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Distinctive morphological variation of saccular otoliths in relation to hermaphroditism type in *Sarpa salpa* and *Serranus scriba* (Teleostei: Perciformes) from the Mediterranean Sea in Bizerte, Tunisia

by

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Abstract

This study aimed to describe and compare the morphological characteristics of saccular otoliths (sagittae) in the protandrous hermaphrodite *Sarpa salpa* and the synchronous hermaphrodite *Serranus scriba* collected from the Bizerte site located in northwestern Tunisia, and to examine the effect of hermaphroditism type on the otolith shape and size at the inter- and intraspecific levels, using elliptical Fourier analysis. At the interspecific level, a significant bilateral asymmetry in shape was observed between the left and right otoliths. At the intraspecific level, a significant bilateral asymmetry in shape was detected between the left and right otoliths only in *S. scriba*. Discriminant function analysis (DFA) produced two separate main groups corresponding to the two species, and intrasexually differentiated between left and right otoliths in *S. salpa*. In addition, a significant bilateral asymmetry was found in Lo, Wo, Ao, and Po in *S. salpa* and in Po only in synchronous *S. scriba*. Thus, protandrous hermaphroditism did not affect otolith shape in *S. salpa*, but showed an apparent bilateral asymmetry in otolith size. However, synchronous hermaphroditism exhibited a significant bilateral asymmetry in otolith shape and Po only in *S. scriba*. The causes of this significant inter- and intraspecific bilateral asymmetry observed in otolith shape and size were discussed.

Key words: bilateral asymmetry, elliptical Fourier descriptors, protandrous hermaphrodite, sagitta shape and size, sagittae, synchronous hermaphrodite

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1. Introduction

The salema, *Sarpa salpa* (Linnaeus, 1758), belongs to the family Sparidae and is a benthopelagic, gregarious marine fish that sometimes forms large schools (Russell et al. 2014). It is common in continental shelf waters up to 5 to 70 m deep. Juveniles are mainly carnivorous, preying on crustaceans, while adults are almost exclusively herbivorous, feeding on seaweeds (Bianchi et al. 1999). It lives in coastal waters near rocks covered with algae or seagrass (Bianchi et al. 1999**)** and sandy bottoms (Méndez Villamil et al. 2002). Geographically, it is widely distributed along the Mediterranean Sea (Jadot et al. 2006), the Black Sea (Pashkov & Reshetnikov 2012), the eastern Atlantic (from the Bay of Biscay to the Cape of Good Hope), and the Western Indian Ocean (from Mozambique to the Cape of Good Hope (Walt & Mann 1998). Interestingly, it has been reported that in the Mediterranean Sea, salema congregate around floating cage farms, feed on uneaten pellets (Colorni & Diamant 2014), and share the feed with seabass and seabream. In this context, Neofitou (2016) reported that large quantities of pellets were found in the stomachs of *S. salpa* captured around the aquaculture cage farms in the Mediterranean Sea.

Sexually, *S. salpa* is a protandrous hermaphrodite (Sellami & Brusle 1975), with males generally ranging from 150 mm to 300 mm and females from 310 mm to 450 mm in total length (TL). As is common in many Sparidae, sex conversion occurs over a wide range of sizes from 230 to 350 mm (Méndez Villamil et al. 2002), and since no external dimorphism was found, sex determination based solely on size remains difficult. According to Joubert (1981), the salema was described as rudimentary hermaphroditic, but is currently characterized by protandric hermaphroditism, with male gonadal tissue maturing first and female tissue developing later (Walt & Mann 1998; Méndez Villamil et al. 2002). In addition, Paiva et al. (2014) reported the presence of solid structures in the ovaries of salema, which could be easily seen macroscopically and which, through histological analysis, indicated the presence of hydrated oocytes. These structures appeared either isolated or arranged in groups to form a cystic structure, and showed a higher prevalence in the months preceding the spawning season, suggesting a relationship with the reproductive strategy of this species.

Over the past 15 years, *S. salpa* from the Mediterranean Sea has attracted the attention of researchers due to its role as a macrograzer of seagrass (Jadot et al. 2002), its biology for developing a management strategy (Méndez Villamil et al. 2002), and its toxicity (Chevaldonne 1990). For instance, Bellassoued et al. (2012) studied the toxicity of dreamfish *S. salpa* from the Gulf of Gabes (Tunisia, Eastern Mediterranean Sea). In Tunisia, *S. salpa* is a ‘staple’ species and is therefore commonly consumed as fresh fish due to its desirable flavor and quality. However, as previously investigated, *S. salpa* can cause poisoning, such as Ciguatera or Caulerpa poisoning when consumed (Chevaldonne 1990).

The painted comber, *Serranus scriba* (Linnaeus, 1758), belongs to the family Serranidae and is a subtropical benthic species found in the Eastern Atlantic from the English Channel and the Bay of Biscay to the Canary Islands and Western Sahara, around the Azores and Madeira, as well as in the Mediterranean and the Black Sea (Zorica et al. 2010). It is found at depths ranging from 5 to 150 m (Reiner 1996), but usually only down to 30 m (Zorica et al. 2010), and lives on rocky seabed and Posidonia beds (Bauchot 1987). *S. scriba* is an ambush and territorial predator, with a diet consisting of cephalopods, bivalves, crustaceans, fish, and worms (Tortonese 1986).

Sexually, *S. scriba* is a true synchronous hermaphrodite, i.e. it retains male and female functional gonads after reaching sexual maturity (Zorica et al. 2006, 2010), and spawns from early spring to early summer (Fischer & Petersen 1987). In addition, it has been previously reported that 50% of individuals of this species with a total length of 93 mm reach sexual maturity in the Adriatic Sea (Zorica et al. 2006).

