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

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Пропорции тела морской свиньи *Phocoena phocoena* (Cetacea, Phocoenidae) в Азовском и Черном морях. Гольдин П. Е. — Исследования относительного роста частей тела морской свиньи впервые показали, что он в постнатальном онтогенезе существенно различается в четырех секторах, соответствующих черепу и отделам позвоночника. Наибольшими темпами относительного роста отличаются грудной и хвостовой отделы. Средняя часть тела отличается наибольшими темпами относительного роста у обоих полов. Выдвинута гипотеза о том, что двухстадийный рост организма определяется периодичностью роста хвостового отдела. Половой диморфизм размеров тела создается за счет частей тела, проявляющих положительную аллометрию или изометрию у обоих полов, однако различия в абсолютных величинах затрагивают лишь анально-генитальное расстояние.

Ключевые слова: морская свинья, Азовское море, Черное море, пропорции тела, аллометрия.

Body Proportions of Harbour Porpoise *Phocoena phocoena* (Cetacea, Phocoenidae) in the Sea of Azov and the Black Sea. Gol'din P. E. — The studies of the allometric growth of the body parts in harbour porpoises have shown that the growth of body parts during the postnatal ontogenesis of the harbour porpoise differs substantially in four body sectors, which correspond to the skull and the parts of vertebral column. The highest rates of allometric growth are observed in the thoracic and caudal departments. The middle part of the body is characterized by maximum rates of allometry in both sexes. The hypothisis was brought forward that the two-stage growth of the organism is determined by the periodicity of growth of the caudal department. Sexual dimorphism of the body size is determined by the body parts, which exhibit positive allometry or isometry in both part. Sexual differences in growth rates are observed in the lumbar part but the differences of absolute length values concern only anus-genital distance.

Key words: harbour porpoise, the Sea of Azov, the Black Sea, body proportions, allometry.

Introduction

Body proportions and regularities of allometric growth in the postnatal ontogenesis of harbour porpoise were studied by several authors (Zalkin, 1938; Van Utrecht, 1978; Stuart, Morejohn, 1980; Read, Tolley, 1997); some results of these studies demonstrated a number of contradictions. Zalkin (1938) was the only one who dealt with porpoises from the Sea of Azov and the Black Sea; however, his research was impeded by the lack of age determination methods. The objective of this study is to describe the patterns of allometry in porpoises from the Black Sea basin and their changes due to postnatal growth.

Material and methods

The material for this study was obtained from 125 harbour porpoises: 97 from the Sea of Azov and 28 from the Black Sea, found dead at the coastline or by-caught during the fisheries operations in 1997—2003. The data on certain measurements taken from 25 animals were kindly provided by V. V. Pavlov (S. I. Georgievsky, Crimean State Medical University), data on 5 animals by N. V. Frolova (Donetsk National University). The rest of the material was collected by the author based on Department of Zoology, V. I. Vernadsky Taurida National University.

Morphometric measurements were taken according to complete or incomplete protocol (fig. 1). The main measurements were taken twice, from the opposite points (tip of rostrum and notch of flukes), to reduce the error of measuring.

Sex was determined in 117 specimens, age in 119 specimens. The age was determined by counting growth layer groups (GLGs) in dentine according to the common techniques, with the use of thin longitudinal sections of decalcified teeth stained by Erhlich's or Mayer's haematoxylin (see details in: Gol'din, in press). The age of 3 specimens was determined from the GLGs number in mandible using the technique developed by author (Gol'din, 2003).

The growth curves were calculated using 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, as well as models including several Gompertz formulae.

The allometry equations were calculated using power formula as follows:

$$y = ax^b.$$

The indices of morphometric measurements were calculated as their ratios to the total body length.

Results and discussion

The main morphometric measurements in harbour porpoise can be compared with the positions of certain skeleton elements. The anterior edge of a flipper basis is located approximately at the level of the first thoracic vertebrae. The anterior edge of the dorsal fin is located at the level of one of the first lumbar vertebrae (from L1 to L5, the most often at L1 or L4); the posterior edge is from L5 to L13, the most often at

