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

Rebeca Rodríguez-Mendoza¹, Marta Muñoz², Fran Saborido-Rey¹

¹Instituto de Investigaciones Marinas (CSIC), Eduardo Cabello 6, 36208 Vigo, Spain

²Departament de Ciències Ambientals, Campus Montilivi, Universitat de Girona, 17071
Girona, Spain

(e-mail: rrodriguez@iim.csic.es)

ABSTRACT

The bluemouth, *Helicolenus dactylopterus dactylopterus* (Delaroche 1809), is a deep-sea scorpionfish widely distributed in the Atlantic Ocean and the Mediterranean. It is a common by-catch species associated with many demersal fisheries. However, there is still little information about the population structure, population 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 the 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 meters (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 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 Catalanian 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 nineties, 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, 1997; White et al., 1998; Kelly et al., 1999; Massutí et al., 2000, 2001; Abecasis et al., 2006; Ribas et al., 2006; Mamie et al., 2007; Muñoz et al., 1999, 2000; Allain, 2001; Sequeira et al., 2003; Mendonça et al., 2006 and 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 and 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; Loy et al., 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., Mosimann, 1970; Burnaby, 1966; Humphries et al., 1981; Thorpe 1983; Claytor and MacCrimmon, 1987; Klingenberg & Froese, 1991; Klingenberg, 1996).

The aim of this work 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.

Material 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 (south-west of the Balearic Sea) and along the Catalanian 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 and Mardia, 1998) using the MorphoJ software package (Klingenberg, 2008). Centroid size is a measure of geometric scale, 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 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, 1999; Rohlf and Slice, 1990; 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 $y = \beta x + \epsilon$ (where y is the row vector of shape variables; β is the regression vector; x is the independent variable; and ϵ is the row vector of error terms), the shape score s can be computed as $s = y\beta(\beta\beta)^{-0.5}$. 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 and 2003b) 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 Catalanian coast to 24.13% for the Gulf of Cadiz. For the Catalanian 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 $35^{\circ}58.44'N$, $2^{\circ}49.53'W$ (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).

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). 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 Catalanian 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 $p = 0.1036$ 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 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 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. 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

286 estimated shape for large specimens showed a considerable up-rightward displacement of
287 landmark 10 (end of the operculum), an up-leftward displacement of landmark 5 (insertion
288 of the hypural plate) and a larger downward displacement of landmarks 8 (insertion of the
289 ventral fin) and 9 (insertion of the pectoral fin).
290

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, 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. (Fig. 7 and 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 - 9 cm in the 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 percooides*, 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 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, 2000). In general, size structure differences (and therefore 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).

391 Interestingly, the growth trend presented by bluemouth from subarea A1 in the Alboran Sea
392 was different than the one exhibited by bluemouth from adjacent areas. Massutí and
393 coworkers (2001) have suggested the existence of a well-developed bluemouth spawning
394 stock in the Alboran basin, contrary to what they found in areas with high fishing pressure
395 north of the Alboran Sea, where older fish are poorly represented. In a more recent study,
396 Abad et al., (2007) also found a high abundance of bluemouth on the small seamount Seco
397 de los Olivos in the eastern Alboran Sea, which is an area where trawled sandy bottoms are
398 interspersed with rocky bottoms, and food is readily available due to strong localized
399 currents and upwelling. Thus, food availability on the continental slope of the Alboran Sea
400 in combination with a lower fishing mortality and the oceanographic conditions in the area
401 are likely to produce a different growth pattern than the patterns observed in adjacent areas.
402 Bluemouth caught in subarea A2 in the Alboran basin showed a similar growth pattern to
403 the ones observed in contiguous areas (i.e., Gulf of Cadiz or Alicante). There is a possibility
404 that a group of individuals from these areas migrated to subarea A2 because occasional
405 migrations of adult specimens may occur (Aboim, 2005) or that especially particular
406 environmental conditions exist in that location that affect the growth of these individuals. In
407 any case, further study is needed to determine the factors that cause different growth
408 patterns within the Alboran basin, and the temporal and spatial stability of the observed
409 patterns has to be confirmed.

