Age, length and reproductive parameters of harbour porpoises
*Phocoena phocoena* (L.) from West Greenland

C. Lockyer, M. P. Heide-Jørgensen, J. Jensen,
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During 1988, 1989 and 1995, 187 harbour porpoises (*Phocoena phocoena*) were sampled from the catches off West Greenland during the months of July, August and September. The samples were taken between 62°N and 69°30’N in Maniitsoq and three more northerly locations (134°, Paamiut (23°), and Nuuk (30°). Comparison of age and length distributions between years and areas, indicated that there were no significant differences between years. However, the Maniitsoq and northerly samples had a modal age in both sexes of about 2 yr and a maximum age of 17 yr, while the more southerly Nuuk and Paamiut samples were biased to younger age classes, with the modal age in both sexes being the first year of life (age class 0 yr) and a maximum age of 12 yr.

Females ovulated from age 3.6 yr at a length of about 142 cm; combined testes weights >200 g indicated maturation in males from age 2.5 yr upwards at a length >125 cm. Several small embryos were found, consistent with a mating season in late summer. Testis hypertrophy in August was also consistent with a late summer breeding. Application of growth models indicated an average asymptotic length of 154 cm in females and 143 cm in males.

Comparisons of the West Greenland data with similar data for porpoises from the Canadian Atlantic, eastern North Atlantic and the North Sea, where genetic studies have shown population differences, indicated differences in biological parameters.

Key words: harbour porpoise, age, growth, reproduction, west Greenland.

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Introduction

The harbour porpoise, *Phocoena phocoena*, is among the most abundant and widespread of the North Atlantic cetaceans, although its distribution is mainly coastal. In West Greenland the species is found from the southern tip to the northernmost inhabited areas, ca. 73°N, with the main distribution between 62°N and 66°N (Teilmann and Dietz, 1998). The harbour porpoise has been hunted for food in Greenland for centuries, perhaps millennia. Periodically, porpoises have been taken as by-catches in drift netting operations for salmon. Christensen and Lear (1977) estimated that 1400 harbour porpoises were caught in the non-Greenlandic driftnet fishery for salmon in 1972, but the fishery ceased during the 1970s and nowadays harbour porpoises are primarily taken in a directed fishery by Inuit hunters and fishermen from West Greenland settlements, and usually shot from small dinghies. The reported catches have remained high (500–1000 animals per year) and have perhaps even increased during this century (Teilmann and Dietz, 1998).

Little is known about the biology and population status of this species off West Greenland. A study undertaken in 1988 and 1989, with a sample size of 84 animals, was reported to the International Whaling Commission in 1990 by Carl Kinze, Thomas Buus...
Sorensen and Hartwig Kremer, but has not been published. We have combined these earlier data with those collected from 103 animals in 1995. This study aims to describe basic features of the biology of harbour porpoises from West Greenland, to compare them to those of adjacent areas and to provide a baseline for future monitoring in West Greenland. Ecological studies of body condition and diet, genetics, pathological and contaminant studies, that are currently under investigation, will be reported elsewhere.

Materials and methods

During July through September in 1988 and 1989, and again in August and September 1995, animals were sampled between 62°N and 69°30′N from Maniitsoq (129) and three other northerly sites [Kangaamiut, Qeqertasuq and Qasigiannguit (5)], and two southerly sites [Paamiut (23) and Nuuk (30)] in the southwestern part of Greenland (Figure 1). The animals were shot at sea. Those sampled in 1988 and 1989 were mainly bought at the local game market in Maniitsoq, where intact carcases were rare. In 1995, the animals were purchased from hunters and frozen whole at the harbours for later examination. The muktuk (the skin with a thin layer of underlying blubber) from these latter animals was removed and weighed for calculating the commercial value of the carcase.

Age determination

Two teeth from the lower jaw were decalcified in RDO (a proprietary decalcifying agent), sectioned on a freezing microtome at 25-μm thickness through the crown and central pulp cavity and stained with Ehrlich’s acid haematoxylin (Lockyer, 1995a). Growth layer groups (GLGs) were counted in dentine and also cementum under low power magnification with transmitted light. GLGs were taken as representing years (Bjørge et al., 1995; Lockyer, 1995a). All tooth sections were read independently of biological information about the specimen, by two readers. Each reader read the teeth independently, and final age was determined after comparing the results. Agreement was reached on all age determinations. Age distributions by sex and area were compared, and mean ages were compared statistically using t-tests (Zar, 1984).

