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EDITED BY

Tomaso Fortibuoni,
Istituto Superiore per la Protezione e
la Ricerca Ambientale (ISPRA), Italy

REVIEWED BY

Sanja Matic-Skoko,
Institute of Oceanography and
Fisheries (IZOR), Croatia
Claudio Vasapollo,
National Research Council (CNR), Italy
Matteo Zucchetta,
National Research Council (CNR), Italy

*CORRESPONDENCE

Francisco Leitão
feitao@ualg.pt

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Environmental variability and fishing effects on artisanal flatfish fisheries along the Portuguese coast

Vânia Baptista¹, Ignacio Pérez Blasco², Juan Bueno-Pardo³,
Maria Alexandra Teodósio¹ and Francisco Leitão^{1*}

¹Centro de Ciências do Mar (CCMAR), Universidade do Algarve, Faro, Portugal, ²Universidade do Algarve, Faro, Portugal, ³Future Oceans Lab, CIM-Universidade de Vigo, Vigo, Spain

Assessing the effects of fishing activity and environmental variability on fishing species might help to understand their fluctuations and to manage them accordingly. However, despite the increasing number of studies linking fisheries and environmental data, few had a multi-species approach considering flatfish species and different age groups. Therefore, this study aims to determine the effects of environmental and fishing related variables on commercial flatfish species across different regions of the Portuguese coast. For that, sea surface temperature, North Atlantic Oscillation, upwelling index, wind components, river discharges and fishing effort were related to landings per unit effort (LPUE) of five commercial flatfish species (*Pleuronectes platessa*, *Dicologlossa cuneata*, *Microchirus* spp., *Solea lascaris*, and *Solea solea*) fished by the artisanal fleet along different regions of Portuguese coast (Northwestern coast, Southwestern coast, and Southern coast), using a multi-model statistical approach from 1989 to 2009. The fishing effort had the same effect along the life cycle and was negatively related with LPUE trends for most of the species. Regarding to environmental variability, during early phases (larval to juvenile – age-group-0) the factors that affected the recruitment, in addition to being related to the physiological needs (e.g., sea surface temperature) of individuals that will trigger growth and survival, were related to larval transport and dispersion from offshore spawning areas to coastal nursery habitats beyond (e.g., wind components and upwelling). For juvenile and young-adult phases (age-groups I and II), the effects of environmental variability appeared to be linked to physiological needs important for growth and maturation (e.g., temperature). Concluding, different effects were observed depending on the region, species, and life-cycle phase. Therefore, these environmental-fishing relationships should be used when managing local fishing resources.

KEYWORDS

Pleuronectiformes, environmental pressure, recruitment, time-series analyses, multi-model approach

Introduction

The variability of fishing stocks and their abundance is one of the main topics of research in fisheries oceanography (e.g., Hjort, 1914; Lehodey et al., 2006). There are several hypotheses that attempt to explain environmental-fisheries recruitment relationships. The classic “critical period” hypothesis suggested by Hjort (1914) pointed out that changes in stock size depend on the strength of the species year-class, determined during early life stages (eggs, larvae, and juveniles) by environmental conditions and food availability. The “match-mismatch” hypothesis proposed by Cushing (1990), indicated that medium-term influences of environmental mechanisms affect larval survival and thereby, inter-annual variability in fish recruitment success. This author highlighted the importance of the matching time of the spawning period and the start of the spring production cycle in coastal areas. Bakun’s triad hypothesis (Bakun, 1996) is an attempt to classify the three main mechanisms favouring early life stages recruitment: i) enrichment (e.g., upwelling events and mixing of waters layers); ii) concentration (e.g., convergence and fronts) and iii) processes favouring the retention within (or toward) an appropriate habitat might improve the chances of larvae stages to reduce their natural mortality and successfully recruit in the fishing stock. In summary, the vulnerability at early life stages crucially determines the recruitment success and consequently, size and structure of fishing stocks.

Currently, in addition to fishing exploitation (Pauly et al., 2002), it is largely recognized that environmental variability can play an important role in fish stock abundance. Climatic and oceanographic variability induces changes on fishing stocks in different ways, at different life-phases (Lloret et al., 2001; Lehodey et al., 2006; Ullah et al., 2012; Leitão et al., 2014; Teixeira et al., 2015) and differently along wide geographic scales (Ravier and Fromentin, 2001). Temperature, salinity, upwelling, winds, tidal currents and oceanic circulation, precipitation and river runoff and nutrients affect productivity, abundance, and distribution of fishing stocks (e.g., Santos et al., 2001; Borges et al., 2003; Erzini, 2005; Lehodey et al., 2006; Brander, 2007; Brander 2010; Baptista and Leitão, 2014; Baptista et al., 2016; Bueno-Pardo et al., 2020). The interaction of fishing activity and climatic variability can act on abundance and distribution of exploited species (direct effects), and affect the productivity, structure and composition of marine ecosystems (indirect effects) (Lehodey et al., 2006; Brander, 2007; Brander 2010). Thus, the environmental changes may reduce, or improve, the productivity of fisheries stocks (Brander, 2007; Brander 2010).

Coastal fishing activity occurs along the Portuguese coast, a transition area dividing cooler temperate waters in the north Europe and warmer subtropical waters in the South. Thus, the Portuguese coast presents distinct oceanographic and climatic regimes (Cunha, 2001; Bettencourt et al., 2004) due to its irregular coastal geography (Mason et al., 2005). Moreover,

fishing activity can highly vary from one region to another because of the habitat distribution of commercial fishing stocks and dissimilarities in the technological resources (Sousa et al., 2005; Duarte et al., 2009; Bueno-Pardo et al., 2017). Also, a variation in species distribution has been observed in this region due to climatic changes, with the probability of sub-tropical species increasing in the Iberian Peninsula in the next coming decades (Vinagre et al., 2009; Teixeira et al., 2014), namely in South of Portugal (Leitão et al., 2018; Encarnação et al., 2019). In this context, the evaluation of combined/synchronic fisheries and environmental effects at a local scale (Lloret et al., 2001; Ullah et al., 2012) can result in a more reliable assessment of the specific processes affecting resources. Several authors suggested that regional analyses rather than meta-analyses (e.g., Teixeira and Cabral, 2009; Ullah et al., 2012; Baptista et al., 2014; Leitão et al., 2014) can improve fisheries stock assessment for management purposes (Leitão et al., 2014). Studies on Portuguese fisheries time-series data have linked the environmental and fishing effects on commercial fishing stocks during larval development and recruitment such as those including pelagic species (Santos et al., 2001; Ullah et al., 2012; Leitão et al., 2014), bivalves (Baptista and Leitão, 2014; Baptista et al., 2014), seabreams (Baptista et al., 2016; Leitão et al., 2016), crustaceans (Herraiz et al., 2009) and cephalopods (Ullah et al., 2012), but few of them had a multi-species approach (e.g. Erzini, 2005; Teixeira and Cabral, 2009; Bueno-Pardo et al., 2020).

The polyvalent fleet is one of the largest fishing segments in the Portuguese mainland fisheries, accounting for more than 40% of the total fish landed and employing more than 70% of the fisher’s population (INE, 2013). Characterized by a wide range of passive gears (gill and trammel nets, lines and hooks, traps, and pots), the polyvalent fleet harvests on a diverse range of coastal species (mixed species), switching between fishing techniques depending on the depth, habitat, and season requirements (Teixeira et al., 2011). This multi-gear fleet is responsible for most of the flatfish landings, mainly by means of passive fishing gears such as gill nets and trammel nets. Although in minor quantity, bottom trawling also exploits this group of species. Flatfish commercial species comprises a relatively small proportion of total landings (less than 4%) but due to their high market value, they represent more than 11% of the landings’ economic value (Teixeira and Cabral, 2009).

The flatfish species (Pleuronectiformes order) are widely distributed over the Portuguese coast (Cabral, 2002), inhabiting marine, estuarine, and freshwater environments (Pauly, 1994; Gibson et al., 2014). Flatfishes perform a life-history strategy in which the larvae adopt a pelagic lifestyle, and the adults are benthonic (Ramos et al., 2010). The “migration triangle” hypothesis, from Harden Jones (1968), describes the general life-history strategy of these species: i) spawning occurs in offshore marine waters; ii) in young early stages, flatfishes are transported towards the coast where they settle in shallow nursery habitats such

as estuaries or coastal lagoons; iii) then, as juvenile mature they move to the adult habitat (Gibson, 1997; Ramos et al., 2009). Migration patterns vary among flatfish species depending on specific ontogenetic and biological features such as age and size at metamorphosis, spawning period, larval behaviour, and environmental conditions (Minami and Tanaka, 1992; Sogard et al., 2001; Bailey et al., 2005). Therefore, recruitment strength in the fishing stocks has been recognized to be widely determined by the migration, settlement, and survival of larvae on an appropriate nursery habitat (Bell et al., 2001; Warlen et al., 2002; Garcia et al., 2003; Ramos et al., 2010). In flatfish species, the recruitment strength has been linked to the hydrodynamic conditions found during pelagic larval phase (Nielsen et al., 1998), freshwater inputs in estuarine nursery grounds (Le Pape et al., 2003), and density-dependent mechanisms affecting food supply and predation pressure (Cowan et al., 2000; Nash and Geffen, 2000), all of them known to vary among geographical areas (van der Veer et al., 2000).

Considering all these premises, the goal of this study is to determine the effects of environmental and fishing variables on some of the most important commercial flatfish species across different regions of the Portuguese coast (Northwestern coast-IXaCN, Southwestern coast- IXaCS, and Southern coast- IXaS) and along larval (age-group 0) and juvenile/young-adults (age-groups I and II) phases. Understanding the temporal variability in catch rates can provide important information to improve species ecological knowledge and local fisheries management.

