



**Abstract**—The population structure of the blue jack mackerel (*Trachurus picturatus*, Osteichthyes, Carangidae), in the northeast Atlantic is still unknown. To identify any distinct population units, three areas were selected: waters off Madeira, Peniche (mainland Portugal), and the Canary Islands. Knowledge of population structure is an aspect of the population dynamics of a species that is essential to effectively assess the existence of stocks and manage fisheries. In this study, geometric morphometrics and otolith shape analysis were successfully applied for population identification. Multivariate analysis of variance (MANOVA) revealed no body shape differences between males and females in each area studied, and therefore the sexes were combined for the analysis. The results of the discriminant analysis showed that a low misclassification occurred among areas; 78.0% of individuals were correctly classified. MANOVA performed on the otolith normalized elliptic Fourier descriptors revealed significant areal differences, but no difference between sexes. An overall classification success of 73.3% in the canonical discriminant analysis was achieved. These results indicate the usefulness of both otolith and body shape analysis for differentiation of blue jack mackerel stocks from the northeast Atlantic and indicate the existence of at least three distinguishable populations of this species.

## Identifying populations of the blue jack mackerel (*Trachurus picturatus*) in the Northeast Atlantic by using geometric morphometrics and otolith shape analysis

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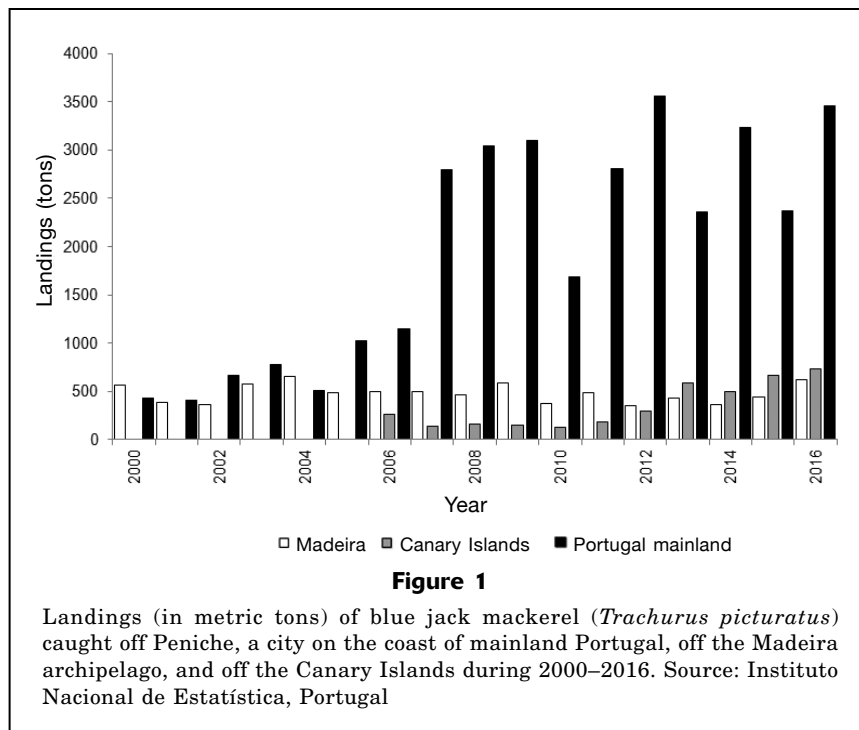
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In fisheries management, understanding population structure is key because a stock is the basic unit in population dynamic models that are used both to determine the status of a stock and to implement management actions appropriate for ensuring the sustainability of a population (Secor, 2014). Begg and Waldman (1999) suggested a holistic approach to understanding populations of fish by using both genetic and phenotypic analyses to define stock boundaries, because this integrative approach

maximizes the likelihood of correctly defining a fish stock and enables a higher degree of confidence than that generated by a single procedure.

The capacity of populations in different environmental conditions to adapt and develop as separate biological entities is counterbalanced by the shifting of individual fish among populations (Turan, 2004). However, each individual fish is characterized by a number of distinctive features that are influenced by environmental and genetic factors (Cadrin and



Friedland, 1999). Consequently, phenotypic and genetic variation among fish within a species can occur as a result of isolation, and such variation can be seen as a basis for separation of fish into groups that can be managed as distinct populations (Turan, 2004). However, areal differentiation within a species may also arise from other factors, such as 1) countergradient variation when environmental influences reinforce the genetic differences between populations (Yamahira and Conover, 2002; Barria et al., 2014), 2) thermal reaction (Yamahira et al., 2007; Yamahira and Takeshi, 2008), and 3) local adaptation and adaptive phenotypic plasticity (Yampolsky et al., 2014).

Identification of fish stocks by using shape analysis has evolved from measuring simple linear distances to deriving geometric variables (Stransky, 2014). The development of image processing tools has facilitated the change from traditional morphometrics to more complex geometric functions (Cadrin and Friedland, 1999) and has increased the power of morphometric analysis for population discrimination (Rohlf and Bookstein, 1990; Marcus et al., 1996; Cadrin and Friedland, 1999; Cadrin et al., 2014). Geometric approaches to morphometric analysis are often classified as either “landmark methods” (Cadrin et al., 2014) or “outline methods” (Bookstein et al., 1985; Marcus et al., 1996). Landmark methods are based on anatomical points or landmarks to analyze morphometry, and outline methods are used to identify different patterns of otolith shapes.

