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Spatio-temporal patterns and environmental controls of small pelagic fish body condition from contrasted Mediterranean areas

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ABSTRACT

Small pelagic fish are among the most ecologically and economically important marine fish species and are characterized by large fluctuations all over the world. In the Mediterranean Sea, low catches and biomass of anchovies and sardines have been described in some areas during the last decade, resulting in important fisheries crises. Therefore, we studied anchovy and sardine body condition variability, a key index of population health and its response to environmental and anthropogenic changes. Wide temporal and spatial patterns were investigated by analyzing separately data from scientific surveys and fisheries in eight Mediterranean areas between 1975 and 2015.

Results showed that anchovy and sardine body condition as well as maximum size in some areas sharply decreased in most Mediterranean areas along years (except in the Northern Alboran Sea). Despite this general pattern, well-marked environmental differences between sub-regions were highlighted by several analyses and variations in body condition were not found to be homogeneous over all the Mediterranean Sea. Further, other analyses revealed that except for the Adriatic where major changes towards a lower body condition were concomitant with a decrease in river runoffs and chl-*a* concentration, no concomitant environmental regime shift was detected in other areas.

Together, these analyses highlighted the current poor body condition of almost all small pelagic fish populations in the Mediterranean. Yet, global environmental indices could not explain the observed changes and the general decrease in condition might more likely come from regional environmental and/or anthropogenic (fishing) effects. A prolonged state of poor fish body condition, together with an observed reduced size and early age-at-maturity may have strong ecological, economic and social consequences all around the Mediterranean Sea.

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1. Introduction

Ocean systems are currently going towards changing environmental conditions especially due to the impact of anthropogenic climate change (Hoegh-Guldberg and Bruno, 2010). In particular, the Mediterranean Sea has been identified as one of the most responsive regions to climate change (Giorgi, 2006), as well as to direct human impacts such as pollution (Halpern et al., 2008). Specifically, recent studies using climate models already highlighted the warming of this sea (both at the surface and in deep waters) and the increasing frequency of extreme events (Bethoux et al., 1990; Theocharis, 2008; Vargas-Yáñez et al., 2008, 2010). Large scale perturbations, such as climate change, are known to affect all biological levels, directly (e.g. by affecting physiological thresholds) and/or indirectly (e.g. by modifying food resources; Jørgensen, 1992), resulting in spatio-temporal changes in the abundance of exploited fish in the Mediterranean Sea (see e.g. Lloret et al., 2015) and elsewhere (see e.g. Drinkwater et al., 2010).

Pronounced small pelagic fish population fluctuations are observed all over the world, especially in the upwelling areas (Baumgartner et al., 1992; Chavez et al., 2003). In the Mediterranean, those variations have been linked to recruitment (Martín et al., 2011), spawning (Agostini and Bakun, 2002; Basilone et al., 2013) or larval survival (Garcia et al., 1998). Such major population changes can have important impacts on the dynamics of marine ecosystems, as these forage fish represent an important biomass at mid-trophic levels, making them a key-component of the ecosystem (Cury et al., 2000; Coll and Libralato, 2012). Thus, the dynamics of this functional group are important both to maintain the integrity of the marine ecosystem, and for socioeconomic stability in the region. The main reason for the renowned population fluctuations of small pelagic is their short life span, as well as their susceptibility to environmental variability (Cushing and Dickson, 1976). Importantly, these characteristics make them excellent indicators of climate-driven environmental changes in marine systems (Drinkwater et al., 2010; Peck et al., 2013). The two most abundant small pelagic fish species in the Mediterranean Sea, the European sardine (*Sardina pilchardus*) and anchovy (*Engraulis encrasicolus*), have been exploited for a long time (Lleonart and Maynou, 2003) and are still intensely exploited, accounting for 35–50% of the reported catch in this area (GFCM, 2014). In recent years, a general decreasing trend has been observed in the landings of the small pelagic fish stocks in different parts of the Mediterranean Sea (GFCM, 2012; Vasilakopoulos et al., 2014), leading to an important fisheries crisis. In addition to this, alarming biological signals also appeared, such as a decrease in growth and body condition of small pelagics in the Gulf of Lions (Van Beveren et al., 2014), and a higher risk of recruitment failure with increasing temperature in the Northern Spain area (Maynou et al., 2014).

Body condition is an important individual physiological trait of marine organisms, influencing other life history traits, such as growth, reproduction (e.g. egg size and number, age at first maturity) and mortality (Lloret et al., 2014; Brosset et al., 2016a). Specifically, body condition indices are proxies of the quantity of stored energy, evaluating individual's health status and fitness (Schulte-Hostedde et al., 2001; Wilson and Nussey, 2010). For example, survival, growth and reproductive success are theoretically higher for individuals in better condition (Millar and Hickling, 1990), resulting in an important link between average population body condition and future population success (Jakob et al., 1996; Adams, 1999). Recently, more evidence emerged showing that variations in body condition can affect ecological processes at scales ranging from individuals to ecosystems (Rätz and Lloret, 2003; Lloret et al., 2014; Van Beveren et al., 2014). Consequently, fish body condition can in part determine ecosystem functioning and fisheries yield, so that this factor can constitute a valuable tool in stock assessment and management (Lloret et al., 2012). Furthermore, condition indices can be computed easily from collected length and weight data, available in numerous areas and at large temporal scale. It has already been demonstrated that environmental factors~~,~~ such as temperature, food availability (Brosset et al., 2015b) or parasitism (Ferrer-Maza et al., 2016) influence fish condition through direct and/or indirect effects. For example, a decrease in body condition due to a lack of food or an increase of metabolic costs under higher temperature has already been advocated in several studies (see e.g. Pörtner and Knust, 2007; Brosset et al., 2015b). Changes in water stratification and currents are known to strongly influence plankton productivity and could thus indirectly act on the body condition of planktivorous small pelagic fish (Costalago et al., 2014; Le Bourg et al., 2015; Brosset et al., 2016b). Furthermore, these effects are easily visible because of the fast response of fish condition to environmental changes (Peck et al., 2013).

However, to our knowledge, a large scale study focusing on small pelagic fish body condition has never been realised in the Mediterranean Sea, so that at present it is still unclear if the recent decreases described in a few areas are truly a common issue. In this study, data of anchovy and sardine body condition from eight Mediterranean areas were compiled for the first time to compare the temporal trend in body condition of the different studied stocks and to assess whether a general decline took place. We also focused on the environmental (including climatic) factors that could potentially affect fish condition, taking into account spatial factors. A dataset of morphometric (i.e. length and weight) variables of more than 250,000 individuals analysed from 1975 to 2016 enabled us to compute the individuals' morphometric condition index, which assumes that for a given length a heavier fish is in better condition.

2. Material and methods

2.1. Study areas

Mediterranean sub-areas (GSA) were selected following the General Fisheries Commission for the Mediterranean (GFCM) delimitations adopted for stock assessments from the westernmost Alboran Sea to the Black Sea in the East (Fig. 1). The Mediterranean Sea is known to be oligotrophic, even if an important variability in productivity is visible with a West to East gradient and enhanced primary productivity areas due to strong river discharge as in the North Western Mediterranean, with the Rhone in the Gulf of Lions and the Ebro in the Catalan Sea, or the Po river in the Northern Adriatic Sea.

