate abundance estimate, rather a means to identify areas where NAHW are aggregating. The summary of effort map represents raw tracklines summarized into grid cells (5 km^2 blocks) for a visual representation of distance covered by boat over the study area between 2012 and 2014.

Here variables were tested to determine if there are features that are important predictors of the type of group associations seen in NAHW off the coast of Puerto Rico. A multinomial logistic regression implemented in the R v3.1.1 package polytomous was performed (Arppe 2012; R Development Core Team 2014). An exhaustive search was used to test for the best model using Akaike Information Criterion (AIC) to compare between models. The independent variables used were bathymetric depth, Euclidean distance from the shelf edge, and slope of the seafloor. These variables were transformed based on the Box-Cox transformation to normalize the data and reduce the influence of extreme values, thereby improving the models’ ability to converge.

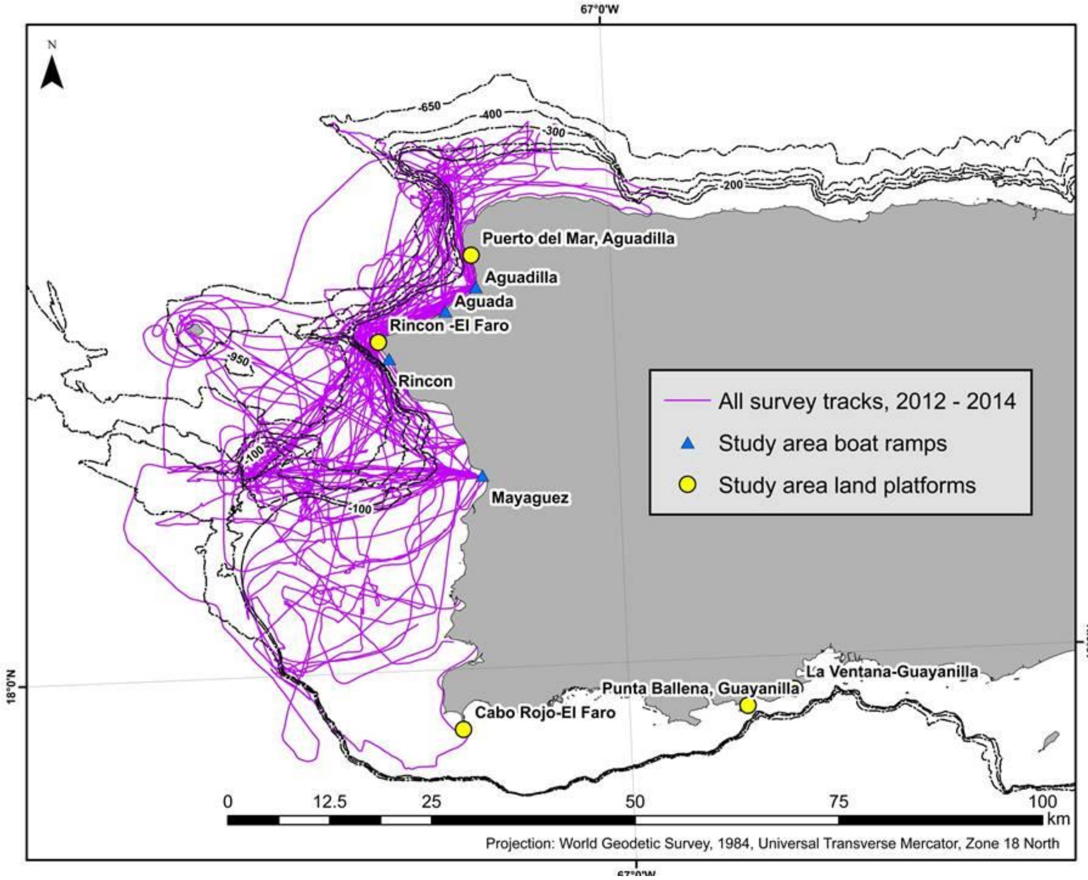

Figure 5. Boat survey tracks in Mona Passage between 2012 and 2014. Purple lines indicate track lines of all boat surveys. Blue triangles denote locations of ramps utilized for launching boat surveys (Aguadilla, Aguada, Mayagüez). Yellow circles denote land platforms (Puerto del Mar, Aguadilla; Rincón -El Faro; Punta Ballena, Guayanilla; La Ventana-Guayanilla; Cabo Rojo-El Faro), including the pilot study in 2011.

Results

Between 11 January 2011 and 01 May 2014, 543.5 h were dedicated to research effort from cliffs and boats (303.6 h from land, 240.9 h from boat) (Table 1, Figure 6). There were a total of 81 days of land effort, 71 days on the boat, and 13 aerial reconnaissance flights. Three hundred thirty-one individual humpback whales in 197 groups were sighted over the study period between winter 2011 and 2014 (Tables 2 and 3, Figures 7 and 8). Groups include M-C, M-C-E, dyads, SAG, singletons, and singers. If one or both individuals in a dyad were singing, they were counted as a single group of dyads, and therefore, singers may be underestimated. Fluke identification photos were difficult to capture, as deep dives were not typical, in favor of “no fluke dives” when whales arched their bodies to move below the surface without raising their flukes above the surface. A local catalog was created and includes fluke photos, dorsal fin photos, and images of other natural markings. Photo-identification images were obtained for 27% of individuals sighted. Resightings of known individuals were rare (1%) within and between years.

The first date of arrival each season was typically between late December and early January with acoustic confirmation of singers in the area off the east and west coasts of Puerto Rico (Table 2). Visual confirmation of humpback whales occurred near the third week in January most years, with exception of 2012 when the first visual confirmation did not occur until February. Acoustic detection with DSG preceded visual detection of whales in the area each year.

Kernel density estimates confirm that sightings were clustered near four bathymetric features including seamounts, ledges (Los Rabos, Rincón, Bajo de Sico [BDS]) and the Cabo Rojo shelf (Figures 8 and 9). Singletons and dyads (non-M-C) were found associated with all four bathymetric features, over and along the edge of each feature (Figures 8 and 9). SAG were associated with bathymetric features near Rincón (Figure 8). M-C pairs were sighted close to the point at Rincón while M-C-E groups were more likely to be offshore (Figure 8). A Mann-Whitney U test resulted in a p value of 0.0003 (test statistic 2.000), rejecting the null hypothesis that there was no significant difference in the distance from shore of M-C and M-C-E (M-C mean distance from shore = 2.69 km; M-C-E mean distance from shore = 18.04 km) (Figures 8 and 9). In 2013, whales were found predominantly off the northwest coast between Rincón and Aguadilla. In 2014, whales were observed predominantly off the southwest coast between BDS and Cabo Rojo. In both years whales aggregated along similar bathymetric features (Figures 8 and 9).

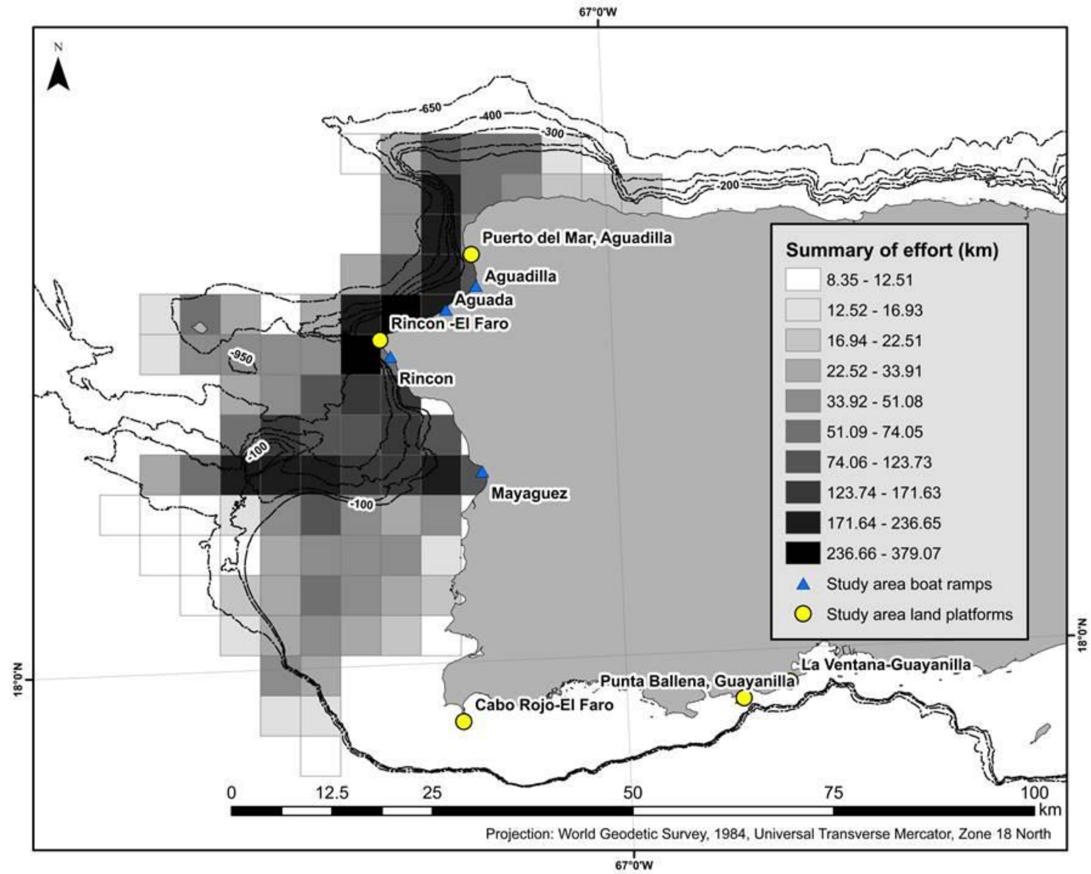

Figure 6. Summary of Effort: The figure represents raw track lines representing the distance traveled by boat between 2012-2014 summarized into grid cells (5 km^2 blocks). This map defines the study area in terms of locations surveyed.

Table 1. Total number of effort hours and days across each platform (land, aerial, and boat) for each year from 2011 to 2014 off western Puerto Rico.

Year	Land Platform (h:mm:ss)	Boat Platform (h:mm:ss)	Aerial Recon Flights	Total Number of Days on Land Effort	Total Number of Days on Boat Effort
2011	129.9	0	0	26	0
2012	76.2	60.1	5	19	16
2013	59.7	90.4	4	21	22
2014	3.8	87.3	4	15	33
Total	**303.6**	**239.8**	**13**	**81**	**71**

Total research effort hours (h) **543:29:07**

Total days on effort (n) **165**

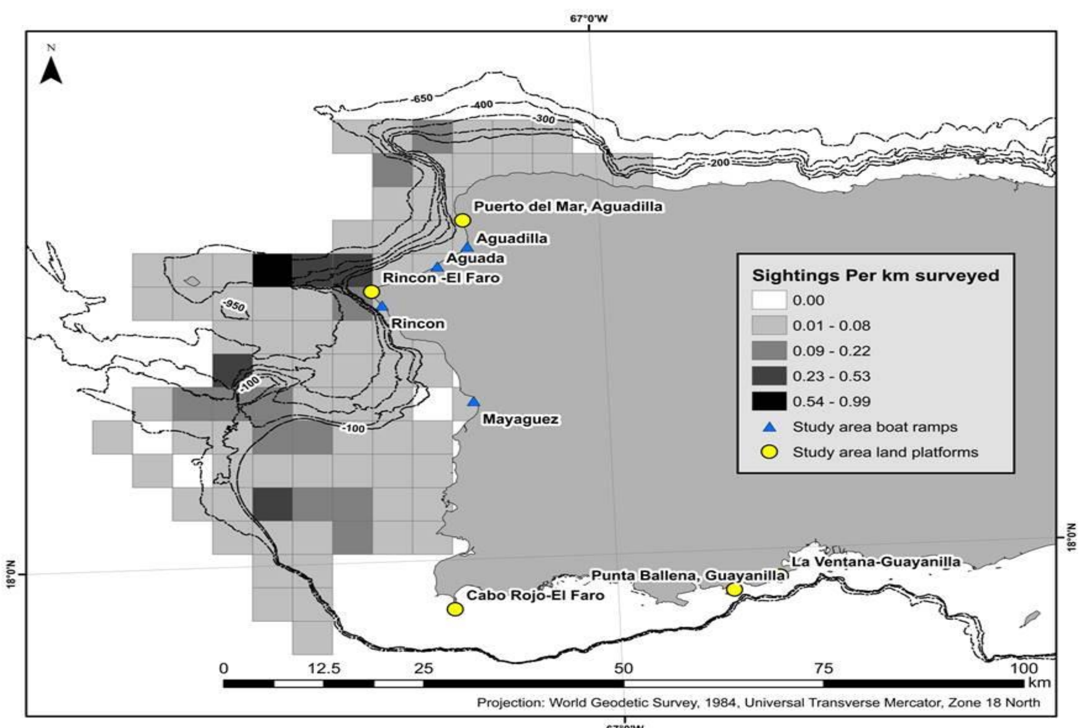

Figure 7. Sightings Per Kilometer Surveyed between (SPKS) 2012 and 2014: This metric is derived by a summation of sightings divided by the summation of distances surveyed (sightings/km). These values were then included in grid cells. In this study SPKS is defined by sightings in each 5 km^2 block surveyed by boat between 2012 and 2014. Four clusters of NAHW sightings can be identified.

Table 2. Summary of first and last arrival of humpback whales in the study area by year.

Study Year*	First Acoustic Detection	Last Acoustic Detection	First Visual Detection	Last Visual Detection	Highest Number of Sightings in a Two Week Period
2007	no data	30-Apr-07	no data	no data	Unknown
2008	19-Jan-08	20-May-08	no data	no data	Unknown
2009	no data	no data	no data	no data	Unknown
2010	19-Jan-10	27-Apr-10	no data	no data	Unknown
2011	29-Dec-10	14-May-11	20-Jan-11	02-Mar-11	Unknown
2012	23-Nov-11	23-Apr-12	13-Feb-2012**	28-Mar-12	27 Feb - 13 Mar
2013	02-Jan-13	16-May-13	23-Jan-13	18-Apr-13	27 Feb - 13 Mar
2014	26-Dec-13	29-Apr-14	17-Jan-14	17-Apr-14	24 Feb - 10 Mar

*years prior to 2011 are only loggers with no visual surveys, DSGs were the first to detect whales by song as they were placed in Mona Passage before land and boat work began each year.
**In March 2012, detection of whales was improved by adding a hydrophone deployed from the boat and January 2013 a directional hydrophone was added to the methods.
***abundance surveys were not conducted; therefore, caution must be exercised in interpretation as this may indicate a "peak" but cannot be confirmed. Peak is defined for this table as the two week period of time in each year with the largest number of individuals observed during boat, aerial, and land surveys combined.