Otolith shape is species specific, is less variable than body growth for fish (Campana and Casselman, 1993), and the appearance and shape of the otolith often vary geographically for any given species (Tuset

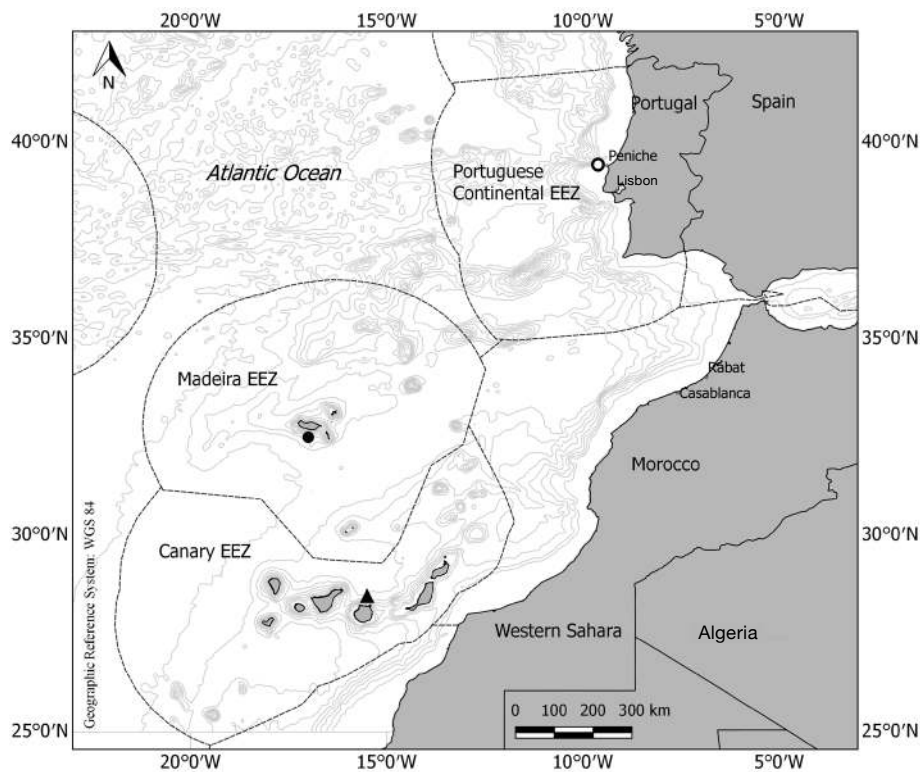
et al., 2008). Unlike scales and bones, otoliths grow during the entire life of a fish, and re-absorption or alteration of otolith material once it has been deposited is unlikely (Campana and Neilson, 1985; Casselman, 1987). Consequently, otoliths remain unchanged during short-term changes in fish condition (e.g. starvation) (Campana and Casselman, 1993). Nevertheless, environmental and genotypic factors can induce differences in metabolism and growth that might influence otolith shape (Cardinale et al., 2004). In addition, the otolith shape can vary substantially if genetic or environmental differences persist and the populations remain partially isolated and inhabit different environments (Bird et al., 1986; Campana and Casselman, 1993; Begg and Brown, 2000; Begg et al., 2001; Smith et al., 2002).

The blue jack mackerel, *Trachurus picturatus* (Bowdich, 1825) (Osteichthyes, Carangidae) is an oceanic pelagic species ranging to depths of at least 370 m (Smith-Vaniz, 1986) (575 m in the Azores, Menezes et al., 2006) and can be found from the Bay of Biscay (France) southward to Morocco and eastward into the Mediterranean Sea (Smith-Vaniz, 1986). It is a commercially important species with highly variable landings. On the Portuguese mainland, for example, landings have doubled over the last decade (INE<sup>1</sup>), while landings off the Canary Islands have tripled (Castro<sup>2</sup>) (Fig. 1).

Apart from one very recent study of parasites in

<sup>1</sup> INE (Instituto Nacional de Estatística). 2013. Estatísticas da Pesca 2012, 133 p. Instituto Nacional de Estatística, I.P., Lisboa, Portugal. [Available from [website](#).]

<sup>2</sup> Castro, J.J. 2017. Personal commun. Faculty of Marine Sciences, University of Las Palmas de Gran Canaria.



**Figure 2**

Map showing the 3 locations where blue jack mackerel (*Trachurus picturatus*) were sampled in 2015 for this study: off Peniche, a city on mainland Portugal (open circle), the Madeira archipelago (black circle), and the Canary Islands (black triangle). Source: Direção de Serviços de Investigação da Direção Regional de Pescas. The dashed lines indicate the exclusive economic zones (EEZs).

the blue jack mackerel, no other work has focused on the possible population structure over the distributional range of this fish (ICES<sup>3</sup>; Vasconcelos et al., 2017a). Interestingly, some studies on reproduction and growth from Madeira (Jesus<sup>4</sup>; Vasconcelos et al., 2006; Vasconcelos et al., 2017b), Azores (Isidro, 1990; Garcia et al., 2015) and the Canary Islands (Shaboneyev and Ryazantseva, 1977; Riviero<sup>5</sup>; Jurado-Ruzafa and Santamaría, 2013) have reported a similar reproductive season, but differences in growth and age at first maturity were observed between individuals from the Azores and those from Madeira (Jesus<sup>4</sup>; Vasconcelos et

al., 2006) and the Canaries (Jurado-Ruzafa and Santamaría, 2013). A number of studies have successfully used parasites of *T. picturatus* as biological tags (Gaevszkaya and Kovaleva, 1985; Costa et al., 2013; Vasconcelos et al., 2017a) and it may be that variation in the occurrence and infection levels of parasites may reflect the existence of different populations of *T. picturatus* in the northeast Atlantic. The goal for this study was to provide a first step toward the identification of geographical variation in blue jack mackerel body and otolith shape by using landmark-based geometric morphometrics and elliptic Fourier analysis, respectively, to determine whether variation in these parameters may have implications for fishery management.