To date, several studies have been conducted on the biology of *S. scriba*, e.g., Papaconstantinou et al. (1994) investigated growth parameters and fork length at first maturity of *S. scriba* in the northern Aegean Sea (Greece), while Politou and Papaconstantinou (1995) studied growth parameters and lifespan trends in northern Greece. Stergiou and Motopoulos (2001) presented data on the length–weight relationship for *S. scriba* from Greek waters, while Gonçalves et al. (1997) examined this relationship on the southwest coast of Portugal. In addition, Stergiou (1997) discussed the spawning seasonality of *S. scriba* in the English Channel and the Mediterranean Sea. Tserpes and Tsimenides (2001) studied the age, growth, and mortality of *S. scriba* on the Cretan shelf. Tuset et al. (2003) applied shape indices to identify regional differences in otolith morphology in the Atlantic and the Mediterranean Sea.

Biologically, otoliths are calcified structures found in the inner ear of fish and are metabolically inert once formed, i.e. there are no chemical changes or reabsorption, and are responsible for fish’s hearing and balance (Krysl et al. 2012). Previous studies have shown that otolith growth was associated with sex change, which can alter otolith composition and sensory-range specificity to optimize life history compatibility with fish's new reproductive modes (Walker & McCormick 2009), as well as maturity (Butler et al. 2021; Roy & Bardhan 2021). Furthermore, Munday et al. (2004) demonstrated that the relationship between otolith and somatic growth significantly varied between the sexes, with otoliths of fast-growing males being smaller than those of slow-growing females. In addition, the otolith phenotype has been found to exhibit inter- and intraspecific and inter- and intra-population differences (Ferri et al. 2018; Mejri et al. 2022a,b). Moreover, numerous studies have used the contour shape of otoliths to identify stocks (Cañás et al. 2012). Furthermore, it has been reported that otolith shape is affected by genetic and environmental parameters (Vignon & Morat 2010). To date, analysis of otolith morphology has been used as a powerful tool to distinguish between different stocks of fish species (Cardinale et al. 2004; Mahé et al. 2021; Mejri et al. 2022b; Ben Mohamed et al. 2019; Ben Labidi et al. 2020a; Khedher et al. 2021). In addition, sagittal otolith structure has been used to estimate population growth and mortality or fisheries management (Cardinale et al. 2004; Cañás et al. 2012; Bakkari et al. 2020). This is because it has been established that otolith structure is affected by many factors, such as sex, growth, maturity, fishery exploitation pattern, as well as genetic and environmental factors (Volpedo & Echeverria 2003; Butler et al. 2021; Roy & Bardhan 2021; Palazzo et al. 2022). Moreover, the three pairs of otoliths have long been considered significant structures in ichthyology, as reading their rings can be used to estimate the age of a fish (Francis & Campana 2004). For example, the composition of calcium carbonate can indicate the environmental conditions (e.g. pollution) in which fish grow (Elsdon et al. 2008). In addition, otoliths are crucial in the trophic ecology of predators that prey on fish due to their resistance to digestion (Meynier et al. 2008).

On the other hand, bilateral asymmetry in the shape of otoliths, which is a deviation from the ideal symmetrical state, has been shown to be fluctuating asymmetry (FA), directional asymmetry (DA) or antisymmetry (A) based on the distribution of their values within and between populations (Van Valen 1962). Of these three types, FA is defined as random individual deviations from perfect bilateral symmetry that lead to a normal distribution with a mean of 0 (Palmer & Strobeck 1986; Palmer 1994). Mahé (2019) declared that FA is associated with the developmental trajectory of otoliths affected by developmental regulatory processes, especially evolutionary canalization. Lemberget & Mccormick (2009) and Díaz-Gil et al. (2015) reported that FA results from developmental instability (DI) and may be an indicator of stress or microenvironmental variability. In particular, Lemberget & McCormick (2009) described FA as an indicator of fish health because it can directly affect their balance and hearing performance. In addition, Jawad & Mahé (2022) indicated that FA can be identified as a functional adaptation to environmental conditions.

To date, morphological characteristics of otoliths in *Serranus* spp. have only been described outside Tunisian waters by Tuset et al. (2003), who compared variation in gross morphology of sagitta otoliths and shape indices with other morphological characters and depth distribution between *Serranus atricauda*, *S. cabrilla*, and *S. scriba* from the Canary Islands. Despite the research to date, many of otolith features in *S. salpa* and *S. scriba* and the effect of hermaphroditism type on otolith morphology remain undefined. Therefore, the present study was conducted in Tunisian waters to describe and compare morphological characteristics of sagittal otolith shape and size (length, width, and area) within and between males and females of the protandrous hermaphrodite *S. salpa* and individuals of the synchronous hermaphrodite *S. scriba*, and to examine the effect of hermaphroditism, particularly protandrous hermaphroditism, on otolith morphology within and between individuals of these species sampled from the Mediterranean Sea in the Bizerte site located in northwestern Tunisia using shape and size indices.

2. Materials and methods

2.1. Sample collection

A total of 120 samples of mature *Sarpa salpa* and *Serranus scriba* fish (60 specimens each) were collected from the Mediterranean Sea in the Bizerte site (37°8′ – 37°14″N; 9°46′ – 9°56″E) located in northwestern Tunisia (Fig. 1) between March and May 2019 using artisanal fishing. Sexual maturity of individuals was confirmed immediately after capture, using similar timing of sexual maturation, which begins within the first two years of life in both *S. salpa* (Paiva et al. 2018) and *S. scriba* (Alós et al. 2010) and length at first maturity (L_m), which is 16.5 cm (Bauchot & Hureau 1990) and 17.3 cm (Tortonese 1986), respectively, as well as by visual inspection or examination under a dissecting microscope when the gonads are so small and thin. Subsequently, the total weight (TW) of each specimen was recorded to the nearest 0.1 g using an electronic balance, and the total length (TL) was measured to the nearest 0.1 mm using an ichthyometer (Table 1).

