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Ocean basin-wide movement patterns of North Atlantic humpback whales

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ABSTRACT

North Atlantic (NA) humpback whales (*Megaptera novaeangliae*) migrate between high-latitude maternal feeding grounds and low-latitude breeding/calving grounds, with one distinct breeding segment currently considered endangered: Cape Verde Islands/northwest Africa (CVI). This study assesses the movement patterns and population spatial structuring of humpback whales across the NA Ocean basin for the first time in three decades. Photo-ID records from collections contributed to the North Atlantic Humpback Whale Catalogue, a dataset of 38,319 records of 9,977 individuals documented between 1980 and 2015 were analysed. Transition probabilities were estimated between all five primary feeding grounds and three breeding/calving areas defined as CVI, Greater

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Antilles and Lesser Antilles, dividing the West Indies distinct population segment into two, based on emerging trends. Breeding-to-feeding area transition probabilities were highest from the Greater Antilles to western feeding grounds (the Gulf of Maine, Atlantic Canada and West Greenland), from the Lesser Antilles to eastern feeding grounds (Norway and Iceland), and from CVI to eastern feeding grounds. The difference in migratory patterns of humpback whales using the Greater Antilles and Lesser Antilles regions within the West Indies indicates that they are behaviourally distinct and may be best managed as separate breeding populations.

KEYWORDS: HUMPBACK WHALE; PHOTO-ID; NORTH ATLANTIC; MIGRATION; MOVEMENTS; BREEDING GROUNDS; FEEDING GROUNDS

INTRODUCTION

Documenting and quantifying the movement of highly migratory species is vital for accurate assessment of the species' population spatial structuring. The seasonal migration that humpback whales undertake between their summer feeding grounds in mid to high-latitudes and their wintering grounds where breeding or calving occurs (henceforth referred to as breeding grounds) at lower latitudes in the North Atlantic Ocean has previously been documented by photo-ID studies (Katona & Beard, 1990; Smith *et al*., 1999; Stevick *et al*., 2003, 2015, 2018; Wenzel *et al*., 2009, 2020; Kennedy *et al*., 2014; Kettemer *et al*., 2022). In the North Atlantic, two breeding populations of humpback whales have been recognised: the West Indies and the Cape Verde Islands (CVI), northwest Africa. The five primary feeding aggregations in the North Atlantic have previously been defined as the Gulf of Maine, including the Bay of Fundy and the Scotian Shelf, Atlantic Canada (Gulf of St. Lawrence and along the coasts of Newfoundland and Labrador), West Greenland, Iceland and northern Norway, including the Barents Sea (Fig. 1) (Stevick *et al*., 2003; Kettemer *et al*., 2022). The CVI population of humpback whales in the eastern North Atlantic, currently estimated at fewer than 300 individuals, primarily migrates to the feeding grounds off northern Norway and Iceland (Wenzel *et al*., 2020). It is likely a remnant of a historically larger breeding population from CVI and northwest Africa which has not yet recovered from commercial whaling and is listed as endangered under the US Endangered Species Act (ESA) (Reeves *et al*., 2002; Bettridge *et al*., 2015; Cooke, 2018).

In the western North Atlantic, comparatively higher numbers of humpback whales are annually observed on the breeding grounds of the West Indies than in the CVI. Humpback whales congregating in the West Indies are currently considered one distinct population segment that is not at risk of extinction under the US ESA (Bettridge *et al*., 2015). Within the West Indies, humpback whales are seasonally documented in the Greater and Lesser Antilles, though they may be distributed anywhere along the West Indies island chain and the Bahamas south to the Caribbean coast of Venezuela (Swartz *et al*., 2003; Kennedy & Clapham, 2017). Humpback whales breeding in the West Indies have been sighted in all five primary feeding grounds: the Gulf of Maine, Atlantic Canada, West Greenland, Iceland and Norway (Stevick *et al*., 2003).

Humpback whales congregate in the highest concentrations in the Greater Antilles, off the islands of Hispaniola (Haiti and the Dominican Republic) and Puerto Rico, with the highest concentrations documented on Silver Bank, Mouchoir/Pañuelo Bank, Navidad Bank and Samana Bay in the Dominican Republic (Whitehead & Moore, 1982; Mattila *et al*., 1989; Mattila *et al*., 1994). Early studies suggested that Silver Bank may host up to 85% of breeding humpback whales from the western North Atlantic (Winn *et al*., 1975; Balcomb & Nichols, 1978). Evaluation of the composition of competitive groups on Silver Bank and in Samana Bay showed spatial and genetic mixing of whales from different feeding areas (Mattila *et al*., 1989; Clapham *et al*., 1993), which led these early studies to assume panmixia in the West Indies (Clapham *et al*., 1993; Smith *et al*., 1999). However, some evidence suggests that whales from the eastern North Atlantic feeding areas of Iceland and Norway are less likely to winter in the Greater Antilles region of the West Indies (Stevick *et al*., 2003).

In the Lesser Antilles, intensive 19th Century whaling operations in the region greatly reduced the population of humpback whales, and their densities have remained low in the Lesser Antilles since the cessation of