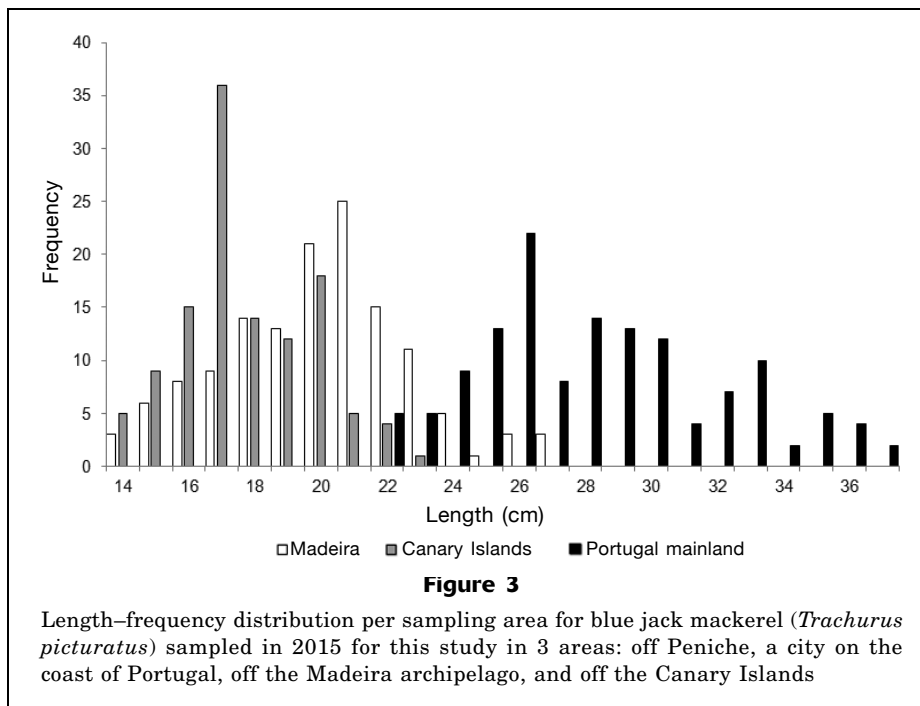
## Materials and methods

A total of 438 specimens of *T. picturatus* (135 from waters off Peniche, mainland Portugal, 155 from the Madeira archipelago and 148 from the Canary archipelago) (Fig. 2) were randomly sampled from commercial catches, per sampling period (quarter), between January and December 2015. The methods and fishing gear used to catch *T. picturatus* varied among locations:

<sup>3</sup> ICES. 2016. Report of the working group on southern horse mackerel, anchovy and sardine (WGHANSA), 24–29 June 2016, Lorient, France. ICES CM 2016/ACOM:17, 588 p. [Available from [website](#).]

<sup>4</sup> Jesus, G. T. 1992. Study of the growth and reproduction of *Trachurus picturatus* (Bowdich, 1825) in Madeira. Doc. XIV/C/1-1991/03 (DG XIV/CE), 66 p. Direção Regional de Pescas da Região Autónoma da Madeira, Funchal, Madeira, Portugal.

<sup>5</sup> Riviero, I. 2006. Biometrics of pelagic fish in Gran Canaria Island waters (Canary Islands), 17 p. Univ. Palmas-Gran Canaria, Las Palmas de Gran Canaria, Canary Islands, Spain. [Available from [website](#).]



purse seine fishing off both Madeira and the Canary Islands; and trawling off Peniche.

Samples from waters off Peniche and off the Canary Islands were stored frozen ( $-20^{\circ}\text{C}$ ) until just before they were measured at the laboratory, and all steps were taken to maintain fish shape. Fish from Madeira were analyzed fresh. From each specimen, total length was measured and, after being photographed for body shape analysis, sex was determined macroscopically. Both sagittal otoliths (hereafter referred to as otoliths) were extracted, rinsed, and stored dry in labeled vials for later otolith shape analysis.

#### Body shape analysis

A total of 300 fish equally distributed among the areas were sampled (Fig. 3): Peniche, 22–37 cm total length (TL), 40 females and 60 males; Madeira, 14–27 cm TL, 48 females and 52 males; Canaries, 16–23 cm TL, 46 females and 54 males.

Twelve anatomical landmarks (e.g., fin insertion point) were defined and used mainly along the left side of the body contour (Fig. 4), in order to be meaningful as systematic terms (Cadrin, 2000; Cadrin et al., 2014), and were based on the 11 anatomical landmarks selected for horse mackerel in a similar study (Murta et al., 2008a).

