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# Anchovy on the rise: Investigating environmental drivers of recruitment strength in the northern Canary Current

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ABSTRACT: Since the mid-2010s, the abundance and recruitment of the European anchovy *Engraulis encrasicolus* has significantly increased off Western Iberia, leading to a 5-fold increase in anchovy catches. The potential environmental drivers impacting recruitment variability in anchovy in Atlantic Northwestern Iberian waters (NW Iberia) are unknown. Using data spanning 1999–2021, we identified regional changes in biological and physical factors most likely responsible for the persistent increased productivity of anchovy. Anchovy recruitment was strongest during periods with weak downwelling events (−500 to 0 $m^3\ s^{-1}\ km^{-1}$), lower salinity (<35), and temperature between 15 and 17°C from April through June, months corresponding with annual peak spawning. Positive Winter North Atlantic Oscillation ($NAO_W$) was also associated with years with strong anchovy recruitment. It is likely that local oceanographic features such as the Iberian Poleward Current and the Western Iberia Buoyant Plume contribute to a higher onshore retention of anchovy larvae, promoting life cycle closure and higher survival. The average lower salinity levels observed during spawning seasons since 2009 support this hypothesis. Moreover, random forest models suggested that years with relatively strong anchovy recruitment tended to be those with low abundance of European sardine *Sardina pilchardus*, suggesting that intra-guild processes such as foraging competition and egg predation are also important in establishing recruitment potential. We highlight future avenues of research needed to gain a mechanistic understanding of recruitment drivers of anchovy in this region to provide robust, science-based advice to managers and improve projections of the potential impacts of climate change.

KEY WORDS: *Engraulis encrasicolus* · NW Iberia · Small pelagic fish · Remote sensing · *Sardina pilchardus*

## 1. INTRODUCTION

Small pelagic fish (SPF) dominate marine ecosystems off eastern boundary upwelling systems (EBUS) (Cury et al. 2000). In these regions, SPF occupy a key position in the trophic web, establishing a crucial link between plankton and the top predators (Cury et al. 2000). Due to their high biomass, they are also crucial for regional fisheries, making up the majority of global marine capture production (FAO 2022). However,

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despite their key role, SPF biomass and catches can be unpredictable. SPF species typically exhibit relatively short life cycles, with fast development and growth (Peck et al. 2021). This makes them highly susceptible to environmental shifts, which frequently leads to rapid changes in biomass and recruitment (boom-and-bust dynamics). While boom-and-bust cycles have been observed for almost all major SPF species, such as Peruvian anchoveta *Engraulis ringens*, Pacific sardine *Sardinops sagax*, northern anchovy *E. mordax*, Japanese anchovy *E. japonicus*, European anchovy *E. encrasicolus*, and the European sardine *Sardina pilchardus* (Alheit & Hagen 1997, Schwartzlose et al. 1999, Cahuin et al. 2009, MacCall et al. 2016, van der Sleen et al. 2018, Thompson et al. 2019, Li et al. 2022), the key environmental drivers and how variability in those drivers cause recruitment fluctuations are still unclear (Peck et al. 2021).

Off Western Iberia, the European sardine has been the most important pelagic species, in both abundance and socioeconomical value, for as long as fish stocks have been monitored in this region, beginning in the early 20th century (Mendes & Borges 2006, Monteiro 2017). However, a sharp decline in sardine abundance and recruitment occurred in the mid-2000s, strongly associated with increasing temperatures during the winter (Malta et al. 2016, Garrido et al. 2017, Szalaj et al. 2021, Ferreira et al. 2023). Concurrently, the abundance of other pelagic species with lower coastal distributions has increased (García-Seoane et al. 2019). For instance, European anchovy typically occurred in very low abundance but has become a highly important fishery along the NW Portuguese coast, particularly in the last decade (ICES 2022a,b). This Iberian anchovy stock extends from the NW Iberian coast to the Gulf of Cadiz, comprising ICES subdivisions 9aN, 9aCN, 9aCS, 9aS-alg, and 9aS-cad (ICES 2018, 2022b). This stock was divided into 2 components (western, including sub-divisions 9aN, 9aCN and 9aCS, and southern, including subdivisions 9aS) due to differences in the fisheries and population dynamics (ICES 2018). In contrast to the western component, the southern component in the Gulf of Cadiz is a persistent population that has shown no clear trend in its stock size, although fluctuations in recruitment success have been linked to environmental variability, such as winds and ocean circulation (Ruiz et al. 2006).

The spawning of European anchovy typically occurs during the warmer months, making it a spring—summer spawner (Peck et al. 2013). In the western component, the spawning season of anchovy spans from April to July (ICES 2022b). Anchovy can also exhibit an important relationship with lagoons and estuaries in early life stages, using them as nursery areas (e.g. Ribeiro et al. 1996, de Carvalho-Souza et al. 2019, Huret et al. 2020). For instance, in NW Portugal, the main area of distribution of the western component of the Iberian stock, anchovy larvae and recruits are frequently found inside, or in the vicinity of, estuaries (e.g. Ré 1996, Ribeiro et al. 1996, Marques et al. 2006, Ramos et al. 2006, França et al. 2009). Diet-wise, anchovy are planktivorous throughout their life cycle and their adult diet composition off NW Iberia is similar to other coastal pelagic species such as chub mackerel and sardine (Garrido et al. 2015, Fonseca et al. 2022). One of the most important prey for sardines off NW Iberia are fish eggs, and a large proportion of anchovy eggs have been found in the stomachs of juvenile and adult sardines (Fonseca et al. 2022). Sardine, therefore, can be an important factor impacting early life stage survival of anchovy and the ability of anchovy to be highly productive in this habitat.

Despite being the most important SPF in nearby regions such as the Gulf of Cadiz or the Bay of Biscay (Uriarte et al. 1996, Ruiz et al. 2017), anchovy abundance and landings off the western coast of Portugal have been historically low (ICES 2022b). However, this has changed from 2016 onwards, with anchovy landings representing up to 9 to 14% of all coastal pelagic fish landings in mainland Portugal (INE 2023). For comparison, anchovy catches accounted for less than 2% from 2011 to 2015 (INE 2023). Moreover, due to the low historical productivity of anchovy in this region, there is still much to understand regarding the environmental parameters that modulate anchovy recruitment. Biological recruitment (i.e. when fish reach first reproduction) depends on the survival of early life stages, which is at its peak when optimal environmental conditions are met (Waldron et al. 1997). In upwelling regions, several studies have reported that SPF biomass follows a dome-shaped relationship with the intensity of coastal upwelling as described in the 'optimal environmental window' hypothesis (Cury & Roy 1989, Roy et al. 1992, Waldron et al. 1997). For the European sardine off NW Iberia, optimal environmental conditions have been linked to relatively low temperatures, shallow mixed layer depths and mild upwelling or downwelling (Ferreira et al. 2023). However, since the current 'boom' of anchovy in this region is so recent, there is a severe lack of knowledge regarding the optimal conditions that may have prompted it.

The main goal of this study was to understand the drivers behind the recent increase ('boom') in the adult biomass and recruitment strength of European anchovy in Atlantic Iberian waters. The biological and physical drivers of anchovy recruitment variability were analysed by comparing estimates of anchovy abundance and recruitment strength to time-series of physical (e.g. temperature, salinity, mixed layer depth, upwelling index) and biological (e.g. chlorophyll *a*, primary production, sardine abundance, sardine recruitment strength) factors over a period of 23 yr (1999–2021).

