Population size and residency patterns of northern bottlenose whales (Hyperoodon ampullatus) using the Gully, Nova Scotia

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ABSTRACT

A population of northern bottlenose whales (Hyperoodon ampullatus) uses the Gully, a submarine canyon off the coast of Nova Scotia, Canada. Eleven years of photo-identification records has permitted estimation of population size using mark-recapture techniques. The population estimate was small (133 individuals, 95% CI = 111-166 from left side identifications; 127 individuals, 95% CI = 106-169 from right side identifications). The population was not closed, with the combined mortality, mark change and emigration rate estimated at 15% per year for left side identifications (95% CI = 9.17%) and 14% for right side identifications (95% CI = 10.18%). There was no significant increase or decrease in the population size between 1988-1999 (change in population size: left side: -0.13% per year, 95% CI = -3.4 to 3.9; right side: -0.43% per year, 95% CI = -4.5 to 3.1). The sex ratio was roughly 1:1, with equal numbers of sub-adult and mature males. Over the summer field season, individuals emigrated from, and re-immigrated into the Gully, spending an average of 20 days within the Gully before leaving (left side identifications 14 days, SE = 17; right side identifications 23 days, SE = 10). Approximately 34% of the population was present in the Gully at any time. Individuals of all age and sex classes displayed similar residency patterns although there were annual differences as individuals spent less time in the Gully in 1996 than in 1990 and 1997. Sighting rates were similar in all years with extensive fieldwork, indicating little variability in the number of whales in the Gully each summer. Accurate estimates of population size and residency patterns will be useful in determining the regulations and required coverage for a marine protected area in the Gully.

KEYWORDS: MARK-RECAPTURE; PHOTO-ID; TRENDS; POPULATION ASSESSMENT; NORTHERN BOTTLENOSE WHALE

INTRODUCTION

Northern bottlenose whales (Hyperoodon ampullatus) are routinely found in the Gully, a submarine canyon off the coast of Nova Scotia, Canada, near the southern and western limits of the species' range. The number of whales in this area has been reduced in the past; whales removed 87 northern bottlenose whales from the Gully and surrounding area from 1962 to 1967 (Reeves et al., 1993). Currently, potential threats are posed by oil and natural gas development near the canyon (Whitehead et al., 1997a; Hooker, 1999). The Gully has recently been declared a ‘Pilot Marine Protected Area’ by the Canadian Department of Fisheries and Oceans, partially to protect northern bottlenose whales, although no boundaries or regulations have yet been established.

A small number of northern bottlenose whales are consistently found in the Gully (Whitehead et al., 1997a), although the extent to which bottlenose whales depend on the Gully has not been specifically studied. This group of bottlenose whales has been declared a ‘vulnerable’ population by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC; Whitehead et al., 1997a) although the genetic isolation of this group has not yet been studied in detail. This paper seeks to (1) evaluate the size of the Gully population and investigate any trends in population growth; and (2) examine the reliance of northern bottlenose whales on the Gully canyons.

METHODS

Field work and photographic catalogue

Photographs of the dorsal fin and surrounding flank of northern bottlenose whales were taken in the deep water areas of the Gully (43°30' - 44°30'N, 58°30' - 50°00'W) during the summers of 1988-1999 from sailing vessels with auxiliary diesel engines. Time spent in the field varied from only a few days in 1991 and 1992 to a few months in 1990, 1996 and 1997; in 1991 and 1992 sighting conditions were poor (Table 1). Sightings were defined as continuous observations of whales at the surface; a sighting was considered ended when 10 minutes had passed with no whales observed at the surface.

Photographs of both left and right sides of the whale were taken when they were within approximately 30m of the boat, although most of the better quality photographs were taken when the whales were within 15m. Except in 1999, attempts were made to photograph all individuals in the group, irrespective of obvious markings on the individual. Photographs were taken throughout the encounter, whether or not photographs had already been taken of the individual.

