ONTOGENETIC VARIATION IN THE SAGITTA OTOLITH OF CENTROPOMUS UNDECIMALIS (ACTINOPTERYGI: PERCIFORMES: CENTROPOMIDAE) IN A TROPICAL ESTUARY

Renato L. Bot Neto 1, 4, Barbara M. Carvalho 2, Roberto Schwarz Júnior 3, and Henry L. Spach 4

1 Post graduate Program in Ecology and Conservation, Federal University of Paraná, Brazil
2 Post graduate Program in Environmental Engineering, Federal University of Paraná, Brazil
3 Laboratory of Estuarine and Marine Ichthyology, Department of Fisheries and Aquaculture Engineering, Federal University of Sergipe, Brazil
4 Laboratory of Fish Ecology, Center for Marine Studies, Federal University of Paraná, Brazil

Bot Neto R.L., Carvalho B.M., Schwarz Júnior R., Spach H.L. 2020. Ontogenetic variation in the sagitta otolith of Centropomus undecimalis (Actinopterygii: Perciformes: Centropomidae) in a tropical estuary. Acta Ichthyol. Piscat. 50 (4): 433–443.

Background. The presently reported study was initiated in order to increase the available information on this species of commercial and sporting importance, thus the study aimed to identify possible differences in the shape of the sagitta otolith during the ontogenetic development of the common snook, Centropomus undecimalis (Bloch, 1792), sampled between May 2017 and April 2018 at the mouth of the São Francisco River along its estuary stretch (approximately 10 km). Morphometric study of otoliths is important as a support for future studies on the trophic ecology of ichthyophagous fishes and studies on fishing stocks using the contour of otoliths of this species.

Materials and methods. The fish were sampled monthly at five sampling sites distributed between the mouth of the São Francisco River and the municipality of Brejo Grande. For the collection, a beach seine (30 m long, 2.8 m high, and 5 mm mesh between opposite knots) was used. In the laboratory, the otoliths were extracted, photographed, described morphologically, and the possible differences in their contour were analyzed using the wavelets.

Results. We analyzed 148 otoliths grouped into six class intervals. Otolith shape varied from rounded to trapezoidal during the ontogenetic growth and showed a gradual decrease in the percentage of presence of the excisura ostii (absent in the largest specimens). PERMANOVA evidenced significant differences in the contour between the smallest size class and the others. For wavelet 4, the LDA correctly reclassified 47.97% otoliths in the size classes, with the best reclassifications occurring in the 5.0–10.0 (43.33%) and 10.1–15.0 cm (65.52%) intervals. While for wavelet 5, the LDA correctly reclassified 59.46% otoliths according to the size class, with the best reclassifications occurring in the length classes 5.0–10.0 (46.67%), 10.1–15.0 (75.86%), 15.1–20.0 (66.67%), and 20.1–25.0 cm (59.38%).

Conclusion. The ontogenetic differences found both in the shape and in the otolith structures are important for the enhancement of knowledge on fish biology and indicate the need for further studies. The lack of such information on estuarine species makes it difficult to conduct studies on the trophic ecology and the management of these species.

Keywords: common snook, Centropomidae, form, morphology, sea bass

INTRODUCTION

Otoliths are mineralized structures formed by the deposition of calcium carbonate in a protein matrix. They are located in the inner ear of bony fishes and assist in the balance and hearing systems (Ladich and Schulz-Mirbach 2016). There are three pairs of otoliths (sagitta, lapillus, and asteriscus) representing different location, size, function, shape and structure (Thresher 1999).

The otolith shape usually has an interspecific pattern among the species (Volpodo and Echeverría 1999, Tuset et al. 2008), however, some internal (physiological) and external factors can modify the shape of otoliths in...
populations of the same species throughout the ontogenetic development. Several studies demonstrate how the shape of the otoliths can vary (Carvalho and Corrêa 2014, Maciel et al. 2019, Carvalho et al. 2020) and the ontogenetic variation influenced by growth has already been described for several species (Capoccioni 2011, Vignon 2012, Carvalho et al. 2015, Yan et al. 2017, Song et al. 2019).

In addition to species physiology, environmental parameters influence the shape of otoliths. Due to hearing adaptation, depth proved to be a significant parameter in the shape of otoliths, as observed by Torres et al. (2000) and Cruz and Lombarte (2004). Changes in otolith shape caused by salinity were also observed (Capoccioni et al. 2011, Avigliano et al. 2012, 2014). It was also possible to detect the influence of temperature on otolith shape. The same fish-species populations living in bodies of water with wide temperature ranges distinctly differ in their otolith shape (Leguá et al. 2013). Recent studies have shown that environmental stress can cause morphological changes, even irregularities, in the deposition of crystals in otoliths (Carvalho et al. 2019, Holmberg et al. 2019).

Several methods are implemented in the description of the morphology and contour of otoliths (Lombarte and Tuset 2015). Among them are:

• polar coordinates (Lombarte and Tuset 2015),
• landmarks (Monteiro et al. 2005, Carvalho et al. 2015),
• Fourier harmonics (Libungan et al. 2015, Bose et al. 2017), and
• wavelets (Sadighzadeh et al. 2014, Tuset et al. 2015).

Fourier harmonics yield better results with phylogenetically distant species, while wavelets provide better results both in distinguishing phylogenetically close species and in identifying intraspecific variations (Sadighzadeh et al. 2012).

