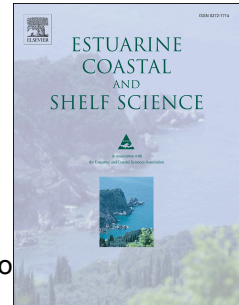


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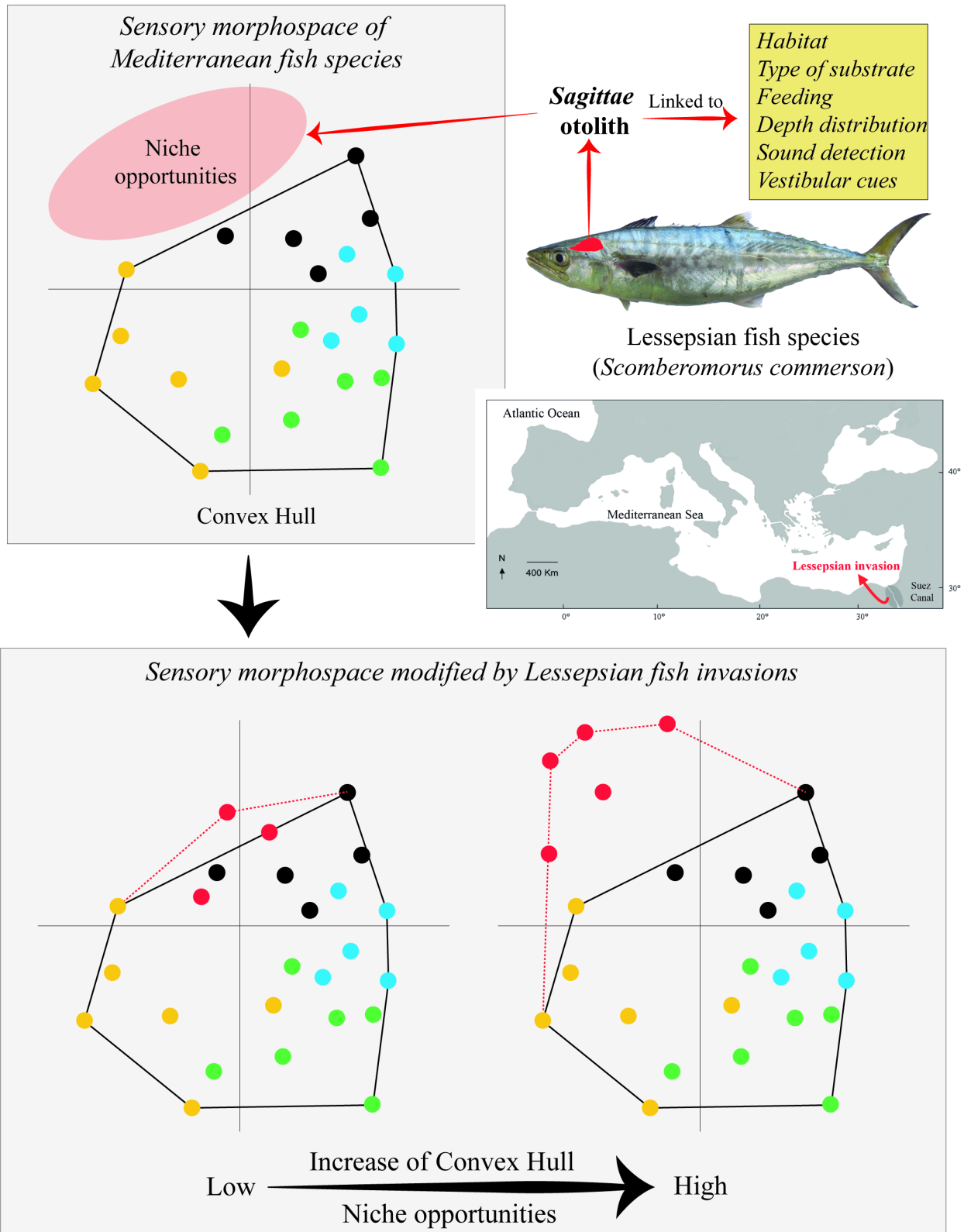
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Otolith morphological divergences of successful Lessepsian fishes on the Mediterranean coastal waters

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Abstract

Here we used a method of morphological niche analysis, previously shown to be an effective predictor of invasion success, to investigate morphological relationships of *sagittae* otoliths of Lessepsian (Red sea species entering the Mediterranean through the Suez Canal) fishes within the morphospace of the corresponding receiving taxonomic groups. Overall, *sagittae* of 13 Lessepsian species and 49 closely related native fishes/taxa, distributed in 9 different families or subfamilies were considered, for a total of 305 analysed otoliths. Based on wavelet functions of 512 Cartesian coordinates, we quantified the degree of morphological disparity produced by the introduction of these species in the hosting community. Lessepsian otoliths tended to be added outside or at the margins of the receiving morphospace, being morphologically divergent from the ones of native species. Considering that many ecological traits of fishes (especially feeding) are mirrored in the shape of otoliths, our findings agree with the idea that these successful invaders may count on novel sensory strategies to compete for available resources and to thrive in newly colonized habitats. Nevertheless, different measurements of morphological disparity did not show any variation before and after invasion and with the specific richness and further investigation is needed to understand to what extent these differentiated sensorial adaptations are linked to novel opportunities along the niche axes, such as in relation to feeding, predatory and anti-predatory behaviour and exploitation of the temporal niche.

