

SC/69A/NH/05

Sub-committees/working group name: NH

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Ocean-basin-wide movement patterns of North Atlantic humpback whales, *Megaptera novaeangliae*

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Abstract

The spatial structure of the North Atlantic humpback whale population has not been studied on an ocean-basin scale in three decades. Larger sample sizes now available throughout their range and regional changes in their spatial patterns in the North Atlantic necessitate a re-evaluation and expansion of past movement analyses. Additional information on the movements and population spatial structure of humpbacks across the North Atlantic Ocean basin is needed considering their various listing statuses under the International Union for the Conservation of Nature, United States' Endangered Species Act (ESA) and International Whaling Commission. Within the North Atlantic, one subpopulation off the Cape Verde Islands/Northwest Africa (CVI) is currently considered endangered under the ESA, while the other subpopulation, breeding/calving in the West Indies, is not considered at risk. The work presented here quantifies the ocean-basin-wide movement patterns of humpbacks from 1980 through 2015 from collections contributed to the North Atlantic Humpback Whale Catalog, a dataset of 37,259 photographic-identification images of 9,566 individual whales from all North Atlantic breeding and feeding regions. Transition probabilities between all major feeding and breeding/calving areas were estimated to detect differences between breeding regions. Based on emerging trends, our analyses further divided the West Indies into two distinct breeding populations: the Greater and Lesser Antilles. Breeding-to-feeding area transition probabilities were highest from the Greater Antilles to western feeding grounds (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. Migratory patterns between feeding areas and the Lesser Antilles were more similar to those from the CVI breeding segment than the geographically closer area in the Greater Antilles,

which suggests that humpbacks from these two regions within the West Indies are behaviorally distinct and may be best managed as such.

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 (*Megaptera novaeangliae*) undertake between their summer feeding grounds in mid to high latitudes and their breeding/calving grounds (henceforth referred to as breeding grounds) at lower latitudes in the North Atlantic Ocean has previously been well-documented. However, the dynamics of this long-distance migration has not been updated across the entire North Atlantic Ocean since the Years of the North Atlantic Humpbacks (YoNAH) project of 1992 and 1993 – a directed effort to survey all major areas and collect photographic-identification (photo-ID) and molecular data (Smith et al., 1999). Updating knowledge of the patterns of long-distance humpback movements is necessary as more data becomes available from regions of low abundance or understudy, and as they experience threats from human interaction and climate change across their migratory corridors.

In the North Atlantic, humpbacks use the breeding grounds of the West Indies or the Cape Verde Islands (CVI), northwest Africa. The CVI population currently includes fewer than 300 individuals, and they migrate to the feeding grounds off Iceland and northern Norway (Wenzel et al., 2020). The CVI population 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 U.S. Endangered Species Act (ESA; Reeves et al., 2002, Bettridge et al., 2015, Cooke 2018).

The largest breeding and calving congregation of humpback whales in the western North Atlantic is the West Indies. Within the West Indies, humpbacks have been documented from the Bahamas to as far south as the Caribbean coast of Venezuela (Kennedy and Clapham, 2018, Swartz et al., 2003). Humpbacks congregate in the highest concentrations in the Greater Antilles, off the islands of Hispaniola and Puerto Rico, primarily on Silver Bank, Mouchoir Bank, Navidad Bank, and Samana Bay in the Dominican Republic (Mattila et al., 1989, Whitehead and Moore, 1982). Early studies suggested that Silver Bank may host up to 85% of breeding humpback whales from the western North Atlantic (Balcomb and Nichols, 1978, Winn et al., 1975). Humpbacks wintering in the Greater Antilles have been re-identified in all five feeding regions, and evaluation of the composition of competitive groups on Silver Bank and in Samana Bay showed both spatial and genetic mixing of whales from different feeding areas (Clapham et al., 1993, Mattila et al., 1989). This has led prior studies to assume panmixia in the West Indies (Clapham et al., 1993, Smith et al., 1999). However, some evidence suggests that whales from feeding areas farther east are less likely to winter in this region of the West Indies (Stevick et al., 2003a).

