From Whaling to Tagging: The Evolution of North Atlantic Humpback Whale Research in the West Indies

AMY S. KENNEDY and PHILLIP J. CLAPHAM

Introduction

The waters surrounding the Greater and Lesser Antilles (otherwise known as the West Indies, Fig. 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 humpback whales, *Megaptera novaeangliae* (Mattila et al., 1989; Mattila and Clapham, 1989; Mignucci-Giannoni, 1998; Roden and Mullin, 2000; Gandilhon, 2012).

Amy S. Kennedy, corresponding author, is with the Joint Institute for the Study of Atmosphere and Oceans, University of Washington, 3737 Brooklyn Ave N.E., Seattle, WA 98105, USA and the Marine Mammal Laboratory, Alaska Fisheries Science Center, NOAA, 7600 Sandpoint Way N.E., Seattle, WA 98115 (email: amy.kennedy@noaa.gov). Phillip J. Clapham is with the Marine Mammal Laboratory, Alaska Fisheries Science Center, National Marine Fisheries Service, NOAA, 7600 Sandpoint Way N.E., Seattle, WA 98115 (email: phillip.clapham@noaa.gov).

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ABSTRACT—North Atlantic humpback whales, Megaptera novaeangliae*, migrate from summer feeding grounds across the temperate and high latitudes to breeding grounds in the West Indies each winter. Humpbacks over-wintering near the Antillean islands comprise one of the most intensely studied populations of large whales in the world. Since scientific research began there in the late 1960's, researchers have worked to describe humpback distribution, abundance, and behavior in this major North Atlantic breeding ground. The progression and advancement of research techniques used in this region are largely representative of humpback studies worldwide. While decades of line-transect, photographic identification, acoustic, and genetic research have given us a good understanding of the occurrence and distribution of humpbacks in much of the West Indies, gaps in our knowledge still exist. This review describes the humpback whale research methods used throughout the West Indies that have evolved over time, from whaling data collection to modern day satellite telemetry, and summarizes the resultant knowledge regarding humpback distribution, abundance, and behavior. For conservation efforts within marine sanctuaries to effectively safe-guard the population, increased multi-national research and collaboration is needed to protect the North Atlantic humpback population from threats encountered throughout its entire life cycle.*

North Atlantic humpback whales migrate to the wider Caribbean region, between Cuba and 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 (Mattila et al., 1989; Katona and Beard, 1990; Smith et al., 1999). Although some breeding behaviors (e.g., singing and competitive groups) are observed in northern feeding grounds, the term "breeding ground" is used to describe low-latitude tropical or subtropical wintering areas where reproductive behaviors, such as singing, sexual competition, and nursing, are predominant, and where little to no feeding takes place (Chittleborough, 1965; Clapham et al., 1993; Clapham, 1996; Clark and Clapham, 2004).

Although humpbacks have historically used habitats off both the Greater (northern) and Lesser (southern) Antilles (Fig. 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 humpbacks are seen on Silver, Navidad, and Mouchoir Banks (north of Hispaniola), as well as in Samaná Bay in the northeastern Dominican Republic (DR). While 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.[1]

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 (Figures 2, 3, and 4 provide an overview of the projects discussed in this review). Modern scientific research on Antillean humpbacks began in the late 1960's, 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 or YONAH, conducted in 1992–93) (Smith et al., 1999), and More of the North

[1]Bonnelly, Idelisa. Fundación Dominicana de Estudios Marinos (FUNDEMAR), Calle Sócrates Nolasco No. 6, Residencial Carla Pamela, Apartamento 401 Ensanche Naco, Santo Domingo, D.R., personal comm., 01 April 2008.

