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Growth and reproduction of three populations of finless porpoise, *Neophocaena phocaenoides*, in Chinese waters

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Summary

We have 189 specimens available for this work. One-hundred and sixty-seven specimens from the Yangtze, Yellow Sea and South China Sea populations were aged and used in studying the growth pattern. A modified power model was employed in fitting the growth curves of the Yangtze and the Yellow Sea populations. The Laird's model was used for the South China Sea population. Testis weight for 75 specimens were available for demonstrating the development of the testis. An adapted S-shaped growth model was used in fitting the testis weight/age curve for the Yangtze and the South China Sea populations. Data from 82 females were available for estimation of reproductive parameters. Sexual maturity was determined by anatomical and histological methods. The results indicate: (1) The growth rate of the body length was pronouncedly higher in the first 4 GLGs of life and ceased to grow at the age of about 8 in the South China Sea population while the Yellow Sea and the Yangtze populations grew relatively slower in the first few GLGs of age, and kept growing in all the ages examined, but the females of the Yangtze population seemed to grow slower than the males after 6. (2) The testis developed earlier and faster in the South China Sea population. (3) The minimum age of the sexually mature finless porpoise is 4 GLGs for males and 5 GLGs for females in the South China Sea population. The minimum age at sexual maturity was about 5 GLGs in both the males and females of the Yellow Sea population, and about 6 in those of the Yangtze population. The age at attainment of sexual maturity varied with individuals. The maximum immature were 8 and 10 GLGs in the males and females of the Yellow Sea population respectively, 7 in the females of the Yangtze River population. (4) The porpoise in the South China Sea population gave birth in June through March with a peak in August through December while that of the Yangtze and the Yellow Sea populations mainly gave birth in April and May. The differences among the three populations in growth and reproduction may be attributed to their different habitats. The higher surface temperature in the tropical water may have enhanced both the rapid growth and the sexual and physical maturity of the South China Sea population.

Introduction

The finless porpoise, *Neophocaena phocaenoides*, is distributed in the form of a narrow band along the coast of tropical and temperate Asia, and in rivers and lakes in China. It reaches the Persian Gulf in the west (Tomilin, 1967; Pilleri and Gihr, 1973–74), the north coast of Java in the south, the northern part of the Liaodong Gulf (41°N latitude) in China in the north (Wang, 1984), and the Sendai Bay (38°20′N latitude) in Japan in the east (Nishiwaki, 1966). Different geographical populations were noted and even were regarded as different species (Pilleri and Ghir, 1972, 1975). According to the external and skeletal characters of 218 specimens, and the mitochondrial DNA polymorphism as well, the finless porpoise in Chinese waters are referred to three populations: the Yangtze population, Yellow Sea population and South China Sea population (Gao, 1991; Gao and Zhou, manuscript).

Harrison and McBrearty (1973–74) studied the reproduction and gonads of the finless porpoise from the waters off Pakistan. Chen, Liu and Harrison (1982) reported the reproduction and reproductive organs based on specimens from the Yangtze River, China. Zhang (1986) aged 52 specimens and studied the growth pattern and sexual maturity with a total of 68 specimens from Yangtze River, Yellow Sea and Bohai Sea in his Masters thesis. Chang (1990) studied the growth and the age at the attainment of sexual maturity of the Yangtze and Yellow Sea populations with 98 aged and 50 unaged specimens. However, the parameters reported by Zhang may not be stable and reliable because of the relatively small sample size, and those reported by Chang included only two of the three populations in Chinese waters. No data on the growth and reproduction have been reported for the South China Sea population so far. The purpose of the present paper, therefore, is to study the growth and reproduction of the three populations separately based on relatively larger samples.

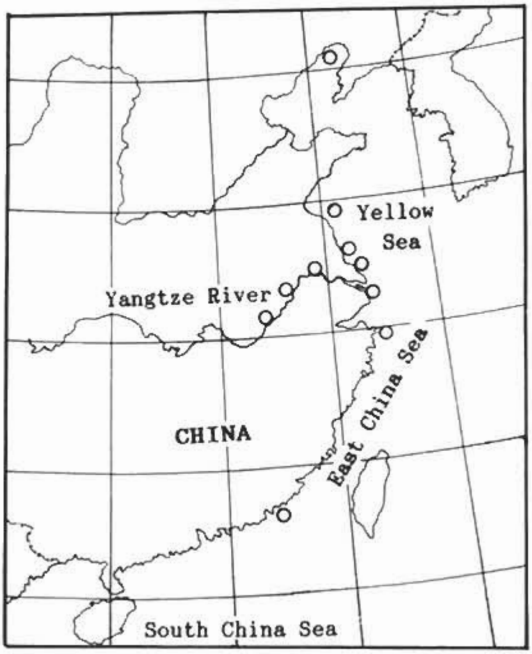

Figure 1. Distribution of *Neophocaena* in Chinese waters, showing collection sites.

