

Survival of adult blue whales *Balaenoptera musculus* in the Gulf of St. Lawrence, Canada

Christian Ramp^{1,2,*}, Martine Bérubé³, Wilhelm Hagen², Richard Sears¹

¹Mingan Island Cetacean Study, 285 rue Green, St. Lambert, Quebec J4P 1T3, Canada

²Marine Zoologie, Universität Bremen, Postfach 330 440, 28334 Bremen, Germany

³Ecosystem Science Division, Department of Environmental Science, Policy & Management, University of California at Berkeley, 151 Hilgard Hall #3110, Berkeley, California 94720-3110, USA

ABSTRACT: Blue whales in eastern Canadian waters are regarded as endangered, mainly due to the lack of knowledge on their abundance and life parameters. Here, we analysed sighting histories of 362 photo-identified blue whales in the Gulf of St. Lawrence over 24 yr to estimate, for the first time, the adult survival rate of this species. The results revealed that some whales have high site fidelity while others are only visitors to the St. Lawrence. Low sighting reliability of transient whales resulted in an age structure for which there is no obvious biological justification and led us to discard the data set with all blue whales. Based on sighting records of individuals of known sex, we consider the best estimate for adult blue whale survival to be 0.975 (95% CI 0.960 to 0.985). This estimate is likely to be biased upwards by long-term records of individuals first sighted in the 1980s and sexed from biopsy samples in the 1990s, but biased downwards by emigration from the study area. The relative magnitude of these biases is, at present, unquantifiable. Trap dependency affects the probability of capture and varies between the sexes, but no significant difference in survival was found between the sexes.

KEY WORDS: Survival rate · Blue whale · Modelling transients · Trap dependence

—Resale or republication not permitted without written consent of the publisher—

INTRODUCTION

Stock health assessments and population dynamics modeling require estimates of adult survival rate (Barlow et al. 1997). Increase in mortality or decrease in survivorship, respectively, can indicate changes in the ecological conditions of a species and reveal potential threats to the stock. The annual adult survival rate of northern right whales *Eubalaena glacialis*, for example, decreased from 0.99 in the early 1980s to 0.94 in the late 1990s. This drop was caused by human-induced mortality such as ship strikes and net entanglements, and could lead to the extinction of that stock in approximately 200 yr (Caswell et al. 1999). Estimating the survival rate of a stock and its changes over time is thus an important tool for the health assessment of that population (e.g. Kraus et al. 2005).

The status of blue whales in Canadian Atlantic waters was recently changed to 'endangered' (Sears & Calambokidis 2002). Blue whale numbers have been described as being in the low hundreds (Mitchell 1974), and there is no evidence that the stock has recovered from the impact of whaling, which for blue whales ceased in the North Atlantic in 1955. Catch records show that blue whales were not as abundant in the western North Atlantic as in the eastern part or around Iceland, where most of the catches were made (Jonsgård 1955). The 'early' whalers also believed that there were 2 different stocks of blue whales in the North Atlantic. However, the International Whaling Commission (IWC) never adopted the hypothesis of different stocks (Donovan 1991). Acoustic studies have led to the speculation that blue whales occur over the entire North Atlantic Ocean basin (Clark 1994) and could thus indicate a single panmictic stock (National Marine Fisheries Service [NMFS] 1998).

*Email: christianramp@web.de

Research by Mingan Island Cetacean Study (MICS) showed that blue whales in eastern Canadian and New England waters belong to 1 stock, as supported by numerous matches (Sears & Calambokidis 2002). In contrast, no matches were found between these animals and an existing photo-identification (ID) catalogue from Iceland (Sears & Calambokidis 2002). Therefore, we regard the animals in the Gulf St. Lawrence (GSL) as part of a western North Atlantic stock. Resolving their relationship with animals in more easterly North Atlantic waters is dependent on future demographic genetic analyses.

In this study, we analysed individual sighting records from the longest study (24 yr) on living blue whales (Sears et al. 1990) to determine a survival rate for adult animals in the northwest Atlantic population. Geographic heterogeneity of the data does not allow an estimation of abundance (Hammond et al. 1990), and also creates difficulties when modeling survivorship. To overcome the problems of heterogeneous data, specific modeling approaches such as transients and trap dependency were used. Furthermore, we investigated potential differences in survivorship between sexes.

MATERIALS AND METHODS

Data set and research area. Individual blue whales can be recognized by the pigmentation on their flanks (Sears et al. 1990). Since 1979, MICS has maintained the blue whale catalogue for the northwest Atlantic, where the emphasis for fieldwork lies in the GSL. Sightings by other stations were also included and represented observations from the Gulf of Maine, Nova Scotia, Newfoundland and West Greenland. A total of 388 animals were included in the catalogue through to the end of 2002. Some animals were identified both in and outside the GSL, while 22 animals were only identified outside. We ignored sightings from outside the GSL because they represented opportunistic sightings, and thereby reduced the data set to 366 animals.

The main sampling period in the GSL took place from June to October, although some data were also collected during early spring and late fall. The vast majority of the sightings were recorded in August and September during peak abundance of blue whales in the GSL (Sears et al. 1999). Observations were

made from small semi-rigid inflatable boats. From these platforms, photos and biopsy skin samples were taken. Since the whole GSL cannot be sampled homogeneously, areas of high productivity such as the Anticosti/Mingan Islands area, the Gaspé area and the Estuary were sampled regularly (Fig. 1). Additional sightings were obtained from secondary sites along the north and the south shore of the GSL. An individual was recorded as identified (and alive) in a given year, regardless of the number or location of its sightings in that year.

