GROWTH AND REPRODUCTION IN THE HARBOR PORPOISE, PHOCOENA PHOCOENA (L.), FROM EASTERN NEWFOUDLAND

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GROWTH AND REPRODUCTION IN THE HARBOR PORPOISE, *PHOCOENA PHOCOENA* (L.), FROM EASTERN NEWFOUNDLAND

BY

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A thesis submitted to the School of Graduate
Studies in partial fulfilment of the
requirements for the degree of
Master of Science

Biopsychology Program
Department of Psychology
Memorial University of Newfoundland
December 1992

St. John's Newfoundland

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ISBN 0-315-82667-3

ABSTRACT

GROWTH AND REPRODUCTION OF THE HARBOR PORPOISE, *PHOCOENA PHOCOENA*, AROUND EASTERN NEWFOUNDLAND

Growth and reproduction characteristics were described for 94 porpoises incidentally caught in gillnets during the summers of 1990 and 1991. Most porpoises (56%) were below five years of age. The oldest female was nine; the oldest male was twelve. Growth rates were similar for males and females until one year of age, at which time females grew longer and weighed more than males of similar ages. Using the Gompertz growth model, asymptotic values for body length were 142.9 cm for males and 156.3 cm for females and asymptotic values for weight were 49.1 kg and 61.6 kg for males and females respectively.

The majority of mature females were pregnant (76%); a high proportion were simultaneously pregnant and lactating (35%). Mean age at sexual maturity for females was 3.1 years at a mean length of 146.4 cm. Younger females appear to have multiple ovulations or an increased proportion of luteinized follicles. Parturition occurred before the sampling period (before late June) and ovulation and conception were estimated to occur from early to late July.

Sexual activity in males as indicated by spermatogenic activity was high during July, supporting estimates for the timing of ovulation and conception. On average, sexual maturity in males was estimated to occur at 3.0 years of age and at a length of 135.1 cm. There was a dramatic increase in testes weight, testes volume, and seminiferous tubule diameter at the onset of age three.

Female porpoises from Newfoundland matured earlier and were larger than females from other areas. Dentinal deposition patterns in the teeth of harbor porpoises from Newfoundland were very different from those of the Bay of Fundy and suggest a new method of stock discrimination.

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ACKNOWLEDGEMENTS

One thing I learned is that it is not only possible, but a valuable experience for government and educational facilities to work together in a cooperative manner, each contributing from their respective strengths and expertise. I thank my committee members for sharing their experience and knowledge with me. Dr. Garry Stenson provided resources, invaluable editing comments, and always had a friendly word of advice. Dr. Jon Lien shared his enthusiasm for science and taught me that "education isn't about filling containers, it's about lighting fires". Dr. Laurel Duquette was always available, providing statistical advice (even from afar) and improving the thesis with her editing skills.

This study would not have had a "porpoise" without the cooperation of the fishermen from the various ports around Eastern Newfoundland. I am also grateful to those people who freely shared their expertise in their respective fields, often saving me time and a bit of frustration. My appreciation extends to Andy Read and Aleta Hohn for showing me the art of aging porpoise teeth and then subsequently having to deal with the frustration of verifying my ages; to Ed Evelly for infinite help and advice (not to mention some good novel recommendations) as I bumbled through his histology lab; to Scott Gilliland for explaining the oh-so-confusing growth

curve models; to 'Flash' King for photography lessons and entertaining stories; to Jack Lawson and Denis Chabot for donuts, introductions to the Mac, and who, along with Beth Perry, shared their words of wisdom of do's and don't's regarding thesis preparation; and to all those (you definitely know who you are) who spent hours elbow deep in porpoise carcasses. Extra special thanks to Fisheries' Finest: Dave McKinnon, Wayne Penney, Dennis Wakeham, Debby Kavanaugh, and Joanne Rowe for providing anything and everything one could imagine.

A special thanks to my fellow zoo-mates and friends who provided the extracurricular activities and reminded me that there's more to grad school than just a thesis. To name but a few: Carl L., Greg B., Hywel M., Janice W., John B., Kristina C., Lesley-Anne H., Lynda W., Mark H., Michelle S., Rosie S., Sue-Anne R., Tracy P., and Wayne C.

And finally, thanks to my family for always believing in me, encouraging me, and loving me.

The manuscript was improved by the comments of Dr. Andrew Read and Dr. David Schneider. Financial support came from the Department of Fisheries and Oceans and two NSERC postgraduate scholarships (PGS 1 and 2).

INTRODUCTION

The harbor porpoise, *Phocoena phocoena*, (Linnaeus, 1758), also called the common porpoise, is one of the smallest of the oceanic odontocetes, rarely exceeding a length of 1.8 m (Harrison 1971). Average adult lengths and weights are 1.5-1.6 m and 45-60 kg, respectively (Gaskin et al. 1974). Harbor porpoises are blackish-gray dorsally and whitish ventrally in appearance and possess a short, triangular dorsal fin. This, combined with their sedentary behavior and non-visible blow, make harbor porpoise sightings difficult, especially at moderate sea states. Harbor porpoises are widespread, being found in the Arctic, North Atlantic, and North Pacific Oceans.

Perrin and Reilly (1984) discuss several effects of geographical variation on life history parameters of the same species. Morphological differences have been found in the skulls of porpoises from the North and Baltic Seas (Kinze 1985; 1990a); Yurick and Gaskin (1987) were able to distinguish between the East Pacific, the western Atlantic and the eastern Atlantic. Aguilar and Borrell (1990) differentiated populations on the basis of pollutant concentration levels in tissues of harbor porpoises within the eastern North Atlantic; similar studies also found discrete differences in porpoises from the eastern Pacific

(Calambokidis and Barlow 1991). Isozyme differences have been found between porpoises from the North and Baltic Seas; preliminary results indicate differentiation between the northeast and northwest Atlantic (Andersen 1990). Growth rates have also been found to differ between regions (Gaskin and Blair 1977; van Utrecht 1978). Such physical differences imply separate and distinct stocks of harbor porpoises in various areas (Gaskin 1984; Yurick and Gaskin 1987). Gaskin (1984) suggests a series of local populations in the northwest Atlantic consisting of a Bay of Fundy/Gulf of Maine, a Gulf of St. Lawrence, a West Greenland, and a Newfoundland stock.

Populations in many regions are thought to be declining due to direct and/or indirect exploitation, as well as habitat degradation in the form of pollution, diminished food sources, etc. (Read 1989; Verwey and Wolff 1981). For these reasons, concern for the status of the harbor porpoise is increasing. Status reports in numerous areas have recently been or are currently being conducted: Norwegian Sea - Bjorge and Oien (1990); California - Barlow and Hanan (1990), Hohn and Brownell (1990); Bay of Fundy/Gulf of Maine - Read (1989), Read and Gaskin (1990a; 1990b); Britain/Ireland - Evans (1990); North Sea/Baltic Sea - Clausen (1990), Kinze (1990b). If any of these studies reveal increasing reproductive rates over time, there may be reason to believe that the population may be declining.

It has been suggested that cetacean reproductive rates exhibit density dependence (Perrin and Donovan 1984; Fowler 1984; Kasuya 1985). In the face of declining numbers, reproductive rates may increase to compensate for the reduced density of the exploited population, thereby increasing net reproduction. Evidence to suggest density dependent responses in reproductive parameters of other species of cetaceans has been found by several authors (Hester 1984; Kasuya 1985; 1991; Perrin and Henderson 1984; Smith 1984; and others). Parameters which may exhibit density dependent responses include pregnancy rate, calving interval, age at attainment of sexual maturity, proportion of simultaneously lactating and pregnant females, growth rates, mean age in the population, and population growth rates (Perrin and Donovan 1984).

Incidental take of harbor porpoise in fishing gear in the Bay of Fundy is high and it is believed that the population may be threatened (Polacheck 1989; Read 1989; Read and Gaskin 1988; Read and Gaskin 1990a; 1990b; Woodley and Read 1991). Growth and reproduction of harbor porpoises from the Bay of Fundy were compared between samples collected in 1969-73 and 1985-88 (Read and Gaskin 1990b). Results suggested intrapopulation parameter changes over time as density dependent responses; calf length increased and sexual maturity occurred at a significantly younger age and shorter body length in the later sample.

While some populations, such as that of the Bay of Fundy/Gulf of Maine, have received extensive study, virtually nothing is known about others, such as the Newfoundland population. Sergeant and Fisher (1957) give an account of harbor porpoise distribution around Newfoundland and Labrador and report frequent catches in cod traps in June and July. More recent studies have shown that the number of harbor porpoises incidentally caught in fishing gear in waters off Newfoundland and Labrador is quite high (Lien 1989; Lien et al. 1988). The impact of incidental takes on a population is difficult to ascertain without accurate estimates of abundance. Population estimates for harbor porpoises are difficult to obtain given their low sightability at sea. Abundance surveys for harbor porpoises typically result in wide confidence intervals which, in turn, pose statistical problems when trying to determine population dynamics (Taylor and Gerrodette 1991). There are no abundance estimates for the harbor porpoise population around Newfoundland. There is ongoing research to obtain estimates of catch levels (G. Stenson, Department of Fisheries and Oceans, pers. comm.) for this population. If it is found that catch per effort is declining, then there will be ample reason to warrant concern over the impact of incidental takes on the Newfoundland population.

