

GROWTH AND REPRODUCTION OF THE FINLESS PORPOISE IN SOUTHERN CHINA

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ABSTRACT. – We studied the growth and reproduction of finless porpoises in southern China, based on 86 specimens collected as strandings or fisheries bycatches in Hong Kong, southern Fujian Province, and Taiwan. Specimens were aged by sectioning and staining thin layers in the teeth, and counting dentinal and cemental growth layer groups (GLGs). There is a general darkening of the colour pattern from neonates through adults, and adults become relatively more slender. Growth is rapid in the first year and thereafter begins to level-off. There is evidence of some sexual dimorphism, with males growing somewhat larger than females. There is a distinct calving peak from October to January. Limited data on age and length at attainment of sexual maturity suggest that females reach maturity at about 137-150 cm and 5-6 years, and males at 138-154 cm and 4-5 years. The growth and reproductive parameters found in this study are similar to those determined previously for other populations of finless porpoises.

KEY WORDS. – Finless porpoise, Hong Kong, Taiwan, Fujian Province, life history, growth, reproduction, sexual maturity.

INTRODUCTION

Despite our general lack of knowledge on the biology of the finless porpoise (*Neophocaena phocaenoides*), there has been quite a bit of work done on the growth and reproductive biology of the species, mainly in China and Japan. Growth and reproductive parameters have been estimated, based largely on animals taken in fisheries (and to a lesser extent, based on observations of captive and stranded animals) for populations in the Inland Sea of Japan (Kasuya & Kureha, 1979; Kasuya et al., 1986); the Kyushu area of Japan (Mizue et al., 1965; Shirakihara et al., 1993); Ise Bay of Japan (Furuta et al., 1989); the Yellow and Bohai seas of China (Zhang, 1992; Gao & Zhou, 1993; Chang & Zhou, 1995); the Yangtze River (Chen et al., 1982; Zhang, 1992; Gao & Zhou, 1993; Chang & Zhou, 1995); the South China Sea (Gao & Zhou, 1993); and the coast of Pakistan (Harrison & McBrearty, 1974).

Growth and reproduction have also been investigated in most other species of the family Phocoenidae, including the harbour porpoise, *Phocoena phocoena* (see Møhl-Hansen, 1954; Fisher & Harrison, 1970; van Utrecht, 1978; Read, 1990a, b; Read & Gaskin, 1990; Sorensen & Kinze, 1994; Read & Hohn, 1995; Lockyer, 1995), Burmeister's porpoise,

Phocoena spinipinnis (see Reyes & Van Waerebeek, 1995), vaquita, *Phocoena sinus* (see Hohn et al., 1996), and Dall's porpoise, *Phocoenoides dalli* (see Kasuya, 1978; Newby, 1982; Kasuya & Shiraga, 1985; Ferrero & Walker, 1999). Only the spectacled porpoise, *Phocoena dioptrica*, has not been studied. Comparisons of finless porpoise studies with the above studies have shown that the finless porpoise is a typical phocoenid, characterized by rapid early post-natal growth, early attainment of sexual maturity, and a short lifespan (see Gaskin et al., 1984).

The growth and reproduction of finless porpoises in southern China was investigated as part of a large-scale, multi-faceted study of the conservation biology of the finless porpoise population that occurs in Hong Kong waters. This study represents the first time that specimens from Hong Kong have been used in studies of finless porpoise life history. The only previous study for the South China Sea used only specimens from near the Xiongdi Islands (southern Fujian Province) (Gao & Zhou, 1993). Although the population structure of finless porpoises in southern China has not yet been resolved, here we assume that finless porpoises from Hong Kong, Taiwan, and southern Fujian Province belong to the same population.

MATERIALS AND METHODS

Sampling and Data Collection. – The overall sample consisted of 86 finless porpoise specimens, from which a minimum of approximate total length had been collected (Table 1). Most of the specimens were collected as beach-cast strandings from the coast of Hong Kong and Taiwan. Some were taken as incidental catches and were obtained from fishermen of Taiwan and Dongshan, southern Fujian Province, PRC. Total length for each specimen was measured in a straight line, using a taut tape measure or calipers, from the tip of the upper jaw to the notch in the tail flukes (Norris, 1961). Two to three teeth were collected from the middle of the lower jaw (or nearby in some cases) and stored in water or alcohol. Reproductive tracts were examined, and gonads were collected and stored in 10% formalin.