Keywords

Otolith shape; Nonindigenous and native species; Convex hull; Morphological disparity

1. Introduction

Understanding biological invasions through predictive factors is an ideal achievement to prioritize management efforts in the preservation of biological native diversity (Mack et al., 2000; Manchester and Bullock, 2000; Sih et al., 2010; Azzurro et al., 2014; Giakoumi et al., 2016). Diverse ecological hypotheses with a broad theoretical framework (e.g., trophic position, niche replacement, biotic resistance, colonization pressure; see more detail in Ricciardi et al., 2013) have been set out in the attempt to distinguishing invaders with major impacts from unsuccessful introductions. Many of these theories, such as the phylogenetic distinctiveness—which argues that the highest impact invaders mainly belong to genera absent in the native community (Ricciardi and Atkinson, 2004)—and the limiting similarity hypotheses—which predicts that invasive species are less likely to establish in communities of species holding similar functional traits (Elton, 1958; MacArthur and Levins, 1967)—are intrinsically connected and explain the importance of functional traits differentiation in successful invasions (Cotê et al., 2013; Elleouet et al., 2014; Thomsen et al., 2014; Fanelli et al., 2015; Nagelkerke et al., 2018). Moreover, a link between morphological distinctness and success probabilities of exotic fishes was recently highlighted by Azzurro et al. (2014). These authors demonstrated that the success probabilities of a newly introduced fish are significantly higher when the species locates outside of the morphological space provided by the hosting community (the native convex hull). Following this methodology, Smith et al. (2016) presented a model for predicting the success of tropical vagrant fishes reaching the coast of Australia due to climate-induced range shifts.

Novel traits may also concern novel sensory capabilities (Falk et al., 2015), such as the auditory and vestibular senses of marine fishes, which are linked to the anatomy and morphology of inner ear and its otolithic organs (*sacculus*, *utricle* and *lagena*). Inside of these organs are located the otoliths (*sagitta*, *lapillus* and *asteriscus*, respectively) (Platt and Popper, 1981; Assis 2003, 2005), acellular concretions of calcium carbonate (ca. 97%) developing over a protein matrix and different elements and isotopes (Carlström, 1963; Blacker, 1969; Degens et al., 1969; Kerr and Campana, 2014), which are in close association with the sensory epithelium or macula (Platt and Popper, 1981; Lombarte and Fortuño, 1992; Schulz-Mirbach et al., 2018). In particular, the *sagittae* otolith (hereafter referred as *sagittae*) shape is an intrinsic feature of each fish species acquired during eco-evolutionary processes, and its morphology has been often linked to the ecological, taxonomical, phylogenetic and functional characteristics of species (e.g., Gaemers, 1984; Tuset et al., 2003, 2016a,b;

Lombarte et al., 2010; Vignon and Morat, 2010). In this context, Tuset et al. (2012) performed a first description the otolith morphological features of 22 Lessepsian species (18 families and 8 orders) and Automated Taxon Identification (ATI) of otolith contour in comparison to species from the Mediterranean Sea using the AFORO database (<http://www.cmima.csic.es/aforo/>) (Lombarte et al., 2006). Although the number of otoliths collected to date was low, the main conclusion was the high morphological variability in the specificity of Lessepsian *sagittae* and may therefore help to thrive in the newly colonized habitat considering its sensory capability as a ‘trait’ not shared with native species.

Here we analyzed the *sagittae* contour in both native and exotic coastal fishes in the Mediterranean Sea, the latter being represented by invasive species of Lessepsian (Red Sea) origin (Por, 1978), which have established successful populations in the Mediterranean Sea. Under the above-mentioned premises, our expectation is that position of successful species will be located at the margins or outside the native otolith morphospace. The advantage of the contour analysis in relation to other morphological options such as morphometry (e.g., area, perimeter, length), shape indices (e.g., circularity, rectangularity, ellipticity) and geometric morphometry (e.g., landmarks and semilandmarks) is the higher level of specific separation (Parisi-Baradad et al., 2010; Sadighzadeh et al., 2014). Moreover, we decided to use wavelets for the contour analysis *versus* Fourier series, because this multiscale analysis allow to identify single morphological points located on the x-axis along the contour (Parisi-Baradad et al., 2005; Piera et al., 2005), whereas Fourier analysis only give a global approximation of outline variability (Reig-Bolaños et al., 2010).

We therefore employed the contour of fish otoliths to test if successful Lessepsian species were of ‘highly diversified nature’ (*sensu* Darwin, 1989; Pearson et al. 2012) compared to closely related indigenous ones in order to avoid the effect of phyletic distance. Our specific aims were to: (i) determine the position a new species when is added within the receiving morphospace; (ii) quantify the degree of morphological disparity produced by the introduction of a new species and; (iii) test a possible relation between the richness of hosting community and the degree of morphological disparity before and after invasion.

