Growth and reproduction in harbour porpoises (*Phocoena phocoena*) in Icelandic waters

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ABSTRACT

A total of 1,268 harbour porpoises were obtained from fishing nets in Icelandic coastal waters from September to June in the years 1991 to 1997. Foetal sex ratio was 1.2:1 (male:female). The bias towards males increased further among older animals in the present collection. The modal year classes were 0 and 1 years but the oldest porpoise was a female estimated at 20 years of age. Length at birth was estimated as approximately 75 cm, and females grew faster and attained larger sizes than males. Asymptotic length was 149.6 cm for males and 160.1 cm for females. Estimated age and length at sexual maturity was 1.9 to 2.9 years and 135 cm for males and 2.1 to 4.4 years and 138 to 147 cm for females. Immature individuals were significantly shorter than pubertal and mature animals in both sexes in age classes 1 to 3. Testes weight increased only slightly with body size in immature males but increased rapidly around maturity. Pronounced seasonality was also observed in testes weight, indicating a peak in testes activity in summer. Lack of data from the summer makes the exact timing of parturition and mating unknown. Births do, however, most likely peak in June and July and lactation lasts at least 7 to 8 months. Ovulation and pregnancy rates were 0.98.

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INTRODUCTION

Interactions of harbour porpoise (*Phocoena phocoena*) with commercial fisheries (IWC 1994) and their susceptibility to pollution in coastal areas (Reijnders *et al.* 1999) have evoked increased concern in recent years. Most studies have put emphasis on investigating population size and structure and life history parameters that may reveal status of populations and their potential vulnerability to human interactions (Bjørge and Donovan 1995). Harbour porpoises are common in Icelandic waters and an offshore population estimate of 27,000 obtained from a shipboard survey in 1987 is most likely downward biased (Sigurjónsson and Víkingsson 1997). Sæmundsson (1939) discussed seasonal migrations of harbour porpoises into shallow waters in Iceland during summer but systematic studies on Icelandic harbour porpoises have not been conducted in any research field to date.

In order to attain basic biological information on the species in Icelandic waters, a wide ranging research project was initiated in 1991. The main emphasis was put on studies of feeding ecology (Víkingsson *et al.* 2003), while studies were also conducted on reproductive biology (Halldórsson and Víkingsson 2003), morphology, genetics (Tolley *et al.* 2001), energetics and toxicology. In this paper biological parameters associated with growth and reproduction will be discussed.

MATERIALS AND METHODS

Harbour porpoises incidentally entangled and drowned in gillnets (6” to 10” (152 to 254 mm) mesh size) set at depths of 10 to 225 m were collected through fish markets or directly from local fishermen in all coastal areas in Iceland from September to June in the years 1991 to 1997 (Víkingsson *et al.* 2003). The carcasses were either necropsied fresh or thawed after being stored frozen (Fig. 1). Life history data (length, weight, sex, and lactating status of females) was obtained from each animal during necropsy. Evidence of lactation in females was observed by pressing and cutting the mammary glands. In case of doubts about lactation, tissue samples were taken from the mammary glands and fixed in neutral buffered formalin for histological examination. Foetuses were removed from the uterus and length, weight and sex recorded. Ovaries and combined testes (excluding epididymis) weights were recorded before preservation in formalin for later analyses. Lower jaws were stored frozen to obtain teeth for age determination.

Sex ratios were compared between age classes using Chi-square tests where significance level was set at 95%. Length distribution of immature *vs.* pubertal and mature animals within each year class was compared for animals obtained in March and April using students t-test.

Age determination

Teeth were removed from the middle region of the lower jaw, cleaned in 0.1 g collagenase D (Activity 0.36 U/mg Lyo) in 100 ml solution of Tris buffer, 0.15 M NaCl at pH=7.6 and 37° C overnight, decalcified in RDO (Apex Engineering Products Corp.) for about 3 hours and finally sectioned on a freezing microtome. Sections were mounted on microscope slides and stained with hemotoxylin. The age reading methodology applied was in accordance with the recommendations from a workshop held in Oslo in 1990 (Bjørge *et al.* 1995). One year’s growth was considered to consist of 2 complete layers; one opaque and one transparent. The 2 layers were sometimes closed by formation of a new opaque layer already in March and April. The date of capture was therefore used to determine completion of a year’s cycle where a new cycle was considered to begin on June 1. Teeth were read separately by 2 readers and re-examined by both readers upon disagreement.

Fig. 1. *Necropsy of bycaught harbour porpoises provides important data on life history parameters, condition and diet. (Photo: Institute of Marine Research, Reykjavik).*

Growth

Total length (from tip of snout to fluke notch) and weight of foetuses was measured in millimetres and grams respectively, while postnatal animals were measured to the nearest cm and 0.1 kg. von Bertalanffy curves were fitted to length-at-age and length-at-weight data:

1) $L = L_{inf}(1.0\text{-}\exp(K(t\text{-}t_0)))$

where L_{inf}, the asymptotic length or weight, is the maximum average length or weight of old individuals, K is the growth rate and t_0 is a theoretical age at zero length (Horwood 1990). Growth curves were fitted by least squares using a non-linear procedure (S-PLUS, MathSoft, Inc.).

Reproductive status

The basic terminology and methods for estimating reproductive status was adopted from Perrin and Donovan (1984).

Females

Ovaries were weighed and sliced in sections about 1 mm thick. Sections were studied under a dissecting microscope to count and measure diameters of follicles, *corpora albicantia* and *corpora atretica* (see March and Kasuya 1984). The magnitude and development of follicles were categorised as the following: 1) none or few scattered primordial follicles in the ovaries, 2) follicles making up to 50% of the area of the ovary sections 3) large follicles filling more than 50% of the ovary sections.