The limited data available on the biology of harbor porpoises around Newfoundland are restricted to lengths and weights of a small number of samples. Sergeant and Fisher (1957) reported length and date of capture for a male harbor porpoise caught in a cod trap in Trinity Bay. Length and weight of a harbor porpoise found in the stomach of a Greenland shark, *Somniosus microcephalus*, caught on the Grand Banks of Newfoundland, is reported by Williamson (1963). Sergeant et al. (1970) give date of capture and weight for two harbor porpoises caught off St. John's.

It is the objective of this study to develop a data base of growth and reproduction data for the Newfoundland harbor porpoise population.

METHODS

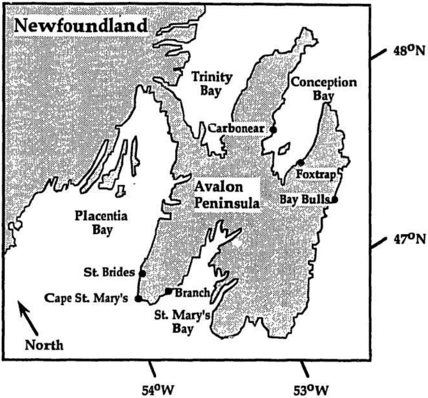
2.1 Collection of specimens

A total of 40 fishermen from the four major bays (Trinity, Conception, St. Mary's, and Placentia - see Figure 1) of the Avalon Peninsula of Eastern Newfoundland were contacted by telephone and were asked to retrieve harbor porpoises that became incidentally caught in their fishing gear. This request was made in late June of 1990 and in early May of 1991. In 1990, some fishermen were paid a small handling fee of 10 or 25 dollars, but in 1991, all fishermen were paid 25 dollars for each porpoise. Animals were caught in gillnets of mesh size 14-20 cm, typically anchored on bottom at depths of 40-90 m, and set 2.2-11.2 km off shore. Target species were primarily cod, *Gadus morhua* (Linnaeus, 1758), and flounder, *Pseudopleuronectes americanus* (Walbaum, 1792).

2.2 Age determination

The most accurate and widely utilized technique for aging harbor porpoise is to count growth layer groups (GLG) in the

Figure 1: Map of the Avalon Peninsula of Eastern Newfoundland showing locations of harbor porpoise by-catch.


Newfoundland
Trinity Bay
Conception Bay
Carbonear
Foxtrap
Avalon Peninsula
Bay Bulls
Placentia Bay
St. Brides
Cape St. Mary's
Branch
St. Mary's Bay
North
48°N
47°N
54°W
53°W

dentine of the teeth, where each GLG is assumed to represent a single year's growth (Hohn 1980; Hohn et al. 1989; Nielsen 1972). Each GLG is composed of two basic parts: 1) a wide zone assumed to be laid down during the winter, a time of slow growth and 2) a narrow zone assumed to be formed during the summer, a time of rapid growth (Nielsen 1972). Lower jaws were extracted from each porpoise during the necropsy. Teeth were removed from the mid-section of the mandibles and were stored in an equal parts mixture of glycerin, 70% ethanol, and water until processing. Teeth were processed for aging similar to the method of Hohn (National Marine Fisheries Service, pers. comm.). Teeth were decalcified in a mixture of sodium citrate and formic acid until flexible and sectioned longitudinally to a thickness of 20 um using a cryostat. Sections were then stained in Erhlich's hematoxylin, differentiated in acid alcohol, blued in Scott's Tap Water (STW), and mounted in a synthetic medium (Eukitt). Tooth sections were viewed using a dissecting microscope (compound, when necessary) under transmitted light and the GLGs were counted. A total of 18 teeth from different animals which ranged in age from one to ten years were sent to experienced readers (A. Read, Woods Hole Oceanographic Institution, and A. Hohn, National Marine Fisheries Service) for verification of GLG counts.

2.3 Growth

Routine necropsies including standard morphometric measurements were performed on each porpoise. Growth curves were fit to cross-sectional length at age and weight at age data for male and female harbor porpoises separately by repeated iterations of the nonlinear regression program of SYSTAT Version 5.1 (Wilkinson 1989). Both Gompertz and von Bertalanffy growth models were used to allow for comparisons with other studies. The regression equation for the Gompertz model is as follows:

$$\text{Length} = A*\exp(-b*\exp(-k*\text{age}))$$

where:

length = straight line distance from snout to fluke notch (cm)

A = asymptotic length (cm)

b = fitted constant (no units)

k = growth rate constant (years^{-1})

age = age (years).

The von Bertalanffy model has the form:

$$\text{Length} = A*(1-b*\exp(-k*\text{age}))^3$$

with the variables being the same as those described for the Gompertz model.

2.4 Reproduction

Ovaries and uteri were removed from female porpoises and preserved in 10% seawater formalin. Lactation was determined by squeezing and cutting the mammary glands. Length and width of each uterine horn were measured using vernier callipers and examined for the presence of a fetus. Ovaries were weighed, measured (length and mean of width and depth) and sectioned by hand to a thickness of 1-3 mm. The largest diameter, defined as the mean of two measurements taken at right angles, was determined for all corpora lutea (CL), corpora albicantia (CA), and the largest follicle in each ovary. The presence of a CL or a CA in the ovary was the criterion for sexual maturity. Females were considered pregnant if a fetus was present in the uterus or a CL was present in the ovary. Female reproductive state was classified following Perrin and Donovan (1984), as modified by Read (1990a), and placed into one of the following categories:

i) immature - no CLs or CAs present,

ii) pregnant - CL present on one ovary and/or the presence of a fetus in the uterus,

iii) lactating - CA present and milk present in the mammary glands, but no fetus nor CL evident,

iv) simultaneously pregnant and lactating - CA present and milk present in the mammary glands and a fetus or CL present, or

v) mature, inactive - CAs present indicating past reproductive events, but no milk present in the mammaries, no fetus present in the uterus, and no CL in the ovary.

Testes and epididymides were removed from male porpoises and were weighed and measured separately. Testicular volume (TV) was estimated using the formula for the volume of an ellipsoid:

$$TV = 4/3 * L/2 * W/2 * D/2$$

where:

L = testis length (cm)
W = testis width (cm)
D = testis depth (cm).

Sections from the outer portion of the right testis and epididymis were embedded in paraffin, sectioned using a microtome (5 um), and stained with hematoxylin and eosin for histological examination. Diameters of 10 round seminiferous tubules were measured using an ocular micrometer, types of cells were examined, and the presence or absence of sperm in both testis and epididymis was noted. Males were considered sexually mature if sperm were present in the testes and/or epididymis.

The relationship between testes weight and age class was assessed using ANCOVA (General Linear Model of SAS) where body size was used as the covariate. Tukey's multiple-range test was used to detect differences between means of testes weight among age classes.

Two methods of estimating mean age at sexual maturity were employed to allow for a greater range of comparisons with other populations. The first method, age at first ovulation (AFO), was estimated by calculating the mean age of females possessing a single corpus (luteum or albicans) in the ovary. The second method (DeMaster 1978) estimated mean age at attainment of sexual maturity (ASM) for both males and females based on the proportion mature in each age class. Similarly, average length at attainment of sexual maturity (LSM) was also calculated for both males and females by partitioning length into 10 cm intervals. The two main underlying assumptions concerning ASM and LSM are that GLGs give accurate, unbiased age estimates and that the sample is unbiased regarding specimen maturity (Myrick et al. 1986).

The annual pregnancy rate (APR) of a population is defined as the fraction of mature females that would be expected to give birth in any given year (Myrick et al. 1986). This was estimated as the number of pregnant females (including those that were simultaneously pregnant and lactating) divided by the number of mature females. Age-specific pregnancy rates were also estimated as the number of pregnant females divided by the total number of females in that age class. These estimates are based on the assumption that the sample of incidentally caught porpoises is representative of the population.

Analyses were tested for year and location effects and were only reported when significant, otherwise pooled. All statistical procedures, with the exception of growth curves, were performed with SAS/STAT (SAS Institute Inc. 1985). For tests of significance for means between populations, a modified t test (t′) was used as described in Snedecor and Cochran (1980). This t′ test assumes that the variances for the two populations are not equal.

RESULTS

3.1 Collection of specimens

Of the 40 fishermen contacted, seven reported catching harbor porpoises in 1990. In 1991, the fishermen who caught porpoises in the St. Brides area were not identified individually.

A total of 94 porpoises were obtained (59 male, 35 female); 19 in 1990 and 75 in 1991. In 1990, 52.6% were collected from Branch in St. Mary's Bay and in 1991, 86.7% came from St. Brides (Table 1 and Figure 1). Fishermen from these two communities often set their nets in the same area, off Cape St. Mary's in Placentia Bay (Figure 1).

The total capture was biased towards males (males: 62.8%, females: 37.2%). To determine if there was a significant difference in the sex ratio, the data were first pooled across years due to small sample sizes within cells (Table 1). Although the sex ratio could vary between years, pooling the data provides a more conservative test of the null hypothesis since the sex ratio in 1990 was virtually 1:1. There were no

Table 1. Origin of harbor porpoise samples from Eastern Newfoundland taken during 1990 and 1991.

Location	1990		1991		Total
	male	female	male	female	
St. Brides	2	0	45	20	67
Branch	5	5	1	3	14
Bay Bulls	1	2	0	1	4
Conception Bay	2	2	3	2	9
Total	10	9	49	26	94

significant differences between location on sex ($G = 6.45$, $df = 3$, $P = 0.09$). The data were then pooled across locations and a chi-square test was performed on the total number of males and females. The overall sex ratio was skewed towards males which comprised 62.8% of the sample (chi-square = 6.2, $0.01 < P < 0.025$, $df = 1$) (Table 1).