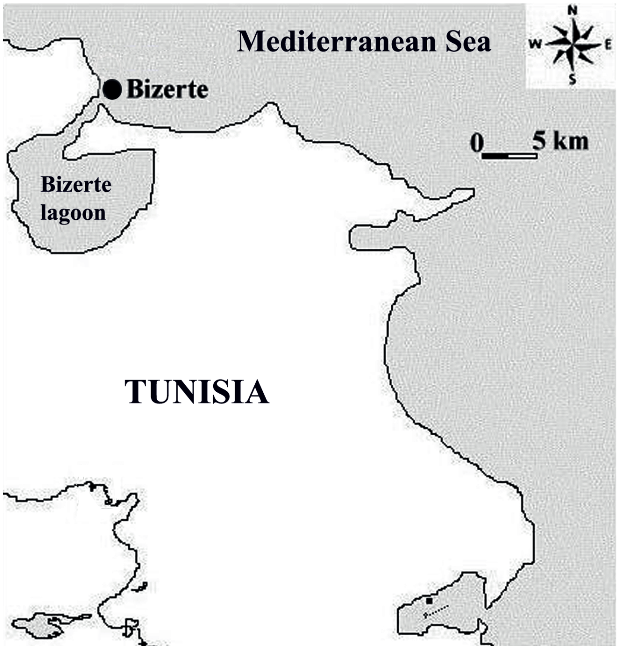

Figure 1

Sampling site from which samples of *Sarpa salpa* and *Serranus scriba* were collected from the Mediterranean Sea in Bizerte (●), northwestern Tunisia.

2.2. Study area

Geographically, the Bizerte lagoon is located on the northern coast of Tunisia and is connected in the northern part to the Mediterranean Sea through a 6 km long inlet, and in the western part to Lake Ichkeul via the Tinja Canal, which has an area of 128 km^2 and an average depth of 7 m (Boukef Ben Omrane et al. 2012). Harzallah (2002) reported that marine inflows are natural in summer, while freshwater is mainly supplied in winter (20 Mm^3 yr^{-1}) from several surrounding streams and Lake Ichkeul. From an ecological point of view, since the lagoon is located in the vicinity of several towns, namely Bizerte, Zarzouna, Menzel Aberrahmen, Menzel Jemil, and Menzel Bourguiba, it is exposed to the effects of various human activities and the impact of the surrounding watershed, such as domestic sewage and industrial waste discharges, atmospheric pollution with chemicals and heavy metals, commercial shipping ports, agricultural and livestock waste, and areas of intensive shellfish farming (Dellali et al. 2004; Barhoumi 2014). In addition, the water temperature ranges from 15°C to 16°C, and the salinity is 37.5‰ (Kaouèche et al. 2017). Moreover, the lagoon is contaminated with persistent organic and metal pollutants, as well as nutrients, the concentrations of which are generally high at the surface of water during the rainy season, characterized by the abundance and quality of food (Barhoumi 2014; Jamila et al. 2016).

2.3. Otolith extraction

Sagittae, the largest of the three otolith pairs, were extracted using pliers. Then, they were cleaned with distilled water, dried on absorbent material, wrapped in cotton wool, labelled, and stored in Eppendorf tubes.

2.4. Otolith imaging and shape analysis

Otoliths were placed under a dissecting microscope at 40X magnification with a black background, and digital images were captured using a Samsung PL210 digital camera with a resolution of 14.2 megapixels. A combination of size variables, including length (Lo), width (Wo), area (Ao), and perimeter (Po), were used to calculate shape indices. The images of otoliths were processed using Adobe Photoshop CS6 software, which converts the original picture of the otolith into a binary image. The binary images of the otoliths' shapes were analyzed using the software SHAPE Ver. 1.3. The shape contours of each otolith were evaluated by the elliptic Fourier analysis (EFA), as previously described by Ben Labidi et al. (2020a, b) and Khedher et al. (2021).

2.5. Data analysis

Analysis of variance (ANOVA) was performed to assess the significance of differences in mean values of total length (TL) and weight (TW) between individuals of the two species. The values were then tested for homogeneity (equality) and normal distribution using Levene's and Shapiro–Wilk's λ tests, respectively.

Table 1

Number of samples (N), range, and mean ± standard deviation (SD) values of the total length (TL) and total weight (TW) of *Sarpa salpa* and *Serranus scriba* collected from the Bizerte site in northwestern Tunisia.

Species	Sex (N)	TL (range) mm	TL (mean ± SD) mm	TW (range) g	TW (mean ± SD) g
Sarpa salpa	♂ (30)	159.4–234.6	190.7 ± 18.9	52.3–179.1	97.9 ± 30.8
	♀ (30)	158.1–230.2	186.3 ± 18.3	51.5–177.3	95.7 ± 28.7
Serranus scriba	⚥ (60)	163.1–217.1	181.4 ± 16.7	27.3–123.1	75.0 ± 28.3

In addition, differences in contour shape and size parameters of otoliths from individuals of the two species were analyzed using discriminant function analysis (DFA). Subsequently, all values of the shape and size variables were checked for normality. If the values did not follow the normal distribution, a Box-cox transformation (Box & Cox 1964) was performed. Finally, Levene's and Shapiro–Wilk's λ tests were performed to assess the homogeneity (equality) and the normal distribution of the variance in the values of the variables for the shape and size of otoliths, respectively. DFA was performed with normalized elliptical Fourier descriptors coefficients (77 coefficients per otolith) to illustrate similarities and differences at the inter- and intraspecific levels. The objective of DFA is to test the integrity of predefined groups of individuals belonging to a given species and the percentage of their correct classification by finding linear combinations of descriptors that maximize the value of Wilk's λ. Wilk's λ test assesses the performance of discriminant analyses. This statistic is the ratio between intra-group variation and total differences and provides an objective method for calculating the corrected percentage chance for agreement. Fisher's distance was also calculated to characterize the differences in the left and right otolith shape and size variables at the inter- and intraspecific levels. All these statistical analyses were performed using XLSTAT 2010.

2.6. Determination of percentage asymmetry

The presence of bilateral asymmetry (OA) between the left and right otoliths within each species was calculated using paired samples Student's *t*-test. The percentage of bilateral asymmetry (P%) in the shape of otolith pairs was then calculated using the following formula:

$$P\% = (OA * 100)/ N,$$

where OA is the number of specimens showing bilateral otolith asymmetry, and N is the total number of specimens.

