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Cyria Meriem Bensebaini, Grégoire Certain, Norbert Billet, Angélique Jadaud, S. Gourguet, Tarek Hattab, Jean-Marc Fromentin

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Bensebaini Meriem [1, *], Certain Gregoire [1], Billet Norbert [1], Jadaud Angelique [1], Gourguet Sophie [2], Hattab Tarek [1], Fromentin Jean-Marc [1]

[1] UMR 9190 MARBEC, University of Montpellier-IRD-Ifremer-CNRS , Av. Jean Monnet, CS 30171, Sète Cedex 34203, France
[2] UMR 6308 AMURE, University of Brest-Ifremer, CNRS-IUEM , Rue Dumont d'Urville 29280 Plouzané, France

* Corresponding author : Meriem Bensebaini, email address : bensebaini.cyria@gmail.com

Abstract :

Environmentally driven changes in small pelagic fish condition and size have been observed in the Gulf of Lions (GOL) since 2008, leading to a significant fishery crisis. However, the effect of changes in environment and/or in the small pelagic community on the demersal community remain unknown. For the first time, this study examines the body condition (bc) and population density of 22 demersal species since 1994, using dynamic factor analysis (DFA). Most (but not all) of demersal species have shown a common shift between 2006 and 2009, which is synchronous with that observed in small pelagic species and the environmental conditions in the GOL. It had been concluded that the environmentally driven changes detected in the pelagic fish community also affected the demersal fish community, but with less drastic and lasting consequences. As the DFA revealed that the bc displayed important variations for several species, notably hake (Merlucius merluccius), the interaction between the bc and population density was investigated using the Multivariate Autoregressive (MAR) model on hake population at three life stages (recruits, juveniles, and adults). Results showed that adult bc, while negatively affected by density, had a positive effect on recruitment. So hake bc could have affected population dynamics by promoting higher recruitment at low densities. Further work is needed to ascertain whether such effects exist in other demersal species.

Keywords : body condition, demersal fish, dynamic factor analysis, Gulf of Lions, Merluccius merluccius, multivariate autoregressive models

Introduction

The Gulf of Lions (GOL) is one of the most productive regions of the Mediterranean Sea, due to its wide continental shelf and a combination of large inflows from the Rhone River and small-scale coastal upwelling (Millot, 1982, 1990). This area has been intensively exploited for decades, with

32 total landings reaching 30,000 to 50,000 tonnes from the 1970s to the 1990s, but only amounting to

33 13,604 tonnes (tuna excluded) in 2018 (STECF, 2019a, 2019b). Today, fish stocks of commercial

34 interest are heavily overfished, according to the report of the State of Mediterranean and Black Sea

35 Fisheries (SoMFi) (FAO, 2018a). It is therefore a high-stakes sector from an ecological, social and

36 economic perspective, where the consequences of unexpected changes could be considerable

37 (Barange *et al.*, 2018).

38 Around 2008, the pelagic ecosystem of the GOL had shown signs of disruption, characterized by the

39 drastic changes in size, age and condition of its two main small commercial pelagic fish stocks

40 (European sardine, *Sardina pilchardus*; European anchovy, *Engraulis encrasicolus*). This "small

41 pelagic crisis" in the GOL was attributed to slower growth and higher natural mortality in the older

42 age groups (Van Beveren *et al.*, 2014). Different hypotheses about the causes of such changes have

43 been tested and finally seemed to result from a bottom-up control induced by a change in plankton

44 composition and/or density (Brosset *et al.*, 2015; Saraux *et al.*, 2019). Subsequent studies indicated

45 that environmental conditions in the GOL broadly changed in the mid-2000s (Feuilloley *et al.*, 2020).

46 These types of large-scale disturbances are known for their effects on fish species biology, directly –

47 physiological threshold – or indirectly – by modifying the food resource (plankton), thereby affecting

48 bottom-up mechanisms (Jørgensen, 1992). This has consequences on the energy storage dynamics of

49 individuals (Jakob *et al.*, 1996), reflected in their body condition (BC), and ultimately in their natural

50 mortality and growth, affecting population dynamics. Fluctuations in population density and BC

51 therefore provide information on population health. The small pelagic crisis first induced a crash in

52 landings, followed by a historic collapse of the fishing activity in the area (Van Beveren *et al.*, 2016)

53 and the shift of fishing efforts towards demersal stocks, which increased an already unsustainable

54 fishing pressure on the demersal species. As such, the demersal stocks became crucial for the survival

55 of the trawl and small-scale fisheries in the region. The captures during the decade preceding the

56 crisis (outside of tuna catches) were composed of around 3/4 of small pelagic species, mainly sardine

57 and anchovy, and around 1/4 of demersal species, while post-crisis (after 2008) the pattern reversed

58 to 1/3 of small pelagic species and almost 2/3 of demersal species (FAO, 2018b).

59 While the small-pelagic shift of the GOL has been the center of an intense research activity

60 (summarized in Saraux *et al.* 2019), not much has been done to discover whether demersal stocks

61 have also been affected, since studies on demersal species' BC in the GOL are over a decade old

62 (Lloret *et al.*, 2002, 2008; Ferraton *et al.*, 2007). Similar changes in BC are likely to be observed in

63 the demersal community, especially since many demersal species depend on environmental

64 conditions when they are in a larval or juvenile stage, and, once adult, certain demersal species feed

65 mainly on small pelagic fishes (Banaru *et al.*, 2013; Mellon-Duval *et al.*, 2017). BC can have a strong

66   impact on growth (Ratz and Lloret, 2003) and natural mortality, as fish in poor condition are more

67   susceptible to disease, predation, and fishery (Martinez *et al.*, 2003). BC can also affect reproduction

68   or reproductive potential, which is crucial for the recovery of a declining stock. Some fish populations

69   in poor condition invest their energy in growth rather than reproduction, reducing fecundity and the

70   quality of the eggs, or leading to delayed maturation (Lambert and Dutil, 2000; Lloret *et al.*, 2008),

71   while others, such as small pelagic fish in the GOL, continue their energy investment in reproduction,

72   whatever their BC, leading to an increased mortality after spawning (Brosset *et al.*, 2016). The search

73   for possible links between BC and population dynamics is therefore interesting.

74   This paper has two goals. First, we explore the demersal species' response to an ecosystem shift

75   detected in the GOL around 2008. Then, we investigate the population dynamics of a highly

76   documented species, the European hake (*Merluccius merluccius)*, to better understand how BC and

77   density interact at a population level. Hence, the first part of the paper is dedicated to determining

78   whether the BC and/or density of demersal species has changed over time. More precisely, we have

79   looked for common trends between 22 demersal species (in terms of BC and density) and investigated

80   if these common trends match those already detected by Feuilloley *et al.* (2020) in the environmental

81   conditions and small pelagic fish species of the GOL. In the second section, we use the European

82   hake as a study model to examine to what extent changes in BC and/or density could affect one

83   another, using Multivariate Autoregressive (MAR) models. The choice of hake was mostly motivated

84   by its central role in the demersal fishery (Mellon-Duval *et al.*, 2017) and by data availability. Hake

85   was the only species which had enough information available to set up a three-stage population

86   dynamics model suitable for searching for interactions between BC and the density of hake at various

87   stages (recruits, juveniles, and adults).

88   With this study, we hope to uncover crucial information that helps provide a better understanding of

89   the dynamics of the demersal stocks in the GOL, and ultimately contribute to the establishment of a

90   more ecosystem-oriented approach to fisheries management in this area.

