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Original Investigation

Timing of ontogenetic changes of two cranial regions in *Sotalia guianensis* (Delphinidae)

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ABSTRACT

Despite the fact that heterochronic processes seem to be an important process determining morphological evolution of the delphinid skull, previous workers have not found allometric scaling as relevant factor in the differentiation within the genus *Sotalia*. Here we analyzed the skull ontogeny of the estuarine dolphin *S. guianensis* and investigate differential growth and shape changes of two cranial regions – the neurocranium and the face – in order to evaluate the relevance of cranial compartmentalization on the ontogeny of this structure. Our results show that, even though both cranial regions stop growing at adulthood, the face has higher initial growth rates than the neurocranium. The rate of shape changes is also different for both regions, with the face showing a initially higher, but rapidly decreasing rate of change, while the neurocranium shows a slow decreasing rate, leading to persistent and localized shape changes throughout adult life, a pattern that could be related to epigenetic regional factors. The pattern of ontogenetic shape change described here is similar to those described for other groups of Delphinidae and also match intra and interspecific variation found within the family, suggesting that mosaic heterochrony could be an important factor in the morphological evolution of this group.

Introduction

The estuarine dolphin *Sotalia guianensis* (van Bénéden 1864) is a small cetacean common in South American shores, occurring from Honduras in Central America to the state of Santa Catarina in the south of Brazil (Geise and Borobia 1987; Simões-Lopes 1988; Borobia et al. 1991; Monteiro-Filho et al. 2006). The ontogeny of this species is well studied. Both males and females reach maximum size between the ages of five and seven years (Borobia 1989; Rosas et al. 2003; Di Beneditto and Ramos 2004; Rosas and Barreto 2008), and the species is known to reach 31 years of age (Ramos et al. 2008). The identification of infant and adult skulls is based on a set of qualitative differences, such as the degree of the fusing of bones, presence or absence of crests and the relative position of some structures (Simões-Lopes and Menezes 2008).

Recently, the species was divided in estuarine populations that dwell in open sea, *S. guianensis*, and riverine populations, *S. fluviatilis*, on the basis of geometric morphometrics studies of the skull (Monteiro-Filho et al. 2002). Despite the fact that riverine individuals possess a smaller skull, the authors found no evidence for the possibility that allometric scaling might account for the differences between species, as there was no apparent correlation between shape differences and size in the sample (Monteiro-Filho et al. 2002).

In a study of the behavior of simulated multivariate ontogenetic trajectories of principal component plots in shape and size space, Mitteroecker et al. (2004) shown that results of the analysis of heterochrony of complex modularized structures could be misleading. The reason is that, given that morphological modules can evolve semi-independently, heterochronic alterations of local rates of development could result in processes that cannot be expressed in terms of global heterochrony. Therefore it is possible that, even though there is no obvious correlation between adult size and shape in *Sotalia*, dissociation of patterns of development, or mosaic heterochrony (*sensu* David 1990), could lead to morphological differences within the genus.

The mammalian skull is a complex structure formed by the coordinated development of various bones, which usually results in different levels of integration and dissociation among different cranial traits (e.g. Cheverud 1982; Steppan 1997; Ackermann and Cheverud 2000; Marroig and Cheverud 2001; Goswami 2006; Hallgrímsson et al. 2007). It is commonly divided in two functional regions, the cerebral skull or neurocranium, associated with

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the brain and the main sensory capsules and the facial skull or snout, associated with the masticatory apparatus (van der Klaauw et al. 1946; Radinsky 1981). Differences in growth rate are thought to alter the relative adult size of these regions, explaining some aspects of shape differences along the ontogeny and among species (Alberch et al. 1979; Shea 1983). Analyses of the morphological integration among various orders of mammals have shown that this neurocranium-face compartmentalization is maintained along the evolutionary history of the group (Porto et al. 2009). Interestingly enough, this pattern was also observed for at least two cetacean genera, including *Sotalia* (Porto 2009), which would make the subdivision between neurocranium and face a natural way of analyzing the possibility of heterogenic rates of development in the skull.

In the present contribution we evaluate the timing of the ontogenetic development of size and shape change of the face and neurocranium of *Sotalia guianensis* in order to look for developmental patterns that could be related to mosaic heterochrony in the skull and, therefore, explain the differences found within the genus. To achieve this goal, we used an integrative methodological framework allowing the analysis of different rates of ontogenetic change.

