

Population spatial structuring on the feeding grounds in North Atlantic humpback whales (*Megaptera novaeangliae*)

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Abstract

Population spatial structuring among North Atlantic humpback whales *Megaptera novaeangliae* on the summer feeding grounds was investigated using movement patterns of identified individuals. We analysed the results from an intensive 2-year ocean-basin-scale investigation resulting in 1658 individuals identified by natural markings and 751 individuals by genetic markers supplemented with data from a long-term collaborative study with 3063 individuals identified by natural markings. Re-sighting distances ranged from < 1 km to > 2200 km. The frequencies (F) of re-sighting distances (D) observed in consecutive years were best modelled by an inverse allometric function ($F = 6631D^{-1.24}$, $r^2 = 0.984$), reflecting high levels of site fidelity (median re-sighting distance < 40 km) with occasional long-distance movement (5% of re-sightings > 550 km). The distribution of re-sighting distances differed east and west of 45°W, with more long-distance movement in the east. This difference is consistent with regional patterns of prey distribution and predictability. Four feeding aggregations were identified: the Gulf of Maine, eastern Canada, West Greenland and the eastern North Atlantic. There was an exchange rate of 0.98% between the western feeding aggregations. The prevalence of long-distance movement in the east made delineation of possible additional feeding aggregations less clear. Limited exchange between sites separated by as little as tens of kilometres produced lower-level structuring within all feeding aggregations. Regional and temporal differences in movement patterns reflected similar foraging responses to varying patterns of prey availability and predictability. A negative relationship was shown between relative abundance of herring and sand lance in the Gulf of Maine and humpback whale movement from the Gulf of Maine to eastern Canada.

Introduction

Movement allows animals to utilize a patchy, unpredictable environment. Where resources are spatially predictable, however, survival and/or reproductive advantages may accrue to individuals that remain in or return to familiar areas, resulting in spatial structuring of populations. To date, there has been an emphasis on the study of philopatry to sites related to reproduction. However, individuals may demonstrate fidelity to any location used during their lives (Robertson & Cooke, 1999), and groups within interbreed-

ing populations may differ in features such as prey specialization (Iverson, Frost & Lowry, 1997), migratory behaviour (Belthoff & Gauthreaux, 1991) and social structure (Richards, 2000). There may also be phenotypic variation (Allen *et al.*, 1994) and differences in mitochondrial genetic markers (Palsbøll *et al.*, 1995) between groups within populations. Estimation of population parameters is also more complex in spatially structured populations (Schwartz & Taylor, 1998; Smith *et al.*, 1999). Segregation has conservation implications as smaller units are more vulnerable to depletion or extinction, and are hampered in recovery

from depletion (Taylor, 1997). There is an increasing recognition, therefore, that biological populations are not always the appropriate units for conservation and management (Taylor, 1997).

As humpback whales *Megaptera novaeangliae* require areas with high prey density to build up and maintain their substantial energy reserves, it might be expected that they would travel extensively in search of these transient prey patches, particularly as the oceans largely lack physical barriers to movement. However, in the most extensively studied feeding areas in the northern hemisphere, they show consistent fidelity to specific foraging areas. Return of individuals to feeding areas is high; movement within them is widely documented and observed movement between them is uncommon (Katona & Beard, 1990; Calambokidis *et al.*, 1996). This pattern of behaviour is maternally based and persists over generations, in some regions resulting in differences in mitochondrial genetic markers between groups from different areas (Palsbøll *et al.*, 1995). The groups of individuals using specific foraging areas have been referred to as feeding aggregations. Feeding aggregations do not necessarily correspond with breeding groups. Individuals from multiple feeding areas may congregate on the same breeding ground, whereas animals from the same feeding area may visit different breeding grounds (Calambokidis *et al.*, 2001; Stevick *et al.*, 2003).

Five feeding aggregations were identified by Katona & Beard (1990) in the western North Atlantic: the Gulf of Maine, Gulf of St Lawrence, Newfoundland-Labrador, West Greenland and Iceland. However, these authors suggested that the re-sighting patterns of individuals from the Gulf of St Lawrence warranted re-evaluation, whereas Whitehead & Glass (1985) found less movement than expected between the Grand Banks and coastal Newfoundland. Humpback whales are also known to occur in summer off the coast of Norway and into the Barents Sea (Christensen, Haug & Øien, 1992*a,b*), although there has been little information on humpback whale movement in this region.

Although humpback whales have been intensively studied in many parts of the world, knowledge of ocean-basin-scale movement patterns has been hampered by the regional nature of most studies, spatial and temporal variability in effort between areas, and often by opportunistic data collection. We present results from the only dedicated study of humpback whale population ecology across an ocean basin, supplemented with data from a long-term study. The ocean-basin-wide nature of this study, large sample size, synoptic and largely systematic data collection, and the use of computed transit distances to examine movement across a range of scales provide new insights into humpback whale movement patterns and spatial structuring on the feeding grounds.