Material and method

We have 167 specimens of finless porpoise available for age determination. Of which, 21 females and 20 males from the lower reaches of the Yangtze River were referred to the Yangtze population, 43 females and 28 males from the coastal waters of the Yellow Sea, Bohai Sea and East China Sea were referred to the Yellow Sea population, 23 females and 32 males from the south part of the East China Sea near Xiongdi Islands (23°5′N, 117°6′E), Fujian Province were referred to the South China Sea population (Fig. 1). We also examined 22 unaged specimens, including 8 males and 3 females from the Yangtze population and 5 males and 6 females from the Yellow Sea population.

Testis weight was available for 75 porpoises. Of which, 24, 24 and 27 were from the Yangtze, Yellow Sea and South China Sea populations respectively. Eighty-two female specimens were available for reproduction data, 19 were from the Yangtze, 41 from the Yellow Sea, and 22 from the South China Sea samples.

All of the specimens were collected in 1974–1991 by the staff of the Cetacean Research Laboratory, Department of Biology, Nanjing Normal University, and are deposited in this laboratory. Most of them were killed incidentally by fishing gear in the fishing season, some were carcasses found lying on the river bank or floating on the river. The samples for the Yangtze and the Yellow Sea populations were mainly collected in April through May, and the samples of the South China Sea population were collected in November through December.

Age determination

The age estimates were based primarily on dentinal growth layer groups (GLGs, terminology of Perrin and Myrick, 1980 p. 48) following Myrick, Hohn, Sloan, Kimura and Stanley (1983) with a few modifications. Two or more teeth were removed from the mid-section of the mandible, decalcified in 5–10% nitric acid and 5% formalin for about 15 hours at room temperature, 2–5°C, in winter. Longitudinal buccalingual sections 20 microns thick were cut passing through the centre of the tooth using an AO 856 Histo Stat freezing microtome at −20°C. Sections were stained with hematoxylin, and mounted in neutral balsam.

Age was calibrated along the vertical axis or through the side wall depending on which was clearer and more regular. For each individual, mounted sections were read at least twice by one reader in a random order. The second scoring was made at least 6 hours later without any reference to the previous count and the body length. If the two readings were different, additional readings were performed until a consistent scoring was obtained.

The pulp cavity occluded generally around the age of 15–20 GLGs. But one specimen from Bohai Sea showed 25 dentinal GLGs with open pulp cavity. For the specimens with closed pulp cavity, age was estimated from the layers in the cementum. Because the number of cemental GLGs appeared to be the same as the number of dentinal GLGs in the teeth with open pulp cavity. The cemental GLGs were much thinner than the dentinal ones, and were not as regular as the dentinal ones. It was assumed that the deposition rate for cemental GLGs was the same before and after the closure of the pulp cavity. Counting of cemental GLGs was difficult. One cemental GLG was composed of one thick layer or two thinner layers. Within one GLG, the constituent layers may run together in one place and separate in another. So correct counting of the cemental GLGs depended on the experiences obtained from careful comparison between the dentinal and cemental GLGs of the tooth whose pulp cavity was not closed. The score based on the most clear layers was accepted. If no region of the cementum had substantially clearer layers than any other regions, the minimum score was accepted.

Testis and ovary

Testes were preserved in 10% neutral formalin during a field necropsy. The sections were cut 20 microns thick using an AO 856 Histo Stat freezing microtome at −15°C, stained with hematoxylin and eosin, and mounted in neutral balsam. Males with spermatozoa concentrated at the centre of the seminiferous tubules were thought to be sexually mature (Hohn, 1985). For females, the presence of either a corpus luteum or a corpus albicans indicated sexual maturity.

