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Use of otolith-shape analysis for stock discrimination of Boops boops along the Algerian coast (southwestern Mediterranean Sea)

Ider Djamila [1], Ramdane Zouhir [1], Mahe Kelig [2], Dufour Jean-Louis [2], Bacha Mahmoud [3], Amara Rachid [3, *]

* Corresponding author : Rachid Amara, email address : rachid.amara@univ-littoral.fr

Abstract :

Otolith-shape analysis was examined to determine its utility for biological stock identification of the bogue Boops boops along the Algerian coast of the Mediterranean Sea. The outlines of 179 sagittal otolith pairs from fish collected at three locations (Oran, Bejaia and Annaba) between 2013 and 2016 were digitised and analysed for shape variation by elliptical Fourier analysis. Potential confounding sources of variation (fish length, age and sex, and left or right otolith position) were examined and accounted for in the analyses before interpretation of spatial differences in distribution of the stock. Redundancy analysis showed a significant difference between the left and right otoliths. No difference was correlated with sex and age, but fish length and sampling location had a significant effect on otolith shape. Differences in otolith shape between fish from the three locations (a span of approximately 1 000 km) were not large enough to support the concept of separate biological stocks of B. boops along the Algerian coast, as illustrated by the scatterplot of discriminant scores. This study emphasises the need to carefully evaluate the confounding effects of the otolith side (left or right) on the Fourier descriptors of otoliths before drawing conclusions about stock structure of the bogue on the basis of otolith-shape differences among samples of fish from different stocks or areas.

Keywords : biological stocks, elliptical Fourier analysis, image analysis, linear discriminant analysis, marine fish, principal components analysis, sex differences

Introduction

Knowledge of population structure and stock identification is of primary importance for successful management and conservation of marine fishery resources. Stock identification of fish is also fundamental for understanding the population dynamics of a species in an ecological sense (Mérigot et al. 2007). Stocks can be defined as intraspecific groups of randomly mating individuals with temporal or spatial integrity (Ihssen et al. 1981). Few fish species form single homogeneous populations and most are composed of discrete stocks (Reiss et al. 2009; Jemaa et al. 2015a). There is growing recognition that many marine fish stocks consist of amalgamations of several isolated geographic components even if they are genetically the same (Baibai et al. 2012; Bacha et al. 2014, 2016; Jemaa et al. 2015a). These local and isolated groups of fish may have unique demographic properties such as growth and reproduction and should be managed separately. Among the methods used to identify stocks, the study of the morphological characteristics of otoliths has been considered an efficient tool (Campana and Neilson 1985). Otolith-shape analysis has been used widely with success in stock-identification studies of various marine fish species (Mérigot et al. 2007; Stransky et al. 2008; Agüera and Brophy 2011; Jemaa et al. 2015b). The otolith shape, among other morphometric traits, like the body shape, is a characteristic that reflects a combined effect of genetic variation and local environmental factors (Campana and Casselman 1993; Cardinale et al. 2004; Vignon 2015). Otoliths are recorders of growth and their structure and development are influenced by external environmental conditions as well as the physiological state of individual fish (Campana and Neilson 1985); these characteristics can vary between populations, and therefore otoliths may show characteristics that are stock-specific.

The bogue *Boops boops* (L.) is a teleost belonging to the family Sparidae. It is a common and ubiquitous species in the North-East Atlantic and Mediterranean. *B. boops* is a gregarious, demersal, semi-pelagic species found as deep as 350 m over a variety of substrata including sand, mud, rocks and seaweeds, though it is more common at depths of less than 150 m and sometimes in coastal waters. This species moves in aggregations, ascending to the surface mainly at night. The bogue was found to grow quickly in length during the first year of life, reaching 53.49% of its final growth **length'** and can live to seven years (Pollard et al. 2014). Sexual maturity is attained at between one and three years of age at about 15.2 cm (Khemiri et al. 2005; Monteiro et al. 2006).

