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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

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 North Sea by French, English and Dutch fleets have been observed from the 1990s onwards. 65 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 the trend for sea-water warming (Poulard & Blanchard, 2005; Marchal, 2008; ICES, 2010). 68 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

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).

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., 2005). Each method offers a unique view of population structure that relates to different 90 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

different growth stages. However, results are difficult to interpret as trace element depositioncan 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 or108 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.

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 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."

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 ($L_{\rm T}\pm 1$ mm), mass 142 $(W\pm 1g)$ 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*

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.

155 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 156 157 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.

178 **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).

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).

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.

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* *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).

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).

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.

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

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282

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



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



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.



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 English477 Channel and the Bay of Biscay respectively. Body segments are identified by the vectors.



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.



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

500 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)
	Number	24	19	14
EVHOE 2003 mean total length (s.d.) 120 (13) 120 (13)	214 (51)	241 (50)
mean total mass (s.d.) 22 (8)			200 (142)	160 (108)