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Hydrographic conditions driving sardine and anchovy populations in a land-locked sea

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Abstract

The aim of this paper is to establish a relationship between long-term variability in sardine and anchovy populations in the Adriatic Sea and ocean dynamics and processes that occur over interannual and decadal timescales in the Adriatic-Ionian basin. This analysis is based on annual time series of sardine and anchovy landings and recruits at age 0 and annual time series of environmental parameters observed at a representative Adriatic station between 1975 and 2010. Pearson correlations and robust dynamic factor analysis (DFA) were applied to quantify the connections between fisheries and environmental parameters. Variations and trends in fishery series were best explained by changes in near-bottom temperature and salinity, which are an appropriate proxy for tracking changes in water mass dynamics and hydrographic conditions in the basin. A prolonged period of decreasing sardine population was characterized by low oxygen availability and environmental conditions in the deep Adriatic waters and was triggered by an extraordinary basin-wide event called the Eastern Mediterranean Transient. A collapse in anchovy population was observed after an exceptional cooling event followed by dense water formation.

Keywords: long-term environmental data, anchovy and sardine populations, ocean dynamics, interannual and decadal variability, synchrony.

Introduction

Multi-decadal variations in populations of small pelagic fish, such as sardine and anchovy, have been repeatedly documented across the oceans with significant impact to fisheries of these commercial species (Tourre *et al*., 2007; Lindegren *et al*., 2013). Different studies connect observed fluctuations to circulation-driven temperature changes and climate shifts (Chavez *et al*. 2003; Lindegren *et al*., 2013; Tzanatos *et al*., 2014). Recent studies indicate that oxygen content might be important for sardine and anchovy population dynamics (Bertrand *et al*., 2011; Grados *et al*., 2012; Gilly *et al*., 2013). This may be particularly relevant for a future ocean in which decreasing trends of oxygen availability are projected (Cocco *et al*., 2013).

In warm, land-locked seas such as the Mediterranean, European anchovy (*Engraulis encrasicolus,* Linnaeus, 1758) and sardine (*Sardina pilchardus*, Walbaum 1792) are abundant small pelagic fish species (Palomera *et al*., 2007; Morello & Arneri, 2009; Antonakakis *et al*., 2011), widely distributed throughout the Mediterranean basin and in the Northeast Atlantic (Whitehead *et al*., 1988; Giannoulaki *et al*., 2013). Both are short-lived and fast-growing fish species with a protracted spawning season. In the Adriatic Sea, the sardine and anchovy tend to spawn from October until April (Mužinić, 1956; Sinovčić *et al*., 2008) and from April until September (Sinovčić & Zorica, 2006), respectively.

Sardine and anchovy populations are found to be highly dependent on climate-induced changes in hydrographic conditions (Katara *et al*., 2011; Martín *et al*., 2012). An observed increase in sea surface temperature (SST) has been found to influence their abundance over the whole Mediterranean basin, but whereas the sardine population is negatively correlated with temperature increase, the anchovy population shows a positive correlation (Tzanatos *et al*., 2014). Fluctuations in numbers of sardine and anchovy in the Adriatic Sea, a Mediterranean sub-basin, have also been attributed to changes in (i) surface environmental variables such as winds and river runoff (Santojanni *et al*., 2006), (ii) upper layer salinity (Zorica *et al*., 2013) and (iii) upwelling/downwelling processes (Agostini and Bakun, 2002). However, sparse long-term fisheries and oceanographic datasets have so far prevented in-depth analyses of connections between long-term changes in sardine and anchovy populationsand physical processes and dynamics at the basin level (Falco *et al*., 2007).

Adriatic circulation is driven by two interconnected thermohaline belts (e.g., Artegiani *et al*., 1997): the first is driven by large northern Adriatic rivers which are responsible for outgoing surface flow along the western basin perimeter (the Western Adriatic Current, WAC) and for the counter-flow along the eastern coastline (the Eastern Adriatic Current, EAC), while the second is a deep thermohaline circulation density current driven by wintertime dense water generation that occurs over the northern Adriatic shelf (e.g., Vilibić, 2003) and deep south Adriatic Sea (e.g., Manca *et al.*, 2002). Dense water formation triggers an inflowing counter-current in intermediate layers along the eastern Adriatic. Outflowing dense water influences the thermohaline properties of the Ionian Sea and of the whole Eastern Mediterranean and, in turn, causes the entrance of water masses with different physical and biogeochemical properties to the Eastern Mediterranean basin and the Adriatic Sea (Bimodal Adriatic-Ionian Oscillation, BIOS, Gačić *et al.*, 2010, 2011; Civitarese *et al.*, 2010). These processes are responsible for driving the strong multidecadal variability of the Adriatic and Ionian Seas and, consequently, of the whole Eastern Mediterranean, resulting in significant variations of oceanographic and dynamic properties in the basin, which have been noted during the mid-twentieth century (Buljan, 1953). On top of these processes, strong anomalies such as the Eastern Mediterranean Transient may occur on the Mediterranean level (Roether *et al.*, 2007), altering basin-scale water masses and biogeochemistry (Conversi *et al.*, 2010). A schematic overview of the basin-wide circulation and relevant transients and of multi-decadal processes is illustrated in Figure 1.

The current work links long-term (36 years) changes in the Adriatic sardine and anchovy populations (recruits at age 0 and landings), including observed fishery collapses and recoveries, to interannual and decadal variability of ocean dynamics in the basin. The effect of fishing is not discussed in this paper due to the lack of official data necessary for its computation. Observed changes in sardine and anchovy populations are related to the most comprehensive *in situ* long-term Adriatic oceanographic series (exposing underlying basin-wide dynamics) and discussed in the context of observed decadal variations and trends in physical and chemical oceanographic properties documented for the region. Pearson correlations and dynamic factor analysis (DFA) are used to assess connections between fisheries and environmental variables. Finally, a perspective for estimating future changes in populations of the most exploited pelagic fishes will be discussed in terms of hydrographic conditions and circulation changes that can be predicted using regional climate models.

