# *Skull ontogenetic variation of the coastal developmental stage of the loggerhead turtle* (Caretta caretta) *in the western South Atlantic Ocean*

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PRIMARY RESEARCH PAPER

# Skull ontogenetic variation of the coastal developmental stage of the loggerhead turtle (*Caretta caretta*) in the western South Atlantic Ocean

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**Abstract** The present study aims to describe the ontogenetic changes in the skull of the loggerhead turtle, *Caretta caretta* by focusing on the stages of development in the western South Atlantic Ocean. Our hypothesis is based on the premise that changes in feeding habits will reflect changes in the shape and/or size of the skull. The existence of changes in skull of the loggerhead turtle were analyzed using traditional and geometric morphometrics on skulls collected from stranded individuals in the southern Brazilian coast. As a general result, a transformation pattern was observed: from younger specimens with smaller, elongated and flattened skulls towards a larger, rounded and more robust skull in older specimens. It is suggested that these skull changes are associated with the diet shift of the loggerhead turtle specimens, providing the skull with greater mechanical resistance and enabling a change in feeding strategy from soft organisms to hard-shelled preys. This result highlights the importance of southern Brazilian coast for the life cycle of the loggerhead turtle. In this region, the individuals undergo the process of ontogenetic diet shift, changing their skull shape to adapt to the newly occupied niche and ensuring the ecological success of the species.

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**Keywords** Sea turtles · Traditional morphometry · Geometric morphometrics · Diet shift · Development

## Introduction

The loggerhead turtle, *Caretta caretta* (Linnaeus, 1758), is the third largest sea turtle in the world, occurring in subtropical, tropical and temperate waters (Marquez, 1990). Due to a slow growth rate, this species needs 25–38 years of development to reach maturity (Piovano et al., 2011; Petitet et al., 2012). The species is listed as vulnerable by IUCN Red List (Casale & Tucker, 2017). In Brazilian coast it is the most abundant sea turtle (Reis et al., 2010) with nesting areas in the States of Rio de Janeiro, Espírito Santo, Bahia and Sergipe (Marcovaldi & Chaloupka, 2007). The Brazilian nesting population is the third largest remaining population in the world (Marcovaldi & Chaloupka, 2007).

Throughout its life cycle, the loggerhead turtle occupies several different marine environments. Hatchlings navigate actively and passively towards the pelagic zone immediately after their emergence in coastal areas (Briscoe et al., 2016), becoming hardly detectable for several years (Carr, 1987). This developmental period, known as the "lost years", is an interval of time when young turtles gain food, thermal benefits and protection from their association with floating *Sargassum* communities (Frazier, 1999; Mansfield et al., 2014). After this period in pelagic waters, juvenile loggerhead turtles recruit to developmental areas, resulting in a habitat transition towards the neritic zone that modifies the selective pressures upon individual foraging performance (Bolten, 2003). The habitat transition in South Brazil occurs when turtles reach ~ 12 years (Lenz et al., 2016) and is followed by a shift in diet, from the consumption of soft-bodied organisms in the pelagic zone to a diet based on hard-shelled benthonic mollusks and crustaceans (McClellan & Read, 2007; Casale et al. 2008; Lazar et al., 2011). Studies in southern and southeastern Brazil confirmed the ingestion of mollusks and crustaceans preys by loggerheads and also identified the ingestion of by-catch disposals indicating the overlapping between feeding and fisheries grounds (Bugoni et al., 2003; Di Beneditto et al., 2015). However, many aspects of loggerhead turtle's natural history are hard to assess, resulting in a gap in knowledge of its biology, mainly related to development, for a good part of its oceanic stages (Ishihara & Kamezaki, 2011).

The coast of the State of Rio Grande do Sul in southern Brazil is an area of extreme importance for the loggerhead turtle populations from the Western South Atlantic Ocean. This region is known as a foraging and development area for the loggerhead turtle population from the Western South Atlantic Ocean (Marcovaldi & Chaloupka, 2007; Sales et al., 2008; Petitet et al., 2012; Lenz et al., 2016), and in these waters loggerheads are threatened by the fisheries activities (Sales et al., 2008) and also suffer with the ingestion of anthropogenic debris (Bugoni et al., 2001), as well as in other Brazilian regions (Gallo et al., 2006; Poli et al., 2014). Stranded sea turtles are consistently reported in southern Brazil, mainly from October to March, when the incidental captures of loggerhead turtles by fishing boats increase in frequency (Monteiro et al., 2016). Such stranded individuals become an important source of information for deciphering key ecological questions about this specific stage of loggerhead turtle development, thanks to the effort of local research institutions that collect the specimens despite their advanced degree of decomposition (Barata et al., 2004; Lenz et al., 2016).

The skeleton, and particularly the skull of stranded individuals are an important source of information for ontogenetic, population, and historical comparisons (Barata et al., 2004; Lenz et al., 2016). The skull is an anatomical structure of extreme morphological and functional complexity, which has the advantage of remaining well preserved, even for specimens under an advanced degree of decomposition. Skull ontogenetic development is determined by intrinsic (genetic) and extrinsic (environmental) factors, conferring changes in terms of shape and size essential for maintaining its functional performance (Hanken & Hall, 1993). Such functional optimization may be driven by the skull's active participation in the acquisition and processing of food (Emerson & Bramble, 1993), when skull shape and size must operate in concert with dietary habits that are dynamic throughout the ontogenetic development of the individuals (see examples in monkeys: Cochard, 1985; Simons & Frost, 2016; rodents: Breno et al., 2011, Maestri et al., 2015a, b; felines: Christiansen, 2012; pinnipeds: Brunner et al., 2004; and freshwater turtles: Claude et al., 2004, Pfaller et al., 2009). The existence of an important diet shift associated with the developmental stage in *C. caretta* suggests that skull shape may respond accordingly. However, there is a lack of information about the ontogeny of the species, with practically no data on its skull development.

In this context, in the present study we searched for ontogenetic changes in the skull of the loggerhead turtle by focusing on the stages of development in coastal habitats. Our rationale is based on the premise that changes in feeding habits are usually associated with changes in the shape and/or size of the skull. We expect to find shape modifications in the loggerhead turtle's skull as a consequence of diet shifts, known to occur in this species in the Western South Atlantic Ocean. Additionally, we aim to describe which cranial characteristics are modified during the development of the species in order to obtain a better anatomical understanding of the skull development of the loggerhead turtle.

## Materials and methods

### Sample design

Samples were obtained opportunistically from dead individuals stranded along the coast, resulting in 97 skulls of *C. caretta* (see Supplementary Material 1). The sampling sites comprised a coastal strip of approximately 270 km between the Barra da Lagoa do Peixe (Mostardas, 31° 22″ S 51° 02″ W) and the Barra do Rio Mampituba (Torres, 29° 19″ S 49° 43″ W) on the coast of Rio Grande do Sul, southern Brazil.

A total of 91 skulls were collected between 1994 and 2010 by the *Grupo de Estudos de Mamíferos Aquáticos do Rio Grande do Sul* (GEMARS), and are deposited in the *Laboratório de Herpetologia da Universidade Federal do Rio Grande do Sul* (UFRGS). The remaining six skulls were collected between 2011 and 2017, and are deposited in the *Museu de Ciências Naturais from the Centro de Estudos Costeiros, Limnológicos e Marinhos at the Universidade Federal do Rio Grande do Sul* (MUCIN/UFRGS).

Specimen ages were previously determined for 79 skull samples by Lenz et al. (2016) using skeletochronological analysis, which consists of counting the growth lines present in the humerus of individuals (Zug et al., 1986; Avens & Snover, 2013). Different scenarios of relative age class in relation to centroid size were evaluated in order to establish what age class interval better explains the size variation in the skulls of *C. caretta*. As a measure of size that is largely independent of variation in shape, we used centroid size, the square root of the sum of squared distances of a set of landmarks from their centroid (Bookstein, 1991). This is the only measure of size mathematically independent from shape (Zelditch et al., 2004). It was tested using Kruskal–Wallis tests. The scenario was chosen in which age classes obtained the most significant value of independence between intervals (see Supplementary Material 2). In this context, three age classes were chosen: individuals from 10 to 13 years, individuals from 14 to 17 years, and individuals aged 18 years or more. It is important to highlight that although the age classes used here have been established a priori, this procedure was made necessary since the maturation of individuals does not necessarily follow somatic growth rates (Bernardo, 1993).

### Morphometric procedures

The ontogenetic changes in the skull of the loggerhead turtles were analyzed by traditional and geometric morphometrics, in order to obtain shape and size information on the structure under evaluation. Though traditional morphometrics offer an intuitive interpretation over linear measurements of the structures, it offers little information about the geometry of the forms (Breno et al., 2011). On the other hand, geometric morphometrics allow a description of the changes in the shape of the specimens independent of those related to their size, helping to synthesize the main transformations of complex biological forms (Zelditch et al., 2004).

### Traditional morphometrics procedures

Traditional morphometric characterization of the skulls was performed from 12 cranial and three mandibular linear measurements (Table 1 and Fig. 1), based on Bever (2008) and Kamezaki & Matsui (1995). A total of 17 samples were excluded from the initial sample set due to missing reference points for measurements in the skull. All cranial and mandibular measurements were performed with a digital caliper (300 mm, Hélios) and automatically stored in a database using the Gage Wedge program interface (TAL Technologies 2006).

