

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 = 106-160 from right side identifications). The population was not closed, with the combined mortality, mark change and emigration rate estimated at 13% 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 19 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; whalers 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 canyon.

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'-60°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-value) 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 Arnborn, 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

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Table 1
Yearly distribution of field work in the Gully (43°30'N-44°30'N; 58°30'W-60°W) and sightings rate, during good sighting conditions (daylight hours (0500 to 2000hrs), Beaufort < 4 and visibility > 500m).

Year	Dates in field	No. search hours	No. sightings	Sighting rate/ hour searching	Sighting rate SE
1988	8-21 Jul.; 25 Jul.-6 Aug.	30	7	0.23	0.088
1989	16-30 Jul.; 1-15 Aug.	170	57	0.34	0.044
1990	14-28 Jun.; 2-18 Jul.; 25 Jul.-12 Aug.	238	125	0.53	0.047
1991	23-26 Jul.	0	0	-	-
1992	24-28 Jul.	0	0	-	-
1993	10-23 Jul.	78	54	0.69	0.094
1994	31 Jul.-18 Aug.	84	25	0.29	0.060
1995	20 Aug.-2 Sep.	31	11	0.35	0.11
1996	7-25 Jun.; 4-21 Jul.; 27 Jul.-12 Aug.; 19 Aug.-2 Sep.	330	172	0.52	0.040
1997	7-23 Jun.; 1-19 Jul.; 24 Jul.- 6 Aug; 10-27 Aug.	304	157	0.52	0.041
1998	12-31 Jul.; 6-23 Aug.	181	107	0.59	0.057
1999	6-26 Jul.; 3-23 Aug.	255	136	0.53	0.046
All		1,701	851	0.50	0.017

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).

Table 2
Summary of photo-identification data ($Q \geq 2$) by year.

Year	No. of frames	No. individuals identified by left fin photographs		No. individuals identified by right fin photographs	
		All individuals	Reliably marked individuals	All individuals	Reliably marked individuals
1988	123	18	12	19	13
1989	1,202	109	56	96	53
1990	3,116	171	81	167	74
1991	27	8	5	5	3
1993	549	46	17	53	26
1994	370	54	20	43	20
1995	82	14	6	17	12
1996	1,751	94	54	86	47
1997	1,531	99	57	90	58
1998	2,404	74	42	68	40
1999	1,409	60	41	56	36

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 ($Q \geq 4$) containing individuals with reliable marks was divided by the total number of photographs ($Q \geq 4$). 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.

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.

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 $Q \geq 4$ photographs of reliably marked individuals using the POPAN module of SOCPROG 1.2 (developed in MATLAB by HW, programs available at: <http://is.dal.ca/~whitelab/index.htm>) with calendar years as units. Three models were fitted to the population estimates using the Akaike 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 (Gowans *et al.*, In press) the assumption of independence was not violated when estimating confidence regions 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, in press):

$$R(\tau) = \frac{P(\tau)}{N} \tag{1}$$

where:

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

Lagged identification rates were estimated from:

$$\hat{R}(\tau) = \frac{\sum_i \sum_{j:t_j=t_i+\tau} m_{ij}}{\sum_i n_i \sum_{j:t_j=t_i+\tau} n_j} \tag{2}$$

where:

- n_i = the number of individuals identified on occasion i ;
- m_{ij} = number of individuals identified on both occasions i and j ;
- t_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 over 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):

$$R = 1/N \tag{3}$$

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

$$R = \left(\frac{1}{N}\right)^{\frac{-\tau}{I}} \tag{4}$$

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

$$R = \frac{Oe^{-\tau(I_0+I/I)} + I}{(I+O)N} \tag{5}$$

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.