In the Lesser Antilles (defined here as from Anegada Passage to the Caribbean coast of Venezuela), intensive 19th century whaling operations greatly reduced the population of humpback whale breeding or calving in the region, and humpback densities have been low since the cessation of commercial whaling operations (Romero and Hayford, 2000, Winn et al., 1975, Reeves et al., 2001, Swartz et al., 2003, Reeves et al., 2004). Prior studies (Mattila and Clapham, 1989, Swartz et al., 2003, Acevedo et al., 2008, Winn et al., 1975) found very few visual and acoustic detections of humpbacks in the Lesser Antilles. An increase in sightings and available photo-ID data since the early 2000s, primarily around the island of Guadeloupe and points south,

allows for examination of humpbacks from the Lesser Antilles in this work. Increased scientific and whale watching activities in the Lesser Antilles have collected additional photo-ID data from January through early May (L. Bouveret 2022, personal communication, October 25). In comparison to humpbacks found at the primary breeding grounds in the Greater Antilles, the average estimated date of arrival to the Lesser Antilles was found to be six weeks later (Stevick et al., 2018). Humpbacks sighted in the Lesser Antilles have been resighted in all five of the North Atlantic feeding grounds (Stevick et al., 1999, Stevick et al., 2015, Robbins et al., 2006). Three whales satellite tagged off Guadeloupe all headed toward the eastern North Atlantic at the start of migration, and the longest-duration tag ceased transmissions approximately 500 miles south of Iceland (Kennedy et al., 2014).

Humpbacks may move within the breeding range in the West Indies and a low level of movement between the Greater Antilles and Lesser Antilles has been documented. One individual was documented by Stevick et al. (1999) to move between the Greater and Lesser Antilles, Dominica and Puerto Rico, and MacKay et al. (2019) found two inter-seasonal and one intra-seasonal resightings between the Lesser Antilles and Puerto Rico, indicating that some level of exchange exists between the Lesser Antilles and breeding areas farther west, but the degree to which movement occurs is under-studied.

Photo-ID images and corresponding sighting data from across the North Atlantic Ocean basin are collected by hundreds of researchers and individuals and contributed to the North Atlantic Humpback Whale Catalog (NAHWC), curated by Allied Whale at the College of the Atlantic (<https://www.coa.edu/allied-whale/>)¹. The NAHWC contains five decades of sightings collected during dedicated research conducted on various scales and opportunistic platforms, such as whale watch cruises.

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Here, we used this multi-decadal dataset from the NAHWC and a novel application of maximum likelihood methods to estimate humpback whale transition probabilities between breeding and feeding grounds in the North Atlantic, with a particular focus on differential movements to the West Indies and the endangered CVI population.

Methods

Photo-ID data processing

The unique pattern on the ventral surface of humpback whale flukes allows for identification of individuals (Katona and Whitehead, 1981). Identification images in the NAHWC were collected throughout the North Atlantic Ocean by over 800 researchers and individuals and submitted to allow for ocean-basin-wide comparison and scientific collaboration. The data analyzed in this work include photo-ID samples from the NAHWC collected by the co-authors and opportunistic encounters from years 1980 through 2015. Fluke photographs are contributed with accompanying sighting information, then compiled in a database and photographic catalog, maintained in iMatch version 5.4.18 (phootools.com) digital asset management software.

Photo-ID comparison methods followed the standards of Katona and Whitehead (1981) with technological updates over the 45-year history of the NAHWC. Visual comparison methods by trained photo-ID technicians were used from 1977 to 2017 to find re-sightings or “matches” and add new whales to the catalog. From 2017 to present, photo-ID methods have gradually evolved to a current standard involving a dual review system where fluke photos are first compared utilizing the automated identification algorithms described in Cheeseman et al. (2021) on a private reference catalog. Every positive match to the NAHWC is confirmed by two trained

reviewers to prevent false positive errors; if the algorithms suggest no match to the NAHWC, the fluke photo is then visually compared to the entire NAHWC by two trained technicians to prevent false negatives or missed matches. Photos with which the algorithms perform poorly, such as half flukes and images of carcasses, are also visually compared by two reviewers. When an individual whale is not successfully identified to an existing animal in the catalog after using both automated identification algorithms and visual comparison, the whale is then assigned a new NA number and added to the NAHWC.

When an individual whale is not successfully identified to an existing animal in the catalog through both automated algorithms and visual comparison, the whale is then assigned a new NA number and added to the NAHWC. Photos of poor quality, where the focus of the photo would significantly affect a reviewer's ability to accurately identify the animal or where less than 20% of the right or left fluke is visible, are not included in the NAHWC database and our analyses.

