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Spatial patterns of humpback whale (*Megaptera novaeangliae*) sightings and survey effort: Insight into North Atlantic population structure

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ABSTRACT

Understanding the population structure of a species is critical to its effective management and conservation. The humpback whale (*Megaptera novaeangliae*) has been the target of numerous research projects in several ocean basins, but no clear picture of its population structure has emerged. In the North Atlantic Ocean, genetic analyses and photo-identification movements have shown significant heterogeneity among the summer feeding grounds. Building on this knowledge, we test the hypothesis that the feeding grounds represent distinct populations by analyzing the spatial pattern of summer humpback whale sightings and survey effort. Controlling for the spatial pattern of effort, sightings are clustered, with peaks at radial distances of 300 km, 600 km, and 1,500 km. These results provide insight into the spatial extent of the summer population structure of humpback whales in the North Atlantic Ocean. Fine-scale clustering at distances of 300 km and 600 km is compatible with multiple populations consisting of the Gulf of Maine, eastern Canada, western Greenland, and Iceland. Broad-scale clustering at distances of 1,500 km may represent divisions between the western and eastern North Atlantic populations. These results provide spatial bounds to the feeding grounds of humpback whales and emphasize their distinct nature as management units.

Key words: spatial statistics, point processes, humpback whale, *Megaptera novaeangliae*, North Atlantic Ocean, population structure.

Knowing the spatial scale and extent of ecological patterns provides insight into underlying ecological processes (Fortin and Dale 2005). This is certainly true in understanding the life history of migratory species. The population structure of the humpback whale (*Megaptera novaeangliae*) in the North Atlantic Ocean has been investigated through mark–recapture studies (Smith *et al.* 1999, Clapham *et al.* 2003), photographs of individually distinct animals (Stevick *et al.* 1999, Jann *et al.* 2003, Larsen and Hammond 2004), genetic analyses (Palsbøll *et al.* 1995, Larsen *et al.* 1996), and commercial whaling catches (Reeves *et al.* 2001, 2002*a*; Reeves and Smith 2002). Despite being one of the most well-studied groups of whales in the world (Reeves *et al.* 2004), there is no overall consensus on the geographic structure of humpback whale populations in the North Atlantic Ocean. The scale, at which populations are structured, including the number of populations, has not been resolved. By examining the spatial pattern of humpback whale sightings, particularly within the context of the survey effort, further insights into the population structure of this species may be obtained.

In all oceans of the world, humpback whales migrate from winter breeding grounds in low latitudes to high-latitude feeding grounds (Martin *et al.* 1984, Baker *et al.* 1985, Clapham and Mattila 1988, Olavarria *et al.* 2007). Traditionally, populations have been defined by the winter breeding grounds because animals consistently return to the same breeding ground each winter (Calambokidis *et al.* 2001, Stevick *et al.* 2003). However, research on the degree of site fidelity to feeding grounds in the North Atlantic Ocean, including genetic analyses that found significant differences in mitochondrial DNA among the feeding grounds (Palsbøll *et al.* 1995, Larsen *et al.* 1996), suggests that whales observed in different feeding grounds may be considered as separate populations within the North Atlantic Ocean (International Whaling Commission 2002*a*, Clapham *et al.* 2003). This has profound implications for the conservation and management of humpback whales. Therefore, determining the number of individual populations, and particularly the spatial extent of each of the feeding grounds, is a top research priority.

Understanding the distribution of humpback whales is complex because a significant portion of the sampling effort has consisted of photo-identification studies (Smith *et al.* 1999). Photo-identification studies are an important part of humpback whale research because animals display individually unique patterns of pigmentation on the underside of their tail flukes when they dive (Katona *et al.* 1979). Using mark–recapture techniques, photo-identification data provide useful insights into the temporal and spatial distribution of individuals, revealing the actual interchange of individuals between areas. For example, broad-scale migration patterns can be determined from resightings between the feeding grounds off Iceland and Norway and the breeding ground in the West Indies (Stevick *et al.* 2003). Fine-scale patterns of spatial fidelity within the feeding grounds can also be discerned from records of sightings and resightings (Stevick *et al.* 2006). However, in order to obtain significant sample sizes, photo-identification studies typically target regions where humpback whales are known to occur, thus imposing bias into analyses of the distribution of humpback whales over broader spatial scales.