**Table 1** Description of the linear measurements used in the study

| Linear measure | Description |
|---|---|
| Skull height (SH) | Vertical measure between the skull base and the highest point of the suture between the parietal and supraoccipital bone |
| Nostril width (NW) | Greater horizontal aperture of the nasal fossa |
| Interorbital width (IOW) | Minimum width between the orbits |
| Orbital length (OL) | Longer orbit length |
| Palate width (PW) | Maximum width between the left and right palatine bones |
| Vomer length (VL) | Maximum vomer length |
| Pterygoid width (PTW) | Minimum waistline width of the pterygoids |
| Pterygoid process (PP) | Distance between bones of the pterygoid process |
| Squamosals width (SQW) | Maximum width between the right and left squamosals |
| Skull length (SL) | Maximum length of the skull between the end of the supraoccipital and the premaxilla |
| Post-orbital skull width (PSW) | Maximum width between post-orbitals |
| Dentary length (DL) | Maximum length of the dentary bone |
| Lower mandibular width (LMW) | Maximum width between the surangular bones |
| Lower mandibular length (LML) | Distance between the end of the dentary and the articular |
| Premaxilla length (PL) | Maximum length of the premaxilla |

### Geometric morphometrics procedures

Geometric morphometrics analyses were based on two-dimensional anatomical landmarks. We independently analyzed the information obtained from three cranial anatomical views (dorsal, lateral, frontal), and two mandibular anatomical views (dorsal, lateral). Skull samples were excluded from the data set of a particular anatomical view in cases of missing landmarks, resulting in unbalanced sample sizes among different anatomical views (cranial dorsal: $n = 70$, cranial lateral: $n = 72$, cranial frontal: $n = 76$, mandibular dorsal: $n = 81$; mandibular lateral: $n = 80$). Each sample view was photographed with a 50 mm lens coupled to a digital camera (Canon 450d) fixed on a tripod, with each specimen aligned with base supports, in order to avoid parallax error. The standard resolution of all images was 800 × 600 pixels, and always included a scale, for subsequent calibration of analyses. All images were saved in jpeg format organized by anatomical view using the software tpsUtil v.1.74 (Rohlf 2016a). One hundred and four anatomical landmarks and semilandmarks (see Fig. 1 and Supplementary Material 3 for details), assumed to be morphologically and topologically equivalent in all specimens, were selected to describe the variation in skull shape and were digitized using the software tpsDig2 v.2.30 (Rohlf 2016b).

All landmarks were always plotted by the same person (EAL). Each landmark was chosen using the following criteria proposed by Bookstein (1991) and emphasized by Zelditch et al. (2004): (1) the anatomical points must be homologous, (2) the relative position between points should be consistent, (3) the anatomical points should provide adequate coverage of the morphology, (4) the points can be found repeatedly and reliably in all specimens, and (5) the points should lie in the same plane. Only type 1 and type 2 landmarks were used (Fig. 1A–F), which are considered the most consistent for shape analysis (Bookstein, 1991). Moreover, semilandmarks were used to improve the geometric information over specific regions of the structure, such as curvatures between adjacent landmarks (Fig. 1E, F). Symmetrical anatomical views (cranial dorsal, cranial frontal and mandibular dorsal) had their landmarks and

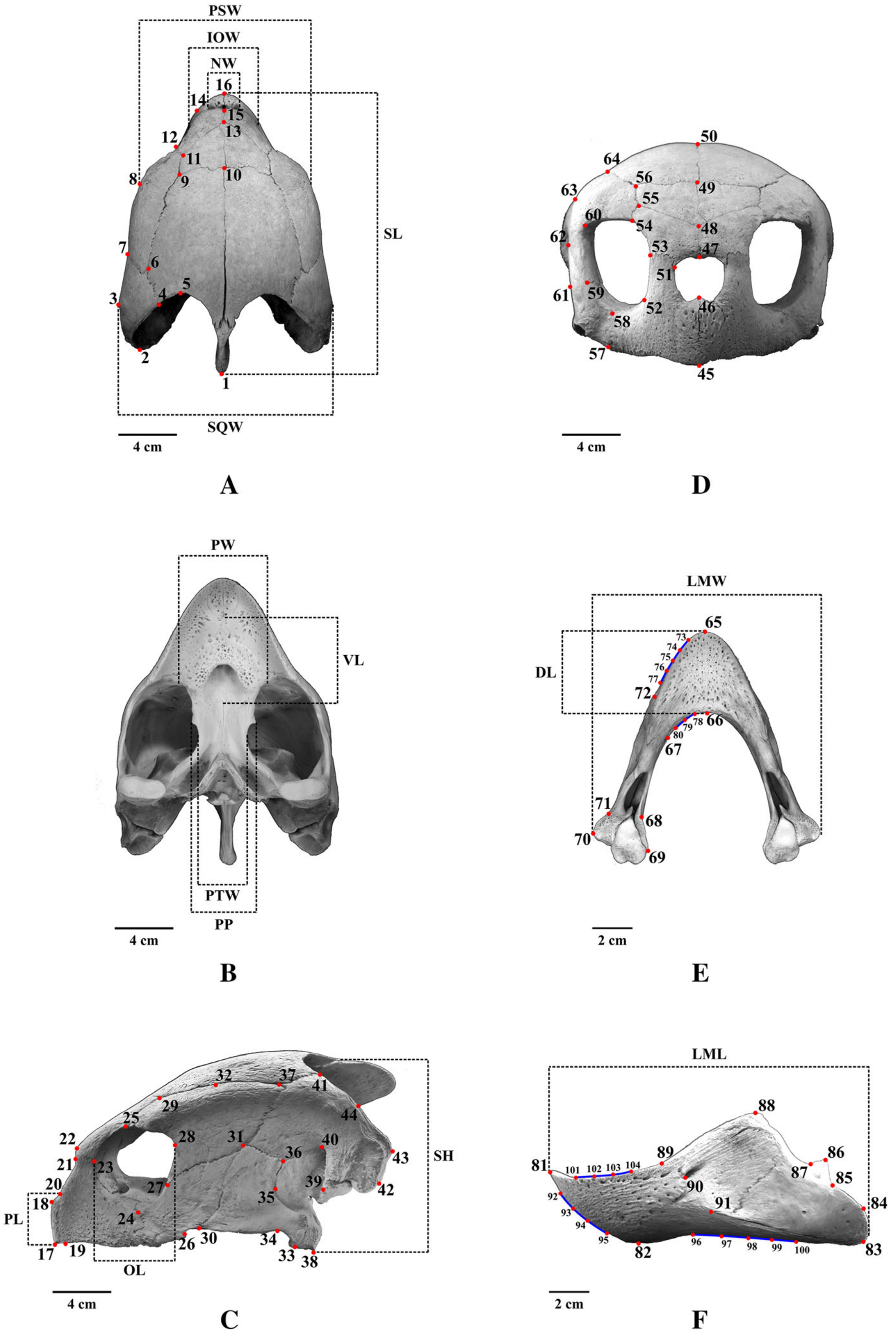

**Fig. 1** Landmarks, semilandmarks and linear measurements of the skull of *Caretta caretta*. **A** Cranial dorsal view. **B** Cranial ventral view. **C** Cranial lateral view. **D** Cranial frontal view. **E** Mandibular dorsal view. **F** Mandibular lateral view

semilandmarks positioned in a single side of their symmetry plane, in order to avoid an inflation of degrees of freedom for the analyses (Oliveira et al., 2005).

Coordinates from the landmarks and semilandmarks were superimposed using a generalized Procrustes Analysis, in order to isolate the shape component from variation regarding scale, position, and orientation. That way, shape was separated from the size (for details see shape analyses below).

## Data analyses

### *Size analyses*

We tested whether the age classes respond to the size variation of the evaluated structures, on the premise that the different age classes had some degree of independence among them, at least in relation to size. Size analyses were performed upon the linear measurements obtained via traditional morphometrics, and also upon the centroid size obtained from geometric morphometrics procedures.

### *Traditional morphometrics*

Skull size evaluation using traditional morphometrics techniques followed two approaches. First, linear dimensions were independently compared among age classes through a one-way ANOVA, or by a Kruskal–Wallis test when the data do not meet the premises of normality and homogeneity of variance. The effect of age class upon skull size estimates was considered significant when $\alpha < 0.05$. The second approach considered the integrated effect of all dimensions, using the first component of a Principal Component Analysis (PCA) based on the original linear measurements. The advantage of PCA in relation to the independent linear dimensions is that it controls for the correlations between the variables, as well as offering a reduction of dimensionality allowing the verification of multivariate patterns in a few dimensions. In addition, the first component of the PCA serves as a global descriptor of the size of the structure, since the loads of all variables for this component are positive (Neff & Marcus, 1980). All analyses were performed in the Past program (version 3.16, Hammer et al., 2001).

### *Geometric morphometrics*

Skull size under the geometric morphometrics perspective was described by the centroid size of each anatomical view, as previously explained (Bookstein, 1991). Centroid size was calculated using the coordinates of the anatomical landmarks in the software MorphoJ (version 1.06 D; Klingenberg, 2011).