Some stranded specimens were very badly decomposed (codes 4 or 5 of the ranking system described by Geraci & Lounsbury, 1993). For most of these, decomposition was too advanced to properly analyze reproductive status, but some specimens for which an accurate length could still be obtained were used in the growth analyses. For some of these decomposed specimens, genders were determined genetically. The sample of specimens with at least length/age data consisted of a total of 58 specimens. The composition of the sample is summarized in Table 1. The sample included specimens of all length categories, with modes for larger specimens 120-170 cm in length (Fig. 1).

Age Determination. – We aged 58 specimens; teeth from 3 others were prepared, but sections were inadequate to obtain a reliable age. Tooth aging was conducted at the Southwest Fisheries Science Center (NOAA, NMFS, La Jolla, CA, USA), generally following the procedures described by Myrick et al. (1983) and Hohn & Lockyer (1995). Teeth were decalcified in RDO™, a commercial rapid-decalcifying agent. Because finless porpoise teeth are small, immersion times in the RDO™ were short, approximately 3-6 hours depending on the length of the animal. The decalcified teeth were sectioned longitudinally into 25 µm-thick sections using a sledge-type sliding microtome, after freezing onto the microtome stage with Tissue Tech™. Sections through the center of the tooth, and encompassing the entire pulp cavity, were stained with Mayer’s hematoxylin stain and mounted on glass slides.

Table 1. Detailed breakdown of the sample, showing the types of data available for the study.

Type of data	Males	Females	Unknown	Total
Length only	11	11	7	29
Length + age	14	18	4	36
Length + maturity	0	1	0	1
Length + age + maturity	14	5	1	20
Total	39	35	12	

Tooth sections were examined under a compound microscope (4X-40X power), without reference to specimen length or other biological data. We assumed that 1 GLG represented 1 year. This assumption is supported by studies of captive porpoises of known age (Kasuya et al., 1986). Growth layer groups (GLGs) were counted in the post-natal dentine. For some older specimens, the pulp cavity was completely occluded, making the GLGs indistinct. In these specimens cementum layers were counted and generally were used to assess the age of the individual. The teeth were read independently by the first two authors 3-4 times on separate days. After the readings were complete, both readers compared their data and agreed on an age for each specimen. If the readers’ GLG counts did not agree, tooth sections were re-examined simultaneously by both readers and a final age was decided upon.

Fitting of Growth Curves. – We used standard logarithmic, as well as Gompertz three-parameter least squares models (Laird, 1966; Kaufman, 1981) to fit growth curves to the age-at-length data, using the software STATISTICA for the Macintosh (StatSoft, Inc., 1994). The Gompertz model takes the general form:

$$S = A \exp(-b \exp(-k t))$$

where S = size (in this case, total length),
 A = asymptotic length,
 b = constant of integration,
 k = growth rate constant, and
 t = age.

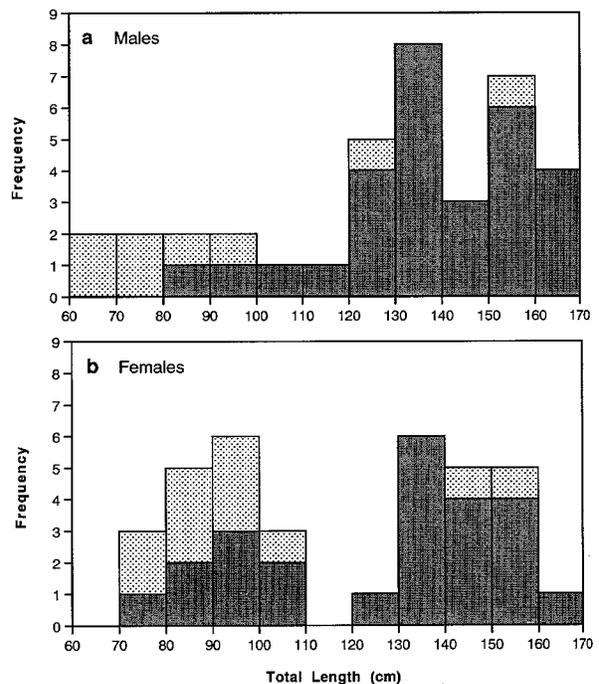


Fig. 1. Details of the sample used in this study. Light shading indicates unaged specimens and dark shading indicates aged specimens: males (a), and females (b).