This study examines the spatial patterns of survey effort and humpback whale sightings during summer months in the North Atlantic Ocean. Spatial statistics provide a means for examining the geographic distribution of point data (Cressie 1993, Bailey and Gatrell 1995, Diggle 2003). The distributions of humpback whale sightings and survey effort are examined to discern spatial patterns (*e.g.,* clustering, randomness, or regularity) in the independent data sets. By accounting for the underlying spatial pattern of survey effort, an unbiased assessment of the distribution of humpback whales can be made and thus yield insight into the population structure of this species.

METHODS

Humpback whales spend the summer in high-latitude feeding grounds. To statistically evaluate their spatial pattern in the North Atlantic Ocean, visual surveys that occurred within the region extending from 40°N to Svalbard in the east (approximately 80°N) and Greenland in the west (65°N) were selected (Fig. 1). Visual surveys were included if they followed traditional line-transect methodology (Buckland *et al.* 2001, 2004) and reported detailed sampling effort data and sightings of humpback whales during the months of July, August, or September. These months were chosen to represent the summer period when humpback whales are found on the feeding grounds and to exclude sightings that might represent migratory transits. Line-transect methodology reduces the likelihood that multiple sightings of individual animals were recorded in a data set. Survey data were obtained from individual researchers (G. Vikingsson and Th. Gunnlaugsson, Marine Research Institute, Iceland) and from the Ocean Biogeographic Information System–Spatial Ecological Analysis of Megavertebrate Populations (OBIS–SEAMAP) (Read *et al.* 2007), with the permissions of the individual data providers (D. Palka, Northeast Fisheries Science Center, National Marine Fisheries Service; R. Kenney, University of Rhode Island; and P. Stevick, Allied Whale and College of the Atlantic). Data were not available for the regions of West Greenland and Norway.

Several steps were needed to prepare the data for analysis. The latitude/longitude locations of the sightings and survey effort were projected from a geographic decimal degree projection to an azimuthally equidistant projection centered on 57°N, 17°W to preserve distance calculations. The survey effort data were converted into a point data set by summarizing the data in grid (raster) format. Because humpback whale sightings that occur beyond approximately 10 km are typically removed from abundance calculations (Forney and Barlow 1998, Bannister and Hedley 2001, Mobley 2005), a grid cell size of 10 km × 10 km was used for the analyses. For each 10 km × 10 km grid cell, we computed the total length of survey trackline (in km). Because our statistical tests required point representation of sampling effort and whale sightings, we assigned one randomly located point inside a grid cell for every 1 km of survey effort that cell contained. For example, a 10 km × 10 km cell that contained 25 km of survey effort would be assigned 25 randomly located points within the bounds of the grid cell to reflect sampling effort. Whale occurrences were mapped as points at the latitude/longitude location of the sighting. For analyses, comparing the spatial distribution of sightings against sampling effort, a point was randomly placed within each grid cell that contained any survey effort. Spatial data

