Modelling the relationships of medium and long-term variations of the anchovy and sardine catches in the Catalan Sea (NW Mediterranean) with the environmental drivers

PhD Thesis 2017

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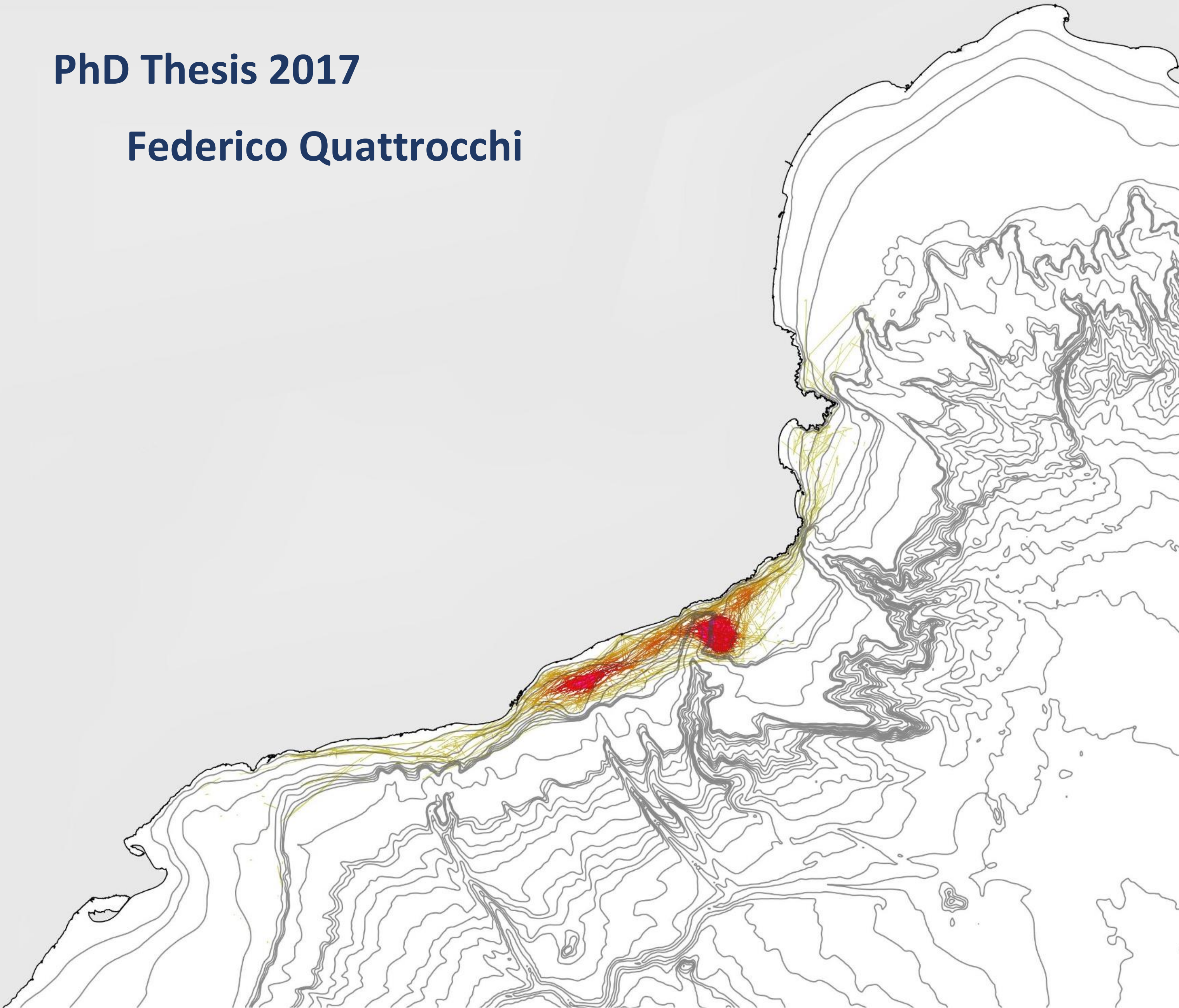

Modelling the relationships of medium and long-term variations of the Anchovy and Sardine catches in the Catalan Sea (NW Mediterranean) with the environmental drivers

Memoria presentada por Federico Quattrocchi
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Resumen/Abstract English

The understanding of the driving forces involved in the abundance fluctuation of fish populations is an important requirement for conservation and management, especially in the context of environmental changes. In the North Western Mediterranean Sea the catches of sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) during the period 1990-2014 have severely decreased. Although neither of the two populations is considered underexploited, it seems unlikely that overexploitation alone has caused the recent decrease. Furthermore, it is even truer considering that changes in the marine environment have occurred in the studied area during the last 40 years. The general objective of this PhD thesis is to detect the main environmental factors involved in the fluctuations of the abundance of the two small pelagic species in the Catalan Sea.

Before focusing on the environmental influences, the spatiotemporal distribution of the purse seine fishery operations was analyzed. The results revealed that the distribution of the fleet captured the features of the distributions of small pelagic populations. These findings contributed to a better understanding and visualization of the spatial distribution of catches, which form the basis of the landings data series studied in the rest of the PhD thesis. We then investigated the local environmental factors and climate index (Western Mediterranean oscillation index; WeMOI) that were strictly linked with landings of both species. We concluded that temperature, salinity, and currents were important drivers for both species, and the WeMOI index favored sardine abundance when it was in positive phase. We highlighted that the relationships between the availability of these small pelagic fishes and these factors were better described by non-linearity. Finally, we provided evidence, independent from the studies directly targeted on early life stages, that the temperature and sea surface height (used as a proxy of mesoscale processes) play an important role in the recruitment variability of these species. Even more importantly we showed that the effects of these drivers were not stationary but transient over time.

Although this work is one step forward in the understanding of the abundance variability of the small pelagic fish in the Catalan Sea further investigation focused especially on the synergic effects of fishing combined with environmental factors will still be needed.

Key words: sardine, anchovy, landings, environmental drivers, VMS, GAM(M), non-stationary relationships, NW Mediterranean Sea

Resumen/Abstract Catalan

La comprensió dels factors implicats en la fluctuació d'abundància de les poblacions de peixos és un requisit important per a la conservació i la gestió, especialment en el context dels canvis ambientals. En la Mediterrània occidental, les captures de sardina (Sardina pilchardus) i l'anxova (Engraulis encrasicolus) durant el període 1990-2014 han disminuït bruscament.

Malgrat que cap de les dues poblacions es consideri subexplotada, és poc probable que només la sobreexplotació hagi causat la recent disminució. Això és encara més cert si es té en compte que dins a la zona estudiada durant els últims 40 anys s'han produït clars canvis en el medi marí. L'objectiu general d'aquesta tesi doctoral és detectar els principals factors ambientals que intervenen en les fluctuacions de l'abundància de les dues espècies de petits pelàgics del mar català.

Abans de centrar-se en les influències mediambientals, s'ha analitzat la distribució espaciotemporal de les operacions de la pesca de teranyina. Els resultats han revelat que la distribució de la flota representa fidelment les característiques de les distribucions de petits pelàgics.

Aquestes troballes han contribuït a una millor comprensió i visualització de la distribució espacial de les captures que formen també la base de la sèrie de dades de desembarcament estudiada a la resta de la tesi doctoral.

A continuació, s'han investigat les relacions entre els desembarcaments d'ambdues espècies i els factors ambientals locals i l'índex climàtic (Índex d'oscil·lació de la Mediterrània occidental, WeMOI).

Es conclou que la temperatura, la salinitat i els corrents són factors importants per ambdues espècies, i l'índex WeMOI afavoreix l'abundància de la sardina quan es troba en fase positiva.

Hem destacat que la relacions entre la disponibilitat d'aquestes espècies de petits pelàgics i aquests factors poden ser millor descrits amb models no-lineals. Finalment, aportem evidències, de manera independent d'altres estudis centrats directament en ous i larves, que la temperatura i el nivell superficial del mar (utilitzat com proxy de processos de mesoescala) tenen un important rol en la variabilitat del reclutament per ambdues espècies. Encara més important, hem mostrat que els efectes d'aquests factors no són estacionaris sinó que han canviat amb el pas del temps

Encara que aquest estudi representa un pas endavant en el coneixement i la comprensió de la variabilitat en l'abundància de petits peixos pelàgics al mar Català, encara és necessària la investigació addicional centrada en l'efecte sinèrgic de la pesca amb els factors ambientals.

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General Introduction

Fish populations fluctuate at a multitude of time scales, from seasonal to centennial and, attempting to comprehend and explain the processes involved in these variations is a key objective for marine scientists. Searching and understanding the driving forces of these fluctuations constitute, in fact, an indispensable requirement in the field of conservation and management especially in the context of environmental changes.

Small pelagic fish populations and their ecological importance

Small pelagic fishes are one species group particularly known for the high interannual and long-term variability in biomass and abundance. These species including sardine (genera *Sardina* and *Sardinops*) and anchovy (genera *Engraulis*) have a very wide distribution. They are predominantly confined to coastal regions and are abundant in the major productive areas of the world (Fig. 1) which differ from each other for their own oceanographic characteristics, *i.e.* the South American west coast (the Humboldt Current), the North American west coast (California current), the waters around Japan (Kuroshio Oyashio current), the waters of Namibia and South-Africa (Benguela Current) the Northeast Atlantic (European Atlantic and Canary Current) and the Australian waters (Checkley et al., 2009; Ganias, 2014). Further, they are also important species in semi-enclosed basins like the Mediterranean Sea and the Black sea (e.g. Lloret *et al.*, 2001; Tugores *et al.*, 2011; Giannoulaki *et al.*, 2013; Bonanno *et al.*, 2014).

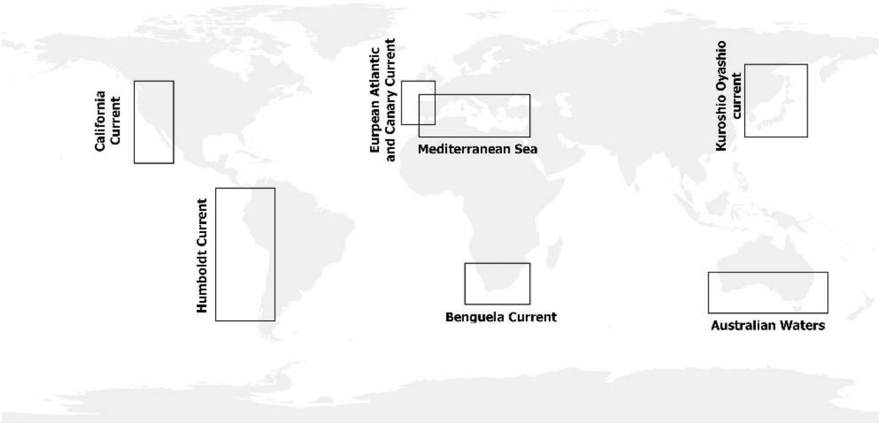

Figure 1. Major systems in which is well known the prevalence of anchovy and sardine (adapted from: Checkley et al., 2009; Ganias et el., 2014)

These small planktivorous fishes generally dominate the intermediate trophic levels (Rice, 1995). For this reason, the bulk of the available energy generated by the primary producers pass through them to become available for predators. Thus, within their ecosystems, they become important both as predator (top-down control) and prey (bottom-up control). Such systems being characterized by an intermediate, energy mediating, abundant species (or at most a few species) capable of having an influence on both lower and higher trophic level are denoted as *wasp-waist* systems (Rice, 1995; Bakun, 2006; Shannon *et al.*, 2008). Small pelagics, operating at the *wasp-waist* levels, as suggested by Bakun (2006) reviewing different marine systems across all oceans, have specific characteristics that together make them pivotal in their respective ecosystems and allow them to play a role which goes further than the simple transfer of perturbations across trophic levels. In summary, these features are:

1. The complex life history (e.g. short- lived, pelagic larvae) which makes the waist populations vulnerable to environmental fluctuations giving large inter-annual variation.
2. The dominance in biomass of their trophic level which allows that each variation of their abundance induces changes to both higher and lower trophic levels (bottom-up and a top-down control).
3. They represent the lowest mobile trophic level. The changes in its distribution force the distribution of their predators and consequently tend to reorganize the spatial pattern of the trophic interactions in the ecosystem.
4. In some systems, they can prey upon the eggs and larval stages of their predators forming a negative feedback loop that keeps them abundant while suppressing that of predators.

Additionally, despite their low commercial value, small pelagic fishes provide a substantial source of income for many countries due principally to their abundance, being employed for aquaculture feed, industrial oil, health supplement and human consumption (Barange *et al.*, 2014). Anchovies and sardines with herring, in fact, made up ca. 50 % of landings of the global capture of the pelagic fisheries and ca 25 % of the marine fishery (FAO, 2015).

Physical process characterizing the habitat of small pelagic fishes

Anchovies and sardines are small bodied fishes and have a short life span (Rochet, 2000). They display early maturation and most of them are pelagic spawners (e.g. Checkley et al., 2009). The fecundity for these species is high and accounts for thousands of eggs produced daily by females during the spawning season, which can vary from a few weeks to several months (e.g. Fréon *et al.*, 2005; Ganias, 2014 and references therein). This strategy of releasing a high number of eggs through a protracted period is adopted in order to enhance the chances of larvae and eggs to meet the ‘survival window’ (Cury and Roy, 1989), since their early life stages are highly vulnerable to predation and have strict requirements in terms of environmental conditions. Despite these reproductive strategies most anchovy and sardine stocks display and have displayed high level of recruitment variability (i.e. variation of how many young fishes survive sufficiently long to enter in the adult population) and, owing to their short life span any fluctuation in recruitment success is translated rapidly into fluctuations at the population scale (Blaxter and Hunter, 1982; Cury and Roy, 1989; Fréon *et al.*, 2005; Checkley et al., 2009). Although the mechanisms of fluctuations of anchovy and sardine vary in their specificity (e.g. species, populations, and stocks) the prevailing view is that the populations' size of small pelagics are controlled primarily by the environmental conditions (Checkley *et al.*, 2017). Thus, the presence and the choice of suitable habitat is crucial to determine the survival during egg-larval and juvenile stages from which the population levels depend (e.g. Katara, 2014).

Comparative studies on fish habitat, have identified the presence of three major classes of physical processes that give rise to a favourable habitat for successful populations (e.g. Cury and Roy, 1989; Bakun, 1996). These three elements are called 'fundamental triad' (Bakun, 1996; Agostini and Bakun, 2002) and are:

- Enrichment processes (upwelling, mixing, river discharge etc.)
- Concentration processes (convergence, water column stability, fronts etc.) which favour larvae to encounter food particles and allow them to grow more rapidly, enabling a quick passage through the size-related intense predation period
- Retention processes inside the appropriate habitat, which avoid the dispersion and the loss of early life stages from the population habitat during their period of passive drift.

This concept became the basis for numerous studies which have attempted to show the environmental effects on the small pelagic population variability across different marine systems (e.g. Bakun, 2010; Katara *et al.*, 2011; Santos *et al.*, 2012). Among these systems, in fact, the presence or high abundance of these species at different life stages have been often associated with different ranges in the value of oceanographic variables, e.g. salinity, temperature, oxygen concentration, sea level anomaly, current velocity and other variables (e.g. Planque *et al.*, 2007; Bertrand *et al.*, 2008; Checkley et al., 2009), leading to no apparent general pattern in regard to the relationships with the hydrographic characteristics. Despite such dissimilarities, the variables and their values characterizing the habitats of these fish were found consistent with the 'triad' and adjusted to the peculiarities of to the water masses containing the source nutrient of each population in question (e.g. Checkley et al., 2009; Bonanno *et al.*, 2014).

Responses to the environmental forces

The exogenous factors affecting individuals and their populations are plentiful, and in general can be distinguished in: a) those whose effects are direct through physiology, including metabolic and reproductive success; b) those whose effects are indirect, because acting on their biological environment e.g. predator, prey, disease (e.g. Ottersen *et al.*, 2004); and finally, c) those which trigger the responses of the population not immediately but temporally lagged (Ottersen *et al.*, 2010).

The biological characteristics of the life cycle of these species make them highly sensitive to the environment and extremely variable in their population's abundance (Lasker, 1981; Cury and Roy, 1989; Bakun, 1996). Although the population-environment relationships have been widely studied, the understanding of these links is yet incomplete (Checkley *et al.*, 2017). This likely depends mainly on the higher complexity of these relationships which generally involve non-linearity, time lags, combined effects and locally diverse manifestations (Katara, 2014). In addition, this topic is further complicated when trying to discern the importance of fishing versus the environment as a cause of population variability (e.g. Rothschild, 2000; Planque *et al.*, 2010). Fishing, in fact, by modifying the size of the spawning stock and altering its age or size, can give rise to substantial consequences on the capacity of the population to buffer the environmental variability (Planque *et al.*, 2010). For instance, fishing can cause the reduction of the duration of the spawning period of the population through the removal of old individuals (the remaining young individuals have a smaller spawning period) followed by a reduction of the viability of eggs and larvae, because forced to experience a restricted range of environmental conditions, leading to potentially higher chance of not survival and recruitment failure (Planque *et al.*, 2010; Hidalgo *et al.*, 2011).

Even though the action of fishing on the population variability is recognized, the role of the environment as driving force on the fluctuations of both anchovy and sardine is evident as demonstrated by analysis performed on sedimentary records, showing the non-constant population size of this species prior to the advent of the large-scale commercial fishing (Finney *et al.*, 2010; Checkley *et al.*, 2017). Either by directly defining mortality or indirectly through altering relationships between life cycle, its role on the recruitment variability is, in fact, undeniable (e.g. Cahuin *et al.*, 2009). Several theories were developed attempting to explain how the environmental factors and processes operate since the early 1900s (Hjort, 1914; 'critical period' hypothesis).

In general, temperature and prey abundance, favored by mechanisms of mixing and advection, have been considered the most influential drivers of recruitment success and consequently on population abundance variability (e.g. Ottersen *et al.*, 2010; Katara, 2014; and references therein). Despite the potentially positive effects that these factors can have on the survival and growth rate on the early stages of the small pelagic fishes, most of the times the relationships with recruitment are not linear taking instead a dome-shaped form, mainly due to the complexity of the combined effects of both the species biology and the environment. For instance, although higher temperatures can lead to a faster development of fish larval stages lowering the mortality rate due to reduced exposure to predators (e.g. Dulčić and Kraljević, 1996; Wang *et al.*, 2009), at the same time it could provoke, among other effects, early maturation at smaller size and reduced per capita fecundity and therefore affecting population productivity (Rijnsdorp *et al.*, 2009). Still, although the match in timing and location between spawning and plankton peaks is a process favouring the recruitment success (match/mismatch hypothesis; Cushing, 1990), as argued by Cushing (1990), processes enhancing nutrient supply, e.g. upwelling turbulences, when increase their intensity, have a reverse effect through a high rate of transport of larvae away from upwelling areas before primary production peaks.

Fish populations, in general, are capable of altering their behaviour in response to the environmental variation (Agenbag *et al.*, 2003). Despite this ability, species and populations usually prefer those environmental conditions most favourable to their survival growth and reproduction (Blaxter and Hunter, 1982). The habitat choice, in fact, in marine fish is widely accepted to being based on the habitat suitability defined according to different biotic and abiotic factors able to optimize the population fitness by maximizing the differences between birth and death ('ideal free distribution'; MacCall, 1990). For this reason, small pelagics, thanks to their features of being good and fast swimmers, may change their spatial distribution annually and or seasonally based on the changes in hydrological factors, and can perform migrations between habitats in order to try to satisfy the different environmental preference among the life stages (e.g. Bertrand *et al.*, 2004b).

Consequently, it is fairly clear that the environmental variability, in addition to the above-mentioned effects on the recruitment, can affect populations by promoting shifts in their distributions. In the most common of the situation, these shifts consist only on alongshore horizontal displacement at short temporal and spatial scale (Fréon and Misund, 1999; Fréon *et al.*, 2005). Conversely, if the non-favourable conditions persist over time, this temporal and local shifts in distribution, can result in contraction or expansion of the distributional range of populations (e.g. Bertrand *et al.*, 2004a; Fréon *et al.*, 2005).

Small pelagic fishes in the Catalan Sea (North Western Mediterranean Sea)

The study focuses on the two most important species in terms of both biomass and commercial interest of small pelagic fishes in the Catalan Sea (NW Mediterranean Sea), the European anchovy (*Engraulis encrasicolus*) and the European sardine (*Sardina philchardus*). These species together with the round sardinella (*Sardinella aurita*) and sprat (*Sprattus sprattus*) are the clupeoids inhabiting this area (Palomera *et al.*, 2007).

In the Western Mediterranean Sea (Gulf of Lion and the Catalan-Balearic Sea, FAO fishery subareas 37.1.1-37.1.2) anchovy and sardine represent the main species landed (ca. 50 % of the total fish landings; Fig 2,GFCM dataset) as well as in the rest of the basin (Stergiou *et al.*, 2016;GFCM dataset Year 2014;Fig. 2). Furthermore, apart from their commercial importance, both species in the area have been described to play important ecological roles in the ecosystem as pointed out by the results of an ecosystem model constructed for the South of the Catalan Sea in which sardine was identified to be involved in wasp-waist control of the trophic flow while anchovy in the bottom-up control (Coll *et al.*, 2006).

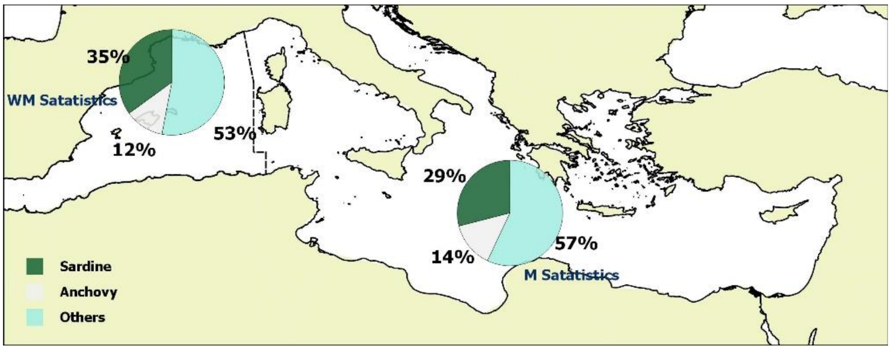

Figure 2. GFCM capture production of the year 2014. WM = Western Mediterranean Sea; M= Whole Mediterranean Sea

In the NW Mediterranean the high biomass of the two small pelagic fishes and its variability have been associated with the favorable environment during the early life stages (e.g. Lloret *et al.*, 2004; Martín *et al.*, 2008). The biology of the two species is relatively well known in the region. In general, they are both planktivorous and feed during their different development stages on a wide range of planktonic species (Tudela and Palomera, 1995; Tudela *et al.*, 2002; Costalago *et al.*, 2012). The two species have a non-overlapping spawning period, in autumn-winter and in spring-summer for sardine and anchovy respectively (Palomera *et al.*, 2007) (Fig. 3). The adult stock abundance and the fecundity of one order of magnitude higher than the other species, allow the early life stages of the two clupeoids to dominate the ichthyoplanktonic fraction along the shelf during the respective spawning seasons (Somarakis *et al.*, 2004;

Sabatés *et al.*, 2007). The shelf in the Catalan Sea is quite narrow and it expands only in the southernmost part near of the Ebro River and in the north part among two major submarine canyons just south to the Gulf of Lions (Fig. 4). Overall, eggs and larvae of anchovy have a maximum density near the edge of the continental shelf (about 200 m isobath) while sardine eggs are located mainly from coastal area to a depth of 100 m and near the shelf when it is narrower, while for both species larvae are more spread than eggs (Palomera, 1992; García and Palomera, 1996; Olivar *et al.*, 2001; Palomera *et al.*, 2007). Anchovy nursery grounds are generally found in shallower waters (between 50–100 m isobaths) compared to spawners, while juveniles of sardine are persistent along the coast where locally increased productivity events occur (Giannoulaki *et al.*, 2011; Tugores *et al.*, 2011). Due to the topographic characteristics (i.e. irregularity of the coastline and bathymetry), the two species' habitats in Catalan Sea as well as in the rest of the Mediterranean Sea show a large degree of overlap between them and among the different life stages (Giannoulaki *et al.*, 2011, 2013).

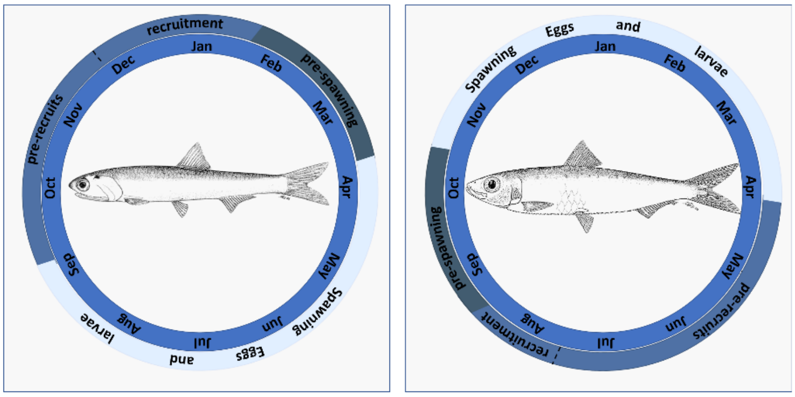

Figure 3. Life cycle schemes of a) *Engraulis encrasicolus* and b) *Sardina philchardus*.

Even if the Mediterranean Sea is generally considered oligotrophic, the complex coastline and bathymetry together with strong seasonality lead to exceptions of this rule. One of these is represented by the NW Mediterranean Sea, in which mechanism of enrichment and concentration processes are recognizable, making it a favorable habitat for both the small pelagic populations. During the year, the physical factors determining productivity depend on the seasonal cycle, and the two species are well adapted to these mechanisms characteristic of their respective spawning season. In general, the upper layer is well mixed in late autumn-winter and strongly stratified during the hot season with the thermocline starting to develop during spring. In winter the convection phenomena are wind-mediated and result in nutrient supply to the surface which sustains high productivity, especially in the wider shelf of the Gulf of Lions and in the Ebro shelf (Salat *et al.*, 2002; Palomera *et al.*, 2007; Sabatés *et al.*, 2007). In these areas, sardine larvae are typically found in high abundance because the environmental conditions favoring their growth (Garcia *et al.*, 2006). These same conditions are also suitable for the juveniles' anchovy which tend to avoid oligotrophic offshore waters (Giannoulaki *et al.*, 2013).

During late spring and summer, the formation of the thermocline prevents vertical motion and the only way to which the productivity could be improved is through river run-offs, which are strong in April -May (Palomera *et al.*, 2007). The riverine waters may spread over wide areas due to the stratification, contributing at about 10% - 20% of the surface productivity. These waters enhance the production of zooplankton during this season (Salat, 1996; Salat *et al.*, 2002) improving both the feeding of the sardine juveniles and the survival of anchovy larvae which are widely distributed from the coast to offshore but with highest density near the Ebro River mouth (García and Palomera, 1996; Palomera *et al.*, 2007; Giannoulaki *et al.*, 2011) (Fig 4, example of the chlorophyll-a production in late winter-spring).

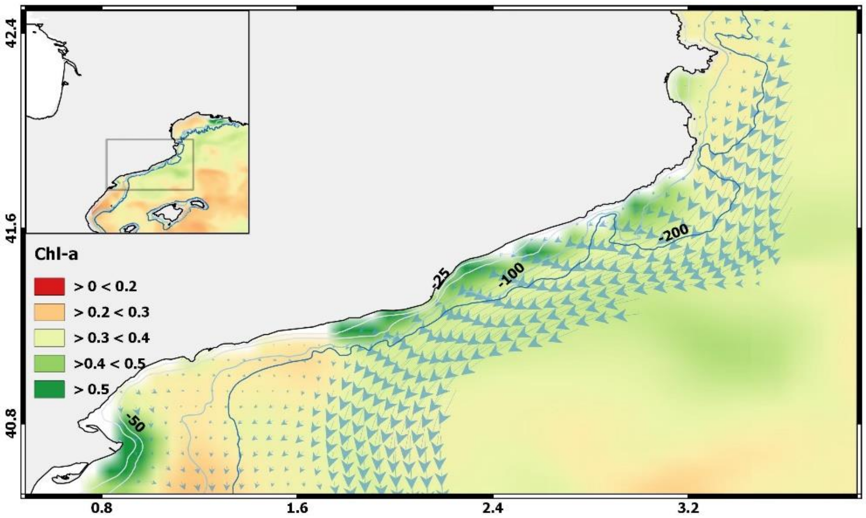

Figure 4. Chlorophyll-a during late winter early spring in 2014 and current direction and intensity calculated by using the meridional and the zonal current (http://marine.copernicus.eu/)

As in the rest of NW Mediterranean Sea, a cyclonic circulation (Northern Current, NC) contouring the continental slope characterize the area (Font *et al.*, 1988). This current is in geostrophic equilibrium with a shelf/slope density front, the so named Catalan front, which is associated with a salinity gradient separating the low salinity-freshwater on the continental shelf, derived by the Atlantic Water and reinforced by the influences of riverine inputs, from the saltiest waters on the open sea (Font *et al.*, 1988). The meandering behavior, generated by a variety of factors (e.g. influxes of freshwater or episodes of strong northerly wind; Font, 1990; Salat, 1996), and its related accumulation mechanisms when the associated front is near the shelf, together with the succession of anticyclonic eddies travelling over the continental shelves, are the most important mesoscale activities of this current flowing southwestwards (Rubio *et al.*, 2005; Sabatés *et al.*, 2007, 2013). Both fronts and eddies are described in the area as important structures which help to ensure better survival conditions for larvae and eggs by enhancing their retention, concentration and feeding (Sabatés *et al.*, 2007, 2013).

Despite these environmental characteristics favouring the spawning, the survival early stages and growing of the two small pelagic species, the catches in the North-eastern Spain (geographical subarea 06, GSA06) during the period 1990-2014 suffered a lasting decrease which after 1994 was consistent also with the biomass estimates by acoustic surveys (GFCM, 2015). Sardine reached the lowest values of both catches and biomass ever during the year 2014, while for anchovy, these values have been slightly increasing since 2008 (GFCM, 2015) (Fig 5a). Similar temporal patterns can be observed, when considering landings of both species along the Catalan coast, characterize by a steadily decline of sardines, and negative trend but less clear regarding anchovy (Fig. 5b).

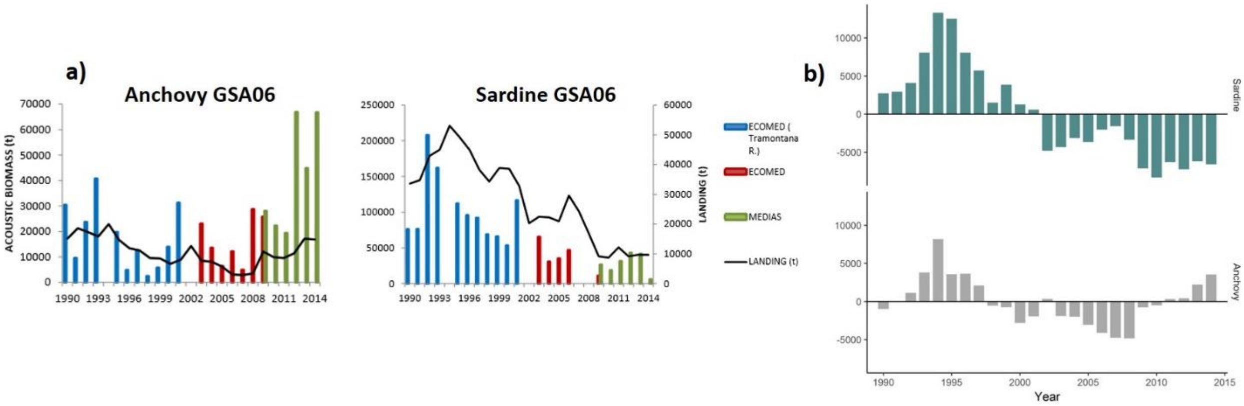

Figure 5. a) Biomass estimates for anchovy and sardine in GSA06 from 1990 to 2014. Surveys ECOMED 1990-2009, MEDIAS 2009-2014 and the respective landings. b) Annual landings form the main Catalan ports standardized in respect to the long term mean.

Even if in the whole GSA06 neither of the two populations is considered underexploited (GFCM, 2015), overfishing alone is an improbable cause of the recent situation. In fact, when looking for example at the estimated summer biomass of both species from 2010 to 2013 from scientific acoustic surveys (MEDIAS) in the whole GSA 06 (Fig 5a), on average was almost three and a half times higher than their respective annual landing estimates. In these estimates, both species seem to maintain high biomass regardless of the preceding fishing pressure, and consequently, it seems unlikely that overexploitation alone has caused the recent decrease (Van Beveren *et al.*, 2016).

On the other hand, changes in the marine environment, although not entirely clear, characterized the area in question. A consistent warming pattern in the entire Western Mediterranean Sea occurred over the last 40 years at different depths (Vargas-Yáñez *et al.*, 2010). Furthermore, salinity gradually have risen especially at the intermediate layers (> 150 of depth) but also an increment at the surface was noticed (Vargas-Yáñez *et al.*, 2010). This salinization might have substantial repercussions on the ocean currents and on the stability of water column with subsequent alterations of the nutrient supply from the deep layers to the photic zones with consequences on the community of the primary producers (Auger *et al.*, 2014) and thus on the tropic levels above them (Calvo *et al.*, 2011). In addition, during the last decade, the zooplankton, which constitutes the bulk of small pelagic fish prey (Palomera *et al.*, 2007; Ganias, 2014 and references therein), has undergone a shift towards smaller plankton species in the Catalan Sea (Calvo *et al.*, 2011).

As pointed out, the environmental factors and their variation can influence small pelagic populations abundance in different ways by, for instance, affecting early life stages and the subsequent recruitment success, or by shifts in distribution at a short or a wide temporal and spatial scale. These effects inevitably affect fisheries which depend upon the total abundance of the target species as well as when and how they are distributed. This work aims at a better understanding of the anchovy and sardine populations variability and their relationships with the environmental drivers in the Catalan Sea.

Thesis outline and objective

The overarching objective of the thesis is to contribute to the better understanding of the roles of the environmental driving forces on the the fluctuations and general decrease of the abundance of small pelagic populations in the NW Mediterranean Sea. The study was developed in four parts.

We started with the analysis of the spatial distribution of the purse seine fishery operations in the area (Chapter 1). Based on the hypothesis that the efficient exploitation of small pelagic fish by fishers relies greatly on the matching of vessels and fish spatial distributions, we used positioning data of fishing vessels obtained by Vessel Monitoring System (VMS) to infer the spatiotemporal dynamics of anchovy and sardine populations. Further, since the data used in this thesis are the high-resolution data of commercial landings for the most important harbors of Catalunya, this chapter, shaping the spatial dimension at which these data can be associated with the local environmental variables, paves the way for the succeeding analysis with the external driving forces.

The three remaining parts of the thesis aim to model the relationships between the environment and landings of both species. Modeling is a necessary tool that can be used to relate abundance, distribution, fluctuations, and production of living organisms to variation in the abiotic environment. When modeling fishery data, it is important to distinguish between the type of influences of environmental drivers have on the availability of the resource *i.e.* immediate or lagged. The immediate effects of the abiotic environment, are those implicated principally on the concentration of fish in a specific area, consequently, when favourable conditions are present the occurrence of small pelagic individuals and thus their availability as a fishing resource are promoted. Whereas, when looking to the delayed influences what we are doing is to look the environmental forces who act on the abundance of the adult fish population by affecting the critical stages of development.

In Chapter 2 and 3 we looked at the immediate effects of the environmental factors on landings per unit effort of anchovy and sardine respectively by using relatively short monthly time series. We considered those environmental drivers which are often used as a proxy of the enrichment, concentration, and retention processes. In Chapter 2 anchovy landings were related with these drivers considering three fishing zones defined along the Catalan Coast. While in Chapter 3 only landings of sardine from the Ebro Delta shelf were considered.

In chapter 4, we looked at the lagged effects of the environment on the small pelagic populations by using forty years of monthly anchovy and sardine landings along the Catalan coast. We searched, by using time series regressions, the environmental factors acting on the temporal windows, defined in respect to the different critical stages of development of both species, which more affected the anchovy and sardine abundance. Furthermore, once these environmental forces affecting the recruitment success were identified we assessed if these effects were stationary or changed over time.

Finally, I discuss the overall results, more relevant findings and the study limitations and provide possible perspectives to pursue this work.

References

Agenbag, J. J., Richardson, A. J., Demarcq, H., Fréon, P., Weeks, S., and Shillington, F. A. 2003. Estimating environmental preferences of South African pelagic fish species using catch size- and remote sensing data. *Progress in Oceanography*, 59: 275–300.

Agostini, V. N., and Bakun, A. 2002. Ocean triads' in the Mediterranean Sea: physical mechanisms potentially structuring reproductive habitat suitability (with example application to European anchovy, Engraulis encrasicolus). *Fisheries Oceanography*, 11: 129–142.

Auger, P. A., Ulses, C., Estournel, C., Stemmann, L., Somot, S., and Diaz, F. 2014. Interannual control of plankton communities by deep winter mixing and prey/predator interactions in the NW Mediterranean: Results from a 30-year 3D modeling study. *Progress in Oceanography*, 124: 12–27.

Bakun, A. 1996. Patterns in the ocean: ocean processes and marine population dynamics. Patterns in the ocean: ocean processes and marine population dynamics.

Bakun, A. 2006. Wasp-waist populations and marine ecosystem dynamics: Navigating the 'predator pit' topographies. *Progress in Oceanography*, 68: 271–288.

Bakun, A. 2010. Linking climate to population variability in marine ecosystems characterized by non-simple dynamics: Conceptual templates and schematic constructs. *Journal of Marine Systems*, 79: 361–373.

Barange, M., Merino, G., Blanchard, J. L., Scholtens, J., Harle, J., Allison, E. H., Allen, J. I., *et al.* 2014. Impacts of climate change on marine ecosystem production in societies dependent on fisheries. *Nature Climate Change*, 4: 211–216.

Bertrand, A., Segura, M., Gutiérrez, M., and Vásquez, L. 2004a. From small-scale habitat loopholes to decadal cycles: a habitat-based hypothesis explaining fluctuation in pelagic fish populations off Peru. *Fish and fisheries*, 5: 296–316.

Bertrand, S., Díaz, E., and Ñiquen, M. 2004b. Interactions between fish and fisher's spatial distribution and behaviour: an empirical study of the anchovy (Engraulis ringens) fishery of Peru. *ICES Journal of Marine Science: Journal du Conseil*, 61: 1127–1136.

Bertrand, S., Díaz, E., and Lengaigne, M. 2008. Patterns in the spatial distribution of Peruvian anchovy (Engraulis ringens) revealed by spatially explicit fishing data. *Progress in Oceanography*, 79: 379–389.

Blaxter, J. H. S., and Hunter, J. R. 1982. The biology of the clupeoid fishes. *Advances in marine biology*, 20: 1–223.

Bonanno, A., Giannoulaki, M., Barra, M., Basilone, G., Machias, A., Genovese, S., Goncharov, S., *et al.* 2014. Habitat Selection Response of Small Pelagic Fish in Different Environments. Two Examples from the Oligotrophic Mediterranean Sea. *PLOS ONE*, 9: e101498.

Cahuin, S. M., Cubillos, L. A., Ñiquen, M., and Escribano, R. 2009. Climatic regimes and the recruitment rate of anchoveta, Engraulis ringens, off Peru. Estuarine, *Coastal and Shelf Science*, 84: 591–597.

Calvo, E., Simó, R., Coma, R., Ribes, M., Pascual, J., Sabatés, A., Gili, J., *et al.* 2011. Effects of climate change on Mediterranean marine ecosystems: the case of the Catalan Sea. *Climate Research*, 50: 1–29.

Checkley, D. M., Asch, R. G., and Rykaczewski, R. R. 2017. Climate, Anchovy, and Sardine. *Annual Review of Marine Science*, 9: 469–493.

Checkley et al. 2009. Climate change and small pelagic fish. *Cambridge University Press, Cambridge, UK; New York*. 372 pp.

Coll, M., Palomera, I., Tudela, S., and Sardà, F. 2006. Trophic flows, ecosystem structure and fishing impacts in the South Catalan Sea, Northwestern Mediterranean. *Journal of Marine Systems*, 59: 63–96.

Costalago, D., Navarro, J., Álvarez-Calleja, I., and Palomera, I. 2012. Ontogenetic and seasonal changes in the feeding habits and trophic levels of two small pelagic fish species. *Marine Ecology Progress Series*, 460: 169–181.

Cury, P., and Roy, C. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Canadian Journal of Fisheries and Aquatic Sciences*, 46: 670–680.

Cushing, D. H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Advances in marine biology*, 26: 249–293.

Dulčić, J., and Kraljević, M. 1996. Weight-length relationships for 40 fish species in the eastern Adriatic (Croatian waters). *Fisheries Research*, 28: 243–251.

Finney, B. P., Alheit, J., Emeis, K.-C., Field, D. B., Gutiérrez, D., and Struck, U. 2010. Paleoecological studies on variability in marine fish populations: a long-term perspective on the impacts of climatic change on marine ecosystems. *Journal of Marine Systems*, 79: 316–326.

Font, J., Salat, J., and Tintore, J. 1988. Permanent features of the circulation in the Catalan Sea. *Oceanologica Acta*, Special issue..

Font, J. 1990. A comparison of seasonal winds with currents on the continental slope of the Catalan Sea (northwestern Mediterranean). *Journal of Geophysical Research: Oceans*, 95: 1537–1545.

Fréon, P., and Misund, O. A. 1999. Dynamics of pelagic fish distribution and behaviour: effects on fisheries and stock assessment. *Fishing News Books*, Oxford. 348 pp.

Fréon, P., Cury, P., Shannon, L., and Roy, C. 2005. Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: a review. *Bulletin of Marine Science*, 76: 385–462.

Ganias, K. 2014. Biology and ecology of sardines and anchovies. CRC Press.

García, A., and Palomera, I. 1996. Anchovy early life history and its relation to its surrounding environment in the Western Mediterranean basin. *Scientia Marina* 60: 155-166.

Garcia, A., Cortes, D., Ramírez, T., Guisande, C., Quintanilla, J., Alemany, F., Rodriguez, J. M., *et al.* 2006. Field comparison of sardine post-flexion larval growth and biochemical composition from three sites in the W Mediterranean (Ebro river coast, bays of Almería and Málaga). *Scientia marina*, 70: 79–91.

Giannoulaki, M., Pyrounaki, M. M., Liorzou, B., Leonori, I., Valavanis, V. D., Tsagarakis, K., Bigot, J. L., *et al.* 2011. Habitat suitability modelling for sardine juveniles (*Sardina pilchardus*) in the Mediterranean Sea: Habitat suitability modelling for sardine juveniles. *Fisheries Oceanography*, 20: 367–382.

Giannoulaki, M., Iglesias, M., Tugores, M. P., Bonanno, A., Patti, B., De Felice, A., Leonori, I., *et al.* 2013. Characterizing the potential habitat of European anchovy *Engraulis encrasicolus* in the Mediterranean Sea, at different life stages: *Habitat of anchovy in the Mediterranean*. *Fisheries Oceanography*, 22: 69–89.

Hidalgo, M., Rouyer, T., Molinero, J., Massutí, E., Moranta, J., Guijarro, B., and Stenseth, N. 2011. Synergistic effects of fishing-induced demographic changes and climate variation on fish population dynamics. *Marine Ecology Progress Series*, 426: 1–12.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. *ICES*.

Katara, I., Pierce, G. J., Illian, J., and Scott, B. E. 2011. Environmental drivers of the anchovy/sardine complex in the Eastern Mediterranean. *Hydrobiologia*, 670: 49–65.

Katara, I. 2014. Recruitment Variability. Biology and Ecology of Sardines and Anchovies: 242.

Lasker, R. 1981. The role of a stable ocean in larval fish survival and subsequent recruitment. *Marine fish larvae: morphology, ecology and relation to fisheries*: 81–87.

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

Lloret, J., Palomera, I., Salat, J., and Solé, I. 2004. Impact of freshwater input and wind on landings of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in shelf waters surrounding the Ebre (Ebro) River delta (north-western Mediterranean). *Fisheries Oceanography*, 13: 102–110.

MacCall, A. D. 1990. Dynamic geography of marine fish populations. *Washington Sea Grant Program Seattle, WA*.

Martín, P., Bahamon, N., Sabatés, A., Maynou, F., Sánchez, P., and Demestre, M. 2008. European anchovy (*Engraulis encrasicolus*) landings and environmental conditions on the Catalan Coast (NW Mediterranean) during 2000–2005. *Hydrobiologia*, 612: 185–199.

Olivar, M. P., Salat, J., and Palomera, I. 2001. Comparative study of spatial distribution patterns of the early stages of anchovy and pilchard in the NW Mediterranean Sea. *Marine Ecology Progress Series*, 217: 111–120.

Ottersen, G., Stenseth, N. C., and Hurrell, J. W. 2004. Climatic fluctuations and marine systems: a general introduction to the ecological effects. *Marine ecosystems and climate variation*: 3–14.

Ottersen, G., Kim, S., Huse, G., Polovina, J. J., and Stenseth, N. C. 2010. Major pathways by which climate may force marine fish populations. *Journal of Marine Systems*, 79: 343–360.

Palomera, I. 1992. Spawning of anchovy *Engra ulis encrasicol* us in the Northwestern Mediterranean relative to hydrographic features in the region. *Mar. Ecol. Prog. Ser*, 79: 215–223.

Palomera, I., Olivar, M. P., Salat, J., Sabatés, A., Coll, M., García, A., and Morales-Nin, B. 2007. Small pelagic fish in the NW Mediterranean Sea: An ecological review. *Progress in Oceanography*, 74: 377–396.

Planque, B., Bellier, E., and Lazure, P. 2007. Modelling potential spawning habitat of sardine (Sardina pilchardus) and anchovy (Engraulis encrasicolus) in the Bay of Biscay. *Fisheries Oceanography*, 16: 16–30.

Planque, B., Fromentin, J.-M., Cury, P., Drinkwater, K. F., Jennings, S., Perry, R. I., and Kifani, S. 2010. How does fishing alter marine populations and ecosystems sensitivity to climate*? Journal of Marine Systems*, 79: 403–417.

Rice, J. 1995. Food web theory, marine food webs, and what climate change may do to northern marine fish populations.

Rijnsdorp, A. D., Peck, M. A., Engelhard, G. H., Möllmann, C., and Pinnegar, J. K. 2009. Resolving the effect of climate change on fish populations. *ICES Journal of Marine Science: Journal du Conseil*: fsp056.

Rochet, M. 2000. A comparative approach to life-history strategies and tactics among four orders of teleost fish. *ICES Journal of Marine Science*, 57: 228–239.

Rothschild, B. J. 2000. 'Fish stocks and recruitment': the past thirty years. *ICES Journal of Marine Science: Journal du Conseil*, 57: 191–201.

Rubio, A., Arnau, P. A., Espino, M., Flexas, M. del M., Jordà, G., Salat, J., Puigdefàbregas, J., *et al.* 2005. A field study of the behaviour of an anticyclonic eddy on the Catalan continental shelf (NW Mediterranean). *Progress in Oceanography*, 66: 142–156.

Sabatés, A., Olivar, M. P., Salat, J., Palomera, I., and Alemany, F. 2007. Physical and biological processes controlling the distribution of fish larvae in the NW Mediterranean. *Progress in Oceanography*, 74: 355–376.

Sabatés, A., Salat, J., Raya, V., and Emelianov, M. 2013. Role of mesoscale eddies in shaping the spatial distribution of the coexisting Engraulis encrasicolus and Sardinella aurita larvae in the northwestern Mediterranean. *Journal of Marine Systems*, 111–112: 108–119.

Salat, J. 1996. Review of hydrographic environmental factors that may influence anchovy habitats in northwestern Mediterranean. *Scientia marina*, 60: 21–32.

Salat, J., Garcia, M. A., Cruzado, A., Palanques, A., Arín, L., Gomis, D., Guillén, J., *et al.* 2002. Seasonal changes of water mass structure and shelf slope exchanges at the Ebro Shelf (NW Mediterranean). *Continental Shelf Research*, 22: 327–348.

Santos, M. B., Gonzalez-Quiros, R., Riveiro, I., Cabanas, J. M., Porteiro, C., and Pierce, G. J. 2012. Cycles, trends, and residual variation in the Iberian sardine (Sardina pilchardus) recruitment series and their relationship with the environment. *ICES Journal of Marine Science*, 69: 739–750.

Shannon, L., Coll, M., Neira, S., Cury, P., and Roux, J.-P. 2008. Exploring the ecological role of small pelagic fish using trophic models: what can be learnt from fishing impacts about the possible impacts of climate change. *Climate Change and Small Pelagic Fish*.

Somarakis, S., Palomera, I., Garcia, A., Quintanilla, L., Koutsikopoulos, C., Uriarte, A., and Motos, L. 2004. Daily egg production of anchovy in European waters. *ICES Journal of Marine Science*, 61: 944–958.

Stergiou, K. I., Somarakis, S., Triantafyllou, G., Tsiaras, K. P., Giannoulaki, M., Petihakis, G., Machias, A., *et al.* 2016. Trends in productivity and biomass yields in the Mediterranean Sea Large Marine Ecosystem during climate change. *Environmental Development*, 17: 57–74.

Tudela, S., and Palomera, I. 1995. Diel feeding intensity and daily ration in the anchovy Engraulis encrasicolus in the northwest Mediterranean Sea during the spawning period. *Marine Ecology Progress Series*, 129: 55–61.

Tudela, S., Palomera, I., and Quílez, G. 2002. Feeding of anchovy *Engraulis encrasicolus* larvae in the north-west Mediterranean. *Journal of the Marine Biological Association of the UK*, 82: 349–350.

Tugores, M., Giannoulaki, M., Iglesias, M., Bonanno, A., Tičina, V., Leonori, I., Machias, A., *et al.* 2011. Habitat suitability modelling for sardine *Sardina pilchardus* in a highly diverse ecosystem: the Mediterranean Sea. *Marine Ecology Progress Series*, 443: 181–205.

Van Beveren, E., Fromentin, J.-M., Rouyer, T., Bonhommeau, S., Brosset, P., and Saraux, C. 2016. The fisheries history of small pelagics in the Northern Mediterranean. *ICES Journal of Marine Science: Journal du Conseil*, 73: 1474–1484.

Vargas-Yáñez, M., Zunino, P., Benali, A., Delpy, M., Pastre, F., Moya, F., García-Martínez, M. del C., *et al.* 2010. How much is the western Mediterranean really warming and salting? Journal of Geophysical Research, 115.

Wang, W.-C., Chau, K.-W., Cheng, C.-T., and Qiu, L. 2009. A comparison of performance of several artificial intelligence methods for forecasting monthly discharge time series. *Journal of Hydrology*, 374: 294–306.

Chapter 1

Spatial structures and temporal patterns of purse seine fishing effort in the NW Mediterranean Sea estimated using VMS data.

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Abstract

Vessel monitoring systems (VMS) represent a tool that can provide information on the spatial and temporal distribution of fishing activity and a quantitative evaluation of the fishing effort on both a spatial and temporal scale. The aim of this study was to characterize the spatio-temporal structure of the Catalan purse-seiner fishing effort directed towards anchovy or sardine, which was estimated by filtering the VMS data (from 2012 to 2014) by species and seasons. Results showed that the mean location of the fishing effort directed towards anchovy did not vary among the summer seasons, in contrast to efforts in spring and autumn, whereas the mean location of the effort directed towards sardine was constant over the seasons. The concentration curves indicated similar fishing effort patterns during all seasons when directed towards sardine, whereas the effort directed towards anchovy was more concentrated during summer. The ranges of the variograms indicated that fishing effort directed towards both species formed patches. The dimensions of these patches changed from season to season with the smallest magnitudes during the summer seasons. In this study, seasonal distribution pattern of the fishing efforts was recognized that apparently adequately captured the features of the distributions of small pelagic populations.

KEYWORDS: spatial analysis, small pelagic fish, purse seine fisheries, northwestern Mediterranean Sea, VMS, Fishing effort

Fisheries Management and Ecology
Under review

Chapter 1

Introduction

Small pelagic fishes are the primary contributors to total fisheries landings in the Mediterranean Sea. Specifically, in the northwestern Mediterranean Sea, sardine (*Sardina pilchardus*, Walb. 1792) and anchovy (*Engraulis encrasicolus*, L. 1758) are the most important species both in biomass and commercial interest (Lleonart & Maynou, 2003; Palomera et al., 2007). Sardines are the primary contributor to fisheries landings in volume, but the landings of anchovy can be more important in value because of the higher unit price (Palomera et al., 2007; Pertierra & Lleonart, 1996).

