Check for updates

Ecomorphological adaptation of *Scorpaena porcus* (Linnaeus, 1758): evidence from two different environments revealed by *sagittae* features and somatic growth rates

Claudio D'Iglio[1], Sergio Famulari[1], Josipa Ferri[2]*,
Marco Albano[3]*, Nunziacarla Spanò[1,4], Gioele Capillo[3,4†]
and Serena Savoca[1,4†]

[1]Department of Chemical, Biological, Pharmaceutical and Environmental Sciences, University of
Messina, Messina, Italy, [2]Department of Marine Studies, University of Split, Split, Croatia, [3]Department
of Veterinary Sciences, University of Messina, Messina, Italy, [4]Department of Chemical, Biological,
Pharmaceutical and Environmental Sciences, Sea in Health and Life Srl, Capo Peloro, Messina, Italy

Improve the knowledge base on the ecomorphological adaptation of teleost
species to different environments, trying to reconstruct how habitat can shape
sagittae, is essential for conservational purposes, evolutionary evaluations, and
population dynamics studies. Here is provided a comparative study between
sagittae features, growth rates and age composition of two *Scorpaena porcus*
populations inhabiting the Mediterranean waters, one from the Strait of Messina
(Central Mediterranean Sea) and one from the Split area (Adriatic Sea).
Additionally, the stomach contents of the Messina specimens have also been
analysed to provide some preliminary information on the diet of *S. porcus*. A total
of ninety individuals, half from each area, have been obtained from two extremely
different environments. Results showed an overall different morphology, shape,
and morphometry of *sagittae* among the size classes of the two investigated
populations. Samples from Messina were characterized by a most elliptical and
slender shape, with a more regular serration of margins than those from Split,
which exhibited a wider *sagitta*, with a most enhanced *anti-rostrum* and longer
rostrum. Concerning diet, specimens from Messina showed a preference for
Crustacea (especially Brachyura and Amphipoda) and Teleost species, showing
some differences with literature data from other geographical areas (Split one
included). Results have confirmed the reliability of *sagittae* to detect the inter-
population variability of *S. porcus* from different geographical areas, an essential
tool for stock assessment, population studies and investigation on
ecomorphological adaptation of teleost species to different habitats.

KEYWORDS

otolith, populations, growth, comparison, morphology, life-history

1 Introduction

The family Scorpaenidae counts more than 1400 species and represents one of the most diverse fish groups worldwide (Turan et al., 2009). It includes species adapted to live in many different environments, from the coastal shallow waters to the deep seas (Costello et al., 2001). Within the family, species belonging to *Scorpaena* genus are among the most abundant in all the temperate marine environments, and in several tropical seas, around the world, with 61 valid species included in the genus (Nelson et al., 2016; Fricke et al., 2018).

Among these, the black scorpionfish, *Scorpaena porcus* (Linnaeus, 1758), is one of the most common in the entire Mediterranean basin, Black Sea, and the Eastern Atlantic Ocean, from the British Islands to the Atlantic Moroccan coasts (Wheeler et al., 1986; Mahé et al., 2014). It dwells rocky, or mixed rocky-sandy, benthic habitats, from the shallow water to the bathyal plan, with a bathymetric distribution in the Mediterranean basin ranging between 20 and 200 m (up to 800 m) with a mean at 20 m (Fricke et al., 2018). It is very common also on seagrass beds, showing a sedentary lifestyle with nocturnal feeding habits (Poutiers, 1987; Pashkov et al., 1999). According to literature, this species is a small-body benthic predator, with a preference for small fishes and crustaceans (Compaire et al., 2018; Aydin and Mazlum, 2020; Ferri and Matić-Skoko, 2021). It is considered, together with the other scorpionfish species, as an essential predator for the well-functioning of the rocky-reefs ecosystems worldwide, both in temperate and tropical areas. Unlike other congeneric species, *S. porcus* is characterized by a slow-growth and a relatively short life, with 12 years as maximum recorded age (Kutsyn et al., 2019), and an enhanced geographical heterogeneity in life span and growth rates within the distribution areas (Jardas and Pallaoro, 1992; Pashkov et al., 1999; Kuzminova et al., 2011; Ferri et al., 2012; Kutsyn et al., 2019; Sahin et al., 2019). This high inter population variability has been related to the influence of the different fishing pressures and environmental factors experienced by the populations within the distribution range (Bradai and Bouain, 1988; Jardas and Pallaoro, 1992; Unsal and Oral, 1994; La Mesa et al., 2010; Kutsyn et al., 2019; Sahin et al., 2019; Ferri and Matić-Skoko, 2021). Many authors have also suggested *S. porcus* as indicator species for biomonitoring and environmental conditions' assessments (Rudneva et al., 2005; Medinets and Medinets, 2010; Kuzminova et al., 2011; Ferri et al., 2012). In the Black Sea, this species showed a significant negative trend in body size related to several factors, as pollution, and temperature rise, being negatively affected by anthropogenetic pressure (Rudneva et al., 2005; Medinets and Medinets, 2010; Kuzminova et al., 2011). While, in the Adriatic Sea, variations in population dynamics, biological traits and biomass, related to fishing pressure, confirmed the sensitivity of the species to fisheries activities (Jardas et al., 1998; Jardas, 1999; Oven et al., 2000; Stagličić et al., 2011; Ferri et al., 2012; Ferri and Matić-Skoko, 2021). *S. porcus* represents one of the main target species of Mediterranean artisanal fisheries (especially in the eastern and western parts of the basin), representing a large portion of the total catch and, consequently, a large source of income (Jardas, 1999; García-Rodríguez et al., 2006;

Forcada Almarcha et al., 2007; Goñi et al., 2008; Forcada et al., 2009; La Mesa et al., 2010; Ferri et al., 2012; Özgül et al., 2019) thanks to its relatively high commercial value in Croatia, Spain, and Italy. *S. porcus* annual total catch was 240 tons in the Eastern part (192 tons in Turkey) of the basin (104 tons from Black Sea, 36 from the Sea of Marmara, 88 from Aegean Sea and 12 from the Mediterranean Sea) in the first decade of 2000 (Bilgin and Çelik, 2009). In Italy the total landings of scorpionfish species in 2021 changed in relation to the geographic areas, from 41.2 tons in the Adriatic Sea, to 446.58 tons in the Ionia Sea (FAO, 2020). Concerning *S. porcus* conservation status, it was recorded a relevant decline in catches and average size during the last two decades in the Ionian coast of the Sicily, strictly related to fishing activities (Tiralongo, 2024). To improve the knowledge base on the intra-specific variability of *S. porcus*, analyzing the different growth and eco-morphological adaptations of populations inhabiting different geographical areas, is essential to enhance its conservation. In fact, in fishery biology, a proper assessment of fishes' populations dynamics and stocks' structure is a fundamental step to establish good management measures, monitoring species and communities' response to management actions and different exploitation levels (Charles, 2001; Cochrane, 2002; Dimech et al., 2012; Perdichizzi et al., 2022). Moreover, being *S. porcus* a benthic species with a low home-range, a high spatial heterogeneity, and an enhanced ecological value, investigate how different habitats can influence its otoliths' features (such as shape, morphology, and morphometry) and growth rates acquires great relevance and scientific interest, also in terms of taxonomical studies and evolution.

Sagittae, as the other otoliths, grow for the entire fishes' life, with a daily metabolically inert deposition of calcium carbonate (Popper et al., 2005; Thomas and Swearer, 2019). Their peculiar physiology and growing mechanism have made otoliths (mainly *sagittae*) (Assis, 2003, 2005; Ladich and Schulz-Mirbach, 2016) an essential tool to study fish ages and growth (Newman and Dunk, 2002; Velasco et al., 2011). Thanks to their high variability in morphology and shape between and within species (Volpedo et al., 2008; Jaramilo et al., 2014; Zhuang et al., 2015a; D'Iglio et al., 2021a; D'iglio et al., 2022a; D'Iglio et al., 2023), they have been widely used also in several research field (e.g., taxonomy, paleontological studies, stomach content analyses, and stocks assessment in fisheries studies) (Benzinou et al., 2013; Higgins et al., 2013; Muniz et al., 2021; Neves et al., 2021; D'Iglio et al., 2021b; D'Iglio et al., 2022b). Concerning the intra-specific variations in shape and morphology, they can be related to many factors, ranging from those genetically driven (Vignon and Morat, 2010), to environmental conditions and diet (Schulz-Mirbach et al., 2010; Higgins et al., 2013). For this reason, *sagittae* are considered a good phenotypic marker, reliable to investigate the ecomorphological adaptation of teleost species to different environmental conditions and ecological dynamics (Abaad et al., 2016; Bose et al., 2020), as highlighted by the shape and morphological differences between stocks and populations (Benzinou et al., 2013; Higgins et al., 2013; Muniz et al., 2021; Neves et al., 2021). Diet composition and feeding habits were assessed as factors which influence on teleosts physiology, metabolism, and, consequently, on otoliths too (Mommsen, 1998;

Sanchez-Jerez et al., 2002). Moreover, molecules incoming deriving from diet strongly influence otoliths' growth process and the geographical differences in feeding habits, added to genetic and environmental variability, could allow their inter-population variability (Mille et al., 2016a, 2016b; Hüssy et al., 2021).

The present paper aims to investigate the intra-specific differences in age composition, growth, diet composition, and *sagittae* shape and morphology, between two populations of *S. porcus* inhabiting, respectively, the tidal ponds in the beach rock formations, along the Strait of Messina coast (Central Mediterranean Sea), and the coastal environment near the Split Area (Eastern Adriatic Sea). The stomach content analysis has been performed only on the specimens from Messina, using the obtained data to make a comparison with the data present in literature for the diet composition of the studied species in the Split area (Ferri and Matić-Skoko, 2021). The main purposes were: (i) to assess how *sagittae* contours, morphology and morphometry change among size classes in the two studied populations; (ii) to evaluate the reliability of shape and morphometrical analysis in the assessment of different *S. porcus* populations; (iii) to provide preliminary observations on growth and age composition between the studied areas; (iv) to analyse the stomach contents of the specimens from Messina, providing preliminary data on the diet composition and feeding habits of the samples of this area, useful to improve the knowledge base on their geographical variability and their influence on the growth and age composition of the specimens from the two different studied areas. These information are important to improve the knowledge base on the influences of the environment on inner ear morphology, otoliths and somatic growth.

2 Materials and methods

2.1 Sample collection and studied areas.

A total number of 90 *S. porcus* specimens were collected in December 2022 from two different localities of the Mediterranean Sea: 45 specimens from the tidal ponds occurring toward the Sicilian coast of the Messina's Strait (Central Mediterranean Sea, 38°15'25"N, 15°36'51"E), and 45 specimens from the coastal environment near the Split area (Eastern Adriatic Sea, 43°26'0"N, 16°26'55"E) (Figure 1).

Thanks to the limited depth (ranging from 0.2 to 1.2 m) of the tidal ponds occurring in the "beach rock" formations, a coastal biotope extending in the north-eastern Messina coast, between the two villages "Ganzirri" and "Torre Faro", toward the Sicilian coast of the Strait of Messina, specimens were caught manually, using a sampling net from the rocky bench present in the beachfront, by local fishermen.

"Beach rock". This sedimentary formation represents a rocky bench (2 kilometres long) that arrive from the beachfront, in the intertidal zone, to a depth of 2-3 meters, at the beginning of the infralittoral zone. It is considered an area of high interest, being part of the Oriented Natural Reserve of "Capo Peloro Lagoon" (Savoca et al., 2020), which, thanks to its irregular shape, is characterized by several tidal ponds, with different surface and connection dynamics to the sea, hosting very complex ecological communities. These are essential nursery areas for several teleost species and a shelter zone for numerous taxa (Gravem and Morgan, 2017; Capillo et al., 2018).

Concerning specimens from the Split area (Figure 1), they were collected using sets of trammel nets, 1.5 m high and 32 m long, with

FIGURE 1
Map of the central Mediterranean Sea with the two studied areas highlighted in the boxes (Strait of Messina area in green and Split area in red).

an inner layer mesh size of 28 mm and 150 mm mesh size of outer layers. Fish samples were captured in the nearshore, coastal waters in the Split area (43.5°N), in the eastern Adriatic, at depths ranging between 10 and 40 m (20 m in average). This biotope is characterized mainly by rocky substrata covered by photophilic algae alternating with patches of sand and *Posidonia oceanica* seagrass beds (Ferri et al., 2012; Ferri and Matić-Skoko, 2021).

2.2 Samples processing, otolith extraction and age reading

All sampled specimens were transported frozen to the laboratory, where they were measured (TL, cm) and weighed (BW, g). *Sagittae* were collected from each specimen, cleaned (15 min in 3% H_2O_2, followed by Milli-Q water) and, once dried, stored in Eppendorf microtubes. To assess the intra-specific variability in *sagittae* shape and morphometries in relation to fish size, all samples were divided into three size classes according to the following TL values: Class I included specimens smaller than 100 mm, Class II those with a TL ranging from 100 mm to 180 mm, and Class III larger than 180 mm. The left *sagittae* of both populations were photographed on the distal side using a stereomicroscope (Olympus SZX10) equipped with an Olympus DP-25 digital camera. Images were converted in binary format for shape analysis, using the ImageJ 1.48p free software, "available at http://rsb.info.nih.gov/ij/". Otoliths morphologies were described following the terminology used by Tuset (Tuset et al., 2008), Nolf (Nolf, 1985) and Assis (Assis, 2000).

After images collection, left *sagittae* were used for age estimation. The reading process was carried out by two different operators, without data on fish length, one with experience in estimating the age of *S. porcus*, and one with experience in estimating the age of other teleost species. Both readers performed two different readings, with one month of distance one from the other. If readings were different for one or two years, it was performed a third reading, with the otolith discarding in the case of persisting differences. The relative precision between readings was tested by the index of average percentage error (APE) (Beamish and McFarlane, 1983) and the coefficient of variation (CV) (Chang, 1982). The annual age of the specimens was estimated with reflected light and on a black background using the stereomicroscope (Olympus SZX10) equipped with an Olympus DP-25 digital camera, at magnification 1.5-2.4x). The pattern of opaque and translucent zones was used for annuli counting. Indeed, according to literature (La Mesa et al., 2010; Carbonara and Follesa, 2019; Ferri and Matić-Skoko, 2021), an annulus is the combination of an opaque and a translucent (or hyaline) ring, appearing, under the reflecting light respectively light and dark. When this pattern was not clear, *sagittae* were grinded to facilitate the rings' counting. It was not necessary the otoliths sectioning, being grinding enough to reveal the opaque and translucent zones' pattern for those samples in which this was not clear from the whole otoliths viewing. Age was estimated by counting translucent zones (Landa and Hernández, 2020) and considering the 1st of July as the birthdate (La Mesa et al.,

2010). In addition, during the age reading process, the edge of otoliths has been classified as opaque or translucent.