In the North Western part of the Mediterranean Sea the Gulf of Lions is the most productive area and covers about 20,400 km^2 (Bănaru et al., 2013). This area has a wide continental margin (>60 km) and productivity depends on strong mixing events induced by NW and N winds and Rhodanian inputs which create a gradient of nutrients from East to West (Darnaude et al., 2004). Also, local upwellings support the high productivity (Millot, 1990). The Northern Spain area, grouping the Catalan Sea and the Gulf of Valencia, is oceanographically connected with the Gulf of Lions through the Northern current flowing to the south-west which enhances the production in the north Catalan Sea. Models have indeed highlighted larval connectivity between the northern spawning grounds of anchovy in the Gulf of Lions and the Catalan Sea due to the hydrodynamic characteristics in the area mediated by the North current and the filament transport in mesoscale eddies (Ospina-Alvarez et al., 2012). The north Catalan Sea has a narrow shelf that widens in front of the Ebro river delta (>60 km

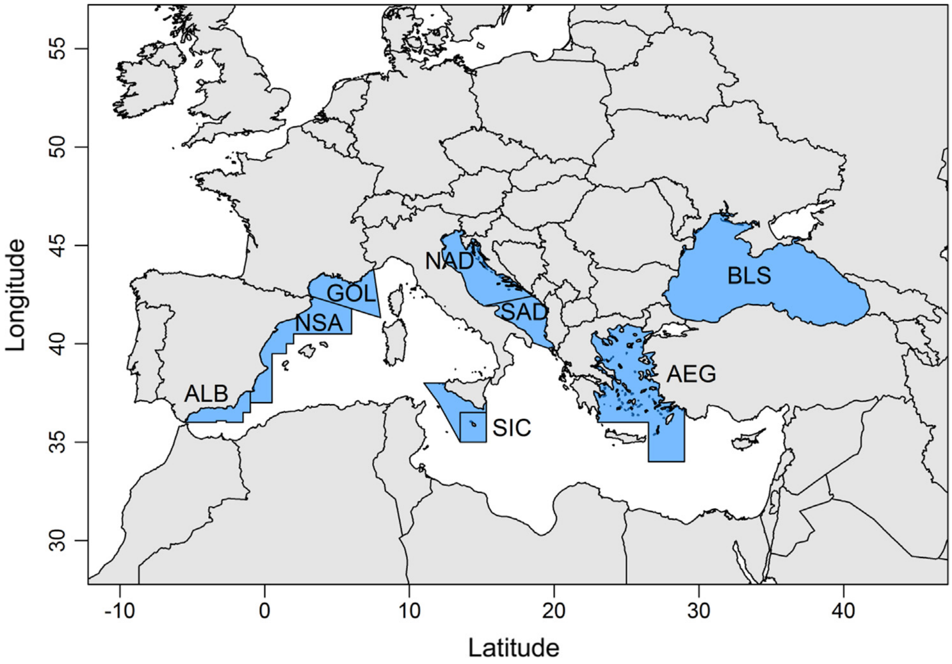

Fig. 1. Main Geographical Subareas of the Mediterranean and Black Seas used in this study according to their number defined by the General Fisheries Commission for the Mediterranean (NAD: Northern Alboran Sea; NSA: Northern Spain area; GOL: Gulf of Lions; SIC: Strait of Sicily (Malta Island and South of Sicily areas combined); NAD: Northern Adriatic Sea; SAD: Southern Adriatic Sea; AEG: Aegean Sea; BLS: Black Sea).

wide) where it is strongly influenced by water discharge and wind mixing allowing phytoplankton to find necessary nutrients, especially during summer period when the water column is strongly stratified (Palomera et al., 2007).

In the south of Spain, the Northern Alboran Sea is the southern- and western-most area in our study, and it is a transitional zone between Mediterranean and Atlantic waters. Two gyres, occurring in the central basin of the Alboran Sea, as well as several upwellings in the north coast associated with vertical and lateral nutrient inputs, make this area especially productive (Macías et al., 2008).

The Adriatic Sea was divided into two areas: the Northern Adriatic Sea and the Southern Adriatic Sea. The Northern Adriatic is characterized by shallow depths and high river discharge, particularly due to the Po River outflow, which has a major impact on the phytoplankton biomass due to the high nutrients loads (Artioli et al., 2008). Furthermore, local upwelling events and eddies, that contribute to spread the Po river discharge offshore, enhance the primary production (Russo and Artegiani, 1996). A decreasing trend in nutrient concentration and in production is observed from North to South (Zavatarelli et al., 1998): the Southern Adriatic is in fact deeper, mostly influenced by eastern Mediterranean waters and exhibits an oligotrophic character with lower phytoplankton abundance and biomass (Zavatarelli et al., 1998).

The Strait of Sicily is the area where the Western and the Eastern Mediterranean basins connect, playing a crucial role in determining the water-mass exchanges. Main water masses present in the Strait of Sicily might be divided into a surface layer composed of Atlantic water flowing eastwards, and intermediate and deep layers mainly composed of Levantine intermediate water, and transitional Eastern Mediterranean deep water flowing in the opposite direction. Their encounter creates local upwellings which enrich the upper water layers, enhancing primary production and creating favorable environmental conditions for small pelagic fish (Basilone et al., 2013; Bonanno et al., 2014).

The North Aegean Sea is among the most productive areas of the Eastern Mediterranean Sea. Black Sea waters, river runoffs and the large continental shelf contribute to increase primary productivity in this area, explaining the high small pelagic catches and the importance as a spawning ground for both anchovy and sardine.

The Black Sea is almost completely isolated, being connected to the Mediterranean only through the Bosphorus Strait. It is therefore mostly influenced by freshwater inputs from rivers (Özsoy and Ünlüata, 1997) and it is characterized by weak water circulation and anoxic waters below the oxycline at about 150 m depth. Only anchovy is found in the Black Sea, where this species is known to migrate between the North, where they reproduce and feed, and the South, where they overwinter (Gucu et al., 2016).

2.2. Fish sampling

Two types of sampling were done. One used commercial vessels (pelagic trawlers and/or purse seiners) all over the year and the other, scientific surveys at sea (trawls), carried out once per year and dedicated to small pelagic fish abundance estimation (Mediterranean International Acoustic Survey (MEDIAS) since 2009). Summarized information on fish sample sizes, temporal coverage and month of collection are provided in Table 1. During scientific surveys, parallel fixed transects perpendicular to the coastline were followed each year. Echosounders enabled to detect fish traces and a pelagic trawl was deployed to determine fish composition when these traces were long enough.

Regardless of the sampling method, a random sample of anchovies and sardines from the catch was directly measured on board or brought to the lab on land for subsequent analyses. Fish measurements included fish total length (TL, depending on the area from the nearest mm to the nearest 0.5 cm for the scientific survey or from the nearest mm to nearest cm for commercial samples) and total weight (W, to the nearest g for both types of sampling).

2.3. Condition and maximum size estimations

2.3.1. Morphometric index of condition

Condition factors are mainly based on length–mass relationships (Bolger and Connolly, 1989). While Fulton's condition factor assumes isometric growth or growth without changes in body pro-

Table 1
Summary of all biological data used in this study by area.

Area	Species	Time period	Data origin	Sampling month	Number of individuals
GSA 1	Anchovy	2001–2009	ECOMED	November-December	666
Northern Alboran Sea		2009–2013	MEDIAS	June-July	182
	Anchovy	1990–1992 & 2003–2013	Fisheries	All months	12,126
	Sardine	2001–2009	ECOMED	November-December	1600
		2009–2013	MEDIAS	June-July	742
	Sardine	1990–1996 & 2003–2013	Fisheries	All months	21,539
GSA 6	Anchovy	1993–2009	ECOMED	November-December	6726
Northern Spain		2009–2013	MEDIAS	June-July	4649
	Anchovy	2004–2013	Fisheries	All months	7049
	Sardine	1993–2009	ECOMED	November-December	6316
		2009–2013	MEDIAS	June-July	8923
	Sardine	2004–2013	Fisheries	All months	13,157
GSA 7	Anchovy	1993–2015	MEDIAS	June-July	8525
Gulf of Lions	Anchovy	2005–2016	Fisheries	All months	12,037
	Sardine	1993–2015	MEDIAS	June-July	9464
	Sardine	1971–1983 & 2003–2016	Fisheries	All months	18,551
GSA 15 & 16	Anchovy	1998–2013	MEDIAS	June-August	1331
Strait of Sicily	Sardine	1998–2013	MEDIAS	June-August	1572
GSA 17	Anchovy	1998–2013	MEDIAS	July-October	14,137
Northern Adriatic Sea	Anchovy	1975–2012	Fisheries	All months	50,826
	Sardine	1998–2013	MEDIAS	July-October	7550
	Sardine	1975–2012	Fisheries	All months	27,164
GSA 18	Anchovy	1998–2013	MEDIAS	June-September	1849
Southern Adriatic Sea	Sardine	1998–2013	MEDIAS	June-September	1046
GSA 22	Anchovy	2003–2008	MEDIAS	June-July	8574
Aegean Sea	Sardine	2003–2008	MEDIAS	June-July	2484
GSA 29	Anchovy	2011–2013	MEDIAS	November-March	3678
Black Sea					

portions, resulting in condition factors that are often length- and species-dependent, the relative condition factor according to Le Cren (1951) compares actual weight to a standard weight predicted by weight-length regression, based on the population from which the fish was sampled (Basilone et al., 2006; and references therein).

