MARINE MAMMAL SCIENCE, 15(1):1–32 (January 1999)

AN OCEAN-BASIN-WIDE MARK-RECAPTURE STUDY OF THE NORTH ATLANTIC HUMPBACK WHALE (*MEGAPTERA NOVAEANGLIAE*)

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ABSTRACT

Although much is known about the humpback whale, *Megaptera novaeangliae,* regional studies have been unable to answer several questions that are central to the conservation and management of this endangered species. To resolve uncertainties about population size, as well as the spatial and genetic structure of the humpback whale population in the North Atlantic, we conducted a two-year ocean-basin-wide photographic and biopsy study in 1992–1993. Photographic and skin-biopsy sampling was conducted of animals in feeding and breeding areas throughout most of the range of this species in the North Atlantic, from the West Indies breeding grounds through all known feeding areas as far north as arctic Norway. A standardized sampling protocol was designed to maximize sample sizes while attempting to ensure equal probability of sampling, so that estimates of abundance would be as accurate and as precise as possible. During 666 d at sea aboard 28 vessels, 4,207 tail fluke photographs and 2,326 skin biopsies were collected. Molecular analyses of all biopsies included determination of sex, genotype using six microsatellite loci, and mitochondrial control region sequence. The photographs and microsatellite loci were used to identify 2,998 and 2,015 individual whales, respectively.

Previously published results from this study have addressed spatial distribution, migration, and genetic relationships. Here, we present new estimates of total abundance in this ocean using photographic data, as well as overall and sex-specific estimates using biopsy data. We identify several potential sampling biases using only breeding-area samples and report a consistent mark-recapture estimate of oceanwide abundance derived from photographic identification, using both breeding and feeding-area data, of 10,600 (95% confidence interval 9,300–12,100). We also report a comparable, but less

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precise, biopsy-based estimate of 10,400 (95% confidence interval of 8,000–13,600). These estimates are significantly larger and more precise than estimates made for the 1980s, potentially reflecting population growth. In contrast, significantly lower and less consistent estimates were obtained using between-feeding-area or between-breeding-area sampling. Reasons for the lower estimates using the results of sampling in the same areas in subsequent years are discussed. Overall, the results of this ocean-basin-wide study demonstrate that an oceanwide approach to population assessment of baleen whales is practicable and results in a more comprehensive understanding of population abundance and biology than can be gained from smaller-scale efforts.

Key words: *Megaptera novaeangliae,* individual recognition, photographic identification, genotypic identification, skin biopsy, abundance, genetic analysis, capture-recapture, sex ratio, migration, North Atlantic Ocean.

In the North Atlantic, the humpback whale (*Megaptera novaeangliae)* ranges from tropical waters north to the arctic pack ice. During winter, the majority of this population congregates to mate and calve in a small number of locations among the reefs and islands of the West Indies. Whales leave these breeding areas in spring and migrate to several high-latitude feeding areas, which they occupy during the months of summer and fall (Whitehead and Moore 1982, Katona and Beard 1990).

The principal breeding areas documented in recent times lie on offshore banks and off insular coasts on the Atlantic margins of the West Indies (Winn *et al.* 1975, Whitehead 1982, Whitehead and Moore 1982). The largest winter concentrations occur in the waters of the Dominican Republic, on Silver Bank, Navidad Bank, and in Samana Bay (Whitehead and Moore 1982; Mattila *et al.* 1989, 1994). Lower densities are found in Mona Passage, Puerto Rico, and on Virgin Bank (Mattila and Clapham 1989). Farther south along the Antillean arc through the Windward Islands, whales appear to occur sparsely today, despite the historical importance of this region as a whaling ground (Winn *et al.* 1975, Mitchell and Reeves 1983, Mattila *et al.* 1994). The West Indies wintering range appears to be characterized by a high turnover of individuals, and there is considerable interchange among areas (Mattila *et al.* 1989, Mattila and Clapham 1989, Katona and Beard 1990). The relationship of humpbacks wintering in the Windward Islands to those elsewhere in the West Indies is also not known. Humpback whales also occur in low numbers in winter months around the Cape Verde Islands in the eastern North Atlantic (Reiner *et al.* 1996). The relationship of the animals in that area to those wintering in the West Indies is not known. However, analysis of humpback song from the Cape Verde Islands and the West Indies suggests that exchange occurs between these two breeding grounds (Winn and Winn 1978).

Humpback whales are also known to remain in high latitudes in the North Atlantic during winter (Williamson 1961, CeTAP 1982, Swingle *et al.* 1993, Wiley *et al.* 1995, Ingebrigtsen 1929, Christensen *et al.* 1992). The proportion of the population that does not migrate to the West Indies breeding areas is unknown, although it has generally been thought to be small (Whitehead 1982).

North Atlantic humpback whales were intensively exploited in the 1800s and early 1900s, and the species was apparently reduced to low levels throughout this ocean (Braham 1984, Mitchell and Reeves 1983, Price 1985, Winn and Reichley 1985). Aboriginal whaling for humpbacks continued in West Greenland until 1985 but was stopped by the International Whaling Commission (IWC) in light of uncertainties regarding the abundance of animals in this area and their relationship to animals in other feeding areas (IWC 1986). Another small native fishery continues today on Bequia in the Windward Islands, with recent catch limits being two whales per year (IWC 1994). The humpback is listed as endangered by the Convention on International Trade in Endangered Flora and Fauna and as either endangered or vulnerable by various governments and international conservation organizations (Klinowska 1991).

Absolute abundance, abundance relative to pre-exploitation abundance, rates of change of abundance, and the relationship of animals using different feeding areas by humpback whales in the North Atlantic are all uncertain (Klinowska 1991). At a regional level, small-scale studies have suggested increasing population sizes in Iceland (Sigurjónsson and Gunnlaugsson 1990) and the Gulf of Maine (Barlow and Clapham 1997). The size of the present population has been variously estimated from photographic and sighting survey data. Mark-recapture estimates for the West Indies using photographic identification data include 2,000–6,000 animals (Whitehead 1982) and 5,505 (Katona and Beard 1990, 95% CI 2,888–8,122)). Estimates for specific feeding and breeding areas have also been given by Whitehead (1982), Balcomb and Nichols (1982), CeTAP (1982), Perkins *et al.* (1984), Katona and Beard (1990), and Christensen *et al.* (1992).

However, there remain several major issues that have not been adequately addressed by the various spatially restricted studies of the past. There is no recent estimate of abundance, and all past estimates are of uncertain reliability and representativeness because of limitations in both sampling methodology and spatial coverage (Hammond 1986). Behavioral differences that may affect the probabilities of individuals being sampled are not well understood. This is especially true in the breeding areas, where animals in different reproductive classes behave quite differently (Rice *et al.* 1987). The boundaries between, and the degree of, physical and genetic interchange among the northern feeding areas and among the various banks and bays within the West Indies are poorly known. Also, our understanding of the reproductive behavior and mating system is limited.

We attempted to overcome the limitations of previous work by designing and conducting a coordinated field study of the entire North Atlantic ocean basin using standardized field sampling and analysis protocols. The study, named Years of the North Atlantic Humpback (YoNAH), combined photo-identification and molecular genetic techniques and used standardized sampling protocols to collect as many photographs and skin biopsies as possible in four sampling periods over a period of two years. Four principal objectives of the study addressed key areas in which increased understanding of the

population biology is needed: (1) abundance in the feeding areas and in total, (2) population genetic structure, (3) rates of exchange among feeding areas, and (4) reproductive behavior and vital rates. Additionally, the study attempted to collect data that could be used to investigate other aspects of population biology and behavior, notably social organization, evolutionary history, and the mating system.

Some results of this study addressing a number of the above uncertainties have been presented, using either the YoNAH data alone (Stevick *et al.* 1988), or in combination with other sources of data (Larsen *et al.* 1996, Palsbøll *et al.* 1997). The suspected migration of whales from all the feeding areas, including Norway, to the West Indies (Katona and Beard 1990, Clapham *et al.* 1993) was confirmed using photographic data (Stevick *et al.* In 1988). Palsbøll *et al.* (1997) showed that this conclusion was consistent with the results of genetic tagging. Previously, Clapham *et al.* (1995) used data from YoNAH and other sources to establish that the sex ratio in the Gulf of Maine feeding area does not differ from parity. Palsbøll *et al.* (1997) extended this to demonstrate that the sex ratio for all feeding grounds and for calves in the breeding areas was even, but that the sex ratio among non-calves in the breeding areas was male biased. Palsbøll *et al.* (1997) also showed that the genotype data provided by this study give further evidence that North Atlantic humpback whales exhibit strong fidelity to specific feeding areas, with limited interannual exchange among these areas. Larsen *et al.* (1996) confirmed Palsbøll *et al.*'s (1995) suggestion that this maternally directed site-specificity has persisted in some areas over an evolutionary time scale. In particular, haplotype frequencies are significantly different among Norway, Iceland, and the western North Atlantic.

Here we present new data from the YoNAH study, focusing on estimating oceanwide abundance. We use photographic and biopsy sampling data from both the feeding and breeding areas, evaluate the consistency of sampling in the breeding areas, and compare the consistency of estimates made using various combinations of those data sets.

Methods

Photographic and biopsy samples were collected in 1992 and 1993 from animals in the West Indies breeding range and in the five principal high-latitude feeding areas: the Gulf of Maine, eastern Canada, West Greenland, Iceland, and Norway. Sampling was organized by individuals based at institutions with extensive research experience in each area, in cooperation with other regional organizations. Of the four main study objectives, greater emphasis was given to evaluating population structure and estimating abundance, using photographic identification and molecular analyses of skin biopsies. Sampling was conducted during summer in all feeding areas known from previous studies to contain significant concentrations of humpback whales, and during winter in four of the most important West Indies breeding areas. Sampling was not attempted in the Cape Verde Islands or in the Windward Islands

because we judged that the apparently low numbers would preclude adequate sample sizes for mark-recapture studies.