Material and methods

Sample

We analyzed 67 skulls of *Sotalia guianensis* from the Instituto de Pesquisa em Cananéia (IPEC), Laboratório de Mamíferos Aquáticos (LAMAQ/UFSC) and Museu de Ciências Naturais da Universidade Federal do Paraná (MCN/UFPR). Absolute age of the specimens was determined through manual wear of teeth followed by decalcification and observation under a stereomicroscope. A complete description of the methodology can be found in Sydney and Monteiro-Filho (2011). Infants with less than one year of age were selected as reference to investigate the rates of ontogenetic shape change (see below).

Both sexes as well as specimens without sex information, and individuals from different localities were pooled together for the statistical analyses since sexual dimorphism or geographical variation in the skull shape were not identified by previous studies (Borobia 1989; Monteiro-Filho et al. 2002).

Geometric morphometrics

We used 3D anatomic landmarks to analyze the shape of the skull of *Sotalia guianensis* (Fig. 1). The landmarks were assigned to different cranial regions according to Porto (2009). This same classification can be found in Porto et al. (2009) for mammalian species belonging to different Orders. We discarded the landmarks situated at the limits between the face and the neurocranium, in order to assign each landmark to only one region. Also, the zygomatic region of the skull is extremely posteriorized in *Sotalia*, suggesting that any modification in the neurocranial region would undoubtfully alter the relative position of the landmarks situated over the zygomatic. For this reason we excluded this cranial region from our analyses. The resulting 37 landmark configurations were digitized using a MicroScribe®-3D.

All configurations were superimposed to the consensus configuration (Rohlf 1998) using a full-Generalized Procrustes Analysis (GPA; Rohlf and Slice 1990), and size was measured as the centroid size. In order to access digitization repeatability, a subset of 25 adults specimens were digitized three times and submitted to an analysis of variance of the Procrustes residuals using individuals as factors to estimate the intraclass correlation coefficient (Falconer and Mackay 1996). This was done to evaluate if the differences between individuals could be distinguished from digitization error.

We tested the neurocranium-face modularity hypothesis found by Porto (2009) in our sample using the procedure described by Klingenberg (2009), wielding significant results (empirical *p value* < 0.0001). Therefore, all the procedures were performed separately for the neurocranium and the face.

Integrated component

To obtain the component of ontogenetic variation that is integrated between the neurocranium and face we employed a Two-Block Partial Least-Squares (2B-PLS) approach (Rohlf and Corti 2000), which is a singular-value decomposition of the covariance submatrix of the Procrustes residuals between both modules. The singular vectors extracted from this analysis are called Singular Warps (SW; Mitteroecker and Bookstein 2008) and are the axes of maximum covariation between two blocks of variables, in this case, the aligned configurations of the neurocranium and the face.

To evaluate if these axes are statistically significant we employed the permutation approach proposed by Mitteroecker and Bookstein (2008), which consists of comparing the singular value of the observed SW with empirical distributions of singular values obtained by permuting the modules across the sample. The significance of each singular warp was calculated separately, removing algebraically all the variation referent to singular warps with singular values superior to the one under evaluation (Mitteroecker and Bookstein 2008). We performed 999 permutations for each SW, and the empirical *p*-value was calculated as the proportion of permuted values superior to the one observed, and considered significant at the level of $\alpha = 0.05$ (Manly 1997). The significant axes were used to reconstruct the shapes corresponding to the integrated shape subspace.

Analysis of ontogeny

Following Galatius and co-workers (Galatius 2010; Galatius et al. 2011; Galatius and Gol'din 2011), we fitted a Gompertz growth function to the trajectories of size and shape. The model can be expressed as follows:

$$S(t) = Ae^{(-be)^{-kt}},$$

where $S(t)$ is the size measure value at time t, A is the asymptotic size measure, e is the Euler's constant, b is a constant of integration and k is the growth rate. The variables used as $S(t)$ were the centroid size (for the investigation of size ontogeny) and the Procrustes distances between each specimen and the youngest individual in the sample (for the investigation of shape ontogeny). We also performed this analysis using the mean shape of the infant age category (see above), following Zelditch et al. (2003). The parameters of the model were estimated through non-linear least-squares optimization. Shape analyses were performed on the sub-space defined by the significant 2B-PLS axis, and on the full shape space of the neurocranium and of the face.