Table 3. Summary of seasonal occurrence of NAHW by groups during 2011-2014 surveys.

Year	**Number of Individuals***	**Number of Groups**	**Number of Mother-Calf Groups**	**Number of Mother-Calf-Escort Groups**	**Number of Surface Active Groups**	**Total Number of Individuals in Surface Active Groups**	**Number of Singletons**	**Number of Dyads****	**Number of Mixed-Species Groups**	**Total Number of Humpback Whales in Mixed-Species Groups**
2011	63	36	8	0	3	9	12	13	0	0
2012	19	12	4	0	0	0	5	3	0	0
2013	145	78	1	2	5	22	28	38	4	11
2014	104	71	4	6	0	0	46	13	2	6
Total	**331**	**197**	**17**	**8**	**8**	**31**	**91**	**67**	**6**	**17**
Percent of Total Individuals			10.3	7.3		9.4	27.5	40.5	6	5.1
Percent of Total Groups			8.6	4.1	4.06		46.2	34.0	3.05	

*Individual counts are exclusively humpback whales
**Excludes mother-calf pairs

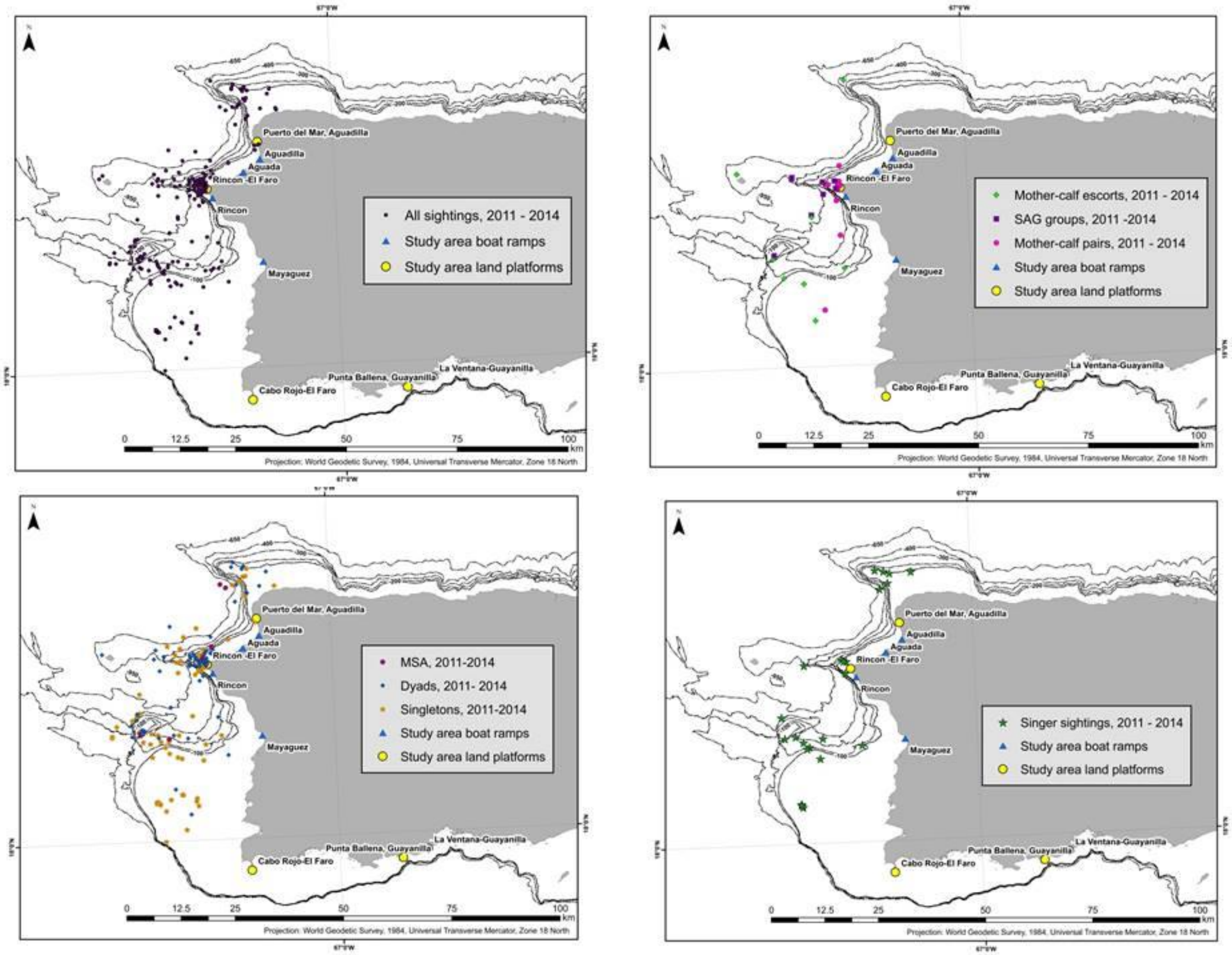

Figure 8. Distribution of 197 groups of North Atlantic humpback whales between 2011 and 2014 in Mona Passage with an overlay of bathymetry in the study area in Mona Passage.

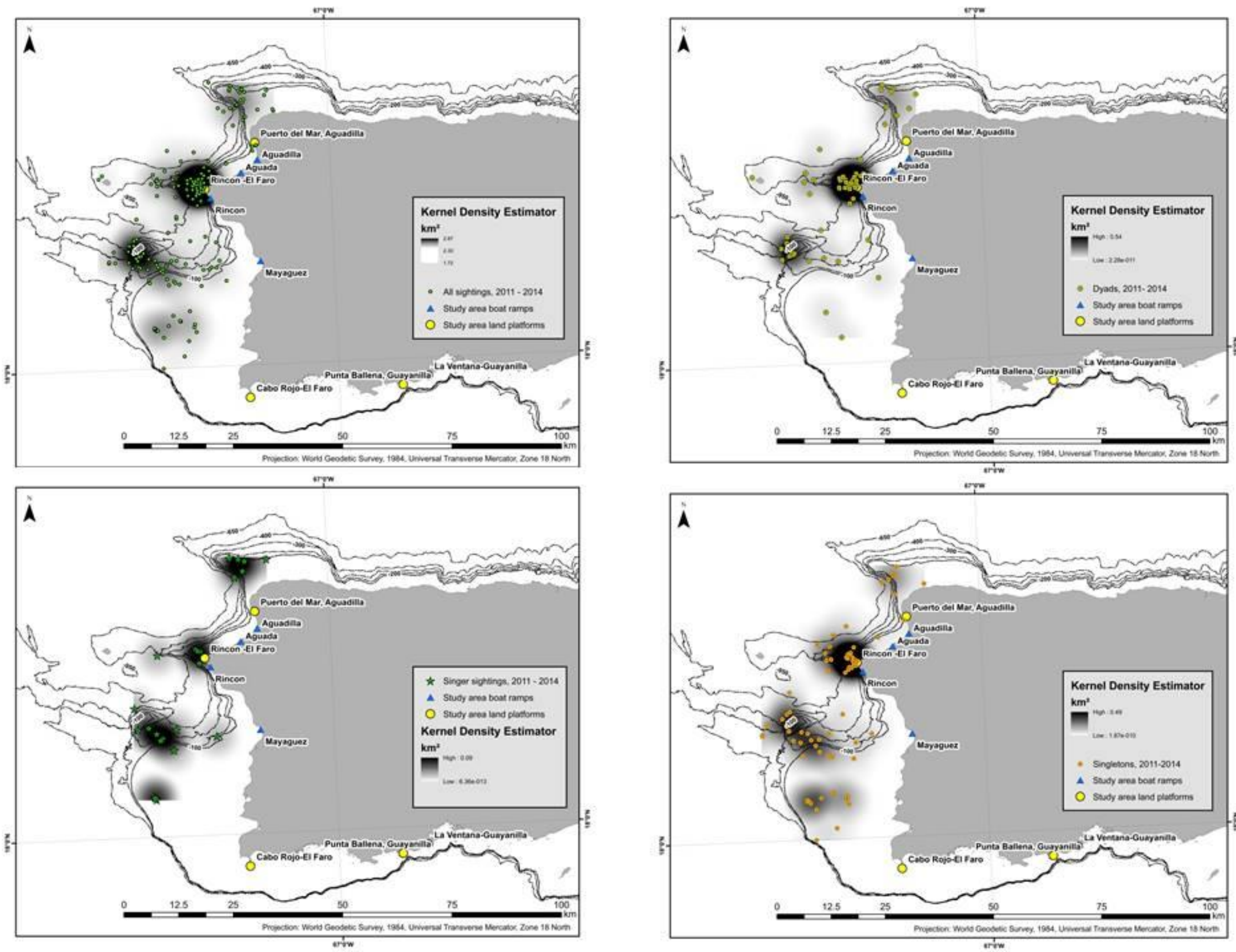

Figure 9. Kernel Density Estimates by group type of North Atlantic humpback whales in Mona Passage. The dark areas indicate whales were aggregated in four "hotspots" associated with 4 distinct bathymetric features between 2011 and 2014.

The result of the multinomial logistic regression models run to test whether bathymetric features (depth, Euclidean distance from the shelf edge and slope of the seafloor) could be used as predictors for finding NAHW group association types with bathymetric features in Mona Passage revealed the following (Tables 4 and 5, Figure 10):

- The best model found based on AIC (Table 4) included the additive effects of Euclidean distance and bathymetric depth (slope did not improve the model),
- M-C pairs were more likely to be sighted in shallower water, with strong trends finding dyads and SAG were more likely to occur in deeper water ($p = 0.006$, 0.074, 0.084 respectively),
- Singletons were significantly more likely to be seen further from the shelf edge, while singing males were more frequently close to the shelf ($p = 0.002$ and $p < 0.001$ respectively),
- M-C-E groups did not demonstrate an association with either depth or Euclidean distance from ledges, and
- The number of group associations for SAG and M-C-E is small ($n = 8$ for each) and must be interpreted with caution.

It appears likely that additional data collected in future years may improve the power of the model with a larger number of each group type.

Table 4. AIC values and parameter inclusion for all tested models.

AIC	Depth	Slope	Euc.Dist	Depth: Slope	Depth: Euc.Dist	Slope: Euc.Dist	Depth: Slope: Euc.Dist
538.5566	X		X				
539.6696			X				
547.11	X	X	X				
548.2323	X		X		X		
550.3347		X	X				
553.6773	X	X	X	X			
554.6618	X	X	X			X	
556.8339	X	X	X		X		
557.5616		X	X			X	
579.3392	X	X	X	X	X	X	X
596.4809	X	X		X			
601.962	X	X					
606.0485		X					
608.1663	X						

An exhaustive search was used to test for the best model using Akaike Information Criterion (AIC) to compare between models (Table 4). The independent variables used were bathymetric depth, Euclidean distance from the shelf edge, and slope of the seafloor. Euclidean distance and depth were significant as predictors for finding North Atlantic humpback whale group association types with bathymetry. Slope did not improve the model.

Table 5. Test statistics of multinomial logistic regression models run in R.*

p.value	MC	dyads	MCE	SAG	singeltons	singer
depth.l	0.006165	0.074658135	0.504490499	0.084136089	0.433335	0.124387
euc.dist.t	0.855594	0.211840531	0.435120065	0.422016769	0.002131	6.20E-09
log.odds	MC	dyads	MCE	SAG	singeltons	singer
depth.l	-0.67006	0.211668838	0.186170386	0.495522621	0.088361	-0.47071
euc.dist.t	0.023838	0.093071335	0.142041917	0.149702705	0.229268	-1.33851
n	17	67	8	8	91	23

*Yellow highlight indicates significant p values and corresponding log.odds.

Test statistics indicated association with depth and/or Euclidean distance. The associations between group types and depth and/or Euclidean distance decrease as values become more negative. Mother-calf (MC) pairs are associated with depth (shallow water indicated by -0.670 log.odds); dyads and surface active groups (SAG) demonstrate a trend towards deeper water. Singletons are more likely to be observed as distance from ledge increases, and singers have a strong association with ledges. Mother-calf-escorts (MCE) did not demonstrate a significant association with depth or Euclidean distance from ledge. The number of groups of M-C-E and SAG (*n* = 8 for each) is small and caution should be taken when interpreting these results.

