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Growth, proportions and variation of the skull of harbour porpoises (*Phocoena phocoena*) from the Sea of Azov

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Skulls of 153 porpoises from the Sea of Azov and the Black Sea were studied. Thirty-seven skull measurements were examined. Skull growth in porpoises can be divided into five periods. The greatest changes in growth patterns occur after the first weeks of life. A 'relay effect' in growth of some structures (e.g. rostrum) was observed. Individual variation usually increases when a given structure grows intensively; however, some structures are highly variable over the entire lifespan. Sexual dimorphism is demonstrated in most of the measurements in adult animals. Temporal variation is minor. Skull structures are characterized by six types of allometry; three of them demonstrate drastic changes of allometry during lifespan, thus requiring two allometric equations to describe them. Skull proportions change critically during the first weeks of life. Six groups of correlated measurements differing in the pattern of correlation links during ontogeny were identified. Three factors play the most important roles in forming the definitive skull proportions: correlation between adjacent structures, impact of total skull size and inclusion in a certain functional complex.

INTRODUCTION

The most comprehensive study of growth and metric variation of the odontocete skull was conducted by Perrin (1975), who investigated two species of *Stenella*. However, to date there have been no similar studies for any cetacean species; thus, there is no basis for a comparative research. The harbour porpoise *Phocoena phocoena* (Linnaeus, 1758) seems to be a promising object for such comparative research as it is a widespread and common species in the northern hemisphere. In addition, being one of the smallest cetaceans, it provides a good reference point for size-related analysis. Some aspects of skull growth in the harbour porpoise have been studied in the North Atlantic (Noldus & de Klerk, 1984; Galatius, 2005) and North Pacific populations (Stuart & Morejohn, 1980; Miyazaki et al., 1987). A number of comparative morphometric studies of porpoise skulls from various geographical areas (Yurick & Gaskin, 1987; Amano & Miyazaki, 1992; Gao & Gaskin, 1996; Borjesson & Berggren, 1997) have also been conducted. Skull size and growth in other phocoenids has been a subject of study in recent years (Amano & Miyazaki, 1993; Yoshida et al., 1994, 1995; Perrin et al., 2000). Growth of bulla tympani in cetaceans, and in the harbour porpoise in particular, has been described in a recent study by de Buffrenil et al. (2004). Porpoises from the Sea of Azov and the Black Sea are especially interesting for size and growth studies as they represent the smallest subspecies of the harbour porpoise, *Phocoena phocoena relicta* Abel, 1905. Taking this into consideration, the current study aims to provide a detailed analysis of skull growth and size-related aspects (proportions and variation of metric characteristics) in porpoises from the Sea of Azov.

MATERIALS AND METHODS

Skulls of 153 porpoises from the Sea of Azov and the Black Sea found stranded on the coastline were studied. Of these, 148 were collected by the author from 2000 to 2005 (collection of the Department of Zoology, V.I. Vernadsky Taurida National University, Simferopol, Ukraine); three were collected by N.V. Frolova from 1996 to 1999 (collection of the Department of Zoology, V.I. Vernadsky Taurida National University, Simferopol, Ukraine); and two were collected by A.M. Volokh in 2001 (collection of the Schmalhausen National Museum of Natural History, Kiev, Ukraine). Mean values were calculated from the sample of 150 skulls of porpoises collected between 1996 and 2003 from the Sea of Azov and the adjoining sea area of the Kerch Strait. In this sample, age was determined in 130 specimens, sex in 104 specimens, and body length in 93 specimens. In addition, comparative studies were conducted on 33 skulls from the Zoological Museum of the Moscow State University (Moscow, Russia) (among these ten from V.I. Zalkin's collection taken in 1936 and 1938, the Kerch Strait; ten from S.E. Kleinenberg's collection taken in 1949, the Black Sea; 12 from V.I. Zhegallo's collection taken in 1988, the Sea of Azov). For a comparative study of the foramen magnum and condylar regions, skulls of 26 animals from French waters (collection of the Centre de Recherche sur les Mammifères Marins, La Rochelle, France) were examined.

The following measurements were taken for analysis of skull growth (the term 'length' always refers to measurements parallel to the longitudinal axis of the skull) (Figure 1):
(1) Condylobasal length; (2) rostrum length; (3) length of the left upper tooth row; (4) length of the right upper tooth row; (5) zygomatic width; (6) orbital width; (7) parietal width;

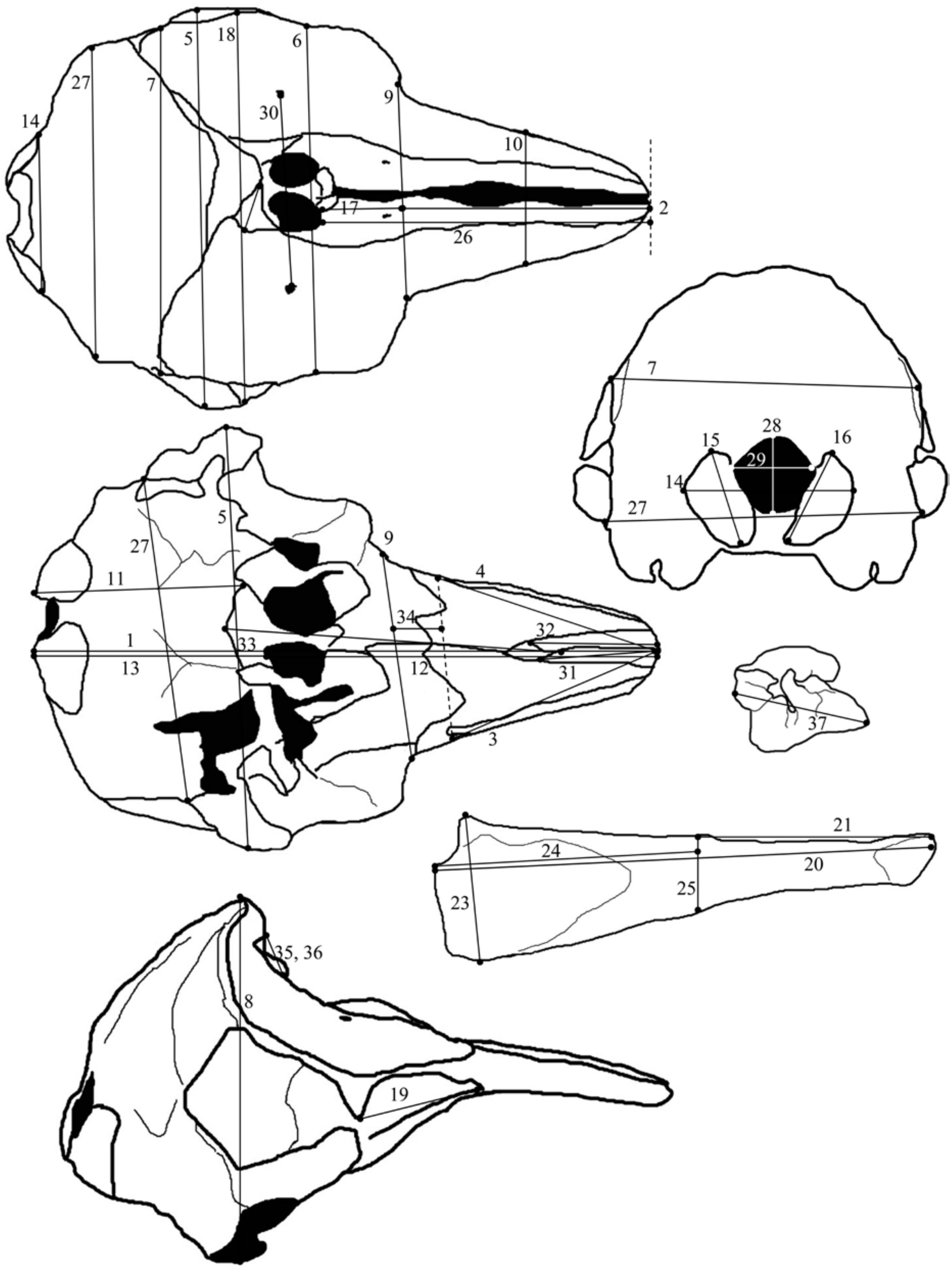

Figure 1. Skull measurements.

(8) skull height; (9) rostrum width at the base; (10) rostrum width at the mid-point; (11) length of basioccipitale (distance from the tips of condyles to the posterior point of the vomer); (12) length of the facial region; (13) length of the braincase (outer); (14) condylar width; (15) condylar height (left); (16) condylar height (right); (17) length of the prenarial region; (18) postorbital width; (19) length of the orbit; (20) length of the mandible; (21) length of the left lower tooth row; (22) length of the right lower tooth row; (23) height of the ramus at the base; (24) length of the ramus (in the strict sense); (25) height of the ramus posterior to the tooth row; (26) distance from tip of the rostrum to the external nares; (27) occipital width; (28) height of the foramen magnum; (29) width of the foramen magnum; (30) distance between back maxillary

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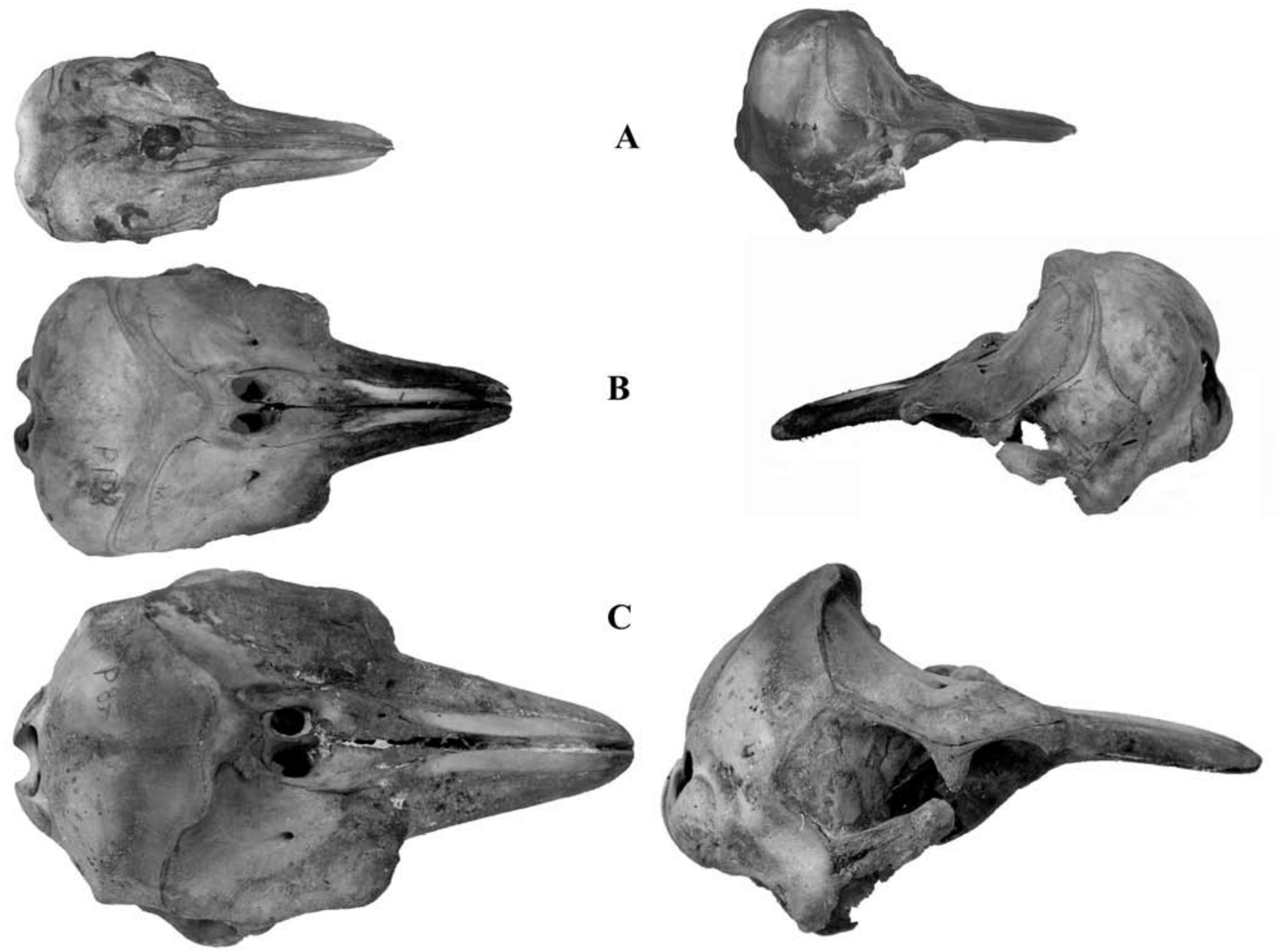

Figure 2. Skulls of females of the harbour porpoise (upper and lateral view): (A) a neonate; (B) a calf; and (C) an adult animal.

fenestra (foramina supraorbitale); (31) length of the anterior part of the left premaxilla (distance from the tip of rostrum to the posterior point of the visible part of the bone on lower surface of the rostrum); (32) length of the anterior part of the right premaxilla; (33) length of the vomer; (34) length of the posterior part of the rostrum (distance from the base of the rostrum to the line connecting the posterior points of the tooth rows, measured along the central axis of the rostrum); (35) length of the left nasal bone; (36) length of the right nasal bone; (37) length of bulla tympani.

Measurements were taken according to the protocol of Kleinenberg (1956) and recommendations by Perrin (1975), Stuart & Morejohn (1980), Yablokov et al. (1983), Noldus & de Klerk (1984), and Kinze (1985). Measurements 11 and 30–36 are introduced or modified by the author.

Counts of growth layer groups (GLGs) in the dentine were used to determine age according to 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. Ages of animals found in spring and early summer, in which the dentinal boundary layer had not been deposited yet, but the intermediate growth layer was already completely formed, were estimated including the layer under formation. As an example, the age of specimens that died in summer and were born the previous summer was estimated as one year, even if the first boundary layer had not been deposited yet (see also Gol'din, 2004). Specimens having an unhealed umbilical scar, non-erupted teeth and inflated lungs were regarded as neonates (similarly to Lockyer, 1995). The age of all calves found in June–September that were not deemed to be neonates was set 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 the dentine. The age of three specimens was determined from the number of GLGs in the mandible (Gol'din, 2003).

Ratio index of measurements was calculated as a ratio of the respective measurement to the condylobasal length.

Coefficient of variation (CV) was calculated as the ratio of the standard deviation to the mean value and expressed as a percentage.

The growth formulae used were the Gompertz equation:

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

and the von Bertalanffy equation:

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

where L is the measurement value at the age of t, L_∞ is the asymptotic measurement value, b and k are constants, and t is age (years).