Material and methods

Study area

The influences of environmental and fishing variables on the Portuguese artisanal flatfish fishery were evaluated in three regions along the Portuguese coast. In its extension of ca. 800 km on the west coast and ca. 200 km on the south coast, the Portuguese coast includes regions with distinct oceanographic, climatic and environmental regimes, such as the Iberian Poleward Current, the Western Iberia Buoyant Plume (river effects), bathymetry, wind regimes and upwelling filaments (Cunha, 2001; Bettencourt et al., 2004; Santos et al., 2007). Also, the Portuguese coast is located in a biogeographical transition zone between temperate and subtropical waters: the Northwestern and the Southwestern coasts represent the subtropical Eastern boundaries of the North Atlantic Ocean (Santos et al., 2001) and the Southern coast which shares characteristics of the Atlantic Ocean and the more saline and warm waters of the Mediterranean Sea (Cunha, 2001). These differences oceanographic environmental and climatic regimes contribute to different fishing regimes across regions (Duarte et al., 2009). According to the International Council of the Exploration of the Sea (ICES), the Portuguese mainland coastal

zone is inside the IXa subdivision area, and thus, these areas can be designated as Northwestern coast (IXaCN), Southwestern coast (IXaCS) and Southern coast (IXaS) (Figure 1).

Fishing data sources

Flatfish (Pleuronectiformes order) fishing data (fishing effort and landings) from the artisanal multi-gear fleet in Portugal were obtained from Direção Geral de Recursos Naturais, Segurança e Serviços Marítimos (DGRM) for the period 1989–2009. A total of five taxa were studied considering their commercial importance: European plaice *Pleuronectes platessa* Linnaeus, 1785, wedge sole *Dicologlossa cuneata* (Moreau, 1881), bastard sole *Microchirus* spp. (Bonaparte, 1833), sand sole *Solea lascaris* (Risso, 1810), and common sole *Solea solea* (Linnaeus, 1785). Yearly Landings per Unit Effort (LPUE) were estimated by dividing the annual landings (in kg) by Fishing Effort (FE: fishing days by boat). Due to their commercial value, flatfishes are not considered as discard in these multispecies fisheries and thus, in this study, we considered that landings of flatfish are directly proportional to catches.

Environmental data sources

In the present study, environmental variable included oceanic, hydrologic and climatic indices. Oceanographic variables included annual and seasonal sea surface temperature (SST; °C), annual and seasonal upwelling index (UPW), and annual and seasonal geostrophic wind data (“u” and “v” wind components). Sea surface temperature data was obtained from Modis-Aqua 4 km satellite imagery available from the NASA Ocean Colour Giovanni website (<http://gdata1.sci.gsfc.nasa.gov>). The monthly upwelling index was obtained from the Pacific Fisheries and Environmental Laboratory website (www.pfeg.noaa.gov) using port position as input coordinate for data acquisition. Then upwelling port data were averaged to estimate each fishing area average upwelling intensity. Geostrophic wind data (“u” and “v” wind components) was obtained from NASA Jet Propulsion Laboratory California Institute of Technology that comprises high-resolution (0.25 degree) gridded datasets – Physical Oceanography Distributed Active Archive Center – PODAAC (http://podaac.jpl.nasa.gov/dataset/CCMP_MEASURES_ATLAS_L4_OW_L3_5A_MONTHLY_WIND_VECTORS_FLK?ids=&values=) (Atlas et al., 2011). The “u” component (UWIND; m.s⁻¹) represents the east-west winds whereas the “v” component (VWIND; m.s⁻¹) represents the north-south winds. Wind magnitude (WMAG; m s⁻¹) was calculated using “u” and “v” wind components (Baptista et al., 2014):

$$WMAG = \sqrt{(u^2 + v^2)}$$

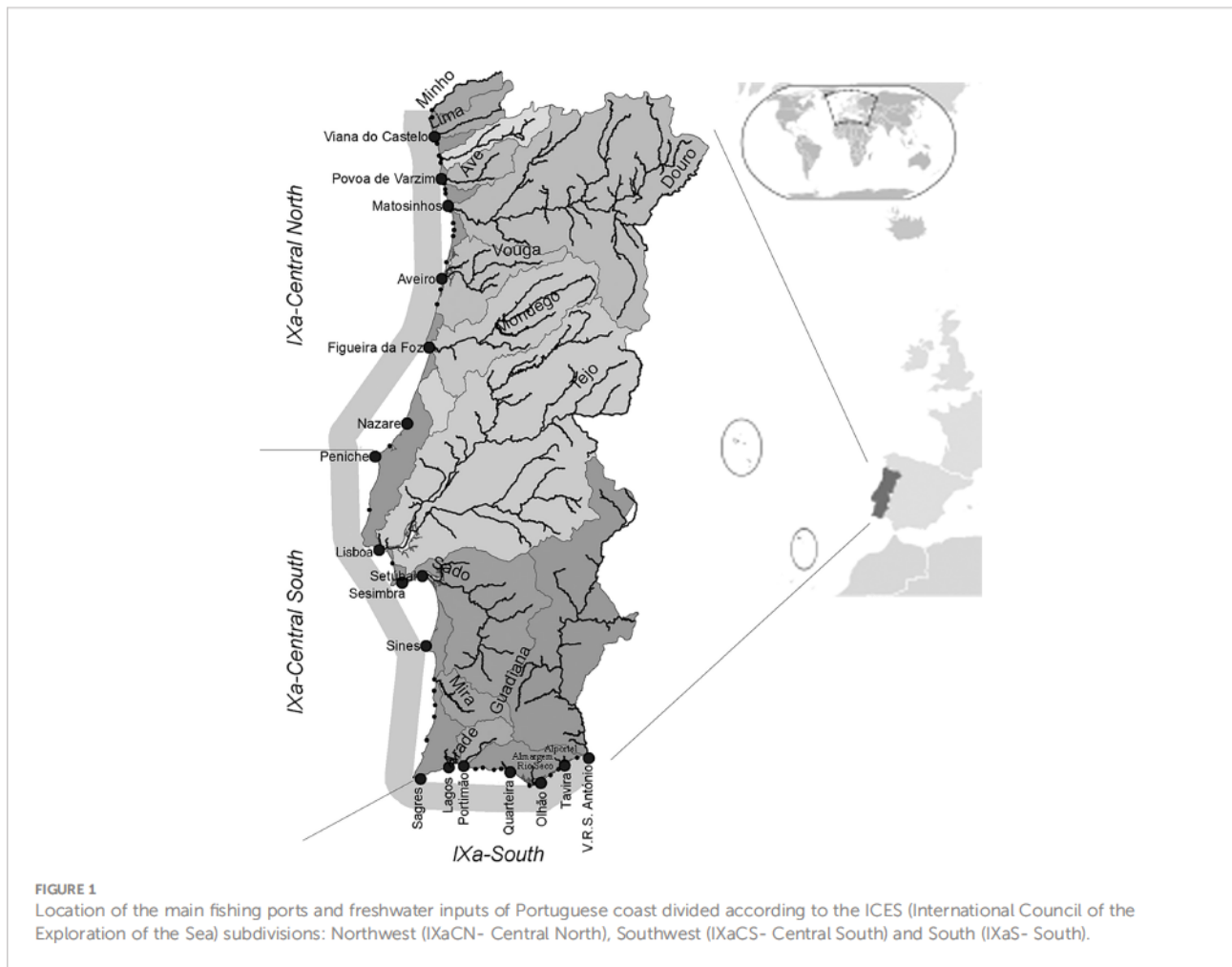


FIGURE 1
Location of the main fishing ports and freshwater inputs of Portuguese coast divided according to the ICES (International Council of the Exploration of the Sea) subdivisions: Northwest (IXaCN- Central North), Southwest (IXaCS- Central South) and South (IXaS- South).

The annual and seasonal river discharges (RD; dam^3) were used as hydrological variables to test the influence of freshwater inputs on flatfish LPUE. Monthly river discharge data were obtained for the period from January to December, for the main Portuguese rivers or basins (Figure 1) including: (i) Cávado, Lima, Douro, Vouga and Mondego for the IXaCN; (ii) Tejo, Sado and Mira for the IXaCS; and (iii) rivers Guadiana, Seco, Rio Arado, Ribeira de Quarteira, Alportel and Almagem for the IXaS. River discharge data were cumulatively grouped in seasons, and the yearly value was estimated by the sum volume contribution of the set of seasons. Monthly flow measurement data from hydrological stations located in the immediacy of the mouth of these rivers were obtained from the Agência Nacional do Ambiente (APA online database, SNIRH: <http://snirh.pt/>).

All the oceanographic and hydrological variables (SST, UPW, UWIND, VWIND and WMAG) were averaged for each geographical area of the Portuguese coast (Northwest- IXaCN, Southwest- IXaCS, and South- IXaS; Figure 1). For the oceanography raster datasets, the procedure to get tabular data

for analyses was the following. The inland port position was extended 12 miles offshore to match with the territorial sea area where most fleet activity is conducted. Then a buffer of 16km were made in each offshore port position. Geospatial operations tools allowed to extract pixel data from raster monthly data sets for each port area vector (area shapefile format). The zonal means values of each oceanographic variable by port were posteriorly averaged by fishing area. Northwest area ranges from Minho at 42° N to Cabo Carvoeiro at $39^\circ 21' 32''$ N, Southwest area from Cabo Carvoeiro to Sagres at $36^\circ 59' 35''$ and South from Sagres at $8^\circ 56' 54''$ W to Vila Real de Santo António at 6° W.

Finally, the yearly and winter North Atlantic Oscillation (NAO) index was also used as a climatic variable (<http://www.cgd.ucar.edu/jhurrell/nao.html>, last accessed 2010; Hurrell, 1995). Since NAO appears to be particularly active during the winter (Rodwell et al., 1999), NAO winter was also considered for the time series analysis. This index represents the differences in atmospheric pressures between the Azores high-pressure zone (placed at middle latitudes) and Iceland low-pressure zone (located at higher latitudes) (Hurrell, 1995; Hurrell et al.,

2003). The NAO index influence precipitation, temperature and wind regimes over most of Northwester Europe (Hurrell, 1995; Witbaard et al., 2005).

