Frontiers in Marine Science

TYPE Original Research
PUBLISHED 17 December 2025
DOI 10.3389/fmars.2025.1703481

OPEN ACCESS

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

REVIEWED BY
Widien Khoufi,
Institut National des Sciences et Technologies de la Mer, Tunisia
Diego Panzeri,
National Institute of Oceanography and Applied Geophysics, Italy
Jade Mogeon,
Université de Nantes, France

*CORRESPONDENCE
Valentina Caserta
valentina.caserta1990@gmail.com

RECEIVED 11 September 2025
REVISED 14 November 2025
ACCEPTED 26 November 2025
PUBLISHED 17 December 2025

CITATION
Cacciamani R, Caserta V, Guizzardi o Guicciardi S, Santojanni A, Colella S, Domenichetti F, Donato F and Angelini S (2025) How fishing pressures and environmental changes can impact the mean size of fish resources: a case study of small pelagics in the Adriatic Sea.
Front. Mar. Sci. 12:1703481.
doi: 10.3389/fmars.2025.1703481

COPYRIGHT
© 2025 Cacciamani, Caserta, Guizzardi o Guicciardi, Santojanni, Colella, Domenichetti, Donato and Angelini. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.

How fishing pressures and environmental changes can impact the mean size of fish resources: a case study of small pelagics in the Adriatic Sea

Roberto Cacciamani[1,2], Valentina Caserta[1,3]*, Stefano Guizzardi o Guicciardi[1], Alberto Santojanni[1], Sabrina Colella[1], Filippo Domenichetti[1], Fortunata Donato[1] and Silvia Angelini[1,4]

[1]National Research Council, Institute for Marine Biological Resources and Biotechnology, Ancona, Italy, [2]CoNISMa–National Interuniversity Consortium for Marine Sciences, Rome, Italy, [3]Department of Biological, Geological and Environmental Sciences, Alma Mater Studiorum - University of Bologna, Bologna, Italy, [4]Fano Marine Center, the Inter-Institute Center for Research on Marine Biodiversity, Resources and Biotechnologies, Fano, Italy

Small pelagic fish, such as European anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*), play a key ecological and economic role in the Adriatic Sea. In recent decades, both species have shown a marked decline in mean body size, raising concerns about the combined impacts of fishing and environmental change. To investigate the main drivers behind this trend, we analyzed 20 years (2000–2021) of fishery-dependent data on weighted mean length (*wML*) derived from Length Frequency Distributions (LFDs) of catches landed in two major Adriatic fishing harbors, Chioggia and Ancona. Generalized Additive Models (GAMs) were applied to explore the relationships between *wML*, fishing effort and key environmental variables (chlorophyll-a, sea surface temperature, salinity, sea surface height and Po River discharge), incorporating both spatial (*Harbor*) and temporal dimensions (*Time* and *Season*). Our results indicated that anthropogenic pressures, particularly the interaction between fishing activity (*Fleet*) and long-term temporal dynamics (*Time*), were the dominant contributors to size reduction. This interaction reflects how long-term exploitation patterns have intensified over time despite nominal reductions in fleet size, suggesting cumulative fishing impacts and limited recovery capacity. Environmental variables contributed to explaining the observed patterns but to a lesser extent, suggesting species-specific and spatially structured responses. Overall, this study highlights that historical overexploitation remains the primary driver of body-size decline in the Adriatic small pelagic species. However, the possibly influence of the environmental variables in the dynamics of these species suggest the development of adaptive, ecosystem-based management strategies that integrate historical fishing pressure, current effort distribution and environmental variability to promote the recovery and resilience of these key fishery resources.

KEYWORDS

small pelagics, Adriatic Sea, generalized additive model, environmental impacts, fishing activity impact, size reduction

1 Introduction

Small pelagic fish, i.e., European anchovy (*Engraulis encrasicolus*, ANE) and European sardine (*Sardina pilchardus*, PIL), are considered the most important commercial species of the Mediterranean Sea (Food and Agriculture Organization [FAO], 2023; Barange et al., 2018; Leonori et al., 2021). They represent the main contributors of total landings within this basin (Lleonart and Maynou, 2003; Carpi et al., 2017), accounting collectively for about 33% (222,610 tons) of fish captures in 2020-2021; of these, about 36% (81,930 tons) are caught in the Adriatic Sea (FAO, 2023).

Beyond their economic value, small pelagic species play a pivotal ecological role (Barausse et al., 2009; Pennino et al., 2020; Schickele et al., 2020; Angelini et al., 2021). As mid-trophic-level organisms, they transfer energy from lower to higher trophic levels, thereby exerting both bottom-up control on top predators and top-down regulation on zooplankton communities (Cury et al., 2000; Bakun, 2006; Coll et al., 2007; Schickele et al., 2020; Malavolti et al., 2021). Because their trophic position tightly links them to primary production and plankton dynamics, small pelagic fish are particularly sensitive to fluctuations in oceanographic conditions that affect food availability and growth. Therefore, higher temperatures, increased stratification, or reduced freshwater input can limit nutrient supply and prey abundance while raising metabolic demands, ultimately leading to smaller body size (Bakun, 2006). Because of their short life span and strong sensitivity to environmental fluctuations, small pelagic species can exhibit size-related responses over very short timescales, making them valuable indicators of climate-induced environmental changes and fishing pressure (Carpi et al., 2015).

Climate change-driven environmental modifications have caused changes in ocean conditions, which have favored a decline in body size; this particularly occurs among short-lived species like anchovy and sardine (Otero and Hidalgo, 2023). In the Adriatic Sea, this trend is particularly pronounced. Regional hydroclimatic variability, influenced by broad-scale phenomena such as the North Atlantic Oscillation (NAO) and the Eastern Mediterranean Transient (EMT), has altered temperature, salinity, and oxygen concentrations over recent decades (Grbec et al., 2015), also impacting biological aspects of fish biology (i.e. recruitment, Santojanni et al., 2006).

Historically, productivity in the northern Adriatic Sea has been sustained by nutrient input from the Po River (Giani et al., 2012). However, recent declines in precipitation (Aragão et al., 2024) and the 1986 Italian regulation limiting phosphate use in detergent, along with broader nutrient load mitigation measures (Reg. 86/91/CEE), have resulted in decreased river discharge and an oligotrophication of coastal waters, diminishing primary production and changing small pelagic species distribution (Sani et al., 2024). Additional stressors—such as the consequences of mismatch between spawning timing and plankton blooms—may have compounded recruitment failures and altered population structures (Malavolti et al., 2021).

Climate-driven declines in productivity combined with management actions (e.g. Rec. GFCM/44/2021/20) aimed at preventing stock collapse, have triggered a severe crisis in the local fishing sector, resulting in a dramatic reduction in the number of active vessels (Supplementary Figure S1).

Understanding the complex interplay between climate variability, hydrological processes, and human pressures on marine ecosystems requires analytical approaches capable of capturing nonlinear and potentially interacting effects. Among the statistical tools increasingly adopted for investigating these dynamics are Generalized Additive Models (GAMs; Wood, 2017), which provide the flexibility needed for ecological data analysis. Their ability to model nonlinear relationships makes them particularly valuable in examining how environmental factors could influence species distribution, abundance, and life-history traits over time and space (Solanki et al., 2017).

In this study, GAM models have been used with the aim of investigating the potential causes of long-term (2000–2021) fluctuations in the mean length of Adriatic anchovy and sardine. The analysis focused on several influencing factors, including i) environmental variables such as primary production, water temperature and salinity, ii) changes in the food-web (e.g. productivity, structure) due to riverine inflow fluctuations and iii) fishing pressure, represented by the number of fishing vessels. Notably, our analysis also considered the temporal dimension that encompassed management measures (e.g., seasonal closures, economic downturns), ecological and socioeconomic changes over the past two decades. This approach aligned with the growing need to embed socio-ecological processes and contextual drivers within fisheries stock assessments. By examining the sensitivity of mean length to both fishing activity and environmental change, our study offers insights into the drivers of stock variability and supports the development of more informed and adaptive management strategies for anchovy and sardine in the Adriatic Sea.

2 Materials and methods

2.1 Study area

The study area included the northern and central Adriatic Sea (Figure 1), which is characterized by high productivity and strong spatio-temporal ecological variability that lead to rich pelagic communities (Coll et al., 2009; Giannoulaki et al., 2013).The shallow northern sector, with an average depth of approximately 35 meters, is fed by numerous rivers, of which the Po River is the most significant, providing nutrient-rich freshwater that drives elevated coastal chlorophyll-a concentrations and periodic eutrophication events (Penna et al., 2004; Pinardi et al., 2004; Giannoulaki et al., 2013).

Figure 1 shows the location of the ports of Chioggia and Ancona, which have historically been among Italy's most important ports for small pelagic fisheries (Cingolani et al., 1996). The samples used to develop this study came from commercial samples performed at these harbors, given their long-standing importance in the Adriatic pelagic fishery and the reliability of biological and fishery data collected through consistent sampling over time (Fortibuoni et al., 2017). The individuals collected for this study originated from pelagic pair trawlers (locally known as "Volante"; PTM), which represent the main gear used to target pelagic species in the study area. These gears operate during daytime and use a minimum mesh size of 20 mm, in agreement with the Council Regulation (EC) No. 1967/2006.

To spatially delineate the fishing grounds, we used the PTM patterns described by Coro et al. (2022), based on the Automatic Identification System (AIS) data that offer high-resolution spatial information on this gear. These operational ranges were validated by comparing them with GPS locations from fishing haul records associated with vessels landing in Ancona and Chioggia, collected through the EU Data Collection Framework (DCF; EC, 2017). Given the natural mobility of small pelagic species, some degree of spatial mixing between adjacent fishing areas is ecologically plausible and consistent with our spatial framework. However, this potential overlap is expected to be limited and therefore represents a negligible source of bias. Moreover, economic constraints, such as fuel costs, discourage vessels from operating far from their home ports (Sabatella et al., 2017), further supporting the spatial consistency between landing ports and fishing grounds.

2.2 Data

2.2.1 Dependent variable

We used the monthly weighted Mean Length (*wML*) by harbor and species as dependent variables in our analysis (Figure 2).

This information was derived from the Length Frequency Distributions (LFDs) collected between 2000 and 2021 by the Institute for Marine Biological Resources and Biotechnology (IRBIM) of the Italian National Research Council (CNR). The data collection was conducted under the framework of the Italian

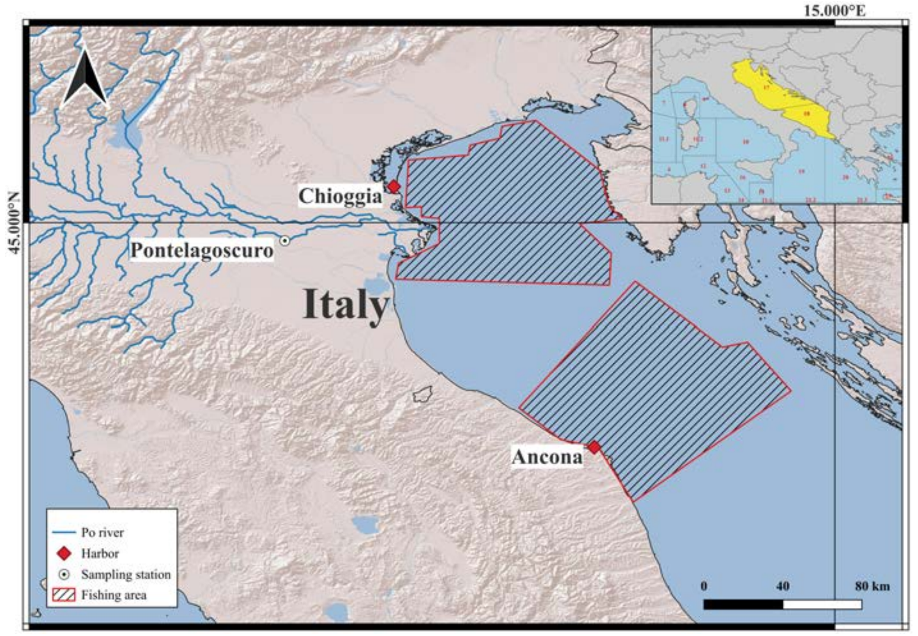

FIGURE 1
Map of the study area including the location of the selected harbors, Chioggia and Ancona, and the corresponding fishing grounds georeferenced using QGIS v.3.20.0 (www.qgis.org). The location of Pontelagoscuro station is highlighted in the map. Mediterranean Geographical Sub-Areas (GSAs) are reported top right; GSAs 17 and 18, corresponding to the whole Adriatic Sea, are highlighted in yellow.

