False killer whales (*Pseudorca crassidens*) from Japan and South Africa: Differences in growth and reproduction

Inês M. Ferreira, Mammal Research Institute, University of Pretoria, ℅ Iziko South African Museum, Box 61, Cape Town, 8000 South Africa; **Toshio Kasuya**, 5-30-32-3 Nagayama, Tama, Tokyo 206-0025, Japan; **Helene Marsh**, School of Earth and Environmental Sciences, James Cook University, JCU Post Office, Townsville, Queensland 4811, Australia; **Peter B. Best**,[1] Mammal Research Institute, University of Pretoria, ℅ Iziko South African Museum, Box 61, Cape Town, 8000 South Africa.

Abstract

Age and reproductive information for 65 false killer whales stranded in South Africa in 1981 are compared with similar material from 156 animals examined from drive fisheries in Japan in 1979 and 1980. Sizes at birth, sexual maturation, and physical maturity all indicated that both sexes were 10%–20% larger in Japan than South Africa. Females reached sexual maturation at similar ages (8–10.5 yr) in both populations, and although sample sizes were too small to establish male ages at puberty precisely the ranges in Japan (10.5–18.5 yr) and South Africa (5.25–17.5 yr) were not inconsistent. The initial ovulation rate for females from South Africa was 65% lower (and the apparent pregnancy rate 82% lower) than those from Japan and there were fewer animals ≤ 2 yr old within the school, but the magnitude of these differences suggests that the stranded school's reproductive performance was probably impaired. Collectively these comparisons and the literature indicate substantive size differences between false killer whales in different populations, although the patterns of growth appear similar. Firm conclusions about any geographical differences in reproduction require additional data.

Key words: false killer whales, *Pseudorca crassidens*, age, growth, reproduction, North Pacific, South Atlantic.

False killer whales, *Pseudorca crassidens*, are distributed worldwide in tropical and warm temperate seas, occasionally extending into cold temperate regions (Baird 2008): approximate polar limits to distribution have been described as 50°N and 50°S (Odell and McClune 1999), although the northern limit of the summer distribution of this species in the western North Pacific is around 40°N (as illustrated in Miyashita 1983). In the southern African subregion, the species has been recorded from Gabon on the Atlantic coast to the Seychelles in the Indian Ocean, with most sightings in water >1,000 m deep but coming close inshore occasionally: at least six mass strandings have occurred in South Africa since 1928 (Best 2007). Despite this widespread distribution, genetic sampling (mainly in the eastern Tropical Pacific but including samples from the North Atlantic, the Indo-Pacific region, and Australia)

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[1] Corresponding author (e-mail: peter.best@axxess.co.za).

has revealed considerable population structure, both between and, in the case of the North Pacific, within ocean basins (Chivers *et al.* 2010). In the latter case, a small population associated with the Hawaiian Islands appears to be genetically distinct from animals occurring further offshore (Chivers *et al.* 2007), and this separation is supported by longitudinal studies of individually identified individuals (Baird *et al.* 2008, Baird 2009) and short-term studies of individual movements (Baird *et al.* 2010). Elsewhere, photo-identification studies have confirmed long-term site fidelity and individual associations for false killer whales off Costa Rica (Acevedo-Gutierrez *et al.* 1997), and morphological comparisons have confirmed interocean population differences (Kitchener *et al.* 1990).

Baird *et al.* (2008) have pointed out that dedicated studies of false killer whales are frequently hindered by the rarity with which the species is encountered at sea, resulting in a very low rate of data accumulation. This situation makes specimen materials from mass strandings and dedicated fisheries important sources of information, not only for investigating population distinction but also for elucidating the basic biology of the species.

In this paper we analyze data from a stranded school in South Africa and from several shore-driven schools in Japan to describe the patterns of growth and reproduction in false killer whales and investigate what differences, if any, exist between these and other populations.

Methods

The South African material was collected from 65 false killer whales that stranded en masse on the west coast of the Western Cape Province on 19 August 1981, of which 56 were found over a 1.5 km stretch of beach in St. Helena Bay (32.781ºS, 18.1ºE). No known attempts to refloat animals were made. As scientists reached the site only two days later, the fixation of the material was suboptimal to poor. Data are available from 63 individuals (41 females and 22 males). Additional information from several other South African strandings was considered when relevant (*e.g.*, length at birth).

The Japanese material originated from 156 specimens (96 females and 60 males) from the following six schools taken in drive fisheries at Iki Island (33.8ºN, 129.718ºE), designed as culling operations to reduce fishery interactions (Kasuya 1985): 20 animals on 8 March (4 females, 1 male examined), 138 on 15 March (20 females, 15 males), 160 on 19 March 1979 (16 females, 12 males), 10 on 22 February (2 females, 4 males), 80 on 27 February (38 females, 18 males), and 155 on 6 March 1980 (16 females and 10 males). The date of capture does not necessarily correspond to the date of death, as groups were kept alive in a netted bay until sampled. As many false killer whales as possible in each school were randomly selected and systematically examined while fishermen independently slaughtered and processed their catch.

Field Procedures

After recording sex and total length (cm), one to three adjacent teeth were removed from the center of the lower jaw of each specimen and fixed in 10% buffered formalin (Japan) or 70% ethanol (South Africa). The presence and color of milk was checked by pressing and then cutting the mammary gland. The maximum thickness (cm) of one gland was recorded at its widest point, and a sample fixed in 10% buffered formalin (South Africa). Both ovaries were collected and the presence of corpora lutea, corpora albicantia, or large follicles recorded before the ovaries were fixed in 10% buffered formalin. The maximum diameters (cm) of the left and right uterine cornua of each female were measured (South Africa), and if a corpus luteum was present but no fetus was obvious, both cornua were opened and searched. The length and sex of any fetus were recorded, and a sample of the uterine mucosa from the larger horn fixed in 10% formalin. Either one (Japan) or both (South Africa) testes were collected, trimmed of the epididymis and weighed to the nearest 0.1 g (while fresh in South Africa, and after fixation in Japan). A mid-length sample was taken from the center of one testis (the left in Japan, the larger in South Africa) and fixed in 10% buffered formalin.

Laboratory Procedures

Age determination—Following methods described in Kasuya and Matsui (1984), teeth were sectioned longitudinally and through the center of the pulp cavity to a thickness of 40–50 μm. Sections were decalcified in 5% formic acid at room temperature (25°C) for approximately 24 h, and washed in running water over night. They were stained with hematoxylin for 30–60 min, washed in running water for 3–10 h and mounted under a coverslip in Canada Balsam. Whales were aged by counting the growth layers in dentine and/or cementum at a magnification of 20–100× without reference to other biological data. The pattern of layering in both tissues tended to be clearer in the Japanese teeth, with portions of unstainable dentine in some South African teeth. A growth layer group (GLG) of alternating high and low mineralization density in the dentine and cementum was assumed to be deposited annually, based on the pattern of dentinal growth-layer deposition observed in short-finned pilot whales (Kasuya and Matsui 1984).

The median values of three independent GLG counts (by TK) were taken in both the dentine and cementum. Results for the same animal were not statistically different for individuals with open or closing pulp cavities. Where discrepancies between dentinal and cemental counts on such teeth occurred, the growth layers in both tissues were repeatedly checked until good agreement was reached between the two counts. The ages of older individuals with closed pulp cavities were determined using cemental GLG counts only.

The ages of individuals below 10 yr were estimated to the nearest 0.25 yr by comparing the thickness of the first and last postnatal dentinal layers, while in older whales the ages were determined to the nearest $n + 0.5$ yr ($n =$ integer). In short-finned pilot whales, *Globicephala macrorhynchus*, the 95% confidence range for the counts at ages 10, 20, 40, and 60 yr were estimated to be ±0.9, ±1.8, ±2.6, and ±3.4 yr, respectively (Kasuya and Matsui 1984), and the same degree of precision has been assumed here, given that readability of *Pseudorca* teeth was generally higher than that experienced for *Globicephala* (TK).

