Neotropical Ichthyology

Original article

https://doi.org/10.1590/1982-0224-2020-0145

Growth stanza in fish life history using otoliths shape: the protandric *Centropomus* case (Carangaria: Centropomidae)

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Morphoanatomical or physiological changes coupled with changes in body size are known as allometric relationships. The objective of this study was to identify the points of growth changes in *Centropomus* based on otolith morphometry and morphogeometry. For this purpose, 455 individuals of *C. undecimalis* and 176 of *C. parallelus* were collected from artisanal fishermen of the coast of the state of Alagoas, Brazil. The sagittal otoliths were measured for length, height, perimeter, area and weighed. The potential and polyphasic models were fitted between total fish length and otolith length. The morphotypes otoliths wen describe by form Fourier descriptors and shape indices. The polyphasic model detected three growth phases. The first stanza for *C. undecimalis* was at 46.8 cm and the second at 75.9 cm. For *C. parallelus*, it was at 18.8 cm and at 41.2 cm. Each stanza has a specific otoliths morphotype in both species. The otoliths of *C. undecimalis* and *C. parallelus* exhibited ontogenetic allometric changes in their growth pattern with two stanzas changing points. The stanzas corresponded to specific lengths reached by individuals over their life cycles, such as their size at maturity and length at sexual reversion.

Keywords: Energy allocation, Hermaphroditism, Morphogeometry, Polyphasic growth, Reproduction.

Submitted December 18, 2020
Accepted September 18, 2021
by Ana Petry
Epub November 30, 2021

Online version ISSN 1982-0224
Print version ISSN 1679-6225

Neotrop. Ichthyol.
vol. 19, no. 4, Maringá 2021

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Mudanças morfoanatômicas ou fisiológicas em conjunto com mudanças no tamanho do corpo, são conhecidas como relações alométricas. O objetivo do estudo foi identificar os pontos de mudanças de crescimento de *Centropomus* com base na morfometria e morfogeometria dos otólitos. Foram coletados 455 indivíduos de *C. undecimalis* e 176 de *C. parallelus*, adquiridos com pescadores artesanais do estado de Alagoas, Brasil. Os otólitos sagitta foram medidos quanto ao comprimento, altura, perímetro, área e pesados. Os modelos potencial e polifásico foram ajustados entre o comprimento do peixe e o comprimento do otólito. Os morfotipos de otólitos são descritos por descritores de Fourier e índices de forma. O modelo polifásico detectou três fases de crescimento. A primeira stanza para *C. undecimalis* foi em 46,8 cm e a segunda em 75,9 cm. Já *C. parallelus*, a primeira foi em 18,8 cm e segunda em 41,2 cm. Cada stanza possui um morfotipo específico de otólitos em ambas as espécies. Os otólitos de *C. undecimalis* e *C. parallelus* exibiram mudanças alométricas ontogenéticas em seu padrão de crescimento com dois pontos de mudança de stanzas. As stanzas corresponderam a comprimentos específicos alcançados por indivíduos ao longo de seus ciclos de vida, como seu tamanho na maturidade e comprimento na reversão sexual.

Palavras-chave: Alocação energética, Crescimento polifásico, Hermafroditismo, Morfogeometria, Reprodução.

INTRODUCTION

The life cycle of living beings is closely related to their maximum size and omset at sexual maturity. Morphoanatomical or physiological changes coupled with changes in body size are known as allometric relationships, and can reflect the compensatory effect necessary to maintain efficiency in bodily functions (Begon *et al*., 2006). Allometry is a common phenomenon in a variety of taxa, from bacteria (Mitchell, 2002) and invertebrates (Shingleton *et al*., 2007; Castro *et al*., 2020) to large mammals, such as whales (Ortega-Ortiz *et al*., 2018). In fish species, allometry has been extensively described (Gisbert, 1999; Su *et al*., 2020; Taylor *et al*., 2020). The beginning of the reproductive life is one of the main causes of changes in growth patterns over the life cycle of fishes, since it implies reallocation of body energy towards reproduction in detriment of growth (Quince *et al*., 2008; Boukal *et al*., 2014; Minte-Vera *et al*., 2016). Several models can be used to evaluate the morphological changes in allometric growth patterns of animals, with the model proposed by Huxley (1924), being one of the most used, because it allows a suitable quantitative description of the growth in a non-linear basis. This model is based on the potential relationship between two morphological variables ($y = ax^b$), assuming that body dimensions increase from an allometric coefficient (b of the equation) (Huxley, 1924). This model is usually applied to the relationship between body mass and size of individuals as an indicator of seasonal or interannual allometric changes (Fabré, Saint-Paul, 1998; Froese, 2006; Sousa *et al*., 2015), as well as of allometry in fish otoliths (Bervian *et al*., 2006).

Otoliths are calcified structures located in the inner ear of fish, being an important component of their mechanoreceptor system (Popper, Coombs, 1982; Cousseau, 2010). These structures allow the understanding of several aspects of fish's life history (Campana, Neilson, 1985; Volpedo, Vaz-dos-Santos, 2015; Assis *et al*., 2020) because otolith growth shows a strict relationship to somatic growth (Francis, 1990). In addition, otoliths are conservative structures that have species-specific morphological characteristics, with the phylogenetic history of a particular taxon being usually reflected in its otolith shape (Nolf, 1985; Monteiro *et al*., 2005; Tuset *et al*., 2008, 2016). Therefore, it is not surprising that otolith morphology and morphometry have been used as powerful tools to detect physiological changes caused by many key factors of fish's life cycle, such as reproduction or sexual maturity (Bervian *et al*., 2006; Capoccioni *et al*., 2011; Carvalho *et al*., 2015; Maciel *et al*., 2019). Otolith allometry has been widely applied in growth studies of both freshwater and marine species (Pérez, Fabré, 2009, 2013; De Queiroz *et al*., 2018), whereas otolith shape analysis has been employed in distinguishing fish stocks, populations and species (Capoccioni *et al*., 2011; Santos *et al*., 2017; Assis *et al*., 2020; Song *et al*., 2020), with Elliptic Fourier Analysis (FEA) being the most commonly used method in shape studies (Santos *et al*., 2017). Nevertheless, up to the present, the use of otolith allometry and its shape study as a response variable in fish reproductive cycle has been little addressed in hermaphroditic fish (Walker, McCormick, 2004; Munday *et al*., 2009; Walker, McCormick, 2009a,b; Mejri *et al*., 2018; Barr *et al*., 2019), especially for protandrous species.