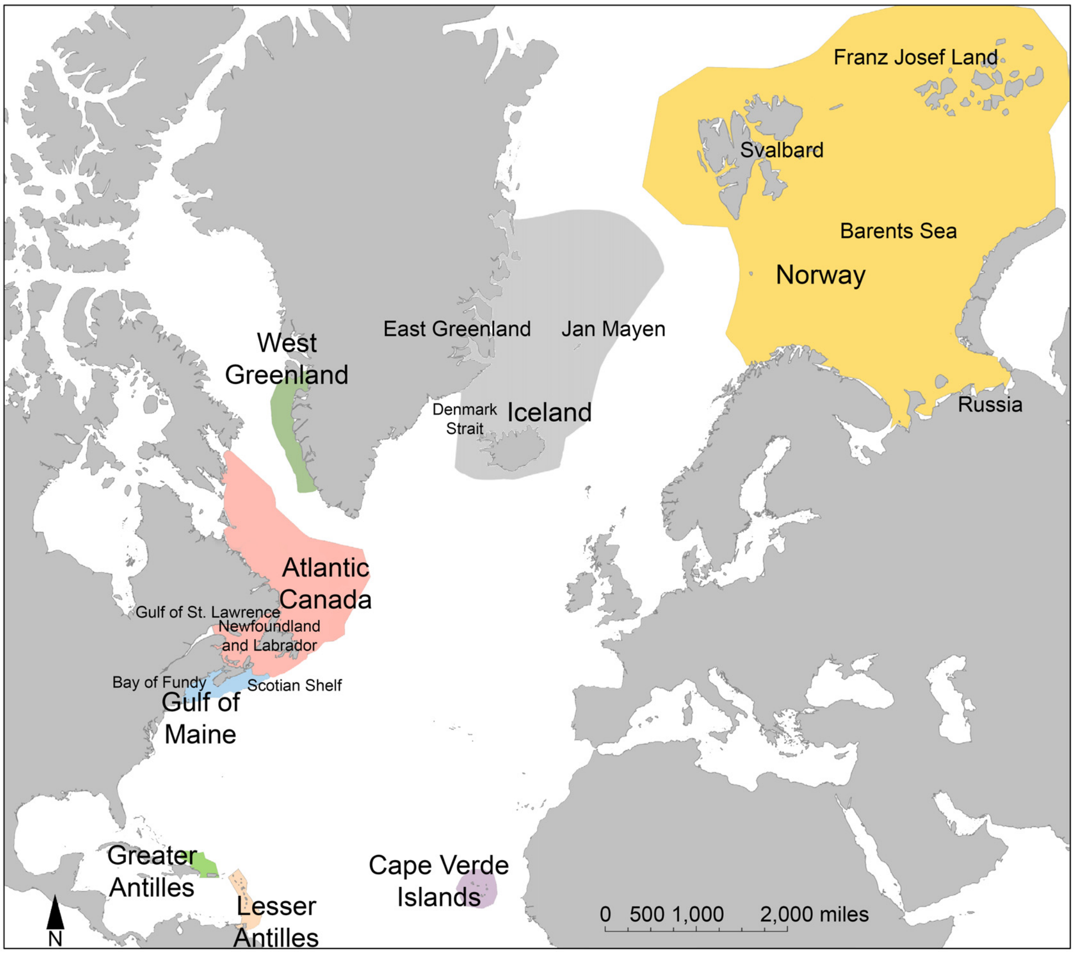

Figure 1. Map of the feeding and breeding areas across the North Atlantic Ocean, as defined in the NAHWC. The text is over each area's general location.

commercial whaling operations (Winn *et al*., 1975; Romero & Hayford, 2000; Reeves *et al*., 2001; Swartz *et al*., 2003; Reeves *et al*., 2004). Early studies (Winn *et al*., 1975; Mattila & Clapham, 1989; Swartz *et al*., 2003; Acevedo *et al*., 2008) documented very few visual and acoustic detections of humpback whales in the Lesser Antilles. An increase in sightings and available photo-ID data since the early 2000s, primarily from whale watching and scientific activities around the island of Guadeloupe and areas south, now allows for closer examination of humpback whales documented from the Lesser Antilles in this study. On average, humpback whales arrive at the Lesser Antilles an estimated six weeks later than the Greater Antilles, demonstrating temporal differences in migratory patterns between the two regions (Stevick *et al*., 2018). A low degree of movement between the Greater Antilles and Lesser Antilles has been documented both inter- and intra-seasonally (Stevick *et al*., 2018; MacKay *et al*., 2019). However, the degree to which this movement occurs is under-studied.

Knowledge of the migratory patterns and population spatial structuring of a species that was commercially depleted is vital for informed resource management, conservation and protection. Humpback whales were one of the first species to be listed as 'Endangered' under the US ESA, and 'Threatened' under Canada's Committee on the Status of Endangered Wildlife in Canada (COSEWIC), while also placed on the International Union for the Conservation of Nature's (IUCN) Red List, due to a long history of depletion by commercial whaling operations (81 FR 62259; IWC, 2002; COSEWIC, 2003; National Marine Fisheries Service, 2016; Cooke, 2018). With most populations experiencing growth since the introduction of a moratorium on commercial whaling in 1985 and conservation actions through various national management processes, the IUCN currently considers the species to be of 'Least Concern' on a global level, with some endangered populations (IWC, 2002; COSEWIC, 2003; National Marine Fisheries Service, 2016; Cooke, 2018). Under the COSEWIC, the entire western North Atlantic population was reassessed and delisted in 2003 (COSEWIC, 2003). Under the US ESA, humpback whales were delisted globally in a listing revision that divided the global species into 14 distinct population segments (DPS) based on breeding grounds, leaving two as 'Endangered' and two DPSs as 'Threatened' (81 FR 62259). In the North Atlantic, two DPSs were identified, one in the West Indies which was considered 'Not at Risk', and a second in the Cape Verde Islands/Northwest Africa population that remains 'Endangered' (Bettridge *et al.*, 2015).

The dynamics of the long-distance migration that humpback whales undertake have not been updated across the entire North Atlantic Ocean since the Years of the North Atlantic Humpback (YoNAH) project of 1992–93, a directed effort to survey all major feeding and breeding grounds and collect both photo-ID and molecular data (Smith *et al.*, 1999). Since then, more data have become available from all areas, including regions of low abundance, such as the Cape Verde Islands, and areas with previously low levels of research activity, such as the Lesser Antilles. Updating our knowledge of the patterns of long-distance humpback movements is imperative to mitigate the increasing disturbance of human activities.

Here, a multi-decadal dataset from the North Atlantic Humpback Whale Catalogue (NAHWC) was analysed using a novel application of maximum likelihood methods to estimate humpback whale transition probabilities between breeding and feeding grounds in the North Atlantic, to test the panmixia hypothesis in the West Indies and compare with the movement patterns from the endangered Cape Verde Islands population. The NAHWC includes photo-ID and corresponding sighting data from across the North Atlantic Ocean basin collected by hundreds of researchers and citizen scientists, curated by Allied Whale at the College of the Atlantic. The data represent five decades of dedicated research, including the YoNAH and More of the North Atlantic Humpback surveys (MONAH; Fulling & Clapham, 2004), and opportunistic platforms, such as whale watching cruises. In this study, photo-ID data from the NAHWC for years 1980 to 2015 were analysed to statistically account for the differences in sample sizes and effort in the feeding and breeding grounds to investigate the movement patterns of humpback whales across the North Atlantic Ocean basin.