Black and white negatives were examined on a light table with a 10x magnifying loupe. All negatives were assigned a qualitative quality rating (Q-values) from 1 to 6 based on focus, exposure, angle of the fin relative to the negative plane and the proportion of the frame filled by the fin (similar to Arnbom, 1987), with Q=6 being the highest quality. Q-values were independent of the markings on the individual. Only photographs of Q ≥ 2 could be assigned an identification number. Quantitative analysis of the marks visible in each quality category indicated that only photographs of Q ≥ 4 contained sufficient information to mark animals and permit recapture between years (Gowans and Whitehead, 2001).

The highest quality negative of each individual in each year was printed and the photographs were compared within years and between years. If a photograph matched an individual present in the catalogue, then that photograph and
all other associated negatives were assigned to the whale’s identification number. If not matched, the individual was given a new number and added to the catalogue. Photographic collections for left and right sides were maintained separately, although some identifications from different sides could be linked. The negative collection contained 12,563 negatives that were assigned an identification (Table 2).

Northern bottlenose whales show sexual dimorphism in the shape of their melon (Gray, 1882). Photographs of the melons, linked to identification photographs, were used to classify individuals as either female/immature male, sub-adult male or mature male. Few individuals in the population showed signs of maturation (Gowans et al., 2000) and individuals were assigned to the age/sex category of their ultimate catalogue identification.

### Table 2

**Summary of photo-identification data (Q ≥ 2) by year.**

<table>
<thead>
<tr>
<th>Year</th>
<th>No. of frames</th>
<th>All individuals</th>
<th>Reliably marked individuals</th>
<th>All individuals</th>
<th>Reliably marked individuals</th>
</tr>
</thead>
<tbody>
<tr>
<td>1988</td>
<td>123</td>
<td>18</td>
<td>12</td>
<td>19</td>
<td>13</td>
</tr>
<tr>
<td>1989</td>
<td>1,262</td>
<td>199</td>
<td>56</td>
<td>56</td>
<td>53</td>
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<tr>
<td>1990</td>
<td>3,116</td>
<td>171</td>
<td>81</td>
<td>167</td>
<td>74</td>
</tr>
<tr>
<td>1991</td>
<td>27</td>
<td>8</td>
<td>5</td>
<td>5</td>
<td>3</td>
</tr>
<tr>
<td>1992</td>
<td>549</td>
<td>46</td>
<td>17</td>
<td>33</td>
<td>26</td>
</tr>
<tr>
<td>1994</td>
<td>370</td>
<td>34</td>
<td>20</td>
<td>43</td>
<td>20</td>
</tr>
<tr>
<td>1995</td>
<td>32</td>
<td>6</td>
<td>6</td>
<td>17</td>
<td>12</td>
</tr>
<tr>
<td>1996</td>
<td>1,731</td>
<td>94</td>
<td>54</td>
<td>86</td>
<td>47</td>
</tr>
<tr>
<td>1997</td>
<td>1,511</td>
<td>99</td>
<td>57</td>
<td>90</td>
<td>58</td>
</tr>
<tr>
<td>1998</td>
<td>2,404</td>
<td>74</td>
<td>42</td>
<td>68</td>
<td>40</td>
</tr>
<tr>
<td>1999</td>
<td>1,409</td>
<td>60</td>
<td>41</td>
<td>56</td>
<td>36</td>
</tr>
</tbody>
</table>

Gowans and Whitehead (2001) found that while all individuals possessed marks that could be used for photo-identification, changes in certain marks can affect re-identification of many individuals over time. However, in their assessment of mark changes they found that notches on the dorsal fin, indentations on the back and ‘mottled patches’ showed no evidence of mark loss over nine years (Gowans and Whitehead, 2001). Therefore all analyses which spanned more than one year, have been conducted only on those individuals (hereafter called ‘reliably marked’). To calculate the proportion of the population that was reliably marked, the number of photographs (Q ≥ 4) containing individuals with reliable marks was divided by the total number of photographs (Q ≥ 4). This calculation was performed separately for each year when more than one month was spent in the field (1989, 1990, 1996 and 1997) and for left and right sides. The mean and standard error were calculated and the overall proportion was then used to scale the population estimate.