## 2. DATA AND METHODS

### 2.1. Study site

Western Iberia is located in the northernmost section of the Canary Current Upwelling System. Although coastal upwelling events occur throughout the year, they are typically stronger between April and October, with a peak during the summer (e.g. Relvas et al. 2007, Favareto et al. 2023). The NW sector of the Western Iberian waters, spanning from the Galician Rías Baixas to central Portugal, is the main upwelling area (Fig. 1). This region is also characterized by the presence of the Iberian Poleward Current (IPC), a surface-intensified northward flowing current located over the slope or shelf that carries warmer and saltier waters from the south and stretches towards the northwestern coast of Spain (Peliz et al. 2003, Teles-Machado et al. 2015). The Western Iberian Buoyant Plume (WIBP) is another important feature of this system, although it is more frequently observed during the winter (Peliz et al. 2002, 2005). The WIBP is a persistent buoyant plume generated by freshwater inputs from rivers off Western Iberia, particularly the Minho and Douro rivers (Peliz et al. 2002, 2005). This study region (hereafter called NW Iberia) ranges from 39.6° to 41.1° N and includes mainly shelf waters. The area roughly coincides with the recruitment hotspots of the European sardine and European anchovy (e.g. ICES 2022b).

### 2.2. Anchovy and sardine data

Yearly data of spring acoustic surveys conducted during 1998–2021 to estimate the abundance of anchovy and sardine along the western coast of Portugal (ICES subarea 9aCN) were used. Monitoring was done along transects perpendicular to the coast within the continental shelf, each separated by 8 nautical miles. Echo-integration was performed from 3 m below the transducer to 20 cm above the seabed. After acoustic detection, pelagic fish trawls were conducted to determine the age and length composition of schools, allowing for the separation of the acoustic measurements into species and length classes. The overall abundance of anchovy and sardine was spatially integrated by taking into account areas where schools with similar length composition were observed (for further details, see Massé et al. 2018). The spawning stock abundance (SSA) was calculated as the total abundance of individuals aged +1, and yearly recruitment was defined as the estimated abundance of recruits (age 1) in the following year (i.e. recruitment of year $Y$ = age 1 individuals estimated for the year $Y$+1). Note that anchovy recruitment in this region occurs rapidly, specifically within the same year the eggs were spawned. For anchovy, while adult abundance was estimated from 1998 to 2021, estimations of recruitment strength were only available from 2007 onwards. However, a near 1:1 correlation existed between anchovy recruitment in year $Y$ and the SSA in year $Y$+1 (N = 13; R = 0.97; data not shown). Therefore, we used the SSA of year $Y$+1 as a proxy of anchovy recruitment in this study (hereafter referred to as the recruitment index).

### 2.3. Environmental data

Satellite and modelled atmospheric and oceanographic data for the NW Iberia region (orange box in Fig. 1) were acquired for the same period as the anchovy dataset (1998–2021). The following environmental parameters were retrieved: (1) chlorophyll *a* (Chl *a*; mg m$^{-3}$); (2) net primary production (NPP; mgC m$^{-2}$ d$^{-1}$); (3) sea surface temperature (SST; °C); (4) sea surface salinity (SSS; unitless); (5) mixed layer depth (MLD; m); (6) upwelling index (UI; m$^3$ s$^{-1}$ km$^{-1}$); (7) the northward ($V$) and eastward ($U$) components of seawater velocity (cm s$^{-1}$); (8) precipitation (mm d$^{-1}$); and (9) the North Atlantic Oscillation (NAO) index (see Table 1 for more details).

For each year of the dataset, monthly means of each environmental parameter assessed were calculated for the months corresponding to the spawning season of anchovy off NW Iberia (April, May, June, July). A full spawning season mean (April to July) was also calculated. Specifically for the NAO, the mean winter NAO preceding the spawning season was also calculated (December to March).

