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Growth and reproduction in false killer whales (*Pseudorca crassidens* Owens, 1846)

by

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Chapter 1

Introduction

The False killer whale (*Pseudorca crassidens*), a member of the family Delphinidae, was first discovered, in sub-fossil form, and described by Owen in 1846 (Odell and McClune 1999). Its complex taxonomic history, reviewed in detail in Purves and Pilleri (1978) and Stacey et al (1994), bears testimony to a prior lack of consensus among scientists with respects to nomenclature and taxonomic status. A single widespread species *P. crassidens* is currently recognised, occurring offshore in all tropical and temperate oceans (Stacey *et al*. 1994, Odell and McClune 1999), and occasionally recorded in higher latitudes in the Northern Hemisphere (Kitchener *et al*. 1990).

While studies of false killer whales in captivity have contributed to our knowledge base (for example: Clarke and Odell 1999, on nursing behaviour; Atkinson *et al*. 1999, on patterns in hormone profiles; Kastelein *et al*. 2000, on energetics), most of what is currently known about these whales has been obtained opportunistically from material collected at mass strandings. In addition to describing distribution, the majority of these latter studies have provided considerable information on the anatomy and morphology of false killer whales (for example: Slijper 1939, Purves and Pilleri 1978, Ross 1984, Kitchener *et al*. 1990). An account of the female reproductive system in *P. crassidens* was (first) given by Comrie and Adam (1938) and later reviewed by Harrison *et al*. (1972), although few data on reproductive rates and related parameters were available, and age of the specimens was unknown. Data on growth and life history characteristics, such as estimates of length at birth, age and size at sexual maturity, are available from a variety of sources (for example: Peacock *et al*. 1936, Smithers 1938, Scott and Green 1975, Purves and Pilleri 1978, Odell *et al*. 1980).

The overall objective of this investigation is to elucidate the life history of, and in particular to expand our knowledge about growth and reproduction in false killer whales. In Chapter Two growth and age-body length relationships in female and male false killer whales are described. Anatomical changes associated with sexual maturity, and the relationship between sexual maturity and age and body size are investigated separately for the sexes. Differences in the above between northern and southern hemisphere groups of false killer whales are compared.

Chapter Three of this thesis is an examination of and comparison between group size of stranded and non-stranded false killer whales. A second objective of this chapter is to compare group composition, with respect to age structure, sex ratio, maturity, and reproductive status of females, between stranded and shore-driven false killer whales. Particular emphasis is given to differences in group size and composition between stranded and non-stranded false killer whales which may account for, or help explain the mass stranding phenomenon in these whales.

In the final chapter, reproduction in female false killer whales is addressed. Differences in fertility between stranded southern hemisphere and shore-driven northern hemisphere groups of false killer whales, suggested to occur in Chapter Three, are explored further. Changes in the ovaries, and in reproductive status with age, are described. Of particular interest, evidence in support of the existence of a post-reproductive phase in female false killer whales is presented.

The objectives of this investigation were addressed by examining two sets of data, collected and examined independently from each other: one at a mass stranding of false killer whales at St Helena Bay, South Africa; and another from several drive fisheries of false killer whales off Iki Island, Japan. The South African material has been previously analysed in some detail with respect to skull morphology and skull growth (Kitchener *et al*. 1990). The Japanese data has similarly been subjected to certain analyses by Kasuya (1986), particularly in relation to age, growth and mortality. In this thesis I both draw on some of the analyses and findings reported in these earlier studies and develop them further, and I also address different questions, as outlined above.

Studies of life histories seek to establish links between aspects of morphology, physiology, phylogeny and behaviour, and to interpret these in the context of trade offs between adaptive responses and constraints (Stearns 1995). Accurate assessment of age is essential in order to analyse growth and reproduction, and to elucidate the natural history of any species (Bryden 1986). Most previous studies on false killer whales have been compromised by either a lack of reliable information on age, the total absence thereof, or a lack of detailed collaborative data from individual animals. In this study both body length and age are available for most specimens, representing an unique opportunity to investigate age-length relationships in detail in false killer whales. Age was determined using dentinal as well as cemental layer growth layer group counts, thereby increasing the accuracy with which age in older individuals has been estimated. In addition, data on reproductive status, as determined macroscopically and histologically, are available, further increasing the information value of the material and enabling previously tentative or speculative inquires to be addressed with more certainty.

I have structured this thesis as three separate papers to be submitted to journals for publication, although a single reference list is provided at the end. Each chapter thus has its own Materials and Methods section, outlining the particular techniques and methodology used as they relate to the relevant chapter objectives. As such, there is a certain measure of overlap and repetition between the three chapters.

Chapter 2

Age and growth in male and female false killer whales, *Pseudorca crassidens*, with emphasis on differences between Northern and Southern Hemisphere populations

Introduction

The oceanic lifestyle of false killer whales is partly responsible for the fact that relatively little is known about them, most of what is known having been opportunistically gathered from mass strandings and drive fisheries or from captive animals. Information relating to their distribution and morphology has formed the bulk of most original studies, and indicates a worldwide distribution, in tropical and temperate waters of all oceans, ranging from between approximately 50° S and 50° N (Odell and McClune 1999).

There were early suggestions, accompanied by varying degrees of support, of a Northern and Southern form of *P. crassidens* (Slijper 1939, Flower 1864 and 1883, Pearson 1931, Deraniyagala 1945, in Leatherwood *et al*. 1991, Purves and Pilleri 1978). Based on skull and dental analyses and other morphometric studies (Slijper 1939, Ross 1984, Kitchener *et al*. 1990), there are indications of regional differences among false killer whales, suggesting that despite their widespread distribution, *Pseudorca crassidens* occurs as a number of disjunct populations. Differences in age and length at sexual maturity between different populations have similarly been reported (Purves and Pilleri 1978, Kasuya 1986). Genetic analyses of false killer whales in the eastern North Pacific Ocean demonstrated that there is a demographically distinct population of these whales around the main Hawaiian Islands (Chivers *et al*. 2007). Geographic variation in morphology is well documented in several species of cetaceans, particularly among the genera *Stenella* and *Tursiops* (see Kitchener *et al*. 1990, Connor *et al*. 2000), and frequently related to variation in water temperature and resource abundance which likely affect energy intake and demand.

The objective of this chapter is to describe aspects of growth in false killer whales using data collected from a mass stranding off the coast of South Africa, and from several drive-fisheries off Iki Island, Japan. Unlike previous studies on false killer whales which have been compromised by lack of detailed collaborative data from individual animals, and where age data has largely been absent, this study maximises information value by drawing on extensive data of individual animals, and by combining data on reproduction with age data. In earlier studies where age has been estimated, age determination techniques have differed, thus being of little comparative value. Furthermore, the practice of using dentinal counts to estimate age is of limited reliability when working with older specimens. By using decalcified, haematoxylin stained sections and both dentinal and cemental layer counts to determine age, the information value of this study is further enhanced and is of particular significance in evaluating the life history of false killer whales.

In addition to describing growth and body size in false killer whales, anatomical changes associated with sexual maturity are considered, and the relationship between growth, size and sexual maturity is investigated. Particular emphasis is made throughout the chapter on potential differences between the South African and Japanese data and how these might relate to differences between Northern and Southern Hemisphere populations of false killer whales.

Materials and Methods

Data Source

The South African material was collected from a mass stranding that occurred on the South African Cape west coast on the 19 August 1981. Of the 65 false killer whales involved in the stranding, 56 were found over a 1500 m stretch of beach in St Helena Bay. Four further specimens were found along 15 km of coast to the west, three specimens were found 10 km to the east, and two outlying, but presumably related, single specimens were reported 77 and 44 km north of the main group, from Lambert’s Bay and Eland’s Bay, respectively. Scientists reached the main site two days after the stranding occurred. The exact timing of the two single strandings is unknown. Due to delays in the onset of sample collecting and fixation, the material examined was not completely fresh, and the quantity and quality of information recorded per individual is varied. Data are available for 63 individuals (41 females and 22 males).

The Japanese whales examined in this study were caught by several drive fisheries at Iki Island, off the south west coast of Japan in February and March of 1979 and 1980 (Table 2.1). The date of capture of the shore-driven false killer whales did not always correspond to the date of death, as groups were kept alive in a netted bay until sampling. In each case, as many false killer whales as possible were randomly examined. Data are available for 156 specimens (96 females and 60 males) from 6 schools.

Table 2.1: Date of capture and number of false killer whales caught and studied at Iki Island, Japan.

School	Date of shore-drive	Date of sampling	No. caught	No. studied	No. studied	
					Females	Males
1	1979 – 03 – 08	03 – 10	20	5	4	1
2	1979 – 03 – 15	03 – 17, 18	138	35	20	15
3	1979 – 03 – 19	03 – 20, 21	160	28	16	12
4	1980 – 02 – 22	02 – 22 to 27, 03 – 18	10	6	2	4
5	1980 – 02 – 27	02 – 28 to 03 – 04	80	56	38	18
6	1980 – 03 – 06	03 – 7 to 9	155	26	16	10

Field Procedures

Data collection and sampling procedures were similar in Japan and South Africa – any differences in protocol and in the data collected are stated in the list below. Data were collected on site at Iki Island by Kasuya, and in St Helena Bay by Best and a team of volunteers respectively. Each whale was assigned an individual school and reference number. The following information was recorded:

1. *Sex*

2. *Body length:* measured to the nearest cm from the tip of the snout to the notch in the tail flukes, on a straight line parallel to the long axis of the body.

3. *Teeth:* 1 to 3 adjacent teeth were removed with a hammer and chisel from the center of the lower jaw of each specimen, and fixed in 10 % buffered formalin (Japan), or in 70 % ethanol (South Africa).

4. *Ovaries:* Both ovaries were collected and the presence of corpora lutea, corpora albicantia and large follicles was recorded before the ovaries were fixed in 10 % buffered formalin. Individual ovary weights were recorded in Japan only.

5. *Foetuses:* The length and sex of any foetus was recorded. If a corpus luteum was found in the ovary but no large foetus was present in the uterus, both uterine horns were opened and searched for a small embryo.

6. *Uteri:* The maximum diameter (cm) of the left and right uterine cornua of each South African female was measured with the uterus lying on a flat surface. Corresponding data for the Japanese specimens are not available.

7. *Mammary glands:* The presence and colour of milk was checked by pressing and then cutting the glands. The maximum thickness (cm) of one gland was recorded at its widest point. Histological samples were taken and fixed in 10 % buffered formalin. Data are available for South African specimens only. The appearance and thickness of the glands was used to help identify mature and lactating females.

8. *Testes:* Both testes were collected, trimmed of the epididymis, and, in South Africa, weighed before being fixed in 10 % buffered formalin. In Japan, the testes were weighted after fixation. A mid-length histological sample was taken from the centre of one testis for all individuals, and fixed in 10 % buffered formalin. In Japan the left testis was used, while in South Africa the larger testis was sampled.

Sexual maturity: Sexual maturity in cetaceans has been defined in a number of ways in previous studies. Both direct and indirect methods of establishing sexual maturity have been used which are typically related to age or body length to determine the onset thereof. The most commonly used criterion of female sexual maturity is the presence of one or more corpus luteum or corpus albicans, which indicates the female has ovulated previously (Clarke 1956, Perrin *et al*. 1976, Perrin *et al*. 1977, Odell *et al*. 1980, Kasuya and Marsh 1984, Kitchener *et al*. 1990, Read and Gaskin 1990, Amano *et al*. 1996; Best and Lockyer 2002). Odell *et al*. (1980) also considered ovary weight of the false killer whales examined when assigning reproductive status to females, while Perrin *et al*. (1976) used the increase in size of the Graafian follicles in female spotted porpoises as indirect evidence of sexual maturity. The presence of one or more corpus luteum or corpus albicans, indicating the female had previously ovulated, was used a direct indication of sexual maturity in females in this study.

The following criteria were used for assigning reproductive status to mature females in the field: A female was classified as pregnant if a foetus was found, and as lactating if milk was found in the mammary gland. Where a corpus luteum was found, but no evidence of a foetus or embryo, a female was classified as ovulating. Where milk was present in the mammary gland and a corpus luteum found in the ovary, but no foetus present, a female was classified as lactating and ovulating. Females with milk in the mammary gland and a foetus were classified as pregnant and lactating. If the foetus was small, the female will have been suckling a previous calf. Mature females not pregnant, lactating, or ovulating were classified as resting. It is an assumption of this study that the corpora regress with age, but persist indefinitely as ovarian scars, whether or not ovulation is followed by pregnancy.

In male cetaceans sexual maturity has largely been based on the histological appearance of the testis. More general histological criteria include the presence of spermatozoa in the testis (e.g. Best 1969, Best 1970, Odell *et al*. 1980); the presence or abundance of sperm in the epididymis (Perrin *et al*. 1976, Perrin *et al*. 1977, Kasuya and Marsh 1984); the relative abundance of interstitium in the testis and the level of maturation of the germinal epithelium (Clarke 1956, Best 1969, Best 1970); and the density of sperm in the epididymis (Kasuya and Marsh 1984, Amano *et al*. 1996). The diameter of the seminiferous tubules has also been used by a number of authors (Clarke 1956, Best 1969, Best 1970, Perrin *et al*. 1976), usually to corroborate evidence given by some other criterion. Other (indirect) measures of male sexual maturity to have been employed include penis length (Best and Lockyer 2002), testis mass (Perrin *et al*. 1976, Best and Lockyer 2002) and the growth rate of the penis (Best 1969). The relative abundance of spermatozoa/ amount of sperm in the testis was used as primary indication of male sexual maturity in this study, as described below

Laboratory Procedures

1. *Age determination:* Age was determined using growth layers in teeth. The use of this method for determining age in cetaceans is widespread (Scheffer and Myrick 1980, Perrin and Henderson 1984, Hohn *et al*. 1989, Read *et al*. 1993, Amano *et al*. 1996, Clark *et al*. 2000, Lockyer *et al*. 2007) despite the various general potential problems and biases with the use of growth layers groups to estimate age (Perrin and Myrick 1980, Hohn and Fernandez 1999). The ageing technique used in this study represents an improvement over most previous methods and currently remains the best method for determining age. Age determination from teeth was carried out by Kasuya following the methods used by Kasuya and Matsui (1984). Whales were aged by counting the growth layers in dentine and/or cementum, and without reference to other biological data. An annual rate of deposition of Growth Layers Groups (GLGs, following Perrin and Myrick 1980) in the dentine and cementum was assumed, based on the pattern of dentinal growth-layer deposition observed in short finned pilot whales by Kasuya and Matsui (1984). While the methods for determining age represent a significant improvement, until growth layer groups in false killer whales are calibrated with actual age in years, the estimates need to be regarded with caution.

Teeth were sectioned longitudinally and through the centre of the pulp cavity to a thickness of between 40 – 50 µm. Sections were decalcified in 5 % formic acid at room temperature (25° C) for approximately 24 hours, and washed in running water overnight. They were stained with haematoxylin for 30 to 60 minutes, washed in running water for 3 to 10 hours and mounted in Canadian balsam. Part of the dentine in some teeth in the South African sample was unstainable. The contrast between cemental and dentinal layers was not always clear. Three independent readings each for dentine and cementum were made at a magnification of 20 – 100x, and the median value in each case taken as the true age. The dentinal and cemental counts of individuals with open or closing pulp cavities, in which dentine deposition was continuing, were found to be statistically similar. Where discrepancies between dentinal and cemental counts on a tooth with an open pulp cavity occurred, the growth layers in both tissues were repeatedly checked until a good agreement was reached between the two tissue counts. The cemental growth layer count was used to estimate the age of older individuals with closed pulp cavities in which dentine deposition had ceased and for which dentinal growth-layer counts were thus not appropriate.

The age of individuals below 10 years was estimated to the nearest 0.25 year by considering the thickness of the first and last postnatal dentinal layers of incomplete thickness. For whales over 10 years the age was grouped into the nearest n + 0.5 years (n = integer). Kasuya and Matsui (1984) estimated the degree of error in these age-determination techniques in their study on short finned pilot whales and concluded that the 95 % confidence range for the age estimates at ages 10, 20, 40 and 60 years were ± 0.9, ± 1.8, ± 2.6 and ± 3.4 years respectively. The same degree of error in estimating age in this study has been assumed.

2. *Ovaries:* Each ovary of the Japanese specimens was trimmed of its bursa and weighed to the nearest 0.1 gm. There are no data on ovarian mass for the South African specimens. The medulla and cortex were hand-sliced at 1-to-2 mm intervals and the numbers of corpora lutea, corpora albicantia, and corpora atretica in both ovaries were recorded. Examination of the ovaries was carried out by Marsh.

3. *Mammary glands:* Histological slides of mammary gland material taken from the South African specimens were prepared using standard techniques and viewed at 100x magnification to help identify mature and lactating females and/or confirm macroscopic observations regarding reproductive status. Mature mammary tissue was distinguishable from immature tissue by the relatively more abundant glandular tissue in the former. Histologically active mammary tissue typical of a lactating female was distinguished from mature, but inactive, non-lactating tissue by the presence of intracellular and intraduct lipid droplets and milk secretions and the relatively larger alveoli.

4. *Testes:* Both testes were weighed to the nearest 0.1 g (Japan), or 10 g (South Africa), and the combined testis weights were used in the study to avoid possible bias. Haematoxylin and eosin (H-E) stained slides were prepared from the paraffin sections of all histological samples by technicians, using standard techniques. Kasuya and Ferreira examined the Japanese and South African slides, respectively, at magnifications of 100 – 400 x. Entire sections, measuring about 5 x 7 mm, were viewed and the relative abundance of immature and mature tubules calculated and used to determine reproductive status, following Kasuya and Marsh (1984). By considering not only the presence, but also the relative abundance of spermatozoa in the testis, this technique takes into account “maturing” males, which contain both immature and mature tubules in varying quantities in adjacent areas of the testis.

Males were classified into different levels of maturity according to the percentage of seminiferous tubules examined which contained spermatozoa, spermatocytes or spermatids. Males with no spermatozoa, spermatocytes or spermatids were classed as immature; those with less than 50 % mature tubules were classed as early maturing; those with between 50 % and 100 % mature tubules were classed as late maturing, and those with 100 % mature tubules were classed as mature. The use of these criteria assumes that males produce sperm more or less continuously throughout the year. The number of tubules examined varied between 5 and 85 tubules (South Africa) and between 70 and 150 tubules (Japan), depending on sample quality. According to Best (1969), different areas of the testis of the sperm whale mature at different times, the centre of the testis maturing much earlier than the periphery. However, various positions along a longitudinally sliced testis of two male short-finned pilot whales were sampled to test whether they were at different stages of maturity, but no significant differences were found between positions (Kasuya and Marsh 1984).

The relative abundance of interstitium was noted for the South African specimens by Ferreira, and used as a more general histological criterion when the presence and abundance of spermatozoa could not be accurately determined, owing to probable post-mortem effects. Whales classed as immature had abundant interstitium and small seminiferous tubules, with mostly closed lumens, while mature males had comparatively small amounts of interstitium and relatively large tubules, with open lumens.

Seminiferous tubule diameter was measured in all testis samples of the South African males. For each whale the diameter of 20 approximately circular seminiferous tubules was measured using a calibrated micrometer eyepiece on two planes at right angles to each other, at a magnification of 100x. Circular tubules were selected to ensure they had been sectioned transversely and samples can thus be considered random for size. An overall mean diameter for each individual was calculated, expressed in µm. No data were available on tubule diameter from the Japanese sample.

A variable amount of information is available for each specimen, for example information relating to sex and body length for a particular specimen may be available, but reproductive status may be unknown. Of the 219 false killer whales examined, age data is available for 186 (65 males, 121 females) and the reproductive status of 198 (73 males, 125 females) is known. Of the 63 South African specimens examined, age data and reproductive status are available for 58 (92 %). Age data are available for 128 (82 %), and reproductive status known for 140 (90 %) of the 156 Japanese specimens examined.

The delay between death and autopsy of the South African specimens is likely to have resulted in the material not being completely fresh when examined. Post-mortem changes due to autolysis are thus likely to have occurred and the quality of samples are affected accordingly.

Statistical analysis: The variable amount of information per specimen is reflected in the corresponding variation in sample sizes used in the analyses.

Growth curves: A number of mathematical models have previously been used to describe growth in relation to age in mammals. By reducing the complex process of growth to a few parameters, one is able to compare growth patterns between sexes, populations, and even species. Furthermore, residual variances in these growth models can be used to identify sources of and estimate variability in the data set, as well as to assess variability between study populations. Growth models relating age and body length were fitted using the Gompertz, Logistic and Von Bertalanffy equations by sex for each site (South Africa and Japan) and in combination.

Comparing body lengths: An analysis of variance was fitted to the data, with age as a covariate of body length, to compare differences in body length by sex between the two sites and in combination. An interaction between site and sex was investigated. The model corrects for imbalances in sample size, and eliminates any possible influence of the covariate age on the comparison of body lengths.

Body length at birth: Confidence intervals for body length at birth, based on a logistic regression of body length at birth using a dummy case with age set to 0, were determined.

Mammary glands: Differences in the mean thickness of mammary glands of females in different reproductive states were investigated with a Mann-Whitney U-test.

Uterine horns: The statistical difference between left and right uterine horn diameter of immature and mature females separately was determined using a Wilcoxon paired t-test, and the difference in combined left and right uterine horns between immature and mature females in various reproductive conditions determined using a Mann-Whitney U-test.

Estimating the onset of sexual maturity:

The length and age at attainment of sexual maturity in cetaceans has previously been estimated using a variety of techniques. A common procedure involves estimating the age or body length at which 50 % of the population is mature, as determined by a pre-established criterion. This has been done by tabulating the % immature or mature for each age or body length interval (Kasuya 1986), or by plotting % mature versus age and interpolating the graph for the age or body length associated with 50 % maturity (Perrin *et al*. 1976, Perrin *et al*. 1977). Another approach involves fitting a linear regression to the data (Kasuya and Marsh 1984) and determining the length or age corresponding to the age or length at which 50 % are mature. In order to reduce variability in his data Best (1969, 1970) smoothed the data by threes before fitting a growth curve. The DeMaster method (DeMaster 1978), another general additive model, was used by Read and Gaskin (1990) and Best and Lockyer (2002). The method is particularly useful in that it provides an estimate of variance, but requires a sample size of 25 if differences of at least ½ year are to be determined. Perrin and Reilly (1984) outline and critique various methods to have been used to estimate size and age at sexual maturity.

Most of the quantitative methods described above could not be applied to this study due to the insufficiently large sample sizes, and particularly to the absence of maturing males (see below). Various other approaches (Logistic regression and ROC analysis) were attempted where possible in the hope of converging on a common result. A logistic regression model was fitted to predict the probability of an individual being immature (i.e. probability modelled is immature). This method of estimating age at sexual maturity was possible for the Japanese females owing to the overlap in ages of immature and mature specimens, but was not used on the South African data or the Japanese males as there is no overlap in ages between immature and mature specimens, and the validity of the model fit would thus be questionable. A logistic regression was similarly fitted to the South African and Japanese female false killer whale data to obtain an estimate of body length at sexual maturity, but was not possible for the Japanese or South African males again owing to the absence of an overlap between immature and mature specimens in the data sets. The estimates for age and body length at sexual maturity given by the ROC analysis represent values where it can be safely assumed that all animals at or above that age/body length are sexually mature, but provide no indication of an average age or body length at maturity. For these reasons, the results of the ROC analysis have not been presented.

Male maturity: The mean combined testis mass of individual mature South African and Japanese false killers was compared using a t-test. Pearson correlation coefficients and their associated significance tests were used to evaluate the relationship between age, body length, combined testis mass, seminiferous tubule diameter and relative sperm abundance.

Growth curves relating age and body length were fitted using SPSS and STATA statistical packages. All the other analyses were done using SAS version 9.1 statistical package (SAS Institute Inc., 2004).

Results

a) Age and Body length relationships

Body length at birth:

In the Japanese sample the largest foetus examined was of unknown sex and measured 174 cm (Table 2.2), while the smallest neonate recorded was a female with a body length of 175 cm. This suggests birth takes place at a body length of approximately 175 cm. A single foetus, 148 cm long, was recorded in the South African sample. Calves 158 cm (in December near the Berg River mouth, in the Western Cape, Smithers 1938), and 161 cm (in February 2006 at Olifantsbos, Western Cape coast of SA) have been measured: length at birth is therefore estimated to be about 155 cm (Best 2007), or 11.5 % less than in the Japanese population. Ohsumi (1966) predicted the relationship between body length at birth (y) and mean female body length at sexual maturity (x) for odontocetes as: $y = 0.532x^{0.916}$. Using an estimate of length at maturity of 3.25 m for the South African specimens, and of 3.59 m for the Japanese females (see below), this equation predicts a birth length of 1.57 m and 1.72 m respectively, which is very close to the estimates above. There are insufficient data to test whether there is a difference in the size of males and females at birth.

Table 2.2: Body length composition of South African and Japanese false killer whale foetuses.

Body length range (cm)	Foetus length (cm)	School	Date of capture	Locality
20 -	29	11	March 1980	Iki Island, Japan
30 -				
40 -				
50 -				
60 -				
70 -	72	10	February 1980	Iki Island, Japan
80 -				
90 -	96	11	March 1980	Iki Island, Japan
100 -				
110 -				
120 -	126	4	March 1979	Iki Island, Japan
130 -	131, 138	10, 11	Feb., March 1980	Iki Island, Japan
140 -	148	13	September 1981	St Helena Bay, SA
150 -	159	3	March 1979	Iki Island, Japan
160 -	167	11	March 1980	Iki Island, Japan
170 -	174	10	February 1980	Iki Island, Japan

Estimates of confidence intervals for body length at birth, based on a logistic regression of body length against age, are shown in Table 2.3. These results are presumably artificially inflated, particularly among the South African specimens, owing to the very small sample of foetal and neonatal data, and indicate the inadequacy of the model in describing early growth in the species.

Table 2.3: Confidence intervals (95 %) for body length at birth for false killer whales.

Site	Sex	Lower end of CI	Upper end of CI
SA	F	282.02	366.57
JAP	F	238.70	431.34
SA	M	270.13	416.40
JAP	M	220.89	408.52

Growth rates and asymptotic length:

Growth curves relating age and body length using the Logistic and Gompertz models were fitted. The residuals showed no obvious patterns. The Von Bertanlanffy model was discarded as it was found to be unstable, particularly among the lower ages. Previous studies have shown it to fit poorly to the youngest animals of youngest cetaceans (Stevick 1999), suggesting it may not be appropriate for all stages of growth. Both the Gompertz and Logistic models (Figures A2.1a and b in Appendix) described the data well (except for the predicted sizes at birth were unrealistically large – see below), and had similar r^2 values. (The growth curve parameters and r^2 values are summarized in Table A2.1 in Appendix). The 3-parameter equations appeared to be strongly influenced by the small number of observations at the lowest ages, particularly among the South African females where the point of maximum growth was given as being -5 years. The B3 parameter was thus removed and the models refitted to each sex and site combination. Given the close fit to the data of the Gompertz model, together with its prevalence in the literature (Read and Gaskin 1990, Read *et al*. 1993, Read and Tolley 1997, Clark *et al*. 2000), and thus its comparative value, only the Gompertz model was refitted to the data. Removing the B3 parameter (point of inflection) and refitting the Gompertz model, however, did not significantly affect the growth curve parameters nor improve the goodness-of-fit (Table A2.1 in Appendix). However, using the 2-parameter Gompertz model the predicted body length at birth is lower and thus more accurate, when compared to the values estimated above. The growth rate until approximately 10 years of age is also higher, and the asymptotic length smaller among both sexes in the South African and Japanese samples. This discrepancy may be due to the 2-parameter model being more sensitive to the small number of specimens at the lower ages, and the relatively higher number of observations at the higher ages, which artificially influence the growth curve parameters. The growth curves for the 2-parameter Gompertz model are shown in Figures 2.1a and 2.1b. The paucity of data for young individuals makes any conclusive analysis of growth in the early years of life difficult (Stevick 1999). The values predicted by the 2- parameter Gompertz model seem biologically more realistic, and unless otherwise stated, have therefore been used in subsequent comparisons between and within the South African and Japanese data sets.

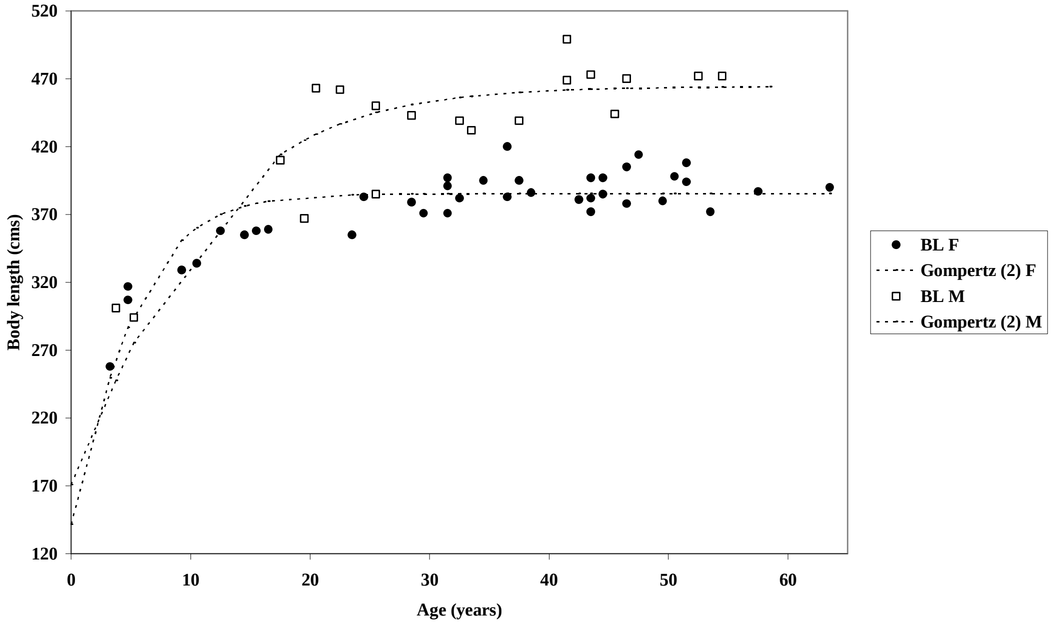

Figure 2.1a: Gompertz growth curves for female (filled circles) and male (open squares) false killer whales stranded at St Helena Bay, South Africa.

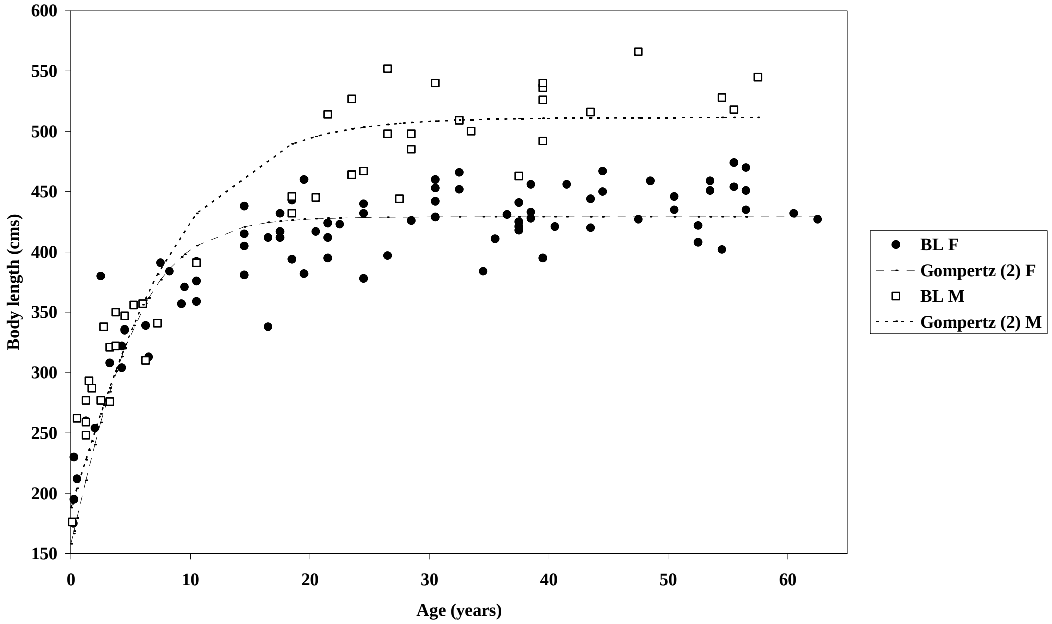

Figure 2.1b: Gompertz growth curves for female (filled circles) and male (open squares) false killer whales taken at Iki Island, Japan.

