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GROWTH AND BODY SIZE OF THE HARBOUR PORPOISE, *PHOCOENA PHOCOENA* (CETACEA, PHOCOENIDAE), IN THE SEA OF AZOV AND THE BLACK SEA

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Growth and Body Size of the Harbour Porpoise, *Phocoena phocoena* (Cetacea, Phocoenidae), in the Sea of Azov and the Black Sea. Gol'din P. E. — Postnatal growth, some aspects of life history, and body size of harbour porpoise were studied. The mean body length of neonates is 72.5 cm; the calving season lasts at least from April to August. The maximum life span is at least 20 years; the age at attainment of sexual maturity is 3–4 years, of physical maturity — 6–12 years. The mean body length of adult males and females is 132–135 cm and 143–145 cm respectively in the Sea of Azov, 122–124 cm and 132– 134 cm in the Black Sea. The question still remains of the existence of two growth stages in postnatal ontogenesis of harbour porpoises. It seems reasonable to distinguish two stages, each with decreasing growth rate. The first evidences are found for the existence of separate populations in the Sea of Azov and the Black Sea: adult specimens from the Sea of Azov are larger than those from the Black Sea in 10–12 cm. During the 20th century body size of the animals has somewhat reduced. The harbour porpoises in the studied region are at present the smallest representatives of *P. phocoena* species.

Key words: harbour porpoise, age, growth, Sea of Azov, Black Sea.

Рост и размеры тела морской свиньи, *Phocoena phocoena* (Cetacea, Phocoenidae), в Азовском и Черном морях. Гольдин П. Е. — Изучены постэмбриональный рост, некоторые особенности биологии и размеры тела морской свиньи. Средняя длина тела новорожденных — 72,5 см; период рождений растянут не менее чем с апреля по август. Максимальная продолжительность жизни — не менее 20 лет, возраст достижения половой зрелости — 3–4 года, физической зрелости — 6–12 лет. Длина тела взрослых самцов и самок в Азовском море в среднем составляет соответственно 132–135 и 143–145 см, в Черном море — 122–124 и 132–134 см. Вопрос о правомерности выделения отдельных периодов роста в постнатальном онтогенезе остается открытым. Целесообразно выделять два периода замедляющегося роста. Впервые обнаружены факты, подтверждающие существование обособленных популяций в Азовском и Черном морях: взрослые азовские особи крупнее черноморских на 10–12 см. В течение последнего столетия произошло некоторое уменьшение размеров особей. Морские свиньи изученного региона являются в наши дни самыми мелкими представителями вида *P. phocoena.*

Ключевые слова: морская свинья, рост, возраст, Азовское море, Черное море.

Introduction

Harbour porpoise *Phocoena phocoena* (Linnaeus, 1758) inhabits temperate waters of the Northern Hemisphere. An isolated fragment of its distribution range is located in the Sea of Azov, the Black, Marmara and Aegean Seas. The harbour porpoise in these waters is distinguished as a separate subspecies — *P. p. relicta* Abel, 1905 (local names — *azovka*, *mutur*). During the 20th century the abundance of these subspecies has substantially decreased due to prolonged take. Now *P. p. relicta* is included into the Red Data Books of several Black Sea countries (conservation status of Category I in Ukraine) and into the European Red List. Many aspects of life history of harbour porpoise in the Black Sea and adjacent waters still remain unstudied or were studied only in 1930–1950s (Zalkin, 1938, 1940; Barabash-Nikiforov, 1940; Kleinenberg, 1956; Tomilin, 1957 etc.) — the fact that impedes the estimation of current population status. At the same time, the comparative studies of harbour porpoises biology in different world regions are essential for understanding of some specific characters of cetaceans as a whole.

The objectives of this study are to find the regularities of growth in body length of harbour porpoise in the Sea of Azov and the Black Sea, and to discover its regional peculiarities. Also, some aspects of life history were specified.

Material and methods

The material for this study was obtained from 217 harbour porpoises: 127 from the Sea of Azov and 90 from the Black Sea, found dead at the coastline or by-caught during the fisheries operations in 1996–2003. The papers were examined concerning the recent findings in the waters off the northern (Tanabe et al., 1997) and north-eastern (Karacam et al., 1990) coast of Turkey, Aegean Sea, Caucasus (Glazov, Lyamin, 2000) — that is, the studies in which the age of animals was determined. Also, some records of porpoise findings during the last years were examined (Krivokhizhin, Birkun, 1999; A. A. Anastasov, A. A. Birkun, Jr., A. Frantzis, D. M. Glazov, S. V. Krivokhizhin, V. V. Pavlov, V. M. Sabodash, A. Tonay, personal communications). The data from 89 specimens were collected in 1997–1999 based on BREMA Laboratory (Simferopol), among them 85 specimens in the frames of BLASDOL Project (general data on the sample were reported in BLASDOL, 1999). Material from 7 specimens was collected by N. V. Frolova in 1996–1999; data on their age, sex and body size were reported in Gol'din and Frolova (2003). The rest of the material was collected by the author in 1999–2003 based on Department of Zoology, V. I. Vernadsky Taurida National University.

The material was collected all year round; however, 85% of findings were made during four months, from May to August.

In 210 specimens total body length was measured point to point from the tip of rostrum to the notch of flukes. Sex was determined in 196 specimens, age in 208 specimens. The age was determined by counting growth layer groups (GLGs) in dentine according to the standard techniques (Bjørge et al., 1995; Klevezal', 1988; Perrin, Myrick, 1980), with the use of thin longitudinal sections of decalcified teeth stained by Erhlich's or Mayer's haematoxylin. The age of animals found in spring and early summer, in which the boundary layer in dentine has not been deposited yet but the intermediate growth layer has already completely formed, was estimated as equal to the number of GLGs including the one being formed. For example, the age of specimens who died in summer and had been born the previous summer was estimated as one year, even if the first boundary layer has not been deposited yet. Such a procedure allowed to examine the growth process more adequately. The neonates were regarded as specimens having unhealed umbilical scar, non-erupted teeth and inflated lungs (similarly to Lockyer, 1995). For the statistical calculations two longest full-term embryos were included in neonate category. The age of all the calves found in June — September and not considered as neonates was estimated as 0.1 year. The age of specimens younger than 8 years found in October — March was estimated as n + 0,5 years, where n is the number of completed GLGs in dentine. The age of 18 specimens (mostly neonates) was determined from the body, skull and teeth size. The age of 3 specimens was determined from the GLGs number in mandible using the author's own technique (Gol'din, 2003). In 5 specimens the age was not determined but the status of sexual maturity was stated.