Data and Methods

An illustration of the investigated area and processes, including the positions of sampling stations and geographical sub-areas (GSA), is displayed in Figure 1, while a schematic diagram of all fisheries and environmental data and methods used in the analyses is depicted in Figure 2.

Environmental data

Time series of temperature, salinity, dissolved oxygen, total inorganic nitrogen (TIN) and orthophosphates (HPO_4^{2-}) collected at Stončica station (station S in Fig. 1) between 1975 and 2010 were used to assess dynamic

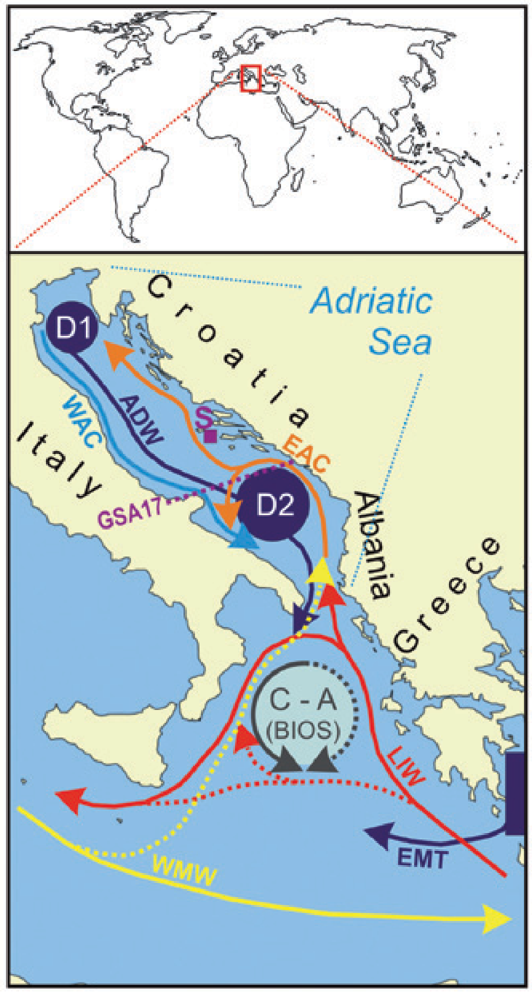

Fig. 1: The geography of the Adriatic-Ionian basin, with major dynamical features and oceanographic processes illustrated. WAC stands for the surface Western Adriatic Current driven by freshwater inputs, ADW denotes the bottom density current which originates from wintertime dense water generation at the shallow northern (D1) and deep southern (D2) Adriatic regions, while EAC stands for the Eastern Adriatic Current flowing at surface and intermediate layers. Ionian Sea circulation includes cyclonic (C) or anticyclonic (A) circular current regime in its northern parts, resulting in warm and saline Levantine Intermediate Water (LIW) and colder and less saline upper-layer Western Mediterranean Waters (WMW) flowing at different pathways depending on the BIOS (Bimodal Adriatic-Ionian Oscillation) phase (full line denotes pathways during cyclonic BIOS phase and dashed line during anticyclonic BIOS phase). Finally, EMT denotes the deep massive outflow of dense waters from the Aegean Sea to the Eastern Mediterranean during the Eastern Mediterranean Transient in early 1990s. Sardine and anchovy data were collected northwest from the GSA 17 line (pink, dashed). Station at which environmental data were collected is marked with S.

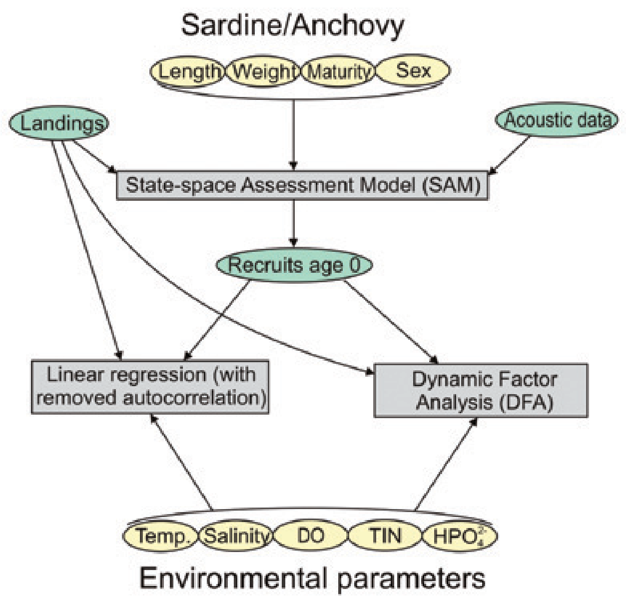

Fig. 2: Schematic diagram of the fisheries and environmental data, methods and models used in analyses.

features and long-term changes in the Adriatic. Sampling was carried out at standard oceanographic depths (0, 10, 20, 30, 50, 75 and 100 m), largely on a monthly basis, altogether encompassing approximately 300 cruises in a 36-year period (1975-2010) for an average of 8.3 cruises per year. The sampling methodology for all parameters was described by Vilibić *et al.* (2012). This station has the longest and best oceanographic series in the Adriatic, with data collection starting in the early 1950s (Vilibić *et al*., 2013), and is positioned in an area favourable for the detection of basin-wide dynamics (e.g., Orlić *et al.*, 1992; Artegiani *et al.*, 1997). The aforementioned time series have been successfully used by Grbec *et al.* (2009), Vilibić *et al.* (2012, 2013) and many others to assess trends and variability in oceanographic properties in the Adriatic and to describe basin-wide dynamics over the Adriatic and Ionian Seas.

Apparent oxygen utilization (AOU) was derived from dissolved oxygen, temperature and salinity measurements. AOU is the difference between the equilibrium saturation concentration of dissolved oxygen and its measured concentration, and may provide information about cumulative biological activity in a water layer since its last contact with the atmosphere; it has been successfully used to trace the deep Adriatic water masses and associated basin-scale dynamics (Vilibić *et al*., 2012).

A rigorous quality check, described in detail by Vilibić *et al.* (2012, 2013), was applied to the data toobtain as high-quality and homogenized series as possible. Seasonal oscillations were removed from the series by a year-day least squares fitting of 12- and 6-month sinusoidal functions to exclude any influence of seasonality. The procedure was separately applied to each depth and parameter. Annual values were estimated by averaging available data over a year, for years with at least three samplings. Correlation analysis and DFA were performed on time series of annual values.