### Sighting rate

The rate at which northern bottlenose whales were encountered was calculated from the number of sightings divided by the hours spent searching when conditions were good (i.e. daylight hours from 05:00 to 20:00, Beaufort sea state < 4, visibility > 500m). The sighting rate was calculated separately for each year and for all years combined. Assuming that the sightings were independent and followed a Poisson distribution, approximate standard errors were calculated by dividing the sighting rate by the square root of the number of sightings. As the sightings may not have been independent, the standard errors may be an underestimate of the true variability.

### Population size and trends

To investigate whether the population was open or closed (to immigration, emigration, mortality or birth) a discovery curve was plotted. The cumulative number of identified individuals (identified by left fin photographs) was plotted against the cumulative number of high quality left fin photographs. The cumulative number of individuals was also plotted for only reliably marked individuals.

Population size and trends were estimated separately for left and right side identifications based on all Q ≥ 4 photographs of reliably marked individuals using the POPAN module of SOCPROG 1.2 (developed in MATLAB by HW, programs available at: http://ss.dai.ac.uk/whitelab/index.htm) with calendar years as units. Three models were fitted to the population estimates using the Aikake Information Criterion (AIC) to determine which model best described the population (see Appendix 1 for model details). Maximum-likelihood methods, conditioned on the first capture, were used to estimate population parameters of each model. The three models were:

1. ‘Closed’ (Schnabel: population has no mortality, birth, immigration or emigration;
(2) 'Mortality': population remains the same with mortality balanced by birth (mortality includes permanent emigration or mark change that prevents recapture and birth includes permanent immigration or mark change that causes a previously identified animal to be identified as a new animal);

(3) 'Mortality + trend': population grows or declines at a constant rate.

Profile likelihood support functions in which other parameters were maximised were used to estimate 95% likelihood confidence intervals for each parameter (Edwards, 1992). As there were few permanent associations, the assumption of independence was not violated when estimating confidence intervals using likelihood methods (Edwards, 1992). Jolly- Seber methods of calculating the population size, mortality/emigration and birth/immigration separately for each year were inappropriate for this dataset, as this method estimates many different parameters resulting in extremely inaccurate estimates (Jolly, 1965).

Age and sex structure
The population size of each age and sex class was estimated and modelled as described above for the entire population. The proportion of the population which was both sexed and reliably marked was calculated by dividing the number of melon photographs linked to a reliably marked fin identification photograph by the number of melon photographs linked to any fin identification. The proportion was calculated separately for each class in each year (1990, 1996 and 1997: years with two months in the field and many melon photographs taken) and then averaged. The estimated number of reliably marked sexed individuals was then scaled to calculate the estimated number of sexed individuals in the population.

Residency in the Gully
The residency of individuals in the Gully was investigated by calculating lagged identification rates. The lagged identification rate for a particular lag tau (τ) is the probability that an individual identified at any time 0 is re-identified in a photograph taken at τ units later (Whitehead, is press):

\[ R(\tau) = \frac{P(\tau)}{N} \]  

where:

τ = time lag;
R(τ) = lagged identification rate for τ;
P(τ) = probability individual is still in the Gully after τ;
N = number of individuals in the Gully.

Lagged identification rates were estimated from:

\[ \hat{R}(\tau) = \frac{\sum_{i} \sum_{j \neq i, j > i} m_{ij}}{\sum_{i} \sum_{j \neq i, j > i} n_{ij}} \]  

where:

n_{i} = the number of individuals identified on occasion i;
m_{ij} = number of individuals identified on both occasions i and j;
i = time of identifications at occasion i.

