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STEPHEN DAWSON, Department of Marine Science, University of Otago, P. O. Box 56, Dunedin, New Zealand; e-mail: steve.dawson@stonebow.otago.ac.nz; FRANZ PICHLER, School for Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand; ELISABETH SLOOTEN, Environmental Science, University of Otago, P. O. Box 56, Dunedin, New Zealand; KIRSTY RUSSELL and C. SCOTT BAKER, School for Biological Sciences, University of Auckland, Private Bag 92019, Auckland, New Zealand. Received 19 July 2000. Accepted 11 September 2000.

MARINE MAMMAL SCIENCE, 17(2):371–381 (April 2001)

OBSERVATION OF A MALE-BIASED SEX RATIO IN THE GULF OF ST. LAWRENCE FIN WHALES (*BALAENOPTERA PHYSALUS*): TEMPORAL, GEOGRAPHICAL, OR GROUP STRUCTURE SEGREGATION?

Knowledge about the migration, behavior, and structural organization of fin whales is limited. Although fin whales (*Balaenoptera physalus*) are characterized as a migratory species, they do not seem to have a single breeding ground as found with the North Atlantic humpback whales (*Megaptera novaeangliae*) (Mattila *et al.* 1989). On the contrary, fin whales in the North Atlantic are believed to be divided into several subpopulations (Bérubé *et al.* 1998). Data on the sex of fin whales obtained from whaling records have been used to estimate the sex ratio in many areas, including the Gulf of Alaska and the Bering Sea, West Greenland, and the northwestern and northeastern North Atlantic (Aguilar and Lockyer 1987, Kapel 1979, Mitchell 1974, Tarasevich 1967). A recent study of the North Atlantic and Mediterranean Sea fin whales detected an even sex ratio for all but two sampling areas (Bérubé *et al.* 1998). The first skewed sex ratio was detected in a sample of 33 Icelandic fin whales taken during whaling operations prior to the international moratorium on

commercial whaling. The second was found during the analysis of 109 skin biopsies collected from free-ranging fin whales in the Gulf of St. Lawrence. While the female-biased sex ratio detected in the Icelandic samples might be due to whalers' preference (females are larger than males), the overrepresentation of males in the Gulf of St. Lawrence raises different questions and requires additional scrutiny. In this study we investigate whether the observed male-biased sex ratio in the Gulf of St. Lawrence might be the result of temporal, geographical, or group structure segregation.

No readily observable dimorphic characters have yet been identified in fin whales. The only means of identifying the sex of a fin whale in the field is if an adult is closely associated (presumed to be a female) with a calf. Because of the difficulty in determining the sex of free-ranging whales, molecular sexing methods using skin biopsies collected from such whales have become increasingly important for the study of cetaceans (Brown *et al.* 1991, Richard *et al.* 1994, Bérubé and Palsbøll 1996).

The concentration of fin whales in the Gulf of St. Lawrence peaks from early June to October (Sergeant 1977, Edds and Macfarlane 1987). During this period fin whales are observed primarily along steep slope contours where biological productivity is high (Sergeant 1977). Skin biopsies were collected off the northern shore of the Gulf of St. Lawrence between 1990 and 1994 in the period from June to November. The primary study area was the Mingan Island/Anticosti Island (50°02′N, 64°25′W) region. However, a few samples were collected in the estuary between the Saguenay River (48°10′N, 69°45′W) and Sept-Iles (50°13′N, 66°22′W), as well as in the Strait of Belle Isle (51°57′N, 55°25′W).

Attempts were made to biopsy all members of a group. For all sampled individuals and non-sampled individuals, information including date, position (longitude and latitude), and group size was noted. For this study, a pair and a pod were defined as two and more than three whales, respectively, swimming side by side within a body length, with coordinated surfacing and diving pattern during the time of the observation. A "mother/calf pair" was defined as a pair of which one was estimated to be equal to or less than half the body length of the accompanying adult.

The biopsy equipment consisted of a crossbow and a bolt with a modified stainless steel tip (Palsbøll *et al.* 1991). The skin part of the biopsy was preserved in saturated NaCl with 20% DMSO (Amos and Hoelzel 1991) and stored at −20°C until DNA extraction. Total-cell DNA was extracted from the skin biopsies using standard protocols (Sambrook *et al.* 1989). Sex was determined for all individuals as described by Bérubé and Palsbøll (1996).

The genotype of six microsatellite loci (one dimer, one trimer, and four tetramers) was determined for each sample as reported previously (Palsbøll *et al.* 1997, Bérubé *et al.* 1998). Linkage between the microsatellite loci was tested using an implementation in the GenePop computer package version 1.2 (Raymond and Rousset 1995). The probability of identity at all analyzed loci for two unrelated individuals by chance was estimated as suggested by Paetkau and Strobeck (1994).