Sightings data used for these analyses include all sightings of non-calf humpback whales for which the photographic comparison process for the NAHWC was complete as of March 2023. The analyses conducted required 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 area in a given year, both sightings are included in the analyses to enable representation of inter-area transitions between and within years. Areas were defined as those of humpback whale aggregation in the North Atlantic Ocean as follows: Gulf of Maine (GOM, including sightings from the Bay of Fundy and the adjacent waters of the Scotian Shelf), Atlantic Canada (the Gulf of the 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 during YoNAH southwest of the island of Jan Mayen), Norway (including the Barents Sea, Svalbard and northwest Russia, to Arctic Franz Josef Land), 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). A line was drawn between the Greater and Lesser Antilles at the Anegada Passage (see Figure 1), around which there are few photographic samples.



Figure 1. Map of the Anegada Passage showing the distinction here between the Greater Antilles and Lesser Antilles.

To improve sample sizes, identifications were subsequently grouped into western North Atlantic feeding regions (GOM, Atlantic Canada, and West Greenland) and eastern feeding regions (Iceland and Norway). Within the West Indies, sightings from the U.S. and British Virgin Islands, though considered part of the Greater Antilles chain, were excluded from all analyses due to lack of photo-ID samples in the NAHWC from the Virgin Islands after the mid-1980s (n = 3 individuals identified in the region from 1990 to 2015). Our definition of the Lesser

Antilles here refers to the Anegada Passage south to the Venezuela coast. The number of individuals identified in each region along the breeding ground range in the West Indies, which were combined into closest geographic regions, are presented in Table 1 together with the sample from the entire island chain of the CVI.

Table 1. N (number of individual humpbacks) identified along the breeding/calving range, segmented by the oceanographic feature or geographic region within the West Indies and the Cape Verde Islands.

Region	N
Banks north of Hispaniola: Silver, Navidad, Mouchoir and Turks	2345
Samana Bay, Dominican Republic	981
Puerto Rico	492
Lesser Antilles – Leeward Islands	286
Lesser Antilles – Windward Islands	24
Cape Verde Islands	211
Total N for all breeding regions	3999

Estimating transition probabilities between seasonal habitats

Collaborative, multidecadal photo-ID collections such as our dataset often include variable and highly clumped sighting records spatially and temporally, which may be an artifact of intensive sampling effort in a region and may not accurately represent any variation in the population’s site fidelity or between-area movements. Photo-ID datasets where effort varies or has not been systematically or randomly distributed in space and time can be problematic for statistical analyses, notably because the homogeneity of capture assumption of capture-recapture models may be violated. To account for different biases in capture-recapture sampling methods

in various locations and years, movement analysis methods that do not require equal probabilities of capture in each region or year studied were selected for these analyses.

The method used most often to quantify movements of individually identifiable animals is that developed by Hilborn (1990) using maximum likelihood techniques to calculate transition probabilities, initially developed for analysis of movement data from tag returns. A transition probability (p_i) is the probability that an individual in one area moves to another area between sampling periods (Whitehead, 2009). Hilborn's method was further developed by Whitehead (2001) to have broad applicability to the quantification of animal movement between areas from capture-recapture data. Maximum likelihood methods applied to identification data allow for the number of identifications to be used as a measure of effort, which enables the use of photo-ID data from any year (Whitehead, 2001).

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 maximize the sample likelihood. The methodology used to estimate transition probabilities between breeding and feeding locations, hereafter referred to as **seasonal migration estimation**, is a maximum likelihood estimation method run in MATLAB R2016b (The Mathworks, Inc., Natick, MA) using data on the number of transitions between each breeding and feeding area. Raw numbers of resightings per paired area (i.e., one breeding and one feeding area) were totaled for comparison.

Sightings records from the NAHWC were restricted to years 1980 to 2015 and the major feeding aggregations: GOM, Canada, West Greenland, Iceland, and Norway. We analyzed a total of 37,259 records of 9,566 individuals using the seasonal migration estimation method.

Consecutive years were paired to increase the number of observed transitions between two regions and improve the performance of this estimation method. Estimates were produced with single years and pairs of years to test the validity of combining years.