Ovarian examination—Each ovary was trimmed of its bursa and weighed to the nearest 0.1 g (Japan). The medulla and cortex of ovaries in both groups were hand-sliced at 1–2 mm intervals and the numbers of corpora lutea, corpora albicantia, and corpora atretica counted (see Perrin and Donovan 1984 for definitions of terms). The diameters of all corpora and Graafian follicles were measured to the nearest 0.1 mm on three planes using vernier calipers, and the mean taken as the cube root of the product of the three. Corpora albicantia were classified as young, medium, or old according to the characteristics used by Marsh and Kasuya (1984). Macroscopically visible Graafian follicles (*i.e.*, those >1 mm in diameter) were classified as atretic or nonatretic on the basis of the macroscopic thickness of the follicle walls.

Histological examination of the ovaries was undertaken to confirm macroscopic observations and reproductive status. Samples of selected tissues were embedded in Paraplast, sectioned at 5 µm, and stained with either Mayer's hemalum and Young's eosin-erythrosin (a variant of Gomori's trichrome), or van Gieson's stain with Celestin blue hemalum. Frozen sections of selected formalin-fixed follicles, corpora lutea, corpora albicantia, and corpora atretica were cut at 8 µm and stained for lipids with a modification of Herxheimer's method using Oil-Red 0 and Sudan IV, or with hematoxylin and eosin (H & E) as above.

Mammary gland—Slides of mammary gland material were prepared using standard histological techniques and viewed at 100× magnification. Mature glands were distinguished from immature glands by their relatively more abundant glandular tissue. Active mammary tissue typical of a lactating female could be distinguished from mature but inactive tissue by the presence of intracellular and intraduct lipid droplets and milk secretions and the relatively larger alveoli.

Uterus—Samples of endometrium collected in Japan were examined histologically using stained hematoxylin and eosin sections to confirm or establish pregnancy (Kasuya and Tai 1993).

Testis—Hematoxylin and eosin stained sections of all testis samples, measuring about 5 × 7 mm, were viewed at magnifications of 100–400× and the relative abundance of immature and mature tubules calculated and used to determine reproductive status. The number of tubules examined per individual varied between 5 and 85 (South Africa) and 70 and 150 (Japan), depending on sample quality. Males with no spermatozoa, spermatocytes, or spermatids were classed as immature, those with less than 50% mature tubules as early maturing, those with between 50% and 100% mature tubules as late maturing, and those with 100% mature tubules as mature. Various positions along a longitudinally sliced testis were sampled in two males to test whether they were at different stages of maturation (Kasuya and Marsh 1984). No consistent differences in maturation status were found between sampling positions.

The relative abundance of interstitium was used as a more general maturation criterion when the presence and abundance of spermatozoa could not be accurately determined because of poor tissue fixation (South Africa). Immature whales had abundant interstitium (and small seminiferous tubules, with mostly closed lumina), while mature males had comparatively small amounts of interstitium (and relatively large tubules, with open lumina).

The diameters of 20 approximately circular seminiferous tubules were measured on two planes at right angles to each other, using a calibrated micrometer eyepiece at a magnification of 100×, and an overall mean diameter for each individual was calculated in µm (South Africa).

Statistical Analysis

Gompertz, Logistic, and Von Bertalanffy growth curves were fitted for each site and sex combination of age and length, using SPSS and STATA statistical packages. All the other analyses were performed using SAS version 9.1 statistical package (SAS Institute Inc. 2004).

Results

Age and Body Length Relationships

Body length at birth—False killer whales from Japan were longer at birth than those from South Africa. The largest fetus from Japan was of unknown sex and measured 174 cm, while the smallest neonate was a female of 175 cm, suggesting that birth in this population takes place at approximately 175 cm. There was a single 148 cm fetus in the South African stranding, but a suckling calf of 157 cm was recorded from an earlier stranding in the same locality (Smithers 1938), and a calf 161 cm long stranded in February 2006 at Olifantsbos, Cape Peninsula, South Africa. The mean of these three measurements (155 cm) has been taken as the length at birth (Best 2007), or 11.5% less than in the Japanese population.

Applying mean lengths at sexual maturation for females of 3.25 m for South Africa and 3.59 m for Japan (see below) to Ohsumi's (1966) equation for predicting body length at birth from mean size at sexual maturation in female odontocetes produces estimates of the birth length of 1.57 m for South Africa and 1.72 m for Japan—very close to the estimates in this paper. There were insufficient data to test whether there is a difference in the size of males and females at birth.

Postnatal growth rate and asymptotic length—The Von Bertalanffy model was discarded as it was found to be unstable, particularly among the lower ages. Both the Logistic and Gompertz growth models described the length age relationships well (except that the predicted sizes at birth were unrealistically large) and had similar r^2 values and residuals showing no obvious patterns. The 2-parameter Gompertz model predicted a body length at birth closer to the values estimated above and was adopted to fit the data (Fig. 1). However the paucity of data for young individuals, particularly in the South African sample, complicated any analysis of growth in the early years of life (Stevick 1999), and extrapolating growth equations when the age structure is skewed is likely to give poor predictions.

The overall pattern of growth and sexual dimorphism was similar for false killer whales from South Africa and Japan. Predicted rates of growth below about 10 yr of age were similar in both sexes, but thereafter males were larger than females at every age and attained an overall larger body size as adults. The point at which growth ceased corresponded to an age of about 25–30 yr in both populations and sexes. At 30 yr or above, South African females were significantly smaller (mean length 390.4 cm, SD = 12.7, $n = 25$) than Japanese females (mean length 437.3 cm, SD = 21, $n = 39$; $t = -9.94$, $P < 0.0001$), while South African males were significantly smaller (mean length 463.5 cm, SD = 22, $n = 11$) than Japanese males (mean length 521.5 cm, SD = 26.5, $n = 13$; $t = -5.75$, $P < 0.0001$): males of these ages were also significantly larger than females in both populations ($t = 12.64$, $P < 0.0001$ for South Africa and $t = -11.6$, $P < 0.0001$ for Japan). For comparison, the asymptotic body length estimates from the Gompertz model were 385.4 and 429.1 cm for South African and Japanese females, and 464.5 and 511.4 cm for South African and Japanese males. The degree of sexual dimorphism in size was therefore the same in false killer whales from South Africa and Japan, with adult females being 83%–84% of the size of adult males in both populations.

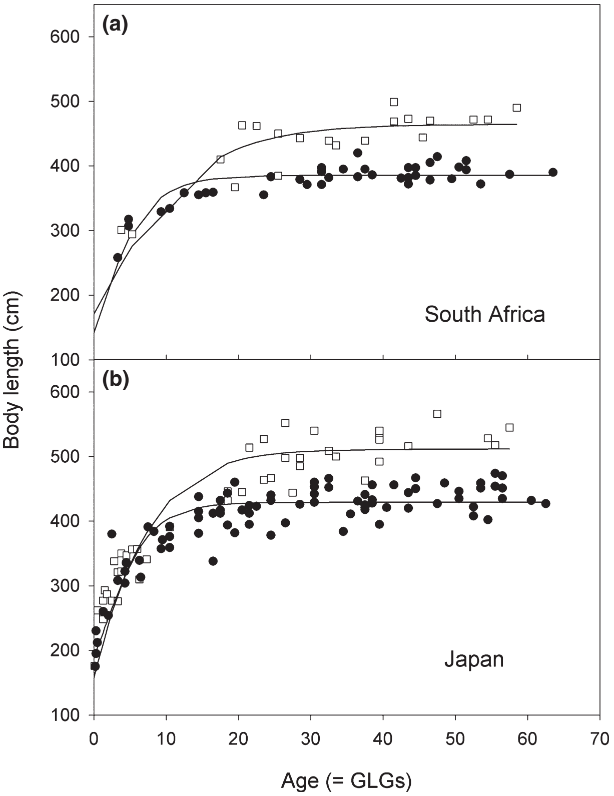

Figure 1. Gompertz growth curves for female (filled circles) and male (open squares) false killer whales from (a) South Africa (20 males, 38 females) and (b) Japan (45 males, 83 females).

