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Ontogenetic allometry of the bluemouth, *Helicolenus dactylopterus dactylopterus* (Teleostei: Scorpaenidae), in the Northeast Atlantic and Mediterranean based on geometric morphometrics

Rebeca Rodríguez-Mendoza · Marta Muñoz · Fran Saborido-Rey

Abstract The bluemouth, *Helicolenus dactylopterus*, is a deep-sea scorpionfish widely distributed in the Atlantic Ocean and the Mediterranean. It is a common by-catch associated to many demersal fisheries. However, there is little information about the stock structure, stock dynamics and life history parameters of the bluemouth. From the perspective of stock identification, it is important to study growth in fish populations to better understand the possible morphological differences among populations and when and why do they arise. Thus, the aim of this study was to determine the growth (allometric) trajectories of shape for several bluemouth populations in Northeast Atlantic and Mediterranean using landmark-based geometric morphometric techniques. In this study, ontogenetic allometry was present in all of the bluemouth samples. Ontogenetic shape changes were most evident in the head and pectoral area, affecting the position of the snout, preopercular spines and pectoral fins, but changes in body depth and length were also important. However, the degree to which these ontogenetic shape changes were present in bluemouth from each of the studied areas was different, indicating that their growth trajectories are not homogeneous. The importance of this finding for size-correction of the shape variables in morphometric studies for stock identification is also discussed.

Keywords *Helicolenus dactylopterus* · Bluemouth · Morphometrics · Growth · Ontogenetic allometry

Introduction

The bluemouth, *Helicolenus dactylopterus dactylopterus* (De la Roche 1809) (Teleostei: Scorpaenidae), is a benthic scorpionfish widely distributed in the Atlantic Ocean and Mediterranean Sea. It dwells on continental shelf edges and upper slopes at depths between 200 and 1,000 m (Whitehead et al., 1986). Although there has been little commercial interest in this species, partially due to its low level of accessibility, it is currently of growing commercial interest as new resources need to be found by fishing fleets because of the depletion of traditional resources. This species is caught by artisanal longline and gillnet fisheries near the Strait of Gibraltar and along the Portuguese continental coast and the Azores (Esteves et al., 1997; Santos et al., 2002; Czerwinski

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et al., 2008). In the western Mediterranean, bluemouth are mostly caught as by-catch in bottom trawl fisheries targeted at deep-sea crustaceans (Moranta et al., 2000; Sánchez et al., 2004). However, in areas such as the Catalonian coast, the bluemouth is the most commercially viable scorpionfish species, with important economic value (Ribas et al., 2006). In other fisheries, such as the Irish demersal fisheries that target prawns (*Nephrops norvegicus*) and/or whitefish (e.g., cod *Gadus morhua* and haddock *Melanogrammus aeglefinus*), bluemouth are caught regularly by otter trawlers, but they are mostly discarded (Borges et al., 2005).

Since the late 90s, the biology of the bluemouth has been studied in the NE and NW Atlantic, the Mediterranean and the North Sea, focusing mainly in the distribution, age, growth, and reproduction of the species (Heessen et al., 1996; Esteves et al., 1997; White et al., 1998; Kelly et al., 1999; Muñoz et al., 1999, 2000; Massutí et al., 2000, 2001; Allain, 2001; Sequeira et al., 2003; Abecasis et al., 2006; Mendonça et al., 2006; Ribas et al., 2006; Mamie et al., 2007; Vila et al., 2007). From these studies, the bluemouth has been characterized as a slow growing and long-lived species reaching up to 30 years of age (Massutí et al., 2000). The growth of male and female bluemouth has been studied systematically in most studies with respect to age and growth, but results among the different reports are not consistent. In the western Mediterranean, Massutí et al. (2000) and Ribas et al. (2006) observed that males grew faster than females. A study in the Azores was not conclusive about possible differences in growth rates between sexes because growth curves estimated using whole otolith readings showed that males grew faster, but growth curves estimated by sliced otoliths failed to show differences between the sexes (Abecasis et al., 2006). Moreover, a very recent study by Sequeira et al. (2009) on bluemouth on the Portuguese continental slope found no significant differences between sexes when comparing female and male growth curves.

At present, most reports regarding the growth of bluemouth include only age–length growth curves with no information on the morphological changes that take place as fish increase in size. Body form in fishes is a product of ontogeny (Cadrin, 2005). It is affected by the genetic makeup of an individual, but it also reflects adaptation to environmental factors such as temperature, food availability, feeding mode, swimming behavior, or habitat use (Barlow, 1961; Wimberger, 1992; Swain et al., 2005). During the growth of fishes, body proportions change as the larvae and juvenile fish adapt to transitions in habitat and diet until they reach adulthood. The change in proportions related to variation in size (i.e., growth) is termed ontogenetic allometry, and it has been studied in fishes for quite some time (e.g., Barlow, 1961; Strauss & Fuiman, 1985; Klingenberg & Froese, 1991). Traditionally, changes in proportion are represented as growth trajectories that describe the growth of an organism from its inception to its mature form (Alberch et al., 1979), and more recently, the tools of geometric morphometrics have allowed us to visualize shape changes to identify what happens during the growth of fish and other organisms (e.g., Loy et al., 1996, 1998; Frost et al., 2003; Mitteroecker et al., 2004; Kouttouki et al., 2006; Drake & Klingenberg, 2008). The study of allometric growth also has an important application for size correction of morphological variables when comparisons of multiple groups of specimens with different size compositions are made (e.g., Burnaby, 1966; Mosimann, 1970; Humphries et al., 1981; Thorpe, 1983; Claytor & MacCrimmon, 1987; Klingenberg & Froese, 1991; Klingenberg, 1996).

The aim of this study was to characterize the shape changes that occur during the growth of bluemouth to better understand the biology and ecology of this species. Thus, we determined ontogenetic shape trajectories for bluemouth from several geographical areas in the NE Atlantic and western Mediterranean and examined the variation of growth patterns in the different environments of the study areas. Growth patterns of males and females were also analyzed to determine if sexual dimorphism exists. Finally, we discuss the implications of our results in the context of phenotypic identification of bluemouth stocks in the NE Atlantic and western Mediterranean.

Materials and methods

Specimens and locations

For this study, a total of 1,012 specimens of bluemouth were caught around the Iberian Peninsula and the Porcupine Bank in Spanish bottom trawl surveys (Table 1). The study areas were divided taking into account their oceanographic characteristics. In the NE Atlantic, specimens were sampled from the Galician shelf (from the Miño River to Cape Finisterre), the Cantabrian Sea (from Cape Estaca de Bares to the mouth of the Bidasoa River), the Gulf of Cadiz and the Porcupine Bank (Irish continental margin). Galicia and the Cantabrian Sea are considered to be divided by Cape Estaca de Bares, which is described as a biogeographic limit (boundary effect) and a larval retention area of mesoscale hydrographic anomalies (i.e., anticyclonic eddies) (Sánchez & Gil, 2000). The other two locations in the NE Atlantic are also interesting in terms of their oceanographic characteristics. The Gulf of Cadiz is the first basin where the dense (i.e., salty and warm) Mediterranean outflow encounters the open ocean after crossing the Strait of Gibraltar, and water mass circulation along its continental shelf results in warm and biologically productive waters that are particularly suitable for the reproduction of many fish species (García-Lafuente, 2006; García-Lafuente et al., 2006). The Porcupine Bank is a submarine shelf break bank that is partly attached to the Irish continental shelf, and it has a high productivity due to closed circulation patterns around the bank that promote the retention of organic matter over it. It is also worth noting that it hosts an important number of deep cold-water ecosystems (White et al., 2005).