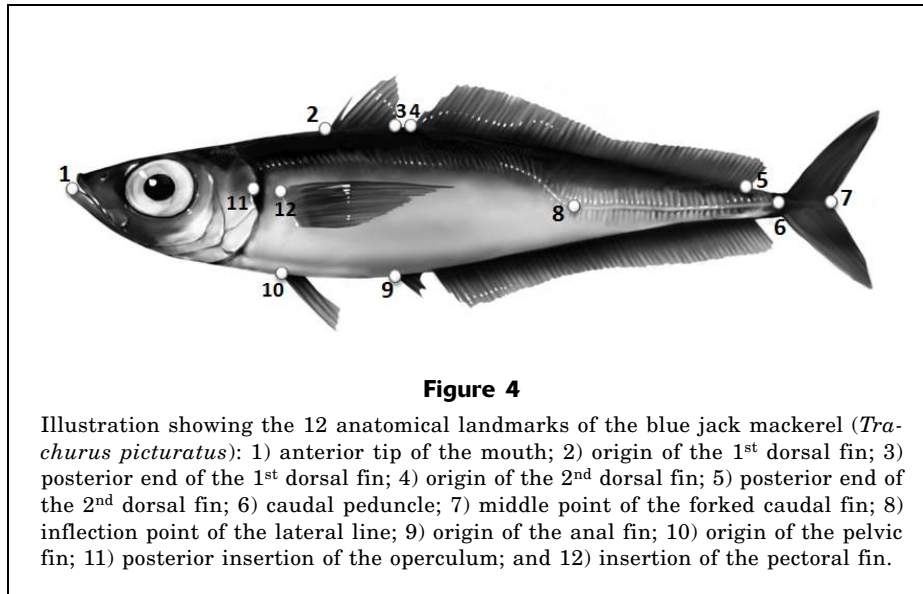
Each of the 100 fish was then photographed with the left side upwards, by using a Canon<sup>6</sup> EOS 700D digital camera (Canon, Inc., Ohta-ku, Tokyo) with

a Canon EF-S 18-55 mm lens that was placed on a firm support to maintain a right angle and adequate height to stabilize and avoid image distortion. From each digital image, a digital TPS (thin-plane spline) file was generated with x and y coordinates for each homologous point with tpsDig software, vers. 2.10 (Rohlf, 2006).

Subsequent methodological procedures followed those of Sequeira et al. (2011) and Porrini et al. (2015). The tpsDig software (Rohlf, 2006) was used to acquire x and y coordinates of the landmarks previously noted, and a generalized least squares Procrustes superimposition (Rohlf, 1990) was used to adjust them. In order to calculate and eliminate the effect of size on shape (allometry), a multivariate (total) regression of the Procrustes coordinates on centroid size was carried out with MorphoJ software, vers. 1.05c (Klingenberg, 2011) and the residuals of this regression were used as ‘size-free’ variables. To test the null hypothesis of independence between shape and size, a permutation test with 10,000 runs was applied (Good, 1994). Possible sexual dimorphism among study areas was tested by using IBM SPSS, vers. 23 (IBM Corp., Armonk, NY) and a multivariate analysis of variance (MANOVA). To detect possible morphometric differences in the body shape of *T. picturatus* among the 3 study areas, a canonical variate analysis was performed with MorphoJ. A canonical discriminant analysis with jackknife cross-validation procedures was carried out with IBM SPSS software to calculate an unbiased estimation of classification success.

A significance level of 0.05 was set for all statistical analyses.

<sup>6</sup> Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.



**Figure 4**

Illustration showing the 12 anatomical landmarks of the blue jack mackerel (*Trachurus picturatus*): 1) anterior tip of the mouth; 2) origin of the 1<sup>st</sup> dorsal fin; 3) posterior end of the 1<sup>st</sup> dorsal fin; 4) origin of the 2<sup>nd</sup> dorsal fin; 5) posterior end of the 2<sup>nd</sup> dorsal fin; 6) caudal peduncle; 7) middle point of the forked caudal fin; 8) inflection point of the lateral line; 9) origin of the anal fin; 10) origin of the pelvic fin; 11) posterior insertion of the operculum; and 12) insertion of the pectoral fin.

### Otolith shape analysis

A total of 277 otoliths were analyzed (Fig. 3): 100 from waters off Peniche (22–37 cm TL, 40 females and 60 males), 100 off Madeira (15–27 cm TL, 50 females and 50 males), and 77 off the Canary Islands (14–23 cm TL, 34 females and 43 males).

The otoliths were positioned on a microscope slide and photographed with the sulcus acusticus facing down and the rostrum to the left on the horizontal plane to reduce distortion errors in the normalization process. High-contrast digital images were captured by a Leica EC3 digital camera (Leica Microsystems, Wetzlar, Germany) linked to a Leica MZ9.5 stereomicroscope that uses transmitted light and with the software Leica Application Suite X Core, vers. 4.5, that delivers dark 2-dimensional objects against a white background. The microscope magnification was adjusted to the largest otolith size to ensure the same magnification (8 $\times$ ) for all otoliths.

The image processing program SHAPE, vers. 1.3 (Iwata and Ukai, 2002), was used to enhance contrast of the images, transforming color or grayscale images to black-and-white silhouettes of the structure (Cadrin and Friedland, 2005). Otolith contours were extracted as chain-codes from the digital image by means of the ChainCoder package that is part of SHAPE. The elliptic Fourier descriptors, or harmonics, were obtained from the SHAPE package Chc2Nef by using a discrete Fourier transformation of the chain-coded contour (Kuhl and Giardina, 1982; Lestrel, 1989, 1997). The four coefficients of each harmonic were normalized in relation to the first harmonic to become invariant to otolith size, rotation, and starting point (Kuhl and Giardina, 1982; Iwata and Ukai, 2002). The first three coefficients of the first harmonic were degenerated to fixed values:  $a_1=1$ ,  $b_1=c_1=0$  (Tracey et al., 2006).