During the entire study (1979 to 2002), 4 out of 13 observed calves were identified. Although for most mammals juvenile mortality is substantially higher than for adults, in whales there is less evidence of this (Evans & Stirling 2001). The determination is difficult to obtain, but for gray whales *Eschrichtius robustus* a higher juvenile mortality rate (10% yr⁻¹) was observed compared with adults (5.5%) (Reilly 1984). For humpback whales, juvenile mortality in their first year is estimated to be 12.5% in the Atlantic (Barlow & Clapham 1997) and 18% in the Pacific (Gabriele et al. 2001). Therefore, the 4 blue whale calves, which were never sighted again, were not included in the analysis to avoid age differences in mortality/survivorship, which lead to an overall data set of 362 animals (Table 1).

Skin samples were obtained by biopsy sampling (Palsbøll et al. 1991) between 1990 and 2002, and sex was determined using Polymerase Chain Reaction (PCR) (Mullis & Faloona 1987). The technique is based upon a set of 3 primers that are specific to either the ZFY or ZFX sequence found on the sex chromosome of

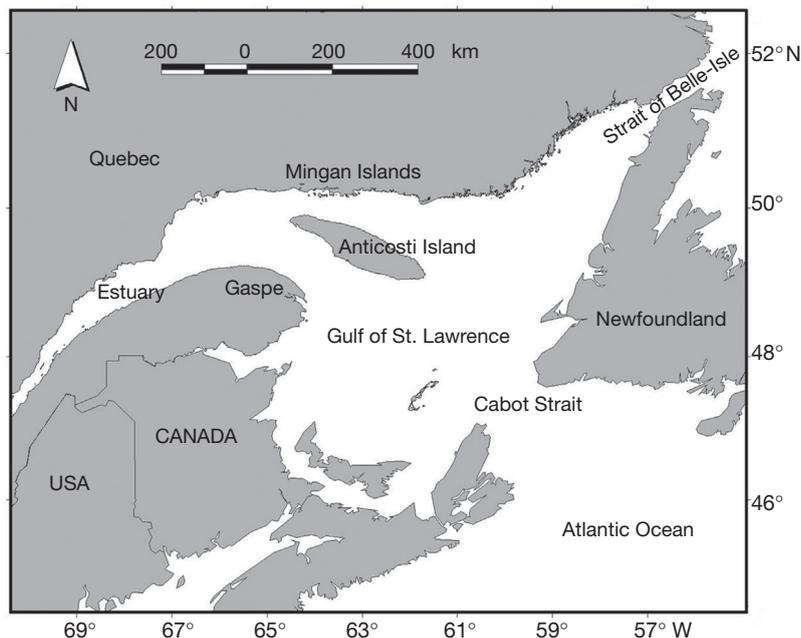


Fig. 1. Study area—the Gulf of St. Lawrence (GSL)

Table 1. *Balaenoptera musculus* data set. Annual number of identified whales (1979 to 2002), separated into new and known animals, those seen exclusively in 1 yr only, plus cumulative numbers of unique animals (catalogue, Cat.)

Year	Total seen	New	Known	Sexed	Only that year	Cat.	Cat. sexed	Sexed (% of total)
1979	8	8	0	3	3	8	3	37.50
1980	16	13	3	7	2	21	8	43.75
1981	21	14	7	7	3	35	11	33.33
1982	19	15	4	2	3	50	13	10.53
1983	35	14	21	14	5	64	21	40.00
1984	51	33	18	17	9	97	29	33.33
1985	91	58	33	36	21	155	49	39.56
1986	19	3	16	6	1	158	49	31.58
1987	33	8	25	13	2	166	51	39.39
1988	55	21	34	29	5	187	63	52.73
1989	29	10	19	19	2	197	70	65.52
1990	61	21	40	30	4	218	77	49.18
1991	61	20	41	37	2	238	89	60.66
1992	62	15	47	45	6	253	100	72.58
1993	91	24	67	62	11	277	113	68.13
1994	97	22	75	72	11	299	126	74.23
1995	49	8	41	40	3	307	130	81.63
1996	59	9	50	41	3	316	132	69.49
1997	74	7	67	63	1	323	138	85.14
1998	22	1	21	17	1	324	138	77.27
1999	55	4	51	39	2	328	139	70.91
2000	91	17	74	63	10	345	144	69.23
2001	93	12	81	60	9	357	146	64.52
2002	71	5	66	48	5	362	146	67.61
Sum	1263	362		770	124			
Mean	52.63	15.08			5.17			
SD	27.89	11.89			4.66			

cetaceans (Palsbøll et al. 1992). The products of the amplification, which indicate sex, can be easily distinguished on an agarose gel electrophoresis due to their different lengths.

This technique has been available since 1990. Sexes determined genetically were applied to all previous sightings of individuals.

Data analysis. The Cormack-Jolly-Seber (CJS) model (Cormack 1964, Jolly 1965, Seber 1965) is an open-population model and was used in this analysis. The model makes several assumptions (see Pollock et al. 1990) that can rarely be met in field studies (Hammond 1986, Lebreton et al. 1992), e.g. all animals must have the same chance of being captured during every sampling occasion. This is particularly true for highly mobile species such as the blue whale that inhabits vast areas such as the whole western North Atlantic. While it appears unlikely to obtain a reliable abundance estimate from sampling the GSL alone (Hammond et al. 1990), analysis of survivorship is less sensitive to geographical heterogeneity of the data (Hammond 1986).