Specimens from the Mediterranean were caught in the Alboran Sea close to the coast of Alicante (southwest of the Balearic Sea) and along the Catalonian coast (Fig. 1). These locations were selected considering studies by Massutí et al. (2000) and Ribas et al. (2006), which indicated several well-defined areas that can be found in terms of oceanographic conditions in the western Mediterranean: (1) the southwestern basin (Alboran Sea), (2) the northwestern basin (Catalonian coast) and (3) the transition zone, from Cape Palos to Sagunto (Alicante sector).

Data acquisition

After collection, the fish were immediately frozen at −20°C and stored in a horizontal position to avoid any deformation of the body until the time of the analysis. Thirteen homologous landmarks were defined (Fig. 2) to provide an adequate coverage of the body shape based on a previous study by Garabana (2005) on similar species (*Sebastes* spp.). To ensure an accurate localization of the selected points, black-headed entomological pins were placed on each landmark. Once the landmarks were located, each fish was placed on its left side on a white polystyrene board with a ruler with 1-cm gradations. A photograph was taken with a Nikon D1X digital camera (Nikon Corporation, Japan) using a focal length of 35 mm to avoid optic distortions of the images. The images were digitized using TpsDig software version 2.10 (Rohlf, 2006) to obtain the *x*,*y* coordinates of the landmarks.

Morphometric and statistical analysis

Size

To quantify the size of a specimen, centroid size (CS) was computed from the raw coordinates of the landmarks (Dryden & Mardia, 1998) using the MorphoJ software package (Klingenberg, 2008). Centroid size is a measure of geometric scale,

Table 1 Number of bluemouth specimens analyzed in each location

Study area	*N*	Size range (CS, cm)	Mean ± SD (CS, cm)	Source (research survey)
Mediterranean Sea				
Alboran Sea	238	6.73–31.59	17.34 ± 5.70	Medits 2007
Alicante	134	6.61–26.14	13.09 ± 4.06	Medits 2007
Catalonian coast	73	5.30–20.13	10.71 ± 3.01	Medits 2007
NE Atlantic				
Gulf of Cadiz	75	5.92–36.81	21.29 ± 6.35	ARSA 2009
Galicia	191	5.23–34.52	15.08 ± 4.42	Demersales 2007
Cantabrian Sea	119	9.42–39.58	18.65 ± 5.37	Demersales 2007
Porcupine Bank	182	8.54–35.02	24.25 ± 6.03	Porcupine 2008

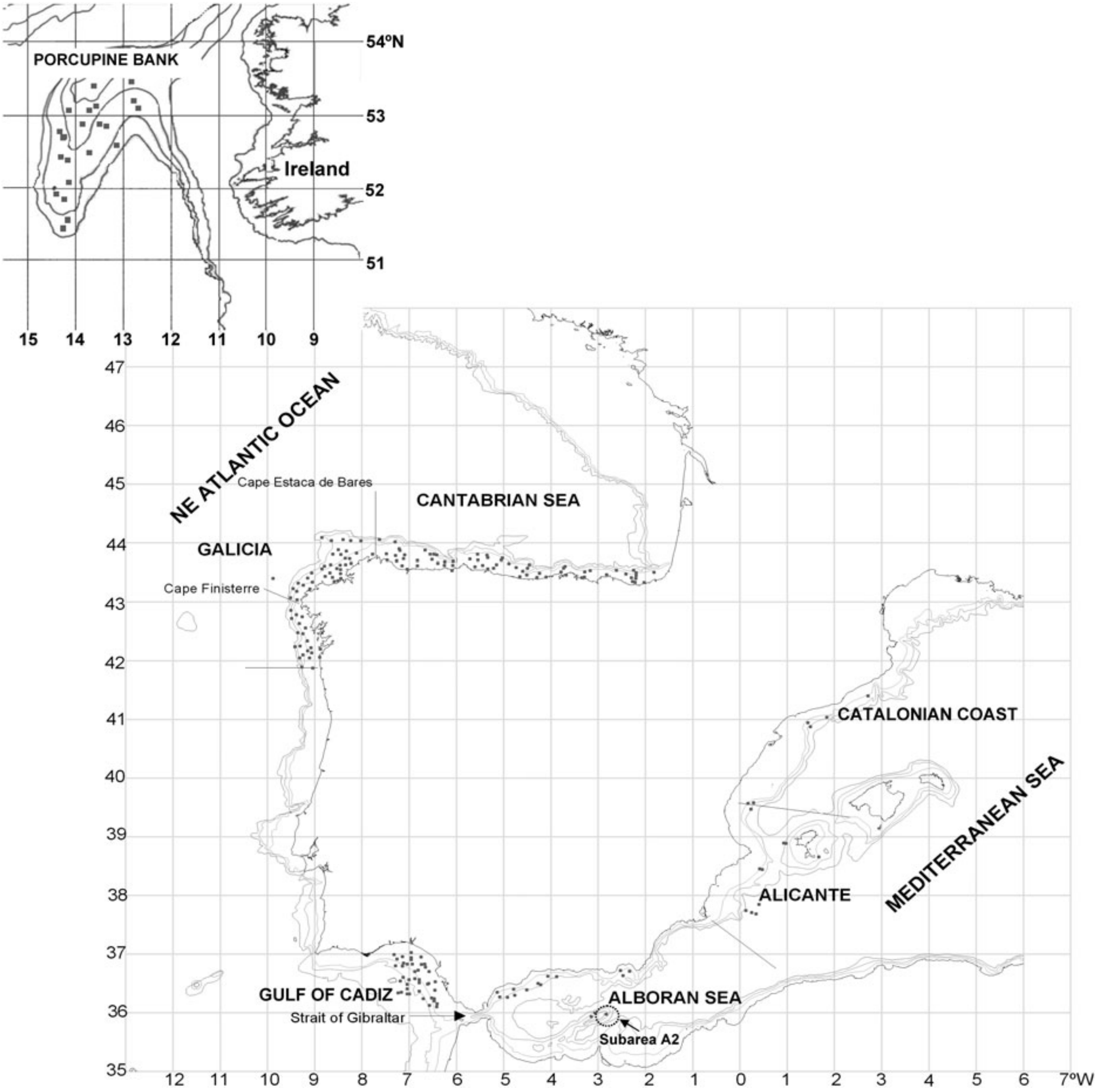

Fig. 1 Map of the study area with the sampling sites in the Northeast Atlantic and Mediterranean

calculated as the square root of the summed squared distances of each landmark from the centroid of the landmark configuration. In the present study, CS was highly correlated with total length of the specimens ($r^2 = 0.9935$, $P < 0.01$) (Fig. 3).