In the Catalan Sea, purse seining is the only technique used to exploit small pelagic species (Pertierra & Lleonart, 1996). By law, purse seiners are obliged to return daily to a port, not necessarily the home port, and also to a minimum docking time of 12 hours per day, during the day-time. This regulation allows the fleet to exploit areas in which the environmental conditions seasonally favour anchovy or sardine aggregations in attempts to maximize fleet catch rates.

Small pelagics aggregate into clusters of schools (e.g., Petitgas 2001; Giannoulaki et al. 2003; Giannoulaki et al. 2006; Brehmer et al. 2007), which can vary in dimensions and in numbers (Giannoulaki et al., 2003, 2006; Petitgas, 2001; Petitgas & Levenez, 1996), and during the night-time, when purse seiners work, they disaggregate forming shoals (Fréon & Misund, 1999). In general, large clusters are more easily located by fishing vessels than smaller ones (Brehmer et al., 2006). These large fish aggregations are detected primarily using acoustical methods (echo sounder), in conjunction with the aggregative behaviour of vessels (Arcos & Oro, 2002), i.e., when a large cluster is detected by a vessel, that vessel becomes more exposed to other vessels, which then aggregate and join the effort to fish the cluster. Consequently, because a fishery is the result of the interaction between the spatial distribution of fish and the application of fishing effort in space (Petitgas, 1998), the presence of large fish aggregations can be reflected in an extended fishing area.

Over the past years, important changes in sardine and anchovy catches were observed in the Catalan Sea (as in other areas of the NW Mediterranean Sea, such as the Gulf of Lions), characterized by a continuous decreasing trend since the mid-1990s. Although signs of anchovy recovery were observed beginning in 2008, overall, both stocks are considered unsustainably exploited, with high biomass but high fishing mortality in the case of anchovy and a depleted stock with low fishing mortality in the case of sardine (SCSA 2015).

In 2000, the European Commission introduced the Vessel Monitoring System (VMS) for all vessels ≥ 24 m LOA, afterwards extending it to all vessels ≥ 12 m (European Commission, 2008), as tool to allow the management authorities to supervise fishing activities, including monitoring the compliance of fishing vessels with spatial and temporal regulations (Lee, South, & Jennings, 2010). VMS is a powerful tool in fishery studies and management, because high resolution analyses of fishing activity and quantitative evaluations of fishing effort can be conducted on both spatial and temporal scales (Bastardie, Nielsen, Ulrich, Egekvist, & Degel, 2010; Lee et al., 2010). Monitoring the daily activity of purse seiners operating on small pelagic fish aggregations can serve as proxy in the study of the spatial distribution of small pelagics, when dedicated acoustic surveys do not exist or do not cover the appropriate spatio-temporal scale of the species. For example, in the NW Mediterranean, the MEDIAS acoustic survey is conducted once a year, in summer, since 2009 (Brosset et al., 2017).

Based on the hypothesis that the efficient exploitation of small pelagic fish by purse seiners relies greatly on the matching of vessels and fish spatial distributions, we used positioning data of fishing vessels obtained by VMS to infer the spatio-temporal dynamics of small pelagic fish. First, the prominent spatial characteristics (location and space occupation) and the changes in aggregation pattern of the seasonal fishing effort directed towards both species were studied. Second, the general characteristics of the spatio-temporal structure of the fishing effort were examined, and finally, the internal organization of the spatial structure of effort aggregations was investigated.

Materials and Methods

The study area spans the entire Catalan coast in the NW Mediterranean Sea and is limited by the 35 m and 200 m isobaths, which correspond to the portion of the continental shelf in which the purse seine fishery is conducted (Fig. 1). In the Catalan Sea, the purse seine fishery targeting small pelagic shoals operates 5 days per week (Pertierra & Lleonart, 1996) at night by using light attraction and is concentrated between Cape Creus and the Ebro River delta (Agostini & Bakun, 2002). To protect the recruitment of anchovy, purse seining is suspended during two months in winter, generally from mid-December to mid-February, although the exact timing varies among harbours.

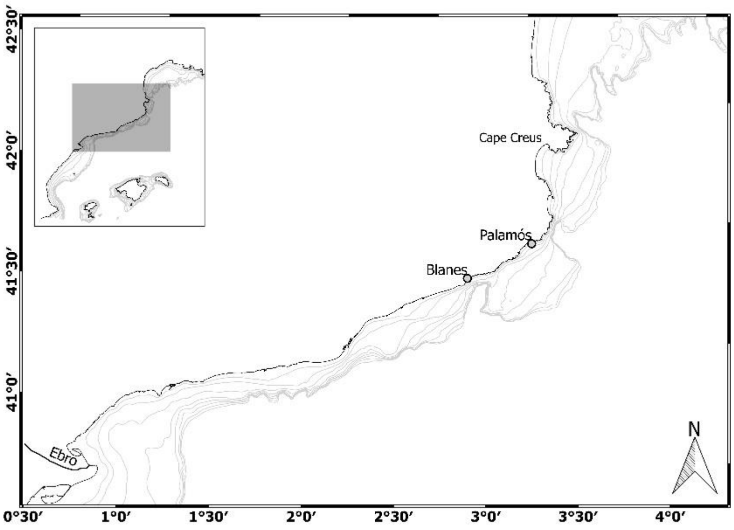

Figure 1. The study area limited by the 35 m and 200 m of the isobaths and the two fishing home ports.

VMS Data and grid effort estimates

The VMS data using 2-hour polling rates of 29 purse seine vessels based in the harbours of Blanes and Palamós and operating along the Catalan Coast were provided by the Secretaria General de Pesca, the fisheries management agency of the Spanish government. The data accounted for the activity of ca. 30% of the entire Catalan purse seiner fleet and included daily records for 2012, 2013 and 2014.

Data processing and data filtering

The coordinates of the VMS data points were expressed as longitude and latitude degrees. Data were projected into a Lambert Azimuthal Equal Area (LAEA) projection, which is suitable for statistical analysis because it is based on an equal area projection (Annoni, Luzet, Gubler, & Ihnde, 2001).

The raw VMS data did not indicate reliably when each vessel was actually engaged in fishing; therefore, the most common approach to overcome this problem is to use the speed of the vessel to define whether the VMS points corresponded to a fishing operation (Lambert et al., 2012; Lee et al., 2010; Murawski, Wigley, Fogarty, Rago, & Mountain, 2005; Russo, Parisi, & Cataudella, 2013). All the VMS data points located at a depth less than 35 m were removed, because purse seiner fishing activity is prohibited landwards from this isobath. Furthermore, VMS records from December to February were deleted, because the purse seine fishery is stopped due to the annual closure (from mid-December until mid-February) in the area. The remaining VMS data (from March to November) were grouped by season: spring (all the VMS data from

March, April and May), summer (all the VMS data from June, July and August) and fall (all the VMS data from September, October and November).

Defining the signature of purse seine operation

Purse seiners spend much of the time searching with the aid of echo sounders for the appropriate location to set the purse seine. Once located, the purse seine is shot, and the fish school is surrounded. This characteristic fishing operation is easily recognized visually in high-frequency monitoring systems, such as the Automatic Identification System (AIS). Using AIS data from online providers such as Marine Traffic (www.marinetraffic.com), the seasonal VMS data were filtered by speed. The filtering procedure was performed by visually examining the daily timeline from AIS data for a sample of vessels, which suggested a starting speed of the fishing of *ca.* 5 knots (Fig. 2); thus, VMS signals with speeds lower than this velocity were retained. Each purse seine cast lasts ca. 1 h, and typically, 2-3 such casts occur each night during the permitted 12 working hours.

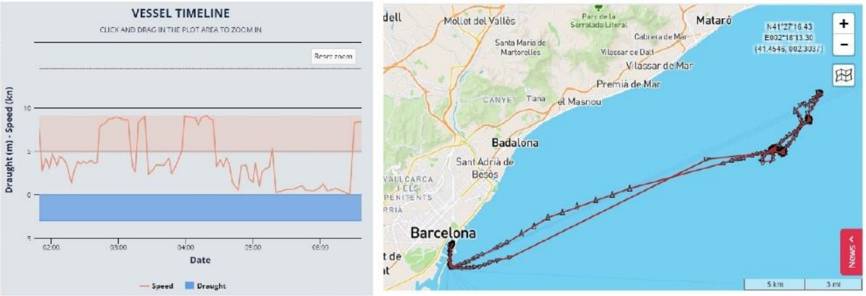

Figure 2. Example of the daily trip of a vessels trip and the timeline associated from AIS data used to filter VMS data (data from WWW.MARINETRAFFIC.COM).

GIS analysis

The filtered VMS records were then combined with the fish sales records provided by the first sale market at the harbour of fish landings, which permitted separation of the records based on the targeted species of the fishing activity of each day and also eliminated the VMS positional information received when a vessel was not involved in fishing activity. With this approach, the seasonal VMS data were divided by species, and each of the VMS records was characterized by a value of Gross Registered Tonnage (GRT), which was used as the fishing capacity parameter to measure the fishing effort.

The seasonal filtered VMS data were then used to represent the fishing effort on a grid (e.g., Gerritsen, Minto, & Lordan, 2013; Lee et al., 2010) by season and species. In general, the skills of the fishermen and good knowledge of the spatial patterns of fish largely influence the success of the purse seines fishery

(Hieu, Brochier, Tri, Auger, & Brehmer, 2014). Small pelagic fishes are described in many pelagic stocks as organized in clusters of schools (e.g., Mackinson, 1999; Pierre Petitgas & Levenez, 1996). In the Mediterranean Sea, the mean size of small pelagic patches varies from < 10 to ca. 25 km^2 (Fréon & Misund, 1999 and references therein; Giannoulaki et al., 2003, 2006); therefore, considering the objective of the study, a 16 km^2 grid (4 x 4 km) was used as the elementary unit, and the centroids were extracted for the subsequent analysis. Based on empirical observation of the daily fishing activity with the use of the online AIS providers, each elementary unit was subdivided into sub-grids with cells of 1 km x 1 km to assign an appropriate estimate of the fishing effort. All the VMS records belonging to a specific vessel that fell inside one of the sub-cells were defined as a singular fishing event in a day, and therefore, the GRT value of the vessel was assigned to that specific sub-cell. Then, the daily fishing effort of a specific vessel in the elementary unit (i.e., 4 x 4 km) was obtained by the sum of the sub-cells representing the GRT value.

The following expression was used to estimate the seasonal fishing effort for a species in each elementary unit:

$$\text{Seasonal fishing effort per species in a cell} = \sum\nolimits^{n}{}_{j=1} Sc_j \times GRT_j \quad (1)$$

where *n* is the total number of vessel x days in a season, Sc_j is the number of sub-cells occupied in a day by a specific vessel and GRT_j is the gross registered tonnage.

Based on the values of equation (1), fishing effort distribution maps were developed using QGIS Ver. 2.10.1. (QGIS, 2015).

Spatial Data analyses

Seasonal Spatial distribution and Concentration patterns of Fishing effort

To capture the spatial patterns of the estimated fishing effort directed towards both species as simply as possible and to investigate season-to-season variations, we calculated the centres of gravity (*CG*) with their associated inertia (Woillez, Rivoirard, & Petitgas, 2009). The *CG* represents the mean location of the population; whereas inertia describes the dispersion of the population around its centre of gravity.

Spatial concentration (or aggregation) of the estimated fishing efforts was compared between season and species by computing geostatistical concentration curves and the derived space concentration index (P. Petitgas, 1998).

The concentration curves (Matheron, 1981; Petitgas, 1998) describe the changes in spatial distribution of a population as a function of its abundance. Overall, the curves represent the maximum proportion of a variable (e.g., biomass, abundance or as in this study, fishing effort) that can be found in any proportion of the area of interest (Petitgas, 1998; Petitgas, 1997). For the construction of the concentration curves, the fishing effort was estimated for the elementary units (i.e., cell), which then were ranked from maximum to minimum, and the cumulative fishing effort and the cumulative area were calculated. These estimates were then expressed as a proportion of total fishing effort $Fe(y)$ and area $A(y)$, respectively, as shown below:

$$Fe(y) = \sum_{i=1}^{k} \frac{f_i}{Fe_{tot}} \qquad (2)$$

$$A(y) = \sum_{i=1}^{k} \frac{a_i}{A_{tot}} \qquad (3)$$

where f_i is the fishing effort in the effort class i and a_i is the cumulative area in which the fishing effort of the class *i* occurs; Fe_{tot} corresponds to the total fishing effort and A_{tot} to the total area.

The concentration curve of fishing effort per season and species obtained by the combination of equations (2) and (3) was used to evaluate whether the effort was homogeneously distributed and also to perform temporal and between species spatial distribution comparisons. Fishing effort is distributed homogeneously when the concentration curve increases at the same rate as that of the area (i.e., linearly in a plot of Fe against A). Consequently, with a greater concentration of effort, the distance between the curve and the 1:1 line is greater. The concavity of this curve represents the space concentration index, which is defined as twice the area between the concentration curve and the 1:1 line (Petitgas, 1998).

Additionally, to evaluate whether the concentration pattern was dependent on the amount of fishing effort, we used linear regressions to relate the seasonal space concentration index for both anchovy and sardine with the corresponding fishing efforts over the 3-year study period.

Spatial structure of Fishing effort

The spatial structure, defined as the spatial autocorrelation between values at different locations, of the fishing effort associated with the two species in each season was investigated using variograms (Matheron, 1963).

A non-parametric method based on the median polish (Cressie, 1993; Cressie & Read, 1989; Tukey, 1977), which helps avoid problems of trends in the mean and is also resistant to outliers, was used to estimate the variograms of seasonal fishing effort on the centroids extracted from the grid for both species. Median polish is an iterative procedure in which the median value of each row of a matrix (the west-to-east points) and the median value of each column of the matrix (south-to-north points) are subtracted from the original values of rows and columns, respectively. The procedure is repeated until no changes occur with the row or column medians (Tuckey, 1977). The omnidirectional variogram for each species and season calculated on the median polish residuals was defined as follows:

$$\gamma(h) = \frac{1}{2N(h)} \sum_{i=1}^{N(h)} [d(x_i) - d(x_i + h)]^2 \quad (4)$$

where $\gamma(h)$ is the estimated semivariance, h is the vector of distance, $N(h)$ is the number of pairs of observations at distance h, and $d(x_i)$ is the value of the median polish residual for the ith data point.

The semivariogram description is based on the quantification of three parameters: *range*, *sill* and the *nugget effect*. The *range* is the distance beyond which the observations are independent; thus, the correlation between them becomes zero. The *sill* is the value at which the variogram reaches the asymptote. The *nugget effect* is the measurement of the spatial variability for distances smaller than *h* (Rossi et al. 1992). To estimate these three variogram parameters for each season and species, the most appropriate model chosen to fit the omnidirectional variogram, determined by the weighted nonlinear least square procedure, was the spherical model (Cressie, 1993).

The features of the study area, which extends in latitude along the entire Catalan coast and longitudinally only in the area between the 35 and 200 m depths, implied that the spatial relationships could depend not only on distance but also on the direction (i.e., anisotropy). Thus, in addition to the omnidirectional variograms, multi-directional variogram plots (Isaaks & Srivastava, 1989) with 45° increments and ± 22.5° (non-overlapping) tolerance were also computed. Furthermore, for each direction, the spherical model was fitted separately to estimate the distance of the spatial continuity of the fishing effort in each direction. The estimated autocorrelation ranges in each direction were then converted to an x-y axis system as follow:

$$x_i = \cos(\alpha_i) * r_i$$
$$y_i = \sin(\alpha_i) * r_i$$

where x_i and y_i are the coordinates in the Cartesian plane, α_i is the direction of the variogram in radians, and r_i is the range estimated. The resulting plots were symmetrical about the origin, because the '*+ range*' values were equal to the '*- range*' values, permitting a better assessment of the direction and magnitude of the spatial structure of the fishing effort.

All analyses were performed using R version 3.3.0 (R Core Team, 2016) and QGIS Ver. 2.10.1. (QGIS, 2015).

Results

Fishing effort distribution and concentration pattern

The total counts of days of fishing operations directed towards anchovy and sardine per vessel and season are shown in Table 1. A seasonal pattern was easily identified for both species in which most of the operations occurred in the summer season, followed by the spring and fall (Tab. 1). However, the seasonal pattern of the operations directed towards anchovy fishing was more evident in which 50%, 52% and 37% of the operations during the three years were conducted during summer, whereas the operations for sardine fishing were more equally distributed.

Table 1. Counts of fishing operations (vessel x day) per season by target species.

	2012			**2013**			**2014**		
	Spring	**Summer**	**Fall**	**Spring**	**Summer**	**Fall**	**Spring**	**Summer**	**Fall**
***A*nchovy**	736	1017	293	530	972	350	759	869	701
Sardine	717	902	435	698	858	569	784	867	751

Fishing effort estimated by equation (1) is shown in Fig. 3. Over the three-year period, estimates for both anchovy and sardine showed an increment in the total annual area occupied (Fig. 3), although the increment was greater for anchovy than for sardine (Fig. 3). The spread of the fishing effort directed towards anchovy showed seasonality, with more effort extended in the summer season (Fig. 3a, c, e), unlike the fishing effort directed towards sardine, which did not show this pattern (Fig. 3b, d, f).

The *CG* of the fishing effort directed towards anchovy did not vary between the summer seasons of the different years, and the distance between CGs ranged from 6.01 to 7.5 km, whereas for spring and fall, they ranged from 8.2 to 22 km and 6 to 39 km, respectively (Fig. 3). For the fishing effort directed towards sardine, the distance between centroids did not vary for the spring and summer seasons (range from 7.1 to 9.1 and 2.2 to 7.4 km, respectively) but did vary for the fall season, although not as clearly as the fishing effort directed towards anchovy (range from 6 to 17.5 km) (Fig. 3).

The associated inertia (Table 2) related to the fishing effort directed towards both species was lower during the summer seasons than in the other seasons. The average root mean square distance between a point of fishing effort directed towards anchovy and sardine for the summer seasons was 51 ± 8.38 km and 48 ± 9 km, respectively, which were distances less than half that between a point of the grid and the gravity centre of the total area (Inertia= 10452.5 km^2, mean distance= 102.24 km); therefore, during the summer seasons, the fishing effort directed towards both species was dispersed in less than half the entire area of the Catalan Sea.

The degree of concentration was apparently similar for both the fishing effort estimates, with average efforts more concentrated during summer as shown in Fig. 4 and confirmed by the space concentration index. However, over the three years, the seasonal space concentration index increased significantly with the increase of fishing effort for anchovy (LM: $y = 0.48 + 0.001x$; R^2adj = 0.45; $p < 0.05$) but not for the one directed towards sardine (LM: $y = 0.53 + 0.0006x$; R^2adj = 0.04; $p > 0.05$).

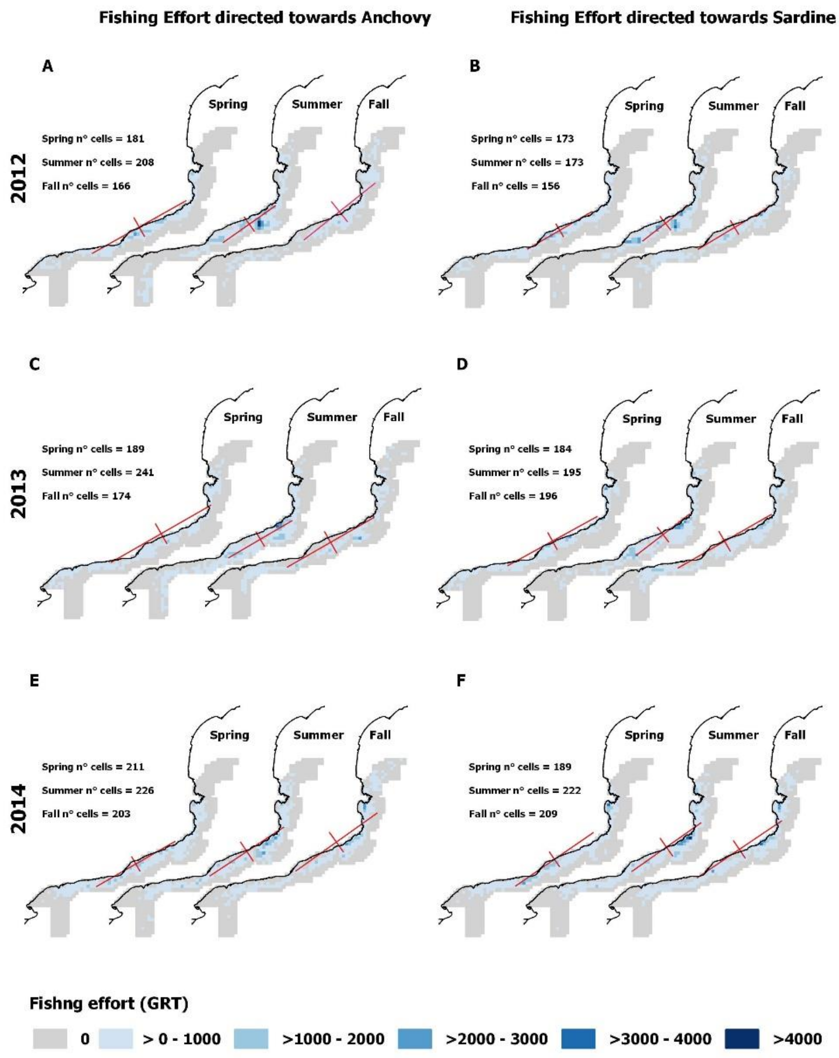

Figure 3. Seasonal maps for each years of the fishing effort estimates directed towards anchovy and sardine with the centres of gravity and inertia in red. n° cells=number of cells occupied by the fishing effort estimates.

Table 2. Values of inertia calculated for each season by target species.

	Spring		Summer		Fall	
	Anchovy	**Sardine**	**Anchovy**	**Sardine**	**Anchovy**	**Sardine**
2012	2587.6	2488.1	1894.1	1562.3	3853.3	3219.2
2013	5975.6	4682.7	2437.5	2104.7	4591.5	4591.5
2014	3681.3	4008.6	3605.6	3288.4	4570.9	4709.7

Spatial structure of Fishing effort

Omnidirectional variograms of the median polish residuals calculated from the fishing effort estimates directed towards both species showed spatial structure (i.e., the variance increased with the increase in the distance between sampling points) for each season during the three years. Therefore, the spatial distributions of fishing effort were not random, as expected, and two points close to one another had a higher probability of having similar values than distant ones. The maximum fishing effort concentrations varied among seasons, with similar patterns shown for both target species. Specifically, the largest concentration patterns of fishing efforts were shown during the spring seasons, with the range of the spherical models varying from ca. 14 to ca. 21 km (Supplementary Fig. A.1, Tab. 3). During the summer seasons, the average dimensions of the concentrations of fishing effort were smaller and the ones directed toward anchovies were more concentrated (Supplementary Fig. A.1, Tab. 3). Although the seasonal pattern was repeated each year, this pattern was less pronounced in 2014 than in the other two years (Supplementary Fig. A.1, Tab. 3).

Table 3. Parameters obtained by fitting spherical models to the omnidirectional variograms of the residuals of the median polish of the seasonal fishing effort (Fe) directed towards anchovy and sardine.

		2012		2013		2014	
		Fe to Anchovy	*Fe to Sardine*	*Fe to Anchovy*	*Fe to Sardine*	*Fe to Anchovy*	*Fe to Sardine*
Spring	**Nuget**	0.80	0.89	1.59	1.12	0.80	0.80
	Partial Sill	4.44	4.14	4.18	4.44	4.30	4.37
	Range	16.85	16.22	20.29	19.49	13.85	15.41
Summer	**Nuget**	0.49	0.66	0.94	1.08	0.94	0.94
	Partial Sill	4.43	4.01	4.57	3.02	4.57	3.76
	Range	9.77	11.40	11.79	13.48	11.79	13.62
Fall	**Nuget**	1.67	0.64	0.86	1.48	1.22	0.64
	Partial Sill	2.32	4.38	3.08	2.79	4.81	4.38
	Range	13.28	12.45	10.36	17.26	13.46	12.45

Anisotropy was apparent for both fishing efforts targeting these species, i.e., the autocorrelation range changed among directions but was inconsistent in direction and magnitude for any particular season (Supplementary Fig. A.2, A.3). When considering the effort towards anchovy, the spatial structures between seasons in 2012 and 2013 and more specifically the differences between spring and the two other seasons were markedly different. The spatial continuities were higher in the north-east direction and east direction (i.e., 45° and 90°) reaching ca. 35 km during the spring season, whereas during summer and fall seasons, the average was ca. 20 km (Supplementary Fig. A.2). Additionally, anisotropy was negligible in summer 2012. In 2014, the structure of the effort concentrations changed, and the smallest magnitudes were observed for all directions and in all seasons, with almost insignificant anisotropy in summer and fall (Supplementary Fig. A.2). Structure of the effort directed towards sardine showed greater magnitudes of spatial continuity in all directions than the effort directed towards anchovy. During spring and fall in 2012 and 2013, equivalent magnitudes of spatial continuity were found in the northeast and east directions (Supplementary Fig. A.3). In 2014, the anisotropic pattern was analogous to the one directed towards anchovy, i.e., negligible for summer and fall seasons (Supplementary Fig. A.3).

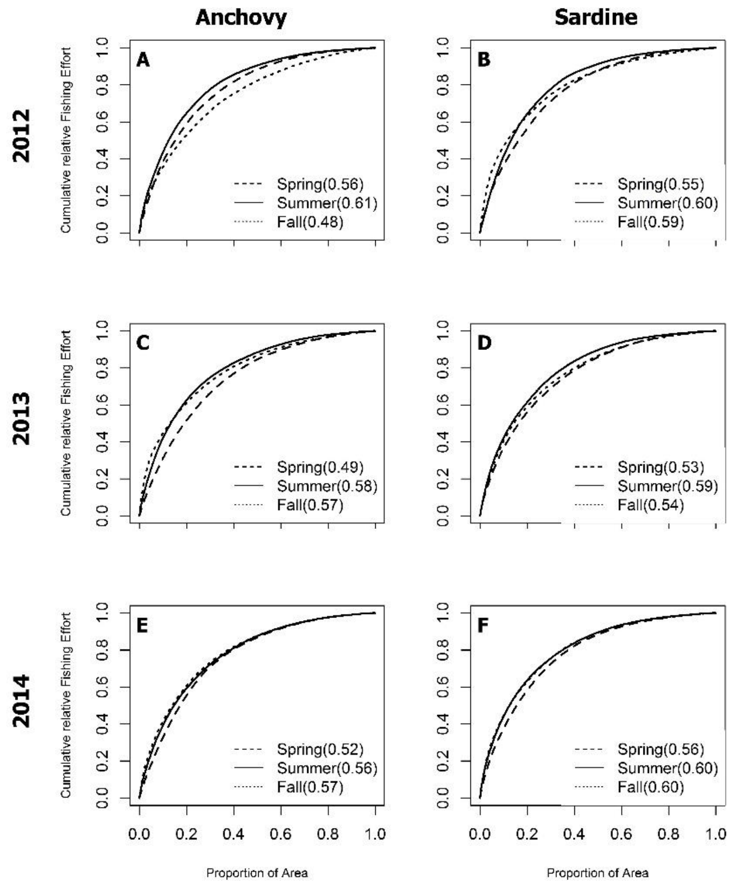

Figure 4. Seasonal concentration curves of fishing effort for each year and species. Number in parentheses indicates the value of the concentration index.

Discussion

This study focused on the spatio-temporal patterns of the fishing effort directed towards the two most important small pelagic species fished in the Catalan Sea. The success of small pelagic catches depends on the perception of fishermen of the spatial patterns of fish and how well they identify high density fish patches (Hieu et al., 2014). Consequently, the spatial distribution of fishing effort and its spatial structure depend on how the resource (i.e., small pelagic fish) is structured, which is dependent on the environmental conditions and how they change spatio-temporally. In this study, we showed definite spatial patterns of the fishing effort directed towards anchovy and sardine and their seasonal variations by applying geospatial techniques. Overall, the total area occupied by the fishing effort directed towards anchovy was greater than that directed towards sardine, and both showed seasonal fluctuations with larger areas occupied during the summer season. The mean location of the fishing effort directed towards anchovy, expressed as the centre of gravity, did not vary during the summer season over the three years, in contrast to the effort during the other two seasons, and moreover, the associated values of inertia were lower during summer than in the spring and fall. The summer season corresponds to the peak of anchovy spawning, and the locations of these summer *CGs* were previously described as an area in which anchovy aggregate to spawn (García & Palomera, 1996; Palomera, 1992). The permanence of the *CGs* and the low inertia suggested that fishermen used the ecology of the exploited species, which in this case, led to encounter with a favourable spawning environment to increase their catches (Parrish, 1999).

The effort directed towards fishing sardine was persistent based on the seasonal CG locations between years. The inertia associated was almost always lower than that directed towards anchovy. Sardine are less important economically (Pertierra & Lleonart, 1996) and along the Catalan coast are more widely distributed than anchovy (Bellido et al., 2008); thus, fishermen were apparently less interested in widening and relocating the effort throughout the area, in contrast to efforts with anchovies during the spring and fall seasons. These results are consistent with the known behaviour of fishermen who do not operate at random but instead follow a process conditioned by the capacity to locate the target species and by the market prices during different seasons (Tsitsika & Maravelias, 2006; Tsitsika & Maravelias, 2008). This behaviour was also confirmed by the concentration curves, which showed similar fishing effort concentration patterns during all seasons when directed towards sardine, whereas the efforts directed towards anchovy were more concentrated during the summer. The preference in fishing anchovy by fishermen was also made evident in the change in the aggregation pattern of the effort directed towards anchovy during summers in which it changed from more concentrated in 2012 and 2013 to less concentrated in 2014, which was a change that was likely associated with the high anchovy biomass registered in the area during this last year (GFCM, 2015) that allowed the fishing effort of fishermen to be more widely scattered. Nevertheless, using the space concentration index to investigate the aggregation patterns in more detail, we found that the concentration of the fishing effort directed towards anchovy increased when the fishing effort itself increased, which suggested an aggregative behaviour of fishing vessels when an anchovy cluster was detected by other fishermen. Contrarily, the space concentration index of the fishing effort directed towards sardine did not vary according to the total fishing effort, which again indicated the importance of anchovy as a species target compared with that of the sardine.

Spatial structure (i.e., spatial autocorrelation) and its seasonal stability were described using omni- and multi-directional variograms. The correlation structure obtained by the omnidirectional variograms reflected patchiness in the distribution of fishing effort directed towards both species, which in general (averages of 13.5 km for anchovy and 14.5 km for sardine), were in the same size range, 12–55 km, consistent with the correlation structures found by other researchers studying acoustic data of small pelagic fishes (Fréon & Misund, 1999 and references therein; Giannoulaki et al., 2003, 2006; Petitgas & Levenez, 1996). Therefore, a strict correspondence of the effort spatial structure distribution with the spatial structure of the small pelagic populations was indicated by the similarities between our findings and the ones obtained by the use of acoustic data, in addition to the reduced probability of concentrations escaping the nets of fishermen because of the technology used (sonar; high resolution radars; (Fréon & Misund, 1999) and the stability of similar effort spatial structures (i.e., magnitude of the range) among the same seasons in the three different years. Hence, based on these results, the use of data completely independent from fishermen control (i.e., VMS) to generate information about the distribution changes in space and in time of the exploited population becomes a possibility when adopting management measures of the resource.

With the spherical models fitted in different directions, we could comprehensively summarize the directional spatial dependence of the fishing effort, which provided an indication of the diameter of the patches in the area. Overall, the geometry of the area affected the organization of the spatial structure of the fishing effort, i.e., the way in which the patches are organized in space (Giannoulaki et al., 2003). As expected, the magnitudes of spatial continuities were the largest in almost all cases in the southwest-northeast directions, following the latitudinal extension of the Catalan coast. Additionally, fishing efforts towards both species did not show a seasonal pattern concerning the direction of spatial continuities. By contrast, the dimensions of the patches tended to change from season to season, although more clearly for the fishing effort directed towards anchovy, which were in smaller patches during the summer seasons. These changes could be interpreted as a reflection of the aggregation behaviour of anchovy, which during the summer season are at the peak of the reproduction period (e.g., Palomera et al., 2007) forming spawning aggregations (Fréon & Misund, 1999), allowing much easier processes of detection and catch (Bertrand, Díaz, & Lengaigne, 2008; Csirke, 1989; Fréon & Misund, 1999) and therefore, a more concentrated fishing effort. The same pattern was not evident for sardine, most likely due to the fishing closures in the area during the time corresponding to the peak of sardine spawning (Martín, Sabatés, Lloret, & Martin-Vide, 2012).

Overall, despite the potential biases that may affect the ability of fishing operations to track small pelagic distributions (Bertrand et al., 2008), from our results, a seasonal distribution pattern of the fishing efforts was recognized that apparently adequately captured the features of the distributions of small pelagic populations (i.e., the extent and patchiness of organization), as described by various authors (Barange & Hampton, 1997; Barra et al., 2015; Petitgas, 2001; Petitgas & Levenez, 1996; Saraux et al., 2014).

Description of the stock size by fishery management authorities is principally affected by the use of indicators, with the primary indicator the Catch per unit effort (CPUE). The use of this index is questionable, particularly for small pelagic fishes because of the high variation in catchability (Bertrand et al., 2008; Csirke, 1989; Fréon & Misund, 1999). However, this variation can be explained by the spatial distribution of the resource exploited and how the fleets fish these resources, as shown by various authors (e.g., Gaertner & Dreyfus-Leon, 2004; Petitgas, 1998). Consequently, using spatially explicit data to determine the organization of the fishing effort in space and how it changes might be useful for improving fish stock assessment and management. Both persistence of the gravity center, inertia, area occupied, as well as the high clustering and the dimension of the patches, are strictly related to fish catchability and vulnerability. The two forage fish in the NW Mediterranean Sea and in other marine ecosystems show highly selective behaviour for suitable areas when they are at both low abundance and biomass values (Saraux et al. 2014, Barra et al. 2015). Accordingly, when the fishing effort is highly clustered, structured by small patches and persistent in the same area along subsequent seasons can correspond to the situation at which fish are concentrated in small suitable areas and for this reason easily to detect and catch (e.e. Fréon & Misund, 1999). Put differently, the stocks are more vulnerable to the fishing operation in these situations. Subsequently, times when fishing operations are spatially structured as described above could be used as warning signals indicating the rise of anchovy and sardine vulnerability to the fishery (Hyperstability, e.g. Hilborn and Walters 1992) and therefore lead to management measures aimed at reduce the fishing effort.

References

Agostini, V. N., & Bakun, A. (2002). Ocean triads' in the Mediterranean Sea: physical mechanisms potentially structuring reproductive habitat suitability (with example application to European anchovy, Engraulis encrasicolus). *Fisheries Oceanography*, *11*(3), 129–142.

Annoni, A., Luzet, C., Gubler, E., & Ihnde, J. (2001). *Map Projections for Europe. European Commission Joint Research Centre, Ispra, Italy. EUR 20120 EN. 131pp*.

Arcos, J., & Oro, D. (2002). Significance of nocturnal purse seine fisheries for seabirds: a case study off the Ebro Delta (NW Mediterranean). *Marine Biology*, *141*(2), 277–286.

Barange, M., & Hampton, I. (1997). Spatial structure of co-occurring anchovy and sardine populations from acoustic data: implications for survey design. *Fisheries Oceanography*, *6*(2), 94–108.

Barra, M., Petitgas, P., Bonanno, A., Somarakis, S., Woillez, M., Machias, A., … Giannoulaki, M. (2015). Interannual Changes in Biomass Affect the Spatial Aggregations of Anchovy and Sardine as Evidenced by Geostatistical and Spatial Indicators. *PLoS ONE*, *10*(8). https://doi.org/10.1371/journal.pone.0135808

Bastardie, F., Nielsen, J. R., Ulrich, C., Egekvist, J., & Degel, H. (2010). Detailed mapping of fishing effort and landings by coupling fishing logbooks with satellite-recorded vessel geo-location. *Fisheries Research*, *106*(1), 41–53. https://doi.org/10.1016/j.fishres.2010.06.016

Bellido, J. M., Brown, A. M., Valavanis, V. D., Giráldez, A., Pierce, G. J., Iglesias, M., & Palialexis, A. (2008). Identifying essential fish habitat for small pelagic species in Spanish Mediterranean waters. *Hydrobiologia*, *612*(1), 171–184. https://doi.org/10.1007/s10750-008-9481-2

Bertrand, S., Díaz, E., & Lengaigne, M. (2008). Patterns in the spatial distribution of Peruvian anchovy (Engraulis ringens) revealed by spatially explicit fishing data. *Progress in Oceanography*, *79*(2), 379–389.

Brehmer, P., Gerlotto, F., Laurent, C., Cotel, P., Achury, A., & Samb, B. (2007). Schooling behaviour of small pelagic fish: phenotypic expression of independent stimuli. *Marine Ecology Progress Series*, *334*, 263–272.

Brehmer, P., Lafont, T., Georgakarakos, S., Josse, E., Gerlotto, F., & Collet, C. (2006). Omnidirectional multibeam sonar monitoring: applications in fisheries science. *Fish and Fisheries*, *7*(3), 165–179. https://doi.org/10.1111/j.1467-2979.2006.00218.x

Brosset, P., Fromentin, J.-M., Van Beveren, E., Lloret, J., Marques, V., Basilone, G., … Saraux, C. (2017). Spatio-temporal patterns and environmental controls of small pelagic fish body condition from contrasted Mediterranean areas. *Progress in Oceanography*, *151*, 149–162. https://doi.org/10.1016/j.pocean.2016.12.002

Council Regulation (EC) No. 199/2008 concerning the establishment of a community framework for the collection, management and use of data in the fisheries sector and support for scientific advice regarding the Common Fisheries Policy

Cressie, N. (1993). Statistics for spatial data: Wiley series in probability and statistics. *Wiley-Interscience, New York*, *15*, 105–209.

Cressie, N., & Read, T. R. (1989). Spatial data analysis of regional counts. *Biometrical Journal*, *31*(6), 699–719.

Csirke, J. (1989). Changes in the catchability coefficient in the Peruvian anchoveta (Engraulis ringens) fishery. *The Peruvian Upwelling Ecosystem: Dynamics and Interactions*, *18*, 207–219.

Fréon, P., & Misund, O. A. (1999). *Dynamics of pelagic fish distribution and behaviour: effects on fisheries and stock assessment*. Oxford: Fishing News Books.

Gaertner, D., & Dreyfus-Leon, M. (2004). Analysis of non-linear relationships between catch per unit effort and abundance in a tuna purse-seine fishery simulated with artificial neural networks. *ICES Journal of Marine Science: Journal Du Conseil*, *61*(5), 812–820.

García, A., & Palomera, I. (1996). Anchovy early life history and its relation to its surrounding environment in the Western Mediterranean basin. Retrieved from http://digital.csic.es/handle/10261/28337

Gerritsen, H. D., Minto, C., & Lordan, C. (2013). How much of the seabed is impacted by mobile fishing gear? Absolute estimates from Vessel Monitoring System (VMS) point data. *ICES Journal of Marine Science: Journal Du Conseil*, *70*(3), 523–531. https://doi.org/10.1093/icesjms/fst017

GFCM 2015. Report of the Working Group on Stock Assessment of Small Pelagic species (WGSASP). Scientific Advisory Committee on Fisheries. General Fisheries Commission for the Mediterranean, FAO, Rome. 82 pp.

Giannoulaki, M., Machias, A., Koutsikopoulos, C., Haralabous, J., Somarakis, S., & Tsimenides, N. (2003). Effect of coastal topography on the spatial structure of the populations of small pelagic fish. *Marine Ecology Progress Series*, *265*, 243–253.

Giannoulaki, M., Machias, A., Koutsikopoulos, C., & Somarakis, S. (2006). The effect of coastal topography on the spatial structure of anchovy and sardine. *ICES Journal of Marine Science*, *63*(4), 650–662. https://doi.org/10.1016/j.icesjms.2005.10.017

Hieu, N. T., Brochier, T., Tri, N.-H., Auger, P., & Brehmer, P. (2014). Effect of Small Versus Large Clusters of Fish School on the Yield of a Purse-Seine Small Pelagic Fishery Including a Marine Protected Area. *Acta Biotheoretica*, *62*(3), 339–353. https://doi.org/10.1007/s10441-014-9220-1

Hilborn, R., Walters, C. J., 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Reviews in Fish Biology and Fisheries, 2: 177–178.

Isaaks, E. H., & Srivastava, R. M. (1989). "An introduction to applied geostatistics. 1989." New York, USA: Oxford University Press. Jones DR, A taxonomy of global optimization methods based on response surfaces. Journal of Global Optimization 23 (2001): 345-383.

Lambert, G. I., Jennings, S., Hiddink, J. G., Hintzen, N. T., Hinz, H., Kaiser, M. J., & Murray, L. G. (2012). Implications of using alternative methods of vessel monitoring system (VMS) data analysis to describe fishing activities and impacts. *ICES Journal of Marine Science: Journal Du Conseil*, *69*(4), 682–693. https://doi.org/10.1093/icesjms/fss018

Lee, J., South, A. B., & Jennings, S. (2010). Developing reliable, repeatable, and accessible methods to provide high-resolution estimates of fishing-effort distributions from vessel monitoring system (VMS) data. *ICES Journal of Marine Science: Journal Du Conseil*, *67*(6), 1260–1271. https://doi.org/10.1093/icesjms/fsq010

Lleonart, J., & Maynou, F. (2003). Fish stock assessments in the Mediterranean: state of the art. *Scientia Marina*, *67*(S1), 37–49.

Mackinson, S. (1999). Variation in structure and distribution of pre-spawning Pacific herring shoals in two regions of British Columbia. *Journal of Fish Biology*, *55*(5), 972–989.

Martín, P., Sabatés, A., Lloret, J., & Martin-Vide, J. (2012). Climate modulation of fish populations: the role of the Western Mediterranean Oscillation (WeMO) in sardine (Sardina pilchardus) and anchovy (Engraulis encrasicolus) production in the north-western Mediterranean. *Climatic Change*, *110*(3–4), 925–939. https://doi.org/10.1007/s10584-011-0091-z

Matheron, G. (1963). Principles of geostatistics. *Economic Geology*, *58*(8), 1246–1266.

Matheron, G. (1981). La sélectivité des distributions. *Note N-686, Centre de Géostatistique, ENSMP, Fontainebleau*. Retrieved from http://cg.ensmp.fr/bibliotheque/public/MATHERON_Rapport_00223.pdf

Murawski, S., Wigley, S., Fogarty, M., Rago, P., & Mountain, D. (2005). Effort distribution and catch patterns adjacent to temperate MPAs. *ICES Journal of Marine Science*. https://doi.org/10.1016/j.icesjms.2005.04.005

Palomera, I. (1992). Spawning of anchovy Engra ulis encrasicol us in the Northwestern Mediterranean relative to. *Mar. Ecol. Prog. Ser*, *79*, 215–223.

Palomera, I., Olivar, M. P., Salat, J., Sabatés, A., Coll, M., Garcia, A., & Morales-Nin, B. (2007). Small pelagic fish in the NW Mediterranean Sea: an ecological review. *Progress in Oceanography*, *74*(2), 377–396.

Parrish, J. K. (1999). Using behavior and ecology to exploit schooling fishes. *Environmental Biology of Fishes*, *55*(1–2), 157–181.

Pertierra, J. P., & Lleonart, J. (1996). NW Mediterranean anchovy fisheries. *Scientia Marina*, *60*(2), 257–267.

Petitgas, P. (1997). Sole egg distributions in space and time characterised by a geostatistical model and its estimation variance. *ICES Journal of Marine Science: Journal Du Conseil*, *54*(2), 213–225.

Petitgas, P. (1998). Biomass-dependent dynamics of fish spatial distributions characterized by geostatistical aggregation curves. *ICES Journal of Marine Science: Journal Du Conseil*, *55*(3), 443–453.

Petitgas, P. (2001). On the relation between schools, clusters of schools, and abundance in pelagic fish stocks. *ICES Journal of Marine Science*, *58*(6), 1150–1160. https://doi.org/10.1006/jmsc.2001.1130

Petitgas, P., & Levenez, J. J. (1996). Spatial organization of pelagic fish: echogram structure, spatio-temporal condition, and biomass in Senegalese waters. *ICES Journal of Marine Science: Journal Du Conseil*, *53*(2), 147–153.

QGIS, D. (2015). *QGIS Geographic Information System. Open Source Geospatial Foundation Project*.

Russo, T., Parisi, A., & Cataudella, S. (2013). Spatial indicators of fishing pressure: Preliminary analyses and possible developments. *Ecological Indicators*, *26*, 141–153. https://doi.org/10.1016/j.ecolind.2012.11.002

SCSA 2015. Report of the 16th session of the Subcommittee on Stock Assessment (SCSA) of the General Fisheries Commission for the Mediterranean (GFCM). 4-6 February 2015, Rome. 47 pp.

Saraux, C., Fromentin, J.-M., Bigot, J.-L., Bourdeix, J.-H., Morfin, M., Roos, D., … Bez, N. (2014). Spatial Structure and Distribution of Small Pelagic Fish in the Northwestern Mediterranean Sea. *PLOS ONE*, *9*(11), e111211. https://doi.org/10.1371/journal.pone.0111211

Team, R. C. (2016). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. 2015, URL h ttp. *Www. R-Project. Org*.

Tsitsika, E. V., & Maravelias, C. D. (2006). Factors affecting purse seine catches: an observer-based analysis. *Mediterranean Marine Science*, *7*(1), 27–40.

Tsitsika, E. V., & Maravelias, C. D. (2008). Fishing strategy choices of purse seines in the Mediterranean: implications for management. *Fisheries Science*, *74*(1), 19–27. https://doi.org/10.1111/j.1444-2906.2007.01492.x

Tukey, J. W. (1977). Exploratory data analysis. Retrieved from http://xa.yimg.com/kq/groups/16412409/1159714453/name/exploratorydataanalysis.pdf

Woillez, M., Rivoirard, J., & Petitgas, P. (2009). Notes on survey-based spatial indicators for monitoring fish populations. *Aquatic Living Resources*, *22*(2), 155–164. https://doi.org/10.1051/alr/2009017

Supplementary Material

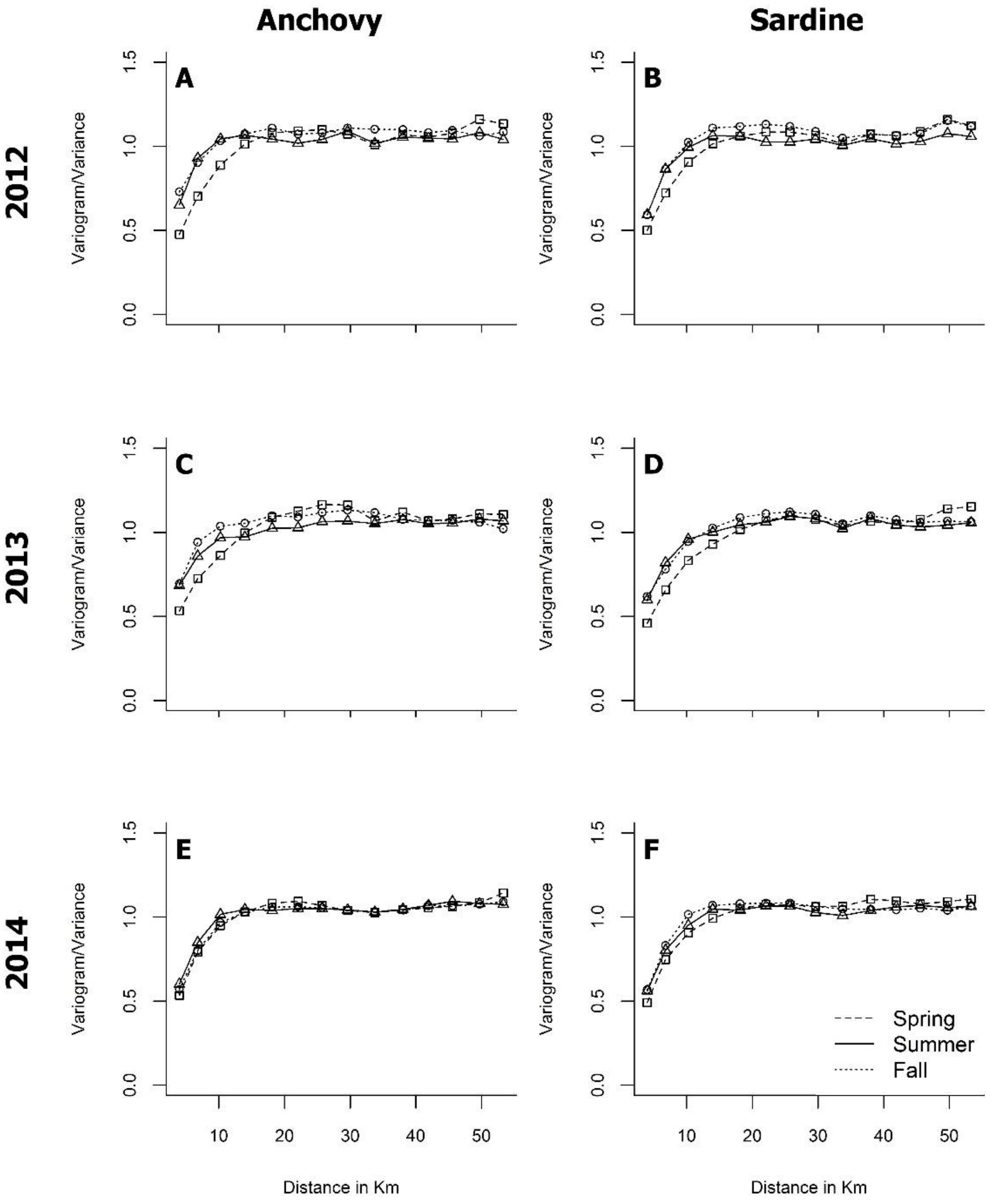

Figure A1. Seasonal omnidirectional variograms of the median polish residuals of the fishing effort directed towards anchovy and sardines.

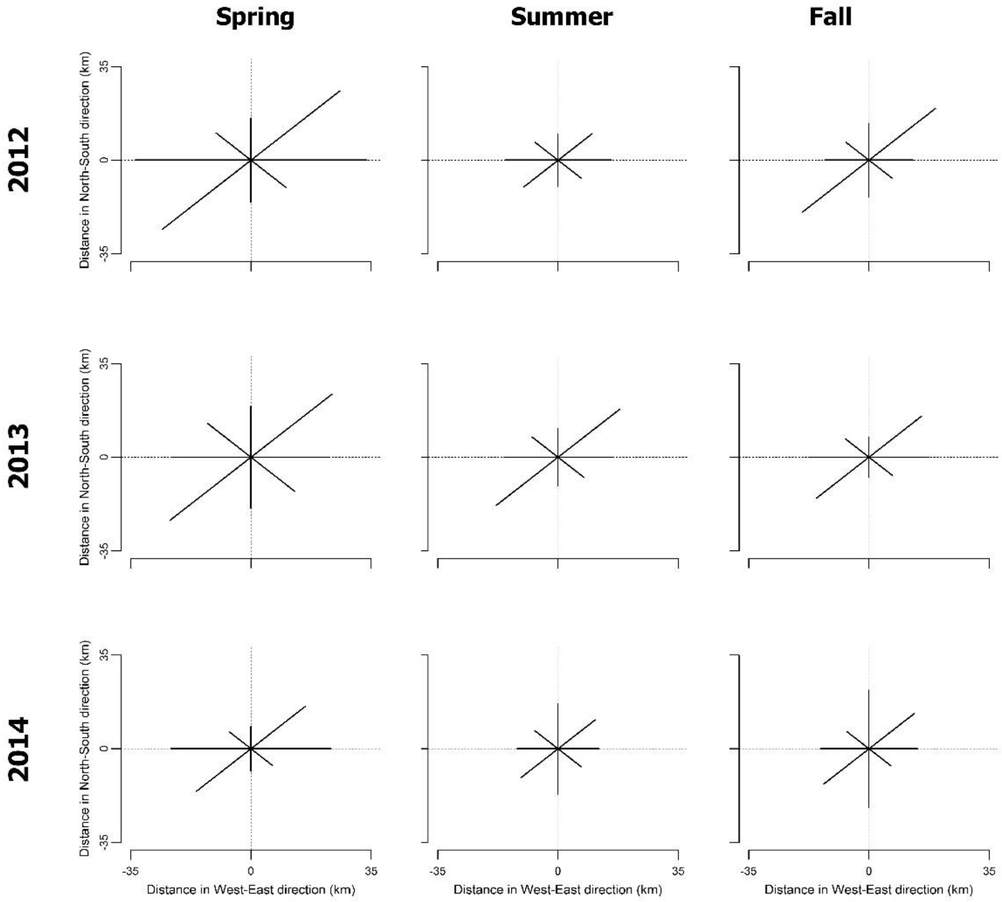

Figure A2. Correlation distances (ranges) estimated by fitting spherical models on omnidirectional variograms of the median polish residuals of the fishing effort directed towards anchovy calculated at 0°, 45°, 90° and 135° directions separately.