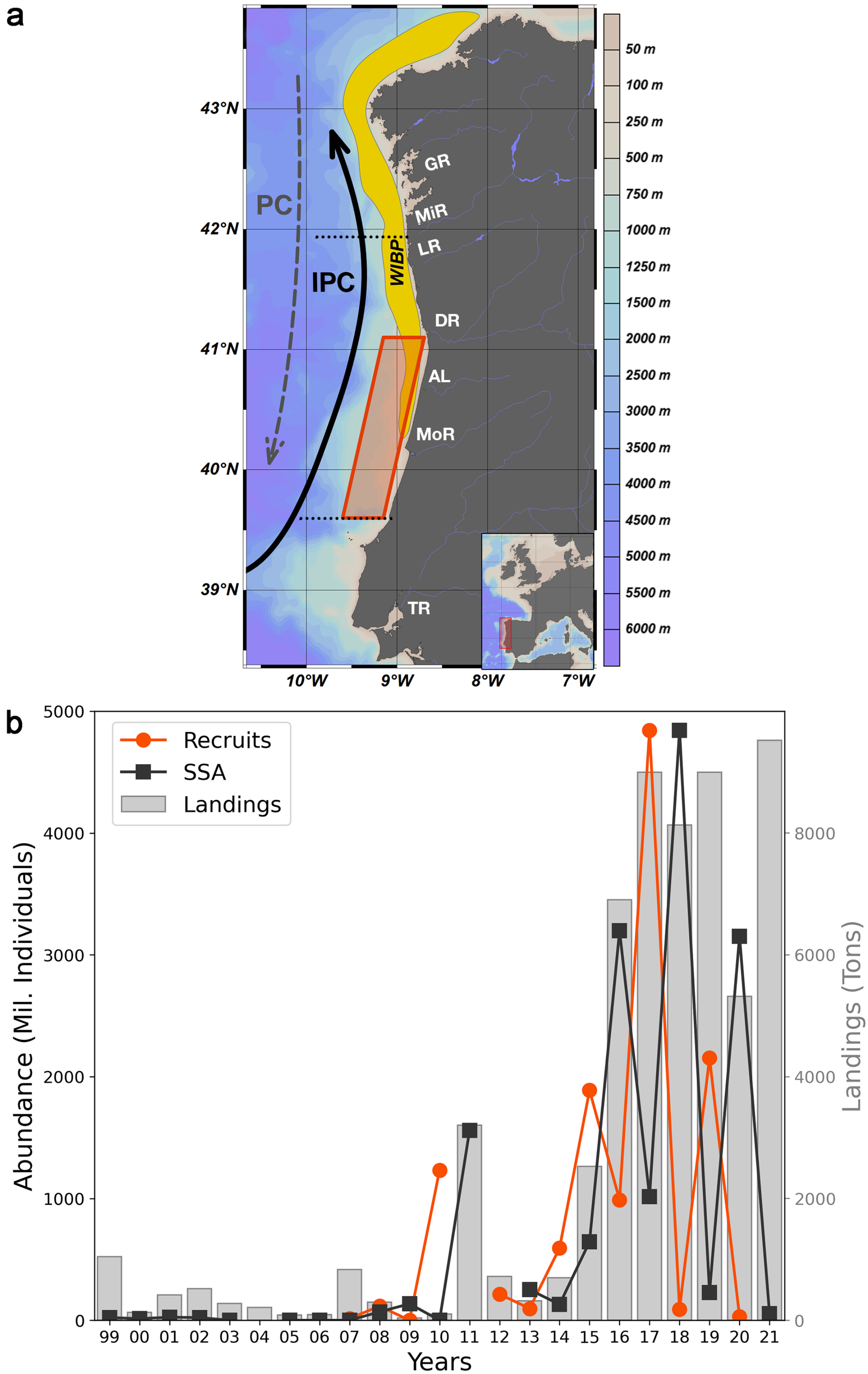


Fig. 1. (a) Setting of Northwestern Iberia (NW Iberia; orange region) within Western Iberia, and (b) yearly estimates of European anchovy recruit abundance and spawning stock abundance (SSA) (Mil.: million), and total European anchovy landings in western Portugal during the period 1999–2021. The main oceanographical features and coastal freshwater systems in the region are also indicated in (a). The dotted lines in (a) indicate the limits of the domain of the acoustic surveys used to estimate European anchovy recruitment strength and SSA. PC: Portugal Current; IPC: Iberian Poleward Current; WIBP: Western Iberia Buoyant Plume; TR: Tagus River; MoR: Mondego River; AL: Aveiro Lagoon; DR: Douro River; LR: Lima River; MiR: Minho River; GR: Galician Rias Baixas

Table 1. Physical and biological variables used to examine environmental controls on European anchovy recruitment that were acquired from satellite and model products. Full names of each variable can be found in Section 2.3. na: not applicable

| Variable | Units | Product | Spatial resolution | Reference |
|---|---|---|---|---|
| Chl *a* | mg m$^{-3}$ | ESA-CCI 6.0 | 4 km | 1, 2 |
| NPP | mgC m$^{-2}$ d$^{-1}$ | NPP-PRIMUS (S05) | 1 km | 3, 4 |
| SST | °C | OSTIA-L4 | 5 km | 5 |
| SSS | Unitless | IBI_MULTIYEAR_PHY_005_002 | ~8 km | 6 |
| MLD | m | IBI_MULTIYEAR_PHY_005_002 | ~8 km | 6 |
| UI (winds)[a] | m s$^{-1}$ | ERA5 Reanalysis | ~25 km | 7 |
| *V* | cm s$^{-1}$ | IBI_MULTIYEAR_PHY_005_002 | ~8 km | 6 |
| *U* | cm s$^{-1}$ | IBI_MULTIYEAR_PHY_005_002 | ~8 km | 6 |
| Precipitation | mm d$^{-1}$ | ERA5 Reanalysis | ~25 km | 7 |
| NAO, $NAO_W$ | Unitless | NOAA NCEP CPC | na | 8 |

[a]The meridional and zonal components of wind were acquired to calculate UI
[1]Sathyendranath et al. (2019)
[2]Ocean Colour Climate Change Initiative dataset, Version 6.0, European Space Agency, www.esa-oceancolour-cci.org/
[3]PRIMUS PP Portal, https://primus.eofrom.space/
[4]Smyth et al. (2005)
[5]Good et al. (2020)
[6]CMEMS Atlantic-Iberian Biscay Irish- Ocean Physics Reanalysis, Version 5.0, doi:10.48670/moi-00028
[7]Hersbach et al. (2023)
[8]NOAA Daily NAO Index since January 1950, www.cpc.ncep.noaa.gov/

## 2.4. Data analysis

### 2.4.1. Environmental shift analysis

In order to visualize the interannual variability of the environmental conditions in NW Iberia between 1998 and 2021, Hovmöller-type diagrams were used (Hovmöller 1949) to depict how NPP, SST, sea surface salinity (SSS), MLD, precipitation, and UI changed with time and latitude. For each environmental variable, a mean was calculated for the period of the spawning season (April to July). A latitudinal step of 0.1° was used for NPP, SST, SSS, and MLD, while a step of 0.25° was used for precipitation and UI (due to the lower resolution of these products). As an example, for every 0.1° between 39.5° and 41.25° N, the spawning season mean of NPP was calculated for each year.

Subsequently, to understand if the sudden rise in anchovy abundance might be related to a shift in environmental conditions, the full environmental dataset was separated into two 10 yr sub-datasets containing data from 1999–2009 (prior to the increase in anchovy) and 2010–2020 (after the increase in anchovy). Means were calculated for each month (April to July) and for the full spawning season (April to July) for all parameters. Wilcoxon rank sum tests (40 tests in total, 5 per variable) were then used to test the existence of statistically significant differences between the 2 periods. A sequential Holm-Šidàk correction (Abdi 2010) was used to limit the occurrence of Type 1 errors due to multiple testing.

### 2.4.2. Optimal environmental windows analysis

Optimal environmental window analysis is an explorative analysis which seeks to identify the favourable environmental conditions for enhanced anchovy recruitment, as well as determine when these conditions are more frequent during the spawning season. The analysis is an extension of the optimal environmental window theory proposed for SPF in coastal upwelling regions (Cury & Roy 1989). Following the 'optimal environmental window' theory, the rationale behind this analysis is that the early weeks of the anchovy life cycle are particularly susceptible to unfavourable environmental conditions. Therefore, a successful recruitment year is partially dependent on the existence of favourable environmental conditions during the anchovy spawning season. Here, we followed a similar methodology to that used for the European sardine by Ferreira et al. (2023). The following variables were chosen: NPP, SST, SSS, UI, and precipitation. Unlike Ferreira et al. (2023), NPP (as a measure of the energy required to support anchovy larvae) and SSS (as a proxy of the WIBP and riverine outflow) were also used.

First, the spawning season period (April to July) was divided into 8 d (weekly) periods (sixteen 8 d weeks per spawning season). For each 8 d period, means were calculated for NPP, SST, SSS, UI, and precipitation. Second, classes were created for each variable (Table 2). For instance, 4 classes were defined for SST: (1) 13 to 15°C; (2) 15 to 17°C; (3) 17 to 19°C; (4) >19°C. The classes were set according to the variability observed for each variable (Table S1 in the Supplement at www.int-res.com/articles/suppl/m741p315_supp.pdf). A control class, for which any value of a given variable was valid (e.g. NPP > 0 mgC $m^{-2}$ $d^{-1}$), was also defined. Third, all possible combinations of the classes (7000) were created.

For each spawning season, we counted the number of 8 d periods matching each combination. As an example, only 1 week within the April to July 2000 spawning season complied with all of the following classes: mean NPP < 800 mgC $m^{-2}$ $d^{-1}$, mean SST between 15 and 17°C, mean SSS between 35 and 35.5, mean UI between −500 and 0 $m^3$ $s^{-1}$ $km^{-1}$, and total precipitation higher than 15 mm. To assess the relationship between the number of weeks complying with each combination and yearly anchovy recruitment, Spearman's correlations were used. Only statistically significant relationships were kept ($p < 0.05$).

#### 2.4.3. Random forest models

Random forest models (Breiman 2001) were used as a tool to disentangle the drivers of anchovy recruitment throughout the dataset period. Random forests are a machine learning ensemble method, structured as the aggregation of multiple regression trees. The response variable used for the random forest model was the anchovy recruitment index. The following variables were considered as predictors: sardine spawning abundance, mean NPP during April to July, mean SST during April to July, mean SSS during April to July, mean MLD during April to July, mean UI during April to July, mean *U* and *V* during April to July, total precipitation (rainfall) during April to July, mean NAO during April to July, and mean winter NAO (December to March).

