



Phenotypic response of a geographically expanding species, *Scomber colias*: Clues in the fish otolith shape

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ABSTRACT

During the last decades, there has been a growing interest in the Atlantic chub mackerel, *Scomber colias*, owing to its northward expansion across the East Atlantic Ocean. This trend has been observed from regions of higher abundance off northwest Africa to the waters of the Atlantic Iberian and the Mediterranean Sea. Changes in abundance and spatial distribution of Atlantic chub mackerel have been previously studied and various theoretical models have been proposed to elucidate the changes in its abundance and biomass. However, within this fishing context, only a limited number of studies have attempted to understand how this species has responded at both the individual and population levels to the changing environmental conditions. The phenotypic variability of 1660 individuals of *S. colias* collected from the Canary Islands, Madeira, the Cantabrian Sea and the Central-Northern Mediterranean Sea was examined, with a specific focus on otolith shape. We identified six morphotypes classified into two groups and associated to the four analyzed regions. Despite of the occurrence of shared phenotypes in varying proportions among the different fishing grounds, this classification might be explained by the adaptation of certain morphotypes to specific environmental conditions and the migratory behavior of this species. The morphotypes M1-M5 were more abundant in the warmer waters of Madeira-Canary Islands region and M6 in the colder waters of Ligurian-Cantabrian. It is plausible that the former set may represent resident contingents, while morphotypes M2-M3 and M4 are likely to exhibit migratory behavior. Therefore, we suggest a complex metapopulation structure, where different contingents coexist.

1. Introduction

Ecosystems worldwide are undergoing environmental transformations due to human activities and climate change. Consequently, novel combinations of physical conditions such as shifts in temperature regimes, precipitation patterns and water chemistry are triggering responses among organisms, populations and ecosystems. These responses manifest through a variety of biological processes (or adaptations),

including acclimatization, evolution, range shifts, and ecological reorganization, occurring across different scales of organization (Webster et al., 2017, 2023). Phenotypic plasticity plays a crucial role in facilitating many of these adaptations, allowing a single genotype to generate multiple phenotypes in response to environmental stimuli (Scheiner, 1993; Schlichting and Pigliucci, 1998; West-Eberhard, 2003) or to other external stressors, such as fishing pressure (Rouyer et al., 2014; Hollins et al., 2018; Morrongiello et al., 2019). The resulting phenotypes can be

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classified as adaptive (positive or negative), non-adaptive (or maladaptive) or neutral concerning an individual's fitness (Ghalambor et al., 2007; Chevin et al., 2010; Storz and Scott, 2021). In particular, adaptive plasticity could enable organisms with a wider tolerance for environmental fluctuations (Pigliucci, 2001; Peck et al., 2013; Schickele et al., 2021), potentially influencing migration and dispersion processes (Bloom et al., 2018). Moreover, differences in life history traits and/or the identification of phenotypic clusters (such as body morphometrics, otolith contour, etc.) are widely used to delineate stocks. These have become essential tools for fishery scientists, assessors, and managers (Begg et al., 1999; Cadrin et al., 2020). However, a gap exists in assessments actively incorporating stock identification requirements. Most stock assessment methods tend to model the dynamics of nearby populations while assuming homogeneity in life history traits (Begg et al., 1999; FAO, 2020). This issue is particularly pronounced in pelagic fish species, where genetic studies reveal low differentiation among stocks or populations, which is commonly attributed to the high gene flow facilitated by the marine environment's extensive dispersal capabilities (Nesbø et al., 2000).

The Atlantic chub mackerel (*Scomber colias*, Gmelin, 1789) is a medium-sized migratory coastal pelagic fish with distribution spanning warm and temperate waters on both sides of the Atlantic Ocean (Castro and Santana, 2000). In East Atlantic waters, its range extends from the Bay of Biscay to South Africa, including Azores, Madeira, the Canary Islands and Saint Helena Islands, and further extending into the Mediterranean and Black Sea (Collette and Nauen, 1983; Whitehead et al., 1984; Collette et al., 2023). Typically inhabiting depths up to 300 m, this species holds a key role in the trophic web, acting as a crucial link between primary producers and top predators, since it feeds mainly on zooplankton and some small pelagic fish, making it an essential component in the diet of larger pelagic fish such as tuna, swordfish and sharks, as well as marine mammals (mainly dolphins and seals) (Machado et al., 2022). As others small and medium pelagic fish (SMPF) give their short generation times and tight coupling to lower trophic levels, these populations exhibit substantial boom-and-bust dynamics, both in productivity and distribution, closely linked to climate variability (Alheit et al., 2014; Garrido et al., 2017). Thus, fluctuations in their populations can exert profound impacts on the overall dynamics of ecosystem structure, giving rise to significant ecological and socioeconomic consequences (Peck et al., 2021). While responses to climate variability vary among SMPF species and stocks, the intrapopulation phenotypic variability observed in species with a relatively short life-spans enhances their resilient to environmental fluctuations. This variability can even result in the development of different intrapopulation life history strategies, allowing them to occupy different "spatio-temporal niches" (Peck et al., 2013; Ma et al., 2022). For example, different energy strategies have been found among autumn and winter spawners of Atlantic herring in the North Sea, in contrast to Norwegian spring-spawning herrings (Jennings and Beverton, 1991; McQuinn, 1997; Winters and Wheeler, 1996) and among closely related groups of European sardines (*Sardina pilchardus*) and anchovies (*Engraulis encrasicolus*) in the Northwest Mediterranean Sea (Albo-Puigserver et al., 2021; Lloret-Lloret et al., 2022). Yet, the intricate interplay between the biology of SMPF, habitat structure, and how these factors collectively shape the complexity of their population demography and responses to fisheries and climate remains not well understood (Otero and Hidalgo, 2023).

