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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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Abstract

Data on *Sardinella aurita* (round sardinella) and *Sprattus sprattus* (European sprat) in the Mediterranean Sea are limited due to their scarce commercial interest, at least in European countries. Yet, these two small pelagic fish, sitting at opposite ends of the thermal range, could be interesting sentinel species to monitor the effects of climate change in the basin. Using the Mediterranean International Acoustic Surveys (MEDIAS) – the most extensive source of information on these species – we analysed their biomass in several geographical subareas of the central and western Mediterranean Sea in relation to satellite-derived environmental parameters. Our findings highlight that the *S. aurita* biomass responded to temperature, salinity, chlorophyll concentration and sea level anomaly, depending on the GSA examined, whereas the *S. sprattus* biomass correlated significantly with salinity in GSA 6, with salinity and chlorophyll concentration in GSA 7 and with sea level anomaly in GSA 17. These data widen our knowledge of the factors that contribute to the ecology of these species. Further studies of their spatial distribution and of their interactions with other small pelagic species, predators and prey are needed to depict a more comprehensive scenario.

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

Introduction

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

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

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

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

Materials and methods

Biomass estimates from acoustic surveys

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

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

The main frequency of the scientific echosounder used for biomass calculation was 38 kHz, the standard international frequency employed to estimate the biomass of small pelagic fish. In accordance with the MEDIAS protocol, noise and reverberation were removed by means of specific filters or manually, based on the researchers' experience with the software used for acoustic data analysis. Echo trace classification was based on visual scrutinization of the echograms by means of direct allocation and allocation on the basis of representative fishing stations. The inherent uncertainty associated with this and other processes involved in biomass estimation from acoustic surveys was expressed through the calculation of a coefficient of variation by means of an R routine according to Walline (2007). As regards the conversion of acoustic density into biomass, the b_{20} values relative to the TS equation used in the different GSAs were either identical (*S. aurita*) or very similar (from -72.6 to -71.2 dB for *S. sprattus*), as listed in Table 1. Since most analyses were made separately for each GSA, the slightly different b_{20} values are not expected to alter the results.

Species and areas

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

Satellite environmental data

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

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

Statistical analysis

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

After this preliminary overview, we performed more detailed and separate analyses for each GSA using the statistical software Minitab 19. We first considered the annual biomass of each species in relation to the average environmental parameters of the survey month, to find any environmental factors inducing fast responses in abundance. Secondly, we considered the biomass estimation in relation to the environmental parameters of the reproductive season prior to survey execution (summer for *S. aurita* and winter for *S. sprattus*), to identify possible delayed influences of the environmental parameters on biomass through effects on larval survival. We tried to fit linear models (LMs) in each GSA. The LMs were run with a forward selection procedure, based on minimization of Akaike's information criterion corrected for small sample sizes and on the Bayesian information criterion, to avoid an excessive number of explanatory variables compared with the size of the sample. To exclude multicollinearity of the environmental parameters, we checked that the variance inflation factor of the variables was < 5, as suggested by Rogerson (2001). Finally, we checked residuals and the goodness of fit of the models to evaluate model fit. In particular, the normality of residuals was assessed through q-q plots and density plots, whereas the presence of temporal autocorrelation was assessed *via* estimation of the partial autocorrelation of residuals. Whenever autocorrelation was present (a violation of LM assumptions merely reflecting the fact that biomass in a given year depends on the biomass of the previous year independently of the environment), the LMs were run again, adding the biomass of the previous year as a covariate. This simple method allowed removing autocorrelation from the residuals.

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

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

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 GSA 7.

Results

Biomass evolution of the studied species

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

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

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

Principal Component Analysis results of pooled data from all GSAs

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

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

S. aurita

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

CCF analysis highlighted a further relationship with T_{sup_S} of the previous year with a time lag k=2 (Fig. 4A), *i.e.* cooler surface temperature 3 summers before resulted in higher *S. aurita* biomass.

In GSA 6 (Northern Spain), biomass at t-1 was added to the model to remove the autocorrelation initially present in the regression residuals. None of the environmental variables of the survey month were retained by the model and the same applied to the average values of the summer before the survey; moreover, CCF analysis found no significant relationship between biomass and the environmental parameters.

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

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

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

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

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

S. sprattus

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

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

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

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

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

CCF analysis highlighted significant relationships with Sla and $Sla_{\_W}$ (both k=1) (Fig. 5C).