Hermaphroditism is a polyphyletic condition that has been documented for approximately 2% of teleost species (Avise, Mank, 2009). It can occur sequentially and is characterized by a sex transition, either from male to female (protandry) or from female to male (protogyny) (Warner, 1975). According to the sex allocation theory, sex change is favored to increase the population's reproductive fitness when the fertility of one particular sex, as a function of size and age, increases more rapidly compared to the other (Charnov, 1982). However, the energetic cost of sex change is as high as that involved in sexual maturation, which means that it can imply in decreased growth rates (Higgins *et al*., 2015; Matthias *et al*., 2016; Neves *et al*., 2017). For many years, sequential hermaphroditism was interpreted as an automatic sex change that occurred when individuals reached a certain body size or age (Allsop, West, 2003; Avise, Mank, 2009). However, some evidence points out that specific conditions in the population structure can trigger the sex change of sequential hermaphrodites (Munday *et al*., 2006; Walker, McCormick, 2009a), as observed by Shapiro (1987) in reef fish species.

In this context of sequential hermaphroditic fishes, two species of the genus *Centropomus*, *C. undecimalis* (Bloch, 1792) and *C. parallelus* (Poey, 1860), stand out in Brazil because of their both wide distribution along the coast and high commercial value. These two species are protandrous hermaphrodites, being commonly found throughout the tropical western South Atlantic (Rivas, 1986; Taylor *et al*., 2000; De Figueiredo-Filho *et al*., 2021). Both species inhabit different habitats throughout their life cycle, being characterized as estuarine dependent fish (they breeding and growing in estuarine areas) that migrate to the sea to grow and feed (Blewett *et al*., 2009; Daros *et al*., 2016; Da Silva *et al*., 2018). They play important ecological roles such as top-down control in tropical coastal ecosystems (Lira *et al*., 2018). In addition, these two species have high commercial value in artisanal and sport fisheries (Alvarez-Lajonchère, Tsuzuki, 2008; Dantas, Barletta, 2016; Garrone-Neto *et al*., 2018). In Brazil, for example, an average of

3,541 tons of snooks are annually caught (considering catches between 2009 and 2018), making it the second highest catching country for this group, behind Mexico only (FAO, 2019). Despite this high catch, there is no evidence to date of population decline for these species. However the rising trend in fishing effort is worrying (Mendonça *et al*., 2019a,b).

Motivated by the biological peculiarities of these species, we hypothesized that the inherent sequential sex change is expressed by changes in otolith allometric patterns and shape. This is based on the assumption that otoliths are able to record changes due to shifts in growth patterns over specific stages of fish's life cycle. Therefore, the objective of this study was to detect changes in the growth pattern of *C. undecimalis* and *C. parallelus* throughout their life cycle, based on the morphometry and shape of sagittal otoliths, as well as to identify what factors are related to these changes.

MATERIAL AND METHODS

Study area and material collection. The coast of the state of Alagoas is 230 km long (08°54'51.3" to 10°30'24.2"S and 35°09'07.1" to 36°23'15.1"W), being characterized by a narrow continental shelf (50 km) with different coastal ecosystems throughout its extension (*e.g*., estuaries, coastal ridges, coral reefs and sandstone reefs) (Dorigo Correia, Sovierzoski, 2008; Oliveira, Kjerfve, 1993). These area has a semi-humid tropical climate, with rainy periods from March to August and dry periods between September and February. There *Centropomus* are targeted by small-scale coastal fisheries, conducted primarily with gillnets at maximum depths of 30 meters (Rangely *et al*., 2010), with young *Centropomus* individuals being very abundant in mangrove areas (Teixeira, 1997; Da Silva *et al*., 2018).

The sampling of individuals were conducted throughout the coast between July 2017 and January 2020, focusing on the main landing point of the state, the Port of Jaraguá (Rangely *et al*., 2010). Individuals were acquired directly from artisanal fishermen right after landing, being captured by different types of fishing gear (*e.g*., gillnet, trawlnet, longline, and hand-line) to collect fish from all size-classes. Specimens were taken to the laboratory to identification following Menezes, Figueiredo (1980).

Data analysis. The total length (TL, cm) of each fish was measured and the sagittal otoliths were removed. Fish lengths were organized by classes following the Sturges rule (Sturges, 1926), thus, *C. undecimalis* was grouped into size classes of 5 cm and *C. parallelus* data was grouped into 3 cm classes. The right otolith of each fish, when available, was weighed (OW, g) on a high precision scale (0.0001 g), then photographed by a Leica S8 APO stereo microscope with camera. Larger otoliths were photographed by a Canon Pc2264 camera in macro mode with a standardized height. Length (OL, mm) and height (OH, mm) were measured from otoliths images (Fig. 1), as well as perimeter (OP, mm) and area (AO, mm^2). All measurements were recorded using ImageJ software version 1.48 (Schneider *et al*., 2012).