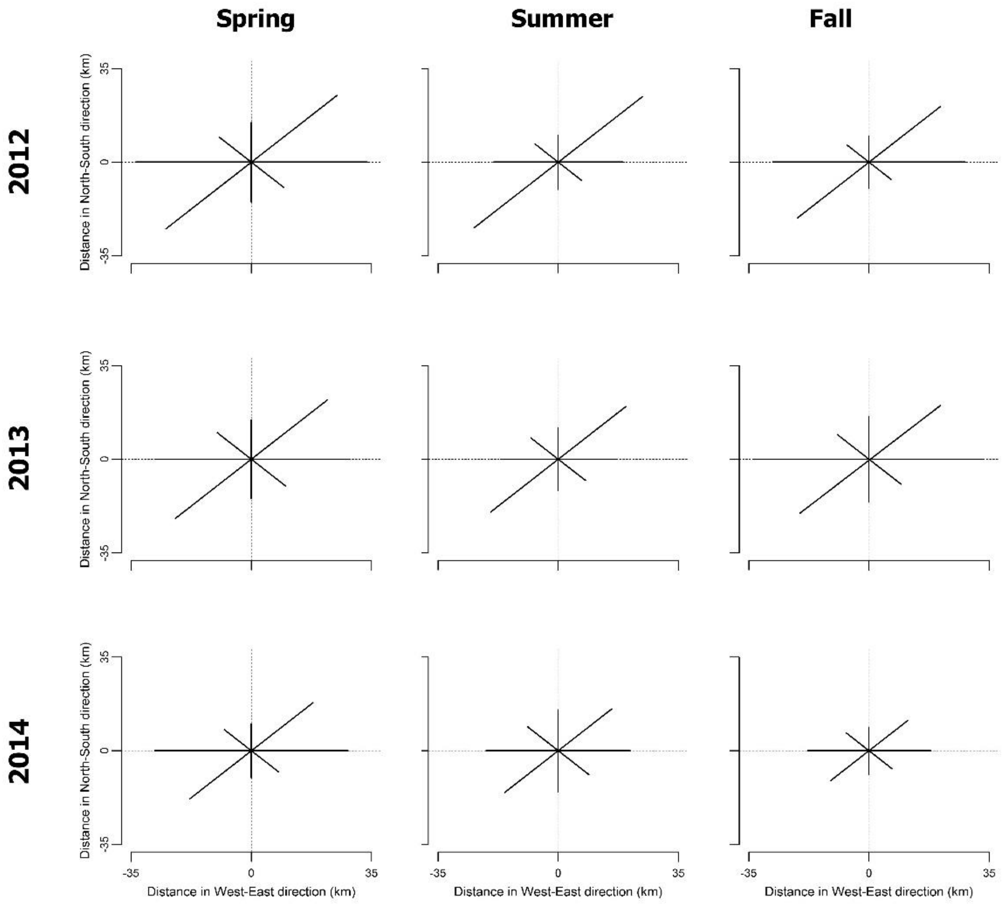

Figure A3. Correlation distances (ranges) estimated by fitting spherical models on omnidirectional variograms of the median polish residuals of the fishing effort directed towards sardine calculated at 0°, 45°, 90° and 135° directions separately.

Chapter 2

Occurrence of adult anchovy in Catalonia (NW Mediterranean) in relation to sea surface conditions

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Abstract

Generalized additive and generalized additive threshold models were used to study the relationship between landings per unit effort (LPUE) of anchovy, *Engraulis encrasicolus*, during the spawning season (May-October) from 2000-2010, and environmental variables, using sea surface data derived from satellite imagery (temperature, salinity, chlorophyll a, and meridional and zonal velocity current) in three fishing zones defined along the Catalan coast. The configuration of the environment where spawning aggregations occur affects early life stages and therefore the future demographic structure of the population. It is therefore fundamental to define the environmental conditions and their variations during the spawning season. Our results show that the low salinity in the Northern and Central sector and the velocity of the zonal and meridional currents in the Central and Southern sector, respectively, implicated in retention processes, increase LPUE during the spawning period. Temperature was related to LPUE in the Southern and in the Northern sectors, in both of which a non-linear positive effect with a local maximum peak at lower temperature values was present. However, in the Northern sector, this relationship held only for the period before 2007. After 2007 the decrease in preferred temperature suggests a reduction of the thermal window in which adult spawner aggregations occur. In agreement with previous studies on this species, the relationships were non-linear, stressing the importance of the match in timing and location between favourable conditions and spawning period as a crucial event for understanding the dynamics of small pelagics populations.

Keywords: *Engraulis encrasicolus*; NW Mediterranean; environmental conditions; anchovy landings; generalized additive models.

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Introduction

Small pelagic fishes are key components of marine ecosystems and support fisheries of global importance (Alheit et al. 2012). These organisms are characterized by a short life span (2-3 years) and they feed on phytoplankton and small zooplankton (Tudela and Palomera 1995) in a short plankton-based food web. Populations of these fishes experience large interannual and long-term variations in abundance (Lluch-Belda et al. 1989), and several hypotheses have been formulated in order to explain these fluctuations (e.g. the "match-mismatch" hypothesis (Cushing 1990); the "optimal environmental window" (Cury and Roy 1989); and the "ocean triad" (Bakun 1996, Agostini and Bakun 2002)). These hypotheses highlight the importance of suitable environmental conditions in time and location during early life stages (eggs and larvae) for recruitment success and failure. Since early life stages are characterized by high sensitivity to environmental changes (Pörtner and Peck 2010), small variations in growth and survival rates of these stages could generate large differences in the annual recruitment (Houde 1997) and therefore in the future structure of the adult population. It is therefore fundamental to define the environmental conditions and their variations during the spawning period of these species.

In the northwest Mediterranean, the anchovy, *Engraulis encrasicolus* (Linnaeus, 1758), is the most important small pelagic fish in terms of biomass along with the pilchard, *Sardina pilchardus* (Walbaum, 1792) (Lleonart and Maynou 2003). Anchovy age-at-first-maturity is 1 year in the area (Lm>9 cm TL) (Pertierra 1992) and 88% of individuals are mature at age 0 (Cardinale et al. 2010)). Anchovy spawns in late spring and summer in coastal waters of continental origin characterized by low salinity (Lloret et al. 2004, Palomera et al. 2007, Sabatés et al. 2007a, 2013). The time of spawning is linked to temperature and, as for species that reproduce in spring/summer, spawning starts earlier in the Southern than in the Northern sector because the surface temperature increases earlier in the south and later extends northwards. For this same reason, the spawning period is longer in the south, where temperatures decrease more slowly (Martín and Sabatés 1991, Martín et al. 2008).

Two main spawning grounds characterize the NW Mediterranean: one is located in front of the Ebro delta and the other one in the Gulf of Lions up to the Rhône delta. Both areas are highly productive and characterized by relatively low salinity due to river runoff if compared with adjacent areas (Palomera et al. 2007). Early stages of development of the anchovy are favoured by these highly productive, low-salinity waters and also by mesoscale structures such as eddies (e.g. Palomera et al. 2007, Sabatés et al. 2013), which appear along the Northern Current coming from the Gulf of Lions (Millot 1991, Rojas et al. 1995). Both conditions cause a greater concentration of nutrients, phytoplankton and zooplankton fluctuations of the anchovy have been associated with local environmental conditions and climate variability (e.g. Lloret et al.

2001, 2004, Martín et al. 2008, 2012). Thus, the positive trends in temperature and salinity data observed during the second half of the twentieth century in the western Mediterranean Sea (Calvo et al. 2011, Vargas-Yáñez et al. 2009, 2010) could have affected the population dynamics of this small pelagic fish.

In the Catalan Sea, the anchovy fishery is concentrated mostly between Cape Creus and the Ebro river delta (Agostini and Bakun 2002); it is carried out for 10 months per year (close season: December-January, generally) and 5 days per week (Pertierra and Lleonart 1996). Discards of this species are negligible (Lloret et al. 2004). Anchovy is caught mainly in spring/summer, when a significant fraction of the population is mature (Cardinale et al. 2010) and has incorporated the recruits from the previous year's spawning, so landings in these seasons can be considered as a proxy of the abundance of adult spawners (e.g. Martín et al. 2008).

The catches in the geographical subarea 06 (GSA06) in the period 1990-2010 were highly variable, suffering a continuous decrease after 1994, with a minimum of 1900 t in 2007 and an average of 11700 t, with two recoveries in 2002 and 2009 (Cardinale et al. 2010). Also, Farrugio (2013) reported decreasing trends in anchovy biomass in the Gulf of Lions between 2001 and 2005 and along the Catalan coasts, where this trend continued until 2010. Cardinale et al. (2010) described the status of this species as overexploited in GSA06, but the decrease and fluctuations in abundance cannot be attributed only to the fishing activities but to a combined effect of overexploitation and unfavourable environmental conditions (e.g. Martín et al. 2008, 2012, Lloret et al. 2000, 2001).

Coupling catches and oceanographic information is one of the main objectives in fisheries science and management. Tools such as generalized additive models (GAMs, Hastie and Tibshirani 1990, Wood 2006) allow these relationships to be described thanks to their flexibility, which allows the non-linear effect of a variable to be assessed independently from the value of another covariate (i.e. additivity). Because of this, they have been largely used in the Mediterranean Sea (e.g. Martín et al. 2008, Bellido et al. 2008, Giannoulaki et al. 2013). A variant of the GAM is the threshold GAM (TGAMs, Ciannelli et al. 2004). Using this modelling approach, composed of two additive formulations, it is possible to test whether a covariate effect changes according to two levels, which are defined by a threshold, of another variable (i.e. non-additive interaction). Therefore, the comparison of the results from the GAM and the TGAM allows us to assess, apart from non-linear relationships, whether the effects of the environmental variables are additive or not.

Through the use of both GAM and TGAM, this study aims to investigate the relation between the anchovy fishery landings and the local environmental conditions in the NW Mediterranean Sea during the spawning season, considering landings per unit of effort (LPUE) as a proxy of abundance of the adult population (spawners), in order to determine potential exogenous drivers of the population spatio-temporal dynamics of this small pelagic fish.

Materials and Methods

Study Area

The study area is located in the Catalan Sea, NW Mediterranean (Fig. 1). The area is characterized by a permanent shelf-slope density front, separating open-sea high-salinity waters from low-salinity continental shelf waters, and a geostrophic Northern Current which flows southwestwards roughly parallel to the coast with an overall transport of around 1 Sv (Castellón et al. 1990). The NW Mediterranean coast receives significant freshwater runoff from two major rivers, the Rhône and the Ebro. The Rhône discharges at the east of the Gulf of Lions and enhances the shelf-slope front by lowering the salinity of shelf waters. The Ebro, with lower runoff, also decreases the salinity of the waters on the relatively wide shelf near its mouth at the southern limit of the area. The water column structure shows a marked seasonal cycle, well mixed in winter and strongly stratified in summer, during the anchovy spawning season, when primary production is limited to a deep chlorophyll maximum (DCM), a thin layer at the deepest levels of the photic zone, ca. 60 m depth (Estrada et al. 1985). Another contribution to local productivity results from freshwater river runoff, which can enrich coastal waters near major river mouths. Summer productivity conditions are highly dependent on interannual variability in temperature and salinity, which in turn depends on the heat balance of air-sea exchanges in the region and fresh water runoff, which are variable from one year to the next. The environmental characteristics and the daily displacement of the fishery operation were used to define three sectors in the study area, Northern, Central and Southern,

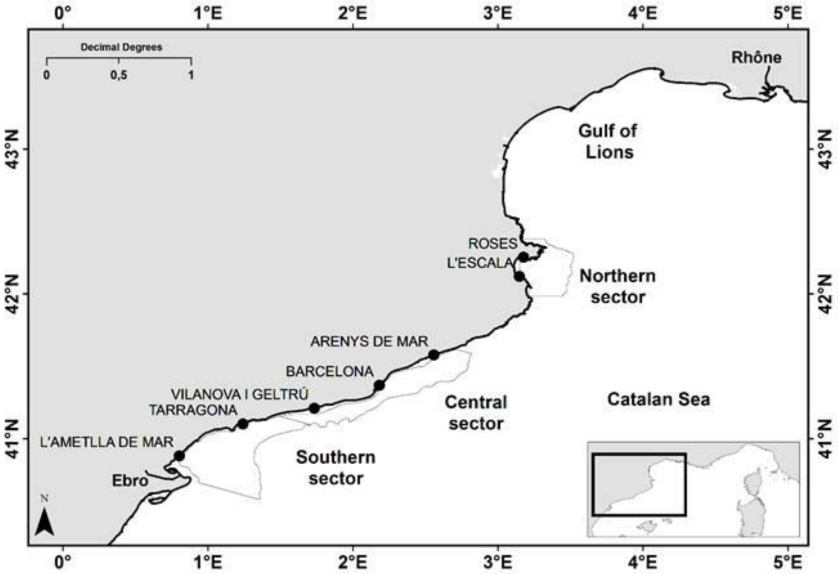

Figure 1. The study area divided into three sectors (Southern, Central and Northern) limited by the 35 m and 200 m isobaths and their major fishing ports.

according to Martín et al. (2008) (Fig. 1). These sectors were limited by the 35 m and 200 m isobaths, which represent the longitudinal expansion where the anchovy fishery is carried out.

Data

Monthly landings (kg) from the main ports with a purse seine fleet (a total of 90 vessels) (Fig. 1) were used to analyse the variations in abundance of *E. encrasicolus* during the period 2000-2010. Landings data for each sector (Northern, Central and Southern sector) were obtained from the daily fish sale database of the Fisheries Directorate of the Autonomous Government of Catalonia. LPUE were computed by dividing the total monthly landings in each sector by the total number of vessels that carried out fishing operations (LPUE as kg/(vessel×day)). The part of the data set analysed represents the whole anchovy spawning period, considered to be from May to October (Palomera 1992, García and Palomera 1996). This period also coincides with the period when most anchovy is caught (62% - 83% of the total annual catch in weight). The average monthly landings and effort are summarized in Table 1. The technical characteristics of the purse seine fleet operating in the area are 18.7 m length-overall (min. 12, max. 25 m), tonnage 37.7 GT (min. 20, max 78 GT) and engine power 209 kW (min. 155, max. 447 kW). Figure 2 shows the age composition of the landings in Geographic SubArea 6 (GSA06, the northern half of which corresponds to the study area), based on the 2010 stock assessment carried out by the Mediterranean subgroup of the Science, Technical, Economic Committee for Fisheries of the European Commission (Cardinale et al. 2010). Depending on the year, between 70% and 90% of the landings in number correspond to year 1 or older individuals, i.e. spawning adults.

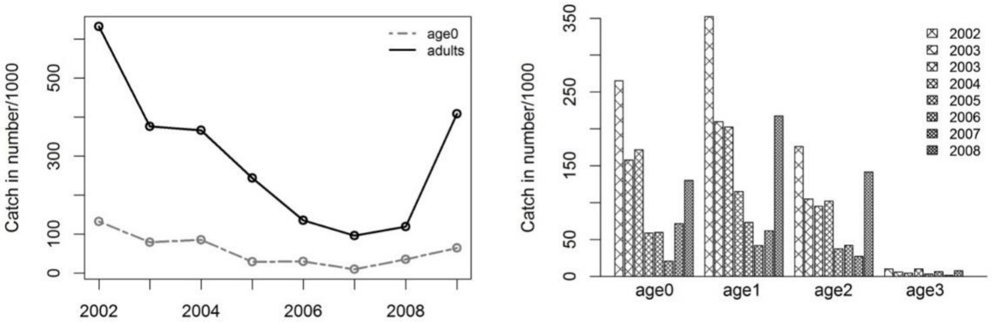

Figure 2. Left: Spawning individuals in age class 0 and age classes 1 and higher, assuming a maturity ogive 0.5, 0.89, 1, 1 for age classes 0 to 3 in GSA06 (Cardinale et al. 2010). Right: age class composition of landings (number of individuals) for the period 2002-2009 in GSA06 (Cardinale et al. 2010).

Table 1. Average anchovy landings (1) and fishing trips (monthly vessel*day) (2) in the three sectors for each year, during the May-October spawning period. All values are reported as mean ± standard error (SE).

		2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
North	1	255.3±78.1	249.1±73.9	265.9±72.8	232.8±61.3	121.1±52.1	104.1±31.8	106.5±30.1	81.5±28.9	100.4±21.1	87.6±26.7	91.1±27.4
	2	184.6±52.1	148±34.8	103.5±23.7	155.3±44.7	94.3±29.8	76.5±22.7	83.1±27.1	66.5±16.7	91.3±25.4	82.6±23.2	74.6±20.9
Centre	1	69.8±25.9	106.1±35.1	274.6±104.8	86.6±38.4	216.7±98.4	155.9±63.4	56.6±17.7	26.2±13.7	25.4±11.9	332.6±87.6	203.6±80.1
	2	77.8±27.4	125.3±35.3	202.3±58.1	113.8±47.1	194.3±68.6	171.2±64.8	107.6±32.3	67±27.3	38.5±5.4	231.2±51.5	199.1±78.1
South	1	87.6±24.1	97.7±34.1	147.9±27.5	93.2±23.9	93.2±39	88.8±27.3	54.8±17	27.2±13.4	85.5±26.8	220.1±17.3	173.1±36.1
	2	146.8±26.1	123.6±27.6	192.6±21.7	177.5±39.3	150.5±32.1	107.6±29.2	114.5±23.2	80.5±29.8	134±32.7	176.1±17.6	175.6±21.1

The explanatory variables used to model the anchovy landings are (Fig. 3): 1) the sea surface temperature (SST in °C), because it has been shown that it determines the species distribution, enhances the growth of larvae and regulates the onset and the duration of the spawning period (García and Palomera 1996, Palomera et al. 2007); 2) the sea surface salinity (SSS in psu), because previous studies have associated the spawning period and the early life stages of anchovy with low-salinity water (e.g. Lloret et al. 2004, Martín et al. 2008); 3) the chlorophyll a concentration (Chl*a* in mg m^{-3}) as an indicator of the primary production; 4) the meridional current (MC in m s^{-1}, north to south); and 5) the zonal current (ZC in m s^{-1}, west to east). Both the MC and the ZC are involved in larva, egg and prey retention and transport (Sabatés et al. 2007a). The above environmental variables were derived from satellite data with a monthly time resolution and a space resolution of 1/16°×1/16° developed within the EU-funded project MyOcean (http://marine.copernicus.eu/). All monthly satellite images were merged to obtain aggregate amounts by sector, using ArcGIS software (ESRI 1994).

Statistical analysis

GAMs (Hastie and Tibshirani 1990, Wood 2006) were used to assess the effect of environmental conditions on the monthly LPUE of the spawning period (May-Oct), log-transformed, in the three sectors (Northern, Central and Southern) from 2000 to 2010. One model for each zone was constructed. Using the backward selection, the best model for each sector was selected based on the minimization of generalized cross-validation criterion (GCV) (Craven and Wahba 1979), which is an estimate of the model's predictive performance and aims at optimizing the trade-off between the model's parsimony (the number of parameters) and goodness of fit.

We used the Gaussian probability distribution as an error distribution and the identity as a link function (Wood 2006), checking the residuals of the model visually for normality and homogeneity, to assess the appropriateness of the choice of probability distribution function. The univariate penalized cubic spline was used as a smoother, and the maximum degree of freedom measured as number of knots (k) was limited to k=5 to avoid over-fitting. For each of the best models obtained we also explored the interaction effect between the time and the other covariates using threshold GAM (TGAM) (Ciannelli et al. 2004).

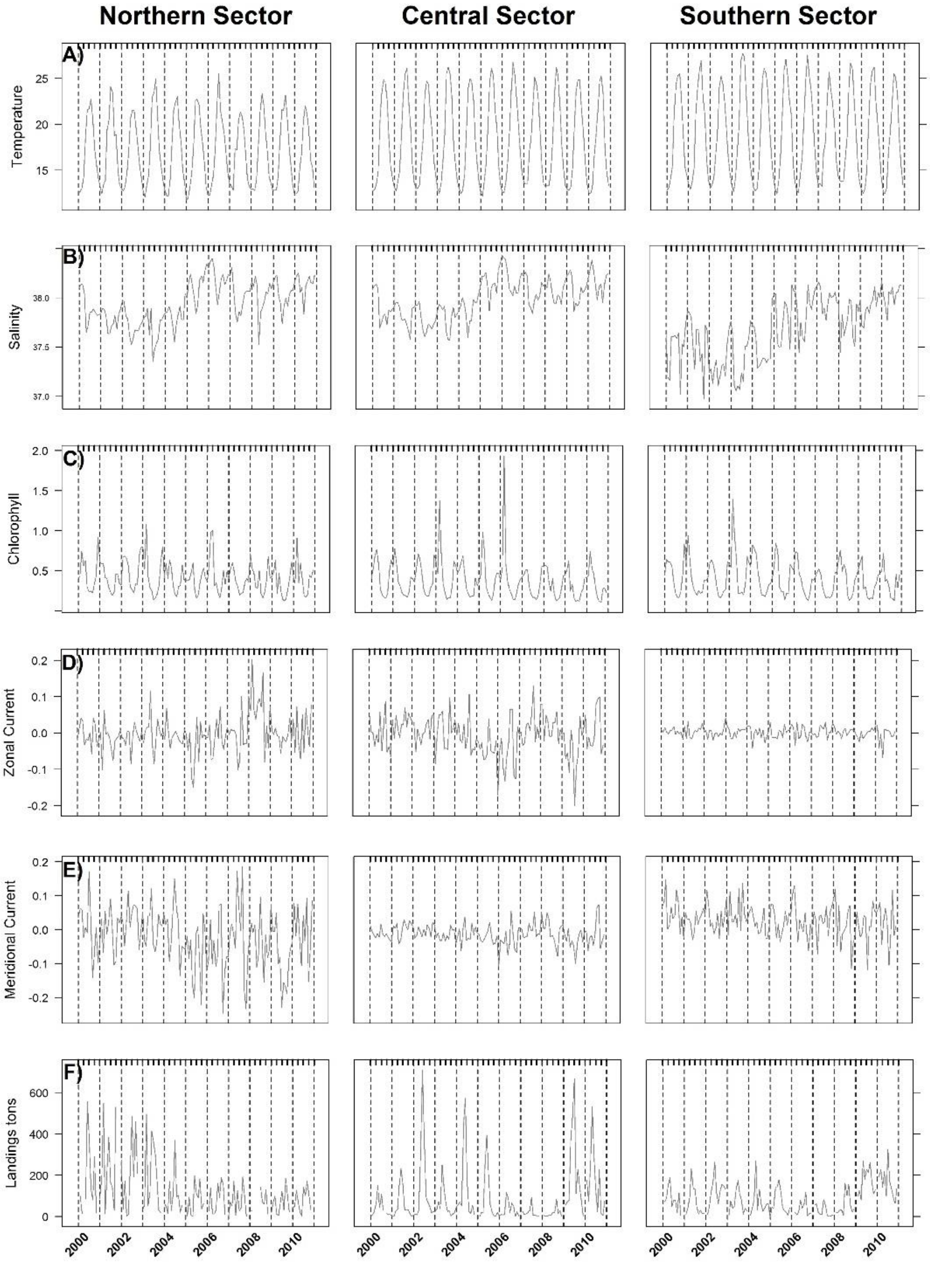

Figure 3. Series of monthly values (mean) for each sector. A, the sea surface temperature (SST); B, sea surface salinity (SSS); C, chlorophyll; D, meridional current; E, zonal current; F, anchovy landings during the years 2000-2010. Top ticks indicate the seasons of the year. Note missing data in winter due to the annual close season to protect anchovy recruitment (usually December and January).

In practice, the TGAM algorithm divides the time (defined as the month expressed in number, in the year), representing the 'threshold variable', into two levels (i.e. a factor variable), before and after the threshold value (Tv). By introducing in the model the interaction between time and another covariate, the covariate effect can change during the observed period. Hence, through this model formulation, the shape of the smoothing function of each covariate was allowed to change over two contrasting periods defined by Tv. The identification of the threshold value was obtained by defining a search grid over an interval given by the 15th to 85th percentiles of the variable time, and the value within this range that produced the model that minimized the GCV score was selected (for details please see Ciannelli et al. 2004).

We used the genuine cross-validation (gCV) to directly compare the selected TGAM and the corresponding GAM models. We calculated gCV scores by excluding randomly about 15% of the entire dataset and using the remaining data to fit a candidate model, and the mean-squared predictive error was estimated (Ciannelli et al. 2004). The routine was repeated 500 times, with the final gCV being the average mean-squared predictive error of all runs for each candidate model (Ciannelli et al. 2004). All the analyses were performed with R v. 2.0.1 statistical package (http:// www.r-project.org/).

Results

Environmental conditions

The environmental data show that the SST has a clear seasonal pattern (Fig. 3A): the maxima during summer show high variability along the latitudinal gradient, decreasing from south to north. For all sectors, the years 2003 and 2006 are the ones with the highest temperatures, while from the year 2007 SST showed a decrease, especially during spring and summer and more evident in the Northern sector. During cold seasons (winter and autumn) SST showed lower variability between the three sectors, with very similar minima. SSS also showed clear latitudinal differences (Fig. 3B), with lower values in the Southern sector. Although salinity did not show a clear seasonal pattern, we observed lower peaks in late summer and early autumn, more evident in the Southern sector, due to the direct influence of river runoff in this period of the year. Salinity increase was evident from 2004 to 2007 in all areas, followed by a gradual stabilization (Fig. 3B), and 2006 showed higher salinity than the other periods (Fig. 3B). Chl a showed the highest peaks in winter and the second-highest in autumn (Fig. 3C). The Central and Southern sectors show the highest production of Chl *a*, with the highest value in the Central sector in winter 2006.

Along the Catalan coast, the zonal current showed a velocity of 5 to 15 cm s^{-1} (Fig. 3D). The Southern sector was characterized mainly by an inshore-offshore flow (eastward flow, positive values), except in 2009 and 2010, which were characterized mainly by a westward flow (negative values, Fig. 3F). During the first half of the decade, in the Central sector currents were slow in both directions, persisting in the range of –5 and 5 cm s–1 until the beginning of 2005 (Fig. 3D). Afterwards, alternating high eastward and westward velocities characterized this sector, with the strongest westward current during the spring of 2009. The Northern sector followed the same pattern as the Central one, but in this case the highest velocity was the eastward one, reaching the uppermost peak in spring 2008 (Fig. 3D). Intense meridional current with high northward and southward current velocities characterized the Northern sector, while in the other two sectors velocities in both directions did not exceed 10 cm s^{-1} (Fig. 3E).

Anchovy LPUE

The LPUE by sector is shown in Figure 3F. In 2000-2008 LPUE was more than twice as high in the Northern sector than in the Central and Southern sectors, while after 2008 it decreased to values closer to the Southern and Central sectors (Fig. 3F). Considering the overall LPUE during spawning periods in each year from 2000 to 2010, all sectors showed decreasing trends starting in 2002, but during 2009-2010 both the Central and Southern sectors showed an increase (Fig. 4). The reduction in abundance was more marked in the Northern sector, with no evidence of recovery. In the Central and Southern sectors the abundances were lower than in the Northern sector and showed a similar decreasing trend until 2008, after which they increased (Fig. 4).

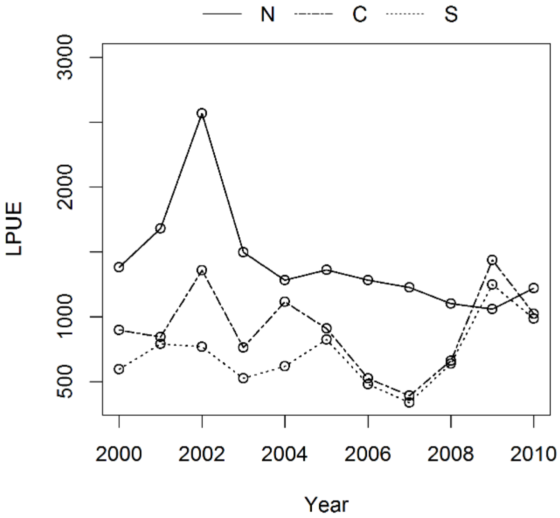

Figure 4. Anchovy LPUE during the spawning season (from May to October) for each sector during the years 2000-2010. N, Northern sector; C, Central sector; S, Southern sector

Environmental influence on spawning season

The threshold model (TGAM) was selected for the Northern sector, while standard GAM models were selected for the other two sectors based on the genuine cross-validation criteria.

The following threshold GAM was the best model fit in the Northern sector:

$$\log(\mathrm{LPUE}) = \begin{cases} \alpha + g_1(\mathrm{SSS}) + f_1(\mathrm{CHL}) + s_1(\mathrm{SST}) + \varepsilon & \text{if time} \leq \textit{June } 2007 \\ \alpha + g_1(\mathrm{SSS}) + f_1(\mathrm{CHL}) + s_2(\mathrm{SST}) + \varepsilon & \text{if time} > \textit{June } 2007 \end{cases}$$

This TGAM formulation, formed by two additive model formulations where α is the intercept while g_1, f_1, s_1, s_2 are the non-parametric smoothing functions specifying the effect of the environmental covariates, showed better results than the corresponding GAM model, with a reduction of the gCV from 0.43 to 0.30 after including time as threshold variable. The TGAM model explained 61.4% of the deviance (Table 2). The effect of the SST changed during the period considered (the smoothing function switched from s1 to s2) and the threshold value estimated for time was at the beginning of the spawning season in 2007 (June), as depicted on the GCV profile in Figure 5.

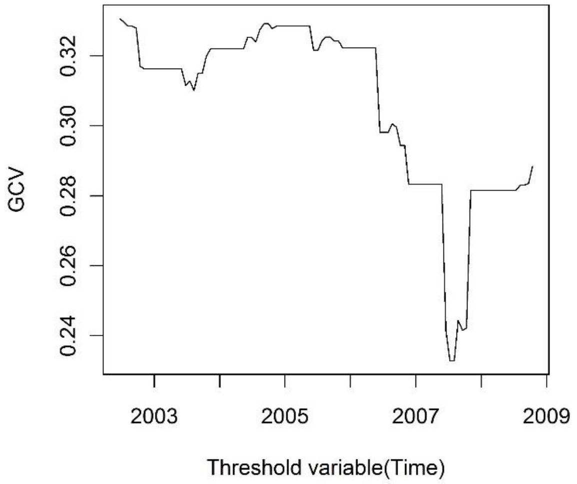

Figure 5. GCV profile for the threshold estimation for the variable time in the Northern sector.

All partial effects are shown in Figure 6A, B, C, D. Results showed a positive effect of the SSS for values lower than ca. 37.7, followed by a small negative effect at values between ca. 37.7 and 38.1 (Fig. 6A). The effect of Chl *a* was linear, and became negative for values higher than 0.3 mg m^{-3} (Fig. 6B). The effect of temperature as described above changed during the period considered. From May 2000 to May 2007 it was positive between ca. 17.5 and ca. 21.3°C, with a peak at ca. 19°C corresponding to spring conditions, and clearly negative at temperatures higher than ca. 21.3°C (Fig. 6C). In the period between June 2007 and October 2010, a linear positive effect was observed for temperatures lower than 19°C, whereas above this value a small negative effect was observed (Fig. 6D).

The following model was the final GAM selected for the Central sector (37.2% of deviance explained) (Table 2):

$$\log(\mathrm{LPUE}) = \alpha + g_1(\mathrm{SSS}) + f_1(\mathrm{ZC}) + s_1(\mathrm{CHL}) + \varepsilon$$

where α is the intercept, g_1, f_1, s_1 the smoothing functions and ε the error term. Relatively low SSS values positively affected LPUE within a range starting from ca. 37.6 to ca. 37.83 with a local peak at ca. 37.7 (Fig. 6E). Negative effects were evident for both high east-and westward velocities of the zonal current. Although less evident, low westward velocities at values around –0.05 m s^{-1} affected the LPUE positively, while no evident effects were present at low eastward velocity values (Fig. 6F). Moderate positive effects were found at values below 0.2 mg m^{-3} of Chl *a* concentration, and a negative effect was found at higher values, excluding the presence of a local non-significant, positive peak at a concentration of 0.35 mg m^{-3} (Fig. 6G).

The final GAM for the Southern sector explained 56.1% of the total deviance (Table 2):

$$\log(\text{LPUE}) = \alpha + g_1(\text{MC}) + f_1(\text{CHL}) + s_1(\text{SST}) + \varepsilon$$

with α representing the intercept, g_1, f_1, s_1 the smoothing functions and ε the errors. LPUE was positively related to meridional current velocity at values lower than –0.01 m s^{-1} (i.e. north-to-south flow of 0.01 m s^{-1} or higher) and negatively related to the intensification of the meridional current velocity, particularly at values higher than 0.01 m s^{-1}, while it showed no effects in the range between ca. –0.01 m s^{-1} and ca. 0.01 m s^{-1} (Fig. 6H). The relationship with Chl *a* was similar to that observed in the Central sector, with a local peak for concentration equal to 0.35 mg m^{-3}, and a slightly positive effect below a Chl *a* concentration of 0.2 mg m^{-3} (Fig. 6I). Positive effects of SST were evident between ca. 19°C and 22°C with a peak at ca. 21°C (Fig. 6J), while no evident effects on LPUE were found for higher values of SST.

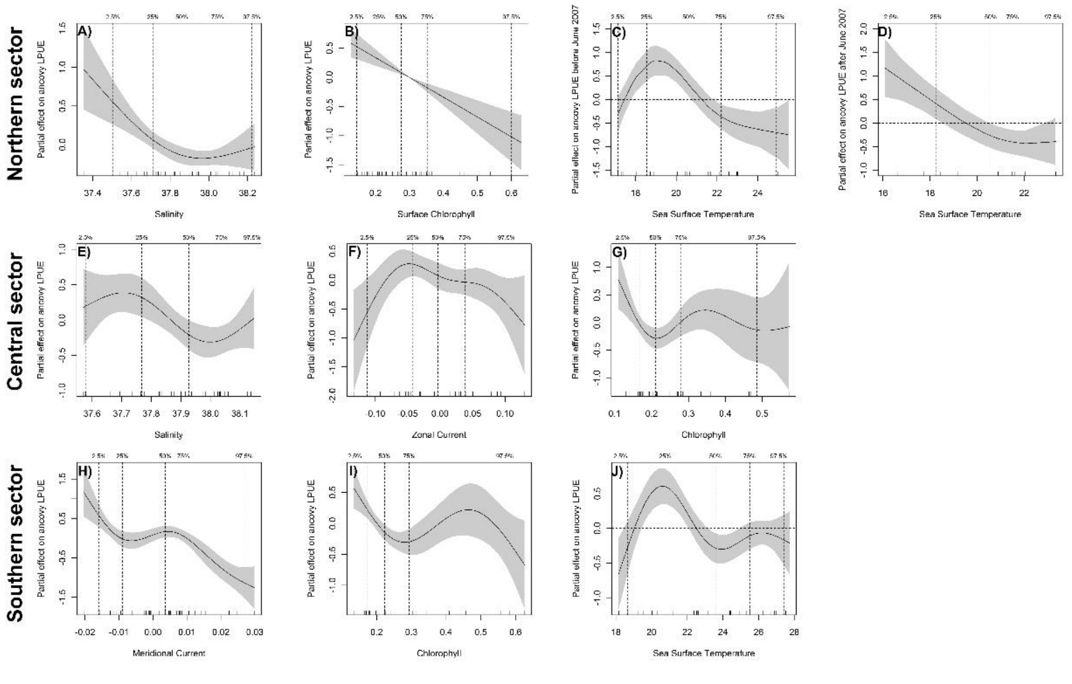

Figure 6. Partial effects of sea surface temperature, sea surface salinity, chlorophyll a concentration, meridional current and zonal current for each sector during spawning periods. The median, 1st and 3rd quartiles and 95% distribution of the explanatory variables are shown along the x-axis as vertical grey lines. The shades areas indicate the 95% confidence interval. A,B,C,D, partial effects on LPUE in the Northern sector, where C and D are the partial effect of the sea surface temperature before and after June 2007, respectively; E,F,G, partial effects on LPUE in the Central sector; H,I,J, partial effects on LPUE in the Southern sector. See models in Table 2.

Table 2. Genuine cross-validation scores (gCV) used to select the models in each sector with the best prediction performance among candidate models and % of the deviance explicated (DVe %). The final models are indicated in bold text with the analysis of deviance of the covariates (SSS, sea surface salinity in psu; SST, sea surface temperature in °C; CHL, Chlorophyll concentration in mg/m^3; ZC, zonal current velocity in m/s; MC, meridional current velocity in m/s).

Sector	Model	Formulation	gCV	DVe %	Edf	Null DV	Res. DV	GCV
North	GAM	$\log(LPUE) = \alpha + g_1(SSS) + f_1(CHL) + s_1(SST) + \varepsilon$	0.43	34.6 %	$\boldsymbol{g_1(SSS) = 3.049}$ $\boldsymbol{f_1(CHL) = 1}$ $\boldsymbol{s_1(SST) = 2.264}$ $\boldsymbol{s_2(SST) = 3.727}$	**0.42**	**0.19**	**0.23**
	TGAM	$\log(LPUE) = \alpha + g_1(SSS) + f_1(CHL) + s_1(SST) + \varepsilon iftime \le r$ $\log(LPUE) = \alpha + g_2(SSS) + f_1(CHL) + s_1(SST) + \varepsilon iftime\varepsilon > r$	0.38	55.2 %				
		$\log(LPUE) = \alpha + g_1(SSS) + f_1(CHL) + s_1(SST) + \varepsilon iftime \le r$ $\log(LPUE) = \alpha + g_1(SSS) + f_2(CHL) + s_1(SST) + \varepsilon iftime\varepsilon > r$	0.94	45.7 %				
		$\boldsymbol{\log(LPUE) = \alpha + g_1(SSS) + f_1(CHL) + s_1(SST) + \varepsilon iftime \le r}$ $\boldsymbol{\log(LPUE) = \alpha + g_1(SSS) + f_1(CHL) + s_2(SST) + \varepsilon iftime > r}$	**0.30**	**61.4%**				
Centre	GAM	$\boldsymbol{\log(LPUE) = \alpha + g_1(SSS) + f_1(ZC) + s_1(CHL) + \varepsilon}$	**0.70**	**37.2%**	$\boldsymbol{g_1(SSS) = 2.761}$ $\boldsymbol{f_1(ZC) = 3.437}$ $\boldsymbol{s_1(CHL) = 3.626}$	**0.53**	**0.39**	**0.54**
	TGAM	$\log(LPUE) = \alpha + g_1(SSS) + f_1(ZC) + s_1(CHL) + \varepsilon iftime \le r$ $\log(LPUE) = \alpha + g_2(SSS) + f_1(ZC) + s_1(CHL) + \varepsilon iftime\varepsilon > r$	0.72	36.2%				
		$\log(LPUE) = \alpha + g_1(SSS) + f_1(ZC) + s_1(CHL) + \varepsilon iftime \le r$ $\log(LPUE) = \alpha + g_1(SSS) + f_2(ZC) + s_1(CHL) + \varepsilon iftime\varepsilon > r$	0.74	44.3%				
		$\log(LPUE) = \alpha + g_1(SSS) + f_1(ZC) + s_1(CHL) + \varepsilon iftime \le r$ $\log(LPUE) = \alpha + g_1(SSS) + f_1(ZC) + s_2(CHL) + \varepsilon iftime\varepsilon > r$	0.90	43.4%				
South	GAM	$\boldsymbol{\log(LPUE) = \alpha + g_1(MC) + f_1(CHL) + s_1(SST) + \varepsilon}$	**0.30**	**56.1 %**	$\boldsymbol{g_1(MC) = 3.542}$ $\boldsymbol{f_1(CHL) = 3.437}$ $\boldsymbol{s_1(SST) = 3.740}$	**0.33**	**0.18**	**0.22**
	TGAM	$\log(LPUE) = \alpha + g_1(MC) + f_1(CHL) + s_1(SST) + \varepsilon iftime \le r$ $\log(LPUE) = \alpha + g_2(MC) + f_1(CHL) + s_1(SST) + \varepsilon iftime\varepsilon > r$	0.33	52.6 %				
		$\log(LPUE) = \alpha + g_1(MC) + f_1(CHL) + s_1(SST) + \varepsilon iftime \le r$ $\log(LPUE) = \alpha + g_1(MC) + f_2(CHL) + s_1(SST) + \varepsilon iftime\varepsilon > r$	0.34	56.3 %				
		$\log(LPUE) = \alpha + g_1(MC) + f_1(CHL) + s_1(SST) + \varepsilon iftime \le r$ $\log(LPUE) = \alpha + g_1(MC) + f_1(CHL) + s_{12}(SST) + \varepsilon iftime\varepsilon > r$	0.32	53.6 %				

Discussion

In this study we investigated the relationships between anchovy LPUE and the local environmental variables on the Catalan coast during the spawning period. The strong influence of environmental factors on small pelagic adult populations is well known, particularly the influence on the location and timing of their reproduction (Lloret et al. 2004, Palomera et al. 2007, Giannoulaki et al. 2013) and on the survival of the early life stages (e.g. Agostini and Bakun 2002, Sabatés et al. 2007b, Maynou et al. 2014). In fact, pelagic eggs and larvae need favourable environmental conditions in order to enhance the probability of success (Bakun 1996). During the period considered, i.e. 2000-2010, anchovy LPUEs showed high fluctuations, with minimum values between 2007 and 2008. The LPUE during the year showed seasonality typical of the species in the Mediterranean Sea, with maxima mainly in spring-summer and minima in late autumn-winter. In this area the anchovy spawning period overlaps with the main fishing season for this species, in spring/summer. During this period catches are composed mainly of individuals of the 1- and 2-year cohort (Pertierra and Lleonart 1996, Cardinale et al. 2010), so peaks in landings can be considered as an index of spawning stock biomass, which in this short-lived species is closely related to recruitment to the fishery from the previous year's spawn (as argued by Lloret et al. 2004, Martín et al. 2008).

The relative lower SSTs (below 22°C) in which high abundance of the anchovy population was found can be indicative of nutrient enrichment processes such as wind mixing or river runoff, which are often associated with favourable conditions for fish. The relationships with temperature found in our results are in accordance with that described by other studies in the same area, using different methodologies (e.g. García and Palomera 1996, Lloret et al. 2004, Palomera 1992, Palomera et al. 2007, Martín et al. 2008). Moreover they also agree with results of Somarakis and Nikolioudakis (2007) and Basilone et al. (2006, 2013) in the Aegean Sea and in the Straits of Sicily, respectively, highlighting the synchrony between the seasonal reproductive cycle and temperature. This synchrony could be a strategy to enhance the probability of success of larval survival, which is favoured by the subsequent stable sea conditions promoting the prey aggregations (Lasker 1981, Basilone et al. 2006). In fact, these temperatures in the Catalan Sea correspond to the period (late April-May, when anchovy starts spawning) immediately before the stratified season (e.g. Palomera et al. 2007, Giannoulaki et al. 2013). Specifically, in the Southern sector higher LPUEs were found at temperatures between 19°C to 22°C, while in the Northern sector LPUE was higher at temperature between 18°C and 21°C and below 19°C, before and after 2007, respectively. The identification of optimal temperature values for the anchovy spawners by several authors (e.g. Motos et al. 1996, García and Palomera 1996, Palomera et al. 2007) may lead one to suppose that stable temperatures are a favorable factor for the reproductive season of anchovies. The northernmost part of the region is characterized by a shorter spawning season related to the thermal cycle (Palomera and Lleonart 1989) in comparison with the other sectors. The apparent decrease in preferred temperature from 2007, corresponding to the threshold value obtained from our analysis, might have further reduced this period and the thermal window in which spawning aggregation occurs.

Results regarding the relationships of Chl *a* concentration with the landings were found to be similar in all sectors. The low values of Chl *a* in late spring and summer, which in this study were associated with higher landings, are typical features of temperate oligotrophic areas such as the Mediterranean Sea (Estrada et al. 1985). In fact, the strong runoffs during early spring from Mediterranean rivers, enhancing the surface primary productivity and the subsequent production of zooplankton (the main food for anchovies) (Tudela and Palomera 1995, Tudela et al. 2002), are followed by a stabilization of the water masses and by the development of the thermocline, which inhibits vertical mixing and determines the depletion of nutrients at the surface (Palomera et al. 2007).

Hydrographic variability influences the spatio-temporal extent of spawning habitat, producing large fluctuations in the recruitment of small pelagic fish (Planque et al. 2007). Our results show that salinity lower than 37.8 enhances the LPUE in the two northernmost areas, closer to the Gulf of Lions, and that this variable is the first to be selected in the models (Fig. 6). During the study period in the Catalan Sea, an alternation between years of high and low salinity was observed, similar to those described by Nicolle et al. (2009) in the Gulf of Lions. This alternation could have reduced the suitable habitat for spawning both spatially and temporally, negatively influencing the fish aggregation for reproduction that takes place along the Catalan coast (Palomera 1992, García and Palomera 1996, Palomera et al. 2007). The influence of salinity on preferred habitat during the spawning might be complex because the survival of larvae results from an interaction between several environmental variables (e.g. temperature, dissolved oxygen, currents, salinity, Chl *a* concentration) (Fréon et al. 2005) and predation. Nevertheless, our results confirm that salinity is important for anchovy, as previously shown by results from echo-survey, egg collection and commercial catch samples in the Mediterranean Sea (e.g. Bellido et al. 2008, Sabatés et al. 2007b), the Bay of Biscay (Massé et al. 1995, Motos et al. 1996, Planque et al. 2007) and the Black Sea (Lisovenko and Andrianov 1996).

The importance of SSS is evident in the Northern (Deviance explained = 21.5%, Fig. 6A) and Central sectors (Deviance explained = 11.5%, Fig. 6E), where low values positively affected anchovy abundances. Our results agree with those of Sabatés et al. (2007b), who found that a gradual decrease in larva and egg concentration occurred towards the south along the Catalan coast when water is extremely salty. They also agreed with previous studies that characterized the spawning habitat, relating anchovy eggs and larvae proliferation to low-salinity periods in the NW Mediterranean Sea (Palomera and Sabatés 1990, Palomera 1992, Martín et al. 2008, Sabatés et al. 2007b, Maynou et al. 2014), and in the Aegean sea (Somarakis and Nikolioudakis 2007), while in the Bay of Biscay salinity was identified as a modest driver of anchovy spawning (Planque et al. 2007) and in the Black Sea anchovy spawning occurs in mesohaline conditions (Lisovenko and Andrianov 1996).

Moreover, we found that other hydrological variables (i.e. currents flowing towards the coast, Fig. 6F) also helped explain the LPUE variability during the spawning periods. The zonal and meridional currents were important environmental drivers in both the Central and Southern sectors, explaining 15.7% (Fig. 6F) and 19.9% (Fig. 6H) of the total deviance, respectively. In the Central sector, negative zonal currents imply water flow towards the coast, facilitating the retention of spawning aggregations, while in the Southern sector negative values of the meridional current suggest north-to-south flow, facilitating retention towards the Ebro Delta area. Retention of eggs and larvae produced by spawning aggregations has been identified as one of the three key processes favouring reproductive success in small pelagic fish (the other two processes of the triad being enrichment and concentration, Bakun 1996).

Overall, mesoscale structures facilitating the aggregation of spawners and highly productive low-salinity waters have been identified as important pelagic conditions for early life stage fish survival and growth (e.g. Lloret et al. 2004, Bakun et al. 2006, Santojanni et al. 2006, Sabatés et al. 2007a). Thus, the match in timing and location between these favourable conditions and the various stages of the life cycle could be crucial in the dynamics of the population. Though LPUE is only an approximation of fish abundance, its analysis improves the understanding of the relationship between small pelagics and the environmental conditions. Specifically, our study confirms the importance of low temperature for the spawning period, in accordance with previous observations, and provides further evidence on the dependence of anchovy adult population on specific oceanographic variables, i.e. salinity and current velocity.

References

Agostini V. N. and Bakun A. 2002. Ocean triads' in the Mediterranean Sea: physical mechanisms potentially structuring reproductive habitat suitability (with example application to European anchovy, *Engraulis encrasicolus*). *Fish. Oceanogr*. 11: 129-142.

Alheit J., Pohlmann T., Casini M., Greve W., Hinrichs R., Mathis M., O'Driscoll K., Vorberg R. and Wagner C. 2012. Climate variability drives anchovies and sardines into the North and Baltic Seas. *Prog Oceanogr* 96: 128-139.

Bakun A. 1996. Patterns in the ocean: ocean processes and marine population dynamics. *California Dea Grant College System*, C.A. 323 pp.

Bakun A. 2006. Fronts and eddies as key structures in the habitat of marine fish larvae: opportunity, adaptive response and competitive advantage. *Sci. Mar.* 70: 105-122.

Basilone G., Bonanno A., Patti B., Mazzola S., Barra M., Cuttitta A. and McBride R. 2013. Spawning site selection by European anchovy (*Engraulis encrasicolus*) in relation to oceanographic conditions in the Strait of Sicily. *Fish. Oceanogr.* 22: 309-323.

Basilone G., Guisande C., Patti B., Mazzola S., Cuttitta A., Bonanno A., Vergara A. and Maneiro I. 2006. Effect of habitat conditions on reproduction of the European anchovy (*Engraulis encrasicolus*) in the Strait of Sicily. *Fish. Oceanogr.* 15: 271-280.

Bellido J. M., Brown A. M., Valavanis V. D., Giráldez A., Pierce G. J., Iglesias M. and Palialexis A. 2008. Identifying essential fish habitat for small pelagic species in Spanish Mediterranean waters. *Hydrobiologia* 612: 171-184.

Calvo, E., Simó R., Coma R., Ribes M., Pascual J., Sabatés A., Gili J. M. and Pelejero C. 2011. Effects of climate change on Mediterranean marine ecosystems: the case of the Catalan Sea. *Clim. Res.* 50: 1-29.

Cardinale M., Cheilari A., Raetz H.J. 2010. Scientific, Technical and Economic Committee for Fisheries (STECF)—Assessment of Mediterranean stocks—Part 1. JCR Publications Repository. Publications Office of the European Union. ISBN: 978-92-79-18754-4. http://publications.jrc.ec.europa.eu/repository/handle/111111111/15362.

Castellón A., Font J. and García E. 1990. The Liguro-Provençal-Catalan current (NW Mediterranean) observed by Doppler profiling in the Balearic sea. *Sci. Mar.* 54: 269-276.

Ciannelli L., Chan K. S., Bailey K. M., and Stenseth N. C.2004. Nonadditive effects of the environment on the survival of a large marine fish population. *Ecology*, 85: 3418-3427.

Craven P. and Wahba G. 1979. Smoothing noisy data with spline functions: estimating the correct degree of smoothing by the method of generalized cross-validation. *Numer. Mat.* 31: 377-403.

Cury, P. and Roy C. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Can. J. Fish. Aquat. Sci.* 46: 670-680.

Cushing, D. H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. *Adv. Mar. Biol.* 26: 249-293.

ESRI (1994) ARC Macro Language. Environmental Systems Research Institute Inc, USA: Redlands, CA, pp. 3 37

Estrada M., Vives F. and Alcaraz M. 1985. Life and the productivity of the open sea. *Western Mediterranean Pergamon Press*, Oxford:148-197.

Farruggio H. 2013. Fisheries in the gulf of Lions. UNEP MAP RAC/SPA. H. Ed. RAC/SPA, Tunis. pp. 79

Fréon, P., Cury P., Shannon L. and Roy C. 2005. Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: a review. *Bull. Mar. Sci. 76*(2): 385-462.

García, A. and Palomera I. 1996. Anchovy early life history and its relation to its surrounding environment in the Western Mediterranean basin. *Sci. Mar.* 60(S2): 155-166.

Giannoulaki M., Iglesias M., Tugores M. P., Bonanno A., Patti B., De Felice A., Leonori I., Bigot J. L., TičIna V., Pyrounaki M. M., Tsagarakis K., Machias A., Somarakis S., Schismenou E., Quinci E., Basilone G., Cuttitta A., Campanella F., Miquel J., OñAte D., Roos D. and Valavanis V. 2013. Characterizing the potential habitat of European anchovy *Engraulis encrasicolus* in the Mediterranean Sea, at different life stages. *Fish. Oceanogr.* 22(2): 69-89.

Hastie T. J. and Tibshirani R. J. 1990. Generalized additive models, vol 43. CRC Press.

Houde E. 1997. Patterns and trends in larval-stage growth and mortality of teleost fish. *J. Fish. Biol.* 51: 52 83.

