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**SATELLITE TELEMETRY AND HUMPBACK WHALES:
A TOOL FOR DETERMINING THE HABITAT USE, DISTRIBUTION AND
BEHAVIOR OF AN ENDANGERED LARGE WHALE SPECIES.**

BY

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Doctor of Philosophy Dissertation

Université Paris-Sud

Centre de Neurosciences

November, 2013



Preface

This dissertation has been prepared in manuscript format and contains four individual papers. Each paper/chapter is formatted for the journal to which it has been, or will be, submitted. In the first manuscript, "From Whaling to Tagging: The evolution of knowledge regarding humpback whales in their North Atlantic breeding grounds", I describe the evolution of humpback whale research from the days of Yankee whaling to the most recent satellite telemetry project in the West Indies breeding grounds. The humpback whales that over-winter in the West Indies are part of one of the most heavily studied whale populations in the world; projects conducted in this area have served as models for humpback whale research world-wide. This manuscript will be submitted for publication in *Mammal Review* in 2014.

In my second manuscript, "Local and migratory movements of humpback whales satellite tracked in the North Atlantic Ocean", I report the results of a satellite telemetry project that was conducted in the winters of 2008 through 2012 in the breeding areas of Silver Bank (Dominican Republic) and Guadeloupe (French West Indies). The results from this project add a level of detail to the current knowledge about North Atlantic humpback whale habitat use, migration, and population structure that could not be obtained without current satellite tagging technology. This paper has been reviewed and accepted for publication by the *Canadian Journal of Zoology* and will be published by November, 2013

In my third manuscript, “Individual variation in movements of humpback whales satellite tracked in the eastern Aleutian Islands and Bering Sea”, I report the results from a satellite telemetry project conducted off Dutch Harbor, (Alaska, USA) in the summers of 2007 through 2011. Satellite telemetry from this project showed the fine-scale use of foraging habitat in a North Pacific feeding ground. Additionally, a long-distance, within-season travel event was recorded in 2010, prompting speculation about the humpback population structure throughout the Bering Sea. This manuscript has been reviewed and accepted for publication by Endangered Species Research and will be published by November, 2013.

In the fourth manuscript, “Assessing implantable satellite tag extrusion using light sensors”, I report the results of a novel approach for remotely quantifying tag rejection; the use of tag-mounted light sensors to indicate extrusion rate. The data for this paper were collected during a 2011 follow-up study aimed at assessing the behavioral and physiological responses of Gulf of Maine humpback whales to current tagging methods. Tag diagnostic technology like this, while still being developed, could significantly improve future telemetry work by updating tag design and placement methods to increase overall project efficiency. This paper has been accepted as a poster presentation at the 20th Biennial Conference on the Biology of Marine Mammals (December 2013, Dunedin New Zealand). It will be updated with the results from the 2013 Gulf of Maine tagging field season and submitted to a peer reviewed journal in 2014.

Acknowledgements

This work would not have been possible without the personal and professional support of a number of people over the past 3, and 35, years. Telemetry projects are logistically complex and require the assistance of many people; chapters 2, 3, and 4 end with a detailed acknowledgement of all those who contributed to the field work and logistics for each project. Additionally, there are several people who have been truly instrumental to this whole endeavor, and I would like to take a moment to thank them personally for their contributions to my work and to my life.

First, I thank my advisors, Olivier Adam and Phil Clapham. Even though we were many thousands of kilometers apart during most of my time as his student, Olivier was always helpful, responsive and readily available whenever I needed advice or support. He helped remind me to think outside the box and to see the bigger picture of any project I was working on. Phil and I, on the other hand, have often been only a few meters apart since I started working for him 6 years ago. During that time, his humor, friendship, impeccable grammar and encyclopedic knowledge of humpback whales have helped me through countless obstacles. In short, Phil has become an advisor to me in the truest sense of the word.

I have worked with many amazing people throughout my career, but few have been more open, patient, and influential than Alex Zerbini. He has repeatedly gone above and beyond the call of duty to teach me about telemetry, and in the process, he has

made me a better scientist. I'd like to thank Jooke Robbins, who has always taken the time to support my work and assist with anything, small and large, crazy or sane, that I need. Oswaldo Vazquez's contributions to the West Indies projects have been invaluable; his ability to think on his feet and carry out field work in some of the most remote, unpleasant, and difficult situations is enviable. I have learned many lessons from him over the years, not least of which are patience and an appreciation for the finer things in life.

On the personal side, I thank my family for always allowing me to follow my own path and for supporting me every single step of the way. Without the safety net that they have provided throughout my life, I would never have dared take the first step. Thanks also to Crescent, Bren and Kim—in addition to your many duties as my personal life coaches, you have helped carry me through the hard times and laugh me through the easy ones. You three are the best “pit crew” anyone could have ever asked for. Finally, I have to thank Ernie for coming into and taking over my life, in the best possible way.

“There are, namely, two things that make the humpback senseless; that is, flirting, and the presence of food. A humpback whale that is busy eating doesn't seem to have thoughts for anything other than food, and a humpback whale in love forgets all regard for safety.”

--Sigurd Risting, 1912

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CHAPTER 1:

From Whaling to Tagging: The evolution of knowledge regarding humpback whales in their North Atlantic breeding grounds.

1.1 ABSTRACT

1. Humpback whales wintering in the waters off the Antillean island chain, and especially those on Silver and Navidad Banks, comprise one of the most intensely studied breeding populations of large whales in the world. From the late 1960s to the early 1980s, humpback research was primarily based upon aerial and shipboard line-transect and acoustic survey methods for abundance, distribution and habitat use estimates. In the 1970s, the discovery that humpbacks could be identified by their fluke patterns spurred a variety of short- and long-term studies of humpback whales in the West Indies and the entire North Atlantic. Advancements in genetic data analyses in the early 1990s added another level to visual, photo-identification, and acoustic datasets. The first satellite telemetry project was conducted from 2008 to 2012 and recorded the first migratory paths between the Antilles and northern feeding grounds, as well as recorded fine-scale habitat use in under-studied waters off Haiti, Turks and Caicos and Anguilla.

2. Historically, humpbacks were heavily hunted in the Lesser Antilles during the late 1800's by sail-based Yankee whalers and shore-based local whalers. The high densities of humpbacks in the Lesser Antilles observed during the 19th century are in sharp contrast to current observations, which today show the highest humpback densities in the Greater Antilles. The reason for this disparity is unknown, as is the question of why the Lesser Antilles have not been significantly repopulated since commercial humpback whaling there ceased in 1927.

3. In addition to the many small-scale, local projects, two large-scale studies (Years of the North Atlantic Humpback (1982-83), YONAH, and More North Atlantic Humpbacks (2004-05), MOHAH) were conducted to address the need for more accurate abundance estimates of North Atlantic humpback whales. These studies combined photo-identification and biopsy-based genetic sampling to further assess population composition and overall abundance in the North Atlantic, and served as a model for subsequent large-scale cetacean studies throughout the world.

4. Today, we know a great deal about the occurrence and distribution of humpbacks in much of the West Indies. The numerous photo-ID matches

between the West Indies and the feeding grounds of the Gulf of Maine, eastern Canada and West Greenland strongly suggests that the Antilles represents the breeding range for the majority of whales from the western North Atlantic. Eastern North Atlantic whales have also been identified in the West Indies, yet the proportion of that population that migrates to Antilles remains unclear. Genetic data suggest the existence of one or more other breeding grounds for whales that feed off Iceland and Norway, although the location(s) of these wintering areas is unknown.

5. The establishment of the Silver and Navidad Banks Sanctuary (Dominican Republic) and the Agoa Sanctuary (French West Indies) represent major conservation milestones for cetaceans in the Antilles. While conservation efforts within marine sanctuaries contribute greatly to safe-guarding the North Atlantic humpback whale population, increased multi-national collaboration is needed to protect this endangered species throughout its entire life-cycle. The application of advanced telemetry tagging, genetic, and acoustic technology to systematic research in the entire region would contribute greatly to efficient humpback whale habitat management and conservation.

1.2 INTRODUCTION

The waters surrounding the Greater and Lesser Antilles (Figure 1.1) are host to a variety of cetacean species, either seasonally or year-round. These include bottlenose dolphins (*Tursiops truncatus*), spotted dolphins (*Stenella* spp.), beaked whales (Family Ziphiidae), killer whales (*Orcinus orca*), sperm whales (*Physeter macrocephalus*) and several mysticetes, notably humpback whales (*Megaptera novaeangliae*)(Mattila et al. 1989; Mattila & Clapham 1989; Mignucci-Giannoni et al. 1998; Roden & Mullin 2000; Gandilhon, 2012).

North Atlantic humpback whales migrate to the wider Caribbean region, from Cuba to the Caribbean coast of Venezuela, to mate and calve each winter; they originate in a broad range of summer feeding grounds across temperate and high latitudes, ranging from the Gulf of Maine to the Arctic (Winn et al. 1975; Mattila et al. 1989; Smith et al. 1999). Although humpback whales have historically used habitats off both the Greater (northern) and Lesser (southern) Antilles (Figure 1.1) as winter breeding grounds, a comparison of modern sighting data to whaling records indicates that the latter region is currently host to a lower density of whales than was apparent in the 19th century (Winn et al. 1975; Reeves et al. 2001; Swartz et al. 2003). Today, the largest concentrations of breeding humpback whales are seen on Silver, Navidad and Mouchoir Banks to the north of Hispaniola, as well as in Samaná Bay in the northeastern Dominican Republic.

Although a population shift from the southeastern to the northern West Indies has been proposed (Reeves et al. 2001), historical records suggest that the lack of 19th century whaling records from Dominican waters relates more to an inability of the whalers to obtain the necessary licenses than to an absence of whales in this region (Bonnely di Calventi, unpublished data).

Humpback whales wintering in the wider Caribbean region, and especially those on Silver Bank, comprise one of the most intensely studied large whale populations in the world (see Figures 1.2 (research project timeline), 1.3, and 1.4 (survey area outlines) for an overview of the projects discussed in this manuscript). Scientific research on Antillean humpback whales began in the late 1960s, and researchers have subsequently worked to establish overall abundance estimates and to describe the spatial and temporal distribution, habitat preference, migration, mating behavior, acoustic repertoire, population identity and genetic structure for the North Atlantic population. In addition to short-term, local studies, two large-scale studies (Years of the North Atlantic Humpback (YONAH; conducted in 1992-93) (Smith et al. 1999), and More North Atlantic Humpbacks (MONAH; conducted in 2004-05) (Clapham et al. 2005)) were undertaken to address the need for reliable abundance estimates of North Atlantic humpback whales. As a result of several decades of this systematic research throughout the Antillean Islands, much is known about humpback whales in this region and in the broader ocean basin. Nonetheless, some aspects of the biology and behavior of this

population - notably the fine-scale movements and habitat use of individual whales - remain poorly understood.

The following is a review of the history and results of humpback whale research conducted in the waters surrounding the Antillean Islands and the Caribbean coast of Venezuela, including a discussion about the significance of this area to the status and management of the overall North Atlantic population. This review chronicles the evolution of scientific research methods, from analysis of historical whaling data to present-day telemetry work, that have been employed by researchers on this major humpback whale breeding ground.

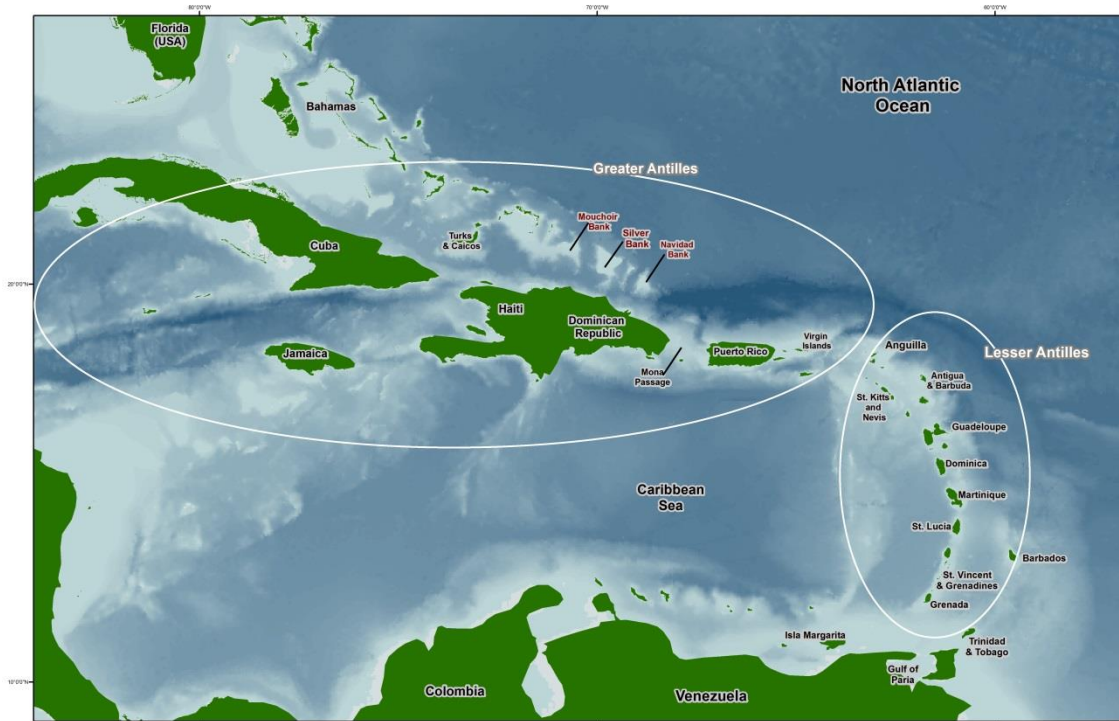


Figure 1.1: The Greater and Lesser Antilles and Caribbean coast of Venezuela

1.3 HISTORICAL OCCURRENCE

The most basic form of humpback whale research is the visual survey. Simple documentation of time, position, and number of whales seen in a particular area often represents the basis for all forthcoming scientific research to expand upon. In essence, whalers collected the first visual survey data when they recorded the date, time and position of a whale sighting or kill. Consequently, much of what we know about the historical occurrence of humpback whales in various parts of the world comes from whaling logbooks and journals, and many modern genetic, acoustic, photographic

identification (photo-ID) and telemetry studies have been designed around historical whaling records of sightings and/or catch distribution.

Commercial exploitation of humpback whales in the West Indies began in the 1820's with whaling by vessels from the great "Yankee" whale fishery. Sailing vessels from New England (notably from Provincetown, Massachusetts) "humpbacked" in the West Indies, either as a primary occupation or as part of broader expeditions targeting sperm whales elsewhere in the North Atlantic (Townsend 1935; Mitchell & Reeves 1983; Reeves et al. 2001; Smith & Reeves 2003). During the sail-based Yankee whaling era, demand for humpback-derived products peaked between 1850 and 1890, and an estimated 1,617 humpback whales were killed in the West Indies during that time (Smith & Reeves, 2003). Whaling logbook data from 19th century American whaling ships show that the highest catches of humpback whales during the winter breeding season occurred from the Windward Islands to Trinidad, and westward along the Venezuelan coast (the Spanish Main) (Townsend 1935; Mitchell & Reeves 1983; Mitchell et al. 1986; Price 1985; Smith & Reeves 2003).

The shore-based killing of whales by local inhabitants in the Antilles was rare until the 1860's. The first permanent humpback whaling station was established in Barbados in 1867 (Mitchell & Reeves 1983). After the establishment of the Barbados station (which killed an estimated 233 humpbacks between 1869 and 1878), shore-based whaling

proliferated throughout the Windward Islands and Trinidad. Although detailed records were not kept, an estimated 44 whales per year were being killed by shore-based whalers between 1880 and 1913 (Mitchell & Reeves 1983). Most of these stations had shut down by 1880, but at least five were still operational in 1912, between St. Vincent and Grenada (Mitchell & Reeves 1983). The St Vincent hunt, which is a native operation that until recently employed traditional methods based upon the Yankee fishery, continues at a low level today in Bequia.

Reeves et al. (2001) analyzed a subsample of logbooks from Yankee whaling vessels from 1823 to 1889 (initially compiled by Mitchell and Reeves (1983)) to further describe the location and number of humpback whales killed or observed by the sail-based whaling fleet in the breeding grounds. Reeves et al.'s (2001) detailed analysis describes the extensive "humpbacking" effort undertaken in the French West Indies (Guadeloupe, St. Lucia, St. Vincent), the Grenadines, Trinidad and Tobago, and the Gulf of Paria (Venezuela). In particular, the highest number of whales "taken, struck or seen" in the 19th century occurred in St. Vincent and the Grenadines (≈ 958 whales), followed by Guadeloupe (≈ 592), Venezuela (≈ 216) and Dominica/Martinique/St. Lucia (≈ 193) (Reeves et al. 2001). Approximately 167 whales were "taken, struck or seen" off the Dominican Republic, yet more than a third of those records come from one voyage in the late 1800's. Records of catches from Samaná Bay and Puerto Rico were rare (Reeves et al. 2001), but so were records of vessels operating there at all.

The occurrence of relatively high humpback whale densities along the Lesser Antilles and Caribbean coast of Venezuela in the late 1800's stands in contrast to the observed density of humpbacks in this region today. After a survey of the Greater and Lesser Antilles, Winn et al. (1975) estimated that 85% of the breeding population is seen on the banks north of Hispaniola. In terms of density, the estimates of 1.15 whales/km² (Balcomb & Nichols, 1982) and 1.13 whales/km² (Whitehead & Moore, 1982) on Silver Bank are significantly higher than estimates for Samaná Bay (0.17 whales/km²; Mattila et al. 1994), Virgin Bank (0.044 whales/km²; Mattila & Clapham, 1989) and 0.005 whales/km² on the "upper chain" (includes Puerto Rico, Virgin Bank and Anguilla Bank) (Winn et al. 1975). The most recent confirmation of low humpback densities outside of the Greater Antilles were reported by Swartz et al. (2003), who saw only 31 whales (between Guadeloupe and Trinidad/Tobago) over nearly 3,200km of effort in the eastern and southeastern Antilles.

Reeves et al. (2001) suggested that the apparent paucity of historical records of whaling effort in the Greater (northern) Antilles indicated that humpback whales were not utilizing the area extensively until the 20th century, and thus that the modern abundance of humpback whales in the waters around Hispaniola is a relatively new, post-whaling phenomenon. The authors suggested that this hypothesized shift in humpback whale distribution from the Lesser to the Greater Antilles after the late

1800's was due to overexploitation in the breeding and/or feeding grounds throughout the NA (Winn & Scott 1977; Reeves et al. 2001).

However, subsequent examination of non-whaling historical documents has provided evidence that the waters of Hispaniola were always host to abundant whales (almost certainly humpbacks) (Idelisa Bonnelly di Calventi, *pers comm*). Documents from France show that they, together with the United States and the United Kingdom, offered to recognize the sovereign status of the newly independent (in 1844) Dominican Republic in exchange for permission to hunt the abundant whales in those waters; Samaná Bay is specifically mentioned in some of these sources. Notes about "abundant" whales in historical documents (Idelisa Bonnelly, *pers comm*.) suggest that Dominican waters have long represented an important humpback habitat and that the absence of records of whaling from this area was more likely related to a failure by whaling vessels to obtain required national licenses.

Regardless of whether the current densities of whales on Silver, Navidad and Mouchoir Banks during the breeding season are a recent phenomenon, the high densities of humpback whales in the Lesser Antilles that are apparent from 19th century catch records stand in sharp contrast to current observations. The reason for this disparity in distribution is unknown, as is the question of why the Lesser Antilles have not been significantly repopulated since commercial humpback whaling ceased in 1927. The

possibility that whales from the Lesser Antilles represent a separate breeding population from those to the northwest seems unlikely given photo-id matches which have linked the former area to western North Atlantic feeding grounds (Robbins et al. 2006, Stevick et al. 1999b).

1.4 MODERN SCIENTIFIC RESEARCH OVERVIEW

Modern studies of humpback whales in the West Indies began in the 1960s and continue today; Figure 1.2 provides a timeline of the development of this research. Here, we provide a brief overview of this history; details of the results of this research are given in topic-specific sections below.

From the late 1960s to the early 1980s, humpback whale research was primarily based upon aerial and shipboard visual line-transect and acoustic survey methods. These were used to establish abundance, distribution, habitat use and overall humpback whale movements. In the 1970s, the discovery that humpback whales could be individually identified by the unique pattern of markings on the ventral surface of the tail (Katona et al. 1979, Katona and Whitehead 1981) inspired the inception of a variety of short- and long-term studies of humpback whales in the West Indies and various summer feeding grounds in the higher-latitude North Atlantic, as well as elsewhere in the species' global range (Clapham 1996).

Humpback whale research in the Antilles effectively began with a brief exploratory acoustics survey conducted in Mona Passage (PR) in 1969 (Winn et al. 1971). After this, Winn et al. (1975) led the first systematic shipboard survey for humpback whales, from Grand Turk to Rio Orinoco in the winters of 1972 and 1973. This study combined passive acoustic listening with line-transect visual surveys. The authors estimated that 85% of the humpback whales in the West Indies breeding grounds were found in the Silver, Navidad and Mouchoir Banks complex (off the northern coast of Hispaniola), and the high calf density there indicated that these areas were critically important breeding and calving grounds.

At about the same time as the Winn et al. (1975) study, the Naval Ocean Research and Development Activity (NORDA) conducted an aircraft-based acoustic survey from Hispaniola to Barbados in January of 1973 (Levenson & Leapley, 1978). Scott and Winn (1980) conducted another visual and aerial survey of Silver and Navidad Banks two years later (1978) to compare and intercalibrate aerial and shipboard survey techniques, and to further document the size, distribution, movement and stock identity of NA humpback whales in the Dominican breeding grounds.

Also in the late 1970s, George Nichols initiated a program of annual research using the 144-foot barquentine *Regina Maris*. Using this platform, Balcomb & Nichols (1978, 1982) and Whitehead & Moore (1982) conducted visual and acoustic surveys in the

winters of 1976 to 1981, from the Gulf of Paria (Venezuela) to Puerto Rico. As with previous surveys, the only large concentrations of whales were found on Silver and Navidad Banks, and peak sightings at the end of January for Navidad Bank, and two weeks later for Silver Bank.

David Mattila and colleagues began a humpback whale study in Mona Passage off the western coast of Puerto Rico in 1978, and collected photo-identification data and song recordings there for the next six winters. The results of this study remain largely unpublished, although selected results were given in Mattila and Clapham (1989), and individual identification photographs from Puerto Rico have been widely used in publications resulting from the North Atlantic Humpback Whale Catalogue. In 1984, Mattila et al. (1989) conducted a six-week photo-ID survey of Silver Bank to further address the scope of genetic mixing of feeding stocks on the breeding ground. In the following two years (1985 and 1986), Mattila and Clapham (1989) conducted the first surveys of Virgin Bank, Anguilla Bank and the northern Leeward Islands.

Herbert Hays and Howard Winn observed a number of humpback whales during a short visit to Samaná Bay in the northeastern Dominican Republic in the late 1970s (unpublished data), but formal research did not begin there until the Center for Marine Biology (CIBIMA) at the Autonomous University of Santo Domingo collaborated with the Center for Coastal Studies (Provincetown, Massachusetts) in 1987 to conduct the first

exploratory survey of the bay. This expedition led to into a series of annual boat-based survey from 1988 to 1991. During the latter study, Mattila et al. (1994) used photo-ID to describe the overall occurrence, population composition and habitat use by humpback whales in Samaná Bay, and the relationship of this habitat to the more populous offshore banks to the northwest.

The collection of individual identification photographs from different parts of the North Atlantic (including the West Indies) resulted in a growing catalogue of humpback whale fluke photos. This permitted the first connections to be made among breeding and feeding areas (Balcomb & Nichols, 1982); furthermore, by the late 1980s, the catalogue (maintained by the College of the Atlantic in Bar Harbor, Maine, USA) was large enough ($n=3,647$ individuals) to allow researchers to employ a photo-ID mark-recapture abundance estimate technique originally suggested by Balcomb & Nichols (1978).

In 1991 and 1992, the first large-scale, ocean-basin-wide photo-ID and genetic mark-recapture project was conducted. This project, called Years of the North Atlantic Humpback (YONAH), incorporated data from all major humpback breeding and feeding grounds. Researchers from seven countries, from the West Indies to Norway, employed standardized sampling methods and demonstrated that a study on such a broad spatial scale, while expensive and logistically complex, can produce a more reliable and comprehensive dataset than multiple small-scale surveys conducted over many years.

YONAH has subsequently been seen as a model for other large-scale studies, notably the Structure of Populations Levels of Abundance and Status of Humpbacks (SPLASH) project in the North Pacific (Barlow et al. 2011).

Although the Lesser Antilles had been sporadically studied by earlier expeditions (Winn et al. 1975; Balcomb & Nichols 1978; Levenson & Leapley 1978), most effort had been focused in the major areas of concentration in the northern West Indies; far less was known about the distribution and occurrence of humpbacks in the Windward Islands and areas to the south. To address this deficiency, in February and March of 2000, Swartz et al. (2003) undertook a visual, genetic and acoustic survey in the Lesser Antilles to describe the regional abundance of humpback whales in areas with lower densities than the Greater Antilles, and to determine the feasibility of using acoustic methods to detect and locate whales. The survey covered the Leeward Islands (except for the Virgin Islands, the islands of Anguilla Bank, and St. Eustatius), the Windward Islands, Barbados, Trinidad and Tobago, and the northern coast and offshore islands of Venezuela. One year later, Swartz et al. (2002) conducted another survey to determine the winter distribution and abundance of cetaceans in the waters surrounding the Bahamas, Turks and Caicos, Puerto Rico and the Virgin Islands.

