

# Genetic diversity and population structure among northern bottlenose whales, *Hyperoodon ampullatus*, in the western North Atlantic Ocean

M.L. Dalebout, S.K. Hooker, and I. Christensen

**Abstract:** To assess population structure and genetic diversity among northern bottlenose whales (*Hyperoodon ampullatus*), we compared mitochondrial DNA control region sequences from three populations in the western North Atlantic Ocean. Skin-biopsy samples were collected from animals in the Gully off Nova Scotia, Canada, in 1996 and 1997 ( $n = 20$ ), and teeth were obtained from whales taken in Davis Strait off northern Labrador ( $n = 20$ ) and off northern Iceland ( $n = 5$ ) between 1967 and 1971 by the historical Norwegian fishery. Only low levels of genetic diversity were found among the 45 animals sampled (three polymorphic sites over 434 base pairs defining four haplotypes; haplotype diversity ( $h$ ) = 0.57, nucleotide diversity ( $\pi$ ) = 0.0015). The cause of this low variability is unclear but may be due to a possible bottleneck event associated with the last glaciation. The distribution of mitochondrial DNA haplotypes between the Gully and Davis Strait populations was suggestive of regional differentiation ( $F_{ST} = 0.118$ ,  $P = 0.024$ ;  $\Phi_{ST} = 0.145$ ,  $P = 0.007$ ). Animals taken off northern Iceland were not included in statistical analyses of population structure, owing to the small sample size. These data, in conjunction with other information collected to date, indicate that the Gully and Davis Strait populations should be considered separate stocks for management purposes.

**Résumé :** Pour évaluer la structure des populations et la diversité génétique chez la Baleine à bec commune (*Hyperoodon ampullatus*), nous avons comparé les séquences de la région de contrôle de l'ADN mitochondrial de trois populations de l'ouest de l'Atlantique-Nord. Des biopsies de la peau ont été pratiquées sur des baleines du Gully, au large de la Nouvelle-Écosse, Canada, en 1996 et 1997 ( $n = 20$ ), et des dents ont été prélevées chez des baleines du détroit de Davis capturées au large de la côte nord du Labrador ( $n = 20$ ) et au large de l'Islande ( $n = 5$ ) entre 1967 et 1971 au cours des pêches commerciales de Norvège de l'époque. La diversité génétique s'est avérée faible chez les 45 animaux étudiés (trois sites polymorphes sur 434 paires de bases définissant quatre haplotypes; la diversité d'haplotype ( $h$ ) = 0,57, la diversité de nucléotide ( $\pi$ ) = 0,0015). La cause de cette faible variabilité reste obscure, mais il est possible qu'il se soit produit un événement aboutissant à un étranglement génétique au cours de la dernière glaciation. La répartition des haplotypes d'ADNmt entre le Gully et le détroit de Davis laisse croire à l'existence d'une différenciation régionale ( $F_{ST} = 0,118$ ,  $P = 0,024$ ;  $\Phi_{ST} = 0,145$ ,  $P = 0,007$ ). Les échantillons du nord de l'Islande n'ont pas été retenus pour les analyses statistiques de la structure des populations car ils sont trop restreints. Ces données, combinées à d'autres informations recueillies à ce jour, indiquent que les populations du Gully et du détroit de Davis doivent être considérées comme des stocks différents pour fins d'aménagement.

[Traduit par la Rédaction]

## Introduction

Of the 20 species of beaked whales (Ziphidae) currently recognised, only the northern bottlenose whale, *Hyperoodon ampullatus*, has been the subject of in-depth study (e.g., Christensen 1973; Benjaminsen and Christensen 1979; Whitehead et al. 1997a, 1997b; Gowans 1999; Hooker 1999; Hooker and Baird 1999). Much of this work has focused on one

small population of this species that frequents the Gully, a submarine canyon on the edge of the Scotian Shelf (44°N, 59°W; e.g., Whitehead et al. 1997a, 1997b). This area appears to be an important year-round feeding ground for northern bottlenose whales (Whitehead et al. 1997a; Hooker 1999). However, little is known about the structure of the Gully population, its relationship to other populations in the North Atlantic Ocean, or the amount of interchange that occurs between them.