Fishes of the family Centropomidae are distributed in the tropical and subtropical regions of the Atlantic and Pacific oceans along the coasts of the American continent (Rivas 1986). The family currently hosts 12 species, four of which are present on the Brazilian coast: *Centropomus undecimalis* (Bloch, 1792), *Centropomus parallelus* Poey, 1860, *Centropomus ensiferus* Poey, 1860, and *Centropomus pectinatus* Poey, 1860 (Froese and Pauly 2019). Species of this family are important because of their high commercial value and the potential for aquaculture (Junior et al. 2007, Ostini et al. 2007). Therefore, centropomids are the target of artisanal, commercial, and recreational fishing (Muller and Taylor 2013, Muller et al. 2015). Even though they are euryhaline species, they are more frequently found in estuarine systems (Seaman and Collins 1983).

The common snook, *Centropomus undecimalis*, popularly known as sea bass, is a protandrous hermaphrodite species, with euryhaline, diadromous, and demersal habits (Taylor et al. 2000, Perera-García et al. 2011). Its distribution extends from North America (Florida, USA) to South America (Rio de Janeiro, Brazil) and is widely distributed along the Brazilian coast (Figueiredo and Menezes 1980). The species is a predator, with primarily piscivorous feeding habit and occupies high levels in the trophic web (Figueiredo and Menezes 1980, Aliaume et al. 2005, Lira et al. 2017). Therefore, the objective of the presently reported study was to identify possible ontogenetic differences in the sagitta otolith of *C. undecimalis*, caught in a tropical estuary, as a support for future studies on the trophic ecology of ichthyophagous fishes in the region and studies on fishing stocks using the contour of otoliths of this species.

**MATERIALS AND METHODS**

**Sample collection and processing.** The specimens of *Centropomus undecimalis* were sampled monthly, between May 2017 and April 2018, at five sampling sites distributed between the mouth of the São Francisco River and the municipality of Brejo Grande (Fig. 1), in the lower São Francisco River (10°28′34.02″S–36°24′27.02″W). For collection, a beach seine (30 m long, 2.8 m high, and 5 mm mesh between opposite knots) was used. Subsequently, the caught fish individuals were refrigerated, identified to the species taxonomic level using specialized literature (Figueiredo and Menezes 1980), measured (total length TL; 0.01 cm), weighed (total weight TW; 0.1 g), divided into six length classes (5.0–10.0, 10.1–15.0, 15.1–20.0, 20.1–25.0, 25.1–30.0, 30.1–35.0 cm). The sagitta otoliths were extracted, packed in identified plastic bags and subsequently photographed.

**Otolith morphology and contour.** The classification of the otolith shape, sulcus acusticus, margins and classification of the anterior and posterior region were performed according to Tuset et al. (2008) and Brenha-Nunes et al. (2016) (Fig. 2 A, C, and D). The contour was obtained using the wavelet function (Paris-Baradad et al. 2010, Sadighzadeh et al. 2014). Wavelets are the result of expanding a signal in a family of functions that represent dilations and translations of a mother function:

\[
Ψ_{s}(x) = 1 \cdot s^{-1} \cdot \Psi \cdot (\varphi \cdot s^{-1})
\]

where \(\Psi\) is the function with local support in an amplitude limited in the abscissa axis, \(\varphi\) is the lowest tone filter and \(s\) is the scale parameter (Mallat 1991). From the wavelets, 512 equidistant coordinates are distributed in each otolith starting from the rostrum (1) and ending at the same (512) (Fig. 2B). The acquisition of wavelets was carried out on the AFORO website as described by Paris-Baradad et al. (2010).

**Statistical analysis of otolith contour data.** Data obtained for the wavelets did not meet the assumptions required for parametric tests (Shapiro–WilK; \(P < 0.05\) and Bartlett’s test; \(P < 0.05\)). Thus, to identify variations in the otolith contour between the class intervals, a Permutational Analysis of Variance (PERMANOVA) was applied. If the test detects significant differences in the otolith shape between the size classes (\(P < 0.05\)), a Bonferroni test was used to identify between which intervals the significant interaction is.

From the principal component analysis (PCA), using the variance-covariance matrix, the wavelet functions were

---

1. http://isis.cmima.csic.es
summarized without losing information (Tuset et al. 2015, 2016). The broken-stick method indicated the principal components (PC) to retain, which further explain the variability in the otolith contour (Gauldie and Crampton 2002). To exclude the effect of otolith allometry, a linear regression was run between the PC and the total length of the fish (TL); from the regressions between PC and TL that showed significance, the residuals were used for the linear discriminant analysis (LDA). Using the PCs and the class intervals, it was possible to employ an LDA to check the percentage of correct reclassification of otoliths within the class intervals.

RESULTS

In total, 148 sagitta otoliths of **Centropomus undecimalis** (3.3–37.6 cm TL; 0.2–362.3 g TW) were analyzed, which were grouped into six fish length classes to better describe the species ontogeny (Fig. 3).