All correlated variables (R > 0.7) were removed prior to running the model (Dormann et al. 2013). The scikit-learn module (Pedregosa et al. 2011) was used to conduct the random forest model. The following hyperparameters were used: 'n_estimators' = 500, 'min_samples_leaf' = 1, 'max_depth' = 50, 'max_features' = 'sqrt', 'min_samples_split' = 2, criterion = 'squared_error'. The most important predictors behind anchovy recruitment were identified by using permutation importance, which uses multiple permutations (N = 500) to assess how randomly shuffling a given predictor's value affects the model performance (based on $R^2$) (Breiman 2001). All analyses in this study were run in Python 3.8.8.

## 3. RESULTS

### 3.1. Anchovy recruitment and SSA

The annual abundance of anchovy recruits (N = 13; only available since 2007) and the spawning stock abundance (N = 22; R = 0.54; p = 0.012) increased from 1999 to 2021 (Fig. 1). The increase in recruitment and SSA was reflected in the total landings of anchovy in Portugal (N = 23; R = 0.76; $p < 0.0001$; Fig. 1). From 2007 to 2021, the mean recruitment was ~945 million individuals, while the mean SSA was only slightly higher at ~1090 million individuals.

The first anchovy recruitment peak in NW Iberia was observed in 2010 (1231.86 million individuals), which coincided with an increase in anchovy landings in the following year (2011). The highest recruitment occurred in 2017, with ~4845 million individuals, 4-fold greater than the first peak in 2010. After 2016, even with constant fluctuations in anchovy recruitment and SSA, landings were consistently high (mean 8061 t).

Table 2. Environmental classes evaluated in the optimal windows analysis for European anchovy recruitment in NW Portugal. For each variable, the tested intervals are presented. The C (Control) class includes any value of a given variable (e.g. NPP > 0 mgC $m^{-2}$ $d^{-1}$). NPP: net primary production; SST: sea surface temperature; SSS: sea surface salinity; UI: upwelling index; precipitation: total precipitation

| Variable | Assessed interval class | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| NPP (mgC $m^{-2}$ $d^{-1}$) | C | <800 | 800 to 1000 | 1000 to 1200 | >1200 | | | |
| SST (°C) | C | 13 to 15 | 15 to 17 | 17 to 19 | >19 | | | |
| SSS (unitless) | C | <34.5 | 34.5 to 35 | 35 to 35.5 | >35.5 | | | |
| UI ($m^3$ $s^{-1}$ $km^{-1}$) | C | −1000 to −500 | −500 to 0 | 0 to 500 | 500 to 1000 | >1000 | | |
| Precipitation (mm) | C | <2.5 | 2.5 to 5 | 5 to 7.5 | 7.5 to 10 | 10 to 12.5 | 12.5 to 15 | >15 |

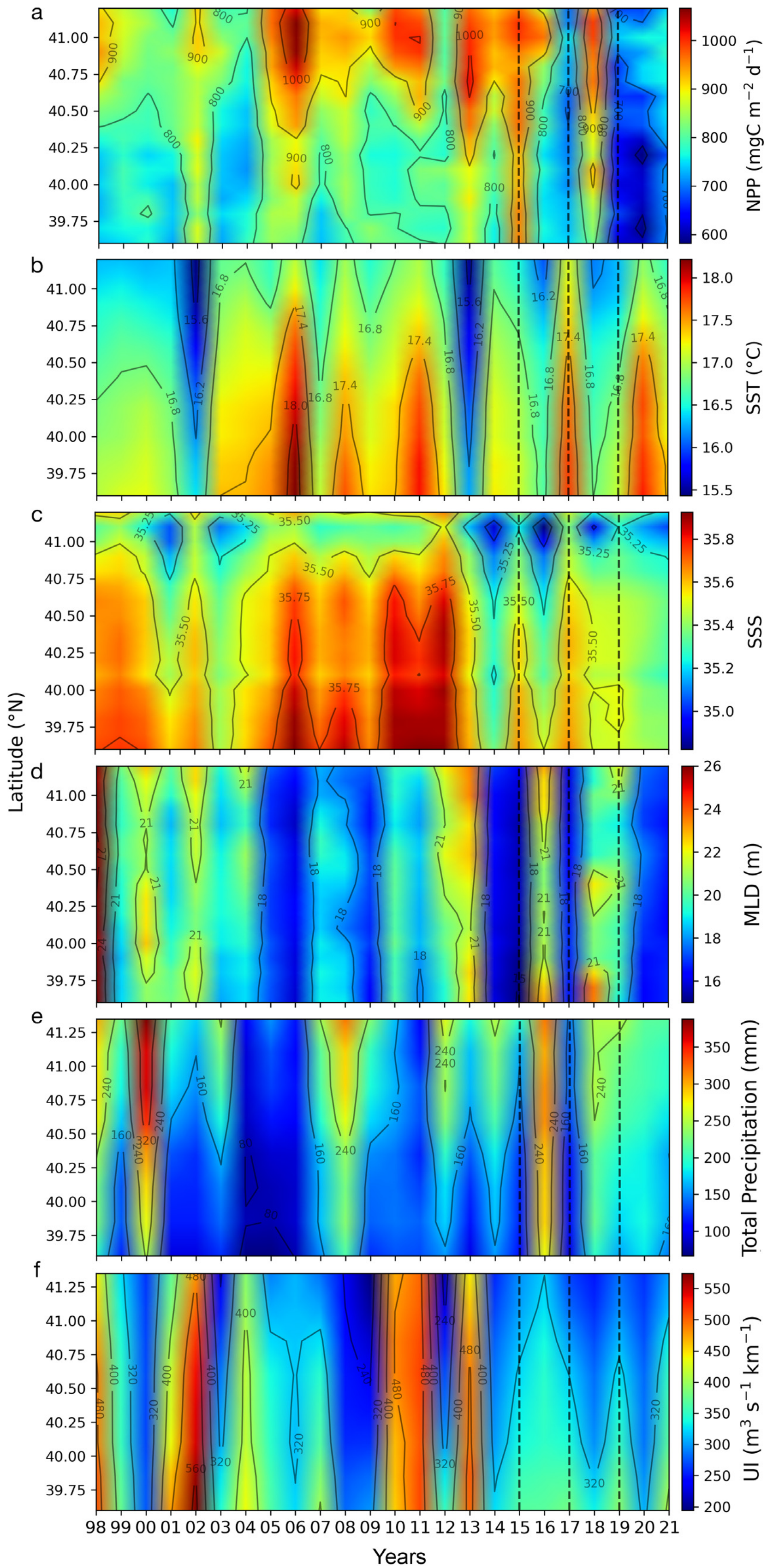


Fig. 2. Interannual variability of the mean (a) net primary production (NPP; mgC $m^{-2}$ $d^{-1}$), (b) sea surface temperature (SST; °C), (c) sea surface salinity (SSS; unitless), (d) mixed layer depth (MLD; m), (e) total precipitation (mm), and (f) upwelling index (UI; $m^3$ $s^{-1}$ $km^{-1}$) during the spawning season (April to July) in NW Portugal. The 3 vertical dashed lines indicate the years with highest recorded European anchovy recruitment (2015, 2017, 2019)

## 3.2. Environmental conditions during the spawning season

Latitudinal and temporal differences existed in the environmental conditions within the study area (Figs. 2 & 3). The mean NPP ranged from 581.8 to 1066.9 mgC $m^{-2}$ $d^{-1}$, and NPP was typically higher at the highest latitudes (>40.5° N). While 2006, 2013, and 2015 were highly productive years, primary production was relatively low (<750 mgC $m^{-2}$ $d^{-1}$) in most spawning seasons after 2016. Mean SST ranged from 15.4 to 18.2°C and tended to be lower at higher latitudes. The years 2002 and 2013 were particularly cold, while 2006, 2011, 2017, and 2020 were relatively warm. A similar latitudinal pattern was observed for SSS. Lower salinities (<35.2) were frequently observed around 41° N, particularly after 2014; therefore, mean SSS throughout the entire study area was lower (~35.4) than in 2004 to 2013 (~35.6).

