NRC Research Press

ARTICLE

Local and migratory movements of humpback whales (*Megaptera novaeangliae*) satellite-tracked in the North Atlantic Ocean

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Abstract: North Atlantic humpback whales (*Megaptera novaeangliae* (Borowski, 1781)) migrate from high-latitude summer feeding grounds to low-latitude winter breeding grounds along the Antillean Island chain. In the winters and springs of 2008 through 2012, satellite tags were deployed on humpback whales on Silver Bank (Dominican Republic) and in Guadeloupe (French West Indies) breeding areas. Whales were monitored, on average, for 26 days (range = 4–90 days). Some animals remained near their tagging location for multiple days before beginning their northerly migration, yet some visited habitats along the northwestern coast of the Dominican Republic, northern Haiti, the Turks and Caicos islands, and off Anguilla. Individuals monitored during migration headed towards feeding grounds in the Gulf of Maine (USA), Canada, and the eastern North Atlantic (Iceland or Norway). One individual traveled near Bermuda during the migration. This study provides the first detailed description of routes used by North Atlantic humpback whales towards multiple feeding destinations. Additionally, it corroborates previous research showing that individuals from multiple feeding grounds migrate to the Antilles for the breeding season. This study indicates that North Atlantic humpbacks use an area broader than the existing boundaries of marine mammal sanctuaries, which should provide justification for their expansion.

Key words: humpback whale, migration, satellite telemetry, North Atlantic, breeding ground, movements.

Résumé : Les rorquals à bosse (*Megaptera novaeangliae* (Borowski, 1781)) de l'Atlantique Nord migrent de leurs aires d'alimentation estivales de haute latitude vers des aires de reproduction hivernales de basse latitude situées le long de la chaîne des Antilles. Durant les hivers et printemps de 2008 à 2012, des émetteurs satellites ont été déployés sur des rorquals à bosse dans le banc Silver (République dominicaine) et dans des aires de reproduction de la Guadeloupe (Antilles françaises). Les rorquals ont été suivis pendant 26 jours en moyenne (plage de 4 à 90 jours). Si certains animaux demeuraient plusieurs jours à l'endroit où ils avaient été marqués avant d'entreprendre leur migration vers le nord, certains visitaient des habitats le long du littoral nord-ouest de la République dominicaine, du nord d'Haïti et des îles Turques et Caïques, ainsi qu'au large d'Anguilla. Les individus suivis durant la migration se sont dirigés vers des aires d'alimentation dans le golfe du Maine (États-Unis), au Canada et dans la partie est de l'Atlantique Nord (Islande ou Norvège). Un individu s'est rendu près des Bermudes durant sa migration. L'étude fournit la première description détaillée des routes empruntées par les rorquals à bosse de l'Atlantique Nord vers différentes destinations où ils vont s'alimenter. Elle corrobore en outre les résultats de travaux antérieurs qui démontraient que des individus provenant de multiples aires d'alimentation migrent jusqu'aux Antilles pour la saison de reproduction. L'étude indique que les rorquals à bosse de l'Atlantique Nord utilisent un territoire plus vaste que celui défini par les limites actuelles des sanctuaires de mammifères marins, ce qui devrait justifier leur agrandissement. [Traduit par la Rédaction]

Mots-clés : rorqual à bosse, migration, télémétrie par satellite, Atlantique Nord, aire de reproduction, déplacements.

Introduction

Humpback whales (*Megaptera novaeangliae* (Borowski, 1781)) travel thousands of kilometres between high-latitude summer feeding areas and low-latitude winter breeding grounds annually (Dawbin 1966; Clapham and Mead 1999). Each winter, North Atlantic humpbacks congregate to mate and calve on the shallow banks that buffer the Antillean island chain, from Hispaniola to the Caribbean coast of Venezuela (Winn et al. 1975; Whitehead and Moore 1982; Mattila and Clapham 1989; Mattila et al. 1989; Katona and Beard 1990; Smith et al. 1999; Acevedo et al. 2008). They then migrate to geographically distinct feeding grounds in

Received 19 July 2013. Accepted 25 October 2013.

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Published at www.nrcresearchpress.com/cjz on 26 October 2013.

the Gulf of Maine, Canada (waters off Newfoundland and Labrador, St. Pierre et Miquelon, and in the Gulf of St. Lawrence), West Greenland, Iceland, and the Barents Sea, where they forage from spring through autumn (IWC 2002; Stevick et al. 2006). Each of these feeding grounds are separated by hundreds or thousands of kilometres, and are characterized by high maternally-directed site fidelity with very little interchange between aggregations (Clapham 1993; Clapham et al. 1993; Palsbøll et al. 1995; IWC 2002; Stevick et al. 2006; Weinrich et al. 2006; Robbins 2007). Studies have shown that migratory timing and speed are heavily influenced by sex, age, reproductive status, and feeding ground preference (Chittleborough 1965; Dawbin 1966; Brown and Corkeron 1995; Brown et al. 1995; Stevick et al. 2003; Weinrich et al. 2006; Noad and Cato 2007); however, these studies were too broad to describe individual, fine-scale migratory variation or to predict the effects of feeding ground origin or life-history status on individual movements.

Whales from all high-latitude feeding aggregations have been observed in the Antilles (Clapham and Mattila 1988; Mattila et al. 1989; Katona and Beard 1990; Palsbøll et al. 1995; Stevick et al. 1998: Bérubé et al. 2004; Robbins et al. 2006), yet Stevick et al. (2003) found that whales from Iceland and Norway are underrepresented on Silver Bank. Additionally, analysis of mitochondrial and nuclear DNA shows evidence of at least one other North Atlantic humpback breeding area outside the Antilles (Palsbøll et al. 1995; Larsen et al. 1996), though its location has yet to be determined. Therefore, while photographic identification (photo ID) and genetic studies support the theory that the western North Atlantic (Gulf of Maine and Canada) humpback whale population constitutes a single panmictic unit (Clapham et al. 1993; Larsen et al. 1996), there is still considerable uncertainty about the stock structure across the entire ocean basin.