Shape

Body shape was analyzed using landmark-based geometric morphometric methods (Rohlf, 1990; Bookstein, 1991). To remove non-shape variation, a generalized Procrustes analysis (GPA) was carried out using MorphoJ software (Klingenberg, 2008). The first step of this procedure is to scale all of the specimens to unit centroid size. The landmark configurations are then superimposed to have a common centroid and rotated to minimize the distances between the corresponding landmarks of all of the configurations. Once the specimens are aligned, the mean configuration of landmarks is

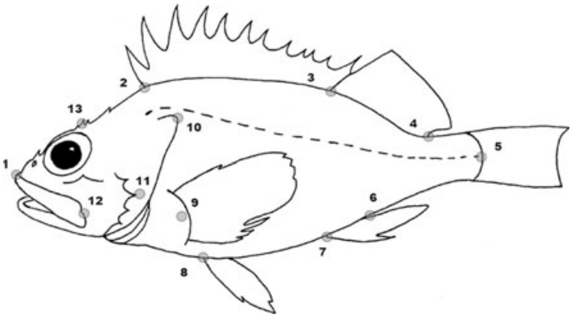

Fig. 2 Schematic representation showing the location of the 13 landmarks used in the analysis

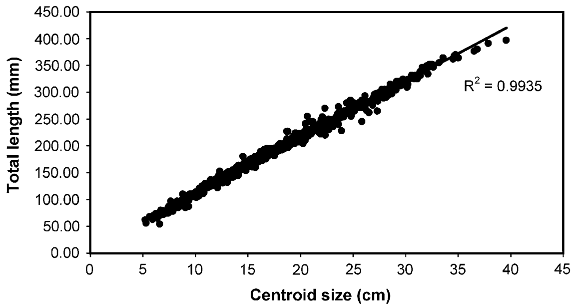

Fig. 3 Relationship between centroid size (CS) and total length (TL) for all the specimens in this study ($r^2 = 0.9935$, $P < 0.01$)

computed, and the specimens are projected to a linear shape tangent space. The mean configuration is usually called the *consensus* or *reference* shape because it is the configuration of landmarks that corresponds to the point of tangency between the exact curved shape space and the approximating tangent space in which the linear multivariate statistical analyses are performed (Rohlf & Slice, 1990; Rohlf, 1999; Slice, 2001). The coordinates of the aligned specimens are the Procrustes coordinates, and they were used as shape variables in the statistical analyses.

Growth trajectories

A multivariate regression of the Procrustes coordinates on the logarithm of centroid size was used to determine growth trajectories and characterize morphological changes in response to size. The amount of shape variation for which each regression accounted was expressed as a percentage of the total variation around the sample means. A permutation test using 10,000 runs (Good, 1994) was used to test the null hypothesis of independence between shape and size.

To visualize the strength of the association between size and shape, we calculated shape scores according to Drake & Klingenberg (2008) and plotted them against log centroid size. A shape score is defined by projecting the shape data onto a line in the direction of the regression vector for the independent variable (centroid size). If the regression model is written as $\boldsymbol{y} = \boldsymbol{\beta}x + \boldsymbol{\varepsilon}$ (where $\boldsymbol{y}$ is the row vector of shape variables; $\boldsymbol{\beta}$ is the regression vector; x is the independent variable; and $\boldsymbol{\varepsilon}$ is the row vector of error terms), the shape score s can be computed as $s = \boldsymbol{y}\boldsymbol{\beta}'(\boldsymbol{\beta}\boldsymbol{\beta}')^{-0.5}$. This shape score is the shape variable associated with the shape changes predicted by the regression model, but it also includes the residual variation in that direction in shape space (Drake & Klingenberg, 2008). These analyses were carried out with the MorphoJ software package (Klingenberg, 2008). The similarity of growth trajectories between sexes and among areas was evaluated following the approach explained in Zelditch et al. (2003a, b) using the VecCompare program (IMP software) (Sheets, 2000). To compare each pair of regression vectors, this program first calculates the angle between these vectors (i.e., between-group angle). That angle is obtained as the arccosine of the signed inner products between normalized regression vectors. Then, the between-group angle is compared with the upper 95% confidence interval of within-group angle ranges assessed by a bootstrapping approach with 900 runs. The null hypothesis is that the observed angle could have been produced by two independent samplings of a single group (i.e., area or sex). If the between-group angle exceeds the 95% confidence interval of the two within-group angles, the difference is judged statistically significant at the 5% level.

Visualization of ontogenetic shape changes

To visualize the shape changes associated with the growth of bluemouth specimens, warped outline drawings were made using the thin-plate spline interpolation function (Bookstein, 1989). Visualizations were made in the MorphoJ software package (Klingenberg, 2008).

Results

Growth trajectories by area

Ontogenetic allometry was present in all of the bluemouth samples, as the multivariate regressions were statistically significant (Table 2). Additionally, the scatter plots used to visualize growth trajectories show an association of the shape scores with centroid size for all of the study areas (Fig. 4). However, the amount of shape variation accounted for by the regressions differed considerably among the studied areas, ranging from 4.57% for the Catalonian coast to 24.13% for the Gulf of Cadiz. For the Catalonian coast, the growth trajectory might not be accurately represented despite the significant relationship between shape and size ($P = 0.0136$) because the sample for this area consisted mainly of small specimens with a mean size of 10.71 cm CS. Thus, the results for this area should be interpreted with some caution. Additionally, some areas from the Iberian Peninsula showed a considerable amount of dispersion around the growth trajectory (e.g., the Cantabrian Sea, the Alboran Sea and Alicante). We examined these locations more closely to determine if there was any pattern indicating a possible substructure of the bluemouth sample within these areas that could explain the observed dispersion and, thus, be considered in the study. In the case of the Alboran Sea, it appears that there are two different growth trends (Fig. 5), one exhibited by bluemouth specimens caught mainly along the coastline (subarea A1, $N = 171$) and another one characteristic of specimens caught off the coast along the slopes of Alboran Island at 35°58.44′N, 2°49.53′W (subarea A2, $N = 67$). Thus, we carried out separate regressions of shape on size for each of the subareas in the Alboran Sea (A1 and A2), and both were statistically significant ($P < 0.0001$). However, the amount of shape variation accounted for by the regressions was noticeably different (7.77% for subarea A1 and 22.82% for subarea A2).

Table 2 Results of the multivariate regression of shape on size for bluemouth specimens within the studied locations

Area	*N*	% Predicted	*P*-value
Alboran Sea	238	9.0962	<0.0001
Subarea A1	171	7.7699	<0.0001
Subarea A2	67	22.8231	<0.0001
Alicante	134	11.2923	<0.0001
Catalonian coast	73	4.5719	0.0136
Gulf of Cadiz	75	24.1378	<0.0001
Galicia	191	8.9842	<0.0001
Cantabrian Sea	119	16.2398	<0.0001
Porcupine Bank	182	12.0634	<0.0001

Growth trajectories for males and females

Multivariate regressions of shape on size were also carried out for males and females separately within the study areas (Table 3 and Fig. 6). Ontogenetic allometry was detected for both sexes from all of the NE Atlantic samples, since the relationship between shape and size was statistically significant ($P < 0.0001$), but no statistical differences between growth trajectories of males and females within these locations were found at the 5% level (Table 4). In the Mediterranean locations, the analysis could not be done for the sample from the Catalonian coast because the number of males and females present in the sample was too low (6 males and 9 females). For the Alboran Sea, the regressions for both sexes from subarea A2 were significant ($P < 0.0001$), but those for subarea A1 were not ($P = 0.2671$ and 0.1036 for males and females, respectively). In the case of subarea A1, the growth trajectories were probably not well defined (and therefore not significant) because the size range of the sexed specimens was very limited. From the 114 males and females in the sample, there was only one specimen smaller than 15 cm CS or 2.7 log centroid size (Fig. 5). Thus, we did not compare the growth vectors for males and females from subarea A1, and we decided to use sexed and unsexed specimens together ($N = 171$) to determine the growth trajectory for comparison with other areas. For subarea A2, the angle between the ontogenetic vectors of males and females was of 44.8° and the 95th percentile of the ranges of the within-sex angles, were 40.9° for females and 44.6° for males. Although the inter-sex angle was significant at the 5% level, its value was very close to the 95th percentile of the range of angles for the males, and this result should also be interpreted with caution. As with subarea A1, we also used all of the available specimens from subarea A2 ($N = 67$) to determine the growth trajectory for comparison with the other

