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Effects of environmental conditions and jellyfish blooms on small pelagic fish and fisheries from the Western Mediterranean Sea

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A B S T R A C T

Sardine and anchovy have shown important changes in landings, biomass, abundance and body condition with time in the Western Mediterranean Sea. Several hypotheses have been proposed to explain these changes, including the negative interaction with jellyfish blooms. Increases in jellyfish blooms may be one of the reasons for a decline in these fish stocks because several jellyfish species have been shown to feed on fish larvae and juveniles. The main aim of the present study was to test the plausible relationship between jellyfish blooms and stock dynamics (abundance, biomass, and fitness) of anchovy and sardine, and its fisheries within an ecological context of the western Mediterranean Sea. Our main hypothesis was that jellyfish blooms, in combination with other environmental drivers, could have negative effects due to their predation on early stages of small pelagic fish (direct mortality) or due to predation on zooplankton, which is also prey of the small pelagic fish at different ontogenetic stages (direct competition). To test our hypothesis, we developed Bayesian Generalized Linear Mixed Models to compare landings, biomass, abundance, and Kn condition factor of both species with several climatic indices, oceanographic variables, and the occurrences of jellyfish blooms. Our results revealed that the jellyfish bloom occurrence had a high probability of negatively and broadly affecting both species in addition to changes in environmental conditions. This suggests that jellyfish blooms should be added to the likely causes of change when analyzing small pelagic fish change.

1. Introduction

There is a general perception of an increase in global jellyfish abundance, with blooms being recorded in different seas throughout the planet (e.g., Boero et al., 2008; Purcell, 2012; Boero, 2013; Condon et al., 2013; Canepa et al., 2014). In the western Mediterranean Sea, recent research highlights an increase in the frequency of these blooms (Bernard et al., 2011), composed mainly by six taxes: *Aurelia spp species complex, Chrysaora hysoscella, Cotylorhiza tuberculata, Pelagia noctiluca, Rhizostoma pulmo* and *Velella velella* (Kogovšek et al., 2010; Purcell et al., 2015; Scorrano et al., 2017). Other gelatinous plankter blooms forming, such as *Mnemiopsis* or the cubozoan *Carybdea marsupialis,* are also

present from Western Mediterranean Sea (Boero et al., 2009; Bordehore et al., 2011).

Jellyfish blooms are perceived with special concern by socio-economic sectors involved in coastal tourism and fisheries because jellyfish blooms or swarms could have a negative effect on local and regional economy (Quiñones et al., 2013; Graham et al., 2014; Canepa et al., 2014). Some jellyfish species are known to prey on larvae of pelagic fish of economic importance such as European anchovy (*Engraulis encrasicolus*), which could cause losses to the local fishing sector (Sabatés et al., 2010; Flynn et al., 2012; Tilves et al., 2016; Tomlinson et al., 2018). In a bloom event, apart from preying on ich-thyoplankton, jellyfish consume high numbers of zooplankton prey,

competing for food with fish species (Tilves et al., 2018a, b). In fact, the increase in gelatinous zooplankton can alter coastal and offshore food web dynamics (Lynam et al., 2006; Houghton et al., 2007; Purcell et al., 2007; Richardson et al., 2009; Robinson et al., 2014; Brodeur et al., 2016), endangering local fisheries (Lynam et al., 2006; Quiñones et al., 2013) and may negatively impact the aquaculture sector (Bosch-Belmar et al., 2017). According to recent studies, jellyfish populations may be one reason for a drop in fish stocks observed in the Mediterranean and Black Sea (Licandro et al., 2010; Boero, 2013) because a large number of them feed on fish larvae and juveniles as well as they often compete for the same food spectra. However, Opdal et al. (2019) did not find a relationship between jellyfish populations and small pelagic fishes. Moreover, many authors suggest that there is not enough evidence to support an increase in jellyfish blooms because the results from studies on jellyfish blooms are not based on long time-series data of jellyfish populations (Brotz et al., 2012; Canepa et al., 2014; Duarte et al., 2014). On the other hand, fish can prey on jellyfish (Milisenda et al., 2014; Thiebot and McInnes, 2020). Moreover, jellyfish species from *Cotylorhiza* and *Rhizostoma* genera often provide shelter for fish juveniles that, indeed, feed on them; thus, jellyfish can also be fish enhancers (Tilves et al., 2018a, b).

Currently sardine and anchovy are considered overfished in the western Mediterranean Sea (GFCM, 2019). Moreover, several studies provided evidence of a decline in biomass, abundance, and catch of European sardine (*Sardina pilchardus*) in the northwestern Mediterranean Sea, while anchovy has shown fluctuations in the central region and declines in the northern region of the Mediterranean Sea (for example, Palomera et al., 2007; Coll et al., 2019; Saraux et al., 2019; Pennino et al., 2020). Moreover, declines in other life history traits of European sardine and anchovy, such as body condition and growth, have been observed since 2007 in the NW Mediterranean Sea (Van Beveren et al., 2014; Brosset et al., 2017). Several hypotheses have been proposed to explain these changes in the pelagic community, including negative interactions with jellyfish (Coll et al., 2019). The main aim of the present study was to test the possible relationship between these blooms of jellyfish and stock biology (abundance, biomass and fitness) of European anchovy and sardine, and its fisheries from the western Mediterranean Sea, in an ecological context taking into account the effect of the environmental variability.

As mentioned above, previous studies have described the high predation of jellyfish blooms on early life stages of small pelagic fish (direct mortality; Lynam et al., 2005; Tilves et al., 2018 a,b), but also on zooplankton, which are prey of the small pelagic fish at different ontogenetic stages (direct competition; Sommer et al., 2002; Tilves et al., 2018a, b). Considering these, the main hypothesis of our study is that, if jellyfish blooms prey on eggs and larval stages of small pelagic fish, it will be observed a lower recruitment the following year and then, a year lag negative effect on pelagic fisheries will be observed. On the other hand, considering the trophic overlap between jellyfish and small pelagic fish, in a situation of food limitation, a negative direct effect on fisheries during the current year will be also expected.

2. Material and methods

2.1. Fisheries data

Landing datasets during the period 2004–2016 were collected for the fishery harbours located in the studied area and provided by the General Secretariat of Fisheries of the Spanish Ministry of Agriculture, Food and Environment (MAPAMA) from the Geographical Subarea (GSA) 06, which corresponds to the eastern region of the Iberian Peninsula, between Cape of Creus and Cape of Palos. This area has been traditionally divided into two zones: Tramuntana (between Cape of Creus and Cape of Nao), and Levante (between Cape of Nao and Cape of Palos) (Fig. 1).