We used centroid size to infer the age class of those samples not described in Lenz et al. (2016) by comparing their cranial centroid sizes with specimens of known age, and subsequently, these samples were placed at a certain age class according to their centroid size. Then, for each anatomical view, we performed a Kruskal–Wallis test ($\alpha < 0.05$) comparing the centroid size among the age classes. All calculations were made using the Past software (version 3.16, Hammer et al., 2001).

### *Shape analyses*

All analyses were performed independently for each view, allowing the visualization of shape changes of the skull and mandible of *C. caretta* across the stages of coastal development. The differences in shape between the groups were evaluated through the Procrustes Distance, which is used as the distance between samples (landmark configurations) in the shape space (Rohlf, 1996). All analyses were performed in the MorphoJ program (version 1.06 D, Klingenberg, 2011).

Landmark configurations were aligned by General Procrustes Analysis (GPA) using MorphoJ (version 1.06 D, Klingenberg, 2011). The GPA method computes a consensus configuration (least-squares Procrustes average) based on the landmark coordinates of all specimens—see Bookstein (1991) and Zelditch et al. (2004) for details. We computed a matrix of partial warp scores—equally weighted regardless of scale—to infer the deviation of each specimen from the consensus configuration (Rohlf 1993). From the covariance matrix of the partial warps scores, we ran a Canonical Variates Analysis (CVA), which is equivalent to principal components (PC) of the distribution of shapes in a space tangent to Kendall's shape space, except that it emphasizes among group comparisons instead of among specimens differences. Each canonical axis expresses a direction of shape change that is orthogonal to the remaining canonical axes, which can be summarized as a thin-plate spline diagram taking as a reference the mean shape of the configuration of landmarks (Zelditch et al., 2004). Since CVA scores only describe the difference of shape among groups, we performed a permutation test (10,000 repetitions) on the matrix of between-groups Procrustes distance to infer if our classification has statistical support. The diagrams representing the shape changes for each anatomical view were created using tpsDig2 v.2.30

(Rohlf, 2016b) and MorphoJ version 1.06d (Klingenberg, 2011), from which we obtained the average configuration of skull and mandibular changes.

### *Shape versus size*

Lastly, in order to explore the association between shape and size variables, the multivariate regression test was performed with the first Procrustes coordinate regression score (shape) on log-transformed centroid size (size). The size of the logarithmic centroid is usually used in ontogeny work, minimizing some disproportionate on the data, which produce a better linear relationship and give a superior analysis performance (Klingenberg, 2016). Through the coefficient of determination ($R^2$) it is possible to obtain in percentage the predictive power of the independent axis variable over the dependent axis variable (Monteiro & Reis, 1999), in this case, how much size predicts shape. The permutation test (10,000 times) of multivariate regression uses the null hypothesis of complete independence between the dependent and independent variables.

## Results

### Size

#### *Geometric morphometrics: validation of relative age classes*

The results of the Kruskal–Wallis test for the centroid size of all anatomical views indicated significant and consistent differences in skull size between age classes as suggested a priori (Table 2, Fig. 2). This confirmed the statistical independence of the proposed age classifications. In this way, the proposed age classification was maintained for all subsequent analyses of cranial shape variation throughout development.

#### *Traditional morphometry: linear measurements*

The results of the analysis of variance showed that all measurements had statistically different means ($P < 0.05$) between the three relative age classes (Table 3), which were suggested a priori by the previous analysis of the centroid size for age classes. In general, the results of size measured by traditional morphometry corroborated those of the centroid size regarding the separation of relative age classes.

Principal component analysis reduced the dimensionality of the data set to two components, where the first principal component (PC1) accounted for 96.4% of the observed variation. The most important measurements for PC1 were those related to the length and width values of the skull of *C. caretta*. The linear skull length (SL) was the one that contributed the most to the PC1, followed by the squamosal width (SQW). The graphical interpretation of the scatter points of principal component analysis, especially along the first principal component, reveals size segregation between younger individuals (from 10 to 13 years and from 14 to 17 years) in relation to older individuals, with partial overlap between the two groups (Fig. 3).

**Table 2** Mean ± standard deviation (sample size) in pixels of the centroid size of the three cranial views and two mandibular views for the relative age classes established a priori for *Caretta caretta* in the coastal development area of southern Brazil. *H*: Statistical value for non-parametric test (Kruskal–Wallis); d.f.: degrees of freedom. For all comparisons: post hoc Bonferroni $P < 0.01$

| Anatomic view | Mean centroid size $\times 10^{15} \pm$ SD $\times 10^{15}$ ($n$) | | | Statistic | $P$ |
|---|---|---|---|---|---|
| | Relative age classes | | | | |
| | 10 to 13 years | 14 to 17 years | ≥ 18 years | | |
| Skull | | | | | |
| Dorsal | 2.05 ± 0.13 (18) | 2.28 ± 0.17 (24) | 2.90 ± 0.37 (28) | $H = 45.9$; d.f. = 65 | < 0.001 |
| Frontal | 1.28 ± 0.10 (21) | 1.41 ± 0.10 (25) | 1.74 ± 0.24 (30) | $H = 41.4$; d.f. = 72 | < 0.001 |
| Lateral | 2.75 ± 0.18 (21) | 3.02 ± 0.22 (23) | 3.64 ± 0.40 (28) | $H = 44.6$; d.f. = 67 | < 0.001 |
| Mandible | | | | | |
| Dorsal | 1.40 ± 0.08 (27) | 1.51 ± 0.14 (24) | 1.84 ± 0.24 (30) | $H = 43.8$; d.f. = 76 | < 0.001 |
| Lateral | 1.69 ± 0.10 (27) | 1.83 ± 0.14 (23) | 2.20 ± 0.25 (30) | $H = 48.2$; d.f. = 76 | < 0.001 |

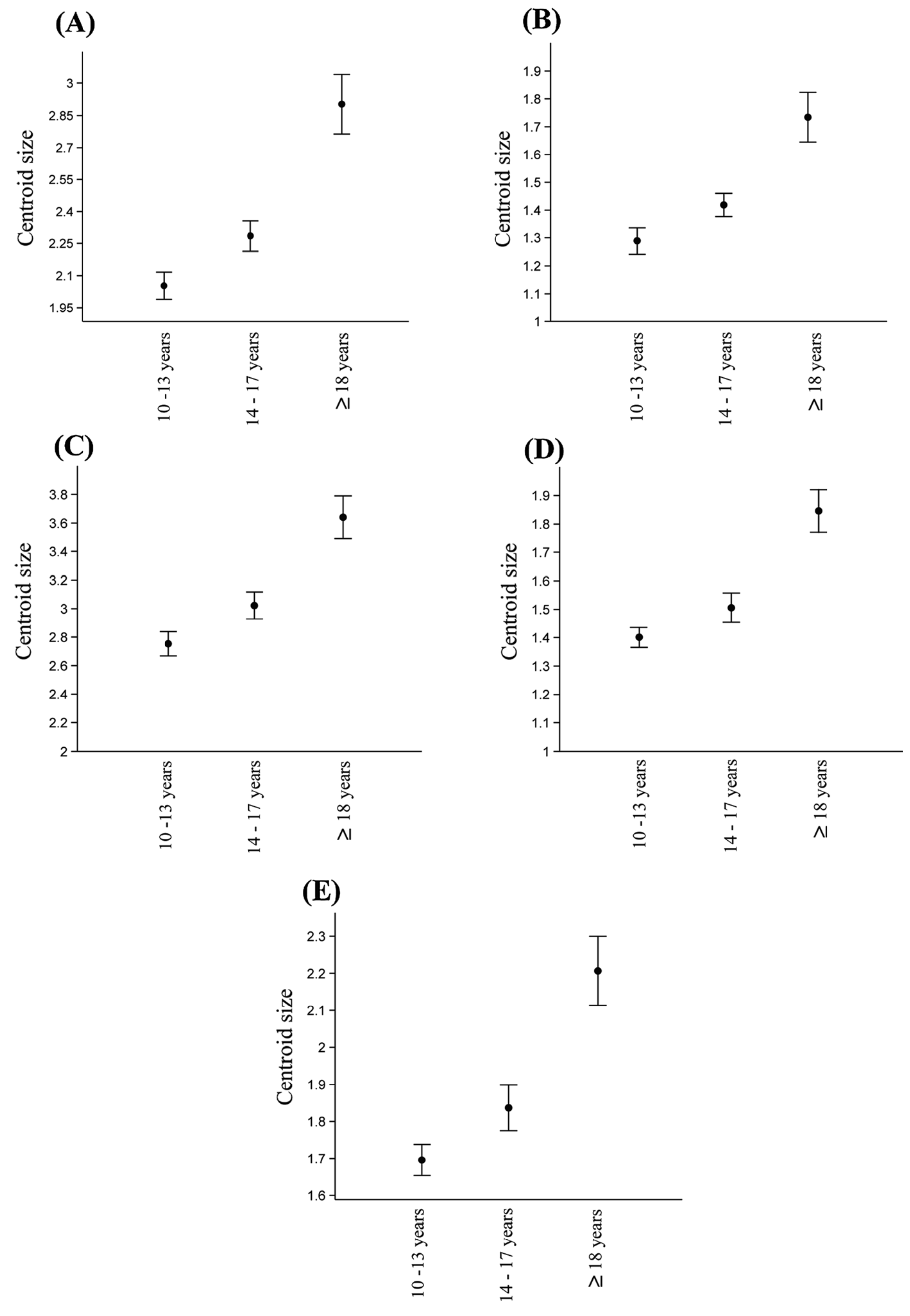

**Fig. 2** Mean of centroid size (black circles) in pixels (× $10^{15}$) and 95% confidence interval of the mean (vertical line) for *Caretta caretta* skulls and mandible of the groups of relative age classes studied (10 to 13 years, 14 to 17 years, ≥ 18 years). **A** Cranial dorsal view; **B** Cranial frontal view; **C** Cranial lateral view; **D** Mandibular dorsal view; **E** Mandibular lateral view