Body length/age curve fitting

Zhang (1986) and Chang (1990) each fitted a growth curve in the model of power function. We found that: (1) the power function curve could not make the body length to be equal to the body length at birth, i.e. at the age of 0 GLG, (2) it did not match the body lengths through all the ages in our samples, and (3) the growth pattern in the South China Sea population was conspicuously different from the other two. So two models were selected in fitting the growth curves. One is a modified power model for the Yangtze and Yellow Sea populations.

$$L = a(t+k)^b + ct \quad [1]$$

where L = body length at age of t, t = age in GLGs, k is defined to make the L equals the body length at birth, ct is designed by the authors to explain the arithmetic fraction which could not be interpreted by the power model. a, b, c and k are constants. The other is the Laird's model for the South China Sea population which was used by Perrin *et al.* (1977) for the eastern spinner dolphin.

$$L = L_0 EXP\{a/b[1 - EXP(-bt)]\} \quad [2]$$

where L = body length, L_0 = body length at birth, t = age in GLGs, a and b = constants. Constants in formulas [1] and [2] were closed iteratively to minimize the residual sums of square.

Testis weight/age curve fitting

The weight of the testis and epididymis on age in GLGs obey the S-shaped model. No difference was found between the left and the right testis and epididymis. We prefer the data of left side. The right data were used only when the left data were not available. The model for the growth curve fitting was adapted by the authors from the common S-shaped curve, $Y = 1/[a + bEXP(-x)]$. It is

$$W = W_{max}/[1 + (W_{max}/W_0 - 1) * EXP(-kx)] \quad [3]$$

where W = testis weight, W_{max} = maximum mean testis weight, W_0 = testis weight at birth, k is the only constant to be defined in this formula.

Results and discussion

Growth

Figure 2a shows the scatterplot of body length on age and the fitted growth curve for the Yangtze population. The growth equations are:

$$L = 1026(t+0.12)^{0.170} - 9.1t \quad [4]$$

($N = 21$, $R^2 = 0.8994$; L in mm, t in GLG) for females and

$$L = 1026(t+0.12)^{0.110} + 18.5t \quad [5]$$

($N = 20$, $R^2 = 0.9416$) for males.

The porpoise from the Yangtze River attained a body length of 1300 mm at the age of 5 years. The adults kept growing all the ages. But the females seem to grow slower than the males after age 6. The maximum records for males were 1765 mm in body length and 17 GLGs in age. The maximum record of body length for females, 1640 mm, was of an unaged specimen. The oldest female recorded in the Yangtze population was 18 GLGs in age and 1600 mm in body length.

Figure 2b is the relationship between the body length and age for the Yellow Sea population. The growth equation is

$$L = 1039(t+0.136)^{0.180} - 4.7t \quad [6]$$

($N = 71$, $R^2 = 0.8292$) for both males and females.

The porpoise of this population reached 1300 mm in body length at the age of 4 GLGs. The adults kept growing and the growth rate of both sexes was similar to each other all the ages. The maximum body length for females, 2060 mm, was of an unaged specimen deposited in Dalian Natural History Museum, Liaoning Province. The oldest female recorded was 25 GLGs in age and 1620 mm in body length. A specimen 1915 mm in body length and 24 GLGs in age was our maximum record for males.

Figure 2c is the relationship between the body length and age for the South China Sea population. The equation of the growth curve is

$$L = 840EXP\{0.372/0.585[1 - EXP(-0.585t)]\} \quad [7]$$

($N = 55$, $R^2 = 0.7580$) for both males and females.

This population grew much faster in the first 4 GLGs of age than that of the other two populations. It reached 1300 mm in body length at the age of about 3 GLGs, approached the maximum length at about 6 years and ceased to grow after 8 years. The maximum records for males were 1680 mm in length and 22 GLGs in age. The maximum record of body length for females, 1710 mm, was of a specimen at the age of 5. The oldest female in the South China Sea samples was 7.5 GLGs in age and 1450 mm in body length.