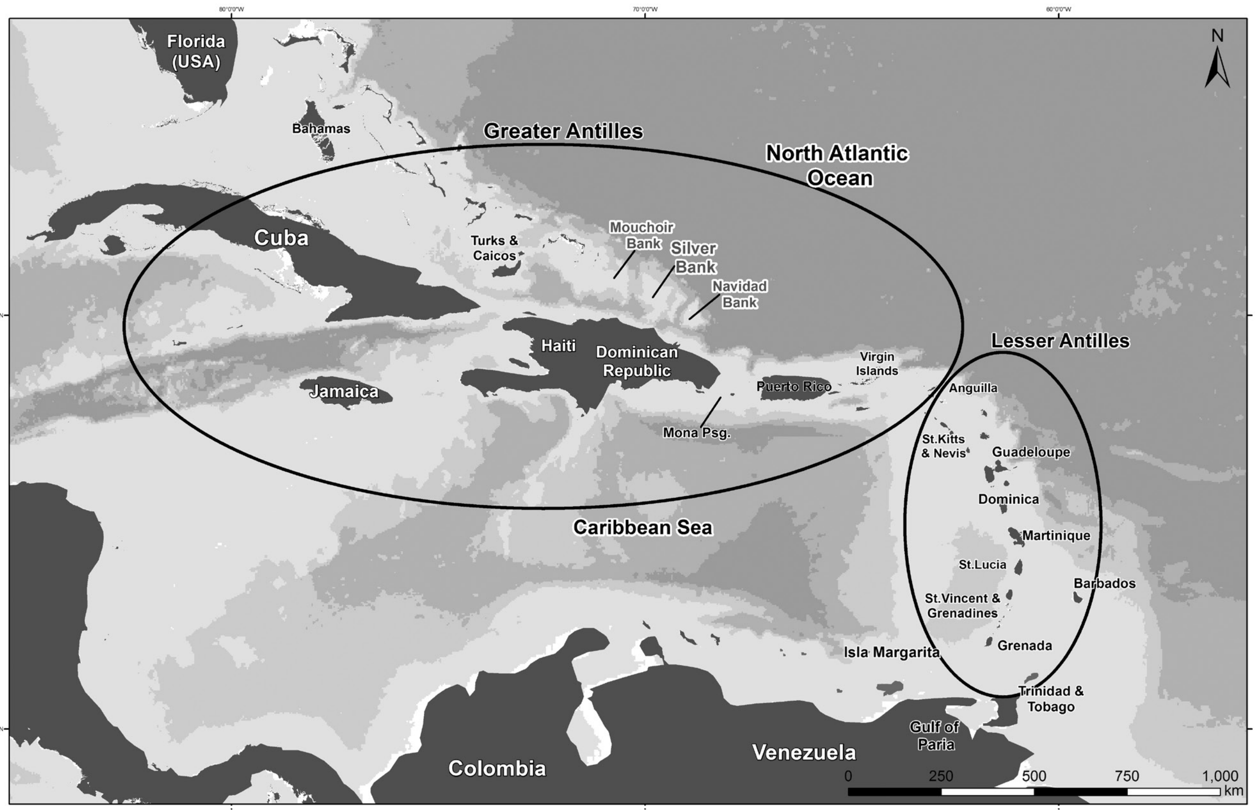

Figure 1.—The Greater and Lesser Antilles and Caribbean coast of Venezuela.

Atlantic Humpbacks or 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 research throughout the Antillean Islands, much is now known about humpback whales in this region and in the broader ocean basin. Nonetheless, some aspects of the biology and structure of this population remain poorly understood.

This review chronicles the evolution of scientific research methods, from the review of historical whaling data to present-day telemetry work, that have been employed throughout the major North Atlantic humpback breeding grounds. Additionally, we will discuss our current gaps in knowledge about the population and suggest future research strategies that may fill in those gaps. Finally, we include a discussion about the significance of this area to the status and management of the overall North Atlantic humpback whale population.

Methods

Whaling Research

The most basic form of 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 humpbacks 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, Mass.) "humpbacked" in the West Indies, either as a primary occupation or as part of broader expeditions targeting sperm whales, *Physeter macrocephalus,* elsewhere in the North Atlantic (Townsend, 1935; Mitchell and Reeves, 1983; Reeves et al., 2001; Smith and Reeves, 2002; Smith and Reeves, 2003a, b). 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 and Reeves, 2003b). Whaling logbook data from 19th century American whalers show that the

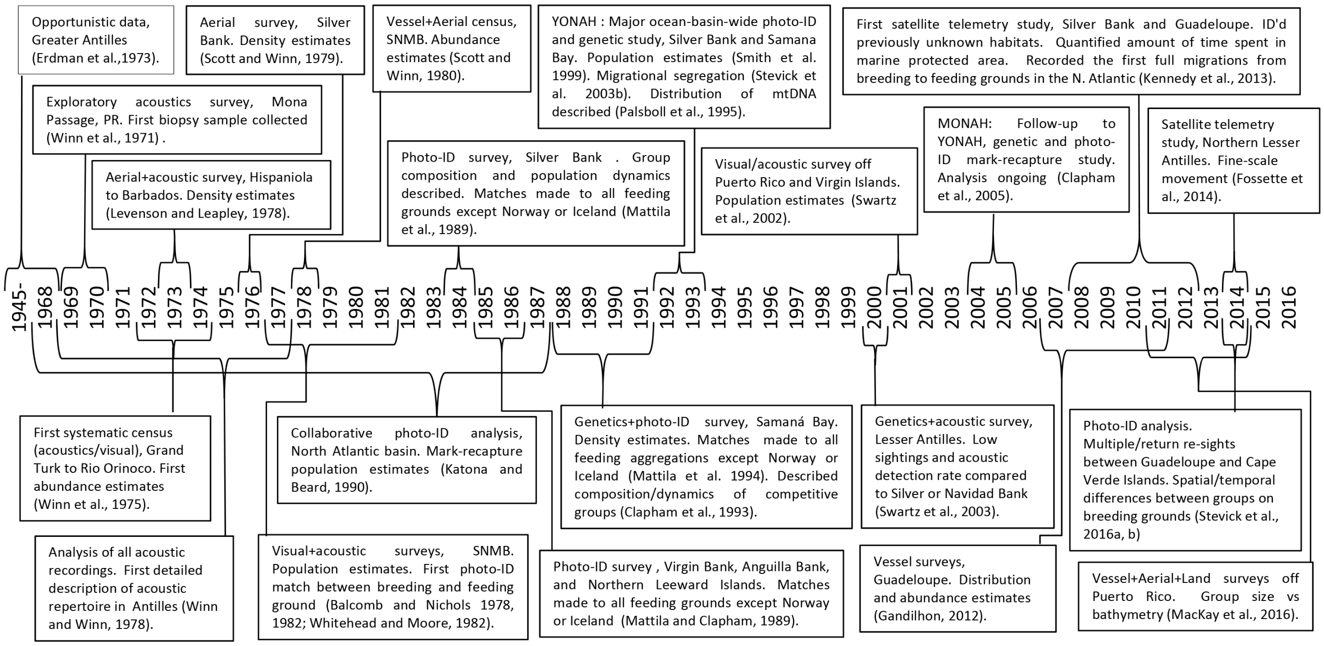

Figure 2.—Timeline of humpback whale research conducted off the Greater and Lesser Antilles.

highest catches of humpbacks during the winter breeding season occurred from the Windward Islands to Trinidad and westward along the Venezuelan coast (the Spanish Main) between January and May (Townsend, 1935; Mitchell and Reeves, 1983; Price, 1985; Smith and Reeves, 2003a, b).