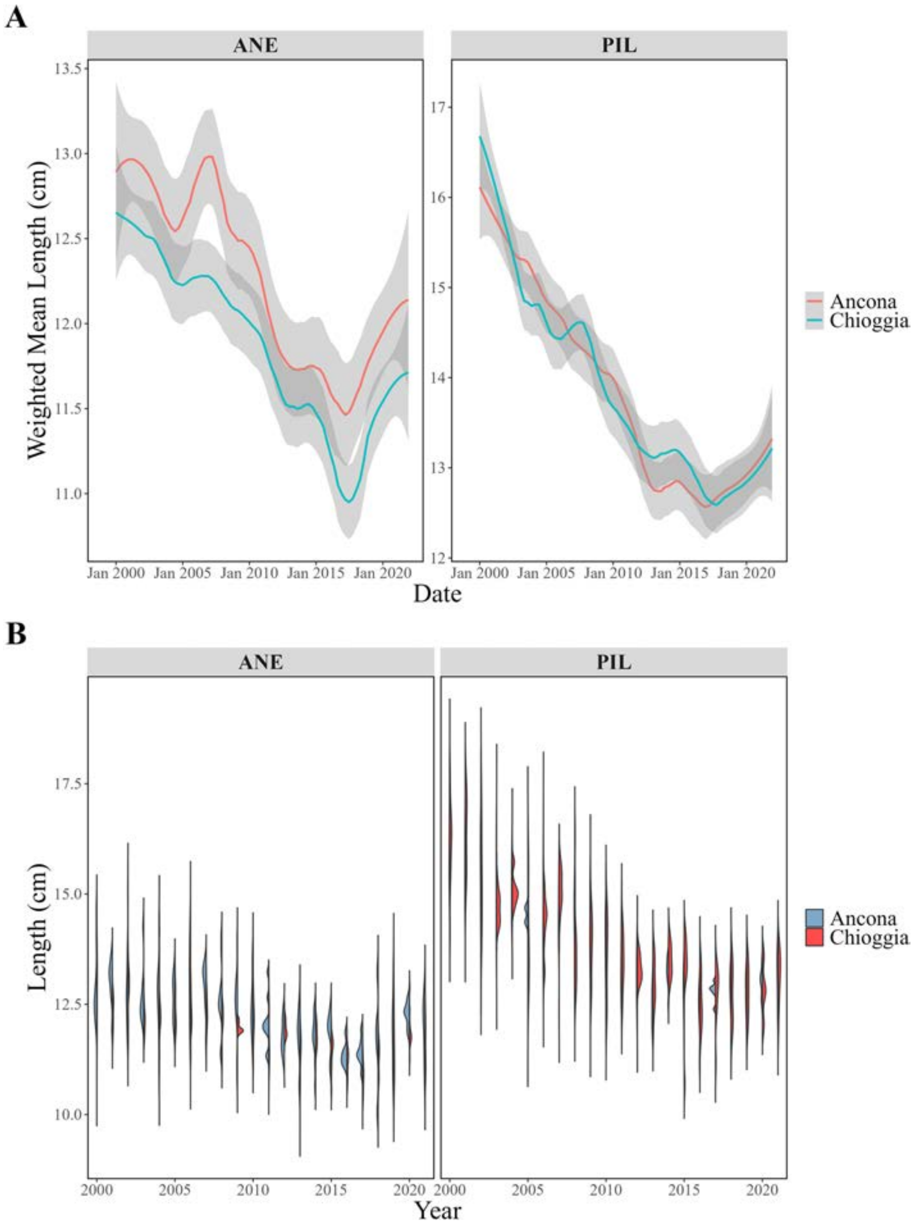

FIGURE 2
(A) Long-term trends in weighted Mean Length of anchovy (ANE, left) and sardine (PIL, right) from January 2000 to December 2021. Colored lines represent smoothed estimates by Harbor (Ancona, orange line; Chioggia light green line) with 95% confidence intervals shown in grey. **(B)** Violin plots that the show the annual length variability and central tendency of individual length measurements across years.

National program for Fisheries in 2000 and 2001, and the EU DCF (EC, 2017), which started in 2002 and is still ongoing. Samples were obtained from the commercial catch landed in the Ancona and Chioggia harbors; discard was not considered since it was negligible for these species (Tsagarakis et al., 2014).

In total, 122,213 anchovy and 66,908 sardine LFDs were collected in Chioggia, while about 148,148 anchovy and 54,675 sardine LFDs were collected in Ancona. Fish lengths were measured using 0.5 cm length classes. For each month, the wML was calculated as showed in Equation 1.

$$wML = \frac{\sum_{i=1}^{k} N_i \ L_i}{\sum_{1=1}^{k} N_i} \tag{1}$$

where L_i is the length of class i, N_i is the number (or relative abundance) of individuals in class i, and k is the total number of length classes. This approach ensured temporal consistency in measuring mean fish size, which served as a proxy for shifts in population structure. Details about the sampling effort are shown in Supplementary Figure S2 for anchovy and Supplementary Figure S3 for sardine.

2.2.2 Covariates

2.2.2.1 Spatio-temporal dimensions

A spatial dimension (*Harbor*) was introduced to investigate potential quantitative differences between the ports of Ancona and Chioggia, specifically regarding fishing strategies (e.g. Chioggia fleet targets sardines as well as anchovies according to seasonal availability; whereas Ancona fleet mainly focuses on anchovies), market conditions (e.g. different market strategies), spatial distribution of the resources and environmental characteristics of the associated fishing grounds (Figure 1). In addition, a long-term temporal dimension (*Time*) was incorporated, defined by sequential numbers from 1 to 264 for each area, corresponding to monthly time steps from 2000 to 2021. This time variable acted as a proxy for broader, less easily quantifiable changes—such as management regulation shifts, economic fluctuations, and long-term environmental trends—that may have influenced ecosystem dynamics and fishing activity over the study period (Bigelow et al., 1999). A short-term temporal dimension (*Season*), corresponding to the calendar seasons, was introduced to capture intra-annual fluctuations in *wML*, reflecting either species-specific biological rhythms or seasonal patterns driven by ecological cycles and fishing activity.

2.2.2.2 Environmental variables

Based on the literature review carried out by Fernández-Corredor et al. (2021), we tested the cited environmental variables, namely temperature (°C, *Temp*), chlorophyll-a concentration (mg/m^3, *Chla*), salinity (PSU, *Sal*) and sea surface height (cm, as proxy for depth, *Ssh*), that may influence small pelagic stocks in the Adriatic Sea. These variables were monthly retrieved from the uppermost layer data from the Copernicus Marine Environment Monitoring Service (CMEMS, 2024). Since Copernicus products for the Mediterranean Sea are delivered at the basin scale, environmental data were subsequently cropped to match the fishing grounds associated with the ports of Ancona and Chioggia, as shown in Figure 1. Besides these, we added the Po River runoff (m^3/s, *Po*), whose flow index was included due to its prominent role in shaping the ecological dynamics of the Adriatic Sea (Coll et al., 2009). As the largest river in the basin, the Po accounts for roughly two-thirds of total freshwater discharge into the Adriatic (Aragão et al., 2024); its influence on the recruitment of small pelagic species is well documented (Santojanni et al., 2006; Marini and Grilli, 2023). Monthly average discharge values (m^3/s) from the Pontelagoscuro station (Figure 1) were obtained via the Regional Open Data Portal (RODP, 2024), provided by the Agenzia Regionale Prevenzione Ambiente Energia Emilia- Romagna (ARPAE-ER).

2.2.2.3 Fishing effort

Fishing effort was measured as the number of active vessels (*Fleet*) in a given period of time, as described by FAO (2025). Data were collected by local fishing cooperatives. For Ancona, data were provided on a monthly scale, whereas for Chioggia only annual data are available. Since no monthly data exist for Chioggia, the annual number of active vessels was assigned to each month of the corresponding year, assuming that fleet size remained constant throughout the year.

2.3 Statistical analysis

To assess spatial variability in environmental conditions between Ancona and Chioggia, independent-sample t-tests were conducted. Variables showing significant differences ($p< 0.05$) were flagged for inclusion with spatial discrimination in the GAMs. In addition, general temporal trends of each environmental variable were visually inspected by plotting the data with fitted local regressions, providing an overview of long-term changes over the study period. This exploratory analysis was conducted to better understand the temporal behavior of environmental covariates and to facilitate the interpretation of the GAM results. Finally, we evaluated correlation among the selected variables using Kendall's tau correlation test, considering collinearity above 0.49 as significant (Wicklin, 2023).

To better understand how far in advance a combination of environmental and anthropogenic covariates influenced the monthly *wML* of anchovy and sardine, we developed a series of GAMs applying time lags from 0 to 12 months, in step of one month, following the approach described by Pennino et al. (2020). This range was chosen to encompass the annual life cycle of anchovy and sardine, as their growth and recruitment can be influenced by environmental conditions over several months. Environmental and *Fleet* data were lagged by directly shifting the monthly time series; for instance, in the case of a one-month lag, the covariate corresponded to the value observed in the month immediately preceding the size data.

We used the mgcv package (Wood, 2017) developed for the R environment, to build GAM models fitted under a Gaussian distribution with an identity link, which is appropriate for modeling the continuous response variable (wML). The general model structure was specified as showed in Equation 2:

$$wML \sim ti(X_j,\ X_j,\ \mathrm{k} = \mathrm{c}(13, 13)) + \sum_j s(X_j,\ \mathrm{k} = 13) + Harbor + Season \tag{2}$$

where X_j represents the set of candidate environmental variables with smoothing terms specified using up to 13 basis functions (i.e., k = 13) to allow sufficiently flexible modeling. To account for potential dependencies between predictors, a partial tensor-product smooth (*ti*) was introduced to model their interaction. This interaction term was applied only to positively correlated variable pairs (based on Kendall's test). In addition, spatial discrimination was retained for fishing effort and for environmental variables that showed significant spatial differences, i.e. p-value< 0.05, based on prior t-tests, and it was also included in the interaction term when at least one of the variables exhibited such spatial discrimination. This allowed the model to account for fishing ground-specific dynamics in both fishing activity and environmental conditions. All models were fitted using Restricted Maximum Likelihood (REML) estimation, which provides more stable and less biased estimates of smoothing parameters compared to maximum likelihood.

We performed model selection using a two-step approach based on training and test data. First, the dataset was randomly split into a training set (70% of the data) and a test set (30%), following the procedure described by James et al. (2023). The training set was used both for variable selection and for model fitting, while the test set was reserved for independent model validation. For each lag scenario, we applied a forward stepwise selection procedure using the FWDselect R package (Sestelo et al., 2016), with GAMs fitted via the qgam interface. Variable selection was guided by Akaike's Information Criterion (AIC; Burnham and Anderson, 2002), retaining the combination of predictors that minimized AIC as the best-fitting model for each lag. This automated procedure (qselection) inherently retains only predictors with statistically significant explanatory power, ensuring that the environmental variables included in the final GAMs contribute meaningfully to model performance. The resulting models—optimized separately for each lag—were then applied to the test set. Predictive performance was evaluated by computing the Root Mean Squared Error (RMSE) between observed and predicted values, as shown in Equation 3.

$$RMSE = \sqrt{\frac{1}{n}\sum_{i=1}^{n}(\widehat{y}_i - y_i)^2} \tag{3}$$

Where *yi* are the predicted values, *yi* are the observed test values and n is the number of observations.

The model yielding the lowest RMSE was selected as the best overall model, as it best captured the relationship between the response variable (*wML*) and the selected covariates. Finally, the contribution of each covariate in the final best models was quantified using the *gam.hp* R package (Lai et al., 2024), which decomposes explained deviance to assess the relative importance of individual predictors. This approach provided insights into the dominant environmental drivers influencing size structure over time.

3 Results

3.1 Environmental variables assessment

Supplementary Figure S4 shows the temporal trends of the environmental variables retained in the analysis. The variables were generally stable (p-value< 0.05), except for the *Chl-a* in Chioggia, which showed an increasing trend, and the *Sal* in Ancona, which decreased throughout the time series. Independent-sample t-tests indicated significant spatial differences (p< 0.05) for *Chla* and *Sal* between Ancona and Chioggia, supporting the inclusion of spatially stratified smoothers for these variables (Supplementary Figure S5).

