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## Environmental drivers influencing the abundance of round sardinella (*Sardinella aurita*) and European sprat (*Sprattus sprattus*) in different areas of the Mediterranean Sea

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3 **Environmental drivers influencing the abundance of round sardinella (*Sardinella aurita*) and**  
4 **European sprat (*Sprattus sprattus*) in different areas of the Mediterranean Sea**

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20 **Abstract**

21 Data on *Sardinella aurita* (round sardinella) and *Sprattus sprattus* (European sprat) in the  
22 Mediterranean Sea are limited due to their scarce commercial interest, at least in European  
23 countries. Yet, these two small pelagic fish, sitting at opposite ends of the thermal range, could be  
24 interesting sentinel species to monitor the effects of climate change in the basin. Using the  
25 Mediterranean International Acoustic Surveys (MEDIAS) – the most extensive source of  
26 information on these species – we analysed their biomass in several geographical subareas of the  
27 central and western Mediterranean Sea in relation to satellite-derived environmental parameters.  
28 Our findings highlight that the *S. aurita* biomass responded to temperature, salinity, chlorophyll

29 concentration and sea level anomaly, depending on the GSA examined, whereas the *S. sprattus*  
30 biomass correlated significantly with salinity in GSA 6, with salinity and chlorophyll concentration  
31 in GSA 7 and with sea level anomaly in GSA 17. These data widen our knowledge of the factors  
32 that contribute to the ecology of these species. Further studies of their spatial distribution and of  
33 their interactions with other small pelagic species, predators and prey are needed to depict a more  
34 comprehensive scenario.

35 **Keywords:** *Sardinella aurita*, *Sprattus sprattus*, environmental factors, acoustic survey,  
36 temporal trends

## 37 **Introduction**

38 Most animal species use migration as a response to climate change, moving towards more  
39 favourable habitats (Poloczanska *et al.*, 2013). This is even truer in the oceans (Lenoir *et al.*, 2020)  
40 and for mobile species such as small pelagic fish (Checkley *et al.*, 2009). Yet, animals already  
41 living at one end of the thermal range may face major problems. The Mediterranean Sea is a semi-  
42 enclosed basin, where the mean water temperature has been showing clear annual and seasonal  
43 upward trends (Azzurro *et al.*, 2011, 2019; Moullec *et al.*, 2019). Whereas the fish inhabiting the  
44 southern Mediterranean coasts can move northward, what will happen to cold-favouring species  
45 living in the northernmost area of the basin? *Sardinella aurita* (round sardinella) and *Sprattus*  
46 *sprattus* (European sprat), two small pelagic species with opposite environmental requirements  
47 throughout their life cycle, have the potential to supply some answers. Little work has been  
48 conducted on these species in the Mediterranean Sea due to their limited commercial value, at least  
49 in the European portion of the Mediterranean. Yet, they have an important ecological role, since  
50 they lie in an intermediate position between planktonic organisms and larger fish, thus contributing  
51 to transfer energy from lower to higher trophic levels (Cury *et al.*, 2000; Bakun, 2006; Coll *et al.*,  
52 2007). Accordingly, any change in their spatial distribution due to climate change has the potential  
53 to alter the entire pelagic ecosystem. Since *S. sprattus* prefers cold waters (MacKenzie *et al.*, 2007;  
54 Petereit *et al.*, 2008) and *S. aurita*, a boreal species, favours warm waters (Sabates *et al.*, 2006;  
55 Palomera *et al.*, 2007; Zgozi *et al.*, 2018), they are rarely found in the same area. In the recent past,  
56 *S. sprattus* has mainly been described in the northern Mediterranean Sea (Tičina *et al.*, 2000),  
57 whereas *S. aurita* has predominantly been found in the southern areas of the basin (Tsikliras *et al.*,  
58 2005; Tsikliras, 2008). If the current trend continues in the future, *S. aurita* is expected to spread to  
59 and settle in the northernmost parts of the basin, as recently described in the north-western (Sabates  
60 *et al.*, 2006) and north-eastern Mediterranean (Tsikliras, 2008). As regards *S. sprattus*, its habitat  
61 could shrink so significantly, through a *cul de sac* effect, as to place it at risk of extinction (Ben  
62 Rais Lasram *et al.*, 2010; Albouy *et al.*, 2012).

63 Still, climate change does not only involve warming, and several other environmental factors,  
64 combined with climate change, can affect the dynamics of small pelagic species. For instance, the  
65 recruitment of *S. aurita* off the Senegalese coast is mostly favoured by coastal upwelling (Diankha  
66 *et al.*, 2017), with surface temperature, chlorophyll concentration, the North Atlantic oscillation  
67 index and wind-induced turbulence also playing important roles. In the Balearic Sea, the recent  
68 increase in mean temperature and salinity and declining chlorophyll concentrations seem to have  
69 favoured *S. aurita*, at least in coastal areas (Maynou *et al.*, 2019). Notably, mass mortality of the  
70 species in the Adriatic and Ionian Seas has been related to low sea temperature (below 10° C) and  
71 strong bora winds (Guidetti *et al.*, 2002). As regards *S. sprattus*, in the Baltic Sea it has proved  
72 sensitive to temperature changes, which may affect growth, reproduction and survival (Frisk *et al.*,  
73 2015; Parmanne *et al.*, 1994); notably, salinity also influenced its stock size, although the latter  
74 effect may be indirect, due to environmental factors acting on the mesozooplankton community  
75 (Cardinale *et al.*, 2002; MacKenzie *et al.*, 2007). In the Black Sea, sprat recruitment correlates  
76 strongly with parental biomass and sea level atmospheric pressure, but an influence of sea surface  
77 temperature, wind speed, zonal wind stress and river run-off has also been described (Daskalov,  
78 1999). However, the negative influence of surface temperature, reported by Daskalov (1999), might  
79 be an indirect effect caused by water convection, which supplies nutrients to the upper layers. The  
80 analysis of recruitment rates in relation to environmental variables in winter indicated that such  
81 effect is more intense at low ambient temperature.

82 These examples demonstrate that the two species are sensitive to environmental changes.

83 This work was conducted to study the possible influence of environmental parameters on the  
84 biomass of these two small pelagic species in seven representative areas of the western and central  
85 Mediterranean Sea. Their preference for the opposite ends of the thermal range in the basin makes  
86 *S. aurita* and *S. sprattus* interesting sentinels of climate change in this area.

87 **Materials and methods**

88 *Biomass estimates from acoustic surveys*

89 Annual biomass estimates of *S. aurita* and *S. sprattus* were obtained from acoustic surveys  
90 conducted in several coastal areas of the Mediterranean Sea, in the framework of the Mediterranean  
91 International Acoustic Surveys (MEDIAS) programme according to the EU Data Collection  
92 Framework (Leonori *et al.*, 2012; Giannoulaki *et al.*, 2013; Brosset *et al.*, 2017). The data  
93 considered in this paper were collected in the western Adriatic Sea, Geographical Subarea (GSA)  
94 17 (GFCM, 2009), by Italy's CNR IRBIM (formerly ISMAR); in the eastern Adriatic Sea (GSA 17)  
95 by Croatia's IOF; in Northern Spain (GSA 6) and the Northern Alboran Sea (GSA 1) by Spain's  
96 IEO; in the Gulf of Lions (GSA 7) by France's IFREMER; and in the Ligurian and Tyrrhenian Seas  
97 (GSAs 9 and 10) and the Strait of Sicily (GSA 16) by Italy's CNR IAS (formerly IAMC), as shown  
98 in Fig. 1.

99

100 The surveys have been standardized through a common protocol since 2008 (see the latest MEDIAS  
101 Handbook, 2021). The data from 2009 to 2018, used in this work, come from the standardized  
102 MEDIAS programme conducted since 2009. Data from surveys conducted before 2009 were used  
103 only if the modifications, introduced for harmonization with the MEDIAS protocol, involved minor  
104 changes. This was the case of GSAs 7, 16 and 17. In contrast, since in Spanish waters the shift of  
105 the survey period from November-December to June-July was considered to involve a major  
106 change, only data from 2009 onwards were used for this area. When the harmonization affected  
107 data analysis rather than survey design, such as when a common target strength (TS) for sardine  
108 was defined in 2012, past data were reanalysed and revised annual estimates produced. In such  
109 cases, estimates obtained before and after the start of the MEDIAS programme were assumed to be  
110 comparable.