Plotting the growth curves of equation [4] through [7] into one figure (Fig. 2d) makes an interesting comparison. Although the patterns are pronouncedly different, the Yangtze and the Yellow Sea populations have a similar body length at birth, and both the males and females of South China Sea and the Yellow Sea populations and the males of the Yangtze

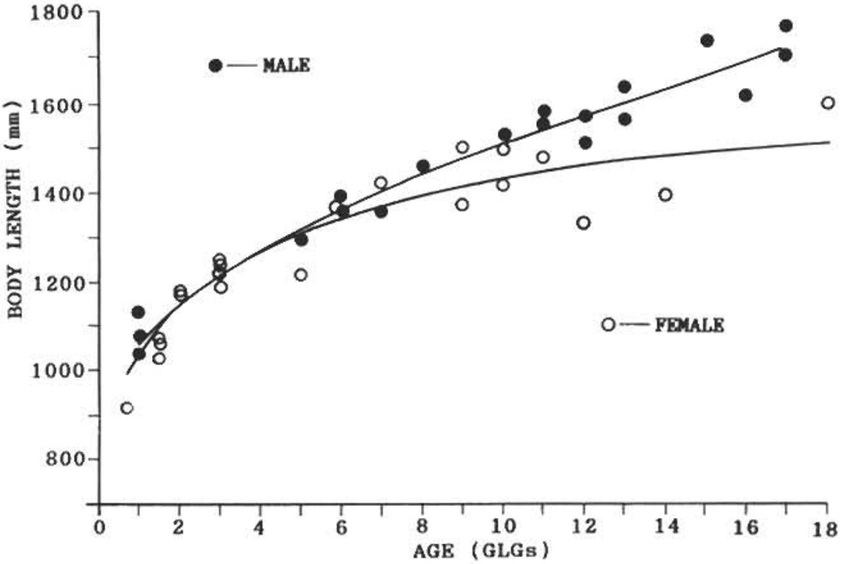

Figure 2a

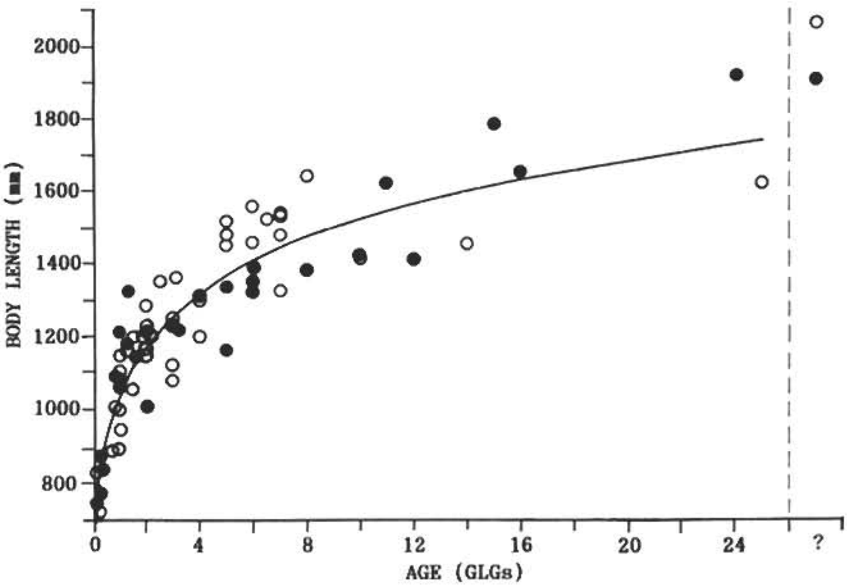

Figure 2b

population reached 1570 mm in body length at the age of about 13 years. Because the sample size we used is small, and the incidental catch on which our data depend was affected by many factors such as the types of the gear, and the behaviour of different sexes and age classes. We were unable to explain why the sample size of the older age classes are rather small at this stage.

Body weight, body length and girth

Weight is proportional to volume, a three-dimensional term including the length (L), width and height. For the finless porpoise, the information of width and height of the body are reflected in the girth (G). So we used the $L*G^2$ to conclude the information of volume as Castellini and Kooyman (1990) did for the Weddell seal.

