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# Detecting the effects of inter-annual and seasonal changes in environmental factors on the striped red mullet population in the Bay of Biscay

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1 **Abstract:**

2 Climate fluctuations affect a wide range of environmental factors that may impact fish populations with  
3 various response mechanisms. For a major part of world fisheries stocks, only abundance time-series are  
4 available. Relations between abundance of these species and ocean variables, including long term trends  
5 and patterns of seasonal change, remain sparsely documented. The main aim of our work is to determine  
6 to what extent effects of inter-annual and seasonal changes in environmental factors can be identified and  
7 quantified on a selected time-series of abundance data-set: the striped red mullet population within the Bay  
8 of Biscay. 8 Landings per unit of effort (LPUE) for striped red mullet data are compared with environmental  
9 covariates extracted from the Copernicus web database. Our strategy is to decompose the patterns of change  
10 in fish populations into long-term and seasonal components and to analyse the possible dependency of both  
11 components on environmental factors. The overall tendencies are a decrease of the long-term component  
12 and a modification of the seasonality, with additional spatial variability. The observed tendencies and  
13 seasonal changes are discussed against the spatio-temporal patterns of change in environmental factors.  
14 High spatial heterogeneity within the Bay of Biscay was found, both for striped red mullet long-term trends  
15 and seasonal changes. Most inter-annual and seasonal changes in striped red mullet abundance can be related  
16 to environmental factors. In addition to the well-known annual fluctuation, most coastal sites revealed a  
17 bi-annual seasonality possibly related to the recruitment process.

18 **Keywords:**

19 Bay of Biscay; Climate change; Environmental modelling; Fisheries indicators; *Mullus surmuletus*; Time-  
20 series decomposition.

## 21 1. Introduction

22 The fluctuations of ocean variables are a primary driver for fish populations (García-Barón et al., 2020).  
23 This environmental control has taken on particular importance in the context of global climate change, which  
24 affects numerous oceanic factors that may impact marine fauna (Brander, 2010). Due to the complexity of the  
25 mechanisms involved and the interactions between space- and time -varying driving factors, understanding  
26 the effect of climate change on these populations may prove to be tricky (Rijnsdorp et al., 2009). The effects  
27 of climate change on environmental factors, such as modifications of the water cycle, are expected to differ  
28 among geographic areas (IPCC, 2007), both at global and regional scales. For instance, river runoff and  
29 precipitation are expected to increase/decrease in northern/southern Europe, respectively (Frei et al., 2006).  
30 Likewise, ocean water properties are exposed to global change-induced modifications, such as the significant  
31 increase in salinity, which was observed during the three last decades in the northern part of the Atlantic  
32 ocean (Stott et al., 2008).

33 Several effects of environmental changes due to global warming on fish populations have already been  
34 reported (Both et al., 2006; Free et al., 2019). The review of Rijnsdorp et al. (2009) highlights that these  
35 changes may result in four response mechanisms. Firstly, changes in environmental parameters can induce a  
36 physiological response (Cohen et al., 2018). Secondly, modifications in environment may induce a behavioural  
37 response, such as moving into new suitable areas. The third type of response may be through population  
38 dynamics (i.e. changes in the balance between rates of mortality, growth, and reproduction in combination  
39 with dispersal) which could result in the establishment of new populations in new areas, [in the abandonment  
40 of traditional sites or in a regime shift, with significantly higher or lower abundance than in other historical  
41 periods](#). Finally, a fourth response to environmental changes may be changes at ecosystem level (i.e. in  
42 productivity and/or trophic interactions). It should be emphasized that, even if this is expected to take on  
43 worrying proportions in the context of global change and increased fishing pressure, the characterization of  
44 the response of fish populations to the fluctuations of ocean variables is already a major challenge for ocean  
45 ecology scientists.

46 From an ecological perspective, the study of the relationships between environmental factors and popula-  
47 tions is generally carried out using three main categories of models (Melo-Merino et al., 2020): mechanistic  
48 models (Kearney and Porter, 2009), process-oriented models (Peterson et al., 2015) and correlative models  
49 (Huntley et al., 1995; Araujo and Guisan, 2006; Franklin et al., 2009; Box, 2012). A direct application of  
50 such modelling strategies in a marine ecosystem remains very challenging. A major limitation is that most  
51 environmental data layers are not known in the entire three-dimensional ocean (Assis et al., 2016). Another  
52 difficulty arises from the lack of knowledge on dynamics and behaviour for most species (Bentlage et al.,  
53 2013). For fisheries stock assessment, the International Council for Exploration of the Sea (ICES) divide  
54 fish stocks into 6 categories. Categories 2 to 6 belong to data-limited categories (Lart, 2019). The majority  
55 of the world’s fisheries, by number, are classified in these categories (Costello et al., 2012; Dowling et al.,  
56 2019). A stock can be considered as data-limited for various reasons, including a lack or a limited amount  
57 of reliable data, incomplete surveys and/or poor sampling leading to uncertainties about the biology of the  
58 species (Le Quesne et al., 2013). For ICES categories 5 and 6, abundance is only indirectly assessed through  
59 selected proxies, and ecology and behaviours are almost unknown. In such a context of data limitation which  
60 inhibits comprehensive understanding of fish behaviour, the alternative approach followed here is first to use  
61 a non-causal statistical approach, i.e. to identify and quantify dependencies between the level of interest and  
62 the available environmental covariates without any *a priori* knowledge of the driving mechanisms, and then  
63 to infer *a posteriori* causal relationships by combining statistical results and expert knowledge.

64 Apart from the data quality issue, the extraction of entangled trends and patterns in time-series data  
65 remains a major challenge for data processing science. A widely used approach is to split the time series  
66 into several components, possibly selected from an *a priori* knowledge of the driving factors (Hyndman and  
67 Athanasopoulos, 2018). A number of decomposition methods are available in literature in relation to the  
68 very variable nature of the data-sets, including for instance intermittency, shortness, nonstationarity, non-  
69 linear response to driving factors (Huang et al., 1998). Standard data processing books, see e.g. Brockwell  
70 et al. (1991), or more recently Shumway and Stoffer (2017), review and detail a large panel of decomposition  
71 methods, the latter with examples of application under R software. [Under global change effect, the data from](#)

72 the Bay of Biscay, situated at mid-latitude, may be expected to respond to climate factors affected by both  
73 global long term trend and annual seasonal fluctuations. A helpful time-series decomposition can be therefore  
74 be based on the extraction of long term trend and seasonality from the time-series, with an additional residual  
75 (Ferguson et al., 2008). Such a time-series decomposition into trend, seasonal and residual components is  
76 still rarely used in fish ecology (Broekhuizen and McKenzie, 1995; Beare and McKenzie, 1999). Among the  
77 rather rare attempts, Plaza et al. (2018) used time-series decomposition as a method of data filtering, to  
78 identify contrasts between data features and technical fisheries literature, and Hsieh et al. (2009) analysed  
79 links between larval anchovy data and environmental variables. More generally, time-series decomposition  
80 methods, while widely used in data processing, are not familiar to ecologists (Hsieh et al., 2009).