3.2 Timing of collections

All porpoises were collected between 21 June and 10 August. The majority (87.2%) were collected within a three week period in July (Table 2). The timing of peak collections was the same for both years, with 15 of the 19 (78.9%) from 1990 and 67 of the 75 (89.3%) from 1991 being collected during this period.

3.3 Age determination

Porpoises ranged in age from zero to twelve; the oldest female was nine; the oldest male was twelve (Figure 2). The majority of the sample (55.9%) was four years of age or less. A tooth from a seven year old animal is shown in Figure 3.

The two experienced readers (A. Hohn and A. Read) agreed with six of the assigned ages. Of the remaining twelve teeth,

Table 2. Temporal distribution of samples of male and female harbor porpoises from Eastern Newfoundland pooled over 1990 and 1991.

Dates (Day of Year)	Male (N)	Female (N)
21 Jun - 27 Jun (172 - 178)	1	0
28 Jun - 04 Jul (179 - 185)	1	1
05 Jul - 11 Jul (186 - 192)	8	5
12 Jul - 18 Jul (193 - 199)	31	21
19 Jul - 25 Jul (200 - 206)	13	4
26 Jul - 01 Aug (207 - 213)	4	2
02 Aug - 08 Aug (214 - 220)	1	0
09 Aug - 15 Aug (221 - 227)	0	2
Totals	59	35

Figure 2: Age frequency distribution of male and female harbor porpoises incidentally caught around Eastern Newfoundland, 1990-1991.

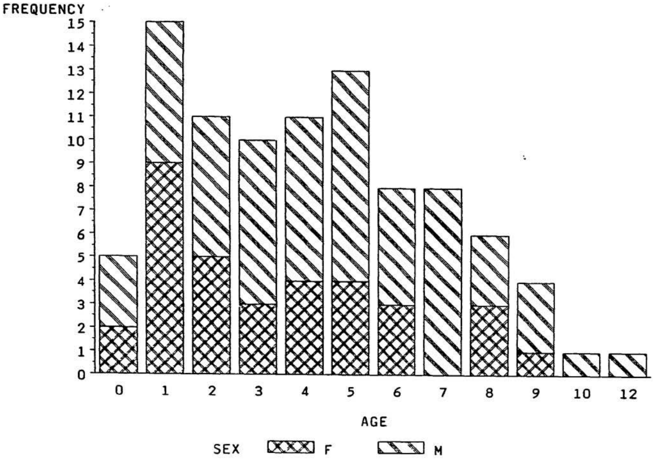
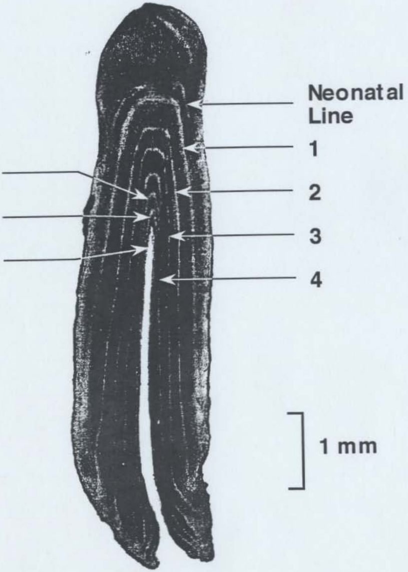

FREQUENCY
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
0
0
1
2
3
4
5
6
7
8
9
10
12
AGE
SEX
F
M

Figure 3: Diagram of the growth layer groups (GLGs) from a seven year old harbor porpoise from Eastern Newfoundland.


Neonatal Line
1
2
3
4
5
6
7
1 mm

three were off by more than one year, usually due to accessory lines which can be difficult for inexperienced readers to distinguish although, once pointed out, become quite recognizable. The other nine teeth were off by exactly one year and in all cases this was due to the variability of the half-year line. A half-year mark is obvious in teeth of porpoises from other areas (A. Hohn, National Marine Fisheries Service, and A. Read, Woods Hole Oceanographic Institution, pers. comm.), but was completely absent in the majority of teeth from Newfoundland and, when its presence was doubtful, it was not consistent with the characteristics typical of half-year lines in other areas. To be consistent in age estimation, half-year lines were not assigned to any of the teeth from Newfoundland.

3.4 Growth

3.4.1 Length at age

Mean length of three male (93.7 cm, SE = 1.7) and two female (88.5 cm, SE = 7.0) calves (porpoises less than one year of age) were compared. There was no significant difference between male and female calf length (t = -0.9095, P = 0.43, df = 3) (Table 3).

Table 3. Growth and reproductive characteristics of by-caught harbor porpoises from Eastern Newfoundland.

Parameter	N	X	SE
Calf Length	5	91.6 cm	2.7
Asymptotic Length: Males	59	142.9 cm	1.2
Asymptotic Length: Females	33	156.3 cm	2.9
Male Age at Maturity	59	3.0 yr	-
Female Age at Maturity	32	3.1 yr	0.07
Male Length at Maturity	59	135.1 cm	0.02
Female Length at Maturity	32	146.4	0.03
Annual Pregnancy Rate	17	0.76	0.10*
Proportion Mature Females	33	0.52	0.09*

* Variance estimator was calculated according to Perrin et al. (1977).

Table 4. Parameter estimates for the Gompertz and von Bertalanffy growth curves from cross-sectional length-at-age data for male and female harbor porpoises from Eastern Newfoundland. Standard errors are in parentheses.

		A	b	k
Gompertz	Males (N=59)	142.9 (1.2)	0.419 (0.03)	0.747 (0.09)
	Females (N=33)	156.3 (2.9)	0.558 (0.06)	0.735 (0.13)
von Bertalanffy	Males (N=59)	143.0 (1.2)	0.131 (0.01)	0.719 (0.09)
	Females (N=33)	156.5 (2.9)	0.171 (0.02)	0.696 (0.12)

where:

A = asymptotic length (cm)
b = fitted constant (no units)
k = growth rate constant (yr^{-1})

Figure 4: Gompertz growth curves fit to length at age data for male harbor porpoises incidentally caught around Eastern Newfoundland, 1990-1991.

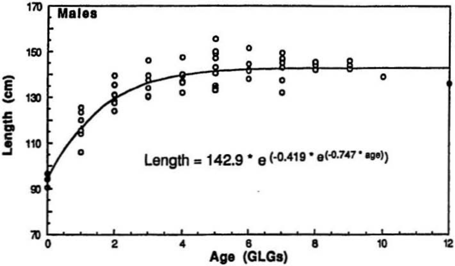
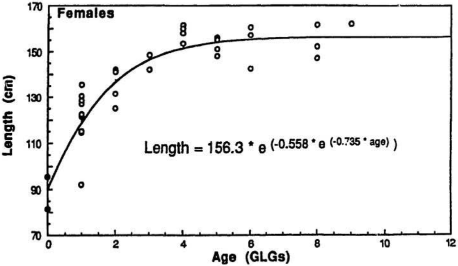

Males
Length (cm)
Age (GLGs)
170
150
130
110
90
70
0
2
4
6
8
10
12
Length = 142.9 * e (-0.419 * e(-0.747 * age))

Figure 5: Gompertz growth curves fit to length at age data for female harbor porpoises incidentally caught around Eastern Newfoundland, 1990-1991.


Females
Length (cm)
170
150
130
110
90
70
0
2
4
6
8
10
12
Age (GLGs)
Length = 156.3 * e (-0.558 * e (-0.735 * age))

The relationship between length and age was described using both Gompertz and von Bertalanffy growth models for males and females separately. Parameter values and standard errors estimated for both models are given in Table 4. Asymptotic values were not significantly different between the two models ($t = 0.049$, $P > 0.9$, $df = 64$ for females; $t = 0.058$, $P > 0.9$, $df = 116$ for males), so only Gompertz models were illustrated (Figures 4 and 5). Both sexes exhibit a rapid increase in growth during the first three years followed by a plateau occurring at approximately age four. The asymptotic value was significantly higher for females than for males (females: 156.3 cm; males: 142.9 cm; $t = 4.97$, $P < 0.001$, $df = 90$). The best fit equation for the Gompertz model for males is:

$$\text{Length} = 142.9\ \text{cm} * \exp(-0.419 * \exp(-0.747 * \text{age}))$$

and for females is:

$$\text{Length} = 156.3\ \text{cm} * \exp(-0.558 * \exp(-0.735 * \text{age}))$$

The longest male recorded was 155.5 cm and the longest female recorded was 162.0 cm.

3.4.2 Weight at age

Gompertz and von Bertalanffy growth models were also fit to weight at age data for both sexes. Parameter values and their standard errors are presented in Table 5 for both models. Asymptotic values were not significantly different between the two models ($t = 0.096$, $P > 0.9$, $df = 64$ for females; $t = 0.104$, $P > 0.9$, $df = 116$ for males). Gompertz curves for weight are presented in Figures 6 and 7 for males and females respectively. An initial rapid increase is followed by a plateau at approximately age five for males and one year later for females. The asymptotic value for females was significantly higher ($t = 6.70$, $P < 0.001$, $df = 90$) than that for males. The Gompertz equation for males is:

$$\text{Weight} = 49.1\ \text{kg} * \exp(-1.069 * \exp(-0.658 * \text{age}))$$

and for females is:

$$\text{Weight} = 61.6\ \text{kg} * \exp(-1.284 * \exp(-0.554 * \text{age}))$$

The heaviest male recorded was 58.0 kg while the heaviest female recorded was 71.0 kg.