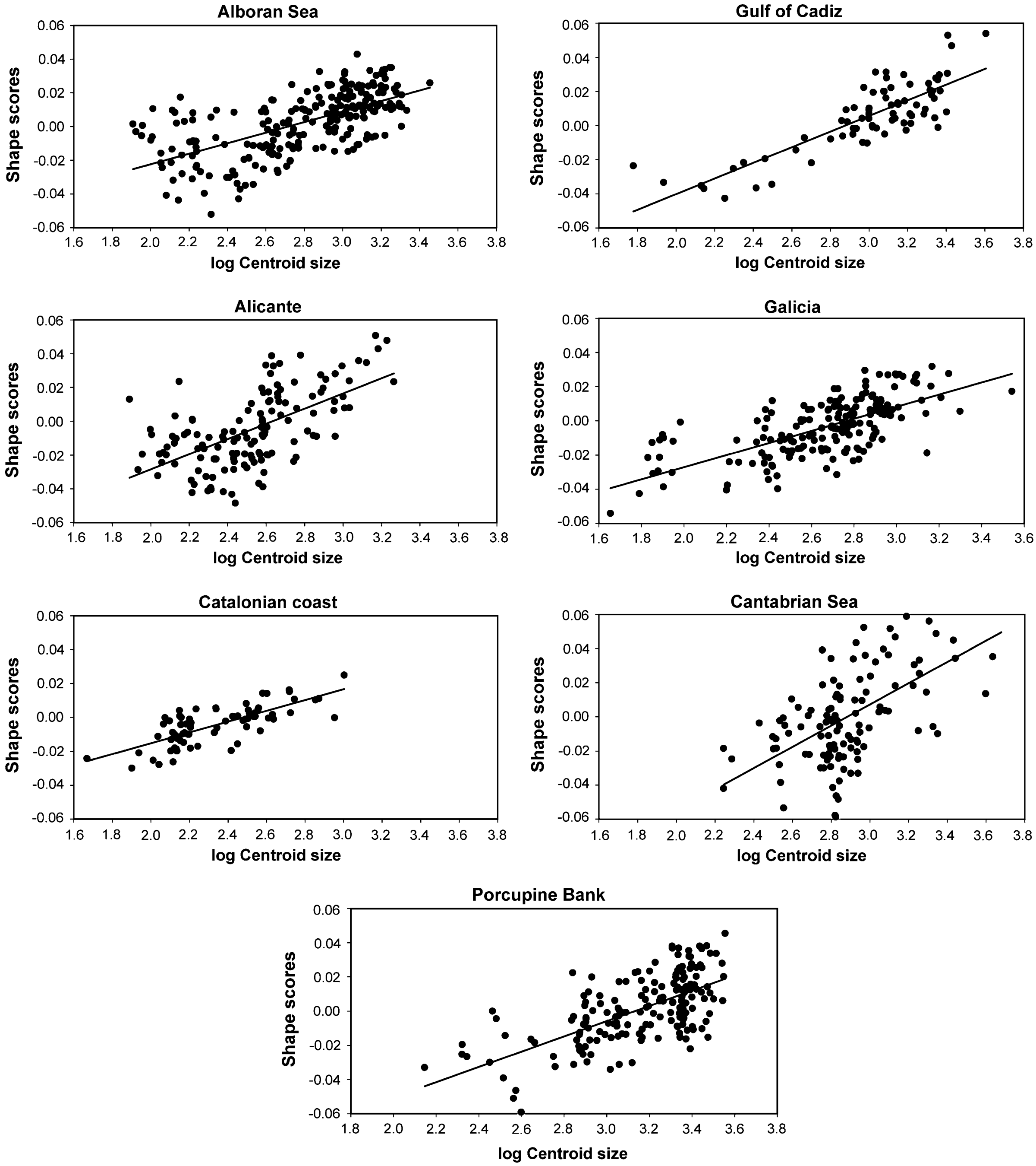

Fig. 4 Ontogenetic allometry for bluemouth from the studied areas. The growth trajectories are represented with shape scores as a function of log-centroid size

areas. For Alicante, the regressions of shape on size for males ($P = 0.0092$) and females ($P = 0.0130$) were significant, and the growth trajectories were similar for males and females in this area (Table 4).

Comparison of growth trajectories between areas

Growth trajectories were compared pairwise by calculating the angle between the regression vectors of the

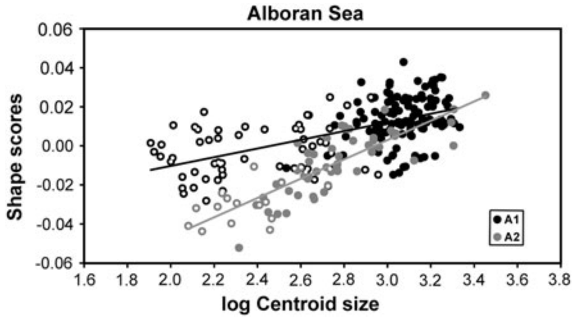

Fig. 5 Growth trajectories for bluemouth from the two subareas in the Alboran Sea (*A1* and *A2*). The trajectories are represented with shape scores as a function of log centroid size. *Filled circles* indicate sexed specimens (males and females) and *open circles* indicate unsexed specimens

Table 4 Angle between growth trajectories of males and females by area

Area	Angle
Alboran Sea–Subarea A2	44.8*
Alicante	28.8
Catalonian coast	–
Gulf of Cadiz	34.1
Galicia	32.4
Cantabrian Sea	18.3
Porcupine Bank	32.8

Growth trajectories for males and females from the Catalonian coast were not determined due insufficient sexed specimens. The comparison between the growth trajectories of males and females from subarea A1 was not performed because the regressions for males and females were not significant at the 5% level

* Significant at the 5% level

studied areas (Table 5). We did not find any clear pattern of geographical variation for the differences between growth trajectories. The pairwise comparisons indicated that bluemouth from the Gulf of Cadiz underwent similar ontogenetic shape changes to those from Galician waters, subarea A2 in the Alboran Sea, Alicante and the Catalonia coast, indicating that there are no growth patterns specific to only the NE Atlantic or the Mediterranean Sea. Interestingly, the growth trajectories for the two subareas within the Alboran Sea differed considerably. Only the growth trajectory for bluemouth from the Cantabrian Sea was different than all others.

Shape changes during growth

The patterns of shape changes during the growth of bluemouth are shown in Fig. 7 for the Mediterranean locations and in Fig. 8 for the NE Atlantic locations.