The replicate samples in the two years allowed all objectives to be addressed, and also permitted calculation of multiple oceanwide abundance estimates. Previous studies had suggested the potential for differences in sampling probabilities among animals in different behavior classes in the breeding areas. For example, sampling could be biased if females with and without calves in consecutive years had different sampling probabilities. We classified animals by behavior class to investigate such potential biases.

Target numbers of individual whales to be photographed were selected to balance the goal of precisely estimating abundance with logistical constraints. Based on the precision and reliability of previously published abundance estimates, and using additional unpublished data, likely ranges of abundance in each area were used to determine sample sizes required to give two-sample Petersen estimates with various levels of precision as measured by the coefficient of variation (CV). Annual target sample sizes of 1,000 and 900 individual whales were established for breeding and feeding areas, respectively, to allow an oceanwide estimate of abundance with a CV of roughly 10%. Annual target sample sizes for the feeding areas were distributed as follows: Gulf of Maine 200, Eastern Canada 350, West Greenland 125, Iceland 125, and Norway 100. These targets reflected expected differences in abundance but in some cases were constrained by logistical limitations.

Skin biopsies were collected for molecular studies. The objectives of the molecular analyses were to obtain insight into population structure, social organization, mating strategies, and phylogeographic patterns. Because the molecular techniques available when the study was planned (1989) were not suitable for large-scale genotypic identification of individuals, no target sample sizes were set.

Field Methods

A standardized sampling protocol for finding aggregations of whales, selecting individual or associated groups of whales from aggregations, and ending sampling after a certain time, was designed based upon previous field experience. The protocol attempted to maximize sample sizes while ensuring equal probabilities of sampling so that estimates of abundance would be as accurate and as precise as possible. Particular attention was given to minimizing the effects of variability in fluking rates and, in the breeding areas, the availability for sampling of animals in different behavioral classes.

To minimize geographic heterogeneity in sampling probabilities, searches for aggregations of whales were primarily conducted using larger vessels (14–35 m) traversing along zigzag paths in known areas of aggregation in the Gulf of Maine and off West Greenland, Iceland, and Norway. Searching began at randomly selected points to ensure that all whales present would have the same probability of being sampled. In Canada, whales occur primarily (although not exclusively) in nearshore coastal waters, and sampling was con-

ducted from small boats working systematically along the shore. In some areas in the Gulf of Maine and in the Gulf of St. Lawrence, sampling was conducted from fixed locations where consistent aggregations occurred.

In the breeding areas, sampling along transects was impractical due to the presence of coral heads and exposure to trade winds. Instead, sampling was conducted using small outboard-powered inflatable boats working from the shore and from anchored mother ships, primarily in the lee areas. The high turnover of whales reported within and among areas (Katona and Beard 1990) implied that a representative sample could be obtained. The more exposed areas on Silver Bank, in Samana Bay, and in Mona Passage were searched when weather conditions allowed. Navidad Bank, in contrast, provided no protection from trade wind swells, and consequently sampling was conducted only under the most favorable conditions. The latter area was sampled using a 14-m sailboat under power, in tandem with a 5-m inflatable boat.

When an aggregation of whales was encountered, contact was made with the closest whale or group of whales, and an attempt was made to obtain photographs from all individuals in that group. Sampling was terminated when all individuals in a group had been photographed, or after 45 min had elapsed, or after 10 terminal dives (*i.e.,* the last dive in a sequence that was followed by a submergence of greater than one minute) had been observed, whichever came first. The vessel moved through the aggregation in a systematic way, attempting to minimize the resightings of sampled individuals.

In the breeding areas, consideration was also given to the differential behavior of whales. Sighted groups of animals and individual animals within groups were classified into behavioral classes based on group size and composition as well as on typical behavior (Tyack and Whitehead 1983, Clapham *et al.* 1992). Sampling crews in the inflatable boats moved from one group of whales to the next closest group, making an effort not to oversample animals in any one behavioral class, thereby distributing sampling among the behavior classes so that the effects of behavioral heterogeneity might be evaluated.

In the breeding areas and the Gulf of Maine feeding area, behavioral data were collected to assess the magnitude of heterogeneity in the probability of sighting whales and of sampling whales once approached. Data collected for at least one whale in each encountered group included the duration of the initial observed dive and the total number of dives made with and without fluking. The number of times an active behavior (defined here as breaches, lobtails, flipper slapping, and tail breaches) was observed was also recorded for all animals approached.

In the first year, biopsies were generally collected only after fluke photographs were obtained, out of concern that biopsying might reduce the probability of obtaining a photograph. After analysis of the effect of biopsying on fluking rates, this requirement was relaxed in the second year. In addition, higher priority was given to biopsying of individuals believed to play key reproductive roles, including mothers and, in competitive groups, nuclear animals, principal escorts, and challengers. Calves were given higher priority to allow for analysis of calf mortality.

Photographs of the ventral side of the flukes were taken with 35-mm cameras equipped with power winders, 70–210-mm or 300-mm lenses, ISO 400 black-and-white print film, and (usually) recording databacks. Biopsies were collected using a 40-mm long bolt with an 8-mm diameter hollow stainless steel tip that penetrated up to 35 mm. The bolt had a molded float and the tip had three internal barbs. The bolt was fired from a 68-kg draw weight crossbow after sterilization of the tip by immersion in 70% ethanol. Biopsies were conserved either in liquid nitrogen or in saturated NaCl with 20% DMSO (Amos and Hoelzel 1991). In some areas, the blubber was separated from the skin and stored in aluminum foil cleaned with analytical-grade acetone separately at 0°C.

In the Gulf of Maine, the Gulf of St. Lawrence, and West Greenland (where many well-known animals would be individually recognized in the field) biopsies were not collected from animals known to have been biopsied at any time in the past. This reduced the likelihood of some animals being included in the sample in the first year, especially in the Gulf of Maine where the population had been intensively studied, and the likelihood that animals biopsied in the first year would be biopsied in the second. This could potentially bias abundance estimates upward.

Data on all aspects of the field protocol were recorded, but with regional variations. In all feeding areas except portions of eastern Canada, details were recorded on the timing and location of searching effort, including date, time, geographic position, vessel speed, and visibility. In the breeding areas, the same, relatively confined, areas were searched each day, making this level of detailed location data unnecessary. In the Gulf of St. Lawrence and at the mouth of the Strait of Belle Isle, a similar procedure was used, surveying a limited area each day, and effort data were not recorded. In all regions, details on the groups and aggregations of whales encountered and of the individuals sampled were recorded.

Laboratory Methods

Initial processing of all photographs was completed by the individuals organizing the field work in each area. Film was developed and contact prints made. Initial analyses included verifying information taken in field notes, isolating and enlarging photographs of individuals, and assigning a temporary identification number to each whale sampled. Enlargements were used to identify individuals observed on more than one occasion within a sampling season in each region. The best fluke photographs from each day that a whale was sampled were forwarded to the laboratory conducting the photographic analysis.

All photographs received by the photographic analysis laboratory were compared manually using a modification of procedures developed previously for the North Atlantic Humpback Whale Catalog (Katona *et al.* 1979, Katona and Beard 1990). All submitted photographs were judged for overall acceptability, and those without a minimum photographic quality were excluded.

The quality of all acceptable photographs was evaluated by an experienced technician. Those judged to represent only the left or right side of the flukes were categorized as "left" or "right," and those judged to show less than 20% of the fluke area were categorized as "partial." All acceptable photographs were also evaluated for overall quality, considering specifically contrast, clarity, and angle to the flukes. Those where overall quality was judged to potentially affect the ability to reidentify the individual were classified as "poor."

All acceptable photographs were compared, in the sequence received, to all previously processed photographs by research assistants selected for patience and skill in pattern recognition. When a new photograph did not match any previously identified whale, it was compared a second time to photographs from the same sampling area. When a photograph was recognized as being of a previously identified individual, the match was confirmed by the photographic laboratory manager, and the appropriate identification number assigned. Otherwise, the whale represented in a photograph was assigned a new identification number and included in all future comparison of incoming photographs. These whales were assumed to be different from all previously identified animals and thus unique in the data set.

Skin and blubber from each biopsy were forwarded to the molecular analysis laboratory for processing, molecular analysis, and archiving. Total cell DNA was extracted from a portion of the skin using standard protocols (Maniatis *et al.* 1982). Three laboratory analyses of the extracted DNA were performed on nearly all biopsies. Sex was determined using the methods described by Palsbøll *et al.* (1992) and Berubé and Palsbøll (1996*a, b*). The sequence of the first 287 or 288 base pairs at the 5' end of the mt control region was determined for all samples by direct sequencing (Saiki *et al.* 1988). Symmetric double-stranded and subsequent asymmetric amplifications of the control region were performed as described in Palsbøll *et al.* (1995). Although not anticipated to be possible when the study was planned, genotype was determined on all samples using one trimer and five tetramer microsatellite loci, using methods described by Palsbøll *et al.* (1998). For all loci, amplification products were electrophoresed through a standard 5% denaturing polyacrylamide gel and visualized by autoradiography.

Data Management and Statistical Analysis

All of the searching effort, sighting, photographic, molecular, and behavioral data from the field sampling were entered into a relational database using commercial software. The data were examined for inconsistencies and other errors and edited to ensure that the data from the different field-sampling programs were consistent. Maps of the locations of sampling effort and groups of animals encountered were used to evaluate the spatial and temporal coverage of the sampling.