Biomass (metric tons) and abundance (number of individuals) data of anchovy and sardine from 2003 to 2016 were retrieved from the
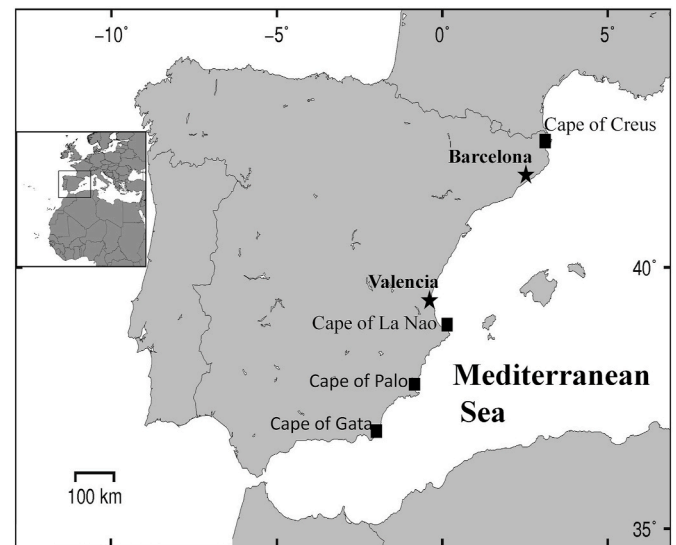
Fig. 1. Map study area. The limits of the old national fishing regions have been highlighted on the map: Tramuntana (between Cape of Creus and Cape of Nao) and Levante (between Cape of Nao and Cape of Palos).

Spanish Acoustic Survey "Eco-MEDiterranean" (ECOMED) and the EU-funded MEDIterranean International Acoustic Survey (MEDIAS) (Pennino et al., 2020). From 2003 to 2008, we used the annual acoustic ECOMED surveys performed by the Instituto Español de Oceanografía (IEO) during November–December (Coll and Bellido, 2018). While acoustic surveys were performed during the day, pelagic trawls were deployed during night time to assess the species composition. The MEDIAS dataset for both species was collected through acoustic surveys from 2009 to 2016 performed during daytime each July by means of scientific 38 kHz split-beam echosounders (Saraux et al., 2014; Pennino et al., 2020). Pelagic trawls were performed when the echosounder detected sufficiently long fish traces or a change in the echogram characteristics. Acoustic data were recorded following the MEDIAS regular sampling design (parallel transects perpendicular to the coastline) at a constant speed of 8–10 knots (1 knot = 1852 m.s-1) (Doray et al., 2010).

As a proxy of the species condition that could be affected by the competition for food when blooms of jellyfish are present, we used the relative condition index (Kn; Le Cren, 1951), which is widely used to analyze species with allometric growth patterns and has been validated for these sardine and anchovy populations (Brosset et al., 2015; Albo-Puigserver et al., 2020). Monthly biological data for sardine and anchovy were collected year-round from commercial landings in the GSA06 from 2004 to 2017 by the Spanish Institute of Oceanography (IEO, CSIC). The relative condition factor was computed as: $Kn = W/Wr$, where W is the mass of an individual and Wr is the theoretical mass of an individual given a total length TL. Wr was predicted by the length–weight relationship calculated from all individuals sampled, $Wr = \alpha TL^{\beta}$, where Wr = total weight minus the gonad weight (g), TL = total fish length (cm) and α and β are the regression coefficients (sardine: $\alpha = 0.0037$, $\beta = 3.2564$; anchovy: $\alpha = 0.0028$, $\beta = 3.3076$). By definition, the values of the Kn are distributed around 1. Values above 1 are individuals in a better condition than a standard individual. Values below 1 are individuals in a worse condition than a standard individual of the same size.

2.2. Environmental data

Annual jellyfish bloom occurrence (JFO) within the Western Mediterranean Sea between 2001 and 2017 (Table 1) was obtained from

Table 1

Source data used for estimated the annual jellyfish bloom occurrence (JFO) within the Western Mediterranean Sea between 2001 and 2017.

Year	Jellyfish outbreak bloom	Source
2001	1	García-Comas et al. (2011); Brotz and Pauly (2012)
2002	1	García-Comas et al. (2011); Brotz and Pauly (2012)
2003	1	García-Comas et al. (2011); Brotz and Pauly (2012)
2004	0	Licandro et al. (2010)
2005	0	Licandro et al. (2010) [a]
2006	0	Licandro et al. (2010) [a]
2007	1	Licandro et al. (2010) [a]
2008	1	Licandro et al. (2010) [a]
2009	0	Bellido et al. (2020)
2010	0	Bellido et al. (2020)
2011	0	Bellido et al. (2020)
2012	1	Bellido et al. (2020)
2013	0	Bellido et al. (2020)
2014	0	Bellido et al. (2020)
2015	1	Bellido et al. (2020)
2016	0	Bellido et al. (2020)
2017	0	Bellido et al. (2020)

[a] Between the years 2005–2008 there is an overlap between Licandro et al. (2010) and Bellido et al. (2020). For these years, information reported by Licandro et al. (2010) has been selected. Furthermore, Bellido et al. (2020) is based on data collected through "citizen science" using a Smartphone application, and the early years of the series by Bellido et al. (2020) could be underestimated.

Licandro et al. (2010) (provided average monthly frequency of Cnidaria from northeast Atlantic between 1958 and 2007; in addition, *Pelagia noctiluca* outbreak bloom during the period 2007–2008 from Western Mediterranean Sea), García-Comas et al. (2011) and Brotz and Pauly (2012) (provided jellyfish bloom data from North Western Mediterranean Sea including all jellyfishes species between 1974 and 2003), and Bellido et al. (2020) (provided jellyfish bloom data from South Western Mediterranean Sea mainly *Pelagia noctiluca* between 2005 and 2018). In addition, we applied a temporal lag of one year for the jellyfish blooms to assess the effect on the species recruitment of the next year for both species. According to Licandro et al. (2010) and Bellido et al. (2020), the main species from Western Mediterranean Sea forming outbreak blooms was *Pelagia noctiluca*.