By 2004, the estimates of abundance produced by YONAH were more than ten years old and there was interest by the U.S. government in conducting a further review of North

Atlantic humpback status relative to the U.S. Endangered Species Act. Consequently, a follow-up study to YONAH, called More North Atlantic Humpbacks (MONAH), was initiated. The goal of MONAH was to obtain North Atlantic humpback abundance estimates using biopsy-based genetic mark-recapture methods, although photo-ID information data were also collected as a secondary objective.

In recent years, satellite telemetry has become a powerful tool to describe the fine-scale local and migratory movements of large whales (Mate & Mesecar 1997; Baumgartner & Mate 2005; Heide-Jørgensen et al. 2006; Zerbini et al. 2006). Kennedy. et al. (in press) conducted the first North Atlantic humpback whale satellite telemetry project between 2008 and 2012. Fine-scale individual movement data, as well as the first documented migration routes from breeding to feeding grounds, were recorded.

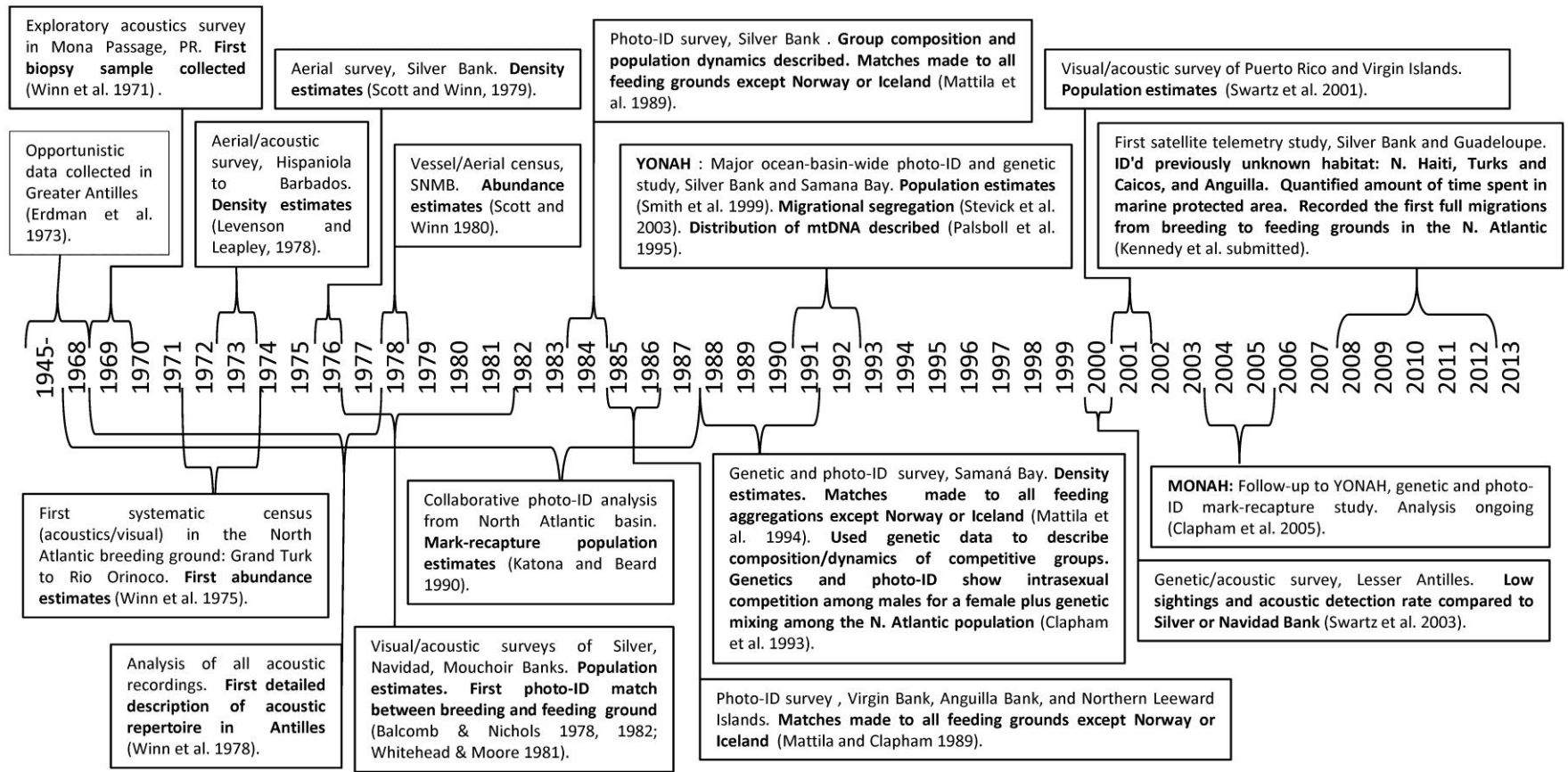


Figure 1.2: Timeline of humpback whale research conducted along the Antillean Island Chain.

1.5 THE DEVELOPMENT OF KNOWLEDGE

1.5.1 Abundance, Density and Distribution

Winn et al.'s (1975) systematic shipboard survey, conducted throughout the Antilles, generated the first North Atlantic humpback whale population estimate of 785-1157 (CI, presumed 95%) animals. Average density estimates of 0.21 (Silver Bank) and 0.23 (Navidad Bank) whales/km² were also calculated; these densities demonstrated that the great majority of whales in the West Indies occurred on the Silver, Navidad and Mouchoir Banks complex off the northern coast of Hispaniola. Levenson and Leapley's (1978) aerial acoustic survey in 1973 deployed eighty-two passive acoustic sonobuoys and recorded visual observations along the predetermined flight track. All but one of the acoustic detections from NORDA's sonobuoys occurred east of 70°W and north of 16°N, with the highest concentrations centered over Silver and Navidad Banks. In 1976, Scott & Winn (1979) conducted two additional aerial survey flights over Silver Bank to explore the utility of different methods (including photogrammetry) for humpback whale stock assessment. The authors calculated a density of 0.311 ± 0.069 (95% CI) whales/km². Since this density was statistically similar to Winn et al.'s (1975) calculation, despite an estimated growth rate of 5% per year (from ACMRR 1976), Scott & Winn (1979) concluded that vertical photographic sampling methods are cost-effective and efficient, yet the precisions of the resulting estimates may be low.

Scott and Winn's (1980) 1978 visual and aerial survey calculated a population of 1069-1377 (95% CI) on Silver Bank and 306-370 (95% CI) whales on Navidad Bank. The density estimates from this study (0.513 whales/km², sd = 0.36) for Silver Bank and 0.554 whales/km², sd = 0.368) for Navidad Bank were over 50% higher than Winn et al.'s (1975) corrected estimate. If this difference was due strictly to population growth, this would equate to an 8.5% annual population increase between 1972 and 1978; however, differences in sampling methods and/or temporal coverage may have contributed to the observed density increase. Additionally, Scott and Winn's (1980) comparison of census techniques found that detection probability during aerial surveys was particularly sensitive to environmental state, and shipboard survey estimates should be considered more accurate, particularly if they include photo-ID.

The sighting data collected in 1977 from *Regina Maris* did not account for detection parameters, yet crude population estimates were reported (Table 1.1). The estimates derived from the 1977 survey roughly equated to a 1.8% population increase per year from Winn et al.'s (1975) previous estimate, yet the authors admit that their number did not account for all potential recruitment and/or bias. The sighting data collected from *Regina Maris* in 1980 and 1981 were ranked and sorted on detection probability parameters (including environmental conditions, sighting cue, and distance to sighting) and produced, in theory, more accurate mean population estimates for Silver, Navidad and Mouchoir Banks (Table 1.1), yet there were still sampling method and/or analysis

biases that needed to be addressed (Balcomb & Nichols 1982). While the authors tentatively compared their results to prior estimates, it was clear that bias from differing survey methods and vastly different spatial and temporal coverage among breeding ground censuses would preclude reliable population trend analyses.

Table 1.1: Mean Population estimates for Silver and Navidad Banks, 1973, 1977, 1980, 1981. Sources: *Winn et al. 1975, **Balcomb and Nichols 1978, ***Balcomb and Nichols 1982.

	Silver Bank	Navidad Bank
*1973	754	110
**1977	809	96
***1980	1432	441
***1981	963	214

Elsewhere in the West Indies breeding range, Mattila and Clapham's 1985-86 surveys found that humpback sightings peaked in mid- to late February on Virgin Bank and Anguilla Bank, with an overall mean of 0.044 whales/nm² (sd = 0.029) on Virgin Bank. Overall, the density of humpbacks on Anguilla Bank was around 50 to 66% lower than either Virgin Bank or Puerto Rico. The seasonal density shifts and within-season photo-ID matches documented in this and other papers (e.g. Balcomb & Nichols 1982) suggested a northeast-to-southwest movement through the Antilles during the winter. In Samaná Bay, Mattila et al. (1994) discovered that whale density (0.17 whales/km²) in

that area was an order of magnitude lower than on Silver or Navidad Banks, but higher than in Mona Passage (Puerto Rico) or on Virgin Bank. Again, a general trend toward peak abundance in February was noted, but this varied among years.

Using the North Atlantic Humpback Whale Catalogue collection of 3,647 individually identified whales, Katona and Beard (1990) conducted a mark-recapture analysis using all available humpback photos taken between 1952 and 1987 to calculate an overall population estimate of $5,505 \pm 2617$ (95% CI) animals, and an unweighted mean population estimate of $3,776 \pm 4,853$ (95% CI) whales on the Silver, Navidad and Mouchoir Banks complex. Katona and Beard (1990) speculated that, in addition to sampling method biases, the highly variable population estimates derived from breeding ground surveys since the late 1970s (see Table 1.1) may be the result of differing sex/age class and/or feeding ground origin occupancy patterns in the breeding grounds.

By the late 1980s, existing abundance estimates were old and suffered from bias relating to use of different survey methods. Furthermore, there had been little sampling in the central and eastern North Atlantic (notably Iceland and Norway). To address these problems, the first ocean-basin-wide photographic and biopsy survey, YONAH (Years of the North Atlantic Humpback), was conducted in 1992 and 1993 (Smith et al. 1999). Consistent spatial and seasonal effort and a standardized sampling protocol across the entire North Atlantic study area significantly reduced sampling bias during

YONAH. Nearly three thousand individuals were photographed, and just over two thousand were biopsied. The resulting population estimates of 10,400 (95% CI = 8,000-13,600 from biopsy data, 10,600 (95% CI = 9,300-12,100) (Smith et al. 1999) and 11,570 (95% CI = 10,290 to 13,390) (Stevick et al. 2003*b*) from photo-ID data were much larger than the estimates from the 1980's and likely reflected a combination of population growth and reduced sampling bias. Palsbøll et al. (1997) used the biopsies from the YONAH study to produce the first mark-recapture abundance estimate based on microsatellite genotyping data.

An important finding of YONAH was that analysis of the breeding ground genetic samples produced significantly different population estimates for females (1,776-4,463(95%CI)) and males (3,374-7,123 (95%CI)), and the total population estimate derived from breeding ground photo-ID and genetic tagging data alone was significantly lower than the ocean-wide estimate. However, the male-only genotype estimate was almost exactly half the winter-summer photo-identification estimate, suggesting that male-specific estimates derived from breeding grounds are more reliable than any estimate that involves sampling of females. The explanation for this is uncertain, and likely relates to sex-based differences in habitat preference, and/or migrational timing. Whatever the reason, the doubled male-only estimate agrees well with Stevick et al.'s (2003*b*) overall photo-id estimate of 11,570, and these two remain the most reliable estimates of North Atlantic humpback whale abundance to date.

The visual and acoustic survey of the Lesser Antilles conducted by Swartz et al. (2000) covered a broad area from Puerto Rico to Venezuela. The low detection rate from this survey (31 visual and at least 142 acoustic detections of humpback whales over the 10,900 kilometers surveyed) reinforced the early findings of Winn et al. (1975) and Levenson and Leapley (1978) that far fewer whales overwinter in the Lesser Antilles than in the Greater Antilles. Silva et al. (2006) conducted a short survey in an area not covered by Swartz et al. (2003) in 2002 and recorded 11 humpback whale sightings just north of Margarita Island and Los Frailes Archipelago (Venezuela).

Swartz et al.'s (2002) subsequent survey from the Bahamas to the Virgin Islands in February and March of 2001 detected humpback whales throughout the entire study area south of the Bahamas, yet the 8:1 acoustic to visual detection ratio showed that visual-only surveys can greatly underestimate true whale densities in winter. Overall, the authors calculated an abundance estimate, based on sighting data, of 532 (95% CI = 260-1,088) humpback whales on the Puerto Rican-Virgin Island insular shelf.

The large-scale follow up to the YONAH project, called MONAH, was conducted over two two-month winter field seasons in 2004 and 2005, on Silver Bank only; additional sampling was also conducted on a single summer feeding ground, the Gulf of Maine. Unlike in YONAH, biopsy sampling for genotyping was the priority over photo-identification, although fluke photos were taken whenever possible. Genetic analyses

from MONAH samples are currently underway, and the preliminary results will be used to generate a male-specific estimate of North Atlantic humpback abundance based upon genotyping.

1.5.2 Population Structure

In the early 1970s, before photo-ID catalogs or genetic analysis technologies had been developed, Mitchell (1973) and Winn and Scott (1977) proposed a distinct spatial separation of three feeding stocks on the breeding grounds with no conclusive evidence of spatial mixing. More than four decades of photo-ID analyses from the late 1970s to the present day have greatly expanded our knowledge of population structure in both the feeding and breeding grounds, and we now know that the three-stock hypothesis is incorrect.

Researchers aboard the *Regina Maris* opportunistically photographed humpback flukes on the breeding ground from 1977 to 1981 (Balcomb & Nichols 1978, 1982) and were able to report the first match between a North Atlantic feeding ground (Tooker Bank, Newfoundland) and breeding ground (Silver Bank), in 1977 (Balcomb & Nichols 1978). Katona and Beard's (1990) extensive photo-ID analyses highlighted the presence of four, probably five, separate feeding aggregations (Iceland-Denmark Strait, western Greenland, Newfoundland, Gulf of St. Lawrence and Gulf of Maine/Scotian Shelf). Stevick et al. (2003b) later used YONAH data to define the feeding aggregation

boundaries as Gulf of Maine, eastern Canada (including Newfoundland, Labrador and the Gulf of St Lawrence), West Greenland and the eastern North Atlantic (Iceland and Norway). Genetic analysis indicated that this strong, maternally directed feeding-area fidelity had persisted over a long enough period to be evident in mitochondrial DNA structure (Palsbøll et al. 1995; see also Clapham et al. 2008) despite extensive genetic mixing on the breeding grounds.

Analysis of photos collected on Silver Bank in 1984 by Mattila et al. (1989) described 97 whales that had been previously seen in summer feeding grounds (Greenland, Newfoundland/Labrador, Gulf of St. Lawrence, Gulf of Maine) or another wintering area (Silver Bank, Puerto Rico, Virgin Bank, Anguilla Bank), as well as off Bermuda (which is generally considered a migratory waypoint rather than a breeding area). Mattila and Clapham's (1989) photo-ID study in the northern Leeward Islands in 1985 and 1986 found nearly the same results as on Silver Bank; matches were made to all major North Atlantic feeding grounds except to Iceland and Norway in the eastern North Atlantic. The lack of representation of eastern North Atlantic whales in these studies (Mattila et al. 1989, Mattila & Clapham 1989) was likely due to the small number of catalogued whales from the eastern feeding grounds. Martin et al. (1984) had matched whales seen off Puerto Rico and Silver Bank to the small (n=17) Icelandic catalog prior to the Mattila and Clapham studies and, as predicted, later studies documented more matches between the Antilles and the eastern North Atlantic (Larsen et al. 1996; Stevick et al.

1999*a*, 1999*b*; Smith et al. 1999; Clapham et al. 1993; Bérubé et al. 2004; Robbins et al. 2006).

While the presence of humpbacks from all North Atlantic feeding grounds on the Antillean breeding grounds is undisputed, genetic analysis of samples collected during YONAH showed that eastern North Atlantic whales were underrepresented compared to western North Atlantic whales on Silver and Navidad Banks (Stevick et al. 2003*a*). Genetic analyses indicates the existence of a second, and perhaps even third, undiscovered breeding ground (Palsbøll et al. 1995; Larsen et al. 1996). Speculation that the Cape Verde Islands (CVI), which today host a relatively small number of whales, may represent one of these unknown breeding grounds has so far been unproven (Larsen et al. 1996), but it seems unlikely that the CVI represent the destination for most whales from what is assumed to be a large population in the eastern NA. Winn et al. (1981) compared songs between the West Indies and the Cape Verdes and found no difference; this might suggest no population separation, but song is known to be at best a crude and sometimes unreliable indicator of stock division (Garland et al. 2012).

The most recent confirmation of genetic mixing between eastern and western North Atlantic feeding stocks in the Antilles came when whales tagged on Silver Bank and off Guadeloupe were tracked over either full or partial migrations to both regions (Kennedy et al. in press). Interestingly, two whales heading toward eastern North Atlantic feeding

grounds showed $\approx 1,300$ km of nearly identical track lines, followed by an additional $\approx 1,600$ km of track with nearly identical heading (separated by roughly 200 km), despite the spatial and temporal separation of the tag deployments. This overlap potentially represents evidence for the existence of specific migratory corridors from the Antillean breeding grounds to eastern North Atlantic feeding grounds, and supports the findings of Horton et al. (2011) that humpbacks can navigate across long distances with remarkable precision.

In addition to apparently unequal occupancy rates by whales from different feeding grounds, Stevick et al. (2003a) found that different sex and age classes arrive on the breeding grounds at different times; males were observed as much as three weeks earlier than females (either with or without calves) in Silver and Navidad Banks. This is consistent with studies based upon whaling catches made in Australia and New Zealand, which also show a migration that is staggered by sex, age class or (for females) reproductive condition (Chittleborough 1965, Dawbin 1966, 1997).

Tagging data have further highlighted a curious issue with humpback whales, namely the vastly different distances over which individuals from different feeding grounds must migrate to reach the winter breeding grounds. For humpback whales that feed in arctic Norway, this distance is approximately three times that of Gulf of Maine whales, and tag data have documented a corresponding large difference in transit times

(Kennedy et al. in press). This raises the possibility that the energy requirements and transit time required for a full migration between the Antilles and the eastern North Atlantic may be high enough to deter a full migration every year.

1.5.3 Habitat Use and Within-season Movement

Winn et al. (1975) noted that, during the breeding season, humpback whales were found “almost exclusively” on banks between 10 and 100 fathoms (18 to 180m) deep, yet there was no effort in the deep waters off the shelf break. Roden and Mullen (2000) recorded 12 humpback sightings in an average depth of 2877m during their cetacean abundance survey (between Guadeloupe and western Cuba). Mignucci-Giannoni (1998) compared humpback sighting data (published and unpublished, up to 1985) off Puerto Rico and the Virgin Islands and found that the whales there also prefer shallow, nearshore waters with little slope. No surveys to date have reported whale sightings on the Caribbean side of the Antillean chain, although whales are known from anecdotal reports to occur there.

An estimated 85% of the whales on the breeding ground are found on Silver and/or Navidad Banks each year, and Silver Bank appeared to have the highest calf density in the breeding range (Winn et al. 1975; Balcomb & Nichols 1982). Virgin and Anguilla Banks, Mona Passage (PR) and Samaná Bay also host mothers and calves, though in much smaller numbers. There was a virtual absence of calf sightings on Navidad Bank

(with very little reef protection) between 1977 and 1981, which led Whitehead and Moore (1982) to speculate that mother-calf pairs prefer the calm waters alee of reefs or large coral heads (ex. Silver Bank). However, calves were observed there during MONAH surveys (Clapham, unpublished data), so the relative suitability of this habitat for mothers is currently unclear.

The preference for Silver and Navidad Banks over other banks with very similar oceanographic characteristics has been a matter of some discussion. The waters around Los Frailes Archipelago and Margarita Island, Venezuela, for example, appear to have once represented populous humpback wintering grounds in the late 1800's (Townsend 1935; Reeves et al. 2001). While they possess similar topographic and bathymetric features as Silver and Virgin Banks, very few humpbacks have been seen there since the 1970s (Winn et al. 1975; Swartz et al. 2003; Silva et al. 2006). Whitehead & Moore (1982) proposed that the appeal of Silver and Navidad Banks is the presence of many whales. In other words, Silver and Navidad Banks seem integral to the humpback whales' mating system in that the males are more likely to congregate and compete in areas which have value to the highest number of females.

Individual movements among different areas of the breeding range had been shown through photo-ID matches of whales seen off Puerto Rico, Anguilla, Virgin Bank and Silver Bank at different times in the same winter (Mattila et al. 1989). Overall, the

observed direction of movement was always east to west along the Antillean Chain; unfortunately, mark-recapture studies do not permit finer-scale habitat-use descriptions. Kennedy et al. (in press) showed that individual whales use well-known breeding habitats (notably Silver Bank), but also travel to areas relatively distant from these densely populated banks, including to waters off the Turks and Caicos Islands, the northern coast of Haiti, and Antigua and Barbuda. While more than 80% of within-season movement occurred on Silver, Navidad and Mouchoir Banks, even small individual movement variations (into or out of the study area) could bias the capture probability assumptions used in mark-recapture analysis and affect population estimates based on such data (Hammond et al. 1990; Friday 1997).

1.5.4 Reproductive Behavior

Howard Winn (Winn et al. 1971) recorded humpback whales producing highly patterned sounds in an ordered sequence during a brief, exploratory acoustic survey in the winter of 1969 in Mona Passage, Puerto Rico; these results were consistent with studies from Bermuda, where the first formal description of humpback whale song was published around this same time (Payne and McVay 1971). While genetic analysis technology was still in its infancy, Winn et al. (1973) managed to collect and analyze a skin sample from a singing whale and found that it lacked the sex chromatin body normally found in the nuclei of mammalian female skin. This fact, coupled with whaling records stating that

the lone individuals (often found outside of calving bays) were always males (Nordhoff 1856), led Winn et al. (1973) to hypothesize that singing whales are generally young, lone males, which suggested that the primary function of singing was related to the mating system. Whitehead and Moore (1982) found that the highest singer density occurred consistently over flat bottom areas of Silver, Navidad and Mouchoir Banks.

Winn & Winn (1978) conducted a detailed analysis of all the acoustic recordings collected from 1969 through 1977 from Grand Turk Island (Bahamas) to Venezuela. Results from this analysis included a detailed description of the humpback whales' acoustic repertoire in the Antilles, a description of yearly changes in the song, and a suggestion of local acoustic dialects throughout the breeding range. The authors hypothesized that the function of the song is to locate breeding areas, establish territory, maintain contact with groups and/or identify individuals. Today, song is widely believed to represent an advertisement by males to attract females (Clapham 1996), and also possibly to mediate male intrasexual interactions (Darling and Bérubé 2001).

Assemblages of humpback whales featuring often highly aggressive behavior, usually termed "competitive groups" from the term coined by Clapham et al. (1993), had been observed with frequency in the West Indies and elsewhere (Tyack and Whitehead 1983). This behavior was seen as intra-sexual competition among male humpbacks for access

to a female. A study in Samaná Bay between 1989 and 1991 used a combination of molecular sexing and photo-identification to confirm this assumption (Clapham et al. 1993). Labels were assigned to each whale in the group by behavioral role, and analysis of the group composition confirmed the hypothesis from earlier work that most competitive groups, although unstable, usually contain a female (nuclear animal, NA), a male principal escort (PE), and various other secondary escorts and challengers. The fact that relatively few principal escort displacements have ever been observed could mean that the PE had already mated with the nuclear female (thus making her less attractive to the other males in the group), or simply that “defense” of a mate is easier than “offense”.

Prior to the Clapham et al. study (1993), competitive groups were often thought to consist exclusively of multiple mature males competing for a mature female. However, the molecular sexing technique allowed the authors to further assess the composition and role of these groups within the breeding system. Several all-male competitive groups were discovered, and such assemblages may serve as an opportunity for dominance sorting between individuals who are likely to encounter each other with some frequency on the breeding grounds. The presence of apparently mutually non-agonistic male pairs within competitive groups may indicate cooperation between males to secure a female, but it is not clear how this cooperative behavior would increase the reproductive success of non-mating, non-kin individuals. Female aggression against a

sub-adult male was noted and suggests active selection, rather than passive acceptance, of a principal escort in some cases (Clapham et al. 1993). Additionally, photo analysis uncovered the presence of some competitive groups containing more than one female or a sub-adult male, urging caution in future research when making sex and age assumptions about such groups (Clapham et al. 1993).

