Migratory destinations of humpback whales from Norwegian and adjacent waters: evidence for stock identity

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ABSTRACT

Migratory destinations of humpback whales (*Megaptera novaeangliae*) in the eastern North Atlantic were investigated using natural markings. A total of 96 individuals was identified from Norwegian and adjacent waters during 1992 and 1993: of these 63 were observed in the Norwegian and Barents Seas and 33 in the Greenland Sea near Jan Mayen. These were compared with other individuals identified throughout the North Atlantic to identify resightings. Ten individuals were identified in both Norway and in the West Indies. There were no significant differences in this rate of exchange to the West Indies between the sample from Norway or either Norwegian sub-area and other feeding areas in the North Atlantic. The mean West Indies sighting date for humpback whales from Norway was 2 March, significantly later than the overall mean for sightings from the West Indies. The individuals identified represent a variety of reproductive classes and both sexes. Observations of mothers with newborn calves, and males in competitive groups, provide the strongest evidence to date that the West Indies is utilised as a breeding and calving ground by humpback whales which feed in Norwegian waters. These results suggest that the West Indies is an important, and likely the primary, breeding destination for individual humpback whales feeding off Norway.

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

INTRODUCTION

The migratory destinations of humpback whales (*Megaptera novaeangliae*) from the western North Atlantic have been well documented through photographic identification (e.g. Katona and Beard, 1991). These data show that while there is considerable site fidelity of humpback whales to specific feeding sites, all or most of the humpback whales from the USA, Canada and Greenland congregate on common breeding grounds in the West Indies (Katona and Beard, 1991; Clapham *et al.*, 1993). While a smaller sample size is available from Iceland, 4 of 20 individuals identified in Iceland were also photographed in the West Indies (Martin *et al.*, 1984; Katona and Beard, 1991). To date, little comparable information has been available to document humpback movements and migratory destinations in the eastern North Atlantic.

An estimated 1,500 humpback whales were taken by Norwegian land stations, mostly off northern Norway between 1881-1904 (Ingebrigtsen, 1929; Christensen *et al.*, 1992). Recently, sightings surveys have shown humpback whales to be seasonally abundant to the north and west of Norway in summer and autumn (Øien, 1990; Christensen *et al.*, 1992); however, the stock identity of these individuals is poorly understood. Several authors have suggested the existence of two breeding stocks of humpback whales in the North Atlantic, one along the western and another along the eastern margin of the ocean basin, although the degree of separation and the precise limits of the two proposed stocks have been the subject of considerable disagreement (Mitchell and Reeves, 1983).

Catches of humpback whales in winter off the coast of Norway (including takes of females pregnant with large foetuses; Ingebrigtsen, 1929) and recent winter sightings off the Finnmark coast (Christensen *et al.*, 1992) indicate that some individuals may not migrate far from the region. Ingebrigtsen (1929) suggested that humpback whales from Norway travel only short distances for breeding, perhaps to waters off the British Isles. Singing by humpback whales has been reported in the region of the British Isles (Clark, 1995), potentially supporting this idea, although humpback songs have occasionally been reported from other feeding grounds (Mattila *et al.*, 1987; McSweeney *et al.*, 1989).

Other authors have proposed that while some humpback whales that summer off Norway may winter in the Arctic, most move south to breeding grounds in the vicinity of the Cape Verde Islands and along the northwestern coast of Africa (Kellogg, 1929; Townsend, 1935; Tomilin, 1957; Winn *et al.*, 1981). Humpback whales were hunted in winter in these areas (Kellogg, 1929; Mitchell and Reeves, 1983), and recent sightings from the Cape Verde Islands demonstrate that humpback whales are still found there in winter (Reiner *et al.*, 1996), although there is little evidence to suggest that large numbers occur in the region today.

Recently, a small number of resightings have been documented between Norwegian waters and the West Indies, suggesting that humpback whales from Norwegian waters travel to the southwestern North Atlantic for breeding (Palsbøll *et al.*, 1997; Stevick *et al.*, 1998). Genetic analyses have suggested that the North Atlantic humpback whale population is panmictic, further supporting this theory (Larsen *et al.*, 1996; Palsbøll *et al.*, 1997).

Previous results, therefore, leave unresolved the extent to which humpback whales from Norway visit the West Indies in winter and use the area as a breeding and calving site. Sightings of individually identified whales provide one source of evidence for documenting migratory destinations of whales from this region. We report here on the most extensive comparison to date of individually identified humpback whales from Norway with those from the West Indies breeding grounds, with the aim of assessing the importance of the West Indies as a breeding ground for humpbacks which feed in Norwegian waters.