Bottlenose whales are found in northern regions of the North Atlantic, have a relatively predictable distribution, and unlike most other ziphids, will often approach slow-moving or stationary vessels (Gray 1882). This behaviour allowed large numbers to be taken as part of a multinational, multi-species whale fishery that began in the second half of the nineteenth century. By the time exploitation ceased in the early 1970s, over 65 000 bottlenose whales had been taken (Reeves et al. 1993). In 1977, the International Whaling Commission recommended that northern bottlenose whales be granted Protected Stock status with zero catch limit (Klinowska 1991). Catch distributions prior to this suggested

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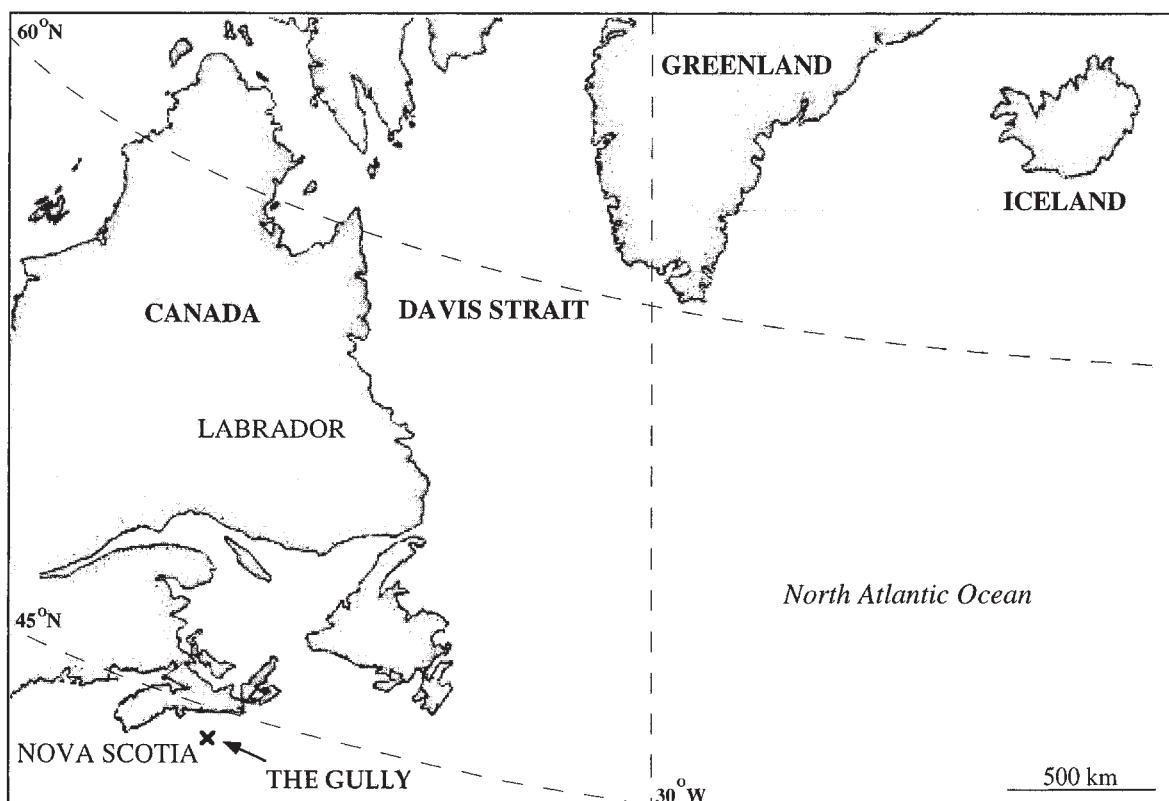
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**Fig. 1.** Map of the western North Atlantic showing the locations of the three northern bottlenose whale (*Hyperoodon ampullatus*) populations sampled: the Gully off Nova Scotia, Davis Strait off the northern Labrador coast, and off northern Iceland.



that there were at least six centers of abundance in the North Atlantic, each potentially a separate stock (Benjaminsen 1972).

