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Acoustic and Visual Survey of Humpback Whale (*Megaptera novaeangliae*) Distribution in the Eastern and Southeastern Caribbean Sea

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ABSTRACT.—Humpback whales (*Megaptera novaeangliae*) historically ranged throughout the eastern and southeastern Caribbean Sea during the winter months. Commercial whaling from the 1820s to the early 1900s depleted the population. A combined passive acoustic and visual survey for humpback whales was conducted to assess the current winter distribution of this species in areas where it was exploited to depletion, and to evaluate the effectiveness of using passive acoustic survey methods to detect and locate humpback whales. Visual surveys were conducted independently but simultaneously with acoustic surveys to compare both detection methods. Humpback whale song was detected throughout the entire survey area, indicating that the species continues to occupy its historical range. A total of 31 sightings were made (n = 46 individuals, including three calves). In contrast, at least 78 unique acoustic detections of different singing males was made. The greater number of whales detected acoustically demonstrated the advantage of passive acoustic methods over visual methods for detecting male singing humpback whales; however, some sightings were not detected acoustically, demonstrating that visual methods are superior for detecting non-vocalizing whales. The number of whales detected indicates that the abundance of humpbacks in the eastern and southeastern Caribbean Sea is considerably lower than it was during the 19th century whaling period, and much lower than present day abundance in the primary wintering areas in the northeastern Greater Antilles.

INTRODUCTION

Most of the North Atlantic population of humpback whales (*Megaptera novaeangliae*) of approximately 10 600 animals (95% CI = 9300-12,100) is believed to winter in the West Indies, where calving and mating occur (Smith et al., 1999). Low numbers are also found in winter around the Cape Verde Islands in the eastern North Atlantic (Reiner et al., 1996; Hazevoet and Wenzel, 2000). Research on humpback whales wintering in the western North Atlantic has focused on the Greater Antilles and the northern portion of the Lesser Antilles, which host the greatest present-day concentration of whales. These well-studied areas include Silver Bank, Navidad Bank, and Samana Bay off the northeastern coast of the Dominican Republic, Mona Passage off western Puerto Rico, and Virgin and Anguilla Banks. Research in the Lesser Antilles from Guadeloupe south to Venezuela has been relatively sparse and was conducted over 25 years ago (Winn et al., 1975; Levenson and Leapley, 1978). These studies and recent anecdotal reports indicate that the present-day abundance of whales in this region is low.

Whaling data indicates that this pattern of humpback whale distribution in the West Indies was reversed in the past. Humpback whales were sufficiently abundant from January through May in the eastern and southeastern Caribbean to support a large-scale fishery in the 19th century

(Townsend, 1935; Mitchell and Reeves, 1983; Price, 1985). Commercial exploitation of this species in the West Indies began in the 1820s, declined in the 1880s, and the fishery was abandoned by 1927 due to scarcity of whales (although a traditional hunt that takes two or three whales per season has continued at Bequia since 1880). A comprehensive review of 19th and early 20th century whale catches and sightings by American whale ships indicated that humpbacks were formerly more abundant during the breeding season throughout much of the Lesser Antilles south to the coast of Venezuela than are found in this region today (Reeves et al., 2001a, b). For example, of 807 records in which 2444 humpback whales were sighted, struck, or caught during 48 winter whaling voyages in the West Indies, the greatest number were reported from St. Vincent and the Grenadines (319 records covering an estimated 958 humpbacks), followed by Guadeloupe (190 records, 592 humpbacks), Dominica/Martinique/St. Lucia (74 records, 193 humpbacks), and Venezuela and the Gulf of Paria (64 records, 216 humpbacks combined). Another study of historical whaling records from Trinidad and Tobago for this same period reveals that at least four shore whaling stations operated in the northeastern Gulf of Paria between 1826 and the 1850s, averaging 25-30 whales in a good year with a maximum documented one-year catch of 35 humpbacks in 1848 (Reeves et al., 2001b). In contrast, there is little evidence that humpback whales were taken on a more than casual basis in the northern waters off Hispaniola and Puerto Rico in the Greater Antilles that host today the major winter concentrations of humpback whales (Reeves et al., 2001a).

The prevalence of strong trade winds in the eastern and southeastern Caribbean reduces the effectiveness of traditional ship-based visual surveys. Therefore we used passive acoustic methods to detect whales that otherwise might be missed by visual methods alone. Passive acoustic surveys offer advantages over visual surveys by allowing the detection of submerged cetaceans, by extending search distances beyond line of sight, and by enabling surveys to be conducted during inclement weather (e.g., high winds and sea states) and at night. Recent attempts to augment visual surveys with acoustic methods include surveys for blue whales (*Balaenoptera musculus*) and fin whales (*Balaenoptera physalus*) (Clark and Fristrup, 1997), bowhead whales (*Balaena mysticetus*) (Zeh et al., 1993; Clark and Ellison, 1989), sperm whales (*Physeter macrocephalus*) (Barlow and Taylor, 1998; Leaper et al., 2000), and humpback whales (Norris et al., 1999). While there are difficulties with integrating acoustic and visual detection methods, the former clearly overcome some limitations of traditional visual surveys and the combination of both techniques provides data that would not be available from either method alone (Clark and Fristrup, 1997). Since male humpbacks sing for prolonged periods, they are good subjects for detection with passive acoustic methods.

The main goals of this survey were to develop a general picture of the regional abundance and distribution of humpback whales in the eastern and southeastern Caribbean relative to their recovery from commercial exploitation, and to provide a foundation on which to develop more quantitative population studies. The specific objectives included surveying areas where humpback whales were depleted by commercial whaling to determine to what extent whales continue to occur in these areas, and evaluating the feasibility of using combined visual and passive acoustic survey methods to locate humpback whales.

