Growth-related changes in testicular mass and plasma testosterone concentrations in long-finned pilot whales, *Globicephala melas*

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Blood samples and testes were collected from long-finned pilot whales (*Globicephala melas*) off the Faroe Islands at irregular intervals over a period of 3 years (July 1986–December 1989). Changes in testis mass ($n = 674$) and plasma testosterone concentrations ($n = 214$), measured by radioimmunoassay, were examined with respect to age, bodylength and bodymass of the animals. Corresponding to a rapid testicular growth (from 0.25 kg up to 1.9 kg), puberty occurred in male pilot whales of 4.6–5.7 m in bodylength, 1.2–1.9 tonnes in bodymass and 11–22 years of age. Changes in plasma testosterone concentrations confirmed this result, with very low values ($< 2 \text{ ng ml}^{-1}$) in immature animals (testis mass $< 0.2 \text{ kg}$), followed by a sharp increase (from 2 to 29 ng ml^{-1}) during the pubertal period, and the maintenance of high concentrations with large variability ($> 1.5 \text{ ng ml}^{-1}$ to 14 ng ml^{-1}) in mature males. Testosterone concentrations were significantly correlated with testis mass ($P < 0.001$), but not with bodylength or age, and very large individual variations were observed in mature males. The average age, length and mass at the attainment of sexual maturity were estimated at 16.99 ± 0.30 years, $5.162 \pm 0.013 \text{ m}$ and 1.403 ± 0.005 tonnes, respectively.

Introduction

Little is known about sexual maturity and gonadal activity of males of many cetaceans, particularly offshore odontocetes. More information is needed for a better understanding of the reproductive strategy and behaviour of these long-living mammals (e.g. up to 46 and 59 years for male and female long-finned pilot whales, respectively; Bloch *et al.*, 1993). Most of the observations made on cetacean male reproduction are based on morphological or gross histological observations and measurements of the masses of sexual organs from species taken in fisheries or stranded animals (Hohn *et al.*, 1985; van Bree *et al.*, 1986; Martin *et al.*, 1987; Collet and Robineau, 1988; Lockyer *et al.*, 1988; and for reviews, see Collet, 1981; Perrin *et al.*, 1984; Bryden and Harrison, 1986; Evans, 1987). The determination of the concentrations of sexual hormones to characterize and specify the reproductive function was developed in cetaceans only during the last decade, because of difficulties in sampling. However, most studies deal mainly with captive females of one species, the bottlenose dolphin, and are oriented towards ovulation and pregnancy diagnosis and artificial insemination (Richkind, 1977; Sawyer-Steffan and Kirby, 1980; Sawyer-Steffan *et al.*, 1983; Kirby, 1984, 1990; Kirby and Ridgway, 1984; Schroeder, 1984; Wells, 1984; Ólafsson and Kjeld, 1986; Yoshioka *et al.*, 1986; Kjeld and

Amason, 1989; Ozharovskaya, 1990; Schroeder and Keller, 1990; Yoshioka, 1991; Yoshioka *et al.*, 1991; Kjeld, 1992). Data on circulating testosterone concentrations are scarce and are mainly for bottlenose dolphins kept in captivity (Harrison and Ridgway, 1971; Judd and Ridgway, 1977; Wells, 1984; Schroeder and Keller, 1989; Kirby, 1990; Iemesh, 1991) and for fin and minke whales taken in fisheries (Ólafsson and Kjeld, 1986; Kjeld and Amason, 1989; Kjeld, 1992; Yoshioka and Fujise, 1993).

In long-finned pilot whales (*Globicephala melas*), a species largely distributed in the North Atlantic Ocean, no gonadal hormonal assay has been reported. In previous attempts to determine sexual maturity in males, results were based on small sample sizes and varied according to authors, criteria and methods of age determination used (Sergeant, 1962; Desportes, 1982; Martin *et al.*, 1987; Bloch, 1992). A unique opportunity to re-examine the reproductive function of male long-finned pilot whales more closely was offered within the framework of a large-scale international programme on the ecology and status of the species (Desportes, 1990; Desportes *et al.*, 1992). Pilot whales are harvested off the Faroe Islands for subsistence purposes in a direct, uncommercial and opportunistic hunt (Bloch *et al.*, 1990; Sanderson, 1991). This catch was the focus of an intensive scientific sampling for 3 years.