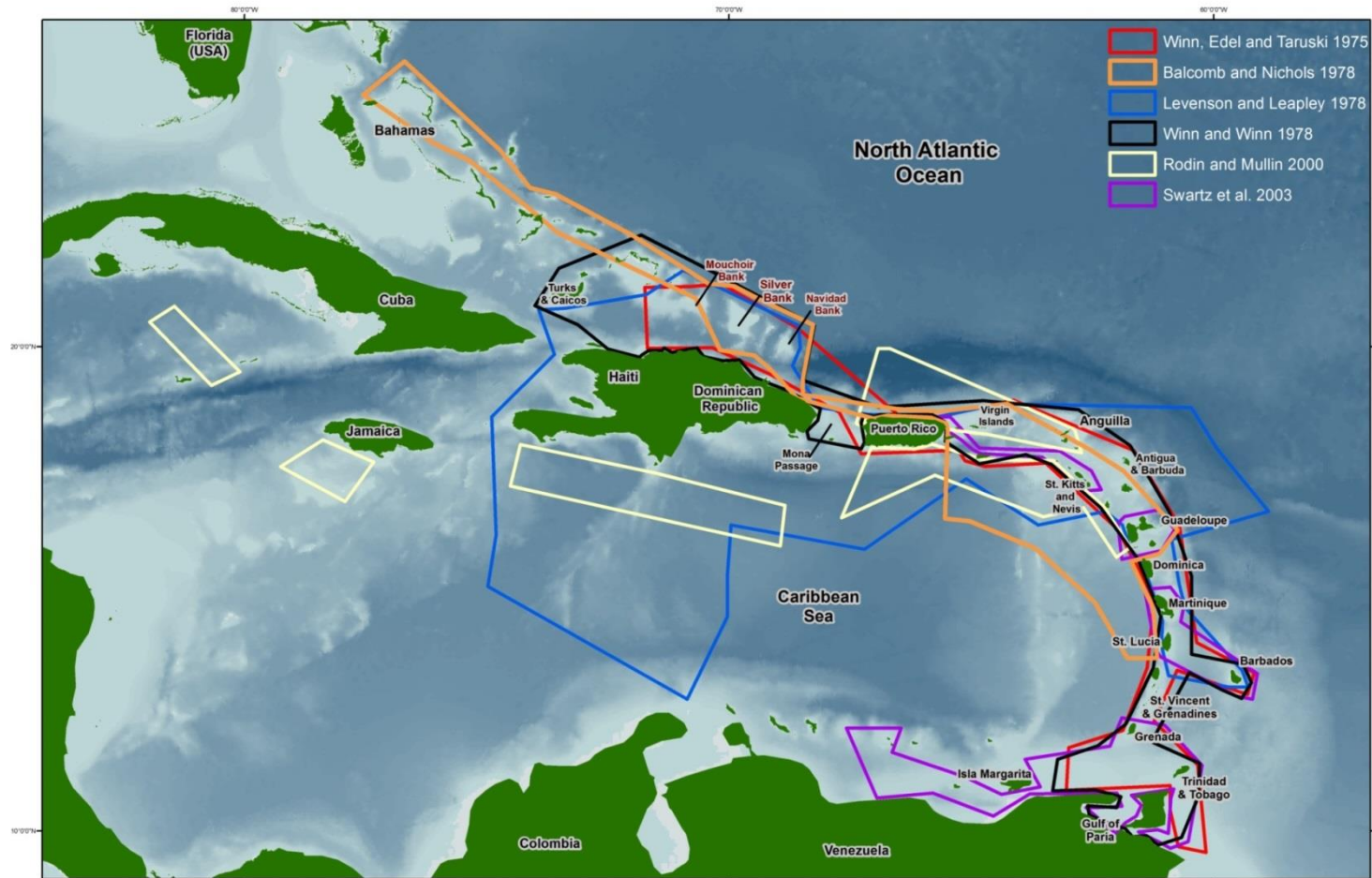


Figure 1.3: Rough outlines of large-scale humpback whale research projects carried out from the late 1960's to present day.

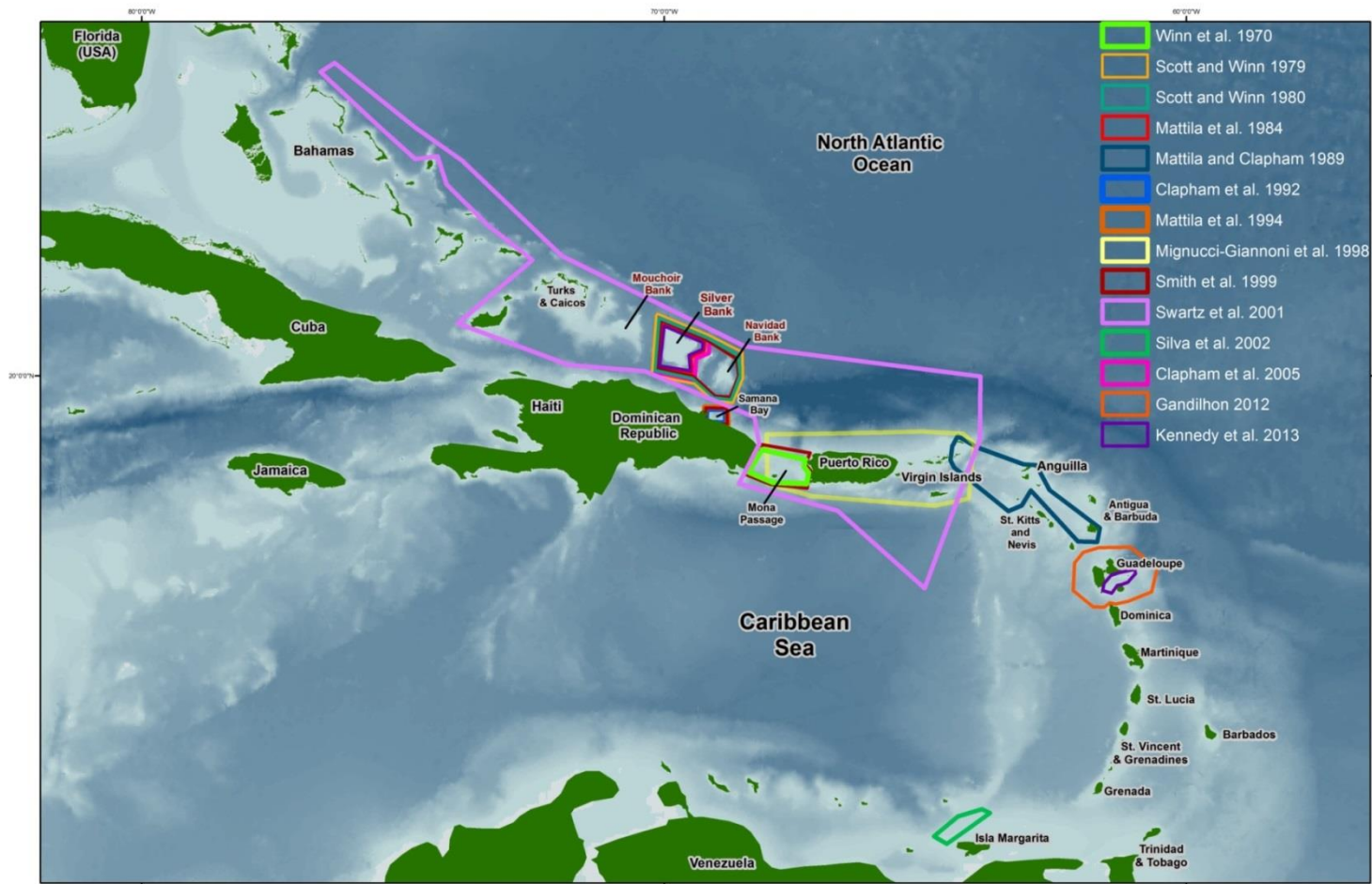


Figure 1.4: Rough outlines of small-scale, local humpback whale research projects carried out from the late 1960s to present day.

1.6 CONSERVATION

The first substantial conservation efforts aimed at protecting humpback whales in the West Indies occurred in the Dominican Republic. The critical importance of Silver, Navidad and Mouchoir Banks to marine mammals in the North Atlantic was reflected in the designation of the Silver and Navidad Banks Sanctuary in October of 1986. This was effectively the world's first national whale sanctuary and, as such, the designation represented a major global conservation milestone. The sanctuary was expanded on 5th July 1996 to include Mouchoir Bank, Navidad Bank, Samaná Bay and the waters in between.

In October of 2010, the French government established a marine sanctuary, named Agoa, which covers the waters surrounding the French territories in the Lesser Antilles (the territorial waters of St. Martin, St. Barthelemy, Guadeloupe and Martinique). These two sanctuaries, together with sanctuaries off Bermuda and Stellwagen Bank (Massachusetts, USA), are part of a larger "sister sanctuary" program designed to improve humpback whale conservation by encouraging collaboration between nations that host breeding, feeding and/or migrating humpback whales.

Since commercial whaling in the West Indies ceased in the late 1920's, there have been relatively few threats to humpback whales in this, their primary North Atlantic breeding range. Elsewhere in this ocean, major threats are entanglement in fishing gear and

collisions with ships (largely though not exclusively on the feeding grounds (Laist et al. 2001; Robbins & Mattila 2004; Johnson et al. 2005). In the breeding range itself, disturbance from eco-tourism and oil and gas exploration (notably off Venezuela) are the principal conservation concerns. Whale-watching in the Antilles began in the 1980s on Silver Bank and in Samaná Bay and by the mid-1990s had spread to the Turks and Caicos, Puerto Rico and a few locations in the Lesser Antilles (Hoyt & Hvenegaard, 2002). The Dominican government has passed regulations requiring permits for access to the Silver and Navidad Banks Sanctuary in an attempt to limit the human disturbance to humpback whales in their waters, but unregulated whale-watching throughout the Antillean breeding range is inevitable and likely to increase over time. Additionally, the growing oil and gas industry off the coast of Venezuela increases the potential for anthropomorphic disturbance and/or mortality of humpback whales overwintering there.

An example of the conservation efforts in the Dominican Republic occurred in 2005, when a group called Los Amigos de los Delfines conducted a cetacean survey of the waters off the Parque Nacional del Este (off the southeastern corner of the Dominican Republic). Whaley et al. (2008) observed a group of four humpback whales (including one calf) just off Saona Island; these were the first confirmed sightings of humpback whales off the southern coast of the Dominican Republic since the early 1980s (opportunistic sightings, Oswaldo Vasquez, pers comm). The authors observed the

group of whales in the same area for two weeks and collected detailed information on the whales' behavior in the presence of tourist vessels that continually approached them, often in a manner which likely constituted harassment. The authors' efforts in detailing the harassment of this small group of animals prompted the government of the Dominican Republic to facilitate the creation of a training program and associated "Guide to Good Practices for the Conservation of Marine Mammals". The need for effective conservation efforts was underscored by a recent passive acoustics study (2008), conducted by the National Marine Mammal Laboratory and the Bioacoustics Research Program at Cornell University, which found that humpback whales in Samaná Bay altered their song production in the presence of vessel noise (Berchok et al. 2009). While adherence is not yet mandatory, the government strongly encourages all mariners within the Dominican Republic to adopt the actions outlined in the Guide.

Understanding the fine-scale spatial and temporal distribution and behavior of animals within regions of high exposure to anthropomorphic threats is essential for conservation and management of humpback whales world-wide. Kennedy et al. (in press) used satellite telemetry to show that current marine mammal sanctuary boundaries cover less than 50% of the overall habitat used by humpback whales tagged in the breeding ground, demonstrating that efforts aimed at the conservation and management of this species need to occur on an ocean-basin-wide level. A management plan for the Silver Bank marine mammal sanctuary was recently finalized and represents major step

forward in further protecting all species which depend upon the waters of the Dominican Republic.

1.7 SUMMARY

The evolution of humpback whale research methods and knowledge in Antillean waters is largely representative of studies of this species elsewhere in the world (for example, Darling & McSweeney 1985; Baker et al. 1994; Helweg et al. 1998; Stevick et al. 2004; Robbins & Mattila 2006; Barlow et al. 2011 and many others). Much has been learned about humpback whales in the wider Caribbean region since the first research conducted there almost half a century ago. Today, we have a reasonably good picture of the occurrence and distribution of the species in much of the West Indies, which clearly represents the principal mating and calving ground for North Atlantic humpback whales. There have been numerous photo-ID matches between the West Indies and the feeding grounds of the Gulf of Maine, eastern Canada and West Greenland, which strongly suggests that the Antilles represents the breeding range for the great majority of whales from the western North Atlantic. Eastern North Atlantic whales have also been identified in the West Indies, yet the proportion of that population that migrates to this breeding ground remains unclear. Genetic data suggest the existence of one or more other breeding grounds for whales that feed off Iceland and Norway, although the location(s) of these wintering areas is unknown.

There is no doubt that the Silver, Navidad and Mouchoir Bank complex hosts the single-largest concentration of humpbacks in the Antilles, with large numbers of animals aggregating there during the peak of the winter in February and March. To the east and south, the densities of whales are one or two orders of magnitude lower, and the apparent failure of humpbacks to repopulate the Windward Islands region to levels suggested by historical whaling catches is difficult to explain given the general resilience of this species elsewhere in the world.

While conservation efforts within marine sanctuaries contribute greatly to safe-guarding the North Atlantic humpback whale population, increased multi-national collaboration is needed to protect this endangered species throughout its entire life-cycle. The application of advanced satellite telemetry, genetic, and acoustic technology to systematic humpback research in the North Atlantic needs to be a major component of future habitat management plans range-wide. In addition, increased research in understudied areas (notably Haiti, Bermuda, the Bahamas, Turks and Caicos, and Venezuelan coastal waters) is needed to better understand the distribution, abundance, and population structure of the humpback whales throughout the North Atlantic Ocean.

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CHAPTER 2:

Local and migratory movements of humpback whales satellite-tracked in the North Atlantic Ocean.

ABSTRACT

North Atlantic humpback whales (*Megaptera novaeangliae*) migrate from high-latitude summer feeding grounds to low-latitude winter breeding grounds along the Antillean Island chain. In the winters and springs of 2008 through 2012, satellite tags were deployed on humpback whales on Silver Bank (Dominican Republic) and off Guadeloupe (French West Indies). Whales were monitored for an average of 26 days (range = 4-90 days). Some animals remained near their tagging location for multiple days before beginning their northerly migration, yet some visited habitats along the northwestern coast of the Dominican Republic, northern Haiti, the Turks and Caicos islands, and off Anguilla. Individuals monitored during migration headed towards feeding grounds in the Gulf of Maine (USA), Canada, and the eastern North Atlantic (Iceland or Norway). One individual travelled near Bermuda during the migration. This study provides the first detailed description of routes used by North Atlantic humpback whales towards multiple feeding destinations. Additionally, it corroborates previous research showing that individuals from multiple feeding grounds migrate to the Antilles for the breeding season. This study indicates that North Atlantic humpbacks use an area broader than

the existing boundaries of marine mammal sanctuaries, which should provide justification for their expansion.

2.2 INTRODUCTION

Humpback whales (*Megaptera novaeangliae*) (Borowski, 1781) travel thousands of kilometers between high-latitude summer feeding areas and low-latitude winter breeding grounds annually (Dawbin 1966; Clapham and Mead 1999). Each winter, North Atlantic humpbacks congregate to mate and calve on the shallow banks that buffer the Antillean island chain, from Hispaniola to the Caribbean coast of Venezuela (Winn et al. 1975; Whitehead and Moore 1982; Mattila and Clapham 1989; Mattila et al. 1989; Katona and Beard 1990; Smith et al. 1999; Acevedo et al. 2008). They then migrate to geographically distinct feeding grounds in the Gulf of Maine, Canada (waters off Newfoundland and Labrador, St. Pierre et Miquelon, and in the Gulf of St. Lawrence), West Greenland, Iceland, and the Barents Sea, where they forage from spring through autumn (IWC 2002; Stevick et al. 2006). Each of these feeding grounds are separated by hundreds or thousands of kilometers, and are characterized by high maternally-directed site fidelity with very little interchange between aggregations (Clapham 1993; Clapham et al. 1993; Palsbøll et al. 1995; IWC 2002; Stevick et al. 2006; Weinrich et al. 2006; Robbins 2007). Studies have shown that migratory timing and speed are heavily influenced by sex, age, reproductive status and feeding ground preference (Chittleborough 1965; Dawbin 1966; Brown and Corkeron 1995; Brown et al. 1995; Stevick et al. 2003; Weinrich et al. 2006; Noad and Cato 2007); however, these studies

were too broad to describe individual, fine-scale migratory variation or to predict the effects of feeding ground origin or life history status on individual movements.

Whales from all high-latitude feeding aggregations have been observed in the Antilles (Clapham and Mattila 1988; Mattila et al. 1988; Katona and Beard 1990; Palsbøll et al. 1995; Stevick et al. 1998; Bérubé et al. 2004; Robbins et al. 2006), yet Stevick et al. (2003) found that whales from Iceland and Norway are underrepresented on Silver Bank. Additionally, analysis of mitochondrial and nuclear DNA shows evidence of at least one other North Atlantic humpback breeding area outside the Antilles (Palsbøll et al. 1995; Larsen et al. 1996), though its location has yet to be determined. Therefore, while photographic identification (photo-ID) and genetic studies support the theory that the western North Atlantic (Gulf of Maine and Canada) humpback whale population constitutes a single panmictic unit (Clapham et al. 1993; Larsen et al. 1996), there is still considerable uncertainty about the stock structure across the entire ocean basin.

The Silver-Navidad-Mouchoir Banks complex, off the northern coast of the Dominican Republic (DR), is arguably host one of the largest breeding aggregation of humpback whales in the world (Mattila et al. 1989; Smith et al. 1999). The importance of this aggregation led to the designation, by the DR, of the Silver and Navidad Banks Sanctuary in 1986. Due to the efficiency associated with working with such a high-density group of animals, many North Atlantic humpback photo-ID, genetic, and acoustic breeding ground studies have been conducted within the sanctuary region (Levenson and Leapley 1978; Winn and Winn 1978; Mattila et al. 1989; Palsbøll et al. 1995; Larsen 1996; Smith

et al. 1999; Stevick et al. 2003; Clapham et al. 2005). Most of these studies have focused primarily on identification of individuals and have yielded significant information about migratory destinations and, to a much lesser extent, insights into within season movement and habitat use (Whitehead and Moore 1982; Mattila et al. 1989; Mattila and Clapham 1989; Clapham et al. 1992; Smith et al. 1999; Swartz et al. 2002). Research effort along the eastern Antillean chain has been comparatively low, yet several studies have produced data describing the distribution and abundance of humpback whales in the French West Indies (Gandilhon 2012) and farther south (Winn et al. 1975; Balcomb and Nichols 1978; Swartz et al. 2002). In order to increase humpback whale protection and foster international research throughout the entire breeding range, a “sister sanctuary” to the Silver and Navidad Banks sanctuary, encompassing 59 square miles of ocean off the French West Indies (known as Agoa) was established in October 2010.

Despite the considerable research effort within the North Atlantic breeding range, there remain many gaps in our understanding of the patterns of individual humpback movements and habitat use along the Antillean chain. In the past decades, satellite telemetry has become a powerful tool when used on large whales to describe such fine-scale habitat use, migration routes and destination, and stock structure (Mate and Mesecar 1997; Baumgartner and Mate 2005; Heide-Jørgensen et al. 2006; Zerbini et al. 2006; Bailey et al. 2009). This technique is particularly useful when whales move into remote areas with low research effort, such as unstudied portions of the Lesser Antilles and near the Mid-Atlantic Ridge. To date, there have been no published studies that examine the extended, day-to-day movements of humpback whales within or beyond

easily accessible study sites. The purpose of this study was to investigate the hypothesis that humpback whales visit areas outside of well-studied, high-density areas within the breeding season. Additionally, we explored the theory that multiple migratory routes from breeding to feeding grounds are used and that those routes vary by individual. Finally, we sought to describe the fine-scale breeding ground habitat use within, and outside of, established marine mammal sanctuaries in order to inform policy for effective sanctuary management.

2.3 MATERIALS AND METHODS

2.3.1 Study areas:

Tagging took place on Silver Bank (21 °N, 69°W), 55 nautical miles to the northeast of Puerto Plata, DR, and off the southeastern coast of Guadeloupe (16 °N, 61 °W). All tagging was conducted within the Silver Bank or Agoa national marine sanctuaries. Silver Bank is a limestone platform reef system that, while still poorly charted, is estimated to have an area of approximately 2404 km² with an approximate mean depth of 30 m (Scott and Winn 1980). The shallow coral heads, notably in the dense barrier reef on the bank's northeastern perimeter, provide shelter from the strong trade winds that dominate the area. In Guadeloupe, the region between the southern coasts of the islands of Grande- and Basse-Terre, and Marie-Galante is also characterized by shallow, well-protected coastal waters that serve as a sanctuary from strong trade winds. Warm, sheltered waters like these appear to be preferred habitat for mating and calving humpback whales (Frankel et al. 1995; Clapham 1996; Craig and Herman 2000; Ersts and

Rosenbaum 2003). Tagging in areas of known abundance facilitates successful deployment by allowing field teams to select whales that are more approachable from a small boat, therefore increasing the chance of proper tag deployment.

2.3.2 Tagging methods:

Once located, whales were approached within a 3-10 m distance for tag deployment from the bow of a small (8-10 m), high-speed vessel capable of maneuvering safely around large whales. Satellite transmitters were placed on the dorsal portion of the body of the whales, near the dorsal fin, using an 8 m-long carbon fiber pole (also known as the Villum pole) in 2008 (Heide-Jørgensen et al. 2006; Zerbini et al. 2006, 2011), and then with the Air Rocket Transmitter System (ARTS), a modified marine safety pneumatic line thrower (Heide-Jørgensen et al. 2001), in all subsequent years. Whales were tagged with the implantable configuration of the SPOT 5 transmitters produced by Wildlife Computers (Redmond, WA). The tags were designed to penetrate into the dorsal surface of the whale, beneath the skin and hypodermis, and anchor within the fascia that lies between the muscle and blubber. Retention of the tag was maintained through actively sprung plates, and/or a circle of passively deployed “petals”. All external components of the tag are built from stainless steel and the tags were sterilized prior to deployment. Most tags were duty cycled to transmit for 6 h during the daytime and 6 h during the nighttime for the first three months after deployment, and then every other day (with the same 6 h on/6 h off pattern) until the end of transmission to preserve battery life. Tags F, H, I, J and K were duty cycled to transmit every other day

from the date of deployment with the same 6 h on/6 h off pattern on during transmission days. All attempts were made to place the tag just forward of the dorsal fin on either side of the dorsal hump (Figure 2.1, right) of the whale in order to facilitate frequent satellite exposure during a duty cycle and to extend the attachment duration.



Figure 2.1: A tag being deployed using the Villum pole (left), and an Air Rocket Transmitter System (ARTS) deployed tag (right).

High-quality identification photos were obtained of the tagged animals pre- and post-deployment whenever possible. Fluke and/or dorsal fin photographs were then compared to the Gulf of Maine Humpback Whale Catalog (curated by the Provincetown Center for Coastal Studies in Provincetown, MA) for insight into the high-latitude origin and life history of tagged whales.

2.3.3 Data processing

Observed locations were calculated by Argos from Doppler-shift data when multiple messages were received during a satellite's passage overhead. The speed-distance-

angle (SDA) Argos filter (Freitas et al. 2008) was applied to all good-quality (B, A, 0, 1, 2, 3) Argos-observed locations in R software (R Development Core Team 2011) in order to remove locations that implied unlikely deviations from the track as well as unrealistic travel speeds. A Bayesian switching state space model (SSSM) (Jonsen et al. 2007) was then applied to the data to estimate positions and behavioral modes. A time-step of 12 hours was selected in order to minimize the number of positions estimated during periods when the tag was not transmitting due to the 6h on/off duty cycle. The estimation procedure applied to the data is presented in more detail in Jonsen et al. (2005, 2006).

A whale was determined to be migrating when it crossed the shelf break and began travelling northward over deep water without returning to the shallow shelf waters. Discrete behavioral modes were quantified by incorporating an index based on mean turning angle and speed/direction autocorrelation parameters into the first-difference correlated random walk model within the SSSM (Jonsen et al. 2005, 2006). Estimated behavioral modes consist of continuous variables between 1 and 2, where behavioral mode 1 (1-1.25) assumes a low turning angle and speed/direction variability and is classified as transit behavior, and behavioral mode 2 (1.75-2) corresponds to higher turning angles and speed/direction variability and is classified as area-restricted search (ARS). Behavior mode values falling between 1.25 and 1.75 were considered unknown (*i.e.* unclassified).

2.4 RESULTS

Seventeen satellite tags were deployed on Silver Bank and 11 were deployed off Guadeloupe at various times during the months of January, April and May during the period 2008 through 2012. Of those 28 tags, 6 failed to transmit entirely and 3 tags did not begin transmitting until 8, 33, and 63 days post deployment, when the animals concerned were already migrating north. The remaining 22 tags transmitted for an average of 26 days (range = 4 to 90 days) and recorded minimum travel distances between 119.8 km and 6960.1 km (Table 2.1). Fourteen tagged animals were migrating north when transmissions ceased. Eleven of those whales spent varying amounts of time on the breeding ground near the tagging location before beginning their northward migration (Figures 2.2 and 2.4). Whales tagged within the same competitive group (a group of whales displaying intra-sexual competition by males for access to a nuclear female; Clapham et al. 1992), did not migrate together.

An average speed of 1.7 ± 0.8 km/h was recorded in the breeding grounds, and average speeds of 4.3 ± 1.2 km/h occurred during migration. Overall, the speed of animals migrating toward the eastern North Atlantic (either Iceland or Norway) (4.5 ± 1.2 km/h) was only slightly, though not significantly, higher (Welch two sample *t*-test, $p=0.451$) than whales travelling toward the Gulf of Maine or Canada (4.0 ± 1.2 km/h). Additionally, the migration speeds of whales that had a calf at the time of deployment (3.9 ± 0.8 km/h), were only slightly lower than those of whales migrating without a calf (4.9 ± 1.5 km/h) (Welch two sample *t*-test, $p=0.222$). During migration, the vast majority

of behavioral mode classifications from the SSSM were considered transiting or unclassified, though there were six individual positions (from three whales) that were classified as ARS (Figure 2.3).

Two tagged whales were identified through comparison of dorsal fin and/or fluke photographs to the Gulf of Maine Humpback Whale Catalog (Provincetown Center for Coastal Studies, www.coastalstudies.org). Whale F, a male named "Tilt", was first seen in the Gulf of Maine in 1997 and in every subsequent year through 2012; he was at least 13 years old at the time of tagging. Whale G, a female named "Vertex", was recorded in the Gulf of Maine as a calf in 1995 and was also seen yearly through 2012; she was 14 years old when tagged.