Despite the wide distribution of Atlantic chub mackerel, 90% of the catches in the northeast Atlantic proceed from northwest African waters, making it a fishery resource crucial for food security in the riparian countries (FAO, 2020). In the last decades, there has been a northwards expansion of the species in the East Atlantic distribution, evidenced by the increased catches in Iberian Atlantic waters, where it has become a target species for the purse seine fisheries (Martins et al., 2013; Punzón et al., 2016; ICES, 2020, 2021). An inverse relationship with European sardine abundance has been demonstrated in Portuguese waters, where

Atlantic chub mackerel competes for food and spawning sites (Martins et al., 2013; Garrido et al., 2015). This expansion has been associated to an increase in sea temperature (Costoya et al., 2015) attributed to climate change (Tasker, 2008; Reid and Valdés, 2011; Vélez-Belchí et al., 2017). Although the Atlantic chub mackerel holds significance in terms of landings and economic value at both regional and subregional levels, it is noteworthy that the regular assessment of this species in ICES and Mediterranean waters is not included in any established European assessment framework (ICES, 2021). Evidence of the need to establish the basis for future assessments of the species in the North-eastern Atlantic waters is the initiation of ICES WKCOLIAS in 2020, an international forum that serves as a platform for sharing the available knowledge of the species in the area, including African and European institutions (ICES, 2020, 2021). Although there is a wealth of information on the life history traits of the Atlantic chub mackerel in its southernmost distribution, the species has also been extensively studied in light of its historical fishing relevance in northern waters. This includes research conducted in both Iberian Atlantic and Mediterranean waters (ICES, 2021) where numerous studies have delved into different life history traits of the species. Regarding their population structure, no discernible genetic patterns have been identified in the eastern geographical distribution of this species (ICES, 2021). The annual assessment of the population in Northwest African waters, carried out under the framework of the Fishery Committee for the Eastern Central Atlantic (CECAF), assumes a metapopulation, with the exception of the fisheries around the Canary Islands (FAO, 2020). In this context, other approaches such as morphometrics, otoliths, and parasites have been applied (ICES, 2021), providing different results. However, we wonder if these studies make sense for a species experiencing a distribution expansion, or whether we could take advantage of it to investigate the impact of climate change on an expanding exploited species. Indeed, the descriptive analyses of the available data gathered during the last ICES WKCOLIAS (ICES, 2021) concluded that latitudinal patterns of different traits seem to occur in Atlantic chub mackerel distributed in East Atlantic waters, with an inflection point in the Strait of Gibraltar. Despite the exclusion of African data, Domínguez-Petit et al. (2022) analyzed in-depth this hypothesis and found clear latitudinal patterns for several reproductive aspects following the Bergmann's rule (Hattab et al., 2021). Particularly, exceptions were observed in the southernmost samples studied, represented by the *S. colias* from the Canary Islands (located in NW African waters) and, in some cases, for the ones from the southern coast of Portugal and the Gulf of Cadiz (SW Spain). Likewise, numerous studies are paying attention to the environmental drivers leading changes on the abundance and/or geographical expansion of the species (e.g., Binet, 1997; Martins et al., 2013; Ebango Ngando et al., 2020; Derhy et al., 2022), which has become an urgent issue to face the global warming.

Recent studies into otolith contour shape analysis in other medium pelagic fish, such as *Trachurus picturatus*, have revealed the coexistence of similar phenotypes in different proportions across different fishing grounds, implying the potential existence of a metapopulation connecting distinct regional populations (Tuset et al., 2019; Vasconcelos et al., 2021). As the Atlantic chub mackerel has shown extensive gene flow, resulting in the establishment of a large panmictic unit in the northeastern Atlantic Ocean and Mediterranean Sea (Scoles et al., 1998; Zardoya et al., 2004), our initial hypothesis postulates the common presence of similar morphotypes across its spatial distribution in the Northeastern Atlantic and the Mediterranean Sea. The main objectives of the present study were as follows: i) to examine the intrapopulation phenotypic variation of the otolith contour using wavelet functions developed by the AFORO team; ii) to assess the accuracy of classification between stocks based on the average phenotype of each region; and iii) to analyze the otolith zones involved in the discrimination of stocks and their relationship with environmental and genetic factors.

2. Material & methods

2.1. Database collections

Between 2016 and 2022, a total of 1660 Atlantic chub mackerels were collected from four fishing grounds in the eastern Atlantic: 718 individuals from the Canary Islands (FAO area 34.1.2), 264 from Madeira (FAO area 34.1.2), 435 from the Cantabrian Sea (FAO area 27.8. c), and 243 from the Ligurian Sea in the Central-northern Mediterranean waters (FAO area 37.1.3) (Fig. 1). These collections were conducted as part of national fishery monitoring programs within the EU Data Collection Framework. Each individual was measured for total length (TL, 0.1 cm) and their otoliths were extracted, cleaned, and storage in labeled vials for subsequent morphological analysis. To remove the effect of size variations, we restricted the size range to between 21.3 and 37.5 cm TL, with the minimum value corresponding to the size of the smallest mature individual found in the Cantabria Sea, while the maximum value corresponds to the largest size observed in the Canary Islands region (Table 1).

Monthly mean Sea Surface Temperature (SST, °C) values from January 2016 to December 2022 were acquired from the IGOSS-IRI database (Reynolds, 2002) for the geographical areas corresponding to the sample collection sites, as well as for a northern area off the coast of West France (Fig. S1).

