



# Landmark-based geometric morphometrics analysis of body shape variation among populations of the blue jack mackerel, *Trachurus picturatus*, from the North-East Atlantic

Cláudia Moreira<sup>a,b</sup>, Elsa Froufe<sup>a</sup>, Paulo Vaz-Pires<sup>a,b</sup>, Raül Triay-Portella<sup>c</sup>,  
Alberto Teodorico Correia<sup>a,d,\*</sup>

<sup>a</sup> Centro Interdisciplinar de Investigação Marinha e Ambiental (CIIMAR), Terminal de Cruzeiros do Porto de Leixões, Avenida General Norton de Matos S/N, 4450-208 Matosinhos, Portugal

<sup>b</sup> Instituto de Ciências Biomédicas Abel Salazar da Universidade do Porto (ICBAS/UP), Rua de Jorge Viterbo Ferreira 228, 4050-313 Porto, Portugal

<sup>c</sup> Instituto Universitario de Estudios Ambientales y Recursos Naturales (i-UNAT), Campus de Tafira, Las Palmas de Gran Canaria, 35017 Las Palmas, Spain

<sup>d</sup> Faculdade de Ciências da Saúde da Universidade Fernando Pessoa (FCS/UFPP), Rua Carlos Maia 296, 4200-150 Porto, Portugal

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## ABSTRACT

Phenotypic variation in fish can indicate exposure to different environmental conditions, affecting species growth and maturation rates and/or be a consequence of genetic factors that allow fish adaptation to different environments. Understanding population structure and dynamics is extremely important for the establishment of sustainable fisheries. The blue jack mackerel, *Trachurus picturatus*, is an important fishery resource of the North-East (NE) Atlantic. Fish were captured in six sampling locations in the NE Atlantic - Azores, Madeira, Canaries and Portugal mainland - Matosinhos, Peniche and Portimão. The phenotypic diversity of the species was studied using body landmark-based geometric morphometrics. A truss box method was followed and 30 distance variables were extracted from digital images. Additionally, the temporal stability of the morphological characters was investigated by comparing samples from two different years: 2016 and 2019. The transformed distances were analysed by univariate and multivariate statistics. The Macaronesia region – Azores, Madeira and Canaries – and Portugal mainland displayed a clear phenotypic pattern. Distances related to the body width and caudal peduncle were the most significant variables explaining the observed phenotypic heterogeneity. Furthermore, this study also showed that *T. picturatus* can exhibit fast phenotypic adaptations to the surrounding environment, observed by the discrimination of Peniche in 2019. Nevertheless, the high overall allocation of individuals to the original location observed for both years (78% in 2016 and 83% in 2019) suggests that the population of *T. picturatus* in the NE Atlantic is phenotypic heterogeneous. These findings corroborate previous studies and have implications for fishery management.

## 1. Introduction

Most of the harvest fish stocks are composed of two or more populations of the same species, with very similar traits, that overlap in space and time (Dahle et al., 2018). Mismatch between the biological processes and the realized management actions frequently occur, since a variety of conflicting aspects, such as biological, economic, social and even political factors, need to be considered (Reiss et al., 2009). Currently, management of fish stocks has changed from the simplistic geographical isolation of populations that exhibit identical rates of growth and mortality (FAO, 2018), to include considerations on the

complex life traits of a fish (Reis-Santos et al., 2018). Insufficient knowledge of the genetic structure, life history diversity and the biological boundaries of a population will lead to failure in protecting distinct fish stocks (Reis-Santos et al., 2018). Nowadays, stock identification highlights the need for holistic approaches, that consider information across multiple spatial and temporal scales (Cadrin, 2020). Fish stock is generally defined to identify a genotypic and/or a phenotypic group. A genotypic stock implies that individuals are isolated, at least, during the spawning season, and across generations, while a phenotypic stock implies that individual differences occur as a result of genetic or environmental differences during the time when the

\* Corresponding author at: Centro Interdisciplinar de Investigação Marinha e Ambiental (CIIMAR), Terminal de Cruzeiros do Porto de Leixões, Avenida General Norton de Matos S/N, 4450-208 Matosinhos, Portugal.

E-mail address: [acorreia@ufp.edu.pt](mailto:acorreia@ufp.edu.pt) (A.T. Correia).

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phenotypic characters are being developed (Hare and Richardson, 2014).