The overall pattern of growth is similar between the South African and the Japanese false killer whales examined (Figures 2.1a and 2.1b). In both samples growth increases linearly from birth, gradually declines, and eventually reaches an asymptotic length. The Japanese specimens are significantly larger than the South African specimens when growth ceases. Apart from an initial period below 10 years of age where growth appears to be similar for males and females in each locality, males in both samples are larger than females at every age, and attain an overall larger body size as adults.

Among the South African female specimens sampled, the point at which growth stops corresponds to approximately 30 years of age (Fig. 2.1a) and the mean body length of 25 females this age or older is 390.4 cm (SD = 12.7). In the Japanese females growth ceases at approximately 25 years (Fig. 2.1b) and the mean body length of 41 females 25 years and older is 436 cm (SD = 21.8). Growth in male false killer whales in both populations ceases at approximately 25 – 30 years (Figures 2.1a and 2.2b). Mean body length of the 11 South African male false killer whales aged 30 years or above is 463.5 cm (SD = 22), while 13 males of the same age from the Japanese population have a mean body length of 521.5 cm (SD = 26.5).

The results of the analysis of covariance, where age is a covariate, are summarized in Table 2.4a, $r^2 = 0.735279$. Residuals showed no pattern. The mean body lengths according to location and sex are shown in Table 2.4b. South African false killer whales sampled were smaller than the Japanese whales, and males were larger than females in both samples. No interaction between site and sex was found to occur ($p = 0.3964$), i.e. the pattern was consistent over both populations irrespective of sex. The model was repeated without the site/sex interaction, and the results shown in Table 2.4c, $r^2 = 0.736441$.

Table 2.4a: Analysis of covariance, with age as a covariate of body length. An interaction between site and sex was investigated. Imm = immature.

Variable	F value	P value
Site	32.99	< 0.0001
Sex	59.33	< 0.0001
Site*Sex	0.72	0.3964
Repro Status(Imm. or Mature)	84.89	< 0.0001
Age	44.59	< 0.0001

Table 2.4b: Least square means for body length (cm) according to site and sex, as given by the analysis of covariance.

		Sex		
		F	**M**	
Site	**SA**	326.4	383.8	355.1
	Jap	371.8	417.7	394.8
		349.1	400.8	

Table 2.4c: Analysis of covariance, with age as a covariate of body length.

Variable	F value	P value
Site	41.35	< 0.0001
Sex	62.55	< 0.0001
Repro Status(Imm. or Mature)	86.62	< 0.0001
Age	44.53	< 0.0001

However, McLaren (1993) advises against using average adult lengths as “they may be more influenced by age-sampling biases” (p. 2 & 4). According to the asymptotic values, as predicted by the growth functions in this study (Table A2.1 in Appendix, p. 1), the Japanese males and females are larger than their counterparts in the South African sample. The females in both samples are smaller than the males. Thus the pattern observed in the analysis of covariance is consistent with the asymptotic values given by the growth curves, and the mean adult body lengths.

Based on the asymptotic body lengths estimated by the 2-parameter Gompertz equations (Table A2.1 in Appendix, p. 1), female body length as a percent of male body length is 83 % (385.4 cm/464.5 cm x 100) in South Africa and 84 % (429.1 cm/511.4cm x 100) in Japan. Using the mean adult body lengths (given above) of 390 cm and 464 cm for the South African females and males (74 cm difference), and 436 cm and 522 cm for the Japanese female and male whales (86 cm), female body length as a percent of male body length is 84 % in both populations. According to the values of the Analysis of covariance (Table 2.4b), female body length as a percent of male body length in the present study is 85 % in the South African sample, and 89 % in Japanese false killer whales. Thus the degree of size dimorphism between South African males and females is the same as that between the Japanese males and females, i.e.: there is no geographic variation in relative size dimorphism between sexes.

b) Female Maturity

Mammary gland thickness:
Mammary gland thickness in immature South African females ranged from 1.3 to 3.0 cm in thickness, with a mean of 1.93 cm (n = 3). Mean thickness increased in mature females to 2.49 cm, ranging from 0.9 to 4.2 cm (n = 35). This difference was not statistically significant (Mann-Whitney U-test: df = 36, p = 0.203). The observed lack of a statistical difference in mean thickness between the two groups could be an consequence of the small sample - even if a biological difference exists between the two groups, it may be concealed by the small number of immature specimens in the present sample. On the other hand, there may be a greater than normal mammary gland involution in older females if the length of the resting period is prolonged. Mammary gland thickness in lactating females (n = 10) ranged from 2.0 to 4 cm, with a mean thickness of 3.11 cm, compared to a mean thickness of 2.24 cm in mature, non-lactating female mammary glands (n = 22), ranging from 0.9 to 4.2 cm. Three of the original females, that were classified as mature on the basis of size and age, but whose exact state of maturity could not be determined, were excluded from this second set of analyses. Despite the overlap in range, mammary glands of lactating females were significantly thicker than those of mature, non-lactating females among the South African sample (Mann-Whitney U-test: df = 30, p = 0.0067).

The presence of milk in the mammary glands of females with histologically active mammary tissue (i.e. large alveoli, sparse amount of connective tissue, secretions in lumen or ducts), was not always detected by gross observations in the field. A possible explanation is that the females were approaching the end of galactopoiesis. Of equal interest is the observation that among several females there were discrepancies in the secretory activities of different areas in their mammary tissue, i.e. some alveoli appeared to be active, while others appeared inactive. The mammary gland thickness of the 4 females with partially active tissue ranged from 2.0 to 3.6 cm, with a mean thickness of 2.78 cm, while the mean thickness of the lactating females when these 4 females were excluded, increased only slightly to 3.3 cm. As many of the histological slides were of poor quality and difficult to interpret, whether these observations represent genuine variations in functional state, terminal stages of lactation, poor histology or post-mortem changes to the tissue, is unclear.

Best and Lockyer (2002) reported a similar increase in mammary gland thickness at sexual maturity in sei whales off the west coast of South Africa. Primigravid females had only slightly larger glands. These enlarged dramatically during lactation, and failed to regress to their former size in resting or multigravid females. According to Matthews (1948) the differences in thickness of the involuted mammary glands in anoestrus females are related to the length of time since the last period of lactation rather than the number of lactations that had occurred. However, Matthews supports his conclusion by demonstrating that there is no relationship between the mammary gland thickness of a group of anoestrus balaenopterids and the number of corpora albicantia, which he equates with the number of pregnancies and subsequent lactations, i.e.: he assumes all ovulations result in a successful pregnancy.

Uterine cornua:

No statistically significant differences between the width of left and right uterine horns were detected among immature females (Wilcoxon paired t-test: df = 3, p = 1.000), nor mature females (Wilcoxon paired t-test: df = 27, p = 0.4196), but the results for immature females must be interpreted with caution due to the small sample size of 4. This suggests the uterine cornua (at least in non-pregnant females) are generally bilaterally symmetrical, thus the average width of the two horns was taken and used in the following analyses. The changes in uterine horn width from immaturity through oestrus, pregnancy and lactation to anoestrus are shown in Figure 2.2.

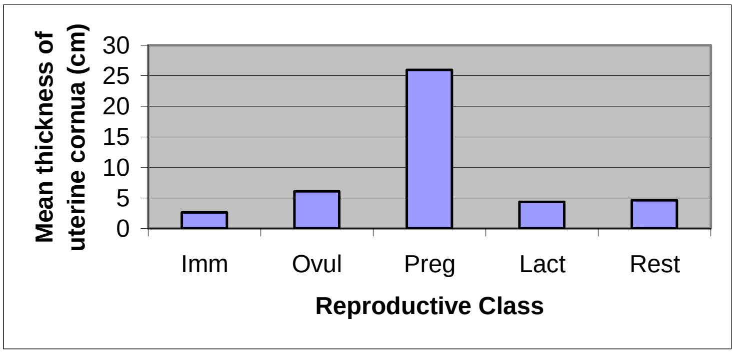

Figure 2.2: Mean diameter of the uterine cornua in immature (Imm), ovulating (Ovul), pregnant (Preg), lactating (Lact), resting (Rest) in South African false killer whales. Left and right uterine cornua combined.

The width of the uterine cornua increases significantly with body length and sexual maturity. Horn width ranged from 2.3 to 2.8 cm, with a mean of 2.65 cm in immature females. The mean uterine horn width in mature females (excluding the single pregnant female) increased to 4.9 cm, ranging from 3.1 cm to 8.5 cm, which is significantly different from that in immature females (Mann-Whitney U test: df = 29, p = 0.0014). Data on uterine horn width is available for only 1 pregnant female, with a horn thickness of 21 cm for the right uterine cornu, and of 31 cm for the left and presumably pregnant cornu. During ovulation the uterine cornua widen considerably, to a mean width of 6.1 cm (n = 7). This increase is probably due to the progestational proliferation brought about through the influence of progesterone produced in the newly formed corpus luteum (Matthews 1948). With a foetal body length of 148 cm, the single pregnant female was presumably in a late stage of pregnancy. Regression of the uterus after birth must be immediate as the uterine cornua of 10 lactating females ranged from 3 cm to 7.6 cm, with a mean of 4.4 cm. This supports the suspicions of Comrie and Adam (1938) that uterine regression in false killer whales, as with mammals in general, is quick after birth. In 14 resting females the combined width of left and right horns averaged 4.6 cm. The trends reported here are consistent with those of Best and Lockyer (2002) for sei whales off the west coast of South Africa, and of Kasuya and Marsh (1984) for short-finned pilot whales.

Age at sexual maturity in females:

The oldest immature South African female was 9.25 years old and the youngest mature female was 10.5 years old, which suggests that the onset of sexual maturity occurs between 9.25 and 10.5 years in this sample (Table 2.5a). The youngest mature Japanese female (pregnant) was 8.25 years old and the oldest immature female 10.5 years (Table 2.5a), which suggests sexual maturity in Japanese females sampled occurs between 8.25 and 10.5 years.

Table 2.5a: Relationship between sexual maturity and age (years) in South African and Japanese female false killer whales. Values in parentheses indicate % mature for each age interval.

	South African Females			Japanese Females		
Age range (yrs)	**Immature**	**Mature**	**Total**	**Immature**	**Mature**	**Total**
0.1 – 2				5		5
2 -	1		1	3		3
4 -	2		2	4		4
6 -				3		3
8 -	1		1	1	2 (67)	3
10 -		1 (100)	1	1	2 (67)	3
12 -		1 (100)	1			
14 -		2 (100)	2		2 (100)	2
16 -		1 (100)	1		5 (100)	5
18 -					4 (100)	4
20 -					4 (100)	4
22 -		1 (100)	1		1 (100)	1
24 -		1 (100)	1		3 (100)	3
26 -					1 (100)	1
28 -		2 (100)	2		1 (100)	1
30 -		3 (100)	3		4 (100)	4
32 -		1 (100)	1		1 (100)	1
34 - 64		21 (100)	21		27 (100)	27

A logistic regression to estimate age at sexual maturity was possible for the Japanese females owing to the overlap in ages of immature and mature specimens, but was not used on the South African data as there is no overlap in ages between immature and mature specimens.

The model for the logistic regression of age at sexual maturity for the Japanese females is: log (p/1-p) = 8.255 – 0.8951x. Thus, a female from the present sample of age x = 7.6

has a predicted probability of 0.81 of being immature. In order to determine the level of probability at which we can safely claim that this female whale is definitely immature, all 74 females in the population were scored and the associated probability of being immature found for each of them. The cut-off probability, representing the point at which the % of females incorrectly classified is minimized and the % correctly classified is highest, is 0.8 i.e. $\log(0.8/1-0.8) = 8.255 - 0.8951x$. Solving for x, the age at and below which the females are likely to be immature, and above which the females are likely to be mature, is 7.7 years, which falls below the age of the youngest mature female. Using the more usual probability of 0.5, the age at sexual maturity is estimated to be 9.2 years. This represents the age at which a female has an equal probability of being immature or mature, or 50 % of females are mature, and seems more realistic. A probability of 0.5 has been used in all subsequent tests.

Body length at sexual maturity in females:

The smallest mature South African female false killer whale sampled measured 320 cm, and the largest immature 329 cm, suggesting that sexual maturity in South African females occurs between a body length of 320 and 329 cm (Table 2.5b). The smallest mature Japanese female measured 338 cm, and the largest immature 392 cm. Sexual maturity in the Japanese female sampled is thus attained between 338 and 392 cm (Table 2.5b).

Table 2.5b: Relationship between sexual maturity and body length (cm) in South African and Japanese female false killer whales. Values in parentheses indicate % mature for each body length interval.

	South African Females			Japanese Females		
Body length range (cm)	**Immature**	**Mature**	**Total**	**Immature**	**Mature**	**Total**
170 -				1		1
190 -				2		2
210 -				1		1
230 -				2		2
250 -	1		1	2		2
270 -						
290 -	1		1	2		2
310 -	2	1 (33)	3	3		3
330 -		1 (100)	1	3	1 (25)	4
350 -		5 (100)	5		2 (100)	2
370 -		16 (100)	16	2	6 (75)	8
390 -		12 (100)	12	2	5 (71)	7
410 -		2 (100)	2		21 (100)	21
430 - 480					32 (100)	32

The model for the logistic regression of body length at sexual maturity for the South African female false killer whales is: log (p/1-p) = 50.36 - 0.15x, and for the Japanese females is: log (p/1-p) = 23.2805 - 0.0648x. The body length at which 50 % of the females are mature (p = 0.5) is 325.1 cm for the South African females, and 359.3 cm for the Japanese females. Thus, sexual maturity in female false killer whales appears to occur at a similar age in South African and Japanese specimens sampled (approximately 8.25 to 10.5 years), but at a shorter body length by approximately 30 - 40 cm in the South African whales.

c) Male maturity

The testicular material of 5 South African specimens was found to contain no sperm, despite having sparse amounts of interstitium, tubules with large diameters and large testes, characteristic of reproductive maturity (Table 2.6). Based on these features, and despite the absence of sperm, I have classified these 5 male specimens as mature. These males have been indicated as M/Z (mature, but no sperm) in the relevant diagrams. Possible explanations for the apparent absence of sperm in these otherwise mature males are discussed below.

Table 2.6: Age, body length, diameter of seminiferous tubules and combined testis mass of 5 male South African false killer whales with no sperm recorded in the seminiferous tubules.

Specimen No.	Age (yrs)	Body length (cm)	Tubule diameter (µm)	Combined testis mass (g)
13	54.5	472	239.3	5800
21	52.5	472	235.9	5700
24	58.5	490	242.3	6300
47	20.5	463	206.1	5300
52	41.5	469	226.1	6000

According to the criterion of sperm abundance, two South African males were classed as late maturing, and two Japanese males were classed as early maturing. Their biological characteristics are shown separately (Table 2.7b) to those of immature and mature males (Table 2.7a). An early maturing Japanese male, 6.25 years of age, was difficult to separate from the immature males. The age of the second early maturing Japanese male is within the range for that of mature males, and the body length and testis weight fall slightly below the respective minimum measurements recorded for mature males. Both of the late maturing South African male specimens have body length, tubule diameter and combined testis mass measurements that fall within the ranges for those of the mature males. In their analyses, Kasuya (1986) combined early maturing male false killer whales with the immature specimens, and Kasuya and Marsh (1984) grouped the early maturing male short-finned pilot whales with the immature specimens and the late maturing males with the mature short-finned pilot whales, as the two “groups” were reportedly distinct from one another.

Table 2.7a: Characteristics of male sexual maturity and body length, age, diameter of seminiferous tubules and combined testis mass in immature (IM) and mature (M) false killer whales. Early maturing and Late maturing males have been excluded.

		Body length (cm)		Age (years)		Tubule diameter (µm)		Combined testis mass (g)	
		Range	**Mean**	**Range**	**Mean**	**Range**	**Mean**	**Range**	**Mean**
SA	**IM**	294 - 323	306	3.75 - 5.25	4.5	57 - 65	62.2	102 - 400	218.7
	M	367 - 473	449.7	17.5 - 58.5	37	154 - 242	213.5	1000 - 7150	5236.7
Jap	**IM**	176 - 391	298	0.1 - 10.5	3.5	-	-	7.3 - 108	50.2
	M	441 - 566	500.8	18.5 - 57.5	33.9	-	-	1680 - 7200	4953

Table 2.7b: Body length, age, diameter of seminiferous tubules and combined testis mass of the 2 late maturing (LM) South African and the 2 early maturing (EM) Japanese false killer whales. The % of seminiferous tubules examined containing sperm is shown (% Mat).

		% Mat	Body length (cm)	Age (years)	Tubule diameter (µm)	Combined testis mass (g)
SA	**LM**	80	385	25.5	159.5	1245
	LM	97	453	unknown	202	6400
Jap	**EM**	1.5	310	6.25	-	88
	EM	12	432	18.5	-	870

Age at sexual maturity in males:

The oldest immature SA male false killer whale was 5.25 years old and the youngest mature male was 17.5 years old. The oldest immature Japanese male was 10.5 years old and the youngest mature Japanese male was 18.5 years old. This suggests maturity is reached between 5.25 and 17.5 years among the South African male false killer whales, and somewhere between 10.5 and 18.5 years of age in the Japanese false killer whales (Table 2.8a). As expected, the abundance of spermatozoa increases abruptly between these ages in the respective populations (Fig. 2.3a and 2.3b). There were no South African male specimens between the ages of 5.25 and 17.5 years, and no Japanese males between the ages of 10.5 and 18.5 years.

Table 2.8a: Relationship between sexual maturity and age (years) in male South African and Japanese false killer whales. Values in parentheses indicate % mature for each age interval.

	South African Males				Japanese Males			
Age (yrs)	**Immature**	**Late maturing**	**Mature**	**T**	**Immature**	**Early maturing**	**Mature**	**T**
0.1 -	1			1	11			11
4 -	1			1	4	1		5
8 -					1			1
12 -								
16 -			2 (100)	2		1	1 (50)	2
20 -			2 (100)	2			5 (100)	5
24 -		1		1			3 (100)	3
28 -			1 (100)	1			2 (100)	2
32 -			2 (100)	2			2 (100)	2
36 -			1 (100)	1			4 (100)	4
40 -			2 (100)	2			1 (100)	1
44 -			2 (100)	2			1 (100)	1
48 -								
52 -			2 (100)	2			2 (100)	2
56 -			1 (100)	1			1 (100)	1

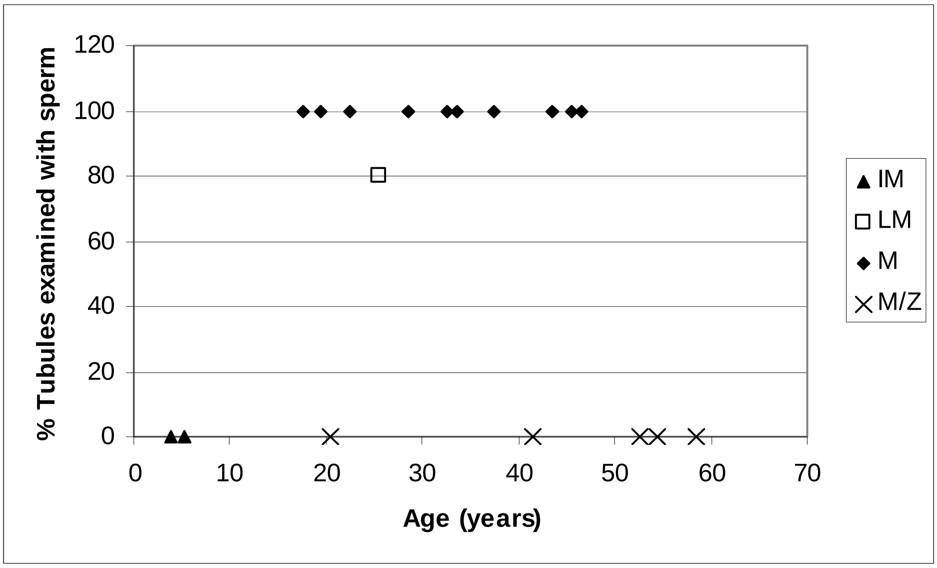

Figure 2.3a: Relationship between age and % tubules examined with sperm in South African male false killer whales. IM = immature, LM = late maturing, M = mature, M/Z = mature, but no sperm.

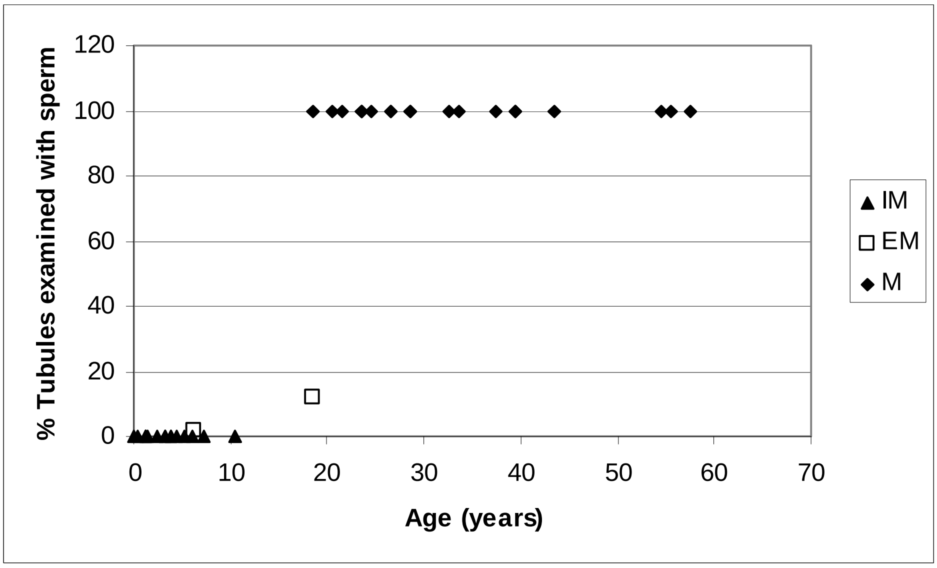

Figure 2.3b: Relationship between age and % tubules examined with sperm in Japanese male false killer whales. IM = immature, EM = early maturing, M = mature.

Body length at sexual maturity in males:

The largest immature South African male measured 323 cm and the smallest mature male measured 367 cm (Table 2.8b). There are no males between these body lengths. Among the sample of Japanese false killer whale males, the smallest mature individual measured 441 cm and the largest immature measured 391 cm (Table 2.8b). With the exception of an early maturing male measuring 432 cm (Table 2.7b), there are no males within this range of body lengths.

Table 2.8b: Relationship between sexual maturity and body length (cm) in male South African and Japanese false killer whales. Values in parentheses indicate % mature for each body length interval.

	South African Males				Japanese Males			
Body length range (cm)	**Immature**	**Late maturing**	**Mature**	**T**	**Immature**	**Early maturing**	**Mature**	**T**
170 -					2			2
200 -								
230 -					3			3
260 -					4			4
290 -	2			2	2	1		3
320 -	1			1	6			6
350 -			1 (100)	1	3			3
380 -		1		1	1			1
410 -			4 (100)	4		1		1
440 -			5 (100)	5			7 (100)	7
470 -			5 (100)	5			9 (100)	9
500 -							8 (100)	8
530 -							4 (100)	4
560 -							2 (100)	2

The proportion of tubules containing sperm increases sharply between these body lengths in the respective populations (Fig. 2.4a and 2.4b). There is a significant positive correlation between the proportion of tubules with sperm and both age and body length among the Japanese male false killer whales (Table 2.9a). However, there is no significant association between the proportions of mature tubules and either age or body length in the South African males (Table 2.9b), presumably reflecting the several mature specimens without sperm. As there is no overlap in the ages or body lengths of immature and mature male false killer whales in either population, it was not appropriate to fit a logistic regression to the data as for the female false killer whales.

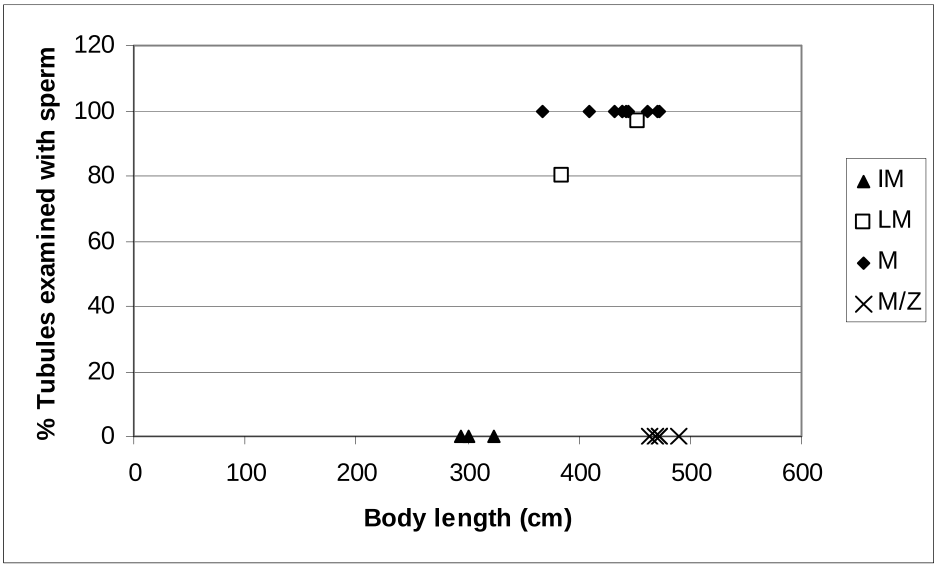

Figure 2.4a: Relationship between body length and % tubules examined with sperm in South African false killer whales. IM = immature, LM = late maturing, M = mature, M/Z = mature, but no sperm.

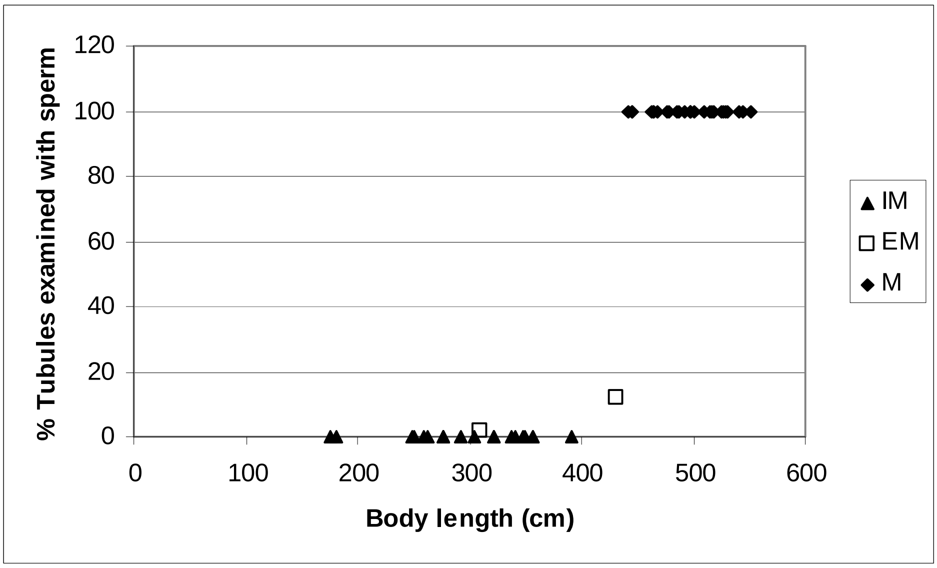

Figure 2.4b: Relationship between body length and % tubules examined with sperm in Japanese false killer whales. IM = immature, EM = early maturing, M = mature.

Table 2.9a: Pearson correlation coefficients for Japanese male false killer whales. Numbers in parentheses refer to sample size.

	No. Tubules with sperm	Combined testis mass
Body length	0.86236 < 0.0001 (50)	0.86997 < 0.0001 (54)
Age	0.82128 < 0.0001 (39)	0.78328 < 0.0001 (42)
Combined testis mass	0.87417 < 0.0001 (49)	-

Table 2.9b: Pearson correlation coefficients for South African male false killer whales. Numbers in parentheses refer to sample size. N/S = not significant.

	No. Tubules with sperm	Combined testis mass	Tubule diameter
Body length	0.22912 N/S (20)	0.87553 < 0.0001 (22)	0.96637 < 0.0001 (19)
Age	0.00309 N/S (18)	0.76235 < 0.0001 (20)	0.83908 < 0.0001 (17)
Combined testis mass	0.41795 N/S (20)	-	0.89975 < 0.0001 (19)
No. tubules with sperm	-	-	0.29416 0.2215 (19)

Testis mass:

The mass of the left and right testes is available for 20 South African and 52 Japanese false killer whales, ranging from 102 g to 7150 g, and from 7.3 g to 7200 g, respectively (Table 2.7a). The mean combined testis mass of 5237 g (n = 15) for mature South African male false killer whales was not significantly different from that of 4953 g (n = 29) for the mature Japanese males (t-test: df = 42; p = 0.6146). The heaviest combined testis mass for an immature South African male was 400 g, and the lowest combined testis mass for a mature South African male was 1000 g (Table 2.7a). There is a distinct gap in testis mass between these values (presumably corresponding to the absent males between the ages of 5.25 and 17.5 years), accompanied by a rapid increase in testis mass at a body length of approximately 370 cm (Fig. 2.5a).

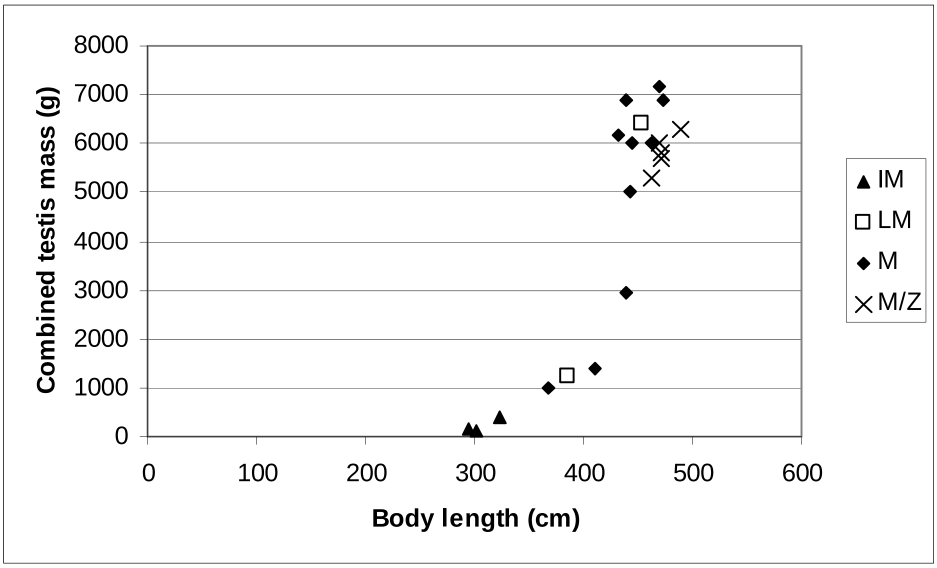

Figure 2.5a: Relationship between body length and combined testes mass in South African false killer whales. IM = immature, LM = late maturing, M = mature, M/Z = mature, but no sperm.

The heaviest combined testis mass for an immature Japanese male was 108 g, and the lowest combined testis mass for a mature Japanese male was 1680 g (Table 2.7a). There is a similar gap in combined testis mass between that of immature and mature Japanese specimens. This is also followed by an abrupt increase in testis mass in males with a combined testis mass of 1680 g. Figure 2.5b indicates that this occurs at a body length of approximately 445 cm. The gaps in combined testis mass and absence of specimens of intermediate testis mass presumably correspond to the absent males between 10.5 and 18.5 years of age.