Time-series analyses (statistical models)

In the present study, we aim evaluate the role of regional and seasonal environmental conditions on flatfish species survival rates along their life cycles. Therefore, regional and seasonal models were considered. Seasons were grouped as follows: winter (January to March), spring (April to June), summer (July to September) and autumn (October to December). Thereby, time-series analyses were carried out for each of the species in each of the regions and seasons independently.

For statistical purposes, LPUE was used as the response variable whereas fishing effort (FE) and environmental variables were used as the explanatory variables. LPUE were used as a proxy for yearly fish biomass production and hence, it was the considered the response variable in the models fitted. The variability of fishing recruitment was assumed to be largely determined by survival during the larval and juvenile stages. Consequently, the survival during its early stages was considered to be influenced beyond starvation and predation (Garrido et al., 2015) by environmental and fishing conditions, and thus a critical period determining the state of the stock in the subsequent years (Lloret et al., 2001; Baptista et al., 2016; Leitão et al., 2016). For this reason, the environmental explanatory variables were lagged depending on the time until species reach the gear recruitment age, ensuring that environmental variability was affecting flatfish during their larval (two years for *D. cuneata*, and three years for *Microchirus* spp., *P. platessa*, *S. lascaris* and *S. solea*; Table 1), juveniles and young adult stages (one year for *D. cuneata*, and two and one years for *Microchirus* spp., *P. platessa*, *S. lascaris* and *S. solea*). Fishing effort can also affect spawning biomass (adults) and recruitment in subsequent years. Thus, to accommodate this effect, FE was also lagged, one, two and three years as environmental variables, to allow reflecting each species LPUE temporal change.

A multi-model approach including different time series analyses techniques was applied to find relationships between explanatory variables and the response variable (LPUE): Dynamic Factor Analysis (DFA), Min/Max Autocorrelation Factor Analysis (MAFA) and Generalised Least Squares (GLS). Since different analyses can provide different results, a selection criterion was implemented to identify the explanatory variables with higher probability to explain variability in flatfish LPUE. The probability was defined according to the number of time series techniques that identified the same significant relationship between explanatory variable and LPUE. This procedure allows classification of variables with either a high (the variable is highlighted in two or more models) or low probability to relate with fisheries (Baptista et al., 2016; Leitão et al., 2016).

Before the analyses, annual and seasonal data (response and explanatory variables) were tested for normality (quantile-quantile plots- QQ-plots) and collinearity (pair-plots) (Zuur et al., 2010). After QQ-plots analyses, no transformation was applied to yearly LPUE and explanatory variables. Since the results of the exploratory analysis over explanatory variables (pair-plots) revealed collinearity between yearly northerly wind (VWIND) and wind magnitude (WMAG), these variables were not taken into account together in the same models. As correlations between variables can be nonlinear the spearman correlation coefficient was used. A coefficient of correlation (R-coefficient correlation) of 80% was used as cut off criteria of collinear variables. Regardless of the time series technique used simple models were firstly tested for significance of the relationship without accounting for more than one variable. In situations where more than one variable was selected, the significance of the relationship was tested by accounting for combined statistically significant variables using surrogate testing. Both response and explanatory variables were standardized to convert the data into the same dimensional scale (2003b; Zuur et al., 2003a). The standardisation method used was the normalisation which consists in centring the data on zero; $(X_i = (Y_i - \hat{Y})/\partial y)$, where \hat{Y} is the sample mean, Y_i the value of the i th sample and ∂y the sample standard deviation. Statistical analyses were performed using Brodgar software package using R version 3.0.1 (<http://www.brodgar.com>).

TABLE 1 Biological and ecological information review of the flatfish species (Pleuronectiformes Order) used in the present study.

Family	Species	Climate	Maturity age (years)	Spawning period
Pleuronectidae	<i>Pleuronectes platessa</i> Linnaeus, 1785	Temperate	3 ^{1*}	December to March ⁵
Soleidae	<i>Dicologlossa cuneata</i> (Moreau, 1881)	Subtropical	2 ²	March to May ⁶
Soleidae	<i>Microchirus</i> spp. Bonaparte, 1833	Temperate	3 ³	February to June ⁷
Soleidae	<i>Solea lascaris</i> (Risso, 1810)	Temperate	3 ^{1*}	February to June ⁵
Soleidae	<i>Solea solea</i> (Linnaeus, 1785)	Temperate	3 ⁴	January to April ⁸

The * indicates that the study area found in the literature was in a location with different climatic conditions that one's presented in Western Iberia Peninsula. ¹Deniel (1990) (France), ²Dinis (1986) (Portugal), ³Afonso-Dias et al. (2005) (Portugal), ⁴Borges (2010) (Portugal), ⁵Félix et al. (2011) (France), ⁶Santos and Lino (2010) (Portugal), ⁷Andrade (1990), ⁸Vinagre et al. (2008).

Min/Max Autocorrelation Factor Analysis

Min/Max Autocorrelation Factor Analysis (MAFA) is a type of principal component analysis (PCA) that can be used for extracting the main trends from time series and for smoothing in short time series. A set of orthogonal linear combinations of the original time series (MAFs) of decreasing smoothness measured by lag-one autocorrelation are constructed (Solow, 1994). The MAFA axes represent a measure of autocorrelation with lag 1. The first axis represents the main trend in the time series, and the others represents less important trends (Solow, 1994). Cross-correlations between MAFA axes and explanatory variables can also be estimated, to allow the identification of significant relationships between trends and explanatory variables (Erzini, 2005; Zuur et al., 2007). The present MAFA analyses considered only a single MAFA trend (autocorrelation time lag 1) for each species and region. Absolute values above the significance cut off level of correlation provided by MAFA were considered to have a significant association with the response variable.

Dynamic Factor Analysis

Dynamic Factor Analysis (DFA) is a multivariate, dimension reduction technique that can be used to analyse short and non-stationary time series in terms of common patterns, evaluate the interactions between response variables (LPUE) and determine the effects of explanatory variables (environmental and fishing) on response variables (2003b; 2007; Zuur et al., 2003a). Time series were modelled as a function of a linear combination of common trends, a constant level parameter, one or more explanatory variables and noise (Zuur and Pierce, 2004). The simplest model (1-time series = trend + noise) was used to establish the cut-value based on the Akaike Information Criteria (AIC) to determine significant relations between explanatory variables and the response variable. A single model with an explanatory variable as a parameter (1-time series = trend + explanatory variable + noise) was used for each species within each region, to account for the different environmental conditions among regions (Baptista and Leitão, 2014; Baptista et al., 2016; Leitão et al., 2016). Models were fitted with a diagonal covariance matrix and the AIC was used to compare models. The t-values obtained from the estimation of regression parameters were considered as an indicator of relationship (positive or negative) and its strength between explanatory and response variables (t-values with the absolute value greater than 3 indicate a strong relationship among variables) (Zuur et al., 2003a).

Generalised Least Square

Generalised Least Square (GLS) is an extended linear mixed-effect model in which errors can be correlated and/or have unequal variance (Pinheiro and Bates, 2000; Lloret et al., 2001). Several GLS models were used without autocorrelation and with an autoregressive process required on the error components to allow

errors with unequal variance (Zuur et al., 2007). Errors were specified following an autoregressive process of degree 1 which was determined using the partial autocorrelation function and the goodness of fit of an auto-regressive moving average (ARMA) model. This approach assumes that the autocorrelation is highest between consecutive years. Generalised Least Square models an autoregressive process of order 1 and without any autoregressive process were tested and compared (only better models are presented) using the lowest AIC coefficient as decision criterion. The simpler model was selected when the difference in AIC coefficients of two models was smaller than 2 (Zuur et al., 2007). Models were considered significant at the 95% level of confidence. The relationship between the explanatory variables and the response variable was evaluated by the sign (positive or negative) of the slope value.

Results

Environmental variables description

Seasonal variability was recorded for all the variables tested (Table 2). Sea surface temperature (SST) was higher in the Southern region than in the Northwestern and Southwestern regions (Table 2). The SST had similar yearly trends in the three regions with the higher peaks registered in 1989-1990, 1995, 1997 and 2006 (Figure 2A). During the study period, the North Atlantic Oscillation (NAO) Index had positive values until 1995 when a prominent decrease occurred, remaining in a steady state (fluctuating around the mean) thereafter (Figure 2B).

The intensity of yearly Upwelling Index (UPW) was higher during spring and summer in the Portuguese mainland coastal zone, predominantly in the Northwestern and Southwestern regions (Table 2). Variations over the time showed different trends principally between the Southern and Western regions (IXaCN and IXaCS, Figure 2C). Important upwelling peaks occurred in the Southern region in 1996 and in 2009. In the Northwestern and Southwestern regions noteworthy peaks in upwelling befell in 1992, 1999-2000, 2005 and 2007-2008.

Yearly wind magnitude (WMAG) trends for the three regions shared similar variations over the time (Figure 2D). Remarkably events occurred in 1996 in the Southern region and also in 2008 where all the regions presented the highest values of the time series. Seasons with strong winds were spring and summer, with the strongest winds occurring in the Southwestern region (Table 2). The easterly yearly wind component (UWind) showed different trends among areas until 1998 (Figure 2E). Afterwards the three regions had similar patterns. Positive anomalies (i.e., values above the mean and wind blew from the west) were striking in 1993-1997, 1998-2004 and 2006-2009. Negative anomalies (i.e., values are below the mean and wind blew from the east) were remarkable

TABLE 2 Yearly and seasonal means and standard deviations (SD) for oceanographic, hydrological and climatic variables used in the time series analysis for the period from 1989 to 2009 along the Portuguese coast: Northwest (IXaCN), Southwest (IXaCS) and South (IXaS).