The age data from the two time periods 1988–1989 and 1995 were the products of different readers. A validation exercise was undertaken to test uniformity of reading methods in the two data sets before combining them. All age data from 1988–1989 were reread by Christina Lockyer independently of information from the previous reader (Hartwig Kremer). The resulting ages were identical except for a few older animals, and statistical analysis using the non-parametric analysis, Kolmogorov–Smirnoff two-sample comparison (Zar, 1984), indicated no differences (p>0.5, d=0.037, n=85). Subsequently, all age data from the northerly sites in 1988—1989 were combined with the 1995 Maniitsoq age data. Most of the age samples from the southerly sites were collected in 1995. They were combined, including two animals from 1988–1989, and compared with the northerly samples.

Length and growth

Body length was measured in a straight line parallel to the carcase from the tip of the lower jaw to the notch in the tail flukes. However, length was unavailable for approximately 43% of the porpoises collected in the years 1988 and 1989. Body size-at-age by sex was investigated, and growth curves (Kaufmann, 1981) were fitted to the data, using both von Bertalanffy and Gompertz methods, where least-squares estimation of the parameters was made with Gauss–Newton minimisation in the nonlinear least-squares algorithm of S-Plus (Math Soft Inc.).

Reproduction

Sexual maturity was determined from examination of the reproductive organs.

Male

The testes were weighed and measured for volume. The criterion of combined testes weight >200 g was used as a guide of sexual maturation (Lockyer, 1995b). The epididymes in males were checked for the presence of sperm. Some 1-cm slices of testes were collected and fixed in 10% neutral buffered formalin during 1988 and 1989, and examined histologically to determine maturity (Sorensen and Kinze, 1994).

Female

The ovaries were weighed and examined for the presence of corpora lutea and corpora albicantia (Perrin et al., 1984) to determine sexual maturity and reproductive status (Read and John, 1995). Ovarian corpora were detected from the surface scar on the ovaries, cut open and measured for diameter, examined under a binocular microscope and classified according to type (Laws, 1961). The ovaries were sliced in 1-mm thick sections. A linear regression of corpora number at age, excluding all females with no corpora, was calculated. The uterine horns were opened, and presence of an embryo was noted, as was the expression of milk from the mammarys.
Figure 1. Map of Greenland showing sites mentioned in the text.
Mean age and length at sexual maturation was estimated, using the method described by DeMaster (1978).

## Results and discussion

### Age

The age frequency distributions for the northerly sites (Table 1), indicate a modal age class of 1–2 yr in females and 2–3 yr in males. Maximum age was 14 yr in females and 17 yr in males. The combined southerly age samples (Table 1), however, showed a modal age of 0 years in both sexes, and a maximum age of 12–13 yr in females and 9–10 yr in males. For females the mean age (± s.e.) was 3.37 ± 0.04 yr in the north and 3.03 ± 0.21 yr in the south; whilst for males, the mean age was 4.90 ± 0.90 yr in the north and 2.43 ± 0.55 yr in the south. A comparison of mean ages using t-tests (Zar, 1984), indicated there was no significant difference between the northern and southern females, but there was a significant difference for males (t = 3.469, p < 0.001, d.f. = 58).

The age compositions of the northerly and southerly samples are similar in females, but in males the southerly sample contains proportionately more young animals than the northerly sample. This may be due to age-, sex- or maturity-related segregation in the population. It has certainly been reported that the distributional pattern of males may differ from that of females in the North Sea area (Walton, 1997) based on mtDNA analyses, and seasonal variations in distribution and movements by sex have been reported in the Skagerrak area (Kinze, 1985, 1990). However, one may also consider the effect of different hunting pressures in the two regions, or a potential seasonal effect on distributional segregation. It is clear that the time of year when these samples were taken closely approximates the breeding season which might arguably be anticipated to have some effect. In harbour porpoises the usual breeding season is late summer (see reproductive results below; also Lockyer, 1995b, c; Lockyer and Kinze, 1999; Sørensen and Kinze, 1994).

The maximum observed age (17 yr) is similar to eastern Canada (Read and Hohn, 1995) where the animals were by-caught, but lower than the 24 yr reported for British Isles (Lockyer, 1995b, c) where most of the sampled animals have been stranded, and in Denmark where ages up to 22 yr have been recorded in strandings and by-caughts (Lockyer and Kinze, 1999). The difference in maximum ages may be artifactual and caused by differences in sample sizes but may also be because strandings generally include very old animals that have died of natural causes, whereas young animals preponderate in by-caughts.