81 The present study is, to our knowledge, the first assessment of the effect of changes in environmental  
82 factors on data-limited fish populations using the time-series decomposition method. The target species  
83 is the striped red mullet, *Mullus surmuletus* Linnaeus, 1758. The striped red mullet is distributed in the  
84 Mediterranean Sea and along the Eastern Atlantic coasts, from the English Channel to the northern part  
85 of West Africa (Labropoulou et al., 1997). At a large scale (Atlantic ocean), northerly migration of striped  
86 red mullet during a phase with demonstrated temperature increases due to climate change has already  
87 been demonstrated (McCarty et al., 2001; Hulme, 2002; Beare et al., 2005). Striped red mullet abundance  
88 increases in the English Channel (Vaz et al., 2004) and the North Sea. Eastern English Channel and the  
89 Bay of Biscay are two main areas of catches of striped red mullet in the Atlantic Ocean (Mahe et al., 2014).  
90 Individuals in the Bay of Biscay belong to the sub-population individualized in Western Europe by ICES.  
91 It extends from the Celtic sea to the waters bordering the Iberian Peninsula with a significant presence in  
92 the Bay of Biscay. It is a predominantly benthic and gregarious species living in small groups of up to a  
93 dozen individuals. It can also be solitary or live just in pairs. Young fishes live in lower salinity coastal areas  
94 while adults have a more offshore distribution (Oskarsson et al., 2019). Pajuelo et al. (1997) find young  
95 striped red mullet between 10 and 60 m deep in Canarias Islands while (Reñones et al., 1995) report values  
96 between 30 and 90m in Majorcan waters. The striped red mullet has an inter-depth migration because  
97 of its reproduction (Kousteni et al., 2019). The recruitment occurs in shallow habitat (García-Rubies and  
98 Macpherson, 1995), spawns in deep habitats and continue to disperse into deep water after reproduction  
99 (Machias and Labropoulou, 2002). On average, striped red mullet abundance is highest in surface waters  
100 down to 100 m depth (easily observable from 0 to 30 m) (Mahé et al., 2005), but large specimens have been  
101 observed below 300 m depth. In the north Atlantic, mature striped red mullet depths is between 100 and 200  
102 m on average (Leaute et al., 2018). Several factor may intervene in the abundance of the striped red mullet.  
103 Benthic habitat composition (Ajemian et al., 2016) or substrate type (Lombarte et al., 2000; Mahé et al.,  
104 2005) are important. As for all other species, other factors can affect striped red mullet and may have an  
105 important impact on its abundance. In particular, population may be affected by trophic web parameters,  
106 such availability of preys and abundance of predators, or factors related to natural mortality such as diseases  
107 and parasites. Recent study reports life-history traits of the striped red mullet in Mediterranean (Kousteni  
108 et al., 2019). Longevity of striped red mullet is estimated at 11.75 years and the length at 50% of maturity  
109 is 153.3 mm for females and 139.2 mm for males.

110 Following the ICES classification categories (ICES, 2012), Bay of Biscay sub-population is currently in  
111 data-limited stocks (DLS) category 5: it is a stock for which only landing data are available, as described  
112 above. From a fish population perspective, the Bay of Biscay remains a limited area with a total surface  
113 aire of approximately 223 000 km<sup>2</sup>. No substantial scientific literature is available to qualify the striped red  
114 mullet stock status within the Bay of Biscay and its relationship with ocean variables, whether in the past,  
115 at present or in the global change context.

116 The aim of the present paper is to determine whether modifications of oceanic environmental factors, such  
117 as changes in long term or seasonal trends, have an impact on the striped red mullet population within the  
118 Bay of Biscay. The analysis will be based on selected professional LPUE (Landing Per Unit Effort) as a proxy  
119 of striped red mullet stock abundance in the Bay of Biscay, as suggested by Caill-Milly et al. (2019). Time-  
120 series decomposition was first applied on striped red mullet abundance to achieve a rough understanding of  
121 the population dynamics through space and time. Secondly, the analysis was dedicated to the identification  
122 and quantification of possible links between trends and seasonal fluctuations of both striped red mullet

123 abundance and environmental covariates. The results and methodology were then discussed, keeping in  
124 mind the challenge of the limited time span of [the available time-series on for striped red mullet index of](#)  
125 [abundance](#).

## 126 2. Methodology

### 127 2.1. Database

#### 128 2.1.1. Fishery data

129 The fishery database used for the present paper (Kermorvant et al., 2020) was provided by the SACROIS  
130 (SACROIS) algorithm developed by Ifremer. SACROIS is a cross validation tool for fisheries statistics,  
131 in response to Article 145 of the EU regulation (EC Reg. 404/2011). SACROIS algorithm cross-checks  
132 information from fishing forms, fishing fleet registers, logbooks, sales notes, VMS data and the scientific  
133 census of fishing activity calendars (Mateo et al., 2016). We have selected this database because we considered  
134 that it is the most complete available database regarding production and fishing effort data for the French fleet  
135 operating in the Bay of Biscay. The SACROIS data are spatially aggregated by ICES rectangles assembled  
136 monthly. ICES rectangles extend about 0.5 and 1 degree in longitude and latitude, respectively, with an  
137 area of approximately 30 nautical squared miles. The present study was based on a set of six coastal ICES  
138 rectangles selected because they were sufficiently documented to allow time and time-frequency analysis  
139 (see Figure 1A). These selected rectangles do not integrate the full ecological niche of striped red mullet  
140 in the Bay of Biscay, but were each inside the niche and contain sufficient information to be considered  
141 as representative of the Bay of Biscay striped red mullet population ICES (2019). LPUE was provided  
142 for a given gear, gear mesh, day and ICES statistical rectangle. Specific vessels, i.e. small trawl vessels  
143 (7.9–15.8 m) with a gear mesh of 70–79 mm, were selected in the SACROIS database following the criteria  
144 of Caill-Milly et al. (2019) for striped red mullet. The time series of the selected mean trawlers LPUE was  
145 available from 2005 to 2018. [LPUE is not a direct estimator of abundance. However, applying, \(i\), a filtering](#)  
146 [on vessel and gear characteristics and, \(ii\), a selection of a period without significant changes in regulation](#)  
147 [\[see Caill-Milly et al. \(2019\)\], we considered that the selected daily LPUE was a relevant proxy for striped](#)  
148 [red mullet abundance](#). In fisheries-dependent data, bias can be introduced to abundance estimates when  
149 sampling was not randomized (Potts and Rose, 2018). Striped red mullet is of high commercial interest  
150 but is not specifically targeted by trawlers in the Bay of Biscay (it is a part of set of sought-after demersal  
151 species). Therefore, even if the sampling scheme was not randomized, it was not directed. Furthermore,  
152 the International Council For the Exploration of the Sea (ICES) identified striped red mullet LPUE as a  
153 potential abundance index for this stock (Oskarsson et al., 2019; ICES, 2020). [Note that, as the present](#)  
154 [analysis requires continuous time-resolved database, other available sources of data at lower sampling rates](#)  
155 [\(such the EVHOE campaign in the Bay of Biscay and Celtic Sea\) were not considered](#).

#### 156 2.1.2. Environmental data

157 Environmental data was extracted from the Copernicus portal (<https://www.copernicus.eu>). Values for  
158 surface temperature (in degree Celcius), surface salinity (in grams per liter), [phytoplankton concentration](#)  
159 [\(in  \$mmolC/m^3\$ \)](#), chlorophyll concentration (in  $mg/m^3$ ), and chemicals (Silicate (Si), Phosphate ( $PO_4^{3-}$ ),  
160 [Ammonium \( \$NH\_4^+\$ \)](#), Nitrate ( $NO_3^-$ ) and Dissolved Oxygen ( $mmol/m^3$ ) were selected from 2005 to 2018  
161 within the Bay of Biscay. For surface temperature and surface salinity, main statistical values (table 1) were  
162 computed for each environmental variable by ICES rectangle. For phytoplankton concentration, chlorophyll  
163 concentration, and chemicals, a first statistical study showed a high correlation. A principal component  
164 analysis (PCA - available in appendix) was therefore used to reduce the number of variables. Based on the  
165 eigenvalues of the three first axes, three new variables were produced, namely PC1, PC2 and PC3. [PC1](#)  
166 [is driven by Si,  \$PO\_4^{3-}\$  and  \$NH\_4^+\$  and explain 57.2% of variability, PC2 by phytoplankton, net primary](#)  
167 [production and  \$NO\_3^-\$  and explain 18.6% of variability. PC3 by Dissolved Oxygen and explain 10.2% of](#)  
168 [variability](#).

169 *Tab.1 here*

170 *2.2. Data processing*

171 *2.2.1. LPUE time-series decomposition*

172 Our strategy to analyse the spatio-temporal dynamics of striped red mullet abundance was to assume an  
 173 additive decomposition of the LPUE in terms of a Long Term Trend (LTT), a Seasonal Trend (ST) and a  
 174 residual R. *LTT* aimed to describe the interannual changes in LPUE while ST was dedicated to characterizing  
 175 the amplitude of the seasonal fluctuations. **LPUE time-series exhibited a very high variance and needed to  
 176 be log transformed to be modelled** at a given time  $t$  (in months from January 2005 to December 2018) and  
 177 location  $r$ ,  $Y_{rt}$  being here below the value of  $\log(LPUE_{rt})$ , the decomposition was written:

$$Y_{rt} = LTT_{rt} + ST_{rt} + R_{rt}. \quad (1)$$

178 *2.2.2. Long Term Trends*

179 For each rectangle  $r$ , a moving median ( $MM(Y_{rt})$ ) over a 48-month window was applied to remove intra-  
 180 annual or seasonal effects and then investigate appropriate model for estimating the *LTT*. We proposed to  
 181 investigate the Long Term Trends applying a smoothing function to time:

$$MM(Y_{rt}) = \alpha_r + f_r(t) + \epsilon_{rt}, \quad (2)$$

182 where  $\epsilon_{rt}$  follows a normal distribution  $\mathcal{N}(0, \sigma^2)$ . The smooth function of each rectangle  $f_r(\cdot)$  is defined  
 183 using spline bases [see Wood (2017)]. In practice we used generalized additive model (GAM) through the  
 184 `mgcv` R package provided by Wood (2017). Note that an intercept  $\alpha_r$  by rectangle was required due to some  
 185 optimization constraints used in `mgcv` (see Chapter 5 and 7 of Wood (2017)).