The mean MLD during the spawning season was typically very shallow and ranged from 16 to 26 m. Unlike MLD, the total precipitation during the spawning season (April to July) exhibited a large range, from 100 to 350 mm. Overall, precipitation was also typically higher in the highest latitudes. The years 2000, 2008, and 2016 had particularly high precipitation, while 2004 to 2006 and 2011 were noticeably drier. The mean UI was always positive, indicating that wind-induced upwelling was constant throughout the spawning season. Stronger upwelling occurred during 2010, 2011, and 2013 (UI > 450 $m^3$ $s^{-1}$ $km^{-1}$), but the UI was relatively low (<320 $m^3$ $s^{-1}$ $km^{-1}$) after 2014.

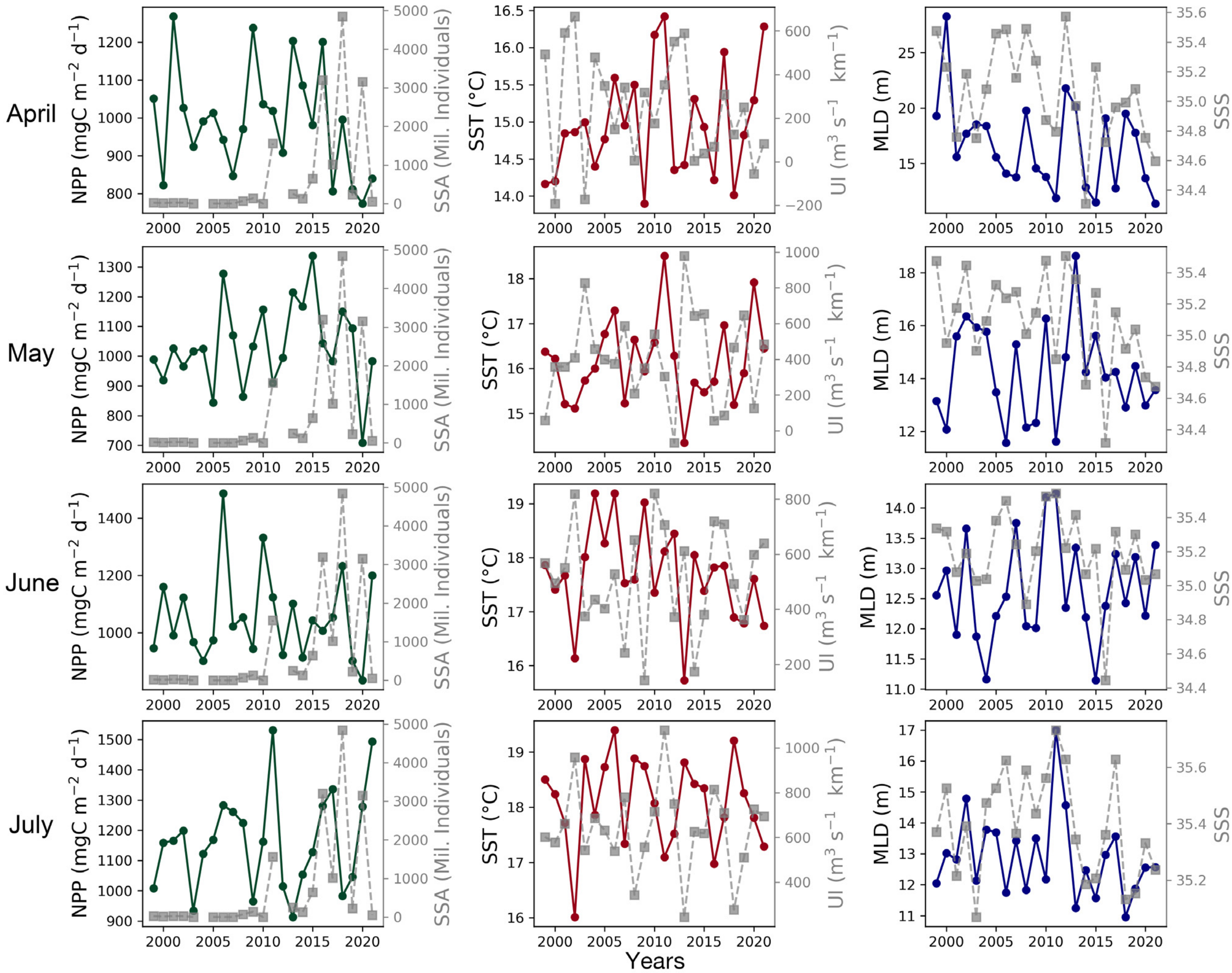


Fig. 3. Interannual variability of the mean net primary production (NPP; mgC $m^{-2}$ $d^{-1}$), sea surface temperature (SST; °C), upwelling index (UI; $m^3$ $s^{-1}$ $km^{-1}$), mixed layer depth (MLD; m), and sea surface salinity (SSS; unitless) for each month of the spawning season (April to July) in NW Portugal. The anchovy spawning stock abundance (SSA; million individuals) is also presented. Left panels: NPP (main axis; green) and SSA (secondary axis; grey). Middle panels: SST (main axis; red) and UI (secondary axis; grey). Right panels: MLD (main axis; blue) and SSS (secondary axis; grey). Note the different scales between months

Differences were also found when comparing the mean environmental conditions for each month (Fig. 3). NPP was typically higher during summer months (June and July). Moreover, interannual changes in summer SST were frequently associated with the UI. As a result, temperatures in June and July could increase (weak upwelling) or decrease (strong upwelling) by up to 3°C (Fig. 3).