Initially, we fitted the potential Huxley model ($y = ax^b$); where a is the angular coefficient and b is the allometric coefficient) and tested for heteroscedasticity of these relationships by the Breusch-Pagan test (Breusch, Pagan, 1979). This test found heteroscedasticity

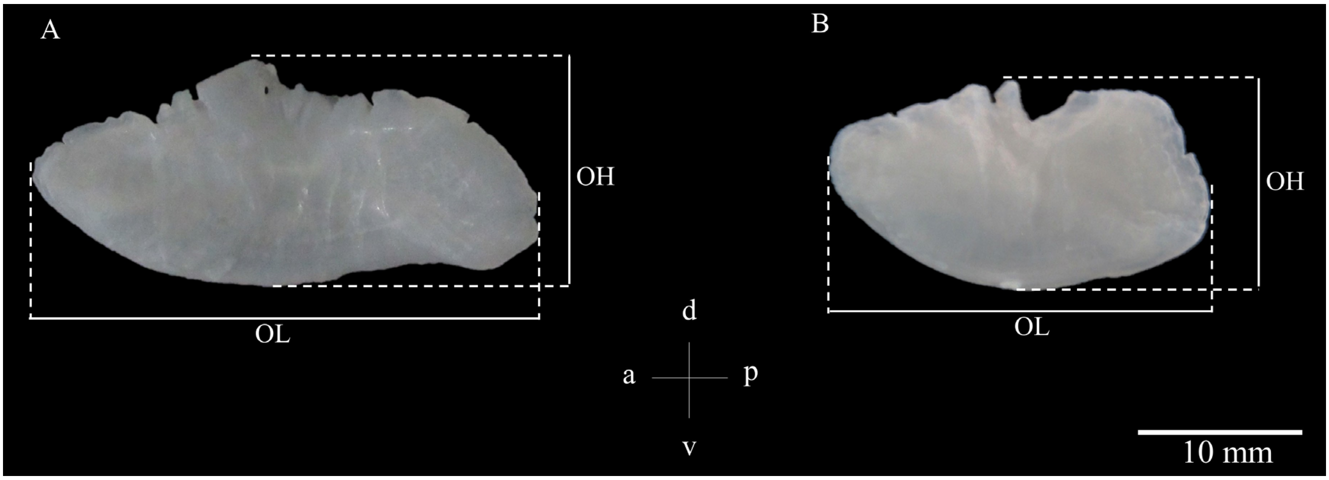

FIGURE 1 | Otoliths of Centropomidae. **A.** *Centropomus undecimalis*. **B.** *Centropomus parallelus*. OL = Otolith length; OH = Otolith height; a = anterior; p = posterior; v = ventral; d = dorsal.

for both species ($P < 0.05$). To correct for this, we calculated the residuals proportional to OL, given by the equation $PR = \frac{OL_o - OL_p}{OL_p}$, where PR is the proportional residual, OL_o is the observed otolith length, and OL_p is the predicted otolith length (Barradas *et al.*, 2016). Proportional residuals were applied because the variance of the error should be constant (homoscedastic) when conditionally analyzing the explanatory variable. We subsequently recalculated the values of *a* and *b* from Huxley's potential relationship applying the nonlinear least-squares method, based on the proportional residuals, using Microsoft Excel Solver (Fylstra *et al.*, 1998).

With this new value of *a*, we used the polyphasic approach which considers the variable *a*, as invariant, and the value of *b* as variant according to size class (Bervian *et al.*, 2006). This approach assumes a growth pattern composed of different phases, separated by a stanza change point (SCP), which indicates the TL at the moment when the growth pattern changes. Therefore, TL (in the size class of 5 and 3 cm for *C. undecimalis* and *C. parallelus*, respectively) was plotted against the mean OL values. Considering the fixed value of *a* (Huxley model), we calculated the allometric coefficient of each size class (*b*sc), from the equation: $OL = aTL^{bsc}$. Then, a third-degree polynomial model was fitted between the *b*sc and the average TL classes. This model was derived (*b*sc'), giving rise to a second-degree equation. The obtained parabola was used to calculate the TL values (*b*sc' = 0), at which growth changes occur.

To validate the growth stanzas, we analyzed whether the otolith contour followed the same changing pattern. For that, we analyzed the harmonics of the Elliptic Fourier Descriptors (EFD) of 120 otoliths from *C. undecimalis* (40 per allometric group) and 90 otoliths from *C. parallelus* (30 per allometric group), using the Shape software (Iwata, Ukai, 2002; Assis *et al.*, 2020). This difference in sample size between species was due to the low number of *C. parallelus* in the study. From the otolith harmonics, a linear discriminant analysis (LDA) was performed to test the power of shape discrimination by growth stanzas, followed by a PERMANOVA test. R statistical software (R Development Core Team, 2013) and its Vegan package (Oksanen *et al.*, 2020) were used to run LDA and PERMANOVA.

Finally, after establishing the morphotypes for both species, a characterization of otoliths' morphotypes was performed for each group. We described the morphotypes by calculating shape indices related to the aspect ratio, circularity, roundness, rectangularity, and ellipticity of otoliths (Tuset *et al*., 2003; Volpedo, Echeverría, 2003; Bani *et al*., 2013) (Tab. 1). Circularity and roundness compare the otolith shape to a perfect circle; whereas rectangularity describes the variation in length and width in relation to the total area; ellipticity indicates whether the changes in the axes are proportional; and the aspect ratio estimates the irregularity of the surface area (Tuset *et al*., 2003; Volpedo, Echeverría, 2003; Bani *et al*., 2013). The Kruskal-Wallis test was used to compare these indices between morphotypes, considering a significance level of 0.05. When significant differences between the various classifications were detected, the Mann-Whitney U-test was subsequently applied for pairwise comparison between species (Zar, 2014).

TABLE 1 | Equations used to estimate the shape indices of the otoliths. OL = otolith length, OH = otolith height, P = perimeter, and A = area.

shape index	Equation
Aspect ratio	OL / OH
Circularity	P^2 / A
Roundness	$4A / \pi \times OL^2$
Rectangularity	$A / OL \times OH$
Ellipticity	$OL - OH / OL + OH$

RESULTS

We collected 455 specimens of *C. undecimalis*, with total length ranging from 9 to 111 cm, with a bimodal distribution (peaks at 15 and 65 cm) (Fig. 2A). The number of *C. parallelus* was smaller, with only 176 individuals ranging in total length from 8 to 57 cm (Fig. 2B).