91   **Materials and methods**

92   **Data description: The MEDITS survey**

93   Data used in the analyses were collected from annual international bottom trawl surveys performed

94   in May-July since 1994 over the continental shelf (10 m to 200 m depth) and the continental slope

95   (200 m to 800 m) of the Mediterranean Sea through the MEDITS scientific program (Bertrand *et al.*,

96   2002). The sampling procedures were standardized according to a common protocol over countries

97   and years. The MEDITS survey (Jadaud, 1994) aims to annually estimate and monitor the demersal

98   fish stocks in the GOL and east of Corsica. The current study focuses on the GOL (Figure 1). The

99   fishing gear used is a bottom trawl GOC-73 with 20 mm of stretched cod-end mesh size. The average

100 vertical and wing opening of the gear are around 2 m and 18 m, respectively. All the tows were

101 performed during daylight hours, 30 min for shelf stations, and 60 min for the continental slope. The

102 MEDITS database documents the distribution and density of roughly 400 Mediterranean species

103 collected over 25 years of sampling. However, for many reasons such as a lack of data or appropriate

104 biological measurements throughout the whole time series (see e.g. Morfin *et al.*, 2012), we restricted

105 our analysis to 22 species that were regularly caught (i.e. there were no missing values in the time

106 series) during the survey and for which length measurements were consistently taken during the

107 whole time period (see Table 1). The survey provides the population density for each species,

108 obtained by dividing the number of individuals of each species obtained in any given trawl by the

109 trawled surface (the annual densities being the average of all densities obtained in any given year for

110 each species, see Supplementary Figure S1). Density is here used as a proxy of abundance in the GOL

111 relative to the trawl catchability, which is assumed to be constant through time, since the fishing

112 protocol has carefully been kept constant since 1994 (Morfin *et al.*, 2012).

113 **Body condition index**

114 To measure the BC, the residual index (Gould, 1975) was used, which is the residual of the length-

115 weight log-linear relationship. Positive residuals indicate the BC is above average, while negative

116 residuals indicate the BC is below average. This index is convenient as it allows to separate the BC

117 from the body size effect (Jakob *et al.*, 1996).

118 The MEDITS protocol includes systematic measurements of individual size for the 22 selected

119 species, but few of them are individually weighed. In the absence of individual weights for each

120 species and in each haul sample, the data available consists of a total biomass and an associated size

121 spectrum. However, it is still possible to estimate a length-weight relationship from these data. The

122 classical length-weight relationship is written as follows:

123 $$w_{s,i} = a_s l_{s,i}^{b_s} \dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots \quad (1)$$

124 The $w_{s,i}$ and $l_{s,i}$ are the weight and length of individual i of species s, respectively. The total biomass

125 in one haul h of a given species s, thereafter denoted $B_{h,s}$, is equal to the sum of the n individuals'

126 weight (w_i) contained in the haul h, as described in equation (2).

127 $$B_{h,s} = \sum_{i=1}^{n} w_{h,s,i} = a_s \sum_{i=1}^{n} l_{h,s,i}^{b_s} \dots\dots\dots\dots\dots\dots\dots\dots\dots\dots\dots \quad (2)$$

128 Where $B_{h,s}$ is the observed biomass of species s in the hth haul and a_s and b_s are the typical constants

129 of the length-weight relationship of the given species s, and $l_{h,s,i}$ is the length of the ith fish in the hth

130 haul of the species s.

131 The number of hauls varies slightly from year to year (the average number being 65). To calculate

132 the residual index based on the same number of hauls each year and produce confidence intervals,

133 the residual index time series were extracted using 100 non-parametric bootstraps. For each species

134   and bootstrap, 40 hauls were randomly selected each year, resulting in a 1000-point data set (40 haul

135   * 25 years). Then the estimates of parameters a_s and b_s were obtained by fitting the equation (2) to

136   the 1000 pairs of $B_{h,s}$ and their corresponding sum of sizes, then finally, residuals were calculated

137   from the fit of the equation (2). Averaging these residuals per year for each bootstrap sample resulted

138   in 100 time series of 25 years, from which the median – and 2.5% and 97.5% quantiles for confidence

139   intervals – were extracted to build the BC index series for each species. These steps are described

140   graphically in Figure 2 and the BC time series can be consulted in Supplementary Figure S2.

141   Furthermore, to check for consistency, bootstrapped estimates of a_s and b_s parameters were compared

142   to parameters from the bibliography, and the obtained results were satisfactory (Supplementary Table

143   S1).

144   **Dynamic Factor Analysis (DFA)**

145   DFA is a dimension reduction technique specifically designed for time series since it takes into

146   account the time factor, unlike other dimension reduction techniques like principal component

147   analysis (PCA) or canonical correspondence analysis (CCA). DFA aims to identify common trends

148   between different time series and relationships between these series (Zuur *et al.*, 2003). It fits linear

149   multivariate autoregressive state-space models with Gaussian errors (Holmes *et al.*, 2018). The model

150   is written as follows:

151    $$y_t = Zx_t + v_t \text{ where } v_t \sim MVN\,(0, R) \quad\text{...} \quad (3a)$$

152    $$x_t = x_{t-1} + w_t \text{ where } w_t \sim MVN\,(0, Q) \quad\text{...} \quad (3b)$$

153   The *y* equation (3a) represents the observation process, and the *x* equation (3b) is termed the state

154   process. The vector y_t of *n* time series (corresponding to the number of analyzed species, *n*=22) is

155   modeled as a linear combination of *m* hidden common trends (x_t vector) and the factor loadings matrix

156   *Z*, and observation errors vector v_t, which were distributed as a multivariate normal distribution with

157   mean vector 0 and variance-covariance matrix *R*. The *m* hidden common trends at time *t* (x_t) follow

158   random walks with process error vector w_t, which was distributed as a multivariate normal distribution

159   with mean vector 0 and variance-covariance matrix *Q* (Holmes *et al.*, 2018). For any given time *t* and

160   species *s*, the linear form of the model can be written as follows:

161    $$y_{st} = z_{s1}x_{1t} + z_{s2}x_{2t} + \text{.....} + z_{sm}x_{mt} + v_{st} \quad\text{..} \quad (4)$$

162   Two DFA were carried out, one for the BC time series and another for the density time series. In both

163   cases, several models were fitted, which had from m=1 to m=3 latent variables, and a covariance

164   matrix *R* starting from its simplest form "diagonal and equal" (i.e. the same variance and no

165   covariance) to a more complex form "equalvarcov" (i.e. one value for the variance and one for the

166   covariance). Model selection was based on Akaike's information criterion for small samples (AICc;

167 Burnham and Anderson, 2002) to identify the most parsimonious model containing the least number

168 of common trends without experiencing much information loss. The Multivariate Autoregressive

169 State-Space (MARSS) package developed in *R* (Holmes *et al.*, 2018; R Core Team, 2020) was used

170 to perform these analyses. As input data for the DFA, we used log-transformed and centered density,

171 and standardized BC time series.

172 Trends identified by this DFA analysis were then compared to the time series retrieved from the study

173 by Feuilloley *et al.* (2020). These authors investigated whether an environmental change could have

174 triggered the small pelagic crisis based on two DFA analyses, one including the time series of 10

175 biological variables (biomass, condition and size for sardine, anchovy and sprat plus abundance for

176 sardine) and one including the time series of 10 environmental variables (chlorophyll-a (Chla)

177 concentration, Rhone flow, thermal fronts, Sea Surface Temperature (SST), Western Mediterranean

178 Oscillation Index, convection, upwelling, stratification index, N and P nutrient concentration). These

179 two DFA analyses revealed common trends with a shift in the mid-2000's, which led the authors to

180 suggest that changes in environmental conditions could have affected plankton production and hence

181 the small pelagic fish community (Feuilloley *et al.*, 2020). Those two common trends have been thus

182 retrieved and compared with the results of the DFA analyses carried out in this study on the demersal

183 community to investigate a potential match between trends in environment, small pelagic and

184 demersal fish communities in the GOL.

185 **Multivariate Autoregressive (MAR) Model**

186 This part of the study looks for interaction between BC and density, using the Granger causality (GC)

187 concept (Granger, 1969). The basic idea of GC is that a variable *x* impacts a variable *y* if it improves

188 the prediction of the latter. This concept can be based on the fitted interaction matrix obtained from

189 a MAR model (Ives *et al.*, 2003; Certain *et al.*, 2018). MAR(p) models, in their linear formula, have

190 demonstrated a particular efficiency in detecting interactions in nonlinear systems (Barraquand *et al.*,

191 2021). This analysis was based on a conditional GC (Geweke, 1984; Barnett and Seth, 2014), in

192 which, when focusing on the causal relationship between two variables, the confounding relationships

193 are accounted for due to the remaining variables.

