

# Changes in the spawning habitat of two small pelagic fish in the Northwestern Mediterranean

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## Abstract

We investigated the effects of three sea surface oceanographic variables (temperature, salinity and chlorophyll *a*) on the abundance of eggs and larvae of two summer-spawning species in the NW Mediterranean sea, the anchovy *Engraulis encrasicolus* and the round sardinella *Sardinella aurita*, based on data from ichthyoplankton surveys carried out in the 1980s, 2000s and 2010s. The environmental data showed an increase in sea water temperature and salinity along time, coupled with a decrease in chlorophyll *a* (proxy for primary production). These long-term directional changes in environmental conditions helped explain the important reduction observed in the abundance of eggs and larvae of anchovy, as well as shrinking of spawning habitat in this species. At the same time, the probability of occurrence of round sardinella has increased from practically zero in the 1980s to probabilities near 1 along the coastal area of the study region in the two decades of the 21<sup>st</sup> century. Given that the trends observed in the environmental variables along the three decades of study are expected to continue during the 21<sup>st</sup> century, as a consequence of climate change, the spawning habitat of anchovy is expected to continue decreasing, while round sardinella habitat can expand. Considering that anchovy is of high commercial importance in NW Mediterranean fisheries, while round sardinella has very low commercial interest, our results show that the viability of small pelagic fisheries in the area may be compromised.

## keywords

*Engraulis encrasicolus*, *Sardinella aurita*, habitat modelling, ichthyoplankton, NW Mediterranean, climate change, GAMs

## 1. Introduction

Small pelagic fishes aggregate at different spatial scales, whose extent and distribution may vary in time. In particular, the spawning grounds of small pelagic fishes are known to expand or contract following changes in abundance of the reproductive stock (Checkley et al., 2009; Giannoulaki et al., 2013; Saraux et al., 2014). The populations of small pelagics are naturally subject to strong abundance fluctuations (Checkley et al., 2017) which may be more pronounced in those species under heavy fisheries exploitation, where age class structure is usually truncated with very low individuals in age classes beyond 1 or 2 year olds. Changes in the location and extent of spawning habitat for species of commercial interest have received a lot of research attention (inter alia, Giannoulaki et al., 2013; Saraux et al., 2014; Brosset et al., 2017). Results have shown that these changes depend on a complex interaction of environmental factors, both physical (temperature, salinity, currents or other oceanographic structures) and biological (productivity, usually estimated with the proxy of satellite-derived chlorophyll). The spawning habitat of small pelagic fish can be characterized from information derived from acoustic surveys (Saraux et al., 2014) or ichthyoplankton surveys (Checkley et al., 2000; Palomera et al., 2007), which if carried out at the appropriate time of the year, provide direct estimates of eggs and larvae production, directly linked to spawning (van der Lingen and Huggett, 2003).

In areas of the world with a strong tradition of fisheries biology applied to fisheries management, standardized ichthyoplankton surveys are routinely employed to monitor the abundance and spatial distribution of early life stages of fishes of commercial interest (Smith and Moser, 2003; van der Lingen and Huggett, 2003). In the western Mediterranean, long-term monitoring programmes are not available, but we re-analysed data from seven ichthyoplankton surveys carried out non-continuously over a 30 year period (1983-2012) along the Catalan coast to monitor the early life stages of summer spawning small pelagic fish, European anchovy (*Engraulis encrasicolus*) and round sardinella (*Sardinella aurita*). European anchovy is a species of high fisheries interest in the Mediterranean and northeast Atlantic, ranking second (after sardine *Sardina pilchardus*) in volume of landings in the south European seas (36 to 44° latitude) (FAO FishStat database, 2018). Evidence from acoustic and ichthyoplankton surveys and fisheries landings suggests that anchovy stocks have decreased markedly in this area (inter alia, Taboada and Anadón, 2016; Brosset et al., 2017),

while round sardinella, a subtropical species, is increasingly abundant in the NW Mediterranean (Sabatés et al., 2006; 2009; Maynou et al., 2014). The main species of commercial interest, the winter-spawning sardine, shows also a strong decrease in biomass (van Beveren et al., 2016; Brosset et al., 2017).

Environmental change has been predicted to cause irreversible changes in the spatial distribution, behaviour and productivity of species, potentially leading to invasions, extinctions and a decrease in the fisheries catch potential (Pörtner et al., 2014). Compared to adult stages, fish early life stages are typically constrained in space and time. This is due to the narrower physiological tolerance of environmental conditions and lower locomotion abilities of larval stages, but also to very specific habitat requirements during spawning and larval phase (Ciannelli et al., 2015). Spatiotemporal changes in egg and larval abundance can be a sensitive indicator of environmental change, and pelagic fishes are particularly sensitive to changes in water masses. Understanding of the mechanisms relating environmental changes to the extent of spatial and temporal location of suitable spawning habitats of small pelagic fish is a key first step to predicting and projecting such future changes, and thereby adapting to these changes (McClatchie et al., 2018).

The causes for the strong reduction in the abundance of small pelagics in the south European seas are complex, but research results usually highlight excessive fishing pressure and adverse environmental conditions in the last two decades (possibly linked with climatic change) (Martín et al., 2012; Taboada and Anadón, 2016; van Beveren et al., 2016; Coll et al., 2018). The combined effect of these drivers has resulted in unbalanced demographic structures of the small pelagic stocks, with individuals in poor condition (Brosset et al. 2017) that delay growth and favour earlier maturity (Brosset et al. 2016). Because the amount of eggs produced (fertility) of fishes is directly, but non-linearly, related to fish size and condition, the overall effect of this unbalanced demographic structure is diminished reproductive potential (Ganias et al. 2014) and, possibly, increasing frequency of years with poor recruitment.

The objectives of the work are to assess trends in abundance and changes in the spatial distribution of early life stages of the two summer spawning small pelagic species in the Mediterranean (anchovy and round sardinella) from ichthyoplankton surveys carried out along a thirty-year period and identify environmental factors that explain these changes.

Establishing a spatial model of dependence of early life stages on environmental factors can be useful to forecast the effect of future changes in these environmental variables (e.g. due to climate change) on fish spawning habitat.

## 2. Material and Methods

### 2.1 Data source

The full data set of ichthyoplankton used came from three biological-oceanographic research programs conducted by the Institute of Marine Sciences in Barcelona (<http://www.icm.csic.es>) along the Catalan coast (Fig. 1): ARECES 1980s (June and July 1983), CACO 2000s (July 2003; June and July 2004), and FISHJELLY 2010s (June 2011; July 2012). Samplings were conducted with the R/V *Garcia del Cid* in June and July, peak of spawning of anchovy and round sardinella in the northwestern Mediterranean (Palomera et al., 2007). In all surveys, the same area was covered and the same sampling methodology was applied. While 2-3 surveys per decade over a thirty year period may seem low, the sampling surveys encompass a wide mesoscale area, covering the spawning grounds of the two study target species. This strengthens the robustness of the results and allows to detect possible changes not only in abundance but also to the spatial distribution. Moreover, the ichthyoplankton samplings include *in situ* measurement of hydrographic parameters allowing to study changes in the spatial distribution in time and in relation to environmental conditions. Sampling stations were placed along 17 transects perpendicular to the shoreline, from near the coast to the shelf break. On each transect, stations were placed between 14 and 16 km apart, and the distance between transects was around 18.5 km. The total numbers of sampled stations, ranged between 44 and 65 (Table 1).

Ichthyoplankton samples were collected both day and night using a bongo net of 300  $\mu$ m mesh size and 60 cm of diameter. Net towing speed was approximately 2 knots. Hauls were oblique from a maximum depth of 200 m to the surface (or from 5 m above the bottom to the surface at stations shallower than 200 m). The volume of filtered water was estimated by a flowmeter placed in the center of the net mouth. Zooplankton samples were fixed immediately after collection in 5% formaldehyde buffered with sodium tetraborate. In the laboratory, fish eggs and larvae were sorted and identified from the preserved samples. Eggs

and larvae of *S. aurita* and *E. encrasicolus* collected at each station were standardized to a number per 10 m<sup>2</sup> of the sea surface.

In all cruises, except in July 1983, hydrographic conditions, temperature and salinity, were obtained at each station with a CTD probe. In July 1983, 5-liter Niskin bottles fitted with reversing thermometers were used with samples collected at standard depths; salinity measurements were taken with an induction salinometer. In all cruises, water samples were collected at different levels of the water column to determine chlorophyll *a* concentration (see Sabatés et al., 2009 for methodological descriptions).