3.2 Influence of covariates on *wML*

Supplementary Table S1 reports all candidate models generated during the variable selection procedure. From these, Table 1 presents the best models for each lag ranked by RMSE. A detailed summary of model parameters, including estimated degrees of freedom (edf), deviance explained and p-values for each smooth term, is provided in Table 2. For ANE, the best-performing model was obtained with a 1-month lag, while for PIL, the optimal model corresponded to a 12-month lag. Notably, *Time* and *Fleet* are recurrent across the top-performing models for both species, underscoring their dominant explanatory role. A strong correlation was observed between these two factors (Supplementary Figure S6), and their interaction was therefore visualized through the partial tensor-product smooth. No major diagnostic anomalies were observed and the Kolmogorov–Smirnov (KS) residual normality tests further supported the adequacy of the fitted models (Supplementary Figures S7, S8). In addition, the comparison between observed and predicted values on the independent test dataset (Supplementary Figure S9) confirmed that the models achieved consistent predictive performance, providing a reliable assessment of their predictive skill.

3.2.1 Anchovy

The best-fitting GAM for anchovy, incorporating a one-month environmental lag, was based on Equation 4 model structure:

$$\begin{aligned} wML\_ANE \sim s(Time) + s(Fleet, by = Harbor) \\ + ti(Time, Fleet, by = Harbor) + s(Po) + s(Chl - a, by \\ = Harbor) + Harbor \end{aligned} \tag{4}$$

The model explained 47.7% of the total deviance, with an adjusted R^2 of 0.451. The estimated REML was 363.97 and the residual variance (0.353) indicated a satisfactory model fit.

Hierarchical partitioning analysis is shown in Figure 3 and revealed that the interaction between *Time* and *Fleet* explained the largest portion of the deviance, highlighting the synergistic influence of temporal dynamics and spatially differentiated fishing activity on anchovy size structure. *Time* underscoring the dominant role of long-term temporal dynamics. These likely encapsulate a wide range of unmeasured processes, including cumulative fishing impacts, regulatory changes, and ecosystem shifts. *Fleet*, with spatial discrimination by *Harbor* was significant in Ancona but not in Chioggia, indicating a stronger linkage between fishing effort and body size in the central Adriatic. Po River discharge smoothness was not statistically significant (p = 0.10), the partial effect showed a decline in predicted *wML* at higher discharge levels, suggesting that high freshwater input may reduce growth conditions, potentially through increased turbidity. Chlorophyll-a was modeled with port-specific smoothers, but neither terms were not statistically significant. Nevertheless, their retention reflected their ecological relevance and their additive contribution to overall model performance. The effect of *Harbor* revealed a significant negative coefficient for Chioggia (estimate = –0.412, p = 0.0049), indicating that, after accounting for covariates, anchovy landed in Chioggia were, on average, significantly smaller than those in Ancona. This result supported the presence of persistent spatial differences in size structure, possibly linked to localized environmental conditions, fishing histories, or spatial targeting practices.

These patterns were clearly illustrated in Figure 4, which displayed the partial effect plots of each model component. The interaction between *Time* and *Fleet* (Figure 4, top panels) revealed marked spatiotemporal contrasts between harbors. In Ancona, the

TABLE 1 Best GAM models selected through variable selection for each environmental lag (0–12 months) and species, anchovy (ANE) and sardine (PIL).

Species	Lag	Formula	Dev. expl (%)	RMSE
ANE	0	wML ~ s(Time, k = 13) + Harbor + s(Fleet, by = Harbor, k = 13) + s(Ssh, k = 13) + s(Temp, k = 13) + ti(Time, Fleet, by = Harbor, k = c(13,13))	48.25	0.644
	1	**wML ~ s(Time, k = 13) + Harbor + s(Po, k = 13)+ s(Fleet, by = Harbor, k = 13) + s(Chla, by = Harbor, k = 13) + ti(Time, Fleet, by = Harbor, k = c(13,13))**	47.67	0.615
	2	wML ~ s(Time, k = 13) + Harbor + s(Po, k = 13) + s(Fleet, by = Harbor, k = 13) + s(Temp, k = 13) + s(Ssh, k = 13) + s(Sal, by = Harbor, k = 13) + ti(Time, Fleet, by = Harbor, k = c(13,13))	48.73	0.633
	3	wML ~ s(Time, k = 13) + Harbor + s(Fleet, by = Harbor, k = 13) + s(Chla, by = Harbor, k = 13) + s(Temp, k = 13) + s(Ssh, k = 13) + ti(Time, Fleet, by = Harbor, k = 13 c(13,13))	47.12	0.647
	4	wML ~ s(Time, k = 13) + s(Fleet, by = Harbor, k = 13) + s(Ssh, k = 13) + Harbor + s(Temp, k = 13) + s(Sal, by = Harbor, k = 13) + ti(Time, Fleet, by = Harbor, k = c (13,13))	48.40	0.701
	5	wML ~ s(Time, k = 13) + s(Fleet, by = Harbor, k = 13) + Harbor + s(Sal, by = Harbor, k = 13) + ti(Time, Fleet, by = Harbor, k = c(13,13))	47.15	0.635
	6	wML ~ s(Time, k = 13) + s(Fleet, by = Harbor, k = 13) + s(Sal, by = Harbor, k = 13) + Harbor + Season + ti(Time, Fleet, by = Harbor, k = c(13,13))	47.79	0.657
	7	wML ~ s(Time, k = 13) + s(Fleet, by = Harbor, k = 13) + Harbor + Season + s(Ssh, k = 13) + ti(Time, Fleet, by = Harbor, k = c(13,13))	46.72	0.669
	8	wML ~ s(Time, k = 13) + s(Fleet, by = Harbor, k = 13) + s(Chla, by = Harbor, k = 13) + Harbor + Season + s(Po, k = 13) + s(Ssh, k = 13) + ti(Time, Fleet, by = Harbor, k = c(13,13))	47.06	0.693
	9	wML ~ s(Time, k = 13) + s(Fleet, by = Harbor, k = 13) + s(Chla, by = Harbor, k = 13) + s(Temp, k = 13) + Harbor + s(Po, k = 13) + Season + ti(Time, Fleet, by = Harbor, k = c(13,13))	46.59	0.625
	10	wML ~ s(Time, k = 13) + s(Fleet, by = Harbor, k = 13) + s(Ssh, k = 13) + Harbor + s(Chla, by = Harbor, k = 13) + s(Temp, k = 13) + ti(Time, Fleet, by = Harbor, k = c (13,13))	47.30	0.634
	11	wML ~ s(Time, k = 13) + Harbor + s(Po, k = 13) + s(Fleet, by = Harbor, k = 13) + s(Temp, k = 13) + ti(Time, Fleet, by = Harbor, k = c(13,13))	47.70	0.626
	12	wML ~ s(Time, k = 13) + s(Chla, by = Harbor, k = 13) + Harbor + s(Fleet, by = Harbor, k = 13) + s(Temp, k = 13) + s(Ssh, k = 13) + s(Sal, by = Harbor, k = 13) + ti(Time, Fleet, by = Harbor, k = c(13,13))	48.28	0.635
PIL	0	wML ~ s(Time, k = 13) + s(Temp, k = 13) + s(Fleet, by = Harbor, k = 13) + Season + s(Po, k = 13) + s(Sal, by = Harbor, k = 13) + s(Chla, by = Harbor, k = 13) + ti (Time, Fleet, by = Harbor, k = c(13,13))	79.24	0.755
	1	wML ~ s(Time, k = 13) + Season + s(Fleet, by = Harbor, k = 13) + s(Po, k = 13) + s (Chla, by = Harbor, k = 13) + Harbor + ti(Time, Fleet, by = Harbor, k = c(13,13))	75.96	0.775
	2	wML ~ s(Time, k = 13) + Season + s(Fleet, by = Harbor, k = 13) + s(Po, k = 13) + s (Sal, by = Harbor, k = 13) + ti(Time, Fleet, by = Harbor, k = c(13,13))	74.64	0.848
	3	wML ~ s(Time, k = 13) + Season + s(Fleet, by = Harbor, k = 13) + s(Chla, by = Harbor, k = 13) + s(Sal, by = Harbor, k = 13) + s(Po, k = 13) + ti(Time, Fleet, by = Harbor, k = c(13,13))	76.71	0.783
	4	wML ~ s(Time, k = 13) + Season + s(Fleet, by = Harbor, k = 13) + ti(Time, Fleet, by = Harbor, k = c(13,13))	74.80	0.773
	5	wML ~ s(Time, k = 13) + s(Temp, k = 13) + s(Fleet, by = Harbor, k = 13) + Season + s(Sal, by = Harbor, k = 13) + ti(Time, Fleet, by = Harbor, k = c(13,13))	77.65	0.739
	6	wML ~ s(Time, k = 13) + s(Temp, k = 13) + s(Fleet, by = Harbor, k = 13) + s(Po, k = 13) + s(Sal, by = Harbor, k = 13) + s(Chla, by = Harbor, k = 13) + ti(Time, Fleet, by = Harbor, k = c(13,13))	77.46	0.765

(Continued)

TABLE 1 Continued

Species	Lag	Formula	Dev. expl (%)	RMSE
	7	wML ~ s(Time, k = 13) + Season + s(Fleet, by = Harbor, k = 13) + s(Po, k = 13) + s (Chla, by = Harbor, k = 13) + s(Temp, k = 13) + ti(Time, Fleet, by = Harbor, k = c (13,13))	76.61	0.737
	8	wML ~ s(Time, k = 13) + Season + s(Temp, k = 13) + s(Fleet, by = Harbor, k = 13) + s(Chla, by = Harbor, k = 13) + Harbor + s(Sal, by = Harbor, k = 13) + ti(Time, Fleet, by = Harbor, k = c(13,13))	75.25	0.750
	9	wML ~ s(Time, k = 13) + s(Fleet, by = Harbor, k = 13) + s(Sal, by = Harbor, k = 13) + s(Temp, k = 13) + Season + s(Chla, by = Harbor, k = 13) + ti(Time, Fleet, by = Harbor, k = c(13,13))	76.68	0.732
	10	wML ~ s(Time, k = 13) + Season + s(Fleet, by = Harbor, k = 13) + s(Temp, k = 13) + ti(Time, Fleet, by = Harbor, k = c(13,13))	76.24	0.733
	11	wML ~ s(Time, k = 13) + s(Temp, k = 13) + s(Fleet, by = Harbor, k = 13) + Season + ti(Time, Fleet, by = Harbor, k = c(13,13))	76.02	0.766
	12	**wML ~ s(Time, k = 13) + s(Temp, k = 13) + Season + Harbor + s(Fleet, by = Harbor, k = 13) + ti(Time, Fleet, by = Harbor, k = c(13,13))**	77.42	0.705

Each row reports the formulas, explained deviance and RMSE. For each species, the model with the lowest RMSE across all lags is highlighted in bold and considered the selected model.

interaction surface showed stronger temporal gradients, with higher predicted *wML* during recent years at low fleet levels, suggesting that reduced fishing intensity may have buffered size declines over time. In contrast, Chioggia exhibited a flatter response surface, indicating weaker coupling between temporal trends and fishing activity, possibly reflecting lower temporal variability in fleet composition or effort distribution. *Time* smoother (Figure 4 middle-left panel) showed a non-linear decline in *wML* from 2000 to the mid-2010s, followed by a modest upward shift in the final years. *Po* river discharge smoother (Figure 4 middle-right panel) showed a decline in *wML* at discharge rates exceeding 1500 m^3/s, a pattern that may reflect less favorable conditions under high freshwater input. The *Fleet* smoother (Figure 4 middle panels) revealed a positive association in Ancona, where higher fleet values corresponded to larger mean lengths; a similar trend was depicted for Chioggia harbor. The smoothers for *Chl-a* (Figure 4, bottom panels) showed a weakly increasing trend for both harbors, slightly more pronounced for Chioggia port, while with higher uncertainty for Ancona, suggesting that growth conditions may vary across the productivity spectrum.

3.2.2 Sardine

The best-fitting GAM for sardine, incorporating a 12-month environmental lag, was specified in the Equation 5:

$$wML\_PIL \sim s(Time) + s(Temp) + s(Fleet, by = Harbor) + ti(Time, Fleet, by = Harbor) + Harbor + Season \quad (5)$$

This model explained 77.4% of the total deviance, with an adjusted R^2 of 0.758, suggesting a strong fit to the data. The REML criterion was 412.45, and the estimated residual variance (0.440) confirmed an overall satisfactory model structure.