194 We focused on European hake because: (i) it is a well-sampled species and the most documented of

195 the MEDITS survey; (ii) its life cycle is well known and the timing of the MEDITS survey (late spring)

196 has been designed to capture hake recruitment; (iii) it is one of the most important and abundant

197 species of the demersal community in the GOL; (iv) it is a major commercial species; and (v) its BC

198 increased significantly through the study period. European hake is widely distributed in the GOL,

199 with juvenile and young adults concentrated mainly on the continental shelf, and the largest

200 individuals deeper on the slope and canyons (Maynou *et al.*, 2003). Hake is a key predator in this

201   area, feeding mainly on crustaceans and small benthic fish when juvenile, then switching to a more

202   piscivorous diet at 15 cm (small pelagics and blue whiting representing 40% to 80% of its diet,

203   Mellon-Duval *et al.*, 2017). It is a highly mobile species, with long lifespan and slow growth (Mellon-

204   Duval *et al.*, 2010). The European hake is a batch spawner that spawns throughout the year with a

205   peak in winter (Ferrer-Maza *et al.*, 2014), and recruitment also happens throughout the year with a

206   peak in late spring. Juveniles are fished as soon as they reach a catchable size (i.e. in their first year

207   of life).

208   A MAR(1) analysis was done using density and BC as variables. Both the BC and density were split

209   into three stages using an age-length key (Bensebaini *et al.*, 2019): juveniles (or recruits) age 0-1;

210   juveniles age 1-2; and adults age 2+ (Supplementary Figure S3). Separating adults from juveniles

211   permits the verification of whether maturation and modifications in physiological processes, leading

212   to changes in the body's energy resources management (Kooijman, 2009), affects the BC-density

213   relationship. In addition, natural mortality is higher in juveniles – which are more vulnerable to

214   predation compared to adults (Vetter, 1988) – and possibly act as a confounding factor. Recruits

215   (juveniles age 0-1) were separated from other juveniles (juveniles age 1-2) in an attempt to acquire

216   recruitment dynamics. The MAR analysis was restricted to a one-year lag due to the shortness of the

217   time series (i.e. 25 points), as increasing the lag also greatly increases model dimensionality.

218   In matrix form, MAR models with one time lag (MAR (1) models) are written as follows:

219    $$x_t = Bx_{t-1} + w_t \text{where } w_t \sim MVN\,(0,\,Q)\;...\;(5)$$

220   with x_t a vector whose elements corresponds to the response variables of the model; either total log-

221   density or BC, each being divided by three stages. B is the 6*6 interaction matrix, with b_{ij} the effect

222   of variable j on variable i. The diagonal of the matrix B represents the effect of the variables on

223   themselves. w_t is a multivariate normally distributed error vector with mean 0 and variance-

224   covariance matrix Q. Matrix B parameters were estimated by a maximum likelihood estimation using

225   a Kalman filter (Harvey, 1989). Each parameter was considered significant with a p-value lower than

226   a significance level of 5% and was associated with a 95% confidence interval.

227   Considering the high number of parameters to be estimated in the full model and the relatively short

228   length of the available time series, we designed a specific approach to avoid a potential overfitting

229   issue. To do so, we first set all parameters that had no biological meaning (see Supplementary Table

230   S2) to 0, such as b_{14}, because the BC of the recruits at time t cannot affect the density of recruits at

231   time t+1 (since the latter are not yet born, see Supplementary Table S3). Then, backward elimination

232   was based on the AICc to keep the most relevant coefficients and to penalize overly complex models.

233   However, some coefficients related to the population dynamics have not been included in the

234 backward elimination because of their key biological meaning: b_{21} and b_{32} (i.e. the growth in density

235 of recruits age 0-1 and of juveniles age 1-2, respectively) as juveniles age from one year to the next;

236 b_{13} (i.e. the adults reproductive output) because adults reproduce and give birth to recruits; and b_{33}

237 (i.e. density-dependent effects within the adult density) because adult density cannot grow

238 indefinitely.

239 Because the aim of this study is to determine whether recruit density is better predicted with an adult

240 BC effect, The sum of squares of residuals (SSR) of recruit density were computed and compared for

241 the models with and without the effect of adult BC on recruit density.

242   **Results**

243   **DFA**

244   For the BC, the AICc (Supplementary Table S4) selected two models as the most parsimonious

245   (ΔAICc=1.9). One contained one common trend and an "equalvarcov" covariance matrix R (i.e. a

246   common variance for all series and common covariance between them), and the other contained two

247   common trends, and an "equalvarcov" covariance matrix R. Both models were tested and showed

248   similar results. However, the model with a common trend (Supplementary Figure S4) had lower factor

249   loadings, probably because a single common trend was insufficient to properly describe the common

250   dynamics of demersal fish BC, which forms the rationale for the selection of the model with two

251   common trends (Figure 3). The first common trend showed a sharp drop in 1994, then a gradual

252   increase from 2006 to 2016. The second common trend displayed a typical regime shift pattern: it

253   dropped sharply between 2006 and 2009, after which it remained below zero until the end of the

254   series. Species with factor loadings (Figure 3) smaller than a threshold of 0.2, in absolute values, have

255   not been included in the interpretation of results (Zuur *et al.*, 2003), as they did not have a particular

256   trend over time. Factor loadings resulting from the DFA on BC (Figure 3) seemed clustered by

257   taxonomic categories, suggesting that the BC of species within a taxonomic group followed a similar

258   temporal dynamics. Cephalopods (three species) mainly displayed negative loadings on trend 2, while

259   perciforms (five species) and John dory displayed positive loadings on trend 2. Pleuronectiforms (two

260   species) were mostly positively associated with trend 1, while gadiforms (four species) and

261   scorpaeniforms (two species) were positively associated with both trends 1 and 2, except hake, which

262   only displayed positive loadings on trend 1. Lophiiforms (two species) were poorly associated with

263   both trends.

264   When looking at the overall model fits for each BC time series (Supplementary Figure S5), most

265   species showed a good fit with the observations, except for a few species (Norway lobster,

266   blackbellied angler, red mullet, and blackspot seabream series). As several species were associated

267   with both common trends, the contribution of each BC time series to the two common trends was

268   plotted in different colors (Figure 4) to determine at which point in the series the model was more

269   driven by trend 1 or 2. In the shift period (2006-2009), almost all species were driven by trend 2 (i.e.

270   blue points) except for European hake, spotted flounder, and angler, whose BCs were only associated

271   with trend 1 (Figure 3).

272   For density, the AICc (Supplementary Table S5) selected the model containing one common trend,

273   and an "equalvarcov" covariance matrix R. This common trend (Figure 5) showed low values until

274   2006, then values quickly increased until 2010, and finally the increase slowed until it reached what

275   appears to be a plateau in 2014. Again, species with factor loadings smaller than 0.2 were not included

276   in the interpretation of results (bottom part of Figure 5 for factor loading; and Supplementary Figure

277   S6 for density model fits versus observed time series), leaving only shortfin squid and three

278   perciforms (blackspot seabream, common pandora, and Mediterranean horse mackerel), which were

279   positively associated with this trend, while blue whiting was negatively associated with it.

280   The common trend from DFA on demersal fish densities, the trend 2 from the DFA on demersal fish

281   BC and the common trends of the DFA analyses on environmental conditions and small pelagic fishes

282   in the GOL performed by Feuilloley *et al.* (2020) are displayed in Figure 6. This figure highlights a

283   strikingly concomitant period of shift (2006-2009), when the strongest changes in these four trends

284   occurred.

