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Morphological variability of the shape of striped red mullet *Mullus surmuletus* in relation to stock discrimination between the Bay of Biscay and the eastern English Channel

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Abstract :

Truss analysis and length measurements were made on 168 striped red mullet *Mullus surmuletus*. Multivariate statistical analyses with principal component analysis and partial redundancy analysis (pRDA) were used on these measurements to evaluate the influence of maturity, sex and geographical area distribution on body shape. Truss measurements were important to quantify and discriminate changing body shape, presumably due to changing environmental conditions. Sexual dimorphism was not observed and juveniles could be distinguished from adults based on their body shape. More importantly, *M. surmuletus* occurring in different geographical areas could be differentiated using this method. Based on pRDA, a significant difference of head morphological dimensions was observed between populations occurring in the eastern English Channel and those occurring in the Bay of Biscay, suggesting that fish from these areas could represent two subpopulations.

Keywords : fish body shape ; head morphology ; morphometric analysis ; stock identification ; Truss model

Introduction

Striped red mullet *Mullus surmuletus* (L. 1758) is an economically important species in the Mediterranean Sea and in the northern Atlantic Ocean, where it is exploited from the Bay of Biscay to the southern North Sea (ICES, 2010). In Atlantic waters there are two main areas where this species is caught, the Bay of Biscay and the Eastern English Channel. This species was initially exploited by the Spanish fleets along the Spanish coast inside the Bay of Biscay. Originally considered as valuable by-catch (Marchal, 2008), the growing exploitation of *M. surmuletus* and a conspicuous increase in landings in the English Channel and the southern North Sea by French, English and Dutch fleets have been observed from the 1990s onwards. This was attributed to an increase in the migratory distribution and abundance of this species in these areas, which is largely heightened by the decline of traditionally targeted species and the trend for sea-water warming (Poulard & Blanchard, 2005; Marchal, 2008; ICES, 2010). Reports indicate a steady increase in Eastern English Channel landings, now reaching ten times the recorded landing levels of 1990 (Marchal, 2008; Carpentier *et al*., 2009). *Mullus surmuletus* is still considered as a non-quota species in the Northeast Atlantic and the evaluation of the level of exploitation only began seven years ago (ICES, 2010).

A stock corresponds to all the individuals that both belong to the same species and live in the same geographical area. The population within a stock is such that breeding is both possible and more likely between any pair within its distribution area than with individuals from other areas. A part or subdivision of a population, often based on geographical consideration, is a subpopulation. Fish stocks may be considered as subpopulations of a particular species of fish, for which intrinsic parameters (growth, recruitment, mortality and fishing mortality) are the only significant factors in determining stock dynamics, while other factors, in particular immigration and emigration, are considered to have limited effect. Information on stock identity and spatial structure provide the basis for understanding fish population dynamics and enable reliable resource assessment for fisheries management (Reiss *et al*., 2009). Each stock may have unique demographic properties and responses or rebuilding capabilities when faced with exploitation. The biological attributes and productivity of the species may be affected if the stock structure considered by fisheries managers is erroneous (Smith *et al*., 1991).

Stock identification aims to identify these subpopulations and several techniques may be used to this end. For example, tagging experiments, analyses of spatial variation in genetic and morphometric markers, life-history parameters, parasite abundance and contaminants can be used to interpret distribution and relative abundance (Pawson & Jennings, 1996; Cadrin *et al*., 2005). Each method offers a unique view of population structure that relates to different definitions of the term "stock" (Begg *et al.*, 1999). Despite a range of difficulties detailed in Jennings *et al.* (2001), morphological analysis has been useful for fish stock identification. Environmentally induced phenotypic variation provides rapid information on stock or sub-population identity (Clayton, 1981). This is especially useful when the time at which stock separation occurred is too recent to have allowed considerable accumulation of genetic differentiation among populations.

In the case of *M. surmuletus*, genetic studies have only been carried out in the Mediterranean Sea (Mamuris *et al*., 1998a,b, 1999; Apostolidis *et al*., 2009; Galarza *et al*., 2009). In the Gulf of Pagasitikos (western Aegean Sea), analyses on three molecular markers revealed panmixia (Apostolidis *et al*., 2009). In the Mediterranean basin, the Siculo-Tunisian Strait seems to be the transition zone between the Mediterranean's eastern and western populations (Galarza *et al*., 2009). A sharp genetic division was detected when comparing populations of *M. surmuletus* originating from the Atlantic Ocean or Mediterranean Sea (Galarza *et al*., 2009).

Otolith microchemistry has also been used to discriminate between subpopulations at different growth stages. However, results are difficult to interpret as trace element deposition can be due to combined effects of physiological, ontogenetic and environmental influences.