As the two studied species exhibited an allometric growth pattern (Brosset et al., 2015a), we used for this study the more suitable relative condition index (K_n, Le Cren, 1951) rather than Fulton's index:

$$K_n = W/W_r$$

where W is the observed weight of an individual and W_r the predicted weight of an individual of a given length TL calculated with ($W_r = \alpha TL^{\beta}$). By definition, the values of the relative condition factor are distributed around 1 and the higher the value the better the condition.

Length-weight relationships were computed by area and species to investigate temporal fluctuations and only by species for the spatial analyses. The advantage of a single regression curve per species is the possibility to compare the values between the different areas (i.e. indicators are standardized for inter-ecosystem comparisons).

As shown by several authors (Schulte-Hostedde et al., 2005; Stevenson and Woods, 2006; McPherson et al., 2011), this morphometric index is related to total lipid content, and its use has previously been validated for individuals outside the reproductive period. During the reproductive period, the variations of condition reflect both lipid and protein variations which represent a global measure of condition (Brosset et al., 2015a).

Maximum size of both species was estimated each year by computing the 95% quantile of fish size distribution rather than the maximal size observed, making this parameter less sensitive to extreme individuals.

2.4. Environmental data

Daily sea surface temperature (SST, in °C), chlorophyll *a* (Chl-*a*, in $mg{\cdot}m^{-3}$) and Eddy kinetic energy (Eke, measuring turbulence in $cm^2{\cdot}s^{-2}$) were obtained from satellite data. These three environmental variables were chosen due to their large coverage in space and time and because they are relevant to explain differences in productivity, water mixing and temperature patterns affecting fish body condition. SST came from version 5 of the AVHRR Oceans Pathfinder SST data set obtained from the NOAA website (http://podaac.jpl.nasa.gov). Surface chlorophyll *a* was extracted using MODIS-aqua data from the OceanColor web site (http://oceancolor.gsfc.nasa.gov). Kinetic energy was extracted from Aviso database. All variables were extracted on the basis of the different area coordinates given by the GFCM. The discharges of three main rivers of the northern Mediterranean, i.e. the Ebro (Northern Spain area), the Po (Northern Adriatic sea) and the Rhône (Gulf of Lions) were used in the breakpoint analysis (see below) to detect any synchrony between river's discharges and fish condition. Note that rivers that discharge in the Black Sea were not considered, as time series of fish condition in the Aegean Sea and Black Sea are too short or too discontinued to conduct such an analysis. A monthly average was taken for all environmental variables per area. Despite the fact that salinity and zooplankton data may be relevant, this type of data was too scarce or heterogeneous in the different Mediterranean areas to be considered. Finally, we also used suitable large-scale climatic indices for the Mediterranean area, such as the Western Mediterranean Oscillation (WeMO, Martin-Vide and Lopez-Bustins, 2006), the North Atlantic Oscillation (NAO, Hurrell and Loon, 1997), the Mediterranean Oscillation (MO, Conte et al., 1989) and the Atlantic Multidecadal Oscillation (AMO, Kerr, 2000) indices. These indices are based on the differences in normalized sea level pressures between two areas and were used as broad scale environmental descriptors. Because most of the variability patterns in the NAO, WeMO or AMO indices takes place during winter (see Hurrell, 1995; Martin-Vide and Lopez-Bustins, 2006), the averages of winter monthly values (December to March) from the previous year were used.

2.5. Data analyses

2.5.1. Fish body condition and maximum size time series analysis

Fish body condition and maximum size time series from annual scientific surveys were analysed together to identify the main characteristics of the time series, as well as to compare them. Correspondence in terms of trend or breakpoints among the different areas could indicate that small pelagic fish condition or size exhibits common patterns of temporal variation at the Mediterranean scale. As the Spanish scientific survey shifted from winter to summer in 2009, we accounted for this change by calculating the mean annual body condition cycle of each species from fisheries data and by adding the obtained winter/summer difference to the winter values (i.e. before 2009). This allowed having a continuous time series from 1993 to 2013 with comparable values before and after 2009.

2.5.1.1. Trends, periodicity and annual cycle of body condition. Twelve MEDIAS (Northern Alboran Sea, Northern Spain area, Gulf of Lions, Northern Adriatic Sea, Southern Adriatic Sea and Strait of Sicily, Table 1) and two fishery time series (Adriatic) were long enough (between 13 and 23 years) to investigate temporal changes for both species. The Aegean Sea and the Black Sea could not be considered in the time series analyses because they were far too short (containing only 5 and 3 years of data with one point per year, respectively, see Table 1). For the other time series, the missing values were filled using either cubic splines or linear interpolation when the analyses imply time continuity.

The Eigen vector filtering (EVF, Colebrook, 1978) was performed on the condition time series for both species at all locations to estimate the percentage of variance of the long-term trend in each series (see Ibanez and Dauvin (1988) for more details).

Periodicity analyses on the other hand were only performed on fisheries data from the Adriatic Sea, which displayed the only long-enough monthly time series for both species (from 1975 to 2012). Fishery time series exist for the Northern Alboran Sea (2003–2013), the Northern Spain area (2004–2013) and the Gulf of Lions (2005–2016) but were considered not long enough to be used in this type of analyses. To do so, wavelets analyses were used, which decompose the variance of a time series over frequencies and over time domains and tolerate non-stationary data. To detect low and high frequencies, β surrogate test were used since it is deemed to be well-suited to ecological time series (for more details, see Rouyer et al., 2008). Final wavelet power spectra were presented as time–frequency plots, with colors indicating intensities of match between wavelets and time series (from blue = low variance to grey = high variance). Additionally to periodicity analyses, temporal changes in the timing of the annual peak of condition in the Adriatic Sea were investigated. The timing of the peak of body condition was computed as the mean number (1 for January, 2 for February, etc.) of the three months with highest condition during each year where all data were available (no year had two peaks of condition that would have affected this calculation).

2.5.1.2. Covariability of small pelagic fish body condition in the Mediterranean. In order to know if similarity in fish body condition was dependent on space, more precisely on distances between sites where the time series come from, we computed pairwise correlations (Mantel test, Mantel, 1967) among fish body condition time series from fisheries data and plotted them again distances (in km) between sites. A nonlinear model was fitted to compute the distance where correlations are reduced to 50% of the estimated correlation at a distance of 0 km ($d_{0.5}$, see Batchelder et al., 2012 for further details). We accounted for year-to-year temporal autocorrelation by using estimated numbers of effective degrees of freedom (typically ~10% smaller than the number of years in the time series) instead of removing autocorrelation by difference filtering (Pyper and Peterman, 1998).

2.5.2. Investigating environmental changes and fish condition relationships

To investigate potential synchrony in temporal changes in fish condition and environmental variables, we computed a breakpoint analysis, i.e. a date (in year) that distinguishes two continuous periods of significant different levels in a given variable. Fish condition and size time series were analysed using the strucchange package (Zeileis et al., 2013) to assess the year(s) (and their 95% confidence intervals) of statistically significant changes in the level of fish condition. The Bayesian Information Criterion (BIC) was consulted to assess a penalty for the number of segments used to describe the data and thus have an objective criterion to determine the most parsimonious number of breakpoints. The same method was used to detect environmental breakpoints (SST, Chl-*a*, Eke, rivers and climatic indices) and check their synchrony with fish biological parameters breakpoints.