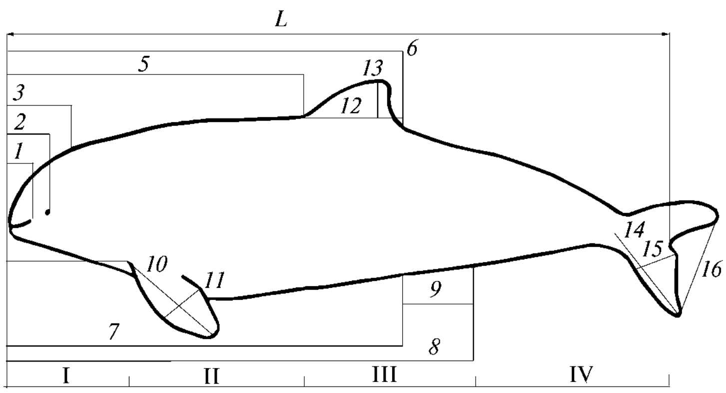

Fig 1. Morphometric measurements of the harbour porpoise: L — total body length, *1* — rostrum to tip of mouth; 2 — rostrum to eye; *3* — rostrum to blowhole; *4* — rostrum to axilla; *5* — rostrum to front edge of base of dorsal fin; *6* — rostrum to back edge of base of dorsal fin; *7* — rostrum to centre of genital slit; *8* — rostrum to centre of anus; *9* — centre of genital slit to centre of anus (anus-genital distance); *10* (Lpect) — length of flipper (max); *11* — width of flipper (max); *12* — base of dorsal fin; 13 — height of dorsal fin; 14 — length of outer edge of tail fluke (from the tail axis); *15* — maximum width of tail fluke; *16* — maximum fluke span; I—IV — number of Sector. Longitudinal measurements are indicated only from tip of rostrum.

Рис. 1. Схема морфометрических измерений морской свиньи: L — общая длина тела; *1* — от рострума до угла рта; *2* — от рострума до переднего угла глаза; *3* — от рострума до переднего края дыхала, *4* — от рострума до переднего края грудного плавника; *5* — от рострума до переднего края спинного плавника; *6* — от рострума до заднего края спинного плавника; *7* — от рострума до центра половой щели; *8* — от рострума до центра анального отверстия; *9* — от центра половой щели до центра анального отверстия (анально-генитальное расстояние); *10* (Lpect) — длина грудного плавника (максимальная); *11* — ширина грудного плавника (максимальная); *12* — длина основания спинного плавника; *13* — высота спинного плавника; *14* — длина внешнего края лопасти хвоста (от хвостового стебля); *15* — максимальная ширина лопасти хвоста; *16* — максимальный размах лопастей хвоста; I—IV — номера секторов. Продольные промеры показаны только от конца рострума.

L10 or L12. The anus is located approximately at the level of the front part of the caudal department, Ca5—Ca8.

Thus, there can be distinguished four conventional sectors corresponding approximately to the skeleton departments:

I — between the tip of rostrum and the axilla; corresponds to the skull and the cervical department of the vertebral column;

II — between the axilla and the basis of the dorsal fin; corresponds to the thoracic department of the vertebral column;

III — between the basis of the dorsal fin and the anus; corresponds to the lumbar department of the vertebral column;

IV — between the anus and the notch of the flukes; corresponds to the caudal department of the vertebral column.

The lengths of Sectors III and IV are on an average 2 cm less than the corresponding measurements of the vertebral column. This is particularly caused by the measuring technique: the external measurements were taken point to point, and measurements of the departments of the vertebral column were taken along the bends with the flexible measuring tape. The length of Sector II is on an average somewhat exceeds the length of the thoracic department, because the former is often influenced by the backward displacement of the dorsal fin in many specimens, and the bend in the thoracic department is not clearly expressed.

Sector I, the anterior part of the body, is characterized by the negative allometry (here and ff. see table 1). This tendency remains during all postnatal ontogenesis, since the moment of birth. The index of Sector I (the ratio of the sector length to the body length), which takes on an average 26.8 and 26.4% of the body length in neonate males and females, decreases to 23.5 and 23.1% during the first year of life and reaches 22 and 21% in adults (here and ff. see table 2). Sector I takes only 19.2—21.1% of the body length in the longest males and 18.1—20.6% in the longest females. It is interesting to

Table 1. Coefficients of allometry equation $y = ax^b$ for body parts of the harbour porpoise from the Sea of Azov

Таблица 1. Коэффициенты уравнения аллометрии $y = ax^b$ для отдельных частей тела морской свиньи из Азовского моря