According to the hierarchical partitioning analysis (Figure 5), interaction *Time* x *Fleet* explained the largest share of the total deviance. Nevertheless, *Time* effect alone accounted for a comparable proportion of the explained deviance, pointing to strong long-term dynamics, possibly reflecting systemic pressures such as continuous exploitation, recruitment shifts, or decadal environmental variability. *Temperature* was also a statistically significant term ($p< 0.001$), and its partial effect suggested the presence of an optimal thermal range for sardine growth.

Fleet activity did not show a significant effect on sardine size in either port. (Chioggia, $p = 0.36$; Ancona, $p \approx 1.00$). This suggests that temporal fluctuations in fleet size or activity over the preceding year (lag 12) had limited influence on sardine size structure across both areas. When the interaction with *Time* was considered, a clearer spatial contrast emerged. The temporal–effort interaction was non-significant in Ancona ($p = 0.55$), indicating that changes in fleet activity over time did not notably affect sardine size there. In contrast, the interaction approached significance in Chioggia ($p = 0.05$), suggesting that the effect of fleet dynamics on sardine size varied through time in the northern Adriatic Sea. This pattern may reflect temporal shifts in fishing intensity or selectivity, possibly linked to local fleet behavior, resource availability, or spatial overlap between sardine aggregations and fishing grounds.

Season and *Harbor* both contributed to explaining variation in sardine *wML*, though with different levels of significance. Seasonal effects were particularly evident: sardines were significantly larger in spring (estimate = 0.26, $p = 0.01$) and summer (estimate = 0.51, $p< 0.01$) compared to winter (estimate = - 0.34, $p< 0.04$), where smaller *wML* were observed. However, this seasonal pattern is not reflecting a true biological signal. Instead, it is more plausibly driven by fishery-dependent biases: during summer, fishers have greater opportunities to target larger individuals offshore, whereas in winter adverse weather conditions often restrict fishing activity to coastal areas, where smaller, spawning fish are more accessible. On the other hand, differences between harbors were less pronounced. Sardines from Chioggia tended to be smaller on average than those from Ancona (estimate = −0.24, $p = 0.09$), although the effect was

TABLE 2 Estimated degrees of freedom (edf), percentage of deviance explained [Dev expl. (%)] and p-values for each smooth term in the selected GAM models for anchovy (ANE) and sardine (PIL).

Species	Term	Harbor	edf	Dev expl. (%)	p-value
ANE	Time		4.139	28.8	0.000
	Fleet	Ancona	1.000	19.5	0.003
		Chioggia	1.000		0.368
	Time x Fleet	Ancona	2.242	38.3	0.07
		Chioggia	1.001		0.44
	Chla	Ancona	2.832	5.2	0.599
		Chioggia	1.000		0.241
	Harbor			4.0	
	Po		3.763	4.2	0.102
PIL	Time		5.443	34.0	0.000
	Temp		5.242	5.5	0.000
	Fleet	Ancona	1.000	20.1	0.998
		Chioggia	2.279		0.360
	Time x Fleet	Ancona	1.001	37.5	0.553
		Chioggia	6.454		0.051
	Season			2.7	
	Harbor			0.3	

only marginally significant. This suggests another potential bias arising from differences in market strategies, that lead to a different representation of size classes during sampling campaigns (Supplementary Figure S3).

Figure 6 visually summarized the partial effects of the covariates included in the final sardine model. The interaction between *Time* and *Fleet* (Figure 6, top panels) revealed distinct temporal and spatial dynamics in the relationship between fishing activity and sardine size.

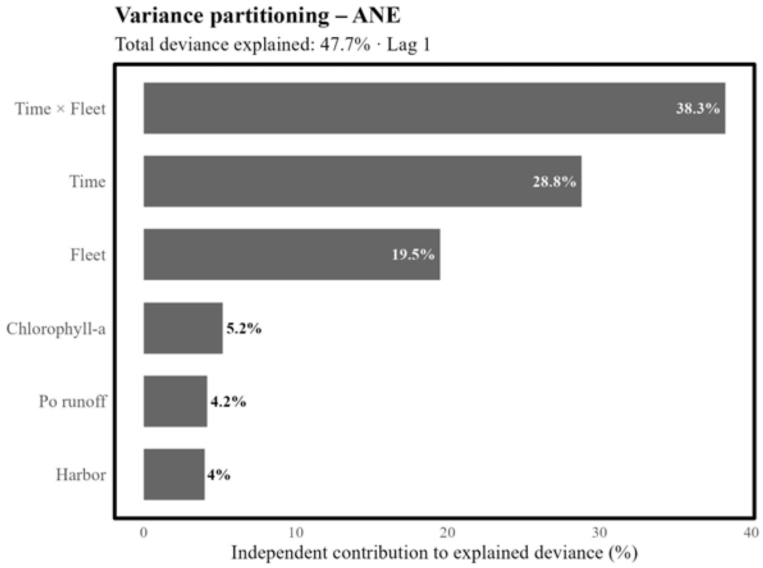

FIGURE 3
Variance partitioning of deviance for the best GAM model of anchovy (ANE). Bars represent the independent contribution of each predictor to the total deviance explained (47.7%), as estimated through hierarchical partitioning of deviance. Percentage values for each predictor are displayed.

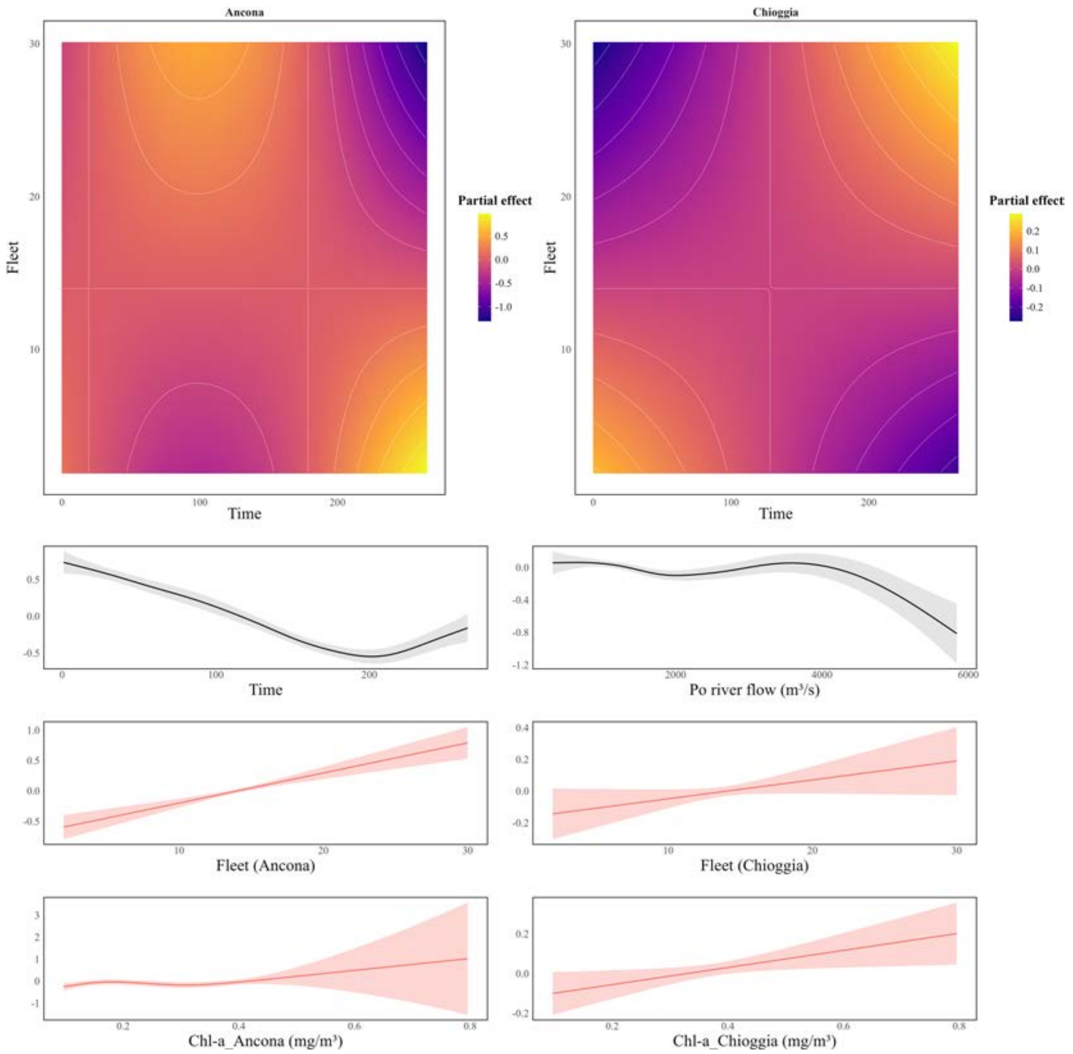

FIGURE 4
Partial effect plots for the best-fitting GAM explaining *wML* of anchovy including the interaction between *Time* and Fleet, temporal proxy (*Time*) and key covariates. Shaded areas represent 95% confidence intervals. Covariates stratified by *Harbor* are indicated in red to distinguish their port-specific effects.

In Ancona, the interaction surface appears relatively flat and symmetrical, indicating a weak or negligible joint effect between *Time* and *Fleet*. This aligns with the statistical results showing a non-significant interaction ($p = 0.55$), suggesting that temporal changes in fleet activity have had little influence on sardine size in this area over the study period. In Chioggia, by contrast, the surface displays more pronounced undulations and localized gradients, with alternating zones of positive and negative partial effects. This pattern points to a more complex temporal modulation of the *Fleet* effect, consistent with the near-significant interaction ($p \approx 0.05$). It suggests that in the northern Adriatic Sea, variations in fleet dynamics through time may have intermittently influenced sardine size—perhaps reflecting shifts in fishing intensity, target composition, or spatial overlap with sardine aggregations during specific periods. *Time* smoother (Figure 6). middle-left panel) showed a gradual decline in *wML* between 2004 and 2016, followed by a moderate upward shift in the final years. This trajectory aligned with patterns often associated with sustained external pressures followed by periods of stabilization. The effect of *Temp* (Figure 6 middle-right panel) followed a sigmoid shape, with *wML* increasing up to approximately 13.5°C, plateauing at 20°C and decreasing above this limit, suggesting the presence of a thermal window beyond which growth conditions may become less favorable. The *Fleet* smoother (Figure 6 bottom panels) indicated port-specific differences: i) in Chioggia, sardine size appeared to decline at a certain number of fishing vessels, coinciding with the rise in landings in Chioggia (Supplementary Figure S1). Conversely, the largest sardine sizes were observed at the beginning of the time series, when a high number of fishing vessels operated in this harbor exerting a fishing activity that has not yet had a notable impact on this species, ii) in Ancona no consistent trend is observed.

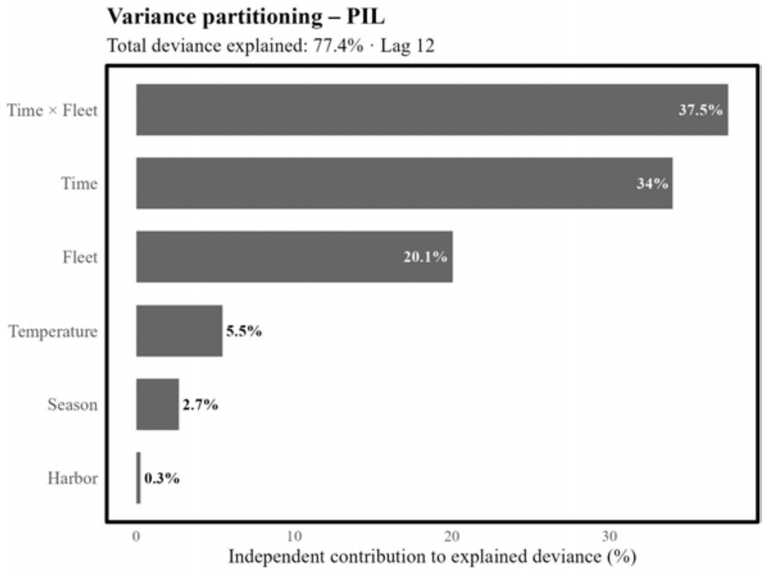

FIGURE 5
Variance partitioning of deviance for the best GAM model of sardine (PIL). Bars represent the independent contribution of each predictor to the total deviance explained (77.4.%), as estimated through hierarchical partitioning of deviance. Percentage values for each predictor are displayed.