Estimates of abundance were calculated using individual identification data from the two breeding and two feeding area samples assuming a closed population. No attempt was made to correct estimates using within-year data for

mortality nor estimates using between-year data for mortality or recruitment. Estimates were calculated using Chapman's modification of Peterson's two-sample estimator (Seber 1982),

$$X_{A,B} = \{(S_A + 1)(S_B + 1)/(M + 1)\} - 1 \quad (1)$$

where S_A and S_B denote the number of individual whales sampled in each of the two sampling periods A and B, and M denotes the number of individual whales that were sampled in both periods. The variance of the estimates of abundance was estimated as (Seber 1982):

$$V(X) = \{(S_A + 1)(S_B + 1)\ (S_A - M)(S_B - M)\}/\{(M + 1)^2(M + 2)\} \quad (2)$$

Estimates from feeding area (F) data alone and breeding area (B) data alone formed one set of estimates. The four estimates combining breeding-area data in one sample with feeding-area data in the other formed another set. Two of these estimates used data collected in the same year and were denoted BF_{92} and BF_{93}. The two other estimates used data collected in different years and were denoted $BF_{92,93}$ and $BF_{93,92}$. Pairs of estimates using data collected in the same area and year are not statistically independent, but the covariance between them is insignificant (Modde *et al.* 1996). Thus, we assumed that they are independent and averaged estimates that were not significantly different to obtain a more precise estimate.

We computed confidence intervals assuming that the sampling distribution of the Peterson estimates were lognormal (Burnham *et al.* 1987). We tested differences between independent estimates by comparing the logarithms of the estimates using a Z-test, where the standard errors of the log transformed variables were computed as

$$SE(\log(X)) = \{\log(1 + CV^2(X))\}^{1/2} \quad (3)$$

Results

Sampling Effort and Sightings

Twenty-eight vessels were used for sampling on 666 vessel-days, during which 4,137 groups of whales were encountered. The areas sampled are depicted in Figure 1. Sampling was conducted from fixed platforms in the West Indies on northern Silver Bank, Navidad Bank, in Samana Bay, and off the west coast of Puerto Rico. The distribution of sampling effort in the feeding areas for 1992 and for 1993 is shown in Figures 2 and 3, respectively. The location of the aggregations of whales sampled in the feeding areas are shown for 1992 and 1993 in Figures 4 and 5, respectively.

Sampling was conducted in all feeding areas during 178 vessel-days from 15 June to 30 September in 1992 and during 158 vessel-days from 2 June to 27 September in 1993. Sampling occurred during somewhat different periods in the several feeding areas, but during similar periods within the same areas in the two years. Vessel-days at sea in 1993 were 50% greater in both Icelandic and Norwegian sampling than in 1992. Icelandic sampling in 1993 included

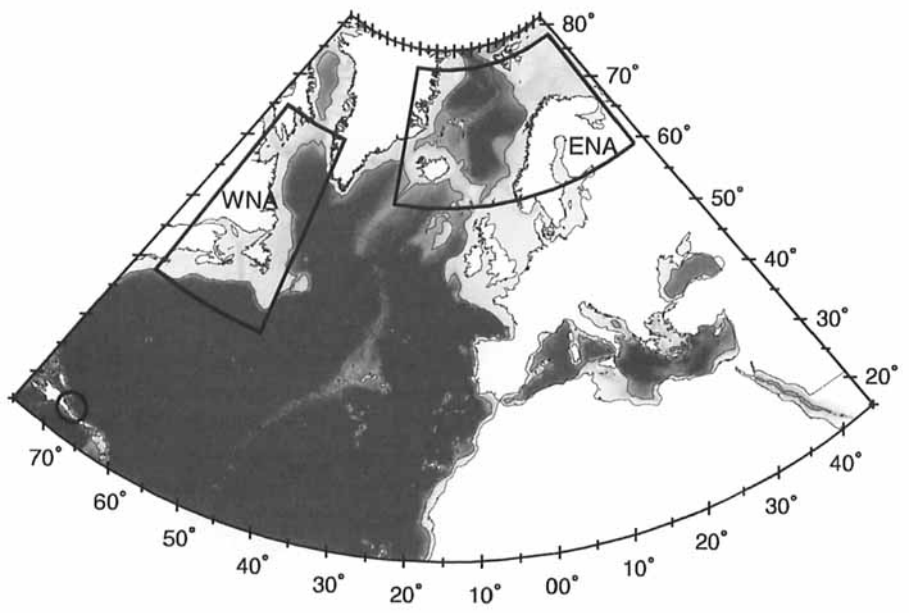

Figure 1. Reference map of North Atlantic Ocean outlining sampling regions. Sampling in four areas in West Indies breeding area is denoted by circle (see text for details). Western North Atlantic region (WNA) included feeding areas in Gulf of Maine, eastern Canada, and West Greenland. Eastern North Atlantic region (ENA) included feeding areas around Iceland and Norway (see Fig. 2–5). Coastlines and 1,000-m depth contours are overlaid on shaded depth using ETOPO5 5-min gridded elevation data (NOAA 1988). Depths deeper than 3,000 m rescaled to 3,000 m to enhance contrast at shallower depths.

the southeastern and eastern coasts of Iceland, as well as portions of the northern coast. Norwegian sampling in 1993 was expanded to include the central Norwegian Sea and the area south and west of Jan Mayen Island (71°N, 8°W), along the Polar Front. Sampling occurred in the breeding areas in nearly the same time period in the two years, from 15 January to 25 March in 1992, and from 19 January to 14 March in 1993.

Photography and Biopsy Sampling

Photographs and biopsies collected from whales on different days were considered sampling events. In 1992 and 1993, YoNAH collected photographs and biopsies during 4,207 and 2,326 such sampling events, respectively. From these sampling events, 2,998 and 2,015 unique individuals were identified by separately comparing the photographs and the genotypes.

For estimating abundance, we omitted photographs that included less than 20% of the fluke area, that included only the left or right side of the flukes, that had poor overall quality, or that were of calves sampled on the breeding areas. This left 3,623 photographic sampling events of non-calf whales; 1,707 in 1992 and 1,916 in 1993 (Table 1). These non-calf photographs represented

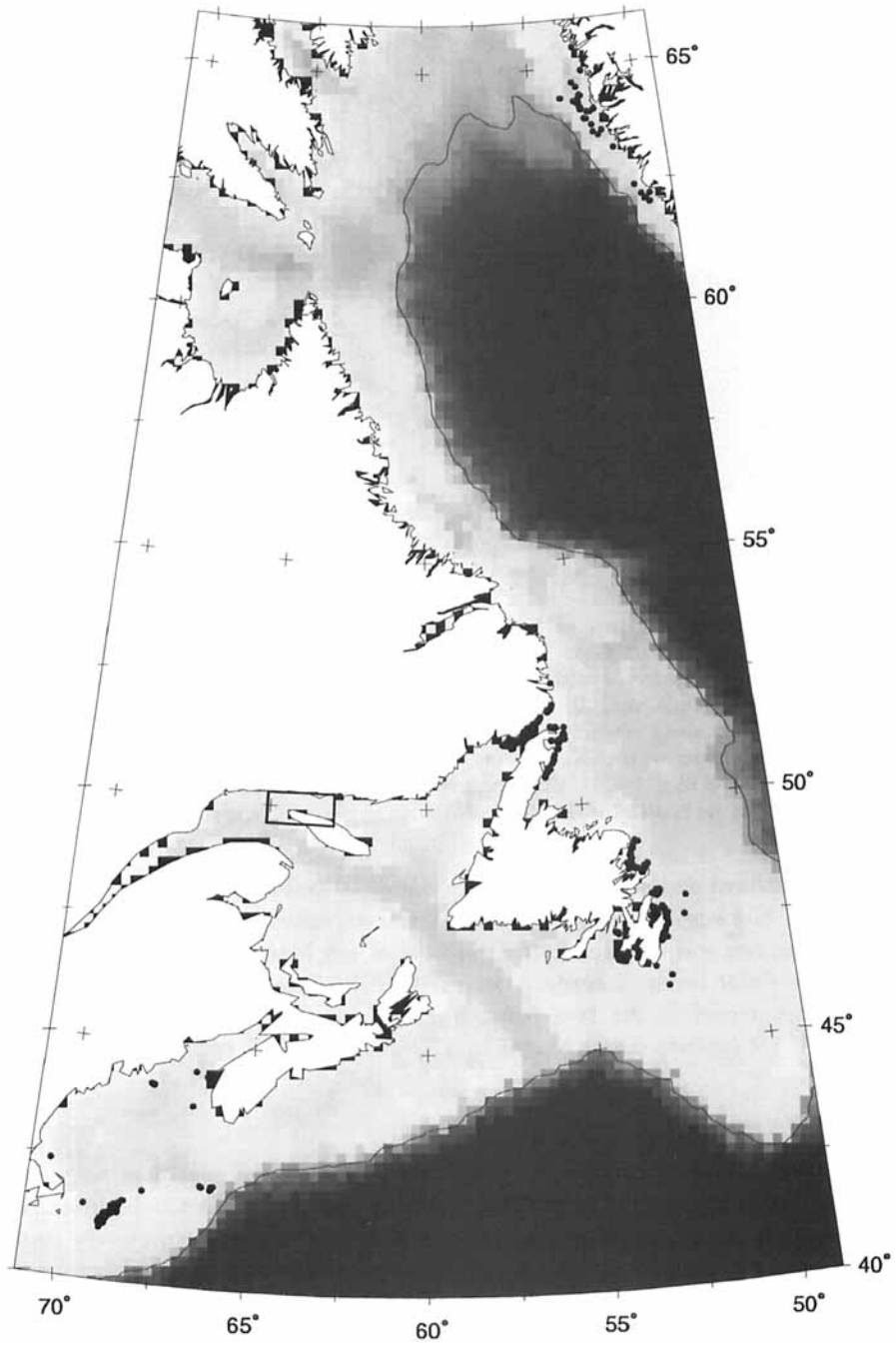

Figure 2. Noon positions of 1992 YoNAH sampling effort in feeding areas, showing lines connecting daily location of mobile sampling platforms. Data shown for western North Atlantic (WNA), where box depicts area where sampling was done but exact locations of sampling effort was not available, and for eastern North Atlantic (ENA).