Multivariate Autoregressive (MAR) Model

286   The model selected by backward elimination is illustrated in Figure 7. Results show that coefficients

287   that have not been included in the backward elimination (b_{21}=0.01±0.32, b_{32}=0.12±0.40,

288   b_{33}=0.1±0.48) were low and not statistically significant, except b_{13}, which revealed the strong positive

289   effect of the density of adults age 2+ at time t on recruits age 0-1 at time $t+1$ (b_{13}=0.90±0.46). The

290   density of adults age 2+ at time t also had a negative effect on the BC of juveniles age 1-2 (b_{53}=-

291   0.22±0.14), and adults age 2+ (b_{63}=-0.33±0.2) at time $t+1$. Finally, the BC of adults age 2+ had a

292   positive effect (b_{16}=0.83±0.69) on the density of recruits age 0-1 at time $t+1$ and was negatively

293   autocorrelated (b_{66}=-0.36±0.29). The calculation of the SSR shows that there was a reduction of the

294   SSR in the model with the effect of the BC, as compared with the model without this effect (a

295   reduction of 17.20%). This means that juvenile density was better predicted when accounting for the

296   BC.

Discussion

One of the first goals of this study was to explore whether the environmentally driven changes in small pelagic fish BC could also be detected in the demersal fish community of the GOL. DFA performed on the BC and density time series of 22 demersal species tended to confirm this impact. This was documented by a common shift between 2006 and 2009 for most (but not all) demersal fishes and a striking synchrony between the common trends extracted from the DFA of this study (on demersal fish) and those performed on the small pelagic fishes and environmental conditions in the GOL (Feuilloley *et al.*, 2020). The authors have clearly depicted an overall change in the environmental conditions of the GOL over the last 30 years, characterized by a rapid decline in Chla concentration in the mid-2000s, a continuous increase in SST, an intensification of coastal upwellings and frontal activities, a decrease in the nutrient inputs from the Rhone river as well as in the deep winter convection and modifications in the regional atmospheric conditions (as described by the Western Mediterranean Oscillation Index). Those environmental changes have probably affected the lower trophic levels (plankton) of the GOL ecosystem, and consequently the small pelagic fish compartment, as already stressed by previous studies (see Saraux *et al.*, 2019; Brosset *et al.*, 2015). The present study shows that these environmental changes may also have affected the demersal fish community. However, the exact cause and pathways of these changes are yet to be discovered. Hence, the processes through which environmental changes might have affected energy storage and fish BC will probably remain a challenging research topic for the next decade, requiring more theoretical approaches before it is solved.

The BC of many demersal species were both positively correlated with trend 1 (a continuous BC improvement) and with trend 2 (the shift in the mid-2000s). For these species, the contribution of trend 2 is substantial during the shift period (blue points in fig 4), while the contribution of trend 1 is more significant at the end of the time series. Hence the BC of these species (blue whiting, greater forkbeard, capelan, Mediterranean and Atlantic horse mackerel, grey gunnard, blackbelly rosefish and John dory), while momentarily altered during the shift, saw an improvement in recent years, contrary to the small pelagic fishes whose BC has still not recovered up to this day (Saraux *et al.* 2019). This study therefore confirms that, as revealed by BC-DFA in trend 2, the impacts of the shift experienced by the small pelagics in the GOL also affected the demersal system, but without triggering the same drastic and long-lasting consequences at the biological (for most species), ecological and economic level.

The pelagic community (3 major species of small pelagics) appears to have a strong and lasting response to the shift, while the demersal community appears to have more diverse responses in both direction and intensity. Depending on their turnover rates, species respond differently to changes in

331   the abiotic environment, for example, small pelagic fish that have fast turnover rates react quickly to

332   an abrupt change (Stenseth *et al.*, 2002). Small pelagic fish communities have lower species diversity

333   (Angel, 1993) and are known to have short trophic chains, a short lifespan, and an explosive

334   demography, making them very sensitive to environmental fluctuations (Alheit and Hagen, 2001).

335   Regime shifts were often observed in these communities, like sardines in the California Current (Hill

336   *et al.*, 2015), or anchovies in the Humboldt Current (Guiñez *et al.*, 2014). Conversely, demersal

337   communities often have a greater species diversity (Angel, 1993), live longer and tend to grow slower

338   (Pauly, 1998). They usually display longer trophic chains and are capable of feeding on both benthic

339   and pelagic resources (Garrison and Link, 2000; Bulman *et al.*, 2001). The demersal community food

340   web is therefore generally characterized by higher complexity and modularity, numerous interactions,

341   and these elements are thought to provide a greater stability and inertia to their dynamics (MacArthur,

342   1955; Paine, 1966; Möllmann and Diekmann, 2012). The difference in responsiveness between small

343   pelagic and demersal systems may explain why the demersal one is usually less affected by

344   environmental changes than the pelagic (Tian *et al.*, 2008; Moyano *et al.*, 2021). It is therefore not

345   surprising that the strong shift signature observed in the small pelagic species of the GOL is only

346   partly mirrored within the demersal community.

347   The shift period seems to be rather advantageous to cephalopods in terms of their BC. This is

348   particularly interesting as cephalopods are species with a short lifespan that respond very quickly to

349   changing environmental conditions compared to other demersal species (Rodhouse *et al.*, 2014). It

350   has been demonstrated that the increase of water temperature (Mangold, 1983), and the intensification

351   of coastal upwelling (Otero *et al.*, 2016) may have a positive impact on the density and growth of

352   cephalopods and especially the common octopus, as this has been shown in the GOL by Feuilloley *et*

353   *al.*, (2020). During the shift, a significant and sudden increase in density was noticed for shortfin

354   squid. Again, the increase of shortfin squid density can be explained by the availability of a favorable

355   environment for the development of cephalopods, such as the rise in the SST (Mangold, 1983) and

356   the intensification of upwellings (Otero *et al.*, 2016) during the mid-2000's.

357   Identifying the precise drivers of BC changes for each species is beyond the scope of the present

358   study, as it requires further species-centered analyses, that would account for both the effects of

359   fishing and the environment. Depending on the species, these drivers are most likely multiple, and

360   our analysis revealed some degree of inter-specific variability in the temporal patterns, but species of

361   the same taxonomic group tended to exhibit similar patterns. In the absence of knowing what

362   triggered the shift in the GOL, it is difficult to provide a clear explanation for this clustering beyond

363   the fact that taxonomically related species may have more similar physiology, diet and behaviour,

364   and so are more likely to be affected in a similar way by any given change.

365   On a more general note, the results of the two DFA show that BC time series have more patterns in
366   common across species than density time series. Such an outcome can emerge from a greater
367   sensitivity of BC to common environmental drivers. If the trend 2 on BC time series displays the
368   same patterns of variations as the small pelagic fish and environmental conditions in the GOL, the
369   gradual increase observed in BC (trend 1), to which most species – except cephalopods and anglers
370   – are positively associated, may result from reduced competition among fishes due to increased
371   fishing pressure. Indeed, it is worth pointing out that the drastic response of the small pelagics to the
372   shift led to a collapse of the fishery, the effort of which has been redirected to the demersal stocks.
373   So increased fishing pressure, due to relaxing (perhaps mostly intra-specific) competition, could be
374   one explanation for improved BC in species positively correlated to trend 1.

375   The objective of the MAR analysis on the hake case study was to determine whether changes in BC
376   may impact population density or vice versa. This analysis displayed the negative effect of the adult
377   density on adult BC, possibly due to intra-specific competition (Hixon and Jones, 2005; Hixon *et al.*,
378   2012), while adult BC positively affected recruitment, most likely through higher reproductive
379   investment, a better quality of eggs and thus higher recruitment success (Booth and Beretta, 2004;
380   Grote *et al.*, 2011). The search for prey by fish larvae and early fish juveniles, as well as predatory
381   escape, is more efficient in developed individuals (with better BC), assuring that they can overcome
382   the critical larval stage with a better survival rate (Brown and Taylor, 1992; Morgan, 2004). Lloret *et*
383   *al.* (2008) also confirmed that maternal condition may affect the reproductive potential of hake in the
384   north-western Mediterranean. Interestingly, hake responded positively to trend 1 of the DFA
385   performed on the BC time series and displayed a continuous positive increase in BC while showing
386   a decrease in density. So, the positive link between BC and recruitment suggests that recruitment of
387   the depleted hake population in the GOL can be enhanced through a higher BC in adults, which may
388   be a mechanism that would partly compensate for population decline due to overfishing (GFCM,
389   2018). The case study of hake clearly demonstrated the importance of investigating the relationship
390   between BC and density for the other species when information is available.