Methods

Individual animals were identified by natural markings on the ventral surface of the flukes (Katona *et al.*, 1979) or by

molecular genetic analysis of skin biopsy samples (Palsbøll *et al.*, 1997). The Years of the North Atlantic Humpback Whale project (YoNAH), a unique ocean-basin-wide study of humpback whales conducted in the North Atlantic during 1992 and 1993 (Smith *et al.*, 1999), provides most of these data. Photographic and genetic samples were collected systematically from humpback whales in all of the major feeding grounds. Effort was allocated in proportion to the expected density of animals on the basis of previous records, additionally constrained by logistical considerations (Smith *et al.*, 1999). Standardized protocols for locating groups of whales and systematically sampling those groups were used to minimize sampling biases. Details of the field sampling protocol, distribution of survey effort, data collection and laboratory methods are provided by Smith *et al.* (1999). Use of dedicated and largely systematically collected data minimizes problems associated with unequal effort distribution (Koenig, Vuren & Hooge, 1996) to an extent unprecedented in large-scale studies of whale movement (Smith *et al.*, 1999). The YoNAH feeding ground records comprise 2586 photographic animal/days representing 1658 individuals and 829 genetic animal/days representing 751 individuals. The YoNAH photographic data were used for most analyses because of more representative sampling effort, greater sampling intensity and availability of precise location information for most sightings. Unless otherwise stated, analyses are based on this sample.

Great-circle distances were calculated (Bowditch, 1977) between YoNAH sighting locations. Distances do not represent swimming distances, as the whales did not travel directly between sightings. In most cases, between-year re-sightings are reported; therefore, many whales would have migrated thousands of kilometres to the tropics between sightings (Stevick *et al.*, 2003). Where multiple transits for the same individual were appropriate for an analysis, only the maximum distance was used, slightly under-representing site fidelity. However, because effort was not random, animals at more remote sites may have moved into under-sampled regions and become less detectable (Koenig *et al.*, 1996), slightly over-representing philopatry.

These YoNAH data are supplemented for some analyses by the North Atlantic Humpback Whale Catalogue (NAHWC), a curation facility for humpback whale fluke identification photographs. Most NAHWC samples were opportunistically collected; therefore, spatial and temporal coverage is highly variable. Most records were from the western North Atlantic; few samples are available from Icelandic waters or further east. These analyses include records of 8049 animal/days representing 3063 individuals collected between 1978 and 1991 and submitted by >350 contributors. Techniques for photographic comparison are detailed in Katona & Beard (1990).

Defining feeding areas

The identified individuals were divided geographically into regions of high whale density (Fig. 1). The regions varied

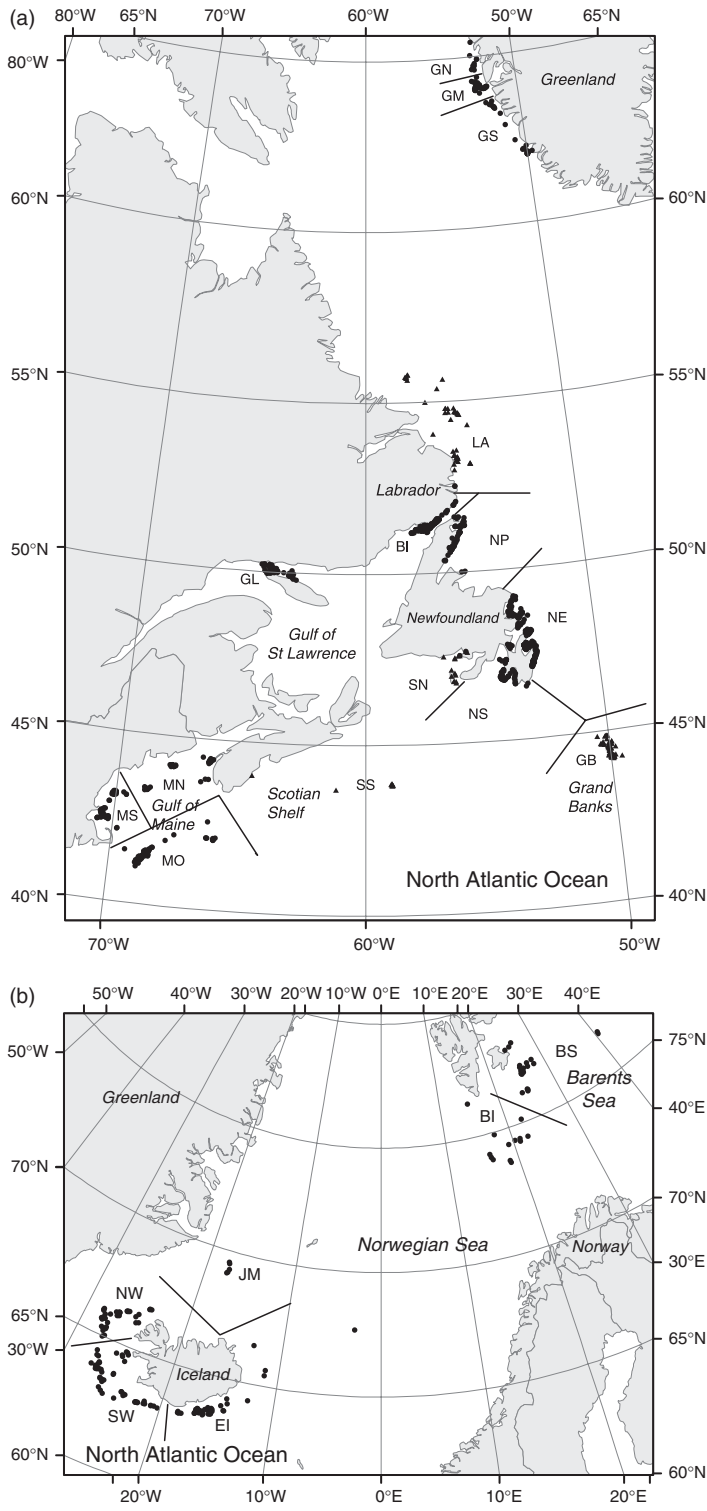


Figure 1 Location of humpback whales *Megaptera novaeangliae* photographically identified during 1992 and 1993 (solid circles) by the Years of the North Atlantic Humpback Whale project (YoNAH) and the regional designations for sampling areas used in analyses. (a) Samples from the western North Atlantic Ocean including samples collected from the Gulf of Maine through west Greenland. Solid triangles represent the locations of North Atlantic Humpback Whale Catalogue samples from four regions in which little or no data were collected during the YoNAH project: SS, GB, SN and LA. (b) Samples collected from the eastern North Atlantic Ocean.

