

# Sex-specific survival in the humpback whale *Megaptera novaeangliae* in the Gulf of St. Lawrence, Canada

Christian Ramp<sup>1,2,\*</sup>, Martine Bérubé<sup>3</sup>, Per Palsbøll<sup>3</sup>, Wilhelm Hagen<sup>2</sup>, Richard Sears<sup>1</sup>

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

<sup>2</sup>Marine Zoologie (FB2), Universität Bremen (NW2), Postfach 330 440, 28334 Bremen, Germany

<sup>3</sup>Department of Genetics, Microbiology and Toxicology, Stockholm University, 106 91 Stockholm, Sweden

**ABSTRACT:** Sex-biased adult mortality is commonly observed in the animal kingdom. In mammals, a predominantly male-biased mortality is found in species with a polygynous mating system, while in monogamous taxa, female-biased mortality prevails. In the largest of all mammals, the Mysticeti, no sex-specific mortality has been found so far apart from that found in biased whaling data. We estimated sex-specific survival rates using an Akaike Information Criterion (AIC<sub>c</sub>)-based model selection of 18 yr of mark-recapture data from a North Atlantic humpback whale feeding aggregation, the Gulf of St. Lawrence, Canada. We found a significantly higher survival rate for females (0.992; 95% CI 0.985–0.999) than for males (0.971; 0.943–0.985). Humpback whales are a typical polygynous species, with males competing intensively for mates while females bear the costs of pregnancy and lactation. However, the existing data did not allow us to test if differential costs of reproduction are causing the skew in mortality. We could not preclude stock-specific differences, such as contamination levels, migratory distances, and reproductive parameters (e.g. calving intervals, age at sexual maturity), and further data are needed to investigate the underlying reasons.

**KEY WORDS:** Sex-specific survival · Mark-recapture models · Humpback whale · Gulf of St. Lawrence · Mating strategies

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## INTRODUCTION

Differences in adult survival between males and females are frequent in the animal kingdom. Sex-biased mortalities are commonly attributed to the different costs of reproduction of both sexes (e.g. Trivers 1972, Promislow 1992). Mate-competition is time and energy consuming and may increase adult mortality, especially in males. On the other hand, parental care, whose costs are often borne by females exclusively, may also lower survival (Clutton-Brock 1991). In mammals, elevated male mortality is common in polygynous mating systems (Trivers 1985), while in monogamous taxa, mortality is frequently female-biased (Promislow 1992). However, there are alternative explanations for sex-specific mortality, especially re-

gional differences such as variation in contamination level or other human-induced mortality in addition to stock-specific trade-offs in life history strategies (Fredriksen et al. 2005).

In cetaceans, male-biased mortality is found in polygynous toothed whales such as sperm whales *Physeter macrocephalus* (Ralls et al. 1980), killer whales *Orcinus orca* (Bigg et al. 1990) and pilot whales *Globicephala macrorhynchus* (Kasuya & Marsh 1984). In mysticete species, however, evidence of sex-specific survival is rare. Two studies based on whaling data found elevated female mortality rates in fin whales *Balaenoptera physalus* (Aguilar & Lockyer 1987) and grey whales *Eschrichtius robustus* (Reilly 1984). At least in the analysis on grey whales, fishery mortality was confounded with natural mortality, and the former

\*Email: christianramp@web.de

was female-biased. Our knowledge of mating systems in baleen whales is very limited. Grey whales and right whales migrate to distinct breeding grounds and appear to be promiscuous (Jones & Swartz 1984, Kraus et al. 2001), and their large testis:body weight ratios suggest sperm competition is an important factor in their mating strategy (Brownell & Ralls 1986). Most rorqual whales (Balaenopteridae) have rather small testis:body weight ratios (Brownell & Ralls 1986), indicating antagonistic male competition as the main male mating strategy, although so far only humpback whales *Megaptera novaeangliae* have been shown to engage in such male–male competition (Clapham 2000).

Humpback whales display a strong annual cycle, spending their summer months in maternally directed high- to mid-latitude feeding grounds and aggregate on common tropical to subtropical breeding grounds during the winter months (Katona & Beard 1990). They feed almost exclusively on the productive feeding grounds and live off their fat reserves the rest of the year (Lockyer 1984). The mating system has been described as polygynous/promiscuous (Clapham 2000, Cerchio et al. 2005), where male humpback whales compete aggressively with one or several males for access to a presumably oestrous female (Tyack & Whitehead 1983). Females bear the cost of rearing the offspring exclusively, representing a considerable investment (Lockyer 1981). Thus, humpback whales are a fairly typical example of a polygynous mammalian species.