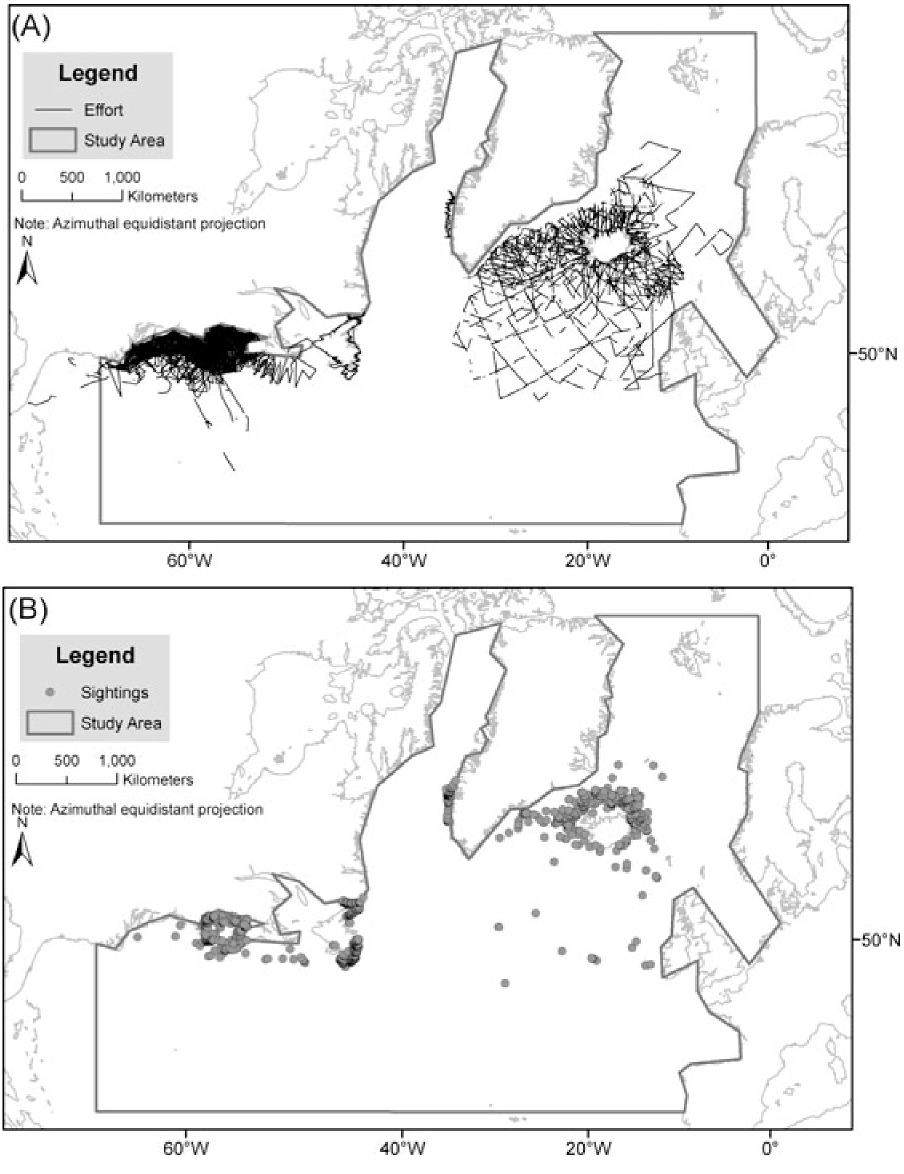

Figure 1. Summer survey effort (A) and humpback whale sightings (B) in the study area.

processing was done using ArcGIS 9.2 (Environmental Systems Research Institute 2007) and Hawth's Tools software (Beyer 2004). Spatial analyses were conducted using the software package R (R Core Development Team 2008).

In this study, we use the terminology that is standard for spatial statistics (Cressie 1993, Bailey and Gatrell 1995, Diggle 2003). Each data set, termed a spatial point process, consists of multiple events that are locations where an item of interest occurred. In this study, an event is either a humpback whale sighting or a point representing survey effort. The null hypothesis is that the point process (*e.g.*, whale sightings or sampling effort) displays complete spatial randomness. In many cases, if the null hypothesis is rejected (*i.e.*, the process is not random), the spatial statistic can indicate whether the spatial pattern exhibits clustering or regularity. Clustering occurs when events are underdispersed or aggregated. Regularity occurs when events are overdispersed or uniformly distributed (Dale *et al.* 2002).

Statistical significance and an analysis of uncertainty are assessed by comparing the measured point process to an envelope created from the maximum and minimum values of multiple simulations of random point processes. Because the envelope is formed by the maximum and minimum values of the multiple random simulations, it bounds the degree of natural variability, or uncertainty, associated with complete spatial randomness. Observed processes that fall along or outside of the envelope derived from the random simulations are statistically different from random.

Spatial Analyses of the Independent Processes

Several spatial analyses were performed to examine the spatial patterns of the two-point processes of humpback whale sightings and survey effort (Cressie 1993, Bailey and Gatrell 1995, Diggle 2003). The first-order properties of the spatial patterns address broad global trends and indicate whether the mean number of points varies across the study region. The Index of Dispersion measures the mean and variance of the intensity of observations, which is defined as the number of events per quadrat (unit area). A second statistic, the Index of Cluster Size (defined as the Index of Dispersion minus one), normalizes the Index of Dispersion for the grid cell size. Comparing the Index of Cluster Size to zero indicates the degree of complete spatial randomness.