2.2. Otolith shape analysis

The left otoliths were positioned with the inner side (*sulcus acusticus*) facing upward and the *rostrum* oriented to the right. Digitalization was carried out against a black background using a digital camera coupled to a stereomicroscope. The shape contour was analyzed using wavelet function, enabling the identification of individual morphological points along the x-axis of the contour (Parisi-Baradad et al., 2005; Lombarte et al., 2006). Due to presence of a long triangular *collicullum ostii* between *rostrum* and *antirostrum* (Tuset et al., 2008), this point was selected as initial reference point. A total of 512 equidistant Cartesian coordinates (points) on each orthogonal projection of the otolith were extracted and analyzed using the wavelet transformed (WLT; see Parisi-Baradad et al., 2005). Among the nine levels obtained from the wavelet function, the 4th level was chosen as the optimal choice for identifying individual variability within populations (Vasconcelos et al., 2021).

2.3. Statistical analysis

To reduce the number of points without losing information, a

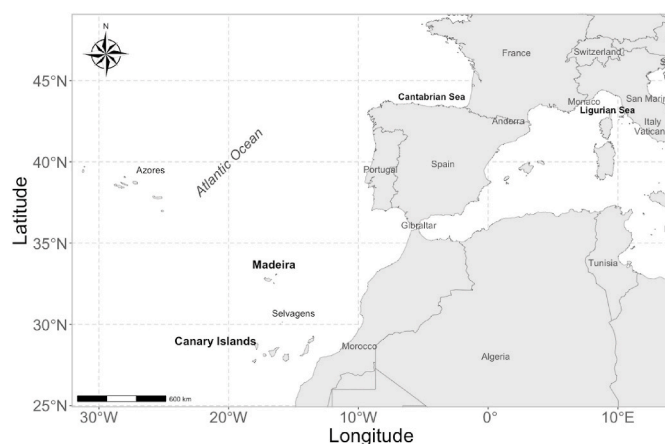


Fig. 1. Geographical areas where *Scomber colias* was sampled in the northeastern Atlantic Ocean and the Mediterranean Sea.

Table 1

Summary of total lengths (cm) of *Scomber colias* collected from the northeastern Atlantic Ocean and the Mediterranean Sea. n, number of individuals; sd, standard deviation; min, minimum; max, maximum.

Origen	Region	n	mean \pm sd	min-max
Mediterranean Sea	Ligurian Sea	264	26.4 \pm 3.93	21.5–38.0
Atlantic Ocean	Cantabrian Sea	435	30.8 \pm 3.80	21.3–38.4
	Madeira	264	26.9 \pm 3.55	21.5–36.7
	Canary Islands	718	25.7 \pm 2.85	21.3–37.5

principal component analysis (PCA) based on the variance–covariance matrix was performed (Sadighzadeh et al., 2012, 2014; Tuset et al., 2015, 2016; Vasconcelos et al., 2021). The percentage of the total explained variation by eigenvectors was plotted against the proportion of variance expected under the “broken stick model” to identify significant eigenvectors (Frontier, 1976; Gauldie and Crampton, 2002). To examine intraspecific differences potentially attributed to allometry, Pearson’s correlations were tested between fish length and principal components. To account for the effect of fish length, residuals based on the common within-group slopes obtained from the linear regressions for each component on fish length were used. These residuals were then used to build a new PCA matrix (Stransky and MacLellan, 2005; Zhuang et al., 2015).

The identification of phenotypes (also named “morphotypes” or “M”, onwards) was conducted using several clustering algorithms, including k-means, pam, clara, som, sota and hierarchical, with the *cValid* R package (Brock et al., 2008) in R environment (R Core Team, 2022). However, only the agglomerative Ward’s hierarchical method employing Manhattan distance yielded a clustering with discernible morphological meaning. Given the observed similarity in the frequency tendencies among regions for morphotypes (see results), our analysis focused exclusively on examining phenotypic variation between regions through permutational multivariate analysis of variance (PERMANOVA, Anderson, 2001), employing 9999 permutations with the Manhattan distance metric. Subsequently, Bonferroni correction was applied for pairwise multiple comparisons using Pillai’s trace. A non-parametric Kruskal-Wallis test was applied to compare the average phenotype of the first component of PCA among regions, using a Wilcoxon rank test for *post hoc* comparisons (O’Dea et al., 2019; Vasconcelos et al., 2021).

Artificial neural network (ANN) was selected for the comparison of otolith shape among regions (El Habouz et al., 2016; Vasconcelos et al., 2021). This classifier operates on a network architecture, with the neuron as its fundamental unit. The network comprises three neuron layers: input layers (comprising morphological variables), hidden layers (with nodules from $i = 1 \dots n$), and an output layer (representing regions). Using a multi-layer perceptron (MLP) architecture and a back-propagation gradient algorithm, we calibrated the ANN (El Habouz et al., 2016; Ciaburro and Venkateswaran, 2017) with the package *caret* (Kuhn, 2008) in R. The whole otolith sample was randomly split into a training dataset (75% of observations) and a validation dataset (25% of observations). The split ensured the preservation of class ratios for the development of the model. The optimal hyperparameters (hidden units) were defined during preliminary tuning (Fig. S2). Following Smoliński et al. (2020) predictor variables (PCA new matrix) underwent scaling and centering in a preprocessing stage. Additionally, a fourfold cross-validation resampling method with 100 repetitions of the entire process was conducted using a ‘*repeatedcv*’ method for training control. To address imbalances in the dataset, we applied a Synthetic Minority Oversampling Technique (SMOTE) using the package *DMwR* (Torgo, 2010) in R. All analysis were performed in R (R Core Team, 2022).