METHODS

Photo-ID data processing

The unique pattern on the ventral surface of humpback whale flukes allows for identification of individuals (Katona & Whitehead, 1981). Identification images and associated sightings data were collected throughout the North Atlantic Ocean by hundreds of researchers and citizen scientists and submitted to the NAHWC for ocean basin-wide comparison and scientific collaboration. The data analysed in this work include photo-ID samples from the NAHWC collected by the co-authors and citizen scientists during dedicated surveys and opportunistic encounters from 1980 through 2015.

Photo-ID comparison methods followed the standards of Katona and Whitehead (1981) for fluke photos with technological updates over the four decade history of the NAHWC. Visual comparison methods by two trained photo-ID technicians were used from 1977 to 2017 to find re-sightings or 'matches' and add new whales to the Catalogue, maintained in iMatch (version 5.4.18). From 2017 to present, photo-ID methods have gradually evolved to the current standard, involving a dual review system where fluke photos are first compared using the automated identification algorithms described in Cheeseman *et al.* (2022) on a private reference catalogue. Every positive match to the NAHWC was confirmed by two trained reviewers to prevent false-positive errors. If the algorithms suggested no match to the Catalogue, the fluke photo was visually compared with the entire NAHWC by an experienced photo-ID technician to prevent false negatives or missed matches. Photos where the algorithms performed poorly, such as images of only one half of the flukes and images of carcasses, were visually compared with the Catalogue by two reviewers. When an individual was not successfully matched to a previously identified individual in the Catalogue after using both automated identification algorithms and visual comparison, the whale was assigned a new permanent (North Atlantic – NA) identification number and added to the NAHWC. Poor quality photos, where the focus would significantly affect a reviewer's ability to accurately identify the animal, or where less than 20% of the right or left fluke was visible, were not included in the NAHWC database and our analyses.

Sightings data used for these analyses include all fluke photos of non-calf humpback whales from 1980 through 2015 for which photographic comparison for the NAHWC was completed as of July 2024. The analyses conducted use only one sighting per year, per area, for every individual to calculate sample sizes and number of transitions between each area. If an animal was sighted in more than one feeding or breeding area in a given year, both sightings were included in the analyses to enable representation of inter-area transitions between and within years. Across all years, the percentage of resightings between a given breeding and feeding area was calculated by dividing the number of individuals sighted in both areas by the total number of individuals that were resighted on any feeding ground, removing any duplicate numbers of whales that were sighted on two feeding grounds. Any inter-matches between the three breeding areas were counted as a percentage of the total sample from the breeding area sample. We analysed a total of 38,319 records/photos of 9,977 individual humpback whales from the feeding or breeding areas defined.

Feeding areas were defined as the Gulf of Maine (including sightings from the Bay of Fundy and the adjacent waters of the Scotian Shelf), Atlantic Canada (the Gulf of St. Lawrence and along the coasts of Newfoundland and Labrador), West Greenland, Iceland (including fewer than a dozen sightings from East Greenland/Denmark Strait and 50 sightings collected during the YoNAH survey near the island of Jan Mayen) and Norway (primarily off northern Norway and the Barents Sea, including the Svalbard Archipelago, and extending northwest to Russia and Franz Josef Land; Fig. 1). To improve sample sizes, identifications were subsequently grouped into western North Atlantic feeding regions (Gulf of Maine, Atlantic Canada and West Greenland) and eastern North Atlantic feeding regions (Iceland and Norway). The breeding areas analysed included the Greater Antilles (primarily from the banks north of the Dominican Republic, Samana Bay in the Dominican Republic and Puerto Rico), the Lesser Antilles and the Cape Verde Islands (CVI). The Greater and Lesser Antilles areas were split at the Anegada Passage (Fig. 2), where there are few sightings and photographic samples in this dataset. The Lesser Antilles was defined as the area extending from the Anegada Passage to the Venezuelan coast. Sightings from the US and British Virgin Islands, though considered part of the Greater Antilles chain, were excluded from all analyses due to a lack of new photo-ID samples in the NAHWC from the Virgin Islands after Mattila and Clapham's (1989) surveys of the region (n = 3 individuals identified in the region from 1990 to 2015). The number of individuals identified in each region of the West Indies breeding range, which were combined into closest geographic regions, are presented in Table 1, together with the sample from the entire island chain of the CVI.

Figure 2. Map of the West Indies breeding area defining the regions included in the text. The distinction drawn here between the Greater Antilles and Lesser Antilles at the Anegada Passage is highlighted in red.

Table 1

N (number of individual humpback whales) identified in the dataset, 1980–2015, along the breeding/calving range, partitioned by the oceanographic feature or geographic region within the West Indies and the Cape Verde Islands. Note: resightings exist between regions; the total N represents the number of unique individuals documented in any breeding region.

Region	N
Greater Antilles – Banks north of Hispaniola: Silver, Navidad, Mouchoir and Turks	2,371
Greater Antilles – Samana Bay, Dominican Republic	1,000
Greater Antilles – Puerto Rico	492
Lesser Antilles – Leeward Islands	288
Lesser Antilles – Windward Islands	24
Cape Verde Islands	212
Total N for all breeding regions	4,038

Estimating transition probabilities between seasonal habitats

Photo-ID datasets where effort varies or sightings are spatially and temporally clumped can be problematic for statistical analyses because animals in intensively-studied areas are more likely to be documented than those in less-studied areas. To address variable sampling effort or distribution, our seasonal migration estimation method using maximum likelihood estimation, designed as a movement-analysis method that does not require equal probabilities of capture in each region or year studied, were selected for these analyses.

Movement was quantified between feeding and breeding regions by calculating transition probabilities using maximum likelihood techniques (Hilborn, 1990; Whitehead, 2001; Stevick *et al*., 2006), a statistical method for estimating the values of unknown model parameters which maximise the sample likelihood. Transition probabilities, the probability that an individual in one area moves to another area between sampling periods, were calculated between all feeding and breeding grounds with a novel maximum likelihood estimation method, hereafter referred to as seasonal migration estimation. This is an extension of the Hilborn (1990) method further developed by Hal Whitehead and modified for this dataset, run in MATLAB R2023a (The Mathworks, Natick, MA), on the number of individual transitions between each breeding and feeding area. Raw numbers of transitions per paired area (i.e., one breeding and one feeding area) were totalled for comparison.