3.4.3 Length at weight

The relationship between length and weight was examined using both linear and quadratic models. The quadratic model explained significantly more variation than the linear model ($F_{(2,87)} = 29.78$, $P < 0.01$), which was expected given the later age of attainment of the weight asymptote in the growth models (Figure 8). The regression lines for males and females were

Table 5. Parameter estimates for the Gompertz and von Bertalanffy growth curves from cross-sectional weight-at-age data for male and female harbor porpoises from Eastern Newfoundland. Standard errors are in parentheses.

		A	b	k
Gompertz	Males (N=59)	49.1 (1.3)	1.069 (0.15)	0.658 (0.13)
	Females (N=33)	61.6 (3.6)	1.284 (0.18)	0.554 (0.15)
von Bertalanffy	Males (N=59)	49.3 (1.4)	0.306 (0.04)	0.598 (0.11)
	Females (N=33)	62.1 (3.8)	0.360 (0.04)	0.495 (0.13)

where:

A = asymptotic weight (kg)

b = fitted constant (no units)

k = growth rate constant (yr^{-1})

Figure 6: Gompertz growth curves fit to weight at age data for male harbor porpoises incidentally caught around Eastern Newfoundland, 1990-1991.

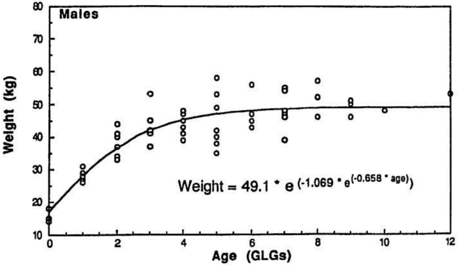
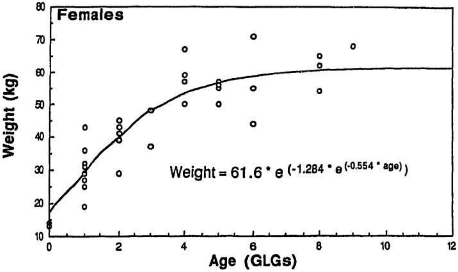

Males
Weight (kg)
80
70
60
50
40
30
20
10
0
2
4
6
8
10
12
Age (GLGs)
Weight = 49.1 * e (-1.069 * e(-0.658 * age))

Figure 7: Gompertz growth curves fit to weight at age data for female harbor porpoises incidentally caught around Eastern Newfoundland, 1990-1991.


Females
Weight (kg)
80
70
60
50
40
30
20
10
0
2
4
6
8
10
12
Age (GLGs)
Weight = 61.6 * e (-1.284 * e (-0.554 * age))

parallel ($F_{(2,87)} = 3.0$, $P > 0.05$), but statistically different ($F_{(1,89)} = 9.04$, $P < 0.01$). The relationship for males is described by:

$$Y = 53.2 + 2.9X - 0.02X^2,$$

and for females is;

$$Y = 52.8 + 2.9X - 0.02X^2,$$

where:

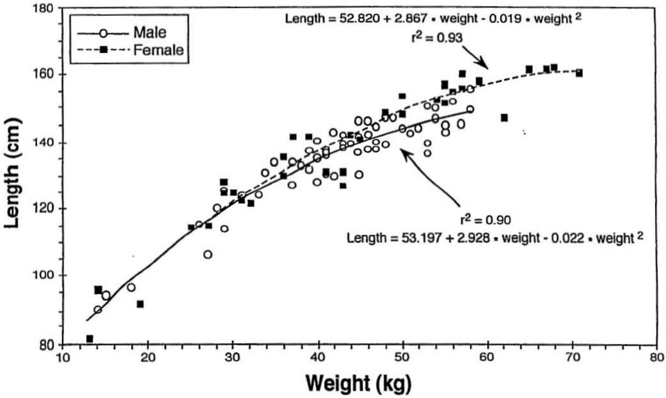
Y = length (cm)
X = weight (kg).

3.5 Female reproduction

The presence of either a corpus luteum (CL) or a corpus albicans (CA) was used as the criterion of sexual maturity. No females less than two years of age possessed corpora. Four of the five (80%) two year olds and one of the three (67%) three year olds were also classified as immature. However, one of the two year olds had a large follicle (8.0 mm) and may have been sampled (15 July) prior to ovulation. All females greater than three years of age contained at least one corpus. None of the females were classified as resting, i.e. mature but neither pregnant nor lactating.

Three females possessed a single corpus luteum in their

Figure 8: Length at weight data for male and female harbor porpoises incidentally caught in fishing gear off Eastern Newfoundland, 1990-1991.


Male
Female
Length = 52.820 + 2.867 * weight - 0.019 * weight 2
r2 = 0.93
r2 = 0.90
Length = 53.197 + 2.928 * weight - 0.022 * weight 2
Length (cm)
180
160
140
120
100
80
10
20
30
40
50
60
70
80
Weight (kg)

Three females possessed a single corpus luteum in their ovaries and were thought to have been sampled in the year in which they first ovulated. One additional female possessed only a single corpus albicans in the ovary and was assumed to have ovulated for the first time during the previous year and was thus included in the age at first ovulation estimation. Mean age of first ovulation (AFO) was estimated to be 3.0 years with a standard error of 0.4 years ($N = 4$). The average age at attainment of sexual maturity (ASM) for females using the method of DeMaster (1978) was estimated to be 3.1 years ($SE = 0.07$) (Table 3). This method takes into account ovulation rates for each age class over the entire range of ages. The two methods employed for estimating age at sexual maturity did not differ significantly in their results ($t = 0.55$, $0.9 > P > 0.5$, $df = 35$).

Entering an age of three into the Gompertz growth model predicted length at sexual maturity (LSM) to be 146.9 cm, similar to the value of 146.4 cm ($SE = 0.03$) determined using DeMaster's algorithm (1978).

No fetuses were evident in the uteri of any of the females and thus the presence of a corpus luteum had to be used as the criterion for pregnancy. Of 17 mature females, seven were pregnant (CL present), four were lactating only (CA present), and six were simultaneously pregnant and lactating. One of four lactating females, collected on 12 July, had a large follicle (10.2 mm) and also may have been sampled prior to ovulation. The size of this follicle is similar to the mean diameter of corpora lutea (11.9 mm, SE = 1.11, N = 13), suggesting that ovulation and conception were occurring during the sampling period. All ovarian activity was sinistral with the right ovary appearing small and dysfunctional, similar to the ovaries of immature porpoises.

The diameter of corpora lutea increased in diameter over time during the sampling period ($F = 9.84$, $P = 0.01$, $df = 9$, $R^2 = 0.50$). The relationship is described by $Y = -45.6 + 0.29X$, where X is the day of the year. Removal of one outlier (studentized residual = -7.14) resulted in a much stronger relationship between CL diameter and time described by $Y = -94.80 + 0.54X$ ($F = 121.26$, $P < 0.0001$, $df = 8$, $R^2 = 0.94$) (Figure 9).

Age-specific pregnancy rates were expressed for the 32 aged females as the number of pregnant females (CL present) divided by the total number of females in that age class (Table 6). The annual pregnancy rate, estimated as the fraction of mature females that were pregnant, was 0.76. If

Figure 9: Increase in diameter of corpora lutea over time from a sample of female harbor porpoises incidentally caught around Eastern Newfoundland, 1990-1991. The relationship is described by $Y = -94.80 + 0.54X$ where X is the day of the year. $R^2 = 0.94$.

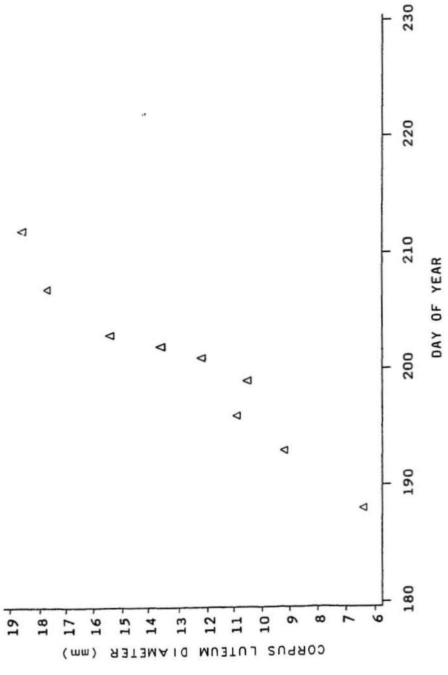

CORPUS LUTEUM DIAMETER (mm)
19
18
17
16
15
14
13
12
11
10
9
8
7
6
DAY OF YEAR
180
190
200
210
220
230

Table 6. Age-specific pregnancy rates of female harbor porpoises from Eastern Newfoundland, using the presence of a corpus luteum as the criterion of pregnancy. Column headings refer to the sample size for each age class (N), the number of mature females (M), and the number and proportion pregnant (P), including those simultaneously pregnant and lactating.

Age class	Sample size (N)	Mature (M)	Pregnant (P)	Preg. rate (P/N)
0	2	0	0	-
1	8	0	0	-
2	5	1	1	0.20
3	3	2	2	0.67
4	4	4	4	1.00
5	3	3	1	0.33
6	3	3	2	0.67
7	0	-	-	-
8	3	3	2	0.67
9	1	1	1	1.00
	32	17	13	

Figure 10: Counts of corpora albicantia with age taken from a sample of female harbor porpoise incidentally caught in fishing gear around Eastern Newfoundland, 1990-1991. The arbitrary line ($Y = X - 3$) represents an ovulation rate of one per year, becoming sexually mature at age 3.