Six different possible predictors were used to assess the variability of anchovy and sardine indexes: Sea Surface Temperature (SST in °C), Sea Surface Salinity (SSS in PSU), Net Primary Productivity (NPP in mg/m³), Atlantic Multidecadal Oscillation (AMO), Western Mediterranean Oscillation (WeMO), and North Atlantic Oscillation (NAO). For SST, SSS, and NPP, monthly averages of oceanographic variables covering the entire study period (2004–2016) were extracted from the Copernicus database (https://www.copernicus.eu/project-database) for the GSA06.

As shown in previous studies, the small pelagic fish resources show a related synchrony to climatic oscillations (e.g., Báez and Real, 2011; Martin et al., 2011; Alheit et al., 2014), such as NAO, WeMO, and AMO. The NAO is the most important source of variability in the North Atlantic region, affecting wind speed and direction and differences in air temperature, sea surface temperature, and rainfall (Hurrell and Deser, 2009). The WeMO is a smaller-scale atmospheric oscillation, affecting mainly the western Mediterranean basin (Martin and Lopez-Bustins, 2006), and it is defined as the difference in pressure between the Po Plain (from Padua station) in the northern part of the Italian peninsula, and the Gulf of Cádiz (from San Fernando station). AMO is a long-term climatic variability index, and it is defined as the North Atlantic SST anomaly between Greenland and the equator. The AMO provides an ongoing series of long-duration changes in the sea surface temperature of the North Atlantic Ocean, with cool and warm phases that may last for 20–40 years at a time (Kerr, 2000; Enfield et al., 2001).

The NAO and AMO monthly time series data were obtained from NOAA (available from the website: https://www.cpc.ncep.noaa.gov/data/teledoc/telecontents.shtml), while WeMO monthly-times series come from http://www.ub.edu/gc/es/wemo/. Subsequently, for each climatic oscillation an annual average was estimated from the monthly values.

Time series of the environmental variables are plotted in Fig. 2. To allow comparison among them, the environmental variables plotted in Fig. 2 were standardized, i.e. difference from the mean divided by the corresponding standard deviation (Gelman, 2008).

2.3. Statistical analysis

As a first step, temporal trends of biomass, abundance, Kn, and landings of the two studied species were plotted using the "ggplot2" package (Wickham, 2011) of the R software version 3.6.3 (R Core Team, 2019) (Figs. 3 and 4). Next, landings, indices of biomass and abundance, as well as the Kn condition factor of both species, were analyzed as dependent variables with respect to the aforementioned climatic indices AMO, WeMO, NAO, the oceanographic variables NPP, SST, and SSS, and the occurrence of jellyfish blooms (JFO). Remaining potential sources of variation on the species indices could be caused by different sources of variability intrinsically due to the area and year. Consequently, we included two random effects in the models as "area effect" (Tramuntana -between Cape of Creus and Cape of Nao-, and Levante -between Cape of Nao and Cape of Palos-) and "year effect."

For each species and dependent variable, a Bayesian Generalized Linear Mixed Model (B-GLMM) was implemented. In the case of the landings, biomass, and abundance time series, a Gaussian distribution was applied after the implementation of a logarithmic transformation of the response variables. For the Kn condition factor we used a beta distribution (Paradinas et al., 2016, 2018). Proportion and ratio data are frequently modelled by transforming the dependent variable using the arcsine square root transformation (Paradinas et al., 2016), but this approach has several drawbacks and inferences can be misleading (Ferrari and Cribari-Neto, 2004). The beta distribution contrasts with this, as it is very flexible in terms of shape and fulfils the required characteristics (Paradinas et al., 2018). However, as beta distribution assumes data ranging from 0 to 1 and Kn could have higher values, each Kn was divided by its maximum value to obtain a range of values varying from 0 to 1.

An additional advantage of the B-GLMM is the possibility of integrating current modeling approaches (such as GLM) and uncertainty analyses into a more general hierarchical framework. Within the Bayesian framework, full inference about uncertainty, given what we have observed (the data) and what we know or assume about the process (the model), comes free with the model estimations (Banerjee et al., 2004). The temporal and spatial correlation can be incorporated into a regression model through random effects that capture the spatial and temporal dependence in the data.

Standardized data exploration techniques were used to identify any outliers and possible correlation and collinearity between explanatory variables (Zuur et al., 2010). No cases of high significant correlation (Spearman correlation, alpha = 0.05) and collinearity were found among explanatory variables and, consequently, all variables were used in the models (Fig. S1). After the exploratory analysis, in order to better interpret both the direction (positive or negative) and magnitudes (effect sizes) of parameter estimates in relation to the others, the explanatory variables were standardized (difference from the mean divided by the corresponding standard deviation) (Gelman, 2008; Hereford et al., 2004).

Following the Bayesian approach, we assigned vague zero-mean Gaussian prior distribution to the fixed effects with a variance of 100 (Held et al., 2010), as no prior information on the parameters of the models was available.