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

Discussion

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

Principal Component Analysis in pooled data from all GSAs

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

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

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

S. aurita

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

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

The forward selection analysis results showed a negative correlation between biomass and temperature at 30 m. CCF analysis yielded a similar result, namely a negative correlation with average surface temperature the summer before the survey. This finding contrasts with several works associating higher temperatures with higher *S. aurita* abundance (Maynou *et al*., 2019; Sabatès *et al*., 2009). However, at least in the case of CCF analysis, the negative correlation and the time lag (2+1 year of time shift) do not seem to indicate a strong relationship, since biomass is unlikely to be influenced by the surface temperature of three years previously. Forward selection analysis also identified a positive correlation with sea level anomaly; this is a highly productive area, where the inflow of nutrients-rich Atlantic waters confers important hydrographic mesoscale features (Albo-Puigserver *et al*., 2021) and exerts an influence on the trophic web from planktonic organisms upwards, possibly also enhancing the abundance of *S. aurita* and of other small pelagic fish.

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

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

Sprattus sprattus

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

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

Based on stomach content, the *S. sprattus* diet – at least in winter in the Adriatic Sea during the spawning season – seems to be dominated by copepods (Tičina *et al.*, 2000). In the Baltic Sea, the copepod biomass has been reported to decline with decreasing salinity (Vuorinen *et al.*, 1998). A possible explanation for our findings is that when salinity decreases, due to higher riverine inputs, local conditions may favour other small pelagic species (*e.g.* anchovy and sardine in the Mediterranean Sea), which compete with *S. sprattus* for the same ecological niche; the opposite would happen in case of lower riverine inputs and increasing local salinity (Feuilloley *et al.*, 2020). A greater knowledge of phytoplankton and zooplankton composition in the previous years and of the dietary preferences of the various small pelagic species would allow verifying this hypothesis.

Biomass correlated significantly with salinity in the deeper strata of the water column. This may simply be due to the similar salinity values at different depths in GSA 6; however, the conditions affecting *S. sprattus* biomass most strongly are probably those found in the first 50 m. Collection of regional data, especially in GSA 6 – whose northern and southern parts differ considerably in oceanographic patterns and species presence – would also allow exploring the characteristic features of each area and provide insights into the dynamics of these species. The salinity values in the winter before the survey could exert a major effect on egg development, duration and survival by acting on their buoyancy, thus indirectly influencing the survival of this crucial life stage (Petereit *et al*., 2009); in particular, greater buoyancy propels them upwards, to a layer characterized by more favourable temperature and dissolved oxygen conditions for egg development and larval survival.