391   In the MAR analysis on hake, the model was unable to detect the growth of recruits age 0-1 to
392   juveniles age 1-2, and then to adult. This lack of apparent connection between ages 0-1 and 1-2, and
393   ages 1-2 and 2+ has multiple explanations. First, natural mortality in the first year is known to be high
394   and variable (because of changes in environmental conditions) for Teleosts, masking cohort tracking
395   from ages 0-1 (Cushing, 1990). Secondly, the area of distribution of the hake population is wider than
396   the GOL (WGSAD, 2019), so immigration/emigration processes with neighboring areas might be
397   another confounding factor. Thirdly, adult hake are known to take refuge in marine canyons (at the
398   shelf break) and are hence more difficult to track by the MEDITS survey. Still, the model was able

399 to recover a strong positive link between adults' (2+) density and recruits, illustrating that spawning
400 stock density affects to some extent the recruitment in the following year. Such relationships are often
401 difficult to observe in fish populations, mostly because recruitment density is more strongly
402 influenced by environmental variations than spawning biomass (Cury *et al.*, 2014) and because the
403 low survival rate of recruits is unrelated to the fishing activity. But in cases when the fishing effort
404 on adults increased beyond a certain threshold (termed recruitment-overfishing by Pauly, 1984;
405 Sparre and Venema, 1992), stock-recruitment relationships can become more visible in the data,
406 which is precisely the case for hake in GSA 7 (GFCM, 2018).

407 To summarize, we detected some changes in the BC and density of the demersal species in the GOL
408 that appeared synchronous with those observed in small pelagic fish populations and in the
409 environmental conditions of the GOL, but to a lesser extent. We also highlighted strong interactions
410 between the BC and density in the European hake population, which could partly explain the rather
411 high resilience of this population to high fishing pressure. This is a good reason to scrutinize
412 relationships between BC and density for commercial fish stocks.

413 **Supplementary material**

414 Supplementary material is available at the ICESJMS online version of the manuscript.

415 **Data availability statement**

416 The data underlying this article will be shared on reasonable request to the corresponding author or
417 to the second author G. Certain (gregoire.certain@ifremer.fr).

418 **Author's contributions**

419 Bensebaini and Certain: conceptualization, methodology, formal analysis, writing and reviewing.
420 Billet, Jadaud and Hattab: data providing and reviewing. Fromentin and Gourguet: conceptualization
421 and reviewing.

422 **Acknowledgements**

428   **Table 1.** List of 22 species selected for the DFA analyses with their contribution to the commercial

429   landings, as well as their estimated density (in number and percentage) in the MEDITS survey catches

430   of 2018 (study area: Gulf of Lions).

Species	Scientific name	Density (%)	Density (individuals)	Commercial landings (%)
Horned octopus	*Eledone cirrhosa*	1,38	15263	16.81
Shortfin squid	*Illex coindetii*	1,54	17010	4.23
Common octopus	*Octopus vulgaris*	0,19	2109	8.96
Norway lobster	*Nephrops norvegicus*	0,65	7145	0.13
European hake	*Merluccius merluccius*	5,62	61943	18.13
Blue whiting	*Micromesistius poutassou*	2,69	29698	0.11
Greater forkbeard	*Phycis blennoides*	0,83	9123	0.43
Capelan	*Trisopterus capelanus*	22,88	252325	10.7
Blackbellied angler	*Lophius budegassa*	0,72	7970	11.1
Angler	*Lophius piscatorius*	0,07	746	1.94
Red mullet	*Mullus barbatus barbatus*	4,78	52751	7.11
Surmullet	*Mullus surmuletus*	0,09	1038	1.93
Axillary seabream	*Pagellus acarne*	0,05	502	3.95
Blackspot seabream	*Pagellus bogaraveo*	0,43	4722	0.7
Common pandora	*Pagellus erythrinus*	0,37	4103	3.6
Mediterranean horse mackerel	*Trachurus mediterraneus*	0,35	3905	9.03
Atlantic horse mackerel	*Trachurus trachurus*	50,63	558400	
Spotted flounder	*Citharus linguatula*	0,20	2233	0.09
Four-spot megrim	*Lepidorhombus boscii*	0,32	3522	0.04
Grey gurnard	*Eutrigla gurnardus*	5,84	64402	0.73
Blackbelly rosefish	*Helicolenus dactylopterus*	0,35	3861	0.04
John dory	*Zeus faber*	0,01	103	0.24

432   **Figure 1.** Map of the sampling stations of the MEDITS survey in the Gulf of Lions.

433   **Figure 2.** Process diagram of BC time series extraction.

434   **Figure 3.** Common trends (top part of the figure) for the residual index series obtained by the model
435   with two common trends and an "equalvarcov" covariance matrix R, and the factor loadings on these
436   trends (bottom part of the figure). The dashed grey lines show the threshold -/+ 0.2 (Zuur *et al*., 2003),
437   above which factor loadings will be interpreted.

438   **Figure 4.** Contribution of the two common trends represented in Figure 2 to the fitted series of BC
439   of each species. The dotted line represents the effect of the first common trend on each BC time series
440   ($z_{s1}x_{1t}$). The dashed line represents the effect of the second common trend ($z_{s2}x_{2t}$). And the solid line
441   is the model fit ($z_{s1}x_{1t} + z_{s2}x_{2t}$). Colored points represent the proportion of contributions from each
442   trend (example for species s and trend 1: $p_{1t} = z_{s1}x_{1t}/(z_{s1}x_{1t} + z_{s2}x_{2t})$) to the fit of the models (red for
443   trend 1, and blue for trend 2). **(a)** is the "shift" phase (2006-2009).

444   **Figure 5**. Common trend (top part of the figure) for the density time series obtained by the model
445   with one common trend and an "equalvarcov" covariance matrix R, and the factor loadings on this
446   trend (bottom part of the figure). The dashed grey lines show the threshold -/+ 0.2 (Zuur *et al*., 2003),
447   above which factor loadings will be interpreted.

448   **Figure 6.** Comparison of all common trends obtained by DFA from the current study and the study
449   of Feuilloley *et al*. (2020). The dashed line in blue represents BC trend 2 and dotted line in green
450   represents density common trend. The brown line with points represents the common trend of small
451   pelagics, while the yellow line with diamonds represents the common trend of environmental factors
452   from the study of Feuilloley *et al*. (2020). The shaded area of the graph delimits the period for the
453   shift between 2006 and 2009.

454   **Figure 7.** Schematic view of the model selected for European hake *M. merluccius*. Red arrows
455   represent negative effects, green arrows represent positive effects, arrows with non-significant p-
456   value were grayed out. x_1: recruits age 0-1 log density, x_2: juveniles age 1-2 log density, x_3: adults
457   age 2+ log density, x_4: recruits age 0-1 BC, x_5: juveniles age 1-2 BC, x_6: adults age 2+ BC.