Morphological studies have long been useful to describe fish spatial distributions (Kaouèche et al., 2017). Previous works have demonstrated morphological divergence in the body of several marine fish species (e.g. Hammami et al., 2013; Kaouèche et al., 2017; Vasconcelos et al., 2018). These changes have been associated with the intrinsic specificities of the particular aquatic environment inhabited by the fish (Hammami et al., 2013). Phenotypic variation within a fish species can occur as a result of isolation, environmental variations, thermal reaction, local adaptation and/or a combination of these (Valladares et al., 2014; Vasconcelos et al., 2018). Different spatial structure within populations can affect the overall dynamics of the species. Growth, maturity, reproduction, recruitment, abundance, and survival of a group of individuals can be greatly influenced by the environmental conditions experienced by these individuals (Abaunza et al., 2008; Cadrin, 2010). Exposure to different environmental factors, such as temperature and salinity, food availability or swimming patterns, can result in individuals following different adaptation strategies, and consequently develop different morphometric features between populations (Sajina et al., 2011). Quantification of these specific characteristics in an individual or group of individuals can demonstrate the degree of isolation and contribute to the definition of different phenotypic stocks (Bailey, 1997). A landmark-based technique called the truss network system (Strauss and Bookstein, 1982) has been increasingly employed for the purposes of stock discrimination, essentially describing phenotypic stocks (Sajina et al., 2011). This approach enables covering the entire fish body in a uniform network, with no restrictions on the direction of variation and localization of shape changes (Rawat et al., 2017). It is a tool highly effective in capturing information about the shape of an individual (Sajina et al., 2011; Kaouèche et al., 2017) and could detect variation among fish populations (Murta et al., 2008; Miyani et al., 2016; Kaouèche et al., 2017).

The blue jack mackerel, *Trachurus picturatus* (Bowdich, 1825), is widely distributed across the North-East (NE) Atlantic, the Mediterranean and Black Seas (Smith-Vaniz, 1986). Although the economic significance of the blue jack mackerel in the Macaronesia islands of Azores and Madeira is recognized, and fluctuations in the catches have been reported (FAO, 2018), the population structure of the species is poorly understood. Furthermore, the International Council for the Exploitation of the Sea (ICES) defined the existence of a single stock for the entire species distribution, simply based on geographical boundaries (ICES, 2018). However, geographical isolation of species with broad distributions, such as *T. picturatus*, can result in the development

of different morphological features between fish populations, leading to the discrimination of phenotypic stocks. The genetic structure of the *T. picturatus* was studied by mtDNA in the Mediterranean Sea (Karaïskou et al., 2003, 2004), and both in the Mediterranean Sea and Macaronesia region (Moreira et al., 2019b), suggesting a lack of genetic structure across the species distribution, with high levels of genetic diversity and inbreeding coefficients showing a high rate of mixing. However, regional studies of *T. picturatus* recorded different growth rates among the Azores, Madeira and the Canary Islands (Isidro, 1990; Vasconcelos et al., 2006, 2017; Jurado-Ruzafa and Santamaría, 2011, 2013; Garcia et al., 2015), which could indicate the existence of different population units in the region. Furthermore, other ecological approaches, such as parasites (Costa et al., 2012, 2013; Hermida et al., 2015; Vasconcelos et al., 2017), geometric morphometrics and otolith shape analysis (Vasconcelos et al., 2018), otolith shape analysis (Moreira et al., 2019a), and otolith elemental and isotopic signatures (Moreira et al., 2018), revealed the existence of different population units in the NE Atlantic. Geometric morphometrics and otolith shape analysis were already applied to study *T. picturatus* populations (Vasconcelos et al., 2018), but as highlighted by the authors, the study area was geographically limited, the collection of individuals did not consider a specific time window, fish were of significantly different size ranges and captured with different fishing methods, which could have somewhat biased the results. To minimize confounding effects of demography, morphometric analyses should be carried out at a time of year when stock mixing is expected to be minimal (e.g. during the spawning season) and the specimens studied should be of similar age or size (Cadrin, 2000; Murta et al., 2008; Heino, 2014). Furthermore, results reported by Moreira et al. (2019a) in a subsequent otolith shape analysis study, revealed that the experimental design set by the previous authors had, in fact, limitations (Moreira et al., 2019a). Therefore, to a better understanding of the population structure of *T. picturatus*, their migration patterns and habitat connectivity, more complete studies are required.

Therefore, the present study aimed to investigate the spatial morphological variation of *T. picturatus* populations in the NE Atlantic using truss network analysis and to assess the temporal stability of the morphological features by comparing two distinct sampling years (2016 and 2019).