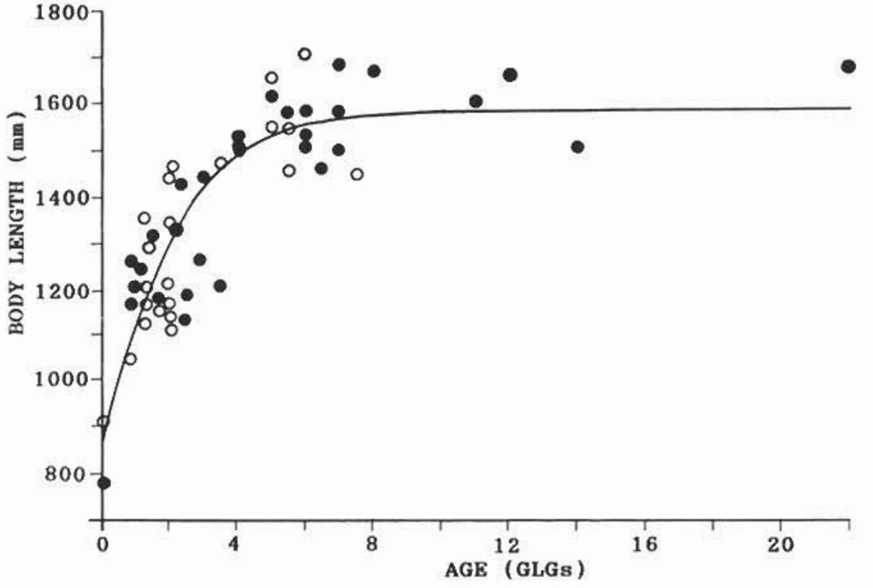

Figure 2c

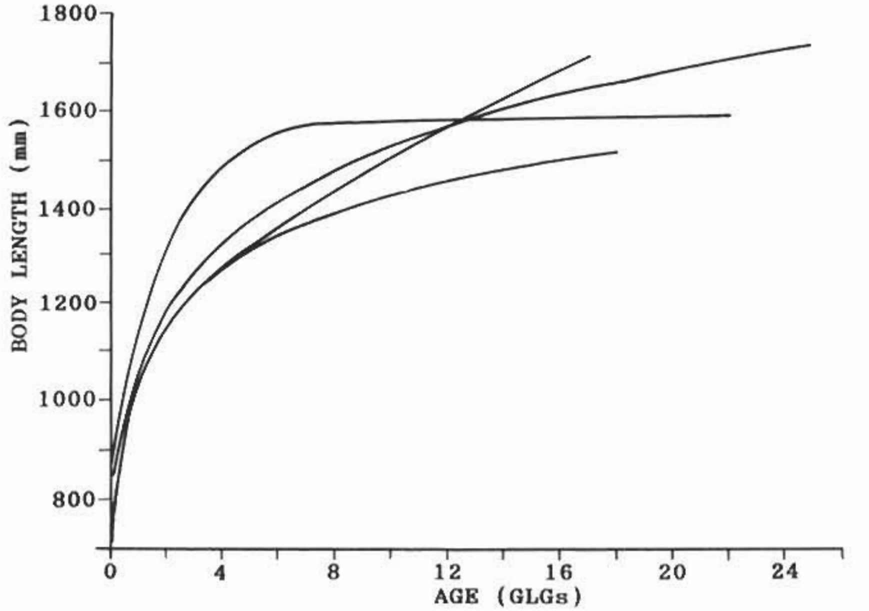

Figure 2d

Figure 2. (a) Scatterplots of body length and age, and the fitted growth curve for the Yangtze population. (b) Scatterplots of body length and age, and the fitted growth curve for the Yellow Sea population. (c) Scatterplots of body length and age, and the fitted growth curve for South China Sea population. (d) Comparison among the growth curves of the Yangtze, the Yellow Sea and the South China Sea populations.