To evaluate wherever there is any significant non-integrated aspect of ontogenetic shape change we tested the growth function estimated for each region against a null model assuming the same b and k parameters as the ones estimated for the integrated shape component. The same was done for size, estimating the growth rate separately for each region and comparing it with a null model assuming the parameters estimated for the centroid size of the full configuration. The models were compared through likelihood-ratio tests. The rate functions of size and shape change were measured as the first derivative of the function ignoring A to allow for graphical comparison between different aspects of ontogenetic change.

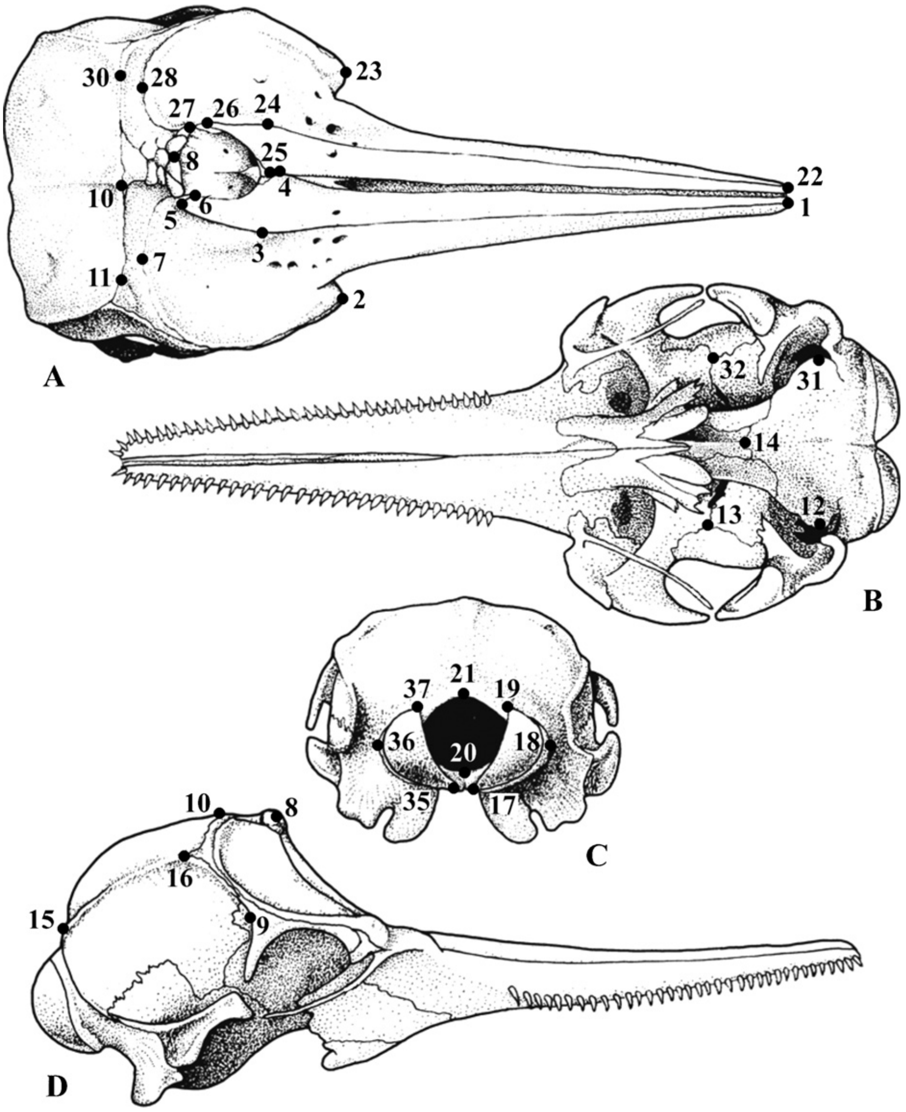

Fig. 1. Anatomical landmarks in dorsal (A), ventral (B), posterior (C) and lateral (D) view of the skull of *Sotalia guianensis* used in the present analysis. Description of the landmarks can be found at Table A-1 of the Appendix.