The results of photoidentification work suggest that a population numbering approximately 130 animals (95% confidence interval = 104–170) uses the Gully area (Gowans 1999). In April 1996 this population was declared "vulnerable" by the Committee On the Status of Endangered Wildlife In Canada (COSEWIC), and in December 1998 the Gully was declared a pilot Marine Protected Area under Canada's Oceans Act, 1997. The primary threats to bottlenose whales in this area are disturbance and potential habitat destruction due to oil and gas exploration and production, shipping, and fisheries activities. Davis Strait, off the coast of Labrador 2000 km north of the Gully (approximate position 62°N, 60°W), is the nearest region where bottlenose whales are also consistently sighted (Fig. 1; Benjaminsen 1972). Examination of length distributions indicates that animals in the Gully are approximately 0.7 m shorter than those caught historically off northern Labrador (Whitehead et al. 1997b), suggesting that the populations in these areas are largely distinct. The threats faced by the small Gully population and the suggestion of regional segregation highlight the importance of investigating the genetic diversity of the animals in this area and their population structure. If informed management decisions are to be made, the degree of distinctiveness and extent of interchange between whales in the Gully, Davis Strait, and other areas in the North Atlantic need to be determined. In this paper we use mitochondrial DNA (mtDNA) control region sequence data to investigate the structure of the bottlenose whale populations in the two centers of distribution in the western North Atlantic: the Gully off Nova Scotia and Davis Strait off northern Labrador. A small number of samples from a population in the central North Atlantic, off northern Iceland, are also included in order to make a preliminary comparison of genetic diversity.

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## Materials and methods

Biopsy samples were collected from 20 animals in the Gully during July and August of 1996 and 1997 (for details of biopsy techniques see Hooker et al. 2001). A small subsample of each biopsy was preserved in salt-saturated dimethyl sulphoxide (DMSO) solution prior to genetic analysis. In general, only one biopsy sample was taken per group of animals encountered. An "encounter" was defined as a group of whales seen after a 10-min interval during which no whales had been observed at the surface. A radio-tracking study of diving animals (using suction-cup tags attached remotely via crossbow; Hooker and Baird 1999) illustrated that individual animals were unlikely to be relocated without the aid of radiotelemetry after dives exceeding 10 min. Sampling individuals during different encounters therefore decreased the likelihood of duplicate sampling of the same animal(s). The field characteristics of each biopsied animal were also noted to further minimise this risk. In addition, 12 of the 20 biopsied animals were photographically identified. There were no obvious associations (possibly suggestive of kinship) between any of these known individuals, based on their past sighting histories (S. Gowans, personal communication). During three encounters, pairs of individuals were sampled, but as associations between groups of bottlenose whales in the Gully are relatively unstable, this is unlikely to indicate relatedness (Gowans et al. 2001). Overall, while we are relatively confident that the majority of the biopsied whales are unlikely to have been

related, it is possible that first- or second-order relatives were included in the sample by chance alone, owing to the small size of this population.

Remnant gum tissue was obtained from the teeth of 20 animals taken in Davis Strait, off the northern Labrador coast, between 1967 and 1971 by Norwegian pelagic whalers (Christensen 1973). Because of the manner in which bottlenose whales were taken by this industry, it is possible that this sample also included related individuals. "When a member of a [group] is harpooned, his fellows do not abandon him; even when he is killed...which gives a good chance of capturing another" (Ohlin 1893, p. 7). However, of the 20 samples, only 2 have consecutive field numbers, the majority being separated from one another by an average of 17 ( $\pm 3.0$  (SE)) numbers. As bottlenose whales were usually found in groups of one to four in this area (Benjaminsen and Christensen 1979), it is likely that the sample was largely composed of animals taken from different, and therefore probably unrelated, groups. Gum-tissue samples were also obtained from the teeth of five animals taken off northern Iceland during the same period. The jaws were boiled for 2 h to facilitate extraction of the teeth (Christensen 1973), which were then stored unpreserved at room temperature in individual paper sachets for up to 30 years prior to this study.

Total DNA was extracted from all samples as described in Gowans et al. (2000). A 434 base pair (bp) fragment of the variable 5' end of the mtDNA control region (D-loop) was amplified via the polymerase chain reaction (PCR) using the primers M13-DlpWH1.5 (t-Pro) and Dlp5 (Dalebout et al. 1998). Previous studies on cetaceans have shown that this locus accumulates mutations rapidly and is usually well suited to addressing questions of population structure (e.g., Hoelzel and Dover 1991; Baker et al. 1993). PCR products were sequenced using BigDye<sup>TM</sup> Dye Terminator Chemistry and run on either an ABI 377 or modified ABI 373 Automated DNA Prism<sup>TM</sup> Sequencer (Applied Biosystems, Inc.). All sequences were aligned by eye, and at least one representative of each haplotype was sequenced in both directions to confirm polymorphic sites.