All the possible combinations among not correlated and collinear
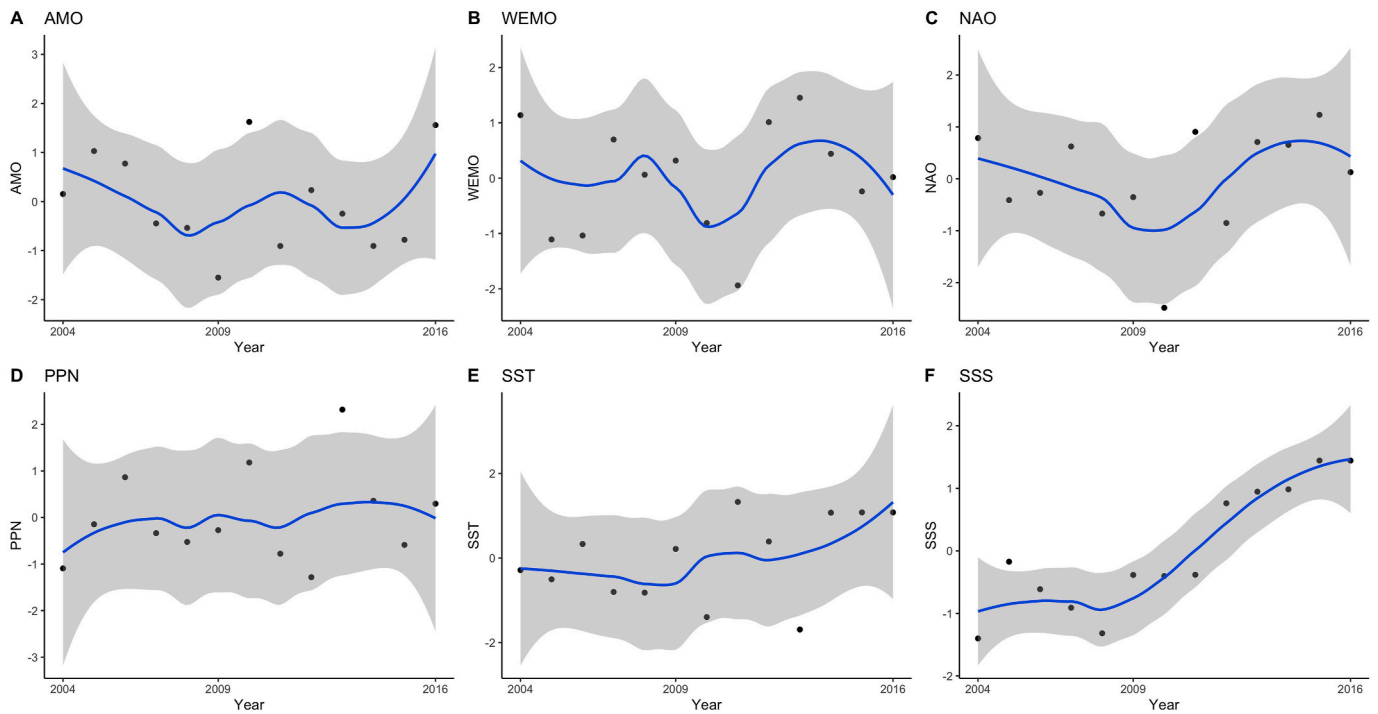
Fig. 2. Time series of the environmental variables used in the models. Before exploration all variables were standardized. Acronyms: SSS, Sea Surface Salinity (SSS in PSU); SST, Sea Surface Temperature (in °C); PPN, Net Primary Productivity (in mg/m^3), AMO, Atlantic Multidecadal Oscillation; WeMO, Western Mediterranean Oscillation; NAO, North Atlantic Oscillation. To better interpret both the direction (positive and negative) and the magnitudes (effect size) of the parameters estimates in relation to others, the environmental variables were standardized, i.e. difference from the mean divided by the corresponding standard deviation.
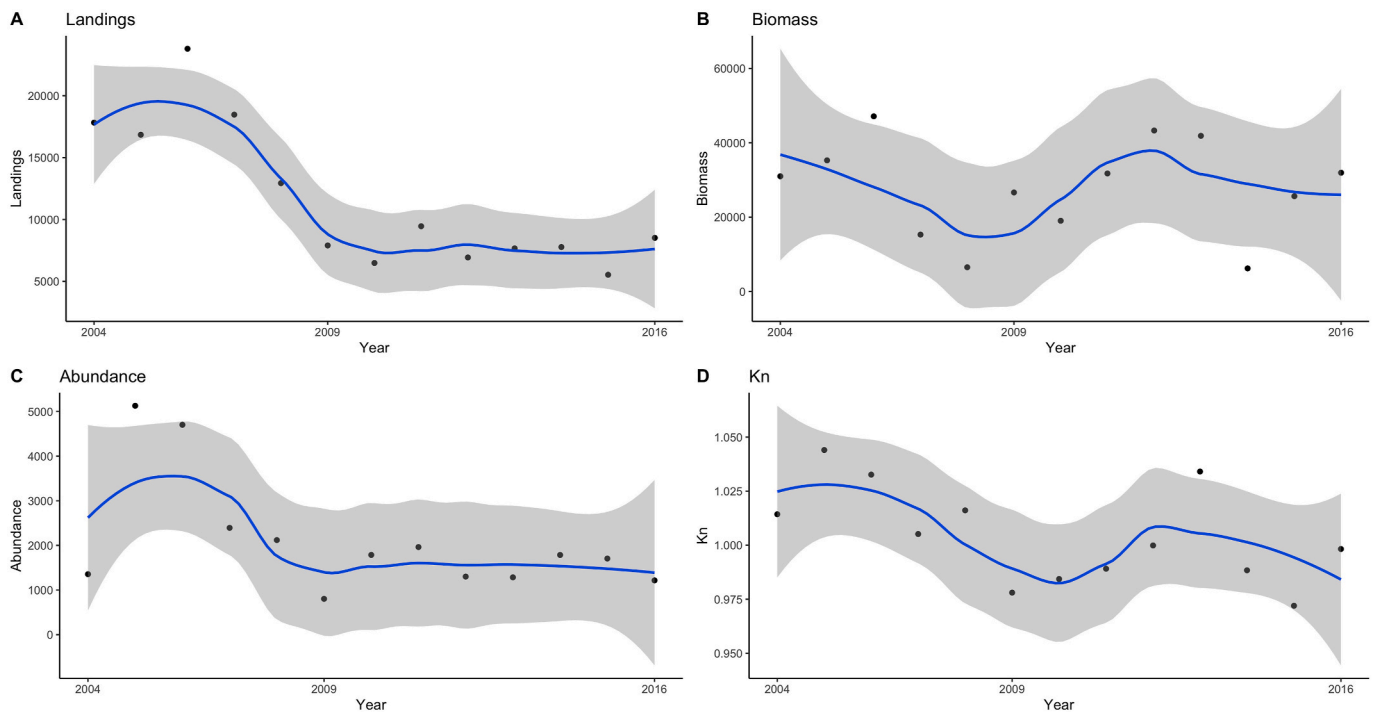
Fig. 3. Landings (A), Biomass (B), abundance (C) and Kn (D) temporal trends of European sardine (*Sardina pilchardus*) in the Geographical Sub-Area 06 from 2004 to 2016.

variables were tested using a loop procedure. The most parsimonious model for each species and dependent variable was selected on the basis of the lowest Watanabe–Akaike information criterion (WAIC) (Watanabe and Opper, 2010), Deviance Information Criterion (DIC) and log-conditional predictive ordinates (LCPO) (Roos and Held, 2011).