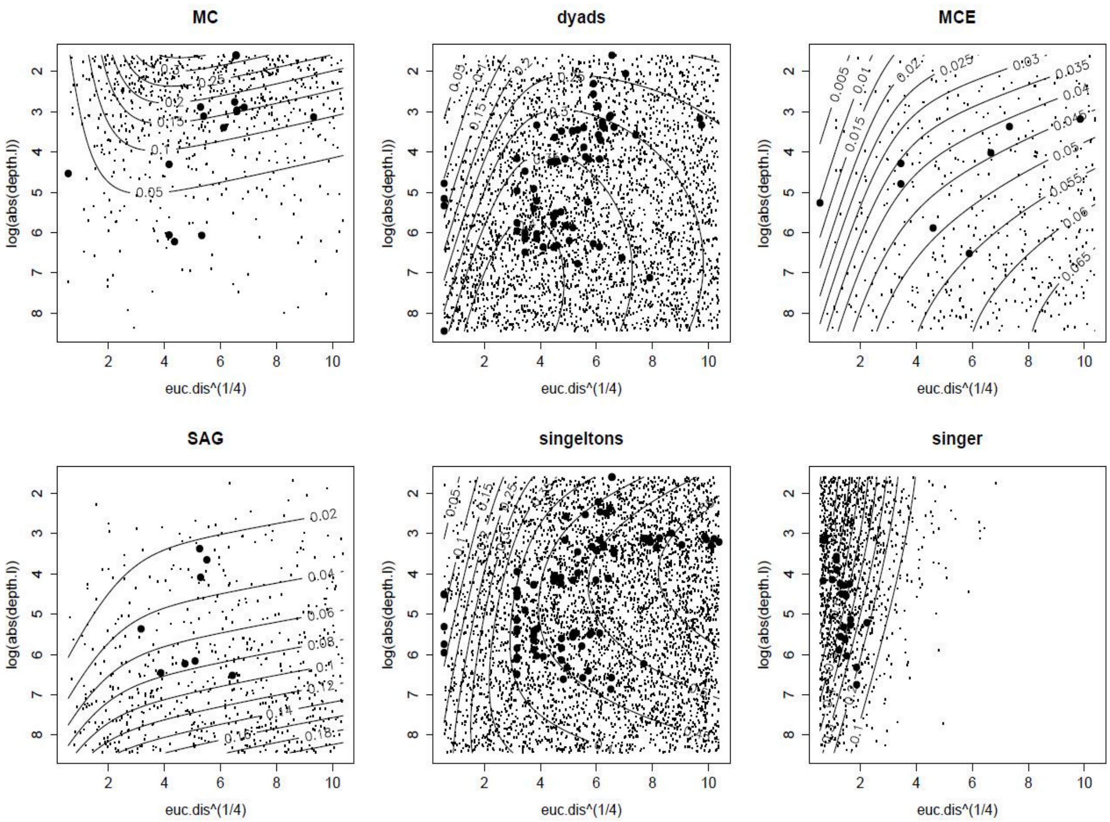

Figure 10. Scattergrams representing the multinomial linear regression models for humpback whale group association types with depth and Euclidean distance from a ledge. The Y axis is the log of the absolute value of depth where water becomes shallow as points move to the top of the scatterplot. The X axis represents Euclidean distance raised to the ¼ power where the strongest association with a ledge occurs at zero. The sum of all group models = 1. MC = mother-calf; MCE = mother-calf-escort; SAG = surface active group.

Discussion

North Atlantic Humpback Whales migrate to the area off Puerto Rico each winter near the beginning of January and return to feeding grounds by the beginning of May. Peak occurrence in Mona Passage is between the middle of February and March, with little variability in occurrence patterns and variability between numbers of groups and individuals between years (Table 2). The occurrence pattern of humpback whales wintering off Hawai'i is similar to but perhaps a bit broader than that of Mona Passage, with whales arriving as early as November, peaking in February and declining throughout May and June (Norris and Reeves 1978; Straley 1990). Although line-transects were not part of our methods and there was no attempt to calculate estimated abundance in any year, the number of humpback whales located each season fluctuated between 19 and 145 individuals throughout the study area (Figure 6 affords a visual representation of the study area by summarizing the survey effort in 5 km^2 blocks). Changes in the numbers of individuals per season in Mona Passage may fluctuate with numbers of individuals migrating from feeding grounds each winter. Because the reason for migration is not known (Corkeron and Connor 1999; Clapham 2001), one can only speculate the reason for variability in this small area in the winter grounds. The difference in number of individuals sighted can be partially explained by the variability in location of aggregating individuals between seasons and improvements in detecting these hotspots. Aerial surveys and PAM were necessary to find the hotspots each season because aggregations shifted within the passage between years surveyed. Variability of movement on the feeding grounds is not unusual and may follow aggregations of prey species; however, the incentive to find prey is absent in the winter areas (Whitehead *et al*. 1980; Tyack and Whitehead 1983). North Atlantic humpback whales in Mona Passage shifted between seasons, north to south, without any obvious cause. Balcomb and Nichols (1982) reported similar movement between 1980 and 1981 off the Dominican Republic. In all years and regardless of movement patterns, humpback whales aggregated in four “hotspots” associated with four distinct bathymetric features between 2011 and 2014 in Mona Passage (Figures 8 and 9).

Resightings of whales were uncommon (1%) or absent within and between years. The small number of resightings can be explained by several factors. Individuals may be transiting through Mona Passage moving between one or more locations throughout the West Indies. NAHW do not often dive deeply (presenting their flukes for photos) in the winter grounds where they do not forage. Shallow dives were observed often; therefore, only a small percentage of fluke identification photos were obtained (27%), leaving the possibility that individuals were resighted but were not able to be identified. The large survey area and limited hours per day collecting photographic data for individual identification impeded our ability to resight individuals remaining in the study area. Photographs from surveys on Silver Bank in 1984 were submitted to the NAHWC where 30.6% were matched (317 photos submitted, 97 individuals matched). Twenty-nine individuals were resighted on Silver Bank in 1984 (9.1%) and may reflect the larger percentage of SAG where individuals are more likely to "fluke-up" compared to Puerto Rico and Virgin Banks (Mattila *et al.* 1989). Surveys off Virgin Bank (British Virgin Islands) (Mattila and Clapham 1989) between 1985 and 1986 had an 8% resighting of individuals in 1986 and the survey in 1985 did not have any resightings. The 1985 (Mattila and Clapham 1989) discontinuous survey methods on Virgin Bank, and the discontinuous surveys in the present study, did not yield many resightings, suggesting that whales may remain in the same location for a short period of time on winter grounds and investigators will have a better chance of resighting individuals with continuous survey effort. An increase in effort hours per day per season with more than one team conducting synchronized surveys over the range of the study area will be needed to investigate whether NAHW are transiting through Mona Passage, remain for at least some period of time, or time is spent residing in the area depending on group type (or other variable). It will be advantageous to tag whales and track movement patterns to discern if they remain in the area rather than rely on photographic resightings alone to determine the length of time whales are in any area.

The aggregations of humpback whales in Mona Passage were comprised of a heterogeneous representation of age, class, and sex (mothers, calves, singers) (Table 3). Singletons, dyads, mothers with calves (and escorts); breeding groups, singers, and MSA were encountered during this study (refer to Chapter IV for detailed description and discussion of association patterns for this study). There are four locations in Mona Passage marked by geographic features, where whales can be found predictably: the first three are Los Rabos (a shelf in the shape of a "tail" in the northeast corner), Rincón (the point of land extending out from the west coast), and BDS (a seamount offshore from Mayagüez, approximately midway down the west coast) (Figure 9). The fourth, the area extending from the southwest coast, Cabo Rojo, is a shelf extending out as far as 20 km and near the Desecheo trench where there is a drop-off into the canyon. SPKS and KDE were mapped for boat effort between 2012 and 2014 (Figures 7 and 9). Each map indicates the increase in the number of groups sighted in areas corresponding to the four bathymetric features (Figures 7 and 9). SPKS (the sum of the sighting in each grid divided by the length of the survey) confirm the KDE associating groups with the bathymetric features. Data collected from land was incorporated into the KDE maps and likely are biased towards a higher probability of sighting groups near Rincón (the primary observation platform from land). However, KDE and SPKS maps revealed clusters of humpback whales associated with the same four bathymetric features, including separate analysis of each group association type. Because SPKS represent observations from the boat, and all analyses support the associations with bathymetric features indicated by the models, it is reasonable to conclude that the results are an accurate representation of humpback whale aggregations associated with bathymetric features.

I predicted that the area along the shore, in shallow locations and near points in Mona Passage, were nursery areas for M-C pairs seeking refuge from the energy of the breeding groups on Silver Bank. M-C pairs were clustered near the point at Rincón and absent in other nearshore, shallow areas or over seamounts in Mona Passage. A preference for shallow water by mothers with calves was supported by the data. It is not a surprise that M-C pairs were sighted nearshore in shallow areas (Figure 8) as this was consistent with observations in other winter habitats of humpback whales, including Brazil (Martins *et al.* 2001), Hawai'i (Smultea 1994; Cartwright *et al.* 2012), the Galapagos (Félix and Haase 2001), and other areas in the West Indies (Whitehead and Moore 1982; Mattila 1984; Mignucci-Giannoni 1998). M-C pairs were sighted almost exclusively near the point at Rincón and, interestingly, when M-C were accompanied by an escort, groups were found offshore (Figure 8). The few data collected for GPS waypoints of M-C-E are not sufficient to test if depth or Euclidean distance to a ledge are predictors for the location of this group type through modeling, although it was possible to determine distance from shore by comparison of M-C and M-C-E with a Mann-Whitney U test. A similar study was carried out on a breeding ground off Madagascar examining spatial variability for humpback whales using depth and distance from shore as variables (Ersts and Rosenbaum 2003). M-C were found nearshore in shallow water and distance from shore increased for all other group types of humpback whales.

I expected few singletons, singers, dyads, and SAG in Mona Passage, as Silver Bank (121 km away) provides a very large aggregation for individuals seeking a breeding opportunity (Mattila and Clapham 1984). This prediction was based on the literature that reported humpback whales migrating for calving and breeding and the assertion that areas with the best opportunity for breeding will attract adults with the exception of lactating females. Singletons were found clustered on the three shelves, and 10 groups of singletons were sighted on top of the shallow shelf in the south (Cabo Rojo) (Figure 8). The models predicted that singletons can be found farther from the shelf edge and depth was not a predictor for location of this group type. The top of plateaus, away from edges, may be where singers rest. A homogeneous group of singletons, such as pregnant females, may indicate why some NAHW cluster on top of the seamount and this may require obtaining age and sex of individuals through biopsy in addition to observations including behaviors.

Surface active groups were not seen often; only seven groups were sighted during the four seasons. Six groups were sighted near Rincón and a single breeding group was sighted over BDS. The reason for the location of these sightings may be as simple as males of SAG potentially seeking out receptive females, and receptive females are likely to be in one of the three aggregations along the ledges and shelves. SAG were more likely to be found in deeper water. SAG were sighted off Rincón in close proximity to the shallow area where M-C pairs data are clustered; however, SAG did not have a calf in any group and the location of SAG near Rincón may not be related to the presence of M-C (Figure 8). The presence of SAG may suggest that the area is becoming repopulated and data collection over future seasons will be needed to determine if the number of SAG increase each year in response to NAHW recovery (see Chapter 4 for a comparison of the proportion of NAHW groups by association in Mona Passage).

Singers were detected vocalizing earlier in the season before observations confirmed other humpback whales migrating into Mona Passage. It is possible that females or males that are not singing arrive prior to the males singing; however, visual observations followed acoustic detection in all years of the study, indicating that the singers were the first to arrive (Table 2). The presence of singers in the study area seems unlikely to be explained by mature, fit males seeking optimum opportunities to locate and breed with females in estrus. If the Dominican Republic is a day's swim away for a humpback whale, it is intriguing that an adult male sings off Puerto Rico in an area with few singletons, instead of traveling to where a majority of the breeding activity is occurring between thousands of NAHW (Whitehead and Moore 1983; Mattila and Clapham 1989). Clapham and Zerbini (2015) explored the possibility through simulation that the higher than plausible increase in humpback whale abundance in some areas in the Southern Hemisphere may be due to a shift of individuals towards areas with larger breeding aggregations in addition to normal population growth rate. The simulation explains the higher than expected, even higher than perpetually sustainable, increase in abundance in some areas if individuals move to a location where breeding opportunities increase. The simulation implies that males looking for breeding opportunities will seek out and move towards larger aggregations. If this is accepted for this area, then there may be some other reason singers are sighted and heard vocalizing in Mona Passage, a low-density area for wintering NAHW, such as subadult males practicing the song away from larger, mature males. This would be a comparable shift of individuals to an area that does not reflect population growth, similar to the Clapham and Zerbini (2015) simulation.

Singers were sighted consistently on ledges associated with seamounts and including the drop-off at the edge of the shelf off Cabo Rojo (Figure 8). The statistical model predicts that singers are found more frequently close to the shelf, which is consistent with our perception in the field. Singers may be gaining some advantage off ledges related to the song, including sound traveling farther or hearing themselves sing (Whitehead and Moore 1982). I noted pairs of singers in which one individual was noticeably smaller than the other, as well as an echo reverberating off the ledges while singers were broadcasting. It is possible that subadults arrive in Mona Passage to practice the song. It may even be worthwhile for these young male singers to hear themselves and other young males sing as a potential advantage to learning the song in an area away from competition between larger, mature whales (Tyack 1983; Mattila *et al.* 1989; Clapham 1992). Furthermore, there may be an acoustic advantage created by ledges to increase the efficiency of singing and to thereby maximize the potential for other whales to detect that song. Mona Passage contains seamounts that provide ledges where NAHW aggregate. These features do not afford protection from high seas and wind similar to the leeward area of an island, atoll, or reef.

The data collected for this study cannot predict if there is an acoustic advantage for whales singing off ledges; however, the presence of singers associated with ledges indicate that future studies should include the approximate size/age of individuals and an acoustical assessment of ledges where males sing. It may eventually be possible to predict the location of singers on winter grounds, and if and how subadults are taking advantage of the area away from the primary aggregation. Singers were the only group type with a strong association to shelf edges, implying that there is not an acoustic advantage for receivers near the same geological feature. It would be interesting to examine the bathymetric features off Madagascar, where depth and distance from shore are associated with group types (Ersts and Rosenbaum 2003), in addition to other winter grounds for Euclidean distance to shelves by group type, to determine if similar patterns of singers near ledges are found.

Dyads were also associated with bathymetric features in Mona Passage (Figure 8) and the model predicts a strong trend towards finding dyads in deeper water. It may be that the dyads are singers vocalizing near the shelf or a pair transiting to a SAG together, similar to singers in Hawai'i (Darling *et al*. 2006). This group type should be observed more closely over the next several seasons and the data divided into locations such as “dyads singing”, “dyads traveling”, and “dyads resting”. This type of analysis will better facilitate a description of behaviors associated with bathymetric features, and genetic sampling has the potential to reveal the importance of physical surroundings to NAHW group association types.

Although NAHW pre-whaling abundance is unknown, the IWC is in general agreement that humpback whales have recovered to approximately 54% of pre-whaling global abundance estimates (Bettridge *et al.* 2015). Management of stocks are generally based on sustainability using estimates of abundance and the rate of increase in the number of individuals based on reports from surveys on feeding and breeding grounds. As NAHW continue to recover from whaling and greater numbers migrate to the West Indies, the possibility of competing with humans for resources, including space in areas used for wintering whales, will also increase. The bathymetric features that NAHW are associated with off Puerto Rico’s west coast are the same areas used for recreational and commercial purposes. Activities that place humans in the same areas with whales will occur more frequently as the number of NAHW continue to increase overall, and as the whales increase nearshore. Predicting where NAHW cluster on winter grounds may enable managers to suggest/enforce minimization of interactions between humans and NAHW in areas where recreational and commercial activities overlap. This is especially important as NAHW are presently considered for delisting as endangered by the U.S. National Marine Fisheries Service, enabling managers to better plan for how best to protect this species as an increase in numbers are anticipated.