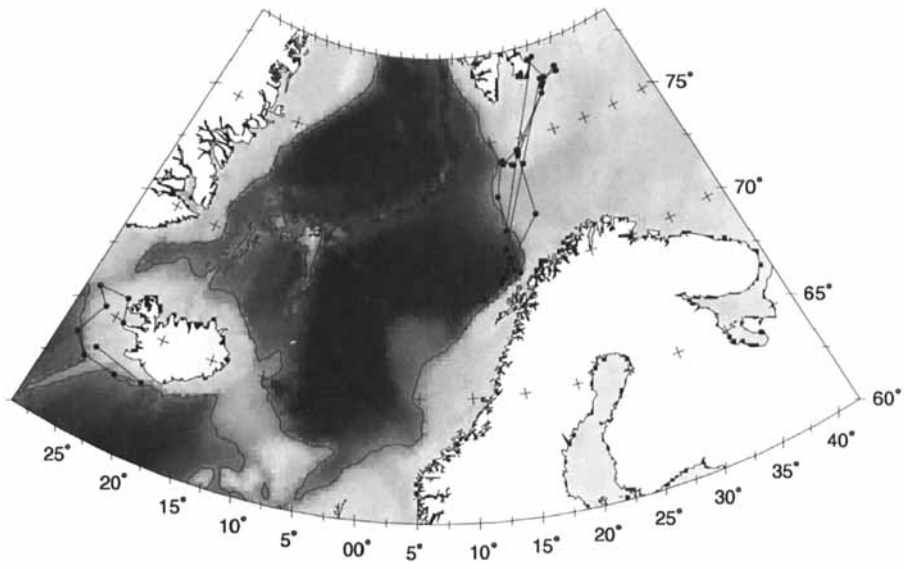

Figure 2. Continued.

1,377 and 1,467 individuals in 1992 and 1993, respectively, with 316 photographed in both years. Thus, 2,528 unique individuals were photographed overall.

Omitting biopsies of calves in the breeding areas (to be consistent with the photographic data) left 2,156 biopsies collected, 1,021 and 1,135 in 1992 and 1993, respectively (Table 1). The expected number of biopsies collected by chance from different animals with identical microsatellite loci was calculated at less than one (Palsbøll *et al.* 1997). Hence, we inferred that all samples with identical genotypes were collected from the same individual. These biopsies represented 933 and 1,049 individuals in 1992 and 1993, respectively, with 109 biopsied in both years. Thus 1,873 unique individuals were biopsied overall.

The numbers of males and females among 2,002 whales sampled in the breeding and feeding areas are given by area and year in Table 2. Significantly fewer females than males were sampled in the breeding areas in both years ($\chi^2(3) = 42.05$ and 38.19, $P = 0$, for 1992 and 1993, respectively, omitting the five biopsies from Puerto Rico to meet the assumptions of the test). Pooling the breeding area data over years, the sex ratios in the three areas tested were not significantly different from one another ($\chi^2(2) = 1.75$, $P = 0.42$). In the feeding areas, the numbers of males and females were not significantly different from parity in the two years over the five areas ($\chi^2(5) = 10.15$, $P = 0.07$, and 2.71, $P = 0.75$, for 1992 and 1993, respectively). Pooling the feeding ground data over areas and years results in a sex ratio of 0.51, with a standard error of 0.018.

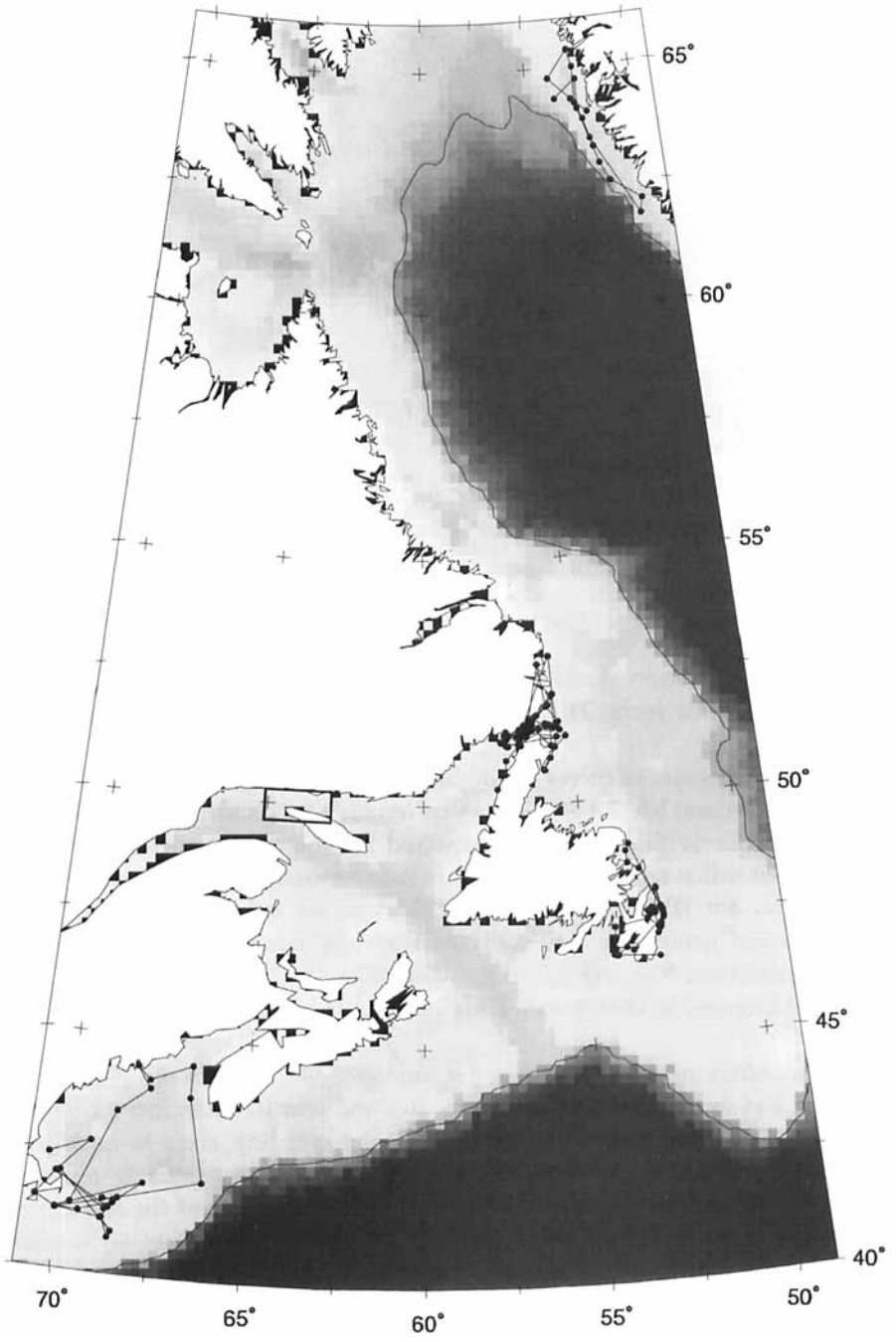

Figure 3. Noon positions of 1993 YoNAH sampling effort in feeding areas, showing lines connecting daily location of mobile sampling platforms. Data shown for western North Atlantic (WNA), where box depicts area where sampling was done but exact locations of sampling effort not available, and for eastern North Atlantic (ENA).

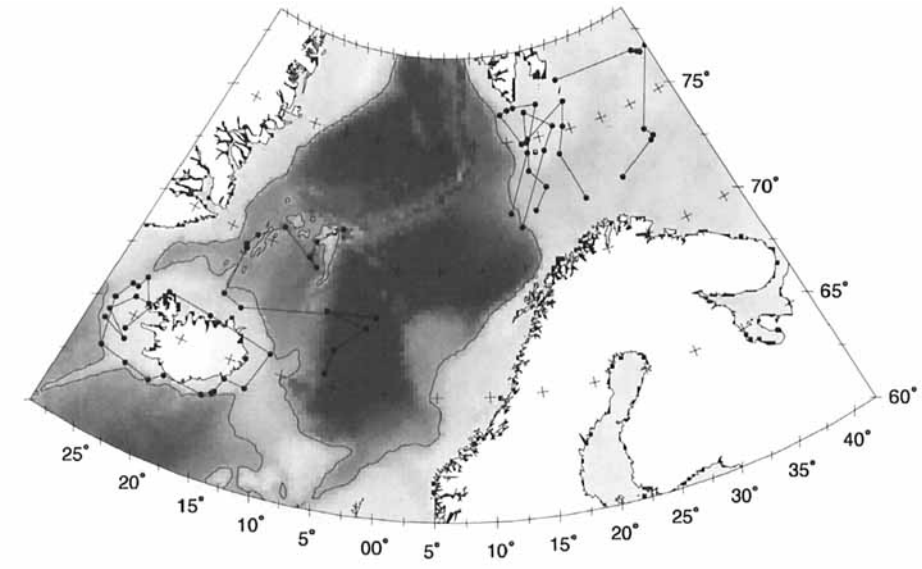

Figure 3. Continued.