111 The main frequency of the scientific echosounder used for biomass calculation was 38 kHz, the  
112 standard international frequency employed to estimate the biomass of small pelagic fish. In

113 accordance with the MEDIAS protocol, noise and reverberation were removed by means of specific  
114 filters or manually, based on the researchers' experience with the software used for acoustic data  
115 analysis. Echo trace classification was based on visual scrutinization of the echograms by means of  
116 direct allocation and allocation on the basis of representative fishing stations. The inherent  
117 uncertainty associated with this and other processes involved in biomass estimation from acoustic  
118 surveys was expressed through the calculation of a coefficient of variation by means of an R routine  
119 according to Walline (2007). As regards the conversion of acoustic density into biomass, the  $b_{20}$   
120 values relative to the TS equation used in the different GSAs were either identical (*S. aurita*) or  
121 very similar (from -72.6 to -71.2 dB for *S. sprattus*), as listed in Table 1. Since most analyses were  
122 made separately for each GSA, the slightly different  $b_{20}$  values are not expected to alter the results.

123

#### 124 *Species and areas*

125 *S. sprattus* was predominantly found in the northern GSAs (6, 7 and 17), whereas *S. aurita* was  
126 mainly found in the southern GSAs 1, 10 and 16 (Table 1). The northward expansion of *S. aurita*,  
127 described in the past few years, was confirmed by its detection in GSAs 6 and 9. However, since its  
128 abundance in the Adriatic Sea has consistently been low for about three decades (Mustać &  
129 Sinovčić, 2012), data on *S. aurita* in the Adriatic Sea were not included in the analysis.

130

#### 131 *Satellite environmental data*

132 Temperature (T), salinity (S), chlorophyll concentration (Chl) and sea level anomaly (Sla) data were  
133 provided by the Copernicus Marine Service Information (<http://marine.copernicus.eu/>). Data *per*  
134 depth stratum and *per* GSA were used with a horizontal resolution of  $1/16^\circ \times 1/16^\circ$  of degree (~ 6.5  
135 km) and 72 unevenly spaced vertical levels (Simoncelli *et al.*, 2019; Teruzzi *et al.*, 2019). The depth  
136 strata were spaced unevenly along the water column; their thickness ranged from 3 m at the surface  
137 (depth, 1.5 m) to 300 m at the bottom (depth, 5,000 m).

138 The environmental data were extracted using SeaDAS software (v. 7.4) at 4 depth strata (surface, 30  
139 m, 50 m and 100 m) based on the authors' knowledge of the spatial distribution pattern of each  
140 species. Notably, in the survey season the bulk of the *S. aurita* and *S. sprattus* populations reside in  
141 the shallower part of the shelf ( $\leq 100$  m bathymetry). The two intermediate strata (30 m and 50 m)  
142 were examined to obtain a more exhaustive picture and to try to identify the one exerting the  
143 strongest influence on abundance. Notably, the layer at 30 m is often associated with the  
144 thermocline, at least in the GSAs explored in this work. Finally, a stratum at 150 m was also  
145 considered in GSA 7, where *S. sprattus* has been recorded at this depth (Saraux *et al.*, 2014).  
146 Hereafter, the depth layers of the environmental variables will be presented as subscripts (*e.g.*  
147 surface temperature,  $T_{\text{sup}}$ ; temperature at 30 m,  $T_{30}$ ). Fish biomass was also explored using the  
148 environmental parameters recorded during the month of the survey and in the previous reproductive  
149 season. The previous reproductive season was the summer preceding the survey for *S. aurita*  
150 (average of the monthly means from June to September,  $T_{\text{sup}_S}$ ) and the winter prior to survey  
151 execution for *S. sprattus* (average of the monthly means from December to March,  $T_{\text{sup}_W}$ ).

152

### 153 ***Statistical analysis***

154 First of all, to identify a potential environmental context justifying the presence of one target  
155 species with respect to the other, we conducted a Principal Component Analysis (PCA) over the  
156 whole set of environmental data, combining means over the survey month and the average of the  
157 previous reproductive period in all seven GSAs.

158 After this preliminary overview, we performed more detailed and separate analyses for each GSA  
159 using the statistical software Minitab 19. We first considered the annual biomass of each species in  
160 relation to the average environmental parameters of the survey month, to find any environmental  
161 factors inducing fast responses in abundance. Secondly, we considered the biomass estimation in  
162 relation to the environmental parameters of the reproductive season prior to survey execution  
163 (summer for *S. aurita* and winter for *S. sprattus*), to identify possible delayed influences of the



164 environmental parameters on biomass through effects on larval survival. We tried to fit linear  
165 models (LMs) in each GSA. The LMs were run with a forward selection procedure, based on  
166 minimization of Akaike's information criterion corrected for small sample sizes and on the  
167 Bayesian information criterion, to avoid an excessive number of explanatory variables compared  
168 with the size of the sample. To exclude multicollinearity of the environmental parameters, we  
169 checked that the variance inflation factor of the variables was  $< 5$ , as suggested by Rogerson  
170 (2001). Finally, we checked residuals and the goodness of fit of the models to evaluate model fit. In  
171 particular, the normality of residuals was assessed through q-q plots and density plots, whereas the  
172 presence of temporal autocorrelation was assessed *via* estimation of the partial autocorrelation of  
173 residuals. Whenever autocorrelation was present (a violation of LM assumptions merely reflecting  
174 the fact that biomass in a given year depends on the biomass of the previous year independently of  
175 the environment), the LMs were run again, adding the biomass of the previous year as a covariate.  
176 This simple method allowed removing autocorrelation from the residuals.

177 For the GSAs for which the data series was less than 10 years, we performed a power analysis with  
178 the R package WebPower (Zhang *et al.*, 2018), to learn which  $\alpha$  value would be more appropriate  
179 according to the number of observations in each GSA, hypothesizing a minimum effect size equal  
180 to 4 (corresponding to an  $R^2$  of 0.8). Models showing a predicted  $R^2$  equal to 0 were discarded due  
181 to insufficient robustness.

182 The autocorrelation function (ACF) and the partial autocorrelation function (PACF) were tested on  
183 log-transformed fish biomass data and on normalized environmental data through a Z-score  
184 standardization (Glantz *et al.*, 2016). Subsequently, cross-correlation function (CCF) analysis was  
185 performed to obtain further information on any delayed relationships between biomass and the  
186 environmental parameters; to avoid spurious correlations with a strong delayed effect of the  
187 environmental variables, only results with time lags of 0 to 2 were considered. Significance  
188 thresholds for CCF analysis were set according to the length of the historical data series, as follows:

189 0.75 for GSA 9, 0.70 for GSA 10, 0.65 for GSAs 1 and 6, 0.475 for GSAs 16 and 17 and 0.425 for  
190 GSA 7.

191

192

193

## 194 **Results**

### 195 *Biomass evolution of the studied species*

196 The fluctuations of *S. aurita* and *S. sprattus* biomass in the seven GSAs are reported in Fig. 2.

197 In the more southern areas (GSAs 1 and 16), the biomass of *S. aurita* exhibited fairly wide  
198 fluctuations, whereas in the northern areas (GSAs 6 and 9) it showed a recent increase. In GSA 1,  
199 peaks (5,715 t in 2012, 10,978 t in 2015 and 7,560 t in 2018) alternated with troughs, with broad  
200 fluctuations that were characterized by a constant periodicity of three years. In GSA 16, biomass  
201 peaked in 2005 (8,127 t) and 2010 (9,721 t) and subsequently decreased. In GSA 6 fluctuations  
202 were smaller and around very low values; values then peaked (27,291 t) in 2017 and declined again  
203 (15,641 t) in 2018. Similarly, in 2009-2018 the biomass of *S. aurita* in GSA 10 showed an upward  
204 trend from fairly low values to 5,590 t and 5,106 t in 2017 and 2018, respectively.

205 The biomass of *S. sprattus* in GSA 6 was fairly low in 2010-2018, except for a peak (29,504 t) in  
206 2013 and a lower peak (13,678 t) in 2018. A similar trend was detected in GSA 7 in the final part of  
207 the period, since the historical series for this area is much longer. Abundance increased from fairly  
208 low values to a peak (70,263 t) in 2013; it then declined, to rise again in 2017-2018 (32,104 t in  
209 2018). In GSA 17, it showed irregular fluctuations with a peak (167,831 t) in 2006 and two lower  
210 peaks (81,219 t) in 2011 and (69,815 t) 2014.