2. Material and methods

2.1. Database

The contour of 58 otoliths belonging to 13 Lessepsian fishes considered as abundant (Azzurro et al., 2014) was analyzed: *Atherinomorus forskali* (Family Atherinidae),

Callionymus filamentosus (Family Callionymidae), *Alepes djedaba*, *Decapterus russelli* (Subfamily Caranginae), *Etrumeus golanii*, *Herklotsichthys punctatus* (Family Clupeidae), *Oxyurichthys papuensis* (Family Gobiidae), *Parupeneus forsskali*, *Upeneus moluccensis*, *Upeneus pori* (Family Mullidae), *Scomberomorus commerson* (Subfamily Scombrinae). We also considered *Liza carinata* (Family Mugilidae) and *Pterois miles* (Family Scorpaenidae), which have currently developed abundant populations in the eastern sectors of the basin (Golani et al., 2017) (Fig. 1). Images were obtained from the AFORO database (<http://aforo.cmima.csic.es/>). Hence, the present study analyzed ca. 50% of the most abundant invader species. The morphology of their otoliths was compared with the ones of 49 native fishes belonging to same taxonomical groups, for a total of 247 native otoliths (Table 1).

2.2. Otolith contour analysis

The analysis of otolith shape was based on a mathematical descriptor named wavelet transformed (WT), which is related to the one-dimensional decomposition of the contour. This procedure is based on expanding the contour into a family of functions obtained as the dilations and translations of a unique function known as a mother wavelet (Mallat, 1991). The advantage of this procedure is the possibility to detect singularities of different sizes favoring the identification of specific zones among species (see details in Parisi-Baradad et al., 2005, 2010). In particular, we considered the wavelet function at 5th scale because several studies have demonstrated that this scale describes better the specific characteristics of otolith contour (Sadighzadeh et al., 2012; Tuset et al., 2015, 2016; Lombarte et al., 2018). A total of 512 equidistant Cartesian coordinates for each otolith were extracted using the *rostrum* (see otolith terminology in Tuset et al., 2008) as origin. Wavelets were obtained online using option AFORO website (http://isis.cmima.csic.es/aforo/upload_img_wav_en.jsp).

For each taxonomic group studied, a principal component analysis (PCA) based on the variance–covariance matrix was performed to reduce the dimensionality of the 512 data obtained for each individual without loss of information. Significant eigenvectors were identified plotting the percentage of total variation explained by the eigenvectors vs. the proportion of variance expected under the ‘broken-stick model’ (Gauldie and Crampton, 2002). Since interspecific differences might be attributed to allometry, linear correlations were tested between otolith length and the principal components (Stransky and MacLellan, 2005). The effect of otolith length was removed using the residuals of the common within-group slopes of the linear regressions of each component on otolith length, building a new PCA matrix.

2.3. Statistical analysis

Significant differences in the otolith morphospace occupation by the arrival of Lessepsian species was tested using nonparametric multivariate analysis of variance (NPMANOVA) (Anderson, 2001) on the PC-scores based on Euclidean distance (9,999 permutations). The first two principal axes of each fish group were used to display the morphospace of Mediterranean and Lessepsian species. In the case of fish groups with more than 1 Lessepsian species (Family Clupeidae and Mullidae, and Subfamily Caranginae), changes in the morphospace were computed sequentially according to the date of first record (Azzurro et al., 2014).

Three different metrics of morphological disparity were estimated from PC-scores: the average dissimilarity distance (*PWD*) among points within morphospace and the sum of variances (*SV*) have the desirable property of being relatively insensitive to variation in sample size (Foote, 1997; Ciampaglio et al., 2001; Goatley et al., 2010). Alternatively, the convex hull volume (*CHV*) is a computational geometry implementation (Cornwell et al., 2006) resulting from niche hypothesis regarding the limit to the ecological similarity of coexisting species (MacArthur and Levins, 1967). To demonstrate the effect of fish invasion in these measurements, the averages of log-transformed data were compared using a paired t-test before and after invasion. Finally, relationships were established between the specific richness (*SD*) and the measurements.

The morphospace and tests were obtained from PAST (PAleontological STatistics, v.3.26) (Hammer et al., 2001), whereas the morphological measurements were obtained with the package *dispRity* and (Guillerme, 2018) in R (R Development Core Team, 2016). The significance level was set at 0.05 for all statistical tests used.

3. Results

The reconstruction of otolith shape with wavelets provided different PC components for each fish group. In most cases, they represented more than 70% of total variance (Appendix A, Table S1), although it attained lesser values (55.08% for Atherinidae and 63.95% for Mullidae) for Families where the native species were only composed by one genus. In general, otoliths of Lessepsian species were allocated outside of the native convex hull as resulting of highly differentiated morphologies with respect to native otoliths (Fig. 2), except for *A. djedaba* (SF. Caranginae) and *S. commerson* (SF. Scombrinae). Invader species did not induce always significant changes in the whole morphospace of receiving communities,

although 61.5% showed significant differences (NPMANOVA, Table 2). However, *PWD* (t -test = -1.344, p = 0.216) and *SV* (t -test = -1.353, p = 0.213) were not significantly altered by the addition of a new invader species, whereas *CHV* (t -test = -3.203, p = 0.013) showed significant changes (Table 3).

The log-*SD* did not show correlation with any metric variable before (r = 0.515, p = 0.156 for log-*PWD*; r = 0.516, p = 0.155 for log-*SV*; r = -0.339, p = 0.373 for log-*CHV*) and after fish invasion (r = 0.600, p = 0.087; r = 0.603, p = 0.086; r = -0.243, p = 0.523; respectively).