B. boops is one of the most abundant species in the Mediterranean Sea, and global captures were of 36 854 tonnes (t) in 2015 according to the Food and Agriculture Organization (FAO) of the United Nations (http://www.fao.org/fishery/statistics/GFCM-capture-production/query/fr). The largest catches in 2015 were reported in the southern part of the Mediterranean Sea; Algeria (4 563 t), Tunisia (3 397 t) and Egypt (2 240 t), and also in the northern part; Greece (2 914 t), Italy (1 117 t) and Turkey (2 208 t). In Algeria, *B. boops* constitute **is the target of'**an important fishery and the Algerian catches of the species are the highest of the Mediterranean Sea.

Although many aspect of its biology have been described (Khemiri et al. 2005; Monteiro et al. 2006; Ramdane et al. 2013; Ichalal et al. 2015; Soykan et al. 2015), there is no information on its population structure. Only Pérez-del Olmo et al. (2010) used, with success, parasites as tags for the delineation of different populations/stocks of *B. boops* from the Mediterranean and NE Atlantic. Previous studies along the Algerian coast showed that for pelagic fish species such as anchovy *Engraulis encrasicolus* or sardine *Sardina pilchardus* there was no population structure (Jemaa et al. 2015a, 2015b). As the bogue is a demersal and sedentary species with limited horizontal displacement (Harmelin 1987) we may suspect some population structure.

The aim of this study was to analyse otolith shape variability in *B. boops*, a gregarious species with limited horizontal migration, along the Algerian coast and to examine its potential to elucidate population structure.

Material and methods

Sample collection

Bogue samples were collected from landing ports along the Algerian coast at three localities (Annaba, Bejaia and Oran) between 2013 and 2016 (Figure 1). In the laboratory, 179 individuals were measured (total length [TL], mm) to the nearest 1 mm, weighed (eviscerated weight [W], g) with a precision of 0.1 g and sexed. Sagittal (left and right) otoliths were then extracted, washed, cleaned in distilled water, and then dried and stored in labelled plastic tubes. Fish sampling details are summarised in Table 1. In order to estimate the age of each individual, whole sagittal otoliths were examined by two different experts in order to limit interpretation error. To increase the visibility of the growth marks, otoliths were covered with essential oil of cloves and then observed with a stereomicroscope under reflected light over a dark background.

Otolith shape analysis

Both left and right otoliths were used for shape analysis. To minimise distortion errors within the normalisation process during image analysis, the otoliths were placed on microscope slide with the sulcus facing downwards and the rostrum pointing leftwards. The otolith outlines were digitised using an image analysis system consisting of a high resolution Sony video camera connected to an optical microscope. High-contrast video images were obtained using reflected light. Each digitised image was analysed using the image-analysis software TNPC (digital processing for calcified structures, www.tnpc.fr). In order to compare left and right otolith shapes, a mirror image of the right otoliths was used. To describe otolith contours, elliptic Fourier analysis (EFA; Lestrel 2008) was carried out. For each otolith, the first 99 elliptical Fourier harmonics (Hi) were extracted and normalised with respect to the first harmonic using the TNPC software and were, thus, invariant to otolith size, rotation and starting point of the shape measurements (Kuhl and Giardina 1982). To determine the number of harmonics required to reconstruct the otolith outline, the Fourier power (PF) was calculated for each individual otolith *k* as a measure of the amount of contour rebuilt by each harmonic $F(n_k) = \mathrm{HI} = 1 n_k \frac{A_{\mathrm{HI}}^2 + B_{\mathrm{HI}}^2 + C_{\mathrm{HI}}^2 + D_{\mathrm{HI}}^2}{2}$

where A_{HI}, B_{HI}, C_{HI} and D_{HI} are the parameters of the HIth harmonic and n_k is the total number of harmonics included. The value of n_k was chosen such that PF (n_k) explains 99.99% of variance in contour coordinates or, in other words, such that shape is reconstructed at 99.99% (Lestrel 2008).