2.3 Stomach content analysis

Concerning stomachs, they were sampled only from Messina's specimens, and stored in ethanol 70% + glycerin 5% for stomach content analysis. Each stomach content of specimens from Messina was analyzed under the stereomicroscope, to identify, at the lowest taxonomic level possible, each prey. Each preys' items were counted and weighted, also detecting the digestion degree (1 = undamaged; 2 = almost digested; 3 = highly digested). The anatomical undigested preys' parts (e.g., otoliths, telsons, carapaces, mouth parts, heads capsules, fish columns) were counted to assess the contribution of each prey taxon to the diet, grouping the unidentifiable preys' items, due to the advanced state of digestion, into undetermined taxa. According to their presence in the stomachs, only one type of anatomical remains was counted for each prey group to avoid the double-counting.

Following indexes were calculated to evaluate the contribution of each preys' taxa to the diet: the percentage of biomass composition (% W), the percentage of abundance composition (%N), and the frequency of occurrence (%F) (Hyslop, 1980). The Relative Importance Index was also calculated [IRI = %F (%N + %P)] expressing it also as percentage 9% IRI = (IRI$_i$ Σ_i^N IRI$_i$) × 100) (Cortés, 1997; D'Iglio et al., 2021b; D'Iglio et al., 2022b). Concerning the empty stomachs, it was calculated the Vacuity Index, VC = (Ne/N) × 100, as the percentage of empty stomachs (Ne) on the total stomach number (N).

2.4 Shape and morphometric analysis

Shape R (R software package, RStudio 2022.07.1 Build 554; R Gui 4.1.3 2022.03.10) was used to perform the Shape analysis from the otoliths' outlines. This package has been developed for inter and inter specific analysis on shape variability in teleost's otoliths (Libungan and Pálsson, 2015). Each binarized *sagitta* photo was analyzed for the outlines' detection using a shape R specific function, with 0.05 as value for intensity threshold greyscale. A data file with studied specimens' information (as body weight and fish length) was linked to extracted contours. These was used for each size classes to perform several otoliths' measurements (maximum width, OW, mm, maximum length, OL, mm, perimeter, OP, mm, and surface, OS, mm^2), through the getMeasurements function. Proper package functions were applied for the extraction, and subsequent adjusting, of Wavelet and Fourier coefficients, to assess the allometric relationships between fish lengths and otolith shapes. Wavelet coefficients were used to provide the comparison between the mean *sagittae* shape of the analyzed populations. The reconstruction's quality was estimated analyzing the deviation of the coefficient's reconstruction from the otolith outline (Supplementary Figure S1). Finally, a g-plots R package's specific function was used to

investigate how the position along the outline can influence the wavelet coefficients variation (Supplementary Figure S2).

Otoliths measurements performed with shape R were used to calculate several indexes. The *sagittae* length increase, related to the total fish length, was evaluated assessing otolith length to total fish length ratio (OL/TL); while, according to literature (Tuset et al., 2003a, 2003b, 2016a; Pavlov, 2016, 2021; Jawad et al., 2018), several shape indexes were used to evaluate intra and inter specific variability of *sagittae* shape: roundness (Ro = $4OS/\pi OL^2$), form factor (FF = $4\pi OS/OP^2$), aspect ratio (AR = OW/OL%), circularity (C = OP^2/OS), rectangularity (Re = OS/[OL×OW]) and ellipticity [E = (OL–OW)/(OL+OW)].

2.5 Statistical analysis

Length frequency distributions of individuals from the two sampling areas were compared using the Kolmogorov–Smirnov two-sample test.

The von Bertalanffy growth model was fitted to the estimated age-length dataset using a non-linear least-square procedure of a Gauss–Newton algorithm, included in the statistical package STATISTICA (version 14.0.0.15). The von Bertalanffy growth parameters (L_∞, K and t_0) were calculated for both fish populations sampled in the Messina's Strait and Split area and compared by the multivariate Hotelling's T^2-test. The growth performance index (Φ' = 2 log L_∞ + log K) was then calculated to compare the different populations of the black scorpionfish throughout its distribution range.

Univariate and multivariate statistical methods were applied to conduct investigations on *sagittae* features of specimens from Messina and Split using Prism V.8.2.1 (Graph- pad Software Ltd., La Jolla, CA 92037, USA), R vegan package V.2.5, and PAST V.4.

The intra-population variability of *sagittae* morphometries, between the different size classes investigated, was detected using a one-way analysis of variance (one-way ANOVA) or Kruskal–Wallis one-way ANOVA, followed by Tukey or Dunn's post-hot test respectively. A Principal Component Analysis (PCA) was conducted to obtain an overview of the differences in otolith parameters between the size classes examined within each population. Additionally, the correlation between the measured parameters and fish body weight (BW) and total length (TL) was tested using the Spearman correlation analysis. To explore the intra-specific variability of otolith contours within each population, the shape indices were extrapolated and analysed through an ANOVA-like permutation test and a PCA, to obtain an overview of the differences in otolith shape between the size classes examined at the intra-population level. The significance level of p-value was set at < 0.05.

Concerning the inter-population variability, a one-way analysis of variance, or a corresponding non-parametric test in case of non-homogeneity of the data, was used to verify the existence of any differences in the *sagittae* extracted between Messina and Split specimens, using the origin site of the samples as the only independent factor, followed by a PCA. For a more detailed description of the two populations examined, a Mann-Whitney test was used to explore the variability of individual otolith morphometric parameters, within each size class, between the sampling sites identified in the current study. Additionally, to obtain an overview of the *sagittae* features of the two populations under examination, a Linear Discriminant Analysis (LDA) was applied to the dataset. A cross-validation of the LDA was carried out to provide a classification of the individuals for both the investigated areas, assessing the classification success rate as the specimens' percentage and number correctly assigned to the original sample. Finally, to investigate the inter-population variability of otolith contours between specimens from Messina and Split, the shape indices were extrapolated and analysed through an ANOVA-like permutation test and a Principal Component Analysis (PCA), to obtain an overview of the differences in otolith shape between the two analyzed populations.

3 Results

The 45 specimens from Messina showed a TL ranging from 6.5 to 23 cm, with a Mean TL ± SD of 12.61 ± 0.69 cm. Concerning Split area, specimens showed a TL ranging from 11.2 to 24.1 cm and a Mean TL ± SD of 14.71 ± 0.41 cm. Length-frequency distributions were significantly different between the two sampling areas (Kolmogorov–Smirnov test; P < 0.001).

3.1 Growth rates and age composition

Age counts were successfully provided for all the otoliths from Messina and Split, with no sample discarded, and a quite low variability of APE and CV indices (4.7% and 9.4%, respectively). The inner structure of sagittal otoliths consisted of a wide opaque nucleus, surrounded by an alternating pattern of translucent and opaque zones. Interpretation of otolith edge types revealed that translucent edge type was dominant in samples from Messina and Split (>90% in both areas). The age composition by area (Table 1) showed 3 to 5 years old as the main estimated ages (57.77%) for the Messina specimens, with a maximum age of 5 years. In Split area, the larger part of the specimens was between 5 and 8 years old (75.57%), with a maximum age of 8 years, showing that the specimens inhabiting the Messina's tidal ponds was younger than that from Split.

The von Bertalanffy growth curves were fitted to age-length dataset, estimated for individuals from the Messina Strait and Split area (Figure 2). Estimated parameters for *S. porcus* from the Messina Strait and Split area were L_∞ = 28.78 cm, K = 0.22 year^{-1}, t_0 = -0.02 year (R^2 = 0.89) and L_∞ = 40.59 cm, K = 0.05 year^{-1}, t_0 = -2.58 year (R^2 = 0.73), respectively. The growth performance index (Φ') was 2.26 for the fish from the Messina Strait and 1.92 for the fish from the Split area. Specimens from Split Area showed a growth rate of slightly more than 1 cm per year between 4 and 7 years old.

The Hotelling's T^2-test indicated that the von Bertalanffy growth curves differed significantly between the two tested groups of individuals (T^2 = 2885.92 > $T^2_{0\ (0.05,\ 3,86)}$ = 12.20). The L_∞ value was higher in fish from the Split area and the K value was higher in fish from the Messina Strait. Therefore, considering the growth

TABLE 1 Age-length keys and Lenght-at-Age of *S. porcus* specimens from Messina and Split area.

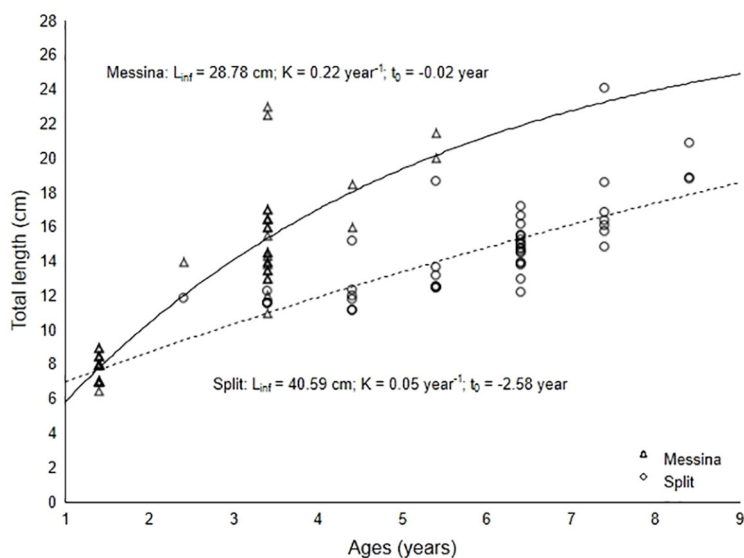| TL (cm)	Messina					Split						
	1	2	3	4	5	2	3	4	5	6	7	8
7	7											
8	6											
9	5											
10												
11			1					2				
12			1			1	4	3		1		
13			2						5	1		
14		1	6						1	3		
15			2					1		7	1	
16			3	1						3	3	
17			5							2	1	
18												
19				1					1		1	2
20					1							
21												1
22					1							
23			2									
24											1	
N	18	1	22	2	2	1	4	6	7	17	7	3
%	40	2.22	48.89	4.44	4.44	2.22	8.89	13.33	15.56	37.78	15.56	6.67
Length-at-Age (cm)	7.77	14.00	15.34	17.25	20.75	11.90	11.77	12.30	13.67	14.82	17.54	19.53

FIGURE 2
Fitted von Bertalanffy growth curve for S. porcus individual from Messina and Split.

coefficient and the growth performance index, fish from the Messina Strait grew faster than fish from the Split area. Statistical difference in length-at-age data (Table 1) was observed between the two investigated areas (t-test for paired comparison, P = 0.025).

3.2 Morphometric and shape analysis

Studied specimens showed an overall morphology of *sagittae* characterized by an oblong to lanceolate outline, with serrate to crenate margins. The anterior region was peaked, with *rostrum*, *antirostrum* and *excisura ostii*, that, together with the notch tilt angle, changed between the two populations in the analyzed size classes (Figures 3A–E). The posterior region was oblique to irregular, and the *sulcus acusticus* was heterosulcoid, ostial and median.

In Supplementary Tables S1, S2 are provided the morphometric mean values of the left *sagittae* for the two investigated populations, with the minimum and maximum range, divided in the three size classes.

Sagittae belonging to Messina specimens showed an oblong shape, with an enhanced margins serration. The *rostrum* and the *antirostrum* were short, with an arrow *excisura ostii*, a not acute notch, and an irregular posterior margin (Figures 4A–C). Concerning the intra specific differences among size classes, morphometrical analyses showed an enhanced variability, confirmed also by the mean otoliths' shapes (Figure 4D). *Sagittae* of specimens belonging to Size Class I showed a most circular contour, then the other classes. Also, the posterior region showed a peculiar organization, with a most oblique margin than the other size classes. In the Size Class II, the contour was less circular than the Class I, with most irregular posterior margin and less acute notch of *excisura*. The Size Class III showed a very different shape,

with an enhanced ellipticity (as highlighted by the highest E value among size classes: 0.41 ± 0.02 mm, see Supplementary Table S1) resulting in a less wide and longer *sagitta* than the other size classes.

Overall, the specimens examined showed significant variations in otoliths' parameters between the size classes considered in the study.

The results of the differences are reported in Supplementary Table S3, showing the absence of significant differences for 90% of the parameters between Class II and Class III. Concerning the comparison between Size Class I and II, and between Size Class I and III, significant differences were detected for all the investigated morphometrical parameters, except for Re values.

PCA confirmed the results obtained by univariate analysis (Figure 5), explaining the main differences observed between the classes I vs II and I vs III.

All *sagittae* measurements showed a significant correlation with specimens' parameters TL and BW. Results of Spearman correlation analyses are reported in Supplementary Table S4.

The mean shape of otoliths differed significantly between the three size classes investigated (p< 0.001). Marked differences in otolith shape have also been confirmed by PCA, mainly between the classes I and III (Figure 5B).