3. Results

3.1. Unveiling and profiling morphotypes

The otoliths of Atlantic chub mackerel exhibited a noticeable variability in shapes across all studied regions (Fig. 2). The position, size (length and height) and orientation of *colliculum ostii* noticeably influenced on the morphology of the *rostrum* and *antirostrum*, resulting in variations in their sizes. Moreover, varying degrees of convexity, concavity and irregularities were observed along the dorsal, posterior and ventral margins. The observed diversity contributed to an expansive PCA-morphospace (PC1 vs PC2, Fig. 3) (see Table S1 for considered PCA components and their variance), and the use of an extensive dataset further favored a high spatial density. These factors influenced the feasibility of the methods to discern between phenotypes, limiting the initial identification to only two morphotypes when using the several clustering algorithms mentioned prior. We opted for a hierarchical clustering approach and identified six morphotypes, which were classified into two primary groups (Fig. 4a): Group-A (comprising M1-M5-M3) and Group-B (M2-M4-M6). This classification was based on the development of the *antirostrum* (larger in Group-A), the ventral pattern of the posterior margin (dorsally more pronounced and ventrally more rounded in Group-A) (Fig. 4b), and the height in the middle of otolith (lesser for the Group-A) (Fig. 4b). Within morphospace (Fig. 3), morphotypes M1 and M5 (negative values) and M6 (positive values) were distributed in the extremes of the PC1 axis (17.3% of variance explained). The morphotype M2 presented a notable concavity, either with or without step, in the middle, whereas M3 showed the less developed *antirostrum* of Group-A morphotypes. The PC2 axis (6.1%) mainly differentiated between morphotype M4 (negative values) and M5 (positive values), which displayed a greater concavity along the ventral margin and a longer *rostrum* (Fig. 4).

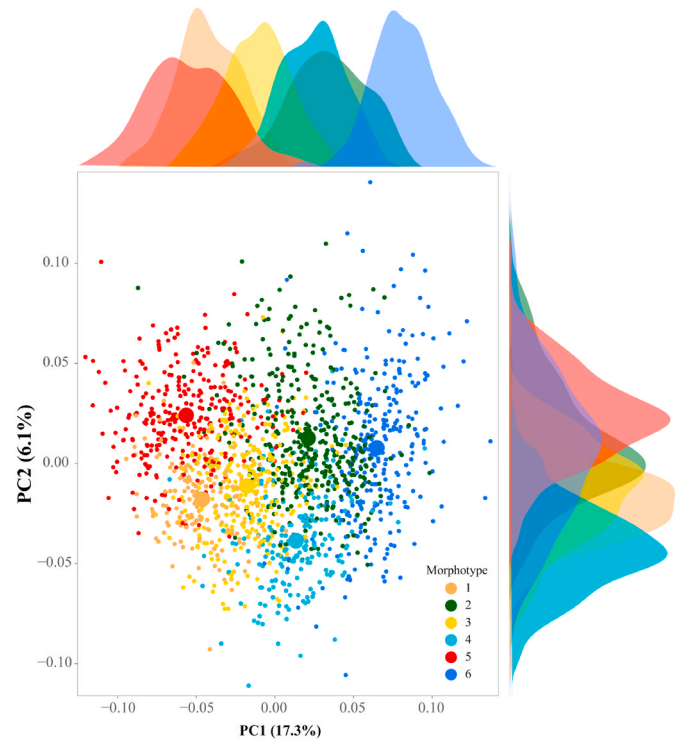


Fig. 3. Scatterplot of the first and second axes of the PCA and marginal density distribution plots for the four morphotypes identified in *Scomber colias* collected from the northeastern Atlantic Ocean and the Mediterranean Sea. Colored circles indicate the centroid of each morphotype. (non-print figure color). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

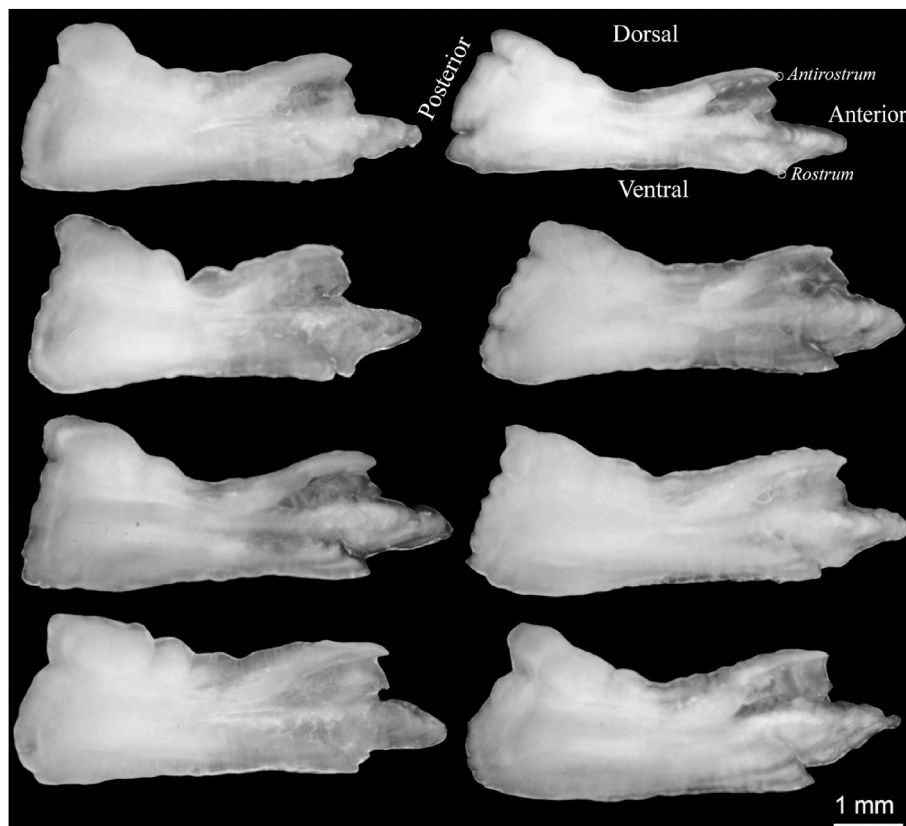


Fig. 2. Mesial surface view of *sagittae* otoliths from *Scomber colias* collected from the northeastern Atlantic Ocean and the Mediterranean Sea.