Female reproductive status was classified as follows 1) immature: ovaries possess solely primordial follicles and no *corpus,* 2) pubertal: ovaries contain secondary or third stage follicles but no *corpus,* 3) mature: ovaries contain at least one *corpus luteum* (CL) or *corpus albicantia* (CA). Mature females were further classified as: 1) pregnant: embryo or foetus in uterus; 2) lactating: active, milk producing mammary glands; 3) resting: non pregnant, mature females. Average age at attainment of sexual maturity (ASM) in females was estimated by 5 methods: 1) one year added to the average age of pubertal animals. Pubertal females are expected to reach maturity in the following mating season when they will be estimated one year older than at the date of capture (see section on age determination above); 2) age when 50% of individuals are mature (Perrin *et al.* 1977); 3) mean age of first time ovulators (DeMaster 1984); 4) simple least-squares regression of combined number of *corpus luteum* and *corpora albicantia* against age (DeMaster 1984) and 5) algorithm described by DeMaster (1978). Methods 1, 2 and 3 were also adopted to estimate the average length at sexual maturity (LSM): 1) average length of pubertal animals; 2) length class of 5 cm intervals when 50% animals are mature and 3) average length of first time ovulators.

Males

Testes were weighed during dissection and fixed in 10% neutral buffered formalin. Two samples, approximately 1 x 1 cm each, were taken from the peripheral (near surface) part and central (core) part of one testicle respectively (see Halldórsson and Víkingsson 2003). For the smallest testes, only one, combined peripheral/central sample was taken. The samples were dehydrated, embedded in paraffin and sectioned on a microtome to 10 mm slices, mounted on glass and stained with hematoxylin and eosin. No spermatogonia, spermatocytes or spermatids were visible in the testes, probably due to sampling entirely outside the main mating season. Males were therefore considered to be immature, pubertal or mature according to the appearance of tubula (Mackintosh and Wheeler 1929, Collet and Saint Girons 1984, Hohn *et al.* 1985, Halldórson and Víkingsson 2003). ASM in males was estimated by: 1) adding one year to the average age of pubertal individuals (see section on females above); 2) calculating age when 50% individuals are mature (Perrin *et al.* 1977) and 3) DeMaster's (1978) algorithm. LSM was derived by methods 1 and 2 (see section on females).

RESULTS

Sample composition

Teeth and/or reproductive organs were sampled from 1,268 harbour porpoises obtained from September to June in the years 1991 to 1997 (Fig. 2). Most samples were collected in March and April, fewer porpoises were obtained from other months and no samples were obtained

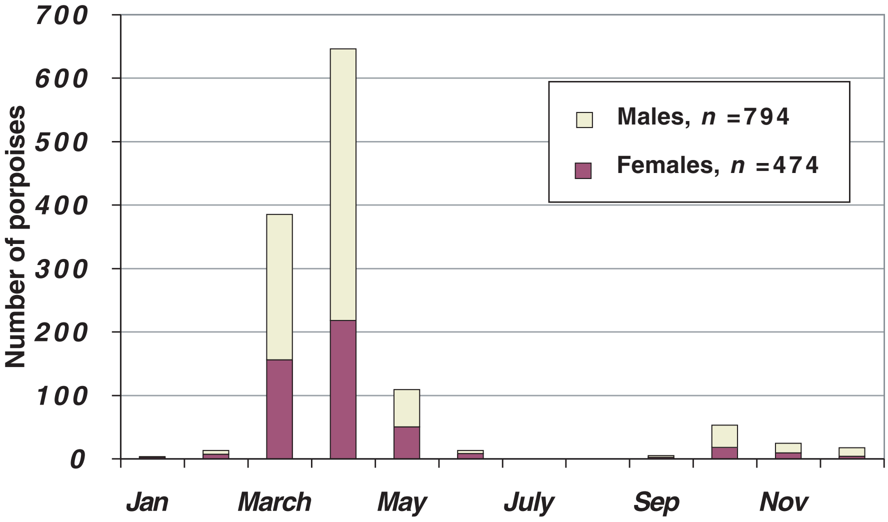

Fig. 2. *Number of life history samples by months.*

from July and August (for geographical distribution of samples see Víkingsson *et al.* 2003). The sampling may reflect porpoise migrations to shallow waters in early spring but it also seems to mirror the gillnet fishing effort in shallow Icelandic waters that peaks in early spring and ceases in many places during the summer months.

Age

Age readings were obtained from 1,025 harbour porpoises. Individuals up to 20 years of age were observed in the study but about 90% of the porpoises were younger than 6 years old. The modal age classes were 0 (calves) and 1 years (Fig. 3). The oldest female was estimated as 20 years old and the oldest male was 16 years old.

Growth

Seventy foetuses were observed from September to mid June. The smallest foetus was collected in September and was 3 cm long and weighed 0.1 g. The largest foetus, obtained in April, was 75 cm long and weighed 7,450 g (Figs 4 and 5). No neonates were obtained and the size of the youngest animals that were caught in October (98 cm) give little information on size at birth. The largest foetuses observed in spring, however, indicate a length at birth of about 75 to 80 cm. Length at age data for postnatal porpoises was obtained from 497 males and 314 females and

