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ECOSYSTEMS AND SUSTAINABILITY

Environmental drivers of the anchovy/sardine complex in the Eastern Mediterranean

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Abstract The anchovy/sardine complex is an important fishery resource in some of the largest upwelling systems in the world. Synchronous, but out of phase, fluctuations of the two species in distant parts of the oceans have prompted a number of studies dedicated to determining the phenomena, atmospheric and oceanic, responsible for the observed synchronicity and the biological mechanisms behind the population changes of the two species. Anchovy and sardine are of high commercial value for the fishing sector in Greece; this study investigates the impact of large-scale climatic indices on the anchovy/sardine complex in the Greek seas using fishery catches as a proxy for fish productivity. Time series of catches for both species were analysed for relationships with teleconnection indices and local environmental variability. The connection between the teleconnection indices and local weather/oceanic variation was also examined in an effort to describe physical mechanisms that link large-scale atmospheric patterns with anchovy and sardine. The West African Summer Monsoon, East Atlantic Jet and Pacific–North American (PNA) pattern exhibit coherent relationships with the catches of the two species. The first two aforementioned patterns are prominent atmospheric modes of variability during the summer months when sardine is spawning and anchovy juveniles are growing. PNA is related with El Niño Southern Oscillation events. Sea Surface Temperature (SST) appears as a significant link between atmospheric and biological variability either because higher temperatures seem to be favouring sardine growth or because lower temperatures, characteristic of productivity-enhancing oceanic features, exert a positive influence on both species. However at a local scale, other parameters such as wind and mesoscale circulation describe air–sea variability affecting the anchovy/sardine complex. These relationships are non-linear and in agreement with results of previous studies

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stressing the importance of optimal environmental windows. The results also show differences in the response of the two species to environmental forcing and possible interactions between the two species. The nature of these phenomena, e.g., if the species interactions are direct through competition or indirect through the food web, remains to be examined.

Keywords Anchovy/sardine complex · Environmental effects · Teleconnections

Introduction

Global fluctuations in the abundance of anchovy and sardine, in particular the apparent alternation of high abundance phases of both species and their possible relationship with climatic cues are an area of intense scientific study. Records of fin-scale deposition in coastal upwelling systems show cycles of expansion and contraction of the sardine and anchovy populations with a periodicity of 30 years for sardine (*Sardinops sagax*), 50–60 years for anchovy (*Engraulis encrasicolus*) and 25 years for both (Lehodey et al., 2006; Valdés et al., 2008).

The regime shift from anchovy (genus *Engraulis*) dominance to sardine (genera *Sardinops* or *Sardina*) dominance during the mid 1970s in the Pacific was one of the most pronounced phenomena of synchronisation of sardine and anchovy landings in distant areas and indicative of opposite phase fluctuations between the two species (Kawasaki, 1983; Schwartzlose et al., 1999; Chavez et al., 2003; Alheit & Bakun, 2009). The movement of the Humboldt current near the coast of Peru, during El Niño events decreases the spatial extent of anchovy (*Engraulis ringens*) spawning habitat thus adversely affecting recruitment and rendering the population more susceptible to predation (Alheit & Niquen, 2004; Lett et al., 2007; Swartzman et al., 2008), while creating favourable feeding conditions for sardine (*S. sagax*). Contemporaneously in the Kuroshio current, sea surface temperature (SST) and productivity fluctuations, attributable to the dislocation of frontal structures and mixed layer depth changes co-varied with anchovy/sardine alternations (Alheit & Bakun, 2009 and references therein). Other mechanisms explaining sardine and anchovy co-variation in the north Pacific involve direct effects of temperature and different optima for sardine (*Sardinops melanostictus*) and anchovy (*Engraulis japonicus*) spawning (Takasuka et al., 2008).

Such coincident changes in oceanographic and biological parameters led to the concept of regime shifts. The complexity of the connections among the different parameters precludes unambiguous conclusions on a mechanism linking the different components, biotic and abiotic, of these ecosystems. However, there is an established agreement that synchronised shifts are forced by large-scale atmospheric and oceanic phenomena (Schwing et al., 2010). In the case of the Humboldt and Kuroshio currents, the North Pacific Gyre Oscillation has been suggested as the synchronising phenomenon between the two distant Pacific ecosystems (Di Lorenzo et al., 2008).

In some cases, synchronicity between different sites is only observed for the Pacific sardine (*S. sagax*) and not for anchovy (*E. ringens*) (Lluch-Belda et al., 1992; Schwartzlose et al., 1999), while short-term events such as the 1997–1998 El Niño do not favour sardine over anchovy (Bertrand et al., 2004). Ultimately, climate variability will cause these stocks to interact through resource competition and predation (Miller & Schneider, 2000).

The striking synchronisation phenomena of anchovy and sardine alternations observed in the Pacific are comparable to synchronous but out of phase fluctuations of another pair of small pelagic species, herring (*Clupea harengus*) and sardine (*Sardina pilchardus*) along the coast of north-east Atlantic. The North Atlantic Oscillation (NAO) is suggested as the climatic phenomenon governing these fluctuations (Alheit & Hagen, 1997; Parsons & Lear, 2001). Synchrony in the abundance of another group of short-lived, pelagic marine organisms, squids, was revealed by Waluda et al. (2004). Moreover, El Niño Southern Oscillation (ENSO) related movement of the Antarctic Circumpolar Wave is suggested as an important factor influencing recruitment strength of *Illex argentinus* in the south Atlantic (Waluda et al., 1999, 2001). The important role of regime shifts and environmental change in driving the variability of squid fisheries in different areas in the world is reviewed by Pierce et al. (2008) and Rodhouse (2009).

The alternation between anchovy-dominated and sardine-dominated ecosystems is a common observation for most upwelling areas where the two species co-exist (Lluch-Belda et al., 1992). Sardine and anchovy are the most exploited small pelagic species in the Mediterranean but causes of large-scale fluctuations in their stock sizes have been undecipherable.

The theory of 'ocean triads' (Agostini & Bakun, 2002) has been an important discussion point for the majority of studies of environmental effects on small pelagic fish in the Mediterranean. Upwelling events and mesoscale features regulate offshore transport and retention of fish eggs and larvae in various areas of the Mediterranean and can thus determine recruitment success (Santos et al., 2004; Lafuente et al., 2005).

In the Adriatic, inter-decadal variability of small pelagic fish is related with an 80-year cycle of climatic oscillations (Grbec et al., 2002). The physical mechanism suggested involves NAO-related atmospheric pressure differences over the Adriatic that modulate the inflow of Levantine Intermediate Water (LIW) into the Adriatic, inducing stock fluctuations in small pelagic fish. Possible biological mechanisms discussed by the authors include bottom-up effects, different environmental optima for the different species and reorganisation of the trophic web.

The hydrology of the Black Sea, strongly connected with the Mediterranean is associated with the NAO and the East Atlantic–Western Russian pattern (Oguz et al., 2006). Regime shifts in the Black Sea ecosystem are related with climate-induced variations in nutrient enrichment of the water column; they are speculated to involve transition from top-down to bottom-up food web structures and are occasional events (Oguz & Gilbert, 2007).