Seasonal migration estimation

We calculated transition probabilities between feeding and breeding areas with a novel maximum likelihood estimation method, an extension of the Hilborn (1990) concept further developed by Hal Whitehead and modified for this dataset, a technique henceforth referred to as seasonal migration estimation. The theory behind this 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, \dots) and feeding areas (V, W, X, \dots) 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:

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

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:

$$L = \prod_y \prod_A \left(\prod_X (p_{AX} \cdot q_{yX})^{z(y,A,X)} \cdot (1 - \sum_X p_{AX} \cdot q_{yX})^{n(y,A) - \sum_X z(y,A,X)} \right) \quad (2)$$

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 $(1 - \sum_X p_{AX} \cdot q_{yX})^{n(y,A) - \sum_X z(y,A,X)}$ 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:

$$\text{Log}(L) = \sum_y \sum_A \left(\sum_X z(y,A,X) \text{Log}(p_{AX} \cdot q_{yX}) + (n(y,A) - \sum_X z(y,A,X)) \text{Log}(1 - \sum_X p_{AX} \cdot q_{yX}) \right) + \text{constant} \quad (3)$$

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

$$q_{yX} = \sum_A z(y,A,X) / \sum_A p_{AX} \cdot n(y,A) \quad (4)$$

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 maximizes equation 3, using values of q_{yX} 's from equation 4, subject to the constraint of equation 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 and Stein, 1981). Bootstrap estimates of variance cannot calculate variance when data are over-populated by zeros, which was true of our dataset with zero transitions between some areas and years. The jackknifing approach is typically conservative in that standard errors are overestimated (Whitehead, 2009, Efron and Stein, 1981).

Estimation methods were run in MATLAB R2016b, scripts available in Appendix 2. Input data were 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 whales identified in each breeding area. The remaining data were the number of transitions between each breeding and feeding area per paired year. Pairing consecutive years increased the number of transitions and sample sizes in each region, and generally reduced standard error estimates.

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 maximization of likelihood and 5000 as the maximum number of iterations, as these procedures gave good convergence.

Results

Photo-ID resightings found between all feeding and breeding areas across all years in our dataset are mapped in Figure 2 and illustrated in Figure 3.

The seasonal migration estimation method produced more robust results, generally with smaller standard errors, when years were paired, and nearby areas were combined. The 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; for example, the transition probability from the Greater Antilles breeding area to western feeding areas was 0.837 ($se = 0.073$; see Table 3), whereas the transition probability from western feeding areas to the Greater Antilles was 0.999 ($se = 0.018$). Our estimates suggest that while almost all the animals in the western feeding areas winter off the Greater Antilles, about 6% of the animals wintering in the Greater Antilles feed in the eastern North Atlantic.

Estimating transition probabilities from breeding to feeding areas produced results with smaller standard errors, estimated with the jackknifing method. Calculations run from breeding areas improved estimates because sample sizes from all breeding grounds are on average smaller than those in all feeding areas, thus the observed transitions are a higher proportion of the number of whales sighted in breeding areas. Therefore, only results from this movement estimation method from given breeding areas to feeding grounds are presented in Tables 2 – 5 and results from feeding to breeding areas are available in Appendix 1.