Since shape is inherently multidimensional, the estimation of ontogenetic shape variation through the use Procrustes distances gives information about the magnitude of shape change, but fails to provide information regarding the direction of shape change, i.e. what shape features are actually changing during the growth. For this reason, we investigated the direction of shape ontogeny dividing the sample into 5 age classes (0–0.5 years; 0.5–4 years; 4–8 years; 8–15 years; 15–31 years). We then obtained 100 bootstrapped mean shapes for each age class, calculating the Procrustes distance between each bootstrapped shape and the reference infant shape. The age of the bootstrapped shapes was assumed to be equal to the mean age of the age class. The bootstrapped shapes that best conformed to the prediction given by the growth functions were chosen to compose a model of the shape ontogeny. To investigate the trajectory of the ontogeny on shape space we employed a principal component analysis (PCA) over the variance/covariance matrix of Procrustes residuals (deviations of each coordinate from each configuration from the mean shape) and projected the bootstrapped models on the two first principal components (PC) of each module.

All the analyses were run under the R v.2.12.1 programming environment (R Development Core Team 2010). The GPA, PCA and the calculation of the CS were all performed with the "shapes" package (Dryden 2009). The 2B-PLS function was implemented in R and is available in the Appendix. The shape changes are graphically visualized through wireframes connecting the landmarks.

Results

Intraclass correlation coefficients for all coordinates were superior to 0.91, indicating that the landmark digitization had a high repeatability, and allowing the use of the full landmark configurations in the subsequent analyses.

The 2B-PLS permutation analysis yielded 4 significant SWs (see Table A-2 of the Appendix), with the first SW explaining more than half of the covariance between the modules (58.72%) and a large portion of the variance in the sample (46.03%). The investigation of the scores of the individuals on both axes of the first SW shows that younger individuals have lower scores and older individuals have higher scores for both axes (Fig. 2).

The investigation of the wireframes depicting the extreme values of the first SW shows the alterations in the skull of *Sotalia guianensis* along the ontogeny (Fig. 2). In dorsal view it is possible to notice that the distance between the posterior extremities of