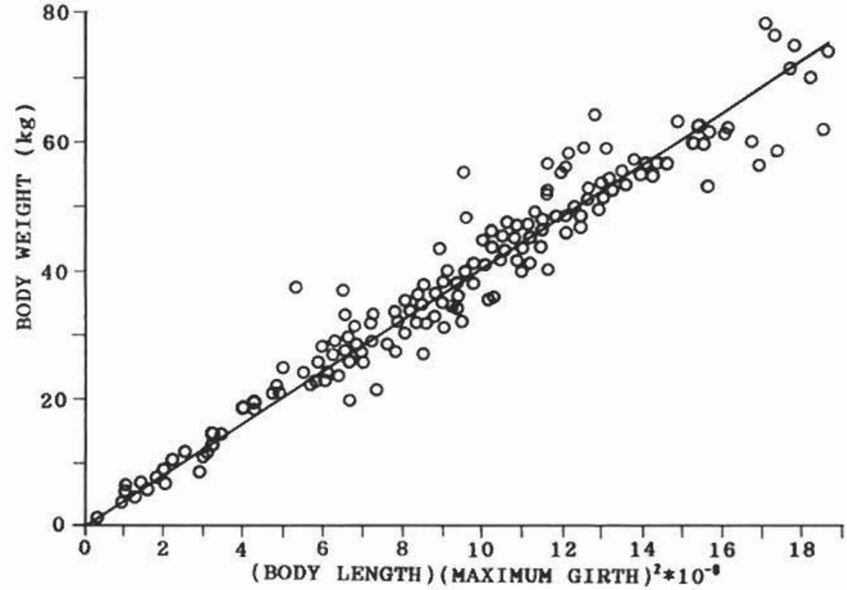

Figure 3. Relationship of body length, maximum girth (in mm) and body weight (in Kg) in *Neophocaena*.

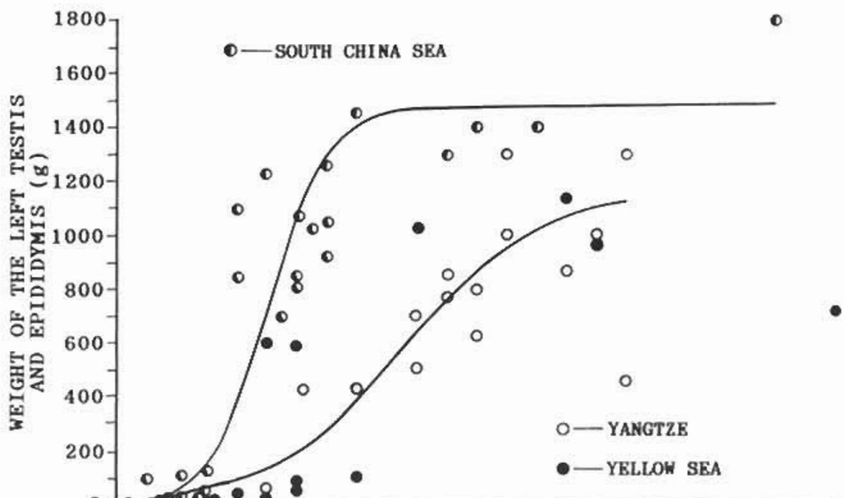

Figure 4. Scatterplots of the weight of left testis and epididymis against the age in GLGs for the Yangtze, the Yellow Sea and the South China Sea populations.

The regression equation for body weight on body length and maximum girth in finless porpoise is:

$$W = 4.05804(LG^2 * 10^{-8}) \qquad [8]$$

($N = 196$, $R^2 = 0.940$; W in kg, L and G in mm). The equation [8] is applicable to all the three populations (Fig. 3).

Reproduction

For males, spermatozoa could often be found in the seminiferous tubules when the diameter of the tubules reached 180 microns and the testis weight reached 305 g or higher as reported by Chang (1990) for the Yangtze and the Yellow Sea population. We

Table 1. Ages and body length for sexually immature and mature individuals in the Yangtze, Yellow Sea and South China Sea populations

	Age in GLGs				Body length in mm			
	Male		Female		Male		Female	
	I[d]	M[e]	I	M	I	M	I	M
YP[a]								
N	5	14	14	5	8	20	14	5
Minimum	0	7[f]	0	6	750	1363	670	1360
Maximum	5	17	7	18	1550	1765	1425	1600
YSP[b]								
N	20	8	30	9	20	13	30	11
Minimum	0.1	5	0	5	750	1320	725	1320
Maximum	8	24	10	25	1385	1915[g]	1455	1640[h]
SCSP[c]								
N	15	16	17	5	15	16	17	5
Minimum	0	4	0	5	780	1505	901	1450
Maximum	3.5	22	3.5	7.5	1442	1681	1470	1710

[a]Yangtze population.
[b]Yellow Sea population.
[c]South China Sea population.
[d]Immature.
[e]Mature.
[f]A male died in captivity at 6.2 GLGs is sexually mature.
[g]A male 2005 mm in body length was reported by Zhang (1986).
[h]A female 2060 mm in body length and 110 Kg in weight was reported by Shi Youren and Wang Xiuyu (1983).