Fishery data

Sardine and anchovy annual landings and recruits at age 0 were determined from official stock data shared among the countries belonging to the GSA 17 area (middle and northern Adriatic, see Fig. 1). These series may be treated as representative for the whole Adriatic area, as the neighbouring GSA 18 area (south Adriatic) has much lower pelagic fish biomass (Adriamed, 2001; STECF, 2013). The stocks of anchovy and sardine recruits were evaluated using the State-space Assessment Model (SAM), which is used for appraisals of several different stocks (Berg *et al*., 2013; STECF, 2013; Nielsen & Berg, 2014). The model allows selectivity to evolve gradually over time, with quantities such as recruitment and fishing mortality modelled as random effects, and has fewer model parameters than full parametric statistical assessment models.

We applied the SAM model to data collected between 1975 and 2010. Data included in the model were (i) biological data (length, weight, age, sex) from the eastern (Croatia, Slovenia) and the western parts (Italy) of the Adriatic sub-area GSA 17, (ii) landings obtained from the official statistics of Italy, Slovenia and Croatia, and (iii) biomass indexes derived from simultaneous eastern and western acoustic cruises throughout the entire GSA 17 and used as a tuning index in the model. We used the SAM model incorporated into the Fisheries Library in R (Kell *et al*., 2007) with version 0.99-3 of the FLSAM package, together with version 2.5 of the FLR library (FLCore).

Because anchovy spawning takes place mostly in spring-summer (Zorica *et al*., 2013), the assessment for the species was carried out conventionally and utilized a birth date of the 1st of June (split-year), as in Santojanni *et al.* (2003). Consequently, anchovy landings and recruits for a given year were computed from the 1st of June of the preceding year until the 31st of May of the current year. For the sardine assessment, the calendar year was used, as the species spawns during the autumn and winter (Sinovčić & Zorica, 2006).

Pearson correlation

Pearson correlation coefficients between fisheries and environmental time series were estimated. Correlations were computed for different time lags between the series, from 0 to 3 years, following the life cycle of the investigated species. Only correlations significant at the 95% level were considered. Autocorrelations have been removed from all series with best matching ARIMA models prior to the correlation analysis.

Dynamic Factor Analysis

DFA is a dimension-reduction technique that allows for estimation of underlying common patterns in a large set of multivariate time series (Zuur *et al*., 2003a). Time series are modelled as a linear combination of common trends, level parameter, explanatory variables and noise. Full details about the mathematics underlying DFA can be found in Zuur *et al*. (2003b).

In this study, time series of sardine and anchovy landings and recruits at age 0 were used as response variables, and time series of environmental parameters (temperature, salinity, AOU, TIN and HPO_4^{2-}) were used as explanatory variables. Different ranges of the DFA parameters were calculated using multivariate autoregressive state-space modelling (Holmes *et al*. 2012). We chose the basic DFA model with three common trends plus noise. Four different structures of noise covariance matrix were used: same variances and no covariances, different variances and no covariance, same variances and covariances, and different variances and covariances. Akaike's information criterion (AIC) was used as a measure of the goodness of fit of the various tested models.

Results

Time series analysis

Figure 3 displays the annual series of landings mass and number of sardine and anchovy recruits at age 0 between 1975 and 2010. A maximum in sardine recruits and landings occurred in the mid-1980s, followed by a steady decrease towards the late 1990s, when the landings and recruits were at approximately 25% and 10%, respectively, of the 1984 maximum. The decrease occurred gradually, implying that the observed decline could be attributed to gradual changes in hydrographic conditions rather than to an extreme-year event. Anchovy maximum landings (year 1980) lagged a few years behind the recruit maximum (year 1977), with both values rapidly decreasing towards the mid-1980s, when their minimum values were recorded. Anchovy recruits and landings at that time were only at 12% and 10% of their maximum value, respectively. The strongest drop in anchovy landings was recorded in 1987, causing a collapse in anchovy fisheries in the Adriatic (Santojanni *et al*., 2006). The total sardine and anchovy landings mass ranged between 116,000 tonnes in 1981 and