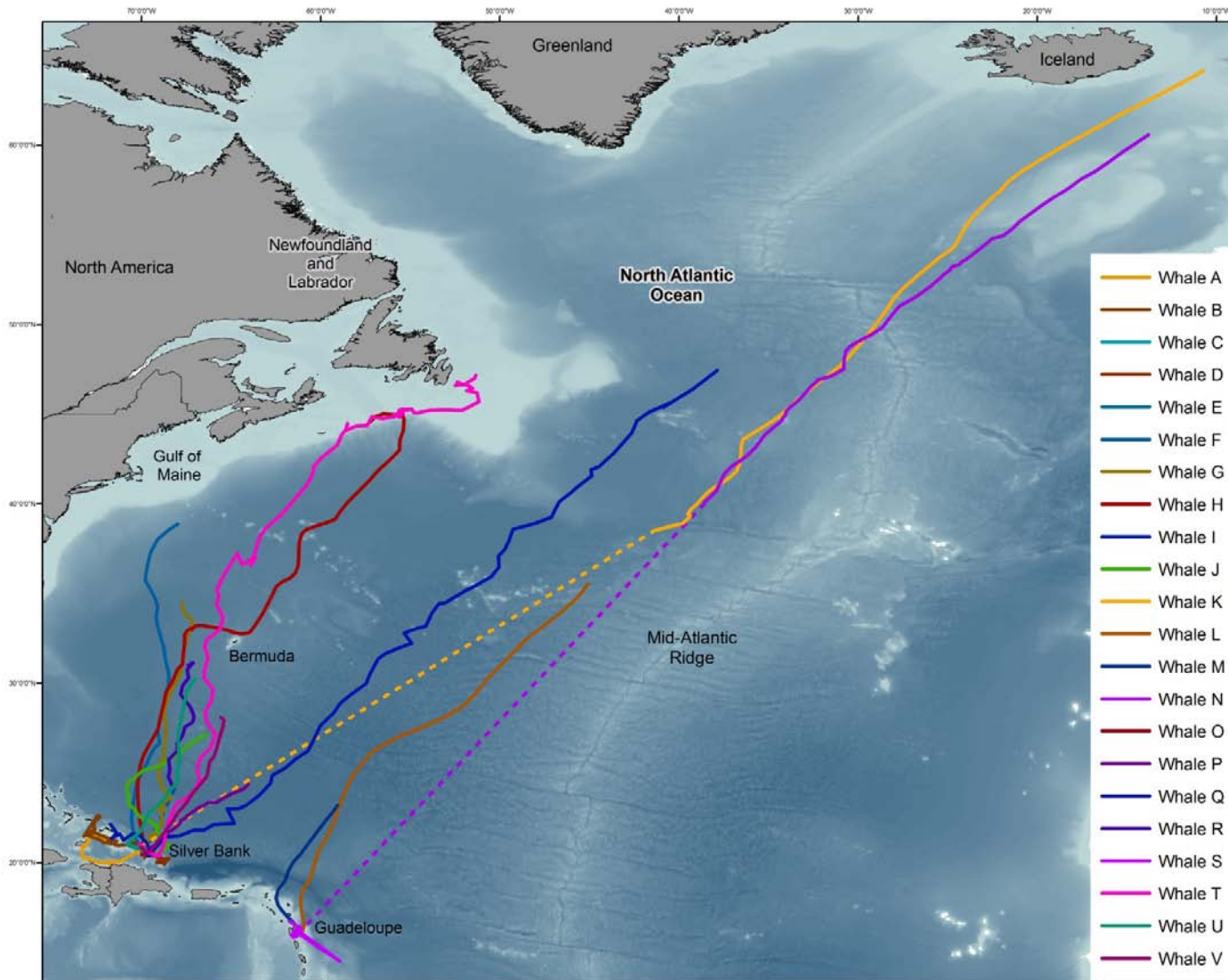


Figure 2.2: Tracks of all 22 tracked humpback whales (*Megaptera novaeangliae*). Track locations were estimated at 12 hour intervals using a Bayesian switching state-space model (SSM). Dashed lines indicate distance between tagging location and first transmission.

Table 2.1: Satellite telemetry results. All results are based on switching state-space model (SSSM) positions estimated every 12 hours. Tagging location: GUAD=Guadeloupe, SB=Silver Bank. The term “challenger” refers to a presumed male occupying a prominent role in the assemblages known as “competitive groups”, which consist primarily of males competing for females. The term “duo” refers to a pair of adult whales with no calf. The term “escort” refers to an adult whale accompanying a mother and calf (Clapham et al. 1992).

Whale	PTT#	Group Type	Tag loc.	Tag date	Longevity (days)	Est. travel dist. (km)	Total est. speed (km/h)	Departure date	Est. migratory speed (km/h)	Est. breeding grnd speed (km/h)
A	81122	Mother-calf	SB	1/29/2008	13	858.3	2.8	--	--	2.8
B	81123	Duo	SB	1/29/2008	17	1221.3	3.0	--	--	3.0
C	81124	Mother-calf	SB	1/29/2008	5	119.8	0.6	--	--	1.2
D	81125	unknown	SB	1/30/2008	22	888.6	1.7	--	--	1.7
E	81126	Duo	SB	1/31/2008	9	249.4	1.3	--	--	1.0
F	87631	Male	SB	4/6/2009	22	2217.2	4.2	4/11/2009	5.2	0.7
G	87760	Mother-calf	SB	4/6/2009	30	2000.6	2.8	4/17/2009	4.0	0.6
H	87632	Mother-calf	SB	4/8/2009	37	3605.1	4.1	4/9/2013	4.2	--
I	87634	Mother-calf	SB	4/8/2009	10	446.1	1.9	--	--	1.9
J	87633	Mother-calf	SB	4/10/2009	27	1314.2	2.0	--	2.3	1.2
K	87635	Mother-calf	SB	4/20/2009	64	6960.1	4.5	--	4.7	--
L	96405	Mother-calf	GUAD	5/6/2010	38	2859.0	3.1	5/9/2010	3.2	2.2
M	87777	Mother-calf	GUAD	4/30/2010	10	939.0	3.9	5/4/2010	5.1	2.2
N	87781	Mother-calf	GUAD	5/2/2010	90	6360.6	2.9	--	4.3	--
O	84484	Mother-calf	SB	4/3/2011	5	130.1	1.4	--	--	1.4
P	84487	Mother-calf	SB	4/3/2011	15	894.3	2.7	4/9/2011	3.5	1.2
Q	87636	Escort	SB	4/3/2011	36	4794.0	6.1	4/9/2011	6.5	1.5
R	84482	Mother-calf	SB	4/4/2011	18	1357.4	3.1	--	3.7	--
S	84488	Duo	GUAD	4/12/2011	12	1037.5	3.9	--	--	3.9
T	87765	Challenger	SB	4/2/2012	58	5010.2	3.6	4/12/2012	5.5	1.4
U	88726	Challenger	SB	4/2/2012	16	1310.0	3.4	4/7/2012	5.0	1.3
V	87624	Challenger	SB	4/2/2012	20	1028.2	2.1	4/6/2012	2.4	1.2
Average					26	2072.8	3.0		4.3	1.7
SD						1.2			1.2	0.8

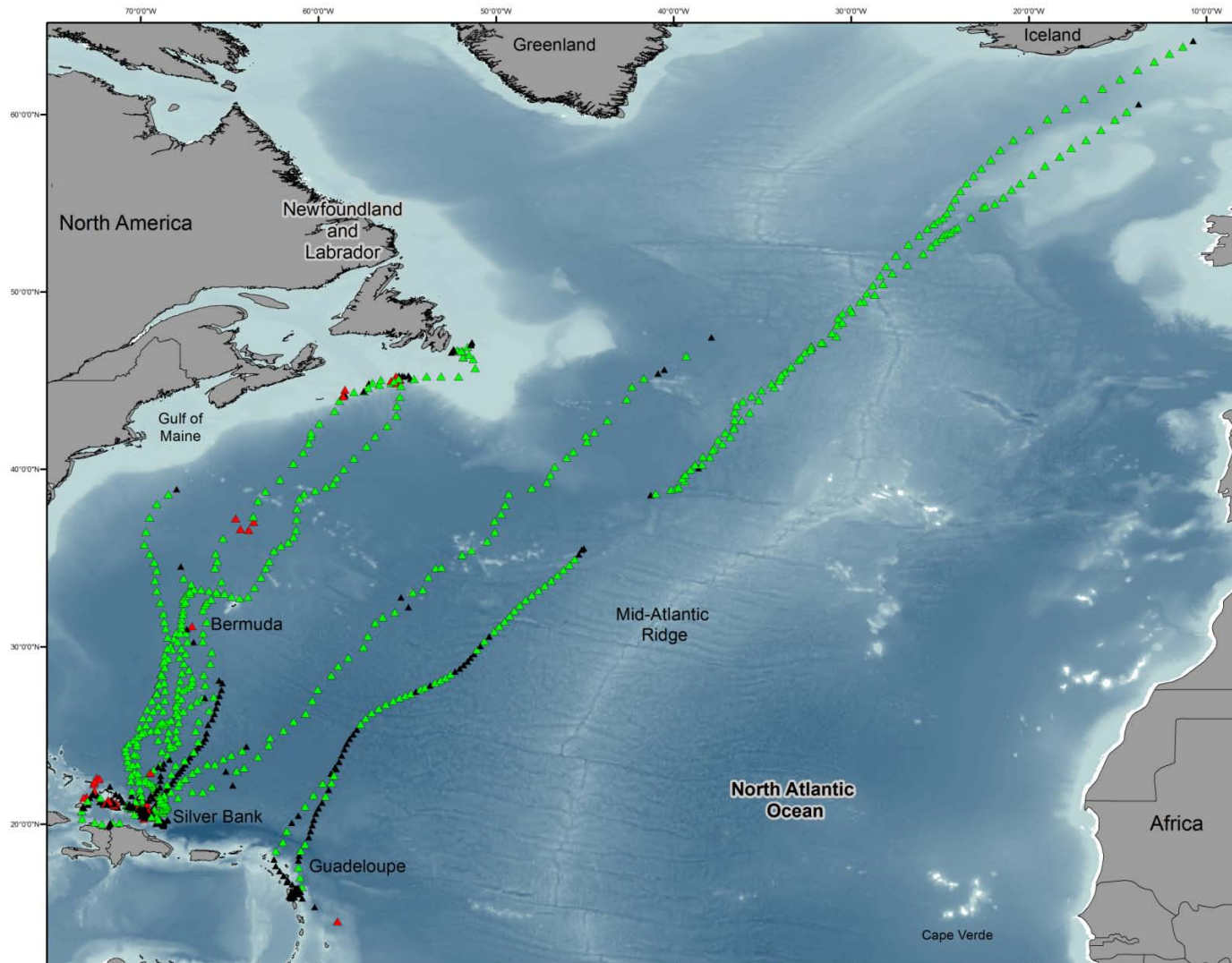


Figure 2.3: Behavioral mode estimates from all tracked whales. Locations and behavioral modes were estimated at 12 hour intervals using a Bayesian switching state-space model (SSSM). Green diamonds = “Transit” (Behavioral Mode 1), Red diamonds = “area-restricted search” (ARS; Behavioral Mode 2), and Black diamonds = unclassified behavior.

2.4.1 Breeding ground movement

Eight whales (A, B, C, D, E, I, O, S) remained in their low-latitude breeding grounds for the duration of tag transmission (Figures 2.1, 2.4 and 2.5). This is likely the result of Whales A-E being tagged significantly earlier in the breeding season than all other whales, and the short tag-duration (5-12 days) of whales I, O and S. No tagged whales traveled into the Caribbean Sea. Only one animal (A) travelled south from the Silver-Navidad-Mouchoir Banks complex to within 30 km of the coast of northwestern DR, then swam along the entire northwestern coast of Haiti. Whale A then travelled north to Great Inagua Island and the southern edge of Caicos Bank. Only whales A, B and I visited Caicos Bank and the coasts of the Turks and Caicos Islands (Figure 2.4). Four whales (B, C, D and U) swam from Silver Bank west to the adjacent Mouchoir Bank, while only Whales D and V travelled east to Navidad Bank, the third bank in the complex (Figure 2.4). Whale D is the only animal to have visited Silver, Navidad and Mouchoir Banks. Of the tagged whales that spent five or more days in the breeding ground, an average of 82% of non-migratory time fell within the Silver and Navidad Banks Sanctuary. However, the overall percentage of time spent within any protected waters was only 44.1% for the full duration of all tags (Figure 2.4).

In Guadeloupe, Whale M initially travelled northwest along the eastern side of Guadeloupe, then traveled to the western side of St. John's (Antigua and Barbuda) before gradually angling north to pass over the Tintamarre Spur and begin migrating (Figure 2.5). Whale L began heading north soon after tagging, yet angled slightly east towards Antigua Valley before exiting the shelf break (Figure 2.5). Whale S swam

rapidly offshore immediately after tagging, crossed the shelf break, and then returned to within 25 km of the tagging position three days later. Whale S then stayed on Colombie Bank (between Marie-Galante Island and southwestern Basse-Terre) for five days; it then moved towards La Desirade and Guadeloupe Passage before migrating (Figure 2.5).

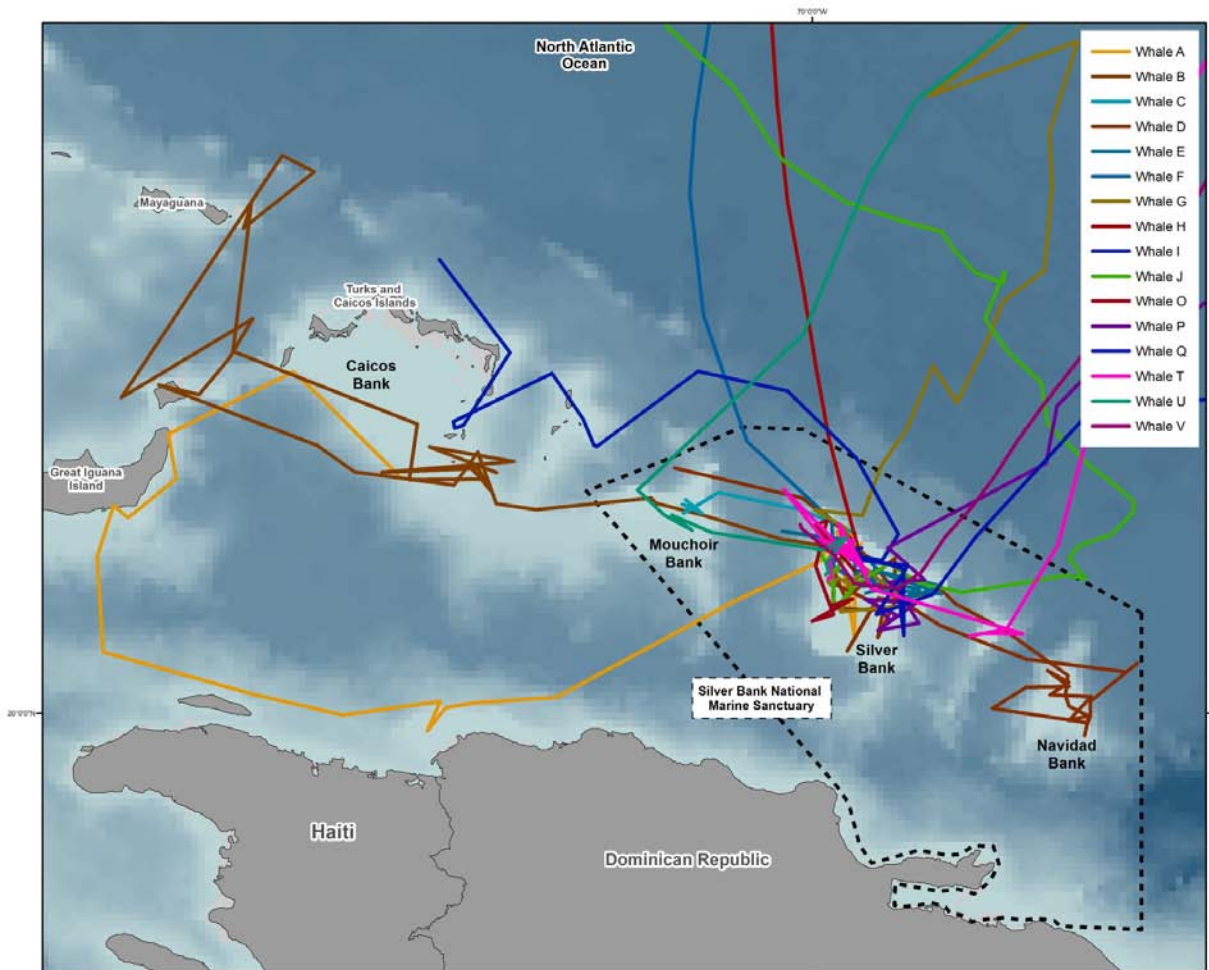


Figure 2.4: Habitat use within the Silver and Navidad Banks Sanctuary (SNBMMS) breeding ground and surrounding waters.

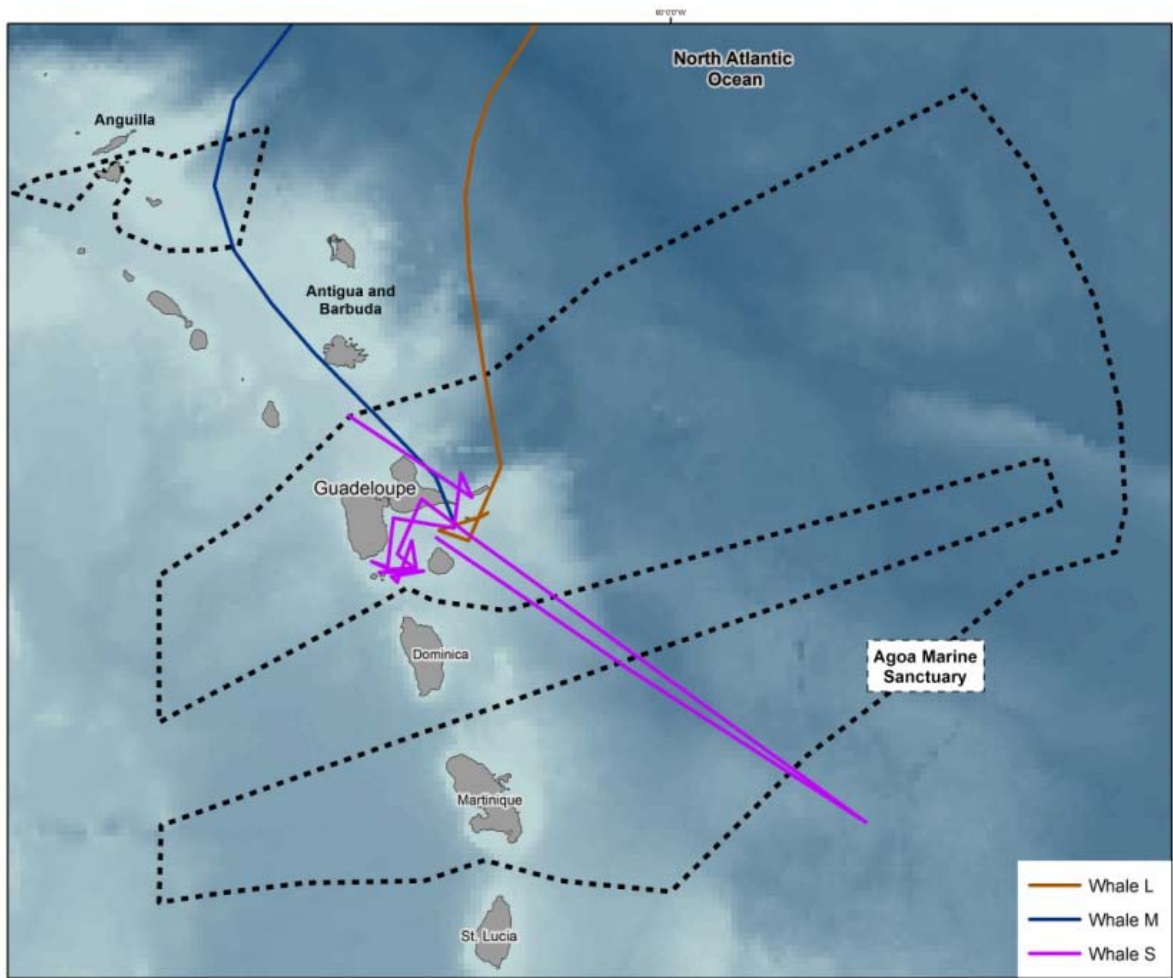


Figure 2.5: Habitat use within the Agoa Marine Sanctuary breeding ground and surrounding waters.

2.4.2 Migratory movement

The animals that appeared to be headed toward the Gulf of Maine or Canada (F, G, H, J, T, U, and V) (Figure 2.2) all travelled within 500 km (longitudinally) of each other until approximately 33°N (*i.e.* the latitude of Bermuda), where they began to spread out and angle more directly toward their presumed feeding ground. Two whales (H and T) were tracked from Silver Bank to the Scotian Shelf, representing the first documented complete humpback whale migration routes in the North Atlantic (Figure 2.2). Whale H first reached the shelf break at St. Pierre Bank and immediately turned southwest to follow the shelf break to the eastern edge of Cabot Strait, yet did not exhibit ARS along the shelf edge. Whale T travelled from SB to the Nova Scotia shelf break at the eastern edge of the canyon known as “the Gully”, and then turned abruptly to follow the shelf break towards the Grand Bank of Newfoundland, presumably to forage. Whale T exhibited ARS on Banquereau and St. Pierre Banks, both known foraging grounds, before transmissions ceased. Whale T recorded four ARS-classified positions at approximately 200 km south of the Kelvin Seamount (Figure 2.3).

Six whales (K, L, M, N, P, and Q) (Figure 2.2) were heading toward the eastern North Atlantic when transmissions ceased. Whale Q traveled towards the Norwegian Sea, yet transmissions stopped just north of the Newfoundland Basin. Whale K did not begin transmitting until it reached the southeastern corner of the Newfoundland Basin, yet the tag transmitted for 31 days until the whale was approximately 167 km off the eastern coast of Iceland. Whale N (tagged in Guadeloupe) had a similar pattern, with

transmissions beginning at the southeastern edge of the Newfoundland Basin and continuing for 28 days until transmissions ceased northeast of the Rockall Rise (Figure 2.2). Whales P (SB) and M (GUAD) both stopped transmitting about 800 km into their northeast migration, and Whale L was just east of the Sohm Plain when transmissions ceased.

The only tagged whale from this study to visit the island of Bermuda (Whale H and calf), showed a nearly 90-degree easterly course change at approximately 250 km abeam of Bermuda that took her to the northeastern corner of the island in three days (Figure. 2.2). Once directly north of Bermuda (at the Bowditch Seamount), she turned sharply NNE and continued her migration on approximately the same heading she had travelled before she diverted to Bermuda.

2.5 DISCUSSION

2.5.1 Breeding ground movement

Our results further confirm that the shallow reef system along the North Atlantic side of the Antillean Chain represents an important habitat for humpback whales, and that whales from several high-latitude feeding grounds congregate in this area to breed each year; this is consistent with previous photo-ID work (Mattila and Clapham 1989; Mattila et al. 1989; Katona and Beard 1990; Clapham et al. 1992; Smith et al. 1999; Bérubé et al. 2004; Robbins et al. 2006). The average speed within the Antillean breeding ground ($1.89 \pm .77$ km/h) calculated here was found to be consistent with Hawaiian mean wintering speeds of 2 km/h (females with calves) and 1.2 ± 0.8 km/h in Mexico (Glockner and Venus 1983; Tyack and Whitehead 1983; Mate et al. 1998; Lagerquist et al. 2008). No North Atlantic breeding ground speeds had been reported prior to this study.

Our results show local travel to areas that are relatively distant from the most densely populated and well-studied breeding aggregations, and suggest that the frequency and extent of inter-island movement may have been underestimated in the past. Previous photographic matches between Silver Bank and Puerto Rico, Anguilla and Virgin Bank (Mattila et al. 1988; Mattila and Clapham 1989) have indicated that some inter-island movement within the breeding range does occur, yet the use of waters off Haiti, Caicos Bank, Caicos Passage, Great Inagua Island, and Antigua and Barbuda shown here had not been previously described (in part because of low or no sighting effort in these

areas). As heterogeneity in occupancy patterns affects capture probability during capture-recapture studies and may bias population estimates (Hammond et al. 1990; Friday 1997; Punt et al. 2007), the scope of within-season movements in the Antilles warrants further investigation.

Whales spent an average of 18% of their time outside the Silver and Navidad Banks Sanctuary boundaries before beginning their northward migration. In order to cover all non-migratory movement of the whales tagged in Silver Bank, the sanctuary would need to expand to approximately three times its current area and include territorial waters off the Bahamas, Turks and Caicos and Haiti. The Dominican government has passed regulations requiring permits for access to the sanctuary in an attempt to limit the human disturbance to humpback whales in their waters, but unregulated vessel traffic throughout the Antillean breeding range is inevitable and likely to increase over time. The evidence of substantial within-season movements shown here highlights the need for multi-national humpback habitat management initiatives that would cover the entire range of this endangered species.