4. Discussion

Our findings emphasize the peculiar otolith morphologies of Lessepsian fishes (Tuset et al., 2012) confirming theoretical expectations as the increase of the convex hull due to localization at the boundaries of the receiving morphospace of the most fish invaders. A large spatial morphological (and hence ecological) distribution within the native community should indicate either the use of different resources or the adoption of novel strategies that provide a different (e.g. Por, 1978; Lundberg and Golani, 1995) and often more efficient (Fanelli et al., 2015) use of resources. Under the niche-based hypothesis—which considers the resource partitioning as the main mechanism to enable coexistence of species (Mookerji et al., 2004; Silvertown, 2004)—, novel ‘niche opportunities’ have been invoked to explain the success of these immigrants (e.g. Oliverio and Taviani, 2003; Azzurro et al., 2014). In this sense, it is highlighted that the less distinct otoliths (see AFORO website <http://aforo.cmima.csic.es/>; Lombarte et al., 2006) belong to low-success species and to families such as Serranidae, Sparidae or Labridae (Por, 1978, 2010; Galil, 2009; Golani et al., 2013; Azzurro et al., 2014), which are well represented in the native assemblages of the Mediterranean coasts (Quignard and Tomasini, 2000).

According to the ‘sensory drive hypothesis’ (Endler, 1992), sensory traits may vary greatly depending on environment where they originate (Sivasundar and Palumbi, 2010; Tuset et al., 2012, 2016a, 2018; Jacobs et al., 2017). It is thus predictable that Lessepsian species, evolved in the Indo-Pacific oceans, may bring sensory novelties favouring potential competitive interactions on native analogues. It is known that Lessepsian species display similar functional traits than native species (Elleouet et al., 2014), but they exploit the more energetic resources (Fanelli et al., 2015). As a matter of fact, novel feeding strategies (e.g., behaviorally) have been described for some invasive fishes such as example in *Pterois volitans* (Morris and Akins, 2009), and are likely to occur in others. The invasive *E. golanii* (Family Clupeidae) has the ability to feed throughout the water column from the bottom to the

surface layer (Osman et al., 2013), a behavior that to the best of our knowledge is unreported by native Mediterranean clupeids. These life-style differences are reflected in the otolith shape narrowing the *excisura ostii*, which are usually wider in shallow pelagic species with respect to deeper ones (Volpedo and Echevarría, 2003; Tuset et al., 2008). In other groups of fishes, otoliths with a larger *rostrum* and higher degree of ellipticity are interpreted as functional adaptations for better vestibular cues affecting the fish's swimming ability, rapidity of action, range of detectable accelerations, and acceleration resolving power (Schulz-Mirbach et al., 2018). These peculiar traits, depicted in *C. filamentosus*, *D. ruselli* and *A. djedaba*, could be associated to substantial differences in the predatory behavior, with respect to native analogues. By contrary, wider otoliths entail short heads (Kéver et al., 2014; Schwarzhans, 2014; Tuset et al., 2018) and likely lesser fish's swimming capability. This noticeable morphological variability may influence in the relation between *sulcus acusticus* and otolith areas (*S:O* ratio), which is linked to sensory capabilities of fish species (Gauldie, 1988; Lombarte, 1992). In fact, otoliths of *O. petersi* have larger ratio morphological traits different to other native species of Family Gobiidae (Lombarte et al., 2018).

The morphological disparity is often used as a surrogate measure of biological diversity in the study of biological communities (Neustupa et al., 2009; Farré et al., 2013). This diversity is historically generated by ecological and evolutionary factors varying across scales of space and time producing variability among different geographical regions (Ricklefs, 2004; Witman et al., 2004; García-Navas et al., 2018). However, these morphological gaps between regions are being increasingly homogenized by human assisted translocation of species to global scale (McKinney and Lockwood, 1999), and the morpho-functional differentiation of nonindigenous species can be the key to gain a competitive advantage and develop invasive populations (Smith and Knapp, 2001; Azzurro et al., 2014; Nagelkerke et al., 2018). This hypothesis is also confirmed by the present study, which illustrates the high morphological distinctness of Lessepsian otoliths, compared to the native background, even if these species are taxonomically close. The introduction of these new species to the receiving assemblage may generate an increase in morphological disparity, which will depend on the distribution of native species in the multidimensional space and on the proximity of the new shapes to them. In our study, only the convex hull provides information for explaining this success *versus* morphological disparity. In fact, taxonomic diversity and morphological disparity are commonly decoupled (Ricklefs and Miles, 1994; Hopkins, 2013; Price et al., 2015), as we have confirmed here.

5. Conclusion

Our findings provide a further evidence of a possible concurrent variation of otoliths and fish body shape, a link that has been only seldom considered in the scientific literature (Kéver et al., 2014; Schwarzhans, 2014; Tuset et al., 2016a, 2018). Considering that the morphology of fish otoliths can mirror sensory adaptations (Gauldie and Crampton, 2002; Volpedo and Echeverria, 2003; Popper et al., 2005; Lombarte and Cruz, 2007; Tuset et al., 2016b), these traits are worth to be better considered in ecological research and further studies can help to better understand to what extent these differentiated sensory adaptations are linked to novel opportunities along the niche axes.

Declarations of interest

None.

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Appendix A. Supplementary material

Supplementary table (Table S1) can be found online.

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Legends

Fig. 1. Sagittae of Lessepsian fish species studied in the present study. a) *Atherinomorus forskali* (Family Atherinidae); b) *Callionymus filamentosus* (Family Callionymidae); c) *Alepes djedaba*; d) *Decapterus russelli* (Subfamily Caranginae); e) *Etrumeus golanii*; f) *Herklotsichthys punctatus* (Family Clupeidae); g) *Oxyurichthys papuensis* (Family Gobiidae); h) *Liza carinata* (Family Mugilidae); i) *Parupeneus forsskali*; j) *Upeneus moluccensis*; k) *Upeneus pori* (Family Mullidae); l) *Scomberomorus commerson* (Subfamily Scombrinae); m) *Pterois miles* (Family Scorpaenidae). Scale bar = 1 mm.