Corpora Albicantia (#)
0
1
2
3
4
5
6
7
0
1
2
3
4
5
6
7
8
9
Age in Years

the two females with large follicles are assumed to have been sampled prior to ovulating and are included, the pregnancy rate increases to 0.83.

To determine if harbor porpoises ovulate once each year, the ovulations for mature females expressed as the total number of corpora albicantia per age class were considered. Several females possessed corpora counts that fell above an arbitrary line based on sexual maturity at age three and one ovulation per year (Figure 10). Three females possessed counts greater than their ages. The maximum number of corpora was seven and appeared to plateau with age. A quadratic model described the relationship between the number of corpora (Y) and age (X): $Y = -4.9 + 2.9X - 0.2X^2$ and provided a significantly better fit than a linear model ($F = 5.96$, $P < 0.03$, $R^2 = 0.57$). However, the sample size was small and the variability high.

3.6 Male reproduction

The mean combined weight of testes for calves (age = 0) was 7.7 g (SE = 1.2), for yearlings was 41.1 g (SE = 3.0) and for two year olds was 216.3 g (SE = 29.0). At age three, testes weight increased to a mean of 971.6 g (SE = 155.7) and for animals age four and up the mean was 1555.9 g (SE = 109.8). To determine if the rate of testes tissue production significantly increased at the onset of sexual maturity (age 3 - see page 55), body weight was controlled for in male porpoises for each age class from zero to four years, at which time testes mass appeared to plateau. The slope defining the relationship between testes weight and body weight did not vary with age (body weight * age: F = 2.72 , P = 0.06). However, Tukey's post hoc test revealed a significant difference of mean testis weight between age two and age three (P = 0.05, df = 23) (Figure 11).

Mean testicular volume for calves was 3.6 cm^3 (SE = 0.6), for yearlings was 17.5 cm^3 (SE = 1.2), and was 92.5 cm^3 (SE = 10.6) for two year olds. Again, a large increase was seen at the onset of age three with a mean of 469.1 cm^3 (SE = 75.7) and a mean of 802.6 cm^3 (SE = 58.2) for males age four and up. To determine if testes volume significantly increased among age classes, an analysis similar to that for testes weight was performed. Once body weight was taken into account, testes volume did not increase disproportionately across age classes (body weight * age: F = 0.75, P = 0.57) (Figure 12), although Tukey's revealed a significant increase in mean testis volume

Figure 11: The relationship between combined testes weight and body weight for male harbor porpoises incidentally caught around Eastern Newfoundland, 1990-1991. Numbers denote age class.

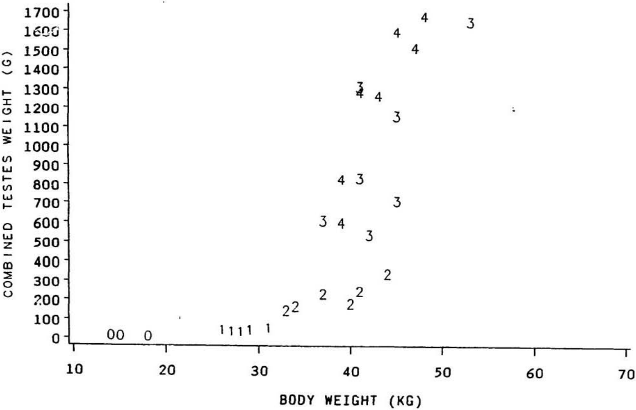
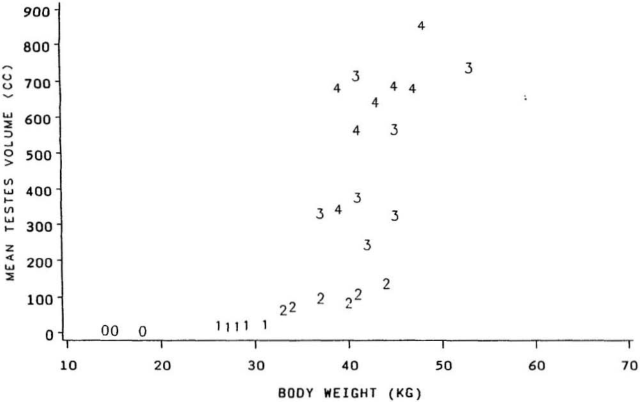

COMBINED TESTES WEIGHT (G)
1700
1600
1500
1400
1300
1200
1100
1000
900
800
700
600
500
400
300
200
100
0
10
20
30
40
50
60
70
BODY WEIGHT (KG)

Figure 12: The relationship between mean testis volume and body weight for male harbor porpoises incidentally caught around Eastern Newfoundland, 1990-1991. Numbers denote age class.



MEAN TESTES VOLUME (CC)
900
800
700
600
500
400
300
200
100
0
10
20
30
40
50
60
70
BODY WEIGHT (KG)
4
3
3
4
4
4
4
4
3
3
3
4
3
3
2
2
2
2
2
2
1
1
1
1
1
0
0
0

between two and three years of age ($P = 0.05$, df = 23).

Mean seminiferous tubule diameter in the testes of calves was 47.6 um (SE = 5.6), for yearlings was 50.6 um (SE = 1.5), and for two year olds was 80.4 um (SE = 7.6). Seminiferous tubule diameter also increased substantially at age three to 146.0 um (SE = 9.0) and animals of age four and above had a mean tubule diameter of 172.8 um (SE = 3.9). Similarly, the increase in seminiferous tubule diameter was not disproportionate across age classes (body weight * age: $F = 0.57$, $P = 0.69$), however, Tukey's revealed a significant increase successively between the ages of one, two, three, and four ($P = 0.05$, df = 23).

Mean reproductive parameters for immature and mature males are given in Table 7. The testes of 16 males (27.1%) were classified as immature. They were small (mean combined weight = 115.4 g, SE = 27.5; mean volume = 49.3 cm^3, SE = 11.5), contained small seminiferous tubules (mean diameter = 64.3 um, SE = 5.3), and displayed little or no spermatogenic activity (spermatogonia present, perhaps a few primary spermatocytes undergoing the first meiotic division, but no secondary spermatocytes, spermatids or spermatozoa).

Table 7. Reproductive characteristics of immature and mature male harbor porpoises from Eastern Newfoundland. Sample size for immatures = 16, for matures = 43. Means, followed by standard errors in parentheses, are presented.

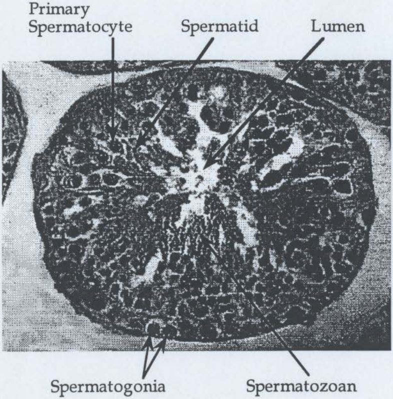
Parameter	Immature	Mature
Combined Testes Weight (g)	115.4 (27.47)	1490.5 (98.86)
Testis Volume (cm^3)	49.3 (11.51)	764.2 (52.58)
Seminiferous Tubule Diameter (um)	64.3 (5.31)	170.1 (3.60)

Sexually mature males had large testes with a mean combined weight of 1490.5 g (SE = 98.9) and a mean volume of 764.2 cm^3 (SE = 52.6), large seminiferous tubules with mean diameter of 170.1 um (SE = 3.6), and spermatogenesis having progressed to the spermatozoa stage (Figure 13). Sperm was present in the testes and epididymides of all mature males with the exception of one male who possessed sperm in the testes but not in the epididymis.

All males below three years of age were immature while all those of age three and above were sexually mature with one exception. A single five year old displayed low levels of spermatogenesis and was considered to be immature (combined testes weight of 278.5 g, testis volume of 118.9 cm^3, mean tubule diameter of 99.9 um, and stages of meiosis visible, but no sperm present) (Figure 14).

The average age of sexual maturity (ASM) for males, estimated using the method of DeMaster (1978), was 3.0 years. A standard deviation for the male estimate could not be generated due to a violation of an assumption in DeMaster's method. The method assumes that the proportion of sexually mature animals increases with each successive age class. When this assumption is not met, the recommendation is to ignore

Figure 13: Seminiferous tubule showing the stages of spermatogenesis in a mature male harbor porpoise.


Primary Spermatocyte
Spermatid
Lumen
Spermatogonia
Spermatozoan

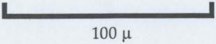
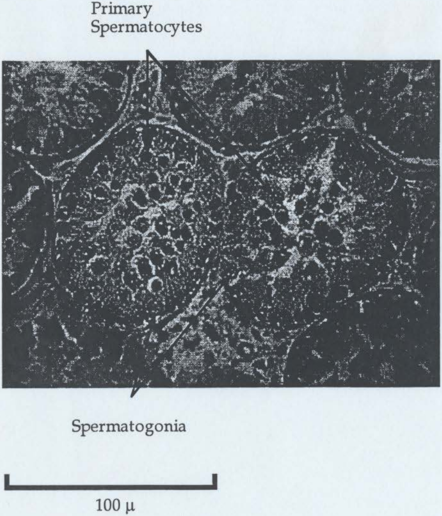

100 µ

Figure 14: Seminiferous tubules from an immature male harbor porpoise near sexual maturity.


Primary
Spermatocytes
Spermatogonia
100 μ

the outliers and use values from a fitted curve of proportion mature versus age. Although a statistical comparison cannot be made, ASM for males appears similar to 3.1 years for females.