Stergiou (1991) was probably the first author to describe the sardine (*S. pilchardus*) /anchovy (*E. encrasicolus*) complex in Greek waters, influenced by an increasing interest in the mechanisms driving this complex. His findings reveal a 3-year periodicity in catches and a negative correlation between the catches of the two species. The author suggests that, along with fishing effort, environmental, biological and economic parameters drive catches. Of the environmental factors, local sea level (atmospheric) pressure and meridian winds have been associated with the ratio of anchovy/sardine in catches (Stergiou & Lascaratos, 1997). Possible mechanisms, suggested by the same authors, include changes in currents, wind-induced productivity favourable for anchovy larvae and different growth rates.

Agostini & Bakun (2002) used the Aegean as a study area to highlight the importance of 'ocean triads' for the recruitment of small pelagic fish, with anchovy as their case study species. They stress the importance of large-scale upwelling in the eastern part of the Aegean (Bakun & Agostini, 2001) and mesoscale fronts in the western part for the spawning and recruitment of the species. Moreover, Giannoulaki et al. (2005) related distribution patterns of anchovy and sardine with anticyclonic features in the north Aegean and with currents carrying water from the Black Sea. Gyres and fronts are retention areas for zooplankton (Somarakis et al., 2002), fish eggs and larvae (Heath, 1992; Somarakis & Nikolioudakis, 2007). Suitable grounds for juvenile sardines in the Aegean are inshore, semi-closed, highly productive areas near estuaries (Tsagarakis et al., 2008).

The large-scale atmospheric patterns driving oceanic circulation in the Mediterranean and the response of anchovy and sardine to environmental cues set the framework for the identification of relationships between the anchovy/sardine complex and teleconnection patterns. In this study, we explored possible mechanisms that link variability in anchovy and sardine fishery catches in the eastern Mediterranean to local and large-scale physical phenomena, mainly teleconnection patterns. Based on previous knowledge of the teleconnections related with oceanic circulation in the eastern Mediterranean and the descriptions of covariance between the anchovy/sardine complex and environmental factors, we tested for empirical relationships between the complex and teleconnection indices; thus, we identified a small number of teleconnections correlated with anchovy and sardine. The effect of local variability, mainly upwelling and frontal structures on the different life stages of the two species has been revealed in various studies mentioned above. Therefore, we hypothesised that oceanic features could modify the impact of teleconnections (Schwing et al., 2010) on anchovy and sardine at a local scale. This hypothesis can be divided into two questions: is there a relationship between the teleconnections and local environmental variability; and is there a relationship between local environmental parameters and the anchovy/sardine complex? Answering these questions will give insights into the mechanistic links connecting teleconnection patterns with anchovy and sardine production, highlighting oceanic features of importance and suggesting possible biological processes involved in these relationships.

Materials and methods

Catch data are used as the only available long-term proxy of population status in this area. The calculation of the catch ratio of the two species is a common practice to prevent fishing effort and gear changes from affecting results in catch–environment relationship studies (Stergiou, 1991). Furthermore, the extraction of temporal trends from the catch time series and their comparison with fishing effort trends and known legislative decisions concerning this fishery has allowed for the unravelling of the different sources of variation.

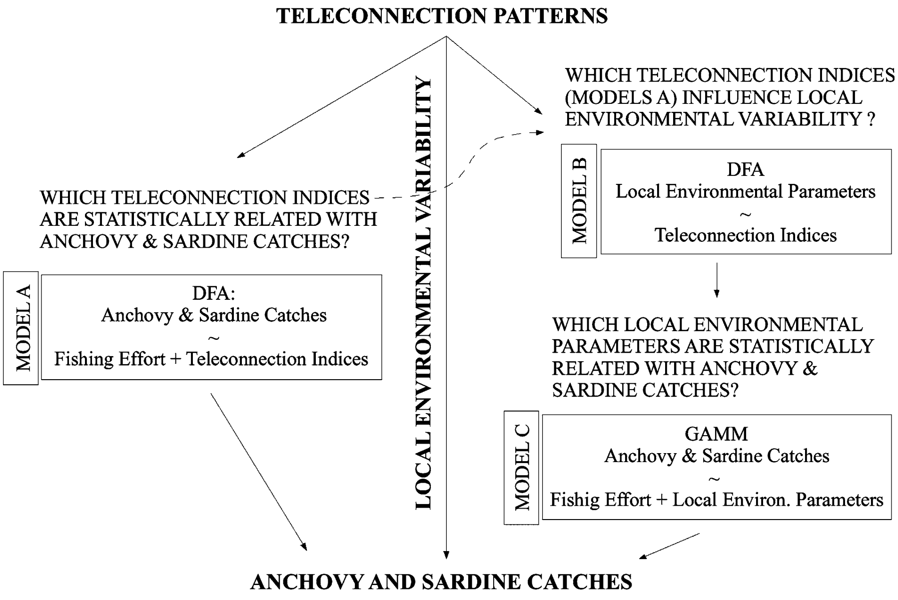
The methodology was designed to answer three interlinked questions (Fig. 1) in an effort to obtain a complete picture of the physical mechanisms through which teleconnection patterns influence anchovy and sardine fishing yield. With the first group of models based on dynamic factor analysis, teleconnection indices associated with anchovy and sardine catches were identified. These indices were used as explanatory variables in the second group of models that investigated the impact of these teleconnections on local environmental variability. Finally, the links between local environmental variability and anchovy–sardine fisheries production were investigated using non-linear regression models.

Catches and environmental data

Catch data on anchovy (*E. encrasicolus*) and sardine (*S. pilchardus*) were obtained through the Greek National Statistics Services (GNSS). The collection scheme of the dataset is described in Stergiou et al. (1997) and Stergiou & Lascaratos (1997); it consists of a network of the major areas around Greece where catches of all commercially important species have been recorded on a monthly basis since 1964. The data are presented in annual reports, the GNSS bulletins. For this study the annual averages of the catches of the two species in 16 areas were used (Fig. 2). The ratio of anchovy over sardine catches was also calculated for each area (Fig. 3). The data therefore consist of annual time series of catches for anchovy, sardine and their ratio for each area over the period 1964–2005. It should be noted that data from the Turkish fishing fleet that operates in some of these areas are not readily available. However, the use of multivariate time series statistics based on the extraction of trends will compensate for this lack of data.