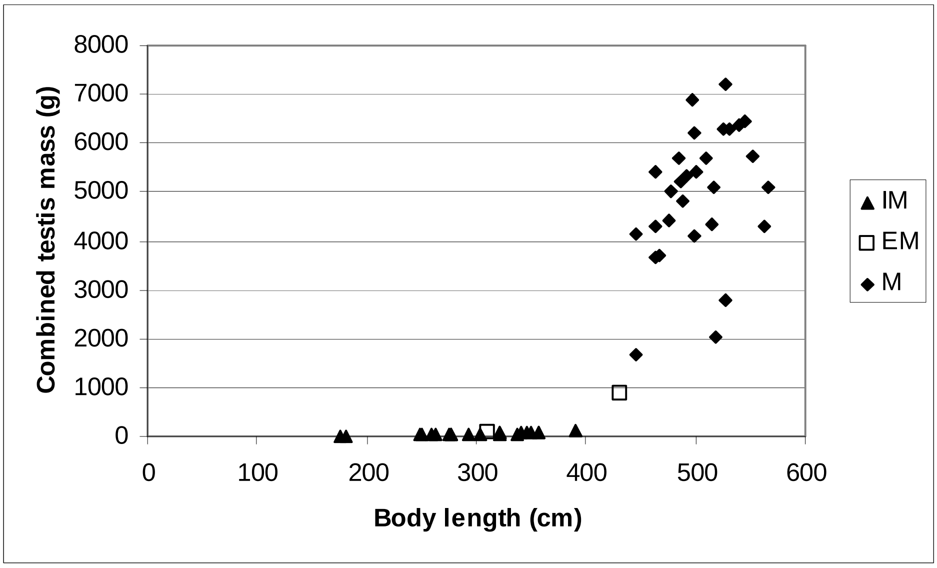

Figure 2.5b: Relationship between body length and combined testes mass in Japanese false killer whales. IM = immature, EM = early maturing, M = mature.

The plots of age against combined testis mass indicate the dramatic increase in testis mass, at 1000 g and at 1680 g, to coincide with an age of 17.5 and 20.5 years, in the South African (Fig 2.6a) and Japanese (Fig. 2.6b) specimens, respectively. Although their accuracy may be affected by the small number of maturing males, the estimates of the age and body length at which testis mass increases dramatically are consistent with the upper end of the ranges previously suggested to represent the onset of sexual maturity based on histological criteria.

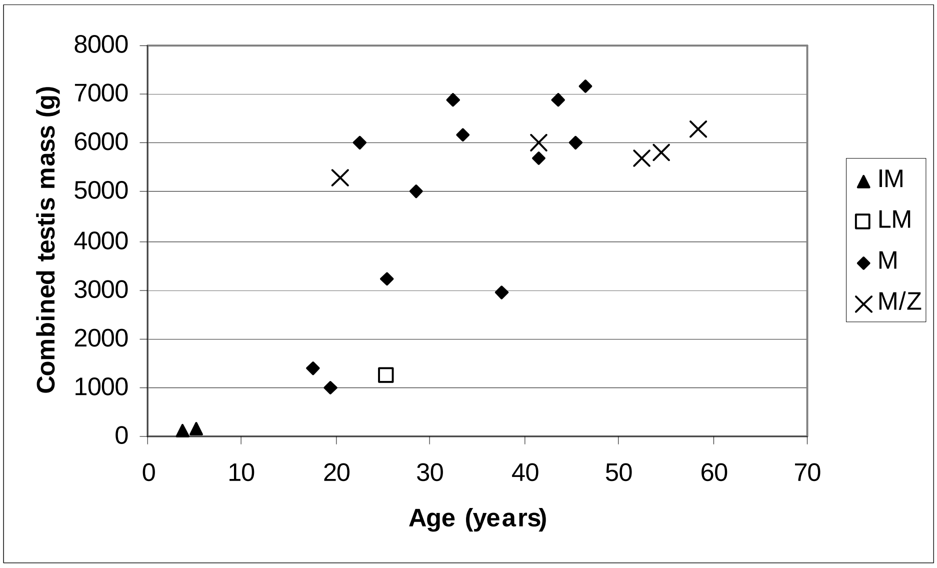

Figure 2.6a: Relationship between age and combined testes mass in South African false killer whales. IM = immature, LM = late maturing, M = mature, M/Z = mature but no sperm.

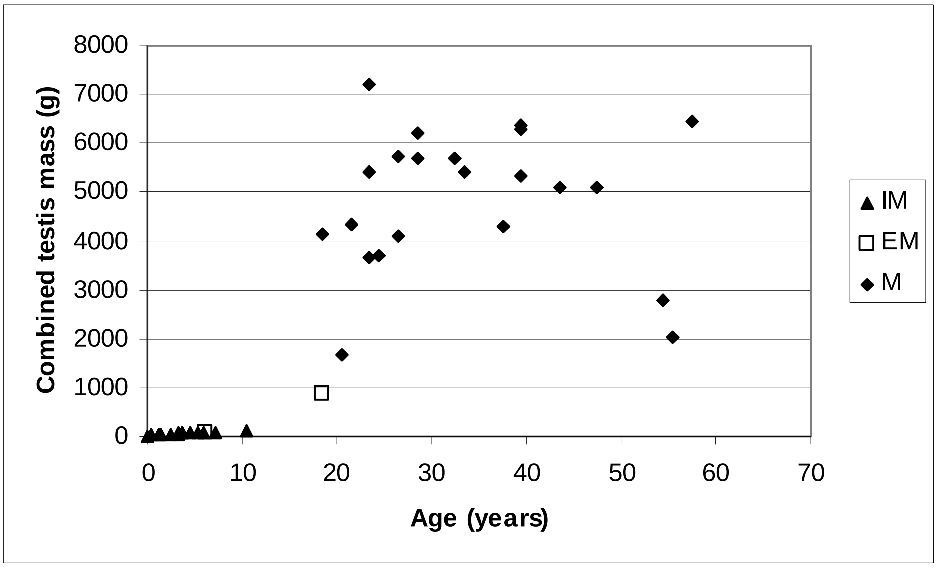

Figure 2.6b: Relationship between age and combined testes mass in Japanese false killer whales. IM = immature, EM = early maturing, M = mature.

There are strong correlations between testis mass and age and body length in both groups of false killer whales (Tables 2.9a and 2.9b). According to plots of testis mass against age and body length, testis mass continues to increase beyond the ages and body lengths at which maturation seems to occur. This increase only levels off at a testis mass of approximately 5000 g, a body length of 430 - 450 cm and an age of 18 - 23 years in the

South African sample (Figures 2.5a and 2.6a), and a testis mass of approximately 4000 g, a body length of 460 - 500 cm and an age of 18 - 23 years in the Japanese sample (Figures 2.5b and 2.6b). Thereafter there is wide variation in testis mass relative to body length and age, with a maximum of approximately 7 kg being recorded in both populations. While there is a strong correlation between combined testis mass and abundance of sperm in the Japanese males (Table 2.9a), there is a poor correlation between the same variables in the South African sample, presumably owing to the 5 mature males without spermatozoa in their tubules (Table 2.9b).

Seminiferous tubule diameter:

Data on seminiferous tubule diameter are available for 19 South African males, but were not recorded for the Japanese whales. Seminiferous tubule diameters ranged from 57.3 - 242.3 µm, and increased from a mean of 62.2 µm among immature males (n = 3) to 213.5 µm among fully mature males (n = 14) (Table 2.7a). The tubule diameters of the two late maturing males fall within the range for that of mature males (Table 2.7b).

The smallest tubule diameter of a mature male, as determined histologically by the amount of tubules recorded with sperm, was 154 µm. However, not all males with a tubule diameter of 154 µm or more were classified as mature. The two South African males classified as late maturing have mean tubule diameters of 159.5 µm and 202 µm. It is possible that these two males, with 80 % and 97 % sperm abundance (Table 2.7b), were actually mature, and that the partially absent/“missing” sperm was the result of post-mortem effects of decomposition to the testicular material before fixation. This possibility is reinforced by the observation that their body length and combined testis mass measurements similarly fall well within the ranges for those of mature males.

From Figure 2.7 it can be seen that there is a sudden increase in seminiferous tubule diameter (to 154 µm), which occurs at a body length of approximately 370 cm. This corresponds to the upper end of the range in body length at which it is estimated that maturity is attained in South African males, and confirms that seminiferous tubule diameter is a reliable indicator of the onset of maturity in false killer whales. Tubule diameter is strongly correlated with body length (Table 2.9b; $r^2 = 0.96637$, $p < 0.0001$), and as with testis mass continues to increase with increasing body length until a length of at least 450 cm (Fig. 2.8). Maximum tubule diameter of 242 µm occurs in a male with a body length of 490 cm.

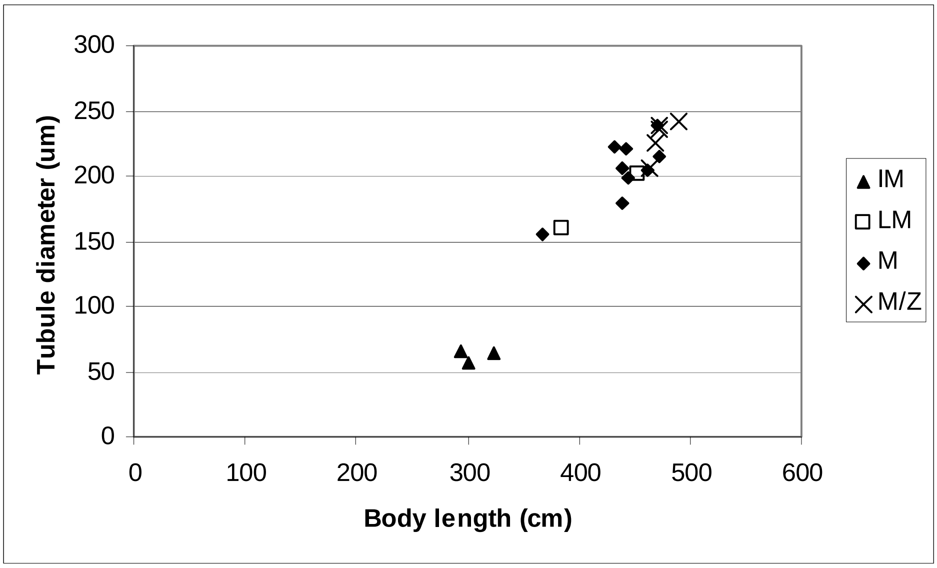

Figure 2.7: Relationship between body length and tubule diameter in South African false killer whales. IM = immature, LM = late maturing, M = mature, M/Z = mature but no sperm.

Combined testes mass in South African males is similarly strongly correlated with tubule diameter (Table 2.9b; $r^2 = 0.89975$, $p < 0.0001$). Figure 2.8 shows the relationship between tubule diameter and combined testes mass for the South African males. Tubule diameter increases dramatically to 150 µm at the combined testis mass of 1000 g which is considered to represent the onset of maturity, and continues to increase until a testis mass of approximately 5000 g, further confirming that tubule diameter is a reliable indicator of sexual maturity in false killer whales.

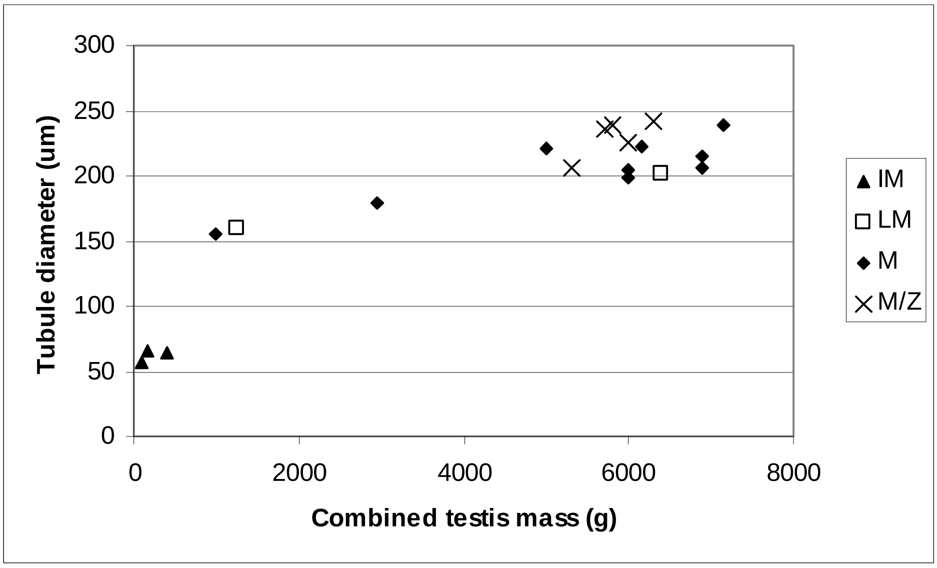

Figure 2.8: Relationship between tubule diameter and combined testes mass in South African false killer whales. IM = immature, LM = late maturing, M = mature, M/Z = mature but no sperm.

Discussion

Female Maturity

According to the results of this study South African female false killer whales attain sexual maturity at a body length of approximately 325 cm (range 320 - 329 cm), which is 30 cm shorter than that of 359 cm estimated for Japanese females (range 338 - 392 cm). Age at the onset of sexual maturity is estimated to be between 9.25 - 10.5 years for the South African females, and between 8.25 - 10.5 years (50 % maturity at 9.2 years) for the Japanese females.

The figures reported above compare favourably with published estimates of age and body length at maturation for female false killer whales. Kitchener *et al*. (1990), in a previous study of the same 1981 St Helena Bay stranding, reported the smallest size for a sexual mature female to be 334 cm. Reporting on a larger data set of female Japanese false killer whales taken at Iki Island, Kasuya (1986) estimated the body length at which 50 % of the females were sexually mature to be approximately 350 cm, and (based on the age of the youngest mature and oldest immature females), age at sexual maturity was suggested to occur between 8 - 11 years. Tomilin (1957) and Purves and Pilleri (1978) reporting on the 1927 Dornoch Firth stranding, Scotland, and Fraser (1936) reporting on the 1935 Donna Nook, England, stranding, suggested sexual maturity in females, based on the presence or absence of corpora lutea and/or foetus among a small group of females, is reached when the animals are from 366 - 427 cm in length, which corresponds to an age of 8 -14 years on the age-length plots of Purves and Pilleri (1978). Although the latter authors used a different age-determination technique, which likely underestimated the age of older individuals, was used by the latter authors, the ages at sexual maturity should not have been affected. The gross breeding condition of female false killers from a mass stranding at Black River Beach, Tasmania, in 1974, was assessed and the smallest female reported to have been “post partum” measured 349 cm (Scott and Green 1975). The smallest pregnant female reported by them was 360 cm. Reviewed collectively, there is some indication that the Southern Hemisphere populations mature at a smaller body length, but this aspect would need to be investigated more extensively before any definitive conclusions can be drawn.

Male Maturity

The observations on male maturity are more difficult to interpret due to the scarcity of maturing males in both samples. Male false killer whales between 5.25 and 17.5 years of age are absent from the South African group, and between 10.5 and 18.5 years from the Japanese group, corresponding to body lengths of between 323 - 367 cm and 391 - 432 cm, respectively. The almost total absence of maturing males and the resulting large gap between immature and mature males is presumably due to the emigration of adolescent males from their maternal group which is discussed in detail in Chapter 3.

Both Kitchener *et al*. (1990) and Kasuya (1986) reported a similar absence of male false killer whales in the body length range of 320 - 370 cm, and between the ages of 10 - 18 years, respectively. No late maturing males were present in the latter study. Kitchener *et al*. (1990) initially suggested male maturity occurs somewhere in this body length range, but later stated that the range over which the males matured was between 370 and 430 cm, and these latter values have since been cited (Stacey *et al*. 1994), causing some ambiguity. The two different ‘options’ apparently result from confusion in terminology, the lower length range indicating the size at which a combined testis weight of 1000 g was achieved, and the higher range a period in which the testes (although heavier than 1000 g) continued to increase in mass with increasing body size.

Sexual maturity in male false killer whales from the 1927 Dornoch Firth stranding was estimated to occur at 8 - 14 years of age, and at a body length of 396 - 457 cm (Purves and Pilleri 1978). Based on the length at which 50 % of the males were sexually mature, Kasuya (1986) estimated body length at sexual maturity in males off the coast of Japan to occur between 430 and 440 cm. The smallest histologically-mature male measured approximately 440 cm. Both the ages of the youngest mature male and of 50 % maturation were reported as 18.5 years (Kasuya 1986), which is several years later than the age at sexual maturity suggested by Purves and Pilleri (1978).

Puberty and Sexual Maturity

The use of a relative measure of sperm abundance and the inclusion of a third, or even fourth, class of "maturing" males (Best 1969, Perrin *et al*. 1976, Perrin *et al*. 1977, Kasuya and Marsh 1984) has enabled researchers to identify different stages of maturity. Definitions for maturity are frequently inconsistent across the studies. According to Perrin *et al*. (1976), onset of puberty is indicated by rapid increase in tubule diameter and in testes mass, and sexual maturity is attained several layers later, with the mid-point between the two representing the average age at attainment of sexual maturity. Best (1969, 1970) defines puberty as the stage at which 50 % of the population is either mature or maturing, i.e. producing some sperm, and the remaining 50 % is immature. According to Best (1969), there is a rapid increase in testis size at this stage which he says is analogous to the "length at sexual maturity" (p. 7) as calculated by the majority of authors who have not recognised a maturing class. The body length and age at which immature and mature whales are found in equal proportions should correspond to those at which the maturing whales are most abundant, and represents the attainment of sexual maturity (Best 1969), which is associated with a further increase in testis size. The shortage of maturing males in both populations of false killer whales in this study and the absence of males in what appears to be a critical range did not allow puberty and sexual maturity to be determined using this approach.

In their study of short-finned pilot whales, Kasuya and Marsh (1984), using the same maturity criteria employed in this study, recorded a sudden increase in seminiferous tubule diameter and testis-weight at a stage corresponding to what they called “functional maturity” (p. 307), analogous to puberty as defined by Perrin et al (1976). According to Kasuya and Marsh (1984), males in this stage are capable of reproducing, but are not necessarily participating in reproduction. As body weight and testis weight continued to increase beyond age of functional maturity, they considered male short-finned pilot whales do not mate successfully until several years after functional maturity is reached, which corresponds to social maturity in the sense of Best (1969). Males in the puberty stage (histological early maturing stage) were considered unlikely to have any reproductive ability (Kasuya and Marsh 1984).

Presumably the onset of puberty in the sense of Kasuya and Marsh (1984) in the false killer whales in the present study occurs during the body length and age range of absent males, and takes place over several years, so that by the time the whales reach approximately 18 years they are capable of reproducing. This corresponds to the state of “functional maturity” employed by Kasuya and Marsh (1984). Thus the initial body length range of 320 - 370 cm, proposed by Kitchener *et al*. (1990) to represent sexual maturity, may actually reflect the predicted onset of puberty, with the first fully mature male (as determined in their study by a combined testis mass criterion of 1000 g) occurring at a body length of 370 cm.

The rapid increase in testis mass at 1000 g, and tubule diameter (at 154 µm) at a body length of 370 cm among the South African false killer whales in this study, and at a testis mass of 1680 g and body length of approximately 445 cm in the Japanese males, is taken to represent the stage of functional maturity, and occurs at 17.5 and 18 years of age, respectively. A study, reporting on false killer whales from Japan, has indicated that the minimum weight of mature testis, estimated as half of the combined testis weight, is approximately 1700 g (Kasuya and Izumisawa, 1981, in Perrin and Reilly 1984), which is close to the value reported for the Japanese males above. According to Fraser (1936), in the false killer whales stranded at Donna Nook, Scotland, the increase in testis size at the onset of sexual maturity occurred between body lengths of 366 cm and 511 cm.

Testis mass and tubule diameter continue to increase beyond the estimated onset of functional maturity. Testis mass continues to increase until approximately 5000 g, at body lengths of between 430 - 450 cm, and between 18 - 23 years of age, in the South African sample. Testis mass similarly increases until an age of between 18 - 23 years, to a testis mass of 4000 g until body lengths of between 460 - 500 cm in the Japanese sample. The continued growth of the testes beyond the stage of functional maturity suggests males do not engage in successful reproduction until social maturity is reached several years later. Such a delay in reproduction may relate to increased fitness of larger males and possible sperm competition. Behavioural observations and studies of social structure in false killer whales are required before the question of social maturity in the sense of Best (1969) can be addressed. Kasuya and Marsh (1984) and Best (1969) reported that social maturity is equivalent to sexual and histological maturity in short-finned pilot whales and sperm whales, respectively, but behavioural studies are required to confirm if this is also the case in false killer whales.

Possible explanations for the absence of sperm in otherwise mature males

Reproductive status in males was originally determined using the presence and abundance of spermatozoa. Despite the lack of evidence of spermatogenesis in 5 South African specimens, the relative abundance of the different testicular tissues (the proportion of interstitium) strongly suggests the individuals were sexually mature. This observation is reinforced by their testis mass and the diameters of their seminiferous tubules. A number of possible explanations exist for the observed absence of sperm in otherwise mature South African males.

Sperm production and abundance may be seasonally related if there is a male sexual cycle. It has been reported for certain cetacean species that males may enter a resting phase, during which testis size decreases and sperm are absent from the epididymis (see Perrin and Reilly 1984). Alternatively, the absence of sperm in some adult males may be due to post-mortem changes to the testicular material as a result of delays in sample collection. Similar states of decomposition to those reported in this study and the resulting difficulty in accurately recording data and interpreting breeding condition have been described elsewhere (Smithers 1938, Clarke 1956, Best 1969). The lack of seasonal coverage of the data offers limited comment on the occurrence of a male reproductive cycle. However, it seems unlikely that the tubule diameters of the false killer whales sampled would not decrease in parallel with the reduction in testis mass. The absence of adult individuals without sperm in the Japanese sample, where there was no post-mortem delay, rather provides stronger evidence at present for the absence of sperm among the South African males being due to autolysis in the post-mortem material.

Given that the absence of sperm in otherwise adult males may be the result of autolysis, this suggests that sperm abundance may not always be a reliable indication of maturity status. It has already been mentioned that, given the characteristics of the two late maturing males, and that the testicular material of the South African false killer whales appears to have been subjected to post-mortem changes, the two late maturing males may actually be mature. Tubule diameter and testis mass, shown in this study to be potential indicators of male maturity, may both be more reliable measures in these circumstances than sperm abundance. However, tubule diameter and testis size may also be subject to seasonal variation, in the event of a male sexual cycle. Clarke (1956) found a correlation between tubule diameter and body length among immature but not mature sperm whales off the Açores, which he claimed is to be expected if a male sexual cycle exists, and provides some evidence of seasonality in tubule diameter in the form of a consistent decline in the diameter from a high range of values in June to a low range in September. Best (1969), on the other hand, reported a correlation between tubule diameter and body length in maturing, but not immature or mature sperm whales off Donkergat, South Africa, and concluded that there is no seasonal cycle of tubule enlargement. The lack of seasonal coverage in this present study affords no comment on changes in tubule diameter associated with a male sexual cycle, and precludes an adequate investigation of a seasonal cycle. In theory, if a male sexual cycle occurs it would be associated with a corresponding cycle in females. The latter occurrence is discussed in more detail in Chapter 4.

In general, and despite the shortage of maturing males and the large gap between immature and mature males, the different indices of sexual maturity appear to confirm previous suggestions that South African false killer whales become mature at smaller body lengths than the Japanese whales. Both combined testes mass and tubule diameter are potentially good indicators of reproductive condition in males. This may be of value in studies where other data are incomplete or not available, and particularly if a seasonal cycle in sperm abundance is shown to exist in false killer whales.

Body length at sex maturity as a % of adult body length

Despite the limitations in the data, particularly the scarcity of males around the apparent age and size at puberty, the results suggest males in both populations defer reproduction while growing to a larger size, providing further evidence that a large size is important, presumably in intra-male competition. In addition to size dimorphism, other differences in morphology between the sexes exist - external appearance of the head (Mead 1975, in Stacey *et al*. 1994), and various skull and dentary measurements (Kitchener *et al*. 1990), suggesting that the mating system in false killer whales may be polygynous.

Based on the results reported, it appears the South African false killer whales mature at a shorter body length than the Japanese whales. This is presumably linked to the smaller adult body size of the South African specimens. In general, body length at sexual maturity in female cetaceans corresponds to 85.1 % of the body length when growth ceases (Laws 1956). A similar rule applies to males, although maturity is typically attained at a later age (Laws 1956). The percentage body length at sexual maturity among males, however, is not so constant, owing to the great variation in growth rates, particularly among polygynous and sexually dimorphic species which typically have a double sigmoid curve, and in which age and size at social maturity may be much higher than that for physiological maturity. The body length at sexual maturity based on the results of the logistic regression, as a percent of asymptotic length (estimated by the 2-parameter Gompertz equation) is 84.4 % for the South African females, and 83.7 % for the Japanese females. These values are in good agreement with Laws' rule.

Age or body length as a better predictor of onset of sexual maturity

The onset of sexual maturity among mammals is generally size- and not age-dependent, and relates to nutritional status, as reflected in body condition. However, growth rate is presumably fixed by heredity, and any animal has an inherent genetically determined growth potential. This forces a minimum age at which those sizes can be reached even under optimal conditions. Under improved nutritional conditions, growth rate is accelerated and optimal body length and therefore attainment of sexual maturity reached at a younger age. It is thus possibly not useful to separate the effects of age and size in the attainment of sexual maturity, as they appear to work in combination with one another, but generally in cetaceans (as in other mammals) puberty is more closely related to size than age.

Body length at birth

Based on the body length at which proportion of foetuses equals proportion of neonates, Kasuya (1986) estimated body length at birth in his analysis of false killer whales off the coast of Japan to be 175 cm, which is consistent with the estimates for the Japanese false killer whales presented above. Compared to a body length of 155 cm at birth for South African false killer whales (Best 2007), this represents a proportional difference in body length (1.13) similar to that for females at sexual maturity in the two samples (1.13), i.e. the body length at birth of 155 cm for South African false killer whales is comparatively smaller, by the same degree (11.5 %), as that for females at sexual maturity in the two samples (11.2 %). The South African female false killer whales are also smaller as adults by 10.6 % and have a smaller asymptotic length by 10.3 %. According to Hinton's unpublished data reported on by Purves and Pilleri (1978), length at birth for the 1927 stranding of false killer whales at Dornoch Firth, is approximately 193 cm. Purves and Pilleri (1978) re-evaluated Hinton's data and report slightly adjusted values for length at birth of about 173 cm - 183 cm. Evans (1987) reported similar differences in body length at birth between false killer whales in the northern hemisphere (193 cm), and the southern hemisphere (160 cm), but the approach used for estimating body length at birth was not disclosed. Both estimates of size at birth presented above are consistent with the predictions of an equation describing the relationship between body length at birth and adult female size (McLaren 1993).

Growth models

Instability (the lack of convergence) and problems with fitting growth models to young animals appear to be general features of most cetacean growth models (Stevick 1999). According to Zullinger *et al*. 1984, for example, the Von Bertalanffy equation underestimates neonatal mass, and overestimates early growth and adult mass; the logistic equation overestimates neonatal mass and underestimates adult mass; while the Gompertz overestimates neonatal mass, and underestimates early growth and adult mass. Winship et al (2001) working on Steller sea lions, discuss how the length-at-age models fail to accurately predict birth length, the birth length in females being underestimated and thus the average growth rate in the first year being overestimated, while the reverse holds true for males. Stevick (1999) tentatively attributed the difficulty of fitting a single growth curve to data from both young and old humpback whales to the lack of convergence in young and to the Von Bertalanffy model not being a good predictor of early growth.

For similar reasons a single growth rate model may not be realistic for false killer whales. Just about any model can fit the long asymptote characteristic of such odontocetes, with the possibility that the r^2 values may be misleadingly high. The real question is whether a model is realistic over the period where most growth occurs. According to Harrison (1969), cetacean growth is quite rapid during the first few weeks of life and throughout the first year. Kasuya (1972, 1976 cited in Kasuya and Matsui 1984) showed that an increase in body length in the first year after birth is between 55 % and 65 % of neonatal length in several species of odontocetes, and concluded that “under these circumstances, calculation of mean growth rate over this entire period is not meaningful” (p. 78). The growth models fitted to the data in this study, and the consequent values estimated for body length at birth, are likely to be strongly influenced by the substantially higher number of specimens in the higher ages, with the result that the growth rates in the lower ages and the predicted body length at birth are likely to be underestimated and overestimated, respectively.

The common difficulty of describing early growth and fitting a single model to the entire range of age data has led some researchers to conclude growth is too complex to be represented by a continuous model, and to suggest using two growth curves. Stevick (1999) fitted separate Von Bertalanffy models to young and old humpback whales, when an attempt to fit a continuous model resulted in a poor fit, which he attributed to the existence of a staged or dynamic growth pattern in this species. McLaren (1993) has similarly stated that no single equation adequately describes growth in pinnipeds over the entire life span, and used two consecutive growth curves. Perrin *et al*. (1976; 1977) fitted separate 2-phase Laird-Gompertz models to their data based on the assumption that growth is discontinuous in spotted and spinner dolphins, respectively. The very small number of neonatal and juvenile false killer whales sampled below 10 years of age did not justify fitting separate curves to young and old individuals, although the evidence suggests that this would be a more appropriate procedure when the sample under investigation adequately covers the entire age spectrum.

Geographic variation in body size

Geographic variation in body size but not in relative sexual size dimorphism was found to occur. The Japanese specimens are significantly larger than the South African specimens in both sexes. Whether size comparisons are based on size at birth, asymptotic lengths as given by the growth curves (as McLaren 1993) argued they should be), on mean body lengths, as given by Analysis of Covariance, on mean adult body length, or on sizes at sexual maturity, male and females false killer whales from the SA population are smaller than those from the Japanese group by a factor of 0.89 – 0.91.

Whereas growth in body length is asymptotic for the South African and Japanese false killer whales, increasing linearly from birth, gradually declining and eventually ceasing, body lengths-at-age previously published for a group of false killer whales stranded at Dornoch Firth, Scotland, 1927, failed to reach an asymptote (Purves and Pilleri 1978). Body lengths of the oldest Scottish specimens, approximately between 18 and 23 years of age, are comparable to those of the oldest Japanese and South African specimens, approximately 55 to 65 years old. Given that different ageing techniques were used on this population - the usual decalcification and staining techniques were not used, and only dentine layers were counted using a low power lens and reflected light (Purves and Pilleri 1978) - it seems reasonable to conclude that their ages were underestimated, particularly in older animals where age is more difficult to determine accurately from dentinal layers only. Age data from the Scottish population are thus of limited comparative value, but the oldest Scottish animals (18 - 23 GLGs) averaged 539 cm and 457 cm in length in males and females respectively. This indicates they were considerably larger than the South African false killer whales, and closer in body size to the Japanese whales.

Body length in false killer whales has previously been reported as follows: Leatherwood and Reeves (1983, in Odell and McClune 1999) reported a maximum body length in males of 610 cm, while a maximum body length of 506 cm in a female from an unspecified location, has been recorded (Perrin and Reilly 1984). The largest male at the mass stranding at the Berg River mouth, South Africa, measured 536 cm, and the largest female measured 450 cm (Smithers 1938). The author also reports that males measuring over 579 cm in length were present in two previous strandings at Kommetjie (1928) and Mamre (1935), in South Africa. In Northern Tasmania (Scott and Green 1975), the largest male measured 533 cm, while the largest body length recorded for females was 409 cm; mean body length for these whales was 414 cm for males, and 355 cm for females, as reported by Odell and McClune (1999). In Florida, the mean length of female false killer whales 416 cm, and the maximum was reported as 494 cm; the mean body length of males was 458 cm, and the maximum body length recorded was 534 cm. A male measuring 589 cm in body length was recorded at Kinkell, near St Andrews, Scotland (Fraser 1936). Maximum recorded body length was 475 cm for females, and 569 cm for males stranded in the Tay Estuary, near Carnoustie, Scotland (Peacock *et al.* 1936).