Previous analyses (Hammond et al. 1990) have shown that our data are heterogeneous. A high proportion of animals were seen only once and these individual differences cause problems in the modelling process, even for the estimation of the survival rate. Here, we chose 2 ways to model heterogeneity in the data, (1) transient whales and (2) trap dependency.

A transient individual is hereafter defined as an individual that is sighted and which then permanently emigrates from the sample, such that is no longer available for encounter in the future (Pradel et al. 1997). Inclusion of these whales with regular animals would result in a lower survival rate estimate. Transients in the population were modeled after Pradel et al. (1997). Two age-class models for survivorship treat the first interval over all cohorts as the first age-class and all other intervals over all cohorts as the second age-class, regardless of the actual unknown age of an animal. Animals captured only once are therefore in the first age-class, and the second class is not biased by them. Pradel et al. (1997) also present an ad hoc method to overcome the transient problem, which is to delete the first sighting of each individual. This left truncation of the data set suppresses the influence of the lower survival estimate of transients.

Trap dependency (Sandland & Kirkwood 1981) was also included in the model. It was not thought to be a genuine trap dependence. Models that include trap dependence are useful to account for other structural effects that mimic trap dependence, for instance general heterogeneity of sighting probabilities among individuals (Pradel 1993). However, for simplicity it will be referred to as trap dependency. We used test statistics of the software 'U-CARE' to determine trap dependency and transients (Choquet et al. 2003).

Parameters and notation. The following parameters and notation were used in this analysis: (1) Survival probability (ϕ) in the population at risk between successive sightings and re-sighting occasions for individuals alive in the trapped population at the first of 2 sample occasions; (2) Probability of capture (p) at an occasion for individuals at risk of sighting at that occasion (Burnham & Anderson 1992). The apparent survival rate is the product of the true survival rate and site fidelity, but for simplicity here will be referred to as survival rate.

The notation of Burnham et al. (1987), Sandland & Kirkwood (1981) and Lebreton et al. (1992) was used also for effects that influence the parameters sex (s), trap dependency (m), time (t) and 2 age-classes ($2a$). A parameter constant over time was noted as (\cdot). These main effects were added singly and in combination, leading to numerous constraints and models. This description follows Burnham & Anderson (1992), to which

the reader is referred for more details. The model ' $\phi_{(t)}p_{(t)}$ ' stands for the full time-dependent CJS model, where the parameters might vary over all intervals and trapping occasions, respectively. For example, ' $\phi_{(s)}p_{(s+t)}$ ' denotes the model with no time effect on survival rates, but different constant survival rates for males and females, while the probability of capture is influenced by sex, time and the interaction sex by time. These are hereafter called interaction models. In contrast, additive models constitute another type of constrained model that makes effects such as time proportional between sexes. They have no interaction term between the effects (time/sex) and are denoted by ' $p_{(s+t)}$ '.

Model selection. A general model was fitted to the data for each data subset, i.e. the fully time-dependent CJS model ' $\phi_{(t)}p_{(t)}$ ', which allows the survival rate and probability of capture to fluctuate between intervals and sighting occasions, respectively. It is a heavily parameterised model but therefore has a greater flexibility that results in smaller variance (deviance).

We applied a goodness-of-fit (GOF) test to verify that the chosen general model fitted the data reasonably well. GOF tests not only provide the test statistics but also give an estimation of the over-dispersion factor (Lebreton et al. 1992), also called variance inflation factor (Burnham & Anderson 1992) noted hereafter as \hat{c} . For the GOF test, the program 'U-CARE' (Choquet et al. 2003) was used. The GOF test statistics include 4 different tests, each testing different aspects of the data. In short, TEST2 components test for differences among individuals between occasions in the probability of capture, hence assessing overall heterogeneity in the data. TEST3 components test for differences in survivorship among individuals between 2 occasions. Both tests compare observed versus expected frequencies in a 2×2 χ^2 table. The results of all 4 test components are pooled together to produce the GOF outcome and to calculate the \hat{c} estimate. For more details and components of TEST2 and TEST3 see Burnham et al. (1987) and Choquet et al. (2003).

Further model selection was based on the likelihood criterion 'Akaike Information Criterion' (AIC) (Akaike 1985) in the program 'MARK' (White & Burnham 1999). The AIC evaluates the fit of the model together with the number of parameters used to achieve this fit. The model with the smallest AIC value has the best model fit with the least parameters, following the 'principle of parsimony' (McCullagh & Nelder 1990). In this analysis, model selection was based on the small sample version of the Akaike Information Criterion (AIC_c) (Burnham & Anderson 2002). Furthermore, we adopted a strategy from the same authors to select the most appropriate model from a set of candidate models. If the difference in the AIC_c (ΔAIC_c) between 2 models is less than 2, both models are believed to have

similar support. Models having an ΔAIC_c between 2 and 7 have considerably less support, and models with an ΔAIC_c exceeding 10 have almost no support. Very often it is not a single model that has all the support, but rather a set of models. In this case, a model-averaging process was used, in which parameters were estimated over the models with most support, proportional to their AIC_c weight (Burnham & Anderson 2002).

Since the appropriate starting model was adjusted for over-dispersion with \hat{c} , the model selection was based on the Quasi Akaike Information Criterion (QAIC_c) and the $\Delta QAIC_c$, respectively. Standard errors (SE) and confidence intervals (CI, 95%) were also computed for the parameter estimates ϕ and p , and in their computation the over-dispersion factor was included.

