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Postnatal cranial growth of Risso's dolphin (*Grampus griseus*)

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Abstract: The short-nosed Risso's dolphin (*Grampus griseus*) is the fifth largest member of Delphinidae, but is one of the least studied dolphin species. We studied the postnatal ontogeny and sexual dimorphism of the skull of Risso's dolphin by applying linear bivariate and multivariate analyses of allometry and discussing our findings in a comparative and functional framework. Comparing a representative of the Globicephalinae subfamily (a typically short-nosed group) with previously studied cetaceans belonging to different families is important for evaluating variations in the growth of splanchnocranium and neurocranium in cetaceans. Results of bivariate and multivariate approaches were mostly similar. The trophic apparatus showed positive allometry or isometry, whereas negative allometry was observed in neurochranial components and in width of external nares. We detected sexual dimorphism in the growth pattern of cranial variables related to trophic functions, suggesting slight differences in the mechanics of the trophic apparatus. Our results indicate a very low degree of sexual dimorphism in skull growth compared with other dolphins with most dimorphic growth rates favoring females; this result can be related to the earlier acquisition of an optimal performance in females, which is important for reproductive requirements. The growth of the splanchnocranium, and especially of those characters associated with the trophic function, exhibits a pattern of higher growth rate than neurochranial components, regardless of the short face of *G. griseus*.

Keywords: allometry; *Grampus*; ontogeny; skull.

Introduction

Cetaceans are specialized mammals, adapted both in their anatomy and physiology, to an entirely aquatic life (e.g. Howell 1930, Slijper 1961, Gaskin 1982). Unlike other mammals, newborn cetaceans represent an extremely precocial state of development, resulting in a suitable morphology and physiology for swimming immediately after birth (e.g. Ito and Miyazaki 1990, Rauschmann et al. 2006, Li et al. 2007, Montie et al. 2007). Among the most important acquisitions in cetacean evolution and development are the increase in brain size (e.g. Oelschläger and Buhl 1985, Oelschläger and Kemp 1998, Marino et al. 2001, Oelschläger et al. 2008, Oelschläger and Oelschläger 2009, Hadad et al. 2012), the obtaining of an hydrodynamic body shape (Pabst et al. 1999, Richardson and Oelschläger 2002), deep modifications of the facial and ear complex, (such as the isolation of the tympano-periotic complex from the skull by means of the development of air sinuses; Mead 1975, Klima 1999, Luo and Gingerich 1999, Ketten 2000, Fordyce and de Muizon 2001), and skull telescoping (Miller 1923, Mead 1975, Oelschläger 2000). Despite all those specializations for an entire aquatic life, odontocete embryos show the general mammalian bauplan (Kemp and Oelschläger 2000, Hadad et al. 2012).

Ontogenetic changes of the skull and their relationship with chronological age in prenatal and postnatal cetaceans were comprehensively documented in several species using different approaches (e.g. *Stenella*: Perrin 1975, Ito and Miyazaki 1990, *Tursiops*: Marino et al. 2001, Kurihara and Oda 2009, *Grampus*: Chen et al. 2011a,b, Phocoenidae: Galatius et al. 2011, Delphinidae: Hadad et al. 2012, *Pontoporia*: del Castillo et al. 2014, 2015, *Cephallorhynchus*: del Castillo et al. 2016). Results of the above-mentioned works demonstrate that, in general terms, the trophic apparatus is highly modified during postnatal growth, in comparison with the braincase, whose development occurs principally during prenatal stages. However, skull morphology of cetaceans shows a large diversity in the splanchnocranium and neurocranium, involving shape, size, and basic construction of the feeding apparatus (e.g. Mead 1975, Berta et al. 1999). Accordingly, variations in the growth pattern commonly assigned to species with long rostrum, such as *Tursiops*

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(Kurihara and Oda 2009), *Stenella* (Perrin 1975, Ito and Miyazaki 1990), *Sotalia* (Sydney 2010), *Pontoporia* (del Castillo et al. 2014) and other long-nosed species, should be compared by studying and quantifying postnatal skull growth of a representative of Globicephalinae, such as the Risso's dolphin (*Grampus griseus*), a group characterized by lack of a distinguished rostrum, having a bulbous forehead. On the other hand, the ontogeny of short-rostrum phocoenids, a group with paedomorphic characters, was also studied in detail (McLellan et al. 2002, Galatius 2010, Galatius et al. 2011), providing an appropriate framework for a comparative analysis of the growth pattern in Risso's dolphin.

The Risso's dolphin, the fifth largest member of Delphinidae (4 m in body length, Bearzi et al. 2011), is one of the least studied dolphin species. The newborns from Japanese waters are 25–136 cm in body length (Kasuya 1985, Mead and Potter 1990) and gestation has been estimated in 13–14 months (Kasuya 1985, Evans and Raga 2001). Age at sexual maturity was estimated to be 8–10 years for females and 10–12 years for males, with a body length of 240–255 cm in females and 253–265 cm in males (Amano and Miyazaki 2004, Chen et al. 2011b). However, there seems be variations in data on body size and age, as Bloch et al. (2012) reported an immature female 2 years of age with 268 cm (235 kg), and mature females being notably longer and heavier. On the other hand, fully mature males between 26 and 27 years old have a body length of 304 cm or longer (Bloch et al. 2012). The approximate longevity of *Grampus griseus* was reported to be 34 years (290 cm; Amano and Miyazaki 2004). Sexual dimorphism was not detected (Kruse et al. 1999, Chen et al. 2011b), although studies in Japan suggest a slight sexual dimorphism in body length relative to appendage size (Kishiro 2001), with males possibly reaching greater length than females (Amano and Miyazaki 2004, Chen et al. 2011b). Although the skeletal characters of *G. griseus* have been scarcely studied, the skull was described in detail (Van Bénéden and Gervais 1868, Flower 1874, True 1889, Ross 1984, Yamagiwa et al. 1999, Chen et al. 2011a). However, the growth pattern of the Risso's dolphin was addressed only by Chen et al. (2011a,b), who studied the relationship among age, body length, and sexual maturity, as well as the ontogeny of suture closure of the skull. Differences in skull growth rate, denoting shape changes during development from birth to adult (and its sexual variations), as well as the form-function relationship have been well studied and interpreted in several cetaceans (e.g. Galatius et al. 2011, del Castillo et al. 2014, 2016, Nakamura and Kato 2014). Most of the patterns of postnatal cranial growth described in odontocetes (e.g. Kurihara and Oda 2009, Chen et al. 2011b, Galatius et al. 2011, del Castillo et al. 2014, 2016) have been associated with the development of structures involved in trophic functions, in comparison with the more precocial neurocranium; therefore, our study of a Globicephalinae representative is important because we test the aforementioned pattern in a large-sized but short-nosed species. Here, we analyzed and compared ontogenetic changes and intraspecific differences in skull shape of *G. griseus* by performing bivariate and multivariate analyses of allometry. We discuss our findings in a comparative and functional framework, focusing on the main factors that influence skull shape changes and sexual dimorphism. This is the first report of a quantitative approach to study the growth of cranial traits in the Risso's dolphin and its sexual dimorphism in populations from the tropical northwest Pacific Ocean.