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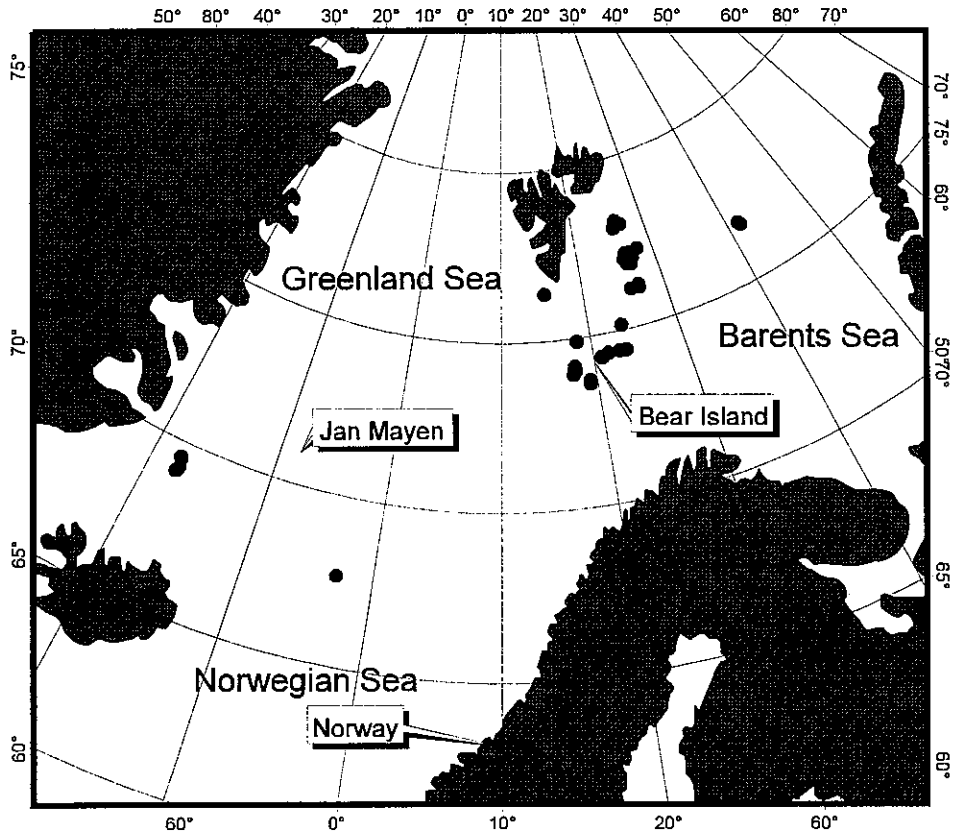

Fig. 1. Location of humpback whales identified in Norwegian and adjacent waters during YoNAH surveys in 1992 and 1993.

METHODS

Photographs of the ventral surface of humpback whale flukes were collected from the waters off Norway during 1992 and 1993 as part of the Years of the North Atlantic Humpback Whale project (YoNAH), an ocean-basin-wide mark-recapture study of humpback whales (Smith *et al.*, 1999). As part of the YoNAH analyses, these individuals from Norway were compared to the approximately 3,000 other individuals identified throughout the North Atlantic during the YoNAH project to identify resightings (Stevick *et al.*, 1998; Smith *et al.*, 1999). Subsequently, all individuals identified by the Norwegian sub-project of YoNAH were compared to the North Atlantic Humpback Whale Catalog (NAHWC) containing approximately 5,000 identified individuals from the North Atlantic, mostly collected between 1978 and 1991 (Katona and Beard, 1990).

Rates of exchange were calculated from Norway to the two West Indies collections separately. A similar rate was calculated from the combined YoNAH feeding ground sub-projects to the YoNAH West Indies for comparison. In 1992 and 1993 YoNAH sampling was conducted in the Norwegian and Barents Seas (Fig. 1). In 1993, additional sampling was conducted in the Greenland Sea near Jan Mayen, well to the west of the area surveyed in 1992. The distribution of whales identified was discontinuous. The distance between the two areas of primary concentration is 1,200km (650 n.miles) in which only a single whale was identified. Given this discontinuous spatial distribution, exchange rates were calculated separately for the Barents Sea sample and the Jan Mayen sample as well as for the entire sample from the Norwegian project. Where comparisons between areas resulted in Chi-square cells with expected values of less than five, the comparisons were made with the Fisher exact test (e.g. Zar, 1984).