CHAPTER III

RESIGHTINGS OF KNOWN HUMPBACK WHALES *(Megaptera novaeangliae)* BETWEEN PUERTO RICO AND THE NORTH ATLANTIC

Introduction

Humpback whales have one of the longest migrations of any mammal (Rasmussen *et al.* 2007; Stevick *et al*. 2011; Horton *et al.* 2011). Individuals migrate between feeding grounds in higher latitudes and breeding grounds in lower latitudes (over 4,000 miles / 6,437 km), although the exact routes of their migration remains unknown (Dawbin 1966; Katona and Beard 1990; Stevick *et al.* 2003a). NAHW mix on the breeding grounds from five discrete feeding grounds, primarily aggregating off the Dominican Republic in three locations. Navidad Bank, Silver Bank, and Samaná Bay have thousands (exact numbers unknown) of NAHW converging from areas that include the Gulf of Maine, Newfoundland, Iceland, Labrador, and Greenland (Martin *et al.* 1984; Mattila and Clapham 1989; Betancourt *et al.* 2012). NAHW with site fidelity to Norway and some NAHW foraging in Iceland migrate during winter to a breeding aggregation off Africa's northwest coast near the Cape Verde Islands, and there appears to be limited mixing between the two primary winter grounds (Stevick *et al.* 2003a). The reason for migration to lower latitudes is unknown, with speculation including predation pressure from killer whales and benefits derived from nursing calves in warmer waters (Corkeron and Connor 1999; Clapham 2001).

The challenges of long-term tracking of individuals make it difficult to understand movement patterns of whales throughout their life cycle. The large number of individuals, size of their habitats, and difficulty of studying whales that live in the ocean largely inaccessible to humans, means that many individuals are sighted and may not be resighted for decades or ever sighted again. Currently, attaching tags to whales for tracking and collecting data is improving but still has limited information on movement patterns as tags do not typically stay attached for long periods, limiting our ability to study movement patterns over months, seasons, or years (Johnson and Tyack 2003;

Southall *et al.* 2012), but see Lagerquist *et al.* (2008) and Mate *et al.* (2015) for modern exceptions). The ability to use natural markings to identify individuals has made photographic capture-recapture studies possible (Katona *et al.* 1979; Katona and Whitehead 1981; Carlson *et al.* 1990; Kniest *et al.* 2010). The shape of the trailing edge and the pigment patterns on the dorsal side of humpback whale flukes are unique to each individual whale (Katona and Whitehead 1981). This information can be used to gain insight into movements throughout their lifetime; including fewer individuals moving past the Dominican Republic throughout the West Indies (Katona and Whitehead 1981; Carlson *et al.* 1990; Stevick *et al.* 2003a; Kniest *et al.* 2010). Images of NAHW flukes and other natural markings (scars, rake marks left from the dentition of a failed killer whale attack) have been collected since at least the early 1970's. The YoNAH and MoNAH surveys in the early 1990's (Palsbøll *et al.* 1997, Stevick *et al.* 2003a; Waring *et al.* 2014) added thousands of fluke images to the NAHW collection curated at COA under the Allied Whale project. Local catalogs are maintained where researchers and tourism operators make an effort to collect and match fluke photographs of NAHW in their area within and between years (*i.e.*, Mingan Island Cetacean Study [MICS], Observatoire des Mammifères Marins de l'Archipel Guadeloupéen or Marine Mammal Guadeloupean Archipelago Observatory [OMMAG], and CCS). In addition to the local catalogs, a repository for all NAHW identification photos is curated at COA in the Allied Whale Project where images of flukes from local catalogs are contributed to the ocean wide data base and matches are attempted between collections (Katona *et al.* 1979; Martin *et al.* 1984; http://www.coa.edu/nahwc.htm). Every photo that is matched provides a clue into the movement of humpback whales within and between winter seasons. There may be more than 20,000 whales in the NAHW NMFS-dedicated stock, based on a 3% increase per annum since the YoNAH survey (P. Stevick, COA, 25 January 2015, personal communication), and there are more than 8,000 individual fluke identifications in the NAHWC (P. Stevick, COA, 30 October 2014, personal communication), making long-term re-matching and descriptions of movements within and between feeding and breeding areas incomplete.

Discovery of the origins and primary destinations of known NAHW migration are possible due to photographic capture-recapture studies, although areas throughout the West Indies, away from the main aggregation off the Dominican Republic, have not been studied recently (Mattila 1984; Mattila and Clapham 1989; Mignucci-Giannoni 1998, Smith *et al*. 1999). Movements of individuals between the high and low latitude habitats are unknown within and between seasons. Here, I examine the number of matches made between humpback whale fluke photos in Puerto Rico and the Allied Whale repository in an attempt to gain insight to movement of NAHW between Puerto Rico and other locations in the North Atlantic. The following null hypotheses were examined: 1) Mona Passage is not occupied by NAHW from all feeding grounds in higher latitudes, and 2) NAHW do not move between areas throughout the West Indies. Because the area was once densely populated enough to lure whaling ships and because of the proximity of Mona Passage to the location of thousands of wintering whales off the Dominican Republic, the following alternative hypotheses are formulated: 1) NAHW migrate to Mona Passage from all feeding grounds in the North Atlantic (with the exception of Norway) in Mona Passage, and 2) NAHW move between and among the islands throughout the West Indies.

Methods

Fluke identification photos were obtained from a small vessel during surveys in Mona Passage in winters (January-April) 2012, 2013, and 2014 (see “methods” Chapter 2). Photos were sorted and attributed to individual whales, then assigned a local catalog number. A local catalog was created from cropped photos taken during surveys in Mona Passage and includes fluke identification photo(s) of individuals along with images of dorsal fins, scars and other natural markings (Figures 2 and 3). Fluke identification photos prior to this study were included from Michael J. Morel, a member of my survey team and a reliable source of data (M. Morel, 02 December 2014, personal communication). Matches within and between years were attempted using our local catalog and then submitted to Allied Whale for matching within the catalog for the North Atlantic. Suitability of photographic images for the NAHWC was determined by the people matching contributions to the NAHWC at COA. Allied Whale does not keep a catalog of dorsal fin photos; therefore, only fluke identification photos were submitted. Each photo was reviewed by at least two people experienced in fluke matching. If matches were not found for a photo in the catalog for the North Atlantic, a unique number was assigned. If matches were found in the NAHWC, data for that individual were updated and Allied Whale informed all contributors of the match. Individuals did not always fluke (lift their flukes out of the water upon beginning a steep dive) and ideal fluke identification photos were not always obtained. Images were counted as a "match" when scars, the shape of the trailing edge, and pigment markings were the same between more than one image. All images of flukes were entered into the local catalog. Competency of research assistants was validated by matching images of 100 pairs of fluke photos with varying image quality and angles and asked to determine which were a match. A score of 95% or greater was deemed "competent" to match fluke and fin images. At least two people reviewed all images for matches within the local catalog to either verify a match or to verify a newly identified individual. Matches between an image of an individual photographed in Mona Passage and a photograph from a catalog in another location were counted as a single match regardless of how many other locations the whale had been recorded.

Results

Three hundred thirty-one NAHW were sighted between 2011 and 2014. Fluke identification photos were available for 90 (27.2%) of the individuals sighted (Table 6) and 57 (17.2%) dorsal fin photos (without flukes) were captured for the local catalog. Submissions into the NAHWC resulted in 24 (26.7%) matches of fluke identification photos. Dorsal fin identification photos were compared within the local catalog and no matches were obtained. The timespan between sightings ranged from one month (MCERC#87) to 35 years (MCERC#98). NAHW were resighted between Puerto Rico and the feeding grounds, including the east coast of Canada (Newfoundland and Labrador), Gulf of Maine, Greenland, and Iceland (Figure 11, Table 6) (n = 24). NAHW were matched to sightings between winter breeding grounds, including Puerto Rico and

Guadeloupe (OMMAG) (*n* = 2, 2.2%), and Puerto Rico and the Dominican Republic (*n* = 5, 5.6%) (Figure 11, Table 6). Three (3.3%) NAHW were sighted off Puerto Rico and then resighted in Puerto Rico during a subsequent winter. Five whales have been photographed off the Dominican Republic and Puerto Rico with a span of three to 31 years between sightings. One whale was matched to a previous sighting off Bermuda in 2010. Further details of my resightings of whales from western Puerto Rico and elsewhere, with references, are found in Table 6.

Discussion

The study of movement of NAHW within and between winter (breeding and calving) and summer (feeding) habitats is difficult even with improvements in satellite/data tags used to track individuals (for example, Lagerquist *et al.* 2008). More data on movement, either from resightings or from tags, are needed to examine the importance of the smaller areas throughout the West Indies. From my data, it is suggested that a heterogeneous group representing multiple feeding grounds is an extension of the primary aggregation. It is possible that the west coast of Puerto Rico serves as an area of importance to those animals that may not be afforded to them in the area off the Dominican Republic, such as mothers/calves staying away from major mating areas, young males "practicing" song, and other adult male activities. It is furthermore possible that certain whales may preferentially use the present area for multiple years and throughout generations, which would imply a potential cultural use of the area for these whales (see, for example, Whitehead and Rendell 2004). Whaling ships plied the West Indies (Ellis 2009), suggesting the West Indies has historically been a single winter breeding and calving ground for NAHW. In addition to large numbers of whales moving through the area historically, the Dominican Republic hosts a mix of whales from all feeding grounds (with the notable exception of Norway), and is located to Puerto Rico’s west coast (Figure A-2 in Appendix A).

Table 6. Matches between the Puerto Rico humpback whale catalog (PRHWC-ID) and the North Atlantic humpback whale catalog (NAHWC). The left-hand column "PRHWC-ID" refers to sightings from this study, with and without resightings made elsewhere.

PRHWC-ID	**NAHWC-ID**	**Other ID Number**	**Puerto Rico Sighting Information**	**Other Sighting Information**	**Acknowledgements***
MCERC#2	na8967		2013 February 06	2011 July 28 Mobile Bay, Newfoundland, Canada	J. Winkel, E. Betteridge
MCERC#3	na2275		2013 February 15 (with a calf)	1982 February 28 March 2-3, Puerto Rico	CCS
MCERC#6	na2988	H616	2013 March 14	1984 March 2 Silver Bank, Dominican Republic 1992 September 8 Strait of Belle Isle, Canada 2004 Gulf of St. Lawrence, Canada	COA/CCS YoNAH MICS
MCERC#13	na4656	N053	2013 February 03	2006 June Húsavík , Iceland	Húsavík Whaling Museum
MCERC#14	na6711	mn155	2013 April 03	2010 October 16 Skjalfandi Bay, Iceland 2014 October 10, 12-15 Húsavík, Iceland	M. Rasmussen - Húsavík M. Rasmussen - Húsavík
MCERC#29	na6191		2012 March 28	2004 Silver Bank, Dominican Republic	MoNAH
MCERC#32	na6542		2013 March 09	2010 March 3 Silver Bank, Dominican Republic	J. Gibson / COA
MCERC#36	na7076	H176 (Kilroy)	2013 March 15	1991 Gulf of St. Lawrence, Canada 2003 July 13 Battle Harbor, Labrador, Canada	MICS MUN
MCERC#41	na7310	H356	2013 March 23 2013 March 25	1992 September 12 Strait of Belle Isle, Canada 1993 July 24-25 Strait of Belle Isle, Canada 2003 July 17 Battle Harbor, Labrador 2005 September 7 Battle Harbor, Labrador	YoNAH YoNAH MUN Wildland Tours
MCERC#45	na2438		2010 March 13	1993 March 1 Puerto Rico	YoNAH
MCERC#47	na8897		2008 February 18	2006 Gulf of Maine	CCS **Puerto Rico
MCERC#52 *	na0349		1997 March 16	1982 -2002 Gulf of Maine	CCS **Puerto Rico

Table 6. continued

PRHWC-ID	NAHWC-ID	Other ID Number	Puerto Rico Sighting Information	Other Sighting Information	Acknowledgements*
MCERC#56	na1030		1998 February 01	1978 June 27, 30, July 1, 11, 15, 17, 20, Trinity Bay Newfoundland Canada 1979 June 21 Trinity Bay Newfoundland Canada	Whitehead Whitehead
MCERC#62	na9368		2012 March (with her first known calf)	2000 Gulf of Maine "Whirlygig"	CCS
MCERC#68	na7194		2013 February 22	1992 July 30 Witless Bay, Newfoundland, Canada.	Hebert/Calbrix/Etcheberry
MCERC#74	na1566		2009 March 01	1979 June 30 Trinity Bay, Newfoundland, Canada 1980 July St. Mary's Bay, Newfoundland, Canada	H. Whitehead MUN **Puerto Rico
MCERC#77	na8469		2014 February 01	2002-"Jabiro"-CCS Gulf of Maine Note: Seen every year in Gulf of Maine since 2002	CCS
MCERC#78	na9488	OMMAG-186	2014 February 12	2013 March 29 Guadeloupe, French West Indies	OMMAG
MCERC#85	na8979		2014 February 19	2009, 2010, 2011 Gulf of Maine	CCS
MCERC#87	na6757	OMMAG-238	2014 February 19	2014 March 25 Guadeloupe, French West Indies	OMMAG
MCERC#90	na3871	H133	2014 March 12	1993 January 30 Samaná Bay, Dominican Republic 1993 July 26-27 Strait of Belle Isle, Canada 1993 August 25 Canada Bay, Newfoundland, Canada 2000 Gulf of St Lawrence, Canada 2003 August 2 Battle Harbor, Labrador, Canada	YoNAH YoNAH YoNAH MICS MUN
MCERC#92	Na4173		2014 March 13	1988 August 16 Fiskenaes, Greenland 1989 July 28 Frederikshab, Greenland 1990 February Samaná Bay, Dominican Republic 1990 July 05 Fiskenaes Banke, Greenland	GINR GINR CCS GINR
MCERC#97	na0498		2014 March 24	1985 Gulf of Maine "Cornucopia"	CCS

Table 6. continued

PRHWC-ID	NAHWC-ID	Other ID Number	Puerto Rico Sighting Information	Other Sighting Information	Acknowledgements*
MCERC#98	na2129		2014 April 17	1979 February 27 Puerto Rico 2010 Bermuda	CCS Whales Bermuda

*CCS = Center for Coastal Studies, COA = College of the Atlantic, YONAH = Years of the North Atlantic Humpback, MICS = Mingan Island Cetacean Study, MONAH = More of the North Atlantic Humpback, MUN = Memorial University of Newfoundland, OMMAG = Observatoire des Mammifères Marins de l'Archipel Guadeloupéen or Marine Mammal Guadeloupean Archipelago Observatory, GINR = Greenland Institute of Natural Resources., MCERC = Marine and Coastal Ecology Research Center.