**Table 3** Summary of the variation of the linear measurements of skull and mandible (in millimeters) and result of the comparison between the relative age classes proposed for *Caretta caretta* in the coastal development area of southern Brazil. *F*: statistical value for parametric test (one-way ANOVA). *H*: statistical value for non-parametric test (Kruskal–Wallis). For all comparisons: d.f. = 79, $P < 0.001$

| Measurements | Relative age classes | | | Statistics |
|---|---|---|---|---|
| | 10 to 13 years (*n* = 25)<br>Mean ± SD<br>(min–max) | 14 to 17 years (*n* = 25)<br>Mean ± SD<br>(min–max) | ≥ 18 years (*n* = 30)<br>Mean ± SD<br>(min–max) | |
| SL | 175.5 ± 15.7<br>(140.4–210.7) | 191.2 ± 17.0<br>(149.0–233.5) | 214.8 ± 27.5<br>(164.3–265.3) | *H* = 42.6 |
| SQW | 127.4 ± 13.4<br>(91.8–162.9) | 144.3 ± 14.7<br>(109.3–179.3) | 162.8 ± 25.5<br>(119.8–205.9) | *H* = 41.6 |
| LMW | 109.3 ± 11.4<br>(81.5–137.2) | 120.4 ± 13.2<br>(88.7–152.2) | 140.8 ± 19.7<br>(102.1–179.5) | *H* = 42.7 |
| LML | 114.0 ± 15.1<br>(89.5–138.5) | 123.1 ± 17.0<br>(93.7–152.6) | 144.5 ± 26.5<br>(109.7–179.4) | *H* = 45.5 |
| SH | 99.7 ± 9.5<br>(77.8–121.6) | 104.2 ± 10.6<br>(79.2–129.2) | 121.2 ± 18.9<br>(88.2–154.1) | *H* = 38.4 |
| PSW | 100.5 ± 8.6<br>(79.6–121.4) | 112.2 ± 9.5<br>(89.3–135.2) | 126.3 ± 16.1<br>(99.1–153.5) | *H* = 42.0 |
| DL | 40.8 ± 4.4<br>(30.3–51.4) | 45.2 ± 4.8<br>(34.0–56.3) | 52.6 ± 7.4<br>(38.8–66.5) | *H* = 44.7 |
| VL | 52.4 ± 5.3<br>(39.1–65.8) | 51.8 ± 5.3<br>(40.5–63.1) | 58.8 ± 7.1<br>(44.0–73.7) | *H* = 37.2 |
| OL | 53.9 ± 4.2<br>(46.7–61.1) | 54.7 ± 4.9<br>(43.6–65.9) | 61.6 ± 8.3<br>(44.6–78.5) | *H* = 21.9 |
| PW | 50.1 ± 3.9<br>(40.7–59.4) | 54.9 ± 4.7<br>(43.5–66.3) | 62.4 ± 6.9<br>(50.7–74.2) | *H* = 43.3 |
| IOW | 42.0 ± 3.4<br>(33.7–50.3) | 45.5 ± 4.2<br>(36.9–54.1) | 53.6 ± 6.0<br>(42.4–64.8) | *F* = 39.9 |
| PL | 29.5 ± 3.3<br>(22.5–36.5) | 31.8 ± 3.9<br>(24.0–39.5) | 39.2 ± 5.2<br>(29.2–49.3) | *F* = 38.0 |
| PTW | 27.6 ± 2.1<br>(23.0–32.3) | 32.8 ± 3.5<br>(24.4–41.3) | 35.9 ± 4.9<br>(26.9–44.9) | *H* = 40.3 |
| PP | 36.6 ± 2.2<br>(31.4–41.7) | 39.2 ± 3.8<br>(31.2–47.1) | 45.9 ± 5.1<br>(35.7–56.2) | *H* = 35.3 |
| NW | 24.3 ± 2.0<br>(20.2–28.4) | 26.2 ± 2.3<br>(20.1–32.3) | 30.5 ± 3.1<br>(24.0–37.0) | *F* = 33.8 |

## Shape

### *Geometric morphometrics*

The skulls of *C. caretta* showed consistent shape modifications throughout development, for all the cranial and mandibular anatomical views. The same segregation between younger (from 10 to 13 years and from 14 to 17 years of age) and older individuals (18 years or older) was observed for every anatomical view (Figs. 4, 5, 6, 7, 8). Only younger classes have no statistically significant differences between them in the cranial and mandibular shape (from 10 to 13 years and from 14 to 17 years).

The contributions of each canonical axis in the elucidation of cranial and mandibular shape variation for each of the considered views, as well as the percentage of general cross-validation correspondence

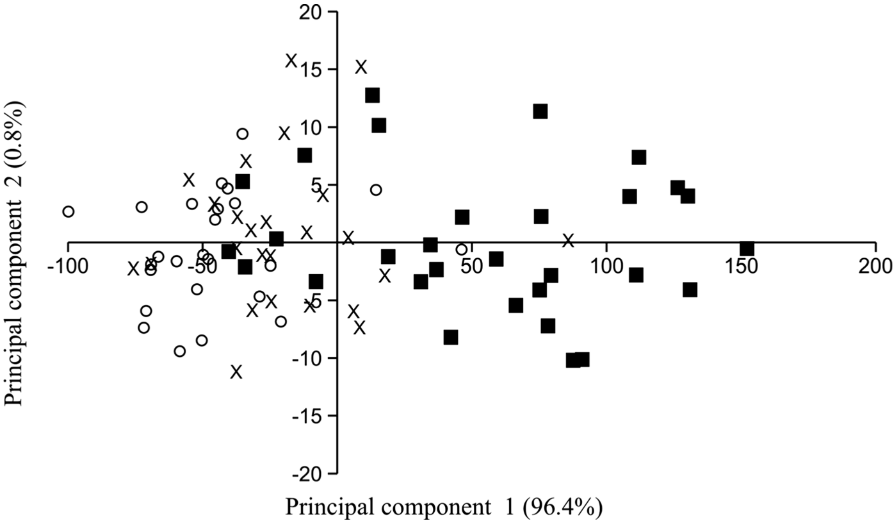

**Fig. 3** *Caretta caretta* ($n = 80$) scores on the first and second axes of the principal components derived from the cranial measurements set. Open circles: specimens with relative ages between 10 and 13 years. X symbols: specimens with relative ages between 14 and 17 years. black squares: specimens of relative age of 18 years or older

between the age classes in the respective views, allows the validation of the allocation of the individuals to their corresponding groups (Table 4).

### *Cranial dorsal view (Fig. 4)*

Throughout the first canonical variable we observed the expansion of certain cranial structures (half skull only) during the development of *C. caretta* individuals, leading to a rounded skull shape in older individuals (Fig. 4). This is mainly due to the expansion of the postorbital and squamosal bones, together with the lateral expansion of the parietal bone. Another change to be highlighted is the shortening of the anterior region of the skull (see also the cranial lateral view, Fig. 5). This change in the anterior region occurred due to premaxilla, maxilla and prefrontal retraction in specimens aged 18 years or older, generating more rounded and robust skulls in *C. caretta*.

Along the second canonical axis there is only a partial separation between groups of younger individuals. This tendency to separate younger age classes according to cranial shape can be explained by the tapering in the position of the anatomical landmarks 11 and 12 during development, which are located in the anterior region of the skull and associated with the intersection of sutures of the postorbital, frontal and prefrontal bones.

In general, the changes in shape seen in the dorsal view indicated that the skulls of *C. caretta* undergo a shortening in the rostral region and a broad rounding during the development of the individuals.

### *Cranial lateral view (Fig. 5)*

The segregation along the first canonical axis was characterized by the shortening of the anterior region of the skull in the older specimens of *C. caretta*. The premaxilla, maxilla, and prefrontal have a reduction in size, whereas a great expansion of the squamosal occurs in the posterior cranial region (Fig. 5). In this region, there is also an expansion of postorbital, jugal and quadratojugal bones. In addition, a reduction in the size of the orbit was observed in older individuals of *C. caretta*. In general, in this view it is observed that throughout the development of the specimens, the *C. caretta* skull transforms from a more elongated and flattened shape in the younger specimens to a more rounded and robust shape in the older individuals.