Determination of the concentrations of hormones was performed in addition to the analysis of parameters previously considered. After adaptation and validation of the testosterone assay to this species, changes in testis mass and hormone concentrations were related to characterize the main gonadal status from birth to adulthood.

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Table 1. Plasma concentrations (means $\pm$ SEM) of testosterone and 5 α -dihydrotestosterone (5 α -DHT) in long-finned pilot whales

Stage of maturity	(n)	Testosterone (ng ml ⁻¹)	5 α -DHT (ng ml ⁻¹)	Testosterone : DHT (ng ml ⁻¹)
Immature	6	1.24 $\pm$ 0.23	0.14 $\pm$ 0.01	8.9
Maturing and mature	5	0.62 $\pm$ 0.11	0.03 $\pm$ 0.01	20.7
	6	4.43 $\pm$ 0.99	0.45 $\pm$ 0.10	9.8
	7	12.89 $\pm$ 1.28	1.46 $\pm$ 0.20	10.1

Results for maturing and mature specimens are presented according to testosterone concentrations: high, medium, and low.

Materials and Methods

Animals

During a period of 3 years (July 1986–December 1989) schools of pilot whales were caught at irregular intervals by the Faroese drive fishery. Forty schools were studied to obtain data on male reproductive status, bodylength, bodymass and age. Testis mass and blood samples were obtained from 674 and 214 specimens, respectively. For logistical reasons, complete data and sample sets were not obtained from all the whales. Exact sample sizes for each set of analyses are given in figure legends and tables.

The age determination, performed by D. Bloch (Zoological Department, Museum of Natural History, FR-100 Tórshavn, Faroe Islands), was carried out by counting groups of growth layers in both dentine and cement on thin sections of decalcified teeth (Kasuya and Matsui, 1984; Bloch *et al.*, 1993).

Blood samples were taken immediately after the animal was killed. They were collected from the neck vessels in 50 ml heparinized tubes and kept on ice until processed in the laboratory. Plasma was divided into aliquots and stored at -25°C until assays were performed. The duration of the drive (from the sighting place to the authorized whaling bay) and the time taken to slaughter the entire school varied; during the sampling period considered, they averaged 142 and 28 min, respectively (Bloch *et al.*, 1990). The state of stress undergone by each individual whale thus varied between and within schools, but was impossible to assess.

Testes were collected a few hours after the death of the animal, when the whales had been moved from the beach to the nearest quay. Desportes (1994) found that the asymmetry in mass and tissue maturation within a testis and within a pair of testes was sufficiently small to allow a single testis and a single histological sample to be used for routine assessment of sexual maturity in long-finned pilot whales. Thus, a single testis from whichever side was the most accessible for sampling was collected, and a single histological sample was taken from the mid-length cross-section of the testis taken from the side opposite to the epididymis. Testes were weighed fresh, without epididymis, to the nearest gram. Histological samples were fixed and preserved in 10% buffered formalin.

Identification of sexual maturity

Sexual maturity was identified by examining testicular tissue histologically. Samples for histology were processed

using standard techniques, and slides were stained with haematoxylin–eosin. The maturity of testicular tissue was assessed by observing an entire section of about 1 cm² and following criteria used for other mammals (see for example Courot *et al.*, 1970). Three stages of histological maturity were used to characterize the maturity of testicular tissue, according to the proportion of mature seminiferous tubules: (1) immature (100% of the tubules were immature); (2) maturing (< 100% of the tubules were mature); and (3) mature (100% of the tubules were mature).

Testosterone assay

Plasma testosterone concentrations were measured in duplicate by radioimmunoassay after steroid extraction with diethyl ether. The average recovery rate of labelled testosterone was 90.4% $\pm$ 0.3%. The accuracy was determined by adding different amounts of testosterone to the same plasma pool and by assaying different volumes of the same plasma. The sensitivity, determined as the smallest detectable quantity of hormone, was < 10 pg per tube, which allows detection of plasma concentrations of about 0.03 ng ml⁻¹. Intra-assay and inter-assay coefficients of variation were 6% and 13%, respectively.