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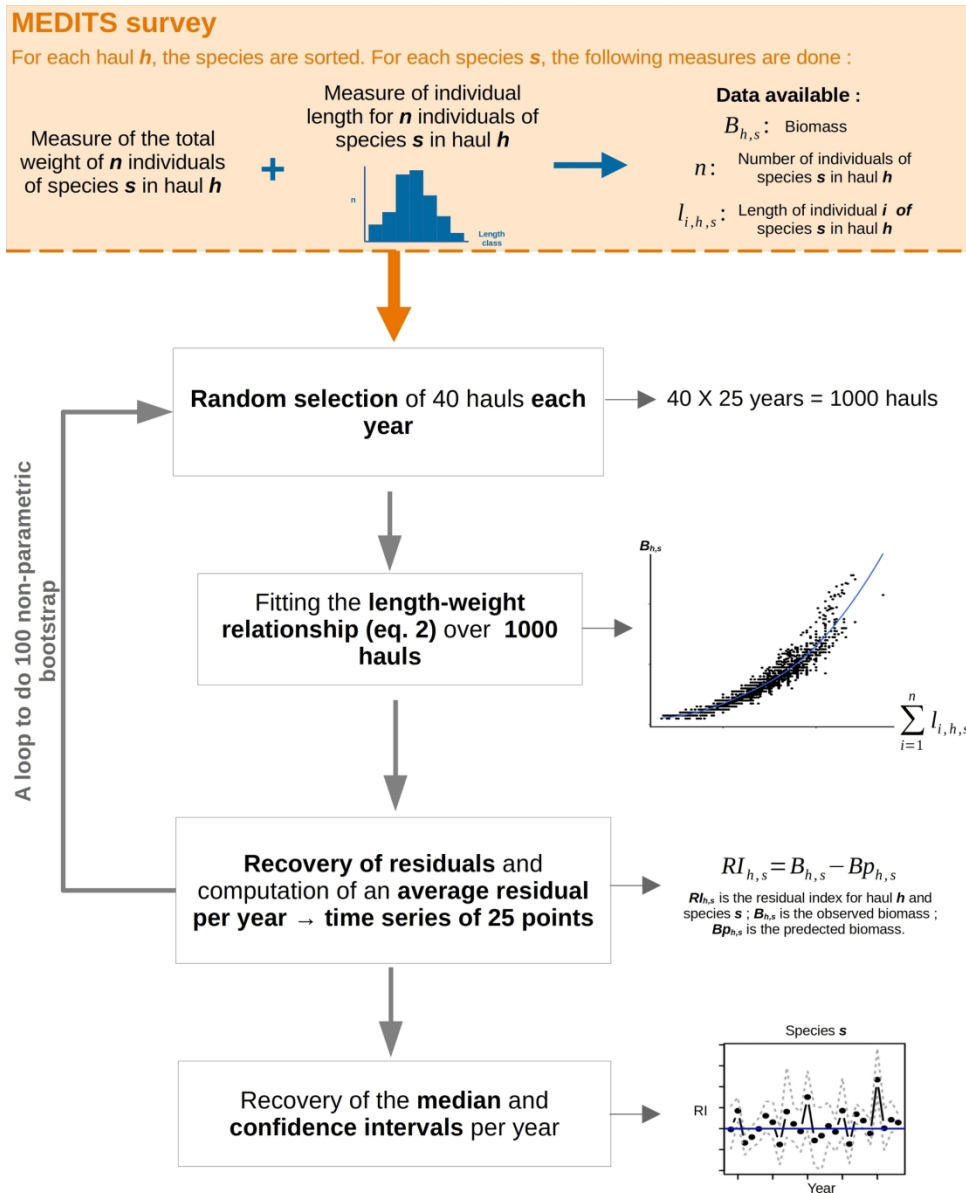595 Pauly, D. 1998. Tropical fishes: patterns and propensities*. Journal of Fish Biology, 53: 1–17.

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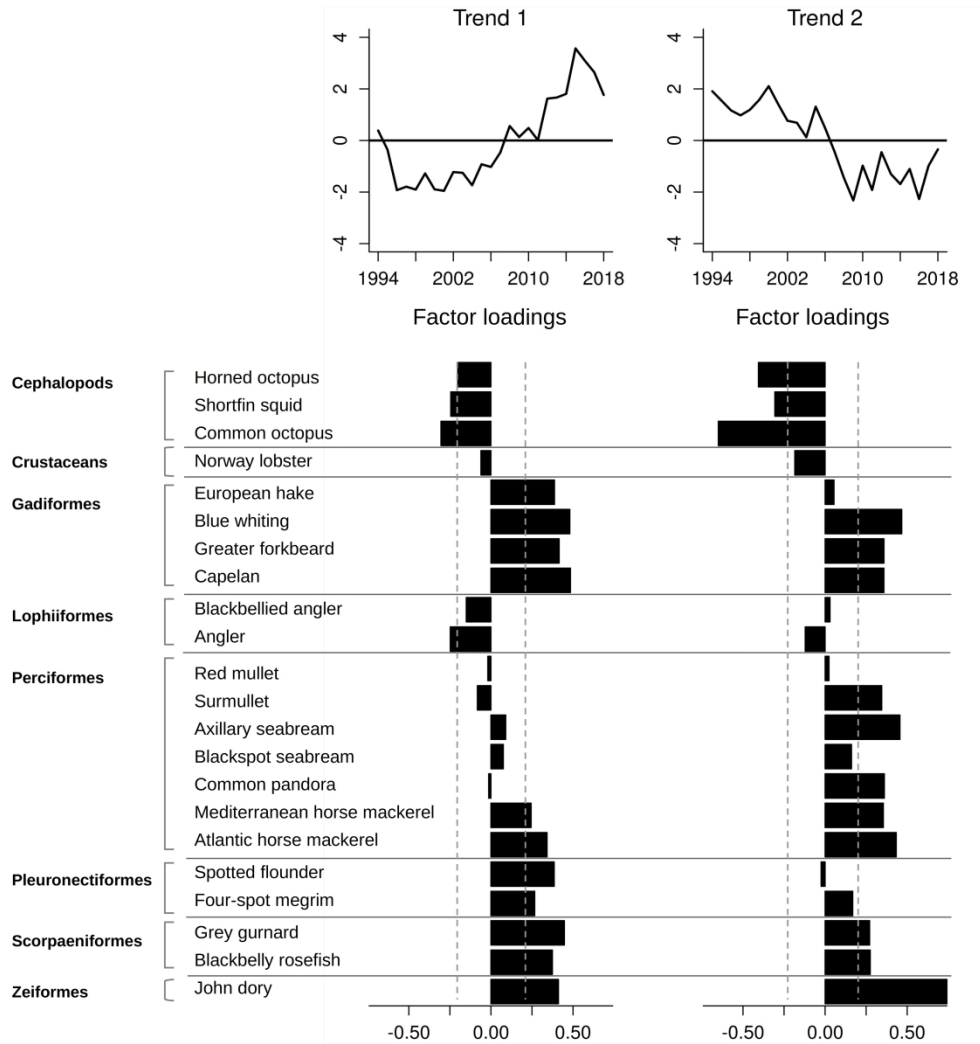631   fisheries time series. Canadian Journal of Fisheries and Aquatic Sciences, 60: 542–552.
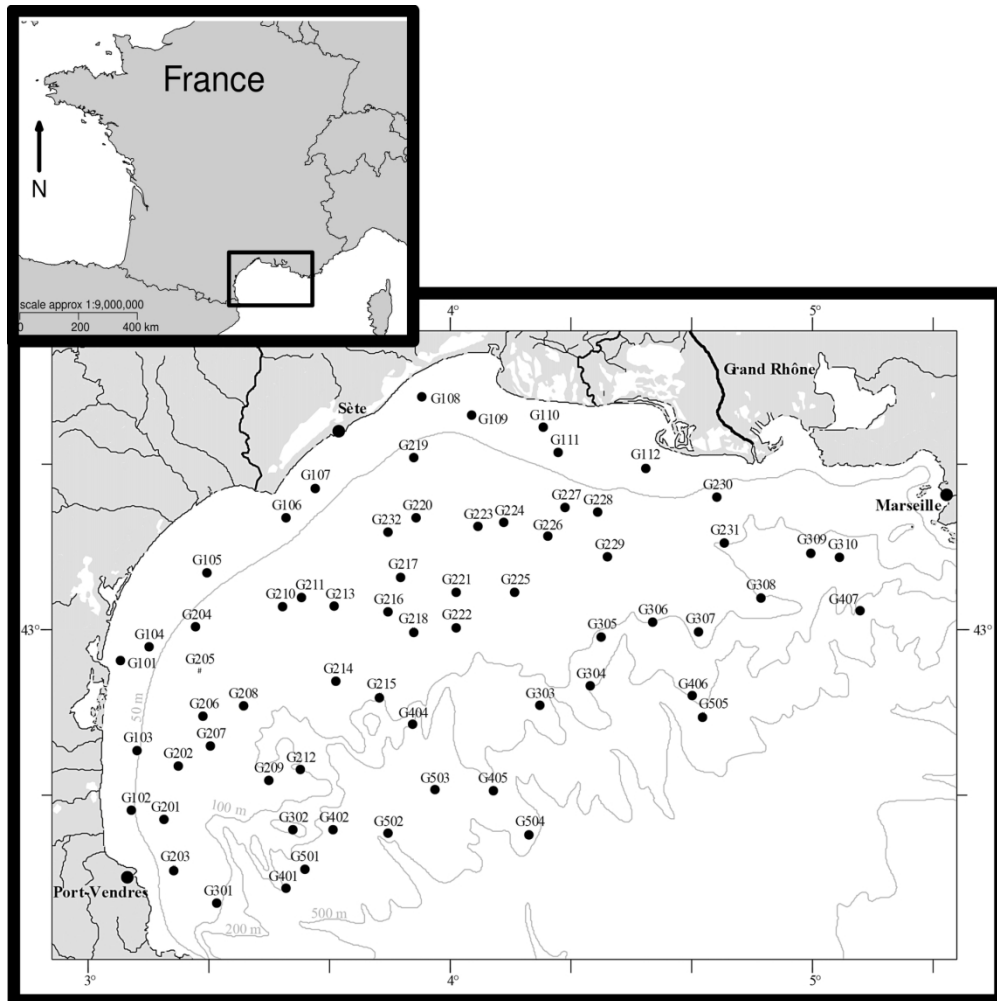
Map of the sampling stations of the MEDITS survey in the Gulf of Lions.