Image quality effects resighting rates and varies between collections and areas (Smith *et al.*, 1999) and thus comparisons of resighting rates were made based only on good quality photographs of whole flukes. Photographs from the YoNAH collection were restricted to include only photographs coded as categories 3+ and better as described in Smith *et al.* (1999) and Friday *et al.* (1999). Photographs from the NAHWC were restricted to photographs of categories 1 and 2 as described by Katona and Beard (1990).

Dates were converted to sequential days following January 1 for computation of means. Photographs of all qualities were used for calculation of sighting dates.

RESULTS

A total of 96 individuals was identified from the Norwegian photographic sample during the YoNAH project. Of these, 63 individuals were identified in the Norwegian and Barents Seas (Barents Sea sample) and 33 in the Greenland Sea (Jan Mayen sample). Distribution of samples is illustrated in Fig. 1. A single whale was identified between the two areas of primary concentration, over 600km from the nearest other sighting. Although this sighting was in the Norwegian Sea, it was not allocated to either sub-region because of this ambiguity. The same individual was identified five days later, however, in the Greenland Sea, and that sighting was assigned to the Jan Mayen sample. Of the individuals identified, 85 were represented by photographs which met the image quality criteria for use in calculation of exchange rates, 55 of these from the Barents Sea sample and 30 from the Jan Mayen sample.

Table 1
Individual humpback whales identified in Norwegian waters and also in the West Indies.

YoNAH ID	NAHWC ID	Date	Location	Latitude/longitude	Gender – Behaviour class
Y0081		12 Mar. 1992	Silver Bank		Mother – Biopsy Female
		27 Sep. 1992	Barents Sea	77°09'N, 27°03'E	Biopsy Female
Y0155	5615	25 Feb. 1988	Samana Bay		Pair
		9 Mar. 1992	Silver Bank		In competitive group – Secondary escort
		25 Mar. 1992	Navidad Bank	20°04'N, 68°50'W	In competitive group – Role unknown
		21 Jul. 1993	Jan Mayen	69°30'N, 17°36'W	
Y0414		12 Mar. 1992	Silver Bank	20°41'N, 69°49'W	In competitive group – Secondary escort
		22 Jun. 1992	Iceland	65°55'N, 27°33'W	
		21 Jul. 1993	Jan Mayen	69°30'N, 17°36'W	
Y1097		24 Jul. 1992	Barents Sea	73°44'N, 19°19'E	
		25 Feb. 1993	Navidad Bank	20°01'N, 68°57'W	In competitive group – Role unknown
Y1132	5540	13 Mar. 1988	Samana Bay		Mother
		16 Mar. 1988	Samana Bay		Mother
		23 Jul. 1992	Barents Sea	73°38'N, 19°14'E	
		22 Sep. 1992	Barents Sea	77°57'N, 25°45'E	Biopsy Female
Y1818		20 Jan. 1993	Silver Bank	20°46'N, 69°51'W	Pair
		19 Feb. 1993	Silver Bank	20°45'N, 69°47'W	Pair
		21 Jul. 1993	Jan Mayen	69°30'N, 17°36'W	
Y2067		6 Mar. 1993	Puerto Rico	18°22'N, 67°17'W	Pair
		20 Jul. 1993	Jan Mayen	69°16'N, 17°26'W	
Y2250		24 Feb. 1993	Silver Bank	20°44'N, 69°48'W	Pair – Biopsy Male
		21 Jul. 1993	Jan Mayen	69°30'N, 17°36'W	Biopsy Male
Y3074	5620	25 Feb. 1988	Samana Bay		In competitive group – Secondary escort
		5 Sep. 1993	Barents Sea	76°07'N, 25°54'E	
Y3077	2307	25 Feb. 1983	Puerto Rico		Singleton
		20 Aug. 1993	Barents Sea	74°21'N, 20°49'E	