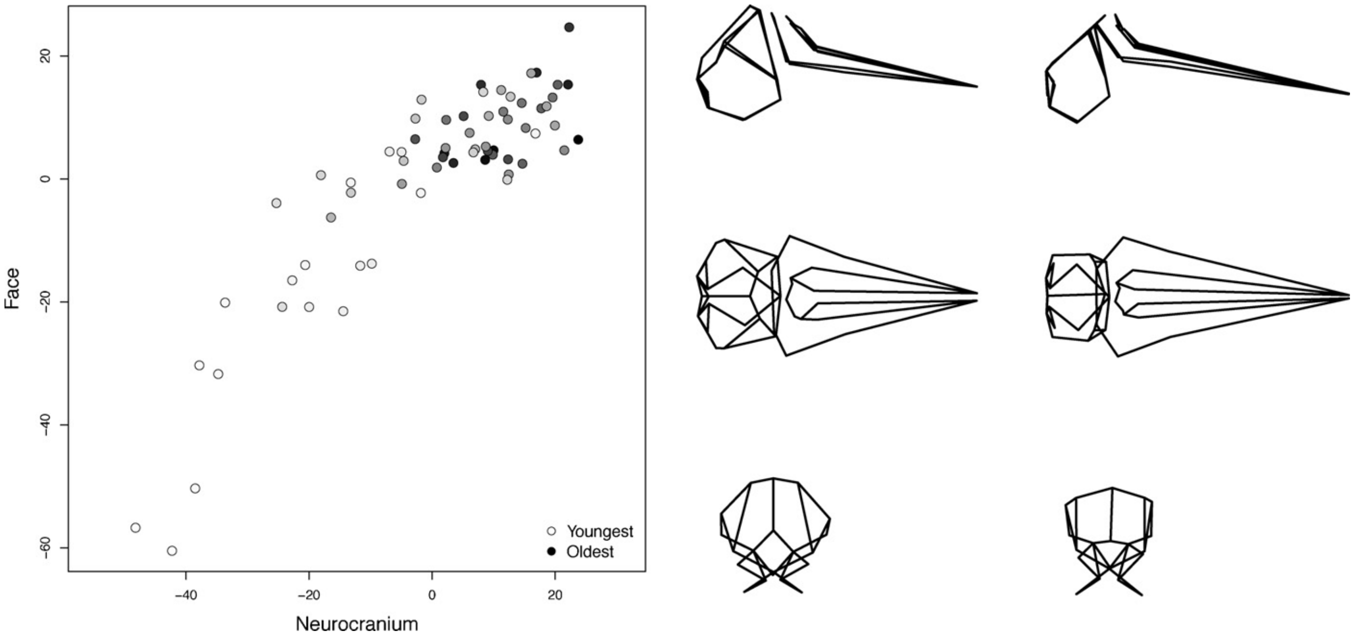

Fig. 2. First singular warp (SW) from the 2B-PLS analysis showing individual scores on the axis of the face and of the neurocranium. Point darkness indicates the relative age of each specimen, with pale dots indicating younger individuals and darker dots indicating older ones. Wireframes on the right depict the ontogenetic changes along the extreme values on the first SW in lateral, dorsal and posterior view.

the maxillaries and the medial extremity of the parietal in contact with the supraoccipital shrinks gradually along the development, reducing the visibility of the frontal, an observation previously made qualitatively (Simões-Lopes and Menezes 2008). The distance between the supraoccipital crest and the nasal shows the same ontogenetic trend. We can also observe an approximation of the ascending process of the pre-maxillary with the nasal, noticing also that the right pre-maxillary is always larger than the same bone on the left side of the skull. In the ventral view we can notice that sutures between the frontal, parietal and alisphenoid bones and the posterior extremities of the vomer shows a tendency to align laterally along the ontogeny. Juvenile individuals show the firsts sutures in a more posterior position than those in adults, probably because of the development of the vomer. In the lateral view it is possible to notice that the posterior extremity of the parietal is more pronounced in older individuals. We can also observe a dorsal displacement of the temporal crest at older ages. Furthermore, in the younger individuals the nasal is ventrally positioned in relation to the middle point of the supraoccipital crest, while in the older ones, they are positioned at the same height. In the posterior view we can observe that the extremity of the parietals gradually approaches the superior portion of the foramen magnum along the development. There is also a relative decrease of the of the foramen magnum size, with a gradually ventral displacement of the dorsal extremity associated with the dorsal displacement of the condyles.

The likelihood ratio tests indicate that the ontogenetic growth of face module and of the neurocranium module are not explained by the growth rates estimated for the full skull (Table 1), suggesting that the growth rates of these regions are different. Additionally, ontogenetic shape change of the face module shows no difference from the rate of shape change estimated for the integrated shape component. On the other hand, ontogenetic shape changes of the neurocranium module showed significant differences from the integrated rate of shape changes, suggesting that there is an individual component of ontogenetic shape change of this cranial region.

The investigation of the rates of ontogenetic change confirms these interpretations (Fig. 3). The rates of the ontogeny of size show that both modules stop growing at about the same age (~6 years), with the neurocranium showing smaller growth rates then those of the face. The rate of ontogenetic shape change of the face is initially very high, but rapidly decreases to almost no shape changes after the adulthood (~8 years). The neurocranium, on the other hand, have small initial values of shape change, but have a less steady decrease, showing persistent growth at ages above 15 years.

The visualization of the first 2 principal components of each module reveals that the ontogenetic shape variation of the neurocranium and of the face share a common pattern, with juvenile specimens having low values of the first and second PC, while adults have high values on the first PC but tend to disperse around the mean value of the second PC (Fig. 4). The visualization of the scores of the bootstrapped models shows that the asymptotic Procrustes distance corresponds to the mean values estimated for the last 3 age categories.

Table 1

Summaries of the log-likelihood ratio tests comparing a full non-linear least-squares fit of a Gompertz model of ontogenetic changes against a null model using some parameters estimated for a fit on the full configuration size (for size tests) and on the integrated shape component (for shape tests). The null model is always the first to be displayed. See text for further details. Res.Df – residual degrees of freedom of the model; Res.Sum Sq – residual sum of squares, Df – degrees of freedom of the test, Sum Sq – sum of squares of the test, *F* value – approximated *F* value, *p* – estimated *p* value.

	Res.Df	Res.Sum Sq	Df	Sum Sq	*F* value	*p*
Size						
Face	65	24817.29				
	63	20847.47	2	3.97E+03	5.9983	0.00412*
Neuro	65	6393.83				
	63	5093.12	2	1.30E+03	8.0446	0.00077*
Shape						
Face	64	0.00646				
	62	0.00613	2	3.32E−04	1.6788	0.19497
Neuro	64	0.01931				
	62	0.01362	2	5.70E−03	12.9704	0.00002*

* Significant differences between models.