Fishing effort data in the form of numbers of fishing vessels and their horsepower are available from the same source (GNSS bulletins) as an average for all the areas on annual basis. To avoid collinearity, when the time-series describing fishing effort are used as

Fig. 1 Models A investigate the possible impact of teleconnection patterns on anchovy and sardine catches. The indices found to be statistically significant are used in the B Models in order to describe their effects on local environmental variability in the study area. C Models were applied to study the relationships of anchovy and sardine catches with local environmental parameters. Thus, possible physical mechanisms were derived, linking teleconnection patterns to biological variability for the two species



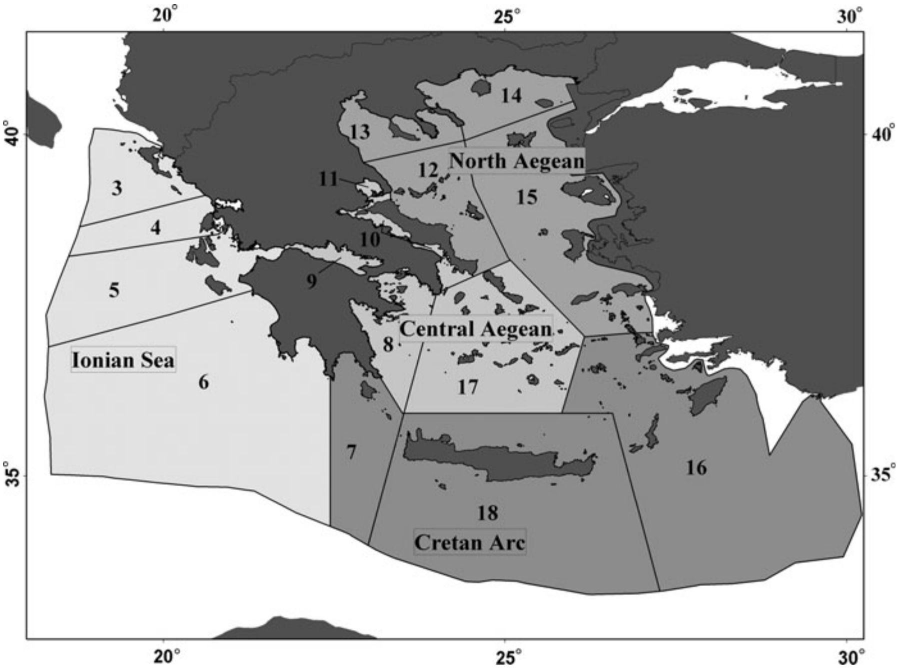


Fig. 2 The collection scheme of the data is organised in 18 areas of which the first area concerns catches from the Atlantic Ocean, the second area concerns catches from the south Levantine Sea and areas 3–18 can be seen in the map. These areas are further grouped into oceanographically coherent larger areas, for the application of GAMMs. These areas are the North Aegean (12–15) influenced by the northwest Aegean upwelling and the intrusion of Black Sea water from the Dardanelles straits; the central Aegean (8–11, 17), including the Cyclades plateau and small bays and enclosed areas around the central continental Greece; the Ionian Sea (3–6) and the Cretan Arc (7, 16, 18) characterised by a row of interconnected cyclonic and anti-cyclonic gyres. Areas 1 and 2 are outside the Greek waters and are not used in the analyses

explanatory variables, Min/Max Autocorrelation Factor Analysis (MAFA) (Solow, 1994) was applied on these time series and the basic trends in fishing effort were derived. Five trends—Fishing Effort (FE) MAFs—were statistically significant and were used to account for fishing effort variability in the subsequent statistical analyses (Supplementary material).

A series of teleconnection indices, previously found to be related to oceanic variability in the Mediterranean (Alpert et al., 2006) are used to account for large-scale atmospheric variability (Table 1). Local environmental variability is described using SST derived from NOAA AVHRR, http://eoweb.dlr.de:8080, sea surface height (SSH), and zonal and meridional wind stress (ZWS and MWS, respectively) from Carton-Giese SODA Version 2.0.2-4, http://iridl.ldeo.columbia.edu/SOURCES/.CARTON-GIESE/SODA/.v2p0p2-4/.ssh/ (Carton & Giese, 2008). The data cover the period 1960–2007. They were processed using ArcGIS modules and annual averages for each of the local environmental parameters were calculated for each of the 16 areas.

Statistical analysis

To identify which teleconnection indices might be related to the anchovy/sardine complex, a DFA model (Molenaar, 1985; Zuur et al., 2003a, b; Huang et al., 2006) was developed using the time series of the ratio of the catches in each area as response variables, fitting one common trend and using the teleconnection indices and fishing effort as explanatory variables. The analysis was also repeated when 1 and 2 (year) time lags were introduced between the explanatory and the response variables. Similar models were built using the original catches of anchovy and sardine separately (Table 2).

The teleconnection indices that were identified as being statistically significant in the above-mentioned models were used to explain the variability of local oceanic parameters for the period 1960–2007. The time series of SST were treated as response variables

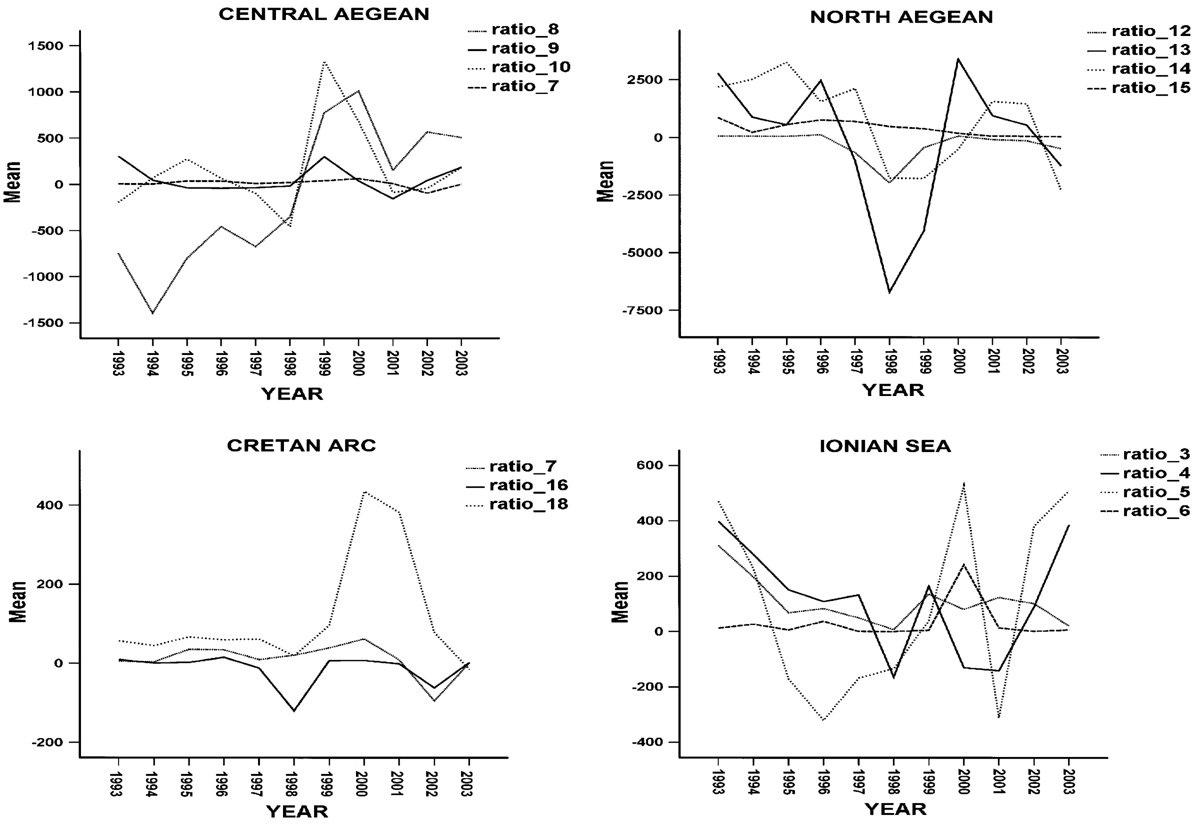


Fig. 3 Ratio of anchovy/sardine for each of the areas of the catches collection scheme. Each time series corresponds to one of the sampled areas as seen in Fig. 2 (ratio_area number)