Specifically, WAIC and DIC were used as measures of goodness-of-fit, and the LCPO indicated predictive ability. Finally, for each estimated parameter of the final selected model we computed the probability (Pr) of each one to be different from 0 (Pr > or < 0) using the Bayes theorem property (Faraway and Augustin, 2018).
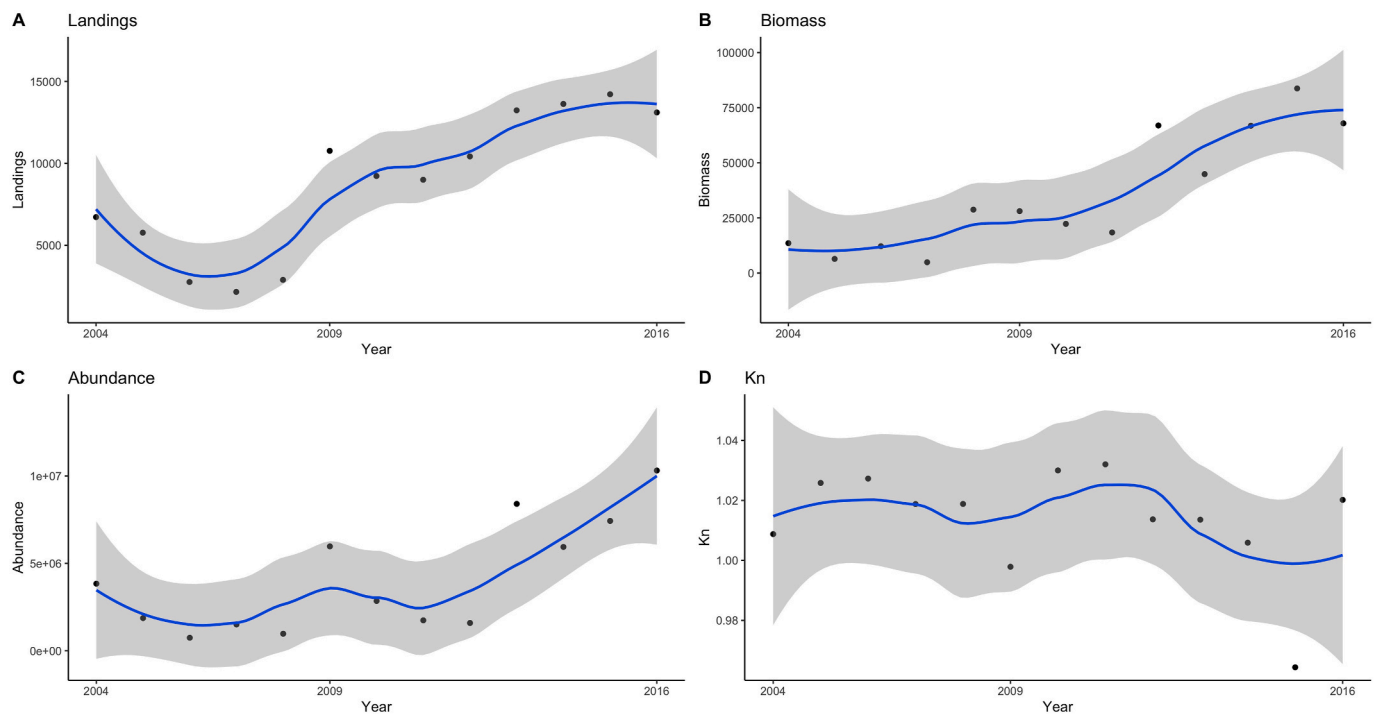
Fig. 4. Landings (A), Biomass (B), abundance (C) and Kn (D) temporal trends of European anchovy (*Engraulis encrasicolus*) in the Geographical Sub-Area 06 from 2004 to 2016.

As explicative variables were standardized, the estimated coefficients could be compared in magnitudes and thus it is possible to assess their effect on the response variables, i.e., higher values of the estimated coefficients indicate a higher effect on the response variable. Using this criterion, we ranked variable's relevance once the final model (selected on the basis of the lowest WAIC, DIC and LCPO values) was selected.

BGLMMs were performed using the R-INLA package (Rue et al., 2009).

3. Results

3.1. European sardine (Sardina pilchardus)

The final B-GLMMs for *S. pilchardus* included different explicative variables depending upon the index analyzed. In particular for landings, the final best model included SSS, NAO, AMO index, and the JFO with a 1-year lag (Table 2). Both the year and area random effects were relevant, suggesting that there were specific differences in the area and in each year for which the landings of this species could change. Overall, the final landings model explained the 74.39% of the total landing variability. A positive relationship was found between the *S. pilchardus* landings and the AMO and NAO index (Table 3), i.e. landings were high with higher AMO and NAO values. On the contrary, the SSS shows a negative relationship with estimated landings for this species (Table 3). Finally, those years where there were jellyfish blooms the previous year showed lower estimates of landings with respect to the reference level (no jellyfish blooms) (Table 3).

The final *S. pilchardus* Bayesian GLMM for the Kn condition factor included SST and the jellyfish occurrence, and year as a random effect (Table 2). The model explained a total of 23.44% of the deviance. The SST showed a negative relationship with the Kn condition factor. There was a 96% probability of having better fish condition when the SST was lower (Table 3). Finally, years when there was a jellyfish bloom showed lower estimates of the Kn condition factor with respect to the reference level (no jellyfish blooms).

Table 2

Model comparison of the 5 most relevant models for each European sardine (*S. pilchardus*) index. Predictor acronyms are: SST = Sea Surface Temperature, SSS = Sea Surface Salinity, NPP = Net Primary Production, AMO = Atlantic Multidecadal Oscillation, WEMO = Western Mediterranean oscillation, NAO = North Atlantic Oscillation, JFO = jellyfish bloom occurrence, JFO^{t-1} = jellyfish bloom occurrence with the temporal lag of 1 year, Y = year random effect, A = area random effect. Statistic acronyms are: WAIC = Watanabe-Akaike information criterion, DIC = Deviance Information Criterion (DIC), LCPO = Log-Conditional Predictive Ordinates (LCPO). The final selected model is highlighted in bold.

	Models	DIC	WAIC	LCPO
Landings	**$1+SSS + NAO + AMO + JFO^{t-1}+Y + A$**	**8.89**	**9.16**	**0.62**
Landings	$1+SSS + NAO + AMO + JFO^{t-1}$	10.92	11.48	0.65
Landings	$1+SSS + NAO + AMO + SST + JFO^{t-1}$	13.67	13.65	0.78
Landings	$1+SSS + NAO + AMO + WEMO + JFO^{t-1}$	13.48	13.76	0.78
Landings	$1+SSS + NAO + AMO + PPN + JFO^{t-1}$	13.26	13.65	0.88
Kn	**$1+SST + JFO + Y$**	**−58.63**	**−58.56**	**−2.20**
Kn	$1+SST + JFO$	−57.14	−56.99	−1.98
Kn	$1+SST + JFO + Y + NPP$	−56.02	−56.24	−2.10
Kn	$1+SST + JFO + Y + NAO$	−56.92	−56.99	−2.05
Kn	$1+SST + JFO + Y + AMO$	−55.44	−55.86	−1.96
Biomass	**$1+AMO + Y$**	**29.82**	**29.97**	**1.17**
Biomass	$1+AMO$	32.07	31.80	1.24
Biomass	$1+AMO + JFO$	32.39	33.10	1.29
Biomass	$1+AMO + WEMO$	33.85	33.50	1.31
Biomass	$1+AMO + WEMO + NPP$	34.63	34.49	1.45
Abundance	**$1+SSS + AMO + JFO^{t-1}+Y$**	**19.20**	**19.06**	**0.80**
Abundance	$1+SSS + AMO + Y$	23.25	23.27	0.95
Abundance	$1+SSS + AMO$	24.38	24.24	0.97
Abundance	$1+SSS + AMO + SST$	26.05	26.19	1.06
Abundance	$1+SSS + AMO + NPP$	26.37	26.37	1.06