211

### 212 *Principal Component Analysis results of pooled data from all GSAs*

213 The PCA results are reported in Fig. 3. PC1 explains 46.5% of the variance and shows the highest  
214 negative correlations with  $T_{sup}$ ,  $T_{30}$  and  $T_{50}$ , whereas the highest positive correlations were with

215 Chl<sub>sup</sub> and Chl<sub>30</sub>. PC2 explains 24.6% of the variance and shows a predominant positive correlation  
216 with S<sub>sup</sub>, whereas the highest negative correlation was with Chl<sub>50</sub>. In other words, the first  
217 component contrasts warm waters with cold, rich waters, whereas the second component contrasts  
218 high-salinity waters with low production at 50 m. Along the first axis, winter and summer values  
219 were distinct and showed a clear seasonal difference in temperature and primary production in all  
220 seven GSAs. When focusing on summer values, clear distinction could also be made among GSAs.  
221 First, a north-south gradient could be identified along the first axis, ranging from cooler and more  
222 productive waters (GSAs 7 and 17) to warmer and less productive waters (GSAs 10, 16, 6 and 9).  
223 Secondly, GSA 1 was clearly isolated from the other GSAs with negative PC1 and very low PC2  
224 values.

225

#### 226 *S. aurita*

227 To overcome the problem of autocorrelation in the model residuals, the *S. aurita* biomass of the  
228 previous year was added as a covariate in both models fitted for GSA 1 (Northern Alboran Sea).  
229 The goodness of fit of the model that included the survey month data was quite good (Table 2),  
230 presenting an adjusted R<sup>2</sup> of 67.1%, of which around 10% was attributed to biomass at t-1. Chl<sub>sup</sub>  
231 showed a negative and highly significant correlation with biomass (Table 3). The model including  
232 the average values of the summer before the survey showed an adjusted R<sup>2</sup> of 49.34%; also in this  
233 case, biomass at t-1 had to be included in the model; T<sub>30</sub> and Sla showed respectively a negative and  
234 a positive correlation with biomass.

235 CCF analysis highlighted a further relationship with T<sub>sup\_S</sub> of the previous year with a time lag k=2  
236 (Fig. 4A), *i.e.* cooler surface temperature 3 summers before resulted in higher *S. aurita* biomass.

237

238 In GSA 6 (Northern Spain), biomass at t-1 was added to the model to remove the autocorrelation  
239 initially present in the regression residuals. None of the environmental variables of the survey  
240 month were retained by the model and the same applied to the average values of the summer before

241 the survey; moreover, CCF analysis found no significant relationship between biomass and the  
242 environmental parameters.

243

244 In GSA 9 (Northern Tyrrhenian Sea), application of forward selection retained no environmental  
245 variable in either model. CCF analysis highlighted no significant correlation between biomass and  
246 the environmental parameters.

247 In GSA 10 (Southern Tyrrhenian Sea), the final model that included the survey month data  
248 presented an adjusted  $R^2$  of 43.9% and showed a significant positive correlation between biomass  
249 and  $T_{100}$  (Tables 2 and 3). The model with the average values of the environmental parameters the  
250 previous summer yielded an adjusted  $R^2$  of 80.9%, where  $S_{sup}$  showed a positive correlation and  
251  $S_{100}$  a negative correlation with biomass, although neither correlation was highly significant (Tables  
252 2 and 3); moreover,  $T_{100}$  and  $S_{1a}$  also presented a positive correlation.

253 CCF analysis yielded the same result as the LM including the survey month data (Fig. 4B).

254

255 In GSA 16 (Sicily Channel), while no variable averaged over the survey month was retained to  
256 explain *S. aurita* biomass,  $T_{100}$  of the previous summer presented a highly significant negative  
257 correlation with *S. aurita* biomass ( $R^2$  adjusted = 52.34%; Tables 2 and 3).

258 Significant results obtained through CCF are given in Fig. 3C; these were the relationships with  
259 surface salinity during the survey ( $S_{sup}$ ,  $k=0$ ), surface salinity of two summers before ( $S_{sup\_S}$ ,  $k=1$ ),  
260 temperature at 100 m of antecedent summer ( $T_{100\_S}$ ,  $k=0$ ), and salinity at 100 m of antecedent  
261 summer ( $S_{100\_S}$ ,  $k=0$ ).

262

### 263 *S. sprattus*

264 In GSA 6 (Northern Spain), the model including the survey month data showed an adjusted  $R^2$  of  
265 49.2% (Table 2), with a significant positive relationship between biomass and  $S_{50}$  (Table 3). The  
266 model with the average data from the winter prior to the survey yielded no significant results.

267 CCF analysis confirmed the significant relationship between biomass and  $S_{50}$  highlighted by the  
268 LM and also one with  $S_{100}$  ( $k=0$ ); the former relationship was strengthened by the correlation  
269 between biomass and  $S_{50}$  of two winters before ( $k=1$ ) (Fig. 5A).

270

271 In GSA 7 (Gulf of Lions), the model with the survey month data yielded an adjusted  $R^2$  value of  
272 29.3% (Table 2); biomass showed a highly significant positive relationship with  $S_{150}$  (Table 3). The  
273 model with the average data of the previous winter showed an adjusted  $R^2$  of 43.7%; again, biomass  
274 showed a highly positive significant relationship with  $S_{150}$  (Tables 2 and 3).

275 According to CCF analysis, only  $Chl_{50}$  showed a significant positive correlation with a time lag of 1  
276 (Fig. 5B).

277

278 In GSA 17 (Northern Adriatic Sea), the model including the survey month data and the average data  
279 from the winter before the survey retained no terms after forward selection.

280 CCF analysis highlighted significant relationships with  $Sla$  and  $Sla_w$  (both  $k=1$ ) (Fig. 5C).

281

282 The significant results of the regression analysis in each GSA are listed in Table 4. The results of  
283 CCF analysis are reported in Table 5.

284

## 285 **Discussion**

286 This study was devised to identify the environmental drivers that affect the abundance of *S. aurita*  
287 and *S. sprattus*, two small pelagic fish, in some geographical subareas of the Mediterranean. Given  
288 their opposite thermal preferences, we expected that temperature would emerge as the most  
289 important variable. In fact, data analysis indicated that in some areas other parameters also played a  
290 major role. A further goal of the study was to gain insights into the possible future spatial  
291 distribution of the two species in a warming Mediterranean Sea.

292

293 ***Principal Component Analysis in pooled data from all GSAs***

294 PCA grouped the seven GSAs into three sets based on shared environmental traits:

- 295 • GSA 1, warm but quite productive and less saline waters (only *S. aurita* found here)
- 296 • GSAs 9, 10 and 16, warm and less productive waters (only *S. aurita* found here)
- 297 • GSAs 7 and 17, cool and more productive waters (only *S. sprattus* found here).

298 These results agree with earlier reports that *S. aurita* prefers warmer waters whereas *S. sprattus*  
299 generally favours colder and productive waters (Frisk *et al.*, 2015; Maynou *et al.*, 2019).  
300 Interestingly, GSA 6, the only area where both species were consistently present, had intermediate  
301 environmental traits between GSAs 9, 10 and 16 on one side and GSAs 7 and 17 on the other, since  
302 the summer values of GSA 6 are closer to those of the former group and the winter values are more  
303 similar to those of the latter.

304

305 ***S. aurita***

306 Different environmental parameters affected the biomass of *S. aurita* in the seven GSAs,  
307 temperature at 100 m being the parameter that most frequently correlated with biomass.

308 In the Northern Alboran Sea (GSA 1), forward selection analysis identified a significant negative  
309 relationship between biomass and surface chlorophyll. Since the chlorophyll concentration is  
310 directly related to zooplankton abundance (Yebra *et al.*, 2020; Oguz *et al.*, 2014), a negative  
311 correlation with biomass may be interpreted in terms of typical predator-prey interactions, with the  
312 alternate peaks and troughs reflecting the slightly delayed reactions of predators (*S. aurita*) to  
313 increases/reductions in plankton abundance.

314 The forward selection analysis results showed a negative correlation between biomass and  
315 temperature at 30 m. CCF analysis yielded a similar result, namely a negative correlation with  
316 average surface temperature the summer before the survey. This finding contrasts with several  
317 works associating higher temperatures with higher *S. aurita* abundance (Maynou *et al.*, 2019;  
318 Sabatès *et al.*, 2009). However, at least in the case of CCF analysis, the negative correlation and the

319 time lag (2+1 year of time shift) do not seem to indicate a strong relationship, since biomass is  
320 unlikely to be influenced by the surface temperature of three years previously. Forward selection  
321 analysis also identified a positive correlation with sea level anomaly; this is a highly productive  
322 area, where the inflow of nutrients-rich Atlantic waters confers important hydrographic mesoscale  
323 features (Albo-Puigserver *et al.*, 2021) and exerts an influence on the trophic web from planktonic  
324 organisms upwards, possibly also enhancing the abundance of *S. aurita* and of other small pelagic  
325 fish.