### *Cranial frontal view (Fig. 6)*

The observed pattern along the first canonical axis represents the expansion of two bones of the posterior (superior) region of the skull: the parietal and the postorbital (Fig. 6). The jugal bone also undergoes an expansion of its upper region, while its lower part contracts. In the superior region of the skull, a clear expansion is observed, making it more rounded in the specimens with age equal or older than 18 years. Another important modification is the stretching of the premaxilla bone, located in the anterior cranial region near the maxilla. Next to this region there is a reduction of the nasal cavity towards the positive values of the axis. In this view, the orbit undergoes a

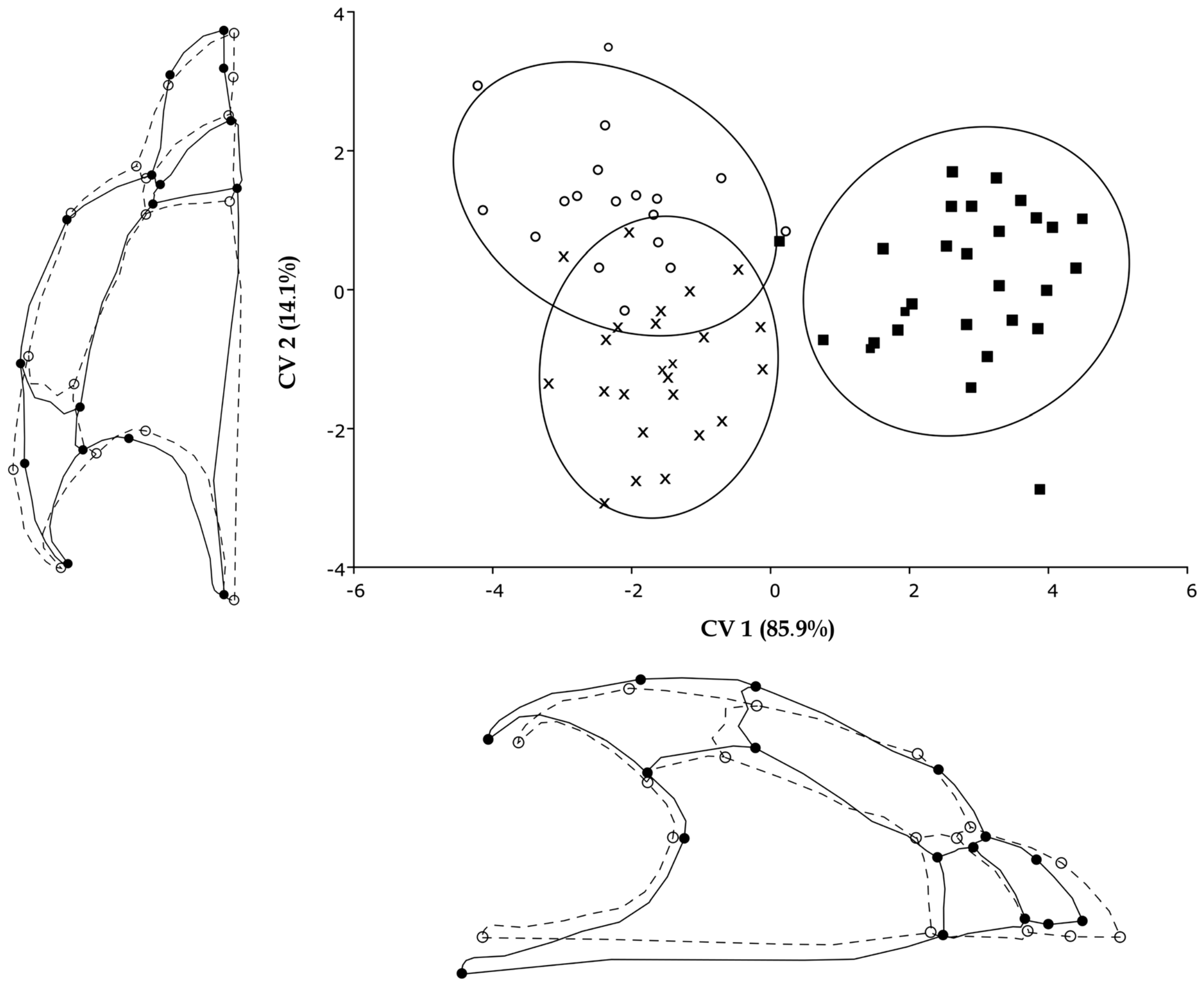

**Fig. 4** Scores of the specimens on the first and second axes of the canonical variates analysis for the cranial dorsal view ($n = 70$) with the outline drawings demonstrating the cranial shape changes (in half skull) along the *Caretta caretta* age classes. The shape changes in the figures are visualized from the average shape in the black dashed lines towards the positive values of the target shape in the continuous black lines. Open circles: interval from 10 to 13 years, X symbols: interval from 14 to 17 years, Black squares: interval ≥ 18 years

reduction throughout its development, as it was also verified in the cranial lateral view. This decrease in orbit size may occur because of the expansion of the bones previously mentioned, primarily the postorbital and jugal bones.

### *Mandibular dorsal view (Fig. 7)*

In this view, there is a large overlap of the scores of the first relative age classes (from 10 to 13 years and from 14 to 17 years) along the first canonical axis (Fig. 8). However, older individuals (≥ 18 years) have only a partial overlap with the younger ones, with the highest scores along CV1. The main change in jaw shape observed in this view is the expansion of the dentary in older individuals, represented by semilandmarks 73–77 and 78–80 (see Fig. 1E), in addition to an expansion in all directions of the articular bone in the posterior portion of the mandible.

### *Mandibular lateral view (Fig. 8)*

There is a relative overlap between the scores of the different relative age classes along the first canonical axis, though individuals with an age equal or older than 18 years showed higher scores along this axis.

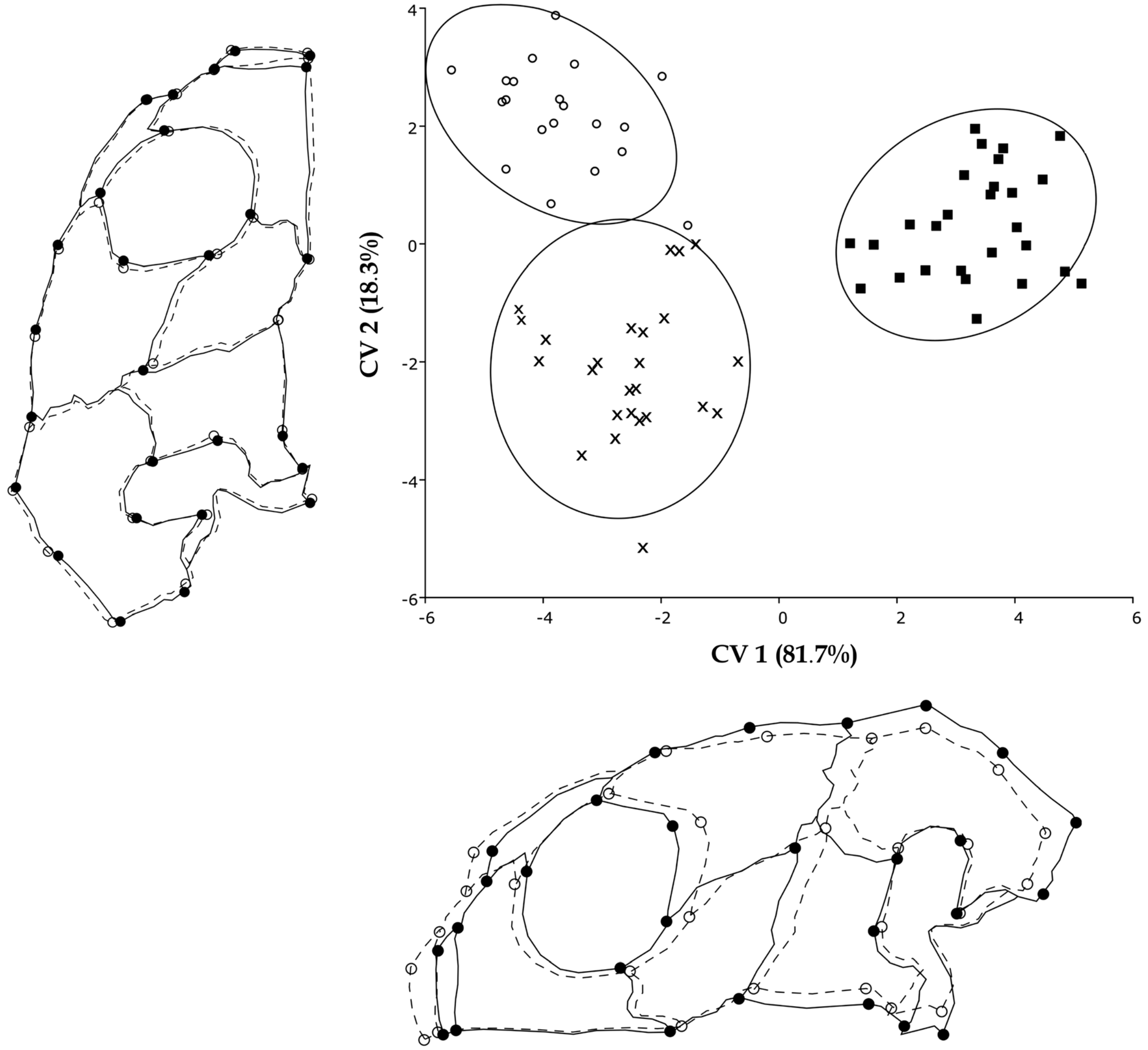

**Fig. 5** Scores of the specimens on the first and second axes of the canonical variates analysis for the cranial lateral view ($n = 72$) with the outline drawings demonstrating cranial shape change over *Caretta caretta* age classes. The shape changes in the figures are visualized from the average shape in the black dashed lines towards the positive values of the target shape in the continuous black lines. Open circles: interval from 10 to 13 years, X symbols: interval from 14 to 17 years, Black squares: interval ≥ 18 years