186 The fitted model (2) provided a smooth estimation of the time-dependent inter-annual trend for each  
 187 rectangle:  $\widehat{LTT}_{rt} = \widehat{\alpha}_r + \widehat{f}_r(t)$ .

188 *2.2.3. Seasonal Trends*

189 The seasonal component was obtained by removing the estimated trends from the initial  $\log(LPUE)$   
 190 data:

$$ST_{rt} = Y_{rt} - \widehat{LTT}_{rt}.$$

191 The subsequent analysis is twofold:

- 192 • The first bulk Seasonal Trend model in each rectangle was obtained from dynamic harmonic regression  
 193 Young et al. (1999):

$$ST_{rt} = \sum_{j=1}^{K_r} \{\alpha_{0,r} \cos(\omega_j t) + \alpha_{1,r} \sin(\omega_j t)\} + \epsilon_{rt} \quad (3)$$

194 where  $\omega_j = \frac{2\pi}{m} j$  are the harmonic frequencies associated with the seasonality in the series,  $m$  being  
 195 the annual number of months, i.e. 12.  $\epsilon_{rt} \sim \mathcal{N}(0, \sigma_r^2)$ . Depending on the selected rectangle, a range of  
 196 harmonics ( $2 < K_r < 6$ ) were tested to provide the best model based on AIC comparisons (Sakamoto  
 197 et al., 1986). This first bulk Seasonal Trend model in each rectangle provided an overview of the LPUE  
 198 seasonality.

- 199 • Further insight on LPUE spatio-temporal dynamics was provided by a time-frequency analysis of the  
 200 seasonal component. A discrete Fourier analysis (Bloomfield, 2004) was performed on the seasonal  
 201 component for each ICES rectangle to provide the spectral density (i) over the complete time-series  
 202 and (ii) over a moving 48-month window for time-resolved analysis. From the latter analysis, the  
 203 amplitude of seasonal fluctuations associated with annual (12 months) and biannual (6 months) periods  
 204 were extracted, named  $ST_{LPUE,rt}^{12}$  and  $ST_{LPUE,rt}^6$ , respectively:

$$ST_{LPUE,rt}^n = \sqrt{\int_{f_1}^{f_2} SD(u) du} \quad (4)$$

205 where  $SD(\cdot)$  is the spectral density (Stoica et al., 2005),  $n = 6$  or  $12$  for biannual and annual fluctua-  
 206 tions, respectively and  $f_1$  and  $f_2$  are the frequency boundaries taken at 5 and 8, and 9 and 16 for the  
 207 biannual and annual fluctuations.

### 208 2.3. Dependency on environmental variables

#### 209 2.3.1. Long Term Trends

210 Models for Long Term Trends were defined for environmental covariates time-series similarly as done  
 211 for LPUE (see Eq. 2). Links between estimated long term trends of LPUE (noted  $\widehat{LTT}_{LPUE}$ ) and various  
 212 environmental covariates were first tested using an uni-variate linear model. Five relevant environmental  
 213 variables were then selected for the multivariate linear model: the fitted trend of median water salinity  
 214  $\widehat{LTT}_{MS}$ , the fitted trend of median surface temperature  $\widehat{LTT}_{MT}$ , and the fitted trends of PC1, PC2 and  
 215 PC3 variables  $\widehat{LTT}_{PC1}$ ,  $\widehat{LTT}_{PC2}$  and  $\widehat{LTT}_{PC3}$ , respectively. For each rectangle, we modeled:

$$\widehat{LTT}_{LPUE,t} = \beta_0 + \beta_1 \widehat{LTT}_{MT,t} + \beta_2 \widehat{LTT}_{MS,t} + \beta_3 \widehat{LTT}_{PC1,t} + \beta_4 \widehat{LTT}_{PC2,t} + \beta_5 \widehat{LTT}_{PC3,t} + \epsilon_t, \quad (5)$$

216 where  $\epsilon_t \sim \mathcal{N}(0, \sigma^2)$ .

#### 217 2.3.2. Seasonality

218 The seasonal component of environmental covariates was processed by time-frequency analysis similarly  
 219 to the LPUE data. For each variable and each rectangle, the annual and biannual amplitudes of seasonal  
 220 fluctuations were obtained from the time-resolved spectral density over a 48-month moving window.

221 A linear model was built by rectangle to test the relationship between the annual and biannual amplitudes  
 222 of seasonal fluctuations of LPUE and environmental covariates data:

$$ST_{LPUE,rt}^n = \gamma_0 + \gamma_1 ST_{MT,t}^n + \gamma_2 ST_{MS,t}^n + \gamma_3 ST_{PC1,t}^n + \gamma_4 ST_{PC2,t}^n + \gamma_5 ST_{PC3,t}^n + \epsilon_t. \quad (6)$$

223 where  $n = 6$  and  $12$  for biannual and annual fluctuations and  $\epsilon_t$  follows  $\mathcal{N}(0, \sigma^2)$ .

#### 224 2.3.3. Models performance

225 Some parameters were selected for each linear model created for  $LTT$  and  $ST$ . Firstly, estimates of the  
 226 coefficient of the linear regression and associated p-value were recorded. Estimates is the mean change in  
 227 the  $LTT$  or  $ST$  for one unit of change in the covariate. A low p-value (e.g.  $<0.05$ ) means changes in the  
 228  $LTT$  or  $ST$  value are related to changes in the covariate. Secondly, the global  $R^2$  and relative importance  
 229 per covariate were calculated. The model global  $R^2$  indicates the proportion of variance of  $LTT$  or  $ST$   
 230 explained by the created model. Relative importance of covariate enables us to determine the share of  
 231 variability accountable for each environmental covariate. In other words, relative importance of covariate is  
 232 the proportionate contribution each covariates makes to global  $R^2$ . Relative importance of covariates was  
 233 calculated with the `relimpo` package of R software (Grömping et al., 2006). The used metric is "lmg", which  
 234 provides a decomposition of the model explained variance (Grömping et al., 2006).