Materials and methods

Sample and measurements

We studied a sample of 47 specimens (23 ♂, 24 ♀) of a well-represented postnatal ontogenetic series of *Grampus griseus* deposited at the Mammal Collection of the National Museum of Nature and Science (NSMT), Tsukuba, Japan (Appendix 1), including young and adult specimens (Figure 1). All specimens in our sample included body length data. The shortest specimens in each sex were 165 cm in body size for females (skull length 350.52 mm; NSMT 24843) and 166 cm for males (skull length 348.61 mm; NSMT 29547), whereas the longest ones were 284 cm for females (skull length 132.76 mm; NSMT 29508) and 289 cm for males (skull length 541.71 mm; NSMT 10507). According to Chen et al. (2011b), our smallest specimen was younger than 1 year old, whereas our largest specimen was a mature individual between 12 and 34 years old (Amano and Miyazaki 2004, Chen et al. 2011b). Although the longevity of *G. griseus* was estimated to be of about 30 years, body size at that age is about 290 cm (Amano and Miyazaki 2004), a size very close to that of our largest specimen. According to body length (Chen et al. 2011b), our sample includes 13 immature males and nine females. The first reproduction in the species (Perrin and Reilly 1984, Kruse et al. 1999) occurs at 11 years old; hence, our sample includes specimens at the period of becoming sexually active. We discard potential geographic variation in our sample because all the individuals are from Japanese waters. Populations from Taiwanese and Japanese waters share similar life history traits (i.e. body size, age at sexual maturity in males and females, and summer-fall calving season), suggesting the existence of a common regional population (Amano and Miyazaki 2004, Chen et al. 2011b). This is an important issue, since some authors (e.g. Gaspari et al. 2007) demonstrated genetic variation of *G. griseus* based on mitochondrial DNA analyses, which could be reflected in morphological differences.

We took 21 cranial measurements (Figure 2) based on Perrin (1975), using a three-dimensional digitizer (Microscribe MX®). We chose measurements that covered the three dimensions of the skull and that involved modules that are not mutually independent in functional terms: the neurocranium and the splanchnochranium. For instance, we addressed, from an allometric perspective, areas for origin and insertion of muscles involved in trophic functions, length, and breadth of the rostrum in different sections, variables associated with nare opening, and others linked to orbits and braincase.

Study of growth

In this report, the time frame is implicitly incorporated (size proxy) but is not specified in order to describe relative modifications as the species grows. Our study of skull growth includes two complementary approaches: bivariate and multivariate allometries, which were applied separately in both sexes in order to obtain statistical data about sexual dimorphism in the growth of each specific

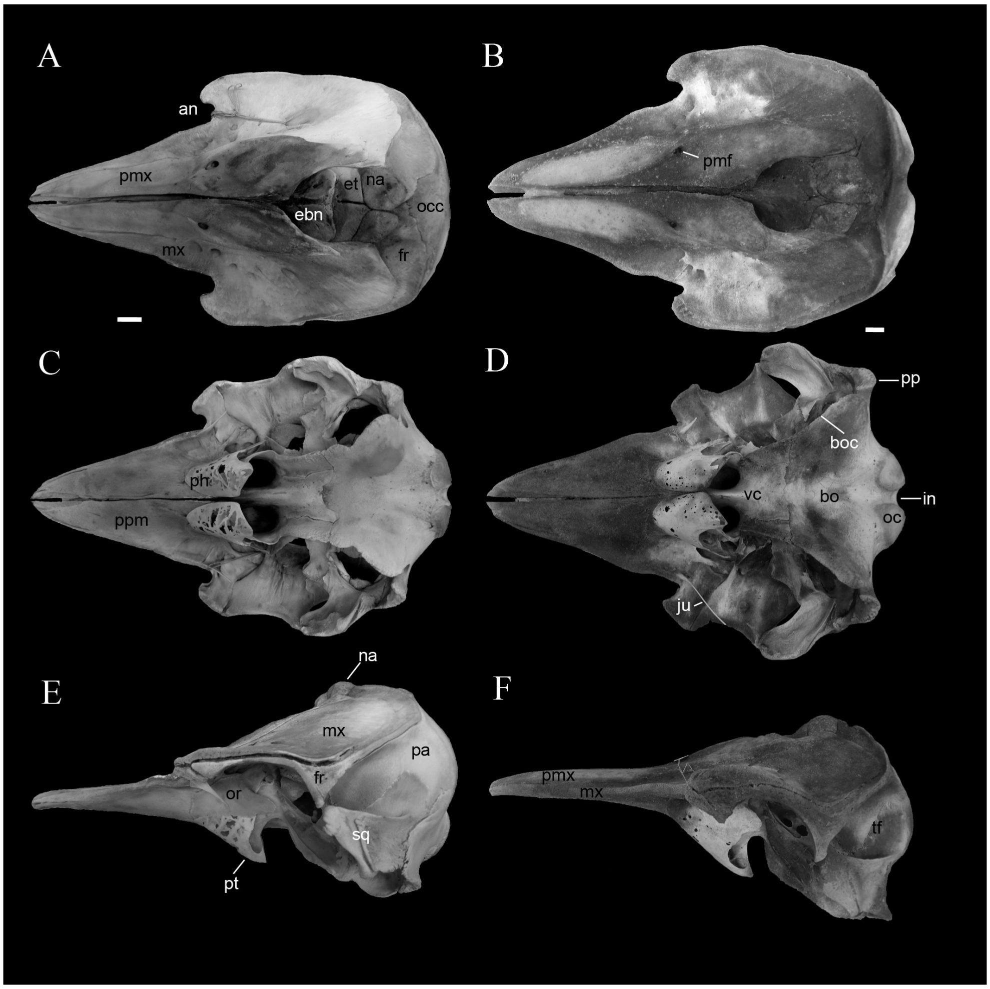

Figure 1: Skull in dorsal, ventral and lateral view of a young (A, C, E; NSMT 24843) and adult (B, D, F; NSMT 29528) Risso's dolphin (*Grampus griseus*).
an, Antorbital notch; bo, basioccipital; boc, basioccipital crest; ebn, external bon nares; et, ethmoid; fr, frontal; ic; infratemporal crest; in, intercondyloid notch; ju, jugal; mf, mandibular fossa; mx, maxilla; na, nasals; oc, occipital condyle; occ, occipital bone; or, orbit; pa, parietal; ph, pterygoid hamulus; pmf, premaxillary foramen; pmx, premaxilla; pp, paraoccipital process; ppm, palatine process of maxilla; pt, pterygoid; sq, squamosal; tf, temporal fossa; vc, vomerine crest. Scale bars = 10 mm.