Table 1 Teleconnection indices used to account for large-scale atmospheric variability and their sources

Teleconnection index	Source
North Atlantic Oscillation (NAO)	NOAA/Climate Prediction Centre
East Atlantic (EA)	NOAA/Climate Prediction Centre
East Atlantic/Western Russia (EA–WR)	NOAA/Climate Prediction Centre
East Atlantic Jet	NOAA/Climate Prediction Centre
Scandinavia (SCA)	NOAA/Climate Prediction Centre
Polar/Eurasia (POL)	NOAA/Climate Prediction Centre
West Pacific (WP)	NOAA/Climate Prediction Centre
East Pacific–North Pacific (EP–NP)	NOAA/Climate Prediction Centre
Pacific/North American (PNA)	NOAA/Climate Prediction Centre
Tropical/Northern Hemisphere (TNH)	NOAA/Climate Prediction Centre
Pacific Transition (PT)	NOAA/Climate Prediction Centre
Indian Monsoon (IM)	Wang & Fan (1999)
Western North Pacific Monsoon (WNPM)	Wang et al. (2001)
Webster and Yang Monsoon Index (WYM)	Webster & Yang (1992)
West African Summer Monsoon Index (WASMI)	Li & Zeng (2005)
Southern Oscillation Index (SOI)	NOAA/Climate Prediction Center

The indices derived from NOAA/Climate Prediction Centre, were calculated by applying Rotated Principal Component Analysis on 500-mb height atmospheric pressure anomalies in the region 20°N–90°N

Table 2 DFA models to identify relationships between the anchovy/sardine complex and the climatic (teleconnection) indices

Ratio ~ 1 trend + fishing effort + lag 0 teleconnection indices
Ratio ~ 1 trend + fishing effort + lag 1 teleconnection indices
Ratio ~ 1 trend + fishing effort + lag 2 teleconnection indices
Anchovy ~ 1 trend + fishing effort + lag 0 teleconnection indices
Anchovy ~ 1 trend + fishing effort + lag 1 teleconnection indices
Anchovy ~ 1 trend + fishing effort + lag 2 teleconnection indices
Sardine ~ 1 trend + fishing effort + lag 0 teleconnection indices
Sardine ~ 1 trend + fishing effort + lag 1 teleconnection indices
Sardine ~ 1 trend + fishing effort + lag 2 teleconnection indices

Table 3 DFA models to identify relationships between local oceanic parameters and climatic indices identified previously as important for the anchovy/sardine complex

SST ~ 1 trend + lag 0 teleconnection indices
SST ~ 1 trend + lag 1 teleconnection indices
SST ~ 1 trend + lag 2 teleconnection indices
SSH ~ 1 trend + lag 0 teleconnection indices
SSH ~ 1 trend + lag 1 teleconnection indices
SSH ~ 1 trend + lag 2 teleconnection indices
ZWS ~ 1 trend + lag 0 teleconnection indices
ZWS ~ 1 trend + lag 2 teleconnection indices
ZWS ~ 1 trend + lag 1 teleconnection indices
MWS ~ 1 trend + lag 0 teleconnection indices
MWS ~ 1 trend + lag 1 teleconnection indices
MWS ~ 1 trend + lag 2 teleconnection indices

in a DFA model in which this subset of teleconnection indices was used as explanatory variables. DFA models with 1 and 2 year time lags between the explanatory and the response variables were also developed. The same approach was followed for SSH, ZWS and MWS (Table 3).

The different DFA models mentioned above describe (a) relationships between atmospheric/climatic variability and oceanic circulation, and (b) relationships between anchovy–sardine and atmospheric–climatic variability. To be able to infer hypotheses on the possible mechanistic links between the teleconnection indices and the anchovy/sardine complex, we also tried to identify local environmental cues that are important for the complex. Generalised Additive Mixed Models (GAMMs) were employed to determine possible significant effects of local parameters, namely SST, SSH, ZWS and MWS on the anchovy/sardine ratio. To account for autocorrelation patterns in the data, autoregressive moving-average structures were introduced into the models. Due to failure of convergence of the maximum likelihood algorithm when a large number of time series is used as response variables in GAMMs, the time series were divided in oceanographically coherent groups corresponding to the following areas: north Aegean, central Aegean, the Ionian Sea and the Cretan Arc (Fig. 2) and a GAMM was applied for each area. The same approach was employed for the time series of sardine and the time series of anchovy catches separately.

DFA models were applied using the statistical software package Brodgar 2.6 (http://www.brodgar.com/) and following the protocols described in Zuur et al. (2003a, b) and Zuur & Pierce (2004). The GAMMs were developed in R, using the package 'mgcv' (Wood, 2006) and following the methodological approach described in Pinheiro & Bates (2000). The analyses presented involve fitting a large number of models with a large number of explanatory variables. To avoid ascribing significance to coincidental relationships, we used $P < 0.001$ to indicate significance rather than $P < 0.05$, reducing the likely frequency of type one errors from 1 in every 20 comparisons to 1 in 1,000 comparisons (Abdi, 2007).

Results

The anchovy/sardine complex and teleconnection indices

Six teleconnection indices are highlighted as statistically significant in all the DFA models: WASMI, EA-Jet, NAO, POL, PNA and EA-WR (Table 4). The importance of fishing effort decreases as the time lag increases from 0 to 2 years whereas the opposite is true for the climatic indices. WASMI is statistically significant in the DFA models for the anchovy/sardine ratio and for sardine catches, especially in the Ionian Sea but also in the north-east Aegean; in all cases the regression

Table 4 DFA models between one of the biological parameters (catch ratio, anchovy or sardine catches per area) and teleconnection indices. Statistically significant variables are indicated with an “x”

	Ratio	Anchovy	Sardine
Lag 0			
FE MAF 1	×	×	×
FE MAF 2	×	×	×
FE MAF 3			
FE MAF 4	×	×	×
FE MAF 5		×	×
EA-WR	×		
Lag 1			
FE MAF 3	×		
FE MAF 4	×		
FE MAF 5	×		
WASMI	×		×
EA-Jet	×	×	×
NAO	×		
PNA	×	×	
POL			×
Lag 2			
WASMI	×		×
EA-Jet	×		
EA-WR	×		

Fishing effort trends were also used as explanatory variables. Three models were applied for each biological parameter at time lags 0, 1 and 2 between the response and explanatory variables

coefficients are positive. EA-Jet is also statistically significant for both species and their ratio, especially in the north-east Aegean where the relationships are negative. The significant regression coefficients for the DFA models at a time lag of 1 year are shown in Fig. 4 and for a 2-year time lag in Fig. 5. EA-WR and the anchovy/sardine ratio are statistically significantly related at lag 0 in areas 6 and 18 and at lag 2 in the north part of the Aegean. PNA is statistically significant related with the anchovy/sardine ratio in the northeast Aegean at lag of 1 year.