The status of sexual maturity in males was determined from general size and weight of testes and epididymides, diameter of seminiferous tubules, active spermatogenesis, in some cases — from size and weight of pelvic bones; in females — from presence of corpora lutea or corpora albicantia on the ovaries, pregnancy or lactation. The data on sexual maturity in specimens examined in the frames of BLASDOL Project are cited after study by A. A. Birkun, Jr. (BLASDOL, 1999).

Mean age at sexual maturity (ASM) in males in the Sea of Azov was calculated using the formula by DeMaster (1978): $ASM = \sum x \cdot [M(x) - M(x-1)]$, where x is the age, M(x) is the frequency of occurrence of sexually mature specimens at given age.

The status of physical maturity was determined on ankylosis of epiphyses in vertebra bodies in the thoracic and lumbar departments. For this purpose, the vertebrae of 47 specimens from the Sea of Azov and 3 specimens from the Black Sea were examined.

The mean values for specimens considered as physically mature were calculated by two methods. According to the first method, the values were calculated for all the specimens aged 8 years and more. According to the second one, after Read and Tolley (1997), the calculations were made for all the specimens aged 7 years and more, plus all the specimens the size of which exceeded the asymptotic size predicted by Gompertz formula.

The growth curves were calculated using von Bertalanffy, Gompertz, Richards, logistic and power growth formulae, as well as models including several von Bertalanffy, Gompertz and power formulae. The calculations for males from the Sea of Azov were made excluding the maximum value of body length (152 cm); however, this value was taken into account while estimating the goodness of model fit. In the calculations for the specimens from the Black Sea the value of the neonate body length was taken as 72.5 cm.

Statistical values were calculated with the use of standard methods. 95% confidence intervals for the mean values are indicated in the text in parentheses.

Results and discussion

C o m p o s i t i o n a n d s t r u c t u r e o f s a m p l e. The sample contains specimens at the age 0 to 13 years from the Black Sea and 0 to 20 years from the Sea of Azov.

The characteristics of the age, sex and size structure of samples containing animals with different causes of death were discussed in a special study on harbour porpoises from Ukrainian waters. The author considers the use of such samples in life history studies of harbour porpoise to be rational and useful (Gol'din, in press).

Life span. In this sample 95% of specimens from the Black Sea were at the age of 11 or younger, from the Sea of Azov — 12 or younger. The oldest female was 20 years old (2001, near Osoviny, Crimea, the Sea of Azov); the oldest male was 14 years old (2000, Tarkhan Cape, Crimea, the Sea of Azov). Thus, the life span of harbour porpoise in the Sea of Azov and the Black Sea is comparable with the values reported from the North Atlantic: the maximum known age of 24 years (Lockyer, 1995), the average life span — about 8–10 years.

Growth in body length

The body length of neonates in our sample falls in the range 58–83 cm, the mean is 72.6 ± 4.0 cm (here and ff. $p < 0{,}05$, except where otherwise indicated), and the maximum length of full-term embryo is 83 cm. The coefficient of variation is 10.8%. Sexual and regional differences in the neonatal body length were not found. Zalkin (1940), examining the animals directly taken in fisheries, wrote that the minimum length of neonates was 82 cm, the maximum length of embryos was 85 cm, and the size of fetuses in May, before the peak of birth, was 62–84 cm (mean — 73 cm). Sabodash and Nazarov (1998) reported the length of 75–82 cm in neonates from the Sea of Azov. Tanabe et al. (1997) reported finding a female 59.5 cm long at the northern coast of Turkey. A. Tonay (personal communication) has found a male 74 cm long at the north-western coast of Turkey. Krivokhizhin and Birkun (1999) recorded finding animals in length categories more than 70 cm in the Black Sea. Glazov and Lyamin (2000) reported finding a male 52 cm long and female 60 cm long at the coast of Caucasus.

Lockyer (1995) pointed out that the length at birth in harbour porpoises in the North Atlantic (*Phocoena phocoena phocoena* (Linnaeus, 1758) was about 65–70 cm, and the range of the neonate size was 60–80 cm.

According to a formula by Mikhalev (1970), the neonatal length of 72.5 cm corresponds to definitive female length of 160 cm. This agrees with the current data on the size of porpoises in the North Atlantic (Lockyer, 1995; Lockyer, Kinze, 2003; Read, Tolley, 1997).

Thus, the mean size of porpoise neonates in the Black Sea and the Sea of Azov does not seem to exceed the value obtained in this study.

The earliest finding of a neonate was recorded on May, 12 (2002, near Balaklava, Sevastopol), the latest one — on August, 5 (1999, Solyanoye, Crimea, the Sea of Azov). However, in early June calves were found with umbilicus healed, erupted teeth with postnatal dentine deposited, and body length up to 107 cm. This is the evidence of an earlier birth period, i. e. not later than April. According to Zalkin (1940), the calving season falls to late April — early July. However, according to my data, this term is even more extended: at least from mid-April to early August. The peak of neonate findings in the southern part of the Sea of Azov falls to early July.

The characteristics of growth. Growth formulae and stages. The linear growth rate is maximum during the first year of life, especially the first months. At the Crimean coast of the Sea of Azov, in the sample for present study, in June the calves with body length of 88–107 cm were found, in July and August — 96–109 cm. It follows that some specimens reach the minimum size of yearlings at the age of approximately two months.

Besides, there are records of smaller specimens found in autumn, winter and early spring. A female 70 cm long was found in October 2002 at the Crimean coast of the Black Sea (Black Sea..., 2003); a female 92.5 cm long was recorded in spring of 1993 in the waters off Turkey (Tanabe et al., 1997). At the southern coast of the Sea of Azov the author of this paper found two specimens: 87 cm long (June 17, 2000) and about 90 cm long (July 2, 2002); their age was determined as about 0.5–1 year as indicated by the skull and teeth size, skeleton ossification, and postnatal dentine depositions. Presumably, it can be explained by the unusual pattern of growth in small neonates, or extraordinarily low growth rate of these specimens. It is also probable that these animals were born in autumn, later than usual.