Behavior Class in the Breeding Areas

Behavior class was established using the definitions in Table 3 for 2,021 groups of whales in the West Indies (Table 4). Pairs were the most frequently sighted group, with singletons and groups involving mothers roughly equally frequently sighted. Competitive groups were the next most frequently sighted. Because the likelihood of sighting varies with behavior, the proportions of groups sighted in each behavior class may not accurately represent the occurrence of each of these groupings of animals in the study area.

Individual behavior class was established for 4,795 whales (Table 5). The numbers of sighted animals photographed and biopsied were similar (1,797 and 1,569, respectively). The percentages of the animals sighted that were photographed varied more than did the percentage biopsied (6% to 89% and 10% to 55%, respectively) and were substantially different for photography and biopsy for most behavior classes. The percentage of the sighted animals that were photographed varied among the behavior classes in part because the likelihood of obtaining a suitable photograph was affected by varying length of dives and frequency of fluking dives by animals in different classes. The percentage of fluking dives varied among behavior class, from less than 4% for calves to more than 45% for singles and nuclear animals (Table 6). The percentages of the sighted animals photographically sampled were larger and less variable over behavior class than the percent of fluking dives, reflecting the requirement of the field protocol of working with groups until all animals were sampled, or until either 45 min or 10 terminal dives were observed.

Nonetheless, animals in the different behavior classes had a variable likelihood of being sampled. Mothers and calves, for example, were more likely

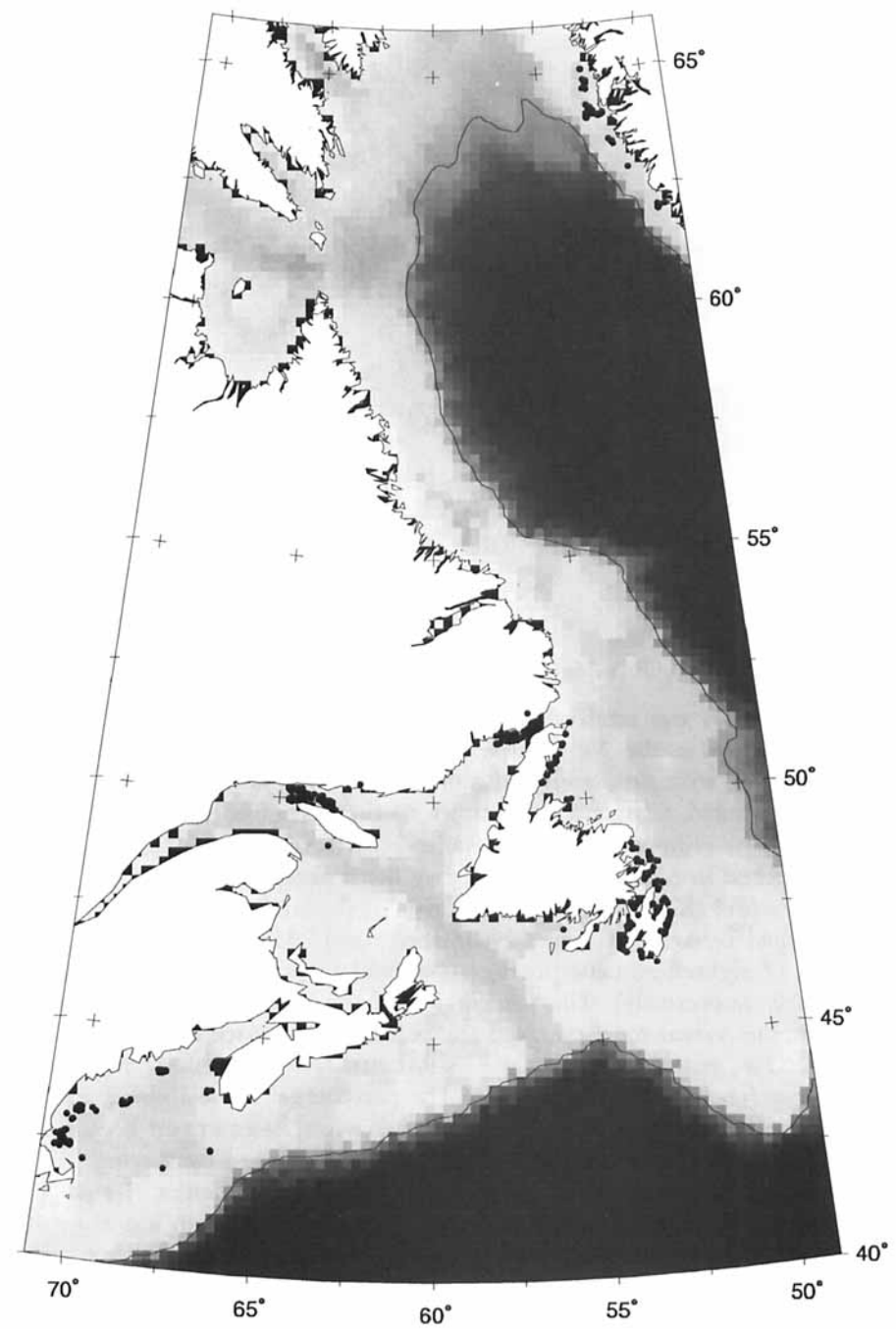

Figure 4. Location of aggregations of humpback whales sampled in 1992 YoNAH sampling effort in feeding areas. Data shown for western North Atlantic (WNA) and for eastern North Atlantic (ENA).

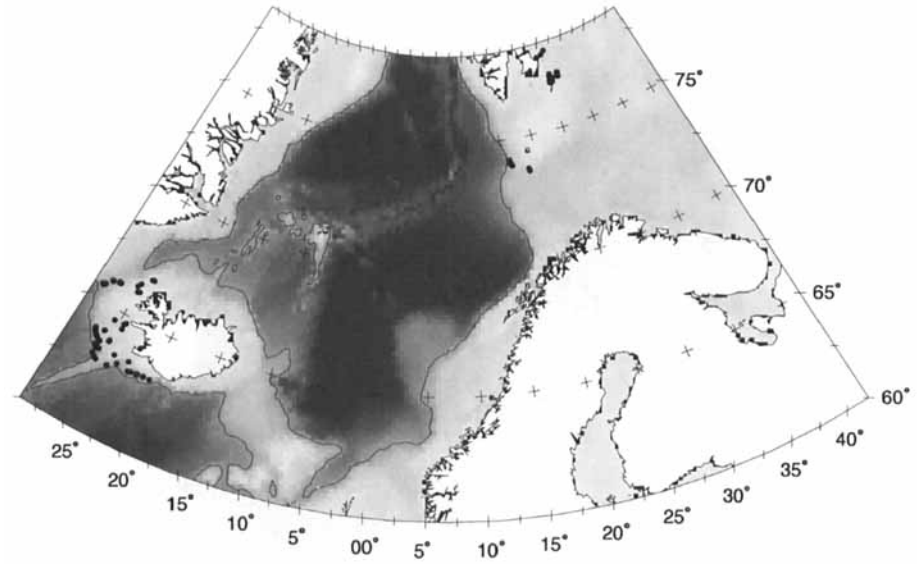

Figure 4. Continued.

to be biopsied than photographed, reflecting their infrequent fluking dives. Among animals in competitive groups, the frequency with which nuclear animals were photographed was higher than for principal escorts. In contrast, singles, pairs, trios, and quartets were less likely to be biopsied than photographed, probably reflecting their being harder to approach closely enough for biopsying. The percentages of nuclear animals, principal escorts, and challengers biopsied was greater than for secondary escorts and other animals, reflecting the planned focus on animals perceived to be in key reproductive roles.

Abundance Estimates

Assuming a closed population, application of the Petersen estimator to the photographic data yielded estimates of the oceanwide abundance of non-calf humpback whales (Table 7) that ranged from 3,600 to 12,400, with coefficients of variation from 0.05 to 0.15. The estimate using the two feeding-area samples was lowest ($F_{92,93}$ = 3,600) and had a low coefficient of variation. The estimate using the two breeding area samples ($B_{92,93}$ = 7,100) was significantly larger (Z = 4.99, P = 0), but much less precise.

The four estimates using both breeding and feeding area samples (BF) were larger still, ranging from 9,400 to 12,400, with coefficients of variation of 0.13–0.15. The differences among these four estimates were not significant at the 5% level, with the Z statistic for the largest of the six possible differences being 1.423. The probability of a more extreme value was 0.077, which is greater than the critical value accounting for the six simultaneous comparisons,