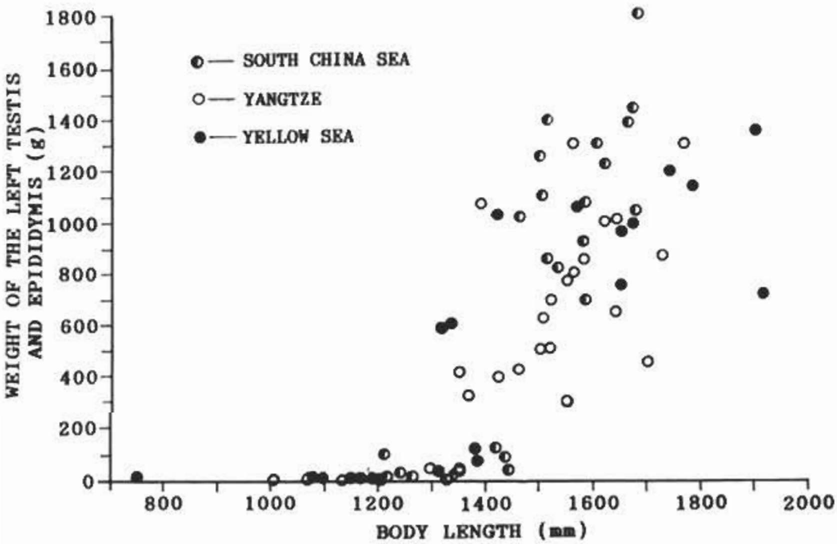

Figure 5. Scatterplots of the weight of left testis and epididymis against the body length for the Yangtze, the Yellow Sea and the South China Sea populations.

found this criteria are also applicable to the South China Sea sample of this species.

The testis weight (left-testis) of the three Chinese populations was plotted against age (Fig. 4). The fitted equation for the relationship between testis weight and age of the Yangtze population is

$$W = 1160/[1 + (1160/14 - 1)EXP(-0.46t)] \quad [9]$$

($N = 16$, $R^2 = 0.86435$).

According to the fitted curve, the testis weight exceeded 305 g in weight at the age of about 7 GLGs and kept growing in a relative stable rate for several GLGs of life. The maximum testis weight, 1300 g, is of a specimen with 17 GLGs.

The equation for relationship between testis weight and age of the South China Sea population is

$$W = 1480/[1 + (1480/8 - 1)*EXP(-1.03t)] \quad [10]$$

($N = 27$, $R^2 = 0.83372$).

The testis growth rate was much higher than that of the Yangtze population before 7 GLGs in age. The curve passed 305 g at the age of about 4 GLGs, and approached 1400 g at the age of about 7. The increase of testis weight may cease to grow in the older animals. The maximum record, 1800 g is of a specimen with 21 GLGs.

The testis weight varies from individual to individual. In the Yangtze sample, the testis of two individuals reached 1300 g in weight at 13 and 17 GLGs, while that of another one was only about 450 g at 17 GLGs. In South China Sea sample, the testis weight was beyond 1000 g in a specimen of about 4 GLGs, while that of another specimen was only 925 g at 7 GLGs. In the Yellow Sea sample, two testes approached 600 g at 5 and 6 GLGs respectively, while in three other specimens of the same age class the testis was less than 100 g in weight, that of another one was only 110 g at the age of 8. The variation was so great that we do not think that the present data of the Yellow Sea sample were sufficient to fit a growth curve. In the Yangtze sample, the smallest functionally mature male was 6.2 GLGs in age. The animal measured 1350 mm in body length when it died after two years of captivity in a holding pool in our laboratory. The smallest functionally mature male from the wild was 7 GLGs in age and 1363 mm in body length. The age of the largest immature male was 5 GLGs. The oldest immature and the youngest mature males were 8 and 5 GLGs in age for the Yellow Sea, and 3.5 and 4 GLGs in age for South China Sea samples respectively (Fig. 4, Table 1).

When the testis weight is plotted against the body length (Fig. 5) and using the testis weight 305 g as a criterion of attainment of sexual maturity (see first paragraph of this section), it showed that the estimated body length at sexual maturation in male finless porpoise was 1300–1400 mm for the Yangtze and Yellow Sea populations, and 1400–1500 mm for the South China Sea population. Harrison and McBrearty (1973–74) reported that sexual activity in the male finless porpoise in the Indus Delta started at the length of 1400–1500 mm. The data for the Indus finless porpoise are similar to that for the South China Sea porpoise. The samples were collected mostly during the fishing season from each region, i.e., in April–June for the Yangtze and the Yellow Sea populations, and in November-December for the South China Sea population. Therefore, the data collected are insufficient to answer whether there are seasonal changes in the testis weight.