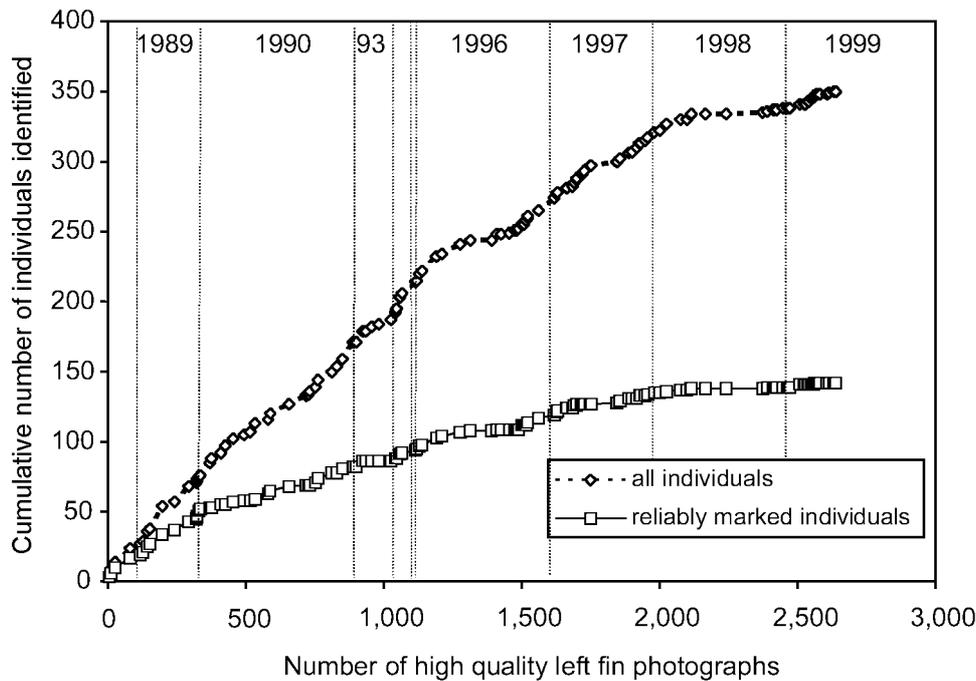


Fig. 1. Discovery curve showing the number of new individuals identified each day. An open population is indicated by the failure of the curves to reach an asymptote even within a single field season.

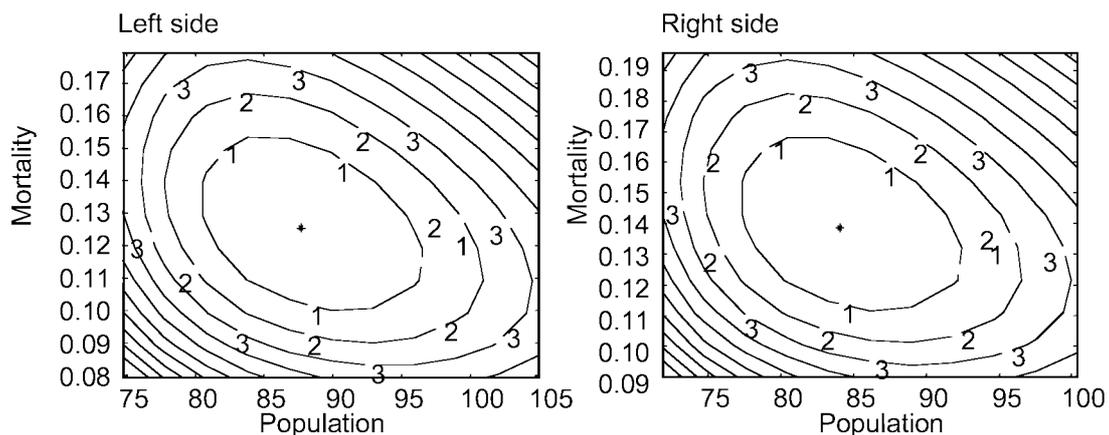


Fig. 2. Support surface contours for estimates of population size and mortality rate of reliably marked individuals, based on mortality model. Support function values less than two approximate the 95% CI region. * Indicates maximum-likelihood estimate.

Table 3

Population estimates for all reliably marked individuals (95% likelihood confidence intervals in brackets). Best-fit models based on Akaike Information Criterion (AIC) are given in *italics*.