Lasker, R. 1981. The role of a stable ocean in larval fish survival and subsequent recruitment. In: *Marine fish larvae: morphology, ecology and relation to fisheries*, 80-89.

Lisovenko L. A. and Andrianov D. P. 1996. Reproductive biology of anchovy (*Engraulis encrasicolus ponticus*, Alexandrov 1927) in the Black Sea. *Sci. Mar.* 60: 209-218.

Lleonart J. and Maynou F. 2003. Fish stock assessments in the Mediterranean: state of the art. *Sci. Mar*. 67: 37-49.

Lloret J., Lleonart J. and Solé I. 2000. Time series modelling of landings in Northwest Mediterranean Sea. *ICES J. Mar. Sci.*: 57: 171-184.

Lloret J., Lleonart J., Solé I. and Fromentin J. M. 2001. Fluctuations of landings and environmental conditions in the north-western Mediterranean Sea. *Fish. Oceanogr.* 10: 33-50.

Lloret J., Palomera I., Salat J. and Sole I. 2004. Impact of freshwater input and wind on landings of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in shelf waters surrounding the Ebre (Ebro) River delta (north-western Mediterranean). *Fish. Oceanogr.* 13: 102-110.

Lluch-Belda D., Crawford R., Kawasaki T., MacCall A., Parrish R., Schwartzlose R. and Smith P. 1989. World wide fluctuations of sardine and anchovy stocks: the regime problem. *S. Afr. J. Mar. Sci.* 8: 195-205.

Martín P. and Sabatés A. 1991. Spatio-temporal distribution pattern of the red band-fish *Cepola rubescens* Linnaeus at different stages of its life cycle in the northwestern Mediterranean. *J. Fish. Biol.* 39: 549-557.

Martín P., Bahamon N., Sabatés A., Maynou F., Sánchez P. and Demestre M. 2008. European anchovy (*Engraulis encrasicolus*) landings and environmental conditions on the Catalan Coast (NW Mediterranean) during 2000–2005. In: Valavanis V.E., Essential Fish Habitat Mapping in the Mediterranean. Series Developments in *Hydrobiology*, vol. 203: 185-199. Springer.

Martín P., Sabatés A., Lloret J. and Martin-Vide J. 2012. Climate modulation of fish populations: the role of the Western Mediterranean Oscillation (WeMO) in sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) production in the north-western Mediterranean. *Clim. Chang.* 110: 925 939.

Massé J., Leroy C., Halgand D. and Beillois P. 1995. Anchovy adult and egg distributrion in the Bay of Biscay in relation to environmental conditions, as observed during acoustic surveys (1990, 1991, 1992). *Actas del IV coloquio Internacional sobre Oceanografía del Golfo de Vizcaya*: 281- 283. Santander

Maynou F., Sabatés A. and Salat J. 2014. Clues from the recent past to assess recruitment of Mediterranean small pelagic fishes under sea warming scenarios. *Clim. Chang.* 126: 175-188.

Millot C. 1991. Mesoscale and seasonal variabilities of the circulation in the western Mediterranean. *Dyn. Atmos. Oceans.* 15:179-214.

Motos L., Uriarte A. and Valencia V. 1996. The spawning environment of the Bay of Biscay anchovy (*Engraulis encrasicolus* L.). *Sci. Mar.* 60: 237-255.

Nicolle A., Garreau P. and Liorzou B. 2009. Modelling for anchovy recruitment studies in the Gulf of Lions (Western Mediterranean Sea). *Ocean dynamics* 59: 953-968.

Palomera I. 1992. Spawning of anchovy *Engraulis encrasicolus* in the Northwestern Mediterranean relative to. *Mar. Ecol. Prog. Ser.* 79: 215-223.

Palomera I. and Lleonart J. 1989. Field mortality estimates of anchovy larvae (Engraulis encrasicolus) in the western Mediterranean. *J.Fish. Biol.* 35 (suppl. A): 133-138.

Palomera I. and Sabatés A. 1990. Co-occurrence of *Engraulis encrasicolus* and *Sardinella aurita* eggs and larvae in the northwestern Mediterranean. *Sci. Mar.* 54: 61-67.

Palomera I., Olivar M. P., Salat J., Sabatés A., Coll M., García A. and Morales-Nin B. 2007. Small pelagic fish in the NW Mediterranean Sea: an ecological review. *Prog Oceanogr* 74: 377-396.

Pertierra J. P. and Lleonart J. 1996. NW Mediterranean anchovy fisheries. *Sci. Mar.* 60(S2): 257-267.

Pertierra J.P. – 1992. Biología pesquera de la anchoa Engraulis encrasicolus del Mar Catalán (NW Mediterraneo). Ph. D. thesis, Univ. Politècnica de Catalunya, Barcelona.

Planque B., Bellier E. and Lazure P. 2007. Modelling potential spawning habitat of sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) in the Bay of Biscay. *Fish. Oceanogr.* 16(1): 16-30.

Pörtner H.-O. and Peck M. 2010. Climate change effects on fishes and fisheries: towards a cause-and effect understanding. *J. Fish. Biol.* 77: 1745-1779.

Razouls C. and Kouwenberg J. 1993. Spatial distribution and seasonal variation of mesozooplankton biomass in the Gulf of Lions (northwestern Mediterranean). *Oceanol. Acta*, 16: 393-401.

Rojas P., Garcia M., Sospedra J., Figa J., Defabregas J., Lopez O., Espino M., Ortiz V., Sanchezarcilla A. and Manriquez M. 1995. On the structure of the mean flow in the Blanes Canyon area (NW Mediterranean) during summer. *Oceanol. Acta*, 18: 443-454.

Sabatés A., Olivar M. P., Salat J., Palomera I. and Alemany F. 2007a. Physical and biological processes controlling the distribution of fish larvae in the NW Mediterranean. *Prog Oceanogr* 74: 355-376.

Sabatés A., Salat J., Palomera I., Emelianov M., Fernández de Puelles M. and Olivar M. P. 2007b. Advection of anchovy (*Engraulis encrasicolus*) larvae along the Catalan continental slope (NW Mediterranean). *Fish. Oceanogr.* 16: 130-141.

Sabatés A., Salat J., Raya V. and Emelianov M. 2013. Role of mesoscale eddies in shaping the spatial distribution of the coexisting *Engraulis encrasicolus* and *Sardinella aurita* larvae in the northwestern Mediterranean. *J. Mar. Syst.* 111: 108-119.

Santojanni A., Arneri E., Bernardini V., Cingolani N., Di Marco M.and Russo A. 2006. Effects of environmental variables on recruitment of anchovy in the Adriatic Sea. *Clim. Res.* 31: 181-193.

Somarakis S. and Nikolioudakis N. 2007. Oceanographic habitat, growth and mortality of larval anchovy (*Engraulis encrasicolus*) in the northern Aegean Sea (eastern Mediterranean). *Mar. Biol.* 152: 1143-1158.

Tudela S. and Palomera I. 1995. Diel feeding intensity and daily ration in the anchovy *Engraulis encrasicolus* in the northwest Mediterranean Sea during the spawning period*. Mar. Ecol. Prog. Ser.* 129: 55-61.

Tudela S., Palomera I., and Quílez G. 2002. Feeding of anchovy *Engraulis encrasicolus* larvae in the north west Mediterranean. *J. Mar. Biol. Ass. UK*, 82(02), 349-350.

Vargas-Yáñez M., Moya F., García-Martínez M., Tel E., Zunino P., Plaza F., Salat J., Pascual J., López-Jurado J. L. and Serra M., 2010. Climate change in the Western Mediterranean sea 1900–2008. *J. Mar. Syst*. 82: 171-176.

Vargas-Yáñez M., Moya F., Tel E., García-Martínez M. C., Guerber E.and Bourgeon M. 2009. Warming and salting in the western Mediterranean during the second half of the 20th century: inconsistencies, unknowns and the effect of data processing. *Sci. Mar.* 73(1): 7-28.

Wood, S., 2006. Generalized additive models: an introduction with R. *CRC/Taylor and Francis*.

Chapter 3

Environmental drivers of sardine (*Sardina pilchardus*) in the Catalan Sea (NW Mediterranean Sea).

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Abstract

In the area surrounding the Ebro Delta, similar to the rest of the north-western Mediterranean Sea, the sardine (*Sardina pilchardus*), one of the most exploited small pelagic fishes, has suffered a decreasing trend in abundance and biomass in the last decade, with low values in evidence since 2007. The dependence of this species on environmental factors makes it vulnerable to environmental changes; consequently, the abundance of the species is highly variable. Using segmented regression, we evaluated the presence of discontinuities in the temporal pattern of the seasonally adjusted landings per unit effort (LPUE), which was used as a proxy of abundance, between 2000 and 2013. The results suggested a sudden increase in mid-2005, followed by a sharp decrease starting in 2006. A generalized additive mixed model (GAMM), incorporating the linear correlation structure, was used to identify relationships between the seasonally adjusted LPUE and trends of the Western Mediterranean Oscillation index (WeMOI), sea surface temperature (SST), salinity (SAL) and the Zonal and Meridional Currents (ZC and MC, respectively). The variance inflation factors (VIFs) were calculated between all environmental variables to avoid high-dimensional collinearities. The final GAMM, selected using the Akaike information criterion, indicated that positive WeMOI values, which favour the productivity of the area, along with SAL (at ca. 38) and a northward-flowing MC, favoured LPUE. Our results, obtained by applying a method in which variation due to season, non-linearity, autocorrelation and collinearity of the covariates was taken into account, provided further evidence of the dependence of the sardine population upon specific hydrographic variables.

Keywords: Sardine; landing; purse seine; GAMM; WeMOI; NW Mediterranean Sea.

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Introduction

Small pelagic fishes are an important component of marine ecosystems due to their role in energy transfer from lower to higher trophic levels (Cury 2000; Palomera et al. 2007). Globally distributed, they support important fisheries around the world (Alder et al. 2008). Early maturation, a short life span, and rapid and drastic responses to changes in the ocean climate (Checkley et al. 2009) characterize their biology.

Large fluctuations in the population abundance of these species in different parts of the world have been associated with shifts in biological and physical processes that particularly affect the recruitment phase (Agostini & Bakun 2002) due to the vulnerability of the species to changing oceanographic conditions during early life stages. Moreover, changes in environmental conditions also influence the adult populations and consequently affect fisheries' production by directly influencing the spatial distribution of fish or their availability to fishing fleets and by indirectly influencing adult mortality (Palomera et al. 2007; Van Beveren et al. 2016).

The effects of climatic components on the variability of small pelagic resources have been studied across various marine ecosystems (e.g. Checkley et al. 2009). Despite the differences encountered across the ecosystems, such as the importance of an environmental factor in one area but not in another area (e.g. in the Mediterranean sea between the Strait of Sicily, where the Atlantic-Ionian Stream was identified as a main driver; Patti et al. 2004; and the Aegean Sea, where the main drivers were depth and river flow; Giannoulaki et al. 2005), patterns of physical mechanisms, summarized as the 'fundamental triads' concept, can generally be identified (Agostini & Bakun 2002). In fact, even if small pelagics inhabit distinguishable areas characterized by different oceanographic characteristics (e.g. circulation patterns, bathymetry, rivers influences), their distribution patterns seem to be driven by environmental processes, which, although specific to each ecosystem, lead to conditions capable of enhancing and maintaining food availability (Bonanno et al. 2014).

Small pelagics dominate the catches in the Mediterranean sea; in particular, European anchovy Engraulis encrasicolus (Linnaeus, 1758) and European sardine Sardina pilchardus (Walbaum, 1792) represent the main species landed (Stergiou et al. 2016). Similar to other Mediterranean fish stocks, sardine spawning stock biomass and age at the time of capture have shown a progressive decrease in the last two decades (Vasilakopoulos et al. 2014).

Since the mid-1990s, sardine and anchovy landings have demonstrated a continuous decreasing trend in the NW Mediterranean Sea (Catalan sea and Gulf of Lions; Van Beveren et al. 2016). This trend has also been observed in the rest of the Mediterranean in recent decades and is consistent with the decline in population biomass in almost all areas where small pelagic stocks are assessed (GFCM 2015; STECF 2015).

In the Catalan sea, sardine reproductive success is enhanced by productivity mechanisms during the spawning season, which occurs from the autumn to spring, with a peak in the winter (January and February; Olivar et al. 2001, 2003; Sabatés et al. 2007). Spawners' abundance is mainly high in inshore waters, where sardine eggs are concentrated in water < 100 m deep (Olivar et al. 2001, 2003). During winter vertical mixing, which is mediated primarily by wind stress, an increased homogenization of the water column enhances biological primary productivity. This condition favours the survival of sardine in their early life stages, which is directly linked to increased landings (Lloret et al. 2004). However, extreme wind speeds can negatively affect sardine populations by increasing larvae mortality via reduced feeding success due to the dispersal of food and larvae to unfavourable locations (Borges et al. 2003; Lloret et al. 2004).

In addition to the wind mixing index, significant positive relationships were found with the Western Mediterranean Oscillation index (WeMOI, Martin-Vide & Lopez-Bustins 2006; Martín et al. 2012), a good proxy for regional atmospheric conditions in this area. Finally, although less significant, negative correlations were found in relation to sea surface temperature (Martín et al. 2012).

These significant relationships (Lloret et al. 2004; Martín et al. 2012) demonstrated that environmental changes influenced sardine population variability by presumably acting principally on the early life stages. However, the results of these analyses were strongly based on correlative or linear models; there is evidence that the relationships between the fisheries' catches (or landings) and the information available on environmental and climate factors can be better modelled using non-linear relationships (Borges et al. 2003). Generalized additive models (GAMs) are a modelling framework well suited to describing this kind of relationship by means of non-linear specification of the dependence of the response variable (Wood 2006); hence, the data allow for the determination of the nature of the relationship rather than the assumption of some form of parametric relationship (Guisan et al. 2002). Furthermore, in cases in which residual autocorrelation is significant (i.e. violation of independence), as in the analysis of time series, generalized additive mixed models (GAMMs) can be used to explicitly model autocorrelation (Wood 2006).

Environmental variability can alter fish distributions over short time-scales and can persist as long as environmental conditions remain unfavourable for fish survival, growth and reproduction, significantly affecting fishery by varying resource availability (Fréon et al. 2005). Thus, in the present study, a characterization of sardine landings in terms of trend and breakpoints was performed to evaluate the presence of marked temporal changes. Then, using GAM and GAMM, we investigated the relationships between the decrease in sardine landings and a combination of potential climate drivers in the Catalan Sea in order to assess their influence.

Materials and methods

General characteristics of the Study Area

The fishing area is situated off the Ebro delta (NW Mediterranean Sea) between 40°56′ N and 41°16′ N latitude and 0°80′ E and 1°72′ E longitude (Figure 1 (a)). This area, which is part of the so-called Ebro shelf, is marked by a drastic change in shelf width, evolving from ca. 15-20 km in the northern part to ca. 70 km in the southern part, and by the presence of a steep slope (Figure 1 (a)). A shelf-slope density front separating the less dense continental influenced waters and the denser open sea waters (Font et al. 1998) and the presence of a quasi-permanent geostrophic slope current (Northern Current, NC) flowing south-westward (Millot 1999; Salat et al. 2002) characterize the Ebro shelf.

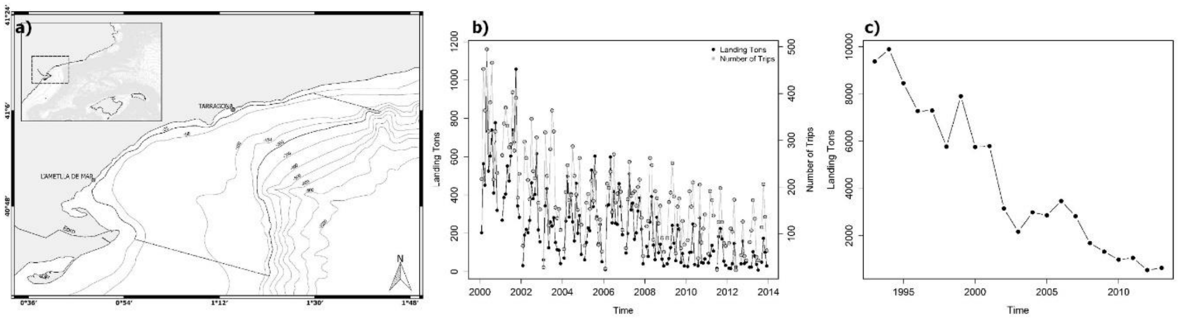

Figure 1. (a) The study area limited by the 35 m and 200 m of the isobaths and the two fishing ports; (b) landings in tons per month and sum of the days per month in which fishing operations were carried out by the fleet. Note the missing data in the winter due to the annual closed season; (c) annual landings in tons from the two ports starting from the year 1993.

The study area receives an important amount of continental fresh water from the Ebro river. On average, its annual water discharge rate ranges from 300 and 600 m3 s-1 with maximum discharge in the spring and autumn (Salat 1996). The seasonal evolution of the stratification is clear in the area. The water column, in fact, is almost homogenous during winter (13-14° C at all depths), in contrast to early spring and late autumn, when it is characterized by a defined thermocline (Salat 1996). Consequently, the river outflow plays an important role, especially immediately before the stratified season, by providing nutrients and enhancing surface productivity during this season (Salat 1996; Palomera et al. 2007).

The sea surface is dominated by winds coming from the north-northwest, which are strong and more frequent in the winter (60-100 km/h). These winds are associated with vertical mixing along the coast, contributing to the formation of the surface mixed layer during the stratified season (Salat 1996).

Furthermore, the north westerly wind predominance, together with the specific features of the shelf, are involved in the intrusion processes of the shelf edge flow into the shelf, allowing the development of anticyclonic eddies (Salat 1996; Xing & Davies 2002), which are important structures for the spawning and reproduction of the small pelagic populations (Bakun 2006). Given these features, the Ebro river continental shelf is considered one of the most important spawning areas for clupeids in the western Mediterranean Sea (Palomera 1992; Palomera et al. 2007).

Data

The monthly data of landings (kg) and the number of fishing days (a measure of fishing effort) (Figure 1 (b)) for purse seine vessels were obtained for the two harbours of the study area with a small pelagic fleet, Tarragona and L'Ametlla del Mar, in the South of Catalonia, from 2000 to 2013 (Figure 1(b)). The selected ports produce 20-30% of the total landings of sardine in the geographical subarea GSA06 (STECF, 2015 p. 110 shows 9-10,000 t in GSA06 in 2012-2103, from 17-20,000 in 2002-2004), while in south Catalonia, production was ca. 6,000 t annually in the early 2000s and has been down to ca. 1000 t in recent years. The fleet was composed of 20 purse seiners in 2013 with the following characteristics: 16-24 m LOA, 30-65 GT and 127-450 kW engines. This purse seine fleet has decreased in the number of vessels (STECF, 2015 p. 109), similar to the other fleets in the Mediterranean Sea, in the last two decades due to poor profitability of fisheries and EU-funded subsidies for the decommissioning of vessels (STECF, 2015 p. 111, 140 vessels in GSA06 in 2013, i.e. our fleet is approximately 15% of the total fleet).

As an index of sardine fishery productivity, the monthly average LPUE (Y_t) was obtained by dividing the landings per month by the sum of the days when fishing operations were carried out by the fleet (LPUE in kg/day).

The environmental monthly time series were derived from satellite datasets, which are commonly used in studies of fisheries data due to their consistent space-time coverage and their ability to highlight the main ocean processes that determine the dynamics of fish populations dwelling near the surface (e.g. Tugores et al. 2011; Bonanno et al. 2013). The environmental variables selected were as follows; Sea Surface temperature (SST in °C), Sea Surface Salinity (SSS), the Meridional Component of the water current (MC in m s-1, positive northward), and the Zonal Component of the water current (ZC in m s-1, positive eastward), which were retrieved from the Myocean Project with a spatial resolution of 1/16° x 1/16° (5.2 x 7.0 km, approximately). The first variables mentioned were useful because they were linked to the population dynamics of small pelagic fishes in the NW Mediterranean Sea (e.g. Lloret et al. 2001, 2004; Martín et al. 2008; Maynou et al. 2014) as well as in other locations around the Iberian Peninsula (Guisande et al. 2001;

Borges et al. 2003; Guisande et al. 2004; Santos et al. 2012). The latter two variables (MC and ZC) were selected because they are indicative of the circulation patterns upon the Ebro shelf, which is characterized principally by a current flowing south-westward (Northern Current) and interrupted by clockwise eddies (structures supporting high level of biological activities; Bakun 2006) and periods of current reversal (i.e. current flowing northward; Font et al. 1990; Salat et al. 2002; Lorente et al. 2015). Furthermore, the monthly Western Mediterranean Oscillation index (WeMOI), resulting from the difference of the standardized atmospheric pressure values in San Fernando-Cadiz (South western of Spain) and Padua (North eastern Italy) (Martin-Vide & Lopez-Bustins 2006), was used as an additional explanatory variable encompassing the overall atmospheric climatology in the area.

All environmental variables (X_t) were averaged over the entire study area (Figure 1 (a)) and examined using statistical modelling to explore their temporal trends and whether they are possible explanatory variables of sardine LPUE. The study area was delimited considering the area fished by the fleet, which was based in the 2 study harbours and the bathymetric range from 35 to 200 m depth (Lleonart & Maynou 2003). The fishing range of the vessels was local because the fleet was obliged to return to port daily, and the boats had to be tied up for a minimum of 12 hours daily (Martín et al. 2012).

The LPUE dataset contained irregularities in terms of missing data in the winter months and in the different number of trips where fishing operations were carried out (Table 1, Figure 1 (b), Figure 2). This was due to the annual closure of the purse seine fishery in the area for 2 months to protect anchovy recruitment. The closure occurs usually in December and January, but may be advanced to mid-November or delayed until mid-February for ad hoc reasons.

Table 1. Sum of landings in tons and number of fishing operation for each month subseries.

	Jan	Feb	Mar	Abr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec
Landings (Tons)	0	1090.72	2815.35	3865.54	4677.89	3463.29	3236.93	4100.31	3868.99	4501.23	2497.49	1094.84
N of trips	0	1335	3034	3160	3050	2246	2615	2710	2439	2558	2039	1289

Statistical analyses

Because the objective of the analysis was to relate trends in the environmental variables to the temporal variation observed in sardine fisheries productivity, to avoid any influence of the monthly cycle (Figure 2), the LPUE series was seasonally adjusted (SaY_s) as follows:

$$(SaY_t) = Y_t - \mu_s$$

where the calculation of the monthly averages (μ_s) using the data from all years was used to correct the time series by subtracting these values from each cycle subseries (months) (Figure 3). This simple seasonal adjustment was chosen because we were not interested in imputing missing LPUE data, which is a requirement for many decomposition methods since they do not allow 'internal' missing values.

The decomposition and extraction of temporal trends in the data series were performed according to 'the seasonal and trend decomposition procedure based on loess' (STL) (first designed by Cleveland et al. 1990) (Figure 4). The STL is an empirical, non-parametric filtering procedure that decomposes a time series (X_t) into three unobservable components using an iterative procedure (inner and outer loop) based on successive smoothing (for more details see Cleveland et al. 1990), resulting in a trend (t_t), seasonal (s_t) and residual or short -term variation (e_t) and is as follows:

$$(X_t) = (t_t) + (s_t) + (e_t)$$

Overall, the STL includes six parameters that determine the degree of smoothing in trend and seasonal components: n_p (Number of observations in each cycle of the seasonal component), n_i (Number of iterations of the inner loop), n_o (Number of iterations of the outer loop), n_l (Smoothing parameter for the low pass filter), n_s (Smoothing parameter for the seasonal component), and n_t (Smoothing parameter for the trend component). The smoothing parameters of the seasonal component were selected using the visual diagnostic method described by Cleveland et al. (1990), while the trend smoothing parameters using the smallest odd integer number that satisfies the following equation:

$n_t \geq \frac{1.5\, n_p}{1 - 1.5 n_s^{-1}}$ (Cleveland et al. 1990).

The seasonally adjusted LPUE (Figure 3) showed relatively stable values around the zero mean until approximately 2007 and decreasing values from 2008 onwards, indicating the possible presence of a change in the trend around the mid-2000s. This change in trend suggests that a better description of the seasonally adjusted LPUE may be provided by segmented regression. The selection of the best explanatory segmented regression was achieved by comparing linear and non-linear (second order polynomial) models and choosing the model with the lowest Akaike Information criterion (AIC). The AICs were the minimum values obtained during the process of the selection of the optimum breakpoint performed for each regression model. The selection of this point, indicating a marked change (in this case on LPUE over time), was performed by doing a search grid throughout a time range starting from the beginning of 2001 to the end of 2012 (ca. 90% of the data) and choosing the break that produced the model that minimized the AIC

(Crawley 2007). Because the objective was not to test the null hypothesis of no effects, no correction for autocorrelation was attempted.

To assess the influence of exogenous factors on the decrease of sardine landings, the environmental trends extracted by the STL procedure were included as explanatory variables in the Generalized Additive Model approach (GAM, Hastie & Tibshirani 1990; Wood 2006) using the seasonal adjusted LPUE as the response variable. The cubic regression spline was used as a one-dimensional non-parametric smoothing function and a double penalty was applied to the penalized regression to reduce the chance of over fitting. As error distribution, the Gaussian with the identity link function was applied, and the restricted maximum likelihood estimation (REML) was used.

To detect possible high-dimensional collinearities, the variance inflation factors (VIFs) between all environmental variables were calculated. The covariates with the highest VIFs were removed from the model until the highest VIF value was <5 (Zuur et al. 2007).

The residuals of the full model were checked using variography, and violations of the independence assumption were detected (Figure 5 (a)). Consequently, to avoid a Type I error, the generalized additive mixed model (GAMM), which is capable of accounting for dependence between observations by adding a correlation structure to the additive model, was used (Wood 2006). Following Pinheiro & Bates (2000) and Zuur et al. (2009), we selected the linear residual correlation based on the minimization of the AIC by comparing models with the same fixed component (i.e. the full model with all the covariates) and different correlation structures. Furthermore, to assess the adequacy of the linear correlation structure, we investigated the sample semi-variogram for the normalized residuals (Figure 5 (b)). The general form of the GAMM used in the analysis has the following structure:

$$y = \beta_0 + \sum_{j=1}^{p} f_j(X_j) + \varepsilon_j$$

$$corr(\varepsilon_{js}, \varepsilon_{jt}) = \begin{cases} 1 \; if \; s = 0 \\ h(s,d) = 1 - \left(\frac{s}{d}\right) \; if \; 0 < s < d \end{cases}$$

where β_0 is the intercept, X_j are the covariates, f_j the cubic spline smoothing function for each covariate and ε_j are the error terms, which are normally distributed with mean 0 and variance σ^2. In the independence assumption, residuals from different time points were not allowed to covary. Next, we modelled the dependence between the residuals of different time points (ε_{js} , ε_{jt}) by the introduction of the linear correlation structure (second equation), where $h(\cdot)$ is the correlation function, s is the temporal distance between ε_j and ε_{jt} and d is the range, which represents the time distance at which residuals are no longer correlated.

The likelihood ratio test (ML) was used to obtain the optimal fixed model formulation, and the final combination of variables was refitted using REML (Zuur et al. 2009).

All analyses were performed with R v. 3.1.2, and the mgcv library was used to implement the generalized additive and mixed models (Wood 2006).

Results

Sardine LPUE exhibited the lowest values in the winter, while the highest LPUE occurred between the spring and fall (Figure 2). Figure 3 shows the seasonally adjusted LPUE and the fitted breakpoint regression. Landings underwent a decreasing trend during the whole period, with higher values between 2000 and 2004, followed by a slow decrease between 2004 and 2006 and a more accentuated decline starting in 2006.

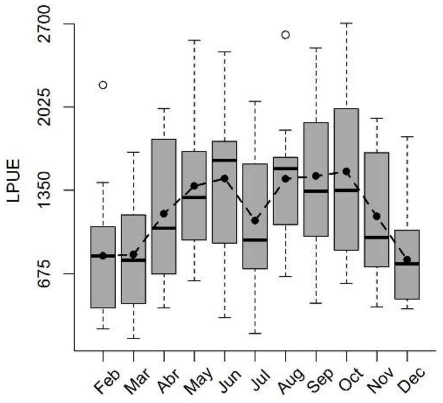

Figure 2. Seasonal cycle of the sardine LPUE. The bold lines indicate the median, while bold points are the mean LPUE values.

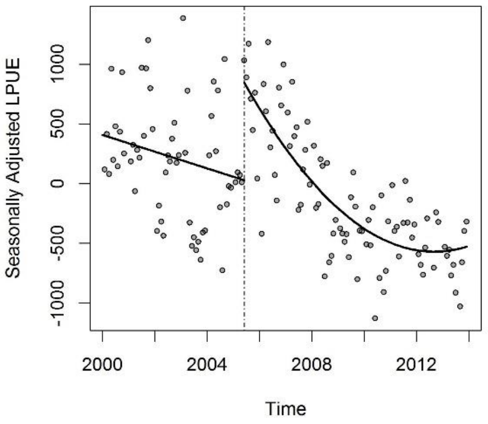

Figure 3. Variation in seasonal-adjusted LPUE series (points) and segmented regression (lines) fitted to identify the possible presence of breaks.

The values of the AIC when comparing the different models suggested that the trend in LPUE was better modelled by dividing the data into two blocks rather than assuming a constant variation over time. The first block was best described with a linear function, while the second was best represented by using a second order polynomial regression. The profile of the AIC indicated that the optimum break was in 2005, and specifically, in June of that year. The seasonally adjusted LPUE decreased linearly and more slowly before the break and was characterized by large fluctuations, followed by a jump in mid-2005 to a higher LPUE.

The second block was characterized by a strong LPUE decrease and slight intra and inter-annual variations, with the minimum values of LPUE almost constant at the end of the series (Figure 3).

Table 2 shows the parameters used for the STL decomposition of the environmental variables.

Table 2. STL decomposition parameters. np, number of observations in each cycle of the seasonal component; ni, number of iterations of the inner loop; no, number of iterations of the outer loop; nl, smoothing parameter for the low-pass filter; ns, smoothing parameter for the seasonal component; nt, smoothing parameter for the trend component.

	Decomposition Parameters					
Environmental Variables	n_p	n_i	n_o	n_l	n_s	n_t
Temperature	12	2	0	13	29	19
Salinity	12	2	0	13	21	19
WeMOI	12	2	0	13	27	19
Meridional Current	12	2	0	13	25	19
Zonal Current	12	2	0	13	21	19

The trend components obtained from the environmental series are shown in Figure 4. Salinity showed two clear increasing trends during 2000-2006 and 2009-2013 and for a period between 2006 and 2009 where the values reached those observed in 2000; overall, the values at the end of the study period were notably higher than those at the beginning of the period (ca. 37.7 vs ca. 38.2) (Figure 4 (a)). Temperature showed a slightly increasing trend with fluctuations during the whole period, although less marked than salinity (from 18.8 at the beginning of the period to 19.0 °C, approximately) (Figure 4 (b)). Figure 4 (c) shows the WeMOI trend, which was characterized by a decrease from 2000 to 2006, followed by stabilization at negative values; the highest positive values were observed between 2000 and 2003 (Figure 4 (c)). Both the Meridional and the Zonal currents showed a decreasing trend from mainly positive values to mainly negative ones starting from the end of 2009. Both currents presented a peak of positive values in 2009, indicating a higher northward flow in the case of the Meridional current and a higher eastward flow for the Zonal current (Figure 4 (d), Figure 4 (e)).

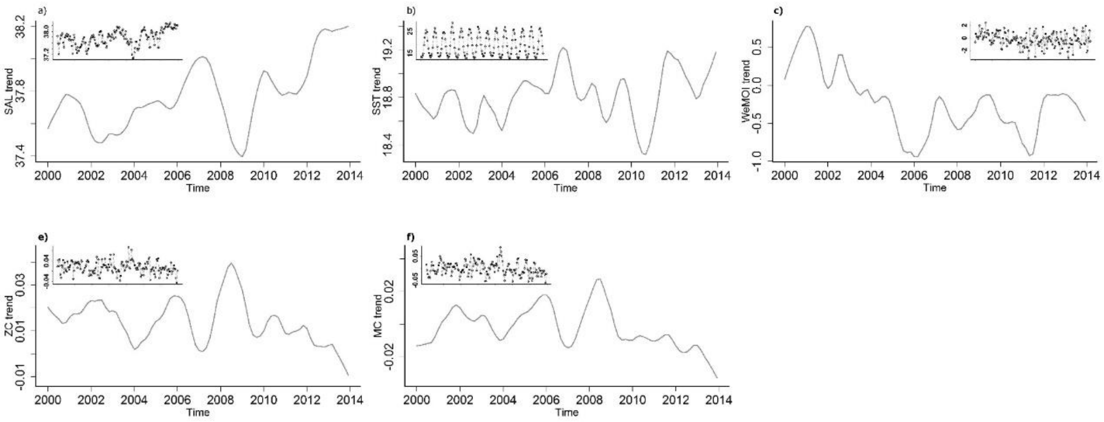

Figure 4. Main graphs: trend components of the environmental drivers obtained by the STL decomposition (SAL, salinity; SST, sea surface temperature; WeMOI, Western Mediterranean oscillation index; ZC, Zonal Current; MC, Meridional Current). Small graphs: monthly mean of each covariate.

The calculation of VIFs to determine variables of high collinearity indicated a value of 5.67 for the Zonal current, and hence, this variable was not included in the model. The other variables showed a maximum VIF of 3.73 and were utilized because they did not introduce major bias in the analyses.

The GAMM formulation, with the incorporation of the linear residual correlation structure, was selected because the semi-variogram on the residuals compared with the GAM full model showed temporal independence (Figure 5) and because it minimized the AIC compared to the GAM formulation.

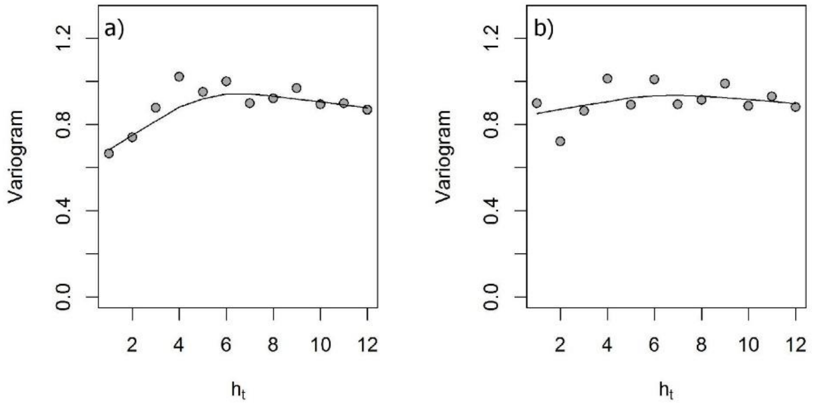

Figure 5. (a) Experimental variogram of the residuals obtained by applying a GAM with all environmental trends. Note that there is evidence that the independence assumption is violated. (b) Experimental variogram of the normalized residual using the GAMM with the linear correlation structure. The horizontal axis (h) in each graph represents the time distance.

The optimal fixed model formulation of the GAMM included Salinity, WeMOI and the Meridional current and explained 47% of the deviation. The parameter estimates of the GAMM are shown in Figure 6 and in Table 3. Significant negative effects on the LPUE were present in relation with WeMOI for negative values between ca. -0.5 to ca. -0.2, while positive values higher than ca. 0.2 positively correlated with abundance. Although not particularly evident, a positive effect was present for WeMOI values lower than ca. –0.8 (Figure 6 (a)). The non-linear relationship with salinity is shown in Figure 6 (b). Negative significant effects were found for values lower than ca. 37.5, followed by values not affecting abundance until ca. 38. Above this value, significant positive effects were recognized and were characterized by a local peak at ca. 38.1, which was followed by a negative non-significant effect (Figure 6 (b)). The meridional current negatively affected LPUE when flowing southward and positively at the opposite direction, with the shape of the relation presenting a local positive peak between 0.01 to 0.02 m/s, and anything above the positive effect started a decrease (Figure 6 (c)).

Table 3. Final GAMM model with the analysis of deviance of the covariate. WeMOI, Western Mediterranean oscillation index; Sal, salinity; MC, Meridional Current). Edf, estimated degree of freedom. DVe, explained deviance.

	edf	F	p-value	DVe	R^2
s(WeMOI)	2.878	5.898	< 0.01	47%	0.43
s(Sal)	5.06	5.144	< 0.01		
s(MC)	3.1	5.24	< 0.01		

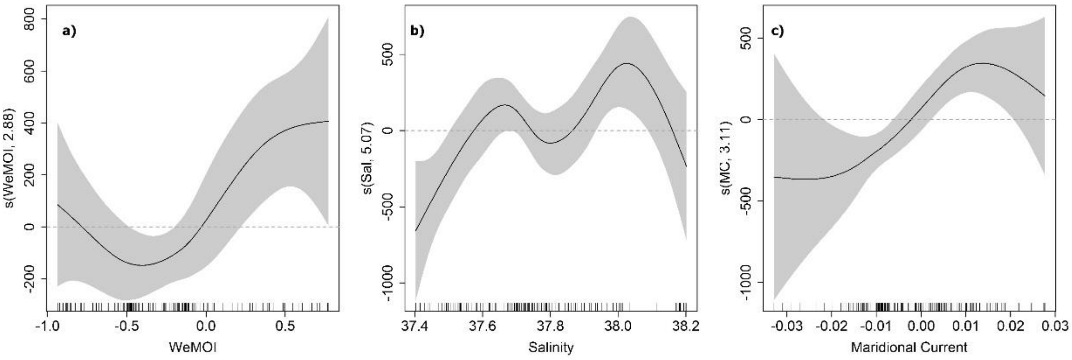

Figure 6. Final GAMM of the seasonal adjusted LPUE in relation to the trend of the environmental variable. The y-axis indicates the smoothers for significant effects of (a) WeMOI, (b) salinity and (c) Meridional Current. Shaded areas show 95% confidence limits for the smoothers.

Discussion

The highly productive waters surrounding the Ebro river represent one of the few exceptions in the essentially oligotrophic coasts of the Mediterranean Sea; they are influenced by the two principal enrichment processes characterizing this semi-enclosed sea: nutrient intake by large river discharge and exposure to strong winds, allowing water mixing (Salat 1996; Salat et al. 2002; Lloret et al. 2004).

During the period of 2000 to 2013, the declining trend of sardine LPUE was characterized by two striking events: the sudden increase in mid-2005, followed by an abrupt decrease until the year 2010, where it stabilized at a lower value for the rest of the investigation period.

The breakdown of the seasonal adjusted LPUE agrees with the findings of Tugores et al. (2010), who, with the use of acoustic surveys, described a general decreasing trend in abundance from 2003 to 2006 with signals of recovery during the year 2005 in the area surrounding the Ebro. Since sardines in the NW Mediterranean Sea spawn from November to March (e.g. Lloret et al. 2004; Palomera et al. 2007), during the early summer, the fished sardine population is mainly composed of adults that are 1 and almost 2 years old (Lloret et al. 2004). The discontinuity observed in the summer of 2005 might have occurred due to more suitable environmental conditions during the spawning season between the late autumn of 2003 and the winter of 2004 compared with the other spawning periods preceding the breakpoint. In particular, temperature during this period was on average relatively low and had small variability (low standard deviation compared to other years) which could indicate a completely broken thermocline in mid-autumn. This homogeneous water column most likely allowed optimal environmental conditions in terms of nutrient supplies that lasted the whole spawning season and therefore increased food availability for sardine early life stages. Although this was only a small recovery, which formed part of the general decreasing trend observed in the area, it could have led to an expansion of the area occupied by this fish and the formation of more dense patches (in areas with favourable environmental conditions), which became more susceptible to fishing pressure (Barra et al. 2015).

The second characteristic event of this period, occurring between 2010 and 2013 and consisting of the stabilization at the lowest values, is in accordance with the findings in the nearby Gulf of Lions (NW Mediterranean Sea), where sardine landings in the same period became even lower than those during the period before the 1960s (Van Beveren et al. 2016).

A part of the landings variation, which are only an approximation of fish abundance, could be explained by a change in fishing effort (Figure 1 (b)), but sudden changes, such as the LPUE shift observed, emphasize the fact that the fluctuations can also be due to variation in the availability of the species to the fishing gear due to environmental conditions, thus leading to low productivity (Cushing 1995; Van Beveren et al. 2016).

Furthermore, when looking at the estimated summer biomass from 2010 to 2013 from scientific acoustic surveys (MEDIAS) in the whole GSA 06, its average was almost three and a half times higher than their respective annual landing estimates (STECF 2015). In these estimates, sardine seems to maintain high biomass regardless of the preceding fishing pressure, and consequently, it seems unlikely that the recent LPUE changes were caused by overexploitation alone. Instead, a combination of overexploitation and an unfavourable environment for the species would better explain these trend changes. On the other hand, the likely increase in the catchability of modern purse seiners, as seen with other fleets in Europe (García-Carreras et al. 2015), may contribute to the problem of decreasing abundance of sardine due to excessive fishing mortality.

The aim of this study was to test the environmental drivers that best explained the variation of sardine LPUE, and to do so we used GAM and GAMM, which are useful tools to describe relationships between biological and environmental variables (e.g. Bellido et al. 2008; Martín et al. 2008; Giannoulaki et al. 2011; Carpi et al. 2015).

In our study, in the final GAMM obtained, the drivers that better explain the LPUE dynamic are WeMOI, SSS and MC. The influences of the WeMOI on fish populations were indirect, with its effects mediated through relationships with local environmental factors (Martín et al. 2012). In fact, during the positive WeMOI, which positively affected LPUEs, the low pressures in the Gulf of Genoa and the high pressure over the Azores (Martin-Vide & Lopez-Bustins 2006) led to two phenomena: one, the prevailing winds affecting the study region came from the northwest (García-Sellés et al. 2010) and two, an augment of the river's discharge rate volume due to an increase in rainfall in the head of the Ebro drainage basin in north Spain (Martín et al. 2012).

When north westerly winds and river discharge are simultaneously propitious, wind pushes the continental and more productive waters across the shelf and causes these waters to be mixed and trapped in the mesoscale eddy structure, which takes form offshore of the Ebro mouth (Font 1990; Xing & Davies 2002; Salat et al. 2002). Furthermore, wind stress allows a rise in the mixing and increases the turbulence in the surroundings of the river mouth, widening the mixing area and thus reducing the salinity gradient (Sierra et al. 2002). The resulting waters become more productive and have salinity values more typical of the shelf-water (ca. 38), which was observed in our results and are positively related with LPUEs.

These favourable, high nutrient conditions enhance phyto- and zooplankton production (Salat 1996; Salat et al. 2002; Lloret et al. 2004) and allow the sardine population to increase in abundance and consequently yield high LPUE (Agostini & Bakun 2002; Lloret et al. 2004; Sabatés et al. 2007; Palomera et al. 2007). Our findings are congruent with those of other studies in the Mediterranean Sea (Lloret et al. 2004; Ganias 2009; Martín et al. 2012) as well as in other areas and for other species of sardine (e.g. Pacific sardine in

Emmett et al. 2005), where the positive relationships between sardine and primary and secondary production, the latter being enhanced by wind and continental water inputs, are described.

The negative values of the WeMOI, which are characterized by an onshore wind flowing from the South (S) and Southeast (SSE), lead to warmer conditions and enhance rain events in the area (Martin-Vide & Lopez-Bustins 2006) and do not allow the discharge water of the river to extend offshore (Xing & Davies 2002); instead, it remains confined to the north and northwest of the Ebro mouth (Mestres et al 2003), probably decreasing primary production. These conditions negatively affect sardine LPUE. Negative relationships are also found with low values of salinity, suggesting that less saline waters or meteorological parameters that lead to a reduction in the salinity of the coastal waters (i.e. rainfall enhanced by WeMOI) are not a suitable environment for this small pelagic fish. As described by Palomera et al. (2007), sardine in early life stages, contrary to anchovy which can be distributed in a wide salinity range and appear to have a lower tolerance to low salinity waters.

Moreover, another environmental variable (i.e. current flowing towards the coast) that contributed to the explanation in the landing per unit effort variability was the meridional current flowing northward, which was positively related with LPUE. This northward current, resulting from the interaction between the cross shelf flow and the topographic structure of the Ebro shelf, which displaces the coastal flow eastward (Lorente et al. 2015), is described as being essential for the generation of the mesoscale anticyclonic eddies along the Catalan coast (Garreau et al. 2011). These structures allow the surface waters and particles to converge in the centre of the anticyclonic circulation, increasing food availability (Bakun 2006) and influencing sardine aggregations.

Overall, with respect to previous studies in the area, our results constitute a step forward by applying a more complex methodology where variation due to the seasonality, non-linear relationships, autocorrelation in the data and collinearity of the environmental covariates were considered and thus provided further evidence of the dependency of sardine LPUEs upon specific hydrographic variables. The study stresses the importance of the additive and non-linear effects on sardine landings production in Catalan Sea via the WeMOI and the local environmental variables (i.e. salinity and northward current). Although LPUEs are only an approximation of the population abundance, they are a function of fishing efforts and stock dimension (Santos et al. 2012); therefore, the environmental influences encountered can also be expected to affect the sardine population in the area.

Sardine landings along the Catalan Coast have been characterized by cyclical fluctuations for the last 40 years (Martín et al. 2012), and the analysed period is part of the long decreasing trend starting from the mid-90s. In the studied area and the whole GSA06, this decreasing trend reached the lowest values of the historical series during the last years of the series. Given the overexploited status of sardine stock and the nonstationary nature of the relationships between the physical factor and the populations' functional response (Schmidt et al. 2014), which may have changed over time, unexpected patterns such as the downfall of cyclic fluctuations may arise and prolong the period of low abundance. The environmental conditions that can be expected in the western Mediterranean Sea, under the current climatic change, is a considerable decrease in rainfall and wind, warmer surface waters and a prolonged stratification period (Calvo et al. 2011). These conditions are in line with the second half (i.e. 2006 and later) of the time series environmental data analysed here. If these trends continue in future decades, a likely scenario of decreased primary productivity and lower sardine fisheries production can be anticipated.

References

Agostini V N, Bakun A. 2002. Ocean triads' in the Mediterranean Sea: physical mechanisms potentially structuring reproductive habitat suitability (with example application to European anchovy, Engraulis encrasicolus). *Fisheries Oceanography* 11:129–42.

Alder J, Campbell B, Karpouzi V, Kaschne, K, Pauly D. 2008. Forage Fish: From Ecosystems to Markets. *Annual Review of Environment and Resources* 33:153–66.

Bakun A. 1996. Patterns in the ocean. California Sea Grant College System. La Paz, Mexico: Centro de Investigaciones Biologicas del Noroeste. 323 pages

Bakun A. 2006. Fronts and eddies as key structures in the habitat of marine fish larvae: opportunity, adaptive response and competitive advantage. *Scientia Marina* 70:105–22.

Barra M, Petitgas P, Bonanno A, Somarakis S, Woillez M, Machias A, et al. 2015. Interannual Changes in Biomass Affect the Spatial Aggregations of Anchovy and Sardine as Evidenced by Geostatistical and Spatial Indicators. *PLoS ONE* 10(8): e0135808. 22 pages.

Bellido J M, Brown A M, Valavanis VD, Giráldez A, Pierce GJ, Iglesias M, Palialexis A. 2008. Identifying essential fish habitat for small pelagic species in Spanish Mediterranean waters. *Hydrobiologia* 612:171–84.

Bergeron J. 2000. Effect of strong winds on the nutritional condition of anchovy (Engraulis encrasicolus L.) larvae in the Bay of Biscay, Northeast Atlantic, as inferred from an early field application of the DNA/C index. *ICES Journal of Marine Science* 57:249–55.

Bonanno A, Zgozi S, Cuttitta A, El Turki A, Di Nieri A, Ghmati H, et al. 2013. Influence of environmental variability on anchovy early life stages (Engraulis encrasicolus) in two different areas of the Central Mediterranean Sea. *Hydrobiologia* 701:273–87.

Bonanno A, Giannoulaki M, Barra M, Basilone G, Machias A, Genovese S, et al. 2014. Habitat Selection Response of Small Pelagic Fish in Different Environments. Two Examples from the Oligotrophic Mediterranean Sea. *PLOS ONE*, 9: e101498. 17 pages.

Borges MF. Santos AMP, Crato N, Mendes H, Mota B. 2003. Sardine regime shifts off Portugal: a time series analysis of catches and wind conditions. *Scientia Marina* 67:235–44.

Calvo E, Simó R, Coma R, Ribes M, Pascual J, Sabatés A, et al. 2011. Effects of climate change on Mediterranean marine ecosystems: the case of the Catalan Sea. *Climate Research* 50:1–29.

Carpi P, Martinelli M, Belardinelli A, Russo A, Arneri E, Coluccelli A, Santojanni A. 2015. Coupling an oceanographic model to a Fishery Observing System through mixed models: the importance of fronts for anchovy in the Adriatic Sea. *Fisheries Oceanography* 24: 521–32.

Checkley D, Alheit J, Oozeki Y, Roy C. 2009. Climate change and small pelagic fish. Cambridge: *Cambridge University Press*. 392 pages.

Cleveland RB, Cleveland WS, and Terpenning, I 1990. STL: A seasonal-trend decomposition procedure based on loess. *Journal of Official Statistics*, 6: 3.

Coll M, Santojanni A, Palomera I, Tudela S, Arneri E. 2007. An ecological model of the Northern and Central Adriatic Sea: Analysis of ecosystem structure and fishing impacts. *Journal of Marine Systems* 67:119–54.

Crawley, M. J. 2007. The R book. Hoboken. NJ: Wiley.

Cury P. 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in ‘wasp-waist’ ecosystems. *ICES Journal of Marine Science* 57:603–18.

Cushing D. 1995. Population production and regulation in the sea: A fisheries perspective. Cambridge: Cambridge University Press. 368 pages

Emmett RL, Brodeur RD, Miller TW, Pool SS, Bentley PJ, Krutzikowsky GK, McCrae J. 2005. Pacific sardine (Sardinops sagax) abundance, distribution, and ecological relationships in the Pacific Northwest. California Cooperative Oceanic Fisheries Investigations Report 46: 122-43.

Espino M, Arcilla AS-, Garcıa MA. 1998. Wind-induced mesoscale circulation off the Ebro delta, NW Mediterranean: a numerical study. *Journal of Marine Systems* 16:235–51.

Font J. 1990. A comparison of seasonal winds with currents on the continental slope of the Catalan Sea (northwestern Mediterranean). *Journal of Geophysical Research*: Oceans 95:1537–45.

Fréon P, Cury P, Shannon L, Roy C. 2005. Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: a review. *Bulletin of Marine Science* 76:385–462.

Ganias K. 2009. Linking sardine spawning dynamics to environmental variability. *Estuarine, Coastal and Shelf Science* 84:402–8.

Garcia A, Cortes D, Ramírez T, Guisande C, Quintanilla J, Alemany F, et al. 2006. Field comparison of sardine post-flexion larval growth and biochemical composition from three sites in the W Mediterranean (Ebro river coast, bays of Almería and Málaga). *Scientia Marina* 70:79–91.

García-Carreras B, Dolder P, Engelhard GH, Lynam CP, Bayliss-Brown GA., and Mackinson S. 2015. Recent experience with effort management in Europe: Implications for mixed fisheries. *Fisheries Research*, 169: 52–59.

García-Sellés C, Peña JC, Martí G, Oller P, and Martínez P. 2010. WeMOI and NAOi influence on major avalanche activity in the Eastern Pyrenees. *Cold Regions Science and Technology*, 64: 137–145.

Garreau P, Garnier V, Schaeffer A. 2011. Eddy resolving modelling of the Gulf of Lions and Catalan Sea. Ocean Dynamics 61:991–1003.

GFCM 2015. Report of the Working Group on Stock Assessment of Small Pelagic species (WGSASP). Scientific Advisory Committee on Fisheries. Rome: General Fisheries Commission for the Mediterranean, FAO. 82 pages.

Giannoulaki M, Machias A, Somarakis S, Tsimenides N. 2005. The spatial distribution of anchovy and sardine in the northern Aegean Sea in relation to hydrographic regimes. *Belgian Journal of Zoology* 135:151-6.

Giannoulaki M, Pyrounaki MM, Liorzou B, Leonori I, Valavanis VD, Tsagarakis K, et al. 2011. Habitat suitability modelling for sardine juveniles (Sardina pilchardus) in the Mediterranean Sea. *Fisheries Oceanography* 20:367–82.

Gjevik B, Moe H, Ommundsen A. 2002. Idealized model simulations of barotropic flow on the Catalan shelf. *Continental Shelf Research* 22:173–98.

Guisan A, Edwards Jr TC, Hastie T. 2002. Generalized linear and generalized additive models in studies of species distributions: setting the scene. *Ecological Modelling* 157:89–100.