When an age of three was entered into the Gompertz growth model, a length at sexual maturity for males was predicted to be 136.7 cm, similar to 135.1 cm (SE = 0.02) calculated via DeMaster (1978). The value of LSM for males was significantly lower than for females ($t = 7674.3$, $P < 0.001$, $df = 89$).

DISCUSSION

4.1 Distribution

Although fishermen were contacted from the entire Avalon Peninsula, the vast majority of porpoises (86.2%) were retrieved from one area, Cape St. Mary's. In a survey of harbor porpoise catches on the Avalon Peninsula, Lien (1980) also found that catches were concentrated in this area. It is not clear if this indicates actual areas of porpoise concentration or rather, a bias in fishing effort or fishermen cooperation.

There was a high proportion (70.1%) of males caught at St. Brides in 1991 (Table 1) which may reflect a sampling bias, a greater likelihood of males becoming entrapped, or sex segregation. A larger proportion of males (66%) was also reported from West Greenland (Kinze et al. 1990) and from the Baltic (Mohl-Hansen 1954). If males segregate and frequent areas of heavy fishing operations and females alternatively are in areas of low fishing effort, then a preponderance of males in the sample might be explained. Evidence for sex segregation in harbor porpoises has also been found by Kinze (1990b). Alternatively, if the two sexes exhibit different grouping behavior, one might also expect to find differences in the by-catch distribution. For example, if males aggregate in high density groups but females remain alone or in small groups, there would be a higher probability of entrapping males simply because where there would be one, there would be many. Piatt and Nettleship (1987) suggest that harbor porpoise form high-density feeding aggregations and, by doing so, likely increase the probability of becoming entangled.

Differences in behavior between the sexes may account for differential entanglement rates. If, for example, males dive to net depths more frequently than females, they run a greater risk of becoming entrapped in a bottom set gillnet.

A preponderance of males in the catches may be representative of the population sex ratio if there is differential mortality between the sexes. However, Mohl-Hansen (1954) found an equal sex ratio among fetuses, although there are no data available on juvenile mortality rates for harbor porpoises.

4.2 Timing of collections

The peak collection period spanned the same three weeks in July for both 1990 and 1991. Preliminary data (G. Stenson, unpubl. data) suggest a change in fishing gear at this time, from lumpfish nets to the smaller-meshed flounder gillnets. Whether a relationship exists between size of net mesh and probability of a porpoise being caught is inconclusive. Data on the timing of collections may have important implications for by-catch management. If the impact of incidental mortalities on the population is high, a reduction in catches may be achieved by a brief closure of the gillnet fishery during the peak entrapment period, i.e. two to three weeks in July. Clearly, the data presented here are preliminary and further research would be necessary to draw conclusions about the exact timing of peak incidental mortalities.

Data on the seasonal movements of this population are not clear, although personal observations and observations by J. Lien (pers. comm.) have noted harbor porpoises being more common in the summer months, but rarely seen during the rest of the year. It must be noted, however, that it is not clear whether harbor porpoises are not present during the winter or, rather, they are present and are just not seen due to higher sea states and/or lack of effort.

4.3 Age structure

The majority of the animals collected were young, i.e. four years or less (Figure 2). Similar results have also been found in other samples of incidentally caught harbor porpoises (Hohn and Brownell 1990; Kinze 1990b; Kinze et al. 1990). Northridge and Lankester (1990) compared the size range of porpoises caught in gillnets versus other sources of samples (trawls and strandings) and found that smaller porpoises were more likely to become entrapped in gillnets than were larger animals. Kinze (1990b) also reported that gillnet-caught specimens are younger than those taken in the drive fishery, indicating that gillnet-caught specimens may not be representative of the age structure of the population. Kinze (1990b) hypothesized that younger animals may get caught more often than older animals because they have not yet learned net avoidance behavior. He also suggested that calves may be vulnerable due to their exploratory behavior and inexperience, and in turn, also put the cows at risk when attempting to rescue their calves. The present study contained four apparent cow-calf pairs, although calves were under-represented in the sample. Alternative explanations for the seemingly lower likelihood of calf entanglement may include possible differences in diving behavior and/or the presence of an experienced attending female (the cow).

A preponderance of younger animals may also occur if porpoises of similar ages travel together and young animals frequent areas of higher fishing intensity. There is some evidence of age segregation presented by Gaskin and Blair (1977) who have found that subadult males appear to be segregated from the rest of the stock. Different foraging strategies may be employed by younger animals if successful prey capture is a learned behavior that comes with experience and thus age. Younger animals may have to resort to raiding nets for food if they have not yet mastered the capture of free-ranging fish.

4.4 Growth

Sorensen and Kinze (1990) reported lengths at birth of 63 to 86 cm for Danish porpoises, similar to 77.3 cm for California harbor porpoises (Hohn and Brownell 1990) and 80.8 cm for West Greenland harbor porpoises (Kinze et al. 1990). Mean calf length was found to be 91.6 cm in the present study. The mean date of collection for Newfoundland was 23 July compared to 9 July for West Greenland. If it is assumed that the timing of reproduction is the same in the two areas, the size of the calves and the collection date suggest that calves in the present study were not neonates. Results of physical examinations of the calves support this; they did not possess any morphological features typical of neonates, such as a folded dorsal fin, a portion of the umbilicus attached, or a fresh umbilical scar. A back calculation to estimate length at birth for the Newfoundland sample was not possible given insufficient data on neonatal growth rates.

Growth rates are similar for male and female harbor porpoises up until approximately 120 cm in length, which is about one year of age (Figure 8). At this time, females grow faster than males and appear to remain larger throughout life (Figures 4 and 5). This is consistent with other studies (Bjorge et al. 1991; Fisher and Harrison 1970; Gaskin and Blair 1977; Gaskin et al. 1984; Hohn and Brownell 1990; Kinze et al. 1990; Martin et al. 1990; Read 1989; Sorensen and Kinze 1990; van Bree 1973; van Utrecht 1978). Statistical comparisons can only be performed with the Bay of Fundy data because no standard errors were reported for other areas. Adult females from this study were not significantly longer than females from the Bay of Fundy ($t' = 0.38$, $0.9 > P > 0.5$, $df = 58$) and not dissimilar to females from Norway (Bjorge et al. 1991) (Table 8). Similarly, males from Newfoundland were not significantly longer than Bay of Fundy males ($t' = 0.51$, $0.9 > P > 0.5$, $df = 177$) and were similar in length to Norwegian males (Table 8).

Both males and females continue to gain weight after reaching their maximum lengths (Figure 6 and 7). Growth models also indicate that females are heavier than males. This is contrary to the results found by Bjorge et al. (1991) who reported that asymptotic weight values were higher for males than for females from Norwegian waters. Males from Norwegian waters were similar in weight to males from Newfoundland, but the females weighed considerably less (49.4 kg versus 61.6 kg) (Table 8). The lighter females in Norwegian waters could be accounted for if they have a lower intrinsic weight than females from Newfoundland waters. Perhaps females in Newfoundland are exposed to a preferable environment, however, this does not explain the similarities in weight between males from Newfoundland and Norway.

Alternatively, the lighter weights of females in Norway may be accounted for if they had been lactating, and thus depleting fat reserves, for a longer period of time than the females in Newfoundland. Approximately 69% of the Norwegian sample were caught between late May and early July, but time of collection was not reported for the remainder of the sample. Rates of mass transfer from mother to calf during lactation are not known for the harbor porpoise, but Gaskin (1982) estimated from an energy budget model that demands could be quite costly. To help offset lactation demands, it

Table 8: Growth and reproductive characteristics of harbor porpoises from various areas. Standard errors are included in parentheses for the Newfoundland population.

Parameter	Newfoundland	Other Populations (see below)
Parturition	before late June	18 May[C], May-June[B], June-July[B]
Ovulation and Conception	early-late July	late June[F], July-August[A,B,I]
ASM: Females (years)	3.1 (0.07)	14 months[A], 3.44[F], 4[H,I,J], 4.6[G], 6[D]
ASM: Males (years)	3.0	3[H,I,J], 5[D]
LSM: Females (cm)	146.4 (0.03)	140[H,I], 143[F], 145[B], 150[A], 152[G]
LSM: Males (cm)	135.1 (0.02)	130[H], 133[B], 135[I]
Length Asymptote: Females (cm)	156.3 (2.9)	155[F], 155.9[J]
Length Asymptote: Males (cm)	142.9 (1.2)	142.3[J], 144[F]
Weight Asymptote: Females (kg)	61.6 (3.6)	49.4[J]
Weight Asymptote: Males (kg)	49.1 (1.3)	52.7[J]

A = Mohl-Hansen, 1954, Baltic
B = Fisher and Harrison, 1970, Bay of Fundy
C = Gaskin and Blair, 1977, Bay of Fundy
D = van Utrecht, 1978, North Sea
E = Stuart-Simons, 1984, California
F = Read, 1989, Bay of Fundy
G = Hohn and Brownell, 1990, California
H = Kinze et al., 1990, West Greenland
I = Sorensen and Kinze, 1990, Denmark
J = Bjorge et al., 1991, Norway

has been suggested that females may increase their food intake by up to 80% during this time (Yasui and Gaskin 1986). Certainly, maternal weight loss during lactation is substantial in seals ranging from 3.1 to 3.8 kg per day for harp and gray seals (Anderson and Fedak 1987; Kovacs et al. 1991) and 16.2% of total maternal body weight for hooded seals (Bowen et al. 1987). So, it might not be unreasonable for the discrepancies in weight between Norwegian and Newfoundland female porpoises to be explained by lactation. However, comparisons between lactating and non-lactating females in the present study did not show any significant differences in body weight (t = 1.05, P = 0.31, N = 15). There were also no significant differences in blubber mass values between lactating and non-lactating mature females from the Bay of Fundy (Read 1990c). However, both studies collected samples in the summer months. It would be interesting to investigate the body condition of porpoises during other times of the year to determine whether prolonged demands of lactation cause females to draw upon their stored fat reserves.