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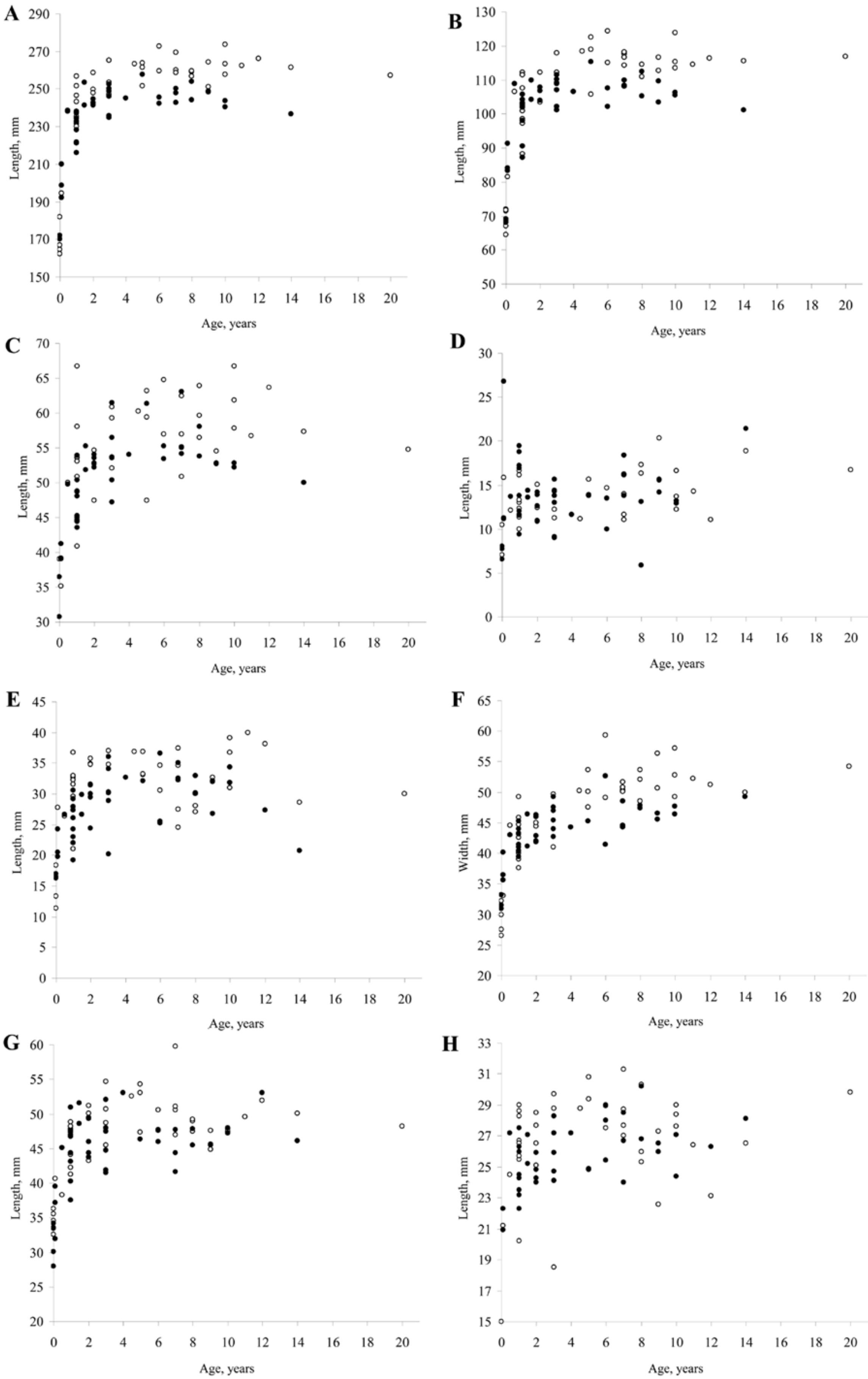

Figure 3. Growth in facial region measurements (○, females; ●, males): (A) condylobasal length; (B) rostrum length; (C) length of the anterior part of the left premaxilla; (D) posterior part of the rostrum; (E) prenarial region length; (F) rostrum width at the mid-point; (G) orbit length; (H) left nasal bone length.

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For the allometry studies, the allometry power formula was used:

$$y = ax^b,$$

where y is the measurement, x is the condylobasal length, and a, b are coefficients.

Correlation pleiades for skull measurements were constructed on the basis of partial positive correlations which were calculated as Pearson partial correlation coefficients, adjusted for age and condylobasal length impact, or age and zygomatic width impact (method of Terentyev, 1959). For the principal components analysis, correlation matrices were used. The number of components used in the analysis was determined as the minimum number of components with initial eigenvalues of more than 1 in all age and sex groups. Rotation was performed using the Varimax method with Kaiser normalization.

RESULTS

Sutures development: general characteristics

Skull sutures in neonates are open, synostosis is only observed in the sphenoid complex. During the first weeks of life synostoses between the braincase bones appear. In calves aged 1–3 months, complete or partial synostosis in the whole braincase is observed, and vomer and nasal bones fuse with the braincase. Squamosal bones and maxilla do not fuse with the braincase; the latter ones partially join with the premaxilla. As a rule, synostosis of skull bones is completed in the first year of life. One of the squamosals occasionally remains unfused until the age of one year.

Ankylosis and suture obliteration is only completed in some parts of the braincase. During the first weeks of life, the sutures between the basioccipital and lateral occipital bones are obliterated. Then the sutures between the upper occipital and lateral occipital bones are obliterated: stages of this process are observed in calves. Suture obliteration is completed sooner on the external surface of the skull; in some calves sutures are only seen on the internal surface. In general, rapid obliteration of sutures is completed in the first year of life. Suture lines in the occipital region (e.g. at the edges of the upper occipital bone) are often visible, even in the oldest specimens. The sutures of the parietal and squamosal bones generally remain unfused for a long time.

Expanded posterior parts of the maxilla cover up to half the length of the frontal bones in neonates (Figure 2). Growth of this part of the maxilla continues for two years; by this time synostosis in the proximal part of the facial region is completed. In the anterior part of the facial region, synostosis of the maxilla, the premaxilla and the vomer is generally completed by 3–4 years. Ankylosis of the rostrum bones does not occur, and their sutures remain visible.

General patterns of skull growth

The total skull lengths in neonate porpoises in this sample range from 162 to 182 mm (Table 1; Figure 3). Specimens with smaller skulls occurred in the current sample but the skulls of the smallest animals were fragmented making measurements impossible.

Table 1. *Skull measurements in porpoises from the Sea of Azov at the age of 0–0.1 years.*

Measurement	Age, years							
	0				0.1			
	N	lim	M	SD	N	lim	M	SD
1	7	162–182	169.7	6.4	6	192–214	205.9	10.9
2	9	60–72	68.1	3.8	6	81–91	85.2	3.8
3	6	52–65	60.4	4.4	6	63–74	69.8	5.8
4	6	52–65	60.1	4.4	5	61–73	69.4	6.7
5	2	73–85	79	8.5	3	110–133	118.1	13.3
6	6	68–84	76.1	6.0	7	94–110	102.1	7.1
7	2	84–88	86.5	2.8	6	105–117	110.0	4.4
8	2	77–80	78.3	2.4	6	97–114	106.2	6.6
9	8	36–49	42.6	4.4	5	49–60	57.3	5.7
10	8	25–33	29.7	2.9	5	33–40	37.2	2.7
11	1	54	54	–	6	58–66	64.3	3.6
12	6	91–100	96.4	3.3	6	101–123	117.6	8.7
13	5	67–82	77.4	11.5	7	77–91	88.4	5.1
14	6	40–46	42.3	2.3	7	43–54	51.1	4.2
15	7	23–29	25.0	2.3	7	26–33	30.4	2.6
16	8	21–28	24.1	1.9	7	27–32	30.4	1.9
17	7	11–18	15.6	2.5	6	20–32	25.7	4.4
18	6	88–101	94.5	4.7	5	110–128	118.4	7.2
19	10	28–36	33.0	2.5	7	32–42	38.0	4.0
20	12	110–129	122.8	5.2	3	149–151	149.9	1.0
21	10	60–69	64.9	3.3	3	72–76	74.1	2.2
22	9	61–68	65.3	2.5	2	77–80	79.0	2.1
23	11	30–36	34.3	2.0	2	45–47	46.0	0.8
24	11	54–66	59.2	3.6	3	72–80	77.9	6.6
25	11	15–19	17.2	1.2	3	22–23	23.0	1.7
26	8	76–90	85.0	4.7	6	103–114	111.3	5.8
27	2	82–83	82.6	0.6	7	82–115	102.7	11.0
28	5	29–37	31.7	3.1	6	33–40	35.0	3.1
29	4	19–30	25.7	5.1	6	25–30	27.8	2.3
30	8	37–43	40.7	2.1	5	47–56	54.3	6.0
31	5	26–39	33.7	5.3	6	30–41	37.6	3.4
32	6	25–39	33.8	5.0	5	30–41	38.3	3.5
33	5	76–93	85.3	6.2	5	109–132	121.7	8.4
34	6	7–10	8.1	1.4	5	11–27	15.7	5.9
35	1	15	15	–	4	21–25	22.4	1.5
36	1	14	14	–	4	21–26	23.0	2.2
37	7	33–37	35.0	1.4	3	35–38	36.9	1.4

N, sample size; lim, limit values; M, mean value; SD, standard deviation.

The facial region elongates during the first weeks of life as a result of growth of the posterior part of the rostrum, the posterior part of the lower jaw, the prenarial region and the orbit. The anterior part of the rostrum does not grow significantly during the first weeks of life, while the mean general lengths of the upper tooth rows, the posterior part of the rostrum, and the prenarial region each increase by 7–10 mm (Table 1; Figure 3). Intensive growth of the anterior part of the rostrum commences somewhat later, between 3 months and 1 year. Growth of the posterior part of the rostrum terminates after the short-term rapid perinatal growth (Tables 1–3; Figure 3). Growth in prenarial region length also ceases within the first year of life.

Table 2. *Skull measurements in porpoises from the Sea of Azov at the age of 1 year.*

Measurement	Males				Females			
	N	lim	M	SD	N	lim	M	SD
1	11	216–253	234.1	9.9	9	221–257	238.7	11.5
2	11	87–110	101.0	6.7	9	88–112	103.2	8.1
3	11	76–95	85.8	6.0	9	78–100	89.5	8.3
4	11	79–95	87.2	5.9	9	76–100	90.9	8.2
5	10	127–145	134.8	4.8	8	130–150	138.3	6.8
6	11	105–121	112.5	5.0	9	108–123	115.1	6.1
7	11	109–125	117.0	5.2	9	110–125	118.0	4.1
8	10	110–122	116.6	4.2	9	109–130	118.1	6.2
9	11	63–74	66.7	4.2	9	59–75	67.8	5.3
10	11	39–46	42.6	2.1	9	38–49	42.5	3.7
11	11	65–73	69.5	3.1	9	65–74	69.4	3.4
12	11	118–155	138.5	11.2	9	126–162	145.3	10.7
13	11	91–101	95.3	3.6	9	88–96	93.3	2.5
14	11	52–61	55.6	2.5	9	49–58	54.5	3.7
15	11	30–37	33.8	2.0	9	32–37	34.0	1.8
16	11	29–37	33.0	2.5	9	30–38	33.4	2.6
17	11	19–31	26.0	3.5	9	21–37	30.3	4.4
18	11	122–139	130.9	4.6	9	122–145	133.1	7.4
19	11	37–51	45.6	4.3	9	41–49	46.0	2.7
20	8	162–191	172.9	9.2	7	162–194	178.3	10.1
21	3	79–91	83.1	7.1	5	82–102	89.4	7.6
22	7	79–96	84.9	7.2	7	81–102	91.2	8.0
23	8	45–54	49.3	3.1	9	46–54	49.2	2.7
24	8	80–96	87.7	6.0	8	79–98	87.9	6.2
25	8	23–29	25.4	2.1	9	20–30	26.7	3.3
26	11	110–136	126.9	7.6	9	118–149	133.1	11.0
27	11	108–122	113.8	3.4	9	110–124	115.6	5.9
28	11	28–36	32.3	2.9	9	25–38	32.5	3.9
29	11	26–32	28.1	1.7	9	23–32	27.2	2.7
30	11	51–65	58.4	4.1	9	57–63	60.0	2.2
31	11	43–55	48.2	4.2	9	41–67	52.1	7.9
32	11	42–58	48.6	4.6	9	42–64	51.9	7.4
33	11	121–148	134.3	8.0	9	122–151	133.6	11.6
34	11	9–19	14.4	3.3	9	10–17	13.1	2.3
35	11	22–27	24.8	1.7	9	20–29	26.3	2.6
36	11	23–28	26.2	1.7	9	20–30	25.9	2.8
37	4	36–38	36.8	0.9	5	36–38	36.9	0.8

N, sample size; lim, limit values; M, mean value; SD, standard deviation.

Table 3. *Skull measurements in porpoises from the Sea of Azov at the age of 3 years and more.*

Measurement	Males				Females			
	N	lim	M	SD	N	lim	M	SD
1	23	235–258	246.4	6.1	24	247–274	260.4	6.4
2	23	101–116	107.6	4.1	24	106–124	115.5	4.3
3	23	79–102	93.0	5.5	22	90–109	101.0	5.5
4	23	80–101	94.2	5.2	23	91–110	101.6	5.2
5	24	139–154	145.9	3.5	26	137–164	153.3	5.8
6	24	111–128	120.1	3.7	25	120–135	126.8	4.1
7	25	117–127	122.0	2.2	26	114–131	122.4	3.7
8	25	114–131	122.0	4.2	26	117–134	128.3	4.3
9	23	66–82	71.5	3.3	25	65–84	77.0	4.5
10	23	41–53	46.4	2.5	24	41–59	51.1	3.6
11	22	65–76	70.3	3.2	26	66–78	73.0	2.5
12	22	145–160	151.3	3.8	24	154–176	162.3	5.7
13	25	89–103	95.1	3.9	26	91–106	98.1	3.7
14	25	52–63	57.1	3.4	26	55–65	60.3	2.6
15	25	32–39	35.3	2.1	26	34–41	37.2	1.8
16	25	32–39	35.2	2.0	26	33–41	37.1	2.0
17	25	20–37	30.1	4.3	26	25–40	33.1	4.1
18	22	133–149	139.8	3.8	25	135–155	147.2	4.8
19	24	41–53	47.0	3.1	26	45–60	49.6	3.2
20	21	177–196	186.8	4.6	21	181–212	199.1	6.8
21	18	82–112	94.2	6.3	19	91–117	102.1	6.7
22	17	82–102	94.2	5.8	21	91–114	101.9	6.7
23	23	49–55	51.6	1.8	21	48–58	53.7	2.8
24	23	81–98	92.5	3.5	20	81–106	97.1	6.1
25	23	25–36	29.2	2.6	23	26–35	31.0	2.4
26	23	121–147	138.3	6.4	24	140–159	148.8	5.3
27	25	115–127	120.6	3.5	26	113–131	124.0	4.3
28	25	28–44	33.4	4.2	26	29–43	33.9	3.1
29	25	25–33	28.4	1.7	26	27–33	29.6	1.6
30	25	55–71	62.1	3.2	26	54–71	64.1	3.3
31	21	47–63	53.9	4.4	24	47–67	58.1	4.6
32	21	45–63	54.0	4.4	24	51–69	59.5	4.5
33	24	133–152	143.1	5.4	25	138–164	144.8	20.1
34	23	6–21	14.1	3.5	21	11–20	14.6	2.6
35	24	24–30	26.6	1.7	26	18–31	27.4	2.8
36	24	23–31	27.2	2.1	26	22–34	28.4	2.9
37	16	36–39	37.2	0.9	10	36–39	37.5	0.9

N, sample size; lim, limit values; M, mean value; SD, standard deviation.

Growth in rostrum length continues due to intensive growth of the tooth row region. After the first year of life growth is only perpetuated in the anterior region in males: the mean increase of rostrum length after one year is 6.8 mm, of which the increment of the anterior parts of the premaxilla is 5.4 mm on the left and 5.6 mm on the right. In females, the central as well as the anterior parts contribute to rostrum growth: only 6.1–6.2 mm of the 12.8 mm overall increase falls to the anterior region. In males, the rostrum grows to the age of three years, while it seems to grow up to 4–5 years in females (Tables 1–3; Figure 3).

Thus, the distinctive feature of rostrum growth in length is a 'relay' pattern: growth processes 'switch' from the posterior part of the rostrum to the anterior one after the first weeks of life.

Growth in rostrum width in males ceases gradually and terminates after three years. In females, intensive and long-term growth starts after 1 year and persists to 5–6 years or more. Rostrum width at the base increases significantly during the second year, while the width at the mid-point increases only after attaining the age of three years (Table 3; Figure 3).

Orbit length increases steadily during the first year of life. Then growth gradually ceases and stops at 2–3 years (Tables 1–3; Figure 3).

Intensive growth of nasals occurs in the first weeks of life; bone length increases by a factor of 1.8. After this, growth declines, though some growth persists up to the ages of at least three years (Tables 1–3; Figure 3). The same growth pattern can be observed in the prenarial region, which gradually elongates at least until 3 years. Before two years this region demonstrates sexual dimorphism: it is 5–6 mm longer in females. Then growth in males intensifies, and sexual differences in adults are evened out (Table 3; Figure 3).