Guisande C, Cabanas JM, Vergara AR, Riveiro I. 2001. Effect of climate on recruitment success of Atlantic Iberian sardine Sardina pilchardus. *Marine Ecology Progress Series* 223:243–50.

Guisande C, Vergara AR, Riveiro I, Cabanas JM. 2004. Climate change and abundance of the Atlantic-Iberian sardine (Sardina pilchardus). *Fisheries Oceanography* 13:91–101.

Hastie TJ., Tibshirani, RJ. 1990. Generalized Additive Models. CRC Press. 356 pp.

Lleonart J, Maynou F. 2003. Fish stock assessments in the Mediterranean: state of the art. *Scientia Marina* 67:37–49.

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

Lloret J, Palomera I, Salat J, Solé I. 2004. Impact of freshwater input and wind on landings of anchovy (Engraulis encrasicolus) and sardine (Sardina pilchardus) in shelf waters surrounding the Ebre (Ebro) River delta (north-western Mediterranean). *Fisheries Oceanography* 13:102–10.

Lorente P, Piedracoba S, Soto-Navarro J, Alvarez-Fanjul E. 2015. Evaluating the surface circulation in the Ebro delta (northeastern Spain) with quality-controlled high-frequency radar measurements. *Ocean Science* 11:921–35.

Martín P, Bahamon N, Sabatés A, Maynou F, SánchezP, Demestre M. 2008. European anchovy (Engraulis encrasicolus) landings and environmental conditions on the Catalan Coast (NW Mediterranean) during 2000–2005. *Hydrobiologia* 612:185–99.

Martín P, Sabatés A, Lloret J, Martin-Vide J. 2012. Climate modulation of fish populations: the role of the Western Mediterranean Oscillation (WeMO) in sardine (Sardina pilchardus) and anchovy (Engraulis encrasicolus) production in the north-western Mediterranean. *Climatic Change* 110:925–39.

Martin-Vide J, Lopez-Bustins J-A. 2006. The Western Mediterranean Oscillation and rainfall in the Iberian Peninsula. *International Journal of Climatology* 26:1455–75.

Maynou F, Sabatés A, Salat J. 2014. Clues from the recent past to assess recruitment of Mediterranean small pelagic fishes under sea warming scenarios. *Climatic Change* 126:175–88.

Mestres M, Sierra JP, Sánchez-Arcilla A, del Río JG, Wolf T, Rodríguez A, and Ouillon S. 2003. Modelling of the Ebro River plume. Validation with field observations. *Scientia Marina*, 67: 379–391.

Millot C. 1999. Circulation in the Western Mediterranean Sea. Journal of Marine Systems 20:423–42.

Olivar MP, Salat J, Palomera I. 2001. Comparative study of spatial distribution patterns of the early stages of anchovy and pilchard in the NW Mediterranean Sea. *Marine Ecology Progress Series* 217:111–20.

Olivar MP, Catalán IA, Emelianov M, Fernández de Puelles,ML. 2003. Early stages of Sardina pilchardus and environmental anomalies in the Northwestern Mediterranean. *Estuarine, Coastal and Shelf Science* 56:609–19.

Palomera I. 1992. Spawning of anchovy Engraulis encrasicolus in the Northwestern Mediterranean relative to. *Marine Ecology Progress Series* 79:215–23.

Palomera I, Olivar MP, Salat J, Sabatés A, Coll M, García A, Morales-Nin B. 2007a. Small pelagic fish in the NW Mediterranean Sea: An ecological review. *Progress in Oceanography* 74:377–96.

Palomera I, Olivar MP, Salat J, Sabatés A, Coll M, García A, Morales-Nin B. 2007b. Small pelagic fish in the NW Mediterranean Sea: An ecological review. *Progress in Oceanography* 74:377–96.

Patti B, Bonanno A, Basilone G, Goncharov S, Mazzola S, Buscaino G. et al. 2004. Interannual fluctuations in acoustic biomass estimates and in landings of small pelagic fish populations in relation to hydrology in the Strait of Sicily. *Chemistry and Ecology* 20:365–75.

Pinheiro JC, Bates DM. 2000. Linear mixed-effects models: basic concepts and examples. *Mixed-effects models in S and S-Plus*: 3–56.

Sabatés A, Olivar MP, Salat J, Palomera I, Alemany F. 2007. Physical and biological processes controlling the distribution of fish larvae in the NW Mediterranean. *Progress in Oceanography* 74:355–76.

Salat J. 1996. Review of hydrographic environmental factors that may influence anchovy habitats in northwestern Mediterranean. *Scientia Marina* 60:21–32.

Salat J, Garcia MA, Cruzado A, Palanques A, Arín L, Gomis, et al. 2002. Seasonal changes of water mass structure and shelf slope exchanges at the Ebro Shelf (NW Mediterranean). *Continental Shelf Research* 22:327–48.

Santos MB, Gonzalez-Quiros R, Riveiro I, Cabanas JM, Porteiro C, Pierce GJ. 2012. Cycles, trends, and residual variation in the Iberian sardine (Sardina pilchardus) recruitment series and their relationship with the environment. *ICES Journal of Marine Science* 69:739–50.

Schmidt A, Botsford L, Eadie J, Bradley R, Di Lorenzo E, Jahncke J. 2014. Non-stationary seabird responses reveal shifting ENSO dynamics in the northeast Pacific. *Marine Ecology Progress Series* 499:249–58.

Sierra JP, Sánchez-Arcilla A, Del Río JG, Flos,J, Movellán E, Mösso C, et al. 2002. Spatial distribution of nutrients in the Ebro estuary and plume. *Continental Shelf Research* 22:361–78.

STECF 2015. Mediterranean assessments, Part 2 (STECF-15-06). Scientfic, Technical and Economic Committee for Fisheries (STCEF). JRC Scientific and Policy Reports. Luxembourg: Publications Office of the European Union, , EUR 27221 EN, JRC 95822, 396 pages.

Stergiou KI, Somarakis S, Triantafyllou G, Tsiaras KP, Giannoulaki M, Petihakis G, et al. 2016. Trends in productivity and biomass yields in the Mediterranean Sea Large Marine Ecosystem during climate change. *Environmental Development* 17: (Supplement 1)57–74.

Tugores M, Giannoulaki M, Iglesias M, Bonanno A, Tičina V, Leonori I, et al. 2011. Habitat suitability modelling for sardine Sardina pilchardus in a highly diverse ecosystem: the Mediterranean Sea. *Marine Ecology Progress Series* 443:181–205.

Tugores MP, Iglesias M, Díaz N, Oñate D, Miquel J, Giráldez A. 2010. Latitudinal and interannual distribution of the European anchovy (Engraulis encrasicolus) and sardine (Sardina pilchardus) in the western Mediterranean, and sampling uncertainty in abundance estimates. *ICES Journal of Marine Science* 67:1574-86.

Van Beveren E, Fromentin J-M, Rouyer T, Bonhommeau S, Brosset P, Saraux C. 2016. The fisheries history of small pelagics in the Northern Mediterranean. ICES Journal of Marine Science 73(6):1474-84.

Vasilakopoulos P, Maravelias CD, Tserpes G. 2014. The Alarming Decline of Mediterranean Fish Stocks. *Current Biology* 24:1643–8.

Wood SN. 2006. Generalized Additive Models: An Introduction with R. Boca Raton, Florida: Chapman and Hall/CRC Press. 410 pages.

Xing J, Davies AM. 2002. Influence of topographic features and along shelf flow upon the Ebro plume. *Continental Shelf Research* 22:199–227.

Zuur AF, Ieno EN, Smith GM. 2007. Analysing Ecological Data. New York: Springer. 648 pages.

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith G. 2009. Mixed Effects Models and Extensions in Ecology with R. New York: Springer. 574 pages.

Chapter 4

Environmental influence on commercial fishery landings of small pelagic fishes in Catalan Sea (NW Mediterranean Sea) and its time variability.

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Abstract

We investigated environmental effects on a population of anchovy and sardine in three fishing areas of the waters off the Catalan Coast (NW Mediterranean Sea), based on a long series of monthly landings from 1973 to 2014). Different statistical analyses were used, including Artificial Neural Networks to fill in missing data in the series, breakpoint analysis to identify co-occurrent temporal shifts, eigen vector filtering to identify the main patterns of the series, generalized linear least square (GLS) regression to identify the relationships with environmental variables and finally, the rolling regression approach to examine temporal changes in these relationships across years. Specifically, we examined the effects of temperature (SST) and salinity (SSS) which are important in determining suitable habitat for the eggs and larval development and survival. Additionally, we examined the effect of kinetic energy (KE), which may influence the recruitment of these species by controlling the trophic environment at the spawning areas and finally, the effects of the sea surface height (SSH), which is indicative of changes of the mesoscale circulation patterns. All the environmental variables were seasonally adjusted and introduced in GLS model formulations after hysteresis in order to identify the critical period of development at which they affected the both populations. SSH and SST represented the most important and recurrent variables affecting the early life stages of both species in the three fishing areas. SST affected the early life stages of both species negatively in each area. Increasing SSH affected negatively sardine in the three zones and anchovy only in the southernmost two. Several previous studies have emphasized the importance of these factors during the critical stages of development of small pelagic fishes. Herein we showed by rolling regressions that the strength of such relationships was transient and non- stationary over time. These time-varying relationships may be due to the coupled effects of the environmental changes and the recent variations in demographic patterns of the two populations which as consequence could have altered the responses to changing environmental conditions.

Introduction

The global distribution of small pelagic fishes, their high biomass at the mid-trophic level of the food webs and the role they play as a link between lower and higher trophic levels make them an essential part in most ecosystems (Cury, 2000; Fréon et al., 2005; Palomera et al., 2007). Small pelagic fishes, which form large dense schools making them easy to catch in large numbers, are targeted species for both artisanal and industrial fishery, and constitute about half of the world's annual fish harvest (Fréon et al., 2005).

Short life span, fast growth, early maturity onset and direct dependence on plankton characterize these species (e.g. Palomera et al., 2007). These features make their populations particularly sensitive to the environment. Since their abundance, is highly dependent on the annual successful recruitment that in turns is extremely susceptible to shifts in physical and biological processes influencing the survival of the early life stages (Bakun, 1996; Cole and McGlade, 1998). Tolerance range of the early life history stages, such as eggs and larvae, is narrower than the tolerance range of juveniles or adults (Pörtner and Peck, 2010) making the former more susceptible to environmental changes. The effects of the environmental fluctuation together with the high exploitation of these species cause small pelagic fish populations to vary widely in abundance and biomass (Checkley et al., 2009). These fluctuations can have substantial consequences for both fishery and ecosystem structure and functioning (e.g. Cury, 2000; Shannon et al., 2000).

In the North-Western Mediterranean Sea, sardine (Sardina philchardus) and anchovy (Engraulis encrasicolus) dominate both the small pelagic fish community and purse seine fishery (Lleonart and Maynou, 2003; Palomera et al., 2007). For both species, the catches in North-eastern Spain (geographical subarea 06, GSA06) during the period 1990-2014, in which on average they were 28000 t and 12000 t for sardine and anchovy respectively, suffered a decrease. After 1994 the trend in landings for both species are consistent with the acoustic biomass estimates, available since the year 1990 (GFCM, 2015). Sardine reached the lowest values of both catches and biomass during the year 2014, while for anchovy, these values have been slightly increasing since 2008 (GFCM, 2015).

In the Catalan Sea, the purse seine fishery is concentrated mostly between Cape Creus and the Ebro river delta (Agostini and Bakun 2002). The reproductive season of these two small pelagic fishes spans opposite periods of the year: autumn-winter and spring-summer, for sardine and anchovy respectively (Palomera et al., 2007). Both species are well adapted to the productivity mechanisms characteristic of their respective spawning seasons, i.e. vertical mixing in winter and spreading of continental runoff at the surface in spring–summer (Sabatés et al., 2007). The minimum landing size of these species is 11 cm and 9 cm for sardine and anchovy respectively (Regulation (EC) No 1967/2006). These conservation sizes are smaller than the average size at first maturity (11.4 cm and 10.8 cm) (GFCM, 2014), which is achieved by both species at one year of age (age at first maturity, GFCM, 2014).

Landings data from the area, standardized or not for fishing effort, have been used to link the fluctuations of small pelagic populations abundance to the surrounding environmental variability (e.g. Lloret et al., 2004; Martín et al., 2008, 2012). These studies singled out the importance of the riverine outputs, the surface chlorophyll and wind mixing on the early life stages of anchovy and sardine, and therefore on recruitment variation. These factors contribute to the enrichment process which, together with concentration and retention, constitute the three key processes that favour reproductive success in small pelagic fish (ocean triads theory; Bakun, 1996).

However, these outcomes were based on the assumption that the response of the populations to the environmental conditions is time-invariant, probably due to the use of relatively short monthly time series. It has been recognized that marine systems can undergo very rapid shift (e.g. Blenckner and Niiranen, 2013), passing from a certain level relatively stable denoted as ‘regime’ to another called ‘regime shift’. This non-stationarity in the environment can cause in turns non- stationarity in population processes (e.g shift in reproductive success, mortality, growth; Szuwalski and Hollowed, 2016) as consequence of the strong links between them. Szuwalski et al., 2015, for example demonstrated that changes in recruitment over time of different fish stocks shifted in coincidence with shifts of environmental conditions. These events being unpredictable could produce as a consequence unexpected responses of the populations in question which in turns result in unexpected results in modelling prospective (Planque, 2016).

Thus, the relationships between populations and environmental signals can change over time (Schmidt et al., 2014) becoming stronger or weaker, in a way that may be better appreciated when looking at a wider temporal scale**.**

However, the small pelagic population is not only shaped by environmental factors. Fishing of these species in NW Mediterranean Sea as well as in the whole basin has existed since ancient time. As discussed in different studies (e.g. Hsieh et al., 2010; Planque et al., 2010; Hidalgo et al., 2011), fishing effects don’t consist simply in the removal of biomass. It can also affect the population dynamics by truncating the age and the size structure of the exploited population since it has been historically directed at large and old individuals, or by reducing intraspecific diversity, or by selecting particular life history strategies (e.g. early maturation) (e.g. Planque et al., 2010; Hidalgo et al., 2011). These changes create populations more sensitive to climate variability for reasons that include the following: the loss of long-lived individuals, the reduction of the number of cohorts which helps the population survive during periods of adverse conditions, and the increase of the coupling between climate fluctuation and recruitment variations (Fromentin and Fonteneau, 2001; Planque et al., 2010).

A general decreasing trend of the body size and body condition of both anchovy and sardine has been reported in the NW Mediterranean sea and in other parts of the basin (Brosset et al., 2017). Considering these changes together with the long-term variation of the environment in the area, constituted by the increase in temperature and salinity in the upper layer (Vargas-Yáñez et al., 2010), the way in which the small pelagic populations are related or respond to the environmental forces may have changed over time. The capacity of these populations to buffer the changing environment might have been altered, for example, by the reduction of their reproductive potential and the time span at which the spawning season occurs due to the lack of large individuals, leading to a diminished probability of encounter the optimal environmental window by eggs and larvae. Furthermore, this situation might have been aggravated due to the intensification of the adverse conditions owing to the environmental changes (Planque et al., 2010; Hidalgo et al., 2011).

Herein we attempt to investigate environmental effects on variation in anchovy and sardine population size using fisheries monthly landing data from the year 1973 to 2014 in the north-western Mediterranean Sea. The purposes are to examine the long-term trend and the variability of the anchovy and sardine population in the Catalan sea in response to the local environmental changes. Specifically, we examined the effects of temperature and salinity which have been proposed to be important in determining suitable habitat for the egg and larval development and survival (e.g. Palomera et al., 2007; Giannoulaki et al., 2011, 2013). We also studied the effect of kinetic energy, which may influence the recruitment of these species because of its hydrodynamic control over the trophic environment at the spawning areas (e.g. Ruiz et al., 2013; Bonanno et al., 2014; Carpi et al., 2015). Finally, we analysed the effects of the sea surface height, which has been suggested as a factor indicative of changes of the mesoscale circulation patterns and the presence of moderate convergence and divergence conditions (e.g. Tugores et al., 2011; Giannoulaki et al., 2013).

Material and Methods

General characteristics of the Study Area

The study area is located in the Catalan Sea, NW Mediterranean (Fig. 1). The area is characterized by a permanent shelf-slope density front, separating open-sea high-salinity waters from low-salinity continental shelf waters, and a geostrophic Northern Current which flows southwestwards roughly parallel to the coast with an overall transport of around 1 Sv (Castellón et al. 1990). The NW Mediterranean coast receives significant freshwater runoff from two major rivers, the Rhône and the Ebro. The Rhône discharges at the east of the Gulf of Lions and enhances the shelf-slope front by lowering the salinity of shelf waters. The Ebro, with lower runoff, also decreases the salinity of the waters on the relatively wide shelf near its mouth at the southern limit of the area. The water column structure shows a marked seasonal cycle, well mixed in winter and strongly stratified in summer, during the anchovy spawning season, when primary production is limited to a deep chlorophyll maximum (DCM), a thin layer at the deepest levels of the photic zone, ca. 60 m depth (Estrada et al. 1985). Another contribution to local productivity results from freshwater river runoff, which can enrich coastal waters near major river mouths. Summer productivity conditions are highly dependent on interannual variability in temperature and salinity, which in turn depends on the heat balance of air-sea exchanges in the region and fresh water runoff, which are variable from one year to the next. The environmental characteristics and the daily displacement of the fishery operation were used to define three sectors in the study area, Northern, Central and Southern, according to Martín et al. (2008) (Fig. 1). These sectors were limited by the 35 m and 200 m isobaths, which represent the longitudinal expansion where the anchovy fishery is carried out.

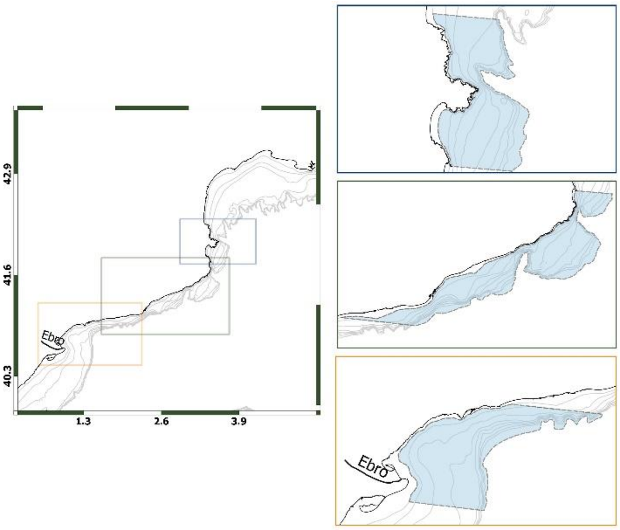

Figure 1. The study area divided and three fishing zones (Southern, Central and Northern) limited by the 35 m and 200 m isobaths.

Landings data

Monthly data of landings (kg) of anchovy and sardine for purse seine vessels were obtained from a total of 18 ports off the Catalan coast. The landing series data obtained were from the years 1973 to 2014 in the southern and central sector, while for the northern sector the first data available were from 1988 and from 1993, for sardine and anchovy respectively. Landings data, which are consistent with the results of the acoustic assessment (GFCM 2015) of both species, were used as estimates of abundance. Data were aggregated without any more subdivisions because the main physical features could be considered similar in each sector (Martín et al., 2008) and because the fishing range of the vessels was local due to daily obligatory return to port of the fleet (Martín et al. 2012). Landings for the years 1990 to 1992 were missing because of the change in the administrative data system and had to be reconstructed. Furthermore, starting from the year 2000, the data corresponding to the months December or January were missing due to the annual closure of the purse seine fishery. These gaps were filled by using the best Artificial Neural network obtained in terms of prediction performance for the former (1990-1992) missing data, and by using linear interpolation for the latter (December/January) missing data (see further in statistical analysis section).

Seasonality

Landings of both species showed strong seasonality (Fig.2). Generally, there was a major peak in all sectors at the end of the spring and in summer for anchovy, while for sardine, the major catch percentage were from mid-spring to mid fall (Fig. 2). Throughout this study, the winter season is defined as January to March, spring season from April to June, summer season from July to September and fall season from October to December, consistent with the conventional calendar seasons.

In the area, anchovy spawns during spring and summer and during fall the juveniles occupy the upper layer until the winter when they recruit at the adult population (Fig 3a). Contrarily, larvae and eggs of sardine occupy the upper layer from late fall to the late winter early spring, during summer the large percentage of the population belong to the juvenile's fraction and at the end of summer and the beginning of the fall sardine can be considered fully recruited (Fig 3b).

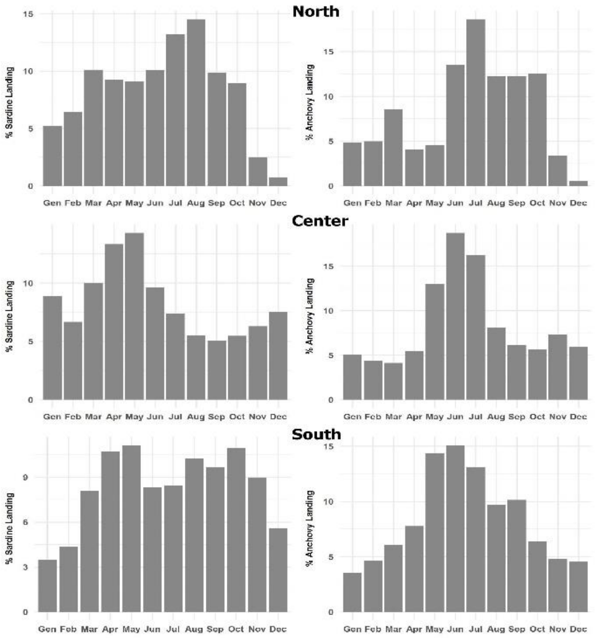

Figure 2. Monthly percentage of sardine and anchovy landings in the three sectors during the whole period. North: From 1988 and from 1993 to 2014 for sardine and anchovy respectively. Central and southern sectors: from the year 1973 to 2014 for both species.

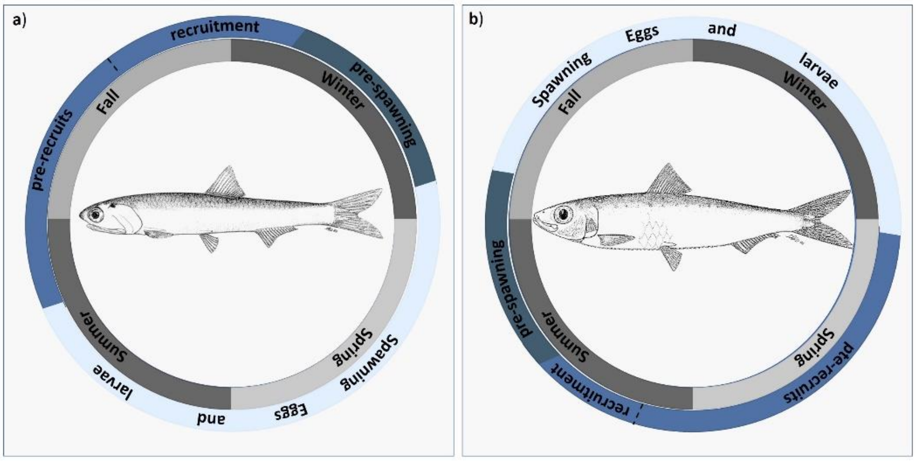

Figure 3. Life cycle scheme of respectively a) *Engraulis encrasicolus* b) *Sardina philchardus*

Environmental data

Remote sensing data series were used for modelling the catches of sardine and anchovy in respect to the environmental conditions. Specifically, the monthly sea surface temperature (SST), salinity (SSS), sea surface height (SSH) and horizontal (u) end meridional (v) current velocity components from the years 1974 to 2014 were obtained from the COPERNICUS Marine Environment Monitoring Service (http://marine.copernicus.eu/), with a spatial resolution of 1/16° x 1/16° (5.2 x 7.0 km, approximately). The last two were used to calculate the kinetic energy (KE) as follows:

$$Ke = (u^2 + v^2)/2$$

where u and v are the velocity components (Ruiz et al., 2013).

These variables were considered important either as direct influence, in terms of physiological suitability of the habitat, on the abundance and on different life stages of small pelagic fishes (e.g. SST, SSS and KE; e.g. Giannoulaki et al., 2011, 2013; Ruiz et al., 2013; e.g. Maynou et al., 2014), or as a proxy of factors enhancing the productivity and favouring the retention of early life stages such as gyres and eddies (SSH; e.g. Tugores et al., 2011; Giannoulaki et al., 2013). All the environmental variables were seasonally averaged by sectors following the conventional year division described above. Summarizing the environmental variables in seasons allowed us to describe and assess the effects of the average conditions of the environment during the main events of the annual cycle of both species (e.g. pre-spawning, spawning and adult feeding shoals, planktonic stages of eggs and larvae, recruitment). This can reflect on the monthly landings series, which in general are mainly composed of adult individuals of one year for anchovy and between one and two years for sardine (Lloret et al., 2004; Martín et al., 2008).

Statistical analysis

Missing data imputation of landing series

Since we were interested in analysing the relationships between catch series and environmental variables, and also because the selected statistical methodology requires contiguity in the data series, the missing values were estimated by using the artificial neural network (ANN) and linear interpolation. The ANNs were used to forecast missing values from 1990 to 1992 for both anchovy and sardine landing series in the central and southern sectors. ANNs are forecasting methods which can be used in time series analysis to predict future observations by using some function of past observations (Faraway and Chatfield, 1998). In general it is an information processing system composed of nonlinear interconnected elements or neurons and it is organized as layers connected via weights (Wang et al., 2009). A common ANN generally consist of three layers. The input layer, in which the data are introduced to the network, the hidden layer or layers, which correspond to the processing part of the network, and the output layer where the results are produced. Throughout the study, the ANN named multi-layer feed forward back propagation network (Haykin, 1994) with only one hidden layer was used. In time series the value at time yt (output) is to be forecasted using the values at lags y_{t-1}, y_{t-2} … y_{t-n} (input). Each of these inputs is connected to the hidden neurons (nodes) which in turn are connected to the outputs. The inputs to each node are combined using a weighted linear combination which is then transformed by mean of a non -linear function (activation function, typically a logistic function) in the nodes of the hidden layer. These neuron values undergo a similar operation to obtain the prediction outputs, although in this case a linear function is applied, which implies the identity activation function at the output stage (Faraway and Chatfield, 1998).

The estimates of the weights between the inputs and the hidden neurons and between the neurons and the outputs were selected in the NN framework using an algorithm that minimizes the sum of square of the within sample one step ahead forecast errors over the part of the monthly series selected as training set (Faraway and Chatfield, 1998). Specifically, for both the central and the southern sector of the anchovy and sardine series, the training sets used were from the years 1973 to 1987, keeping the last two years i.e. 1988 and 1989 as the test set. The general process can be written as:

$$y_t = \phi_0 \{\beta_k + \textstyle\sum_j \; w_{jk}\phi_h \left(\beta_j + \textstyle\sum_l \; w_{lj} y_{t-li} \right)\}$$

where y_{t-li} are the input signals (lags of the series), y_t are the output signals, w_{lj} are the weights between the input neuron *i* to hidden neuron *j*, and w_{jk} are the weights between the hidden neuron j and the output neuron k. β_k and $\beta_j$are the bias which behave like the intercepts in the regression, and ϕ_0 and ϕ_h are the activation function for the hidden and the output layers. The network is 'trained' in order to find a series of weight that yield an output signal that has a small error relative to training sets, and it is performed by using the back-propagation training procedure. In practice this procedure adjusts the weights starting from the output layer and ending with the input layer in a looping pattern (Chen and Ware, 1999). Since the objective of our analysis was imputing the three years missing values, we were not interested in fitting the best NN on the training set but instead in fitting NN models to obtain the best forecasts of the test set data. Consequently, we chose the best model based on the forecast accuracy and in particular on the minimization of the root mean square errors between the forecast estimates and the test set observations. To do so we compared different feed forward NN models prediction accuracy using different input (lagged) variables and different architecture. Specifically, we considered different NN models composed by inputs lagged values p of the time series up to the last 12 observations (y_{t-1}, y_{t-2} … y_{t-12}) and inputs lagged seasonal values P up to the last 3 seasonal observations (since our series were seasonal monthly data), and the number of nodes in the hidden layer varying from 2 up to 6. For each structure, a total number of 1000 networks were trained and their prediction averaged.

Missing values during the winter season (in December or January) due to the annual fishing closure starting from the year 2000 of the anchovy and sardine series in the three sectors were instead imputed by using linear interpolation. A periodic seasonal trend decomposition procedure based on loess (Cleveland et al., 1990) was first fitted onto the data to remove the seasonal component from the series. On the remaining component a linear interpolation was performed to impute the values and subsequently, to obtain the complete series, the seasonal components were again added (Hyndman et al., 2014; Moritz et al., 2015).

Time series main pattern and Seasonal adjustment

Time series are, in general, considered as a set of three components: the slow varying trend, the oscillatory or seasonal component, and the white noise. In order to describe the main pattern of both landings and environmental variables (i.e. identify what of the components above mainly characterize the 'shape' of the series) the Eigen vector filtering (EVF, Colebrook, 1978) was performed for each standardized time series (i.e. landings monthly series and environmental quarterly series, of which the KE log transformed). The EVF method is identical to the Principal component analysis (PCA), in which the components are calculated on the autocovariance matrix, which is constructed based on the original series plus several copies of it lagged by one-unit time (Colebrook, 1978; Ibanez and Etienne, 1992). The choice of the number of the lagged series to construct the matrix was based on the observation of the autocorrelation function and by selecting this number equals to the lags just less than the shortest significant cycle (see Ibanez and Dauvin, 1988 for details). The variance explained by the main temporal pattern, this being the first axis of the PCA, may be calculated, giving us the possibility to quantify its importance (Van Beveren et al., 2016).

Subsequently all series were seasonally adjusted in order to avoid spurious relationships (i.e. obtain apparently significant relationships from unrelated variables), as the aim was to relate the origin of the trend in the landing series in relation to the local environmental factors. The seasonal adjustment method employed was the follow:

$$y_{ts} = y_t - \mu_s$$

Where y_{ts} was the seasonal adjusted series, y_t the observation value of a particular month (for the landing series) or season (for the local environmental factors) in the year, μ_s the mean of the monthly/season values. These resultant series, composed by the trend – residuals component were used for the subsequent analysis.

Breakpoints and relationships with the environment

Since environmental and landing series were analyzed together, the time series characteristics like patterns and sudden shifts could be identified and compared. The existence of synchronous temporal changes, in fact, could indicate if the local environmental forces have been influencing the small pelagic landings.

For all the seasonal adjusted environmental variables and landing series in each sector, a breakpoints analysis was computed using the 'strucchange package' (Zeileis et al., 2003) to assess the period(s) and the 95% confidence interval of significant changes, which were then checked for their synchrony.

The breakpoints procedure detects a structural change in regression relationships (Zeileis et al., 2003) by searching a break where the regression coefficients shift from one stable regression relationship to a different one. It works in two steps. First, the ordinary-least-squares moving sum (MOSUM) test, which uses the residuals of a series of regressions to determine if the coefficients are stable or varying over time, is used to test for the existence of breakpoints in the time series. Second, if significant structural changes are identified, different breakpoints are then iteratively tested. The optimal number of segments (breakpoints + 1) and the optimal position of a breakpoint are estimated by minimizing the Bayesian Information Criterion (BIC) and by minimizing the residual sum of squares of this regression respectively (Bai and Perron, 2003; Zeileis et al., 2003).

In addition, to determine and quantify the possible relationships between the local environmental variables and the landings of both species in each sector, multiple linear regression models were used. In particular, based on the hypothesis that the variability of fishing landings was largely determined by survival during the larval and juvenile stages, we related the seasonal environmental variables with lags up to 6 seasons (corresponding to 18 month) for sardine and up to 4 seasons (12 months) for the anchovy, with landings of both species at the time t.

In standard linear regression, the errors are assumed to be independent and identically distributed, but when dealing with time series regression, it is generally implausible to assume that errors are independent. For this reason, Generalized least squares (GLS) models in the nlme package (Pinheiro and Bates, 2006) were used to relate the landings with the local environment. GLS extends the ordinary least square (OLS) estimation of the normal linear model by providing for possible correlations between different errors and so allowing one to avoid the Type I errors. Since we related current values of the landings (dependent variable) with lagged values (past period at t-1 t-2… and so forth) of the different local environmental variables, which could likely be correlated among them, serious problems of violation of the assumption of independence of predictors could have arisen. To avoid the model producing parameter estimates with highly inflated standard errors, resulting in an overall significant model with no significant predictors, we identified collinear predictors by calculating a Variance inflation factor (VIF). This represents the proportion of variance in one predictor explained by all the other predictors in the model. We calculated a VIF of each predictor and excluded sequentially the predictor with the highest VIF. As suggested by Zuur et al., 2010 the predictors were dropped until all VIF values were below a cutoff of 3. These remaining variables were used to formulate the GLS models.

Final model selection for each sector and species was performed by the top-down strategy suggested by Diggle, 2002 and Zuur et al. 2009. It consists in estimating the model by restricted maximum likelihood estimation (REML) with all the predictor variables and with different errors correlation structures, limited for simplicity up to the third-order autoregressive structure. These models were compared in order to find the optimal correlation structure based on the minimization of the AIC. Once it was found, the best combination of explanatory variables was obtained by fitting the model with the maximum likelihood estimation (ML) and by using the likelihood ratio test to compare nested models obtained by dropping the terms basing on its significance. Finally, the best model was refitted using the REML estimation.

Multivariate rolling regressions

In order to investigate whether the relationships between anchovy and sardine landings with the local environmental variables were persistent over time, we adopted the rolling regression method, a technique used to investigate time-based effects in a specific coefficient (Jank and Shmueli, 2008).

Specifically, the rolling regression technique fits a regression model multiple times by moving forward in a rolling fashion (Brown et al., 1975). The rolling regression procedure consists in the selection of the dimension of the window, i.e. the number of observations on which the regression model has to be fitted, and on the slide this window forward of a determined step size (the increment by which the window is moved each iteration) up to the end of the series. The outcome of this procedure is the production of multiple sets of coefficient estimates. The number of regressions and their resulting sets of coefficients depend on the window size, the number of observations in the dataset, and the step size (Jank and Shmueli, 2008).

In our study we used as regression model the best GLS formulation for each sector and species of above, assuming that the residuals correlation structures found were optimal also for the rolling regressions. Consequently, the significance of the obtained coefficients was used to infer the strength of the association between landings and the local environmental variables. For each sector, the models were fitted on a number of observations selected by predetermining a window size basing on the mean length of the segments obtained with breakpoints analysis, which for the northern, central and southern sector, were of 8, 10 and 10 years respectively. The use of these windows allowed us to evaluate the associations in different periods of stability and not-stability (i.e. the shifts detected with the breakpoints analysis). Then, the window for each sector was slid forward once a year and the fitting procedure was repeated each time. Doing so, we obtained different coefficient estimates and their significance and how they changed over time.

Results

Landing series description and main patterns

The best ANN models, based on the forecast accuracy, were applied to reconstruct the three years of missing values of landing series in the central and southern sectors, which are summarized in Table 1.

Table 1. Neural Network models used to reconstruct the three years (1990-1992) of Anchovy and Sardine landing series. RMSE= Root mean square errors

		Lags - Seasonal Lags	Number of Hidden Neurons	Forecast Accuracy (RMSE)
Central Sector	**Sardine**	1,2 - 12,24	2	133.27
	Anchovy	1,2,3,4,5,6,7,8,9,10 - 12,24,36	2	146.9
Southern Sector	**Sardine**	1,2,3,4,5,6 - 12,24,36	6	376.66
	Anchovy	1,2,3,4 - 12,24	2	219.34

Over the investigated period the Southern area was the most important in terms of quantity of landings of both anchovy and sardine, accounting on average 247 t and 646 t per month respectively. It was followed by the Central sector (219 t for anchovy and 338 t for Sardine) and, lastly, the Northern sector (179 t for anchovy and 152 t for sardine). The maximum reported annual landings of anchovy and sardine were, in order of quantity, 6757.8 t (year 1982) and 13604.7 (year 1994) in the Southern sector, 7364.7 (year 1994) and 10745.8 (year 1994) in the Central sector, and finally 1121.8 (year 1992) and 3661.9 t (year 1988) for the Northern sector. Anchovy landings in the Northern sector, despite having started in 1988, had a pattern similar to that of the Central sector (Fig. 4), with the highest peaks during summer in the 1990s followed by a sharp decrease until ca. the year 2010, after which signs of landing recovery can be observed (Fig 4).

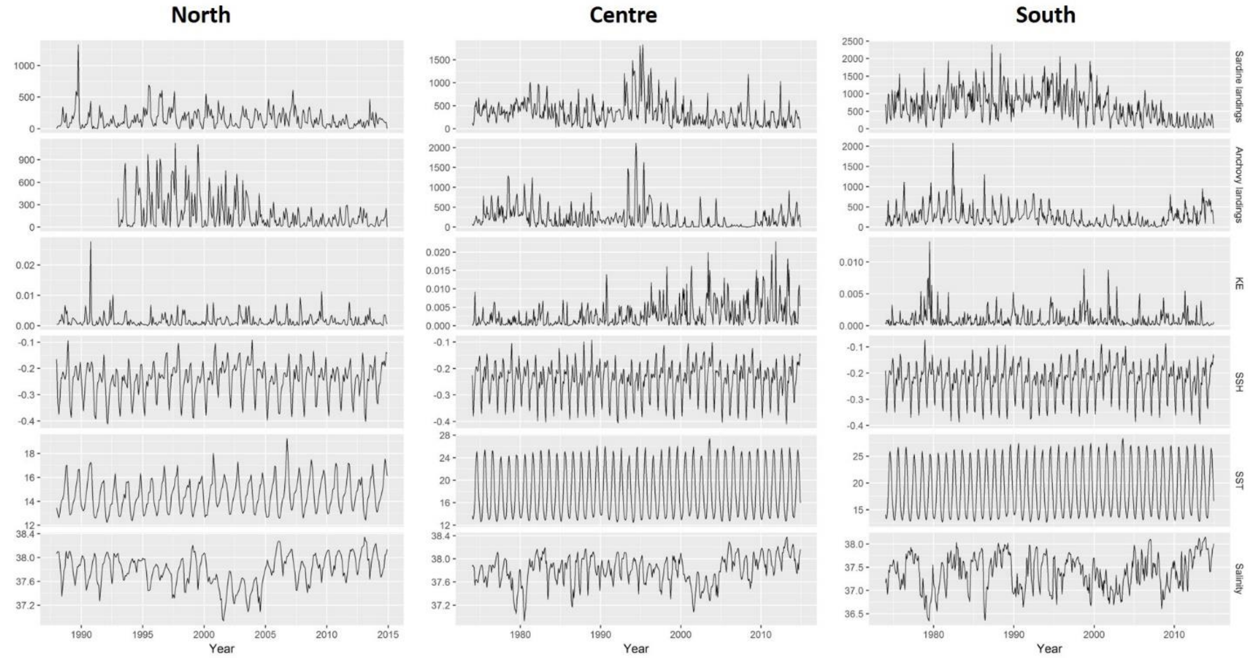

Figure 4. Landing and environmental variables series. Ke= Kinetic energy; SSH= sea surface height (m). SST=sea surface temperature.

The long-term patterns showed an increase during the 90s before stabilizing and the deviances explained were 29.07 % and 21.76 % for the central and the northern sector respectively (Fig. 5). In the southern sector, the decreasing trend started earlier, more precisely from the second half of the 1980s until ca. the year 2008, after which landings started to increase (variance explained 29.45%, Fig. 5). Regarding the landings of sardine, in all sectors, they were characterized by a long-term decreasing trend. The trend decreased more slowly in the Northern sector (deviance explained 23.45%, Fig. 5), while it was more pronounced in the other two sectors, explaining 35.92 % of the variance for the Central area while in the

South it was the 41.53 % Fig. 5. In the Southern area the period preceding the sharper decrease at ca. the year 2000 was characterized by a certain stability at high values Fig. 4, while in the Central sector landings increased rapidly during the 90s but suffered a strong decline in the subsequent years Fig. 4 and Fig. 5. When looking at the seasonally adjusted series (Fig. A1, supplementary material) a significant decreasing trend could be appreciated in all the time series of both sardine and anchovy landings in the whole areas.

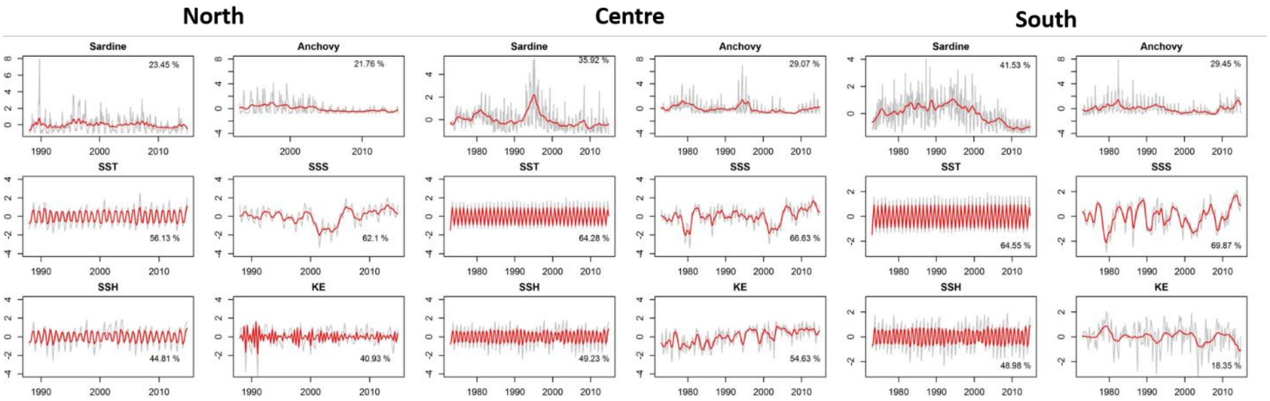

Figure 5. Standardized time series of anchovy and sardine landing. The red line represent the first eigen vector, and the percentage of deviance explained by this is indicated in the upper left corner for landing series and in the bottom left corner for the environmental series. SST= Sea surface temperature; SSS= sea surface salinity; SSH= sea surface height and KE =kinetic energy.

Environmental Series description and main patterns

Fig. 4 shows the monthly environmental series and Fig. A1 (supplementary material) the series averages per season and seasonal adjusted. Kinetic energy showed stable patterns in the Northern and Southern sectors. The North did not show long-term trend and was characterized by random noise pattern (variance explained 40.9 %) while in the south the trend was relatively stable, explaining the 18.35 % of the variance (Fig. 5). In the central sector, KE started to fluctuate more after the second half of the 90s Fig. 3-5 and was characterized by a long-term increasing trend, explaining the 54.6 % of the variance (Fig 5).

SSH was similar in all sectors, showing peaks during the fall season Fig 4 The main pattern explained from approximately 45 % to 50% of the variance from south to north (Fig 5) and all sectors were characterized by strong seasonality (Fig 4; 5). SST showed similar values during the colder months in all three sectors (Fig 4). During summer seasons the lowest values were in the north with the hottest peak reached during the year 2006, while in the other two sectors, which showed similar higher values, the highest peak was reached in the year 2003. For both SSH and SST, seasonality was the main characterizing pattern in the whole study area (Fig 5) explaining 56.3 % ,64.28% and 64.55% of the variance in the Northern, Central and southern sector respectively (Fig 5). SSS showed similar fluctuations across sectors, with the lowest values in the southern sectors (Fig 4). In all three areas, SSS increased during the period studied and was more evident in the last 15 years (Fig 4). The deviance explained by the long trend in the northern sector was 62.1%, Fig 5) and in the central and in the southern explained 66.63% and 69.87 % respectively (Fig 5).

The seasonally adjusted series for both SST and SSS showed a linearly increasing trend in all areas (Fig A1, supplementary material). SSH increased in the northern sector while it did not show a trend in the other two sectors (Fig A1, supplementary material). KE showed a positive long-term trend in the Central sector, contrary to the South where it decreased and to the northernmost area where it didn’t show long-term variation (Fig A1, supplementary material).

Breakpoint analysis

For landing series of both species, the breakpoints analysis detected between one and four significant discontinuities (Fig 6). The last breakpoints regarding the sardine landings were detected in the southern and northern sector between the years 2008 and 2009, consistently leading to low landing values. A co-occurring breakpoint was detected in the central and in the southern sectors between the years 1998 and 2000 (Fig 6). Regarding the anchovy landings, a breakpoint during the second half of the 90s co-occurred in all areas, and one co-occurred in the central and southern areas at ca. the year 2010 (Fig 6). In the Central area two more breakpoints were detected in the early 80s and at ca. the year 1990, consistent with the subsequent sharp increase in landing values which characterized the first half of the nineties (Fig 6).

Regarding the environment, breakpoints were detected in Salinity time series around the year 2000 and the year 2005 in all sectors (Fig 6). In the Centre and in the south around the year 1980, a coinciding breakpoint was identified, and during the period from the second half of the 80s and earlier 90s the only breakpoints detected were in the southern sector. Between ca. the year 2000 and the year 2005 co-occurring breakpoints were detected regarding the SSH in all three sectors (Fig 6) and a coinciding breakpoint was detected in the central and in the northern sector between the year 1990 and 1992. In the Northern sector, no breakpoints were detected on the kinetic energy series, while for both the central and the southern sector two and one discontinuities were identified respectively (Fig 6). Despite being in opposite directions, the last break of the central sector co-occurred with the only break of the southern area around the year 2005.

In all zones, three breakpoints were detected on the SST series (Fig 6). In the central and southern sectors, the last breakpoint coincided around the year 1999 and the second breakpoint of both areas concurred with the first breakpoint of the northern sector around the year 1992 (Fig 6). The last breakpoint in the North was instead detected around the year 2007 (Fig 6).

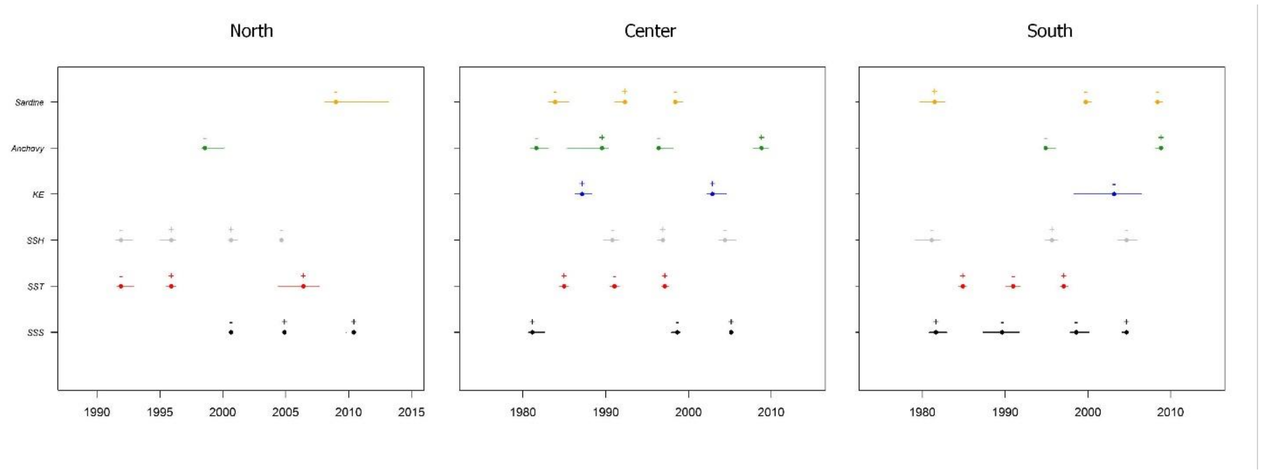

Figure 6. Breakpoint analyses of landing series and the environmental variables. SST= Sea surface temperature; SSS= sea surface salinity; SSH= sea surface height and KE =kinetic energy. Horizontal lines indicate confidence interval around the detected breakpoint and the sign (plus or minus) indicate the direction of the breakpoint toward an increase or a decrease.

Relationships with the environment

VIFs were calculated to identify variables with high collinearity. Regarding the anchovy landings in the southern sector, the salinity at the seasonal lag equal to 2 resulted in a VIF value greater than 3, and was therefore removed from the model. For the sardine landings, the variable removed from the model was the salinity at the time lag equal to 3 seasons. The procedure was repeated for the Central sector and for both species it led to the removal of SSS at time lags of 3 and 4 seasons for anchovy and sardine landing respectively. Regarding the sardine landings in the North, we removed SSH at the time lag of 5 and SSS at the time lags equals to 4, whilst for the anchovy landings we removed the SSS at the time lags of 4 seasons. Table 2 and Fig A2, A3 A4 (in supplementary material) show the final GLS models obtained for each sector and species.

The Final model for the northern zone regarding the anchovy landings contained SST and SSH as significant explanatory variables, the former negatively affecting the landings, and the latter positively affecting them at time lags of 3 and 4 seasons, respectively (Fig A2). Sardine landings, instead, were related negatively with SSS, SST, and SSH at the time lags of 1, 5 and 4 respectively (Tab2; Fig A2).

In the Central area, SST and SSH were the variables which resulted significantly related with both anchovy and sardine landings (Table 2, Fig A3). SSH at a time lag of 3 seasons influenced negatively both landings of the sardine and anchovy. SST negatively affected the sardine landings at the time lags of 1, 3 and 5 seasons and the anchovy landings at the time lags of 2 and 4 seasons (Table 2, Fig A3).

In the southern area SST was the only environmental factor which was significantly related with the anchovy landings (Table 2, Fig A4). This relationship involved the time lags at 2 and 4 seasons and was negative in both cases (Table 2, Fig A4). Landings of sardine were negatively affected by SST at the time lags of 3 and 5 seasons, by SSS at the time lags of 2 seasons and by SSH at the time lags of one and 5 seasons (Table 2, Fig A4).

The rolling regression analysis in Figures 7, 8, 9 showed that the relationships and their strengths (measured in terms of magnitude of the coefficients and their significance) between landings and the environmental variables changed over time. During the early period in the northern sector SSS with a lag of 1 seasons significantly affected sardine landings until 2009 (Fig 7). Afterwards, although the relationship continued to be negative, it lost strength and didn't influence the sardine landings significantly until the last decade of the series (Fig 7). SST with a lag of 5 seasons negatively affected sardine landings during the middle years of the study period until the 2008 (Fig 7). During the later years of the series, the SSH with a lag of 4 seasons was the one to influence the sardine landing most significantly (Fig 7).

In the Central sector, SST with lag at 1, 2 and 5 seasons, negatively influenced the sardine landings until 2005 in a significant manner. In the first and in the last case, this negative relationship was very pronounced in the early period, and losing practically all of its effect afterwards, with regression coefficients reaching values equals to ca. zero. While SST and SSH both with the lag at 3 seasons, significantly affected the sardine landings in the period between 1995 and 2005 (Fig 8).