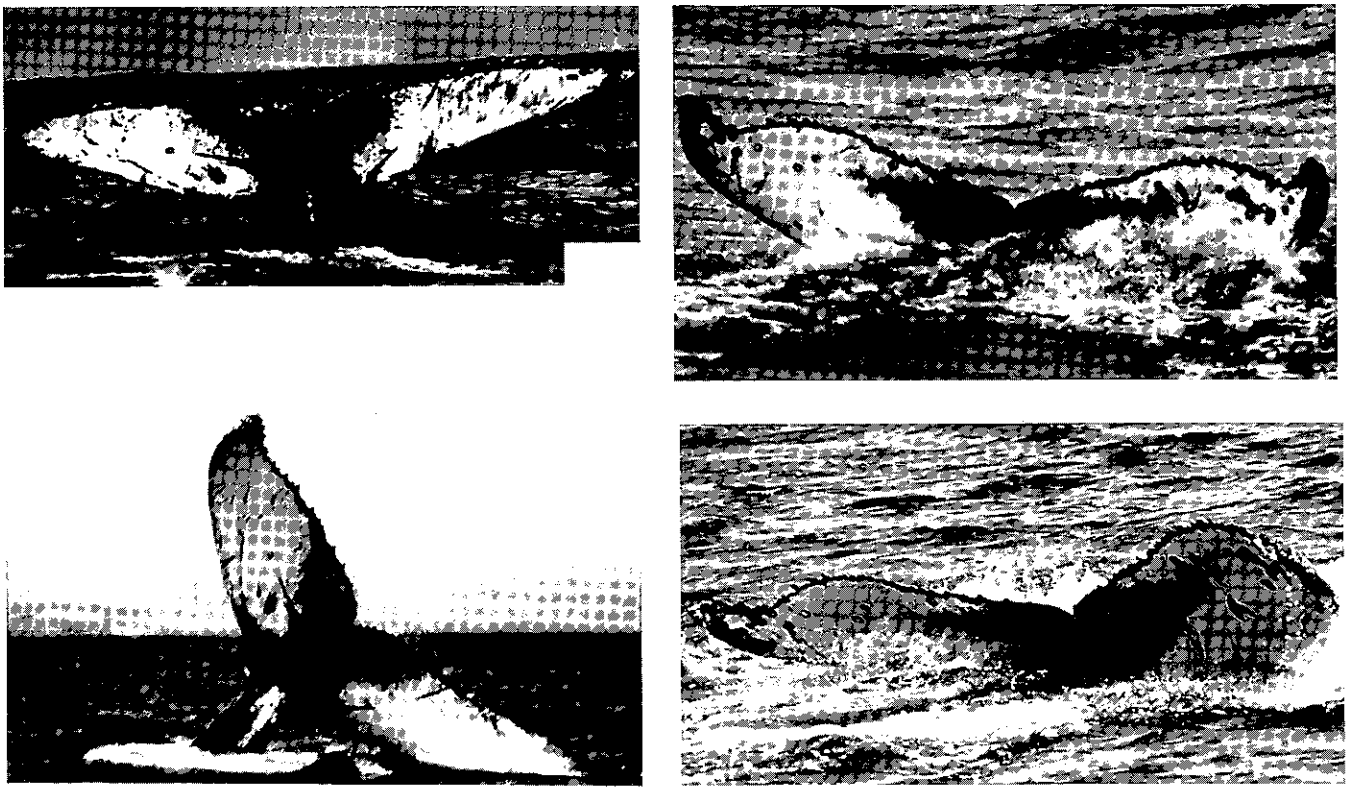

Plate I. Photographs of two humpback whales identified in reproductively active roles in the West Indies and also identified off Norway. Whale number Y1132 (left) photographed in March 1988 in Samana Bay, Dominican Republic accompanied by a newborn calf (bottom), and in July 1992 South of Bear Island in the Barents Sea (top). Whale Y3074 (right) photographed in February 1988 in Samana Bay as a secondary escort in a competitive group (bottom) and in September 1993 near Hopen Island in the Barents Sea (top).

Migration to the West Indies

A total of 10 individuals was identified in Norway and also in the West Indies (Table 1; and see Plate I). Seven of these individuals were identified from the YoNAH collection, while four were identified from the NAHWC with one appearing in both collections. The pattern of resightings differed between the two West Indies collections, with the overall higher resighting rate being to the YoNAH collection. Of the Barents Sea sample, two individuals were identified in the YoNAH and three in the NAHWC West

Indies collection, whilst of the Jan Mayen sample, five individuals were identified in the YoNAH and one in the NAHWC West Indies collection. There were no significant differences, however. Resighting rates between Norway and the West Indies were not significantly different between collections ($\chi^2 = 0.875$; $p = 0.350$). Neither were the resighting rates different when comparing the returns from the Barents Sea and Jan Mayen samples to the West Indies samples from the NAHWC (Fisher exact test; $p = 1.00$) or YoNAH (Fisher exact test; $p = 0.091$). Similarly, there were no differences in exchange with the YoNAH West Indies collection between the total from the feeding grounds in YoNAH and the sample from Norway ($\chi^2 = 0.426$; $p = 0.514$), the Barents Sea ($\chi^2 = 2.760$; $p = 0.106$) or Jan Mayen (Fisher exact test; $p = 0.228$).