In this assay 5 α -dihydrotestosterone (DHT) gives the only significant crossreaction (45%) with the testosterone antiserum used. In adult mammals the testosterone:DHT ratio usually ranges between 5 and 20, and the total testosterone–DHT complex is accepted as representing the testosterone concentration (for review, see Maurel, 1981). To check whether the same assimilation was acceptable for pilot whales, specific assays were performed for testosterone and DHT on 24 plasma samples from immature, maturing and mature animals. After steroid extraction with diethyl ether, DHT and testosterone were separated by chromatography on chromatolite-A columns, and two specific radioimmunoassays were performed. The recovery rate of the labelled DHT was 60–80%. The volume of plasma extracted had no influence on DHT concentration. The sensitivity was 10–15 pg of DHT per tube. The variations in DHT and testosterone concentrations are presented in Table 1. The testosterone:DHT ratio was low and practically constant (< 21) in adults and immature animals and was within the range for terrestrial mammals. Taking into account the low concentration of DHT and the crossreactivity of 45% with the antiserum used, we therefore considered the direct assay of testosterone without chromatography (i.e. total testosterone concentration plus 45% of the DHT

Table 2. Ranges of testicular masses and plasma testosterone concentrations observed in long-finned pilot whales caught from March to September and from October to February according to reproductive stage

Parameter	Stage of maturity	March–September	October–February
Testis mass (kg)	Immature	0.010–0.346 (197, $P < 0.001$)	0.009–0.340 (168, $P < 0.001$)
	Maturing	0.248–1.922 (18, $P < 0.001$)	0.300–1.450 (44, $P < 0.001$)
	Mature	1.068–6.150 (106)	0.807–4.240 (141)
Testosterone (ng ml ⁻¹)	Immature	0.04–29.39 (58, $P = 0.183$)	0.04–2.80 (64, $P < 0.001$)
	Maturing	1.19–11.17 (5, $P = 0.149$)	0.53–6.17 (16, $P < 0.001$)
	Mature	1.87–22.07 (30)	1.01–8.26 (41)

Sample sizes and probability of *t* test values comparing means from one stage with the next are in parentheses.

concentration) as acceptable to be used routinely for pilot whale plasma samples.

Estimation of age, length and mass at the attainment of sexual maturity

Techniques used to estimate the average age at attainment of sexual maturity in cetaceans have been reviewed by Hohn (1989). The nonparametric method of the sum of the fraction of immature animals, as described by Hohn (1989), is used here to estimate the average age, length and mass at attainment of sexual maturity. These were calculated as the sum of the fraction of animals immature in each age or length or mass class between that of the youngest mature and that of the oldest immature animal, added to the age or length or mass of the first indeterminate age, length or mass class. The method was applied to the proportion of immature animals within an age class of 1 year, a length class of 5 cm (the sum of the fraction of immature animals and the variance was multiplied by five, i.e. the number of cm per length class), and a mass class of 100 kg (the sum of the fraction of immature animals and the variance was multiplied by 100, i.e. the number of kg per mass class).

Statistical analyses

The results are expressed as means $\pm$ SEM. Student's *t* tests were performed for statistical comparisons, and Pearson's correlations were used (Sokal and Rohlf, 1981).

Presentation of results

Although this paper does not focus on the study of reproductive seasonality, which is dealt with elsewhere (Desportes *et al.*, 1993), point data from mature males and a range of values are given according to the period of testicular activity to illustrate the variation due to seasonality (March–September and November–February).