## 2. Material and methods

Specimens of *T. picturatus* were acquired from fish markets at Portugal mainland (Matosinhos, Peniche and Portimão) and at the

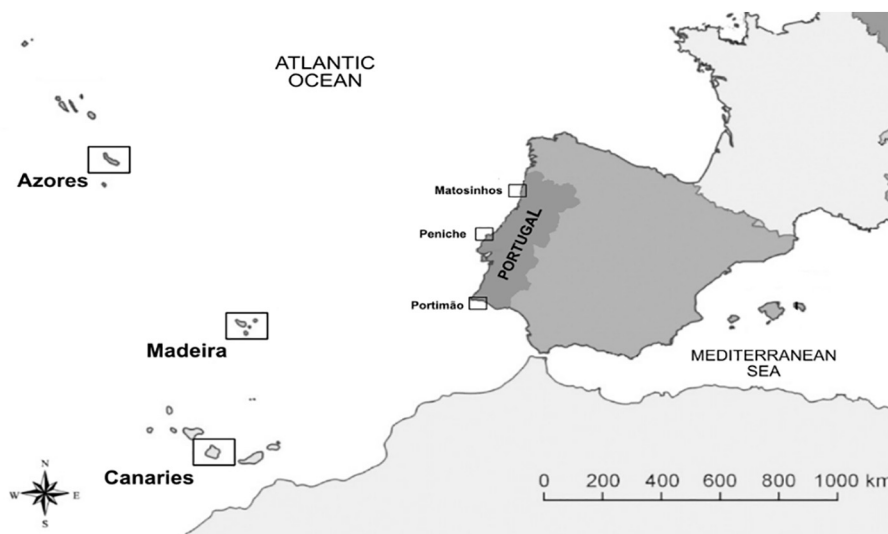


Fig. 1. Sampling locations of *Trachurus picturatus* individuals collected in 2016 and 2019 in the Northeast Atlantic Ocean.

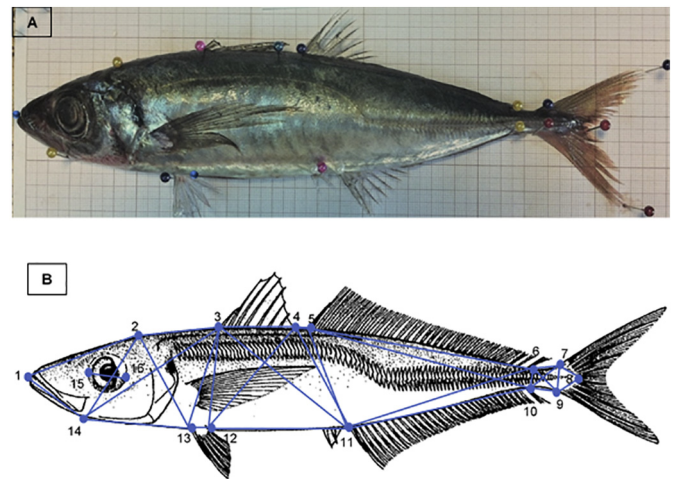
**Table 1**  
Sampling locations, year, sample size (n), standard length (SL) of *Trachurus picturatus* used in this study. Values are presented as mean  $\pm$  standard error (SE).

Regions	Sites	Sampling location	Year	n	SL (mm)
Azores	–	37°42'6.39"N	2016	30	21.59 $\pm$ 0.19
		25°29'15.12"W	2019	30	23.88 $\pm$ 0.26
Madeira	–	32°42'18.79"N	2016	30	22.39 $\pm$ 0.03
		16°56'52.75"W	2019	30	22.33 $\pm$ 0.20
Canaries	–	27°48'42.12"N	2016	30	15.23 $\pm$ 0.30
		15°35'6.33"W	2019	25	16.66 $\pm$ 0.16
Portugal Mainland	Matosinhos	41°10'49.50"N	2016	30	24.63 $\pm$ 0.17
		8°42'11.25"W	2019	30	24.89 $\pm$ 0.18
	Peniche	39°21'51.11"N	2016	30	21.69 $\pm$ 0.27
		9°23'56.58"W	2019	30	23.06 $\pm$ 0.18
	Portimão	37° 6'14.20"N	2016	30	23.56 $\pm$ 0.17
		8°31'25.99"W	2019	30	22.90 $\pm$ 0.42

Macaronesian Islands of Azores, Madeira and Canaries (Fig. 1). Fish were caught in shallow coastal waters (up to 75 m water depth) by the artisanal purse-seine fleets to ensure a correct location of the capture. Unfortunately, small fishing boats targeting jack mackerel could suffer several inter-annual constraints, due to adverse weather conditions or by the displacement to other fish species due to market reasons. Anyway fish were collected for both years (October to December 2016 and February to May 2019) within the main protracted spawning season for the species. Moreover, to minimize confounding demographic effects, individuals of similar length were selected (Table 1). The fish were stored on ice and transported to the laboratory to be processed.