Materials and Methods

Study area, survey timing and survey vessel

The area of primary interest included the waters of the Lesser Antilles around the Leeward Islands (except for the Virgin Islands, the islands on the Anguilla Bank, and Saint Eustatius), the Windward Islands, Barbados, Trinidad and Tobago, the islands north of Venezuela, and the Caribbean coast of Venezuela (Fig. 1). Country clearance was received to conduct the survey in the waters of St. Kitts and Nevis, Guadeloupe, Martinique, St. Lucia, Barbados,

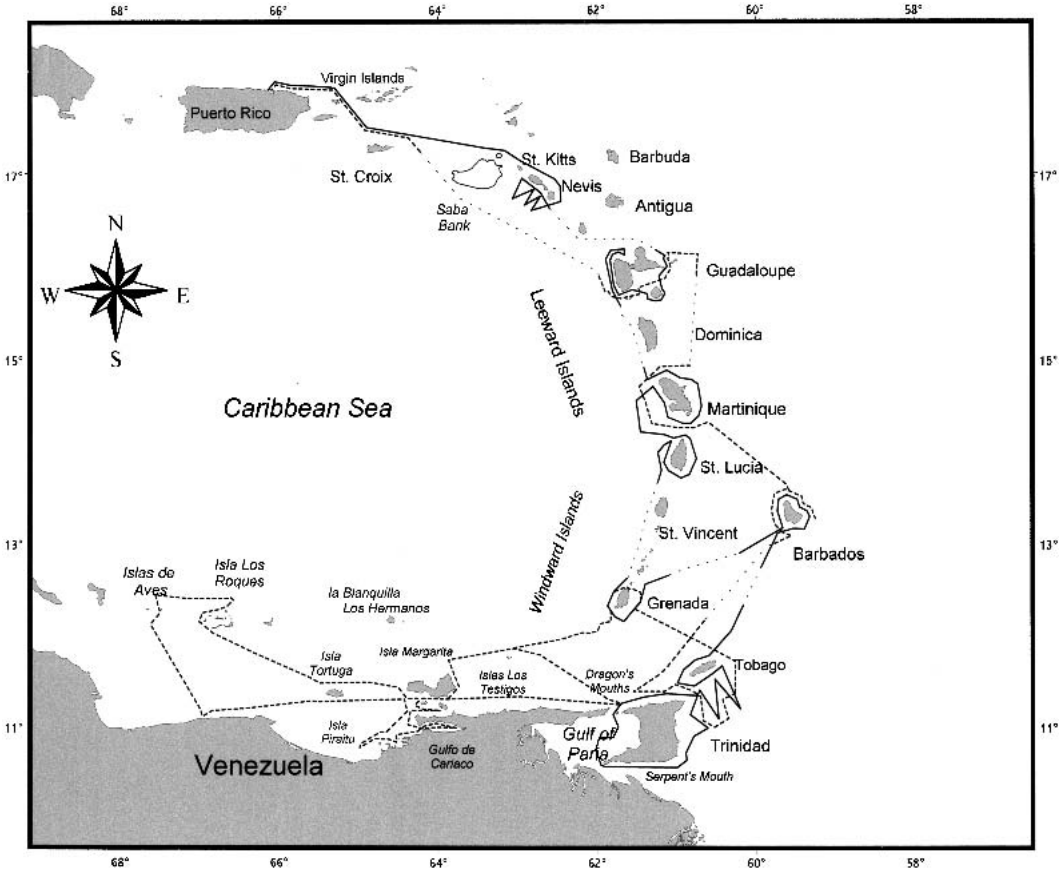

FIG. 1. Survey trackline: Leg 1 (solid black line), Leg 2 (dashed line), and closed areas (dotted line).

Grenada, Trinidad and Tobago, and Venezuela. The nations of Antigua and Barbuda, Dominica, and St. Vincent and the Grenadines declined to provide vessel clearances and the survey did not include their waters. Clearance for Saba (including Saba Bank) and Montserrat was not requested.

Historical whaling records indicate that humpback whales formerly occurred throughout the Lesser Antilles from January through May (Reeves et al., 2001a, b). Recent research in the Greater Antilles and northern Leeward Islands indicates that the winter humpback population there peaks from mid-February to mid-March (Mattila et al., 1994; Mignucci-Giannoni, 1998). Thus, our survey was scheduled during February and March to coincide with the peak of the humpbacks' winter breeding season. The survey was conducted from the 75 m U.S. NOAA ship *RV Gordon Gunter*; this former U.S. Navy vessel was engineered to support passive acoustic operations and is well suited for visual and acoustic surveys. The ship is powered by diesel-electric engines that are acoustically quiet compared to power plants in other vessels, and produce minimal low-frequency background noise during survey operations. The observation deck, located approximately 14 m above the water's surface, provides good visibility for observers.

Acoustic and visual survey

The survey was designed to provide a general picture of the distribution of humpback whales, and not to estimate absolute abundance. Thus, rather than follow ran-

domized transect lines and standard line transect survey protocols (Barlow, 1995), our track lines circumnavigated the islands to allow coverage of their coastal waters, the channels between the islands, and to cover the coastal waters of northern Venezuela. Visual and acoustic surveys were conducted simultaneously during "on-effort" periods to allow comparison of both methods for detecting whales. The dual survey mode switched to an "off effort" survey mode when visual conditions deteriorated (due to sea state > Beaufort 5) and when the ship left the survey track line to locate whales detected acoustically.

Visual survey.—Ship survey speed averaged 10 knots during "on effort" visual survey mode. Observations were conducted continuously from 0630 hrs to sunset (approximately 1930 hrs) each day. Two teams of three observers operated rotating 2-hr shifts, weather permitting (i.e., no rain, Beaufort Sea state $\leq$ 5, winds below approximately 22 knots). Observations were made from the flying bridge, which provided a viewing distance to the horizon of approximately 11 km. A port and a starboard observer searched for cetaceans within a 90^0 quadrant from the bow to the beam on each side of the ship using 25× "big eye" binoculars mounted on fixed supports. A third observer recorded data and searched the area near the ship using unaided eye or 7× handheld binoculars. When cetaceans were sighted, the ship broke from its track and approached the animals to confirm species and to estimate group size. Sighting data were recorded on a computer using a data acquisition and logging software program interfaced with the ship's global positioning system (GPS). Sighting data included species, group size, presence of calves, bearing from the bow, linear distance from the ship when detected, and behavioral observations. Environmental data were recorded every 30 min with the rotation of observer positions, when conditions changed during a shift, and at the time of each sighting. Environmental data included sea state, surface temperature, water depth, weather (rain, fog, and cloud cover), visibility, wind direction and speed, and sun glare in the observer's field of view. A continuous record of the ship's position, sea surface temperature (SST), and water depth was collected via the ship's onboard Scientific Sensor Collection System (SSCS).

Acoustic survey.—Acoustic surveys began before sunrise and continued after dark to supplement data gathered during daytime. Acoustic monitoring to detect humpback whale song was conducted with Directional Fixing and Ranging (DIFAR) sonobuoys (AN-SSQ-53D). To optimize sound reception, the sonobuoy hydrophone depths were set at 27 m, 121 m, or 303 m depending on the presence and/or depth of the thermocline. The sonobuoy sensor contains a compass, east/west and north/south particle velocity sensors, and an omni-directional hydrophone with a frequency response up to 3.5 kHz. Sonobuoy data were continually transmitted to the ship for up to 8 h on a VHF radio carrier in an analog multiplexed format.

During "on-effort" survey mode, an attempt was made to place sonobuoys at intervals such that the VHF radio signal detection ranges overlapped to allow continuous coverage while underway, and thus emulate the continuous daytime visual search effort. When singing whales were detected, additional sonobuoys were placed along the trackline to locate singers by triangulation (see below). If the singing whale's location was within a few kilometers of the vessel, the vessel went "off-effort" and proceeded to those locations.