2.5.2 Migratory movement

This study confirms the findings of Reeves et al. (2004), who examined 19th century North Atlantic whaling logbook data and found what appeared to be diffuse humpback whale dispersion across the North Atlantic Ocean over several months of the migratory period. However, while the migrations documented in this study were spatially and temporally diffuse, there were some noticeable movement patterns. Animals migrating

towards the eastern North Atlantic feeding grounds (Iceland and Norway) travelled on a fairly direct and consistent course of roughly 35°, while those traveling towards the Gulf of Maine or Canada exhibited a general heading of approximately 20° until they neared Bermuda. Additionally, Whales K and N were heading toward the eastern North Atlantic and showed ≈1,300 km of nearly identical track lines, followed by an additional 1,600 km of track with nearly identical heading (separated by roughly 200 km), despite having been tagged in two separated locations (Guadeloupe and Silver Bank) in different years (Figure 2.2). Whales L (Guadeloupe) and P (Silver Bank) also appeared to be heading for similar tracks as K and N (Figure 2.2), despite the spatial and temporal separation. This overlap supports the idea that migratory corridors for whales feeding in the eastern North Atlantic may exist (Charif et al. 2001), or that migrations are governed by the same navigational cues (Horton et al. 2011).

Historically, humpbacks observed and/or killed by 19th century whaling vessels were occasionally documented along the western margins of the Mid-Atlantic Ridge from June through August, prompting speculation of a feeding aggregation in pelagic waters well south of their current known range (Reeves et al. 2004). However, while the telemetry data cannot entirely rule out feeding while travelling, no animals from this study exhibited area-restricted search (ARS) (which generally characterizes foraging; Kareiva and Odell 1987; Mayo and Marx 1990) near the margins of the Mid-Atlantic Ridge. Overall, only six individual points from three migrating whales were categorized as ARS (Figure 2.3), and the general lack of pronounced meandering movement patterns during migration suggest that no typical feeding aggregations occur along the western

margin of the Mid-Atlantic Ridge. Furthermore, humpbacks have been seen in the Antilles as late as June (Reeves et al. 2001; Gandilhon 2012); if they began their migration the eastern North Atlantic in mid-June, they would be over the Corner Rise seamounts around the beginning of July. This is consistent with historical sightings (Reeves et al. 2004), and indicates that humpbacks seen well south of known coastal feeding aggregations during summer months could easily have been late migrants still on their northbound migration, rather than being part of a separate feeding aggregation.

Whale T was the only whale to exhibit more than one position classified as ARS during migration, spending two days presumably foraging about 200 km south of the Kelvin Seamount (Figure 2.3). Humpbacks have been known to visit seamounts during the breeding season (Garrigue et al. 2010) and during periods of peak oceanographic productivity (Mate et al. 2007), yet the scope of seamount habitat use is largely unknown. Virtually no humpback research effort exists for this area of the North Atlantic, and the frequency and purpose of ARS on the New England Seamounts warrants further investigation.

Humpbacks from all major feeding aggregations, including Iceland, are consistently seen near Bermuda from February to May during the northward (but not the southward) migration (Stone et al. 1984, 1987; Reeves et al. 2006), yet none of the eastern North Atlantic whales tagged in this study travelled toward Bermuda. Given our findings of consistent linear travel toward the eastern North Atlantic from the start of migration, it

is plausible that decisions about specific migratory movements (including travel to Bermuda) may be made on or before breeding ground departure and may be influenced by age, sex, and/or reproductive state. Opportunistic feeding has been hypothesized (Stone et al. 1984) in Bermuda waters, yet the habitat use of humpbacks visiting this region is largely unknown. Whale H made a nearly 90° course change to the east during her northward migration before making an equally abrupt course change to the north after reaching the Bowditch Seamount, yet no ARS was observed during this diversion. The lack of evidence for foraging behavior (*i.e.* lack of ARS) by Whale H may indicate an absence of prey, or that humpbacks visit Bermuda for navigational, mating, or other unknown purposes. However, our sample size is small and existing information does not permit further speculation about the scope of use of Bermudan waters. As a populated offshore island in a migratory path, Bermuda provides a unique opportunity to study the behavior of migrating humpback whales in mid-ocean, and further research there would potentially be very useful to our understanding of the ecology of this species.

Telemetry from this study shows an overall average minimum speed during migration of 4.21 ± 1.3 km/h, yet humpbacks travelling toward the eastern North Atlantic were slightly faster than those heading toward Gulf of Maine or Canada (4.67 ± 1.5 km/h vs. 3.87 ± 1.1 km/h). These results fall within the range of speeds of tagged humpbacks migrating from Mexico (4 km/h) (Lagerquist et al. 2008), Hawaii (4.5 km/h) (Mate et al. 1998) and Brazil (3.83 km/h and 3.48 km/h) (Zerbini et al. 2006, 2011), but are slower than migrating gray whales (mean=6.5 km/h)(Mate et al. 2011a) and southern right

whales (4.4 to 6.5 km/h)(Mate et al. 2011*b*). Previous photo-ID mark-recapture studies in the Gulf of Maine have documented migration rates of 34 days (male), 43 days (male) (Clapham and Mattila 1988) and 41 days (mother and calf) (Robbins 2007), yet these estimated speeds are likely low due to poor coverage of departure and arrival points. The two complete migrations between Silver Bank and the Scotian Shelf recorded here took 34 days (Whale H and calf) and 24 days (Whale T), and are the fastest mother-calf and non-calf adult migrations recorded for the North Atlantic population. Furthermore, since we know that Whale F (“Tilt”) and G (“Vertex”) exhibit strong site-fidelity to the Gulf of Maine, we can extrapolate their track and speed to the Georges Bank shelf break and predict an overall migration time of 19 days for Tilt and 26 days for Vertex and calf, which would be much faster than any previously reported migration durations (Clapham and Mattila 1988; Gabriele 1996; Robbins 2007; Lagerquist et al. 2008; Zerbini et al. 2011).

Historical whaling records (Ingebrigtsen 1929) suggest a scenario in which eastern North Atlantic whales begin their feeding season off Jan Mayen, and move in a clockwise direction to Bear Island and Finnmark as the summer progresses. At the speeds we observed, it would have taken Whales K and N at least 68 and 71 days (respectively) to reach Jan Mayen from their tagging location. Thus, an eastern North Atlantic whale would need at least five months just to transit between breeding and feeding grounds each year. If this is correct, it is plausible that the energetic and time requirements for a full eastern North Atlantic migration, particularly for a nursing mother, are high enough that it could not be completed each year. Late-summer mid-Atlantic sightings (Reeves

et al. 2004), documented singing and mating behavior in feeding grounds (Weinrich 1995; Clark and Clapham 2004; Vu et al. 2011), and recent telemetry showing some southward migration from Iceland beginning as late as February (Gisli Vikingsson, pers comm), could all be taken as evidence for the idea that the distance between Iceland or Norway and the Antilles forces individual eastern North Atlantic whales to choose between an incomplete southward migration, a truncated or off-peak breeding season, or a truncated or off-peak feeding season, annually. If we may extend this speculation a little farther, these decisions could result in fewer (and less diverse) breeding opportunities or a shorter feeding season unless eastern North Atlantic whales spatially and/or temporally extend their seasonal ranges. Extension of the breeding range, to include breeding while migrating or breeding on feeding grounds, could partially explain the genetic evidence for the existence of unknown breeding areas (Larsen 1996), as well as previous observations that not all feeding grounds are equally represented among whales in the North Atlantic breeding ground during peak abundance (Stevick et al. 2003).

While the above is inevitably speculative, it does highlight the substantial disparity - and presumably energetic consequences - that exists in the distances that humpback whales from different North Atlantic feeding grounds must travel on migration; for example, the difference is a factor of three for Norwegian whales compared to those from the Gulf of Maine. While it would be logistically challenging, tagging of humpback whales in Norwegian waters in late autumn to assess their winter movements and destinations would potentially provide data to address this interesting question

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CHAPTER 3:

Individual variation in movements of humpback whales satellite-tracked in the eastern Aleutian Islands and Bering Sea.

3.1 ABSTRACT

Humpback whales utilize the Aleutian Islands and Bering Sea as foraging grounds during summer months. Currently, the fine-scale movements of humpback whales within these feeding grounds are poorly understood. In the summers of 2007-2011, eight humpback whales were tracked with satellite tags deployed near Unalaska Bay. Individuals were tracked for an average of 28 days (range = 7-67 days). Three individuals remained within 50 km of their tagging locations for approximately 14 days, while 2 others explored areas near the northern shore of Unalaska Bay and Unimak Pass. Two whales moved west; one traveled to the Island of Four Mountains and returned to the northern side of Umnak Island, while the other moved through Umnak Pass and explored feeding areas on both sides of Umnak Island. Remarkably, one individual left Unalaska Bay soon after tagging and moved ~1500 km (in 12 days) along the outer Bering Sea shelf to the southern Chukotka Peninsula, Russia, then east across the Bering Sea basin to Navarin Canyon, where it remained until transmissions ceased. Most area-restricted search was limited to waters shallower than 1000 m, while movement into deeper water was often associated with travel behavior. Tagged animals preferred the Bering Sea shelf and slope to that of the North Pacific. Movement

patterns show individual variation, but are likely influenced by seasonal productivity. This study provides evidence that while humpbacks aggregate in well-known areas, individuals may perform remarkably long trips during the feeding season.

3.2 INTRODUCTION

The humpback whale (*Megaptera novaeangliae*) is a globally distributed, highly mobile species that typically undertakes long annual migrations between energy-rich, high-latitude summer feeding grounds and low-latitude winter breeding and calving grounds (Dawbin 1966, Clapham & Mead 1999). While humpbacks are arguably one of the most well-studied large whales in the world, habitat use and within-season movements are poorly understood range-wide, and particularly in remote, offshore regions like the Bering Sea. Most of our existing knowledge of North Pacific humpback whale distribution is the result of historical whaling data analysis together with modern photo-identification, genetic mark-recapture (Baker 1985, Darling & McSweeney 1985, Baker et al. 1987, 1990, Perry et al. 1990, Calambokidis et al. 2001), and line-transect studies (Moore et al. 2002, Zerbini et al. 2006a). A large-scale, ocean-basin-wide mark-recapture study, called Structure of Populations, Levels of Abundance and Status of Humpback Whales (SPLASH) was conducted between 2004 and 2006 and provides the most comprehensive data regarding the status of North Pacific humpback whales today (Calambokidis et al. 2008, Barlow et al. 2011); however, SPLASH and similar studies yield only coarse-scale distribution and abundance information and are limited by low spatial

and temporal effort. Here we present the first fine-scale humpback whale telemetry data collected from the eastern Aleutian Islands and Bering Sea feeding grounds.

Since predation by killer whales (*Orcinus orca*) on humpback whales in high-latitude feeding grounds is rare (Dolphin 1987, Mehta et al. 2007), the latter's distribution in the North Pacific is almost certainly driven by prey abundance. Humpbacks feed on discrete, variable patches of small fish or eupausiids (Nemoto 1957, 1962, Krieger & Wing 1984) in a nearly continuous arc from Russia to the western coast of the United States, within five loosely defined feeding areas: California and Oregon, Northern Washington and British Columbia, Southeast Alaska, Northern Gulf of Alaska, Aleutian Islands/Bering Sea, and waters off the Russian mainland and Commander Islands (Calambokidis et al. 2001, Fleming & Jackson 2011). Humpback distribution in the eastern Aleutian Islands/Bering Sea feeding grounds is thought to be related to proximity of the nearest passes, which are dominated by strong tidal currents and mixing (Reed & Stabeno 1994; Byrd et al. 2005, Sinclair et al. 2005). Eddies and fronts generated by water circulating through these passes create reliable prey aggregations between Unimak and Samalga Passes each year (Coyle 2005; Ladd et al. 2005a, b).

As in other well-studied humpback populations (Katona & Beard 1990, Baker et al. 1992, Clapham et al. 1993), maternally directed site fidelity is a key factor driving North Pacific feeding area selection (Witteveen et al. 2009, Baker et al. 1985, Darling & McSweeney 1985, Waite et al. 1999, Calambokidis et al. 1996, 2008, Riley 2010). A number of photo-identification and genetic mark-recapture studies have described some interchange

between eastern Aleutian Islands humpbacks and Kodiak (Alaska) whales, but there is very little documented interchange between the Aleutians and more southerly feeding stocks (Darling & McSweeney 1985, Baker et al. 1985, 1986, Calambokidis et al. 1996, 2008, Waite et al. 1999, Riley 2010). Due to low humpback survey effort throughout most of the Bering Sea (particularly offshore), there are insufficient data to say whether eastern Aleutian Island humpbacks can be considered a discrete feeding aggregation from the rest of the Bering Sea. However, scant existing data (Omura and Ohsumi 1964; this study) suggests that eastern Aleutian Island humpbacks also visit unstudied areas throughout the Bering Sea. The scope of this long-distance, within-season movement variation is currently unknown.

In the past decade, satellite telemetry studies have consistently yielded fine-scale individual movement data that cannot be obtained, or even predicted, through other methods (e.g., Mate et al. 1998, Heide-Jørgensen et al. 2006, Mate et al. 2007, Horton et al. 2011, Zerbini et al. 2011). For this descriptive study, we use data from satellite tags attached to humpback whales off Unalaska Island (in the eastern Aleutian Islands) during the summers of 2007 to 2011 to describe their fine-scale movement and foraging patterns in a North Pacific humpback whale feeding ground.

3.3 MATERIALS AND METHODS

3.3.1 Study area:

The eastern Aleutian Island region lies between Samalga Pass and Unimak Pass (between 54°20'N, 164°55'W and 53°46'N, 169°15'W) to the west of mainland Alaska

(Figure 3.1). Unimak Pass is the first major pass encountered by the westward-flowing Alaska Coastal Current (Royer et al. 1979, Ladd et al. 2005a) and is dominated by high water-flow and mixing. The resulting water property fronts, together with current, bathymetry, depth and slope, structure the nearby ecosystem to consistently concentrate prey in coastal waters of the eastern Aleutian Islands (Ladd et al. 2005a, 2005b). Aside from the relatively high density of humpbacks in that area, Unalaska Bay was the tagging site during all 5 summers of the study because of its protected waters and proximity to Dutch Harbor.

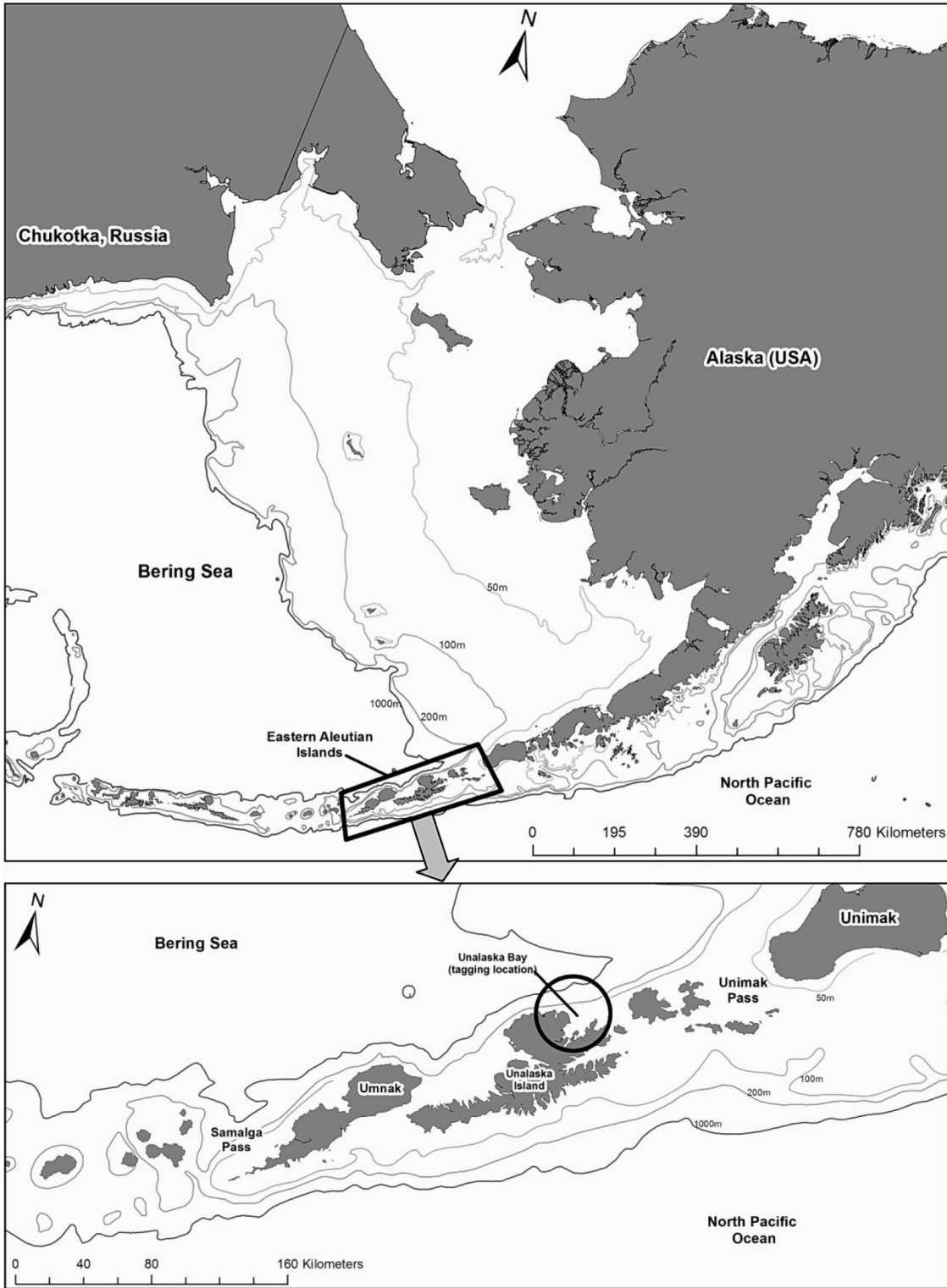


Figure 3.1: Location of eastern Aleutian Islands and Bering Sea study area.

3.3.2 Satellite telemetry and tagging:

Nine whales were tagged with the deep implantable configuration of the SPOT5 transmitter (Wildlife Computers, Redmond, WA, USA), and one whale (2009) was tagged with a Low Impact Minimally Percutaneous External-electronic Transmitter (LIMPET) tag (Andrews et al. 2008, Schorr et al. 2009). Deep implantable tags were attached to the blubber and fascia/muscle layer of the whale's body using a fiberglass pole (Heide-Jørgensen et al. 2003, Zerbini et al. 2006b) and/or a custom-modified pneumatic line thrower (the Air Rocket Transmitter System, ARTS, Heide-Jørgensen et al. 2001). The LIMPET tag was deployed using a compound crossbow. Tags were duty-cycled to transmit every day for 6 h during daytime and 6 h during nighttime for the first 3 months of transmission. After the first 3 months, the transmitters were programmed to transmit every other day, following the same duty-cycle, to conserve the battery life of the tag. Satellite tags were monitored by Argos Data Collection and Location Service receivers on NOAA TIROS-N weather satellites (Argos 1990), and locations were calculated by Argos, from Doppler-shift data when multiple messages were received during a satellite's passage overhead, using a standard least-squares filtering method. The Argos Filter (Freitas 2010) was then applied to all Argos observed locations in software R (R Core Team 2011) in order to remove locations that implied extreme, unlikely deviations from the track's path.

3.3.3 Switching state-space model (SSSM):

A Bayesian SSSM (Jonsen et al. 2007) was applied to all Argos Filtered data to estimate a position every 12 hours. The SSSM uses a first-difference correlated random walk (DCRW) model (Jonsen et al. 2005) to simulate the whale's movement process and assumes a correlated random walk on the differences between locations. The model was fit using R and WinBUGS software (Lunn et al. 2000, Spiegelhalter et al. 2003). Two chains were run in parallel, producing a total of 40,000 Markov Chain Monte Carlo (MCMC) samples each. The first 20,000 samples were discarded as burn-in and one out of every 20 remaining sample was retained (in order to reduce autocorrelation), for a total of 1,000 samples to form the posterior distribution of model parameter estimates.

In order to quantify discrete behavioral modes, the DCRW model we used incorporated an index based on mean turning angle and speed/direction autocorrelation parameters. Behavioral modes are estimated from the means of the MCMC samples within the model, producing continuous variables between 1 and 2; higher values representing higher turning angle and speed/direction variability. Modes are then classified (conservatively) as follows: behavioral mode 1 (1-1.25) assumes a low turning angle and speed/direction variability and is classified as transit behavior, and behavioral mode 2 (1.75-2) corresponds to higher turning angles and speed/direction variability, and is classified as area-restricted search (ARS). Unclassified behavior mode values fall between 1.25 and 1.75. While it is impossible without real-time confirmation to be certain that all ARS classifications are indicative of active foraging, the slower speed and

higher turning angles observed during ARS generally correspond to foraging behavior in marine predators (Kareiva and Odell, 1987, Mayo and Marx, 1990). Therefore, for the sake of this discussion, ARS will be referred to hereafter as “foraging”.

3.4 RESULTS

A total of ten tags were deployed on humpback whales in August and September of 2007 through 2011 in Unalaska Bay, Alaska (Figure 3.1). Judged by their size and behavior, all tagged whales were identified as adults and no tagged whales were associated with a calf. One tag transmitted intermittently for only 3 days and is not considered further in this study. Another tag was deployed but did not transmit, for unknown reasons. The remaining eight tags transmitted for an average of 28 d (range = 8-67 d). All whales exhibited differing speed, direction and overall distance traveled within and between years (Table 3.1, Figure 3.2). Whales traveled a minimum average of 46.0 km/day (range = 31.1-109.6 km/day), and spent a significant portion of their time foraging (Table 3.1). All but one whale (Whale G) remained relatively close to the tagging location for the period they were monitored (Figure 3.2). Tagged whales visited habitats on the Bering Sea (north) side of the Aleutian Islands more often than the North Pacific side, yet two whales traveled through Umnak Pass and spent brief periods foraging in the North Pacific. The tagged animals largely remained over shelf and slope habitat (1000 m or shallower) (Figures 3.2 and 3.3).

In 2007, Whale A made a trip west to the Island of Four Mountains and returned to the northern side of Umnak Island over a period of 28 days. This animal spent 98% of its time foraging. The other whale tagged on the same day in 2007 (Whale B) explored presumed feeding areas to the east of the tagging location, crossing Unalaska Bay and Unimak Pass before transmissions ceased (Figure 3.2). In 2008, Whale C traveled nearly 3 times farther than the other whale tagged on the same date (Whale D). After tag deployment, Whale C traveled east to Unimak Pass, then west to Unalaska Bay for several days, then farther southwest to the Pacific side of Umnak Pass (Figure 3.2). This animal spent 68% of its time in ARS. Whale D, however, remained within 50 km of Unalaska Bay for the duration of the tag transmissions, spending 99% of the time in foraging mode. The single whale tagged in 2009 (Whale E, Figure 3.2) remained within Unalaska Bay during the 7 days of tag transmission with 85% of its time spent presumably foraging. The animal tracked in 2011 (Whale H, Figure 3.2) headed east to the northern side of Akutan Island and then across Unimak Pass. It remained largely near shore during tag transmission and spent 75% of its time in foraging mode.

Table 3.1 - Summary of satellite telemetry and switching state-space model (SSSM) results from humpback whales tagged in Unalaska Bay from 2007 to 2011. Minimum distances represent the sum of distances between positions estimated every 12 hours. Average locations per day = average number of good locations (of qualities 0, 1, 2, 3, A, and B that passed the applied Argos Filter (Freitas 2010)) used to generate the switching state-space modeled results. ARS=Area-restricted search and is considered foraging for the purpose of this study.