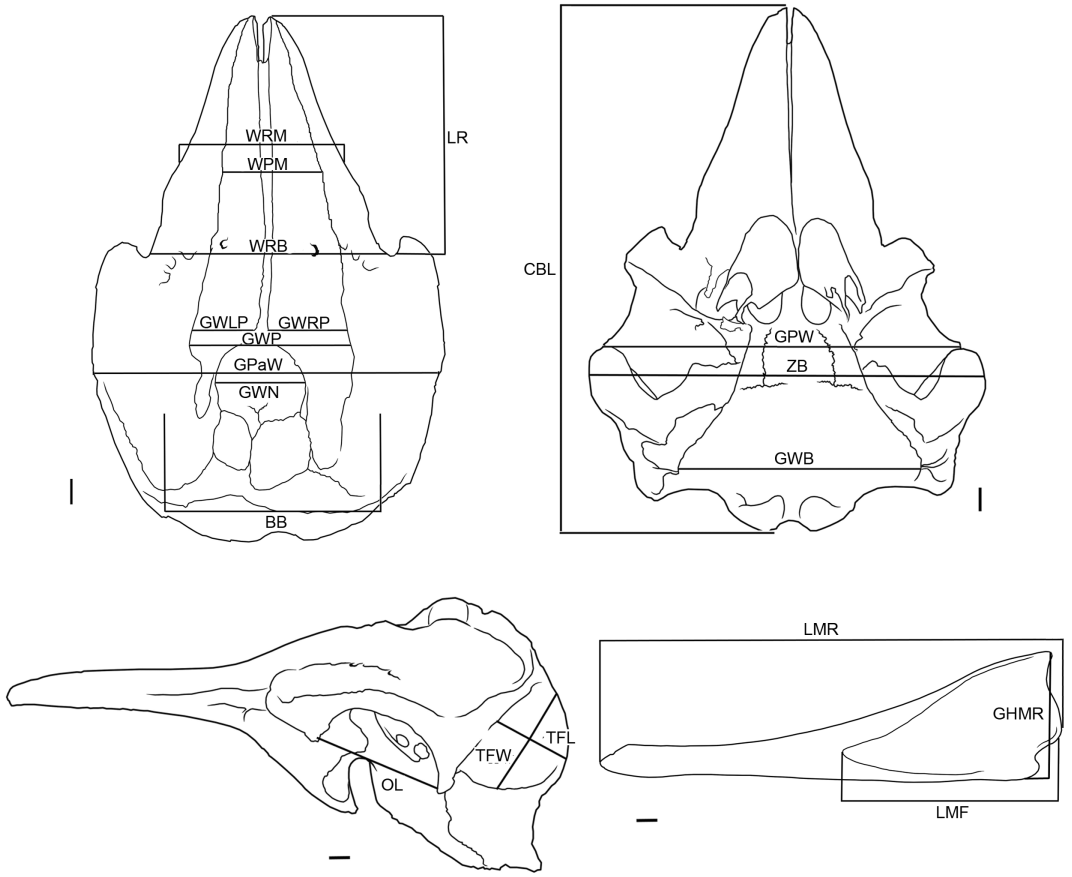

Figure 2: Skull of *Grampus griseus* in dorsal, ventral, lateral, and mandibular views showing measurements analyzed in the analyses. BB, Breadth of the braincase; CBL, condylo-basal length; GHMR, greatest height of mandibular ramus; GPaW, greatest parietal width; GPW, greatest postorbital width; GWB, greatest width of basioccipital; GWLP, greatest width of left premaxillar, GWN, greatest width of external nares; GWP, greatest width of premaxillaries; GWRP, greatest width of rigth premaxillar; LLT, length of lower toothrow; LMF, length of mandibular fossa; LMR, length of mandibular ramus; LR, length of rostrum; OL, orbit length; TFL, greatest length of postemporal fossa; TFW, greatest width of posttemporal fossa; WPM, width of premaxillaries at midlength of rostrum; WRB, width of rostrum at base; WRM, width of rostrum at midlength; ZB, zygomatic breadth.

cranial variable. We performed both approaches because bivariate allometry is suitable for statistical comparison of slopes and intercepts for two regressions (e.g. males and females, see below), whereas multivariate allometry is more realistic, since it considers size as a latent variable affecting all measured variables simultaneously, being less suitable for statistical comparisons of rate values, beyond the allometric trend (Flores et al. 2015). In addition, some qualitative observations in young and adult specimens were done in order to detect changes not covered by our measurements (e.g. development of the pterygoid hamulus).

Bivariate allometry

Under bivariate allometry, we consider the logarithmic (base 10) expression of the power equation of allometry (Alexander 1985, Silva 1998): $\log y = \log b_0 + b_1 \log x + \log e$, where y is any of the measured skull variables, b_0 is the y-intercept, b_1 is the slope of the regression or coefficient of allometry, x is the variable considered as the independent term, and e is the error term. We tested the deviation from isometry of each dependent variable by means of two tailed t-tests, after corroborating normal distribution of the independent variable (Shapiro-Wilk test, males: $w = 0.85$; $P = 0.17$, females: $w = 0.78$; $P = 0.13$). Allometric coefficients are interpreted as isometric when they cannot be distinguished statistically from unity. Statistically significant deviations from isometry represented cases of negative allometry if $b_1 < 1.0$ and positive allometry if $b_1 > 1.0$. However, in bivariate analyses, the scaling of any measurement can be affected by the choice of the independent variable (Smith 1981, Wayne 1986). The independent term is usually the total length of the skull, which is a good proxy of body size (e.g. Emerson and Bramble 1993, Abdala et al. 2001). However, this measurement is not always isometric with respect to the skull as a whole (e.g. Flores et al. 2010, Tarnawski et al. 2014a,b); hence, we employed a different linear variable as the geometric mean (Mosimann 1970, Meachen-Samuels and Van Valkenburgh 2009, Tarnawski et al. 2014a,b), which is more suitable as an independent term. The geometric mean is a size variable derived from the Nth root of the product of N measurements, being a good predictor of individual size and skull measurements. We used the reduced major axis regression model (RMA) (e.g. Abdala et al. 2001, Flores et al. 2003) and a likelihood

Table 1: Summary of bivariate regressions for skull elements of *Grampus griseus*, using geometric mean of the skull as proxy of size (independent variable, see text for details).