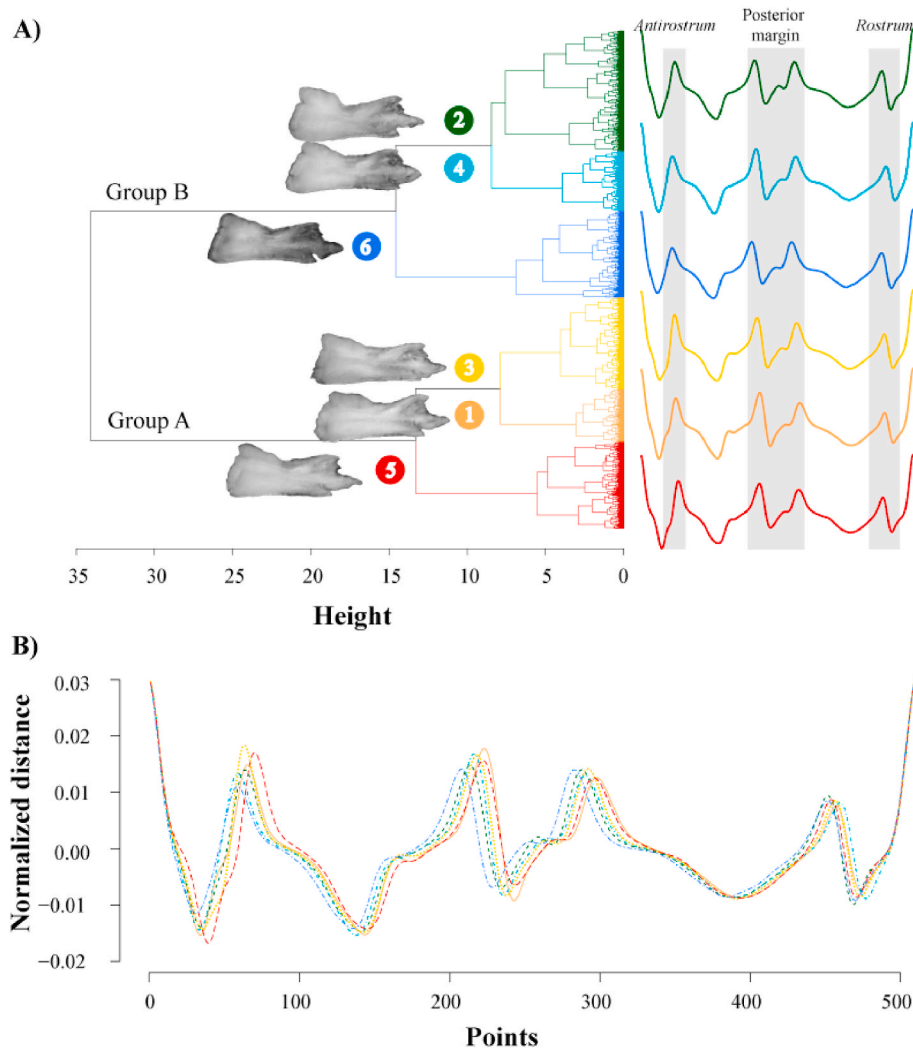


Fig. 4. (A) Dendrogram illustrating the outcomes of a hierarchical cluster analysis (Ward's method) based on Manhattan distance as similarity index to identify morphotypes, along with the average decomposition of otolith contour using the 4th wavelet for each morphotype; (B) average decomposition of otolith contour using the 4th wavelet for all morphotypes. Grey color highlights the sections more relevant for discriminating between morphotypes. (non-print figure color). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

3.2. Morphological homogeneity among stocks

In general, the relative phenotypic frequency of morphotypes exhibited a consistent pattern across all examined regions (Fig. 5). However, morphotypes M1 and M5 were more frequent in warm waters, specifically in Madeira and the Canary Islands, whereas M6 was more predominant in colder waters of the Ligurian Sea and the Cantabria Sea (see Sea Surface Temperatures in Fig. S1). Additionally, although morphotype M2 showed higher frequencies across all regions (>21%), it was notably more abundant in the Ligurian Sea, where it reached 34.6%.

The PERMANOVA analysis unveiled significant phenotypic differences in otolith shape between regions ($F = 15.86$, $p < 0.001$; pairwise-test, $p = 0.006$ for all cases). Additionally, the average value of PC1 exhibited significant variations across regions (Kruskal-Wallis test, $\chi^2 = 128$, $df = 3$, $p < 0.001$) (Fig. 6). Subsequent *post hoc* testing revealed similarities in the otolith shape between Madeira and the Canary Islands ($p = 0.131$), as well as between the Ligurian Sea and the Cantabria Sea ($p = 0.240$); although notable differences were observed between them ($p < 0.001$). Upon application of the neural classification model (ANN), the accuracy of classifying regional populations only reached 47.8%, with a Cohen's kappa (κ) value of 0.288. This indicates an efficiency in the classification that was 29% better than chance alone (Table 2). The

accuracy ranged between 40 and 50%, except for samples from the Ligurian Sea, which acquired a 62.7% accuracy rate (Table 2). Overall, the misidentification of otoliths exhibited a discernible geographical pattern, in which otoliths from the Canary Islands and Madeira showed greater similarity, as did otoliths from Madeira and those from the Cantabria Sea. In contrast, otoliths from the Ligurian Sea exhibited a distinct pattern (Table 2). Finally, the principal components PC3 (with a stronger correlation linked to *rostrum* size), PC1 (practically related to the entire signal), P11 (associated with morphological shifts in the dorsal margin variability) and PC19 (connected with the length of *colliculum ostii*) significantly contributed to the maximum discrimination observed between regions (Fig. 7; see Table S2 for importance of PC components).