RESULTS

Full data set

The sighting histories of 362 individual blue whales were used in this analysis. Altogether they account for 1263 sightings and re-sightings over 24 yr, an average of 3.48 sightings ind.⁻¹. The number of identified individuals sighted fluctuated considerably among years (Fig. 2).

Among the 362 animals, there was a wide variety in the number of different years that they were observed. While 1 individual was observed in 18 different years, 124 (34%) animals were sighted in only 1 year. Frequency of observation is shown in Fig. 3. The GOF test rejected the full time-dependent CJS model with probability < 0.001.

Since 124 animals were seen only once, heterogeneity was an important factor for the rejection of the model. To overcome the transient problem, the first sighting of each individual was deleted. This truncation reduced the data set to 23 yr and 238 animals; thereafter, the CJS model was applied to the reduced data set. The GOF test still rejected the model (probability = 0.0119), but only 1 of the TEST2 components was significant. The rejection of that test then led to the immediate trap response model ' $\phi_{(t)}p_{(t+m)}$ ' (Pradel 1993). The over-dispersion factor was applied with $\hat{c} = 1.364$.

The trap response model with 65 parameters did not improve the QAIC_c value. However, the additive model ' $\phi_{(t)}p_{(t+m)}$ ' fitted the data better than the CJS model. Reducing time as an effect of the survival rate also improved the fit of the model. A two age-class model was applied to the survival rate (both constant) and this model had by far the most support (Table 2).

Parameter estimates for the best model (Table 2) were ϕ (first class) = 0.845 (SE = 0.0377, CI = 0.7566/0.9061), and ϕ (second class) = 0.946 (SE = 0.009, CI =

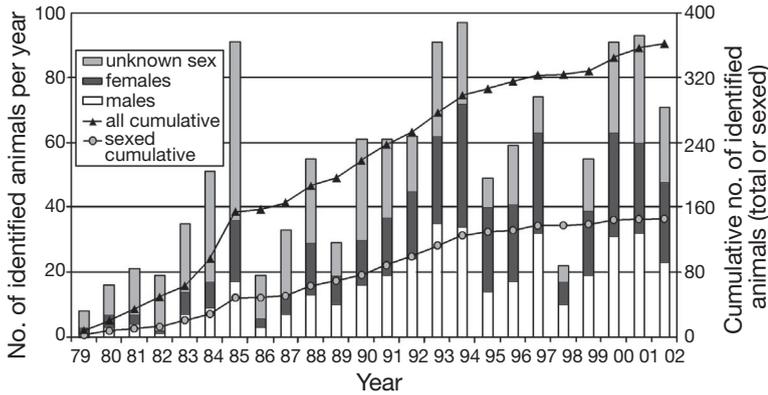


Fig. 2. *Balaenoptera musculus*. Number of identified whales (ind. yr⁻¹ by sex) in the Gulf of St. Lawrence, and cumulative number of identified (total and sexed) individuals

0.09255/0.9615). The second-best model $\phi_{(t)}P_{(t+m)}$ with a constant survival rate over all cohorts estimated $\phi = 0.933$ (SE = 0.0086, CI = 0.9145/0.9486).

Sexed animals

The sex of 146 ind. was known, representing 40 % of the 362 total ind., but accounting for over 60 % (n = 770) of the sightings and re-sightings. More males (77) than females (69) were included in the data set, but females accounted for more sightings (389) than males (381). Thus, a female was seen on average in 5.64 different years and a male in 4.94.

The fluctuation of the sightings of identified and sexed whales per year is very similar to the fluctuation of the sightings of all blue whales (Fig. 2). There was no clear indication if one sex was sighted more regularly per year than the other. The main difference between the 2 data sets (i.e. sexed versus all individuals) is in the frequency of capture (Fig. 3). Sexed animals were seen more often (on average 5.37 sightings).

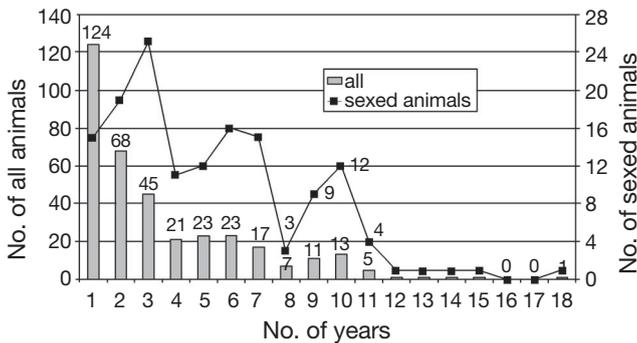


Fig. 3. *Balaenoptera musculus*. Sighting/capture frequency of all identified blue whales and sexed individuals

The full time-dependent CJS model was fitted to the data. The GOF test rejected the model (probability = 0.0139). Closer examination of the test results revealed that there was a significant difference between sexes. All tests for males were non-significant, and the CJS model thus fitted the data adequately well (probability = 0.148). For females, 3 tests were non-significant, but one of the TEST2 components was rejected (probability < 0.001) indicating that the assumption of equal catchability was not met. Due to this single test, the entire CJS model was rejected for females (probability = 0.017) and for both groups combined (probability = 0.0139).

The 3 other non-significant tests led to the immediate trap response model $\phi_{(t)}P_{(t^*m)}$ as a starting point. Additional tests for trap dependency showed that males were also influenced by this effect, even though it did not lead to the rejection of the CJS model for that group.