Environmental Variables	Northwest (IXaCN)		Southwest (IXaCS)		South (IXaS)	
	MEAN	SD	MEAN	SD	MEAN	SD
SST Annual	16.02	0.46	17.04	0.38	18.51	0.33
SST Winter	14.11	0.66	15.05	0.61	16.18	0.45
SST Spring	15.88	0.71	16.68	0.61	17.98	0.48
SST Summer	18.53	0.64	19.15	0.68	21.04	0.70
SST Autumn	15.86	0.94	17.06	0.83	18.82	0.75
NAO	0.30	0.62	0.30	0.62	0.30	0.62
NAO Winter	1.01	1.70	1.01	1.70	1.01	1.70
UPW Annual	-4.66	17.80	13.20	9.80	-0.48	7.72
UPW Winter	-25.70	40.47	-4.24	22.65	-13.62	25.58
UPW Spring	26.39	15.69	29.91	17.12	12.02	9.87
UPW Summer	43.01	12.38	49.46	14.26	8.69	7.12
UPW Autumn	-48.60	53.20	-21.86	30.62	-3.29	28.14
WMag Annual	2.87	0.60	3.71	0.56	2.45	0.46
WMag Winter	1.93	0.93	3.11	0.88	2.48	0.54
WMag Spring	3.83	0.80	5.02	0.88	3.56	0.65
WMag Summer	4.46	0.70	5.34	0.65	3.75	0.58
WMag Autumn	2.69	1.03	2.78	1.29	2.25	0.82
UWind Annual	1.02	0.43	1.28	0.46	0.94	0.54
UWind Winter	0.69	1.14	0.27	1.35	-0.83	1.74
UWind Spring	1.72	0.65	2.00	0.57	2.19	0.66
UWind Summer	1.35	0.36	1.81	0.29	2.02	0.58
UWind Autumn	0.18	1.29	0.29	1.43	0.20	1.49
VWind Annual	-2.52	0.64	-3.21	0.60	-2.06	0.46
VWind Winter	-1.25	1.27	-2.91	1.07	-1.90	0.74
VWind Spring	-3.55	1.10	-4.45	1.04	-2.64	0.68
VWind Summer	-4.41	0.76	-5.05	0.71	-3.21	0.55
VWind Autumn	-1.87	2.17	-2.13	1.67	-1.53	1.23
River Annual	27050.41	13363.74	6999.66	6348.43	1134.55	2417.12
River Winter	10799.63	11327.00	1772.88	4797.06	339.79	1592.59
River Spring	5443.01	2945.85	1092.84	633.51	140.97	135.77
River Summer	2775.88	769.97	777.55	485.12	74.64	58.58
River Autumn	6480.82	5486.53	2059.98	3039.02	317.86	1363.22

SST, Sea surface temperature (°C); NAO, North Atlantic Oscillation Index; UPW, Upwelling Index; WMAG, Wind magnitude ($m.s^{-1}$); UWIND, Easterly wind component ($m.s^{-1}$); VWIND, Northerly wind component ($m.s^{-1}$) and RD, River discharges (dam^3).

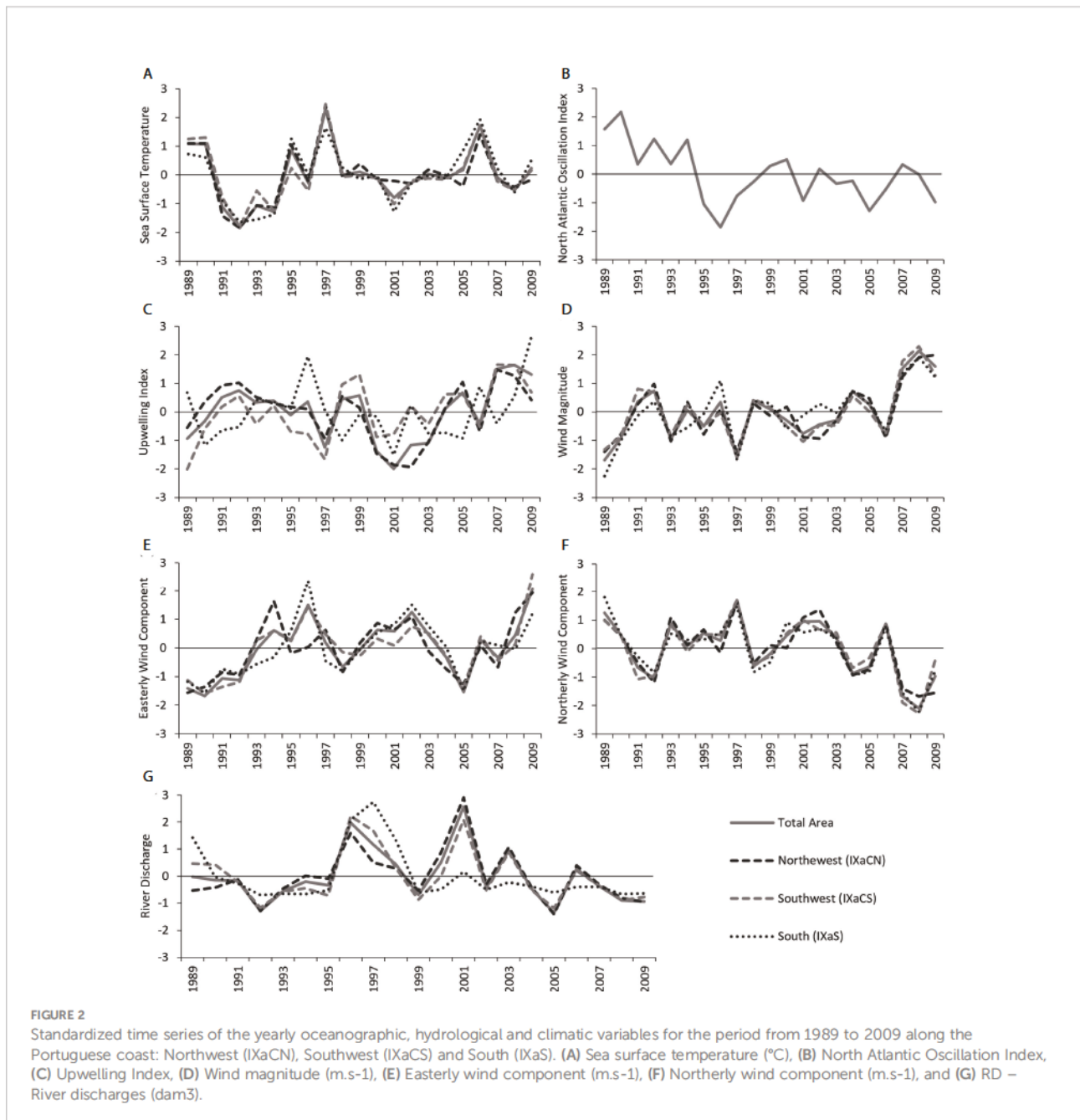
during the period before 1992 and in 2005. The yearly northerly wind component (VWind) presented similar trends among all the regions varying smoothly along the mean (Figure 2F). The dominance of positive values represents winds coming from the south whereas negative values denote winds blowing from the north. After 2006, an outstanding decrease befell peaking in the lowest values in 2008 regardless of the areas.

Maximum river discharge (RD) volumes occurred during winter and the lowest occurred in summer, for all the regions (Table 2). The discharges were higher in the Northwestern region regardless of season, and significantly lower in the

Southern region. The Northwestern and Southwestern regions had similar trends, peaking in 1996, 2001 and 2003 (Figure 2G). The larger volumes discharged in the Southern region occurred in 1989 and in 1996-1997.

Fishing variables description

Fishing effort and LPUE regional trends showed high variability among areas and for each flatfish species (Figure 3). Landings per unit effort values were higher in IXaCN. The FE of *P. platessa*



showed a decreasing trend in IXaCS (Figure 3A) and was highly variable in IXaCN and IXaS, with a peak in 2004 in IXaCN. The LPUE of *P. platessa* also revealed decreasing trends in all the regions, with a high isolated peak in 2003 in IXaCN (Figure 3B). The FE of *D. cuneata* showed an increasing pattern in IXaCN and IXaCS, contrarily to registered in IXaS (Figure 3A). Its LPUE was higher in 1991 and 1993 in IXaCN, in 1991 in IXaCS, and between

1997 and 2003 in IXaS (Figure 3B). *Microchirus* spp. had highly variable FE and LPUE trends in all the regions, with no clear patterns (Figures 3A, B). The FE of *S. lascaris* increased along the years in IXaCN and IXaCS and showed more variability in IXaS increasing in 1990 and 2003 and decreasing in 1998 (Figure 3A). Contrarily, its LPUE decreased over the years, with the highest values registered in 1991 and 1993 in IXaCN, and 1995 in IXaCS