Local oceanic/atmospheric variability and teleconnection indices

In the DFA models where parameters describing local environmental conditions were used as response variables, the relationships between WASMI and SST, and EA-Jet and SSH are significant at all time lags (Fig. 6). Statistically significant relationships include: NAO with wind stress; SST with NAO, EA-Jet and WASMI; EA-Jet and SSH at all time lags; and SSH with POL.

Anchovy/sardine complex and local oceanic/atmospheric variability

At 0 lag, the common trends in fishing effort are the significant explanatory variables present in the majority of the models of fish catches (Table 5). At lag 1, SST, SSH and MWS also show statistically significant correlations (Table 6). At lag 0, SST has a statistically significant effect for area 5 in the Ionian Sea.

The shape of the statistically significant relationships of SST at lag 1 with anchovy, sardine and their ratio are shown in Fig. 7. Although extremely high temperatures create unfavourable conditions for both species, anchovy seems to be doing better than sardine under these adverse conditions. A weak dome-shaped relationship between SST at lag 1 and sardine catches is observed in the north Aegean.

Sardine catches in areas 10 and 8 are related with MWS; sardine catches decrease when MWS increases above a level of 5 N/m^2 (Fig. 8). Anchovy catches in the central Aegean show a U-shaped relationship with SSH (Fig. 8).

Discussion

Inter-decadal cycles of the alternate dominance of anchovy and sardine have been attributed to ocean temperatures, productivity of coastal and open sea ecosystems and climatic variability (Schwartzlose et al., 1999; Chavez et al., 2003; Valdés et al., 2008). In the Mediterranean, a combination of hydrological features that enhance productivity and retain fish eggs and larvae, the ‘ocean triads’, seems to be crucial for successful recruitment, especially of small pelagic fish (Agostini & Bakun, 2002; Santos et al., 2004; Lafuente et al., 2005). In this study, we linked climate-induced oceanic variability with fluctuations of the anchovy/sardine complex in the northeastern Mediterranean.

Most of the correlations between the environmental parameters and fishery catches, observed in this study, are enhanced after hysteresis (i.e. time-lagged effects) has been introduced into the models, reinforcing the

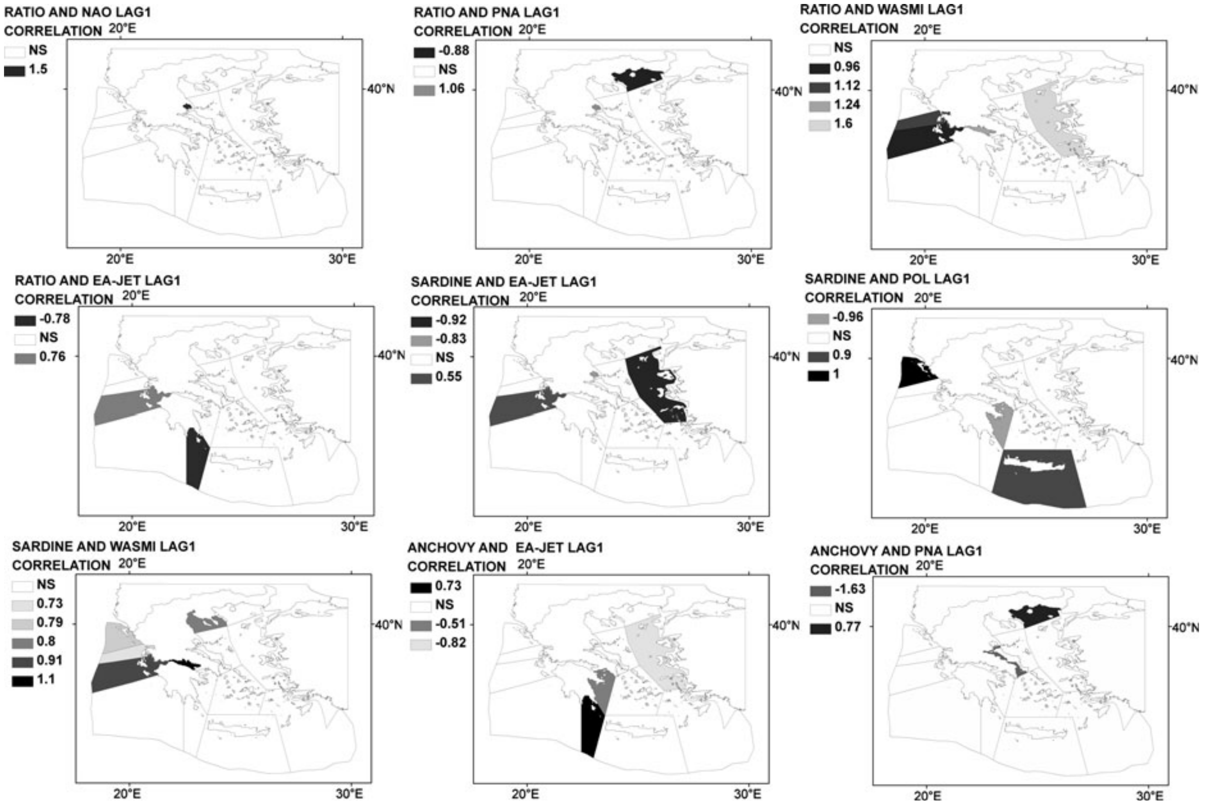
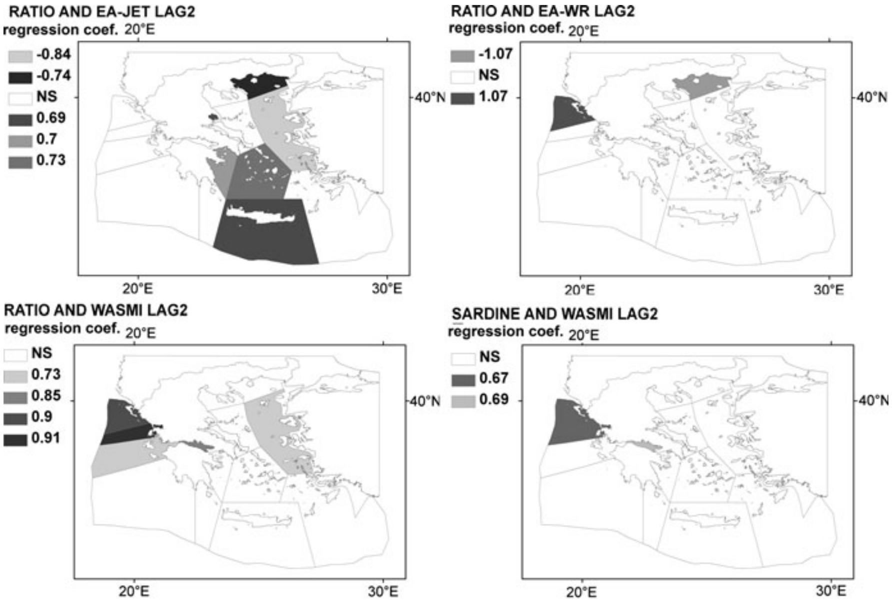


Fig. 4 Regression coefficients derived from the DFA models relating sardine and anchovy catches (response variables) with teleconnection indices at lag 1 (explanatory variables). *NS* non significant

Fig. 5 Regression coefficients derived from the DFA models relating sardine and anchovy catches (response variables) with teleconnection indices at lag 2 (explanatory variables). *NS* non significant