A random subsample of 10 otoliths for each sex and area was used to define the minimum number of harmonics needed (99% accumulated variance) for the multivariate analysis. For each otolith, 100 harmonics were generated. Possible effect of area and sex on otolith normalized elliptic Fourier descriptors (NEFDs) was tested by using MANOVA. To detect possible morphometric differences in the contour shape of otoliths from the three studied areas, a canonical discriminant analysis was performed and a jackknife cross-validation procedure was carried out with IBM SPSS software to validate similarities between groups by listing the misclassification of individuals within other areas (Neves et al., 2011; Vieira et al., 2014).

A significance level of 0.05 was set for all statistical tests used.

### Results

#### Body shape analysis

No shape differences were found between males and females within the three areas under study (Madeira:  $F=0.15$ ,  $P=0.72$ ; Peniche:  $F=0.68$ ,  $P=0.83$ ; Canary Islands:  $F=0.40$ ,  $P=0.59$ ), and therefore sexes were pooled for each region.

A significant difference in the mean body shape of blue jack mackerel was found for each of the three study areas (Table 1). The overall assignment of blue jack mackerel individuals in their original sample was correctly classified for 78.0% of the total number of specimens (Table 2). In the jackknifed classification matrix of the discriminant analysis, a proportion of 33.0% of the specimens from Madeira were incorrectly assigned to the Canary Islands (23.0%) and Peniche (10.0%). Misclassifications also occurred between the

**Table 1**

Procrustes distances for the mean body shape of blue jack mackerel (*Trachurus picturatus*) from the 3 areas sampled in this study in 2015, off the Madeira archipelago, off Peniche on mainland Portugal, and off the Canary Islands. Corresponding *P*-values (in parentheses) obtained from a permutation test (10,000 permutation runs) are also given. The results indicate that all of the mean body shapes are statistically different between the 3 areas.

Region	Madeira	Mainland Portugal	Canary Islands
Madeira	-	0.03 (<0.0001)	0.03 (<0.0001)
Mainland Portugal	-	-	0.03 (<0.0001)

**Table 2**

Classification matrix from the discriminant analysis performed by using a jackknife procedure for cross-validation of the body shape of individual blue jack mackerel (*Trachurus picturatus*) sampled from 3 areas in the northeast Atlantic Ocean in 2015: off the Madeira archipelago, off mainland Portugal, and off the Canary Islands. Values are percentages of individuals sampled in the areas (given in rows) that were classified into the area given in columns (values for correct classification are presented in bold). Overall classification success was 78.0%.

Region	Madeira	Mainland Portugal	Canary Islands
Madeira	<b>67.0</b>	10.0	23.0
Mainland Portugal	13.0	<b>83.0</b>	4.0
Canaries	11.0	5.0	<b>84.0</b>

Canary Islands and Peniche (5.0%) and Madeira (11.0%), as well as between Peniche and the Canary Islands (4.0%) and Madeira (13.0%). However, the percentage of individuals incorrectly classified between the referred locations was low. The proportion of correctly classified samples off Peniche (83.0%) and the Canary Islands (84.0%) to their original group was highest, showing a clear separation from samples off Madeira (67.0%).

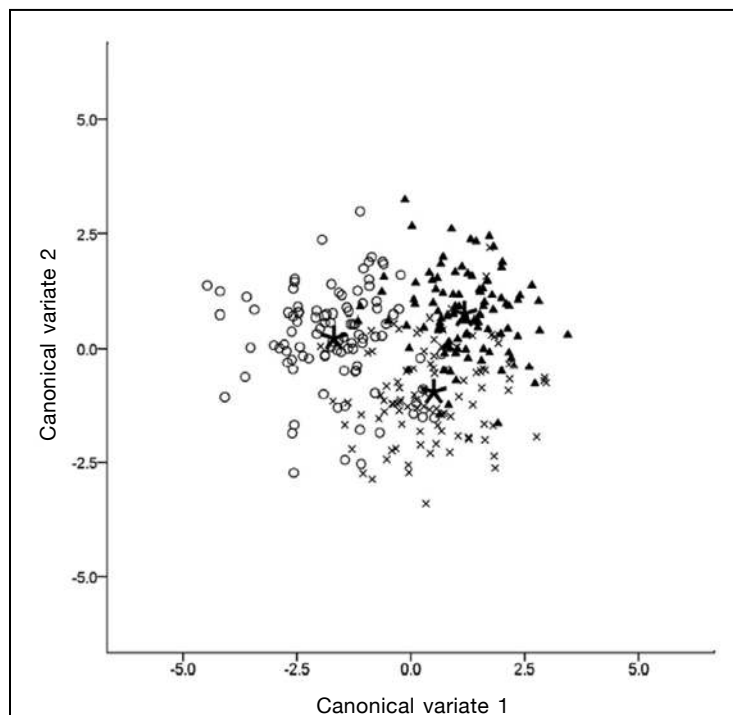
The 2-dimensional ordination plot (Fig. 5) showed a differentiation of stocks for the three areas studied, but with some overlapping of stocks mainly between Madeira and the two other areas; the Canary Islands and Peniche seem to be more distinct from each other. The first two canonical variate analysis accounted for 74.5% and 25.5% of the between-group variability.

#### Otolith shape analysis

The mean and standard deviations of the cumulative variance of the harmonics are shown in Figure 6. Only the first 15 harmonics were used for multivariate analysis because these were responsible for over 99% of the otolith shape variation.

Figure 7 represents the outlines of the mean NEFDs, by region, plotted as an overlay picture to enhance differences in average otolith shapes. Overall, the highest shape variation among areas occurred in the excisura ostii and antirostrum. Variations also occurred in the dorsal and ventral edges of the otolith.