Concerning *sagittae* belonging to Split specimens, they showed a lanceolate contour, with a marked irregularity of margins. The *rostrum* and *antirostrum* were long, with a wide *excisura* and a very acute notch (Figures 6A, B). Concerning the intra-specific differences among size classes, shape analysis showed a general uniform shape (Figure 6C). Class II was characterized by a more enhanced circular contour than the other class, with an oblique posterior margin and an acute notch. In Class III the *sagittae* were more elliptic than the Class II, as highlighted by the highest E value (0.41 ± 0.02 mm, see Supplementary Table S2), with an enhanced length and a reduced width.
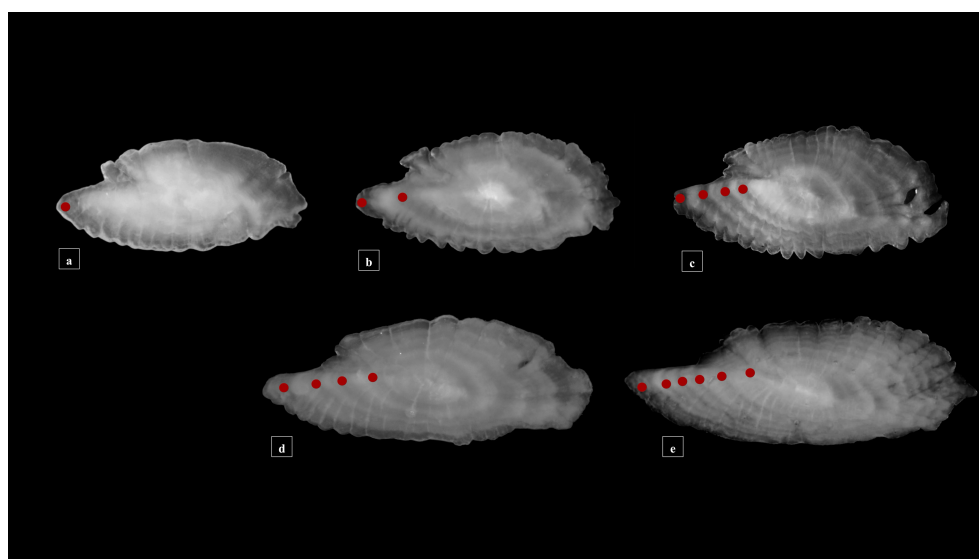

FIGURE 3
Stereoscope images of the medial view of the sagittae belonging to specimens from Messina **(A-C)** and Split **(D, E)** for the three investigated size classes [Class I: **(A)** Class II: **(B−D)** Class III: **(C−E)**]. Red dots indicate the end of each hyaline annulus in the reading area of each otoliths' image.
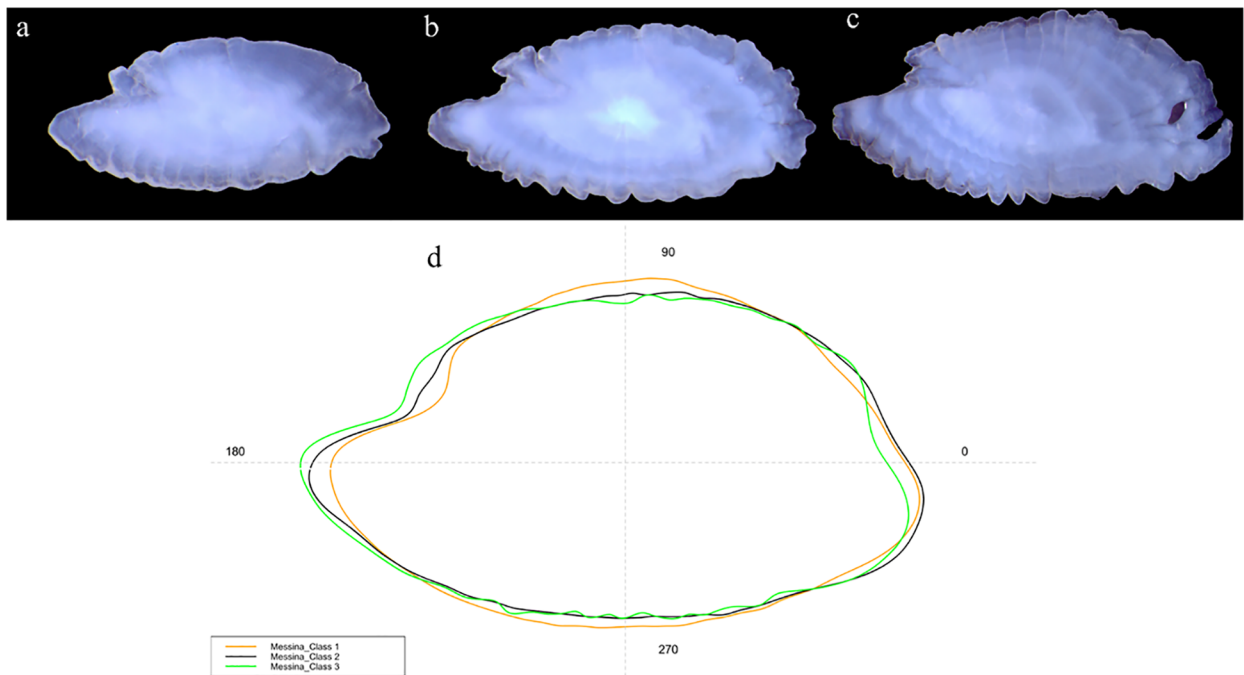
FIGURE 4
Stereoscope images of the medial view of the sagittae belonging to specimens from Messina, for the three investigated size classes [**(A)** Class I, **(B)** Class II, **(C)** Class III], with their mean otoliths shape **(D)**.

The specimens examined showed overall a significant variation in *sagittae* parameters between the two size classes investigated in the study ($p<0.05$).

The results of the variations observed for the individual parameters of the otoliths extracted from each size class are reported in Supplementary Table S5. Significant differences between the two size classes (Size Classes II and III) of the Split population were detected for all the investigated morphometrical parameters, except for Re values.

PCA confirmed the results obtained by univariate analysis (Figure 7A), explaining the main differences observed between the size.

Almost all *sagittae* measurements showed significant correlation with specimen parameters TL and BW. Results of Spearman correlation analyses are reported in Supplementary Table S6.

The mean shape of otoliths differed significantly between the two size classes investigated ($p< 0.009$). Slight differences in otolith shape have also been confirmed by PCA (Figure 7B).

FIGURE 5
Principal Component Analysis (PCA) plot between the specimens belonging to size classes I (fill triangle dark magenta), II (dot orange red) and III (fill square forest green), calculated on sagittae p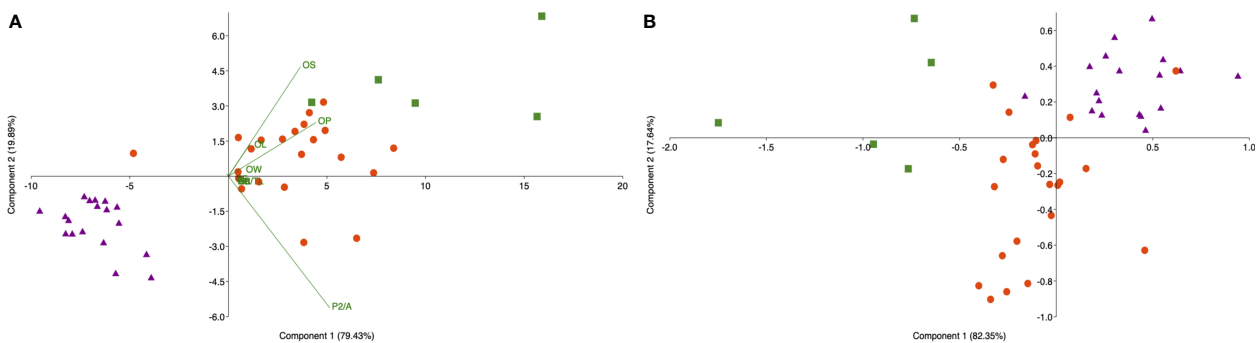arameters of Messina population **(A)**; Principal Component Analysis (PCA) plot between the Messina's specimens belonging to size classes I (fill triangle dark magenta), II (dot orange red) and III (fill square forest green), calculated on elliptic Fourier descriptors **(B)**.
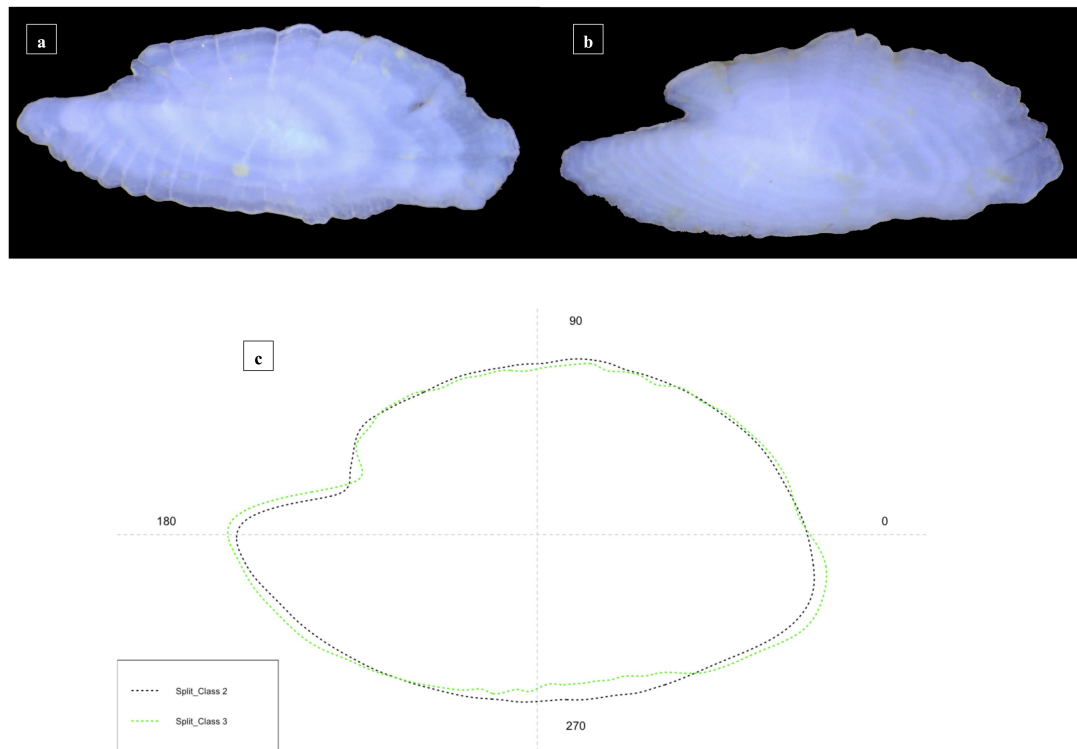
FIGURE 6
Stereoscope images of the medial view of the sagittae belonging to specimens from Split, for the two investigated size classes [(A) Class II, (B) Class III], with their mean otoliths shape (C).

3.3 Geographical differences between sagittae features

Concerning the number of individuals compared between the two zones, specimens belonging to Class III were much lesser than those belonging to Class II in both the studied areas. Overall, despite quite an overlap between the two areas, the two groups of individuals examined were different both for fish parameters and *sagittae* features (P<0.05), as well confirmed by PCA analysis (PC1 96.10%; PC2 3.51%) (Figure 8).

Class I of the specimens from Messina was eliminated from subsequent analyses, as it was not comparable to a class equally represented in the other group from Split.

The results obtained through the Mann-Whitney test are reported in Table 2, showing, for the compared size Classes III, the presence of significant differences only for the Ro shape index.

As highlighted by the LDA (Figure 9), the major differences concerned size classes II. An overall successful classification rate of 83.12% was achieved, concerning the LDA, for both the size classes combined (Supplementary Table S7). Specimens belonging to Class II
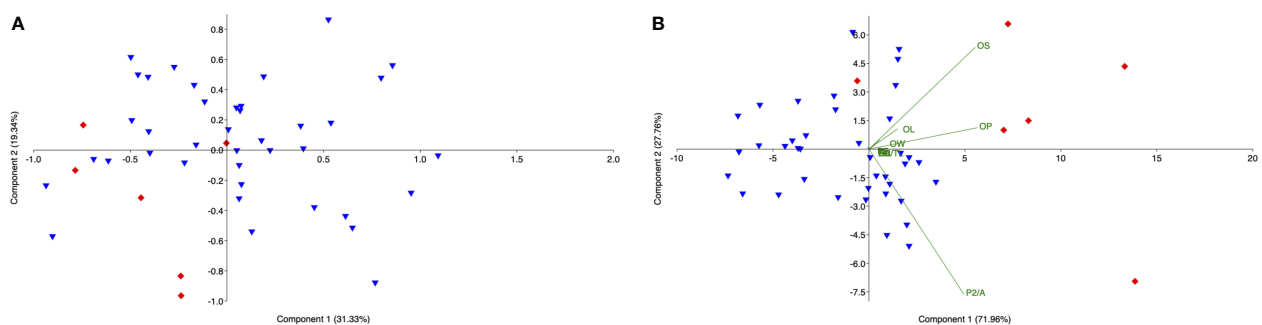

FIGURE 7
(A) Principal Component Analysis (PCA) plot between the specimens belonging to size classes II (Blue fill inverted triangle) and III (Red fill diamond), calculated on sagittae parameters from Split population; (B) Principal Component Analysis (PCA) plot between the specimens belonging to size classes II and III, from Split calculated on elliptic Fourier descriptors.
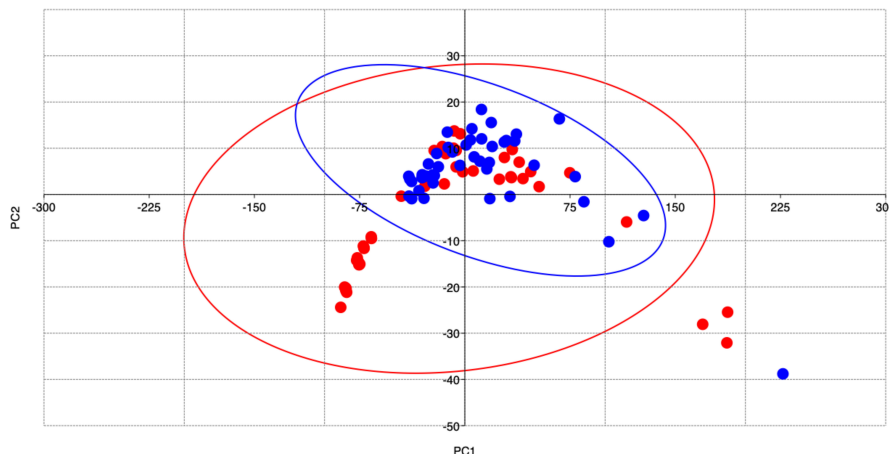
FIGURE 8
Principal Component Analysis showing fish and sagittae features differences between the sampling sites: Messina (red dots) and Split (blue dots).

showed the highest classifications, with values of 90.9% (from Messina) and 89.7% (from Split). Specimens belonging to Class III showed slightly lower values: 83.3% from Split and 80% from Messina.

The analysis of the *sagittae* contours of the two populations examined showed an evident variability between the specimens of class II (p=0.001) and class III (p=0.017). Results of PCA and mean otoliths shapes confirmed the differences observed for each class between the sampling sites, showing a variance of 41.75% (PC1) and 17.16% (PC2) for Class II, and 53.67% (PC1) and 17.5% (PC2) for Class III (Figures 10A, B).

In Figures 10C, D is provided a comparison of the mean otoliths' contours for the three investigated size classes. Specimens from Class II showed visible inter-population

differences regarding *rostrum* and overall mean contour, oval in individuals from Split and elliptical in those from Messina. In the Class III, the differences detected for the second size class were confirmed, with more marked *excisura ostii* showed by Split specimens than Messina ones, which reported a less marked irregularity of the margins, a shorter *rostrum* and a less pointed *antirostrum*.

The shape analysis performed on the total interclass samples showed mean *sagittae* shapes clearly different between the two analyzed populations (Figure 11). The main differences were detected in the *rostrum* organization (longer and more pointed in Split population than in the Messina one), in the *excisura ostii* (deeper in Split population than in the Messina one), in the *antirostrum* organization (more prominent and pointed in Split population than in the Messina one), and in the overall *sagittae* shape, oval in Split specimens and elliptical in Messina ones.