235 **3. Results**

236 *3.1. LPUE time-series decomposition*

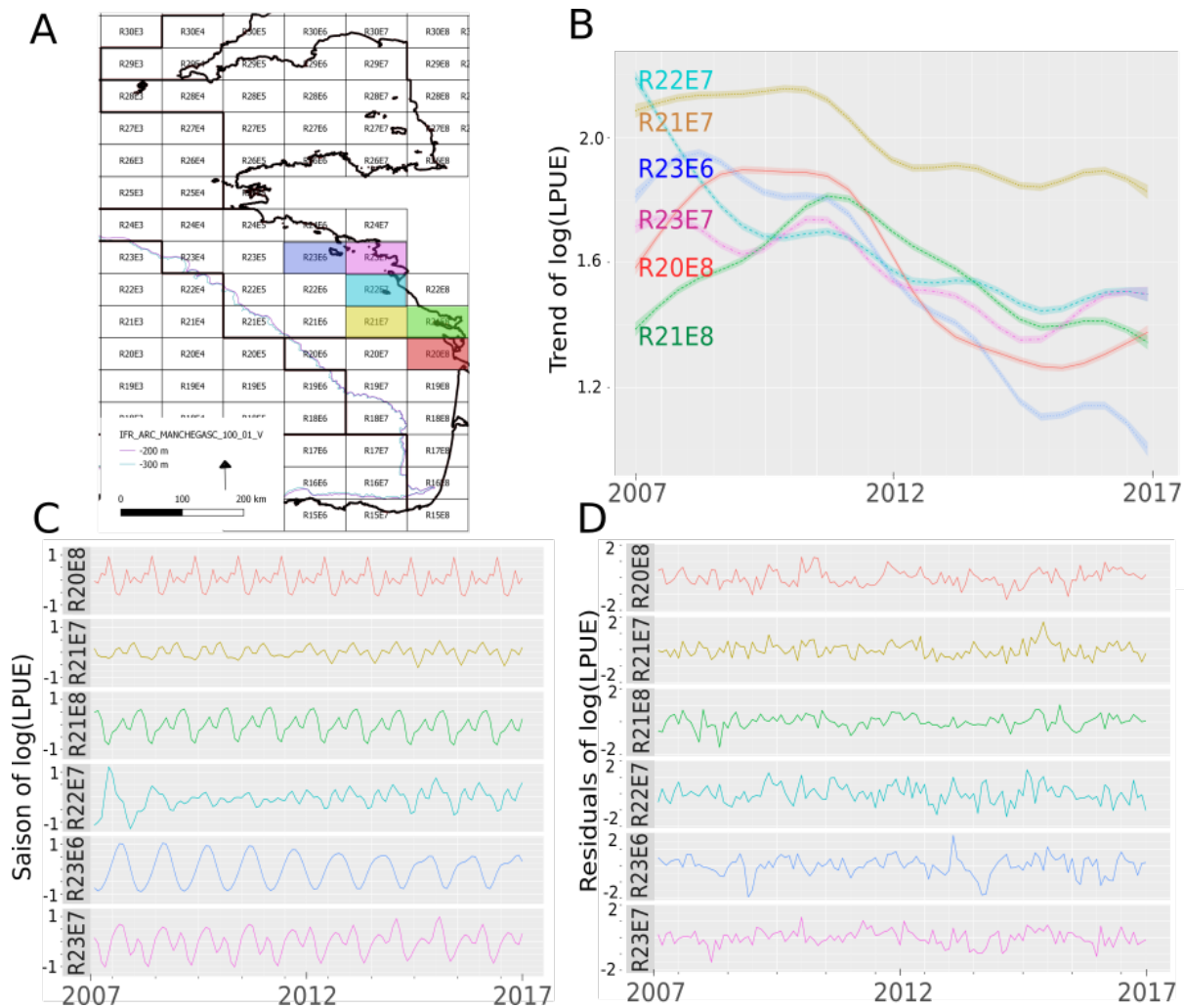


Figure 1: Time-series decomposition in striped red mullet abundance. A: Map of studied rectangles. B, C and D: Long Term Trend (LTT) and associated GAM error, Seasonal Trend (ST) and Residual (R) of  $\log(LPUE)$  by ICES statistical rectangle, respectively.

237 Figure 1A presents the locations of the ICES rectangles in this study. Data were recorded from 01/01/2005  
 238 to 12/31/2018. Due to moving average processing, the two first and the two last years of data were deleted.  
 239 Data are so presented from 01/01/2007 to 12/31/2016. The first observation in Figure 1B was an overall  
 240 decreasing of  $\widehat{LTT}$  of  $\log(LPUE)$  during time, with an average value of approximately 20 % between 2006  
 241 and 2017. To go further we used a linear model by rectangle to assess the ability of  $\widehat{LTT}$  to explain initial  
 242  $\log(LPUE)$ .  $\widehat{LTT}$  variable is significant (p-value < 0.01) in almost all linear models to explain  $\log(LPUE)$   
 243 data, but not for rectangles R23R7 and R22E7. A finer analysis of Figure 1B revealed a significant spatial  
 244 variability in time evolution of striped red mullet abundance with three main periods: 2006-2010, 2010-2014  
 245 and 2014-2017. First, during the 2006-2010 period, R23E7, R23E6 and R21E7 showed weakly fluctuating  
 246 values, R20E8 and R21E8, situated at the southeast of the study area, showed a significant increase and

247 R22E7 showed a clear decreasing trend. The second and third periods, respectively 2010-2014 and 2014-  
248 2017, showed more spatial consistency. The former period was characterized by a global decrease for all  
249 zones while the latter period showed overall more stable values.

250 Seasonal patterns computed using Equation 3 also highlighted spatial variability, see Figure 1C. Sig-  
251 nificant intra-annual fluctuations were observed for most ICES rectangles. A striking observation was the  
252 time and space variability of these seasonal fluctuations. Such variability in the frequency domain calls for  
253 more detailed spectral analysis which will be presented in Section 3.3. The only zone clearly dominated by  
254 uni-modal distribution is R23E6, i.e. the most north-westerly rectangle studied. Other rectangles showed  
255 additional periodic bi-modal or higher frequencies fluctuations. The time-change was also spatially variable,  
256 with a quite steady seasonal shape for R20E8, R21E8, R23E6 and R23E7 rectangles and more visible change  
257 for R21E7 and R22E7. For this latter area, the seasonal signal nearly drops to zero between 2009 and 2011  
258 before regaining values similar to other zones.

259 Figure 1D shows decomposition residuals. For all sites, the residuals did not exhibit any discernible pat-  
260 tern. This confirmed that the selected additive decomposition had extracted most of the relevant information  
261 in the striped red mullet abundance time-series.

### 262 3.2. Long term effects

263 Figure 2 depicted the comparison between  $\widehat{LTT}$ s for striped red mullet abundance and selected environ-  
264 mental covariates. Results were first presented in qualitative terms, while a more quantitative analysis is  
265 provided hereafter by the linear model.  $\widehat{LTT}$  for  $\log(LPUE)$  was described and compared in the previous  
266 section (see Figure 1B).  $\widehat{LTT}$  for environmental covariates generally shown a strong spatial variability. The  
267 surface salinity (MS) was lower for coastal rectangles R23E7, R21E8 and R20E8 due to the continental  
268 freshwater inputs, in particular by the Garonne and Charente rivers. For most rectangles, the overall trend  
269 was a slight decrease of salinity affected by a rise during the 2010-2012 period. The surface temperature  
270 (MT) shown the expected meridional variation (higher temperature in the south) and an overall increase for  
271 all rectangles. For the northern areas (R23E6, R23E7 and R22E7), the temperature tended to vary in the  
272 opposite way to the salinity: low temperatures were associated with high salinity during the 2009-2012 period  
273 while rising temperatures were associated with lowering salinity after 2012. This trend was less marked for  
274 the southern rectangles. The PCA-reduced environmental variables were generally well connected in space.  
275  $\widehat{LTT}$  for PC1, PC2 and PC3 were maximal in coastal regions R21E8, R20E8 and R22E7 and decreased off-  
276 shore in R21E7 and R23E6. The only exception was the R23E7 coastal rectangle for which PC1 was maximal  
277 while PC2 and PC3 was minimal. Changes over time for PC1 were generally very weak. Stronger dynamics  
278 were observed for PC2, for which low values were associated with low temperatures and high salinity events  
279 and, inversely, to rise after 2012 when salinity/temperature are generally decreasing/increasing. For PC3,  
280 the signal was nearly stable for R20E8 and R21E7 and mainly decreasing for R21E8, R22E7 and R23E6,  
281 without any straightforward relation with other environmental covariates. For R23E7, PC3 followed PC2  
282 trends, with a strong link with surface temperature.