The theory behind the seasonal migration estimation method is as follows for transitions from a breeding area to a feeding area: Suppose an individual in breeding area A migrates to feeding area X with probability P_{AX}. There can be numerous breeding areas (*A, B, C,* ...) and feeding areas (*V, W, X,* ...) within the species' distribution. Each probability of transitioning from one seasonal habitat to another is assumed to be independent of study year. We assume that each animal makes this annual migration, so:

$$\sum_X P_{AX} = 1, \forall A \tag{1.1}$$

The sum of each whale's probability of migrating from area A to any of the areas X is equal to 1 for all of area A. Given that a whale migrates to a feeding area X, then the animal's probability of being identified in year y is q_{yX}. Each transition probability includes the probability of the animal dying before identification on either the feeding or breeding ground.

We then define $n(y,A)$ as the number of animals identified in breeding area A in year y and $z(y,A,X)$ as the number of animals identified in year y in both breeding area A and feeding area X. Then, conditioning on breeding area observations, we find that the likelihood of the data is proportional to:

$$L = \prod_y \prod_A \left(\prod_X (P_{AX} \cdot q_{yX})^{z(y,A,X)} \cdot \left(1 - \sum_X P_{AX} \cdot q_{yX} \right)^{n(y,A) - \sum_X z(y,A,X)} \right) \tag{1.2}$$

The probability of the observed movement between breeding and feeding areas is: $\prod_X (P_{AX} \cdot q_{yX})^{z(y,A,X)}$. The second part of the equation $\left(1 - \sum_X P_{AX} \cdot q_{yX}\right)^{n(y,A) - \sum_X z(y,A,X)}$ adds in each probability for individuals that were not observed in a feeding area in a given year but were observed in a breeding area. Then the log-likelihood is:

$$Log(L) = \sum_y \sum_A \left(\sum_X z(y,A,X) Log(P_{AX} \cdot q_{yX}) + \left(n(y,A) - \sum_X z(y,A,X) \right) Log\left(1 - \sum_X P_{AX} \cdot q_{yX} \right) \right) + \text{constant} \quad (1.3)$$

The log-likelihood should be maximised to estimate the P_{AX}'s. After testing with simulated data, the following shortcut to estimate the q_{yX}'s gave good convergence:

$$q_{yX} = \sum_A z(y,A,X) / \sum_A P_{AX} \cdot n(y,A) \quad (1.4)$$

The probability of being identified in year y in feeding area X is the number of animals that were identified in that area during that year, divided by the number of animals identified the previous winter in a breeding area A who are estimated to have moved to area X based on the transition probabilities P_{AX}. Then, we numerically find the P_{AX} that maximises Equation 1.3, using values of q_{yX}'s from Equation 1.4, subject to the constraint of Equation 1.1. This seasonal migration estimation method was tested on simulated data and was successful in reproducing input P_{AX}'s used to generate the data with up to three breeding areas and three feeding areas.

Standard errors of transition probabilities were calculated using Tukey's jackknifing approach, which are produced by omitting observations in turn and calculating an estimate based on the remaining n – 1 observations over 100 iterations (Efron & Stein, 1981). Bootstrap estimates of variance cannot calculate variance when data are over-populated by zeros, which was true for our dataset with zero transitions between some areas and years. The jackknifing approach is typically conservative in that standard errors are overestimated (Efron & Stein, 1981; Whitehead, 2009).

Estimation methods were run in MATLAB R2023a (scripts available in Supplementary Material 1), with input data in two formats: from breeding area to feeding area or from feeding area to breeding area. When run from breeding area to feeding area, for instance, sample sizes were the number of unique whales identified in each breeding area. The remaining data were the number of transitions between each breeding and feeding area per sampling period. The sampling period includes paired years between 1980 to 2015. Consecutive years were lumped to create two-year capture opportunities which better document transitions between two areas and improve the performance of the seasonal migration estimation method.

After estimating transition probabilities from breeding to feeding area and from feeding to breeding area, results were compared. All estimates were produced with 10 replications of starting parameters for maximisation of likelihood and 5,000 as the maximum number of iterations, as these procedures gave good convergence. The areas with high resulting transition probabilities (maximum of 1) indicate a migratory preference between these areas; lower values indicate areas where whales are less likely to migrate in relation to the other available regions.

RESULTS

Migratory connections between all feeding and breeding areas that were found in our photo-ID dataset across years 1980–2015 are presented in Table 2 and described in Figs. 3 and 4. Resightings were found between all five primary feeding grounds (Gulf of Maine, Atlantic Canada, West Greenland, Iceland and Norway) and the Greater and Lesser Antilles, and between the eastern feeding grounds of Iceland and Norway to CVI. Table 3 presents data from all years on the number of whales from each of the five feeding grounds and the overall percentages from Western and Eastern North Atlantic feeding grounds. Percentages in Table 3 on resightings are given as the number of individual whales from a feeding area that were resighted on a given breeding ground out of the total number of resightings to any feeding ground. Across all years, the percentage of resightings between a given breeding and feeding area was calculated by dividing the number of individuals sighted in both areas by the total number of individuals that were resighted on any feeding ground.

Table 2

Number of individual humpback whales resighted between feeding areas and the breeding sites of the Greater Antilles (G. Antilles), Lesser Antilles (L. Antilles), and Cape Verde Islands (CVI) across all years 1980 to 2015. The number of individuals photo-identified in each area are provided as 'n' under each area.

		Feeding area				
		Western			Eastern	
		Gulf of Maine n = 2,414	Atlantic Canada n = 2,791	West Greenland n = 569	Iceland n = 945	Norway n = 704
Breeding area	G. Antilles n = 3,541	379	716	111	55	25
	L. Antilles n = 312	3	9	4	11	36
	CVI n = 212	0	0	0	9	30