Fig. 2. Sensory morphological position of native and Lessepsian fish species by taxonomic group. Black lines indicate the convex hull of native species and dashed red lines illustrate the increase of convex hull due to non-indigenous species invasion. All species are represented by different symbols and one representative otolith image is also provided.

Table 1

Species and taxonomic groups (Families or Subfamilies) of abundant Lessepsian fish invaders and native species from the Mediterranean Sea with otolith and total fish size range and location. In bold, Lessepsian species, including year of first presence. NA, data not available.

Group	Species	n	Otolith length (mm)	Fish length (mm)	Region
F. Atherinidae	<i>Atherina boyeri</i>	6	2.32-2.67	69- 76	Tirrenian Sea
	<i>Atherina hepsetus</i>	6	3.66-4.21	121- 132	NW Mediterranean
	<i>Atherina presbyter</i>	3	2.58-4.76	NA	Alboran Sea
	<i>Atherinomorus forskali</i> 1902	6	3.50-4.31	130- 151	NW Mediterranean
F. Callionymidae	<i>Callionymus lyra</i>	6	3.12-4.51	190- 285	Alboran Sea
	<i>Callionymus maculatus</i>	6	1.85-2.33	75- 120	NW Mediterranean
	<i>Callionymus pusillus</i>	2	0.90-0.94	65- 73	NW Mediterranean
	<i>Callionymus risso</i>	6	1.05-1.67	47- 70	NW Mediterranean
	<i>Synchiropus phaeton</i>	6	2.90-3.84	125- 205	NW Mediterranean
	<i>Callionymus filamentosus</i> 1953 or before	4	2.06-3.31	113- 170	Eastern Mediterranean
SF. Caranginae	<i>Caranx crysos</i>	3	3.99-7.53	160- 438	Alboran Sea
	<i>Caranx rhonchus</i>	6	5.84-9.61	230- 385	NW Mediterranean
	<i>Pseudocaranx dentex</i>	3	5.98-9.94	320- 572	Alboran Sea
	<i>Trachurus mediterraneus</i>	6	5.42-9.67	160- 360	NW Mediterranean
	<i>Trachurus picturatus</i>	6	4.16-7.26	137- 255	NW Mediterranean
	<i>Trachurus trachurus</i>	6	3.37-11.43	95- 363	NW Mediterranean
	<i>Alepes djedaba</i> 1927 or before	6	3.32-4.93	133- 211	Eastern Mediterranean
	<i>Decapterus russelli</i> 2005	4	3.01-6.71	114- 121	Eastern Mediterranean
F. Clupeidae	<i>Sardina pilchardus</i>	6	1.88-3.40	105- 185	NW Mediterranean
	<i>Sardinella aurita</i>	6	1.78-4.01	83- 231	NW Mediterranean
	<i>Sardinella maderensis</i>	6	2.21-4.61	94- 207	NW Mediterranean
	<i>Sprattus sprattus</i>	6	0.97-1.57	65- 122	NW Mediterranean
	<i>Herklotsichthys punctatus</i> 1943	4	2.43-9.36	90- 105	Eastern Mediterranean
	<i>Etrumeus golanii</i> 1961	6	2.61-3.45	120- 203	Eastern Mediterranean
	<i>Buenia affinis</i>	6	0.88-1.06	20- 24	Adriatic Sea
F. Gobiidae	<i>Delentosteus quadrimaculatus</i>	6	2.82-3.74	70- 86	NW Mediterranean
	<i>Lesuerigobius friesii</i>	6	2.35-2.92	52- 75	NW Mediterranean
	<i>Lesuerigobius sueri</i>	6	1.89-2.48	45- 55	NW Mediterranean
	<i>Gobius niger</i>	6	4.23-5.71	95- 151	NW Mediterranean
	<i>Pomatoschistus marmoratus</i>	6	1.13-1.41	33- 42	Adriatic Sea
	<i>Odondebuenia balearica</i>	6	1.06-1.47	27- 34	Adriatic Sea
	<i>Oxyurichthys papuensis</i> 1982	5	4.46-5.81	135- 194	Eastern Mediterranean
	<i>Chelon auratus</i>	6	6.95-10.75	225- 520	NW Mediterranean
F. Mugilidae	<i>Chelon labrosus</i>	6	4.88-10.40	145- 460	NW Mediterranean
	<i>Chelon ramada</i>	6	6.11-11.82	120- 441	NW Mediterranean
	<i>Chelon saliens</i>	5	4.88-7.54	140- 321	Tirrenian Sea
	<i>Mugil dephalus</i>	6	6.44-12.17	208- 490	NW Mediterranean
	<i>Liza carinata</i> 1924	5	5.46-6.92	NA	NW Mediterranean
	<i>Mullus barbatus</i>	6	1.85-3.35	108- 200	NW Mediterranean
F. Mullidae	<i>Mullus surmuletus</i>	6	3.26-4.51	145- 260	NW Mediterranean
	<i>Upeneus pori</i> 1942	5	2.43-2.66	105- 115	Eastern Mediterranean
	<i>Upeneus moluccensis</i> 1946 or before	6	3.15-3.98	116- 178	Eastern Mediterranean
	<i>Parupeneus forsskali</i> 2000	2	3.14-3.51	220- 230	Eastern Mediterranean
	<i>Acanthocybium solandri</i>	1	7.92	1204	Alboran Sea
	<i>Auxis rochei</i>	2	3.42-4.04	406- 480	NW Mediterranean
SF. Scombrinae	<i>Auxis thazard</i>	1	5.00	630	Alboran Sea
	<i>Euthynnus alletteratus</i>	2	3.25-4.13	348- 440	NW Mediterranean
	<i>Katsuwonus pelamis</i>	2	5.07-5.85	500- 610	Alboran Sea
	<i>Sarda sarda</i>	6	4.97-8.70	360- 650	NW Mediterranean
	<i>Scomber colias</i>	6	4.50-7.23	203- 405	NW Mediterranean
	<i>Scomber scombrus</i>	6	3.55-5.94	210- 380	NW Mediterranean
	<i>Thunnus alalunga</i>	3	8.87-13.37	730-1237*	NW Mediterranean
	<i>Thunnus thynnus</i>	5	4.29-13.11	238-1100*	NW Mediterranean
	<i>Scomberomorus commerson</i> 1935 or before	2	5.46-6.79	298- 430	Eastern Mediterranean
	<i>Pontinus kuhlii</i>	3	10.24-15.0	220- 375	Alboran Sea
F. Scorpaenidae	<i>Scorpaena elongata</i>	6	7.18-11.08	135- 234	NW Mediterranean
	<i>Scorpaena loppei</i>	6	4.32-6.55	78- 119	NW Mediterranean
	<i>Scorpaena maderensis</i>	2	2.50-4.61	60- 105	Alboran Sea