## 2.2 Environmental variables

At the ichthyoplankton sampling stations, CTD casts (Niskin bottles in July 1983) were obtained which allowed to derive the following environmental variables:

- Sea Surface (5 m) Temperature (SST, °C)
- Sea Surface (5 m) Salinity (SSS)
- Sea Surface (5 m) Chlorophyll *a* (Chl *a* 5m; mg m<sup>-3</sup>)
- Intermediate (20 m) Chlorophyll *a* (Chl *a* 20m; mg m<sup>-3</sup>)
- Depth of Chlorophyll *a* Maximum (DCM, m)
- Chlorophyll *a* at the DCM (Chl *a* DCM; mg m<sup>-3</sup>)
- Deep (60 m) Temperature (T60, °C)
- Deep (60 m) Salinity (S60)
- Deep (60 m) Chlorophyll *a* (Chl *a* 60m; mg m<sup>-3</sup>)
- Deep (75 m) Temperature (T75, °C)
- Deep (75 m) Salinity (S75)
- Deep (75 m) Chlorophyll *a* (Chl *a* 75m; mg m<sup>-3</sup>)

However, not all variables could be determined at all sampling stations. In particular, missing data for the variables at the deep levels (Chl *a* DCM, T60, S60, Chl *a* 60m, T75, S75 and Chl *a* 75m) accounted for over 20% of the total in the 1980s samplings. Pairwise correlations showed that several variables were correlated (Pearson's  $|r| > 0.6$ ), suggesting that statistical analysis might reveal problems of multicollinearity. For these reasons, only 3 uncorrelated environmental variables were selected as explanatory variables: SST, SSS, Chl *a* 20m. Intermediate Chl *a* 20 m was chosen to represent surface chlorophyll over the reading at 5 m

because it had more complete data and both variables provide essentially the same information (Pearson's  $r = 0.75$ ).

### 2.3 The study area

The dynamics of the Western Mediterranean sea is subject to the influence of the North Atlantic climate at decadal scales. The temperature of the upper layers has significantly increased since the early 1970s, at a rate of 0.25 °C per decade (Vargas Yáñez et al., 2009), tracking the trends of the Atlantic Meridional Oscillation (AMO) (Vargas Yáñez et al., 2010; Tsikliras et al., 2019). Superimposed on this long-term decadal trend, local oceanic climate is modulated by local drivers (Vargas Yáñez et al., 2010), such as the Western Mediterranean Oscillation (WeMOI, Martín et al., 2012), which is linked to local precipitation and the river flow regime of Western Mediterranean rivers, viz. the Rhone and the Ebro. The flow of the Rhone, for instance, was very high in the early 1980s, at its lowest in the first years of the 21<sup>st</sup> c. and increasing again in the current decade, while the Ebro river flow has been decreasing steadily for the past 4 decades (Cozzi et al., 2019). The variations in river flow are accompanied in all cases by a decrease in the nutrient load (Cozzi et al., 2019), which might explain the observed decrease in chlorophyll *a* concentration in the Gulf of Lions and NE Spain in the last two decades (Colella et al., 2016).

The study area covers the Catalan Sea continental shelf and the slope (NW Mediterranean, Fig. 1). The continental shelf is, in general, narrow and widens in the southernmost part, in the vicinity of the Ebre River Delta, and in the north between the main submarine canyons, south of the Gulf of Lions. The area is characterised by a permanent shelf-slope density front along the shelf break separating open sea high-salinity waters from lower salinity coastal waters (Font et al., 1988). A permanent geostrophic current (the Northern Current) associated to the front flows from NE to SW, roughly parallel to the coast, with maximum speed of 0.60 m/s and an overall transport of around 1 Sv (Castellón et al., 1990). The front and associated current are subjected to high mesoscale variability that causes oscillations, meandering and eddy generation (Rubio et al., 2005). The northern sector, which is more directly influenced by strong northerly winds, is generally colder than the central and southern parts, and a surface thermal front roughly coincides with the limit of frequent northerly winds (Sabatés et al., 2009). The NW Mediterranean coast also receives significant runoff from two major western Mediterranean rivers, the Rhone and the Ebre, which enhance the shelf-slope front by lowering the salinity of shelf waters (Salat, 1996). Over the southern shelf, low salinity patches can be found on the surface layer near the Ebre mouth or quite far away, trapped by



eddies (Font et al., 1990; Wang et al., 1988). In the northern area, Rhone influence can also be felt through relatively low salinity at surface just along the Northern Current path (Salat 1996; Sabatés et al., 2007).

The water column structure presents a marked seasonal cycle with strong stratification in summer. In this period, vertical water movement is very limited, and almost all the surface nutrients become depleted, resulting in primary production restricted to the deep chlorophyll maximum (DCM), a thin layer at the deepest levels of the photic zone (Estrada et al., 1993). According to Estrada and Salat (1989), the presence of the shelf-slope front contributes to enhance the productivity at the DCM level. Surface productivity is restricted to areas influenced by river runoff that can be identified by a lower salinity surface layer; down to ~ 20-30 m, accounting for the typical surface mixed layer above the thermocline (Salat et al., 2002; Masó et al., 1998). These average summer conditions show interannual variations due to the changes in the heat balance of air-sea exchanges in the region and fresh water influx, both variable from year to year.

## 2.4 Statistical analysis

We used General Additive Models (GAMs: Hastie and Tibshirani, 1990; Wood, 2006) to assess the influence of environmental variables on the abundance of eggs and larvae of *Engraulis encrasicolus* and *Sardinella aurita* as a proxy for determining the spatial extent of spawning habitat in both species during the spawning peak (June and July, summer in the northern hemisphere). GAMs are a flexible class of mathematical models that allow incorporating smooth functions to model the non-linear effect of continuous explanatory variables (Wood 2006). The total number of explanatory variables was reduced before the formal GAM selection procedure by examining the correlation matrix between pairs of environmental variables and discarding one variable of each pair when  $|r| > 0.6$ , following Wintle et al. (2005). For each pair of correlated variables, the variable retained was that with higher correlation with total ichthyoplankton abundance or lower amount of missing values, see above. The 3 candidate explanatory variables were: sea surface temperature (°C, SST), surface salinity (SSS), and log-transformed chlorophyll *a* at 20 m depth (log Chl20) as a proxy for surface chlorophyll *a*. We restricted the form of the smooth function to an equivalent polynomial of a maximum of degree 5, by setting the number of knots *k* to 5, to avoid over fitting the models with complex shapes of little biological significance (Wintle et

al., 2005). The decade (1980s, 2000s, 2010s) was added as linear intercept to the GAM models as a proxy for the spawning stock condition in each sampling period. We used a modelling approach based on information theory (Burnham and Anderson, 2002) building sets of candidate models of increasing complexity and choosing the “best” model based on minimizing an information criterion, in our case Generalized Cross Validation (GCV). In all cases, decreasing the GCV score coincided with decreasing values of Akaike’s Information Criterion (AIC) and increasing percentage of deviance explained, two other criteria often used in model selection (Burnham and Anderson, 2002; França et al., 2012). Selection of variables was based on the GCV score and followed a forward model selection algorithm (Wood, 2006): Starting from a null model (intercept-only model), we added each explanatory variable one at a time and selected the model which produced the lowest GCV. Then we added a second explanatory variable and continued adding variables to the model while GCV decreased. We used the quasi-poisson probability distribution function as error distribution and the logarithm as link function for eggs and larvae abundance of anchovy. In the case of round sardinella, the data on early life stages contained a high number of zeros and the GAM models were built using presence/absence only, with a binomial distribution function and logit link. The GAMs models were fitted with the mgcv package v. 1.8-15 (Wood, 2006) of the statistical package R v. 3.3.2 (R Development Core Team, 2016). We interpreted the effect of the selected explanatory variables on the early life stages of both species by inspecting the partial plots in the range of values containing 95% of the observations, i.e. excluding the extreme lowest and highest 2.5% quantiles because predicted effects may be subject to the influence of outliers. We highlight the neutral effect (0) in the partial plots to discuss the environmental effects in terms of negative or positive.

## 2.5 Habitat models

Predictive maps of distribution of eggs and larvae for each decade were computed over a 4 km square grid on the sampling domain with the results of the GAM models. Four km was chosen as a (round) average of the distance among replicates of the same sample station across years (Fig. 1). Predictors SST, SSS and chlorophyll *a* were calculated as June-July averages per decade at each grid cell. For each species early life stage, the GAM model selected was projected onto each grid cell to derive the abundance in the case of anchovy (number / 10 m<sup>2</sup>) or probability of encounter in the case of round sardinella. In addition to the distribution maps, the percentage of surface area occupied by high-density patches of

eggs and larvae was also computed, defining high density as grid cells with  $n \geq 500$  eggs or larvae /  $10 \text{ m}^2$  in the case of anchovy and cells with probability  $> 0.5$  of encountering eggs or larvae in the case of round sardinella.

## 3 Results

### 3.1 Environmental variables

The spatial distribution of temperature showed, as expected for the summer period, a gradient from south to north with higher values in the southern part of the area (maps of horizontal distribution of the environmental variables are shown in Supplementary material 1, Fig. S1a-c). In the 2000s and 2010s surveys, a clear temperature front, perpendicular to the coastline, was apparent around  $41^{\circ}45' \text{ N}$ ,  $3^{\circ}20' \text{ E}$  (Palamós canyon), especially in July (see also Sabatés et al., 2009; 2018), but it was not evident in the 1980s. Overall, temperatures tended to be higher near the coast (Fig. S1a). Salinity showed higher values offshore and the presence of low salinity patches over the southern continental shelf, in the vicinity of the Ebro River delta, where continental fresh water runoff has a marked influence even in summer (Fig. S1b). In June 1983, a significant input of low salinity waters from the Rhone River was evident in the northernmost part of the area, resulting in exceptionally low values (30.5 to 32.0). Note that the maximum values recorded for salinity in the 1980s were lower than 38, while in the 21<sup>st</sup> c. samplings values higher than 38.0 were found offshore. Chlorophyll *a* showed higher values near the coast, in the vicinity of the river mouths, particularly the Ebro and the Rhone (Fig. S1c), but also the Francolí, Llobregat and Besós, which are secondary rivers located in the central part of the area (Fig. 1). A decreasing chlorophyll *a* trend was detected along the 3 decades, with peak values higher than 2.0 in June 1983 to readings typically lower than 0.3 in June 2011 and June 2012.