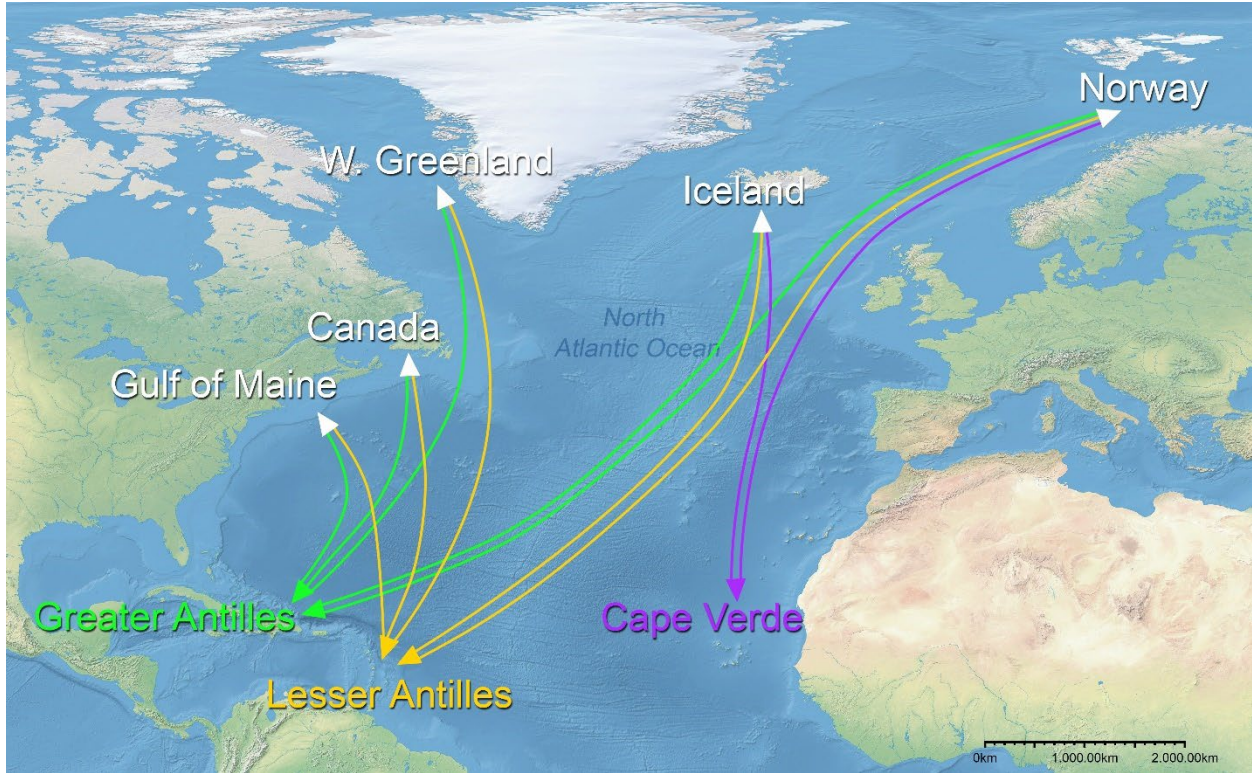


Figure 2. Map of the documented resightings from the NAHWC dataset between northern feeding regions and breeding regions across the North Atlantic Ocean, 1980-2015. The text is over each area's general location; lines connect migratory endpoints and are not meant to represent routes.

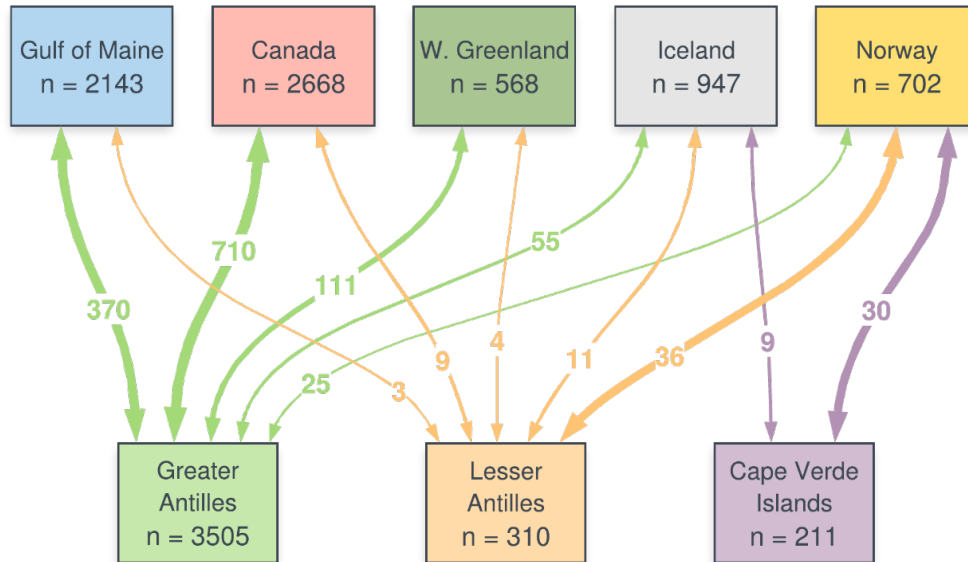


Figure 3. All observed transitions between feeding and breeding areas in the North Atlantic, years 1980-2015. Number of individual whales sighted in each region are provided as n for a given area and the number of whales identified between one breeding and feeding area are presented on the connecting lines.

The following tables present the resulting transition probabilities from the seasonal movement estimation method for paired years 1980-2015, from breeding areas to feeding areas. Different combinations of feeding areas are presented though the results in Table 3 have the smallest standard errors and give the most accurate results.

Table 2. Observed transitions of individual whales between feeding areas and the breeding sites of the Greater Antilles (G. Antilles), Lesser Antilles (L. Antilles), and Cape Verde Islands (CVI) across any years 1980 to 2015.