Scorpaena notata

Journal Pre-proof

6 6.73-10.52

120- 200

NW Mediterranean

Scorpaena porcus

6 6.46-9.89

194- 311

NW Mediterranean

Scorpaena scrofa

6 9.26-15.05

200- 360

NW Mediterranean

***Pterois miles* 1991**

3 4.38-5.49

240- 345

Eastern Mediterranean

* fish length is expressed as fork length

Table 2

Results of significance testing (NPMANOVA) by phylogenetic groups (Families or Subfamilies) on the morphospace occupation of abundant Lessepsian fish invaders using the PC components of otolith contour analysis. The invasion year is provided for each Lessepsian species. In bold, the significant differences.

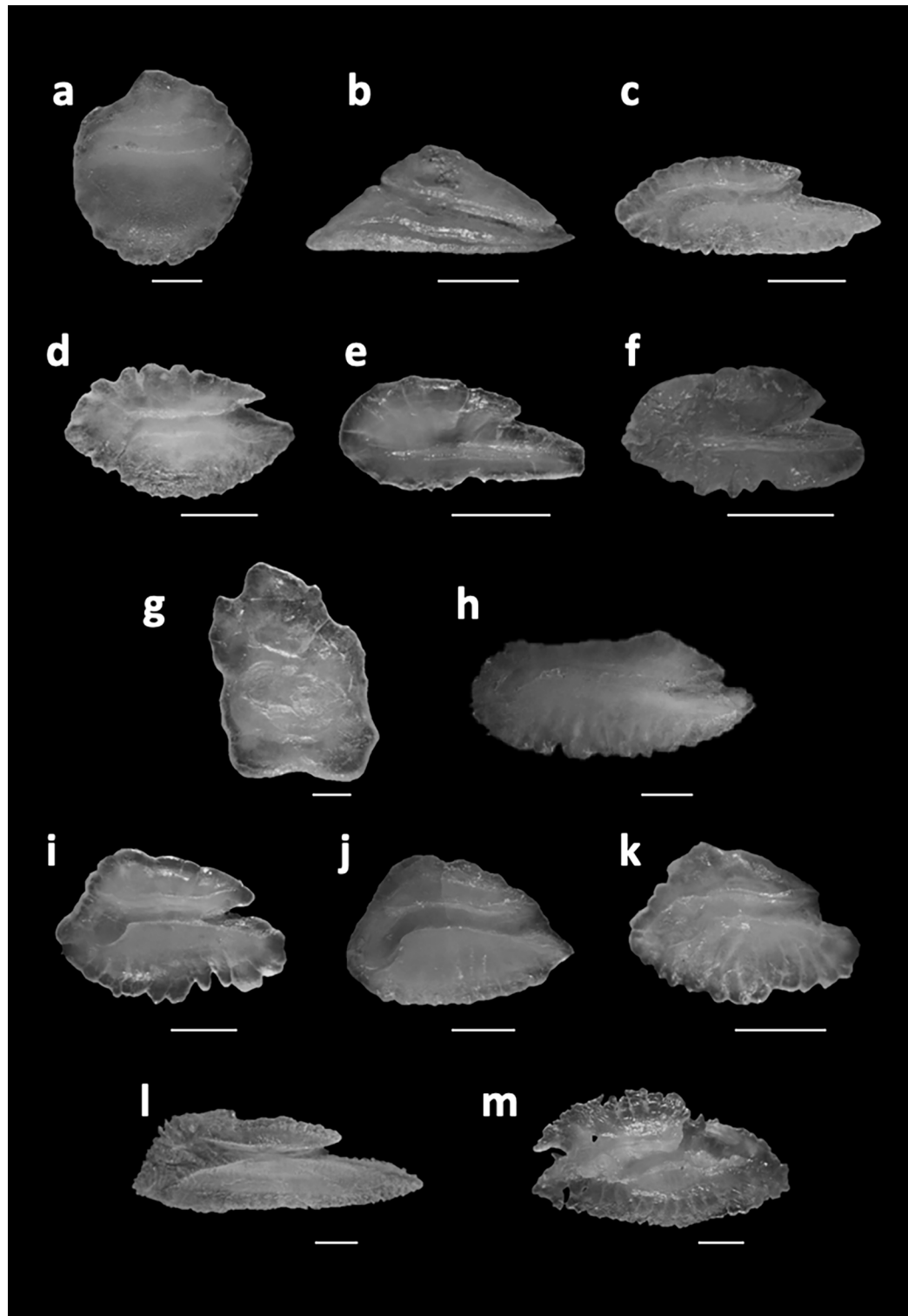
Groups	Lessepsian species	Pseudo-F	df ₁	df ₂	P
F. Atherinidae	<i>Atherinomorus forskali</i> 1902	48.749	1	19	0.001
F. Callionymidae	<i>Callionymus filamentosus</i> 1953 or before	2.812	1	28	0.054
SF. Caranginae	<i>Alepes djedaba</i> 1927 or before	2.167	1	35	0.099
	<i>Decapterus russelli</i> 2005	3.422	1	38	0.032
F. Clupeidae	<i>Herklotsichthys punctatus</i> 1943	2.985	1	26	0.073
	<i>Etrumeus golanii</i> 1961	5.234	1	32	0.022
F. Gobiidae	<i>Oxyurichthys papuensis</i> 1982	2.161	1	45	0.077
F. Mugilidae	<i>Liza carinata</i> 1924	2.163	1	32	0.032
F. Mullidae	<i>Upeneus pori</i> 1942	4.430	1	15	0.005
	<i>Upeneus moluccensis</i> 1946 or before	7.888	1	19	<0.001
	<i>Parupeneus forsskali</i> 2000	4.715	1	23	0.005
SF. Scombrinae	<i>Scomberomorus commerson</i> 1935 or before	0.306	1	34	0.887
F. Scorpaenidae	<i>Pterois miles</i> 1991	5.697	1	36	0.006