By the end of the first year of life, the body length of males in the Sea of Azov reaches 104–125 cm (mean is 111.8 ± 2.9 cm), of females — 105–122 cm (mean is 113.9 ± 4.2 cm). Among the animals of undetermined sex the minimum length is 101 cm. The body length of males in the Black Sea reaches 98–117 cm (mean is 108.6 ± 3.2 cm), of females — 103–118 cm (mean is 109.4 ± 6.2 cm). No significant sexual differences are found. Any differences in mean values during April–August are not observed. Some differences in body length between the specimens from the Sea of Azov and the Black Sea are observed but remain insignificant. In the Sea of Azov males reach the minimum size recorded for physically mature specimens, in the Black Sea they approach it.

During the second year of life the growth rates in animals in the Sea of Azov and the Black Sea (especially females) are different. In the Sea of Azov males reach the length of 118–126 cm (mean is 122.2 ± 3.1 cm), females — 128–145 cm (mean is 133.7 ± 11.1 cm). There was also found an animal 109 cm long of undetermined sex. In the body length of animals in the Sea of Azov sexual differences are exhibited. In the Black Sea males reach the length of 109–125.5 cm (mean is 116.4 ± 4.4 cm), females — 110–132 cm (mean is 118.4 ± 7.3 cm).

During the third year of life almost all the males and Azov females reach the minimum length of physically mature specimens. The females from the Black Sea are the most slowly growing group; their mean length is only 122.7 ± 3.7 cm. Later the growth gradually ceases in all sexual and regional groups. The variability of the body length remains high enough. For instance, the body lengths of 3-year-old males in the Sea of Azov vary in the range of 115–137 cm (CV = 7.5%), and in an animal 115 cm long the synarthrosis of epiphyses in thoracic and lumbar vertebrae was already in progress.

The best results in describing the postnatal growth with one growth curve were obtained when fitting von Bertalanffy formula as follows:

$$L_t = L_\infty \ (1 - be^{-kt}),$$

or Gompertz formula as follows:

$$L_t = L_\infty \cdot e^{-be^{-kt}},$$

where t is age in years, L is body length in cm, b and k are constants, L^∞ is asymptotic length in cm.

In general, the growth models suggesting two stages of growth describe the process of growth somewhat better than the corresponding models suggesting only one stage. This is especially true for the first year of life (tabl. 1, fig. 1). However, the differences between the coefficients of determination r^2 for models with one and two growth stages are not significant for all groups. The best method for describing growth with several stages is to apply the models including two von Bertalanffy or two Gompertz equations with different coefficients. In males from the Sea of Azov the best formula for the first stage was calculated for animals aged 0–1.5 years, for the second stage — 2 years and more. The intersection point for the two curves is at the age of 1.4 year. In females from the Sea of Azov the best formula for the first stage was calculated for animals aged 0–1.5 years, for the second stage — 1 year and more. The intersection point for the two curves is at the age of 1 year. In males from the Black Sea the best formula for the first stage was calculated for animals aged 0–2 years, for the second stage — 2.5 years and more. The intersection point for the two curves is at the age of 2 years. A two-stage model fitting for females from the Black Sea has failed.

Table 1. Parameters of growth equations for linear growth of harbour porpoise, their standard errors (SE), residual sum of squares (S_{resid}) and the coefficients of determination (r^2)

Таблица 1. Коэффициенты уравнений линейного роста морской свиньи, их стандартные ошибки (SE), остаточные суммы квадратов (S_{resid}) и коэффициенты детерминации (r^2)

Formula	$L_\infty \pm$ SE	b ± SE	k ± SE	S_{resid}	r^2
Males (the Sea of Azov) (n = 53)					
von Bertalanffy	132.1 ± 2.2	0.3915 ± 0.0241	0.9130 ± 0.1462	4360.6	0.8031
von Bertalanffy — the first growth stage	112.4 ± 1.9	0.3948 ± 0.0275	11.8162 ± 2.8329	1040.0	0.8953
von Bertalanffy — the second growth stage	132.2 ± 1.7	0.7109 ± 1.4102	1.1178 ± 0.9667	1096.8	0.8953
Gompertz	131.9 ± 2.2	0.4936 ± 0.0393	1.0583 ± 0.1609	4374.5	0.8022
Gompertz — the first growth stage	112.4 ± 1.9	0.5022 ± 0.0454	13.5842 ± 3.0422	1040.0	0.8953
Gompertz — the second growth stage	132.2 ± 1.7	0.7790 ± 1.5678	1.1440 ± 0.9787	1096.6	0.8953
Females (the Sea of Azov) (n = 45)					
von Bertalanffy	144.7 ± 1.6	0.4468 ± 0.0187	0.7651 ± 0.0837	2074.4	0.9194
von Bertalanffy — the first growth stage	115.1 ± 1.9	0.3442 ± 0.0239	5.5132 ± 1.9251	117.8*	0.9345
von Bertalanffy — the second growth stage	144.4 ± 1.6	0.5051 ± 0.1283	0.8719 ± 0.2389	1569.1	0.9345
Gompertz	144.4 ± 1.5	0.5877 ± 0.0333	0.9127 ± 0.0953	2064.8	0.9198
Gompertz — the first growth stage	115.0 ± 1.9	0.4214 ± 0.0372	6.5530 ± 2.1657	75.7*	0.9361
Gompertz — the second growth stage	144.4 ± 1.6	0.6017 ± 0.1628	0.9333 ± 0.2494	1571.0	0.9361
Males (the Black Sea) (n = 48)					
von Bertalanffy	122.8 ± 0.9	0.4007 ± 0.0374	1.2064 ± 0.1335	1003.6	0.7926
von Bertalanffy — the first growth stage	118.5 ± 4.2	0.3886 ± 0.0529	1.5311 ± 0.4351	651.3	0.7990
von Bertalanffy — the second growth stage	123.1 ± 1.0	0.3969 ± 2.4589	1.1014 ± 2.2685	321.4	0.7990
Gompertz	122.7 ± 0.9	0.5049 ± 0.0622	1.3783 ± 0.1591	1018.7	0.7894
Gompertz — the first growth stage	118.1 ± 3.8	0.4880 ± 0.0855	1.7613 ± 0.4437	651.3	0.7990
Gompertz — the second growth stage	123.1 ± 1.0	0.4052 ± 2.5174	1.1052 ± 2.2801	321.4	0.7990
Females (the Black Sea) (n = 41)					
von Bertalanffy	132.4 ± 1.5	0.4166 ± 0.0426	0.7102 ± 0.1052	1525.5	0.7745
Gompertz	132.1 ± 1.5	0.5154 ± 0.0694	0.8011 ± 0.1240	1573.2	0.7675

* S_{resid} was calculated for the specimens aged less than 1 year (S_{resid} рассчитана для особей возрастом менее одного года).