### 3.3. Drivers of anchovy recruitment

The biological and environmental conditions were significantly different between the periods prior to (1999–2009) and after (2010–2020) the increase in the abundance and landings of anchovy (Table 3). In biological terms, the mean spawning stock abundance of the European sardine decreased from ~7000 to ~2200 million individuals in 1999–2009 to 2010–2020, respectively. The anchovy recruitment index was inversely related to the sardine spawning abundance (Spearman's correlation: N = 21; R = −0.71; $p < 0.001$). Compared to 1999–2009, SSS significantly decreased throughout the spawning season in 2010–2020 (Table 3), particularly in April −0.28; Wilcoxon rank test: $p < 0.0001$; $W$ = 0) with most of the decrease in SSS occurring in nearshore regions (Fig. S1 in the Supplement). We also observed an increase in the mean NPP in May (~8%) between 1999–2009 and 2010–2020 ($W$ = 84; p = 0.0013). Unlike SSS and NPP, the changes observed in SST were not homogeneous throughout the spawning season, as it increased during spring months (+0.3°C

Table 3. Results of the Wilcoxon tests, showcasing the environmental variables that exhibited differences between 1999–2009 (before the increase in anchovy recruitment) and 2010–2020 (after the first peak in anchovy recruitment) at a statistically significant level (α = 0.05). NPP: net primary production (mgC $m^{-2}$ $d^{-1}$); SST: sea surface temperature (°C); SSS: sea surface salinity (unitless). The Wilcoxon tests were corrected using a sequential Holm-Šidàk correction

| Variable | 1999–2009 Mean | 2009–2019 Mean | Wilcoxon Rank | p-value |
|---|---|---|---|---|
| NPP May | 997.86 | 1085.46 | 84 | 0.0013 |
| SST April | 14.74 | 15.08 | 48 | 0.0001 |
| SST May | 16.05 | 16.23 | 18 | <0.0001 |
| SST June | 18.00 | 17.46 | 7 | <0.0001 |
| SSS April | 35.21 | 34.93 | 0 | <0.0001 |
| SSS May | 35.18 | 35.03 | 0 | <0.0001 |
| SSS July | 35.42 | 35.39 | 64 | <0.001 |
| SSS April–July | 35.25 | 35.14 | 705 | <0.0001 |

in April and +0.2°C in May) but was significantly lower in June (–0.5°C; $W = 7$; $p < 0.0001$).

The frequency of 'optimal windows', i.e. 8 d periods showing environmental conditions with statistically significant positive correlations with anchovy recruitment, increased in recent years (Spearman's correlation: N = 24; R = 0.44; p = 0.031; Fig. 4). The optimal windows occurred mostly in April and May, highlighting the importance of late spring for the spawning season (Fig. 4). When comparing 1999–2009 and 2010–2020, we observed that there was an increase in optimal windows, particularly in the months of April (+11) and June (+19) (Fig. 4). The optimal windows were characterized by SST between 15 and 17°C, relatively low salinity (34.5 to 35), mild downwelling (–500 to 0 $m^3$ $s^{-1}$ $km^{-1}$) and relatively low NPP (800 to 1000 mgC $m^{-2}$ $d^{-1}$).

The random forest model highlighted that both biological and physical factors were important drivers of the interannual variability of anchovy recruitment in NW Iberian waters ($R^2$ = 0.84; mean absolute error = 433.02 million individuals; Fig. 5). The 2 main factors driving the recruitment strength of anchovy were the spawning stock abundance of sardine and the winter NAO index. The partial dependence plots indicated that high anchovy recruitment was favoured by a low abundance of adult sardine (<2500 million individuals) and a positive NAO index (>0.5) during the winter preceding the spawning season.

## 4. DISCUSSION

The size and productivity of SPF populations can abruptly shift depending on environmental conditions. Frequently, changes in abundance are associated with bottom-up processes impacting the survival and growth of early life stages (Peck et al. 2021). For instance, temperature can change intrinsic factors such as spawning phenology, egg hatching success, and rates of embryonic development that impact egg and larval survival (Moyano et al. 2023). In some cases, boom-bust dynamics can also be shaped by biological drivers such as changes in prey abundance or predation pressure (Moyano et al. 2023). Overall, it can be difficult to disentangle physical and biological drivers, particularly when some changes are amplified by fishing exploitation and other anthropogenic influences (Alheit & Peck 2019). In the waters off the NW Portuguese coast, we found evidence that the current increase in anchovy abundance may be related to both biological and physical changes. Successful anchovy recruitment was favoured by more weeks with relatively low SST (15 to 17°C), weak downwelling, and low salinities (<35) during the spawning season. The decrease in salinity was observed prior to the bloom in anchovy. An inverse relationship with sardine abundance was also observed, suggesting the importance of intraguild processes such as competition and or predation in controlling the productivity in anchovy.

Water temperature is a key driver of the recruitment dynamics of SPF populations. Anchovy is typically considered a summer spawner, thereby being associated with higher temperatures compared to other SPF in the region (Peck et al. 2013), such as the European sardine (Basilone et al. 2004, Stratoudakis et al. 2007, Petitgas et al. 2012, Garrido et al. 2016, Fernández-Corredor et al. 2021). For instance, in northern Europe, regional warming has led to an increase in the productivity of relict anchovy populations since the mid-1990s (Petitgas et al. 2012). Intense coastal upwelling during summer in NW Iberia, however, promotes cooler water temperatures (Relvas et al. 2007). Nonetheless, our analysis identified that temperatures occurring during periods of high recruitment of anchovy were up to 4°C higher than those (13 to 15°C) associated with high sardine recruitment in this region (Ferreira et al. 2023). The temperatures observed here for anchovy agree with the temperatures associated with the spawning of anchovy in the Bay of Biscay (14 to 18°C; Motos et al. 1996). A link between successful recruitment and