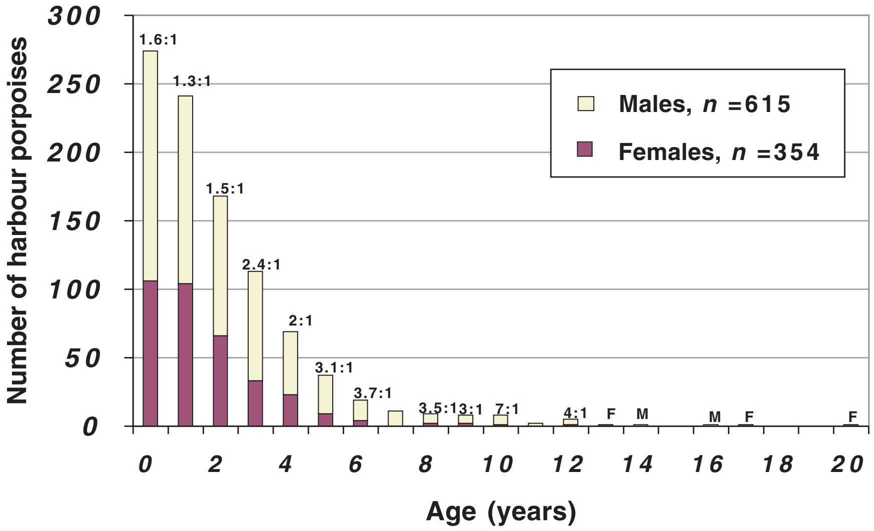

Fig. 3. *Number of life history samples by age. Labels on top of columns show M:F ratio.*