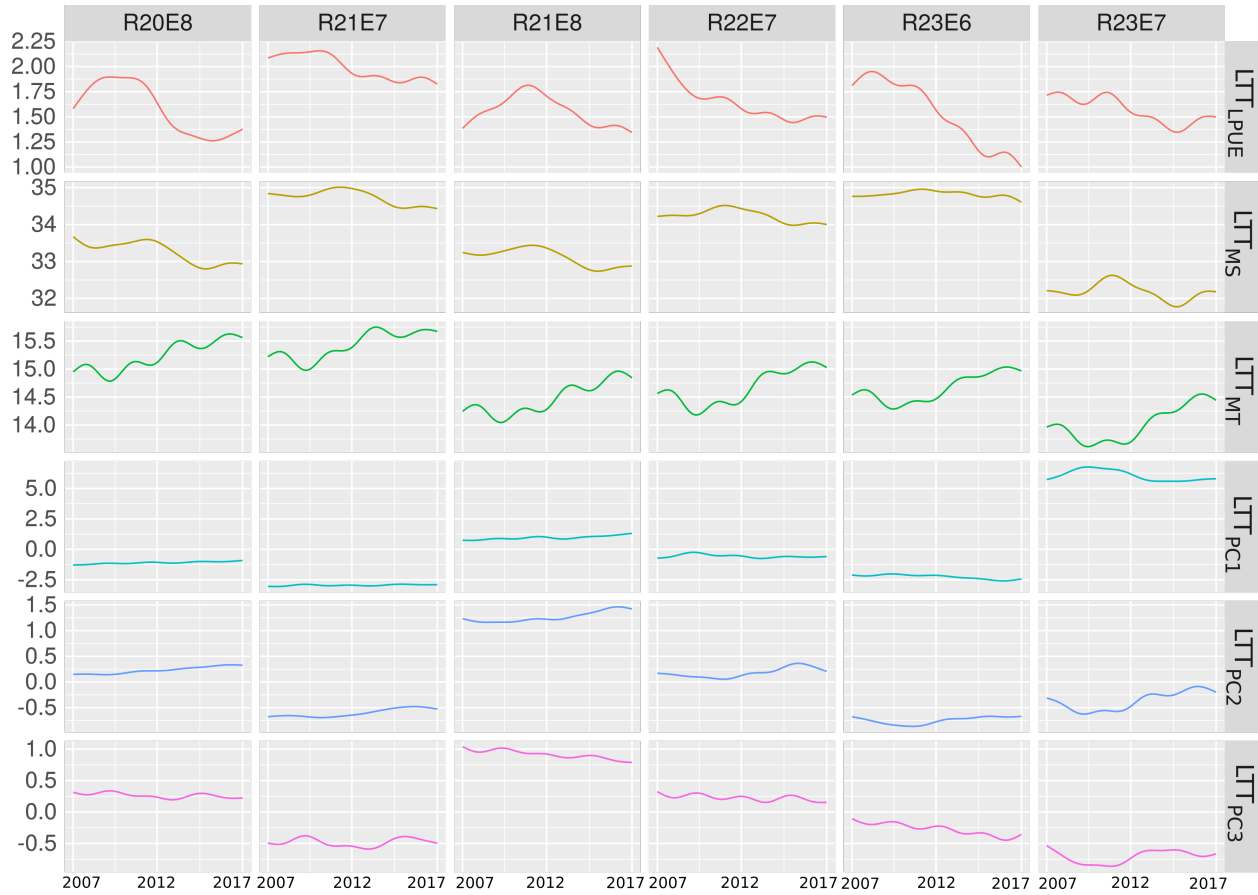


Figure 2: Long Term Trends (LTT) for striped red mullet abundance and environmental covariates for all studied ICES rectangles. LPUE is landing per unit of effort, expressed in monthly mean of daily kg by rectangle, MS is salinity in grams per liter and MT is temperature in degrees Celsius.

283 The linear model presented in Equation (5) was used to assess quantitatively the relationships between  
 284  $\widehat{LTT}$  for striped red mullet abundance and environmental variables. The results were summarized in Table  
 285 2. The first observation was that all  $R^2$  values were above 0.8 (excepting R22E7 which shows  $R^2 = 0.65$ ),  
 286 meaning that trends in environmental variables were able to explain at least 80% of trends in striped red  
 287 mullet abundance. Note that these  $R^2$  values were not directly related to the raw data and they had to  
 288 be interpreted on the explained variance of the extracted long term trends  $\widehat{LTT}$  of the LPUE obtained  
 289 from 2 by the long term trends of environmental variables. Our main goal was to investigate and highlight  
 290 the importance of variables to explain striped red mullet LPUE. Another observation was that striped red  
 291 mullet abundances were predominantly positively affected by salinity for five out of six rectangles. For the  
 292 coastal rectangles R20E8, R21E08 and R23E7, striped red mullet abundance could be linked to continental  
 293 freshwater inputs. The role of temperature was mainly significant in the two northern zones R23E6 and  
 294 R23E7, with striped red mullet abundance favored by higher temperature. PC1 generally played a weak  
 295 role except in the most northwestern zone R23E6/R23E7. PC2 was negatively correlated to abundance  
 296 in all rectangles except the most southeastern ones R21E8 and R20E8. PC3 displayed stronger positive  
 297 correlations only for the northern zones R23E6, R23E7 and R22E7.

298 *Tab. 2 here*

299 3.3. Seasonality

300 Figure 1 revealed the spatial and temporal variability of the LPUE seasonal component using a bulk  
 301 harmonic approach. Further insight was provided by the spectral density computed, for each rectangle, over  
 302 the complete time series, see Figure 3. The spatial discrimination was straightforward: coastal rectangles  
 303 R20E8, R21E8 and R23E7 were the only ones to show both biannual (6-month period) and annual (12-  
 304 month period) fluctuations. The offshore rectangles R23E6 and R21E7 shown a single annual seasonality,  
 305 although less marked for R21E7 than for the northwestern R23E6. The remaining rectangle R22E7 had a  
 306 noisy spectral density. This lack of consistency for the spectrum was related to the fluctuations of seasonality,  
 307 both in amplitude and period, during the acquisition period revealed in Figure 1.

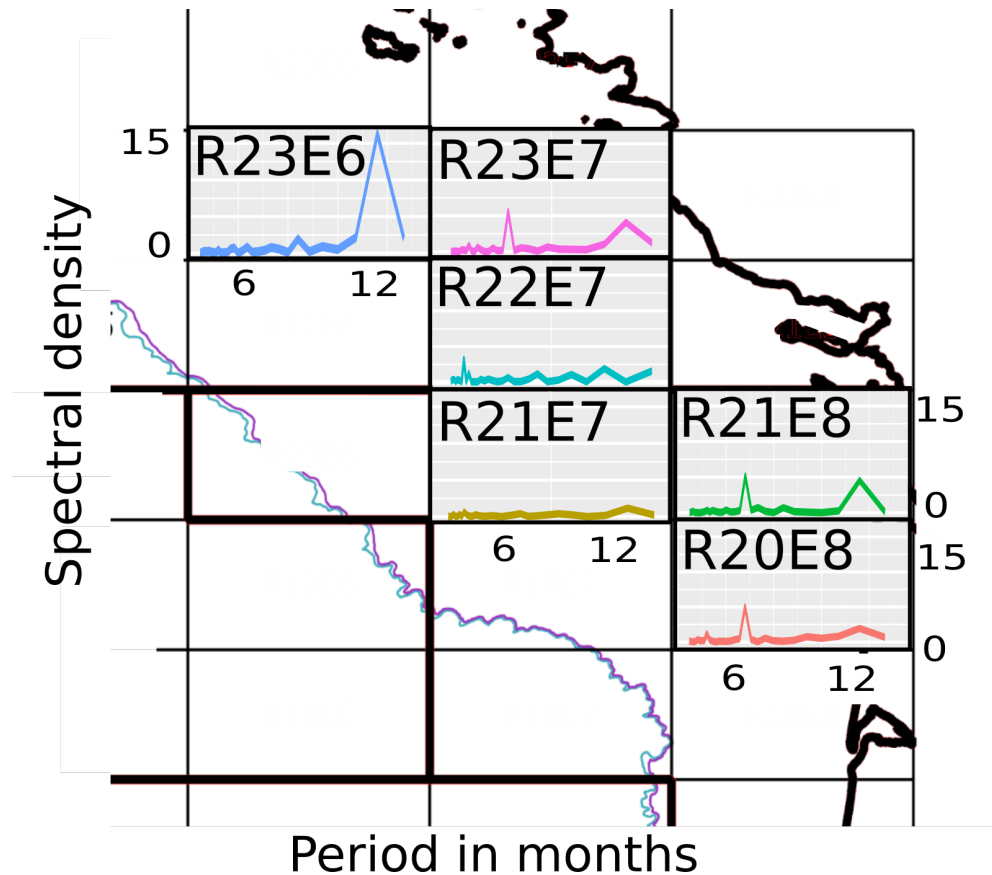


Figure 3: Spectral density of  $\log(LPUE)$  for each ICES rectangle over the complete time series.

308 Based on the time-resolved spectral density over a 48-month moving window, the amplitudes of annual  
 309 and biannual seasonal fluctuations (Eq. 4) were computed in each rectangle for  $\log(LPUE)$  and environmen-  
 310 tal covariates. An illustration of the results for rectangle R23E7 is presented in Figure 4. The spectral density  
 311 computed over the complete time-series (Figure 4A) revealed that the biannual (6-month) peak observed in  
 312  $\log(LPUE)$  can not be connected to any similar seasonal component in the selected set of environmental  
 313 covariates while the annual (12-month) peak in  $\log(LPUE)$  surely had a link with the annual peak observed  
 314 in all selected environmental covariates.

315  
 316 The time-resolved spectral analysis of biannual and annual fluctuations over a 48-month moving window  
 317 was shown in Figures 4B and C, respectively. Biannual seasonality of abundance was variable but the level  
 318 observed between the start and the end of the studied period did not show any trend and was qualitatively

319 uncorrelated to environmental covariates. Annual seasonality for  $\log(LPUE)$  shown slightly greater change  
 320 over time, with minimal values reached between 2009 and 2013. Annual seasonality for environmental  
 321 covariates also revealed more consistent patterns over time.