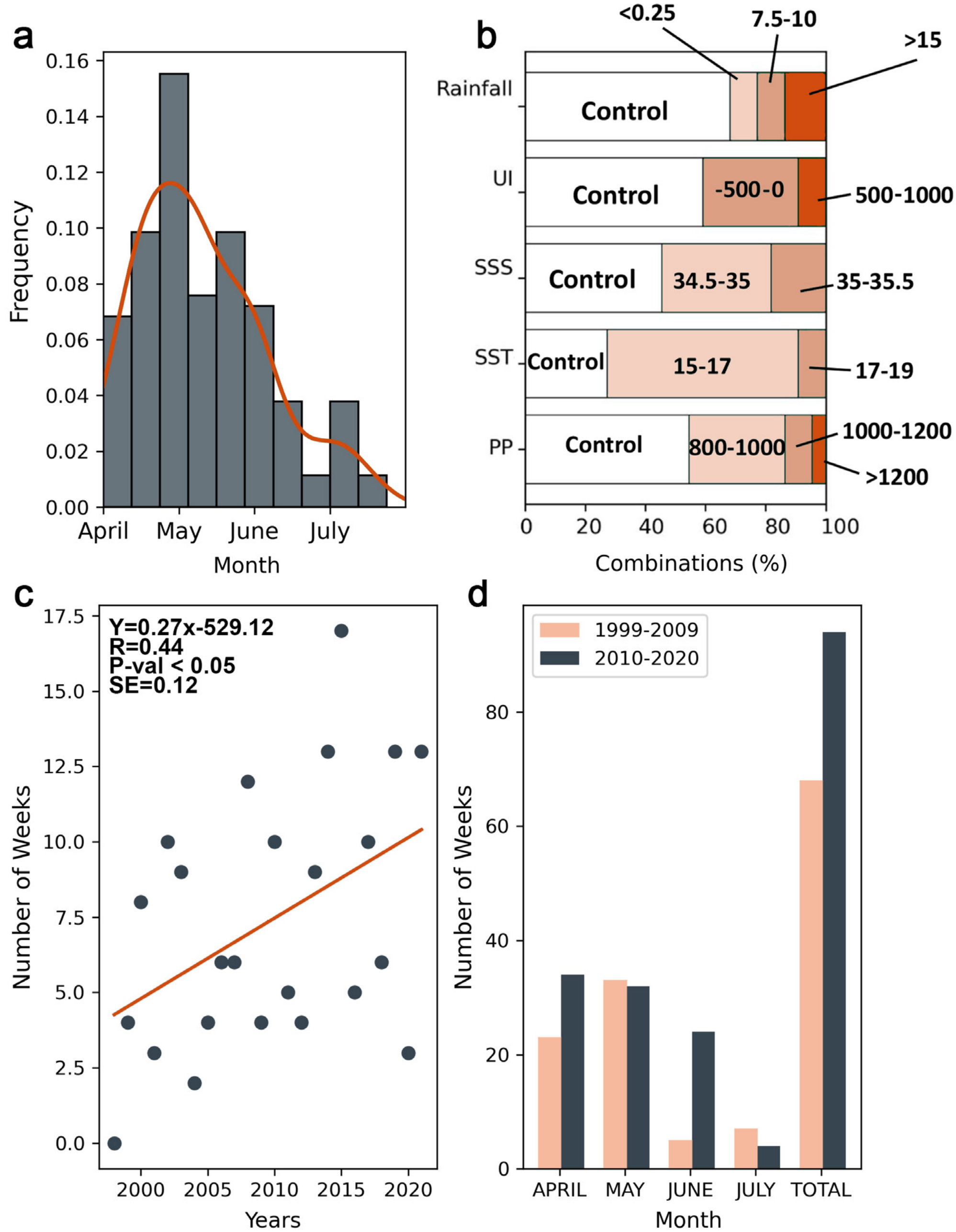


Fig. 4. Results from the optimal window analysis for European anchovy recruitment. (a) Optimal window frequency within the spawning season (April–July). (b) Percentage of each class within each environmental variable in relation to the total number of statistically significant optimal window combinations observed. (c) Interannual variability of the number of weeks corresponding to significant optimal window (1998–2021). (d) Comparison of the number of weeks corresponding to optimal windows occurring within the spawning season between 1999–2009 (before the increase in anchovy recruitment) and 2010–2020 (after the first peak in anchovy recruitment). Rainfall: cumulative rainfall (mm), UI: upwelling index ($m^3$ $s^{-1}$ $km^{-1}$), SSS: sea surface salinity (unitless), SST: sea surface temperature (°C), NPP: net primary production (mgC $m^{-2}$ $d^{-1}$)

relatively low temperatures has also been observed for other anchovy species in other regions. For example, increased productivity of the Peruvian anchoveta in the northern Humbolt Current System tends to occur during climate regimes characterized by relatively low (<17°C) temperatures (Cahuin et al. 2009). Similarly, the recruitment of Japanese anchovy in the Yellow Sea was negatively correlated with summer temperatures, particularly in July (Yu et al. 2020). In the present study, all years with successful anchovy recruitment (>1 million individuals) in NW Iberian waters coincided with spawning season temperatures of ~16 to 17°C (Fig. S2 in the Supplement). However, low recruitment also occurred in years with

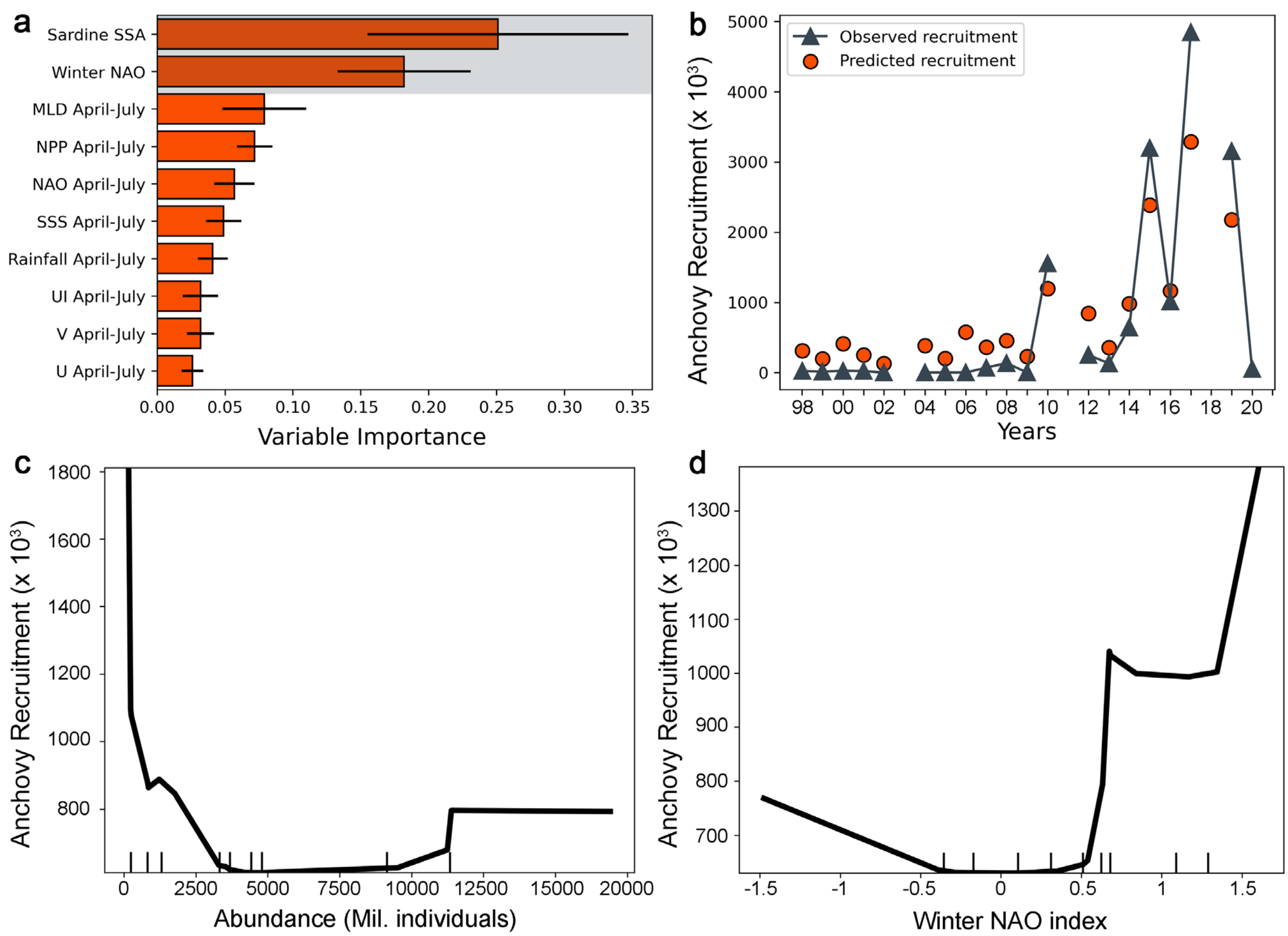


Fig. 5. European anchovy recruitment in NW Portugal. (a) Variables ranked by importance (i.e. how much the variable contributes to increasing the accuracy of the model), (b) comparison of the observed and model-predicted anchovy recruitment ($10^3$), and partial dependence plots for the (c) European sardine spawning stock abundance (SSA) and (d) Winter North Atlantic Oscillation ($NAO_W$), the 2 most important variables for anchovy recruitment according to the model, showcasing the average model-predicted response of European anchovy recruitment to changes in each variable. The ticks on the *x*-axes correspond to the percentile distribution for each variable

this range of temperatures suggesting that temperature may be necessary but not sufficient for high recruitment of anchovy in this system.