The boxplots of SST in Supplementary material 2 show that temperatures were lower in June than in July in the three decades studied (Fig. S2a), as expected, although June temperatures were lower in 1980s than in the two decades of the 21<sup>st</sup> century. Conversely, July temperatures were higher in 1983 and 2003 and decreased in the later surveys. Note that water temperature at deeper layers (60 and 75 m, Figs. S2a) also appeared to increase, but the temperature difference between months was not appreciable. The boxplots of SSS (Fig. S2b)

show that salinity was lower in the June than in the July surveys, but with a clear increasing trend along the three decades in both months. Salinity readings were typically below 37.5 in the 1980s while they became closer to 38.0 in the samplings carried out in 2000s and 2010s. In the first survey (June 1983), a low-salinity intrusion from the Rhone river into the northern sector of the study area resulted in some stations producing readings as low as 30 to 36 (Fig. S1b). Salinity at deeper layers (60 and 75 m) were observed to increase along time as well (Figs. S2b).

The boxplots of Chl *a* (Fig. S2c) did not show significant differences between months within each decade, but values in the 1980s were significantly higher than in later surveys, both at the surface (5 m level) and at the 20 m level, with a clear decreasing trend. This trend to decreasing Chl *a* concentration was also apparent in readings at other depth levels (Figs. S2c), with a concomitant increase of the depth of the deep chlorophyll maximum (DCM), from ca. 55 m in June 1983 to ca. 62 m in July 2011 (Fig. S2d).

The abundance of anchovy eggs and larvae was highest in the 1980s (Figs. S1d, e), with no significant differences between June and July in the three decades (Figs. S2e, f). Round sardinella eggs and larvae were not detected in the first survey (June 1983) (Figs. S1f, g and Figs. S2g, h). Their abundance was highest in (2000s) and decreased in the 2010s.

### 3.2 GAM models

The results of the GAM fitting are shown in Table 2 and Fig. 2. The best model fit was obtained with 2 or 3 explanatory variables (Table 2). The deviance explained by these models was between 25.2% and 44.4 %.

In the case of anchovy eggs, the model identified SSS, Chl *a* 20 m and SST, in this order, as the explanatory variables. Salinities between 37.3 and 37.8 had a positive effect on egg abundance, while very low and very high salinities also showed a positive effect, but the number of data points to support the model at the extremes was low. Values of Chl *a* 20 m between 0.10 and 0.30 mg m<sup>-3</sup> also had a positive effect on anchovy egg abundance, with a few data points supporting high abundance at chlorophyll values above 1.1 mg m<sup>-3</sup>. The effect of temperature on anchovy eggs was positive between 20 and 24.5 °C, becoming

negative quickly at higher temperatures. Note the important decrease in the value of the model intercept, indicator of total abundance, from the 1980s to the later decades (Fig. 2a).

In the case of anchovy larvae the model selected Chl *a* 20 m, SSS and SST in this order. Chl *a* 20 m had a positive effect over a wider range of values compared to eggs, with a positive effect of chlorophyll between 0.08 and 0.37 mg m<sup>-3</sup>. However, the range of salinities with a positive effect on anchovy larvae was higher than for eggs: 37.7 to 38.1. Very low salinity values (below 36.5) also had a positive effect, although with very low number of data points supporting the model. The range of temperatures with a positive effect on anchovy larvae was similar than for eggs, 20 to 25 °C. At higher temperature values the abundance fell strongly. Note also the important decrease in the value of the intercept along the 3 decades.

In the case of round sardinella eggs, the model identified Chl *a* 20 m, SST and SSS, in this order, as the explanatory variables. The probability of encountering round sardinella eggs was higher than 50% at chlorophyll values higher than 0.14 mg m<sup>-3</sup> and higher than 98% at chlorophyll values 1.0 mgm<sup>-3</sup>. The probability of encountering round sardinella eggs increased nonlinearly with increasing temperature until 25.5 °C and decreased at higher temperatures. Conversely, the probability of finding round sardinella eggs decreased with increasing salinity, becoming lower than 50% at salinities higher than 37.8. The effect of decade on the model intercept was positive, with practically null probability of encountering sardinella eggs in the 1980s.

In the case of round sardinella larvae, the model identified only SSS and SST, in this order, as the explanatory variables. The probability of encountering round sardinella larvae was higher than 80% at salinities below 37.5, decreasing rapidly at higher salinity. The probability of encountering larvae increased nonlinearly with temperature, never reaching 100%, but with probabilities higher than 50% at temperatures above 23 °C. The effect of decade was similar than for round sardinella eggs.

### 3.3 Habitat models

With the results of the GAM models, predictive maps of distribution of eggs and larvae in each decade were computed over a 4 km square grid on the sampling domain. Fig. 3 shows the results. Spawning areas for anchovy (Fig. 3a, left panels), defined as grid cells with high

habitat suitability, are mainly located in the northeast area (east of 2.75° E, approximately) and over the southern shelf off shore the Ebro delta. However, the predicted density by the habitat model decreases importantly from the 1980s. The suitable habitat for anchovy larvae remains relatively constant overtime in the northeast area (Fig. 3a, right panels) but decreased in the Ebro delta area. The pattern shown in the distribution maps are summarized in Table 3, which indicates that habitat in the 1980s was suitable for eggs and larvae in 100% of the study area, but decreased to less than 1% for eggs and 55% for larvae by the 2010s. The eggs and larvae of round sardinella show the opposite pattern: in the 1980s the probability of suitable habitat conditions was null, while it increased to 30% (eggs) and 22% (larvae in the 2010s).

In the case of round sardinella, predicted high suitability areas were located in the southern half of the study area (Barcelona as northernmost latitude) and closer to the coast, both for eggs and larvae. In the 2000s the range of suitable areas expanded considerably to the north, while in the 2010s habitat suitability decreased slightly, but is still considerably larger than in the 1980s.

## 4 Discussion

We detected clear changes in the values of the environmental variables along the three decades of the study period. There was a temperature increase (particularly marked for the June surveys) at all depth levels studied, even in the 60 and 75 m readings (Supplementary material 2). This trend is in accordance with the continuous warming documented in the Mediterranean at surface, intermediate levels and in deep waters in recent decades (Vargas Yañez et al., 2009; Calvo et al., 2011; Skliris et al., 2012; Schroeder et al., 2016). Skliris et al. (2012) analysed sea surface temperature from satellite observations and the NOCS<sup>1</sup> data set and estimated an average increase of 0.29 °C / decade over the 1985-2008 period in summer in the Western Mediterranean (nearly half the rate than in spring, 0.54 °C /decade, but higher than in autumn or winter). In the Spanish coasts, the temperature increase is higher than the regional average in the Western Mediterranean (Skliris et al. 2012: Fig. 3).

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<sup>1</sup> National Oceanography Centre Southampton, global monthly mean gridded data set of marine surface variables.

Surface salinity and chlorophyll *a* showed opposite trends, increasing and decreasing, respectively, along the three decades. The salinity increase could be related with a diminution of the river runoff waters, in particular from the Rhone River, that in the early 1980s was exceptionally high (Sabatés, 1990). In the study area, at the end of spring, low salinity waters from riverine outflow may spread over wide areas due to the well-established stratification (Salat, 1996). In that period, river runoff is the main mechanism that can supply nutrients to the surface, and a good correspondence between low salinity and high chlorophyll *a* at surface is characteristic of that period (Masó et al., 1998; Sabatés et al., 2009; 2013). A decrease in chlorophyll *a* concentration has also been documented from satellite measurements off the Rhone River mouth, likely due to a decrease of the riverine runoff waters, and elsewhere in the Gulf of Lions and the Catalan coast for the period 1998-2009; a result also found in the outflow of other Mediterranean rivers (Colella et al., 2016: Fig. 2). In a recent paper, Cozzi et al. (2019) documented the reduction in river flow and main nutrients (nitrogen, phosphorus) of the Ebro and Rhone rivers over the last four decades. On the other hand, and at local scale, a decreasing trend in the abundance of most phytoplankton groups has been documented in the Catalan coastal waters (Blanes Bay), associated with a reduction in nutrient availability (Nunes et al., 2018). According to these authors, the possible drivers for this oligotrophication would include stronger stratification (due to increased temperature or freshwater input) and the improvement of wastewater treatment in the region.