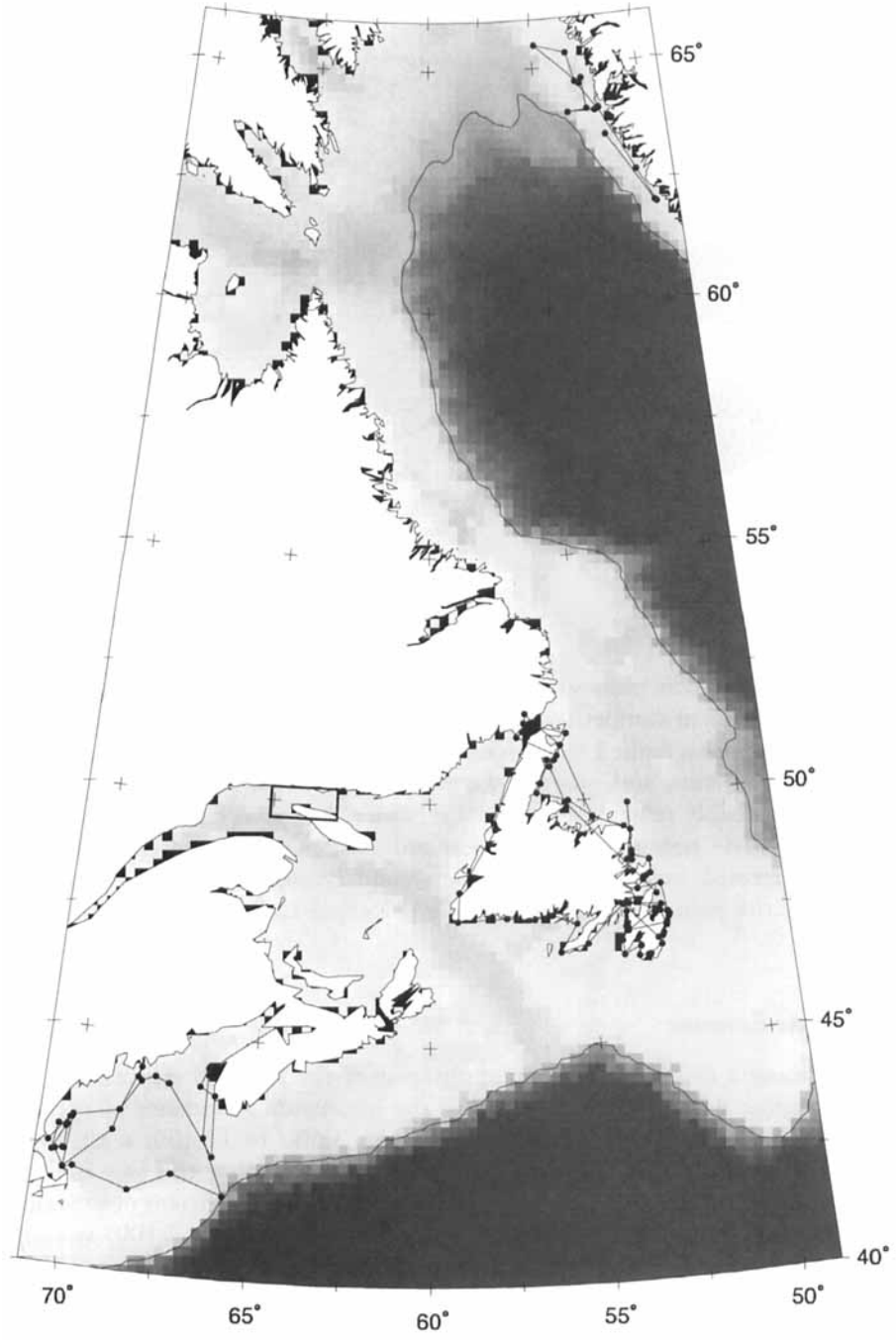

Figure 5. Location of aggregations of humpback whales sampled in 1993 YoNAH sampling effort in feeding areas. Data shown for western North Atlantic (WNA), where box depicts area where sampling done but exact positions of encountered whales not available, and for eastern North Atlantic (ENA).

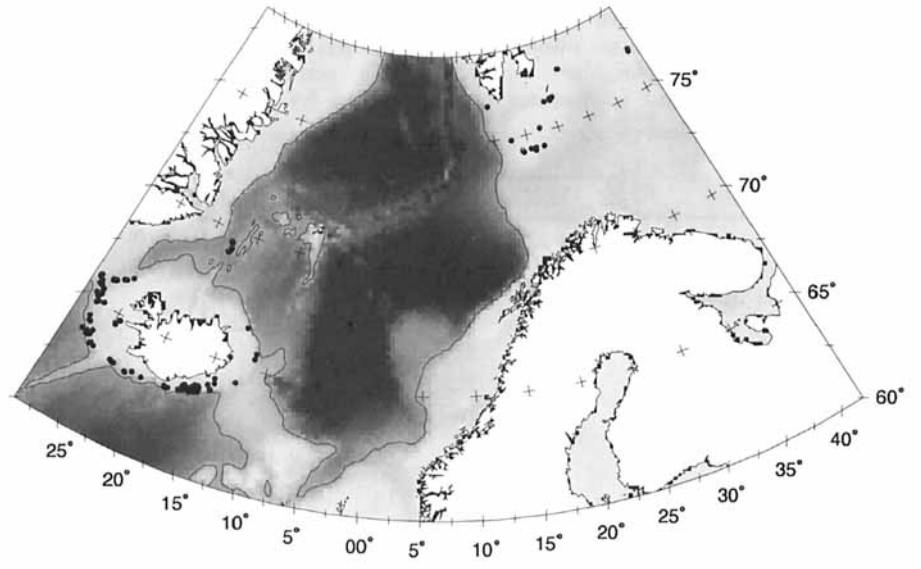

Figure 5. Continued.

Table 1. Numbers of photographs and biopsies collected by YoNAH, and number of unique individuals in those samples, by year and sampling region, and in total, omitting photographs of left or right side, covering less than 20% of fluke area, and with poor overall quality, and photographs and biopsies of individuals collected on same day and of calves. Numbers of unique individual animals sampled in breeding and feeding areas are less than or equal to sum of number of unique animals sampled in component regions because some individuals were sampled in more than one region within a year.

Sampling region	Photographic identification				Molecular identification			
	Photographs		Unique animals		Biopsies		Unique animals	
	1992	1993	1992	1993	1992	1993	1992	1993
				Breeding areas				
Silver Bank	525	479	488	453	554	587	511	557
Navidad Bank	65	16	65	16	12	25	12	25
Samana Bay	76	90	76	82	40	108	37	101
Puerto Rico	17	38	17	38	0	5	0	5
Total	683	623	629	582	606	725	555	684
				Feeding areas				
Gulf of Maine	204	118	152	108	106	68	97	68
Canada	593	922	439	593	211	245	202	224
W. Greenland	145	89	117	83	33	38	33	36
Iceland	44	111	44	105	44	36	44	33
Norway	38	53	36	49	21	23	21	23
Total	1,024	1,293	787	937	415	410	396	383
Overall	1,707	1,916	1,377	1,467	1,021	1,135	933	1,049

Table 2. Numbers of males and females determined molecularly from biopsies collected by YoNAH in each sampling region within breeding and feeding areas in 1992 and 1993, excluding calves. Sum of number of males and females differs slightly from totals in Table 1 because sex was not determined for a few biopsy samples.

Sampling region	1992		1993	
	Males	Females	Males	Females
	Breeding areas			
Silver Bank	323	183	337	217
Navidad Bank	9	3	18	7
Samana Bay	22	15	63	36
Puerto Rica	0	0	3	2
Total	351	199	418	261
	Feeding areas			
Gulf of Maine	48	49	35	31
Canada	115	86	101	122
W. Greenland	20	13	20	16
Iceland	23	20	16	16
Norway	5	14	12	11
Total	211	182	184	196

0.009 ($= 1 - (1 - 0.05)^{1/6}$). The inverse variance-weighted average of these four estimates was 10,600, with a coefficient of variation of 0.067 and a 95% confidence interval of 9,300–12,100. This average was significantly different from the breeding-breeding estimate ($Z = 2.82$, $P = 0.0024$).

Again assuming a closed population, genotypic estimates of humpback whale population size (Table 8) ranged from 5,100 to 16,400, with coefficients of variation ranging from 0.13 to 0.26. These estimates exhibited the same general patterns as the photography-based estimates. The estimate using data from the two feeding areas was the smallest, although higher than the corresponding photographic estimate. The breeding-breeding estimate was significantly larger than the feeding-feeding estimate ($Z = 2.18$, $P = 0.0145$).

Estimates using both the feeding and breeding area samples ranged from 9,700 to 16,400. The two between-area estimates using 1993 feeding area data ($BF_{92,93}$ and BF_{93}) were higher than the corresponding photography-based estimates. In contrast, the three genotypic estimates that did not use the 1993 feeding area sample ($B_{92,93}$, BF_{92}, and $BF_{93,92}$) were more similar to the corresponding photographic estimates. This was probably because animals recognized as having been previously biopsied were not biopsied again in some feeding areas. The genotypic estimates not using 1993 feeding area samples were 9,700 and 12,300, with coefficients of variation of 0.18 and 0.22, respectively (Table 8) and with an inverse variance weighted average of 10,400 with a coefficient of variation of 0.138 and a 95% confidence interval of 8,000–13,600. This average was significantly different from the average of the two biopsy breeding-feeding estimates using the 1993 feeding area data ($Z = 2.10$,

Table 3. Definition of behavior classes defined for groups of whales and for individual whales used during YoNAH sampling in the breeding areas.

Group class	Individual class	Definition of individual class
Singleton	Single	Whale observed alone, either not singing or singing behavior not checked.
	Singer	Long-diving whale whose continuous, stereotypical vocalizations corresponded with its dive pattern and were heard through the hull.
Pair	Member	Member.
Trio	Member	Member.
Quartet	Member	Member.
Mother-calf	Mother	Whale exhibiting close and continuous association with significantly smaller animal.
	Calf	Small whale consistently in close association with larger whale, often positioned above and slightly behind head of its partner.
Mother-yearling	Mother	See above.
	Yearling	Small whale which exhibited calf-like association with larger whale, but too large to have been born this year.
Mother-calf-escort	Mother	See above.
	Calf	See above.
	Escort	Whale which accompanied a mother and her calf.
Competitive group	Nuclear animal	Centrally placed animal in group of three or more animals displaying agonistic behavior.
	Principal escort	Animal most closely associated with nuclear animal.
	Challenger	Animal attempting to displace principal escort.
	Secondary escort	Member not nuclear animal, principal escort, or challenger.
	Undifferentiated	Role not determined.
Unknown	Unknown	Role not determined.

Table 4. Number of groups of humpback whales sighted during YoNAH sampling in breeding area in 1992, 1993, classified by group behavioral class, as defined in Table 3.