The relationship between TL and OL, using the proportional residuals, in *C. undecimalis* individuals showed positive allometry, $b > 1$ ($OL = 0.235 \times TL^{1.09}$, $r^2 = 0.948$, P = 0.001) (Fig. 3A), with the residual analysis showing three growth phases (Fig. 3B). The third-degree polynomial model resulted in the following equation $bsc = 7E^{-7} \times TL^3 - 1.4E^{-4} \times TL^2 + 8E^{-3} \times TL + 0{,}99$ ($r^2 = 0.529$) (Fig. 3C). The model fitted for the allometry coefficient derivative (bsc') as a function of the TL($bsc' = 2E^{-6} \times TL^2 - 3E^{-4} \times TL^2 + 8E^{-3}$), detected two growth stanzas, one at 46.8 cm and another at 75.9 cm (Fig. 3D).

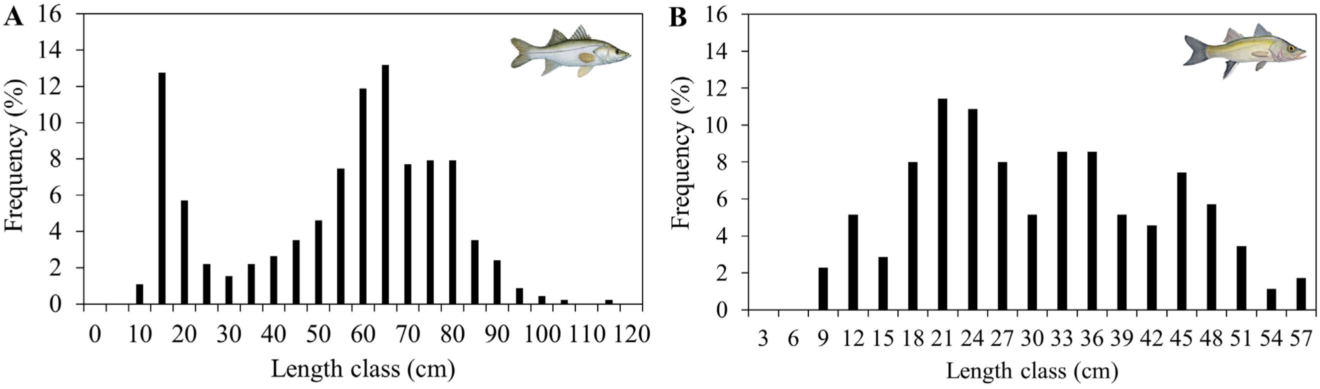

FIGURE 2 | Frequency distribution of *Centropomus undecimalis* (**A**) and *Centropomus parallelus* (**B**) collected in the state of Alagoas, Brazil.

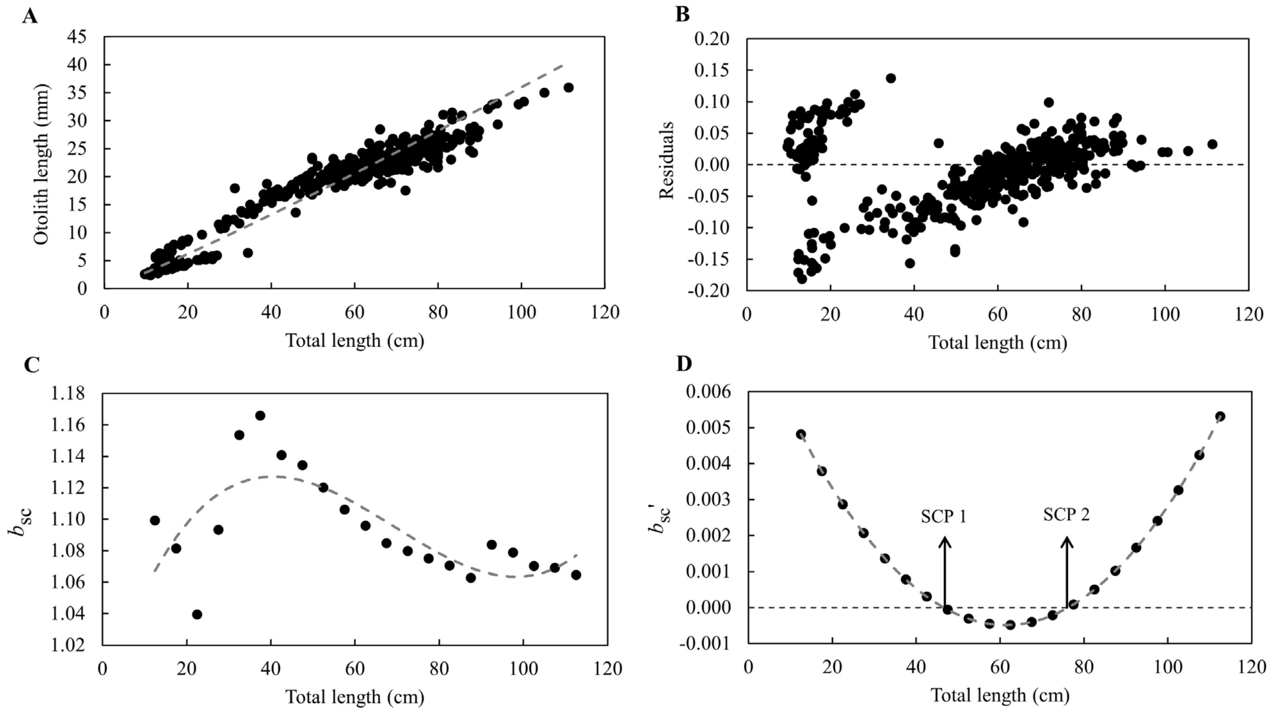

FIGURE 3 | Growth changes in *Centropomus undecimalis* based on a polyphasic growth model. **A.** Potential regression for fish total length as a function of otolith radius; **B.** Residual distribution; **C.** Exponential coefficient (*bsc*) for length class; **D.** Derivative of the third-degree polynomial function, and indication of the change points of the stanza (SCP 1 and SCP 2).

Reconstruction of the otolith shape of *C. undecimalis* indicated three different morphotypes. Morphotype 1, with OL smaller than 15.4 mm, morphotype 2 with OL between 15.4 and 26.1 mm, and the third comprising otoliths with lengths greater than 26.1 mm (Fig. 4A). The LDA showed high jack-knifed classification success (91.7%) (Fig. 4B), with significant differences among the three morphotypes (P = 0.0001).