Sexual Maturation in Females

Body length—The length of females at sexual maturation was larger in the Japanese samples than in the South African samples. In South Africa the smallest of 37 mature female false killer whales measured 320 cm and the largest of four immature animals 329 cm, suggesting that sexual maturation occurred between these body lengths, while in Japan the smallest of 67 mature females measured 338 cm and the largest of 20 immatures 392 cm.

A logistic model fitted to the incidence of mature females (p) at body length (x) for South Africa is

$$\log(p/1-p) = 50.36 - 0.15x,$$

and for Japan

$$\log(p/1-p) = 23.2805 - 0.0648x.$$

These equations indicated body lengths at 50% maturation of 325.1 cm for South Africa and 359.3 cm for Japan, confirming that sexual maturation occurs at a 30–40 cm shorter length in the South African population. Mature females from South

Africa (mean 381.5 cm, SD = 20.6, $n = 37$) were significantly smaller than those from Japan (mean 427.3 cm, SD = 31.2, $n = 65$; $t = 8.01$, $P < 0.0001$). These body lengths at sexual maturation as a percent of asymptotic length (84.4% for South Africa and 83.7% for Japan) were in good agreement with the mean of 85.1% proposed by Laws (1956) for female cetaceans in general.

Age—The age at sexual maturation appeared to be similar in the two populations. The oldest of four immature South African females was 9.25 yr and the youngest of 34 mature females 10.5 yr old, while the youngest of 57 mature Japanese females was 8.25 yr and the oldest of 16 immature females 10.5 yr old. These results defined limits within which the age at which sexual maturation occurred in the two populations.

A more quantitative estimate of the age at sexual maturation was possible only for the Japanese females owing to the lack of specimens from South Africa in the range where the transition seemed to occur. A logistic regression of the proportion of mature females (p) against age (x)

$$\log(p/1-p) = 8.255 - 0.8951x$$

indicated that 50% of females in Japan were mature at 9.2 yr.

Sexual Maturation in Males

Criteria—Using the criterion of sperm abundance, two South African males were classed as late maturing, and two Japanese males as early maturing. One early maturing Japanese male, 6.25 yr of age, was difficult to separate from the immature males. The age of the second early maturing Japanese male was within the range of that for mature males, and the body length and testis mass fell slightly below the respective minimum measurements recorded for mature males. Both of the late maturing South African specimens had body length, tubule diameter and combined testis mass measurements that fell within the ranges for those of mature males. We grouped early maturing males with immature males, and late maturing males with mature males following Kasuya (1986) and Kasuya and Marsh (1984).

Five large African specimens were shown histologically to contain no sperm, although they had large testes, seminiferous tubules with expanded lumina, and sparse amounts of interstitium, all characteristic of reproductive maturation. These individuals were classified as mature but without sperm. Although they could have been seasonally inactive, the lack of any such individuals in the Japanese sample (where there was no postmortem delay in collection) suggested that the absence of sperm was more likely due to autolysis.

Testes mass—The testes of the South African whales were generally smaller than those of Japanese false killer whales of equivalent reproductive status. The mean testis mass of 15 mature South African false killer whales (including those without sperm), ranged from 500 to 3,575 g with a mean of 2,454.7 g, significantly less than that of 4,953 g for 29 mature Japanese males, that ranged from 1,680 to 7,200 g (two-tailed $t = 5.97$, df = 42, $P < 0.0001$). A plot of testis mass against body length showed that this difference was a reflection of the greater body size of Japanese whales, with the size of the testis following a similar allometric relationship in both populations (Fig. 2). Mean testis mass increased dramatically from a maximum of 200 g for an immature male to a minimum of 500 g for a mature South African male, and an even greater increase in single testis mass (from 108 to 1,680 g) for Japanese males.

Although this increase undoubtedly reflected the proliferation of testicular tissue associated with maturation, the lack of adolescent males in the samples from both populations (Fig. 3) probably contributed to the contrast. Despite this hiatus in the data, it seems the testes mass at sexual maturation was greater in the animals from Japan than in those from South Africa.

Mean seminiferous tubule diameters (South Africa) in three immature males ranged from 57 to 65 μm with an overall mean of 62.2 μm, but in two late maturing, 10 mature and five mature males without sperm ranged from 154.8 to 242.3 μm with means of 180.8, 204.4, and 229.9 μm, respectively. Sexual maturation was therefore estimated to occur at around a mean testis mass of 500 g (South Africa) and a single testis mass of 1,680 g (Japan), and a seminiferous tubule diameter of about 150 μm (South Africa). Testis mass continued to increase beyond the body lengths at which maturation occurs in both populations (Fig. 4). This increase only leveled off at a body length of 430–450 cm in the South African sample and 460–500 cm in the Japanese sample. Thereafter the variation in testis mass relative to body length was high, with a maximum mass of 3,575 g being recorded in South Africa and 7,200 g in Japan. Combined testes mass in 19 South African males was strongly correlated with tubule diameter, at least over a body length of 300 cm ($r^2 = 0.89975$, $P < 0.0001$). Tubule diameter continued to increase beyond a combined testis mass of 1,000 g (or the onset of maturation), and up to a testis mass of approximately 5,000 g.

Body length—Japanese male false killer whales were larger at sexual maturation than those from South Africa. The largest of three immature South African males measured 323 cm and the smallest of 17 mature males 367 cm. No males were sampled between these body lengths. The largest of 21 immature individuals in the Japanese sample measured 391 cm and the smallest of 29 matures 441 cm: with the exception of an early maturing male (at 432 cm), no individuals between these body lengths were examined. Maturation presumably occurred within these size ranges; a more precise figure cannot be given because of the lack of adolescent males in the samples (Fig. 3).

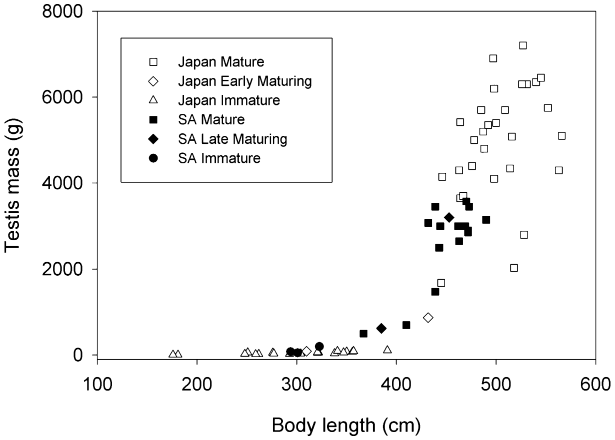

Figure 2. Relationship between body length and single testis mass in 20 South African and 52 Japanese false killer whales.