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

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

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

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

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

Conclusions

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

Acknowledgements

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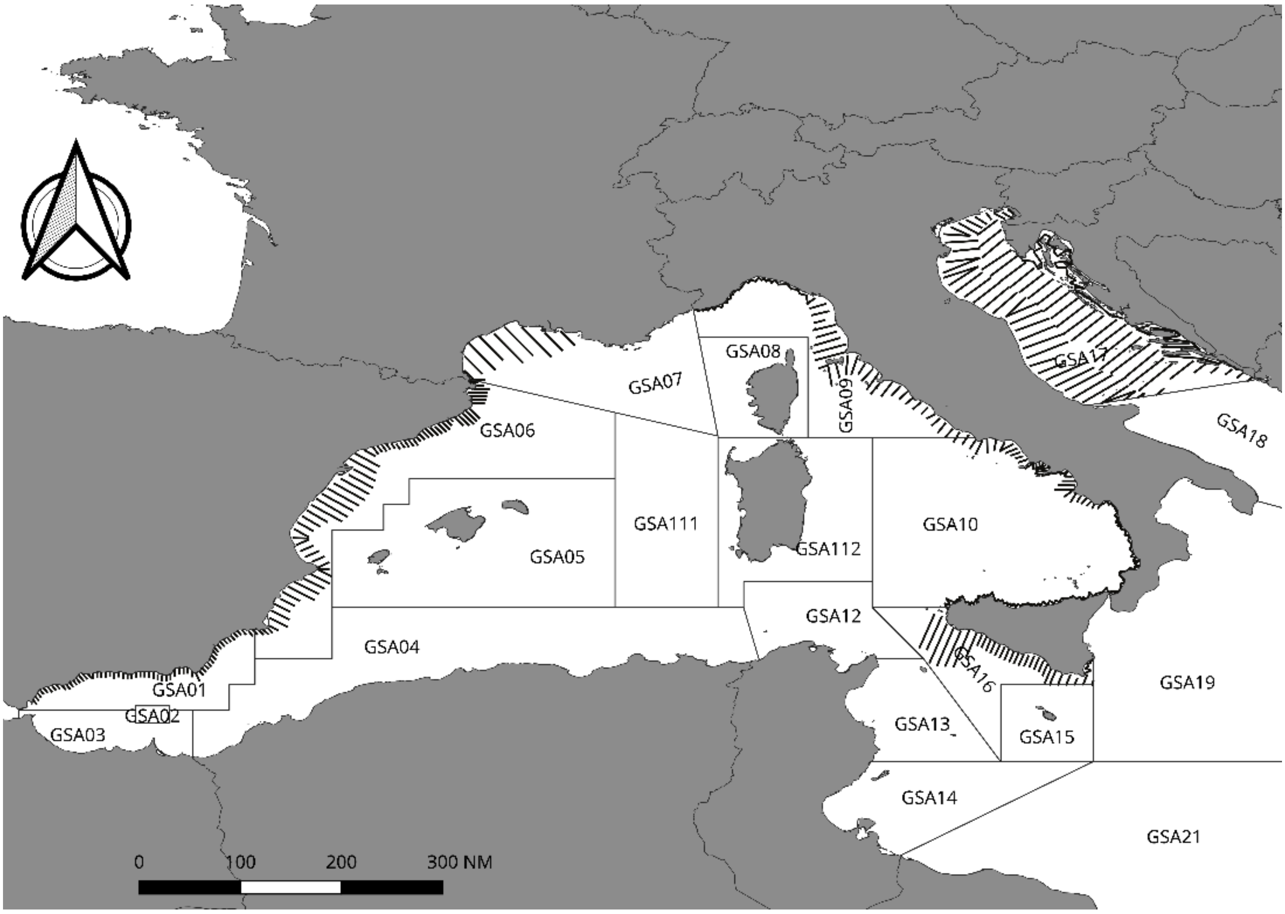


Fig. 1. MEDIAS surveys transects conducted in the Geographical Subareas (GFCM, 2009) considered in this work.