The Silver–Navidad–Mouchoir banks complex, off the northern coast of the Dominican Republic, is arguably host to one of the largest breeding aggregation of humpback whales in the world (Mattila et al. 1989; Smith et al. 1999). The importance of this aggregation led to the designation, by the Dominican Republic, of the Silver Bank and Navidad Bank Sanctuary in 1986. Due to the efficiency associated with working with such a high-density group of animals, many North Atlantic humpback photo ID, genetic, and acoustic breeding ground studies have been conducted within the sanctuary region (Levenson and Leapley 1978; Winn and Winn 1978; Mattila et al. 1989; Palsbøll et al. 1995; Larsen et al. 1996; Smith et al. 1999; Stevick et al. 2003; Clapham et al. 2005). A majority of these studies have focused primarily on identification of individuals and have yielded significant information about migratory destinations and, to a much lesser extent, insights into within-season movement and habitat use (Whitehead and Moore 1982; Mattila et al. 1989; Mattila and Clapham 1989; Clapham et al. 1992; Smith et al. 1999; Swartz et al. 2002). Research effort along the eastern Antillean chain has been comparatively low, yet several studies have produced data describing the distribution and abundance of humpback whales in the French West Indies (Gandilhon 2012) and farther south (Winn et al. 1975; Balcomb and Nichols 1978; Swartz et al. 2002). To increase humpback whale protection and foster international research throughout the entire breeding range, a "sister sanctuary" to the Silver Bank and Navidad Bank Sanctuary, encompassing 59 square miles (1 square mile = 2.5899 km²) of ocean off the French West Indies (known as Agoa) was established in October 2010.

Despite the considerable research effort within the North Atlantic breeding range, there remain many gaps in our understanding of the patterns of individual humpback movements and habitat use along the Antillean chain. In the past decades, satellite telemetry has become a powerful tool when used on large whales to describe such fine-scale habitat use, migration routes and destination, and stock structure (Mate and Mesecar 1997; Baumgartner and Mate 2005; Heide-Jørgensen et al. 2006; Zerbini et al. 2006; Bailey et al. 2009). This technique is particularly useful when whales move into remote areas with low research effort, such as unstudied portions of the Lesser Antilles and near the Mid-Atlantic Ridge. To date, there have been no published studies that examine the extended, day-to-day movements of humpback whales within or beyond easily accessible study sites. The purpose of this study was to investigate the hypothesis that humpback whales visit areas outside of well-studied, high-density areas within the breeding season. Additionally, we explored the theory that multiple migratory routes from breeding to feeding grounds are used and that those routes vary by individual. Finally, we sought to describe the fine-scale breeding ground habitat use within, and outside of, established marine mammal sanctuaries to inform policy for effective sanctuary management.

Materials and methods

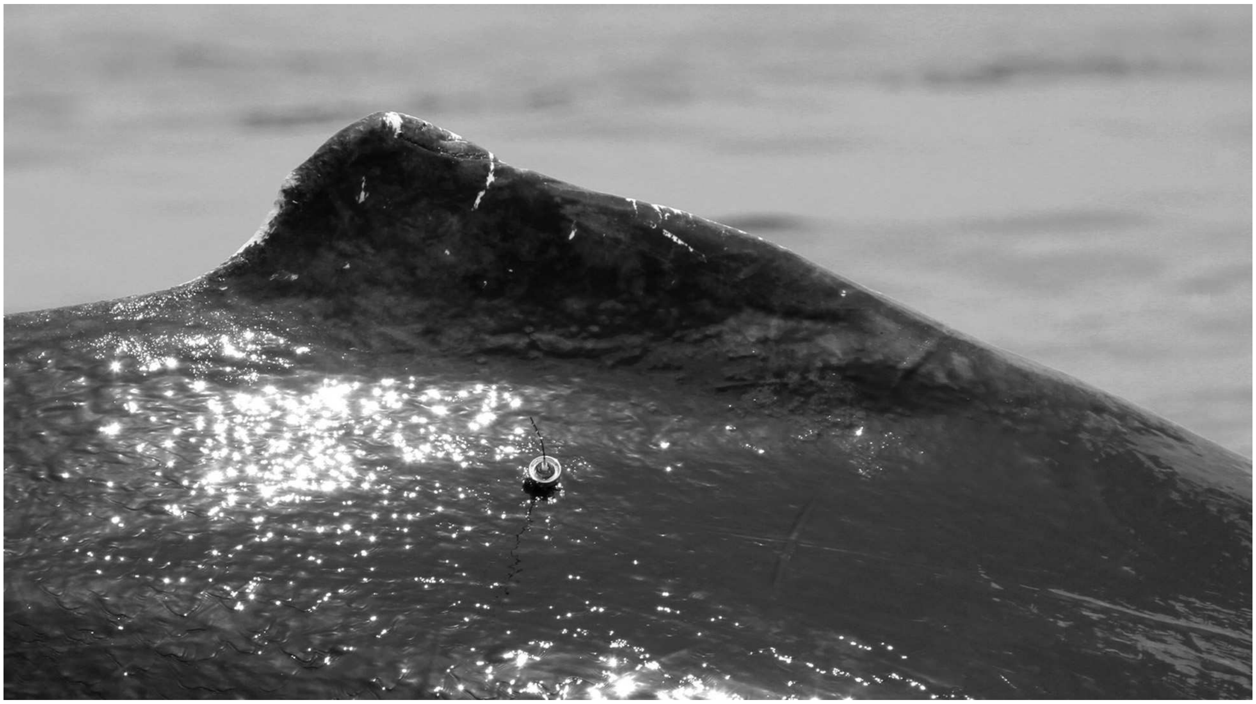
Study areas

Tagging took place on Silver Bank (approximately 21°N, 69°W), 55 nautical miles (1 nautical mile = 1.852 km) to the northeast of Puerto Plata, Dominican Republic, and off the southeastern coast of Guadeloupe (approximately 16°N, 61°W). All tagging was conducted within the Silver Bank or Agoa national marine sanctuaries. Silver Bank is a limestone platform reef system that, while still poorly charted, is estimated to have an area of approximately 2404 km² with an approximate mean depth of 30 m (Scott and Winn 1980). The shallow coral heads, notably in the dense barrier reef on the bank's northeastern perimeter, provide shelter from the strong trade winds that dominate the area. In Guadeloupe, the region between the southern coasts of the islands of Grande-Terre and Basse-Terre, as well as Marie-Galante, is also characterized by shallow, well-protected coastal waters that serve as a sanctuary from strong trade winds. Warm, sheltered waters like these appear to be preferred habitat for mating and calving humpback whales (Frankel et al. 1995; Clapham 1996; Craig and Herman 2000; Ersts and Rosenbaum 2003). Tagging in areas of known abundance facilitates successful deployment by allowing field teams to select whales that are more approachable from a small boat, therefore increasing the chance of proper tag deployment.