The maximum lag (τ) between photographs considered was 100 days, which was greater than the number of days in a single field season. Individuals did not have to be reliably marked to be included in these analyses as marks were unlikely to have experienced sufficient change to preclude re-identification within 100 days (Gowans and Whitehead, 2001). Mortality and birth rates were considered to be zero in these analyses as few births or deaths were likely to have occurred in the 100-day sampling period. Three models of residency were fitted to the residency rate data using AIC methods to determine the best model. Jack-knife techniques (in which data from each date were sequentially eliminated from the dataset) were used to calculate 95% confidence interval error bars and standard errors for each model parameter. The three models were:

(1) 'Closed' (no changes in the individuals present in the Gully):

\[ R = \frac{1}{N} \]  

(2) 'Emigration' (individuals could leave the Gully, but never return):

\[ R = \left( \frac{1}{N} \right)^{\tau} \]  

(3) 'Emigration and re-immigration' (individuals could enter and leave the Gully, then re-enter the Gully; Whitehead, 1990):

\[ R = \frac{Oe^{-\lambda I \tau} + \lambda I}{(I + O)N} \]  

where:

N = number of individuals in the Gully;
I = mean time spent inside the Gully;
O = mean time spent outside the Gully.

Lagged identification rates were calculated and models fitted for each age and sex class separately and for each year with more than two months spent in the field. The proportion of individuals in the Gully at any given time was calculated by dividing the estimated number of whales in the Gully by the total estimated population size.

RESULTS

Sighting rate

The sighting rate varied by a factor of about 2.5 between years (Table 1), although all years with extensive field effort (1990, 1996 and 1997) had similar sighting rates, revealing relatively small levels of inter-annual variability in the mean number of whales in the Gully. The sighting rate was low in 1988, as much of the search effort was spent in areas further north than those in which northern bottlenose whales were typically found.

Population size and trends

The discovery curve indicated that new individuals continue to be recruited to the population throughout the study period, especially if individuals with unreliable marks were included (Fig. 1). There was some levelling off in the discovery curve of reliably marked individuals in the last few years of the study, although new reliably marked individuals were sighted each year. New recruits to the population may represent births, immigration into the population, mark change or captures in subsequent years of individuals which had been previously unphotographed. Within a single year the population was not closed as new individuals were continually identified throughout each field season, even in the long field seasons.
Fig. 1. Discovery curve showing the number of new individuals identified each day. An open population is indicated by the failure of the curves to reach an asymptote even within a single field season.

Fig. 2. Support surface contours for estimates of population size and mortality rate of reliably marked individuals, based on mortality model. Support function values less than two approximate the 95% CI region. * Indicates maximum-likelihood estimate.

Table 3

<table>
<thead>
<tr>
<th>Dataset</th>
<th>Model</th>
<th>Population estimate</th>
<th>Mortality (% per year)</th>
<th>Trend (% per year)</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Left side (n=147)</td>
<td>Closed</td>
<td>151 (134-174)</td>
<td>13 (9-17)</td>
<td>-</td>
<td>760</td>
</tr>
<tr>
<td></td>
<td>Mortality</td>
<td>88 (79-109)</td>
<td>13 (9-17)</td>
<td>-</td>
<td>682</td>
</tr>
<tr>
<td></td>
<td>Mortality + trend</td>
<td>88 (78-101)</td>
<td>13 (9-17)</td>
<td>-0.13</td>
<td>684</td>
</tr>
<tr>
<td>Right side (n=146)</td>
<td>Closed</td>
<td>153 (135-176)</td>
<td>-</td>
<td>-</td>
<td>763</td>
</tr>
<tr>
<td></td>
<td>Mortality</td>
<td>84 (75-97)</td>
<td>14 (10-19)</td>
<td>-0.45</td>
<td>675</td>
</tr>
<tr>
<td></td>
<td>Mortality + trend</td>
<td>84 (75-97)</td>
<td>14 (10-19)</td>
<td>-0.45</td>
<td>675</td>
</tr>
</tbody>
</table>