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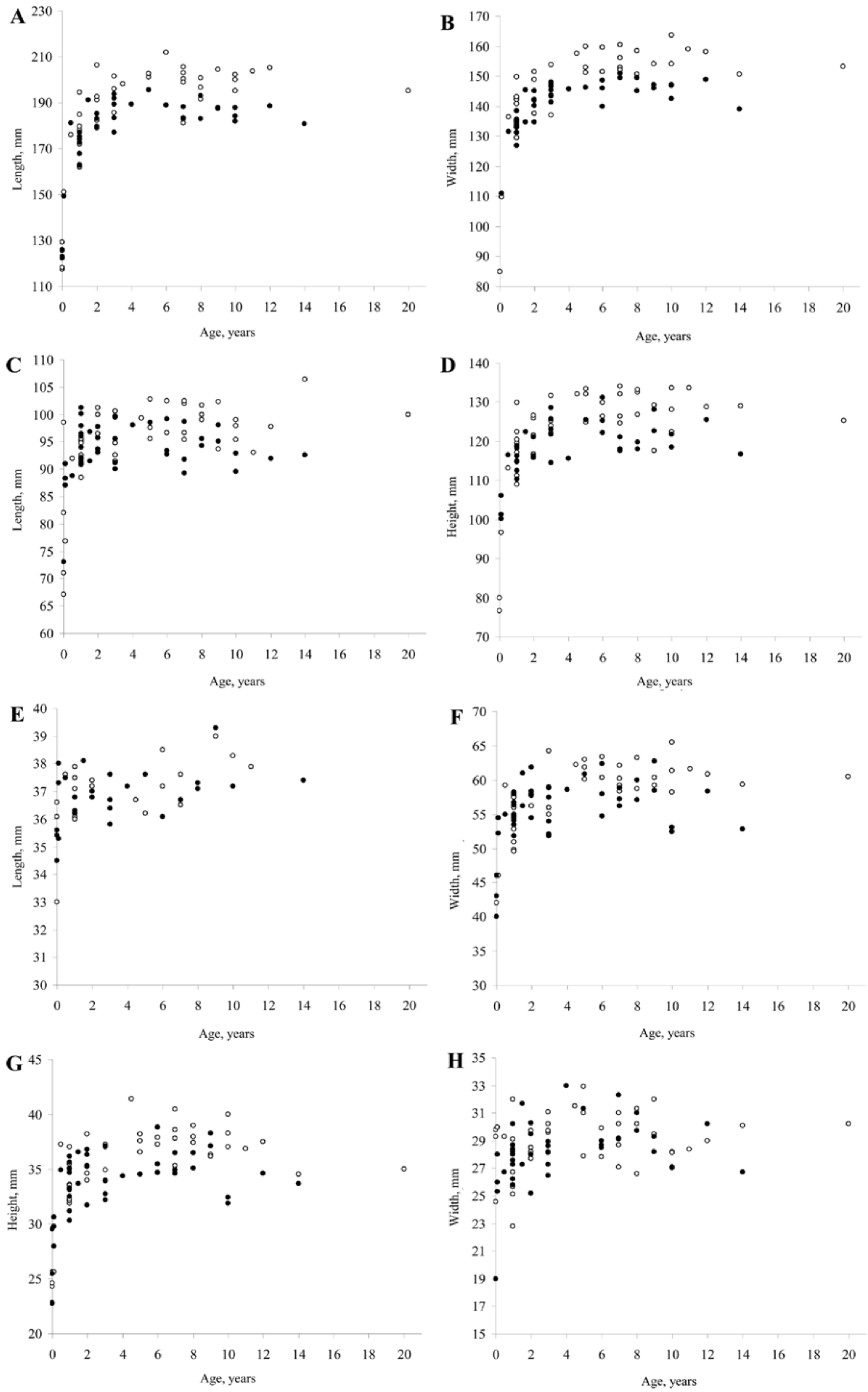

Figure 4. Growth in mandible and braincase measurements (○, females; ●, males): (A) mandible length; (B) zygomatic width; (C) braincase length; (D) skull height; (E) bulla tympani length; (F) condylar width; (G) left condyle height; (H) foramen magnum width.

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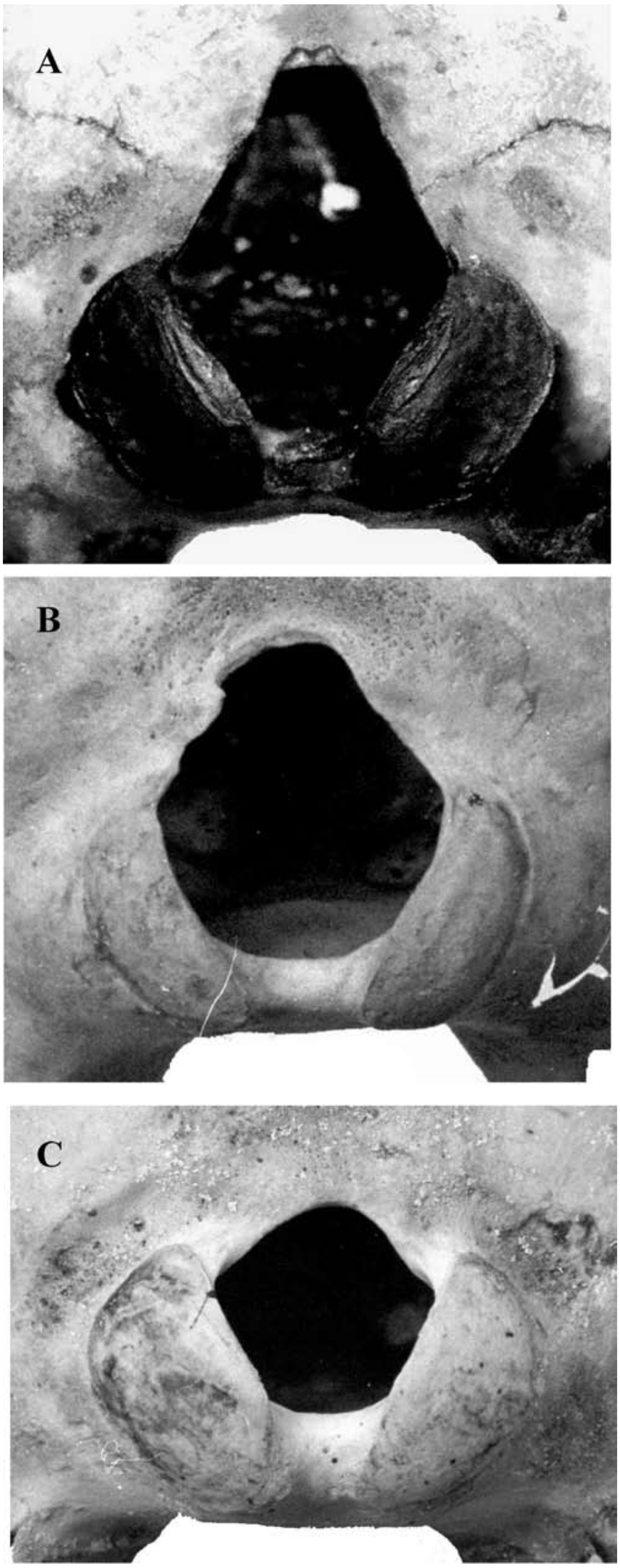

Figure 5. Foramen magnum and condylar region of females of the harbour porpoise (scale is not observed): (A) a neonate; (B) a calf; and (C) an adult animal.

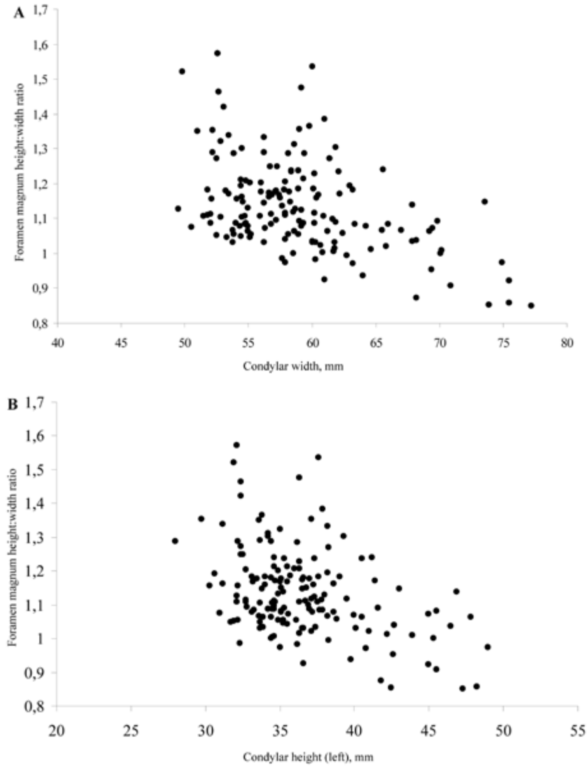

Figure 6. Ratio of height and width of foramen magnum plotted against (A) condylar width; and (B) condylar height in porpoises from the Sea of Azov and Atlantic Ocean (mixed sample).

Rapid growth in mandible length occurs in the first weeks of life; from 110–129 mm in neonates to ~150 mm in calves (Figure 4). This is primarily caused by an enlargement of the ramus (in the strict sense), i.e. the posterior part of the jaw, the length of which increases by 19 mm on average. There is also some growth in the tooth row region, however. Subsequently, rapid growth of the anterior part of the mandible commences, while the growth in ramus length ceases. Mean mandible length at the age of one year is 172.9 mm in males and 178.3 mm in females, and the emerging sexual dimorphism is determined solely by differences in tooth row length. Then the growth in ramus length becomes much slower in males and stops after one year. In females, the ramus growth either lasts longer, or has a higher rate; generally, it lasts for two years or less. Growth of the tooth row region is more intensive and lasts longer, at least to 3 years in males and 4–5 years in females (Tables 1–3).

Ramus height (both at the base and at the posterior end of the tooth row) grows rapidly during the first weeks of life. Later, ramus height at the base increases insignificantly and ceases growth between one and three years. Growth in ramus height at the posterior end of the tooth row continues longer and terminates at the age of about three years in males, and 3–5 years or later in females (Tables 1–3).

Growth in skull width lasts relatively long. Orbital width grows intensively for two years. In females, a growth spurt in orbital width occurs in the second year of life; then growth ceases. In males such a spurt takes place in the third year (Tables 1–3). Preorbital width grows intensively to three years in males, and to 4–5 years in females, without abrupt spurts. Zygomatic width is extremely variable in calves; in this sample, it spans a range of 110–133 mm. At the age of one year it reaches 131–139 mm in males and 133–150 mm in females. In the animals of undetermined sex, even smaller skulls were found; the minimum width recorded was 129 mm. Zygomatic width increases to three years in males

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Table 4. *Increment of some skull measurements in porpoises from the Sea of Azov during the lifetime (calculated as a ratio of mean values in adults and neonates).*

Measurement	Males	Females
Length of the prenarial region	1.93	2.11
Zygomatic width	1.85	1.94
Length of the left nasal bone	1.78	1.82
Length of the posterior part of the rostrum	1.75	1.81
Height of the ramus posterior to the tooth row	1.69	1.80
Rostrum width at the base	1.68	1.81
Length of the vomer	1.68	1.70
Length of the front part of the left premaxilla	1.60	1.72
Rostrum length	1.58	1.70
Orbital width	1.58	1.66
Rostrum width at the mid-point	1.57	1.72
Length of the ramus (in the strict sense)	1.56	1.64
Skull height	1.56	1.64
Length of the left upper tooth row	1.54	1.67
Distance between back maxillary fenestra (foramina supraorbitale)	1.53	1.57
Length of the mandible	1.52	1.62
Height of the ramus at the base	1.50	1.56
Postorbital width	1.48	1.56
Occipital width	1.46	1.50
Length of the left lower tooth row	1.45	1.57
Length of the orbit	1.42	1.51
Condylobasal length	1.42	1.50
Condylar height (left)	1.41	1.49
Parietal width	1.41	1.41
Condylar width	1.35	1.42
Length of the braincase	1.23	1.27
Width of the foramen magnum	1.13	1.15
Length of bulla tympani	1.07	1.07
Height of the foramen magnum	1.06	1.07

and approximately five years in females, with a secondary growth spurt after three years in females. Mean width is 145.9 mm in males at the age of three years and older, and 153.3 mm in females of the same age (154.9 mm in females of four years and older) (Tables 1–3; Figure 4).

The brain division elongates significantly during the first year of life. Growth in braincase length is further maintained until at least two years, especially due to the growth of the condylar region. In the animals with the longest skulls, this region is remarkably bulb-shaped (Tables 1–3; Figure 4). Growth of the braincase in width displays a similar pattern but lasts longer, approximately to three years. Growth in skull height also lasts for approximately three years. Growth in skull height is partly determined by growth of the occipital crest but also by growth of the lateral occipital bones. The latter factor also affects growth in occipital width (measurement 27); growth in this dimension lasts longer in females than in males, to 4–5 years (Tables 1–3; Figure 4).

The bulla tympani has almost obtained its definitive size by the moment of birth, and its postnatal growth generally completes in the first weeks of life. In neonates, its mean length is 35.0 mm, in calves it is 36.9 mm. After that, the size of bulla tympani does not change significantly (Figure 4).

Condylar width gradually increases during the first year of life; its growth ends at two years in males and at 4–5 years in females (Tables 1–3). Growth in condylar height is similar (Figure 4). Foramen magnum virtually does not grow in height during the postnatal period, and its growth in width is rather limited (Figure 4). Location of the condyles changes with age. In neonates, the condyles form an open semi-ring encircling the lower part of the foramen magnum, their lower margins almost touching each other. Then, as a result of growth of the occipital bones, the lower parts of the condyles begin to separate, and the top parts approach each other, thus encircling the foramen magnum laterally. This process is evident during the first weeks of life; however, it probably lasts longer, with growth of the occipital region in length as well as width. As a result, the ratio between the height and width of the foramen magnum changes: it becomes lower and wider in animals with a large condylar region (Figure 5). This tendency is clearly seen in a combined sample of animals from the Sea of Azov and the Atlantic Ocean (the latter with larger condyles) (Figure 6). This phenomenon was observed by Brauner (1923) who defined foramen magnum proportions as a diagnostic feature distinguishing the Black Sea porpoises from the Atlantic ones.

Growth in skull length is completed with the growth of the facial region: it ends at the age of about three years in males and about five years in females. Skull length is 235–258 mm (mean value is 246.4 mm) in adult males and 247–274 mm (mean value is 260.4 mm) in females (Table 3; Figure 3). In some animals, however, the size, proportions, and distinctive features (such as well-developed occipital crests in females) of the skull, typical for adult animals, can be observed as early as at the end of the first year of life. Furthermore, the skulls of two calves (male and female) in the sample were disproportionally over-developed for their age and were similar in ossification and size to specimens at the age of one year: condylobasal lengths were 239 and 238 mm, zygomatic widths 131 and 136 mm, rostrum lengths 106 and 107 mm, braincase lengths 89 and 92 mm. Thus, occasionally, postnatal growth and development rate can be significantly accelerated.

Life-long increment value of the measurements can be estimated using the ratio of mean sizes in adults and neonates (Table 4). In all facial measurements the increment is more than that of total skull length, while it is less in all the braincase measurements. The largest increment values were observed for the structures in the posterior part of the facial region: e.g. length of the prenarial region increases 1.94 times in males and 2.11 times in females.

Thus, the skull and its parts are generally characterized by gradually decelerating growth, which eventually ceases. Such a process is accurately described by the Gompertz equation:

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

or the von Bertalanffy equation:

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

In Tables 5 and 6, the Gompertz equation parameters are presented; however, the von Bertalanffy equation allows the growth of these structures to be described with similar accuracy.