A total of 109 samples was collected and analyzed. Exact tests for linkage disequilibrium between microsatellite loci detected no significant incidences of linkage between loci. The probability of identity across all loci combined was estimated at 7.32×10^{-9}, thus the probability that two unrelated individuals have the same genotype across all loci is one in 140 million. Consequently, any two samples with identical genotypes across all loci were inferred to represent re-captures of the same individual. Among the 109 biopsies, eleven pairs of samples had identical genotypes. Only four of these recaptures were between different years: two were individuals sampled in 1990 and recaptured in 1991, one was sampled in 1991 and recaptured in 1992, and one was sampled in 1993 and recaptured 1994 (Table 1). The remaining recaptures were observed within the same year. The low recapture rate in itself suggests that we probably were sampling from a relatively large population. The most recent estimate for the St. Lawrence fin whale population was of approximately 340 individuals (Mitchell 1974).

We used the Chi-square (χ^2) test (Lindgren 1975, p. 296) for goodness of fit of the proportion of males to females against the 1:1 ratio observed in other areas. Various partitionings of the samples were tested, such as between years, months, and groups. Of the 98 individual fin whales sexed, 68 (69%) were male and 30 (31%) female. This ratio of 2.3 males for each female differs significantly from parity ($\chi^2_{1d} = 14.73$, $P < 0.0001$). The high number of males relative to females was observed in all years and months, ranging from a ratio of 1.7 to 3.6 males for 1 female.

As mentioned above, the only estimates of the sex ratio among fin whales reported so far originate from whaling data (Tarasevich 1967, Mitchell 1974, Kapel 1979, Aguilar and Lockyer 1987). It has been suggested that samples collected from commercial whaling operations could be biased toward males due to catch restrictions (*e.g.,* on lactating females, Holt 1977) or females (as hunters might aim for larger individuals, which tend to be the females). Despite these possible sources of bias, reported estimates of the sex ratio in fin whales calculated from whaling logbook data have yielded a 1:1 ratio of males to females. The collection of biopsies from free-ranging fin whales might also be subject to bias, *e.g.,* individuals of one sex are more approachable than the other. Hence, if females were more evasive than males, this could explain the observed bias. However, if we compare the sex ratio in completely and incompletely sampled groups (including pairs and pods, Table 1), no significant differences are detected ($G\text{-test}_{1d} = 0.18$, $P > 0.50$). This result strongly suggests that individuals within groups are sampled randomly.

In our study groups sizes in the Gulf of St. Lawrence ranged from one to fourteen individuals ($n = 78$, mean = 5.89, SE = 1.39). More specifically, we sampled from 23 single individuals (29.5%), 21 pairs (26.9%), and 34 (43.6%) pods. Except for one instance (biopsy LM), all duplicate samples were biopsied on different days, months, and/or years (Table 1). For this reason, only the duplicated sample of the individual LM was excluded from the group composition sex ratio analysis (Table 2). The two completely sampled trios

Table 1. Group composition of all biopsied fin whales in the Gulf of St. Lawrence between 1990 and 1994.

Years Months/ Groups	1990		1991		1992		1993		1994	
	Size	Members	Size	Members	Size	Members	Size	Members	Size	Members
June					1	***HF***	4	03F, 04M, X, X		
June					4	*06M, 07M,* **GM, *IM***				
June					5	*10M,* ***LM*, LM****, *13M, 14M, 15F*				
June					10	**IM,** 18M, **HF,** X, X, X, X, X, X, X				
June					3	**GM,** X, X				
June					1	*20M*				
June					1	*21M*				
July			4	02M, X, X, X	1	*30F*	3	07M, 08M,X	4	101M, X, X, X
July			6	03M, X, X, X, X, X	1	*38F*	1	*09F*	*3*	*102M, X, X*
July			3	**DM,** 05M, X	6	103M, 102F, 104F, X, X, X	2	10F, X		
July			2	**EM,** X	1	*106M*				
July			1	*07M*	5	107M, X, X, X, X				
July			4	**EM,** 10M, 08F, X	2	108F, X				
July			1	*12M*	3	*109M, 111M, 110F*				
July					1	*112F*				
Aug.			3	*15M,* ***DM,*** *17F*	3	66F, X, X	2	63F, X	4	30M, X, X, X
Aug.			1	***AM***	10	68M, 69M, 70M, X, X, X, X, X, X, X	14	64M, X, X, X, X, X, X, X, X, X, X, X		

Table 1. Continued.