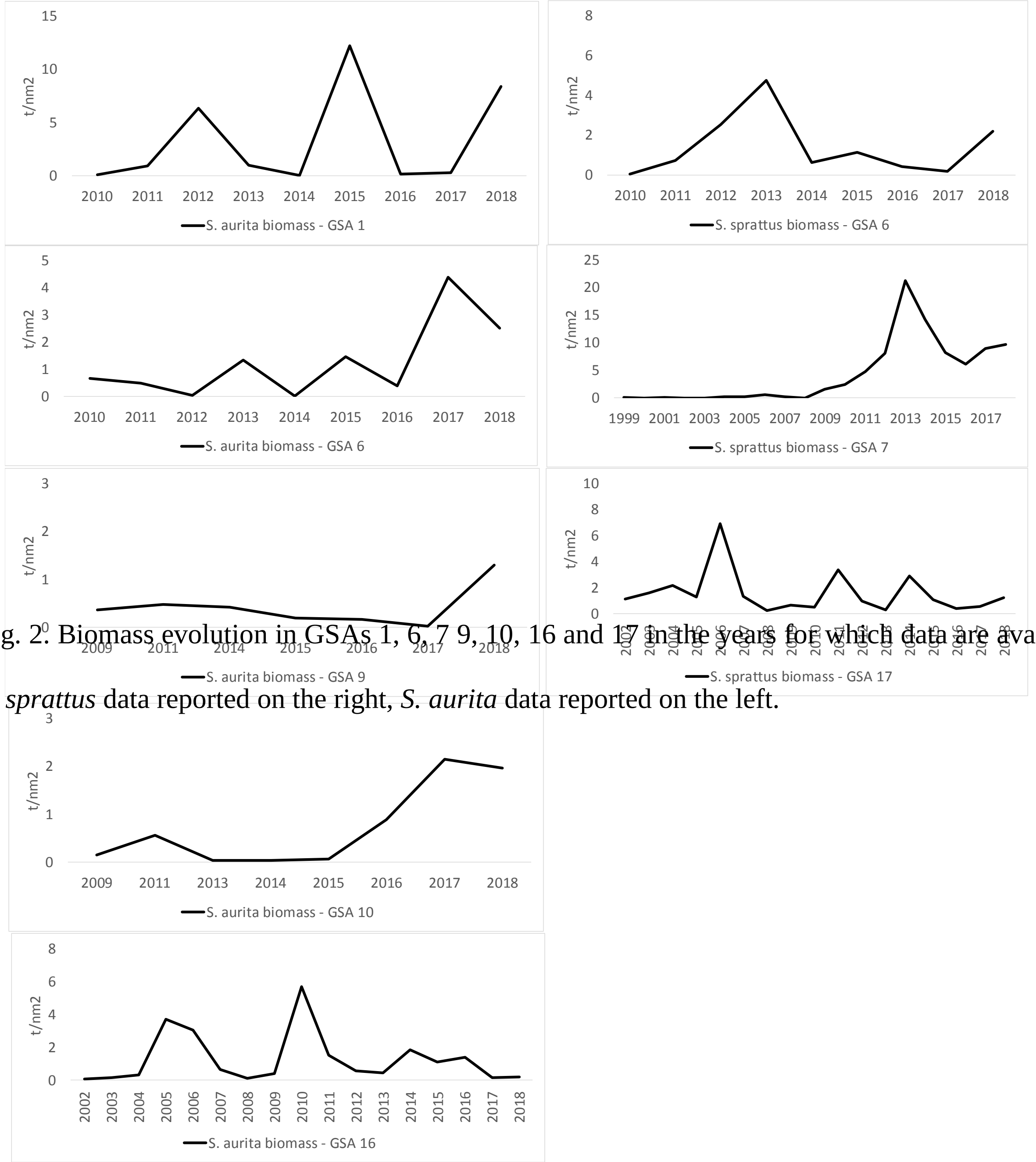
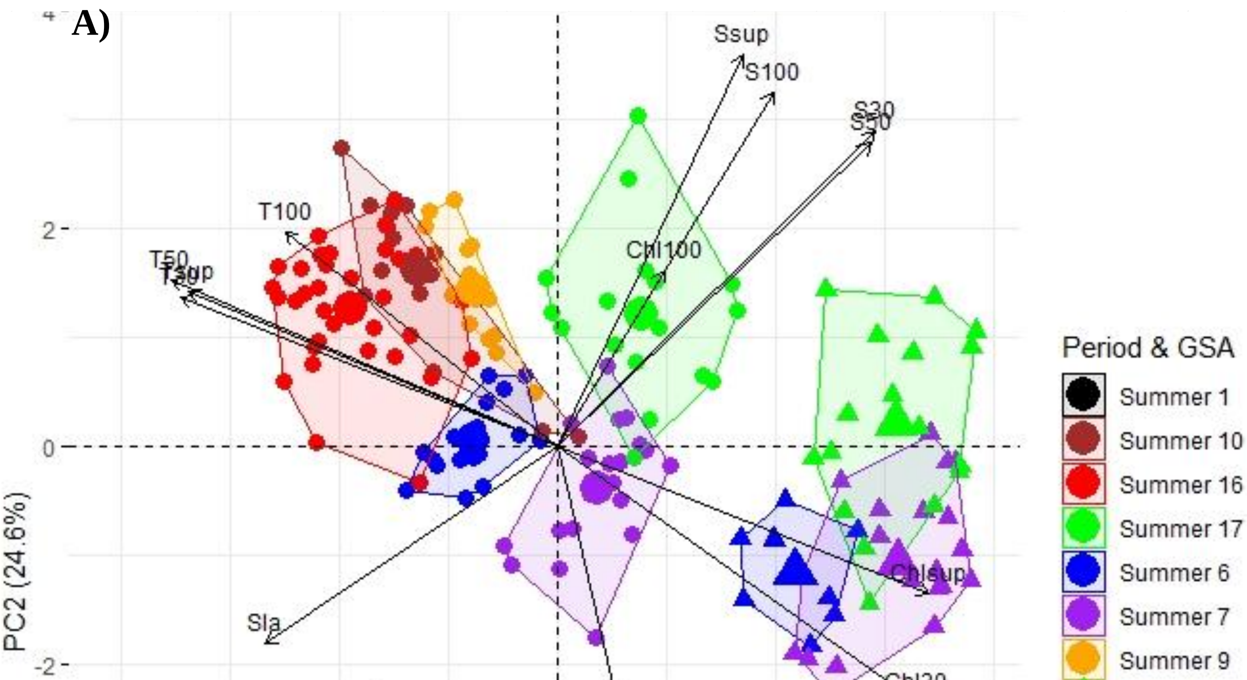