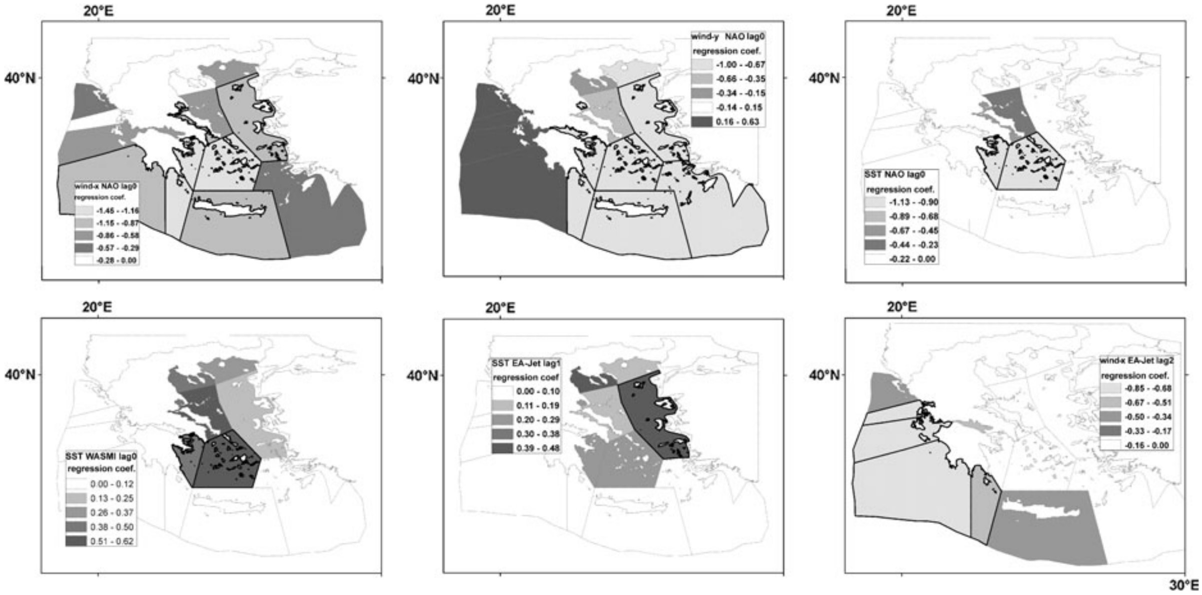


Fig. 6 Regression coefficients for relationships of local environmental parameters (response variable) with teleconnection indices (explanatory variables). The statistically significantly correlated areas (99% confidence) are highlighted with a *black border*

Table 5 Final GAMMs for the different areas at lag 0

Ionion
- Ratio (normalised) ~ FE4***
- Pilchard (normalised) ~ SST
- Anchovy ~ SST(by region)*

North Aegean
- Ratio (normalised) ~ FE3(by region)** + FE5(by region)*** + FE2*** + SST
- Pilchard (normalised) ~ FE2(by region)*** + FE5(by region)*** + FE4(by region) + MWS
- Anchovy(normalised) ~ FE2(by region)*** + SST

Central Aegean
- Ratio (normalised) ~ FE4(by region)*** + SST
- Pilchard (normalised) ~ FE4(by region)*** + SST
- Anchovy (normalised) ~ FE3(by region)***

Cretan Arc
- Ratio (normalised) ~ FE3*** + SST
- Pilchard ~ SST
- Anchovy (normalised) ~ FE2(by region)*** + FE4(by region)

FE *fishing effort* and the number for the MAF, *ZWS* zonal wind stress, *MWS* meridional wind stress. 'by region' indicates that the relationship with the explanatory variable is different for each area, i.e. an interaction between the explanatory variable and the 'area' treated as a factor. (Significance codes: 0 '***', 0.001 '**', 0.5 '*')

hypothesis that environmental impacts on small pelagic fish are mainly felt through recruitment or growth with the subsequent effects this may have on population dynamics. Some relationships become apparent with a time lag of 2 years. Effects on egg production, hatching success and growth and survival of early life stages would be expected to impact on the fished populations of sardine and anchovy with a lag of one or more years. In the northeast Atlantic, sardine (*S. pilchardus*) and anchovy (*E. encrasicolus*) typically recruit to the fishery at age one (e.g. ICES, 2010). Such effects can be additive if the same or other forcing factors persist for consecutive periods. Different theories such as of changes in the migratory behaviour of the species (*S. pilchardus*: Muzinic, 1963; Škrivanić & Zavodnik, 1973), interactions between anchovy and sardine such as the 'school trap' mechanism and trophic relations (Miller & Schneider, 2000 on *S. sagax*; Cubillos & Arcos, 2002 on *E. ringens* and *Strangomera betincki*), differences in the adaptations of the species to adverse conditions (Irigoien et al., 2007 on *E. encrasicolus*) or density-dependent effects (Shepherd & Cushing, 1980; Voulgaridou & Stergiou, 2003 on *S. pilchardus*) are discussed as possible explanations for the relationships that arise from our results.

Table 6 Final GAMMs for the different areas at lag 1

Ionion

Ratio (normalised) ~ SST

Pilchard (normalised) ~ SST

Anchovy ~ SST*

North Aegean

Ratio (normalised) ~ FE5(by region)** + SST*

Pilchard (normalised) ~ FE2(by region)*** + FE5(by region)*** + FE4*** + SST**

Anchovy(normalised) ~ FE2(by region)*** + SST*

Central Aegean

Ratio (normalised) ~ FE2(by region)**

Pilchard ~ FE1(by region)*** + MWS(by region)***

Anchovy (normalised) ~ FE1 + SSH** + SST

Cretan arc

Ratio (normalised) ~ FE3(by region)*** + SST

Pilchard (normalised) ~ SST*

Anchovy (normalised) ~ FE2(by region)*** + SST

FE *fishing effort* and the number for the MAF, *ZWS* zonal wind stress, *MWS* meridional wind stress. 'by region' indicates that the relationship with the explanatory variable is different for each area i.e. an interaction between the explanatory variable and the 'area' treated as a factor. (Significance codes: 0 '***', 0.001 '**', 0.5 '*')

Teleconnection patterns and the Anchovy/sardine complex

The role of three teleconnection patterns, namely the East Atlantic jet, West African Summer Monsoon and PNA pattern, as forcing factors for the anchovy/sardine complex was highlighted in this study. These patterns are related to a number of local phenomena describing air-sea interactions in the Mediterranean with the potential to influence anchovy and sardine population dynamics in the area.

The EA-Jet is the third mode of low frequency variability found over the North Atlantic from April to August. One of its anomaly centres is located over Northern Africa and the Mediterranean Sea (NOAA-CPC, 2005) and the EA-Jet index presents inter-decadal variability. Wind variability, cyclone tracks over the Mediterranean, precipitation and chlorophyll concentration at the northern coast of the Sea are associated with the EA-Jet (Barnston & Livezey, 1987 Alpert et al., 1990; Trigo et al., 1999*;* Dünkeloh & Jacobeit, 2003; Katara et al., 2008).