The main apparent change in this view is the enlargement of the upper region of the mandible, where the coronoid and the dentary are located. It is also possible to observe the shortening of the mandible, generated by the reduction of the mandibular posterior region, of which the *surangular* bone is part, as well as the retraction of the semilandmarks 92–95 in the anterior and inferior dentary regions. Changes in mandible shape of *C. caretta* throughout development can be summarized from a narrower initial formation in the younger individuals to a wider jaw in individuals aged 18 years or older.

### *Shape versus size*

Part of the variation in the shape of the skull of *C. caretta* can be explained by the centroid size in all cranial and mandibular views (all views $P < 0.0001$)

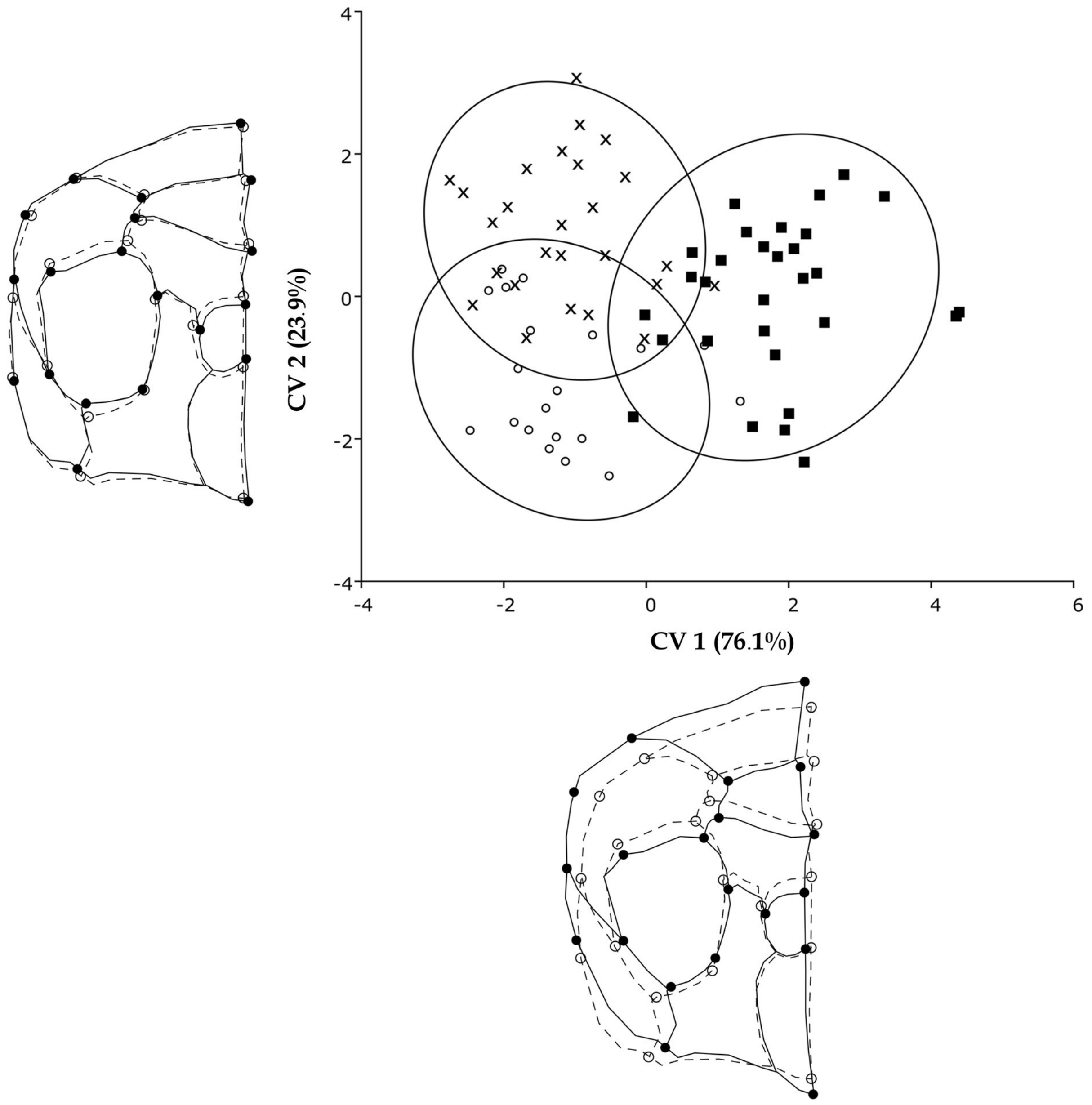

**Fig. 6** Scores of the specimens on the first and second axes of the canonical variates analysis for the cranial frontal view ($n = 76$) with the outline drawings demonstrating the cranial shape changes (in half skull) along the *Caretta caretta* age classes. The shape changes in the figures are visualized from the average shape in the black dashed lines towards the positive values of the target shape in the continuous black lines. Open circles: interval from 10 to 13 years, X symbols: interval from 14 to 17 years, Black squares: interval ≥ 18 years

(Fig. 9). This positive relationship of the shape with the centroid size indicates that the *C. caretta* skull undergoes an allometric transformation throughout development. However, the size explained only a small part of the changes in the skull shape of individuals of *C. caretta* (skull: dorsal 8.3%, frontal 11.8%, lateral 8.0%, and mandible: dorsal 8.1%, and 9.6% lateral).