A \hat{c} estimate of 1.055 was applied to the model set. The adjusted trap response model $\phi_{(t)}P_{(t^*m)}$ had the lowest deviance, but since it was heavily parameterised its QAIC_c was larger than that of the CJS or the additive model $\phi_{(t)}P_{(t+m)}$. This was true for all interaction models. After fitting a series of combinations, it became apparent that a model with a sighting probability including time and trap dependence $P_{(t+m)}$ performed best (Table 3). Results also showed that time did not play an important role for ϕ' and therefore could be disregarded.

Differences between the sexes were expected in light of the GOF test results. Including sex as an effect on survival and/or sighting probability did improve the models until trap dependency was added. Subsequently, the influence of the factor sex became diminished. Adding this factor into the sighting probability slightly improved the final model set. It is important to

Table 2. *Balaenoptera musculus*. Model selection for left-truncated data set (n = 238). Applied over-dispersion factor $\hat{c} = 1.364$. Models ordered by their Quasi Akaike Information Criterion (QAIC_c). para.: parameters

Model	QAIC _c	ΔQAIC _c	QAIC _c weights	No. para.	Qdeviance
$\phi_{(2a)}P_{(t+m)}$	1767.08	0.0000	0.9167	25	1715.48
$\phi_{(t)}P_{(t+m)}$	1771.90	4.8193	0.0824	24	1722.42
$\phi_{(t)}P_{(t)}$	1780.85	13.7673	0.0009	23	1733.49
$\phi_{(t)}P_{(t+m)}$	1802.34	35.2599	0.00	44	1709.33
$\phi_{(t)}P_{(t)}$	1812.83	45.7479	0.00	43	1722.05
$\phi_{(t)}P_{(t)}$	1830.48	63.3963	0.00	2	1826.47
$\phi_{(t)}P_{(t^*m)}$	1835.93	68.8460	0.00	65	1694.78

Table 3. *Balaenoptera musculus*. Model selection for survival rate estimation of sexed animals (n = 142). Applied over-dispersion factor $\hat{c} = 1.055$. This is only a selection of models applied to the data set, which led to the 4 most supported models. QAIC_c: Quasi Akaike Information Criterion; para.: parameters

Model	QAIC _c	ΔQAIC _c	QAIC _c weights	No. para.	Qdeviance
$\phi_{(.)}P(t+s+m)$	2060.03	0.000	0.531	25	2008.16
$\phi_{(.)}P(t+m)$	2061.98	1.956	0.200	24	2012.26
$\phi_{(s)}P(t+s+m)$	2062.17	2.147	0.182	26	2008.15
$\phi_{(s)}P(t+m)$	2063.64	3.609	0.087	25	2011.77
$\phi_{(t)}P(t+s+m)$	2077.93	17.904	0.000	47	1977.24
$\phi_{(t)}P(t+m)$	2079.39	19.366	0.000	46	1980.99
$\phi_{(s)}P(s+t)$	2089.17	29.141	0.000	25	2037.30
$\phi_{(.)}P(s+t)$	2089.21	29.178	0.000	25	2037.34
$\phi_{(.)}P(t)$	2091.84	31.814	0.000	24	2042.12
$\phi_{(s)}P(t)$	2093.61	33.583	0.000	25	2041.74
$\phi_{(t)}P(s+t)$	2099.23	39.200	0.000	46	2000.82
$\phi_{(t)}P(t)$	2102.08	42.055	0.000	45	2005.96
$\phi_{(t)}P(t^*m)$	2111.93	51.898	0.000	68	1961.56
$\phi_{(.)}P(s^*t)$	2121.55	61.523	0.000	47	2020.86
$\phi_{(t)}P(s^*t)$	2134.19	74.162	0.000	68	1983.82

note, however, that the second-best model did not have sex added as an effect at all.

The estimates of ϕ from the 4 best models are shown in Table 4. All models fell into a $\Delta QAIC_c$ interval smaller than 3, indicating that they all have considerable support. The fifth estimates in Table 4 represent a weighted average of the 4 models. Since 2 models estimated different survival rates for males and females, the average estimates also distinguish between both sexes.

The best estimate for the survival rate of blue whales was 0.975 for males, 0.976 for females, and 0.975 for both sexes combined. The CI intervals for males were always slightly smaller than for females.

However, the difference between the sexes regarding probability of sighting was more pronounced. The re-sighting rate of females is consistently higher than

Table 4. *Balaenoptera musculus*. Results for sexed animals: estimates of ϕ from the 4 best-supported models with SE, 95% CI, and weighted average. M: male; F: female

Model	Sex	ϕ	SE	CI lower	CI upper
$\phi_{(.)}P(t+s+m)$		0.9758	0.0061	0.9602	0.9854
$\phi_{(.)}P(t+m)$		0.9754	0.0061	0.9602	0.9849
$\phi_{(s)}P(t+s+m)$	M	0.9754	0.0083	0.9524	0.9874
	F	0.9762	0.0079	0.9543	0.9877
$\phi_{(s)}P(t+m)$	M	0.9721	0.0080	0.9511	0.9842
	F	0.9792	0.0076	0.9575	0.9899
Weighted average	M	0.9753	0.0067	0.9579	0.9856
	F	0.9761	0.0066	0.9588	0.9862

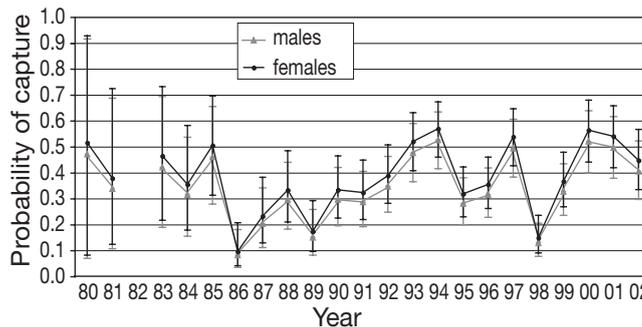


Fig. 4. *Balaenoptera musculus*. Estimates of probability of capture for males and females over sampling period (95% CI). No estimate is available for 1982 because no previously identified individuals were re-sighted

that of males (Fig. 4). Values were also calculated by the weighted average of the 4 models. The 2 models without sex as a constraint diluted the differences between sexes.