The sex of all animals was determined, or confirmed for comparison with whaling records, using the zinc-finger protein (ZFY) method of Palsbøll et al. (1992) and the sex determining region Y gene (SRY) method of Richards et al. (1994) as described in Gowans et al. (2000). The  $\chi^2$  test of independence was used to assess the significance of sex-ratio deviation from parity between the Davis Strait and Gully samples.

Standard indices of genetic variation, nucleotide diversity ( $\pi$ ) and haplotype diversity ( $h$ ), were calculated for each population and over all samples ( $n = 45$ ). The selective neutrality of the mtDNA control region in this species was assessed using Tajima's  $D$  statistic (Tajima 1989). An exact test (Raymond and Rousset 1995) and an analysis of molecular variance (AMOVA) incorporating both  $F_{ST}$  and  $\Phi_{ST}$  statistics were used to investigate the degree of geographic differentiation between the Gully and Davis Strait populations. The northern Iceland animals were not included in these analyses, as the sample ( $n = 5$ ) was too small for statistical comparison with the other populations. The exact test is analogous to Fisher's exact test, haplotype frequency data being used to build the contingency table. The statistical significance of this test was assessed by means of 10 000 Markov chain steps. For the AMOVA,  $F_{ST}$  evaluates the difference in overall haplotype frequency, while  $\Phi_{ST}$  takes into account the relationships between the haplotypes based on molecular distance (Excoffier et al. 1992). Because of the low level of variation, uncorrected pairwise distances ( $p$ ) were used for this estimate. The statistical significance of the  $F_{ST}$  and  $\Phi_{ST}$  values was tested by 10 000 permutations of the data. To assess the effect of possible duplicates among the biopsied animals from the Gully, the analyses were run twice, once using all Gully samples available ( $n = 20$ ) and once using only those samples known to represent unique individuals ( $n = 15$ ). Of the 20 animals biopsied, 12 were known from photoidentification, so the remain-

ing 8 could have been duplicates. Given an estimated population size of approximately 130 animals, the probability of duplicates among eight samples is low (approximately 0.2). Information on the sex and haplotype of the animals reduced the number of possible duplicates to 5, leaving a total sample of 15 confirmed unique animals. An AMOVA partitioning all animals sampled by sex and a hierarchical AMOVA partitioning each population by sex were also performed to investigate whether a possible sex bias in the animals sampled would affect the degree of structuring observed. The formula  $M = (1 - F_{ST})/2F_{ST}$  was used to provide an estimate of  $N_{mf}$ , where  $N$  is the population (sample) size and the mutation rate is assumed to be negligible compared with the migration rate,  $m$  (Wright 1951; Takahata and Palumbi 1985). As the influences of drift and gene flow are difficult to separate,  $N_{mf}$  can be interpreted as the absolute number of females exchanged between the two populations per generation. All analyses were carried out using the program ARLEQUIN 1.1 (Schneider et al. 1997).

## Results

Analysis of 434 bp of sequence data from the 5' end of the mtDNA control region revealed three variable sites defining four unique haplotypes among the sample of 45 whales from the Gully, Davis Strait, and off northern Iceland (Table 1). All substitutions were transitions. Relationships among the haplotypes were inferred from a parsimony network (Fig. 2). The overall frequency distribution of haplotypes differed between the putative stocks (Table 2): haplotype A was the most common in all three areas (50–75% of individuals sampled), haplotype B was also found in all areas but was less common (15–20% of individuals sampled), haplotype C was found only in Davis Strait and off northern Iceland (20–35% of individuals sampled), and haplotype D was found only in the Gully (10% of individuals sampled). Within the overall sample ( $n = 45$ ),  $h = 0.57$  and  $\pi = 0.0015$  (Table 2). The lowest haplotype and nucleotid diversity were found among the Gully animals:  $h = 0.43$ ,  $\pi = 0.0011$ . Northern Iceland animals had the highest haplotype and nucleotid diversity, with three haplotypes found among the five animals sampled:  $h = 0.70$ ,  $\pi = 0.0018$ . The results of Tajima's  $D$  test of selective neutrality were not significant ( $P > 0.05$ ), suggesting that this locus is not under selection in this species.