Statistical analysis

Before investigating spatial variation in otolith shape, differences due to factors such as fish length and sex and the effect of inner-ear location (side) were investigated. Firstly, principal components analysis (PCA) was applied to selected elliptical Fourier descriptors (EFDs) matrix (EFDs as columns and individual otoliths as rows) of otolith contours (Rohlf and Archie 1984) and a subset of the resulting principal components were selected as otolith shape descriptors according to the broken-stick model, where relevant principal components (PCs) explaining more variance than expected by chance alone were evaluated according to the model *sensu* Jackson (1993) and Legendre and Legendre (2012). This allowed us to decrease the number of variables used to describe otolith-shape variability while ensuring that the main sources of shape variation were kept, as well as to avoid co-linearity between shape descriptors (Rohlf and Archie 1984). Subsequently, the relevant PCs were used as input variables of a partial redundancy analysis (pRDA) with side (left/right) as a potentially influential variable. RDA is an extension of multiple regressions to multivariate response data and an extension of principal components analysis (Legendre and Legendre 2012), combined with permutation tests (marginal effect, type II; Fox and Weisberg 2011) on the selected principal components (PC) matrix generated from the broken-stick model. To visualise differences in otolith shape between right and left sides, an average otolith shape of each side group was rebuilt based on average EFDs. To investigate variation sources for otolith shape differences due to other factors such as fish length, sex and sampling area, the same statistical process was carried out on the otolith from only one side, by specimen. Using an RDA, the potential effects of total length, sex, sampling year and geographic area were tested with the explained matrix combined with permutation tests on the selected PC matrix (generated from the broken-stick model applied on the PCA). To test the significance of each explanatory variable, a permutation test (marginal effect, type II) was used (Legendre and Legendre 2012).

To discriminate fish classified in three sampled areas based on their otolith shapes, a linear discriminant analysis (LDA) with jackknifed prediction was applied on the residuals of the RDA model to remove the significant effects tested previously on the otolith shape (Rencher and Christensen 2012). To evaluate the resulting discriminant functions, the percentage correct classification of individuals to sampling area was calculated using jackknife cross-validation and Wilk's lambda criteria (Klecka 1980).

All statistical analyses were performed using the 'Vegan' (Oksanen et al. 2013), 'MASS' (Venables and Ripley 2002), 'CAR' (Fox and Weisberg 2011), 'FactoMinR' (Lê et al. 2008), 'HH' (Heiberger and Holland 2004) and 'Ellipse' (Murdoch and Chow 1996) packages in the statistical environment R (R Core Team 2014).

Results

There was a significant linear relationship between fish length and otolith length (Figure 2). Among the 99 Fourier harmonics extracted to describe otolith contours from left and right otoliths of 179 individuals, the individual Fourier power was calculated and the first 23 harmonics explained more than 99.99% of the otolith shape variation for all individual shapes. As the fish analysed ranged between 12.9 and 26 cm in length, shape differences between the right and left otoliths were analysed for all the fish and separately for the smaller fish (TL < 15 cm) and larger fish (>15 cm). In all cases, the redundancy analysis (RDA) tests of both saggital otoliths showed a significant difference between the left and right otoliths (p = 0.001) (Figure 3).

As the effect of side was significant, only right sagittal otoliths were used for the following analyses. Only the first seven PCs of principal components analysis were significant as determined by their eigenvalues exceeding the threshold eigenvalue generated randomly by the broken-stick model (>3.36% of the total variance). The effect of total length, sex, age and sampling **location** were tested by an RDA. Sex (p = 0.124) and age (p = 0.561) have no significant effect on otolith shape. Only fish length (p = 0.001) and sampling area (p = 0.003) had a significant effect on the otolith shape. Consequently, the LDA was carried out on the residuals of RDA to remove the length effect. The analysis showed significant differences among groups of bogue sampled in the three locations along the Algerian coast (Wilks' λ = 0.622; F = 7.638; p = 0.001). The overall jackknifed classification success was 67%. The misclassification percentage for each sampling location was explained by the proximity of the sites (Table 2). Fish from Bejaia had the highest percentage of individuals successfully classified (83%). The misclassification percentage was very low between the two extreme sites, Annaba in the east and Oran in the west. To visualise differences in average shapes between geographical areas, the reconstructed outlines of the mean Fourier harmonics of the three sampling locations were plotted as overlay picture (Figure 4). Only minor differences between average shapes were observed. The main shape difference between the three geographical areas occurs in the area between antirostrum and rostrum. The differences found in the otolith shape between the three areas were not large enough to support the concept of separate biological stocks of *B. boops* along the Algerian coast as illustrated by the scatterplot of discriminant scores (Figure 5).