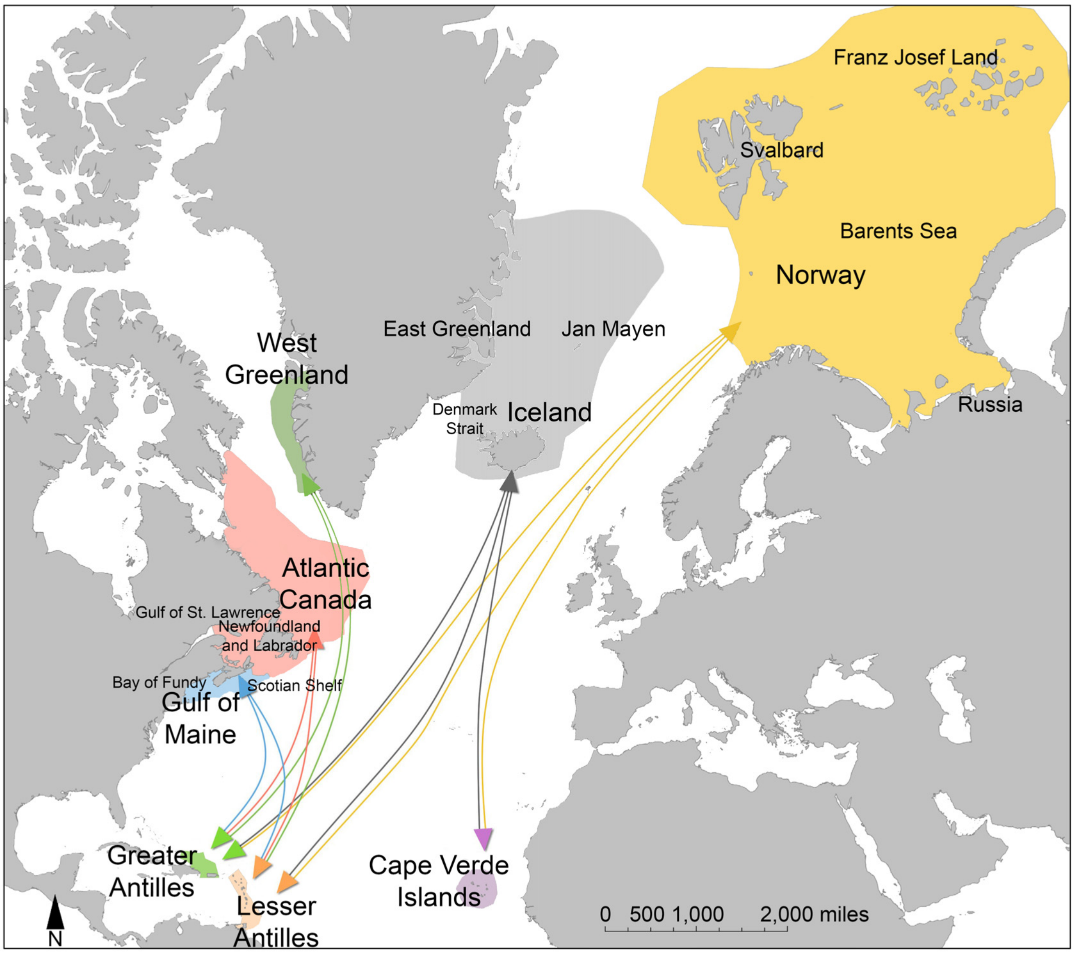

Figure 3. Map of the feeding and breeding areas across the North Atlantic Ocean, as defined in the NAHWC. The text is over each area's general location. Lines represent observed transitions or photo-ID resightings between each area in the dataset and not the migratory pathways.

Inter-breeding area resightings were found between the Greater and Lesser Antilles (22 individuals; 7.1% of the whales in the Lesser Antilles sample), including two individuals sighted in both areas in the same year, and between the Lesser Antilles and CVI (five individuals; 1.6% of whales in the Lesser Antilles sample). Zero resightings were found between the Greater Antilles and CVI.

The seasonal migration estimation method used to calculate transition probabilities produced more robust results with smaller standard errors when years were paired and neighbouring feeding areas combined. The

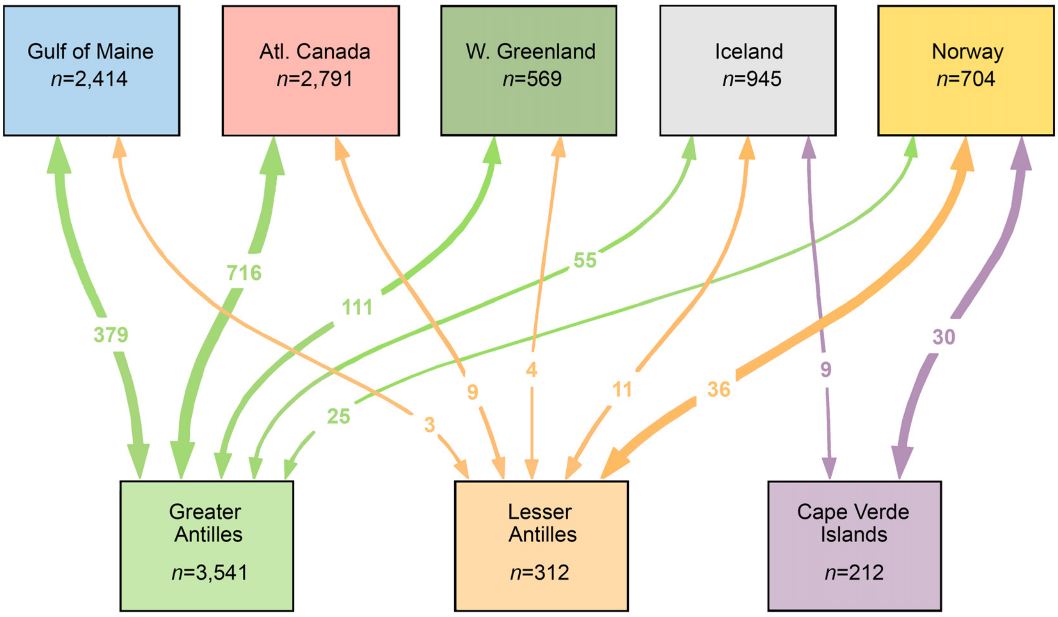

Figure 4. All observed transitions between feeding and breeding areas in the North Atlantic, years 1980–2015. Number of individual whales sighted in each region are provided as 'n' for a given area and the number of whales photo-identified in both the breeding and feeding area in question are presented on the connecting lines.

number of observed inter-annual transitions between breeding and feeding areas increased considerably when areas and years were pooled. Transition probabilities were not equal to and from two given areas (cf., Table 4, Tables S2–4). Estimating transition probabilities from breeding to feeding areas produced results with smaller standard errors, estimated with the jackknifing method, because the observed transitions are a higher proportion of the total breeding area sample sizes compared with the larger sample sizes from the feeding areas. The best results from this movement-estimation method from given breeding areas to feeding grounds are presented in Table 4 and results from feeding to breeding areas are available in Tables S2–4. Different combinations of feeding areas are presented in the Supplementary Material, though the results in Table 4 have the smallest standard errors and give the most accurate results.