Results

Testis growth

In Faroese pilot whales, the mass of a single testis at birth was about 0.009 kg and it was 6 cm long. In adults, the mass may reach 6.150 kg and the length 51 cm. The epididymis mass was linearly correlated with testis mass ($n = 275$, $P < 0.001$). In immature animals, the testis mass increased very slowly and linearly with bodylength (rate < 1 g cm⁻¹ of bodylength; Fig. 1a), bodymass (Fig. 1b) and age (Fig. 1c). A sharp upsurge in testis mass occurred roughly between 4.60 and 5.20 m in bodylength, 1 and 1.5 tonnes in bodymass and 11 and 18 years of age, the testis mass increasing at a rate of about 50 g cm⁻¹ of bodylength. After this period of sharp increase, and despite large individual variations, testis mass continued to increase with bodylength ($n = 236$, $P < 0.001$) and bodymass ($n = 45$, $P < 0.001$) but it was no longer correlated with age after 21 years ($n = 275$, $P = 0.07$). These different profiles suggest that fully grown males of large body size tend to have heavier testes than do smaller males, and that testis mass depends more on bodymass than on body length. Seasonality explained part of the individual variation observed in mature animals (Fig. 1; Table 2).

The rapid increase in growth rate of the testis corresponded to the time of maturation. Male pilot whales smaller than 4.55 m, weighing less than 1.2 tonnes and younger than 11 years of age were immature. Testes weighing less than 0.248 kg were all histologically immature and testes heavier than 1.922 kg were all histologically mature. The maturing period appeared protracted from the overall data, taking place in testes weighing between 0.250 kg and 2 kg.

The average age, length and mass of whales at the beginning of testis maturation were estimated to be 13.82 ± 0.22 years, 4.859 ± 0.012 m and 1.214 ± 0.003 tonnes, respectively. Full histological maturity was attained on average at 16.99 ± 0.30 years, 5.162 ± 0.013 m and 1.403 ± 0.005 tonnes.

Plasma testosterone concentrations

Testosterone concentrations in Faroese pilot whales ranged from 0.01 to 29.4 ng ml⁻¹. The relationship between

Fig. 1. Changes in testis mass in relation to (a) bodylength ($n = 669$), (b) body mass ($n = 178$) and (c) age ($n = 602$) in long-finned pilot whales. (+) Immature testis; (▲) maturing testis; (□) mature testis from animals caught between October and February; (×) mature testis from animals caught between March and September. The lines connect the arithmetic means of testis mass for (a) length classes (10 cm), (b) mass classes (200 kg) and (c) age classes (1 year).

testosterone concentration and testis mass is presented in Fig. 2. A high concentration of testosterone (5 ng ml^{-1}) was observed in males in which a single testis weighed between

Fig. 2. Relationship between plasma testosterone concentration and testis mass ($n = 156$) in long-finned pilot whales. (+) Immature testis; (▲) maturing testis; (□) mature testis from animals caught between October and February; (×) mature testis from animals caught between March and September.

200 and 250 g, about 1 kg and 2 kg or more. In the group with a single testis mass of $> 2 \text{ kg}$, plasma testosterone concentrations were significantly correlated with testis mass ($P < 0.001$, $n = 54$).

In animals younger than 8 years old, testosterone concentrations were undetectable or less than 1 ng ml^{-1} , except in a few calves. From 11 years of age and after the whales had reached 4.60 m in bodylength (i.e. simultaneously with the spurt in testis growth described above), plasma testosterone concentration began to increase. In animals 15 years old and older and longer than 5 m, the testosterone concentration varied greatly and ranged from 1 ng ml^{-1} to 22 ng ml^{-1} . The highest concentrations (i.e. $> 10 \text{ ng ml}^{-1}$) were observed between 15 and 32 years of age only and in animals caught between March and September. Part of the large variation observed in mature animals is explained by seasonality (Figs 2 and 3; Table 2).

Unexpectedly, comparatively high testosterone concentrations (Table 3) were observed in a few young immature individuals, or considered to be such on the basis of their age, bodylength and testis mass (although no testicular histology was performed in these instances).

Discussion

The present results correlated the lifelong testicular activity of long-finned pilot whales, determined by changes in testicular mass and plasma testosterone concentrations, with the evolution of morphological parameters such as bodylength, body-mass and age. The amount of data collected over a period of 3 years made it possible to obtain a representative sample for the characterization of each reproductive state from birth to adulthood in this long-living species of which males may reach at least 46 years. The pattern of testicular growth and histological examination of testicular tissue showed that puberty occurred between 11 and 22 years of age in males measuring between 4.6 and 5.7 m long and weighing between

Fig. 3. Relationship between plasma testosterone concentration and (a) bodylength ($n = 214$) and (b) age ($n = 194$) in long-finned pilot whales. (+) Immature testis; ($\blacktriangle$) maturing testis; ($\square$) mature testis from animals caught between October and February; ($\times$) mature testis from animals caught between March and September.