Second-order properties address the variance of the point processes by evaluating the distance between events. The nearest neighbor distance can be an event–event distance (the distance between a randomly selected event and the next closest event) or a point–event distance (the distance between a random point in the study region and the closest event) (Cressie 1993, Bailey and Gatrell 1995, Diggle 2003). Several comparisons of the nearest neighbor distances were made to measure the spatial pattern of sampling effort and sightings. The first test compared the cumulative distribution function (CDF) of the observed event–event distances to the CDF envelope (*i.e.*, maximum and minimum values) of event–event distances for 99 spatially random simulations. Under spatial randomness, the observed CDF would fall within the simulation envelope. The second test compared the observed distribution to the distribution of a random process with the same intensity using the Kolmogorov–Smirnov test. Finally, the point–event distances were compared to the event–event distances. Under spatial randomness, it is expected that the event–event and point–event distances would be nearly equal.

Spatial patterns at a broader range of scales were evaluated using the L function, a modification of Ripley's K (Bailey and Gatrell 1995). The L function calculates the distances between each event and every neighbor (every other event). To evaluate the null hypothesis of complete spatial randomness, the CDF of the observed distances was compared to the CDF envelope (*i.e.*, maximum and minimum values) of distances for 99 spatially random simulations. Under spatial randomness, the observed CDF would fall within the simulation envelope, whereas it would fall above or below the envelope if the process is clustered or regular, respectively.

Spatial Analyses of the Two Processes

Once the point processes are examined individually, it is important to consider them together, particularly where the distribution of the sightings is certainly a function of the distribution of survey effort. The Cross *K* Function (Bailey and Gatrell 1995) addresses the null hypothesis of no interaction of the two processes by calculating the distances between each humpback whale sighting (process one) and each survey effort point (process two). Statistical significance and an analysis of uncertainty are determined by comparing the Cross *K* Function to an envelope created from 99 simulations of random point processes. An observed Cross *K* Function that falls along or above the upper envelope of the random processes represents attraction between the two processes, whereas along or below the lower envelope indicates repulsion between the two processes.

The second null hypothesis is that the distribution of humpback whale sightings is not different from the distribution of survey effort. This addresses the question of whether the spatial pattern seen in the humpback whale sightings is real or an artifact of the spatial pattern of the survey effort. To test this hypothesis, the difference [$D(h)$] between the Ripley's *K* functions of all of the humpback whale sightings [$K_{11}(h)$] and all the survey effort points [$K_{22}(h)$] was calculated at different distances (h). To test statistical significance and provide a measure of uncertainty, an envelope of the maximum and minimum values was calculated by randomly allocating the labels on the observations and then estimating the difference between the Ripley's *K* functions in 99 simulations. Peaks above the upper envelope (maximum random value), indicate clustering of the humpback whale sightings (process one) over and above clustering in the survey effort (process two), whereas troughs below the lower envelope (minimum random value) indicate clustering of survey effort over and above clustering of the humpback whale sightings.

RESULTS

In total, 20 surveys met the criteria of this study; that is, they reported detailed effort data and observed humpback whales during July, August, or September within the defined study region. This provided 343,628 km of survey effort and 2,752 sightings of humpback whales (Fig. 1). The surveys spanned the time period from the Cetacean and Turtle Assessment Program, begun in 1978 (Shoop and Kenney 1992) to the 2004 NOAA Northeast Fisheries Science Center shipboard and aerial surveys (Read *et al.* 2007).

Independent Analyses

All of the spatial tests suggested that the humpback whale sightings and the survey effort were not random, but exhibited clustered spatial patterns. The Indices of Dispersion were much greater than the upper critical values of the chi-square test statistic, thus rejecting the null hypotheses of complete spatial randomness ($P < 0.001$). The Indices of Cluster Size for the sightings and survey effort were much greater than 0, providing additional evidence for clustering in whale sightings and sampling effort.

The nearest neighbor calculations also rejected the hypothesis of complete spatial randomness and supported the conclusion of clustering in both the sightings and survey effort. The CDFs of the event–event nearest neighbor distances for the humpback whale sightings and the survey effort rose rapidly. In addition, upper and lower envelopes, representing the maximum and minimum values, respectively, of 99 random simulations, plotted below the whale sighting and sampling effort CDFs, indicating significant clustering. Using the Kolmogorov–Smirnov Test to compare the observed CDFs with CDFs for random point processes with the same intensity, the distributions were significantly different ($P < 0.001$). If the processes exhibited complete spatial randomness, the CDF of the point–event distances would be similar to the CDF of the event–event distances. However, the point–event distances were longer for both the humpback whale sightings and the survey effort.