Thus, the question remains of the existence of two growth stages in postnatal ontogenesis of harbour porpoise. However, as an operational hypothesis it seems reasonable to distinguish two stages, each with decreasing growth rate. The secondary growth spurt marking the shift of stages falls to different ages in the samples of different origin.

It is remarkable that Gaskin and Blair (1977) found similar growth regularities in harbour porpoise from the Bay of Fundy but came to the opposite conclusion, i. e. that in practice it was better not to distinguish the two stages. However, they worked with a sample where the ratio of neonates was very low.

The two-stage growth models suggest that in the animals from the Sea of Azov the growth curve attains the asymptotic length of the first stage at the age of 3–6 months,

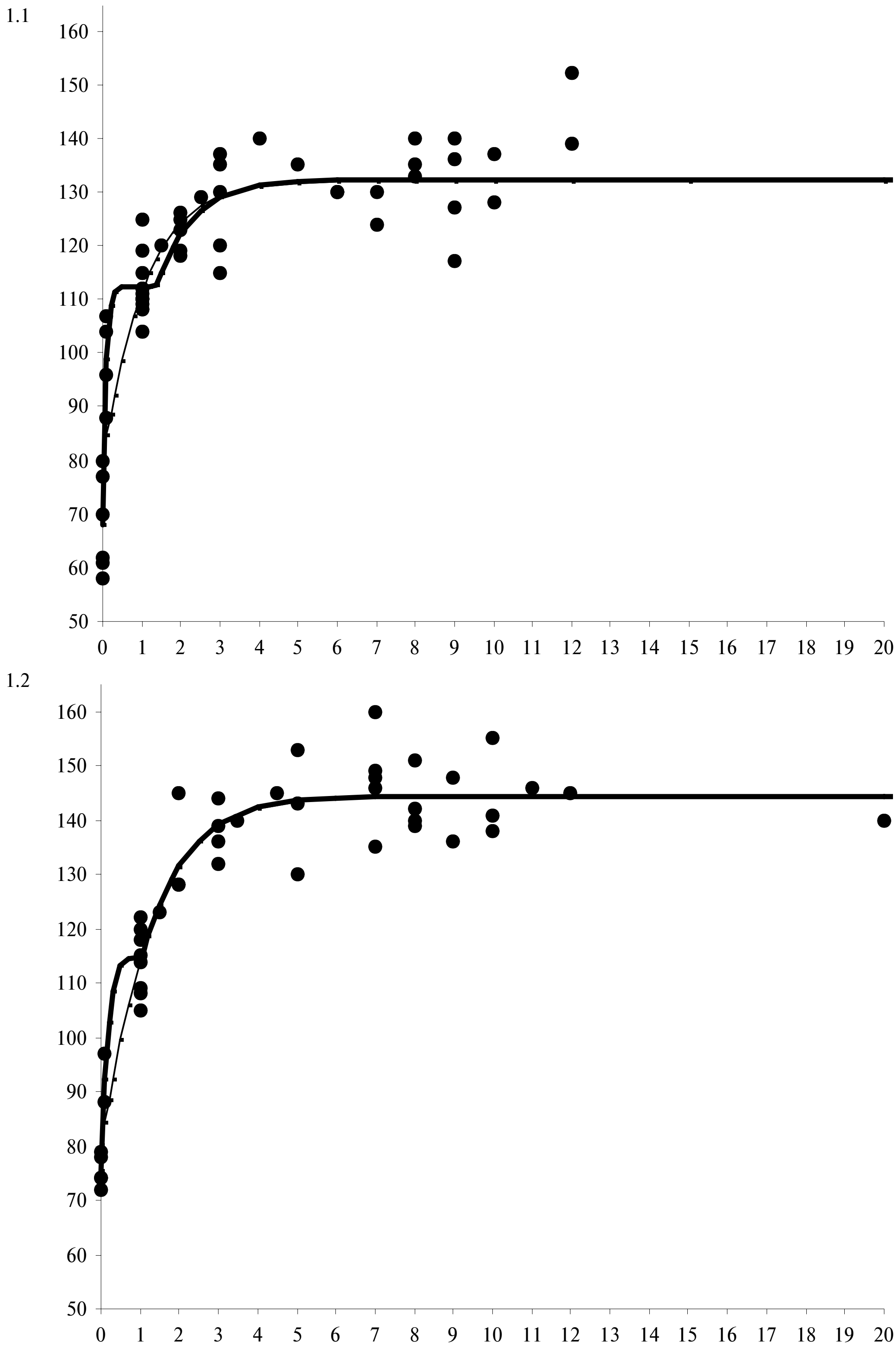
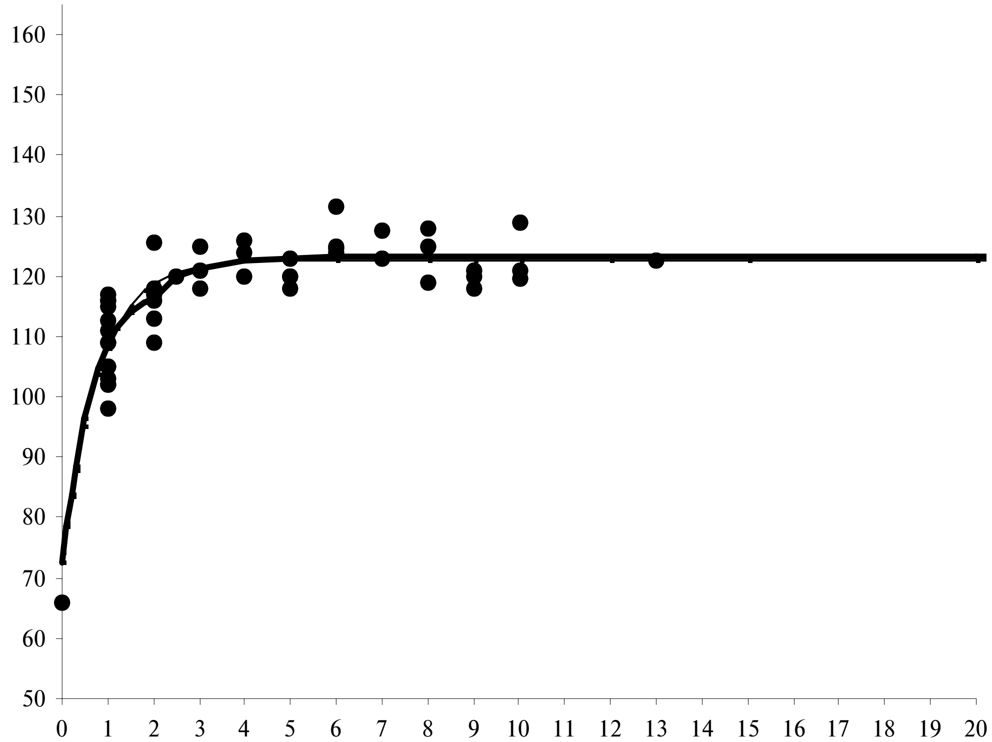