410 In this study, we also compared growth trajectories between males and females. Information
411 about sexual dimorphism is required for understanding the ecology, behavior, and life
412 history of a fish species (Kitano et al., 2007), and allometry has been suggested to be a main
413 component of sexual shape dimorphism because it accounts for size dimorphism
414 (Gidaszewski et al., 2009). Up to the present, only differences in sexual size dimorphism
415 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; Ribas et al., 2006; Abecasis 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 and coworkers (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; Humphries et al., 1981; Thorpe 1976 and 1983; 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 Material and Methods), 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, 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.

Acknowledgements

RRM's work was funded by a Marie Curie fellowship from the Early Stage Training site ECOSUMMER (MEST-CT-2005-020501) and a CONACyT- Mexico scholarship. This research was also supported by the project CTM2006-13964-C03-00 of the Spanish Ministry of Science and Innovation. We would like to thank the anonymous reviewers whose comments and suggestions helped to improve this manuscript.

515

516 Table 1. Number of bluemouth specimens analyzed in each location.

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

517

518

519 Table 2. Results of the multivariate regression of shape on size for bluemouth specimens

520 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

521

Table 3. Results of the multivariate regression for males and females within the studied locations. The shape variation predicted by each regression is expressed as a percentage of the total shape variation. The regressions for the Catalanian coast were not performed due to insufficient sexed specimens in the area.

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 ^a
	Males	60	1.99	0.2671 ^a
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

^a Not significant at the 5% level

Table 4. Angle between growth trajectories of males and females by area. Growth trajectories for males and females from the Catalanian 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.

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

* 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.

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

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 ($r^2 = 0.9935$, $p < 0.01$).

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.

564

565 Fig. 5 Growth trajectories for bluemouth from the two subareas in the Alboran Sea (A1 and

566 A2). The trajectories are represented with shape scores as a function of log centroid size.

567 Filled circles indicate sexed specimens (males and females) and open circles indicate

568 unsexed specimens.

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. 4 (see *Results- Growth trajectories for males and females* section).

577

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

Estimated shape - small specimen

Mean shape

Estimated shape - large specimen

Porcupine Bank

Cantabrian Sea

Galicia

Gulf of Cadiz

585

586

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

594

595 References

- 596 Abad E., I. Preciado, A. Serrano & J. Baro, 2007. Demersal and epibenthic assemblages of
597 trawlable grounds in the northern Alboran Sea (western Mediterranean). *Scientia*
598 *Marina* 71: 513–524.
- 599 Abecasis, D., A. R. Costa, J.G. Pereira & M.R Pinho, 2006. Age and growth of bluemouth,
600 *Helicolenus dactylopterus* (Delaroche, 1809) from the Azores. *Fisheries Research*
601 79: 148–154.
- 602 Abelló, P., A. Carbonell, & P. Torres, 2002. Biogeography of epibenthic crustaceans on the
603 shelf and upper slope off the Iberian Peninsula Mediterranean coasts: implications
604 for the establishment of natural management areas. *Scientia Marina*, 66: 183-198.
- 605 Aboim, M.A., G.M. Menezes, T. Schlitt & A.D. Rogers, 2005. Genetic structure and history
606 of populations of the deep-sea fish *Helicolenus dactylopterus* (Delaroche, 1809)
607 inferred from mtDNA sequence analysis. *Molecular Ecology* 14: 1343–1354.
- 608 Alberch, P., S. J. Gould, G. F. Oster & D. B. Wake, 1979. Size and shape in ontogeny and
609 phylogeny. *Paleobiology* 5: 296–317.
- 610 Allain V., 2001. Reproductive strategies of three deep-water benthopelagic fishes from the
611 northeast Atlantic Ocean. *Fisheries Research* 51: 165-176.
- 612 Barlow, G. W., 1961. Causes and significance of morphological variation in fishes.
613 *Systematic Zoology* 10: 105–117.
- 614 Begg, G. A., 2005. Life history parameters. In Cadrin, S.X., K.D. Friedland & J.R.
615 Waldman (eds), *Stock Identification Methods: Applications in Fishery Science*.
616 Elsevier Academic Press, San Diego, California: 119–150.