4. Discussion

This study presents the first approach to explore the otolith phenotypic variability of Atlantic chub mackerel across regions spanning from the North and Central Eastern Atlantic Ocean and the Mediterranean Sea. Our findings unveiled the presence of six morphotypes, although the high morphological variability in this species posed challenges in phenotypic identification. As a result, there was a notable degree of

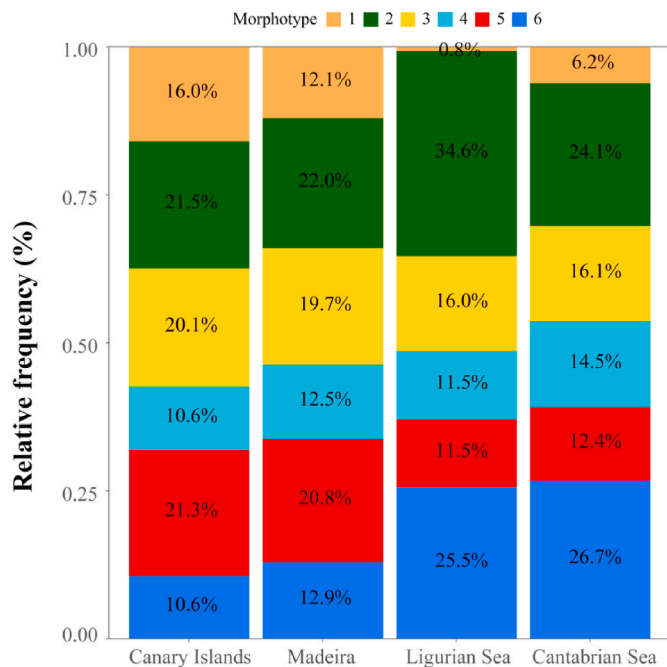


Fig. 5. Relative frequencies of morphotypes found in *Scomber colias* collected from the northeastern Atlantic Ocean and the Mediterranean Sea. (non-print figure color). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

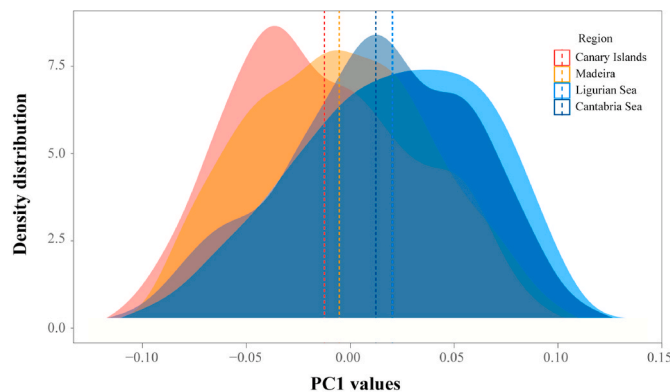


Fig. 6. Density distributions of the PC1 representing the overall phenotype of *Scomber colias* collected from the northeastern Atlantic Ocean and the Mediterranean Sea. The lines show the average values of each region. (non-print figure color). (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

Table 2

Confusion matrix and accuracy achieved by the Multilayer Perceptron (MLP) classifier using wavelets to define the otolith contour in *Scomber colias* specimens collected from the northeastern Atlantic Ocean and the Mediterranean Sea. CI, Canary Islands; CS, Cantabrian Sea; M, Madeira, LS, Ligurian Sea. The highest regional classification is highlighted in black.

Prediction	References				Performance		
	CI	M	LS	CS	Accuracy	Kappa	% accuracy
CI	87	13	6	20			49.2
M	44	30	8	27			43.5
LS	24	5	37	18			62.7
CS	22	21	8	42			39.3
Total					0.476	0.288	

morphological similarity among the morphotypes introducing uncertainty in the decision-making process. To address this issue, we explored a broad spectrum of clustering methods and wavelet levels, ranging from signals with higher detail (3rd level) to smoother ones (5th level). Finally, we opted for the grouping option that provided the most coherent morphological interpretation of the observed phenotypic diversity. The distinct otolith shape of this species sets it apart from other small and medium pelagic fishes like *Trachurus* spp., *Decapterus* spp. and *Engraulis* spp., which exhibit more conventional otolith shapes, making the differentiation of morphotypes easier (Lombarte et al., 2006).