Male and female humpback whales both suffer clear costs of reproduction, but these are difficult to quantify and to distinguish from other possible causes of sex-biased mortality. Thus, it is hard to predict which sex, if any, will exhibit lower survival. However, based on the generality of patterns observed in other mammals (including other cetaceans), we can hypothesize that polygynous humpback whales may show a male-biased mortality. Thus far, studies on the survival of humpback whales have presented a single specific survival rate (Barlow & Clapham 1997, Chaloupka et al. 1999, Mizroch et al. 2004), although it is not clear whether they found any evidence for sex-specific survival or if this subject was not investigated. Here we try to investigate if sex-specific survival exists in a humpback whale population. To do so, we analyzed 18 yr of mark-recapture data of humpback whales from one of the North Atlantic feeding aggregations, the Gulf of St. Lawrence.

## MATERIAL AND METHODS

**Data collection.** We conducted multiple annual research surveys in the Jacques-Cartier Passage in the Gulf of St. Lawrence (GSL), Canada (Fig. 1) between 1988 and 2005. This region has the highest density of humpback whales in the GSL during the summer (Ramp 2008). Surveys were conducted on a daily basis (weather permitting) from June to October, with an average of 500 survey hours per year. Additional surveys targeted the regions around Sept-Iles, the Estuary, and Gaspé (Fig. 1).

Individual humpback whales were identified from photographs of the ventral pigmentation pattern of the fluke (Katona & Whitehead 1981). Photographs were taken using either 35 mm black and white film or digital imaging from semi-rigid inflatable boats as platforms. Collection of identification photographs continued over multiple days in a specific area, until it was assumed that all individuals had been photographed. We considered an individual as captured for a given year when a high-quality photo was taken (Friday et al. 2000), regardless of how many times or where the animal was sighted in the GSL. The sex of an individually identified humpback whale was determined by molecular analysis (Bérubé & Palsbøll 1996) of genomic DNA extracted from remotely collected skin biopsy samples (Palsbøll et al. 1992).

**Data analysis.** We used the Cormack-Jolly-Seber (CJS) model (Cormack 1964, Jolly 1965, Seber 1965),

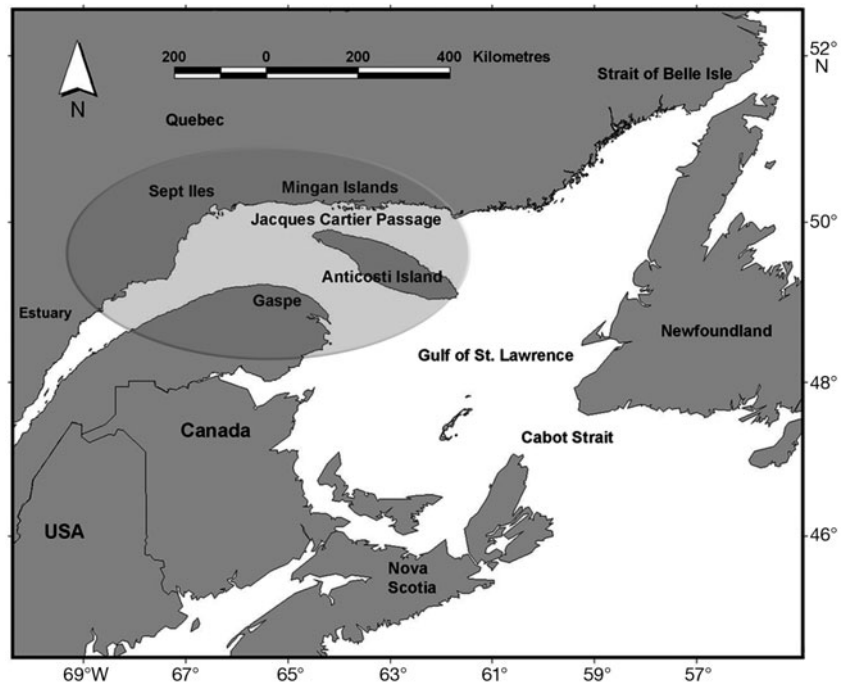


Fig. 1. *Megaptera novaeangliae*. Research area and approximate distribution of the St. Lawrence humpback whales (grey oval)

an open population model to estimate 2 parameters: the survival probability ( $\phi$ ) in the population at risk of capture in the interval between 2 successive sampling occasions for individuals alive in the first sampling event, and the probability of capture ( $p$ ) at an occasion for individuals at risk on that sampling occasion (Burnham & Anderson 1992). The apparent survival rate is the product of the true survival rate and the return of animals to the study area (site fidelity), but for simplicity we will refer to it as survival rate.