A principal component analysis (PCA) was implemented to describe the multivariate relationships among the annual values of both fish biological parameters (fish body condition and maximum size) and environmental factors (SST, Chl-*a* and Eke). A correlation-based matrix on Euclidean distances among all variables was used. The PCA reduced the spatial population and environmental variability into a few dimensions. Since sardine is not present in the Black Sea, this area was not considered in the sardine PCA.

All statistical analyses were performed with R version 3.0.2 (R Development Core Team, 2013). Values are indicated as mean ± standard error (SE) and all statistical tests were performed at a significance level of 0.05.

3. Results

3.1. Annual fish condition and maximum size trends

Anchovy and sardine mainly displayed a decreasing trend in their body condition in most studied areas (Fig. 2). Anchovy body condition showed a pronounced decrease in the Gulf of Lions (63% of deviance explained), in both Adriatic Sea areas (72% and 78% of deviance explained in the North and South part, respectively) and in the Strait of Sicily (60% of deviance explained). While the decreasing trend has been linear along years since 1998 in the Southern Adriatic Sea, anchovy condition has started to drop only since 2004 in the Strait of Sicily and in the Northern Adriatic and since 2007 in the Gulf of Lions. Anchovy body condition was increasing before being stable in the Northern Alboran Sea and stable over the time series in the Northern Spain area (43% and 46% of deviance explained). All areas except the Northern Alboran Sea displayed an overall decreasing trend for sardine body condition (Fig. 2). Similarly to anchovy, the decrease was mostly linear in the Southern Adriatic, and began later in the 2000s in other areas (in 2004, 2007, 2007 and 2009 in respectively the Northern Spain area, the Gulf of Lions, the Northern Adriatic and the Strait of Sicily, Fig. 2). The deviance explained by this trend was relatively high in all areas (from 57% to 85%), except for the Strait of Sicily where it only explained 49%. The trend was different in the North-

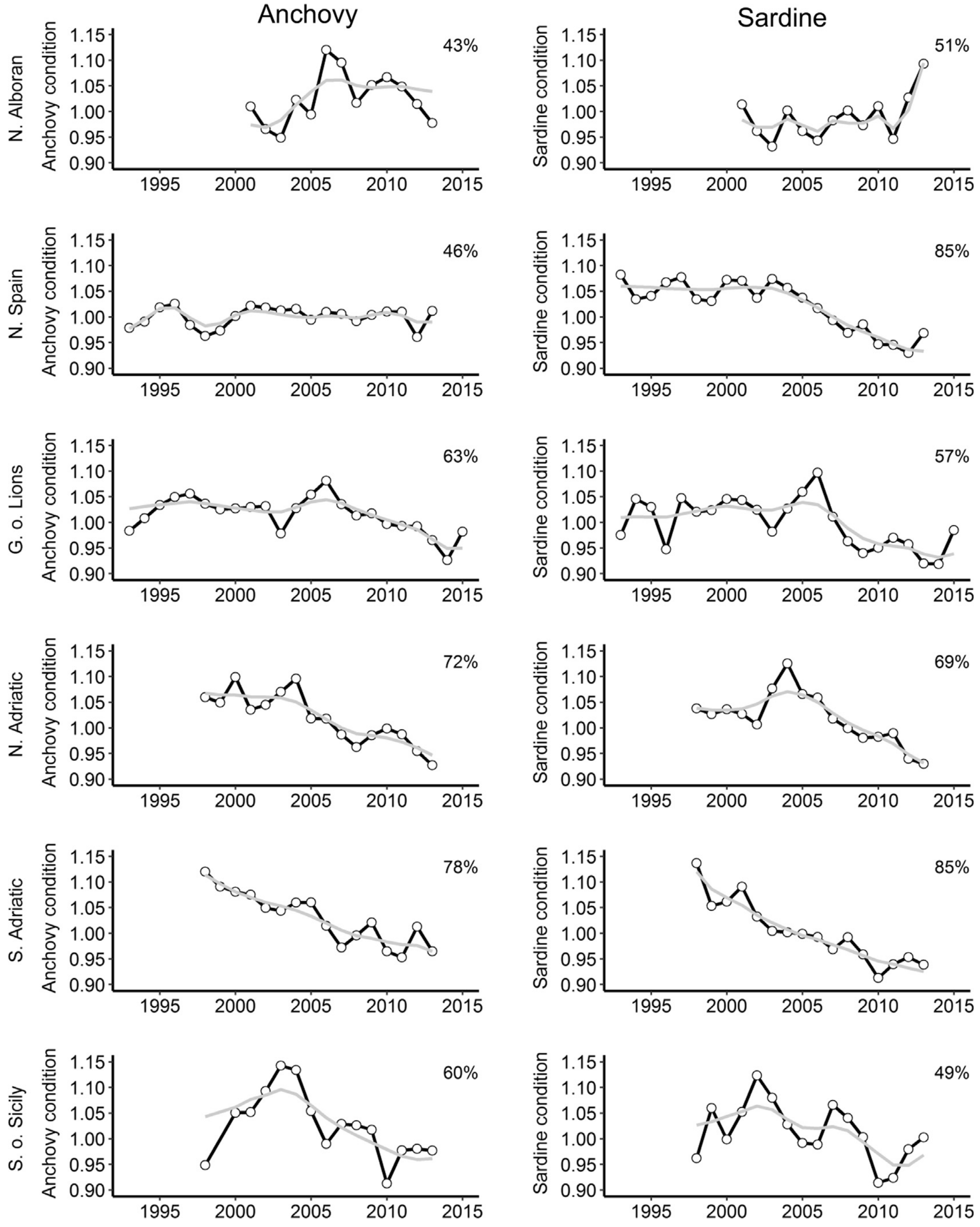

Fig. 2. Time series of the annual anchovy and sardine body condition of the six different areas studied from MEDIAS data. The black line with markers represents the time series and the grey line the trend from Eigen Vector Filtering. The percentage of deviance explained by the main trend is indicated in the upper right corner.

ern Alboran Sea, where sardine body condition was stable before it greatly increased during the last two years (Fig. 2).

As for fish condition, the Northern Alboran Sea did not exhibit pronounced trend in fish maximum size and the same applies to the Northern Spain area (between 40 and 50% of deviance explained, Fig. 3). The Gulf of Lions (especially after 2008), and Northern Adriatic (linearly) on the other hand showed a strong negative trend for both species and a high percentage of deviance explained (Fig. 3). The decrease was also observed but less pronounced in the Southern Adriatic Sea (Fig. 3). Finally, a decrease in sardine size only was found in the Strait of Sicily, though not really strong (49% of deviance explained, Fig. 3).

3.2. Fish body condition, size and environmental breakpoint analysis

Fish body condition time series showed between zero and two statistically significant breakpoints, which mostly occurred in the middle of the 2000s (Fig. 4). The last breakpoints in sardine condition (consistently towards lower condition values) occurred simultaneously between 2006 and 2008 in all areas (except in the Northern Alboran Sea and the Strait of Sicily where no breakpoint occurred, Fig. 4). Regarding anchovy, the last breakpoints were much more widely spread in time between 2005 and 2009 (Fig. 4). Breakpoints in maximum fish size appeared in the areas where fish body condition have also shifted and often occurred