The rapid swift northwards expansion of the Atlantic chub mackerel within the East Atlantic distribution (Martins et al., 2013; Garrido et al., 2015) and its migratory behavior may account for the remarkable similarity in the phenotypic structure found at regional level. This similarity suggests an extensive gene flow, resulting in the establishment of a large panmictic unit in the north-eastern Atlantic Ocean and Mediterranean Sea (Scoles et al., 1998; Zardoya et al., 2004). Indeed, a recent small-scale study conducted in the northernmost Atlantic African waters has revealed a weak genetic structure within Moroccan-Mauritanian waters, attributed to the irregular distribution of the fishing pressure, which disrupts the natural gene flow (Stroganov et al., 2023). However, all studies describe distinct fish groups inhabiting a wide geographic distribution, with populations intermixing within a large metapopulation. For instance, size-segregations linked to ontogenetic/bathymetric migrations of individuals towards deep bottoms far from the coast have been observed around Atlantic islands, probably linked to breeding (Menezes et al., 2006). Similarly, latitudinal breeding/feeding migrations have been documented in the northern CECAF waters (García, 1982; Martins et al., 2013; Ebango Ngando et al., 2020), indicating the species as a transboundary shared stock. In Ghana, Kwei (1971) observed seasonal migrations inshore for spawning during the upwelling period in summer, followed by a movement of individuals to greater depths for feeding in autumn. It also suggested that in the northeast Atlantic, including both African and European waters, the Atlantic chub mackerel undergoes migration from wintering areas—mainly located in Mauritanian waters, southern Portugal and in the inner part of the Bay of Biscay—towards northern waters in the summer (ICES, 2021). Additionally, in the case of the Bay of Biscay, the migration extends towards the western Iberian Peninsula. Hence, the high number of morphotypes identified in the present study may be linked to these migratory processes, posing significant implications (and challenges) to understand the metapopulation dynamics and accurately describing the complexity of the species' population structure. Firstly, this raises concerns about the reliability of studies conducted to date with small sample sizes, such as in Muniz et al. (2020) (using otolith shape and body morphometrics in 45 specimens by region) and Correia et al. (2021) (examining otoliths' elemental and isotopic signatures for 30 individuals by region), both encompassing Portugal mainland, Azores, Madeira, and the Canary Islands; and Sbiba et al. (2024) along NW African coast (exploring the otolith shape for 30 individuals for nine localities). Secondly, the morphotypes M2-M3 and M4 here described, represent ca. 51–60% of all the individuals analyzed and appear in similar frequencies in each origin, except for the higher predominance of M2 in the Ligurian Sea. However, an inversely proportional rate was evident between the morphotypes M1-M5 and M6 in the regions of Madeira-Canary Islands vs Ligurian-Cantabrian Seas. These findings may suggest that certain morphotypes have effectively adapted to specific environmental conditions, such as temperature. Drawing on Vasconcelos et al. (2021) insights into the relationship between morphotypes and contingents (resident versus migratory) in the Atlantic distribution of the blue jack mackerel (*T. picturatus*), we suggest, based on our findings, that morphotypes M2-M3 and M4 might demonstrate migratory behavior, explaining their similar presence in all the considered fishing grounds; in contrast, M1-M5 and M6 could represent the resident contingents. The lack of information on the seasonal distribution of these morphotypes currently hinders our ability to explore and clarify alternative

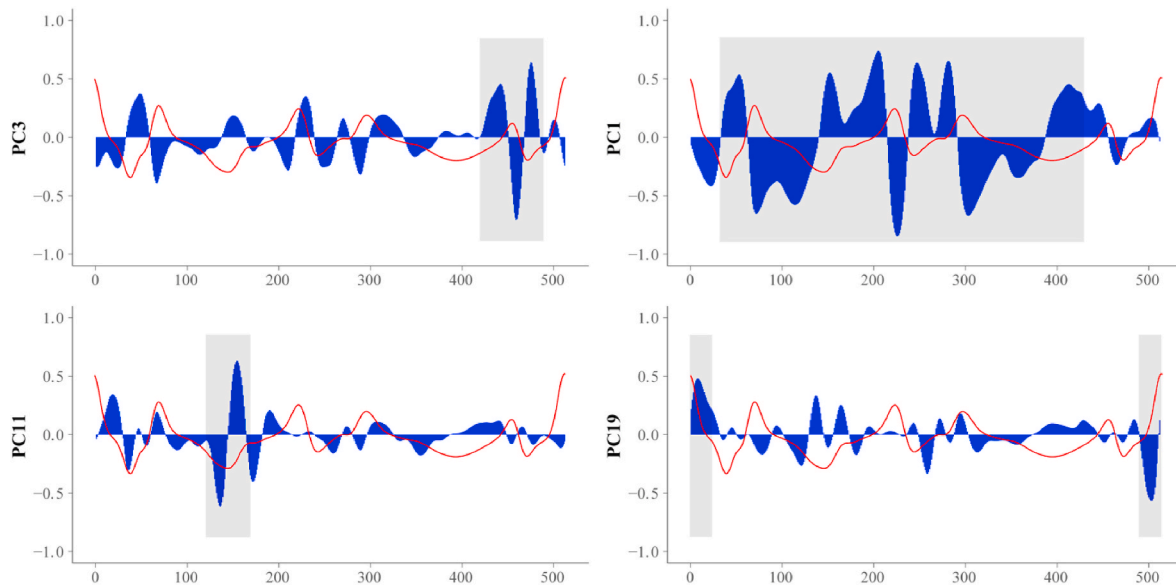


Fig. 7. Correlation between the PCs with higher relative importance obtained in the classification model and the values of the wavelet along the 512 points.

hypotheses. Future studies will be necessary to address this gap.