With all 20 animals from the Gully included in the analyses, the results of both the exact test and the AMOVA ( $F_{ST}$  and  $\Phi_{ST}$ ) indicated significant geographic differentiation ( $P < 0.05$ ) between the two western North Atlantic populations (exact test,  $P = 0.008$ ;  $F_{ST} = 0.118$ ,  $P = 0.024$ ;  $\Phi_{ST} = 0.145$ ,  $P = 0.007$ ; Table 3). When only the known unique Gully animals were included ( $n = 15$ ), similar results were obtained, except for the  $F_{ST}$  statistic, which was marginally non-significant ( $F_{ST} = 0.010$ ,  $P = 0.059$ ). The  $\Phi_{ST}$  values from both analyses suggest that 14–15% of the overall molecular variance is explained by the division of the Gully and Davis Strait. The estimated absolute number of female migrants ( $M = N_{mf}$ ) moving between these populations per generation, calculated from  $F_{ST}$  and  $\Phi_{ST}$  values, ranged from 2.94 to 3.75 if all samples were included and from 3.10 to 4.33 if only the known unique samples were included (Table 3). Generation time for female bottlenose whales is approximately 8–13 years (Christensen 1973). Sequences representing each of the four haplotypes have been submitted to GenBank (Accession Nos. AF350437–AF350440).

Among the Gully sample, the sex ratio was 7 males : 13

**Table 1.** Variable sites within 434 bp of the mtDNA control region of the northern bottlenose whale (*Hyperoodon ampullatus*), defining four unique haplotypes.

Haplotype	Position			Sex ratio (M:F)		
	15	106	213	The Gully	Davis Strait	Northern Iceland
A	G	C	T	5:10	5:5	1:2
B	•	•	C	1:2	1:1	1:0
C	•	T	•	—	6:1	0:1
D	A	•	•	1:1	—	—
Total				7:13	12:7	2:3

Note: A dot indicates identity with the reference sequence, haplotype A. Position 15 corresponds to position 15903 of the mtDNA genome of the fin whale, *Balaenoptera physalus* (Arnason et al. 1991). The sex ratio by haplotype for each of the three populations is also shown. Note that one animal from Davis Strait is excluded, as the results from molecular sexing are in conflict with whaling records.

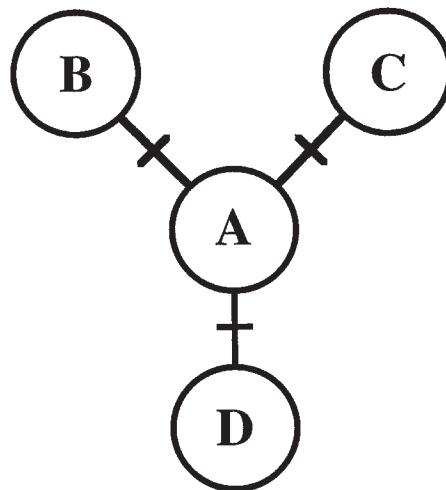
females, and in Davis Strait, 12 males : 7 females (Table 1). One animal from Davis Strait was excluded, as results from molecular sexing were in conflict with whaling records (for further discussion see Gowans et al. 2000). The results of the test of independence indicated that the difference in sex ratio between the Gully and Davis Strait did not deviate significantly from parity ( $\chi^2_{1 \text{ df}} = 3.09, P > 0.05$ ). The results of the AMOVA partitioning all animals by sex and partitioning the two populations by sex were not significant ( $P > 0.05$ ).

## Discussion

While the 5' end of the mtDNA control region is highly variable in many cetacean species (e.g., Baker et al. 1993; Rosel et al. 1995; Brown-Gladden et al. 1997), only low levels of variation were found at this locus among bottlenose whales in the western and central North Atlantic ( $n = 45$ ), with three polymorphic sites (transition substitutions) over 434 bp defining four haplotypes ( $h = 0.57, \pi = 0.0015$ ). In contrast, analyses of four animals from the sister-species, the southern bottlenose whale, *Hyperoodon planifrons*, revealed 17 polymorphic sites (13 transitions, 3 transversions) defining four unique haplotypes ( $h = 1.00, \pi = 0.0288$ ) over a smaller segment (362 bp) nested within the same fragment of the mtDNA control region (M.L. Dalebout, unpublished data). The average intraspecific pairwise sequence divergence (uncorrected  $p$  distances) for *H. ampullatus* over this segment was 0.19% ( $\pm 0.007\%$  (SE)), while for *H. planifrons* it was 2.70% ( $\pm 0.547\%$ ). The average interspecific pairwise sequence divergence was 5.51% ( $\pm 0.151\%$ ). No haplotypes were shared between these species.