Variable	Sex	Range	R^2	b_{rma}	T_{iso}	P_{iso}	y-Intercept	Trend
CBL	Male	348.61–541.71	0.975	0.833	15.0674	2.78e-05	0.905	–
	Female	350.52–517.83	0.973	0.962	8.838	0.277	0.629	=
LR	Male	166.22–281.28	0.963	1.113	0.177	0.018	0.017	+
	Female	162.42–258.86	0.955	1.318	−3.343	3.26E-06	−0.423	+
WRB	Male	117.63–218.10	0.965	1.299	−4.457	1.80E-06	−0.493	+
	Female	124.69–207.15	0.939	1.440	−4.926	4.19E-07	−0.788	+
WRM	Male	70.31–150.83	0.943	1.543	−6.993	2.41E-08	−1.174	+
	Female	82.23–146.52	0.879	1.625	−5.233	7.63E-07	−1.331	+
WPM	Male	44.69–106.07	0.874	1.515	−5.234	1.76E-05	−1.220	+
	Female	58.01–104.68	0.832	1.492	−4.440	0.0001	−1.286	+
GWP	Male	76.24–128.45	0.952	1.000	−0.842	0.984	−0.084	=
	Female	86.16–120.08	0.873	0.867	1.465	0.073	0.203	=
GWN	Male	50.04–65.84	0.547	0.439	6.195	3.32E-06	0.837	–
	Female	47.88–67.38	0.302	0.811	0.183	0.2479201	0.055	=
ZB	Male	202.69–354.27	0.985	1.253	−2.476	2.00E-08	−0.170	+
	Female	211.54–338.71	0.957	1.322	−2.595	1.62E-06	−0.317	+
GPW	Male	197.29–339.21	0.947	1.065	1.892	0.216	0.210	=
	Female	207.02–322.55	0.952	1.226	−1.062	0.0002	−0.128	+
GWRP	Male	38.77–71.33	0.796	1.003	−1.796	0.968	−0.371	=
	Female	42.84–63.74	0.515	0.985	−1.068	0.921	−0.329	=
GWLP	Male	28.28–54.31	0.866	1.037	−4.832	0.013	−0.998	+
	Female	31.74–48.59	0.733	1.053	−2.472	0.641	−0.605	+
GPaW	Male	159.25–260.38	0.849	0.881	2.951	0.149	0.461	=
	Female	171.10–235.47	0.764	0.924	1.847	0.454	0.373	=
BB	Male	129.43–189.67	0.909	0.787	5.244	0.001	0.567	–
	Female	137.44–182.74	0.931	0.791	5.985	0.0003	0.556	–
TFL	Male	73.15–137.31	0.899	1.238	−3.125	0.005	−0.561	+
	Female	79.22–127.32	0.779	1.268	−2.358	0.025	−0.631	+
TFW	Male	45.00–72.56	0.688	1.136	−2.142	0.305	−0.621	+
	Female	43.77–70.83	0.477	1.379	−2.561	0.045	−1.149	+
OL	Male	58.00–87.39	0.781	0.768	1.584	0.016	0.260	–
	Female	62.07–85.56	0.640	0.867	0.225	0.277	0.052	=
LLT	Male	41.67–78.82	0.247	1.121	−1.282	0.014	−0.560	+
	Female	40.03–80.47	0.139	1.570	−2.397	0.027	−1.572	+
LMR	Male	270.86–442.18	0.974	0.949	8.234	0.147	0.566	=
	Female	273.41–417.11	0.970	1.029	4.986	0.439	0.394	=
GHMR	Male	67.61–114.03	0.960	1.140	−4.043	0.006	−0.418	+
	Female	74.65–108.77	0.836	0.991	−0.598	0.920	−0.107	=
LMF	Male	118.63–201.57	0.891	1.122	−0.815	0.121	−0.137	=
	Female	128.39–190.34	0.804	1.097	−0.435	0.335	−0.095	=
GWB	Male	101.29–186.96	0.954	1.266	−4.066	4.76E-05	−0.505	+
	Female	103.89–173.44	0.918	1.348	−3.960	5.41E-05	−0.685	+

Abbreviations (variable acronyms) as in Figure 2. Variables that show different trends for both sexes are listed in bold script. R^2, adjusted coefficient of correlation; b_{rma}, allometric coefficient in reduced major axis analysis; T_{iso}, two-tailed Student’s t-value under the assumption of isometry; P_{iso}, p-value for T_{iso}, isometry; +, positive allometry; –, negative allometry.