617 Blaber, S. J. M. & C. M. Bulman, 1987. Diets of fishes of the upper continental slope of
618 eastern Tasmania: content, calorific values, dietary overlap and trophic relationships.
619 Marine Biology 95: 345- 356.

620 Bookstein, F.L., 1991. Morphometric tools for landmark data: geometry and biology.
621 Cambridge University Press, Cambridge.

622 Bookstein, F.L., 1989. Principal warps: thin-plate splines and the decomposition of
623 deformations. IEEE Transactions on Pattern Analysis and Machine Intelligence 11:
624 567–585.

625 Borges L., E. Rogan & R. Officer, 2005. Discarding by the demersal fishery in the waters
626 around Ireland. Fisheries Research 76: 1–13.

627 Burnaby, T. P., 1966. Growth-invariant discriminant functions and generalized distances.
628 Biometrics 22: 96–110.

629 Cadrin, S. X., 2000. Advances in morphometric identification of fishery stocks. Reviews in
630 Fish Biology and Fisheries 10: 91–112.

631 Cadrin, S. X., 2005. Morphometric Landmarks. In Cadrin, S.X., K.D. Friedland & J.R.
632 Waldman (eds), Stock Identification Methods: Applications in Fishery Science.
633 Elsevier Academic Press, San Diego, California: 153–172.

634 Cartes, J. E., A. Serrano, F. Velasco, S. Parra, F. Sanchez, 2007. Community structure and
635 dynamics of deep-water decapod assemblages from Le Danois Bank (Cantabrian
636 Sea, NE Atlantic): Influence of environmental variables and food availability.
637 Progress in Oceanography 75: 797-816.

638 Czerwinski, I. A., J. C. Gutiérrez-Estrada, M. C. Soriguer & J. A. Hernando, 2008.
639 Morphometric relations for body size and mouth dimensions for four fish species in
640 the Strait of Gibraltar. Acta Ichthyologica et Piscatoria 38: 81-90.

641 Claytor R. R. & H. R. MacCrimmon, 1987. Partitioning size from morphometric data: A
642 comparison of five statistical procedures used in fisheries stock identification
643 research. Canadian Technical Report of Fisheries and Aquatic Services No. 1531.

644 Demestre, M., P. Sánchez & P. Abelló, 2000. Demersal fish assemblages and habitat
645 characteristics on the continental shelf and upper slope of the north-western
646 Mediterranean. Journal of the Marine Biological Association of the UK 80: 981–988.

647 Drake A. G. & C. P. Klingenberg, 2008. The pace of morphological change: historical
648 transformation of skull shape in St Bernard dogs. Proceedings of the Royal Society
649 B 275: 71–76.

650 Dryden, I. L. & K.V. Mardia, 1998. Statistical Shape Analysis. John Wiley & Sons, New
651 York.

652 Esteves, E., J. Aníbal, H. Krug & H. Marques da Silva, 1997. Aspects of age and growth of
653 bluemouth, *Helicolenus dactylopterus dactylopterus* (Delaroche, 1809) from the
654 Azores. Arquipélago. Life and Marine Sciences 15A: 83–95.

655 Fariña A. C., J. Freire & E. González-Gurriarán, 1997. Megabenthic decapod crustacean
656 assemblages on the Galician continental shelf and upper slope (north-west Spain).
657 Marine Biology 127: 419–434.

658 Frost, S. R., L. F. Marcus, F. L. Bookstein, D. P. Reddy & E. Delson, 2003. Cranial
659 allometry, phylogeography and systematics of large-bodied papionins (Primates:
660 Cercopithecinae) inferred from geometric morphometric analysis of landmark data.
661 Anatomical Record 275: 1048–1072.

662 Furlani, D. M., 1997. Development and ecology of ocean perch larvae, *Helicolenus*
663 *percoides* (Richardson, 1842) (Pisces: Scorpaenidae), from southern Australian
664 waters, with notes on the larvae of other sympatric scorpaenid genera. Marine and
665 Freshwater Research 48: 311–320

666 Garabana, D., 2005. The genus *Sebastes* Cuvier, 1829 (Pisces, Scorpaenidae) in the North
 667 Atlantic: species and stock discrimination using traditional and geometric
 668 morphometrics. PhD Thesis. University of Vigo, Spain.