The African monsoon is associated with dry and hot summers over the Mediterranean (Ziv et al., 2004; Alpert et al., 2006). Intense West African Monsoon effects enhance the meridional Hadley circulation, thus strengthening the north-easterly winds over the eastern Mediterranean (Gaetani et al., 2008, 2009).

PNA is a principal mode of low-frequency variability in the Northern Hemisphere mid-latitudes. It is associated with ENSO episodes and over the western Mediterranean cold ENSO events become apparent as PNA-like variability (Alpert et al, 2006). Thus, its impact could be perceived as a strong ENSO signal over the Mediterranean.

Although the influence of the teleconnection patterns mentioned above on local weather and oceanic circulation in the Mediterranean has already been established, the combination of hypotheses tested in this study allows for a more thorough description of possible physical mechanisms modulating the influence of these teleconnections on the anchovy/sardine complex.

Physical mechanisms

Sea surface temperature, one of the most important oceanographic variables influencing biological indicators appears as a crucial factor affecting sardine and anchovy catch fluctuations and is suggested to be the mediator between the teleconnection patterns and the anchovy/sardine complex. Variability in SST has been related to various oceanic processes such as current advection, direct surface heating, upwelling and changes in mixing (Miller & Schneider, 2000).

The positive relationship between sardine and WASMI, at time lags of 1 and 2 years, might be related with the elevated SST in most of the area during the positive phase of the WASM. Sardine shows a preference for warm and shallow waters (Giannoulaki et al., 2005); it spawns during winter, and its association with warm waters during the summer confers the benefit of increased growth rate (Ursin, 1979).

The most plausible mechanism, through which teleconnection indices can influence the anchovy/sardine complex in the Mediterranean, seems to be climate-induced variability of oceanic features that interrupt the oligotrophic regime dominating this area. These features, mainly upwelling and gyres are characterised by cold nutrient-rich waters that reach the sea surface through wind-induced mixing. This

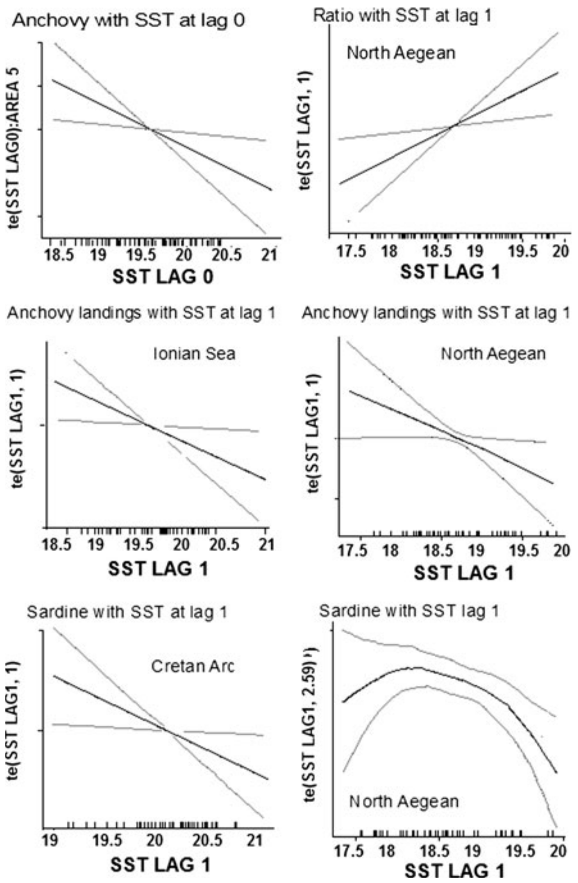


Fig. 7 A negative relationship of anchovy catches (response variable) and SST at lag 0 is observed for area 5, also between anchovy catches (response variable) and SST at lag 1 in the Ionian and north Aegean seas and between SST and sardine catches (response variable) for the Cretan arc. A weak dome-shaped relationship between sardine catches (response variable) and SST is observed for the north Aegean. The anchovy/sardine ratio time series (response variable) has a positive linear relationship with SST

relationship is manifested in various forms and areas for both study species.

Anchovy and sardine catches are both negatively correlated with SST at a time lag of 1 year. The relationship is the same for anchovy in the Aegean and the Ionian; although the two seas are inhabited by two different populations (Kristoffersen & Magoulas, 2008). In agreement with the 'oscillating control hypothesis' (Hunt et al., 2002), 'cold' climate regimes have been associated in the Black sea with systems controlled by small planktivorous fish that thrive under this regime due to the climate-induced increase in nutrient enrichment of the surface sea layers (Oguz et al., 2006; Oguz & Gilbert, 2007).

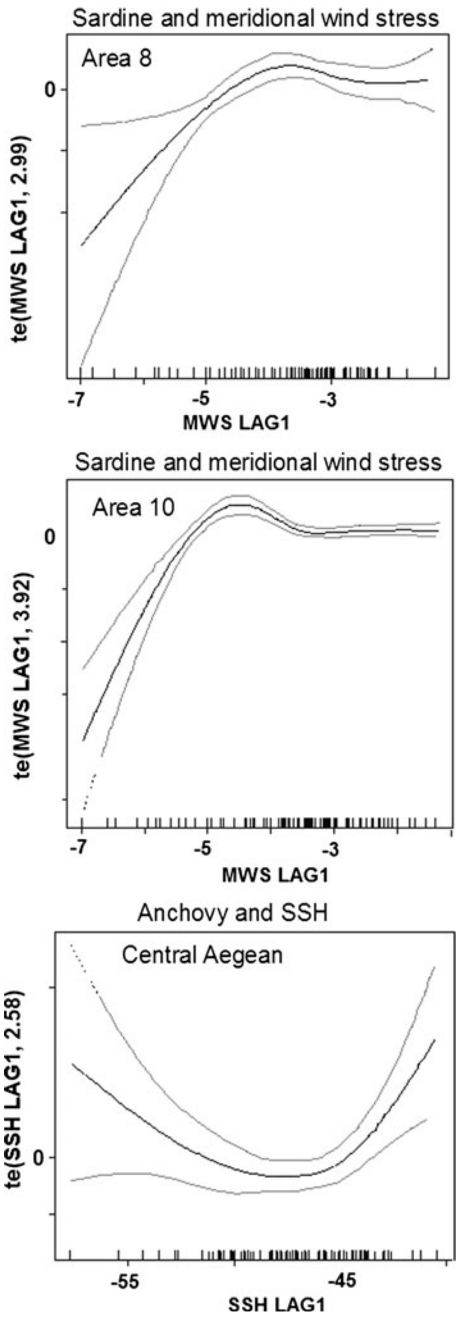


Fig. 8 Non- linear relationships are observed between sardine catches (response variable) and meridional wind stress at lag 1 in areas 8 and 10. Anchovy catches (response variable) are related to Sea Surface Height at lag 1, with a U-shaped relationship, in the central Aegean

As for a physical mechanism through which PNA influences anchovy and sardine production in the Thracian Sea, it seems to be related with gyres retaining nutrient-rich and cold Black Sea water; these oceanic features constitute auspicious spawning grounds (Somarakis et al., 2002, Giannoulaki et al., 2005). The resolution of the data used did not allow for a thorough investigation of such a link but the observed relationships of the species with PNA and SST do support this hypothesis.