Discussion

To use otolith-shape variability properly for stock identification studies, it is important to consider the intrinsic factors that may affect shape variability. In the present study, the use of redundancy analysis (RDA) showed that the shapes of the right and left otoliths of *B. boops* were significantly different. Such otolith-shape differences between the right and left inner ears are common in flatfish species (Mérigot et al. 2007; Mille et al. 2015), due to body morphology asymmetry and lateralised behaviour. These differences are usually not observed for roundfish (Panfili et al. 2002; Lychakov and Rebane 2005), although some differences were reported in species such as whiting *Merlangius merlangus* (Mille et al. 2015) and annular seabream *Diplodus annularis* (Trojette et al. 2015). Differences observed in roundfish species are difficult to explain and further studies are needed to improve knowledge on otolith biomineralization and the physiological mechanisms that produce changes in otolith asymmetry (Mille et al. 2015). In the light of our result, it is recommended that *B. boops* studies based on otolith shape should always use otoliths from the same side.

We found no significant difference in otolith shape between sexes, which is also the case in, for example, Atlantic mackerel *Scomber scombrus* (Castonguay et al. 1991), Atlantic cod *Gadus morhua* (Cardinal et al. 2004) and blue whiting *Micromesistius poutassou* (Mahé et al. 2016), but not, for example, Atlantic herring *Clupea herengus* (Bird et al. 1986; Mille et al. 2015), silver hake *Merluccius bilinearis* (Bolles and Begg 2000) and forkbeard *Phycis phycis*

(Vieira et al. 2014). Although no sexual dimorphism in otolith shape was observed in the bogue, the effect of sex on otolith shape must be checked to avoid introducing bias into the analysis of otolith-shape variation.

Not accounting for age effects may result in falsely attributing shape differences between samples to a stock effect, whereas they may in fact reflect differences in age structure (Castonguay et al. 1991) because the age of fish can have a considerable influence on otolith shape (Campana and Casselman 1993). We found no significant effect of age on bogue otolith shape. This is probably because we have analysed only fish older than 2 years, corresponding to the period of slowdown in growth (Pollard et al. 2014). Indeed, for the majority of fish species, most of the growth generally occurs during the first year of life, which results in a distinct otolith shape of younger fish compared to that of older age groups (e.g. Jemaa et al. 2015b; Bacha et al. 2016).
In otolith-shape studies, size must be considered as a confounding factor and source of variability since it is associated with individual growth (Campana and Casselman 1993). In the present study, otolith-shape analyses were carried out on the residuals of RDA to remove the length effect.

The elliptical Fourier analysis used in this study has proven to be the most powerful and appropriate method for otolith-shape analysis since it can capture the entire shape variation and small-scale individual differences in the otolith outline (Campana and Casselman 1993). The RDA analysis showed differences among groups of bogue sampled in the three locations along the Algerian coast. The overall jackknifed classification success was 67% higher than the random value (33%). The misclassification percentage was low between the two extreme sites, Annaba in the eastern part and Oran in the western part of the Algerian coast. The central site, Bejaia, seems to correspond to a mixing zone for fish from the eastern and western parts of the coast. However, the differences in otolith shape between the three locations studied, which were spaced by about 1 000 km in total, were not large enough to support the concept of separate biological stocks of *B. boops* along the Algerian coast. These results agree with a previous study suggesting the existence of one anchovy stock along the Algero-Provencal Basin (Bacha et al. 2014). It has been suggested that differences in environmental conditions can have a considerable influence on how otoliths grow and consequently how otolith shapes are formed (Campana and Neilson 1985). Many studies have demonstrated that otolith morphology can vary in response to differences in growth regimes for a range of species (Cardinale et al. 2004). Gauldie and Nelson (1990) found that growth rates had a direct link to otolith shape because faster growth usually produces longer and thinner otoliths. A recent study (Vignon 2015) established that local environmental conditions induce an important change in otolith shape. Indeed, various environmental factors such as water temperature, depth and feeding conditions (Gauldie and Crampton 2002; Cardinale et al. 2004; Gagliano and McCormick 2004) influence fish growth, which in turn can affect otolith growth and hence produce variations in otolith shape.