** Puerto Rico photo credit: Michael J. Morel.

Figure 11. Representation of matches of humpback whales between Mona Passage and the North Atlantic (including previous and subsequent sightings). Whales sighted in Mona Passage include individuals from Iceland, Greenland, Newfoundland, Labrador, Gulf of Maine, Bermuda, Dominican Republic, and Guadeloupe. Numbers correspond to "PRHWC-ID" sightings from this study, (left column Table 6) and indicate movement between summer and winter grounds. Lines indicate the general location of endpoints between sightings of individuals.

Abundance estimates for the North Atlantic are based on historical data and include the latest extensive surveys in the 1990's. Based on a 3% optimistic population growth rate (determined as a result of the YoNAH and MoNAH studies) and assuming a steady, uninterrupted recovery, currently we can predict that there are more than 20,000 humpback whales in the North Atlantic Ocean (Stevick *et al.* 2003a). This estimate is sufficient as a basis of comparison for examining the mix of individuals from the feeding grounds to Mona Passage. There are 8,000 known whales in the NAHWC out of an estimated 20,000 in the North Atlantic Ocean (approximately 40%). There are 90 known whales (identified with a photograph) from the Puerto Rico catalog matched with 24 of the known whales in the NAHWC (27%), demonstrating the ability to use capture-recapture methods as an indication of movement patterns from NAHW. The individuals are from five discrete feeding grounds (excluding Norway), confirming that from 2011 to 2014, Mona Passage was occupied by individuals from all known feeding grounds in higher latitudes with the exception of Norway. A single individual was sighted in Puerto Rico in 1979, Bermuda in 2010, and four years later in Mona Passage, putting Bermuda on the route of migrating whales. It is possible that Mona Passage is being repopulated as the number of individuals increase in the North Atlantic, and NAHW throughout the West Indies are returning to winter habitats historically occupied by previous generations. Smaller areas throughout the West Indies may have a specific utility, such as site fidelity corresponding to reproductive status as has been noted in Hawai'i for females (Cartwright *et al.* 2012). Similarly, the possibility remains that singers may be individuals benefiting from seeking mating opportunities away from mature and successful males, or it may simply be an area that will eventually mirror the behaviors off the Dominican Republic. Modern epigenetic age assay sampling (Polanowski *et al.* 2014) may be considered to determine age of singers, which may indicate if subadults are broadcasting song some distance away from large mature males where an aggressive response could be anticipated (Tyack 1981; Tyack and Whitehead 1983; Darling and Bérubé 2001; Darling *et al.* 2006).

There is a gap of more than three decades for two whales between the first sighting on the feeding grounds and the sighting off Puerto Rico. The timespan illustrates the difficulty in tracking NAHW and, unlike the killer whales of the northeastern Pacific (where almost all or all individuals of most pods are identified, Parsons *et al.* 2009); whales cannot be presumed deceased or missing when individuals are not resighted (Allen and Angliss 2014). Other NAHW were seen multiple times in the same feeding grounds, including consecutive seasons, before being sighted off Puerto Rico (as summarized in Table 6). Movement within the West Indies appears to indicate that NAHW utilize the entire area (Mattila and Clapham 1989). This may be a result of site fidelity to specific locations on winter habitats (for reasons yet undetermined) or it is possible that movement throughout the entire winter breeding grounds is a typical behavior pattern for NAHW. Because individual movement patterns are not well understood, the importance of smaller habitats are also not well explained, leaving the potential for a greater impact to a segment of the NAHW population as the result of a single event or due to long-term changes. For example, if a single feeding ground has high site fidelity to a small secondary habitat and that habitat is compromised, the magnitude of the impact of the NAHW stock will be more profound than if multiple feeding grounds utilize the same area.

The reason for migration for NAHW is still unknown, and there is speculation that NAHW migrate to avoid predation from killer whales (Corkeron and Connor 1999), calves benefit from by being born and spending their first few months nursing in warmer waters (Corkeron and Connor 1999; Clapham 2001; Rasmussen *et al.* 2007; Cartwright and Sullivan 2009b), or some other unexplained benefit for individuals to travel thousands of miles in winter. Determining where the individuals move on the winter habitats has the potential to help determine where they migrate and why they migrate at all. Continuous surveys will be important for understanding the importance of small areas throughout the West Indies where humans and whales overlap, providing marine managers with information regarding "end-point of migration" occurrence patterns, especially important as NAHW increase in numbers and ahead of the proposed U.S. delisting of NAHW as endangered.

CHAPTER IV
HUMPBACK WHALE (*Megaptera novaeangliae*) ASSOCIATION PATTERNS IN WINTER OFF PUERTO RICO, USA

Introduction

Winter habitats for NAHW are in lower latitudes where the large primary aggregation occurs off the Dominican Republic, and consists of a mixing of individuals from discrete feeding grounds in higher latitudes (Clapham *et al.* 1993b) (Chapter 1, Figure 1). Few NAHW continue their migration through the West Indies where the association patterns in the smaller secondary habitats are not well-known (Mattila and Clapham 1989; Smith *et al.* 1999). Association patterns differ between the higher latitudes (where most foraging takes place) and lower latitudes (where reproductive behaviors and caring for calves are the primary activities) (Chittleborough 1965; Baker and Herman 1984; Baraff *et al*. 1991; Clapham *et al.* 1992). Natural markings can be used to identify individuals and place them in the context of social and reproductive group associations (Katona *et al.* 1979; Katona and Whitehead 1981; Kaufman *et al*. 1990). Long-term investigations, including DNA evidence (Palsbøll *et al.* 1997), continue to aid in understanding association patterns with conspecifics. The YoNAH (1992-1993) and MoNAH (2004-2005) surveys describe associations on the winter habitat where the presence of SAG and M-C pairs give a clear indication that this area is for breeding and calving (Clapham and Mattila 1993; Clapham *et al.* 1993a; Mattila *et al.* 1994; Stevick *et al.* 2003a).

NAHW sociality includes group associations of varying numbers and well described behaviors such as milling, singing, traveling, resting, playing, percussive, and SAG (see Table 7 for definitions). The frequency of any individual joining, separating, and rejoining a group of a particular size and composition is unknown. However, group associations can be generalized as short in duration on feeding and breeding habitats, with the exception of the M-C pair (Chittleborough 1958; Clapham and Mayo 1987) and some notable exceptions during consecutive seasons on at least one feeding ground (Weinrich 1991; Ramp *et al.* 2010). M-C associations last from birth (pregnant females give birth in the warmer waters of the winter habitats or on the migration route) throughout the winter, and continue beyond the time of the migration back to the feeding grounds. The calf is weaned before the next seasonal migration to warmer latitudes (Chittleborough 1958, 1965; Baker *et al.* 1987; Craig *et al.* 2003). Associations with conspecifics are of short duration and include SAG comprised of a focal female, primary escort, and varying number of males engaging in energetic behaviors. SAG form and disband in time periods of minutes to hours while aggressive males attempt to gain access to the focal female (Tyack and Whitehead 1983; Baker and Herman 1984; Mattila *et al.* 1989). The frequency of males participating in SAG is unknown. Singletons and dyads (a pair of whales that are not M-C) are not uncommon, although the duration of their associations on the breeding ground is unknown (Clapham 1992; Hakala 2004; Félix and Novillo 2015).

Interactions with other species of cetaceans (and, indeed, any other animals) are termed as "mixed species associations" (MSA) (Waser 1984; Stensland et al. 2003; Cords and Würsig 2014). MSA include coincidental occurrences where aggregations of common prey species attract heterospecific dolphins and whales in close proximity (Cords and Würsig 2014). The reasons for humpback whales in MSA are largely unknown, with the exception of occurrences that appear to be "play" and coincidental foraging opportunities (Glockner-Ferrari and Ferrari 1985; Deakos *et al.* 2010). Specific examples of MSA have been described with humpback whales in the Pacific off California and Hawai'i (Glockner-Ferrari and Ferrari 1985; Black 1994; Deakos *et al*. 2010; Smultea and Bacon 2012, 2013). Descriptions are of dolphins and humpback whales playing, humpback whales reacting with trumpeting and to killer whales attacking gray whale calves (A. Schulman-Janiger, American Cetacean Society, 24 January 2015, personal communication), and a single occurrence of humpback whales with short-finned pilot whales (*Globicephala macrorhynchus*) off Norway (Ciano and Jørgensen 2000). Pilot whales at times appear to harass other species of cetaceans

(Norris and Prescott 1961; Kraus and Gihr 1971; Overholtz and Waring 1991; Shane 1995a, b; Weller *et al.* 1996; Baraff and Asmutis-Silvia 1998; Pereira 2008), although there are no previously documented occurrences of pilot whales aggressively interacting with NAHW in the North Atlantic on mating/calving grounds in winter.

Association patterns in the small secondary NAHW habitats off western Puerto Rico are described for a future attempt to understand the connection to the large aggregation of whales off the Dominican Republic. Data were collected during winters (January through April) of 2011 through 2014, and a comparison to other wintering areas is made. Association patterns of NAHW with conspecifics and other cetacean species were observed from multiple platforms in an attempt to understand the habitat use in the context of social dynamics where whales are fasting, and where competition or cooperation for food is therefore not a consideration. The following null hypotheses (H_0) were tested:1) Mona Passage will not have a heterogeneous mix of all groups defined by association patterns (M-C, M-C-E, SAG, dyads, singers, and singletons), 2) The frequency of encounters of NAHW group associations in Mona Passage will be equal, and 3) Groups (defined by associations) are not more likely to be exhibiting behaviors indicating they are staying in the area (milling, resting, percussive, singing) than what would be expected by chance. Alternative hypotheses, based on studies of NAHW off the Dominican Republic and other humpback whale winter areas and the recovery of NAHW numbers post-whaling (Mattila and Clapham1989; Mattila *et al.* 1994), Brazil (Martins *et al.* 2001), and Hawaii (Silber 1986; Smultea 1994), are as follows: 1) Mona Passage will have a heterogeneous mix of associations by group including M-C, M-C-E, SAG, dyads, singers, and singletons, 2) M-C pairs will be encountered more frequently than other group association types, and 3) Groups are more likely to exhibit behaviors indicating they are remaining in the area for at least some period of time rather than behaviors indicating transiting through (traveling, SAG) than what would be expected by chance.

Methods

The study area is located in Mona Passage between the Dominican Republic and

Puerto Rico (refer to Chapter 2 for additional details and a description of the study area and Figure A-2, Appendix A for a map of the study area). Data were collected from aerial, small vessel, and land platforms in areas where a pilot study and data from previous surveys in the West Indies (such as the YoNAH and MoNAH projects) indicated that NAHW were likely to be detected (Winn *et al.* 1975; Winn and Winn 1978; Clapham and Mattila 1993; Clapham *et al.* 1993a; Mattila *et al.* 1994; Stevick *et al.* 2003a). Aerial reconnaissance was flown when NAHW were difficult to locate or fishers indicated that whales were offshore, and boat survey effort was then directed towards the areas where sightings had been made from the air. No attempt was made to obtain an abundance estimate or collect behavioral data from the air. If NAHW were sighted from the aircraft, a GPS point was obtained and the reconnaissance flight continued.

Group focal follows were conducted from land and boat when whales were first sighted at the surface. NAHW groups were defined by the presence of at least one individual and included MSA. Activities were noted and general behavioral state of groups was described. Although an ethogram was followed (Table 7) to describe behaviors, data collection was *ad libitum,* as it was not always possible to attribute behaviors to any single individual (where the group size was greater than one) and some individuals may have been observed more often than others. The general behaviors of milling, traveling, resting, singing, and percussive were described for a group as the predominant activity of that group during the focal follow, and listed as a new general behavior when that predominance changed.

From the boat, a GPS waypoint was obtained either by entering the distance and bearing of the group into the program *Mysticetus* or by motoring to where a fluke print (flattening of the water surface as a result of fluke movement underwater) was evident, and recording the GPS point at that location. When the team encountered groups with NAHW and other cetaceans (MSA), group behavior was characterized and individual behaviors were noted for all individuals whenever possible. Groups were defined using a modified chain rule and coordinated activity (see Mobley and Herman 1985 ["pod"], Smolker *et al.* 1992 [10-m chain rule] and Mann 2000 [coordinated activity]) when the following criteria were met:

a. All individuals in a group were within 150 m (approximately 10 body lengths [BL]) of the closest whale. It was therefore possible for two whales in the same group to be spaced greater than 150 m apart and be included in the same group;
b. Individuals within 5 BL were included in the group without consideration for coordinated activity (for example, direction and speed of travel or direct interaction (mothers and calves, breeding behaviors, harassment); and
c. Individuals spaced between 5 and 10 BL apart were engaged in coordinated activities;
d. When whales were observed approaching a group from a distance greater than 150 m, they were treated as a separate group until the groups merged (the number for the first group was maintained as long as the groups were merged). An attempt was made to collect photographic data (flukes, fins, and scars) in advance of a merge of both groups. If a group split, the focal whale(s) remained with the original group designation (and data were collected by continuing to observe the original group) and the next sequential group number was assigned to the individual(s) moving away in another direction or the follow was discontinued.