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Table 5. *Parameters of the Gompertz equation for growth of skull measurements in males.*

Measurement	N	L_∞ ±SE	*b* ±SE	*k* ±SE	S_{resid}	r^2
1	42	244.9 ±1.7	0.3114 ±0.0216	2.1589 ±0.3495	2581.0	0.87
2	42	105.2 ±0.9	0.4293 ±0.0449	7.7677 ±2.0489	1077.9	0.80
3	42	93.0 ±1.2	0.3743 ±0.0406	1.7066 ±0.3662	1224.7	0.75
4	42	94.3 ±1.2	0.3927 ±0.0397	1.8275 ±0.3719	1154.1	0.77
5	37	146.0 ±0.9	0.2763 ±0.0345	1.1509 ±0.1720	453.5	0.80
6	44	118.6 ±1.0	0.3938 ±0.0305	2.2781 ±0.4005	1092.4	0.85
7	40	122.1 ±0.8	0.1179 ±0.0190	0.9741 ±0.2667	364.6	0.58
8	40	121.7 ±0.9	0.1882 ±0.0289	1.3413 ±0.3262	633.8	0.62
9	42	69.4 ±0.6	0.5092 ±0.0509	7.9861 ±1.9262	515.1	0.83
10	42	46.3 ±0.6	0.3058 ±0.0333	1.2803 ±0.2681	239.6	0.73
11	38	70.1 ±0.7	0.0921 ±0.0396	1.9598 ±1.4812	350.4	0.17
12	39	151.4 ±1.8	0.3621 ±0.0420	1.4314 ±0.2677	2027.0	0.75
13	42	94.6 ±0.6	0.2586 ±0.0474	13.991 ±4.005	459.4	0.54
14	44	56.5 ±0.5	0.2732 ±0.0416	14.263 ±5.3487	376.4	0.58
15	44	34.7 ±0.3	0.2894 ±0.0461	5.6603 ±2.7826	177.1	0.60
16	44	34.8 ±0.4	0.2492 ±0.0362	1.6472 ±0.4983	179.3	0.59
17	43	30.5 ±0.9	0.4706 ±0.0977	1.0896 ±0.3742	604.0	0.47
18	40	139.1 ±1.0	0.3307 ±0.0262	1.7255 ±0.2381	805.2	0.85
19	44	46.6 ±0.6	0.3770 ±0.0474	3.0676 ±1.2067	476.9	0.68
20	39	186.2 ±1.5	0.3634 ±0.0249	1.8058 ±0.2759	1824.7	0.89
21	30	94.3 ±1.6	0.3182 ±0.0412	1.4252 ±0.5102	1037.2	0.73
22	29	94.1 ±1.9	0.2895 ±0.0487	1.2102 ±0.4237	1216.5	0.62
23	40	50.8 ±0.4	0.4057 ±0.0367	13.946 ±3.8629	217.7	0.82
24	41	91.6 ±1.0	0.4222 ±0.0380	2.8896 ±0.7698	931.8	0.82
25	41	29.4 ±0.5	0.4608 ±0.0523	1.1181 ±0.2408	192.7	0.74
26	42	137.6 ±1.6	0.3898 ±0.0355	1.7204 ±0.3080	1994.7	0.81
27	41	120.5 ±0.8	0.1666 ±0.0218	1.0459 ±0.2208	427.4	0.68
28	–	–	–	–	–	–
29	42	28.9 ±0.4	0.2080 ±0.0517	2.2286 ±1.1286	141.7	0.36
30	44	61.6 ±0.7	0.3261 ±0.0371	1.9685 ±0.4831	502.1	0.71
31	41	54.8 ±0.9	0.4094 ±0.0490	1.1692 ±0.2396	504.9	0.72
32	41	54.9 ±1.0	0.3895 ±0.0524	1.1257 ±0.2621	602.9	0.67
33	39	142.7 ±1.5	0.2023 ±0.0412	0.9911 ±0.2969	1415.6	0.52
34	42	13.9 ±0.6	0.6262 ±0.2891	201.5	525.5	0.18
35	39	26.8 ±0.5	0.1754 ±0.0520	0.7161 ±0.3615	104.2	0.33
36	39	–	–	–	–	–
37	28	37.9 ±1.3	0.0437 ±0.0327	0.1620 ±0.2582	20.3	0.21

N, sample size; L_∞, *b*, *k*, equation coefficients; SE, standard errors, S_{resid}, residual sum; r^2, determination coefficient.

Table 6. *Parameters of the Gompertz equation for growth of skull measurements in females.*

Measurement	N	L_∞ ±SE	*b* ±SE	*k* ±SE	S_{resid}	r^2
1	42	260.8 ±1.5	0.4172 ±0.0204	1.4392 ±0.1279	2123.5	0.94
2	43	115.6 ±1.0	0.4918 ±0.0310	1.3198 ±0.1530	1042.6	0.90
3	38	101.6 ±1.2	0.4818 ±0.0534	1.2045 ±0.1913	1078.5	0.80
4	39	101.6 ±1.2	0.4729 ±0.0548	1.3019 ±0.2153	1169.5	0.78
5	41	153.1 ±1.3	0.5722 ±0.0493	1.6860 ±0.2036	1833.3	0.86
6	43	126.8 ±1.0	0.4303 ±0.0338	1.5388 ±0.1955	1103.5	0.86
7	41	122.0 ±0.8	0.2634 ±0.0344	2.1480 ±0.4435	610.6	0.68
8	42	128.2 ±1.0	0.4438 ±0.0368	1.6157 ±0.1394	940.0	0.86
9	44	77.3 ±0.9	0.5160 ±0.0470	1.3423 ±0.1998	856.6	0.83
10	42	51.8 ±0.7	0.5314 ±0.0450	0.7420 ±0.1141	377.1	0.85
11	41	73.5 ±0.5	0.2979 ±0.0358	1.6666 ±0.2687	234.5	0.73
12	43	162.3 ±1.4	0.4974 ±0.0297	1.3495 ±0.1482	1860.7	0.91
13	45	98.6 ±1.0	0.2379 ±0.0290	1.4852 ±0.3859	1085.7	0.66
14	43	60.7 ±0.5	0.3569 ±0.0303	1.1159 ±0.1550	241.6	0.83
15	44	37.3 ±0.3	0.4233 ±0.0341	1.4491 ±0.2046	126.8	0.84
16	45	37.2 ±0.4	0.4468 ±0.0380	1.3341 ±0.2073	185.4	0.83
17	45	33.1 ±0.8	0.6880 ±0.1660	2.2491 ±0.7038	712.2	0.65
18	42	147.4 ±1.1	0.4340 ±0.0296	1.3826 ±0.1516	1197.3	0.89
19	45	49.7 ±0.6	0.3471 ±0.0383	1.5509 ±0.3469	396.9	0.72
20	39	198.6 ±1.9	0.4543 ±0.0308	1.5973 ±0.2180	2848.4	0.90
21	34	102.3 ±1.5	0.4388 ±0.0412	0.9830 ±0.1990	1226.3	0.83
22	38	101.6 ±1.5	0.4302 ±0.0471	1.3047 ±0.2676	1582.3	0.77
23	39	53.6 ±0.5	0.4430 ±0.0341	1.4122 ±0.1976	231.4	0.87
24	38	97.0 ±1.4	0.4733 ±0.0480	1.9960 ±0.4611	1535.0	0.80
25	42	31.2 ±0.5	0.5295 ±0.0567	1.0166 ±0.1953	237.4	0.77
26	43	148.8 ±1.4	0.5364 ±0.0337	1.5133 ±0.1754	1853.9	0.91
27	42	123.9 ±0.9	0.3995 ±0.0335	1.5821 ±0.1953	785.1	0.85
28	–	–	–	–	–	–
29	43	29.6 ±0.6	0.0792 ±0.0343	0.4668 ±0.4938	157.0	0.13
30	44	63.9 ±0.6	0.4496 ±0.0353	1.9927 ±0.3150	373.3	0.85
31	41	58.3 ±1.1	0.5480 ±0.0807	1.3073 ±0.2952	1029.3	0.67
32	39	59.6 ±1.1	0.5456 ±0.0751	1.1686 ±0.2465	901.5	0.71
33	43	148.7 ±1.5	0.5110 ±0.0390	1.4646 ±1.1856	2178.9	0.87
34	37	17.9 ±6.6	0.3996 ±0.3402	0.0873 ±0.1406	213.5	0.22
35	41	27.3 ±0.5	0.4748 ±0.1229	2.2873 ±0.8481	263.1	0.40
36	41	28.1 ±0.5	0.5268 ±0.1239	1.8752 ±0.5364	266.2	0.47
37	22	37.5 ±0.3	0.0623 ±0.0177	1.4546 ±0.9585	18.5	0.40

N, sample size; L_∞, *b*, *k*, equation coefficients; SE, standard errors, S_{resid}, residual sum; r^2, determination coefficient.

Definitive size values estimated with the Gompertz equation agree with the true mean values of the same measurements with an accuracy of 1–2 mm (Tables 3,5&6). The best accuracy and best determination coefficients (r^2) are obtained in regressions for long-growing structures with relatively low variability. In particular, r^2 of the regression for the growth of condylobasal length is 0.87 in males and 0.94 in females, for mandible length it is 0.89 in males and 0.90 in females, for postorbital length it is 0.85 in males and 0.89 in females (Tables 5&6).

Sexual dimorphism

At the age of three years and older, significant sexual differences of the mean values between males and females are observed in the absolute majority of measurements ($P<0.05$) (Table 7). In the younger animals, sexual dimorphism is only seen in braincase length (at the age of two years) and in prenarial region length (after one year). In all cases females are larger than males.

Sexual di morphism is not observed in many measurements of the brain division: parietal width, foramen magnum height and width, bulla tympani size. In contrast to this, sexual differences in the facial region are only absent in nasals size and the length of the posterior part of the rostrum. In several measurements (prenarial region length, ramus height at its base, etc.) differences are minor.

Thus, sexual dimorphism is expressed due to structures with a long growth period, and it is determined by the fact that males complete their growth at the age of three years while females do so at the age of 4–5 years. Galatius (2005) comes to a similar conclusion in his study of sexually dimorphic proportions forming in harbour porpoise skeletons. Indeed, sexual dimorphism cannot be explained by differences in growth rates, which decline remarkably after the first year. Indices of allometric growth are also similar in males and females at the age of one year and older: significant differences in *b* coefficient were only found for the rostrum width at the mid-point.

Individual variation

In some skull measurements individual variation expressed as a coefficient of variation CV is the highest in neonates; in others, it peaks in calves or animals of one year. As a rule, increase in variation occurs in the period of positive allometric growth. So in many measurements of the skull width CV decreases in the first year coinciding with the changes in allometry (see below). However, in some cases, the variation remains high even after growth slows down.

The highest individual variation persisting during the entire lifespan is observed in prenarial region length, length of nasal bones, length of the anterior parts of the premaxilla, length of the posterior part of the rostrum and foramen magnum height. In particular, the coefficient of variation for prenarial region length is 15.7 ±6.7% in neonates (hereinafter CV error is indicated), 17.2 ±8.8% in calves, 15.9 ±3.6% at the age of one year, and some less in adults: 14.2 ±3.9% in males and 12.3 ±3.2% in females.

In addition, in neonates high variation is observed in foramen magnum width (CV=19.6 ±8.4%), length of the brain division (CV=14.8 ±6.4%), rostrum width at the base (CV=10.4 ±4.5%) and at the mid-point (CV=9.6 ±4.2%). In calves, variation in width measurements increases: width between foramina supraorbitale (CV=11.0 ±5.7%), occipital width (CV=10.7 ±5.6%), zygomatic width (CV=1.2 ±5.8%); and variation of rostrum width at the base remains high (CV=10.0 ±5.2%). At the age of 1 year, variation is relatively high in ramus height at the posterior margin of the tooth row (CV=10.9 ±2.5%, incl. 12.3 ±6.0% in females) and foramen magnum width (CV=11.2 ±2.6%). In older groups, high individual variation (CV=10% and more) is only seen in the measurements that remain highly variable over the entire lifespan.

The lowest individual variations in adults are observed in measurements of the total skull size: condylobasal length, lengths of the rostrum, the facial and brain divisions, the mandible; zygomatic, orbital, braincase, occipital widths; and maximum skull height. CV values for these measurements do not exceed 4%. However, during the rapid growth at age younger than one year, variation of these measurements is remarkably higher and fluctuates in the range of 4–8%.

Temporal variation

Data on skull size in harbour porpoises of various ages in the Black Sea and the Sea of Azov in the first half of the 20th century are based on collections and studies by Zalkin (1938), Kleinenberg (1956) and Tomilin (1957). Most of their collections are lost, so the possibilities for study of temporal variation are limited.

In the past, animals with larger body sizes evidently had smaller skulls, e.g. in Kleinenberg's sample the condylobasal lengths of seven males were 223–239 mm at the body length of 120–132 cm (while in my recent sample, males of the same body-length range have condylobasal lengths of 231–253 mm) while another male had a body length of 142 cm and condylobasal length of only 228 mm. Relative skull size was also smaller in adults: according to Zalkin (1938), skull length:body length ratio was 17.7% on average, in contrast to 18.4% in the current sample.

During the last decades (in comparison with Zalkin's data), the condylobasal length of adults decreased slightly in females (from 262.9 to 260.4 mm on average) and more dramatically in males (on average, from 254.8 to 246.4 mm). No animals with remarkably large skulls have been observed recently: in Zalkin's sample maximum skull length was 293 mm, but in my recent sample it is only 274 mm. At the same time, minimum size did not change: 238 mm in Zalkin's sample, 235 mm in the current sample. Mean length of the rostrum somewhat increased, especially in adult females (from 113.7 to 115.5 mm, i.e. from 43.0 to 44.4% of the skull length), as well as rostrum width at the base (from 73.1 to 77.0 mm, i.e. 48.7 to 50.1% of the skull width) (compared to the data from Zalkin, 1938). However, rostrum length and width in the female skulls that remained from Zalkin's collection are much larger than average values reported by Zalkin (1938). The ratio between rostrum length and prenarial region length also increased: sexual dimorphism of skull length was

Table 7. *Skull measurements demonstrating sexual dimorphism (age 3 years and more).*

Measurement	*P*
Condylobasal length	**
Rostrum length	**
Length of the left upper tooth row	**
Length of the right upper tooth row	**
Zygomatic width	**
Orbital width	**
Skull height	**
Rostrum width at the base	**
Rostrum width at the mid-point	**
Length of basioccipitale	**
Length of the facial region	**
Length of the braincase	**
Condylar width	**
Condylar height (left)	**
Condylar height (right)	**
Length of the prenarial region	*
Postorbital width	**
Length of the orbit	**
Length of the mandible	**
Length of the left lower tooth row	**
Length of the right lower tooth row	**
Height of the ramus at the base	**
Length of the ramus (in the strict sense)	**
Height of the ramus back to the tooth row	*
Distance from tip of the rostrum to the external nares.	**
Occipital width	**
Distance between back maxillary fenestra (foramina supraorbitale)	*
Length of the front part of the left premaxilla	**
Length of the front part of the right premaxilla	*
Length of the vomer	**

*, $P<0.05$; **, $P<0.01$)

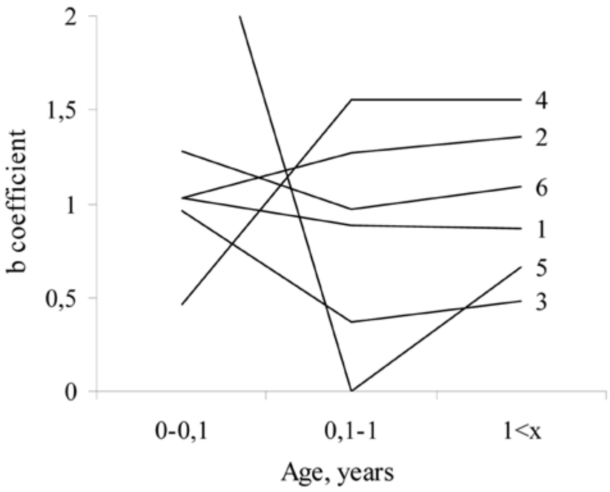

Figure 7. Types of changes in allometry of skull structures.

mainly determined by prenarial region length in Zalkin's sample, but by rostrum length in my sample. Zygomatic width increased slightly; on average, from 57.4 to 59.2% of skull length in males, and from 57.7 to 59.0% in females.