Transition probabilities from the Greater Antilles were highest to the western feeding grounds of the Gulf of Maine, Atlantic Canada and West Greenland. Transition probabilities from the Lesser Antilles were highest to the eastern feeding grounds of Iceland and Norway; transition probabilities from CVI were highest to eastern feeding grounds.

Table 3

Resightings from each feeding ground to a given breeding area are a percentage of the total number of humpback whales from the given breeding area resighted to any feeding ground. Percentages of feeding area sample sizes are provided individually and grouped by Western North Atlantic (NA): Gulf of Maine, Atlantic Canada and West Greenland, and Eastern NA: Iceland and Norway.

Note: the values agree across columns, not rows, and any whales that were sighted on two feeding grounds were only counted once in the number of individuals (n) in the Western or Eastern NA.

	% Feeding ground sample	% Greater Antilles resightings	% Lesser Antilles resightings	% CVI resightings
Western NA	78% (n = 5,644)	91% (n = 1,168)	24% (n = 15)	0% (n = 0)
Gulf of Maine	33%	29%	4.7%	0%
Atlantic Canada	38%	56%	14%	0%
West greenland	7.7%	8.6%	6.3%	0%
Eastern NA	22% (n = 1,635)	6.1% (n = 78)	75% (n = 47)	100% (n = 39)
Iceland	13%	4.3%	17%	23%
Norway	9.5%	1.9%	57%	77%

Table 4

Transition probabilities from breeding to feeding areas, calculated with the seasonal migration estimation method on paired years 1980–2015. Areas Gulf of Maine, Atlantic Canada, and West Greenland (GOM + Can + W.Grl), and Iceland and Norway (Ice + Nor) were combined to improve performance. Values in parentheses are the jackknife estimates of the standard errors.

		Western Feeding Areas	**Eastern Feeding Areas**
		GOM + Can + W Grl	Ice + Nor
Breeding area	G. Antilles	0.841 (0.0710)	0.159 (0.0710)
	L. Antilles	0.0422 (0.0482)	0.958 (0.0481)
	CVI	$6.98*10^{-9}$ ($2.354*10^{-8}$)	1.00 ($2.354*10^{-8}$)

DISCUSSION

This study analyses the largest number of records of photo-identified individuals from the North Atlantic Ocean basin to date: 38,319 photos of 9,977 whales, from 1980 through 2015. The Lesser Antilles dataset, an area formerly underrepresented in studies due to either low abundance of humpback whales or limited survey effort, includes a total of 312 individual humpback whales, with more regular sightings beginning in the late 2000s. Our results indicate that humpback whales breeding in the Lesser Antilles preferentially migrate to eastern North Atlantic feeding areas, even though they have been documented in all five feeding grounds (Stevick *et al*., 1999; Bérubé *et al*., 2004; Robbins *et al*., 2006; Rinaldi *et al*., 2009). The highest number of resightings are to the Norwegian feeding region (eastern NA). The seasonal migration estimation method, which statistically accounts for variable effort between regions and years, further confirms that individuals breeding in the Lesser Antilles have the highest probability of migrating to either Norway or Iceland (eastern NA) and the lowest probability of migrating to the Gulf of Maine, West Greenland or Atlantic Canada feeding grounds (western NA).

Early photo-ID studies focused primarily on the Greater Antilles and concluded that humpback whales in the West Indies were likely a single, panmictic population (Palsbøll *et al*., 1997; Smith *et al*., 1999; NMFS, 1991). However, our results along with those of Stevick *et al.* (2018), a study which used a subset of the same dataset from the NAHWC, question the panmixia assumption by demonstrating differences in the migratory patterns and timing of arrival and departure of humpback whales from the Lesser Antilles compared with the Greater Antilles. The seasonal migration estimation method shows that humpback whales from different regions within the West Indies breeding range do not use each feeding area equally, instead displaying preferences for different feeding areas, with a higher proportion of whales from the Greater Antilles migrating to western feeding grounds (Gulf of Maine, Atlantic Canada, West Greenland) and a higher proportion of whales from the Lesser Antilles migrating to the eastern North Atlantic feeding grounds (Iceland and northern Norway).

Table 3 presents the percentage of whales from each breeding area that were resighted on each feeding ground and the relative size of each feeding ground in our sample for comparison. The raw percentages and the more robust transition probability results demonstrate that humpback whales breeding in the Greater Antilles have the highest probability of migrating to the western NA feeding grounds and are less likely to use eastern NA feeding areas. Resightings from the Greater Antilles to Norway, the easternmost feeding ground, were lowest and represent only 1.9% of the total resightings between any feeding region and the Greater Antilles. The probability of transitioning between the Greater Antilles and Norway was found to be consistently much lower than the probability of moving between the Greater Antilles and the Gulf of Maine or Canada (western NA). The higher resighting rates between Norway and the breeding areas of CVI and the Lesser Antilles suggests that most Norwegian whales are not using the Greater Antilles as their primary breeding ground and may be less likely to mate with whales from western feeding stocks.

Observed transitions from the Greater Antilles to the Iceland feeding area (eastern NA) are more numerous compared with Norway. A study of the breeding ground destination of humpback whales feeding in Iceland, analysing a subset of the same data used in this study, found unequal use of such areas, with more resightings from Iceland to CVI and the Lesser Antilles and fewer from Iceland to the Greater Antilles (Chosson *et al*., 2015). Transition probabilities reported here indicate the same pattern for the migratory destinations of whales feeding in Iceland. Movement between the Greater Antilles and West Greenland (western NA), the feeding area with the fewest whales in our dataset, was low as well which suggests that humpback whales feeding in West Greenland might be using other breeding grounds or are less likely to be sampled in the Greater Antilles.

Previous studies have shown temporal differences in the migratory patterns of whales from the Greater and Lesser Antilles as well as differences in feeding ground destinations. Photo-ID data suggest that, on average, humpback whales are present in the Greater Antilles earlier, with peak distribution in Dominican Republic six weeks earlier than in the Lesser Antilles (Stevick *et al*., 2016, 2018). This difference may be due in part to temporal differences in observation effort in either location, or that whales are potentially photographed in the Greater Antilles during their transit to the Lesser Antilles. Acoustic recordings from seven sites throughout the Antilles chain suggests that humpback whales are present on Silver Bank, Dominican Republic, for a longer time than the period during which whale watching groups are operating (Heenehan *et al*., 2019).