Methods

Once located, whales were approached within a 3–10 m distance for tag deployment from the bow of a small (8–10 m), high-speed vessel capable of maneuvering safely around large whales. Satellite transmitters were placed on the dorsal portion of the body of the whales, near the dorsal fin, using an 8 m long carbon fiber pole (also known as the Villum pole) in 2008 (Heide-Jørgensen et al. 2006; Zerbini et al. 2006, 2011), and then with the air rocket transmitter system (ARTS), a modified marine safety pneumatic line thrower (Heide-Jørgensen et al. 2001), in all subsequent years. Whales were tagged with the implantable configuration of the SPOT 5 transmitters produced by Wildlife Computers (Redmond, Washington, USA). The tags were designed to penetrate into the dorsal surface of the whale, beneath the skin and hypodermis, and anchor within the fascia that lies between the muscle and the blubber. Retention of the tag was maintained through actively sprung plates and (or) a circle of passively deployed "petals". All external components of the tag are built from stainless steel and the tags were sterilized prior to deployment. Most tags were duty cycled to transmit for 6 h during the daytime and 6 h during the nighttime for the first 3 months after deployment, and then every other day (with the same 6 h on and 6 h off pattern) until the end of transmission to preserve battery life. Tags F, H, I, J, and K were duty cycled to transmit every other day from the date of deployment with the same 6 h on and 6 h off pattern on during transmission days. All attempts were made to place the tag just forward of the dorsal fin on either side of the dorsal hump (Fig. 1) of the

Fig. 1. A photograph of an air rocket transmitter system (ARTS) deployed SPOT 5 tag on the dorsal surface, near the dorsal fin, of a humpback whale (*Megaptera ovaeangliae*) in the West Indies.



whale to facilitate frequent satellite exposure during a duty cycle and to extend the attachment duration.

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

Data processing

Observed locations were calculated by Argos from Doppler-shift data when multiple messages were received during a satellite's passage overhead. The speed–distance–angle (SDA) Argos filter (Freitas et al. 2008) was applied to all good-quality (B, A, 0, 1, 2, 3) Argos-observed locations in R software (R Development Core Team 2011) to remove locations that implied unlikely deviations from the track as well as unrealistic travel speeds. A Bayesian switching state–space model (SSSM) (Jonsen et al. 2007) was then applied to the data to estimate positions and behavioral modes. A time-step of 12 h was selected to minimize the number of positions estimated during periods when the tag was not transmitting because of the 6 h on and 6 h off duty cycle. The estimation procedure applied to the data are presented in more detail in Jonsen et al. (2005, 2006).

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

Results

Seventeen satellite tags were deployed on Silver Bank and 11 were deployed off Guadeloupe at various times during the months of January, April, and May during the period 2008 through 2012. Of those 28 tags, 6 failed to transmit entirely and 3 tags did not begin transmitting until 8, 33, and 63 days after deployment, when the animals concerned were already migrating north. The remaining 22 tags transmitted, on average, for 26 days (range = 4–90 days) and recorded minimum travel distances between 119.8 and 6960.1 km (Table 1). Fourteen tagged animals were migrating north when transmissions ceased. Eleven of those whales spent varying amounts of time on the breeding ground near the tagging location before beginning their northward migration (Figs. 2, 4). Whales tagged within the same competitive group (a group of whales displaying intrasexual competition by males for access to a nuclear female; Clapham et al. 1992) did not migrate together.

A mean (±SD) speed of 1.7 ± 0.8 km·h^{-1} was recorded in the breeding grounds, whereas 4.3 ± 1.2 km·h^{-1} occurred during migration. Overall, the speed of animals migrating toward the eastern North Atlantic (either Iceland or Norway) (4.5 ± 1.2 km·h^{-1}) was only slightly, though not significantly, higher (Welch two-sample t test, p = 0.451) than whales traveling toward the Gulf of Maine or Canada (4.0 ± 1.2 km·h^{-1}). Additionally, the migration speeds of whales that had a calf at the time of deployment (3.9 ± 0.8 km·h^{-1}) were only slightly lower than those of whales migrating without a calf (4.9 ± 1.5 km·h^{-1}) (Welch two-sample t test, p = 0.222). During migration, the vast majority of behavioral mode classifications from the SSSM were considered transiting or unclassified, though there were six individual positions (from three whales) that were classified as ARS (Fig. 3).

Two tagged whales were identified through comparison of dorsal fin and (or) fluke photographs to the Gulf of Maine Humpback Whale Catalog. Whale F, a male named "Tilt", was first seen in the

Table 1. Satellite telemetry results based on switching state–space model (SSSM) positions estimated every 12 h.

Whale	PTT No.	Group type	Tag location	Tag date	Longevity (days)	Estimated travel distance (km)	Total estimated speed (km·h^{-1})	Departure date	Estimated migratory speed (km·h^{-1})	Estimated breeding ground speed (km·h^{-1})
A	81122	Mother–calf	SB	29/1/2008	13	858.3	2.8	—	—	2.8
B	81123	Duo	SB	29/1/2008	17	1221.3	3.0	—	—	3.0
C	81124	Mother–calf	SB	29/1/2008	5	119.8	0.6	—	—	1.2
D	81125	Unknown	SB	30/1/2008	22	888.6	1.7	—	—	1.7
E	81126	Duo	SB	31/1/2008	9	249.4	1.3	—	—	1.0
F	87631	Male	SB	6/4/2009	22	2217.2	4.2	11/4/2009	5.2	0.7
G	87760	Mother–calf	SB	6/4/2009	30	2000.6	2.8	17/4/2009	4.0	0.6
H	87632	Mother–calf	SB	8/4/2009	37	3605.1	4.1	9/4/2013	4.2	—
I	87634	Mother–calf	SB	8/4/2009	10	446.1	1.9	—	—	1.9
J	87633	Mother–calf	SB	10/4/2009	27	1314.2	2.0	—	2.3	1.2
K	87635	Mother–calf	SB	20/4/2009	64	6960.1	4.5	—	4.7	—
L	96405	Mother–calf	GUAD	6/5/2010	38	2859.0	3.1	9/5/2010	3.2	2.2
M	87777	Mother–calf	GUAD	30/4/2010	10	939.0	3.9	4/5/2010	5.1	2.2
N	87781	Mother–calf	GUAD	2/5/2010	90	6360.6	2.9	—	4.3	—
O	84484	Mother–calf	SB	3/4/2011	5	130.1	1.4	—	—	1.4
P	84487	Mother–calf	SB	3/4/2011	15	894.3	2.7	9/4/2011	3.5	1.2
Q	87636	Escort	SB	3/4/2011	36	4794.0	6.1	9/4/2011	6.5	1.5
R	84482	Mother–calf	SB	4/4/2011	18	1357.4	3.1	—	3.7	—
S	84488	Duo	GUAD	12/4/2011	12	1037.5	3.9	—	—	3.9
T	87765	Challenger	SB	2/4/2012	58	5010.2	3.6	12//42012	5.5	1.4
U	88726	Challenger	SB	2/4/2012	16	1310.0	3.4	7/4/2012	5.0	1.3
V	87624	Challenger	SB	2/4/2012	20	1028.2	2.1	6/4/2012	2.4	1.2
Mean					26	2072.8	3.0		4.3	1.7
SD						1.2			1.2	0.8