Examining a broader range of distances than the nearest neighbor functions, the *L* function provided insight into spatial scales of relevance to the two processes. The *L* function for humpback whale sightings plotted above the upper limit of the simulation envelope at all distances, with peaks in intensity at approximately 600 km and 1,500 km. The *L* function for the survey effort also plotted above the upper limit of the simulation envelope at all distances, with a parabolic behavior over a distance of 2,000 km.

Analyses of the Two-Point Processes

Because both the humpback whale sightings and the survey effort exhibited clustered spatial patterns, it is necessary to examine the two processes together. Inasmuch as humpback whale sightings can only be found where survey effort has been conducted, the spatial distribution of survey effort might influence patterns detected in whale sightings.

Whale sightings were not random with respect to the distribution of the survey effort. The Cross *K* Function was at or above the upper envelope of random simulations until approximately 200 km (Fig. 2A). This indicates that the sightings and survey effort strongly interacted at that spatial scale. At greater distances, the function declined slightly but continued to follow the upper envelope, suggesting that the distribution of the humpback whale sightings was influenced by the distribution of the survey effort at all spatial scales.

Using the clustered spatial pattern of the survey effort as the baseline, the humpback whale sightings continued to exhibit a clustered spatial pattern. Examining the Ripley's *K* Test Statistic, the sightings (process one) clustered above and beyond the clustering seen in the survey effort (process two) at distances of 0–800 km and greater than 1,400 km (Fig. 2B). In addition, the survey effort (process two) clustered above and beyond the clustering seen in the sightings (process one) at distances of 800–1,400 km. The significance of these patterns is shown by the extreme departure from randomness, with the peaks and troughs falling above and below, respectively, the envelope of maximum and minimum values of 99 random simulations. There were peaks in the degree of clustering of the sightings at distances of 300 km, 600 km, and 1,500 km. These peaks are approximately seven orders of magnitude larger than the maximum value obtained from 99 random simulations, indicated by the upper dashed line in Figure 2B. Given this extreme result, the peaks strongly indicate clustering of humpback whale sightings at these spatial scales.

To obtain a qualitative sense of what clustering at these spatial scales might indicate for the population structure of humpback whales, circles with radii of 300 km,

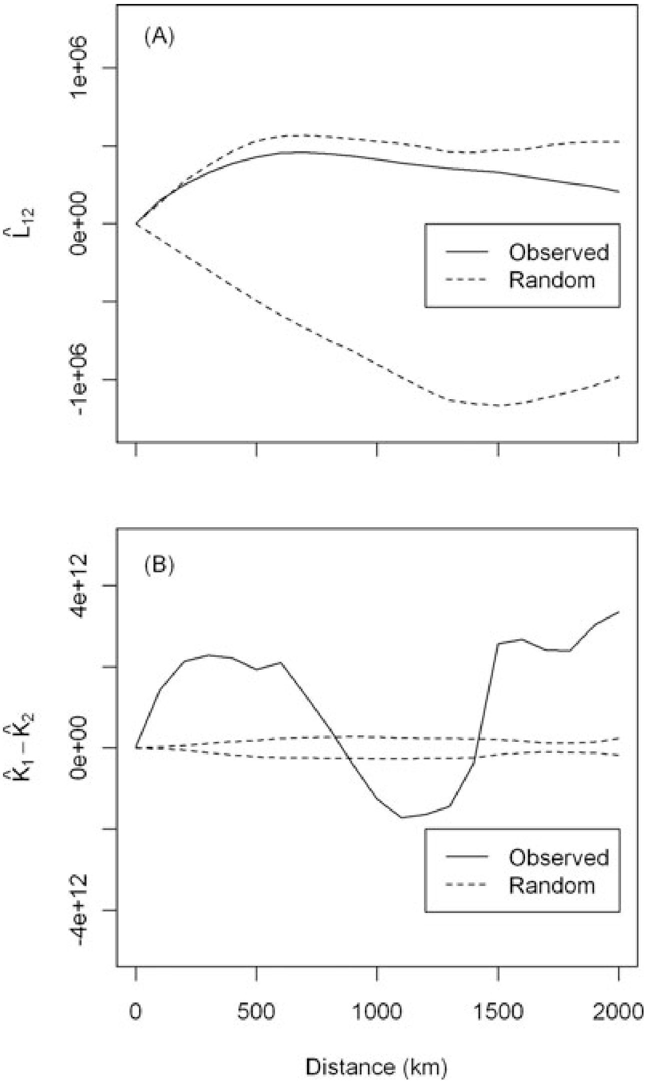

Figure 2. Analyses of two-point processes. (A) Cross *K* function. (B) Two-point process Ripley's *K* function.