We tested numerous effects (e.g. sex) on survival and the probability of capture (Table 1). The notation follows Burnham et al. (1987), Lebreton et al. (1992), and Sandland & Kirkwood (1981). Age classes did not correspond to the real age of the animals but to the time they were first recorded in this study (i.e. time since first marking). We used 2 age classes to model transients to adjust for heterogeneity of survival among individuals (Pradel et al. 1997). Pradel et al. (1997) define transient animals as individuals that are sighted once and emigrate permanently afterwards from the population, such that they are no longer available for encounter in the future. The resulting survival of 0 would bias the survival rate downwards. To account for transients in a model the first interval over all cohorts is defined as the first age class and all other intervals over all cohorts as the second age class, regardless of the actual (usually unknown) age of the animals. Transient animals are therefore included in the first age class, leaving the survival of the second age class unbiased (Pradel et al. 1997, see also Sandercock 2006). In fact, the survival estimate of the first age class is the survival of the residents (second age class) multiplied by the proportion of residents in the sample. This confinement does not represent a biological meaningful survival rate and is just applied to obtain an unbiased estimate for the second age class.

The notation a2 indicated 2 age classes. A model  $\phi$  (a2 t/t) represented time-varying survival in both age classes, while  $\phi$  (a2 t/c) stands for time-varying survival

in the first age class, but constant in the second (i.e. the slash separates the 2 age classes).

We tested the effect of 2 more factors on the probability of capture. We added effort in hours of surveys per year to account for annual variation in the detection probability. Trap dependency ( $m$ ) (Sandland & Kirkwood 1981) was also applied to some models. It was not thought to represent genuine trap dependency but rather to account for structural effects mimicking trap dependency, such as heterogeneity of sighting probabilities among individuals (Pradel 1993). We included the effect as an individual covariate, taking into account whether or not an animal was sighted on the previous sampling occasion.

The main effects were added individually and combined in the model set, yielding numerous constraints and models (see Burnham & Anderson 1992 for more details). The model  $\phi_{(t)} p_{(t)}$  represents the full, time-dependent CJS model, where the parameters can vary over all intervals and capture occasions, respectively. The model  $\phi_{(s)} p_{(s \times t)}$  indicates no time effect on survival but sex-specific survival rates, while the probability of capture is influenced by sex, time and the interaction of sex and time. These are hereafter called interaction models. Models with time and sex as effects that are proportional to each other and without the interaction term are called additive models. They are denoted through  $p_{(s+t)}$ .

**Model selection.** We applied a general model to the data set and conducted a goodness-of-fit (GOF) test to determine if that model adequately fitted the data (Lebreton et al. 1992). The GOF test results also make possible the estimation of extra binominal variation, the so-called over-dispersion factor  $\hat{c}$  (Burnham & Anderson 2002). We used the U-CARE program (Choquet et al. 2005) to conduct the GOF test, which is divided into 4 different components (see Burnham et al. 1987, Choquet et al. 2005 for details), each testing a different aspect of the model fit. U-CARE also provides additional directional tests for trap dependency and

Table 1. *Megaptera novaeangliae*. Effects and notation used for modelling the survival rate of humpback whales

Parameter	Effect	Notation	Description
<b>Survival</b>	Time	$\phi_t$	Time varying survival
	Constant	$\phi_c$	Constant survival over time
	Sex	$\phi_s$	Survival as function of sex (male, female, sexed, and unknown)
	Age (class)	$\phi_{a2}$	Survival as a function of 2 age classes
	Calf	$\phi_{\text{calf}}$	Survival as a function of being a calf at first sighting
	Trend (linear)	$\phi_T$	Survival as a linear trend over time
<b>Probability of capture</b>	Time	$p_t$	Time varying probability of capture
	Sex	$p_s$	Probability of capture as a function of sex (male, female, and unknown)
	Age (class)	$p_{a2}$	Probability of capture as a function of 2 age classes
	Trap dependency	$p_m$	Probability of capture as a function of being sighted in previous year
	Effort	$p_{\text{effort}}$	Effort in $\text{h yr}^{-1}$
	Trend (linear)	$p_T$	Probability of capture as a linear trend over time

transients in the data. Trap dependency and non-random (Markovian) temporary emigration can both lead to significant GOF test results (TEST.2CT), but the 2 can be distinguished by the direct test for trap dependency (Schaub et al. 2004). Random temporary emigration is allowed under the model assumptions (Burnham 1993) and leaves the survival estimates unbiased (Kendall et al. 1997), in contrast to Markovian emigration, which has to be modeled in a multi-state mark-recapture approach (Schaub et al. 2004).