As a result, morphological analysis offers a rapid and inexpensive method for population or subpopulation structure identification.

To date, very few studies dealing with otolith shape have been conducted on stock structure of *M. surmuletus* in the north-eastern Atlantic Ocean (Mahé *et al*., 2005; Benzinou *et al.,* 2013). This region is nevertheless divided into two areas by the International Council for the Exploration of the Sea (ICES) as distinct areas of stock management. The objective of this paper is to evaluate if morphological variations may discriminate populations of *M. surmuletus* sampled in two different ICES areas using geometric morphometric tools.

Materials and methods

Study sites and sampling

Two ICES areas within the northeast Atlantic are considered in this study: the Bay of Biscay and the Eastern English Channel (Fig. 1) where annual research surveys are conducted to evaluate commercial fish abundance. The Bay of Biscay (ICES areas VIIIa and b) has a large continental shelf with water depth reaching down to 200 m. Average annual water temperature increases from the northern part (11.2 °C at 48 °N) to the southern part (15.6 °C at 36°N) of the North-eastern Atlantic region. The substrate varies from a muddy bottom along the shelf break to rocky or sandy substrates along the inner shelf (depth < 100 m). The eastern English Channel (ICES area VIId) is an epicontinental area characterized by a strong tidal regime. Water depth declines from 70 m off Cherbourg to 40 m in the centre of the Dover Strait. Seabed sediment types vary from west to east and are strongly influenced by the tidal currents. Pebbly bottoms occur in open waters off Cherbourg followed by a progression towards gravel, then coarse to fine sands toward the eastern coasts and even mud in the sheltered estuarine bays. Pebbles and rocks are found again in the narrows of the Dover strait where tidal currents are very strong. Average annual water temperature is 13.3 °C (Carpentier *et al*., 2009).

Mullus surmuletus were sampled during two annual scientific surveys using GOV bottom trawls (very high vertical opening, square mesh size in the cod end: 10 mm side). In the Bay of Biscay, fish were collected during the Western Europe fisheries resources evaluation (EValuation des resources Halieutiques de l'Ouest de l'Europe, EVHOE) survey in October-November 2003 onboard the research vessel (RV) "Thalassa". In the Eastern English Channel, samples were collected during the Channel Ground Fish Survey (CGFS) during October-November 2002 and 2003 onboard the RV "Gwen-Drez."

A total of 168 individuals were sampled: 111 in the Eastern English Channel and 57 in the Bay of Biscay. All fresh *M. surmuletus* were measured for total length (L_T±1mm), mass (W±1g) and sexed. The total length ranged from 82 to 345 mm for individuals collected in the Bay of Biscay, and from 90 to 372 mm for those sampled in the Eastern English Channel (Table I). The total mass (W) varied from 10 to 625 g and 6 to 692 g for individuals collected in the Bay of Biscay and in the eastern English Channel respectively. Macroscopic observation of gonads based on scale proposed by Mahé *et al.* (2005) was used to determine individual sex and maturity. In the Bay of Biscay, this species principally occurs along the northern area close to the Loire estuary (Fig. 1) while in the eastern English Channel this species is mainly found in the Dover Strait and Bay of Seine areas.

Image analyses

Each individual was photographed using a digital camera. A calibrated image of each individual (positioned head on the left and deployed fins) was obtained using the Optimas 6 software (Anonymous, 1996). This software was used to enable identification of homologous points or landmarks and to calculate distances between these points.

The Truss network method (Strauss & Bookstein, 1982) was used and 10 landmark points were identified on the outline of the body (head: 1-2; dorsal fin: 3; adipose fin: 4-5; caudal fin: 6-7; anal fin: 8-9; pelvic fin: 10; see Fig. 2). Three categories of clearly defined landmarks are identified: Type 1 is a mathematical point such as a local juxtaposition of two different tissues (3-7, 9-10), Type 2 is a point marking the geometrical structure of the individual (1-2) and Type 3 is based on another structure or point (8) (Slice *et al.*, 1996). Consequently from these 10 selected points, 21 segments (or distances) are established and measured with a precision of 0.001 mm (Fig. 2).

Data processing

To investigate possible variations of fish shape according to five explanatory variables (geographical area, maturity, body length, body mass and sex), the normal distribution of segments was checked using kurtosis and skewness coefficients. Principal component analysis (PCA) was applied to truss size variables to outline groups of samples and to identify influential variables. Principal components were extracted from the covariance matrix. Allometric analyses and PCAs showed that these distances are related to the overall length of individuals. Partial redundancy analysis (pRDA) was primarily carried out using CANOCO by extracting the variance explained by total length used as a covariate (ter Braak & Smilauer, 2002). In the resulting partial analysis, it is possible to test and extract the relevant explanatory variables related to the variation in fish morphology independently from the individual total length. The pRDA was used in combination with Monte Carlo permutation tests to explore the multi-linear relationships between morphometric data and un-biased geographical and sex descriptors.

Results

Principal component analysis of truss variables reveals that the first principal component accounts for 96.7% of the total variance. There is an unbiased correlation between segments, body size and body mass which is directly related to individual size (Fig. 3).

The strong correlation with the fish size potentially masks morphological differences between sexes and geographical sectors. A pRDA was therefore carried out (Fig. 4) to remove the observed effect of fish size. No significant morphological differences are observed from inter-annual (2002-2003) individual samples analysed in the Eastern English Channel (Fig. 4). Likewise, the pRDA does not reveal any significant sexual dimorphism (p=0.134). However, this analysis clearly separates individuals from the Bay of Biscay (EVHOE) from those of the Eastern English Channel (CGFS). Segments D1-2, D1-3, D1-10, D2-3 and D4-5 are associated to the EVHOE survey (Fig. 2). All these segments are on the head, except for D4-5 (adipose fin).

The individuals collected from the Bay of Biscay appear to have a more ventrally positioned mouth than those captured in the Eastern English Channel and this significant difference indicates two stock components (Fig. 5). Shape divergences are also observed between juvenile (smaller bodied) and adult (larger bodied) stages collected within the Eastern English Channel. Multivariate analyses were also performed on body mass data, but results show that this factor does not discriminate between populations of *M. surmuletus* from different areas.

Discussion

The truss network analysis identifies two distinct subpopulations of *M. surmuletus* from the Bay of Biscay and the Eastern English Channel. This study demonstrates that populations in the two areas can be discriminated based on morphology, even when fish size effect is removed. These results corroborate those obtained from a study of otolith shape (Benzinou *et* *al*., 2013). Little morphological variability was observed between sexes. This weak sexual dimorphism may be attributed to the sampling period, which did not coincide with spawning period. All samples were collected in October and November, whereas the reproductive season of *M. surmuletus* occurs between May and September in the North-Eastern Atlantic (N'Da & Deniel, 1993).

In general, morphological variability may result from genetic variation (Griffiths *et al*., 2010) or phenotypic plasticity (Schlichting & Pigliucci, 1998; Moe *et al*., 2004) induced by different environmental conditions prevailing in each geographic area (Corti *et al*., 1996; Clabaut *et al*., 2007). In particular, morphological variability may reflect local food availability and feeding conditions prevailing in each area; a relatively low rate of egg and larval transportation or migration for the adult fish; limited swimming performance or geographical constraints imposed on the subpopulations; and last but not least, the differential impact of fisheries (i.e. different fishing patterns), which might determine different selection effects (for example, smaller lengths at maturity).

External shape and internal anatomical development are affected by the environmental conditions of growth (e.g., climate, food limitation, interaction, exploitation, other stressors), especially during juvenile (developmental) stages (Loy *et al*., 2000; Moe *et al*., 2004). Food availability has been observed in other studies as a factor affecting fish morphology and behaviour (Moe *et al*., 2004; Borcherding & Magnhagen, 2008). Consumption of more energy rich prey may also contribute to change in body shape development.

Mullus surmuletus exhibits an opportunistic and benthivorous feeding habit on sandy and rocky bottoms (Lombarte & Aguirre, 1997; Mazzola *et al*., 1999). In our study, *M. surmuletus* from the Bay of Biscay were found mainly over sandy and rocky bottoms. In the eastern English Channel, the habitats of *M. surmuletus* also include rocky and sandy substrates but are dominated by coarse sands, gravels and pebbles. Species that can occupy several habitat (substrate) types may develop a wider dietary breadth and morphological variation, which may have resulted in head shape modifications of *M. surmuletus* in the eastern English Channel.

Previous studies have investigated the diet of *M. surmuletus*. In these studies, juveniles consume large quantities of polychaetes and other prey such as copepods, harpacticoids, amphipods and *Tanaidacea* (N'Da, 1992; Labropoulou *et al*., 1997; Mazzola *et al*., 1999; Bautista-Vega *et al*., 2008). Adults fed mainly on crustaceans (shrimps and crabs) and other benthic organisms such as polychaetes, molluscs and echinoderms, as well as on small forage fish (Badalamenti & Riggio, 1989; Golani & Galil, 1991; N'Da, 1992; Mazzola *et al*., 1999; Bautista-Vega *et al*., 2008). The observed ontogenetic changes in feeding habits may explain shape divergences between juvenile and adult of *M. surmuletus*.

The truss network has been a useful tool to discriminate subpopulations of *M. surmuletus* from two different ecosystems based on fish shape and directly comparable with the results obtained by the study of otolith shape (Benzinou *et al*., 2013). Similar patterns of differentiation have been observed for others species, based on morphological, otolith and genetic characters (Cadrin *et al*., 2005; Kristoffersen & Magoulas, 2008). Morphological variation may be greater than the differentiation found at the genetic level (Stepien *et al.*, 1994). These morphological differences between habitats, could, to some extent, reflect phenotypic plasticity (Mamuris *et al.*, 1998b; Uiblein *et al.*, 1998). In this study, the significant morphometric divergence observed could indicate isolation between these two populations. Fage (1909) distinguished a southern and a northern form of *M. surmuletus* based mainly on head shape. Moreover, the strong increase in numbers of individuals of *M. surmuletus* reported in landings from the English Channel and the southern North Sea since the 1990s has also been observed in the northern North Sea (Beare *et al.*, 2005; Engelhard *et al.*, 2011). Beare *et al.* (2005) observed that the increased abundance of *M. surmuletus* in the northern North Sea could be due to a winter migration of a larger resident population in the southern North Sea, when water temperatures in the northern part of the North Sea are higher than in the southern part. There is a positive relationship between the abundance of this species and water temperature (Cushing, 1982; Vaz *et al.*, 2004; Beare *et al.*, 2005). Hence, the increasing presence of *M. surmuletus* in northern parts of its distribution range could be in response to warming climate (Engelhard *et al*., 2011). Recently, Mahé *et al*. (2013) showed that growth rate of *M. surmuletus* in the eastern English Channel and southern North Sea is higher than those observed in southern areas. Feeding behaviour is a well-known factor that influences head morphology (Hyndes *et al*., 1997; Delariva & Agostinho, 2001; Palma & Andrade, 2002; Silva, 2003; Janhuen *et al*., 2009) and an organism's (somatic) growth (Loy *et al.*, 2000). Thus, fish trophic ecology might be one of the principal explanatory factors for morphological divergences observed in the current study. Unfortunately, the effects of trophic ecology on variation of the morphology of *M. surmuletus* cannot be quantitatively accounted for because food and feeding patterns of *M. surmuletus* have not been considered on samples collected for this study. Spline values observed on head dimensions of *M. surmuletus* are likely to be related to trophic differences and exposure to various environmental conditions in different habitats during important developmental periods. Genetic, otolith and trophic characterisation studies are future research programs that can be combined to this method to achieve a more reliable determination of stock structure, which is critically relevant to its successful management.

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Figure 1 : Map showing location of sampling areas with ICES divisions (IVc, VIId, VIIe, VIIIa & VIIIb).

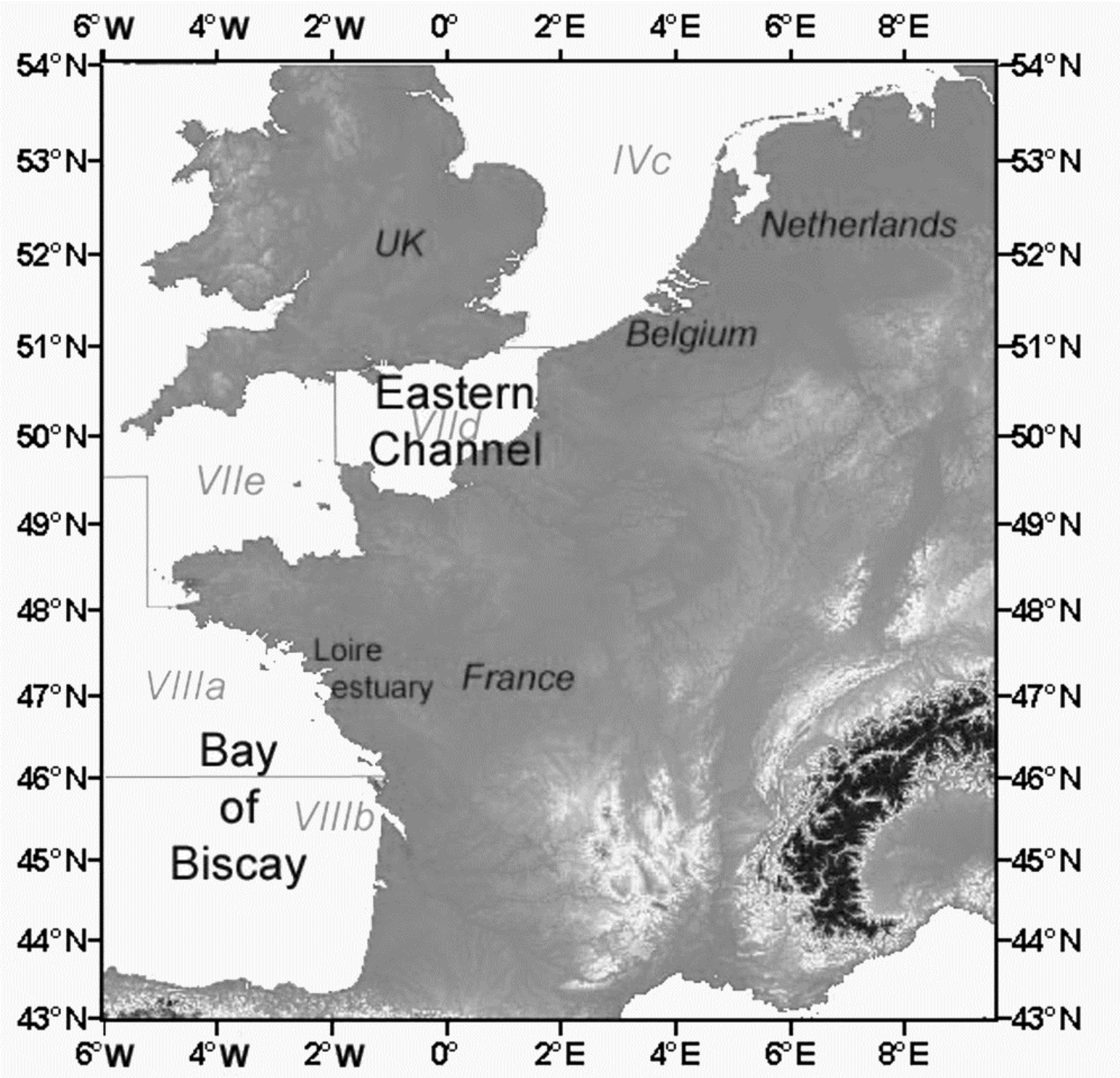
6°W
4°W
2°W
0°
2°E
4°E
6°E
8°E
54°N
53°N
52°N
51°N
50°N
49°N
48°N
47°N
46°N
45°N
44°N
43°N
IVc
UK
Netherlands
Belgium
Eastern
VIId
Channel
VIIe
Loire
estuary
France
VIIIa
Bay
of
VIIIb
Biscay

Figure 2 : The 10 homologous landmarks used to calculate the truss networks (lines) on *M. surmuletus*.

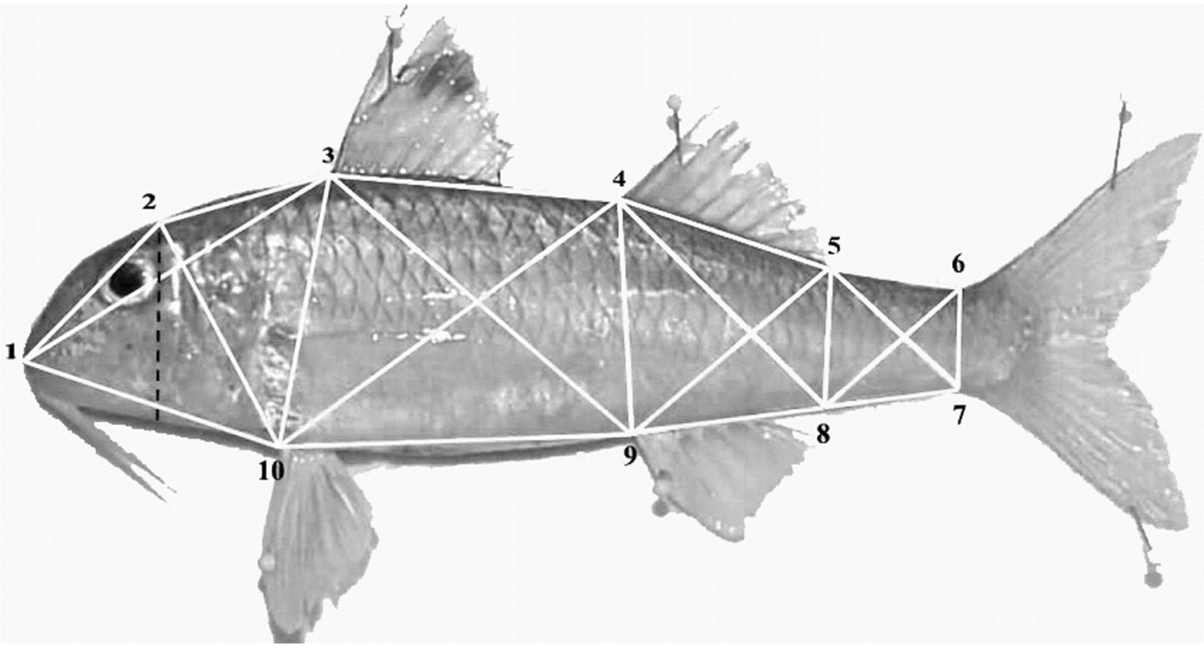

Figure 3: Main results of the principal components analysis. Open squares and circles represent individual fish specimens analyzed from the Eastern English Channel and the Bay of Biscay, respectively.

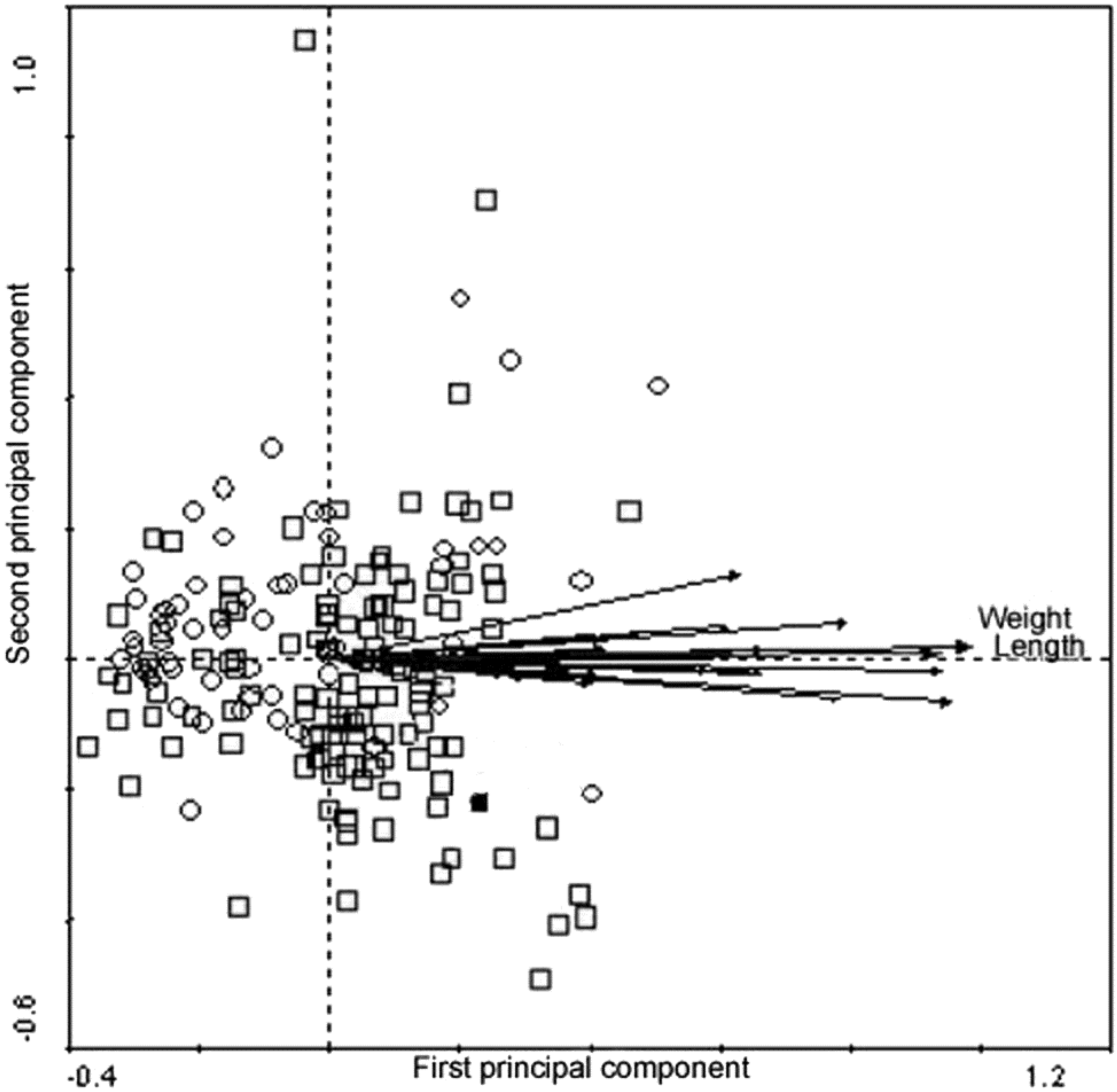

Figure 4: Main results of the Redundancy Partial Analyses. Squares (black: 2002 & open: 2003) and circles represent individual fish specimens analyzed from the Eastern English Channel and the Bay of Biscay respectively. Body segments are identified by the vectors.

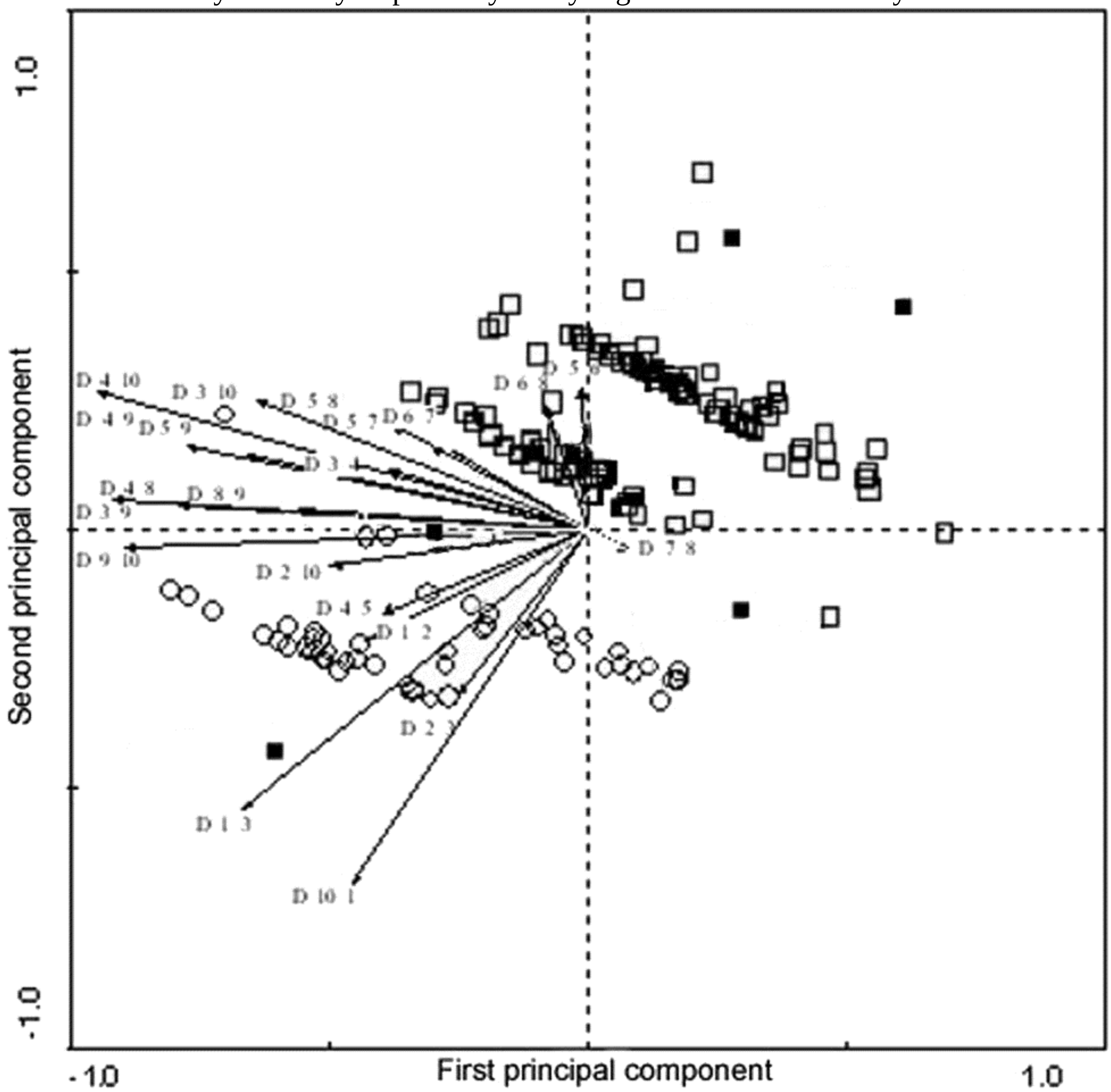

Figure 5: Averaged forms of *M. surmuletus* in the Bay of Biscay and in the Eastern English Channel. Reconstructed forms are scaled in centimetres and represent body total length of 20 cm.

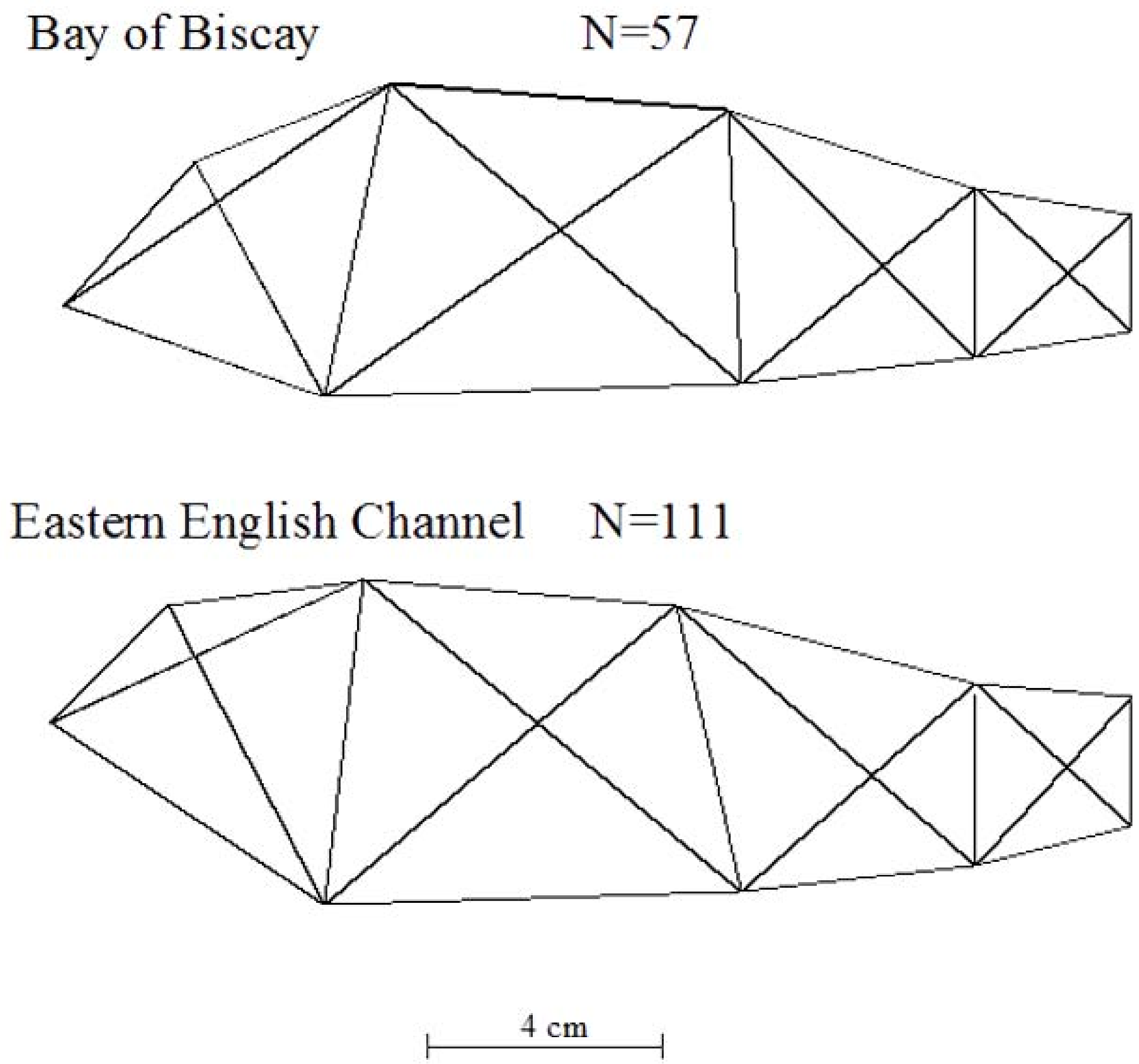

Table I: Number, total length (mean+s.d.; mm) and total mass (mean+s.d.; g) of samples of *M. surmuletus* used in groundfish surveys according to the stage of sexual maturity and sex. CGFS: Channel Ground Fish Survey; EVHOE: Evaluation des ressources halieutiques de l'ouest de l'Europe.

Groundfish surveys		Juveniles	Females	Males
CGFS 2002	Number	0	20	30
	mean total length (s.d.)		250 (41)	223 (22)
	mean total mass (s.d.)		236 (140)	145 (49)
CGFS 2003	Number	16	28	17
	mean total length (s.d.)	122 (22)	251 (51)	204 (44)
	mean total mass (s.d.)	17 (8)	219 (120)	109 (53)
EVHOE 2003	Number	24	19	14
	mean total length (s.d.)	120 (13)	214 (51)	241 (50)
	mean total mass (s.d.)	22 (8)	200 (142)	160 (108)