Fig. 1. Growth curves for length at age of harbour porpoise in the Sea of Azov and the Black Sea calculated using one and two Gompertz formulae. Age (in years) is displayed at X-axis, length (in cm) is displayed at Y-axis: 1.1 — males, the Sea of Azov; 1.2 — females, the Sea of Azov; 1.3 — males, the Black Sea; 1.4 — females, the Black Sea. —— One-stage growth curve. ▬ Two-stage growth curve.

1.3



1.4

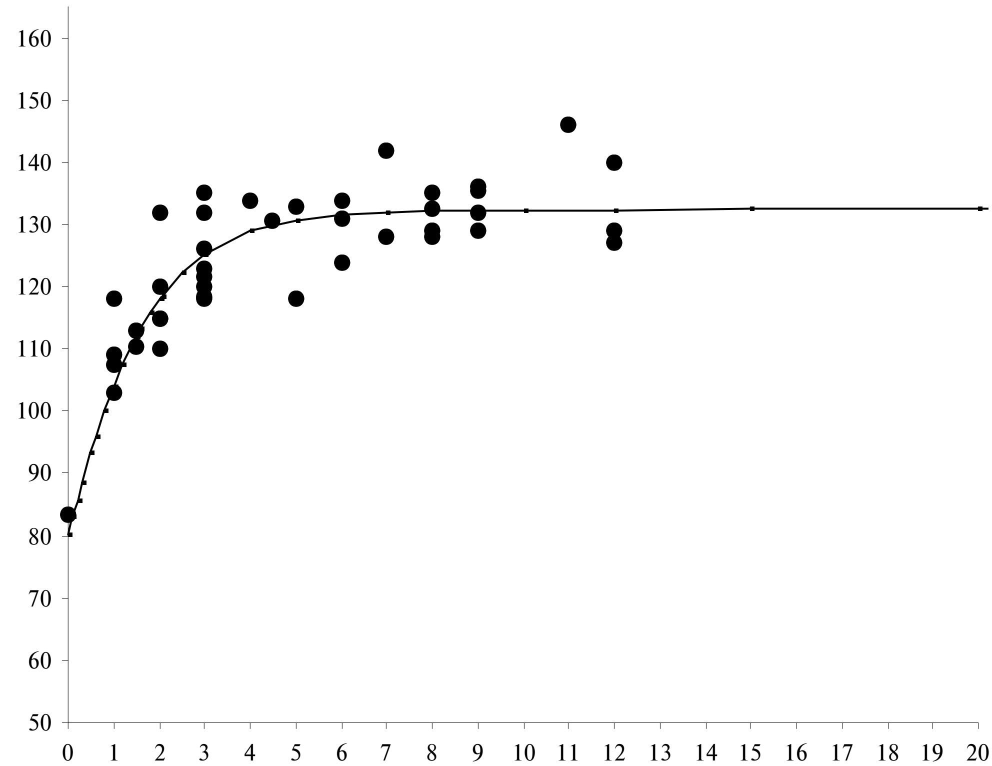


Рис. 1. Кривые линейного роста морской свиньи в Азовском и Черном морях, выраженные одним и двумя уравнениями Гомпертца. По оси абсцисс — возраст (год), по оси ординат — длина тела (см). 1.1 — самцы, Азовское море; 1.2 — самки, Азовское море; 1.3 — самцы, Черное море; 1.4 — самки, Черное море. —— Кривая, соответствующая одной стадии роста. ▬ Кривая, соответствующая двум стадиям роста.

and then the growth interrupts for 0.5–1 year. There are no direct evidences for this phenomenon but it is implicated by the growth rates of the calves. In such a case the interruption of growth immediately follows the weaning. This hypothesis is confirmed by a poor-stained line, which is often layered in dentine in the middle of GLG of the first year and divides the secondary growth layers of contrasting dentine structure.

A. Galatius (personal communication) suggested that the interruption of growth between the two stages could be caused by difficulties in foraging after weaning and by the infestation of parasites entering the organism with prey. Yet there can be another explanation: the accelerated perinatal linear growth can be associated with the forming of the hydrodynamic body parameters necessary for active movement and food search. During this period other processes of growth and development are delayed, and the ossification rate is slow. After the weaning the equilibrium is re-established; the body weight grows, the facial bones fuse with skull, the bodies and arches of vertebrae fuse, the metacarpal bones ossify. Thus, the growth strategy "switches" to other processes.

The hypothesis about the several-staged postnatal growth in toothed whales was first experimentally grounded by Kasuya (1972) in a study of striped dolphin *Stenella coeruleoalba* (Meyen, 1833), and then by Perrin et al. (1976) in a study of spotted dolphin *Stenella attenuata* (Gray, 1846). Different hypotheses were suggested for the growth stage pattern in *Phocoena phocoena*. Benke et al. (1998) believe that the change of growth stages occurs in the beginning of the first year of life; Galatius (personal communication) — at the age between 1 and 2 years; Gaskin and Blair (1977) — between 3 and 4 years (i. e. just before or during attaining the sexual maturity); and Van Utrecht (1978) — at the age of 4–5 years (i. e. in mature specimens, and only in males). Furthermore, in many reports (Lockyer, 1995; Read, Tolley, 1997; Lockyer et al., 2003; Lockyer, Kinze, 2003) the growth of harbour porpoise is described by one formula, without distinguishing any stages.