3.4 Stomach content analysis

The analysis of the 49 sampled stomachs from Messina (9 empty stomachs, with a Vacuity Index of 4.9) has shown a total of 80 preys, belonging to 29 taxa. As reported in Table 3, Crustacea and Osteichthyes were the major taxa with the highest number of preys, with also the highest values of IRI %. The infraorder Brachyura was the taxon which showed the highest IRI % value (IRI % = 32.81), followed by the species, belonging to the infraorder Brachuyra, *Pachygrapsus marmoratus* (Fabricius, 1787) (IRI % = 27.59), that was the taxon with the highest relative abundance (N % = 18.75) among the preys. The order Amphipoda (IRI % = 10.74) and the species *Xantho pilipes* (A. Milne-Edwards, 1867) (IRI % = 9.86), belonging to the infraorder Brachuyra, were the other two most relevant taxa for relative importance. Concerning the Osteichthyes preys, those belonging to the species *Chelon auratus* (Risso, 1810) (IRI % = 3.24) and *Thalassoma pavo* (Linnaeus, 1758) (IRI % = 2.36) were the most relevant preys, with the genus *Parablennius* as taxon with the highest relative abundance value (N % = 2.50). Concerning

TABLE 2 Mann Whitney test results obtained for otoliths' morphometric parameters comparison the same size classes from different sampling sites, Strait of Messina, and Split.

Sagittae parameters	Messina *vs* Split Class II	Messina *vs* Split Class III
	P value	P value
OS	0.0116*	0.3290 ns
OL	0.5636 ns	0.2468 ns
OW	<0.0001***	0.1255 ns
OP	0.0328*	0.4286 ns
Ro	<0.0001***	0.0043**
FF	0.5459 ns	0.9307 ns
E	<0.0001***	0.5368 ns
P^2/A	0.5459 ns	0.9307 ns
Re	0.0382*	0.7922 ns
AR	<0.0001***	0.5368 ns
OL/TL	0.0440*	0.1255 ns

P value legend: >0.05, not significant (ns); 0.03*, moderately significant; 0.002 **, significant; 0.001 *** highly significant.
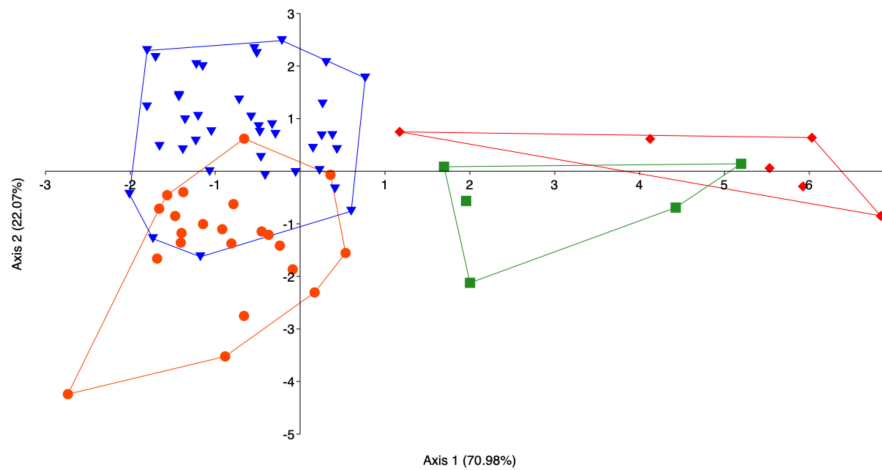
FIGURE 9
Linear Discriminant Analysis (LDA) between morphometric parameters (OL, OW, OP, OS, OL/TL, C, Re, E, AR, FF, Ro) of the investigated populations for the size classes II (orange-red dot Messina, Blue fill inverted triangle Split) and III (Forest green fill square Messina; Red diamond Split).

the class Polychaeta, it was the major taxa with the less relative importance (IRI % = 0.15).

4 Discussion

Data provided by the present work indicated a geographical variability for some biological features of *S. porcus* inhabiting two different biogeographic districts of the Mediterranean Sea: the Central Mediterranean Sea (Strait of Messina) and the Adriatic Sea (Split area) (Spanò and De Domenico, 2017). The relevant differences mainly involved the *sagittae* features of the black scorpionfish, also suggesting the reliability of otolith shape and morphometrics analyses as a useful tool for its populations' discrimination.

Concerning growth and age composition, our preliminary observations indicated an estimated maximum age higher in Split (8) than in Messina (5), with the von Bertalanffy growth curves which have shown K parameters higher in Messina, and L_∞
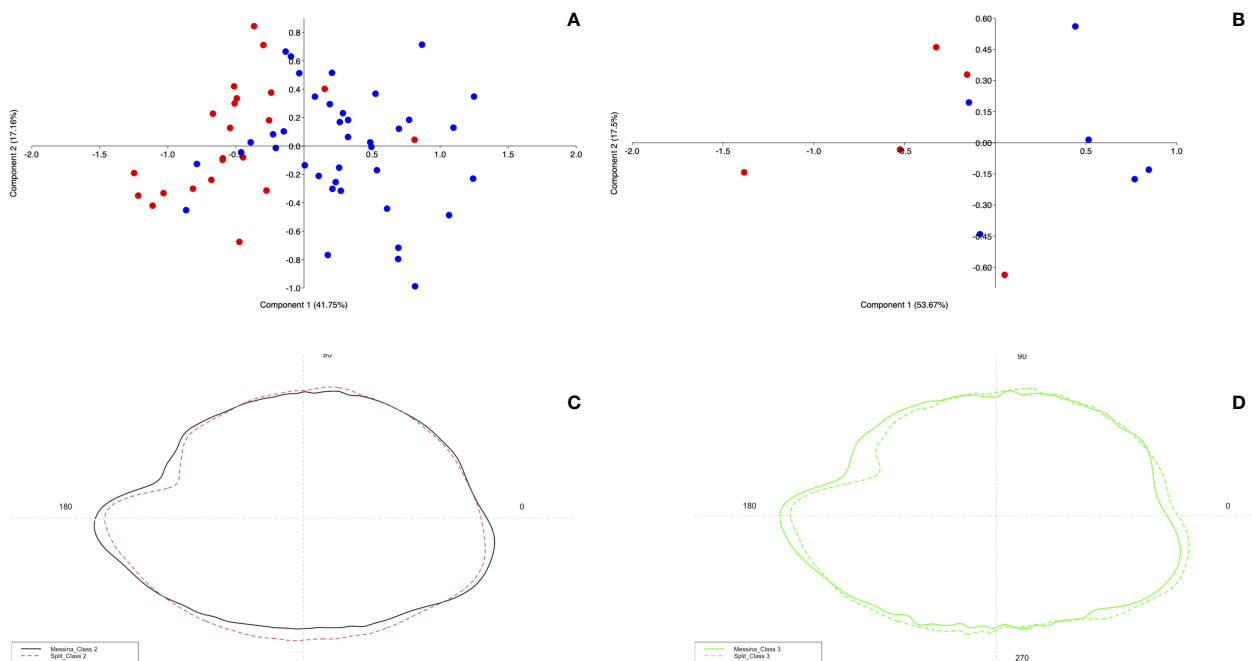
FIGURE 10
Results of PCA performed on Wavelet coefficient obtained by sagittae contours of specimens collected from Messina (red dots) and Split (blue dots). Results are reported for Class II and III, figures **(A, B)** respectively. Wavelet coefficient variance for each size classes investigated is expressed as percentage. Comparison of the mean otoliths shapes from the two populations is provided in figures **(C, D)** respectively for Class II and III.

FIGURE 11
Mean shape of sagittae contours of the investigated *S. porcus* population.
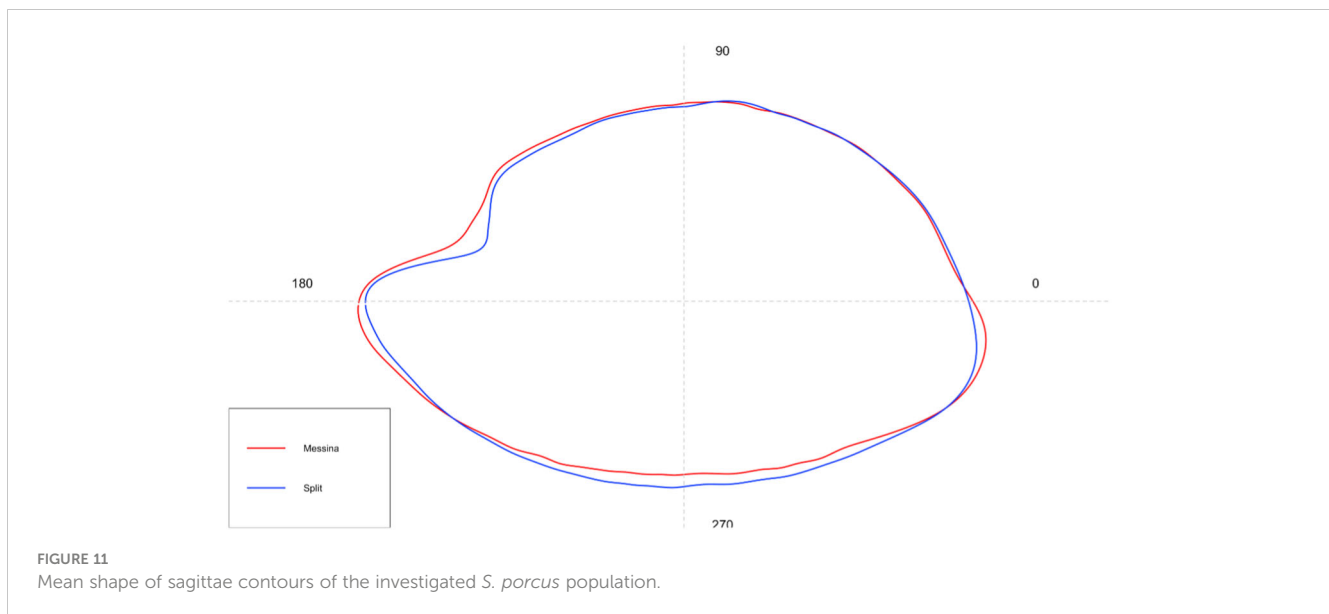
parameters higher in Split. The age composition was very different, with specimens from Messina that were mainly composed of individuals belonging to the third age class (3), with length-at-age values significantly higher than those shown by those from Split. All these data indicated a faster growth rate of the studied species in the Strait of Messina, as also highlighted by the growth performance index, which was higher in Messina specimens than Split. The high degree of population separation in *S. porcus* was widely reported, as highlighted by the differences in growth parameters and age composition detected between literature data from different geographical areas (Siblot-Boutéflika, 1976; Bradai and Bouain, 1988; Jardas and Pallaoro, 1992; Koca, 1997, 2002; Silvestri et al., 2002; Passalacqua et al., 2005; Bilgin and Çelik, 2009; La Mesa et al., 2010; Kendallha et al., 2018; Kutsyn et al., 2019; Sahin et al., 2019; Ferri and Matić-Skoko, 2021) (Table 4). Indeed, the overall comparison of the growth studies on this species from the Mediterranean basin highlighted a variability of Φ' index between 1.92 and 2.3 (excluding the extreme value of 2.71 reported by Bilgin and Çelik, 2009, being based on an unrealistic L∞ of 140 cm). The Φ' values shown by results were within the range of the previous studies, but with extreme values (1.92 and 2.26), reflecting the plasticity of *S. porcus* growth. The L∞ values reported by results were also in line with previous literature, in which they range from 19.8 and 60.94 cm. The only parameter not in line was the t_0 from Messina specimens, lower than those reported by literature data from other Mediterranean geographical areas.

Despite this, it must be considered also the effect of the length composition of samples from the two studied areas, influencing the curve trajectory of the younger age classes, and, consequently, the reconstruction of the entire growth rate. Further analyses with wide length classes composition, especially regarding the Messina population, are required to confirm the differences reported by results for the growth rate in the two studied geographical areas. *S. porcus* is a low-range benthic species with a high site fidelity capable of exhibiting a high phenotypic heterogeneity in its biological traits, often responding to local environmental conditions (Özgül et al.,

2019). The Strait of Messina represents a singularity inside the Mediterranean Sea, with a unique hydrographic regime and a peculiar seawater masses chemistry (Cucco et al., 2016; Savoca et al., 2020). It is located at the junction area between the Ionian and Tyrrhenian Sea. The meeting of these two water masses, different in physiochemical properties, occurs in an area with an enhanced morpho-bathymetrical irregularity of the bottom, resulting in a mixing process of the water masses, with strong currents regulated by tidal phases (Cucco et al., 2016; Longhitano, 2018). This intense hydro dynamism, with the massive presence of "upwelling" events, and the peculiar waters' physio chemistry, have meant that this area has become an "Atlantic Island" inside the Mediterranean basin (as highlighted by the oxygen concentrations, nutrients, and temperature similar to those reported for the Atlantic Ocean) and a hot spot of biodiversity, with the presence of unique biological communities (De Domenico, 1987; Cortese and De Domenico, 1990; Spanò and De Domenico, 2017). Otherwise, the Adriatic Sea generally shows a pronounced seasonality and an enhanced longitudinal gradient in dissolved oxygen, temperature, nutrients, salinity, and chlorophyll-a (Lipizer et al., 2014), with urbane discharges, aeolian inputs, underground waters and surface runoff which represent the main nutrients sources. The eastern Adriatic Sea, to which Split area belongs, is outflowed by the East Adriatic current, bringing Levantine Intermediate Water from the Ionian Sea (Orlić et al., 2006; Zorica et al., 2019), with the water column characterized by a high homogeneity during winter, becoming more stratified during Summer (Vilibić and Orlić, 2001). According to literature, different oceanographic features can influence the growth of species, resulting in a faster growth in populations inhabiting cold and productive water masses, than those from less productive and warmer ones (Kikuchi et al., 2021). In addition to the oceanographic differences between the water masses, also the environmental conditions experienced by the studied groups in the two different habitats were completely different. Specimens from Messina were sampled in the tidal ponds present in the beach rock formations, with reduced depth and large variations, also daily, of

TABLE 3 Diet composition of *S. porcus* individuals with %N (relative abundance), %W (percentage in biomass), %F (frequency of occurrence), IRI (index of relative importance) and %IRI (index of relative importance expressed as percentage) expressed for each prey items.