For *C. parallelus*, the relationship between TL and OL, using the proportional residuals, showed an isometric growth, $b = 1(OL = 0.389 \times TL^{1.01}$, $r^2 = 0.931$, $P = 0.001)$ (Fig. 5A), with residual analysis pointing to three growth phases (Fig. 5B). The third-

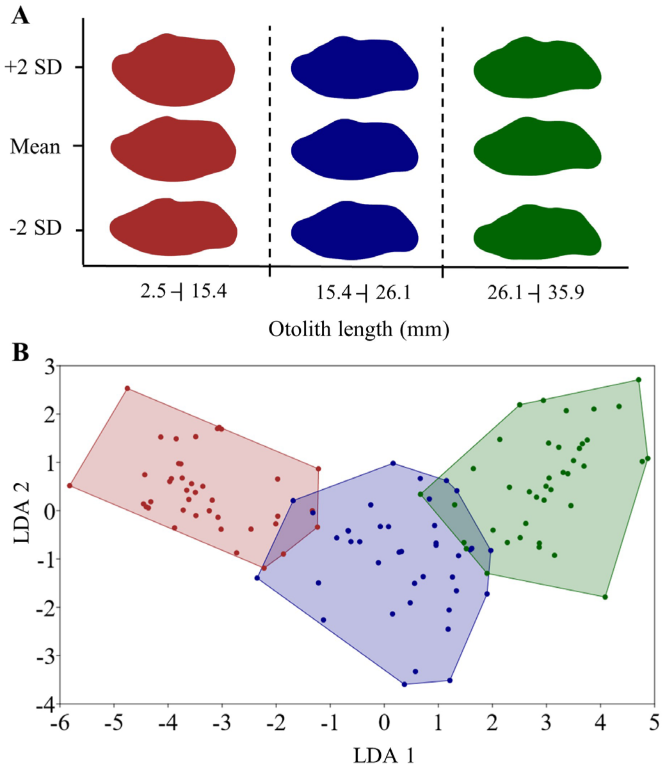

FIGURE 4 | Shape of otoliths of *Centropomus undecimalis* by morphotypes. **A.** Otolith mean outline and standard deviation (SD). **B.** Linear discriminant (LD) analysis of harmonics of elliptic Fourier descriptors of otoliths. red = Morphotype 1; blue = Morphotype 2; green = Morphotype 3.

degree polynomial model resulted in ($bsc = 2E^{-6} \times TL^{2} - 3E^{-4} \times TL^{2} + 8E^{-3}$) ($r^{2} = 0.559$) (Fig. 5C). The model fitted for the allometry coefficient derivative ($bsc' = 2E^{-6} \times TL^{2} - 3E^{-4} \times TL + 8E^{-3}$), also detected two growth stanzas, first at 18.8 cm and the second at 41.2 cm (Fig. 5D).

The otolith contours also indicated three morphotypes: first composed of the otoliths with OL smaller than 7.5 mm; second between 7.5 and 16.5 mm; and the last one OL larger than 16.5 mm (Fig. 6A). The LDA showed a jack-knifed classification success of 92.2% (Fig. 6B), with a significant difference between morphotypes (P = 0.0001).

Therefore, both species exhibited three morphotypes. In *C. undecimalis*, the ratios between OL/OH and OL/OW grow differently among the morphotypes. Furthermore, all shape indices showed a significant difference. Morphotype 1 presented a less elongated aspect and a higher circularity value than the other two morphotypes. Morphotype 2, on its turn, is elongated and presents higher rectangularity and roundness, and Morphotype 3 presented higher aspect ratio and ellipticity values (Tab. 2). The otoliths of *C. parallelus* showed a similar trend to its congener *C. undecimalis*, with different relative growth between the biometric proportions of their morphotypes. Two shape indices showed some similarities among the groups (roundness and circularity), but the other indices were significantly different among morphotypes. Morphotype 1 was less elongated and had a higher circularity value, whereas Morphotype 2 presented the greatest roundness, and Morphotype 3 was the most elongated and the most rectangular (Tab. 2).

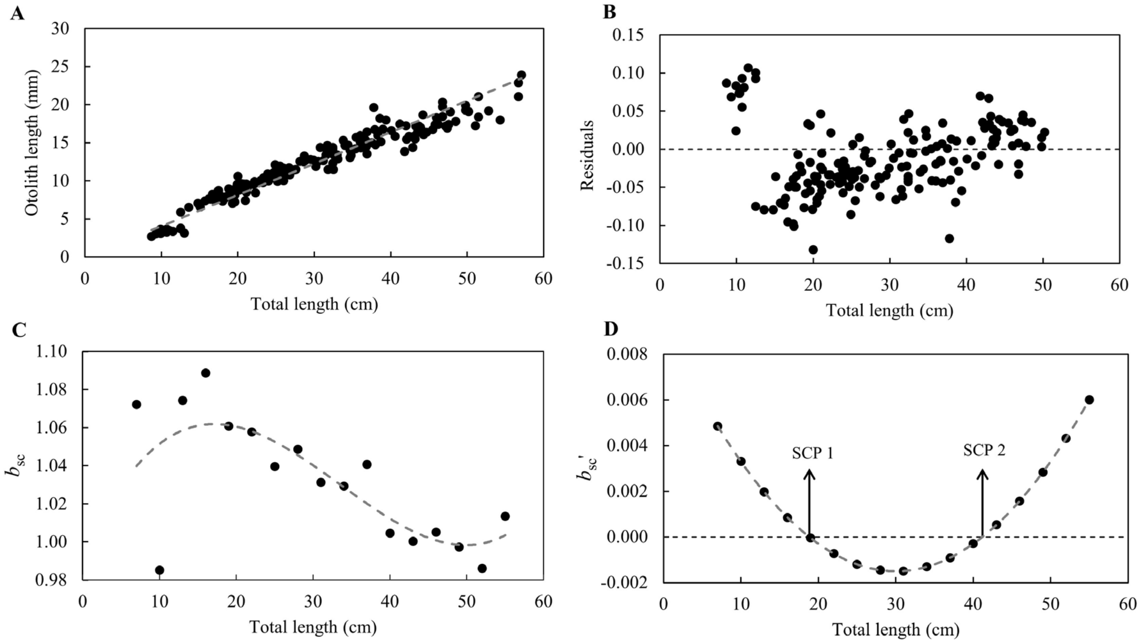

FIGURE 5 | Growth changes in *Centropomus parallelus* based on a polyphasic growth model. **A.** Potential regression for fish total length as a function of otolith radius; **B.** Residual distribution; **C.** Exponential coefficient (*b*sc) for length class; **D.** Derivative of the third-degree polynomial function, and indication of the change points of the stanza (SCP 1 and SCP 2).