2.7. Determination and analysis of otolith biometric parameters

The length (Lo), width (Wo), area (Ao), and perimeter (Po) of the otoliths (in mm) were determined using ImageJ software. According to Javor et al. (2011) and Dehghani et al. (2016), the Lo is defined as the distance between points a and b, while Wo is the distance between points c and d (Fig. 2). Before proceeding to statistical analyses, one-way ANOVA was used to determine whether there were any significant differences between the mean values of Lo, Wo, Ao, and Po for the left and right otoliths. Mean values of the four variables were analyzed using paired samples Student's t-test to determine the difference, i.e. asymmetry, and similarity, i.e. symmetry, between the left (L) and right (R) otoliths at the inter- and intraspecific levels.

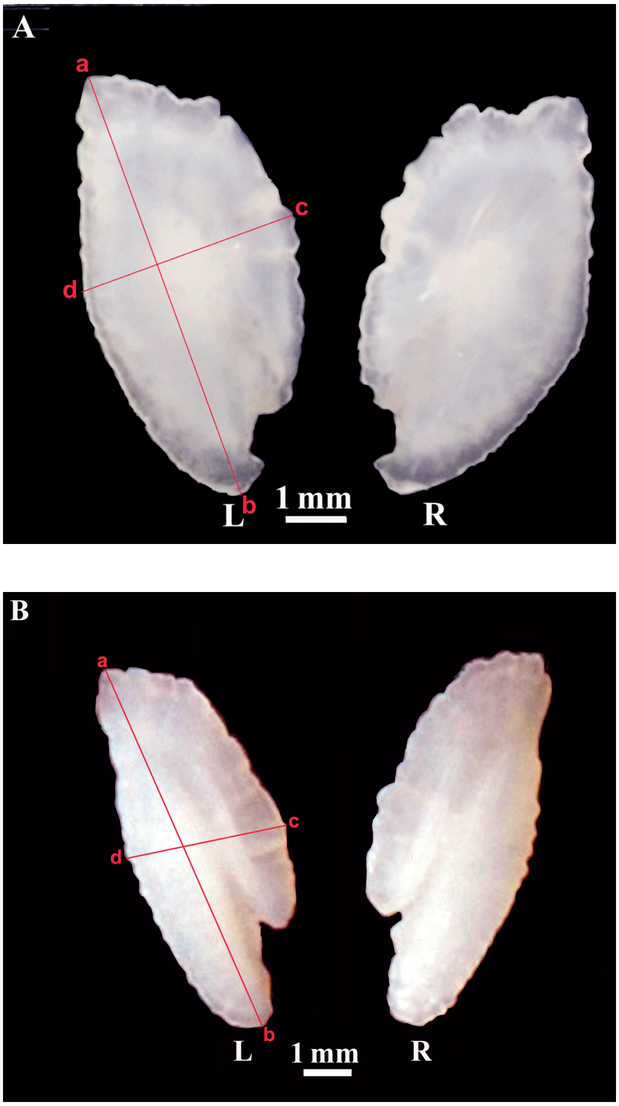

Figure 2

Actual images of the left (L) and right (R) otoliths extracted from (A) *Sarpa salpa* and (B) *Serranus scriba* showing the length (Lo) and width (Wo) parameters examined among individuals collected from the Bizerte site, northwestern Tunisia. Lo is defined as the distance between points a and b, while Wo is the distance between points c and d.

3. Results

3.1. Total weight (TW) and total length (TL) variation

As shown in Table 1, the total weight (TW) and length (TL) of males and females of protandrous hermaphrodite *S. salpa* ranged from 52.3 to 179.1 g and 159.4 to 234.6 mm for males and from 51.5 to 177.3 g and 158.1 to 230.2 mm for females, respectively. However, in the synchronous hermaphrodite *S. scriba*, TW and TL varied from 27.3 and 123.1 g and from 163.1 to 217.1 mm, respectively.

3.2. Otolith shape variation

Levene's and Shapiro–Wilk's λ tests confirmed that all values of shape variance were equally and typically distributed for the two species with a *p*-value > 0.05. At the interspecific level, one-way MANOVA and Shapiro–Wilk's λ tests for otolith shape values showed statistically significant differences (Wilk's λ = 0.016; *p* < 0.0001), i.e. there was a bilateral asymmetry in the shape of left and right otoliths between individuals of *S. scriba* and *S. salpa*. Similarly, Fisher's distances showed significant bilateral asymmetry (*p* < 0.0001) in the shape of L and R otoliths between individuals of the two species (Table 2). At the intraspecific level, both Wilk's λ test (Wilk's λ = 0.0277; *p* > 0.05) and Fisher's distance revealed a non-significant difference (*p* > 0.05), i.e. there was a symmetry in the left and right otoliths among males and females of the protandrous hermaphrodite *S. salpa* (Table 3). Conversely, a significant bilateral asymmetry (*p* < 0.0001) was detected in the left and right otoliths among individuals of the synchronous hermaphrodite *S. scriba* (Table 2).

Table 2

Fisher's distance matrix (above diagonal) and *p*-values (below diagonal) between the left (L) and right (R) otoliths of *Sarpa salpa* and *Serranus scriba* collected from the Bizerte site, northwestern Tunisia. SSCR = *Serranus scriba* right otolith; SSCL = *Serranus scriba* left otolith; SSR = *Sarpa salpa* right otolith; SSL = *Sarpa salpa* left otolith.

	SSCR	SSCL	SSR	SSL
SSCR	-	8.747	45.409	34.589
SSCL	< 0.0001	-	62.436	49.058
SSR	< 0.0001	< 0.0001	-	4.445
SSL	< 0.0001	< 0.0001	0.056	-

Table 3

Fisher's distance matrix (above diagonal) and *p*-values (below diagonal) between the left (L) and right (R) otoliths of males and females of *Sarpa salpa* collected from the Bizerte site, northwestern Tunisia. The value marked in bold is statistically significant (*p* < 0.05). SSLF = *S. salpa* left female otolith; SSLM = *S. salpa* left male otolith; SSRF = *S. salpa* right female otolith; SSRM = *S. salpa* right male left otolith.