Groups sighted from land were often too far away to positively identify the same individuals between surfacings. To avoid a false and significant increase in the number of groups reflected by our data, multiple surfacings were attributed to the same group from a land platform when the number of individuals remained constant and whales remained in the same area or traveled in the same direction over a short distance between surfacings. This was possible due to the low-density aggregation. An attempt was made to describe group size and composition.

Photographic data were collected from the boat (and rarely from shore, and only when the whales were close enough for large-lens photography) to confirm group composition and dynamics as well as identification of individuals through natural markings (Katona *et al*. 1979; Katona and Whitehead 1981). Species identification for individuals other than NAHW was confirmed with photographs and/or video from a small underwater video camera on a PVC pole in cases of MSA. Once sampling of each group was completed (group size, composition, location, and predominant behavior of the group, individual behaviors were noted) the focal follow was discontinued and survey effort resumed.

"Singing" was used to describe NAHWs positioned in the water column and confirmed vocalizing using a hydrophone from the boat. SAG describes a group with a focal female and at least two males in energetic competition, when lunging, tail throws, trumpeting and other aggressive behaviors dominated the activity within the group. Percussive behavior was added to the ethogram in the second year, when it became apparent that these activities occurred often enough for meaningful descriptions by whale association type. Percussive behaviors consisted of flipper slapping, tail slapping, and any other sound made by the body abruptly hitting the surface or a conspecific (Darling 1983; Frazer and Mercado 2000; Deakos 2002; Deecke *et al.* 2005) (Table 1 in Chapter 2). In the case of MSA, no attempt was made to identify individual behaviors of the other cetaceans. All behaviors were recorded in *Mysticetus* and a manual log. Statistical analyses were carried out by Chi-square goodness of fit test to determine whether behaviors appeared to occur with equal or unequal likelihood, and a Freeman Tukey Deviate test to determine which behaviors contributed to the significance Chi-square tests. Similarly, I ran a Chi-square goodness of fit test to determine whether group types occurred differently from what was expected by chance.

Age and maturational class were noted as follows: singers (confirmed by PAM) were presumed males (Payne and McVay 1971; Winn *et al.* 1975; Winn and Winn 1978; Darling 1983; Darling and Bérubé 2001; Darling *et al.* 2006; Herman *et al.* 2013) and adults with a calf were presumed females. All other determination of sex was confirmed by photo-identification of a matched individual from the NAHW catalog, or marked "undetermined".

Table 7. Ethogram characterizing group behaviors of North Atlantic humpback whales wintering off Puerto Rico*

Singing	Vocalizations made by males during the breeding season nearly 30 minutes long and consisting of discrete units.
Traveling	Whales swimming in a single direction without resting.
Percussive	Activity including flipper slapping, fluke slapping, breaching, lobtailing, chin slapping, when a part or all of the whale's body slaps the surface of the water. In this study, "percussive" is used to characterize the group behavior when more than one of these actions was occurring during the same focal follow.
Resting	Whales are on the surface without any obvious signs of directed locomotion.
Milling	Swimming in different directions without moving away from the immediate area, often associated with play or social interaction.
Mixed-Species Association (MSA)	Humpback whales and at least one other species of cetacean directly interacting. In general, both species must be within 10 body lengths of the humpback whale to be considered closely interacting.
Surface Active Group (SAG)	Breeding group with a focal female, primary escort and males competing for access to the female. Groups were identified by aggressive behaviors (lunging, trumpeting, blowing bubbles, tail slapping, flipper slapping, fluke slapping, chuffing) in a group of at least 3 individuals traveling quickly.

*definitions of behaviors are paraphrased from Darling 1983 and Clapham 2009

Results

A total of 246 marine mammal sightings (i.e., groups) comprised an estimated 598 individuals (Table 8). Most sightings were NAHW (n = 331, 55%) within 197 groups (80%) of one or more individuals. A total of six MSA were encountered and consisted of

NAHW with short-finned pilot whales, common bottlenose dolphins (*Tursiops truncatus*), or Atlantic spotted dolphins (*Stenella frontalis*) (Table 9) to be described in detail later. A majority of groups (N = 197) were singletons (*n* = 91, 46.2%) followed by humpback whale dyads (excludes M-C pairs) (*n* = 67, 34.0%), M-C groups (*n* = 17, 8.6%), M-C-E (*n* = 8, 4.1%), and SAG (*n* = 8, 4.1%) (Table 3 in Chapter 2, figure 12). Static behaviors (milling, singing, resting, percussive) (70%) and transiting behaviors (traveling, SAG) (30%) were noted (figure 13). SAG were not seen in 2012 and 2014 and group size varied between 3 and 6 individuals in 2011 and 2013. Mean size of all group types (excluding MSA) is 1.64 individuals (SD 0.81, *n* = 197), with the SAG mean of 3.88 individuals (SD 1.64, *n* = 8). The smallest number of groups was of MSA (*n* = 6, 3.1%). The most common behaviors observed among groups and individuals were milling and traveling (Table 10, Figures 11 and 12). The most common behavior observed among singletons was traveling, and among dyads was milling (Table 10; Figure11). The most common behavior among M-C pairs and M-C-E was resting. On one occasion an escort actively and deliberately placed itself between our small research vessel and a M-C pair even at distances greater than 200 m and with a slow approach (3-4 kt [5.5-7.5 km per h (kilometers per hour)]) by our research vessel. Video capture of the M-C-E indicated that the presence of the escort did not elicit an avoidance response from the M-C, however; the M-C did appear to change direction avoiding the approach from the boat even at distances greater than 100m.

The null hypothesis that group types (M-C, M-C-E, SAG, dyads, singers, and singletons) did not differ from what was expected by chance was rejected (Chi-square = 154.21, df = 4, $p<0.001$). Dyads of NAHW exhibited behaviors with a frequency that differs from what would be expected by chance (Chi-square = 17.96, df = 4, $p<0.01$). Dyads (not M-C) were more likely to be traveling (35%) than resting (8%). Percussive actions (21%), milling (20%), and singing (16%) did not contribute to the significance of Chi-square (Freeman-Tukey deviate test). However, singletons exhibited behaviors with a frequency that differs from what would be expected by chance (Chi-square=22.33, df = 4 $p<0.001$). Singletons were more likely to be milling (37%) and traveling (28%) than resting (5%), and singing (14%). As before, for singletons, percussive behaviors (16%) did not occur significantly more than other behaviors. It was not possible to run a Chi-square test to examine the frequencies of behaviors of other groups: M-C (n = 17) or M-C-E (n = 8) due to low sample size.

Table 8. Summary of cetacean species observed in Mona Passage, Puerto Rico from 2011 to 2014 during winter (January through April).

Species Common Name	**Species Scientific Name**	**No. Groups Sighted**	**Estimated No. Individuals Sighted**
Humpback Whale	*Megaptera novaeangliae*	197	331
Unidentified Dolphin	Delphinidae	39	189
Short-Finned Pilot Whale	*Globicephala macrorhynchus*	4	31
Atlantic Spotted Dolphin	*Stenella frontalis*	2	10
Common bottlenose Dolphin	*Tursiops truncatus*	1	6
Rough-toothed Dolphin	*Steno bredanensis*	1	10
Risso's Dolphin	*Grampus griseus*	1	1
Spinner Dolphin	*Stenella longirostris*	1	20
Total		**246**	**598**

Table 9. Mixed-Species Associations: North Atlantic humpback whale groups that include individuals of a second cetacean species observed during winter between 2011 and 2014.

Date	Species 1	Number of Individuals	Species 2	Number of Individuals	Behavior Type
2/01/2013	NAHW	1	Common bottlenose Dolphin	6	Traveling
2/15/2013	NAHW	3	Probable Atlantic Spotted Dolphin	16	Play
2/27/2013	NAHW	1	Probable Atlantic Spotted Dolphin	5	Milling
3/21/2013	NAHW	3	Short-Finned Pilot Whale	9	Harassment
2/12/2014	NAHW	3	Short-Finned Pilot Whale	5	Harassment
2/19/2014	NAHW	3	Atlantic Spotted Dolphin	10	Play

Table 10. Behaviors of Humpback Whale Groups observed in winter between 2012 and 2014 from a small vessel platform*.

Behavior	2012**	2013**	2014**	Total # of groups	Percent of the total # of groups
Milling	1	25	15	**41**	**25**
Singing	1	9	14	**24**	**15**
Traveling	1	20	20	**41**	**25**
Resting	1	3	10	**14**	**9**
Percussive	8	12	10	**30**	**19**
Mixed-Species Association	0	4	2	**6**	**4**
Surface Active Group	0	5	0	**5**	**3**
Total	**12**	**78**	**71**	**161**	**100**

*2011 data excluded (singers unable to be determined)
**Values represent the number of groups observed in each behavior
Note: "Play" was excluded from this table because it was never attributed to a group during this study.

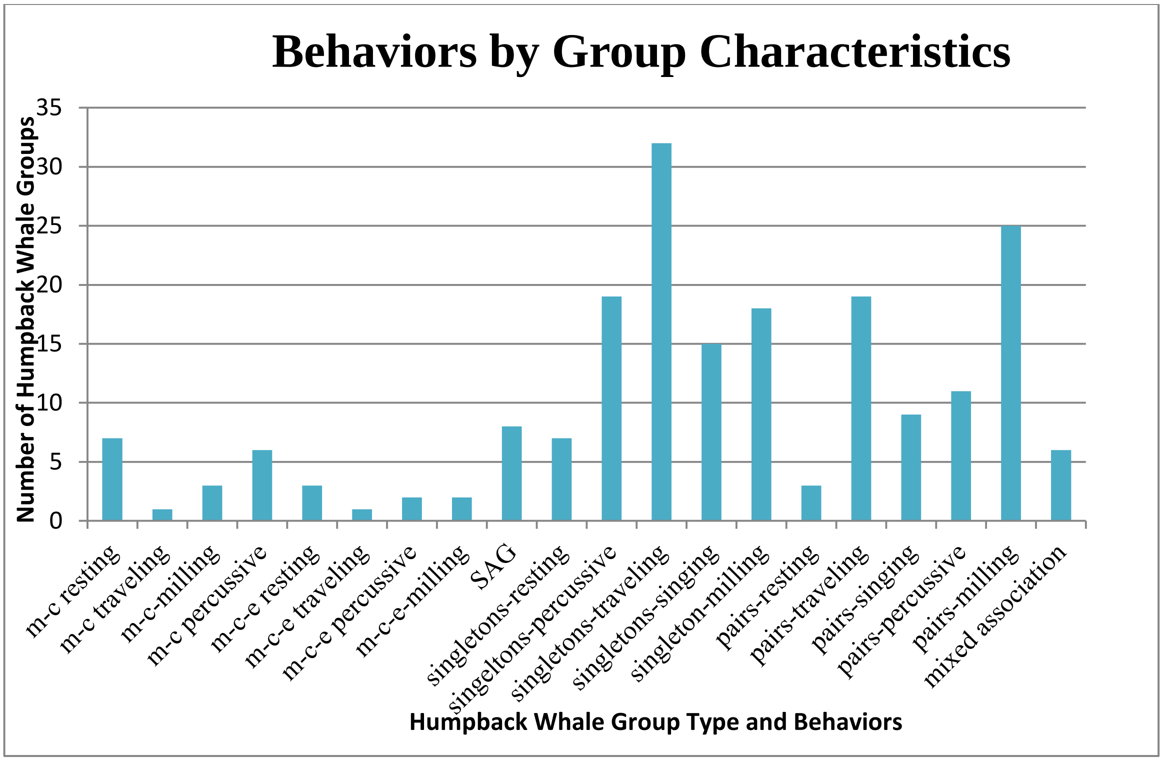

Figure 12. Distribution of North Atlantic humpback whale group assocations (*n* = 197) characterized by behaviors. This histogram represents 331 whales in 197 groups defined by associations with conspecifics and in mixed associations with another cetacean species during winter between 2011 and 2014.

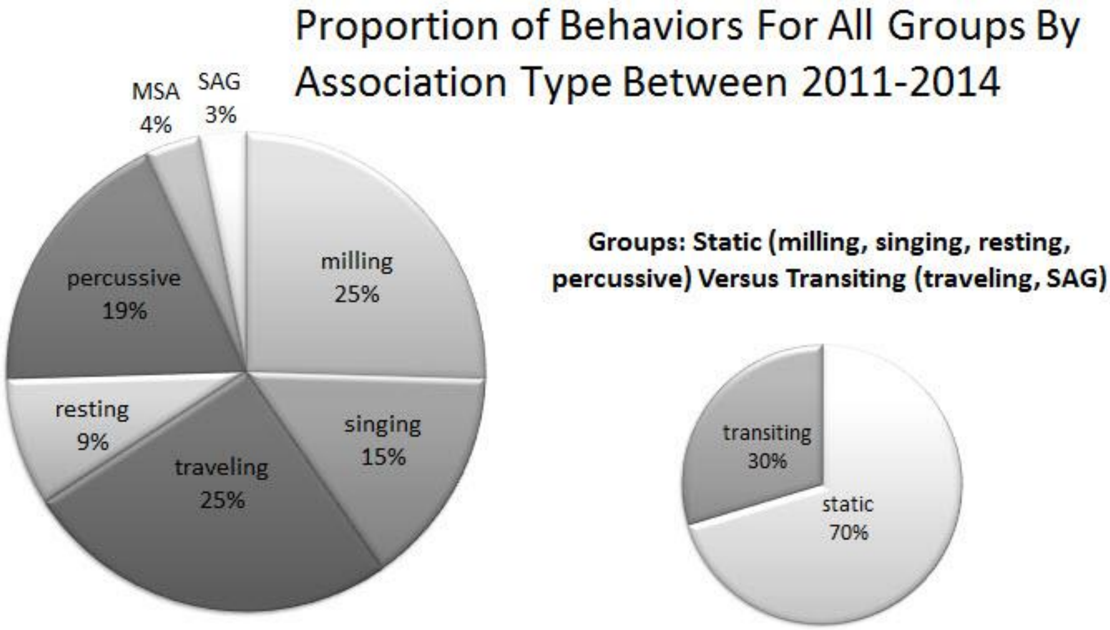

Figure 13. Summary of group behaviors by association type as an indication of movement within Mona Passage between 2011 and 2014.