600 km, and 1,500 km can be placed over regions where sightings were concentrated. When 600-km circles are placed over regions where sightings were concentrated, four distinct aggregations are discernible in the regions of the Gulf of Maine, eastern Canada, western Greenland, and Iceland (Fig. 3). Smaller 300-km circles correspond to concentrations of sightings within these broader aggregations. The broadest spatial scale of 1,500 km might suggest spatial separation between sightings in the western and eastern North Atlantic.

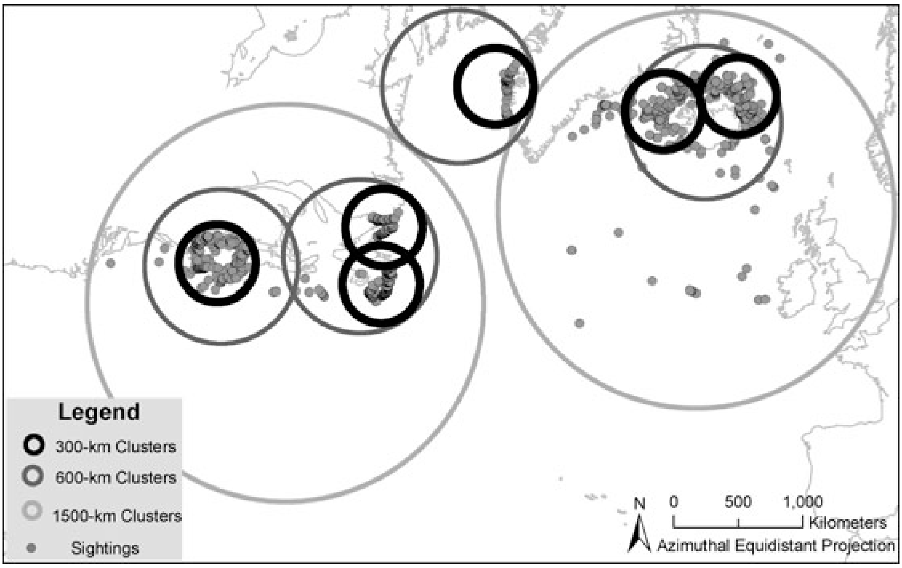

Figure 3. 300-km, 600-km, and 1,500-km clusters of summer humpback whale sightings.

DISCUSSION

The population structure of humpback whales has been examined using a variety of methods including mark–recapture techniques (Smith *et al.* 1999, Clapham *et al.* 2003), analysis of photographs of individually distinct animals (Stevick *et al.* 1999, Jann *et al.* 2003, Larsen and Hammond 2004), genetic analyses (Palsbøll *et al.* 1995, Larsen *et al.* 1996), and commercial whaling catches (Reeves *et al.* 2001, 2002*a*; Reeves and Smith 2002). The locations of commercial whaling catches provide historical insight into the occurrence and distribution of marine mammals, possibly indicating important regions of consistent aggregations of animals (Reeves *et al.* 2002*b*). Genetic analyses indicate the degree of mixing between individuals from specific regions, though often at longer temporal scales than mark–recapture and photo-identification methods. Mark–recapture and photo-identification techniques provide direct evidence of individual animal movements at multiple temporal scales, from daily to seasonal to interannual periods. This evidence results in the knowledge of site fidelity to given regions and exchange rates among broad-scale areas, providing direct insight into population structure.

Our study takes an innovative approach by using spatial statistics to describe the geographic distribution of summer sightings of humpback whales compiled over several decades. Spatial statistics quantitatively identify the spatial pattern by defining the spatial scale and extent of significant aggregations. Because our analyses covered the time period from the late 1970s through the mid-2000s, the results indicate consistent clusters of humpback whales, providing insight into the spatial extent of feeding aggregations in the North Atlantic Ocean. Coupled with previous knowledge from mark–recapture, photo-identification, and genetic analyses, insights into the underlying ecological processes, such as population structure, can be obtained. Humpback whales provide a unique opportunity for cross-correlating multiple lines of evidence for stock structuring across an ocean basin. The fact that all lines of evidence converge on a similar structure demonstrates that spatial analyses provide a valuable tool, which would be useful on populations where photo-identification is difficult or impossible and where biopsy sampling is not possible (*i.e.*, aerial surveys or historical data).