Geographic variation in life histories and organismal traits has been the subject of much research, and led to the formulation of several ecogeographic rules or patterns. Of these, probably the best known is Bergmann's rule, which originally stated that within a genus of endothermic vertebrates, the larger species occur in cooler environments (Bergmann 1847; translated in James 1970). In addition to the debate over whether Bergmann's rule is actually valid, the actual mechanism(s) responsible for this pattern has generated considerable debate. The original explanation that larger size is favoured in colder environments because it provides a relative decrease in surface area to volume ratio, which results in a lower thermoregulatory cost per unit mass, has largely been discredited (Ralls and Harvey 1985). However, there remains little agreement over the exact mechanism responsible (McNab 1971, Lindstedt and Boyce 1985, Ashton *et al*. 2000, Freckleton *et al*. 2003). Assuming variation in body size is genetically based and an evolved response (and not merely a physiological one), the observed differences between the South African and the Japanese samples could be the result of any one, or a combination, of several selective forces to which the populations are and/or have been exposed in their respective environments. The larger adult body size of the Japanese and Scottish false killer whales could, for example, be due to a faster growth rate, which in turn could reflect improved quality of food and resources.

Alternatively, the reduced surface area to volume ratio and proportionately lower metabolic rate of the larger Japanese and Scottish animals may confer a thermoregulatory advantage in their colder (also typically more seasonal) environments. It has been argued, however, that increasing fur density (and, by logical extension, blubber) should be more effective in conserving heat than increasing body size (Stetudel *et al*. 1994, in Freckleton *et al*. 2003). Strong correlations between geographic variation in body size and seasonality have been shown to occur in mammals (Boyce 1978), including cetaceans whose adult body size was found to be inversely correlated with the length of the feeding season and directly correlated with prey availability during that period (Brodie 1975). Larger bodied individuals, with proportionally more energy-yielding adipose tissue, and, in the case of whales, an optimal surface area for deposition of a portable lipid cache, might be better able to tolerate periods of food shortage (Boyce 1978, Boyce 1979, Lindstedt and Boyce 1985). These effects might be further reinforced by a reduction in competition and an increase in resources in more temperate and seasonal climates due to high over-wintering mortality, which may further promote growth. This latter influence would be a physiological response to environmental conditions, and not constitute an evolutionarily selected response.

However, McNab (1971) challenged the use of weight-specific expressions, stating that "an animal does not live on a per-gram basis" (p. 846), and that an increase in body size would result in an absolute increase in the cost of thermoregulation. Following on from the logic of this argument, one could expect small body sizes to evolve in response to low temperatures, or food shortages, as smaller animals have a lower total metabolic rate. Alternatively, there may be selection for smaller size in hot environments to avoid internal heat loading (Brown and Lee 1969, in Lindstedt and Boyce 1985, James 1970, McNab 1979). Thus, the mechanism at play may still be thermoregulatory, but occur in the opposite direction. Perhaps there are two entirely separate forces acting on body length in the South African and Japanese populations. With their history of being exploited, one might expect the Japanese specimens to be larger as a result of the smaller ones being easier to drive ashore, and that over generations, selection would have resulted in a larger body size. However, there is no obvious evidence that smaller whales are in fact easier to drive ashore, in addition to which the Japanese populations may not have been exploited for long enough to result in such an effect. Furthermore, social cohesion would likely cause the school to remain together. Finally, the stranded Dornoch Firth specimens are even large and there have been no drive fisheries in Scotland.

Sexual size dimorphism

Based on asymptotic lengths from growth curves or mean adult body lengths, females are smaller than males by a factor of 0.83 - 0.84 in both samples, despite the overall difference in body length between false killer whales off Japan and South Africa. Although there is a smaller absolute size difference between males and females in the South African sample, the proportional degree of dimorphism between the South African males and females appears to be the same as between the Japanese males and females, i.e. there is no geographic variation in relative sexual size dimorphism.

Without accurate ageing techniques and explicit information relating to the parameters given (i.e. average body length of adults or maximum recorded body lengths, etc), published statements on size differences between male and false killer whales in other populations offer limited comparative value. Nevertheless, and without being able to quantify the degree of size dimorphism between the sexes, male false killer whales in other populations have been shown to be larger than females. According to the growth curves presented by Purves and Pilleri (1978), after the age of 2 years, the growth rate is similar in both sexes, but males are approximately a foot (30.48 cm) longer than females at every age, and therefore attain larger maximum body lengths than females. Reporting on the November – December 1935 series of strandings off the coast of Scotland, Peacock *et al*. (1936) stated that based on a "comparison of the mean of the two largest groups" (p. 98) males are larger by about 3 feet (approximately 91 cm). Caldwell *et al*. (1970) reported a similar average difference of 2 to 3 feet among male and female false killer whales stranded along the southeastern coast of Florida in 1970; while male and female false killer whales stranded on Loggerhead Key, Dry Tortugas, differed in mean length by approximately 40 cm. According to Smithers (1938), males were "on the whole" (p. 28) only about 45 to 60 cm larger than females in the 1936 Berg River mouth stranding.

It is common among mammals for males to delay sexual maturation, and concentrate on somatic growth, particularly if a large body size enhances mating success. There are two main hypotheses proposed to account for this sexual dimorphism. The first suggests that sexual size dimorphism serves to bring about resource partitioning, and thus to reduce intersexual competition for food, while the second argues that in polygynous species, intrasexual competition between males for access to and matings with females will select for large size in males relative to females. Ralls and Harvey (1985) have taken this further and suggested that sexual selection is possibly not the only force in operation, and that selection for small body size in females may also contribute. Post *el al*. 1999 argue that in red deer, and other polygynous mammals the differential response of the sexes, as a result of dichotomous selection regimes acting on the two sexes, to environmental variation underlies sexual dimorphism. Feeding niche differences and sexual segregation, where males and females live separately outside of the breeding season, have been documented in many polygynous and sexually dimorphic species of mammals (see Ralls and Harvey 1985), including cetaceans (see Chapter 3). The observed sexual size dimorphism is thus likely to be the result of a polygynous mating system and sexual selection reflecting the differential investment in growth and reproduction between male and female false killer whales. Furthermore, the continued growth in testes mass and tubule diameter beyond the age and body length where sexual maturity is estimated to occur may relate to the increased fitness of larger males.

Several researchers have argued that this sexual size dimorphism is brought about by a secondary growth spurt among adolescent males. The idea of a secondary growth spurt in whales was suggested as far back as 1962 by Sergeant, working on long-finned pilot whales, and again in 1970 by Best in a paper on sperm whales. However, the evidence given by Best is somewhat problematic, given that the inflection point on the graph of age against body length was drawn freehand and not mathematically generated. Christensen (1984) demonstrated an increase in growth rate in adolescent male killer whales, on a plot of body length against age similarly fitted by eye. Both studies are based on cross-sectional data, which makes it more difficult to detect a growth spurt, even if one does exist. McLaren (1993) modelled what he refers to as a growth spurt in pinnipeds using two consecutive age-body length models, without actually providing evidence of its occurrence. Perrin *et al*. (1976) for spotted porpoises, and Perrin *et al*. (1977) for spinner dolphins fitted a 2 - phase version of the Laird growth model to their data in which separate equations were simultaneously and repeatedly fitted to the upper and lower range of means, with the convergence of the curves reflecting the secondary growth spurt, as represented by an inflection point on the age-body length graphs. Winship *et al*. (2001) on Steller sea lions, similarly state a growth spurt in mass occurs based on their observed break down/change in the allometric relationship between body length and mass at puberty, which corresponds to the age at which a rapid increase in other physiological indices of maturity occurs.

However, the observed sexual size dimorphism need not result from a secondary growth spurt in males, but could be due to different growth rates between males and females, female growth slowing down at sexual maturity relative to that of males, or to a larger birth size in males. Very little information about differences in body size and mass at birth between males and females cetaceans exists, and where values have been reported it is normally combined for males and females. The observed size dimorphism in false killer whales could alternatively result from males continuing to grow beyond the point at which female growth stops, and reflect a differential investment in reproduction between males and females. For example, Duffield and Miller (1988) suggest the larger body size of male killer whales is due a longer period of growth in males, relative to females. Clarke (1956) on sperm whales of the Açores states that males and females mature at the same length, and, assuming that they mature at the same age, then the great difference in adult size between the sexes must develop after maturity is attained, “when the physiological demands of the female’s protracted breeding cycle are likely to slow down her growth relative to that of the male” (p. 277).

The various explanations for these differences in body size, between populations and even sexes, need not be mutually exclusive. Many selective pressures affect size and the observed variations in body length are likely to be the result of a combination of selective forces. The present dataset does not allow for any conclusive arguments on this subject to be made for false killer whales. Future research may reveal that rather than being attributable to a single factor, differences in body size may be due to a combination of multiple forces, which include both a genetic and an environmental or geographical component.

Conclusion

The findings reported in this study indicate that the South African false killer whales are smaller than the Japanese whales. Females in both populations appear to attain sexual maturity at approximately the same age, but the South African females do so at a smaller body length. The paucity of maturing males in both groups (presumably owing to their dispersal), makes estimating age and size at sexual maturity in these male false killer whales difficult. It appears that males become sexually mature several years later than females in both populations, and the South African males similarly mature at a relatively smaller body length than the males from Japan. Despite some differences from previously published results that were probably due to different ageing techniques, methods of analysis and/or interpretation, the findings of this study confirm previous suggestions that false killer whales in the Southern Hemisphere are generally smaller and become sexually mature at a shorter body length than those in the Northern Hemisphere. These differences are likely to be the result of different environmental and selective forces operating in the respective regions. Larger samples are required before the taxonomic implications, if any, and the significance/ distinctness of these North-South differences can be properly evaluated.

CHAPTER 3

A comparison of group size and composition between stranded and non-stranded false killer whales, *Pseudorca crassidens*

Introduction

Although the subject of much speculation, the reasons behind mass strandings of cetaceans remain unclear. Among those species known to commonly strand are false killer whales, pilot whales, killer whales, sperm whales and common dolphins. Various explanations have been advanced for this phenomenon, *inter alia*, anomalies in the earth's magnetic field, by which the whales are thought to navigate (Klinowska 1986); the topography of the ocean floor – a gradually shelving sea floor may interfere with echolocation; and large fluctuations in water level which may result in whales becoming unwittingly entrapped in unfamiliar waters (Best 1989), perhaps while feeding inshore. In addition, it has been suggested that one whale, perhaps a focal individual, may become hurt or debilitated, and possibly as a result of social cohesion the other group members may remain with and eventually follow the injured animal ashore (Best 1989). At a population level, Sergeant (1982) attributed the mass stranding phenomenon to a density-dependent population response and the build up of high density herds in coastal waters when the population is abundant.

A previous comparison between stranded North West Atlantic long-finned pilot whales (*Globicephala melaena*) and those driven ashore did not reveal differences in their length-specific blubber thickness (Sergeant 1982). However, to date no studies have considered differences in group size and composition between stranded and non-stranded populations of cetacean species which frequently strand en masse that may contribute to or account for mass strandings. Among the species of odontocetes reported to strand en masse, the frequency of these strandings is highest among those exhibiting higher sociality (Sergeant 1982).

This chapter compares group composition and size between stranded and non-stranded false killer whales (*Pseudorca crassidens*), and specifically looks for evidence of differences between the two which may account for and help explain the mass stranding phenomenon in these whales. Differences in sex ratios, maturity status, age profile, and in particular, the possibility that a particular age or female reproductive class is absent from the stranded population, are investigated. The majority of the comparison is between a group of false killer whales that mass stranded in 1981 at St Helena Bay, off the coast of South Africa, and several shore-driven groups of false killer whales, taken at Iki Island, Japan, in 1979 and 1980. However, the group size comparison draws on data of mass strandings of *P. crassidens* extracted from the literature.

Materials and Methods

Data Source

The stranded material examined in this study was collected from a single mass stranding that occurred on the South African Cape west coast on 19 August 1981. Of the 65 false killer whales involved in the stranding, 56 were found over a 1500 m stretch of beach along St Helena Bay. Four specimens were found along 15 km of coast to the west, three specimens were found 10 km to the east, and two outlying, but presumably related, single specimens were reported 77 and 44 km north of the main group, from Lambert’s Bay and Eland’s Bay, respectively. Scientists reached the main site two days after the stranding occurred. The exact timing of the two single standings is unknown. Due to delays in the onset of sample collecting and fixation, the material examined was not completely fresh, and the quantity and quality of information recorded per individual is varied. Data are available for 63 individuals (41 females and 22 males).

The stranded data were compared with data on false killer whales derived from several drive fisheries taken at Katsumoto, near Iki Island, off the south west coast of Japan. The false killer whales were caught simultaneously with bottlenose dolphins, *Tursiops truncatus*, during February and March of 1979 and 1980 (Table 3.1). The date of capture of the shore-driven false killer whales did not always correspond to the date of death, as groups were kept alive in a netted bay until sampling. In each case, as many false killer whales as possible were randomly examined. Data are available for 156 specimens (96 females and 60 males) from 6 shore drives. For consistency the 6 groups are referred to as discrete schools, although it is possible that they actually represent short-term aggregations of these schools, or mixed groupings of individuals from various schools herded together during the drive. The possible significance of the unit groupings are discussed in more detail later. Data was initially examined separately for the 6 schools, and then merged to increase sample size, following Kasuya's (1986) investigation of the same Japanese drive fisheries using a larger data set. Even if differences in composition exist between the schools, these may not have been detectable owing to the small number of specimens in each school. In addition to differences between the schools, it is also possible that there may be biases common to most or all of the schools. These are discussed in the relevant sections. It has been assumed that Japanese school structure remained unchanged during the 2 year sampling period.

Of the 63 South African specimens examined, age and reproductive data are both available for 58 (92 %) whales. Age data are available for 128 (82 %), and reproductive status known for 140 (90 %) of the 156 Japanese specimens examined.

Table 3.1: Date of capture and number of false killer whales caught and studied at Iki Island, Japan.

School	Date of shore-drive	Date of sampling	No. caught	No. studied	No. studied Females	Males
1	1979 – 03 – 08	03 – 10	20	5	4	1
2	1979 – 03 – 15	03 – 17, 18	138	35	20	15
3	1979 – 03 – 19	03 – 20, 21	160	28	16	12
4	1980 – 02 – 22	02 – 22 to 27, 03 – 18	10	6	2	4
5	1980 – 02 – 27	02 – 28 to 03 – 04	80	56	38	18
6	1980 – 03 – 06	03 – 7 to 9	155	26	16	10

Data collection and sampling procedures were similar in Japan and South Africa. Differences in protocol are noted in Chapter 2 of this thesis. Data were collected on site

at Iki Island by Kasuya, and in St Helena Bay by Best, each with a team of volunteers respectively. Each whale was assigned an individual school and reference number.
The sex of each specimen was recorded. One to three adjacent teeth were removed with a hammer and chisel from the centre of the lower jaw of each specimen, and fixed. Age determination was done by Kasuya by counting the annual growth layers in dentine and cementum in longitudinal, haematoxylin-stained sections of the decalcified teeth, as outlined in Chapter 2. An annual dentinal and cemental growth layer deposition was assumed and age expressed as the number of growth layer groups (GLGs). Reproductive condition of males and females was determined as detailed in Chapter 2. As body length is unlikely to be a contributing factor in false killer whale strandings, differences in body length between the two data samples are not included in this chapter, but are discussed in Chapter 2 with respect to geographical location.

Statistical analyses:

Group size: Additional data on group size of stranded and sighted populations of false killer whales were extracted from the literature, and compared with the number of stranded South African false killer whales in the present study using a Mann-Whitney test.

Age frequency distribution: Age frequency distributions of the stranded and shore-driven schools were compared by combining ages into categories, using a Kolmogorov-Smirnov test. The test measures the difference between the two distributions and tests specifically for a difference in the numbers within each category.

Sex ratio, Maturity status and Reproductive class: Sex ratios and differences in the proportions of the maturity status, and of the various reproductive classes were compared using Chi-squared analyses or Fisher's Exact Test where the sample size was small.

Results

a) School size

Table 3.2 summarizes the group size of various schools of stranded false killer whales, taken from the literature, and includes the 65 whales stranded in 1981 at St Helena Bay. Group size for the 29 stranded schools of false killer whales listed ranges from 4 – 835, with an average of 104.7 (sd = 155; mode = 30; median 54).

Table 3.2: Records of mass strandings of *Pseudorca crassidens* taken from the literature.

Source	N	Locality & Date	Reference	Notes
Stranding	4	Gansbaai, SA, 1958	Best 2007	
Stranding	4	Berg River Mouth, St Helena Bay, SA, 1973	Best 2007	
Stranding	5	Elizabeth Bay, Namibia, 1982	Best 2007	
Stranding	19	Florida Keys, Florida, 1972	Odell *et al*. 1980	-
Stranding	21	Glamorgan, SE Wales, 1934	Fraser 1936	“contemporaneous reports of individual animals, evidently stranglers, near the place where the main body stranded”p.106
Stranding	26	Colorado River Delta, Mexico	Liebig *et al*. 2007	“26 skulls found”, which provide “best estimate of the min. number of individuals”p.384
Stranding	30	Loggerhead Key, Dry Tortugas, Florida, 1976	Odell *et al*. 1980; Porter 1977	“Herd was divided in 2 groups at time of stranding”p.172
Stranding	30	Bay of Kiel, NW Germany, 1861	Reinhardt 1862 (in Kitchener *et al*. 1990)	Purves&Pilleri (1978) describe how the whales arrived in the Bay & were attacked & driven into the Harbour by fishermen, p.70
Stranding	30	Dundee, Scotland, 1927	Tomilin 1957	
Stranding	34	Near Albany, SW Australia, 1964	Mell 1988 (in Leatherwood *et al*. 1991)	
Stranding	40	Near Roebourne, NW Australia, 1981	Mell 1988 (in Leatherwood *et al*. 1991)	
Stranding	41	Tay Estuary,	Peacock *et al*.	

		Carnoustie, Scotland, 1935	1936	
Stranding	43	Perkins Island, Tasmania, 1974	Scott and Green 1975	
Stranding	50	Seal Bay, King Island, Tasmania, 1958	Scott and Green 1975	
Stranding	54	Mtoni Beach, N of Zanzibar, 1933	Anon. (in Leatherwood *et al*. 1991)	
Stranding	58	Berg River Mouth, St Helena Bay, SA, 1936	Smithers 1938	
Stranding	65	St Helena Bay, SA, 1981	Present study	-
Stranding	90	Stanley, NW Tasmania, 1936	Scott and Green 1975	"90 – 100 individuals"p.95
Stranding	97	Mudtur, Sri Lanka, 1934	Tomilin 1957	
Stranding	100	Kommetjie, SA, 1928	Best 1989, 2007; Fraser 1936	"..although more than 100 came ashore, we saw as many in the sea which did not."p.100 Best (1989); "over 100"p.105 Fraser (1936)
Stranding	114	Augusta, W. Australia, 1986	McNamara 1986 (in Kitchener *et al*. 1990); Mell 1988 (in Leatherwood *et al*. 1991)	
Stranding	127	Dornoch Firth, Scotland, 1927	Tomilin 1957; Purves and Pilleri 1978; Fraser 1936	"about 150"p.105 Fraser (1936)
Stranding	150	Ft Pierce, Florida, 1970	Caldwell *et al.* 1970	150 - 175; "reliable, yet conservative, estimate"p.634
Stranding	167	Velanai Island, Sri Lanka, 1929	Pearson 1931	-
Stranding	170	Black River Beach, NW Tasmania, 1974	Scott and Green 1975	170 – 172, p.91; "they were in 2 groups", separated by "some 400 m"p.93
Stranding	181	NE Strait of Magellan, Chile, 1989	Alonso *et al.* 1999	"at least 181 individuals"p.713
Stranding	250	Port Prime, Australia, 1944	Hale 1944 (in Leatherwood *et al*. 1991); Aitken, 1971	"main body of 200 came ashore at Port Prime" "about 50 whales landed approx. 2.5 km further north"p.100 Aitken (1971)

Stranding	200	Seaspray, Mamre, SA, 1935	Tomilin 1957; Best 2007	200 – 300, p.11 Best (2007)
Stranding	835	Mar del Plata, Buenos Aires, Argentina, 1946	Tomilin 1957	

In addition to the individual values reported in Table 3.2, various authors have made some more general comments on group size of mass stranded false killer whales. Small to very large groups of up to 231 individual false killer whales have been reported (Kitchener *et al*. 1990). Ross (1984) reporting on several published results, stated group size of false killer whales stranded en masse ranged from 50 – 835 animals, with an average of 180 for 14 such strandings.

Best (2007) states that sightings of false killer whales in the South African Subregion varied in size from 1 – 100 individuals, with an average of 20.2 (n = 26; sd = 25; mode = 8; median = 8). Only 8 schools contained 30 whales or more. Other sighting data of false killer whales (mostly from the Northern Indian Ocean and North Atlantic – Mörzer-Bruyns 1969; Balance *et al*. 1996; Mullin *et al*. 1994, 2004) range from 1 – 150 individuals in group size, with a mean of 25.1 (n = 23; Best, pers. comm.). Confirmed sightings from the Indian Ocean between 1890 – 1986, reported in Leatherwood *et al*. (1991), range from 1 – over 100 animals, with the majority (83 %, n = 47) containing 30 or fewer animals. Odell and McClune (1999) reported 157 sightings of false killer whales in the North Pacific, ranging from 1 – 89 individuals, with an average of 18. Estimates of group size of false killer whales off the Pacific Ocean of Japan based on aerial sighting records range from 2 – 200 individuals, with a mean of 55, among 6 schools (Kasuya 1971 in Stacey *et al*. 1994, and in Odell and McClune 1999), although aerial data may be biased towards larger groupings. Acevedo-Guttierrez *et al*. (1997) recorded 15 boat-based sightings of false killer whales in Golfo Dulce and at Isla del Coco, in Costa Rica. Group size estimates were possible for 13 of these sightings, with a reported average of 16 individuals per group, and ranging from 13 – 14 individuals at Golfo Dulce and from 5 – 34 at Isle del Coco. The numbers of false killer whales caught per drive fishery off Iki Island in Japan in February and March 1979 and 1980 and analysed in this study (Table 3.1), range from 10 to 160, with a mean of 94 (n = 6; sd is 67; median = 109). In his study of a larger sample of shore-driven false killer whales off Iki Island, Japan, Kasuya (1986) reports on an additional 3 groups, with 40, 201 and 84 specimens. Data from other drive fisheries were not available to include in this comparison.

A Mann-Whitney test comparing the 29 stranded group sizes in Table 3.2 against the group sizes for the 49 sightings provided by Best (2007; pers. comm.) confirms that the difference in group size between stranded and sighted false killer whales is significant (p = 0.0001), with stranded groups being 4 – 5 times larger on average.

b) Age frequency distribution

Frequency distributions of age are represented separately for male and female stranded and shore-driven whales (Figures 3.1a-d). Ages range from 3.25 to 63.5 years for the stranded female whales (Fig. 3.1a), and from 3.75 to 58.5 years for the stranded males (Fig. 3.1c). The youngest and oldest shore-driven female and male false killer whales were 0.2 and 62.5 years (Fig. 3.b), and 0.1 and 62.5 years (Fig. 3.1d), respectively.

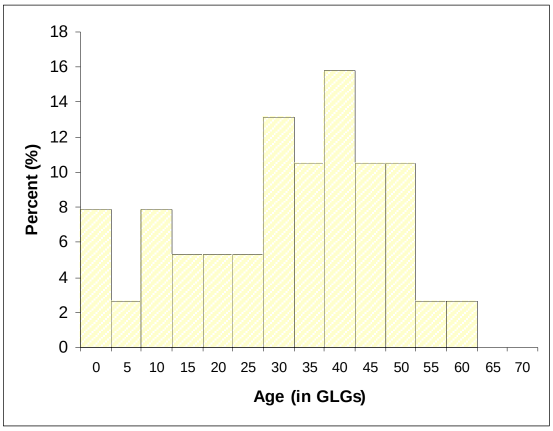

Figure 3.1a: Age distribution of female false killer whales stranded at St Helena Bay, South Africa. GLG = Growth layer group; 1 GLG corresponds to 1 year.

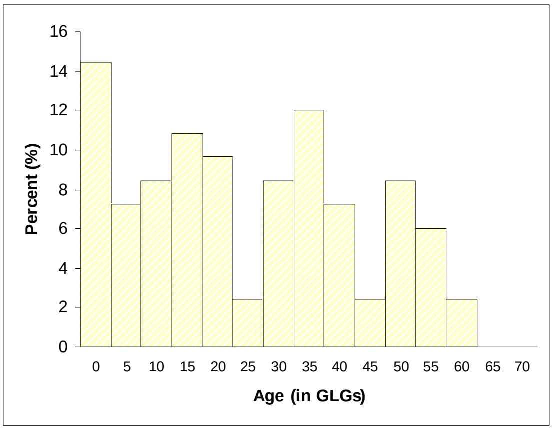

Figure 3.1b: Age distribution of female false killer whales captured at Iki Island, Japan. GLG = Growth layer group; 1 GLG corresponds to 1 year.

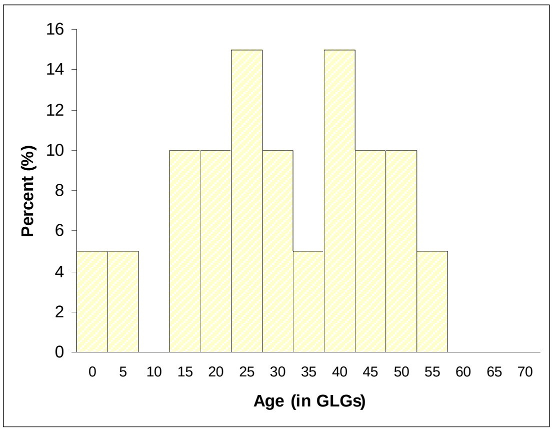

Figure 3.1c: Age distribution of male false killer whales stranded at St Helena Bay, South Africa. GLG = Growth layer group; 1 GLG corresponds to 1 year.

Figure 3.1d: Age distribution of male false killer whales captured at Iki Island, Japan. GLG = Growth layer group; 1 GLG corresponds to 1 year.

Stranded and shore-driven females appear to be evenly distributed across age (Figures 3.1a and b). There is no obvious peak in age frequency (Figures 3.1c and d) among the shore-driven and stranded male false killer whales examined. However, among the stranded males there is a distinct absence of specimens between the ages of 5.25 and 17.5 years (Fig. 3.1c). The 5.25 year old is an immature specimen and the 17.5 year old specimen is a mature male. There are no Japanese specimens between 10.5 and 18.5 years of age (Fig. 3.1d). The 10.5 year old Japanese male is the oldest immature male shore-driven specimen, while the 18.5 year old male is classified as early maturing. There also appear to be relatively fewer non-stranded males over 40 years of age. (Fig. 3.1d).

The stranded specimens are on average older than the shore-driven whales (Table 3.3). However, there is no significant statistical difference between the mean age of the stranded and shore-driven immature females, and males ($p = 0.3983$; $p = 0.6232$, respectively), nor between the stranded and shore-driven mature females, and males ($p = 0.1299$; $p = 0.3350$, respectively; maturing males have been combined with mature males). Despite a difference in the overall distribution of ages between the stranded and shore-driven data (KS = 0.117432; $p = 0.0118$), with stranded whales being older, there is no significant difference between the age distribution of stranded and shore-driven females (Test statistic value = 0.109633; $p = 0.1091$), nor between that of the stranded and shore-driven males (Test statistic value = 0.148718; $p = 0.1128$). This indicates that the overall difference is not specifically due to any differences within either sex between the samples.

Table 3.3: Mean age (in years) according to sex and reproductive status for shore-driven and stranded false killer whales sampled. N represents the number of specimens sampled of known age.

Sample	Sex	Maturity status	N	Mean Age (yrs)	Min	Max
Shore-driven	**F**	Immature	17	3.997	0.200	10.5
		Mature	57	32.526	8.25	62.5
	M	Immature	16	3.490	0.100	10.5
		Early maturing	2	12.375	6.25	18.5
		Mature	22	33.909	18.5	57.5
Stranded	**F**	Immature	4	5.500	3.25	9.25
		Mature	34	37.235	10.5	63.5
	M	Immature	2	4.500	3.75	5.25
		Late maturing	1	25.5	-	-
		Mature	15	36.967	17.5	58.5

c) Sex ratio

With the exception of 1 small school (School 4, n = 6), there are more females then males among the shore-driven groups (Table 3.4). Following Kasuya (1986), the Japanese schools have been combined in subsequent analyses of sex ratio.

There are significantly fewer males than females overall when the shore-driven groups are combined (Table 3.5), with a sex ratio (indicated by the percent of females hereafter) of 0.62 ($\chi^2 = 8.308$; $p < 0.001$). The sex ratio, of 0.65, for the stranded whales is similarly female biased ($\chi^2 = 5.73$; $p < 0.05$).

Table 3.4: Sex ratio for shore-driven schools (Japan). Values given in parentheses represent % females in each school.

School	**1**	**2**	**3**	**4**	**5**	**6**
Females	4 (80 %)	20 (57 %)	16 (57 %)	2 (33 %)	38 (68 %)	16 (62 %)
Males	1	15	12	4	18	10
TOTAL	**5**	**35**	**28**	**6**	**56**	**26**

Table 3.5: Sex ratio for the stranded and shore-driven groups. Values given in parentheses represent % females.

	Stranded (South Africa)	Shore-driven (Japan)	TOTAL
Females	41 (65 %)	96 (62 %)	137 (63 %)
Males	22	60	82
TOTAL	63	156	219

Both sex and maturity status is known for 41 female and 18 male stranded specimens, and for 87 and 51 female and male shore-driven whales respectively (Table 3.6). Information relating to maturity status was not recorded and could not be determined from the available data for 9 shore-driven females, all belonging to School 5, and for 7 shore-driven males from various schools.

Table 3.6: Overview table showing the number of female and male false killer whales in the stranded and shore-driven groups, according to maturity status (excludes maturing males).

	Stranded (South Africa)		Shore-driven (Japan)	
	Females	Males	Females	Males
Overall	41	22	96	60
Immature	4	3	20	21
Mature	37	15	67	30

The sex ratios among the immature whales of the stranded and shore-driven groups appear to be close to parity (Table 3.6), with 4 immature females and 3 immature males in the stranded population, and 20 immature females and 21 immature males in the shore-driven population. However, the sex ratios, of 0.71 and 0.69 among the mature stranded and shore-driven adults (operational sex ratio), respectively, are significantly female-biased (Chi-squared test, stranded: $p = 0.0273$; shore-driven: $p = 0.0084$), with less than half the number of males in both groups, i.e. there are fewer adult males than adult females in both groups (Table 3.7). There is no significant difference in sex ratio between the stranded and shore-driven adult false killer whales overall (Chi-squared test: $p = 0.7919$), i.e. there is an almost equal proportion of females in both samples.

Table 3.7: Operational sex ratio. Values expressed in parentheses represent % mature whales which are female, in the respective sample. The 2 SA male specimens classified as LM (late maturing) and the 2 Japanese specimens classified as EM (early maturing) have been excluded.

	Stranded (South Africa)		**Shore-driven (Japan)**	
	Immature	**Mature**	**Immature**	**Mature**
Female	4 (58 %)	37 (71 %)	20 (49 %)	67 (69 %)
Male	3	15	21	30
TOTAL	7	52	41	97

d) Maturity status

Sexually immature false killer whales are present in all 6 of the shore-driven Japanese schools, but in equal or proportionately fewer numbers than mature specimens (Table 3.8). Schools 1 and 3 each contain an equal number of males and females of known maturity status. Based on the age and body length values of the 3 unclassified specimens in School 3, it can be reasonably assumed that 2 are mature, and the remaining 1 is immature, thus biasing the ratio towards mature specimens in that school. Schools 1 and 3 also each contain an early maturing male, not shown in the table.

Table 3.8: Number of immature and mature false killer whales in the shore-driven schools (Japan). Two schools (marked with *) each contain 1 early maturing male not shown. Information relating to maturity status was not recorded for 9 shore-driven females, all belonging to School 5, and for 6 shore-driven males from various schools.