BREEDING AREA	FEEDING AREA					
	Gulf of Maine	Canada	W. Greenland	Iceland	Norway	
G. Antilles	370	710	111	55	25	
L. Antilles	3	9	4	11	36	
CVI	0	0	0	9	30	

Table 3. Transition probabilities from breeding to feeding areas, calculated with the seasonal migration estimation method. Areas Gulf of Maine, Canada, and West Greenland (GOM + Can + Grl), and Iceland and Norway (Ice + Nor) were combined to improve performance. Values in parentheses are the jackknife estimates of the standard errors.

BREEDING AREAS:	WESTERN FEEDING AREAS	EASTERN FEEDING AREAS
	GOM + Can + Grl	Ice + Nor
G. Antilles	0.837 (0.0723)	0.163 (0.0723)
L. Antilles	0.046 (0.056)	0.954 (0.056)
CVI	3.14*10 ⁻⁹ (1.30*10 ⁻⁸)	1.000 (1.30*10 ⁻⁸)

Table 4. Transition probabilities from breeding to feeding areas, calculated with the seasonal migration estimation method. Areas Gulf of Maine and 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.

	GOM + Can	W. Greenland	Ice + Nor
G. Antilles	0.279 (0.292)	0.605 (0.331)	0.116 (0.071)
L. Antilles	0.013 (0.019)	0.610 (0.456)	0.376 (0.447)
CVI	2.85*10 ⁻⁸ (3.86 *10 ⁻⁷)	1.33*10 ⁻⁵ (0.002)	0.999 (0.002)

Table 5. Transition probabilities from breeding to feeding areas, calculated with the seasonal migration estimation method. Areas Gulf of Maine and Canada were combined to improve performance. Values in parentheses are the jackknife estimates of the standard errors.

	GOM + Canada	W. Greenland	Iceland	Norway
G. Antilles	0.276 (0.310)	0.175 (0.377)	0.512 (0.415)	0.038 (0.060)
L. Antilles	0.010 (0.031)	0.001 (0.024)	0.761 (0.303)	0.229 (0.288)
CVI	2.41*10 ⁻⁹ (0.001)	7.66*10 ⁻¹⁴ (0.998)	3.92*10 ⁻⁵ (1.01)	0.999 (1.176)

Discussion

Knowledge of the movement patterns and population spatial structuring of a highly migratory species such as the humpback whale is vital for informed management and conservation of the species. Humpback whales were one of the first species listed as Endangered under the United States' Endangered Species Act (ESA), Threatened under Canada's Committee on the Status of Endangered Wildlife (COSEWIC) in Canada, and 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 (80 FR 22303, COSEWIC 2003, Cooke, 2018). The North Atlantic Ocean was the first to receive protection from commercial whaling in 1955 and conservation actions through national management processes, which has allowed for population growth (National Marine Fisheries Service 1991, IWC, 2002, Stevick et al., 2003b). Currently, the IUCN considers the species to be of 'Least Concern' (Cooke, 2018). Under COSEWIC, the entire western North Atlantic population was re-assessed and delisted in 2003 (COSEWIC, 2003). Under the ESA, humpbacks 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 (80 FR 22303). In the North Atlantic, two DPSs were identified – one for the West Indies which was considered not warranted for listing under

the ESA ('Not at Risk'), and a second DPS for the Cape Verde Islands/Northwest Africa population, that remains 'Endangered' (81 FR 62259, Bettridge et al., 2015).

In the West Indies, whaling focused in the Lesser Antilles, where humpbacks were subject to commercial exploitation from the mid-1700s until 1926 (Reeves et al., 2001, Romero and Hayford, 2000, Romero, 2012). Intensive whaling operations were rare in the Greater Antilles and this breeding population is recovering from global whaling operations faster than the historically large population using the Lesser Antilles (Kennedy and Clapham, 2018, Reeves et al., 2001). Early surveys of the Lesser Antilles region post-depletion by whaling found zero to very few humpbacks (Winn et al., 1975, Reeves et al., 2001, Swartz et al., 2003) in areas where they are now sighted frequently in the winter. Prior to our study, few photographic samples were available from the southeastern portion of the West Indies range and previous research was limited in this area of their range due to low abundance, though now the Lesser Antilles area appears to be of increasing importance for North Atlantic humpback whales.

With few data previously available from the Lesser Antilles, early studies assumed humpbacks in the West Indies were of a single, panmictic population (Palsbøll et al., 1997, Smith et al., 1999, Service, 1991). Our results along with that of Stevick et al. (2018), using a subset of the same dataset, question the panmixia assumption as our results show differences in the migratory patterns of whales from the Lesser Antilles compared to 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, but instead display different migratory preferences to northern feeding areas. The areas with high resulting transition probabilities indicate a migratory preference between these areas. Lower values may indicate

habitat avoidance or areas where whales are less likely to migrate to in relation to the other available feeding regions.