A deepening over time of the depth of the deep chlorophyll maximum (DCM) was also evident in the data (Supplementary material 2), which can be interpreted as a further evidence for a trend towards oligotrophication. The DCM is a permanent feature during the stratification period in the Mediterranean Sea (e.g. Estrada et al., 1993; Siokou-Frangou et al., 2010), and their seasonal evolution is characterized by a deepening from May to July in coincidence with the deepening of the pycnocline (Lavigne et al., 2015). In a context of sea warming, the period of water column stratification will likely increase in the Western Mediterranean, leading to deeper DCM in the future, as observed in the more oligotrophic Eastern Mediterranean (Siokou-Frangou et al. 2010). In the Catalan coast, Coma et al. (2009) already showed enhanced stratification with ca. 40% lengthening of summer conditions since 1974. These marked changes in the local environmental variables, with a consistent direction, would help to explain in large part the decrease in abundance of anchovy early life stages observed in the data. Temperatures higher than ca. 25° C produced a negative effect on the



abundance of anchovy eggs and larvae (Fig. 2a, b). A narrow range of intermediate salinities around 37.5 generate a positive impact, with decreasing abundance both at high and low salinities (Fig. 2a, b). A notable exception was observed in the northern sector with salinity < 36.5, where the influx of eggs and larvae from the spawning area in the Gulf of Lions is the main explanatory factor for their high abundance (see also Sabatés et al., 2007). Intermediate values of chlorophyll *a* (~0.1 - 1 mg m<sup>-3</sup>) showed to have a positive effect on anchovy eggs and larvae. The observed decrease of chlorophyll *a* along the three decades and the increase of temperature and salinity help explain the decreasing abundances of anchovy eggs and larvae. The trends projected for the next few decades (Durrieu de Madron et al., 2011; Calvo et al., 2011) for our three explanatory variables agree well with the trends observed in the study period and suggest that the habitat of anchovy may shrink even further in the coming decades. The forecast decrease in surface chlorophyll *a* combined with a likely future deepening of the DCM could negatively affect the ability of large (post-flexion) larval anchovy to obtain food at the DCM, where high concentrations of zooplankton have been found during daylight hours (Saiz et al., 2014). Previous studies conducted in the region have been reported that post-flexion anchovy larvae perform diel vertical migrations to feed at the DCM during the day, while the low temperatures (~15°C) detected at the DCM level restrict the vertical migration of *S. aurita*, which feeds preferentially at the surface (Olivar et al., 2001; Sabatés et al., 2008).

Excessive fishing pressure can also contribute to explain the decreasing abundance in eggs and larvae of anchovy along the 1980s-2010s period, by reducing the spawning stock biomass (round sardinella has very low commercial interest in the area). Tsikliras et al. (2019) and recent stock assessment of anchovy in the study area (Supplementary material 3) show how the late 1970s and early 1980s were years of high landings of anchovy in the Western Mediterranean, contrasting with the low productivity of the stock in the 2000s and 2010s. Spawning stock biomass started to decrease from the late 1970s to early 1980s and reached its lowest levels in the first decade of the 21<sup>st</sup> c (Supplementary material 3, Fig. S3a). During this entire period fishing mortality was 2-3 times above sustainable levels, being highest in the first years of the 21<sup>st</sup> c., coinciding with our second sampling programme. In recent years, since 2013 (i.e. after our third sampling programme) catches and SSB are increasing again.



The probability of encountering round sardinella eggs and larvae was also positively correlated with chlorophyll *a*, and negatively with salinity (Fig. 2c, 2d): the trend of decreasing chlorophyll *a* and increasing salinity could explain the decline of this species after a maximum in the 2000s. However, temperature had a different effect in eggs and larvae. Round sardinella eggs appeared to be negatively affected by temperatures higher than 26.5 °C, while the probability of occurrence of larvae levelled off at very high temperatures (> 25 °C). These effects on the probability of occurrence mean that conditions defining the habitat of round sardinella may persist over the next few decades and are likely to start to contract only if sea surface temperatures reach very high values or salinity increases further. The landings of round sardinella for the entire Spanish Mediterranean (i.e. an area larger than the study area) show indeed a peak during the first decade of the 21<sup>st</sup> c. and a decreasing trend afterwards (Supplementary material 3, Fig. S3b).

Previous studies conducted in the area showed that under high temperature conditions, the abundance of different zooplanktonic groups, indicator of larval food resources, was very low (Atienza et al., 2016; Maynou et al., 2014), which would negatively affect fish larval abundance. In addition to trophic limitation of fish larvae, changes in plankton composition and abundance may have important effects on the condition of juvenile and adult fishes, determining demographic parameters such as reproduction, growth and mortality, and these changes have been proposed as important drivers of small pelagics population variability in the NW Mediterranean (Brosset et al., 2016; Coll et al., 2018; Saraux et al. 2018). Another indirect factor related to changing plankton dynamics is the increasing abundance and changes in gelatinous plankton composition that have been recorded in the NW Mediterranean (Molinero et al., 2008; Guerrero et al., 2018). Jellyfish, specifically scyphozoan medusae, may negatively affect pelagic fish due to competition for food or through direct predation on their fish eggs and larvae (Purcell and Arai, 2001). In particular, *Pelagia noctiluca*, one of the most abundant jellyfish species in the NW Mediterranean, has been described as an important predator of anchovy eggs and larvae with a high potential impact on their populations (Tilves et al., 2016). The combination of all these adverse factors, and possible synergies among them, likely contribute to explain the demise of this and other small pelagic species (viz. sardine) in the western Mediterranean (Coll et al. 2018; van Beveren et al., 2016).

In addition to the temporal changes detected along the three decades, changes in relative abundance in space were also evident. The main spawning areas of anchovy in the NW Mediterranean are located in the vicinity of the mouths of the Rhone and the Ebro rivers (Palomera, 1992; Palomera et al., 2007). These areas are highly productive in terms of phytoplankton and zooplankton concentrations (Razouls and Kouwenberg, 1993; Sáiz et al., 2014) and provide suitable conditions for anchovy adult feeding (Blaxter and Hunter, 1982) and larval development (Peebles et al., 1996; Sabatés et al., 2007). In the Mediterranean during summer, trophic resources in the surface layers, where anchovy larvae dwell, are very limited since phytoplanktonic biomass in the water column is generally confined to the DCM. In that period, river run-off is the main mechanism that can supply nutrients to the surface offering significant trophic resources to fish larvae. Although the contribution of riverine water to the total primary productivity has been estimated to be between 10% and 20% of the annual productivity (Salat et al., 2002), its ecological importance lies in it being the only relevant surface contribution to the primary production during the fully stratified season (Blanc et al., 1969). A close link between Rhone and Ebro river discharge and anchovy recruitment has been established for the north and southern zones of the Catalan coast, respectively (Lloret et al., 2001; 2004; Martín et al., 2008). These authors suggested that river runoff enhances spawning and survival rate of the anchovy early stages and, hence, recruitment. Our habitat maps along the three decades show that anchovy eggs became particularly scarce in the formerly (Palomera, 1992) important spawning area of the Ebro delta (Fig. 3a, three left panels). It has been shown that a strong correlation exists between spawning stock abundance and the extension of the spawning area in anchovy (Somarakis et al., 2004) and our results provide additional evidence of this relationship by showing that years with low estimated spawning stock biomass (Supplementary material 3) correspond to years with low eggs and larvae for anchovy. The northern sector (influenced by the important spawning derived from the Gulf of Lions) (Sabatés et al., 2007) showed favourable habitat conditions along the three decades, albeit with decreasing egg abundance (Fig. 3a, three left panels) and larval abundance (Fig. 3a, three right panels).

The habitat of round sardinella, as defined by the probability of occurrence higher than 50%, showed notable expansion from the 1980s to the later decades, both for eggs and larvae, with maximum probability of occurrence in the 2000s, and lower in the most recent surveys (Fig. 3b: three left panels for eggs; three right panels for larvae). Note also that the probability of occurrence was patchy and localized to the southern part in the 1980s, not reaching beyond

41.50° N, becoming more extended in later decades. Round sardinella is a warm water species that, in the last decades, has experienced an increasing abundance and northward expansion in the western Mediterranean in relation to the water temperature increase (Sabatés et al., 2006; 2009). The abundance of eggs and larvae markedly increased in the 2000s and their distribution extended further north, being their abundance extremely low in the northernmost part in accordance with the low temperatures detected in that area and the low abundance of adult population (Sabatés et al., 2006). However, this expansion has been restricted in the last decade of study to the coastal areas and the overall abundance has also decreased (compare with the reported landings in the Spanish Mediterranean, Supplementary material 3, Fig. S3b).