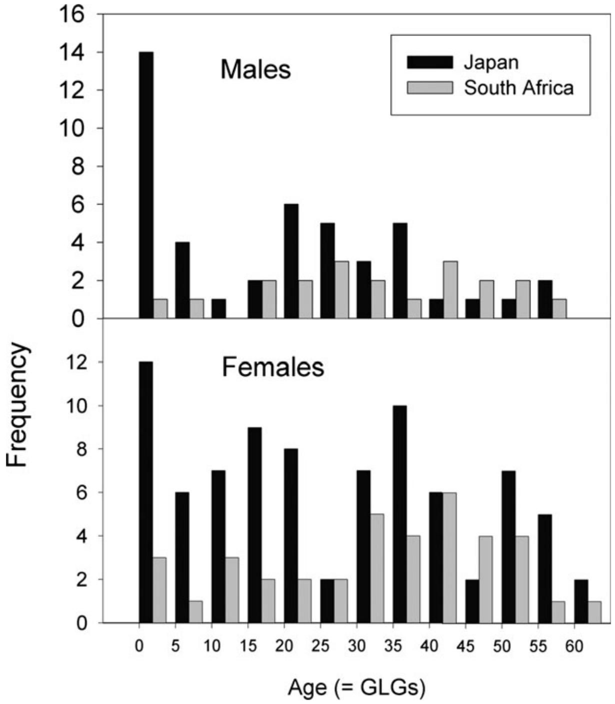

Figure 3. Age composition by sex of false killer whales from Japan (n = 128) and South Africa (n = 58).

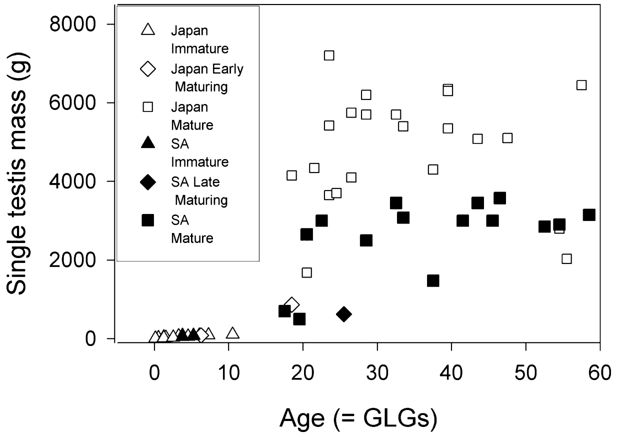

Figure 4. Relationship between age and single testis mass in false killer whales from South Africa (n = 18) and Japan (n = 40).

Age—The preliminary results are consistent with the hypothesis that the age of male sexual maturation was similar in the two populations, but this conclusion cannot be confirmed because a lack of adolescent males prevents accurate determination of the age at sexual maturation (Fig. 3). The older of two immature South African males examined was 5.25 yr and the youngest of 16 mature males 17.5 yr old, while the oldest of 17 immature Japanese males was 10.5 yr and the youngest of 23 mature males 18.5 yr old. Maturation therefore must have occurred at some age between 5.25 and 17.5 yr in males from South Africa, and between 10.5 and 18.5 yr in males from Japan.

Both testis size and tubule diameter apparently indicated a role for the larger and older males beyond the mere attainment of physiological maturation. Testis mass stabilized in mature males around 2,500–3,000 g in South Africa and 5,000–6,000 g in Japan, and at about an age of 30 yr (= GLGs) in both populations, far greater than the estimated mean mass and age at puberty (Fig. 4).

Group Composition

There were significantly more females than males in both the Japanese (61.5%, $n = 156$) and South African (65.1%, $n = 63$) samples of false killer whales (Chi-square with Yates correction = 7.86 and 5.14, $P = 0.0051$ and 0.0234, respectively).

There were fewer young whales in the South African sample, where the youngest ages were 3.75 and 3.25 yr in males and females (compared to 0.1 and 0.2 yr in Japan). The proportion of animals less than 10 yr old was significantly less in the South African sample (6/58) than in the Japanese sample (36/128) (Chi-square with Yates correction = 6.24, $P = 0.0125$). There were no juvenile males in either sample (Fig. 3) as explained above.

The reproductive composition of the samples of 34 mature females from South Africa and 67 from Japan also differed. Pregnant females were less frequent in the South African sample (2.9% *vs.* 14.9%), and there were no young calves (≤ 2 yr), but 13 in the Japanese sample (excluding three animals 148–196 cm in length for which there were no ages). The combined frequencies of pregnant females and young calves differed significantly between the two regions (Chi square with Yates correction = 8.07, $P = 0.0045$). Excluding pregnant females, however, the proportions of lactating, ovulating (including simultaneously lactating and ovulating), and resting females were similar in both populations (Chi-square with Yates correction = 0.094, $P = 0.9541$). Whales in the two samples reached similar maximum ages, 58.5 and 57.5 yr in 20 and 45 males and 63.5 and 62.5 yr in 38 and 83 females from South Africa and Japan, respectively.

Reproduction

In order to increase sample size, data from South African and Japanese females were combined ($n = 120$, of which 24 were immature) for most of this section. Only where there were obvious differences have the analyses been separated by population.

Follicular development—The number of macroscopically visible Graafian follicles in mature females varied greatly between individuals, with 42.1% having none. Although the proportion of animals with visible follicles was higher in younger (<39 yr old) than in older females (19/53 compared to 16/30), the difference was not statistically significant (Chi-square with Yates correction = 1.74, $P = 0.1871$). The diameter of the largest Graafian follicle ranged from 1 to 45 mm. Most (87.5%) of the follicles 10 mm or more in diameter were found in resting or ovulating females, while 88.9% of the largest follicles in immature, 75% in pregnant, and 90% in lactating females (that were not simultaneously pregnant) were less than 10 mm.

Follicles 30 mm or more in diameter were only found in resting females, and although several (57%) of these were atretic, it seems likely that 30 mm was close to the diameter that the follicle attains at ovulation.

Development of corpora lutea—A corpus luteum (CL) was found in 29 false killer whales, 10 of which also contained a fetus, indicating that these were corpora lutea of pregnancy (CLPs). A female from Japan with a CL measuring 38.3 mm was classified as pregnant although no fetal length was recorded, possibly because the fetus was aborted or lost and endometrial histology or the presence of a fragment of placenta or umbilical cord indicated pregnancy (Kasuya and Tai 1993), while no data on CL size were available for another pregnant female as only one ovary was collected. An accessory CL 11.6 mm in diameter was found in a whale from Japan carrying a fetus 138 cm in length and with a main CL of 100.9 mm. No fetus was found in the uterus of the remaining 20 females, so the CLs of these females were assumed to be corpora lutea of ovulation (CLOs). No data were available for the diameters of one CLP and two CLOs. The remaining 10 CLPs (excluding the accessory corpus luteum) ranged in diameter from 38.3 mm to 100.9 mm, with a mean of 54.4 mm. There was no significant correlation between the mean diameter of the CLP and fetal length ($r^2 = 0.1315$, two-tailed $P = 0.337$), suggesting no systematic change in the mean diameter of CLPs throughout pregnancy. The diameters of the 20 CLOs (from 18 females) ranged from 4.2 mm to 49.7 mm, with a mean of 26.2 mm, substantially smaller than the CLPs. The size distribution of the CLOs tended to be bimodal, with 13 having diameters ≤ 29.6 mm and seven diameters ≥ 39.3 mm. As the latter group coincided with the size range for known CLPs, it is possible that some of the larger CLOs may actually have been undiagnosed CLPs (perhaps associated with very small undetected embryos).

The ovaries of two ovulating South African females contained two CLs, with diameters of 8 mm and 45 mm, and 27.5 mm and 46.9 mm, respectively. The two corpora in each individual could have represented successive ovulations or it is possible that the females were in a very early stage of pregnancy and that the larger corpora were CLPs and the smaller were accessory CLs.

Evidence of the regression and persistence of corpora albicantia with age—Each corpus albicans (CA) was graded as young, medium, or old according to morphological criteria. The mean diameters for these three classes became successively smaller with age (15.2 ± 4.0, $n = 27$; 10.7 ± 2.7, $n = 70$; 6.2 ± 1.8 mm, $n = 636$, respectively), providing support for our contention that the morphological criteria represent stages in the regression of the CA.