For each year and location, a total of 25 to 30 individuals were one-side photographed. The use of this sample size is according to the recommendations for this methodological approach (Reist, 1985), and followed previous works (e.g. Murta et al., 2008; Kaouèche et al., 2017; Neves et al., 2018). Moreover, it allowed to use the same individuals (namely from 2016) to which we have already otolith's shape analysis (Moreira et al., 2019a) and microsatellites (Moreira et al., 2020) data, allowing a holistic discussion. Individuals of both sexes were analysed together since there is no sexual dimorphism in this species (Vasconcelos et al., 2018), such as in other related species, including *T. trachurus* (Murta et al., 2008) and *T. mediterraneus* (Turan, 2004). Furthermore, a visual inspection of the specimens at the time of sampling did not show any obvious genera morphological differences, like females with protracted abdomens. It means that the existence of any sexual difference was very unlike in this work. As general rule, including a previous published work on this species (Vasconcelos et al., 2018), for fish bilaterally symmetric, landmarking one side, instead of both, reduces the number of variables, as well as the time and costs of data collection. A total of 16 anatomic landmarks were defined on fish left-side (Fig. 2A, Table 2), corresponding to hard structures (e.g. fin insertions points), distributed along the fish body contour (Cadrin, 2000; Cadrin, 2014 Murta et al., 2008). Location coordinates of homologous landmarks were digitized using tpsDig (Rohlf, 2018) and used to derive box-truss dimensions (Strauss and Bookstein, 1982; Fig. 2B, Table 3). Morphometric measurements correlation with fish standard length was verified using analysis of co-variance (ANCOVA). Each distance was corrected to remove the size-effect and possible allometric relationship between variables following Reist (1985) and Kaouèche et al. (2017):  $V_{trans} = \log V - b (\log SL - \log SL_{mean})$  where  $V_{trans}$  is the corrected measurement,  $V$  is the original measurement,  $b$  is the within-group slope regression of  $\log V$  against  $\log SL$ ,  $SL$  is the standard length of the individual and  $SL_{mean}$  is the overall mean of the standard length for all locations.

One-way analysis of variance (ANOVA) was used to explore the statistical differences of each distance measured in the body shape of *T. picturatus* between the years and among the sampling locations,



**Fig. 2.** Specimen of *Trachurus picturatus* collected from Madeira in 2019 showing the selected landmarks (A). Illustration of *T. picturatus* (adapted from Sanches, 1992) with the indication of the landmarks (1 to 16) and the Truss network represented by the blue lines (B) (see Tables 2 and 3 for more details). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

**Table 2**

Morphometric landmarks of *Trachurus picturatus* used to derive the morphometric distances (see Fig. 2).

Landmark	Description
1	Anterior tip of snout
2	Most posterior aspect of neurocranium
3	Origin of dorsal fin
4	End insertion of dorsal fin
5	Origin of second dorsal fin
6	End insertion of second dorsal fin
7	Anterior attachment of dorsal membrane from caudal fin
8	Posterior end of vertebrae column
9	Anterior attachment of ventral membrane from caudal fin
10	End insertion of anal fin
11	Origin of anal fin
12	End insertion of pelvic fin
13	Origin of pelvic fin
14	Posterior most point of maxillary
15	Posterior end of the eye
16	Anterior end of the eye

followed by a Tukey post-hoc test if needed (ANOVA:  $p < .05$ ). Multi-distances variations among sampling locations for each year using a permutational multivariate analysis of variance (PERMANOVA) based on the Euclidean distance measure using Monte-Carlo simulations (9999 random permutations). The body truss network was analysed with a stepwise linear discriminant function analysis (LDFA). Re-classification accuracies of the discriminant functions for each location were evaluated using a jackknifed (leave-one-out) cross-validation. A canonical analysis of principal coordinates (CAP) was performed to detect morphometric differences among locations.

All statistical analyses were performed using Systat (v 12) and PRIMER 6 + PERMANOVA software, with a statistical level of significance ( $\alpha$ ) of 0.05. Data are presented as mean Log distances  $\pm$  standard errors (SE).