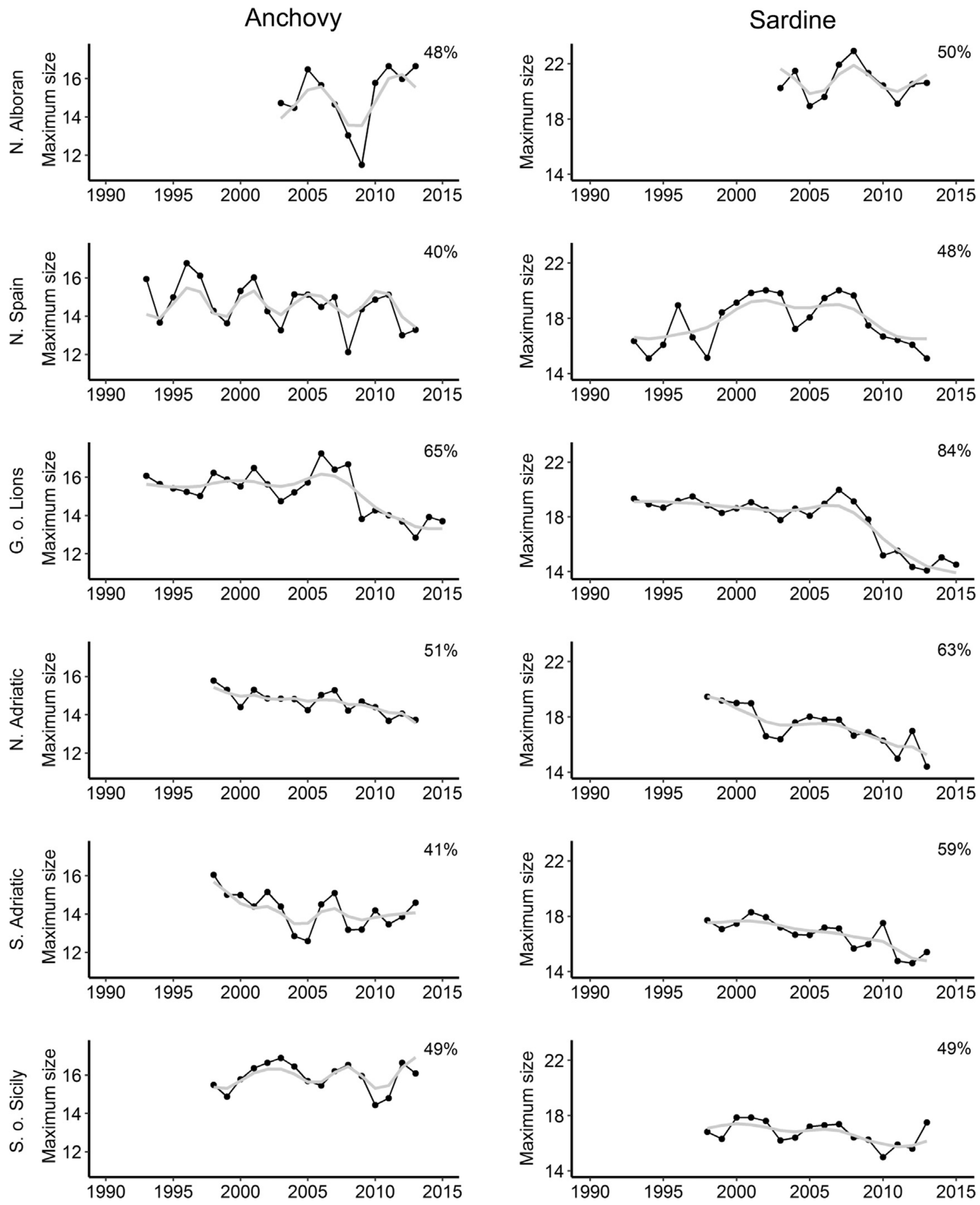

Fig. 3. Time series of the annual anchovy and sardine maximum size of the six different areas studied from MEDIAS data. The black line with markers represents the time series and the grey line the trend from Eigen Vector Filtering. The percentage of deviance explained by the main trend is indicated in the upper right corner.

simultaneously or just after those ones (Fig. 4). Regarding the environment, no breakpoints were detected in either the Eke time series, nor in the climatic indices (except for AMO in 1995) nor in the chl-*a* concentration of certain areas (Fig. 4). Depending on the area, SST had one or two breakpoints. The first ones co-occurred around 1996 while the second one only occurred in 2006 in Sicily and in 2010 in both Adriatic areas. The three river discharges also showed breakpoints, the first one being similar around 2002 but the second one only occurred in the Adriatic in 2008 (Fig. 4). In the Northern Adriatic, the anchovy decreasing body condition led to a breakpoint in 2004, which coincided with the decline in Po river runoff and chl-*a* for which breakpoints have been also detected in the same period, in 2002 and 2003, respectively (Fig. 4). The breakpoint in sardine condition reflecting a drop occurred in 2006 (Fig. 4). In the Southern Adriatic, the both anchovy decreasing breakpoint co-occurred with a decrease in chl-*a*. Sardine's first decreasing breakpoint co-occurred with a decrease in chl-*a* while the second sardine condition decreasing breakpoint co-occurred with an increase of temperature (Fig. 4). Apart from the Adriatic, only two breakpoints of fish body condition and size time series co-occur with any environmental breakpoint (Fig. 4). An increase in sardine size occurred with increasing SST in the North Spain area

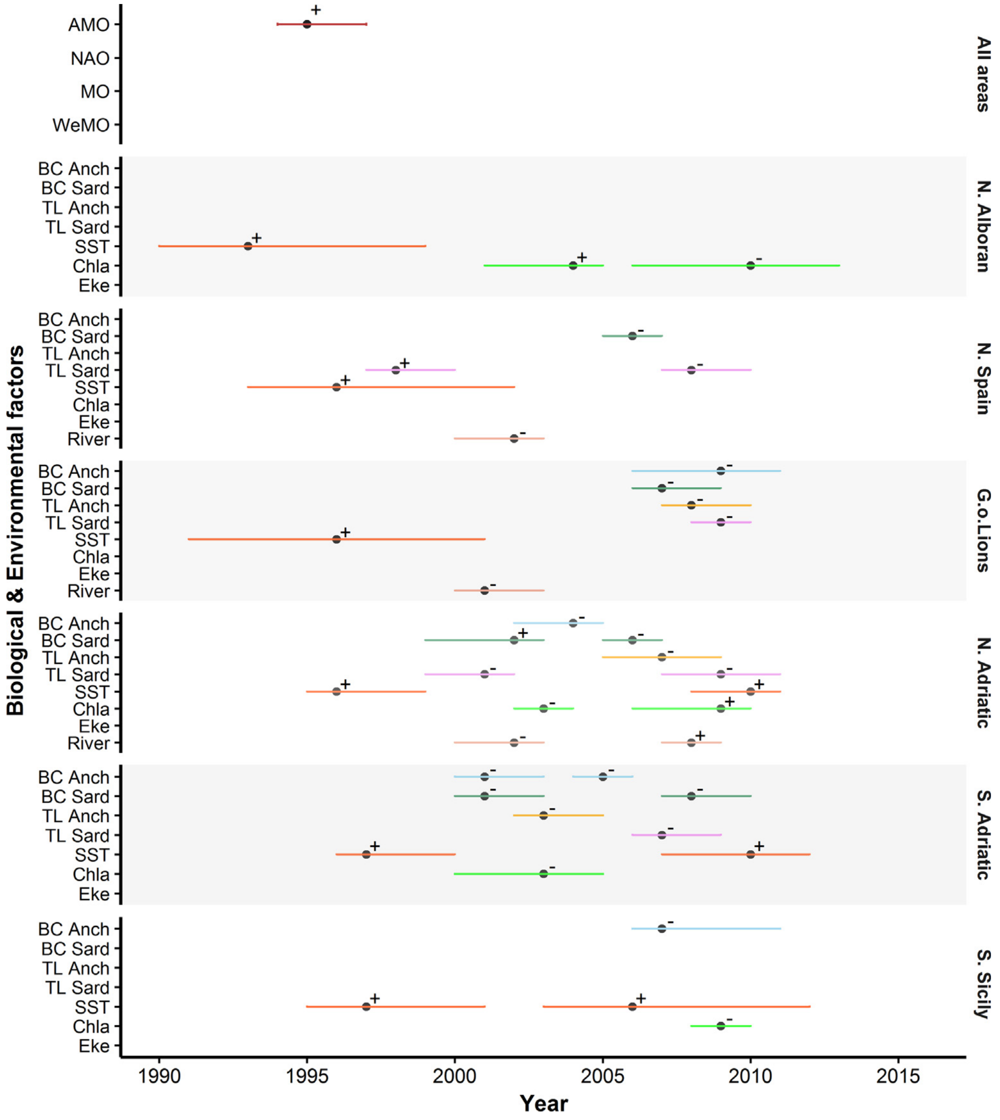

Fig. 4. Breakpoint analyses of fish biological parameters from MEDIAS data and environmental factors time series per Mediterranean Sea region (BC and TL mean body condition and total length, respectively). Horizontal lines indicate the confidence interval around the detected breakpoint and the sign (plus or minus) indicated the direction of the breakpoint towards an increase or a decrease.

while a decreasing anchovy body condition has been concomitant with decreasing chl-*a* quantity and increasing SST in the strait of Sicily (Fig. 4).