TAXA	N%	W%	F%	IRI	IRI%
Polychaeta	1.25	0.04	1.59	2.044	0.15
Total Polychaeta	**1.25**	**0.04**	**1.59**	**2.044**	**0.15**
Xantho pilipes	6.25	14.39	6.35	131.036	9.86
Brachynotus sexdentatus	1.25	1.74	1.59	4.742	0.36
Pachygrapsus marmoratus	18.75	14.24	11.11	366.524	27.59
Pachygrapsus sp.	1.25	2.11	1.59	5.341	0.40
Inachus dorsettensis	1.25	0.30	1.59	2.464	0.19
Percnon gibbesi	1.25	1.74	1.59	4.742	0.36
Brachyura	16.25	4.87	20.63	435.843	32.81
Palemon sp.	3.75	1.02	4.76	22.7	1.71
Lysmata sp.	1.25	0.38	1.59	2.58	0.19
Athanas nitescens	1.25	0.04	1.59	2.0	0.15
Palaemon elegans	1.25	0.26	1.59	2.40	0.18
Dendrobranchiata	6.25	0.94	7.94	57.10	4.30
Decapoda n.d.	1.25	0.04	1.59	2.04	0.15
Total Decapoda	**61.25**	**42.07**	**63.49**	**1039.57**	**78.26**
Lysianassa sp.	1.25	0.04	1.59	2.04	0.15
Dexamine spinosa	1.25	0.04	1.59	2.0	0.15
Microdeutopus sp.	1.25	0.04	1.59	2.04	0.15
Amphipoda	12.50	0.34	11.11	142.67	10.74
Dynamenella sp.	1.25	0.04	1.59	2.04	0.15
Sphaeroma sp.	7.50	0.68	3.17	25.97	1.95
Isopoda	1.25	0.11	1.59	2.16	0.16
Total Peracarida	**26.25**	**1.28**	**22.22**	**178.97**	**13.47**
Crustacea n.d	1.25	0.08	1.59	2.10	0.16
Total Crustacea	**88.75**	**43.43**	**87.30**	**1220.65**	**91.90**
Chelon auratus	1.25	25.83	1.59	42.99	3.24
Tripterygion delaisi	1.25	0.08	1.59	2.10	0.16
Gobius sp.	1.25	4.34	1.59	8.88	0.67
Gobius incognitus	1.25	6.34	1.59	12.05	0.91
Thalassoma pavo	1.25	18.50	1.59	31.36	2.36
Parablennius sp.	2.50	0.83	1.59	5.29	0.40
Osteichtyes n.d.	1.25	0.60	1.59	2.94	0.22
Total Osteichtyes	**10.00**	**56.53**	**11.11**	**105.61**	**7.95**

both biotic and abiotic conditions, related to tidal cycles and storms (Capillo et al., 2018). This results in marked physiochemical differences between the two studied areas, with higher temperature and salinity values in tidal pools from Messina than

those from Split, probably allowing for the higher growth rate and mean length at age found in specimens from Messina than those from Split. Indeed, tidal pools represent an "extreme" environment, and they are considered a perfect case of study to explore the behavioural, physiological and morphological adaptations of marine species to peculiar hydrographic and ecological conditions (Gomes et al., 1998; Capillo et al., 2018; Savoca et al., 2020). They are a shelter from the intense hydro-dynamism affecting the area, a nursery area and a perfect hunting ground for many predators, *S. porcus* included. Indeed, beach rock represents the only natural substrate for benthic species present at these depths (Spanò and De Domenico, 2017), and a shelter from the strong currents that make the coastal areas of the Strait of Messina a difficult environment for habitat exploitation (Gravem and Morgan, 2017). This biotope hosts very peculiar benthic communities, with substantially different species composition and richness to those found in other similar Mediterranean environments (Spanò and De Domenico, 2017). It also houses extended vermetid formations (protected by the European Community) with a unique arrangement, being on the substrate surface, and not in the typical trottoir formation, as in the rest of the Mediterranean Sea (Ingrosso et al., 2018). Conversely, the biotope of the coastal waters near Split is the classical environment inhabited by the studied species, and other Scorpaenids, in the Mediterranean Sea. It is characterized by depths ranging from 10 and 40 m, the presence of rocky bottoms covered by algae, sandy bottoms, and patches of *P. oceanica*, with a relatively high biodiversity (up to 27 different recorded fish species, belonging to Sparidae, Mullidae, Mugilidae, Centracanthidae, Labridae and Gobiidae families) (Institute of Oceanography and Fisheries, 2023). Specimens from Split here analyzed were sampled at an average depth of 20 m, very different from the 2-3 m depth of the tidal ponds of Messina's beach rock formations. According to the literature, these differences in biotic and abiotic environmental conditions could drive the geographical variability in growth shown by results between the two studied areas (Bacha et al., 2010; Lek et al., 2012; Ferri and Matić-Skoko, 2021).

It is well known that temperature can influence the metabolism, and consequently the growth rates, of several teleost species (Atkinson, 1994; Kozłowski et al., 2004; Jobling, 2011), but also food availability and quality can shape them (Mommsen, 1998; Bacha et al., 2010). Concerning diet composition, a comparison between the data provided by the stomach content analysis of the specimens from Messina, and the literature data regarding the studied species from Split, showed a similarity between the feeding habits of the black scorpion fish in the two areas, especially regarding the major taxa of the main preys. Results from the stomach content analysis on specimens sampled in Messina showed a high selectivity for decapods' preys, as assessed also for other Scorpaenidae species from other geographical areas (Harmelin-Vivien et al., 1989; Başçinar and Sağlam, 2009; Compaire et al., 2018; Aydin and Mazlum, 2020; Ferri and Matić-Skoko, 2021). The high relevance of brachyuran decapods (e.g., *X. pilipes, P. marmoratus*, Brachyura) reported by results was in line with literature data on the studied species, but some differences regarding the contribution of teleost fishes, peracarids crustaceans and molluscs were detected. The differences in feeding habits with *S.*

TABLE 4 Von Bertalanffy growth parameters and derived growth performance index (Φ') of *S. porcus* from literature and the present study.

L• (cm)	K (year^{-1})	t_0	Φ'	Area	Authors
140.745	0.026	-1.557	2.711	Black Sea	Bilgin and Çelik, 2009
40.810	0.107	-2.227	2.250	Black Sea	Koca, 1997
19.8	0.35	-0.48	2.14	Black Sea	Kutsyn et al., 2019
40.8	0.11	-2.23	2.26	Black Sea	Koca, 2002
22.15	0.287	-1.577	2.149	Black Sea	Sahin et al., 2019
23.1	0.16	–	1.93	Gulf of Gabes	Bradai and Bouain, 1988
24.377	0.161	-1.191	1.981	Marmara Sea	Unsal and Oral, 1994
28.200	0.182	–	2.161	Adriatic Sea	Jardas and Pallaoro, 1992
60.94	0.03	-5.18	2.05	Adriatic Sea (Split Area)	Ferri and Matić-Skoko, 2021
41.99	0.06	-3.54	2.02	Adriatic Sea (Pag Area)	Ferri and Matić-Skoko, 2021
22.30	0.23	-3.43	2.07	Adriatic Sea	La Mesa et al., 2010
21.80	0.29	-2.51	2.29	Adriatic Sea	Scarcella et al., 2011
32.4	0.18	-0.93	2.28	Ligurian Sea	Silvestri et al., 2002
29.3	0.16	0.97	2.14	Algerian Sea	Siblot-Boutéflika, 1976
23.5	0.28	-0.03	–	Tyrrhenian Sea	Passalacqua et al., 2005
23.96	0.68	0.058	–	Central Mediterranean Sea	Kendallha et al., 2018
28.78	0.22	-0.02	2.26	Strait of Messina	Present study
40.59	0.05	-2.58	1.92	Adriatic Sea (Split Area)	Present study

porcus specimens from Split mainly consisted of the complete absence of Molluscs and Anomura from the diet of Messina's specimens. According to the literature, these prey items represent an important source of food for Split population, together with teleost fishes and Caridea decapods, which showed a reduced occurrence in Messina specimens (Ferri and Matić-Skoko, 2021). Concerning peracarids crustaceans (e.g., Amphipoda and Isopoda), they were well represented in the stomach content from Messina, but they are very marginal in the diet composition reported in literature from Split. This variability in peracarids' preys could be strictly related to the biocenosis present in the tidal pools of the beachrock formations of Messina, rich in Amphipods and Isopods (being the perfect habitats for them) (Dias, 2013). Indeed, the presence of these crustaceans in the diet of this Scorpaenidae species has been assessed also in other similar formations present in Spain (Gulf of Cadiz) (Compaire et al., 2018). The wide variability in feeding habits between groups of individuals inhabiting different geographical areas probably reflects the capability of this species to adapt its diet according to the prey's availability, indicating a generalist and opportunistic feeding strategy (Harmelin-Vivien et al., 1989; Başçinar and Sağlam, 2009; Rafrafi-Nouira et al., 2016; Compaire et al., 2018; Aydin and Mazlum, 2020; Ferri and Matić-Skoko, 2021). This is an essential feature which allowed this species to inhabit a wide range of Mediterranean areas and habitats. Further analyses on a wider

temporal scale, with a larger samples' number, representative of the different ontogenetic classes, are required to better reconstruct the feeding habits and diet composition of *S. porcus* specimens, during the entire year, in the tidal ponds of the Strait of Messina. This is essential to understand how much diet variations, added to the other genetic and environmental features, can allow for the geographical differences in growth rates between the two groups of individuals highlighted by results.

Fish growth and metabolism, such as biotic and abiotic habitat features, can also influence otoliths growth and, consequently, their morphometry and shape (Grønkjær, 2016). Lifestyle, diet composition, food quality and feeding fitness have a role in otoliths' morphology, shape, growth patterns and physiology (Popper and Lu, 2000; Popper and Schilt, 2008; Schulz-Mirbach et al., 2019). According to the literature, otoliths' shape and morphometry are influenced by water temperature, depth (e.g., the size of otoliths increases with greater depths and warmer water masses), genetics and lifestyle of the species (e.g., epipelagic species show smaller and more elongated *sagittae* than benthic ones) (Lombarte and Lleonart, 1993; Lombarte and Cruz, 2007; Volpedo et al., 2008; Lombarte et al., 2010; Tuset et al., 2015). Thanks to this high sensitivity to environmental conditions, otoliths (especially *sagittae*) have become an essential tool in fish stock assessment and population discrimination. This was confirmed by the results of *sagittae* analyses. The overall morphology and shape

of both studied groups of individuals were in line with data from the literature, with several differences in morphometry. Tuset et al (Tuset et al., 2008). reported rectangularity and circularity values, for specimens from the western and central Mediterranean Sea, different from those of both Split and Messina specimens, with a most marked rectangular overall shape of the *sagittae* than the studied ones; while Yedier et al. (YediEr and Bostanci, 2021). reported, from the Black Sea, Aegean Sea and Sea of Marmora, different shape indices values, e.g., roundness, ellipticity and aspect ratio, with a most marked elliptical shape of the *sagittae* than the studied ones. This shape heterogeneity of *sagittae* was also evident when comparing Split and Messina specimens. As highlighted by the overall contours and the statistical analysis on the morphometrical parameters between the two groups of individuals, specimens from Split showed wider, double-picked (with an enhanced *antirostrum*) more circular *sagittae*, than those from Messina. Otherwise, these last showed more lanceolate, larger, with a most marked *rostrum*, *sagittae*, characterized by higher otolith surface values and a more elliptical than circular shape. Based on the obtained results, the morphology and morphometry of the *sagittae* from both the analyzed geographical areas showed peculiar features, different from those reported in the literature from other ones, highlighting the high geographical heterogeneity of the studied species' otoliths.

Several factors could have induced these differences, being otoliths under a double control of genetic and environment, and sensitive to variation in physiological and metabolic individuals' conditions. According to Vignon and Morat (Vignon and Morat, 2010), different environmental factors can reshape the overall *sagittae* outlines, while genetic variations at the intra-specific level, related to the long-time separation between the populations, only influence the shape of the otoliths locally (mainly at *rostrum* and *antirostrum* level). Concerning the environmental conditions experienced by the two groups of individuals, one of the most evident differences between the two sampling areas was the depth range, significantly higher in Split than in Messina. Indeed, it is widely reported how species and populations inhabiting deeper habitats show wider, more circular *sagittae* than those from shallower ones (Lombarte and Lleonart, 1993; Monteiro et al., 2005; Lombarte and Cruz, 2007). This finding is in line with results, which showed also a most lanceolate *sagittae* in specimens from Messina, inhabiting a very shallow environment, then those from Split. The soundscape can be another factor that can strongly influence the otolith morphology and development. Indeed, according to the sensory drive hypothesis postulated by Endler (Endler, 1992, 1993), there is a coevolution between detected signals and sensory systems, with the speciation that may be strongly influenced by the diversification of the organisms' sensory interactions and environment. This is strongly evident in deep species and in species that use sound to communicate (such as rockfishes) (Tuset et al., 2016b). The soundscapes experienced by individuals drive a selection on the form-function of the fishes' auditory system, with species or groups of individuals sharing a similar surrounding soundscape that could express an inner ears' phenotypic similarity, expressed by otolith morphology and shape (Bose et al., 2020; Chapuis et al., 2023). This could be also the case of

the two analyzed groups of individuals of *S. porcus*, with the differences related to the soundscapes of the two different studied areas that may have also influenced the detected *sagittae* variability in morphology, morphometry and shape. Also, metabolic rate and somatic growth can influence otolith features, such as morphometry, size and shape (Popper et al., 2005; Schulz-Mirbach et al., 2019). Messina specimens showed faster growth than the Split ones, which (if confirmed by the further analyses required to deeply investigate the growth rates of the studied species in the two studied areas) could be related to several environmental factors, such as the most enhanced availability of food in the tidal ponds habitats (Dias, 2013), probably resulting in a major food intake, and the "extreme" environmental conditions (such as high temperature and salinity, with large seasonal values' fluctuation) experienced by specimens from Messina. Indeed, in addition to the enhanced availability of food in tidal ponds biocenosis, another factor strongly influencing growth and, consequently, *sagittae* features is the water temperature. It is widely reported how teleost species show enhanced growth rates in environments characterized by higher temperatures (Pepin, 1991; Jobling, 1997). The tidal ponds are characterized by large fluctuation of temperature, with a range (between 14 and 23° C) (Savoca et al., 2020) higher than that reported for the Split area (data reported in the literature for the first meter of the water column between 10 to 23°C) (Kraus et al., 2019). This different range of temperature which specimens from Messina probably experienced, in addition to other factors (such as food intake), could allowed for the faster growth shown by the results. It is necessary to enlarge the sample size also to obtain more solid data from the analyses on the intra and inter-population variability of *sagittae*, considering the differences in specimen numbers between size classes (especially between Size classes I, totally absent in Split, and III) in both the studied areas. Indeed, data from a larger number of specimens, with a similar sample size composition between the analyzed Size Classes, can be essential to obtain an even more complete picture of the inter and intra-population variability of the studied species. Bias related to sample size has great relevance, especially in inter-population studies involving otoliths' shape and morphometrical data, with a non-representative number of specimens, or a not-comparable number of specimens from each population, representing one of the major concerns in this research field (Hilborn and Walters, 1992; Campana and Casselman, 1993; Lleonart and Maynou, 2003; Biolé et al., 2019). Future studies, involving more specimens, and combining otoliths' shape analysis with biological or genetic analyses, are necessary to confirm and improve the data provided by results. This is essential to deepen the knowledge base regarding the inter-population differences in *sagittae* features and growth rates of the studied species for further stocks' discrimination and population studies.