### 3. Results

The truss network obtained with the 16 landmarks allowed the calculation of 30 body distances (Fig. 2). For both years, all the distances showed a significant correlation with the fish standard length (ANCOVA,  $p < .05$ ) and had to be corrected. Correction by allometric

**Table 3**  
Morphometric distances and associated landmarks for *Trachurus picturatus* (for details see Fig. 2 and Table 2).

Truss network Distances	Landmarks	Description
D1	1–2	Head length
D2	1–14	Maxilla length
D3	2–3	Distance from most posterior aspect of neurocranium to 1st dorsal fin
D4	2–13	Anterior diagonal height of head
D5	2–14	Anterior height of head
D6	3–13	Posterior height of head
D7	3–14	Posterior diagonal head height
D8	13–12	Length of the pelvic fin base
D9	13–14	Distance from maxilla to pelvic fin insertion
D10	3–4	Length of 1st dorsal fin
D11	3–11	Anterior diagonal of body height
D12	3–12	Anterior body height
D13	4–11	Posterior body height
D14	4–12	Posterior diagonal of body height
D15	11–12	Distance between anal and pelvic fins
D16	4–5	Distance between 1st dorsal fin and 2nd dorsal fin
D17	5–6	Length of 2 <sup>nd</sup> dorsal fin
D18	5–10	Anterior diagonal height of posterior body
D19	5–11	Anterior height of posterior body
D20	6–10	Anterior caudal peduncle height
D21	6–11	Posterior diagonal height of posterior body
D22	10–11	Length of anal fin
D23	6–7	Distance between 2nd dorsal fin and caudal fin
D24	6–9	Anterior diagonal of caudal peduncle
D25	7–9	Posterior height of caudal peduncle
D26	7–10	Posterior diagonal of caudal peduncle
D27	9–10	Distance between anal fin and caudal fin
D28	7–8	Distance between dorsal insertion of caudal fin and posterior end of vertebrae column
D29	8–9	Distance between ventral insertion of caudal fin and posterior end of vertebrae column
D30	15–16	Eye diameter

transformation successfully removed the effect of body length in all distances (ANCOVA,  $p > .05$ ). ANOVA of all the 30 truss measurements showed significant differences between years (ANOVA,  $p < .05$ ) and among locations (ANOVA,  $p < .05$ ), although with no recognizable pattern (Table 4).

PERMANOVA analysis of all the truss measurements resulted in significant differences among all locations for each year (pseudo- $F_{5,174} = 17.917$ ,  $p$  (MC) = 0.0001, and pseudo- $F_{5,169} = 14.857$ ,  $p$  (MC) = 0.0001, respectively for 2016 and 2019).

The stepwise analysis for all sampling locations in 2016 eliminated 5 distances from the analyses - D7, D19, D24, D28 and D29. The plot obtained in the stepwise LDA showed clear discrimination of the Azores, Madeira and Canary individuals, with a high overlap of individuals from Portugal mainland (Fig. 3A). The overall assignment of individuals to their original location was 78%, with values ranging from 60% for Peniche to 97% for the Azores (Table 5). For the year 2019, the stepwise analysis eliminated 9 distances from the analyses - D3, D6, D7, D17, D19, D20, D22, D27 and D28. The plot obtained in the stepwise LDA showed clear discrimination of Canaries and Peniche, with a high overlap of individuals captured in Matosinhos and Portimão (Fig. 3B). The overall assignment of individuals to their original locations was 83%, ranging from 70% for Madeira and Matosinhos to 100% for Canaries (Table 5).

CAP for 2016 identified four main groups, i.e. Azores (Group 1), Madeira (Group 2), the Canaries (Group 3), and Portugal mainland (Group 4) (Fig. 4A). Distances D4, D6, D12, D14, D24 and D27 allowed the discrimination of group 1 (Azores); distances D3, D5, D7, D9 and D23 allowed the discrimination of group 2 (Madeira); and distances D1, D2 and D30 allowed the discrimination of group 3 (Canaries); all other distances measured overlapped the locations of Portugal mainland,

with no clear indication to which distances were more discriminant. CAP for 2019 identified five main groups, i.e. Azores (Group 1), Canaries (Group 2), Madeira (Group 3), Peniche (Group 4), and Matosinhos and Portimão (Group 5) (Fig. 4B). Distances D21, D22, D24 and D27 allowed the discrimination of group 1 (Azores); distances D4, D6 and D12 allowed the discrimination of group 2 (Canaries); distances D2, D5, D9, D16 and D30 allowed the discrimination of group 3 (Madeira); distance D8 allowed the discrimination of group 4 (Peniche).