The differences in body weight between Newfoundland and Norway female harbor porpoises may reflect seasonal changes in fat deposition, if indeed some of the porpoises in Norway have been caught during the winter months.

4.5 Female reproduction

If age at sexual maturity (ASM) varies with exploitation as a density dependent response, then it becomes a vital parameter in stock and status assessment studies (Eberhardt and Siniff 1977; Perrin and Reilly 1984). Techniques for estimating ASM vary in their assumptions. Age at first ovulation (AFO) is an unbiased estimate, but usually has wide confidence intervals due to the typically small sample size of first time ovulators (DeMaster 1984) (N = 4 in the present study). The method of DeMaster (1978) on the other hand, considers all age classes, but weights them evenly. This will positively bias the estimate when there are fewer older specimens in the sample (DeMaster 1984). Statistical comparisons of ASM between populations should only be done when the same methods have been employed.

Females reached sexual maturity at approximately age three. Estimates of mean age of sexual maturity (ASM) for female porpoises have ranged between 14 months and six years for various populations (Table 8). Mohl-Hansen's (1954) estimate of 14 months for harbor porpoise in the Baltic was discredited by Fisher and Harrison (1970) who reported sexual maturation to occur between the third and fourth years for porpoises from the Bay of Fundy. Estimates from the North Sea range from four years (Sorensen and Kinze 1990) to six years (van Utrecht 1978); from Norway, four years (Bjorge et al. 1991); from West Greenland, four years; and from California, 4.6 years (Hohn and Brownell 1990). It appears that females in Newfoundland achieve sexual maturity about a year earlier than females from other areas. Statistical comparisons could only be made with estimates from the Bay of Fundy (Read 1989 - ASM = 3.44 years). Females in the Newfoundland sample attained sexual maturity at a lower age than females in the Bay of Fundy ($t' = 4.30$, $P < 0.001$, $df = 34$) (Table 8), although the relatively small size of the Newfoundland sample should be noted ($N = 35$). There are several possible explanations for a lower ASM. Interpopulation variation in maturation rates is one possibility; perhaps Newfoundland females have a higher intrinsic growth rate and can therefore mature earlier. A lower ASM may reflect a more favorable environment. If food resources in Newfoundland waters are more plentiful or have a higher energy density, then it would presumably be possible for females to grow faster and also mature earlier. There is some evidence to suggest that age at sexual maturity lowers in response to a reduction in population density (Kasuya 1991, Perrin and Donovan 1984, Read and Gaskin 1990b). If harbor porpoises around Newfoundland have been exposed to substantial exploitation, then a decrease in age at sexual maturity may be a response to the decreased density of the population.

Length at attainment of sexual maturity (LSM) is useful in yielding maturity status of samples for which only length data is available (Perrin and Reilly 1984). LSM values for female porpoises from other areas are presented in Table 8. Females from Newfoundland are longer at attainment of sexual maturity than females from the Bay of Fundy (Read 1989) ($t' = 70.03$, $P < 0.001$, $df = 135$). This also may suggest a higher intrinsic growth rate or better food resources for Newfoundland porpoises. Based on the data available, female harbor porpoises from Newfoundland mature earlier at a larger size than females from other areas.

The timing of parturition in the Newfoundland sample could not be directly estimated. Kinze et al. (1990) obtained fetuses from West Greenland females as late as mid-July, so it would seem that parturition in Newfoundland porpoises is earlier as no near term fetuses were recovered during the sampling period. There is a recent report of a heart rate recording taken from a small porpoise (umbilical cord still attached) that was found swimming alone with difficulty near Carbonear (eastern Newfoundland) in late June (S. Todd, Memorial University of Newfoundland, pers. comm.). Parturition can only be estimated to occur sometime before the sampling period. Gaskin and Blair (1977) back calculated the mean date of birth as 18 May for Bay of Fundy porpoises based on dentinal deposition rates and thickness of postnatal dentine in calves. Estimates from other areas range from May to July (Table 8).

In Newfoundland, ovulation and conception appear to occur during early to late July. Most corpora lutea were small and developing (mean diameter = 11.9 mm) and two females were sampled with very large follicles (8.0 and 10.2 mm) in mid-July. Few porpoises were sampled early in the season so it is difficult to put much confidence in this estimate. Read's (1990a) estimate of late June to early July for porpoises from the Bay of Fundy was about a month earlier than estimates from other areas. Estimates of ovulation and conception ranging from late July to early August have been given by Fisher and Harrison (1970) for the Bay of Fundy, by Sorensen and Kinze (1990) for the North Sea, and by Mohl-Hansen (1954) for the Baltic.

Pregnancy rate was estimated as 0.76. Inclusion of the two females with large follicles would raise this to 0.83 which is similar to 0.86 reported by Read (1989) for the Bay of Fundy sample. Because no fetuses were found, the presence of a corpus luteum (CL) had to be used as the criterion for pregnancy. This value is, in reality, a minimum estimate of the ovulation rate rather than a true pregnancy rate. This ovulation rate will over-estimate pregnancy rate if some of the females with corpora lutea did not become pregnant or if inter-uterine mortality occurs. This estimate is also based on the assumption that the distribution of reproductive conditions in the sample is representative of those in the population. A violation of this assumption cannot be ruled out given the nature of the sample.

Diameter of corpora lutea increased over the duration of the sampling period (Figure 9). The one outlier was a first time ovulator and may possibly have been late in ovulating or conceiving due to lack of experience. However, the other two first time ovulators fit the line very well, suggesting that the outlier may have been an example of an infertile ovulation and thus, an indication of the extent that the pregnancy rate may be positively biased when corpora lutea are the criterion of pregnancy.

Because of the risk of over-estimating pregnancy rates when using the presence of a CL as the criterion for pregnancy, an alternative method would be to consider the number of lactating females divided by the number of females that had the potential to become pregnant in the previous year (those possessing at least one CA). This value (0.71) was less than the rate based on CL presence (0.76 in the most conservative estimate). This difference may be due to small samples sizes or may indicate the extent of infertile ovulations and/or inter-uterine mortalities. This estimate may under-estimate the birth rate but, depending on the level of neonatal mortality, the timing of sampling, and the time lag between the death of a suckling calf and termination of lactation, it may give a better indication of calf survivorship.

Based on the assumption that age estimates are correct, examination of corpora albicantia counts versus age suggested that some females ovulate more than once per year. Individual variability in ASM may account for some scatter of values, but is not likely to explain all values above the arbitrary line ($Y = X - 3$), representing a rate of one ovulation per year with sexual maturity occurring at age 3. The younger females have corpora counts that are greater than or equal to their age (Figure 10). Large numbers of CAs do not always represent previous pregnancies; some may result from unfertilized ovulations or from luteinization of unruptured follicles (Brodie 1971). The number of CAs is therefore an unreliable estimate of past production (Brodie 1971). All CAs were similar in appearance, so if luteinized follicles (corpora atretica) existed, they were not distinguished. Certainly the data are inconclusive with the small sample size, especially with the paucity of older females, but the apparent quadratic relationship between corpora counts and age suggests that the number of corpora plateau and may not persist throughout the lifetime of the individual, as suggested by Perrin and Donovan (1984) and Read (1989). If this is the case, perhaps it is the luteinized follicles or the corpora of infertile ovulations that fail to persist.

The proportion of females simultaneously pregnant and lactating in the present study was quite high (35.3%). Read (1989) found that 23.6% of mature females were both pregnant and lactating in the Bay of Fundy. This concurs with Mohl-Hansen (1954) who suggests that porpoises breed every year. Alternatively, Fisher and Harrison (1970), Hohn and Brownell (1990), and Martin et al. (1990) conclude that the calving interval for the harbor porpoise must be greater than one year due to the low proportions of simultaneously pregnant and lactating females that they found. A higher fecundity in Newfoundland porpoises suggests either interpopulation variation that is genetically based or a more favorable environment which allows Newfoundland porpoises to invest more energy into reproduction. Alternatively, it is also conceivable that an increase in the number of simultaneously pregnant and lactating females would reduce the length of the calving cycle and thereby increase production. This may reflect a density dependent response if population abundance has been reduced because of high exploitation rates (Perrin and Donovan 1984).

No fetuses were recovered over the duration of the sampling period. Kinze et al. (1990) did not find any fetuses in August. Fisher and Harrison (1970) did not find an embryo until 15 August and Read (1989) also reported the earliest fetus as mid-August. Sorensen (1991) reported the first detectable fetus in early September for porpoises in Danish waters. One explanation for the delay in fetus visibility is Read's (1989) suggestion of a pre-implantation period of 6 to 7 weeks after ovulation and conception, allowing the left uterine horn time to recover before the next pregnancy (harbor porpoise do not appear to alternate uterine horns). Alternatively, it may reflect failure to recover the very small embryos during gross lab necropsies prior to this time (T. Sorensen, Institute of Cell Biology, Denmark, pers. comm.).