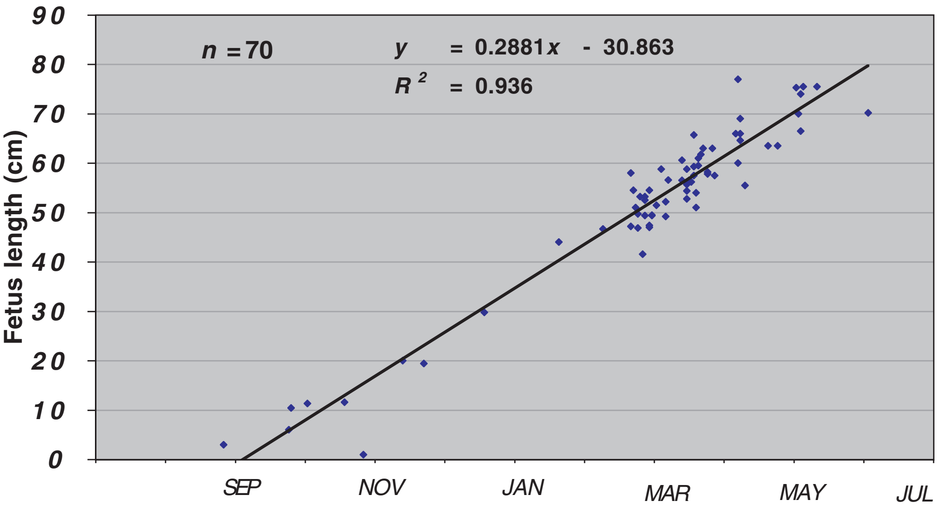

Fig. 4. *Growth of harbour porpoise foetuses from Icelandic waters.*

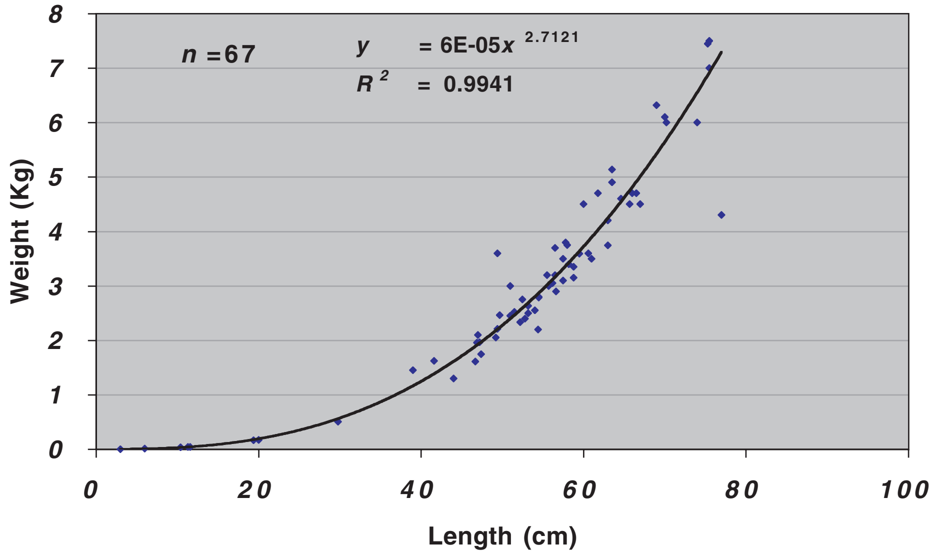

Fig. 5. *Foetus weight on length for harbour porpoises in Icelandic waters*

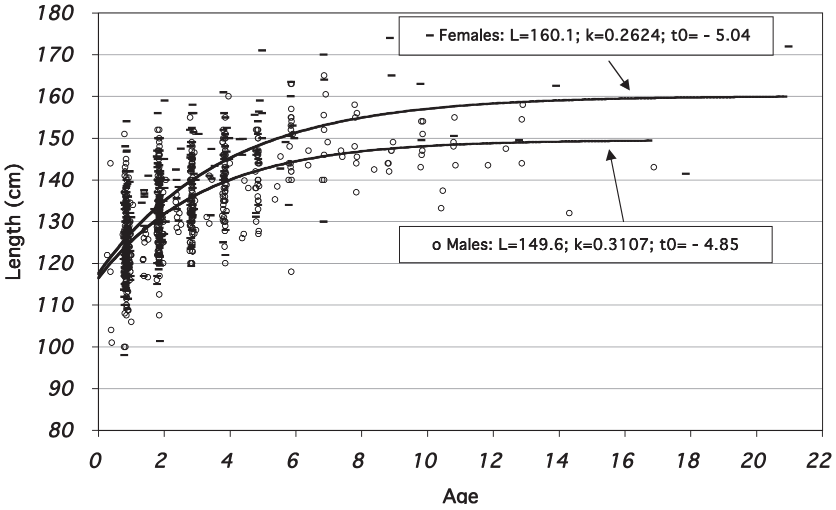

Fig. 6. *Length at age for harbour porpoises from Icelandic waters.*

weight at age data from 280 males and 216 females. Harbour porpoises grew rapidly during the first year but growth rate declined in the following years (Figs 6 and 7). Large variance is observed in growth between individual harbour porpoises but females grow in general faster and become larger than males. The youngest calves were collected in October and measured 101 cm and 104 cm but the smallest animal was a 98 cm female collected in March. Growth curves could not be constructed separately for each sex for the first year since no calves were collected in November to February. In March-April the mean length of calves had reached 126.1 cm (s = 11.11, n = 89) and 124.6 cm (s = 9.44, n = 124) in females and males respectively. The largest porpoise in the sample was a 174 cm female and the largest male was 165 cm. The asymptotic lengths and weights were 160.1 cm and 77.5 kg respectively for females and 149.6 cm and 51.7 kg for males (Figs 6 and 7).

Sex ratio

The overall ratio of male to female foetuses was 1.2:1 (n=65), mainly from data obtained in March and April. Foetuses from September and October were not sexed and the gender was known only for five foetuses from November to February. Lack of information from early pregnancy therefore precludes investigation of potential changes of sex ratio during the prenatal stage. In postnatal animals the overall M:F ratio was 1.7:1. The sex ratio did not change significantly between age classes but the male preponderance in the sample declined slightly between age classes 0 and 1 and increased again to the ages of 10 to 12 years. Thus, the proportion of males aged 0 to 2 years was 57% to 61% while males comprised 67% to 100% of age classes 3 to 12 (Fig. 3). The two oldest animals, 17 and 20 years old, were, on the other hand, females.

Reproductive cycle

Seasonally biased sampling resulted in a gap in the data on reproductive biology from June to August. Information obtained from samples in spring and autumn show that parturition, ovulation and conception take place in the summer but the exact time interval for each event remains unknown. Foetal growth indicates parturition in late spring or summer (Fig. 4). Ten pregnant females were obtained in May and one in June. No newborn calves or post-partum females

Table 1. Comparison of length distribution of immature vs pubertal and mature male and female harbour porpoises from March and April in Iceland.

	Females						
	Immature			Pubertal and mature			
Age class	Mean length	n	s	Mean length	n	s	
0	124.0	56	10.3	133.5	8	6.64	*
1	132.1	40	10.06	138.3	19	5.89	*
2	131.7	14	7.21	141.1	22	9.29	**
3	134.5	4	11.36	148.0	11	9.66	*
	Males						
	Immature			Pubertal and mature			
Age class	Mean length	n	s	Mean length	n	s	
0	123.6	106	8.90	138.8	7	7.78	***
1	130.2	79	7.92	141.1	16	8.35	***
2	129.4	23	6.62	138.0	47	7.73	***
3	131.4	10	6.30	141.3	44	6.72	***

*: p<0.05; ** : p<0.01; *** : p<0.001

Table 2. Reproductive status of harbour porpoises entangled in sink nets in Icelandic waters in 1991-1997.

	Females (n)	Males (n)
Immature	61% (223)	51% (290)
Pubertal	19% (68)	5% (28)
Mature	20% (74)	44% (250)
Pregnant	20% (73)	
Resting	<1% (1)	
Total	365	568

were, however, collected in these months or earlier. It is therefore very unlikely that parturition begins in April. While it cannot be excluded that some births occur in May, the peak in births is certainly not reached before June. Increased testes weight in mature males in spring and subsequent reduction in autumn indicates mating in the summer (Fig. 11). Pubertal males were mainly observed in spring, also implying that mating occurs in the summer.

The single mature female sampled in September and all 3 sampled in October were pregnant. There are therefore no signs of a prolonged mating season in the autumn, but with such a small sample size it can not be excluded that some mating may occur later than August.

Three out of 4 mature females with 1 or more *corpus albicans* that were obtained from September to January were lactating. Information on lactation is missing from February but none of the 38 mature females obtained from March and April were lactating. Assuming that births occur in mid June, this suggests a duration of lactation of at least 7 months but not longer than 9 months.

Reproductive status

Immature individuals were significantly smaller than pubertal and mature animals of the same age in March and April. The significance held for animals within age classes 0 to 3 years for both females and males (Table 1).

Females

Of the 335 female porpoises sampled 22% were sexually mature and all but one of these were pregnant (Table 2). The exceptional female was 17 years old with ovaries possessing only small follicles, 15 old *corpora albicantia* and no *corpus luteum*. Microscopical examination was not

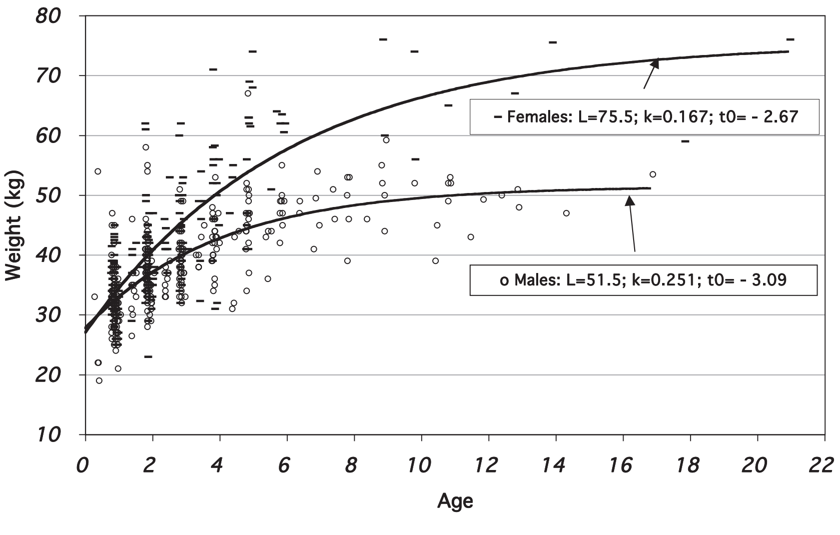

Fig. 7. *Weight at age for harbour porpoises from Icelandic waters.*

Table 3. Proportion mature animals at age for female and male porpoises entangled in fishing nets in Iceland 1992-1997.