Years Months/ Groups	1990		1991		1992		1993		1994	
	Size	Members	Size	Members	Size	Members	Size	Members	Size	Members
Aug.			3	19M, X, X	2	71M, X	6	66M, X, X, X, X, X		
Aug.			1	***BM***	4	73M, X, X, X	2	**KM**, X		
Aug.			2	21M, X						
Aug.			1	*23F*						
Aug.			1	*24M*						
Aug.			1	*25F*						
Aug.			5	26F, X, X, X, X						
Aug.			1	*31M*						
Aug.			8	**CM**, 33M, **JF**, X, X, X, X, X						
Sept.	2	01M, X	4	35M, X, X, X	2	90M, X	2	70F, X	1	***KM***
Sept.	2	*05F, 06M*	4	53M, X, X, X	2	91M, X	2	71M, X	5	55F, X, X, X, X
Sept.			1	***JF***	5	94M, 95M, X, X, X	2	*73F, 72M*		
Sept.			2	60F, X	2	*96M, 97M*				
Sept.			4	106M, X, X, X	2	98M, X				
Sept.			2	110M, X	6	114M, X, X, X, X, X				
Sept.			2	*112F, 113F*	6	121M, X, X, X, X, X				
Oct.	1	*08M*							1	*74F*
Oct.	4	10F, 09M, X, X			1	***CM***				

Table 1. Continued.

Years Months/ Groups	1990		1991		1992		1993		1994	
	Size	Members	Size	Members	Size	Members	Size	Members	Size	Members
Oct.	1	***AM***								
Oct.	4	13F, X, X, X								
Oct.	2	**BM**, X								
Oct.	1	*26M*								
Oct.	2	02M, X								
Total	N_s	8M, 3F, 8X		23M, 10F, 34X		34M, 11F, 46X		8M, 6F, 26X		4M, 2F, 12X
	N_t	6M, 3F		20M, 9F		31M, 10F		7M, 6F		4M, 2F

Note. Following the identification number, M denotes male, F female, and X unknown sex. All duplicated samples are in bold and their identification number has been changed to a letter followed by their sex. Only the individual noted by * has been sampled twice during the same sighting. N_s denotes total number of biopsies collected per year and N_t denotes total number of individuals biopsied per year. ***Highlighted*** cells indicate completely sampled groups.

consisted of two males and one female, of which one trio was identified, and confirmed by the genotypes, as a mother/calf and a male adult.

Fin whales in the waters of western Australia (Chittleborough 1953) have been mainly observed in groups of less than four individuals, mostly singles and pairs. In the Gulf of St. Lawrence fin whales have been found in groups ranging from single to fourteen individuals (mean of 2.2, SD = 1.6; unpublished data). In our study the sampling was performed mainly on pods. As pods are more visible (more blows at each surfacing), far more approachable and certainly more attractive in a results-to-effort perspective than single individuals and pairs, it is likely that there was a bias towards sampling from pods.

Statistically significant deviations weighted towards males from the expected proportions of males and females (1:1) were found in both completely and incompletely sampled pods (Table 2). In contrast, no significant deviation from the expected 1:1 sex ratio was observed for singles and pairs (Table 2), as well as with the combination of completely sampled singles and pairs ($\chi^2 = 0.81$; $P = 0.369$). Although based on a small sample size, we could hypothesize that the presence of a male-biased sex ratio in the Gulf of St. Lawrence was the result of sampling mainly pods. However, to verify if the high proportion of pods observed in this study (43.6%) is an artifact of the sampling effort, an estimation of the relative proportions of the three group categories in the Gulf of St. Lawrence has to be undertaken. Two studies on the group composition of fin whales hunted in the Antarctic and North Pacific Oceans included observations collected from the whaling operations during the spring migration to the feeding grounds and in the summer while at the feeding grounds (Nemoto 1964, Tarasevich 1967). In both studies, despite the possible whaling bias, groups consisting entirely of, or dominated by, males were larger and more common than groups consisting entirely of, or dominated by, females. In the Atlantic Ocean pods dominated by males have been described for North Atlantic humpback whales on the West Indies breeding ground (Competitive Groups, CG) (Mattila *et al.* 1989, Clapham *et al.* 1992), as well as for the North Atlantic right whale (*Eubalaena glacialis*) on the continental shelf of Nova Scotia (Surface Active Group, SAG) (Stone *et al.* 1988). These SAG or CG groups are most likely related to mating and courtship behavior, where males are in competition for access to a female.

Whaling data suggest that the migration of fin whales is characterized by a partial age segregation, as determined either by the difference in length frequencies, or by age as determined from earplug laminations (Mitchell 1974, Rørvik *et al.* 1976, Sergeant 1977). A study on group composition of fin whales hunted off Alaska and in the Bering Sea in 1963 and 1964 was performed during migration to the feeding grounds and during the foraging there (Tarasevich 1967). Analysis revealed segregation during the migration that was due not only to age, but also to sex and physiological condition (*e.g.*, pregnant, lactating, resting state, approaching sexual maturity) generating variations in departure time. The unusually high ratio of males to females, which we observed in the biopsied individuals from the Gulf of St. Lawrence is

Table 2. Observed and expected (assuming sex ratio of 1:1) numbers of male and female fin whales in different categories of completely and incompletely sampled groups.