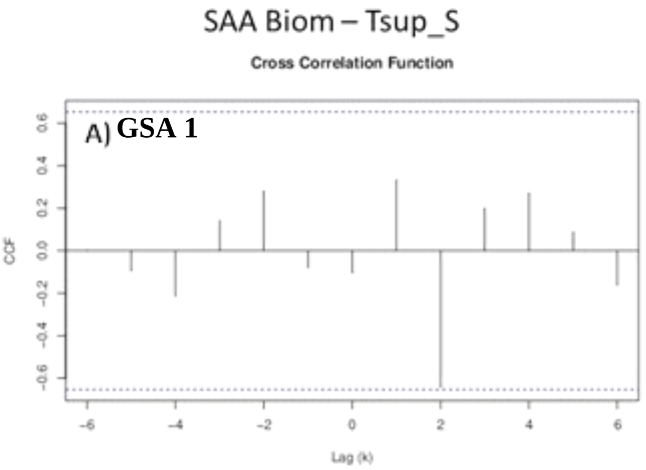
Fig. 2. Biomass evolution in GSAs 1, 6, 7 9, 10, 16 and 17 in the years for which data are available. *S. sprattus* data reported on the right, *S. aurita* data reported on the left.

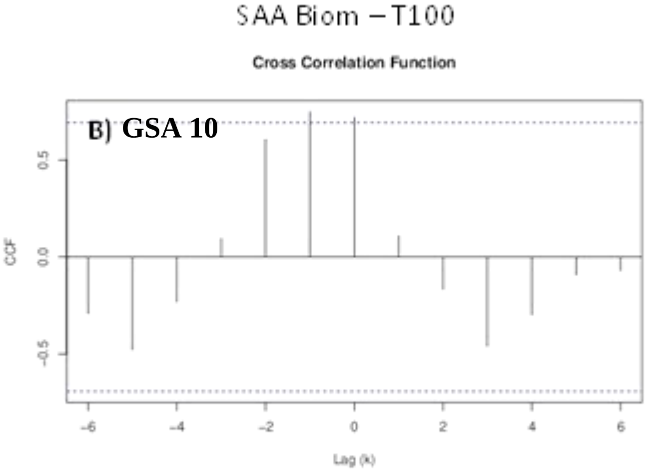


B)

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
A) GSA 1
CCF
0.6
0.4
0.2
0.0
−0.2
−0.4
−0.6
−6
−4
−2
0
2
4
6
Lag (k)


SAA Biom – T100
Cross Correlation Function
B) GSA 10
CCF
0.5
0.0
−0.5
−6
−4
−2
0
2
4
6
Lag (k)