The final model for the biomass of the *S. pilchardus* only retained the AMO index and the year random effect as relevant variables. Inclusion of all the other variables resulted in higher WAIC, DIC, and LCPO values

Table 3

Numerical summary of the posterior distributions of the fixed effects of the selected model for each European sardine (*S. pilchardus*) index. This summary contains the posterior mean of the estimated parameters (mean), the standard deviation (sd), the median ($Q_{0.50}$) and 95% credible interval, which is a central interval containing 95% of the probability under the posterior distribution ($Q_{0.025}$ - $Q_{0.975}$). Effects of categorical variables are considered for k-1 of the k factor levels, with the remaining one being considered as the base level. Hence the estimated posterior mean of each factor level will indicate the deviation with respect to the value of the base level. Pr = probability of each variable to be different from 0 (Pr > or < 0) using the Bayes theorem property.

Model	Variable	Mean	Sd	$Q_{0.025}$	$Q_{0.50}$	$Q_{0.975}$	Pr ≠ 0
Landings	Intercept	9.29	0.10	9.08	9.29	9.49	1
	SSS	−0.42	0.08	−0.59	−0.42	−0.24	0.99
	NAO	0.29	0.10	0.08	0.29	0.49	0.99
	AMO	0.26	0.09	0.06	0.26	0.46	0.99
	JFO^{t-1} (1)	−0.10	0.16	−0.43	−0.10	0.22	0.75
Kn	Intercept	0.00	0.00	0.00	0.20	0.00	1
	SST	−0.01	0.00	−0.02	−0.01	−0.01	0.96
	JFO (1)	−0.09	0.01	−0.03	−0.09	0.01	0.77
Biomass	Intercept	10.07	0.18	9.71	10.07	10.43	1
	AMO	0.22	0.19	−0.15	0.22	0.60	0.89
Abundance	Intercept	7.74	0.14	7.46	7.75	8.03	1
	SSS	−0.19	0.11	−0.43	−0.19	0.04	0.95
	AMO	0.16	0.11	−0.07	0.16	0.40	0.92
	JFO^{t-1} (1)	−0.59	0.23	−1.06	−0.59	−0.12	0.99

(Table 2). The biomass model explained only the 13.31% of the total variability. The AMO index showed a positive relationship with respect to the biomass of the *S. pilchardus*. Results showed that with higher AMO the biomass values are expected to be higher (Table 3).

For the abundance of *S. pilchardus* the final model included the SSS, the AMO index and the jellyfish occurrence with the lag of 1-year, as well as the year random effect. Inclusion of all other variables led to higher WAIC, DIC, and LCPO values (Table 2). Overall, the abundance model explained 49.96% of the total variability. The AMO index showed a positive relationship with respect to the biomass of the *S. pilchardus*, which means that with higher AMO values were estimated higher abundance of *S. pilchardus* (Table 3). On the contrary, the SSS presented a negative relationship (Table 3). Finally, years where there was a jellyfish bloom, the previous year showed lower estimation of abundance with respect to the reference level (no jellyfish blooms).

3.2. European anchovy (Engraulis encrasicolus)

The final B-GLMMs for *E. encrasicolus* included different explicative variables depending upon the index analyzed. For landings, the final best model included SSS, SST, NPP, the AMO, and the occurrence of jellyfish in addition to the random effects of area and year. The NAO index and the LCPO index was not included in the most parsimonious model (Table 4). Overall, this model explained the 83.4% of the total variability in the *E. encrasicolus* landings. The AMO index, NPP all showed a negative relationship with respect to the *E. encrasicolus* landings. This means that with lower values of NPP, SST, and the AMO index, there is a higher probability to have more landings (Table 5). On the contrary, the SSS showed a positive relationship, meaning that with higher SSS values were estimated higher landings (Table 5). Finally, years with the occurrence of a jellyfish bloom showed lower estimates of landings with respect to the reference level (no jellyfish blooms).

For the Kn condition factor in anchovy, the final model retained SSS, the AMO index, the random effect of the year, and the jellyfish bloom occurrence (Table 4). The model explained 51.92% of the total variability of the *E. encrasicolus* Kn condition factor. The SSS showed a negative relationship with the *E. encrasicolus* Kn condition factor with a probability to be negative equal to 97% (Table 5). On the contrary, the

Table 4

Model comparison of the five most relevant models for each European anchovy (*E. encrasicolus*) index. Predictor acronyms are: SST = Sea Surface Temperature, SSS = Sea Surface Salinity, NPP = Net Primary Production, AMO = Atlantic Multidecadal Oscillation, WEMO = Western Mediterranean oscillation, NAO = North Atlantic Oscillation, JFO = jellyfish bloom occurrence, JFO^{t-1} = jellyfish bloom occurrence with the temporal lag of 1 year, Y = year random effect, A = area random effect. Statistic acronyms are: WAIC = Watanabe-Akaike information criterion, DIC = Deviance Information Criterion (DIC), LCPO = Log-Conditional Predictive Ordinates (LCPO). The final selected model is highlighted in bold.