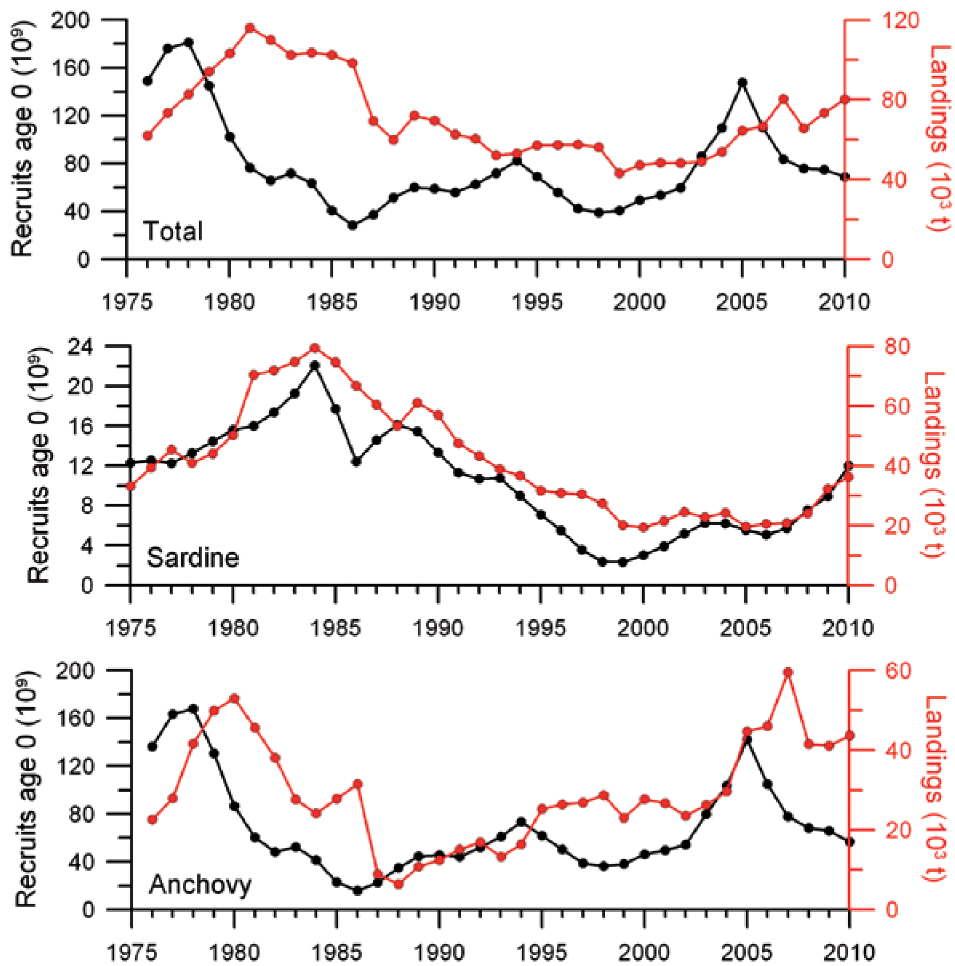

Fig. 3: From top to bottom: annual time series of total (sardine+anchovy) recruits and landings; sardine recruits and landings; and anchovy recruits and landings, all between 1975 and 2010.

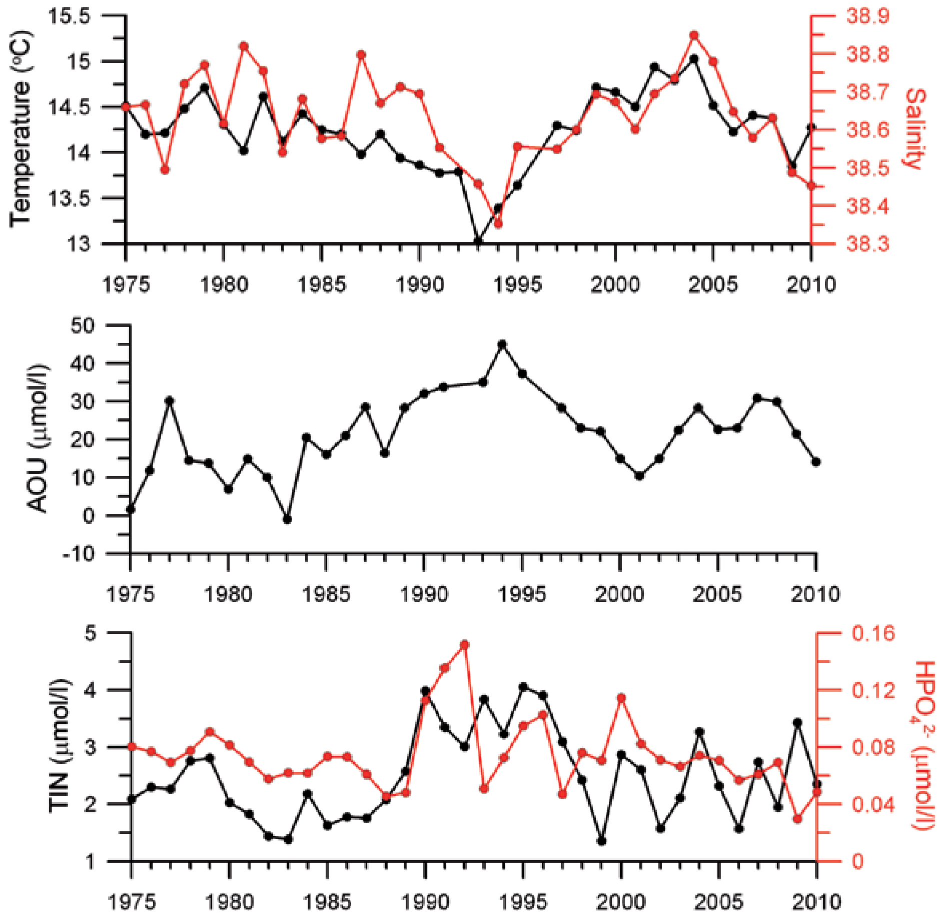

Fig. 4: Annual time series of temperature, salinity, apparent oxygen utilisation (AOU), total inorganic nitrogen (TIN) and ortho-phosphates (HPO_4^{2-}), all collected at station S between 1975 and 2010.

43,000 tonnes in 1999, whereas total number of recruits age 0 ranged between $182 \cdot 10^9$ (1978) and $30 \cdot 10^9$ (1986) individuals, largely driven by the anchovy recruit time series. After the 1999 minimum, total landings increased steadily and were almost doubled in 2010.

Time series of annual oceanographic parameters collected at station S at 100 m (Fig. 4) indicate that, starting in the late 1980s, a well-pronounced climate anomaly characterized by significantly decreased temperature and salinity and increased AOU, TIN and HPO_4^{2-} values occurred. This climatic anomaly lasted until the late 1990s, when temperature and salinity recovered to pre-anomaly values, whereas AOU, TIN and HPO_4^{2-} continued fluctuating around values that were elevated relative to pre-anomaly levels. In the early 2000s, temperature and salinity at 100 m depth rose to even higher levels, peaking in 2004 and decreasing substantially in the following years. Overall, decadal variability appears to be the dominant scale of variability, although strong interannual variability of temperature and salinity can be observed in the 1970s and the 1980s and in nutrients in the 1990s and the 2000s.

Observed changes in environmental variables are a good indicator of water mass dynamics in the Adriatic Sea and, in particular, of the inflow of warm and saline Levantine Intermediate Water (LIW). LIW, which enters the northern Adriatic crossing over the middle and deep layers of the Palagruža Sill, is detectable at a depth of 100 m at station S (Vilibić *et al.*, 2013). Observations indicate a decline of the LIW inflow from the late 1980s to the late 1990s and its recovery in the 2000s. Both processes are consistent with different phases of the BIOS (Gačić *et al.*, 2010).