Weight/length and other curves were fitted using a variety of models (including standard exponential and linear functions).

Determination of Calving Seasonality. – Calving seasonality was determined by computing an estimated birthdate for each neonate (defined as < 100 cm in length) and fetus in the sample, based on the average length at birth along with fetal and early neonatal growth rates from the literature. Birthdates for neonates were estimated using 84 cm as the average length at birth, and the age at 1 year as 117 cm (after Gao & Zhou, 1993). Assuming linear growth in the first year, this translates to a first year growth rate of 2.75 cm/mo. For fetuses, linear growth was assumed during gestation. Assuming an 11 month gestation period (Gao & Zhou, 1993), this corresponds to a fetal growth rate of 7.64 cm/mo. The estimated month of birth was then calculated from the average length at birth and the appropriate growth rate.

Assessment of Reproductive Status. – Ovaries and testes were processed according to the procedures described in Akin et al. (1993). Length and width measurements were taken with calipers to the nearest 0.1 cm and weight was obtained to the nearest 1.0 g. All corpora were counted and classified according to the system of Perrin et al. (1976), which is described in detail and figured in Akin et al. (1993). Sexual maturity for females was defined by the presence of at least one corpus luteum or corpus albicans, or the presence of a fetus in some females for which ovaries were not collected.

For males, a 1 cm² section was taken from the middle of the right testis and prepared histologically for detailed examination (Akin et al., 1993). Hematoxylin and Eosin stained slides were prepared by a commercial laboratory (A Cut Above Histology Lab, San Diego, CA). Stained testis sections were examined under a compound microscope (40X power), and sexual maturity was determined by the presence of products of spermatogenesis (stocytes, satids, and satozoa) and the size and shape of the seminiferous tubules and the interstitial space (see Hohn et al., 1985; Akin et al., 1993). Five tubule diameters were measured in microns at 40X using a micrometer disc (later converted to μm) for each specimen, and the mean of these five measurements was used as the average tubule diameter. Specimens were classified as immature (state 1), maturing/prepubescent (state 2), or mature (state 3), based on a subjective assessment of all of the above (after Collet & Saint Girons, 1984).

RESULTS

Growth. – Finless porpoises in southern China can be classified into a number of age/sex classes (Fig. 2). Neonates are characterized by relatively large flippers, a shallow forehead, lighter colour than adults, a very light patch around the lips, and a gape-to-flipper stripe (Fig. 2a). Very young newborns may still show prominent fetal folds. Juveniles have a steeper forehead, are light gray in colour (or sometimes fawn), and still show the prominent light lip patch

and dark gape-to-flipper stripe (Fig. 2b). Subadults are nearly the size of adults, with steep foreheads, and show a varying darkness of body coloration; the light lip patch is less prominent, but the gape-to-flipper stripe may still be obvious (Fig. 2c,d). Adults are uniformly dark gray (almost black in some specimens), with no light lip patch, and with steep or overhanging foreheads (Fig. 2e). The increase in maximum girth slows down as specimens get larger (Fig. 3), which results in neonates and juveniles appearing relatively robust and large adults looking relatively slender. We found no evidence of sex-related differences in coloration or external morphology.