Concerning somatic growth, it is not clear its relation to metabolic rate, food intake and otoliths' size and growth, also because faster fish growth and a most enhanced food intake do not always result in larger otoliths (Hoff and Fuiman, 1993; Grønkjær, 2016). Concerning the geographical differences among the size classes, the statistical analyses highlighted significant shape differences in intermediate specimens (11-18 cm), but no significant

differences in morphometry between specimens from the two studied areas were found in those larger than 18 cm. This could be related to the life habits of the specimens from Messina, which could pass more time inside the tidal ponds of the beach rock formations during the first part of their life, searching for shelter and good hunting ground, as reported for other teleost species in the area (Capillo et al., 2018; Savoca et al., 2020). Indeed, tidal pools are recognized worldwide as an important nursery area for several teleost families, that in these environments can find shelter from predators and increased preys' availability (Dias, 2013; Dias et al., 2016; Mendonça et al., 2019). This could explain the more significant morphometrical differences at the geographical level between specimens smaller than 18 cm than the larger ones. Future studies comparing the otoliths belonging to specimens smaller than 10 cm from both areas can confirm this thesis, being these absent from the Split samples here analyzed. Indeed, according to the literature, otolith shape and morphometry are under the control of both genetic and environmental influences (Cardinale et al., 2004). The environment can strongly shape the sensory organs, as also highlighted by the sensory drive hypothesis, tested by Tuset et al. (Tuset et al., 2015) on the *sagittae* of others Scorpaenidae species (*Sebastes* spp.). Specimens smaller than 18 cm, belonging to the first and second age groups, could be more influenced by the beach rocks' tidal ponds than the third, spending more time in these habitats. Getting larger, *S. porcus* individuals could, conversely, spend more time in the nearshore coastal waters (re-entering in the tidal pounds searching for food, as reported for several transient species inhabiting these environments worldwide) (Dias, 2013), with biotopes and depths like those present in the Split area.

As shown by age composition results, tidal ponds in Messina represent a nursery area for *S. porcus*, characterized by a relevant abundance of small-age specimens. Considering the commercial and ecological value of this species, it is required an improved conservation of this sensitive and extreme biotope. It is necessary to enhance the management practice of commercial and recreational fishing, especially in the areas near this biotope. Moreover, being this area so close to the city, it is required to preserve it against increasing urbanization, creating buffer zones between the beach rock formation and the most anthropized zones. The conservation of these ecologically relevant habitats can improve not only the abundance and distribution of *S. porcus*, but also those of the several species inhabiting them, preserving the biodiversity of the entire marine coastal environment.

5 Conclusion

Assess and exploring the variations in ecomorphological features and population parameters at the geographical level is essential for both conservation purposes (being morphological features, such as those related to otoliths, and population dynamics widely used in stock assessment) and ecological studies (Aguirre and Lombarte, 1999; Lombarte et al., 2010; Zhuang et al.,

2015b; Assis et al., 2020). The eco-morphological adaptation of species to different habitats and environmental features is the basis of phenotypic plasticity (i.e., the capability to express different phenotypes related to different environmental factors) (Via et al., 1995). This becomes an essential concept for the identification of marine teleost populations, being assumed that each population, living under peculiar environmental conditions, can display specific phenotypes under the regulation of genetic and/or environmental mechanisms (Swain and Foote, 1999; Grabowski et al., 2009; Berg et al., 2018). This process, being also the basis of the stock's differentiation, assumes relevant importance in the conservation of fishery resources and the maintenance of marine ecosystems' well-being.

In this regard, the present paper assessed both the reliability of *S. porcus* as a model species to explore the eco-morphological variability of otoliths and population dynamics plasticity, and the reliability of otoliths shape and morphometric analysis for the populations' discrimination in the studied species. The low home-range distribution of this benthic species, its heterogeneity in growth somatic patterns and feeding habits related to different environments, added to the high geographical variability of *sagittae* in shape and morphometry reported by results, make *S. porcus* perfect to explore the influence of different environmental conditions on teleost species. Specimens inhabiting the tidal ponds of the beachrock formations could be a perfect case study to understand how teleost species can adapt to extreme environmental conditions and peculiar habitat features. Future analyses on population dynamics and seasonal distribution of the studied species in this peculiar environment are required, to understand the ecology of this species and its life habits in these habitats. Moreover, it will be also essential to provide valuable data about the species composition and ecological inter-specific dynamics existing in tidal ponds, recognized worldwide as fundamental nursery areas, and feeding grounds for several marine species, and, consequently, as important biocenosis for the well-being and the conservation of the marine biodiversity.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material. Further inquiries can be directed to the corresponding authors.

Ethics statement

Ethical approval was not required for the studies involving animals because ethical approval was not required for the study involving animals in accordance with the local legislation and institutional requirements because biological samples were obtained from landings of commercial fishing vessels and fisherman. The studies were conducted in accordance with the local legislation and institutional requirements.

Author contributions

CD: Writing – original draft, Visualization, Validation, Software, Investigation, Data curation, Conceptualization. SF: Writing – review & editing, Visualization, Software, Methodology, Investigation, Formal analysis, Data curation. JF: Writing – review & editing, Visualization, Validation, Supervision, Software, Methodology, Investigation, Conceptualization. MA: Writing – review & editing, Visualization, Validation, Supervision, Methodology, Investigation, Data curation, Conceptualization. NS: Writing – review & editing, Conceptualization, Validation, Supervision, Resources, Investigation, Funding acquisition. GC: Writing – review & editing, Visualization, Validation, Project administration, Methodology, Investigation, Data curation, Conceptualization. SS: Writing – review & editing, Visualization, Software, Project administration, Methodology, Investigation, Formal analysis, Data curation, Conceptualization.

Funding

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2024.1347897/full#supplementary-material

References

Abaad, M., Tuset, V. M., Montero, D., Lombarte, A., Otero-Ferrer, J. L., and Haroun, R. (2016). Phenotypic plasticity in wild marine fishes associated with fish-cage aquaculture. *Hydrobiologia* 765, 343–358. doi: 10.1007/s10750-015-2428-5

Aguirre, H., and Lombarte, A. (1999). Ecomorphological comparisons of sagittae in Mullus barbatus and M. surmuletus. *J. Fish Biol.* 55, 105–114. doi: 10.1111/j.1095-8649.1999.tb00660.x

Assis, C. A. (2000). Estudo morfológico dos otólitos sagitta, asteriscus e lapillus de Teleóstei (Actinopterygii, Teleostei) de Portugal continental. Sua aplicação em estudos de filogenia, sistematica e ecologia. *Ecologia* 1005, 1-1004.

Assis, C. A. (2003). The lagenar otoliths of teleosts: Their morphology and its application in species identification, phylogeny and systematics. *J. Fish Biol.* 62, 1268–1295. doi: 10.1046/j.1095-8649.2003.00106.x

Assis, C. A. (2005). The utricular otoliths, lapilli, of teleosts: Their morphology and relevance for species identification and systematics studies. *Sci. Mar.* 69, 259–273. doi: 10.3989/scimar.2005.69n2259

Assis, I. O., da Silva, V. E. L., Souto-Vieira, D., Lozano, A. P., Volpedo, A. V., and Fabré, N. N. (2020). Ecomorphological patterns in otoliths of tropical fishes: assessing trophic groups and depth strata preference by shape. *Environ. Biol. Fishes* 103, 349–361. doi: 10.1007/s10641-020-00961-0

Atkinson, D. (1994). Temperature and organism size—A biological law for ectotherms? *Adv. Ecol. Res.* 25, 1–58. doi: 10.1016/S0065-2504(08)60212-3

Aydin, M., and Mazlum, R. E. (2020). Feeding ecology of black scorpion fish (Scorpaena porcus Linnaeus 1758) in SE black sea region, (Ordu) Turkey. *J. Mar. Biol. Assoc. United Kingdom* 100, 435–444. doi: 10.1017/S002531542000020X

Bacha, M., Moali, A., Benmansour, N. E., Brylinski, J. M., Mahé, K., and Amara, R. (2010). Relationships between age, growth, diet and environmental parameters for anchovy (Engraulis encrasicolus L.) in the Bay of Bénisaf (SW Mediterranean, west Algerian coast). *Cybium* 34, 47–57. doi: 10.26028/cybium/2010-341-006

Başçınar, N. S., and Sağlam, H. (2009). Feeding habits of black scorpion fish scorpaena porcus, in the South-Eastern Black Sea. *Turk J. Fish Aquat Sci.* 9, 99–103.

Beamish, R. J., and McFarlane, G. A. (1983). The forgotten requirement for age validation in fisheries biology. *Trans. Am. Fish Soc.* 112, 735–743. doi: 10.1577/1548-8659(1983)112<735:TFRFAV>2.0.CO;2

Benzinou, A., Carbini, S., Nasreddine, K., Elleboode, R., and Mahé, K. (2013). Discriminating stocks of striped red mullet (Mullus surmuletus) in the Northwest European seas using three automatic shape classification methods. *Fish Res.* 143, 153–160. doi: 10.1016/j.fishres.2013.01.015

Berg, F., Almeland, O. W., Skadal, J., Slotte, A., Andersson, L., and Folkvord, A. (2018). Genetic factors have a major effect on growth, number of vertebrae and otolith shape in Atlantic herring (Clupea harengus). *PloS One* 13, e0190995. doi: 10.1371/journal.pone.0190995

Bilgin, S., and Çelik, E.Ş. (2009). Age, growth and reproduction of the black scorpionfish, Scorpaena porcus (Pisces, Scorpaenidae), on the Black Sea coast of Turkey. *J. Appl. Ichthyology* 25, 55–60. doi: 10.1111/jai.2009.25.issue-1

Biolé, F. G., Callicó Fortunato, R., Thompson, G. A., and Volpedo, A. V. (2019). Application of otolith morphometry for the study of ontogenetic variations of Odontesthes argentinensis. *Environ. Biol. Fishes* 102, 1301–1310. doi: 10.1007/s10641-019-00908-0

Bose, A. P. H., Zimmermann, H., Winkler, G., Kaufmann, A., Strohmeier, T., Koblmüller, S., et al. (2020). Congruent geographic variation in saccular otolith shape across multiple species of African cichlids. *Sci. Rep.* 10, 1–14. doi: 10.1038/s41598-020-69701-9

Bradai, M. N., and Bouain, A. (1988). Age et croissance de Scorpaena porcus et Scorpaena scrofa du golfe de Gábes. *Oebalia* 15, 13–38.

Campana, S. E., and Casselman, J. M. (1993). Stock discrimination using otolith shape analysis. *Can. J. Fisheries Aquat. Sci.* 50, 1062–1083. doi: 10.1139/f93-123

Capillo, G., Panarello, G., Savoca, S., Sanfilippo, M., Albano, M., Volsi, R. L., et al. (2018). Intertidal ponds of messina's beachrock faunal assemblage, evaluation of ecosystem dynamics and communities' interactions. *AAPP Atti della Accademia Peloritana dei Pericolanti Classe di Sci. Fisiche Matematiche e Naturali* 96, A41–A416. doi: 10.1478/AAPP.96S3A4

Carbonara, P., and Follesa, M. C. (2019). *Handbook on fish age determination: a Mediterranean experience* (Rome: FAO).

Cardinale, M., Doering-Arjes, P., Kastowsky, M., and Mosegaard, H. (2004). Effects of sex, stock, and environment on the shape of known-age Atlantic cod (Gadus morhua) otoliths. *Can. J. Fisheries Aquat. Sci.* 61, 158–167. doi: 10.1139/f03-151

Chang, W. Y. B. (1982). A statistical method for evaluating the reproducibility of age determination. *Can. J. Fisheries Aquat. Sci.* 39, 1208–1210. doi: 10.1139/f82-158

Chapuis, L., Yopak, K. E., and Radford, C. A. (2023). From the morphospace to the soundscape: Exploring the diversity and functional morphology of the fish inner ear, with a focus on elasmobranchs. *J. Acoust Soc. Am.* 154, 1526–1538. doi: 10.1121/10.0020850

Charles, A. T. (2001). *Sustainable Fishery Systems* Vol. 10 (Oxford: Blackwell Science, Ltd).

K. Cochrane (Ed.) (2002). *A fishery manager's guidebook – Management measures and their application* (Rome: FAO Fisheries Technical Paper No. 424. Food & Agriculture Org).

Compaire, J. C., Casademont, P., Cabrera, R., Gómez-Cama, C., and Soriguer, M. C. (2018). Feeding of Scorpaena porcus (Scorpaenidae) in intertidal rock pools in the Gulf of Cadiz (NE Atlantic). *J. Mar. Biol. Assoc. U. K.* 98, 845–853. doi: 10.1017/S0025315417000030

Cortés, E. (1997). A critical review of methods of studying fish feeding based on analysis of stomach contents: Application to elasmobranch fishes. *Can. J. Fisheries Aquat. Sci* (3), 726-738. doi: 10.1139/f96-316

Cortese, G., and De Domenico, E. (1990). Some considerations on the levantine intermediate water distribution in the Straits of Messina. *Boll. Ocean. Teor. Appl.* 8, 197–207.

Costello, M. J., Emblow, C., and White, R. J. (2001). *European register of marine species: a check-list of the marine species in Europe and a bibliography of guides to their identification* Vol. 50 (Paris: Collection Patrimoines Naturels. Paris: Muséum national d'Histoire naturelle).

Cucco, A., Quattrocchi, G., Olita, A., Fazioli, L., Ribotti, A., Sinerchia, M., et al. (2016). Hydrodynamic modelling of coastal seas: The role of tidal dynamics in the Messina Strait, Western Mediterranean Sea. *Natural Hazards Earth System Sci.* 16, 1553–1569. doi: 10.5194/nhess-16-1553-2016

De Domenico, E. (1987). Caratteristiche fisiche e chimiche delle acque nello Stretto di Messina. *Doc. Trav. IGAL* 11, 225–235.

Dias, M. A. D. (2013). Tidal pools as nursery areas for marine fish larvae and juveniles – habitat use and trophic ecology. *Mestrado em Ecologia Marinha*, 1–92.