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

Although detailed records were not kept, an estimated average of 44 whales per year were killed by shore-based whalers between 1880 and 1913 (Mitchell and Reeves, 1983). Most of these stations had shut down by 1880, but at least 5 were still operational in 1913, between St. Vincent and Grenada (Mitchell and Reeves, 1983; Smith and Reeves, 2002). The St. Vincent hunt, a native operation that until recently employed traditional Yankee whaling methods, continues at a low level today from the island of 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. Their 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 DR, 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 are records of vessels operating there at all.

The occurrence of relatively high humpback densities along the Lesser Antilles and Caribbean coast of Venezuela in the late 1800's stands in sharp contrast to the observed density of humpbacks observed in this region today. After a survey of the Greater and Lesser Antilles, Winn et al. (1975) estimated that 85% of the North Atlantic humpback breeding population is seen on the banks north of Hispaniola. In terms of density, the estimates of 1.15 whales/km^2 (Balcomb and Nichols, 1982) and 1.13 whales/km^2 (Whitehead and Moore, 1982) on Silver Bank are significantly higher than estimates for Samaná Bay (0.17 whales/km^2; Mattila et al., 1994), Virgin Bank (0.044 whales/km^2; Mattila and Clapham, 1989), and 0.005 whales/km^2 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 the Greater Antilles were reported by Swartz et al. (2003), who saw only 31 whales (between Guadeloupe and Trinidad/

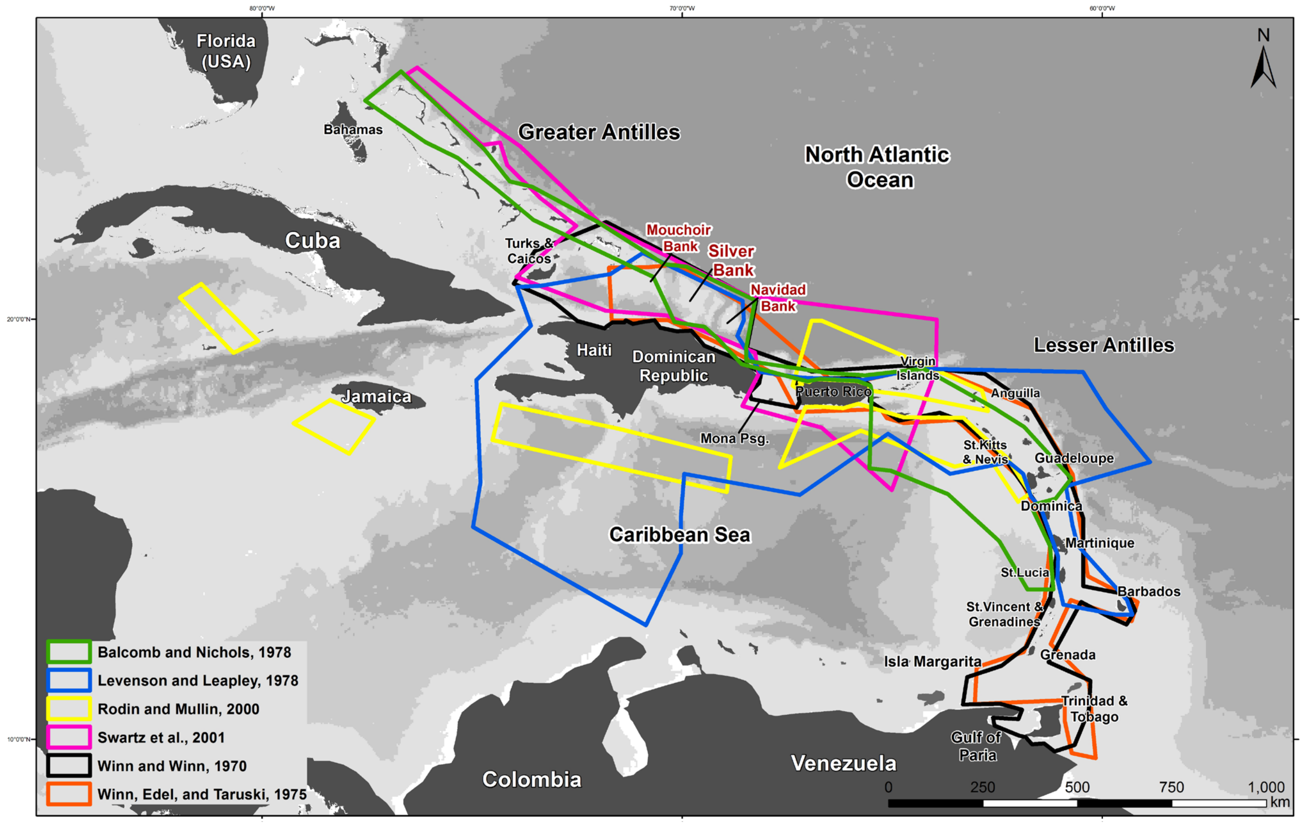

Figure 3.—Rough outlines of large-scale humpback whale research projects carried out from the late 1960's to present day off the Greater and Lesser Antilles.

Tobago) over nearly 3,200 km of effort in the eastern and southeastern Antilles in February and March of 2000. In addition to those sightings, there were acoustic detections of singing humpbacks throughout the Lesser Antilles between St. Croix and Isla Margarita, yet group size and/or population density cannot be estimated from sonobuoy data (Swartz et al., 2003).

Reeves et al. (2001) suggested that the apparent paucity of historical records of whaling effort in the Greater Antilles indicated that humpback whales were not utilizing the area extensively until the 20th century, and thus the modern abundance of humpbacks in the waters around Hispaniola was a post-whaling phenomenon. The authors suggested that this 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 North Atlantic (Winn and Scott, 1977; Reeves et al., 2001).