	SSLF	SSLM	SSRF	SSRM
SSLF	-	0.8326	1.6111	2.7314
SSLM	0.7555	-	1.1068	1.8042
SSRF	**0.0453**	0.3639	-	1.0414
SSRM	**0.0003**	**0.0185**	0.4505	-

On the other hand, a comparison of the percentage (P%) of bilateral asymmetry (OA) in the otolith shape on the left and right sides between the two species revealed a significant difference (*p* < 0.05), with only 4% asymmetry (OA) in *S. salpa* compared to 80% OA in *S. scriba*.

At the intraspecific level, the barycentric projection of the contour shape values for the left and right otoliths among and within males and females of *S. salpa* on the first axes *F1* and *F2* of the DFA indicated that the two axes explained 66.61% and 18.09% of the total variation, respectively, showing that the otoliths from males and females were more segregated on the positive and negative parts of the *F1* axis than on the *F2* axis (Fig. 3). Therefore, the two axes accounted for 84.70% of the total shape variance and clearly differentiated between the left and right otoliths, as well as between otoliths of the same side (L–L) and (R–R) of the two sexes into two distinct main groups. The first group comprised R–R otoliths of both sexes in the positive part of *F1*, while the second included L–L otoliths in the negative part. Moreover, the *F2* axis separated the left and right otoliths of males in the positive part, the right otoliths of females in the negative part, and the left otoliths were segregated in between.

At the interspecific level, the barycentric projection, based on EFDs of the contour shape of the left and right otoliths from individuals of the two species on the first axes *F1* and *F2* of the DFA, revealed that the two axes explained 89.42% and 7.08% of the total variation, respectively, showing that the otoliths from individuals of the two species were more segregated on the positive and negative parts of the *F1* axis than on the *F2* axis (Fig. 4). Therefore, the two axes

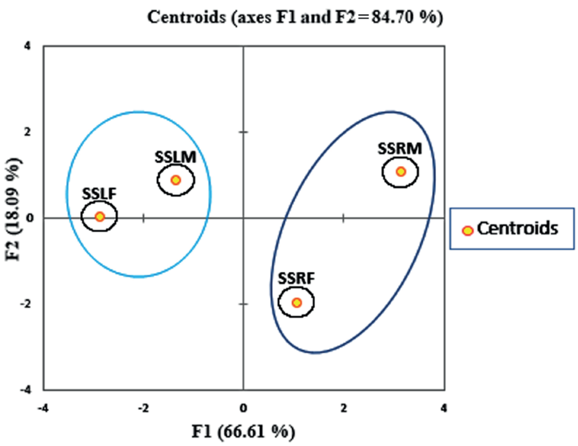

Figure 3

Discriminant function analysis (DFA) showing the barycentric projection (●) of the left (L) and right (R) shape values of otoliths in males and females of *Sarpa salpa* samples collected from the Bizerte site, northwestern Tunisia. SSLF = *S. salpa* left female otolith; SSLM = *S. salpa* left male otolith; SSRF = *S. salpa* right female otolith; SSRM = *S. salpa* right male left otolith.

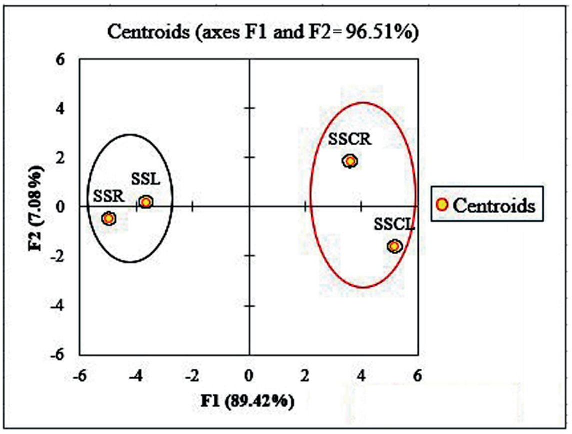

Figure 4

Discriminant function analysis (DFA) showing the barycentric projection (●) of the left (L) and right (R) shape values of otoliths in *Sarpa salpa* and *Serranus scriba* samples collected from the Bizerte site, northwestern Tunisia. SSR = *Sarpa salpa* right otolith; SSL = *Sarpa salpa* left otolith; SSCR = *Serranus scriba* right otolith; SSCL = *Serranus scriba* left otolith.

accounted for 96.50% of the total shape variance and clearly separated the otoliths of the two species into two distinct main groups. The first group comprised the left and right otoliths of *S. scriba* in the positive part of *F1*, while the second included those of *S. salpa* in the negative part. Moreover, the *F2* axis separated the left otoliths of *S. scriba* in the positive part and the right otoliths in the negative part, while it placed both the left and right otoliths of *S. salpa* in the positive part.

3.3. Otolith biometric variation

The results of Student's t-test for the biometric measurements showed significant differences ($p < 0.05$), i.e. there was asymmetry between the left and right otoliths in Lo, Wo, Ao, and Po among and within males and females of the protandrous hermaphrodite *S. salpa* (Table 4). However, significant symmetry ($p > 0.05$) was detected in Lo, Wo, and Ao, while significant asymmetry ($p = 0.05$) in Po between the left and right otoliths among individuals of the synchronous hermaphrodite *S. scriba* (Table 5).

Table 4

Paired samples Student's *t*-test analysis of range, mean ± standard deviation (SD), and *p*-values of the length (Lo), width (Wo), area (Ao), and perimeter (Po) measurements of the left (L) and right (R) otoliths among males and females of *Sarpa salpa* collected from the Bizerte site, northwestern Tunisia. The values marked in bold are statistically significant ($p < 0.05$).