326

327 In GSA 10 (Southern Tyrrhenian Sea), temperature at 100 m showed a positive significant  
328 relationship with biomass. This was confirmed by CCF analysis, which identified a positive  
329 significant correlation with no time lag between abundance and average temperature at 100 m in the  
330 month of the survey; in fact, in GSA 10 *S. aurita* is still found at a depth of 100 m (A. Bonanno,  
331 personal communication). Although the temperature near the bottom did appear to exert an  
332 influence on biomass, the limited data available for this subarea prevented drawing firm  
333 conclusions. In GSA 10, biomass increased in the past few years; so did water temperature at 100  
334 m, though not in the higher strata. The biomass data collected in this subarea confirm the general  
335 tendency of this species to expand northwards as a result of the recent temperature increase. There  
336 were also significant correlations with surface salinity and salinity at 100 m in the summer prior to  
337 survey execution; this could affect the buoyancy of *S. aurita* eggs and larvae, with different effects  
338 on surface (positive relationship) and deeper layers (negative relationship). Altogether, data on *S.*  
339 *aurita* behaviour in relation to the environment are limited, except for some information on feeding  
340 habits (Lomiri *et al.*, 2007). In GSA 10, *S. aurita* may spawn near the 100 m bathymetry, which is  
341 not very distant from the coast, given the narrow continental shelf. The temperature increase may  
342 have enhanced spawning and egg development conditions; a similar effect, albeit on a longer time  
343 scale, may have been exerted by salinity (Palomera *et al.*, 2007). A possible interpretation of the

344 positive correlation with sea level anomaly is that local gyres may favour plankton enrichment, thus  
345 contributing to increase the biomass of small pelagic fish.

346

347 In the Strait of Sicily (GSA 16), multiple regression analysis showed that temperature at 100 m the  
348 summer before survey execution exhibited a highly significant negative relationship with biomass.  
349 CCF analysis confirmed the relationship, albeit with the average values of the summer prior to the  
350 survey. Other CCF results show a positive correlation with surface salinity (both in the survey  
351 month and the previous summer) and a negative correlation with salinity at 100 m the previous  
352 summer. Although the above findings seem to contrast with the habitat preferences of *S. aurita*  
353 (Palomera *et al.*, 2007; Tsikliras, 2008; Maynou *et al.*, 2019), the results for the Strait of Sicily  
354 should be interpreted in relation to coastal upwelling, the main enrichment process in this GSA  
355 (Bonanno *et al.*, 2014; Basilone *et al.*, 2017). Here, the effects of coastal upwelling on temperature  
356 and salinity have already been described (*e.g.* Patti *et al.*, 2010; Bonanno *et al.*, 2014); in particular,  
357 lower temperature and higher salinity values are found mainly along the south-western coast of  
358 Sicily in summer, whereas the eastern coast is less influenced by the process (Bonanno *et al.*, 2014).  
359 Furthermore, the easternmost area of the Strait of Sicily (the Sicilian-Maltese platform) is affected  
360 by the Atlantic Ionian Stream (Robinson *et al.*, 1999), a fresher water vein of Atlantic origin, which  
361 exerts a strong influence on the upper layer circulation. Studies of *S. aurita* spatial distribution (Ben  
362 Abdallah *et al.*, 2018; Zgozi *et al.*, 2018) have described a more abundant presence in the Sicilian-  
363 Maltese platform, where temperatures are higher than in the rest of GSA 16. Taking into account  
364 the complexity of this area from an oceanographic point of view, the obtained relationships could be  
365 masked when considering the average environmental values in the area. A spatially explicit  
366 approach would probably help to account for the effects of these variables on *S. aurita* biomass.

367

368 *Sprattus sprattus*



369 The biomass of *S. sprattus* correlated with different environmental parameters in different GSAs; in  
370 particular, salinity was the key parameter in GSAs 6 and 7, whereas sea level anomaly showed a  
371 significant correlation in GSA 17.

372 In Northern Spain (GSA 6), *S. sprattus* abundance showed a positive correlation with average  
373 salinity at 50 m in the month of the survey. Moreover, CCF analysis indicated that it positively  
374 correlated with average salinity at 50 and 100 m in the survey month; the result was strengthened by  
375 a similar correlation with average salinity at 50 m the previous winter. In GSA 6, *S. sprattus* favours  
376 the area near the coast; it is scarce from 100 m to 150 m and is not found further down. Its  
377 concentrations are highest in the Gulf of Rosas – which may be affected by environmental  
378 influences from the Gulf of Lions – and in the Ebro Delta, mainly its northern part (Vives & Suau,  
379 1956; MEDIAS Report, 2019), which is strongly influenced by river runoff. Since the sprat biomass  
380 showed a positive correlation with salinity, its abundance is unlikely to be favoured by higher  
381 riverine (*i.e.* nutrients) inputs. A possible explanation is that a different, and more advantageous,  
382 plankton composition is available in years characterized by less abundant river runoff and higher  
383 salinity.

384 Based on stomach content, the *S. sprattus* diet – at least in winter in the Adriatic Sea during the  
385 spawning season – seems to be dominated by copepods (Tičina *et al.*, 2000). In the Baltic Sea, the  
386 copepod biomass has been reported to decline with decreasing salinity (Vuorinen *et al.*, 1998). A  
387 possible explanation for our findings is that when salinity decreases, due to higher riverine inputs,  
388 local conditions may favour other small pelagic species (*e.g.* anchovy and sardine in the  
389 Mediterranean Sea), which compete with *S. sprattus* for the same ecological niche; the opposite  
390 would happen in case of lower riverine inputs and increasing local salinity (Feuilloley *et al.*, 2020).  
391 A greater knowledge of phytoplankton and zooplankton composition in the previous years and of  
392 the dietary preferences of the various small pelagic species would allow verifying this hypothesis.  
393 Biomass correlated significantly with salinity in the deeper strata of the water column. This may  
394 simply be due to the similar salinity values at different depths in GSA 6; however, the conditions

395 affecting *S. sprattus* biomass most strongly are probably those found in the first 50 m. Collection of  
396 regional data, especially in GSA 6 – whose northern and southern parts differ considerably in  
397 oceanographic patterns and species presence – would also allow exploring the characteristic  
398 features of each area and provide insights into the dynamics of these species. The salinity values in  
399 the winter before the survey could exert a major effect on egg development, duration and survival  
400 by acting on their buoyancy, thus indirectly influencing the survival of this crucial life stage  
401 (Petereit *et al.*, 2009); in particular, greater buoyancy propels them upwards, to a layer characterized  
402 by more favourable temperature and dissolved oxygen conditions for egg development and larval  
403 survival.

404 In the Gulf of Lions (GSA 7), the models including the data of the month of the survey and the  
405 average values of the environmental parameters of the previous winter both showed that biomass  
406 had a significant positive relationship with salinity at 150 m. In this area, *S. sprattus* is abundant  
407 throughout the continental shelf, without a clear gradient related to river inputs (MEDIAS report,  
408 2019). Since its abundance correlated positively with salinity, the same hypothesis advanced for  
409 GSA 6 could apply here, also considering that the two subareas are contiguous. Given the very  
410 similar salinity trends found at different depths in GSA 7, it is conceivable that the strongest  
411 influence on *S. sprattus* biomass is exerted by surface salinity and that the relationship with  $S_{150}$  is  
412 only due to statistical selection to avoid collinearity. Based on our findings, salinity should exert  
413 effects both on juveniles and adults. Interestingly, *S. sprattus* showed similar trends in GSAs 6 and  
414 7 and relationships between biomass and salinity were highlighted in both areas. These findings  
415 deserve further investigation.

416 As regards CCF analysis, the only significant positive correlation was with average chlorophyll  
417 concentration at 50 m in the month of the survey. Its time lag of 1 indicates that the chlorophyll  
418 concentration positively influenced *S. sprattus* biomass the following year. Even though *S. sprattus*  
419 does not seem to concentrate around river estuaries, a higher abundance of phytoplankton, and  
420 consequently of zooplankton, is likely to result in higher *S. sprattus* abundance in this area.

421

422 In the Northern Adriatic Sea (GSA 17), the multiple regression analysis highlighted no significant  
423 relationship between biomass and the environmental parameters. CCF analysis showed a significant  
424 negative correlation with sea level anomaly in the survey month of the previous year and with the  
425 average winter values of two years before. These correlations seem to indicate that the sprat  
426 biomass in GSA 17 could be influenced by the circulation dynamics of the water masses.