The bogue is an opportunistic and omnivorous species and feeds on benthic prey (with no variation in diet according to sex) (Derbal and Kara 2008). It is an erratic species with a high capacity for vertical displacement but with limited horizontal displacement, and hence can be considered a sedentary species (Harmelin 1987). The bogue is one of the most common of the Sparidae on the Algerian coast but its biology is still little-studied (Derbal and Kara 2008). There are no studies that have compared the growth or the feeding of the bogue along the Algerian coast. As fish growth may affect otolith size (Campana and Casselman 1993), the absence of difference in the otolith shape may suggest that the bogue finds relatively similar growth conditions along the Algerian coast.

It has been shown that the presence of hydrographic features may act as barriers to fish dispersal and migration (Schunter et al. 2011; Bacha et al. 2014, 2016). Except the existence of the quasi-permanent Almeria-Oran front (AOF) located on the west side of Oran, which induces different environmental conditions between the Alboran Sea and the Algéro-Provencal Basin (Tintore et al. 1988), the oceanographic conditions are similar along the Algerian coast.

Some studies have found that classification success from otolith shape increases as genetic discreteness or geographic separation increases (Castonguay et al. 1991; Burke et al. 2008; Vignon and Morat 2010; Jemaa et al. 2015a). It is therefore necessary to study at a larger spatial scale (e.g. the Mediterranean Sea) the population structure of the bogue based on both the analysis of the shape of the otoliths and genetic studies.

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Figure legends

Figure 1: Map showing the three locations along the Algerian coast where *B. boops* individuals were sampled

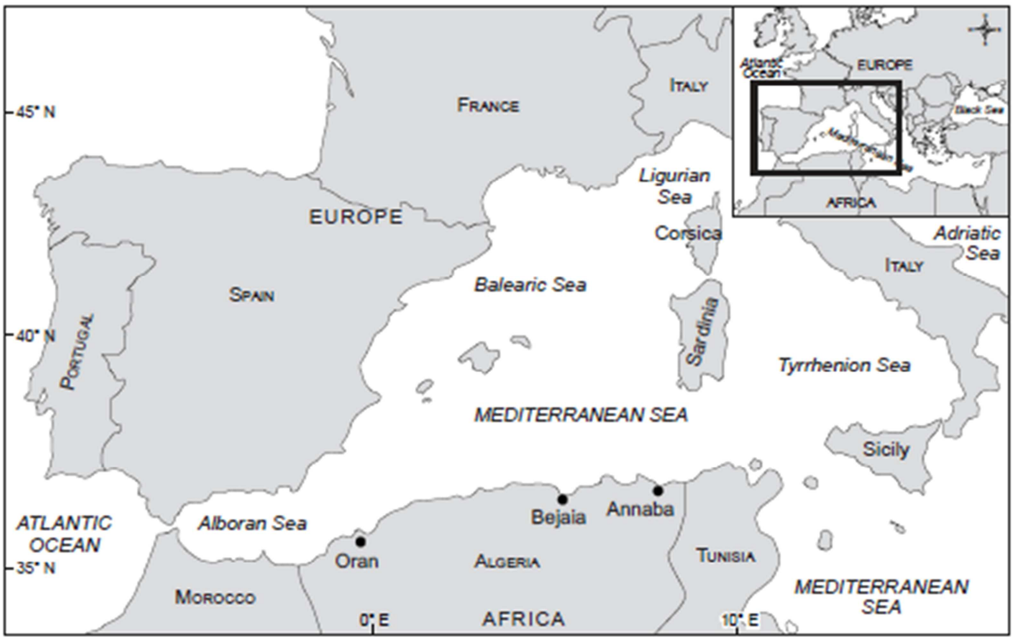

Figure 2: Fish length (cm) and otolith length (mm) relationship of *B. boops* individuals analysed showing the linear regression fitted to the data