Overall, trends in environmental conditions show that the quality of the spawning habitat of anchovy has decreased, while the spawning habitat of round sardinella has increased. In addition to deterioration of environmental conditions, fishing reduces the size of populations, making them more sensitive to additional stressors such as climate change (Cheung et al., 2013), and can reduce the reproductive potential of small pelagics, the first step in the recruitment process (Somarakis et al., 2018). The combination of these effects can help explain the important reduction in fisheries landings of anchovy observed in the NW Mediterranean, and elsewhere in the Mediterranean and the Black Sea (FAO 2010). These trends in environmental conditions are expected to continue through the 21st century. However, the existence of complex, non-linear relationships in marine ecosystems and inter-species interactions make it difficult to assess future trends in small pelagics populations because a mix of direct and indirect anthropogenic drivers, such as climate change, species invasion, and fisheries exploitation are also likely to affect small pelagic populations (Checkley et al., 2017). Fisheries managers should incorporate information on the variations in natural productivity of stocks and be proactive to reduce fishing pressure during less productive years in order to avoid stock collapse, as it has conclusively been shown that late reaction can lead to grave socioeconomic consequences (for instance the closure of the anchovy fishery in the Bay of Biscay during 5 years due to stock collapse, Taboada and Anadón 2016).

**Data Availability Statement:** Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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**Authors contributions:** FM made the statistical analyses and prepared the figures, AS contributed with data, VR prepared figures in the supplementary material. All authors contributed to the analyses of results and writing of the manuscript.

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## 595 REFERENCES

596

597 Atienza, D., Sabatés, A., Isari, S., Saiz, E., & Calbet, A. (2016). Environmental boundaries of  
598 marine cladoceran distributions in the NW Mediterranean: implications for their  
599 expansion under global warming. *Journal of Marine Systems*, 164, 30–41. doi :  
600 10.1016/j.jmarsys.2016.08.003.

601 Blanc, F., Leveau, M., & Szekiolda, K.H. (1969). Effets eutrophiques au débouché d'un grand  
602 fleuve (Grand Rhône). *Marine Biology*, 3(3) : 233-242. doi : 10.1007/BF00360956.

603 Blaxter, J.H.S., & Hunter, J.S. (1982). The biology of Clupeoid fishes. *Advances in Marine*  
604 *Biology*, 20, 1-223.

605 Brosset, P., Lloret, J., Muñoz, M., Fauvel, C., Van Beveren, E., Marques, V., Fromentin, J.-  
606 M., Ménard, F., & Saraux, C. (2016). Body reserves mediate trade-offs between life-  
607 history traits: new insights from small pelagic fish reproduction. *Royal Society Open*  
608 *Science*, 3, 160202. doi: 10.1098/rsos.160202.

609 Brosset, P., Fromentin, J.M., van Beveren, E., Lloret, J., Marques, V., Basilone, G., Bonanno,  
610 A., Carpi, P., Donato, F., Čikeš Keč, V., De Felice, A., Ferreri, R., Gašparević, D.,  
611 Giráldez, A., Gücü, A., Iglesias, M., Leonori, I., Palomera, I., Somarakis, S., Tičina, V.,  
612 Torres, P., Ventero, A., & Zorica, B. (2017). Spatio-temporal patterns and environmental  
613 controls of small pelagic fish body condition from contrasted Mediterranean areas.  
614 *Progress in Oceanography*, 151, 149-162. doi: 10.1016/j.pocean.2016.12.002.

615 Burnham, K.P., & Anderson, D.R. (2002). Model Selection and Multimodel Inference.  
616 Springer: New York.

617 Calvo, E., Simó, R., Coma, R., Ribes, M., Pascual, J., Sabatés, A., Gili, J.M., & Pelejero, C.  
618 (2011). Effects of climate change on Mediterranean marine ecosystems: the case of the  
619 Catalan Sea. *Climate Research*, 50, 1-29. doi: 10.3354/cr01040.

620 Castellón, A., Font, J., & García Ladona, E. (1990). The Liguro-Provençal-Catalan current  
621 (NW Mediterranean) observed by Doppler profiling in the Balearic sea. *Scientia Marina*,  
622 54, 269-276.

623 Checkley Jr., D.M., Dotseon, R.C., & Griffith, D.A. (2000). Continuous, underway sampling  
624 of eggs of Pacific sardine (*Sardinops sagax*) and northern anchovy (*Engraulis mordax*)

625 in spring 1996 and 1997 off southern and central California. *Deep-Sea Research Part II*,  
626 47(5-6), 1139-1155. doi: 10.1016/S0967-0645(99)00139-3.

627 Checkley Jr., D.M., Alheit, J., Oozeki, Y., & Roy, C. (Eds.) (2009). *Climate Change and*  
628 *Small Pelagic Fish*. Cambridge, UK: Cambridge Univ. Press.

629 Checkley Jr. D.M., Asch, R.G. & Rykaczewski, R.R. (2017). Climate, Anchovy and Sardine.  
630 *Annual Review of Marine Science*, 9, 469-493. doi: 10.1146/annurev-marine-122414-  
631 033819.

632 Cheung, W.W.L., Watson, R., & Pauly, D. (2013). Signature of ocean warming in global  
633 fisheries catch. *Nature* 497: 365–369. doi: 10.1038/nature12156.

634 Ciannelli, L., Bailey, K., & Olsen, E.M. (2015). Evolutionary and ecological constraints of  
635 fish spawning habitats. *ICES Journal of Marine Science*, 72(2): 285-296. doi:  
636 10.1093/icesjms/fsu145.

637 Coll, M., Albo-Puigserver, M., Navarro, J., Palomera, I., & Dambacher, J.M. (2018). Who is  
638 to blame? Plausible pressures on small pelagic fish population changes in the  
639 northwestern Mediterranean Sea. *Marine Ecology Progress Series*,  
640 doi.org/10.3354/meps12591

641 Colella, S., Falcini, F., Rinaldi, E., Sammartino, M., & Santoleri, R. (2016). Mediterranean  
642 Ocean Colour Chlorophyll Trends. *PLoS ONE*, 11(6), e0155756.  
643 doi:10.1371/journal.pone.0155756.

644 Cozzi, S., Ibáñez, C., Lazar, L., Raimbault, P. & Giani, M. (2019). Flow regime and nutrient-  
645 loading trends from the largest South European watersheds: Implications for the  
646 Productivity of Mediterranean and Black Sea’s coastal areas. *Water*, 11(1), 1:27.  
647 doi:10.3390/w11010001.

648 Durrieu de Madron, X., Guieu, C., Sempéré, R., Conan, P., Cossa, D., D'Ortenzio, F.,  
649 Estournel, C., Gazeau, F., Rabouille, C., Stemmann, L., Bonnet, S., Diaz, F., Koubbi, P.,  
650 Radakovitch, O., Babin, M., Baklouti, M., Bancon-Montigny, C., Belviso, S.,  
651 Bensoussan, N., Bonsang, B., Bouloubassi, I., Brunet, C., Cadiou, J.-F., Carlotti, F.,  
652 Chami, M., Charmasson, S., Charrière, B., Dachs, J., Doxaran, D., Dutay, J.-C., Elbaz-  
653 Poulichet, F., Eléaume, M., Eyrolles, F., Fernandez, C., Fowler, S., Francour, P.,  
654 Gaertner, J.C., Galzin, R., Gasparini, S., Ghiglione, J.-F., Gonzalez, J.-L., Goyet, C.,  
655 Guidi, L., Guizien, K., Heimbürger, L.-E., Jacquet, S.H.M., Jeffrey, W.H., Joux, F., Le

656 Hir, P., Leblanc, K., Lefèvre, D., Lejeusne, C., Lemé, R., Loÿe-Pilot, M.-D., Mallet, M.,  
 657 Méjanelle, L., Mélin, F., Mellon, C., Méricot, B., Merle, P.-L., Migon, C., Miller, W.L.,  
 658 Mortier, L., Mostajir, B., Mousseau, L., Moutin, T., Para, J., Pérez, T., Petrenko, A.,  
 659 Poggiale, J.-C., Prieur, L., Pujo-Pay, M., Pulido-Villena, B., Raimbault, P., Rees, A.P.,  
 660 Ridame, C., Rontani, J.-F., Ruiz Pino, D., Sicre, M.A., Taillandier, V., Tamburini, C.,  
 661 Tanaka, T., Taupier-Letage, I., Tedetti, M., Testor, P., Thébault, H., Thouvenin, B.,  
 662 Touratier, F., Tronczynski, J., Ulses, C., Van Wambeke, F., Vantrepotte, V., Vaz, S., &  
 663 Verney, R. (2011). Marine ecosystems' responses to climatic and anthropogenic forcings  
 664 in the Mediterranean. *Progress in Oceanography*, 91, 97-166. doi:  
 665 10.1016/j.pocean.2011.02.003.

666 Estrada, M., & Salat, J. (1989). Phytoplankton assemblages of deep and surface water layers  
 667 in a Mediterranean frontal zone. *Scientia Marina*, 53, 203–214.

668 Estrada, M., Marrasé, C., Latasa, M., Berdalet, E., Delgado, M., & Riera, T. (1993).  
 669 Variability of the deep chlorophyll maximum characteristics in the Northwestern  
 670 Mediterranean. *Marine Ecology Progress Series*, 92, 289-300.

671 FAO FishStat database, 2018. FishStatJ, a tool for fishery statistics analysis. Release: 3.04.4.  
 672 FAO, Fishery and Aquaculture Department, Statistics and Information Branch.  
 673 <http://www.fao.org/fishery/statistics/software/fishstatj/en>

674 Font, J., Salat, J., & Tintoré, J. (1988). Permanent features of the circulation in the Catalan  
 675 sea. In H.J. Minas & P. Nival (Eds.), *Pelagic Mediterranean oceanography*.  
 676 *Oceanologica Acta*, 9, 51-57.