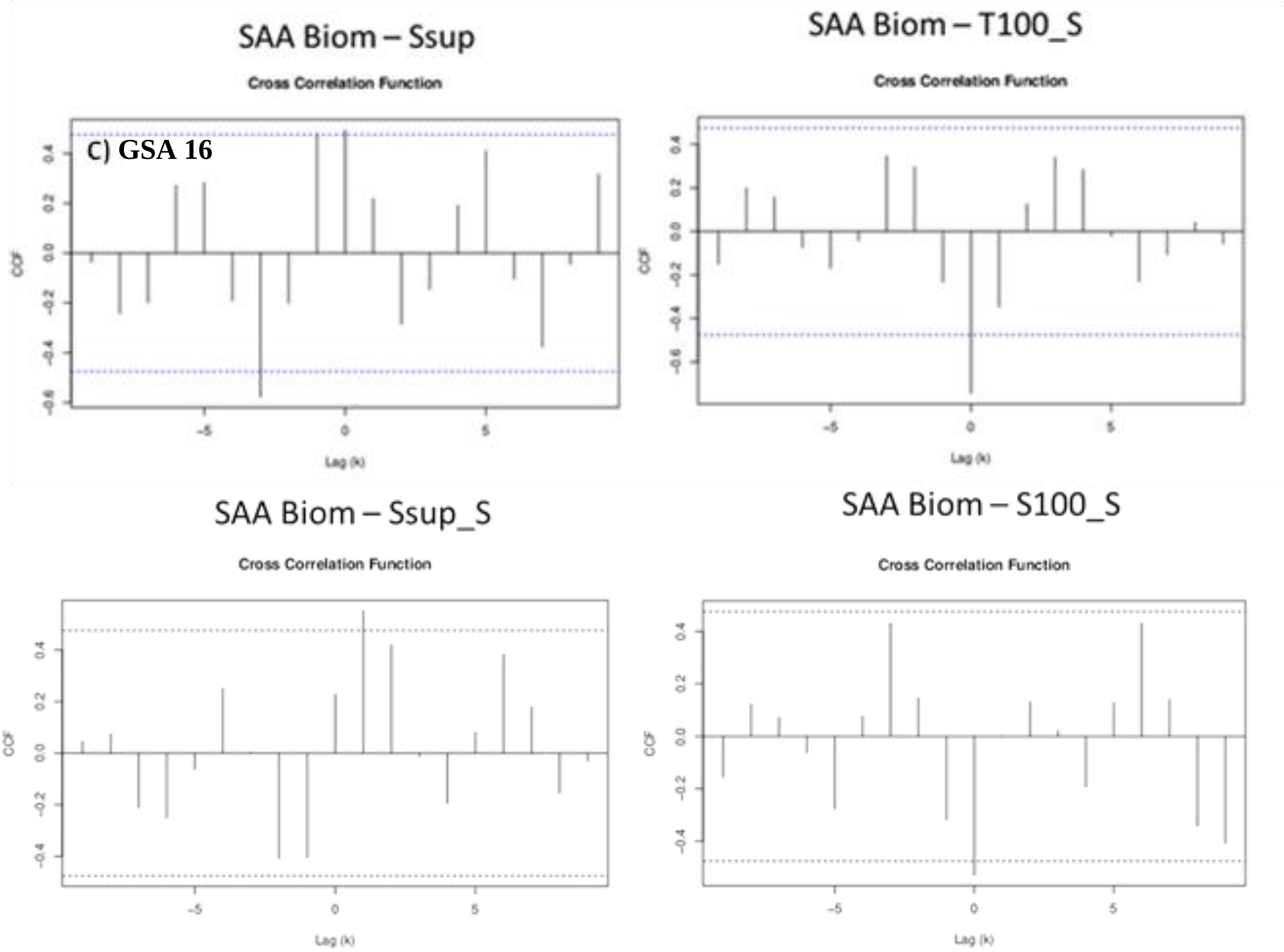
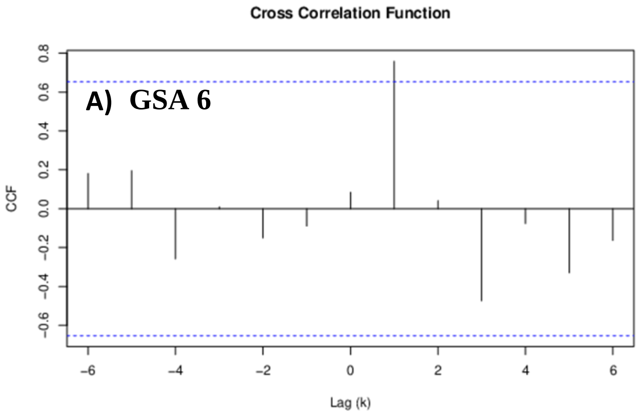

SAA Biom – Ssup
Cross Correlation Function
C) GSA 16
CCF
0.4
0.2
0.0
−0.2
−0.4
−0.6
−5
0
5
Lag (k)
SAA Biom – T100_S
Cross Correlation Function
CCF
0.4
0.2
0.0
−0.2
−0.4
−0.6
−5
0
5
Lag (k)
SAA Biom – Ssup_S
Cross Correlation Function
CCF
0.4
0.2
0.0
−0.2
−0.4
−5
0
5
Lag (k)
SAA Biom – S100_S
Cross Correlation Function
CCF
0.4
0.2
0.0
−0.2
−0.4
−5
0
5
Lag (k)