Dataset	Model	Population estimate	Mortality (% per year)	Trend (% per year)	AIC
Left side (n=147)	Closed	151 (134-174)	-	-	760
	<i>Mortality</i>	88 (79-109)	13 (9-17)	-	682
	Mortality + trend	88 (78-101)	13 (9-17)	-0.13 (-3.4 + 3.9)	684
Right side (n=146)	Closed	153 (135-176)	-	-	763
	<i>Mortality</i>	84 (75-97)	14 (10-18)	-	673
	Mortality + trend	84 (75-97)	14 (10-19)	-0.45 (-4.5 + 3.1)	675

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

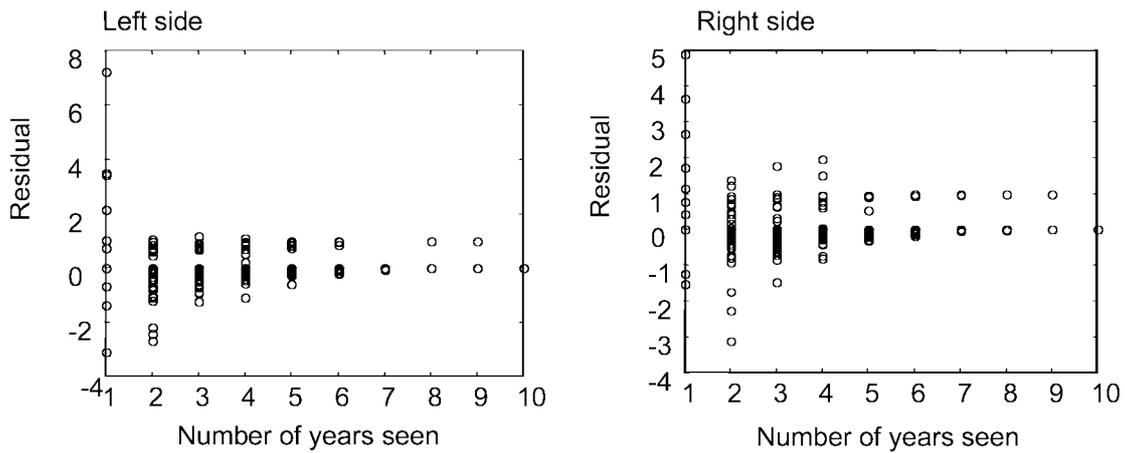


Fig. 3. Residual difference between the expected and observed number of individuals (based on mortality model) with each identification history plotted against the number of years identified for that identification history.

Table 4

Population estimates of reliably marked individuals within each age and sex class (95% CI). Results were for right side identifications, however, the left side results were similar. Best-fit models based on Akaike Information Criterion (AIC) are given in *italics*.

Dataset	Model	Population estimate	Mortality (%)	AIC	Population of sexed individuals (95% CI)
Female/immature male (n=45)	Closed	42 (36-52)	-	272	-
	<i>Mortality</i>	31 (27-38)	7.9 (3.2-14)	257	57 (45-77)
Sub-adult male (n=17)	Closed	18 (13-28)	-	70	-
	<i>Mortality</i>	15 (13-21)	12 (1.1 - 30)	67	22 (16-39)
Mature male (n=25)	Closed	25 (21-32)	-	162	-
	<i>Mortality</i>	18 (15-22)	6.7 (2.5-13)	145	27 (19-39)

estimate of reliably 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 79-101 individuals (left side) and 75-97 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 Gully 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/immatures 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).

Table 5

Estimated residency parameters (\pm SE) for all individuals in all years ($Q \geq 4$). Best-fit models based on Akaike Information Criterion (AIC) are given in *italics*.

Dataset	Model	Estimated number of individuals in Gully at given time	Mean number of days whales remain in the Gully	Mean number of days whales remain outside of the Gully	AIC
Left side ($n=346$)	Closed	81 \pm 21	-	-	7,873
	Emigration	52 \pm 12	37 \pm 10	-	7,750
	<i>Emigration and re-immigration</i>	44 \pm 5	19 \pm 17	62 \pm 272	5,736
Right side ($n=313$)	Closed	78 \pm 9	-	-	6,685
	Emigration	49 \pm 6	35 \pm 8	-	6,568
	<i>Emigration and re-immigration</i>	44 \pm 6	23 \pm 10	104 \pm 113	6,564