Humpback whales breeding in the Greater Antilles, the best-studied area in the breeding range, have rarely been resighted in high-latitude feeding regions in the eastern North Atlantic. From the NAHWC dataset, only 25 of 3,505 individuals sighted in the Greater Antilles region have been documented in the Norway feeding region. Resightings from the Greater Antilles to Norway represent only 2% of the total resightings between the Greater Antilles and any feeding region, though the Norwegian sample size represents 10.2% of all feeding area samples. 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. The higher rate of resightings between Norway and breeding regions other than the Greater Antilles appears to indicate that Norwegian whales are not using the Greater Antilles as their primary breeding ground.

Observed transitions from the Greater Antilles to the Iceland feeding area are more numerous, but not as high as the number of transitions to western feeding grounds; only 4.3% of feeding area resightings from the Greater Antilles have been to Iceland. A study on the breeding ground destination of humpback whales feeding in Iceland found unequal use of breeding grounds, with the Greater Antilles region under-represented in the sample, and CVI and the Lesser Antilles over-represented (Chosson et al., 2015). Calculated transition probabilities indicate the same pattern for the Iceland feeding area destinations.

This study analyzes the largest number of photo-identified individuals from the Lesser Antilles to date – a total of 310 individual humpback whales sighted from 1980 through 2015, with more regular sightings reported beginning in the late 2000s. Our results indicate that

humpback whales breeding in the Lesser Antilles region preferentially migrate to eastern North Atlantic feeding areas, even though they have been resighted in all five feeding destinations (Bérubé et al., 2004, Rinaldi et al., 2009, Stevick et al., 1999, Robbins et al., 2006). The highest number of resightings from the Lesser Antilles are to the Norway feeding region. Approximately 58.1% of feeding ground resightings from the Lesser Antilles are to Norway and 17.7% are to Iceland, both much higher than the resighting rates to western feeding grounds (GOM = 4.8%, Canada = 12.9%, W. Greenland = 6.5%). The seasonal migration estimation method, which statistically accounts for variable effort between regions and years, shows that individuals breeding in the Lesser Antilles have the highest probabilities of migrating to either Norway or Iceland and the lowest probability of migrating to the feeding grounds of GOM, W. Greenland or Canada.

Whales wintering in the Lesser Antilles display distinct movement patterns from humpback whales in the Greater Antilles, as demonstrated by divergent transition probabilities. Humpback whales documented in the Lesser Antilles are much more likely to migrate to eastern feeding regions than to western feeding regions. This is the opposite of the resulting pattern found for whales breeding in the Greater Antilles, which may migrate to any feeding area, but have a higher probability of migrating to western feeding areas, primarily Atlantic Canada and the Gulf of Maine.

The populations breeding in the Greater Antilles and the Lesser Antilles differ in the temporal patterns on these breeding sites. On average, humpbacks arrive earlier to the Greater Antilles compared to the Lesser Antilles, with peak distribution in the Lesser Antilles six weeks later than in the Dominican Republic (Stevick et al., 2018, Stevick et al., 2016). This difference may be due in part to temporal differences in effort in either location, but anecdotal evidence

from whale watching and research groups searching for humpbacks in the Lesser Antilles report that their efforts are unsuccessful in January and February. Visual and acoustic surveys in the Lesser Antilles conducted by Swartz et al. (2003), which began on 17 February, documented five sightings visually at the end of February and 26 sightings in March, also demonstrating late presence at this breeding ground. A recent satellite tagging study found one female humpback tagged off Norway arrived at the Greater Antilles breeding ground, specifically Mona Passage between Puerto Rico and Hispaniola, on 21 April 2021, suggesting that some humpbacks from eastern feeding grounds may also arrive later to the Greater Antilles breeding grounds (Kettner et al., 2022).

Whales arriving later in the Lesser Antilles as compared to the Greater Antilles have reduced opportunities to mate with humpback whales from western feeding areas (Stevick et al., 2018). Delayed breeding ground presence 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.