Growth curves were constructed, based on age-at-length data for 56 specimens (28 males, 23 females, and 5 animals of unknown sex) (Fig. 4). Separate curves were plotted for males and females, and showed some evidence of sexual dimorphism, with males growing larger than females (Fig. 4a). Stratified sample sizes for each sex were relatively small (some specimens were unsexed), and the logarithmic curve did not fit the female data well for older specimens. Therefore, a single, sex-independent growth curve was also

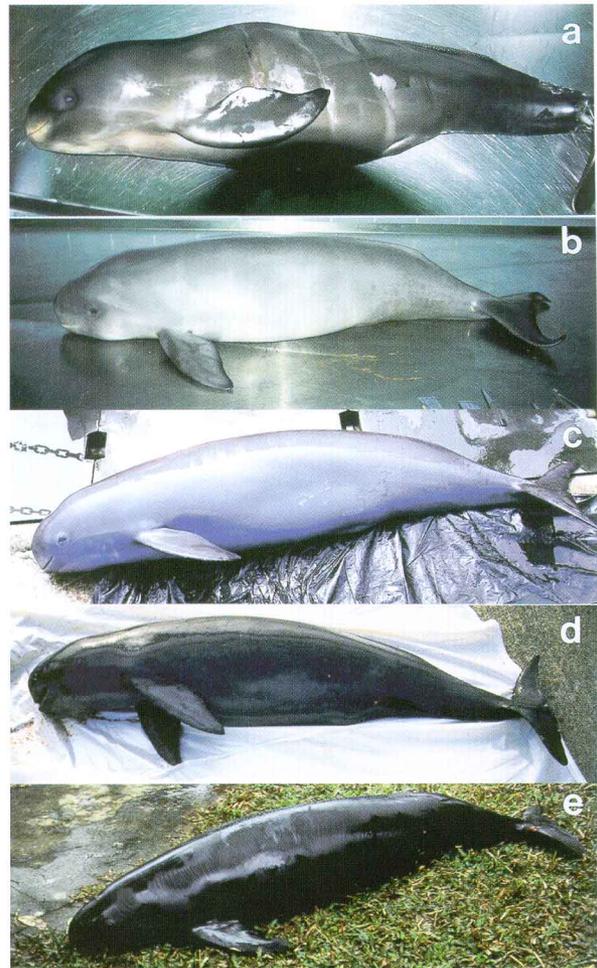


Fig. 2. Development of external appearance of finless porpoises from Hong Kong: 67-cm male neonate (NP96-23/01 - a); 84-cm male calf (NP96-25/04 - b); 124-cm, 2.5-year old juvenile male (NP00-12/02 - c); 137-cm, 4-year old subadult male (NP97-11/10 - d); and 168-cm, 13-year old adult male (NP96-12/01 - e).

constructed, using the combined male and female data, as well as data from several unsexed specimens (Fig. 4b). A Gompertz model (which assumes asymptotic growth) fit the pooled-sex data well. An asymptote was reached at 161 cm and 13 GLGs. Growth during the first year was extremely rapid and linear, and the growth rate decreased significantly after the first several years (Fig. 4). The oldest specimen in the sample (a female) was estimated to be 33 years old.

The length vs. weight relationship appeared to be linear (Fig. 5). Newborns appeared to weigh about 5 kg, and the maximum weight reached by specimens in the sample was 52 kg. Based on this curve, the largest specimens in the population (about 168-170 cm) probably reach weights of at least 60 kg.

Reproduction. – The distribution of the estimated month of birth for neonates and fetuses showed clear evidence of reproductive seasonality (Table 2; Fig. 6). Although a few births occurred in other months, 77% (17 of 22) were estimated to occur in the late autumn and early winter months of October to January.

Data on sexual maturity for specimens over 120 cm in length were available for six females and 11 males (Table 3). For females, one specimen aged 5 years and 137 cm in length, was immature. The rest, all 6 years or older and at least 150 cm in length, were mature. This small sample suggests that females reach sexual maturity at ages between 5 and 6 and lengths between 137 and 150 cm.

For males, five specimens (aged 2-4 and 124-138 cm) were immature or maturing, and six others (aged 4.5-13 and 154-168 cm) were mature (Table 3). There was a rapid increase in testis weight between specimens < 140 cm and those > 154 cm (Fig. 7). All immature or maturing males had single testis weights < 30 g and all mature males had testis weights of > 200 g. Unfortunately, there were no specimens between 140 and 154 cm to allow us to define more precisely the length at which the rapid increase occurs. Immature and maturing male specimens had average seminiferous tubule diameters of < 80 μm, and mature males had diameters of > 130 μm (Fig. 8). Collectively, these data suggest that male sexual maturity is reached at between 4 and 5 years and between 138 and 154 cm.