4 Discussion

Currently, the reduction small pelagic fish size is a major concern for fishers in the Adriatic Sea and can also have relevant implication for the entire basin ecosystem. In this study, long-term fishery-dependent data covering 22 years has been used to investigate changes in the mean length of anchovy and sardine living in this basin in relation to a suite of environmental and anthropogenic drivers. Although fishery-dependent data have known limitations, such as lack of standardization, dependence on fleet behavior (e.g., changes in fishing gear, technology, grounds, and effort) and sensitivity to market dynamics (Pauly et al., 1998; Fortibuoni et al., 2017), they have proven valuable in tracking changes in marine populations (Azzurro et al., 2011; Tzanatos et al., 2014; Fortibuoni et al., 2015).

4.1 Long-term effects of unmanaged fishing pressure

The temporal smoother (*Time*) in our GAMs encompassed phenomena that were not quantified, and its strong statistical signal suggested that persistent processes acting over time have had a major influence on the size structure of small pelagic fish in the Adriatic Sea. Therefore, its inclusion may more effectively capture dynamic ecosystem and fishery processes or account for non-stationary catchability and shifting effort allocation over time—particularly when other covariates (i.e. environmental variables) fall short (Maunder and Punt, 2004). One of the most plausible interpretations is that this effect reflects the cumulative impact of unmanaged or poorly regulated fishing pressure over the past decades. In the Adriatic Sea, fisheries policy historically lacked coordinated spatial and temporal measures, and enforcement has been limited (Carpi et al., 2017; FAO, 2023). Until recent years, effort controls were almost absent, and capacity reductions were not always accompanied by limits on fishing efficiency (Lucchetti et al., 2018). As a result, fishing practices have intensified, favoring short-term gains over sustainability. This pattern is strongly suggestive of legacy effects from decades of largely unmanaged fishing pressure. In the Adriatic Sea, regulatory mechanisms for small pelagics have historically lagged ecological signals. Weak enforcement and the absence of total allowable catch (TAC) systems in the Mediterranean Sea (FAO, 2023; Carpi et al., 2017) until recent years, allowed for chronic overexploitation, particularly during the 1980s and 1990s when fleet modernization and size-selective harvesting intensified. Several studies (Cingolani et al., 1996; Santojanni et al., 2005; Colloca et al., 2011; Tsikliras et al., 2015) highlighted the persistent targeting of large individuals during peak spawning, contributing to demographic truncation and potential shifts in life-history traits in small pelagic populations.

This phenomenon is further exacerbated by technological creep—enhancements in engine power, sonar and GPS-based navigation—that effectively increase fishing capacity without expanding the nominal fleet size (Hilborn and Walters, 1992; Fortibuoni et al., 2017). These changes, which are under-represented in traditional effort statistics, align with what Pauly et al. (1998) described as “creeping capacity”—a silent driver of stock erosion. The rising trend in effective fishing power, despite stagnating or declining vessel numbers, supports the notion that fishing intensity has remained high or even increased.

Such effects mirror those observed in other regions. In the North Sea, Baudron et al. (2014) demonstrated that size declines in cod were linked to prolonged overfishing. Similarly, Van Beveren et al. (2014) linked long-term shifts in body size and life history to

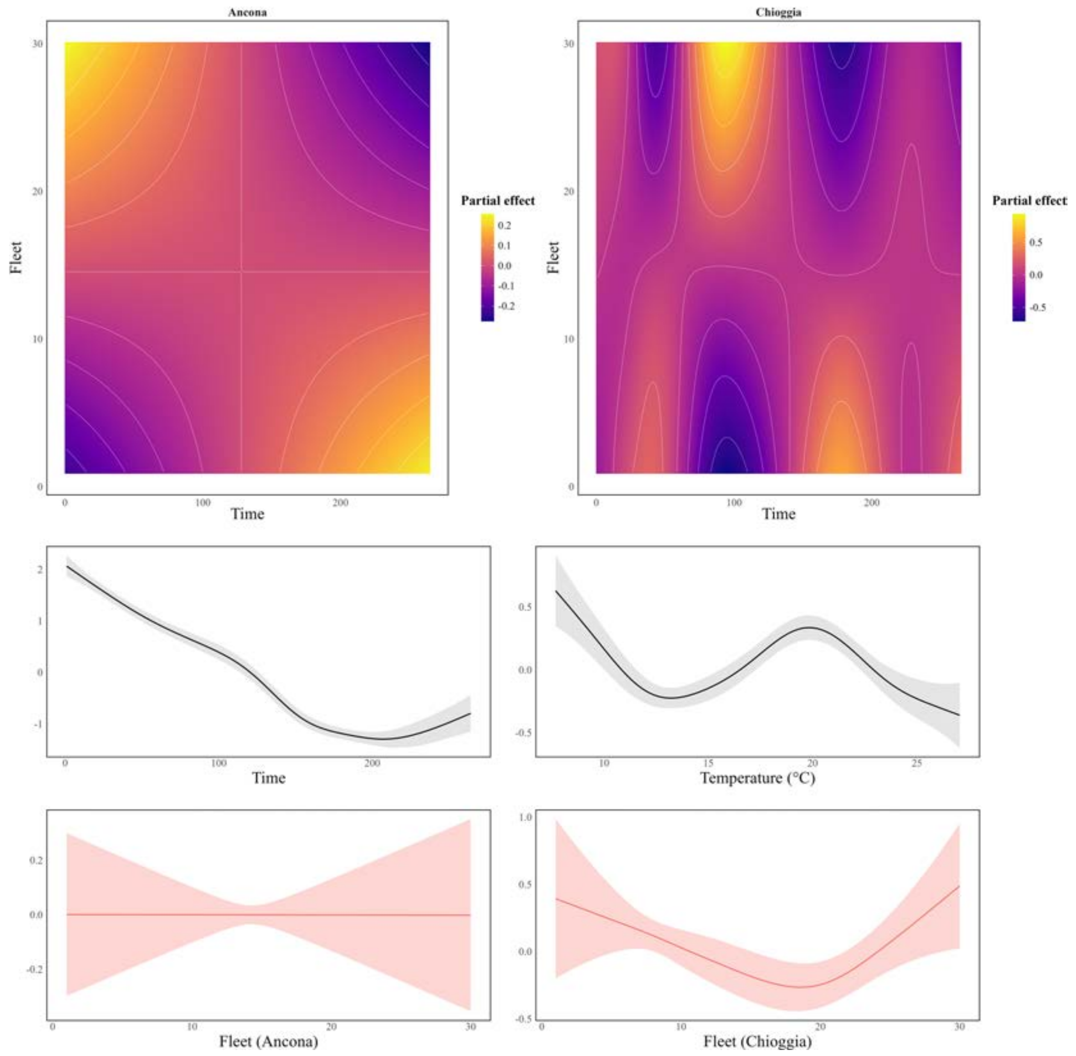

FIGURE 6
Partial effect plots for the best-fitting GAM explaining *wML* of sardine including the interaction between *Time* and Fleet, temporal proxy (*Time*) and key covariates. Shaded areas represent 95% confidence intervals. Covariates stratified by *Harbor* are indicated in red to distinguish their port-specific effects.

fishery-induced evolution in Peruvian anchoveta. Our findings contributed to this literature flow, suggesting that the Adriatic may represent another case in which insufficient management response has led to enduring demographic and phenotypic shifts.

From a management standpoint, the implication is clear: historical overfishing may have altered the baseline state of these populations, reducing their responsiveness to future management interventions. This adds urgency to calls for adaptive, ecosystem-based management frameworks that consider historical legacies alongside current exploitation rates (Pikitch et al., 2004; Trenkel, 2018; Halpern et al., 2019).

4.2 Fishing pressure and its impact on size structure

Our GAM results revealed spatially heterogeneous relationships between *Fleet* size and *wML*, along with species-specific responses to fishing pressure. For anchovy, we observed a positive association: the relationships were moderately increasing for both harbors (Figure 4, middle panels). While this trend may initially appear counterintuitive, a better look on the interaction between *Fleet* and *Time* (Figure 4, top panels) it reflects underlying historical dynamics. In earlier decades, both fleet size and *wML* were higher, whereas recent years are characterized by fewer vessels but smaller individuals, suggesting that technological improvements and spatial expansion of fishing activities have compensated for the numerical decline in fleet size (Supplementary Figure S1).

For sardine, the relationship between *wML* and fleet size differed between the two harbors and appeared more complex (Figure 6, middle panels). In Ancona, the trend was nearly flat, with a slight negative slope, suggesting a weak effect of this covariate on the dependent variable. In contrast, the pattern in Chioggia followed a U-shaped curve, with a local minimum at intermediate fleet sizes (around 17 vessels). These differing responses likely reflect context-dependent effects of fishing pressure. In Ancona, sardines are not a target species, which may explain the lack of a statistically significant trend. Conversely, in Chioggia, where fishers show higher commercial interest for this species, fishing pressure may be shaped by interactions with environmental conditions or fleet dynamics, such as vessel aggregation near spawning grounds (Russo et al., 2015; Coro et al., 2022). It is also important to note that the number of vessels in Chioggia was reported on an annual basis, under the assumption of constant activity throughout the year. Furthermore, fleet sizes exceeding 17 vessels only occurred during the first nine years of the time series. This limited variability, combined with the low representation of high fleet sizes, likely constrained the model's ability to detect a robust relationship between *wML* and this proxy for fishing effort.

Despite these differences, the biological interpretation remains consistent with ecological theory. In exploited fish populations, size structure often reflects the balance between somatic growth and size-selective mortality imposed by fishing (Swain et al., 2007). Larger individuals are more vulnerable to capture because they are more visible to fishing gears, occupy shallower or more accessible habitats, and are preferentially retained due to market demand and gear selectivity (Jennings et al., 1999; Andersen and Brander, 2009). Consequently, sustained fishing pressure typically leads to size truncation under sustained fishing (Patterson, 1992; Planque et al., 2010). Anchovy, due to its short lifespan and rapid growth, is particularly sensitive to such pressure (Peck et al., 2013), whereas sardine, with a longer life cycle and different spatial dynamics, exhibits more complex responses (Mustać et al., 2020; Otero and Hidalgo, 2023). Historical CPUE and VPA analyses have confirmed that declines in size are linked to persistent fishing intensity, particularly in high-effort areas (Cingolani et al., 2001; Santojanni et al., 2002). Management measures—including effort reductions and seasonal closures (e.g. Rec. GFCM/37/2013/1, Rec. GFCM/44/2021/20) —have led to a sharp decline in the number of active vessels (Supplementary Figure S1). This reduction may have helped to lower the fishing pressure on the anchovy stock. This is supported by the most recent stock assessments of both species, which showed a slight recovery of Spawning Stock Biomass (SSB) and a decreasing trend of fishing mortality, which was closed to the reference value for this species (Angelini et al., 2024). Notwithstanding this sign of improvements, size-at-age and overall mean sizes of the stock have still declined or have not fully recovered, likely due to slower growth, truncated age structures, and recruitment failures (Van Beveren et al., 2014; Brosset et al., 2017). In contrast, sardine stock remains under notable fishing pressure, particularly following an increase in Croatian landings over the past two decades (Cikes-Kéc et al., 2024). Furthermore, the use of highly selective traditional gear such as the purse seine (Lampara)—more size-selective than the pelagic trawler (Volante)—intensifies exploitation on larger individuals (Carpi et al., 2017). This may be reinforcing selection for early maturation and smaller adult size, as documented in other intensively exploited systems (Sharpe and Hendry, 2009; Law, 2000; Heino et al., 2015; Albo-Puigserver et al., 2021).

In this study, we used the number of active vessels targeting small pelagic fish as a proxy for fishing pressure. While this metric is consistently available across years, it does not fully capture the true intensity of exploitation, particularly considering technological improvements and changes in fleet composition over time. For example, although the number of vessels has decreased—especially in the Italian fleet—the modern fleet is more efficient, with higher engine power, more effective gear types, and broader spatial reach (Villasante and Sumaila, 2010). This suggests that modern fleets, despite being smaller in number, may exert equivalent or greater selective pressure due to technological advancements and broader spatial coverage. The apparent paradox of fewer vessels but smaller fish thus reflects a shift toward more efficient fishing practices. This pattern underscores the importance of considering both technological change and spatial effort distribution when interpreting exploitation indicators.

To more accurately represent fishing pressure in ecosystem-based analyses, we recommend using higher-level indicators—such as standardized CPUE, effort in kilowatt-days, or fishing mortality (F) from stock assessments—as proposed by Piet et al. (2006). These metrics better capture fleet efficiency, spatial patterns of effort, and technological improvements over time, particularly in areas with vulnerable spawning aggregations.