#### 4. Discussion

In the present study, the differences in the body shape of *T. picturatus* along the NE Atlantic were investigated using truss network morphometrics. It was assumed that genus *Trachurus* shows no sexual dimorphism across its distribution range (e.g. Turan, 2004; Murta et al., 2008; Vasconcelos et al., 2018). The analysis showed that the NE Atlantic *T. picturatus* populations are phenotypically heterogeneous regarding the fish body shape. Furthermore, comparing the morphological characters between two distinct years - 2016 and 2019 - revealed that the species can exhibit fast phenotypic adaptations to the environment (e.g. Heino, 2014). The statistical discrimination of populations was driven by several morphometric distances, but the most significant ones were essential those related to body width and caudal peduncle, a relation that was already reported for other fish species, namely for 92 species of the Sparidae family (e.g. Antonucci et al., 2009) and for *Phycis phycis* (Vieira et al., 2016).

For both years a clear isolation of the Macaronesian region (i.e., Azores, Madeira and Canaries) was observed. However, the truss measurements responsible for this regional differentiation were different between the years. For example, the Azores individuals caught in 2016 showed differences for distances related to the anterior body width (D4, D6, D12 and D14), while individuals caught in 2019 showed differences for distances related to posterior body width (D21 and D22). The discrimination of Madeira and the Canaries was mainly caused by distances related to head morphology, while the Azores region was discriminated by distances related to body height (in 2016) and peduncle region (in 2019). Head morphological variation can be related to different feeding behaviours, while peduncle morphological variation is usually associated with swimming behaviour (Vieira et al., 2016; Kouèche et al., 2017; Mounir et al., 2019). The diet of the blue jack mackerel is still poorly understood, but crustaceans appear to be the main food item (ICES, 2018). Moreover, different fish size distributions have been observed between the Azores islands shelf and offshore areas, presumably related to different diet preferences (Menezes et al., 2006). The migration of juvenile fish to different adult feeding grounds can result in significant phenotypic variations, accordingly to the new feeding regimes and habitats. Additionally, the correlation between fish length, water depth and diet variations has been reported for several pelagic fish species off the Portuguese coast, such as *Trachurus trachurus* (Cabral and Murta, 2002; Garrido and Murta, 2011) and *Micromesistius poutassou* (Cabral and Murta, 2002). However, if different diets could help explain the differences in the head variables, the morphological peduncle variation is more difficult to clarify. Body form, fin size and location are fish's adaptations for movement and manoeuvrability (Webb, 1984), indicating differences in habitat exploitation (Neves et al., 2018). Indeed, several authors have observed that morphological variations in the peduncle area are mostly associated with different hydrodynamic systems (e.g. Sajina et al., 2011; Vieira et al., 2016). The hereby study area (NE Atlantic) is known to be influenced by currents with different hydrodynamic features - e.g. the Azores and the Canaries currents (Sala et al., 2013; Neves et al., 2018) - which could induce morphological variances in body shape, namely in the peduncle area. Furthermore, Azores and Canaries are volcanic islands with special topographic conditions, such as narrow shelves and steep slopes (Menezes et al., 2006), leading to the formation of regional distinctive habitats. Additionally, the sampling locations are influenced by a sea



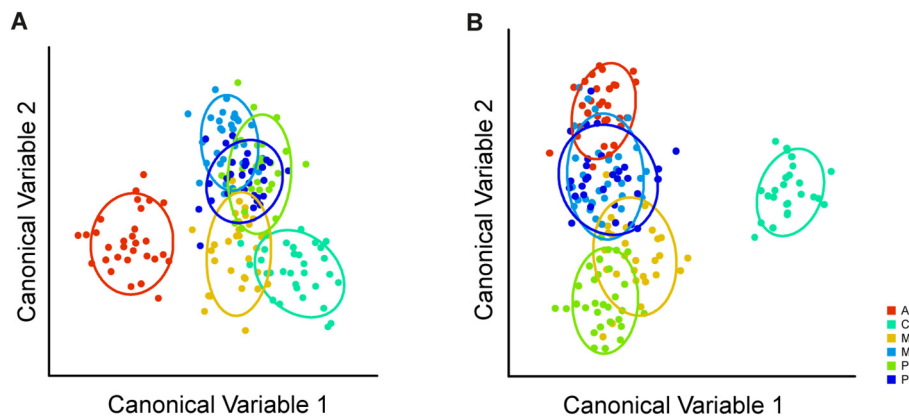


Fig. 3. Canonical variable plots displaying spatial differences in the morphometric distances calculated for *Trachurus picturatus* collected in the six sampling locations of the NE Atlantic in 2016 (A) and 2019 (B). Legend: Azores (AZ), Canaries (CN), Madeira (MD), Matosinhos (MT), Peniche (PE) and Portimão (PT). Ellipses represent 95% confidence intervals around the data, and data points represent individual fish.