427 The Adriatic Sea circulation is dominated by two currents, the West Adriatic Current, which flows  
428 in southeast direction along the western coast, and the East Adriatic Current, which flows in  
429 northwest direction along the eastern coast (Artegiani *et al.*, 1997a, b). Cyclonic and, to a lesser  
430 extent, anticyclonic gyres are also present. Some are temporary, like those that form between  
431 Trieste and Rovinj after strong bora events (Kuzmic *et al.*, 2006); others last longer, albeit showing  
432 different seasonal current velocities, like the three cyclonic gyres identified from the north to the  
433 south Adriatic (Poulain, 2001). The dynamics of these gyres, especially those lasting longer, may  
434 favour local enrichment processes in the areas where *S. sprattus* is abundant due to plankton  
435 transport. At the local scale, wind action could also generate upwelling of colder, denser and food-  
436 rich waters near the coast that would combine with nutrients-rich river inputs which in the northern  
437 Adriatic Sea are particularly robust. The negative correlations between biomass and sea level  
438 anomaly in GSA 17 could indicate an effect of strong local gyres on plankton composition, which  
439 would favour other small pelagic species thus exerting a negative influence on the sprat biomass.

440

441 As a final general comment, since several ecological factors influence the dynamics of small  
442 pelagic species (Planque *et al.*, 2011), this preliminary analysis of the environmental parameters  
443 driving the biomass of *S. aurita* and *S. sprattus* requires integration with data on competitors,  
444 predators and prey.

445

446 **Conclusions**

447 Due to their scarce commercial interest, data on *S. aurita* and *S. sprattus* are limited in the European  
448 part of the Mediterranean Sea. Yet, these species play an important role in the trophic chain and  
449 their abundance is very likely to affect the stocks of several other species, including commercially  
450 valuable ones. The biomass of *S. aurita* was found to be influenced by temperature in GSAs 1, 10  
451 and 16, by salinity in GSAs 10 and 16, by sea level anomaly in GSAs 1 and 10 and by chlorophyll  
452 concentration in GSA 1. The *S. sprattus* biomass correlated with salinity, chlorophyll concentration  
453 and sea level anomaly, depending on the area. Our findings confirm that the stocks of the two  
454 species depend strongly on environmental factors and would considerably be strengthened by  
455 information on how the species interact with each other and with predators and prey. The  
456 indications provided by the analysis of our dataset warrant further investigation.

457

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464

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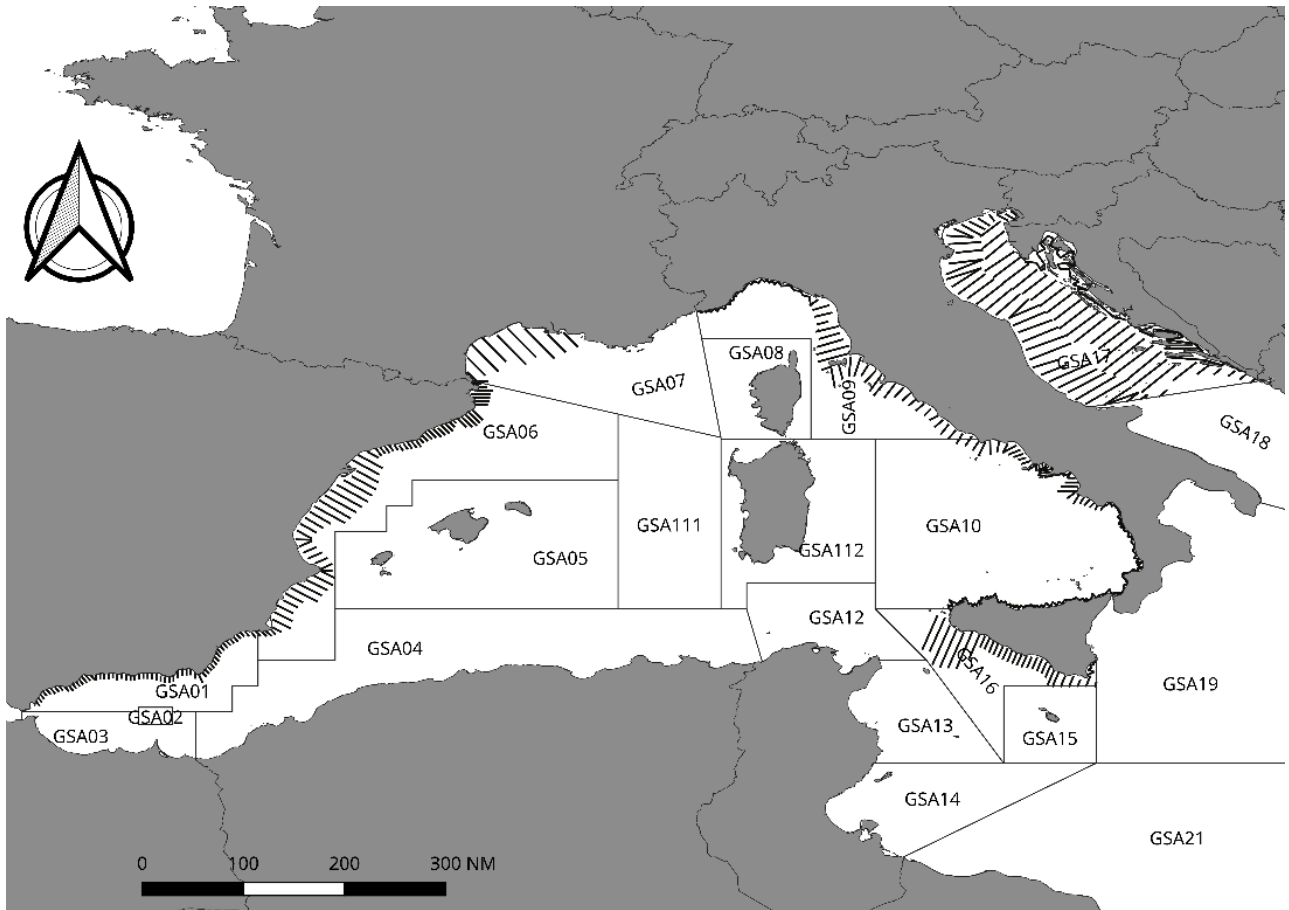
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613 Fig. 1. MEDIAS surveys transects conducted in the Geographical Subareas (GFCM, 2009)

614 considered in this work.