4.3 Environmental drivers

Aside from anthropogenic pressures, which emerged as the dominant driver of growth decline in Adriatic small pelagic species, our findings reveal a complex, lagged, and species-specific influence of environmental variability on somatic growth. Although the exact life-history phases affected remain uncertain, *wML* likely reflects the average age structure of these short-lived populations (maximum lifespan ~2 years). Within such a narrow age window, the incorporation of environmental lags provides a proxy to link covariate effects to specific life-cycle phases (e.g., recruitment, juvenile growth, or early adult stage), thereby clarifying how environmental forcing may differentially affect anchovy and sardine.

4.3.1 Anchovy

The combination of Po River discharge and chlorophyll-a at 1-month lag likely reflects the immediate influence of environmental variability, possibly affecting anchovy size throughout the life span of this species. In the Adriatic Sea, anchovy spawning generally occurs from late spring through summer, but recruitment becomes ecologically critical in early autumn, when juveniles must locate sufficient food and suitable environmental conditions to support growth and survival (Morello and Arneri, 2009). Santojanni et al. (2006) reported a significant positive effect of Po River discharge on anchovy recruitment. However, Hopkins (2002) suggested that elevated freshwater input could trigger advection processes, transporting larvae and eggs offshore into less nutrient rich environments characterized by different phytoplankton communities (Mozetič et al., 2012).

Water transparency also plays a key role in anchovy foraging efficiency by enhancing prey visibility (Aldanondo et al., 2010). High chlorophyll concentrations, particularly when associated with riverine input, can increase turbidity and hinder visual predation (Brosset et al., 2017). Anchovies possess a flexible feeding strategy, alternating between filter-feeding and active biting depending on prey size and density (Bulgakova, 1993; Zorica et al., 2021). However, this plasticity also makes them more sensitive to turbidity, which directly affects their visual hunting capacity. Anchovies tend to avoid nutrient-rich freshwater plumes (Palomera et al., 2007), and their abundance has been shown to increase in areas farther from turbid estuarine zones (Drake et al., 2007). For instance, Basilone et al. (2017) observed that adult anchovies forage more frequently in offshore waters, where prey availability may be lower, but water clarity is greater, improving detection of prey.

Nonetheless, some studies suggested that anchovy juveniles may occasionally utilize moderately turbid coastal areas as temporary refuge habitats. Drake et al. (2007) and Costalago (2015) noted this behavior, while Tugores et al. (2011) and Giannoulaki et al. (2013) proposed that intermediate levels of chlorophyll and turbidity may benefit early-stage survival by providing food and partial protection from predators.

Our model results are consistent with this interpretation. We found that chlorophyll-a and Po River discharge positively influence anchovy size structure—but only within specific thresholds. In particular, predicted size increased when chlorophyll-a remained below 0.2 mg/m^3 and Po discharge below 4000 m^3/s (Figure 4). These conditions typically occur in areas farther from the river mouth, such as Ancona, where chlorophyll concentrations rarely exceeded 0.4 mg/m^3 (Supplementary Figure S5, panel C). Beyond this threshold, the model produced increasingly wide confidence intervals, reflecting a lack of data support and greater uncertainty for higher chlorophyll values in this area. Conversely, in Chioggia, where chlorophyll-a values reached up to 0.81 mg/m^3, the model showed a more regular, upward trend in predicted size.

Importantly, our findings also indicated that this environmental combination operates at a 1-month lag, which may be explained by the income breeding strategy of anchovy. This reproductive strategy relies on recently acquired energy rather than stored reserves (Schismenou et al., 2024), making anchovy particularly sensitive to short-term changes in food availability and water quality during and just after the spawning season. As such, episodic autumnal events—such as floods and heavy rainfall, increasingly frequent in the northern Adriatic in recent years (Montanari et al., 2023)—may have immediate and direct effects on recruitment success by altering prey accessibility and habitat quality during this critical developmental window.

4.3.2 Sardine

In our model, temperature was selected showing a sigmoidal response that indicates the existence of an optimal thermal window (Figure 6, middle-right panel). This supports earlier observations by Palomera et al. (2007), who reported a phenological shift in sardine populations: while the timing of spawning has remained stable, the period of peak condition has moved from autumn to early summer, likely in response to shifting seasonal prey dynamics. This may also explain why predicted *wML* in our model plateaued when sea surface temperatures exceeded 20°C. Although elevated temperatures enhance metabolic rates, food limitation or misalignment with prey peaks may constrain somatic growth (Brosset et al., 2015, 2016; Van Beveren et al., 2016; Patti et al., 2020; Hattab et al., 2021).

Notably, the selection of both environmental variables at a 12-month lag aligns well with the sardine's capital breeding strategy. Unlike anchovies, sardines spawn during the winter months—when food availability is lowest—and rely on energy reserves accumulated during the previous productive season (Morello and Arneri, 2009; Gkanasos et al., 2019; Albo-Puigserver et al., 2020). This strategy renders them highly dependent on conditions experienced in the spring and summer of the preceding year. Supporting this, Schismenou et al. (2024) found that sardines in the North Aegean Sea exhibited peak condition in summer–early autumn, with significantly reduced energy and lipid content during the reproductive season. Furthermore, while higher autumn and winter temperatures may favor metabolism, they may also disrupt the delicate energy balance required for successful reproduction if prey availability is low or poorly timed. In recent years, sea temperatures during autumn and winter in the Adriatic have remained relatively high (Salini et al., 2024), which may interfere with the effectiveness of capital breeding (Varpe et al., 2009; Sainmont et al., 2014).

In addition to the sigmoidal temperature response, our length data revealed a marked seasonal component that offers further insight into the thermal sensitivity of sardine growth. Analyses on length data (unpublished) showed that the highest variance in *wML* occurs during winter months, coinciding with the spawning period and the presence of multiple cohorts in the population. Conversely, in summer, variance reaches its minimum, as the population becomes dominated by larger individuals. This seasonal stabilization likely results from the growth of age-0 sardines and, at the same time, from thermal constraints on somatic growth as summer sea surface temperatures in the Adriatic Sea often exceed 26 °C, well above the optimal range indicated by our model.

Experimental and field evidence supports this interpretation. Schismenou et al. (2016) identified an optimal growth temperature for juvenile sardines around 24 °C, beyond which growth declines, while Thoral et al. (2023) demonstrated that food deprivation under warm (20 °C) conditions led to rapid depletion of energy reserves and high mortality, in contrast to the energy-saving mechanisms observed at cooler winter temperatures (12°C). These findings suggest that high summer temperatures amplify metabolic stress, limiting energy storage and ultimately constraining growth. Similarly, Albo-Puigserver et al. (2020) described strong seasonal fluctuations in sardine energy density and lipid content, with maximum values in spring–summer and a sharp decline by early autumn, reflecting the depletion of energy reserves under thermal and trophic stress. This pattern is consistent with the capital breeding strategy described above, where energy accumulated during the productive season is subsequently mobilized for winter reproduction (Morello and Arneri, 2009; Albo-Puigserver et al., 2020).

From a broader biogeographical perspective, Dimarchopoulou and Tsikliras (2022) showed that sardine asymptotic length is negatively correlated with sea temperature and positively with oxygen concentration, implying that warming and oxygen limitation can drive a reduction in body size. The same conclusion is echoed by the Gill-Oxygen Limitation Theory (Pauly, 2021) and supported by habitat-suitability projections from Lima et al. (2022) and Pennino et al. (2020), which identified optimal sardine habitats at sea surface temperatures between 10°C and 22°C, with future warming expected to reduce suitable areas in the Mediterranean basin.

In conclusion, these findings suggest that the seasonal modulation in size structure observed in the Adriatic sardine population results from the interaction between temperature-driven metabolic constraints, prey availability and the species' reproductive strategy. During the summer, when temperatures exceed the thermal optimum and prey composition shifts toward smaller, less energetic plankton (Thoral et al., 2023), growth and condition are likely limited despite the apparent dominance of larger individuals. In winter, by contrast, the coexistence of multiple cohorts and increased size variance reflect both active recruitment and the redistribution of stored energy toward reproduction. This dynamic interplay highlights how ongoing warming trends in the Adriatic Sea may progressively narrow the thermal and energetic window within which sardines can sustain both somatic growth and reproductive output, ultimately threatening the resilience of this capital-breeding population.

4.4 Socio-economic implications

The reduction in *wML* of anchovy and sardine observed in the Adriatic Sea has had clear ecological implications but also significant economic consequences for coastal communities reliant on these stocks. In ports such as Chioggia and Ancona, which historically constituted major hubs for pelagic fisheries, a sharp decline in average fish size has coincided with a parallel drop in both landings and fleet size (Supplementary Figure S1), indicating a contraction of the fishery sector. According to the FAO (2023), Italy remains among the top contributors to capture small pelagics in the Mediterranean; however, its production declined by nearly 29% between 2018 and 2021, a trend partly attributable to the reduced commercial value of smaller individuals and increased operational costs.

Smaller fish yield lower prices per kilogram and are less suited for high-value processing, reducing profit margins and disincentivising long trips or fleet maintenance (Colloca et al., 2017). This situation is especially critical in the northern Adriatic, where pelagic pair trawling has historically supported a sizable portion of the local economy (Cingolani et al., 1996; Barausse et al., 2009). The loss of size structure thus translates into reduced economic returns per unit effort (Quezada-Escalona et al., 2025), creating a negative feedback loop between resource condition and fishing capacity. Moreover, Carpi et al. (2015) noted that fisheries targeting small pelagics in the Adriatic are highly vulnerable to combine environmental and anthropogenic stressors, which can amplify socio-economic risks. Furthermore, as previously noted by Basilone et al. (2017), persistent reductions in mean fish length may also affect recruitment and long-term stock productivity, triggering a feedback loop that further destabilizes local economies.

In ports like Ancona and Chioggia, the reduction in average catch size exacerbates existing vulnerabilities, contributing to ageing fleets, job loss, and community-level economic instability. These findings reinforce the need for adaptive management strategies that not only target stock recovery but also consider the socio-economic resilience of fishing communities.

Our GAM results confirm that fishing effort (*Fleet*) remains a key predictor of size structure, with port-specific interactions pointing to different exploitation regimes. The economic effects of this biological contraction are compounded by external pressures, including rising fuel costs (Sabatella et al., 2017) and reduced consumer demand for smaller fish.

Studies such as the present work, along with others focused on GAM modeling and small pelagic fisheries (e.g., Falco et al., 2007; Tugores et al., 2011; Giannoulaki et al., 2013; Carpi et al., 2015), as well as research promoting ecosystem-based fisheries management (EBFM) approaches (e.g., Coll et al., 2007, 2016, Coll et al., 2016; Piroddi et al., 2017; Russo et al., 2015), have contributed to the development of more targeted and integrated regulatory frameworks. In particular, findings highlighting long-term changes in size structure and the combined influence of fishing and environmental pressures have supported the implementation of precautionary and adaptive management strategies. These include transitional catch limits and seasonal closures, as outlined in GFCM/44/2021/20 Recommendation. Encouragingly, recent assessments—such as the 2023 Stock Assessment Form (SAF) for anchovy in GSAs 17–18 (Angelini et al., 2024)—report early signs of stock stabilization, suggesting that such measures may be beginning to reverse previous declines.

5 Conclusion

This study underscored the value of integrating long-term fishery-dependent data with flexible modeling approaches to uncover the complex drivers of size structure in Adriatic small pelagic species. Our study highlighted the primary impacts of fishing pressure, followed by the influence of specific environmental variables on the size of these species. In addition, spatial resolution and temporal lags proved to be essential components of this type of analysis, as the effects of the examined variables influence these stocks at different scales, depending on the feeding and breeding strategy of each species. In fact, anchovy appears to be more responsive to short-term productivity pulses but negatively affected by freshwater surges, while sardine is shaped by delayed environmental conditions, particularly thermal regimes, with regional differences in the role of primary productivity. This differentiation is critical in the context of climate change, which is expected to reduce freshwater input, raise sea surface temperatures, and modify phytoplankton dynamics across the Adriatic Sea (Giannoulaki et al., 2013; Lindmark et al., 2022). Understanding how these environmental changes interact with fishing pressure will be essential for the sustainable management of small pelagic fish under shifting ecological baselines (Quezada-Escalona et al., 2025; Planque et al., 2010; Van Beveren et al., 2014). This knowledge supported the urgent need for adaptive, ecosystem-based management strategies that consider historical legacies and species-specific responses to exploitation.