The VHF radio signal from the sonobuoys was received by a pair of antennas mounted on the aft mast of the ship, located 26 m above the waterline. To receive the sonobuoy signals, we used five ICOM R-100 radio recievers specially modified and calibrated by Greeneridge Sciences to provide flat frequency response from 10 Hz to 20 kHz. Radio reception range from the sonobuoys averaged 20-24 km and allowed each sonobuoy to be monitored for approximately 70 min before the ship moved out of radio reception range. When in monitoring mode to locate whales, sonobuoys were monitored continuously for up to 8 h and/or additional sonobuoys were deployed to allow extended periods of

monitoring. The signals from the radios were recorded at a 48 kHz sampling rate on Sony TCD-D8 digital audio tape recorders for processing and archival purposes. Signals were monitored in real time both aurally and visually on computers running the commercial signal-analysis software program SpectraPlus Version 2.

The magnetic bearing to calling animals was found by using the SpectraPlus software program to select a segment of the humpback song from the sonobuoy signal. This signal sample was stored as a binary file, de-multiplexed using software developed by Greeneridge Sciences, and then processed by custom software written in Matlab to obtain the bearing. The processing scheme outputs a plot showing signal intensity as a function of frequency and bearing angle from 0° to 360°. The bearing accuracy to a sound source using these buoys had a standard deviation of two degrees. Magnetic bearing angles from the sonobuoys to calling animals were plotted as true bearings on navigational charts to determine the direction to the calling whale relative to the position of the ship. Range to the calling whales could not be determined by received signal amplitude alone due to the variation of acoustic propagation in the ocean. However, when the same singing whale was detected on two or more sonobuoys, the location of the singing whale was determined by triangulation of the directional vectors obtained from the sonobuoys.

Survey phases.—The survey was conducted in two phases or legs. The first leg began on February 17, 2000 in the waters off St. Kitts and Nevis in the north, continued southward to Guadeloupe, Martinique, St. Lucia, Grenada, plus the island nations of Barbados and Trinidad and Tobago, and concluded in Trinidad on March 7, 2000. The second leg began on March 11, 2000 moving west from Trinidad to survey the Caribbean coast of Venezuela to the Gulfo de Trise; the leg then turned north to Islas de Aves and eastward along the islands of northern Venezuela (Los Roques, Isla Tortuga, Isla Piraitu, Isla de Margarita, the Gulfo de Cariaco, and Islas Los Testigos) and returned to Trinidad and Tobago before moving northward to Grenada, Barbados, Martinique, and Guadeloupe. The vessel continued north transiting the closed territorial waters around Saba and resumed surveying up to the northeast of St. Croix, where the survey concluded on March 26, 2000 (Fig. 1). Areas surveyed during both legs included Guadeloupe, Martinique, Grenada, Barbados, and Trinidad and Tobago.

Our original goal was to conduct visual and passive acoustic surveys simultaneously for side-by-side comparison of whale detection rates using both methods. Unfortunately, poor weather conditions and high winds severely limited the visual survey effort, and the low number of sightings precluded any meaningful statistical comparison of the two survey methods.

RESULTS

Visual survey

A total of 10 900 km were transited during both surveys (Fig. 1). However, only 3189 km or 29 % was visually surveyed during a total of 194.8 h with sea state conditions $\leq$ Beaufort 5 (Fig. 2). Although daily visual effort averaged 7.2 h/day and 131 km/day of trackline, effort ranged widely from 0.3 h/day and 4.3 km/day to 14.6 h/day and 227.5 km/day, depending upon weather conditions.

A total of 31 sightings of humpback whales were made during the "on-effort" and "off-effort" portions of both survey legs. The sightings comprised 46 individual whales including three calves: 21 sightings were of single whales, 6 were sightings of 2 whales, 3 were sightings of 3 whales (including 2 mother-calf pairs), and 1 sighting corresponded to 4 whales which also included a mother-calf pair (Table 1, Fig. 2). Twenty-two (71 %) sightings were in waters up to 100 m deep while the remaining nine (29 %) were in deeper waters, including 1 sighting in water over 2700 m deep. The three mother-calf pairs were sighted in water 38 m or less in depth (Table 1).

Seven of the 31 visual detections (23 %) occurred during periods of simultaneous "on-effort" visual and acoustic surveys

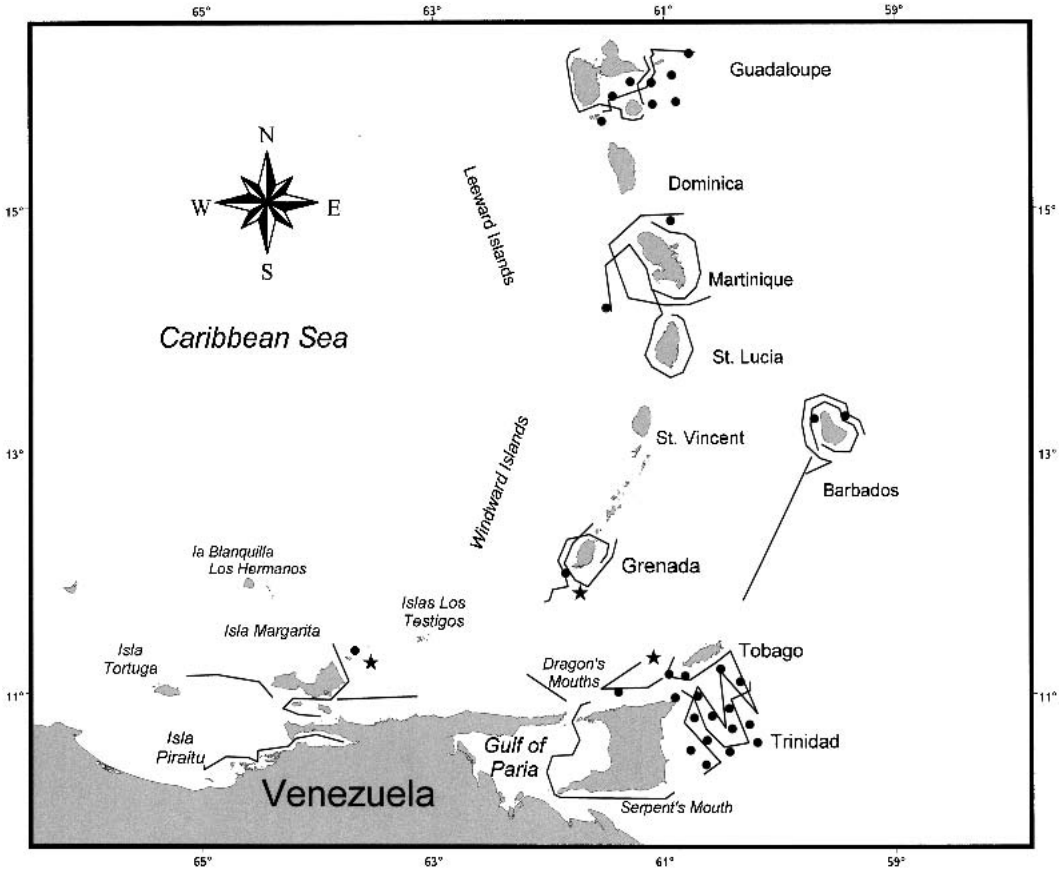

FIG. 2. Visual survey effort in Beaufort sea state < 5 (black lines) and location of 31 humpback whale sightings totaling 46 individual whales (black circles) including three mother-calf pairs (stars).