Otoliths of *C. undecimalis* presented some morphological variations throughout ontogeny, being rounded otoliths (Fig 4. A) in the lowest interval of 5.0–10.0 cm, becoming trapezoidal throughout the ontogenetic growth (Fig 4. B–F). The development of the rostrum and the excisura ostii varied throughout ontogeny; 87% otoliths in the 5.0–10.0 cm length class had a well-developed rostrum with excisura ostii; 53% otoliths in 10.1–15.0 cm, between 23% and 27% in the intervals 15.1–20.0 and 20.1–25.0 cm, respectively, 6% in the 25.1–30.0 cm interval had developed rostrum and excisura ostii, and were absent in the 30.1–35.0 cm interval. Throughout ontogeny, it was possible to identify smooth and crenulated margins. The crenulated margins were dominant in all intervals, assuming the following dominance values: 90% in the 5.0–10.0 cm interval, 77% in the intervals 10.1–15.0, 15.1–20.0, and 20.1–25.0 cm, 81% and 100% in the intervals 25.1–30.0, and 30.1–35.0 cm, respectively. The posterior region varied between double-peaked and round. There was a dominance of the round posterior region with 97%, 53%, 63% and 75% in the 5.0–10.0, 10.0–15, 25.1–30.0, and 30.1–35.0 cm intervals, respectively. The 20.1–25.0 cm interval showed 57% dominance of the double-peaked posterior region. Meanwhile, in the 15.1–20.0 cm interval, 50% otoliths presented a double-peaked posterior region and 50% round posterior region. The sulcus acusticus of the analyzed otoliths presented the cauda section curved towards the posterior ventral region, and this curvature seems to intensify along the ontogenetic growth of the species (Figs. 4A, 4F). The only constant traits throughout ontogeny of *C. undecimalis* otoliths were:

---

**Fig. 1.** Sampling sites in the lower São Francisco River, State of Sergipe, Brazil

**Fig. 2.** (A) Schematic drawing of the sagitta otolith of *Centropomus undecimalis* caught in the lower São Francisco River, Sergipe, Brazil; (B) Contour of the otolith using 512 equidistant coordinates in the sagitta otolith; (C) Double-peaked posterior region; (D) Round posterior region; abbreviations: a = anterior region, d = dorsal region, v = ventral region, p = posterior part of the otolith, sa = sulcus acusticus, r = rostrum, e = excisura ostii, dd = dorsal depression
heterosulcoid sulcus acusticus, anterior round region, and deep dorsal depression.

The contour of the otoliths showed variability in wavelet 4 and wavelet 5, in the posterior (286–363) and ventral (370–460) regions of the otoliths (Fig. 5).

The results of PERMANOVA indicated significant differences in the contours between size class intervals ($F = 9.583$, $P < 0.0001$) and the Bonferroni test pointed out that these differences are caused by the first class interval, which differed from all others (Table 1).

Figure 6 shows a high variability in the shape of otoliths of *C. undecimalis* along its ontogeny obtained by wavelet 4. Axis 1 explained 61.63% variability in the shape of otoliths. On the positive axis 1, the otoliths from the 5.0–10.0, 25.1–30.0, and 30.1–35.0 cm intervals were grouped, which are intervals with the highest percentage of crenulated margins in the otoliths. In the negative axis 1, the intervals 10.1–15.0, 15.1–20.0, and 25.1–30.0 cm with dorsal depression with less depth. Axis 2 explained only 17.14% variability in otolith shape. In the negative axis 2, the intervals 5.0–10.0, 15.1–20.0, 20.1–25.0, and 25.1–30.0 cm were grouped, which are intervals with the highest percentage of crenulated margins in the otoliths, as also observed in wavelet 4. In the negative axis 1, the intervals 10.1–15.0, 15.1–20.0, and 20.1–25.0 cm were grouped together, these intervals showed similar percentages of the posterior region type, well-developed rostrum and excisura ostii.

For wavelet 5, LDA presented 59.46% correct reclassifications of otoliths between the defined class intervals. The wavelet 5 LDA presented a better reclassification between the intervals 5.0–10.0, 10.1–15.0, 15.1–20.0, and 20.1–25.0 cm with percentages of 46.67%, 75.86%, 66.67%, and 59.38%, respectively (Table 3).
DISCUSSION

The morphology of otoliths of *Centropomus undecimalis* in the presently reported study indicates as a diagnostic trait of this species the otolith shape (from elliptical to trapezoidal, varying ontogenetically), heterosulcoid sulcus acusticus and the presence of dorsal depression. Some characteristics varied a lot during the ontogenetic development, such as type of margins, excisura ostii, and stages of development of the rostrum. The absence of in-depth studies like this on the ontogenetic variation of *C. undecimalis* otoliths makes it difficult to compare and identify differences influenced by the environment in all life stages of this species. Otoliths from adult individuals of this species, however, caught both in Florida (USA)* and on the Brazilian coast (Brenha-Nunes et al. 2016) show morphological similarity with those observed in the presently reported study.

The otoliths analyzed in the present study presented a shape that varies from elliptical to trapezoidal, a characteristic diagnostic trait for the genus *Centropomus*, as already observed in previous studies (Lombarte et al. 2006, Brenha-Nunes et al. 2016, Granados-Amores et al. 2016).