Age class	% mature males (*n*)	% mature females (*n*)
0-0.9	3.3 (153)	0 (74)
1-1.9	14.3 (126)	4.6 (80)
2-2.9	52.6 (95)	10.6 (50)
3-3.9	80.3 (71)	45.8 (24)
4-4.9	92.5 (40)	70.0 (20)
5-5.9	95.6 (23)	87.5 (8)
6-6.9	100 (14)	66.7 (3)
7-7.9	100 (10)	-
8+	100 (26)	100 (9)

performed on the ovarian histology so we do not know whether the female was senescent (see Sørensen and Kinze 1994). The observed pregnancy rate per year is therefore 0.98 and regression analysis of the number of *corpora* against age indicated an ovulation rate about one per year (Fig. 8):

Number of *corpora* = 0.9773 * age – 1.103; SE = 1.763; *n*=50.
The highest number of *corpora* was 19 in a 20 year old pregnant female.

Foetuses were observed in 2 females in their second year of life. The oldest immature female was, however, 6 years old (Table 3). The average age of pubertal females was 1.5 years, implying an ASM of 2.5 years (Table 4). The mean length of pubertal females was 138.0 cm, indicating a slightly greater LSM since all pubertal females were obtained in spring, 2 to 3 months prior to the mating season. The average age and length of first time ovulators was 2.81 years and 147.6 cm respectively. The estimated age and length when 50% of the individuals are mature was 3.20 years and 146 cm respectively. Regression of the number of *corpora* against age gave ASM at 2.1 years (Fig. 8) and DeMaster's (1978) method 4.4 years ($s = 0.318$, $n = 293$).

Males

Of the 664 males sampled, 43% were mature and 51% and 6% immature and pubertal respectively (Table 2). Mature males were observed late in their second year of age (Table 3). The oldest

Table 4. Average age (years) and length (cm) at sexual maturity in harbour porpoise females from Iceland.

Method	Age (*n*)	*s*	Length (*n*)	*s*
Average for pubertal individuals	2.5 (62)	0.971	138.0 (72)	7.837
First time ovulators	2.8 (21)	1.030	147.6 (30)	7.154
Average when 50% mature	3.2 (269)		146	
Regression corpora~age	2.1 (51)			
DeMaster 1978	4.4 (293)	0.318		

Table 5. Average age (years) and length (cm) at sexual maturity in harbour porpoise males from Iceland.

Method	Age (*n*)	*s*	Length (*n*)	*s*
Average for pubertal individuals	2.9 (21)	1.108	135.6 (33)	8.129
Average when 50% mature	1.9 (493)		135	
DeMaster 1978	2.6 (526)	0.099		

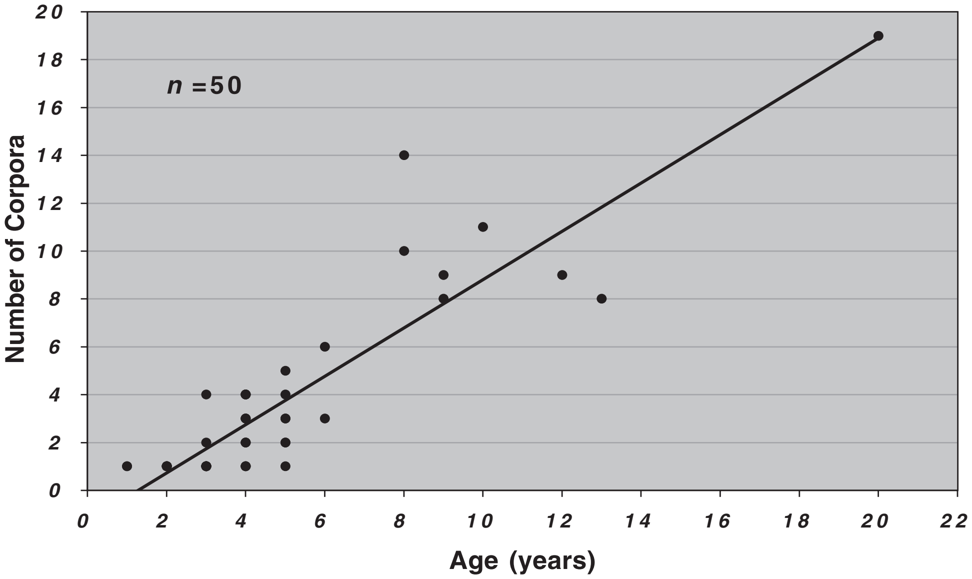

Fig. 8. *Number of corpora albicantia and corpora lutea at age in harbour porpoises from Icelandic waters.*

immature male, on the other hand, was estimated as 5 years old. The average age of pubertal males was 1.9 years and therefore an ASM of 2.9 years assuming that these individuals would have reached maturity around the following mating season (Table 5). The mean length of the pubertal males was 135.6 cm. Age and length when 50% of the individuals were mature was 1.9 years and 135 cm respectively. DeMaster's (1978) method estimated ASM as 2.6 years.