ID	PTT#	Date deployed	Tag Longevity (d)	Total km (min)	km/d (min)	Avg. locations/d	Behavioral Modes		
							% Travel	%ARS	% unclassified
Whale A	21809_07	8/11/2007	28.0	1160.0	41.4	3.6	0	98	2
Whale B	21810_07	8/11/2007	17.0	879.0	51.7	7.9	15	9	76
Whale C	21810_08	8/26/2008	67.0	2341.0	34.9	5.7	2	68	30
Whale D	21809_08	8/26/2008	36.0	813.0	22.6	6.6	0	99	1
Whale E	87769_09	8/5/2009	8.0	249.0	31.1	5.9	0	85	15
Whale F	88720_10	8/1/2010	15.0	589.0	39.3	8.9	3	56	41
Whale G	88721_10	8/1/2010	26.0	2849.0	109.6	6.2	85	8	7
Whale H	87771_11	9/10/2011	29.0	1082.0	37.3	2.8	0	75	25
AVERAGE			28.3	1245.3	46.0	5.9	13.1	62.3	24.6
(SD)			(18.0)	(890.5)	(27.0)	(2.0)	(29.5)	(36.2)	(25.1)

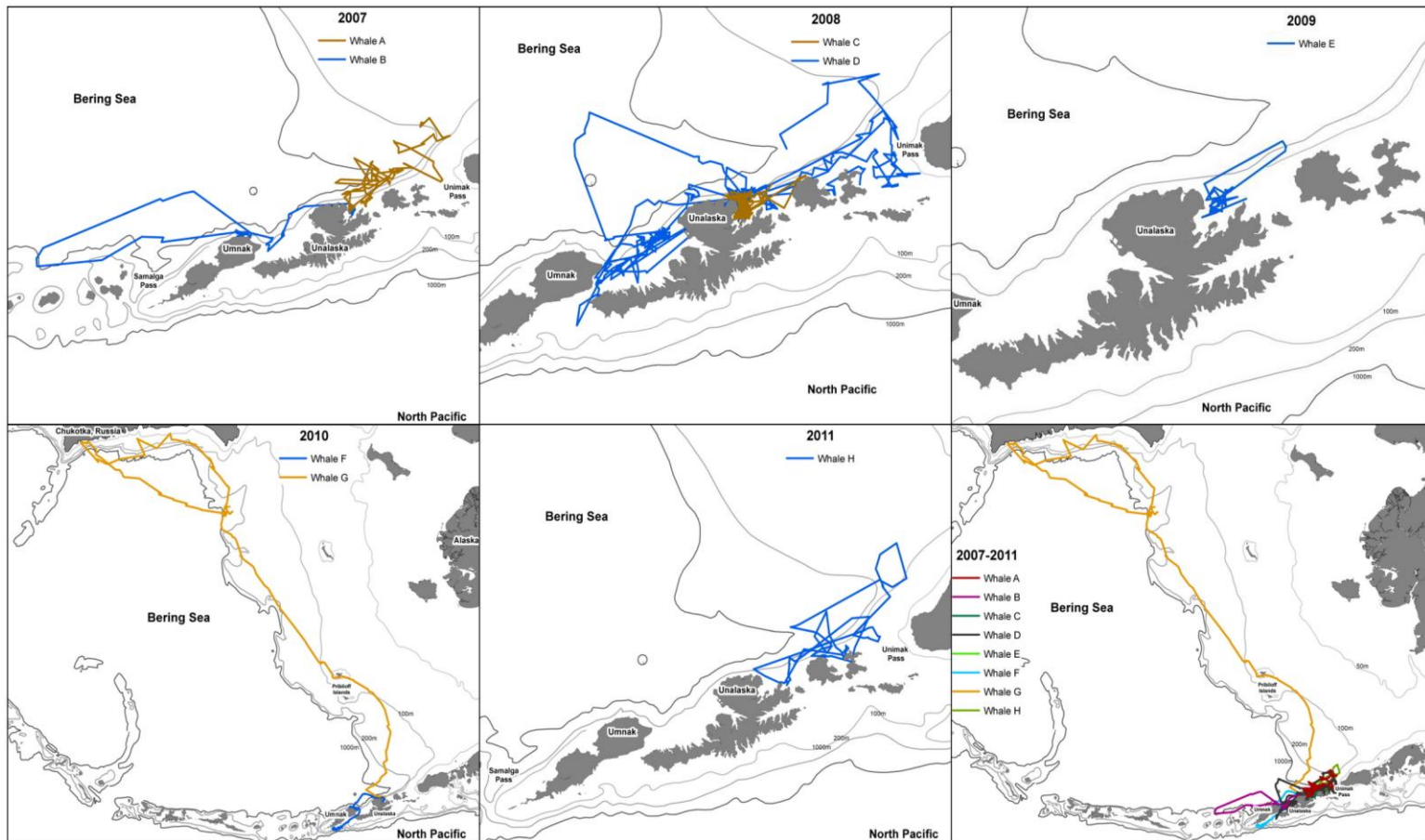


Figure 3.2: Tracks of all whales from 2007 to 2011. Tracks based on Switching State-Space modeled positions.

The 2 whales tagged in 2010 showed the most marked variation in movement observed throughout the study. Whale F (Figure 3.2) traveled from Unalaska Bay west to northeastern Umnak Island, then southeast through Umnak Pass, presumably to forage on the Pacific side of the island, spending 56% of its time foraging. The other animal tagged that year (Whale G, Figure 3.2) left Unalaska Bay 3 days after tagging and over a period of 16 days traveled at least 1,500 km northwest along the outer Bering Sea shelf to the southern Chukotka Peninsula, Russia (reaching the northern extent of Vityaz Valley on August 14th and then heading west along the shelf break)(Figure 3.2). Over the next several days, Whale G moved east across the Bering Sea basin before turning southeast. Whale G stopped in Navarin Canyon (60°30'N, 179°20'W), where it remained until transmissions ceased 2 days later on 26 August. Whale G spent 85% of its time travelling. The long-range movement of this individual, encompassing nearly 3,000 km in 26 days, equates to an average travel rate of 110 km/day.

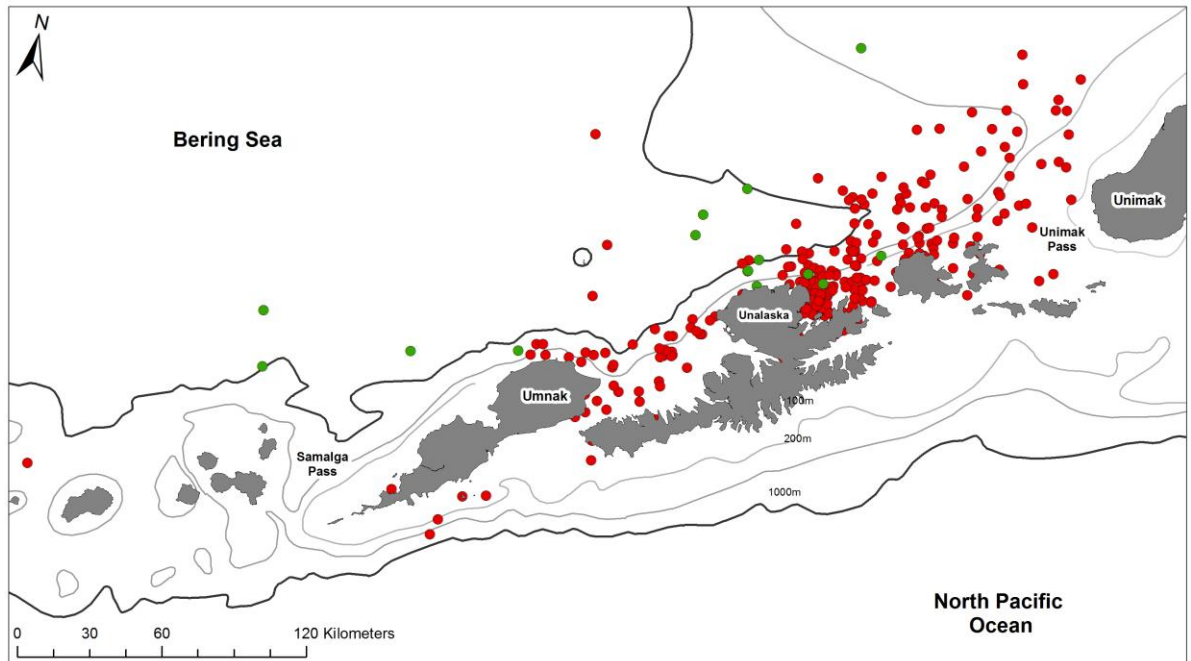


Figure 3.3: Locations of Area-restricted search (ARS) (red dots) and travel (green dots) modes of all tagged whales except Whale G (see Figure 3.4). Unclassified behavior modes are not shown.

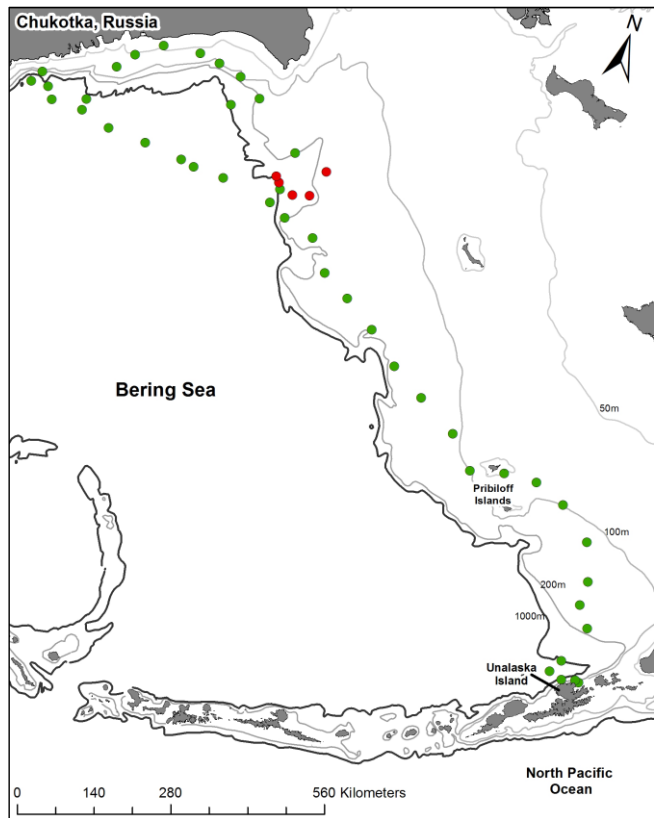


Figure 3.4: Locations of foraging (ARS; red dots) and travel (green dots) modes of Whale G. Unclassified behavior modes are not shown.

3.5 DISCUSSION

Telemetry data from this study largely support the findings of historical and current studies (Moore et al. 2002, Zerbini et al. 2006a, Calambokidis et al. 2008, Riley 2010) which showed that humpback whales congregate in the shallow, highly productive coastal waters north of the eastern Aleutian Islands between Unimak and Samalga Passes (Figure 3.1). The extremely high proportion of foraging (Table 3.1) within the narrow band 200 km east and west of Unalaska Bay further emphasizes the importance of the waters off the eastern Aleutian Islands for humpback whales (Figures 3.3 and

3.4). However, the spatial and temporal movement variation evident in these telemetry data suggest that whales are making individual decisions about fine-scale movement and that these decisions can lead to long-distance travel to remote, under-studied habitat within a feeding season.

There is an abrupt division of water mass properties at Samalga Pass (200 km west of Dutch Harbor): waters east of the pass are consistently warmer and fresher, with significantly higher primary productivity than those to the west (Ladd et al. 2005a, 2005b, Mordy et al. 2005, Hunt et al. 2010). Correspondingly, the highest concentrations of humpback sightings along the Aleutian chain have consistently occurred from Samalga Pass east to Unimak Pass (Moore et al. 2000, Hunt & Stabeno 2005, Zerbini et al. 2006a, Calambokidis et al. 2008, Friday et al. 2013) with very few humpbacks seen west of Samalga Pass. Telemetry data align with those findings; only one tagged animal traveled west of Samalga Pass for 3 days in 2007, but it looped back to the northern side of Unalaska Island without lingering in the pass itself (Figures 3.2 and 3.3). Additionally, Whales B, C, and F spent several days (presumably foraging) just north of Umnak Island, as well as in Umnak Pass (Figure 3.3). Previous surveys near Umnak Island have shown low humpback encounter rates (Zerbini et al. 2006a, Riley 2010), yet the telemetry data suggest that those areas may be used more often than previously thought.

The majority of foraging behavior occurred over the shelf/slope habitat (1,000 m or less) on the Bering Sea side of the Aleutian Island chain rather than the bathymetrically similar North Pacific side (Figure 3.3). This preference for the northern side of the Aleutian Islands has also been observed in previous visual surveys (Zerbini et al. 2006a, NMML unpublished data), and is likely the result of the oceanographic processes that create consistent prey concentrations just west of Unimak Pass (Ladd et al. 2005a, b, Mordy et al. 2005). Although the Bering Sea shelf/slope area appear to be used more often, Mate et al. (2007) tracked 2 whales from Hawaii to the Pacific side of the Aleutian Islands; one of those tagged whales stayed on the shelf/slope south of Umnak for 59 days. Additionally, two whales from this study (Whales C and F) also travelled through Umnak Pass to forage (Figure 3.5) in the Pacific in different years. Fine-scale oceanographic and biological productivity studies are needed to help describe conditions that warrant the use of this historically less-productive habitat.

Vessel surveys conducted throughout the Bering Sea in 2002, 2008 and 2010 recorded an increase in humpback sightings (as well as overall cetacean diversity and density) in 2010 in the Pervenets and Navarin canyons when compared to other survey years (Brueggeman et al. 1984, Friday et al. 2013). The increased cetacean sightings in this area in 2010 overlapped with the track of Whale G, who spent several days foraging in Navarin Canyon that same year (Figure 3.4) before transmissions ceased. Interestingly, the animal initially traveled through the canyon (without foraging) 11 days earlier, then looped back to forage there for three days before transmissions ceased. The extent of

use of these submarine canyons in the Bering Sea is unknown, but these data suggest that canyons may represent important humpback whale foraging habitat.

Average daily distances traveled during this study were similar to those in other feeding grounds (Heide-Jørgensen & Laidre 2007, Dalla Rosa et al. 2008), with the exception of Whale G, who traveled more than two times faster and farther than the average speed and distance of the 7 other tagged whales (Figures 3.2 and 3.4). Heide-Jørgensen and Laidre (2007) tagged feeding humpbacks off West Greenland and found that some animals moved up to 200 km per day, presumably in search of food. Dalla Rosa et al. (2008) tracked a humpback that traveled a similar straight-line distance as Whale G, averaging ≈ 108 km/day while traveling between presumed feeding sites off the Antarctic Peninsula. The speed and distance traveled by Whale G more closely resemble migratory travel rates foraging rates (Mate et al. 1998, Zerbini et al. 2006b, Garrigue et al. 2010), yet the late-summer sighting (August) and the fact that Whale G was tagged while part of a large, surface-feeding group, make it unlikely that this animal was still migrating so late in the season (August).

Long-distance travel between feeding aggregations has been documented through photo-identification in the Gulf of Maine, yet 95% of the across-aggregation resightings occurred within 550 km of their original sighting location (Stevick et al. 2006). Less than 1% of all whales photographed on a feeding ground during the SPLASH project ($n=4,328$) were re-sighted more than 740 km from their original sighting (Calambokidis et al. 2008). Furthermore, only two individually identified humpbacks (out of hundreds) seen

in the Bering Sea/Aleutian Islands were resighted elsewhere during a large, ocean-basin-wide study undertaken from 2004 to 2006; one was seen in southeastern Alaska, and one in the northern Gulf of Alaska (Calambokidis et al. 2008). Although humpbacks are commonly seen off the Chukotka Peninsula (Russia) (Tomilin 1937, Omura & Ohsumi 1964) there have been no photo-identification matches between eastern Aleutian Island and Chukotka humpbacks, probably due to the near total lack of this type of study effort in the latter area. However, Omura and Ohsumi (1964) documented a humpback whale tagged with a Discovery mark near Unimak Pass that was recovered by a Japanese whaling vessel 8 years later off Chukotka. The Omura and Ohsumi (1964) record and the telemetry data from 2010 prove that at least some whales that feed along the eastern Bering Sea shelf and slope also visit the eastern coast of Russia. Long-distance movement variation has the potential to bias any population density estimate (Hammond et al. 1990; Friday 1997; Punt et al. 2007), and the scope of this phenomenon within the Bering Sea warrants further investigation.

The impact of anthropogenic injury or mortality on humpback whales throughout the Bering Sea is not well known, but fishing gear entanglements and ship-strikes have been observed in Alaskan waters (Gabriele et al. 2007, Angliss and Outlaw 2008, Neilson et al 2009). Although Unalaska Bay has been a heavily trafficked fishing port for many years, human activity from the Aleutian Islands to the Chukchi Sea will likely increase as newly opened oil and gas lease areas in the Alaskan Arctic are developed. Telemetry data from this study highlight the overlap of humpback whale foraging habitat with areas of heavy shipping and fishing vessel traffic, such as Unalaska Bay and Unimak Pass, and

management strategies should incorporate these results in order to strengthen the current conservation policies.

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CHAPTER 4:

Assessing implantable satellite tag extrusion using light sensors

4.1 ABSTRACT:

Advances in satellite telemetry technology have greatly improved over the years, yet satellite tag duration has been highly variable and is often below longevity expected based upon battery life alone. Causes of tag failure are difficult to determine and may include transmitter failure during deployment, post-deployment tag damage, or natural removal/rejection of the tag. A follow-up study aimed at assessing tag retention and wound healing in Gulf of Maine humpback whales (*Megaptera novaeangliae*) was initiated in 2011; the high re-sighting rates of identified individuals in this population permitted repeated assessments of tag status and placement. The tags were equipped with a light sensor to investigate whether they could serve as an indicator of tag extrusion. Comparisons of high-quality follow-up photos of each tag to recorded light levels show correlation between the amount of tag extrusion and daytime light levels. Tag extrusion was described by zones based on lines etched onto each tag; 0=fully flush to 1.75cm (stopper to first etch marks), 1=1.75cm to 3.75cm (between first and second etched marks), 2=3.75cm to 4.75cm (second etch mark to sensor), or 3=fully exposed sensor. As expected, tags extruding to zones 0 recorded no light, while tags at zone 3 recorded full light levels during daylight, variable light during dawn, and no light at night. Tags in zones 1 and 2 consistently showed variable light levels throughout

daylight hours, likely due to irregular or partial exposure of the light sensor. These results show that light levels may be used as a guide for determining the rate of tag extrusion, which may help to identify at what levels tag detachment occur. Ultimately, this type of information can be used to understand the factors responsible for tag rejection and may assist in advancing satellite tagging technology.

4.2 INTRODUCTION:

Satellite monitoring of large whales provides valuable habitat-use, migration, stock structure and individual movement data that have been used to protect and manage cetaceans worldwide (e.g. Baumgartner and Mate 2003; Mate et al. 2007; Gales et al. 2009; Heide-Jorgensen and Laidre 2007; Hauser et al. 2009, Zerbini et al. 2011). While there have been significant technological advances in tag design, electronics, deployment methods, and satellite network coverage in the past decade, implantable satellite tags used on cetaceans typically stop transmitting before their battery life ends. This premature tag detachment often leads to widely varying datasets within and between study seasons, and can bias resulting behavior prediction models, home range density estimates, and fine-scale movement statistics.

Telemetry data are collected using remote systems and, tagged whales are rarely re-encountered during the transmission period of a telemetry study. Without visual confirmation of tag removal or breakage, there is no method for determining the cause of tag cessation. Reasons for premature tag cessation in large whales are poorly understood, but may include hardware damage, software malfunction (during or after

deployment) or natural rejection of the tag (Mate et al. 2011, Robbins et al. 2013, Zerbini, unpublished data). The underlying reasons for tag rejection may vary by individual, but are likely the result of the natural physiological response to a foreign body within tissue, anchor breakage or malfunction, or improper tag placement during deployment. Tag extrusion, as a result of the rejection process, has been observed during opportunistic re-sightings of tagged animals and is generally thought to begin over varying periods of time, from hours to days (Kennedy, unpublished data, Zerbini, unpublished data, Robbins et al. 2013). Regardless of the reasons for tag rejection, a tag that has completely penetrated the animal (the stopper is fully flush with a whale's body) will, on average, transmit for a longer period than a tag that is extruded by any amount (Mate et al. 2011; Robbins et al. 2013). Increasing the external surface area of the tag will result in greater drag forces being applied to the tag and tissue, and should also increase the chance of contact with external objects, which could result in complete breakage and/or removal of the tag.

The ability to ascribe extrusion values to real-time telemetry data could improve future tagging projects by allowing researchers to make short- and long-term changes to their tag design and deployment techniques. For example, comparing extrusion and failure rate with tag deployment statistics could inform field teams about ideal tag placement and/or anchor configuration. Here, we report the results of a novel approach for remotely quantifying certain aspects of tag rejection: the use of a light sensor on the tag body to indicate whether portions of the tag were exposed after deployment. Potential

uses of this technology, including its utility in the assessment of tag-design and placement efficiency, are discussed.

4.3 MATERIALS AND METHODS:

4.3.1 Study population

The Gulf of Maine is host to a population of humpback whales that feed in local waters in spring, summer and autumn every year. Individual whales are identified by variations in ventral fluke pattern (Katona et al. 1979) and by the size, shape and scarring of the dorsal fin (Clapham et al. 1993); individuals are typically given names based upon prominent field marks, and some names are referred to in this report. Because of extensive data collection aboard commercial whale-watching vessels and regular dedicated research cruises, individuals in this population typically have a high re-sighting rate, both within a season and from year to year (Clapham et al. 1993). This re-sighting rate was the basis for choosing Gulf of Maine humpbacks as the target population for a study aimed at assessing behavioral, physical and physiological effect of tagging and improving satellite tag technology for large whales (Robbins et al., 2013).

4.3.2 Tag and sensor specifications

The implantable (Type 1, ONR 2009) tags used in this study consisted of an electronics package (transmitter, Mold 193H manufactured by Wildlife Computers, Redmond, WA, USA) coupled with an attached anchoring system (Gales et al., 2009) (Figure 4.2). The electronics package contained a SPOT-5 transmitter and light level sensor custom designed by Wildlife Computers, housed in a 160mm long by 22mm diameter stainless

steel cylinder. The tags were designed to penetrate beneath the hypodermis and anchor in the fascia between the blubber and muscle of the animal; maximum penetration depth for all tags was 270mm. Lines were etched into the transmitter cylinder at varying intervals (see Figure 4.2).

The light sensor, located in the communications port, 4.75cm from the stopper (Figure 4.2) recorded the level of irradiance from 300 to 1100nm wavelength light as integers between 1 (no light) and 255 (maximum reading). The tag recorded a light level immediately before positioning information was transmitted to the satellite, only when the wet/dry sensor indicated that the tag was out of the water. A test of three tags on land showed that the sensitivity of the light sensor was high enough to reliably detect dawn and dusk events (Figure 4.1).

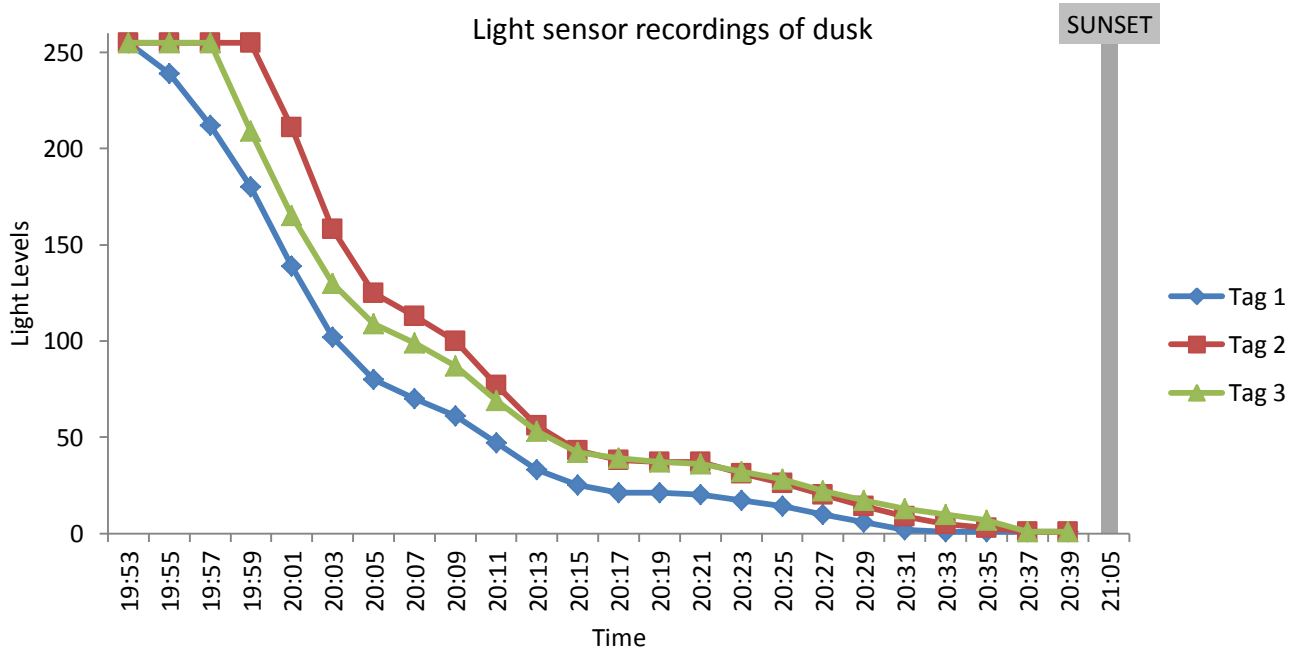


Figure 4.1: An experimental comparison of light level sensor values from three tags exposed to the sun during dusk.

4.3.3 Post-deployment follow-up

After deployment, a focal-follow of at least one-hour was conducted to evaluate tag positioning and the animal’s physiological responses to the deployment procedure. After the initial focal follow, regular attempts (daily to weekly) to re-encounter tagged individuals (either by travelling to transmitted positions or by visiting high-density feeding areas) were made in order to further evaluate the condition of the tag and the overall health of the whale. During both the initial focal-follow and the subsequent re-sightings, high-resolution images were collected of the tag site from many angles, to ensure proper description of tag extrusion. Opportunistic high-resolution photographs taken by naturalists working aboard commercial whale watching vessels were also used if they were found to be of sufficient quality to assess the level of tag extrusion.

Photographs were rejected if the extrusion level could not be determined. The most common reasons for photo rejection were inadequate angle to the tag, poor focus, or improper image exposure.

4.3.4 Data analysis

Tag extrusion was described by zones, which were based on the lines etched into the transmitter cylinder (Figure 4.2, Table 4.1, and Appendix A). Multiple photographs taken on the same day were assessed whenever possible, and the highest zone (farthest extruded) observed was recorded as the extrusion value for the day. If the extrusion zone remained constant throughout the day, one zone value was assigned to the day, per whale. If the tag had extruded or intruded between daily re-sightings, multiple zone values were assigned to that day. Light level readings from 06:00 to 15:00 local time (after sunrise to the end of the duty cycle) were averaged and used to represent the overall daily light level value for the observed extrusion zone, per tag. Average light levels from multiple-zone days were excluded from statistical data analysis since the exact time of extrusion zone and/or light level changes could not be determined. However, zone to light level correlation could still be confirmed (see Draco, Appendix B) on multi-zone days.

Table 4.1: Extrusion zone descriptions. See Appendix A for photographic examples.