Comparative analysis of the data concerning the growth of the North Atlantic harbour porpoise does not allow to make any definite conclusions about the age when the interruption and the secondary spurt of growth could occur. The diagrams show that in females from the Bay of Fundy the growth interruption can occur at age between 2 and 3 years, while in males it is not evident at all (Read, Tolley, 1997); in the waters off Denmark the interruption in males can occur at the age between 1 and 3 years, in females — between 2 and 3 years (Lockyer, Kinze, 2003); in males from Greenland waters — before 2 years, in females — between 2 and 3 years (Lockyer et al., 2003); in the waters off Britain and Germany the interruption is not evident (Lockyer, 1995; Benke et al., 1998).

In any of the studies of large samples the growth spurt after attaining the sexual maturity was not observed.

The difficulty in distinguishing growth stages in harbour porpoise can be explained by small body size, early age of attaining the sexual maturity, high variability in the body size in the age groups, and variability between different populations. Besides, there are no good criteria for age determination within the accuracy better than 1 year. The only conclusion that can be made is that there are at the most two growth stages in postnatal ontogenesis; the shift in the growth stages, if it takes place, occurs before attaining sexual maturity, as in other delphinids and phocoenids (the list of references see in Ferrero, Walker, 1999); the growth interruption can be associated with weaning.

Age at attainment of sexual maturity. Body size of sexually mature specimens. The mean age at attainment of sexual maturity in males from the Sea of Azov calculated by DeMaster formula was 3.25 years. Among the females from the Sea of Azov all specimens at the age of 3.5 years and more were sexually mature. In the animals from the Black Sea the mean age at attainment of sexual maturity also seems to be about 3–4 years (BLASDOL, 1999).

Table 2. Body length (cm) of sexually and physically mature harbour porpoises from the Black Sea and the Sea of Azov: number of specimens (n), limit values (lim), mean values ($\bar{x}$) with standard deviations (s_x)

Таблица 2. Длина тела (см) половозрелых и физически зрелых морских свиней из Азовского и Черного морей: объем выборки (n), предельные значения (lim), средние значения ($\bar{x}$) и их среднеквадратичные отклонения (s_x)

Age/category	Male				Female			
	n	lim	$\bar{x}$	s_x	n	lim	$\bar{x}$	s_x
	The Sea of Azov							
Sexually mature	21	115–152	132.0	8.6	26	130–160	143.5	7.1
Physically mature:								
– at age of 8 years and more	10	117–152	134.5	9.3	13	135–160	143.1	5.6
– calculated after Read and Tolley (1997)	16	117–152	135.0	7.5	24	135–160	144.9	6.4
	The Black Sea							
Physically mature:								
– at age of 8 years and more	10	118–131.5	122.3	3.8	12	127–146	133.2	5.6
– calculated after Read and Tolley (1997)	21	118–131.5	123.9	3.5	18	127–146	133.6	5.2

The maximum length in immature males recorded in the Sea of Azov was 137 cm, in females — 145 cm. The mean and limit values for mature specimens from the Sea of Azov are presented in table 2. In the Black Sea (BLASDOL, 1999; Gol'din, 2000) the maximum length recorded in immature males was 126 cm, in females 132 cm; the minimum length in mature males was 118 cm (specified data), in females 121.5 cm (124 cm in a specimen having *corpora albicantia*).

In the sample of Tanabe et al. (1997) the length of sexually mature males was 112–121 cm, of females 129.5–138.5 cm.

Age at attainment of physical maturity. The earliest case of attainment of physical maturity, i. e. complete ankylosis in all vertebral column, was recorded in a specimen at the age of 6 years (supposedly female). The rest of physically mature animals were at the age of 10 and 12 years. Partial epiphyseal ankylosis in all the vertebrae was recorded, starting from the age of 5 years, in more than half animals at the age of 7–8 years, and in all older specimens up to 12 years. The mean age at attaining the physical maturity can be regarded as about 8 years, like in harbour porpoises in the North Atlantic (Lockyer, 2003); however, further research is needed to verify this value, in light of the last data (Galatius, Kinze, 2003).

According to the growth formulae used in this study, the asymptotic value of the body length (with accuracy of 0.1 cm) is attained at the age of 6–10 years, and 99% of asymptotic length is attained at the age of 3–4 years in males and 4–5 years in females. Thus, the age when 99% asymptotic length is attained corresponds approximately to early partial ankylosis in all the vertebral column.

Asymptotic body size of adult specimens. Size characteristics of adults (conditionally regarded as physically mature specimens — see "Material and Methods") calculated by two methods are presented in table 2. The length values of the two males at the age of 10 and 12 years from the Sea of Azov are not included; their length could not be determined exactly but did not exceed 120 cm.

The variability of the body length is rather high, as in other marine mammals (Yablokov, 1965). The coefficient of the variation fluctuates between 3.1–6.9% in different samples, the limit values are recorded in the males from the Black Sea and the Sea of Azov respectively.

Sexual dimorphism of the body length is exhibited in statistical values: mean, minimum, and maximum size of adult specimens (see table 2). As in the other populations of harbour porpoise, females are larger than males. The differences of the mean values, according to a number of estimation methods, average 9–11 cm in the Sea of Azov, 10–11 cm in the Black Sea; all the differences are significant (t-test, $p < 0.05$ in the Sea of Azov, $p < 0.01$ in the Black Sea). Similar differences are observed in the studied sample between the maximum lengths of adult males and females in the Sea of Azov (152 and 160 cm) and minimum lengths in the Black Sea (118 and 127 cm). Hence it can be predicted that the specimens filling the "gaps" will be found in categories not matching these values: physically mature females with the length of 125–130 cm in the Sea of Azov, males with the length up to 140 cm in the Black Sea.

The difference in the mean length of sexually mature specimens in the Sea of Azov is 11.5 cm. Zalkin (1938), basing on material from both the Sea of Azov and the Black Sea, indicated the difference as 7 cm.

Sexual differences are exhibited somewhat weaker than in the North Atlantic populations, where they average about 15 cm (Read, Tolley, 1997; Lockyer, Kinze, 2003 etc.).

Differences in body size in harbour porpoises from the Sea of Azov and the Black Sea

Animals from the Sea of Azov are longer than those from the Black Sea. The differences in the mean length of specimens at the age of 7 years and more average 11–12 cm; they are strictly significant ($p < 0.01$ for males, $p < 0.001$ for females). The same concerns the asymptotic values predicted by the growth formulae. Significant differences were also discovered in the values of the body length of all sexually mature animals. In females significant differences in the body length are exhibited since the age of 3 years.