DISCUSSION

Survival rate

The full data set with all blue whales could not be used for the analysis due to overall heterogeneity in the data. Many whales appear to pass through the GSL only once and never return, or at least not for a long time. Truncation of the data set solved part of the problem. However, even with the reduced data set, a two age-class model performed best, suggesting that there were further transient whales in the data set even if test statistics were unable to detect this. There are blue whales that were observed for the second time 18 yr after their first sighting. Certainly, these are also whales that visit the Gulf only sporadically. One could subtract such animals that are seen only occasionally, e.g. twice in 10 yr, but any such choice would be arbitrary. Furthermore, the number of identified blue whales (362) in our final data set was too low to allow subtraction of many animals, especially since the left truncation had already removed 124 whales. This is also true for other approaches such as the robust design model (Kendall & Nichols 1995), which enables one to estimate temporary emigration.

Including trap dependency appeared to improve the model and to reduce heterogeneity, but did not solve the problem completely. The estimate of survival rate from the model that takes into account both trap dependence and transients is 0.946 for the second age-class. It appears, however, that not all effects could be modelled and that the value is biased low and does not represent a realistic value of blue whale survivorship.

The survival rate of 0.975 for sexed animals represents the best estimate of adult blue whale survival. However, there are several potential biases associated with this estimate, apart from the reduction of the data set itself. First, sexed animals were sighted more regularly than un-sexed blue whales: the more frequently an individual was sighted, the higher the chances that a biopsy skin sample could be obtained. Second, individuals that were only observed in the 1980s were excluded since no biopsy skin sample could be obtained. Only individuals that were sighted in both the 1980s and 1990s and from which a biopsy skin sample was obtained were included in this analysis. These animals were observed over a longer period, and therefore using them in the analysis resulted in an upward bias of the survival rate.

Best & Kishino (1998) provide several examples of potential biases in photo-identification data sets in general. Errors in comparing the pigmentation pattern of blue whales, for example, are more likely to result in the failure of recognizing a match rather than making a false match. More animals would lead to an overestimate of mortality and thus to a downward bias of the survival rate.

The age of all blue whales was not known, so juveniles could have been inadvertently included in the data set. Juveniles are thought to have a lower survival rate than adults (Reilly 1984), and their inclusion could therefore result in a downwards bias of adult survivorship estimate. We regard the influence of juveniles as small, since the data set of sexed animals included animals sighted more regularly and over longer periods. In addition, the result of the GOF test (TEST3) did not show any significant difference in survival among individuals. The test would have been significant if there were animals with different ages and different survival rates in the data set. Hence, there were either not many juveniles included in the data set, or differences between juveniles and adults were negligible.

In this analysis, one of the main sources of bias is emigration, which lead to an underestimate of the survivorship. Emigration of whales out of the research area leads to non-availability of certain individuals on the next sampling occasion. This heterogeneity in the data was the main problem in our analysis and appears to be of different significance for males and females.

The survival rate of 0.975 is thus biased both up- and downwards. The magnitude of both trends is not known. This value lies in the range of other baleen whale species such as bowhead whales *Balaena mysticetus*, for which a survival rate of 0.984 was estimated (Zeh et al. 2002). Best & Kishino (1998) presented similar values for reproductively active southern right whale females *Eubalaena australis*. For humpback

whales *Megaptera novaeangliae* in the Gulf of Maine, a non-calf survival rate of 0.96 was estimated (Barlow & Clapham 1997); for the North Pacific, Mizroch et al. (2004) gave estimates ranging from 0.963 to 0.984.

Our knowledge of the sources of mortality of blue whales is limited. Since 1979, 3 blue whales in the GSL have been reported to have drowned due to entanglement in fishing gear (Sears & Calambokidis 2002). Lethal ship strikes have so far not been documented in the GSL, but blue whales were occasionally killed or injured by ship strikes in other parts of the North Atlantic (NMFS 1998) and off California (Barlow et al. 1997). Sixteen per cent of the blue whales identified in the GSL bear scars that were likely to be caused by collisions with vessels. It is possible that lethal collisions might happen unnoticed, if a whale sinks after death (Sears & Calambokidis 2002).