in size because of the local distribution of whales, but were typically about 200km across. Regional designations used in the NAHWC database were combined to represent as similar a distribution as possible.

The transition probability, pt , between two regions was estimated using maximum likelihood methods (Hilborn, 1990; Whitehead, 2001). The log-likelihood that m_{ij} of the n_i animals identified in area i were also identified from n_j

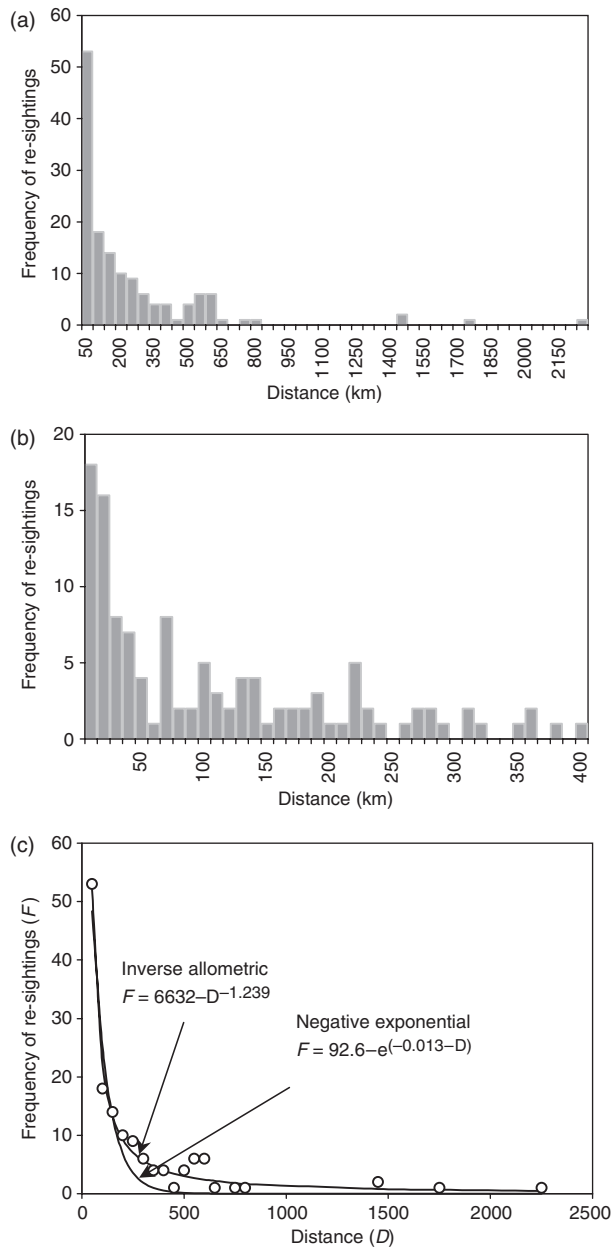


Figure 2 Frequency of distances observed for re-sightings between years. Only the maximum distance reported for each individual is shown. (a) All calculated distances are included. (b) Only distances less than 400 km are included for greater resolution. (c) Negative exponential and inverse allometric functions fit to the frequency distribution. The comparatively poor fit of the negative exponential represents over-dispersion in these data resulting from a combination of strong site fidelity and some long transits.

animals sampled in area j given a population of n individuals is given as the Poisson approximation (Whitehead, 2001):

$$L = (m_{ij} \log(\hat{m}_{ij}) - \hat{m}_{ij}) + \text{constant}$$

where the expected number of re-sightings is

$$\hat{m}_{ij} = pt_{ij}n_i(n_j/n)$$

The likelihood was maximized over 5000 transition probabilities drawn from a uniform distribution. For each iteration, n was drawn from a uniform distribution with a range from 2000 to 10 000.

Because photographic quality influences re-sighting rates (Stevick *et al.*, 2001) and varies between feeding areas ($\chi^2_8 = 116.3$, $P = 2.8 \times 10^{-17}$), photographs given the poorest overall quality code [code 3 for the NAHWC, Katona & Beard (1990); code 3- for the YoNAH collection, Friday *et al.* (2000)] were excluded in the calculation of regional transition probabilities and only photographs showing whole flukes were used.

Hierarchical cluster analysis was used to help describe feeding aggregations by grouping areas between which there was a high transition probability. Ward's algorithm was used as this method identifies compact, well-defined clusters (R Core Development Team, 2005).