Group sizes			Single	Pair	Pods	Total excluding singles
Completely sampled groups	No. of occurrences		23	4	4	
	Observed	Male	14	4	12	16
		Female	9	4	3	7
	Expected (1:1)	Male	11.5	4	7.5	
		Female	11.5	4	7.5	
	χ^2_{1df}		1.09	0	5.40*	
Incompletely sampled groups	No. of occurrences		—	17	30	
	Observed	Male	—	12	34	46
		Female	—	5	11	16
	Expected (1:1)	Male	—	8.5	22.5	
		Female	—	8.5	22.5	
	χ^2_{1df}		—	2.88	11.76***	

Note. The analyses included recaptures excepted if the individual had been resampled within the same sighting. According to the Table of χ^2 (p. 112) in Fisher (1948), $P \leq 0.025$ = *; $P \leq 0.001$ = ***.

consistent between years and months and thus appears unrelated to the timing of arrival on, or departure from, the feeding ground (Table 1).

The study area constitutes only a small part of the Gulf of St. Lawrence, mainly its northern shore (50°02'N, 64°25'W). For the Gulf of Maine fin whales, it has been suggested that segregation by sex or age classes may occur, since lower proportions of mothers and calves were found more in the northern than in the southern part of the Gulf (Agler *et al.* 1993). As with right whales (Schaeff *et al.* 1993), pregnant or lactating females may abandon other females and males to bear and nurse their young. A stomach content study in fin whales off Alaska and in the Bering Sea found that pregnant and lactating females have better-filled stomachs than animals in larger mixed groups or male dominated groups (Tarasevich 1967). One could therefore assume that these females are intentionally choosing a geographically separate feeding ground to insure a maximum chance of survival for their offspring. For this reason it is possible that these females escape sampling.

Mitchell (1974) reported some reproductive parameters for female fin whales harvested along the Canadian east coast. At three whaling stations he calculated that immature females represented an average of 30% of the sample and of the mature females (70% of the catches); 20% were resting, 25% lactating, and 25% pregnant animals. As only one mother/calf pair was sampled during the five-year period, we suggest that mainly resting and immature females (50% of the females) are present in the study areas. This would result in a sex ratio similar to our findings of two males to one female and thus could explain the observed male-biased sex ratio along the northern shore of the Gulf of St. Lawrence. However, sampling of a larger proportion of the Gulf of St. Lawrence is needed to support this hypothesis.

In conclusion, despite the limited sample size, the data suggest a male-biased sex ratio in pods of fin whales, while this may not be the case for smaller groups or single individuals. Our finding is in agreement with previous studies of the sex composition in groups of fin whales in the Antarctic and the North Pacific Ocean (Nemoto 1964, Tarasevich 1967). The limited spatial and temporal distribution of our samples precludes a more thorough analysis of the cause of the observed sex bias.

Acknowledgments

The authors would like to thank the research team of the Mingan Island Cetacean Study Inc. for their help with the sample and data collection. All behavioral data and biopsy samples have been collected under Fisheries and Oceans Canada permits (#6350–3). This research was funded by the International Whaling Commission; the Commission for Scientific Research in Greenland, Denmark; and the Greenland Home Rule and Aage V. Jensens Charity Foundation, Denmark. Thanks to Drs. P. J. Palsbøll, P. J. Clapham, F. Larsen, D. Mattila, D. E. Sergeant, and two reviewers for their comments on the manuscript.

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MARTINE BÉRUBÉ,[1] Population Biology Department, Zoological Institute, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen, Denmark and Natural Resource Sciences Department, Macdonald Campus of McGill University, 21,111 Lakeshore Road, Ste-Anne de Bellevue, Quebec H9X 3V9, Canada; CATHERINE BERCHOK and RICHARD SEARS, Mingan Island Cetacean Study Inc., 285 Green Street, Saint-Lambert, Quebec J4P 1T3, Canada.
Received 15 May 1998. Accepted 17 August 2000.

[1] Current address: School of Biological Sciences, University of Wales, Bangor, Gwynedd LL57 2UW, Wales, United Kingdom; e-mail: martine@sbs.bangor.ac.uk.

MARINE MAMMAL SCIENCE, 17(2):381–387 (April 2001)

PINNIPED SURVIVAL IN CAPTIVITY: ANNUAL SURVIVAL RATES OF SIX SPECIES

Under U.S. law, institutions maintaining marine mammals in captivity for the purposes of display, public education, and basic research are required to submit information on the status of individual animals for inclusion in the Marine Mammal Inventory Report (MMIR). The MMIR is currently maintained by the National Marine Fisheries Service (NMFS), and in a Cooperative Agreement with the International Species Information System (ISIS), the da-