This phenomenon can be explained either by spatial segregation based on the body size, or by the existence of a separate population group in the Sea of Azov.

Segregation in cetaceans is caused, as a rule, by age and sex factors (about the possibility of age segregation in harbour porpoise — see Cox et al., 1998); the body size merely reflects these factors. However, no differences in age and sex structure were found in the animals at the age of 1 year and more in the samples from Ukrainian waters of the two seas (Gol'din, in press).

Harbour porpoise inhabits the Sea of Azov from spring to autumn. The majority of animals migrate simultaneously with the autumn mass migration of anchovy through the Kerch Strait to the Black Sea, where they spend winter. According to the local residents' reports, only in warm winters single specimens are observed in the southern part of the Sea of Azov.

The peak of parturition of harbour porpoise falls to warm season (July–October after the data of Zalkin, 1940), preceding the migration of the Azov animals to the Black Sea, i. e. at the time of their geographical isolation. This fact supports a hypothesis of the existence of a separate population in the Sea of Azov. Earlier harbour porpoise in the region was considered to be a single herd migrating from the Black Sea to the Sea of Azov and back in spring and autumn respectively (Kleinenberg, 1956). Nowadays, however, there is no doubt that harbour porpoise is distributed throughout all the area of the Black Sea in summer season.

Obviously, the isolation of porpoises in the Sea of Azov and the Black Sea cannot be total. Some animals migrate from the Sea of Azov through the Kerch Strait to the Black Sea in summer. This is supported by the reports of local residents. E. g., in July 2000 small migrating groups were observed. The question of summer migrations from the Black Sea to the Sea of Azov has not been studied at all. Winter distribution of animals from the Sea of Azov also requires further study. Finally, nothing is known about how strictly individual specimens are associated with a certain local geographical area in summer and whether they can migrate from one basin to another not annually.

Determination of the ranks of harbour porpoise groupings in the Sea of Azov and the Black Sea requires further investigation, primarily genetic. However, irrespective of the fact whether these groupings represent the true populations, it is obvious that different morphological or ecological "races" have formed in the two seas. Hence the grouping of harbour porpoise in the Sea of Azov has to be regarded as a separate stock, especially in regard to conservation and management policies.

The small body size of harbour porpoises from the Black Sea was reported recently by many researchers. According to the data by Krivokhizhin and Birkun (1999) and the results of BLASDOL Project (BLASDOL, 1999), among several hundreds of porpoises found at the Black Sea coast of the Crimea in 1989—1998, the maximum length of females was 148 cm. Tanabe et al. (1997) recorded the maximum length of 130.5 cm in males, 138 cm in females in the sample of 49 specimens. A. Tonay (personal communication) recorded the maximum length of 140 cm in females in the sample consisting of several dozens of animals studied in 1997—2003. Rosel et al. (2003) reported finding a male 126 cm long and 13—14 years old.

At the same time, Karacam et al. (1990) observed specimens with the length up to 160—166 cm in a small sample from the waters off the northern coast of Turkey, and Rosel et al. (2003) reported a 157 cm female from the Aegean Sea. These data can also be related to migrating specimens from the Sea of Azov. The body size of the porpoises noted in Karacam et al. (1990) as a whole corresponds to the measurements obtained in this study for the specimens from the Sea of Azov.

Sabodash and Nazarov (1998) reported large porpoises from the Sea of Azov (females up to 163—165 cm long, males up to 156 cm). Krivokhizhin and Birkun (1999) reported findings animals up to 180 cm long; however, their data concerning the largest specimens were obtained from volunteers; in 1994 a female 156 cm long was found (S. V. Krivokhizhin, personal communication).

The sample studied by Glazov and Lyamin (2000) at the coast of Caucasus could include specimens originated from both the Black Sea and the Sea of Azov. The maximum body length recorded was 150 cm in females, 147 cm in males.

Thus, the differences in body size of harbour porpoise from the two seas are confirmed by most studies.

The data on the body size of harbour porpoise in the first half of the 20th century implicate that such differences could also exist in the past. Zalkin (1938), while examining the material in the Sea of Azov and the Black Sea, reported the body length in males up to 167 cm, in females up to 180 cm. At the same time, Barabash-Nikiforov (1940) and Kleinenberg (1956), basing on the Black Sea material only, recorded the maximum body length of 148 and 157 cm respectively; however, they dealt with much smaller samples.

The differences in body size between the animals from the Sea of Azov and the Black Sea can be explained from the ecological perspective. For many years the Sea of Azov has been characterized by the highest fish productivity (7 times more than the Black Sea (data by Moiseev, 1989) and high variety of prey species for harbour porpoise (Zalkin, 1940). Besides, the shallowness of the sea facilitates the availability of prey. The abundance and biomass of gobies has critically decreased during the last 30—40 years, but at present the population growth is observed (Demchenko, Mitiay, 2001). The anchovy abundance substantially decreased at the end of the 1980s (Chashchin, 1997) but is gradually increasing in recent years (Animal life..., 2001). Nowadays the productivity of fish species, which are prey for harbour porpoise, is relatively high in the Sea of Azov (Animal life..., 2001); so in this respect the Sea of Azov still can have advantage over the Black Sea.

The significant differences in the body length in the neighbouring regions indicate high ecological plasticity of this characteristic.

The minimum lengths of adult males at the age of 8 years and older in the Black Sea and the Sea of Azov remain the same: 117—118 cm. This value (the bottom limit of size range) can be a more conservative index. It is remarkable that this value is the same (117 and 118 cm) in the two dolphin species with body length close to that of harbour porpoise from the Black Sea — Hector's dolphin *Cephalorhynchus hectori* (Van Beneden, 1881) (Slooten, 1991) and Commerson's dolphin *Cephalorhynchus commersonii* (Lacepede, 1804) (Lockyer et al., 1988). These seem to be the smallest body lengths recorded in the adult cetaceans.

Changes in body size of specimens through the 20th century

On the basis of 1394 measurements of the body length, Zalkin (1938, 1940) concluded that the mean lengths of sexually mature males and females were respectively 141.5 and 148.5 cm, the maximum lengths were 167 and 180 cm, and the minimum length of pregnant females was 130—135 cm. Therefore, the values he got were significantly greater than those obtained in this study.