3.3. Periodicity and phenology in fish condition of the Adriatic Sea

Time series of monthly body condition from 1975 to 2012 derived from fisheries data in the Adriatic Sea displayed long term decreases. A first drop occurred in the mid-80s for both species. It is followed by a slight decrease (1995) and increase (2005) for anchovy and a final decrease between 2008 and 2012 only for sardine (from 42% to 48% of deviance explained, Fig. 5A). Periodicities at lower frequency were also observed for anchovy with periods of 3 years between 1996 and 2012 or 6–7 years between 1975 and 1995 (Fig. 5A). Periods of 6–7 years were detected all along the temporal windows in sardine body condition (Fig. 5A). The annual cycles during the entire period is well pronounced, as revealed by wavelet analyses (Fig. 5A), but the peak in condition moved earlier in the season for both species along the series, with a stronger change for anchovy (from October/November in the 1970s to June/August in the 2000s) than for sardine (from September/October in the 1970s to July at the end of the 2000s, Fig. 5B).

3.4. Environmental parameters determining pelagic fish body condition in the Mediterranean

In the PCA performed on anchovy body condition, maximum size and environmental factors, the first (F1) and second (F2) components accounted for respectively 40% and 22% of the total variance (Fig. 6). Positive values of F1 represented areas with high mean annual SST while positive values of F2 indicated areas with high mean annual chl-*a*. Anchovy mean annual body condition and maximum size were positively related to mean annual Eke rather than to mean annual chl-*a* and temperature in the Mediterranean Sea. In the PCA performed on sardine, F1 and F2 represented 37% and 28% of the total variance, respectively (Fig. 6). F1 represented the contrast between mean annual temperature and mean annual chl-*a*, while F2 is mostly characterized by the mean

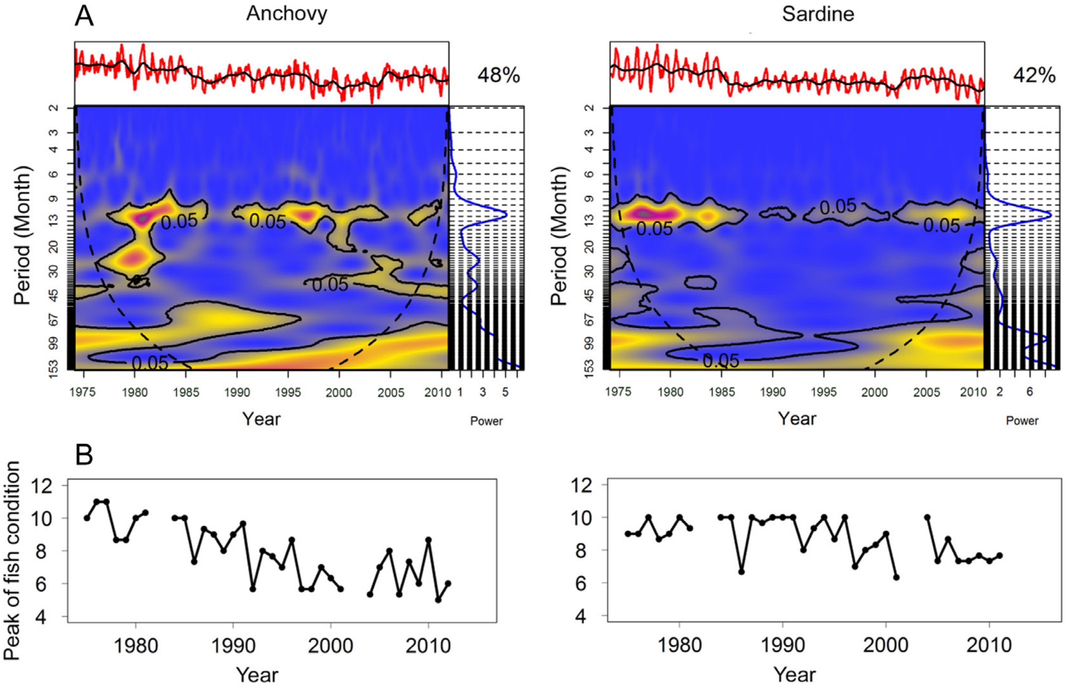

Fig. 5. Wavelet analyses and timing of the peak in condition for anchovy and sardine from Adriatic fisheries data. (A) Wavelet power spectra (mean panels). Power values range from blue (low) to grey (high). The black dashed line forming a cone delimits the region not influenced by edge effects. Continuous black lines show 5% significance areas. The top panel represents the standardized data time series (in red) as well as the EVF result (in black). The right panel is the global spectrum. (B) Yearly moment of maximum fish condition. Peaks were calculated as the average of the three successive months of highest condition values. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

annual Eke. Contrary to anchovy, sardine annual body condition and maximum size were strongly related to annual mean chl-*a*, opposed to annual mean temperature and almost independent of Eke. For both species, even if interannual variability within areas was sometimes important (e.g. Northern Alboran Sea), points of a same area were closer to each other than to points from other areas, indicating a spatial variability much higher than the temporal one (Fig. 6). This regional coherency was especially visible for sardine where areas were ordered according to the latitudinal gradient (from South to North) on the first component and where the northern the area, the higher the sardine body condition (except for the Northern Alboran Sea, Fig. 6). Particularly, the Strait of Sicily and the Northern Alboran Sea were totally isolated, mainly due to their strong Eke values. A last point of interest relies on the discrimination of the different areas, such as the Gulf of Lions against the Alboran Sea for sardine or Sicily against Northern Adriatic for anchovy (Fig. 6), which indicates that regions inhabited by anchovy and sardine display different environmental conditions.

3.5. Covariability of small pelagic fish body condition in the Mediterranean

Covariability of both anchovy and sardine body condition declined exponentially with increasing distance between harbors, as expected (Fig. 7). The 50% decorrelation distance of the pairwise correlation between GSAs was estimated as 948 km (845–1075 km, 95% CI) for anchovy and 843 km (732–1031 km, 95% CI) for sardine. However, some harbors separated by small distance could also display a low Pearson correlation coefficient (e.g. between Split and Chioggia for anchovy, respectively on the eastern and western coast of the Northern Adriatic Sea, Table 2), indicating occasional strong local variability in fish body condition, mainly for anchovy (Table 2).

4. Discussion

Anchovy and sardine exhibited a decreasing trend in body condition in most of the studied areas, i.e. four or five over six for anchovy and sardine, respectively. None of the studied species in the different Mediterranean areas displayed a long term increase in body condition. The general decrease in small pelagic fish body condition is in agreement with other observations, such as a decreasing biomass of several stocks and weakened biological state for both species at the Mediterranean scale (Tsikliras et al., 2015; Vasilakopoulos et al., 2014; Vilibic et al., 2016). This is particularly clear in some areas, such as the NW Mediterranean, where small sized less fecund individuals (McBride et al., 2015) in a low health status (i.e. lower lipid content and higher intensity of certain parasites, Ferrer-Maza et al., 2016; Van Beveren et al., 2016b) are dominant in the population.