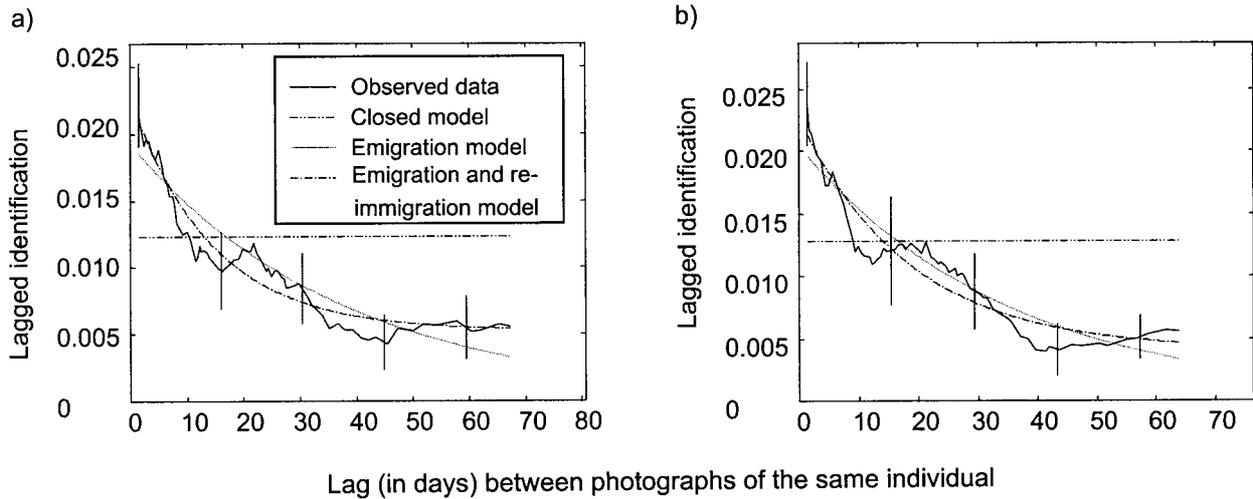


Fig. 4. Lagged identification rate (probability of re-identifying animal after a certain time lag) of northern bottlenose whales in the Gully for (a) left side identifications and (b) right side identifications. Vertical lines are jack-knife error bars.

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, female/immature males 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

Table 6

Estimated residency parameters (\pm SE) for each age/sex class based on left fin identifications in all years ($Q \geq 4$). Best-fit models based on Akaike Information Criterion (AIC) are given in *italics*.

Age/sex class	Model	Number of individuals in Gully at given time	Mean number of days whales remain in the Gully	Mean number of days whales remain outside of the Gully	AIC
Female/immature male ($n=91$)	Closed	25 \pm 3	-	-	2,845
	Emigration	16 \pm 2	36 \pm 16	-	2,790
	<i>Emigration and re-immigration</i>	15 \pm 2	30 \pm 16	236*	2,791
Sub-adult male ($n=17$)	Closed	10 \pm 2	-	-	386
	Emigration	7 \pm 3	57 \pm 64	-	384
	<i>Emigration and re-immigration</i>	4 \pm 2	7 \pm 4	18 \pm 18	377
Mature male ($n=33$)	Closed	14 \pm 1	-	-	1,445
	Emigration	11 \pm 5	60 \pm 10	-	1,431
	<i>Emigration and re-immigration</i>	9 \pm 2	22 \pm 35	35*	1,430

* SE very large (over 1 million).