Pearson correlations

Correlations were run between environmental parameters and the anchovy and sardine recruits and landings at an annual level, with autocorrelation removed prior to the analysis and by varying the lag between the environmental and fishery time series between 0 and 3 years (Table 1). The best correlation for the bottom layer (100 m) is found between AOU and sardine landings (r=-0.631, p=0.000) and recruits age 0 (r=-0.373, p=0.028), both at atime lag of 1 year, indicating that, as AOU increases (less oxygen available), sardine population declines, and vice versa. Significant correlation is also found between salinity at 100 m and sardine landings (r=0.376, p=0.026) fora time lag of two years.

For the surface layer, significant correlations are found between temperature and sardine landings for a 0-year time lag (r=-0.357, p=0.035) andbetween temperature and anchovy landings for a 3-year time lag (r=-0.402, p=0.017). Sardine landings are also correlated with AOU for a 1-year time lag (r=-0.376, p=0.026), similar to the bottom layer. Anchovy recruits at age 0 are correlated with surface salinity at two time lags, 0 years (r=0.343, p=0.044) and 2 years (r=0.398, p=0.018), indicating a connection between salinity fluctuations and their spawning, as previously documented by Zorica *et al*. (2013). Finally, significant correlations are documented for sardine and anchovy recruits age 0 with surface salinity for a 0-year time lag (r=0.373, p=0.027) and with surface AOU at a 2-year time lag (r=0.357, p=0.036).

DFA results

The testing of different structures of the noise covariance matrix (not shown) with no explanatory variable introduced to the method yielded the lowest AIC values when using an unconstrained matrix with different variances and covariance, and these values were much lower than for any other structure of covariance matrix. Therefore, we used such a setup (different variances and covariances) for introducing the DFA method with one to five explanatory variables (temperature, salinity, AOU, TIN, HPO_4^{2-}). Associated AIC values were computed for each of the explanatory variables, separately for surface (0 m) and bottom (100 m) layers, and for each combination of explanatory variables, and also for their surface and bottom layers (resulting in 23 combinations at each layer). The results are presented in Table 2.

Better fitting of the model is achieved when the number of trends is increased. When introducing one explanatory variable, the best model performance is obtained for temperature at 100 m (AIC=-208.7 for three trends), while the AOU values at 100 m yield the worst model performance; these results are the opposite of the results obtained using Pearson correlation analysis. When introducing two explanatory variables to the method, the best fitting of the model to the observed time series is achieved for temperature and salinity at 100 m (AIC=-218.4); this is the lowest AIC value among all the experiments, and it indicates that 100 m temperature and salinity are the variables that best describe the observed changes in anchovy and sardine landings and recruits at age 0. Introducing three variables to the model does not increase the model performance, although a good fit is achieved for temperature, salinity and AOU values at 100 m (AIC=-212.6). It is interesting to note that the best fit for the one- and two-trend model experiments is achieved precisely for these three parameters (AIC=-172.9 for one trend and AIC=-208.7 for two trends), indicating the importance of deep oxygen availability to the observed sardine and anchovy changes.

The model performance does not improve when increasing the number of explanatory variables to four and five (all variables). Adding TIN to the temperature, salinity and AOU values at 100 m yields better results (AIC=-205.4) than adding HPO_4^{2-} (AIC=-166.4). Additionally, the DFA generally performs better when the explanatory variables are deepwater (100 m) and not surface (0 m). At the surface, the best fit is achieved when temperature only (AIC=-203.5) and temperature and AOU (AIC=-203.7) are introduced as explanatory variables. Thus, the surface temperature is also important for the observed annual changes in fishery parameters, but less important than the 100 m temperatures and other 100 m variables.

The common trends and factor loadings for the best fitting model (three trends with temperature and salinity at 100 m as explanatory variables) are displayed in Figure 5, while Figure 6 contains the modelled and fitted values for all response variables (sardine and anchovy landings and recruits at age 0). The model qualitatively reproduces

Table 1. Pearson's correlation coefficients with significance levels (in brackets) estimated between fisheries (L – landings, R0 recruits at age 0) and environmental series in the surface (0 m) and bottom (100 m) layers at station S for different time lags (0 to 3 years, the number of stars denote the phase lag). Autocorrelations are removed from the series. Only correlations significant at 95% level are presented.

	Sardine L	Sardine R0	Anchovy L	Anchovy R0	Total L	Total R0
T (0 m)	-0.357 (0.035)	-	0.402 (0.017)***	-	-	-
S (0 m)	-	-	-	0.343 (0.044), 0.398 (0.018)**	-	0.373 (0.027)
AOU (0 m)	-0.376 (0.026)*	-	-	-	-	-0.357 (0.036)**
TIN (0 m)	-	-	-	-	-	-
HPO_4^{2-} (0 m)	-	-	-	-	-	-
T (100 m)	-	-		-	-	-
S (100 m)	0.376 (0.026)**	-	-	-	-	-
AOU (100 m)	-0.631 (0.000)*	-0.373 (0.028)*		-		-
TIN (100 m)	-	-	-	-		-
HPO_4^{2-} (100 m)	-	-	-	-	-	-

Table 2. Akaike's information criteria (AIC) values for different combinations of explanatory variables (ExpVar, 0 stands for 0 metres, 100 stands for 100 m) and number of common trends (tr) introduced to the DFA. Bolded values stand for the best fitting model, depending on number of utilized common trends.