	Models	DIC	WAIC	LCPO
Landings	**1+SSS + SST + NPP + AMO + JFO + Y + A**	**10.49**	**10.49**	**0.71**
Landings	1+SSS + SST + NPP + AMO + JFO	16.90	16.84	0.80
Landings	1+SSS + SST + NPP + JFO	18.13	18.43	0.78
Landings	1+SSS + SST + NPP + NAO + JFO	20.70	21.13	0.96
Landings	1+SSS + SST + NPP + AMO	26.78	26.98	1.12
Kn	**1+SSS + AMO + JFO + Y**	**−68.02**	**−67.04**	**−2.44**
Kn	1+SSS + AMO + JFO	−66.43	−66.73	−2.40
Kn	1+SSS + NAO + JFO	−65.37	−65.91	−2.39
Kn	1+SSS + WEMO + JFO	−63.33	−63.89	−2.32
Kn	1+SSS + WEMO + JFO	−62.32	−64.14	−2.18
Biomass	**1+SSS + JFO^{t-1} +Y**	**24.94**	**24.80**	**1.01**
Biomass	1+SSS + JFO^{t-1}	28.38	28.38	1.12
Biomass	1+SSS + JFO^{t-1}+AMO	29.33	29.62	1.17
Biomass	1+SSS + JFO^{t-1}+NAO	29.74	30.03	1.18
Biomass	1+SSS + JFO^{t-1}+NPP	29.21	29.56	1.16
Abundance	**1+SSS + JFO + Y**	**26.10**	**26.23**	**1.04**
Abundance	1+SSS + JFO	32.20	32.36	1.29
Abundance	1+SSS + JFO + NAO	31.72	32.06	1.27
Abundance	1+SSS + JFO + SST	32.35	32.75	1.32
Abundance	1+SSS + JFO + NPP	33.14	33.26	1.34

Table 5

Numerical summary of the posterior distributions of the fixed effects of the selected model for each European anchovy (*E. encrasicolu*) index. This summary contains the posterior mean of the estimated parameters (mean), the standard deviation (sd), the median ($Q_{0.50}$) and 95% credible interval, which is a central interval containing 95% of the probability under the posterior distribution ($Q_{0.025}$ - $Q_{0.975}$). Effects of categorical variables are considered for k-1 of the k factor levels, with the remaining one being considered as the base level. Hence the estimated posterior mean of each factor level will indicate the deviation with respect to the value of the base level. Pr = probability of each variable to be different from 0 (Pr > or < 0) using the Bayes theorem property.

Model	Variable	Mean	Sd	$Q_{0.025}$	$Q_{0.50}$	$Q_{0.975}$	Pr ≠ 0
Landings	Intercept	9.21	0.13	8.96	9.21	9.47	1
	SSS	0.77	0.15	0.47	0.77	1.07	0.99
	SST	−0.36	0.17	−0.71	−0.36	−0.00	0.98
	NPP	−0.45	0.18	−0.82	−0.45	−0.08	0.99
	AMO	−0.18	0.10	−0.39	−0.18	0.03	0.95
	JFO (1)	−0.98	0.29	−1.57	−0.99	−0.41	1
Kn	Intercept	0.01	0.00	0.00	0.01	0.02	1
	SSS	−0.08	0.00	−0.01	−0.08	0.00	0.97
	AMO	0.08	0.00	−0.01	0.08	0.01	0.97
	JFO (1)	−0.01	0.00	−0.02	−0.01	0.00	0.88
Biomass	Intercept	9.94	0.21	9.52	9.94	10.36	1
	SSS	0.73	0.39	0.73	1.08	0.73	1
	JFO^{t-1} (1)	0.53	0.34	−0.15	0.53	1.21	0.94
Abundance	Intercept	15.07	0.22	14.63	15.07	15.50	1
	SSS	0.58	0.19	0.19	0.57	0.95	1
	JFO (1)	−0.54	0.39	−1.33	−0.54	0.24	0.92

AMO index showed a positive relationship with the Kn (Table 5). Finally, years with the occurrence of a jellyfish bloom showed a lower estimate of Kn condition factor with respect to the reference level (no jellyfish blooms).

The final biomass model included as the relevant variables the SSS

and the jellyfish bloom occurrence with the lag of 1 year, as well as the year random effect (Table 4). The final model explained the 62.53% of the total biomass variability of the *E. encrasicolus*. In particular, SSS showed a positive relationship with *E. encrasicolus* biomass which means that higher biomass values were estimated in salter waters (Table 5). Finally, years in which the previous year showed a jellyfish bloom had lower estimates of biomass with respect to the reference level (no jellyfish blooms).

The final model for the abundance of the *E. encrasicolus* included SSS and the jellyfish bloom occurrence in addition to the random effect of year (Table 4). The model explained the 64.69% of the total variability. The SSS showed a positive relationship with the *E. encrasicolus* abundance, with higher abundance values in salter waters (Table 5). Finally, years with the occurrence of a jellyfish bloom showed lower estimates of abundance with respect to the reference level (no jellyfish blooms).

4. Discussion

According to our findings, both sardines and anchovies from the western Spanish Mediterranean were negatively affected by jellyfish blooms (Table 6) both at a population level (biomass, abundance, and body condition) and at their exploitation (landings) level.

Both species are typical small pelagic fishes, and therefore r-selected species (Caddy and Sharp, 1986). Thus, many eggs and larvae of sardine (in winter) and anchovy (spring and summer; Palomera et al., 2007) are present in the ichthyoplankton and jellyfish blooms could potentially prey on the larvae of these fishes, and the recruitment could be affected as was demonstrated by Tilves et al. (2016). Moreover, it is common to observe mass concentrations of anchovy and sardine eggs and larvae in the borders of submarine canyons (Garcia and Palomera, 1996; Würtz, 2012), and simultaneously jellyfish outbreaks mainly occur in the proximity of submarine canyons. Thus, submarine canyons could funnel *P. noctiluca* blooms towards shore during upwelling (Würtz, 2012; Berline et al., 2013). Therefore, jellyfish blooms and anchovy and sardine eggs overlap in the same areas, which could favor egg depredation by

jellyfishes (Benedetti-Cecchi et al., 2015).

Sardine and anchovy have many predators (for example tunas and large pelagic sharks) (Cardona et al., 2015) and potential competitors (for example round sardinella, *Sardinella aurita*) (Morote et al., 2008), but jellyfish have strong and fluctuating blooms (in contrast to other predators and competitors), especially in June (Boero et al., 2008; Boero, 2013; Ottmann et al., 2021), coinciding with the spawning of anchovy (Sabatés et al., 2018), and the season with the highest productivity of the Mediterranean Sea. This seasonal overlap could explain the stronger relationship found between jellyfish blooms and changes in landings and biomass of anchovy than for landings and biomass of sardine.