Mechanisms that promote onshore larval retention have also been associated with increased productivity of anchovy populations (Peck et al. 2021). Mesoscale structures, for example, can play a key role in promoting larval retention and overall higher recruitment in upwelling regions (e.g. Roy 1998, Lett et al. 2007, van der Sleen et al. 2018). While coastal upwelling leads to an increase in phyto- and zooplankton biomass, it also promotes offshore transport of SPF eggs and larvae. Therefore, coastal features — e.g. river plumes, counter-coastal currents and eddies (Santos et al. 2004, 2007, Condie et al. 2011, Moyano et al. 2014) — can help prevent SPF early life stages from drifting to offshore waters, where conditions are less favourable for growth and survival. Young larvae, in particular, benefit from onshore retention due to their poor swimming ability. In NW Iberian waters, coastal upwelling is more frequent and intense during the summer, and periods of post-upwelling relaxation may help stabilize the water column and entrap anchovy larvae and their prey within the upper layer, facilitating larval feeding. This may explain the link between successful recruitment and downwelling that we found in this study.

The recruitment of sardine in this region is known to benefit from onshore retention, which is aided by lower-density structures such as the IPC and the WIBP (Santos et al. 2004, 2007). While the IPC and WIBP are more associated with the winter season, it is possible that the WIBP may benefit anchovy recruitment during spring, when river runoff is high. This is suggested by the observation of lower salinity in years with successful anchovy recruitment. The existence of a freshwater plume is corroborated by the lower salinities found around 41° N (near the Douro Estuary) (Fig. 2). Moreover, other recent studies underscore the importance of taking into account lower-density structures for understanding the recent success of anchovy in NW Iberian waters. For instance, a decreasing trend in SSS since 2011 has already been observed for the waters along Western Iberia (Biguino et al. 2022). Numerical modelling by Campuzano et al. (2018) also suggested the existence of another important low-salinity plume (the West Iberian Central Plume, WICP). The WICP, derived from freshwater inputs from the Sado and Tagus estuaries, could interact with the WIBP to create a common, low salinity field across NW Iberian waters (Campuzano et al. 2018).

Finally, the random forest model revealed that the winter NAO index was also associated with successful years of anchovy recruitment. For Western Iberia, positive values of the winter NAO index are linked to drier winters, lower spring river flow, and upwelling-favourable winds in the winter (Borges et al. 2003, Trigo et al. 2004). In the Gulf of Cadiz, inhabited by the southern component of the Iberian anchovy stock, positive values of the winter NAO index have been associated with decreased anchovy landings (Báez & Real 2011, Castro-Gutiérrez et al. 2022). Báez & Real (2011) suggested that this might be due to the reduced river runoff in this region that occurs under positive NAO phases. In NW Iberian waters, several studies have hinted towards a negative relationship between winter NAO and the recruitment and abundance of sardine (e.g. Guisande et al. 2001, 2004, Borges et al. 2003). These studies associated the stronger upwelling observed during positive NAO phases with enhanced offshore larval transport and subsequent mortality. Therefore, it is curious that we observed a direct correlation between positive values of the winter NAO index and successful anchovy recruitment. In our analysis, positive winter NAO index values were related to less intense upwelling, higher precipitation, and lower phytoplankton biomass during the period of anchovy spawning (April to July) (Fig. S3 in the Supplement), 2 factors linked to successful recruitment. While the mechanisms linking the winter NAO to conditions in spring and summer remain unclear, the correlation is consistent with our optimal window analysis and the comparison between 1999–2009 and 2010–2020. It is possible that positive winter NAO values benefit anchovy recruitment by negatively impacting sardine recruitment, although no significant relationship between sardine abundance and winter NAO was found prior to running the random forest analysis.

Our results highlight the important effect that sardine may have on the recruitment dynamics of anchovy in Western Iberian waters. Alternating periods of high abundance of sardine and anchovy have been described for other EBUS, mainly thought to be associated with changes in climate regimes (e.g. Cahuin et al. 2009, Checkley et al. 2017, Sánches-Garrido et al. 2021). Nevertheless, intraguild competition between anchovy and sardine is also frequent as they both feed mainly on zooplankton (Garrido & van der Lingen 2014). While trophic differences between these species tend to minimize competition (van der Lingen et al. 2006, Espinoza et al. 2009), Nakayama et al. (2018) reported an interspecific effect of sardine on anchovy in the Northwestern Pacific.

Unlike in other EBUS, sardine has been the dominant species off Western Iberia for nearly a century (since monitoring started) and anchovy landings have been consistently low since at least 1969 (Fig. S4 in the Supplement). Thus, there is no historical evidence of an 'anchovy regime'. It is possible that competition between each species could be occurring and that successful recruitment of anchovy in NW Iberia may be dependent on low sardine abundance, similar to that observed by Nakayama et al. (2018). There are several reasons why sardine may outcompete anchovy in this region. (1) Since the sardine spawning season (October to April) starts a few months prior to the anchovy spawning season (April to July), a significant portion of newborn sardine individuals have already reached the juvenile stage when anchovy eggs start to hatch. (2) Sardine is typically much more abundant in this region: even with the recent drop in sardine abundance, the average sardine SSA since 1999 has still been 2 to 3 times higher than the average anchovy SSA (Fig. S5 in the Supplement). (3) The impact of sardine predation on anchovy egg mortality can be substantial (Fonseca et al. 2022). Nevertheless, it is important to note that without evidence of resource limitation, it is impossible to definitely ascertain if there is effectively competition between both species. Thus, our results can only suggest that potential competition exists, although more studies are required to fully understand these interactions in NW Iberia. While sardine abundance in NW Iberia has sharply declined since the mid-2000s, particularly since 2012, it has been slowly recovering since 2019. Winter SST has been identified as the main factor modulating sardine recruitment (Szalaj et al. 2021, Ferreira et al. 2023), and this is expected to continue rising in the NE Atlantic (IPCC 2023), although a slowing of the rate of increase in SST has been reported (Biguino et al. 2023). Under these circumstances, if the success of anchovy is truly dependent on lower sardine abundance (or an inverse effect of the same environmental drivers), anchovy abundance may remain high in the future, establishing itself as an important SPF for the fisheries off NW Iberia.

## 5. FINAL CONSIDERATIONS

This study was the first to investigate the potential environmental drivers causing the recent rise in anchovy abundance in NW Iberian waters and offers important insight into the environmental conditions promoting the productivity of anchovy in this system. The increase in anchovy was associated with the concurrent decline in the abundance of sardine and with physical changes in the marine environment that may increase the retention of anchovy larvae onshore, such as weaker upwelling and lower salinity. Another important finding was that the optimal weeks for anchovy recruitment appear to primarily occur in the mid-spring (April to May). However, there has also been a significant increase in the number of optimal weeks in June since 2010. This suggests that environmental changes in June may also have contributed to the increased anchovy abundance, given that peak spawning occurs through this month in this area. While there is no way of knowing if the abundance of anchovy will continue to increase in the future, it is clear that this rise has already impacted fisheries in Western Iberia.

This study contributes to better understanding the boom-and-bust dynamics of SPF in other EBUS by demonstrating that a positive regime in anchovy appears to have been promoted by changes in both physical and biological factors. Although this study is a first step, it is important to continue studying and monitoring anchovy off the Portuguese coast. Moreover, future studies should focus on improving our understanding of the relationship between anchovy and sardine in the broader Canary Coastal Current System, specifically by attempting to quantify the importance of intraspecific interactions for the recruitment variability of both species.

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