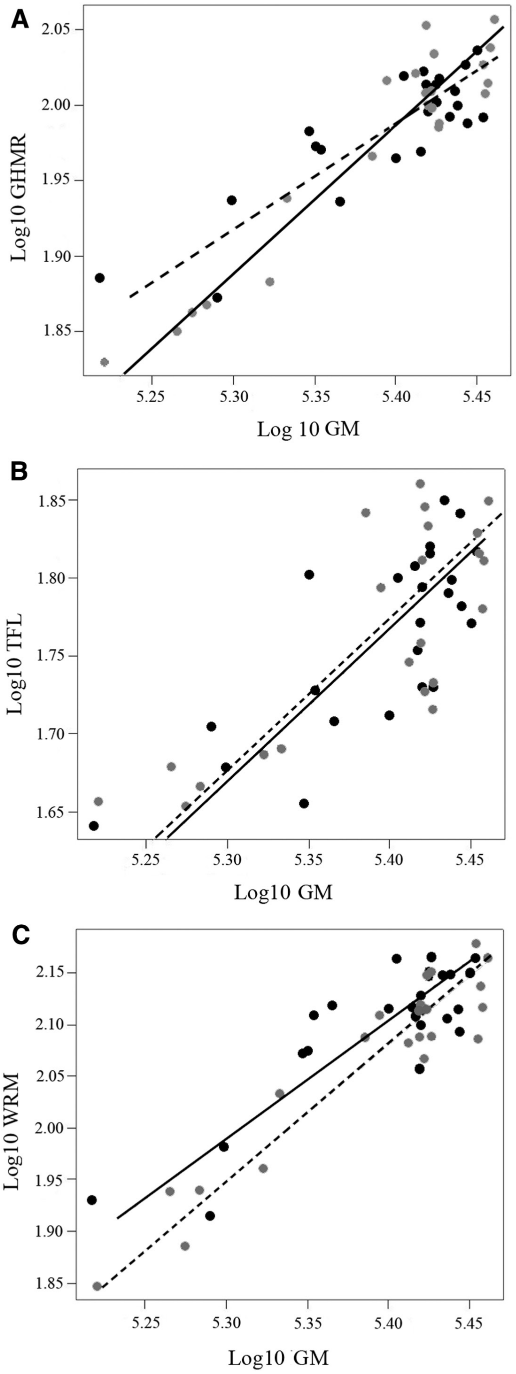

Figure 3: Bivariate RMA regressions of selected variables (*Log* base 10) versus geometric mean (GM).
(A) Different slopes between the growth trajectories of males and females; (B) same slope and intercepts for females and males; (C) same slope and different intercepts between females and males. Symbols: black circles, females; gray symbols, males; lines, RMA regression; dash line, females; solid line, males. Abbreviations as in Figure 2.

ratio test for the common RMA slope, following Warton et al. (2006). If the species shared a common slope, we compared the significance of the common y-intercepts using the Wald test (as described in Warton et al. 2006). All these regression coefficients, statistical parameters, and tests were performed using the SMART package in R (Warton and Weber 2002).

Multivariate allometry

In this analysis, size is considered a latent variable affecting all measured variables simultaneously. Multivariate coefficients of allometry are obtained from a principal component analysis (PCA) based on a variance–covariance matrix of all cranial variables (Jolicoeur 1963), excluding the geometric mean used in bivariate allometry. Then, a resampling strategy was performed using jackknife pseudovalues of coefficients to generate confidence intervals (CIs) for the coefficients (see Giannini et al. 2004, Flores et al. 2006). The CI may include a specific isometric value that depends on the number of variables, *p*, and therefore be statistically indistinguishable from isometry, or may exclude such value and therefore be considered allometric. The isometric value for 21 variables is 0.218 (calculated as $1/21^{0.5}$); therefore, all the coefficients whose intervals do not include this value are considered positive if >0.218 and negative if <0.218). We used untrimmed and also trimmed pseudovalues to calculate the CIs (Manly 1997). Trimming the largest and smallest jackknife pseudovalues for each variable significantly decreases CI width, reflecting a more realistic allometric estimation (see Giannini et al. 2004). Untrimmed and trimmed CIs differing significantly in width can be interpreted as extreme pseudovalues affecting standard errors. We report untrimmed and trimmed pseudovalues. For statistical analyses (PCA + jackknife resampling) the R-script (R Development Core Team 2012) of Giannini et al. (2010) was used (which is available from the authors).

Results

Bivariate allometry

Our bivariate analysis (Table 1) showed high values of coefficient of determination (R^2) in almost all variables, except in LLT (0.24 and 0.14 for males and females, respectively), GWN (0.54 and 0.3) and TFW (0.69 and 0.48). The highest R^2 indices were obtained for CBL (0.97 for both sexes), ZB (0.98 and 0.95), LMR (0.97 for both sexes) and GPW (0.94 and 0.95). Under bivariate allometry, only

Table 2: Test for common slopes and common intercepts for male and female of *Grampus griseus*.

Variable	Common slope			Common intercept		
	Lr	P_{b1}	b_1 com	$W_{(logb0)}$	$P_{(logb0)}$	Log (b_0)com
CBL	7.589	0.006	Female > male			
LR	6.742	0.009	Female > male			
WRB	2.258	0.133	1.350	0.00007	0.993	– 0.597
WRM	0.318	0.573	1.570	4.342	0.037	Male > female
WPM	0.016	0.900	1.505	4.264	0.039	Male > female
GWP	2.413	0.120	0.962	2.633	0.105	– 0.020
GWN	6.575	0.010	Female > male			
ZB	1.066	0.302	1.271	0.224	0.636	– 0.203
GPW	3.992	0.046	Female > male			
GWRP	0.011	0.917	0.998	0.088	0.767	– 0.366
GWLP	1.358	0.244	1.172	0.426	0.514	– 0.873
GPaW	0.124	0.725	0.898	0.098	0.755	0.422
BB	0.004	0.953	0.790	0.356	0.551	0.567
TFL	0.038	0.846	1.248	0.899	0.343	– 0.564
TFW	0.946	0.331	1.224	1.375	0.241	– 0.772
OL	0.533	0.465	Female > male			
LLT	1.624	0.203	1.305	1.366	0.243	– 0.946
LMR	2.447	0.118	0.986	1.724	0.189	0.497
GHMR	2.009	0.156	Male > female			
LMF	0.037	0.848	1.113	2.733	0.098	– 0.091
GWB	0.642	0.423	1.296	2.667	0.102	– 0.546

$b_1$com, common slope from reduced major axis analysis; log(b_0)com, common intercept from reduced major axis analysis; Lr, likelihood ratio (Warton et al. 2006); W, Wald statistic (Warton et al. 2006); P_{b1}, p-value of Lr parameter; $P_{(logb0)}$, p-value of W parameter. Abbreviations as in Figure 1.

five variables were isometric in both sexes (GWP, GWRP, GPaW, LMR, and LMF). Three of them belong to the cranium and affect some width dimensions, whereas the remaining ones correspond to length of the mandible. Ten variables showed positive allometry in both sexes (LR, WRB, WRM, WPM, ZB, GWLP, TFL, TFW, LLT, and GWB), which were principally related to rostrum growth (both in length and width), basicranium, and postemporal fossa. Finally, only one variable (BB) showed negative allometry in both sexes, which was related to the breadth of the braincase.

Sexual dimorphism in skull growth was detected in eight variables (Figure 3A, C; Table 2). Five of them (CBL, GWN, GPW, OL, and GHMR) showed different allometric trends, of which only GHMR favored males. In one variable (LR), both sexes shared a positive allometric trend, but females exhibited a statistically higher allometric trend than males. Finally, two variables related to breadth of the rostum and premaxillaries at midlength of the rostrum (WRM, WPM) showed the same slope, but the intercept of the trajectories was statistically different, favoring males (Figure 3C). In the remaining variables, both slopes and intercepts were statistically similar (Figure 3B).