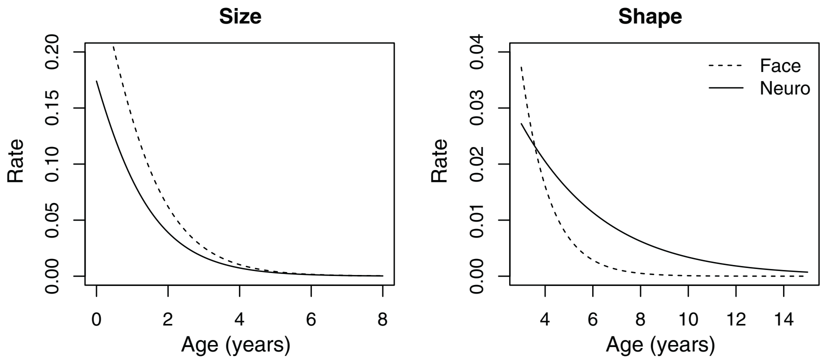

Fig. 3. Rates of ontogenetic size and shape change for both cranial modules. Rates are normalized to be a fraction of the asymptotic size *A*.

Discussion

Monteiro-Filho et al. (2002) were the first authors to describe and quantify the geometric differences between the skull of marine and riverine dolphins from the genus *Sotalia*, separating *S. guianensis* from *S. fluviatilis*, respectively. While the first have a larger and longer skull with the rostrum aligned with the foramen magnum opening (and therefore with the axial skeleton), the latter have a smaller and shorter skull, with a downward inflection of the rostrum in relation to the foramen magnum. Despite differences in size between the two species, the authors found no evidence of allometric scaling as a mechanism for between-species difference within *Sotalia* because of the apparent lack of correlation of within and between population allometry. However, the possibility of evolution through mosaic heterochrony resulting in the observed patterns (Mitteroecker et al. 2004) was not evaluated. Our results show that different cranial regions of the skull of *S. guianensis* develop at different rates and attain adult morphology at different ages, suggesting that the skull of *Sotalia* could have suffered mosaic heterochronic changes, thus producing the differences detected between species. This would explain why the ontogenetic shape changes of *S. guianensis* described here are similar to the differences between species of *Sotalia*: younger *S. guianensis* shows a relatively larger braincase and a shorter rostrum, exhibiting a downward inflection of the rostrum and a ventrally placed foramem magnum. This pattern is consistent with the interpretation of