Further model selection was based on the Akaike Information Criterion (Akaike 1985, Burnham & Anderson 2002), corrected for small sample size ( $AIC_c$ ) using the program MARK (White & Burnham 1999). The model with the lowest  $AIC_c$  value has the best fit with the fewest parameters. When the difference in the  $AIC_c$  ( $\Delta AIC_c$ ) between 2 models was  $<2$ , both models were inferred to have similar support. A  $\Delta AIC_c >2$  but  $<7$  was inferred as low support for the least likely model, and a  $\Delta AIC_c >10$  was inferred as no support for the least likely of the 2 models. When several models showed some support, we applied a model-averaging procedure during which the parameters were estimated from the models in question proportional to their  $AIC_c$  weights (Burnham & Anderson 2002). We included effects (Table 1) to model the parameters and used the  $AIC_c$  to determine whether the effect improved the fit of the model. The magnitude of an effect, e.g. the difference between the sexes, is called effect size. If the 95% CI did not include 0, the effect size was statistically significant. When the variance-inflation

factor  $\hat{c}$  was applied, model selection was based on the quasi Akaike information criterion ( $QAIC_c$ ) (Burnham & Anderson 2002).

## RESULTS

We identified a total of 208 humpback whales among which 126 (68 females, 58 males) individuals were sexed using biopsy techniques exclusively. The data set also included 53 calves, 40 of them sexed (27 males, 13 females). The GOF test rejected the general model  $\phi_{(t \times s)} P_{(t \times s)}$  for the entire data set ( $p < 0.0001$ ). We then distinguished between sexed ( $n = 126$ ) and unsexed ( $n = 82$ ) animals accounting for 651 and 123 encounters, respectively. These 2 groups could not be pooled, and we disregarded the unsexed animals. The GOF test was then applied to the dataset of sexed animals with the starting model  $\phi_{(t \times s)} P_{(t \times s)}$ . The test was rejected ( $\chi^2 = 124.77$ ,  $df = 86$ ,  $p = 0.004$ ), although only one test component was significant for both sexes, indicating the presence of transients in the sample. There was no evidence of non-random temporary emigration. The direct test for transients was significant for both sexes, as was the directional test for trap dependency for females (trap-happy). We adjusted for transients following Pradel et al. (1997) and started with a 2 age class model for both sexes,  $\phi_{(2a \ t \times s/t \times s)} P_{(t \times s)}$ , thus including the survival of calves in the first age class. This general model (Model 17) (Table 2) was accepted ( $\chi^2 = 39.75$ ,  $df = 64$ ,  $p = 0.99$ ) and made a  $\hat{c}$

Table 2. *Megaptera novaeangliae*. Model selection for apparent survival. List includes only selected models leading to the best-supported ones and is in order of the Akaike Information Criterion ( $AIC_c$ ) value.  $AIC_c$  wt:  $AIC_c$  weights. See Table 1 for definitions of modelling notations

No.	Model	$AIC_c$	$\Delta AIC_c$	$AIC_c$ wt	No par	Deviance
1	$\phi_{(a2 \ T + \text{calf} + s/c + s)} P_{(a2 \ T + s + m/t + s + m)}$	1049.20	0.00	0.44	24	999.09
2	$\phi_{(a2 \ T + s/c + s)} P_{(a2 \ T + s + m/t + s + m)}$	1050.34	1.13	0.25	23	1002.40
3	$\phi_{(a2 \ T + \text{calf} + s/c + s)} P_{(a2 \ T + m/t + m)}$	1051.34	2.14	0.15	23	1003.40
4	$\phi_{(a2 \ T + \text{calf} + s/c + s)} P_{(a2 \ T + s + m/t + m)}$	1053.47	4.27	0.05	24	1003.36
5	$\phi_{(a2 \ T + \text{calf} + s/c + s)} P_{(a2 \ t + m/t + s + m)}$	1053.78	4.58	0.04	25	1001.50
6	$\phi_{(a2 \ T + \text{calf} + s/c)} P_{(a2 \ T + s + m/t + s + m)}$	1055.38	6.18	0.02	24	1005.27
7	$\phi_{(a2 \ T + \text{calf}/c + s)} P_{(a2 \ T + s + m/t + s + m)}$	1055.97	6.77	0.02	24	1005.86
8	$\phi_{(a2 \ T + s/c + s)} P_{(a2 \ t + s + m/t + s + m)}$	1056.49	7.29	0.01	24	1006.38
9	$\phi_{(a2 \ T + \text{calf}/c)} P_{(a2 \ T + s + m/t + s + m)}$	1059.12	9.92	0.00	23	1011.18
10	$\phi_{(a2 \ T + \text{calf} + s/c + s)} P_{(t + s + m)}$	1063.91	14.71	0.00	24	1013.80
11	$\phi_{(a2 \ t + s/c + s)} P_{(a2 \ t + s + m/t + s + m)}$	1066.95	17.75	0.00	39	983.32
12	$\phi_{(a2 \ c + \text{calf} + s/c + s)} P_{(a2 \ t + s + m/t + s + m)}$	1070.87	21.67	0.00	24	1020.76
13	$\phi_{(a2 \ c + \text{calf}/c + s)} P_{(a2 \ t + s + m/t + s + m)}$	1071.95	22.74	0.00	24	1021.84
14	$\phi_{(a2 \ c + \text{calf} + s/c + s)} P_{(t + s + m)}$	1080.38	31.18	0.00	23	1032.45
15	$\phi_{(a2 \ c + s/c + s)} P_{(t + s)}$	1112.99	63.78	0.00	21	1069.37
16	$\phi_{(a2 \ c \times s/c \times s)} P_{(t \times s)}$	1135.46	86.26	0.00	38	1054.12
17	$\phi_{(a2 \ t \times s/t \times s)} P_{(t \times s)}$	1166.56	117.36	0.00	93	945.60
18	$\phi_{(t \times s)} P_{(t \times s)}$	1249.26	200.06	0.00	66	1100.48