Abundance of prey

Relative abundance data for herring, sand lance and mackerel from the Gulf of Maine were obtained from trawl surveys conducted twice annually by the United States National Marine Fisheries Service (NMFS). The stratified mean number of individuals per standard tow was determined for stations covering the Gulf of Maine and Georges Bank (NMFS strata 23–40). Data were provided by the Population Dynamics Branch, Northeast Fisheries Science Center, Woods Hole, MA, USA. A regression was fitted with the mean transition probability from the Gulf of Maine to eastern Canada in the same year or the following year as the dependent variable and the prey indices from the preceding year and their interaction terms as independent variables. Movement data from 1980 to 1993 were used in the model. A reverse stepwise selection procedure was used to select the most parsimonious variables for the final model.

Results

Distance of individual movements

Three hundred and ninety-two individuals were identified by natural markings and 54 by genetic methods on >1 day during 1992 and 1993. Re-sighting distances ranged from <1 km to >2200 km. The frequency of between-year re-sighting is greatest at distances <10 km (Fig. 2). The median distance was 40 km; 5% of distances were >550 km. The frequency distribution (F) of between-year re-sighting distances (D) was well fitted by both inverse allometric ($F = 6631D^{-1.24}$, $r^2 = 0.984$) and negative exponential functions ($F = 92.6e^{-0.013D}$, $r^2 = 0.934$; Fig. 2). The inverse allometric function is a better descriptor of over-dispersed data, modelling more effectively both high site fidelity and

Table 1 Pattern of re-sightings between areas as represented by the regional transition probability

	<i>n</i>	MN	MS	MO	NS	NE	NP	SB	GL	GS	GM	GN	SW	NW	JM	EI	BI
<i>(a) Results of identification by natural markings from the YoNAH project for 1992 and 1993</i>																	
GOM																	
	MN	56															
	MS	111	0.9986														
	MO	95	0.6066	0.9986													
Canada																	
	NS	80															
	NE	357		0.1896	0.9986												
	NP	146			0.4633	0.8985											
	SB	340			0.7061	0.7878	0.9986										
	GL	51				0.6204	0.7063	0.9986									
Greenland																	
	GS	38															
	GM	137						0.1378	0.6712	0.9986							
	GN	16								0.9986	0.9986						
ENA																	
	SW	49															
	NW	54											0.9696				
	JM	29												0.9986			
	EI	44															
	BI	19															^a
	BS	38												0.9986		0.9986	0.9986
<i>(b) Results of identification by genetic markers from the YoNAH project for 1992 and 1993</i>																	
GOM																	
	MN	37															
	MS	67	0.9996														
	MO	63		0.9996													
Canada																	
	NS	40															
	NE	153			0.9996												
	NP	53			0.8603	0.2251											
	SB	127				0.4831	0.9996										
	GL	24					0.9996	0.7758									
Greenland																	
	GS	24															
	GM	38								0.9996							
	GN	7															
ENA																	
	SW	39															
	NW	24											0.9996				
	JM	9															
	EI	14															
	BI	15											0.9996			0.9996	
	BS	20															
<i>(c) Results from the NAHWC through 1991 for the western North Atlantic only</i>																	
	<i>n</i>	MN	MS	MO	SS	GB	SN	NS	NE	NP	SB	GL	LA	GS	GM		
GOM																	
	MN	196															
	MS	705	0.9177														
	MO	298	0.7777	0.9551													
Canada																	
	SS	9		0.5816	0.6978												
	GB	249		0.0193		0.7910											
	SN	27		0.2173													
	NS	136		0.0312				0.0612									
	NE	898		0.0065		0.2844	0.2832	0.1353	0.6724								

Table 1c Continued
(c) Results from the NAHWC through 1991 for the western North Atlantic only

	<i>n</i>	MN	MS	MO	SS	GB	SN	NS	NE	NP	SB	GL	LA	GS	GM
NP	87				0.9900			0.9520	0.4565						
SB	150		0.1081	0.1514				0.3186	0.2770	0.6092					
GL	94	0.7149	0.3789	0.4404		0.1849	0.3521	0.5566	0.1492	0.2514	0.9644				
LA	263					0.0481		0.2185	0.3075	0.9302	0.2754	0.1371			
Greenland															
GS	134		0.0383				0.7295		0.1332				0.0614		
GM	166							0.1697						0.9900	
GN	89										0.6268			0.9900	0.9900

The areas and abbreviations are presented in Fig. 1. Only regions between which movement was observed are included.

^a A re-sighting between these areas was observed, but it is not included in calculation of the transition probability for this table because of poor photographic quality.

YoNAH, Years of the North Atlantic Humpback Whale project; NAHWC, North Atlantic Humpback Whale Catalogue.