Parameter	Sex	Side	Range (mm)	Mean ± SD (mm)	*p*-value
Length (Lo)	F	L	6.09–8.48	7.70 ± 0.47	**0.04**
		R	6.50–9.08	7.80 ± 0.51	
	M	L	6.11–8.39	7.71 ± 0.49	**0.04**
		R	6.49–9.20	7.79 ± 0.49	
Width (Wo)	F	L	3.75–5.43	4.36 ± 0.36	**0.03**
		R	3.79–5.47	4.39 ± 0.38	
	M	L	3.71–5.41	4.34 ± 0.35	**0.03**
		R	3.75–5.42	4.36 ± 0.35	
Area (Ao)	F	L	20.50–30.61	22.57 ± 2.21	**0.02**
		R	20.28–34.27	22.18 ± 2.12	
	M	L	21.41–32.52	22.71 ± 2.17	**0.03**
		R	20.68–33.68	22.80 ± 33.87	
Perimeter (Po)	F	L	19.01–25.14	21.14 ± 1.61	**0.03**
		R	20.14–26.24	22.61 ± 1.69	
	M	L	19.20–25.48	22.07 ± 1.63	**0.03**
		R	20.24–25.61	22.16 ± 1.64	

Table 5

Paired samples Student's *t*-test analysis of range, mean ± standard deviation (SD), and *p*-values of the length (Lo), width (Wo), area (Ao), and perimeter (Po) measurements of the left (L) and right (R) otoliths among individuals of *Serranus scriba* collected from the Bizerte site, northwestern Tunisia. The value marked in bold is statistically significant ($p = 0.05$)

Parameter	Side	Range (mm)	Mean ± SD (mm)	*p*-value
Length (Lo)	L	9.598–10.41	9.97 ± 0.14	0.17
	R	9.548–10.19	9.96 ± 0.13	
Width (Wo)	L	4.62–8.81	5.29 ± 0.60	0.14
	R	4.54–5.94	5.22 ± 0.40	
Area (Ao)	L	23.13–33.12	31.29 ± 1.38	0.61
	R	29.85–33.01	31.37 ± 0.91	
Perimeter (Po)	L	25.91–28.61	27.14 ± 0.45	**0.05**
	R	21.10–28.51	26.94 ± 0.89	

4. Discussion

The shape of fish otolith has long been used to discriminate between species and populations and their stocks in different habitats, as well as between sexes, age classes, and reproductive morphs, as it shows a high inter- and intraspecific variability in shape (Ben Labidi et al. 2020a, b; Bose et al. 2020; Echreshavi et al. 2021; Khedher et al. 2021; Yedier and Bostanci 2021, 2022; Purrafee Dizaj et al. 2022; Mejri et al. 2022a, b). Furthermore, otolith growth has been associated with sex change in protandrous hermaphroditism (Walker & McCormick 2009), maturity (Butler et al. 2021; Roy & Bardhan 2021), and somatic growth (Munday et al. 2004). To date, morphological differences in the shape of otoliths have been studied by comparing characteristics of their shape and size across species and populations living in a varying range of geographic environments (Bose et al. 2020). In the present study, we examined the variation of saccular otolith shape and size and their relationship to the type of hermaphroditism between and within individuals of *S. salpa* and *S. scriba* collected from the Mediterraneas Sea in the Bizerte site located in northwestern Tunisia. In this regard, it is worth mentioning that only adult samples from the two species were examined to eliminate the effect of sexual immaturity, which can affect the contour shape of otoliths (Cardinale et al. 2004), as well as to avoid the effect of confounding factors resulting from allometric growth from the larval stage to the adult stage, where the shape stabilizes (Santos et al. 2017). Elliptical Fourier analysis for otolith contour shape values as well as Fisher's distance matrix showed a statistically significant difference ($p < 0.0001$), i.e. bilateral asymmetry in the shape between the left and right otoliths among individuals of the two species and also among individuals of synchronous *S. scriba*. In addition, the DFA based on the EFDs of the contour shape of the left and right otoliths distinctly separated the otoliths of the two species into two distinct groups corresponding to the two species. This interspecific variation in the shape of otoliths has previously been recorded in *Serranus atricauda*, *S. cabrilla*, and *S. scriba* (Tuset et al. 2003), *Sicyopterus lagocephalus*, *S. aiensis*, and *S. sarasini* (Lord et al. 2012), *Neogobius caspius*, *Ponticola bathybius*, and *P. gorlap* (Bani et al. 2013), *Sardinella gibbosa*, *S. longiceps*, and *S. sindensis* (Homayuni et al. 2013), *Lutjanus argentiventris* and *Hyporthodus acanthistius* (Puentes-Granada et al. 2019), *Mulloidichthys flavolineatus*, *M. vanicolensis*, and *Parupeneus forsskali* (Osman et al. 2020), and *Liza aurata* and *Chelon ramada* (Mejri et al. 2022b). Moreover, the asymmetry in otolith shape among individuals of *S. scriba* is consistent with that found in *Scorpaena porcus* (Trojette et al. 2014), *Diplodus annularis* (Trojette et al. 2015), *Liza ramada* (Rebaya et al. 2016), *Oblada melanura* (Barhoumi et al. 2018), *Pagellus erythrinus* (Mejri et al. 2020, 2022a), *Boops boops* (Ben Labidi et al. 2020a, b), and *D. vulgaris* (Khedher et al. 2021) collected from different geographic localities in Tunisian waters. Similarly, this asymmetry in the shape of otoliths was also recorded in *Sphyraena sphyraena* (Yedier 2021), *Scorpaena* spp. (Yedier & Bostanci 2022), as well as in other species found elsewhere outside the Tunisian waters (for details on these species, see Ben Labidi et al. 2020a, b; Khedher et al. 2021; Mejri et al. 2022a; Ben Mohamed et al. 2023). Previous studies have shown that differences in the shape of otoliths are affected by feeding habits, including food availability (quantity and quality), shifts in diet during ontogenetic development (Cardinale et al. 2004; Mahé et al. 2019), and the depth at which fish live (Fashandi et al. 2019), as well as physiology (e.g. hearing abilities associated with acoustic communication (Schulz-Mirbach et al. 2019), phylogeny (Torres et al. 2000), sex, growth and maturity (Cardinale et al. 2004), as well as spatial isolation between demographic populations (Turan et al. 2006). In addition, as described by Simoneau et al. (2000) and Vaux et al. (2019), differences in age and sex among fish species may lead to a significant difference in the shape of otoliths within fish stocks. As far as is known, *S. salpa* is a benthopelagic species, living at a depth range of 5 to 70 m, with juveniles being mainly carnivorous, preying on crustaceans, and adults being almost exclusively herbivorous, feeding on seaweed (Bianchi et al. 1999). *S. scriba*, on the other hand, is a benthic species, living at a depth range of 5 to 150 m (Reiner 1996), but usually only down to 30 m (Zorica et al. 2010), and feeds on fish and crustaceans (Tortonese 1986). In terms of age and sex, the two species studied are mature, and *S. salpa* is a protandrous hermaphrodite with a sex change of males to females that occurs at 25.0 cm TL and an age of 3.75 years (Allsop & West 2003), while *S. scriba* is a synchronous hermaphrodite that matures at L_m of 17.3 cm (Tortonese 1986). Therefore, we can assume that this clear distinction between the two species can be most likely attributed to the changes that occurred in the morphology of the otoliths of the two species in relation to their living and feeding behavior and growth during the ontogenetic development of the larvae, hearing abilities, and the type of hermaphroditism and sex change. However, the bilateral asymmetry in otolith shape between the left and right sides among individuals of the synchronous hermaphrodite *S. scriba* can be explained as differences in hearing function. This is because it has been suggested that the relative movement pattern between the otolith and the sensory epithelium is affected by the shape of the otolith and thus affects hearing (Popper et al. 2005). In addition to these factors, many other factors have also been found to affect differences in the otolith shape, including ontogenetic (Capoccioni et al. 2011), genetic (Jawad et al. 2020), and environmental factors, such as water depth, temperature and salinity, light regime, substrate and pollution (Ferri et al. 2018; Ben Labidi et al. 2020a, b; Khedher et al. 2021; Mejri et al. 2022a, b). More specifically, Jawad and Sadighzadeh (2013) reported that the asymmetry between the left and right sides of otoliths is due to the exposure of individuals to environmental stress resulting from changes in particular environment factors, including pollution, severe physical conditions and habitat quality (Al-Rasady et al. 2010). In addition, Popper et al. (2005) reported that the complex shape of otoliths may provide richer information for hearing or balance, while Deng et al. (2013) suggested that the complex shape of otoliths may alter the dynamics of otoliths' responses to sounds. Moreover, Gauldie & Crampton (2002) indicated that saccular otoliths with more complex shapes are found in more hearing-dependent species than in non-hearing ones. Consequently, we can suggest that the differences in the shape of otoliths between the two species may be related to their differences in response to sounds and differences in hearing and balance levels, an assumption that needs further investigation. However, as assumed by Panfili et al. (2005), the intra-individual variation may reflect the fluctuating asymmetry of otoliths, and the intra-population variation may result from inter- and intra-individual, or even inter-population variations (Mejri et al. 2018, 2020, 2022a, b; Ben Labidi et al. 2020a, b; Khedher et al. 2021). On the other hand, it should be noted that protandrous hermaphroditism had no effect on the shape of otoliths in males and females of *S. salpa*, which is inconsistent with the results obtained by Mejri et al. (2022a) in the protandrous hermaphrodite *P. erythrinus*. This finding can be attributed to the effect of sex change and its association with hearing function and the similarity of hearing ability in males and females.