669 García-Lafuente J., 2006. Topical Studies in Oceanography: the Gulf of Cadiz
 670 Oceanography: A Multidisciplinary View. Deep Sea Research Part II: 53: 1141-
 671 1143.

672 García-Lafuente J., J. Delgado, F. Criado-Aldeanueva, M. Bruno, J. del Río, J. Miguel
 673 Vargas, 2006. Water mass circulation on the continental shelf of the Gulf of Cadiz.
 674 Deep Sea Research Part II 53: 1182-1197.

675 Gidaszewski N. A., M. Baylac & C. P. Klingenberg, 2009. Evolution of sexual dimorphism
 676 of wing shape in the *Drosophila melanogaster* subgroup. BMC Evolutionary
 677 Biology 9: 110.

678 Good, P., 1994. Permutation tests: A practical guide to resampling methods for testing
 679 hypotheses. Springer, New York.

680 Hayes, D. B., C. P. Ferreri & W. Taylor, 1996. Linking fish habitat to their population
 681 dynamics. Canadian Journal of Fisheries and Aquatic Sciences 53: 383-390.

682 Heessen H. J. L., J. R. G. Hislop & T. W. Boon, 1996. An invasion of the North Sea by
 683 blue-mouth, *Helicolenus dactylopterus* (Pisces, Scorpaenidae). ICES Journal of
 684 Marine Sciences 53: 874-877.

685 Humphries J. M., Jr., F. L. Bookstein, B. Chernoff, G. R. Smith, R. L. Elder & S. G. Poss,
 686 1981. Multivariate discrimination by shape in relation to size. Systematic Zoology
 687 30: 291–308.

688 Ihssen, P. E., H. E. Booke, J. M. Casselman, J. M. McGlade, N. R. Payne & F. M. Utter,
 689 1981. Stock identification: materials and methods. Canadian Journal of Fisheries and
 690 Aquatic Sciences 38: 1838–1855.

691 Jolicoeur, P., 1963. The multivariate generalization of the allometry equation. *Biometrics*
692 19: 497–499

693 Karpouzi, V. S. & K. I. Stergiou, 2003. The relationships between mouth size and shape and
694 body length for 18 species of marine fishes and their trophic implications. *Journal of*
695 *Fish Biology* 62: 1353–1365.

696 Kelly, C. J., P. L. Connolly & J. J. Bracken, 1999. Age estimation, growth, maturity, and
697 distribution of the bluemouth rockfish *Helicolenus d. dactylopterus* (Delaroche
698 1809) from the Rockall Trough. *ICES Journal of Marine Science* 56: 61–74

699 Kitano, J., S. Mori & C. Peichel, 2007. Sexual dimorphism in the external morphology of
700 the threespine stickleback (*Gasterosteus aculeatus*). *Copeia* 2: 336–349.

701 Klingenberg, C. P. & R. Froese, 1991. A multivariate comparison of allometric growth
702 patterns. *Systematic Zoology* 40: 410–419.

703 Klingenberg, C. P., 1996. Multivariate allometry. In L. F. Marcus, M. Corti, A. Loy, G. J. P.
704 Naylor & D. E. Slice (eds). *Advances in morphometrics*. Plenum Press, New York:
705 23–49.

706 Klingenberg, C.P., 2008. MorphoJ software/ documentation. Version 1.00i. Faculty of Life
707 Sciences, University of Manchester, UK.
708 http://www.flywings.org.uk/MorphoJ_page.htm

709 Kouttouki, S., E. Georgakopoulou, P. Kaspiris, P. Divanach & G. Koumoundouros, 2006.
710 Shape ontogeny and variation in the sharpsnout seabream, *Diplodus puntazzo* (Cetti
711 1777). *Aquaculture Research* 37: 655–663.