Corpora albicantia apparently persist indefinitely as ovarian scars. If they did not, one would expect the size-frequency distribution of old CAs to be negatively skewed (Marsh and Kasuya 1984). In practice, old CAs have a slight positive skew to their distribution (coefficient of skewness = 0.30192671).

Despite the absence of ovulations after age 47–48 (Ferreira 2008), the mean number of old CAs per female increased steadily with age until age 56 but decreased thereafter in the very oldest whales (Fig. 5). This could either signify a cessation of ovulation some years earlier or that some CAs may eventually be resorbed. The modal diameter of old CAs in mature females fluctuated between 6.2 and 7.2 mm from the ages of 14 to 44 yr but thereafter decreased slightly to between 5.2 and 5.7 mm (Fig. 5), indicating that the corpora continued to shrink in size in old age; some may have become too small to be distinguishable. Nonetheless, there was no sign of a decline in the total corpora count in old age (Fig. 6), suggesting that if corpora resorption takes place in false killer whales it is likely to be at a slow rate and confined to the oldest females.

As a further test of whether resorption of corpora might occur, we have examined whether corpora counts in pregnant females are lower than those in nonpregnant females, as found for *Delphinus delphis* by Dabin *et al.* (2008).Total corpora counts in both pregnant and nonpregnant false killer whales from Japan increased linearly up to the age of the oldest pregnant individual examined, 43.5 yr (r = 0.871, one-tailed P = 0.001; and r = 0.8099, one-tailed P < 0.0001 respectively). A comparison of corpora counts in three age groups of false killer whales from Japan (8–20, 20–32, and 32–44 yr) failed to demonstrate a significant difference in the mean numbers of corpora in pregnant and nonpregnant animals (3.8 *vs.* 3.9, t = 0.162, P = 0.437; 7 *vs.* 8.2, t = 0.569, P = 0.294; and 12.5 *vs.* 13.9, t = 0.771, P = 0.261 respectively), even though in all three age groups the means were lower in pregnant animals, albeit weakly so in the younger animals. These results do not support the resorption of CLs in false killer whales.

Ovulation rate—The relationship between age and corpora count for both the South African and Japanese females is clearly non-linear and declines with age (Fig. 6), with South African females apparently ovulating less frequently than the Japanese false killer whales and ceasing to ovulate at an earlier age. Such a phenomenon would be consistent with the comparatively lower reproductive output of South African females suggested by the lower incidence of pregnant females and nursing age calves indicated earlier.

An alternative explanation could be that the lower counts in South African females were a consequence of the poorer state of fixation of their ovaries, leading to some of the smaller corpora being overlooked. To test this hypothesis, the size distribution of old CAs was compared between South African and Japanese females. The data were stratified into three age groups (6–20 yr, 20–45 yr, 45 + yr), to control for the naturally occurring decrease in corpus size with age. Overall the old CAs of the South African females ranged in diameter from 2.3 to 13.4 mm with a mean of 5.8 mm

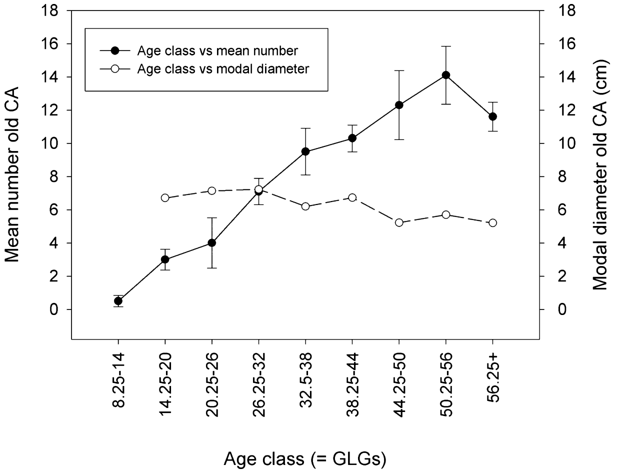

Figure 5. Trends in mean number of old CAs per mature female and the modal diameter (cm) of all old CAs against age in false killer whales, South Africa and Japan combined (n = 82). Modes calculated using 0.5 cm intervals and the Dalenius (1965) method.

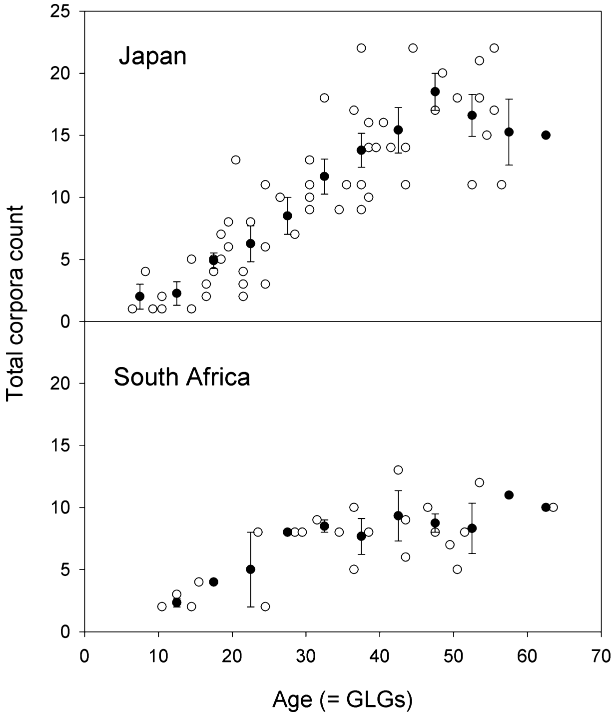

Figure 6. Relationship between age and corpora count in mature female false killer whales from Japan (n = 58, above) and South Africa (n = 25, below), including means ± SE for 5 yr age groups.

(n = 177), while those of the Japanese females were significantly larger, ranging from 1.2 to 13.3 mm with a mean of 6.3 mm (n = 599, t = 2.85, two-tailed P = 0.0045). The mean corpus size was smaller in the South African sample for all three age groups (5.9 ± 1.2 *vs.* 7.5 ± 1.9 cm, 6.2 ± 1.7 *vs.* 6.4 ± 1.7 cm, and 5.3 ± 1.7 *vs.* 5.8 ± 1.9 cm, respectively), and significantly so in the 6–20 and 45 + age groups (t-test, P = 0.0326 and 0.0155, respectively). Contrary to the prediction that a postmortem effect would result in smaller corpora not being as detectable, old CAs in the South African whales were consistently smaller than those from Japan across all age groupings. Accordingly, the hypothesis that the lower ovulation rate in the South African false killer whales is an artifact arising from poorer fixation was not supported by the results of this analysis. The generally larger size of the old corpora in the Japanese females could reflect their larger body size.

Quantitative expression of the overall ovulation rate in both populations is complicated by the high individual variation, trend with age and (especially in South African whales) the relatively low sample size (Fig. 6). In both populations the rate appears initially to be roughly linear but then declines and ceases in old age: the transition seems to occur around 40-45 yr in Japanese whales and 30–35 yr in those from South Africa. A linear regression fitted to the data for mature females from Japan for ages 10–44.5 yr produces the following relationship

$$y = 0.449x - 3.353,$$

where x = age in GLGs and y = corpora count ($r^2 = 0.667$). An equivalent regression for mature South African whales up to the age of 34.5 yr produces the following relationship

$$y = 0.29x - 1.129,$$

where x = age in GLGs and y = corpora count ($r^2 = 0.686$). This result indicates an initial ovulation rate that is only 65% of that in Japanese false killer whales. Above these ages the ovulation rate is either very much reduced (South Africa, $b = 0.081$) or does not differ significantly from zero (Japan: $b = -0.016, P > 0.25$). These calculations are predicated on an assumption (that all ovulations are represented by detectable CAs) that has been challenged in the case of some smaller dolphins (Brook *et al.* 2002, Dabin *et al.* 2008).