677 Font, J., Salat, J., & Julià, A. (1990). Marine circulation along the Ebro continental margin.  
 678 *Marine Geology*, 95(3-4), 165-177.

679 França, S., Vasconcelos, R.P., Fonseca, V.F., Tanner, S.E., Reis-Santos, P., Costa, M., &  
 680 Cabral, H.N. (2012). Predicting fish community properties within estuaries: Influence of  
 681 habitat type and other environmental features. *Est Coast Shelf Sci*, 107, 22-31. doi:  
 682 10.1016/j.ecss.2012.04.013.

683 Ganas, K., Somarakis, S., & Nunes, C. (2014) Reproductive potential. In K. Ganas (Ed.)  
 684 *Biology and Ecology of Sardines and Anchovies* (pp. 79-121). Boca Raton, FL: CRC  
 685 Press, Taylor and Francis.

686 Giannoulaki, M., Iglesias, M., Tugores, M.P., Bonanno, A., Patti, B., De Felice, A., Leonori,  
687 I., Bigot, J.L., Tičina, V., Pyrounaki, M.M., Tsagarakis, K., Machias, A., Somarakis, S.,  
688 Schismenou, E., Quinci, E., Basilone, G., Cuttitta, A., Campanella, F., Miquel, J., Oñate,  
689 D., Roos, D., & Valavanis, V. (2013). Characterizing the potential habitat of European  
690 anchovy *Engraulis encrasicolus* in the Mediterranean sea, at different life stages.  
691 Fisheries Oceanography, 22(2), 68-89. doi: 10.1111/fog.12005.

692 Guerrero, E., Gili, J.M., Grinyó, J., Raya, V., & Sabatés, A. (2018). Long-term changes in the  
693 planktonic cnidarian community in a mesoscale area of the NW Mediterranean. *PLoS*  
694 *ONE* 13 (5): e0196431. <https://doi.org/10.1371/journal.pone.0196431>.

695 Hastie, T.J., & Tibshirani, R.J. (1990). Generalized Additive Models. New York: Chapman  
696 and Hall.

697 Lavigne, H., D’Ortenzio, F., Ribera D’Alcalà, M., Claustre, H., Sauzède, R., & Gacic, M.  
698 (2015). On the vertical distribution of the chlorophyll a concentration in the  
699 Mediterranean Sea: a basin-scale and seasonal approach. *Biogeosciences*, 12, 5021–  
700 5039. doi : 10.5194/bg-12-5021-2015.

701 Lloret, J., Lleonart, J., Solé, I., & Fromentin, J.M. (2001). Fluctuations of landings and  
702 environmental conditions in the north-western Mediterranean Sea. *Fisheries*  
703 *Oceanography*, 10, 33–50.

704 Lloret, J., Palomera, I., Salat, J., & Solé, I. 2004. Impact of freshwater input and wind on  
705 landings of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in shelf  
706 waters surrounding the Ebre River Delta (northwestern Mediterranean). *Fisheries*  
707 *Oceanography*, 13, 102–110.

708 McClatchie, S., Gao, J., Drenkard, E.J., Thompson, A.R., Watson, W., Ciannelli, L., Bograd,  
709 S.J., & Thorson, J.T. (2018). Interannual and secular variability of larvae of mesopelagic  
710 and forage fishes in the Southern California Current system. *Journal of Geophysical*  
711 *Research*, 123(9), 6277-6295. doi: 10.1029/2018JC014011.

712 Martín, P., Bahamon, N., Sabatés, A., Maynou, F., Sánchez, P., & Demestre, M. (2008).  
713 European anchovy (*Engraulis encrasicolus*) landings and environmental conditions on  
714 the Catalan Coast (NW Mediterranean) during 2000–2005. *Hydrobiologia*, 612, 185–  
715 199. doi : 10.1007/s10750-008-9482-1.



716 Martín, P., Sabatés, A., Lloret, J., & Martin-Vide, J. (2012). Climate modulation of fish  
 717 populations: the role of the Western Mediterranean Oscillation (WeMO) in sardine  
 718 (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) production in the north-  
 719 western Mediterranean. *Climatic Change*, 110, 925-939. doi : 10.1007/s10584-011-0091-  
 720 z.

721 Masó, M., Sabatés A., & Olivar M.P. (1998). Short-term physical and biological variability in  
 722 the shelf-slope region of the NW Mediterranean during the spring transition period.  
 723 *Continental Shelf Research*, 18, 661-675.

724 Maynou, F., Sabatés, A., & Salat J. (2014). Clues from the recent past to assess recruitment  
 725 of Mediterranean small pelagic fishes under sea warming scenarios. *Climatic Change*,  
 726 126(1-2), 175-188. doi : 10.1007/s10584-014-1194-0.

727 Molinero, J.C., Ibanez, F., Souissi, S., Buecher, E., Dallot, S., & Nival, P. (2018). Climate  
 728 control on the long-term anomalous changes of zooplankton communities in the  
 729 Northwestern Mediterranean. *Global Change Biology*, 14(1), 11-26.

730 Nunes, S., Latasa, M., Gasol, J.M., & Estrada, M. (2018). Seasonal and interannual variability  
 731 of phytoplankton community structure in a Mediterranean coastal site. *Marine Ecology*  
 732 *Progress Series*, 592: 57-75. doi: 10.3354/meps12493.

733 Olivar, M.P., Salat, J., & Palomera, I. (2001). A comparative study of the spatial distribution  
 734 patterns of the early stages of anchovy and pilchard in the NW Mediterranean Sea.  
 735 *Marine Ecology Progress Series*, 217, 111–120. Palomera, I. (1992). Spawning of  
 736 anchovy *Engraulis encrasicolus* in the North Western Mediterranean relative to  
 737 hydrographic features in the region. *Marine Ecology Progress Series*, 79, 215–223.

738 Palomera, I., Olivar, M.P., Salat, J., Sabatés, A., Coll, M., García, A., & Morales-Nin, B.  
 739 (2007). Small pelagic fish in the NW Mediterranean Sea: an ecological review. *Progress*  
 740 *in Oceanography*, 74, 377-396. doi: 10.1016/j.pocean.2007.04.012.

741 Peebles, E.B., Hall, J.R., & Tolley, S.G. (1996). Egg production by the bay anchovy *Anchoa*  
 742 *mitchilli* in relation to adult and larval prey fields. *Marine Ecology Progress Series*,  
 743 131(1-3), 61-73.

744 Pörtner, H.O., Karl, D.M., Boyd, P.W. , Cheung, W.W.L. , Lluch-Cota, S.E., Nojiri, Y.,  
 745 Schmidt, D.N., & Zavialov, P.O. (2014). Ocean systems. In *Climate Change 2014:*  
 746 *Impacts, Adaptation, and Vulnerability. Part A: Global and Sectoral Aspects* (pp. 411-

747 484). Contribution of Working Group II to the Fifth Assessment Report of the  
748 Intergovernmental Panel on Climate Change, Cambridge University Press, USA.

749 Purcell, J. E., & Arai, M.N. (2001). Interactions of pelagic cnidarians and ctenophores with  
750 fish: a review. *Hydrobiologia*, 451, 27–44.

751 Razouls, C., & Kouwenberg, J.H.M. (1993). Spatial distribution and seasonal variation of  
752 mesozooplankton biomass in the Gulf of Lions (northwestern Mediterranean).  
753 *Oceanologica Acta*, 16(4), 393-401.

754 Rubio, A., Arnau, P.A., Espino, M., Flexas, M.M., Jordà, G., Salat, J., Puigdefàbregas, J., &  
755 Arcilla, A.S. (2005). A field study of the behaviour of an anticyclonic eddy on the  
756 Catalan continental shelf (NW Mediterranean). *Progress in Oceanography*, 66, 142-156.  
757 doi: 10.1016/j.pocean.2004.07.012.

758 Sabatés, A. (1990). Changes in the heterogeneity of mesoscale distribution patterns of larval  
759 fish associated with a shallow coastal haline front. *Estuarine, Coastal and Shelf Science*,  
760 30(2), 131-140. doi: 10.1016/0272-7714(90)90059-Z.

761 Sabatés, A., Martín, P., Lloret, J., & Raya, V. (2006). Sea warming and fish distribution: the  
762 case of the small pelagic fish, *Sardinella aurita*, in the western Mediterranean. *Global*  
763 *Change Biology*, 12, 2209-2219. doi: 10.1111/j.1365-2486.2006.01246.x.

764 Sabatés, A., Salat, J., Palomera, I., Emelianov, M., De Puelles, M.L.F., & Olivar, M.P.  
765 (2007). Advection of anchovy (*Engraulis encrasicolus*) larvae along the Catalan  
766 continental slope (NW Mediterranean). *Fisheries Oceanography*, 16, 130-141. doi:  
767 10.1111/j.1365-2419.2006.00416.x.