Mixed association patterns of humpbacks with other cetacean species

In 2011-2014, MSA occurred between humpback whales and other cetaceans in six groups of 197 (3%) observations. Atlantic spotted dolphins were observed with humpback whales on three dates; two groups in 2013 (three whales with 16 dolphins and one whale with five dolphins) and one group in 2014 (three whales and 10 dolphins) (Table 9). Each calf exhibited percussive "splashing" behaviors (fluke slapping, lobtailing) with the mother within 10 BL and often subsurface. Common bottlenose dolphins were observed in close association with humpback whales only once (one whale and six dolphins, 01 February 2013).

Short-finned pilot whales approached NAHW in a manner that elicited signs of agitation or distress (Ciano and Jørgensen 2000; Whaley *et al.* 2008) including trumpeting, chuffing, and tail slapping (refer to Table 7 for definitions) on two occasions (once in 2013 and once in 2014) (Table 9). Three NAHW and nine short-finned pilot whales were sighted in a group in 2013 off the northwest coast. A second MSA with three NAHW and five short-finned pilot whales was sighted on 12 February 2014 in similarly apparently aggressive interaction between groups. In both encounters, our team sighted the group by the NAHW blows and approached to where whales were blowing, trumpeting, chuffing, and thrashing at or just below the surface. The groups were first thought to be competitive groups due to the high energetic behaviors until it was possible to distinguish smaller blows of short-finned pilot whales in the white waters of the thrashing group. The short-finned pilot whales continued to appear in very close contact with the humpback whales, although it was not possible to determine if there was any physical contact between species. The NAHW dove below the surface and the short-finned pilot whales remained near our boat while vocalizing. Just prior to the NAHW resurfacing, the short-finned pilot whales turned simultaneously in a single direction and the NAHW surfaced in the direction that the short-finned pilot whales were facing. The short-finned pilot whales swam quickly to the humpback whales on the surface (sometimes moving in the direction of the NAHW prior to surfacing) and repeated the following cycle; apparent harassment during four-five min of surface interaction, NAHW dive below the surface for two-three min, NAHW resurfacing while the short-finned pilot whales moved towards the location where NAHW resurfaced, and NAHW finally left the area with the short-finned pilot whales in apparent pursuit. A total of 22 min of apparently aggressive interaction was observed in 2013 and 48 min of similar interaction in 2014, between the time observations began and the whales left the area, traveling rapidly.

The final cetacean MSA of NAHW included photographic documentation of a humpback whale calf being attacked by a group of killer whales. A single episode was documented by USA Homeland Security from a small fixed-wing plane in Mona Passage in April 2014. A separate M-C-E group was observed in 2014 with evidence of a very recent killer whale attack including rake marks across the dorsal ridge behind the dorsal fin, fresh abrasions along the dorsal ridge, and a torn fluke. It was not possible to determine if this was the same calf or evidence of a second event.

Discussion

Results of this study reject the null hypothesis (H_01) that a heterogeneous mix of groups would not be represented in Mona Passage. As the population recovers from exploitation (Smith *et al*. 1999; Stevick *et al*. 2003a; Bettridge *et al.* 2015), SAG, M-C, M-C-E, dyads, singers, and singletons were observed, indicating that the area is an overflow or extension of the primary aggregation off the Dominican Republic. The null hypothesis (H_02) predicting group associations will be equally represented in Mona Passage was rejected; however, M-C pairs were not encountered more frequently than other group types. I expected M-C pairs to represent a larger proportion than other group associations secondary to the suppositions that: a) areas throughout the West Indies are geographically consistent with preferences of M-C pairs, b) as the NAHW population recovers from exploitation, nursery areas may become apparent away from the primary aggregation, and c) individuals seeking mating opportunities would be expected to be in the primary aggregation consisting of thousands of NAHW. The expectation that NAHW use Mona Passage for a nursery area (for the purpose of giving birth and nursing calves, typically nearshore and at a depth of approximately 20 m) was derived from previous surveys in the North Atlantic Ocean (*e.g.*, Mattila 1984; Reeves *et al.* 2001; Swartz *et al.* 2002; Dennis *et al.* 2005) indicating recovery of NAHW (thus anticipating a larger number of M-C pairs) and the availability of shallow waters along the west coast of Puerto Rico. The number of M-C pairs represents a small percentage of the groups in all years, contrary to what was expected in an area where bathymetric features would seem to favor a nursery area. Individuals seeking breeding opportunities, or SAG groups competing for access to a female in estrus, would favor Silver Bank, Dominican Republic.

It was not possible to determine how long any group or individual stayed in the study area. Resightings of identified humpback whales were low (1%), and may indicate that groups were transient rather than resident throughout the winter; however, it is possible that our low number of resightings was the result of a limited number of days per week of effort as it is consistent with resighting data for a period of discontinuous survey effort in 1985 off Virgin Bank (Mattila *et al.* 1989). Resightings of NAHW off Virgin Bank during a period of continuous surveys by the same group in 1984 yielded a higher resighting rate (8%). There were few SAG (4.1%) in the four years of data collection during this study compared to Samaná Bay (10.3%) (Mattila *et al.* 1994), indicating that this area is either just beginning to be repopulated with enough whales to present opportunities for males and females seeking breeding opportunities to encounter each other, or that this area has another purpose for singing males. In 2012, a total of 19 whales were sighted during the field season. It is not known if whales did not migrate as far south as Puerto Rico, moved past Puerto Rico into the Lesser Antilles, or more whales stayed on the feeding grounds.

Singing in Mona Passage, a low-density area on the periphery of the main aggregation and away from the thousands of females in estrus, does not appear to have an advantage for males seeking a breeding opportunity. Males unable to compete successfully in a high-density area may be seeking opportunities in a lower density area (which may be a “fringe” area) where competition is less likely to be encountered (Mattila and Clapham 1989) (similar to sneakers in pinniped aggregations [Coltman *et al.* 1998; Flatz *et al.* 2012]). Other explanations for males singing in Mona Passage may be that the area is being repopulated as a result of increasing numbers following cessation of whaling or that subadult males are practicing the song away from larger and mature males who may respond with aggression (Tyack and Whitehead 1983; Darling *et al*. 2006). Epigenetic age assay testing may reveal information regarding age (Polanowski *et al.* 2014) and sex relatedness of individuals, and thereby lead to a better understanding of why singers are in this low-density area.

The role of the escort is still not understood (Tyack and Whitehead 1983; Felix and Novillo 2015), and perhaps the present small sample size of observations hints that escorts may serve as a means of protection for M-C pairs from other male humpback whales competing for a breeding opportunity or predators. This appears to be supported by observations of escorts intercepting approaching boats and finding M-C farther offshore when accompanied by an escort. This “bodyguard” behavior from an escort

(Norris 1967; Wilson and Mesnick 1997; Mesnick 1997; Cartwright and Sullivan 2009b) is neither predictable nor uncommon in the West Indies or the winter areas of Pacific humpback whales off Hawai'i. Humpback whale escorts have been observed blocking access between boats, divers, swimmers and M-C pairs, including positioning their length perpendicular to the boat and "surfing" with rostrum, tail stock, and flippers fully extended, resurfacing directly in front of small boats with the BL lined up "stem to stern" and rostrum breaking the surface directly in front of the bow, and (in one instance in Hawai'i) bumping the boat (A. Zoidis, Cetos Research Organization, 28 June 2014, personal communication). It is unclear if the humpback whales are aware that the boat is not a whale and takes a defensive posture to any object that approaches the M-C pair, or if the events are a reaction elevated by breeding activity; although our escort was not in competition with any other adult males at the time of our encounter. One consideration for the presence of an escort with a M-C pair may be that all three individuals benefit from a larger group as they migrate to and from an area with killer whales.

Behaviors of groups and individuals were described in an attempt to understand the social dynamics of NAHW in Mona Passage that may help to explain the association patterns of NAHW wintering in the study area. The group behaviors over four winters between 2011 and 2014 indicate that M-C are more likely to be found resting and generally non-transient, and with other group types generally likely to be static (staying in the area at least some period of time) rather than transient (Figure 13), with the exception of SAG moving quickly while engaged in breeding activities. Observations over several more winters and consecutive days may make it possible to determine if M-C are resident, at least for some period of time, and if other groups move through or throughout Mona Passage. Percussive behavior was noted in 19% of groups without any indication of a connection between group type or composition. It was not possible to determine if the percussive behavior was associated with any particular demographic of NAHW (young, mature, male or female); however, including this type of data in future studies may indicate a connection to percussive activity and breeding or calving groups.

Data mining from studies on multiple breeding grounds was attempted as a means of comparing behaviors of NAHW to other humpback whale populations. Table 11 is a summary of data for the purpose of comparing winter habitats in Brazil, Hawai'i, and the West Indies. The data in other studies were collected with an aim at answering different questions (as indicated); therefore, the following information should be considered: Smultea (1994) had similar proportions of group association types on Hawaiian winter grounds but did not collect photo-identification data; therefore, resighting information is not known. Silber (1986) investigated questions related to understanding SAG off Hawai'i and the data collection methods were skewed towards a higher proportion of SAG than other winter grounds. Two studies in the West Indies (Mattila 1984; Mattila and Clapham 1989) were conducted on Silver Bank and the Virgin Bank (USVI); however, the study conducted of Virgin Bank had a higher proportion of M-C (12% on Virgin Bank; 9% on Silver Bank; 9% off western Puerto Rico). It may be that data collected in Mona Passage will demonstrate a comparable ratio of group associations with several more seasons of observations. It is also possible that the percentage of M-C pairs are higher on Virgin Bank because they are further from the high-density aggregation on Silver Bank, or that the mothers photographed are related to females that gave birth or were born in the same area before the cessation of whaling. The study off Silver Bank (Mattila *et al.* 1994) had very similar proportions of group types to this study with the exception of SAG. The higher percentage of SAG off the Dominican Republic (10%) may be an indication that individuals seeking a breeding opportunity are moving to an area with a larger aggregation consistent with the predictions in the Clapham and Zerbini (2015) model, and similar shifts were the premise for the hypotheses that singers were expected to be observed as a lower proportion of groups and M-C were expected to be observed as a higher proportion of groups off Puerto Rico (4%). Virgin Bank had (1%) SAG observed and may indicate that M-C pairs may have a bias for areas in the West Indies farther from the Silver Bank aggregation. Mignucci-Giannoni (1998) provided a compilation of data collected in the West Indies by at least one other researcher combined with information obtained from residents and fishers via interviews. This represents a very different methodology from the present study, and therefore, may not be directly comparable. The long-term study off Brazil (Martins *et al*. 2001) yielded some similar results compared to this study. Studies compared here had a heterogeneous mix of group types on winter habitats with similar methods yielding similar proportions of group associations. These similarities may indicate that humpback whales either 1) have small areas away from the primary aggregation in breeding grounds as part of their reproductive strategies, 2) populations of humpback whales in more than one ocean are still recovering from pre-whaling numbers and the low-density areas away from primary winter aggregations indicate that these same populations have not rebounded to pre-whaling abundance, or 3) both. With further continuous winter season data collection, association patterns off Puerto Rico and throughout the West Indies can be examined to evaluate shifts in population dynamics, and to determine if the numbers of groups are increasing.

Table 11. Comparison of Associations on Winter Breeding Grounds.

Other Winter Area Studies*	**Year and Location of Study**	**Number of Mother-Calf Groups**	**Number of Mother-Calf-Escort Groups**	**Number of Surface Active Groups**	**Number of Surface Active Group With Calves**	**Number of Singletons**	**Number of Dyads**
MacKay 2015	2011-2014 Mona Passage, Puerto Rico	17 (9%)	8 (4%)	8 (4%)	0	91 (46%)	67 (34%)
Martins *et al.* 2001	1992-1998 Brazil	331 (23%)	205 (14%)	195 (14%)	62 (4%)	226 (16%)	418 (29%)
Mignucci-Giannoni 1998	Up to 1989 Puerto Rico and Virgin Islands	0	0	160 (10%)	0	686 (43%)	607 (38%)
Smultea 1994	1988-1989 Hawaii	36 (7%)	45 (8%)	41 (8%)	10 (2%)	241 (45%)	163 (30%)
Mattila *et al.* 1994	1988-1989 Dominican Republic	58 (9%)	35 (5%)	67 (10%)	6 (1%)	273 (42%)	204 (31%)
Mattila and Clapham 1989	1985-1986 Virgin Bank, Virgin Islands	21 (12%)	13 (7%)	3 (1%)	1 (1%)	85 (49%)	52 (30%)
Silber 1986	1981-1982 Hawaii	7 (5%)	14 (9%)	49 (32%)	0	34 (22%)	49 (32%)

*Publications listed in the Literature Cited Section

Humpback whales interact with other species of cetaceans worldwide (Ciano and Jørgensen 2000). Six events were recorded when NAHW were interacting with other cetaceans, where apparent harassment, play, milling or traveling was observed. It was not surprising that a small number of MSA were encountered in this area where cetaceans are not abundant (Mignucci-Giannoni 1998; Smith *et al.* 1999). The behaviors observed are consistent with MSA. Dolphin encounters with humpback whales are not uncommon and are often described as play (Brownell 1964; Glockner-Ferrari and Ferrari 1985; Deakos *et al.* 2010). In the four incidents of dolphins with NAHW, they interacted with a calf at < 3 BL distances while other adults were within a short distance (< 10 BL) regardless of the general group behavior. In two encounters, the calf flipper slapped and the dolphins were next to the calf. It was unclear if the calf was slapping the surface in response to the dolphins nearby, if the dolphins were attracted to the splashing, or if the calf was playing or slapping the water for some other purpose. The mother appeared to be unconcerned with the presence of the dolphins and rested at or below the surface for (at least) the length of our follows. Behaviors of the bottlenose dolphins were similar to those of the Atlantic spotted dolphins. Both dolphin species appeared to be exhibiting "play" behaviors (Glockner-Ferrari & Ferrari 1985; Deakos *et al.* 2010; Würsig 2009; Würsig and Pearson 2014). The dolphins appeared to be distracted by our small boat and left the calves to investigate our boat until the engines were placed into idle or slowed down below 6 kt (11 km / h), at which point the dolphins left our boat and headed back to the splashing calf.