adjustment unnecessary; thus the model selection was based on  $AIC_c$ .

We applied different age structures to the survival and found a difference between the sexes. For males, the classic 2 age class model (Pradel et al. 1997) fitted the data best: the first age class included only the first sampling interval, while the first age class for females spanned the first 2 intervals, due to further heterogeneity of survival among individuals (transients). Thus, 31 females (11 calves) and 33 males (22 calves) fell under the definition of transients and were treated in the first age class. Time varying survival was not supported in both age classes (Model 16 vs. 17). The estimates of the first age class did vary with time, but most values were on the boundaries (0, 1) and thus were inestimable. A linear trend was applied and was better supported than models with time-varying or constant survival (Model 8 vs. 12). In the first age class, the distinction between males and females was supported (Model 1 vs. 7) and the covariate 'calf' improved the model fit further (Model 1 vs. 2). In the second age class, sex was the only supported factor (Model 1 vs. 6). All effects were applied as additive models; interaction models were not supported due to the number of inestimable parameters.

This was also true for the probability of capture, where time variation and sex were supported but not the interaction term (Model 15 vs. 16). We added trap dependency to females due to the direct test results under U-CARE, but the application for both sexes fitted the data best (Model 14). We applied several age structures, and a 2 age class model performed best, in which the first age class included the first 2 recaptures (Model 12 vs. 14). The same age structure was supported for both sexes. The estimates of the second age class were time varying, while for the first age class a linear trend performed best due to numerous parameters on the boundaries (Model 2 vs. 8). We applied sex and trap dependency in various combinations to both age classes (Models 2–5). The differences were marginal, but both effects were supported. Adding effort as covariate did not improve the model fit.

Several models had considerable support (Table 2). Therefore, the estimates

were model-averaged over the model set. The model-averaged survival estimates for the first age class of both genders is declining rapidly over the years (Fig. 2), indicating an increasing proportion of transients. The initial estimate is lower for males, and its decrease is also more pronounced than for females. For the second age class, the estimate of survival for females was 0.992 (95% CI 0.985–0.999) and for the males 0.971 (0.943–0.985). The effect size was 0.021 (0.004–0.380) and therefore statistically significant. Model 6 (Table 2) was the only model included in the model averaging giving a single survival estimate

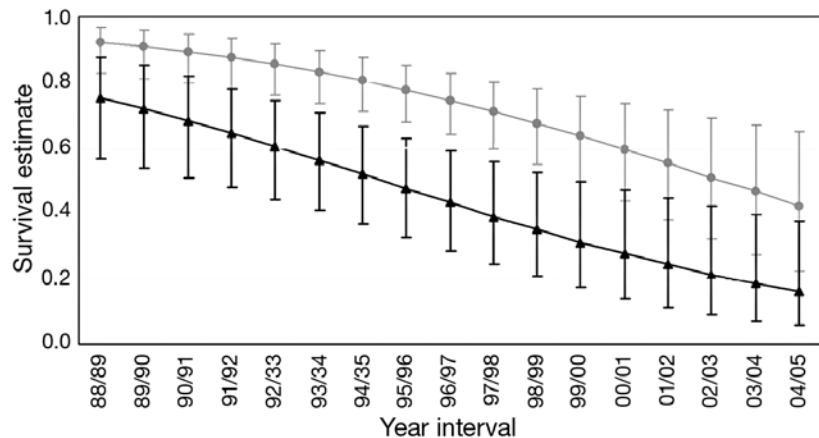


Fig. 2. *Megaptera novaeangliae*. Model-averaged apparent survival estimates for males (▲) and females (●) of the first age class with 95% CI