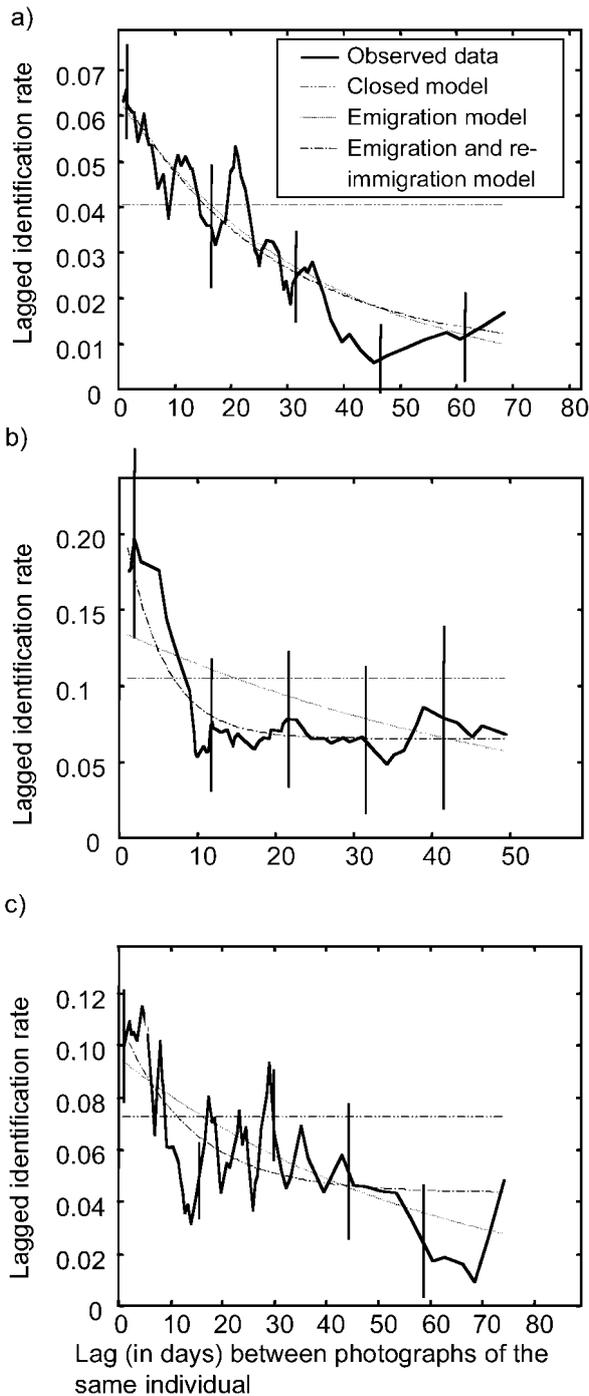


Fig. 5. Lagged identification rate (probability of re-identifying animal after a certain time lag) of northern bottlenose whales in the Gully for each age/sex class: (a) female/immature male; (b) sub-adult male; (c) mature male. Vertical lines are jack-knife error bars.

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. 6). 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