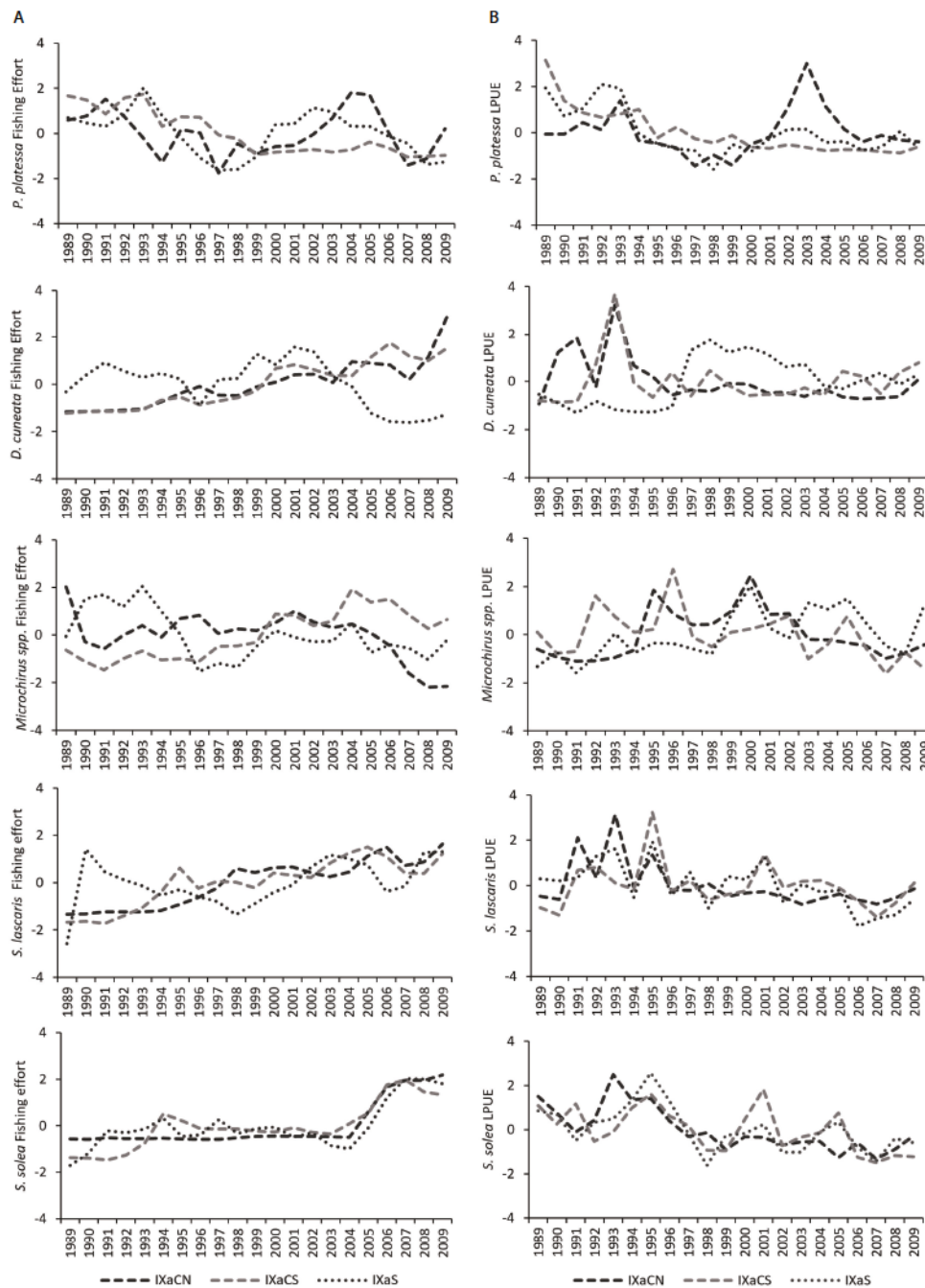


FIGURE 3
 (A) Standardised yearly fishing effort (number of fishing days by boat, and (B) Landings per unit effort (LPUE: kg per fishing days by boat) for *Pleuronectes platessa*, *Dicologlossa cuneata*, *Microchirus* spp., *Solea lascaris*, and *Solea solea* between 1989 and 2009 in Northwestern (IXaCN), Southwestern (IXaCS) and Southern (IXaS) coasts of Portugal.

(Figure 3B). *Solea solea* FE was concentrated close to the mean, showing an increasing pattern from 2005 in all the three regions (Figure 3A). The LPUE of *S. solea* showed a decreasing pattern, peaking in 1993 in IXaCN, 1995 in all regions, and 2001 and 2005 in IXaCS (Figure 3B).

Modelling flatfish LPUEs

Explanatory variables selected as significant in more than one model have a high probability to influence flatfish LPUE. Summarized results of explanatory variables with significant

relationship with flatfish LPUE for each region are given in Table 3 (age-group 0), Table 4 (age-group I), and Table 5 (age-group II) (for the detailed results of all model approaches see Supplementary Table 1 in Supplementary Material).

Considering the sign of the effect of explanatory variables on the age-group 0, FE had positive effects on *P. platessa* in IXaCS, and negative effects on *D. cuneata* and *S. lascaris* in IXaCN, *S. solea* in IXaCS, and on *Microchirus* spp. in IXaCN and IXaS (Table 3). The SST negatively affected *P. platessa* during spring (IXaCS), and *S. solea* in spring (IXaCS and IXaS), summer (IXaCN) and autumn (IXaCS) (Table 3). On the other hand, SST had positive effects on *D. cuneata* and *Microchirus* spp. during winter and spring (IXaS). The NAO Index in winter positively affected *P. platessa* (IXaCN and IXaS), *Microchirus* spp. and *S. lascaris* (IXaCN) (Table 3). Upwelling (UPW) Index showed negative effects in *P.*

platessa during summer (IXaCS) and on *D. cuneata* during spring (IXaS) (Table 3). Upwelling had also positive effects on *Microchirus* spp. in summer (IXaCN and IXaCS) and autumn (IXaS), and on *S. solea* during spring and summer (IXaCS). Wind magnitude (WMag) had negative effects on *P. platessa* during summer (IXaS), *Microchirus* spp. in spring (IXaCN) and winter (IXaCS), and on *S. solea* during autumn (IXaCN) (Table 3). However, WMag showed positive effects during summer on *Microchirus* spp. (IXaS) and *S. lascaris* (IXaCS). U-wind component (UWind) negatively affected *P. platessa* during summer (IXaCS and IXaS), *D. cuneata* and *S. solea* during spring (IXaCS), and *S. lascaris* during winter (IXaS). *Dicologlossa cuneata* was also positively affected by VWind during summer (IXaS), as well as *Microchirus* spp. during autumn (IXaCN and IXaS) (Table 3). V-wind component (VWind) showed negative effects on *D. cuneata* during

TABLE 3 Summary of results of relationships (significant in two or more time series analysis) between each flatfish species (Landings per unit effort- LPUE) and explanatory variables (fishing effort and environmental factors) using Min/Max Autocorrelation Factor Analysis (MAFA), Dynamic Factor Analysis (DFA) and Generalised Least Squares (GLS) corresponding to the age-group 0 (Lag3 for *Pleuronectes platessa*, *Microchirus* spp., *Solea lascaris* and *Solea solea*, and Lag2 for *Dicologlossa cuneata*), along the Portuguese coast: Northwest (IXaCN), Southwest (IXaCS) and South (IXaS).

Explanatory variables	<i>Pleuronectes platessa</i>			<i>Dicologlossa cuneata</i>			<i>Microchirus</i> spp.			<i>Solea lascaris</i>			<i>Solea solea</i>		
	IXaCN	IXaCS	IXaS	IXaCN	IXaCS	IXaS	IXaCN	IXaCS	IXaS	IXaCN	IXaCS	IXaS	IXaCN	IXaCS	IXaS
Fishing Effort		(+)		(-)				(-)	(-)	(-)					(-)
SST Win						(+)			(+)						
SST Spr		(-)			(+)	(+)			(+)					(-)	(-)
SST Sum															(-)
SST Aut															(-)
NAO Win	(+)		(+)					(+)			(+)				
UPW Win															
UPW Spr					(-)									(+)	
UPW Sum		(-)					(+)							(+)	
UPW Aut									(+)						
WMag Win								(-)							
WMag Spr							(-)								
WMag Sum			(-)						(+)		(+)				
WMag Aut															(-)
UWind Win												(-)			
UWind Spr					(-)									(-)	
UWind Sum		(-)	(-)			(+)									
UWind Aut							(+)		(+)						
VWind Win									(+)						
VWind Spr				(-)	(-)										
VWind Sum											(-)			(-)	
VWind Aut															
River Win						(+)									
River Spr			(+)				(+)		(+)				(-)		
River Sum															
River Aut									(+)						

SST, Sea surface temperature (°C); NAO, North Atlantic Oscillation Index; UPW, Upwelling Index; WMAG, Wind magnitude (m.s⁻¹); UWIND, Easterly wind component (m.s⁻¹); VWIND, Northerly wind component (m.s⁻¹); and RD, River discharges (dam³); the - and + signs indicate explanatory variables with negative and positive relationships, respectively.

TABLE 4 Summary of results of relationships (significant in two or more time series analysis) between each flatfish species (Landings per unit effort- LPUE) and explanatory variables (fishing effort and environmental factors) using Min/Max Autocorrelation Factor Analysis (MAFA), Dynamic Factor Analysis (DFA) and Generalised Least Squares (GLS) corresponding to the age-group I (Lag2 for *Pleuronectes platessa*, *Microchirus* spp., *Solea lascaris* and *Solea solea*, and Lag1 for *Dicologlossa cuneata*), along the Portuguese coast: Northwest (IXaCN), Southwest (IXaCS) and South (IXaS).

Explanatory variables	<i>Pleuronectes platessa</i>			<i>Dicologlossa cuneata</i>			<i>Microchirus</i> spp.			<i>Solea lascaris</i>			<i>Solea solea</i>		
	IXaCN	IXaCS	IXaS	IXaCN	IXaCS	IXaS	IXaCN	IXaCS	IXaS	IXaCN	IXaCS	IXaS	IXaCN	IXaCS	IXaS
Fishing Effort		(+)		(-)				(-)		(-)					(-)
SST Win						(+)									
SST Spr	(-)					(+)		(-)					(-)		(-)
SST Sum			(+)												
SST Aut					(-)										
NAO Win				(+)		(-)				(+)			(+)		
UPW Win	(-)						(+)								
UPW Spr			(-)												
UPW Sum		(-)													
UPW Aut															
WMag Win										(-)				(+)	
WMag Spr										(-)				(+)	
WMag Sum			(-)		(+)							(-)			
WMag Aut			(-)		(+)	(+)		(+)	(+)					(-)	
UWind Win							(-)								
UWind Spr															
UWind Sum			(-)								(+)			(+)	
UWind Aut							(+)								
VWind Win							(+)								
VWind Spr															
VWind Sum			(-)		(-)							(+)			
VWind Aut									(-)						
River Win	(+)					(+)									
River Spr							(+)								
River Sum				(-)											
River Aut					(-)										

SST, Sea surface temperature (°C); NAO, North Atlantic Oscillation Index; UPW, Upwelling Index; WMAG, Wind magnitude ($m.s^{-1}$); UWIND, Easterly wind component ($m.s^{-1}$); VWIND, Northerly wind component ($m.s^{-1}$); and RD, River discharges (dam^3); the - and + signs indicate explanatory variables with negative and positive relationships, respectively.

spring (IXaCN and IXaCS), and on *S. lascaris* and *S. solea* during summer (IXaCS); and positive effects on *Microchirus* spp. during winter (IXaS). River discharges positively affected *P. platessa* during spring (IXaS), *D. cuneata* in winter (IXaS), and *Microchirus* spp. during spring (IXaCN and IXaS) and autumn (IXaS); and negatively affected *S. solea* during spring (IXaCN) (Table 3).