Group behavior class	Number sighted	Percent
Singleton	414	20.5
Pair	781	38.6
Mother-calf	138	6.8
Mother-calf-escort	244	12.1
Mother-yearling	8	0.4
Trio	71	3.5
Quartet	6	0.3
Competitive groups	212	10.5
Unknown	147	7.3
Total	2,021	100.0

$P = 0.018$), but not significantly different from the biopsy breeding-breeding estimate ($Z = 1.30$, $P = 0.096$).

Biopsy abundance estimates were also calculated for males and females separately (Table 9). The sum of the male and female estimates was similar to the corresponding unstratified estimates (Table 8), although the samples sizes in some cases were too small for reliability (Seber 1982). The only significant difference between the male and female estimates was between those from the breeding-breeding comparison (2,800 females *vs.* 5,100 males, $Z = 2.29$, $P = 0.011$). The sum of those two estimates (7,900) is similar to the unstratified estimate (8,100).

Discussion

The data gathered by the YoNAH study have resulted in substantially improved photography-based estimates of total population abundance (10,600, 95% confidence interval of 9,300–12,100). They also resulted in a comparable but less precise biopsy-based estimate (10,400, 95% confidence interval of 8,000–13,600) and corresponding sex-specific estimates. These estimates are substantially larger than estimates made in the 1980s (Katona and Beard 1990), perhaps reflecting population growth over the intervening years (Barlow and Clapham 1997).

These new estimates are substantially more reliable than those previously available for several reasons. First, the feeding areas were sampled more in proportion to abundance and included areas previously sampled only opportunistically. Second, the spatial and seasonal distribution of sampling was largely consistent in the two years. Third, the standardized sampling protocol resulted in a more representative sample. This occurred in two ways. The requirement to work with groups of animals until a photograph was obtained, or for a fixed period of time, resulted in photographs being collected from animals that were more difficult to approach or which fluked less frequently. Additionally, in the breeding areas the requirement to sample the next closest

Table 5. Numbers of sighted humpback whales during YoNAH that were photographed and biopsied in breeding areas in 1992, 1993, classified by individual behavioral class as defined in Table 3.

Individual behavior class	Number sighted	Photographed		Biopsied	
		Number	Percent	Number	Percent
Singer	43	23	53.5	18	41.9
Single	371	177	47.7	91	24.5
Pair	1,563	739	47.3	363	23.2
Mother	389	77	19.8	217	55.8
Calf	381	21	5.5	177	46.5
Yearling	9	8	88.9	5	55.6
Escort to mother	244	95	38.9	121	49.6
Trio	219	87	39.7	53	24.2
Quartet	24	11	45.8	4	16.7
Nuclear animal	212	135	63.7	104	49.1
Principal escort	255	79	31.0	141	55.3
Challenger	262	99	37.8	113	43.1
Secondary escort	295	100	33.9	109	36.9
Undifferentiated	381	82	21.5	37	9.7
Unknown	147	64	43.5	16	10.9

group of animals resulted in a lower proportion of the competitive group animals being sampled than during previous sampling efforts (*e.g.*, see Katona and Beard 1990). Finally, the estimates are more reliable because of the agreement in estimates based on two types of sampling with different potential sampling biases.

There are several aspects of the sampling that should be noted. The total number of individuals photographed in the feeding areas taken together was similar to the combined sampling targets for all feeding areas, although there were differences from the individual area targets, primarily related to logistics. The number of unique individuals photographed in the breeding areas was

Table 6. Number of dives observed for 2,536 animals, classified by individual behavior class (Table 3), and percentage of those dives where flukes were exposed.

Behavior class	Number of dives observed	Percent fluking exposed
Singer	106	34.9
Single	701	46.5
Pair	3,662	38.6
Mother	1,077	9.3
Calf	700	3.9
Nuclear animal	552	42.2
Principal escort	602	9.8
Challenger	293	24.9
Secondary escort	881	21.7

Table 7. Photography-based estimates of abundance of North Atlantic humpback whales older than calves, showing estimates (n) to nearest 100, standard errors (SE) to nearest 10, and coefficients of variation (CV), along with numbers of individual animals photographed in each sampling period (S_A and S_B) and in both periods (M), using Equations 1 and 2.

Estimators		n	SE	CV	S_A	S_B	M
		Within breeding or feeding areas					
Between	$F_{92,93}$	3,600	190	0.05	787	937	204
years	$B_{92,93}$	7,100	890	0.13	629	582	51
		Between breeding and feeding areas					
Within	BF_{92}	12,400	1,830	0.15	629	787	39
years	BF_{93}	10,300	1,300	0.13	582	937	52
Between	$BF_{92,93}$	12,100	1,590	0.13	629	937	43
years	$BF_{93,92}$	9,400	1,230	0.13	582	787	48

less than the sampling target, reflecting a substantially greater average time per whale sampled under the YoNAH sampling protocol than during earlier studies (Mattila *et al.* 1989, 1994).

There were differences in the numbers of animals sampled by photography and by biopsy in the two years. One difference was that more individual whales were photographed in the breeding areas than were biopsied in 1992, while the opposite was true in 1993. This probably reflected the change in the field protocol in 1993 of not requiring a fluke photograph before obtaining a biopsy. In contrast, in the feeding areas more photographs than biopsies were obtained in both years. This probably reflects the shorter time required to collect photographs in the feeding areas, which decreased the opportunity for biopsy collection. Also, the proportion of photographs collected that were from unique animals varied among the sampled areas, reflecting differences in sampling and in behavior of whales in the breeding and feeding areas (Table 1).

Table 8. Biopsy-based estimates of abundance of North Atlantic humpback whales older than calves, showing estimates (n) to nearest 100, standard errors (SE) to nearest 10, and coefficients of variation (CV), along with numbers of individual animals biopsied in each sampling period (S_A and S_B) and in both periods (M), using Equations 1 and 2.

Estimators		n	SE	CV	S_A	S_B	M
		Within breeding or feeding areas					
Between	$F_{92,93}$	5,100	840	0.17	396	383	29
years	$B_{92,93}$	8,100	1,080	0.13	555	684	46
		Between breeding and feeding areas					
Within	BF_{92}	12,300	2,700	0.22	555	396	17
years	BF_{93}	16,400	3,860	0.23	684	383	15
Between	$BF_{92,93}$	16,400	4,260	0.26	555	383	12
years	$BF_{93,92}$	9,700	1,700	0.18	684	396	27

Table 9. Biopsy-based estimates of abundance of North Atlantic humpback whales older than calves, stratified by sex and summed, showing estimates (n) to nearest 100, standard errors (SE) to nearest 10, and coefficients of variation (CV), along with numbers of individual animals biopsied in each sampling period (S_A and S_B) and in both periods (M) for which sex was reliably determined, using Equations 1 and 2.

Estimate	Sex	n	SE	CV	S_A	S_B	M
$F_{92,93}$	Males	2,200	450	0.21	211	184	17
	Females	3,000	780	0.26	182	196	11
	Sum	5,200	900	0.17			
$B_{92,93}$	Males	5,100	860	0.17	351	418	28
	Females	2,800	560	0.20	199	261	18
	Sum	7,900	1,030	0.13			
BF_{92}	Males	5,700	1,460	0.25	351	211	12
	Females	6,100	2,230	0.37	199	182	5
	Sum	11,800	2,670	0.23			
BF_{93}	Males	8,600	2,630	0.31	418	184	8
	Females	6,500	2,070	0.32	261	196	7
	Sum	15,100	3,350	0.22			
$BF_{92,93}$	Males	7,200	2,200	0.30	351	184	8
	Females	7,900	3,140	0.40	199	196	4
	Sum	15,100	3,830	0.25			
$BF_{93,92}$	Males	5,200	1,160	0.22	418	211	16
	Females	4,000	1,050	0.26	261	182	11
	Sum	9,200	1,560	0.17			

In Iceland and Norway, sampling vessels covered large areas, and almost every photographed animal was sampled only once. In West Greenland, Canada, and the Gulf of Maine, sampling vessels covered smaller areas, and a greater number of animals were resampled. Fixed point sampling as conducted in the Gulf of St. Lawrence produced the lowest proportions of unique animal photographs. In the breeding areas, in contrast, fixed point sampling produced proportions of unique animal photographs close to unity, reflecting the high turnover of animals in these regions as well as the greater number of animals present.

In the breeding areas, the proportions of biopsies from unique animals were similar to those for photographs (Table 1). In contrast, in the Gulf of Maine, Canada, and West Greenland, the proportions of unique animal biopsies were larger than the corresponding proportions of photographs. This difference reflected the tendency not to biopsy whales recognized as having been previously biopsied in these feeding areas.

There were consistent differences among estimates using different types of data. Although the photography and biopsy-based abundance estimates using feeding- and breeding-area samples were consistent, those using only feeding-area samples or only breeding-area samples were not. For example, both the genotypic and photographic estimates using only feeding-area data were significantly lower than those using only breeding-area data. The estimates based on data from only the breeding or only the feeding areas may suffer more

from sampling biases than do estimates based on data from both areas because whatever sampling biases existed were likely different in the two areas (Hammond 1986).

Estimates based on the two feeding-area samples were the lowest, possibly because the sampling was not proportional to abundance across the areas. To evaluate this explanation, we computed estimates for the individual feeding areas, combining Norway and Iceland because of the low number of recaptures. The sum of these estimates was roughly 6,000 whales, still substantially less than the feeding-breeding estimate, indicating that stratification at the feeding-area level does not entirely explain the low estimates. The apparent downward bias of the estimate could be due to the existence of a still-unknown feeding area that was not sampled. Alternately, it could be due to spatial heterogeneity in the probability of animals being sampled in known feeding areas, or heterogeneity in the probability of being sampled that was related to other individual animal characteristics. However, the cause of the downward bias is not simply related to differences between the sexes, because the estimates of male and female abundance were not significantly different.