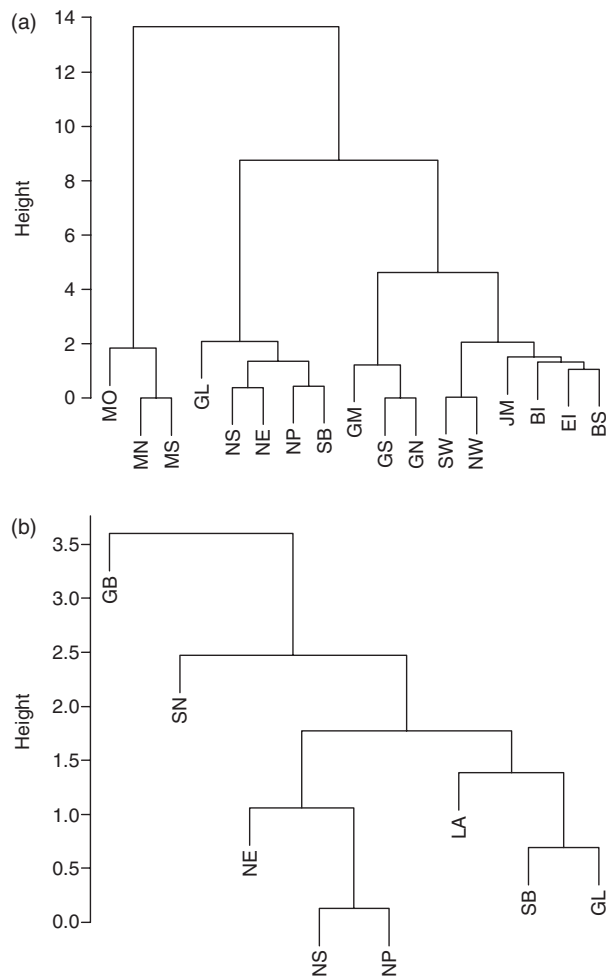


Figure 3 Feeding aggregations of humpback whales *Megaptera novaeangliae* in the North Atlantic Ocean defined by cluster analysis. (a) All feeding area results from the Years of the North Atlantic Humpback Whale project. Feeding aggregations shown from left: the Gulf of Maine, eastern Canada, West Greenland and the eastern North Atlantic. (b) Structuring within the eastern Canada aggregation shown using the North Atlantic Humpback Whale Catalogue data.

Table 2 Number of individuals observed to move between western North Atlantic feeding areas

Region	Gulf of Maine		Canada	
Canada	25	1		
Greenland	1	0	13	2

Results from the North Atlantic Humpback Whale Catalogue (left) and the Years of the North Atlantic Humpback Whale project (right).

Table 3 Results of multiple linear regression on transition probabilities of individual humpback whales *Megaptera novaeangliae* from the Gulf of Maine to Newfoundland, Labrador or the Gulf of St Lawrence against indices of relative finfish abundance from 1980 to 1993

Coefficients	Estimate	SE	<i>t</i>	<i>P</i>
Intercept	0.4052	0.07511	5.395	0.000303
Sand lance	-0.001922	0.000642	-2.994	0.013490
Atlantic herring	-0.004533	0.00129	-3.841	0.005675
Sand lance:Atlantic herring	0.000152	0.000086	1.756	0.109653

occasional long-distance movement (Hill, Thomas & Lewis, 1996; Baguette, Petit & Queva, 2000).

The distribution of re-sighting distances was significantly different between animals sampled east and west of 45°W. The median re-sighting distance for all animals identified more than once either within or between years in the east was 148 km corresponding to 25 km in the west ($U = 0.0024$, $P = 0.0012$). All of the re-sightings separated by > 1800 km were from the eastern North Atlantic.

Feeding aggregations

This pattern of individual movement is reflected in the exchange between regions. Most individuals seen during both years returned to the same region: 138 of 204 in the west and two of four in the east. Very high transition probabilities prevailed between adjacent regions, rapidly declining as the distance between areas increased (Table 1).

There were four feeding aggregations apparent in the results of cluster analysis (Fig. 3): the Gulf of Maine, West

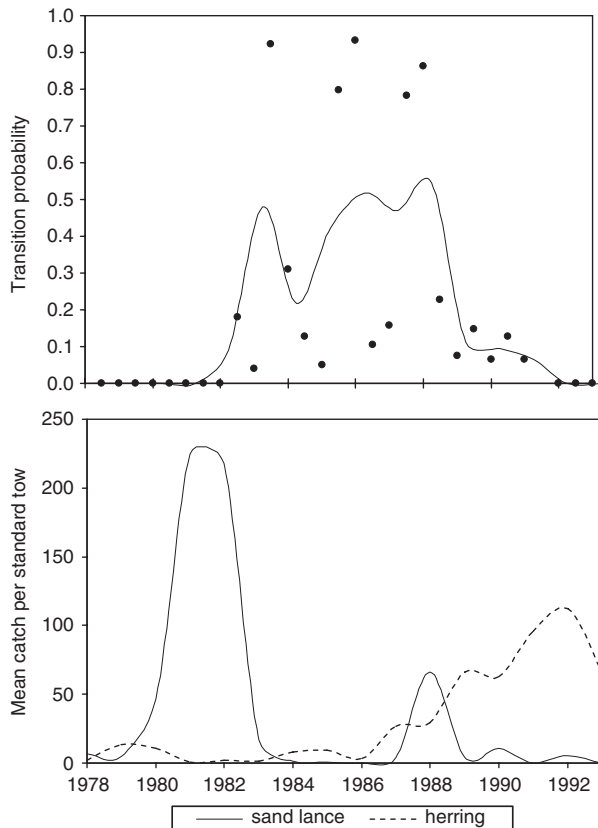


Figure 4 Movement responses to changes in prey fields. Movement of individuals between the Gulf of Maine and eastern Canada, represented by the probability of transition for movement within a single year or in 2 adjacent years (top). The line represents the 12-month running mean. Indices of relative abundance for two primary forage species in US waters (bottom).

Greenland, eastern Canada and the eastern North Atlantic. All four aggregations are geographically distinct, have a substantial return of individuals to the area and limited exchange to other regions. Fine-scale philopatry produces low-level segregation within all areas.