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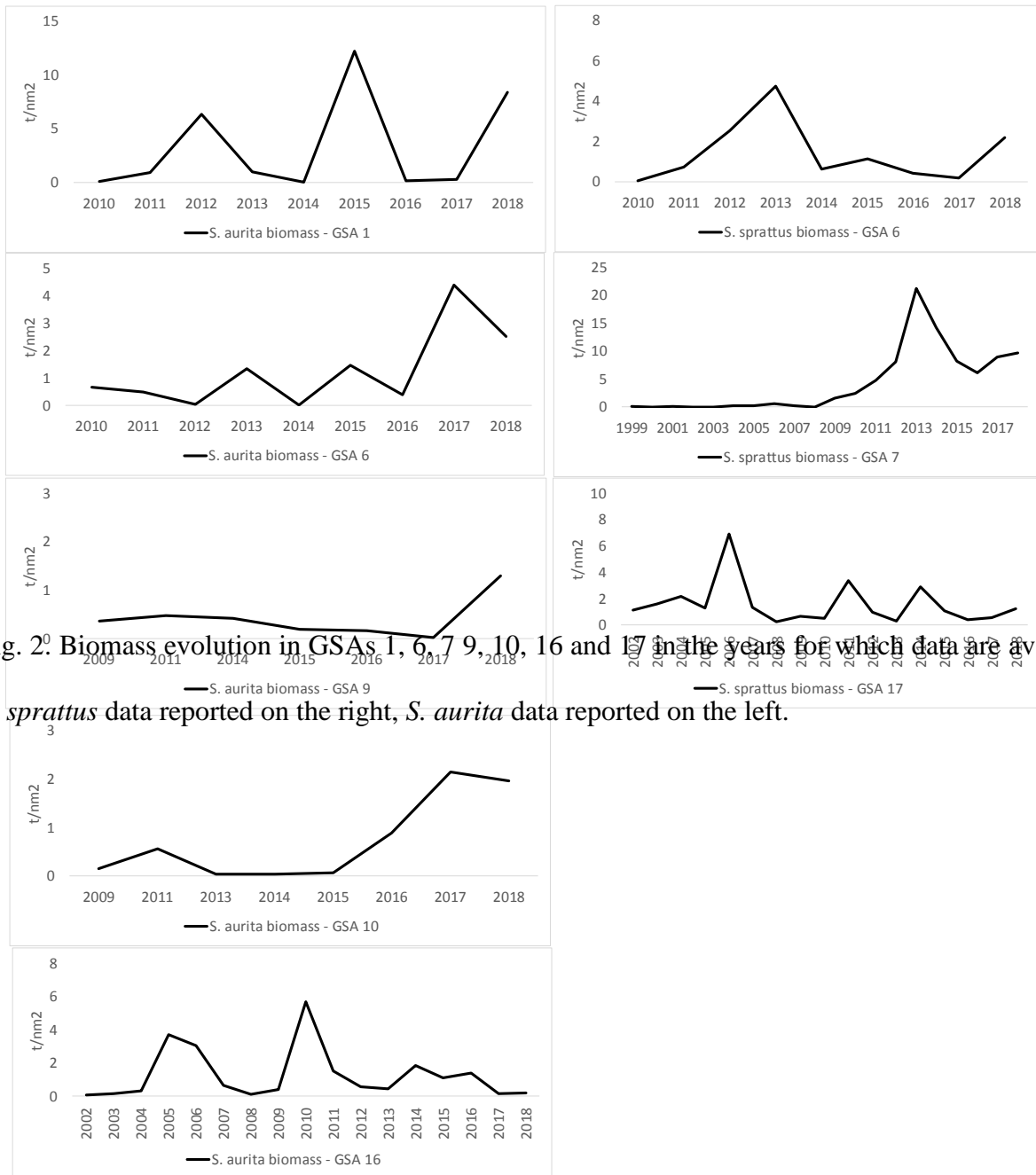
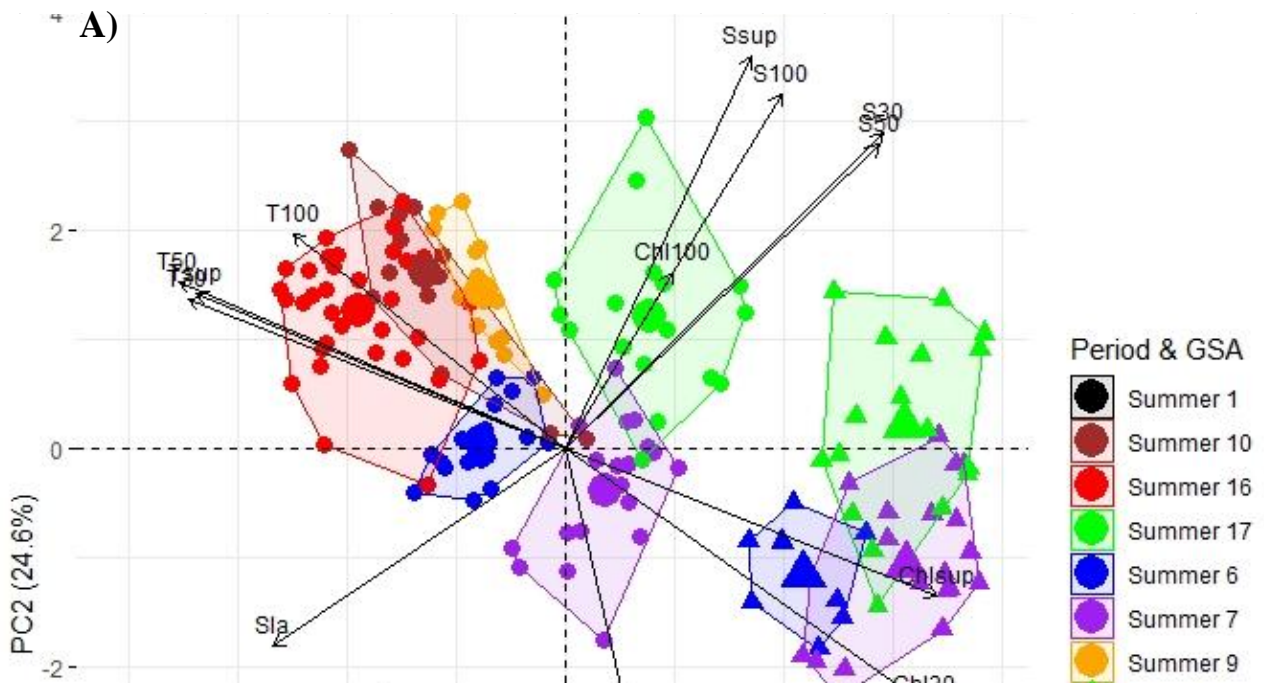


Fig. 2. Biomass evolution in GSAs 1, 6, 7, 9, 10, 16 and 17 in the years for which data are available.

*S. sprattus* data reported on the right, *S. aurita* data reported on the left.



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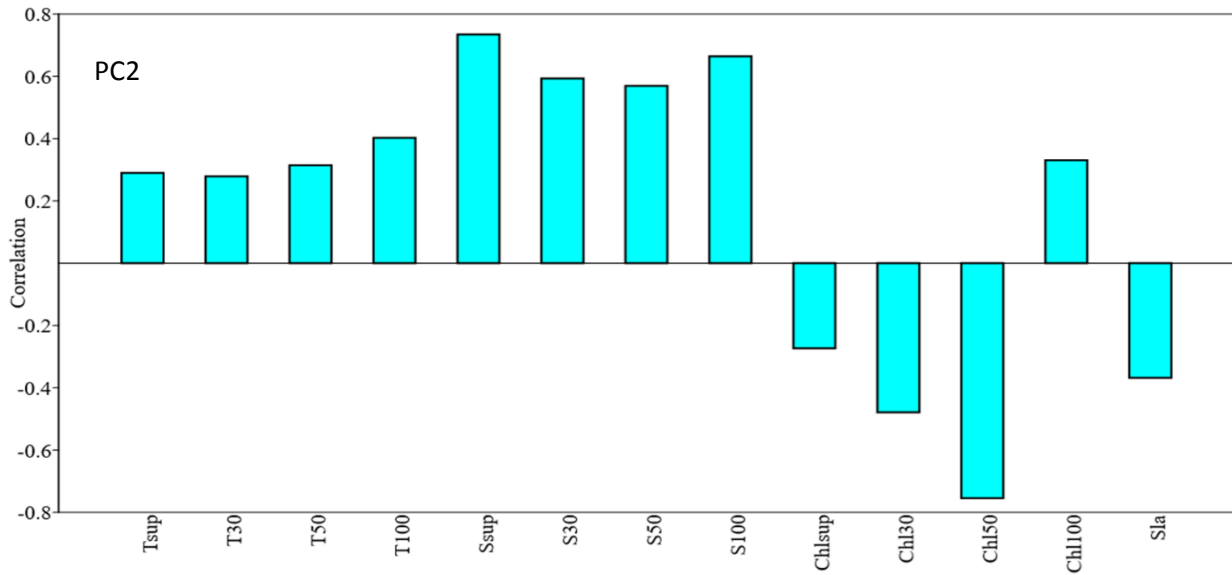
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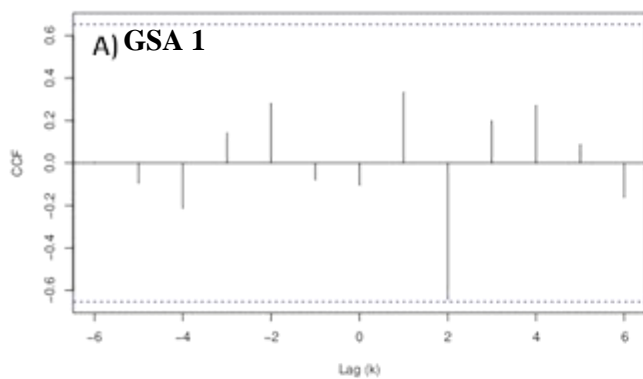
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Fig. 3. A) XY plot of PCA results for the pooled data of all seven GSAs. B) Correlation values for each of the environmental variables considered for PC1 and PC2.

$T_{sup}$  = surface temperature,  $T_{30}$  = temperature at 30 m,  $T_{50}$  = temperature at 50 m,  $T_{100}$  = temperature at 100 m in the survey month,  $S_{sup}$  = surface salinity,  $S_{30}$  = salinity at 30 m,  $S_{50}$  = salinity at 50 m,  $S_{100}$  = salinity at 100 m,  $Chl_{sup}$  = surface chlorophyll concentration,  $Chl_{30}$  = chlorophyll concentration at 30 m,  $Chl_{50}$  = chlorophyll concentration at 50 m,  $Chl_{100}$  = chlorophyll concentration at 100 m,  $Sla$  = sea level anomaly.