Thus, skull size and proportions in porpoises from the Sea of Azov and the adjoining area have changed insignificantly during the last decades: condylobasal length has decreased somewhat, while measurements of anterior parts (rostrum, primarily) have increased. Skull proportions became more 'mature', and the ratio between skull length and body length has become more 'juvenile' (because of a decrease in the total body size) (Gol'din, 2004). Main patterns of skull growth, briefly characterized by Zalkin (1938), have not changed.

Allometric growth. Growth types and periods

The following types of changes in allometry during the postnatal ontogenesis can be distinguished (Tables 8–11; Figures 7&8):

Table 8. *Ratio indices of skull measurements.*

Age, years	0		0.1		1		3 and more (males)		3 and more (females)	
Measurement	i	SD	i	SD	i	SD	i	SD	i	SD
2	0.405	0.015	0.416	0.020	0.432	0.018	0.437	0.009	0.444	0.010
3	0.364	0.010	0.337	0.032	0.370	0.018	0.377	0.017	0.388	0.015
4	0.361	0.008	0.336	0.041	0.373	0.020	0.382	0.017	0.389	0.015
5	0.517	0.082	0.582	0.035	0.577	0.014	0.592	0.015	0.590	0.013
6	0.455	0.050	0.494	0.019	0.485	0.015	0.488	0.017	0.487	0.011
7	0.538	–	0.540	0.027	0.496	0.016	0.495	0.012	0.470	0.013
8	0.453	0.019	0.519	0.019	0.496	0.018	0.493	0.014	0.493	0.016
9	0.251	0.028	0.275	0.018	0.285	0.013	0.290	0.012	0.295	0.013
10	0.181	0.015	0.182	0.008	0.181	0.013	0.188	0.011	0.196	0.011
11	0.328	–	0.316	0.025	0.294	0.016	0.283	0.009	0.281	0.007
12	0.568	0.016	0.570	0.026	0.599	0.021	0.614	0.009	0.623	0.013
13	0.432	0.016	0.429	0.026	0.401	0.021	0.386	0.010	0.377	0.013
14	0.255	0.013	0.255	0.015	0.235	0.011	0.230	0.010	0.232	0.007
15	0.147	0.015	0.145	0.008	0.144	0.006	0.143	0.007	0.143	0.006
16	0.141	0.011	0.147	0.007	0.142	0.008	0.142	0.007	0.143	0.006
17	0.091	0.013	0.124	0.021	0.118	0.017	0.124	0.017	0.128	0.016
18	0.557	0.048	0.567	0.024	0.560	0.012	0.566	0.014	0.566	0.010
19	0.197	0.012	0.190	0.020	0.193	0.013	0.190	0.011	0.191	0.013
20	0.723	0.020	0.768	0.015	0.753	0.025	0.759	0.010	0.767	0.016
21	0.383	0.011	0.379	0.010	0.379	0.020	0.383	0.020	0.394	0.020
22	0.385	0.015	0.404	0.021	0.375	0.023	0.383	0.019	0.391	0.021
23	0.199	0.014	0.235	0.000	0.209	0.010	0.209	0.006	0.207	0.008
24	0.341	0.017	0.385	0.024	0.377	0.021	0.375	0.015	0.375	0.020
25	0.102	0.007	0.114	0.007	0.111	0.008	0.119	0.010	0.119	0.008
26	0.499	0.023	0.536	0.013	0.550	0.019	0.561	0.018	0.571	0.014
27	0.506	0.009	0.509	0.030	0.484	0.012	0.490	0.013	0.477	0.012
28	0.185	0.029	0.176	0.009	0.138	0.014	0.134	0.016	0.130	0.014
29	0.148	0.029	0.133	0.012	0.120	0.010	0.117	0.007	0.114	0.007
30	0.239	0.021	0.255	0.011	0.254	0.011	0.251	0.012	0.246	0.010
31	0.198	0.036	0.184	0.023	0.208	0.019	0.219	0.016	0.223	0.016
32	0.200	0.038	0.189	0.027	0.209	0.019	0.219	0.016	0.223	0.016
33	0.516	0.049	0.586	0.019	0.573	0.030	0.581	0.019	0.571	0.017
34	0.049	0.011	0.078	0.029	0.061	0.013	0.057	0.015	0.056	0.010
35	0.091	–	0.109	0.005	0.109	0.008	0.108	0.008	0.105	0.011
36	0.085	–	0.111	0.011	0.112	0.010	0.110	0.009	0.109	0.012
37	0.204	0.003	0.180	0.011	0.156	0.009	0.152	0.004	0.143	0.004

i, mean values; SD, standard deviations.

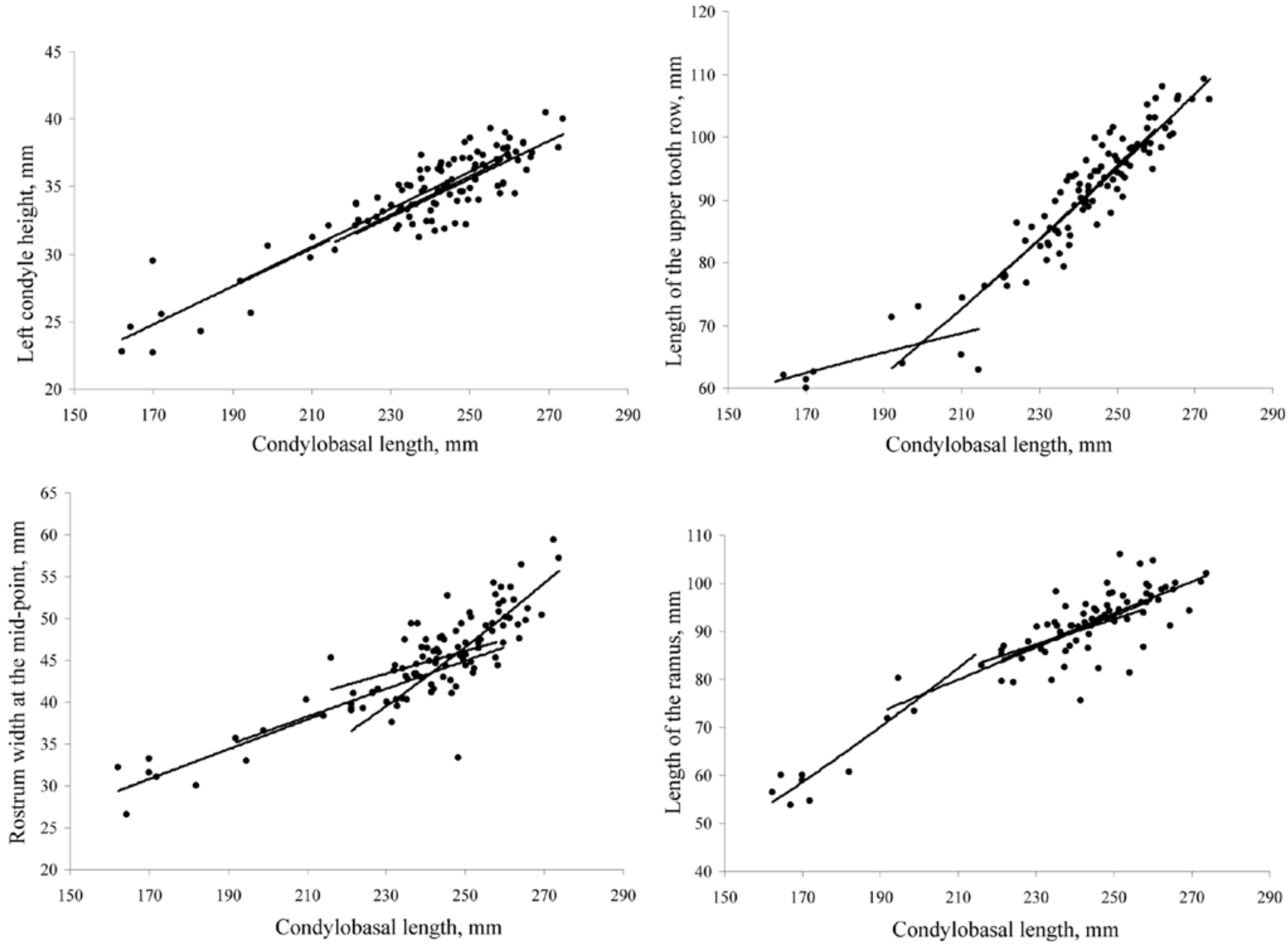

Figure 8. Examples of sustaining and changing allometry during the lifetime.

1. Isometry is demonstrated over most of the lifespan (measurements: condylar height, postorbital width). The ratio index does not change significantly over the lifetime. Growth of condylar width and orbit length is similar but demonstrates slightly negative allometry.

2. Allometric growth rate is constant or rising (measurements: rostrum length, rostrum width at the base, facial region length, lengths of lower tooth rows, ramus height at the posterior end of the tooth row, distance from the tip of the rostrum to the external nares). Allometry is positive, or isometry is replaced by the positive allometry after the first weeks of life; *b* coefficient remains constant or increases; ratio index increases.

3. Allometric growth rate is constant or declining (measurements: parietal width, brain division length, basioccipitale length, foramen magnum and bulla tympani measurements). Allometry is negative; *b* coefficient remains constant or decreases; ratio index decreases.

An extreme example of such a growth type is observed when a structure does not grow or only grows in a short period (e.g. foramen magnum or bulla tympani).

4. Allometric growth rate is slow (or no growth occurs) during the first weeks of life; then it accelerates and remains high until the end of the growth period (measurements: lengths of upper tooth rows, rostrum width at the mid-point in females, lengths of the anterior parts of the premaxillae). Negative allometry is replaced by positive allometry. The *b* coefficient increases significantly and then remains stable (Figure 8); ratio index decreases and then increases (the curve of ratio index changes is V-shaped) (Table 8).

5. Allometric growth rate is high during the first weeks of life, after which it declines and growth ceases early (measurements: posterior part of the rostrum). Positive allometry is replaced by negative allometry. The *b* coefficient decreases significantly and then remains stable (Figure 8); ratio index increases and then decreases (the curve of ratio index changes is an inverted V-shape) (Table 8).

6. Allometric growth rate is high during the first weeks of life, after which it declines, but growth continues until the skull growth is completed (measurements: maximum skull height, orbital width, prenarial region length in females, mandible length, ramus height at the base in females, length of nasals, distance between foramina supraorbitale, vomer length). Positive allometry is replaced by isometry. The *b* coefficient decreases and then remains stable; ratio index increases and then remains stable.

Growth in zygomatic width is close to type 6; however, for the most part of life it is not characterized by isometry but by slightly positive allometry.

Growth in occipital width is intermediary between types 3 and 6; during the first weeks of life it demonstrates slightly positive allometry, then slightly negative allometry.

Table 9. *Parameters of allometry equations* (y=ax^b) *for skull measurements (all ages).*

Measurement	Males				Females			
	a	*b*	$\pm s_b$	r^2	*a*	*b*	$\pm s_b$	r^2
2	0.14	1.21	0.03	0.96	0.15	1.20	0.03	0.97
3	0.047	1.38	0.15	0.69	0.09	1.27	0.07	0.91
4	0.06	1.33	0.16	0.65	0.10	1.24	0.07	0.90
5	0.20	1.20	0.10	0.78	0.18	1.21	0.05	0.94
6	0.48	1.00	0.10	0.68	0.53	0.99	0.05	0.94
7	7.53	0.50	0.07	0.57	3.95	0.62	0.05	0.81
8	1.67	0.78	0.07	0.76	0.41	1.03	0.06	0.89
9	0.10	1.20	0.12	0.70	0.50	1.32	0.07	0.89
10	0.16	1.03	0.15	0.56	0.01	1.53	0.10	0.85
11	13.92	0.29	0.11	0.15	1.68	0.68	0.07	0.77
12	0.037	1.51	0.07	0.92	0.27	1.15	0.04	0.96
13	19.70	0.29	0.10	0.18	1.38	0.77	0.06	0.79
14	1.19	0.70	0.07	0.70	0.61	0.83	0.05	0.87
15	0.31	0.86	0.08	0.73	0.13	1.02	0.06	0.89
16	0.29	0.87	0.07	0.76	0.10	1.06	0.06	0.87
17	0.007	1.51	0.30	0.39	0.002	1.78	0.18	0.73
18	0.26	1.14	0.05	0.92	0.56	1.00	0.04	0.93
19	0.15	1.04	0.15	0.55	0.43	0.85	0.08	0.75
20	0.40	1.12	0.03	0.98	0.39	1.12	0.03	0.98
21	0.42	0.98	0.06	0.94	0.30	1.05	0.06	0.93
22	0.37	1.00	0.10	0.88	0.33	1.03	0.05	0.93
23	0.16	1.05	0.12	0.83	0.15	1.06	0.05	0.95
24	0.59	0.92	0.14	0.55	0.34	1.02	0.08	0.84
25	0.031	1.24	0.21	0.50	0.02	1.32	0.12	0.81
26	0.12	1.29	0.12	0.85	0.14	1.26	0.04	0.97
27	1.96	0.75	0.08	0.73	0.80	0.91	0.04	0.93
28	–	–	–	–	–	–	–	–
29	0.47	0.75	0.12	0.46	8.47	0.22	0.10	0.11
30	0.30	0.97	0.08	0.75	0.39	0.92	0.05	0.87
31	0.010	1.56	0.19	0.64	0.004	1.70	0.13	0.83
32	0.016	1.47	0.20	0.58	0.004	1.71	0.13	0.83
33	0.45	1.04	0.10	0.74	0.43	1.05	0.06	0.90
34	–	–	–	–	1.66	0.38	0.31	0.04
35	0.25	0.85	0.23	0.37	0.08	1.04	0.25	0.54
36	0.35	0.79	0.36	0.17	0.06	1.11	0.30	0.48
37	16.09	0.15	0.08	0.13	9.25	0.25	0.05	0.66

a and *b*, coefficients; s_b, standard error of *b* coefficient; r^2, determination coefficient.

Growth in ramus length (in males also height of ramus at its base) is intermediary between types 3 and 6; after the first weeks of life growth slows down abruptly but still persists for about two years.

It is obvious that describing allometric growth of structures demonstrating drastic changes in growth rate (growth types 4, 5, 6) by only one allometric equation leads to misunderstanding of the growth patterns and observation of 'paradoxical' phenomena, e. g. mandible length seems to display a higher allometric coefficient (*b*=1.12) than each of its parts: for the anterior part *b*=0.98–1.00 in males and 1.03–1.05 in females, for the posterior part *b*=0.92 in males and 1.02 in females (Table 9). The allometric growth patterns of the tooth row and the ramus (in a narrow sense) change significantly over the lifetime, so describing growth of these structures by only one allometric equation would be inaccurate. In fact, the growth rate of the mandible is intermediary between the growth of the tooth row and the ramus in every growth period: at first, the ramus grows more intensively, and then the tooth row does. This is evident from the allometric coefficients for the different periods (Tables 10 and 11; Figure 8).

In some structures a secondary growth spurt is observed. Growth is divided into two stages, and during each of them rapid growth occurs, and eventually slows down. These structures include: prenarial region length (in males) (Figure 3), orbital width (in males), condylar width (in females) (Figure 4), zygomatic width (in females) (Figure 4), height of the right condyle (in females), length of the lower right tooth row (in females). The secondary growth spurt occurs between two and three years in the former three cases and between three and five years in the latter three cases. Such a growth pattern is reflected in changes of allometry: the growth retardation is associated with a decline of coefficient *b*, while the secondary spurt is associated with an increase (Figure 8). The secondary growth spurt is short-term in all cases, and soon after it growth stops. In all cases this spurt is sexually dimorphic; it is observed only in animals of the sex indicated above. The growth spurt does not depend on the type of allometry.