Zone	Amount of Extrusion	Description
0	0 to 1.75cm	Stopper to bottom of the first etch marks
1	1.75 to 3.75cm	Bottom of the first to top of the second etch marks
2	3.75 to 4.75cm	Top of the second etch marks to com. port
3	4.75cm to end	Fully exposed com. port

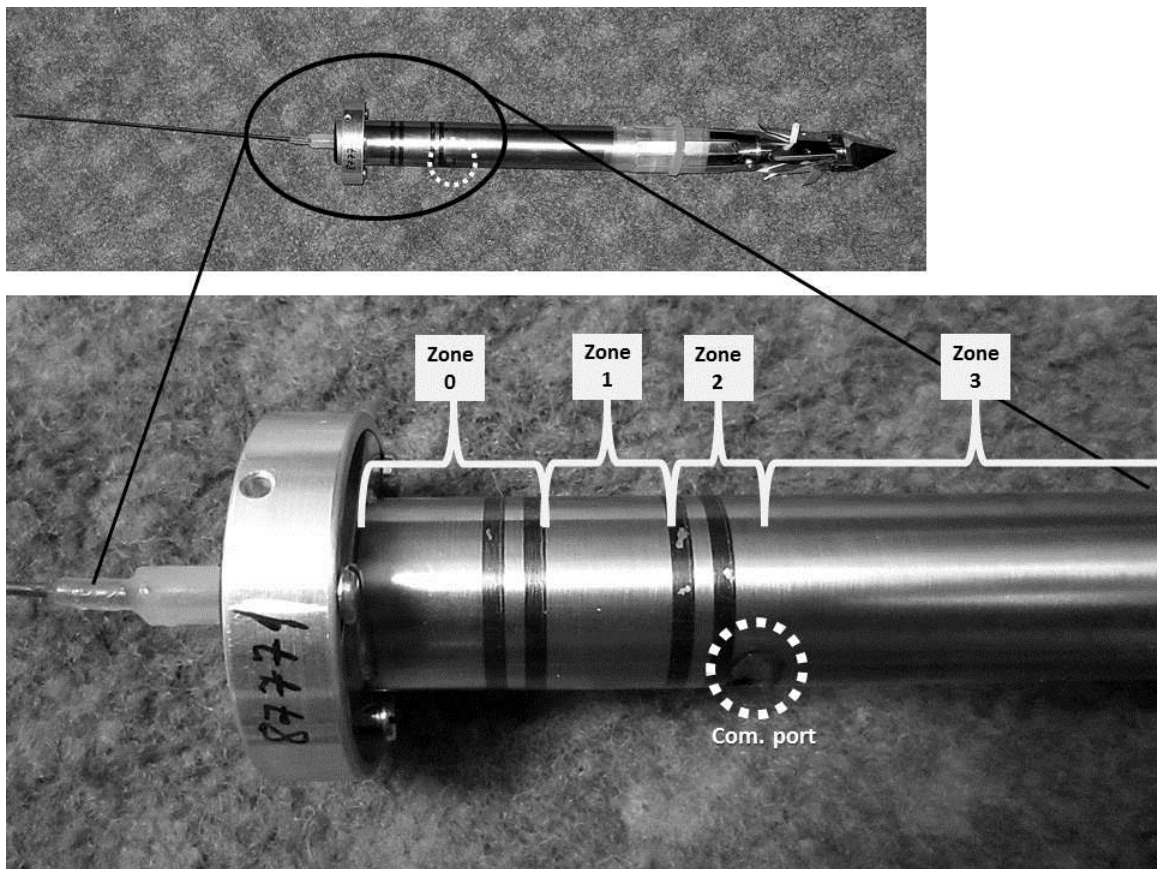


Figure 4.2: Photograph of the tag used in this study, with brackets indicating extrusion zone. Dashed circle indicates com. port location.

4.4 RESULTS

Light sensor readings and follow-up photographs from ten whales tagged in the summer of 2011 were analyzed during this study (Tables 4.2 and 4.3). Follow-up photographs were obtained on an average of 5.1 days, or 19% (range 7-48%) of total transmission days. Of these ten whales, Etch-a-sketch was the most frequently re-sighted individual for zone determination (15 non-consecutive days after deployment, or 48% of total transmission days). Overall, light sensor readings clearly show that the amount of tag extrusion is directly correlated with increased light level readings (Figure 4.3 and Appendix B). Photographic documentation validated that fully embedded or fully exposed sensors consistently recorded minimum and maximum light levels, respectively, with very low variability (Table 4.4 and Figure 4.3). The highest variation in light level readings occurred during zones 1 and 2 (Table 4.4 and Figure 4.3). While light levels recorded in zone 1 were, on average, lower than those recorded in zone 2, there was considerable variation across all values (1-255) in both zones (See Appendix C for examples of typical daily light level readings per zone).

Table 4.2: Total number of days each whale was re-sighted (*with high enough photo quality for zone determination), and proportion of re-sightings per overall tag duration.

	# of resightings (d)	Resight./ duration
Buckshot	4	0.24
Colt	10	0.29
Draco	1	0.17
Etch-a-sketch	15	0.48
Fern	2	0.12
Jabiru	5	0.16
Nile	2	0.07
Pele	7	0.24
Timberline	3	0.03
Zap	2	0.10
Average (sd):	5.1(4.4)	0.19(.13)

Table 4.3: Dates of photographic documentation for all 10 tagged whales (re-sighting dates with no or poor photo-documentation of extrusion zone are omitted). Numbers 0-3 indicate extrusion zone. Light grey box indicates tag deployment date. Dark grey box indicates the last day of transmission. *Draco progressed through 3 zones throughout the day: 0, 1, and 3, respectively. X indicates re-sightings with no associated light level due to poor tag transmission.

Whale Name	7/10	7/13	7/15	7/16	7/17	7/18	7/19	7/20	7/22	7/23	7/24	7/25	7/26	7/27	7/28	7/30	7/31	8/1	8/2	8/3	8/4	8/5	8/6	8/8	8/9	8/11	8/12	8/13	8/15	8/17	8/20	8/31	10/18	
Buckshot				0			1	2				2			2																			
Colt	0	0					2		2	1	3	3				3			2	2							3							
Draco		0*	3																															
Etch-a-sketch		0x		1	2		2	2	3	3		3			3				3			3	3	3		3	3							
Fern							3	2		1																								
Jabiru					1										1				1						3		3			3				
Nile							0x	0																			1							
Pele										1			2		2					2					2		3			3	3			
Timberline		0x																								1	1					2		
Zap				0											3	3																		

Of the ten tags used in this study, eight were observed extruding from a low to high zone over time, as expected. Surprisingly, two tags (on whales named Colt and Fern) were also observed intruding during the study period. On July 19th, Fern's tag was extruded to zone 3. The next day, the tag had intruded to zone 2, and finally zone 1 on July 23rd. Average daily light levels corresponded with these zone changes (Appendix B). Colt's tag was seen both intruding and extruding between July 10th (deployment date) and August 13th. From deployment to July 13th, Colt's tag was fully flush (zone 0). The tag was later observed in zone 2 on July 19th, zone 1 on the 22nd and 23rd, zone 3 on the 24th, 25th and 30th, zone 2 again on August 2nd and 3rd, and finally in zone 3 on August 12th. Again, these intrusion and extrusion events were reflected in the average daily light levels recorded, with lower light levels corresponding with lower extrusion zones (Appendix B). These deviations from previously assumed natural progression from low to high extrusion provide further validation of the utility of light sensor readings in remote extrusion estimates.

Table 4.4: Overall average light level readings per zone.

Zone	Avg. Light Level (SD)
0	2 (1.5)
1	31 (58.6)
2	125 (100.2)
3	255 (0)

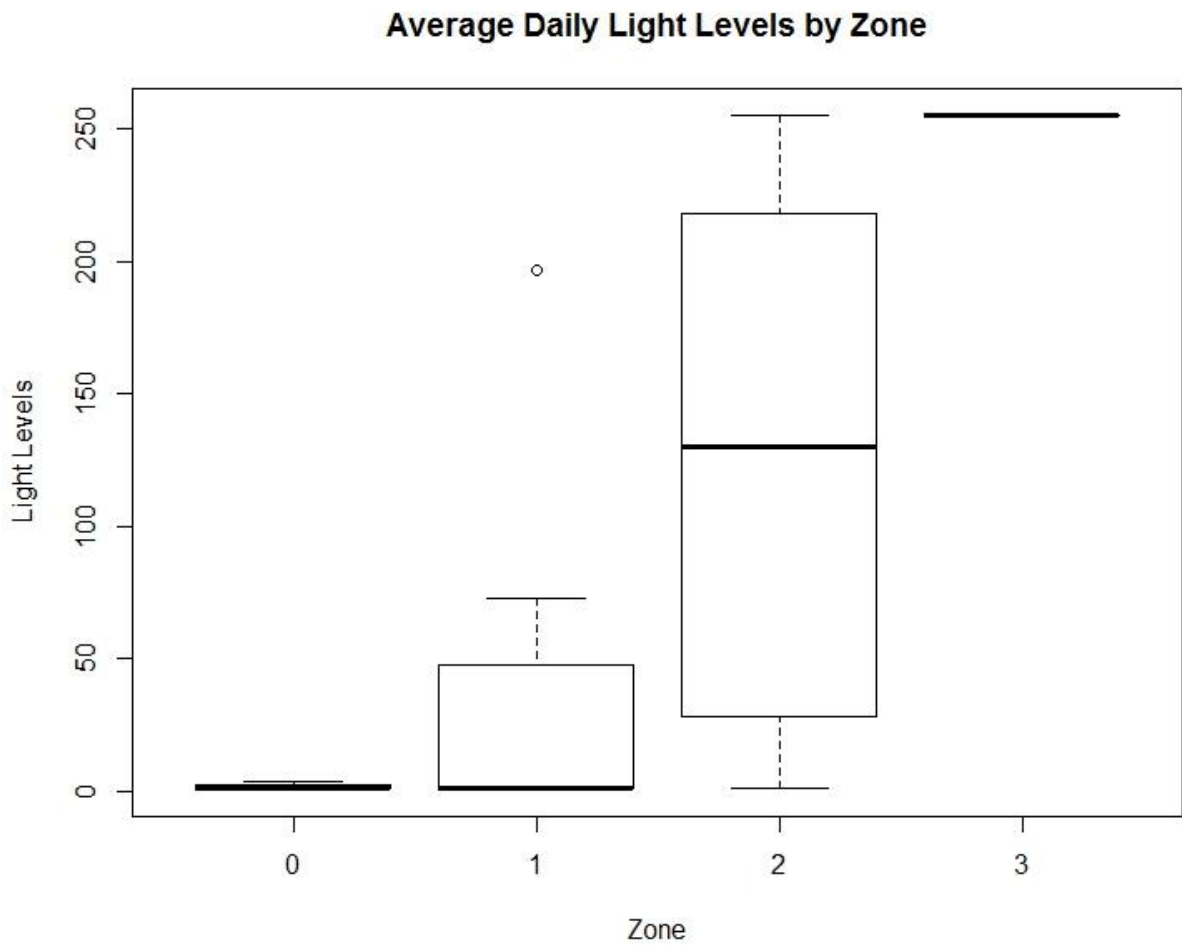


Figure 4.3: Box and whisker plot of average daily light level readings per zone, for all 10 whales combined.

4.5 DISCUSSION

The ultimate goal of using light sensors is to provide a reliable method to assess the rate at which tags are extruded post-deployment. Understanding the level at which tags are detached from the whale's body can assist in improving technology. Results from this study validate that light level readings were consistent with observed extrusion levels and confirm that tag-mounted sensors can be used to describe tag extrusion. Examination of remote light level data should allow researchers to predict when a tag was nearly fully penetrated, or extruded past the sensor. Differentiation between extrusion zones 1 and 2 would be more difficult without visual confirmation, yet the highly variable light level readings should at least reliably indicate extrusion to somewhere between 1.75 and 4.75 cm outside of the whale.

While the results reported here show that it is possible to remotely monitor certain physical properties of implantable satellite tags, it is clear that additional tag design modifications are needed to reduce sensor errors and allow researchers to assess the effects of tag design and placement on tag failure rate. Given that tagging projects are expensive, tag deployment requires specialized personnel, and telemetry technology is almost always used in the study of endangered species, improvements that increase tag longevity and/or decrease unnecessary harassment of an animal would be beneficial on many levels.

4.5.1 Potential Error

There are two situations that may lead to inaccurate light level readings, and subsequently bias the extrusion analyses: inaccurate levels due to sensor malfunction, or readings that are biased due to tag orientation/wound healing. Both of these situations may result in light level measurements that don't necessarily reflect the true tag extrusion level, and both will vary with each deployment. Researchers have no control over the orientation of the light sensor after deployment, and the sensor's responsiveness to changing light levels at different orientations may affect the readings. Tissue swelling, scarring, or other wound-healing processes are also variable, and may affect light sensor data on some whales. For example, several whales were observed with necrotic tissue extruding from the tag insertion point. Because this tissue could have shifted to cover the light sensor during surface readings at any time, the overall effect of the obstruction on the average light level readings is unknown. In addition, the natural flexion and extension of the whale's muscles during feeding, resting, diving or travelling may influence light level data by pulling tissue away from, or pushing it into, the sensor at different extrusion levels. Similarly, localized swelling near the tag site may cover and/or uncover the sensor as the tagging wounds heal.

The effects of flexion/extension and swelling/subsidence are the most likely causes of the highly variable sensor readings observed in extrusion zones 1 and 2. Furthermore, pronounced localized swelling could lead to inaccurate zone descriptions and potentially account for the unique tag intrusions seen in Colt and Fern (Appendix B). Although distinctions between

localized swelling and true tag intrusion can be made only with visual confirmation, the light sensor should still indicate partial or full obstruction, regardless of the reason.

There have been several attempts to assess the effects of tagging on the overall health and behavior of large whales (Watkins et al. 1981; Kraus et al. 2000, Best and Mate 2007, Mate et al. 2007, Mizroch et al. 2011), yet these studies have been largely opportunistic and were based upon small sample sizes. Detailed, long-term monitoring studies of the effects of tag placement on wound healing and tag longevity, such as those currently being undertaken by Robbins et al. (2013), should allow for more informed estimates of the common physiological responses associated with each type of tag deployment. Future projects combining the knowledge of wound type/tag placement relationships with tag-mounted diagnostic sensors will hopefully allow for more informed assumptions about the causes of premature cessation.

4.5.2 Suggested Modifications

Advancements in remote tag monitoring technology could lead to tag designs that would allow researchers to assess the tag extrusion rate in relation to tag placement and quantify the differences in tag extrusion between species' or sub-populations. In lieu of costly, large-scale tag modifications, some basic adjustments would improve light level assessment. The addition of more horizontal lines, from the stopper to the anchor attachment, has already been implemented for the 2012 and 2013 field seasons, yet a vertical line etched along the transmitter cylinder to indicate the location of the light sensor would also help quantify extrusion rate and the effects of sensor orientation on light level recordings. Also, since tag

extrusion can occur rapidly and could easily be missed during long non-transmitting periods, adjustment of the duty cycle programming would increase the likelihood of recording significant extrusion events. Third, an increase (or thorough calibration) of sensor sensitivity may make it possible to discern extreme meteorological events; examination of changes in animal behavior during those events would be extremely valuable to any behavioral study.

More complex tag modifications should also be considered. The light sensor used in this study was located 4.75 cm from the stopper, leaving an additional 22.75 cm to extrude before full tag removal. The addition of more light sensors, placed at specific intervals along the length of the transmitter body, would allow for fine-scale extrusion rate calculations. The inclusion of different types of sensors (e.g. temperature or pressure) should be explored; sensors that do not need to be exposed outside the animal's body would aid in nighttime data collection, intercalibration with other diagnostic sensors, and description of the internal physiological responses to tag deployment.

4.6 ACKNOWLEDGEMENTS

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including the Dolphin Fleet, Captain John Boats, Whale Center of New England, Whale and Dolphin Conservation Society and Blue Ocean Society. Tag deployment, photo-identification and biopsy sampling were performed according to regulations and restrictions specified in existing permits issued by the National Marine Fisheries Service to PCCS (permits #16325 and #633-1778 and NMML (permit # 14245).

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Zone 3

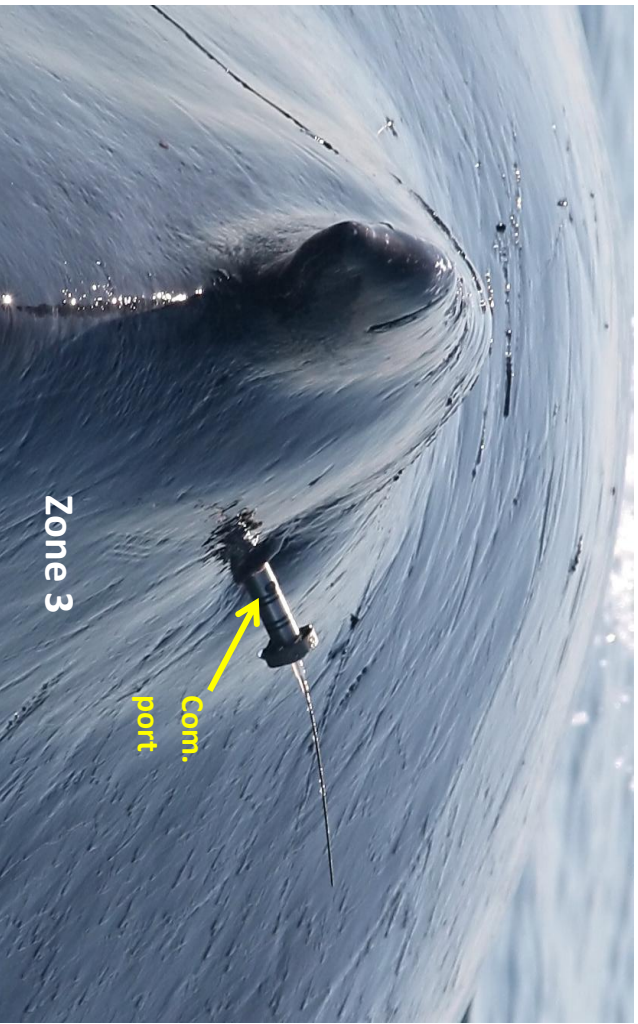
APPENDIX A: Examples of each extrusion zone, based on lines etched on the electronics cylinder.



APPENDIX A continued: Examples of each extrusion zone.



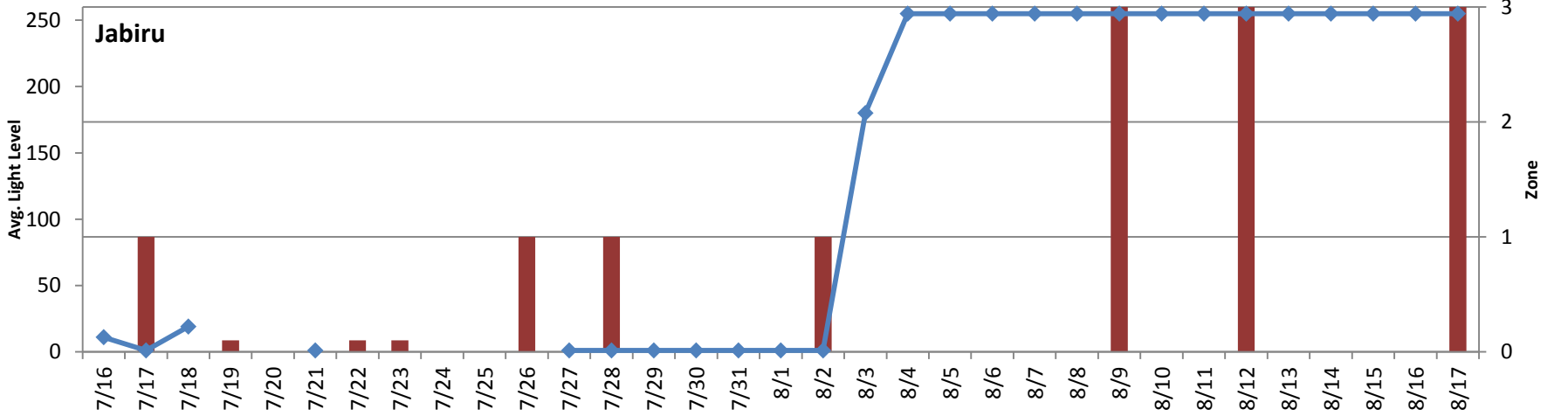
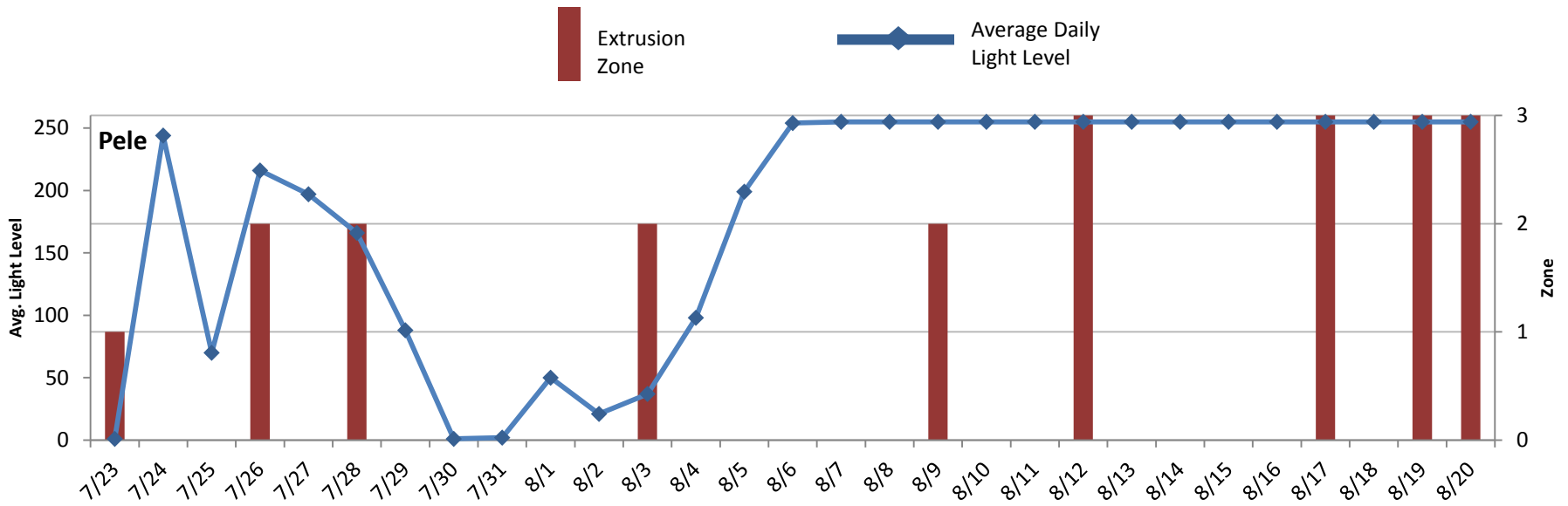
Zone 2



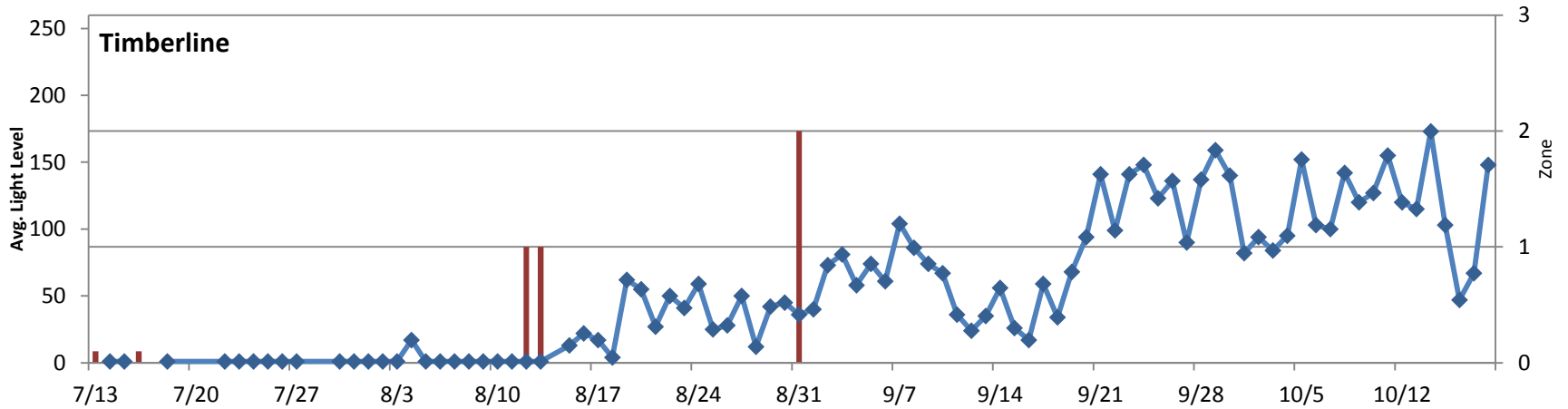
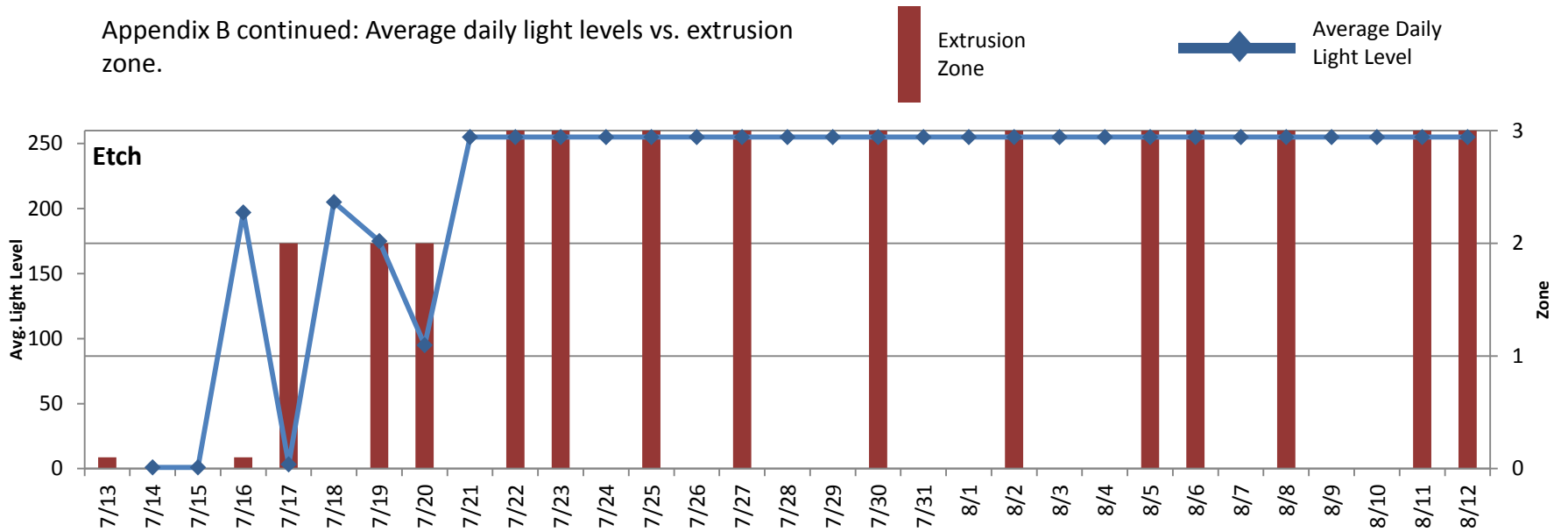
Zone 3

Appendix B: Average daily light levels per whale, with daily extrusion zone.