ExpVar	AIC			ExpVar	AIC		
	1 tr	2 tr	3 tr		1 tr	2 tr	3 tr
none	-51.3	-51.3	-51.3	-			
T_0	-116.1	-171.4	-203.5	T_{100}	-121.2	-177.2	**-208.7**
S_0	-106.8	-163.0	-190.9	S_{100}	-110.5	-163.8	-197.9
AOU_0	-106.3	-155.5	-167.1	AOU_{100}	-56.3	-112.3	-151.6
TIN_0	-116.3	-163.1	-175.7	TIN_{100}	-115.0	-162.1	-174.5
$HPO_4^{2-}{}_0$	-117.0	-163.9	-176.8	$HPO_4^{2-}{}_{100}$	-117.0	-163.9	-176.8
T_0, S_0	-144.9	-190.9	-200.3	T_{100}, S_{100}	-163.5	-205.2	**-218.4**
T_0, AOU_0	-103.2	-167.2	-203.7	T_{100}, AOU_{100}	-119.0	-178.2	-204.6
T_0, TIN_0	-127.9	-164.4	-192.3	T_{100}, TIN_{100}	-122.6	-169.5	-194.7
T_0, $HPO_4^{2-}{}_0$	-126.4	-164.4	-193.5	T_{100}, $HPO_4^{2-}{}_{100}$	-126.3	-169.0	-192.2
S_0, AOU_0	-98.7	-162.5	-191.8	S_{100}, AOU_{100}	-108.6	-166.6	-194.6
S_0, TIN_0	-128.7	-159.3	-180.4	S_{100}, TIN_{100}	-123.7	-159.7	-184.2
S_0, $HPO_4^{2-}{}_0$	-126.9	-159.5	-179.5	S_{100}, $HPO_4^{2-}{}_{100}$	-128.7	-159.8	-183.5
AOU_0, TIN_0	-121.2	-163.5	-184.4	AOU_{100}, TIN_{100}	-113.6	-158.1	-169.7
AOU_0, $HPO_4^{2-}{}_0$	-121.4	-163.9	-185.1	AOU_{100}, $HPO_4^{2-}{}_{100}$	-116.3	-160.2	-172.9
TIN_0, $HPO_4^{2-}{}_0$	-114.6	-160.9	-170.7	TIN_{100}, $HPO_4^{2-}{}_{100}$	-127.7	-165.5	-173.1
$T_{0,}$ S_0, AOU_0	-146.5	-184.1	-180.2	$T_{100,}$ S_{100}, AOU_{100}	**-172.9**	-208.7	-212.6
T_0, S_0, TIN_0	-125.5	-184.5	-193.8	T_{100}, S_{100}, TIN_{100}	-151.1	-199.4	-158.8
T_0, S_0, $HPO_4^{2-}{}_0$	-124.4	-183.8	-186.0	T_{100}, S_{100}, $HPO_4^{2-}{}_{100}$	-152.6	-198.8	-176.6
S_0, AOU_0, TIN_0	-114.3	-160.8	-189.6	S_{100}, AOU_{100}, TIN_{100}	-122.4	-160.8	-186.8
S_0, AOU_0, $HPO_4^{2-}{}_0$	-109.4	-160.7	-189.9	S_{100}, AOU_{100}, $HPO_4^{2-}{}_{100}$	-127.1	-159.3	-187.0
AOU_0, TIN_0, $HPO_4^{2-}{}_0$	-117.7	-160.1	-179.9	AOU_{100}, TIN_{100}, $HPO_4^{2-}{}_{100}$	-120.0	-159.5	-170.2
T_0, S_0, AOU_0, TIN_0	-120.7	-177.9	-193.6	T_{100}, S_{100}, AOU_{100}, TIN_{100}	-164.3	-202.3	-205.4
S_0, AOU_0, TIN_0, $HPO_4^{2-}{}_0$	-96.4	-129.8	-175.7	S_{100}, AOU_{100}, TIN_{100}, $HPO_4^{2-}{}_{100}$	-130.9	-154.7	-166.4
T_0, S_0, AOU_0, TIN_0, $HPO_4^{2-}{}_0$	-140.5	-180.3	-170.8	T_{100}, S_{100}, AOU_{100}, TIN_{100}, $HPO_4^{2-}{}_{100}$	-48.5	-133.6	-199.1

all of the response variables well (i.e., their decadal and interannual variability, see Fig. 6), whereas the amplitude of variability is somewhat overestimated. This particularly refers to sardine recruits at age 0, where the maxima and minima of the observed and modelled series match, but with all three maxima (1976, 1987, 2005) overestimated. In contrast, sardine landings are well-reproduced, qualitatively and quantitatively. The anchovy recruits at age 0 minima and maxima are again well-reproduced, but with consistently overestimated values, while modelled and observed series of anchovy landings match better, except in the late 1990s and the early 2000s. In general, the series describing landings are reproduced better than the recruit series.

Discussion

Several significant Pearson correlations between annual time series of fisheries parameters and environmental variables (in particular temperature, salinity and AOU) were estimated for both the bottom and surface layers. According to the DFA, trends of fisheries parameters are best explained by temperature and salinity at a 100 m depth, and then by temperature, salinity and AOU at a 100 m depth. Both methods thus stress temperature, salinity and AOU as significant and TIN and HPO_4^{2-} as less important variables for explaining fisheries parameters. The DFA overestimates amplitudes of the interannual and decadal variations, indicating that these variations cannot be fully explained by physical and chemical parameters and that trophic relations and fisheries effects should be taken into account in further studies.

Temperature, salinity and AOU values below the seasonal pycnocline are major conservative tracers of deepwater mass changes in the Adriatic Sea (e.g., Zore-Armanda, 1963; Artegiani *et al.*, 1997; Vilibić & Orlić, 2001; Mihanović *et al.*, 2013). Very low values of AOU (high oxygen content) in the early and mid-1980s can be related to periods of frequent ventilation of deep waters in the Adriatic Sea, when, due to several very harsh win-