Within eastern Canadian waters, few animals were identified in common to the most widely separated regions, but the division of Newfoundland/Labrador from the Gulf of St Lawrence presented by Katona & Beard (1990) is not pronounced. The NAHWC contains records from four geographic areas of eastern Canada where YoNAH coverage was limited or lacking (Fig. 1). Only nine individuals were identified on the Scotian Shelf, limiting potential analysis. However, two of these were also identified in the Gulf of Maine, one on the Grand Banks and one off the east coast of Newfoundland (Table 3). The other areas demonstrate a good deal of structuring, but no clear divisions (Fig. 3b). The Grand Banks segregates early from other areas. Unfortunately, as there was no offshore YoNAH effort in Canadian waters, it is difficult to evaluate the level of segregation between these areas beyond the analysis

presented by Whitehead & Glass (1985). Re-sightings from southern Newfoundland followed a pattern different from that seen elsewhere. Although the sample size is small, little movement was evident to adjacent waters to the east, whereas movement was observed to the more distant Gulf of St Lawrence and to Greenland.

Only three individuals identified during both 1992 and 1993 were seen in more than one of these feeding aggregations (Table 2). This yields a rate of exchange of 0.98% between western feeding aggregations in successive years. No within-year re-sightings were observed. Individuals identified in the Gulf of Maine before 1992 were re-sighted off Newfoundland, Labrador and the Gulf of St Lawrence, whereas most re-sightings from Greenland were to the east coast of Newfoundland. A single whale was identified in the Gulf of Maine, south-east of Newfoundland and off Greenland. The majority (14 of 25) of individuals sighted in >2 feeding aggregations were observed to return to the initial area. A total of 12 individuals was identified in two aggregations in the same year, all moving between the Gulf of Maine and eastern Canada (interval 14–143 days). Most of the re-sightings between the Gulf of Maine and eastern Canada within a year or in adjacent years occurred between 1983 and 1989 (Fig. 4). There is a significant negative relationship between humpback whale movement from the United States to Canada from 1980 to 1993 and estimates of sand lance and herring abundance in the Gulf of Maine ($F_{3 \text{ and } 10} = 5.107$, $P = 0.02129$; Table 3). The most parsimonious model includes sand lance, herring and their interaction term but not mackerel.

In contrast to the west, long-distance movements were commonly observed in the eastern North Atlantic. No between-year re-sightings were identified in Norwegian waters, but three within-year and two between-year re-sightings were made between Norway and Iceland. There were no re-sightings between eastern Iceland and western Iceland. However, one individual was identified off western Iceland and in the Greenland Sea, whereas there were two re-sightings from eastern Iceland to the Barents Sea and one to the Bear Island area. This may suggest that animals from western Iceland and the Greenland Sea constitute one feeding aggregation, with another extending from eastern Iceland into the Barents Sea. The movement of an individual from north-west Icelandic waters to the Barents Sea does not fit this pattern, however, and small regional sample sizes limit the ability to interpret these data further.

Discussion

Animals must forage on a scale over which resources are predictably available, and thus their distribution is linked in a scale-dependent manner to the distribution and predictability of their principal prey (Whitehead, 1996; Fauchald, Erikstad & Skarsfjord, 2000). Humpback whales must locate and exploit localized and often ephemeral high-density concentrations of prey (Brodie, Sameoto & Sheldon, 1978). Thus regional and temporal patterns of movement broadly reflect prey distribution and predictability.

Western North Atlantic

The level and scale of site fidelity observed among western North Atlantic humpback whales is consistent with exploitation of prey that occurs predictably over scales of kilometres or tens of kilometres. Although local diet preferences are not always well described, humpback whales in the western North Atlantic prey primarily on schooling fish, *inter alia* capelin, sand lance, herring and mackerel, and also on euphausiids (NMFS, 1991). The spawning sites for capelin are restricted to beaches or shoals with highly specific substrate characteristics and their occurrence is correlated with water temperature and tidal oscillation (Scott & Scott, 1988). Similarly, sand lance regularly burrow in sediment; hence they are restricted to shoal areas with appropriate substrate for burrowing (Nizinski, 2002). Herring are observed to make regular annual return migrations to and from specific spawning sites and to seasonally inhabit waters of consistent temperature and depth characteristics (Munroe, 2002). These fish and also euphausiids are largely planktivorous with a wide overlap in diet (Sameoto, 1980; Collette & Klein-MacPhee, 2002). Zooplankton distribution is exceedingly patchy on small scales, and this patchiness may be associated with physical oceanographic features that occur with seasonal predictability at moderately small scales (Wishner *et al.*, 1988, 1995).

These circumstances suggest that revisiting geographic areas where foraging has been successful is likely to be a productive foraging strategy in the western North Atlantic. Because prey at individual sites will vary in abundance through a season and between years, regular return to a number of proximal sites with occasional exploration at greater distances is likely, with the duration of stay at and tendency to return to each site related to relative prey density. Thus, at scales of tens of kilometres, individuals may show preference for habitat patches, but will frequently move between them. At scales of hundreds of kilometres, high degrees of site fidelity to specific habitat patches will be observed, but considerable movement will still occur between these. At scales of thousands of kilometres, the predictability of prey within habitat units is high, and hence there will be little incentive for movement between units.

Eastern North Atlantic

Although some small-scale return is observed in the eastern sample, with one between-year re-sighting at 15 km, long-distance movement over short periods of time appears to be more common. Indeed, within-feeding-area movements reported here are equivalent to the seasonal migratory distance from the Gulf of Maine to the West Indies. This may reflect response to a larger scale of resource predictability in the region with seasonally predictable but spatially transitory food resources associated with oceanographic features that are less geographically stable.