### Length and growth

Length frequency distributions for the northerly samples in both time periods were comparable, and were therefore combined by sex. The northern and southern female length distributions are presented in Table 2. The mean lengths (± s.e.), of 129.0 ± 3.5 cm (northern) and 129.3 ± 4.6 cm (southern), are not significantly different. The equivalent length frequency distributions for males are shown in Table 2, where the mean lengths of 130.7 ± 2.1 cm for the northern samples and 122.8 ± 3.4 cm for the southern samples are significantly different (d = 2.001, p < 0.05). The length ranges in the two regions are broadly similar, although in females the minimum length is lower and the maximum length is higher in the south. In males the opposite occurs, with a lower minimum and higher maximum in the north, although fewer animals were sampled in the south. The length distributions of each sex, combined over regions, are shown in Figure 2. Females ranged in length from 74–166 cm (mean: 128.2 ± 3.5 cm) and males from 84–158 cm (mean: 128.2 ± 1.8 cm).

When length is plotted at age, by sex, there is no apparent difference between the two regions, and therefore the length at age data have been combined (Figure 3). The parameters of the fitted length at age growth curves are presented in Table 3. Both von Bertalanffy and Gompertz growth models indicate an asymptotic length of about 154 cm in females and 143 cm in males. These lengths are smaller than those reported for harbour porpoises off the British Isles (mainly North
Reproduction

Male

Testes weight and sexual maturity. Testes weights of all males were recorded, but not all testes were examined histologically for presence of sperm, spermatogonia or tubule diameter and character (open/closed), and the histological method was used mainly to confirm the testes weight diagnosis in animals from 1988–1989. In Figure 4, the combined testes weights are plotted against age and length. Using the 200 g criterion, the switch from immature to mature appears to occur at 2 yr, and all males are mature at 3 yr. Maturation occurs from a length of 123 cm and all males are mature at a length of 130 cm. The average age at sexual maturation is 2.45 yr using the method described by DeMaster (1978). These data are compared with data for harbour porpoises from elsewhere in Table 4.

Female

Ovarian corpora and sexual maturity. The presence of at least one corpus luteum/albicans was used as a criterion for sexual maturity (Lockyer, 1995b). Other criteria used for assessing maturity were evidence of pregnancy and/or lactation. The youngest animal in this sample with a corpus was 3 yr, and the oldest was 12 yr with 11 corpora (Table 5). A linear relationship between ovarian corpora (both lutea and albicantia) number and age was fitted for these 31 animals which had at least one corpus.

Number of corpora=0.731 × Age − 0.628

(1)

The coefficient (0.731) above has a standard error of 0.157, giving 95% confidence limits of 0.410 and 1.052. If one calculates the apparent ovulation interval from

Age=(Number of corpora+0.628)/0.731

(2)

using the 95% confidence limits, the apparent ovulation interval is 0.95–2.44 yr. The regression coefficient (0.731)
is similar to that observed for Danish (Lockyer and Kinze, 1999) and Canadian Bay of Fundy (Read, 1990) porpoises. The data, however, indicate a strong seasonality of reproduction (see below); thus the most likely scenario is that females either ovulate each year or every two years. The main point is that not all porpoises ovulate or become pregnant every year. On the other hand, some females appear to have ovulated more frequently than every year (Table 5), and this may be a result of polyovul y.

It is worth noting that if the calculation of regression of corpora against age is done excluding the one individual aged 12 yr with only two corpora (Table 5), on the grounds that this animal is an outlier, the equation becomes

\[ \text{Number of corpora} = 1.018 \times \text{Age} - 1.999 \]  

With a standard error of the regression coefficient of 0.142 giving 95% confidence limits of 0.727–1.309, the recalculated apparent ovulation interval becomes 0.76–1.38 yr, which clearly implies an annual ovulation rate.

An estimation of mean age at sexual maturation was made using the method of DeMaster (1978). The mean age at first ovulation was 3.6 yr which concurs with the observation in this data set that no female has a corpus before age 3 yr.

Reproductive parameters are compared with those for porpoises from British and Danish waters (mainly North Sea) and eastern Canada (Table 4). In males, length and age at maturation are less than those reported in the North Sea and off eastern Canada; in females, the age at maturation is similar to porpoises elsewhere in the North Atlantic, but size is smaller than generally reported elsewhere.

**Breeding season**

A plot of testes weight ± s.e. by month indicates a significant increase in weight during August (Figure 5). This is consistent with findings from other areas of the Northeast Atlantic where a similar hypertrophy has been reported in August (Lockyer, 1995b; Lockyer and Kinze, 1999; Sorensen and Kinze, 1994). Sperm were found in all males >129 cm and in one measuring 128 cm (total mature=15) in a sample of 23 males (length range 108–158 cm) collected during August and early September 1989, which suggests that mating, and probably conception, may be especially likely at this time. No information was available for July.