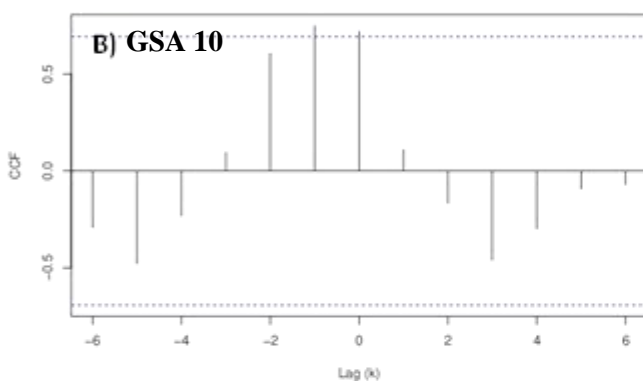
### SAA Biom – Tsup\_S

Cross Correlation Function



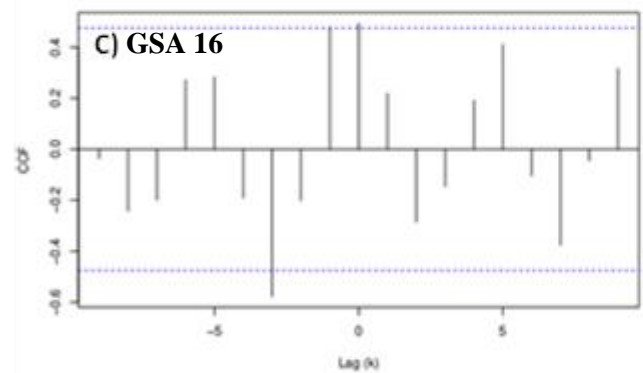
### SAA Biom – T100

Cross Correlation Function



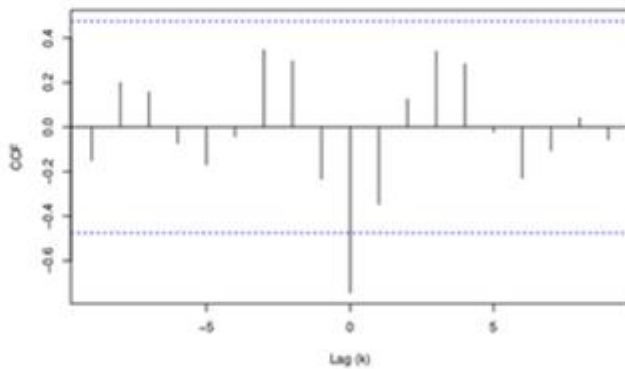
### SAA Biom – Ssup

Cross Correlation Function



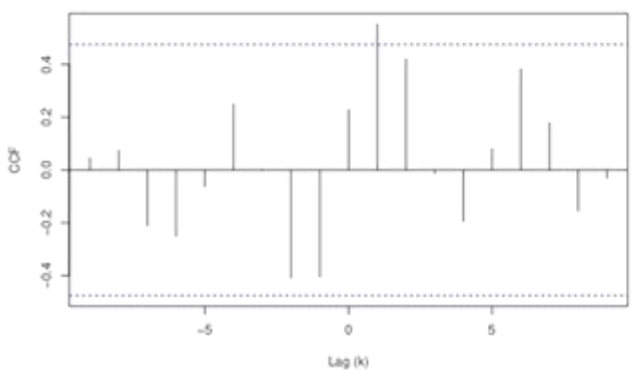
### SAA Biom – T100\_S

Cross Correlation Function



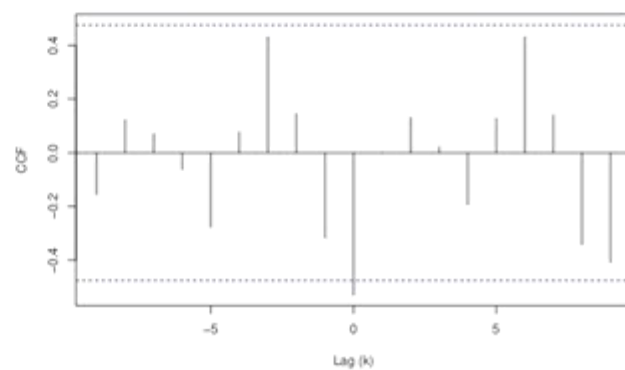
### SAA Biom – Ssup\_S

Cross Correlation Function



### SAA Biom – S100\_S

Cross Correlation Function



727 Fig. 4. A) Significant results of CCF analysis between *S. aurita* biomass (SAA Biom) and  
728 environmental parameters in GSA 1. Blue dotted lines: significance threshold ( $\pm 0.65$ ); B)  
729 Significant results of CCF analysis between *S. aurita* biomass and environmental parameters in  
730 GSA 10. Blue dotted lines: significance threshold ( $\pm 0.70$ ). C) Significant results of CCF analysis  
731 between *S. aurita* biomass and environmental parameters in GSA 16. Blue dotted lines: significance  
732 threshold ( $\pm 0.475$ ).

733  $T_{\text{sup}_S}$  = surface temperature in the summer before the survey,  $T_{100}$  = temperature at 100 m in the  
734 survey month,  $T_{100_S}$  = temperature at 100 m in the summer before the survey,  $S_{\text{sup}}$  = surface salinity  
735 in the survey month,  $S_{\text{sup}_S}$  = surface salinity in the summer before the survey,  $S_{100_S}$  = salinity at  
736 100 m in the summer before the survey.

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### SPR Biom – S50\_W

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Cross Correlation Function

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**A) GSA 6**

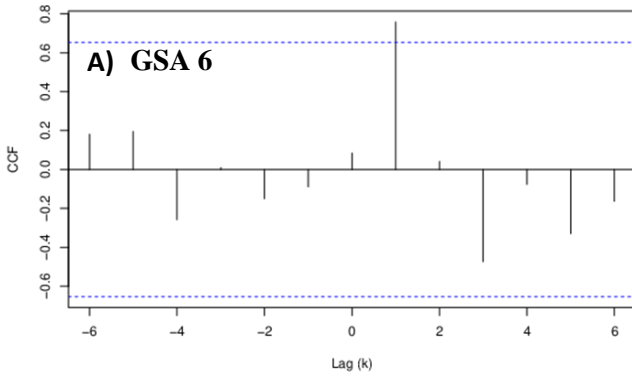
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### SPR Biom – S50

Cross Correlation Function

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### SPR Biom – S100

Cross Correlation Function

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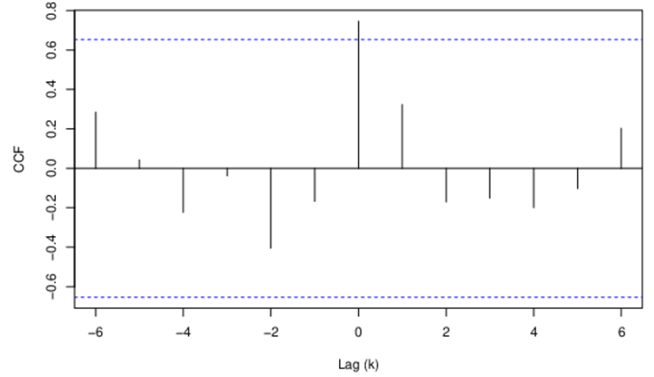
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### SPR Biom – Ch150

Cross Correlation Function

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**B) GSA 7**

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### SPR Biom – Sla

Cross Correlation Function

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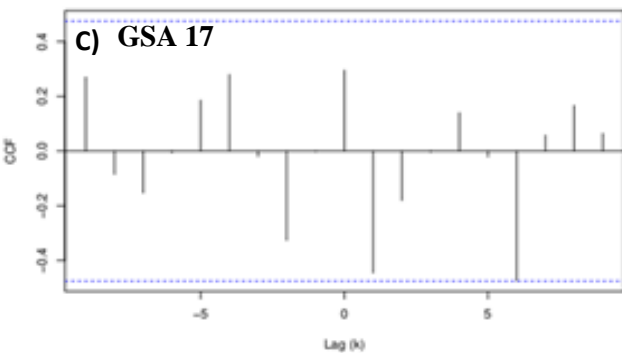
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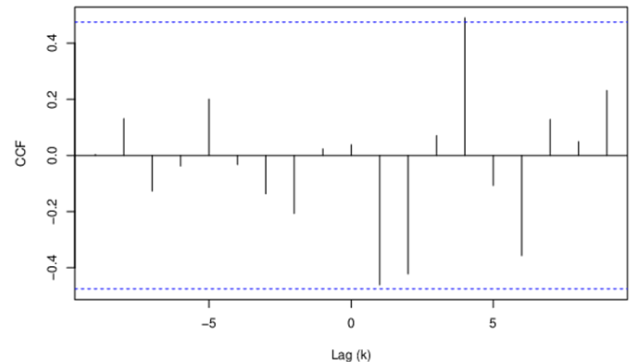
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### SPR Biom – Sla\_W

Cross Correlation Function



797 Fig. 5. A) Significant results of CCF analysis between *S. sprattus* biomass (SPR Biom) and  
798 environmental parameters in GSA 6. Blue dotted lines: significance threshold ( $\pm 0.65$ ). B)  
799 Significant results of CCF analysis between *S. sprattus* biomass and environmental parameters in  
800 GSA 7. Blue dotted lines: significance threshold ( $\pm 0.425$ ). C) Significant results of CCF analysis  
801 between *S. sprattus* biomass and environmental parameters in GSA 17. Blue dotted lines:  
802 significance threshold ( $\pm 0.475$ ).