Multivariate allometry

Overall, the mean difference in absolute bias clearly favored untrimmed over trimmed values, with 0.0008 and 0.0044 average absolute bias in males and females, respectively, towards males, and 0.0034 and 0.0064 towards females. Therefore, our interpretations are based on untrimmed values (Table 3). In males, the lowest departure from the isometric value was detected in GPW (0.002) and LMF (0.003), whereas in females, it was observed in LMR (0.0003) and LMF (0.008). Five variables showed positive allometry for both sexes (WRB, WRM, WPM, ZB, and GWB), all of which are related to the breadth of the rostrum and skull in general. Three variables, all related to sensory capsules (GWN, BB, and OL), showed negative allometry in both sexes. Finally, five variables were isometric in both sexes (GWRP, GWLP, TFL, TFW, and LMF), which are related to the premaxillaries and areas for muscle attachment in the cranium and mandible. Sexual dimorphism was detected in eight variables (CBL, LR, GWP, GPW, GPaW, LLT, LMR, and GHMR), of which five favored females and the remaining three variables (GWP, GPaW, and GHMR) favored males.

Table 3: Results of the multivariate analysis of cranial allometry in male and female of *Grampus griseus*.

Variable	Sex	Expected	Observed	Untrimmed				Trimmed			
				Resampled	Bias	CI 95%	Trend	Resampled	Bias	CI 95%	Trend
CBL	Male	0.218	0.173	0.174	−0.0007	0.164–0.184	−	0.172	0.0004	0.164–0.179	−
	Female	0.218	0.198	0.204	−0.0029	0.186–0.221	=	0.203	−0.0027	0.194–0.212	−
LR	Male	0.218	0.230	0.23	−0.0002	0.209–0.251	=	0.233	−0.0017	0.217–0.249	=
	Female	0.218	0.270	0.279	−0.0044	0.253–0.304	+	0.264	0.0029	0.253–0.274	+
WRB	Male	0.218	0.268	0.269	−0.0007	0.248–0.291	+	0.261	0.0035	0.247–0.275	+
	Female	0.218	0.293	0.300	−0.0034	0.262–0.337	+	0.288	0.0024	0.267–0.309	+
WRM	Male	0.218	0.316	0.32	−0.0020	0.285–0.355	+	0.324	−0.0043	0.296–0.353	+
	Female	0.218	0.323	0.332	−0.0047	0.289–0.376	+	0.314	0.0044	0.292–0.335	+
WPM)	Male	0.218	0.299	0.304	−0.0024	0.241–0.367	+	0.289	0.0052	0.250–0.327	+
	Female	0.218	0.288	0.299	−0.0055	0.266–0.332	+	0.291	−0.0014	0.263–0.318	+
GWP	Male	0.218	0.205	0.206	−0.0006	0.181–0.231	=	0.204	0.0002	0.185–0.224	=
	Female	0.218	0.170	0.173	−0.0012	0.139–0.206	−	0.17	0.0001	0.154–0.185	−
GWN	Male	0.218	0.068	0.066	0.0005	0.038–0.095	−	0.062	0.0028	0.038–0.085	−
	Female	0.218	0.093	0.102	−0.0045	0.003–0.020	−	0.094	−0.0010	0.054–0.134	−
ZB	Male	0.218	0.262	0.262	−0.0003	0.244–0.279	+	0.264	−0.0011	0.252–0.274	+
	Female	0.218	0.272	0.272	0.00001	0.252–0.292	+	0.282	−0.0049	0.271–0.293	+
GPW	Male	0.218	0.218	0.22	−0.0012	0.191–0.250	=	0.231	−0.0064	0.210–0.251	=
	Female	0.218	0.251	0.258	−0.0034	0.237–0.279	+	0.247	0.0016	0.236–0.259	+
GWRP	Male	0.218	0.188	0.19	−0.0012	0.139–0.240	=	0.176	0.0056	0.139–0.214	−
	Female	0.218	0.147	0.158	−0.0058	0.068–0.248	=	0.123	0.0116	0.095–0.151	−
GWLP	Male	0.218	0.242	0.244	−0.0014	0.206–0.282	=	0.24	0.0005	0.211–0.270	=
	Female	0.218	0.188	0.198	−0.0053	0.155–0.241	=	0.181	0.0034	0.150–0.210	−
GPaW	Male	0.218	0.170	0.167	0.0015	0.113–0.220	=	0.194	−0.0121	0.170–0.218	−
	Female	0.218	0.169	0.171	−0.0010	0.150–0.191	−	0.173	−0.0023	0.156–0.190	−
BB	Male	0.218	0.158	0.159	−0.0007	0.132–0.186	−	0.171	−0.0067	0.156–0.186	−
	Female	0.218	0.160	0.162	−0.0014	0.148–0.177	−	0.159	−0.0001	0.150–0.169	−
TFL	Male	0.218	0.248	0.25	−0.0012	0.214–0.286	=	0.245	0.0013	0.219–0.271	+
	Female	0.218	0.237	0.233	0.0021	0.148–0.316	=	0.254	−0.0090	0.223–0.285	+
TFW	Male	0.218	0.200	0.198	0.0004	0.161–0.236	=	0.202	−0.0016	0.171–0.233	=
	Female	0.218	0.204	0.187	0.0083	0.0949–0.279	=	0.248	−0.0219	0.204–0.290	=
OL	Male	0.218	0.143	0.145	−0.0012	0.112–0.178	−	0.145	−0.0010	0.117–0.171	−
	Female	0.218	0.144	0.138	0.0028	0.066–0.209	−	0.155	−0.0056	0.133–0.176	−
LLT	Male	0.218	0.110	0.11	−0.0002	0.043–0.177	−	0.123	−0.0063	0.071–0.173	−
	Female	0.218	0.112	0.165	−0.0266	0.022–0.353	=	0.018	0.0471	0.049–0.085	−
LMR	Male	0.218	0.197	0.198	−0.0007	0.187–0.209	−	0.2	−0.0019	0.194–0.207	−
	Female	0.218	0.212	0.219	−0.0033	0.183–0.253	=	0.208	0.0019	0.195–0.220	=
GHMR	Male	0.218	0.235	0.235	−0.0001	0.218–0.252	+	0.233	0.0009	0.218–0.248	+
	Female	0.218	0.190	0.193	−0.0016	0.153–0.232	=	0.187	0.0012	0.166–0.208	−
LMF	Male	0.218	0.222	0.222	0.0001	0.192–0.252	=	0.228	−0.0033	0.204–0.253	=
	Female	0.218	0.207	0.210	−0.0012	0.180–0.239	=	0.22	−0.0065	0.200–0.240	=
GWB	Male	0.218	0.260	0.26	0.0000	0.232–0.289	+	0.27	−0.0052	0.250–0.291	+
	Female	0.218	0.272	0.266	0.0033	0.234–0.297	+	0.278	−0.0030	0.259–0.296	+