Comparatively low levels of diversity have previously been documented only in species or populations with (i) overall low abundance or declining population size, e.g., Hector's dolphins, *Cephalorhynchus hectori*, in the North Island of New Zealand ( $h = 0.00, \pi = 0.0000$ ; Pichler and Baker 2000), belugas, *Delphinapterus leucas*, in Cook Inlet ( $h = 0.52, \pi = 0.0023$ ; O'Corry-Crowe et al. 1997), and harbour porpoises, *Phocoena phocoena*, in the Black Sea ( $h = 0.42, \pi = 0.0011$ ; Rosel et al. 1995); or (ii) matrilineal social organisation (Whitehead 1999), e.g., sperm whales, *Physeter macrocephalus*, worldwide ( $h = 0.74, \pi = 0.0038$ ; Lyrholm et al. 1996) and killer whales, *Orcinus orca*, in the eastern

**Fig. 2.** Relationships among northern bottlenose whale haplotypes, represented by a parsimony network. Circles (nodes) represent haplotypes, labelled A–D as in Table 1. The crossbars on the links represent single nucleotide changes.



North Pacific Ocean ( $\pi = 0.0054$ ; Hoelzel et al. 1998). Except for the group utilising the Gully ( $n \sim 130$  animals), no current abundance estimates are available for northern bottlenose whales. Before the onset of whaling, at least 40 000 to 50 000 animals are thought to have frequented the area east of Greenland (Christensen 1976). Whales were scarcely seen in this region by the 1960s, when the Norwegian fishery began to exploit the stocks in the western North Atlantic (Christensen 1975). By 1972, as a result of this transfer of effort, the number of whales in Davis Strait had also decreased (Christensen et al. 1977). During this time, 87 animals were also taken from the Gully – Grand Banks area by the Canadian whale fishery (Mitchell 1974). The small size of the Gully population, perhaps further diminished by whaling, may be sufficient to explain the low nucleotide diversity observed there. However, modern whaling takes alone are unlikely to account for the low nucleotide diversity also observed in the Davis Strait population. No additional haplotypes were found among the small sample of animals from northern Iceland. This suggests that low levels of genetic diversity are widespread in this species, and may instead be the result of a historical population bottleneck pre-dating human intervention, perhaps associated with range restrictions during the last glacial epoch 18 000 years ago. The shallow, starlike relationship of the haplotypes (Fig. 2), with haplotype A representing the majority of animals sampled (Table 1), also supports this hypothesis (Page and Holmes 1998). During the last glaciation, sea-surface temperatures in some parts of the North Atlantic were up to 10°C lower than present-day ones (COHMAP members 1988), and permanent sea ice covered much of the northern regions, including Davis Strait and off northern Iceland (Wilson et al. 2000). These climatic conditions would have excluded northern bottlenose whales from many parts of their present-day range.

It has been suggested that reduced genetic diversity could also result from cultural selection of maternally inherited traits (Whitehead 1999). For diversity to be reduced by this mechanism, social groups should be composed primarily (95.5%) of related individuals (i.e., all animals share the

**Table 2.** Distribution of haplotypes, numbers of animals sampled, and indices of genetic diversity for the three populations included in this study.

	Haplotype					Haplotype diversity ( $h$ )	Nucleotide diversity ( $\pi$ )
	<i>n</i>	A	B	C	D		
The Gully	20	0.75	0.15	0	0.10	0.43	0.0011
Davis Strait	20	0.50	0.15	0.35	0	0.67	0.0017
Northern Iceland	5	0.60	0.20	0.20	0	0.70	0.0018

**Table 3.** Results of the exact test for population structure, and AMOVA  $F_{ST}$  and  $\Phi_{ST}$  statistics, comparing regional samples of northern bottlenose whales from the Gully and Davis Strait; estimates of the numbers of females dispersing between these populations per generation ( $N_{mf}$ ) are also shown.