Note: Tagging locations are Guadeloupe (GAUD) and Silver Bank (SB). The term "challenger" refers to a presumed male occupying a prominent role in the assemblages known as "competitive groups", which consist primarily of males competing for females. The term "duo" refers to a pair of adult whales with no calf. The term "escort" refers to an adult whale accompanying a mother and calf (Clapham et al. 1992).

Gulf of Maine in 1997 and in every subsequent year through 2012; he was at least 13 years old at the time of tagging. Whale G, a female named "Vertex", was recorded in the Gulf of Maine as a calf in 1995 and was also seen yearly through 2012; she was 14 years old when tagged.

Breeding ground movement

Eight whales (A, B, C, D, E, I, O, S) remained in their low-latitude breeding grounds for the duration of tag transmission (Figs. 4, 5). This is likely the result of whales A–E being tagged significantly earlier in the breeding season than all other whales, and the short tag duration (5–12 days) of whales I, O, and S. No tagged whales traveled into the Caribbean Sea. Only one animal (A) traveled south from the Silver–Navidad–Mouchoir banks complex to within 30 km of the coast of northwestern Dominican Republic, then swam along the entire northwestern coast of Haiti. Whale A then traveled north to Great Inagua Island and the southern edge of Caicos Bank. Only whales A, B, and I visited Caicos Bank and the coasts of the Turks and Caicos Islands (Fig. 4). Four whales (B, C, D, and U) swam from Silver Bank west to the adjacent Mouchoir Bank, while only whales D and V traveled east to Navidad Bank, the third bank in the complex (Fig. 4). Whale D is the only animal to have visited Silver, Navidad, and Mouchoir banks. Of the tagged whales that spent 5 or more days in the breeding ground, a mean of 82% of nonmigratory time fell within the Silver Bank and Navidad Bank Sanctuary. However, the overall percentage of time spent within any protected waters was only 44.1% for the full duration of all tags (Fig. 4).

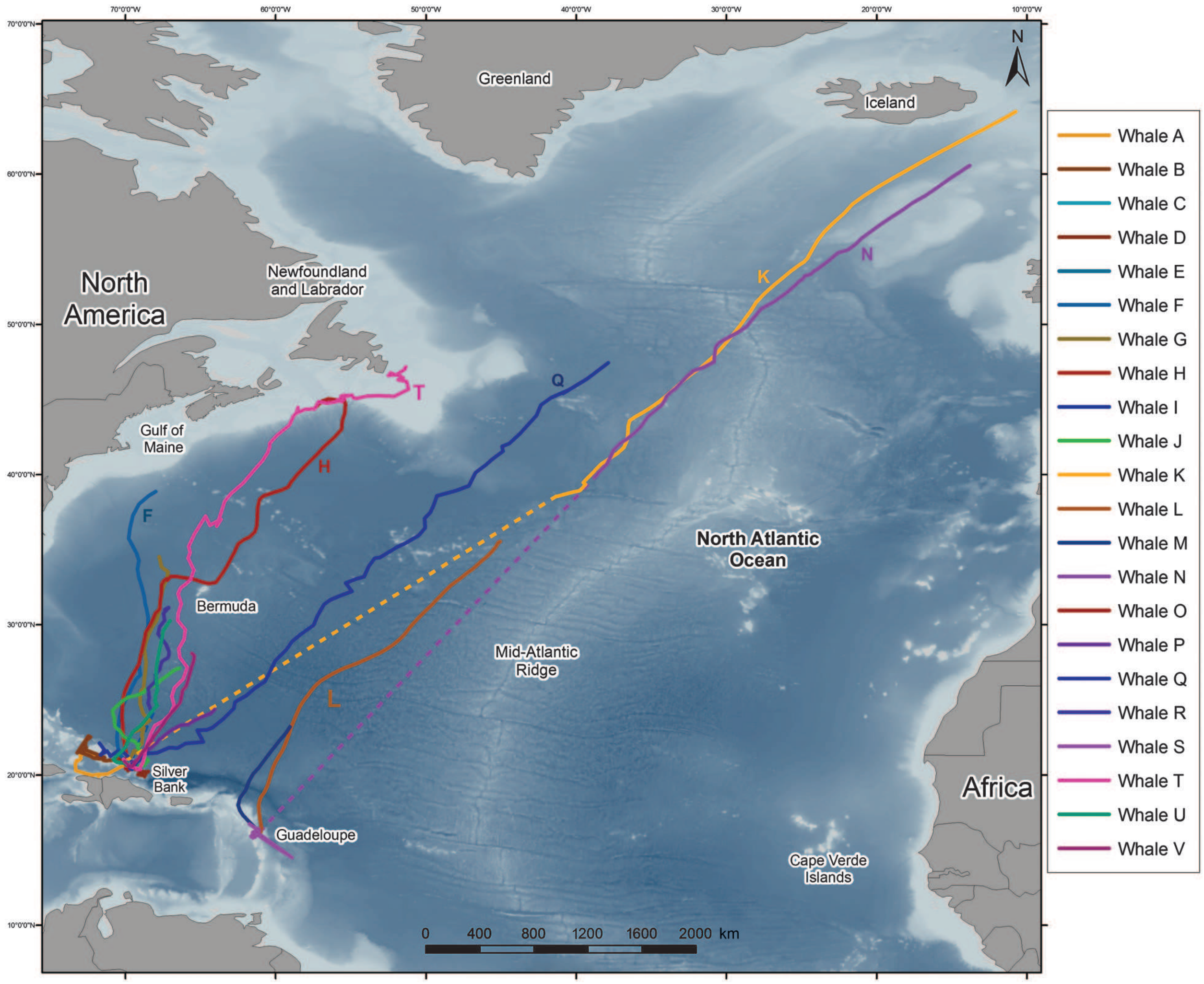
In Guadeloupe, whale M initially traveled northwest along the eastern side of Guadeloupe, then traveled to the western side of St. John's (Antigua and Barbuda) before gradually angling north to pass over the Tintamarre Spur and begin migrating (Fig. 5). Whale L began heading north soon after tagging, yet angled slightly east towards Antigua Valley before exiting the shelf break (Fig. 5). Whale S swam rapidly offshore immediately after tagging, crossed the shelf break, and then returned to within 25 km of the tagging position 3 days later. Whale S then stayed on Colombie Bank (between Marie-Galante Island and southwestern Basse-Terre) for 5 days; it then moved towards La Desirade and Guadeloupe Passage before migrating (Fig. 5).