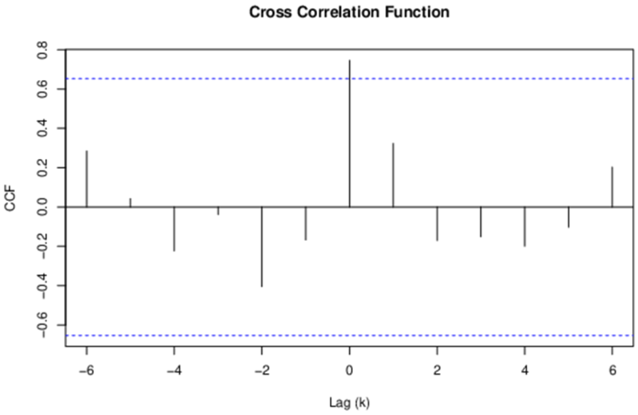
Fig. 4. A) Significant results of CCF analysis between *S. aurita* biomass (SAA Biom) and environmental parameters in GSA 1. Blue dotted lines: significance threshold (±0.65); B) Significant results of CCF analysis between *S. aurita* biomass and environmental parameters in GSA 10. Blue dotted lines: significance threshold (±0.70). C) Significant results of CCF analysis between *S. aurita* biomass and environmental parameters in GSA 16. Blue dotted lines: significance threshold (±0.475).

T_{sup_S} = surface temperature in the summer before the survey, T_{100} = temperature at 100 m in the survey month, T_{100_S} = temperature at 100 m in the summer before the survey, S_{sup} = surface salinity in the survey month, S_{sup_S} = surface salinity in the summer before the survey, S_{100_S} = salinity at 100 m in the summer before the survey.