The first three data columns show results using all specimens. The remaining columns show jackknife results calculated with untrimmed and trimmed (m = 1) sets of pseudovalues (see section "Bivariate allometry" for details). The allometric coefficient of a variable is the corresponding element of the first (unit) eigenvector per variable. The expected coefficient is the value under the assumption of isometry (0.218 for all variables). The observed coefficient is the value obtained with all specimens included. The resampled coefficient is the value generated by first-order jackknife resampling. Bias is the difference between the resampled and observed coefficients. The jackknifed 99% confidence interval (CI) is provided; allometric variables are those whose CIs exclude the expected value under the assumption of isometry (0.258). Abbreviations (variable acronyms) as in Figure 2. Variables that show different trends for the sexes (untrimmed) are listed in bold script. =, isometry; +, positive allometry; −, negative allometry.

Our results of bivariate and multivariate allometry were mostly in agreement; however, the bivariate approach showed higher allometric trends for those variables for which both approaches showed different trends. For instance, in variables in which the allometric trend was recovered as isometric in multivariate analysis, it was positively allometric in bivariate analysis, whereas those variables negatively allometric in the former were isometric in the latter analysis. These trends describe a pattern of postnatal growth in the Risso's dolphin skull that can be interpreted as follows (Figure 1).

Grampus griseus's rostrum growth during postnatal ontogeny (both in width and length) is greater than the neurocranium. The skull of young specimens is relatively narrow compared to that of adults and becomes wider as a consequence of the high growth rate of most variables related to rostrum and zygomatic breadth (Figure 1A–D). Other few variables remain in similar proportions with respect to the whole skull when the animal grows, such as the post-temporal fossa width and the length of the mandibular fossa. Three variables exhibit little change throughout skull growth, being proportionally large in young specimens and affecting the neurocranium: breadth of the braincase, orbit, and size of external nares. Finally, males and females show several differences in growth pattern. For instance, rostrum length of females grows faster than that of males; the same occurs with the length of the mandibular ramus and the postorbital width. On the other hand, males show higher rates of growth in the parietal and premaxillary width and in the height of the mandibular ramus.

Discussion

Studies focusing on the morphological basis of the function in the cetacean skull (e.g. Owen 1868, Perrin 1975, Cranford et al. 1996, Oelschläger 2000, Mead and Fordyce 2009) show a good overview of the complex form-function in odontocete skull. Although previous reports studying patterns of skull growth in odontocetes did not apply exactly the same methodological approaches used here, the growth patterns described in literature provide us an opportunity to make a clear comparison with those obtained for *Grampus griseus*. Our results indicate that the postnatal skull growth of Risso's dolphin exhibits higher rates in variables associated with trophic apparatus (rostrum, mandible) than with neurochranial components (braincase, orbits), even considering the typical short rostrum in this species. That is, although the short rostrum suggests that allometric trends in these variables could not be as positive as in other cetacean species with longer rostra, results showed positive trends in these variables. This result is in accordance with those observed by Gol'din (2007), who also found positive trends on rostrum variables on another short-nosed species such as the harbor porpoise.

This pattern (i.e. positive allometry or isometry of the trophic apparatus, and negative allometry of the neurocranial component) which is evident in terrestrial mammals (e.g. Flores et al. 2015), seems to be also a common pattern in odontocetes (e.g. Perrin 1975, Kurihara and Oda 2009, Sydney 2010, Sydney et al. 2012, Nakamura and Kato 2014). Several long-nosed odontocetes (e.g. Bottlenose dolphin, *Tursiops truncatus*, Kurihara and Oda 2009; Guiana dolphin, *Sotalia guianensis*, Sydney et al. 2012, Striped dolphin, *Stenella coeruleoalba*, Ito and Miyazaki 1990; Franciscana dolphin, *Pontoporia*, del Castillo et al. 2014) showed an accelerated development of the trophic apparatus, as detected here for *Grampus griseus*. The allometry of both dimensions of the post-temporal fossa was isometric or positively allometric in *G. griseus*, as well as the greatest height of the mandibular ramus and the zygomatic breadth (Tables 1–3), suggesting an increase in the area of the temporalis and masseteric muscles. However, the well-developed internal pterygoid muscle also shows a high influence on the occlusal force in odontocete (as observed in *T. truncatus*; Seagers 1982). Although the development of such muscle was not described for *G. griseus*, its well-developed palatine surface of the pterygoid (as well as the pterygoid hamulus; Figure 1C–D) suggests a notable participation of this muscle in occlusion force. LLT was the only variable with low correlation with the geometric mean (Table 1), which could be due to the unclear landmarks defining this measurement. Clarke (1986) stated that the morphology of the jaw and the

Figure 4: Dorsal aspect of lower dentition of *Grampus griseus* showing variations in alveolous and dental elements between specimens and hemimandibles. Scale bar = 1 cm.

number of teeth reflects the diet of odontocetes, indicating that predominantly cephalopod-eating odontocetes have fewer teeth than predominantly fish eaters. Accordingly, the reduced number of teeth in the mandible of *G. griseus* (Figure 4) and the absence of upper teeth reflect their diet, which is almost exclusively composed of cephalopods (Wang et al. 2012). In addition, a short and broad rostrum, with a short mandible showing a well-developed mandibular fossa, suggests a great mechanical advantage at the anterior section of the trophic apparatus, where the lower teeth are placed. Another interesting trend is the negative allometry of the greatest width of external nares (Table 2), as also observed for *S. attenuata* (Perrin 1975) and *T. truncatus* (Rauschmann et al. 2006). The negative allometry of the external nares suggests a well-developed capacity for external nasal passage (Mead 1975) from early stages of growth.

Although the rostrum of *Grampus griseus* grows with positive allometry in length, its short and wide aspect is evident in adults, because of the strong positive allometry in its width at the base and especially at the midlength (Tables 1–3). Such notably broad platform in the anterior portion of the nares serves as support for the well-developed melon, clearly visible in the head of this species. In a lateral view (Figure 1E–F), the skull of *G. griseus* lacks the characteristic long rostrum and frontal concavity found in other dolphins (e.g. *Stenella coeruleoalba*, Loy et al. 2011; *Delphinus delphis,* Jordan 2012), with the melon becoming more notable on the external aspect of the head, as observed in other Globicephalinae taxa such as *Peponocephala, Feresa,* and *Globicephala* (i.e. a distinctive broad melon, squarish in profile, with a longitudinal furrow extending down to the top of the upper jaw; Nachtigall et al. 2005).