Dias, M., Roma, J., Fonseca, J., Pinto, M., Cabral, H. N., Silva, A., et al. (2016). Intertidal pools as alternative nursery habitats for coastal fishes. *Mar. Biol. Res.* 12, 331–344. doi: 10.1080/17451000.2016.1143106

D'Iglio, C., Albano, M., Famulari, S., Savoca, S., Panarello, G., Di Paola, D., et al. (2021a). Intra- and interspecific variability among congeneric Pagellus otoliths. *Sci. Rep.* 11, 16315. doi: 10.1038/s41598-021-95814-w

D'Iglio, C., Albano, M., Tiralongo, F., Famulari, S., Rinelli, P., Savoca, S., et al. (2021b). Biological and ecological aspects of the Blackmouth Catshark (Galeus melastomus rafinesque 1810) in the southern Tyrrhenian Sea. *J. Mar. Sci. Eng.* 9, 967. doi: 10.3390/jmse9090967

D'Iglio, C., Famulari, S., Albano, M., Carnevale, A., Di Fresco, D., Costanzo, M., et al. (2023). Intraspecific variability of the saccular and utricular otoliths of the hatchetfish Argyropelecus hemigymnus (Cocco 1829) from the strait of Messina (Central Mediterranean sea). *PloS One* 18, 1–31. doi: 10.1371/journal.pone.0281621

D'iglio, C., Natale, S., Albano, M., Savoca, S., Famulari, S., Gervasi, C., et al. (2022a). Otolith analyses highlight morpho-functional differences of three species of mullet (Mugilidae) from transitional water. *Sustainability (Switzerland)* 14, 1-25. doi: 10.3390/su14010398

D'Iglio, C., Porcino, N., Savoca, S., Profeta, A., Perdichizzi, A., Armeli, E., et al. (2022b). Ontogenetic shift and feeding habits of the European hake (Merluccius merluccius L . 1758) in Central and Southern Tyrrhenian Sea (Western Mediterranean Sea): A comparison between past and present data. *Ecol. Evol.* 12, 1-12. doi: 10.1002/ece3.8634

Dimech, M., Kaiser, M. J., Ragonese, S., and Schembri, P. J. (2012). Ecosystem effects of fishing on the continental slope in the Central Mediterranean Sea. *Mar. Ecol. Prog. Ser.* 449, 41–54. doi: 10.3354/meps09475

Endler, J. A. (1992). Signals, signal conditions, and the direction of evolution. *Am. Nat.* 139, S125–S153. doi: 10.1086/285308

Endler, J. A. (1993). Some general comments on the evolution and design of animal communication systems. *Philos. Trans. - R. Soc. London B* 340, 215–225. doi: 10.1098/rstb.1993.0060

FAO. (2020). *FAO Fisheries and Aquaculture - FishStatJ - Software for Fishery and Aquaculture Statistical Time Series* (FAO Fisheries and Aquaculture Division). Available online at: https://www.fao.org/fishery/en/topic/166235?lang=en (Accessed February 8, 2024).

Ferri, J., and Matić-Skoko, S. (2021). The spatial heterogeneity of the black scorpionfish, scorpaena porcus (Scorpaenidae): Differences in length, dietary and age compositions. *Appl. Sci. (Switzerland)* 11, 11919. doi: 10.3390/app112411919

Ferri, J., Stagličić, N., and Matić-Skoko, S. (2012). The black scorpionfish, Scorpaena porcus (Scorpaenidae): Could it serve as reliable indicator of Mediterranean coastal communities' health? *Ecol. Indic* 18, 25–30. doi: 10.1016/j.ecolind.2011.11.004

Forcada, A., Valle, C., Bonhomme, P., Criquet, G., Cadiou, G., Lenfant, P., et al. (2009). Effects of habitat on spillover from marine protected areas to artisanal fisheries. *Mar. Ecol. Prog. Ser.* 379, 197–211. doi: 10.3354/meps07892

Forcada Almarcha, A., Bayle Sempere, J. T., and lizaso, J. L. S. (2007). Evaluación de las áreas marinas protegidas y su efecto en pesquerías artesanales del Mediterráneo Occidental. *Departamento Cienc. del Mar. y Biología Aplicada*, 402. pp.

Fricke, R., Golani, D., Appelbaum-Golani, B., and Zajonz, U. (2018). Scorpaena decemradiata new species (Teleostei: Scorpaenidae) from the gulf of aqaba, northern red sea, a species distinct from scorpaena porcus. *Sci. Mar.* 82, 169–184. doi: 10.3989/scimar.2018.82n3

García-Rodríguez, M., Fernández, Á.M., and Esteban, A. (2006). Characterisation, analysis and catch rates of the small-scale fisheries of the Alicante Gulf (SE Spain) over a 10 years time series. *Fish Res.* 77, 226–238. doi: 10.1016/j.fishres.2005.09.002

Gomes, P. B., Belém, M. J., da, C., and Schlenz, E. (1998). Distribution, abundance and adaptations of three species of Actiniidae (Cnidaria, Actiniaria) on an intertidal beach rock in Cameiros beach, Pemambuco, Brazil. *Miscellania Zoologica* 21, 65–72.

Goñi, R., Adlerstein, S., Alvarez-Berastegui, D., Forcada, A., Reñones, O., Criquet, G., et al. (2008). Spillover from six western Mediterranean marine protected areas: Evidence from artisanal fisheries. *Mar. Ecol. Prog. Ser.* 366, 159–174. doi: 10.3354/meps07532

Grabowski, T. B., Young, S. P., Libungan, L. A., Steinarsson, A., and Marteinsdóttir, G. (2009). Evidence of phenotypic plasticity and local adaption in metabolic rates between components of the Icelandic cod (gadus morhua l.) stock. *Environ. Biol. Fishes* 86, 361–370. doi: 10.1007/s10641-009-9534-z

Gravem, S. A., and Morgan, S. G. (2017). Shifts in intertidal zonation and refuge use by prey after mass mortalities of two predators. *Ecology* 98, 1006–1015. doi: 10.1002/ecy.1672

Grønkjær, P. (2016). Otoliths as individual indicators: A reappraisal of the link between fish physiology and otolith characteristics. *Mar. Freshw. Res.* 67, 881–888. doi: 10.1071/MF15155

Harmelin-Vivien, M. L., Kaim-Malka, R. A., Ledoyer, M., and Jacob-Abraham, S. S. (1989). Food partitioning among scorpaenid fishes in Mediterranean seagrass beds. *J. Fish Biol.* 34, 715–734. doi: 10.1111/j.1095-8649.1989.tb03352.x

Higgins, R., Isidro, E., Menezes, G., and Correia, A. (2013). Otolith elemental signatures indicate population separation in deep-sea rockfish, Helicolenus dactylopterus and Pontinus kuhlii, from the Azores. *J. Sea Res.* 83, 202–208. doi: 10.1016/j.seares.2013.05.014

Hilborn, C. R., and Walters, J. (1992). *Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty* (Chicago: Springer Science & Business Media). doi: 10.1086/417864

Hoff, G. R., and Fuiman, L. A. (1993). Morphometry and composition of red drum otoliths: Changes associated with temperature, somatic growth rate, and age. *Comp. Biochem. Physiol. A Physiol.* 106, 209–219. doi: 10.1016/0300-9629(93)90502-U

Hüssy, K., Limburg, K. E., de Pontual, H., Thomas, O. R. B., Cook, P. K., Heimbrand, Y., et al. (2021). Trace element patterns in Otoliths: the role of biomineralization. *Rev. Fisheries Sci. Aquaculture* 29, 445–477. doi: 10.1080/23308249.2020.1760204

Hyslop, E. J. (1980). Stomach contents analysis—a review of methods and their application. *J. Fish Biol.* 17, 411–429. doi: 10.1111/j.1095-8649.1980.tb02775.x

Ingrosso, G., Abbiati, M., Badalamenti, F., Bavestrello, G., Belmonte, G., Cannas, R., et al. (2018). Mediterranean bioconstructions along the Italian coast. *Adv. Mar. Biol.* 79, 61–136. doi: 10.1016/bs.amb.2018.05.001

Institute of Oceanography and Fisheries. (2023). *Database and indicators of the state of the marine environment, mariculture and fisheries.* Available online at: http://baltazar.izor.hr/azopub/bobazi.

Jaramilo, A. M., Tombari, A. D., Benedito Dura, V., Eugeni Rodrigo, M., and Volpedo, A. V. (2014). Otolith eco-morphological patterns of benthic fishes from the coast of Valencia (Spain). *Thalassas* 30, 57–66.

Jardas, I. (1999). Review of long-term changes in trammel bottom set catches, crustacean, cephalopoda and fish communities along the eastern Adriatic (Croatian) coastal area. *Acta Adriat* 40, 67–78.

Jardas, I., and Pallaoro, A. (1992). Age and growth of black scorpionfish, Scorpaena porcus L. 1758 in the Adriatic Sea. *Rapport la Commission Internationale pour Mer Méditerranean* 33, 296.

Jardas, I., Pallaoro, A., Kraljević, M., Dulčić, J., and Cetinić, P. (1998). Long-term changes in biodiversity of the coastal area of the eastern Adriatic: Fish, crustaceam and cephalopoda communities. *Period Biol.* 100, 19–28.

Jawad, L. A., Sabatino, G., Ibáñez, A. L., Andaloro, F., and Battaglia, P. (2018). Morphology and ontogenetic changes in otoliths of the mesopelagic fishes Ceratoscopelus maderensis (Myctophidae), Vinciguerria attenuata and V. poweriae (Phosichthyidae) from the Strait of Messina (Mediterranean Sea). *Acta Zoologica* 99 (2), 126-142. doi: 10.1111/azo.12197

Jobling, M. (1997). "Temperature and growth: modulation of growth rate via temperature," in *Global warning: implication for freshwater and marine fish* (Cambridge, Cambridge: Cambridge University Press, Cambridge), 225–253.

Jobling, M. (2011). Temperature and growth: modulation of growth rate via temperature change. *Global Warming*, 225–254. doi: 10.1017/cbo9780511983375.010

Kendallha, K., Shtewi, H. H., Elsalini, O. A., and Shakman, E. A. (2018). Biological aspects of black scorpionfish, Scorpaena porcus (Linnaeus 1758) in the western coast of Libya. *Libyan J. Sci.* 21, 13–23. doi: 10.55276/ljs.v21iA.138

Kikuchi, E., Cardoso, L. G., Canel, D., Timi, J. T., and Haimovici, M. (2021). Using growth rates and otolith shape to identify the population structure of Umbrina canosai (Sciaenidae) from the Southwestern Atlantic. *Mar. Biol. Res.* 17, 272–285. doi: 10.1080/17451000.2021.1938131

Koca, H. U. (1997). *A research on the determination of some parameters of Scorpion fish (Scorpaena porcus Linnaeus 1758) caught by bottom nets in the area of Sinop from the vievpoint of fishery biology* (Sinop: Science and Engineering, Ondokuz Mayıs University).

Koca, H. U. (2002). A Study on the determination of some parameters of the scorpion fish (Scorpaena porcus Linne. 1758) caught by bottom nets in the area of Sinop in terms of fishery biology. *Turk J. Vet. Anim. Sci.* 26, 65–69.

Kozłowski, J., Czarnołęski, M., and Dańko, M. (2004). Can optimal resource allocation models explain why ectotherms grow larger in cold? *Integr. Comp. Biol.* 44, 480–493. doi: 10.1093/icb/44.6.480

Kraus, R., Grilli, F., Supić, N., Janeković, I., Brailo, M., Cara, M., et al. (2019). Oceanographic characteristics of the Adriatic Sea–support to secondary HAOP spread through natural dispersal. *Mar. pollut. Bull.* 147, 59–85. doi: 10.1016/j.marpolbul.2018.10.062

Kutsyn, D. N., Skuratovskaya, E. N., and Chesnokova, I. I. (2019). Body size, age structure, growth, and maturation of black scorpionfish Scorpaena porcus (Scorpaenidae) from southwestern Crimea (Black Sea). *J. Ichthyol* 59, 864–869. doi: 10.1134/S0032945219060067

Kuzminova, N., Rudneva, I., Salekhova, L., Shevchenko, N., and Oven, L. (2011). State of black scorpionfish (Scorpaena porcus Linnaeus 1758) inhabited coastal area of Sevastopol region (Black sea) in 1998-2008. *Turk J. Fish Aquat Sci.* 11, 101–111. doi: 10.4194/trjfas.2011.0114

Ladich, F., and Schulz-Mirbach, T. (2016). Diversity in fish auditory systems: One of the riddles of sensory biology. *Front. Ecol. Evol.* 4. doi: 10.3389/fevo.2016.00028

La Mesa, M., Scarcella, G., Grati, F., and Fabi, G. (2010). Age and growth of the black scorpionfish, *Scorpaena porcus* (Pisces: Scorpaenidae) from artificial structures and natural reefs in the Adriatic Sea. *Sci. Mar.* 74, 677–685. doi: 10.3989/scimar.2010.74n4677

Landa, J., and Hernández, C. (2020). Age estimation, corroboration and back-calculation of four-spot megrim (Lepidorhombus boscii) on the Porcupine Bank using otoliths. *Estuar. Coast. Shelf Sci.* 243, 106890. doi: 10.1016/j.ecss.2020.106890

Lek, E., Fairclough, D. V., Hall, N. G., Hesp, S. A., and Potter, I. C. (2012). Do the maximum sizes, ages and patterns of growth of three reef-dwelling labrid species at two latitudes differ in a manner conforming to the metabolic theory of ecology? *J. Fish Biol.* 81, 1936–1962. doi: 10.1111/j.1095-8649.2012.03446.x

Libungan, L. A., and Pálsson, S. (2015). ShapeR: An R package to study otolith shape variation among fish populations. *PloS One* 10, 1–12. doi: 10.1371/journal.pone.0121102

Lipizer, M., Partescano, E., Rabitti, A., Giorgetti, A., and Crise, A. (2014). Qualified temperature, salinity and dissolved oxygen climatologies in a changing Adriatic Sea. *Ocean Sci.* 10, 771–797. doi: 10.5194/os-10-771-2014

Lleonart, J., and Maynou, F. (2003). Fish stock assessments in the Mediterranean: State of the art. *Sci. Mar* 67 (S1), 37-49. doi: 10.3989/scimar.2003.67s137

Lombarte, A., and Cruz, A. (2007). Otolith size trends in marine fish communities from different depth strata. *J. Fish Biol.* 71, 53–76. doi: 10.1111/j.1095-8649.2007.01465.x

Lombarte, A., and Lleonart, J. (1993). Otolith size changes related with body growth, habitat depth and temperature. *Environ. Biol. Fishes* 37, 297–306. doi: 10.1007/BF00004637

Lombarte, A., Palmer, M., Matallanas, J., Gómez-Zurita, J., and Morales-Nin, B. (2010). Ecomorphological trends and phylogenetic inertia of otolith sagittae in Nototheniidae. *Environ. Biol. Fishes* 89, 607–618. doi: 10.1007/s10641-010-9673-2

Longhitano, S. G. (2018). Between Scylla and Charybdis (part 2): The sedimentary dynamics of the ancient, Early Pleistocene Messina Strait (central Mediterranean) based on its modern analogue. *Earth Sci. Rev.* 179, 248–286. doi: 10.1016/j.earscirev.2018.01.017

Mahé, K., Goascoz, N., Dufour, J. L., Iglesias, S. P., and Tetard, A. (2014). Black scorpionfish Scorpaena porcus (Scorpaenidae): A first record in the eastern English Channel. *Mar. Biodivers Rec* 7, e6. doi: 10.1017/S1755267214000037

Medinets, S., and Medinets, V. (2010). Results of investigations of atmospheric pollutants fluxes in zmeiny island in western part of the black sea in 2003-2007 years. *J. Environ. Prot. Ecol.* 11, 1030–1036. doi: 10.4194/1303-2712-v12_2_42

Mendonça, V., Flores, A. A. V., Silva, A. C. F., and Vinagre, C. (2019). Do marine fish juveniles use intertidal tide pools as feeding grounds? *Estuar. Coast. Shelf Sci.* 225, 106255. doi: 10.1016/j.ecss.2019.106255

Mille, T., Ernande, B., Pontual, H., Villanueva, C., and Mahé, K. (2016a). Sources of otolith morphology variation at the intra-population level : directional asymmetry and diet marine fishes. *SFI Days* 2016.