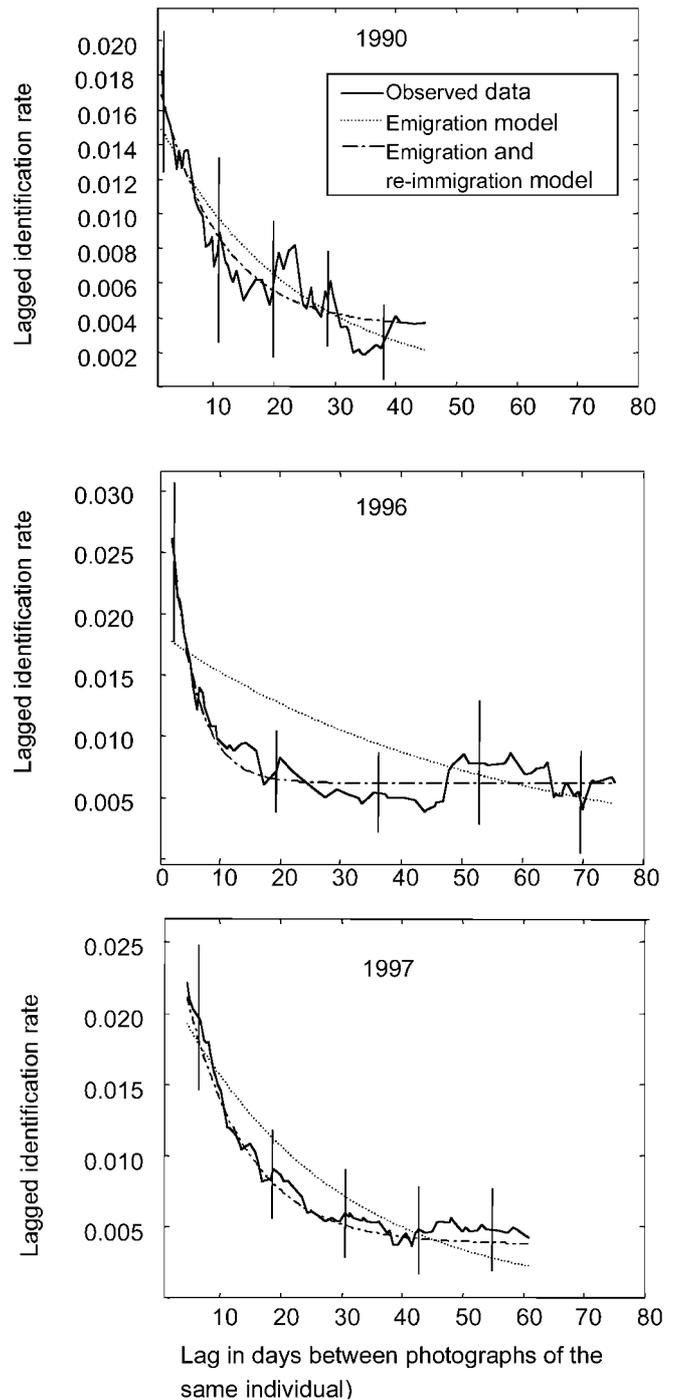


Fig. 6. Lagged identification rate (probability of re-identifying animal after a certain time lag) of northern bottlenose whales in the Gully for each field season that extended over two months. Vertical lines are jack-knife error bars.

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

Table 7

Estimated residency model parameters (\pm SE) for individuals based on left fin identifications in each of the years with long field seasons ($Q \geq 4$). Best-fit models based on Akaike Information Criterion (AIC) are given in *italics*.

Year	Model	Estimated number of individuals in Gully at given time	Mean number of days whales remain in the Gully	Mean number of days whales remain outside of the Gully	AIC
1990 ($n=119$)	Closed	124 \pm 21	-	-	2,018
	Emigration	63 \pm 17	22 \pm 8	-	1,975
	<i>Emigration and re-immigration</i>	53 \pm 19	12 \pm 12	55*	1,974
1996 ($n=81$)	Closed	95 \pm 20	-	-	1,131
	Emigration	54 \pm 16	53 \pm 30	-	1,110
	<i>Emigration and re-immigration</i>	27 \pm 9	5 \pm 3	25 \pm 17	1,096
1997 ($n=79$)	Closed	103 \pm 21	-	-	858
	Emigration	43 \pm 11	26 \pm 8	-	823
	<i>Emigration and re-immigration</i>	32 \pm 16	12 \pm 10	84 \pm 136	822

* SE very large (over 1 million).

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 Sigurjónsson, 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 (*Xiphius 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; Jarmillo-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 (Sigurjónsson *et al.*, 1989; Gunnlaugsson and Sigurjónsson, 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 is suggested 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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[Appendix 1 is overleaf]