Migratory movement

The animals that appeared to be headed toward the Gulf of Maine or Canada (F, G, H, J, T, U, and V) (Fig. 2) all traveled within 500 km (longitudinally) of each other until approximately 33°N (i.e., the latitude of Bermuda), where they began to spread out and angle more directly toward their presumed feeding ground. Two whales (H and T) were tracked from Silver Bank to the Scotian Shelf, representing the first documented complete humpback whale migration routes in the North Atlantic (Fig. 2). Whale H first reached the shelf break at St. Pierre Bank and immediately turned southwest to follow the shelf break to the eastern edge of Cabot Strait, yet did not exhibit ARS along the shelf edge. Whale T traveled from Silver Bank to the Nova Scotia shelf break at the eastern edge of the canyon known as "the Gully", and then turned abruptly to follow the shelf break towards the Grand Bank of Newfoundland, presumably to forage. Whale T exhibited ARS on Banquereau and St. Pierre Banks, both known foraging grounds, before transmissions ceased. Whale T recorded four ARS-classified positions at approximately 200 km south of the Kelvin Seamount (Fig. 3).

Six whales (K, L, M, N, P, and Q) (Fig. 2) were heading toward the eastern North Atlantic when transmissions ceased. Whale Q traveled towards the Norwegian Sea, yet transmissions stopped just north of the Newfoundland Basin. Whale K did not begin transmitting until it reached the southeastern corner of the Newfoundland Basin, yet the tag transmitted for 31 days until the whale was approximately 167 km off the eastern coast of Iceland. Whale N (tagged in Guadeloupe) had a similar pattern, with transmissions beginning at the southeastern edge of the Newfoundland Basin and continuing for 28 days until transmissions ceased northeast of

Fig. 2. Movement of all 22 humpback whales (*Megaptera novaeangliae*) tracked in this study. Track locations were estimated at 12 h intervals using a Bayesian switching state–space model (SSSM). Broken lines indicate distance between tagging location and first transmission. Some longer tracks are labeled for clarity.



the Rockall Rise (Fig. 2). Whales P (Silver Bank) and M (Guadeloupe) both stopped transmitting about 800 km into their northeast migration, and whale L was just east of the Sohm Plain when transmissions ceased.

The only tagged whale from this study to visit the island of Bermuda (whale H and calf), showed a nearly 90° easterly course change at approximately 250 km abeam of Bermuda that took her to the northeastern corner of the island in 3 days (Fig. 2). Once directly north of Bermuda (at the Bowditch Seamount), she turned sharply north-northeast and continued her migration on approximately the same heading that she had traveled before she diverted to Bermuda.