In the Norwegian Sea, euphausiids have been reported as a principal prey of humpback whales in spring and early summer (Hjort & Ruud, 1929; Ingebrigtsen, 1929). There are few data on humpback whale prey off Iceland, but

euphausiids are the primary prey of fin whales caught to the south and west of Iceland (Vikingsson, 1998). Capelin are also reported to be a major prey item in the eastern North Atlantic (Ingebrigtsen, 1929; Christensen *et al.*, 1992a,b). One capelin stock occurs to the north and west of Iceland and another in the Barents Sea (Vilhjálmsón, 1994; Gjørseter, 1998). Capelin distribution in these waters is highly unpredictable. However, both stocks are associated with meso-scale oceanographic features. The Icelandic stock spawns to the southwest of Iceland, moving north and east through the summer in association with the Polar Front (Vilhjálmsón, 1994). This current boundary is highly dynamic, but generally extends from the Denmark Strait east and north in the waters between Iceland and Jan Mayen. In summer and autumn, the Barents Sea stock is associated with oceanographic features related to warm water intrusions into the Barents Sea and the resulting boundary of the ice (Gjørseter, 1998). Substantial year-to-year variation in capelin abundance and distribution in both regions has been correlated with sea temperature, reflecting changes in these larger-scale features (Astthorsson & Gislason, 1998; Gjørseter, 1998), and substantial declines in the Barents Sea stock have been associated with shifts in humpback distribution (Christensen *et al.*, 1992a,b).

This reduced temporal and spatial predictability of prey is consistent with greater mobility of predators, with larger-scale predictability resulting in regular seasonal distribution shifts. These factors suggest that humpback whales initially congregate in areas of euphausiid concentration, following capelin later in the season. Abundance patterns from sighting surveys and catch records indicate such a seasonal progression of humpback whales (Martin *et al.*, 1984; Christensen *et al.*, 1992a,b). The possible segregation of individuals from eastern and western Iceland is also consistent with this prey distribution, suggesting that those whales to the west of Iceland in early summer follow the Icelandic capelin stock north along the Polar Front into the Greenland Sea, whereas those to the east are more likely to move to the Barents Sea.

Inter-annual shifts in prey abundance

Lack of inter-annual predictability may lead whales to make longer movements. Although such forays may in some cases be exploratory, they are likely to occur more frequently during periods of changing food supplies. Local changes in humpback whale abundance and distribution in the western North Atlantic have been correlated with prey variation (Whitehead & Carscadden, 1985; Payne *et al.*, 1986; Weirich *et al.*, 1997), whereas a larger-scale distributional shift in Norwegian waters has been associated with a collapse in the Barents Sea capelin stock (Christensen *et al.*, 1992a,b). Thus it is even possible, although it appears unlikely, that the east–west difference reported here is anomalous and related to a perturbation in food availability during 1992 and 1993.

The relationships presented here suggest that the simultaneously low abundance of two principal prey in the Gulf of Maine led to more whales travelling long distances for

foraging. Herring, sand lance and mackerel populations in the western North Atlantic are inter-related through predation and competition. They have widely overlapping food preferences, whereas mackerel, and to some extent also herring, prey upon sand lance, especially the larval and juvenile stages (Bowman, Warzocha & Morris, 1984). During the period of this study, both mackerel and herring underwent substantial recovery from fishery-related low abundance (Sherman *et al.*, 1996). As herring and mackerel stocks reached their lowest levels in about 1976, the relative abundance of sand lance across the Northeast Shelf increased dramatically, likely as a result of a combination of competitive release and reduced predation (Sherman *et al.*, 1981; Nelson & Ross, 1991). An increase in abundance of mackerel beginning in 1982 corresponded to a precipitous decline in sand lance during 1983 and 1984 (Nelson & Ross, 1991; Sherman *et al.*, 1996). Herring increased exponentially during this time, reaching an estimated 1 mmt biomass by 1989 (Sherman *et al.*, 1996).

These shifts in relative finfish species abundance correspond to changes in observed movement from the Gulf of Maine to eastern Canada. Initially, when sand lance predominated, little or no long-distance movement was observed. Relatively high levels of movement from 1984 to 1988 correspond to the simultaneously low abundance of herring and sand lance. By 1989 herring had recovered, and from 1989 to 1993 long-distance movement was again largely absent. The lack of support for inclusion of mackerel abundance in the model suggests that, although mackerel have been identified as prey of humpback whales in the region (Mitchell, 1973; Geraci *et al.*, 1990), they are taken incidentally or in the absence of alternative prey.

These relationships between movement and prey are stronger than might be expected given the probable complexity of foraging interactions and the limited nature of data available on prey abundance. Humpback whales feed on prey such as euphausiids for which regional abundance data are not available and thus these cannot be included in the model. Pelagic fish are not the target of the trawl surveys and thus this method is not optimal for sampling these species. Energetic factors related to size or age of prey may influence predation by humpback whales (Whitehead & Carscadden, 1985). However the indices used here do not reflect age or size classes. Local patch density may also influence foraging responses to similar large-scale prey concentrations (Brodie *et al.*, 1978; Payne *et al.*, 1986). Finally, to the extent that foraging is a threshold response to prey availability, the predator-prey relationship may be non-linear (Piatt & Methven, 1992). Nonetheless, the data presented here show that large-scale humpback whale movement patterns in the western North Atlantic altered during the 1980s in response to relative prey scarcity.