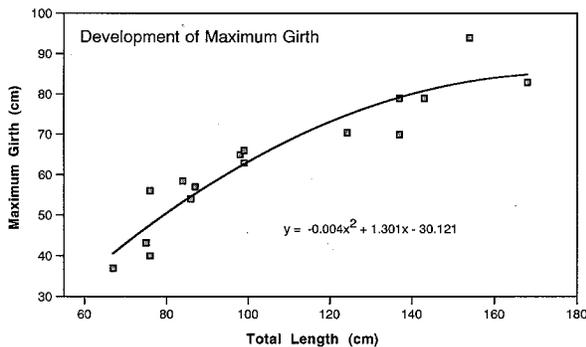


Fig. 3. Curve showing development of maximum girth for southern Chinese finless porpoises.

DISCUSSION

General Discussion. – Overall, the growth and reproductive parameters determined in this study fit in well with other

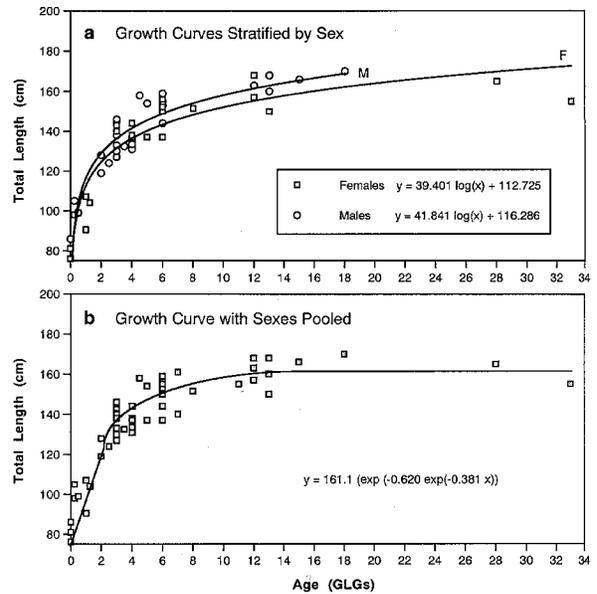


Fig. 4. Growth curves for southern Chinese finless porpoises, with the sexes stratified (a), and with both sexes pooled along with unsexed specimens (b).

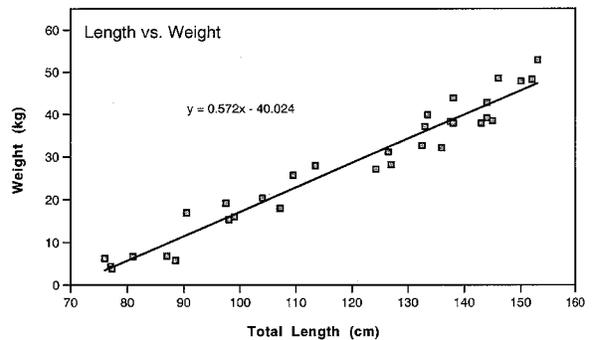


Fig. 5. Length vs. weight relationship for southern Chinese finless porpoises.

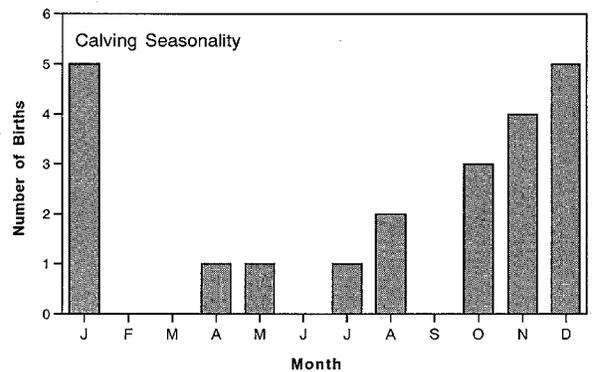


Fig. 6. Bar graph showing the predicted month of birth for southern Chinese finless porpoise fetuses and neonates.

studies of finless porpoises, and with studies of porpoises (family Phocoenidae) in general. Phocoenids are known to be relatively short-lived, with early development and relatively 'r-selected' growth and reproductive features.