Probability of capture

The results of probability of capture (Fig. 4) show that there is a large variation over the years: sighting probability is certainly time-dependent. This high fluctuation, especially pronounced at the beginning of the data set, was also caused by the small sample sizes. Thus, the CI and SE values of the estimates for the first years were rather large. There are potentially several reasons to account for this. In particular, survey effort was still increasing during the first third of the study period, and it was not until 1988 that effort became consistent over time and space. Sighting probability did not show an increasing trend during these early years. Usually, increasing effort results in more chances of encountering individuals. For the most part, variation in the probability of capture over time was not caused by variations in the survey effort. Environmental factors were more likely to have accounted for variability in the number of animals seen per year and thus in 'p'. Distribution and availability of food inside and outside the GSL are more likely explanations for the presence and absence of animals in these waters (e.g. Simard & Lavoie 1999). This phenomenon is very difficult to quantify and cannot yet be modelled. Furthermore, a shift in distribution of blue whales in the GLS has been observed (MICS unpubl. data). Between 1979 and 1992, an aggregation of blue whales was regularly found along the Quebec north shore and west of the Mingan Islands (Fig. 1); however, since the early to mid-1990s, this area seems to have lost its attraction to blue whales even though it remains intensively sampled. In general, only a few blue whales have been sighted along the north shore in the Mingan/Anticosti area since this time. Individuals that were regularly observed in this area are now sighted in other parts of the Gulf, but the majority

of animals known to have frequented this area vanished and were never seen again.

Comparison between males and females initially showed a difference in survival rate, until sex was included as a factor in the probability of capture. The GOF test revealed that females are more prone to trap dependency than males. Females are seen slightly more regularly than males. Additionally, temporary distribution during a season varies (Sears et al. 1999). While males only show one peak in abundance in August, females show 2: one in August and a second in October, closer to the breeding season. Trap dependence or effects mimicking this could disguise a real difference in survival rate, but this is impossible to prove at the moment.

CONCLUSIONS

The models could not clearly distinguish if the survival of blue whales varies by sex. The current data set does not allow this inference. Therefore, a survival rate of 0.975 is the best estimate for both sexes.

The data set has its limitations, which directly lead to limitations in analysis. Such limitations are particularly common in data sets of endangered species, which — almost without exception — do not occur in large numbers. Highly mobile species such as the blue whale cause even greater problems, because they inhabit vast regions that cannot be sampled homogeneously.

The magnitude of human-induced mortality is unknown, but it appears to be less significant than that of e.g. northern right whales in the North Atlantic. Human-induced mortality reduced the natural survival rate of that population significantly (Caswell et al. 1999). Nonetheless, future research must be undertaken to determine the potential influence of human-induced mortality on the GSL blue whale population.

The survival estimate is likely subject to both up- and downwards biases. Neither of these trends could not be quantified. In the future, research on blue whales should include methods to determine these biases, such as the Pollock robust design that estimates temporary and permanent emigration (Kendal & Nichols 1995).

Future studies should be designed to provide a reliable population estimate. In order to properly achieve this aim with regard to the GSL population, the study area should be extended to the offshore waters of eastern Canada and the USA. Investigations should be undertaken to determine trends in abundance of this population and underlying parameters, such as reproduction and (natural and human-induced) mortality. These have to be monitored on a long-term basis in

order to detect any significant changes. A stock health assessment for northwest Atlantic blue whales is necessary to provide the basis for any management plan to guarantee the survival of blue whales in eastern Canadian waters.

Acknowledgements. We thank the following organisations and persons for continuous effort and contribution to data collection: the GREMM and J. Giard in particular, H. Whitehead and associates, Team Meriscope, J. Gelinau, Y. Belanger, R. Roy and many others. We also thank numerous team members who worked hard over all these years to collect and process data. We are grateful to S. Mizroch, R. Barker, G. White and many members of the MARK online forum for suggestions, critiques/critical assessments and advice; T. Doniol-Valcroze and P. Hammond for comments on analyses and on multiple versions of our draft; 3 anonymous reviewers for improving the manuscript.

LITERATURE CITED

- Akaike H (1985) Prediction and entropy. In: Atkinson AC, Fienberg SE (eds) Celebration of statistics: the ISI centenary volume. Springer Verlag, New York, p 1–24
- Barlow J, Clapham PJ (1997) A new birth-interval approach to estimating demographic parameters of humpback whales. *Ecology* 78:535–546
- Barlow J, Forney KA, Hill PS, Brownell RL Jr and 6 others (1997) U.S. Pacific marine mammal stock assessment: 1996. NOAA Tech Mem NMFS Southwest Fish Sci Center 248
- Best PB, Kishino H (1998) Estimating natural mortality rate in reproductively active female southern right whales, *Eubalaena australis*. *Mar Mamm Sci* 14:738–749
- Burnham KP, Anderson DR (1992) Data based selection of an appropriate biological model: the key to modern data analysis. In: McCullough DR, Barrett RH (eds) *Wildlife 2001: populations*. Elsevier Applied Science, London, p 16–30
- Burnham KP, Anderson DR (2002) *Model selection and inference: a practical information theoretic approach*, 2nd edn. Springer Verlag, New York
- Burnham KP, Anderson DR, White GC, Brownie C, Pollock KH (1987) Design and analysis methods for fish survival experiments based on release recapture. *Am Fish Soc Monogr* No. 5, Bethesda, MD
- Caswell H, Fujiwara M, Brault S (1999) Declining survival probability threatens the North Atlantic right whale. *Proc Natl Acad Sci USA*, 96:3308–3313
- Choquet R, Reboulet AM, Pradel R, Gimenez O, Lebereton JD (2003) User's guide for U-CARE. CEFE/CNRS, Montpellier
- Clark CW (1994) Deep voices: insights from the Navy's whales '93 program. *Whalewatcher* 28:6–11
- Cormack RM (1964) Estimates of survival from the sighting of marked animals. *Biometrika* 51:429–438
- Donovan G (1991) A review of IWC stock boundaries. *Rep IWC Spec Issue* 13:39–68
- Evans PGH, Sterling I (2001) Life history strategies of marine mammals. In: Evans PGH, Raga JA (eds) *Marine mammals: biology and conservation*. Kluwer Academic, New York p 7–62
- Gabriele CM, Straley JM, Mizroch SA, Baker CS and 10 others (2001) Estimating the mortality rate of humpback whale calves in the central North Pacific Ocean. *Can J Zool* 79:589–600