As for the environmental characteristics of the study site, previous studies have reported that the water temperature ranges from 15°C to 16°C, and the salinity is 37.5‰ (Kaouèche et al. 2017). Furthermore, the Bizerte lagoon, where the site is located, is polluted with organic matter, heavy metals, and persistent nutrients, the concentrations of which generally affect the abundance and quality of food (Barhoumi 2014; Jamila et al. 2016). In addition, it has been shown that the shape of otoliths is sensitive to environmental temperature, as it affects the rate and trajectory of otolith morphogenesis (Mahé et al. 2019). Moreover, trace elements can be absorbed into either the organic or inorganic component of the developing otolith, and the incorporation of metal contaminants in the aragonite matrix of the otolith is not a simple function, as the process is species-specific (Chang & Geffen 2013), driven by environmental conditions (Campana 1999), and the route of exposure (Ranaldi & Gagnon 2008). Therefore, the morphological asymmetry shown here between the left and right otoliths of the two species can be attributed either to the impact of the surrounding environment during their lifespan or to a decline in some factors such as fertility, sexual maturity, survival or growth (Trojette et al. 2015), or due to genetic factors (Vaux et al. 2019). However, the latter factor cannot be discussed here due to the lack of genetic data on the two species at the Bizerte site. In addition, differences in the tolerance to temperature, salinity, and pollution between individuals of the two species may also be key factors in altering the shape of otoliths (Bremm and Schulz 2014; Ben Labidi et al. 2020a, b; Khedher et al. 2021; Mejri et al. 2022a, b). Similar explanations for the effects of these environmental factors on otolith shape diversity have also been reported for sparid fish that live in Tunisian waters, such as *D. annularis* (Trojette et al. 2015), *B. boops* (Ben Labidi et al. 2020a, b) and *P. erythrinus* (Mejri et al. 2018, 2020, 2022a).