---

*Fig. 5.* Decomposition of the *sagitta* otolith contour through the ontogeny of the specimens of *Centropomus undecimalis* caught in the lower São Francisco River, Sergipe, Brazil; the x-axis represents the 512 Cartesian coordinates that form the contour and the y-axis presents the means of the points by length class; length class intervals: 5.0–10.0, 10.1–15.0, 15.1–20.0, 20.1–25.0, 25.1–30.0, 30.1–35.0 cm

*Table 1* Probability values obtained through permutational analysis of variance (PERMANOVA) with Bonferroni’s correction applied to the otolith contour, within the total length class intervals, of *Centropomus undecimalis* caught in the lower São Francisco River, Sergipe, Brazil

| Length class | 5.0–10.0 | 10.1–15.0 | 15.1–20.0 | 20.1–25.0 | 25.1–30.0 |
|--------------|----------|-----------|-----------|-----------|-----------|
| 10.1–15.0    | 0.0015   |           |           |           |           |
| 15.1–20.0    | 0.0015   |           |           | 1.0000    |           |
| 20.1–25.0    | 0.0015   | 0.1740    |           | 1.0000    |           |
| 25.1–30.0    | 0.0015   | 0.4620    | 1.0000    | 1.0000    |           |
| 30.1–35.0    | 0.0015   | 1.0000    | 1.0000    | 0.5085    | 1.0000    |

*Values of *P* <0.05 were considered significant and are marked with *S*.

---

*https://www.flickr.com/photos/myfwc/albums/72157625872804969*
In the internal part of the otoliths, the presence of a well-developed heterosulcoid sulcus acusticus was noted, with a notable differentiation between ostium and cauda, agreeing with the studies performed by Lombarte et al. (2006), Martínez et al. (2007), Brenha-Nunes et al. (2016), Gallardo-Cabello et al. (2017), Espino-Barr et al. (2019).

It is still possible to denote that the analyzed otoliths have the cauda curved towards the posterior ventral region of the otoliths, and this is considered a standard for the genus. It is also worth noting the presence of a heterosulcoid sulcus acusticus in this species, and this characteristic is common to the order Perciformes, however, it is also present in the orders Atheriniformes and Clupeiformes (see Carvalho and Corrêa 2014, Siliprandi et al. 2014, Carvalho et al. 2015).

The presence of an elongated, rounded and pronounced rostrum are characteristics pointed out by Gallardo-Cabello et al. (2017) and Espino-Barr et al. (2019) for the genus Centropomus and are characteristics that were also observed in the presently reported study. Gallardo-Cabello et al. (2017) also point out that for otoliths of the species Centropomus nigrescens Günther, 1864 there is an absence of pronounced notches (excisura major and minor) causing the absence of both antirostrum and pararostrum, this seems to be a characteristic of the genus in larger individuals, since that the presently reported study detected that the prevalence of the excisura decreases along with the ontogenetic development of Centropomus undecimalis. The prevalence of crenulated borders was constant during the analyzed ontogenetic development,

### Table 2

Reclassification of the otolith contour for wavelet 4 between the length class intervals of Centropomus undecimalis caught in the lower São Francisco River, Sergipe, Brazil, obtained through the linear discriminant analysis (LDA)

| Length class | 5.0–10.0 | 10.1–15.0 | 15.1–20.0 | 20.1–25.0 | 25.1–30.0 | 30.1–35.0 |
|--------------|----------|-----------|-----------|-----------|-----------|-----------|
| 5.0–10.0     | 13 (43.33) | 3 (10.00) | 3 (10.00) | 0         | 5 (16.67) | 6 (20.00) |
| 10.1–15.0    | 3 (10.34)  | 19 (65.52) | 3 (10.34) | 1 (3.45)  | 3 (10.34) | 0         |
| 15.1–20.0    | 3 (9.09)   | 6 (18.18)  | 13 (39.39) | 6 (18.18) | 5 (15.15) | 0         |
| 20.1–25.0    | 1 (3.13)   | 3 (9.38)   | 7 (21.88)  | 16 (50)   | 4 (12.50) | 1 (3.13)  |
| 25.1–30.0    | 3 (18.75)  | 3 (18.75)  | 1 (6.25)   | 2 (12.5)  | 6 (37.50) | 1 (6.25)  |
| 30.1–35.0    | 2 (25.00)  | 0          | 0          | 1 (12.5)  | 1 (12.50) | 4 (50.00) |

The number in parentheses corresponds to the frequency of reclassification; the information in bold print is the number and percentage of otoliths correctly reclassified when comparing the size class with itself. It is highlighted to show that the reclassifications have had a good success rate.
Ontogenetic variation in otoliths of *Centropomus undecimalis* agreeing with what was observed by Espino-Barr et al. (2019). Gallardo-Cabello et al. (2017) and Espino-Barr et al. (2019) also indicated that the otoliths of species within the genus *Centropomus* have a concave exterior, according to the presently reported study, and that along the growth both the flexion and the thickness of the otolith tend to increase.

Ontogenetic changes in otolith contour have been widely observed in several species (Capoccioni et al. 2011, Vignon 2012). In *C. undecimalis*, variations in the contour throughout ontogeny were also found (Table 1 and Table 2), studies that describe the ontogenetic variations in the shape of otoliths are of paramount importance for the identification of prey of ichthyophagous fishes (Bugoni and Vooen 2004, Carvalho et al. 2019, Rodrigues et al. 2019). The lack of morphological studies on otoliths at different stages of life makes it difficult to identify species, causing an erroneous identification among ingested prey or an increase in the number of specimens in the “unidentified” category. For example, otoliths from *C. undecimalis* at the intermediate phases have characteristics very similar to other perciform fishes, such as *Pomadasys corvinaeformis* (Steindachner, 1868), otoliths from *C. undecimalis* at the adult phases are similar to otoliths from *Lutjanus analis* (Cuvier, 1828) (see Martinez et al. 2007, Brenha-Nunes et al. 2016).