School	**1***	**2**	**3***	**4**	**5**	**6**
Immature	2	11	12	1	11	4
Mature	2	22	12	5	35	21
Unclass.	0	2	3	0	10	1
TOTAL	**4**	**35**	**27**	**6**	**56**	**26**

The number of mature whales exceeded immature whales in both the shore-driven groups combined, and in the stranded group of whales (Table 3.9). However, the proportion of immature whales among the stranded whales (12 %) is significantly less than that of 30 % for the shore-driven whales (Chi-squared test: $p = 0.0075$), i.e. there are relatively more immature shore-driven false killer whales than immature stranded whales.

Table 3.9: Group composition according to sexual maturity. Values in parentheses represent % immature specimens in each sample. The 2 shore-driven specimens classified as EM (early maturing) and 2 stranded male specimens classified as LM (late maturing) have been excluded.

	Stranded	Shore-driven
Immature	7 (12 %)	41 (30 %)
Mature	52	97
TOTAL	59	138

Table 3.10: Group composition according to sexual maturity and sex. Values in parentheses represent % immature female and male specimens in each sample. The 2 SA male specimens classified as LM (late maturing) and the 2 Japanese specimens classified as EM (early maturing) have been excluded.

	Female		Male	
	Stranded	**Shore-driven**	**Stranded**	**Shore-driven**
Immature	4 (10 %)	20 (23 %)	3 (17 %)	21 (41 %)
Mature	37	67	15	30
TOTAL	41	87	18	51

Table 3.10 shows the group composition in the two samples according to sexual maturity and sex. There are comparatively fewer immature male stranded whales relative to immature shore-driven whales, although this difference is not statistically significant (Chi-squared test: p = 0.0605). There are also fewer immature stranded females relative to the shore-driven females, but the difference is not as pronounced as between males (Chi-squared: p = 0.0735).

e) Reproductive classes among mature females

Among the Japanese schools of false killer whales (Table 3.11), resting females are represented in all except 1 school (School 4), which contains 2 females, both ovulating, 3 mature males and 1 immature male. School 1 (n = 5) similarly contains only two females, both resting (and 2 immature males and 1 early maturing male). Apart from these two schools, pregnant, ovulating and lactating females are represented in all schools.

Table 3.11: School composition of sexually mature shore-driven females of known reproductive status.

School	1	2	3	4	5	6
Pregnant	0	2	1	0	3	4
Lactating	0	4	4	0	1	4
Ovulating	0	1	2	2	2	3
Resting	2	7	3	0	16	3
Ovulating/Lactating	0	1	0	0	1	1
TOTAL	**2**	**15**	**10**	**2**	**23**	**15**

Although there is an almost equal proportion of females in both samples, the age structure of females is different. Ninety percent of the stranded false killer whales are sexually mature, whereas 77 % of the shore-driven whales are mature, i.e. there are relatively more sexually mature stranded than driven females. Of the 37 mature female stranded false killer whales, data on reproductive status are known for 34 animals. Reproductive status is known for all of the 67 mature female shore-driven whales. The reproductive compositions of the shore-driven schools combined, and the stranded females are shown in Table 3.12.

There is only one pregnant whale in the stranded sample, representing 3 % of the females of known reproductive status, compared to 10 pregnant whales (15 %) in the shore-driven samples combined. There are more lactating than pregnant females in both samples of false killer whales, but the ratio of pregnant to lactating females is more pronounced among the stranded females (1:9) compared to the shore-driven females (1:1.3), i.e. there are proportionately more lactating females relative to pregnant whales in the stranded group. Despite these differences, there are no significant statistical differences in the proportions of the various reproductive classes between the shore-driven and the stranded groups sampled (Fisher’s exact test: p = 0.3841).

Table 3.12: Number and relative proportions of females in each reproductive class in the stranded and shore-driven groups of false killer whales. Imm represents the total number of female and male immature whales in each sample. Values in parentheses represent % total number of mature females in each sample. T represents the total number of mature females of known reproductive status.

	Imm	Pregnant	Lactating	Ovulating	Resting	Ovul/Lact	T
Stranded	*7*	1 (3 %)	9 (26 %)	7 (21 %)	16 (47 %)	1 (3 %)	34
Shore-driven	*41*	10 (15 %)	13 (19 %)	10 (15 %)	31 (46 %)	3 (5 %)	67

The number of lactating females (9) exceeds the number of immature specimens in the stranded sample (7; Table 3.12). The age of 6 of the 7 immature stranded specimens is known, of which none are 2 years or less in age. Lactation has previously been reported to last 18 months to 2 years in false killer whales (Odell and McClune 1999).The situation is reversed in the shore-driven group, with more than double the number of immature specimens (41) relative to lactating females (13). The age of 33 of the 41 immature shore-driven specimens is known, 12 of which are 2 years or below in age.

Discussion

Group size

The comparison of group size between stranded and sighted schools of false killer whales in this study clearly indicates that the sighted schools are smaller than the stranded schools. Differences in herd size between stranded, shore-driven and sighted schools have been reported for other species. Sergeant (1962), for example, reported that the herd size of long-finned pilot whales, *Globicephala melaena*, averaged about 20 whales in pelagic sightings and rarely exceeded 100, but that the size of schools stranded or driven ashore averaged about 85 whales, and frequently exceeded 200. These reported differences compare favourably with the results of this study. The few data available from drive fisheries suggest that group size of the shore-driven false killer whale schools is intermediate between the stranded and sighted schools, although a more thorough investigation of this is required.

The comments from the individual studies included in Table 3.2 suggest that the specimens that strand are often part of a larger group at sea. Purves and Pilleri (1978) state that a review of strandings of false killer whales on the North Pacific coast of America by Mitchell (1965, in Purves and Pilleri 1978) led him to conclude that the numbers collected (sic) represented only a few animals in each case and “that there was evidence that these had been part of much larger schools” (p. 72). Shore-driven groups could similarly represent temporary feeding aggregations, associated with inshore movements of food. It is also possible that they could represent an amalgamation of schools, or individuals from several widely dispersed schools, that were herded at the drive by the several hundred boats which participated in the drive.

A variety of possible groupings within and between cetacean species are recognised - group, pod, herd, school (see Sergeant 1982, Connor *et al*.1998). However, in any discussion on group size it is important to recognise that definitions of what constitutes a “group” or “school” tend to change across studies and sometimes remain unstated. Not only are terms often inconsistently used across studies, but their meaning is often not subjected to scrutiny, and is assumed rather than stated. The implications of this are that there is ambiguity in what constitutes a group or school. Thus, even though it has been assumed that the values reported in this study represent actual school sizes, what these groupings represent biologically is at present unclear.

The implications of this are that it is possible that specimens found at mass strandings, and analysed as a “group” in most studies, including the present one, could in fact belong to various different schools, i.e. the large number of individuals recorded as a single group at mass strandings could reflect several schools. It is possible that mass strandings are composed of several smaller groups that have come together for a common purpose, for example, for the exploitation of locally abundant, inshore migrating populations of a prey species. Several researchers have reported inshore migrations and movements by false killer whales, possibly associated with the distribution and respective movements of prey species (Fraser 1936, Tomilin 1957, Ross, 1984, Acevedo-Gutierrez *et al*. 1997). Perhaps once in these unfamiliar waters, the whales could become disorientated and subsequently strand. Similarly, it is also possible that individuals from several widely dispersed schools were herded at the drive by the several hundred boats which participated in the drive.

Values obtained from sightings are similarly subject to bias, but in the opposite direction. According to Baird *et al*. (in press) sighted groups of false killer whales are often subsets of a larger actual group, travelling in the same direction and in vocal communication, even though scattered over a wide area. These subgroups may join and split over time frames of several hours, so the actual ‘school” is probably much larger than what observers typically record. A relationship between the duration of a sighting and the number of specimens observed has been demonstrated previously in a boat-based study of false killer whales (Baird *et al*. 2005).

Differences in methodology represent another source of variation in group size. Boat-based estimates frequently underestimate group size, when compared to independent counts of the same group taken from aerial photographs (Gerrodette *et al*. 2002). Another potential source of bias is whether the sighting was part of a directed/focused survey, or whether it was incidental. Group size is less likely to be consistently and accurately recorded during incidental sightings as groups may be spread over a large area.

The ecological and behavioural context of a particular sighting is also an important consideration. The size of a group is likely to vary according to the particular behaviour the group members are engaged in, for example, foraging, socialising, and mating. Furthermore, differences in group size of feeding groups could also be related to diet. For example, differences in the group size and dispersal patterns between the mammal-eating transient and the fish-eating resident killer whales have been linked to their respective differences in diet and foraging strategy (Baird and Dill 1996). According to an interspecific comparison of group size in delphinids, pilot whales tended to associate in smaller units when feeding more on fish and less on cephalopods (Gygax 2002). Based on what is known of their diet from stomach contents, there appear to be differences in their respective diets between Northern and Southern populations of false killer whales.

False killer whales are typically reported to feed on deep sea cephalopods and fish (Stacey et al. 1991, Odell and McClune 1999) and are considered teuthoichthophagic (Tomilin 1957). However, Ross (1984) reporting on cetaceans off the coast of Southern Africa, stated that the remains of only cephalopods were found in the stomach of a single false killer whale specimen. Best (2007) similarly reports that all food items identified in the stomachs of 13 false killer whales from the Subregion were cephalopods. According to an analysis of the stomach contents of 25 false killer whales collected from a mass stranding off both coasts of the Strait of Magellan, Chile, 9 of the 11 prey items identified were cephalopods, and the remaining were 2 species of neritic fish (Alonso *et al*. 1999). While stomach analyses may not be reliable indications of prey consumed if false killer whales break up their food, as suggested by Best (2007), if real, such a difference in diet could produce corresponding differences in prey distribution, foraging strategies, and typical herd size, as per the transient and resident killer whales.

Therefore the only conclusion regarding group size that can be drawn from this study is that stranded groups of false killer whales are significantly larger than either shore-driven or sighted groups. However, this conclusion needs to be interpreted against the various biases in the data and other factors such as the ambiguous use of terminology, and the transient nature of groups according to their behavioural and ecological demands. Such issues cannot be clarified through carcass studies, and require long-term observational studies, using standardized methodologies to reduce sampling variability and allow for meaningful comparisons.

Group composition

Based on the results presented in this study, it appears that false killer whales occur in units composed of immature specimens of both sex, relatively few maturing and adult males, and adult females of various reproductive classes. On average, the stranded whales are older overall. This could be due to there being relatively fewer immature stranded female and male false killer whales, compared to the immature female and male false killer whales in the shore-driven sample. A second explanation for the age difference between the two samples could be the relative absence of males over 40 years of age in the shore-driven sample.

The overall sex ratio is female-biased in both stranded and shore-driven groups.
The sex ratio in stranded groups of false killer whales has previously been reported as approximately equal (Smithers 1938, Tomilin 1957, Stacey *et al*. 1994, Norman and Fraser (1948, in Ross 1984). Elsewhere (Fraser 1936; Odell *et al*. 1980), stranded females have been in excess of males. Of the 77 false killer whales of known sex to have stranded at Dornoch Firth, Scotland (Purves and Pilleri 1978), 43 were females and 34 males. Kasuya (1986) reporting on a larger sample of the shore-driven false killer whales off Japan similarly found proportionately more females, 159/101. The results in this study confirm those previous studies that indicate female false killer whales occur in excess of males in some stranded and most shore-driven groups.

The situation is not so straight forward, however, when looking at sex ratio according to maturity status. Among the immature false killer whales in both the stranded and shore-driven samples the sex ratio is close to parity. Birth sex ratios of 1: 1 are typical of cetacean populations and mammals in general (Whitehead and Mann 2000). Among mature false killer whales, however, the sex ratio is female-biased, with less than half the numbers of mature males than there are mature females in both groups. Using data from several studies of stranded false killer whales in Britain, Florida, South Africa, and Tasmania, Sergeant (1982) determined the ratio of mature females to mature males, as estimated from a minimum body length of 400 and 500 cm, respectively, to be 90/34. Both short- and long-finned pilot whales (Bernard and Reilly 1999) and killer whales (Bigg 1981, in Sergeant 1982) have female-biased adult sex ratios comparable to those reported for false killer whales in this study.

According to Sergeant (1982), the delay in attainment of male sexual maturity in Orcininae is associated with greater male mortality and together these result in a lower overall male sex ratio than in Delphininae. The female-biased sex ratio in the samples of false killer whales investigated in this study could therefore reflect differences in natural mortality rate between males and females, as has been found for long-finned (Bloch *et al.* 1993) and short-finned pilot whales (Kasuya and Marsh 1984), in which males may live for 10 years less than females. In his analysis of a larger sample of shore-driven false killer whales off Iki Island, Kasuya (1986) reported males have a slightly higher mortality. Although mortality rates were not estimated in this analysis, the differences in apparent longevity of the sexes in both samples (Table 3.2) likely correspond to differences in mortality rate between the sexes. This is consistent with the findings reported in Chapter 2 that males attain sexual maturity at a later stage relative to females. However, there is no obvious evidence of a difference in sex ratio between stranded and shore-driven false killer whales, as reported by Sergeant (1982) for stranded and shore-driven pilot whales.

In addition to both samples having a female-biased sex ratio overall, another feature common to both is the occurrence of fewer immature male and female animals than mature specimens. Based on their estimates of age at sexual maturity, as determined from teeth, Purves and Pilleri (1978) similarly reported comparatively fewer immature specimens in the mass stranded school at Dornoch Firth, Scotland. Assuming an average age at sexual maturity of 10 GLGs, and based on age and body length data presented in Tables 22 and 23 (Purves and Pilleri 1978), 24 of the 77 whales (31 %) were immature. In a second example, and using a body length at sexual maturity criterion of between 330 cm and 370 cm for South African female and male false killer whales, respectively, (see Chapter 2), only 11 % and 10 % of female and male false killer whales, respectively, of known body length (n = 40), as reported by Smithers (1938), that mass stranded at Varkvlei, South Africa, were immature. In contrast, according to data presented by Kasuya and Marsh (1984) on shore-driven short-finned pilot whales, just below half (48.8 %) of the whales of known maturity status (n = 387) were immature. Therefore it appears that in general groups of false killer whales have fewer immature specimens.

There are, however, proportionately fewer immature specimens among the stranded than among the shore-driven whales in this study. As discussed above, this likely contributes to the stranded whales being older, on average than the shore-driven whales. A possible explanation for the relatively larger number of immature shore-driven whales may be that they are over-represented, possibly due to their lesser stamina during the drive fishery process (compare Perrin et al. 1977 on spinner dolphins caught up in the yellow tuna purse seine fishery). Alternatively, the differences in the relative proportions of immature specimens in the stranded and shore-driven samples could reflect differences in fecundity.

Both the shore-driven and the stranded samples are also characterized by a large age gap among the males, between 5 - 18 years in the stranded sample, and between 10 - 19 years in the shore-driven group. In Chapter 2, it was reported that there is a large gap between immature and mature male specimens, with few maturing males. The observed absence of male false killer whales between the above reported ages thus presumably corresponds to the intermediate stage between immature and mature males. In his report on a larger data set of shore-driven Japanese false killer whales caught at Iki Island, Kasuya (1986) suggests that the gap in males between these ages is due specifically to the absence of males in the late maturing stage (2 early maturing males were present, no late maturing males were reported). However, the stranding data in this study - no early maturing, and 2 late maturing males - suggest that the absence may involve maturing males in general.

Segregation is a common feature to several dolphin species, for example: among striped, pantropical spotted and fraser’s dolphins mature and immature are segregated, with females of a particular reproductive status usually predominating in schools mostly composed of mature dolphins (Kasuya 1986, Amano *et al*. 1996). Kasuya and Marsh (1984) reported a similar shortage of maturing males for short-finned pilot whales stranded or caught off the Pacific coast of Japan. However, unlike in Kasuya and Marsh’s (1984) study, there does not appear to be an aggregation of maturing males in any single shore-driven school in this study. School 4 (which contains 4 males and only 2 females), has only one immature male, aged 1.5 years, and three adult males, all over 26 years of age. Instead of indicating social segregation of maturing males within a school, data on age composition and sexual maturity strongly indicate that maturing males actually leave their breeding school. The question thus arises at to what happens to the maturing males.

Comparatively little is known about association patterns and social organization in false killer whales, most of what is known having been inferred from carcass studies, or free ranging observations of short duration. While carcass studies are valuable, they provide little information about social organization. Thus it is not known what becomes of these maturing males during their adolescent years, or what happens to them when they reach maturity.

Several odontocete species display a variety of dispersal patterns. Dispersal by all females and all but the first born male has been proposed for transient killer whales (Baird 2000), while, in what is considered a rarity among mammals, neither male nor female resident killer whales disperse from their natal group (Bigg *et al*. 1990). Although the evidence is more ambiguous (Ottensmeyer and Whitehead 2003), a microsatellite DNA analysis similarly suggests that female and male long-finned pilot whales do not disperse although there does not appear to be inbreeding within a pod (Amos *et al*. 1993). Rather it seems that male pilot whales may segregate socially in bachelor herds, and occasionally leave their natal group and perhaps rove between schools when several such schools unite (Kasuya and Marsh 1984, Amos *et al*. 1993). Male sperm whales on the other hand, are known to leave their breeding school at puberty and form bachelor groups or remain single (Best 1979, in Connor *et al*. 1998, Weilgart *et al*. 1996). As they age adult male sperm whales become progressively more solitary and tend to move into higher latitudes. The reason for male whales dispersing may be that it enables them to avoid competition for resources with the breeding population. If one also assumes, based on sexual dimorphism and delayed male sexual maturity, that these species are polygynous, males might also segregate to reduce or avoid inter-male competition and aggression.

Based on what is known about dispersal patterns in other species, several possibilities emerge as to what happens to maturing false killer whale males: a) the males join up with other groups, b) form bachelor groups, or c) rove singly. In the present study, there are two early maturing males in the shore-driven sample and two late maturing males in the stranded sample. This, together with the presence of mature males, albeit in small numbers, of various ages and body lengths in both samples suggests that some maturing males might leave their breeding school permanently, but that at least one or a few males remain with, or return to their natal group. There is a growing body of evidence to suggest that false killer whales exhibit strong social bonds and long term association and philopatry (Acevedo-Gutierrez *et al*. 1997, Baird *et al*. 2007). Alternatively, these maturing and adult males may be unrelated to the rest of the group and have emigrated from other breeding schools. The absence of predominantly male groups of false killer whales at mass strandings and in drive fisheries does not support the possibility that male false killer whales form bachelor groups like the sperm whales. However, one cannot completely discount it, as such schools might be less socially cohesive and thus less likely to strand en masses or be easily driven ashore. The alternative, that males rove singly, is thus by default a more likely scenario. As there is no reason why single male false killer whales should not make occasional inshore migrations, perhaps for food, as suggested for groups of false killer whales, they could similarly subject themselves to stranding. A potentially valuable study would be to investigate whether most single or small strandings of false killer whales are of males.

The issues of what becomes of maturing males, and what happens to them upon reaching maturity, await further investigation. Long term studies are required to determine the movements of these males, while genetic data will establish relatedness within a group and clarify issues of natal philopatry. Regardless of what happens to these maturing males, their absence is common to both samples in the present study, and is thus unlikely to offer insight into or contribute to the stranding phenomenon in false killer whales. Among the mature female false killer whales of known reproductive status, there are relatively fewer pregnant false killer whales among the stranded group (3% vs 15%). The relatively low incidence of immature specimens and pregnant females in the stranded population could indicate that they are under-represented in the stranded sample, or suggest that the stranded group is inherently less fertile than the shore-driven group.

The number of lactating whales in both populations exceeds the number of pregnant whales, although the margin of difference is greater in the stranded group. Slight differences in criteria used to identify lactating females in the stranded and shore-driven samples may also have contributed to this discrepancy (Chapter 2). Although the presence of milk in the mammary glands was used to identify lactating females in both samples, histological preparations of the mammary glands were subsequently used to confirm lactating status only for the South African females, and several females that did not initially present obvious signs of lactating were reclassified as lactating. As no histology was available for the Japanese females, it is possible that the actual number of lactating females in the shore-driven group has been underestimated.

This methodological difference, however, does not account for the relatively fewer number of immature whales in the stranded group, none of which are of presumed suckling age. False killer whale calves nurse for about 18 months to 2 years (Odell and McClune 1999). All of the immature specimens of known age in the stranded sample are over 3 years of age. Given the relatively lower ovulation rate of the stranded females (see Chapter 4), the comparatively lower pregnancy rate is to be expected, and, together with their lower annual gross reproductive rate, provides further evidence that the stranded group is relatively less fecund. The disproportionately high number of stranded lactating females in relation to the few immature specimens could perhaps be a response to a low population reproductive rate. Older lactating females who fail to fall pregnant again could be stimulated through suckling to continue lactating. Thus, through lactation being prolonged, some of the older lactating females may have been nursing older immature individuals, i.e. older than 2 years of age. If these lactating females are also providing milk to non-offspring, they may help increase the chance of survivorship of immature false killer whales. Best *et al*. (1984) report a similar excess of lactating sperm whales relative to calves of presumed suckling age, which they suggest may be due to an underestimation of the duration of lactation, or to the fact that calves may be suckling from more than one female.

The subject of fertility was not an initial consideration in this chapter, but has emerged as a potentially significant factor in explaining certain differences in group composition between the stranded and shore-driven samples. Differences in reproductive parameters and fertility between and within species have often been attributed, at least partly, to different histories of exploitation, and resulting density-dependent population responses, i.e. as density within a population decreases the reproductive rate increases. Perrin *et al*. (1976) reported differences in the reproductive rates between eastern Pacific and Japanese spotted dolphins (*Stenella attenuata*), which they related to the historically greater exploitation of the former population. Similarly Perrin *et al*. (1977) reported the gross reproductive rate of eastern Pacific spinner dolphin (*Stenella longirostris*) was lower than that for the highly exploited offshore eastern Pacific spotted dolphin.

Although Perrin and Henderson (1984) found no major difference in pregnancy rate between the heavily exploited eastern and the less exploited northern whitebelly Pacific spinner dolphins, the former population had a larger proportion of immature females despite their lower mean age at sexual maturity, presumably reflecting a higher mortality. A comparison between the intensely hunted Newfoundland population of long-finned pilot whales and the relatively unexploited Faroe Island population of long-finned pilot whales revealed that the age at sexual maturity in females was demonstrably lower in the former, which the authors suggested may have been a density-dependent response to exploitation pressure (Martin and Rothery 1993). There was no observable difference in the age at sexual maturity between Japanese shore-driven and South African stranded female false killer whales in this study, but there were proportionally more immature specimens and a relatively higher ovulation and pregnancy rate among the shore-driven whales.

False killer whales were often targeted by drive and harpoon fisheries in the Pacific (Miyazaki 1983), for food in Japan (Odell and McClune 1999), and especially at Iki Island, Japan, due to perceived conflict with the yellowtail fishery (Kasuya 1986). There are no records of false killer whales being exploited off the coast of Southern Africa. Thus, the observed differences in reproductive parameters between the two samples of false killer whales in this study, and in particular the relatively higher productivity in the Japanese group, could reflect a density-dependent population response to previous exploitation.

Another possibility is that the differences in fertility could reflect inherent racial differences and be the result of genetic isolation between the two geographically separated populations. Considering the number of morphological differences between the two populations, this possibility cannot be ruled out at present, although the current data does not allow for comments on the taxonomic significance of these various differences. Alternatively, the differences could be environmentally based, relating to likely differences in water temperature and food availability and quality between the two populations. As discussed in Chapter 2, strong correlations between geographic variation in body size and seasonality have been shown to occur in mammals (Boyce 1978), including cetaceans, whose adult body size was found to be inversely correlated with the length of the feeding season and directly correlated with prey availability during that period (Brodie 1975). Differences in prey items (as discussed above), resource availability and quality between the Japanese and South African waters could similarly manifest in differential reproductive parameters and levels of fertility. Kasuya and Marsh (1984), for example, suggested that the earlier maturation and higher pregnancy rate of the long-finned pilot whale, *Globicephala melas/melaena*, compared to that of the short-finned pilot whale, *G. macrorhyncus*, may reflect differences in environment and food availability, as well as differences in the history of exploitation.

Almost half of the mature females in the shore-driven schools and in the stranded group showed no evidence of being reproductively active at the time of death. In some cases the female may have been anoestrus but, given the large number of resting females, coupled with certain other features of these whales, it is possible that some may actually be in a post-reproductive state (see Chapter 4). If this is the case, the apparent female-biased operational sex ratio is misleadingly high. The theme of post-reproductivity is explored in detail in the following chapter.

Conclusion

Stranded groupings of false killer whales tend be significantly larger than either shore-driven or sighted schools of false killer whales and appear to represent an amalgamation of several schools that have maybe come together shortly before the stranding. It is possible that these schools joined together for a common purpose, perhaps to take advantage of locally abundant food, or represent a social unit that is normally more fragmented. Their inshore movements into unfamiliar waters, coupled perhaps with disturbances in the earth's magnetic field, or certain topographic features could subsequently result in their stranding en masse.

In both samples there is an overall female-biased sex ratio and an absence of maturing males, likely owing to their dispersal. There are relatively fewer immature specimens in the stranded sample, which coupled with the scarcity of shore-driven males over 40 years of age resulted in the stranded group on average being older. There is a similar proportion of resting females in both groups. There are significantly fewer pregnant females in the stranded sample. Together with the relatively fewer number of immature specimens in the stranded group, this suggests that the stranded group is less fertile than the shore-driven group. If indeed the stranded sample is made up of several schools then the presence of a single pregnant female further emphasises the comparatively low reproductive output of the stranded sample. There are more lactating than pregnant females in both groups, but the difference is more pronounced among the stranded whales. Among the shore-driven whales, there are more immature individuals than lactating females, while in the stranded group the situation is reversed, so presumably some lactating females are nursing older immatures. If the stranded group is intrinsically less fertile, it is possible that females responded by increasing the duration of lactation. Despite the various differences in composition, and in productivity, between the stranded and shore-driven false killer whale populations investigated in this study, it is not possible to conclude that these were related to the act of stranding, or were singly an expression of genetic or environmentally based differences between populations.

Chapter 4

Reproduction in the female false killer whale and changes in the ovaries and reproductive activity with age: evidence for a post-reproductive phase?

Introduction

Reproduction in female false killer whales, *Pseudorca crassidens*, was first described in detail by Comrie and Adam (1938), who reported on the reproductive systems of several females stranded at the Tay estuary, near Carnoustie, Scotland, in 1935. Since that publication, very little information on the reproductive biology of false killer whales has been forthcoming. Using ovarian material obtained from a mass stranding in St Helena Bay, along the west coast of South Africa in 1981, and from several drive fisheries off Iki Island in Japan in February and March of 1979 and 1980, this paper attempts to augment the existing knowledge about reproduction in female false killer whales.

The differences in fertility between the stranded South African and shore-driven Japanese samples, suggested in Chapter 3, is explored further with respect to ovulation, gestation and gross annual reproductive rate. Furthermore, in addition to improving our current understanding of reproduction in female false killer whales, evidence of seasonality, and changes in fertility and in reproductive activity with age are examined. Anatomical changes in the ovaries with age, as determined macroscopically and histologically, (and age-specific patterns of fecundity) are investigated as measures of fertility. The information value in this study is increased by combining macroscopic and histological observations of reproductive condition, with the absolute age of each individual, using improved ageing techniques. Evidence of a post-reproductive phase in false killer whales, comparable to menopause in humans, is presented, together with a discussion of the possible functions and adaptive significance of such a seemingly counter-selective phenomenon.

Current literature often uses the terms ‘senescence’, ‘reproductive senescence’, post-reproductive females’ and ‘menopause’ loosely, providing no clear criteria for distinguishing between them, and conflating different processes under the same term. Some authors, for example Marsh and Kasuya (1984), have used the terms ‘menopause’ and ‘post-reproductive’ interchangeably with ‘reproductive senescence’. However, following S. Austad (pers. comm., 2007), this study understands reproductive senescence to begin with the decline in fertility, and is thus considered separate to menopause, which is here understood to be the complete cessation of reproduction, which is then followed by a post-reproductive or post-menopausal phase.

Materials and Methods

Data source

A mass stranding of false killer whales occurred on the South African Cape west coast on the 19th August, 1981. Of the 65 false killer whales involved in the stranding, 56 were found over a 1500 m stretch of beach in St Helena Bay. Four further specimens were found along 15 km of coast to the west, three specimens were found 10 km to the east, and two outlying, but presumably related, single specimens were reported 77 and 44 km north of the main group, from Lambert’s Bay and Eland’s Bay, respectively. Scientists reached the main site two days after the stranding occurred. The exact timing of the two single strandings is unknown. Due to delays in the onset of sample collecting and fixation, the material examined was not completely fresh, and post-mortem changes may have occurred. The quantity and quality of information recorded per individual is varied. Data are available for 41 females.

Mixed schools of false killer whales and bottlenose dolphins, *Tursiops truncatus*, were caught by several drive fisheries at Iki Island, off the south west coast of Japan in

February and March of 1979 and 1980. Data are available for 96 female *P. crassidens*. Information relating to age and reproductive status was recorded as detailed in Chapter 2 of this thesis.

Preparation and subsequent examination of the ovarian material of the South African and Japanese samples was carried out by Marsh. During the examination of ovarian material the medulla and cortex were hand-sliced at 1-to-2 mm intervals and the numbers of corpora lutea, corpora albicantia, and corpora atretica in both ovaries were recorded. Regressed or regressing corpora lutea, indicated by the residual scar tissue, were referred to as corpora albicantia. No attempt was made to distinguish corpora albicantia resulting from corpora lutea of pregnancy from those of corpora lutea of ovulation. Despite earlier reports that the two types of corpora albicantia (CA) are distinct, the claims have been strongly contested and largely unsubstantiated to date (Perrin and Donovan 1984). Three diameters each of all corpora lutea, corpora albicantia, corpora atretica and Graafian follicles were measured to the nearest 0.1 mm using vernier callipers. The mean diameter of each corpus was calculated as the cube root of the product of the three diameters. The corpora albicantia were classified as young, medium or old according to the characteristics used by Marsh and Kasuya (1984), shown in Table 4.1, which are assumed collectively to be a more reliable indication of age than the diameter. It is another assumption of this study that the corpora albicantia regress with age, but do not disappear completely, thus serving as a permanent record of previous ovulations. Graafian follicles were classified as atretic or non-atretic on the basis of the macroscopic thickness of the follicle walls. Corpora atretica (yellow bodies) were distinguished from other atretic follicles by the presence of lipid accumulation, indicating luteinization of unruptured (corpora atretica b) and ruptured (corpora a) follicles (Marsh and Kasuya 1984; Perrin and Donovan 1984).

Histological examinations of the ovaries from the South African and Japanese samples were undertaken to confirm macroscopic observations and reproductive status. The slides were prepared using standard techniques. Samples of selected tissues were dehydrated through a graded series of ethanols, cleared in xylene, embedded in Paraplast and sectioned at 5um. The slides were stained with either Mayer's haemalum and Young's eosin-erythrosin, a variant of Gomori's trichrome, or van Gieson's stain with Celestin blue haemalum. A cryostat was used to cut frozen sections of selected formalin-fixed follicles, corpora lutea, corpora albicantia and corpora atretica at 8 um. The sections were stained for lipids using with a modification of Herxheimer's method using Oil-Red 0 and Sudan IV, or with haematoxylin and eosin as above.

Table 4.1: The characteristics on which the classification of corpora albicantia as young, medium and old was based, as used by Marsh and Kasuya (1984). CA = corpus albicans, CL = corpus luteum.