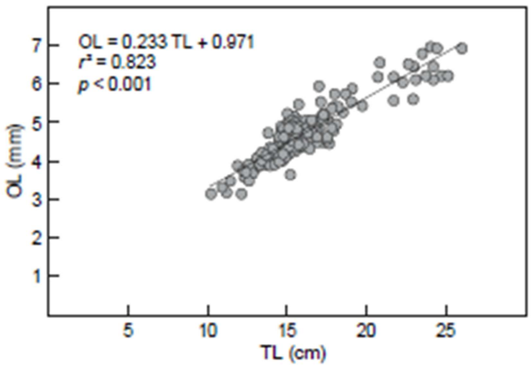

Figure 3: Otolith outline shapes formed with reverse Fourier transform of the outline using the first 23 harmonics showing the difference between the right and left otolith shape of *B. boops* from the Algerian coast for (a) small fish (TL <15 cm) and (b) large fish (TL >15 cm). Grey: left otolith, white: right otolith

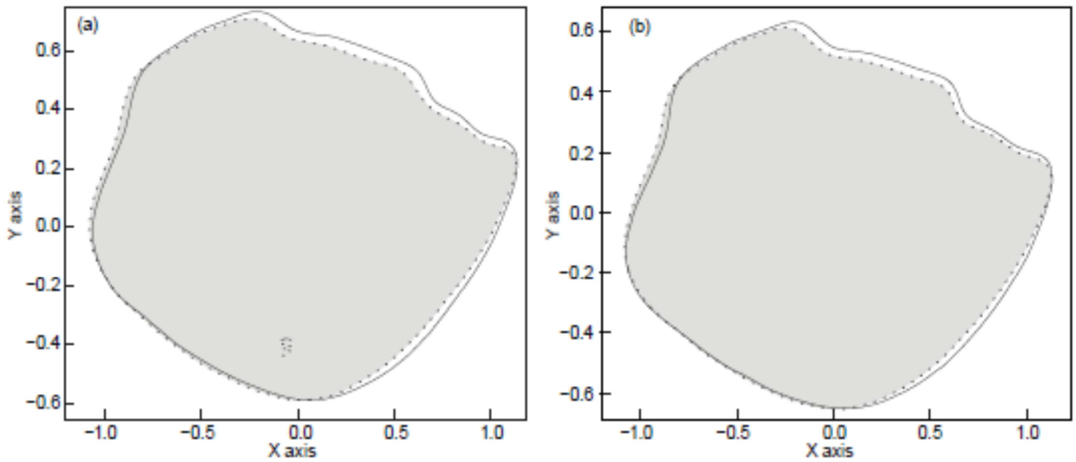

Figure 4: Otolith outline shapes formed with reverse Fourier transform of the outline showing the difference between sampling areas on the Algerian coast (grey continuous line: Oran, black continuous line: Annaba, fine dotted line: Bejaia)

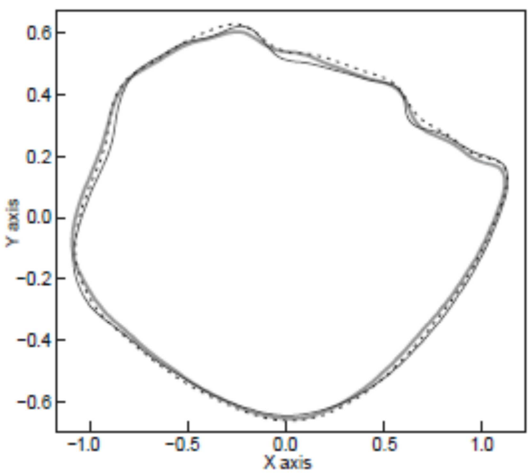

Figure 5: Discriminant function scores for the size-corrected Fourier descriptors (FDs) of *B. boops* otoliths from the three locations along the Algerian coast