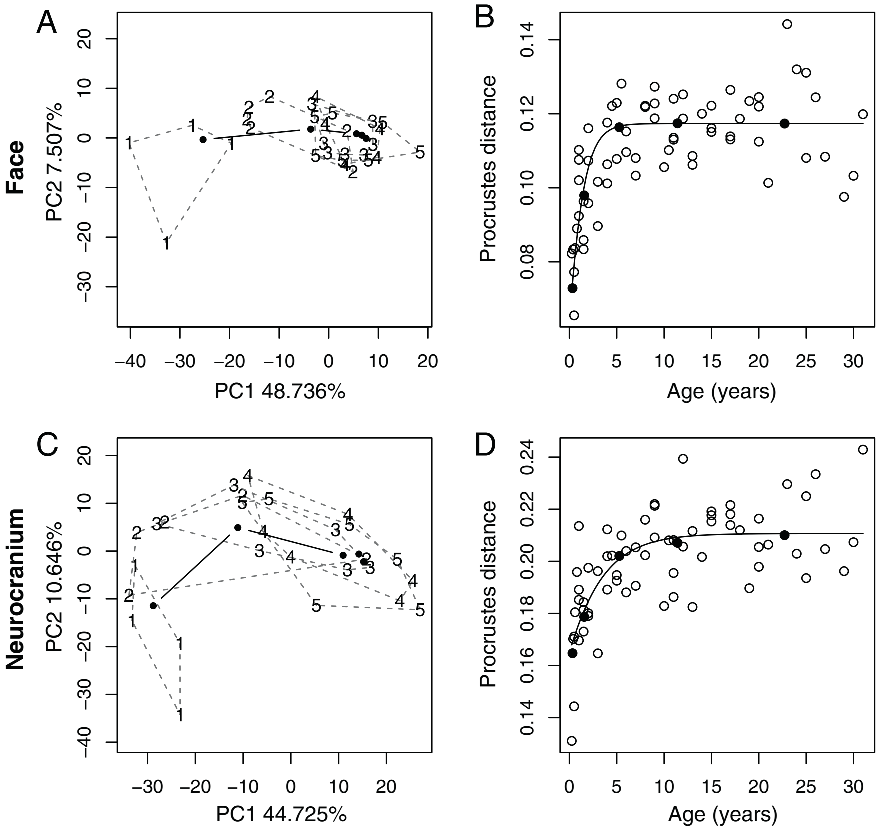

Fig. 4. Ontogenetic changes in the neurocranium (A–B) and face (C–D), representing the first two shape principal components of the morphospace relative to each module (A and C) and the ontogenetic shape functions (B and D). Dashed lines limits the convex hull referent for each age category (different age categories are delimited by different numbers). Solid points represent the bootstrapped means for each age category that best fitted the ontogenetic function prediction. Percentage of shape variance explained by each principal component is between parenthesis.

S. fluviatilis as a neotenic form of *S. guianensis*. Moreover, Fettuccia et al. (2009) found that some localized non-metric characters of *S. fluviatilis* were neotenic in comparison to *S. guianensis*, reinforcing the idea that differences in timing of ontogenetic processes can have local effects that are not clear through the investigation of the full skull.

The evaluation of ontogenetic rates of change indicates that face and neurocranium shows different rates of development for both size and shape. The face have a rapid initial development, reaching adult size at ~6 years and adult shape at ~8 years old. The neurocranium showed low early rates of change and despite the fact that it reached adult size at the same time as the face (~6 years), there is some shape change throughout adult life (>8 years). The faster development of the face could be imposed to functional demands related to ecological factors. In Odontoceti the relative size of the snout is negatively correlated to suction feeding ability (an adaptation for capturing prey underwater), with animals with smaller snouts having a better performance (Werth 2006). Moreover, even though skull asymmetry is usually regarded as related to the use of biosonar (e.g. Moore 1981; Yurick and Gaskin 1988; Thomson and Richardson 1995), there are evidences that it could also be related to larynx asymmetry, which in turn determines maximum prey size (Macleod et al. 2007). These ecomorphological correlations suggest that the attaining of the adult morphology of the face is essential for various aspects of the species life history. On the other hand, the persistence of shape development in the neurocranium can be related to the loosening of mechanical pressures on the cetacean skeleton provided by the aquatic habitat. In fact, while terrestrial mammals show positive allometry between bone weight and total weight, aquatic animals show a proportional relationship between both variables (Reynolds 1977), suggesting that the aquatic habitat can loosen stabilizing selection on bone density and resistance imposed by the terrestrial habitat, allowing a more flexible exploration of heterochrony and allometry (Galatius 2010). Another possible explanation is that the persistence of shape change on the neurocranium is caused by epigenetic factors, such as muscle use and development, promoting bone remodeling and the development of crests and ridges that extends into adulthood.

In a recent analysis of skull ontogeny of Phocoenidae, Galatius and colleagues (Galatius 2010; Galatius et al. 2011) found a common allometric component between phocoenid and delphinid species that are similar to the ontogenetic patterns shown here for *S. guianensis*. Some morphological aspect described here and by those authors, namely the downward inflexion of the rostrum and the ventral displacement of the foramen magnum seems to be common not only to ontogenetic trends, but also for between (Galatius 2010) and within species variation (Loy et al. 2010). While these aspects are suggested to be related to foraging in shallow waters (Monteiro-Filho et al. 2002), forms with the rostrum more aligned with the vertebral column, such as the ones associated with older individuals here, are though to be related do pelagic feeding (Galatius 2010; Loy et al. 2010). The reoccurrence of these morphological patterns within Delphinidae, its correlation with ontogenetic trends and its apparent correlation with different aquatic habitats, suggests that there might be an underling genetic and developmental phenomenon that could facilitate adaptation to different environments (Schluter 1996). Therefore, more investigations of the ontogeny of the *Sotalia* and other Delphinidae species are warranted in order to test these possibilities.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.mambio.2012.04.007.

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