comprising 14 whales: 4 of these sightings (the 3 mother-calf pairs and 1 other group, n = 11 whales) were seen by observers without being detected acoustically because the whales were not vocalizing. Three sightings (n = 3 whales) were detected by visual and acoustic surveys. The remaining 24 sightings (77 %, n = 32 whales) were detected first by the acoustic survey during "off-effort" survey mode, and the vessel was directed toward the source of the calls before the whales were seen by the observers.

Although humpback whale song was detected throughout the entire study area (see below), visual sightings were made only from Guadeloupe south to Trinidad and Tobago and off northern Venezuela. Eight sightings (n = 9 individuals) occurred off Guadeloupe, two occurred off Martinique (n = 2 individuals), two occurred off Barbados (n = 2 individuals), and a mother and calf and two single animals (n = 4 individuals) were sighted off the southern end of Grenada. Seventeen humpback sightings occurred north and east of Trinidad and south of Tobago (n = 26 individuals including one calf), and a mother and calf plus another individual (n = 3 individuals) were sighted off Isla Margarita (Table 1, Fig. 2).

Acoustic survey

At least 142 singing humpbacks were detected on 88 of 141 (62 %) sonobuoys deployed during 3189 km of "on effort" survey mode (simultaneous visual and acoustic surveys), compared to 7 "on ef-

TABLE 1. Humpback whale sightings.

Date	Group size (n = 46)	Location	Position I at I on	Surface temp (°C)	Depth (m)	Sighting effort	Acoustic detection
21-Feb-00	1	Martinique	14° 13′ 61° 30′	26.7	2745	Off	Yes
23-Feb-00	4*	Grenada	11° 57′ 61° 50′	26.9	33	On	No
27-Feb-00	1	Tobago	11° 07′ 60° 31′	27.2	77	Off	Yes
28-Feb-00	1	Trinidad	10° 30′ 60° 36′	27.2	33	On	Yes
28-Feb-00	1	Trinidad	10° 25′ 60° 47′	27.3	31	On	Yes
01-Mar-00	1	Trinidad	10° 50′ 60° 55′	27.1	53	Off	Yes
02-Mar-00	3*	Tobago	11° 04′ 60° 56′	26.8	38	On	No
02-Mar-00	1	Trinidad	10° 30′ 60° 38′	27.0	40	Off	Yes
03-Mar-00	2	Trinidad	10° 34′ 60° 34′	26.7	48	Off	Yes
03-Mar-00	2	Trinidad	10° 29′ 60° 36′	27.1	40	Off	Yes
03-Mar-00	2	Trinidad	11° 04′ 60° 56′	26.8	38	Off	Yes
03-Mar-00	1	Trinidad	10° 30′ 60° 38′	26.8	40	Off	Yes
03-Mar-00	2	Trinidad	10° 34′ 60° 34′	26.8	48	Off	Yes
03-Mar-00	2	Tobago	10° 29′ 60° 36′	27.1	40	Off	Yes
05-Mar-00	3	Trinidad	10° 36′ 60° 25′	27.0	71	Off	Yes
05-Mar-00	1	Trinidad	10° 49′ 60° 27′	27.3	84	Off	Yes
06-Mar-00	1	Trinidad	10° 52′ 60° 26′	27.1	71	Off	Yes
17-Mar-00	3*	Venezuela	11° 10′ 63° 48′	23.9	31	On	No
20-Mar-00	1	Trinidad	10° 49′ 60° 43′	27.3	44	Off	Yes
21-Mar-00	1	Tobago	10° 55′ 61° 24′	27.3	44	Off	Yes
22-Mar-00	1	Barbados	13° 16′ 59° 41′	27.6	295	Off	Yes
23-Mar-00	1	Barbados	13° 17′ 59° 27′	28.1	522	Off	Yes
24-Mar-00	1	Martinique	14° 58′ 60° 57′	27.7	71	On	No
25-Mar-00	1	Guadeloupe	16° 24′ 60° 47′	26.2	390	On	Yes
25-Mar-00	1	Guadeloupe	16° 09′ 61° 09′	26.3	27	Off	Yes
25-Mar-00	1	Guadeloupe	16° 09′ 61° 09′	26.4	27	Off	Yes
25-Mar-00	1	Guadeloupe	16° 06′ 61° 12′	26.6	309	Off	Yes
25-Mar-00	1	Guadeloupe	16° 06′ 61° 12′	26.6	309	Off	Yes
25-Mar-00	1	Guadeloupe	16° 05′ 61° 16′	26.6	311	Off	Yes
25-Mar-00	2	Guadeloupe	15° 59′ 61° 28′	27.2	309	Off	Yes
25-Mar-00	1	Guadeloupe	15° 57′ 61° 29′	27.3	306	Off	Yes

*Includes a female-calf pair not detected acoustically.

fort" visual sightings representing 14 individual whales (Table 2, Figs. 3, 4). Of the 142 acoustic detections, examination of magnetic bearings to the source of the calls and cross bearings from 2 or more sonobuoys suggested that a minimum of 78 unique whales were detected during the "on-effort" survey (Table 3). Three of the acoustic detections (4 %) of 3 individual whales were both heard and seen by the visual observers, while 4 sightings of 11 individual whales (including 3 mother-calf pairs) were seen by the visual observers but not detected acoustically. The remaining 75 acoustic detections (96 %) were heard first or heard and never seen.

Bearings to the sources of the whales' calls were used to direct the vessel to the

TABLE 2. "On effort" acoustic detections and visual sightings of humpback whales.