Estimates based on the two breeding-area samples were also low, contrary to a concern with which we began the study, that these estimates could be biased upward by differential sampling probabilities of females with and without calves in consecutive years. The photographic estimate based on breeding-area data was significantly lower than the average of the breeding-feeding photographic estimates, although this was not true for the biopsy-based estimates. However, the breeding-breeding estimates of male and female abundance were significantly different, suggesting that the overall biopsy breeding-breeding estimate was downwardly biased (Palsbøll *et al.* 1997).

The apparent downward bias of the breeding-breeding estimates could be due to sampling biases among behavioral classes. Our data showed that different behavioral classes in the breeding areas were differentially sampled, both by photography and by biopsying. A notable example is that photographs of mothers accompanied by a calf were much less likely to be collected than were photographs of animals in pairs, while the opposite is true for biopsies (Table 5). However, except for competitive groups, there is no evidence that animals within these groups were differentially sampled. Differential sampling of behavior classes and between sexes could account for the pattern of lower breeding-breeding estimates.

However, the male estimate (5,100) was consistent with the observed equal sex ratio in the feeding areas and the total abundance estimates from the breeding- and feeding-area biopsy and photographic data (10,400 and 10,600, respectively). This suggests that the problem lies with the females. A negative bias in the female abundance estimate can occur only if there was a range of capture probabilities, and the capture probability for each individual was consistent in the two years (Hammond 1986). Therefore, to obtain the observed downward bias, the same females must have been differentially available for sampling both years. Further, a large number of females must have been differentially available to account for an apparent downward bias of 45%. It is

difficult to envisage how this could occur due to differential sampling of animals among behavioral classes.

One more likely mechanism for the low apparent abundance of females is differential migration by sex, as it is believed that some animals remain in high latitudes during winter (*e.g.*, Williamson 1961, Christensen *et al.* 1992). Further, Brown *et al.* (1995) off eastern Australia showed that migrating animals were disproportionately male. Alternatively, the low apparent abundance could be due to differential habitat use within the breeding areas in combination with differential sampling among breeding area. For example, if females show site specificity to one of the four breeding areas that we sampled, they would have been unequally represented in our samples because our effort was heavily focused in one area. Similarly, if some females occupied an, as yet, unstudied breeding area (*e.g.*, the Cape Verde Islands or the Windward Islands), they would have been unavailable to our sampling. At this stage, we can speculate only that our results reflect some combination of sampling biases, possibly differential habitat use by females within the known breeding areas as well as non-migration of some females. However, our results can be explained only if the differential behavior involves the same individual females in both years. The migratory behavior and breeding-area habitat use of humpback whales in the North Atlantic require further study.

Violations of the assumption of a closed population would affect the abundance estimates differently, and the magnitude of these effects needs to be considered further. For example, the estimates formed from the feeding- and breeding-area samples in the same year should be unbiased estimates of the abundance in the winter, while those formed from breeding and feeding samples in subsequent years may be biased upwards by natural mortality and by likely population increases (Sigurjónsson and Gunnlaugsson 1990, Barlow and Clapham 1997). However, the between-year estimates were lower than the corresponding within-year estimates, suggesting that such biases were not large compared to the variance of the estimates.

As shown by Palsbøll *et al.* (1997), molecular tagging can be used as the primary means of identifying individual animals, and the resulting microsatellite data can be employed to estimate animal abundance using mark-recapture techniques. This technique has broad applicability to other taxa because molecular tags are both present and permanent in all species of animals, even those with insufficient phenotypic variation to permit individual identification by photography. An especially important aspect of molecular tagging is the ability to also determine sex of each animal, allowing abundance to be estimated for males and females separately. In the present case, this allowed the identification of differential behavior by females as the most likely cause of apparent biases in abundance estimates based only on breeding area data. Further, this allowed the demonstration that the male estimate was not similarly biased, allowing the possibility of estimating total abundance by simply dividing by the estimated sex ratio using the feeding area data. In this case, the estimate would be 10,000 (= 5,100/0.51), with a standard error, approximated using the delta method (Seber 1983), of 1,720. This approach to es-

timating total abundance is worth further consideration because the breeding areas are better known than the feeding areas for many populations of humpback whales, and because obtaining representative samples in the restricted breeding areas may be easier. However, it assumes that all males migrate each year, a belief which appears reasonable but which remains untested.

An Ocean-Basin-Wide Study

Populations of baleen whales frequently range over entire ocean basins during the course of a year. Ocean-basin-wide studies would be expected to provide more comprehensive understanding of the population biology of baleen whales than regional studies. The YoNAH study was a first attempt at such an ocean-basin-wide study of a cetacean species. Although such broad spatial-scale studies are logistically complex, we suggest that this study was a more productive strategy for obtaining much of the data required to support conservation and management than even many years of smaller-scale studies.

YoNAH was successful in obtaining more representative samples over nearly the full migratory range of the North Atlantic humpback whale, resulting in a large and spatially extensive collection of photographs and biopsies that better reflects the population's characteristics and structure. The study was able to collect data to address each of its objectives, and results presented to date have answered several outstanding questions that were suggested by previous regional studies. Although some of our findings confirmed existing ideas, the large sample sizes involved in YoNAH have lent greater confidence to these interpretations.

As reported here, the study resulted in estimates of abundance based on both photography and biopsy that are much more precise and reliable. Further, the study allowed the identification of the degree of potential non-representativeness of sampling animals in different behavioral classes in the breeding areas and by sex in both the breeding and feeding areas. In addition, further analyses of these data are underway to address reproductive behavior, social organization, evolutionary history, and mating systems. Finally, the data collected have been archived as a reference collection for future work as new ideas and new methods of analysis are developed and for comparison with future studies.

The improvement in our understanding of the population abundance and biology of the North Atlantic humpback whale from this study results directly from its ocean-basin scope. The results gained by an equivalent research investment in a series of small-scale studies could not have provided the answers that this study did. Thus, conducting studies of whale populations on a much larger spatial perspective than has been previously employed has the potential of providing much information and should be strongly considered. Further, the techniques of individual identification used here, both photography and (especially) genotype determination from biopsy, provide the possibility of conducting such studies on a variety of other endangered species.

ACKNOWLEDGMENTS

We thank our home institutions for our personal support throughout YoNAH: Center for Coastal Studies, College of the Atlantic, Greenland Institute for Natural Resources, Iceland Marine Research Institute, Memorial University of Newfoundland, Norwegian Institute of Marine Research, Norwegian Research Council, Northeast Fisheries Science Center, Sea Mammal Research Unit, and the University of Copenhagen. We are indebted to the following organizations and individuals for the necessary funds to complete YoNAH: American Cetacean Society, Brier Island Ocean Survey, Vaughan Brown Charitable Trust, Canadian Department of Fisheries and Oceans, Cetacean Society International, Cetacean Research Unit, Commission for Scientific Research in Greenland, Coral Bay Cruises, Danish Natural Science Research Council, Dorr Foundation, Edmund Scientific Co., European Union Biotechnology Program, Exxon Corporation, Greenland Fisheries Research Institute, Greenland Home Rule Government, Ruth Heibert, L. Knife and Sons, Iceland Marine Research Institute, Aage V. Jensen Charity Foundation, KNAPK (Greenland Hunters and Fishermen's Association), Marine Dream Co. of San Juan, Marine Mammal Conservation Program of Nantucket, Nature Conservancy, Feodor and Kirsten Pitcairn, Puerto Rico Department of Natural Resources, University of Copenhagen, University of Puerto Rico, US Department of State, US Marine Mammal Commission, US National Fish and Wildlife Foundation, US National Marine Fisheries Service, and World Wildlife Fund-DK.

A veritable army of individuals assisted with YoNAH, including individuals from Argentina, Brazil, Canada, Columbia, Denmark, Dominican Republic, Germany, Iceland, Norway, Puerto Rico, Scotland, Spain, UK, and USA. While we cannot acknowledge by name everyone who helped in the field and laboratories, we would like to thank the following for their extra effort on behalf of YoNAH: Thomas Hviid Andersen, Peter Arctander, Wayne Barney, Martine Bérubé, Bob Bowman, Idelisa Bonnelly de Calventi, Carol Carlson, Gerry Conway, Kjell Arne Fagerheim, Tonnie P. Feddersen, Tom Fernald, Jim Hain, John Hoenig, Richard R. Hudson, John Nicolas, Jette Jensen, Hanne Jórgensen, Charles Karnella, Anja Holm Larsen, Frank Nygaard, Megan McOsker, Antonio Mignucci, Kim Balnks Pedersen, Dwayne Pittman, David Potter, Durita Poulsen, Janeen Quintal, Poul Raahauge, Jooke Robbins, Richard Sears, Renate Sponer, Oswaldo Vasquez, Mason Weinrich, and Erika Widén.

For their assistance and support during the field work, we thank the Governor of Samana Province (DR), the women of the Renovacion of Puerto Plata (DR), the Dominican Navy, Department of Fisheries and Oceans and the Canadian Wildlife Service, Canada, the Norwegian Coast Guard, Jose Miguel Martinez of PRONATURA, Capt. Tom Conlon of Coral Bay Cruises, the Captain and crew of the *Rachel B. Jackson,* Gary Pittman and the crew of the *Dawnsailor,* and Wayne Ledwell and the crew of the *L.M. Tuck.*

For assistance throughout the analysis and with the preparation of the maps, we thank Nancy Friday and Daniel Sheehan. We also thank two anonymous reviewers for their helpful comments and suggestions, which strengthened both the analysis and the presentation of this work.

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Received: 22 September 1997
Accepted: 11 March 1998