The results obtained in the presently reported study show changes in the shape of otoliths of *C. undecimalis* throughout the ontogenetic development (from elliptical to trapezoidal). Such an effect can be caused by the

---

**Table 3**

| Length class | 5.0–10.0 | 10.1–15.0 | 15.1–20.0 | 20.1–25.0 | 25.1–30.0 | 30.1–35.0 |
|--------------|----------|-----------|-----------|-----------|-----------|-----------|
| 5.0–10.0     | 14 (46.67)| 3 (10.00) | 3 (10.00) | 1 (3.33)  | 6 (20.00) | 3 (10.00) |
| 10.1–15.0    | 0        | 22 (75.86)| 3 (10.34) | 2 (6.90)  | 2 (6.90)  | 0         |
| 15.1–20.0    | 0        | 6 (18.18) | 22 (66.67)| 5 (15.15)| 0         | 0         |
| 20.1–25.0    | 1 (3.13) | 3 (9.38)  | 7 (12.50) | 19 (59.38)| 2 (6.25)  | 0         |
| 25.1–30.0    | 4 (25.00)| 1 (6.25)  | 2 (12.50) | 1 (6.25)  | 7 (43.75) | 1 (6.25)  |
| 30.1–35.0    | 3 (37.50)| 0         | 0         | 1 (12.50)| 0         | 4 (50.00) |
| Total        | 22       | 35        | 37        | 29        | 17        | 8         |

The number in parentheses corresponds to the frequency of reclassification. The information in bold print is the number and percentage of otoliths correctly reclassified when comparing the size class with itself. It is highlighted to show that the reclassifications have had a good success rate.
change of habitat and by the exposure of individuals to different salinity throughout their development since the salinity is recognized for causing changes in the shape of otoliths (Capoccioni et al. 2011, Avigliano et al. 2012, 2014). As mentioned above, *C. undecimalis* had a diadromous habit, moving to places of higher salinity (close to the mouth of estuarine systems) in reproductive periods. After hatching, young individuals tend to migrate to more internal areas of the estuaries where they remain until the reproductive period (Perera-García et al. 2011).

According to Avigliano et al. (2012), elliptical-shaped otoliths are associated with fish found in environments with higher salinity. Therefore, the change in otolith shape for *C. undecimalis* (from elliptical to trapezoidal) may be reflecting the species migrations in the estuarine environment throughout development. Nevertheless, other variables (such as diet and physiological stress) may also be influencing this change in the otolith shape, so further studies are still required to define which variables are actually causing this change.

In addition to changes in shape, otoliths of *C. undecimalis* also showed morphological variations in the rostrum and in the excisura ostii during ontogenetic development. The results indicate a tendency to decrease the percentage of otoliths with the excisura ostii and a decrease in the development of rostrum with the growth of individuals. The development of the rostrum and the excisura ostii were considered by Volpedo and Echeverría (2003) as a diagnostic trait for the position in the water column and swimming ability. Otoliths that have a prominent rostrum and deep excisura ostii are characteristic of fish with a pelagic habit, while otoliths with little pronounced rostrum and a shallow or absent excisura ostii are characteristic of fish that have a demersal habit (Volpedo and Echeverría 2003). These changes in the rostrum and the excisura ostii among the ontogeny of *C. undecimalis* may be the result of the change in habitat caused by the diadromous habit, with smaller individuals more present in the water column and larger individuals more associated with substrate and rigid structures, according to Froese and Pauly (2019), the species is associated with rigid structures like rocks or tree branches.

Studies using wavelets in otoliths usually employ this technique for the characterization of fish stocks (Wiff et al. 2019), characterization of populations (Libungan et al. 2015), or for ecomorphological studies (Sadighzadeh et al. 2014), however, the use of this technique to identify differences in the morphology of otoliths during ontogenetic development is still scarce. It is also worth mentioning that the presently reported study is a pioneer in testing separately wavelet 4 and 5 by class interval, in which wavelet 5 obtained a good rate of correct reclassification of otoliths between intervals; perhaps this wavelet is sensitive to ontogenetic differences, however further studies are required to confirm this.

**Conclusions and future perspectives.** The ontogenetic differences found in the presently reported study highlight the importance of conducting further studies of this type, as for the majority of species (commercially important or not) information such as these is still lacking. The lack of this information makes it difficult to develop studies on the trophic ecology of ichthyophageous fishes, leading to the identification failure of many of the otoliths in the stomach contents or the confusion between close species that may present similarities in their otoliths. Moreover, this study indicated the possibility that the wavelet 5 is sensitive to ontogenetic variations, however, more studies are needed to confirm it.

**ACKNOWLEDGEMENTS**

The authors would like to thank the Coordination for the Improvement of Higher Education Personnel (CAPES) for the scholarship granted to Renato L. Bot Neto (Doctoral Scholarship) in the Graduate Program in Ecology and Conservation at the Federal University of Paraná (PPG-ECO UFPR); National Council for Scientific and Technological Development (CNPq Process Numbers: 153090/2019-7) to Barbara Maichak de Carvalho, to students of the Fisheries Engineering Program at the Federal University of Sergipe (UFS) Luane, Kléverton, Paulo, and Priscilla who assisted in the collection and sorting of the material; to our boatman and friend Ronaldinho (Tito) always happy to sail with us through Velho Chico. And special thanks to the artist Giorgio Alberto for kindly helping us with the illustrations in this study.