768 Sabatés, A., Zaragoza, N., Grau, C., & Salat, J. (2008). Vertical distribution of early  
769 developmental stages in two coexisting clupeoid species, *Sardinella aurita* and *Engraulis*  
770 *encrasicolus*. *Marine Ecology Progress Series*, 364, 169–180.

771 Sabatés, A., Salat, J., Raya, V., Emelianov, M., & Segura-Noguera, M. (2009). Spawning  
772 environmental conditions of *Sardinella aurita* at the northern limit of its distribution  
773 range, the western Mediterranean. *Marine Ecology Progress Series*, 385, 227-236. doi:  
774 10.3354/meps08058.

775 Sabatés, A., Salat, J., Raya, V., & Emelianov, M. (2013). Role of mesoscale eddies in  
776 shaping the spatial distribution of the coexisting *Engraulis encrasicolus* and *Sardinella*

777        *aurita* larvae in the northwestern Mediterranean. *Journal of Marine Systems*, 111, 108–  
778        119. doi: 10.1016/j.jmarsys.2012.10.002.

779        Sabatés, A., Salat, J., Tilves, U., Raya, V., Purcell, J.E., Pascual, M., Gili, J.M., & Fuentes,  
780        V.L. (2018). Pathways for *Pelagia noctiluca* jellyfish intrusions onto the Catalan shelf  
781        and their interactions with early life fish stages. *Journal of Marine Systems*, 187, 52-61.  
782        doi: 10.1016/j.jmarsys.2018.06.013.

783        Sáiz, E., Sabatés, A., & Gili, J.-M. (2014). The zooplankton. In S. Goffredo & Z. Dubinsky  
784        (Eds.), *The Mediterranean Sea: Its History and Present Challenges* (pp. 183–211).  
785        Dordrecht: Springer. doi: 10.1007/978-94-007-6704-1.

786        Salat, J. (1996). Review of hydrographic environmental factors that may influence anchovy  
787        habitats in northwestern Mediterranean. *Scientia Marina*, 60(Suppl. 2), 21-32.

788        Salat, J., Garcia, M.A., Cruzado, A., Palanques, A., Arín, L., Gomis, D., Guillén, J., De León,  
789        A., Puigdefàbregas, J., Sospedra, J., & Velásquez, Z.R. (2002). Seasonal changes of  
790        water mass structure and shelf slope exchanges at the Ebro shelf (NW Mediterranean).  
791        *Continental Shelf Research*, 22(2), 327-348.

792        Saraux, C., Fromentin, J.-M., Bigot, J.-L., Bourdeix, J.-H., Morfin, M., Roos, D., van  
793        Beveren, E., & Bez, N. (2014). Spatial structure and distribution of small pelagic fish in  
794        the Northwestern Mediterranean Sea. *PLoS ONE*, 9(11), e111211. doi:  
795        doi:10.1371/journal.pone.0111211.

796        Saraux, C., Van Beveren, E., Brosset, P., & Queiros Q. (2018). Small pelagic fish dynamics:  
797        a review of mechanisms in the Gulf of Lions. *Deep-Sea Res II* (in press),  
798        doi:10.1016/j.dsr2.2018.02.010.

799        Schroeder, K., Chiggiato, J., Bryden, H.L., Borghini, M., & Ben Ismail, S. (2016). Abrupt  
800        climate shift in the Western Mediterranean Sea. *Scientific Reports*, 6, 23009. doi:  
801        10.1038/srep23009.

802        Siokou-Frangou, I., Christaki, U., Mazzocchi, M.G., Montresor, M., Ribera d'Alcalà, M.,  
803        Vaqué, D., & Zingone, A. (2010). Plankton in the open Mediterranean Sea ; a review.  
804        *Biogeosciences*, 7, 1543-1586. doi: 10.5194/bg-7-1543-2010.

805        Skliris, N., Sofianos, S., Gkanasos, A., Mantziafou, A., Vervatis, V., Axaopoulos, P., &  
806        Lascaratos, A. (2012). Decadal scale variability of sea surface temperature in the

807 Mediterranean Sea in relation to atmospheric variability. *Ocean Dynamics*, 62, 13-30.  
808 doi: 10.1007/s10236-011-0493-5.

809 Smith, P.E., & Moser, H.G. (2003). Long-term trends and variability in the larvae of Pacific  
810 sardine and associated fish species of the California Current region. *Deep Sea Research*  
811 *Part II*, 50, 2519–2536.

812 Somarakis, S., Palomera, I., García, A., Quintanilla, L., Koutsikopoulos, C., Uriarte, A., &  
813 Motos, L. (2004). Daily egg production of anchovy in European waters. *ICES Journal of*  
814 *Marine Science*, 61, 944-958.

815 Somarakis, S., Tsoukali, S., Giannoulaki, M., Schismenou, E., & Nikolioudakis, N. (2018).  
816 Spawning stock, egg production and larval survival in relation to small pelagic fish  
817 recruitment. *Marine Ecology Progress Series*, doi.org/10.3354/meps12642.

818 Taboada, F.G. & Anadón R. (2016). Determining the causes behind the collapse of a small  
819 pelagic fishery using Bayesian population modelling. *Ecological Applications*, 26(3),  
820 886-898. doi: doi/10.1890/15-0006.

821 Tilves, U., Purcell, J.E., Fuentes, V.L., Torrents, A., Pascual, M., Raya, V., Gili, J.-M. &  
822 Sabatés, A. (2016). Natural diet and predation impacts of *Pelagia noctiluca* on fish eggs  
823 and larvae in the NW Mediterranean. *Journal of Plankton Research* 38(5): 1243–1254.  
824 doi:10.1093/plankt/fbw059.

825 Tsikliras, A.C., Licandro, P., Pardalou, A., McQuinn, I.H., Gröger, J.P., & Alheit, J. (2019).  
826 Synchronization of Mediterranean pelagic fish populations with the North Atlantic  
827 climate variability. *Deep-Sea Research Part II*, 159, 143-151.

828 van Beveren, E., Bonhommeau, S., Fromentin, J.-M., Bigot, J.-L., Bourdeix, J.-H., Brosset,  
829 P., Roos, D., & Saraux, C. (2014). Rapid changes in growth, condition, size and age of  
830 small pelagic fish in the Mediterranean. *Marine Biology*, 161(8), 1809-1822. doi:  
831 10.1007/s00227-014-2463-1.

832 van Beveren, E., Fromentin, J.-M., Rouyer, T., Bonhommeau, S., Brosset, P., & Saraux, C.  
833 (2016). The fisheries history of small pelagics in the Northern Mediterranean. *ICES*  
834 *Journal of Marine Science*, 73(6), 1474-1484. doi:10.1093/icesjms/fsw023.

835 van der Lingen, C.D., & Huggett, J.A. (2003). The role of ichthyoplankton surveys in  
836 recruitment research and management of South African anchovy and sardine. In H.L.

837 Browman & A.B. Skiftesvik (Eds.), *The Big Fish Bang*. Proceedings of the 26th Annual  
838 Larval Fish Conference (pp. 303–343). Bergen: Institute of Marine Research.

839 Vargas-Yáñez, M., Moya, F., Tel, E., García-Martínez, M.C., Guerber, E., & Bourgeon, M.  
840 (2009). Warming and salting in the western Mediterranean during the second half of the  
841 20th century: Inconsistencies, unknowns and the effect of data processing. *Scientia*  
842 *Marina*, 73(1), 7-28. doi: 10.3989/scimar.2009.73n1007

843 Vargas-Yáñez, M., Moya, F., García-Martínez, M.C., Tel, E., Zunino, P., Plaza, F., Salat, J.,  
844 Pascual, J., López-Jurado, J.L., & Serra, M. (2010). Climate change in the Western  
845 Mediterranean Sea 1900-2008. *Journal of Marine Systems*, 82, 171-176.

846 Wang, D.P., Vieira, M.E.C., Salat, J., & Tintoré, J. (1988). A shelf slope filament off the  
847 northeast Spanish coast. *Journal of Marine Research*, 46, 321–332.

848 Wintle, B.A., Elith, J., & Potts, J.M. (2005). Fauna habitat modelling and mapping: a review  
849 and case study in the Lower Hunter Central Coast region of NSW. *Australian Ecologist*,  
850 30, 719-738. doi: 10.1111/j.1442-9993.2005.01514.x.

851 Wood, S.N. (2006). Generalized additive models: an introduction with R. Boca Raton, FL:  
852 CRC / Taylor and Francis.

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855 [Tables](#)

856 Table 1. Characteristics of the ichthyoplankton surveys: Sampling dates, number of stations  
857 and depth range.

survey code	dates	Nb stations	Depth min (2.5%)	Median depth (50%)	Depth max (97.5%)
ARECES3	8-12 June 1983	44	24.15	90.50	364.23
ARECES4	18-25 July 1983	44	24.75	87.00	655.15
CACO1	18-25 July 2003	65	29.60	117.00	1034.00
CACO3	23-30 June 2004	65	26.20	113.00	1028.20
CACO4	21-29 July 2004	65	29.60	118.00	973.40
Fishjelly11	15-29 June 2011	64	28.00	110.00	1052.33
Fishjelly12	1-23 July 2012	58	29.00	113.00	1043.55

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Table 2. Forward stepwise selected GAMs with goodness of fit statistics of ichthyoplankton abundance data (AIC: Akaike's information criterion, Edf: estimated degrees of freedom, GCV: generalized cross validation). For each species life stage, each term (explanatory variable) was added onto the previous model until GCV could no further be minimized. Error distribution function: quasi-poisson with log transformation for *Engraulis encrasicolus*; binomial with logit transformation for *Sardinella aurita*.