Data availability statement

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

Author contributions

RC: Data curation, Formal Analysis, Methodology, Validation, Writing – original draft, Writing – review & editing. VC: Data curation, Formal Analysis, Methodology, Writing – original draft, Writing – review & editing. SG: Formal Analysis, Methodology, Supervision, Writing – review & editing. AS: Supervision, Writing – review & editing, Data curation. SC: Data curation, Writing – review & editing. FiD: Data curation, Writing – review & editing. FoD: Data curation, Writing – review & editing. SA: Supervision, Writing – original draft, Writing – review & editing, Data curation.

Funding

The author(s) declared that financial support was not received for this work and/or its publication.

Acknowledgments

The authors acknowledge the Italian National Program and the DCF program for providing the length data. The authors thank all the CNR-IRBIM colleagues involved in the sampling of these two projects. The research leading to these results was conceived as part of the International Ph.D. Program "Innovative Technologies and Sustainable Use of Mediterranean Sea Fishery and Biological Resources" (www.FishMed-PhD.org) and represents partial fulfillment of the requirements for VC's Ph.D. thesis.

Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

The author(s) declared that generative AI was not used in the creation of this manuscript.

Any alternative text (alt text) provided alongside figures in this article has been generated by Frontiers with the support of artificial intelligence and reasonable efforts have been made to ensure accuracy, including review by the authors wherever possible. If you identify any issues, please contact us.

Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2025.1703481/full#supplementary-material

References

Albo-Puigserver, M., Pennino, M. G., Bellido, J. M., Colmenero, A. I., Girldez, A., Hidalgo, M., et al. (2021). Changes in life history traits of small pelagic fish in the western mediterranean sea. *Front. Mar. Sci.* 8. doi: 10.3389/fmars.2021.570354

Albo-Puigserver, M., Sánchez, S., Coll, M., Bernal, M., Sáez-Liante, R., Navarro, J., et al. (2020). Year-round energy dynamics of sardine and anchovy in the north-western Mediterranean Sea. *Mar. Environ. Res.* 159, 105021. doi: 10.1016/j.marenvres.2020.105021

Aldanondo, N., Cotano, U., Tiepolo, M., Boytra, G., and Irigoien, X. (2010). Growth and movement patterns of early juvenile European anchovy (Engraulis encrasicolus L.) in the Bay of Biscay based on otolith microstructure and chemistry. *Fish. Oceanogr.* 19, 196–208. doi: 10.1111/j.1365-2419.2010.00537.x

Andersen, K. H., and Brander, K. (2009). Expected rate of fisheries-induced evolution is slow. *PNAS.* 106, 11657–11660. doi: 10.1073/pnas.0901690106

Angelini, S., Armelloni, E. N., Costantini, I., De Felice, A., Isajlović, I., Leonori, I., et al. (2021). Understanding the dynamics of ancillary pelagic species in the adriatic sea. *Front. Mar. Sci.* 8. doi: 10.3389/fmars.2021.728948

Angelini, S., Biagiotti, I., Bratina, P., Cikes-Kéc, V., Costantini, I., De Felice, A., et al. (2024). *Stock assessment form small pelagics—Anchovy—GSA 17 and 18.* Available online at: https://www.fao.org/gfcm/data/safs/en (Accessed July 2024).

Aragão, L., Mentaschi, L., Pinardi, N., Verri, G., Senatore, A., and Di Sabatino, S. (2024). The freshwater discharge into the Adriatic Sea revisited. *Front. Clim.* 6. doi: 10.3389/fclim.2024.1368456

Azzurro, E., Moschella, P., and Maynou, F. (2011). Tracking signals of change in Mediterranean fish diversity based on local ecological knowledge. *PLoSONE.* 6, e24885. doi: 10.1371/journal.pone.0024885

Bakun, A. (2006). Wasp-waist populations and marine ecosystem dynamics: Navigating the "predator pit" topographies. *Progr. Oceanogr.* 68, 271–288. doi: 10.1016/j.pocean.2006.02.004

Barange, M., Bahri, T., Beveridge, M. C. M., Cochrane, K. L., Funge-Smith, S., and Poulain, F. (2018). "Impacts of climate change on fisheries and aquaculture. Synthesis of current knowledge, adaptation and mitigation options," in *FAO fisheries and aquaculture technical paper no. 627* (Rome, Italy: FAO), 654.

Barausse, A., Duci, A., Mazzoldi, C., Artioli, Y., and Palmeri, L. (2009). Trophic network model of the Northern Adriatic Sea: analysis of an exploited and eutrophic ecosystem. *Estuar. Coast. Shelf* S. 83, 577–590. doi: 10.1016/j.ecss.2009.05.003

Basilone, G., Mangano, S., Pulizzi, M., Fontana, I., Giacalone, G., Ferreri, R., et al. (2017). European anchovy (Engraulis encrasicolus) age structure and growth rate in two contrastedareas of the Mediterranean Sea: the paradox of faster growth in oligotrophic seas. *Medit. Mar. Sci.* 18, 504–516. doi: 10.12681/mms.2059

Baudron, A. R., Needle, C. L., Rijnsdrop, A. D., and Marshall, C. T. (2014). Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes. *Glob. Change Biol.* 20, 1023–1031. doi: 10.1111/gcb.12514

Bigelow, K. A., Boggs, C. H., and He, X. (1999). Environmental effects on swordfish and blue shark catch rates in the US North Pacific longline fishery. *Fish. Oceanogr.* 8, 178 –198. doi: 10.1046/j.1365-2419.1999.00105.x

Brosset, P., Fromentin, J. M., Van Beveren, E., Lloret, J., Marques, V., Basilone, G., et al. (2017). Spatio-temporal patterns and environmental controls of small pelagic fish body condition from contrasted Mediterranean areas. *Prog. Oceanogr.* 151, 149–162. doi: 10.1016/j.pocean.2016.12.002

Brosset, P., Lloret, J., Muñoz, M., Fauvel, C., Van Beveren, E., Marques, V., et al. (2016). Body reserves mediate trade-offs between life-history traits: new insights from small pelagic fish reproduction. *R. Soc Open Sci.* 3, 160202. doi: 10.1098/rsos.160202

Brosset, P., Ménard, F., Fromentin, J.-M., Bonhommeau, S., Ulses, C., Bourdeix, J.-H., et al. (2015). Influence of environmental variability and age on the body condition of small pelagic fish in the Gulf of Lions. *Mar. Ecol. Prog. Ser.* 529, 219–231. doi: 10.3354/meps11275

Bulgakova, Y. V. (1993). Daily feeding dynamics of the Black Sea anchovy, Engraulis encrasicholus. *J. Ichthyol.* 33, 78–88.

Burnham, K. P., and Anderson, D. R. (2002). "Model selection and multimodel inference," in *A practical information-theoretic approach*, *2nd* (Springer-Verlag Inc, New York).

Carpi, P., Martinelli, M., Belardinelli, A., Russo, A., Arneri, E., Coluccelli, A., et al. (2015). Coupling an oceanographic model to a Fishery Observing System through mixed models: The importance of fronts for anchovy in the Adriatic Sea. *Fish. Oceanogr.* 24, 521–532. doi: 10.1111/fog.12126

Carpi, P., Scarcella, G., and Cardinale, M. (2017). The saga of the management of fisheries in the Adriatic Sea: History, flaws, difficulties, and successes toward the application of the common fisheries policy in the Mediterranean. *Front. Mar. Sci.* 4. doi: 10.3389/fmars.2017.00423

Cikes-Kéc, V., Angelini, S., Biagiotti, I., Bratina, P., De Felice, A., Juretic, T., et al. (2024). *Stock assessment form small pelagics—Sardine—GSA 17 and 18.* Available online at: https://www.fao.org/gfcm/data/safs/en (Accessed July 2024).

Cingolani, N., Arneri, E., Giannetti, G., Santojanni, A., Belardinelli, A., Colella, S., et al. (2001). The small pelagic fisheries on the Western coast of the Adriatic Sea: monitoring and assessment. Priority topics related to small pelagic fishery resources of the Adriatic Sea in FAO-MiPAF Scientifc Cooperation to Support Responsible Fisheries in the Adriatic Sea. GCP/RER/010/ITA/TD-03. *AdriaMed Tech. Documents.* 3, 39–52.

Cingolani, N., Giannetti, G., and Arneri, E. (1996). Anchovy fisheries in the adriatic sea. *Sci. Mar.* 60, 269–277.

Coll, M., Santojanni, A., Palomera, I., and Arneri, E. (2009). Food-web changes in the Adriatic Sea over the last three decades. *Mar. Ecol. Prog. Ser.* 381, 17–37. doi: 10.3354/meps07944

Coll, M., Santojanni, A., Palomera, I., Tudela, S., and Arneri, E. (2007). An ecological model of the Northern and Central Adriatic Sea: Analysis of ecosystem structure and fishing impacts. *J. Mar. Syst.* 67, 119–154. doi: 10.1016/j.jmarsys.2006.10.002

Coll, M., Shannon, L. J., Kleisner, K. M., Juan-Jordá, M. J., Bundy, A., Akoglu, A. G., et al. (2016). Ecological indicators to capture the effects of fishing on biodiversity and conservation status of marine ecosystems. *Ecol. Ind.* 60, 947–962. doi: 10.1016/j.ecolind.2015.08.048

Colloca, F., Cardinale, M., Maynou, F., Giannulaki, M., Scarcella, G., Jenko, K., et al. (2011). Rebuilding Mediterranean fisheries: a new paradigm for ecological sustainability. *Fish Fish.* 14, 89–109. doi: 10.1111/j.1467-2979.2011.00453.x

Colloca, F., Scarcella, G., and Libralato, S. (2017). Recent trends and impacts of fisheries exploitation on Mediterranean stocks and ecosystems. *Front. Mari Sci.* 4. doi: 10.3389/fmars.2017.00244

Copernicus Marine Environment Monitoring Service (2024). Available online at: http://marine.copernicus.eu/ (Accessed July 2024).

Coro, G., Tassetti, A. N., Armelloni, E. N., Pulcinella, J., Ferrà, C., Sprovieri, M., et al. (2022). COVID-19 lockdowns reveal the resilience of Adriatic Sea fisheries to forced fishing effort reduction. *Sci. Rep.* 12, 1–14. doi: 10.1038/s41598-022-05142-w

Costalago, D. (2015). Review on the links between the distribution of larvae and juveniles of anchovy and sardine with their ecological dynamics in the Northwestern Mediterranean. *Vie Milieu.* 65, 101–113.

Cury, P., Bakun, A., Crawford, R. J. M., Jarre, A., Quiñones, R. A., Shannon, L. J., et al. (2000). Small pelagics in upwelling systems: Patterns of interaction and structural changes in "wasp-waist ecosystems. *ICES J. Mar. Sci.* 57, 603–618. doi: 10.1007/s10641-022-01229-5

Dimarchopoulou, D., and Tsikliras, A. (2022). Linking growth patterns to sea temperature and oxygen levels across European sardine (Sardina pilchardus). *Environ. Biol. Fish.* 105:1335–1345. doi: 10.1007/s10641-022-01229-5

Drake, P., Borlán, A., González-Ortegón, E., Baldó, F., Vilas, C., and Fernández-Delgado, C. (2007). Spatio-temporal distribution of early life stages of the European anchovy Engraulis encrasicolus L. within a European temperate estuary with regulated freshwater inflow: effects of environmental variables. *J. Fish. Biol.* 70, 1689–1709. doi: 10.1111/j.1095-8649.2007.01433.x

European Commission (2017). *Regulation (EU) 2017/1004 on the establishment of a Union framework for the collection, management and use of data in the fisheries sector and support for scientific advice regarding the common fisheries policy and repealing Council Regulation (EC) No 199/2008* (Brussels: European Commission).

Falco, P., Belardinelli, A., Santojanni, A., Cingolani, N., Russo, A., and Arneri, E. (2007). An observing system for the collection of fishery and oceanographic data. *Ocean Sci.* 3, 189–203. doi: 10.5194/os-3-189-2007

Fernández-Corredor, E., Albo-Puigserver, M., Pennino, M. G., Bellido, J. M., and Coll, M. (2021). Influence of environmental factors on different life stages of European anchovy (Engraulis encrasicolus) and European sardine (Sardina pilchardus) from the Mediterranean Sea: A literature review. *Reg. Stud. Mar. Sci.* 41, 101606. doi: 10.1016/j.rsma.2020.101606

Food and Agriculture Organization (2023). "The state of mediterranean and black sea fisheries 2023 – special edition," in *General fisheries commission for the mediterranean* (Rome: FAO). doi: 10.4060/cc8888en

Food and Agriculture Organization (2025). *Number of fishing vessels: fishing effort indicator*. Available online at: https://www.fao.org/cwp-on-fishery-statistics/handbook/capture-fisheries-statistics/fishing-effort/en/ (Accessed January 28, 2025).