Although no individuals from Norway were resighted in the Cape Verde Islands, it is clearly difficult to reach any firm conclusions from this as effort in the region has been limited. Given the fact that sea conditions are often difficult and whales are scattered, only three individuals have been photographically identified from the Cape Verde region to date. The lack of resightings is not, therefore, surprising.

Of the three individuals from which biopsy samples were collected, one was determined to be a male and two female. Four individuals were sighted in competitive groups; one of these individuals on two separate occasions on different banks. The designation of three of these individuals as secondary escorts in competitive groups suggests that these individuals are males, while the other individual was in a competitive group where the nuclear animal was identified, so it is also most likely a male (Tyack and Whitehead, 1983; Clapham *et al.*, 1992). Two mothers with newborn calves were also identified.

Transit distances of individuals reported here range from about 6,425km between Jan Mayen and Silver Bank to 8,080km between the Barents Sea and Samana Bay.

Sighting dates in the West Indies (see Fig. 2)

The dates of the West Indies sightings for humpback whales from Norway ranged from 20 January to 25 March. However, there was only one sighting before 19 February. The rest were heavily concentrated in a period of about three weeks in late February and early March, with a mean date of 2 March. In contrast, the mean sighting date for all West Indies whales from the NAHWC was 19 February, while the mean West Indies date for the YoNAH project was 21 February. Thus, humpback whales from the Norwegian feeding grounds were resighted in the West Indies significantly later than expected from the total NAHWC ($t = 2.79$; df = 13; $p = 0.015$) and YoNAH ($t = 2.24$; df = 13; $p = 0.043$) data. In order to minimise the influence of multiple sightings of single individuals within a year, the mean date was re-calculated using only the earliest date for each individual during any single season. While reducing the influence of individual whales on the calculations, this also reduced the already small sample size from Norway, decreasing the precision of the test. The mean breeding ground date for individuals from Norway calculated in this manner was 27 February. Using this date, the difference is still significant compared to that for the NAHWC (breeding ground date 17 February, $t = 2.36$; df = 10; $p = 0.040$), while the difference with the YoNAH collection is not significant (breeding ground date 20 February, $t = 1.74$; df = 10; $p = 0.11$).

The mean West Indies sighting dates for the Barents Sea sample alone are 4 March for all samples and 2 March for earliest sightings only. For the Jan Mayen sample the comparable dates are 28 February and 25 February. The Barents Sea sample is significantly later than the mean for either West Indies collection (NAHWC all sightings $t = 3.89$; df = 5; $p = 0.012$; earliest sightings $t = 3.65$; df = 4; $p = 0.022$; YoNAH all sightings $t = 3.30$; df = 5; $p = 0.022$; earliest sightings $t = 2.93$; df = 4; $p = 0.043$). The Jan Mayen sample is later than the West Indies means, but not significantly so (NAHWC all sightings $t = 1.34$; df = 7; $p = 0.22$; earliest sightings $t = 0.99$; df = 5; $p = 0.37$; YoNAH all sightings $t = 1.01$; df = 7; $p = 0.35$; earliest sightings $t = 0.63$; df = 5; $p = 0.55$).

DISCUSSION

The results presented here support the hypothesis that humpback whales feeding in the waters off Norway winter in the West Indies (Palsbøll *et al.*, 1997; Stevick *et al.*, 1998).