Table 3

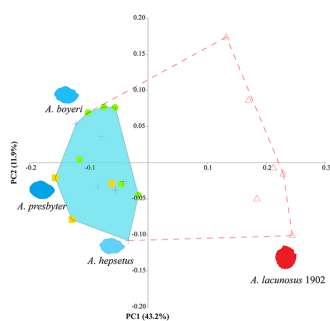
Changes in the morphological disparity by phylogentic groups (Families or Subfamilies) after the invasion of abundant Lessepsian fishes. The morphological data are given from the otolith contour analysis. *CHV*, convex hull volume; *n*, number of otoliths analyzed; *PWD*, average pairwise distance; *SV*, sum variances. In bold, Lessepsian species and invasion year.

Groups	Species	n	Morphological disparity		
			<i>PWD</i>	<i>SV</i>	<i>CHV</i>
F. Atherinidae	<i>Atherina boyeri</i>	6			
	<i>Atherina hepsetus</i>	6			
	<i>Atherina presbyter</i>	3			
	Natives		0.089	0.005	0.017
	<i>Atherinomorus forskali</i> 1902	6	0.180	0.022	0.076
F. Callionymidae	<i>Callionymus lyra</i>	6			
	<i>Callionymus maculatus</i>	6			
	<i>Callionymus pusillus</i>	2			
	<i>Callionymus risso</i>	6			
	<i>Synchiropus phaeton</i>	6			
	Natives		0.232	0.033	0.016
	<i>Callionymus filamentosus</i> 1953 or before	4	0.249	0.038	0.023
SF. Caranginae	<i>Caranx crysos</i>	3			
	<i>Caranx rhonchus</i>	6			
	<i>Pseudocaranx dentex</i>	3			
	<i>Trachurus mediterraneus</i>	6			
	<i>Trachurus picturatus</i>	6			
	<i>Trachurus trachurus</i>	6			
	Natives		0.214	0.030	0.017
	<i>Alepes djedaba</i> 1927 or before	6	0.214	0.029	0.020
	<i>Decapterus russelli</i> 2005	4	0.211	0.029	0.201
F. Clupeidae	<i>Sardina pilchardus</i>	6			
	<i>Sardinella aurita</i>	6			
	<i>Sardinella maderensis</i>	6			
	<i>Sprattus sprattus</i>	6			
	Natives		0.318	0.066	0.200
	<i>Herklotsichthys punctatus</i> 1943	4	0.301	0.059	0.213
	<i>Etrumeus golanii</i> 1961	6	0.306	0.061	0.238
F. Gobiidae	<i>Buenia affinis</i>	6			
	<i>Crystallogobius linearis</i>	6			
	<i>Deltentosteus quadrimaculatus</i>	6			
	<i>Lesueurigobius friesii</i>	6			
	<i>Lesueurigobius suerii</i>	6			
	<i>Gobius niger</i>	6			
	<i>Odondebuenia balearica</i>	6			
	Natives		0.307	0.055	1.476*10 ⁻⁵
	<i>Oxyurichthys papuensis</i> 1982	5	0.315	0.057	2.748*10 ⁻⁵