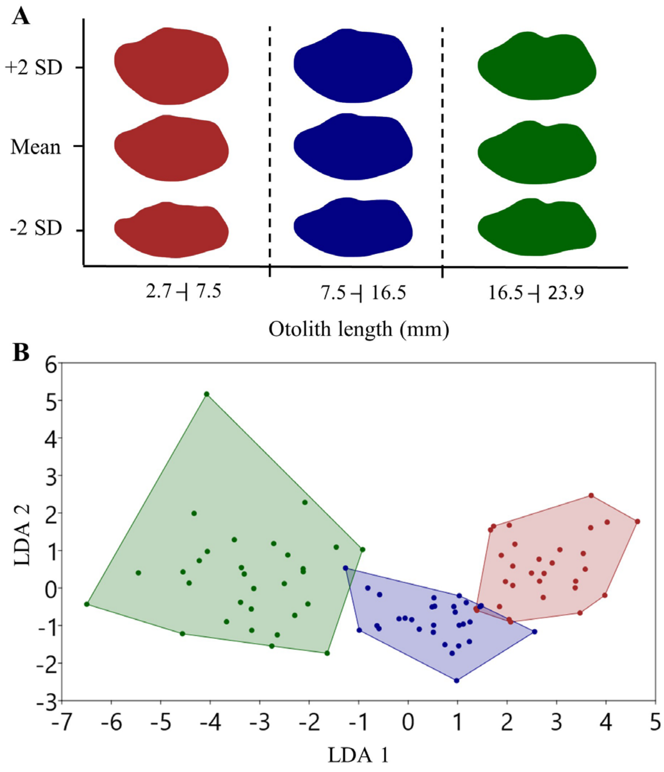

FIGURE 6 | Shape of otoliths of *Centropomus parallelus* by morphotypes. **A.** Otolith mean outline and standard deviation (SD). **B**. Linear discriminant (LD) analysis of harmonics of elliptic Fourier descriptors of otoliths. red = Morphotype 1; blue = Morphotype 2; green = Morphotype 3.

TABLE 2 | Morphometric relations and shape index of the otoliths of *Centropomus undecimalis* and *C. parallelus* per morphotype. Means with the different lower-case letter superscripted are significantly different ($P < 0.05$). OW = Otolith weigh.

Species	Class	N	OW	Aspect ratio	Roundness	Circularity	Rectangularity	Ellipticity
Centropomus undecimalis	All	455	0.423 ± 0.329	2.031 ± 0.154	0.425 ± 0.082	23.605 ± 4.573	0.680 ± 0.138	0.339 ± 0.033
	Morphotype 1	146	0.085 ± 0.098	1.904 ± 0.115^{a}	0.377 ± 0.124^{a}	26.859 ± 6.501^{a}	0.567 ± 0.198^{a}	0.310 ± 0.027^{a}
	Morphotype 2	238	0.489 ± 0.134	2.075 ± 0.120^{b}	0.454 ± 0.030^{b}	21.870 ± 1.661^{b}	0.737 ± 0.026^{b}	0.349 ± 0.025^{b}
	Morphotype 3	71	0.917 ± 0.329	2.146 ± 0.156^{c}	0.430 ± 0.038^{c}	22.728 ± 2.372^{c}	0.721 ± 0.027^{c}	0.363 ± 0.031^{c}
Centropomus parallelus	All	176	0.157 ± 0.121	1.814 ± 0.156	0.510 ± 0.075	19.999 ± 5.037	0.724 ± 0.102	0.287 ± 0.037
	Morphotype 1	33	0.035 ± 0.023	1.727 ± 0.152^{a}	0.445 ± 0.129^{a}	24.804 ± 9.736^{ab}	0.602 ± 0.181^{a}	0.264 ± 0.040^{a}
	Morphotype 2	103	0.135 ± 0.071	1.797 ± 0.111^{b}	0.529 ± 0.036^{b}	18.241 ± 1.464^{a}	0.743 ± 0.025^{b}	0.284 ± 0.028^{b}
	Morphotype 3	40	0.318 ± 0.121	1.919 ± 0.193^{c}	0.517 ± 0.065^{b}	20.689 ± 2.045^{b}	0.772 ± 0.059^{c}	0.312 ± 0.040^{c}

DISCUSSION

The otoliths of *C. undecimalis* and *C. parallelus* exhibited clear ontogenetic changes in their growth pattern with two stanzas changing points (SCPs) ($P < 0.001$ for both species). There stanzas corresponded to specific lengths reached by individuals over their life cycles, such as their size at maturity (L_{50}) and length at sexual reversion (SRL_{50}) (Fig. 7). In both species, SCPs (SCP 1 and SCP 2) allowed us to identify three growth phases, which were expressed by significant morphogeometric variations in otoliths' shape ($P < 0.001$ for both species) (Fig. 7), creating a specific morphotype for each phase (Morphotype 1, Morphotype 2 and Morphotype 3). Interspecific differences were observed in the ontogenetic development of the otoliths, in which for both species Morphotype 1 was less elongated and rectangular, typical of more sedentary fish conversely as the structure grows it becomes more rectangular and elongated, which are features of more active fish (Volpedo *et al*., 2008; Tuset *et al*., 2015). There were high shape differences by morphotypes (classification = 90%), with the greatest similarities occurring especially in otoliths close in size to the transition lengths between morphotypes. However, the limitations of these results for Morphotype 1, can be attributed to intra-population variations, which could not be tested due to uncertainty of the type of environment where they were caught. Comparing the timing of the changes in growth pattern, it was observed that the first stanza occurs earlier in *C. parallelus* (31.4% of the maximum length) than in *C. undecimalis* (39.1%). In contrast, the second stanza occurs earlier in *C. undecimalis* (63.3%), with *C. parallelus* only changing its growth pattern when it reaches 68.6% of its maximum length (Fig. 7). Allometric changes in the otoliths of *Centropomus* are observed in the first phase as a greater energetic investment in increasing fish size to the detriment of otolith size. The second allometry is produced by an inverse process, where otoliths grow more than fish size proportionally. Therefore, the morphogeometry of otoliths of *Centropomus* may be an appropriate indicator of their ontogenetic phases.

The allometry found in our study is well known in fish (Bervian *et al*., 2006; Carvalho *et al*., 2015; Barradas *et al*., 2016; Maciel *et al*., 2019). In gonochoric fish, this pattern is commonly associated with the onset of sexual maturity as observed by Carvalho *et al*. (2015), for *Anchoa tricolor*; Barradas *et al*. (2016) for *Corydoras paleatus*; and Maciel *et al*. (2019) for *Genidens genidens*. These authors also made use of the polyphasic method and found two growth stanzas, the first being very similar to the maturation size (L_{50}) of these species. This occurs because sexual maturation is a key-point in the life history of fish, where changes in energy allocation typically occurs. Before sexual maturation, it is exclusively directed to body growth, whereas after first maturation, the energy allocation changes to support the development of reproductive structures (Quince *et al*., 2008; Wilson *et al*., 2018).

For sequential hermaphroditic fishes, this polyphasic growth methodology to break down when growth changes occur had not yet been applied. However, it did not show any difference for the gonochoric fishes, as the growth stanzas found were also very similar with estimated reproductive parameters for *C. undecimalis* and *C. parallelus* (Tab. 3). In both species, the first stanza was within the estimated L_{50} size, and the second stanza was close to the sexual reversal of males into active female size (SRL_{50}). Therefore, the reproductive factor was also the main possible cause, similar to that found for gonochoric fishes (Bervian *et al*., 2006; Carvalho *et al*., 2015; Barradas *et al*., 2016; Maciel

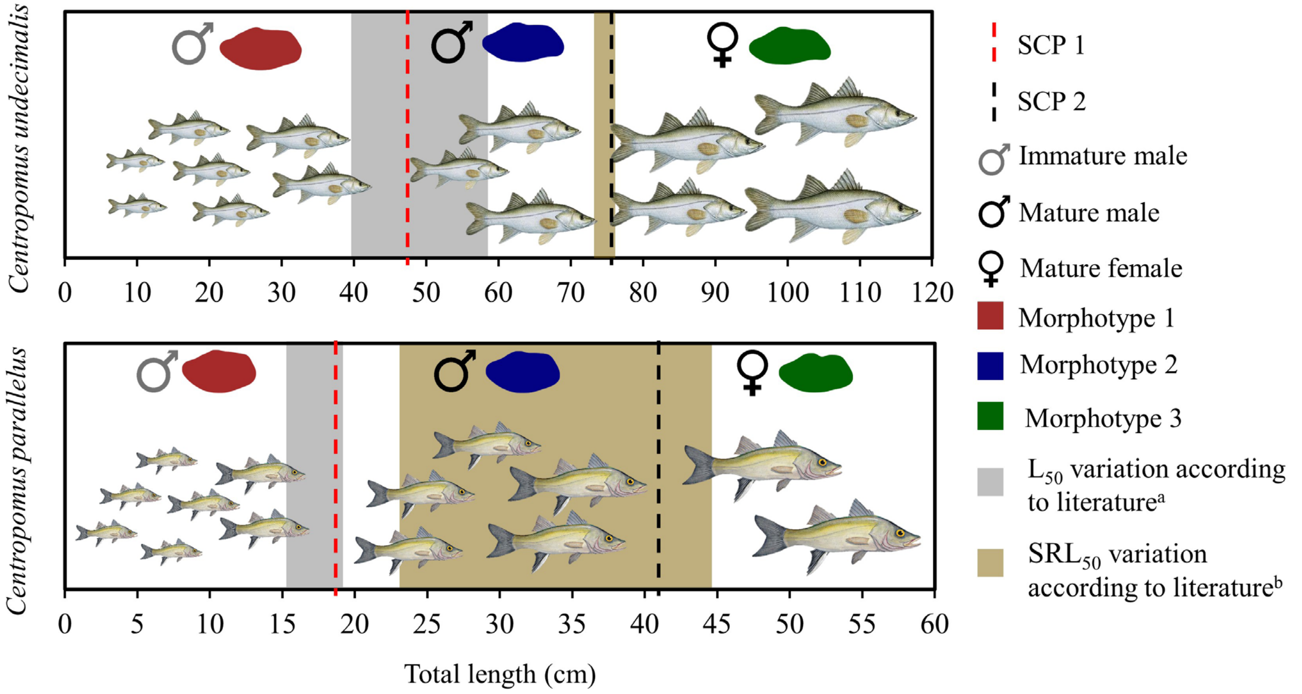

FIGURE 7 | Ontogenetic phases for *Centropomus undecimalis* and *Centropomus parallelus*, and indications of growth stanzas. L_{50} = maturation length; SRL_{50} = sexual reversion length; literature[a] for *C. undecimalis* = Gassman *et al.* (2017) and Cruz-Botto *et al.* (2018); literature[a] for *C. parallelus* = Cunha Chaves, Nogueira (2018), Assis *et al.* (2019) and Costa e Silva *et al.* (2021); literature[b] for *C. undecimalis* = Gassman *et al.* (2017) and Young *et al.* (2020); literature[b] for *C. parallelus* = Cerqueira (2005), Gómez-Ortiz *et al.* (2011) and Assis *et al.* (2019).

et al., 2019). Sequential hermaphroditic species also require high energetic demands due to the amount of complex physiological processes involved in gametogenesis and subsequent sex change (Higgins *et al*., 2015; Matthias *et al*., 2016).