**REFERENCES**

Aliaume C., Zerbi A., Miller J.M. 2005. Juvenile snook species in Puerto Rico estuaries: Distribution, abundance and habitat description. Proceedings of the 47th Gulf and Caribbean Fisheries Institute: 499–519.

Avigliano E., Martínez C.F.R., Volpedo A.V. 2014. Combined use of otolith microchemistry and morphometry as indicators of the habitat of the silverside (*Odontesthes bonariensis*) in a freshwater–estuarine environment. Fisheries Research 149: 55–60. DOI: 10.1016/j.fishres.2013.09.013

Avigliano E., Tombari A., Volpedo A.V. 2012. ¿El otolito de pejerrey (*Odontesthes bonariensis*), refleja el estrés ambiental? Biología Acuática 27: 9–15.

Bose A.P., Adragna J.B., Balshine S. 2017. Otolith morphology varies between populations, sexes and male alternative reproductive tactics in a vocal toadfish *Porichthys notatus*. Journal of Fish Biology 90 (1): 311–325. DOI: 10.1111/jfb.13187

Brenha-Nunes M.R., Santificetur C., Conversani V.R.M., Giaretta M.B., Rossi-Wongtschowski C.L.D.B., Siliprandi C.C. 2016. Atlas of marine bony fish otoliths (sagittae) of southeastern-southern Brazil Part IV: Perciformes (Centropomidae, Acropomatidae, Serranidae, Priacanthidae, Malacanthidae, Pomatomidae, Carangidae, Lutjanidae, Gerreidae and Haemulidae). Brazilian Journal of Oceanography 64 (Spe 1): 23–75. DOI: 10.1590/S1679-875920161100064(sp1)

Bugoni L., Vooren C.M. 2004. Feeding ecology of the common tern *Sterna hirundo* in a wintering area...
in southern Brazil. Ibis 146 (3): 438–453. DOI: 10.1111/j.1474-919X.2004.00277.x

Capocciioni F., Costa C., Aguzzi J., Menesatti P., Lombarte A., Ciccotti E. 2011. Ontogenetic and environmental effects on otolith shape variability in three Mediterranean European eel (Anguilla anguilla, L.) local stocks. Journal of Experimental Marine Biology and Ecology 397 (1): 1–7. DOI: 10.1016/j.jembe.2010.11.011

Carvalho B.M., Corrêa M.F.M. 2014. Morphometry of the sagitta otolith from Atherinella brasiliensis (Quoy and Gaimard, 1824) (Actinopterygii – Atherinopsidae), at the coast of Paraná. Tropical Oceanography 42: 54–59. DOI: 10.5914/tropicalocean.v42i1.5801

Carvalho B.M., Spach H.L., Vaz-Dos-Santos A.M., Volpedo A.V. 2019. Otolith shape index: Is it a tool for trophic ecology studies? Journal of the Marine Biological Association of the United Kingdom 7: 1–8. DOI: 10.1017/S0025315419000729

Carvalho B.M., Vaz-Dos-Santos A.M., Spach H.L., Volpedo A.V. 2015. Ontogenetic development of the sagittal otolith of the anchovy, Anchoa tricolor, in a subtropical estuary. Scientia Marina 79: 409–418. DOI: 10.3989/scimar.04218.31A

Carvalho B.M., Volpedo A.V., Fávaro L.F. 2020. Ontogenetic and sexual variation in the sagitta otolith of Menticirrhus americanus (Teleostei; Sciaenidae) (Linnaeus, 1758) in a subtropical environment. Papéis Avulsos de Zoolôgia 60: e20206009. DOI: 10.11606/1807-0205/2020.60.09

Cruz A., Lombarte A. 2004. Otolith size and its relationship with colour patterns and sound production. Journal of Fish Biology 65: 1512–1525. DOI: 10.1111/j.0022-1112.2004.00558.x

Espino-Barr E., Gallardo-Cabello M., Puente-Gómez M., García-Boa A. 2019. Study of the age of Centropomus robalito by otolith analysis of sagitta, asteriscus and lapillus in Mexican Central Pacific. HSQA Journal of Aquatic Fisheries 3: e013. DOI: 10.24966/AAF-5523/100013

Figueiredo J.L., Menezes N.A. 1980. Manual de Peixes Marinhos do Sudeste do Brasil, III Teleostei (2), Museu de Zoológia, Universidade de São Paulo, São Paulo.

Froese R., Pauly D. (eds.) 2019. FishBase. [Version 18/2019] http://www.fishbase.org

Gallardo-Cabello M., Espino-Barr E., Puente-Gómez M., García-Boa A. 2017. Age analysis of Centropomus nigrescens by otoliths sagitta, asteriscus and lapillus in Mexican Central Pacific. International Journal of Development Research 7 (11): 16499–16507.