803  $S_{50\_w}$  = surface salinity in the winter before the survey,  $S_{50}$  = salinity at 50 m in the survey month,  
804  $S_{100}$  = 100 m salinity in the survey month,  $Chl_{50}$  = chlorophyll concentration at 50 m in the survey  
805 month,  $Sla$  = sea level anomaly in the survey month,  $Sla\_w$  = sea level anomaly in the winter before  
806 the survey.

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808 Table 1. Main survey data information and reference acoustic parameters for biomass estimation in  
 809 each GSA.

810 SAA = *S. aurita*, SPR = *S. sprattus*

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GSA	Time interval	Survey month	Survey name	Species biomass	b <sub>20</sub> value (dB)
1	2010-2018	July	MEDIAS	SAA	-72.6
6	2010-2018	July	MEDIAS	SPR, SAA	-72.6 for both species
7	1995-2018	July	PELMED, MEDIAS	SPR	-71.2
9	2009-2018	Mainly August, sometimes June	EVATIR, MEDIAS	SAA	-72.6
10	2009-2018	May-August	EVATIR, MEDIAS	SAA	-72.6
16	2002-2018	Mainly July, sometimes June, August, October	ANCHEVA, MEDIAS	SAA	-72.6
17	2002-2018	Mainly September, sometimes June in western side	ECHOADRI, PELMON, MEDIAS	SPR	-71.7
all	on the base of availability		all above surveys	SPR, SAA	

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813 Table 2. Summary table of the multiple regression analysis. Only GSAs presenting significant  
 814 models are shown.

815  $T_{100}$  = 100 m temperature,  $S_{sup}$  = surface salinity,  $S_{30}$  = 30 m salinity,  $S_{50}$  = 50 m salinity,  $S_{100}$  = 100  
 816 m salinity,  $S_{150}$  = 150 m salinity,  $Chl_{sup}$  = surface chlorophyll concentration,  $Sla$  = sea level  
 817 anomaly.

818 ° environmental parameters of the summer prior to the survey

819 °° environmental parameters of the winter prior to the survey

Species	Area	Model	Adjusted R square	P-value	$\alpha$ value
<i>Sardinella aurita</i>	GSA1	$LOGbiomass=3.061-0.704*Chl_{sup}$	67.10%	0.008	0.57
	GSA 1°	$LOGbiomass=4.126 - 0.442 LOG biomass-1 - 0.778*T_{30} + 0.563*Sla$	49.34%	0.141	0.36
	GSA 10	$LOGbiomass=2.761+0.559*T_{100}$	43.86%	0.044	0.35
	GSA 10 °	$LOGbiomass=2.761+0.285*T_{100}+0.892*S_{sup} -0.598*S_{100}+0.509*Sla$	80.86%	0.056	0.35
	GSA 16 °	$LOGbiomass=3.1399 - 0.3882*T_{100}$	52.34%	0.001	0.05
<i>Sprattus sprattus</i>	GSA 6	$LOGbiomass=3.655-0.460*S_{50}$	49.19%	0.021	0.05
	GSA 7	$LOGbiomass=3.115+0.877*S_{150}$	29.31%	0.008	0.05
	GSA 7 °°	$LOGbiomass=3.115+1.041*S_{150}$	43.65%	0.001	0.05

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826 Table 3. Details of the environmental variables used in the multiple regression models *per* species  
 827 and GSA.

828  $T_{100}$  = temperature at 100 m,  $S_{sup}$  = surface salinity,  $S_{30}$  = salinity at 30 m,  $S_{50}$  = salinity at 50 m,  
 829  $S_{100}$  = salinity at 100 m,  $S_{150}$  = salinity at 150 m,  $Chl_{sup}$  = surface chlorophyll concentration,  $Sla$  =  
 830 sea level anomaly.

831 ° environmental parameters of the summer prior to the survey

832 °° environmental parameters of the winter prior to the survey

Species	Area	Term	Coefficient	Degrees of freedom	Contribution	P-value
<i>S. aurita</i>	GSA1	Constant	3.061			0.000
		$Chl_{sup}$	-0.704	1	71.80%	0.008
	GSA 1°	Constant	4.126			0.009
		LOG biomass-1	-0.442	1	20.20%	0.217
		$T_{30}$	-0.778	1	29.28%	0.057
		$Sla$	0.563	1	21.58%	0.159
	GSA 10	Constant	2.761			0.000
		$T_{100}$	0.559	1	51.88%	0.044
	GSA 10 °	Constant	2.761			0.000
		$T_{100}$	0.285	1	33.07%	0.229
		$S_{sup}$	0.892	1	24.48%	0.019
		$S_{100}$	-0.598	1	17.54%	0.049
		$Sla$	0.509	1	16.70%	0.090
	GSA 16 °	Constant	3.1399			0.000
$T_{100}$		-0.3882	1	55.32%	0.001	
<i>S. sprattus</i>	GSA 6	Constant	3.655			0.000
		$S_{50}$	0.460	1	55.55%	0.021
	GSA 7	Constant	3.115			0.000
		$S_{150}$	0.877	1	33.03%	0.008
	GSA 7 °°	Constant	3.115			
		$S_{150}$	1.041	1	46.61%	0.001

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835 Table 4. Environmental parameters significantly correlated with *S. sprattus* or *S. aurita* biomass in  
 836 each GSA according to regression analysis.

837 SAA = *S. aurita*, SPR = *S. Sprattus*. Chl<sub>sup</sub> = surface chlorophyll concentration, T<sub>100</sub> = 100 m  
 838 temperature, S<sub>50</sub> = 50 m salinity, S<sub>150</sub> = 150 m salinity, S<sub>100</sub> = 100 m salinity, S<sub>sup</sub> = surface  
 839 salinity, Sla = sea level anomaly. y = years

GSA	Species	Environmental parameters	Positive/Negative Correlation (+/-)	P-value	Delay in biomass response to changes in the environmental variable
1	SAA	Chl <sub>sup</sub>	-	0.008	0 y
1	SAA	T <sub>30</sub> , Sla	-, +	0.057, 0.159	1 y
6	SAA	None			
6	SPR	S <sub>50</sub>	+	0.021	0.5 y
7	SPR	S <sub>150</sub>	+	0.008	0 y
7	SPR	S <sub>150</sub>	+	0.001	0.5 y
9	SAA	None			
10	SAA	T <sub>100</sub>	+	0.044	0 y
10	SAA	T <sub>100</sub> , S <sub>sup</sub> , S <sub>100</sub> , Sla	+, +, -, +	0.229, 0.019, 0.049, 0.090	1 y
16	SAA	T <sub>100</sub>	-	0.001	1 y
17	SPR	None			

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848 Table 5. Environmental parameters significantly correlated with *S. sprattus* or *S. aurita* biomass for  
 849 each GSA according to CCF analysis.

850 SAA = *S. aurita*, SPR = *S. sprattus*. Tsup\_S = surface temperature in the summer before the survey,  
 851 T100 = temperature at 100 m in the survey month, T100\_S = temperature at 100 m in the summer  
 852 before the survey, Ssup = surface salinity in the survey month, Ssup\_S = surface salinity in the  
 853 summer before the survey, S50 = 50 m salinity in the survey month, S100 = 100 m salinity in the  
 854 survey month, S50\_W = salinity at 50 m in the winter before the survey, S100\_S = 100 m salinity in  
 855 the summer before the survey, Chl50 = 50 m chlorophyll concentration in the survey month, Sla =  
 856 sea level anomaly in the survey month, Sla\_W = sea level anomaly in the winter before the survey,  
 857 y = years

GSA	Species	Environmental parameters	Positive/Negative Correlation (+/-)	Delay in biomass response to changes in the environmental variables
1	SAA	T <sub>sup_S</sub>	-	3 y
6	SAA	None		
6	SPR	S <sub>50</sub> , S <sub>50_W</sub> , S <sub>100</sub>	+,+,+	0 y, 1 y, 0 y
7	SPR	Chl <sub>50</sub>	+	1 y
9	SAA	None		
10	SAA	T <sub>100</sub>	+	0 y
16	SAA	S <sub>sup</sub> , S <sub>sup_S</sub> , T <sub>100_S</sub> , S <sub>100_S</sub>	+,+,-,-	0 y, 1 y, 0 y, 0 y
17	SPR	Sla, Sla <sub>w</sub>	-, -	1 y, 1 y

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