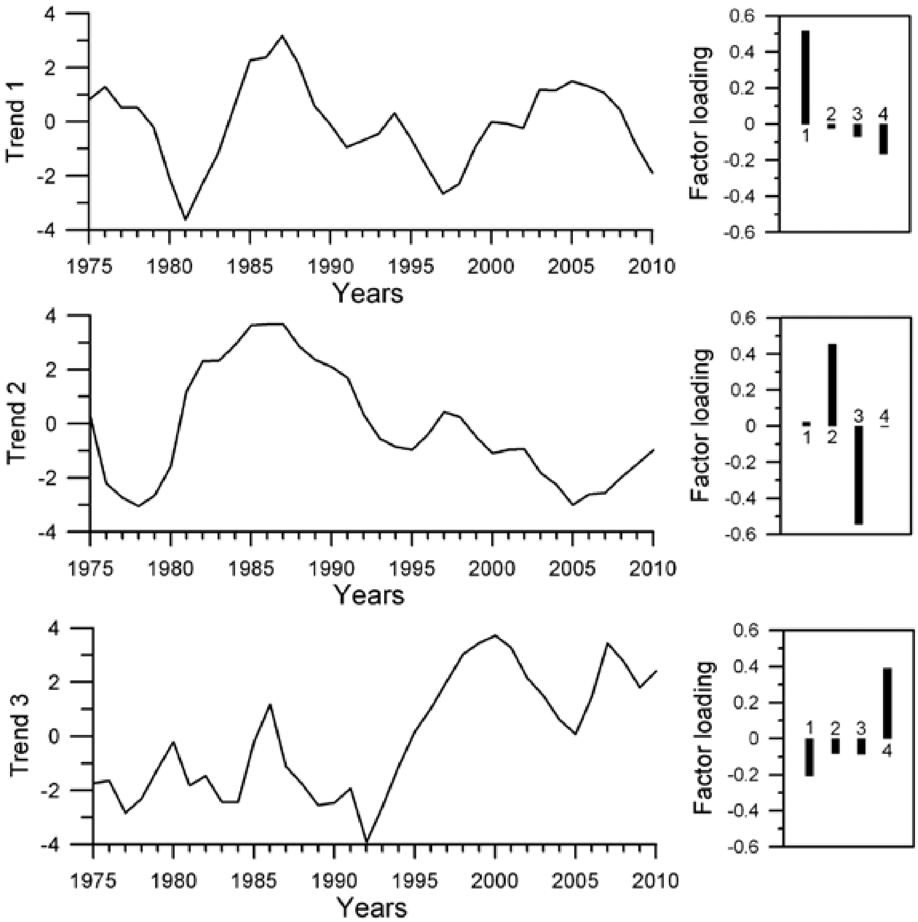

Fig. 5: Common trends (uniteless) and factor loadings of anchovy and sardine landings and recruits at age 0. Trends were calculated with DFA using three common trends and two explanatory variables (T_{100}, S_{100}). Factor loadings are plotted for: 1 - sardine recruits age 0, 2 - sardine landings, 3 - anchovy recruits, 4 - anchovy landings.

ters, dense water was generated not only in the northern Adriatic (e.g., Artegiani & Salusti, 1987; Vilibić, 2003) but also likely (through deep convection processes up to several hundred metres depth) in the rest of the Adriatic (Manca *et al.*, 2002). Dense water outflow from the Adriatic was compensated by an increased inflow of LIW, which is evidenced by higher temperature and salinity values. This period of frequent dense water generation and increased LIW inflow corresponds to the period of large populations of anchovy and, in particular, sardine. Observed temperature and salinity drops and a strong increase of AOU in the late 1980s to the late 1990s closely corresponded to a strong decrease in anchovy and sardine populations, with minimum values observed in the late 1980s (anchovy) and the late 1990s (sardine). In 1998 the BIOS switched from an anticyclonic to a cyclonic regime, and LIW inflow to the Adriatic started to increase once more (higher temperature and salinity, lower AOU). It is noteworthy that exactly at this time, the sardine population started to recover, whereas 3 to 4 years later, during a period of even stronger LIW inflow, recovery of the anchovy population (which started already in 1988) accelerated (Fig. 3).

From DFA results and Pearson correlations for a depth of 100 m, we may conclude that periods of strong LIW inflow associated with higher temperature and salinity and lower AOU values (related to dense water generation events) are more beneficial for sardine abundance in the Adriatic Sea than are periods of diminished LIW inflow. The reason for this relationship might lie in a number of different processes, including more appropriate ranges of temperature and salinity and food availability. The necessity to include additional processes is further emphasized by the fact that the DFA model reproduces well the occurrences of minima and maxima of fishery parameters, but not the rate of decadal variability and changes.

As opposed to a 100 m layer, where complex basin-wide water mass dynamics play a dominant role, the surface layer at station S is influenced by atmospheric forcing and by the eastern Adriatic coastal current, which advects freshened water from the eastern Adriatic rivers towards the north (Vilibić *et al.*, 2013). Pearson correlations and DFA indicate that temperature is the most important surface variable related to