Several small embryos of approximately 6–8 weeks developmental age were found throughout September (one at the end of August), consistent with a mating season in late summer. The inferred breeding and calving periods differ from the Canadian Bay of Fundy harbour porpoise where testicular activity peaks in late June and the main calving season is May (Read, 1989). Read suggested that there may be an embryonic diapause which could reconcile early seasonal testicular

![Figure 3. Length at age, with fitted Gompertz curve, of female (a) and male (b) Greenland porpoises, all areas.](image)

### Table 3. Growth parameters fitted to length at age data in West Greenlandic harbour porpoises, using different models.

<table>
<thead>
<tr>
<th>Parameter ± s.d.</th>
<th>Length at age (cm) – von Bertalanffy</th>
<th>Length at age (cm) – Gompertz</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Females</td>
<td>Males</td>
</tr>
<tr>
<td>( L_{\infty} ) (asymptotic body length)</td>
<td>154.716 ± 2.820</td>
<td>143.095 ± 1.824</td>
</tr>
<tr>
<td>( b ) (constant)</td>
<td>0.387 ± 0.016</td>
<td>0.313 ± 0.017</td>
</tr>
<tr>
<td>( k ) (exp. coefficient)</td>
<td>0.483 ± 0.066</td>
<td>0.457 ± 0.065</td>
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</table>
activity in Canadian animals with a birth season similar to other areas. However, this physiological phenomenon would appear to be inconsistent with information on reproduction in porpoises from elsewhere, and does not fit with findings here.

Conclusions

There appear to be some differences in biological parameters between West Greenland, Canada and eastern North Atlantic populations. However, there is the possibility that the source of the samples (catches by hunters) may have introduced some biases. Genetic findings from allozyme (Andersen, 1993) and DNA-microsatellite analyses (Rosel et al., 1999) have indicated differences between porpoises from these areas. Andersen (1993) and Andersen et al. (1995, 1997), using allozyme DNA-microsatellite analyses, found differences between West Greenland, inner Danish waters and the North Sea, indicative of population sub-structure.

Additional information on harbour porpoise sub-populations, based on tooth ultrastructure in different regions of the North Atlantic, indicates clear differences between West Greenland and the Canadian Bay of Fundy, and also with eastern North Atlantic populations (Lockyer, 1999). Furthermore, Lockyer (1999) reported differences in tooth structure between Maniitsoq and more southerly areas (Nuuk and Paamiut), which could not be explained by arguments for sex or age segregation.

Møller (1999) has recently shown further differences between porpoises from Maniitsoq, and Nuuk and Paamiut, based on fatty acid signatures in the blubber of the animals from 1995 examined in this paper. Whilst these differences may be argued as transient and a reflection of local feeding ecology, differences between teeth (Lockyer, 1999) are permanent.

There is evidence, therefore, that the West Greenland harbour porpoise population is distinct from other

<table>
<thead>
<tr>
<th>Region and period of sampling</th>
<th>Mean age at sexual maturity (yr)</th>
<th>Mean length at sexual maturity (cm)</th>
<th>Mean adult length (L∞) (cm)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Male</td>
<td>Female</td>
<td>Male</td>
<td>Female</td>
</tr>
<tr>
<td><strong>West Greenland</strong> 1988–1995</td>
<td>2.45</td>
<td>3.6</td>
<td>127*</td>
<td>142*</td>
</tr>
<tr>
<td><strong>Eastern Canada</strong> 1969–1973</td>
<td>&gt;3</td>
<td>3.97</td>
<td>134</td>
<td>147</td>
</tr>
<tr>
<td><strong>Denmark</strong> mainly 1980–1988</td>
<td></td>
<td></td>
<td>150</td>
<td>160</td>
</tr>
</tbody>
</table>

*Estimated from length at mean age at sexual maturity from the length at age curves [Figure 3(a) and (b)].

Figure 4. Total testes weight at age (a) and length (b) for Greenland porpoises, all areas.
geographical areas, and may well itself comprise sub-
populations or stocks and, at the very least, have a
probable seasonal sex and age segregation. The biology
of the porpoises in this area presents an interesting
challenge in the management arena, and begs further
attention.

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Table 5. Total ovarian corpora (lutea and albicantia) counts by
age.

![Figure 5. Total mean testes weight ± s.e., by month, for Green-
land porpoises, all areas.](image-url)