However, subsequent examination of non-whaling historical documents by researchers with the Centro de Investigación de Biología Marina (CIBIMA) at the Autonomous University of Santo Domingo has provided evidence that the waters of Hispaniola were always host to abundant whales (almost certainly humpbacks).[1] 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.[1] Notes about "abundant" whales in archived historical documents suggest that Dominican waters have long represented an important humpback habitat and that the absence of whaling records 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 humpbacks 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 whaling ceased in 1927 in the West Indies and in 1955 throughout the North Atlantic. The possibility that whales from the Lesser Antilles represent an entirely separate breeding population from those to the northwest seems unlikely given that photo-ID matches have linked both

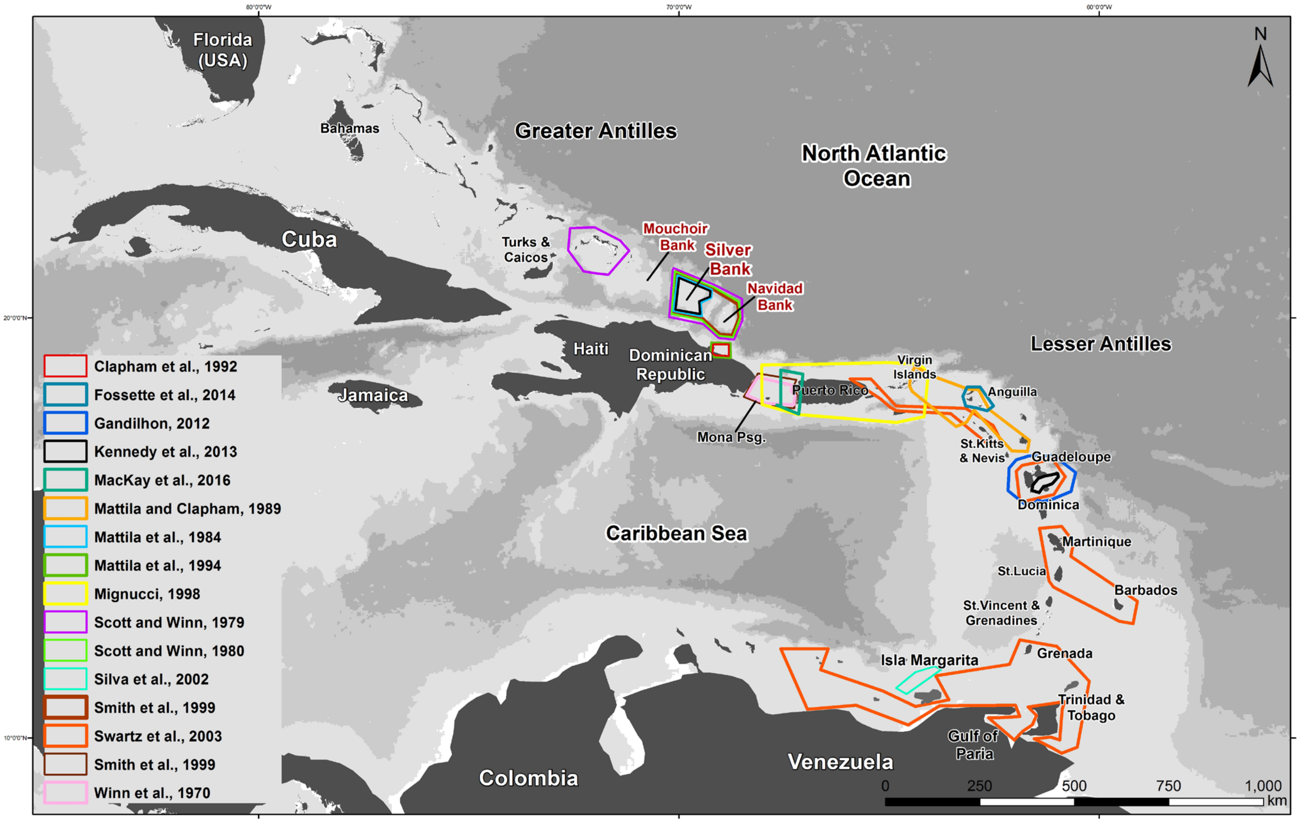

Figure 4.—Rough outlines of small-scale humpback whale research projects carried out from the late 1960's to present day off the Greater and Lesser Antilles.

areas to the same western North Atlantic feeding grounds (Stevick et al., 1999b; Robbins et al., 2006), yet new research suggests that this separation may be more significant than previously thought.

Modern Scientific Research

Although there had been some opportunistic humpback observations in the West Indies beginning in the mid-1940's (Erdman et al., 1973), modern studies of humpback whales in the West Indies began in the 1960's and continue today; Figure 2 provides a timeline of the development of this research. From the late 1960's to the early 1980's, 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 1970's, 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 also in 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 (Puerto Rico) in 1969 (Winn et al., 1971). After this, Winn et al. (1975) led the first systematic shipboard survey for humpback whales, from Grand Turk (Turks and Caicos) to Rio Orinoco (Venezuela) in the winters of 1972 and 1973. This study combined passive acoustics with 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, 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 and Leapley, 1978). Scott and Winn (1980) conducted shipboard and aerial visual surveys of Silver and Navidad Banks two years later to compare and inter-calibrate the two survey techniques, and to further document the size, distribution, movement, and stock identity of North Atlantic humpback whales in the Dominican breeding grounds.