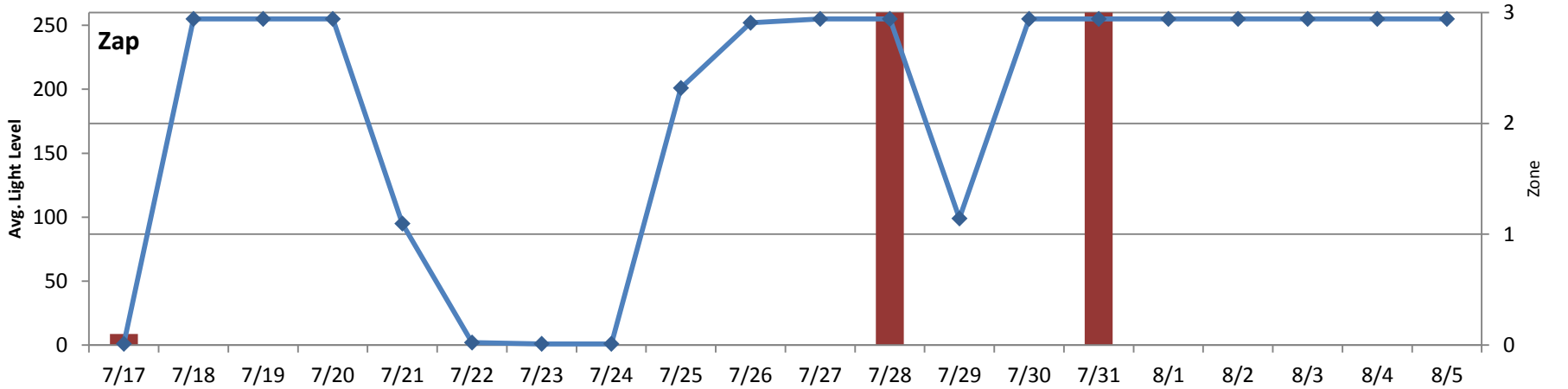
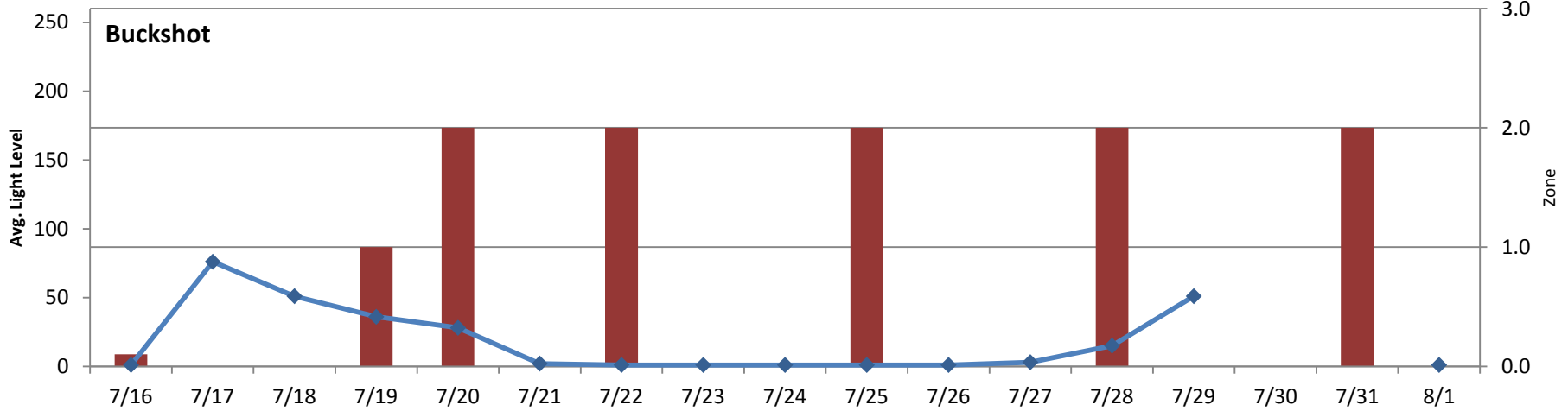
The following graphs represent the average daily light levels for each of the ten tagged whales. The corresponding extrusion zone for each re-sight day is also shown.



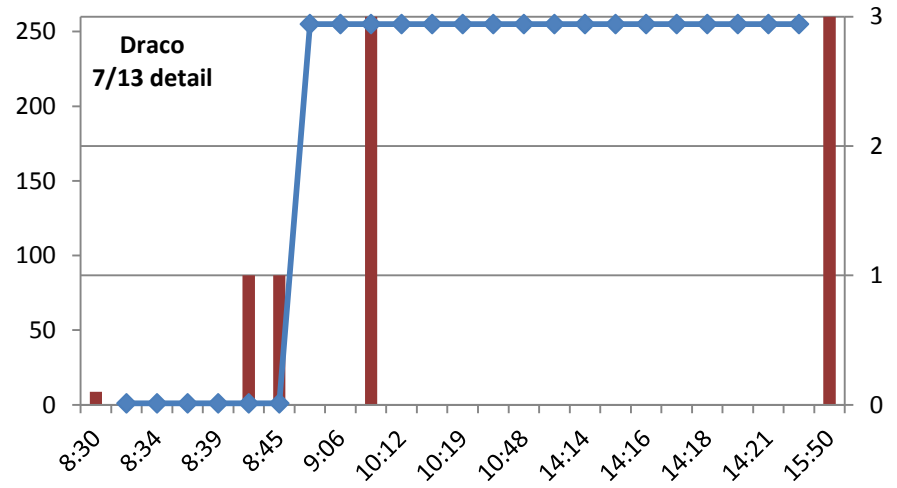
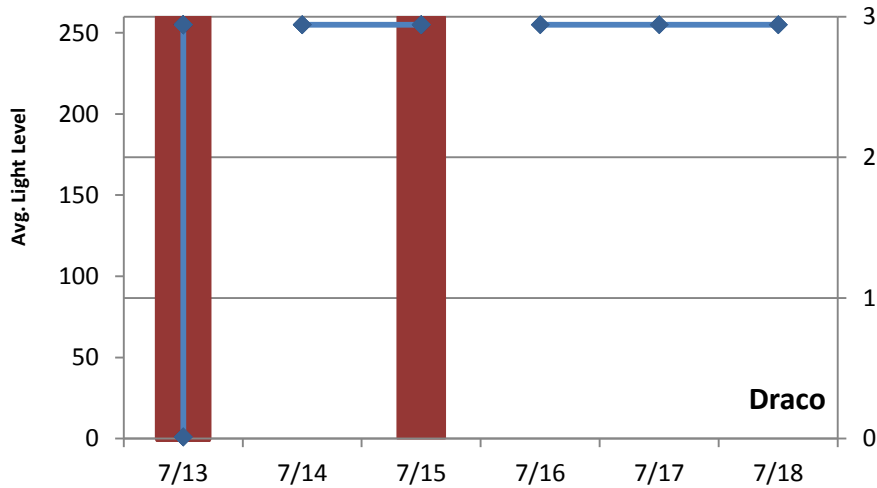
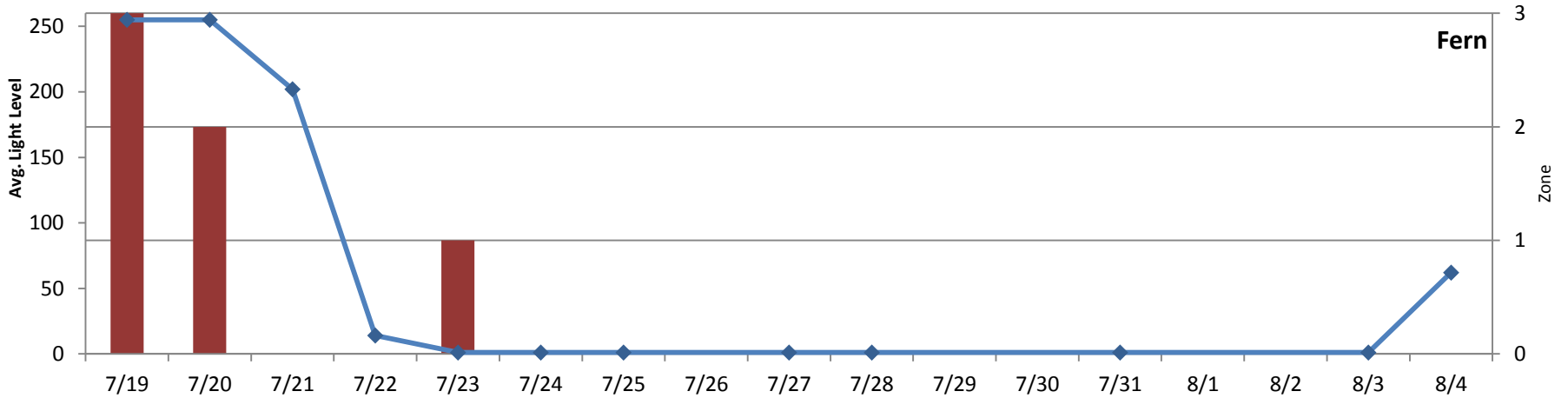
Appendix B continued: Average daily light levels vs. extrusion zone.



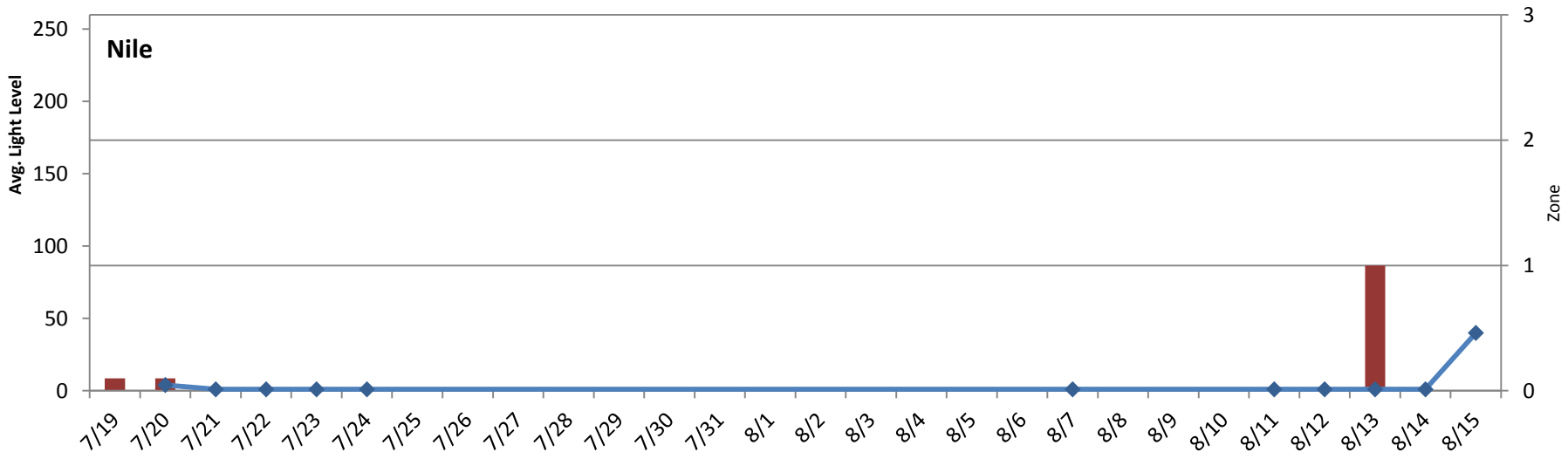
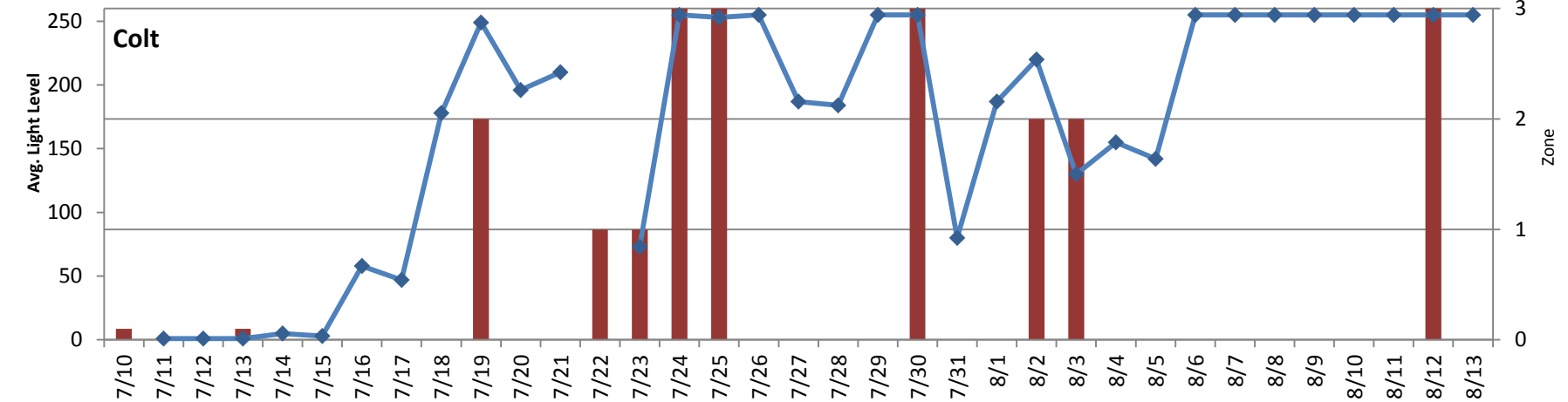
Appendix B continued: Average daily light levels vs. extrusion zone.



Appendix B continued: Average daily light levels vs. extrusion zone.



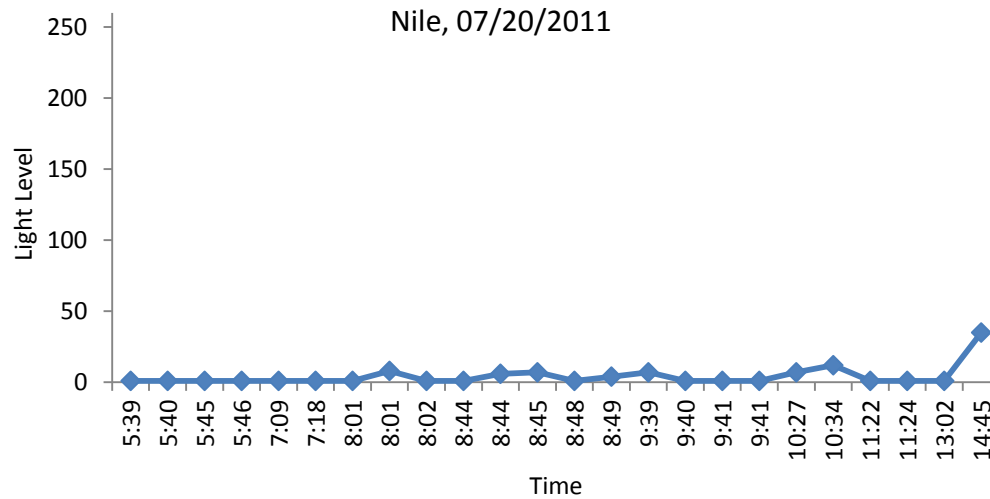
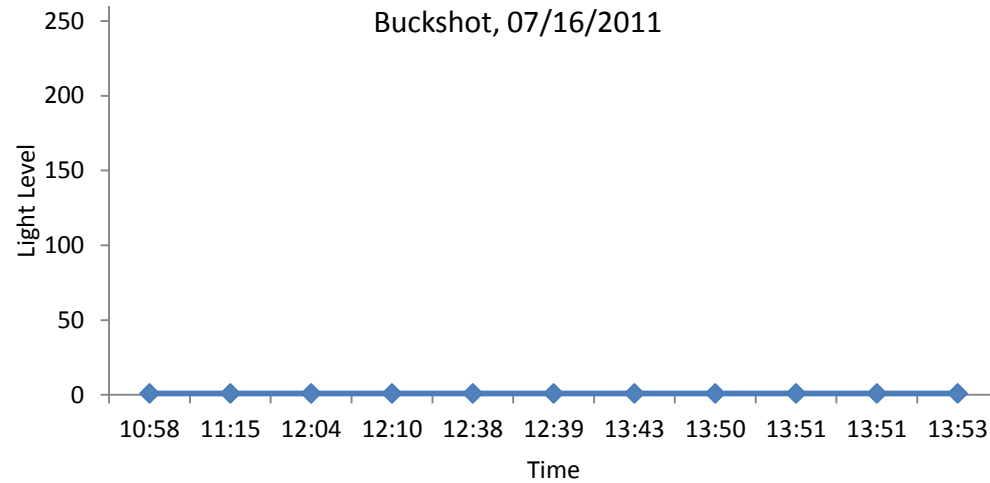
Appendix B continued: Average daily light levels vs. extrusion zone.



Appendix C: Examples of typical daily light levels for each extrusion zone.

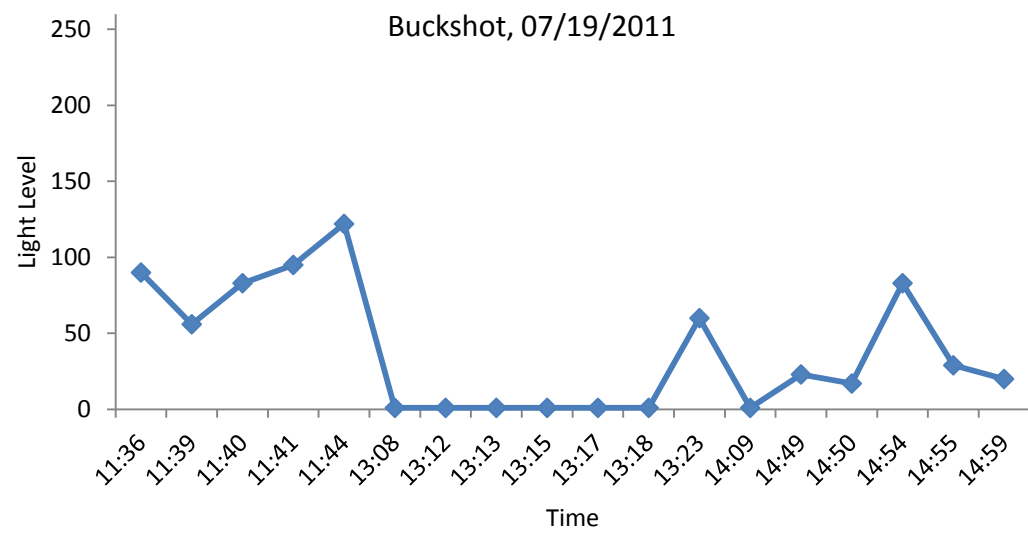
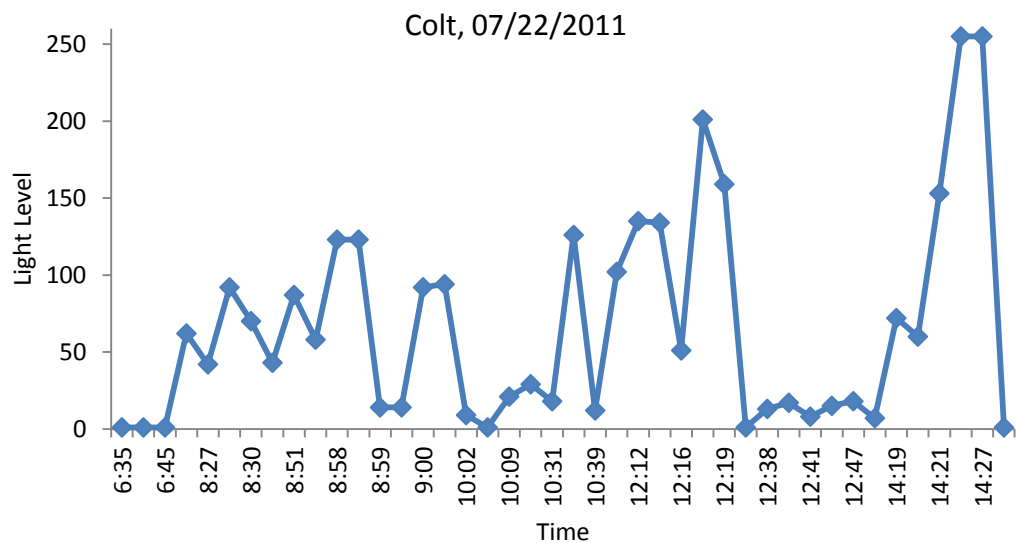
The following graphs are examples of the average daily light levels for all 4 extrusion zones for a select number of tags.

Typical **Zone 0** Daily Light Levels



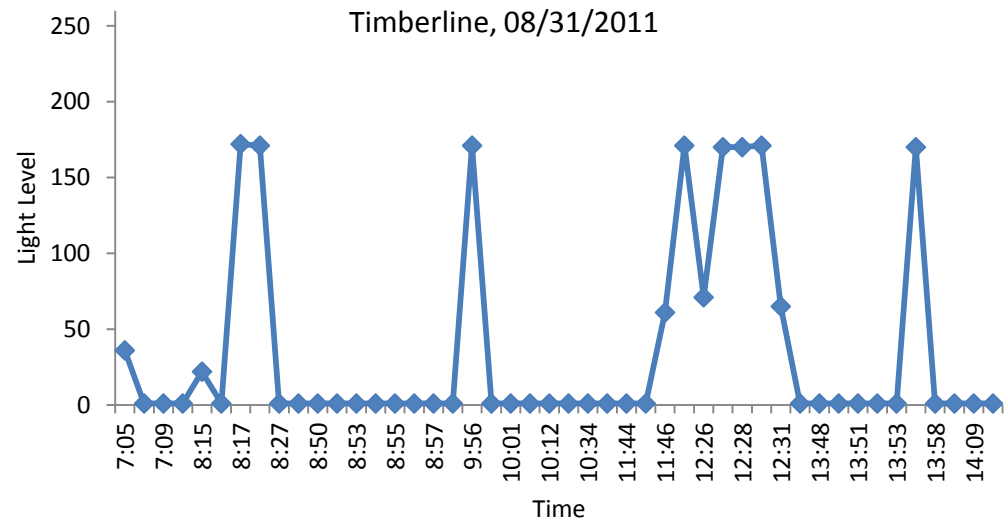
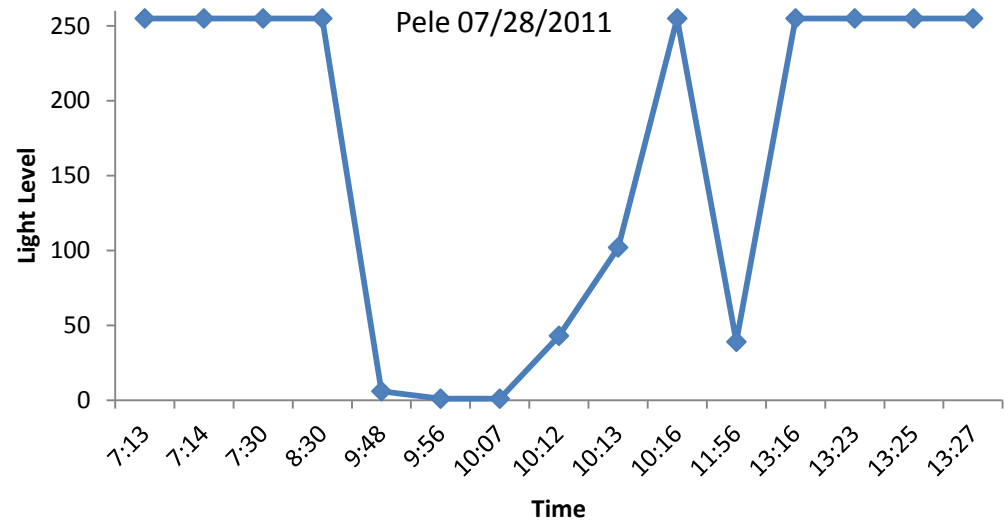
Appendix C continued: examples of typical light levels per zone.

Typical **Zone 1** Daily Light Levels



Appendix C continued: examples of typical light levels per zone.

Typical **Zone 2** Daily Light Levels



Appendix C continued: examples of typical light levels per zone.

Typical **Zone 3** Daily Light Levels