85x85mm (600 x 600 DPI)

MEDITS survey

For each haul **h**, the species are sorted. For each species **s**, the following measures are done :

Measure of the total weight of **n** individuals of species **s** in haul **h**

+

Measure of individual length for **n** individuals of species **s** in haul **h**

n

Length class

Data available :

$B_{h,s}$: Biomass

n : Number of individuals of species **s** in haul **h**

$l_{i,h,s}$: Length of individual **i** of species **s** in haul **h**

A loop to do 100 non-parametric bootstrap

Random selection of 40 hauls **each year**

→ 40 X 25 years = 1000 hauls

Fitting the **length-weight relationship (eq. 2)** over **1000 hauls**

$B_{h,s}$

$$\sum_{i=1}^{n} l_{i,h,s}$$

Recovery of residuals and computation of an **average residual per year** → time series of 25 points

$$RI_{h,s} = B_{h,s} - Bp_{h,s}$$

$RI_{h,s}$ is the residual index for haul **h** and species **s** ; $B_{h,s}$ is the observed biomass ; $Bp_{h,s}$ is the predicted biomass.

Recovery of the **median** and **confidence intervals** per year
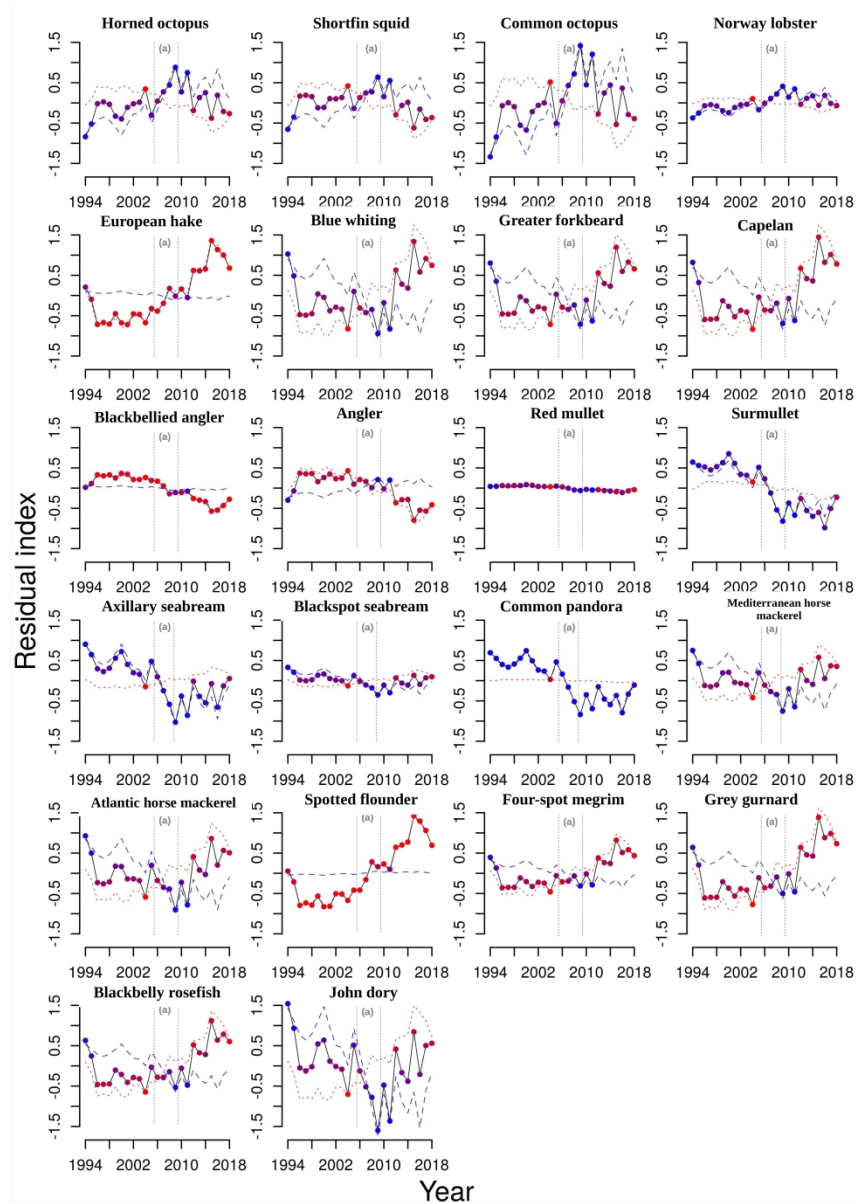
Species **s**

RI

Year

Process diagram of BC time series extraction.
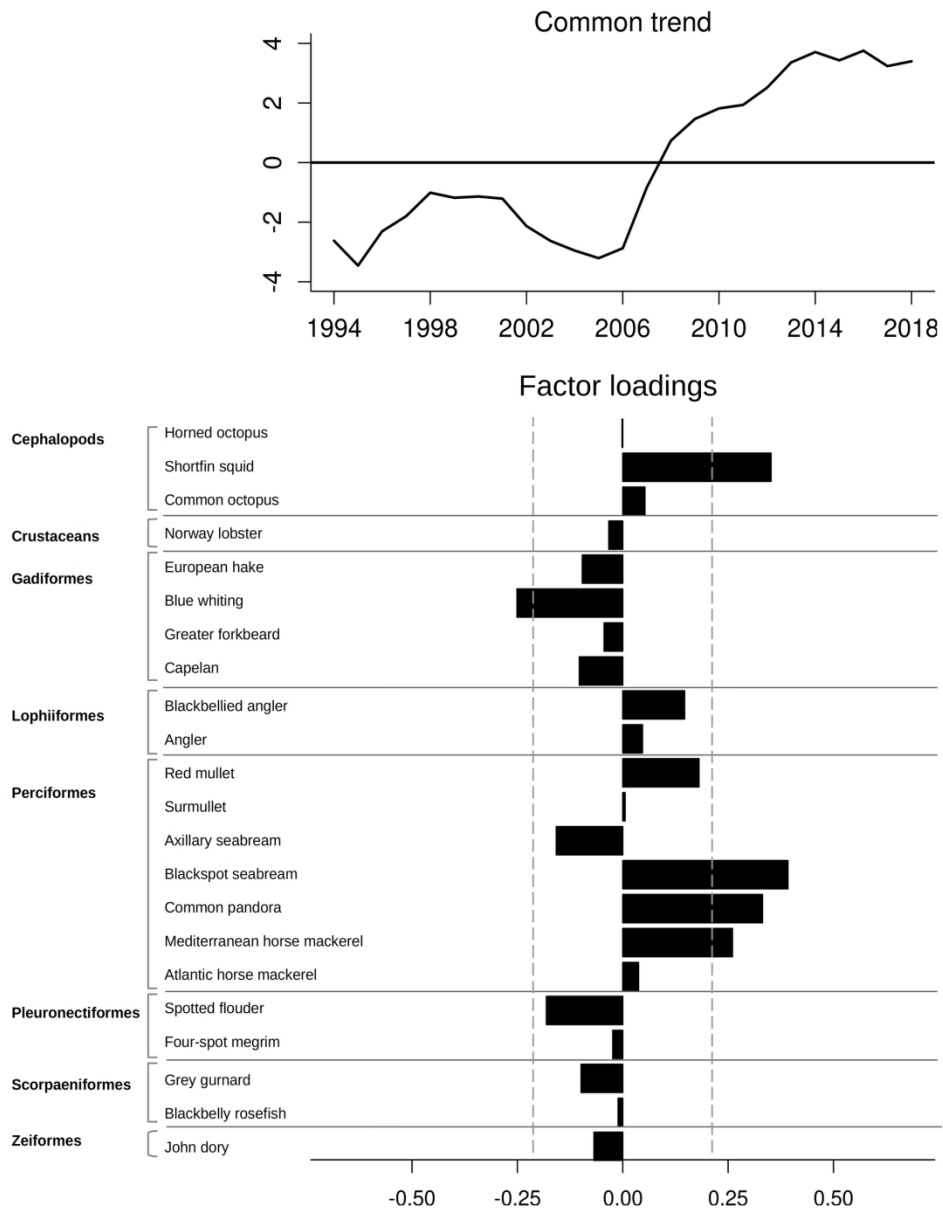
85x105mm (600 x 600 DPI)