Survey leg	On effort track (km)	Total sonobuoys	Sonobuoys with whale detections	Number singing whales	Visual sightings	Number whales sighted
Leg 1	1424	65	45	73	4	9
Leg 2	1765	76	43	69	3	5
Total	3189	141	88	142	7	14

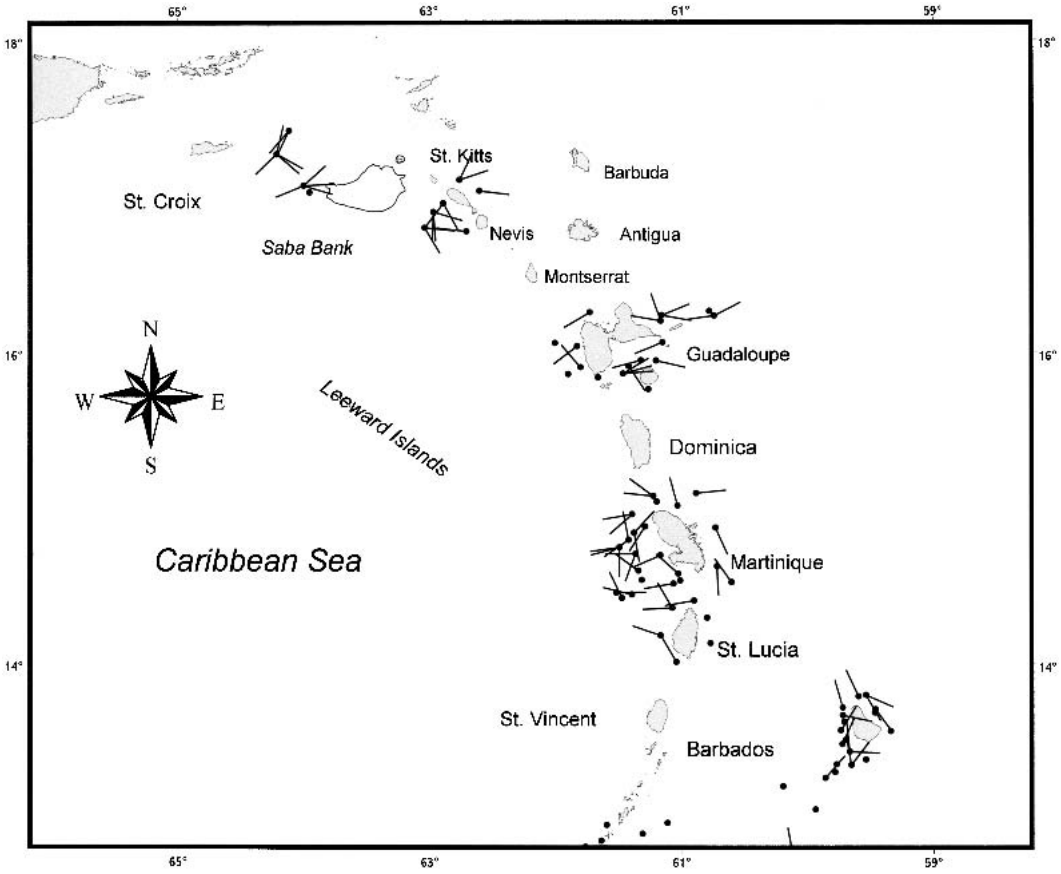

FIG. 3. Location of sonobuoys deployed along the survey trackline (black circles) in the northern portion of the eastern Caribbean showing magnetic bearings (radials from circles) to the position of singing humpback whales. Radials do not indicate range or signal strength of the received song.

source of calling whales if the distance to the whale was less than 10 km. Some whales were never seen because their exact location could not be determined due to poor signal reception, poor visibility conditions (e.g., Beaufort > 5), or the estimated distance to the calling whale was over 10 km. The distance at which whales were detected acoustically varied from less than 10 km in shallow water with a high sea state, to as much as 57 km in deep water with a strong thermocline and relatively low sea state (Fig. 5). Some singing whales were accompanied by other humpbacks that were not vocalizing, indicating that the number of singing whales detected represents a minimum number of individuals. Occasionally two or more singing whales were detected on the same or similar bearings, as evidenced by a difference in the received amplitude of the acoustic signals and/or differences in the starting and stopping patterns of songs by the different whales.

Humpback whale song was detected throughout the Lesser Antilles and the southeastern Caribbean. The northernmost detections were made from sonobuoys located south of St. Croix. Bearings to these sources suggested that the whales were on Saba Bank (southwest of Saba Island) and toward Antigua and Barbuda (Fig. 3). Seven singing whales were located off the west coast of St. Kitts and Nevis in waters approximately 1000 m deep. Singing humpback whales were detected off the west, south, and eastern coasts of Guadeloupe (7 whales were detected during Leg 1 and 10 during Leg 2).