4.6 Male reproduction

Most studies focus on the reproductive characteristics of females and put little emphasis on those of males. In animals such as the harbor porpoise, which are believed to display reproductive seasonality, information on male reproduction is not only important in and of itself, but can also reveal or confirm information regarding the timing of the female cycle. It is not unreasonable to suspect that peak sexual activity in males will coincide with ovulation in females. Because the sampling window was narrow, the peak of sexual activity in male porpoises was not possible to determine. However, all mature males sampled were actively producing sperm and comparisons with other studies (see below) suggest that this was high, if not peak, sexual activity. This concurs with the estimate of timing of ovulation in females.

Age and length at sexual maturity are important in revealing any sex differences in growth or maturation rates. ASM was not dissimilar for males (3.0) and females (3.1) within the Newfoundland population. Several authors have reported that males attain sexual maturity one year earlier than females (Bjorge et al. 1991; Kinze et al. 1990; Sorensen and Kinze 1990; van Utrecht 1978). The use of different methods in estimating ASM for other porpoise populations does not permit statistical comparisons with the estimate of sexual maturity in males obtained from this study. ASM has been estimated as three years for male harbor porpoises from the Norwegian population (Bjorge et al. 1991) and from the Danish North Sea population (Sorensen and Kinze 1990). Gaskin et al. (1984) estimated that males in the Bay of Fundy become sexually mature between the ages of three and four and van Utrecht (1978) has estimated ASM for North Sea porpoises to be five years of age. It would seem that the estimate of van Utrecht (1978) reflects interpopulation variation, sampling bias, or errors in determination of reproductive condition or age estimation. van Utrecht's (1978) age data may not be accurate according to much of the recent work that has been done on standardization of age determination in harbor porpoises. His age estimates would be positively biased if a half-year line existed in his samples but was counted as a complete GLG.

Length at sexual maturity was lower for males than for females in the Newfoundland sample ($t = 6.7$, $P < 0.001$, $df = 90$). This is a common finding in other harbor porpoise populations (Fisher and Harrison 1970; Kinze et al. 1990; Sorensen and Kinze 1990). LSM for Newfoundland harbor porpoises is similar to those from the Bay of Fundy, West

Greenland, and the Danish North Sea (Fisher and Harrison 1970; Kinze et al. 1990; Sorensen and Kinze 1990) (Table 8).

Mean testes weight was not dissimilar among adult males (age four and up) from Newfoundland (1555.9 g), Norway (1553.0 g - Bjorge et al. 1991), and the Gulf of St. Lawrence (1373.3 g - Fontaine 1991). Testes weight can reach 3.5 to 4.0% of the body weight for mature males (Fontaine 1991; Gaskin et al. 1984); the present study found a maximum of 6.2% of the body weight. From an energetics point of view, seasonal decrease in testes mass would presumably be favorable outside of the breeding season. Such a seasonal change in testes size, peaking from May to July and declining from August to October, was found by Fisher and Harrison (1970) for porpoises in the Bay of Fundy. Gaskin et al. (1984), Read (1989), and Sorenson and Kinze (1990) also found similar changes in testis size. A significant trend of this nature was not found in the Newfoundland sample, but this was likely due to the narrow time period sampled each year.

Mean seminiferous tubule diameter for mature males was similar among porpoises from Newfoundland, the Gulf of St. Lawrence (Fontaine 1991), and the Bay of Fundy (Fisher and Harrison 1970), while Gaskin et al. (1984) reported a lower mean of 124.2 um for mature males also from the Bay of Fundy.

This value may be lower due to a wider sampling period which began in mid-July and extended to early September. Seasonal decrease in seminiferous tubule diameter has been found by Fisher and Harrison (1970) and Gaskin et al. (1984), although was not apparent in the Newfoundland sample, possibly relating to the restricted sampling period.

Seasonal trends in testicular volume have also been reported for mature males in the Bay of Fundy (Gaskin et al. 1984). They found that immature males could easily be distinguished from mature males during the summer months on the basis of single testis volume. Mean testicular volumes for immature and mature Newfoundland harbor porpoises (Table 7) are larger than those from the Bay of Fundy (immatures = 17.7 cc, matures = 236.4 cc), probably reflecting the later sampling period of Gaskin et al. (1984). No significant decrease in testicular volume over time was found for the Newfoundland sample.

Generally male harbor porpoises from Newfoundland were similar in their growth and reproductive characteristics to males from other areas. The interpopulation differences that were apparent for females did not appear to exist for males.

4.7 Stock identification

There has been recent debate concerning population distribution of harbor porpoises in the northwest Atlantic (Marine Mammal Investigation 1992). Gaskin (1984) suggests that porpoises occur in a series of local populations consisting of a Bay of Fundy/Gulf of Maine stock, a Gulf of St. Lawrence stock, a West Greenland stock, and a Newfoundland stock. While there is evidence to suggest such a segregation, there is also support for the alternative hypothesis of one large harbor porpoise population in the northwest Atlantic. The importance of this discussion is realized when determining the extent of incidental mortalities on the potential growth of the population based on by-catch levels and population abundance. The evidence is by no means conclusive, but certain findings lend support to the proposition that the Newfoundland porpoises are indeed a different stock of animals.

Peak times for sightings and incidental catches of porpoises around Newfoundland are typically June and July (Piatt and Nettleship 1987; Sergeant and Fisher 1957; J. Lien, Memorial University of Newfoundland, pers. comm.), although it is not certain whether fishing and/or sighting efforts introduce biases. The peak sighting times in the Bay of Fundy coincide with those in Newfoundland (Gaskin 1991; Gilpin 1878; Neave and Wright 1968; Read and Gaskin 1988; Smith et al. 1983). Similar timing of concentrations in two geographically separate areas suggests two separate populations (Mercer 1973). Bay of Fundy porpoises are thought to migrate north/south seasonally (Marine Mammal Investigations 1992) while at least some of the Newfoundland population may occur off the Grand Banks in winter (Stenson and Reddin 1991) and may display a seasonal inshore/offshore migration. There are also reports of small overwintering populations in both the Bay of Fundy and around Newfoundland (Gaskin 1991; Gilpin 1878; Neave and Wright 1968; J. Lien, Memorial University of Newfoundland, pers. comm.), which may suggest a resident population in each area and another migratory population or, more simply, that a migration does exist, but not all porpoises participate in it.

Differences in growth and reproductive characteristics of porpoises from different areas may also suggest different stocks. The earlier age at sexual maturity and longer length for females from Newfoundland compared to those from the Bay of Fundy may indicate different intrinsic rates and thus different stocks of animals.

A separate Newfoundland stock is indicated by the differences observed in dentinal deposition patterns. The GLGs were not as clearly defined in the Newfoundland sample as they were in porpoise teeth from California and the Bay of Fundy (A. Read, Woods Hole Oceanographic Institution, pers. comm.). Teeth from Newfoundland were harder to read and it was harder to achieve consensus between the two experienced readers (A. Hohn and A. Read). A half-year mark laid down at approximately six months was common in the other populations but was completely absent, or extremely variable, in the Newfoundland sample. The inconsistency of this mark may suggest environmental fluctuations, mixing of stocks, or changes in diet. The Newfoundland sample of teeth also had structural anomalies prevalent in the dentine that were not commonly seen in the other populations (A. Hohn, National Marine Fisheries Service, pers. comm.). These anomalies may be the result of some type of nutritional and/or physical stressors (A. Read, Woods Hole Oceanographic Institution, pers. comm.).

4.8 Future research

The extent of incidental mortalities on the population is critical as porpoise populations have been calculated to grow at a maximum rate of less than 10.0% per year (Barlow and Hanan 1990). These authors suggest a maximum allowable take of 2.0% per year, a conservative value given the lack of information on actual population growth rates. Recommendations have been made to reduce the level of by-catch of harbor porpoises from the Gulf of Maine/Bay of Fundy population as levels are now estimated to be 4.0 to 5.0% of the estimated abundance (Marine Mammals Investigation 1992). Although there are some estimates of harbor porpoise by-catch around Newfoundland (Lien 1980; Lien 1987; Lien 1989; Lien et al. 1988; Piatt and Nettleship 1987), the impact of these takes cannot be evaluated until estimates of porpoise abundance become available. Future studies should therefore initiate population surveys for the Newfoundland area and improve existing estimates of by-catch.

Research on population structure should be continued to better define the stocks of the northwest Atlantic. A new method may be possible if the differences in the deposition patterns in the teeth of porpoises from the various populations can be quantified. Radio or satellite tagging and skull morphometric studies may also reveal evidence to suggest population boundaries. Mitochondrial DNA studies of northwest Atlantic harbor porpoises are presently incomplete (J. Wang, U. of Guelph, pers. comm.). It is uncertain if genetic techniques are sensitive enough to determine such differences, if indeed they exist. Differences in the concentrations of pollutants have also been used to distinguish stocks (Aguilar and Borrell 1990; Calambokidis and Barlow 1991; Granby and Kinze 1991). There is ongoing research to analyze organochlorine and heavy metal concentrations in the blubber of porpoises from the areas in question, although results are not yet available (A. Westgate, U. of Guelph, pers. comm.).

Finally, the present study was important in providing the first growth and reproduction data for harbor porpoises in the Newfoundland area, but conclusions are preliminary. A more in-depth study should include a larger sample size from a wider time period, especially from the winter months, in order to better investigate migration patterns and seasonal cycles in reproduction. If a single population can display changes in life history parameters over time in response to changes in density, then potential impacts of reduced density caused by exploitation may be realized by time lapse studies. This population monitoring technique may become increasingly important, especially given the difficulties associated with obtaining population counts with this species.

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