Common trends (top part of the figure) for the residual index series obtained by the model with two common trends and an "equalvarcov" covariance matrix R, and the factor loadings on these trends (bottom part of the figure). The dashed grey lines show the threshold -/+ 0.2 (Zuur *et al*., 2003), above which factor loadings will be interpreted.

170x177mm (600 x 600 DPI)

Contribution of the two common trends represented in Figure 2 to the fitted series of BC of each species. The dotted line represents the effect of the first common trend on each BC time series ($z_{s1}x_{1t}$). The dashed line represents the effect of the second common trend ($z_{s2}x_{2t}$). And the solid line is the model fit ($z_{s1}x_{1t} + z_{s2}x_{2t}$). Colored points represent the proportion of contributions from each trend (example for species s and trend 1: $p_{1t}=z_{s1}x_{1t}/(z_{s1}x_{1t}+z_{s2}x_{2t})$) to the fit of the models (red for trend 1, and blue for trend 2). (a) is the "shift" phase (2006-2009).

170x240mm (600 x 600 DPI)

Common trend (top part of the figure) for the density time series obtained by the model with one common trend and an "equalvarcov" covariance matrix R, and the factor loadings on this trend (bottom part of the figure). The dashed grey lines show the threshold -/+ 0.2 (Zuur *et al.*, 2003), above which factor loadings will be interpreted.

85x105mm (600 x 600 DPI)
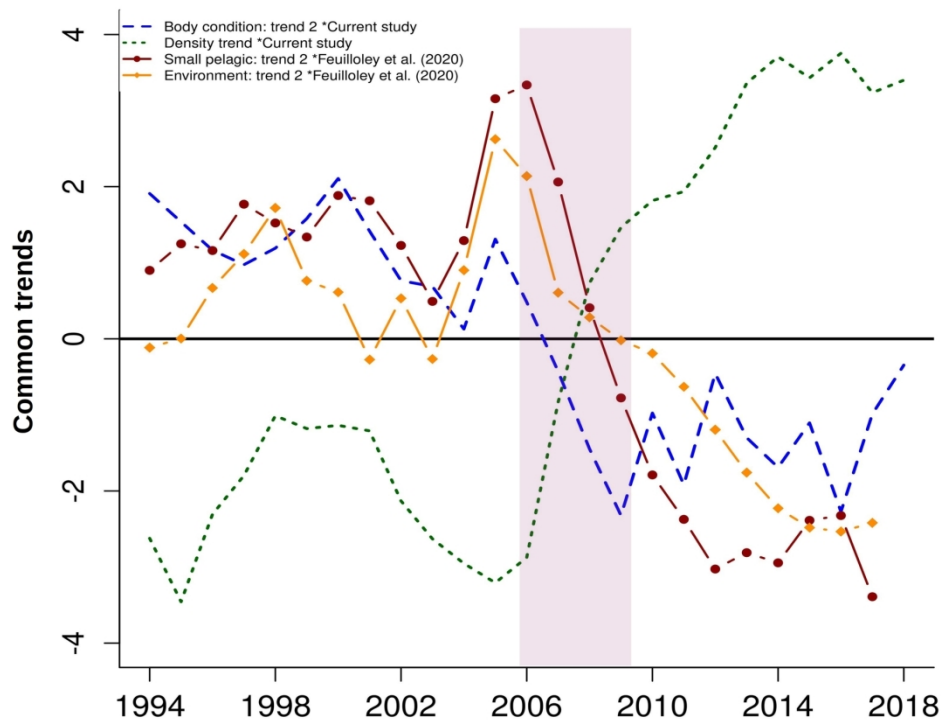
Comparison of all common trends obtained by DFA from the current study and the study of Feuilloley *et al*. (2020). The dashed line in blue represents BC trend 2 and dotted line in green represents density common trend. The brown line with points represents the common trend of small pelagics, while the yellow line with diamonds represents the common trend of environmental factors from the study of Feuilloley *et al*. (2020). The shaded area of the graph delimits the period for the shift between 2006 and 2009.

85x68mm (600 x 600 DPI)

European hake
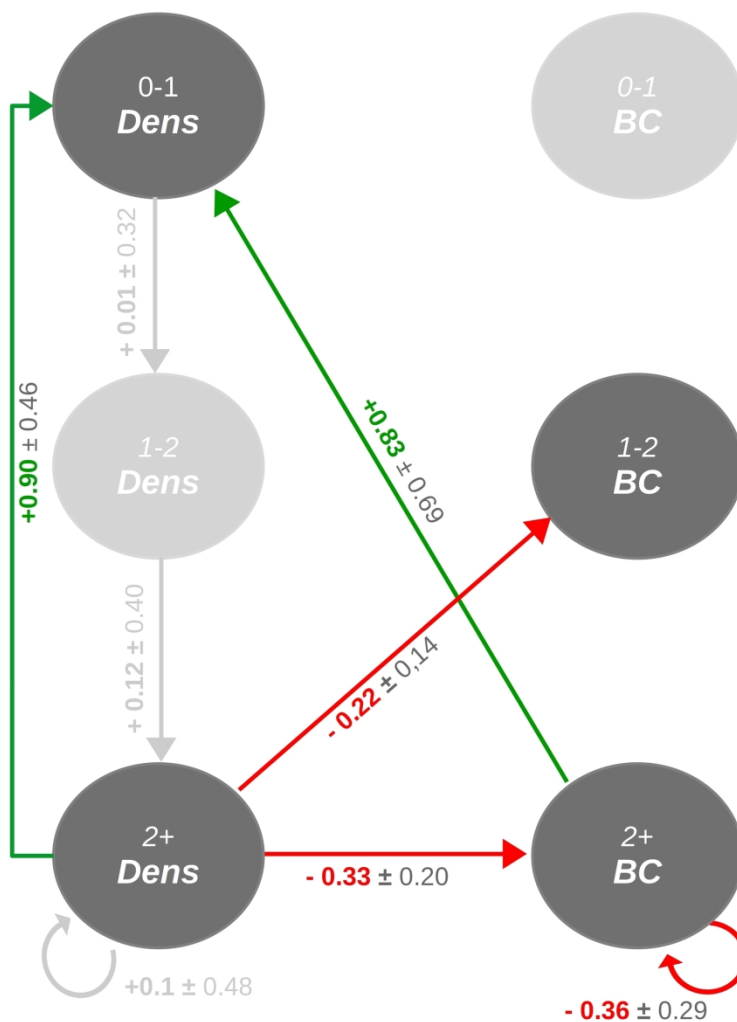
Schematic view of the model selected for European hake M. merluccius. Red arrows represent negative effects, green arrows represent positive effects, arrows with non-significant p-value were grayed out. x_1: recruits age 0-1 log density, x_2: juveniles age 1-2 log density, x_3: adults age 2+ log density, x_4: recruits age 0-1 BC, x_5: juveniles age 1-2 BC, x_6: adults age 2+ BC.

85x127mm (600 x 600 DPI)