In relation to the effects on age-group I, FE showed positive effects on *P. platessa* in IXaCS, and negative effects on *D. cuneata* and *S. lascaris* in IXaCN, and on *Microchirus* spp. and *S. solea* in IXaCS (Table 4). The SST had negative and positive effects on *P. platessa* in spring (IXaCN) and summer (IXaS), respectively (Table 4). *Dicologlossa cuneata* was negatively affected by SST in autumn (IXaCS) and positively during winter and spring (IXaS). The SST had also negative effects on *Microchirus* spp. (IXaS) and *S. solea* (IXaCN and IXaCS) during spring. The NAO Index in

winter had positive effects on *D. cuneata* (IXaCN), *S. lascaris* (IXaCS) and *S. solea* (IXaCN) (Table 4). *Dicologlossa cuneata* was also negatively affected by NAO winter (IXaS). Upwelling index showed negative effects on *P. platessa* during winter (IXaCN), spring (IXaS) and summer (IXaCS); and positive effects on *Microchirus* spp. in winter (IXaCN) (Table 4). Wind magnitude negatively affected *P. platessa* during summer and autumn (IXaS), *Microchirus* spp. during spring (IXaS), *S. lascaris* during winter (IXaCN) and summer (IXaS), and *S. solea* during autumn (IXaCN) (Table 4). On the other hand, WMag showed positive effects on *D. cuneata* in summer (IXaCS) and autumn (IXaCS and IXaS), on *Microchirus* spp. during autumn (IXaCS and IXaS), and on *S. solea* during winter and spring (IXaCN). U-wind component had negative effects on *P. platessa* during summer (IXaS), and positive effects on *S. lascaris* and *S. solea* during summer (IXaCS) (Table 4). *Microchirus* spp. was

TABLE 5 Summary of results of relationships (significant in two or more time series analysis) between each flatfish species (Landings per unit effort- LPUE) and explanatory variables (fishing effort and environmental factors) using Min/Max Autocorrelation Factor Analysis (MAFA), Dynamic Factor Analysis (DFA) and Generalised Least Squares (GLS) corresponding to the age-group II (Lag1 for *Pleuronectes platessa*, *Microchirus* spp., *Solea lascaris* and *Solea solea*), along the Portuguese coast: Northwest (IXaCN), Southwest (IXaCS) and South (IXaS).

Explanatory variables	<i>Pleuronectes platessa</i>			<i>Microchirus</i> spp.			<i>Solea lascaris</i>			<i>Solea solea</i>		
	IXaCN	IXaCS	IXaS	IXaCN	IXaCS	IXaS	IXaCN	IXaCS	IXaS	IXaCN	IXaCS	IXaS
Fishing Effort		(+)	(+)				(-)				(-)	
SST Win												
SST Spr	(-)		(-)									(-)
SST Sum												(-)
SST Aut			(-)					(-)	(-)			
NAO Win												
UPW Win												
UPW Spr	(+)											
UPW Sum						(+)						
UPW Aut												
WMag Win				(+)						(-)	(+)	
WMag Spr			(+)									
WMag Sum		(+)										
WMag Aut												
UWind Win				(+)								
UWind Spr		(+)										
UWind Sum		(-)										
UWind Aut												
VWind Win				(-)								(-)
VWind Spr										(-)		(-)
VWind Sum		(-)				(+)						
VWind Aut			(-)			(-)						
River Win												
River Spr	(-)											
River Sum		(+)	(+)									
River Aut			(-)		(-)			(-)				(-)

SST, Sea surface temperature (°C); NAO, North Atlantic Oscillation Index; UPW, Upwelling Index; WMAG, Wind magnitude ($m.s^{-1}$); UWIND, Easterly wind component ($m.s^{-1}$); VWIND, Northerly wind component ($m.s^{-1}$); and RD- River discharges (dam^3); the - and + signs indicate explanatory variables with negative and positive relationships, respectively.

negatively affected by UWind during winter and positively during autumn (IXaCN). V-wind component showed negative effects during summer on *P. platessa* (IXaS) and *D. cuneata* (IXaCS), and during autumn on *Microchirus* spp. (IXaS) (Table 4). *Microchirus* spp. was also positively affected by VWind during winter (IXaCN), as well as *S. solea* during summer (IXaS). River discharges had positive effects on *P. platessa* (IXaCN) and *D. cuneata* (IXaS) during winter, and on *Microchirus* spp. during spring (IXaCN); and negative effects on *D. cuneata* during summer (IXaCN) and autumn (IXaCS) (Table 4).

Concerning to the effects on age-group II, FE showed positive effects on *P. platessa* in IXaCS and IXaS, and negative effects on *S. lascaris* in IXaCN and *S. solea* in IXaCS (Table 5). The SST negatively affected *P. platessa* during spring (IXaCN and IXaS) and autumn (IXaS), *S. lascaris* during autumn (IXaCS and IXaS),

and *S. solea* during spring and summer (IXaS) (Table 5). Upwelling index had positive effects on *P. platessa* during spring (IXaCN) and on *Microchirus* spp. during summer (IXaS) (Table 5). Wind magnitude had positive effects on *P. platessa* during spring (IXaS) and summer (IXaCS), and on *Microchirus* spp. and *S. solea* during winter (IXaCN); and negative effects on *S. lascaris* during winter (IXaS) (Table 5). U-wind component positively affected *P. platessa* during spring (IXaCS) and *Microchirus* spp. during winter (IXaCN) (Table 5). *Pleuronectes platessa* was also affected by UWind during summer (IXaCS). V-wind component showed negative effects on *P. platessa* during summer (IXaCS) and autumn (IXaS), on *Microchirus* spp. during winter (IXaCN) and autumn (IXaS), and on *S. solea* during winter (IXaS) and spring (IXaCN and IXaS) (Table 5). *Microchirus* spp. was also positively affected by VWind during summer (IXaS). *Pleuronectes platessa* was positively affected by river discharges during summer (IXaCS and IXaS) and

negatively during spring (IXaCN) and autumn (IXaS) (Table 5). River discharges had also negative effects on *Microchirus* spp. (IXaCS), *S. lascaris* (IXaCS) and *S. solea* (IXaS) during autumn.

Discussion

Overall, we have different variable relationships between the LPUE of flatfish in Portuguese coast and the explanatory variables considered (FE, SST, NAO, UPW, WMAG, UWIND, VWIND and RD). Also, we have found that these relationships vary between species and regions, and that these relationships are species and region dependent, in agreement with previous works (van der Veer et al., 2000). The environmental variability affects flatfish species in different ways along their life cycle, seasons, and regions along the Portuguese coast. Similarly, FE had opposite effects on the LPUE depending on the region or the species (sometimes positive, sometimes negative). This finding is related to the indirect (sometimes not clear) relationship between LPUE and fish stocks. Hence, positive relationships between LPUE and FE are only expected on healthy stocks, while negative relationships might be found in situations of decreasing stocks or in the case of species that do not form large schools (as is the case of flatfish) (Bueno-Pardo et al., 2020). In the following subsections we discuss the effects of fishing pressure and environmental variability on the age-group 0 (larvae and juveniles), and age-groups I and II (juveniles to young-adults) separately.

Effects of fishing effort

In parallel with environmental variables, it has been widely demonstrated that fishing can cause great impacts on fishing stocks (Pauly et al., 2002; Gibson et al., 2014). Our results show that FE is the most relevant variable (more times identified as significant) of the analysed variables, for almost all species and age-groups of flatfish studied. A negative relationship between FE and LPUE was detected for *Dicologlossa cuneata* and *Solea lascaris* in the Northwestern region (IXaCN), and for *Microchirus* spp. and *Solea solea* in the Southwestern (IXaCS) and Southern (IXaS) regions. As mentioned before, the relationship between LPUE (as for the catch per unit effort, CPUE) has been shown to not be necessarily related to the state of the stock (Harley et al., 2001), but negative relationships between LPUE and FE could only be related to decreasing stocks. The limitation in the management measures of flatfish fisheries in Portugal and the lack of stock assessment have generated some problems in legislation, for example, the minimum landing sizes, local quotas, and total admissible captures (TAC) were regulated only for a couple of species (Teixeira and Cabral, 2009). Consequently, these resources have yet presented evidences of over-exploitation (Rice and Cooper, 2003; Rijnsdorp et al., 2007; Teixeira and Cabral, 2009). Although there are minimum landing

sizes defined for flatfish species (e.g., 15 cm for *D. cuneata*, 18 cm for *Microchirus* spp., and 24 cm for *Solea* spp.), undersized flatfishes are being caught, belonging to the age-groups 0 and I (i.e., immature individuals) (Ribeiro et al., 1999; Afonso-Dias et al., 2005). Also, some authors (Teixeira and Cabral, 2009; Andersen et al., 2010; Teixeira et al., 2011) described that flatfish species were caught mainly during the spawning season, a sensitive period for these species, as they concentrate near the coast to spawn and become more vulnerable for fishery. Thus, the fishing pressure exercised on these species could have reduced the spawning stock biomass influencing the recruitment in subsequent years. It is worth to note, however, that the LPUE of *Pleuronectes platessa* is positively related to FE in the region IXaCS. Here the LPUE time-series presented a decreasing trend, being also the region with lowest effort for this species.