	Status of corpora albicantia		
Characteristic	**Young**	**Medium**	**Old**
External structure			
Protuberance from ovarian surface	As small CL	Usually slight except for stigma	Stigma only
Shape	As small CL	May be round or flattened against surface	Irregular, may be round or flattened against surface
Stigma	Obvious as on CL	Smaller than young CA	White, usually puckered plaque
Nature of surface	Smooth	Smooth	White, usually puckered plaque
Internal structure			
Trabeculae	Obvious	Less obvious	Not visible
Periphery	Obvious	Obvious	Traced with difficulty
Colour	Pale orange to	Usually white, may	White, may have

	white	have orange/brown pigment esp. near centre	trace of brown pigment
Blood vessels	Mainly around periphery	Relatively much more obvious	Form bulk of structure
Avascular connective tissue	Forms bulk of structure (still vascular in very young CA)	Much less	Very reduced, may be almost absent

Ovarian scars (from the corpora albicantia) and corpora lutea were used to estimate ovulation rate. This technique assumes that regression of the corpus luteum at the end of an ovarian cycle results in the formation of a corpus albicans (in the presence and absence of pregnancy), which persists indefinitely in the ovary, and has been used in studies of many cetacean species, including spinner and spotted dolphins, common dolphins, pilot whales, sperm whales, and sei, fin and humpback whales (e.g. Marsh and Kasuya 1984; Perrin and Donovan 1984; Martin and Rothery 1993). However, it is possible that not every ovulation results in the formation of a corpus luteum (Perrin and Donovan 1984), in which case the ovulation rate determined using this method would be under-estimated, and it remains uncertain whether all corpora albicantia persist indefinitely (Brook *et al*. 2002). For the purpose of estimating an ovulation rate for the false killer whales in this study, however, it has been assumed that the corpora regress with age, but persist indefinitely as ovarian scars, whether or not ovulation is followed by pregnancy, thus also serving as a record of past ovulations.

Data collection protocol was similar at the two sites. Differences in procedure are noted in Chapter 2. A total of 137 female *P. crassidens* were examined (41 South African, 96 Japanese). Age data, determined from dentinal and cemental layer groups, are available for 121 females: 38 South African females (93 %), and 83 Japanese females (86 %). Reproductive status was determined for 125 females: 38 South African females (93 %) and 87 Japanese females (91 %).

Statistical analyses:

Ovulation rate: The annual ovulation rate was calculated by regressing the corpora count (number of corpora lutea and corpora albicantia) against age (as determined by the number of growth layer groups). As per Perrin and Donovan (1984) and Marsh and Kasuya (1984), corpora atretica were not included in the count. The difference in the mean corpora counts between South African and Japanese false killer whales was evaluated with a Mann-Whitney U-test.

Pregnancy: The proportions of mature females in the South African and Japanese samples that were pregnant were compared using a two-tailed Fisher exact test.

Results

a) Seasonality

Table 4.2 gives details of the size and occurrence of false killer whale foetuses. There was a single South African foetus recorded, with a body length of 148 cm. The body length of the 9 Japanese foetuses ranged from 29 cm to 174 cm with a mean of 121 cm. In schools where there was more than one foetus body length ranged from 29 cm to 167 cm (school 11), and from 72 cm to 174 cm (school 10). Their size distributions together with the sampling dates do not indicate a strong seasonality of conception.

Table 4.2: Body length composition of South African and Japanese false killer whale foetuses.

Body length range (cm)	Foetus length (cm)	School	Date of capture	Locality
20 -	29	11	March 1980	Iki Island, Japan
30 -				
40 -				
50 -				
60 -				
70 -	72	10	February 1980	Iki Island, Japan
80 -				
90 -	96	11	March 1980	Iki Island, Japan
100 -				
110 -				
120 -	126	4	March 1979	Iki Island, Japan
130 -	131, 138	10, 11	Feb., March 1980	Iki Island, Japan
140 -	148	13	September 1981	St Helena Bay, SA
150 -	159	3	March 1979	Iki Island, Japan
160 -	167	11	March 1980	Iki Island, Japan
170 -	174	10	February 1980	Iki Island, Japan

b) Gestation

The gestation period can be calculated by the method of Huggett and Widdas (1951) and using Laws' correction (1959) for length instead of weight data, which is the most commonly used technique for estimating gestation for cetaceans in general (Perrin and Reilly 1984), including delphinids (for example: Purves and Pilleri 1978 for false killer whales; Perrin *et al*. 1976 for the spotted porpoise; Amano *et al*. 1996 for Fraser's dolphins). According to this approach, two distinct phases occur – a short nonlinear phase, followed by a much longer linear phase (the slope of which can be taken to represent the foetal growth rate). Kasuya (1977) proposed the following linear interspecific relationship between the mean body length at birth and foetal growth rate of the delphinid foetus during the latter phase: $y = 0.001462x + 0.1622$, where x is length at birth in cm and y is growth rate of foetus in cm/day. Thus, for a body length estimate of 175 cm at birth, the foetal growth rate for the Japanese false killer whales would be 0.418 cm/day. Using the method of Huggett and Widdas (1951)/Laws (1959), as described by Amano *et al*. (1996), the total gestation period for the Japanese false killer whales is estimated as $(175/0.418)/0.91 = 460$ days = 15.1 months (using months of 30.4 days).

The corresponding foetal growth rate for the South African whales is 0.389 cm/day, and with a birth length of 155 cm, gives a total gestation period of 438.9 days or 14.4 months.

The gestation period for false killer whales can also be extrapolated using the following relationship between body length at birth and the duration of gestation derived for four delphinid species (Perrin *et al*. 1977) : $\log (t_g) = 0.4586 \log (L_b) + 0.1659$, where L_b is length at birth in cm. Using the body length at birth estimates of 175 cm for the Japanese whales and 155 cm for the South African whales, the gestation lengths would be 15.7 months and 14.8 months, respectively, which are close to the above estimates.

c) Ovaries

Follicular development and atresia with age

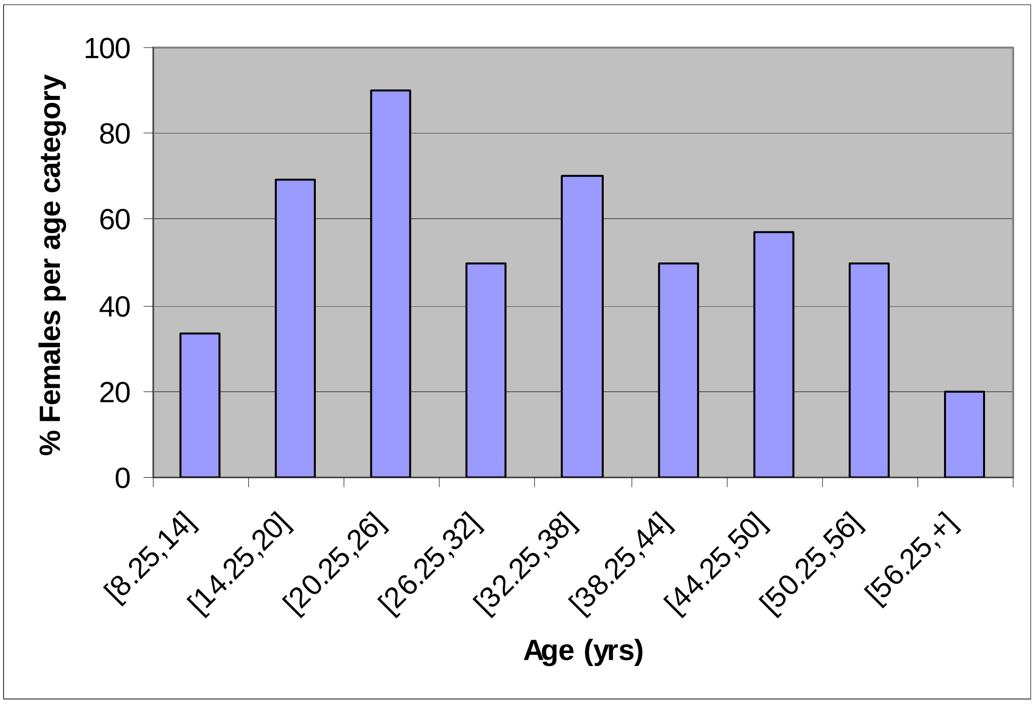

Figure 4.1: Incidence of false killer whales with Graafian follicles, atretic and non-atretic, according to age (Japan and South Africa combined).

Data on the nature and incidence of ovarian follicles and corpora in mature false killer whales with age, using dentinal and cemental layer groups, are available for 83 females. The incidence of females containing Graafian follicles, according to age, is shown in

Figure 4.1, and the relative proportions of these Graafian follicles which are non-atretic and atretic are shown in Figures 4.2 and 4.3, respectively. Following Marsh and Kasuya (1984), non-atretic, macroscopically-visible (> 1 mm in diameter) follicles have been referred to as macroscopic follicles. The percent of females with Graafian follicles increased from 57.9 % in females below 20 years of age, to 82.8 % in females aged between 20 and 40 years. Only 44.8 % (13/29) of females 40 years of age and older had Graafian follicles. Although the proportion of females with Graafian follicles that are non-atretic (i.e. macroscopic) does not appear to decrease with age, the average number of macroscopic follicles per female decreases with age (Fig. 4.2), particularly after approximately 40 years of age.

No macroscopic follicles were observed in the ovaries of 45 of the 83 (54.2 %) whales examined. This is higher than the 44 % reported by Marsh and Kasuya (1984) for short-finned pilot whales. As found by Marsh and Kasuya (1984), the proportion of false killer whales without macroscopic follicles is greater in older females - 48.1 % in females under 40 years compared to 65.5 % in females 40 years of age and older. No females 56 years of age or over contained macroscopic follicles in their ovaries.

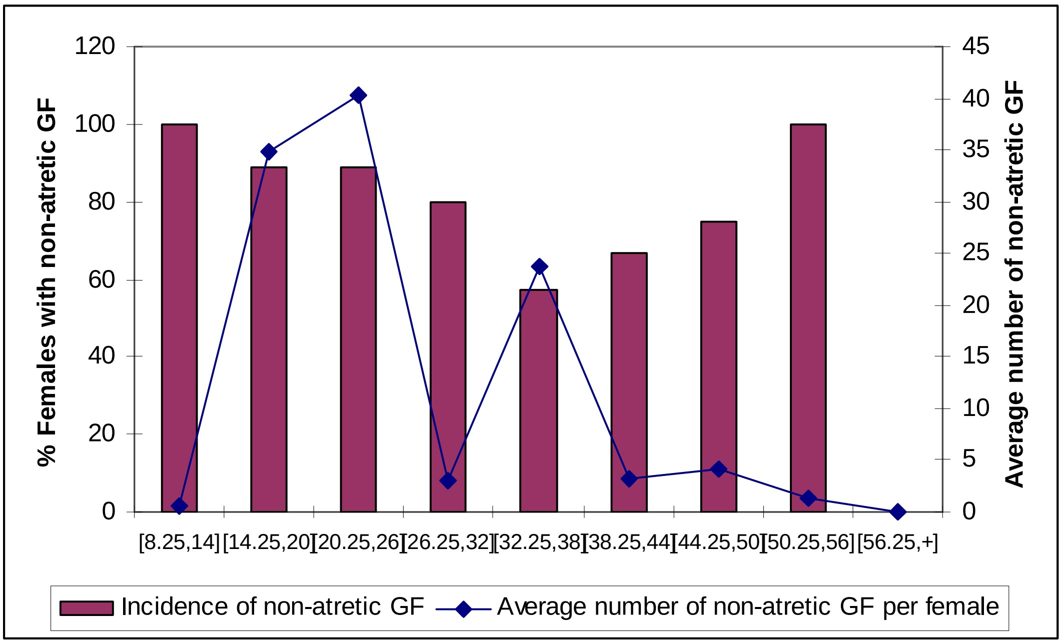

Figure 4.2: Change in the proportion of female false killer whales with Graafian follicles that are non-atretic, and average number of macroscopic Graafian follicles per female, according to age (Japan and South Africa combined).

Follicular atresia is as natural to the follicular cycle as normal follicular development, and relatively more Graafian follicles actually become atretic than proceed to ovulation (Perrin and Donovan 1984). As shown in Figure 4.3, the proportion of females with Graafian follicles that are atretic increases with age, from an average of 16.7 % in females below the age of 40 years, to over 20 % in females 40 years of age and older. The average number of atretic follicles per female is highest among older females.

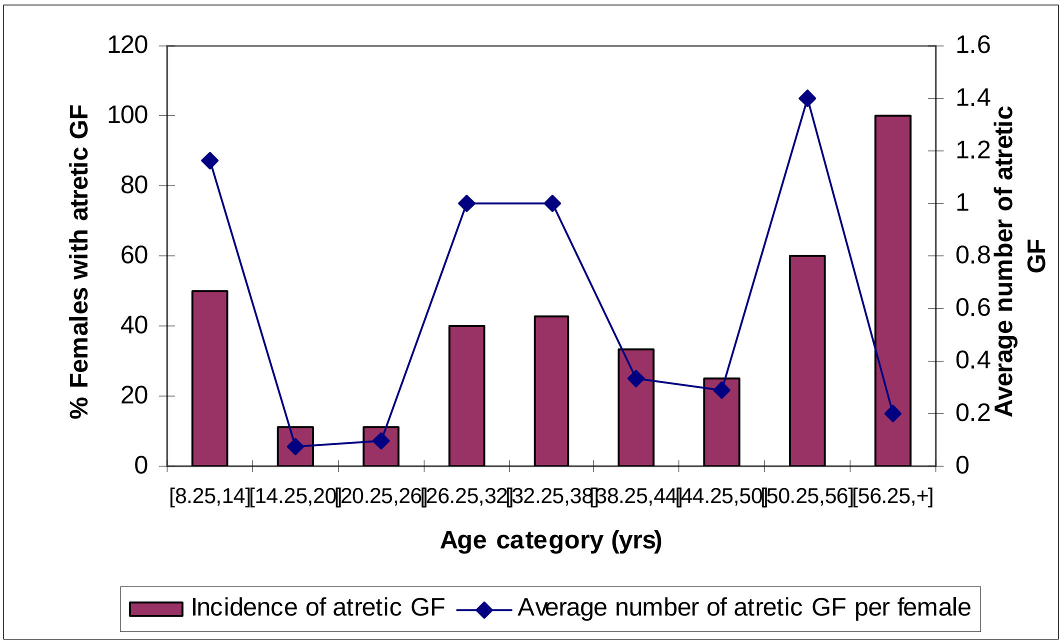

Figure 4.3: Change in the proportion of female false killer whales with atretic Graafian follicles, and average number of atretic Graafian follicles per female, according to age (Japan and South Africa combined).

The proportion of females with yellow bodies (resulting from the atresia of luteinized Graafian follicles) similarly increases with age, as does the average number of yellow bodies per females with age (Fig. 4.4).

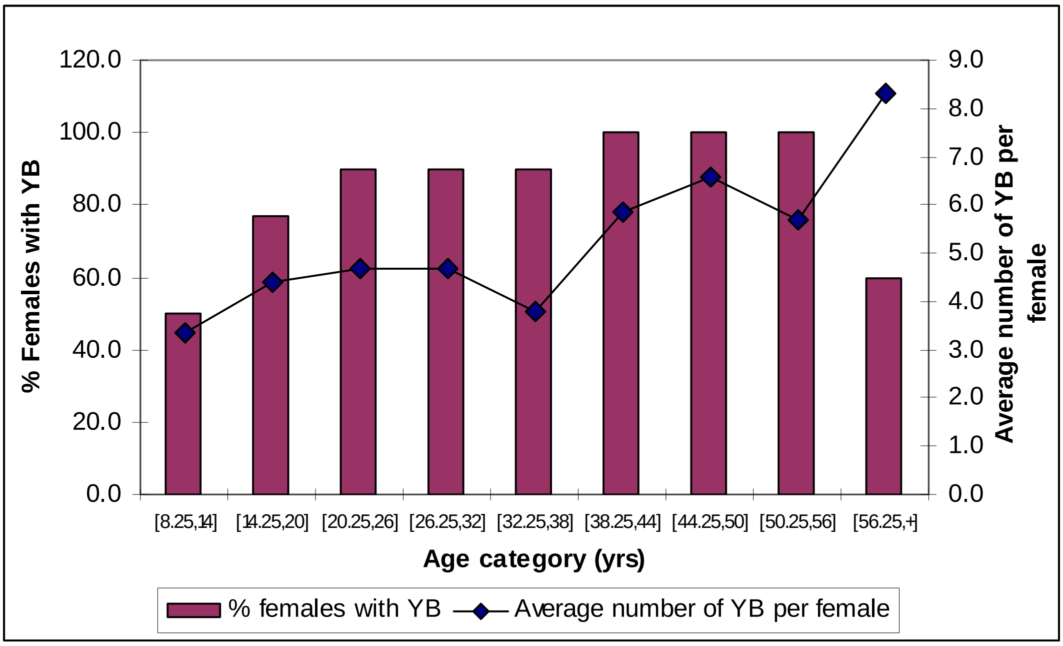

Figure 4.4: Change in the proportion of female false killer whales with yellow bodies, and average number of yellow bodies, according to age (Japan and South Africa combined).

Development of corpora

Twenty females were classed as ovulating, and 11 females as pregnant. A corpus luteum (CL) was observed in the ovaries of 29 false killer whales. A foetus was present in the uterus of 10 of these females, so the CL of these 10 females would be corpora lutea of pregnancy (CLP). A female from the Japanese sample, with a CL measuring 38.3 mm, was classified as pregnant, but no foetus length recorded. Presumably a foetus was found, but body length may not have been recorded if it was severely decomposed. Assuming the reproductive status is correct, its CL was classed as a CLP. A second pregnant female, with a foetus measuring 72 cm, had no corpora lutea recorded in the left ovary, but no data was recorded for the right ovary, which presumably contained the corpus luteum. Two corpora lutea, 11.6 and 100.9 mm in diameter, were found in the right ovary of a pregnant Japanese whale (school 11, spec 29), with a foetal body length of 138 cm. The smaller of the two corpora may be what Marsh and Kasuya (1984) and Perrin and Donovan (1984) referred to as an accessory corpus luteum, formed from an unruptured follicle, and which the former authors speculate may have an endrocrinological function. Although rare (Perrin and Reilly 1984), more than one corpus luteum per foetus in a single pair of ovaries has been documented in some species of cetaceans, most commonly in the odontocete genera *Delphinapterus* and *Monodon* (Perrin and Donovan 1984). Alternatively, the older (smaller) corpus could be from a previous unsuccessful ovulation, and nearing the final stage of regression, as described in Comrie and Adam (1938), while the larger corpus may have resulted from a successive ovulation that was followed by fertilisation (see below).

No foetus was found in the uteri of the remaining 20 ovulating females. The CL of these females were by default assumed to be corpora lutea of ovulation (CLO). No data are available for the diameters of 1 CLP and 2 CLO. The remaining 10 CLP (excluding the smaller (accessory) corpus, 11.6 mm in diameter) ranged in diameter from 38.3 mm to 100.9 mm, with a mean diameter of 54.4 mm (Fig. 4.5). The pregnant Japanese female with a CL measuring 38.3 mm but no foetus, is not shown in the figure.

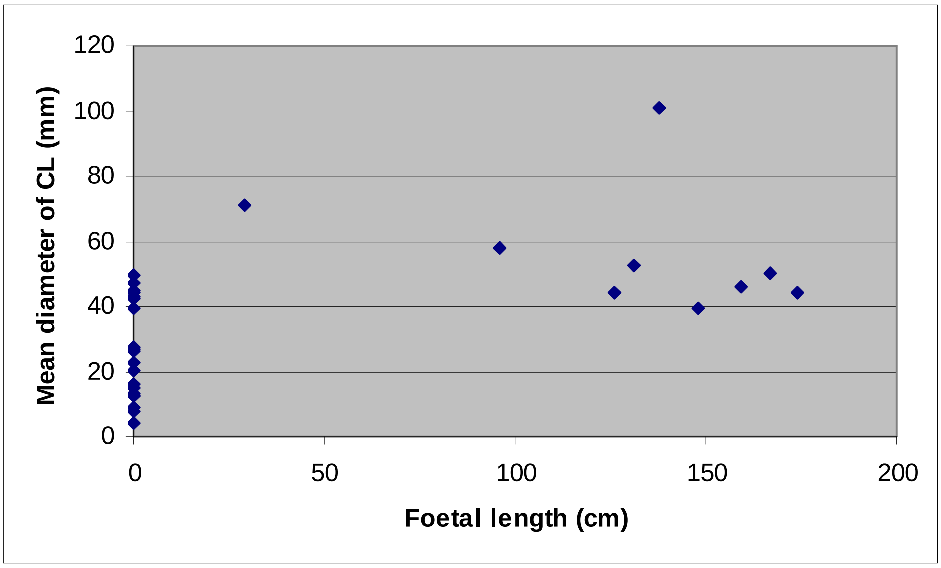

Figure 4.5: Scatter plot of the diameters of the corpora lutea of ovulation (at a foetal body length of 0 cm) and of corpora lutea of pregnancy throughout gestation of false killer whales. The pregnant Japanese female with a CL measuring 38.3 mm but no foetus, is not included, nor are any accessory CLO.

The mean diameter of 20 CLO (from 18 females) ranged from 4.2 mm to 49.7 mm (Fig. 4.5), with a mean of 26.2 mm. As can be seen from the plot, there is considerable overlap in the mean diameter of the larger CLO and of the smaller CLP. There is also no evidence of a systematic change in the mean diameter of CLP throughout pregnancy. This is consistent with the findings of Marsh and Kasuya (1984) and Dans *et al*. (1997) that there is no obvious shrinkage in the corpora lutea of pregnancy in short-finned pilot whales and dusky dolphins, respectively, throughout gestation. Perrin *et al*. (1976) reported a decline in the size of the corpus luteum of spotted porpoises during pregnancy.

The ovaries of two ovulating SA females (spec 2 and spec 9) contained two CL, with a diameter of 8 mm and 45 mm, and 27.5 mm and 46.9 mm, respectively. It is generally upheld that whales have one ovulation at each oestrus, and that in all odontocetes (and some mysticetes) several short polyoestrous cycles occur in rapid succession in the absence of fertilization (Comrie and Adam 1938; Matthews 1948; Whitehead and Mann 2000). The two corpora could thus represent successive ovulations, with or without the intervention of pregnancy. Assuming the corpora regress at the same rate, their discrepancy in size could suggest they were at different stages of regression. Another possibility is that the larger corpora in the ovaries of the two "ovulating" females were corpora lutea of pregnancy (CLP), and that these females were in an early stage of pregnancy, following on from a previous unsuccessful ovulation. Best and Lockyer (2002) acknowledged that some of the apparently ovulating sei whales with large corpora lutea in their study may actually have been in early pregnancy, and the small embryo or blastocyst went undetected. Matthews (1948) and Marsh and Kasuya (1984) similarly report that ova and blastocysts in the uterine tube are often not detected during examination. Thus, a small embryo, even if present may have been overlooked during examination of the South African and Japanese material, if it had not reached the uterus.

Comrie and Adam (1938) tabulate details of the ovaries of four false killer whales, with between 5 and 9 corpora lutea in each pair of ovaries, while the single ovaries of two unspecified females reportedly contained 10 and 12 corpora lutea. A single *active* corpus luteum of pregnancy was found, a mushroom-shaped structure, about 40mm in diameter, which falls within the range of CLP in this study. The remaining corpora lutea, in various stages of regression, ranged in thickness from 3mm to 30mm, the latter being a regressing apparently inactive corpus luteum (Comrie and Adam 1938). According to the authors, from this stage “a series can be traced down to a star-shaped corpus albicans” (p. 526). It is likely that a different terminology was used in their study and that the inactive corpora “lutea” were equivalent to corpora albicantia in the present study.

Despite their being generally larger and more compact in structure, it was not always possible to separate the CL of pregnancy of short-finned pilot whales from CL of ovulation using the criteria of size or morphology, according to Marsh and Kasuya (1984). It is possible however, that some of the “CLO” were from females which had recently aborted a small foetus or which contained a very small embryo overlooked during sampling, thus artificially inflating the mean diameter of CLO. There is in fact some indication of bimodality in the size distribution of the CLO – a group 30 mm or less in diameter and a second group 39 mm or more in diameter (Fig. 4.5). As the latter group overlaps the size distribution of known CLP, it is tempting to assume that these are actually misclassified pregnant animals (that either have very small embryos or whose foetuses were not detected owing to abortion during or immediately preceding stranding). It might be interesting to see the incidence of such “misclassified” CL in both populations and with age.

Evidence that CA regress with age

Each corpus albicans was graded as young, medium or old according to the criteria outlined in Materials and Methods. As regression is a continuous process, this gradation is somewhat arbitrary, but has been used for convenience as a comparison with the state of regression recorded in other studies (Comrie and Adam 1938; Marsh and Kasuya 1984; see Perrin and Donovan 1984 for more examples). If these relative age classifications are correct, the diameters of old corpora albicantia should all be relatively smaller than those of both the medium-sized and small corpora albicantia. Twenty seven corpora albicantia were classified as young, seventy as medium, and six hundred and thirty six as old. The mean diameters for young, medium and old corpora albicantia, summarised in Table 4.3, confirm that the corpora albicantia follow the expected pattern and regress in size with age.

Table 4.3: Diameter (in mm) of young, medium and old corpora albicantia. Skewness refers to the coefficient of skewness.

Status	N	Mean (mm)	Std Dev	Min	Max	Mode	Skewness
Young	27	15.185	4.004	7.5	23	12.30000	0.36302217
Medium	70	10.652	2.696	5	20.8	11.10000	1.01638591
Old	636	6.150	1.820	1.7	13.4	6.300000	0.30192671

Persistence of corpora with age

It is another assumption of this study that corpora albicantia persist indefinitely as ovarian scars. If the CA did not persist, one would expect the size-frequency distribution of old corpora albicantia to be negatively skewed (Marsh and Kasuya 1984). As can be seen by the coefficient of skewness in Table 4.3, this is not the case – the old corpora albicantia have a slightly positively skewed distribution. Figure 4.6 shows the change in modal diameter with age in old CA. No mode is indicated for the first age category as there are only 3 old CA, all of which differ in diameter. Modal diameter fluctuates between 6 and 6.8 mm between the ages of 14 and 44 years, but then decreases slightly, ranging between 5.2 and 5.5 mm thereafter. The change with age in mean diameter of the smallest corpus albicans in each mature female is shown in Figure 4.7. The mean diameter varies greatly in females between approximately 8 and 45 years of age. Unlike the corresponding figure in Marsh and Kasuya (1984), in which the smallest diameter remains unchanged after about 20 years of age, the trend in Figure 4.7 appears to indicate there is a reduction in diameter of the smallest corpus albicans per female with age, until at least 45 years of age, but appears to remain more or less unchanged thereafter. Despite ovulations not continuing into old age (see below), the average number of old CA per female actually increases with age (Fig. 4.6), as is expected if they do not disappear from the ovaries. However, there is a slight decrease in the incidence of old CA per female in very old whales (56 years of age and older), which suggests that some CA may be resorbed. On the other hand, there is no sign of a decline in the total corpora count in old age (Fig. 4.8), suggesting that such loss (if any) is small.

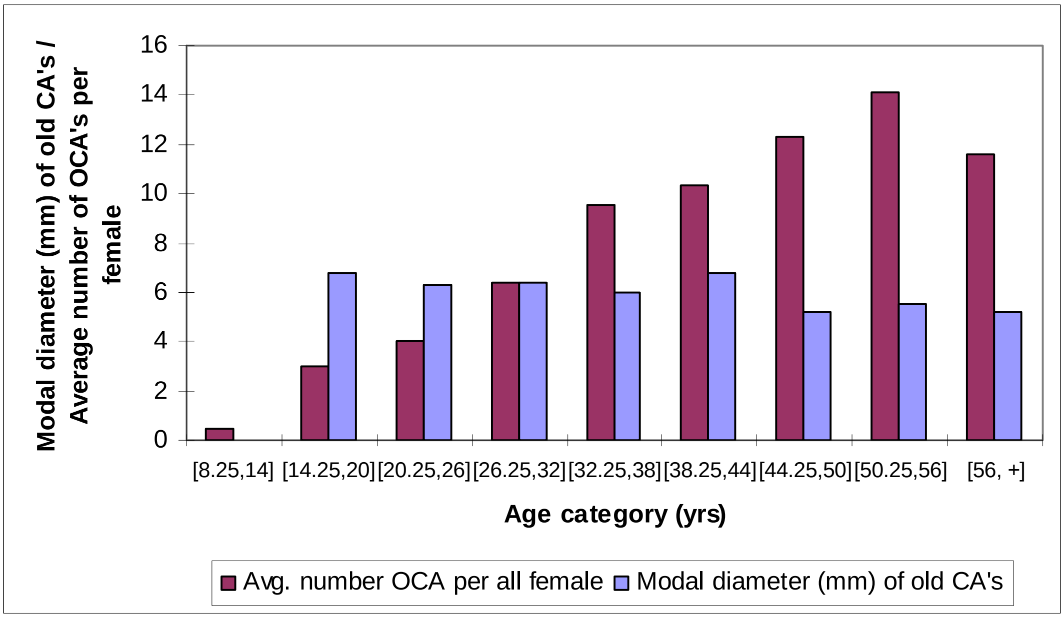

Figure 4.6: Change in modal diameter of old corpora albicantia (CA) in false killer whales, and average number of old corpora albicantia per female, according to age (Japan and South Africa combined).

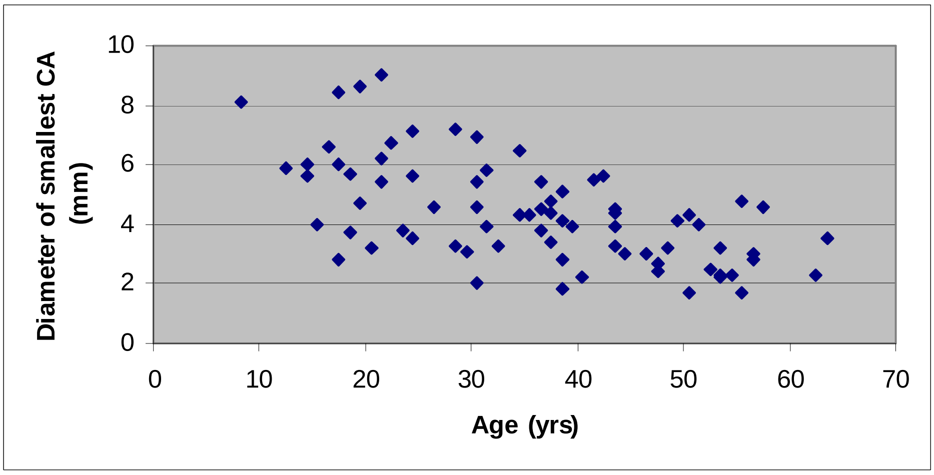

Figure 4.7: Trend in the size of the smallest corpus albicans (CA) in the ovaries of false killer whales with age (Japan and South Africa combined).

Ovulation Rate:

As discussed previously (see Chapter 2), the female false killer whales in the South African and Japanese samples were estimated to ovulate for the first time between the ages of approximately 8 and 10.5 years. The ovarian scars, resulting from the degeneration of the corpora lutea into corpora albicantia, and assumed to persist indefinitely, were used together with functioning corpora lutea to evaluate the ovulation rate. The relationship between age, as determined by the number of Growth Layer Groups, and corpora count, the number of corpora albicantia and corpora lutea per female, for the combined sample of South African and Japanese false killer whales is shown in Figure 4.8. Only reproductively mature females (with at least one or more corpora albicantia or corpora lutea observed) were included.