Table 1. Final GLS models for each sector and species. The Subscript (*S-i*) indicates the lags in seasons while (*t*) lags in months

Sector	Landings for Species	Final Model	Errors autoregressive forms
North	**Sardine**	$y_t = -0.04 - 0.17 * SSS_{s-1} - 0.09 * SST_{S-5} - 0.22 * SSH_{S-4} + W_t$	$W_t = 0.33W_{t-1} + 0.09W_{t-2} + Z_t$ $Z_t \sim N(0, \sigma^2)$
	Anchovy	$y_t = 0.005 - 0.33 * SST_{s-3} - 0.15 * SSH_{S-4} + W_t$	$W_t = 0.32W_{t-1} + Z_t$ $Z_t \sim N(0, \sigma^2)$
Centre	**Sardine**	$y_t = -0.009 - 0.15 * SST_{s-1} - 0.14 * SST_{S-2} - 0.24 * SST_{S-5} - 0.16 * SSH_{s-3} + W_t$	$W_t = 0.59W_{t-1} + Z_t$ $Z_t \sim N(0, \sigma^2)$
	Anchovy	$y_t = -0.002 - 0.18 * SST_{s-2} - 0.15 * SST_{s-4} - 0.12 * SSH_{S-3} + W_t$	$W_t = 0.67W_{t-1} - 0.17W_{t-2} + Z_t$ $Z_t \sim N(0, \sigma^2)$
South	**Sardine**	$y_t = -0.03 - 0.16 * SSS_{s-2} - 0.11 * SST_{s-3} - 0.20 * SST_{S-5} - 0.19 * SSH_{s-1} - 0.16 * SSH_{s-5} + W_t$	$W_t = 0.41W_{t-1} - 0.22W_{t-2} + Z_t$ $Z_t \sim N(0, \sigma^2)$
	Anchovy	$y_t = -0.004 - 0.15 * SST_{s-2} - 0.16 * SST_{s-4} + W_t$	$W_t = 0.48W_{t-1} + Z_t$ $Z_t \sim N(0, \sigma^2)$

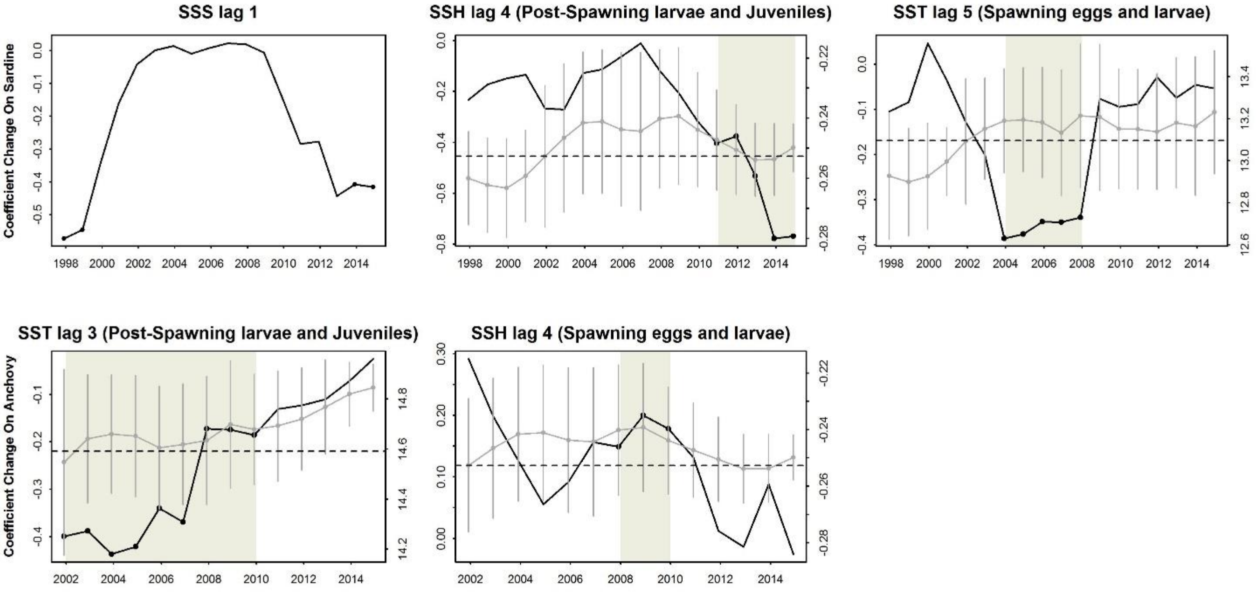

Figure 7. Temporal variability (based on a sliding window of 8-yr) of the sign and magnitude of the GLS coefficients (black line) of the relationships between the sardine and anchovy landings and the environmental variables in the northern sector. Filled circles indicate significant relationships. Grey lines represent the temporal variability of the mean value (based on a sliding window of 8-yr) and grey segments the standard deviation, of the specific environmental variable.

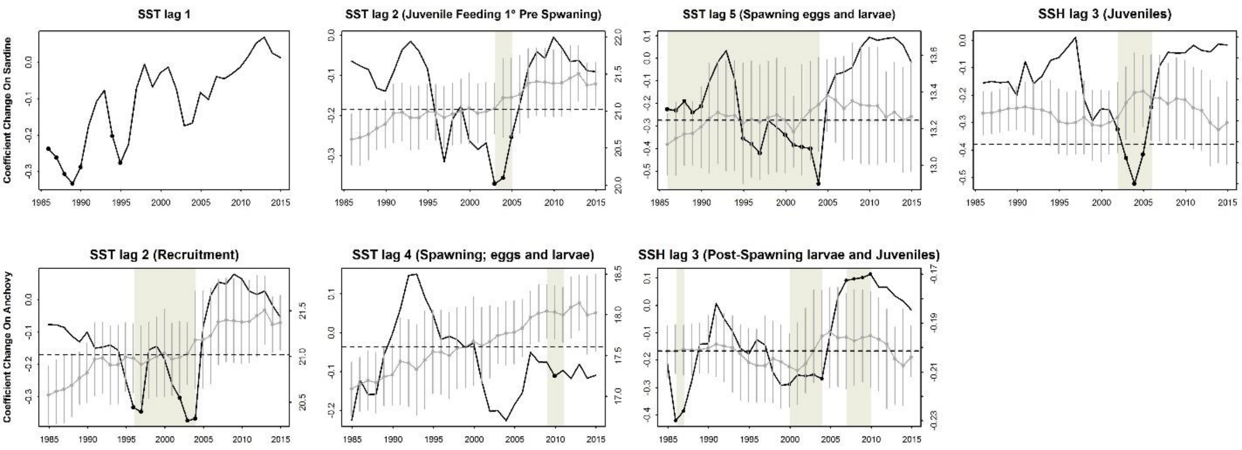

Figure 8. Temporal variability (based on a sliding window of 10-yr) of the sign and magnitude of the GLS coefficients (black line) of the relationships between the sardine and anchovy landings and the environmental variables in the Central sector. Filled circles indicate significant relationships. Grey lines represent the temporal variability of the mean value (based on a sliding window of 10-yr) and grey segments the standard deviation, of the specific environmental variable.

In the south concurrent negative effects on sardine landings, with coefficients showing similar patterns i.e. local minimums during the period between the years 1995 -2008, were accomplished by SSS, SST and SSH at a lag of 2, 3 and 5 seasons respectively. The negative relationship with SST at a lag of 5 seasons showed only one significant negative value during the period between 1997-2007 (Fig 9). SSH at a lag of 1 season was significantly related with sardine during the early period and slowly diminished its negative effect over time (Fig 9).

In relation to the anchovy landings in the northern sector, regression coefficients of SST at a lag of 3 seasons gradually decreased its negative effect until it reached non-significant values during the last decade. SSH always affected anchovy positively, observing significant effects only between 1999 and 2010 (Fig 7).

In the central sector, significant negative relationships between SST at the time lag of 2 seasons and anchovy landings occurred between 1995 to 2005, after which it became insignificant and almost null. SST at a lag of 4 seasons negatively affected anchovy landings in the period included between 2000 and 2010 (Fig 8). During the years 1990 to 2010 the regression coefficient of the relationship between SSH at a lag of 3 seasons and anchovy changed from a significantly negative relationship to a positive one which, although relatively low, was significant (Fig 8).

Finally, in the southern sector, SST at the time lag of 2 and 4 seasons negatively influenced the anchovy landings during the middle part and the second half part of the study period. SST at a lag of 2 seasons negatively affected anchovy from the year 1986 to the 2004 and later it started again to influence negatively anchovy during the last two decades. While the SST at the lag of 4 seasons influenced negatively anchovy from 1992 until the end of the series (Fig 9).

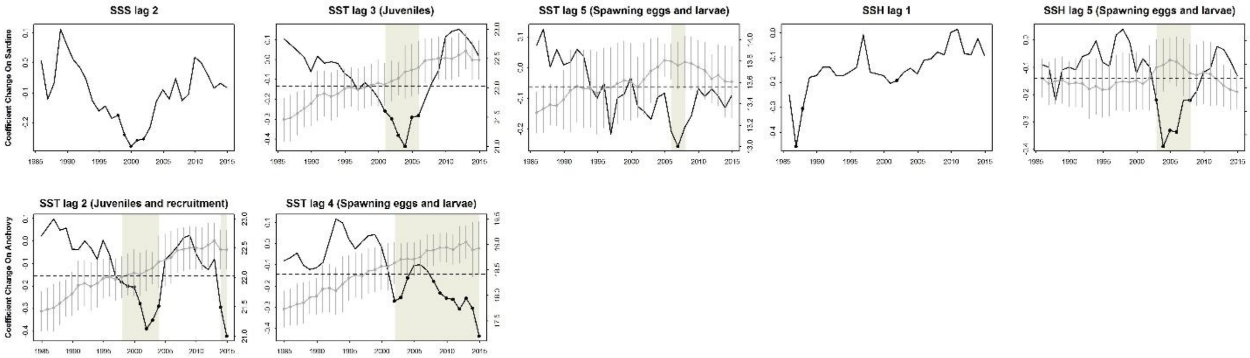

Figure 9. Temporal variability (based on a sliding window of 10-yr) of the sign and magnitude of the GLS coefficients (black line) of the relationships between the sardine and anchovy landings and the environmental variables in the Southern sector. Filled circles indicate significant relationships. Grey lines represent the temporal variability of the mean value (based on a sliding window of 10-yr) and grey segments the standard deviation, of the specific environmental variable.

Discussion

In this study, we investigated the characteristics of the long-term trend and the potential causes of variability of the anchovy and sardine landings in the Catalan sea. Because of the consistence between catches and the annual biomass estimates observed in the last ca. 15 years in the GSA06 (GFCM, 2015), landings can be an acceptable proxy of abundance for both species. But when interpreting the results, it is important to consider and keep in mind the various problems related to any kind of official fisheries landings data e.g. "black" market, misreporting or discards, although the latter could be considered negligible in our case study (Martín et al., 2008). To achieve the purpose, we needed as much long-term information of small pelagic landings as possible for subsequent analysis. Such kind of series generally are hard to obtain as long-term data are often fragmented, not digitized, partially lost etc. Here, in order to get exceptional extended time series, the three years gap (1990-1992) in the central and southern fishing area were estimated by using the ANN methods on the set of data before the 1990. Generally, in time series forecasting past observations of the same variable are collected and analysed to develop a model which describes the underlying relationships of these variable allowing to estimate its future realizations (Zhang, 2003). Although there are many kinds of time series analyses such as exponential smoothing method, Box–Jenkins autoregressive integrated moving average (ARIMA) models, which have been used to forecast small pelagic landings (e.g. Stergiou *et al.*, 1997; Koutroumanidis *et al.*, 2006; Tsitsika *et al.*, 2007), recently ANN methods have attracted increasing attention due to their flexible non-linear capacity (Czerwinski *et al.*, 2007, Zhang,2003) and to their ability of identify inputs and output rather than considering causality of data, i.e. using a black box approach (Gutiérrez-Estrada *et al.*, 2007; Kim *et al.*, 2015). With ANNs there is in fact no need to specify a model form. Rather the model is adaptatively formed based on the features presented from the data (Zhang,2003). Despite ANN method is difficult to understand due to its 'black box' nature, it has a superior and reliable forecasting power compared to the other empirical methods (Gutiérrez-Estrada *et al.*, 2007; Kim *et al.*, 2015). This is especially true when a consistent repetitive pattern does not characterize the data such as landings time series, which are instead susceptible to drastic environmental changes or are influenced by fish age, growth, or natural mortality (Kim *et al.*, 2015). Since the purpose of the reconstruction of our landing series was not in the sense of the interpretative aspect (e.g. the relation between the landing of a specific month compared to the same month from the previous year) but instead was the realization of the largest anchovy and sardine series to be subsequently modeled, the choice of ANN method because of its characteristics seemed to be the most appropriate.

Excluding the last four years, sardine was the most important species in volume (tons) caught and exhibited peaks during the spring and at the end of the summer. Regarding reproductive strategies, this species is a multiple spawner, producing batches of eggs during an extended season, covering the colder period of the year, from November to March in the Catalan sea, when the water is vertically homogenous (Olivar et al., 2001). Sardine is a species following the 'capital breeder' strategy (e.g. Albo-Puigserver et al. 2017; Ganias et al., 2007). Even though the two landing peaks were not so evident, they suggest individuals' aggregation of which, the first during spring, reflect this strategy, i.e. the accumulation of energy during the spring season. While the second peak reflect the spawning aggregation starting at the beginning of the fall season (Palomera and Olivar, 1996).

Seasonality was more evident for anchovy landings and showed a latitudinal evolution in terms of peaks, starting earlier at the lower latitudes at the end of the spring and during late summer in the northernmost latitudes. These latitudinal differences could be related to the species reproduction cycle, characterized by the high temperature-dependence of the spawning onset (Palomera, 1992).

Sardine landings exhibited a general decreasing trend and none of the three sectors showed signs of recovery, reaching instead the lowest values during the last ten years, most evident in the southern area. Regarding anchovy, a general reduction in landings was observed in the northern and central sector. In the southern zone, despite the differences of peaks of the last years during the summer seasons respect to the peaks during the first half of the years 90s which were extremely high, overall, they remained at rather high levels compared to the sardine landings. Furthermore, in the two southernmost sectors we actually observed a slight increase of anchovy landings during the latest years. This increase could be the result of both the capacity of anchovy to recover more quickly when good feeding conditions reappear, thanks to its reproductive strategy ('income breeder', McBride et al., 2015), and to the annual closed fishing season, which coincides with the period of its recruitment. These results concur with the findings of the adjacent area (Gulf of Lions), as well as with the general decrease in other areas of the Mediterranean Sea (Van Beveren et al., 2016, GFCM 2015).

One of the most noticeable events in this study was the synchronous breakdown of the landings of both species with the rise of SST and SSH and the decrease in SSS during the second half of the 90s and the beginning of the 2000s. These breakpoints matched the start of the most pronounced decrease of landings for both species. In the case of anchovy, it stopped with signs of recovery starting in ca. 2009 also evidenced by the breakpoint analysis for the southern and central sector (Fig 6). The combined effect between the long term fishing exploitation (in fact, none of the stocks of these species are described as underexploited in the GSA06; GFCM, 2015), which could have eroded the age structure of the populations making them increasingly juvenescent, together with the negative effects of sudden environmental changes acting on these populations mainly composed by juveniles more susceptible to the environmental variations (combined effects of fishing and environmental variability; e.g. Anderson et al., 2008; Planque et al., 2010; Hidalgo et al., 2011) could be hypothesized as an explanation of the downfalls of the two small pelagic fishes.

Although we did not analyse data regarding the age structure of these populations during the period considered, the recent findings regarding the decrease in size structures of both the anchovy and sardine population in NW Mediterranean Sea (Van Beveren et al., 2014; Brosset et al., 2017) indirectly strengthen this hypothesis.

Our analysis is grounded on the hypothesis that the environmental impacts on small pelagic fish should be mainly felt through recruitment depending on eggs and larvae survival and juveniles growth, with the subsequent effects on the population dynamics (Bakun, 1996; Agostini and Bakun, 2002; Fréon et al., 2005). So as to study these impacts on the adult population (landings), we introduced the environmental parameters in the models after hysteresis (i.e. time lagged-effects, considering seasons).

SST and SSH appeared to be the most important and frequent factors among the local environmental factors considered in influencing the landing variations along the Catalan coast. SSS was related only with the sardine landings in the North and in the South, which are the sectors influenced more directly by the continental waters, i.e. from the Rhone river and the Ebro river respectively. Considering that the bulk of landings was during the late spring and summer for both species, the significant seasonal lags of SST and SSH encountered affected mainly their early stages of the life cycle. For anchovy, the seasonal time lags found were considered representative of the spawning period of the prior year (spring-summer, time lag of 4 seasons), the juvenile aggregation shoals (fall, time lag of 3 season), and the period at which anchovy reach ca. 1 year old, which is when they are almost sufficiently mature to contribute to spawning and to recruit in fishery (winter, time lag of 2 season). The sardine population during the late spring and summer is a mixture of both juvenile (age 0) and adults (age 1 and older) (Tugores et al., 2011; Bonanno et al., 2014). The significant seasonal lags were considered to be the related with the spawning period of the previous year (late fall and winter, seasonal lags of 5-4), the juveniles feeding period, and recruitment (summer-fall, 3 and 2 seasonal time lag).

SST negatively affected both anchovy and sardine during the different life stages in the whole area. These negative relationships a coincided with other findings in this area (Martín et al., 2012) as well as in other parts of the Mediterranean sea where both anchovy and sardine catches were negatively correlated with SST (Katara et al., 2011). In the NW Mediterranean sea, cold years tend to be more productive, because winter mixing may reach greater depth (Salat, 1996). This enhanced productivity during the colder months of winter and spring also meant an increase in micro and meso-zooplankton (Fernandez de Puelles et al., 2004), the main food for the early life stages and adult individuals. Oppositely warm periods, were likely to trigger and anticipate strong thermal stratification preventing the mixing of water masses and therefore, leading to a reduction of nutrient supply in the upper layers with a consequent reduction of the zooplankton (Fernandez de Puelles et al., 2004) and in a modification of its composition (Auger et al., 2014).

Regarding anchovies, the low productivity during the spawning period of the previous year (as a consequence of the high SST) might have affected the trophic environment for spawners and, subsequently, the eggs production, which therefore negatively affected landings. In fact, in another area of the basin Somarakis et al., 2004; Somarakis and Nikolioudakis, 2007 showed that waters cooler and much richer in zooplankton represent a favourable trophic environment for the spawning adults, which in these conditions enhanced the anchovy eggs production. In addition to food limitation, the high temperature values during the early life stages in the summer and fall of the previous year, could have led to a lower growth rate of larvae and juveniles owing to physiological limitations (dome-shaped relationship between temperature and growth larval and juveniles; Takasuka and Aoki, 2006; Urtizberea et al., 2008), negatively affecting landings due to the smaller chances of survival that young individuals have (Miller, 1997; Sogard, 1997). As described in a recent study in the Bay of Biscay by Aldanondo et al., 2016, the size-dependent mortality could be a significant regulating process of the anchovies recruitment strength.

Temperature affected sardine landings by acting on the spawning period in winter and on the juvenile aggregation shoals in summer and fall, just before the first breeding season. During both periods temperature probably played an indirect role in determining the early life stages survival, similar to what occurs with anchovy, by limiting prey availability. The growth and survival of the pilchard eggs and larvae developing in this area were described to be highly dependent on high food availability (Catalán et al., 2006). This dependence was also seen for the growth of juveniles, which in the western Mediterranean sea (Alemany et al., 2006) seems to be strongly affected by a poor feeding environment due to the extended period of water column stability.

The other factor recurrently linked to both anchovy and sardine landings in the whole area was the SSH, which is a variable that describes processes such as gyres meanders and eddies (Pujol and Larnicol, 2005). These hydrological features are known to enhance the enrichment and retention processes and are therefore crucial structures for successful recruitment, especially of small pelagic fish (Agostini and Bakun, 2002; Lafuente et al., 2002; Sabatés et al., 2007; Checkley et al., 2009). Low SSH during fall/winter favoured the following year landings for both sardine (eggs and larvae) and anchovy (recruitment) in the southern and central sectors. These relationships were in agreement with other studies aimed at describing favourable environments for larvae and juveniles of both species in the Mediterranean sea (Giannoulaki et al., 2011, 2013; Tugores et al., 2011; Bonanno et al., 2014). Lower SSH generally indicate zones of divergence characterized by an uplift of subsurface and nutrient rich water (Nieto et al., 2014), which along the Catalan shelf were described to be caused by the strong downslope winds that originate in the Ebro valley (Bakun and Agostini, 2001). The positive relationships between anchovy landings and SSH in the northern sector during spring summer of the previous year seemed to be in contrast to what occurred in the other two sectors. Nevertheless, anchovy as shown by Katara et al., 2011; and Bonanno et al., 2014 in the Aegean Sea, was favoured by a wide range of SSH. The rise of SSH could be indicative of the start of processes like the mesoscale anticyclonic eddies which retains food and prevents larval dispersion favouring growth and survival (Sabatés et al., 2007). Convergent ocean surface transport and downwelling is indeed a typical situation occurring during, the summer season along the Catalan coast, and it is caused by the wind pattern characterizing this season (Bakun and Agostini, 2001).

The rolling regression analysis allowed us to identify the period in which the strength (in terms of magnitude and significance of the coefficient estimates) of the main local factors causing variation of landings of both species changed. For both sardine and anchovy, the period in which the strength of most relationships with SST and SSH increased both negatively and positively was between the 90s and ca. 2010. The abrupt rise in sea surface temperature during this period, according to Vargas-Yáñez et al., 2010, and changes in the mesoscale patterns as evidenced by the breakpoints analysis could have reduced the chances of survival of the early life stages and affected the recruitment of both species. Concerning SST, the negative effects became stronger during the summer/fall and winter for sardine and during spring/summer and fall for anchovy from the 90s to ca. 2010. During this period a change in mean temperature values was extremely noticeable and could have influenced sardine and anchovy larvae both directly on the foraging and growth capacity (Garrido et al., 2016), or indirectly by food limitation (e.g. Alemany et al., 2006; Catalán et al., 2006). The negative relationships between SST and anchovy landings during the last decades in the southern sector coincided both with the highest temperature values observed and with the slight recovery of landings. In general, higher temperatures during spring/summer, such as those observed during this period, might have favoured the growth rate of larvae and, therefore, lowered the mortality rate due to reduced exposure to predators (e.g. Dulčić and Kraljević, 1996; Wang et al., 2009), favouring the overall recruitment and recovery of anchovy. Nevertheless, this positive effect, useful for the anchovy recovery, likely turned into a negative one when the water temperature exceeded a threshold value and became a factor which prevented productivity of phytoplankton and subsequently zooplankton, which as suggested by Garcia et al., 1998, represents one of the major factors limiting anchovy eggs and larvae growth in the area.

SSH always had a negative impact on sardine, observing an increased strength of the relationship during the middle years of the period studied. During this time period SSH was, on average, high during the winter spawning season as well as during the growing period in summer-fall, indicating a low divergence pattern and hence a lack of enrichment of the upper layer. The relationship between anchovy and SSH showed instead a controversial pattern, changing in spring/summer from a negative to a positive effect in the central sector, and always positively influencing anchovy landing in the northern sector. In the Central zone, during the late summer and fall of the previous year a fairly clear divergence pattern characterized the area (lowest value of mean SSH, Fig 8), indicating a mixed upper layer which sustained high productivity after the break of thermocline (Salat, 1996; Sabatés et al., 2007). Consequently, an increase of SSH, which negatively affected landings, could be indicative of the failure of this break. Contrarily, significant positive effects on landings appeared when SSH values were on average highest (Fig 8). The rise in SSH likely could be indicative of convergent patterns, which therefore favoured retention of nutrients, favouring anchovies. The loss of significant relationships during the last period, especially for sardine landings, was not surprising, considering the complex effects the environmental factors have on a biological population (Hsieh et al., 2009). Variability of small pelagic fishes cannot indeed be explained by single environmental factor, but by a set of different drivers which permit these populations to prosper. The effect of a rise in temperature can be, for example, positive for the growth rate of early life stages but limiting for food availability. This latter effect could be mitigated if mesoscale processes are formed, permitting convergence, with the associated opportunities for the concentration of small organisms.

In addition, the population responses to the environmental variability as shown by various studies could be further complicated by fishing, which by modifying demographic parameters of the stocks could enhance the nonlinear dynamics of the populations (e.g. Anderson et al., 2008; Planque et al., 2011) and alter their capacity to cope with changing environments (Hidalgo et al., 2011).

This study was designed to investigate whether local environmental factors may have affected landings variation in the Catalan sea. Although some aspects of the long-term effects of the temperature and the role of productivity-enhancing oceanic features acting on the critical periods of the life cycle are revealed, the exploitation state of both species in this area might not allow unambiguous conclusions about the impacts of the environment on the population of these two small pelagic fishes. From this study, it is evident that the decline of both stocks is not only a result of environmental changes but rather the combined effects of these with the lengthy period of exploitation, and calls for studies oriented towards understanding the interaction between climate and fishing of these two species.

References

Agostini, V. N., and Bakun, A. 2002. Ocean triads' in the Mediterranean Sea: physical mechanisms potentially structuring reproductive habitat suitability (with example application to European anchovy, *Engraulis encrasicolus*). *Fisheries Oceanography*, 11: 129–142.

Albo-Puigserver, M., Muñoz, A., Navarro, J., Coll, M., Pethybridge, H., Sánchez, S., and Palomera, I. (n.d.). Ecological energetics of forage fish from the Mediterranean Sea: Seasonal dynamics and interspecific differences. Deep Sea Research Part II: Topical Studies in Oceanography.

Aldanondo, N., Cotano, U., Goikoetxea, N., Boyra, G., Ibaibarriaga, L., and Irigoien, X. 2016. Interannual differences in growth and hatch-date distributions of early juvenile European anchovy in the Bay of Biscay: implications for recruitment. *Fisheries Oceanography*, 25: 147–163.

Alemany, F., Álvarez, I., García, A., Cortés, D., Ramírez, T., Quintanilla, J., Álvarez, F., *et al.* 2006. Postflexion larvae and juvenile daily growth patterns of the Alborán Sea sardine (*Sardina pilchardus* Walb.): influence of wind. *Scientia Marina*, 70: 93–104.

Anderson, C. N. K., Hsieh, C., Sandin, S. A., Hewitt, R., Hollowed, A., Beddington, J., May, R. M., *et al.* 2008. Why fishing magnifies fluctuations in fish abundance. *Nature*, 452: 835–839.

Auger, P. A., Ulses, C., Estournel, C., Stemmann, L., Somot, S., and Diaz, F. 2014. Interannual control of plankton communities by deep winter mixing and prey/predator interactions in the NW Mediterranean: Results from a 30-year 3D modeling study. *Progress in Oceanography*, 124: 12–27.

Bai, J., and Perron, P. 2003. Computation and analysis of multiple structural change models. *Journal of Applied Econometrics*, 18: 1–22.

Bakun, A. 1996. Patterns in the ocean: ocean processes and marine population dynamics. Patterns in the ocean: ocean processes and marine population dynamics.

Bakun, A., and Agostini, V. N. 2001. Seasonal patterns of wind-induced upwelling/downwelling in the Mediterranean Sea. *Scientia Marina*, 65: 243–257.

Blenckner, T., and Niiranen, S. 2013. Biodiversity-marine food-web structure, stability, and regime shifts. Climate vulnerability. *Oxford Academic Press*. p: 203–12.

Bonanno, A., Giannoulaki, M., Barra, M., Basilone, G., Machias, A., Genovese, S., Goncharov, S., *et al.* 2014. Habitat Selection Response of Small Pelagic Fish in Different Environments. Two Examples from the Oligotrophic Mediterranean Sea. *PLOS ONE*, 9: e101498.

Brosset, P., Fromentin, J.-M., Van Beveren, E., Lloret, J., Marques, V., Basilone, G., Bonanno, A., *et al.* 2017. Spatio-temporal patterns and environmental controls of small pelagic fish body condition from contrasted Mediterranean areas. *Progress in Oceanography*, 151: 149–162.

Brown, R. L., Durbin, J., and Evans, J. M. 1975. Techniques for testing the constancy of regression relationships over time. *Journal of the Royal Statistical Society. Series B (Methodological)*: 149–192.

Carpi, P., Martinelli, M., Belardinelli, A., Russo, A., Arneri, E., Coluccelli, A., and Santojanni, A. 2015. Coupling an oceanographic model to a Fishery Observing System through mixed models: the importance of fronts for anchovy in the Adriatic Sea. *Fisheries Oceanography*, 24: 521–532.

Catalán, I. A., Olivar, M. P., Palomera, I., and Berdalet, E. 2006. Link between environmental anomalies, growth and condition of pilchard Sardina pilchardus larvae in the northwestern Mediterranean. *Marine Ecology Progress Series*, 307: 219–231.

Checkley, D., Alheit, J., Oozeki, Y., and Roy, C. 2009. Climate change and small pelagic fish. *Cambridge University Press* pp. 372

Chen, D.-G., and Ware, D. M. 1999. A neural network model for forecasting fish stock recruitment. *Canadian Journal of Fisheries and Aquatic Sciences*, 56: 2385–2396.

Cleveland, R. B., Cleveland, W. S., and Terpenning, I. 1990. STL: A seasonal-trend decomposition procedure based on loess. *Journal of Official Statistics*, 6: 3.

Cole, J., and McGlade, J. 1998. Clupeoid population variability, the environment and satellite imagery in coastal upwelling systems. *Reviews in fish biology and fisheries*, 8: 445–471.

Colebrook, J. M. 1978. Continuous plankton records-zooplankton and environment, northeast Atlantic and North-Sea, 1948-1975. *Oceanologica acta*, 1: 9–23.

Czerwinski, I. A., Gutiérrez-Estrada, J. C., and Hernando-Casal, J. A. 2007. Short-term forecasting of halibut CPUE: Linear and non-linear univariate approaches. Fisheries Research, 86: 120–128.

Cury, P. 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in ‘wasp-waist’ ecosystems. *ICES Journal of Marine Science*, 57: 603–618.

Diggle, P. 2002. Analysis of longitudinal data. *Oxford University Press*. pp.379

Dulčić, J., and Kraljević, M. 1996. Weight-length relationships for 40 fish species in the eastern Adriatic (Croatian waters). *Fisheries Research*, 28: 243–251.

Faraway, J., and Chatfield, C. 1998. Time series forecasting with neural networks: a comparative study using the airline data. *Applied statistics*: 231–250.

Fernandezdepuelles, M., Valencia, J., and Vicente, L. 2004. Zooplankton variability and climatic anomalies from 1994 to 2001 in the Balearic Sea (Western Mediterranean). *ICES Journal of Marine Science*, 61: 492–500.

Fréon, P., Cury, P., Shannon, L., and Roy, C. 2005. Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: a review. *Bulletin of Marine Science*, 76: 385–462.

Fromentin, J.-M., and Fonteneau, A. 2001. Fishing effects and life history traits: a case study comparing tropical versus temperate tunas. *Fisheries Research*, 53: 133–150.

Ganias, K., Somarakis, S., Koutsikopoulos, C., and Machias, A. 2007. Factors affecting the spawning period of sardine in two highly oligotrophic Seas. *Marine Biology*, 151: 1559–1569.

Garcia, A., Cortes, D., and Ramirez, T. 1998. Daily larval growth and RNA and DNA content of the NW Mediterranean anchovy *Engraulis encrasicolus* and their relations to the environment. *Marine Ecology Progress Series*, 166: 237–245.

Garrido, S., Cristóvão, A., Caldeira, C., Ben-Hamadou, R., Baylina, N., Batista, H., Saiz, E., *et al.* 2016. Effect of temperature on the growth, survival, development and foraging behaviour of Sardina pilchardus larvae. *Marine Ecology Progress Series*, 559: 131–145.

Giannoulaki, M., Pyrounaki, M. M., Liorzou, B., Leonori, I., Valavanis, V. D., Tsagarakis, K., Bigot, J. L., *et al.* 2011. Habitat suitability modelling for sardine juveniles (Sardina pilchardus) in the Mediterranean Sea: Habitat suitability modelling for sardine juveniles. *Fisheries Oceanography*, 20: 367–382.

Giannoulaki, M., Iglesias, M., Tugores, M. P., Bonanno, A., Patti, B., De Felice, A., Leonori, I., *et al.* 2013. Characterizing the potential habitat of European anchovy *Engraulis encrasicolus* in the Mediterranean Sea, at different life stages: *Habitat of anchovy in the Mediterranean*. Fisheries Oceanography, 22: 69–89.

Gutiérrez-Estrada, J. C., Silva, C., Yáñez, E., Rodríguez, N., and Pulido-Calvo, I. 2007. Monthly catch forecasting of anchovy Engraulis ringens in the north area of Chile: Non-linear univariate approach. Fisheries Research, 86: 188–200.

Haykin, S. 1994. Neural Networks: A Comprehensive Foundation: *Macmillan College Publishing Company. New York*. Pp.696

Hidalgo, M., Rouyer, T., Molinero, J., Massutí, E., Moranta, J., Guijarro, B., and Stenseth, N. 2011. Synergistic effects of fishing-induced demographic changes and climate variation on fish population dynamics. *Marine Ecology Progress Series*, 426: 1–12.

Hsieh, C., Yamauchi, A., Nakazawa, T., and Wang, W.-F. 2010. Fishing effects on age and spatial structures undermine population stability of fishes. *Aquatic Sciences*, 72: 165–178.

Hsieh, C.-H., Chen, C.-S., Chiu, T.-S., Lee, K.-T., Shieh, F.-J., Pan, J.-Y., and Lee, M.-A. 2009. Time series analyses reveal transient relationships between abundance of larval anchovy and environmental variables in the coastal waters southwest of Taiwan. *Fisheries Oceanography*, 18: 102–117.

Hyndman, R. J., Athanasopoulos, G., Razbash, S., Schmidt, D., Zhou, Z., Khan, Y., and Bergmeir, C. 2014. forecast: Forecasting functions for time series and linear models. R package version, 5.

Ibanez, F., and Dauvin, J.-C. 1988. Long-term changes (1977 to 1987) in a muddy fine sand *Abra alba–Melinna palmata* community from the Western English Channel: multivariate time-series analysis. *Marine Ecology Progress Series*: 65–81.

Ibanez, F., and Etienne, M. 1992. Le filtrage des séries chronologiques par l'analyse en composantes principales de processus (ACPP). *J. Rech. Océanogr*, 16: 27–33.

Jank, W., and Shmueli, G. (Eds). 2008. Statistical methods in e-commerce research. Statistics in practice. *Wiley, Hoboken*, N.J. 429 pp.

Katara, I., Pierce, G. J., Illian, J., and Scott, B. E. 2011. Environmental drivers of the anchovy/sardine complex in the Eastern Mediterranean. *Hydrobiologia*, 670: 49–65.

Kim, J. Y., Jeong, H. C., Kim, H., and Kang, S. 2015. Forecasting the monthly abundance of anchovies in the South Sea of Korea using a univariate approach. Fisheries Research, 161: 293–302.

Koutroumanidis, T., Iliadis, L., and Sylaios, G. K. 2006. Time-series modeling of fishery landings using ARIMA models and Fuzzy Expected Intervals software. Environmental Modelling & Software, 21: 1711–1721.

Lafuente, J. G., Garcia, A., Mazzola, S., Quintanilla, L., Delgado, J., Cuttita, A., and Patti, B. 2002. Hydrographic phenomena influencing early life stages of the Sicilian Channel anchovy. *Fisheries Oceanography*, 11: 31–44.

Lleonart, J., and Maynou, F. 2003. Fish stock assessments in the Mediterranean: state of the art. *Scientia Marina*, 67: 37–49.

Lloret, J., Palomera, I., Salat, J., and Solé, I. 2004. Impact of freshwater input and wind on landings of anchovy (*Engraulis encrasicolus*) and sardine *(Sardina pilchardus*) in shelf waters surrounding the Ebre (Ebro) River delta (north-western Mediterranean). *Fisheries Oceanography*, 13: 102–110.

Martín, P., Bahamon, N., Sabatés, A., Maynou, F., Sánchez, P., and Demestre, M. 2008. European anchovy (*Engraulis encrasicolus*) landings and environmental conditions on the Catalan Coast (NW Mediterranean) during 2000–2005. *Hydrobiologia*, 612: 185–199.

Martín, P., Sabatés, A., Lloret, J., and Martin-Vide, J. 2012. Climate modulation of fish populations: the role of the Western Mediterranean Oscillation (WeMO) in sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) production in the north-western Mediterranean. Climatic Change, 110: 925–939.

Maynou, F., Sabatés, A., and Salat, J. 2014. Clues from the recent past to assess recruitment of Mediterranean small pelagic fishes under sea warming scenarios. Climatic Change, 126: 175–188.

McBride, R. S., Somarakis, S., Fitzhugh, G. R., Albert, A., Yaragina, N. A., Wuenschel, M. J., Alonso-Fernández, A., *et al.* 2015. Energy acquisition and allocation to egg production in relation to fish reproductive strategies. *Fish and Fisheries*, 16: 23–57.

Miller, T. J. 1997. The use of field studies to investigate selective processes in fish early life history. *In Early life history and recruitment in fish populations*, *Springer.* pp. 197–223..

Moritz, S., Sardá, A., Bartz-Beielstein, T., Zaefferer, M., and Stork, J. 2015. Comparison of different Methods for Univariate Time Series Imputation in R. *arXiv*:1510.03924

Nieto, K., McClatchie, S., Weber, E. D., and Lennert-Cody, C. E. 2014. Effect of mesoscale eddies and streamers on sardine spawning habitat and recruitment success off Southern and central California. *Journal of Geophysical Research: Oceans*, 119: 6330–6339.

Olivar, M. P., Salat, J., and Palomera, I. 2001. Comparative study of spatial distribution patterns of the early stages of anchovy and pilchard in the NW Mediterranean Sea. *Marine Ecology Progress Series*, 217: 111–120.

Palomera, I. 1992. Spawning of anchovy Engra ulis encrasicol us in the Northwestern Mediterranean relative to. *Mar. Ecol. Prog. Ser*, 79: 215–223.

Palomera, I., and Olivar, M. P. 1996. Nearshore ichthyoplankton off the Costa Brava (northwest Mediterranean Sea). Publicaciones Especiales del Instituto Espanol del Oceanografıa, 22.

Palomera, I., Olivar, M. P., Salat, J., Sabatés, A., Coll, M., García, A., and Morales-Nin, B. 2007. Small pelagic fish in the NW Mediterranean Sea: An ecological review. *Progress in Oceanography*, 74: 377–396.

Pinheiro, J., and Bates, D. 2006. Mixed-effects models in S and S-PLUS. *Springer Science & Business Media*. pp.528

Planque, B., Fromentin, J.-M., Cury, P., Drinkwater, K. F., Jennings, S., Perry, R. I., and Kifani, S. 2010. How does fishing alter marine populations and ecosystems sensitivity to climate? *Journal of Marine Systems*, 79: 403–417.

Planque, B., Loots, C., Petitgas, P., LINDSTRøM, U., and Vaz, S. 2011. Understanding what controls the spatial distribution of fish populations using a multi-model approach: Spatial distribution of fish populations. *Fisheries Oceanography*, 20: 1–17.

Planque, B. 2016. Projecting the future state of marine ecosystems, ‘la grande illusion’? *ICES Journal of Marine Science: Journal du Conseil*, 73: 204–208.

Pörtner, H. O., and Peck, M. A. 2010. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *Journal of Fish Biology*, 77: 1745–1779.

Pujol, M.-I., and Larnicol, G. 2005. Mediterranean sea eddy kinetic energy variability from 11 years of altimetric data. *Journal of Marine Systems*, 58: 121–142.

Ruiz, J., Macías, D., Rincón, M. M., Pascual, A., Catalán, I. A., and Navarro, G. 2013. Recruiting at the Edge: Kinetic Energy Inhibits Anchovy Populations in the Western Mediterranean. *PLoS ONE*, 8: e55523.

Sabatés, A., Olivar, M. P., Salat, J., Palomera, I., and Alemany, F. 2007. Physical and biological processes controlling the distribution of fish larvae in the NW Mediterranean. *Progress in Oceanography*, 74: 355–376.

Salat, J. 1996. Review of hydrographic environmental factors that may influence anchovy habitats in northwestern Mediterranean. *Scientia marina*, 60: 21–32.

Schmidt, A., Botsford, L., Eadie, J., Bradley, R., Di Lorenzo, E., and Jahncke, J. 2014. Non-stationary seabird responses reveal shifting ENSO dynamics in the northeast Pacific. *Marine Ecology Progress Series*, 499: 249–258.

Shannon, L. J., Cury, P. M., and Jarre, A. 2000. Modelling effects of fishing in the Southern Benguela ecosystem. *ICES Journal of Marine Science: Journal du Conseil*, 57: 720–722.

Sogard, S. M. 1997. Size-selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of marine science*, 60: 1129–1157.

Somarakis, S., Palomera, I., Garcia, A., Quintanilla, L., Koutsikopoulos, C., Uriarte, A., and Motos, L. 2004. Daily egg production of anchovy in European waters. *ICES Journal of Marine Science*, 61: 944–958.

Somarakis, S., and Nikolioudakis, N. 2007. Oceanographic habitat, growth and mortality of larval anchovy (*Engraulis encrasicolus*) in the northern Aegean Sea (eastern Mediterranean). *Marine Biology*, 152: 1143–1158.

Stergiou, K. I., Christou, E. D., and Petrakis, G. 1997. Modelling and forecasting monthly fisheries catches: comparison of regression, univariate and multivariate time series methods. Fisheries Research, 29: 55–95.

Szuwalski, C. S., Vert-Pre, K. A., Punt, A. E., Branch, T. A., and Hilborn, R. 2015. Examining common assumptions about recruitment: a meta-analysis of recruitment dynamics for worldwide marine fisheries. *Fish and Fisheries*, 16: 633–648.

Szuwalski, C. S., and Hollowed, A. B. 2016. Climate change and non-stationary population processes in fisheries management. *ICES Journal of Marine Science*, 73: 1297–1305.

Takasuka, A., and Aoki, I. 2006. Environmental determinants of growth rates for larval Japanese anchovy Engraulis japonicus in different waters. *Fisheries Oceanography*, 15: 139–149.

Tsitsika, E. V., Maravelias, C. D., and Haralabous, J. 2007. Modeling and forecasting pelagic fish production using univariate and multivariate ARIMA models. Fisheries Science, 73: 979–988.

Tugores, M., Giannoulaki, M., Iglesias, M., Bonanno, A., Tičina, V., Leonori, I., Machias, A., *et al.* 2011. Habitat suitability modelling for sardine Sardina pilchardus in a highly diverse ecosystem: the Mediterranean Sea. *Marine Ecology Progress Series*, 443: 181–205.

Urtizberea, A., Fiksen, O., Folkvord, A., and Irigoien, X. 2008. Modelling growth of larval anchovies including diel feeding patterns, temperature and body size. *Journal of Plankton Research*, 30: 1369–1383.

Van Beveren, E., Bonhommeau, S., Fromentin, J.-M., Bigot, J.-L., Bourdeix, J.-H., Brosset, P., Roos, D., *et al.* 2014. Rapid changes in growth, condition, size and age of small pelagic fish in the Mediterranean. *Marine Biology*, 161: 1809–1822.

Van Beveren, E., Fromentin, J.-M., Rouyer, T., Bonhommeau, S., Brosset, P., and Saraux, C. 2016. The fisheries history of small pelagics in the Northern Mediterranean. *ICES Journal of Marine Science: Journal du Conseil*, 73: 1474–1484.

Vargas-Yáñez, M., Moya, F., García-Martínez, M. C., Tel, E., Zunino, P., Plaza, F., Salat, J., *et al.* 2010. Climate change in the Western Mediterranean Sea 1900–2008. *Journal of Marine Systems*, 82: 171–176.

Wang, W.-C., Chau, K.-W., Cheng, C.-T., and Qiu, L. 2009. A comparison of performance of several artificial intelligence methods for forecasting monthly discharge time series. *Journal of Hydrology*, 374: 294–306.

Zeileis, A., Kleiber, C., Krämer, W., and Hornik, K. 2003. Testing and dating of structural changes in practice. *Computational Statistics & Data Analysis*, 44: 109–123.

Zhang, G. P. 2003. Time series forecasting using a hybrid ARIMA and neural network model. Neurocomputing, 50: 159–175.

Zuur, A. F., Ieno, E. N., and Elphick, C. S. 2010. A protocol for data exploration to avoid common statistical problems: Data exploration. *Methods in Ecology and Evolution*, 1: 3–14.

Supplementary Material

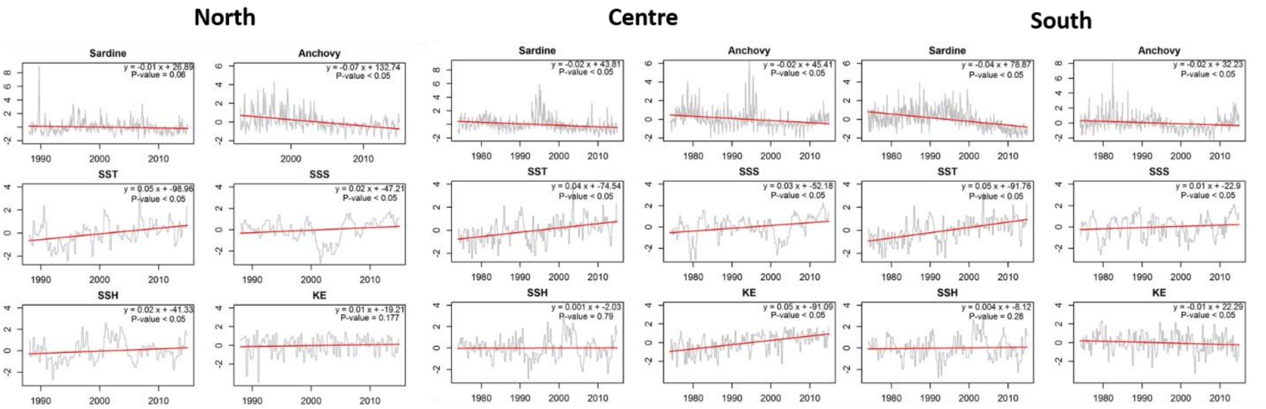

Figure A1. Seasonal adjusted series and long-term linear trend of sardine and anchovy landings and the environmental series.

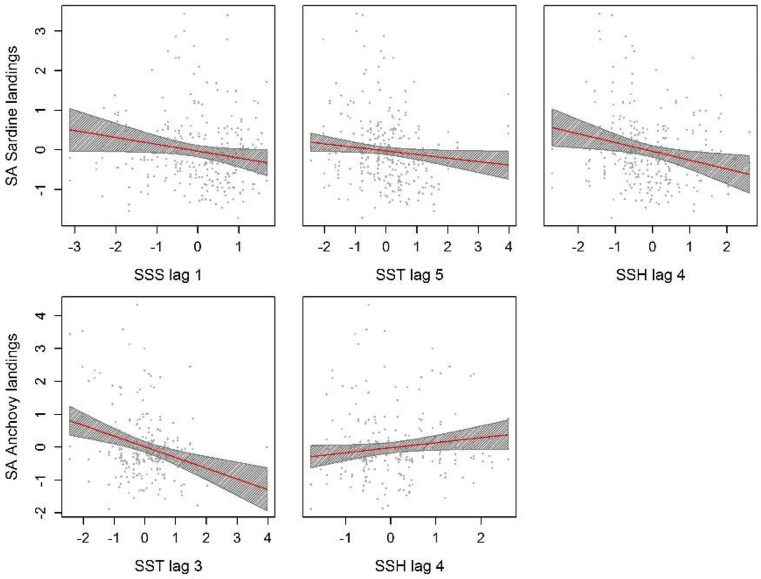

Figure A2. Final GLS models for the northern sector. Red line indicate the fitted model and the 95 % of confidence interval. SA= Seasonally adjusted.

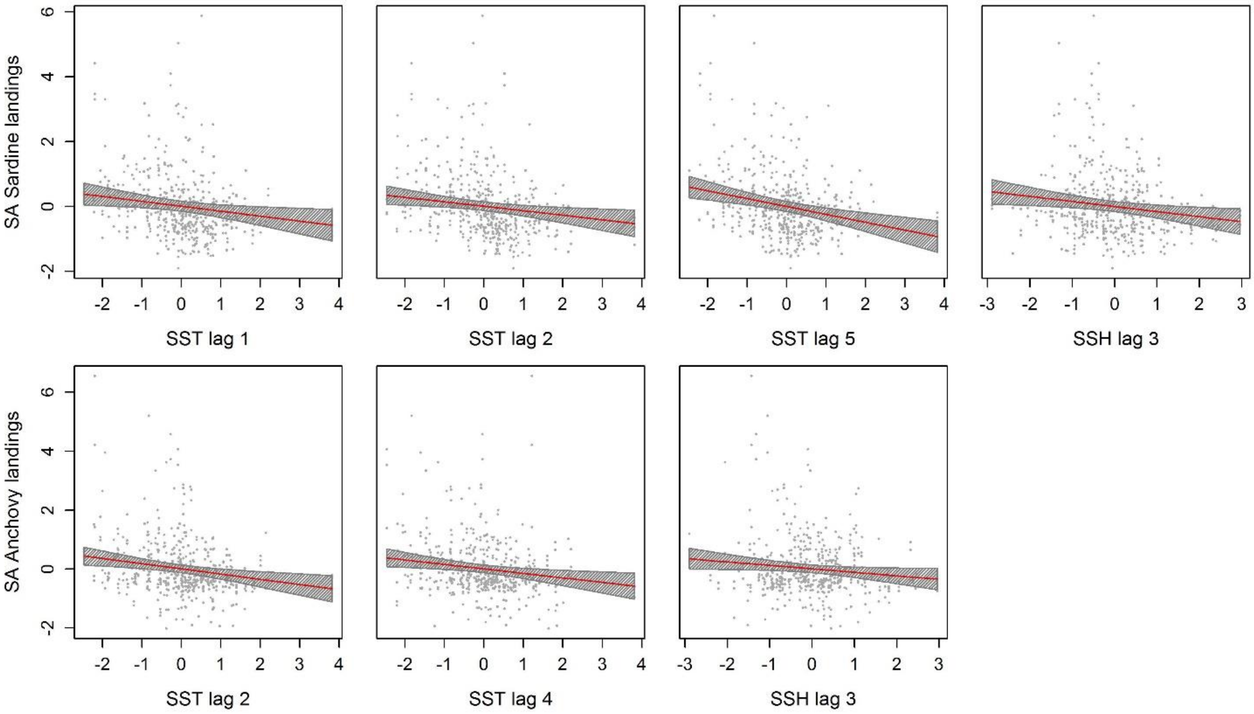

Figure A3. Final GLS models for the Central sector. Red line indicate the fitted model and the 95 % of confidence interval. SA= Seasonally adjusted.

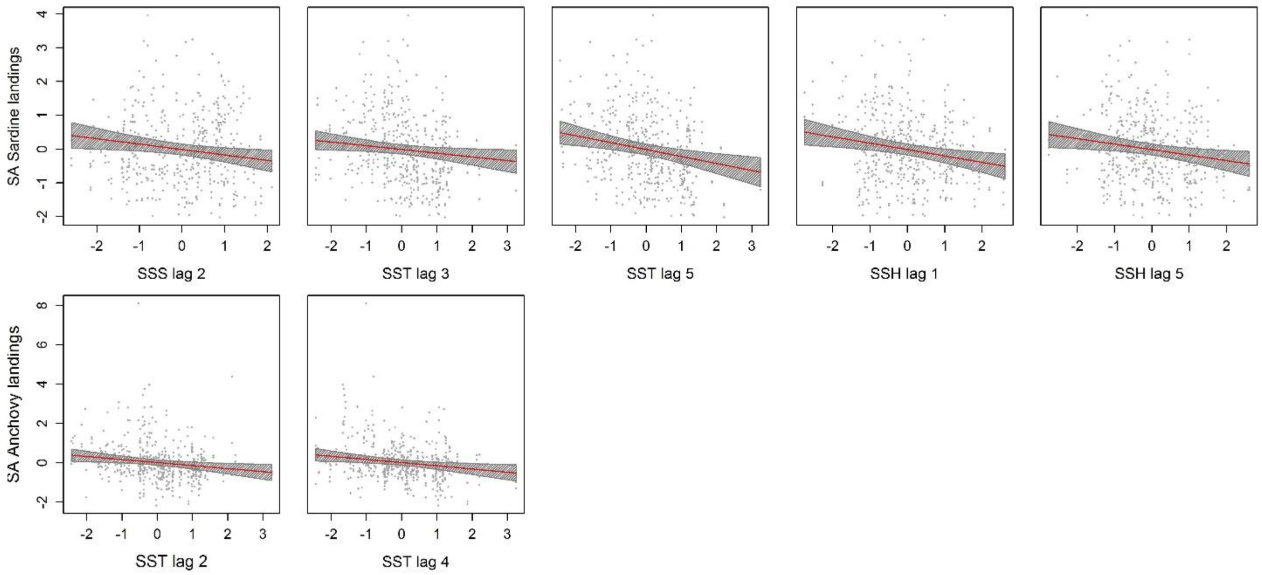

Figure A4. Final GLS models for the Southern sector. Red line indicate the fitted model and the 95 % of confidence interval. SA= Seasonally adjuste

General Discussions and Conclusions

Discussions

The objective of this PhD thesis was to detect the main environmental factors involved in the fluctuations of the abundance of small pelagic fishes (Sardine and Anchovy) along the coast of the North-East Spain, whose catches were historically one of the highest of the entire Mediterranean Sea, which after some anomalies have been observed to decrease strongly, especially regarding Sardine.

Before focusing on the environmental influences, the spatial pattern of the fishing effort directed toward both species by using VMS data was studied to understand the behavior of the purse seine fleet targeting this species. This analysis showed that the fleet spatial distribution captured the features of the distributions of small pelagic populations in the area (Chapter 1). The results of this chapter led to a better understanding and visualization of the spatial distribution of catches, which form the basis of the landings data series[1] studied in the rest of the PhD thesis. Then I considered both local environmental factors (Chapters 2 and 3) and climate index (WeMOI) (Chapter 3) and searched which of these was strictly linked with landings of both species. Results of these chapters showed that non-linearity better described the relationships between the availability of the resource and the environmental factors than previous studies effectuated in the area (e.g. Lloret *et al.*, 2001; Martín *et al.*, 2012). The results highlighted the importance of temperature, salinity and currents for both species, and the role of the WeMOI index in favoring sardine abundance when it was in a positive phase.