The age and body length of the smallest functionally mature female in the Yangtze River sample were 6 GLGs and 1360 mm respectively. The largest female was a specimen of 7 GLGs in age and 1425 mm in body length and with a number of follicles in different sizes on the right ovary. In the Yellow Sea sample, 2 lactating females in 5 GLGs were recorded in the length of 1450 mm and 1515 mm respectively. One corpus luteum and 1 corpus albicans were found in 2 females of 6 GLGs and 7 GLGs in age and 1560 mm and 1320 mm in body length respectively. However, the attainment of sexual maturity was delayed in some of the individuals in the Yellow Sea population. The largest immature female was a 10-GLG specimen, 1410 mm in length and with a number of follicles in different sizes on the left ovary. In the South China Sea sample, the smallest functionally mature female was a 5-GLG female, 1550 mm in body length, and the largest immature we recorded was a 3.5-GLG female (Table 1).

According to a Yangtze specimen which was 4.5 GLGs in age and whose two testis weighted to 505 g, Zhang (1986) regarded it as a sexually mature male. He did not mention if there was any spermatozoa in the seminiferous tubules of this specimen. Furthermore, he estimated the body length at attainment of sexual maturity in males on the basis of this only specimen for both the Yangtze and Yellow Sea populations. In our samples, the finless porpoise was found mature when its two testis exceeded 610 g in weight (Chang, 1990). Zhang (1986) also reported that the females of the Yangtze population attained sexual maturity at 4 GLGs of age when the body length was 1280–1300 mm long. He assumed that the female porpoise in the Yellow Sea and Bohai Sea samples also attained sexual maturity at 4 GLGs of age, then estimated the body length at attainment of sexual maturity according to the growth curve he obtained. The age at sexual maturity estimated by Zhang looked smaller than that of ours. It may result from different criteria, or from individual variation in the development of the gonads.

The mean body length at birth was 710 mm ($N = 2$) for the Yangtze population which is similar to the estimation of 680–740 mm reported by Chen *et al.* (1982). Mean body length at birth was 760 mm (N = 8) for the Yellow Sea population, and 840 mm (N = 2) for the South China Sea population. For the South China Sea population, 14 calves were collected in December in addition to the 2 neonates, 5 were 0 or 1 GLG, 1 was 0.8 GLG, 1 was 0.9 GLG, 2 were 1.2 GLGs and 3 were 1.3 GLGs, 1 was 1.4 and 1 was 1.5 GLG. It suggests that the South China Sea population probably gives birth in June through March, with a peak in August through December.

For the South Asia finless porpoise, Kükenthal (1890) described a pregnant female of 1190 mm long with a 520 mm foetus. Allen (1923) recorded a 1270 mm pregnant female. Pilleri and Gihr (1973–74) reported a preserved specimen with a body length of 1300 mm and a foetus of 770 mm from Songkhla, Thailand. The above data suggest that the females of the South Asia finless porpoise attained sexual maturity at 1200–1300 mm in body length, and the body length at birth be over 770 mm. However, the reproduction parameters for the South Asia finless porpoise were insufficient and further investigation was needed.

The narrow and long banded distribution of the porpoise made the habitat of the populations relatively stable and isolated from each other. The Yangtze population is the only population which inhabits the freshwater where the topographical features, salinity and food supplies are different from that of the ocean. The coastal waters along the Chinese mainland has a large span in latitudes, from 20°15′N to 41°N latitude. The surface temperature differs greatly from the north to the south. For example, the monthly mean surface temperature was 22.2–28.8°C with an annual average of 25.8°C at Dongshan, Fujian province, 5.7–25.6°C with an annual average of 14.9°C in the middle part of the Yellow Sea, and 0.2–24.8°C with an annual average of 11.6°C in the Bohai Sea. The higher surface temperature in the tropical water may have enhanced both the rapid growth and the sexual and physical maturity of the South China Sea population. The difference among the ecological factors in different habitats has apparently influenced the evolution of the finless porpoise and led to the formation of different geographical populations.

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