One finding of particular interest is the presence in the sample of two old individuals (28 and 33 years). An examination of the literature on phocoenid age and growth (see review in Gaskin et al., 1984) suggests that these are the two oldest specimens ever recorded in the family Phocoenidae. This finding may suggest that finless porpoises live longer than other species in the family. However, we suggest that the explanation may lie, at least partially, in sampling bias. Most previous studies of porpoise life history have been of populations that had been exploited by fisheries for many years, which might result in few animals reaching their maximum possible longevity. Our sample of finless porpoise specimens, on the other hand, contained a large proportion of stranded specimens. As such, we might expect that our sample would have a higher chance of containing older individuals. We should caution the reader that this is only one possible explanation, and there are certainly others.

It should be cautioned that our estimate of asymptotic length is based on both sexes pooled, and we consider it to be highly preliminary. There were no old males in the sample (the

oldest was 17 years), and therefore a reliable estimate of the sex-stratified asymptotic length is not possible at this point. This is something that will be examined in future studies based on larger samples, but in the mean time we present the sex-pooled asymptotic length estimate (161 cm) as a tentative figure.

We were surprised to find that a linear function fit the length vs. weight data better than an exponential or power curve (Fig. 5). However, this may be explained by the fact that finless porpoises become proportionately more slender as they grow (Fig. 3). Thus, as the animals get longer, their increasing slenderness may counteract the tendency for weight to increase exponentially. It should also be recognized that our largest specimens in the analysis were < 155 cm, and that larger specimens may show more evidence of a power relationship. We plan to examine this in the future with a larger dataset.

In the histological examination of testes and ovaries, we found that the advanced level of decomposition of some specimens (codes 3 and 4) did not seriously hinder our ability to assess their reproductive status. This was a welcome finding, as we are limited mostly to stranded specimens for

Table 2. Summary of fetuses and neonates, and estimates of their date of birth.

Collection Locality	Age Class	Length (cm)	Collection Date	Estimated Birth
Hong Kong	Fetus	70	1 October	November
Hong Kong	Fetus	87	15 November	November
Hong Kong	Neonate	67	23 January	January
Hong Kong	Neonate	67	7 January	January
Hong Kong	Neonate	75	4 January	January
Hong Kong	Neonate	76	15 December	December
Hong Kong	Neonate	76	10 October	October
Hong Kong	Neonate	77	26 May	May
Hong Kong	Neonate	77.3	12 January	January
Xiamen	Neonate	82	January	January
Hong Kong	Neonate	83	2 November	November
Hong Kong	Neonate	84	25 April	April
Hong Kong	Neonate	86	14 January	December
Hong Kong	Neonate	87	15 January	December
Hong Kong	Neonate	87	21 November	October
Hong Kong	Neonate	88.5	31 August	July
Xiamen	Neonate	90.5	February	December
Hong Kong	Neonate	94	9 March	November
Xiamen	Neonate	96	December	August
Hong Kong	Neonate	98	4 January	August
Hong Kong	Neonate	99	18 May	December
Hong Kong	Neonate	99	9 April	October

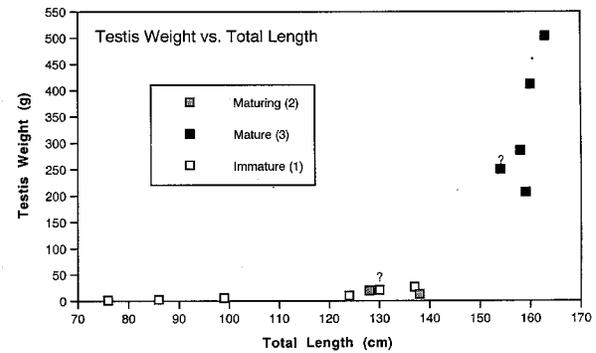


Fig. 7. Plot showing development of testis weight with length for southern Chinese finless porpoises. The two symbols with question marks indicate specimens in which maturity was not evaluated based on histological examination of gonads.