Finally, I described the main driving forces acting on the critical stages of development of both species in the area and provided evidence, independent from the studies directly targeted on early life stages of development, that the temperature and sea surface height (used as a proxy of mesoscale processes) play an important role in the recruitment variability of the species studied (Chapter 4). In addition, we highlighted how the effects of these drivers were not stationary but transient over time (Chapter 4).

The decreasing trend and the shifts (i.e. breakpoints) of both sardine and anchovy landings of the Northeast Coast of Spain during the 90's, together with the relationships found with concentration and enrichment processes (positive phase of WeMOI characterized by low temperature and strong wind mixing, or low

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[1] In these purse seine fisheries, it is commonly assumed that discards are negligible and catches are equated to landings (cf. for instance recent stock assessments in GFCM or STECF).

salinity continental waters), concurred with the ones found in the adjacent northernmost area, i.e. the Gulf of Lions (e.g. Van Beveren et al. 2016). These similarities lead to think that these drivers act and have acted on a larger scale, that is, the NW Mediterranean basin rather than just the Catalan Sea. This is even truer when considering the dynamics of the coastal circulation of the Northwestern basin. This is characterized by the Northern Current flowing along the continental slope from the Gulf of Lions toward the Catalan Shelf perturbed by significant mesoscale activity like meanders eddies and filament (Millot 1987) which greatly influence biological activity (Garreau et al. 2011; Sabatés et al. 2001). This main permanent flow southward allows the transport of biological material, including pelagic eggs and passive larvae, from the Gulf of Lions toward the Catalan Coast (e.g. Sabatés et al. 2001, 2007). A recent study aimed to depict the transport of anchovy fish larvae in NW Mediterranean Sea (Ospina-Alvarez et al., 2015), by considering both hydrodynamic forcing and spawning behavior, identified the connectivity between the Gulf of Lions and the Catalan Coast as being characterized by an occasional two-way exchange of larvae, and by a marked but not uniform, in time and location, exchange southward, as also previously suggested by Sabatés et al. 2001. Consequently, this exchange can play an important role in structuring the adult population in terms of abundance, acting as a transport from spawning areas toward the nursery areas. Therefore, when modeling local adults fish abundance (landings) as in this case study, it is important to note that it could be the result depending on the year (even if in small fraction especially in the central and southern parts of the Catalan Coast), of loss or gain of a fraction of recruited individuals due to the exchange between the Gulf of Lions and the Catalan Coast (Ospina-Alvarez et al., 2015). At the same time, our results regarding the northern part of the Catalan Coast being characterized by a strict connectivity with the Gulf of Lions (Ospina-Alvarez et al., 2015), could be extended, even if with extreme caution, to the nearby area. Although the scientific knowledge is less extensive for sardine, it is plausible to think that the exchanges of the passive early life stages between the two areas occur also for this forage fish.

The reader may find here a final discussion in which information from the chapters and other studies is given in order to provide a general overview and explain the small pelagic populations’ trend in the area. The discussion is organized by distinguishing the two kinds of relationships considered; those related with favorable environmental conditions which shape the abundance of the small pelagic fishes by promoting their distribution and concentration, which unavoidably it is reflected on landings values; and those related with the recruitment success and their changes over time.

The central hypothesis of this study was that environmental changes were the main drivers of the small pelagic populations in the area, but, the lack of data on biomass and abundance precluded making direct links with the environmental factors. Actual biomass and abundance of small pelagics is usually estimated through acoustic surveys (MEDIAS, Mediterranean acoustic surveys), which have also the advantage of providing also geo-located information but are of complex logistics and high costs (e.g. Carpi *et al.*, 2015). The use of landings as proxy for biomass or abundance of small pelagic populations is common in studies of these species (e.g. Lloret *et al.*, 2004; Katara *et al.*, 2011; Ruiz *et al.*, 2013; Leitão, 2015; Teixeira *et al.*, 2016). Although we are aware that these data are only an approximation, landings offer the possibility of inferring, to a certain level, the population variation thanks to the strong consistency between them and annual biomass estimates (GFCM, 2015).

Populations responses at immediate and intermediate temporal scales

The success of small pelagic catches depends on the ability of the fishermen to recognize the spatial patterns of fish and identify high-density patches (Hieu *et al.*, 2014). In NW Mediterranean Sea the purse seiners fleet has a very mobile behaviour and the vessels usually perform migration along the coast to search and reach areas where the resource is abundant (Pertierra and Lleonart, 1996). The search of pelagic resources is basically a problem of localization which can be summarised as follows: each vessel explores the sea using information about past fishing ground positions and its own present information from echosounders or other detection devices, but also evaluates the activity of the other vessels simultaneously exploiting the same fishing grounds, so if another finds the resource all vessels can converge into this area and fish (Russo *et al.*, 2015). Consequently, the spatial distribution of the fishing effort and its spatial structure depends on how the resource (i.e., small pelagic fish) is structured, which in turn is dependent on the environmental conditions and how they change spatiotemporally.

Gregarious fish such as anchovy and sardine have different levels of aggregation (rarely are they observed alone), from core concentrations or nuclei within a school to large concentration or sub-stocks, passing though schools/shoals and clusters (Fréon *et al.*, 2005). The importance of the environmental processes influence on fish distribution rises with the increase of the level of aggregations (Fig. 1) (Bertrand *et al.*, 2008). The distribution and structure and size of the clusters, which correspond to the aggregation level in which fishers operate, depend mainly on those mesoscale processes which shape the zooplankton distribution patches like eddies or fronts (Bertrand *et al.*, 2008). In addition, cluster distribution depends on those environmental forces such as temperature and salinity which, apart from acting directly on the physiological requirements of the fish (e.g. Pörtner and Peck, 2010), are responsible for the zooplankton availability and quality in terms of community composition. This can be altered over time owing to its increase together with the increase in stratification or changes in ocean currents circulations (Calvo *et al.*, 2011).

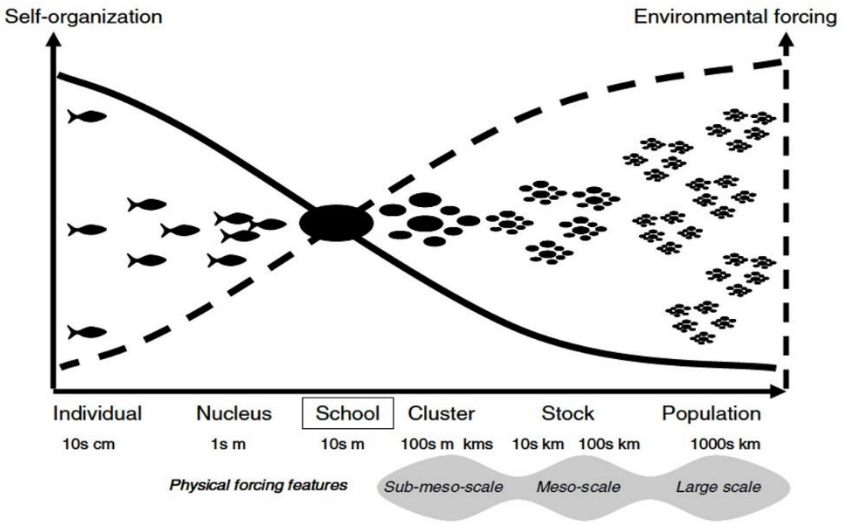

Figure 1. A conceptual model describing the relative importance of factors regulating aggregation as a function of spatial scale. y-axis=oneself-organization, x-axis= environmental forcing. From Bertrand et al. 2008

In Chapters 2 and 3 we stated the importance of salinity, temperature and current velocity of both meridional and zonal directions, used as a proxy of concentration and retention processes, for landings of both species and the importance of WeMOI index for sardine when is in its positive phase indicating strong river runoff and wind mixing (García-Sellés et al., 2010; Martín et al., 2012). These relationships were non-linear and allowed identification of ranges of values of these variables which favor the abundance of both species. By superimposing this information with the spatial distribution of the effort obtained in Chapter 1 it seems that effectively fishermen, according to our findings, allocate and assemble their efforts where environmental conditions are more favorable for the concentration of high abundance of fish (Fig. 2).

Although fishing vessels can migrate among different harbors the fishing range is local because the fleet is obliged to return to port daily, and the boats must be moored for a minimum of 12 hours daily (Pertierra and Lleonart, 1996). Even though adults of small pelagic have less strict habitat requirements than their early life stages (e.g. Bellido *et al.*, 2008; Giannoulaki *et al.*, 2013; Petitgas *et al.*, 2013) it is likely that those large fish aggregations, which are easier to be located by fishermen (Hieu *et al.*, 2014), shift their distribution in response to changes in the environment so as to maximize the individuals fitness (Bertrand *et al.*, 2008). This makes them more available for certain local fishing operations and unavailable for others.

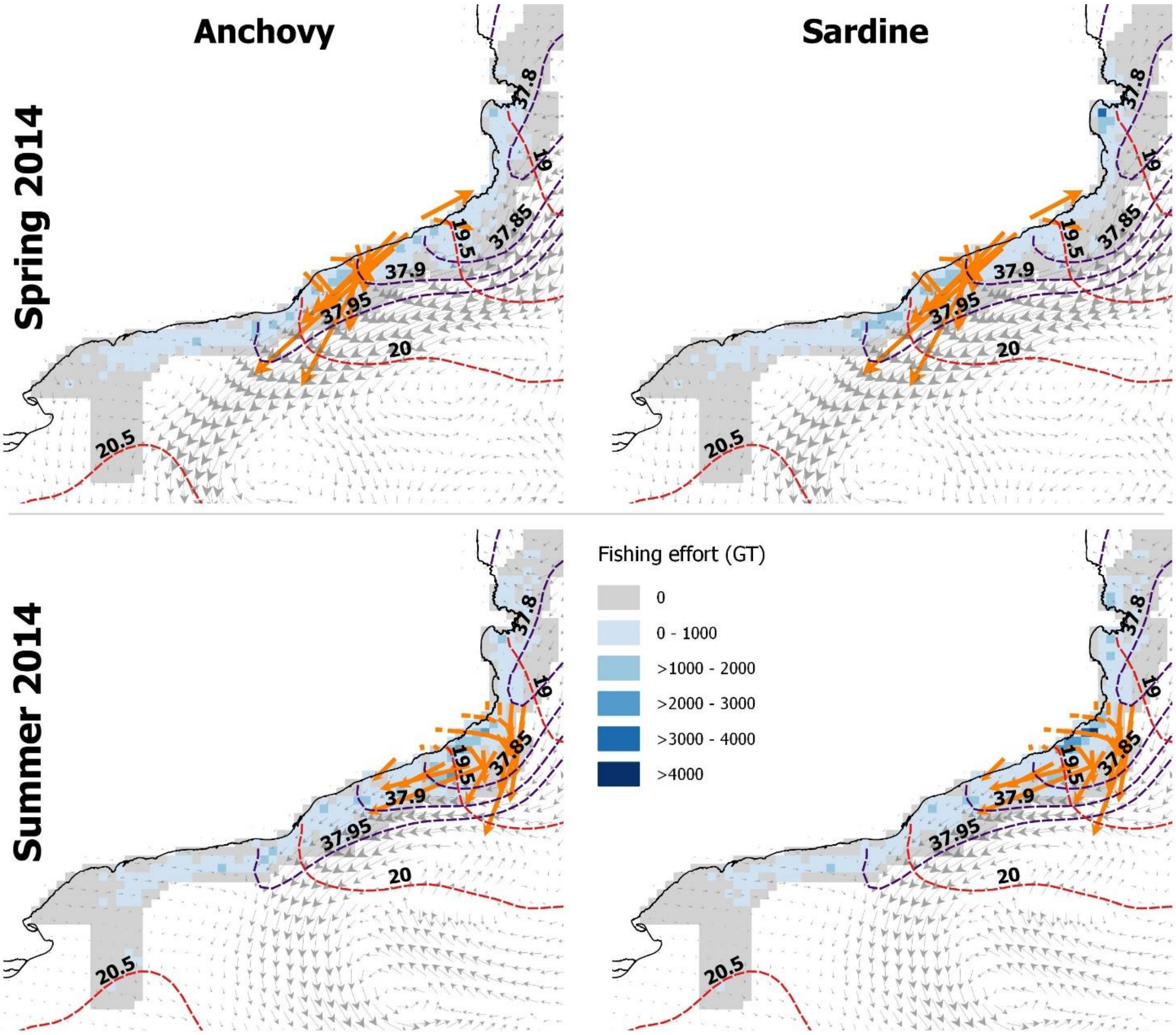

Figure 2. Fishing effort direct toward anchovy and sardine in spring and summer 2014. Isotherm and isohalines in red and purple respectively. Direction and Magnitude of the current velocity estimated from Meridional and Zonal current. For a better visualization of the possible concentration process the style of the vector representing the Magnitude of the currents in the area at which the highest fishing effort occurred was amplified. GT=Gross tonnage.

The size or geographical area occupied by the aggregation formation of small pelagic fishes clearly does not depend only on the environmental forces but also on the size of population (MacCall, 1990; Bertrand et al., 2004b). In a recent study Saraux et al., 2014 described the spatial organization of small pelagics in the Gulf of Lions and identified a different behavior in terms of aggregation of the two species. According to their results, anchovy seems to follow the relationship between the geographical area occupied and abundance proposed by MacCall, 1990 and known as the 'basin model', where density and area vary with abundance. Such kind of spatial organization was also observed in other systems (i.e. water off South Africa, Kuroshio

Current and in the Humboldt Current) by Barange et al., 2009. On the other hand, according to the findings of Saraux et al., 2014, sardines seem to follow the ‘proportional model’, where the area occupied remains constant and local density varies in proportion to abundance (Hilborn et al., 1992; Petitgas, 1997).

Part of the lasting decrease in landings of sardine and the unclear trend regarding anchovy could be hypothetically explained in a summarized way by combining our findings concerned with: 1) relationships with the environmental forces stressed to be non-linear (Chapters 2 and 3); 2) the changes in the aggregation distribution of the small pelagics which is reflected unavoidably on the fishing operations distribution (Chapter 1); 3) the kinds of the aggregation behavior of these species mentioned above, and 4) the environmental changes observed in the Catalan Sea.

Over the last 40 years evident changes in the environment such as the increase in temperature and salinity and the diminution of wind stress and water mixing have been observed in the NW Mediterranean Sea (Vargas-Yáñez et al., 2010a, 2010b; Calvo et al., 2011). These changes have inevitably affected sub-mesoscale and mesoscale processes by acting on the hydrology as well as on the stratification, and on the ocean currents patterns which in turn affects the distribution and the abundance of the zooplankton communities (Molinero et al., 2008; Calvo et al., 2011; Villate et al., 2014). Such variations lead to an alteration of the distribution and to the decrease of the abundance of the prey patches, which influences the distribution of the cluster aggregations of both species due to their biological requirement (Bertrand et al., 2008). The general oceanographic and topographic features of the areas which forces the distribution of these population to be associated with the few point sources of nutrient (e.g. Giannoulaki et al., 2013) together with the catchability of these populations which depends on how well fishers perceive their spatial patterns and how successfully they identify high-density fish patches (Hieu et al., 2014), make these clusters more likely to be identified by fishermen during fishing operation. Fewer suitable areas due to the changing environment could have thus caused a reduction of the aggregations of both species, as evidenced for instance with the use the Threshold-GAM in the relationship between anchovy LPUE and temperature (Chapter 2), but the effects of the less suitable conditions were probably different for the two species owing to the different behaviour they have (Saraux et al., 2014; Barra et al., 2015). Specifically, sardines don’t spread their area, being capable of structuring high-density patches. This increases their availability to fishermen, resulting in a magnification of catchability when the population is at the same time particularly vulnerable to the unfavorable environment conditions, determining a drastic reduction of the abundance. On the contrary, anchovy is capable of spreading into areas less suitable and could thereby have avoided the rapid overfishing caused by the formation of these extremely dense patches. This hypothesis about the changes in the ranges of anchovy and sardine habitat to explain the variation of their populations is not new. In fact, authors such as Bertrand et al., 2004a or Gutiérrez et al., 2007 proposed the 'habitat-based' hypothesis to explain fluctuations and shifts in abundance in pelagic fish populations in upwelling ecosystems and emphasized the role of the aggregation as an important parameter to explain variation in abundance because it reflected how the fish distribution responded to changing environmental conditions.

Lagged populations response to environmental drivers

So as to compensate for the low lifetime fecundity small pelagic species display several characteristics such as early maturation or the production of many eggs released in batches throughout protracted periods of time (Blaxter and Hunter, 1982). These characteristics make their life history traits highly sensitive to the environment (e.g. Cury and Roy, 1989; Bakun, 1996; Checkley et al., 2009), and because these traits can influence population dynamics years later, when cohorts reach reproductive maturity, direct effects of environment on development and reproduction can produce lagged population responses to environmental changes (e.g. Katara et al., 2011; Santos et al., 2012; Teixeira et al., 2016). In Chapter 4 temperature and sea surface height, which is indicative of convergent and divergent processes, were identified as the main forces driving the landings variation in the Catalan Sea. These drivers were found to have a significant influence on the early stages of development of both species, as has been previously outlined by other authors in other parts of the Mediterranean Sea (e.g. Giannoulaki et al., 2011, 2013; Katara et al., 2011; Tugores et al., 2011; Bonanno et al., 2014) as well as in other systems (e.g. Asch and Checkley, 2013; Nieto et al., 2014). Although significant relationships were encountered, the presence of long-term trends and the shifts (evidenced by the breakpoint analysis) of both landings and environmental data lead to think that the relationships might not be statistically stationary i.e. the functional form of the relationships changed over time (e.g. Hidalgo et al., 2012; Schmidt et al., 2014; Szuwalski and Hollowed, 2016) due to the evident non-stationary properties of the variables in question. This implied that even if the local environmental variables significantly affect the early life stages of sardine and anchovy, they might not extend into the future and that the effects inferred from the past may not be relevant today (e.g. Planque, 2016). Since one of the obvious advantages of using lagged regression models is just that of producing prediction (Post, 2004), evaluating if such relationships were stationary resulted to be an important issue. For this reason, I decided to use the rolling regression approach which was particularly useful in this context since it allowed me to examine temporal changes both within and across years without choosing an arbitrary point (Hsieh et al., 2009; Hidalgo et al., 2011; Schmidt et al., 2014). As a result of the analysis of the long-term relationships between landings of sardine and anchovy and local environmental variables, we were able to take the first step in identifying when the relationships with seas surface high and temperature began to emerge and how they have changed over time. Obviously, understanding what led to the non-stationarity in the response of the individuals and populations to physical processes is a complex issue, and based on the results presented here it can only be hypothesized. Non-stationary responses to the environment are mainly due to an alteration of the population processes such as shifts in reproductive success, mortality, growth, or maturation rate (Planque et al., 2010; Szuwalski and Hollowed, 2016). Both anthropogenic and environmental factors (e.g. Anderson et al., 2008; Hidalgo et al., 2011) can cause alteration of these processes. For instance, warmer temperature values within the optimal temperature range for sardines increases their growth and development rates (e.g. Garrido et al., 2016). In addition, the fishery can alter the reproductive success of the population due to the removal of adult individuals (e.g. Hsieh et al., 2006). The total annual number of spawns, in fact, depends on the duration of the spawning period and the spawning frequency of individuals. Both these spawning parameters can be size/age dependent in anchovies and sardines, so as a consequence of the removal of the adult individuals, the total annual number of spawns can decrease when the size/age decreases (Ganias et al., 2014 and references therein).

Considering this, a plausible hypothesis could be the co-occurrent effects of the changing environment and the effects of the fishery. Fishing exists in the area since ancient time (Lleonart and Maynou, 2003; Palomera et al., 2007), and because fishing typically targets the larger individuals of a species, the average size and thus the age of the target population could, in turn, be decreased (Anderson et al., 2008; Hsieh et al., 2010; Planque et al., 2010). Changes in both size structure and age of both species have been observed in the NW Mediterranean Sea and were mainly attributed to the changes in prey availability and composition due to environmental variability (Van Beveren et al., 2014; Brosset et al., 2015). Obviously, as specified above, both fishing and environmental factors are not mutually exclusive, in fact, they might have acted synergistically on the age-size reduction of the two populations (Van Beveren et al., 2014). The reduced demographic structure of both populations could have in turn reduced the capacity to buffer the changing environment by reducing the duration of the spawning season, thereby reducing the probability of the eggs and larvae encountering the optimal environmental window because of the reduced reproductive potential young individuals have compared to the older and larger (Planque et al., 2010; Ganias et al., 2014).

Therefore, the reported decrease of the age-size structure of both populations in the area (Van Beveren et al., 2014; Brosset et al., 2017) together with the likely changes in population processes (e.g. growth, maturation), which can result from both linkages to non-stationary environmental variables (Fulton, 2011) and fishing exploitation (Anderson et al., 2008), might be a possible explanation of the transient responses of sardine and anchovy in relation to the local environmental drivers observed over time.

A possible signal which strengthens this hypothesis was shown in chapter 2. A shift towards lower values inside the range of temperature preferred by the anchovy for spawning was observed. This reduction in the preferred temperature can be indicative of smaller temporal windows in which the spawning aggregations occurred owing to an increasingly juvenile population. This consideration is further supported by the recent findings on the reduction in size reported for anchovy during the same period (2006-2007) by Brosset et al., 2017.

Study limitations and Perspectives

Despite having a better understanding of the environmental driving forces acting on the two small pelagic populations along the Catalan Coast many questions remain unanswered. The two hypothesis specified above could be considered possible starting points for future research while at the same time highlighting some limitations of the study, specially in regard to the kind of data which could add to our findings.

For example, one of the limitations of this study could be the use of landings data as a proxy of the abundance of both populations. Commercial fishing data provide an inexpensive sampling of the exploited species with wide spatiotemporal scale coverage and in the area, thanks to both the fishing regulations and the topography, offer a fairly good representation of the small pelagic populations size. However, since these data rely on the variability of catchability which varies with the behavior of fish, fishers and their interactions (e.g. Fréon and Misund, 1999), a step further might be coupling available data from acoustic surveys with spatial explicit fishing data. Doing so, a better understanding of the concentration behavior of vessels in relation to the changes in biomass of anchovy and sardine related to the adjustment of their density and range of distribution could be provided.

In addition, inferring the possible results for a whole year (acoustic estimates are effectuated once a year) by discriminating for example the cluster size by using similarities in the VMS tracks, the distribution and the aggregation patterns could be analyzed in relation to the temperature, salinity, currents and nutrient concentrations in order to evaluate in a spatially explicit way the effects of these on the small pelagic aggregations and how these relationships change over time.

Another gap of the study is the lack of the size/age structure of commercial catches whose availability could improve our findings. By using historical monthly time series of biological parameters of commercial catches to analyze the evolution of the average size and weight over time, the non-stationary response observed in relation to the local drivers could be refuted or demonstrated. However, the relevant time series over sufficiently long-time scales (e.g. 10 years or more) are simply unavailable. Trends and breakpoints might be analyzed using, for example, similar time series analyses, as used in chapter 4, and compared with both landings and the local environmental drivers. In addition, the changing effects on landings of environmental drivers as a function of the size-age structure could be explored by the use of different threshold models in which the demographic parameters could be used as a fixed threshold (likewise in chapter 2) or as a variable coefficient model *e.g* Ciannelli *et al.*, 2012.

Despite these unanswered questions that could be looked into, this work is one step forward in the understanding of the small pelagic populations abundance variability in the Catalan Sea.

Conclusions

The main conclusions derived from this study can be summarized as follows:

1) The use of spatial indicators applied to the fishing efforts showed that the temporal and spatial organization of fishing operations differed when directed toward anchovy or sardine. When directed toward anchovy the fishing effort's spatial distribution changed between seasons and revealed a clear application of the fishermen's knowledge of the spawning aggregation behavior of this species when allocating and concentrating their fishing effort. In addition, fishing effort increased when the level of spatial concentration (concentration index) rose, suggesting an aggregative behavior of fishing vessels when an anchovy cluster was detected. On the contrary, when directed toward sardine these spatial patterns described did not occur. The fishing effort's concentration curve and its related index, which provide information on the proportion of the area occupied by the fishing operations, could give, if coupled with available catch data, a preliminary idea of the status of the exploitation of the small pelagic fishes.

2) Fishing effort distribution directed toward both species reflected spatial patchiness which was highly consistent with the spatial structures described by other authors using acoustic surveys data. Therefore, we should consider the possibility of using these data as a complementary tool for studying the spatial distribution of small pelagic fishes for management or assessment purpose, and also take advantage of the fact that it provides information of a whole year, unlike acoustic survey data.

3) High productive low salinity waters together with the currents flowing southward and westward, both of which indicate the occurrence of concentration and retention processes during the spring and summer seasons, favoured the Landing per unit effort (LPUE) used as a proxy of the anchovy adult abundance.

4) During the decade 2000-2010, the threshold GAM allowed to identify a threshold effect of temperature on adult anchovy abundance in the northernmost part of the Catalan Sea, suggesting a reduction of the spawning period and the thermal window in which the spawning aggregation occurred.

5) The Western Mediterranean Oscillation index (WeMOI), which was used as a proxy of productivity-enhancing oceanic features, played an important driving role in favouring Sardine LPUE, but the relationship between them was non-linear. Our results expand those of other studies by showing that this relationship became almost or totally insignificant when WeMOI reached high absolute values.

6) Sardine tended to prefer a restricted range of salinity values, avoiding both low and high salty waters, and their abundance was favoured by the current flowing northward, which is essential for the generation of the mesoscale anticyclonic eddies implicated in retention and concentration processes along the Catalan coast.

7) Sea surface height (SSH), used as a proxy of convergence and divergence processes, together with the sea surface temperature (SST) were the two main environmental drivers which, by acting on the eggs/larvae and juvenile stages of both species, explained the abundance fluctuations of Sardine and Anchovy in the Catalan Sea.

8) The strength with which the SSH and SST affected the abundance of both populations changed over time owing to the non-stationary behaviour of the environmental variables (*i.e.* their mean values steadily changed) together with the extended exploitation of both species in the area. The effects of both environmental factors became stronger during the periods characterized by a sudden increase or decrease in their mean values or when they were higher compared to other periods. The variation over time of the strength of the relationship between these environmental variables and the population abundance are supposed to be due to the synergic effects of the environmental changes and the variations in demographic patterns described for both populations in the NW Mediterranean.

References

Anderson, C. N. K., Hsieh, C., Sandin, S. A., Hewitt, R., Hollowed, A., Beddington, J., May, R. M., *et al.* 2008. Why fishing magnifies fluctuations in fish abundance. *Nature*, 452: 835–839.

Asch, R. G., and Checkley, D. M. 2013. Dynamic height: A key variable for identifying the spawning habitat of small pelagic fishes. *Deep Sea Research Part I: Oceanographic Research Papers*, 71: 79–91.

Bakun, A. 1996. Patterns in the ocean: ocean processes and marine population dynamics. Patterns in the ocean: ocean processes and marine population dynamics.

Barange, M., Coetzee, J., Takasuka, A., Hill, K., Gutierrez, M., Oozeki, Y., Lingen, C. van der, *et al.* 2009. Habitat expansion and contraction in anchovy and sardine populations. *Progress in Oceanography*, 83: 251–260.

Barra, M., Petitgas, P., Bonanno, A., Somarakis, S., Woillez, M., Machias, A., Mazzola, S., *et al.* 2015. Interannual Changes in Biomass Affect the Spatial Aggregations of Anchovy and Sardine as Evidenced by Geostatistical and Spatial Indicators. *PLoS ONE*, 10.

Bellido, J. M., Brown, A. M., Valavanis, V. D., Giráldez, A., Pierce, G. J., Iglesias, M., and Palialexis, A. 2008. Identifying essential fish habitat for small pelagic species in Spanish Mediterranean waters. *Hydrobiologia*, 612: 171–184.

Bertrand, A., Segura, M., Gutiérrez, M., and Vásquez, L. 2004a. From small-scale habitat loopholes to decadal cycles: a habitat-based hypothesis explaining fluctuation in pelagic fish populations off Peru. *Fish and fisheries*, 5: 296–316.

Bertrand, A., Gerlotto, F., Bertrand, S., Guti?rrez, M., Alza, L., Chipollini, A., D?az, E., *et al.* 2008. Schooling behaviour and environmental forcing in relation to anchoveta distribution: An analysis across multiple spatial scales. *Progress in Oceanography*, 79: 264–277.

Bertrand, S., Díaz, E., and Ñiquen, M. 2004b. Interactions between fish and fisher’s spatial distribution and behaviour: an empirical study of the anchovy (Engraulis ringens) fishery of Peru*. ICES Journal of Marine Science: Journal du Conseil*, 61: 1127–1136.

Blaxter, J. H. S., and Hunter, J. R. 1982. The biology of the clupeoid fishes. Advances in marine biology, 20: 1–223.

Bonanno, A., Giannoulaki, M., Barra, M., Basilone, G., Machias, A., Genovese, S., Goncharov, S., *et al.* 2014. Habitat Selection Response of Small Pelagic Fish in Different Environments. Two Examples from the Oligotrophic Mediterranean Sea. *PLOS ONE*, 9: e101498.

Brosset, P., Ménard, F., Fromentin, J., Bonhommeau, S., Ulses, C., Bourdeix, J., Bigot, J., *et al.* 2015. Influence of environmental variability and age on the body condition of small pelagic fish in the Gulf of Lions. *Marine Ecology Progress Series*, 529: 219–231.

Brosset, P., Fromentin, J.-M., Van Beveren, E., Lloret, J., Marques, V., Basilone, G., Bonanno, A., *et al.* 2017. Spatio-temporal patterns and environmental controls of small pelagic fish body condition from contrasted Mediterranean areas. *Progress in Oceanography*, 151: 149–162.

Calvo, E., Simó, R., Coma, R., Ribes, M., Pascual, J., Sabatés, A., Gili, J., *et al.* 2011. Effects of climate change on Mediterranean marine ecosystems: the case of the Catalan Sea. *Climate Research*, 50: 1–29.

Carpi, P., Martinelli, M., Belardinelli, A., Russo, A., Arneri, E., Coluccelli, A., and Santojanni, A. 2015. Coupling an oceanographic model to a Fishery Observing System through mixed models: the importance of fronts for anchovy in the Adriatic Sea. *Fisheries Oceanography*, 24: 521–532.

Checkley et al. 2009. Climate change and small pelagic fish. *Cambridge University Press, Cambridge, UK* ; New York. 372 pp.

Ciannelli, L., Bartolino, V., and Chan, K.-S. 2012. Non-additive and non-stationary properties in the spatial distribution of a large marine fish population. *Proceedings of the Royal Society B: Biological Sciences*, 279: 3635–3642.

Cury, P., and Roy, C. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. *Canadian Journal of Fisheries and Aquatic Sciences*, 46: 670–680.

Fréon, P., and Misund, O. A. 1999. Dynamics of pelagic fish distribution and behaviour: effects on fisheries and stock assessment. *Fishing News Books*, Oxford. 348 pp.

Fréon, P., Cury, P., Shannon, L., and Roy, C. 2005. Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: a review. *Bulletin of Marine Science*, 76: 385–462.

Fulton, E. A. 2011. Interesting times: winners, losers, and system shifts under climate change around Australia. ICES Journal of Marine Science: *Journal du Conseil*, 68: 1329–1342.

Ganias, K., Somarakis, S., and Nunes, C. 2014. Reproductive potential. Biology and Ecology of Sardines and Anchovies. *CRC Press, Boca Raton*: 79–121.

García-Sellés, C., Peña, J. C., Martí, G., Oller, P., and Martínez, P. 2010. WeMOI and NAOi influence on major avalanche activity in the Eastern Pyrenees. *Cold Regions Science and Technology*, 64: 137–145.

Garreau, P., Garnier, V., and Schaeffer, A. 2011. Eddy resolving modelling of the Gulf of Lions and Catalan Sea. Ocean Dynamics, 61: 991–1003.

Garrido, S., Cristóvão, A., Caldeira, C., Ben-Hamadou, R., Baylina, N., Batista, H., Saiz, E., *et al.* 2016. Effect of temperature on the growth, survival, development and foraging behaviour of Sardina pilchardus larvae. *Marine Ecology Progress Series*, 559: 131–145.

Giannoulaki, M., Pyrounaki, M. M., Liorzou, B., Leonori, I., Valavanis, V. D., Tsagarakis, K., Bigot, J. L., *et al.* 2011. Habitat suitability modelling for sardine juveniles (Sardina pilchardus) in the Mediterranean Sea: Habitat suitability modelling for sardine juveniles. *Fisheries Oceanography*, 20: 367–382.

Giannoulaki, M., Iglesias, M., Tugores, M. P., Bonanno, A., Patti, B., De Felice, A., Leonori, I., *et al.* 2013. Characterizing the potential habitat of European anchovy *Engraulis encrasicolus* in the Mediterranean Sea, at different life stages: *Habitat of anchovy in the Mediterranean*. Fisheries Oceanography, 22: 69–89.

Gutiérrez, M., Swartzman, G., Bertrand, A., and Bertrand, S. 2007. Anchovy (*Engraulis ringens*) and sardine (*Sardinops sagax*) spatial dynamics and aggregation patterns in the Humboldt Current ecosystem, Peru, from 1983 to 2003. *Fisheries Oceanography*, 16: 155–168.

Hidalgo, M., Rouyer, T., Molinero, J., Massutí, E., Moranta, J., Guijarro, B., and Stenseth, N. 2011. Synergistic effects of fishing-induced demographic changes and climate variation on fish population dynamics. *Marine Ecology Progress Series*, 426: 1–12.

Hidalgo, M., Gusdal, Y., Dingsor, G. E., Hjermann, D., Ottersen, G., Stige, L. C., Melsom, A., *et al.* 2012. A combination of hydrodynamical and statistical modelling reveals non-stationary climate effects on fish larvae distributions. *Proceedings of the Royal Society B: Biological Sciences*, 279: 275–283.

Hieu, N. T., Brochier, T., Tri, N.-H., Auger, P., and Brehmer, P. 2014. Effect of Small Versus Large Clusters of Fish School on the Yield of a Purse-Seine Small Pelagic Fishery Including a Marine Protected Area. *Acta Biotheoretica*, 62: 339–353.

Hilborn, R., Walters, C. J., and others. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. *Reviews in Fish Biology and Fisheries*, 2: 177–178.

Hsieh, C., Reiss, C. S., Hunter, J. R., Beddington, J. R., May, R. M., and Sugihara, G. 2006. Fishing elevates variability in the abundance of exploited species. *Nature*, 443: 859–862.

Hsieh, C., Yamauchi, A., Nakazawa, T., and Wang, W.-F. 2010. Fishing effects on age and spatial structures undermine population stability of fishes. *Aquatic Sciences*, 72: 165–178.

Hsieh, C.-H., Chen, C.-S., Chiu, T.-S., Lee, K.-T., Shieh, F.-J., Pan, J.-Y., and Lee, M.-A. 2009. Time series analyses reveal transient relationships between abundance of larval anchovy and environmental variables in the coastal waters southwest of Taiwan. *Fisheries Oceanography*, 18: 102–117.

Katara, I., Pierce, G. J., Illian, J., and Scott, B. E. 2011. Environmental drivers of the anchovy/sardine complex in the Eastern Mediterranean. *Hydrobiologia*, 670: 49–65.

Leitão, F. 2015. Time series analyses reveal environmental and fisheries controls on Atlantic horse mackerel (Trachurus trachurus) catch rates. *Continental Shelf Research*, 111: 342–352.

Lleonart, J., and Maynou, F. 2003. Fish stock assessments in the Mediterranean: state of the art. *Scientia Marina*, 67: 37–49.

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

Lloret, J., Palomera, I., Salat, J., and Solé, I. 2004. Impact of freshwater input and wind on landings of anchovy (Engraulis encrasicolus) and sardine (Sardina pilchardus) in shelf waters surrounding the Ebre (Ebro) River delta (north-western Mediterranean*). Fisheries Oceanography*, 13: 102–110.

MacCall, A. D. 1990. Dynamic geography of marine fish populations. Washington Sea Grant Program Seattle, WA. http://www.sidalc.net/cgi-bin/wxis.exe/?IsisScript=libri.xis&method=post&formato=2&cantidad=1&expresion=mfn=017548 (Accessed 31 May 2017).

Martín, P., Sabatés, A., Lloret, J., and Martin-Vide, J. 2012. Climate modulation of fish populations: the role of the Western Mediterranean Oscillation (WeMO) in sardine (Sardina pilchardus) and anchovy (Engraulis encrasicolus) production in the north-western Mediterranean. *Climatic Change*, 110: 925–939.

Molinero, J. C., Ibanez, F., Souissi, S., Buecher, E., Dallot, S., and Nival, P. 2008. Climate control on the long-term anomalous changes of zooplankton communities in the Northwestern Mediterranean. *Global Change Biology*, 14: 11–26.

Nieto, K., McClatchie, S., Weber, E. D., and Lennert-Cody, C. E. 2014. Effect of mesoscale eddies and streamers on sardine spawning habitat and recruitment success off Southern and central California. *Journal of Geophysical Research: Oceans*, 119: 6330–6339.

Ospina-Alvarez, A., Catalán, I. A., Bernal, M., Roos, D., and Palomera, I. 2015. From egg production to recruits: Connectivity and inter-annual variability in the recruitment patterns of European anchovy in the northwestern Mediterranean. Progress in Oceanography, 138: 431–447.

Palomera, I., Olivar, M. P., Salat, J., Sabatés, A., Coll, M., García, A., and Morales-Nin, B. 2007. Small pelagic fish in the NW Mediterranean Sea: An ecological review. *Progress in Oceanography*, 74: 377–396.

Pertierra, J. P., and Lleonart, J. 1996. NW Mediterranean anchovy fisheries. Scientia Marina, 60: 257–267.

Petitgas, P. 1997. Sole egg distributions in space and time characterised by a geostatistical model and its estimation variance. *ICES Journal of Marine Science*, 54: 213–225.

Petitgas, P., Rijnsdorp, A. D., Dickey-Collas, M., Engelhard, G. H., Peck, M. A., Pinnegar, J. K., Drinkwater, K., *et al.* 2013. Impacts of climate change on the complex life cycles of fish. *Fisheries Oceanography*, 22: 121–139.

Planque, B., Fromentin, J.-M., Cury, P., Drinkwater, K. F., Jennings, S., Perry, R. I., and Kifani, S. 2010. How does fishing alter marine populations and ecosystems sensitivity to climate? *Journal of Marine Systems*, 79: 403–417.

Planque, B. 2016. Projecting the future state of marine ecosystems, 'la grande illusion'? *ICES Journal of Marine Science*, 73: 204–208.

Pörtner, H. O., and Peck, M. A. 2010. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. *Journal of Fish Biology*, 77: 1745–1779.

Post, E. 2004. Time lags in terrestrial and marine environments. Marine Ecosystems and Climate Variability. Stenseth NC, Ottersen G, Hurrell JW, Belgrano A editors. *Oxford University Press Oxford UK*: 165–167.

Ruiz, J., Macías, D., Rincón, M. M., Pascual, A., Catalán, I. A., and Navarro, G. 2013. Recruiting at the Edge: Kinetic Energy Inhibits Anchovy Populations in the Western Mediterranean. *PLoS ONE*, 8: e55523.

Russo, T., Pulcinella, J., Parisi, A., Martinelli, M., Belardinelli, A., Santojanni, A., Cataudella, S., *et al.* 2015. Modelling the strategy of mid-water trawlers targeting small pelagic fish in the Adriatic Sea and its drivers. *Ecological Modelling*, 300: 102–113.

Sabatés, A., Salat, J., and Olivar, M. P. 2001. Advection of continental water as an export mechanism for anchovy, *Engraulis encrasicolus*, larvae. *Scientia Marina*, 65: 77–88.

Sabatés, A., Olivar, M. P., Salat, J., Palomera, I., and Alemany, F. 2007. Physical and biological processes controlling the distribution of fish larvae in the NW Mediterranean. *Progress in Oceanography*, 74: 355–376.

Santos, M. B., Gonzalez-Quiros, R., Riveiro, I., Cabanas, J. M., Porteiro, C., and Pierce, G. J. 2012. Cycles, trends, and residual variation in the Iberian sardine (*Sardina pilchardus*) recruitment series and their relationship with the environment. *ICES Journal of Marine Science*, 69: 739–750.

Saraux, C., Fromentin, J.-M., Bigot, J.-L., Bourdeix, J.-H., Morfin, M., Roos, D., Beveren, E. V., *et al.* 2014. Spatial Structure and Distribution of Small Pelagic Fish in the Northwestern Mediterranean Sea. *PLOS ONE*, 9: e111211.

Schmidt, A., Botsford, L., Eadie, J., Bradley, R., Di Lorenzo, E., and Jahncke, J. 2014. Non-stationary seabird responses reveal shifting ENSO dynamics in the northeast Pacific. *Marine Ecology Progress Series*, 499: 249–258.

Szuwalski, C. S., and Hollowed, A. B. 2016. Climate change and non-stationary population processes in fisheries management. *ICES Journal of Marine Science*, 73: 1297–1305.

Teixeira, C. M., Gamito, R., Leitão, F., Murta, A. G., Cabral, H. N., Erzini, K., and Costa, M. J. 2016. Environmental influence on commercial fishery landings of small pelagic fish in Portugal. *Regional Environmental Change*, 16: 709–716.

Tugores, M., Giannoulaki, M., Iglesias, M., Bonanno, A., Tičina, V., Leonori, I., Machias, A., *et al.* 2011. Habitat suitability modelling for sardine Sardina pilchardus in a highly diverse ecosystem: the Mediterranean Sea. *Marine Ecology Progress Series*, 443: 181–205.

Van Beveren, E., Bonhommeau, S., Fromentin, J.-M., Bigot, J.-L., Bourdeix, J.-H., Brosset, P., Roos, D., *et al.* 2014. Rapid changes in growth, condition, size and age of small pelagic fish in the Mediterranean. *Marine Biology*, 161: 1809–1822.

Vargas-Yáñez, M., Zunino, P., Benali, A., Delpy, M., Pastre, F., Moya, F., García-Martínez, M. del C., *et al.* 2010a. How much is the western Mediterranean really warming and salting? *Journal of Geophysical Research*, 115..

Vargas-Yáñez, M., Moya, F., García-Martínez, M. C., Tel, E., Zunino, P., Plaza, F., Salat, J., *et al.* 2010b. Climate change in the Western Mediterranean Sea 1900–2008. *Journal of Marine Systems*, 82: 171–176.

Villate, F., Uriarte, I., Olivar, M. P., Maynou, F., Emelianov, M., and Ameztoy, I. 2014. Mesoscale structure of microplankton and mesoplankton assemblages under contrasting oceanographic conditions in the Catalan Sea (NW Mediterranean). *Journal of Marine Systems*, 139: 9–26

ANNEXES

Annex I

Occurrence of adult anchovy in Catalonia (NW Mediterranean) in relation to sea surface conditions

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Annex II

Environmental drivers of sardine (Sardina pilchardus) in the Catalan Sea (NW Mediterranean Sea)

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ANNEX I

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Occurrence of adult anchovy in Catalonia (NW Mediterranean) in relation to sea surface conditions

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Summary: Generalized additive and generalized additive threshold models were used to study the relationship between landings per unit effort (LPUE) of anchovy, *Engraulis encrasicolus*, during the spawning season (May-October) from 2000-2010, and environmental variables, using sea surface data derived from satellite imagery (temperature, salinity, chlorophyll *a*, and meridional and zonal velocity current) in three fishing zones defined along the Catalan coast. The configuration of the environment where spawning aggregations occur affects early life stages and therefore the future demographic structure of the population. It is therefore fundamental to define the environmental conditions and their variations during the spawning season. Our results show that the low salinity in the Northern and Central sector and the velocity of the zonal and meridional currents in the Central and Southern sector, respectively, implicated in retention processes, increase LPUE during the spawning period. Temperature was related to LPUE in the Southern and in the Northern sectors, in both of which a non-linear positive effect with a local maximum peak at lower temperature values was present. However, in the Northern sector, this relationship held only for the period before 2007. After 2007 the decrease in preferred temperature suggests a reduction of the thermal window in which adult spawner aggregations occur. In agreement with previous studies on this species, the relationships were non-linear, stressing the importance of the match in timing and location between favourable conditions and spawning period as a crucial event for understanding the dynamics of small pelagics populations.

Keywords: *Engraulis encrasicolus*; NW Mediterranean; environmental conditions; anchovy landings; generalized additive models.

Ocurrencia de anchoa adulta en Cataluña (Mediterráneo noroccidental) en relación a las condiciones superficiales del mar

Resumen: Con el objeto de estudiar la relación entre descargas por unidad de esfuerzo (LPUE) de la anchoa, *Engraulis encrasicolus*, durante la época de puesta (Mayo-Octubre) y variables ambientales marinas obtenidas por observación de satélite (temperatura, salinidad, clorofila-a, velocidad de corriente zonal y meridional) se analizaron series de datos para el periodo 2000-2010 mediante modelos aditivos generalizados, con y sin umbral, en tres zonas de pesca de la costa catalana. La configuración del ambiente en que ocurren las agregaciones de puesta afecta a los estadios tempranos y, por consiguiente, a la estructura demográfica futura de las poblaciones. Por lo tanto es de gran importancia definir las condiciones ambientales y sus variaciones durante la época de puesta. Los resultados del análisis muestran que bajas salinidades en los sectores norte y central, y las velocidades zonal y meridional de la corriente, en los sectores central y sur respectivamente, implicadas en los procesos de retención hacen aumentar la LPUE durante el periodo de puesta. La temperatura se relacionó con la LPUE en los sectores sur y norte. En ambas zonas se observó un efecto positivo y no lineal con un pico máximo a valores de temperatura bajos. Sin embargo, en el sector norte esta relación se mantuvo solamente hasta 2007. Después de 2007, la disminución en la temperatura preferencial sugiere una reducción en la ventana térmica en la que ocurren las agregaciones de puesta. Las relaciones obtenidas son no lineales, coincidiendo con estudios previos en esta especie, haciendo resaltar la importancia del ajuste espacio-temporal entre condiciones favorables y periodo de puesta como evento crucial para entender la dinámica poblacional de los pequeños pelágicos.

Palabras clave: *Engraulis encrasicolus*; Mediterráneo noroccidental; condiciones ambientales; descargas; Modelos Aditivos Generalizados**.**

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INTRODUCTION

Small pelagic fishes are key components of marine ecosystems and support fisheries of global importance (Alheit et al. 2012). These organisms are characterized by a short life span (2-3 years) and they feed on phytoplankton and small zooplankton (Tudela and Palomera 1995) in a short plankton-based food web. Populations of these fishes experience large interannual and long-term variations in abundance (Lluch-Belda et al. 1989), and several hypotheses have been formulated in order to explain these fluctuations (e.g. the "match-mismatch" hypothesis (Cushing 1990); the "optimal environmental window" (Cury and Roy 1989); and the "ocean triad" (Bakun 1996, Agostini and Bakun 2002)). These hypotheses highlight the importance of suitable environmental conditions in time and location during early life stages (eggs and larvae) for recruitment success and failure. Since early life stages are characterized by high sensitivity to environmental changes (Pörtner and Peck 2010), small variations in growth and survival rates of these stages could generate large differences in the annual recruitment (Houde 1997) and therefore in the future structure of the adult population. It is therefore fundamental to define the environmental conditions and their variations during the spawning period of these species.

In the northwest Mediterranean, the anchovy, *Engraulis encrasicolus* (Linnaeus, 1758), is the most important small pelagic fish in terms of biomass along with the pilchard, *Sardina pilchardus* (Walbaum, 1792) (Lleonart and Maynou 2003). Anchovy age-at-first-maturity is 1 year in the area (Lm>9 cm TL) (Pertierra 1992) and 88% of individuals are mature at age 0 (Cardinale et al. 2010)). Anchovy spawns in late spring and summer in coastal waters of continental origin characterized by low salinity (Lloret et al. 2004, Palomera et al. 2007, Sabatés et al. 2007a, 2013). The time of spawning is linked to temperature and, as for species that reproduce in spring/summer, spawning starts earlier in the Southern than in the Northern sector because the surface temperature increases earlier in the south and later extends northwards. For this same reason, the spawning period is longer in the south, where temperatures decrease more slowly (Martín and Sabatés 1991, Martín et al. 2008).

Two main spawning grounds characterize the NW Mediterranean: one is located in front of the Ebro delta and the other one in the Gulf of Lions up to the Rhône delta. Both areas are highly productive and characterized by relatively low salinity due to river runoff if compared with adjacent areas (Palomera et al. 2007). Early stages of development of the anchovy are favoured by these highly productive, low-salinity waters and also by mesoscale structures such as eddies (e.g. Palomera et al. 2007, Sabatés et al. 2013), which appear along the Northern Current coming from the Gulf of Lions (Millot 1991, Rojas et al. 1995). Both conditions cause a greater concentration of nutrients, phytoplankton and zooplankton compared with other areas (e.g. Razouls and Kouwenberg 1993, Bakun 2006, Sabatés et al. 2007a, Martín et al. 2008). In previous studies, abundance fluctuations of the anchovy have been associated with local environmental conditions and climate variability (e.g. Lloret et al. 2001, 2004, Martín et al. 2008, 2012). Thus, the positive trends in temperature and salinity data observed during the second half of the twentieth century in the western Mediterranean Sea (Calvo et al. 2012, Vargas-Yáñez et al. 2009, 2010) could have affected the population dynamics of this small pelagic fish.

In the Catalan Sea, the anchovy fishery is concentrated mostly between Cape Creus and the Ebro river delta (Agostini and Bakun 2002); it is carried out for 10 months per year (close season: December-January, generally) and 5 days per week (Pertierra and Lleonart 1996). Discards of this species are negligible (Lloret et al. 2004). Anchovy is caught mainly in spring/summer, when a significant fraction of the population is mature (Cardinale et al. 2010) and has incorporated the recruits from the previous year's spawning, so landings in these seasons can be considered as a proxy of the abundance of adult spawners (e.g. Martín et al. 2008).

The catches in the geographical subarea 06 (GSA06) in the period 1990-2010 were highly variable, suffering a continuous decrease after 1994, with a minimum of 1900 t in 2007 and an average of 11700 t, with two recoveries in 2002 and 2009 (Cardinale et al. 2010). Also, Farrugio (2013) reported decreasing trends in anchovy biomass in the Gulf of Lions between 2001 and 2005 and along the Catalan coasts, where this trend continued until 2010. Cardinale et al. (2010) described the status of this species as overexploited in GSA06, but the decrease and fluctuations in abundance cannot be attributed only to the fishing activities but to a combined effect of overexploitation and unfavourable environmental conditions (e.g. Martín et al. 2008, 2012, Lloret et al. 2000, 2001).

Coupling catches and oceanographic information is one of the main objectives in fisheries science and management. Tools such as generalized additive models (GAMs, Hastie and Tibshirani 1990, Wood 2006) allow these relationships to be described thanks to their flexibility, which allows the non-linear effect of a variable to be assessed independently from the value of another covariate (i.e. additivity). Because of this, they have been largely used in the Mediterranean Sea (e.g. Martín et al. 2008, Bellido et al. 2008, Giannoulaki et al. 2013). A variant of the GAM is the threshold GAM (TGAMs, Ciannelli et al. 2004). Using this modelling approach, composed of two additive formulations, it is possible to test whether a covariate effect changes according to two levels, which are defined by a threshold, of another variable (i.e. non-additive interaction). Therefore, the comparison of the results from the GAM and the TGAM allows us to assess, apart from non-linear relationships, whether the effects of the environmental variables are additive or not.

Through the use of both GAM and TGAM, this study aims to investigate the relation between the anchovy fishery landings and the local environmental conditions in the NW Mediterranean Sea during the spawning season, considering landings per unit of effort (LPUE) as a proxy of abundance of the adult

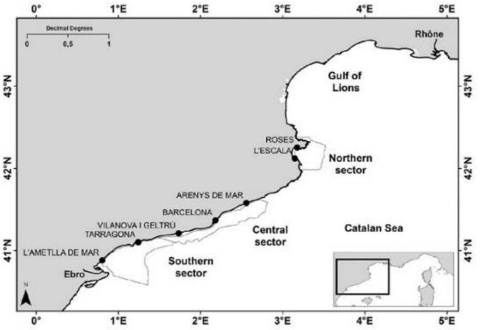


Fig. 1. – The study area divided into three sectors (Southern, Central and Northern) limited by the 35 m and 200 m isobaths and their major fishing ports.

population (spawners), in order to determine potential exogenous drivers of the population spatio-temporal dynamics of this small pelagic fish.