Thus, the following periods of postnatal skull growth can be distinguished:

1. The first weeks of life. The skull (including the brain division) grows rapidly in length, width and height. The anterior part of the jaws and bulla tympani are the only structures to show limited growth. The most intensive growth occurs in the width and height dimensions and in the posterior part of the facial region.

2. From one to three months to one year. Rapid growth of the anterior part of the jaws starts. Growth of the posterior part of the rostrum and bulla tympani is completed. Growth in the length of the brain division, the prenarial region and the ramus (in a narrow sense) becomes much slower. Growth in the skull width slows down and becomes isometric.

3. From one to two years. Growth in the length of the brain division, the ramus (in a narrow sense), and the orbit is completed, as well as growth of the condylar region in males.

4. From two to three years (in males) or 4–5 years (in females). A short-term secondary growth spurt occurs in some structures. Growth in rostrum length (and, naturally, the facial region and the whole skull), skull width and height is completed, as well as growth of the condylar region (in females).

5. After three years (in males) or 4–5 years (in females). Growth in rostrum width and mandible height is completed.

The most profound changes of the growth pattern occur during the first weeks and months of life; so in a broader sense it is useful to distinguish two growth periods: perinatal and strictly postnatal. The most evident feature of the shift of the periods is when the posterior part of the rostrum ceases to grow and the anterior part commences growth.

Skull proportions

Skull proportions change significantly during the first 1–3 months of life. In this period, the skull grows at a much higher rate in the width and height dimensions than in the length

Table 10. *Parameters of allometry equations* ($y=ax^b$) *for skull measurements (ages of 0–0.1 and 0.1–1.5 years).*

Measurement	Age, years							
	0–0.1				0.1–1.5			
	a	*b*	$\pm s_b$	r^2	*a*	*b*	$\pm s_b$	r^2
2	0.34	1.03	0.13	0.86	0.10	1.27	0.09	0.83
3	5.90	0.46	0.22	0.36	0.018	1.55	0.25	0.47
4	12.10	0.31	0.27	0.17	0.017	1.56	0.16	0.71
5	0.019	1.64	0.16	0.97	0.81	0.94	0.08	0.81
6	0.08	1.34	0.25	0.77	1.05	0.86	0.07	0.78
7	1.06	0.87	0.22	0.76	9.14	0.47	0.06	0.58
8	0.018	1.63	0.21	0.91	1.72	0.77	0.08	0.70
9	0.069	1.25	0.33	0.62	0.13	1.15	0.11	0.73
10	0.20	0.98	0.23	0.68	0.28	0.92	0.16	0.45
11	2.07	0.65	0.31	0.47	9.61	0.36	0.10	0.25
12	0.51	1.02	0.12	0.89	0.055	1.44	0.06	0.92
13	0.53	0.96	0.15	0.81	12.47	0.37	0.09	0.28
14	0.35	0.94	0.16	0.79	2.69	0.55	0.10	0.41
15	0.17	0.97	0.24	0.63	0.17	0.97	0.10	0.70
16	0.05	1.19	0.19	0.78	0.29	0.87	0.11	0.60
17	$2.0\cdot10^{-5}$	2.64	0.44	0.78	0.65	1.11	0.38	0.17
18	0.48	1.03	0.24	0.75	1.09	0.88	0.07	0.80
19	2.15	0.54	0.30	0.35	0.21	0.98	0.17	0.44
20	0.17	1.28	0.15	0.91	0.87	0.97	0.07	0.88
21	0.33	1.03	0.13	0.90	0.26	1.07	0.14	0.77
22	0.19	1.14	0.23	0.78	0.63	0.91	0.18	0.53
23	0.004	1.76	0.44	0.70	2.02	0.58	0.13	0.42
24	0.056	1.35	0.28	0.77	0.72	0.88	0.14	0.59
25	0.011	1.44	0.45	0.77	0.08	1.07	0.19	0.50
26	0.06	1.41	0.33	0.86	0.13	1.26	0.07	0.89
27	0.96	0.87	0.35	0.68	2.38	0.71	0.07	0.70
28	–	–	–	–	11.76	−0.23	0.24	0.02
29	5.10	0.31	0.52	0.06	6.16	0.28	0.16	0.06
30	0.22	1.03	0.14	0.90	0.60	0.84	0.11	0.58
31	2.56	0.50	0.58	0.11	0.002	1.85	0.20	0.67
32	1.37	0.62	0.62	0.15	0.004	1.71	0.22	0.60
33	0.14	1.27	0.11	0.98	0.58	1.00	0.11	0.65
34	3·10-7	3.31	0.99	0.58	–	–	–	–
35	0.0015	1.80	0.23	0.97	0.22	0.88	0.47	0.12
36	0.0004	2.03	0.58	0.86	0.89	0.62	0.40	0.09
37	4.85	0.38	0.15	0.57	3.96	0.40	0.47	0.03

a and *b*, coefficients; s_b, standard error of *b* coefficient; r^2, determination coefficient.

Table 11. *Parameters of allometry equations* ($y=ax^b$) *for skull measurements (age 1 year and more).*

Measurement	Males				Females			
	a	*b*	$\pm s_b$	r^2	*a*	*b*	$\pm s_b$	r^2
2	0.07	1.33	0.10	0.82	0.06	1.36	0.08	0.88
3	0.017	1.56	0.18	0.68	0.018	1.55	0.11	0.85
4	0.04	1.41	0.19	0.60	0.037	1.42	0.13	0.78
5	0.40	1.07	0.14	0.62	0.29	1.13	0.11	0.76
6	0.75	0.92	0.14	0.55	0.42	1.03	0.09	0.77
7	3.07	0.67	0.10	0.53	7.77	0.50	0.09	0.44
8	1.98	0.75	0.14	0.44	0.88	0.90	0.11	0.63
9	0.19	1.08	0.20	0.44	0.019	1.49	0.14	0.75
10	0.86	0.72	0.26	0.17	0.001	1.95	0.19	0.73
11	17.05	0.26	0.19	0.05	2.68	0.60	0.12	0.41
12	0.03	1.54	0.11	0.84	0.10	1.33	0.07	0.90
13	27.91	0.22	0.17	0.05	6.28	0.49	0.12	0.32
14	0.54	0.85	0.20	0.34	0.19	1.17	0.11	0.75
15	0.36	1.00	0.22	0.36	0.12	1.03	0.13	0.63
16	0.04	1.23	0.21	0.40	0.03	1.27	0.16	0.64
17	0.001	1.83	0.64	0.18	0.08	1.08	0.43	0.15
18	1.17	0.87	0.10	0.69	0.29	1.12	0.08	0.85
19	0.60	0.79	0.29	0.17	0.40	0.86	0.20	0.33
20	0.54	1.06	0.11	0.78	0.46	1.09	0.08	0.87
21	0.04	1.42	0.31	0.52	0.036	1.43	0.19	0.68
22	0.02	1.52	0.27	0.61	0.05	1.36	0.20	0.62
23	0.86	0.74	0.17	0.40	0.18	1.02	0.14	0.63
24	1.96	0.70	0.25	0.20	0.71	0.88	0.19	0.43
25	0.002	1.63	0.35	0.45	0.001	1.79	0.27	0.58
26	0.05	1.43	0.14	0.74	0.12	1.28	0.08	0.86
27	1.35	0.81	0.12	0.56	0.95	0.88	0.09	0.72
28	–	–	–	–	2.27	0.48	0.34	0.05
29	1.45	0.54	0.25	0.11	0.29	0.83	0.21	0.30
30	0.30	0.97	0.20	0.39	0.72	0.81	0.14	0.49
31	0.004	1.74	0.30	0.49	0.009	1.58	0.26	0.49
32	0.004	1.72	0.32	0.44	0.006	1.65	0.25	0.55
33	0.27	1.14	0.15	0.60	0.15	1.24	0.11	0.76
34	–	–	–	–	0.69	0.54	0.60	0.02
35	–	–	–	–	1.31	0.54	0.45	0.09
36	–	–	–	–	–	–	–	–
37	9.68	0.25	0.17	0.10	24.9	0.07	0.10	0.04

a and *b*, coefficients; s_b, standard error of *b* coefficient; r^2, determination coefficient.

dimension. In particular, the ratio index for maximum skull height increases by 6.5% of skull length (Table 8). Among the proportions of the length dimensions, the contribution of the prenarial region and the posterior part of the rostrum increases. Due to these processes, the skull shape changes remarkably. In neonates, the condylar region is shifted in the skull-base direction in such a way that the inion point is located at the same level as the posterior margins of the condyles. The maximum width of the skull is the postorbital width; parietal width is a bit smaller. Zygomatic processes are poorly developed. In calves, on the contrary, the condyles shift backwards, and after this age, condylobasal length becomes the maximum length of the skull; zygomatic processes grow intensively, and zygomatic width becomes the maximum width of the skull (Figure 2). Intensive growth in skull height occurs due to the growth of the frontal bones and proximal parts of the maxilla, on the one side, and the occipital bones, on the other side, while the growth in length is less intensive. Because of this pattern of growth, a typical cetacean skull profile appears, with a slightly concave frontal surface and a strongly convex occipital one. The interparietal bone becomes compressed between the upper occipital and frontal bones and forms the occipital crest. In calves, the skull attains its typical shape (Figure 2).

After calf age (1–3 months), most of the width and height measurements demonstrate isometry relative to the condylobasal length for the remaining growth period; allometry, if present, is slight. Thus, the ratios of these measurements to the condylobasal length remain constant. This growth pattern is demonstrated during most of the animal's life in maximum skull height, condylar heights, ramus height at the base, orbital and postorbital widths.

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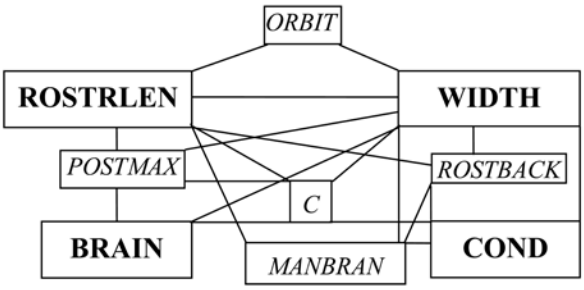

Figure 9. General scheme of correlations between measurements of the bone structures. Pleiad names are bold-typed.

The ratio index increases insignificantly in zygomatic width and decreases in occipital width. The maximum skull width: maximum skull length ratio in neonates is 0.50–0.62. After calf age, when zygomatic width becomes maximum width, it varies within the range of 0.54–0.62 (up to 0.64 in the North Atlantic animals), on average 0.58–0.59. This ratio changes slightly with age; it is neither dependent on sex nor geographical region, nor does it demonstrate any temporal variation.

On the contrary, the proportions of skull length measurements change significantly during the first years of life. In particular, the ratio index of upper tooth rows increases by 4–5% of the condylobasal length in adults relative to calves, while the braincase division ratio index declines by approximately the same value. Proportions of the posterior part of the facial region do not change (Table 8; Figure 2).

Correlations of skull measurements

Correlation pleiades

'Correlation pleiades' (term introduced by Terentyev, 1959) are clusters of characteristics interconnected by relatively strong correlation links while having weaker correlations with other clusters. Four correlation pleiades, two major and two minor ones, were identified (Figure 9):

1. Measurements associated with facial division length (ROSTRLEN): rostrum length, lengths of upper and lower tooth rows, facial division length, distance from the tip of the rostrum to the external nares, lengths of the anterior parts of premaxillae, mandible length, ramus heights and also foramen magnum height.
2. Measurements associated with skull width (WIDTH): zygomatic width, orbital width, postorbital width, rostrum widths at the base and the mid-point, parietal width, occipital width and maximum skull height.
3. Measurements associated with the braincase base (BRAIN): brain division length, basioccipitale length and foramen magnum width.
4. Condylar heights (COND).

In addition, certain 'inter-pleiad' measurements can be associated with several pleiades simultaneously or alternately:

1. Condylar width (C).
2. Orbit length (ORBIT).
3. Length of the ramus (in a narrow sense) (MANBRAN).
4. Distance between foramina supraorbitale (POSTMAX).
5. Length of the posterior part of the rostrum (ROSTBACK).

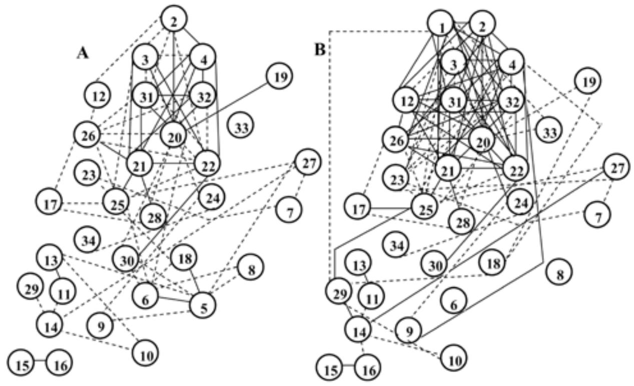

Figure 10. Graph of partial correlations in the porpoise skull adjusted (A) for the condylobasal length impact; and (B) for the zygomatic width impact (age of 0.1–1 years, both sexes). __________, r>0.6; ----------------, 0.6>r>0.4.

Measurements of bulla tympani and the nasal bones are not involved in any pleiad. Bulla tympani size does not correlate with any skull measurements, and lengths of the nasals have few correlations with various measurements in different sex and age groups.

Correlation patterns change over lifetime. In animals at the age of 0.1–1 years the greatest number of correlation links is observed. Measurements of the facial bones (ROSTRLEN pleiad) are the most closely correlated; orbit and ramus lengths are associated with them. The WIDTH pleiad is well expressed, when adjusted for the condylobasal length impact. When adjustment is made for the impact of zygomatic width, only a few links of this pleiad remain; so width measurements and their correlations are strongly determined by the maximum skull width. The WIDTH pleiad is connected with the ROSTRLEN pleiad by a number of correlations, including links with 'inter-pleiad' measurements (POSTMAX, ROSTBACK). In addition, the WIDTH pleiad is connected with the BRAIN pleiad through a number of measurements, e.g. condylar width. Thus, the skull correlation pleiades are interconnected in early life (Figure 10).

The pattern of correlations then changes significantly. In males and females aged 1–2 years, the weak links disappear, and only the strong positive correlations remain. In males they are not numerous: four separate pleiades are observed (ROSTRLEN, WIDTH, BRAIN, COND), and the WIDTH pleiad is expressed only in the correlations adjusted for condylobasal length impact. Many measurements are 'isolated', i.e. do not correlate with others. In particular, orbit length (ORBIT) in males has no partial correlations in neither this nor any older age group. In females, on the contrary, strong correlations are numerous, and all skull measurements are, in fact, united into one pleiad: only the BRAIN pleiad is autonomous. A close link between zygomatic width and maximum skull height is evident in young animals of both sexes (Figure 11).

In adult animals (three years and more) partial correlations between skull measurements become weaker, and most of the links are weak (r <0.6). In males, ROSTRLEN pleiad remains; while the WIDTH pleiad fuses with BRAIN and COND. Thus, another large pleiad—'braincase pleiad'—is

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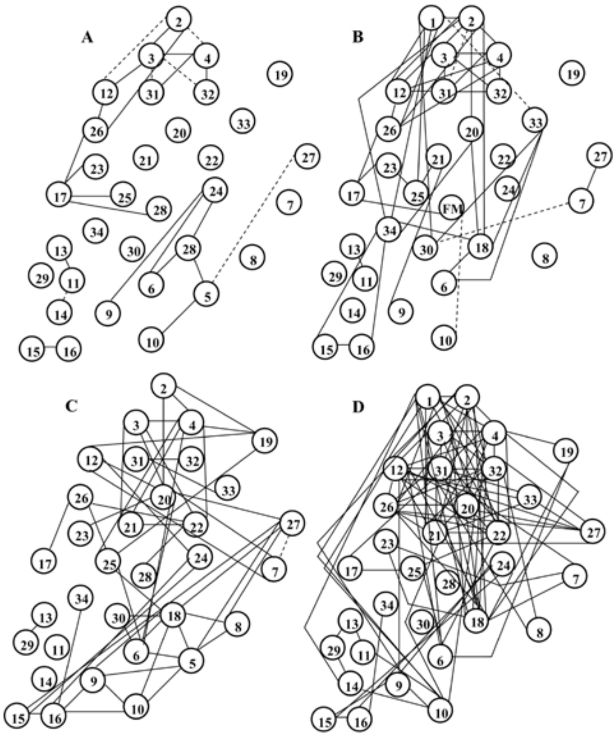

Figure 11. Graph of partial correlations in the porpoise skull adjusted (A) for the condylobasal length impact (males); (B) for the zygomatic width impact (males); (C) for the condylobasal length impact (females); and (D) for the zygomatic width impact (females) (age of 1–2 years), __________, r>0.6; ----------------, 0.6>r>0.4.