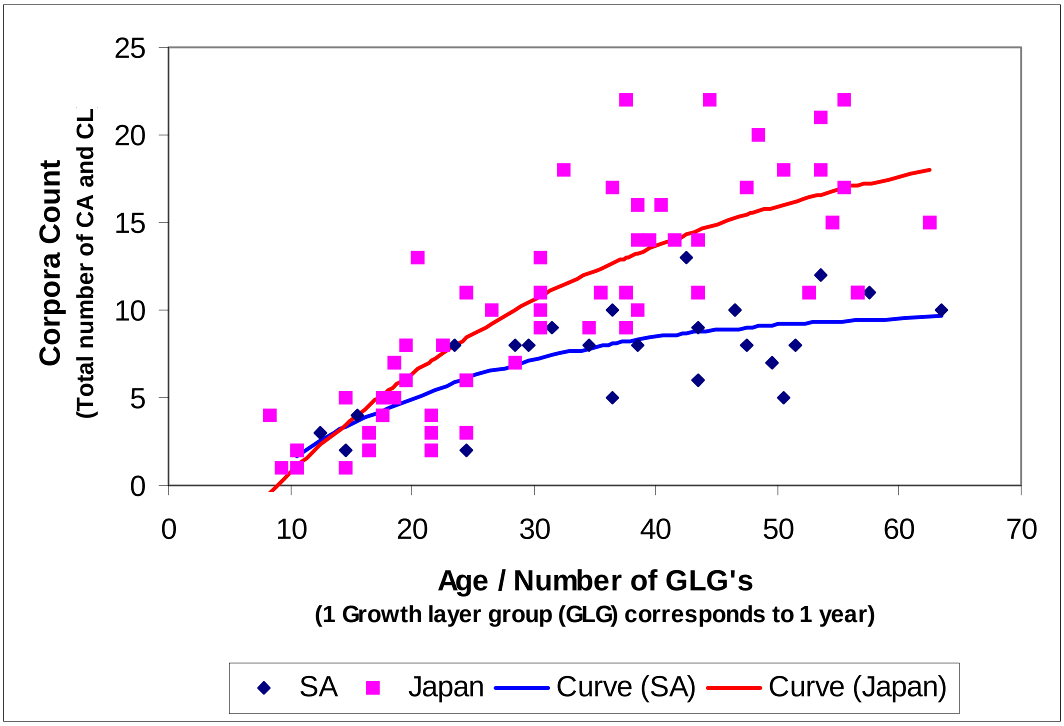

Figure 4.8: Relationship between age and corpora count in South African and Japanese false killer whales. A single-phase exponential curve has been fitted independently to the South African and Japanese female false killer whales.

Until the age of approximately 30 years, the relationship between age and corpora count for the South African and Japanese females appears to be linear (Figure 4.8). Thereafter the corpora count appears to level off in both populations, gradually reaching an asymptote. The average corpora count for the South African false killer whales (mean = 7.35; sd =3.15; min = 2; max = 13) is less than that for Japanese whales (mean = 10.87; sd = 5.90; min = 1; max = 22; Mann-Whitney U-test: $p = 0.0036$), and the corpora count in general tends to be lower for South African than for Japanese females over most of the age range. This difference becomes more pronounced with increasing age. It is most likely that the lower corpora counts in the South African sample are due to the females ovulating less frequently than the Japanese false killer whales, which would be further evidence of a comparatively lower reproductive output in the South African sample. However, the lower counts could be due to some corpora being overlooked during the examination of the South African ovaries, owing to the longer post-mortem times and the changes that might have occurred before fixation and examination. The subsequent difficulty in detecting the ovarian bodies in the poorly preserved material may have resulted in the corpora count of the South African females being underestimated, and the corpora count thus not serving as an accurate reflection ovulation history of these females. According to Matthews (1948), such post-mortem changes are to be expected as it is very difficult to obtain completely fresh material for histological purposes from whales, and decomposition starts very soon after death in these animals. Long delays between death and autopsy resulted in similar difficulties in obtaining ovarian material in a satisfactory condition from the whales stranded in the Dornoch Firth, Scotland, in 1927 (Purves and Pilleri 1978).

Testing for a post-mortem effect

In order to eliminate this possibility, a post-mortem effect was investigated. The size distribution of old corpora albicantia in females of equivalent ages was compared between the South African and Japanese samples. Under the hypothesis that the poorer condition of the South African ovarian material would result in the smaller ovarian corpora becoming less discernible and passing undetected, then the corpora from the South African sample should be relatively larger, on average, within any given age group than those from the Japanese sample. As a result of the Japanese females being more fecund, they naturally appear to have larger corpora as they contain relatively more young and medium corpora albicantia. The analysis was thus limited to old corpora albicantia to account for the lower fecundity and the relatively few young (large) and medium corpora of the South African females.

Females were stratified into three age groups (6 – 20 years; 20 – 45 years; 45 < years), to control for the naturally occurring decrease in corpus size with age, and the corpora sizes of the South African and Japanese whales within each of the groups were compared. The size distributions of old corpora albicantia in the South African and Japanese samples overall, and according to age category, are shown in Figures 4.9 and 4.10, respectively.

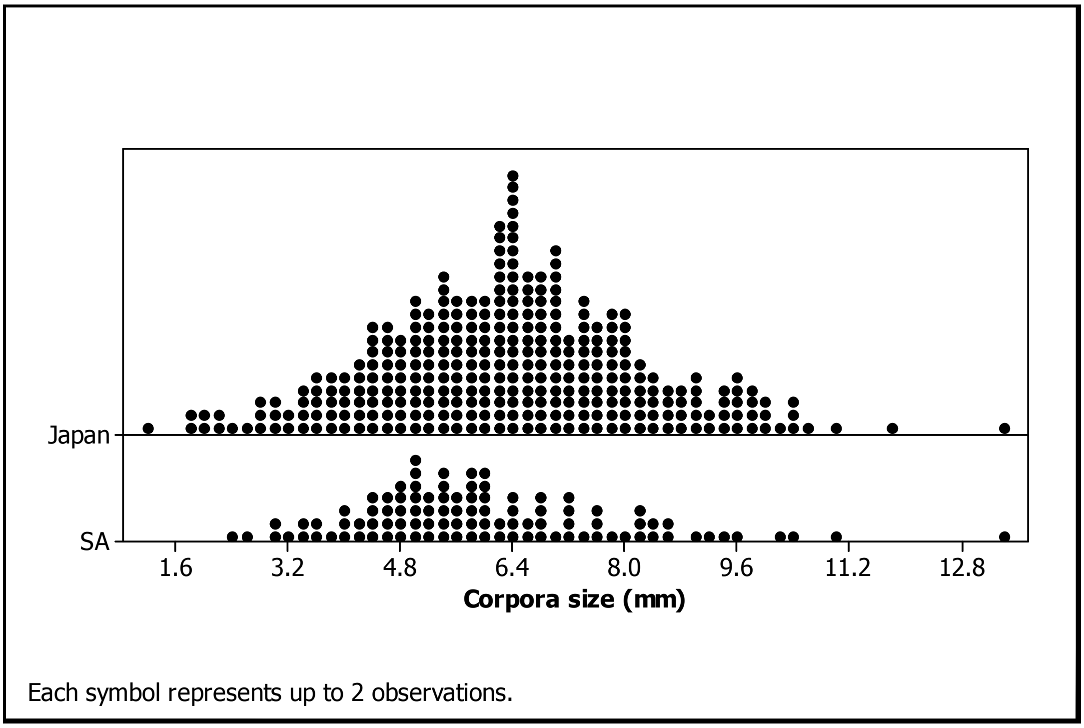

Figure 4.9: Size distributions (mm) of old corpora albicantia in South African and Japanese false killer whales.

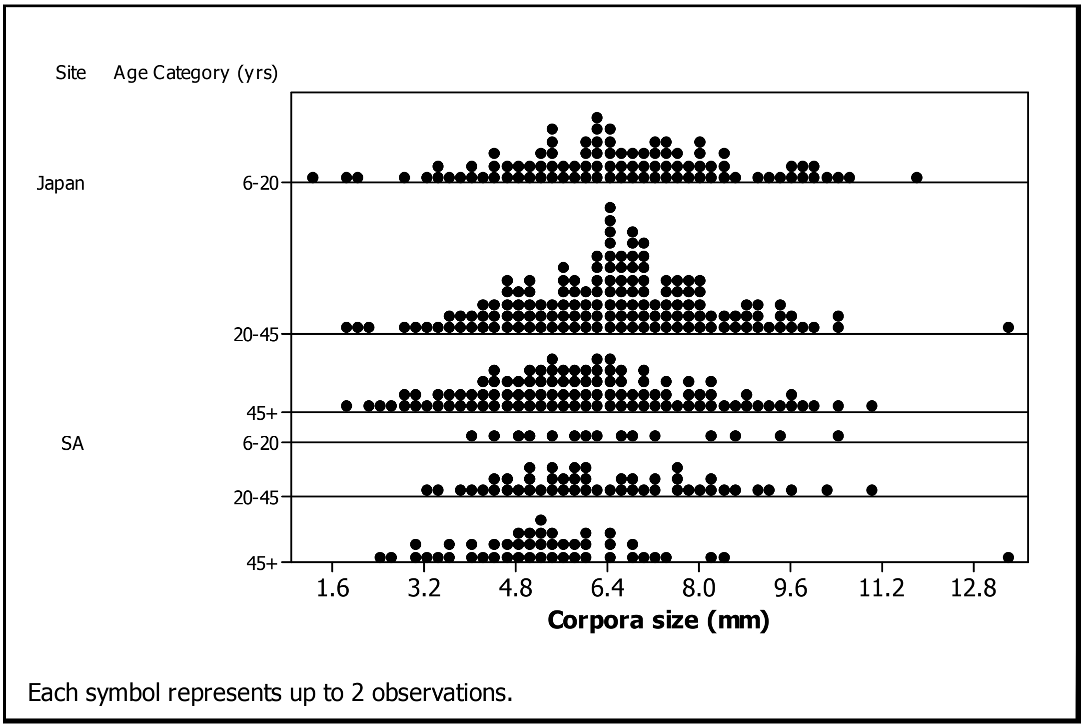

Figure 4.10: Size distributions (mm) of old corpora albicantia according to age category in South African and Japanese false killer whales.

Corpus size for the South African false killer whales (over the entire age range sampled) ranged from 2.3 mm to 13.4 mm, with an overall mean size of 5.83 mm (n =177). The corpus size for Japanese females was significantly larger (Mann-Whitney U-test: p = 0.0004), ranging from 1.2 mm to 13.3 mm, with a mean size of 6.28 (n = 599). The mean corpus size was lower among the South African females than the Japanese females in all 3 age groups (Table 4.4). The difference was statistically significant within the 6 – 20 years and the 45 + years age groups.

Table 4.4: Descriptive statistics and p-values testing for a post-mortem effect using old corpora albicantia i.e. H_0: corpus size (mm) (SA) = corpus size (mm) (Japan) *vs.* H_1: corpus size (mm) (SA) > corpus size (mm) (Japan) using the Mann-Whitney U-test. SD = Standard deviation.

Age category	Mean Corpus size (mm)		*SD*		p-value
	SA	Japan	SA	Japan	
Entire age range	5.83	6.28	1.77	1.84	0.0004*
6 – 20 years	5.92	7.52	1.19	1.86	0.0326**
20 – 45 years	6.23	6.42	1.72	1.68	0.1797
45 + years	5.28	5.82	1.70	1.87	0.0155**

*Significant at a 1% level; **Significant at a 5 level.

The hypothesis that the lower ovulation rate in the South African sample of false killer whales is due to a post-mortem effect is not supported by the results of this study. Contrary to the prediction of the hypothesis, that a post-mortem effect would have resulted in the smaller corpora not being discernible and that the South African corpora should therefore be larger on average, the South African corpora were consistently smaller on average than the Japanese corpora across all the age groupings. The larger corpus size of the Japanese females could reflect their relatively larger body size, i.e. there could be an allometric relationship between corpora size and body length. This would be consistent with the findings of other comparisons of morphometric data between the larger Japanese false killer whales and the smaller South African specimens (see Chapter 2).

Modelling the relationship between age and corpora count

The relationship between age and corpora count was subsequently studied separately for the South African and Japanese false killer whale samples. A linear model, and a single-phase exponential curve (as suggested by Marsh and Kasuya 1984), were fitted independently to the South African and Japanese data sets.

Linear model

Applying a straight line, the relationship between age (x) and corpora count (y) for the South African females is given by the equation $y = 0.149x + 1.884$, where the slope (0.149) represents the ovulation rate. The amount of variation in corpora count as explained by age in this regression was 49 % ($r^2 = 0.490$). The relationship between age and corpora count for the Japanese females is given by the equation $y = 0.333x - 0.452$, with an ovulation rate of 0.333. The amount of variation in corpora count as explained by age was 64.8 % ($r^2 = 0.648$).

Single-phase curve

The single-phase exponential model for the relationship between age and corpora count for the South African females is given by $y = 10.175 - (14.932)(0.95)^x$, where x represents age and y represents the corpora count. The curve is displayed in Figure 4.8. The amount of variation in corpora count as explained by age increased (from 49 %) to 55 % ($r^2 = 0.551$) when using this model.

The single-phase exponential model for the relationship between age and corpora count for the Japanese females (Fig. 4.8) is given by $y = 22.560 - (29.366)(0.97)^x$. The amount of variation in corpora count as explained by age similarly increased (from 64.8 %) to nearly 70 % ($r^2 = 0.683$) when fitting the exponential model. This suggests that in both cases the curve is a better fit to the data than the linear model.

Change in ovulation rate with age

The ovulation rate for the South African females, given by the derivative of the curve, $(0.797)(0.95)^x$, decreases continuously with age from 0.5287 ovulations per year in 8 year old South African females to 0.0367 ovulations per year in 60 year old females (Fig. 4.11). Among the Japanese false killer whales the ovulation rate is $(0.895)(0.97)^x$, which similarly decreases continuously with age from 0.70145 ovulations per year in 8 year old Japanese females to 0.14424 ovulations per year in 60 year old females (Fig. 4.11).

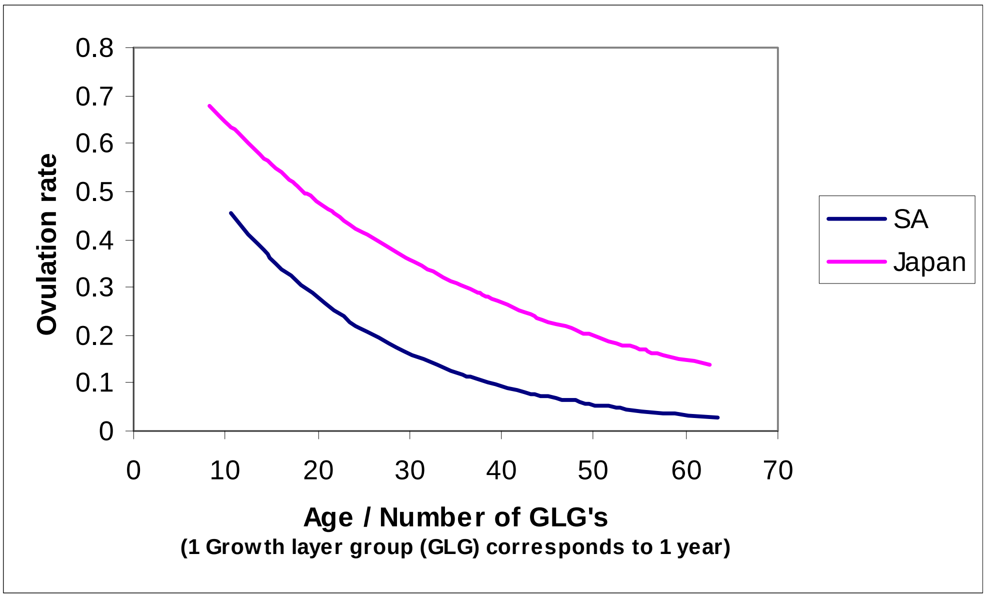

Figure 4.11: Change in ovulation rate with age in South African and Japanese false killer whales. Calculated using the formula: $dy/dx = (0.937)(0.96)^{x}$.

Pregnancy:

A total of 11 pregnant females was encountered across the two samples, 10 Japanese and 1 South African. Foetal body lengths are available for only 10 of the pregnant females. The pregnancy rate, expressed as the proportion of mature females in the group which are pregnant, is 14.93 % (10/67) for the Japanese schools combined, and 2.7 % (1/37) for the South African sample. The relative numbers of pregnant and non-pregnant females in the two populations are not significantly different at the 5 % level (Fisher exact test, two-tailed p = 0.093). As the gestation period of the Japanese females is approximately 15.7 months, the annual pregnancy rate (corrected for the length of gestation) is 11.41 %. This represents the probability of a female to conceive in a given year. Assuming a gestation period of 14.8 months, the corresponding annual pregnancy rate for the South African sample is estimated to be 2.19 %.

The apparent pregnancy rate (not corrected for the length of gestation) of mature Japanese false killer whales in successive age classes is shown in Table 4.5. The apparent pregnancy rate rose from 25 % in newly matured whales to over 37 % in females aged 20 - 26 years. Thereafter the apparent pregnancy rate declined to 25 % in 38 - 44 year old females. The oldest pregnant female was 43.5 years old. None of the 13 whales above 44 years of age was pregnant.

In contrast to the high proportion of pregnant females in very young short-finned pilot whales observed by Marsh and Kasuya (1984), the low numbers of pregnant false killer whales at a young age in this study may indicate that these young females are sub-fertile and not able to sustain a pregnancy, as reported by Sergeant (1962) for very young long-finned pilot whales. A similar description of the change in apparent pregnancy rate with age for the South African females was not possible as there was only one pregnant female in the group sampled.

Table 4.5: Apparent pregnancy rate (not corrected for length of gestation) of mature Japanese false killer whales in various age classes. Preg = pregnant.

Apparent Pregnancy Rate			
Age class (yrs)	**No. Preg. females**	**Total No. females**	**%**
8 - 14	1	4	25
14 – 20	3	11	27.3
20 - 26	3	8	37.5
26 - 32	1	6	16.7
32 - 38	0	7	0
38 - 44	2	8	25
44 - 50	0	3	0
50 - 56	0	7	0
56 +	0	3	0

Recent ovulation or pregnancy: Is there an age-related change in the incidence of females having recently ovulated or given birth?

Figure 4.12 presents the proportion of mature non-pregnant females in each age class which show evidence of having recently ovulated or given birth, as indicated by a young corpus albicans or a corpus luteum of ovulation (CLO). The frequency of such females having recently ovulated or given birth fluctuates with age, but is highest between the ages of 32 and 38 years. Thereafter the frequency falls. Only two of the 31 females over 40 years of age had any young corpora albicantia: the oldest female was a 48.5 year old resting female and the second oldest female was aged 40.5 years and was ovulating/lactating. Only five (non-pregnant) of the 31 females over 40 years contained a

CLO, the oldest being 47.5 years. None of the 16 females over 49 years of age showed signs of having recently ovulated or given birth, confirming that ovulations do not continue into old age.

Ten whales over 40 years of age contained macroscopic follicles in their ovaries; the oldest whale aged 55.5 years with 8 follicles. Two of these females, aged 40.5 and 48.5, contained both macroscopic follicles (2 and 3, respectively) and young corpora albicantia (3 and 1, respectively). None of the remaining 29 whales over 40 years of age contained both young corpora albicantia and macroscopic follicles in their ovaries.

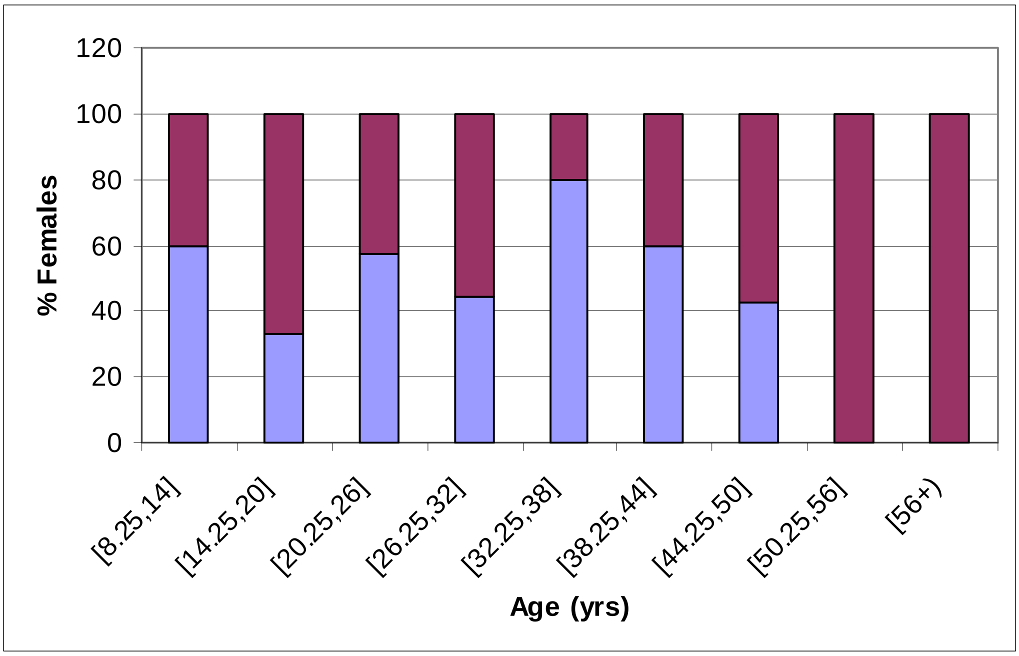

Figure 4.12: Incidence of mature, non-pregnant false killer whales with a corpus luteum or young corpus albicans according to age.

Changes in freq. of CLP and CLO with age: Does the fertility of ovulating females change with age?

Table 4.6 shows the change in frequency of CLO and CLP with age in 26 females. Age data were not available for several females. The secondary corpora lutea of the two ovulating females and one pregnant whale were excluded from the analyses.

Table 4.6: Number of females with a corpus luteum of ovulation (CLO) and pregnancy (CLP) in whales below 25 years of age, and 25 years of age and older. The proportion of pregnant females in each age class is shown.

	AGE (yrs)		**Total**
	< 25	> = 25	
CLO	5	10	**15**
CLP	8	3	**11**
Proportion Preg.	**0.615385**	**0.230769**	**26**

There is a significant decrease in the proportion of females with a CLP with age, indicating that ovulation is less likely to be followed by pregnancy in older females (χ^2 = 3.939394, p = 0.047168).

Gross Annual Reproductive Rate:

An almost equal proportion of females in the stranded and shore-driven groups are resting and not currently actively reproducing (47 % and 46 %, respectively). The proportion of pregnant and lactating females combined in each population were compared, but found not to be significantly different (p = 0.6186). Gross annual reproductive rates as per Perrin and Henderson (1984) were estimated as the female proportion of population x proportion females sexually mature (not post-reproductive) x annual pregnancy rate. The results were: 0.013 for the stranded females, compared to 0.05 for the shore-driven females.

d) Changes in reproductive activity with age/Change in proportion of various reproductive classes with age:

The youngest sexually mature female in each of the South African and Japanese samples was 10.5 and 8.25 years, respectively. By the age of 14.5 years all females (South African and Japanese) had ovulated at least once. Figure 4.13 illustrates the relationship between age and reproductive class of 88 mature females from the South African and Japanese false killer whale samples combined. Four females who were ovulating and lactating simultaneously (3 Japanese and 1 South African) are shown in a separate category. Three mature South African females were excluded as their particular reproductive status was not recorded, and could not be determined with the available data.

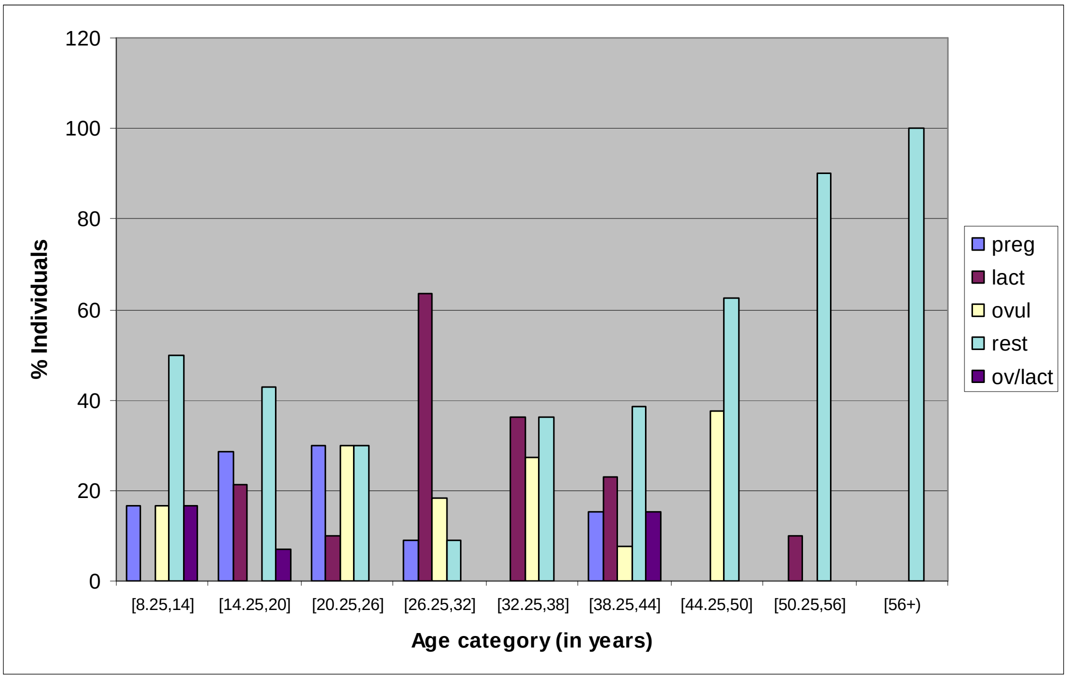

Figure 4.13: Relationship between age class and reproductive status among mature South African and Japanese false killer whales. The 4 females simultaneously ovulating and lactating are shown in a separate class (ov/lact).

The proportion of resting females (mature but neither pregnant, lactating nor ovulating) among the youngest females is quite high (ca 50 %), and then declines to a minimum (of ca 10 %) in females 26.25 - 32 years old before increasing again in older females and dominating in females over 44 years of age (60 - 100 %). Pregnant and lactating females occur in equal, relatively small (< 20 %) proportions in young, newly mature females. The proportions of pregnant and lactating false killer whales increase with age, peaking at 20.25 - 26 years of age for pregnant females and at 26.25 - 32 years for lactating females, before gradually decreasing, with the oldest pregnant female being 43.5 years old (Japan), and the oldest lactating female 53.5 years old (Japan). With the exception of the latter individual, all females 48 years of age and older were resting. The oldest female was aged at 63.5 years (South Africa). As discussed above, the oldest ovulating female was 47.5 years old (Japan), and the oldest female showing sign of having recently ovulated was 48.5 years of age (Japan).

Discussion

Seasonality

The small foetal and neonatal samples and the lack of seasonal coverage in the present data prevent an examination of seasonality in mating and calving in false killer whales. In his analysis of a larger foetal sample of false killer whales off the coast of Japan, Kasuya (1986) concluded from the widely dispersed foetal length distribution that breeding occurs more or less continuously throughout the year. However, based on the observed bimodal length composition of foetuses in his data, he tentatively suggested that two foetal peaks might occur, with an estimated interval of time between them of close to 1 year and with a parturition peak around March to April. From his calculation of a gestation period of approximately 15 months, Kasuya (1986) concluded that there is a mating peak in January to December, which would provide evidence, albeit weak, of some seasonality in breeding.

Previously, Comrie and Adam (1938) reporting on observations of fewer than 20 specimens, stated that, with the exception of 2 pregnant females, most of the ovaries of the false killer whales examined contained corpora lutea [sensu albicantia in this paper] in an advanced state of regression and no mature follicles. From this they surmised that most females were in a state of anoestrum, the duration of which lasted for some period of the winter months. More recently, hormonal studies in 2 captive female false killer whales (Atkinson *et al*. 1999) have shown a seasonal pattern of elevated levels of progesterone in summer and lower levels in winter, which, in spite of the small sample size, is suggestive of an inherent seasonality in reproduction.

The apparent seasonal in-shore migrations of false killer whales off Iki Island in Japan, between February and April, which are presumably associated with the yellowtail tuna fishery (Kasuya 1985, in Stacey *et al*. 1994), and the higher volume of food in the stomach of false killer whales in Japanese waters during winter months (Tsutsumi et al 1961, in *Stacey et al*. 1994), may be further evidence of seasonality in breeding linked to a cycle of migration and feeding. The present (cross-sectional) data allows limited comment on this due to the restricted seasonal coverage. Larger foetal samples, long term studies and female hormone profiles are needed before the possibility of seasonality in breeding in false killer whales can be properly investigated.

Gestation

The gestation lengths of 14.8 months and 15.7 months reported for the South African and Japanese false killer whales, respectively, are consistent with those calculated for false killer whales off the south west coast of Japan, which ranged from 15.1 to 15.6 months (Kasuya 1986), depending on the method used. These values also correspond to the estimates of total gestation time of 15 ½ months given for false killer whales stranded at Dornoch Firth, Scotland, by Purves and Pilleri (1978) using the method of Huggett and Widdas 1951/Laws 1959, but are somewhat longer than the length of pregnancy of 14 months determined for a captive *Pseudorca* female at Sea World, Florida using urine and blood serum hormone analyses (Robeck *et al*. 1994, in Odell and McClune 1999). While studies of captive animals can provide valuable insight into the life history of cetaceans (for example: Kasuya *et al*. 1986), the shorter duration of pregnancy observed by Robeck *et al*. (1994, in Odell and McClune 1999) could be a result of the artificial conditions of a captive environment, but is more likely a reflection of the difference between a longitudinal and cross-sectional study. Total gestation period for the closely-related pilot whale, off Newfoundland, for instance, was estimated to be 15.5 - 16 months by Sergeant (1962), while Martin and Rothery (1993), using a larger sample size over a greater part of the year, estimated gestation to last 12 months in pilot whales from the Faroe Islands. Differences in estimated gestation length between various populations may thus reflect different methodologies used in analysis rather than intrinsic differences in population reproduction.

Ovulation

Individual differences in the age at first ovulation and in the rate of accumulation of ovarian scars, and changes in ovulation rate during an individual’s reproductive life span (as well as possible errors in age determination) may all contribute to the spread of corpora counts against age that is shown in Figure 4.8. Perrin *et al*. (1976) corrected for individual differences in age at first ovulation when estimating ovulation rate in spotted dolphins, *Stenella attenuata*. This approach was not used in this study, as the sample size is too small to make a significant correction. Huge variation in the number of corpora with age has been shown to occur in many odontocetes, including short- and long-finned pilot whales (Marsh and Kasuya 1984; Martin and Rothery 1993), spinner dolphins (Perrin *et al*. 1977; Perrin and Henderson 1984) and spotted dolphins (Perrin *et al*. 1976). According to the results presented, the South African sample of false killer whales has a lower ovulation rate than the Japanese group. It is possible that the relatively higher ovulation rate in the Japanese population reflects a higher level of exploitation. Perrin *et al*. (1976) found that estimated ovulation rates were higher in the eastern Pacific population of *Stenella attenuata* than in a relatively unexploited population of the same species in Japanese waters. False killer whales off the coast of Japan have been the object of drive- and harpoon-fisheries (Miyazaki 1983). There is no known record of false killer whales being subjected to hunting or drive-fisheries off the South African coast. Thus, the higher gross reproductive rate of the Japanese false killer whales could be the result of density-dependent changes that have occurred in response to exploitation. Perrin *et al*. (1977) further suggested that the females in an exploited population could on average become sexually mature at a younger age (but be less fertile). This was not detected in a comparison of Japanese and South African false killer whales (Chapter 2).

An alternative explanation to an adaptive population response to exploitation could be that the South African false killer whales may be inherently less productive. A possible reason for this could relate differences in climate and water temperatures between the two populations of false killer whales under investigation. The colder waters inhabited by the Japanese whales are likely more productive and abundant in food than the warmer waters around Southern Africa. This would likely result in relatively higher energy intake (which could also account for the comparatively larger size of the Japanese whales) and possibly even higher fertility. Although inconclusive, analyses of stomach contents suggest there may also be differences in diet between Southern and Northern Hemisphere populations of false killer whales (see Chapter 3). These differences, if real, may translate into differences in the nutritional value of the respective prey items, and could possibly similarly affect energy intake and fertility. Another possibility, that the low reproductive rate of the South African school was somehow associated with its stranding, must remain speculation until comparable data are available for non-stranded animals from the same population.

Variability in ovulation rate is high both between and within cetacean species (Perrin and Donovan 1984; Perrin and Reilly 1984). The ovulation rate for the false killer whales stranded at Dornoch Firth, was initially reported by Comrie and Adam (1938) to be possibly several times per year, and later estimated by Purves and Pilleri (1978) to be once per year, both of which are higher than those presented in this study, almost certainly due to differences in age determination methodologies. The decreases in ovulation rate with age reported in this study compare favourably with published trends in ovulation rate with age in short-finned pilot whales, which decreases from 0.7 ovulations/year in 7 year old females to 0.14 ovulations/year in 39 year old female short-finned pilot whales off the Pacific Coast of Japan (Marsh and Kasuya 1984).