Of the three models tested to describe the population (closed, mortality, mortality + trend), the mortality model fitted best (Table 3). The mortality + trend model fitted the data no better than the simpler mortality model, although a small non-significant population decline was indicated by the model. Based on the mortality model, the population...
The estimated reliability of marked individuals was 88 (for left side identifications) or 84 (right side identifications). The estimated mortality, emigration and mark change rate was 13% per year (left side) and 14% per year (right side). Support surfaces indicate the 95% CI of the estimation of the population size and mortality rate (Fig. 2). The population estimate of reliably marked individuals (using the mortality model) ranged from 79 to 101 individuals (left side) and 75 to 97 individuals (right side; Table 3). The overall percentage of the population that was reliably marked was estimated to be 66% (5% SE) for all photographs (left side photographs 61%, SE = 6%; right side photographs 69%, SE = 3%). Therefore, the total number of individuals in the population was estimated to be 133 (95% CI = 111-166) and 127 (95% CI = 106-160) for left and right side identifications respectively.

When using mark-recapture analysis to estimate population size, the capture probabilities must not be heterogeneous, with some individuals more identifiable than others, which could lead to negative bias in the population estimate (e.g. Hammond, 1986; 1990). To test for heterogeneity, the residual differences between the observed identification histories and the expected histories (from the fitted model) were plotted against the number of years observed (Fig. 3), with a U-shaped curve indicating heterogeneity (Cormack, 1985). This did not occur when the mortality model was fitted indicating that particular members of the population were not much more or less likely to be identified in the Gally in any year.

**Age/sex structure**

Data for all age/sex classes showed best fit with the mortality model (Table 4). However, there were insufficient data to test the mortality + trend model on these datasets. Some heterogeneity was observed in the residual plots (not shown), indicating that these age/sex class estimates may be negatively biased. The combined estimated number of individuals in each age and sex class was lower than the estimated total population size as there were some individuals in the population that had not been sexed (Table 4). Estimated mortality rates for each of the age/sex classes were lower than for the whole population (Table 3 and 4). However, the mortality rates of individuals would be expected to be biased downwards since they were more likely to have been sexed if they had survived long-term. The ratio of female/immature to males (sub-adult and mature combined) was close to parity (1.06:1) for the total estimated population, indicating that there were slightly more female/immatures than the combined numbers of maturing and mature males, which was not surprising as some immature males were included in the female/immature class. The ratio of sub-adult males to mature males was (1:1).
Residency

The emigration and re-immigration model best described the data, indicating that, within a summer, individuals may enter, leave and re-enter the Gully (Table 5 and Fig. 4). On average, there were 44 individuals in the Gully at any given time (33.1% of the population) and individuals resided in the Gully for approximately 20 days (19 days by left side identifications and 23 days by right side identifications). The standard error of the estimate of the residency period outside of the Gully was large in comparison to the actual estimate, which could indicate that individuals spend variable time periods outside the Gully and/or that the summer field seasons have not been able to sample a large number of exits from and re-entries to the Gully.

**Age/sex class differences**

The emigration and re-immigration models best described all three datasets (Table 6 and Fig. 5). Based on the emigration and re-immigration model, females/immaurates and mature males spent longer in the Gully than sub-adult males, but the standard errors for these estimates were large (Table 6). Similarly, the standard errors on the