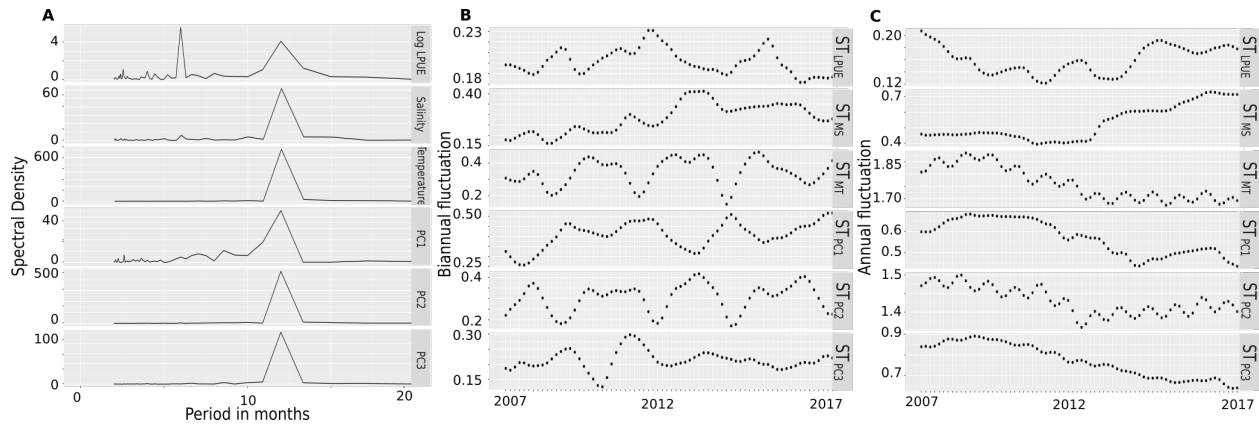


Figure 4: Time-frequency analysis for rectangle R23E7. A: spectral density for  $\log(LPUE)$  and environmental covariates over the full time-series. B and C: time-resolved magnitude of seasonal fluctuations over a 48-month moving window for biannual and annual components, respectively, for  $\log(LPUE)$  and environmental covariates.

322 The multivariate linear model presented in Equation 6 was used to evaluate comprehensively the rela-  
 323 tionship between abundance and covariate seasonality. Complete results were shown in Table 3.  
 324 Figure 3 previously demonstrated that the annual seasonality of striped red mullet abundance was well devel-  
 325 oped for rectangles R21E8, R23E6 and R23E7 and to a lesser extent for rectangles R20E8 and R21E7. Table  
 326 3 further indicates that the dependency of abundance seasonality on environmental covariates seasonality  
 327 was not systematic and not spatially uniform. PC1 annual seasonality appeared to affect abundance annual  
 328 seasonality in rectangles R20E8 and R23E6, with negative and positive correlations, respectively. R20E8  
 329 was furthermore connected to the annual fluctuations of salinity and temperature: abundance seasonality  
 330 was favored by strong temperature and weak salinity fluctuations. R21E7 and R21E8 were connected to  
 331 salinity and temperature annual fluctuations, respectively, while R23E7 annual seasonality did not show any  
 332 significant relation with environmental parameters.

333 Biannual seasonality of  $\log(LPUE)$  was well established in the three coastal rectangles R20E8, R21E8  
 334 and R23E7 (Fig.3). For the latter rectangle, the biannual seasonality was not related to environmental  
 335 covariates seasonality, similarly as for annual seasonality. PC1 biannual seasonality was observed to affect  
 336 both R20E8 and R21E8, while salinity biannual seasonality only affected R20E8.

337 *Tab. 3 here*

#### 338 4. Discussion

339 The aims of the present study were (i) to assess long-term and seasonal changes in striped red mullet  
 340 abundance in the Bay of Biscay, and (ii) to identify the possible relationships between changes in abundance  
 341 and environmental factors. This study was carried out on the basis of an indicator of abundance, which  
 342 was the sole information available for striped red mullet natural fish populations within the Bay of Biscay.  
 343 As no appropriate methodology to tackle this problematic with these data already existed in literature, we  
 344 had to develop a new one. Thus, the main aim of this study was not to present a new methodology, but  
 345 to better understand the effects of the environment on striped red mullet abundance. Here, we will discuss  
 346 results and compare them with other studies, but some conclusion will remain hypothetical due to a very  
 347 poor documentation in literature on the ecology of striped red mullet.

348

349 Long term trends were inferred from the abundance data using a moving average with a smoothing  
350 function. The resulting trends were clearly non-linear, thus ruling the use of linear approaches (see Hess  
351 (2001); Lentka and Smulko (2019) for trends detection). Seasonal components were processed using time-  
352 frequency analysis with moving-window spectral computations, which highlighted the strong fluctuations of  
353 the abundance seasonality both in space and time. Other tools for time-frequency analysis could have been  
354 used here such as the wavelet analysis (Huang et al., 1998). It is important to note that time-frequency  
355 analysis is strongly constrained by the need to have continuous and long enough time-series.  
356 The selected environmental variables also shown non-linear long term trends. These observations result from  
357 the complex interactions between a large number of processes affected by fluctuations over wide ranges of  
358 space and time scales which were outside of the scope of the present study. However, from a data-processing  
359 perspective, it is again worth noting to note that, in our study zone, coupled ocean-atmosphere systems such  
360 as the North-Atlantic Oscillation (NAO) (Hurrell, 1995) or other fluctuating large scale climate patterns  
361 (Castelle et al., 2017) provided additional variability to the global change track. For instance, the overall  
362 warming of the ocean surface observed from the present analysis of Copernicus database, well documented  
363 in the literature (Peck and Pinnegar, 2019; deCastro et al., 2009; Koutsikopoulos et al., 1998; Planque et al.,  
364 2003), combines with inter- and intra-annual oscillations and spatial variability. Similarly, salinity and PCA-  
365 reduced environmental variables showed strong time and space variability. Such results could be related  
366 with climate-driven patterns (Roessig et al., 2004) of atmosphere properties, precipitation, land runoff, river  
367 discharge, etc. This reinforces the relevance of the present approach to determine trends and relationships  
368 between fish populations and environmental factors.

369 the study of long term trends in striped red mullet abundance shown a high spatial heterogeneity within  
370 the Bay of Biscay even on a relatively small scale. The dominant trend was a decrease in striped red  
371 mullet abundance. This decrease varied among the studied ICES spatial rectangles. But, for almost all  
372 rectangles, we could link 80% of this trend variance to environmental covariates trends. The dependency on  
373 environmental covariates was also spatially variable. In coastal rectangles, long term trends of abundance  
374 can had a slight positive link with surface salinity trends. While for more off-shore rectangles, striped red  
375 mullet abundance increased along with salinity. Striped red mullet salinity preference was detected to be  
376 between 35.1 and 35.6 grams per liter (Desbrosses, 1935). These values were for adults fishes at depths  
377 between 100 and 200 meters. One possible explanation for positive link in trends between striped red mullet  
378 abundance and salinity in coastal rectangles is that the striped red mullet is at the lower limit of its salinity  
379 ecological niche in coastal rectangles (see table 1). When salinity decreases in coastal zones, due to inland  
380 freshwater inputs, striped red mullet abundance decreases. More precise information about the striped red  
381 mullet ecological niche is needed to consolidate this hypothesis of a positive link between striped red mullet  
382 abundance trends and salinity in coastal zones.

383 In the southern Bay of Biscay, striped red mullet have already been detected as species with an affinity  
384 for warm temperatures (García-Rodríguez et al., 2011). In our study area, in the northern Bay of Biscay,  
385 mean sea surface temperature was around 14.5 degrees Celsius for the colder rectangles and 15 degrees  
386 Celsius for the warmer rectangles. We did not detect links between temperature trends and striped red  
387 mullet abundance except for the two coldest rectangles. In these two northern rectangles, abundance trends  
388 decreased when temperature trends decreased and conversely, which tends to confirm the observation of  
389 García-Rodríguez et al. (2011). For a similar species *M. barbatus* in Aegean Sea, abundance has been proved  
390 to be higher in warm bottom water (19°C) than in colder waters (Maravelias et al., 2007). In addition, this  
391 species seems to avoid the cold bottom waters (< 16°C) (Maravelias et al., 2007). An hypothesis to explain  
392 the freshness of the two northern rectangles is they are in a river freshwater inputs and up-welling zone.  
393 This hypothesis is favoured by the study of Puillat et al. (2006) demonstrating some events of up-welling-  
394 favourable winds exactly in the zone were we found the lowest temperature, and a positive link with striped  
395 red mullet abundance. In these rectangles, red-mullet is at the edge of its favoured life condition regarding  
396 temperature. When water temperature decreases, striped red mullet falls outside its life *preferendum* and  
397 abundance decreases.