1.2 and 1.9 tonnes. Maturing testes weighed between 0.250 and 1.922 kg. Thus, the maturation period appeared to be protracted from the overall data. However, this apparent protracted duration of the pubertal stage is probably a sampling artifact and does not necessarily represent the individual rate of change. Indeed, if pilot whales progress through the pubertal stage at a rapid rate, but not in synchrony with their chronological peers as occurs in other species such as humans (Sinclair, 1973), then the overall data will underestimate the individual rate of change and overestimate the period over which the changes take place.

Previous data on testes obtained from 41 Faroese pilot whales caught during 1984 and 1985 (Bloch, 1992) gave a pattern of testis growth that fits well with the pattern presented in this study. The pattern of testis growth obtained from other locations in the North Atlantic for the same species is not inconsistent with our data, although the age at which the testicular growth spurt is said to occur is imprecise and somewhat variable because of very limited sample sizes and inadequate techniques of age determination. For example, the growth spurt took place when the animals had a bodylength of about 4.50 m and were 12–13 years old

in 90 males caught off Newfoundland (Sergeant, 1962), 4.25–5.00 m long and 9–14 years old in 11 males stranded on the British coast (Martin *et al.*, 1987), and just under 5.00 m long in males 11 years old or older in 12 specimens stranded on the Icelandic coast (Sigurjónsson *et al.*, 1993). Using the macroscopical detection of seminal fluid in the epididymis of 18 males as a criterion of sexual maturity, Sergeant (1962) found that the smallest mature male was 4.65 m long with a testis weighing just over 1.5 kg and that the largest immature animal was 5.1 m long with a testis also weighing just over 1.5 kg. The smaller congeneric species, the short-finned pilot whale, shows a similar pattern of testicular growth (Kasuya and Marsh, 1984). The testes stop growing at about 25 years of age, with larger males having heavier testes, and histological maturity (i.e. full maturity of testicular tissue observed on histological slides) is reached between 15 and 29 years of age.

In this study, the characterization of the reproductive status from birth to adulthood was also assessed for the first time in pilot whales by determining plasma testosterone concentrations by radioimmunoassay. The present results showed a wide range of testosterone concentrations in long-finned pilot whales with generally low concentrations in immature animals and large variations in mature males. A similar range of plasma testosterone concentrations was reported for bottlenose dolphins (Harrison and Ridgway, 1971), with low concentration in three immature males (from 0.07 to 3.9 ng ml⁻¹) and a large variation in a mature male monitored over 2 years (from about 1.2 to 24.5 ng ml⁻¹). Wells (1984) found a wider range in an adult male spinner dolphin monitored for 1 year, from <1 ng ml⁻¹ to >60 ng ml⁻¹, with a baseline range of 0–8 ng ml⁻¹. Ranges reported for baleen whales also vary according to species: 0.03–7.0 ng ml⁻¹ for mature fin whales; and 0.3–0.7 ng ml⁻¹ for mature sei whales caught off Iceland in summer (J. Sigurjónsson and M. Kjeld, personal communication). Thus, ranges of testosterone concentrations vary between cetacean species, as in land mammal species (Gustafson and Shemesh, 1976). Consequently, the present results constitute a unique reference for *Globicephala melas*, but cannot be extended to another species without sufficient investigation.

From birth to the beginning of the pubertal period, testicular mass and plasma testosterone concentrations were usually low, although increasing slowly from birth onwards. However, in two very young suckling calves, probably <3 months old, high plasma testosterone concentrations were observed. These might possibly be compared to the transient neonatal increase occurring in different species (e.g. men: Forest *et al.*, 1974; pigs: Meusy-Desolle, 1975; guinea-pigs: Pelardy and Delost, 1978). As in those species, this increase may be related to a first imprint of the nervous structures involved in postnatal sexual development (Harris, 1964).