Table 3 Results of the multivariate regression for males and females within the studied locations

Area	Sex	*N*	Predicted shape variation (%)	*P*-value
Alboran Sea	Females	78	20.77	<0.0001
	Males	89	12.35	<0.0001
Subarea A1	Females	54	3.17	0.1036*
	Males	60	1.99	0.2671*
Subarea A2	Females	24	23.71	0.0001
	Males	29	20.96	<0.0001
Alicante	Females	35	9.48	0.0130
	Males	27	11.94	0.0092
Catalonian coast	Females	9	–	–
	Males	6	–	–
Gulf of Cadiz	Females	35	30.38	<0.0001
	Males	31	11.33	0.0038
Galicia	Females	87	9.69	<0.0001
	Males	75	11.26	<0.0001
Cantabrian Sea	Females	64	21.18	<0.0001
	Males	48	15.64	<0.0001
Porcupine Bank	Females	67	9.95	<0.0001
	Males	108	15.26	<0.0001

The shape variation predicted by each regression is expressed as a percentage of the total shape variation. The regressions for the Catalonian coast were not performed due to insufficient sexed specimens in the area

* Not significant at the 5% level

Table 5 Results for the pairwise comparisons of growth vectors for bluemouth from the studied areas

	Alboran Sea (A1)	Alboran Sea (A2)	Alicante	Catalonian coast	Gulf of Cadiz	Galicia	Cantabrian Sea	Porcupine Bank
Alboran Sea (A1)	0							
Alboran Sea (A2)	62.5*	0						
Alicante	57.9*	27.4	0					
Catalonian coast	54.5	66.4*	51.1	0				
Gulf of Cadiz	57.4*	20.5	20.9	57.0	0			
Galicia	40.2*	38.8*	35.7*	45.1	34.7	0		
Cantabrian Sea	76.1*	26.3*	29.7*	70.1*	29.3*	49.6*	0	
Porcupine Bank	51.8*	30.9*	31.9*	60.9*	20.5	38.8*	41.8*	0

* Growth trajectories are significantly different at the 5% level

In general, the shape changes associated with increases in size in bluemouth specimens consisted of: (a) a relative expansion of the area comprised by landmark 9 (midpoint of the insertion of the pectoral fin), landmark 11 (tip of the second-preopercular spine) and landmark 12 (midpoint of the end of the jaw), (b) a contraction of the head area in relation to body size accompanied in most cases by an upward shift of the tip of the snout and (c) a dorsoventral expansion together with a relative shortening of the body. Thus, as expected, we observed a trend towards a more robust body morphology as the fish become larger. Still, some specific shape changes were identified in bluemouth specimens from the Cantabrian Sea. The estimated shape for large specimens showed a considerable up-rightward displacement of landmark 10 (end of the operculum), an up-leftward displacement of landmark 5 (insertion of the hypural plate) and a larger downward displacement of landmarks 8 (insertion of the ventral fin) and 9 (insertion of the pectoral fin).

Discussion

Body form in fishes is a product of their ontogeny (Cadrin, 2005). It is affected by the genetic makeup of an individual, but it also reflects adaptation to environmental factors such as temperature, food availability, feeding mode, swimming behavior and habitat use (Barlow, 1961; Wimberger, 1992; Swain et al., 2005). During the growth of fishes, body proportions change as the larvae and juvenile fish adapt to habitat and diet transitions until they reach adulthood. According to our results, bluemouth specimens from both NE Atlantic and Mediterranean locations seem to follow a pattern of ontogenetic shape changes that is probably related to the changing ecology of the species over the course of its life history: bluemouth juveniles have a streamlined body shape during their pelagic stage (Furlani, 1997 and references therein), while adults have robust but flexible muscular bodies typical of benthic sit-and-wait predators (Webb, 1984; Uiblein et al., 2003). For most of the studied areas, ontogenetic shape changes were most evident in the head and pectoral area, affecting the position of the snout, preopercular spines and pectoral fins, but changes in body depth and length were also important (Figs. 7, 8). Changes in body depth and length are mostly related to swimming capacity and locomotor adaptations to food capture and escape from predators (Webb, 1984). Functionally, mouth shape changes also have many repercussions in the life of fish because mouth morphology plays an essential role in determining the type of prey consumed, and morphological variations can lead to changes in foraging/predation ability and subsequently differential exploitation of food resources (Karpouzi & Stergiou, 2003). Thus, the observed changes in mouth shape and position are very likely to be related to ontogenetic changes in the diet of bluemouth. In general, their diet consists of benthic decapod crustaceans (Natantia, Brachyura, and Macrura), demersal fish and sometimes pyrosomes, polychaetes and echinoderms (Macpherson, 1979, 1985; Nouar & Maurin, 2000; Serrano et al., 2003), but the proportions of these prey types in their diet vary according to the size of the fish. For example, Macpherson (1979) reported that the diet of small bluemouth individuals from 4 to 9 cm in the

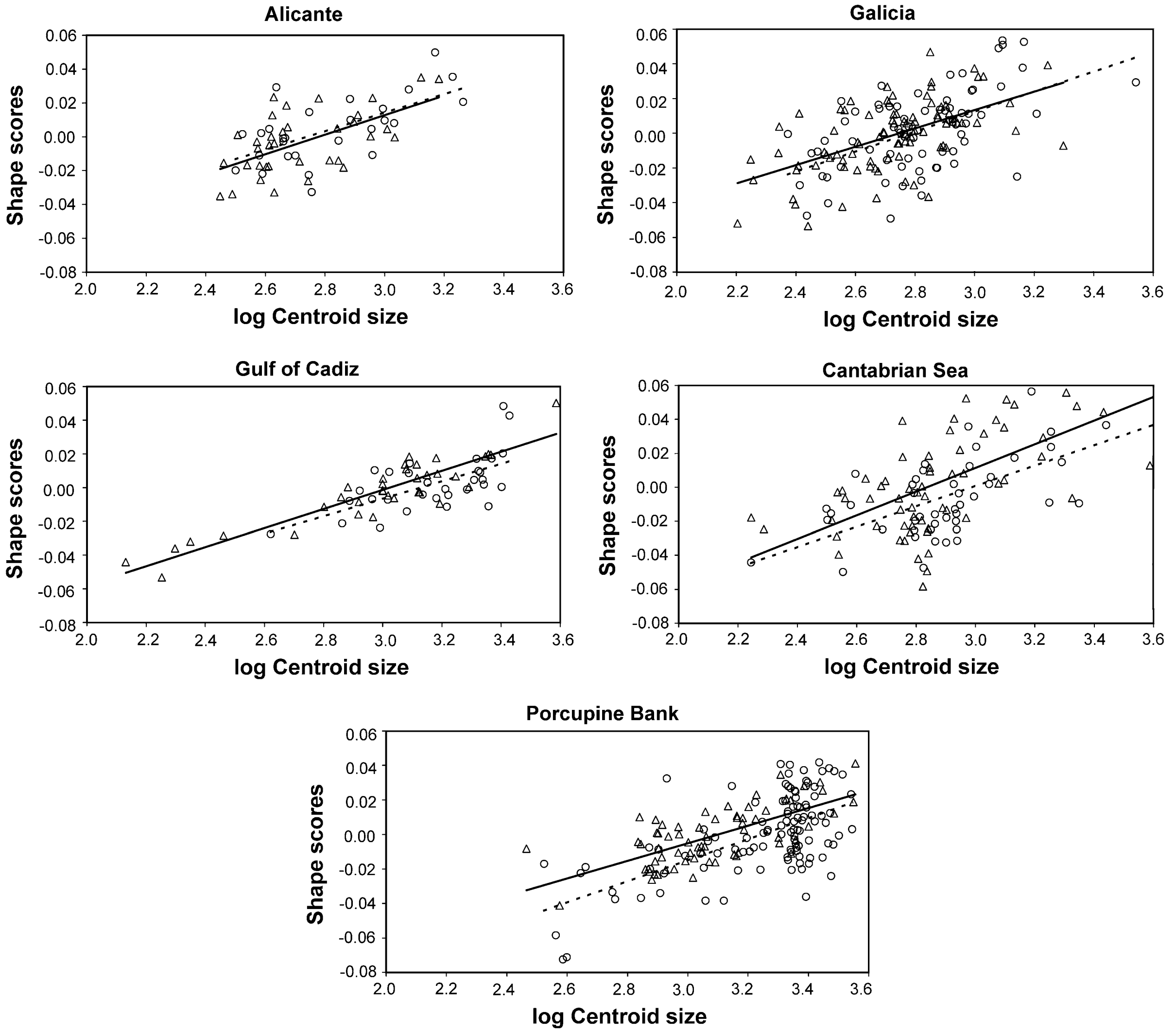

Fig. 6 Growth trajectories for bluemouth males (*open black circles* and *dashed line*) and females (*open black triangles* and *solid line*) for some of the studied areas in the NE Atlantic and Mediterranean. The growth trajectory for the Alboran Sea is shown separately in Fig. 5 (see "Growth trajectories for males and females" section)