398 Up-welling and river discharges also induce chemical transports or dissolution from sediments. In this study,  
399 we have attempted to find a relationship between striped red mullet abundance and chemical concentrations

400 in the sea water. As strong correlations were initially observed between different chemical species, we chose  
401 to perform a dimension reduction with PCA. But, interpretation of linear model estimates of PCA reduced  
402 dimensions can be delicate. Only the two southern rectangles do not shown a link with PCA reduced  
403 dimensions. For the four other rectangles, trends in striped red mullet abundance were linked to chemicals  
404 and primary production. The link was positive with PC3. As PC3 had a positive contribution of  $O_2$   
405 concentration, we can say striped red mullet abundances were positively linked to  $O_2$  concentration. This  
406 result is consistent with studies highlighting an increase of capture probability of an other mullet species  
407 along with dissolved oxygen rate (Maes et al., 2007). In the four northern rectangles, trends in striped  
408 red mullet abundance were also positively linked with PC1. PC1 is built from a negative contribution of  
409  $Si$ ,  $PO_4^{3-}$  and  $NH_4^+$ , meaning that striped red mullet abundance was negatively linked to  $Si$ ,  $PO_4^{3-}$  and  
410  $NH_4^+$  concentrations. The effect of chemicals, phytoplankton and net primary production rates on striped  
411 red mullet abundance were never investigated. Further investigations are required to confirm the present  
412 original observations.

413 The seasonal study revealed high variability of striped red mullet abundance seasonality within the  
414 Bay of Biscay. In the most off-shore rectangle, striped red mullet abundance shown well defined annual  
415 oscillations while in the most shoreward ICES rectangles, additional biannual oscillations were observed.  
416 In the two remaining ICES rectangles, no clear periodic pattern was observed. Multiple peaks per year  
417 when studying seasonality in fisheries stock abundance were already reported in the case of multiple species  
418 studies (Hsieh et al., 2009), but such a variability for a single species was not reported before, to the best  
419 of our knowledge. One peak in seasonality of annual abundance occurred at intermediate depth. Following  
420 the literature on striped red mullet ecology, spawning commonly occurs in spring and early summer (May  
421 and June) (Desbrosses, 1935; N'Da and Déniel, 1993; Mahé et al., 2005; Leaute et al., 2018). Even if  
422 massive movement of spawners during reproduction has not been reported for striped red mullet, our best  
423 hypothesis regarding the annual seasonal peak in striped red mullet abundance may reflect movements during  
424 reproduction process. But, to our knowledge, it has to date never been statistically proven. We also modeled  
425 this one peak annual seasonal fluctuation of striped red mullet abundance along with similar environmental  
426 annual seasonal fluctuations. This dependency was not systematic and not spatially uniform. Temperature  
427 was the most relevant parameter linked with seasonal fluctuation in our study, but it was only significant  
428 in three rectangles. This result supports our hypothesis of the annual spawning peak. Higher sea water  
429 temperature has been reported during striped red mullet spawning in Israel and Canary Islands (Suquet and  
430 Person-Le Ruyet, 2001). For Brittany, striped red mullet spawning is observed in relation with increasing  
431 photo-period and temperature (Suquet and Person-Le Ruyet, 2001). One hypothesis is that the second peak  
432 may be explained by the recruitment process corresponding to the arrival in the catches of the individuals  
433 born the year before. This hypothesis is supported by the fact that biannual abundance seasonality occurs in  
434 shallow coastal rectangles and that multiple recruitment peaks have also been observed for different species  
435 (see, for example Abella et al. (1995) or Hatfield (1996)). We tried to model the biannual peak of seasonality  
436 in striped red mullet abundance with the corresponding peak in environmental covariates but we were not  
437 able to link the three coastal rectangles to the same set of environmental variables. One rectangle can be  
438 linked to low fluctuation of PC1, one to low fluctuation of PC3 and the third to all variables excepting  
439 PC3. The two rectangles where no seasonality was detected are in deep zones. Seasonality of striped red  
440 mullet abundance was clearly depth driven. Further studies will be needed to better reveal the link between  
441 seasonality in striped red mullet abundance and environmental variables.

442 A critical issue for a deeper understanding of the dependency of fish abundance on the oceanic variable is  
443 the proper definition of space and time scales. The focus was here on the Bay of Biscay over the 2005-2018  
444 period. The Copernicus database used to define environmental covariates revealed a mean increasing trend of  
445 surface temperature over the considered period, following a century-long tendency (Garcia-Soto and Pingree,  
446 2012) for the Bay of Biscay. This trend may appear contradictory with the large scale decrease of North  
447 Atlantic sea surface temperature noted for instance by Piecuch et al. (2017) over the 2005-2015 period, but  
448 is indeed an indicator of the heterogeneity of the ocean dynamics. This underlines that any generalization of  
449 local findings should be made with particular caution and vice versa. [From an ecological point of view, the use  
450 of ICES rectangles to study the impact of the environment on the red mullet population in the Bay of Biscay](#)

451 raises questions. ICES rectangles correspond to the finest spatial mesh common to the mandatory declarative  
452 data of fishermen and not homogeneous ecological units. For example, several habitats may be represented  
453 in the same rectangle or conversely, a single habitat may occupy several rectangles. The development of an  
454 habitat-delimited analysis will certainly be a fruitful but ambitious and long-term challenge. The present  
455 study was strictly bounded by the source data, i.e. by the fishermen’s logbooks and fishing forms filled in  
456 by ICES rectangle. Moreover there is a crucial need to simultaneously dynamically refine and extend in  
457 space and time the mapping of both marine environmental parameters and fish abundance. Developing a  
458 model for such a small portion of the ocean is useful to be able to understand the effect of environmental  
459 changes on local fisheries. At this scale, most of the fisheries are local small industries. Understanding  
460 the link between environment and resources preserves local socio-economic activities, and it is of very high  
461 importance. While costly, such an approach appears now to be a prerequisite to decipher the response of  
462 marine fauna to the fluctuations of ocean variables. This is already true for the relationships existing at the  
463 present time (García-Barón et al., 2020; Véron et al., 2020) and it will become even more necessary to move  
464 forward towards a resource-preserving marine spatial planning strategy in the context of global change.

465 The approach we developed to tackle our applied research question can be applied in a wide range of  
466 fish population studies, in order to monitor the effect of climate change on fish population distribution  
467 at various scales and to help fishermen anticipate changes. The analysis was carried out from abundance  
468 time-series, which is the sole information available for a number of natural fish populations. It had also  
469 been performed considering the main environmental factors available over the study area, mainly focused in  
470 the surface layers. When available, additional factors can be easily implemented and tested such as more  
471 complete three-dimensional information (Assis et al., 2016). For the study of striped red mullet, knowledge  
472 on benthic habitat composition (Ajemian et al., 2016) or on substrate type (Lombarte et al., 2000; Mahé  
473 et al., 2005) can improve the study. Substrate type layer is not yet available for the entire Bay of Biscay.  
474 One perspective will be to include new layers in this study, once one is available. **Finally, a comprehensive  
475 understanding of the time-resolved population dynamics should encompass each driving factor, including  
476 trophic web parameters and additional mortality causes.**

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481 Mathematical and Statistical Frontiers (ACEMS). The data that support the findings of this study is openly  
482 available in SEANOE (Kermorvant et al., 2020).