The SRL_{50} shows high variation, especially for *C. parallelus* (Tab. 3). This may be related to fishing (Hunter *et al*., 2015), since overfishing can directly affect size at maturity, longevity, and fecundity (Hutchings, 2002; Hunter *et al*., 2015; Da Silva *et al*., 2019). In addition, sex allocation theory points out that sex change occurs when reproductive potential in the first sex is no longer as efficient (Charnov, 1982). However, Charnov, Skúladóttir (2000) proposed a dimensionless model, which presents the idea that sex change occurs when individuals reach a certain size/age (low variability). In contrast to this approach, in some species sex changes take place as a response to known social or demographic conditions of local populations, such as local sexual proportion (Shapiro, Lubbock, 1980; Shapiro, 1987). Since empirical evidences associate body size and otolith morphometry in both species, our study supports the model proposed by Charnov, Skúladóttir (2000). By applying the same conceptual approach, Allsop, West (2003) predicted sex change at 80% of maximum body size as an invariant relation modeled for over 50 species. If it is assumed that the second stanza coincides with the sex change in both examined species, this phenomenon should occur at 63% of maximum body size for *C. undecimalis* and 68% of maximum body size for *C. parallelus*. These changes, which could be considered early according to the empirical model proposed by Allsop, West (2003), may be related to higher growth rates, which are typical of tropical regions (Houde, 1989). Therefore, for both species, the first stanza may be related to sexual maturation and the second stanza may be related to sexual reversion.

TABLE 3 | Reproductive parameters of *Centropomus undecimalis* and *C. parallelus*. L_{50} = length at first sexual maturation; SRL_{50} = length at sexual reversal of males into active female size; NI = Not informed.

Species	L_{50} (cm)	SRL_{50} (cm)	Geographical coordinates	References
C. undecimalis	40–50	NI	10°58’55”N 74°18’29.1”W	Cruz-Botto *et al.* (2018)
C. undecimalis	59	73.6	10°11’30” – 10°20’20”N 65°41’10” – 65°57’20”W	Gassman *et al.* (2017)
C. undecimalis	NI	73.1	27°50’00” – 26°50’00”N 80°00’00” – 80°30’00”W	Young *et al.* (2020)
C. parallelus	19	NI	25°52’00”S 48°39’00”W	Chaves, Nogueira (2018)
C. parallelus	15	23	15°43’00”S 38°55’00”W	Assis *et al.* (2019)
C. parallelus	18	NI	25°45’00”S 48°20’00”W	Costa e Silva *et al.* (2021)
C. parallelus	NI	45	27°35’02”S 48°26’35”W	Cerqueira (2005)
C. parallelus	NI	32	21°30’00” – 22°48”00”N 97°36’00” – 98°00’00”W	Gómez-Ortiz *et al.* (2011)

Although some features of the reproductive biology of the species may impact the overall shape of otoliths, which could explain why three otoliths morphotypes were found for both studied species, there are many other factors that may also be related to changes in otoliths shape. For instance, habitat type can also be an important factor as changes in habitat use can directly impact otolith shape (Tuset *et al*., 2003, 2018; Vignon, 2012; Zischke *et al*., 2016). In this context, it might be expected that *C. undecimalis* and *C. parallelus* would present different morphotypes as found in this study, due to their migratory behaviour between marine, estuarine and continental waters throughout their life history (Daros *et al*., 2016; Bot Neto *et al*., 2020; Purtlebaugh *et al*., 2020; Stevens *et al*., 2021). However, since we acquired specimens from fishermen at the time of landing, we cannot state whether habitat type, feeding, depth, or temperature influenced the morphotypes due to the uncertainties of where the fish were captured. Therefore, we can observe that the allometry present in the otoliths of *C. undecimalis* and *C. parallelus* represents complex processes associated with evolutionary and demographic issues that need to be better studied by evaluating growth rates and the effect of habitat changes characteristic of these estuarine dependent species.

Finally, we can conclude that *C. undecimalis* and *C. parallelus* show polyphasic growth, with observed changes in growth resulting from reproductive processes such as maturation and sexual reversion. Furthermore, we detected that the otolith shape also followed the pattern of allometric relationships, indicating three different morphotypes for each species. This study reinforces the importance of life-history studies of *C. undecimalis* and *C. parallelus*.

ACKNOWLEDGMENTS

The present study is part of the Projeto Ecológico de Longa Duração da Costa dos Corais – Alagoas, funded by the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq, process number 441657/2016–8), the Alagoas Research Foundation (process number 60030.1564/2016), and the Coordenação de Aperfeiçoamento de Pessoal de Ensino Superior (CAPES) (process number 23038.000452/2017–16). The authors would like to express their gratitude to CNPq for providing a grant to N. Fabré, PhD (process number 306624/2014–1); to all the fishermen who helped in the field work; and to all members of the Laboratory of Ecology, Fish, and Fishery and the Laboratory of Conservation and Management of Renewable Resources at the Universidade Federal de Alagoas.

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AUTHORS' CONTRIBUTION

Reginaldo Medeiros: Conceptualization, Data Curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Writing-original draft, Writing-review and editing.
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ETHICAL STATEMENT

The research was carried out in accordance with the principles of the Basel Declaration and following the recommendations of Brazilian Animal Protection Law. Sampling procedures were approved by the Sistema de Autorização e Informação em Biodiversidade (SISBIO committee) under the license #56293–1.

COMPETING INTERESTS

The authors declare no competing interests.

HOW TO CITE THIS ARTICLE

- **Medeiros R, Oliveira CD, Souto D, Rangely J, Fabré NN.** Growth stanza in fish life history using otoliths shape: the protandric *Centropomus* case (Carangaria: Centropomidae). Neotrop Ichthyol. 2021; 19(4):e200145. https://doi.org/10.1590/1982-0224-2020-0145

Neotropical Ichthyology

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SBI
Official Journal of the
Sociedade Brasileira de Ictiologia