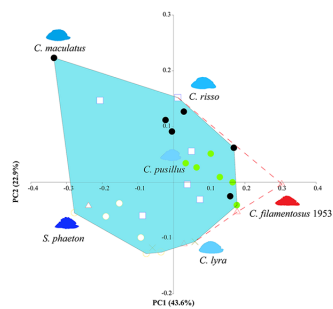
Journal Pre-proof					
F. Mugilidae	<i>Chelon aurata</i>	6			
	<i>Chelon ramada</i>	6			
	<i>Chelon saliens</i>	5			
	<i>Chelon labrosus</i>	6			
	<i>Mugil cephalus</i>	6			
	Natives		0.306	0.050	4.050×10^{-8}
	<i>Liza carinata</i> 1924	5	0.298	0.047	5.481×10^{-8}
F. Mullidae	<i>Mullus barbatus</i>	6			
	<i>Mullus surmuletus</i>	6			
	Natives		0.229	0.031	0.007
	<i>Upeneus pori</i> 1942	5	0.231	0.032	0.012
	<i>Upeneus moluccensis</i> 1946 or before	6	0.232	0.032	0.016
	<i>Parupeneus forsskali</i> 2000	2	0.257	0.040	0.026
SF. Scombrinae	<i>Acanthocybium solandri</i>	1			
	<i>Auxis rochei</i>	2			
	<i>Auxis thazard</i>	1			
	<i>Euthynnus alletteratus</i>	2			
	<i>Katsuwonus pelamis</i>	2			
	<i>Sarda sarda</i>	6			
	<i>Scomber colias</i>	6			
	<i>Scomber scombrus</i>	6			
	<i>Thunnus alalunga</i>	3			
	<i>Thunnus thynnus</i>	5			
	Natives		0.499	0.146	4.377×10^{-4}
	<i>Scomberomorus commerson</i> 1935 or befo	2	0.486	0.139	4.413×10^{-4}
F. Scorpaenidae	<i>Pontinus kuhlii</i>	3			
	<i>Scorpaena elongata</i>	6			
	<i>Scorpaena loppei</i>	6			
	<i>Scorpaena maderensis</i>	2			
	<i>Scorpaena notata</i>	6			
	<i>Scorpaena porcus</i>	6			
	<i>Scorpaena scrofa</i>	6			
	Natives		0.178	0.019	4.894×10^{-4}
	<i>Pterois miles</i> 1991	3	0.203	0.026	0.002



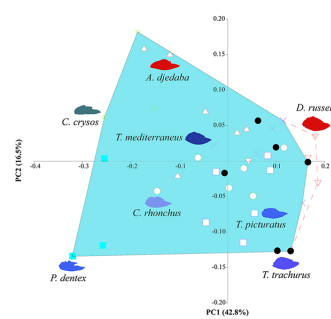
F. Atherinidae



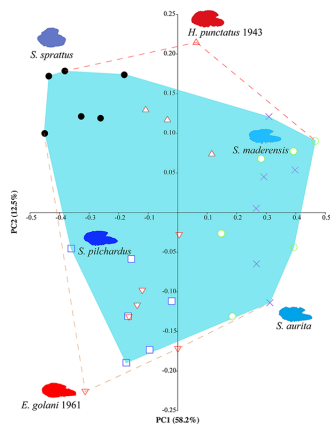
F. Callionymidae



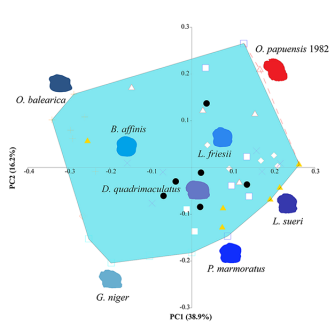
SF. Caranginae



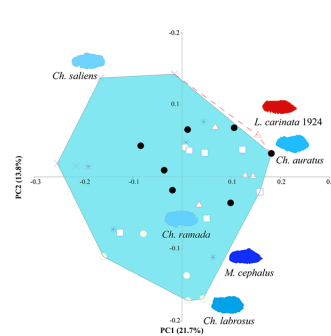
F. Cupleidae



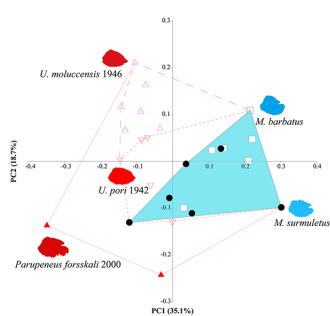
F. Gobiidae



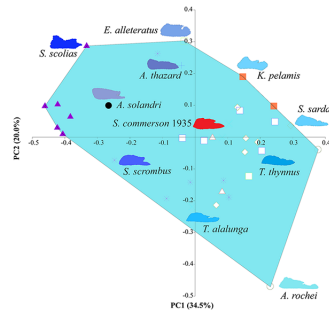
F. Mugilidae



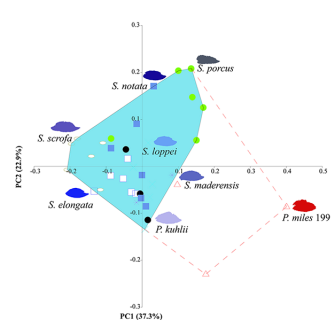
F. Mullidae



SF. Scombrinae



F. Scorpaenidae



Highlights

- Otoliths of successful Lessepsian fishes are morphologically divergent from the ones of closely related native species.
- Morphological disparity after invasion is uncorrelated to specific richness of native community.
- Novel sensory strategies might contribute to explain the success of Lessepsian fishes.

Declaration of interests

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

☐ The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: