



**HAL**  
open science

# 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

K. Mahé, M. C. Villanueva, S. Vaz, F. Coppin, P. Koubbi, A. Carpentier

► **To cite this version:**

K. Mahé, M. C. Villanueva, S. Vaz, F. Coppin, P. Koubbi, et al.. 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. *JOURNAL OF FISH BIOLOGY*, 2014, 84 (4), pp.1063-1073. 10.1111/jfb.12345 . hal-03502771

**HAL Id: hal-03502771**

<https://hal.science/hal-03502771v1>

Submitted on 26 Dec 2021

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License

---

## 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

K. Mahe<sup>1,\*</sup>, M. C. Villanueva<sup>1</sup>, S. Vaz<sup>1</sup>, F. Coppin<sup>1</sup>, P. Koubbi<sup>2</sup> and A. Carpentier<sup>1</sup>

<sup>1</sup> IFREMER, Laboratoire Ressources Halieutiques, 150 quai Gambetta, BP699, 62321 Boulogne-sur-Mer, France

<sup>2</sup> UPMC Université Paris VI, UMR 7093, Laboratoire d'Océanographie de Villefranche, 06230 Villefranche-sur-Mer, France

\*: Corresponding author : Kelig Mahe, tel. +33 3 21 99 56 02 ; email address : [Kelig.Mahe@ifremer.fr](mailto:Kelig.Mahe@ifremer.fr)

---

### 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

57 **Introduction**

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

73 A stock corresponds to all the individuals that both belong to the same species and live in the  
74 same geographical area. The population within a stock is such that breeding is both possible  
75 and more likely between any pair within its distribution area than with individuals from other  
76 areas. A part or subdivision of a population, often based on geographical consideration, is a  
77 subpopulation. Fish stocks may be considered as subpopulations of a particular species of  
78 fish, for which intrinsic parameters (growth, recruitment, mortality and fishing mortality) are  
79 the only significant factors in determining stock dynamics, while other factors, in particular  
80 immigration and emigration, are considered to have limited effect. Information on stock  
81 identity and spatial structure provide the basis for understanding fish population dynamics and

82 enable reliable resource assessment for fisheries management (Reiss *et al.*, 2009). Each stock  
83 may have unique demographic properties and responses or rebuilding capabilities when faced  
84 with exploitation. The biological attributes and productivity of the species may be affected if  
85 the stock structure considered by fisheries managers is erroneous (Smith *et al.*, 1991).

86 Stock identification aims to identify these subpopulations and several techniques may be used  
87 to this end. For example, tagging experiments, analyses of spatial variation in genetic and  
88 morphometric markers, life-history parameters, parasite abundance and contaminants can be  
89 used to interpret distribution and relative abundance (Pawson & Jennings, 1996; Cadrin *et al.*,  
90 2005). Each method offers a unique view of population structure that relates to different  
91 definitions of the term “stock” (Begg *et al.*, 1999). Despite a range of difficulties detailed in  
92 Jennings *et al.* (2001), morphological analysis has been useful for fish stock identification.

93 Environmentally induced phenotypic variation provides rapid information on stock or sub-  
94 population identity (Clayton, 1981). This is especially useful when the time at which stock  
95 separation occurred is too recent to have allowed considerable accumulation of genetic  
96 differentiation among populations.

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

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

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

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

115

## 116 **Materials and methods**

### 117 *Study sites and sampling*

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

131 where tidal currents are very strong. Average annual water temperature is 13.3 °C (Carpentier  
132 *et al.*, 2009).

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

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

#### 150 *Image analyses*

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

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

### 163 *Data processing*

164 To investigate possible variations of fish shape according to five explanatory variables  
165 (geographical area, maturity, body length, body mass and sex), the normal distribution of  
166 segments was checked using kurtosis and skewness coefficients. Principal component  
167 analysis (PCA) was applied to truss size variables to outline groups of samples and to identify  
168 influential variables. Principal components were extracted from the covariance matrix.  
169 Allometric analyses and PCAs showed that these distances are related to the overall length of  
170 individuals. Partial redundancy analysis (pRDA) was primarily carried out using CANOCO  
171 by extracting the variance explained by total length used as a covariate (ter Braak & Smilauer,  
172 2002). In the resulting partial analysis, it is possible to test and extract the relevant  
173 explanatory variables related to the variation in fish morphology independently from the  
174 individual total length. The pRDA was used in combination with Monte Carlo permutation  
175 tests to explore the multi-linear relationships between morphometric data and un-biased  
176 geographical and sex descriptors.

177

178 **Results**

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

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

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

197

198 **Discussion**

199 The truss network analysis identifies two distinct subpopulations of *M. surmuletus* from the  
200 Bay of Biscay and the Eastern English Channel. This study demonstrates that populations in  
201 the two areas can be discriminated based on morphology, even when fish size effect is  
202 removed. These results corroborate those obtained from a study of otolith shape (Benzinou *et*



203 *al.*, 2013). Little morphological variability was observed between sexes. This weak sexual  
204 dimorphism may be attributed to the sampling period, which did not coincide with spawning  
205 period. All samples were collected in October and November, whereas the reproductive  
206 season of *M. surmuletus* occurs between May and September in the North-Eastern Atlantic  
207 (N'Da & Deniel, 1993).

208 In general, morphological variability may result from genetic variation (Griffiths *et al.*, 2010)  
209 or phenotypic plasticity (Schlichting & Pigliucci, 1998; Moe *et al.*, 2004) induced by different  
210 environmental conditions prevailing in each geographic area (Corti *et al.*, 1996; Clabaut *et al.*,  
211 2007). In particular, morphological variability may reflect local food availability and feeding  
212 conditions prevailing in each area; a relatively low rate of egg and larval transportation or  
213 migration for the adult fish; limited swimming performance or geographical constraints  
214 imposed on the subpopulations; and last but not least, the differential impact of fisheries (i.e.  
215 different fishing patterns), which might determine different selection effects (for example,  
216 smaller lengths at maturity).

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

223 *Mullus surmuletus* exhibits an opportunistic and benthivorous feeding habit on sandy and  
224 rocky bottoms (Lombarte & Aguirre, 1997; Mazzola *et al.*, 1999). In our study, *M. surmuletus*  
225 from the Bay of Biscay were found mainly over sandy and rocky bottoms. In the eastern  
226 English Channel, the habitats of *M. surmuletus* also include rocky and sandy substrates but  
227 are dominated by coarse sands, gravels and pebbles. Species that can occupy several habitat

228 (substrate) types may develop a wider dietary breadth and morphological variation, which  
229 may have resulted in head shape modifications of *M. surmuletus* in the eastern English  
230 Channel.

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

239 The truss network has been a useful tool to discriminate subpopulations of *M. surmuletus*  
240 from two different ecosystems based on fish shape and directly comparable with the results  
241 obtained by the study of otolith shape (Benzinou *et al.*, 2013). Similar patterns of  
242 differentiation have been observed for others species, based on morphological, otolith and  
243 genetic characters (Cadrin *et al.*, 2005; Kristoffersen & Magoulas, 2008). Morphological  
244 variation may be greater than the differentiation found at the genetic level (Stepien *et al.*,  
245 1994). These morphological differences between habitats, could, to some extent, reflect  
246 phenotypic plasticity (Mamuris *et al.*, 1998b; Uiblein *et al.*, 1998). In this study, the  
247 significant morphometric divergence observed could indicate isolation between these two  
248 populations. Fage (1909) distinguished a southern and a northern form of *M. surmuletus*  
249 based mainly on head shape. Moreover, the strong increase in numbers of individuals of *M.*  
250 *surmuletus* reported in landings from the English Channel and the southern North Sea since  
251 the 1990s has also been observed in the northern North Sea (Beare *et al.*, 2005; Engelhard *et*  
252 *al.*, 2011). Beare *et al.* (2005) observed that the increased abundance of *M. surmuletus* in the

253 northern North Sea could be due to a winter migration of a larger resident population in the  
254 southern North Sea, when water temperatures in the northern part of the North Sea are higher  
255 than in the southern part. There is a positive relationship between the abundance of this  
256 species and water temperature (Cushing, 1982; Vaz *et al.*, 2004; Beare *et al.*, 2005). Hence,  
257 the increasing presence of *M. surmuletus* in northern parts of its distribution range could be in  
258 response to warming climate (Engelhard *et al.*, 2011). Recently, Mahé *et al.* (2013) showed  
259 that growth rate of *M. surmuletus* in the eastern English Channel and southern North Sea is  
260 higher than those observed in southern areas. Feeding behaviour is a well-known factor that  
261 influences head morphology (Hyndes *et al.*, 1997; Delariva & Agostinho, 2001; Palma &  
262 Andrade, 2002; Silva, 2003; Janhuen *et al.*, 2009) and an organism's (somatic) growth (Loy *et*  
263 *al.*, 2000). Thus, fish trophic ecology might be one of the principal explanatory factors for  
264 morphological divergences observed in the current study. Unfortunately, the effects of trophic  
265 ecology on variation of the morphology of *M. surmuletus* cannot be quantitatively accounted  
266 for because food and feeding patterns of *M. surmuletus* have not been considered on samples  
267 collected for this study. Spline values observed on head dimensions of *M. surmuletus* are  
268 likely to be related to trophic differences and exposure to various environmental conditions in  
269 different habitats during important developmental periods. Genetic, otolith and trophic  
270 characterisation studies are future research programs that can be combined to this method to  
271 achieve a more reliable determination of stock structure, which is critically relevant to its  
272 successful management.

273

#### 274 **Acknowledgements**

275 We would like to express our gratitude to all people involved in the collection of *M.*  
276 *surmuletus* required in this study. Thanks are expressed to the crew of the RV « Thalassa »  
277 and the RV « Gwen Drez » during the EVHOE and CGFS surveys. This work is a part of the

278 " Le rouget barbet de roche *Mullus surmuletus* (L. 1758) en Manche orientale et mer du Nord  
279 " regional project. We acknowledge the help of Willie McCurdy for improvement of the  
280 language. We are grateful for the constructive comments provided by the reviewers and the  
281 associated editors.

282

### 283 **References**

284 Anonymous (1996). OPTIMAS 6. User guide and technical reference, 8th eds. Silver Spring,  
285 Maryland: Media Cybernetics.

286 Apostolidis, A. P., Moutou, K. A., Stamatis, C. & Mamuris, Z. (2009). Genetic structure of  
287 three marine fish from the Gulf of Pagasitikos (Greece) based on allozymes, RAPD, and  
288 mtDNA RFLP markers. *Biologia* **64**, 1005-1010.

289 Badalamenti, F. & Riggio, S. (1989). Polychaetes in the gut contents of *Mullus surmuletus* L.  
290 (Pisces, *Mullidae*) in the Bay of Palermo. *Oebalia* **15**, 79-87.doi:10.1046/j.1439-  
291 0426.1999.00135.x

292 Bautista-Vega, A. A., Letourneur, Y., Harmelin-Vivien, M. & Salen-Picard, C. (2008).  
293 Difference in diet and size-related trophic level in two sympatric fish species, the red mullets  
294 *Mullus barbatus* and *Mullus surmuletus*, in the Gulf of Lions (north-west Mediterranean Sea).  
295 *Journal of Fish Biology* **73**, 2402-2420.doi:10.1111/j.1095-8649.2008.02093.x

296 Beare, D.J., Burns, F., Peach, K. & Reid, D. G. (2005). Red mullet migration into the northern  
297 North Sea during late winter. *Journal of Sea Research* **53**, 205-  
298 212.doi:10.1016/j.seares.2004.06.003

299 Begg, G. A., Friedland, K. D. & Pearce, J. B. (1999). Stock Identification : Its role in stock  
300 assessment and fisheries management. *Fisheries Research Special Issue* **43**, 1-252.

301 Benzinou, A., Carbini, S., Nasreddine, K., Elleboode, R. & Mahé, K. (2013). Discriminating  
302 stocks of striped red mullet (*Mullus surmuletus*) in the Northwest European seas using three

303 automatic shape classification methods. *Fisheries Research* **143**, 153-160.  
304 doi:10.1016/j.fishres.2013.01.015

305 Borcharding, J. & Magnhagen, C. (2008). Food abundance affects both morphology and  
306 behaviour of juvenile perch. *Ecology of Freshwater Fish* **17**, 207-218.doi:10.1111/j.1600-  
307 0633.2007.00272.x

308 Cadrin, S. X., Friedland, K. D. & Waldman, J. R. (2005). *Stock identification methods:  
309 applications in fishery science*, Academic Press.

310 Carpentier, A., Martin, C. S. & Vaz, S. (2009). *Channel Habitat Atlas for marine Resource  
311 Management (CHARM phase II)*, INTERREG 3a Programme, IFREMER, Boulogne-sur-mer.

312 Clabaut, C., Bunje, P. M. E., Salzburger, W. & Meyer, A. (2007). Geometric morphometric  
313 analyses provide evidence for the adaptive character of the Tanganyikan cichlid dish  
314 radiations. *Evolution* **61**, 560-578.

315 Clayton, J. W. (1981). The stock concept and the uncoupling of organismal and molecular  
316 evolution. *Canadian Journal of Fisheries and Aquatic Sciences* **38**, 1515-  
317 1522.doi:10.1139/f81-204

318 Corti, M., Loy, A. & Cataudella, S. (1996). Form changes in the sea bass, *Dicentrarchus  
319 labrax* (Moronidae Teleostei), after acclimation to freshwater: An analysis using shape  
320 coordinates. *Environmental Biology of Fishes* **47**, 165-175.

321 Cushing, D. H. (1982). *Climate and Fisheries*. London: Academic Press.

322 Delariva, R. L. & Agostinho, A. A. (2001). Relationship between morphology and diets of six  
323 neotropical loriciariids. *Journal of Fish Biology* **58**, 832-847.doi:10.1111/j.1095-  
324 8649.2001.tb00534.x

325 Engelhard, G. H., Ellis, J. R., Payne, M. R., ter Hofstede, R., & Pinnegar, J. K. (2011).  
326 Ecotypes as a concept for exploring responses to climate change in fish assemblages. *ICES  
327 Journal of Marine Science* **68**, 580-591.doi:10.1093/icesjms/fsq183

328 Fage, L. (1909). Etude de la variation chez le rouget (*Mullus barbatus* L.M. *surmuletus* L.).  
329 *Archives de Zoologie Expérimentale et Générale* **5**, 389-445.

330 Galarza, J. A., Turner, G. F., Macpherson, E. & Rico, C. (2009). Patterns of genetic  
331 differentiation between two co-occurring demersal species: the red mullet (*Mullus barbatus*)  
332 and the striped red mullet (*Mullus surmuletus*). *Canadian Journal of Fisheries and Aquatic*  
333 *Sciences* **66**, 1478-1490. doi:10.1139/F09-098

334 Golani, D. & Galil, B. (1991). Trophic relationships of colonizing and indigenous goatfish  
335 (*Mullidae*) in the Eastern Mediterranean with special emphasis on decapod crustaceans.  
336 *Hydrobiologia* **218**, 27-33. doi:10.1007/BF00006415

337 Griffiths, A. M., Machado-Schiaffino, G., Dillane, E., Coughlan, J., Horreo, J. L., Bowkett, A.  
338 E., Minting, P., Toms, S., Roche, W., Gargan, P., McGinnity, P., Cross, T., Bright, D.,  
339 Garcia-Vazquez, E. & Stevens, J. R. (2010). Genetic stock identification of Atlantic salmon  
340 (*Salmo salar*) populations in the southern part of the European range. *BMC Genetics* **11**, 1-31.

341 Hyndes, G. A., Platell, M. E. & Potter, I. C. (1997). Relationships between diet and body size,  
342 mouth morphology, habitat and movement of six sillaginid species in coastal waters:  
343 implications for resource partitioning. *Marine Biology* **128**, 585-598.

344 ICES. (2010). Report of the Working Group on Assessment of New MoU Species  
345 (WGNEW). ICES CM 2010/ACOM: 21.

346 Janhunen, M., Peuhkuri, N. & Piironen, J. (2009). Morphological variability among three  
347 geographically distinct Arctic charr (*Salvelinus alpinus* L.) populations reared in a common  
348 hatchery environment. *Ecology of Freshwater Fish* **18**, 106-116. doi:10.1111/j.1600-  
349 0633.2008.00329.x

350 Jennings, S., Kaiser, M. J. & Reynolds, J. D. (2001). *Marine Fisheries Ecology*. Blackwell  
351 Science, Oxford, England.

352 Kristoffersen, J. B. & Magoulas, A. (2008). Population structure of anchovy *Engraulis*  
353 *encrasicolus* L. in the Mediterranean Sea inferred from multiple methods. *Fisheries Research*  
354 **91**, 187-195. doi:10.1016/j.fishres.2007.11.024.

355 Labropoulou, M., Machias, A., Tsimenides, N. & Eleftheriou, A. (1997). Feeding habits and  
356 ontogenetic shift of the striped red mullet, *Mullus surmuletus* Linnaeus, 1758. *Fisheries*  
357 *Research* **31**, 257-267. doi: 10.1016/S0165-7836(97)00017-9

358 Lombarte, A. & Aguirre, H. (1997). Quantitative differences in the chemoreceptor systems in  
359 the barbels of two species of *Mullidae* (*Mullus surmuletus* and *M. barbatus*) with different  
360 bottom habitats. *Marine Ecology Progress Series* **150**, 57-64. doi:10.3354/meps150057

361 Loy, A., Busilacchi, S., Costa, C., Ferlin, L. & Cataudella, S. (2000). Comparing geometric  
362 morphometrics and outline fitting methods to monitor fish shape variability of *D. puntazzo*  
363 (*Teleostea: Sparidae*). *Aquaculture Research* **21**, 271-283. doi :10.1016/S0144-  
364 8609(99)00035-7

365 Mahé, K., Destombes, A., Coppin, F., Koubbi, P., Vaz, S., Le Roy, D. & Carpentier, A.  
366 (2005). *Le rouget barbet de roche Mullus surmuletus* (L. 1758) en Manche orientale et mer  
367 du Nord. Rapport de Contrat IFREMER/CRPMEM Nord-Pas-de-Calais, IFREMER,  
368 Boulogne-sur-mer.

369 Mahé, K., Coppin, F., Vaz, S., & Carpentier, A. (2013). Striped red mullet (*Mullus*  
370 *surmuletus*, Linnaeus, 1758) in the eastern English Channel and southern North Sea: growth  
371 and reproductive biology. *Journal of Applied Ichthyology* **29**, 1067-1072. doi:  
372 10.1111/jai.12266

373 Mamuris, Z., Apostolidis, A. P. & Triantaphyllidis, C. (1998a). Genetic protein variation in  
374 red mullet (*Mullus barbatus*) and striped red mullet (*M. surmuletus*) populations from the  
375 Mediterranean Sea. *Marine Biology* **130**, 353-360.

376 Mamuris, Z., Apostolidis, A. P., Panagiotaki, P., Theodorou, A. J. & Triantaphyllidis, C.  
377 (1998b). Morphological variation between red mullet populations in Greece. *Journal of Fish*  
378 *Biology* **52**, 107-117.

379 Mamuris, Z., Stamatis C., Triantaphyllidis, C. (1999). Intraspecific genetic variation of  
380 striped red mullet (*Mullus surmuletus*, L.) in the Mediterranean Sea assessed by allozyme and  
381 Random Amplified Polymorphic DNA (RAPD) analysis. *Heredity* **83**, 30-38.

382 Marchal, P. (2008). A comparative analysis of métiers and catch profiles for some French  
383 demersal and pelagic fleets. *ICES Journal of Marine Science* **65**, 674-  
384 686.doi:10.1093/icesjms/fsn044

385 Mazzola, A., Lopiano, L., La Rosa, T. & Sara, G. (1999). Diel feeding habits of juveniles of  
386 *Mullus surmuletus* (Linneo, 1758) in the lagoon of the Stagnone di Marsala (western Sicily,  
387 Italy). *Journal of Applied Ichthyology* **15**, 143-148.doi: 10.1046/j.1439-0426.1999.00135.x

388 Moe, B., Brunvoll, S., Mork, D., Brobakk, T. E. & Bech, C. (2004). Developmental plasticity  
389 of physiology and morphology in diet-restricted European shag nestlings (*Phalacrocorax*  
390 *aristotelis*). *Journal of Experimental Biology* **207**, 4067-4076.doi:10.1242/jeb.01226

391 N'Da, K. & Deniel, C. (1993). Sexual cycle and seasonal changes in the ovary of the red  
392 mullet *Mullus surmuletus* Linné 1758, from the southern coast of Brittany. *Journal of Fish*  
393 *Biology* **43**, 224-244.doi:10.1111/j.1095-8649.1993.tb00425.x

394 Palma, J. & Andrade, J. P. (2002). Morphological study of *Diplodus sargus*, *Diplodus*  
395 *puntazzo*, and *Lithognathus mormyrus* (*Sparidae*) in the Eastern Atlantic and Mediterranean  
396 Sea. *Fisheries Research* **57**, 1-8.

397 Pawson, M. G. & Jennings, S. (1996). A critique of methods for stock identification in marine  
398 capture fisheries. *Fisheries Research* **25**, 3-4.



399 Poulard, J. C. & Blanchard, F. (2005). The impact of climate change on the fish community  
400 structure of the eastern continental shelf of the Bay of Biscay. *ICES Journal of Marine*  
401 *Science* **62**, 1436-1443.doi:10.1016/j.icesjms.2005.04.017

402 Reiss, H., Hoarau, G., Dickey-Collas, M. & Wolff, W. J. (2009). Genetic population structure  
403 of marine fish: mismatch between biological and fisheries management units. *Fish and*  
404 *Fisheries* **10**, 361-395.doi:10.1111/j.1467-2979.2008.00324.x

405 Schlichting, C. D. & Pigliucci, M. (1998). *Phenotypic evolution: A reaction norm perspective*.  
406 Sunderland: Sinauer.

407 Silva, A. (2003). Morphometric variation among sardine (*Sardina pilchardus*) populations  
408 from the northeastern Atlantic and the western Mediterranean. *ICES Journal of Marine*  
409 *Science* **60**, 1352-1360.doi:10.1016/S1054e3139(03)00141-3

410 Slice, D. E., Bookstein, F. L., Marcus, F. & Rohlf, F. J. (1996). A glossary for geometric  
411 morphometrics. In *Advances in morphometrics* (Marcus, L. F., Corti, M., Loy, A., Naylor, G.  
412 J. P. and Slice, D. E. E., eds), pp. 531-551. Springer Publishing.

413 Smith, P. J., Francis, R. I. C. C. & McVeagh, M. (1991). Loss of genetic diversity due to  
414 fishing pressure. *Fisheries Research* **10**, 309-316.doi:10.1016/0165-7836(91)90082-Q

415 Stepien, C. A., Randall, J. E. & Rosenblatt, R. H. (1994). Genetic and morphological  
416 divergence of a circumtropical complex of goatfishes: *Mulloidichthys vanicolensis*, *M.*  
417 *dentatus*, and *M.martinicus*. *Pacific Science* **48**, 44-56.

418 Strauss, R. E. & Bookstein, F. L. (1982). The TRUSS : body form reconstructions in  
419 morphometrics. *Systematic Zoology* **31**, 113-135.

420 ter Braak, C. J. F. ter. & Smilauer, P. (2002). *CANOCO Reference Manual and CanoDraw for*  
421 *Windows User's Guide: Software for Canonical Community Ordination*, Ithaca, New-York.

422 Uiblein, F. (2007). Goatfishes (*Mullidae*) as indicators in tropical and temperate coastal  
423 habitat monitoring and management. *Marine Biology Research* **3**, 275-288.

424 Uiblein, F., Köhler, C. & Tian, M. C. (1998). Quantitative examination of morphological  
425 variability among goatfishes of the genus *Upeneus* from the Malayan Province (Pisces:  
426 Perciformes: *Mullidae*). *Senckenbergiana Maritime* 28, 123-132.

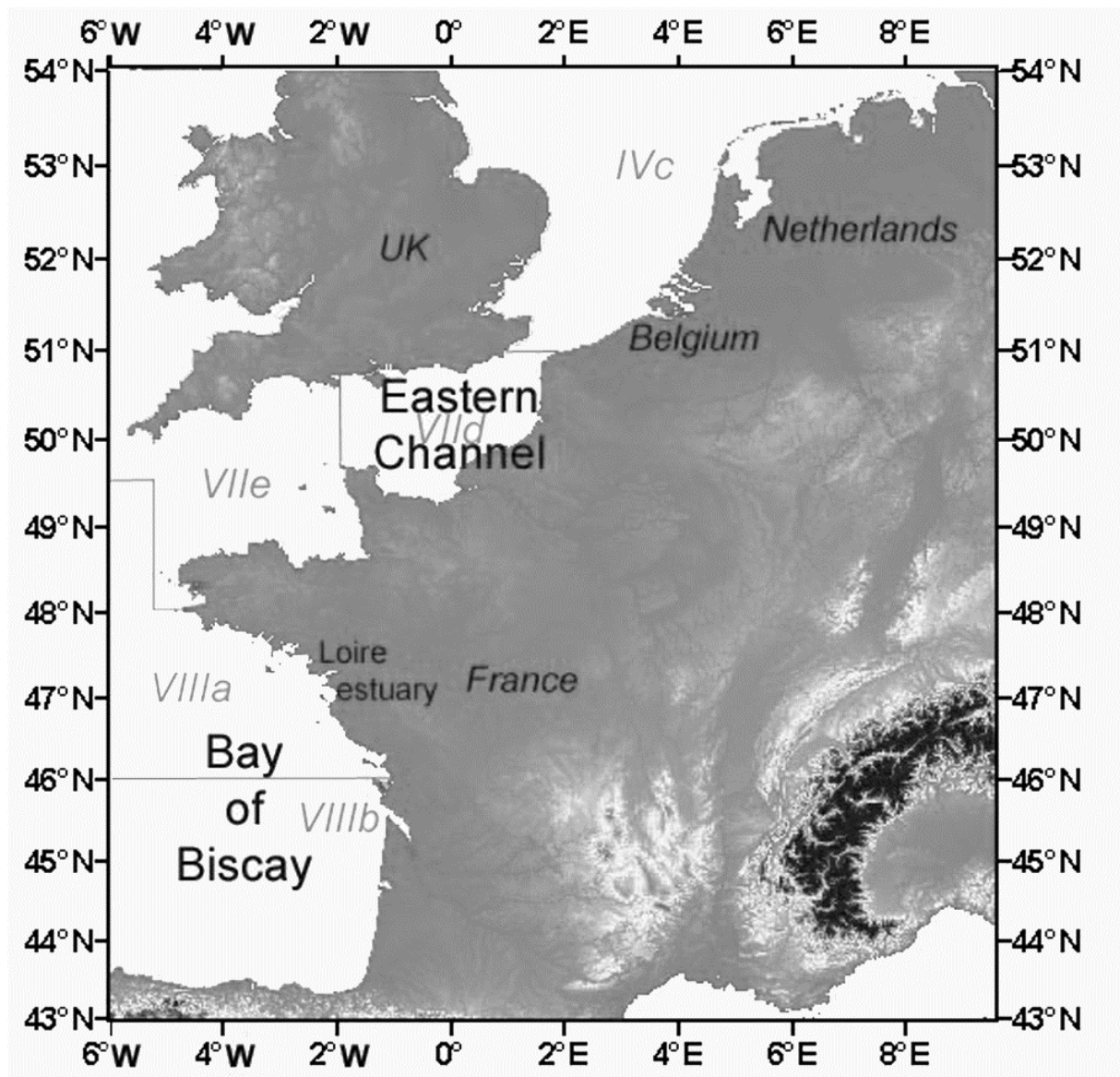
427 Vaz, S., Carpentier, A. & Coppin, F. (2004). Eastern English Channel fish community from  
428 1988 to 2003 and its relation to the environment. ICES CM 2004/K:40.

429

430

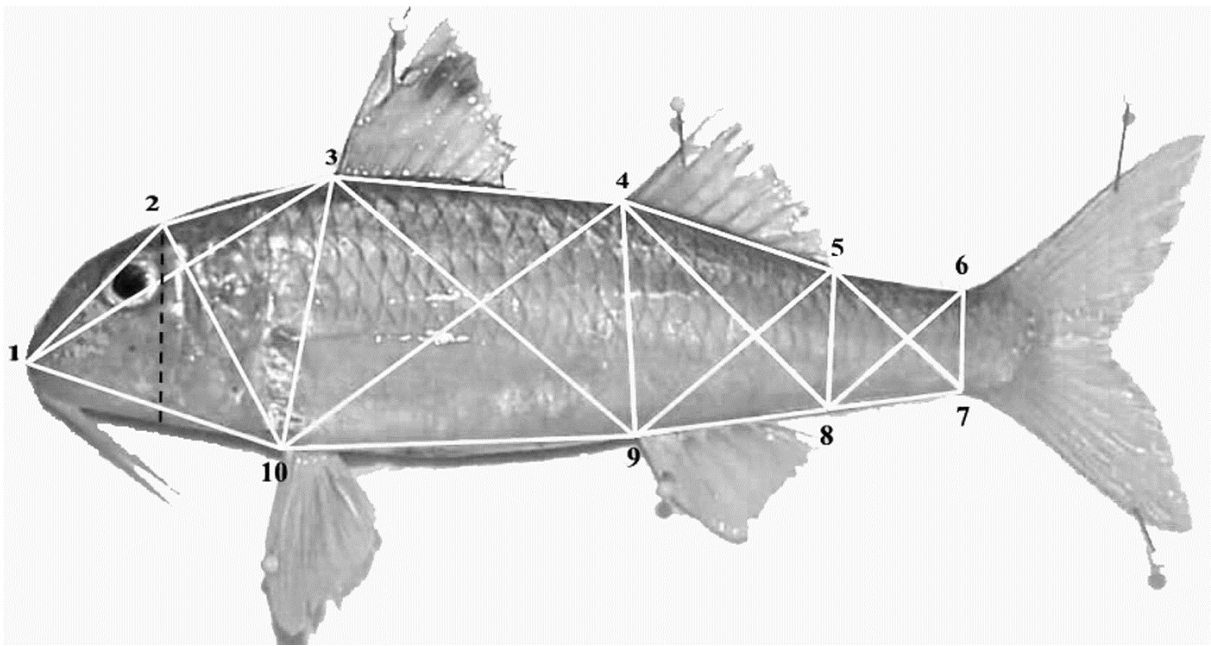
431

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



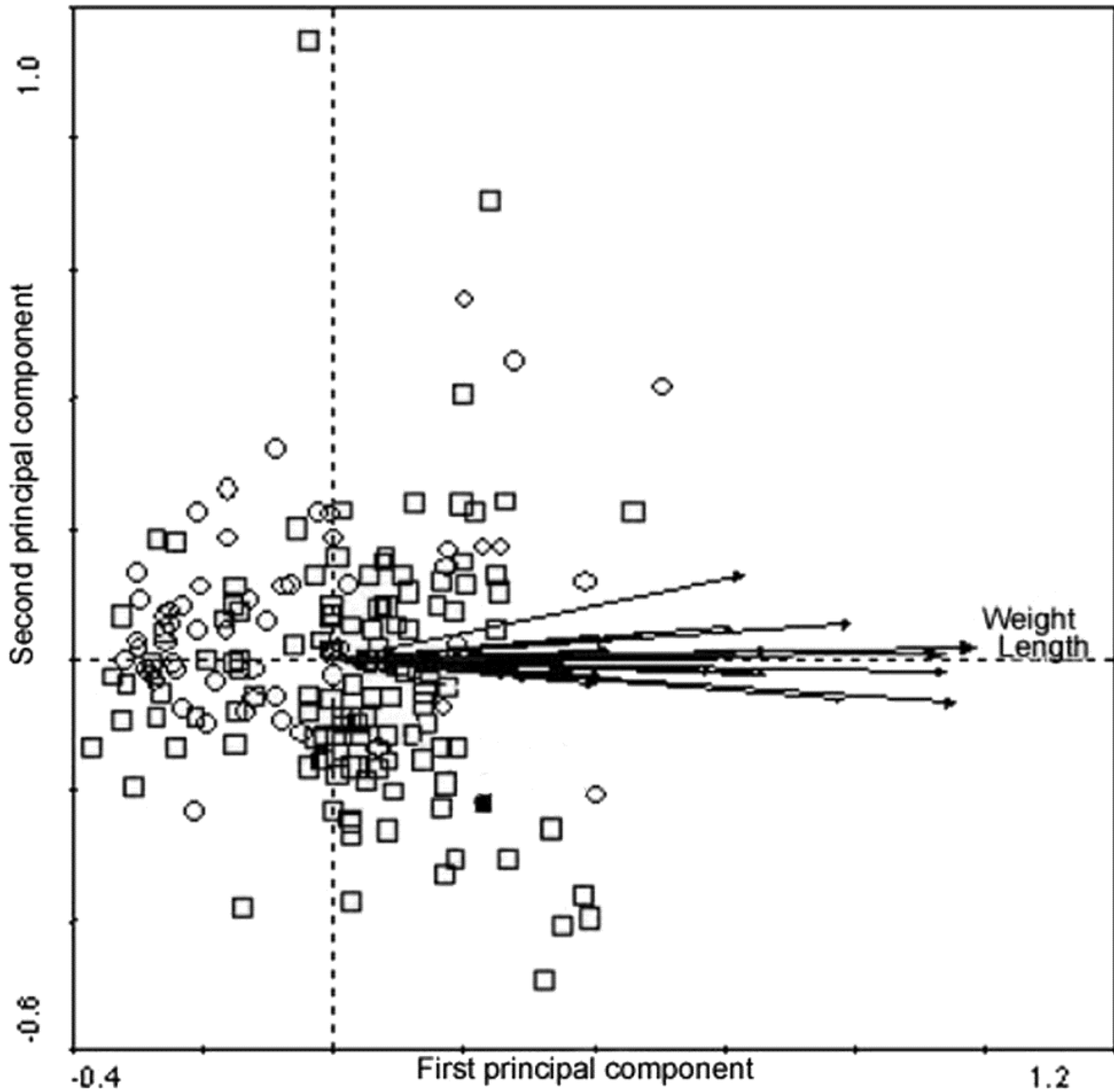
434  
 435  
 436  
 437  
 438  
 439  
 440  
 441  
 442

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



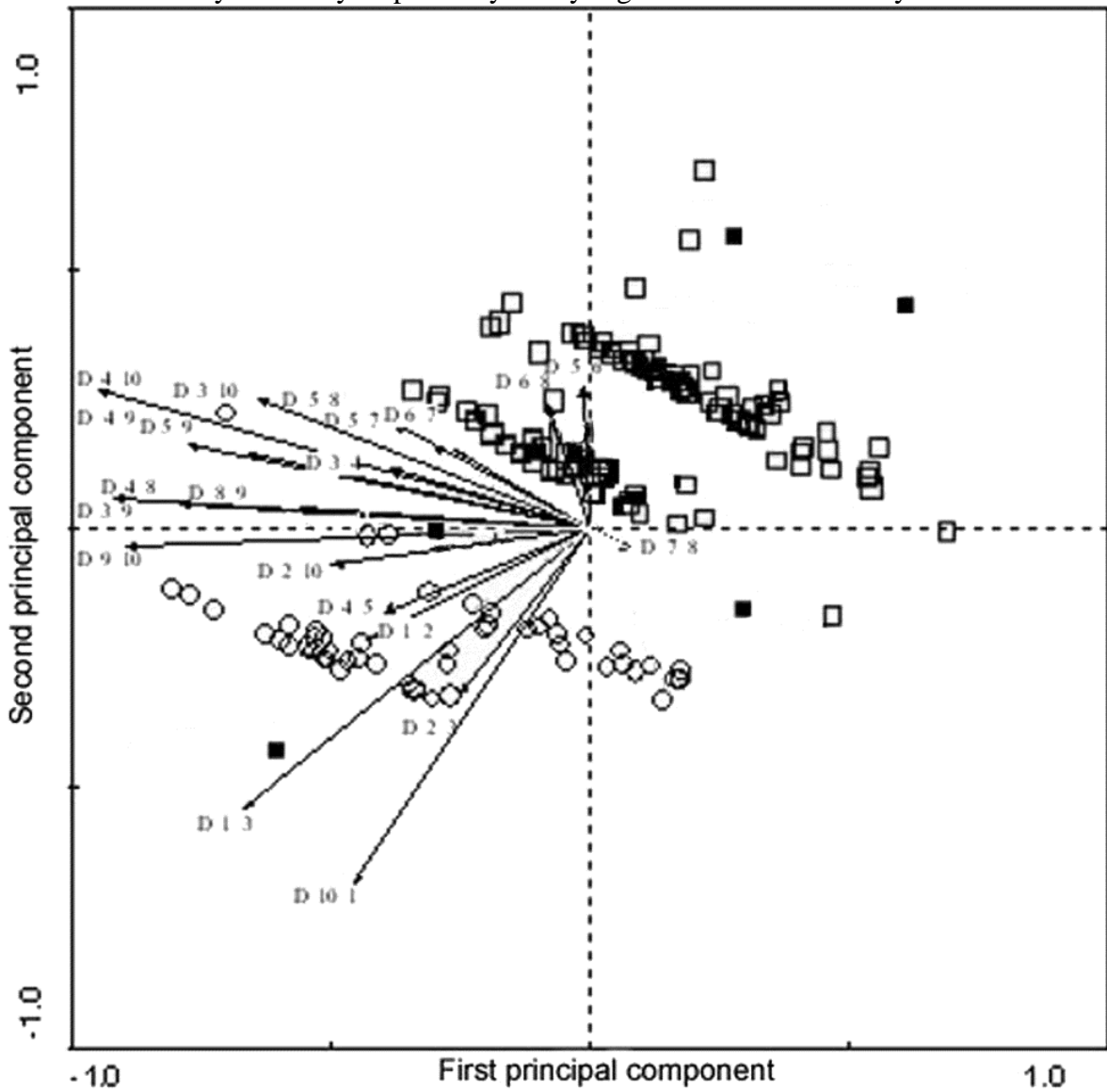
445  
446  
447  
448  
449  
450  
451  
452  
453  
454  
455  
456  
457  
458  
459

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



463  
464  
465  
466  
467  
468  
469  
470  
471  
472  
473  
474

475 Figure 4: Main results of the Redundancy Partial Analyses. Squares (black: 2002 & open:  
476 2003) and circles represent individual fish specimens analyzed from the Eastern English  
477 Channel and the Bay of Biscay respectively. Body segments are identified by the vectors.

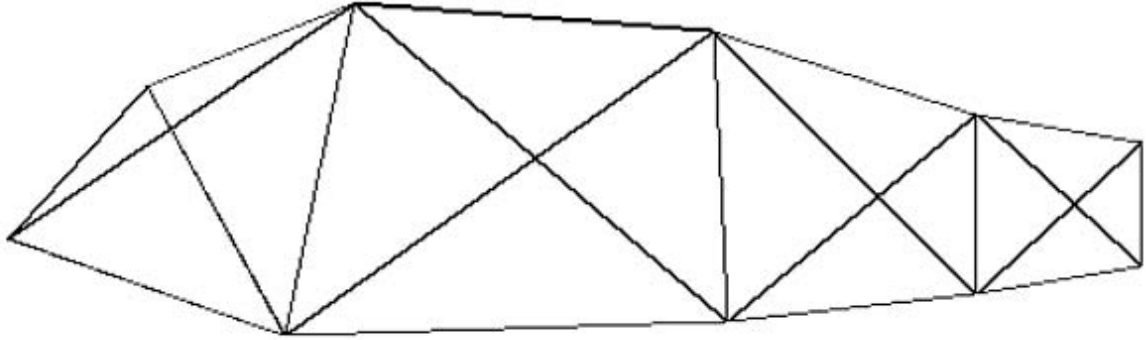


478  
479  
480  
481  
482  
483  
484  
485  
486

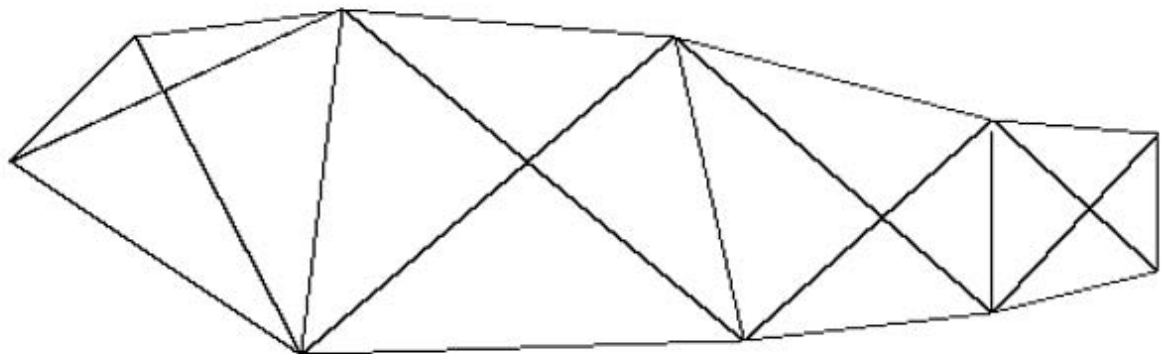
487 Figure 5: Averaged forms of *M. surmuletus* in the Bay of Biscay and in the Eastern English  
488 Channel. Reconstructed forms are scaled in centimetres and represent body total length of 20  
489 cm.

Bay of Biscay

N=57



Eastern English Channel N=111



4 cm

490

491

492

493

494

495

496

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

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

501

502

503

504