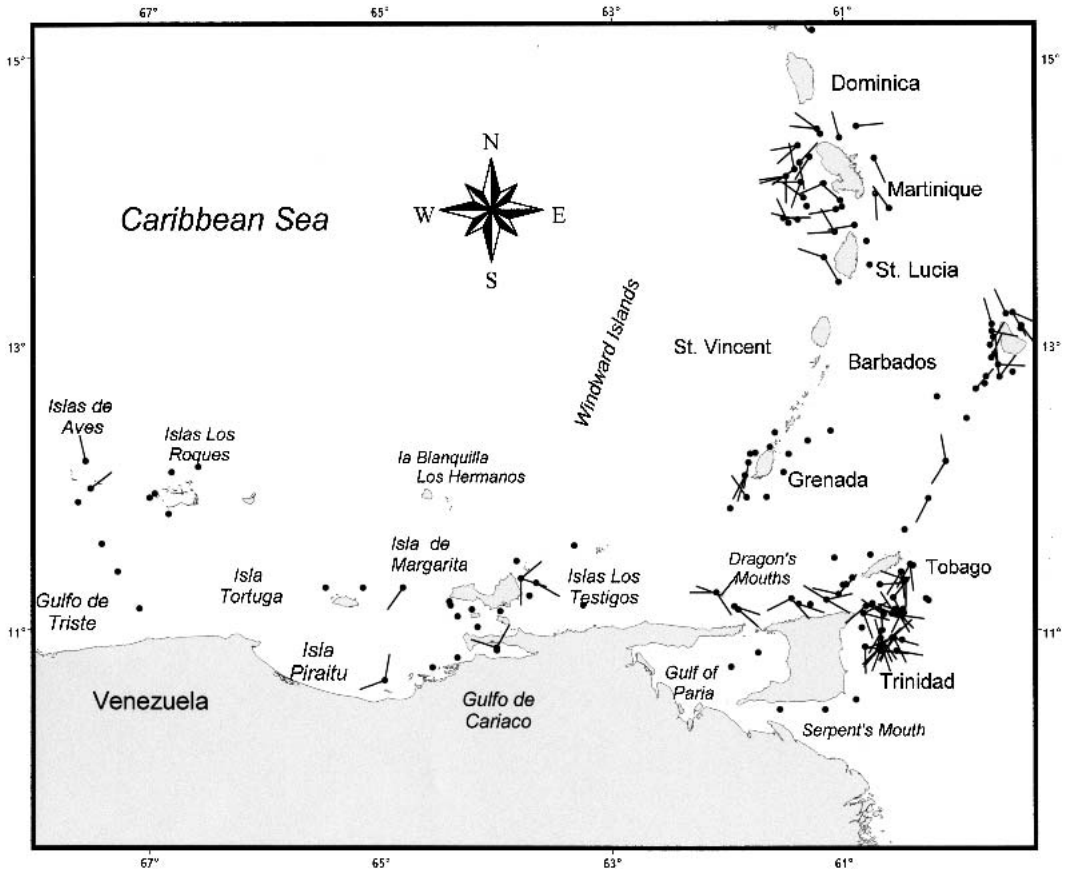

FIG. 4. Location of sonobuoys deployed along the survey trackline (black circles) in the southern portion of the eastern Caribbean showing magnetic bearings (radials from circles) to the position of singing humpback whales. Radials do not indicate range or signal strength of the received song.

In the Windward Islands, seven singing humpbacks were detected around Martinique during Leg 1 and seven during Leg 2 one month later, with most whales occurring on the Caribbean side in water depths of 1000 m to 2600 m. Two singing whales were located to the west and northwest of St. Lucia, distant and over deep water. No acoustic detections were made to the north, south, or east of St. Lucia. Acoustic detections of four whales were made off the west and southwest coasts of Grenada during Leg 2, but not during Leg 1 (Fig. 4). East of the Windward Islands, humpback whales were detected around Barbados (one during Leg 1 and five during Leg 2). The locations of some whales were confirmed visually to be within a few kilometers of the western shore of the island, while other calls appeared to be originating from undetermined locations some distance at sea to the north, east, and southeast of the island (Fig. 4).

Singing whales were located to the southwest and southeast of Tobago, as well as off the north, northeast, and east coasts of Trinidad (8 during Leg 1 and 6 during Leg 2); all in waters 50 m to 100 m deep (Fig. 4). Some of these whales were found along the north coast of Trinidad near the Dragon's Mouths Passage (between Trinidad and Venezuela) during Leg 2, but none were in this area during Leg 1 a month earlier. No singers were detected off the southeast or south coast of Trinidad in the Serpent's Mouth Channel or in the Gulf of Paria. Fourteen whales were detected along the northern coast of Venezuela; these in-

TABLE 3. Locations of the 78 singing male humpback whales detected acoustically.

Area	Date	Number
St. Kitts & Nevis	17-18 Feb	7
Guadeloupe	19 Feb	7
Martinique	20-21 Feb	7
St. Lucia	22 Feb	2
Grenada	23 Feb	0
Barbados	24 Feb	1
Trinidad & Tobago	27-28 Feb	8
Venezuela:		
Islas de Aves	11 Mar	2
Isla Piraitu	14 Mar	2
Golfo de Cariaco	14 Mar	2
Dragons Mouth	16 Mar	4
Isla de Margarita	17 Mar	4
Grenada	19 Mar	4
Trinidad & Tobago	20-21 Mar	6
Barbados	22-23 Mar	5
Martinique	24 Mar	7
Guadeloupe	25 Mar	10
Survey total		78

cluded 2 whales off Islas de Aves at the northern edge of the Golfo de Triste, 4 around Isla de Margarita, 2 off Isla Piraitu, 2 in the Golfo de Cariaco, and 4 northeast of the Dragon's Mouths between Venezuela and Trinidad (Fig. 4).

DISCUSSION

The low abundance of humpback whales detected during this survey supports the conclusions of Winn et al. (1975) and Levenson and Leapley (1978) that relatively few whales visit this region compared to the current primary wintering areas in the eastern Greater Antilles. Winn et al. (1975) surveyed what they presumed was the entire range of humpback whales in the West Indies, based on Townsend's (1935) analysis of catch distributions of 19th century whalers. They detected relatively few whales in the areas of the eastern and southeastern Caribbean included in our survey (visual detections = 8, acoustic detections = 24). In contrast, they observed many more whales (172 visual detections) on Silver and Navidad Banks in the northern Greater Antilles' portions of the humpbacks' winter range.

Winn et al. (1975) proposed that the low number of whales detected in 1972 could be the result of the ongoing hunt at Bequia of

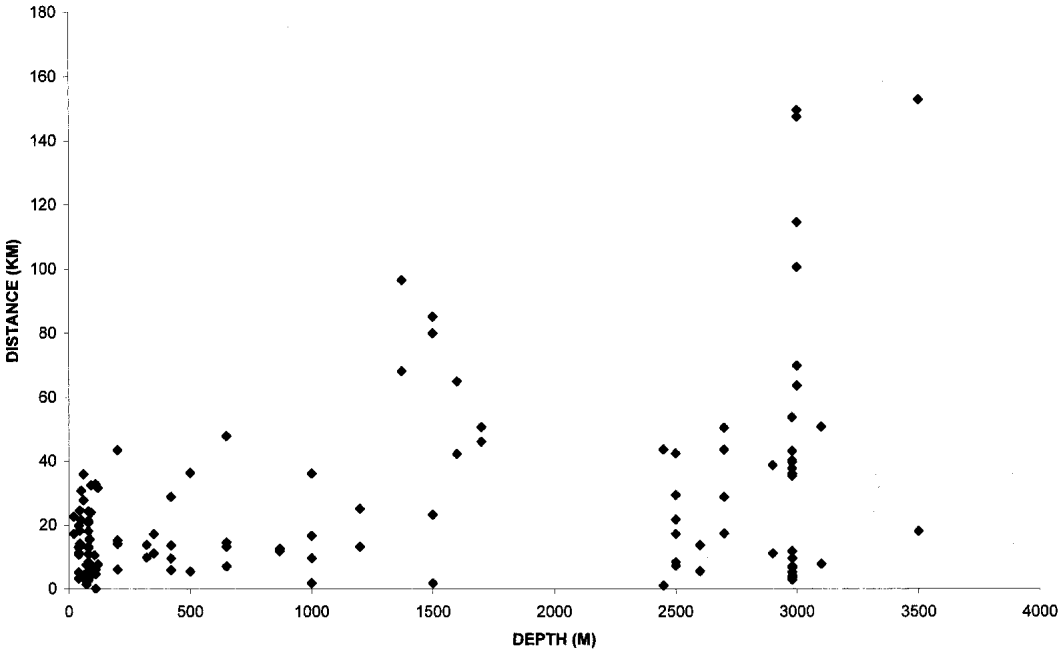

FIG. 5. Distance (km) and water depth (m) to the location of singing humpback whales calculated from sonobuoy detections.