Discussion

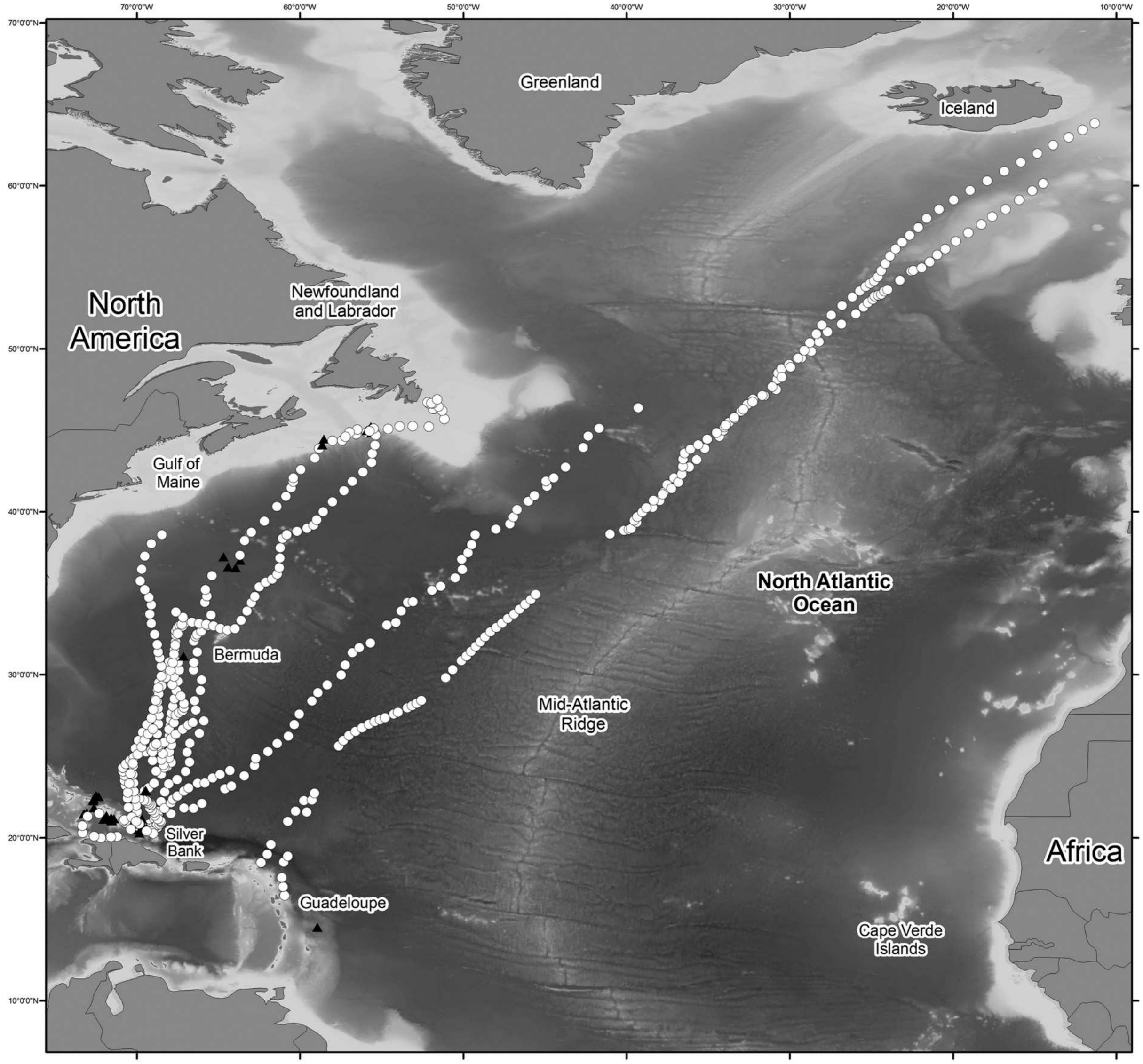
Breeding ground movement

Our results further confirm that the shallow reef system along the North Atlantic side of the Antillean island chain represents an important habitat for humpback whales, and that whales from several high-latitude feeding grounds congregate in this area to breed each year; this is consistent with previous photo ID work (Mattila and Clapham 1989; Mattila et al. 1989; Katona and Beard 1990; Clapham et al. 1992; Smith et al. 1999; Bérubé et al. 2004; Robbins et al. 2006). The mean (±SD) speed within the Antillean breeding ground (1.89 ± 0.77 km·h^{-1}) calculated here was found to be consistent with speeds observed in breeding grounds off Hawai'i (2 km·h^{-1}) and off Mexico (1.2 ± 0.8 km·h^{-1}) (Glockner and Venus 1983; Tyack and Whitehead 1983; Mate et al. 1998; Lagerquist et al. 2008). No North Atlantic breeding ground speeds had been reported prior to this study.

Our results show local travel to areas that are relatively distant from the most densely populated and well-studied breeding aggregations, and suggest that the frequency and extent of interisland movement may have been underestimated in the past. Previous photographic matches between Silver Bank and Puerto Rico, Anguilla and Virgin Bank (Mattila et al. 1989; Mattila and Clapham 1989) have indicated that some interisland movement within the breeding range does occur, yet the use of waters off Haiti, Caicos Bank, Caicos Passage, Great Inagua Island, and Antigua and Barbuda shown here had not been previously described (in part because of low or no sighting effort in these areas). As heterogeneity in occupancy patterns affects capture probability during capture–recapture studies and may bias population estimates (Hammond et al. 1990; Friday 1997; Punt et al. 2007), the scope of within-season movements in the Antilles warrants further investigation.

Whales spent, on average, 18% of their time outside the Silver Bank and Navidad Bank Sanctuary boundaries before beginning their northward migration. To cover all nonmigratory movement

Fig. 3. Behavioral mode estimates from all tracked humpback whales (*Megaptera novaeangliae*). Locations and behavioral modes were estimated at 12 h intervals using a Bayesian switching state–space model (SSSM). White circles represent "transit" (behavioral mode 1) and black triangles represent "area-restricted search" (ARS; behavioral mode 2). Unclassified behavioral states are not shown.



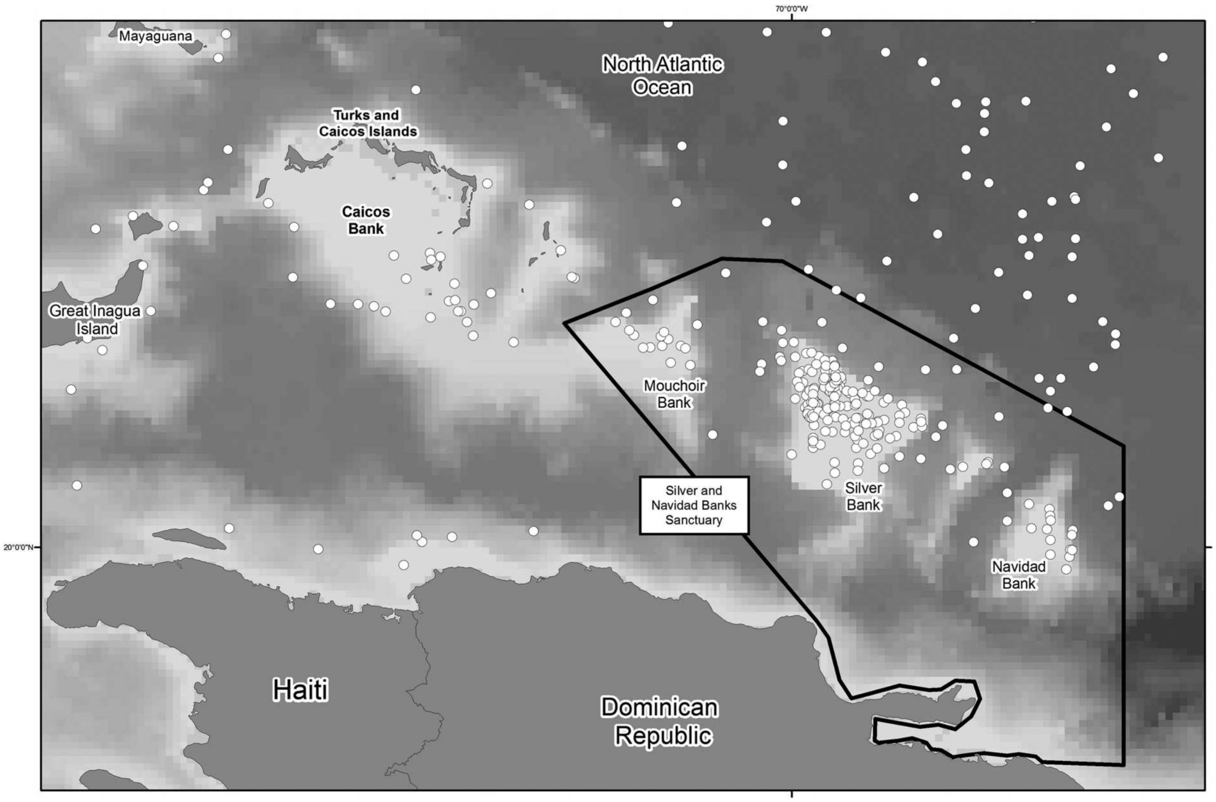
of the whales tagged in Silver Bank, the sanctuary would need to expand to approximately three times its current area and include territorial waters off the Bahamas, Turks and Caicos, and Haiti. The Dominican government has passed regulations requiring permits for access to the sanctuary in an attempt to limit the human disturbance to humpback whales in their waters, but unregulated vessel traffic throughout the Antillean breeding range is inevitable and likely to increase over time. The evidence of substantial within-season movements shown here highlights the need for multinational humpback habitat management initiatives that would cover the entire range of this endangered species.