With ovulations ceasing at age 47–48 but females living to age 62.5–63.5 yr, a significant postreproductive phase seems a distinct possibility (Ferreira 2008).

Pregnancy rate—The Japanese false killer whales were more likely to be pregnant than those from South Africa, if our samples were representative of the pregnancy rates of the populations. Ignoring any age-related effects, the apparent pregnancy rate (proportion of pregnant females in sexually mature females sampled) was 14.9% (10/67) for the Japanese schools and 2.7% (1/37) for the South African sample. Assuming a gestation period of 15 mo (Kasuya 1986), these results correspond to annual pregnancy rates (probability of a female conceiving in a given year) of 11.9% in Japanese whales and 2.2% in South African whales. Use of a gestation length of 14 mo, as proposed from captive studies (O'Brien and Robeck 2010), produced correspondingly higher annual pregnancy rates but the interpopulation differences remained.

Mammary gland development—Mammary gland thickness averaged 1.9 cm in immature South African females (range 1.3–3.0 cm, $n = 3$), and 2.5 cm in mature females (range 0.9–4.2 cm, $n = 35$). This difference was not statistically significant (Mann-Whitney U-test: df = 36, $P = 0.203$), possibly as a consequence of small sample size, although mammary gland involution may be greater than normal in older females if the length of the resting period is prolonged. Mammary gland thickness in lactating females averaged 3.1 cm (range 2.0–4.0 cm, $n = 10$), compared to a mean thickness of 2.2 cm (range 0.9–4.2 cm, $n = 22$) in mature, nonlactating females. Despite the overlap in range, this difference was statistically different (Mann-Whitney U-test: df = 30, $P = 0.0067$).

The presence of milk in females with histologically active mammary tissue was not always detected in the field, possibly because they were approaching the end of galactopoiesis. Four females showed discrepancies in the secretory activities of different areas in their mammary tissue, with some alveoli appearing to be active and others inactive: their mammary gland thickness averaged 2.8 cm (range 2.0–3.6 cm). Whether these represented genuine variations in functional state, terminal stages of lactation, poor histology or postmortem changes to the tissue, is unclear.

Uterine development—The uterine cornua were generally bilaterally symmetrical in nonpregnant females. No statistically significant differences between the width of left and right uterine horns were detected in 4 immature or 28 mature females (Wilcoxon paired t-test: $P = 1.000$ and $P = 0.4196$, respectively). Mean cornua width was used in the following analyses.

The width of the uterine cornua increased significantly with body length, sexual maturation and some reproductive states. The mean cornua width was 2.7 cm (range 2.3–2.8 cm) in 4 immature females and 4.9 cm (range 3.1–8.5 cm) in 30 mature nonpregnant females, a significant increase (Mann-Whitney U-test: df = 29, $P = 0.0014$). In ovulating females the uterine cornua increased in width to a mean of 6.1 cm ($n = 4$), probably due to the influence of progesterone produced in the newly formed CL (Matthews 1948). In the single female in late pregnancy (with a fetus of 148 cm), the right cornu measured 21 cm and the left (pregnant) cornu 31 cm. Regression of the uterus after birth must be rapid as the width of the uterine cornua in 7 lactating females ranged from 3 to 7.6 cm, with a mean of 4.4 cm. In 14 resting females the combined width of left and right horns averaged 4.6 cm.

Seasonality of reproduction—The limited annual coverage of samples from both regions makes it difficult to detect any seasonality in the incidence of births (Table 1). Nonetheless the results are broadly consistent with plasma progesterone concentrations in two captive false killer whales that reflected ovarian activity for most of the year but with increased concentrations in the spring and summer (Atkinson *et al.* 1999). There was insufficient contrast to test for seasonal variations in testicular activity, with material only being available from late winter (August in South Africa, February in Japan) or early spring (March in Japan). However the fact that the Japanese and South African samples were six to seven calendar months apart and so in roughly equivalent seasons in Northern and Southern Hemispheres respectively indicated that the differences seen in testis size could not be attributed to the effects of any seasonal variation in testicular activity.

Discussion

Geographical Comparisons

Male and female false killer whales from the South African population were smaller than those from the Japanese population by a factor of 0.89–0.91, irrespective of whether comparisons are based on size at birth, asymptotic lengths as given by the growth curves (as McLaren (1993) argued they should be), mean adult body length, or on sizes at sexual maturation. Determining whether this difference represents regional, oceanic or wider population differences is difficult when age-length relationships are available only for a few populations worldwide.

In the absence of such information, the mean length of the 50% largest animals of each sex in each population has been used as a proxy for asymptotic length (excluding animals below 2.5 m to avoid confounding effects of any seasonality of reproduction): comparisons of these proxy asymptotic lengths (PAL) with the previously calculated asymptotic lengths for the South African and Japanese populations suggest that they are either equivalent or slightly larger. A one-way ANOVA rejected the null hypothesis that the mean PALs are similar between regions, both for females ($F = 47.38$, $P < 0.0001$) and males ($F = 10.53$, $P < 0.0001$). *Post hoc* Tukey HSD tests (using harmonic means to adjust for unequal sample sizes) revealed significant differences between 61.9% of female and 47.6% of male population comparisons (Table 2). Whales of both sexes from South Africa in 1936 or 1983 were smaller than those from the Tay Estuary, Scotland, while those from the 1983 stranding were also smaller than both sexes from Japan or Chile, and Chilean whales of both sexes were larger than those from Tasmania. No significant differences were found between whales of both sexes from the Tay Estuary, Japan, and Chile. In other examples, a significant

Table 1. Possible seasonality of birth calculated for calves and fetuses of false killer whales from the Japanese drive fishery. Possible months of birth calculated for nine fetuses assuming a length at birth of 175 cm and a mean fetal growth rate based on either a 14 mo (O'Brien and Robeck 2010) or 15 mo pregnancy (Kasuya 1986). Reverse calculations made for eight calves from Japan estimated to be less than 1 yr old, assuming immediate post-natal growth is similar to that in late pregnancy.

	Number of births predicted	
Season	14 mo gestation	15 mo gestation
Spring (March–May)	4	5
Summer (June–August)	6	6
Autumn (September–November)	4	4
Winter (December–February)	3	2

difference in size between areas was confined to only one sex. Overall geographical patterns are difficult to establish, and perhaps should not be sought, given the sparse nature of the data and in most cases a lack of accompanying age information. Nevertheless, it appears that adult false killer whales from different areas (and even from the same area) can differ significantly in mean body size by as much as 0.5–0.6 m.

Assuming variation in body size is genetically based and an evolved response, the observed differences in body size could be the result of any one, or a combination, of several selective forces to which the populations have been exposed in their respective environments. These include different ambient sea temperatures and differing food availabilities, especially seasonally and/or spatially—current data on the diet and feeding behavior of (particularly South African) false killer whales are insufficient to determine whether there are differences with those from Japan. Further regional studies of growth, especially in tropical regions, are needed to clarify the issue.

The growth curves constructed in this paper differed greatly from those previously published by Purves and Pilleri (1978) for a group of false killer whales stranded at Dornoch Firth, Scotland, which failed to reach an asymptote. Even though the body lengths of the oldest Scottish specimens were roughly comparable to those of the oldest Japanese specimens, their ages were much younger, 18–23 compared to 55–65 yr. The teeth from the Scottish animals were not decalcified or stained, and only dentine layers were counted using a low power lens and reflected light (Purves and Pilleri 1978). Thus it seems likely that their ages were underestimated, particularly in older animals where age is more difficult to determine accurately from dentinal layers only. Consequently the differences between the growth curves of the Scottish sample and our samples from South Africa and Japan were methodological rather than real.