The average combined testes weight in immature individuals was 46.1 g ($s = 23.803$, range: 13-212, $n = 290$) and exceeded 100 g in only 3 individuals (Figs 9 and 10). The weight of the testes in immature males increased only slightly with body length or weight but increased greatly around maturity (Figs 9 and 10). Average combined testes weight in pubertal males was 125.8 g ($s = 58.087$, range: 56-313, $n = 24$) and 327.6 g ($s = 152.718$, range: 111-1,278, $n = 214$) in mature males. Less than 10% of mature males had a combined testis weight below 200 g. Testes weight increased with body mass in mature males and a pronounced seasonality was also observed, showing drastic hypertrophy in the summer months (Fig. 11).

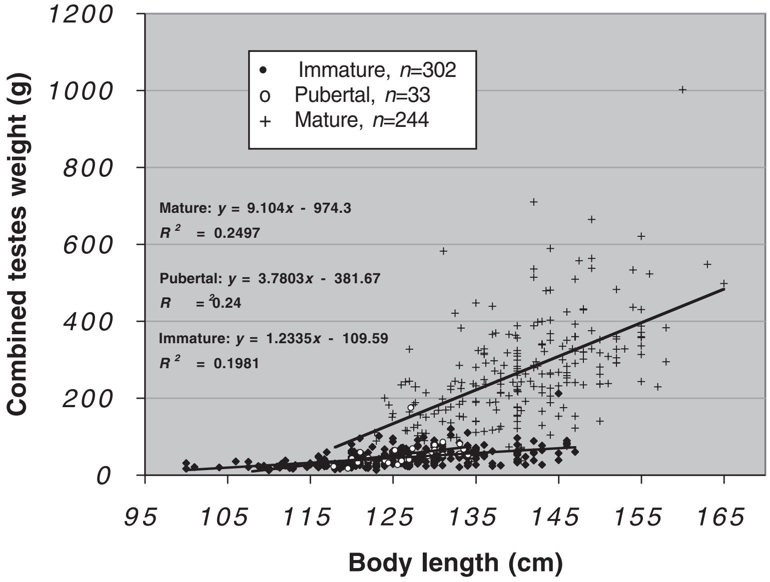

Fig. 9. *Combined testes weight (g) at body length (cm) for harbour porpoise males in Icelandic waters*

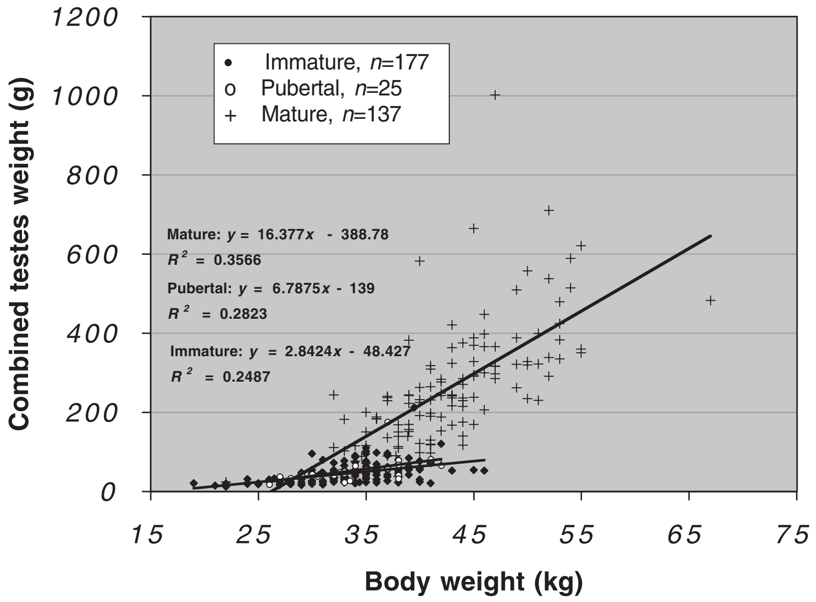

Fig. 10. *Combined testes weight (g) at body weight (kg) for harbour porpoise males in Icelandic waters.*

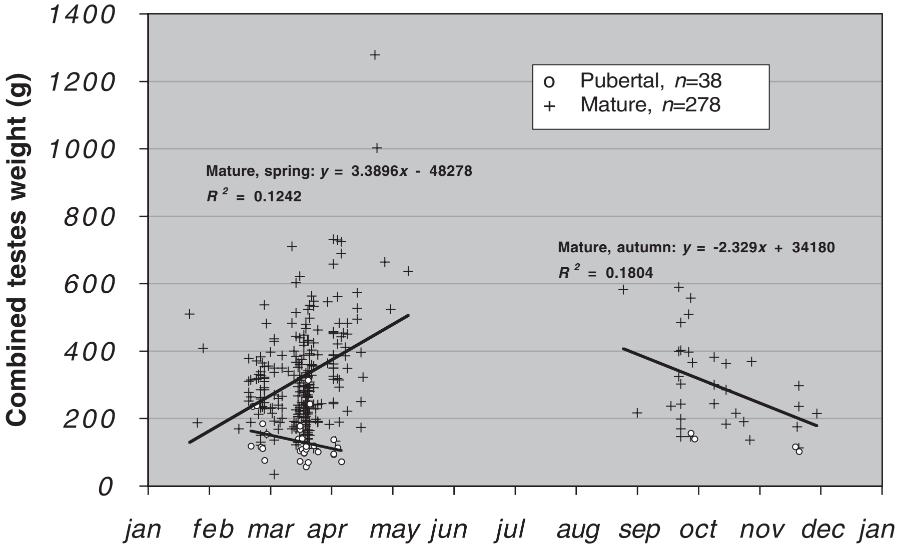

Fig. 11. *Combined testes weight (g) by months for harbour porpoise males in Icelandic waters.*

DISCUSSION

Age

Similar age distribution is observed in the net entangled harbour porpoises in Iceland as reported from stranded and net entangled animals from other populations in the North Atlantic. Few individuals live for over 20 years and the majority die before reaching an age of 10 years (Lockyer 1995a, Lockyer and Kinze 2003, Lockyer *et al.* 2001, Read and Hohn 1995, Palka *et al.* 1996, Addink *et al.* MS 1996, Rogan and Berrow MS 1996, Benke *et al.* 1998). Vulnerability to net entanglement may however be age specific, resulting in non-representative age distribution in samples obtained from bycatch.