Migratory movement

This study confirms the findings of Reeves et al. (2004), who examined 19th century North Atlantic whaling logbook data and found what appeared to be diffuse humpback whale dispersion across the North Atlantic Ocean over several months of the migratory period. However, while the migrations documented in this study were spatially and temporally diffuse, there were some noticeable movement patterns. Animals migrating towards the eastern North Atlantic feeding grounds (Iceland and Norway) traveled on a fairly direct and consistent course of roughly 35°, while those traveling towards the Gulf of Maine or Canada exhibited a general heading of approximately 20° until they neared Bermuda. Additionally, whales K and N were heading toward the eastern North Atlantic and showed approximately 1300 km of nearly identical track lines, followed by an additional 1600 km of track with nearly identical heading (separated by roughly 200 km), despite having been tagged in two separated locations (Guadeloupe and Silver Bank) in different years (Fig. 2). Whales L (Guadeloupe) and P (Silver Bank) also appeared to be heading for similar tracks as K and N (Fig. 2), despite the spatial and temporal separation. This overlap supports the idea that migratory corridors for whales feeding in the eastern North Atlantic may exist (Charif et al. 2001), or that migrations are governed by the same navigational cues (Horton et al. 2011).

Historically, humpbacks observed and (or) killed by 19th century whaling vessels were occasionally documented along the western margins of the Mid-Atlantic Ridge from June through August, prompting speculation of a feeding aggregation in pelagic waters well south of their current known range (Reeves et al.

Fig. 4. Habitat use by humpback whales (*Megaptera novaeangliae*) within the Silver Bank and Navidad Bank Sanctuary (SNBS) and surrounding waters. Each white circle represents a 12 h switching state–space modeled position from 1 of the 16 whales that used habitat off the Dominican Republic.



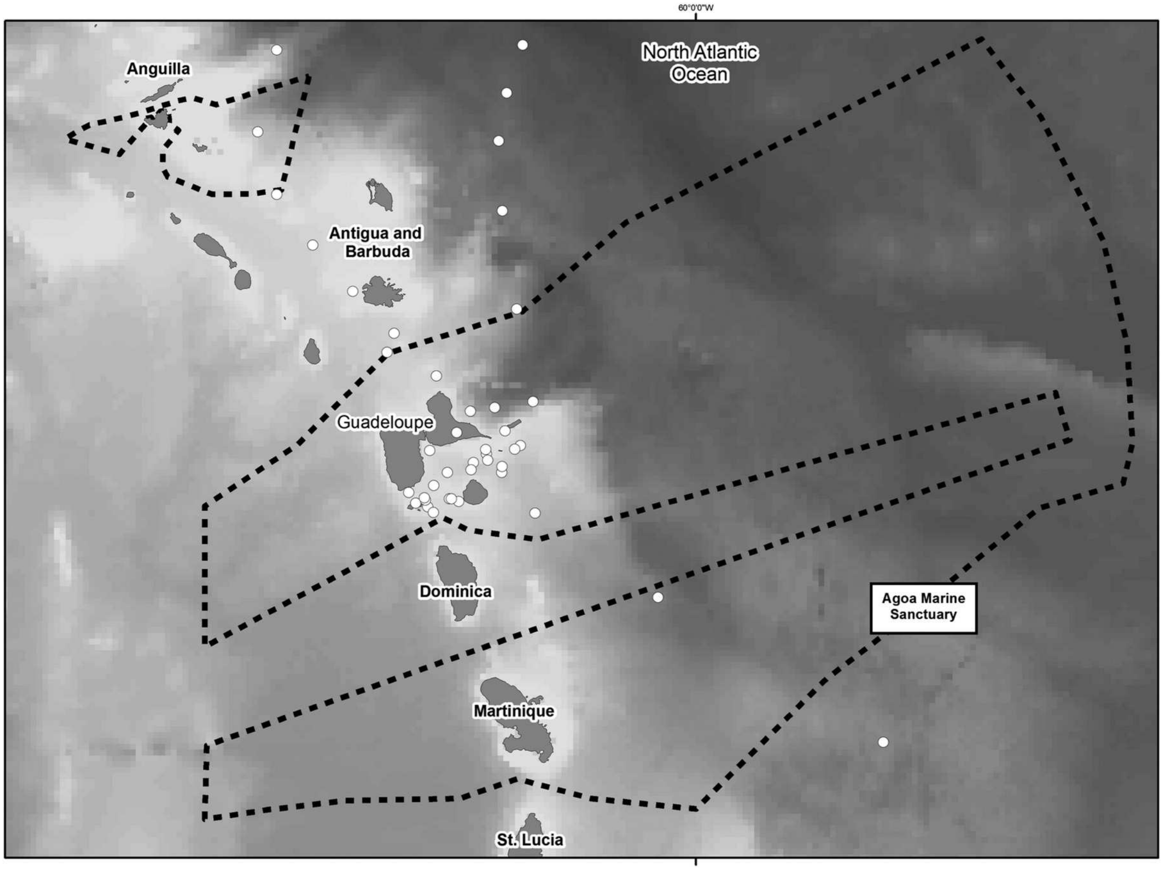
2004). However, while the telemetry data cannot entirely rule out feeding while traveling, no animals from this study exhibited ARS (which generally characterizes foraging; Kareiva and Odell 1987; Mayo and Marx 1990) near the margins of the Mid-Atlantic Ridge. Overall, only six individual points from three migrating whales were categorized as ARS (Fig. 3), and the general lack of pronounced meandering movement patterns during migration suggest that no typical feeding aggregations occur along the western margin of the Mid-Atlantic Ridge. Furthermore, humpbacks have been seen in the Antilles as late as June (Reeves et al. 2001; Gandilhon 2012); if they began their migration the eastern North Atlantic in mid-June, then they would be over the Corner Rise seamounts around the beginning of July. This is consistent with historical sightings (Reeves et al. 2004) and indicates that humpbacks seen well south of known coastal feeding aggregations during summer months could easily have been late migrants still on their northbound migration, rather than being part of a separate feeding aggregation.