	TERM	AIC	Res dev	Expl dev%	Edf	UBRE (GCV)
Eggs E. encr.	NULL	7985.6	704415.4	0.0%	--	1747.92
	decade	7704.7	704415.4	21.1%	--	1392.31
1	+ SSS	7535.2	681513.1	31.3%	3.963	1220.83
2	+ log (Chl a 20m)	7307.8	635438.6	38.6%	3.573	1068.61
3	+ SST	7017.6	635438.6	41.5%	2.360	1030.10
Larvae E. encr.	NULL	7596.7	548950.5	0.0%	--	1362.15
	decade	7519.3	548950.5	25.3%	--	1027.70
1	+ log (Chl a 20m)	7061.5	449628.2	22.4%	3.169	851.17
2	+ SSS	6956.1	418467.1	31.2%	3.814	786.20
3	+ SST	6896.7	418467.1	34.2%	2.611	762.49
Eggs S. aur	NULL	485.2	483.2	0.0%	--	0.20
	decade	458.0	452.0	6.5%	--	0.13
1	+ log (Chl a 20m)	407.0	393.7	15.6%	1.00	0.05
2	+ SST	381.1	360.4	22.7%	3.713	0.02
3	+ SSS	365.2	347.8	25.2%	1.000	0.02
Larvae S. aur	NULL	563.4	561.4	0.0%	--	0.39
	decade	407.1	401.1	28.6%	--	0.21
1	+ SSS	357.4	347.6	36.8%	1.984	0.10
2	+ SST	319.7	306.0	44.4%	1.880	0.09

868 Table 3. Habitat occupancy (surface occupied by favourable habitat, according to an arbitrary  
869 threshold, grid cells > 500 n/10 m<sup>2</sup> for *Engraulis encrasicolus* and probability of occurrence >  
870 0.5 for *Sardinella aurita*). Surface of the study area 12 000 km<sup>2</sup>.

	1980s	2000s	2010s
<i>E. encrasicolus</i>			
eggs	100%	18%	<1%
larvae	100%	77%	55%
<i>S. aurita</i>			
eggs	0%	17%	30%
larvae	0%	30%	22%

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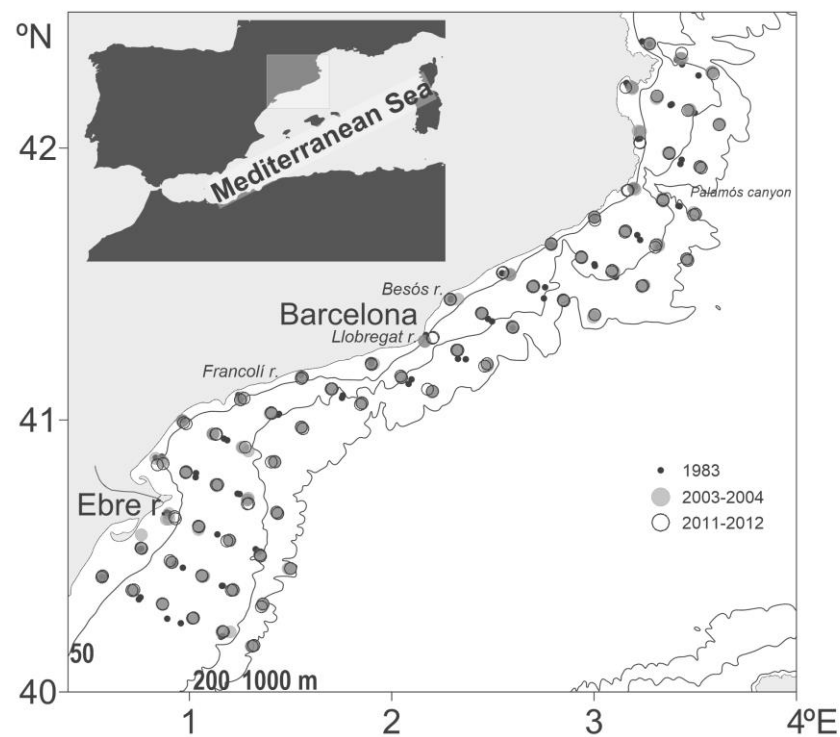
## Figure legends

Fig. 1. Map of the sampling stations, with inset showing the location of the study area. Depth contours 50, 200 and 1000 m depth shown.

Fig. 2. GAM partial effects on anchovy eggs (a), anchovy larvae (b), round sardinella eggs (c), round sardinella larvae (d), with model intercept (decade). To aid interpretation of results the data percentiles are shown as vertical bars. The range of percentiles 2.5% to 97.5% cover 95% of the observed data.

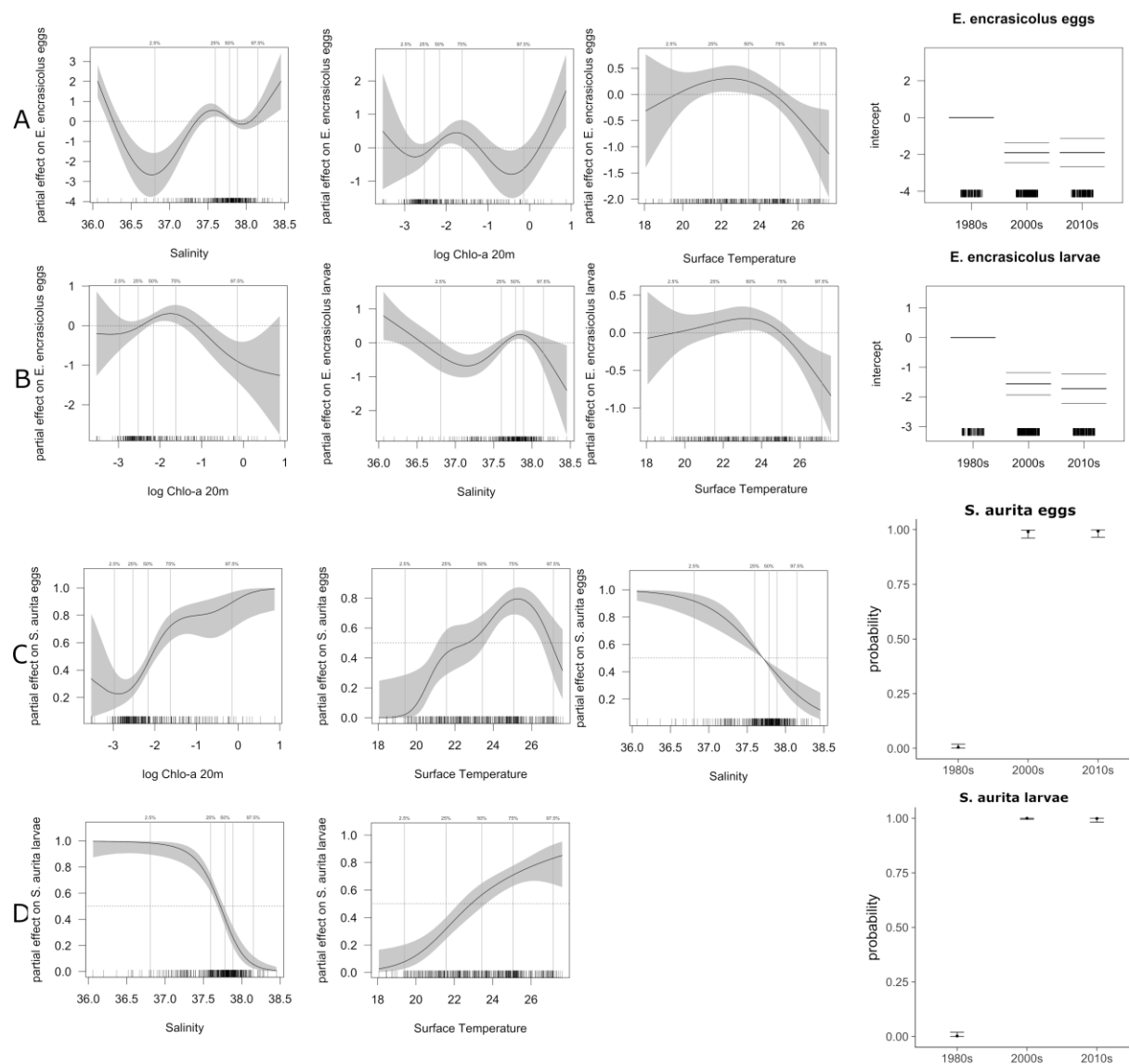
Fig. 3. Predicted habitat maps of (a) of anchovy eggs and larvae (colour scale: density as  $n/10\text{ m}^2$ ), and (b) probability of occurrence of round sardinella eggs and larvae (colour scale: probability between 0 and 1).

888 Fig. 1



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891 Fig. 2



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