Effects of environmental variability

Larvae and juveniles – age-group 0

Sea surface temperature (SST) is considered one of the main environmental factors driven biological and ecological changes in the marine environment (Teixeira and Cabral, 2009; Baptista et al., 2018). Larval development in fish species is highly affected by the increase of temperature, accelerating planktonic larval duration and consequently survivorship (Pauly and Pullin, 1988; Pepin, 1991). In the case of flatfish species, SST has been reported to affect growth, maturity, spawning, and development of eggs, larvae, and juveniles (Rijnsdorp and Vingerhoed, 1994; Henderson and Seaby, 2005; Petitgas et al., 2012; Vinagre et al., 2013). In the present study, negative relationships between SST and LPUE of *P. platessa* were found in the Southwestern region during spring, corresponding to the end of the spawning season and development of early phases (eggs and larvae). These results are in accordance with previous findings reporting negative relationships between *P. platessa* year-class strength and water temperature in North Atlantic during spawning (van der Veer et al., 2000) and early life periods (van der Veer and Witte, 1999). Teal et al. (2008) also suggested that growth of age-group 0 *P. platessa* is determined by temperature. LPUE of *Solea solea* had also a negative relation with SST in Southwestern (spring and summer) and Southern coasts (spring and autumn). Although several studies found positive correlations between SST and *Solea* spp. in Portuguese estuaries (e.g., Vinagre et al., 2008; Ramos et al., 2009; Gamito et al., 2015), Rijnsdorp et al. (1992) reported that lower SST at the spawning season might enhance the reproductive success of *S. solea*. Cozzi and Giani (2011) also registered low recruitment rates in years with warm temperatures in Adriatic Sea. *Solea solea* is a temperate species with a metabolic optimum temperature estimated of 18.8°C (Lefrançois and Claireaux, 2003), possibly suffering thermal stress in Southwestern and Southern regions of Portuguese coast, with temperatures varying

between 18.4 and 22.5°C during spring, summer, and autumn (Table 2). During these conditions, the ingestion rates decrease (Yamashita et al., 2001) as well as the growth rates, since the energy is spent to face unfavourable conditions, as previously described in Tagus Estuary (Southwestern coast- IXaCS) (Vinagre and Cabral, 2008; Vinagre et al., 2008). Still, egg mortality in *P. platessa* and *S. solea* has also been associated with the increase of pathogens activity caused by warm temperatures (Fonds, 1995; Henderson, 1998).

In addition, time-series analysis also revealed positive relationships between LPUE and SST for *D. cuneata* and *Microchirus* spp., benefiting from winter (IXaS) and spring SST (IXaCS and IXaS), and matching with spawning and larval periods (Andrade, 1990; Santos and Lino, 2010; Table 1). As reported by Lange and Greve (1997), temperature influences the rate of gonadal maturation and spawning time, and consequently recruitment of flatfish species. Désaunay et al. (2006) also reported that winter warming can be favourable for growth and survival of *D. cuneata* early phases in the Bay of Biscay. Increases in SST may also influence other marine trophic levels such as phytoplankton and zooplankton communities (Colebrook, 1982; Tunberg and Nelson, 1998), important food resources for flatfish larvae. Furthermore, *D. cuneata* had a subtropical range distribution (Froese and Pauly, 2016) tolerating warmer temperatures than other flatfish species occurring in these waters. In fact, Teixeira et al. (2014) reported the increase of *D. cuneata* landings in warm years in Portuguese coast. *Microchirus* spp. LPUE was also positively related with both winter and spring SST, corresponding to their spawning period (February to June; Andrade, 1990; Table 1). Therefore, favourable SST conditions might determine an early spawning and decrease pelagic larval duration (O'Connor et al., 2007) increasing the settlement success through larval retention (Lacroix et al., 2018). *Microchirus* spp. are a temperate species with a remarkably southern distribution (Quéro et al., 1986) taking advantage of warmer SST conditions. Teixeira and Cabral (2009) reported that temperature was the most important predictor explaining *Microchirus azevia* landings, by its effects on food resources. Also, Teixeira et al. (2014) and Gamito et al. (2015) demonstrated that *Microchirus* spp. landings were higher in warm years and lower during cold periods.

Although the same North Atlantic Oscillation (NAO) Index was used for all the regions, LPUE of different flatfish species were associated to it in different regions of the Portuguese coast. The NAO Index was positively related to LPUE of *P. platessa* (IXaCN and IXaS), *Microchirus* spp. and *S. lascaris* (IXaCS) during winter, coinciding with their spawning season and the beginning of the larval period (Andrade, 1990; Félix et al., 2011; Table 1). Thus, high biomass was observed during positive NAO periods, characterized, in the Southern Europe, by a predominance of relatively lower SST (Henriques et al., 2007) and Northern wind conditions favouring upwelling and productivity (Huthnance et al., 2002; Borges et al., 2003;

Santos et al., 2004). The correlation between NAO and recruitment of *Microchirus* spp. and *S. solea* was previously observed in the Portuguese coast (Gamito et al., 2015). It was related with *S. solea* growth, due to the possible relation with productivity and food availability (phytoplankton and zooplankton) (Henderson and Seaby, 2005). Also, cold winters could favour the spawning processes of some flatfish species, as previously reported for *P. platessa* and *S. solea* (e.g., Rijnsdorp et al., 1992; van der Veer and Witte, 1999), and may also reduce eggs and larval mortality due to lower predator activity or to the match between larval production and their food (Cushing, 1972; Leggett and Deblois, 1994).

Upwelling (UPW) events usually occur along the Portuguese coast during spring and summer (Leitão et al., 2019; Table 2) when equatorward winds occur for consecutive days (Relvas et al., 2007; Vinagre et al., 2007). During upwelling events, the surface water is pushed offshore being replaced by deep, cool, and nutrient enriched waters favouring biological production. Generally, drifting larvae is hampered by these oceanographic events, threatening the chance of flatfish early stages to reach the nursery grounds close to the coast (2008; Vinagre et al., 2007). Thus, upwelling events can have opposite effects on fish larvae and juveniles. *Pleuronectes platessa* and *D. cuneata* were negatively correlated with upwelling in summer (Southwest) and spring (South), respectively. These seasons corresponded to the higher upwelling index registered in each region (Table 2), increasing the offshore advection of larvae (Guisande et al., 2001; Landaeta and Castro, 2002) and affecting the recruitment success. Contrarily, *Microchirus* spp. LPUE was found to be positively related with summer (IXaCN) and autumn (IXaS) upwelling, as well as *S. solea* with spring and summer upwelling (IXaCS). Although upwelling provokes the offshore advection of the surface water layer, several mechanisms can retain larvae in the nursery grounds near the coast (Gibson, 1994; Moita et al., 2003; Vinagre et al., 2007). It is the case of upwelling shadow zones that may play an important role in the retention of flatfish early stages preventing their offshore advection (Moita et al., 2003; Mason et al., 2005).

Coastal drift currents are affected by wind strength and direction (Moita, 1986; Melo, 1989; Vila-Concejo et al., 2003) influencing the transport and/or the retention of eggs and larvae along the coastline through changes in hydrodynamics (Jager, 2001; Borges et al., 2007; Vinagre et al., 2009; Lacroix et al., 2018), and food supply (Fernández et al., 1993; Santos et al., 2012). Wind magnitude also influences the dispersal of the river plumes into the sea, helping larvae to successfully reach estuarine nursery areas (Tanaka, 1985; Vinagre et al., 2007) by using the chemical cues released by the river discharge and spread by the force of the wind (e.g., Gibson, 1997; Arvelund and Takemura, 2006). Thus, as reported by several authors, the recruitment of flatfish species is related to prevailing wind conditions (e.g., Werner et al., 1997; Nielsen et al., 1998; van der Veer et al., 2000). In the present study, the increase of wind

strength negatively affected the LPUE of *P. platessa* and *S. solea* during summer (IXaS) and autumn (IXaCN) probably by promoting the larval dispersion from the nursery areas in a way that larval mortality was also enhanced (Vinagre et al., 2009; Lacroix et al., 2018) and by increasing turbidity in shallow waters (Gibson, 1994; Laffargue et al., 2007). On the other hand, *S. lascaris* larvae have been also found to benefit from the increase of river plumes (Vinagre et al., 2007) and retention in coastal areas (Vinagre et al., 2009) caused by the increase of summer wind magnitude (Southwest). The LPUE of *Microchirus* spp. was negatively related to wind magnitude during winter (IXaCS) and spring (IXaCN), and positively during summer (IXaS), revealing the importance of regionality and seasonality for recruitment.

Together with wind magnitude, the variability of the wind direction also played an important role on larval transport (Lacroix et al., 2018). In fact, in our study, *D. cuneata* and *Microchirus* spp. LPUE were positively related with Westerly winds (UWIND) in Southern coast (IXaS) during spring and autumn, respectively, meaning that recruitment was higher when the wind blew from the west. These winds are responsible for upwelling conditions in the Southern coast of Portugal (Fiúza, 1983; Baptista et al., 2016), but with less intensity than on the Western coast (IXaCN and IXaCS) due to the oceanographic characteristics. Therefore, it is more likely that these winds might influence the surface coastal drift current retaining eggs and larvae in the coastal areas and preventing them to run away to the open sea. On the contrary, negative relationships were found in *P. platessa* (IXaCS and IXaS), *S. lascaris* (IXaS), *D. cuneata* and *S. solea* (IXaCS). In these cases, recruitment enhanced when the winds blow from the East, corresponding to downwelling conditions in Southern coast of Portugal (Fiúza, 1983; Baptista et al., 2016). Therefore, winds blowing from the east may enhance the retention of flatfish eggs and larvae in coastal areas (Moita, 1986; Vinagre et al., 2009; Baptista et al., 2016). Furthermore, specific characteristics, such as temperature, salinity, and nutrients of the water transported by the Easterly winds (e.g., from the Mediterranean Sea in Southern regions) might have a positive effect on the survivorship of flatfish larvae, improving the recruitment success and consequently, the landings on the following years. In relation to the Northerly wind component (VWIND), winds from South increased the recruitment of *Microchirus* spp. during winter in Southern region. These winds seem to transport and retain larvae in coastal nursery areas (Vinagre et al., 2009). Contrarily, in Western coast, winds from North (negative values) improved the recruitment of *D. cuneata* during spring (IXaCN and IXaCS), and *S. lascaris* and *S. solea* during summer (IXaCS). In Western coast of Portugal, these winds are responsible for upwelling events (Relvas et al., 2007), increasing biological production (Vinagre et al., 2007) and recruitment of flatfish species.