712 Law, R., 2000. Fishing, selection, and phenotypic evolution. *ICES Journal of Marine*
713 *Science* 57: 659–669.

714 Loy, A., S. Cataudella & M. Corti, 1996. Shape changes during the growth of the sea bass,
715 *Dicentrarchus labrax* (Teleostei: Perciformes), in relation to different rearing

716 conditions. In Marcus, L. F., M. Corti, A. Loy, G. J. P. Naylor & D. E. Slice (eds),
 717 Advances in Morphometrics. Plenum Press, New York: 399–405.

718 Loy, A., L. Mariani, M. Bertelletti & L. Tunesi, 1998. Visualizing allometry: Geometric
 719 morphometrics in the study of shape changes in the early stages of the Two-banded
 720 sea bream, *Diplodus vulgaris* (Perciformes, Sparidae). Journal of Morphology 237:
 721 137–146.

722 Macpherson, E., 1979. Estudio sobre el régimen alimentario de algunos peces en el
 723 Mediterráneo occidental. Miscelánea Zoológica 5: 93–107

724 Macpherson, E., 1985. Daily ration and feeding periodicity of some fishes off the coast of
 725 Namibia. Marine Ecology Progress Series 26: 253–260.

726 Mamie J. C. J., D. J. Beare, E. G. Jones, M. Kienzle, H. Dobby, M. R. Heath & D. G. Reid,
 727 2007. Aspects of the distribution and growth of bluemouth (*Helicolenus*
 728 *dactylopterus*, Delaroche 1809) since its invasion of the northern North Sea in 1991.
 729 Fisheries Oceanography 16: 85–94.

730 Massutí, E., B. Morales–Nin & J. Moranta, 2000. Age and growth of blue-mouth,
 731 *Helicolenus dactylopterus* (Osteichthyes: Scorpaenidae), in the western
 732 Mediterranean. Fisheries Research 46: 165–176.

733 Massutí, E., J. Moranta, L. Gil de Sola, B. Morales–Nin & L. Prats, 2001. Distribution and
 734 population structure of the rockfish *Helicolenus dactylopterus* (Pisces: Scorpaenidae)
 735 in the western Mediterranean. Journal of the Marine Biological Association of the
 736 United Kingdom 81: 129–141.

737 Massutí, E., J. Gordon, J. Morata, S. Swan, C. Stefanescu, & N. Merrett, 2004.
 738 Mediterranean and Atlantic deep-sea fish assemblages: differences in biomass
 739 composition and size-related structure. Scientia Marina, 68: 101–115.

740 Mendonça, A., E. Isidro, G. Menezes, M. Rui Pinho, O. Melo & S. Estácio, 2006. New
 741 contribution to the reproductive features of bluemouth *Helicolenus dactylopterus*
 742 *dactylopterus* from northeast Atlantic (Azores Archipelago). *Scientia Marina* 70:
 743 679-688.

744 Mitteroecker, P., P. Gunz, M. Bernhard, K. Schaefer & F. L. Bookstein, 2004. Comparison
 745 of cranial ontogenetic trajectories among great apes and humans. *Journal of Human*
 746 *Evolution* 46: 679–698. *Marine Sciences* 53: 874-877.

747 Moranta J., E. Massutí & B. Morales-Nin, 2000. Fish catch composition of the deep-sea
 748 decapod crustacean fisheries in the Balearic Islands (western Mediterranean).
 749 *Fisheries Research* 45: 253-264.

750 Mosimann, J. E., 1970. Size allometry: Size and shape variables with characterizations of
 751 the lognormal and generalized gamma distributions. *Journal of the American*
 752 *Statistical Association* 65: 930–945.

753 Muñoz M., M. Casadevall & S. Bonet, 1999. Annual reproductive cycle of *Helicolenus*
 754 *dactylopterus dactylopterus* (Teleostei: Scorpaeniformes) with special reference to
 755 the ovaries sperm storage. *Journal of the Marine Biological Association of the UK*
 756 79: 521-529.

757 Muñoz M. & M. Casadevall, 2002. Reproductive indices and fecundity of *Helicolenus*
 758 *dactylopterus dactylopterus* (Teleostei: Scorpaenidae) in the Catalan Sea (western
 759 Mediterranean). *Journal of the Marine Biological Association of the UK* 82: 995-
 760 1000.