MATERIALS AND METHODS

Study area

The study area is located in the Catalan Sea, NW Mediterranean (Fig. 1). The area is characterized by a permanent shelf-slope density front, separating open-sea high-salinity waters from low-salinity continental shelf waters, and a geostrophic Northern Current which flows southwestwards roughly parallel to the coast with an overall transport of around 1 Sv (Castellón et al. 1990). The NW Mediterranean coast receives significant freshwater runoff from two major rivers, the Rhône and the Ebro. The Rhône discharges at the east of the Gulf of Lions and enhances the shelf-slope front by lowering the salinity of shelf waters. The Ebro, with lower runoff, also decreases the salinity of the waters on the relatively wide shelf near its mouth at the southern limit of the area. The water column structure shows a marked seasonal cycle, well mixed in winter and strongly stratified in summer, during the anchovy spawning season, when primary production is limited to a deep chlorophyll maximum (DCM), a thin layer at the deepest levels of the photic zone, ca. 60 m depth (Estrada et al. 1985). Another contribution to local productivity results from freshwater river runoff, which can enrich coastal waters near major river mouths. Summer productivity conditions are highly dependent on interannual variability in temperature and salinity, which in turn depends on the heat balance of air-sea exchanges in the region and fresh water runoff, which are variable from one year to the next. The environmental characteristics and the daily displacement of the fishery operation were used to define three sectors in the study area, Northern, Central and Southern, according to Martín et al. (2008) (Fig. 1). These sectors were limited by the 35 m and 200 m isobaths, which represent the longitudinal expansion where the anchovy fishery is carried out.

Data

Monthly landings (kg) from the main ports with a purse seine fleet (a total of 90 vessels) (Fig. 1) were used to analyse the variations in abundance of *E. encrasicolus* during the period 2000-2010. Landings data for each sector (Northern, Central and Southern sector) were obtained from the daily fish sale database of the Fisheries Directorate of the Autonomous Government of Catalonia. LPUE were computed by dividing the total monthly landings in each sector by the total number of vessels that carried out fishing operations (LPUE as kg/(vessel×day)). The part of the data set analysed represents the whole anchovy spawning period, considered to be from May to October (Palomera 1992, García and Palomera 1996). This period also coincides with the period when most anchovy is caught (62%-83% of the total annual catch in weight). The average monthly landings and effort are summarized in Table 1. The technical characteristics of the purse seine fleet operating in the area are 18.7 m length-overall (min. 12, max. 25 m), tonnage 37.7 GT (min. 20, max 78 GT) and engine power 209 kW (min. 155, max. 447 kW). Figure 2 shows the age composition of the landings in Geographic SubArea 6 (GSA06, the northern half of which corresponds to the study area), based on the 2010 stock assessment carried out by the Mediterranean subgroup of the Science, Technical, Economic Committee for Fisheries of the European Commission (Cardinale

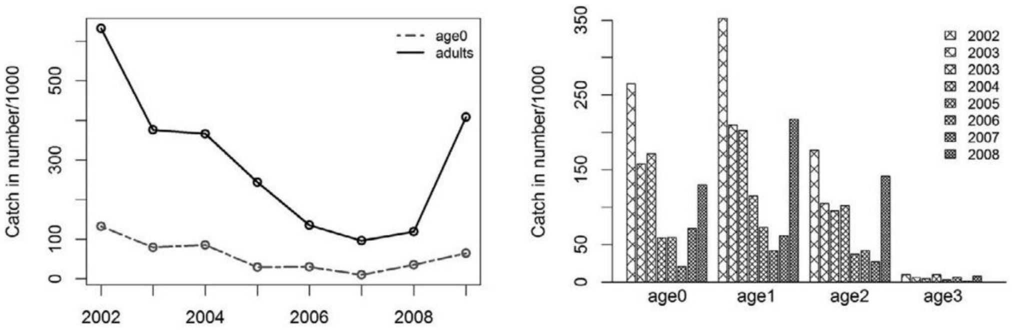


Fig. 2. – Left: Spawning individuals in age class 0 and age classes 1 and higher, assuming a maturity ogive 0.5, 0.89, 1, 1 for age classes 0 to 3 in GSA06 (Cardinale et al. 2010). Right: age class composition of landings (number of individuals) for the period 2002-2009 in GSA06 (Cardinale et al. 2010).

Table 1. – Average anchovy landings (1) and fishing trips (monthly vessel*day) (2) in the three sectors for each year, during the May-October spawning period. All values are reported as mean ± standard error (SE).

		2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010
North	1	255.3±78.1	249.1±73.9	265.9±72.8	232.8±61.3	121.1±52.1	104.1±31.8	106.5±30.1	81.5±28.9	100.4±21.1	87.6±26.7	91.1±27.4
	2	184.6±52.1	148±34.8	103.5±23.7	155.3±44.7	94.3±29.8	76.5±22.7	83.1±27.1	66.5±16.7	91.3±25.4	82.6±23.2	74.6±20.9
Centre	1	69.8±25.9	106.1±35.1	274.6±104.8	86.6±38.4	216.7±98.4	155.9±63.4	56.6±17.7	26.2±13.7	25.4±11.9	332.6±87.6	203.6±80.1
	2	77.8±27.4	125.3±35.3	202.3±58.1	113.8±47.1	194.3±68.6	171.2±64.8	107.6±32.3	67±27.3	38.5±5.4	231.2±51.5	199.1±78.1
South	1	87.6±24.1	97.7±34.1	147.9±27.5	93.2±23.9	93.2±39	88.8±27.3	54.8±17	27.2±13.4	85.5±26.8	220.1±17.3	173.1±36.1
	2	146.8±26.1	123.6±27.6	192.6±21.7	177.5±39.3	150.5±32.1	107.6±29.2	114.5±23.2	80.5±29.8	134±32.7	176.1±17.6	175.6±21.1

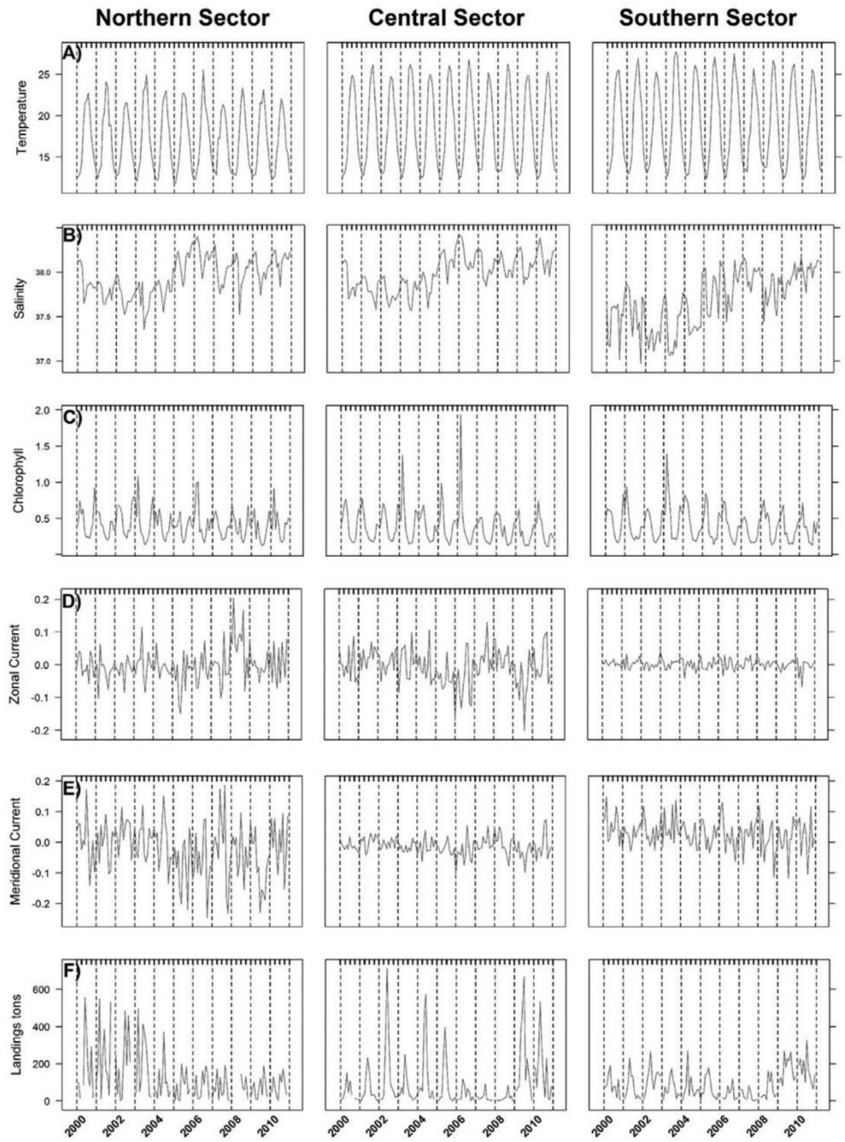


Fig. 3. – Series of monthly values (mean) for each sector. A, the sea surface temperature (SST); B, sea surface salinity (SSS); C, chlorophyll; D, meridional current; E, zonal current; F, anchovy landings during the years 2000-2010. Top ticks indicate the seasons of the year. Note missing data in winter due to the annual close season to protect anchovy recruitment (usually December and January).

et al. 2010). Depending on the year, between 70% and 90% of the landings in number correspond to year 1 or older individuals, i.e. spawning adults.

The explanatory variables used to model the anchovy landings are (Fig. 3): 1) the sea surface temperature (SST in °C), because it has been shown that it determines the species distribution, enhances the growth of larvae and regulates the onset and the duration of the spawning period (García and Palomera 1996, Palomera et al. 2007); 2) the sea surface salinity (SSS in psu), because previous studies have associated the spawning period and the early life stages of anchovy with low-salinity water (e.g. Lloret et al. 2004, Martín et al. 2008); 3) the chlorophyll *a* concentration (Chl *a* in mg m^{-3}) as an indicator of the primary production; 4) the meridional current (MC in m s^{-1}, north to south); and 5) the zonal current (ZC in m s^{-1}, west to east). Both the MC and the ZC are involved in larva, egg and prey retention and transport (Sabatés et al. 2007a).

The above environmental variables were derived from satellite data with a monthly time resolution and a space resolution of 1/16°×1/16° developed within the EU-funded project MyOcean (http://marine.copernicus.eu/). All monthly satellite images were merged to obtain aggregate amounts by sector, using ArcGIS software (ESRI 1994).

Statistical analysis

GAMs (Hastie and Tibshirani 1990, Wood 2006) were used to assess the effect of environmental conditions on the monthly LPUE of the spawning period (May-Oct), log-transformed, in the three sectors (Northern, Central and Southern) from 2000 to 2010. One model for each zone was constructed. Using the backward selection, the best model for each sector was selected based on the minimization of generalized cross-validation criterion (GCV) (Craven and Wahba 1979), which is an estimate of the model's predictive performance and aims at optimizing the trade-off between the model's parsimony (the number of parameters) and goodness of fit.

We used the Gaussian probability distribution as an error distribution and the identity as a link function (Wood 2006), checking the residuals of the model visually for normality and homogeneity, to assess the appropriateness of the choice of probability distribution function. The univariate penalized cubic spline was used as a smoother, and the maximum degree of freedom measured as number of knots (k) was limited to k=5 to avoid over-fitting. For each of the best models obtained we also explored the interaction effect between the time and the other covariates using threshold GAM (TGAM) (Ciannelli et al. 2004).

In practice, the TGAM algorithm divides the *time* (defined as the month expressed in number, in the year), representing the 'threshold variable', into two levels (i.e. a factor variable), before and after the threshold value (Tv). By introducing in the model the interaction between *time* and another covariate, the covariate effect can change during the observed period. Hence, through this model formulation, the shape of the smoothing function of each covariate was allowed to change over two contrasting periods defined by Tv. The identification of the threshold value was obtained by defining a search grid over an interval given by the 15th to 85th percentiles of the variable *time*, and the value within this range that produced the model that minimized the GCV score was selected (for details please see Ciannelli et al. 2004).

We used the genuine cross-validation (gCV) to directly compare the selected TGAM and the corresponding GAM models. We calculated gCV scores by excluding randomly about 15% of the entire dataset and using the remaining data to fit a candidate model, and the mean-squared predictive error was estimated (Ciannelli et al. 2004). The routine was repeated 500 times, with the final gCV being the average mean-squared predictive error of all runs for each candidate model (Ciannelli et al. 2004). All the analyses were performed with R v. 2.0.1 statistical package (http://www.r-project.org/).

RESULTS

Environmental conditions

The environmental data show that the SST has a clear seasonal pattern (Fig. 3A): the maxima during summer show high variability along the latitudinal gradient, decreasing from south to north. For all sectors, the years 2003 and 2006 are the ones with the highest temperatures, while from the year 2007 SST showed a decrease, especially during spring and summer and more evident in the Northern sector. During cold seasons (winter and autumn) SST showed lower variability between the three sectors, with very similar minima. SSS also showed clear latitudinal differences (Fig. 3B), with lower values in the Southern sector. Although salinity did not show a clear seasonal pattern, we observed lower peaks in late summer and early autumn, more evident in the Southern sector, due to the direct influence of river runoff in this period of the year. Salinity increase was evident from 2004 to 2007 in all areas, followed by a gradual stabilization (Fig. 3B), and 2006 showed higher salinity than the other periods (Fig. 3B). Chl *a* showed the highest peaks in winter and the second-highest in autumn (Fig. 3C). The Central and Southern sectors show the highest production of Chl *a*, with the highest value in the Central sector in winter 2006.

Along the Catalan coast, the zonal current showed a velocity of 5 to 15 cm s^{-1} (Fig. 3D). The Southern sector was characterized mainly by an inshore-offshore flow (eastward flow, positive values), except in 2009 and 2010, which were characterized mainly by a westward flow (negative values, Fig. 3F). During the first half of the decade, in the Central sector currents were slow in both directions, persisting in the range of –5 and 5 cm s^{-1} until the beginning of 2005 (Fig. 3D). Afterwards, alternating high eastward and westward velocities characterized this sector, with the strongest westward current during the spring of 2009. The Northern sector followed the same pattern as the Central one, but in this case the highest velocity was the eastward one,

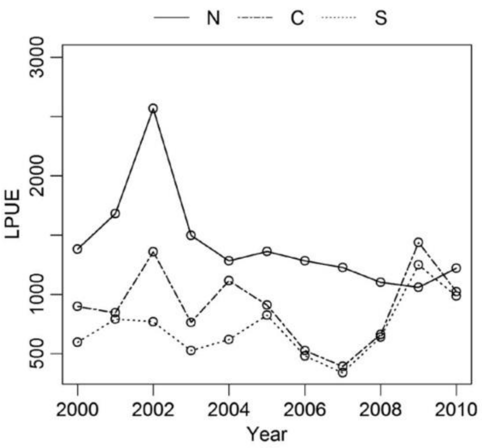


Fig. 4. – Anchovy LPUE during the spawning season (from May to October) for each sector during the years 2000-2010. N, Northern sector; C, Central sector; S, Southern sector.

reaching the uppermost peak in spring 2008 (Fig. 3D). Intense meridional current with high northward and southward current velocities characterized the Northern sector, while in the other two sectors velocities in both directions did not exceed 10 cm s^{-1} (Fig. 3E).

Anchovy LPUE

The LPUE by sector is shown in Figure 3F. In 2000-2008 LPUE was more than twice as high in the Northern sector than in the Central and Southern sectors, while after 2008 it decreased to values closer to the Southern and Central sectors (Fig. 3F). Considering the overall LPUE during spawning periods in each year from 2000 to 2010, all sectors showed decreasing trends starting in 2002, but during 2009-2010 both the Central and Southern sectors showed an increase (Fig. 4). The reduction in abundance was more marked in the Northern sector, with no evidence of recovery. In the Central and Southern sectors the abundances were lower than in the Northern sector and showed a similar decreasing trend until 2008, after which they increased (Fig. 4).

Environmental influence on spawning season

The threshold model (TGAM) was selected for the Northern sector, while standard GAM models were selected for the other two sectors based on the genuine cross-validation criteria.

The following threshold GAM was the best model fit in the Northern sector:

$$\log(\text{LPUE})=\begin{cases}\alpha+g_1(\text{SSS})+f_1(\text{CHL})+s_1(\text{SST})+\varepsilon & \text{if time} \le \text{June 2007}\\ \alpha+g_1(\text{SSS})+f_1(\text{CHL})+s_2(\text{SST})+\varepsilon & \text{if time} > \text{June 2007}\end{cases}$$

This TGAM formulation, formed by two additive model formulations where α is the intercept while g_1, f_1, s_1, s_2 are the non-parametric smoothing functions specifying the effect of the environmental covariates, showed better results than the corresponding GAM model, with a reduction of the gCV from 0.43 to 0.30 after including time as threshold variable. The TGAM model explained 61.4% of the deviance (Table 2). The effect of the SST changed during the period considered (the smoothing function switched from s_1 to s_2) and the threshold value estimated for time was at the beginning of the spawning season in 2007 (June), as depicted on the GCV profile in Figure 5.

All partial effects are shown in Figure 6A, B, C, D. Results showed a positive effect of the SSS for values lower than ca. 37.7, followed by a small negative effect at values between ca. 37.7 and 38.1 (Fig. 6A). The effect of Chl *a* was linear, and became negative for values higher than 0.3 mg m^{-3} (Fig. 6B). The effect of temperature as described above changed during the period considered. From May 2000 to May 2007 it was positive between ca. 17.5 and ca. 21.3°C, with a peak at ca. 19°C corresponding to spring conditions, and clearly negative at temperatures higher than ca. 21.3°C (Fig. 6C). In the period between June 2007 and October 2010, a linear positive effect was observed for temperatures lower than 19°C, whereas above this value a small negative effect was observed (Fig. 6D).

The following model was the final GAM selected for the Central sector (37.2% of deviance explained) (Table 2):

$$\log(\text{LPUE})=\alpha+g_1(\text{SSS})+f_1(\text{ZC})+s_1(\text{CHL})+\varepsilon$$

where α is the intercept, g_1, f_1, s_1 the smoothing functions and ε the error term. Relatively low SSS values positively affected LPUE within a range starting from ca. 37.6 to ca. 37.83 with a local peak at ca. 37.7 (Fig. 6E). Negative effects were evident for both high east- and westward velocities of the zonal current. Although less evident, low westward velocities at values around –0.05 m s^{-1} affected the LPUE positively, while no evident effects were present at low eastward velocity

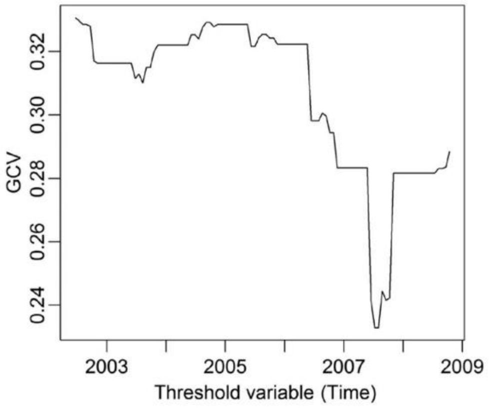


Fig. 5. – GCV profile for the threshold estimation for the variable *time* in the Northern sector.

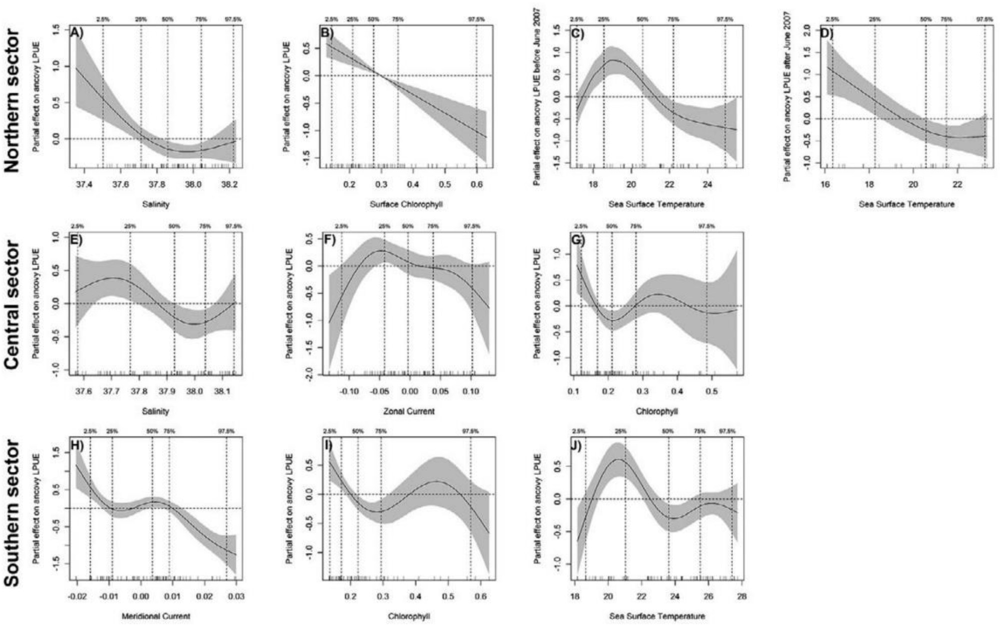


Fig. 6. – Partial effects of sea surface temperature, sea surface salinity, chlorophyll *a* concentration, meridional current and zonal current for each sector during spawning periods. The median, 1st and 3rd quartiles and 95% distribution of the explanatory variables are shown along the x-axis as vertical grey lines. The shades areas indicate the 95% confidence interval. A,B,C,D, partial effects on LPUE in the Northern sector, where C and D are the partial effect of the sea surface temperature before and after June 2007, respectively; E,F,G, partial effects on LPUE in the Central sector; H,I,J, partial effects on LPUE in the Southern sector. See models in Table 2.

Table 2. – Genuine cross-validation scores (gCV) used to select the models in each sector with the best prediction performance among candidate models and % of the deviance explicated (DVe %). The final models are indicated in bold text with the analysis of deviance of the covariates (SSS, sea surface salinity; SST, sea surface temperature; CHL, Chlorophyll concentration; ZC, zonal current velocity; MC, meridional current velocity).

Sector	Model	Formulation	gCV	DVe %	Edf	Null DV	Res. DV	GCV
North	GAM	$\log(\mathrm{LPUE})=\alpha+g_1(\mathrm{SSS})+f_1(\mathrm{CHL})+s_1(\mathrm{SST})+\varepsilon$	0.43	34.6%				
	TGAM	$\log(\mathrm{LPUE})=\alpha+g_1(\mathrm{SSS})+f_1(\mathrm{CHL})+s_1(\mathrm{SST})+\varepsilon$ if time ≤r $\log(\mathrm{LPUE})=\alpha+g_2(\mathrm{SSS})+f_1(\mathrm{CHL})+s_1(\mathrm{SST})+\varepsilon$ if time >r	0.38	55.2%	**$g_1(\mathrm{SSS})=3.049$** **$f_1(\mathrm{CHL})=1$** **$s_1(\mathrm{SST})=2.264$** **$s_2(\mathrm{SST})=3.727$**	**0.42**	**0.19**	**0.23**
		$\log(\mathrm{LPUE})=\alpha+g_1(\mathrm{SSS})+f_1(\mathrm{CHL})+s_1(\mathrm{SST})+\varepsilon$ if time ≤r $\log(\mathrm{LPUE})=\alpha+g_1(\mathrm{SSS})+f_2(\mathrm{CHL})+s_1(\mathrm{SST})+\varepsilon$ if time >r	0.94	45.7%				
		$\log(\mathrm{LPUE})=\alpha+g_1(\mathrm{SSS})+f_1(\mathrm{CHL})+s_1(\mathrm{SST})+\varepsilon$ if time ≤r **$\log(\mathrm{LPUE})=\alpha+g_1(\mathrm{SSS})+f_1(\mathrm{CHL})+s_2(\mathrm{SST})+\varepsilon$ if time >r**	**0.30**	**61.4%**				
Centre	GAM	**$\log(\mathrm{LPUE})=\alpha+g_1(\mathrm{SSS})+f_1(\mathrm{ZC})+s_1(\mathrm{CHL})+\varepsilon$**	**0.70**	**37.2%**				
	TGAM	$\log(\mathrm{LPUE})=\alpha+g_1(\mathrm{SSS})+f_1(\mathrm{ZC})+s_1(\mathrm{CHL})+\varepsilon$ if time ≤r $\log(\mathrm{LPUE})=\alpha+g_2(\mathrm{SSS})+f_1(\mathrm{ZC})+s_1(\mathrm{CHL})+\varepsilon$ if time >r	0.72	36.2%	**$g_1(\mathrm{SSS})=2.761$** **$f_1(\mathrm{ZC})=3.437$** **$s_1(\mathrm{CHL})=3.626$**	**0.53**	**0.39**	**0.54**
		$\log(\mathrm{LPUE})=\alpha+g_1(\mathrm{SSS})+f_1(\mathrm{ZC})+s_1(\mathrm{CHL})+\varepsilon$ if time ≤r $\log(\mathrm{LPUE})=\alpha+g_1(\mathrm{SSS})+f_2(\mathrm{ZC})+s_1(\mathrm{CHL})+\varepsilon$ if time >r	0.74	44.3%				
		$\log(\mathrm{LPUE})=\alpha+g_1(\mathrm{SSS})+f_1(\mathrm{ZC})+s_1(\mathrm{CHL})+\varepsilon$ if time ≤r $\log(\mathrm{LPUE})=\alpha+g_1(\mathrm{SSS})+f_1(\mathrm{ZC})+s_2(\mathrm{CHL})+\varepsilon$ if time >r	0.90	43.4%				
South	GAM	**$\log(\mathrm{LPUE})=\alpha+g_1(\mathrm{MC})+f_1(\mathrm{CHL})+s_1(\mathrm{SST})+\varepsilon$**	**0.30**	**56.1%**				
	TGAM	$\log(\mathrm{LPUE})=\alpha+g_1(\mathrm{MC})+f_1(\mathrm{CHL})+s_1(\mathrm{SST})+\varepsilon$ if time ≤r $\log(\mathrm{LPUE})=\alpha+g_2(\mathrm{MC})+f_1(\mathrm{CHL})+s_1(\mathrm{SST})+\varepsilon$ if time >r	0.33	52.6%	**$g_1(\mathrm{MC})=2.761$** **$f_1(\mathrm{CHL})=3.437$** **$s_1(\mathrm{SST})=3.626$**	**0.33**	**0.18**	**0.22**
		$\log(\mathrm{LPUE})=\alpha+g_1(\mathrm{MC})+f_1(\mathrm{CHL})+s_1(\mathrm{SST})+\varepsilon$ if time ≤r $\log(\mathrm{LPUE})=\alpha+g_1(\mathrm{MC})+f_2(\mathrm{CHL})+s_1(\mathrm{SST})+\varepsilon$ if time >r	0.34	56.3%				
		$\log(\mathrm{LPUE})=\alpha+g_1(\mathrm{MC})+f_1(\mathrm{CHL})+s_1(\mathrm{SST})+\varepsilon$ if time ≤r $\log(\mathrm{LPUE})=\alpha+g_1(\mathrm{MC})+f_1(\mathrm{CHL})+s_2(\mathrm{SST})+\varepsilon$ if time >r	0.32	53.6%				

values (Fig. 6F). Moderate positive effects were found at values below 0.2 mg m^{-3} of Chl *a* concentration, and a negative effect was found at higher values, excluding the presence of a local non-significant, positive peak at a concentration of 0.35 mg m^{-3} (Fig. 6G).

The final GAM for the Southern sector explained 56.1% of the total deviance (Table 2):

$$\log(\mathrm{LPUE})=\alpha+g_1(\mathrm{MC})+f_1(\mathrm{CHL})+s_1(\mathrm{SST})+\varepsilon$$

with α representing the intercept, g_1, f_1, s_1 the smoothing functions and ε the errors. LPUE was positively related to meridional current velocity at values lower than –0.01 m s^{-1} (i.e. north-to-south flow of 0.01 m s^{-1} or higher) and negatively related to the intensification of the meridional current velocity, particularly at values higher than 0.01 m s^{-1}, while it showed no effects in the range between ca. –0.01 m s^{-1} and ca. 0.01 m s^{-1} (Fig. 6H). The relationship with Chl *a* was similar to that observed in the Central sector, with a local peak for concentration equal to 0.35 mg m^{-3}, and a slightly positive effect below a Chl *a* concentration of 0.2 mg m^{-3} (Fig. 6I). Positive effects of SST were evident between ca. 19°C and 22°C with a peak at ca. 21°C (Fig. 6J), while no evident effects on LPUE were found for higher values of SST.

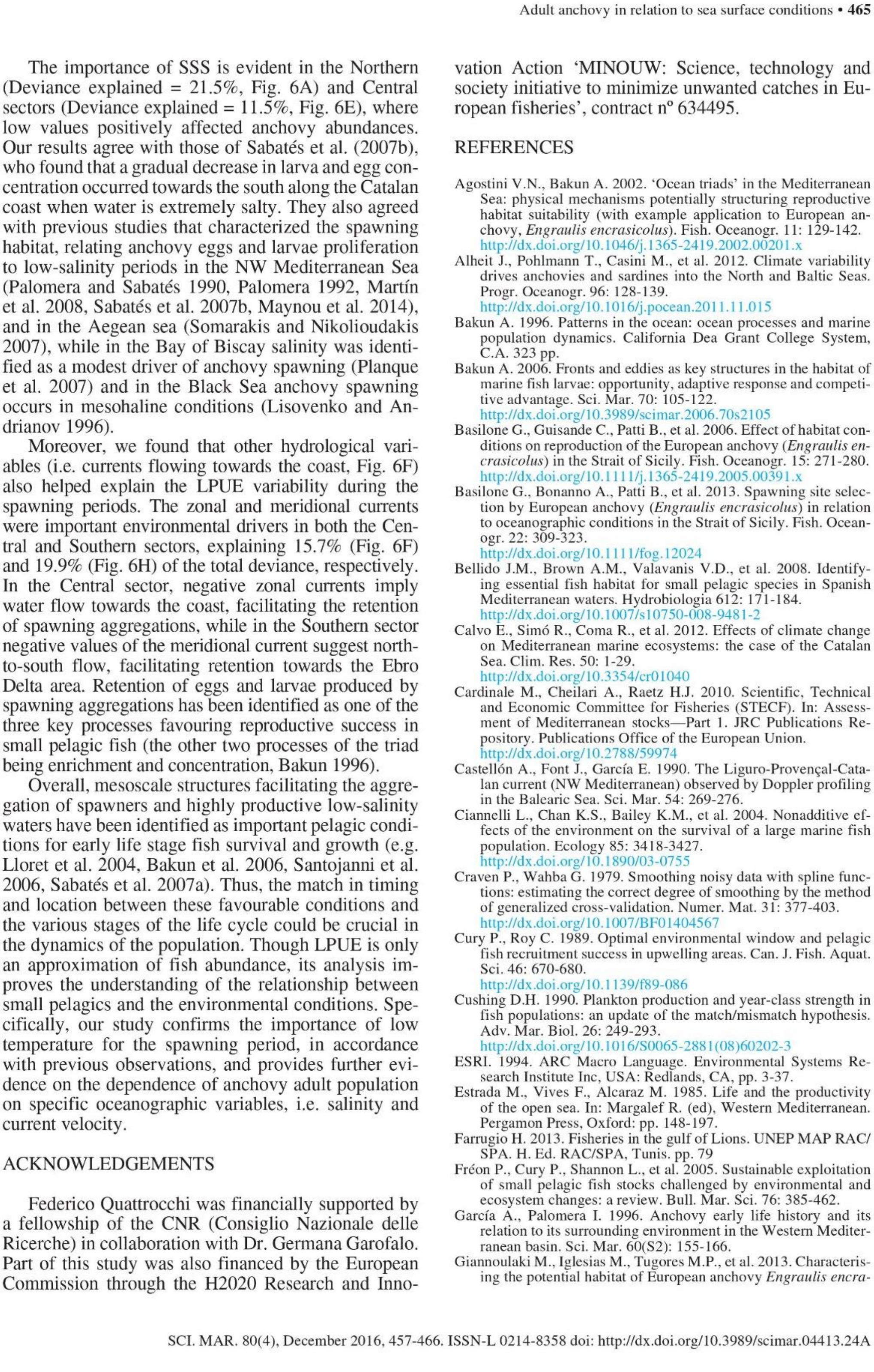
DISCUSSION

In this study we investigated the relationships between anchovy LPUE and the local environmental variables on the Catalan coast during the spawning period. The strong influence of environmental factors on small pelagic adult populations is well known, particularly the influence on the location and timing of their reproduction (Lloret et al. 2004, Palomera et al. 2007, Giannoulaki et al. 2013) and on the survival of the early life stages (e.g. Agostini and Bakun 2002, Sabatés et al. 2007b, Maynou et al. 2014). In fact, pelagic eggs and larvae need favourable environmental conditions in order to enhance the probability of success (Bakun 1996). During the period considered, i.e. 2000-2010, anchovy LPUEs showed high fluctuations, with minimum values between 2007 and 2008. The LPUE during the year showed seasonality typical of the species in the Mediterranean Sea, with maxima mainly in spring-summer and minima in late autumn-winter. In this area the anchovy spawning period overlaps with the main fishing season for this species, in spring/summer. During this period catches are composed mainly of individuals of the 1- and 2-year cohort (Pertierra and Lleonart 1996, Cardinale et al. 2010), so peaks in landings can be considered as an index of spawning stock biomass, which in this short-lived species is closely related to recruitment to the fishery from the previous year's spawn (as argued by Lloret et al. 2004, Martín et al. 2008).

The relative lower SSTs (below 22°C) in which high abundance of the anchovy population was found can be indicative of nutrient enrichment processes such as wind mixing or river runoff, which are often associated with favourable conditions for fish. The relationships with temperature found in our results are in accordance with that described by other studies in the same area, using different methodologies (e.g. García and Palomera 1996, Lloret et al. 2004, Palomera 1992, Palomera et al. 2007, Martín et al. 2008). Moreover they also agree with results of Somarakis and Nikolioudakis (2007) and Basilone et al. (2006, 2013) in the Aegean Sea and in the Straits of Sicily, respectively, highlighting the synchrony between the seasonal reproductive cycle and temperature. This synchrony could be a strategy to enhance the probability of success of larval survival, which is favoured by the subsequent stable sea conditions promoting the prey aggregations (Lasker 1981, Basilone et al. 2006). In fact, these temperatures in the Catalan Sea correspond to the period (late April-May, when anchovy starts spawning) immediately before the stratified season (e.g. Palomera et al. 2007, Giannoulaki et al. 2013). Specifically, in the Southern sector higher LPUEs were found at temperatures between 19°C to 22°C, while in the Northern sector LPUE was higher at temperature between 18°C and 21°C and below 19°C, before and after 2007, respectively. The identification of optimal temperature values for the anchovy spawners by several authors (e.g. Motos et al. 1996, García and Palomera 1996, Palomera et al. 2007) may lead one to suppose that stable temperatures are a favourable factor for the reproductive season of anchovies. The northernmost part of the region is characterized by a shorter spawning season related to the thermal cycle (Palomera and Lleonart 1989) in comparison with the other sectors. The apparent decrease in preferred temperature from 2007, corresponding to the threshold value obtained from our analysis, might have further reduced this period and the thermal window in which spawning aggregation occurs.

Results regarding the relationships of Chl *a* concentration with the landings were found to be similar in all sectors. The low values of Chl *a* in late spring and summer, which in this study were associated with higher landings, are typical features of temperate oligotrophic areas such as the Mediterranean Sea (Estrada et al. 1985). In fact, the strong runoffs during early spring from Mediterranean rivers, enhancing the surface primary productivity and the subsequent production of zooplankton (the main food for anchovies) (Tudela and Palomera 1995, Tudela et al. 2002), are followed by a stabilization of the water masses and by the development of the thermocline, which inhibits vertical mixing and determines the depletion of nutrients at the surface (Palomera et al. 2007).

Hydrographic variability influences the spatio-temporal extent of spawning habitat, producing large fluctuations in the recruitment of small pelagic fish (Planque et al. 2007). Our results show that salinity lower than 37.8 enhances the LPUE in the two northernmost areas, closer to the Gulf of Lions, and that this variable is the first to be selected in the models (Fig. 6). During the study period in the Catalan Sea, an alternation between years of high and low salinity was observed, similar to those described by Nicolle et al. (2009) in the Gulf of Lions. This alternation could have reduced the suitable habitat for spawning both spatially and temporally, negatively influencing the fish aggregation for reproduction that takes place along the Catalan coast (Palomera 1992, García and Palomera 1996, Palomera et al. 2007). The influence of salinity on preferred habitat during the spawning might be complex because the survival of larvae results from an interaction between several environmental variables (e.g. temperature, dissolved oxygen, currents, salinity, Chl *a* concentration) (Fréon et al. 2005) and predation. Nevertheless, our results confirm that salinity is important for anchovy, as previously shown by results from echo-survey, egg collection and commercial catch samples in the Mediterranean Sea (e.g. Bellido et al. 2008, Sabatés et al. 2007b), the Bay of Biscay (Massé et al. 1995, Motos et al. 1996, Planque et al. 2007) and the Black Sea (Lisovenko and Andrianov 1996).



The importance of SSS is evident in the Northern (Deviance explained = 21.5%, Fig. 6A) and Central sectors (Deviance explained = 11.5%, Fig. 6E), where low values positively affected anchovy abundances. Our results agree with those of Sabatés et al. (2007b), who found that a gradual decrease in larva and egg concentration occurred towards the south along the Catalan coast when water is extremely salty. They also agreed with previous studies that characterized the spawning habitat, relating anchovy eggs and larvae proliferation to low-salinity periods in the NW Mediterranean Sea (Palomera and Sabatés 1990, Palomera 1992, Martín et al. 2008, Sabatés et al. 2007b, Maynou et al. 2014), and in the Aegean sea (Somarakis and Nikolioudakis 2007), while in the Bay of Biscay salinity was identified as a modest driver of anchovy spawning (Planque et al. 2007) and in the Black Sea anchovy spawning occurs in mesohaline conditions (Lisovenko and Andrianov 1996).

Moreover, we found that other hydrological variables (i.e. currents flowing towards the coast, Fig. 6F) also helped explain the LPUE variability during the spawning periods. The zonal and meridional currents were important environmental drivers in both the Central and Southern sectors, explaining 15.7% (Fig. 6F) and 19.9% (Fig. 6H) of the total deviance, respectively. In the Central sector, negative zonal currents imply water flow towards the coast, facilitating the retention of spawning aggregations, while in the Southern sector negative values of the meridional current suggest north-to-south flow, facilitating retention towards the Ebro Delta area. Retention of eggs and larvae produced by spawning aggregations has been identified as one of the three key processes favouring reproductive success in small pelagic fish (the other two processes of the triad being enrichment and concentration, Bakun 1996).

Overall, mesoscale structures facilitating the aggregation of spawners and highly productive low-salinity waters have been identified as important pelagic conditions for early life stage fish survival and growth (e.g. Lloret et al. 2004, Bakun et al. 2006, Santojanni et al. 2006, Sabatés et al. 2007a). Thus, the match in timing and location between these favourable conditions and the various stages of the life cycle could be crucial in the dynamics of the population. Though LPUE is only an approximation of fish abundance, its analysis improves the understanding of the relationship between small pelagics and the environmental conditions. Specifically, our study confirms the importance of low temperature for the spawning period, in accordance with previous observations, and provides further evidence on the dependence of anchovy adult population on specific oceanographic variables, i.e. salinity and current velocity.

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REFERENCES

Agostini V.N., Bakun A. 2002. 'Ocean triads' in the Mediterranean Sea: physical mechanisms potentially structuring reproductive habitat suitability (with example application to European anchovy, *Engraulis encrasicolus*). Fish. Oceanogr. 11: 129-142. http://dx.doi.org/10.1046/j.1365-2419.2002.00201.x

Alheit J., Pohlmann T., Casini M., et al. 2012. Climate variability drives anchovies and sardines into the North and Baltic Seas. Progr. Oceanogr. 96: 128-139. http://dx.doi.org/10.1016/j.pocean.2011.11.015

Bakun A. 1996. Patterns in the ocean: ocean processes and marine population dynamics. California Dea Grant College System, C.A. 323 pp.

Bakun A. 2006. Fronts and eddies as key structures in the habitat of marine fish larvae: opportunity, adaptive response and competitive advantage. Sci. Mar. 70: 105-122. http://dx.doi.org/10.3989/scimar.2006.70s2105

Basilone G., Guisande C., Patti B., et al. 2006. Effect of habitat conditions on reproduction of the European anchovy (*Engraulis encrasicolus*) in the Strait of Sicily. Fish. Oceanogr. 15: 271-280. http://dx.doi.org/10.1111/j.1365-2419.2005.00391.x

Basilone G., Bonanno A., Patti B., et al. 2013. Spawning site selection by European anchovy (*Engraulis encrasicolus*) in relation to oceanographic conditions in the Strait of Sicily. Fish. Oceanogr. 22: 309-323. http://dx.doi.org/10.1111/fog.12024

Bellido J.M., Brown A.M., Valavanis V.D., et al. 2008. Identifying essential fish habitat for small pelagic species in Spanish Mediterranean waters. Hydrobiologia 612: 171-184. http://dx.doi.org/10.1007/s10750-008-9481-2

Calvo E., Simó R., Coma R., et al. 2012. Effects of climate change on Mediterranean marine ecosystems: the case of the Catalan Sea. Clim. Res. 50: 1-29. http://dx.doi.org/10.3354/cr01040

Cardinale M., Cheilari A., Raetz H.J. 2010. Scientific, Technical and Economic Committee for Fisheries (STECF). In: Assessment of Mediterranean stocks—Part 1. JRC Publications Repository. Publications Office of the European Union. http://dx.doi.org/10.2788/59974

Castellón A., Font J., García E. 1990. The Liguro-Provençal-Catalan current (NW Mediterranean) observed by Doppler profiling in the Balearic Sea. Sci. Mar. 54: 269-276.

Ciannelli L., Chan K.S., Bailey K.M., et al. 2004. Nonadditive effects of the environment on the survival of a large marine fish population. Ecology 85: 3418-3427. http://dx.doi.org/10.1890/03-0755

Craven P., Wahba G. 1979. Smoothing noisy data with spline functions: estimating the correct degree of smoothing by the method of generalized cross-validation. Numer. Mat. 31: 377-403. http://dx.doi.org/10.1007/BF01404567

Cury P., Roy C. 1989. Optimal environmental window and pelagic fish recruitment success in upwelling areas. Can. J. Fish. Aquat. Sci. 46: 670-680. http://dx.doi.org/10.1139/f89-086

Cushing D.H. 1990. Plankton production and year-class strength in fish populations: an update of the match/mismatch hypothesis. Adv. Mar. Biol. 26: 249-293. http://dx.doi.org/10.1016/S0065-2881(08)60202-3

ESRI. 1994. ARC Macro Language. Environmental Systems Research Institute Inc, USA: Redlands, CA, pp. 3-37.

Estrada M., Vives F., Alcaraz M. 1985. Life and the productivity of the open sea. In: Margalef R. (ed), Western Mediterranean. Pergamon Press, Oxford: pp. 148-197.

Farrugio H. 2013. Fisheries in the gulf of Lions. UNEP MAP RAC/SPA. H. Ed. RAC/SPA, Tunis. pp. 79

Fréon P., Cury P., Shannon L., et al. 2005. Sustainable exploitation of small pelagic fish stocks challenged by environmental and ecosystem changes: a review. Bull. Mar. Sci. 76: 385-462.

García A., Palomera I. 1996. Anchovy early life history and its relation to its surrounding environment in the Western Mediterranean basin. Sci. Mar. 60(S2): 155-166.

Giannoulaki M., Iglesias M., Tugores M.P., et al. 2013. Characterising the potential habitat of European anchovy *Engraulis encra-*

sicolus in the Mediterranean Sea, at different life stages. Fish. Oceanogr. 22: 69-89. http://dx.doi.org/10.1111/fog.12005

Hastie T.J., Tibshirani R.J. 1990. Generalized additive models, vol 43. CRC Press.

Houde E. 1997. Patterns and trends in larval stage growth and mortality of teleost fish. J. Fish. Biol. 51: 52-83. http://dx.doi.org/10.1111/j.1095-8649.1997.tb06093.x

Lasker R. 1981. The role of a stable ocean in larval fish survival and subsequent recruitment. In: Lasker R. (ed.), Marine fish larvae: morphology, ecology and relation to fisheries, vol. 1, Univ. Washington Press, Seattle, pp. 80-89.

Lisovenko L.A., Andrianov D.P. 1996. Reproductive biology of anchovy (*Engraulis encrasicolus ponticus*, Alexandrov 1927) in the Black Sea. Sci. Mar. 60: 209-218.

Lleonart J., Maynou F. 2003. Fish stock assessments in the Mediterranean: state of the art. Sci. Mar. 67: 37-49. http://dx.doi.org/10.3989/scimar.2003.67s137

Lloret J., Lleonart J., Solé I. 2000. Time series modelling of landings in Northwest Mediterranean Sea. ICES J. Mar. Sci. 57: 171-184. http://dx.doi.org/10.1006/jmsc.2000.0570

Lloret J., Lleonart J., Solé I., et al. 2001. Fluctuations of landings and environmental conditions in the north-western Mediterranean Sea. Fish. Oceanogr. 10: 33-50. http://dx.doi.org/10.1046/j.1365-2419.2001.00151.x

Lloret J., Palomera I., Salat J., et al. 2004. Impact of freshwater input and wind on landings of anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*) in shelf waters surrounding the Ebre (Ebro) River delta (north-western Mediterranean). Fish. Oceanogr. 13: 102-110. http://dx.doi.org/10.1046/j.1365-2419.2003.00279.x

Lluch-Belda D., Crawford R., Kawasaki T., et al. 1989. World-wide fluctuations of sardine and anchovy stocks: the regime problem. S. Afr. J. Mar. Sci. 8: 195-205. http://dx.doi.org/10.2989/02577618909504561

Martín P., Sabatés A. 1991. Spatio-temporal distribution pattern of the red band-fish *Cepola rubescens* Linnaeus at different stages of its life cycle in the northwestern Mediterranean. J. Fish. Biol. 39: 549-557. http://dx.doi.org/10.1111/j.1095-8649.1991.tb04385.x

Martín P., Bahamon N., Sabatés A., et al. 2008. European anchovy (*Engraulis encrasicolus*) landings and environmental conditions on the Catalan Coast (NW Mediterranean) during 2000-2005. In: Valavanis V.E., Essential Fish Habitat Mapping in the Mediterranean. Series Developments in Hydrobiology, vol. 203: 185-199. Springer. http://dx.doi.org/10.1007/978-1-4020-9141-4_14

Martín P., Sabatés A., Lloret J., et al. 2012. Climate modulation of fish populations: the role of the Western Mediterranean Oscillation (WeMO) in sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) production in the north-western Mediterranean. Clim. Chang. 110: 925-939. http://dx.doi.org/10.1007/s10584-011-0091-z

Massé J., Leroy C., Halgand D., et al. 1995. Anchovy adult and egg distribution in the Bay of Biscay in relation to environmental conditions, as observed during acoustic surveys (1990, 1991, 1992). Actas del IV coloquio Internacional sobre Oceanografía del Golfo de Vizcaya: 281- 283. Santander.

Maynou F., Sabatés A., Salat J. 2014. Clues from the recent past to assess recruitment of Mediterranean small pelagic fishes under sea warming scenarios. Clim. Chang. 126: 175-188. http://dx.doi.org/10.1007/s10584-014-1194-0

Millot C. 1991. Mesoscale and seasonal variabilities of the circulation in the western Mediterranean. Dyn. Atmos. Oceans. 15: 179-214. http://dx.doi.org/10.1016/0377-0265(91)90020-G

Motos L., Uriarte A., Valencia V. 1996. The spawning environment of the Bay of Biscay anchovy (*Engraulis encrasicolus* L.). Sci. Mar. 60: 237-255.

Nicolle A., Garreau P., Liorzou B. 2009. Modelling for anchovy recruitment studies in the Gulf of Lions (Western Mediterranean Sea). Ocean Dynamics 59: 953-968. http://dx.doi.org/10.1007/s10236-009-0221-6

Palomera I. 1992. Spawning of anchovy *Engraulis encrasicolus* in the Northwestern Mediterranean relative to hydrographic features in the region. Mar. Ecol. Prog. Ser. 79: 215-223. http://dx.doi.org/10.3354/meps079215

Palomera I., Lleonart J. 1989. Field mortality estimates of anchovy larvae (*Engraulis encrasicolus*) in the western Mediterranean. J. Fish. Biol. 35 (suppl. A): 133-138. http://dx.doi.org/10.1111/j.1095-8649.1989.tb03054.x

Palomera I., Sabatés A. 1990. Co-occurrence of *Engraulis encrasicolus* and *Sardinella aurita* eggs and larvae in the northwestern Mediterranean. Sci. Mar. 54: 61-67.

Palomera I., Olivar M.P., Salat J., et al. 2007. Small pelagic fish in the NW Mediterranean Sea: an ecological review. Prog. Oceanogr. 74: 377-396. http://dx.doi.org/10.1016/j.pocean.2007.04.012

Pertierra J.P. 1992. Biología pesquera de la anchoa *Engraulis encrasicolus* del Mar Catalán (NW Mediterráneo). PhD thesis, Univ. Politècnica de Catalunya, Barcelona.

Pertierra J.P., Lleonart J. 1996. NW Mediterranean anchovy fisheries. Sci. Mar. 60(Suppl. 2): 257-267.

Planque B., Bellier E., Lazure P. 2007. Modelling potential spawning habitat of sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*) in the Bay of Biscay. Fish. Oceanogr. 16: 16-30. http://dx.doi.org/10.1111/j.1365-2419.2006.00411.x

Pörtner H.O., Peck M. 2010. Climate change effects on fishes and fisheries: towards a cause-and-effect understanding. J. Fish. Biol. 77: 1745-1779. http://dx.doi.org/10.1111/j.1095-8649.2010.02783.x

Razouls C., Kouwenberg J. 1993. Spatial distribution and seasonal variation of mesozooplankton biomass in the Gulf of Lions (northwestern Mediterranean). Oceanol. Acta 16: 393-401.

Rojas P., Garcia M., Sospedra J., et al. 1995. On the structure of the mean flow in the Blanes Canyon area (NW Mediterranean) during summer. Oceanol. Acta 18: 443-454.

Sabatés A., Olivar M.P., Salat J., et al. 2007a. Physical and biological processes controlling the distribution of fish larvae in the NW Mediterranean. Prog. Oceanogr. 74: 355-376. http://dx.doi.org/10.1016/j.pocean.2007.04.017

Sabatés A., Salat J., Palomera I., et al. 2007b. Advection of anchovy (*Engraulis encrasicolus*) larvae along the Catalan continental slope (NW Mediterranean). Fish. Oceanogr. 16: 130-141. http://dx.doi.org/10.1111/j.1365-2419.2006.00416.x

Sabatés A., Salat J., Raya V., et al. 2013. Role of mesoscale eddies in shaping the spatial distribution of the coexisting *Engraulis encrasicolus* and *Sardinella aurita* larvae in the northwestern Mediterranean. J. Mar. Syst. 111: 108-119. http://dx.doi.org/10.1016/j.jmarsys.2012.10.002

Santojanni A., Arneri E., Bernardini V., et al. 2006. Effects of environmental variables on recruitment of anchovy in the Adriatic Sea. Clim. Res. 31: 181-193. http://dx.doi.org/10.3354/cr031181

Somarakis S., Nikolioudakis N. 2007. Oceanographic habitat, growth and mortality of larval anchovy (*Engraulis encrasicolus*) in the northern Aegean Sea (eastern Mediterranean). Mar. Biol. 152: 1143-1158. http://dx.doi.org/10.1007/s00227-007-0761-6

Tudela S., Palomera I. 1995. Diel feeding intensity and daily ration in the anchovy *Engraulis encrasicolus* in the northwest Mediterranean Sea during the spawning period. Mar. Ecol. Prog. Ser. 129: 55-61. http://dx.doi.org/10.3354/meps129055

Tudela S., Palomera I., Quílez G. 2002. Feeding of anchovy *Engraulis encrasicolus* larvae in the north-west Mediterranean. J. Mar. Biol. Ass. UK 82: 349-350. http://dx.doi.org/10.1017/S0025315402005568

Vargas-Yáñez M., Moya F., Tel E., et al. 2009. Warming and salting in the western Mediterranean during the second half of the 20th century: inconsistencies, unknowns and the effect of data processing. Sci. Mar. 73: 7-28. http://dx.doi.org/10.3989/scimar.2009.73n1007

Vargas-Yáñez M., Moya F., García-Martínez M., et al. 2010. Climate change in the Western Mediterranean sea 1900-2008. J. Mar. Syst. 82: 171-176. http://dx.doi.org/10.1016/j.jmarsys.2010.04.013

Wood S., 2006. Generalized additive models: an introduction with R. CRC/Taylor and Francis.