North Atlantic feeding aggregations

The extent of movement of humpback whales between any two areas in the North Atlantic is a function of the distance

between them. Individuals allocate their time preferentially to specific sites, presumably those associated with resources. The limited nature of movement over small distances observed in western areas is striking, given the swimming capabilities of humpback whales. Although humpback whales may traverse > 100 km in a day (Mate, Gisiner & Mobley, 1998), individuals consistently return to within a few kilometres of the same location after intervening migrations of thousands of kilometres. Site fidelity, coupled with highly clumped, discontinuous distribution, produces consistent geographic whale concentrations that are referred to as feeding aggregations.

There are four feeding aggregations within the North Atlantic: the Gulf of Maine, eastern Canada, West Greenland and the eastern North Atlantic. Because humpback whale habitat in eastern Canada covers a broad area, little movement is observed between remote sites. However, intervening areas have high rates of exchange to both. Thus there are no unambiguous divisions within these waters comparable to the other feeding aggregations, and exchange rates across any delimited boundary will be high. Because of the lower sampling intensity and more frequent observations of long-distance movement in the eastern North Atlantic, it is less clear if multiple feeding aggregations occur in the east and, if so, what the boundaries of these are. The existence of genetic differences between individuals sampled off Iceland and Norway (Larsen *et al.*, 1996) suggests considerable discreteness between individuals from these areas that is not evident in the movement results. The data are few and the area is large; hence more samples, including broader geographic and seasonal coverage, are required to clarify the status. Analysis of the genetic sample from the eastern North Atlantic on a finer geographic scale may also clarify the grouping pattern suggested by this analysis.

These results demonstrate neither random mixing of individuals within feeding aggregations nor lack of movement between them. Separating the feeding aggregations are regions of 900–1300 km within which few humpback whales have been observed. Because some whales occur in these intervening low-density areas, some individuals move between aggregations, and because prey abundance may shift in intermediate habitats, delineation of aggregation boundaries will inevitably be somewhat arbitrary. For example, although only nine humpback whales were identified on the Scotian Shelf through 1993, recent work suggests that there are substantial numbers there (Clapham *et al.*, 2003). This may simply reflect limited prior effort in the region. However, the biomass of small pelagic fish, principally sand lance, capelin and herring, increased by two orders of magnitude on the Scotian Shelf beginning in the mid-1980s and pelagic fish have been dominant from 1993 to 2002 in a region where they were previously scarce (DFO, 2003). This suggests that increases in food supply may have led to a substantial increase in humpback use of what was formerly a low-density habitat.

A higher rate of re-sighting between feeding aggregations might be expected, given probable migratory routes. Whales bound from the West Indies to waters off Greenland, Iceland or Norway by the shortest route would have to pass

near Newfoundland or over the Grand Banks. Asymmetric migration is common in some bird groups where routes are associated with prevailing weather patterns (Rappole, 1995). Acoustic tracking of humpback whales off Britain showed an offshore southerly migration in the autumn and winter, but failed to identify a northward migration in spring (Charif, Clapham & Clark, 2001), perhaps indicating that northbound individuals are following a track farther to the east. Thus a migration pattern following the North Atlantic gyre is possible. Although YoNAH sampling specifically avoided early and late season sampling in order to avoid the confounding factors associated with migration, of 13 instances in the NAHWC of individuals identified on different feeding grounds in the same year (12 individuals), 11 were seen in the area nearest to the West Indies earlier in the season, many during the early spring.

We demonstrate site fidelity at a scale well below that of a feeding aggregation. Little previous attention has been given to this smaller-scale fidelity and sub-regional preference within feeding aggregations. Recently, however, the rate of re-sighting between southern and northern sectors of the West Greenland feeding aggregation has been shown to be low compared with the rate of return to those areas, and this difference persisted over multiple years (Larsen & Hammond, 2004). Persistence of fidelity to areas visited early in life may lead to clusters of related individuals over scales smaller than feeding aggregations, even in the absence of long-term social relationships.

Individual preference for travel routes follows logically from feeding site fidelity in humpback whales and may further explain the observed pattern of exchange. Fidelity to migratory staging areas and routes has been shown in many birds (Schwartz & Ganter, 1995; Reed *et al.*, 1998) and in some mammals (Boyce, 1991). Preferred routes of travel may be reflected in the re-sighting patterns observed in eastern Canada as individuals travelling to the west or east of Newfoundland may reach the Strait of Belle Isle or Labrador. This indicates that population structuring may not be adequately modelled by geographically discrete groups of individuals. Semi-geographical structuring, in which groups of individuals with different patterns of movement occur in common areas during parts of the year, has been observed in some migrants and may be common (Rappole, 1995; Dingle, 1996).

Thus feeding aggregations are the result of the fidelity of individual animals to foraging sites and travel routes, coupled with discontinuous distribution related to patchy distribution of prey. In the North Atlantic, humpback whales demonstrate high levels of persistent site fidelity on the feeding range. However, the specific patterns of movement observed vary between areas and over time. Such differences appear to reflect foraging responses to patterns of prey abundance. Specifically, differences in movement patterns in the eastern and western North Atlantic reflect a similar strategy of return to areas of concentrated prey. In eastern regions, however, these prey are principally associated with meso-scale features that are spatially less predictable. The primary factor separating aggregations is discontinuity in

feeding habitat. In areas with no discontinuity in distribution or sampling, population divisions may not be clearly defined, yet movement between remote locations will be low.

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