The results of the MANOVA applied to compare the NEFDs by area and sex are shown in Table 3. Because neither differences in otolith shape between males and females within the three areas, nor interaction between

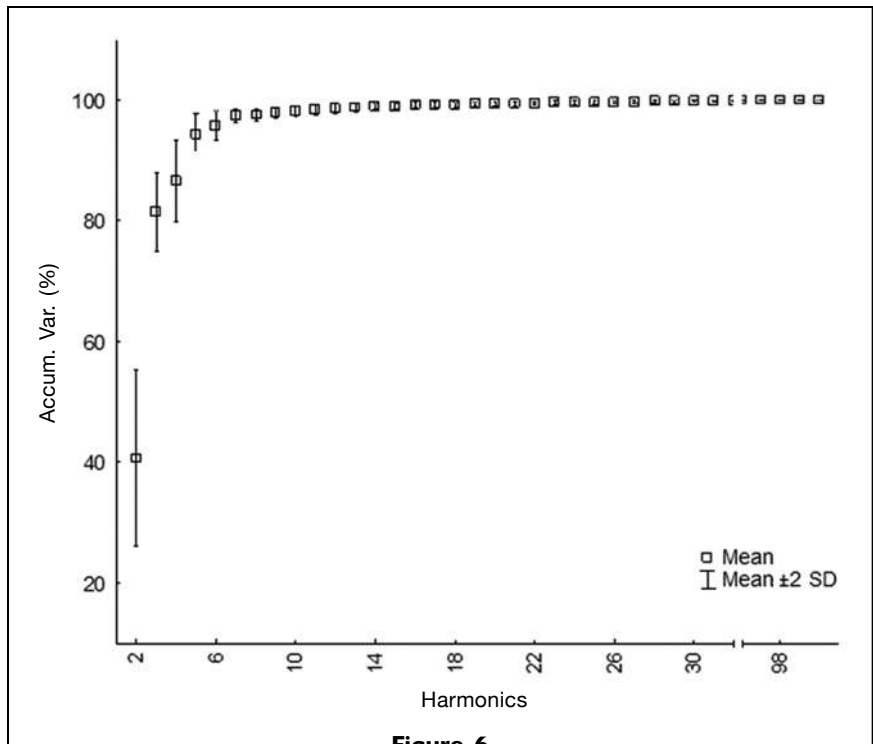
**Figure 5**

Two-dimensional ordination plot of the samples of blue jack mackerel (*Trachurus picturatus*), collected in 2015 from off the Madeira archipelago (black crosses), off mainland Portugal (open circles), and off the Canary Islands (black triangles), based on canonical variate analysis. Stars indicate class centroids per sampled area (each individual was allocated to the group with the nearest centroid).

area and sex, were found, all subsequent analyses were performed for sexes combined.

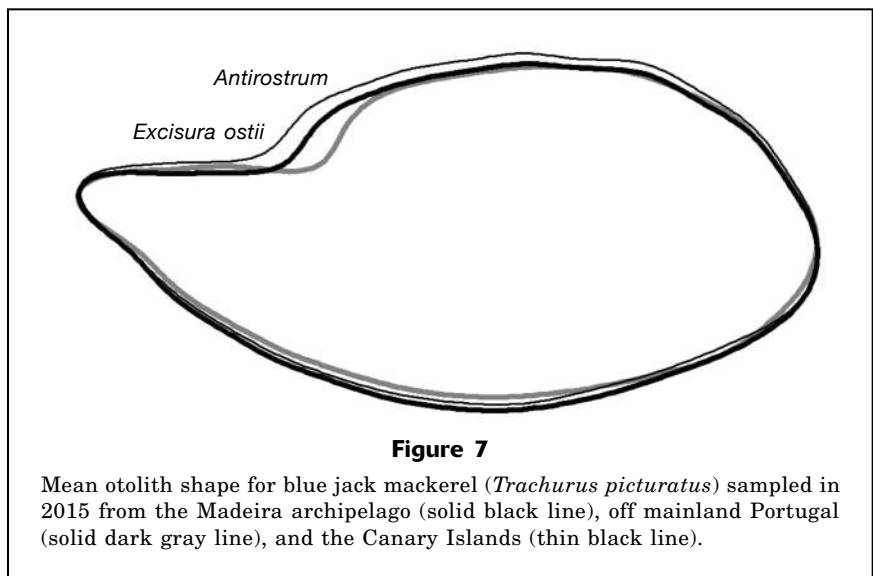
The variables used in the stepwise discriminant analysis are represented in Table 4. For the analysis





**Figure 6**

Mean and standard deviation (SD) of the cumulative variance of 100 harmonics for 60 randomly selected otoliths of blue jack mackerel (*Trachurus picturatus*) taken from fish sampled in 2015 in the northwest Atlantic Ocean. Mean (open squares) and standard deviation (whiskers) values represent the accumulated percentage of variance (% accum. var.) explained by the *n*th harmonic.



**Figure 7**

Mean otolith shape for blue jack mackerel (*Trachurus picturatus*) sampled in 2015 from the Madeira archipelago (solid black line), off mainland Portugal (solid dark gray line), and the Canary Islands (thin black line).