A marked geographic difference between our samples was the lower incidence of pregnant animals and juveniles of presumed suckling age in the South African sample. While this could be attributed to a temporary loss of fertility in the population (or a biased representation of reproductive classes in the stranding), the significantly lower ovulation rate in the South African whales suggested that these alternative explanations are unlikely, and that the St. Helena Bay school had an inherently lower reproductive rate compared to the samples from Japan. Once again, determining

Table 2. Comparison of lengths (in cm) of 50% largest individual false killer whales among five regions and seven data sets, with (below) significant differences derived from Tukey HSD tests (** $P < 0.01$, * $P < 0.05$, NS = not significant). Data from Chile revised by Goodall.[2]

	Females			Males			
Population	*n*	Mean	SE	*n*	Mean	SE	Source
South Africa 1983	21	394.76	2.24	11	470.27	4.33	This paper
South Africa 1936	10	432.56	3.53	11	477.29	8.99	Smithers (1938)
Tasmania	13	415.31	7.09	17	477.82	6.53	Scott and Green (1975)
Chile	10	445.08	4.57	7	529.33	3.32	Koen Alonso *et al.* (1999)
Japan	45	447.4	2.31	29	511.31	5.23	This paper
Tay, Scotland	14	455.07	2.61	11	537.09	7.45	Peacock *et al.* (1936)
Dornoch Firth, Scotland	21	451.71	2.44	17	493.36	9.28	Purves and Pilleri (1978)

Females Males	South Africa 1983	South Africa 1936	Tasmania	Chile	Japan	Tay, Scotland	Dornoch Firth, Scotland
South Africa 1983	-	−37.8**	−20.5**	−50.3**	−52.6**	−60.3**	−56.9**
South Africa 1936	NS	-	17.3*	NS	NS	−22.5**	−19.1**
Tasmania	NS	NS	-	−29.8**	−32.1**	−39.8**	−36.4**
Chile	59.1**	52**	51.5**	-	NS	NS	NS
Japan	41**	34*	NS	NS	-	NS	NS
Tay, Scotland	66.8**	59.8**	59.3**	NS	NS	-	NS
Dornoch Firth, Scotland	NS	NS	NS	−36*	NS	−43.7**	-

whether this is a general characteristic of southern *vs.* northern false killer whales is difficult given the lack of systematically recorded data.

Unfortunately there is no information on age or maturation status for the animals from the 1936 St. Helena Bay stranding and 14 were unsexed. Nevertheless, adopting 3.25 m as the mean length of the female at maturation, and (as an upper limit) assuming all unsexed individuals between this length and 4.5 m (the largest female measured) were mature females, there would be a minimum of 17 and a maximum of 26 mature females in the school. Smithers (1938) recorded the presence of a 0.58 m fetus and one individual less than 2.8 m long (a calf of 1.57 m) which was presumably the only whale of suckling age. These observations indicate that the incidence of fetuses and individuals of suckling size was between 2/26 (7.7%) and 2/17 (11.8%), depending on whether the upper or lower estimates of the number of mature females is adopted. These values are closer to the same statistic for the 1981 school (1/34 or 2.9%) than for those from Japan (23/67 or 34.3%). Nevertheless, it is not clear how thoroughly the 1936 whales were examined for fetuses, so their incidence could be underestimated. In another mass stranding of false killer whales in South Africa (200 –300 animals at Sea Spray, near Mamre, in November 1935), G. W. Rayner, a

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[2] R. N. P. Goodall, Museo Acatushún de Aves y Mamíferos Marinos Australes, Argentina, 21 October 2012.

member of the Discovery Investigations, and scientists from the South African Museum examined 18 females for the presence of a fetus but found none. Rayner commented that the females must all have calved shortly before stranding, although no newborn calves were found amongst the stranded animals (Birkby 1935).

Different methods of estimating annual pregnancy rates, different possible criteria for establishing pregnancy and inherent biases (for example, representativeness of the sample), precluded a substantive comparison of the pregnancy rates reported in this study with those of other delphinids. However, the apparent pregnancy rates of false killer whales in this study, as well as elsewhere (10%–17%, Purves and Pilleri 1978), are lower than those estimated for 28 populations of eight other species of delphinids, which apart from a single value of 13.7% (for a killer whale population) fall within the range of 26.5%–80.4% (Perrin and Reilly 1984). Nevertheless, the apparently low reproductive rates of the three false killer whale schools from South Africa are remarkable. Although survival rates have not been calculated, it is obvious that they would have to be extremely high for the population to be biologically viable. Assuming an equal sex ratio at birth, the annual pregnancy rate of 2.2% calculated for the school stranded in 1981 and reported here equates to only 1.1 female calves being produced annually per 100 mature females, so that allowing for some mortality between birth and maturation the annual survival rate of adult females would have to be substantially greater than 99% to prevent the population from declining. Such survival rates are unknown amongst odontocetes. It seems more likely that the school stranded in 1981 was somehow reproductively compromised, and not typical of the population as a whole: only examination of further material from southern African false killer whales will resolve this issue.

Insights into Life History

Both the shore-driven and stranded samples are characterized by a hiatus in the age distribution of males (between 10 and 19 yr and 5 and 18 yr, respectively; Fig. 3) and an apparent gap between immature and mature males (*i.e.*, few maturing individuals). Kasuya (1986) suggested that this discontinuity in shore-driven groups is due to the absence of males in the late maturing stage (two early maturing males were present but no late maturing males). However, the stranded St. Helena Bay school contained no early maturing but two late maturing males, suggesting that the absence may involve maturing males in general. Koen Alonso *et al.* (1999) reported that amongst 91 animals examined from a mass stranding of 181 false killer whales in Chile there were only large and small animals and that larger juveniles and subadults were absent: measurements given for a sample of 33 suggest this applied to both sexes.

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 (and a scarcity of maturing and young mature males is also apparent in schools of long-finned pilot whales driven ashore at the Faroe Islands; Desportes *et al.* 1993). 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 (although few in number). School 4 (which contained four males and only two females), had only one immature male, aged 1.5 yr, and three adult males, all over 26 yr of age.

The dispersal pattern of male false killer whales from their natal school is unknown. The presence of maturing and 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 at least temporarily, but that at least one or a few males may remain with, or return to their natal group, in line with the evidence for strong social bonds and long term association and philopatry (Acevedo-Gutierrez *et al.* 1997, Baird *et al.* 2008). Alternatively, these maturing and adult males may be unrelated to the rest of the group and have emigrated from other breeding schools. The formation of bachelor groupings like sperm whales, or as observed in at least one case for long-finned pilot whales (Desportes *et al.* 1994), has not yet been observed at mass strandings or in drive fisheries for false killer whales, leading to speculation that these males may rove singly or in very small groups.

Conclusion

Although based on an instantaneous and possibly not fully representative sample of the South African and Japanese false killer whale populations, the results of this paper provide a valuable background to the longer-term individual identification programs for this species. Further such studies of mass strandings, including systematic genetic sampling, are encouraged. The sex composition of strandings of single or small groups of false killer whales should be investigated, while genetic data from mass strandings or shore-driven samples would help establish relatedness within a group and clarify issues of fidelity to natal schools.

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References

Acevedo-Gutierrez, A., B. Brennan, P. Rodriguez and M. Thomas. 1997. Resightings and behavior of false killer whales (*Pseudorca crassidens*) in Costa Rica. Marine Mammal Science 13:307–314.

Atkinson, S., C. Combelles, D. Vincent, P. Nachtigall, J. Pawloski and M. Breese. 1999. Monitoring of progesterone in captive female false killer whales, *Pseudorca crassidens*. General and Comparative Endocrinology 115:323–332.