Pilot whales apparently harass other cetaceans in what appears to be "fun" (i.e. play) (Norris and Prescott 1961; Shane 1995a, b; Ciano and Jørgensen 2000; Pereira 2008). The NAHW appeared agitated when pilot whales approached the group (see detailed description of NAHW response to pilot whales in Chapter 4, Results) while the pilot whales appeared to be the source of the NAHW distress. It is possible to deduce that the two groups of pilot whales observed were having such "fun" and another benefit to harassing the NAHW was not obvious. Speculation exists that cetaceans may harass other cetaceans causing them to regurgitate a recent meal (kleptoparasitism) to save the energy expenditure of foraging for themselves (Weller *et al.* 1996; Palacios and Mate 1996; Smultea *et al.* 2014; Cords and Würsig 2014); however, NAHW are not foraging in winter and it appears that the pilot whales were playing by causing the NAHW to thrash about, trumpet and chuff. These are the first documented cases of apparent harassment of NAHW by pilot whales in this area, but with at least one documented event in Norway, the latter on or near humpback whale feeding grounds (Ciano and Jørgensen 2000).

Killer whale attacks on humpback whales between the feeding grounds and the winter grounds is evident in the form of rake marks and scarring (Whitehead and Glass 1985; Jefferson *et al.* 1991; Steiger *et al*. 2008; McCordic *et al.* 2014), although there had not been a documented sighting of a killer whale attack on a humpback whale calf in this area until the present one. Killer whales were observed during the calving season off Puerto Rico since 2012, by fishermen who reported sightings along with photographs and GPS coordinates to our team, although my research team did not see these directly. Effort in subsequent seasons will include the area where the photos of the calf and killer whales were taken, in an attempt to determine if this is a hot spot for killer whales waiting for an opportunity to attack M-C pairs as they migrate away from larger groups. The area of this sighting is between the west coast of Puerto Rico and Navidad Bank, Dominican Republic. The area is located away from NAHW aggregations, and is difficult to study (and not likely to be the focus of research effort for the same reason). Anecdotal evidence (citizen science, including photos) suggests that killer whales are resident off-shore pods taking advantage of NAHW migrating to the area each winter for opportunities to forage on calves. Reports of killer whales in the area, from citizens and fishers, appear to correlate with the arrival and departure of NAHW, and a study is needed to ascertain if killer whales from other areas are migrating to the West Indies or coming closer to shore during winter.

NAHW are represented by a heterogeneous mix of groups, including M-C, M-C-E, singers, SAG, dyads, and MSA. The area off Puerto Rico's west coast in Mona Passage has a similar composition of group associations as humpback whales wintering in other oceans and breeding/calving grounds, and the proportion of each group is similar to the data from as much as three decades ago in the Lesser Antilles (Mattila *et al.* 1994). It is possible this area is low-density because NAHW have not rebounded after exploitation during centuries of whaling, or there may other reproductive strategies in these low-density areas in addition to the behaviors of the primary aggregation, but perhaps no less important to the reproductive success of the population. NAHW appear to be remaining in Mona Passage for at least some period of time, as indicated by group behaviors. My data set is admittedly small and should be augmented with a continuous survey to increase the possibility of resighting groups and individuals remaining in the same area for many or just a few days. Because the current data are similar in proportions of group associations to data collected on Silver Bank decades ago, Puerto Rico may be an economically efficient venue for a continuous study as an indicator of changes in population dynamics of NAHW wintering in the West Indies. These are important considerations ahead of possible U.S. delisting of NAHW as endangered (79 FR 36281; Bettridge *et al.* 2015)).

CHAPTER V
CONCLUSIONS

Summary

North Atlantic humpback whales migrate to Mona Passage each winter, arriving around the first week in January and leaving near the end of April, with peak occurrence close to the first week in March. Individual and group behaviors along with group composition are varied, indicating that the area is not used for a single purpose. As indicated by PAM and visual surveys, NAHW occupy waters off the west and east coasts of Puerto Rico. The north and south coasts were not included in this study and it is not known if groups occupy these areas other than to use them to transit between other locations within the range of the winter habitat. NAHW may be repopulating this area as they recover post-whaling harvests, or they may simply use the entire West Indies as a single habitat, moving within the region during each winter when calving and breeding occur (Mattila and Clapham 1989). Mona Passage, the area between the Dominican Republic and Puerto Rico, consists of ledges, seamounts, and shallow coastal areas where NAHW are clustered into four hotspots associated with four discrete bathymetric features. Singers, dyads, and singletons are associated with ledges in three locations. Singletons are closely associated with the edge of a shelf that may be providing some acoustic advantage. Data from this study indicate that M-C are clustered nearshore at Rincón near the point at El Faro, and SAG are in the same location and farther offshore along the ridge extending from that point. M-C pairs with an escort are more likely to be found offshore.

NAHW migrate to Puerto Rico from all known North Atlantic feeding grounds with the exception of Norway (Stevick *et al*. 2003a). This study did not collect evidence that individuals from Norway occasionally intermix with the West Indies aggregation. Occasional mixing of individuals between the Cape Verde Islands and the West Indies would not be surprising because evidence of humpback whales deviating from the current understanding of migration routes has been indicated in other areas (Garland *et* *al.* 2011). Occurrence patterns vary between seasons with behavioral and sighting data, suggesting that individuals are using the entire West Indies as a single winter habitat. This study matched NAHW wintering in Mona Passage to sightings of the same individuals off the Dominican Republic and Guadeloupe, and the matches support the suggestion that at least some whales are transiting through the West Indies (Mattila and Clapham 1989). It was not possible to determine if individuals have site fidelity to Mona Passage, as resighting using photo-identification was very low (1%). Individuals on breeding and calving grounds do not always fluke up as they dive, and are not included in the analysis. Twenty-seven percent of the sightings during this study yielded a photograph suitable for submitting to the NAHWC for an attempt at matching to previous sightings in the North Atlantic. It is possible that some of the remaining 73% included resightings of the same individuals. Group behaviors also indicate that NAHW may be remaining in Mona Passage for at least some period of time. It is possible that group association type may predict whether any NAHW will reside in Mona Passage or transit throughout the West Indies.

Mixed species associations were infrequent and it is not known whether these are coincidental or if other cetaceans seek out NAHW groups. NAHW were observed in Mona Passage with three different species of cetaceans. Atlantic spotted dolphins and common bottlenose dolphins appeared to have a preference for calves flipper slapping or fluke slapping. Pilot whales apparently harass many cetacean species (Shane 1995a, b; Weller *et al.* 1996; Baraff and Asmutis-Silvia 1998; Pereira 2008); therefore, it is not surprising that short-finned pilot whales were encountered during two events when they were apparently harassing NAHW in Mona Passage. One theory has been presented that pilot whales may harass other cetaceans in an attempt to gain a regurgitated meal and thereby benefit from the energy expended by another group of individuals (Weller *et al.* 1996; Palacios and Mate 1996; Smultea *et al.* 2014; Cords and Würsig 2014). If kleptoparasitism is the reason for harassment by pilot whales in other areas, it is not the reason for this activity in winter habitats where humpback whales are not known to be feeding. Play is often a form of training for young animals (Bekoff 1997), and it is possible that pilot whales are teaching their young skills at the expense and "frustration" of other cetaceans, or the activity may simply be for play by the pilot whales. Caution must be taken when interpreting results of MSA in this study because few opportunities to observe NAHW with other cetaceans were encountered.

Analysis of acoustic events has been valuable for this study. Mona Passage is challenging to conduct surveys from any platform. Land-based studies are best conducted from high cliffs with a clear view of the water. In spite of the topography of the island that includes mountains, a clear view of the water from a high vantage point was difficult to find on the west coast, due to obstructions by nearby headlands, vegetation, or human-made structures. The trade winds also posed a challenge, with the weather often prohibiting collection of data in the afternoon when seas became rough and sighting whales was unlikely. Loggers attached to the sea floor (passive acoustic monitoring, PAM) detected singers arriving in Mona Passage. Data collected using this method helped to determine when NAHW arrived and departed each season. Detection of song by DSG off the east coast between Puerto Rico and St. Thomas, USVI, determined the presence of whales when observation effort was not possible due to limited resources. Finding whales was difficult in 2012, the first season data were collected from our small boat, until hydrophones and occasional aerial reconnaissance were added to the methods. Singers led us to locations where whales were aggregating despite an apparent shift along the west coast each season. Experience augmented the directional hydrophones and behavioral data helped predict where NAHW would be found. Expanding the coverage of PAM would contribute to understanding movement patterns of singers throughout Mona Passage and the West Indies.

Future Research Effort

Mona Passage has similar proportions of NAHW group association types as the aggregation off the Dominican Republic from previous studies. As NAHW stocks recover from whaling and other anthropogenic impacts, the monitoring of small areas similar to Mona Passage may represent a relatively inexpensive and rapid means of assessing fluctuations in humpback whale population dynamics. SAG, M-C, M-C-E, dyads, singers, and singletons were observed, indicating that the area is an overflow or extension of the primary aggregation off the Dominican Republic. This investigation took advantage of the smaller aggregations where behaviors are more readily attributed with confidence to a single animal or group. Additionally, the waters off Puerto Rico are a favorable study area with boat traffic limited to small boats (with the exception of the north coast's Metro Area near the city of San Juan), high visibility underwater, and limited anthropogenic noise.

Genetic relationship and epigenetic age studies coupled with size information as potentially gleaned from photogrammetric work would be able to augment the behavioral, acoustic and photographic data by determining the relatedness, age, and sex of individuals. It is possible that singers are younger males practicing the song and keeping up with the changes that occur each season without the challenge of older males, and a genetic survey along with detailed photogrammetry could help answer this question. Dyads are not uncommon in this area, and it would be valuable to know if these are pairs of related males, perhaps transiting through the area in search of a SAG. It is also possible that they are unrelated subadult males singing in the area, and that they find protection from older males that may respond to their song with aggression. Males with possible long-term associations on feeding and breeding grounds could join for the purpose of cooperating in a SAG similar to males in other areas (Darling *et al.* 2006), or associate for another reason. To more definitively answer any of these possibilities, more detailed and longer-term studies are needed.

NAHW continue to attract local and international visitors to Puerto Rico in search of a chance to see them in their winter habitat. The tourism bureaus take advantage of the charisma of NAHW through advertising in areas where whales can be seen from land, such as our observation point at Rincón - El Faro. There are commercial operators of dive boats advertising whale watches and at least one company boasts of close approaches to NAHW by boat or diving, although permits for whale watching have not been issued from local management agencies since the 1990's. There appears to be a growing interest in the NAHW by residents of the island. When a pair of NAHW was chased by four men on jet skis close to shore off Crash Boat Beach, Aguadilla, in 2014, a response from local residents included appeals to local and federal agencies for action to prevent such disruptive activities. It is difficult to predict what the effects of tourism will be in an area showing signs of indifference, exploitation, and concern for NAHW. Fishing nets can be seen floating in the same areas where NAHW are sighted by our team, placed from small boats owned by local fishermen making a living from the sea in Mona Passage. As fisheries and humpback whales recover, it will be important to have an entanglement response team and mitigation measures in place ahead of collisions between nets and whales. This study should not conclude with the information presented here. A long-term effort of data collection over decades rather than seasons should include PAM, behavioral data collection, genetics, and tagging. Tracking movement through the range of the winter habitat and determining the age, sex, and reproductive status of individuals and their associations may provide more information leading to understanding why NAHW migrate and how important it is to protect their entire suite of habitats. As NAHW are being considered for delisting under the ESA, the impact of this decision can be weighed only with a thorough understanding of their life history.

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APPENDIX A

Figure A-1. Lunging humpback whales from a surface active group. Two North Atlantic humpback whales engaging in aggressive behaviors typical in a competitive breeding group. Marine and Coastal Ecology Research Center [MCERC], Photograph taken 15 March 2013 by Mithriel M. MacKay under National Marine Fisheries Permit #15682.

Figure A-2. Winter grounds for North Atlantic humpback whales off Dominican Republic. Silver Bank, Navidad Bank, and Samana Bay are the areas where a large majority of humpback whales will migrate from higher latitude feeding grounds. The area along Puerto Rico's west coast, in Mona Passage, is the focus of this study.

APPENDIX B

GLOSSARY

Blow	Obvious expiration, often evidenced by the heart shape mist in humpback whales.
Breach	Whale propels itself from the water vertically and re-enters the water by spinning and landing on the dorsal side on impact.
Chin slap	Whale raises just the head out of the water and slaps it down on the surface.
Chuffing	Forceful exhalation through the blowhole resulting in a grunt.
Flipper slap	Whale slaps the flipper on the surface of the water. This often occurs multiple times resulting in a loud, percussive sound.
Fluke slap	Whale slaps the fluke on the surface of the water. This often happens once and laterally directed at another whale in close proximity.
Fluke-up dive	Whale arches back for a deep dive with the fluke leaving the water. Fluke is vertical as whale dives.
Harassment	Behavior (by an individual or group) that elicits a response indicative of agitation, annoyance, or distress including (but not limited to) a change in direction, chuffing or percussive activity.
Lobtail	Whale slaps the peduncle and flukes on the surface of the water. The tail stock is raised high in the air out of the water.
Lunging	Whale moves forward rapidly with head out of the water.
Milling	Swimming in different directions without moving away from the immediate area, often associated with play or social interaction.
No fluke dive	Whale arches back for a deep dive without the fluke leaving the water.
Nursing	Indications of nursing when calf's rostrum is placed beneath mother's abdomen in the area of the mammary slit. Nursing will be noted as "probable" if calf alternates between both sides of mother in nursing position.

Play	Any activity for the purpose of apparent enjoyment and does not appear to have any immediate benefit to the individual(s) but may have an important role in learning skills needed for another situation, perhaps later in life. "Play", in this study, is used to characterize behavior fitting this description and excluding other behaviors in this ethogram.
Singing	Vocalizations made by males during the breeding season nearly 30 minutes long and consisting of discreet units.
Social-sexual	Indicated by the behaviors associated with a competitive breeding group.
Spy hop	Whale is vertical in the water raising its head above the surface without a slap.
Traveling	Whales swimming in a single direction without resting.
Trumpeting	Whale vocalizes by forcing air from the blowhole while at the surface. The sound is loud and long as if blowing through a trumpet or letting air out of a small balloon forcefully.

*paraphrased from Darling 1983 and Perrin et al. 2009, refer to for definitions of these behaviors