Measurement/body part	Males					Females				
	n	a	b	SE_b	r^2	n	a	b	SE_b	r^2
Sector I (промер 4)	38	1.0	0.69	0.06	0.77	33	1.34	0.63	0.06	0.78
Sector II	33	0.07	1.22	0.09	0.85	23	0.05	1.32	0.17	0.72
Sector III	19	0.17	1.07	0.18	0.68	16	0.27	0.73	0.21	0.47
Sector IV	20	0.28	1.02	0.09	0.88	20	0.19	1.10	0.08	0.95
Sector I+II (промер 5)	35	**0.60**	**0.94**	0.04	0.94	30	**0.60**	**0.94**	0.07	0.86
Sector II+III	19	**0.26**	**1.12**	0.06	0.94	18	**0.27**	**1.11**	0.07	0.94
Sector III+IV	33	**0.42**	**1.05**	0.03	0.96	30	**0.44**	**1.04**	0.06	0.91
Measurement 1	17	0.72	0.56	0.16	0.44	19	0.74	0.55	0.10	0.63
Measurement 2	29	0.59	0.66	0.10	0.63	30	0.46	0.71	0.08	0.72
Measurement 3	17	2.39	0.36	0.13	0.34	20	0.52	0.69	0.11	0.68
Measurement 6	30	0.90	0.92	0.03	0.98	28	1.06	0.88	0.06	0.90
Measurement 7	17	2.24	0.69	0.09	0.80	16	0.71	0.98	0.04	0.98
Measurement 8	19	0.76	0.98	0.04	0.96	20	0.89	0.94	0.04	0.96
Measurement 9	13	$1.6 \cdot 10^{-8}$	4.35	0.48	0.88	16	0.25	1.07	0.39	0.35
Measurement 10	27	0.37	0.80	0.07	0.82	26	0.52	0.72	0.09	0.74
Measurement 11	20	0.27	0.66	0.14	0.54	19	0.21	0.72	0.08	0.81
Measurement 12	30	0.34	0.82	0.10	0.68	28	0.28	0.86	0.13	0.62
Measurement 13	14	0.35	1.12	0.25	0.63	11	0.37	0.66	0.23	0.48
Measurement 14	13	0.60	0.72	0.11	0.77	9	0.65	0.71	0.18	0.68
Measurement 15	24	0.25	0.77	0.18	0.43	20	0.32	0.71	0.13	0.61
Measurement 16	12	0.88	0.71	0.11	0.79	9	0.19	1.03	0.19	0.81

Table 2. Indices of body parts in age groups of the harbour porpoise from the Sea of Azov calculated as percentages of total body length

Таблица 2. Индексы различных частей тела в возрастных группах морской свиньи из Азовского моря, выраженные в долях общей длины тела

Age (years)	Sector I	Sector II	Sector III	Sector IV	Sector I+II	Sector II+III	Sector III+IV	L_{pect}
				Males				
0	0.268	0.207	0.220	0.303	0.475	0.444	0.525	0.161
0.1	0.243	0.219	0.187	0.354	0.462	0.385	0.538	0.156
1	0.235	0.233	0.242	0.286	0.470	0.479	0.529	0.138
2	0.215	0.243	0.261	0.296	0.452	0.485	0.548	0.149
3	0.220	0.235	0.225	0.316	0.461	0.460	0.538	0.145
3—20	0.224	0.230	0.226	0.308	0.458	0.470	0.542	0.143
8—20	0.219	0.233	0.246	0.302	0.459	0.484	0.541	0.144
				Females				
0	0.264	0.192	0.241	0.305	0.456	0.431	0.544	0.164
0.1	0.267	—	—	0.306	—	0.426	—	—
1	0.231	0.240	0.219	0.308	0.471	0.462	0.529	0.135
2	0.229	0.260	0.187	0.310	0.488	0.457	0.512	0.134
3	0.221	0.253	0.250	0.312	0.458	0.475	0.526	0.136
3—20	0.212	0.241	0.219	0.327	0.447	0.463	0.549	0.130
8—20	0.210	0.245	0.232	0.320	0.447	0.469	0.553	0.127

note that in the examined Black Sea specimens the index of Sector I is remarkably less; it takes on an average 20% of the body length in both sexes.

The data on the proportions of Sector I in the specimens from the Sea of Azov match exactly the results obtained by V. I. Zalkin (1938).

The negative allometry expresses itself in the growth of all the measurements within Sector I (tip of rostrum to edge of mouth, eye, blowhole). The coefficients of the allometry equations for the distance from the tip of rostrum to the blowhole differ significantly in males and females but there are no significant differences in the absolute values of this measurement.

Sector II demonstrates positive allometry in both sexes. Its rapid growth continues during the first year of life. The index of Sector II takes 20.7 and 19.1% in neonate males and females, rises up to 23.4 and 24.0% by the end of the first year, and then remains at the level about 23% in males. In females the index of Sector II grows up to 25—26% by the age of 2—3 years, and then decreases approximately to 24% due to increase of the posterior part of the body. In adult animals Sector II demonstrates a tendency to positive allometry in regard to the total body length; in some of the longest males it reaches 27%, in females 29%. Sector II is one of the two sectors determining the total body length.