The fact that the oldest animals were females might indicate a higher natural mortality of males, or that higher fishing mortality of young males eventually leads to a low proportion of old males in the population The low sample size in the older age classes and the non-random nature of the sampling precludes, however, calculation of age specific mortality rates from the observed age distribution.

Growth

The Icelandic porpoises reach lengths similar to those observed in the Northeast Atlantic (Bjørge and Kaarstad MS 1996, Benke *et al.* 1996, Lockyer 1995a, Lockyer and Kinze 2003), but seem to grow slightly larger than harbour porpoises from eastern Canada (Read and Gaskin 1990, Read and Hohn 1995, Palka and Read 1996, Read and Tolley 1997) and West Greenland (Lockyer *et al.* 2001). Large asymptotic weights in the Icelandic female porpoises (75 kg), compared to 65 kg in Danish waters (Lockyer and Kinze 2003) and 55 kg in British waters (Lockyer 1995a) may be explained by the seasonally biased sampling in the present study. All the largest females, except one, were pregnant and most were obtained late in the gestation period. Weight is therefore not a reliable parameter when comparing growth in different populations unless seasonal variations in body condition are taken into account.

Sex ratio

The preponderance of males among foetuses and postnatal animals in the present study is in accordance with most studies harbour porpoises in the North Atlantic (see Lockyer 2003). The overall sex ratio for postnatal animals in the Icelandic sample showed, however, a somewhat higher bias towards males than found elsewhere. The observed sex ratio for foetuses is likely to be unbiased whereas the sex ratio for postnatal animals observed in bycaught animals may be influenced by spatial or temporal sex segregation (Víkingsson *et al.* 2003). Males may also be more vulnerable to fishing activity due to size selectivity of fishing gear or differences in diving or other behaviours between the sexes leading to the observed sex ratio. Consequently, higher mortality of males may eventually lead to the dominance of females in the oldest age classes.

The decline in the proportion of males between year classes 0 and 1 seen in this study is also known from other studies (Lockyer 1995a, Lockyer and Kinze 2003). Lockyer (1995a, b) suggested that poorer condition of male neonates relative to females in British waters led to higher mortality of male calves and a subsequent decline in the proportion of males in year classes 1 and 2. Female neonates are larger than males in the southern North Sea and German waters (vanUtrecht 1978, Benke *et al.* 1998), which may support this hypothesis. The lack of neonates in the present sample makes it impossible to verify for Icelandic porpoises.

Reproductive cycle

The summer seems to be eventful in the reproductive cycle of harbour porpoises in Iceland, encompassing the periods of parturition, ovulation and conception. The gap in sampling from June to August is therefore very unfortunate and the exact timing of the peak in births and mating remains unknown. The information on foetal growth, pregnancy status, testes weight (present study) and histological changes in gonads (see Halldórsson and Víkingsson 2003) from the Icelandic porpoises in late spring and autumn, however, indicates similar timing of the reproductive cycle as observed in northern European porpoises (vanUtreckt 1978, Sørensen and Kinze 1994, Lockyer 1995a, Lockyer and Kinze 2003) and West Greenland (Lockyer *et al.* 2001) where parturition peaks in June and mating seems to occur in July and August. Histological studies on the testes of the Icelandic porpoises, furthermore, show that the mating period may be prolonged to the autumn (Halldórsson and Víkingsson 2003). Parturition and conception seem occur about one month earlier in harbour porpoises from eastern Canada than from the central North and Northeast Atlantic (Read and Hohn 1995, Palka and Read 1996).

Females have been found lactating in March in Danish waters, indicating that lactation there lasts up to 9 months (Sørensen and Kinze 1994). No sign of lactation was found in the present study in any of the 10 mature females in March that was not pimiparous. Assuming that the date of birth is in mid June, the present data do not support a period of lactation of more than 7 months. One lactating female was sampled in January, in accordance with a lactation period of 7 months or less.

Ovulation and pregnancy rates observed for Icelandic porpoises strongly suggest annual reproduction in most females after they reach maturity. Several females had more *corpora* than their estimated age. This may indicate multiple ovulation in some years but it cannot be excluded that these findings were effected by inaccurate age estimation. The high pregnancy rate observed in the Icelandic porpoises is even more surprising as most animals were obtained late in spring just before parturition, when the possibility of catching females that have aborted their foetuses should be highest. A high pregnancy rate has also been reported from porpoises from the Gulf of Maine (0.93) (Read and Hohn 1995). Most studies in the North Atlantic have, on the other hand, shown considerably lower values (Møhl-Hansen 1954, Lockyer 2003, Lockyer and Kinze 2003, Lockyer *et al.* 2001, Read and Gaskin 1990, Sørensen and Kinze 1994, Bjørge and Kaarstad MS 1996). Pregnancy rates in Norwegian and Swedish porpoises were estimated as 0.73 and 0.67 based on the presence of foetuses and *corpora lutea*, respectively (Bjørge and Kaarstad MS 1996). Sørensen and Kinze (1994) reported a pregnancy rate of 0.73 from Danish waters in September, and a pregnancy rate of 0.76 has been reported from eastern Newfoundland (Palka *et al.* 1996). Ovulation rates from Danish waters (0.64 *corpora*/year) (Lockyer and Kinze 2003) and West Greenland (0.73 *corpora*/year) (Lockyer *et al.* 2001) also indicate lower fecundity in porpoises from these areas than in Icelandic waters.