13 variables were used. The differences among the three areas shown by the MANOVA were also supported by the MANOVA performed on the otolith NEFDs. An overall successful classification rate of 73.3% in the

canonical discriminant analysis was achieved for both sexes combined (Table 4). The highest classification rate was found for specimens from Peniche with 89.0% classification success, whereas specimens from the Ca-

**Table 3**

Summary of results from a multivariate analysis of variance (MANOVA) ( $n=300$ ) on normalized elliptic Fourier descriptors for otoliths of blue jack mackerel (*Trachurus picturatus*) sampled in 2015 from the Madeira archipelago, off mainland Portugal and off the Canary Islands. Results include the test statistics Pillai's trace and Wilks'  $\lambda$ . df=degrees of freedom (numerator, nominator).

	Pillai's trace	Wilks' $\lambda$	df	P-value
Area	1.09	0.15	114.43	<0.0001
Sex	0.23	0.77	57.22	0.27
Area * sex	0.43	0.62	114.43	0.41

nary Islands showed the lowest classification success with 62.3%.

The two discriminant functions were significant and discriminated the three areas studied (f1:  $\lambda=0.26$ ,  $P<0.0001$ ; f2:  $\lambda=0.85$ ,  $P<0.0001$ ). The score plots for the first 2 discriminant functions (Fig. 8) showed a separation between the 3 areas studied, but some overlapping can be observed. The first discriminant function explained 92.6% of between-group variance.

## Discussion

The blue jack mackerel population structure in the southern part of the northeast Atlantic (Peniche–Madeira–Canary Islands) was unknown before this study. The present results reveal the usefulness of anatomical geometric morphometric and otolith shape analysis in supporting the existence of three stock units of blue jack mackerel in the southern northeast Atlantic. The same holistic approach that we applied was also used to discriminate the stocks of another species of the genus *Trachurus* in the northeast Atlantic Ocean and Mediterranean Sea, the horse mackerel (*Trachurus trachurus*). The body shape (Murta et al., 2008a) and otolith shape (Stransky et al., 2008) analysis provided evidence of a consistent separation between Atlantic and Mediterranean locations, with 90% correct allocation of individuals of each stock in the otolith shape analysis (Murta et al., 2008a; Stransky et al., 2008).

Ideally, a sampling strategy should focus on a specific time scale (e.g. spawning season) and on a specific length or age range of fish. Adherence to this strategy would have enhanced our results, but different fishing methods did not allow the implementation of an ideal sampling strategy. To overcome this potential weakness, the corrections used in both analyses removed the effect of size on shape. High values of classification success (78.0% and 73.3%) were achieved in the canonical discriminant analysis used in both anatomical morphometric and otolith shape analysis, respectively,

**Table 4**

Classification matrix of the discriminant analysis performed by using a jackknife procedure for cross-validation of the otolith shape of individual blue jack mackerel (*Trachurus picturatus*) sampled from 3 areas in the northeast Atlantic Ocean in 2015: off the Madeira archipelago, off mainland Portugal, and off the Canary Islands. Values are percentages of individuals sampled in the areas given in rows that were then classified into the areas given in columns (values for correct classification are presented in bold). Overall classification success: 73.3%, Wilks'  $\lambda=0.26$ . In the discriminant analysis, 13 variables were used.

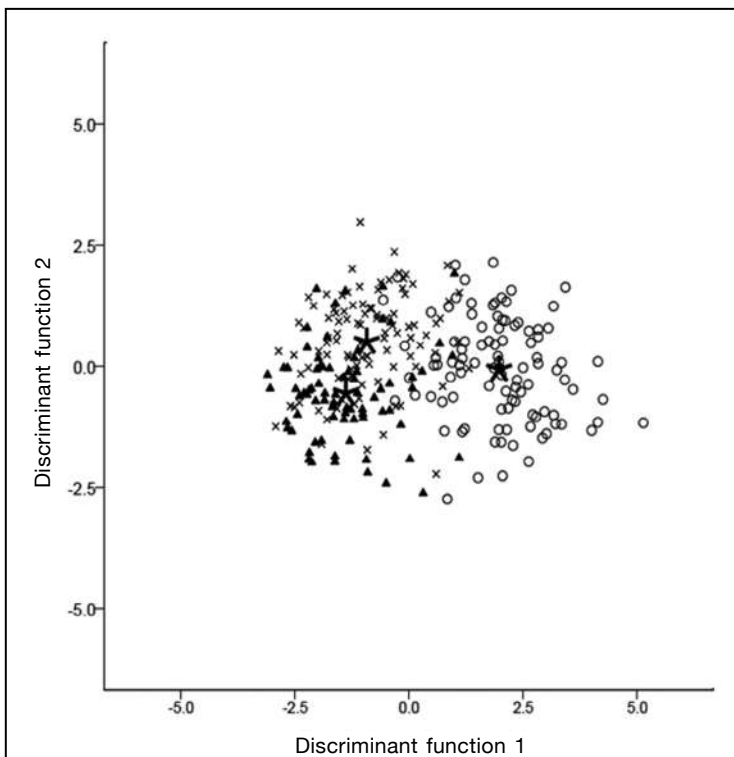
Region	Madeira	Mainland Portugal	Canary Islands
Madeira	<b>66.0</b>	10.0	24.0
Mainland Portugal	9.0	<b>89.0</b>	2.0
Canaries	31.2	6.5	<b>62.3</b>
Variables	d7, b9, c8, b8, c13, c15, d13, d12, d15, c5, a5, c14, c9		

indicating three phenotypically distinct local populations. No differences between sexes were observed by using either technique.