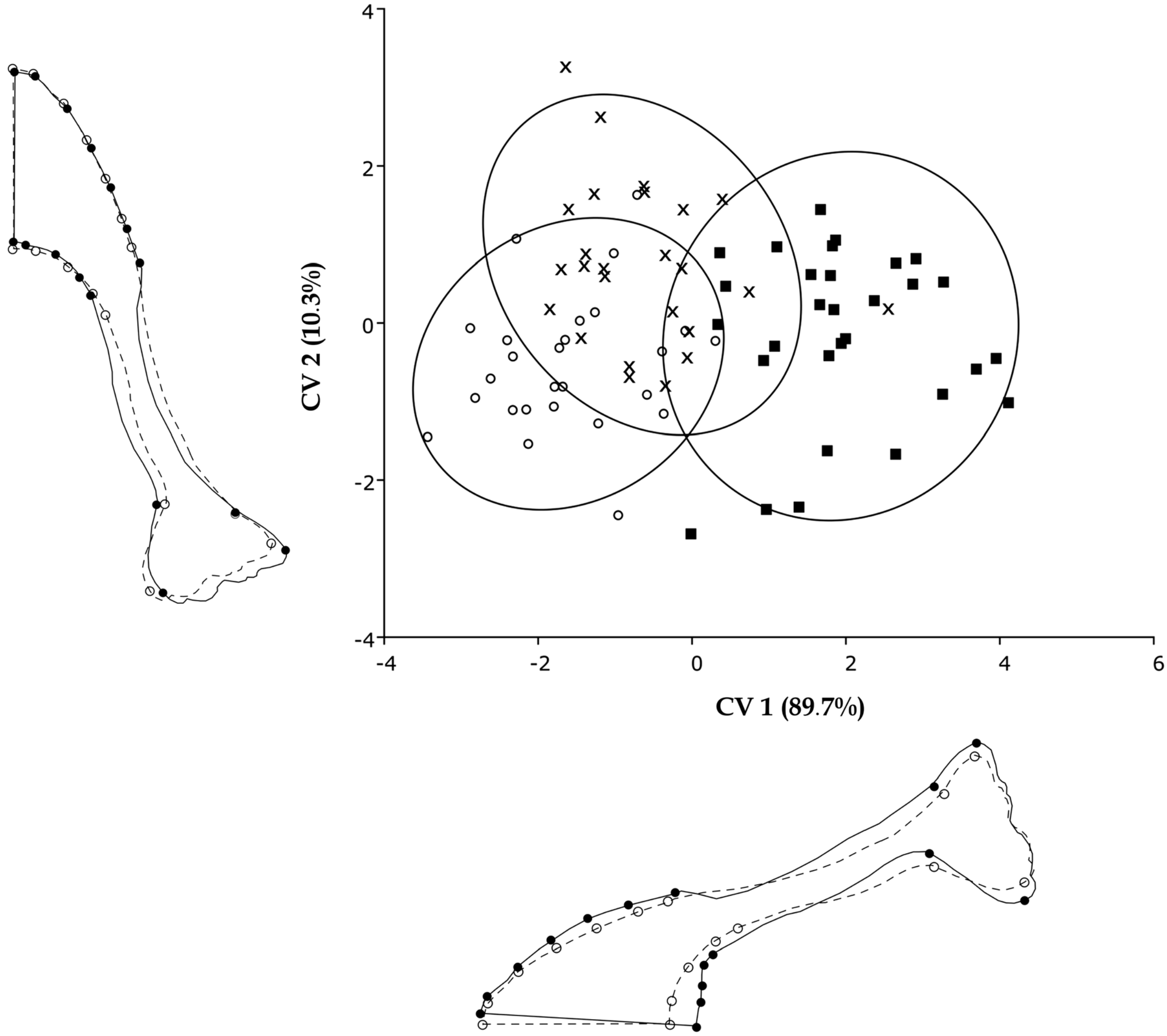

**Fig. 7** Scores of the specimens on the first and second axes of the canonical variates analysis for the mandibular dorsal view ($n = 81$) with the outline drawings demonstrating the shape change of the mandible along the *Caretta caretta* age classes. The shape changes in the figures are visualized from the average shape in the black dashed lines towards the positive values of the target shape in the continuous black lines. Open circles: interval from 10 to 13 years, X symbols: interval from 14 to 17 years, Black squares: interval ≥ 18 years

## Discussion

In the present study, the shape and size of skulls of loggerhead turtles were described in three different age classes based on the analyses of specimens collected on the coast of Rio Grande do Sul, southern Brazil. This area is known to be used by individuals of this species during the coastal stages of development, with ages predominantly ranging between 10 and 20 years (Di-Bernardo et al., 2003; Lenz et al., 2016).

The statistical difference found between *C. caretta* skull size distributions in the three relative age classes (from 10 to 13 years, from 14 to 17 years and ≥ 18 years) gives us the ability to interpret the biological consequences of the observed shape patterns. Perhaps the clearest pattern has been the transformation of the skull shape of *C. caretta*, from an elongated and flattened shape in the younger specimens to a more rounded and robust/wider shape in older individuals. In general, the observed patterns corroborated our

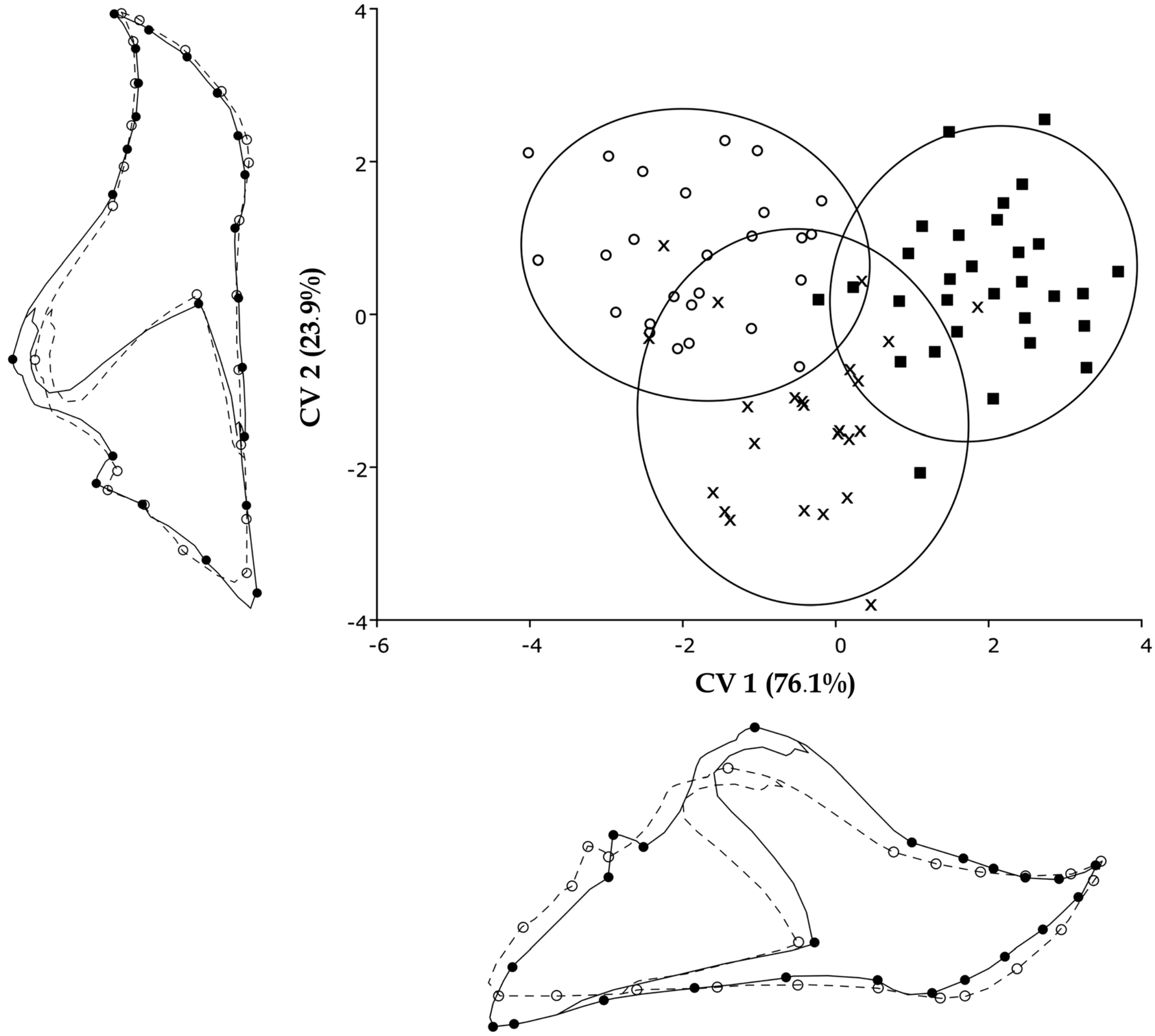

**Fig. 8** Scores of the specimens on the first and second axes of the canonical variates analysis for the mandibular lateral view ($n = 80$) with the outline drawings demonstrating the shape change of the mandible along the *Caretta caretta* age classes. The shape changes in the figures are visualized from the average shape in the black dashed lines towards the positive values of the target shape in the continuous black lines. Open circles: interval from 10 to 13 years, X symbols: interval from 14 to 17 years, Black squares: interval ≥ 18 years

hypothesis that there would be changes in the shape and size of loggerhead turtle specimens across the coastal stages of development. The evidence presented here represents the first description of cranial changes in the shape and size of individuals of *C. caretta* in a developmental and foraging area. Usually, similar studies involving chelonian species only describe the relationship between the shape of the skull and the individuals' way of life and diet, as well as the use of freshwater turtle species as model (Lemell et al., 2000; Herrel et al., 2002; Claude et al., 2004). The most similar study to the present one was published by Nishizawa et al. (2010), where the authors investigated changes in cranial shape along with the ontogenetic diet shift in green turtles, *Chelonia mydas* (Linnaeus, 1758).

**Table 4** Relative contributions of the first canonical axes in explaining the variation of *Caretta caretta* skull and mandibular shape and decimals of classification correspondence according to the informed age class (general cross-validation). CV1: first canonical variate and CV2: second canonical variate

| View | CV1 | CV2 | General cross-validation | Figure |
|---|---|---|---|---|
| Skull | | | | |
| Dorsal (*n* = 70) | 0.859 | 0.141 | 0.806 | Figure 4 |
| Lateral (*n* = 72) | 0.817 | 0.183 | 0.725 | Figure 5 |
| Frontal (*n* = 76) | 0.761 | 0.239 | 0.554 | Figure 6 |
| Mandible | | | | |
| Dorsal (*n* = 81) | 0.897 | 0.103 | 0.612 | Figure 7 |
| Lateral (*n* = 80) | 0.761 | 0.239 | 0.571 | Figure 8 |

### Biological relevance of the chosen age classes

The three age classes adopted in this study explained a significant part of the variation observed in size and shape patterns of the analyzed structures and were sufficient to demonstrate a rapid shape change in the transition to the third age class. This indicates that it was possible to capture the change in diet. Though the proposed age classes comprised three arbitrary levels, biologically they seem to encompass two different moments of the life history of the species. The first moment represents a recruitment stage towards the development area, while the second moment characterizes the individuals that are potentially migrating towards the adult stage areas. In this context, a more general classification would be one that aggregates individuals from 10 to 17 years old into a single category. The aggregation of the first two age intervals may be related to the individual variation that exists at the time of recruitment of these specimens, making this wide age class representative of the moment of habitat change (Monteiro, 2017).

In this context and taking into account the contributions of the measurements to the first principal component, the cranial measurement of *C. caretta* that contributed most to the characterization of the individuals' development was the skull length, followed by the squamosals width, lower mandibular width, lower mandibular length and skull height. From these results, we suggest that individuals are recruited from the pelagic area to the neritic area with a minimum skull length of 140.4 mm ($\sim$ 12 years of age), while specimens with 265.3 mm of skull length ($\sim$ 29 years of age) would be leaving the neritic development region towards adult feeding areas. However, it is important to mention that adult specimens may return to the neritic area to feed (Pinedo, 1997), resulting in an overestimation of the maximum skull size for the individuals inhabiting in the developmental area.