Matosinhos and Portimão) and later on aged with 3 years old, not only confirmed the main scenario but also made it more robust. The overall assignment of individuals to their original location was 95%, with values ranging from 100% for Azores and Canaries, and 90% for Madeira and Peniche, for both years. It means that any fish age effect, to exist, was minimal in this study. However, among the Portuguese coast, differences in morphometric patterns were less evident, although a high percentage of correct assigned individuals was obtained for most locations. Furthermore, in 2019, individuals from Peniche showed an unexpected separation from the other coastal locations. Regarding the Portuguese coast, the continental shelf contributes to a more hydrodynamic stable environment, which is reflected by the existence of a phenotypic homogeneous population among the coastal locations. Nevertheless, seasonal upwelling of nutrient-rich waters in summer, buoyant plumes from river discharge during winter (Santos et al., 2007), along with the existence of several submarine canyons (Aquarone et al., 2008) could be sufficient to create phenotypic patterns in the region. Data from the year 2016 suggest migratory movements among Portuguese coastal sampling locations - Matosinhos, Peniche and Portimão - with an apparent phenotypic homogeneous pattern across the sampling locations. However, individuals captured in 2019 showed clear isolation of Peniche. This location was discriminated by differences in fin related distances, meaning that fish from this location could have adapted for different swimming needs (Webb, 1984). Fluctuations in the upwelling events and/or size of the plumes can result in isolation and consequently local adaptation of these individuals. Additionally, Peniche is located about 40 km of the largest canyon

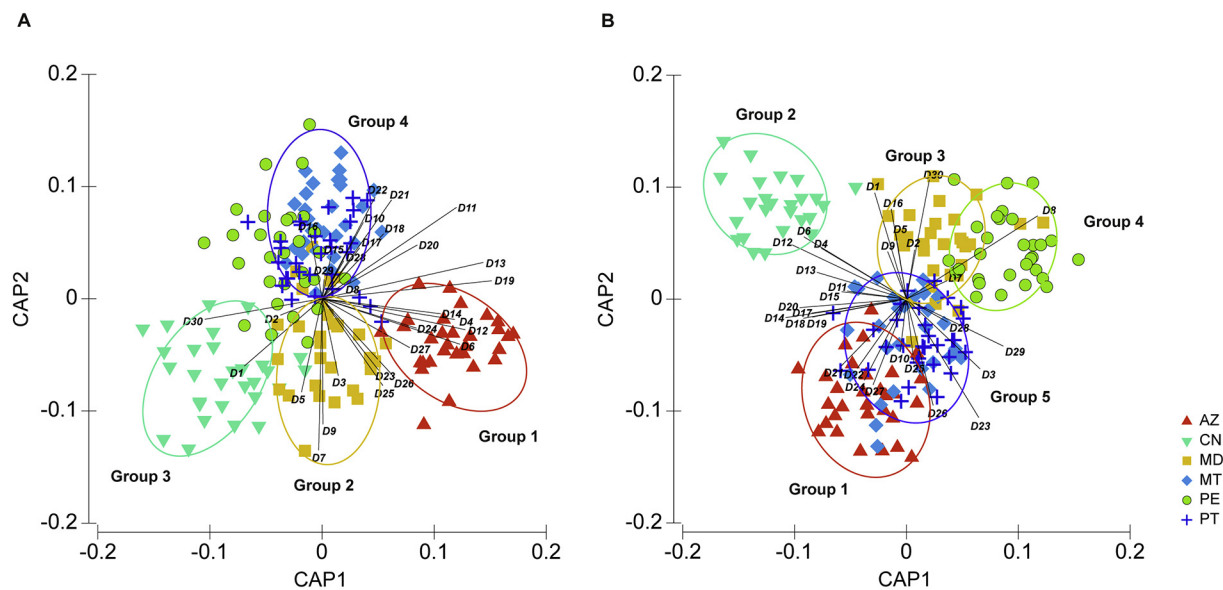
found in the Iberian continental shelf - Nazaré Canyon. This canyon has been reported has a clear marine community boundary, creating distinct fish assemblages between north and south (Sousa et al., 2005). Furthermore, considering the different body shape patterns observed between the years, *T. picturatus* seems to exhibit fast phenotypic adaptations to the surrounding environments. The specificities of each environment have been indicated as probable causes for phenotypic heterogeneity in several marine fish, including *T. picturatus* in Madeira, Canaries and Peniche (Vasconcelos et al., 2018), and closed related species, such as *T. trachurus* in the Iberian and North African Atlantic (Murta, 2000) and *T. mediterraneus* in the Mediterranean Sea (Turán, 2004). This phenotypic heterogeneity was also observed in the current study taking into consideration the high overall re-allocation of individuals to the original location for both years - 78% in 2016 and 83% in 2019.