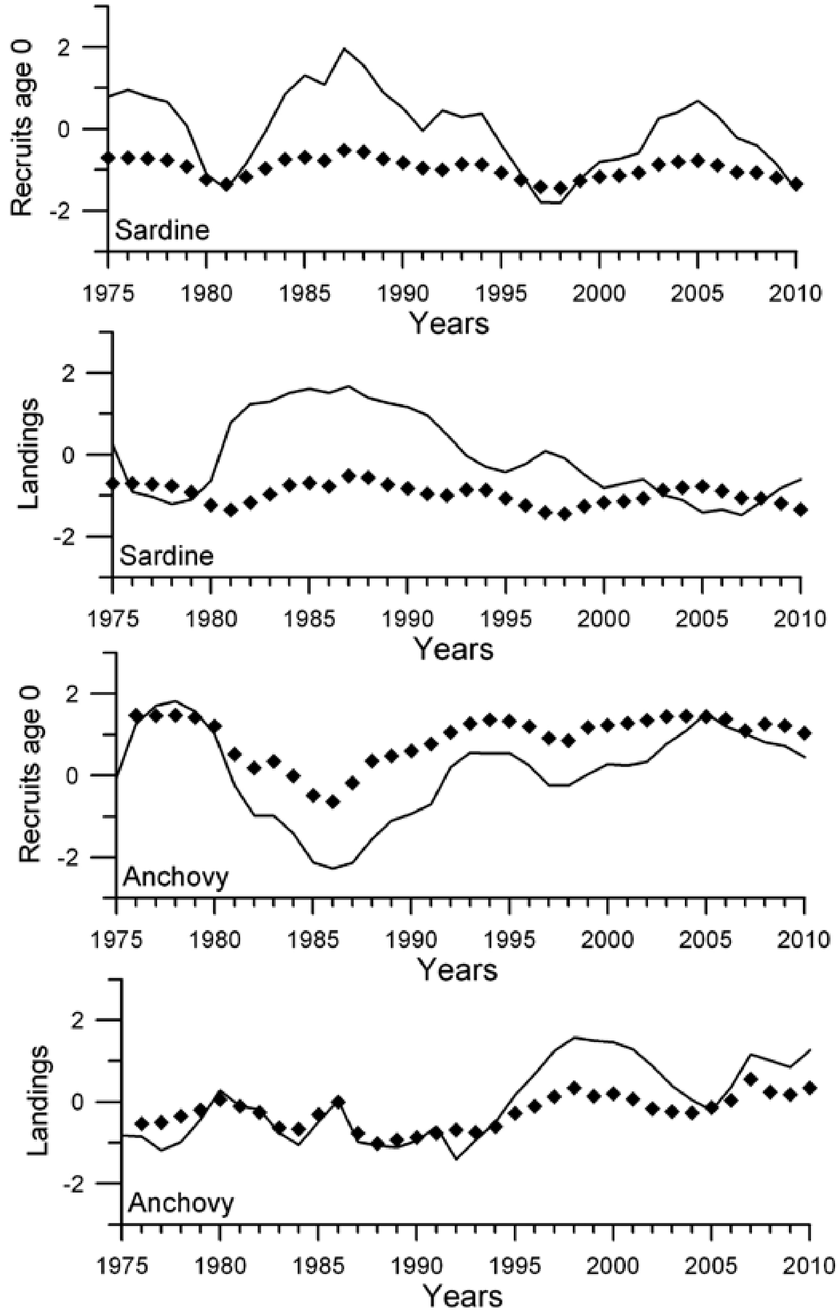

Fig. 6: Observed values (diamonds) and fitted values (black lines) of: sardine recruits age 0, sardine landings, anchovy recruits age 0, anchovy landings. Fitted values were calculated with DFA using three common trends and two explanatory variables (T_{100},S_{100}).

sardine and anchovy abundance, althoughs alinity and AOU are crucial as well. In good agreement with a recent study on the effect of climate change on the Mediterranean fisheries (Tzanatos *et al*., 2014), we have shown that sardine landings are negatively correlated with SST. While Tzanatos *et al*. (2014) obtained a positive correlation between the landing numbers of anchovy and temperature, we found no significant correlation, except at a time lag of 3 years, which exhibited a positive correlation. Furthermore, AOU content at the surface layer showed a negative correlation with sardine landings at a time lag of 1 year, which infers a direct correlation between more oxygen (lower values of AOU) in a preceding year and an increase in sardine abundance. Such a strong correlation corroborates with the documented sardine sensitivity to oxygen availability (Bertrand *et al*., 2011). Unlike oxygen content in deeper layers that is more likely correlated to fishery parameters as an indicator of water mass dynamics, oxygen content in surface layers might influence sardine numbers directly (e.g., Kreiner *et al*., 2009; Bertrand *et al*., 2011). By contrast, the anchovy is probably better adapted to lower oxygen concentrations, and it is thus unlikely that the observed oxygen decrease would influence their population size (van der Lingen, 1995; Bertrand *et al.*, 2011). Additionally, Bertrand *et al.* (2010) showed that the anchovy does not seem to be affected by a very shallow oxycline (<10 m), while the sardine avoids such areas; this observation is also consistent with the results obtained in this study.

We are left to discuss one more interesting phenomenon observed in Figure 3, the difference in sardine and anchovy populations. Although the species peak at a different time (sardine in 1985, and anchovy in 1978-1980), what is more interesting is the nature of their decline. Whereas sardine numbers (both of landings and recruits at age 0) slowly decrease from 1985 to the late 1990s, a drop in anchovy numbers (in particular of landings) is very dramatic and concentrated mostly in the year 1987. Many hypotheses have been put forward regarding the drop in anchovy abundance—surface temperature decreases (Azzali *et al.*, 2002), negative effects of the abundant plankton blooms (Regner, 1996), increasing quantities of mucilaginous aggregates and marine snow (Dulčić, 1995), increased predation of larval stages caused by a high abundance of the jellyfish *Pelagia noctiluca* (Specchi *et al.*, 1998), heavy overfishing (Klanjšček & Legović, 2007)—but it is most likely that the drop was caused by a combination of all the abovementioned processes. The winter of 1987 was very harsh and anomalous. Vilibić and Orlić (2001) document extremely high rates of dense water generation in both the northern Adriatic and within the South Adriatic Pit in 1987, resulting in changed characteristics of source water masses and significantly lowered temperatures in intermediate and deep waters (see their Figs. 6, 16 and 17). Thus, a collapse in anchovy numbers could have been driven by extreme cooling and mixing during the wintertime, but further analyses taking into account the interactions of all the abovementioned hypotheses should be conducted.

In conclusion,we might argue that, when assessing physical processes and ocean phenomena, small pelagic fish dynamics in the Adriatic Sea are governed by a complex interaction of (i) long-term processes occurring due to direct forcing of the atmosphere (increase of heat input at the surface layers), (ii) processes due to internal changes in the Adriatic-Ionian Sea-Eastern/Western Mediterranean dynamics, and (iii) shorter (even daily) time-scale processes occurring due to extreme wintertime cooling. All of these processes are in turn connected to the deep Adriatic and Eastern Mediterranean water masses and their interchange in the Adriatic Sea. Naturally, biological-ecological development, species interactions and their exploitation are important as well, but are not considered in this study.

Conclusions

Through an assessment of long-term changes in anchovy and sardine landings and recruits and oceanographic parameters (temperature, salinity, dissolved oxygen and nutrients), we have attempted to relate oscil lations, trends and rapid changes in fishery populations tooceanographic processes that occur over different time scales, from a month (wintertime cooling events) to a decade (BIOS mechanism, EMT-driven changes), and drive the water mass dynamics in the Adriatic Sea. Our results show that populations of both species are significantly influenced by ocean dynamics. These relationships indicate the importance of a spectra of ocean processes that can be connected to past and future decadal time scales through regional climate studies (Somot *et al.*, 2008; L'Heveder *et al.*, 2013); these studies are already used in assessments of marine environmental conditions (Weinmann *et al.*, 2013; Pairaud *et al.*, 2014). Our study aims to establish a basis for predicting long-term changes of small pelagic fish populations, driven by changes in environmental conditions, which should be included in future fishery projection studies.

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