Additionally, sardine body condition dropped synchronously in 2006 and 2007 in four areas, indicating potential broad-scale causes affecting nearly simultaneously the majority of studied stocks. The range of breakpoint years was more spread between areas for anchovy than sardine, as body condition dropped between 2004 and 2009. Further, maximum size, a relevant parameter to monitor population changes due to its impact on survival, growth and reproduction (e.g. larger fish are more fecund, McBride et al., 2015) also decreased concomitantly with fish body condition for both species in most areas. A general and rapid change affecting the entire Mediterranean Sea could thus be involved to explain the synchrony observed. Small pelagic fish body condition is known to be primarily affected by food availability, especially the zooplanktonic compartment which constitutes the bulk of small pelagic fish preys (Basilone et al., 2006; Brosset et al., 2015b). Lower quality and/or quantity in food resources may have negatively affected fish growth, lowering overall mean and maximum fish size. Changes in the zooplanktonic community

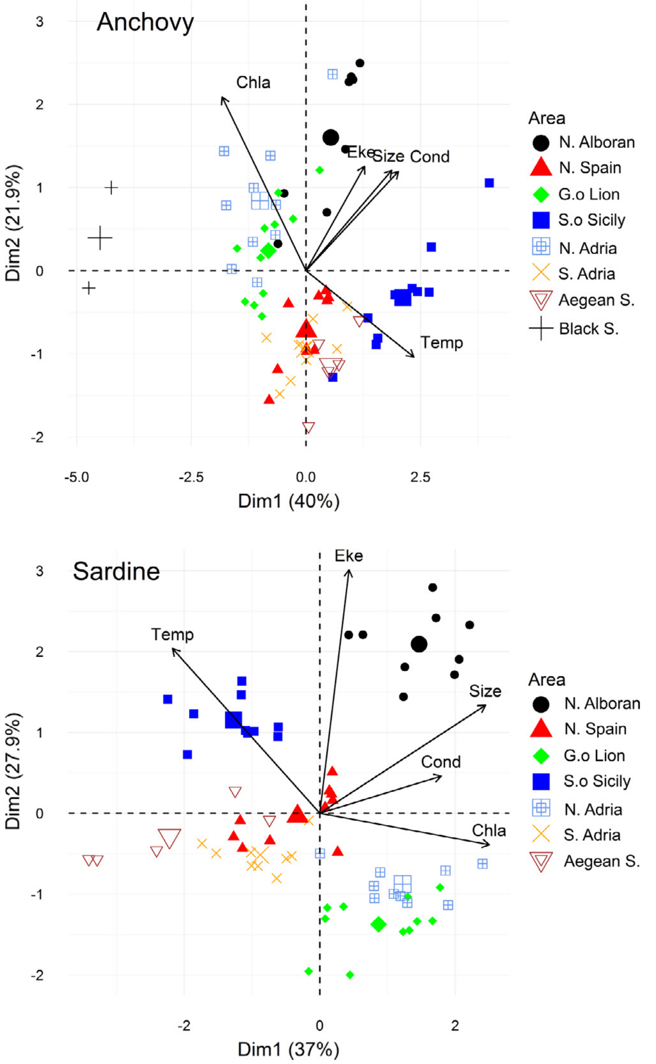

Fig. 6. Principal component analysis for anchovy and sardine using MEDIAS data, showing the relative importance of two fish biological parameters and three environmental factors of 8 different Mediterranean areas. The variance explained by each axis is indicated between brackets. Larger symbols reflect the barycenter of each area. Sardine does not inhabit the Black Sea, so this area was excluded from this analysis.

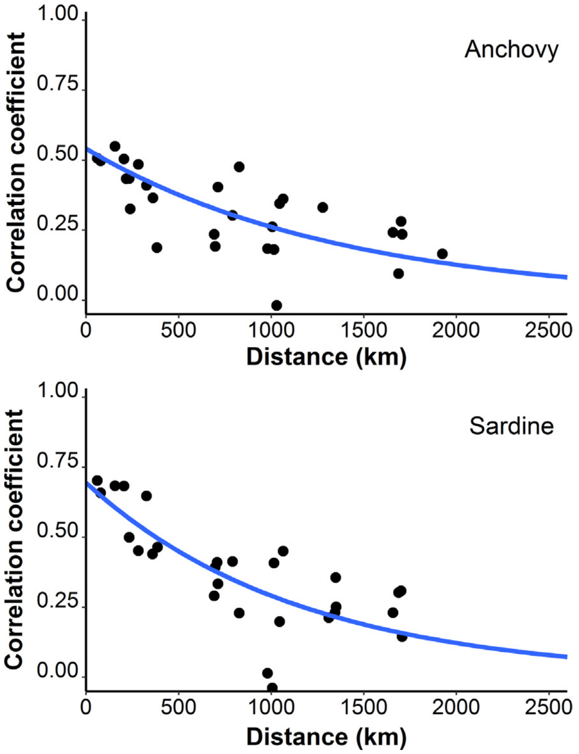

Fig. 7. Exponential decline over distance of pairwise correlations between anchovy or sardine body condition time series from 9 different harbors (5 in the Adriatic Sea: Split, Ancona, San Benedetto, Chioggia and Porto Garibaldi; 2 in the Northern Alboran Sea: Màlaga and Torrevieja, 1 in the Northern Spain area: Tarragona and 1 in the Gulf of Lions: Sète).

have been observed in different parts of the Mediterranean. For example, a shift towards smaller zooplankton biomass in 2003 in the Adriatic (Mozetič et al., 2012) or a change towards smaller plankton species in the Northern Spain area since 2000 related to increasing temperature and stratification (Calvo et al., 2011) were described. Few data are available in other areas, even if similar changes are suspected to have occurred in for example the Gulf of Lions (Auger et al., 2014). Although chl-*a* is a proxy of primary production available thanks to satellite data, longer precise plankton time series (with at least main functional groups) are required to link food availability to fish body condition and size fluctuations.

Even if a general decrease in body condition was visible for both species, this pattern could not be explained with global environmental factors, such as climatic indices which did not display synchronous breakpoints with fish body condition. Furthermore, the importance of regional factors was highlighted by both the results of the PCAs and the analyses of spatial covariability. For the latter, a 50% decorrelation distance of about 900 kms (i.e. 950 and 850 kms for anchovy and sardine, respectively) was detected. In other words, small pelagic fish body condition may not vary in synchrony at the Mediterranean scale, but rather at the scale of subregions. Because of the small number of time series and the resulting uncertainties of the underlying fish condition autocorrelation functions, we can only make a preliminary and rough comparison with correlograms for other species. Nevertheless, when we compare those correlograms to the spatial autocorrelation of zooplankton (biomass and abundance or even phenology), which represents the main prey of small pelagic fish and greatly influence their body condition (Brosset et al., 2015b), similar values up to 950 km were found (Batchelder et al., 2012; Mackas et al., 2012). For example, Mackas et al. (2012) computed a 50% decorrelation distance around 1000 km in the Mediterranean and NE Atlantic zooplankton phenology time series, while Batchelder et al. (2012) found decorrelation to occur between 643 and 673 km depending on the length of zooplankton abundance time series used, so some values in the vicinity of those found for anchovy and sardine in this study. As mentioned above, this strong regionalization of the environment in the Mediterranean Sea was also confirmed by the results of the PCAs. For both species, areas were mostly marked by spatial (inter-area) variability and were aggregated into three main groups: the eastern areas (the Strait of Sicily and the Aegean Sea), the northern areas (the Gulf of Lions and the Northern Adriatic) and the southern areas (the Southern Adriatic and the Northern Spain area). The Alboran Sea mainly stands apart, probably due to the strong influence of the Atlantic waters which are characterized by low deviations on the annual average values of biological parameters (Renault et al., 2012), and are richer in zooplankton biomass (Youssara and Gaudy, 2001), creating a relatively stable environment. Areas were thus distinct in terms of demographic and environmental characteristics, a result in coherence with the scale of about 900 kms displayed by covariability analyses. Although the Mediterranean Sea is strongly affected by large atmo-

Table 2

Pairwise correlation (Pearson coefficient) between fish body condition time series from 9 different harbors. Orange data come from anchovy and blue data from sardine. Harbors are classified from West to East (Málaga (Northern Alboran Sea); Torrevieja, Tarragona (Northern Spain area); Sète (Gulf of Lions); Chioggia, Porto Garibaldi, Ancona, San Benedetto, Split (Adriatic Sea)). Statistical significances of correlation are indicated by bold values.