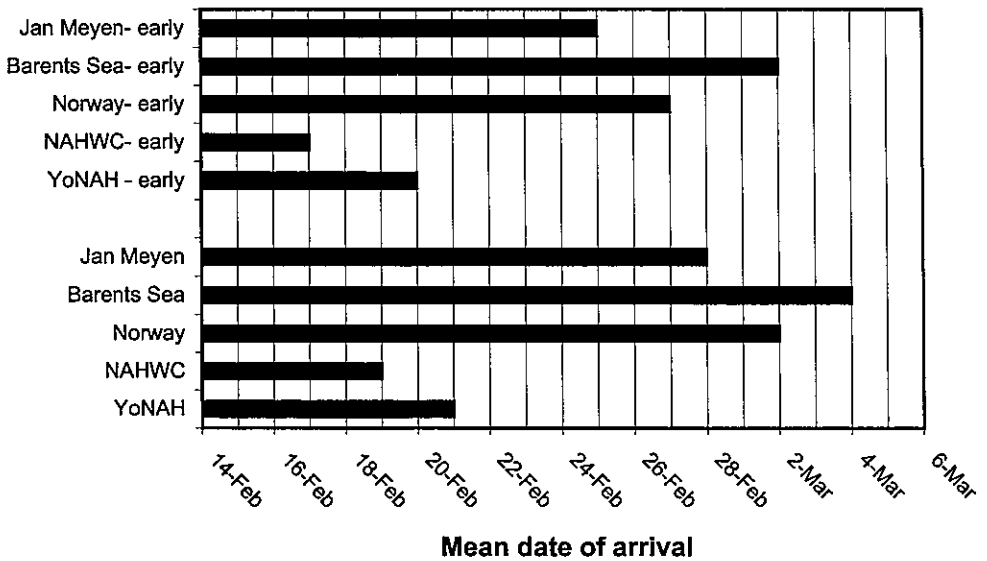

Fig. 2. Mean dates of arrival on the breeding grounds in the West Indies, for different components of the North Atlantic humpback population; 'early' refers to only the first sighting date of an individual in the West Indies (see text for a full description).

They further indicate that this applies to a variety of reproductive classes of both sexes. The observations of mothers with newborn calves, and of males in competitive groups, provides the strongest evidence to date that the West Indies is utilised as a breeding and calving ground by humpback whales which feed in Norwegian waters. The extent of movement of humpback whales between Norway and the West Indies is similar to that from other feeding grounds. The exchange rate from the Barents Sea to the YoNAH West Indies sample was lower than from other regions, but the difference was not significant, and the trend was reversed in comparisons to the NAHWC.

One reason to suppose that whales from Norway might not travel to the West Indies is the transit distance between the two areas. Humpback whales in Norwegian waters have the most polar distribution of any members of this species, with many individuals occurring north of 70ºN. While the transit distances reported here are longer than those of most reported humpback whale migrations, these distances are not inconsistent with some documented migratory transits between seasonal habitats in other waters. The longest distance between marking and recovery for a Discovery tag (Brown, 1978) in a humpback whale is a transit of 7,400km of a whale marked in Tonga and caught in the Bellingshausen Sea (Dawbin, 1964). A migration of over 8,300km between Colombia and the Antarctic Peninsula has been photographically documented (Stone *et al.*, 1990). In the North Pacific, a transit of 7,900km was recorded between Japan and British Colombia (Darling *et al.*, 1996). The distance from Bear Island to the region of the Cape Verde Islands with the highest rate of humpback sightings (Reiner *et al.*, 1996) is 6,890km, only 430km shorter than the distance from the same location to Silver Bank, the major breeding site in the West Indies.

The implications of the later mean West Indies sighting date of whales from Norway are not clear. If, as Ingebrigtsen (1929) and Christensen *et al.* (1992) suggest, food in the form of capelin is abundant in Norwegian waters in winter, whales may delay departure for the breeding grounds in order to continue feeding. Alternatively, the timing may be a function of distance travelled. The distance from Bear Island to the West Indies is more than twice that from Newfoundland, and nearly three times that from the Gulf of Maine. Thus if all animals depart the feeding grounds at the same time, individuals from Norway might be expected to arrive later. This would imply, however, that either these individuals spend less time in the West Indies than do conspecifics from other areas, or that they remain longer into the spring, arriving on the feeding grounds considerably later than individuals from other areas. There are currently no data to support this. Furthermore, the sample is too small to account for the potential effects of age and sex-structured segregation in humpback whale migration (Dawbin, 1997). Temporal differences in occupancy in the West Indies would reduce mating opportunities between animals from different feeding areas, although during the middle of the season individuals from all areas are present and substantial segregation seems unlikely.

These findings are consistent with the conclusions of Larsen *et al.* (1996), that North Atlantic humpback whales constitute a single panmictic population. It is possible that some individuals from this region winter outside the West Indies (in the Cape Verde Islands for example; Reiner *et al.*, 1996), or do not migrate to the tropics at all (Ingebrigtsen, 1929; Christensen *et al.*, 1992). However, these results demonstrate the presence in Norway of individuals which have also been identified on the West Indies breeding grounds in apparently reproductively active roles, and a rate of exchange with the West Indies comparable to that from other feeding areas. This suggests that the West Indies is an important, and likely the primary, breeding destination for the humpback whales from this relatively unstudied feeding stock.

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