In the Lesser Antilles, anecdotal evidence from whale watching and research groups searching for humpback whales report that their efforts are unsuccessful in January and February. Acoustic and satellite tagging efforts in the Lesser Antilles have demonstrated late arrival or presence at this breeding ground compared with the Greater Antilles (Swartz *et al*., 2003; Heenehan *et al*., 2019; Kettemer *et al*., 2022). Delayed breeding ground arrival in the Lesser Antilles compared with the Greater Antilles could have population-level effects if animals from certain northern feeding regions have a reduced likelihood of encountering and mating with individuals from other feeding areas while wintering in the Lesser Antilles, further questioning the panmixia assumption in the West Indies.

In the West Indies, historical whaling focused on the Lesser Antilles, where humpback whales were subject to commercial exploitation from the mid-1700s until 1926 (Romero & Hayford, 2000; Reeves *et al*., 2001; Romero, 2012). Formal surveys conducted in the Lesser Antilles region prior to 2002 found zero to very few humpback whales (Winn *et al*., 1975; Reeves *et al*., 2001; Swartz *et al*., 2001, 2003). Few photographic samples were therefore available from this southeastern portion of the West Indies range and previous research was limited in this area of their range due to low abundance.

Humpback whales from the Cape Verde Islands/Northwest Africa breeding population that remains endangered fit the pattern previously documented, with movement detected only to the eastern NA feeding grounds of Iceland and Norway (Bettridge *et al*., 2015; Wenzel *et al*., 2020). Transition probabilities calculated were close to one from CVI to eastern NA feeding grounds. In a year outside our study period, 2021, the first resighting between CVI and any western NA feeding ground was found in the NAHWC, in this case to West Greenland (Chosson *et al*., 2024). Increased photo-ID efforts in West Greenland are needed to investigate further how much of the CVI population might be using that feeding ground, where a small number of indigenous takes of humpbacks are allowed annually (Government of Greenland, 2018).

Inter-breeding area movements are important to the overall picture of humpback population dynamics and require further study. Movement between the breeding regions of the Greater Antilles and the Lesser Antilles is known to occur at a low level (Stevick *et al*., 1999; MacKay *et al*., 2019). Within our dataset, 22 resightings were found between the Lesser Antilles (n = 312) and the Greater Antilles (n = 3,541), representing only 7.1% of the whales wintering in the Lesser Antilles. Examining the resightings between the Lesser Antilles and Greater Antilles more closely, we found that three of the 22 individuals have only been sighted on Anguilla Bank and one near Saba Bank, the northernmost areas here considered as the Lesser Antilles. This may suggest that whales sighted in the northern section of the currently defined Lesser Antilles region have greater affinity for the Greater Antilles region than whales using areas further south. A lower level of exchange between the Lesser Antilles and CVI was found: five humpback whales were sighted in both CVI and the Lesser Antilles, all in different years, an increase of one compared with Stevick *et al*. (2016). Zero resightings were found between the Greater Antilles and CVI during our study period. Sex information is not available for the majority of these whales and none of the inter-breeding area movement occurred within the same season. Between seasons, we speculate that these are more likely to be males searching for additional mates.

The differences in ocean basin-wide migratory patterns found between the Greater Antilles and Lesser Antilles suggest that these two regions in the West Indies host breeding humpback whale populations that may be behaviourally and/or genetically distinct. The question remains where a boundary may exist between these two populations. To be considered a distinct population segment under the US ESA, a population's discreteness and significance is evaluated based on information about distribution, ecological situation, genetics and other factors (Bettridge *et al*., 2015). Additional lines of evidence, such as genetic analyses and song structure, will aid in evaluating the past assumption of panmixia in the West Indies. Genetic sampling and analysis of individuals specifically in eastern feeding areas would also be necessary to better understand the degree to which multiple breeding stocks overlap on the feeding grounds in Iceland and Norway. Migrations are thought to be matrilineally directed and learned by calves as they follow their mothers on their first migration north to the feeding grounds (Katona & Beard, 1990; Palsbøll *et al*., 1995). Determining whether site fidelity is equally strong in females and males as they recruit into a breeding stock will be an interesting goal for future analyses.

This new analysis and larger dataset, which includes more survey efforts and sightings of humpback whales in historically depleted areas, such as the Lesser Antilles and Cape Verde Islands, should be used to guide future management actions and conservation status designations, including the IUCN Red List and national listings. Management decisions should be based on the most up-to-date analyses and data available for the best possible outcomes for the species. Highly migratory species, such as North Atlantic humpback whales, should regularly be assessed across their migratory range to detect changes in seasonal habitat use and distribution, especially in relation to concurrent changes in ocean environments and anthropogenic activities.