0-6 animals per year, which may have kept the population suppressed because it targeted mother and calf pairs, and/or the timing of their survey (January 25 to February 24) being too early to coincide with the main seasonal influx of whales. The contention that the annual catches at Bequia might have suppressed the population is unlikely due to the small catch and the resilience of humpback whale populations elsewhere (Clapham et al., 1999). While Winn et al. generally covered the main areas we surveyed, they did so about a month earlier than the period of greatest abundance of humpbacks in the region (mid-February to mid-March); still, we also encountered low numbers of humpback whales although our survey coincided with the period of maximum abundance. Our preliminary data support the findings of Winn et al. (1975) and Levenson and Leaply (1978) that the abundance of humpbacks using the eastern and southeastern Caribbean was relatively low in 1972, and suggest that it remains low 28 years later.

Historical whaling records indicate that humpback whales were formerly common throughout the Lesser Antilles, along the Caribbean coast of Venezuela, in the Gulf of Paria, and along the southern coast of Trinidad during January through May (Reeves et al., 2001b, a). While humpback whale calls were heard throughout the entire survey area, visual sightings represented only a fraction of the number of acoustic detections of singing whales. The paucity of visual sightings compared to the number of singing whales detected acoustically can be partly attributed to the generally high Beaufort sea state (5+ on average) and the relatively brief periods that humpback whales spend at the surface. Another possibility to account for low numbers of humpback whales in the eastern and southeastern Caribbean compared to more northerly areas of the Greater Antilles is that the catch records from American whale ships were not wholly representative of the 19th century distribution and the relative abundance of humpbacks in different parts of the West Indies. Reeves et al. (2001a) point out that the numbers of humpback whales encountered and/or taken represent a minimum number because many logbooks and journals for this period of whaling have not survived or are unavailable for study. However, historical catches in the more northern Greater Antilles would have to be greatly underrepresented in records for that area to have hosted the numbers of humpback whales observed there today.

Our observations of whales, including mother and calf pairs, indicate that the Lesser Antilles and the Caribbean coast of Venezuela continue to serve as nursing, mating, and possibly calving grounds, although surely in a lesser capacity than during the whaling period. An exception is the Gulf of Paria between northeastern Venezuela and Trinidad. This area was a major gathering ground for humpbacks before their exploitation to depletion between the 1830s to 1880s (Reeves et al., 2001b), but we found no evidence of its use by humpbacks. The failure of whales to reoccupy the Gulf of Paria could be due to the effects of disturbance and noise associated with the development of extensive oil and gas production facilities in the gulf, and to heavy commercial shipping traffic since the turn of the 20th century. Avoidance of continual industrial noise has been observed with bowhead whales (Ljungblad et al., 1988; Richardson et al., 1990) and gray whales (Malme et al., 1983, 1984; Jones et al., 1994).

The numbers of visual and acoustic detections reported here do not represent the total abundance of humpback whales around each island or in the survey region. At best, the acoustic detections represent a minimum number of male humpbacks that reside in or move through this region during the winter months. Nonetheless, it is difficult to reconcile the low numbers observed in this and previous studies with the seasonal distribution and numbers of whales implied from the historical catch data. The apparent low abundance of whales in the formerly important breeding habitats of the eastern and southeastern Caribbean suggests failure to reoccupy their former range despite the protection provided by various conservation measures.

One explanation for the current low

abundance of humpbacks is that they descended from a population greatly reduced by whaling that has failed to recover from exploitation. However, Stevick et al. (1999) reported photographic matches of two humpback whales between the Lesser Antilles and the North Atlantic feeding grounds: one animal was photographed on the Saba Bank and then in Newfoundland, and the second match was between Grenada and Greenland. A third individual photographed in the Lesser Antilles was resighted in Puerto Rico and Dominica, showing an exchange between the eastern Caribbean and the more northerly breeding area in the Greater Antilles. Although a small sample, these matches support the view that humpbacks wintering in the West Indies belong to a single population.

The failure of the whale population to reoccupy the eastern and southeastern Caribbean as it recovered from depletion does not explain the apparent shift of the location of the primary breeding aggregations from the southeastern Caribbean to the northern Greater Antilles. Clapham and Hatch (2000) suggest that this shift reflects a characteristic of the humpback's mating system whereby only one major aggregating point occurs in any oceanic breeding range. They argue that this aggregation point shifted (largely stochastically) from the southeastern Lesser Antilles to the eastern portion of the Greater Antilles following overexploitation in the 1800's and early 1900's.

Clearly, passive acoustic survey methods have an advantage over visual methods for detecting whales singing in areas with high winds and poor visibility, and during night. Currently, however, passive acoustic methods are limited to detecting singing males. We do not know how often a male humpback sings or the duration of singing bouts. The visual survey confirmed that non-singing whales often accompany singers, so singing alone is not a reliable indicator of the number of individuals in an area. The combination of visual and acoustic surveys provides reliable information on presence or absence and distribution of humpbacks in the Caribbean but can only provide minimum estimates of relative abundance due to uncertainties common to both methods. Adapting passive acoustic detection methods to abundance estimation will require, at minimum, development of statistical techniques and correction factors for estimating acoustic detection range, number of male humpbacks not singing during a survey, and number of females and young accompanying singers.

Future surveys for humpback whales should include a more complete coverage of this portion of their winter range to better assess the status of this species in the region, and to delineate the diversity of habitats and conditions that are most conducive to reproduction and continued recovery. This coverage should include even lesser-known areas of occurrence, like the Colombian coast, where a few humpbacks have been reported between January and March (Vidal, 1990; Florez-González and Capella-Alzueta, 1995). Genetic analyses, analyses of identification photographs, and analyses of humpback song throughout the region will improve our understanding of the relationship of humpback whales in the eastern and southeastern Caribbean to those in the northern Caribbean in winter, and to humpbacks that frequent summer feeding grounds in the North Atlantic. In addition, future studies may help to determine if humpbacks from the West Indies mix with those that winter in the Cape Verde Islands (Reiner et al., 1996), and whether humpbacks from the South Atlantic visit the southern Caribbean during the boreal winter and mix with North Atlantic humpback whales (as has been noted for Pacific humpback whales by Acevedo and Smultea, 1995).

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LITERATURE CITED

Acevedo, A. and M.A. Smultea. 1995. First records of humpback whales including calves at Golfo Dulce and Isla del Coco, Costa Rica, suggesting geographical overlap of northern and southern hemisphere populations. Mar. Mammal Sci. 11(4):554-560.

Barlow, J. 1995. Abundance of cetaceans in California waters: I. Ship surveys in summer/fall 1991. Fish. Bull., 93:1-14.