Whale T was the only whale to exhibit more than one position classified as ARS during migration, spending 2 days presumably foraging about 200 km south of the Kelvin Seamount (Fig. 3). Humpbacks have been known to visit seamounts during the breeding season (Garrigue et al. 2010) and during periods of peak oceanographic productivity (Mate et al. 2007), yet the scope of seamount habitat use is largely unknown. Virtually no humpback research effort exists for this area of the North Atlantic, and the frequency and purpose of ARS on the New England Seamounts warrants further investigation.

Humpbacks from all major feeding aggregations, including Iceland, are consistently seen near Bermuda from February to May during the northward (but not the southward) migration (Stone and Katona 1984, Stone et al. 1987; Reeves et al. 2006), yet none of the eastern North Atlantic whales tagged in this study traveled toward Bermuda. Given our findings of consistent linear travel toward the eastern North Atlantic from the start of migration, it is plausible that decisions about specific migratory movements (including travel to Bermuda) may be made on or before breeding ground departure and may be influenced by age, sex, and (or) reproductive state. Opportunistic feeding has been hypothesized (Stone and Katona 1984) in Bermuda waters, yet the habitat use of humpbacks visiting this region is largely unknown. Whale H made a nearly 90° course change to the east during her northward migration before making an equally abrupt course change to the north after reaching the Bowditch Seamount, yet no ARS was observed during this diversion. The lack of evidence for foraging behavior (i.e., lack of ARS) by whale H may indicate an absence of prey, or that humpbacks visit Bermuda for navigational, mating, or other unknown purposes. However, our sample size is small and existing information does not permit further speculation about the scope of use of Bermuda waters. As a populated offshore island in a migratory path, Bermuda provides a unique opportunity to study the behavior of migrating humpback whales in mid-ocean, and further research there would potentially be very useful to our understanding of the ecology of this species.

Telemetry from this study shows an overall mean (±SD) minimum speed during migration of 4.21 ± 1.3 km·h^{-1}, yet humpbacks traveling toward the eastern North Atlantic were slightly faster than those heading toward Gulf of Maine or Canada (4.67 ± 1.5 vs. 3.87 ± 1.1 km·h^{-1}). These results fall within the range of speeds of tagged humpbacks migrating from Mexico (4 km·h^{-1}) (Lagerquist et al. 2008), Hawai‘i (4.5 km·h^{-1}) (Mate et al. 1998), and Brazil (3.83 and 3.48 km·h^{-1}) (Zerbini et al. 2006, 2011), but are slower than migrating gray whales (*Eschrichtius robustus* (Lilljeborg, 1861)) (mean = 6.5 km·h^{-1}) (Mate et al. 2011*a*) and southern right whales (*Eubalaena australis* (Desmoulins, 1822)) (4.4–6.5 km·h^{-1}) (Mate et al. 2011*b*). Previous photo ID mark–recapture studies in the Gulf of Maine

Fig. 5. Habitat use by humpback whales (*Megaptera novaeangliae*) within the Agoa Marine Sanctuary and surrounding waters. Each white circle represents a 12 h switching state–space modeled position from one of the three whales that used habitat off the French West Indies.



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

Historical whaling records (Ingebrigtsen 1929) suggest a scenario in which eastern North Atlantic whales begin their feeding season off Jan Mayen, and move in a clockwise direction to Bear Island and Finnmark as the summer progresses. At the speeds that we observed, it would have taken whales K and N at least 68 and 71 days, respectively, to reach Jan Mayen from their tagging location. Thus, an eastern North Atlantic whale would need at least 5 months just to transit between breeding and feeding grounds each year. If this is correct, it is plausible that the energetic and time requirements for a full eastern North Atlantic migration, particularly for a nursing mother, are high enough that it could not be completed each year. Late-summer mid-Atlantic sightings (Reeves et al. 2004), documented singing and mating behavior in feeding grounds (Weinrich 1995; Clark and Clapham 2004; Vu et al. 2011), and recent telemetry showing some southward migration from Iceland beginning as late as February (G. Vikingsson, personal communication) could all be taken as evidence for the idea that the distance between Iceland or Norway and the Antilles forces individual eastern North Atlantic whales to choose between an incomplete southward migration, a truncated or off-peak breeding season, or a truncated or off-peak feeding season, annually. If we may extend this speculation a little farther, these decisions could result in fewer (and less diverse) breeding opportunities or a shorter feeding season unless eastern North Atlantic whales spatially and (or) temporally extend their seasonal ranges. Extension of the breeding range to include breeding while migrating or breeding on feeding grounds could partially explain the genetic evidence for the existence of unknown breeding areas (Larsen et al. 1996), as well as previous observations that not all feeding grounds are equally represented among whales in the North Atlantic breeding ground during peak abundance (Stevick et al. 2003).

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

Acknowledgements

We are greatly indebted to G. Flipse from Conscious Breath Adventures and T. Conlin from Aquatic Adventures who provided invaluable logistical and vessel support on Silver Bank. Y. Geyer,

F. Mazeas, Y. Ivashchenko, G. Clapham, S. Cerchio, D. Cholewiak, R. Sears, J. Lemire, and the volunteers from BREACH and OMMAG in Guadeloupe greatly assisted with tagging operations, data collection, logistics, and fieldwork. Tag deployment, photo ID, and biopsy sampling were performed according to regulations and restrictions specified in the existing permits issued by the NMFS to the National Marine Mammal Laboratory (permit Nos. 782-1719-03 and 14245). Research in the Silver Bank and Navidad Bank Sanctuary was permitted and supported by the Minister of Environment and Natural Resources of the Dominican Republic. The findings and conclusions in the paper are those of the authors and do not necessarily represent the views of the NOAA–NMFS. Reference to trade names does not imply endorsement by the NMFS.

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