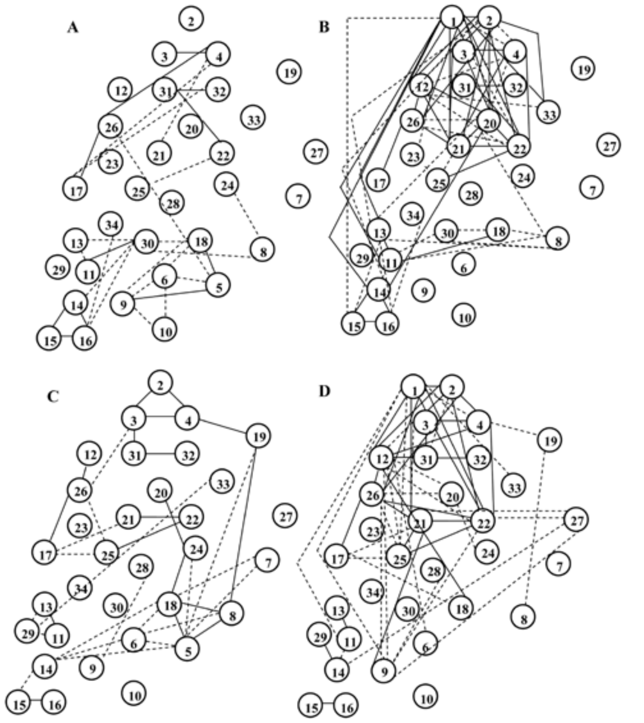

Figure 12. Graph of partial correlations in the porpoise skull adjusted (A) for the condylobasal length impact (males); (B) for the zygomatic width impact (males); (C) for the condylobasal length impact (females); and (D) for the zygomatic width impact (females) (age of 3 years and more). ________, r>0.6; -----------, 0.6>r>0.4.

formed. These two pleiades are interconnected by a few measurements, determining total skull size, e.g. condylobasal or mandible length. Correlation links of measurements characterizing total skull size are determined exclusively by the condylobasal length. Among such measurements are rostrum length, facial division length, mandible length, vomer length and occipital width. In females, unlike in males, the pleiades are relatively separate. BRAIN and COND pleiades are observed. The WIDTH pleiad is distinct when adjusted for the impact of condylobasal length (Figure 12).

The length of the prenarial region has a remarkable place in the ROSTRLEN pleiad. In addition to the distance from the rostrum tip to the nares (of which it is a part), it has stable partial correlations in various sex and age groups with ramus heights only, and also with foramen magnum height in young animals. Adjustments for condylobasal length or zygomatic width do not affect these correlation links.

Principal components

Analysis of correlation links with the help of principal component analysis generally confirms the regularities found while studying correlation pleiades. When dealing with various age and sex groups, eight principal components were analysed. 90–94% of the total variance at the age of 1–2 years and 76–79% at the age of 3 years and more were explained.

Four groups of measurements forming the same principal component at various ages can be distinguished (Tables 12–15):

1. Facial division length and measurements associated with it: condylobasal length, rostrum length, lengths of the upper tooth rows and distance from the tip of the rostrum to the external nares. This corresponds to the ROSTRLEN pleiad. These measurements are included in the 1st component in males of 1–2 years, males and females of three years and older and in the 2nd component in females of 1–2 years.

The length of the anterior part of the right premaxilla and the vomer length also belong to this group, whereas they contribute to a separate sixth component in males of three years and older.

2. Measurements associated with skull width: zygomatic width, orbital width, postorbital width, rostrum widths at the base, parietal width and occipital width. This corresponds to the WIDTH pleiad. These measurements are included in the 1st component in females of 1–2 years, in the 1st and 2nd components in males of 1–2 years, in the 2nd component in females of three years and older and in the 3rd (except parietal width) in males of three years and older.

3. Measurements associated with the braincase base: brain division length, basioccipitale length, foramen magnum width. This corresponds to the BRAIN pleiad. These measurements are included in the 2nd component in males of three years and older, in the 3rd component in males and females of 1–2 years, and in the 6th in females of three years and older. Foramen magnum width is included into this group in females only.

4. Condylar heights. This corresponds to COND pleiad. These measurements are included in the 1st component

Table 12. *Principal components for correlations of skull measurements (males, age 1–2 years).*

Measurement	Component 1	2	3	4	5	6	7	8
AGE	**0.782**	0.134	0.309	0.112	−0.144	−0.081	0.274	0.074
1	**0.784**	0.490	0.069	0.043	0.319	0.033	−0.016	0.083
2	**0.852**	0.312	−0.234	−0.190	0.224	0.141	−0.048	0.003
3	**0.898**	0.195	−0.211	0.147	0.208	0.150	0.058	0.006
4	**0.927**	0.011	−0.099	0.248	0.156	0.180	0.014	0.039
5	**0.517**	0.386	0.184	0.224	0.218	0.457	0.309	0.193
6	**0.618**	0.577	−0.060	−0.088	0.231	0.318	0.144	−0.023
7	0.452	**0.520**	0.423	0.299	0.263	−0.002	−0.105	−0.129
8	0.115	**0.734**	0.104	0.114	−0.160	0.083	0.375	0.166
9	0.495	0.110	0.371	0.142	0.167	**0.653**	−0.039	−0.085
10	0.159	0.277	0.158	0.361	0.019	0.408	0.436	**0.470**
11	−0.181	0.265	**0.824**	0.103	0.064	0.015	0.316	−0.022
12	**0.816**	0.408	−0.202	0.068	0.292	−0.023	−0.015	0.067
13	−0.393	0.037	**0.831**	−0.063	−0.080	0.136	0.008	0.007
14	0.404	0.405	0.414	**0.494**	0.178	0.252	−0.127	0.086
15	0.326	**0.813**	0.120	0.058	0.002	0.279	−0.281	−0.032
16	0.373	**0.762**	0.238	0.015	0.103	0.071	−0.204	0.055
17	0.392	0.163	−0.196	**0.750**	−0.290	−0.097	−0.143	0.024
18	**0.706**	0.534	0.014	−0.029	0.229	0.343	0.055	−0.078
19	0.108	0.492	−0.285	−0.045	0.463	0.002	**0.538**	0.132
20	**0.757**	0.299	−0.022	−0.182	0.252	0.270	0.089	0.266
21	**0.694**	−0.032	−0.103	−0.036	−0.302	−0.482	−0.207	0.193
22	0.378	0.120	−0.141	0.086	**0.789**	0.077	−0.164	0.115
23	0.237	0.450	0.045	**0.691**	0.228	0.016	−0.040	0.081
24	0.194	0.462	0.029	−0.135	−0.017	**0.784**	0.007	−0.014
25	**0.733**	0.356	0.152	0.314	0.007	−0.106	−0.038	0.286
26	**0.881**	0.306	−0.258	0.175	0.039	0.029	−0.092	0.012
27	**0.570**	0.459	0.252	0.323	0.271	0.271	0.117	−0.094
28	−0.212	−0.020	−0.217	0.390	**−0.701**	−0.320	−0.126	0.199
29	0.106	−0.014	0.046	0.065	−0.057	−0.168	−0.125	**0.953**
30	**0.550**	0.405	0.149	0.111	**0.568**	−0.148	0.171	−0.153
31	0.029	−0.278	0.008	−0.044	−0.045	0.000	**0.891**	−0.174
32	**0.866**	0.028	0.039	0.358	0.187	−0.067	0.116	0.079
33	**0.778**	0.052	−0.019	0.338	0.043	0.351	−0.005	0.098
34	0.401	**0.690**	−0.152	2·10-6	0.377	0.068	−0.152	0.114
35	0.366	0.147	**0.443**	−0.033	−0.114	**−0.563**	0.388	0.365
36	−0.104	**0.447**	−0.173	**−0.821**	0.095	−0.046	−0.179	−0.042
37	**0.411**	0.056	**−0.703**	0.029	0.356	−0.084	0.364	−0.101

Loading coefficients are presented in columns. Maximum (in modulus) loading coefficients for each measurement are bold-typed.

Table 13. *Principal components for correlations of skull measurements (females, age 1–2 years).*

Measurement	Component 1	2	3	4	5	6	7	8
AGE	0.462	−0.048	**0.719**	−0.030	0.327	−0.004	−0.141	0.141
1	0.403	**0.789**	0.438	0.090	0.016	−0.022	0.042	0.006
2	0.402	**0.860**	0.183	−0.003	−0.072	0.161	0.106	0.134
3	0.296	**0.853**	0.300	0.072	0.136	0.088	0.226	0.083
4	0.364	**0.862**	0.097	0.044	0.106	0.090	0.247	0.149
5	**0.904**	0.146	0.133	0.106	0.068	−0.110	0.171	−0.085
6	**0.862**	0.290	0.125	−0.040	0.296	−0.069	0.108	0.074
7	**0.524**	0.457	−0.219	0.481	0.029	−0.023	0.117	0.421
8	**0.755**	0.497	0.071	−0.023	−0.100	0.039	−0.128	−0.286
9	**0.855**	0.346	0.206	0.140	−0.113	−0.025	−0.040	0.200
10	0.545	**0.623**	0.185	0.234	−0.347	−0.113	0.187	−0.193
11	0.201	0.280	**0.821**	−0.060	−0.151	−0.323	−0.069	−0.102
12	0.431	**0.876**	0.148	0.085	−0.053	0.029	−0.028	0.049
13	0.173	0.098	**0.910**	0.075	0.220	−0.081	0.173	−0.128
14	0.286	0.434	**0.657**	0.189	−0.291	0.241	0.012	0.142
15	**0.824**	0.183	0.137	0.379	−0.135	−0.076	−0.188	0.092
16	**0.856**	0.253	0.071	0.201	−0.199	0.124	−0.225	−0.057
17	0.338	0.462	0.197	0.218	**0.625**	−0.138	0.086	−0.295
18	**0.870**	0.432	0.073	0.100	0.122	−0.008	0.086	0.034
19	**0.587**	**0.574**	−0.033	−0.309	0.253	0.161	0.051	0.098
20	**0.722**	0.379	0.220	0.015	0.249	0.181	0.031	0.412
21	−0.089	**0.633**	0.191	−0.007	0.122	**0.671**	0.186	0.149
22	0.400	0.457	0.118	−0.057	**0.501**	0.337	0.393	0.171
23	**0.542**	0.509	−0.014	0.118	0.083	−0.239	0.364	0.320
24	**0.695**	0.069	0.379	0.019	−0.046	−0.042	−0.355	0.455
25	**0.603**	0.488	−0.132	−0.140	0.332	0.025	0.436	−0.172
26	0.369	**0.871**	0.222	0.079	0.137	0.037	0.102	−0.026
27	**0.852**	0.356	−0.033	0.275	0.159	0.016	0.001	−0.111
28	0.183	0.067	0.075	−0.052	**0.883**	0.019	−0.067	0.072
29	0.038	0.425	**0.557**	0.105	0.086	0.343	**0.566**	−0.094
30	**0.812**	0.182	0.126	−0.174	0.199	−0.210	0.250	0.122
31	0.202	0.047	0.068	**0.962**	0.050	−0.050	0.047	−0.035
32	0.229	**0.836**	−0.144	0.293	0.069	0.199	−0.223	−0.199
33	0.149	**0.865**	−0.048	0.235	0.247	0.064	−0.182	−0.213
34	**0.703**	0.354	0.236	0.273	0.352	0.183	0.009	−0.212
35	0.440	0.343	0.090	**0.792**	−0.028	0.075	−0.043	−0.055
36	0.251	−0.025	−0.069	−0.224	**−0.705**	0.259	−0.481	0.060
37	0.106	−0.320	0.120	−0.154	−0.016	**−0.845**	0.073	0.009

Loading coefficients are presented in columns. Maximum (in modulus) loading coefficients for each measurement are bold-typed.

in females of 1–2 years, in the 2nd component in males of 1–2 years and females of three years and older, in the 4th in males of three years and older. In animals three years and older, condylar width is included into this group.

In males at the age of 1–2 years, the 1st component includes measurements of facial division length and some width measurements. The 2nd component includes height measurements (with condyles heights); the 3rd component includes skull base measurements. Minor components are mainly contributed by groups of posterior facial measurements. In females, the 1st component includes measurements of skull width and height, mandible length and condylar heights; the 2nd component includes facial length measurements, while, the 3rd includes skull base measurements and the age value (Tables 12&13).

In animals at the age of three years and older, the 1st component includes measurements of facial division length. The 2nd component includes width and occipital measurements, and in males also some measurements of width, height, skull base and some facial measurements. In males, the 3rd component consists of width measurements, in females it consists of mandible and orbit measurements, and skull height. Minor components are contributed by various small groups of measurements: anterior facial structures, occipital region, and foramen magnum (Tables 14&15).

Some principal components are contributed by pairs of measurements: maximum skull height and orbit length; length of the anterior part of the right premaxilla and vomer length; foramen magnum height and width; lengths of the prenarial region and the posterior part of the rostrum. Many

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Table 14. *Principal components for correlations of skull measurements (males, age 3 years and more).*

Measurement	Component							
	1	2	3	4	5	6	7	8
AGE	−0.154	−0.208	−0.001	0.099	0.168	−0.022	0.074	**0.804**
1	**0.827**	0.282	0.162	0.276	−0.057	0.147	0.158	0.080
2	**0.772**	0.052	0.322	0.322	−0.094	0.138	0.258	−0.025
3	**0.769**	0.061	0.268	−0.176	0.027	0.081	0.319	−0.316
4	**0.726**	0.122	0.171	−0.273	−0.005	0.239	0.373	−0.243
5	0.347	0.225	**0.684**	0.028	−0.261	0.113	0.236	0.059
6	−0.010	0.423	**0.690**	0.054	−0.075	−0.187	0.038	0.080
7	**0.735**	−0.151	0.272	−0.134	−0.080	−0.332	−0.197	−0.122
8	0.471	**0.637**	0.099	0.082	0.166	−0.163	−0.342	−0.030
9	0.152	0.216	**0.729**	0.205	−0.203	0.102	0.289	0.016
10	−0.061	−0.150	**0.753**	0.096	0.305	0.151	−0.239	0.168
11	0.222	**0.712**	0.169	0.179	0.081	0.035	0.211	0.217
12	**0.881**	−0.073	0.144	0.130	−0.042	0.243	−0.045	0.170
13	0.392	**0.622**	0.119	0.303	−0.118	0.057	0.266	0.039
14	0.440	0.467	0.015	**0.511**	−0.076	0.220	0.337	0.155
15	0.159	0.358	0.101	**0.791**	0.045	0.079	0.238	−0.018
16	0.184	0.410	0.145	**0.757**	−0.024	0.047	0.237	−0.030
17	0.382	0.066	−0.097	**−0.610**	−0.456	0.153	0.200	0.038
18	0.290	**0.542**	**0.569**	−0.018	−0.179	−0.017	0.090	−0.072
19	0.257	0.132	0.059	0.171	**0.387**	−0.176	0.243	0.122
20	**0.825**	0.306	−0.134	0.086	0.230	0.073	0.026	−0.099
21	**0.747**	−0.029	−0.192	0.000	0.312	0.280	0.148	0.182
22	**0.605**	0.195	0.075	−0.072	−0.049	0.335	0.127	−0.344
23	**0.399**	0.275	0.168	−0.073	**0.375**	0.381	−0.237	0.004
24	0.071	**0.483**	−0.006	0.217	−0.402	−0.419	−0.074	−0.278
25	0.209	0.127	0.004	0.003	0.294	**0.812**	−0.004	0.034
26	**0.769**	0.135	0.142	−0.171	−0.353	0.212	0.313	−0.050
27	0.388	0.323	**0.632**	0.094	0.014	−0.057	−0.222	−0.144
28	0.157	0.011	0.084	0.044	−0.007	−0.126	**0.807**	0.063
29	0.415	−0.086	−0.117	0.141	−0.112	0.208	**0.589**	−0.186
30	−0.131	**0.861**	0.133	0.206	−0.007	0.129	−0.152	0.004
31	−0.099	**0.525**	0.166	−0.093	0.104	−0.013	0.000	−0.132
32	0.356	−0.075	0.065	0.023	−0.297	**0.733**	−0.034	−0.168
33	0.446	−0.142	−0.031	0.041	−0.532	**0.618**	0.048	−0.048
34	**0.516**	−0.208	0.059	0.466	0.288	−0.236	−0.122	0.172
35	0.015	−0.159	−0.012	−0.043	**0.711**	0.014	−0.035	0.087
36	−0.238	−0.077	0.038	**0.710**	−0.126	−0.080	−0.224	0.395
37	−0.029	0.019	−0.400	0.249	**0.543**	0.208	0.270	0.065

Loading coefficients are presented in columns. Maximum (in modulus) loading coefficients for each measurement are bold-typed.