Mediterranean consisted mainly of fish (51.9%) such as silvery pout (*Gadiculus argenteus argenteus*) and gobies (*Deltentosteus quadrimaculatus* and *Lesueurigobius friesii*) and decapods including *Alpheus glaber* (20.9%), *Calocaris macandreae* (5.9%), and *Goneplax rhomboides* (4.2%). In contrast, the main prey of adult specimens (20–29 cm in length) was the decapod crustacean *Goneplax rhomboides* (49.4%), followed by other decapods, such as *Calocaris macandreae* (17.6%) and *Alpheus glaber* (14.1%), and a small percentage of pyrosomes (9.4%) and fish (8.2%). In the case of *Helicolenus percoides*, ontogenetic diet changes have been also observed, as the proportions of Crustaceans and fish are inversely related as length increases. For this species, Brachyura were the single most important prey in fish of less than 20 cm, but they were replaced by *Pyrosoma atlanticum* and teleosts in larger size classes (Blaber & Bulman, 1987).

However, the degree to which the above described ontogenetic shape changes were present in bluemouth from each of the studied areas was different, reflecting the differences in growth trajectories that we found in this study. The factors that cause these growth differences are likely to be complex. Phenotypic variation can result from either genetic differentiation or

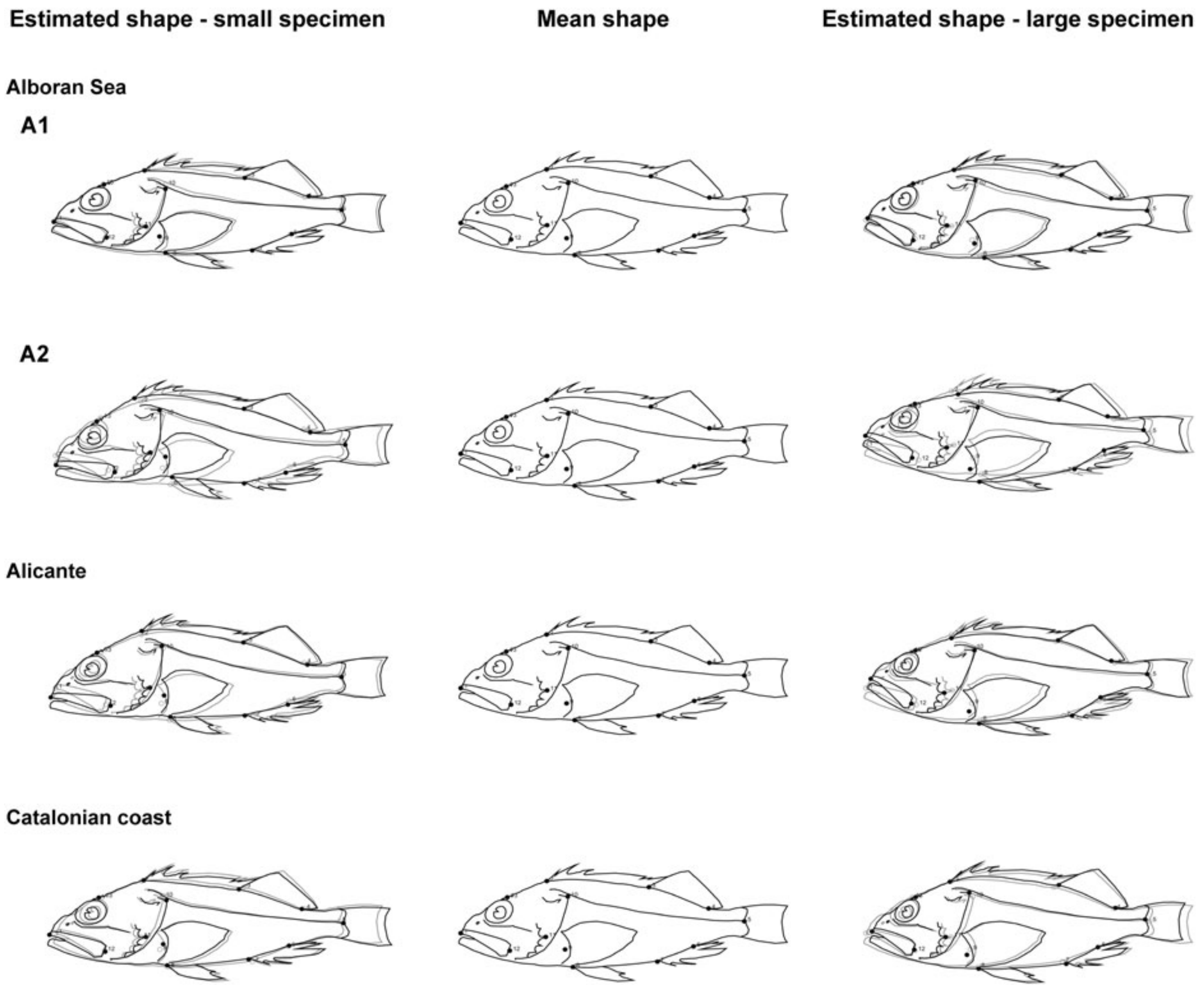

Fig. 7 Visualization of shape changes associated with growth for bluemouth from the western Mediterranean. The mean shape is shown in the center and is also represented as *light gray outlines* drawn in the figures in the *left* and *right columns*. *Left column*: the *black outline* shows the shape change for an arbitrary decrease in log centroid size by 1.5 units, representing the shape for a small specimen. *Right column*: the *black outline* shows the shape change for an arbitrary increase in log centroid size by 1.5 units, representing the shape for a large specimen

phenotypic plasticity. Genetic information on bluemouth populations is still scarce. To our knowledge, only one study has focused on the genetic population structure of the bluemouth in the north Atlantic (the Azores, Madeira and Cape Verde, the coast of Portugal (Peniche) and the northwest Atlantic off the coast of South Carolina, USA) (Aboim et al., 2005). In that study, no significant genetic differentiation was detected between populations within the NE Atlantic region (Azores, Peniche, and Madeira).