According to Armfield et al. (2011), large heads in cetaceans include positive allometry of growth during pre-and postnatal growth periods, unlike most mammals in which overall head size is negatively allometric in the postnatal period (e.g. Pagel and Harvey 1990, Emerson and Bramble 1993). However, our results in *Grampus griseus* indicate isometry in females and negative allometry in males in condylo-basal length with respect to the geometric mean of the skull (Table 1). A possible cause of such differences may be that the results of Armfield et al. (2011) referred to head growth with respect to body size instead of the geometric mean used here. In this sense, the election of the independent variable used for comparison in bivariate allometry, can give different results. However, our experimental approach using body size as independent variable results in negative allometry of condylo-basal length in both sexes (b_1 females = 0.68; males = 0.71). Accordingly, a generalization about postnatal head growth in cetaceans may not be plausible, with some cetacean species showing the typical accelerated mammalian growth head during prenatal period and slow postnatal growth (Miyazaki et al. 1981, McLellan et al. 2002, Oelschläger et al. 2008, Oelschläger and Oelschläger 2009, Armfield et al. 2011, Hadad et al. 2012). The proportions between skull and body size does not seem to be uniform in odontocetes, as well as in whales (*Balaenoptera*), in which this proportion is related to feeding strategies (Nakamura et al. 2012). Studies addressing comparative frames of prenatal and postnatal growth in cetaceans (e.g. Armfield et al. 2011, Huang et al. 2011, Moran et al. 2011, Hadad et al. 2012) suggest that social cetaceans, such as *G. griseus* (Gaspari 2004), have slow prenatal growth, which implies low prenatal energetic effort and high costs of lactation. Our results seems to support this idea; although the condylo-basal length and neurocranial variables (such as breadth of the braincase and orbit length) showed negative postnatal allometry (i.e. accelerated prenatal growth), most variables (17 out 21 variables) showed isometry or positive allometry of growth (especially in bivariate analysis), denoting a high rate of postnatal growth. However, prenatal analyses and studies of energetic costs should be done in order to shed light on this issue. These findings suggest a pattern of skull growth in *G. griseus* basically similar to that of long-nosed species, representing perhaps, a plesiomorphic mode of growth evidenced not only in odontocetes, but also in several terrestrial mammals.

Sexual dimorphism

While sexual dimorphism was not detected in body size of *Grampus griseus* (Kruse et al. 1999), here, sexual dimorphism was detected in the allometric growth pattern of some cranial variables (Tables 2 and 3; Figure 3). Although rostrum width grows with similar positive allometry in both sexes, rostrum length grows at a higher rate in females (multivariate analysis), as well as the greatest postorbital width. Other variables related to trophic functions, such as the greatest height of the mandibular ramus, also showed sexual dimorphism in growth, suggesting possibly slight sexual differences in the mechanics of the trophic apparatus. For instance, while we did not detect sexual dimorphism in the shape of the posttemporal fossa, the dimorphism detected in the greatest height of the mandibular ramus favored males (Tables 2 and 3; Figure 3), suggesting differences in the area for masseteric attachment.

Despite the dimorphism detected in the mandibular ramus (favoring males), most of the few dimorphic variables (in either methods) favored females in their slopes and intercepts (Tables 2 and 3), indicating an earlier onset of the optimal morphological performance in females with respect to males. Similar conclusions were obtained for body growth of *Stenella cureoalba* (Calzada et al. 1997), with males growing at a lower rate than females. Although a different growth rate does not mean larger final size, the inverted sexual dimorphism in size observed in other cetaceans (e.g. *Pontoporia blainvillei*, *Phocoena phocoena*, *Platanista gangetica*, *Berardius bairdii*, and species of the genus *Cephalorhynchus*; Kasuya and Brownell 1979, Lockyer et al. 1988, McLellan et al. 2002, Ralls and Mesnick 2002, del Castillo et al. 2014) has been related to breeding strategies in females (competition for resources in females, or the capacity for large offspring, Ralls 1976, McLellan et al. 2002). However, the lack of sexual dimorphism in body length is also related to possible reproductive strategies in *Grampus griseus*. In general, delphinid species whose males are larger than females (in body size and skull) typically exhibit intraspecific male-male aggression for access to reproductive females (Schaeff 2007), whereas monomorphic species as *G. griseus*, (or only moderately dimorphic in body length) usually have large testes relative to body size (McLellan et al. 2002, Murphy and Rogan 2006, Westgate and Read 2007), probably in association with sperm competition (Ralls and Mesnick 2002, Murphy et al. 2005, Neuenhagen et al. 2007). *G. griseus* possesses relatively large testes (43–86 cm, 15.9–26.5% of body length; Orr 1966; Ross 1984) and seasonal breeding, suggesting sperm competition as part of a male mating strategy (Plön and Bernard 2007). In fact, the absence of strong size dimorphism in adults of this species, suggest morphological differences in the skull of males and females, considering our detection of variables statistically dimorphic in its growth trend.

The pattern of skull growth and the weak sexual dimorphism observed in *Grampus griseus* show an association with the species' life history during ontogeny (e.g. negative allometry of external nares, positive allometry of rostrum width, slight sexual dimorphism), while maintaining the growth pattern observed in other dolphins (i.e. accelerated postnatal growth of trophic apparatus, and neurocranium with lower growth rate). This method to quantify skull growth, taking in account functional demands based on ecological or behavioral traits, can be applied in further analyses of related Globicephalinae dolphins with the aim of detecting common patterns in the group related to its particular morphology or differences based on alternative behaviors and life history patterns.

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Appendix 1

Specimens examined in this work. All specimens are deposited in the mammal collection of the National Museum of Nature and Science, Japan (NSMT).

Males: NMNS 29493, 29498, 29481, 29507, 29530, 29523, 29547, 29529, 29529, 29531, 29550, 29540, 29528, 29476, 29475, 29489, 27479, 24665, 29513, 29574, 10507, 30728, 21400. Females: 29487, 29494, 29495, 29483, 29484, 29482, 29492, 29491, 29509, 29511, 29485, 29485, 29508, 29536, 29537, 29539, 29525, 29527, 24842, 24843, 29477, 29478, 29480, 80202.

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