### Adaptive significance of observed cranial variation patterns

Through the outline drawings of the anatomical views analyzed, it was possible to visualize the regions that underwent the major modifications in the cranial shape of *C. caretta* during the ontogeny of the individuals. The interpretations that follow about these patterns were based on premises linked to the adaptive maintenance of the structures. Through this analytical exercise we intend to introduce functional interpretations of the structures and to hypothesize how the interaction of these organisms with the environment in which they live could generate the morphological patterns described by us.

In all the cranial views (Figs. 4, 5 and 6) an important enlargement of the cranial posterior part was observed. This increase is probably due to the expansion of the mandible muscles (also called adductors of the mandible), which play a role in mastication (Schumacher, 1993) and adhere to the posterior cranial part. More specifically, the two adductor muscles *mandibulae externus Pars profundus* and *mandibulae externus Pars superficialis* have their origins in the parietal, supraoccipital and squamosal bones and are of great importance for the power of mandibular closure (Jones et al., 2012).

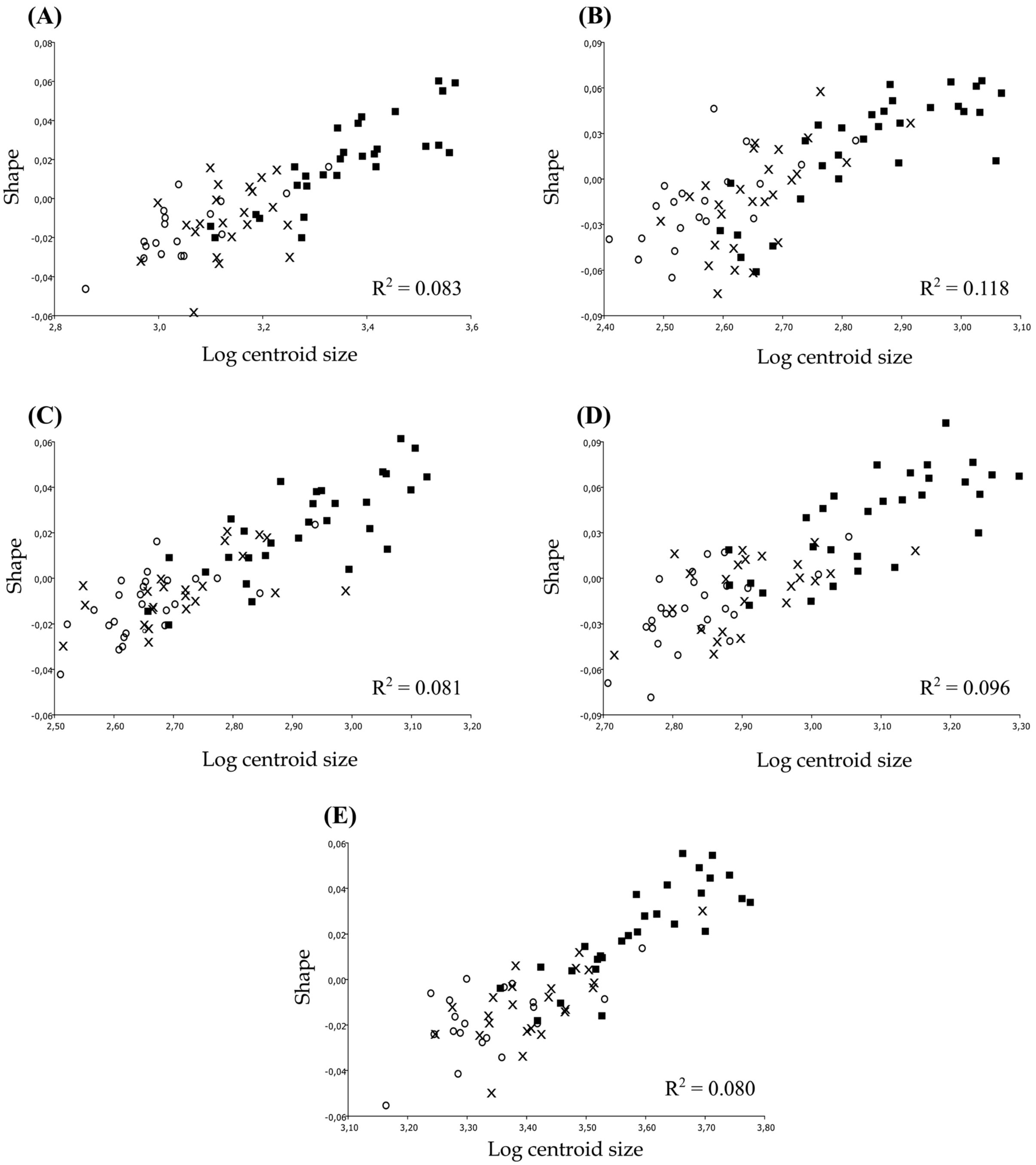

**Fig. 9** Multivariate regression analysis between the first Procrustes coordinate regression score (shape) and log-transformed centroid size (size) of *C. caretta* individuals. **A** Cranial dorsal view. **B** Cranial frontal view. **C** Mandible dorsal view. **D** Mandible lateral view. **E** Cranial lateral view. Age classes: Open circles: interval from 10 to 13 years, X symbols: interval from 14 to 17 years, Black squares: interval of ≥ 18 years

A second pattern of modification relates to the relative decrease in the orbit of younger specimens to older specimens (Figs. 5 and 6), which may be related to the importance of vision in juvenile stages of the species (Nishizawa et al., 2010). However, Narazaki et al. (2013) argued that vision would also be of great importance for the foraging ability of these individuals in later stages. An alternative situation would be that from the juvenile stages the main cognitive path of the turtles would pass through vision, which would lead to acceleration in the development of the orbital region to develop a visual system compatible with their requirements. Once formed, the system would not undergo further modifications, giving the false impression of a minor adjustment in the eye orbits region. However, it is important to note that many vertebrates exhibit this same pattern, possibly also associated with a phylogenetic pattern of Tetrapoda (e.g., Kardong, 1994; Liem et al., 2013).

Regarding the cranial changes, the premaxilla stretching (Fig. 6), also called "beak", was probably related to a greater efficiency in the feeding behavior of these individuals. The beak allows a point of greater pressure to be generated in the closing of the mandible of a loggerhead turtle, facilitating the rupture of the hard shell of its prey, such as benthic mollusks. In addition, the relative shortening observed in the frontal cranial region (Figs. 4 and 5) along the ontogeny of *C. caretta* could be related to penation (changes in the orientation of the muscle fibers) and relative decrease of the length of the mandible muscles, which would assign greater bite force even if speed were reduced (Schenk & Wainwright, 2001). Associated with this, the shrinkage of the anterior region was also observed, together with the posterior cranial expansion, which would provide a greater perpendicular orientation of the adductor muscles of the mandible and generate greater strength (Herrel et al., 2002).

In relation to the mandible, it was observed that this structure was transformed during ontogeny into a broader shape when compared to the initial developmental intervals (Fig. 8). This final conformation was generated mainly by the relative increase of the superior part of the mandible and the lower mandibular length isometry along the ontogeny (LML: allometric coefficient = 1.0), giving a greater area of insertion for the mandibular adductor muscles (Jones et al., 2012), resulting in greater bite efficiency. In addition, a relative increase of the dentary bone (Fig. 7), both in length and width, was observed, expanding the crushing surface of the mandible. This expansion also refers to the ontogenetic change in the dietary preference of *C. caretta* specimens, allowing greater efficiency in the capture of hard-shelled animals such as mollusks and benthic crustaceans (Eckert & Grobois, 2001). This diet shift and mandibular expansion has also been reported in the freshwater turtle, *Sternotherus minor* (Agassiz, 1857), by Zappalorti & Iverson (2006).

In summary, the data presented here offer indirect evidence in support of the niche change premise, where changes in the shape of the skull and mandible result in response to the different niche spaces occupied. In this context, size could not be the only variable that determines the development of the loggerhead turtle, being also attributed to any another environmental variable (Klingenberg, 2016). A recent study provided additional evidences of environmental variable that can also affect the development of *C. caretta*. Gaube et al. (2017) provided evidence of the preferential use of the interiors of the anticyclone's eddies by juvenile loggerheads in Western South Atlantic. Some hypotheses were proposed for this behavior and the possible increased foraging success is one of them (Gaube et al., 2017).

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## Compliance with ethical standards

**Conflict of interest** All authors (Eduardo Araujo Lunardon; Luiz Ernesto Costa-Schmidt; Ana Júlia Lenz; Márcio Borges-

Martins; Larissa Rosa De Oliveira) declare they had no conflicts of interest whatsoever.

**Ethical approval** The study was based on voucher specimens deposited in scientific collections. All specimens in the scientific collections were found dead, stranded along the coast. No animal was intentionally caught or killed during the summarized research. Consequently, no submission to the institutional ethics committee on the use of animals is required in Brazil.

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