761 Nouar, A. & C. Maurin, 2000. Régime alimentaire de *Helicolenus dactylopterus*
 762 *dactylopterus* (Pisces: Scorpaenidae) des fonds chalutables des côtes algériennes.
 763 *Cahiers de Biologie Marine* 41:313–320.

764 Ribas, D., M. Muñoz, M. Casadevall & L. Gil de Sola, 2006. How does the northern
765 Mediterranean population of *Helicolenus dactylopterus dactylopterus* resist fishing
766 pressure? Fisheries Research 79: 285–293.

767 Rochet, M. J., 1998. Short-term effects of fishing on life history traits of fishes. ICES
768 Journal of Marine Science 55: 371–391.

769 Paul, L. J. & P. L. Horn, 2009. Age and growth of sea perch (*Helicolenus percoides*) from
770 two adjacent areas off the east coast of South Island, New Zealand. Fisheries
771 Research 95: 169–180.

772 Rohlf, F. J. & F. L. Bookstein, 1987. A Comment on shearing as a method for "size
773 correction". Systematic Zoology: 36: 356–367.

774 Rohlf, F.J., 1990. Morphometrics. Annual Review of Ecology and Systematics 21: 299–316.

775 Rohlf, F. J., & Slice, D., 1990. Extensions of the Procrustes method for the optimal
776 superimposition of landmarks. Systematic zoology 39: 40–59.

777 Rohlf, F. J., 1999. Shape statistics: Procrustes superimpositions and tangent spaces. Journal
778 of Classification 16: 197–223.

779 Rohlf, F. J., 2006. TpsDig. Version 2.10 . SUNY, Stony Brook, NY.

780 Sánchez, F., 1993. Las comunidades de peces de la plataforma del Cantábrico.
781 Publicaciones Especiales. Instituto Español de Oceanografía 13: 1–137.

782 Sánchez, F. & J. Gil, 2000. Hydrographic mesoscale structures and Poleward Current as a
783 determinant of hake (*Merluccius merluccius*) recruitment in the southern Bay of
784 Biscay. ICES Journal of Marine Science 57: 152–170.

785 Sánchez, P., M. Demestre & P. Martín. 2004. Characterisation of the discards generated by
786 bottom trawling in the northwestern Mediterranean. Fisheries Research 67: 71-80.

787 Sánchez, F., A. Serrano, S. Parra, M. Ballesteros & J.E. Cartes, 2008. Habitat characteristics
788 as determinant of the structure and spatial distribution of epibenthic and demersal

789 communities of Le Danois Bank (Cantabrian Sea, N. Spain). *Journal of Marine*
790 *Systems* 72: 64–86.

791 Sánchez Lizaso J. L., R. Goñi, O. Reñones, J. A. García Charton, R. Galzin, J. T. Bayle, P.
792 Sánchez Jerez, A. Pérez Ruzafa & A. A. Ramos, 2000. Density dependence in
793 marine protected populations: a review. *Environmental Conservation* 27:144–158.

794 Santos, M. N., M. B. Gaspar, C. C. Monteiro & P. Vasconcelos, 2002. Gill net and long–line
795 catch comparisons in a hake fishery: the case of southern Portugal. *Scientia Marina*
796 66: 433–441.

797 Sequeira, V., A. Neves, A. R. Vieira, I. Figueiredo & L. S. Gordo, 2009. Age and growth of
798 bluemouth, *Helicolenus dactylopterus*, from the Portuguese continental slope. *ICES*
799 *Journal of Marine Science* 66: 524–531.

800 Serrano, A., F. Velasco, I. Olaso & F. Sánchez, 2003. Macrobenthic crustaceans in the diet
801 of demersal fish in the Bay of Biscay in relation to abundance in the environment.
802 *Sarsia* 88:36-48.

803 Sequeira, V., I. Figueiredo, M. Muñoz & L. S. Gordo, 2003. New approach to the
804 reproductive biology of *Helicolenus dactylopterus*. *Journal of Fish Biology* 62:
805 1206-1210.