Along the east coast of the Aegean, a physical mechanism linking both species with EA-Jet through SST is revealed. This area is dominated by strong upwelling that have been suggested to be a part of an 'ocean triad' affecting small pelagic fish recruitment in the Aegean (Bakun & Agostini, 2001; Schismenou et al., 2008). WASMI also appears as an important climatic forcing in the area at lags of 1 and 2 years favouring anchovy. Although a physical mechanism is not apparent from the results, the effect of WASMI on MWS and the impact of wind-induced upwelling in the area are known from previous studies and could constitute a tenable process linking atmospheric to biological variability.

The positive effects of WASMI and EA-Jet on sardine and the anchovy/sardine ratio are most profound in the Ionian Sea. The main hydrographical feature of the area is the LIW, which has been shown to influence productivity and species distribution in the Adriatic and has been related with climate oscillations (Grbec et al., 2002).

Non-linear effects of local environmental variability

The recognition of non-linear relationships between species abundance and physical characteristics of their environment has been suggested as a step forward to improve our understanding of the processes behind climatic impacts on ecosystems (Ottersen et al., 2010). Such relationships were observed in this study for a number of local parameters and provide an insight into different aspects of the impact of the environment on anchovy and sardine.

The shape of the relationship of sardine abundance with southerly winds at a time lag of a year, at two of its important spawning grounds in the central Aegean, is in agreement with other studies that have suggested that low to medium wind forcing is advantageous for recruitment of small pelagic fish (Bay of Biscay, Borja et al., 1998). A possible reason is that intense mixing could prevent the development of phytoplankton blooms (Bakun & Agostini, 2001) or hinder the feeding activity of larvae and juveniles (Mackenzie, 2000). A preference of sardine for an enriched but stable environment has also been suggested by Cury & Roy (1989, for *S. sagax*) and Bakun & Parrish (1990, for *Sardinella aurita*). On the other hand, anchovy in the central Aegean prefers extreme values for SSH (i.e. abundance is lowest around the mean value of SSH), indicative of changes in the mesoscale circulation patterns in the area, increased turbulence and nutrient enrichment of the surface layers. Tsagarakis et al. (2008) also found important relationships between sea level anomalies and distribution of juvenile sardines in the Aegean. Our results also agree with the findings of Skogen (2005), who found a positive relationship of anchovy (*S. sagax*) recruits with productivity-enhancing oceanic processes and an optimal environmental window for sardine in the Benguela upwelling. In contrast, both Allain et al. (2001) and Uriarte et al. (2002) showed a negative correlation between wind-induced stratification disruption events and anchovy (*E. encrasicolus*) recruitment levels in the Bay of Biscay. Roy et al. (1992) and Roy (1993) suggest a dome-shaped relationship between upwelling strength and anchovy (*Engraulis mordax*) recruitment. The differences in our results could be attributed to the oligotrophic nature of the Mediterranean, where oceanic processes, which increase primary productivity such as the northwest Aegean upwelling, the Rhodes Gyre, the east Aegean fronts etc, are crucial for the survival of the ecosystems. Therefore, the Mediterranean might only show features on the 'inclining' arch of relationship.

Different responses of the two species and implications

Interactions between the two study species, differences in their preferences and adaptations towards environmental change and possible migratory movements as response to climatic variability are phenomena that add to the complexity of the interactions of these fish species with their environment. Such implications also arise in this study and are interpreted with reference to integrative hypotheses that combine biological interactions and migrations with environmental forcing (Bakun, 2009).

Anchovy and sardine have a negative relationship with temperature in the North Aegean. However, the anchovy/sardine ratio in this area is positively associated with temperature indicating that anchovy might be able to find a spatial or temporal ‘loophole’ and outperform sardine under unfavourable conditions. A similar mechanism has been suggested for anchovy (*E. ringens*) off Peru, which is able to exploit small-scale spatiotemporal ‘loopholes’ during short-term El Niño events (Bertrand et al., 2004) and for the anchovy (*E. encrasicolus*) population in the Bay of Biscay, where anchovy is taking advantage of lower predation in offshore waters (Irigoien et al., 2007).

In the Thracian sea (area 14), although anchovy abundance is positively correlated with PNA at lag 1, the anchovy/sardine ratio is negatively related with the same index at lag 1 suggesting an indirect effect on sardine such as a biological mechanism of interaction between the two species (*Strangomera benthincki* and *E. ringens*: Cubillos & Arcos, 2002; Pedraza-Garcia & Cubillos, 2008). A similar mechanism can be suggested for the WASMI and EA-Jet effects on the anchovy/sardine complex in the Ionian Sea. Both sardine catches and the anchovy/sardine ratio are positively correlated to the two aforementioned teleconnection indices, indicating indirect effects on anchovy through interactions of the two species. Such mechanisms pertain to interactions between species in mixed schools; when climate favours the growth of one species, another species that schools with it might be disadvantaged.

The interpretation of the results for the northern Aegean becomes more complicated, if we consider the possibility of inflow of recruits from the Black sea as observed for anchovy (Mantzouni et al., 2007). Such enrichment in recruits could counteract negative effects of the environment on the recruitment of the resident population and obscure environmental relationships in quantitative analyses. Furthermore, this phenomenon impedes our effort to disentangle environmental effects on fisheries productivity in the area as any correlation observed can be attributed either to local oceanic variation or input from the Black Sea.

The anchovy/sardine ratio in the central Aegean is positively related with EA-Jet at a lag of 2 years whereas anchovy is negatively related with EA-Jet at a lag of 1 year in Saronikos Bay (area 8). At the same time, in the area west of Crete, an area dominated by the west Cretan gyre (Robinson & Golnaraghi, 1993), the correlation sign for anchovy and EA-Jet at lag 1 is reversed and a positive relationship between anchovy and EA-Jet at lag 1 is observed. A definite mechanism for the impact of this teleconnection pattern in the area cannot be deduced from the results. It is however obvious that both species are affected by EA-Jet-related variability in the west Cretan Gyre. The complexity of the results might be a manifestation of climate-related changes in migrations of the two species to more favourable areas when the conditions become adverse or due to higher levels of competition or predation when primary productivity increases.

Conclusions

There are a number of issues that might blur our perception of the mechanistic links between climatic variation and the anchovy/sardine complex. The over-exploited state of the stocks might not allow solid conclusions about the impact of the environment on population dynamics of the two species (Daskalov, 2003). Also the relationship between abundance and catches might be clear for anchovy but less so for sardine because anchovy is the target species for the Mediterranean fleets (Abad et al., 1998; Stergiou & Lascaratos, 1997). Long time series and better spatiotemporal resolution of biological indicators are needed for an in-depth investigation of the possible mechanisms of climate-biological relationships for the small pelagic fish studied here. However, it becomes apparent that such a relationship does exist and could potentially assist in improving our predictions, and therefore management for anchovy and sardine in the Greek Seas. Some aspects of this relationship are revealed in this study and could provide guidance for the finer-scale studies that are proving to be essential in such a variable environment as the Mediterranean. Our results highlight the role of productivity-enhancing oceanic features as the physical link between atmospheric and biological variability and stress the implications of non-linear relationships, interactions between species and migrations for our interpretation of biological-environmental relationships for the anchovy/sardine complex.

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