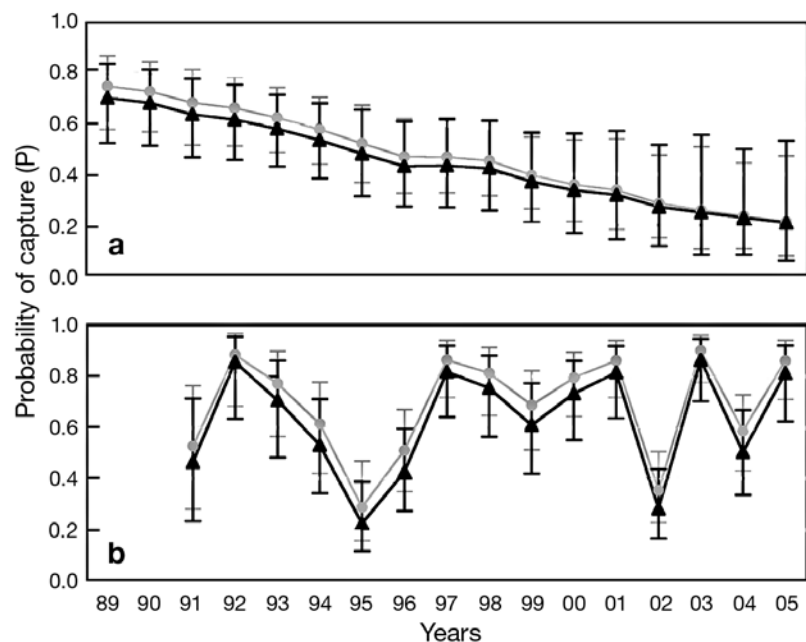


Fig. 3. *Megaptera novaeangliae*. Probability of capture for the (a) first and (b) second age class for males (▲) and females (●) with 95% CI

(0.982, CI 0.966, 0.991). It had only marginal support (AIC weight 0.02), but it is given here for comparison. The model-averaged estimates for the probability of capture are shown in Fig. 3. Due to the additive character of the models, the  $p$  estimates for different age and sex classes paralleled each other, with females having slightly higher  $p$  values than males in both age classes.

## DISCUSSION

### Modelling survival

The declining trend of the first age class was caused by the increasing number of transients, reflecting the rising number of calves in the second half of the study periods and does not represent a decrease in survival as such. Calves have a lower survival (Barlow & Clapham 1997, Gabriele et al. 2001, Rosenbaum et al. 2002), and their inclusion in the first age class left the second age class unbiased. We were not able to estimate calf or juvenile survival and limit the following discussion to the estimates of the second age class, i.e. to adult survival of humpback whales.

We used the 2 age class approach to obtain homogeneous estimates of adult survival among the individuals of both sexes. In humpback whales, as in most mammals, we would expect a third (juvenile) age class, but the survival was homogenous among the individuals in the second age class. This indicated either a marginal number of juveniles in the sample, or a low difference between juvenile and adult survival. Given the low number of re-sighted calves, the former appears more likely. There were just not many juveniles among the sample. The survival estimates of 0.971 for adult males and 0.992 for adult females in the GSL humpback whales were in a range similar to those reported by other studies that did not distinguish between the sexes. Barlow & Clapham (1997) estimated a non-calf survival rate of 0.96 (SE 0.008) among Gulf of Maine humpback whales; estimates for North Pacific humpback whales range between 0.957 (95% CI 0.943–0.967) and 0.983 (0.954–0.995) (Mizroch et al. 2004), while post-yearling survival off Australia was 0.966 (0.88–1.00) (Chaloupka et al. 1999). Whales sighted more frequently have a higher chance of being biopsied; thus, our estimates of survival rates, which included only genetically sexed animals, might be biased high. Best & Kishino (1998) list several potential biases in mark-recapture studies (e.g. misidentifications), most of them leading to an overestimate of mortality. Thus, our estimates may be biased in either direction. It is not possible to quantify the magnitude of these biases, but they should affect both sexes equally.

We estimated the apparent survival of humpback whales, which is the product of true survival and site fidelity, and differences in apparent survival between sexes could be caused by variation in site fidelity. However, we regard the differences in apparent survival as differences in the true survival, since there are few indications of different site fidelity between males and females on the feeding grounds, in contrast to the breeding grounds (Craig & Herman 1997). Both sexes did not differ significantly in their mean occurrence and occupancy within a season, nor in the average number of seasons sighted (Ramp 2008). In the North Atlantic, females are more likely to move between different feeding areas than males (Palsbøll et al. 1997), thus having a lower site fidelity resulting in a lower apparent survival. The opposite is the case in our study, and we therefore regard it as highly likely that the difference shown represents a difference in true survival.