483 We do not declare any conflict of interest.

## 6. Tables

Table 1: Main statistical values of two environmental variables (temperature and salinity) recorded over the 2005–2018 period in the selected ICES rectangles. Temperature is expressed in degrees Celcius, salinity in grams of salt per liter of water

		<b>R20E8</b>	<b>R21E7</b>	<b>R21E8</b>	<b>R22E7</b>	<b>R23E6</b>	<b>R23E7</b>
<b>Salinity</b>	<b>Min</b>	28.51	32.36	29.10	31.80	32.27	26.76
	<b>Max</b>	34.65	35.72	34.57	35.53	35.67	34.58
	<b>Med</b>	33.17	34.85	33.12	34.13	34.80	32.10
	<b>Sd</b>	1.27	0.67	0.88	0.66	0.65	1.52
<b>Temperature</b>	<b>Min</b>	7.32	8.56	7.09	7.76	8.57	7.32
	<b>Max</b>	22.16	22.54	21.22	21.64	21.52	20.89
	<b>Med</b>	15.26	15.25	14.85	14.84	14.44	14.47
	<b>Sd</b>	4.23	3.77	4.16	3.79	3.34	3.80



Table 2: Results of the linear model to assess the relationship between long term trends of stripped red mullet abundance and environmental variables. Models estimates ( $\beta$ ), P-values,  $R^2$  and relative importance (Imp) of variables obtained with linear models on each rectangle. Results with P-values  $< 0.005$  are in bold. Standard deviations of models estimates are available in appendix.

	Type	Intercept	$\widehat{LTT}_{MS}$	$\widehat{LTT}_{MT}$	$\widehat{LTT}_{PC1}$	$\widehat{LTT}_{PC2}$	$\widehat{LTT}_{PC3}$	$R^2$
<b>R20E8</b>	$\beta$	-6.906	0.433	-0.35	0.438	-0.879	0.373	.
	P_value	0.358	<b>&lt;0.001</b>	0.219	0.141	0.337	0.611	.
	Imp.	.	0.231	0.246	0.102	0.214	0.069	0.862
<b>R21E7</b>	$\beta$	-7.495	0.102	0.205	-0.873	-1.739	1.743	.
	P_value	0.036	0.142	0.1	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	.
	Imp.	.	0.147	0.308	0.083	0.295	0.069	0.902
<b>R21E8</b>	$\beta$	-15.951	0.524	0.071	0.358	-0.731	-0.31	.
	P_value	0.004	<b>&lt;0.001</b>	0.772	0.096	0.097	0.67	.
	Imp.	.	0.366	0.163	0.051	0.162	0.087	0.828
<b>R22E7</b>	$\beta$	31.395	-0.959	0.177	-0.842	-3.379	2.824	.
	P_value	0.011	<b>&lt;0.001</b>	0.618	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>0.002</b>	.
	Imp.	.	0.091	0.153	0.077	0.19	0.136	0.647
<b>R23E6</b>	$\beta$	-56.003	0.732	1.855	-1.067	-5.673	6.577	.
	P_value	<b>&lt;0.001</b>	<b>0.001</b>	<b>&lt;0.001</b>	<b>0.003</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	.
	Imp.	.	0.04	0.214	0.22	0.164	0.254	0.892
<b>R23E7</b>	$\beta$	-23.493	0.434	0.632	0.574	-0.922	2.213	.
	P_value	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	.
	Imp.	.	0.215	0.14	0.207	0.16	0.15	0.8725

Table 3: Results of the linear model to assess the relationship between seasonal trends of stripped red mullet abundance and environmental variables. Model estimates( $\beta$ ), P-values,  $R^2$  and relative importance (Imp) of environmental covariates seasonality in abundance seasonality obtained with lm models on each rectangles. ".12" and ".6" notations correspond to the annual and biannual fluctuations, respectively. Results with p-values  $< 0.005$  are in bold. Standard deviations of models estimates are available in appendix.

	Type	Intercept	$\widehat{ST}_{MS}$	$\widehat{ST}_{MT}$	$\widehat{ST}_{PC1}$	$\widehat{ST}_{PC2}$	$\widehat{ST}_{PC3}$	$R^2$
<b>R20E8.6</b>	$\beta$	0.171	0.063	0.077	-0.365	0.298	0.069	.
	P_value	<b>&lt;0.001</b>	0.441	0.031	<b>&lt;0.001</b>	0.008	0.598	.
	Imp.	.	0.009	0.119	0.146	0.059	0.051	0.383
<b>R20E8.12</b>	$\beta$	-0.167	-0.28	0.278	-0.721	-0.207	0.462	.
	P_value	0.087	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.456	<b>0.003</b>	.
	Imp.	.	0.152	0.28	0.272	0.27	0.008	0.982
<b>R21E7.6</b>	$\beta$	0.141	-0.271	-0.045	-0.182	0.2	-0.056	.
	P_value	<b>&lt;0.001</b>	<b>0.002</b>	0.006	<b>&lt;0.001</b>	0.007	0.286	.
	Imp.	.	0.167	0.088	0.244	0.075	0.095	0.668
<b>R21E7.12</b>	$\beta$	0.232	0.225	-0.141	0.073	0.64	-0.212	.
	P_value	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.177	0.571	0.161	0.404	.
	Imp.	.	0.289	0.04	0.034	0.057	0.046	0.466
<b>R21E8.6</b>	$\beta$	0.343	-0.765	-0.193	-0.906	0.629	0.024	.
	P_value	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.895	.
	Imp.	.	0.261	0.089	0.138	0.069	0.012	0.569
<b>R21E8.12</b>	$\beta$	0.227	0.16	-0.25	0.123	-0.018	0.693	.
	P_value	0.011	0.014	<b>&lt;0.001</b>	<b>0.004</b>	0.877	<b>&lt;0.001</b>	.
	Imp.	.	0.144	0.305	0.1	0.266	0.095	0.910
<b>R22E7.6</b>	$\beta$	0.152	-0.128	-0.006	0.087	0.092	-0.24	.
	P_value	<b>&lt;0.001</b>	0.231	0.82	0.07	0.062	<b>0.002</b>	.
	Imp.	.	0.015	0.044	0.021	0.025	0.123	0.229
<b>R22E7.12</b>	$\beta$	0.648	0.478	0.37	0.157	-0.973	-1.629	.
	P_value	<b>&lt;0.001</b>	0.252	<b>0.003</b>	0.253	<b>&lt;0.001</b>	<b>&lt;0.001</b>	.
	Imp.	.	0.102	0.068	0.027	0.066	0.256	0.520
<b>R23E6.6</b>	$\beta$	0.103	-0.026	-0.08	0.26	-0.236	0.24	.
	P_value	0.012	0.897	0.128	0.211	0.253	0.089	.
	Imp.	.	0.008	0.023	0.054	0.012	0.078	0.175
<b>R23E6.12</b>	$\beta$	0.403	-0.131	-0.248	1.124	-0.588	-0.092	.
	P_value	<b>0.003</b>	0.647	0.026	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.456	.
	Imp.	.	0.032	0.243	0.409	0.036	0.241	0.961
<b>R23E7.6</b>	$\beta$	0.183	-0.024	0.068	-0.016	-0.076	0.148	.
	P_value	<b>&lt;0.001</b>	0.307	<b>0.001</b>	0.505	<b>0.004</b>	<b>0.002</b>	.
	Imp.	.	0.02	0.072	0.007	0.097	0.077	0.273
<b>R23E7.12</b>	$\beta$	-0.341	0.025	0.241	-0.228	0.192	-0.106	.
	P_value	<b>0.002</b>	0.532	0.029	<b>0.005</b>	0.13	0.347	.
	Imp.	.	0.097	0.074	0.131	0.057	0.084	0.442

## 7. Figure legends

Figure 1: Time-series decomposition in striped red mullet abundance. A: Map of studied rectangles. B, C and D: Long Term Trend ( $\widehat{LTT}$ ), Seasonal Trend (ST) and Residual (R) of  $\log(LPUE)$  by ICES statistical rectangle, respectively.

Figure 2: Long Term Trends ( $\widehat{LTT}$ ) for striped red mullet abundance and environmental covariates for all studied ICES rectangle. LPUE is landing per unit of effort, expressed in monthly mean of daily kg by rectangle MS is salinity in gram per liter and MT is temperature in degree Celsius, PC1, PC2 and PC3 are the

three first axes of PCA of phytoplankton concentration, chlorophyll concentration, and chemicals variables. Figure 3: Spectral density of  $\log(LPUE)$  for each ICES rectangle over the complete time series. Figure 4: Time-frequency analysis for rectangle R23E7. A: spectral density for  $\log(LPUE)$  and environmental covariates over the full time-series. B and C: time-resolved magnitude of seasonal fluctuations over a 48-month moving window for biannual and annual components, respectively, for  $\log(LPUE)$  and environmental covariates. MS is salinity in gram per liter and MT is temperature in degree Celsius, PC1, PC2 and PC3 are the three first axes of PCA of phytoplankton concentration, chlorophyll concentration, and chemicals variables.

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