Mille, T., Mahé, K., Cachera, M., Villanueva, M. C., De Pontual, H., and Ernande, B. (2016b). Diet is correlated with otolith shape in marine fish. *Mar. Ecol. Prog. Ser.* 555, 167–184. doi: 10.3354/meps11784

Mommsen, T. P. (1998). Growth and metabolism. *Physiol. fishes* 2, 65–97.

Monteiro, L. R., Di Beneditto, A. P. M., Guillermo, L. H., and Rivera, L. A. (2005). Allometric changes and shape differentiation of sagitta otoliths in sciaenid fishes. *Fish Res.* 74, 288–299. doi: 10.1016/j.fishres.2005.03.002

Muniz, A. A., Moura, A., Triay-Portella, R., Moreira, C., Santos, P. T., and Correia, A. T. (2021). Population structure of the chub mackerel (Scomber colias) in the North-east Atlantic inferred from otolith shape and body morphometrics. *Mar. Freshw. Res.* 72, 341–352. doi: 10.1071/MF19389

Nelson, J. S., Grande, T. C., and Wilson, M. V. H. (2016). *Fishes of the World, Fifth Edition.* WILEY. doi: 10.1002/9781119174844

Neves, J., Silva, A. A., Moreno, A., Veríssimo, A., Santos, A. M., and Garrido, S. (2021). Population structure of the European sardine Sardina pilchardus from Atlantic and Mediterranean waters based on otolith shape analysis. *Fish Res.* 243, 106050. doi: 10.1016/j.fishres.2021.106050

Newman, S. J., and Dunk, I. J. (2002). Growth, age validation, mortality, and other population characteristics of the red emperor snapper, Lutjanus sebae (Cuvier 1828),

off the Kimberley coast of north-western Australia. *Estuar. Coast. Shelf Sci* 55, 67–80. doi: 10.1006/ecss.2001.0887

Nolf, D. (1985). "Otolithi piscium," in *Handbook of Paleoichthyology*, vol. 10 . Ed. G. Fischer(Stuttgart, New York: Gustav Fischer Verlag).

Orlić, M., Dadić, V., Grbec, B., Leder, N., Marki, A., Matić, F., et al. (2006). Wintertime buoyancy forcing, changing seawater properties, and two different circulation systems produced in the Adriatic. *J. Geophys Res. Oceans* 111, 1-21. doi: 10.1029/2005JC003271

Oven, L. S., Rudneva, I. I., and Shevchenko, N. F. (2000). Responses of Scorpaena porcus(Scorpaenidae) to anthropogenic impact. *J. Ichthyol* 40, 70–73.

Özgül, A., Lök, A., Tansel Tanrıkul, T., and Alós, J. (2019). Home range and residency of Scorpaena porcus and Scorpaena scrofa in artificial reefs revealed by fine-scale acoustic tracking. *Fish Res.* 210, 22–30. doi: 10.1016/j.fishres.2018.10.008

Pashkov, A. N., Shevchenko, N. F., Oven, L. S., Giragosov, V. E., and Kruglov, M. V. (1999). Distribution, numbers and principal population indexes of Scorpaena porcus under anthropogenic pollution of the Black Sea. *J. Ichthyol* 39, 634–641.

Passalacqua, M., Canta, S., Bono, G., and Beltrano, A. (2005). Scorpaena porcus Nell'area Marina Protetta (Amp) delle isole egadi. *Biol. Mar. Medit* 12, 418–421.

Pavlov, D. A. (2016). Differentiation of three species of the genus Upeneus (Mullidae) based on otolith shape analysis. *J. Ichthyol* 56, 37–51. doi: 10.1134/S0032945216010094

Pavlov, D. A. (2021). Otolith morphology and relationships of several fish species of the suborder Scorpaenoidei. *J. Ichthyol* 61, 33–47. doi: 10.1134/S0032945221010100

Pepin, P. (1991). Effect of temperature and size on development, mortality, and survival rates of the pelagic early life history stages of marine fish. *Can. J. Fisheries Aquat. Sci.* 48, 503–518. doi: 10.1139/f91-065

Perdichizzi, A., D'Iglio, C., Giordano, D., Profeta, A., Ragonese, S., and Rinelli, P. (2022). Comparing life-history traits in two contiguous stocks of the deep-water rose shrimp Parapenaeus longirostris (H. Lucas 1846) (Crustacea: Decapoda) in the southern Tyrrhenian Sea (Central Mediterranean sea). *Fish Res.* 248, 106206. doi: 10.1016/j.fishres.2021.106206

Popper, A. N., and Lu, Z. (2000). Structure-function relationships in fish otolith organs. *Fish Res.* 46, 15–25. doi: 10.1016/S0165-7836(00)00129-6

Popper, A. N., Ramcharitar, J., and Campana, S. E. (2005). Why otoliths? Insights from inner ear physiology and fisheries biology. *Mar. Freshw. Res.* 56, 497–504. doi: 10.1071/MF04267

Popper, A. N., and Schilt, C. R. (2008). Hearing and acoustic behavior: basic and applied considerations. *Fish Bioacoustics* 17–48, 17-48. doi: 10.1007/978-0-387-73029-5_2

Poutiers, J. M. (1987). Fiches fao d'identification des especes pour les besoins de la peche. Mediterranee et mer noire zone de peche 37 révision 1 volume 1 vegetaux et invertebres. *Vertebres* 2, 1290-1300.

Rafrafi-Nouira, S., El Kamel-Moutalibi, O., Boumaïza, M., Reynaud, C., and Capapé, C. (2016). Food and feeding habits of black scorpionfish, Scorpaena porcus (Osteichthyes: Scorpaenidae) from the northern coast of Tunisia (Central Mediterranean). *J. Ichthyol* 56, 107–123. doi: 10.1134/S0032945216010112

Rudneva, I. I., Shevchenko, N. F., Zalevskaya, I. N., and Zherko, N. V. (2005). Biomonitoring of the coastal waters of the Black Sea. *Water Resour.* 32, 215–222. doi: 10.1007/s11268-005-0028-x

Sahin, C., Erbay, M., Kalayci, F., Ceylan, Y., and Yesilcicek, T. (2019). Life-history traits of the Black Scorpionfish (Scorpaena porcus) in southeastern Black Sea. *Turk J. Fish Aquat Sci.* 19, 571–584. doi: 10.4194/1303-2712-v19_7_04

Sanchez-Jerez, P., Gillanders, B. M., and Kingsford, M. J. (2002). Spatial variability of trace elements in fish otoliths: Comparison with dietary items and habitat constituents in seagrass meadows. *J. Fish Biol.* 61, 801–821. doi: 10.1111/j.1095-8649.2002.tb00912.x

Savoca, S., Grifó, G., Panarello, G., Albano, M., Giacobbe, S., Capillo, G., et al. (2020). Modelling prey-predator interactions in Messina beachrock pools. *Ecol. Modell* 434, 1-17. doi: 10.1016/j.ecolmodel.2020.109206

Scarcella, G., Grati, F., Polidori, P., Domenichetti, F., Bolognini, L., and Fabi, G. (2011). Comparison of growth rates estimated by otolith reading of Scorpaena porcus and Scorpaena notata caught on artificial and natural reefs of the northern Adriatic sea. *Brazilian Journal of Oceanography* 59, 33–42. doi: 10.1590/S1679-87592011000500006

Schulz-Mirbach, T., Ladich, F., Plath, M., and Heß, M. (2019). Enigmatic ear stones: what we know about the functional role and evolution of fish otoliths. *Biol. Rev.* 94, 457–482. doi: 10.1111/brv.12463

Schulz-Mirbach, T., Ladich, F., Riesch, R., and Plath, M. (2010). Otolith morphology and hearing abilities in cave- and surface-dwelling ecotypes of the Atlantic molly, Poecilia mexicana (Teleostei: Poeciliidae). *Hear Res.* 267, 137–148. doi: 10.1016/j.heares.2010.04.001

Siblot-Boutéflika, D. (1976). *Contribution à l'etude des Scorpaeni- dae de la région Alger* (Marseille: Univ. Aix-Marseille II).

Silvestri, R., Voliani, A., and Zucchi, A. (2002). Nota sulla biologia di Scorpaena porcus Linneo 1758 nel Mar Ligure meridionale. *Biol. Marina* 9, 813–817.

Spanò, N., and De Domenico, E. (2017). Biodiversity in central Mediterranean sea. *Mediterr. Identities - Environment Society Culture* 6, 129–148. doi: 10.5772/intechopen.68942

Stagličić, N., Matić-Skoko, S., Pallaoro, A., Grgičević, R., Kraljević, M., Tutman, P., et al. (2011). Long-term trends in the structure of eastern Adriatic littoral fish assemblages: Consequences for fisheries management. *Estuar. Coast. Shelf Sci.* 94, 263–271. doi: 10.1016/j.ecss.2011.07.005

Swain, D. P., and Foote, C. J. (1999). Stocks and chameleons: The use of phenotypic variation in stock identification. *Fish Res.* 43, 113–128. doi: 10.1016/S0165-7836(99)00069-7

Thomas, O. R. B., and Swearer, S. E. (2019). Otolith biochemistry—a review. *Rev. Fisheries Sci. Aquaculture* 27, 458–489. doi: 10.1080/23308249.2019.1627285

Tiralongo, F. (2024). Unraveling the story of the black Scorpionfish (Scorpaena porcus linnaeus 1758): exploring local ecological knowledge and the exploitative history of a marine species. *Fishes* 9, 1-11. doi: 10.3390/fishes9010031

Turan, C., Gunduz, I., Gurlek, M., Yaglioglu, D., and Erguden, D. (2009). Systematics of Scorpaeniformes species in the Mediterranean Sea inferred from mitochondrial 16S rDNA sequence and morphological data. *Folia biologica (Kraków)* 57, 219–226. doi: 10.3409/fb57_1-2.219-226

Tuset, V. M., Farré, M., Otero-Ferrer, J. L., Vilar, A., Morales-Nin, B., and Lombarte, A. (2016a). Testing otolith morphology for measuring marine fish biodiversity. *Mar. Freshw. Res.* 67, 1037–1048. doi: 10.1071/MF15052

Tuset, V. M., Imondi, R., Aguado, G., Otero-Ferrer, J. L., Santschi, L., Lombarte, A., et al. (2015). Otolith patterns of rockfishes from the northeastern pacific. *J. Morphol* 276, 458–469. doi: 10.1002/jmor.20353

Tuset, V. M., Lombarte, A., and Assis, C. A. (2008). Otolith atlas for the western Mediterranean, north and central eastern Atlantic. *Sci. Mar.* 72, 7–198. doi: 10.3989/scimar.2008.72s1

Tuset, V. M., Lombarte, A., González, J. A., Pertusa, J. F., and Lorente, M. J. (2003a). Comparative morphology of the sagittal otolith in Serranus spp. *J. Fish Biol.* 63, 1491–1504. doi: 10.1111/j.1095-8649.2003.00262.x

Tuset, V. M., Lozano, I. J., Gonźlez, J. A., Pertusa, J. F., and García-Díaz, M. M. (2003b). Shape indices to identify regional differences in otolith morphology of comber, Serranus cabrilla (L. 1758). *J. Appl. Ichthyology* 19, 88–93. doi: 10.1046/j.1439-0426.2003.00344.x

Tuset, V. M., Otero-Ferrer, J. L., Gómez-Zurita, J., Venerus, L. A., Stransky, C., Imondi, R., et al. (2016b). Otolith shape lends support to the sensory drive hypothesis in rockfishes. *J. Evol. Biol.* 29, 2083–2097. doi: 10.1111/jeb.12932

Unsal, N., and Oral, M. (1994). An investigation on the growth and reproduction characteristics of the black Scorpionfish in the Sea of Marmara. *Turkish J. Zoology* 20, 303–308.

Velasco, E. M., Jiménez-Tenorio, N., Del Arbol, J., Bruzón, M. A., Baro, J., and Sobrino, I. (2011). Age, growth and reproduction of the axillary seabream, Pagellus acarne, in the Atlantic and Mediterranean waters off southern Spain. *J. Mar. Biol. Assoc. United Kingdom* 91, 1243–1253. doi: 10.1017/S0025315410000305

Via, S., Gomulkiewicz, R., De Jong, G., Scheiner, S. M., Schlichting, C. D., and Van Tienderen, P. H. (1995). Adaptive phenotypic plasticity: consensus and controversy. *Trends Ecol. Evol.* 10, 212–217. doi: 10.1016/S0169-5347(00)89061-8

Vignon, M., and Morat, F. (2010). Environmental and genetic determinant of otolith shape revealed by a non-indigenous tropical fish. *Mar. Ecol. Prog. Ser.* 411, 231–241. doi: 10.3354/meps08651

Vilibić, I., and Orlić, M. (2001). Least-squares tracer analysis of water masses in the South Adriatic, (1967-1990). *Deep Sea Res. 1 Oceanogr Res. Pap* 48, 2297–2330. doi: 10.1016/S0967-0637(01)00014-0

Volpedo, A. V., Tombari, A. D., and Echeverría, D. D. (2008). Eco-morphological patterns of the sagitta of Antarctic fish. *Polar Biol.* 31, 635–640. doi: 10.1007/s00300-007-0400-1

Wheeler, A., Whitehead, P. J. P., Bauchot, M.-L., Hureau, J.-C., Nielsen, J., and Tortonese, E. (1986). Fishes of the north-eastern Atlantic and the Mediterranean. *Copeia 1986* 1, 266. doi: 10.2307/1444931

YediEr, S., and Bostanci, D. (2021). Morphologic and morphometric comparisons of Sagittal otoliths of five Scorpaena species in the Sea of Marmara, Mediterranean Sea, Aegean Sea and Black Sea. *Cah Biol. Mar.* 62, 357–369. doi: 10.21411/CBM.A.6B8915B2

Zhuang, L., Ye, Z., and Zhang, C. (2015a). Application of otolith shape analysis to species separation in Sebastes spp. from the Bohai Sea and the Yellow Sea, northwest Pacific. *Environ. Biol. Fishes* 98, 547–558. doi: 10.1007/s10641-014-0286-z

Zhuang, L., Ye, Z., Zhang, C., Ye, Z., Li, Z., Wan, R., et al. (2015b). Stock discrimination of two insular populations of diplodus annularis (Actinopterygii: Perciformes: Sparidae) along the coast of Tunisia by analysis of otolith shape. *J. Fish Biol.* 46, 1–14. doi: 10.3750/AIP2015.45.4.04

Zorica, B., Čikeš Keč, V., Pešić, A., Gvozdenović, S., Kolitari, J., and Mandić, M. (2019). Spatiotemporal distribution of anchovy early life stages in the eastern part of the Adriatic Sea in relation to some oceanographic features. *J. Mar. Biol. Assoc. United Kingdom* 99, 1205–1211. doi: 10.1017/S0025315418001145