As a result, the anterior part of the body constituted by Sectors I and II demonstrates slightly negative allometry (b = 0,94). Zalkin (1938) considered this tendency to be the main direction of the body proportions change in the ontogenesis. Van Utrecht (1978), basing on the measurements made along the body contour, reported the negative allometry pattern of the anterior part of the body; however, at the same time he recorded isometry in males and positive allometry in females as for the measurement from the blowhole to the basis of the dorsal fin. A. J. Read and K. A. Tolley (1997) calculated the coefficients of the allometry equations for the measurements from the tip of rostrum to the basis of the dorsal fin as 0.81 and 0.88 respectively and noted the slightly negative allometry of the basis of dorsal fin. Galatius (personal communication) specially emphasizes the necessity to study separately the two zones in the anterior part of the body, which correspond to Sectors I and II and exhibit dramatically contrasting growth patterns.

Sector III demonstrates the most intricate growth pattern. The length of this sector least correlates with the total body length in both sexes. The coefficient estimates in the allometry equations are rather rough. This is the only sector characterized by the tendency of sexual differences in growth rate. In general, Sector III demonstrates positive allometry in males in the course of growth, taking 22% of total body length in neonates and 24.2% in specimens at age of 1 year. In adult males this index remains constant on an average, about 24%. In females the allometry is negative in juveniles, and in adults this measurement does not correlate with the body length at all. The index decreases from 24% in neonates to 23.2% in specimens at the age of 8—10 years. At the same time, no sexual differences were found in the absolute length of Sector III.

The length of the basis of the dorsal fin, which is located within Sector III, demonstrates slightly negative allometry and does not differ by growth rate in the sexes. The sexual differences in allometry of dorsal fin height are not significant.

Therefore, it follows that the sexual differences in growth rates concern mostly the posterior part of Sector III. In particular, this explains the outwardly paradoxical fact that b coefficient in the allometry equation for the distance from the tip of the rostrum to the centre of the genital slit (measurement 7) in females is somewhat greater than for the distance to the anus (measurement 8). However, the data by A. J. Read and K. A. Tolley (1997) do not confirm such a tendency.

The rapid early growth of Sector III in males is explained by the necessity for the development of large genitalia, which are the specific character for harbour porpoise. The testes weight in this species can reach to 4% of the body weight (Read, 1990). Due to the comparatively small body size of the animals from the Sea of Azov and the Black Sea, this tendency can be exhibited in them more clearly than in porpoises from other regions.

Sector IV demonstrates isometry or slightly positive allometry in growth of both sexes. The index of this sector changes on an average from 30.2 to 30.5% in males, from 30.8 to 32% in females. In the majority of adult animals of a given sex the lengths of Sector IV are approximately equal; they do not depend on the total body length. However, in the longest females the absolute size and index of this sector increase, the latter up to 35—41%. Sector IV is characterized by stable growth of the absolute size at the age of 1—4 years, when the growth of the other body parts already ceases. Thus, Sector IV, as well as Sector II, determines the total body length.

A. Galatius and C. C. Kinze (2003) report the partial ankylosis in the forepart of the caudal department of the vertebral column in males begins at the age of more than 3 years and in females at the age of more than 4 years. Approximately at the same time the growth of Sector IV ceases, and the further increment of the total body length becomes very insignificant.

The length of Sector IV shows a strong correlation with the total body length. In its growth, like in the growth of the whole organism, two stages can be distinguished, which are best demonstrated in the growth of males from the Sea of Azov. The coefficients of determination r^2 of the two-stages growth equations (the Gompertz formula) for Sector IV are significantly higher in males than those of the one-stage equation. At the same time, there are no significant differences in the coefficients of determination of the growth equations for the rest of the body (sum of Sectors I-III). Thus, it is in the growth of Sector IV where the periodicity is exhibited. The shift of the growth stages takes place at the age between 1.5 and 2 years in males; in females this regularity is not so clearly expressed, as well as in the growth of the total body length (Gol'din, 2004). Thus, it is reasonable to suggest that it is Sector IV that is responsible for exhibiting the stages in the growth of the organism.

Sector IV contains a great mass of the skeletal musculature. It is the caudal part that is the main driver of a cetacean's body. Thus, the periodicity of the growth of organism in the porpoise is determined by the growth regularities of the locomotor musculoskeletal complex.