The results are based on a relatively small sample size, but in mark-recapture experiments the precision of the estimates improves with a high recapture rate, many sampling occasions, and a high survival of individuals (Pollock et al. 1990), which was the case for our study. The question remained if the sample was representative of the entire population. A study performed on the same GSL individuals as those we examined did not find any evidence for sex-segregation, with males and females selecting areas with identical habitat characteristics (Doniol-Valcroze 2008). Thus, we are confident that the sample represents the humpback whale population summering in the Gulf of St. Lawrence.

### Probability of capture

The time variation in the probability of capture represented the fluctuation of animals sighted annually. In the CJS model,  $p$  is defined as the probability of capturing an individual in the population at risk on a given occasion (i.e. the detection probability). Temporary emigration, leading to the absence of animals in some years, is only allowed when it is random (Burnham 1993), which leaves the survival estimates unbiased (Kendall et al. 1997). The fluctuation in  $p$  was likely caused by the presence and absence of animals due to environmental factors such as prey availability (Simard & Lavoie 1999) and was not influenced by our relatively consistent effort. The observed temporary emigration was random and left the survival estimates unbiased. Females returned more regularly in the GSL, as indicated by a slightly higher capture probability in both age classes.

We found evidence of a difference between 2 age classes. Juveniles (non-calves) have a lower  $p$  than the

adult resident animals. Juvenile animals are often observed at the peripheries of the main aggregations (Weinrich et al. 1997, Robbins 2007). In addition to their smaller size, they raise their tail less frequently, which leads to a lower detection and identification probability. The time-varying models resulted in some inestimable parameters, and a linear trend was better supported. The decreasing trend in  $p$  was attributed to the fact that all animals seen initially in the beginning of the study had a high recapture rate, and there were few calves or juveniles among them. The proportion of animals with a lower recapture chance increased during the study period, causing the negative trend.

### Sex-specific adult survival

We showed that the survival rate for adult female humpback whales (0.992) was significantly higher than for males (0.971) in the Gulf of St. Lawrence. This is, to our knowledge, the first time that sex-biased adult mortality has been shown for a baleen whale species, apart from whaling data. Sex-specific mortality is common in mammals, and humpback whales do not seem to be an exception. Furthermore, one could argue that elevated male mortality in humpback whales was to be expected due to their polygynous mating system and the associated costs of reproduction, as found in many other mammalian species (Trivers 1985), but we did not possess the data to test this. In the following we discuss this hypothesis but also examine alternative explanations.

### Costs of reproductive behavior

Males engage in competitive groups that are often violent, and superficial wounds have been noted among the participating males (Tyack & Whitehead 1983, Baker & Herman 1984b), although serious or even lethal consequences are rare (Pack et al. 1998). In addition to the unknown, but nonetheless potentially high, energy expenditure, the fighting and resulting wounds (Tyack & Whitehead 1983) could make them more prone to parasites and infections, resulting in elevated mortality of the sex engaged in mate competition, as shown in other mammals (Moore & Wilson 2002).

The annual migration between winter breeding and summer feeding grounds of humpback whales is one of the most extensive among mammals (Stone et al. 1990), with migration distance ranging from 2000 to over 8000 km in the North Atlantic (Stevick et al. 2003). Adult finback and blue whales *Balaenoptera musculus* might use up to 25% of the annual energy budget during migration (Lockyer 1981), which might be even

higher for humpback whales due to their longer migration distances (Craig & Herman 1997). Several studies have identified a significant excess of males on the breeding grounds (Brown et al. 1995, Palsbøll et al. 1997), in contrast to the parity observed in the whole population (Palsbøll et al. 1997). The reason for this is still under debate, and it has been suggested that either some females do not migrate to the breeding grounds annually but winter at higher and more productive latitudes (Brown et al. 1995), that female residency time on the breeding ground is much shorter than for males (Palsbøll et al. 1997, Craig et al. 2001), or that females already impregnated during migration return to the feeding grounds before reaching the breeding areas (Craig & Herman 1997). Regardless of the underlying reason, adult male humpback whales spend more time on, or on the way to, the breeding grounds and may have considerably less time overall to forage compared to females, which in turn is likely to adversely affect survival rates.

The investment of female humpback whales in reproduction such as gestation and lactation is considerable (Lockyer 1981). However, the number and intensity of constraints due to male reproductive behavior, such as the annual migration, longer residency time on the breeding grounds, and the intense mate competition between males, could outweigh the female investment of rearing the offspring.