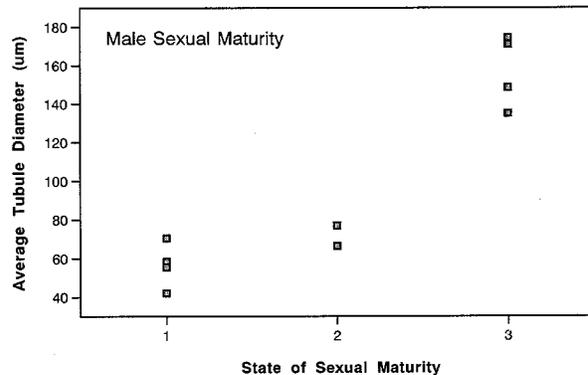


Fig. 8. Seminiferous tubule diameter vs. state of sexual maturity for southern Chinese finless porpoises. Maturity states: 1 = immature, 2 = maturing, and 3 = mature. Since our criteria for determining state of sexual maturity was based partly on average tubule diameter, there may be some element of circularity.

Table 3. Summary of finless porpoise specimens >120 cm in length, in which sexual maturity was assessed by examination of reproductive tracts.

Specimen #	Age (GLGs)	Length (cm)	Status	Comments
FEMALES				
NP96-08/03	5	137	Immature	No corpora on ovaries
N14	6	ca. 150	Mature	Pregnant
NP97-23/01	12	157	Mature	Large corpus luteum (13.9 X 8.8 mm)
NP98-15/11	12	168	Mature	Pregnant
NP96-13/01	13	150	Mature	Uterus enlarged and engorged with blood
NP97-26/01	nd	150	Mature	Uterus enlarged and engorged with blood
MALES				
NP96-13/03	2	128	Maturing	Testis weight = 20 g
NP00-12/02	2.5	124	Immature	Testis weight = 10 g
NP96-08/01	3	138	Maturing	Testis weight = 13 g
NP98-23/06	3	130	Immature or maturing?	Testis weight = 21 g
NP97-11/10	4	137	Immature	Testis weight = 27 g
NP98-06/03	4.5	158	Mature	Testis weight = 286 g
NP99-16/07	5	154	Mature?	Testis weight = 250 g
NP99-17/02	6	ca. 159	Mature	Testis weight = 207 g
NP99-17/11	12	163	Mature	Testis weight = 504 g
NP99-30/01	13	160	Mature	Testis weight = 412 g
NP96-12/01	13	168	Mature	Testis weight = >500 g Testis length = 28 cm

life history studies, and these specimens are often badly decomposed.

Geographical Variation in Growth and Reproductive Parameters. – A comparison of some finless porpoise growth and reproductive parameters among populations is presented in Table 4. Although some apparent differences may simply reflect different study techniques and biases, some aspects show apparent geographical variation among different populations of this species. For instance, the maximum length from each area (except for Pakistan) is based on a relatively large sample, so these differences are probably real. As noted by Kasuya (1999), these differences follow a predictable pattern, with the largest size reached by the northernmost populations along the northern China coast, and the smallest apparently reached by the more tropical populations in Hong Kong and probably Pakistan.

There is some question as to whether the maximum size of 155 cm from Pakistan is indeed typical of growth in the Indian Ocean populations. To examine this, we searched the literature for records of finless porpoises from the Indian Ocean and Southeast Asia south of China, in which the total lengths of specimens were reported. Reported lengths (n = 75) ranged from 58–180 cm (Murray, 1884; Keswal, 1886; van Bommel, 1939; Dawson, 1959; Pilleri & Gühr, 1972, 1974; Harrison & McBrearty, 1974; Al-Robaee, 1975; Balan,