Also in the late 1970's, George Nichols initiated an annual research program using the 144-ft barquentine *Regina Maris*. From this platform, Balcomb and Nichols (1978, 1982) and Whitehead and 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 humpbacks were found on Silver and Navidad Banks, with peak sightings made at the end of January for Navidad Bank, and two weeks later for Silver Bank.

David Mattila and colleagues began a humpback study in Mona Passage off the western coast of Puerto Rico in 1978, and collected photo-ID 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 (NAHWC, curated and published by the College of the Atlantic in Bar Harbor, Maine). 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, 1986), Mattila and Clapham (1989) conducted the first surveys of Virgin Bank, Anguilla Bank, and the northern Leeward Islands using similar techniques.

Herbert Hays and Howard Winn observed a number of humpback whales during a short visit to Samaná Bay in the northeastern DR in the late 1970's (unpub. data), but formal research did not begin there until CIBIMA researchers collaborated with the Center for Coastal Studies, in Massachusetts, in 1987 to conduct the first exploratory survey of the bay. This expedition led to a series of annual vessel surveys between 1988 and 1991. During the latter study, Mattila et al. (1994) used photo-ID to describe the occurrence, population composition, and habitat use by humpback whales in Samaná Bay, and the relationship of this bay to the more populous offshore banks.

The collection of identification photographs from the entire North Atlantic resulted in a growing catalogue of humpback fluke photos. This permitted the first connections to be made among breeding and feeding areas (Balcomb and Nichols, 1978). Furthermore, by the late 1980's, the NAHWC was large enough (n=3,647 individuals) to allow researchers to employ a photo-ID mark-recapture abundance estimate technique originally suggested by Balcomb and Nichols (1978) (Katona and Beard, 1990).

By the late 1980's, existing abundance estimates were outdated and it was apparent that they 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, was conducted in 1992 and 1993 (Smith et al., 1999). 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 and less biased 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 and Nichols, 1978; Levenson and 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 U.S. and British Virgin Islands. Between 2008 and 2011, Gandilhon (2012) conducted systematic line-transect studies for all cetaceans, including humpbacks, using the waters around Guadeloupe. Most recently, MacKay et al. (2016) conducted vessel, aerial, and land-based surveys for humpback whales off western Puerto Rico between 2011 and 2014 and described habitat preferences based on group size in that area.

By 2004, the estimates of abundance produced by YONAH were more than 10 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 of the North Atlantic Humpback (MONAH), was initiated. The goal of MONAH was to obtain humpback abundance estimates using biopsy-based genetic mark-recapture methods, although photo-ID data were also collected as a secondary objective.

In recent years, satellite telemetry has become a powerful tool used to describe the fine-scale movements of large whales (Baumgartner and Mate, 2005; Heide-Jørgensen et al., 2006; Zerbini et al., 2006). Kennedy et al. (2013) conducted the first North Atlantic humpback telemetry project between 2008 and 2012. Fine-scale individual movement data, as well as the first documented migrations from breeding to feeding grounds, were recorded. A second satellite telemetry project was conducted in April of 2014 from Anguilla that revealed movement throughout the French West Indies and Virgin Islands (Fossette et al., 2014).

Results

Distribution and Abundance

The Winn et al. (1975) systematic shipboard survey of the Antilles generated the first North Atlantic humpback population estimate of 785–1,157 (CI, presumed 95%) animals. Average density estimates of 0.21 whales/km^2 (Silver Bank) and 0.23 whales/km^2 (Navidad Bank) were also calculated; these densities demonstrated that the great majority of breeding whales in the West Indies were spending time in the Silver, Navidad, and Mouchoir Banks complex.

Levenson and Leapley's (1978) aircraft-based acoustic survey in 1973 deployed 82 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 longitude 70°W and north of latitude 16°N, with the highest concentrations centered over Silver and Navidad Banks.

In 1976, Scott and Winn (1979) conducted two additional aerial survey flights over Silver Bank to explore the utility of using different methods (including photogrammetry) for humpback whale stock assessment. The authors calculated a density of 0.311 ± 0.069 (95% CI) whales/km^2. Since this density was statistically similar to the Winn et al. (1975) calculation, despite an estimated growth rate of 5% per year (from ACMRR, 1976), Scott and 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 surveys calculated an abundance estimate of 1,069–1,377 (95% CI) on Silver Bank and 306–370 (95% CI) whales on Navidad Bank. The density estimates from this study (0.513 whales/km^2, sd = 0.36) for Silver Bank and 0.554 whales/km^2, sd = 0.368) for Navidad Bank were over 50% higher than the corrected estimate calculated by Winn et al. (1975). 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). The estimates derived from the 1977 survey roughly equated to a 1.8% population increase per year from the Winn et al. estimate (1975), yet the authors admit that their number did not account for all potential recruitment and/or sampling bias.

Sighting data collected from *Regina Maris* in 1980 and 1981 were ranked and sorted on detection probability parameters and produced, in theory, more accurate mean population estimates for Silver, Navidad, and Mouchoir Banks, yet there were still sampling method and/or analysis biases that needed to be addressed (Balcomb and 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 analyses of population trends (Table 1).

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/nmi^2 (sd = 0.029) on Virgin Bank. The density of humpbacks on Anguilla Bank was approximately 50–66% 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 and Nichols, 1982) suggested a northeast-to-southwest movement through the Antilles during the winter.

Table 1.—Differing mean population estimates for Silver and Navidad Banks, 1973, 1977, 1980, 1981.

	Mean Population Estimates	
Year	Silver Bank	Navidad Bank
1973[1]	754	110
1977[2]	809	96
1980[3]	1432	441
1981[3]	963	214

[1]Winn et al., 1975.
[2]Balcomb and Nichols, 1978.
[3]Balcomb and Nichols, 1982.