The northward latitudinal expansion has entailed an increase of fish mean size, length at first maturity, a delay in the peak of spawning and the spawning season, and a decrease in the somatic growth rate, all likely influenced by surface sea temperature (ICES, 2021; Domínguez-Petit et al., 2022). In this sense, we have also found a similar pattern in total lengths for all morphotypes across regions. Individuals within the Group-A exhibited smaller mean and maximum sizes compared to those in Group-B (Fig. S3). Besides, the occurrence of small-sized individuals in all cases suggest that the morphotypes found are not related to fish length or age. Certainly, otoliths undergo ontogenetic changes throughout their growth; specifically, contour alterations (e.g., convexity or concavity) response to specific exogenous factors (Hüssy, 2008; Tuset et al., 2015), whereas the *rostrum* and *antirostrum* size are genetically codified (Reichenbacher et al., 2009; Vignon and Morat, 2010; Reichenbacher and Reichard, 2014). In this context, our findings revealed that PC1, explaining a greater variability in the otolith contour (Table S1) and contributing significantly to partial population differentiation, did not showed correlation with fish length (Table S3). On the other hand, the PC3 component, linked to *rostrum* size and its connectivity with the *colliculum ostii*, deemed the most crucial component in the population identification, was significantly influenced by fish length (Table S3). This zone of the otolith exhibited greater development in the Group-B, consisting of larger Atlantic chub mackerels. Neves et al. (2024) found variability in the otolith shape linked to age, particularly in 1-year-old individuals. However, this conclusion may be debatable due to significant variability and overlap in fish size-ranges by age among age groups (Navarro et al., 2021) and among morphotypes (present study). Additionally, a study on otolith elemental and isotopic signatures in the NE Atlantic revealed population differences among the Macaronesia archipelagos and mainland Portugal (Correia et al., 2021). The authors proposed a limited movement of adult individuals between isolate regions (i.e., islands), with larval retention mechanisms or a self-recruitment process operating at large spatial scales. Our primary concern with this hypothesis is, once again, the representativeness of morphotypes when only 30 individuals were analyzed per region, although we do not entirely rule it out. We agree that further research into the population structure, fish movement and habitat connectivity of this species is still needed.

The Atlantic chub mackerel congener, *S. scombrus*, is recognized to consist of a northern (in Canada) and a southern contingent (in USA) in the Northwest Atlantic population, which spawn in distinct areas and

periods, occasionally overlapping seasonally in the fished regions of the USA (Arai et al., 2021; Bourret et al., 2023). Given the complexity of the fishery dynamism in which both components seem to present different trends in productivity and depletion, higher levels of contingent mixing appear to be related to greater landings of the less favored contingent. Arai et al. (2021) recommended spatially explicit stock assessment models to preserve both productivity and stability in this two-component population. Currently, stock identification methods have uncovered discrepancies between the spatial structure of biological populations and assumed stock units, leading to mismatches that compromise accurate stock assessment and hinder sustainable fisheries management. A fundamental ecological concern revolves around the potential overexploitation of unique spawning components, which could result in a loss of productivity, reduced biodiversity, and destabilization of local and regional stock dynamics (Kerr et al., 2017). Fishing managers must grasp that phenotypic richness mirrors the health and potential plasticity of species to inhabit different (and new) niches or adopt complementary life history patterns (Tuset et al., 2019). Challenges associated to the use of averaged phenotypes for identifying SMPF stocks have been highlighted in other SMPF species, like *T. picturatus* from the central-eastern Atlantic (Vasconcelos et al., 2021). This underscores the significance of integrating phenotypic diversity into any fishery management considerations, particularly in the context of ongoing global warming. Presently, continuous monitoring programs aligned with the *European Data Collection Framework* (Regulation (EU) 2017/1004) for the collection, management and usage of fishery data, should promote the extraction and creation of otoliths collections. This would allow the ongoing monitoring of temporal shifts in phenotype frequencies for both targeted and by-catch species over the long term. This information is valuable for developing adaptive fishing management strategies, especially for SMPF species facing the challenges of global change. In the East Atlantic waters, the most productive region for the Atlantic chub mackerel is situated just south of the origins covered in this study (i.e., between Morocco and Mauritania) (ICES, 2021). This region falls within one of the four Eastern Boundary Upwelling Systems, recognized as one of the current thermal refuges for marine organisms amid climate change (García-Reyes et al., 2023).

5. Conclusion

The presence of otolith morphotypes in the Atlantic chub mackerel highlights a complex population structure, indicating the existence of a

metapopulation. This metapopulation may comprise different contingents cohabiting in varying proportions, depending on local environmental conditions. A well-documented northward latitudinal trend reveals an increase in mean fish size, length at first maturity, a postponement in the peak of spawning and the spawning season, and a decrease in the somatic growth rate. This trend is likely influenced by surface sea temperature (ICES, 2021). Although further research is needed at species level, the new insights presented in this study contribute to a more comprehensive understanding of the biological aspects and population dynamics of chub mackerel. Our findings, derived from a substantial number of samples for the first time, represents a significant stride toward the development of future assessments of chub mackerel stocks, thereby facilitating sustainable stock management.

CRedit authorship contribution statement

A. Jurado-Ruzafa: Writing – original draft, Validation, Resources, Investigation, Data curation, Conceptualization. **J. Vasconcelos:** Writing – review & editing, Validation, Supervision, Resources, Methodology, Investigation, Data curation, Conceptualization. **J.L. Otero-Ferrer:** Software, Formal analysis. **M.R. Navarro:** Writing – review & editing, Resources, Investigation. **A. Massaro:** Writing – review & editing, Resources, Investigation. **C. Hernández:** Writing – review & editing, Resources, Investigation. **V.M. Tuset:** Writing – original draft, Supervision, Methodology, Formal analysis.

Declaration of competing interest

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

J. Vasconcelos reports financial support was provided by Fundação para a Ciência e a Tecnologia I.P. (FCT). J. Vasconcelos reports financial support was provided by Government of the Canary Islands and University of Las Palmas of Gran Canaria. A. Jurado-Ruzafa reports financial support was provided by European Maritime and Fisheries and Aquaculture Fund (EMFAF). If there are other authors, they declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

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