Variability in river discharges has important consequences for recruitment of fish species, leading to changes in salinity,

organic matter input, food abundance and currents (Vinagre et al., 2007). *Pleuronectes platessa* and *Microchirus* spp. LPUE were positively related with spring river discharge, and *D. cuneata* with winter river discharge, that matches with the seasons where these species spawn and larval development occurs (Andrade, 1990; Santos and Lino, 2010; Félix et al., 2011; Table 1). *Microchirus* spp. LPUE also were positively related to river discharges during autumn, corresponding to a post-metamorphosis and juvenile phase. In fact, larvae living on the coast take advantage of the increase of food abundance driven by the inputs of organic matter from the river discharges (Cushing, 1996; Lloret et al., 2001). The positive relationship between river discharge and the landings of marine fish in Portugal has been recently described using multiple DFA models (Bueno-Pardo et al., 2020), resulting to be especially relevant in the South region during winter. Larvae of various organisms can follow cues released by river plumes such as odour, temperature, salinity and turbidity (e.g., Gibson, 1997; Arvelund and Takemura, 2006) which could orient them to the coastal nursery areas where food resources and refuge are available (Tanaka, 1985; Tamburri et al., 1996). Thus, high river discharge increases the river plumes to a wider area, increasing the possibility of being detected by flatfish larvae spawned on the coast (Vinagre et al., 2007). On the other hand, river discharges can also have negative impacts on flatfish LPUE, such as *S. solea* during spring at the Northwestern region. Despite being described that *S. solea* larvae benefit from the increase of river discharges to ingress into Portuguese estuaries (2010; Vinagre et al., 2007; Martinho et al., 2009), Ramos et al. (2009) reported that this species is not able to migrate into Lima estuary (Northwest) due to the increase of river flow enhancing turbidity. Turbidity, an indirect consequence of the river runoff, can affect the passive tidal migration of flatfish larvae (Ramos et al., 2009). Thus, years with high river discharges during spring, when larvae ingress into nursery habitats, could compromise their estuarine migration, and consequently the recruitment of *S. solea*.

Juveniles to young-adults – age-groups I and II

After spending the first months (at least six months) in coastal nursery grounds to complete their development, many juveniles of flatfish species migrate into deeper coastal waters (Dorel et al., 1991; Gibson, 1997), where they will grow and reach sexual maturity, returning or not to inshore habitats during their life cycle (Gibson, 1997). Thus, as shown by present results, the effects of environmental variability on age-groups I and II of flatfish species seems to be related with growth and maturation. In fact, Fuiman (1997) described the juvenile phase as a period dominated by growth, and the adulthood a period dominated by reproduction. As previously reported, the SST could affect metabolic and physiological rates (Brander et al., 2003) and food availability (Cushing, 1990) which in

turn affect growth of flatfish juveniles (Yamashita et al., 2001; Teal et al., 2008), since the energy expended for growth will be diverted to face adverse temperatures (Vinagre et al., 2008). In fact, despite flatfishes are quite sedentary, they can perform small migrations to avoid unfavourable conditions, like temperature (Marchand, 1991). Temperature could also affect the duration of maturation of flatfish species by its influence on gonadal maturation (Lange and Greve, 1997). Beyond the thermal conditions, hydrographic conditions could also have an impact on distribution and abundance of juvenile and young-adult flatfishes (Yeung and Yang, 2017), such as coastal currents affected by wind strength and direction. Yet, juveniles and adults living on the coast could also take advantage of the increase of food abundance driven by the inputs of organic matter from the river discharges (Cushing, 1996; Lloret et al., 2001).

It should be noted that in most cases where the environmental effect was repeated from one year to the next, this effect occurred in the following year, that is, if the effect occurred in the age-group 0, it was repeated in the age-group I and not in the age-group II. In other words, it appears that the effects of environmental variability over the life cycle of flatfish species have a gradual transition over the life cycle phases. Also, although there are some effects of environmental variability during the juvenile-young-adults' phases (age-groups I and II), these effects are stronger during the larval-juvenile phase (age-group 0), as previously described. For example, it was reported that the year-class abundance is determined by environmental factors experienced early in life in many temperate flatfish species, like plaice (*P. platessa*) (e.g., van der Veer et al., 1990), sole (*S. solea*) (Rijnsdorp et al., 1992; Henderson and Seaby, 1994), flounder (*Platichthys flesus*) (van der Veer et al., 1991; Henderson and Seaby, 1994), and dad (*Limanda limanda*) (Henderson and Seaby, 1994). Thus, the year-class strength of flatfish species is fixed by the end of the first year (Henderson and Seaby, 1994).

Conclusion

In conclusion, LPUE of *P. platessa* age-group 0 (recruitment) is favored by an increase in NAO index and river discharge, and a decrease in SST, UPW, WMag and UWind, for age-group I by an increase in river discharge, and a decrease in UPW, WMag, UWind and VWind, and for age-group II by an increase in UPW and WMag, and a decrease in SST and VWind; LPUE for *D. cuneata* age-group 0 is enhanced by an increase in SST and river discharge, and a decrease in UPW and VWind, and for age-group I by an increase in SST and WMag, and a decrease in VWind and river discharge; LPUE of *Microchirus* spp. age-group 0 is favored by an increase in SST, NAO index, UPW, UWind, VWind and river discharge, and a decrease in WMag, for age-group I by an increase in UPW, WMag and river discharge, and a decrease in SST, and for age-group II by an increase in UPW, WMag and UWind, and a decrease in VWind and river discharge; LPUE for *S. lascaris* age-

group 0 is enhanced by an increase in NAO index and WMag, and a decrease in UWind and VWind, for age-group I by an increase in NAO, UWind and VWind, and a decrease in WMag, and for age-group II by a decrease in SST, WMag and river discharge; LPUE for *S. solea* age-group 0 is enhanced by an increase in UPW, and a decrease in SST, WMag, UWind, VWind and river discharge, for age-group I by an increase in NAO, WMag and UWind, and a decrease in SST, and for age-group II by an increase in WMag, and a decrease in SST, VWind and river discharge. From the point of view of management, we have evidenced that an increase in fishing effort is negative for all the species and age-groups evaluated except for *P. platessa*.

In this multi-species study, it has been found that relationships between explanatory variables (environmental and fishing) and response variables (LPUE) vary among species, regions, and life cycle phase. Intra-specific biological differences within the Pleuronectiformes order and species ecological distribution range result in different patterns among flatfishes regarding environmental-fisheries associations. Furthermore, the heterogenic geography of the Portuguese coast and the different climatic and oceanographic conditions that occur along it, could explain the variability found between regions. Environmental variables tend to function in reactional cascades frequently depending on the pattern of another one (e.g., changes in sea surface temperature might be in part the result of upwelling events enhanced by an increase in the wind magnitude in a certain region). Thus, it can be observed that significant results are usually linked to this "domino effect" between environmental variables. Flatfish early (age-group 0) phases are enhanced when they can successfully reach the nursery grounds. Consequently, the retention or transport of eggs and larvae toward the coast is an important factor being reflected in the LPUE of subsequent years. Food availability is also an essential aspect influencing larval recruitment. Food resources can increase in response to several environmental conditions such as upwelling, sea surface temperature or winds. Therefore, matching the events of high productivity with the recruitment of flatfish early stages could make the difference between a good fishing year and a bad one (high LPUE vs low LPUE). On the other hand, during juveniles to young-adult phase (age-groups I and II), the increase of LPUE in the next years seems to be related to environmental variables that affect growth and maturation. Thus, SST – a variable consistently identified in this study across regions and species as fundamental for understanding LPUE – plays a fundamental role in the maturation processes of the organisms, determining the time that the species spends in the plankton before reaching the nursery areas to conduct metamorphoses into the next life phase and influencing the growth and maturation of juveniles and young-adults.

LPUE are key for fisheries management as it is directly related to the revenues obtained by fishers. This parameter has a different meaning than the total landings or captures, with which LPUE are not necessarily related. Managers of marine fisheries should consider both perspectives and understand the links between them, the environmental variables and fishing effort for a

correct decision making. In this work we have identified the main potential drivers of LPUE of flatfish in Portugal, providing a better understanding of their effects and the different age-groups of the species. The strong importance of fishing effort determining LPUE, and the region-species specific influence of the environmental variables, in a scenario of climate change, makes necessary to adopt recurrent monitoring of the stocks and environmental variables to manage fishing effort in the most sustainable way.

Data availability statement

Publicly available datasets were analyzed in this study. This data can be found here: this data was requested to Portuguese STAT fisheries office and can only be used for scientific proposes.

Ethics statement

Ethical review and approval was not required for the animal study because N/A - this is fisheries time series statistical data.

Author contributions

Conceptualization – VB and FL; Investigation – VB and IP; Methodology – VB and IP; Resources – MT and FL; Supervision – FL; Writing, original draft – VB, IP, and JB-P; Writing, review & editing – VB, IP, JB-P, MT, and FL. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2022.844158/full#supplementary-material>

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