Barlow, J. and B. Taylor. 1998. Preliminary abundance of sperm whales in the northeastern temperate Pacific estimated from a combined visual and acoustic survey. Rep. Intl. Whal. Comm. SC/50/CAWS 20. 18 p.

Clapham, P.J., S.B. Young, and R.L. Brownell. 1999. Baleen whales: conservation issues and the status of the most endangered populations. Mam. Rev. 29:35-60.

Clapham, P.J. and L.T. Hatch. 2000. Determining spatial and temporal scales for population management units: lessons from whaling. Rep. Intl. Whal. Comm. SC/52/SD2. 11 p.

Clark, C.W. and W.T. Ellison. 1989. Numbers and distributions of bowhead whales, *Balaena mysticetus*, based on the 1986 acoustic study off Pt. Barrow, Alaska. Rep. Int. Whal. Comm. 39:297-303.

Clark, C.W. and K.M. Fristrup. 1997. Whales 95: A combined visual and acoustic survey of blue and fin whales off Southern California. Rep. Int. Whal. Comm. 47:583-600.

Florez-González, L. and J. Capella-Alzueta. 1995. Mamíferos acuáticos de Colombia. Una revisión y nuevas observaciones sobre su presencia, estado del conocimiento y conservación. Informe Museo del Mar (Universidad de Bogotá Jorge Tadeo Lozano) Bogota, Colombia 39:1-29.

Hazevoet, C.J. and F.W. Wenzel. 2000. Whales and dolphins (Mammalia, Cetacea) of the Cape Verde Islands, with special reference to the humpback whales *Megaptera novaeangliae* (Borowski 1781). Cont. Zool. 69:197-211.

Jones, M.L., S.L. Swartz, and M.E. Dahlheim. 1994. Census of gray whale abundance in San Ignacio Lagoon: a follow-up study in response to low whale counts recorded during an acoustic playback study of noise-effects on gray whales. U.S. Department of Commerce, NTIS Report No. PB94-195062. 32 pp.

Leaper, R., D. Gillespie and V. Papastavrou. 2000. Results of passive acoustic surveys for odontocetes from the British Antarctic Survey research vessel James Clark Ross in the Southern Ocean, 30^0W to 70^0W. J. Cetacean Res. Manage. 2(3):187-196.

Levenson, C. and W.T. Leapley. 1978. Distribution of humpback whales (*Megaptera novaeangliae*) in the Caribbean by a rapid acoustic method. J. Can. Res. Bd. Can. 35:1150-1152.

Ljungblad, D.K., B. Wursig, S.L. Swartz, and J.M. Keen. 1998. Observations on the behavioral responses of bowhead whales (*Balaena mysticetus*) to active geophysical vessels in the Alaskan Beaufort Sea. Arctic 41(3): 183-194.

Malme, C.I., P.R. Miles, C.W. Clark, P. Tyack, and J.E. Bird. 1983. Investigations of the potential effects of underwater noise from petroleum industry activities on migrating gray whale behavior. BBN Rep. 5366. Rep. From Bolt Beranek & Newman Inc., Cambridge, MA. For U.S. Minerals Management Serv., Anchorage, AK. NTIS PB86-174174.

Malme, C.I., P.R. Miles, C.W. Clark, P. Tyack, and J.E. Bird. 1984. Investigations of the potential effects of underwater noise from petroleum industry activities on migrating gray whale behavior/Phase II: January 1984 migration. BBN Rep. 5586. Rep. From Bolt Beranek & Newman Inc., Cambridge, MA. For U.S. Minerals Management Serv., Anchorage, AK. NTIS PB86-218377.

Mattila, D.K., P.J. Clapham, O. Vasquez, and R. Bowman. 1994. Occurrence, population composition and habitat use of humpback whales in Samana Bay, Dominican Republic. Can. J. Zool. 72: 1898-1907.

Mignucci-Giannoni, A.A. 1998. Zoogeography of cetaceans off Puerto Rico and the Virgin Islands. Carib. J. Sci. 34:173-190.

Mitchell, E. and R.R. Reeves. 1983. Catch history, abundance, and present status of northwest Atlantic humpback whales. Rep. Intl. Whal. Comm., Special Issue 5:153-212.

Norris, T.F., M. McDonald, and J. Barlow. 1999. Acoustic detections of singing humpback whales (*Megaptera novaeangliae*) in the eastern North Pacific during their northbound migration. J. Acoust. Soc. Am. 106:506-514.

Price, W.S. 1985. Whaling in the Caribbean: historical

perspective and update. Rep. Intl. Whal. Comm. 35:413-420.

Reeves, R.R., S.L. Swartz, S.E. Wetmore, P.J. Clapham. 2001a. Historical occurrence and distribution of humpback whales in the eastern and southern Caribbean Sea, based on data from American whaling logbooks. J. Cetacean Res. Manage. 3(2):37-59. 22 p.

Reeves, R.R., J. Kahn, R.R. Olsen, S.L. Swartz, and T.D. Smith. 2001b. History of whaling in Trinidad and Tobago. J. Cetacean Res. Manage. 3(1):45-54. 11 p.

Reiner, F., M.E. Dos Santos, and F.W. Wenzel. 1996. Cetaceans of the Cape Verde Archipelago. Mar. Mamm. Sci. 12(3):434-443.

Richardson, W.J., B. Wursig, and C.R.Green, Jr. 1990. Reactions of Bowhead whales, *Balaena mysticetus*, to drilling and dredging noise in the Canadian Beaufort Sea. Mar. Envir. Res. 29(2):135-160.

Smith, T.D. et al. 1999. An ocean-basin-wide mark-recapture study of the North Atlantic humpback whale (*Megaptera novaeangliae*). Mar. Mamm. Sci. 15(1):1-32.

Stevick, P.T., C.A. Carlson, and K. Balcomb. 1999. A note on migratory destinations of humpback whales from the eastern Caribbean. J. Cetacean Res. Manage. 1(3):251-254.

Townsend, C.H. 1935. The distribution of certain whales, as shown by logbook records of American whaleships. Zoologica 19(1):1-50.

Vidal, O. 1990. Lista de los mamíferos acuaticos de Colombia. Informe Museuo del Mar (Universidad de Bogotá Jorge Tadeo Lozano) Bogota, Colombia 37:1-18.

Winn, H.E., R.K. Edel, and A.G. Taruski. 1975. Population estimate of the humpback whale in the West Indies by visual and acoustic techniques. J. Fish. Res. Board Can. 32:499-506.

Zeh, J.E. et al. 1993. Current population size and dynamics. *In*: J.J. Burns et al. (Eds.) *The Bowhead Whale*, pp. 409-489. Special Publication No. 2, Society for Marine Mammalogy. Allen Press, Lawrence, Kansas.