Movement between the breeding regions of the Greater Antilles and the Lesser Antilles is known to occur, and inter-breeding area movements are important to the overall picture of humpback population dynamics (Stevick et al., 1999, MacKay et al., 2019). Within a breeding season, movement between Puerto Rico and the Lesser Antilles has been documented (MacKay et al., 2019). There is a small level of interchange between the Lesser Antilles and Greater Antilles, within our dataset 22 resightings were found between the Lesser Antilles ($n = 310$) and the Greater Antilles ($n = 3,505$), representing a proportion of only 0.07 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 humpbacks were sighted in both CVI and the Lesser Antilles, all in different years, an increase of one from Stevick et al. (2016). In contrast, the breeding populations in CVI and Greater Antilles are distinct; our data contained zero resightings between the Greater Antilles and CVI during the study period.

Together, 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 may be largely distinct, though the question remains of where exactly to draw the line between them. Furthermore, molecular genetic research is needed to evaluate the past assumption of panmixia in the West Indies, and to determine whether there are genetic differences between humpbacks wintering in the Greater Antilles and the Lesser Antilles. There is known exchange among these areas (Stevick et al., 1999, MacKay et al., 2019), but the degree to which mixing and interbreeding occurs is unknown. Genetic analysis of individuals 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.

The population structure and movement patterns of a historically depleted species must be monitored over time for effective management and conservation. Highly migratory species such as the North Atlantic humpback whale 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.

Acknowledgements

The NAHWC and this work is only possible through collaboration with hundreds of researchers, whale watching groups, and people photographing humpback whales throughout the North Atlantic Ocean and contributing to the 45-year history of the NAHWC, thank you all for your devoted efforts. This work is the result of decades of identification and cataloging work by people working around the ocean basin, as well as many past and present Allied Whale researchers and College of the Atlantic students who cannot all possibly be named here; thank you all very much. The NAHWC is funded by donors and an anonymous foundation.

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Appendix 1.

Results: Feeding to breeding area transition probabilities

Table 3. Transition probabilities from breeding to feeding areas, calculated with the seasonal migration estimation method. Areas Gulf of Maine, Canada, and West Greenland (GOM + Can + Grl), and Iceland and Norway (Ice + Nor) were combined to improve performance. Values in parentheses are the jackknife estimates of the standard errors.

BREEDING AREAS:	WESTERN FEEDING AREAS	EASTERN FEEDING AREAS
	GOM + Can + Grl	Ice + Nor
G. Antilles	0.999 (0.018)	0.352 (0.177)
L. Antilles	0.001 (0.018)	0.011 (0.241)
CVI	1.36*10 ⁻⁷ (2.90*10 ⁻⁸)	0.637 (0.274)

Table 4. Transition probabilities from breeding to feeding areas, calculated with the seasonal migration estimation method. Areas Gulf of Maine and 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.

	GOM + Can	W. Greenland	Ice + Nor
G. Antilles	0.999 (0.006)	0.771 (0.248)	0.343 (0.173)
L. Antilles	0.001 (0.005)	4.04*10 ⁻⁸ (5.23*10 ⁻⁶)	0.014 (0.079)
CVI	2.73*10 ⁻⁹ (4.90*10 ⁻³)	0.229 (0.248)	0.642 (0.199)

Table 5. Transition probabilities from breeding to feeding areas, calculated with the seasonal migration estimation method. Areas Gulf of Maine and Canada were combined to improve performance. Values in parentheses are the jackknife estimates of the standard errors.

	GOM + Can	W. Greenland	Iceland	Norway
G. Antilles	0.765 (0.384)	0.555 (0.654)	0.298 (0.685)	0.098 (0.143)
L. Antilles	0.235 (0.386)	2.90*10 ⁻⁹ (0.533)	0.693 (0.899)	0.147 (1.02)
CVI	1.56*10 ⁻⁶ (0.038)	0.445 (0.632)	0.009 (0.342)	0.755 (0.973)

Appendix 2: MATLAB script for seasonal migration estimation

```

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]};
wintcats={[1 2 3],[4 5]};
[A,B]=xlsread('SightingPerYearPerArea_WtoSum20230403-YearsPairedGAnt.xlsx','IDs');
%[A,B]=xlsread('seassimx.xlsx');wintcats={1,2,3};sumcats={1,2};%simulated
%data
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
end

for s=1:length(wintcats)
    namsu{s}=strcat(nams{wintcats{s}});
    uzv=sum(zzv(:,wintcats{s},:),2);
    if s==1
        zzu=uzv;
    else
        zzu=cat(2,zzu,uzv);
    end
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(' ')

```

```

zsn=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),zzu);
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,0.000001);
            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
```