Baird, R. W. 2008. False killer whale *Pseudorca crassidens*. Pages 405–406 *in* W. F. Perrin, B. Würsig and J. G. M. Thewissen, eds. Encyclopedia of marine mammals. 2nd edition. Academic Press, San Diego, CA.

Baird, R. W. 2009. A review of false killer whales in Hawaiian waters: Biology, status, and risk factors. Report prepared for US Marine Mammal Commission (unpublished). 40 pp.

Baird, R. W., A. M. Gorgone, D. J. McSweeney, *et al.* 2008. False killer whales (*Pseudorca crassidens*) around the main Hawaiian Islands: Long-term site fidelity, inter-island movements, and association patterns. Marine Mammal Science 24:591–612.

Baird, R. W., G. S. Schorr, D. L. Webster, D. J. McSweeney, M. B. Hanson and R. D. Andrews. 2010. Movements and habitat use of satellite-tagged false killer whales around the main Hawaiian islands. Endangered Species Research 10:107–121.

Best, P. B. 2007. Whales and dolphins of the Southern African Subregion. Cambridge University Press, Cape Town, South Africa.

Birkby, C. 1935. Two hundred false killers hurl themselves ashore: A mysterious stranding near the Cape, which is paralleled by cases of false killers recently stranded on the east coast of England. The Illustrated London News, December 21, 1935:1124–1125.

Brook, F. M., R. Kinoshita and K. Benirschke. 2002. Histology of the ovaries of a bottlenose dolphin, *Tursiops aduncus*, of known reproductive history. Marine Mammal Science 18:540–544.

Chivers, S. J., R. W. Baird, D. J. McSweeney, D. L. Webster, N. M. Hedrick and J. C. Salinas. 2007. Genetic variation and evidence for population structure in eastern North Pacific false killer whales *Pseudorca crassidens*. Canadian Journal of Zoology 85:783–794.

Chivers, S. J., R. W. Baird, K. M. Martien, *et al.* 2010. Evidence of genetic differentiation for Hawai'i insular false killer whales (*Pseudorca crassidens*). US Department of Commerce, NOAA Technical Memorandum Series NOAA-TM-NMFS-SWFSC-458. 51 pp.

Dabin, W., F. Cossais, G. J. Pierce and V. Ridoux. 2008. Do ovarian scars persist with age in all cetaceans: New insight from the short-beaked common dolphin (*Delphinus delphis* Linnaeus, 1758). Marine Biology 156:127–139.

Dalenius, T. 1965. The mode—a neglected statistical parameter. Journal of Royal Statistical Society, Series A 128:110–117.

Desportes, G., M. Saboureau and A. Lacroix. 1993. Reproductive maturity and seasonality of male long-finned pilot whales, off the Faroe Islands. Report of the International Whaling Commission (Special Issue 14):233–262.

Desportes, G., L. W. Andersen, P. E. Aspholm, D. Bloch and R. Mouritsen. 1994. A note about a male-only pilot whale school observed in the Faroe Islands. Fróðskaparrit 40:31–37.

Ferreira, I. 2008. Growth and reproduction in false killer whales (*Pseudorca crassidens* Owen, 1846). M.Sc. thesis, University of Pretoria, Pretoria, South Africa. 152 pp.

Kasuya, T. 1985. Fishery-dolphin conflict in the Iki Island area of Japan. Pages 253–273 *in* J. R. Beddington, R. J. H. Beverton and D. M. Lavigne, eds. Marine mammals and fisheries. George Allen & Unwin, London, U.K.

Kasuya, T. 1986. False killer whales. Pages 178–187 *in* T. Tamura, S. Ohsumi and S. Arai, eds. Report of investigation in search of solution for dolphin-fishery conflict in the Iki Island area. Report prepared for the Japan Fisheries Agency. English translation by N. Inagaki.

Kasuya, T., and H. Marsh. 1984. Life history and reproductive biology of the short-finned pilot whale, *Globicephala macrorhynchus*, off the Pacific coast of Japan. Report of the International Whaling Commission (Special Issue 6):259–310.

Kasuya, T., and S. Matsui. 1984. Age determination and growth of the short-finned pilot whale off the Pacific coast of Japan. Scientific Reports of the Whales Research Institute, Tokyo 35:57–91.

Kasuya, T., and S. Tai. 1993. Life history of short-finned pilot whale stocks off Japan and a description of the fishery. Report of the International Whaling Commission (Special Issue 14):439–473.

Kitchener, D. J., G. J. B. Ross and N. Caputi. 1990. Variation in skull and external morphology in the false killer whale, *Pseudorca crassidens*, from Australia, Scotland and South Africa. Mammalia 54:119–135.

Koen Alonso, M., S. N. Pedraza, A. C. M. Schiavini, R. N. P. Goodall and E. A. Crespo. 1999. Stomach contents of false killer whales (*Pseudorca crassidens*) stranded on the coasts of the Strait of Magellan, Tierra del Fuego. Marine Mammal Science 15:712–724.

Laws, R. 1956. Growth and sexual maturity in aquatic mammals. Nature 178:193–194 [erratum 299].

Marsh, H., and T. Kasuya. 1984. Changes in the ovaries of the short-finned pilot whale, *Globicephala macrorhynchus*, with age and reproductive activity. Report of the International Whaling Commission (Special Issue 6):311–335.

Matthews, L. H. 1948. Cyclic changes in the uterine mucosa of balaenopterid whales. Journal of Anatomy 4:207–232.

McLaren, I. A. 1993. Growth in pinnipeds. Biological Reviews 68:1–79.

Miyashita, T. 1983. Abundance of dolphin stocks in the western North Pacific taken by the Japanese drive fishery. Report of the International Whaling Commission 43:417–437.

O'Brien, J. K., and T. R. Robeck. 2010. The value of *ex situ* cetacean populations in understanding reproductive physiology and developing assisted reproductive technology for *ex situ* and *in situ* species management and conservation needs. International Journal of Comparative Physiology 23:227–248.

Odell, D. K., and K. M. McClune. 1999. False killer whale *Pseudorca crassidens* (Owen, 1846). Pages 213–243 *in* S. H. Ridgway and R. J. Harrison, eds. Handbook of marine mammals. Volume VI. The second book of dolphins and the porpoises. Academic Press, New York, NY.

Ohsumi, S. 1966. Allomorphosis between body length at sexual maturity and body length at birth in the Cetacea. Journal of the Mammalogical Society of Japan 3:3–7.

Peacock, A. D., D. L. Comrie and F. Greenshields. 1936. The false killer whales stranded in the Tay Estuary. The Scottish Naturalist 220:93–104.

Perrin, W. F., and G. P. Donovan. 1984. Report of the workshop. Report of the International Whaling Commission (Special Issue 6):1–27.

Perrin, W. F., and S. B. Reilly. 1984. Reproductive parameters of dolphins and small whales of the family Delphinidae. Report of the International Whaling Commission (Special Issue 6):97–134.

Purves, P., and G. Pilleri. 1978. The functional anatomy and general biology of *Pseudorca crassidens* (Owen) with a review of the hydrodynamics and acoustics in Cetacea. Investigations on Cetacea 9:67–227.

SAS Institute Inc. 2004. SAS/STAT 9.1 user's guide. SAS Institute Inc., Cary, NC.

Scott, E. O. G., and R. H. Green. 1975. Recent whale strandings in northern Tasmania. Papers and Proceedings of the Royal Society of Tasmania 109:91–96.

Smithers, R. H. N. 1938. Notes on the stranding of a school of *Pseudorca crassidens* at the Berg River mouth. Transactions of the Royal Society of South Africa 25:403–411.

Stevick, P. 1999. Age-length relationships in humpback whales: a comparison of strandings in the western North Atlantic with commercial catches. Marine Mammal Science 15:725–737.