It cannot be excluded that segregation of mature females by reproductive status may cause the observed lack of resting females. Immature females were, however, frequently obtained and it is rather unlikely that resting females are totally separated from, or less likely to be entangled, than other female porpoises.

Reproductive status

Combined testes weight was less than 100 g in most immature individuals and less than 10% of mature males had testes lighter than 200 g. These results support Lockyer's (1995a) assumption that maturity is initiated when the testes reach around 200 g combined weight.

Comparison of length distributions of immature and mature porpoises within each year class revealed a significant relationship between maturity and body size. Attainment of maturity may thus be indirectly connected with age and we would expect LSM to be superior to ASM for comparisons of maturity between populations with different growth curves.

The estimates of ASM and LSM for males and female harbour porpoises using different methodologies in the present study are somewhat variable. Apparently, the seasonally biased sampling affects the estimates obtained by various methods and each sex differently. Pubertal females are observed in spring, but according to the criteria used to define maturity, females first attain sexual maturity at first ovulation. The definition of maturity in males is based on tubule size and appearance and males may thus be defined as sexually mature before they become sexually active. The large bulk of samples from spring in the present study, therefore, affects the estimation of ASM differently for males and females. Since both age and maturity stage in females reflect the situation in the last mating season prior to sampling, the estimated ASM for females is likely to be accurate. These animals have, however, attained almost one year's growth between mating and sampling, leading to a relatively high estimated LSM. Mature males observed in spring might recently have reached maturity, however they first will become sexually active in the following mating season when they will be one year older. ASM for males is therefore estimated about 1 year lower than the actual age when they become sexually active. The continuous attainment of maturity over a longer period in males is likely to lead to unbiased estimate of LSM.

In addition to the effects of the seasonally biased sampling on the estimates of ASM and LSM, various methods may serve differently for evaluating ASM and LSM from the present data. The mean age deduced by DeMaster's (1978) method is commonly used to assess ASM in marine mammals. This method, however, evenly weights all age classes regardless of sample sizes. In the present study the oldest age classes with immature females are comprised of few individuals, leading to a relatively high estimation of ASM. ASM ranging from 2.1-3.2 years deduced by the other methods are likely more accurate for the present data.

The differences in estimates of LSM for females using different methods are probably due to the severe seasonality in sampling mentioned above. The LSMs calculated from first time ovulators and the average length when 50% have reached maturity are obtained from animals that have been sexually mature for almost one year when they were caught and measured. The value of 146 to 148 cm derived by these methods is therefore positively biased. The LSM of 138 cm obtained from pubertal animals in spring is, on the other hand, probably negatively biased since these animals have yet 2 to 3 months of growth before the mating period begins. Consequently, the true LSM for females probably lies between these estimates and is probably similar to the observed values from the British Isles (140-145 cm) (Lockyer 1995a) and the North Sea (143 cm) (Lockyer and Kinze 2003).

The estimates of ASM and LMS for males obtained by different methods do not vary as much as those observed for females. The number of males was sufficient in all year classes that contained immature individuals and DeMaster's (1978) method is therefore likely to give a better estimate of ASM for males than for females in the present study.

The relatively lower ASM observed for males in the present study as compared to other areas in the North Atlantic (see Lockyer 2003) is probably again influenced by the seasonally biased sampling. The same argument cannot be adopted for the relatively low ASM for the female porpoises in Iceland compared to other harbour porpoise populations in the North Atlantic.

Concluding remarks

Harbour porpoises in Icelandic waters have a similar life history to that observed in other populations in the North Atlantic. Individuals may reach over 20 years of age, but most die by the age of 10. A slight preponderance of males is observed in foetuses. The increased dominance of males observed in postnatal animals may be a result of sex segregation and/or selectivity of and vulnerability to fishing gear. Alternatively, the natural mortality of males and females may differ. Foetal growth, length at birth and postnatal growth in Icelandic porpoises are similar to those observed in northern European porpoises, which seem to become larger than those from West Greenland and eastern Canada. The timing of the life cycle seems also to be similar to that of the northern European populations. This is inconsistent with results of studies of the homogeneity between putative populations of harbour porpoises in the North Atlantic, which have shown a closer relationship between Icelandic porpoises and populations in the Northwest Atlantic than the Northeast Atlantic (Tolley *et al.* 2001).

The Icelandic porpoises differ from other populations in the North Atlantic in having a slightly lower age at attainment of sexual maturity and high ovulation and pregnancy rates. No historical data are available on Icelandic porpoises and it is not known whether these life history characteristics are due to recent developments in the population. The age distribution of porpoises in the Icelandic bycatch seems similar to those from other areas in the North Atlantic. There are therefore no reasons to presume that fishing mortality of harbour porpoises has caused a higher selective pressure for increased fecundity at lower age in the Icelandic porpoises than in other populations in the North Atlantic. Cetacean populations are generally assumed to be regulated by density dependent processes (Perrin and Donovan 1984, Fowler 1984). These are often expressed in processes associated with recruitment and the causes may involve increased resource levels and possibly social or behavioural factors. Evidence of density dependence in reproduction has been observed in some populations of cetaceans with a history of exploitation or fishing gear entrapment (Lockyer 1984, Kasuya 1976, Read and Gaskin 1990). Investigation of the body condition of Icelandic porpoises compared to other populations may reveal whether decreased feeding competition as a consequence of a decline in population size is likely for harbour porpoises in Iceland. The difference in reproductive rates between the Icelandic and other populations may also be associated with differences in pollutant burdens between regions within the North Atlantic.

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