Table 15. *Principal components for correlations of skull measurements (females, age 3 years and more).*

Measurement	Component							
	1	2	3	4	5	6	7	8
AGE	0.060	−0.076	0.124	0.158	**0.793**	0.175	−0.015	0.075
1	**0.652**	0.555	0.192	0.243	0.089	0.267	−0.074	−0.021
2	**0.706**	0.426	0.056	0.310	0.076	0.008	0.049	−0.239
3	**0.661**	0.418	0.030	0.453	−0.209	0.129	0.054	−0.057
4	**0.589**	0.407	0.278	0.224	−0.460	0.130	0.051	−0.105
5	0.372	**0.676**	0.435	0.165	0.127	0.213	0.063	0.005
6	0.414	**0.545**	0.314	0.367	0.193	0.040	0.045	−0.007
7	0.081	**0.600**	0.439	0.045	−0.118	0.248	0.132	0.063
8	−0.031	0.449	**0.632**	0.237	−0.187	0.337	−0.057	−0.107
9	0.554	**0.605**	−0.073	0.121	0.288	0.034	−0.094	0.328
10	0.355	**0.563**	0.209	0.088	0.452	0.069	−0.224	−0.174
11	0.261	0.374	0.082	0.049	−0.148	**0.767**	−0.064	0.024
12	**0.672**	0.505	0.184	0.305	−0.100	−0.144	−0.290	0.048
13	0.107	0.121	0.014	−0.124	0.280	**0.803**	0.225	−0.083
14	0.277	**0.680**	0.261	0.006	0.082	0.362	0.092	0.177
15	0.200	**0.792**	0.133	0.129	−0.266	0.007	0.220	0.063
16	0.275	**0.794**	0.088	0.008	−0.198	0.013	0.104	−0.036
17	0.323	−0.041	−0.121	−0.121	−0.230	−0.028	−0.256	**0.681**
18	0.451	**0.517**	0.427	0.324	0.011	0.268	0.120	0.161
19	0.091	0.123	**0.602**	0.174	−0.523	0.128	0.181	−0.009
20	0.503	0.169	**0.626**	−0.072	0.086	−0.109	−0.151	0.055
21	**0.791**	0.163	−0.127	0.036	−0.012	0.125	0.174	0.250
22	**0.894**	0.110	0.000	−0.071	0.000	0.118	−0.066	−0.123
23	0.458	0.327	**0.686**	−0.214	0.140	0.035	−0.071	0.006
24	−0.167	0.075	**0.764**	0.037	0.051	−0.059	0.117	−0.056
25	**0.821**	0.076	0.123	−0.092	0.005	0.199	−0.119	0.129
26	**0.785**	0.289	0.075	0.175	−0.173	−0.094	−0.099	0.288
27	0.466	**0.501**	0.219	−0.037	−0.007	0.331	0.047	0.359
28	−0.003	0.218	−0.314	**−0.615**	0.080	−0.307	0.222	0.384
29	−0.089	0.170	−0.034	**−0.625**	−0.161	**0.462**	−0.259	0.148
30	0.268	**0.473**	0.389	0.145	0.250	0.143	0.004	0.443
31	0.116	0.231	0.070	0.243	0.386	0.211	0.081	**0.621**
32	0.203	0.223	−0.153	**0.807**	−0.024	−0.111	0.110	0.041
33	−0.032	0.300	0.129	**0.735**	−0.054	0.043	−0.107	0.245
34	0.237	**0.619**	−0.144	0.054	−0.045	0.332	−0.395	0.001
35	0.279	0.131	0.061	0.001	0.215	0.253	−0.293	**−0.593**
36	−0.279	−0.103	−0.116	−0.275	**0.744**	−0.133	0.008	−0.261
37	0.080	0.178	0.228	0.084	0.141	−0.014	**0.753**	0.132

Loading coefficients are presented in columns. Maximum (in modulus) loading coefficients for each measurement are bold-typed.

of these paired measurements are topographically close to each other.

The major principal components are only associated with the age value at the age of 1–2 years: in males, age is associated with the 1st component characterizing fast-growing structures, while in females it is associated with the 3rd component characterizing braincase measurements completing their growth.

Relationships between growth and correlations

During the first year of life, the period of intensive growth of most structures, correlations between the various measurements are highly diverse. The length measurements in the facial division displaying the highest growth rates closely correlate with each other and with condylobasal length. Weaker correlations exist between the measurements differing in growth rate that are topographically close and thus growing concurrently for a certain period. Finally, some correlations are caused merely by similar growth rates during a certain period. For example, correlations between rostrum width at the mid-point and braincase measurements in the first year of life are caused by their relatively low growth rates. Later, most of these correlations disappear as a result of emerging differences in growth rates. For example, the length of the ramus (in a narrow sense) correlates with the length of the posterior part of the rostrum during the first year of life (Figure 10).

After the first year of life, growth in skull length is primarily determined by growth of the central and anterior

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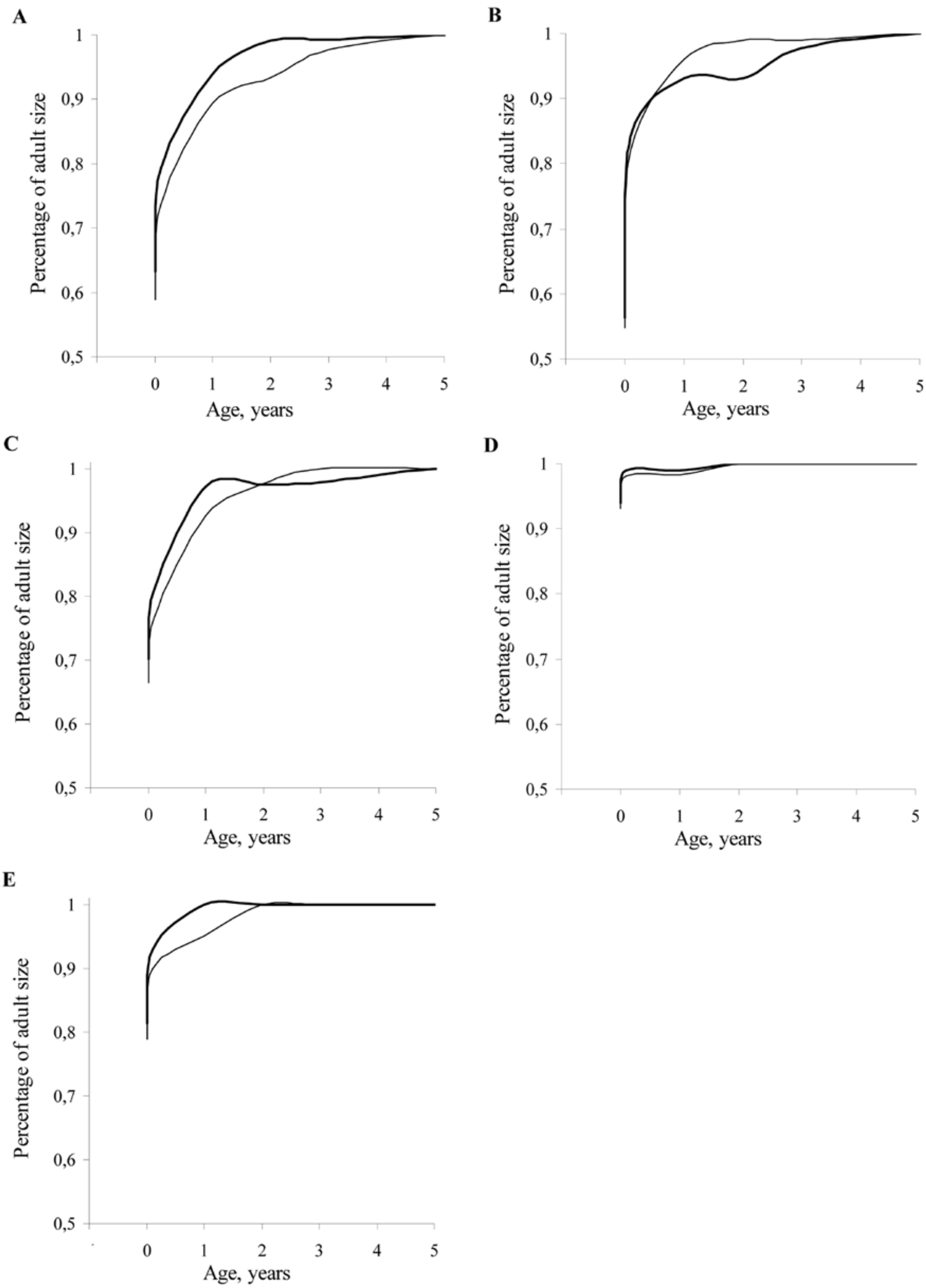

Figure 13. Examples of growth of the structures associated with (A) feeding; (B) breathing; (C) vision; (D) hearing; and (E) brain, percentage of definitive size. Growth of males is indicated with bold lines, females with thin lines.

parts of the rostrum, while growth in skull width and height is proportional to growth in length (see above). Thus, until a certain time, growth in length of the anterior facial region remains concurrent with growth in skull width and height. This is clearly seen in males at the age of 1–2 years: length, width and height measurements contribute to the 1st principal component. In this period, the male skull grows intensively and almost reaches its definitive size. The 1st principal component includes measurements of intensively growing structures, while the 2nd one includes measurements of bones completing or having completed their growth (condylar heights, vomer length). In females at the age of 1–2 years, on the contrary, the rate of skull growth in length slows down compared to growth in skull width. In particular, the mean increase in rostrum length in females in the second year of life is 4.6 mm (in males 5.6 mm), while the mean increase in postorbital width is 7.8 mm (in males 4.8 mm). As in males, the 1st principal component is made up by measurements of rapidly growing bones; however, unlike in males, these are measurements of skull width, ramus length and height, condylar height, and the correlations between them are determined by the impact of skull width (Table 13; Figure 11).

While growth is ceasing, total skull size becomes the main factor affecting the size of certain structures. Sizes of major structures, which have complicated growth patterns and determine the total skull size, do not depend any more on the size of their parts, which have grown intensively for a certain period. Sizes of such structures are less variable than the definitive sizes and ratios of their contributing parts (like the tooth rows and the posterior part of the rostrum, or the tooth rows and the ramus in a narrow sense). Total skull size becomes the only factor determining size ratios of these major structures. That is why such measurements as rostrum length, facial division length and mandible length 'fall out' from correlation pleiades adjusted for condylobasal length impact. Similarly, skull width measurements during the period of isometric growth are primarily determined by the total skull size, namely by parameters of its maximum width (Figures 11&12).

Thus, six groups of measurements differing in the structure of correlation links during the growth process can be identified in the harbour porpoise skull:

1. Measurements of facial division length.
2. Measurements of skull width and height.
3. Measurements of braincase base and brain division length.
4. Condylar heights.
5. Measurements of nasal bones.
6. Measurements of bulla tympani.

Most of these groups (except for the skull width measurements) can be interpreted as structures located close to each other. Another factor is the overall skull size: it strongly affects skull width measurements as well as facial length measurements.

Some measurements, such as condylar width, prenarial region length, orbit length, ramus length, length of the posterior part of the rostrum and foramen magnum height, have a specific place in the system of correlations being associated with several groups or with none of them during the majority of the lifespan. It should be noted that most of these measurements are located in the posterior part of the facial region.

DISCUSSION

Growth, correlations and functional components

When studying variation in skulls of spotted and spinner dolphins *Stenella attenuata* and *Stenella longirostris*, Perrin (1975) defined five main functional components in the marine mammal skull: structures associated with feeding, breathing and sound generation, vision, hearing and the braincase.

According to Perrin (1975), at the moment of birth the structures associated with hearing and some structures associated with breathing and sound generation are the most developed; they are followed by the vision apparatus, the braincase, certain structures associated with breathing and structures associated with feeding. As a result, the slowest growth rates and the shortest growth terms are seen in the structures associated with hearing, and the highest rates and longest terms are found in the structures associated with feeding; a very long growth period is also observed in the braincase. The structures associated with several functional components simultaneously demonstrate intermediary patterns. For example, the posterior part of the mandible, which is associated with both hearing and feeding, has an intermediary position between the two components in the growth rate and growth period.

This study demonstrates that growth patterns of functional components of the harbour porpoise skull are similar to the regularities described above (see Figure 13). However, some differences can be observed. First, the growth of many structures ceases after sexual maturation, while in *Stenella* it stops at the time of maturation. Second, braincase growth terminates much earlier than the growth of the structures associated with feeding. Third, the structures associated with breathing grow faster and demonstrate greater increments than the structures associated with feeding, while the latter ones grow for a longer time. Finally, the growth patterns and size values of width measurements in the structures belonging to different functional components are closer to each other than to other measurements and structures associated with the same components.

The functional components of the skull allow explanation of some aspects of growth of the posterior part of the facial region. The nasal bones, the prenarial region and the posterior part of the rostrum are associated with breathing and sound generation. Their intensive growth during the first weeks of life is caused by growth of the nasal sacs participating in the sound generation. The variation of lengths of the prenarial region and the posterior part of the rostrum is very high, while the variation of their combined length is much lower in all age and sex groups. Accordingly, they should be analysed as a functional unit, although their sizes do not correlate.

Thus, the posterior part of the rostrum appears to be a key element in the composition of two long-growing structures with little variation: the rostrum and the bony base of the air pathways. It should be noted that the posterior part of the rostrum does not grow after the first weeks of life, and its length correlates neither with the size of the structures of which it is a part, nor with the sizes of other components of these structures.

Growth of the structures associated with breathing and sound generation influences growth patterns of all elements of the posterior part of the facial region independent of their functional role, e.g. orbit and ramus (in a narrow sense).

Sexual dimorphism, which is common in the structures of the facial region, is not observed in measurements of the structures associated with breathing and sound generation. In addition, growth of the structures of the prenarial region associated with vision as well as with breathing, demonstrates unusual patterns of sexual differences. Unlike the measurements of the rostrum, the braincase and the skull width, growth of these structures stops earlier in females than in males (at the age of about two years). Due to this pattern, males 'catch up' with females during the third year of life. In some measurements (prenarial region length, orbital width), males demonstrate a growth pause, which is later followed by a secondary spurt coinciding with sexual maturation (see above). Such a growth pattern may be explained by increasing communication activity in males attaining maturation.

Thus, three main factors determining the growth patterns and the definitive size of skull structures can be defined:

1. Overall skull size.
2. Mutual topographical proximity of structures.
3. Association with a functional component.

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