- Hammond PS (1986) Estimating the size of naturally marked whale populations using capture-recapture techniques. Rep IWC Spec Issue 8:253–282
- Hammond PS, Sears R, Bérubé M (1990) A note on problems in estimating the number of blue whales in the Gulf of St. Lawrence from photo-identification data. Rep IWC Spec Issue 12:141–142
- Jolly GM (1965) Explicit estimates from capture-recapture data with both death and immigration stochastic model. Biometrika 52:225–247
- Jonsgård A (1955) The stocks of blue whales (*Balaenoptera musculus*) in the northern Atlantic Ocean and adjacent Arctic waters. Norsk Hvalfangsttid 44:505–519
- Kendall WL, Nichols JD (1995) On the use of secondary capture-recapture samples to estimate temporary emigration and breeding proportion. J Appl Stat 22:751–762
- Kraus SD, Brown MW, Caswell H, Clark CW and 12 others (2005) Ecology: North Atlantic right whales in crisis. Science 309:561–562
- Lebreton JD, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecol Monogr 62:67–118
- McCullagh P, Nelder JA (1990) Generalized linear models, 2nd edn. Chapman & Hall, New York
- Mitchel E (1974) Present status of northwest Atlantic fin and other whale stocks. In: Schevill WE (ed) The whale problem: a status report. Harvard University Press, Cambridge, MA, p 108–169
- Mizroch SA, Herman LM, Straley JM, Glockner-Ferrari DA, and 6 others (2004) Estimating the adult survival rate of central North Pacific humpback whales (*Megaptera novaeangliae*). J Mammal 85:963–972
- Mullis KB, Faloona F (1987) Specific synthesis of DNA in vitro via a polymerase-catalyzed chain reaction. Methods Enzymol 155:335–350
- National Marine Fisheries Services (NMFS) (1998) Recovery plan for the blue whale (*Balaenoptera musculus*). Prepared by Reeves RR, Clapham PJ, Brownell RL Jr, Silber GK for NMFS, Silver Spring, MD
- Palsbøll PJ, Larsen F, Sigurd Hansen E (1991) Sampling of skin biopsies from free ranging large cetaceans in West Greenland: development of new biopsy tips and bolt designs. Rep IWC Spec Issue 13:71–79
- Palsbøll PJ, Vader A, Bakke I, El-Gewely MR (1992) Determination of gender in cetaceans by the polymerase chain reaction. Can J Zool 70:2166–2170
- Pollock KH, Nichols JD, Brownie C, Hines JE (1990) Statistical inferences for capture-recapture experiments. Wildlife Monogr 107
- Pradel R (1993) Flexibility in survival analysis from recapture data: handling trap dependence. In: Lebreton JD, North PM (eds) Marked individuals in the study of bird populations. Birkhaeuser Verlag, Basel, p 29–37
- Pradel R, Hines JE, Lebreton JD, Nichols JD (1997) Capture-recapture survival models taking account of transients. Biometrics 53:60–72
- Reilly S (1984) Observed and published rates of increase in gray whales, *Eschrichtius robustus*. Rep IWC Spec Issue 6:389–399
- Sandland RL, Kirkwood GP (1981) Estimation of survival in marked populations with possibly dependent sighting probabilities. Biometrika 68:531–541
- Sears R, Calambokidis J (2002) Status of the blue whale, *Balaenoptera musculus*, in Canada. Report to the Committee on the Status of Endangered Wildlife in Canada (COSEWIC). Canadian Wildlife Service, Ottawa
- Sears R, Williamson MJ, Wenzel F, Bérubé M, Gendron D, Jones P (1990) Photographic identification of the blue whale (*Balaenoptera musculus*) in the Gulf of St. Lawrence, Canada. Rep IWC Spec Issue 12:335–342
- Sears R, Berchok C, Palsbøll P, Doniol-Valcroze T, Ramp C (1999) Gender related structure in blue whale (*Balaenoptera musculus*) pairs from the Gulf of St. Lawrence. In: Proc 13th Bienn Conf Biol Mar Mamm, 28 Nov–3 Dec, 1999, Oahu, HI. The Society for Marine Mammalogy, Lawrence, KS, p 169
- Seber GAF (1965) A note on the multiple recapture census. Biometrika 52:249–259
- Simard Y, Lavoie D (1999) The rich krill aggregation of the Saguenay-St. Lawrence Marine Park: hydroacoustic and geostatistical biomass estimates, structure, variability, and significance for whales. Can J Fish Aquat Sci 56:1182–1197
- White GC, Burnham, KP (1999) Program MARK Survival estimation from populations of marked animals. Bird Study 46 (Suppl):120–139
- Zeh J, Poole D, Miller G, Koski W, Baraff L, Rugh D (2002) Survival of bowhead whales, *Balaena mysticetus*, estimated from 1981–1998 photo-identification data. Biometrics 58:832–840

Editorial responsibility: Otto Kinne (Editor-in-Chief), Oldendorf/Luhe, Germany

Submitted: August 19, 2005; Accepted: January 23, 2006
Proofs received from author(s): July 25, 2006