Our results suggest that humpback whales and survey effort are clustered within the high latitudes of the North Atlantic Ocean during the summer. These results are consistent with previous findings. Since the 1600s, humpback whales have been the target of whaling operations in the North Atlantic due to their predictable seasonal availability (Reeves and Smith 2002, Reeves *et al.* 2002*a*). Humpback whales tend to congregate near bathymetric features that appear to be associated with high concentrations of their preferred prey, such as sand lance (*Ammodytes* spp.), Atlantic herring (*Clupea harengus*), capelin (*Mallotus villosus*), and euphausiids (*Thysanoessa inermis* and *Meganyctiphanes norvegica*) (Hjort and Ruud 1929; Ingebrigtsen 1929; Brodie *et al.* 1978; Hain *et al.* 1982; Payne *et al.* 1986, 1990; Sigurjónsson and Gunnlaugsson 1990; Christensen *et al.* 1992). High prey regions are often located close to shore in shallow water, making these areas easily accessible to whalers (Reeves and Smith 2002).

In addition, the location of these clusters has been used to design surveys of humpback whales. Sampling effort targeting the humpback whale typically consists of photo-identification studies that occur in regions where whales are expected (Punt *et al.* 2006). In order to obtain a statistically significant number of photographs and to meet sampling requirements to equally photograph all age and sex components of the population, appropriately designed photo-identification surveys require a fundamental understanding of the distribution of the species. For example, for the Years of the North Atlantic Humpback project, summer photo-identification sampling occurred in regions that had been identified in previous studies to contain significant concentrations of humpback whales (Smith *et al.* 1999). The *a priori* knowledge of areas where animals aggregate produced adequate sample sizes for mark–recapture analyses.

Given that the effort of surveys used in our study was clustered, the distribution of the humpback whale sightings needed to be examined within the context of the clustered distribution of the effort. The spatial patterns of sightings and survey effort were found to interact at all scales, with strong interactions at distances of up to 200 km (Fig. 2A). As expected, the sightings and the survey effort were not independent; one can only have sightings in regions where survey effort has occurred and the surveys were designed to occur in regions where humpback whales were believed to congregate. Because of this co-dependence, the distribution of the sightings needed to be considered within the underlying spatial pattern of the survey effort.

This study shows that there are two spatial scales important to the distribution of humpback whales in the North Atlantic Ocean. The sightings clustered above and beyond the clustering in the effort at spatial scales <800 km and >1,400 km (Fig. 2B). There were peaks in the degree of clustering of the sightings at 300 km, 600 km, and 1,500 km. Circles with radii of 300 km, 600 km, and 1,500 km placed over the visible concentrations of sightings indicate statistically significant groupings (Fig. 3) and suggest four clusters of humpback whales in the North Atlantic: the Gulf of Maine, eastern Canada, western Greenland, and Iceland. Furthermore, whales in the western and eastern North Atlantic appear to be distinct.

The spatial patterns resulting from our analyses are similar to the International Whaling Commission (IWC) assessment model that defines five feeding grounds, which it identifies as sub-stocks and recommends as the appropriate management unit in the North Atlantic (International Whaling Commission 2002*a*). To reconcile historical data with current abundance estimates within this population structure, a sophisticated spatially-explicit, age- and sex-structured population dynamics model was developed (Punt *et al.* 2006). It attempted to model each feeding ground–breeding ground combination as a stock. The data did not fit the model well, indicating the possibility of a third, as yet unidentified, breeding ground or significant, long-term shifts in distribution on the feeding grounds. A full understanding of the population structure of humpback whales in the North Atlantic has yet to be obtained.