In Samaná Bay, Mattila et al. (1994) discovered that whale density (0.17 whales/km^2) 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 slightly among years.

Using the NAHWC collection of 3,647 individual 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 $\pm$ 2,617 (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 1970's (see Table 1) may be the result of differing sex/age class and/or feeding ground origin occupancy patterns in the breeding grounds.

During the YONAH project, nearly 3,000 individuals were photographed, and just over 2,000 were biopsied throughout the North Atlantic in 1992 and 1993 (Smith et al., 1999). The resulting ocean-basin-wide population estimates of 10,400 (95% CI = 8,000–13,600) from biopsy data, and 10,600 (95% CI = 9,300–12,100) 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 (Smith et al., 1999).

Palsbøll et al. (1995) used the biopsies from the YONAH study to produce the first mark-recapture abundance estimate based on microsatellite genotyping data. Stevick et al. (2003b) later applied strict photo-ID protocols and more robust statistical analyses to the pooled mark-recapture data from YONAH and all NAHWC records collected between 1979 and 1991 to produce an abundance estimate of 11,570 (95% CI = 10,290 to 13,390) humpbacks in the North Atlantic. The Stevick et al. (2003b) method of pooling the data and applying advanced statistical analyses likely reduced the heterogeneity and small sample size biases associated with the estimates from YONAH alone (Smith et al., 1999).

An important finding of YONAH was that sex-specific abundance calculations derived from the breeding ground genetic samples produced significantly different 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-ID 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 migratory timing. Whatever the reason, the doubled male-only estimate agrees well with the Stevick et al. (2003b) overall photo-ID estimate of 11,570, and these two remain the most reliable estimates of North Atlantic humpback whale abundance to date.

A visual and acoustic survey of the Lesser Antilles conducted by Swartz et al. (2002) 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 humpbacks over the 10,900 km surveyed) reinforced earlier findings (Winn et al., 1975; 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 2002 in an area not covered by Swartz et al. (2003) and recorded 11 humpback whale sightings just north of Margarita Island and Los Frailes Archipelago (Venezuela). Gandilhon's (2012) line-transect surveys, which took place between January and June, 2008–11, resulted in a population estimate of 442 (95% CI = 302–442) humpbacks using the territorial waters of Guadeloupe. Peak abundance was recorded in April.

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, MONAH, was conducted in January and February of 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-ID, 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. However, telemetry studies have shown movement throughout the greater Caribbean region within the breeding season (Kennedy et al., 2013, Fossette et al., 2014); while much of this within-season movement occurred on Silver, Navidad, and Mouchoir Banks, even small individual movements into or out of a 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).

Population Structure

In the early 1970's, before photo-ID catalogs or genetic analysis technologies had been developed, Mitchell and Reeves (1983) 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 1970's 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 and 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 and Nichols, 1978). Extensive photo-ID analysis by Katona and Beard (1990) highlighted the presence of four, or probably five, separate feeding aggregations (Iceland/Denmark Strait, western Greenland, Newfoundland/Labrador, Gulf of St. Lawrence, and the Gulf of Maine/Scotian Shelf). Stevick et al. (2003b) later used YONAH data to define the feeding aggregation boundaries as the 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. 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 and Clapham, 1989) was originally attributed to the small number of catalogued whales from the eastern feeding grounds, but may also be the result of survey timing or behavioral differences between eastern and western North Atlantic whales (Stevick et al., 2016b). 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 (Clapham et al., 1993; Larsen et al., 1996; Stevick et al., 1999a, 1999b; Smith et al., 1999; Bérubé et al., 2004).

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., 2003a). Furthermore, a recent examination of photos collected between 1972 and 2014 from Antigua to Venezuela suggest that humpbacks wintering in the southeastern Caribbean are not a representative subset of those wintering off the Dominican Republic (Stevick et al., 2016b). Stevick et al. (2016b) found that animals that typically feed in the eastern North Atlantic are significantly over-represented in the southeastern Caribbean compared to animals that summer in the western North Atlantic. These findings suggest that southeastern Caribbean humpbacks represent a group of behaviorally distinct whales within the Antillean breeding grounds.

The most recent confirmation of mixing between eastern and western North Atlantic feeding stocks in the Antilles came when whales tagged on Silver Bank, Guadeloupe, and Anguilla were tracked over either full or partial migrations to both regions (Kennedy et al., 2013; Fossette et al., 2014). Interestingly, two satellite-tagged whales heading toward eastern North Atlantic feeding grounds 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 the spatial and temporal separation of the tag deployments (Kennedy et al., 2013). This overlap may represent evidence for the existence of specific migratory corridors from the Antillean breeding grounds to eastern North Atlantic feeding grounds (Charif et al., 2001), and supports the findings of Horton et al. (2011) that humpbacks, like other marine animals (Gaspar et al., 2006; Trathan et al., 2008), can navigate across long distances with remarkable precision.

In addition to apparently unequal breeding ground occupancy rates by whales from different feeding grounds (Stevick et al., 2016b), 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 (with or without calves) on 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 female reproductive condition (Chittleborough, 1965; Dawbin, 1966, 1997).

Genetic analyses indicate the existence of a second, and perhaps even third, as-yet undiscovered North Atlantic breeding ground (Palsbøll et al., 1995; Larsen et al., 1996). However, speculation that the Cape Verde Islands (CVI) may represent one of these unknown breeding grounds seems unlikely (Larsen et al., 1996) due to the relatively small local humpback population size. Additionally, Winn et al. (1981) compared songs between the West Indies and the CVI and found no difference; this might suggest no stock separation, but song is known to be at best a crude and sometimes unreliable indicator of stock division (Garland et al., 2012).