A remarkable characteristics in the pattern of growth of Sector IV is that the periodicity of the growth does not reveal itself in any allometry changes. This phenomenon is explained by a very strong correlation of the length of Sector IV and total body length during all the life span.

The maximum length of Sector IV was observed in the largest animals. That is why studying the populations of harbour porpoises of the largest body size – in the waters off Pyrenean peninsula, Africa, Pacific Ocean – is a subject of special interest.

The distance from the tip of the rostrum to the anus (measurement 8), including the length of Sectors I—III, demonstrates slightly negative allometry or isometry (the differences between the b coefficient and 1 are insignificant). The slightly negative allometry is also characteristic for measurement 6 (the distance from the tip of the rostrum to the posterior edge of the dorsal fin basis) (the differences between the b coefficient and 1 are significant).

The allometry of the posterior part of the porpoise body was studied in detail by Van Utrecht (1978). According to his study, all the measurements in Sectors III and IV in both sexes are characterized by isometry.

Almost all the measurements of the flippers and tail flukes are characterized by negative allometry. Similar regularities were reported by other authors (Zalkin, 1938; Van Utrecht, 1978; Read, Tolley, 1997; Galatius, personal communication).

The measurements of the dorsal fin and tail flukes (except the flukes span), as well as the head measurements, are characterized by low correlation with the total body length.

Negative allometry and low correlation with total body size are observed in structures early developing and undergoing high pressures since the moment of birth: head and fins. The lengths of Sector I and flippers better correlate with the total body length, so the growth of these structures should last longer.

When comparing the lengths of pairwise summed sectors (I+II, II+III, III+IV) it appears that only the middle body part (Sectors II+III) shows stable positive allometry in both sexes – both during the growth period and in adult animals. The index of this part increases in 4% during the lifespan in both sexes. However, two sectors, II and III, contribute to the increment in males, while in females it is only Sector II, which at the same time compensates the decrease of the portion of Sector III. Changes in the ratio of the anterior and posterior parts of the body, mentioned by all the authors who studied allometry in harbour porpoise (Zalkin, 1938; Van Utrecht, 1978; Stuart, Morejohn, 1980; Read, Tolley, 1997), are also observed in our sample, yet they appear less significant. The allometry equations for the pairwise summed sectors are exactly equal in both sexes (the coefficients are printed in bold type in table 1). Thus, every value of the body length is characterized by a specific dynamic ratio of proportions determined by a strict regularity. The functional meaning of this ratio requires further study.

Sexual dimorphism of absolute sizes is exhibited in the lengths of Sectors II and IV, which are characterized by isometry or positive allometry in both sexes. These sectors cause sexual dimorphism in the total body length. The mean length of these sectors starts to differ in males and females since the age of 2 years. Among sexually mature specimens the length of Sector II in females is 4 cm more and the length of Sector IV is 6 cm more than in males. However, due to high variability the differences in the length of Sector II do not reach the 95% confidence level.

The position of the genital slit is another apparent and repeatedly reported intersexual difference in harbour porpoises. In neonates the slit, with the anus at its caudal edge, is located in the posterior part of Sector III. Soon after birth, along with the growth of Sector III, the genital slit in males gets displaced forward, to the anterior edge of this sector. By the end of the first year of life the distance from the centre of the genital slit to the anus increases from 2—3 cm to 12—22 cm and can reach 32 cm in adult males. In females, the length of the genital slit increases with age but its location does not change. This fact accounts for significant sexual differences in the allometry equations for measurements 7 and 9.

Conclusions

1. On the basis of studies of the allometric growth of the body parts it was first shown that the growth of body parts during the postnatal ontogenesis of harbour porpoise differs substantially in four body sectors corresponding to the skull and departments of vertebral column. The anterior part and fins — the structures undergoing high pressures since the moment of birth — are characterized by negative allometry, and many of their measurements have low correlation with the total body size. The highest rates of allometric growth are observed in the thoracic and caudal departments.

2. The obtained results have allowed to hypothesize that the two-stage growth of the organism is determined by the periodicity of growth of the caudal department and the locomotor musculoskeletal complex associated with it.

3. The anterior, posterior and partly overlapping them middle body parts are interconnected by a ratio of proportions expressed by allometry equations and not depending on sex. The middle part of the body is characterized by maximum rates of allometry in both sexes.

4. Sexual dimorphism of the body size is determined by body parts, which exhibit positive allometry or isometry in both sexes. Sexual differences in growth rates are observed in the lumbar department, which grows faster in males. However, these differences do not influence the absolute size except the anus-genital distance.

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