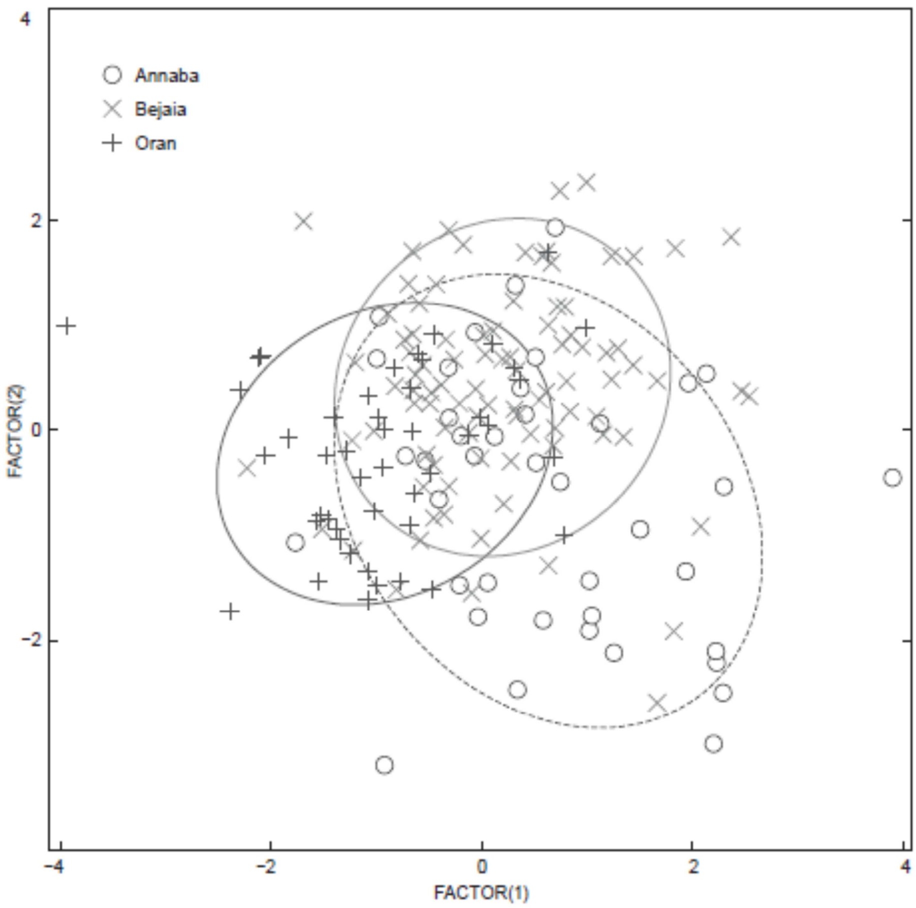
Annaba
Bejaia
Oran
FACTOR(2)
FACTOR(1)
4
2
0
-2
-4

Table1: Number of bogue otolith samples by geographical area and sex. The length (cm) and eviscerated weight (g) is indicated

Area	Number of fish	Number of females	Number of males	Total length (cm) Mean ±SD [range]	Eviscerated weight (g) Mean ±SD [range]
Annaba	40	14	26	18.98 ±4.07 [12.9–26]	64.41 ±45.78 [11.3–151.9]
Bejaia	92	49	43	15.04 ±1.93 [10.2–21.7]	36.90 ±8.09 [17.2–54.2]
Oran	47	41	6	15.76 ±1.11 [12.4–17.8]	25.88 ±10.52 [8.2–76]

Table 2: Jackknifed correct classification matrix of the LDA for bogue (n = 179) between three sampling areas based on the selected seven-PC matrix. The percentages in each row represent the classification into the sampling area in each column (the correct classification appears in bold on the diagonal)

	Annaba	Bejaia	Oran	%
Annaba	**17**	21	2	43
Bejaia	7	**76**	9	83
Oran	1	19	**27**	57