On the other hand, examination of the biometric dimensions of the otoliths revealed a clear bilateral asymmetry ($p < 0.05$) between the left and right otoliths in Lo, Wo, Ao, and Po among and within males and females of the protandrous hermaphrodite *S. salpa* with a TL range of 15.8–23.5 cm. This finding is consistent with that found in *Merlucius merlucius* by Palazzo et al. (2022), who attributed the differences in the increase in otolith length, width, area, perimeter, volume, and weight between females and males with a TL range of 15–50 cm to the difference in hearing adaptation to reproductive behavioral strategies during the spawning season. In addition, the significant asymmetry ($p < 0.05$) in otolith Lo, Wo, Ao, and Po within males of protandrous *S. salpa* having a TL range of 15.9–23.5 cm is also consistent with that found within males of protogynous *Eleutheronema tetradactylum* (Roy & Bardhan 2021), as well as other protogynous Perciformes, i.e. *Polydactylus virginicus*, *Sparidentex hasta*, *Acanthopagrus berda* and *Acanthopagrus latus* (Santificetur et al. 2017; Abdulsamad 2017). However, a highly significant symmetry ($p > 0.05$) was detected in Lo, Wo, and Ao, as well as a distinct bilateral asymmetry ($p = 0.05$) in Po between the left and right otoliths among individuals of the synchronous hermaphrodite *S. scriba*. Indeed, as reported by Ben Labidi et al. (2020b) for *B. boops*, Khedher et al. (2021) for *D. vulgaris*, and Ben Mohamed et al. (2023) for *Mullus barbatus* also collected from the Bizerte lagoon, the bilateral asymmetry observed in Lo, Wo, Ao, and Po and only in Po between the left and right otoliths among individuals of *S. salpa* and *S. scriba*, respectively, may be due to fluctuating asymmetry (FA) resulting from exposure of individuals to environmental stress. This stress may be due to water contamination in the Bizerte lagoon by persistent organic, metal, and nutrient pollutants (Barhoumi 2014; Jamila et al. 2016). In this context, Lychakov & Rebane (2005) found that bilateral asymmetry in otolith dimensions among individuals could result from abnormal swimming activity and interference with correct sound identification, resulting in the inability of individuals to blend in with the environment in which they live. As far as is known, the Bizerte lagoon is exposed to various types of industrial effluents, including chemical, petrochemical, mineral, and cement wastewater, which lead to chemical contamination with various toxic compounds and reduce the pH of water (Dellali et al. 2004). Therefore, we can assume that the short and narrow otoliths of *S. salpa* may be associated with a narrow range of hearing compared to the long and wide otoliths in *S. scriba*, which provide the best hearing and highest survival rate. Accordingly, the level of pollution present in the Bizerte lagoon may be responsible for the bilateral asymmetry that developed in Lo, Wo, Ao, and Po in *S. salpa* and Po in *S. scriba* and Po in S. scriba collected from the study site. In addition, it has been reported that the parasite load can reflect differences in the rate of fish somatic growth, which in turn results in differences in sagittal otolith growth (Palacios-Fuentes et al. 2012). Furthermore, Gauldie & Jones (2000) described that parasite infection leads to slow growth of fish, and thus leads to the formation of wide and thick dust otoliths. Regarding the parasite load in the two species examined from the Bizerte lagoon, Gargouri Ben Abdallah et al. (2011) reported that *S. salpa* is infected with a variety of digenean species, while *S. scriba* showed a wide range of parasites, including Myxozoa, Digenea, Nematoda, Copepoda, Isopoda, and Hirudinea (Bouderbala et al. 2019). Therefore, we can attribute the differences recorded in the otolith biometric indices between the two species to the variation in the parasite load.

5. Conclusion

Comparison of the saccular otolith contour shape at the interspecific level revealed a statistically significant difference ($p < 0.0001$), i.e. bilateral asymmetry between the left and right otoliths. In addition, discriminant function analysis (DFA) using otolith contour shape values confirmed the presence of two separate main groups corresponding to the two species. At the intraspecific level, a significant bilateral asymmetry in shape was observed between the left and right otoliths only among individuals of the synchronous hermaphrodite *S. scriba*. Moreover, a significant bilateral asymmetry ($p < 0.05$) was found in Lo, Wo, Ao, and Po among and within males and females of the protandrous hermaphrodite *S. salpa* and in Po only ($p = 0.05$) among individuals of the synchronous hermaphrodite *S. scriba*. This inter- and intraspecific bilateral asymmetry observed between left and right otoliths was discussed in terms of differences in living and feeding behavior and growth during the ontogenetic development of larvae, hearing and balance abilities, the type of hermaphroditism and sex change, and differences in the tolerance to temperature, salinity, and pollution of water. Therefore, it is worth noting here that protandrous hermaphroditism with sex change had no effect on the shape of otoliths, but exhibited a marked bilateral asymmetry in the otolith size indices among individuals of *S. salpa*. Synchronous hermaphroditism, on the other hand, exhibited a significant bilateral asymmetry in the otolith shape and Po only among individuals of *S. scriba*. These findings contribute largely to data using otolith shape and size as an effective indicator for identifying and discriminating between fish species, and highlight the effect of hermaphroditism type on otolith shape and size within and between species.

Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work presented in the paper.

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Authorship contribution statement

WB and MM: suggested the topic of the study, collected the fish samples, extracted and photographed the otoliths, performed the data analysis, prepared the figures, and wrote the main draft of the manuscript. NB, SM, and AC reviewed and validated the main draft and figures. AABS edited and revised the main draft, with tables and figures, wrote the final version of most of the manuscript, and submitted it to the journal. J-PQ, MT, and ABF read and validated the final manuscript. All authors approved the final version of the manuscript.

Consent for publication

All authors of this manuscript agreed to submit it for publication in Oceanological & Hydrobiological Studies.

Ethical approval

The Laboratory of Ecology, Biology and Physiology of Aquatic Organisms, and the Laboratory of Biodiversity, Biotechnology and Climate Change, the Faculty of Sciences of Tunis, the University of Tunis El Manar, Tunis, Tunisia, approved this research. In addition, all procedures in this study were performed following the guidelines for the Proper Conduct of Animal Experiments outlined by the University of Tunis El Manar, Tunis, Tunisia (No. 1474, certificated on 14 August 1995), as well as all applicable international, national, and/or institutional guidelines for the care and use of animals in research.

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