Populations compared	<i>n</i>	Exact test	AMOVA	
All samples				
Gully	20	—	$F_{ST} = 0.118$	$\Phi_{ST} = 0.145$
Davis Strait	20	$P = 0.008^*$	$P = 0.024^*$	$P = 0.007^*$
			$N_{mf} = 3.75$	$N_{mf} = 2.94$
Known unique samples only				
Gully	15	—	$F_{ST} = 0.104$	$\Phi_{ST} = 0.139$
Davis Strait	20	$P = 0.019^*$	$P = 0.059$	$P = 0.015^*$
			$N_{mf} = 4.33$	$N_{mf} = 3.10$

\*Significant at the 0.05 level.

same maternal haplotype). However, long-term observations of known individuals in the Gully suggest that in this species it is males rather than females which form stable associations (Gowans et al. 2001). Alternatively, the low mitochondrial diversity seen here and in several other wide-ranging odontocete species may be due either to ongoing natural selection at this locus, perhaps associated with the physiological demands of an aquatic life-style, or to a selective sweep some time in the past (Lyrholm et al. 1996; Mesnick et al. 1999). While Tajima's *D* statistic was not significant ( $P > 0.05$ ), suggesting that the mtDNA control region is not under selection in bottlenose whales, it is recognised that in many circumstances such tests may in fact have little power to detect selection (Wayne and Simonsen 1998).

Although the number of samples available was relatively small, the distribution of mtDNA haplotypes between the two main populations, in the Gully and Davis Strait, was suggestive of geographic subdivision, as reflected in the  $\Phi_{ST}$  value of 14.52% (all samples included). This regional differentiation was found to be statistically significant at the  $P < 0.05$  level, for both  $F_{ST}$  and  $\Phi_{ST}$  statistics and the exact test. However, if only the known unique samples were used to represent the Gully ( $n = 15$ ), the  $F_{ST}$  value was marginally nonsignificant ( $P = 0.059$ ). Incorporation of rapidly evolving nuclear markers (e.g., microsatellites) would allow us to eliminate possible duplicates among the Gully samples and determine whether close relatives from either population had been included in the analyses. Both could produce spurious evidence concerning population structure. Until such data are collected, the findings presented here can offer only a preliminary evaluation of stock divisions among northern bottlenose whales in the western North Atlantic.

The observed differentiation between these putative stocks suggests an average long-term exchange of only a few females per generation ( $N_{mf} < 5$ ) despite the absence of obvious geographic barriers. Similar low amounts of gene flow have been documented for humpback whales, *Megaptera novaeangliae*, and right whales, *Eubalaena australis*, frequenting different wintering grounds (Baker et al. 1999), and provide evidence that such stocks should be considered independent management units (Baker and Palumbi 1997). It should be noted, however, that the island model on which the calculation of  $N_{mf}$  is based assumes both that samples are representative of the populations as a whole and that the populations being compared are of equal size (Takahata and Palumbi 1985). Although we have sampled approximately 15% of the Gully population, the proportion of Davis Strait animals represented by our sample is not known. In addition, the 30-year (~3 generations) interval in collecting samples from these populations may also be problematic. For example, cohort effects have been documented for humpback whales sampled at different times on some feeding grounds (e.g., Baker et al. 1998). Whaling records suggest that there may be a seasonal pattern to the distribution of bottlenose whales but conflict in the directionality of such movements (i.e., south in summer (Ohlin 1893) or south in winter (Gray 1882)). The overall predominance of males in the Davis Strait sample is likely due to whalers' preference for the larger adult males (Mead 1989), and therefore may also not reflect the true sex ratio in this population. Much of the population structure detected by our analyses was driven by the large proportion of animals of haplotype C in Davis Strait, the majority of which were males (85.7%). However, partitioning the molecular variance by sex within each population suggested that sex-ratio differences did not strongly influence detected structure.

Although females predominated among the animals biopsied in the Gully, the overall sex ratio of this population, determined from melon-profile photographs, appears close to parity (Gowans 1999).

Overall, the evidence to date suggests that the Davis Strait and Gully populations should be considered separate management units, based on significant differences in haplotype frequencies that indicate low levels of interchange between the two regions (Baker and Palumbi 1997; Vogler and DeSalle 1994). The null hypothesis of panmixia was rejected for all analyses bar one, for which the results were marginally nonsignificant. Even in the latter case, however, the two populations still warrant recognition as discrete stocks for management purposes according to the precautionary approach suggested by Taylor and Dizon (1999). This argument is strengthened by the small size of the Gully population and its vulnerability to stochastic events, especially those associated with industrial developments in this region. Together with previous observations of length differences between bottlenose whales in the Gully and Davis Strait (Whitehead et al. 1997a), our results support the putative distinctiveness of these populations. The inclusion of animals from other known centers of abundance, together with information from biparentally inherited nuclear markers, would allow us to provide a more comprehensive assessment of genetic variation and gene flow, including sex-biased dispersal, in bottlenose whales, which should in turn allow better management and conservation of this unique North Atlantic odontocete.

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