REFERENCES

- Arnbom, T. 1987. Individual identification of sperm whales. *Rep. int. Whal. Commn* 37:201-4.
- Caswell, H., Fujiwara, M. and Brault, S. 1999. Declining survival probability threatens the North Atlantic right whale. *Proc. Natl Acad. Sci. USA* 96(6):3,308-13.
- Cormack, R.M. 1985. Examples of the use of GLIM to analyse capture-recapture studies. pp. 243-73. In: B.J.T. Morgan and P.M. North (eds.) *Statistics in Ornithology*. Springer-Verlag, Berlin. 418pp.
- Edwards, A.W.F. 1992. *Likelihood*. John Hopkins University Press, Baltimore. 275pp.
- Gowans, S. and Whitehead, H. 2001. Photographic identification of northern bottlenose whales (*Hyperoodon ampullatus*): sources of heterogeneity. *Mar. Mammal Sci.* 17:76-93.
- Gowans, S., Dalebout, M.L., Hooker, S.K. and Whitehead, H. 2000. Reliability of photographic and molecular techniques for sexing northern bottlenose whales (*Hyperoodon ampullatus*). *Can. J. Zool.* 78:1224-9.
- Gowans, S., Whitehead, H. and Hooker, S.K. In press. Social organisation in northern bottlenose whales (*Hyperoodon ampullatus*): not driven by deep water foraging? *Anim. Behav.*
- Gray, D. 1882. Notes on the characters and habits of the bottlenose whale (*Hyperoodon rostratus*). *Proc. Zool. Soc. Lond.* 1882:726-31.
- Gunnlaugsson, T. and Sigurjónsson, J. 1990. NASS-87: Estimation of whale abundance based on observations made onboard Icelandic and Faroese survey vessels. *Rep. int. Whal. Commn* 40:571-80.
- Hammond, P.S. 1986. Estimating the size of naturally marked whale populations using capture-recapture techniques. *Rep. int. Whal. Commn* (special issue) 8:253-82.
- Hammond, P.S. 1990. Heterogeneity in the Gulf of Maine? Estimating humpback whale population size when capture probabilities are not equal. *Rep. int. Whal. Commn* (special issue) 12:135-9.
- Harrison, G. and Fenton, D. 1998. The Gully: a scientific review of its environment and ecosystem. Department of Fisheries and Oceans Canadian Stock Assessment Secretariat Research Document 98/83. 282pp. [Available from: <http://www.ncr.dfo.ca/csas>].
- Hooker, S.K. 1999. Resource and habitat use of northern bottlenose whales in the Gully: Ecology, diving and ranging behaviour. Ph.D. Thesis, Dalhousie University, Halifax. 211pp.
- Jarmillo-Legorreta, A.M., Rojas-Bracho, L. and Gerrodette, T. 1999. A new abundance estimate for vaquitas: First step for recovery. *Mar. Mammal Sci.* 15:957-73.
- Jolly, G.M. 1965. Explicit estimates from capture-recapture data with both death and immigration - a stochastic model. *Biometrika* 52:225-47.
- Reeves, R.R., Mitchell, E. and Whitehead, H. 1993. Status of the northern bottlenose whale, *Hyperoodon ampullatus*. *Can. Field-Nat.* 107(4):490-508.
- Sigurjónsson, J., Gunnlaugsson, T. and Payne, M. 1989. NASS-87: Shipboard sightings surveys in Icelandic and adjacent waters June-July 1987. *Rep. int. Whal. Commn* 39:395-409.
- Small, R.J. and DeMaster, D.P. 1995. Survival of five species of captive marine mammals. *Mar. Mammal Sci.* 11(2):209-26.
- Stacey, P.B., Johnson, V.A. and Taper, M.L. 1997. Migration within metapopulations: The impact upon local population dynamics. pp. 267-91. In: I. Hanski and M.E. Gilpin (eds.) *Metapopulation Biology: Ecology, Genetics and Evolution*. Academic Press, San Diego. 512pp.
- Whitehead, H. 1990. Mark-recapture estimates with emigration and re-immigration. *Biometrics* 46:473-9.
- Whitehead, H. In press. Analysis of animal movement using opportunistic individual-identifications: Application to sperm whales. *Ecology*
- Whitehead, H., Faucher, A., Gowans, S. and McCarrey, S. 1997a. Status of the northern bottlenose whale, *Hyperoodon ampullatus*, in the Gully, Nova Scotia. *Can. Field-Nat.* 111:287-92.
- Whitehead, H., Gowans, S., Faucher, A. and McCarrey, S. 1997b. Population analysis of northern bottlenose whales in the Gully, Nova Scotia. *Mar. Mammal Sci.* 13(2):173-85.

Appendix 1

POPULATION ESTIMATION MODELS

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

$$p_i = n_i / N \quad (1)$$

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

$$q_{ij} = p_j \prod_{k:i < k < j} (1 - p_k) \quad (2)$$

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

$$r_i = \prod_{k:i < k \leq I} (1 - p_k) \quad (3)$$

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

$$L = \sum_{i=1, \dots, I-1} \left[\sum_{j=i+1, \dots, I} m_{ij} \text{Log}(q_{ij}) \right] + s_i \text{Log}(r_i) \quad (4)$$

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 (δ) per animal per year), equations (2) and (3) are changed by:

$$q_{ij} = e^{-\delta(t(j)-t(i))} p_j \prod_{k:i < k < j} (1 - p_k), \text{ and} \quad (5)$$

$$r_i = \prod_{j:i < j \leq I} \left[e^{-\delta(t(j-1)-t(i))} (1 - e^{-\delta(t(j)-t(j-1))}) \prod_{k:i < k < j} (1 - p_k) \right] + e^{-\delta(t(I)-t(i))} \prod_{k:i < k \leq I} (1 - p_k) \quad (6)$$

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

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

$$p_i = n_i / (N_M e^{\mu(t(i)-0.5(t(I)-t(1)))}) \quad (7)$$

where N_M is the population size at the midpoint of the sampling, $0.5(t(I)-t(1))$

Now we choose both N_M , μ and δ to maximise L in equation (4).