1976; Thomas, 1983; Tas'an & Leatherwood, 1984; James & Lal Mohan, 1987; James et al., 1987; Leatherwood & Reeves, 1989; Ganapathy, 1992; Nammalwar et al., 1994; Lal Mohan, 1995; Muthiah, 1995; Mahakunlayanakul, 1996; Robineau & Fiquet, 1996; Rudolph et al., 1997; Andersen & Kinze, 1999; Chantrapornsy et al., 1999; TAJ unpubl. data). However, only two specimens were reported to be over 158 cm in length, both from India; they were both reported to be 180 cm (Thomas, 1983). Both of these measurements are highly suspect, however. It is possible that the measurements were taken over the curve of the body, rather than in a straight line. Also, the measurements reported in Thomas' (1983) paper were almost all in 5-cm intervals. Thus, it is likely that these were simply estimates (or were at least rounded), rather than true measurements. We think these measurements should be treated as inaccurate. If we exclude these two questionable lengths, the longest specimen reliably measured from the Indian Ocean and tropical southeast Asia appears to be 158 cm.

One reproductive parameter that appears to be highly variable is the calving season. In various populations, calving apparently peaks in summer, spring, or winter. This is considered to be a real difference, and is probably related to local conditions (calving presumably peaking at a time of year that is favorable for newborn calves and mothers with greater nutritional requirements). The gestation period, on

Table 4. Summary of reproductive parameters estimated for various finless porpoise populations. Zhang (1992) is not included, because that study mixed information from the Yangtze River and North China coastal populations. ASM refers to age at sexual maturity and LSM length at sexual maturity.

Parameter	Japan	N. China Coast	Yangtze River	Hong Kong/ S. China Sea	Southern China	Pakistan
Neonatal length (cm)	79 ^a 78 ^b 75-85 ^c	77	73	84 ^d	70-75 ^d	> 77 ^d
Min. male ASM (yr.)	3 ^a 4 ^b	5.5	5.8	4	4 ^d	—
Min. female ASM (yr.)	< 4 ^a 5 ^b	5	5.5	5	5 ^d	—
Min. male LSM (cm)	145 ^a 135 ^b	132	136	151	138 ^d	140 ^d
Min. female LSM (cm)	< 140 ^a 135 ^b	132	135	145	137 ^d	120 ^d
Asymptotic length female (cm)	157.7 ^b	ca. 152	ca. 146	ca. 158 ^e	ca. 161 ^e	—
Asymptotic length male (cm)	165.5 ^b	—	—	ca. 158 ^e	ca. 161 ^e	—
Maximum length (cm)	194 ^a 175 ^b 194 ^c	227	177	171	168	155 ^d
Maximum age (yr.)	23	25	18	22	33	—
Gestation period (mo.)	10.6-11.2	10.4-11.1	10.1-10.8	10.9-11.5	—	—
Calving season	Apr.-Aug. ^a Nov.-Dec. ^b April ^c	Apr.	Mar.-May	Jun.-Mar.	Oct.-Jan.	—
Reference(s)	Kasuya & Kureha, 1979; Kasuya et al. 1986; Furuta et al., 1989; Shirakihara et al., 1993; Kasuya, 1999	Chang & Zhou, 1995; Wang, 1989	Chang & Zhou, 1995	Gao & Zhou 1993	This study	Harrison & McBrearty, 1974

a Estimate for Inland Sea population.

b Estimate for Kyushu populations (Omura Bay and Tachibana/Araiike Sound).

c Estimate for Ise Bay population.

d Estimate is based on a very small sample, and should therefore be considered preliminary.

e Estimate for both sexes pooled.

the other hand, does not appear to be highly variable (see Perrin & Reilly, 1984).

This study has provided some detailed information on life history of the finless porpoise in the northern South China Sea off southern China, a previously poorly-studied part of its range. The descriptions we provide of finless porpoise age and sex classes may be of use in future ecological and behavioral studies. While this study has clarified many aspects of growth and reproduction of these animals in this area, the limitations of the sample (small to moderate sample sizes, and advanced level of decomposition of many of the specimens) have prevented us from examining many finer details. We hope that the increased interest in the finless porpoise in recent years will result in additional studies and the availability of fresher specimens. These in turn will

hopefully be used to effectively manage and conserve the populations of this species.

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