### Stock (region)-specific differences

The different migration distances among humpback whale stocks raise the question whether mortality in humpback whales is correlated with the extent of migration. The constraints of a longer migration and a potentially shorter feeding season apply to both sexes. However, if females do not migrate annually (Brown et al. 1995), males would suffer from comparatively higher costs of migration, and sex-biased mortality could be more pronounced in feeding aggregations at greater distances from the breeding grounds, such as the GSL (ca. 4000 km) compared with the Gulf of Maine (2500 km).

Sex-specific survival has not been examined in other mark-recapture studies on humpback whales (Barlow & Clapham 1997, Mizroch et al. 2004), despite the availability of larger sample sizes. Inter-population variation in life parameters was hypothesized to be an underestimated factor in some taxa (Frederiksen et al. 2005) and could explain potential differences between the GSL and other populations. Females in the GSL have longer calving interval (3.5 yr) (Ramp 2008) compared with females in the Gulf of Maine (2.4 yr) (Barlow & Clapham 1997). This could indicate reduced cost of reproduction over time and result in elevated survival.

Male balaenopterid whales in the GSL are more contaminated with poly-chlorinated biphenyls (PCBs) and organochlorines (such as DDT) than females, reflecting maternal transfer of contaminants to offspring (Gauthier et al. 1997, Metcalfe et al. 2004). Whether the elevated bioaccumulation of these contaminants in males increases mortality is unknown. Thus far, no evidence has been presented that the reported levels of these substances are sufficient to have lethal effects on baleen whales (O'Shea & Brownell 1994). Nonetheless, differences in contamination levels between areas (Hobbs et al. 2001) could not only cause inter-population variation in mortality, but could also drive sex-specific mortality. Further research is needed to investigate the potential effects of toxics on baleen whales, especially in semi-enclosed seas such as the GSL.

At this point we have listed potential explanations but cannot provide any evidence that stock-specific variables unique to the GSL were causing the sex-specific mortality in humpback whales. This is mainly due to the lack of sex-specific survival estimates for other humpback whale stocks, making a quantitative comparison impossible. We are aware that our results of sex-specific survival are based on one small population, and we recommend strongly that other stocks be studied in a similar manner. Although elevated male mortality falls within the expectation of a polygynous mammalian species, we could not test and therefore prove the hypothesis that the costs of reproduction cause the differential survival. Combining sighting data from the winter and summer grounds could be used to model the transition of becoming a breeding animal in the multi-state modelling framework. Especially the survival of females could be correlated with their reproductive transitions (lactating vs. pregnant vs. resting) and hence be linked with the associated costs of reproduction. Ultimately, more precise data on exoecology are needed to quantify the costs of reproduction for both sexes.

#### **Mortality, mating system, and sexual size dimorphism**

We presented evidence that male humpback whales in the GSL suffered from a higher mortality than females, and we suggest that at least one possible cause is differential costs of reproduction associated with their polygynous mating system (Trivers 1985). However, humpback whales are the only known balaenopterid species exhibiting intense physical fights among males, although the fact that all balaenopterids have small testes (Brownell & Ralls 1986) suggests antagonistic mate competition as the main mating strategy for the entire family. This would lead to the

question of whether other balaenopterids also display elevated male mortality. The 2 other Mysticeti families, the grey and right whales, are promiscuous (Jones & Swartz 1984, Kraus et al. 2001) and sperm competition seems to be their main mating strategy (Brownell & Ralls 1986). Under the hypothesis that such mating strategies put less constraint on males, we expect the mortality to be less skewed towards males. Thus, mortality in baleen whales might be primarily driven by male mating strategies, as observed in birds (Liker & Székely 2005), and we recommend investigating sex-specific survival in other baleen whale species.

Humpback whales, as all mysticetes, display a female-biased sexual size dimorphism (SSD) (Ralls 1976), in contrast to most polygynous mammalian species in which males compete for mates and where a male-biased SSD is observed (Clutton-Brock et al. 1977). Some studies also found a positive correlation between SSD and mortality (e.g. Promislow 1992, Moore & Wilson 2002), although recent reviews found no evidence that the larger sex suffers higher mortality (Blanckenhorn 2005, Isaac 2005). Liker & Székely (2005) argue that the use of SSD as a proxy for the intensity of sexual selection between sexes is unjustified, and that sex-biased mortality is correlated to the mating system but not to SSD. Our results of male-biased mortality in a species with a polygynous male mating system but reversed SSD are in agreement with this statement. Under this hypothesis, larger sizes of female humpback whales would be driven by factors outweighing sexual selection among males, e.g. being better mothers (Ralls 1976), producing larger offspring (Pack et al. 2009), female choice (Clapham et al. 1992), and defending calves against predators (Clapham 2000). These factors apply to all baleen whales and could explain why the entire Mysticeti suborder exhibits a female-biased SSD despite different mating strategies among species.

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