To explain this fact, one can resort to the following hypotheses. First, there are certain differences in measurement techniques: in Zalkin's study the total body length was measured along the ventral side, while in this study it was measured point to point. However, when a measured animal lies on its belly (like the one in the photo in Zalkin (1938)), these measurements are just identical or, in any case, cannot differ so dramatically. Second, V. I. Zalkin has examined a much greater sample than this one, so it could be suggested than in an analogous sample one would obtain similar values. But, as it was already noted above, none of the researchers in this field during the last 20 years has found an animal longer than 165—166 cm. Furthermore, in this study only one male had the length more than 141.5 cm, which is the mean value reported by V. I. Zalkin; two more specimens were recorded by Sabodash and Nazarov (1998) and Glazov and Lyamin (2000) respectively. The only remaining hypothesis is that some changes in the body size took place in the last decades.

There are numerous reports on the body size of harbour porpoises in different regions of the North Atlantic during the twentieth century (Clausen, Andersen, 1988; Read, Gaskin, 1990). During less than 20 years the asymptotic length of males has reduced by 2 cm, of females — by 8 cm in the Bay of Fundy (Read, Gaskin, 1990) (according to another study, by 3 and 5 cm respectively) (Read, Tolley, 1997) under the pressure of an anthropogenic factor, namely the incidental by-catch.

Assuming that the data by Zalkin (1938) refer primarily to the animals from the Sea of Azov, the changes of mean length in the 20th century (9.5 cm in mature males, 5 cm in mature females) seem to agree with the general trend of body size reducing in harbour porpoise within its whole distribution range.

Comparison of body size in harbour porpoise in the Sea of Azov and the Black Sea with animals from other geographical areas

Lockyer (2003) in the paper summarizing the results of recent studies in the North Atlantic concluded that the asymptotic lengths of males in different populations were 141—149 cm, females — 153—163 cm. The maximum body lengths recorded were 167 cm in males, 189 cm in females (Lockyer, Kinze, 2003). The smallest mean lengths were recorded in the adult specimens from Greenland waters, 141 and 154 cm respectively (Lockyer et al., 2003); the lengths of animals from German waters of the North Sea were close to them, 144 and 152 cm respectively (Benke et al., 1998). The minimum length recorded in animals 8 years old and more was 126 cm in males, 135 cm in females (Lockyer, Kinze, 2003). Harbour porpoises in the waters off the Southern Europe and the Northern Africa were characterized by remarkably larger body size; the maximum body length exceeded 2 m (Smeenk et al., 1992; Sequeira, 1996).

The mean values of the body length of the porpoises from the Sea of Azov and the Black Sea are remarkably smaller (tabl. 2). The differences in the body length in comparison with that of the adult animals from the Bay of Fundy (North America) (Read, Tolley, 1997) are highly significant for all the groups ($p < 0.01$ or $p < 0.001$). The differences between the asymptotic body size values calculated from the growth formulae are also highly significant. What is especially remarkable is the extremely small body size of many adult males, which is less than 120 cm.

Harbour porpoises of the Sea of Azov and the Black Sea are obviously the smallest representatives of the *Ph. phocoena* species nowadays. As for the body size, they are similar to the smallest species of Phocoenidae family, vaquita *Phocoena sinus* Norris, McFarland, 1958, in which the asymptotic length is 135 cm in males, 141 cm in females (Hohn et al., 1996).

The differences in the mean size of specimens could also exist at the first half of the 20th century, when the porpoises were larger both in the Atlantic and in the Black Sea basin. In the material examined by Zalkin (1938), only 5 of 744 males and 24 of 650 females were longer than 160 cm, whereas in the material reported by Möhl-Hansen (1954) that ratio was 11 of 225 males and 55 of 164 females. At that, the maximum lengths of the animals in both samples were 180 cm.

Thus, harbour porpoises from the Sea of Azov differ in the body size from those from the Black Sea, and both populations differ from the North Atlantic ones, the animals from the Sea of Azov possessing the intermediate body size between the Black Sea and Atlantic porpoises.

Perrin (1984) considered the emergence of dwarf forms in inner seas to be a general tendency to variability in cetaceans and confirmed the idea with the examples of the Black Sea and Mediterranean populations of two species: short-beaked common dolphin *Delphinus delphis* Linnaeus, 1758, and bottlenose dolphin *Tursiops truncatus* (Montagu, 1821). The causes of this phenomenon are unclear and require further investigation.

Conclusions

1. Investigations of the growth and life history of harbour porpoise in the Sea of Azov and the Black Sea have shown that the mean body length of neonates is 72.5 cm, like in harbour porpoises in the other regions. The calving season lasts at least from April to August. The peak of neonates' findings in the Sea of Azov falls to early July. The greatest increment of body length occurs during the first months of life. The maximum life span is at least 20 years; the age at attainment of sexual maturity is 3–4 years, of physical maturity — 6–12 years. 99% of the body length is possessed at 3–4 years in males and 4–5 years in females. The mean body length of adult males and females is 132–135 cm and 143–145 cm respectively in the Sea of Azov, 122–124 cm and 132–134 cm in the Black Sea. The body size is characterized by high variability. Adult females are larger than males in 9–11 cm; sexual dimorphism is exhibited in statistically calculated values.

2. The question still remains of the existence of two growth stages in postnatal ontogenesis of harbour porpoises. It seems reasonable to distinguish two stages, each with decreasing growth rate. The shift of the stages takes place before attaining sexual maturity. The age when the shift occurs depends on sex and stock. The growth interruption at the end of the first stage can be associated with weaning.

3. The results of the comparative analysis of the body size of the porpoises in the Sea of Azov and the Black Sea demonstrate that adult specimens of both sexes from the Sea of Azov are larger than those from the Black Sea in 10–12 cm on an average. These are the first evidences for the existence of separate populations in the Sea of Azov and the Black Sea. The Azov grouping of the harbour porpoise should be regarded as a separate conservation and management stock.

4. The minimum length of adult males in both seas is 117—118 cm. This value, as well as the minimum size in dolphins of genus *Cephalorhynchus*, is the smallest length known in adult cetaceans.

5. During the 20th century the size of specimens somewhat reduced. This phenomenon agrees with the general trend observed within all the distribution range of the harbour porpoise.

6. The results obtained show that the harbour porpoises in the Sea of Azov and the Black Sea are at present the smallest representatives of *Ph. Phocoena* species; as for the body size, the animals from the Sea of Azov are intermediate between the Black Sea and Atlantic porpoises.

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