The period of puberty was characterized by the testicular development and a parallel increase in plasma testosterone concentrations, attesting that maturational changes in spermatogenic as well as in steroidogenic components occurred simultaneously. The high concentrations of testosterone observed in a few calves approaching or at puberty are not unique; they may be compared with those reported during puberty in other mammals (McCann *et al.*, 1974; Ghanadian

Table 3. Plasma concentrations of testosterone with respect to age of long-finned pilot whales

Age (years)	Length (m)	Testis mass (kg)	Testis histology	Testosterone (ng ml ⁻¹)	Month
0	2.24	0.014	Immature	1.4	November
0	2.11	0.013	Immature	2.8	November
8	4.89	0.184	Immature	3.1	April
11	4.92	0.158	Immature	3.1	April
13	4.49	0.160	ND	7.2	April
12	5.06	0.232	ND	7.4	April
5	4.70	0.248	ND	28.1	September
6	4.30	0.140	ND	29.4	September

ND: not determined.

et al., 1975; Berger *et al.*, 1976; Bedair and Thibier, 1979; Saboureaux and Dutourné, 1981). The high values of testosterone concentration and testis mass found in some young mature males have also been reported for males of other mammals at a similar stage (rat: Ghanadian *et al.*, 1975; hedgehog: Saboureaux and Dutourné, 1981). This increase in circulating steroid concentrations reflects changes in testicular sensitivity to gonadotrophins and the establishment of pituitary–testicular feedback.

In adult long-finned pilot whales, a wide range of testosterone concentrations was observed during life, the very low concentrations occurring only in immature animals. Such large individual variations are also reported in fin whales (Ólafsson and Kjeld, 1986; M. Kjeld and A. Arnason, personal communication), and may be due to several parameters. A seasonal factor widened the range of individual variations (see also Desportes *et al.*, 1993), but the variations remained important among mature males caught from October to February. Part of the variation is probably the expression of diurnal patterns or pulses of testosterone, such as those described in many terrestrial species (bulls: Katongole *et al.*, 1971; men: Naftolin *et al.*, 1973; rats and mice: Bartke *et al.*, 1973; rabbits: Rowe *et al.*, 1973; badger: Maurel *et al.*, 1981). Such diurnal and pulsatile variations are less apparent in longitudinal studies in which animals are bled several times a day or a month, and where results are presented as means. The variations observed may also be related to numerous factors such as nutritional state, exposure to receptive females, social status, muscular exercise and stress, which have been shown to influence reproduction (Perry and Rowlands, 1973; Bertram, 1975; Bronson, 1985; Frank, 1986), and particularly the pattern of testosterone secretion (McMillin *et al.*, 1976). Stress, for example, might be of importance when animals are caught in a drive fishery. The last phase of the drive, the beaching and the killing are obviously stressful for the animals, but with a very variable state of stress undergone by individual males within the same pod and between pods. Social cues are also known to influence strongly the concentration of circulating testosterone in various land mammals (Faulkes and Abbott, 1991; Faulkes *et al.*, 1991; van Jaarsveld and Skinner, 1991). This factor might be of importance in pilot whales since mating in this species appears to occur reciprocally between pods, with no evidence of strong reproductive dominance (Amos *et al.*, 1991a, b, 1993).

In conclusion, the determination of plasma testosterone concentrations as well as testicular mass and testicular histology allowed the specification of the changes in reproductive activity in the long-finned pilot whales during their lifetime. The large individual variations and overlap between stages of maturity with the highest concentrations found in immature males approaching puberty, suggests that plasma testosterone concentrations cannot be used as a single indicator of sexual maturity in pilot whales. However, testosterone concentrations provide a suitable tool for following the sexual activity of male pilot whales over time. This is probably also the case for males of other cetacean species. The assessment of the reproductive status of individual males by measuring the concentration of testosterone present is widely used in land mammals, and is a particularly interesting tool in cetaceans because it is a harmless method that can be used in nonlethal investigations. As such, the study of sexual hormones in male cetaceans should be continued, with special emphasis on seasonal cycles and a longitudinal analysis of individual whales to understand individual rates of change better.

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