806 Sheets, H. D., 2000. VecCompare6 software (Integrated Morphometrics Package series).
807 Department of Physics, Canisius College, Buffalo, NY.

808 Slice, D. E., 2001. Landmark coordinates aligned by Procrustes analysis do not lie in
809 Kendall's shape space. *Systematic Biology* 50: 141–149.

810 Slice, D. E. & J. Stitzel, 2004. Landmark-based geometric morphometrics and the study of
811 allometry. S.A.E. conference on Digital Human Modeling for Design and
812 Engineering (DHM) June, 2004, Oakland University, Rochester, MI. Pub. No.:
813 04DHM–36.

814 Stefanescu, C., J. Rucabado & D. Lloris, 1992. Depth-size trends in western Mediterranean
815 demersal deep-sea fishes. *Marine Ecology Progress Series* 81: 205-213.

816 Strauss, R. E. & L. A. Fuiman, 1985. Quantitative comparisons of body form and allometry
817 in larval and adult Pacific sculpins (Teleostei: Cottidae). *Canadian Journal of*
818 *Zoology* 63: 1582–1589.

819 Swain, D. P., J. A. Hutchings & C. J. Foote, 2005. Environmental and genetic influences on
820 stock identification characters. In Cadrin, S.X., K.D. Friedland & J.R. Waldman
821 (eds), *Stock Identification Methods: Applications in Fishery Science*. Elsevier
822 Academic Press, San Diego, California: 45–85.

823 Thorpe, R. S., 1976. Biometric analysis of geographic variation and racial affinities.
824 *Biological Reviews* 51: 407–452.

825 Thorpe, R. S., 1983. Morphometric studies in inbred and hybrid House mice (*Mus sp.*):
826 Multivariate analysis of size and shape. *Journal of Zoology* 199: 421–432.

827 Uiblein, F., P. Lorance & D. Latrouite, 2003. Behaviour and habitat utilisation of seven
828 demersal fish species on the Bay of Biscay continental slope, NE Atlantic. *Marine*
829 *Ecology Progress Series* 257: 223–232.

830 Webb, P. W., 1984. Body Form, locomotion and foraging in aquatic vertebrates. *American*
831 *Zoologist* 24: 107–120

832 White, D. B., D. M. Wyanski & G. R. Sedberry, 1998. Age, growth, and reproductive
833 biology of the blackbelly rosefish from the Carolinas, U.S.A. *Journal of Fish*
834 *Biology* 53: 1274–1291.

835 White, M., C. Mohn, H. de Stitger & G. Mottram, 2005. Deep-water coral development as a
836 function of hydrodynamics and surface productivity around the submarine banks of
837 the Rockall Trough, NE Atlantic. In Freiwald A. & J. M. Roberts (eds), *Cold-water*
838 *Corals and Ecosystems*. Springer Verlag Berlin: 503-514.

839 Whitehead, P.J.P., M. L. Bauchot, J. C. Hureau, J. Nielsen & E. Tortonese, 1986. Fishes of
 840 the North-eastern Atlantic and Mediterrean. UNESCO, Paris.
 841 Wimberger, P. H., 1992. Plasticity of fish body shape. The effects of diet, development,
 842 family and age in two species of *Geophagus* (Pisces: Cichlidae). Biological Journal
 843 of the Linnean Society 45: 197–218.
 844 Withell A. F. & J. W. Wankowski, 1988. Estimates of age and growth of ocean perch,
 845 *Helicolenus percoides* (Richardson), in south-eastern Australian waters. Australian
 846 Journal of Marine and Freshwater Research 39: 441–457.
 847 Zelditch, M.L., B. L. Lundrigan, D. H. Sheets & T. Garland, 2003. Do precocial mammals
 848 develop at a faster rate? A comparison of rates of skull development in *Sigmodon*
 849 *fulviventer* and *Mus musculus domesticus*. Journal of Evolutionary Biology 16: 708-
 850 720.
 851 Zelditch, M.L., D. H. Sheets & W. L. Fink, 2003. The ontogenetic dynamics of shape
 852 disparity. Paleobiology 29: 139-156.
 853
 854