Phenotypic plasticity is the ability of a genotype to produce different phenotypes in response to different environmental stimuli (Wimberger, 1992). In fishes, as with most indeterminately growing organisms, the influence of the environment on life history traits is realized primarily through factors that affect body size and the rate at which body size changes throughout an individual's life (Swain et al., 2005). Therefore, fish growth and survival depend on many components of the habitat in which fish live (i.e., prey resources, predation risk, temperature, sediment type, water depth, etc.) (Hayes et al., 1996). In addition to environmental factors, growth in fish can be affected by population density and fishing mortality (Rochet, 1998; Law, 2000; Sánchez Lizaso et al., 2000). In general, size structure differences (and therefore

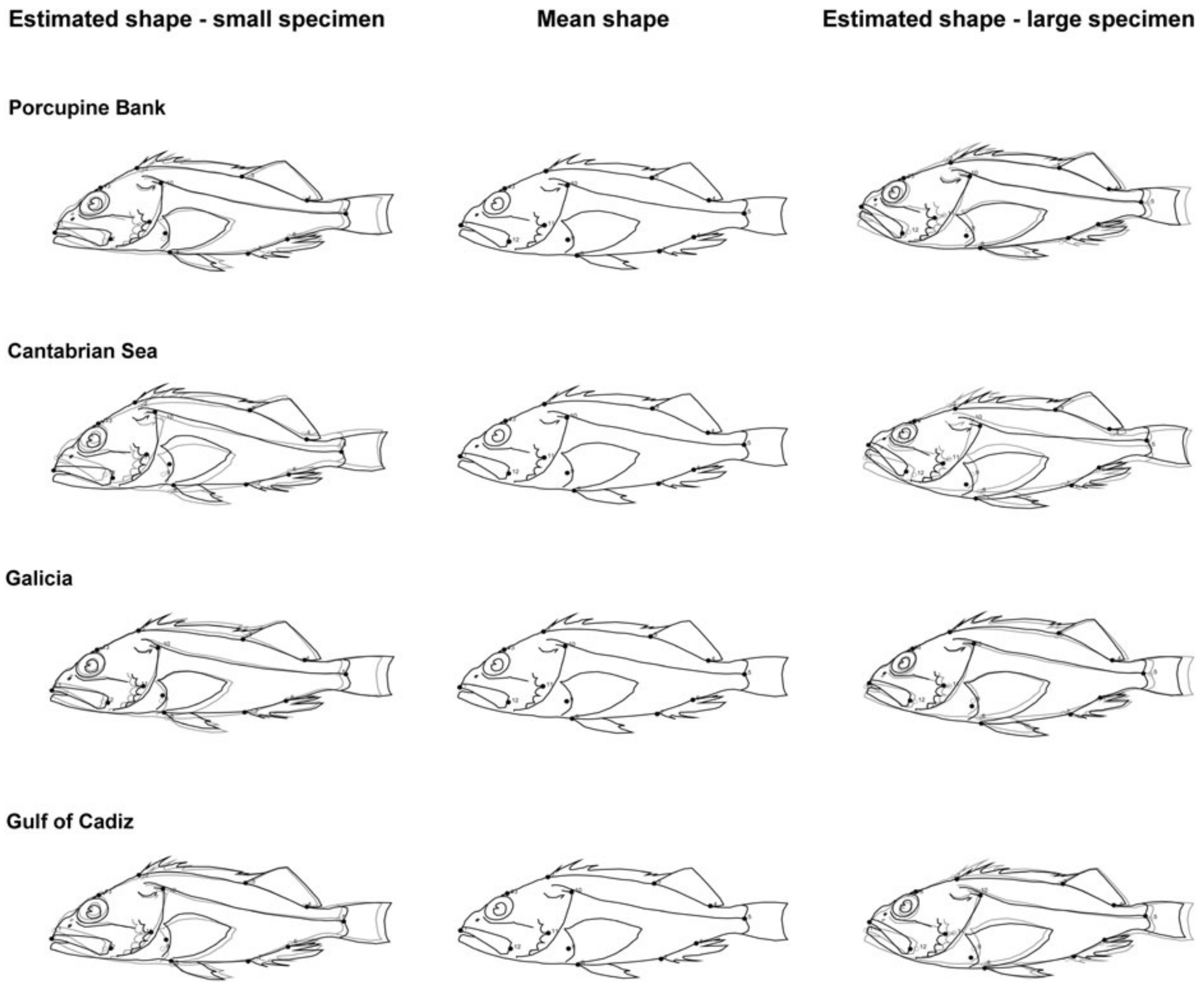

Fig. 8 Visualization of shape changes associated with growth for bluemouth from the NE Atlantic. The mean shape is shown in the center and is also represented as *light gray outline* drawn in the figures in the *left* and *right columns*. *Left column*: the *black outline* shows the shape change for an arbitrary decrease in log centroid size by 1.5 units, representing the shape for a small specimen. *Right column*: the *black outline* shows the shape change for an arbitrary increase in log centroid size by 1.5 units, representing the shape for a large specimen

differences in growth) of deep-sea fishes occur between the NE Atlantic and the Mediterranean (Tortonese, 1960; Stefanescu et al., 1992). More recently, Massutí et al. (2004) compared the deep-sea fish assemblages between these areas, and they also found evidence that for almost all species, those in the Mediterranean tended to grow to a smaller adult size. As a consequence, these fish will have smaller mouths and will, therefore, utilize a different component of the available food resources (Massutí et al., op. cit.). The authors of that study suggested that the primary cause of the differences they observed in size structure were a result of adaptations at both the species and ecosystem level to different trophic relationships between these two areas. However, they also indicated that a high temperature in the Mediterranean (~13°C, compared to ~10°C in the eastern Atlantic areas) could also play an important part in explaining size structure differences. In the same study, size differences between NE Atlantic and Mediterranean bluemouth were found, as the minimum size for locations in the NE Atlantic was at least double than that found in the Mediterranean, and the maximum size was found in the Porcupine Seabight (west of Ireland, NE Atlantic). In our study, bluemouth from the NE Atlantic generally reached larger sizes, but we did not find that NE Atlantic growth patterns were clearly differentiated from those presented by bluemouth from Mediterranean locations. For example, bluemouth specimens from the Gulf of Cadiz, which is located next to the Strait of Gibraltar, exhibited similar ontogenetic shape changes to bluemouth from Galicia and the Porcupine Bank (NE Atlantic) but also to bluemouth from subarea A2 in the Alboran Sea and Alicante (western Mediterranean). In this study, bluemouth from the Cantabrian Sea presented a unique growth pattern that is probably caused by a combination of factors (i.e., food availability along with a low fishing mortality and unique environmental conditions). The Cantabrian Sea is a well delimited area in the Bay of Biscay with particular characteristics that differentiate it from the rest of the Atlantic (Sánchez, 1993), and it also supports an important demersal ecosystem (Le Danois Bank) where no regular fishery operates, allowing for a well-preserved bluemouth spawning stock (Sánchez et al., 2008). In the Cantabrian Sea at the summit of Le Danois Bank where bluemouth are more abundant (400–550 m depth), some of the decapods that are considered to be the main prey of adult bluemouth (i.e., the crab *Goneplax rhomboides*, and the shrimp *Calocaris macandreae* and *Alpheus glaber*) are scarce or even absent due to the low proportion of mud in the sediments, which is required by these burrowing species (Cartes et al., 2007). Therefore, morphological adaptations of the snout in bluemouth from the Cantabrian Sea could arise as the fish use other food resources in the area.