Gauldie R.W., Crampton J.S. 2002. An ecophenological explanation of individual variability in the shape of the fish otolith: comparison of the otolith of Hoplostethus atlanticus with other species by depth. Journal of Fish Biology 60 (5): 1204–1221. DOI: 10.1111/j.1095-8649.2002.tb01715.x

Granados-Amores E., Granados-Amores J., Zavala-Leal O.I., Flores-Ortega J.R. 2020. Geometric morphometrics in the sulcus acusticus of the sagittae otolith as tool to discriminate species of the genus Centropomus (Centropomidae: Perciformes) from the southeastern Gulf of California. Marine Biodiversity 50 (1): 10. DOI: 10.1007/s12526-019-01030-1

Holmberg R.J., Wilcox-Freeburg E., Ryhne A.L., Trusty M.F., Stebbins A., Nye S.W. Jr., Honig A., Johnston A.E., San Antonio C.M., Bourque B., Hannigan R.E. 2019. Ocean acidification alters morphology of all otolith types in Clark’s anemonefish (Amphiprion clarkii). PeerJ 7: e6152. DOI: 10.7717/peerj.6152

Junior J., Almeida V.G., Souza-Filho J.I. 2007. Adaptação de juvenis selvagens de Centropomus undecimalis (Bloch, 1792) (Pisces, Centropomidae) ao ambiente controlado. [Adaptation of wild juveniles of Centropomus undecimalis (Bloch, 1792) (Pisces, Centropomidae) to the controlled environment.] Cândombá–Revista Virtual 3 (1): 15–26. [In Portuguese.]

Ladich F., Schulz-Mirbach T. 2016. Diversity in fish auditory systems: One of the riddles of sensory biology. Frontiers in Ecology and Evolution 4: 28. DOI: 10.3389/fevo.2016.00028

Leguá J., Plaza G., Pérez D., Arkhipin A. 2013. Otolith shape analysis as a tool for stock identification of the southern blue whiting, Micromesistius australis. Latin American Journal of Aquatic Research 41: 479–489. DOI: 10.3856/vol41-issue3-fulltext-11

Libungan L.A., Oskarsson G.J., Slotte A., Jacobsen J.A., Pálsson S. 2015. Otolith shape: a population marker for Atlantic herring Clupea harengus. Journal of Fish Biology 86 (4): 1377–1395. DOI: 10.1111/jfb.12647

Lira A.S., Frédou T., Vaz-dos-Santos A.M., Spach H.L., Vaz-Dos-Santos A.M., Junior J., Almeida V.G., Souza-Filho J.J. 2007. Adaptação de juvenis selvagens de Centropomus undecimalis (Bloch, 1792) (Pisces, Centropomidae) ao ambiente controlado. [Adaptation of wild juveniles of Centropomus undecimalis (Bloch, 1792) (Pisces, Centropomidae) to the controlled environment.] Cândombá–Revista Virtual 3 (1): 15–26. [In Portuguese.]

Lombarte A., Ciccotti E. 2007. Otolith shape analysis as a tool for stock identification of the southern blue whiting, Micromesistius australis. Latin American Journal of Aquatic Research 41: 479–489. DOI: 10.3856/vol41-issue3-fulltext-11

Lombarte A., Ciccotti E. 2007. Otolith shape analysis as a tool for stock identification of the southern blue whiting, Micromesistius australis. Latin American Journal of Aquatic Research 41: 479–489. DOI: 10.3856/vol41-issue3-fulltext-11

Lombarte A., Tuset V. 2015. [3.] Morfometria de otolitos. Pp. 59–91. Volpedo A.V., Vaz-dos-Santos A.M. (eds.) Métodos de estudos com otólitos: princípios e aplicações. Métodos de estudos com otólitos: princípios e aplicações. CAFP-BA-PIESC, Buenos Aires, Argentina.

Maciel T.R., Vaz-dos-Santos A.M., Barradas J.R.D.S., Vianna M. 2019. Sexual dimorphism in the catfish Genidens genidens (Siluriformes: Ariidae) based on otolith morphometry and relative growth.
Neotropical Ichthyology 17 (1). DOI: 10.1590/1982-0224-20180101

Mallat S. 1991. Zero-crossings of a wavelet transform. IEEE Transactions on Information theory 37 (4): 1019–1033. DOI: 10.1109/18.86995

Martínez J.A., Arteaga M.M.C., Musi J.L.T., Aranda A.A.M. 2007. Utilización de otolitos como herramienta en la determinación de especies. Revista de Zoología 18: 13–18.

Monteiro L.R., Di Benedetto A.P.M., Guillermo L.H., Rivera L.A. 2005. Allometric changes and shape differentiation of sagitta otoliths in sciaenid fishes. Fisheries Research 74 (1–3): 288–299. DOI: 10.1016/j.fishres.2005.03.002

Muller R.G., Taylor R.G. 2013. The 2013 stock assessment update of common snook, Centropomus undecimalis. In House Report IHR 2013-004. Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, St. Petersburg, FL, USA. http://myfwc.com/media/2573521/snook-2013.pdf

Muller R.G., Trotter A.A., Stevens P.W. 2015. The 2015 stock assessment update of common snook, Centropomus undecimalis. Technical Report IHR 2015-004. Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, St. Petersburg, FL, USA. https://myfwc.com/media/13332/snook-2015.pdf

Ostini S., Oliveira I.R., Serralheiro P.C.S., Sanches E.G. 2007. Criação do robalo-peva (Centropomus parallelus) submetido a diferentes densidades de estocagem. [Rearing of fat snook (Centropomus parallelus) at different stocking densities.] Revista Brasileira de Saúde e Produção Animal 8 (3): 250–257. [In Portuguese.]

Parisi-Baradad V., Manjahacas A., Lombarte A., Olivella R., Chic Ó., Pera J., García-Ladona E. 2010. Automated taxon identification of teleost fishes using an otolith online database-AFORO. Fisheries Research 105 (1): 13–20. DOI: 10.1016/j.fishres.2010.02.005

Perera-Garcia M.A., Mendoza-Carranza M., Contreras-Sánchez W.M., Huerta-Ortiz M., Pérez-Sánchez E. 2011. Reproductive biology of common snook Centropomus undecimalis (Perciformes: Centropomidae) in two tropical habitats. Revista de Biología Tropical 59 (2): 669–681.