In the case of abundance, both species showed a strong negative relationship with jellyfish blooms in the previous year. This could not only be related to predation of jellyfish on sardine and anchovy early life-stages, but also with the impact in the body condition of adult stages. In both species, the increase of jellyfish blooms had a direct negative effect on the body condition of the late juvenile and adult fish, most likely due to competition for resources (Tilves et al., 2018a, b), that could lead to lower reproduction rates and higher mortality the following year. In this context, jellyfish could be an important inhibitor for the recovery of fish populations from depleted ecosystems (Lynam et al., 2006). Jellyfish could also compete with sardines and anchovies for similar prey taxa (Brodeur et al., 2008; Tilves et al., 2018a, b). Declines in food availability or changes in the quality of prey have been previously suggested as the main driver of the declines in body condition of small pelagic fish in the area of study (Saraux et al., 2019; Feuilloley et al., 2020; Biton-Porsmoguer et al., 2020).

Jellyfish proliferate in ecosystems with increasing overfishing, and in turn are driven by the climate condition (Mills, 2001; Lynam et al., 2006; Purcell, 2012; Boero et al., 2016). In this context, it is widely known that population dynamics of small pelagic clupeoid fish, such as sardines and anchovies, are affected by large-scale climate phenomena (e.g., Alheit et al., 2014; Checkley et al., 2017; Pennino et al., 2020). Related to this, the AMO index was one of the most important

Table 6
Summary of the results obtained with all the B-GLMMs for both species and indexes. As explicative variables were standardized, the estimated coefficients could be compared in magnitudes and thus it is possible to assess their effect on the response variables, i.e., higher values of the estimated coefficients indicate a higher effect on the response variable. Using this criterion, we ranked variable's relevance once the final model was selected. The relevance of the variable is expressed through the color scale, from red (more important) to light orange (less important). The signal (−) (+) indicates the relationship found between the explanatory variable and the examined index in the B-GLMM. Area and year are random effects and thus there was no estimated coefficient. Blank cells imply that for a determinate target variable, its corresponding environmental variable or jellyfish variable was not part of the B-GLMM explanatory model. Acronymous: SSS, Sea Surface Salinity (SSS in PSU); SST, Sea Surface Temperature (in °C); NPP, Net Primary Productivity (in mg/m^3), AMO, Atlantic Multidecadal Oscillation; WeMO, Western Mediterranean Oscillation; NAO, North Atlantic Oscillation; Jellyfish, Annual jellyfish bloom occurrence; Jellyfish^{-1}, Annual jellyfish bloom occurrence in previous year.

Sardina pilchardus	SSS	SST	NPP	AMO	NAO	WeMO	Jellyfish	Jellyfish[t-1]	Area	Year
Landings	-			+	+			-	X	X
Kn index		-					-			X
Biomass				+						X
Abundance	-			+				-		X
Engraulis encrasicolus	SSS	SST	NPP	AMO	NAO	WeMO	Jellyfish	Jellyfish[t-1]	Area	Year
Landings	+	-	-	-			-		X	X
Kn index	-			+			-			X
Biomass	+							-		X
Abundance	+						-			X

explanatory variables of the observed variability in landing, fitness, abundance, and biomass of both species examined here, at least during the period studied (Table 6). According to Enfield et al. (2001), AMO showed warm phases and cool phases regime shift per multidecadal periods. Since the mid-1990s, the AMO has been in a warm phase (NOAA, 2005). The AMO affects air temperatures and rainfall over much of the Northern Hemisphere (Knight et al., 2006). There are many examples that show that AMO drives the populations of many fish (Alheit et al., 2014; Faillettaz et al., 2019). Contrary to the previous research of Martin et al. (2011), we did not find an effect of WeMO on sardines and anchovies. However, it should be noted that Martin et al. (2011) analyzed the effect of WeMO on sardine and anchovy production in a restricted area of the north-western part of the Mediterranean Sea, while the present study covers a larger area (the entire GSA06 area). The WeMO could have a major impact from a particular area (Martin-Vide and Lopez-Bustins, 2006).

Another important environment variable was salinity (Table 6), which showed mixed effects between species (anchovy and sardine) and the explored indexes. For anchovy, the effect was positive in landings, abundance, and biomass. The results of the models with landings as a dependent variable showed great coherence with the results of the models with abundance variable (Table 6). Our results are in accordance with Carpi et al. (2015), which found that marked salinity gradients could have a positive effect on anchovy catches in the Adriatic Sea. Additionally, Pennino et al. (2020) found a positive relationship between salinity and anchovy biomass and landings measures in the GSA06. In contrast, landings of sardines presented a negative relationship with salinity. Sardine aggregations tend to be higher in shallower areas characterized by lower salinity that probably are less favorable for this species (Quattrocchi and Maynou, 2017). These results are also in agreement with Pennino et al. (2020), which found a negative relationship between landings of sardine in the GSA06 and sea surface salinity using random forest models and several temporal lags. The primary production indicator was correlated only with anchovy landings showing a negative relationship. Negative relationships were also found between anchovy adults and primary productivity in other Mediterranean areas (Giannoulaki et al., 2013; Quattrocchi et al., 2016). Recent studies point out that areas with high primary productivity concentration could affect water transparency, increasing the difficulty of finding prey (Pennino et al., 2020). Sea surface temperature was mainly relevant for the sardine Kn showing a negative relationship. This result is in accordance with the literature where the effect of temperature on sardine was found negative in different Mediterranean areas (Bellido et al., 2008; Bonanno et al., 2016; Brosset et al., 2015; Giannoulaki et al., 2013; Pennino et al., 2020).

Human impacts on the marine environment seem to favor the occurrence of jellyfish blooms (Boero et al., 2008; Purcell, 2012; Boero, 2013; Duarte et al., 2013; Dong, 2019). Thereby, in the current context of cumulative human and environmental impacts (Ramírez et al., 2018), an ecosystem approach to manage marine resources is required to ensure that the exploitation of small pelagic fishes in the Mediterranean Sea is done under a "safe operating space" that can guarantee their conservation in the future and avoid total depletion of these important stocks. In this sense, it seems necessary to include the potential effects of jellyfishes along with environment variables in stock assessment models, integrated analyses and fisheries management.

CRediT authorship contribution statement

J.C. Báez: Conceptualization, Investigation, Methodology, Data curation and Writing - original draft. Maria Grazia Pennino: Software, Validation, Formal analysis, Data curation, Writing - review & editing. Marta Albo-Puigserver: Investigation, Methodology, Writing - review & editing. Marta Coll: Methodology, Funding acquisition, Investigation, Project administration, Resources, Supervision, Writing - review and editing. Ana Giráldez: Investigation, Data curation, and Writing - review

& editing. José María Bellido: Methodology, Funding acquisition, Investigation, Writing - review and editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

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