In contrast, these decapods are very abundant in other areas considered in this study such as the southern part of the Galician shelf and the upper slope, where there are fine sediments due to outwelling from the Rías Baixas (Fariña et al., 1997). On the Mediterranean coasts of the Iberian Peninsula, the abundance of *Goneplax rhomboides*, *Calocaris macandreae* and *Alpheus glaber* also varies in the different geographical sectors, with the most abundant regions being found in the Alboran Sea and the northern Catalonia (Abelló et al., 2002). In general, the Alboran Sea has been described as an area with particular hydrographical characteristics due to the influence of Atlantic waters and with a high productivity within the general oligotrophic context of the Mediterranean (Massutí et al., 2001; Abad et al., 2007). Interestingly, the growth trend presented by bluemouth from subarea A1 in the Alboran Sea was different than the one exhibited by bluemouth from adjacent areas. Massutí et al. (2001) have suggested the existence of a well-developed bluemouth spawning stock in the Alboran basin, contrary to what they found in areas with high fishing pressure north of the Alboran Sea, where older fish are poorly represented. In a more recent study, Abad et al. (2007) also found a high abundance of bluemouth on the small seamount Seco de los Olivos in the eastern Alboran Sea, which is an area where trawled sandy bottoms are interspersed with rocky bottoms, and food is readily available due to strong localized currents and upwelling. Thus, food availability on the continental slope of the Alboran Sea in combination with a lower fishing mortality and the oceanographic conditions in the area are likely to produce a different growth pattern than the patterns observed in adjacent areas. Bluemouth caught in subarea A2 in the Alboran basin showed a similar growth pattern to the ones observed in contiguous areas (i.e., Gulf of Cadiz or Alicante). There is a possibility that a group of individuals from these areas migrated to subarea A2 because occasional migrations of adult specimens may occur (Aboim et al., 2005) or that especially particular environmental conditions exist in that location that affect the growth of these individuals. In any case, further study is needed to determine the factors that cause different growth patterns within the Alboran basin, and the temporal and spatial stability of the observed patterns has to be confirmed.

In this study, we also compared growth trajectories between males and females. Information about sexual dimorphism is required for understanding the ecology, behavior, and life history of a fish species (Kitano et al., 2007), and allometry has been suggested to be a main component of sexual shape dimorphism because it accounts for size dimorphism (Gidaszewski et al., 2009). Up to the present, only differences in sexual size dimorphism and growth rates between sexes have been studied for the bluemouth in the NE Atlantic and Mediterranean (White et al., 1998; Kelly et al., 1999; Massutí et al., 2000; Abecasis et al., 2006; Ribas et al., 2006; Sequeira et al., 2009). However, both of these topics are still being studied for bluemouth, as some of these authors have found that females grow faster and achieve a larger asymptotic length, while others have found the opposite trend, and in some studies, no differences in growth rates were detected at all.

Recently, Sequeira et al. (2009) suggested that these discrepancies in results could be related to differences in the length ranges sampled in the various studies. For other species of the same genus, such as *Helicolenus percoides* in southeastern Australian waters, Withell & Wankowski (1988) found that the growth rates of the sexes seemed to be comparable, though females attained a larger size, but a recent study found that males grew slightly faster than females (Paul & Horn, 2009). In the case of *Helicolenus lengerichi*, no differences in growth rates were observed between males and females (Petrova & Chekunova, 1979, as cited in Withell & Wankowski, 1988).

Regarding ontogenetic shape changes, no difference in the growth patterns of males and females was observed within any of the NE Atlantic locations. However, in the Mediterranean, we could only compare growth trajectories for males and females from two of the four areas included in this study: Alicante and subarea A2 in the Alboran Sea (see "Results" section). For Alicante, we did not find differences in allometric growth between sexes. However, our study was inconclusive about possible differences between sexes for subarea A2 due to a relatively low sample size and because the angle between the regression vectors was marginally significant. Perhaps in future studies, a combination of the study of growth rates and allometric shape changes between sexes can be used to better understand sexual dimorphism in bluemouth populations.

In fisheries, differences in life history parameters between groups of fish are assumed to be evidence that populations are geographically and/or reproductively isolated and can be considered discrete stock units for management purposes (Ihssen et al., 1981; Begg, 2005). Thus, the information provided in the present study can be used to complement further studies regarding stock identification of bluemouth around the Iberian Peninsula. Moreover, in the context of stock identification, morphological discrimination among groups of fish is often difficult because samples may differ in size composition and because allometric growth is taking place. This situation implies the risk of confounding real differences between fish populations with accidental differences in size composition of the samples. Thus, in morphometric studies, it is necessary to eliminate shape variation associated with size before we can compare multiple groups (Burnaby, 1966; Mosimann, 1970; Thorpe, 1976, 1983; Humphries et al., 1981; Rohlf & Bookstein, 1987; Klingenberg, 1996). According to our results, bluemouth from around the Iberian Peninsula and the Porcupine Bank exhibit allometric growth. Therefore, this fact has to be taken into account if morphological comparisons of bluemouth from different areas are to be made for the purpose of stock identification in Iberian waters.

In geometric morphometrics, one of the preferred methods for size-correction of variables is to use the residuals of a pooled-within group regression as 'size-free' variables (Klingenberg, 2008) because in this way, we only remove shape variation that is due to size variation, in contrast to what happens with other methods, such as principal components analysis (PCA) (Jolicoeur, 1963) or Burnaby's method (Burnaby, 1966), where an entire dimension is removed from the analysis. In addition to this issue, PCA may not work well for geometric morphometric data because during the generalized Procrustes analysis (see "Materials and methods" section), isometric size is factored out from the samples in the rescaling step. In this way, only in cases where allometric growth is substantially present will the first Principal component be associated with size (Slice & Stitzel, 2004). However, the central assumption of all methods for size-correction is that the groups in the analysis share the same allometric trajectories (Klingenberg, 1996), and in this study, we found evidence that the growth trajectories for bluemouth among the study areas are not homogeneous, representing a problem for size-correction of the shape variables that should be addressed prior to morphometric analysis. Another way to avoid size effects would be to compare samples with similar size compositions or to only use fish of the same size (selective sampling). However, for demersal species like the bluemouth, it is not easy to obtain homogeneous samples from all of the study areas because most of the time, sampling depends on fisheries that target other species (e.g., European hake, *Merluccius merluccius*, or Blue and red shrimp, *Aristeus antennatus*), and the size range of the captured specimens in each area can be affected by factors such as depth and the type of bottom of the fishing area and the fishing gear used (i.e., trawling nets, long-lines or gill-nets) (Demestre et al., 2000; Massutí et al., 2001; Santos et al., 2002). In addition, bluemouth samples from trawling research surveys also vary in size composition, as in this study. In the case of size selective sampling, shape variation outside the chosen size range is ignored, the covariance is reduced; and the ability to distinguish groups is, therefore, weakened (Cadrin, 2000). Another potential drawback of size selective sampling is that if the growth rate is very different among putative populations and it is uncoupled from shape changes, we could be comparing specimens of very different ages, thus resulting in confounding effects.

Conclusions

In this study, geometric morphometric techniques allowed us to determine and visualize ontogenetic shape trajectories for bluemouth specimens from around the Iberian Peninsula and the Porcupine Bank. The general pattern of ontogenetic changes seemed to be related to the changing ecology of the species (i.e., ontogenetic diet and habitat adaptations) and consisted of a relative expansion of the area between the second-preopercular spine and the pectoral fin, a relative deepening and shortening of the body and an upward shift of the snout as the head becomes more compact in relation to the body. However, the degree to which the above described ontogenetic shape changes were present in bluemouth from each of the studied areas was different, indicating that the growth trajectories are not homogeneous. The factors that cause these growth differences are likely to be complex, but a combination of factors such as food availability along with a low fishing mortality and unique environmental conditions is likely to produce distinctive growth patterns such as the ones that we found in areas including the Cantabrian Sea and the Alboran Sea. For the purpose of fisheries management, these observed differences in the way that bluemouth grow could be an indicator that different populations exist and should be further studied. However, if morphological comparisons are to be used as a tool to identify phenotypic stocks, the fact that growth differences exist should be considered because most size-correction methods assume equal or parallel growth trajectories to remove the effect of size from shape variables. Finally, this kind of shape information could be also used to complement traditional growth curves, showing what shape changes occur and when they take place during growth.

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