More recently, Jann et al. (2003) documented a photo-ID match between a whale seen in the CVI and the Denmark Strait (off Iceland), yet the low photographic sample size in both regions cannot conclusively support the hypothesis that the CVI is the primary migratory destination for eastern North Atlantic humpbacks. While a surprising recent discovery of 4 humpback whales photographically identified in both Guadeloupe and Boa Vista (CVI) (Stevick et al., 2016a) further underscores the suggestion that there are behaviorally distinct groups within the overall North Atlantic population, it cannot fully explain the undiscovered breeding ground.

Telemetry results highlight the vastly different distances over which individuals from different feeding grounds must migrate to reach the breeding grounds. For humpback whales that feed off Norway, this distance is approximately three times that of Gulf of Maine whales, and tag data have documented correspondingly large differences in transit times (Kennedy et al., 2013). The cost of this extended migration vs. the overall benefit to an individual humpback are difficult to define or measure, yet the energetic requirements for a full migration between the Antilles or the CVI and the eastern North Atlantic may be high enough to deter yearly full migrations. This disparity in migratory distance and the resultant decisions made by individuals regarding migratory timing and extent may partially explain the spatial and temporal segregation of humpbacks that feed in the eastern vs. western North Atlantic on the breeding ground.

Habitat Use and Within-season Movement

Winn et al. (1975) noted that, during the breeding season, humpbacks were found "almost exclusively" on banks between 10 and 100 fathoms (18–180 m) deep, yet there was little or no sighting effort in the deep waters off the shelf break. Roden and Mullen (2000) recorded 12 humpback sightings in an average depth of 2,877 m during their cetacean abundance survey between Guadeloupe and western Cuba. Mignucci-Giannoni (1998) compared humpback sightings (published and unpublished, up to 1985) off Puerto Rico and the Virgin Islands and found that those whales also prefer shallow, nearshore waters with little slope. A recent study off the western coast of Puerto Rico found that mother-calf pairs were most often found nearshore in shallow water, while singers were found more frequently along the shelf edge than other areas in Mona Passage (MacKay et al., 2016). Depth did not appear to be a factor for the presence of single non-singing whales (MacKay et al., 2016).

From earlier studies, it was estimated that approximately 85% of the whales on the breeding ground were found on Silver and/or Navidad Banks each year, and Silver Bank appeared to have the highest calf density in the West Indies (Winn et al., 1975; Balcomb and Nichols, 1982). Virgin and Anguilla Banks, Mona Passage (Puerto Rico), and Samaná Bay (DR) 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 like those on Silver Bank. However, calves were observed there during YONAH surveys (Robbins et al., 2001; Mattila et al.[2]), so the relative suitability of this habitat for mothers is 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 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 1970's (Winn et al., 1975; Swartz et al., 2003; Silva et al., 2006). Whitehead and 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 a small number of 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 east to west along the Antillean Chain. Unfortunately, mark-recapture studies do not permit finer-scale habitat-use descriptions.

Telemetry studies have shown that individuals travel to areas relatively distant from densely populated banks, including to waters off the Turks and Caicos Islands, the northern coast of Haiti, Antigua, Barbuda, Anguilla, and the Virgin Islands (Kennedy et al., 2013; Fossette et al., 2014). These studies also show that whales tagged in the West Indies breeding grounds also travel relatively long distances throughout the island chain within a breeding season.

Reproductive Behavior

Winn et al. (1971) recorded humpbacks 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, which resulted in the first formal description of humpback whale song 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; this 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. That singers are male has been confirmed by numerous subsequent studies worldwide (Glockner-Ferrari and Ferrari, 1981; Glockner, 1983).

Winn and Winn (1978) conducted a detailed analysis of all 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

[2]Mattila, D. K., M. Bérubé, R. Bowman, C. Carlson, P. J. Clapham, A. A. Mignucci-Giannoni, P. Palsbøll, J. Robbins, P. Stevick, and O. Vasquez. 2001. Humpback whale habitat use on the West Indies breeding grounds. Sci. Committee Doc. SC/53/NAH3 (unpubl.), Int. Whal. Comm., Camb. Engl. (avail. from IWC, Camb., U.K.).

of local acoustic "dialects" within 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 highly aggressive behavior, often termed "competitive groups" (Clapham et al., 1993) or "rowdy groups" (Tyack and Whitehead, 1983), had been observed with frequency in the West Indies and elsewhere. This behavior was seen as intra-sexual competition among males for access to a female. A study in Samaná Bay between 1989 and 1991 used molecular sexing and photo-ID to confirm this assumption (Clapham et al., 1993). 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 authors noted that the fact that relatively few principal escort displacements have ever been observed could mean that the PE had already mated with the NA and was mate-guarding (thus making her less attractive to the other males in the group).

Prior to the Clapham et al. (1993) study, 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; 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 PE in some cases (Clapham et al., 1993). Additionally, photo-ID 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).

Conservation

The first conservation efforts aimed at protecting humpback whales in the West Indies occurred in the DR. The critical importance of Silver and Navidad Banks to humpback whales and other cetaceans was reflected in the designation of the Silver Bank Marine Mammal Sanctuary in October of 1986. This was effectively the world's first national humpback whale sanctuary and, as such, the designation represented a major global conservation milestone for the species. The sanctuary (now named the Silver and Navidad Banks Sanctuary) was expanded on 5 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 territorial waters of St. Martin, St. Barthelemy, Guadeloupe, and Martinique in the Lesser Antilles. This new sanctuary is governed under the Specially Protected Areas and Wildlife (SPAW) protocol, established under the Cartagena Convention. The Silver and Navidad Banks and Agoa sanctuaries, together with protected waters off Bermuda and Stellwagen Bank (off Massachusetts), are part of a larger "sister sanctuary" program designed to improve humpback conservation by encouraging management collaboration between nations that host breeding, feeding, and/or migrating humpback whales.