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**Table 5**

<table>
<thead>
<tr>
<th>Dataset</th>
<th>Model</th>
<th>Estimated number of individuals in Gully at given time</th>
<th>Mean number of days whales remain in the Gully</th>
<th>Mean number of days whales remain outside of the Gully</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Left side (n=346)</td>
<td>Closed</td>
<td>81±21</td>
<td>-</td>
<td>-</td>
<td>7,873</td>
</tr>
<tr>
<td></td>
<td>Emigration</td>
<td>52±12</td>
<td>32±10</td>
<td>-</td>
<td>7,750</td>
</tr>
<tr>
<td></td>
<td>Emigration and re-immigration</td>
<td>44±5</td>
<td>19±17</td>
<td>62±272</td>
<td>5,736</td>
</tr>
<tr>
<td>Right side (n=133)</td>
<td>Closed</td>
<td>78±9</td>
<td>-</td>
<td>-</td>
<td>6,665</td>
</tr>
<tr>
<td></td>
<td>Emigration</td>
<td>49±6</td>
<td>35±8</td>
<td>-</td>
<td>6,685</td>
</tr>
<tr>
<td></td>
<td>Emigration and re-immigration</td>
<td>44±6</td>
<td>23±10</td>
<td>104±113</td>
<td>6,564</td>
</tr>
</tbody>
</table>

**Table 6**

<table>
<thead>
<tr>
<th>Age/sex class</th>
<th>Model</th>
<th>Number of individuals in Gully at given time</th>
<th>Mean number of days whales remain in the Gully</th>
<th>Mean number of days whales remain outside of the Gully</th>
<th>AIC</th>
</tr>
</thead>
<tbody>
<tr>
<td>Female/immaurates (n=91)</td>
<td>Closed</td>
<td>25±3</td>
<td>-</td>
<td>-</td>
<td>2,845</td>
</tr>
<tr>
<td></td>
<td>Emigration</td>
<td>16±2</td>
<td>38±16</td>
<td>-</td>
<td>2,790</td>
</tr>
<tr>
<td></td>
<td>Emigration and re-immigration</td>
<td>15±2</td>
<td>30±16</td>
<td>-</td>
<td>2,791</td>
</tr>
<tr>
<td>Sub-adult male (n=17)</td>
<td>Closed</td>
<td>10±2</td>
<td>-</td>
<td>-</td>
<td>386</td>
</tr>
<tr>
<td></td>
<td>Emigration</td>
<td>7±3</td>
<td>57±64</td>
<td>-</td>
<td>384</td>
</tr>
<tr>
<td></td>
<td>Emigration and re-immigration</td>
<td>4±2</td>
<td>7±4</td>
<td>18±18</td>
<td>377</td>
</tr>
<tr>
<td>Mature male (n=33)</td>
<td>Closed</td>
<td>14±1</td>
<td>-</td>
<td>-</td>
<td>1,445</td>
</tr>
<tr>
<td></td>
<td>Emigration</td>
<td>11±5</td>
<td>62±10</td>
<td>-</td>
<td>1,445</td>
</tr>
<tr>
<td></td>
<td>Emigration and re-immigration</td>
<td>9±1</td>
<td>22±55</td>
<td>-</td>
<td>1,430</td>
</tr>
</tbody>
</table>

* SE very large (over 1 million)

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estimates of time spent in and out of the Gully by each age/sex class were large (Table 6), so it was difficult to determine whether the different classes have differing residency times in the Gully.

Year differences
Although there were some differences in the residency rate of different age and sex classes (Table 6), all classes were pooled together to increase sample sizes for looking at yearly differences (Fig. 9). Residency rates were calculated for 1990, 1996 and 1997 (all years with more than two months in the field and reasonably large sample sizes). The lagged identification rates for 1990 and 1997 were similar and best fit the emigration and re-immigration model (Table 7). The field season in 1990 was shorter than in 1996 and 1997, which may account for the reduced maximum lag values. In 1990 and 1997, individuals spent 12 days on average in the Gully. In 1996 however, individuals spent fewer days in the Gully (mean = 5 days).