In most of the dolphin and whale species that have been intensively studied, ovulation can occur during lactation, although in general when this occurs in toothed whales it is towards the end of lactation (Whitehead and Mann 2000). Perrin *et al*. (1976) reported that almost 10 % of the lactating spotted porpoises they studied were also pregnant, most of which had ovulated and fallen pregnant halfway through the lactation period. Marsh and Kasuya (1984) similarly observed three simultaneously lactating and pregnant short-finned pilot whales in their study. Assuming a mean gestation period of approximately 515 days (Walker *et al*. 1988, in Olesiuk *et al*. 1990), the calving intervals of resident killer whales from British Colombia of 2 - 12 years (Olesiuk *et al*. 1990) would imply that some females are able to conceive while still nursing a calf. The occurrence of simultaneously lactating and ovulating females in highly social toothed whales may be of significance to species with co-operative breeding and communal suckling (see below). For example, if a lactating female falls pregnant, her young calf may continue suckling from older females within the group, while the mother concentrates on future offspring.

Pregnancy rate

The annual pregnancy rate of 11.4 % reported for the Japanese false killer whales is slightly lower than the annual pregnancy rate of 14.5 % previously calculated by Kasuya (1986) for false killer whales off the coast of Japan. Of the 89 mature females sampled in his study, 19 were pregnant, representing a proportion of 19 % (apparent pregnancy rate). Estimates of the percentage of mature females pregnant for several delphinid species ranged from 26.8 - 80.4 %, with a single value of 13.7 % falling outside the range (Perrin and Reilly 1984). On the basis of the age at sexual maturity, as deduced from the teeth, Purves and Pilleri (1978) estimated there to have been at least 30 mature females in the Dornoch Firth school. Only three females were pregnant, representing a proportion of 10 % (apparent pregnancy rate).

Different methods of estimating annual pregnancy rates, different criteria for pregnancy (foetus present; corpus luteum present), and the inherent biases of both (for example, representativeness of the sample), preclude a serious comparison of the pregnancy rates reported in this study with those of other delphinids. However, the pregnancy rates of false killer whales presented in this study, as well as elsewhere, appear to be considerably lower than those for most other delphinids. Reporting on a group of pilot whales (*G. melaena*) stranded at Dunbar, in April 1950 that they examined, Purves and Pilleri (1978) state that 12 of the 30 mature females were pregnant, representing a pregnancy rate of 40 %. A similarly high pregnancy rate (37.9 %) was reported by Sergeant (1962) for a large sample of pilot whales in Canada, while Martin and Rothery (1993) describe pregnancy in the same species from the Faroes as declining from approximately 40 % in the youngest mature females to near zero at age 55. Pregnancy rates in Puget Sound resident killer whales varied from 40.9 to 61.4 % depending on the season (Olesiuk *et al*. 1990). Thus, false killer whales may have a much lower reproductive output than other closely related species.

Persistence of corpora albicantia

Implicit in the use of ovarian scars as an indicator of reproductive history are the assumptions that every ovulation results in the formation of a CL, and that its regression in turn results in the formation of a CA which persists indefinitely and thus serves as an accurate and complete record of ovulation events.

However, not all ovulations necessarily result in the formation of a CL (Perrin and Donovan 1984), nor has evidence for the persistence of corpora albicantia been unequivocally demonstrated for all cetacean species (Perrin and Donovan 1984). While they appear to persist in some species, (for example: *Physeter macrocephalus*, Ohsumi, in Perrin and Donovan 1984; *Globicephala macrorhynchus*, Marsh and Kasuya 1984), some CA in certain species, such as *Tursiops truncatus* and perhaps *Stenella spp*., may be resorbed (or at least not detected), particularly those of successive infertile ovulations (Harrison *et al*. 1972). More recently, the validity of the above assumptions was challenged by the lack of correlation between the known reproductive history (determined by ultrasound imaging and progesterone monitoring) of a captive bottlenose dolphin and the number of ovarian scars found – the female was known to have ovulated 18 times but only three corpora albicantia were detected in the ovaries at the time of her death (Brook *et al*. 2002). Future studies with larger samples of cetaceans of known reproductive history, coupled with ovarian histology, will hopefully clarify the relationship between ovarian scars and reproductive activity. On the basis of the evidence presented in this study, it would appear that there may be some (albeit slight) resorption of corpora albicantia in *P. crassidens*, and it cannot therefore be concluded that CA persist indefinitely in this species. Consequently the ovulation count and thus ovulation rates reported in this study may be underestimated, although the degree of error is likely to be small, and mostly likely to affect the oldest females.

Follicular abundance, atresia and corpora

In conjunction with the reported decline in follicular abundance with age, there is an age-related increase in the incidence of atretic follicles and yellow bodies in the South African and Japanese false killer whales sampled. The ovulation rate declines with age in both populations. The proportion of false killer whales that have recently ovulated and/or given birth falls sharply at 40 years. Ovulation was also shown to be less likely to be followed by pregnancy in older females, i.e. the fertility of ovulation decreases with age, and there is evidence of an age-specific reduction in apparent pregnancy rates for the Japanese females.

Females are born with their full complement of oocytes, which decrease continuously until the entire stock is depleted or the animal dies (Talbert 1977). A corpora-related increase in atretic follicles was reported for sperm whales (Best 1967). The age-related decline in follicle abundance observed in false killer whales parallels the observations on short-finned pilot whales reported by Marsh and Kasuya (1984).

Age-related changes in fertility and a drop in fertility with age are well documented among mammals, including odontocetes (Marsh and Kasuya 1986). Ovulation rate and apparent pregnancy rate have been shown to decline with age in short-finned pilot whales, caught in drive fisheries off the Pacific coast of Japan (Kasuya and Marsh 1984, Marsh and Kasuya 1984). Female long-finned pilot whales around the Faroe Islands also showed reduced fertility (increased interval between births and duration of lactation) with age (Martin and Rothery 1993). A decline in pregnancy rate with age was reported for spotted porpoises (Perrin *et al*. 1976) and spinner dolphins (Perrin *et al*. 1977). Olesiuk *et al*. (1990) similarly reported a decrease in fecundity (and fertility) rate in killer whales. Marsh and Kasuya (1986) list data from several studies showing a decline with age in ovulation and/or pregnancy rates in several odontocetes species. The pattern shown for false killer whales is thus consistent with these previous studies.

In most animals the end of a female's period of reproductive capacity, reproductive cessation, corresponds to the death of the animal. However, a prolonged post-reproductive period, comparable to the post-menopause phase in human females, in which females cannot conceive or sustain a pregnancy successfully, has been shown or suggested to occur in a few species. Apart from humans, the single most convincing example of such a post-reproductive phase is provided by short-finned pilot whales (Marsh and Kasuya 1984). Female short-finned pilot whales cease to breed by 40 years of age, when they still have a mean life expectancy of 14 years (Marsh and Kasuya 1986). Using demographic data collected over many years, Olesiuk *et al*. (1990) provided evidence that strongly suggests female killer whales live well beyond the age of reproductive cessation, lending support to previous behavioural work on killer whales by Bigg (1982). Although there are indications that other odontocetes, for example spotted porpoises and spinner dolphins (Perrin *et al*. 1976, 1977), may have a similar post-reproductive phase, the evidence is inconclusive (Marsh and Kasuya 1986).

Various criteria have been utilized to identify post-reproductive females in previous studies, making interpretation of the findings often ambiguous, and meaningful comparisons difficult. In their study of short-finned pilot whales Marsh and Kasuya (1984) classified females as post-reproductive based on macroscopic and histological age-related changes to the ovaries, including semi-quantitative measures of follicular abundance, and suggested that all females older than 40 years and with only old CA and no macroscopic follicles were post-reproductive. According to their definition, a female could be lactating and post-reproductive. The same criteria were adopted by Martin and Rothery (1993) in their study on long-finned pilot whales. Olesiuk *et al*. (1990) defined post-reproductive killer whales as mature females that had not given birth for at least 10 years. Perrin *et al*. (1976) tentatively classified several spotted female porpoises as post-reproductive based on the obviously regressed appearance of their ovaries, and the absence of corpora lutea or young corpora albicantia, while Perrin *et al*. (1977) described post-reproductive spinner dolphins using a series of criteria, including: neither pregnant nor lactating, having small, withered ovaries, no developing follicles, and no young corpora albicantia.

Although a standard criterion of post-reproductivity is preferable, this may not necessarily be feasible. Researchers are frequently limited by their data – detailed histology of the ovaries may not be available for example. Furthermore, for reasons explained in Marsh and Kasuya (1986), there is no single completely reliable indicator of reproductive cessation. A decrease in ovulation and pregnancy rate with age is typical of many mammals, few of which show a post-reproductive phase. The age-related decline in fertility is not just the result of changes in the ovaries, but actually due to the total sum of changes to the reproductive system. Due to ageing of the uterus, a female can become post-reproductive and still have large numbers of follicles. Thus, the existence of a post-reproductive phase is best investigated on the basis of a variety of evidence.

In addition to the age-related decline in the various measures of fertility, the results presented here, based on macroscopic and histological examination of the ovaries, strongly suggest there is a post-reproductive phase in the false killer whales examined. Of the ten whales over 40 years of age that contained macroscopic follicles, only two contained both macroscopic follicles and young corpora albicantia. The oldest of these females was aged 48.5 years, and the second oldest was aged 40.5 years. None of the remaining 29 whales over 40 years of age contained both young corpora albicantia and macroscopic follicles in their ovaries. Similarly, with the exception of these two individuals, none of the females above 40 years of age contained young corpora albicantia. Five (non-pregnant) females between 40 and 47.5 years each contained a corpus luteum. None of the 16 females over 49 years of age showed signs of having recently ovulated or given birth. The oldest pregnant female was aged 43.5 years. The oldest Japanese female sampled was 62.5 years, and the oldest South African female was aged 63.5 years. This does not necessarily represent absolute longevity, as stated by Stacey *et al*. (1994), but provides some indication of the age to which female false killer whales can live. Given the observed decline in frequency of ovulations, and the reduced proportion of these that are followed by conception, with age, the likelihood of females above 45 years of age conceiving and successfully sustaining a pregnancy appears to be very low. Thus, assuming female false killer whales cease to reproduce at approximately 45 years of age, and assuming, as per Marsh and Kasuya (1984), that lactation continues after conceptions cease, there would appear to be a potential post-reproductive period of at about 15 years.

According to life history theory there should be no selection for living beyond the end of one’s ability to reproduce (Williams 1957, Hamilton 1966). Questions thus arise about the nature of the selective pressure for the evolution of such a seemingly counter-selective phenomenon, and the mechanism(s) responsible. Presumably a post-reproductive lifespan evolved to maximise life-time productivity and is adaptive in that it confers some sort of selective fitness advantage. In their cautionary paper, Gould and Lewontin (1979) advised against attributing an adaptive explanation to every feature or characteristic observed, and describe how not all features and behaviours are necessarily adaptive. A post-reproductive period could have no adaptive function - it could be a by product of genetic drift and non-Darwinian selection (King and Jukes, 1969, in Mayer 1982), a result of pleiotropy (Williams 1957), or, in humans, merely an artefact of our recently extended lifespan (Austad 1994). However, the relatively large number of post-reproductive females in pilot whale and killer whale groups, and the fact that the cetacean species which exhibit menopause have a matrilineal social system, are believed to indicate that the phenomenon is functional (Whitehead and Mann 2000, McAuliffe and Whitehead 2005).

Several hypotheses have been advanced as to how or why a post-reproductive phase may have evolved, each with varying support (Packer *et al*. 1998, Whitehead and Mann 2000, Shanley and Kirkwood 2001, Macdonald Pavelka *et al*. 2002, Lahdenpera *et al*. 2004). According to the “Grandmother” Hypothesis selection will favour a prolonged life after reproductive cessation through mother-child food sharing – and post-reproductive females may increase their inclusive fitness by directly investing in and providing additional parental care to grandoffspring (Hawkes *et al*. 1998). The “Stop-early” Hypothesis proposes selection acts to terminate reproductive ability ahead of natural mortality and the increased risk of child-bearing, and that post-reproductive females gain greater fitness success by concentrating on and helping to improve the survival of their existing offspring than they would through continued reproduction. Central to both theories, and adaptive menopause theories in general (Austad 1994), is the assumption that there is a continually increasing maternal mortality risk with age, and that menopause results from a trade-off between calf-bearing and calf-rearing. The main difference between the “Stop-early” and the “Grandmother” Hypotheses lies in whether post-reproductive females enhance the survival of offspring only, or if there is also a grand-offspring benefit. As with many theories on the evolution of particular life history characteristics or behaviour, the reality might involve a combination of elements from both, and/or be species-specific.

Adaptive significance of a post-reproductive phase

False killer whales share several life history characteristics with the two other species, killer whales and short-finned pilot whales, shown to have a post-reproductive phase. All three species have low life-time productivity, and produce a single calf at a time, are sexually dimorphic indicating male parental care is likely to be low or non-existent, and are known or believed to exist in stable matrilineal groups of closely related females, with strong, mother-child associations and a long period of dependency (Kasuya and Marsh 1984, Bigg 1982, Whitehead and Mann 2000).

False killer whale calves can continue to suckle for over two years (Clarke and Odell 1999). With such a long period of dependency and heavy maternal investment, and low fecundity, the survival of any one calf is very important. Post-reproductive females may help to ensure better calf survival (even if not their own offspring) through protection and provisioning of resources, nutritional and otherwise, and thereby increase their own inclusive fitness because calves are likely to be genetically related in these matrilineal pods. Food sharing among false killer whales has been reported by Connor and Norris (1982), and was frequently observed in a study of false killer whales around the main Hawaiian Islands (Baird *et al*. in press).

Lactation is also energetically expensive (Lockyer 1981 in Best *et al*. 1984). Thus, in species with co-operative breeding, post-reproductive females may relieve daughters from their lactating duties so enabling the daughter to redirect her energies on producing more offspring. Another advantage of communal suckling is that if a lactating female should die, her calf could obtain milk from another lactating female, or alternatively, if the mother should lose its newborn calf, she could provide milk to and contribute to the survival of other nursing calves in the group. Best *et al*. (1984) speculated that a mother sperm whale that loses her newborn may resume nursing a previous calf or the juvenile of another female, while Gordon (1987 in Whitehead and Weilgart 2000) describes observations of an identified sperm whale calf suckling from different females, and two similar-sized calves simultaneously suckling from the same adult. Although there is no direct evidence of communal suckling in false killer whales, the presence of more lactating females than calves among the relatively less fertile South African whales in this study could suggest communal suckling. In species with low reproductive potential and stable groups of closely related females, this seems to be an advantageous strategy to adopt. There exist several examples of how cetaceans can respond to adverse environmental changes. Seemingly in response to increased whaling pressure, the proportion of pregnant females at higher ovarian counts, and thus presumably age, increased in sperm whales off Durban (Best 1980). This ability for ovulation success to improve in females close to reproductive senescence may provide an important buffer in the event of the school being subjected to environmental conditions that adversely affect survival. At the opposite end of the reproductive window period, the age at sexual maturity was found to be demonstrably lower in heavily hunted populations of long-finned pilot whales (Martin and Rothery 1993) and spotted porpoises (Perrin *et al*. 1976), possibly in response to exploitation pressure, as discussed in Chapter 3.

Old, post-reproductive females may also serve as a reservoir of social/cultural information and knowledge (McAuliffe and Whitehead 2005). In their paper Weilgart *et al*. (1996) discussed the similarities in life histories and social organisation of sperm whales and elephants. In addition to being large sized, both species are long-lived, and large-brained, which may account for the complex social organisation they both appear to have (Connor *et al*. 1998). Females of both typically live in highly social, closely related family units, providing communal care of offspring, while males live more solitary lives. These shared characteristics of elephants and sperm whales are thought to have given rise to a number of associated benefits, one of which might conceivably be the accumulation and storage of experience and knowledge among the group’s older members (Weilgart *et al*. 1996). The idea that older elephant females may serve as reservoirs and conduits of social knowledge was later expanded on by McComb *et al*. (2001), who indicated that their absence (through removal) could be detrimental to the population. Although still a relatively under-researched topic, culture similarly appears to be an integral aspect of the lives of matrilineal whales (Whitehead 1998, Rendell and Whitehead 2001) and may offer insight into the adaptive role of older, post-reproductive females.

Conclusion

Based on the limited data analysed in this regard there is no evidence of seasonality in conception in the false killer whales studied. Several population differences have emerged. South African females have a lower fertility/productivity than the Japanese females, as indicated by their relatively lower ovulation and pregnancy rates, and gross annual reproductive rate. Gestation is estimated to last 14.8 months in the South African false killer whales, and 15.7 months in the Japanese false killer whales. There is a decrease in follicular development and in the incidence of macroscopic follicles with age in both groups. The incidence of atresia and the proportion of yellow bodies increase with age. There may be some resorption of corpora albicantia in old female false killer whales. Ovulation rate declines with age in both groups. Apparent pregnancy rate declines with age in the Japanese false killer whales, while the proportion of resting females increases with age. The frequency of females that have recently ovulated or given birth declines sharply at 40 years, and ceases completely in females over 48.5 years of age. The fertility of ovulations also decreases with age. Anatomical changes in the ovaries and age-specific patterns of fecundity collectively indicate that female false killer whales cease to reproduce at approximately 45 years of age, while they still have a life expectancy of at least 10 - 15 years. Although the exact role of post-reproductive females is presently unclear, the development of a significant post-reproductive phase may be an adaptive response to the overall low reproductivity of the species, and contribute to the survival of offspring and possibly grandoffspring.

CHAPTER 5

CONCLUSION

> "They (the false killer whales) had struggled vigorously and some were still alive more than 24 hours after stranding. By their exertions they only succeeded in embedding themselves more firmly in the sand, so that when examination was made some were half buried in silted sand and others were lying partly immersed in troughs they themselves had made…It is easy to imagine that, when the animals do get away from their normal environment, the form of coast on which they have habitually been found would be precisely the one to represent the greatest degree of embarrassment to animals accustomed to deep water."

An extract from a Scottish Naturalist article, quoted in Norman and Fraser (1948, p. 298)

Along with the degree of accompanying embarrassment, the reason why cetaceans in general, and false killer whales in particular, mass strand remains unknown. This stranding phenomenon has however, enabled researchers to achieve a better understanding of cetaceans, particularly the rarely encountered species, such as *Pseudorca crassidens*, about which very little would otherwise be known.

In this study I set out to expand our current understanding of the life history, growth and reproduction of false killer whales. I had at my disposal two data sets with which to address this objective: data collected from a mass stranding of 65 false killer whales off the coast of SA, and a set of data obtained from several drive fisheries off Iki Island, Japan.

Limitations and shortcomings

Despite the auspicious opportunity that they have provided, the two data sets have individual biases/shortcomings, as well as limitations common to both. On a personal level, I experienced some difficulty reconciling all the data distributed among several data sheets, often as a result of inconsistencies in the data material. Various people had at different stages contributed to the collection of this data, sometimes working on the same specimens and recording different information (e.g. macroscopic information about the ovaries vs number of dentinal and cemental growth layers groups in the teeth), sometimes capturing similar but additional information from the same specimens (number of corpora lutea in the ovaries vs the number and diameter of corpora lutea in the ovaries). Specimen numbers given did not always correspond between the various data sheets, which required some sleuth work and the process of elimination to match the relevant data to the correct specimen.

The difficult working conditions at a mass stranding, and in particular the delay between death and data capturing of the South African material, are also likely to have resulted in post-mortem changes to the material. A second drawback of material used in this study relates to the cross-sectional nature of both the stranded and shore-driven data, i.e. both are event-driven data. Thus, there are once-off single observations for individuals; there are no long-term repeated observations of several animals, or even repeated observations of different animals over a time period. Furthermore, where previously modeled relationships between various parameters were used, it is important to acknowledge that these estimates are often tentative. For example, in the determination of foetal growth rates, a prior estimate of body length at birth was used. Uncertainty in this estimate of body length, resulting from an inadequate sample size, for example, casts doubts on further calculations involving body length at birth, such as foetal growth rate and/or gestation period. Where direct comparisons are made between the two data sets, for example, between stranded and shore-driven, the possible confounding effects of population differences due to geography are difficult to evaluate.

Despite these limitations, many interesting findings have emerged from this study on false killer whales. The results presented in Chapter Two indicate clearly that there are consistent differences in growth and size between the Japanese and South African samples of false killer whales. This is the first such study to provide firm evidence of a distinct difference between southern- and northern occurring populations of false killer whales. Male false killer whales are larger than females irrespective of geographical location, and there is no geographical variation in the relative degree of size dimorphism. The delay in attainment of sexual maturity in males is consistent with the observed sexual dimorphism, and may be associated with a polygynous mating system.

Although the reason why false killer whales mass strand are still unclear, stranded groupings of false killer whales were found to be significantly larger than either shore-driven or sighted schools of false killer whales. The whales involved in mass strandings may thus represent an amalgamation of several units that have come together shortly before the stranding. Maturing males are largely absent from both the stranded and shore-driven samples, likely owing to their dispersal during this period. An unexpected finding in Chapter Three is the apparent existence of differences in fertility between the stranded South African and the shore-driven Japanese specimens. These differences in reproductive output may explain part of the differences in group composition observed between the two samples. The same reasons cited for differences in body size and growth between the South African and Japanese samples, namely food availability and nutritional levels, could be responsible for the relatively lower reproductive output of the South African specimens. This reduced fertility could be a feature of stranded groups of false killer whales in general, or could merely reflect environmental differences.

In addition to confirming the difference in fecundity between the stranded South African and shore-driven Japanese samples, Chapter Four provides convincing evidence of the existence of a post-reproductive phase in female false killer whales. Anatomical changes in the ovaries, together with the age-specific patterns of fecundity collectively indicate that female false killer whales cease to reproduce at approximately 45 years of age while still having a life expectancy of 15 years.

Future research

Several issues remain unresolved, and many further questions have arisen. The taxonomic significance of the observed differences between the South African and Japanese samples remains at present unclear. Given what is presently known about false killer whales, namely their strong social bonds, tendency towards site philopatry, the existence of genetic differentiation between adjunct populations, the several differences in morphological growth between geographically dispersed populations is interesting. These features and observations suggest they already reflect genetically distinct populations, which, given the correct circumstances, could eventually speciate. Alternatively, the observed differences in morphology and growth could merely reflect racial/population differences and/or environmental/geographical differences to which each is subjected. Larger samples are required before the taxonomic implications, if any, and the significance of these North-South differences can be rigorously evaluated.

Due to the ephemeral and dynamic nature of cetacean groupings, the study of group structure and composition necessitates a context specific approach. The composition and size of groups is likely to depend on the function, geography, energetic requirements, and levels of predation. Furthermore, the relationships between factors affecting group size and sociality are complex and not necessarily the product of only one factor; there may a multitude of contributing factors interacting with each other. While carcass studies have provided much of what is known about false killer whales, the association patterns and social organisation of false killer whales will be best elucidated by long-term behavioural studies of individually recognised whales, coupled with genetic analyses to determine relatedness, and confirm philopatry. The questions of where maturing males go and what becomes of them when they reach maturity can also only be addressed with such long-term behavioural and genetic studies to determine relatedness within group. Thus, no single methodological approach will necessarily yield all the answers. Long-term studies of individually recognised individuals will answer some questions, but do not allow researchers to obtain age estimates from teeth, or information on reproductive status from ovarian or testicular samples. Carcass studies, on the other hand, offer those opportunities and information, but have there own limitations, as discussed above.

In order for the incidence of post-reproductivity in cetaceans to be properly investigated, some standard criteria for identifying post-reproductive females is required. At present various definitions have been employed, which not only make meaningful comparisons between studies impossible, but essentially reflect our lack of detailed understanding of the biology underlying this phenomenon in cetaceans. According to Marsh and Kasuya's (1984) criteria, a lactating female can be post-reproductive. Thus, part of the female's reproductive system is still operational. This is not merely an issue of semantics or criteria, because if Marsh and Kasuya are correct that a female can be post-reproductive and still lactating, this suggests that there may be a number of stages of gradual shutdown of the reproductive system until complete cessation of all reproductive function. Ideally we need to consider the total changes to the female's reproductive tract at menopause and beyond. Secondly, in order to elucidate the adaptive role of post-reproductive females, and the fitness currency they might provide to kin, individual-based behavioural and molecular studies are necessary. A useful approach for future studies would be to examine closely the relationship of post-reproductive females with other members in the group. Comparative studies of how the presence/absence of post-reproductive females affects the fitness of their offspring and grandoffspring (and hence themselves) may also yield answers. The evaluation of the costs of parturition and a quantitative assessment of how these costs might vary with age is also indicated. The relationship between length of lactation and maternal age needs to properly investigated and may also provide clues to the role of post-reproductive females.

The approach of "we'll take what we can get" and "making the best of the available data" appears to underpin many studies of cetacean biology. Researchers have admittedly been constrained on a number of fronts, not least of which is the usual inaccessibility to the study animal, an unavoidable consequence of their aquatic and frequently wide-ranging and off-shore lifestyle. Advances in our knowledge and understanding of the biological systems of cetaceans thus occur in often painful increments. However, as our knowledge increases, we can re-position earlier findings within a broader comparative framework and identify additional avenues of potential enquiry. It is through this gradual accumulation, and continued innovations in research methods that we will be able to fill in the gaps in our current knowledge and better understand the biology of cetaceans.

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APPENDIX

Table A2.1: Growth curve parameters for the 2- and 3- parameter logistic equation: y = b1/(1 + exp(-b2. (age – b3))), and the 2- and 3- parameter Gompertz equation: y = b1.exp (-b2. exp(-b3age)), where y is the length of the animal, b1 is the asymptotic value, b2 is the growth rate constant, and b3 is the point of inflection, C.I. is the 95 % confidence interval for the growth rate, and r^2 is the coefficient correlation.

SITE SEX	N	MODEL	Asymptotic value (b1)	Growth rate constant (b2)	Point of inflection (b3)	Confidence Interval	r^2
South African Females	38	Logistic 3	391.3619	0.1153	-5.226350	0.0743-0.1563	0.83928
		Logistic 2	387.4943	0.2074			0.78214
		Gompertz 3	391.7198	0.1067	-7.295565	0.0683-0.1451	0.84111
		Gompertz 2	385.3993	0.2565			0.74011
Japanese Females	83	Logistic 3	432.4405	0.1924	-0.500319	0.1478-0.2369	0.83111
		Logistic 2	431.8896	0.2110			0.82928
		Gompertz 3	433.2932	0.1604	-2.35447	0.1293-0.2048	0.83751
		Gompertz 2	429.1490	0.2722			0.78612
South African Males	20	Logistic 3	476.2148	0.0851	-1.849334	0.0408-0.1295	0.80546
		Logistic 2	473.8516	0.0964			0.79911
		Gompertz 3	478.9073	0.0734	-5.913934	0.0319-0.1149	0.80702
		Gompertz 2	464.4835	0.1237			0.73597
Japanese Males	45	Logistic 3	527.3476	0.1058	0.563640	0.0765-0.1352	0.92743
		Logistic 2	525.3436	0.1030			0.92609
		Gompertz 3	530.6982	0.0892	-3.162110	0.0628-0.1155	0.93008
		Gompertz 2	511.4311	0.1694			0.88570

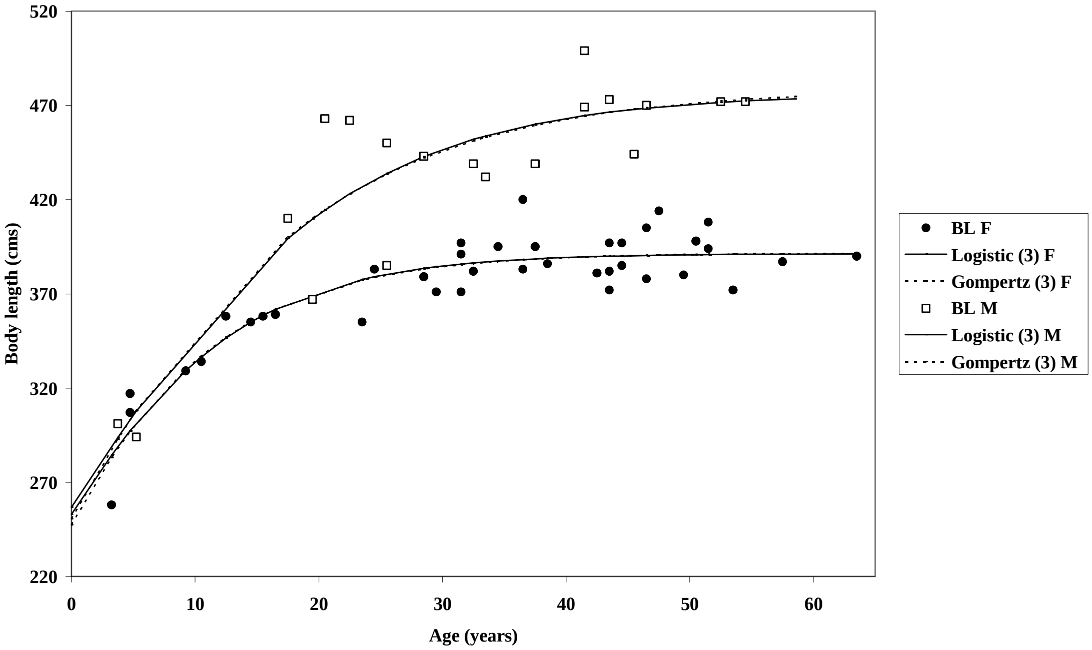

Figure A2.1a: 3-Parameter Logistic (solid lines) and Gompertz (broken lines) growth curves for female (filled circles) and male (open squares) false killer whales stranded at St Helena Bay, South Africa.

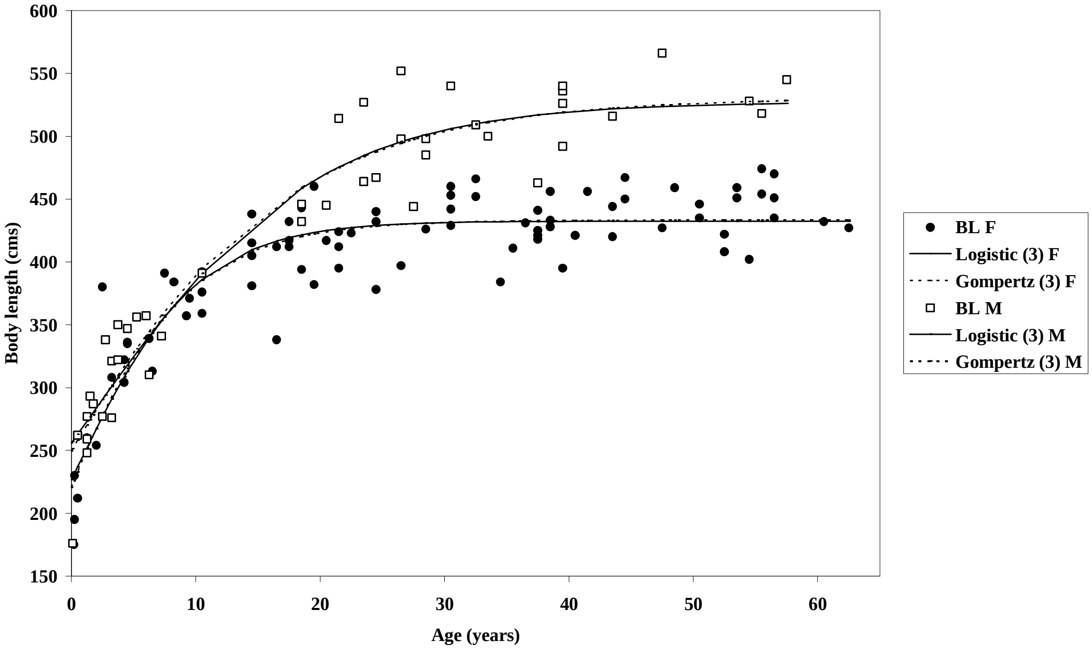

Figure A2.1b: 3-Parameter Logistic (solid lines) and Gompertz (broken lines) growth curves for female (filled circles) and male (open squares) false killer whales taken at Iki Island, Japan.