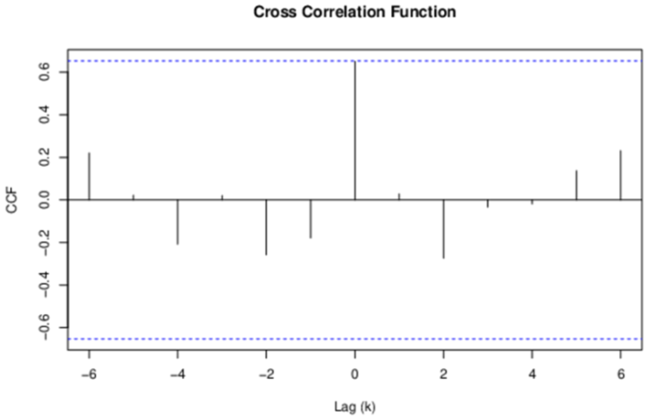
SPR Biom – S50_W



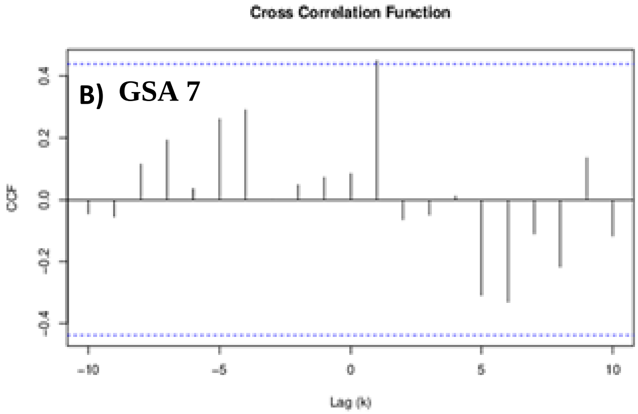
SPR Biom – S50



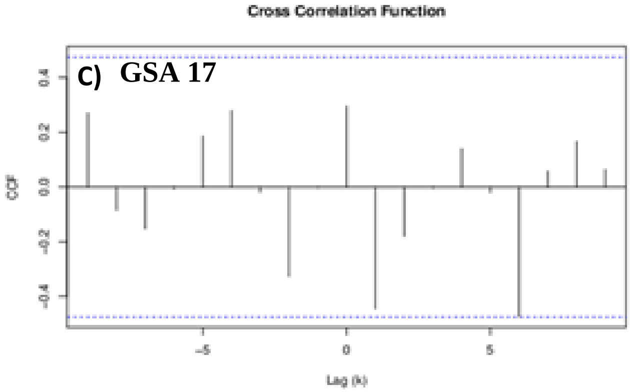
SPR Biom – S100



SPR Biom – Chl50



SPR Biom – Sla



SPR Biom – Sla_W

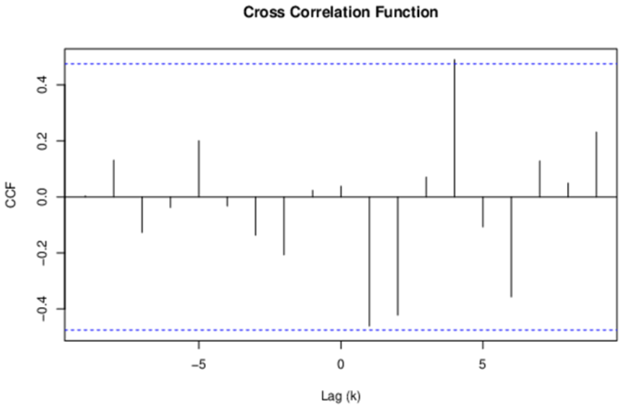


Fig. 5. A) Significant results of CCF analysis between *S. sprattus* biomass (SPR Biom) and environmental parameters in GSA 6. Blue dotted lines: significance threshold (±0.65). B) Significant results of CCF analysis between *S. sprattus* biomass and environmental parameters in GSA 7. Blue dotted lines: significance threshold (±0.425). C) Significant results of CCF analysis between *S. sprattus* biomass and environmental parameters in GSA 17. Blue dotted lines: significance threshold (±0.475).

S_{50_W} = surface salinity in the winter before the survey, S_{50} = salinity at 50 m in the survey month, S_{100} = 100 m salinity in the survey month, Chl_{50} = chlorophyll concentration at 50 m in the survey month, Sla = sea level anomaly in the survey month, $Sla_{\_W}$ = sea level anomaly in the winter before the survey.

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

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

GSA	**Time interval**	**Survey month**	**Survey name**	**Species biomass**	**b_{20} 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	

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

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

° environmental parameters of the summer prior to the survey

°° environmental parameters of the winter prior to the survey

Species	Area	Model	Adjusted R square	P-value	α value
Sardinella aurita	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
Sprattus sprattus	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

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

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

° environmental parameters of the summer prior to the survey

°° environmental parameters of the winter prior to the survey

Species	Area	Term	Coefficient	Degrees of freedom	Contribution	P-value
S. aurita	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
S. sprattus	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

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

SAA = *S. aurita*, SPR = *S. Sprattus*. Chl_{sup} = surface chlorophyll concentration, T_{100} = 100 m temperature, S_{50} = 50 m salinity, S_{150} = 150 m salinity, S_{100} = 100 m salinity, Ssup = surface 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_{sup}	-	0.008	0 y
1	SAA	T_{30}, Sla	-, +	0.057, 0.159	1 y
6	SAA	None			
6	SPR	S_{50}	+	0.021	0.5 y
7	SPR	S_{150}	+	0.008	0 y
7	SPR	S_{150}	+	0.001	0.5 y
9	SAA	None			
10	SAA	T_{100}	+	0.044	0 y
10	SAA	T_{100}, S_{sup}, S_{100}, Sla	+, +, -, +	0.229, 0.019, 0.049, 0.090	1 y
16	SAA	T_{100}	-	0.001	1 y
17	SPR	None			

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

SAA = *S. aurita*, SPR = *S. sprattus*. Tsup_S = surface temperature in the summer before the survey, T100 = temperature at 100 m in the survey month, T100_S = temperature at 100 m in the summer before the survey, Ssup = surface salinity in the survey month, Ssup_S = surface salinity in the summer before the survey, S50 = 50 m salinity in the survey month, S100 = 100 m salinity in the survey month, S50_W = salinity at 50 m in the winter before the survey, S100_S = 100 m salinity in the summer before the survey, Chl50 = 50 m chlorophyll concentration in the survey month, Sla = sea level anomaly in the survey month, Sla_W = sea level anomaly in the winter before the survey, y = years

GSA	Species	Environmental parameters	Positive/Negative Correlation (+/-)	Delay in biomass response to changes in the environmental variables
1	SAA	T_{sup_S}	-	3 y
6	SAA	None		
6	SPR	S_{50}, S_{50_W}, S_{100}	+,+,+	0 y, 1 y, 0 y
7	SPR	Chl_{50}	+	1 y
9	SAA	None		
10	SAA	T_{100}	+	0 y
16	SAA	S_{sup}, S_{sup_S}, T_{100_S}, S_{100_S}	+,+,-,-	0 y, 1 y, 0 y, 0 y
17	SPR	Sla, $Sla_{\_W}$	-,-	1 y, 1 y