**DISCUSSION**

**Population size and trends**
A previous estimate of the Gully population size (230 animals; Whitehead et al., 1997b) was much larger than found in this study (130 animals). However this difference was not due to a declining population, but to a difference in
the estimated proportion of the population that was reliably
marked. In the earlier estimate, only individuals with notches
on the dorsal fin were included in the population estimate
analysis, and it was estimated that 29% of the population was
notched. The estimated number of notched individuals
(based on mark-recapture modelling) was similar to the
estimated number of reliably marked individuals in this
study. However, quantitative analysis of mark change
(Gowans and Whitehead, 2001) indicated that 66% of the
population can be considered reliably marked. Thus, the
difference between the previous estimates of the proportion
of notched individuals (29%) and the current estimated
proportion of reliably marked individuals (66%) accounted
for most of the difference in estimated total population size.
The recent analysis of reliable markings was more rigorous
than that used by Whitehead et al. (1997b) and therefore the
new population estimate is more accurate.

The Gully population is small and may be largely distinct from
other populations of northern bottlenose whales in the
North Atlantic. Differences in sizes of individual whales
found in the Gully and those found elsewhere in the North
Atlantic (Whitehead et al., 1997b) suggest that this
population may be reproductively isolated. The small
population size found here also suggests that the Gully
population may be relatively isolated; if whales from the
Gully were freely mixing with other North Atlantic
bottlenose whales, our estimate of 130 animals would apply
to the entire North Atlantic. Recent sightings of northern
bottlenose whales off Labrador, Iceland and the Faroe
Islands indicate that the North Atlantic population is much
larger than 130 animals (Gunnlaugsson and Sigurjonssson,
1990; Reeves et al., 1993). Furthermore, there is a
statistically significant difference between the distribution of
mtDNA haplotypes between the Gully and Labrador (M.L.
Dalebout, pers. comm.). The Gully population has probably
always been small, although it may still be recovering from
the whaling catch of up to 87 individuals between 1962 and
1967 (Reeves et al., 1993). While no significant trend in
population size was detected when the mortality + trend
model was fitted (Table 3), the size of this small population
should continue to be monitored as a larger sample size may
indicate a significant trend.

Estimated mortality rates (which also included mark
change and permanent immigration) were imprecise (see
95% CI in Table 3) and were higher than expected for a
long-lived marine mammal (e.g. Small and DeMaster,
1995). The rate at which individuals gain reliable marks was
estimated to be 3.3% per year and such marks were not lost
over time (Gowans and Whitehead, 2001), although some
marks may be obscured by the gain of new ones. If mark
change is estimated at 3% per individual per year, then the
mortality + permanent emigration rate can be estimated at 10
or 11% per year for left and right identifications respectively.
This is still higher than those found by Small and DeMaster
(1995) for other long-lived marine mammals. There are few
indications of causes of mortality for the Gully population.
However, in August 1999, one immature individual was
observed entangled, almost certainly fatally, in monofilament fishing line, probably from the longlines that are set for swordfish (Xiphias gladius) across the Gully in
late summer and autumn.

Small population sizes and high mortality rates are
implicated in the decline and likely extinction of certain
cetacean species and populations (e.g. North Atlantic right
whales, Eubalaena glacialis and vaquita, Phocoena sinus;
Caswell et al., 1999; Jaramillo-Legorreta et al., 1999). The
small size of the Gully population of northern bottlenose
whales does not indicate that bottlenose whales are likely to
become extinct as recent surveys off Iceland and the Faroe
Islands, as well as sightings from the Davis Strait, indicate
that northern bottlenose whales are routinely sighted
further north than the Gully (Sigurjonsson et al., 1989;
Gunnlaugsson and Sigurjonsson, 1990; Reeves et al., 1993).
However, little is known about the size of the more northern
aggregations. While there is some evidence for reproductive
isolation between northern bottlenose whales in the Gully
and other areas of the North Atlantic (see above), low levels
of migration (one or two individuals per generation) can
reduce inbreeding (Stacey et al., 1997) and low levels of
migration may be occurring. However, the small population
size in the Gully does indicate that the population could
easily be threatened by human activity.