In addition to the environmental factors, phenotypic variation within species is also influenced by the individual genetic input (Cadrin, 2010). However, several authors have shown that heritability of morphometric characters is generally low to moderate (Swain et al., 2005; Cadrin, 2010; Costa et al., 2010), suggesting that “local stocks” can be better identified based on phenotypic variations. Accordingly, while some fish species show morphological divergence due to genetic differentiation, others show phenotypic variations that cannot be related to the genetic component (e.g. Domingues et al., 2007; González-Wangüemert et al., 2010; Kaouèche et al., 2017). For instance, Costa et al. (2010) demonstrated that, in reared conditions, the shape of the European sea bass *Dicentrarchus labrax* was primarily influenced by the

Table 5

Jackknifed cross-validation re-classification matrix of the stepwise linear discriminant analysis for the truss measurements of *Trachurus picturatus* for all sampling locations in the year 2016 and 2019.

Original location	Predicted location						% correct
	Azores	Canaries	Madeira	Matosinhos	Peniche	Portimão	
<b>2016</b>							
Azores	29	0	1	0	0	0	97
Canaries	0	27	2	0	1	0	90
Madeira	1	0	23	0	1	5	77
Matosinhos	0	0	1	23	3	3	77
Peniche	0	0	3	5	18	4	60
Portimão	0	0	2	5	3	20	67
Total	30	27	32	33	26	32	78
<b>2019</b>							
Azores	26	0	0	2	0	2	87
Canaries	0	25	0	0	0	0	100
Madeira	1	0	21	0	4	4	70
Matosinhos	3	0	1	21	0	5	70
Peniche	0	0	1	0	28	1	93
Portimão	0	0	1	4	0	25	83
Total	30	25	24	27	32	37	83



**Fig. 4.** Canonical analysis of principal coordinates (CAP) plots for the morphometric distances calculated for *Trachurus picturatus* collected in the six sampling locations of the NE Atlantic in the year 2016 (A) and 2019 (B). Legend: Azores (AZ), Canaries (CN), Madeira (MD), Matosinhos (MT), Peniche (PE) and Portimão (PT).

culturing conditions (i.e., temperature, hydrodynamics, food) and secondly by the parental origins. Moreover, the relationship between morphological and functional traits of fish and ecological niches, i.e., body-shape adaptation to habitat use, has been described by several authors (Price et al., 2011; Farré et al., 2013). This seems to be case for *T. picturatus* since the genetic component of this species showed a lack of genetic structure across the species distribution (i.e., NE Atlantic and the Mediterranean Sea), high levels of genetic diversity and high rates of mixing (Karaiskou et al., 2003, 2004; Moreira et al., 2019a).

Finally, the present results show the existence of phenotypic heterogeneity across the NE Atlantic *T. picturatus* populations, with the discrimination of four phenotypic stocks – Azores, Madeira, Canaries and Portugal mainland. Adding more sampling locations to the analyses provided a more extensive view of the species' population structure than the one reported by Vasconcelos et al. (2018). These results are consistent with previous observations achieved with otolith shape analysis (Moreira et al., 2019a), and otolith elemental and isotopic signatures (Moreira et al., 2018). However, data for both years showed that the species can exhibit relatively fast phenotypic adaptations, an approach that was considered for the first time in this work. Nevertheless, results indicate that, even though the species seems to function as a panmictic population, phenotypic stocks seem to exist, as a result of local adaptation to different environments. In terms of fisheries management, these stocks should be treated as separate populations, and manage accordingly. Additionally, studies on life-history parameters across all the species distribution should be enhanced and all integrated, since information structure is essential to accurately assess and manage fisheries.

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#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to

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