Since commercial whaling in the North Atlantic ceased in the mid-1950's, there have been relatively few threats to humpback whales in their primary North Atlantic breeding range. Elsewhere in the North Atlantic (particularly on the feeding grounds), the major anthropogenic threats are entanglement in fishing gear and ship strikes (Laist et al., 2001; Robbins and Mattila, 2004; Johnson et al., 2005).

In the breeding range itself, disturbance from nature-focused tourism and oil and gas exploration (notably off Venezuela) are the principal conservation concerns. Whale-watching in the Antilles began in the 1980's on Silver Bank and in Samaná Bay and by the mid-1990's had spread to the Turks and Caicos, Puerto Rico, and several locations in the Lesser Antilles (Hoyt and Hvenegaard, 2002). The DR government has passed regulations requiring permits for access to the Silver and Navidad Banks Sanctuary in an attempt to limit the human disturbance to the whales in their territorial waters, but unregulated whale-watching throughout the breeding range is almost inevitable and likely to increase over time. Additionally, the growing oil and gas industry off the coast of Venezuela increases the potential for anthropogenic disturbance and/or mortality of humpbacks overwintering there.

An example of directed conservation efforts in the DR occurred in 2005, when a group called Los Amigos de los Delfines conducted a cetacean survey of the waters off the southeastern corner of Hispaniola. Whaley et al. (2008) observed a group of 4 humpbacks (including a calf) just off Saona Island; these were the first confirmed sightings of humpbacks off the southern coast of the DR since the early 1980's (Whaley et al., 2008). The authors' efforts in detailing the harassment of these animals prompted the Dominican government 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 NMFS 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.[3]) While adherence is not yet mandatory, the government strongly encourages all mariners within the DR 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 anthropogenic threats is essential for conservation and management of humpbacks world-wide. Satellite telemetry has shown that tagged humpbacks spent less than half of the tag duration within marine sanctuary boundaries (Kennedy et al., 2013), proving that efforts aimed at the conservation and management of this species need to occur on an ocean-basin-wide level in order to protect these highly mobile animals. A management plan for the Silver and Navidad Banks Sanctuary was recently finalized and represents a major step forward in the protection of all species which depend upon the waters of the DR, yet effective multi-national collaboration is still lacking range-wide.

Conclusions

The evolution of humpback whale research methods and knowledge in Antillean waters is largely representative of studies of this species elsewhere in the world (i.e. Darling and McSweeney, 1985; Baker et al., 1994; Helweg et al., 1998; Stevick et al., 2004; Robbins and Mattila, 2006; Barlow et al., 2011, and many others). Much has been learned about humpbacks in the wider Caribbean region since research began there more than 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.

[3]Berchok, C., J. Crance, and L. Morse. 2009. Humpback song and ship noise impact: A passive acoustic study. Unpublished final report to NOAA/NMFS/AFSC National Marine Mammal Laboratory, 7600 Sandpoint Way N. E., Seattle WA 98115.

Knowledge Gaps

Smith and Pike (2009) outline the seven major unknown factors, or enigmas, of North Atlantic humpback whale population dynamics and biology. While many of these enigmas pertain to feeding season population dynamics, large gaps in knowledge of the breeding ground population structure, temporal distribution, and population abundance still exist, despite decades of research throughout the region.

The apparent failure of humpbacks to repopulate the Windward Islands region to levels suggested by historical whaling catches is difficult to understand, given the general resilience of this species elsewhere in the world, and has yet to be explained. Genetic analysis, a recent reexamination of over 40 years of fluke photographs showing unequal representation of animals from different feeding grounds on the breeding ground, and differences between population abundances estimated on the feeding ground vs. the breeding ground suggest two things: that there is a 3rd as-yet-undiscovered breeding ground in the North Atlantic (Palsbøll et al., 1995; Larsen et al., 1996; Smith and Pike, 2009; Stevick et al., 2016b), and that there are likely behaviorally distinct groups of humpbacks on the breeding grounds as well as the feeding grounds (Stevick et al., 2003a; Stevick et al., 2016b). Humpbacks have been known to overwinter and engage in breeding behavior (notably singing and competitive group activity) on the feeding grounds and during migration (Swingle et al., 1993; Robbins et al., 2001; Barco et al., 2002; Clark and Clapham, 2004) yet whether breeding outside of well-described areas occurs on a large enough scale to influence the population's genetic profile and abundance estimates is unknown. While the recent discovery of multiple instances of exchange between Guadeloupe and the CVI (Stevick et al., 2016b) is an important piece of the puzzle, it seems unlikely that this exchange could fully account for the feeding vs. breeding ground population estimates or the undiscovered breeding ground.

Knowledge gaps regarding breeding ground population dynamics exist, in part, due to the bias resulting from inadequate spatial and temporal survey coverage in the West Indies. In order to increase genetic, photographic, and/or acoustic sample sizes, the vast majority of projects conducted in the area were designed to coincide with the highest densities of animals (e.g., January through March within the Silver, Navidad, and Mouchoir Banks complex). Unfortunately, this strategy likely excludes members of behaviorally distinct groups from being sampled, thus biasing the resulting conclusions about North Atlantic humpback populations overall. Additional telemetry, photo-ID, and biopsy studies that cover a greater spatial and temporal scale are clearly needed in order to fully understand North Atlantic humpback whale population dynamics. Continued and expanded multi-national research collaboration is essential to the success of such projects and should be considered the highest priority for creating and executing an effective management plan.

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