Rivas L.R. 1986. Systematic review of the perciform fishes of the genus Centropomus. copeia 1986 (3): 579–611. DOI: 10.2307/1449490

Rodrigues V.L.A., Wedekin L.L., Marcondes M.C.C., Barbosa L., Farro A.P.C. 2019. Diet and foraging opportunism of the Guiana dolphin (Sotalia guianensis) in the Abrolhos Bank, Brazil. Marine Mammal Science 36 (2): 436–450. DOI: 10.1111/mms.12656

Sadigzhadeh Z., Otero-Ferrer J.I., Lombarte A., Fatemi M.R., Tuset V.M. 2014. An approach to unraveling the coexistence of snappers (Lutjanidae) using otolith morphology. Scientia Marina 78 (3): 353–362. DOI: 10.3989/scimar.03982.16C

Sadigzhadeh Z., Tuset V.M., Valinassab T., Dadpour M.R., Lombarte A. 2012. Comparison of different otolith shape descriptors and morphometrics for the identification of closely related species of Lutjanus spp. from the Persian Gulf. Marine Biology Research 8 (9): 802–814. DOI: 10.1080/17451002.2012.692163

Seaman W., Collins N.M. 1983. Species profiles: Life histories and environmental requirements of coastal fishes and invertebrates (south Florida): Snook. Biological Report FWS/OBS 82/11.16. US Fish and Wildlife Service.

Siliprandi C.C., Rossi-Wongtschowski C.L.D.B., Brenha M.R., Gonsales S.A., Santificetur C., Vaz-Dos-Santos A.M. 2014. Atlas of marine bony fish otoliths (sagittae) of southeastern-southern Brazil Part II: Perciformes (Carangidae, Sciaenidae, Scombridae and Serranidae). Brazilian Journal Oceanography 62: 28–100.

Song Y., Cheng F., Zhao S., Xie S. 2019. Ontogenetic development and otolith microstructure in the larval and juvenile stages of mandarin fish Siniperca chuatsi. Ichthyological Research 66 (1): 57–66. DOI: 10.1007/s10722-018-0648-1

Taylor R.G., Whittington J.A., Grier H.J., Crabtree R.E. 2000. Age, growth, maturation, and protandric sex reversal in common snook, Centropomus undecimalis, from the east and west coasts of South Florida. Fishery Bulletin 98 (3): 612–612.

Torres G.J., Lombarte A., Morales-Nin B. 2000. Variability of the sulcus acusticus in the sagittal otolith of the genus Merluccius (Merluccidae). Fisheries Research 46: 5–13. DOI: 10.1016/S0165-7836(00)00128-4

Thresher R.E. 1999. Elemental composition of otoliths as a stock delineator in fishes. Fisheries Research 43 (1–3): 165-204. DOI: 10.1016/S0165-7836(99)00072-7

Tuset V.M., Farré M., Otero-Ferrer J.I., Vilar A., Morales-Nin B., Lombarte A. 2016. Testing otolith morphology for measuring marine fish biodiversity. Marine and Freshwater Research 67 (7): 1037–1048. DOI: 10.1071/MF15052

Tuset V.M., Immondi R., Aguado G., Otero-Ferrer J.I., Santschi L., Lombarte A., Love M. 2015. Otolith patterns of rockfishes from the Northeastern Pacific. Journal of Morphology 276 (4): 458–469. DOI: 10.1002/jmor.20353

Tuset V.M., Lombarte A., Assis C.A. 2008. Otolith atlas for the western Mediterranean, North and central eastern Atlantic. Scientia Marina 72: 7–198. DOI: 10.3989/scimar.2008.72s17

Vignon M. 2012. Ontogenetic trajectories of otolith shape during shift in habitat use: Interaction between otolith growth and environment. Journal of Experimental Marine Biology and Ecology 420: 26–32. DOI: 10.1016/j.jembe.2012.03.021

Volpeado A.V., Echeverría D.D. 1999. Morfología de los otolitos sagitale de juveniles y adultos de Micropogonias
Ontogenetic variation in otoliths of *Centropomus undecimalis* and *S. furnieri* (Desmarest, 1823) (Sciaenidae). Revista Ciências Marina Thalassas 15: 19–24.

**Volpedo A., Echeverría D.D.** 2003. Ecomorphological patterns of the sagitta in fish on the continental shelf off Argentine. Fisheries Research 60 (2–3): 551–560. DOI: 10.1016/S0165-7836(02)00170-4

**Wiff R., Flores A., Segura A.M., Barrientos M.A., Ojeda V.** 2019. Otolith shape as a stock discrimination tool for ling (*Genypterus blacodes*) in the fjords of Chilean Patagonia. New Zealand Journal of Marine and Freshwater Research 54 (2): 218–232. DOI: 10.1080/00288330.2019.1701047

**Yan T., Hu J., Cai Y., Xiong S., Yang S., Wang X., He Z.** 2017. Otolith development in larval and juvenile *Schizothorax davidi*: Ontogeny and growth increment characteristics. Chinese Journal of Oceanology and Limnology 35 (5): 1197–1204. DOI: 10.1007/s00343-017-6138-x

Received: 14 July 2020
Accepted: 11 November 2020
Published electronically: 7 December 2020