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Supplementary Material 1

MATLAB code for seasonal migration estimation method

```
function seasmigration
%seasonal migration
% jackknife version
jackgo=1;%does jackknife standard errors
numrep=10;%No. of replications of starting positions for maximization of likelihood.
sumcats={[1 2 3],[4 5]};
wintcats={[1],[2,[3]};
[A,B]=xlsread('data.xlsx','IDs');
nwa=sum(cellfun('length',B)==1);%number winter-breeding areas
nsa=(length(B)-1-nwa)/nwa;%number of summer-feeding areas
namw=B(2:(1+nwa));
nams=B((2+nwa):(1+nwa+nsa));
for k=1:nsa
    nams{k}=nams{k}(2);
end
n=A(:,2:(1+nwa));%Numbers seen in each wintering area each year
z=A(:,(2+nwa):end);
nyy=length(A(:,1));
zz=reshape(z,nyy,nsa,nwa);
for w=1:length(sumcats)
    namwu{w}=strcat(namw{sumcats{w}});
    unw=sum(n(:,sumcats{w}),2);
    uzw=sum(zz(:,:,sumcats{w}),3);
    if w==1
        nu=unw;
        zzv=uzw;
    else
        nu=[nu unw];
        zzv=cat(3,zzv,uzw);
    end
end

for s=1:length(wintcats)
    namsu{s}=strcat(nams{wintcats{s}});
    uzw=sum(zzv(:,wintcats{s},:),2);
    if s==1
        zzu=uzw;
    else
        zzu=cat(2,zzu,uzw);
    end
end
[nyy,nsa,nwa]=size(zzu);
ppq=estpp(reshape(zzu,nyy,nsa*nwa),nu,numrep,1,nyy,nsa,nwa);
disp('  ')
disp('Observed transitions:')
disp(array2table(squeeze(sum(zzu,1))','rownames',namwu,'variablenames',namsu))
disp('  ')
disp('Estimated transition probabilities:')
disp(array2table(ppq,'rownames',namwu,'variablenames',namsu))
disp('  ')
zzn=reshape(zzu,nyy,nsa*nwa);
if jackgo
jackstat = jackknife(@estpp,zzn,nu,numrep,0,nyy,nsa,nwa);
    jse=reshape(std(nyy*(ppq(:)*ones(1,length(jackstat(:,1))))'-(nyy-1)*jackstat)/sqrt(nyy-
1),nwa,nsa);
    disp('Estimated SE transition probabilities using jackknife')
    disp(array2table(jse,'rownames',namwu,'variablenames',namsu))
    disp('   ')
end
```

```
if numboot
    [ci,bootstat] =
bootci(numboot,{@estpp,reshape(zzu,nyy,nsa*nwa),nu,numrep,0,nyy,nsa,nwa},'type','per');
    bootstat=reshape(bootstat,numboot,nwa,nsa);
    sees=squeeze(std(reshape(bootstat,numboot,nwa,nsa)));
    disp('Estimated SE transition probabilities using bootstrap')
    disp(array2table(sees,'rownames',namwu,'variablenames',namsu))
    if numboot>=100
          for i=1:nwa;for j=1:nsa;af{i,j}=sprintf('%6.4f (%6.4f -
%6.4f)',ppq(i,j),ci(1,i,j),ci(2,i,j));end;end;
          disp(['Estimated 95% C.I.''s for transition probabilities using '
num2str(numboot) ' bootstrap replicates:'])
         disp(array2table(af,'rownames',namwu,'variablenames',namsu))
     end
end



function ppq=estpp(zzut,nu,numrep,givelike,nyy,nsa,nwa)
nyyy=length(zzut(:,1));
zzu=reshape(zzut,nyyy,nsa,nwa);
pp=ones(nwa,nsa)/nsa;
ppp=pp(:,1:(end-1))-0.2;
%ll=likkecalc(ppp(:),nu,zu);
fll = @(x)likkecalc(x,nu,zzu);
options = optimset('MaxFunEvals',5000);
for du=1:numrep
    pppq=ppp.*(1.3-0.6.*rand(size(ppp)));
    [xx,efval,exitflag,output]  = fminsearch(fll,pppq(:),options);
[x,fval(du),exitflag,output]  = fminsearch(fll,xx, options);
    x=reshape(x,[nwa,(nsa-1)]);
    ppj{du}=[x 1-sum(x,2)];
end
[a1,a2]=min(fval);
ppq=ppj{a2};
if givelike
    disp(sprintf('Estimates of log-likelihood:  %7.2f  %7.2f  %7.2f  %7.2f  %7.2f  %7.2f
%7.2f  %7.2f  %7.2f  %7.2f',-fval))
    disp(sprintf('    Best log-likelihood:  %7.2f',-a1))
end



function ll=likkecalc(ppp,nu,zu)
[nyy,nsa,nwa]=size(zu);
ppp=reshape(ppp,[nwa,(nsa-1)]);
pp=[ppp 1-sum(ppp,2)];
if min(pp(:))<0  | max(pp(:))>1;
    ll=10000000000;
else
    may=squeeze(sum(zu,2));
    ll=0;
    for  y=1:nyy
        if sum(sum(squeeze(zu(y,:,:))));
            %actual likelihood estimates of qtt
            qtt=sum(squeeze(zu(y,:,:)),2)'./(nu(y,:)*pp);%shortcut estimate
            qtt=max(qtt,0.0000001);
            qtt=min(qtt,1);
            ll=ll-(sum(sum(squeeze(zu(y,:,:))'.*log((ones(nwa,1)*qtt).*pp)))+(nu(y,:)-
may(y,:))*log(1-pp*qtt'));
            qt(y,:)=qtt;
        else
            qt(y,:)=0;
        end
    end
end
```

Supplementary Material 2

Table S1

Transition probabilities from breeding to feeding areas, calculated with the seasonal migration estimation method on paired years 1980–2015. Areas Gulf of Maine, Atlantic Canada (GOM + Can), and Iceland and Norway (Ice + Nor) were combined to improve performance. Values in parentheses are the jackknife estimates of the standard errors.

		Feeding Areas		
		GOM + Can + W. Greenland	W. Greenland	Ice + Nor
Breeding Areas	G. Antilles	0.308 (0.521)	0.580 (0.561)	0.113 (0.0725)
	L. Antilles	0.0137 (0.0572)	0.611 (0.637)	0.375 (0.604)
	CVI	$2.13*10^{-9}$ (0.000558)	$1.45*10^{-8}$ (0.00851)	1 .00 (0.00847)

Table S2

Transition probabilities from feeding to breeding areas, calculated with the seasonal migration estimation method on paired years 1980–2015. Areas Gulf of Maine, Atlantic Canada, and West Greenland (GOM + Can + W.Greenland), and Iceland and Norway (Ice + Nor) were combined to improve performance. Values in parentheses are the jackknife estimates of the standard errors.

		Breeding Areas		
		G. Antilles	L. Antilles	CVI
Western feeding areas	GOM + Can + W. Greenland	0.999 (0.0422)	0.000818 (0.0422)	$5.412*10^{-8}$ ($5.627*10^{-8}$)
Eastern feeding areas	Ice + Nor	0.344 (0.175)	0.0110 (0.606)	0.644 (0.618)

Table S3

Transition probabilities from feeding to breeding areas, calculated with the seasonal migration estimation method on paired years 1980–2015. Areas Gulf of Maine and Atlantic Canada (GOM + Can), and Iceland and Norway (Ice + Nor) were combined to improve performance. Values in parentheses are the jackknife estimates of the standard errors.

		Breeding Areas		
		G. Antilles	L. Antilles	CVI
Western feeding areas	GOM + Can	0.999 (0.0322)	0.00171 (0.0322)	$5.16*10^{-8}$ (0.000678)
	W. Greenland	0.748 (0.259)	$8.32*10^{-8}$ (0.793)	0.252 (0.245)
Eastern feeding areas	Ice + Nor	0.330 (0.178)	0.0199 (0.399)	0.650 (0.350)

Supplementary Material 3

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