Residency rate
Throughout the summer field season, individuals enter the
Gully, spend on average approximately 20 days there and
then leave, to re-enter at some later time. The inter-annual
variability in the use of the Gully (by both proportion of
individuals found in the Gully and residency period) could
be linked to either ecological factors or human activity.
Annual patterns of distribution and abundance of northern
bottlenose whales in the Gully were correlated with some
oceanographic features (e.g. depth of scattering layer; Hooker, 1999). However changes in ecological factors between 1990, 1996 and 1997 (such as prey density or distributions) have not been directly studied (e.g. Harrison and Fenton, 1998 and references therein). There have been marked differences in human activity near the Gully over this time period. In 1990, there was an active fishery for groundfish along the edges of the Gully and little activity related to natural gas exploration or exploitation. However, in 1996 and 1997 there was no groundfish fishery in the area (due to a moratorium imposed in 1993) but there was an increase in activities related to gas exploration and exploitation.

CONCLUSION

Results from this study indicate that the Gully population of bottlenose whales is smaller than previously estimated, although a declining population is not indicated. Analysis of the residency patterns of individuals in the Gully indicates that individuals routinely visit the Gully (likely several times a year) for days to months at a time, and thus the Gully area appears to be an important habitat for these whales. Establishment of a marine protected area, which prohibits the activities that threaten these whales, is an excellent way of ensuring the survival of this unique population. However, since individuals appear to leave the Gully regularly, it suggests that protection in the Gully alone may not be sufficient. Further work is needed to assess the importance of other potential habitats along the shelf edge and deeper offshore waters.

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REFERENCES


[Appendix 1 is overleaf]
Appendix 1

POPULATION ESTIMATION MODELS

Beginning with the closed (Schnabel) model, let \( N \) be the population size. There are \( I \) samples, \( i = 1, ..., I \), at times \( t_1, ..., t_I \), and on the \( i \)th sample \( n_i \) individuals are identified. Then the identification rate on the \( i \)th sample is:

\[
p_i = \frac{n_i}{N} \tag{1}
\]

The probability that an animal sighted on the \( i \)th sample is next sighted on the \( j \)th sample is:

\[
q_{ij} = p_j \prod_{k<i \land k<j} (1-p_k) \tag{2}
\]

And the probability that an animal sighted on the \( i \)th sample is not sighted again is:

\[
r_i = \prod_{k<i \land k<\geq i} (1-p_k) \tag{3}
\]

If, of the \( n_i \) individuals identified on the \( i \)th sample, \( m_{ij} \) are next sighted on the \( j \)th sample, and \( a_i \) are not sighted again, then the log-likelihood of the dataset (conditioning on first capture) is approximately:

\[
L = \sum_{i=1}^{I} \left[ \sum_{j<i} m_{ij} \log(q_{ij}) + a_i \log(r_i) \right] \tag{4}
\]

\( N \) is simply chosen to maximise \( L \) in equation (4) using the Nelder-Mead Simplex method.

For the mortality model (with mortality plus emigration plus mark change of delta \( \delta \) per animal per year), equations (2) and (3) are changed by:

\[
q_{ij} = e^{-\delta(t_j-t_i)} p_j \prod_{k<i \land k<j} (1-p_k), \tag{5}
\]

\[
r_j = \prod_{j<i \land j<\geq i} \left[ e^{-\delta(t_j-t_i)} (1-e^{-\delta(t_j-t_i)}) \prod_{k<i \land k<j} (1-p_k) \right] + e^{-\delta(t_j-t_i)} \prod_{k<i \land k<j} (1-p_k) \tag{6}
\]

Now we choose both \( N \) and \( \delta \) to maximise \( L \) in equation (4).

Finally, for the mortality plus trend model, with a rate of growth of the population at \( \mu \) per year, equation (1) is changed by:

\[
p_i = \frac{n_i}{(N_M e^{\mu(t_i-t_f)} - 0.5(t_i-t_f))} \tag{7}
\]

where \( N_M \) is the population size at the midpoint of the sampling, \( 0.5(t_i-t_f) \)

Now we choose both \( N_M \), \( \mu \) and \( \delta \) to maximise \( L \) in equation (4).