Using both analytical techniques, we found the highest percentages of misclassification for specimens from Madeira that were classified in the Canary Islands group and vice-versa. This overlap between areas may be indicative of some degree of migration between these two populations. In general, the migratory movements of the blue jack mackerel are driven by feeding and spawning requirements (Menezes et al., 2006) and where seamounts are used as feeding areas in their preadult and adult phase, but it is likely that there are immigrants to the seamount from the island shelf areas (Menezes et al.<sup>7</sup>). Differences in the biological and physical environments of hatchery and nursery areas can also result in morphometric variations between these populations (Robinson et al., 1993; Chipps et al., 2004; Vila-Gispert et al., 2007). Other, non-environmental factors may also contribute to differences among populations. For example, a greater growth capacity in high-latitude populations reflects an adaptation that would counteract a slowing of growth rate over the growing season; otherwise a reduction in annual growth rates of individuals with increasing latitude would be expected because of the shorter growing seasons at higher latitudes that result in a reduction in body size (Conover and Present, 1990; Yamahira et al., 2007). Yamahira et al. (2007) observed that individ-

<sup>7</sup> Menezes, G., A. Rogers, H. Krug, A. Mendonça, B. M. Stockley, E. Isidro, M. R. Pinho, and A. Fernandes. 2001. Seasonal changes in biological and ecological traits of demersal and deep-water fish species in the Azores, 164 p. Univ. Açores, Dep. Oceanogr. (DOP), Arquivos DOP Sér. Estud. 1/2001.





**Figure 8**

Plots of function scores determined with discriminant analysis, with sexes combined, for blue jack mackerel (*Trachurus picturatus*) sampled in 2015 from off the Madeira archipelago (black crosses), off mainland Portugal (open circles), and off the Canary Islands (black triangles). Scores were based on 57 normalized elliptical Fourier descriptor coefficients of the first 15 harmonics. Stars indicate class centroids per area sampled (each individual was allocated to the group with the nearest centroid).

uals at higher-latitudes did not only grow faster than lower-latitude individuals but also at all temperatures that they examined and suggested that populations moving to higher latitudes have developed a capacity for growth by vertically shifting the thermal reaction norms for ascendant growth rates. These thermal reactions results in an increase in the growth rates of individuals at a certain temperature (Yamahira and Takeshi, 2008). Local adaptation in its two forms (temperature adaptation and countergradient variation) may also be expected to vary within and among species (Yamahira and Conover, 2002).

The results of this study reveal a clear differentiation between Peniche and the Macaronesian archipelagos, especially between Peniche and the Canary Islands. This differentiation may be due to an adaptation of the population off mainland Portugal to high-latitude environments, and therefore to a faster growth rate than that of the Canary Islands population. Considering that the northeast Atlantic system, the Canary Islands, and the region of the Iberian Peninsula form two quite distinct subsystems (Dias, 2015), their separation

is not only geographic but also a result of the unique oceanographic features of the northeast Atlantic region; the discontinuity of currents imposed by the flow of the Mediterranean Sea through the Strait of Gibraltar to the Gulf of Cadiz (Dias, 2015). These subsystems may be seen as biogeographic breaks that often result in abrupt changes in phenotypic traits among resident populations (Barria et al., 2014). This separation may explain our results that show low levels of population mixture between the Canary Islands and Peniche.

Both archipelagos, i.e. Madeira and the Canary Islands, are under the influence of the subtropical gyre of the eastern central Atlantic, which would facilitate the transport of planktonic larvae to these archipelagos from American, European, and northwest African coasts. This gyre may influence the mixing levels found between the two archipelagos in our study. In the case of the Canary Islands (relatively close to Africa—104 km from Cape Juby, Morocco), a strong mesoscale distribution of the larval community has been recently described from filaments of the upwelling system from Africa reaching the southeast of this archipelago (Rodríguez et al., 2004; Bécognée et al., 2009). This pattern in the larval community corroborates our findings and supports the distinction of the Madeira and Canary Islands stocks, although some mixing of fish from these two archipelagos exists.

The final determination of the existence of stocks of blue jack mackerel in the northeast Atlantic for assessment and ultimately the management of the fisheries must obviously be based on more than one method or single result. Clearly, the most successful way of defining stock limits is through a holistic approach, involving a combination of a broad spectrum of complementary techniques (Begg and Waldman, 1999) which will, in combination, provide considerable insight into the practical identification and delineation of individual population subunits or stocks (Elliott et al., 1995; Cadrin et al., 2005; Waldman, 2005; Waples et al., 2008). The different methods (e.g., life history parameters, tagging, otolith elemental composition, fatty acid profiles, parasites as biological tags, morphometric landmarks, morphometric outlines, and genetic analysis) that can be used to identify stocks were exhaustively compiled by Cadrin et al. (2005) and updated by Cadrin et al. (2014). Considering the existence of three possible *T. picturatus* populations as suggested by the results of the present work and in order to maintain the sustainability and genetic biodiversity (Begg and Waldman, 1999) of this resource in Madeira, the management strategy should be one in which a precautionary approach is taken (e.g., to regard the fish in the three areas studied as separate stocks) while other avenues of research are being pursued. A failure to ac-

knowledge these stocks as separate stocks may lead to flawed management actions and ultimately to overexploitation. However, the results obtained here suggest that there may be a mix (below 32% misclassification) of individuals of different stocks, namely between Madeira and the Canary Islands, which could offer a buffer against any regional overexploitation. This finding implies that, for an accurate assessment of the overall population and state of each stock, its boundaries should not only be defined but also an estimate should be made of the proportion of mixing of fish from the different population units, by location and time of year during which the mixing of stocks occurs (Murta et al., 2008b).

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