	Málaga	Torrevieja	Tarragona	Sète	Chioggia	P. Garibaldi	Ancona	S. Benedetto	Split
Málaga		NA	**0.24**	0.18	0.10	**0.24**	**0.28**	**0.24**	0.17
Torrevieja	**0.44**		NA	NA	NA	NA	NA	NA	NA
Tarragona	**0.29**	**0.46**		**0.41**	**0.26**	0.18	**0.35**	**0.36**	**0.33**
Sète	**0.41**	**0.41**	**0.65**		**0.38**	0.21	**0.30**	**0.48**	-0.02
Chioggia	0.30	0.23	-0.04	0.33		**0.51**	**0.51**	**0.49**	0.19
P. Garibaldi	0.23	0.21	0.02	**0.39**	**0.70**		**0.55**	**0.44**	**0.37**
Ancona	0.31	**0.36**	0.20	**0.41**	**0.68**	**0.68**		**0.50**	**0.33**
S. Benedetto	0.15	0.25	**0.45**	0.23	**0.45**	**0.50**	**0.66**		**0.43**
Split	NA	NA	NA	NA	NA	NA	NA	NA	

spheric transfers (Vargas-Yáñez et al., 2008; Martín et al., 2011), forceful influences are also attributable to more local factors, such as river runoff, which induce contrasted conditions at small temporal and spatial scales. As a consequence, more local drivers had to be investigated in order to better understand these fluctuations. For example, anchovy optimal habitat is usually seen to be related to high frontal activities and river inputs (Agostini and Bakun, 2002; Morais et al., 2012; Giannoulaki et al., 2013; Carpi et al., 2015), resulting in strong water mass mixing. River runoffs are known to potentially affect fish condition (Lloret et al., 2004), but because of a lack of appropriate measures to evaluate correctly river discharges in the different areas (i.e. when no major river is present), this parameter was not taken into account in the PCA but it will necessitate to be correctly incorporated in further spatial work. Sardine is known to prefer colder waters than anchovy (Palomera et al., 2007), explaining the opposition between its body condition and high temperature. Chlorophyll *a* plays an important role on sardine body condition which may be explained by the fact that sardine also feeds on diatoms additionally to zooplankton when anchovy do not (Costalago and Palomera, 2014; Nikolioudakis et al., 2014) even if phytoplankton consumption remains minor. Yet, despite the important covariation of environmental parameters with body condition and size of sardine and anchovy to explain spatial differences, synchronies in the breakpoints of fish body condition and other environmental factors considered were only rare in most of the areas. This might come from the importance of even more local factors (e.g. small rivers runoff, local upwellings) or the lack of data on small pelagic fish main preys (e.g. zooplankton species). Another explanation could be the delay and/or the complexity of the interactions between environmental variations and fish body condition responses.

The higher level of detection of breakpoints and environmental relationships in the Adriatic (more specifically river runoff, chlorophyll *a* and SST for that area) might be related to its geographic situation. The Adriatic Sea (especially in the northern part) is a quasi-closed basin in comparison to more open areas (e.g. the Gulf of Lions or the Catalan Sea), which might reinforce the effects of local environmental factors. Further, the length of the fisheries monthly time series in the Adriatic (37 years) also enabled us to study long-term patterns in terms of periodicity. Small pelagic fish body condition is known to display a clear annual pattern together with a strong low frequency signal in the major upwelling regions of the world (Lluch-Belda et al., 1989; Chavez et al., 2003; Lindegren et al., 2013). In addition, it's seasonality also changed in both species. The condition's peak moved earlier over the years, modifying fish energy storage during the year as already underlined by Zorica et al. (2013). This may results from environmental changes in the Adriatic Sea between 1975 and 2012 (as underlined for the period 1997–2015 in the breakpoint analysis). Phytoplankton production mostly depends on nutrients, light and temperature. As warmed waters promoted earlier phytoplankton development and stronger water stratification led to a reduced second peak of primary production (Edwards and Richardson, 2004), primary production and zooplankton bloomed earlier. This may explain why the peak in fish energy storage shifted towards earlier months for both species. The timing of the peak in anchovy body condition, even if shifted earlier (from October/November to June) still occurs during the reproductive period (late spring and summer). Thus, anchovy can allocate large reserves to reproduction, a phase highly demanding on energy (Williams, 1966) and still survive to the following winter. On the contrary, sardine has to store a maximum of energy before winter reproduction when few resources are available. However, body condition peaked just before reproduction until the mid 90s (September/November) and now peaks in July, longer before reproduction takes place, preventing sardine to reach the reproductive period with maximal fat storage. This difference can make the sardine population more sensitive to current environmental changes in the Adriatic Sea, as has already been observed in the Gulf of Lions (Brosset et al., 2016b), where sardine has less energy to both overwinter and reproduce. Longer time series on a monthly basis will be required to provide conclusions for other areas, and see if the Adriatic Sea situation is unique or if the body condition's annual peak has moved earlier in all areas.

Apart from environmental factors, fishing can also affect fish condition and size, which is important to stress as most of the stocks are overexploited in the Mediterranean (GFCM, 2014). Fishing can impact fish condition through overfishing on their main preys, as demonstrated for demersal species (Hiddink et al., 2005). As small pelagic fish depend on planktonic preys, which are not exploited, such a process remains however very unlikely. A more likely process relies on the catchability that is often size and condition-dependent. Indeed, fisheries-induced selection is known to magnify shifts towards young, small and more quickly maturing individuals in targeted populations (Devine et al., 2012; Audzijonyte et al., 2013a; Mollet et al., 2016; Kuparinen et al., 2016), but difficulties remain in distinguishing phenotypical responses from true evolutionary changes. Phenotypic plasticity deals with the adaptive response of an organism faced with fishing pressure and/or changing environment. As fishing can reduced fish density, resulting in a decrease in food and space competition, faster growth and earlier maturation can occur. Alternatively, faster growth and earlier maturation can be a consequence of changing genetic composition of population for certain trait values, fishing also determines evolutionary dynamic. The decreasing trend in body size may be also due to an evolutionary response to intensive size selective fishing in overexploited Mediterranean areas (see also Conover and Munch, 2002). This appears unlikely for the Gulf of Lions because of the asynchrony between fishing pressure and the decline in size and condition and the historical low harvest rates (Van Beveren et al., 2016a). However, major changes observed in other areas might be explained by the combined effect of exploitation and environmental changes, especially in areas where anchovy and sardine were clearly overexploited, such as the Adriatic Sea (FAO, 2014). Unfortunately, no proper long-term information on fishing effort directed to each stock was available, preventing us to quantify ecological feedbacks of such life-history changes. Indeed, effort monitoring programs differ between countries and Mediterranean fisheries are often opportunistic (multispecific in some areas), making it impossible to quantify precisely fishing effort on all these stocks.

Based on scientific surveys and fisheries data linked to environmental data, this study evaluates for the first time the temporal and spatial variability in body condition of the two main small pelagic fish at the Mediterranean scale. The results highlighted a general decrease in fish body condition and maximum size, probably related to changes in planktonic quantity and/or quality. The forecasted trend for the near future is an increase in mean Mediterranean SST, sea surface salinity and water stratification (Vargas-Yáñez et al., 2010; Adloff et al., 2015), favoring lower size classes of plankton (Herrmann et al., 2013). In such conditions, small pelagic fish condition may remain poor or even continue to decline as smaller plankton has lower energetic values (Vijverberg and Frank, 1976; Zarubin et al., 2014). Further, due to a lack of reliable data, this analysis did not take into account the exploitation pressure, that we know is high in several stocks and that might well explain part of the decline in some areas. This decreasing trend in the condition of small pelagic fish may have long-lasting negative effects on the Mediterranean fisheries through an effect on life-history traits such as growth, reproduction or natural mortality hampering stock productivity and hence future fisheries yield, as well as on other ecosystem components such as predators preying on small pelagic fish (e.g. Wanless et al., 2005). Considering fish population body condition through scientific surveys and fisheries landings samplings should now be gathered with environmental regular monitoring (including planktonic sampling) and considered in order to implement and provide effective and efficient management plans in the Mediterranean Sea.

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