The population structure of humpback whales in the North Atlantic has been the subject of extensive scientific research (International Whaling Commission 2002*a*). While several population models have been suggested, none capture the complexity of the available data. Genetic studies have found distinctions between the nuclear DNA of the western North Atlantic (Gulf of Maine, Gulf of St. Lawrence, and west Greenland) and Iceland (Valsecchi *et al.* 1997) and among the mitochondrial DNA of whales on the different feeding grounds (Palsbøll *et al.* 1995, Larsen *et al.* 1996). Managers believe that maternally-directed site fidelity, as seen in photo-identification data, occurs on a timescale sufficient to consider individual feeding grounds as distinct populations (Clapham *et al.* 2003). Photo-identification data document the exchange of individuals between regions. Stevick *et al.* (2006), examining the distances between resightings of individually recognized animals on the feeding grounds, could not distinguish between the two eastern North Atlantic feeding grounds of Iceland and Norway, and therefore defined four feeding grounds. The authors also found spatial structuring between sub-regions on the feeding grounds separated by as little as 10 km (Stevick *et al.* 2006). Only with additional data collection can these inconsistencies be resolved.

Similar studies in other ocean basins demonstrate the complexity of humpback whale population structure (International Whaling Commission 2002*b*). In the North Pacific, photo-identification studies have shown a high rate of resightings in the same feeding ground in different years and a low rate of interchange among different feeding grounds (Calambokidis *et al.* 2001). Only four of the 709 whales seen more than once were found to have traveled to different feeding areas, whereas eight whales traveled between different wintering grounds. Unfortunately, migrations between wintering and feeding grounds did not follow a distinct pattern, though high match rates were found between Mexico and California, and between Hawaii and southeastern Alaska. With these conflicting data, the population structure in the North Pacific is not known (International Whaling Commission 2002*b*).

Understanding the population structure in the Southern Hemisphere is complicated by limited data (Baker *et al.* 1998). Stocks were historically defined by gaps in distribution on the summer feeding grounds documented by commercial whaling fleets. Defined as Groups I through VI, longitudinal lines divided Antarctic waters into six broad regions that functioned as management units during the whaling period. Since the end of commercial whaling in 1966, few data have been collected to review or refine the historical population boundaries (Baker *et al.* 1998). However, given the lack of any distinct geographic features between the feeding grounds, the IWC currently finds it most useful to define populations in the Southern Hemisphere by the wintering grounds (International Whaling Commission 2002*b*, Olavarria *et al.* 2007). This also appears most appropriate when variations in the rate of population recovery after exploitation are considered (Baker *et al.* 1998).

The focus of our study was to determine spatial scales that are important to North Atlantic humpback whales. The results identified three spatial scales (300 km, 600 km, and 1,500 km) that appear to define boundaries for feeding aggregations, feeding sub-stocks, and breeding stocks, respectively. While these distances provide insight into the spatial extent of these population units, distinct boundary lines are not realistic (Cui *et al.* 2002). Exchanges among the feeding grounds have been documented, and as the ocean is an open, unconstrained environment, there are no absolute restrictions to animal movement. Any boundary simply represents a compromise between aberrant, broad-scale movements, and site fidelity to an individual ground. Therefore, the suggested spatial extents should be viewed as regions that minimize the proportion of intermingling among animals on the feeding grounds. The results also point to regions where additional genetic sampling might provide the most insight into population structure.

The results of this study also pose a series of interesting questions regarding efforts to define critical habitat and develop a consistent management plan for a species listed as endangered by the United States Endangered Species Act (16 U.S.C. 1531–1545), although classified as Least Concern internationally (IUCN 2008). In order for a species to persist, its requirements must be met at all spatial scales of the environment, from individual requirements at the local habitat level to population requirements within the landscape mosaic (Storch 1997). This study demonstrates that over decadal temporal scales in the North Atlantic Ocean, there are statistically significant patterns of use at three spatial extents—300 km, 600 km, and 1,500 km. There may be significant environmental features at these spatial extents that are influencing the observed clustering behavior, and may, in fact, drive the matrilineal site fidelity to the feeding grounds and ultimately the population structure (Palsbøll *et al.* 1995, Larsen *et al.* 1996). Studies at finer spatial and temporal resolutions provide insight into finer scale processes, such as foraging. Stevick *et al.* (2006), analyzing the distances between resightings in consecutive years on the feeding grounds, found limited exchange between sub-regions separated by as little as 10 km. In addition, it is believed that humpback whales off Norway shift the center of their concentration on an annual basis. Work is ongoing to understand the finer scale environmental processes that might be contributing to these shifts. Through detailed studies of the spatial patterns seen in humpback whales, an understanding of the significant environmental components for this species can be realized.

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