Fortibuoni, T., Aldighieri, F., Giovanardi, O., Pranovi, F., and Zucchetta, M. (2015). Climate impact on Italian fisheries (Mediterranean Sea). *Reg. Environ. Change* 15, 931:937. doi: 10.1007/s10113-015-0781-6

Fortibuoni, T., Giovanardi, O., Pranovi, F., Raicevich, S., Solidoro, C., and Libralato, S. (2017). Analysis of long-term changes in a Mediterranean marine ecosystem based on fishery landings. *Front. Mar. Sci.* 4. doi: 10.3389/FMARS.2017.00033

Giani, M., Djakovac, T., Degobbis, D., Cozzi, S., Solidoro, C., and Umani, S. F. (2012). Recent changes in the marine ecosystems of the northern Adriatic Sea. *Estuar. Coast. Shelf* S. 115, 1–13. doi: 10.1016/j.ecss.2012.08.023

Giannoulaki, M., Iglesias, M., Tugores, M. P., Bonanno, A., Patti, B., De Felice, A., et al. (2013). Characterizing the potential habitat of European anchovy Engraulis encrasicolus in the Mediterranean Sea, at different life stages. *Fish. Oceanogr.* 22, 69–89. doi: 10.1111/fog.12005

Gkanasos, A., Somarakis, S., Tsiaras, K., Kleftogiannis, D., Giannoulaki, M., Schismenou, E., et al. (2019). Development, application and evaluation of a 1-D full life cycle anchovy and sardine model for the North Aegean Sea (Eastern Mediterranean). *PloS One* 14, e0219671. doi: 10.1371/journal.pone.0219671

Grbec, B., Morović, M., Matić, F., Gladan, Ninćević, Marasović, I., Vidjak, O., et al. (2015). Climate regime shifts and multi-decadal variability of the Adriatic Sea pelagic ecosystem. *Acta Adriat.* 56, 66.

Halpern, B. S., Frazier, M., Afflerbach, J., Lowndes, J. L., Micheli, F., O'Hara, C., et al. (2019). Recent pace of change in human impact on the world's ocean. *Sci. Rep.* 9, 11609. doi: 10.1038/s41598-019-47201-9

Hattab, T., Gucu, A., Ventero, A., De Felice, A., Machias, A., Saraux, C., et al. (2021). Temperature strongly correlates with regional patterns of body size variation in Mediterranean small pelagic fish species. *Mediterr. Mar. Sci.* 22, 800–811. doi: 10.12681/mms.26525

Heino, M., Pauli, B. D., and Dieckmann, U. (2015). Fisheries-induced evolution. *Annu. Rev. Ecol. Evol.* S. 46, 461–480. doi: 10.1146/annurev-ecolsys-112414-054339

Hilborn, R., and Walters, C. J. (1992). Quantitative fisheries stock assessment: Choice, dynamics and uncertainty. *Rev. Fish Biol. Fisheries* 2, 177–178. doi: 10.1007/BF00042883

Hopkins, T. H. (2002). Abiotic variability and biocomplexity in the Northern Adriatic, some research perspectives. *Biol. Mar. Medit.* 9, 1–47.

James, G., Witten, D., Hastie, T., and Tibshirani, R. (2023). *An introduction to statistical learning with applications in R. 2ed* (New York, NY: Springer).

Jennings, S., Greenstreet, S. P. R., and Reynolds, J. D. (1999). Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *J. Anim. Ecol.* 68, 617–627. doi: 10.1046/j.1365-2656.1999.00312.x

Lai, J., Tang, J., Li, T., Zhang, A., and Mao, L. (2024). Evaluating the relative importance of predictors in Generalized Additive Models using the gam.hp R package. *Plant Divers.* 46, 542–546. doi: 10.1016/j.pld.2024.06.002

Law, R. (2000). Fishing, selection, and phenotypic evolution. *ICES J. Mar. Sci.* 57, 659–668. doi: 10.1006/jmsc.2000.0731

Leonori, I., Tičina, V., Giannoulaki, M., Hattab, T., Iglesias, M., Bonanno, A., et al. (2021). History of hydroacoustic surveys on small pelagic fish species in the European Mediterranean Sea. *Mediterr Mar. Sci.* 22, 751–768. doi: 10.12681/mms.26001

Lima, A. R. A., Baltazar-Soarez, M., Garrido, S., Riveiro, I., Carrera, P., Piecho-Santos, M. A., et al. (2022). Forecasting shift in habitat suitability across the distribution range of a temperate small pelagic fish under different scenarios of climate change. *Sci. Total Environ.* 804, 15167. doi: 10.1016/j.scitotenv.2021.150167

Lindmark, M., Audzijonyte, A., Blanchard, J. L., and Gardmark, A. (2022). Temperature impacts on fish physiology and resource abundance lead to faster growth but smaller fish sizes and yields under warming. *Glob. Change Biol.* 28, 6239–6253. doi: 10.1111/gcb.16341

Lleonart, J., and Maynou, F. (2003). Fish stock assessments in the Mediterranean: state of the art. *Sci. Mar.* 67, 37–49. doi: 10.3989/scimar.2003.67s137

Lucchetti, A., Belardinelli, A., D'Andrea, L., Marčeta, B., Martinelli, M., Russo, T., et al. (2018). Small pelagic purse seines in the Adriatic Sea: A spatial analysis and technical overview in relation to Mediterranean Regulation provisions. *Mar. Policy.* 98, 104–114. doi: 10.1016/j.marpol.2018.09.031

Malavolti, S., Ruggeri, P., Fioravanti, T., Tičina, V., Costantini, I., De Felice, A., et al. (2021). Temporal and spatial genetic variation of Engraulis encrasicolus in the Adriatic Sea. *Mediterr. Mar. Sci.* 22, 843–857. doi: 10.12681/mms.25990

Marini, M., and Grilli, F. (2023). The role of Nitrogen and Phosphorus in eutrophication of the Northern Adriatic Sea: History and future scenarios. *Appl. Sci.* 13, 9267. doi: 10.3390/app13169267

Maunder, M. N., and Punt, A. E. (2004). Standardizing catch and effort data: a review of recent approaches. *Fish. Res.* 70, 141–159. doi: 10.1016/j.fishres.2004.08.002

Montanari, A., Nguyen, H., Rubinetti, S., Ceola, S., Galelli, S., Rubino, A., et al. (2023). Why the 2022 Po River drought is the worst in the past two centuries. *Sci. Adv.* 9, eadg8304. doi: 10.1126/sciadv.adg8304

Morello, E. B., and Arneri, E. (2009). Anchovy and sardine in the Adriatic Sea — an ecological review. *Oceanogr. Mar. Biol. Annu. Rev.* 47, 256. doi: 10.1201/9781420094220.ch5

Mozetič, P., Francé, J., Kogovšek, T., Talaber, I., and Malej, A. (2012). Plankton trends and community changes in a coastal sea (northern Adriatic): bottom-up vs. top-down control in relation to environmental drivers. *Estuar. Coast. Shelf S.* 115, 138–148.

Mustać, B., Cukar, G. Z., and Vidović, A. (2020). Comparison of growth parametres between sardine sardina pilchardus (Walbaum 1792) and anchovy engraulis encrasicolus (Linnaeus 1758) from the eastern adriatic sea. *J. Marit. Transport. Sci.* 3, 325–333. doi: 10.18048/2020.00.24.

Otero, J., and Hildago, M. (2023). Life-history traits and environment shape small pelagic fish demography and responses to fishing and climate across European Atlantic seas. *ICES J. Mar. Sci.* 80, 1447–1461. doi: 10.1093/icesjms/fsad072

Palomera, I., Olivar, M. P., Salat, J., Sabatés, A., Coll, M., García, A., et al. (2007). Small pelagic fish in the NW Mediterranean Sea: An ecological review. *Prog. Oceanogr.* 74, 377–396. doi: 10.1016/j.pocean.2007.04.012

Patterson, K. (1992). Fisheries for small pelagic species: an empirical approach to management targets. *Rev. Fish Biol. Fisher.* 2, 321–338. doi: 10.1007/BF00043521

Patti, B., Torri, M., and Cuttitta, A. (2020). General surface circulation controls the interannual fluctuations of anchovy stock biomass in the Central Mediterranean Sea. *Sci. Rep.* 10, 0–14. doi: 10.1038/s41598-020-58028-0

Pauly, D. (2021). The gill-oxygen limitation theory (GOLT) and its critics. *Sci. Adv.* 7, eabc6050. doi: 10.1126/sciadv.abc6050

Pauly, D., Christensen, V., Dalsgaard, J., Froese, R., and Torres, F. Jr. (1998). Fishing down marine food webs. *Science.* 279, 860–863. doi: 10.1126/science.279.5352.860

Peck, M. A., Reglero, P., Takahashi, M., and Catalan, I. A. (2013). Life cycle ecophysiology of small pelagic fish and climate-driven changes in populations. *Progr. Oceanogr.* 116, 220–245. doi: 10.1016/j.pocean.2013.05.012

Penna, N., Capellacci, S., and Ricci, F. (2004). The influence of the Po River discharge on phytoplankton bloom dynamics along the coastline of Pesaro (Italy) in the Adriatic Sea. *Mar. pollut. Bull.* 48, 321–326. doi: 10.1016/j.marpolbul.2003.08.007

Pennino, M. G., Coll, M., Albo-Puigserver, M., Fernández-Corredor, E., Steenbeek, J., Giráldez, A., et al. (2020). Current and future influence of environmental factors on small pelagic fish distributions in the Northwestern Mediterranean Sea. *Front. Mar. Sci.* 7. doi: 10.3389/fmars.2020.00622

Piet, G. J., Quirijns, F. J., Robinson, L., and Greenstreet, S. P. R. (2006). Potential pressure indicators for fishing and their data requirements. *ICES J. Mar. Sci.* 64, 110–121. doi: 10.1093/icesjms/fsl006

Pikitch, E. K., Santora, C., Babcock, E. A., Bakun, A., Bonfil, R., Conover, D. O., et al. (2004). Ecosystem based fishery management. *Science.* 305, 346–347. doi: 10.1126/science.1098222

Pinardi, N., Zavatarelli, M., Arneri, E., Crise, A., and Ravaioli, M. (2004). "The physical, sedimentary and ecological structure and variability of shelf areas in the Mediterranean Sea," in *The global coastal ocean*, vol. 14 . Eds. R. R. Robinson and K. H. Brink (Harvard University press, Cambridge), 1243–1272.

Piroddi, C., Coll, M., Liquete, C., Macias, D., Greer, K., Buszowski, J., et al. (2017). Historical changes of the Mediterranean Sea ecosystem: modelling the role and impact of primary productivity and fisheries changes over time. *Sci. Rep.* 7, 44491. doi: 10.1038/srep44491

Planque, B., Fromentin, J. M., Cury, P., Drinkwater, K. F., Jennings, S., Perry, R. I., et al. (2010). How does fishing alter marine populations and ecosystems sensitivity to climate? *J. Mar. Syst.* 79, 403–417. doi: 10.1016/j.jmarsys.2008.12.018

Quezada-Escalona, F. J., Tommasi, D., Kaplan, I. C., Hernvann., P.-Y., Frawley, T. H., Garcia, D., et al. (2025). Socio–economic impacts and responses of the fishing industry and fishery managers to changes in small pelagic fish distribution and abundance. *Rev. Fish. Biol. Fisheries.* 35, 1063–1093. doi: 10.1007/s11160-025-09949-4

Regional Open Data Portal (2024). Available online at: https://simc.arpae.it/dext3r/ (Accessed February 2024).

Russo, T., Pulcinella, J., Parisi, A., Martinelli, M., Belardinelli, A., Santojanni, A., et al. (2015). Modelling the strategy of mid-water trawlers targeting small pelagic fish in the Adriatic Sea and its drivers. *Ecol. Modell.* 300, 102–113. doi: 10.1016/j.ecolmodel.2014.12.001

Sabatella, E. C., Colloca, F., Coppola, G., Fiorentino, F., Gambino, M., Malvarosa, L., et al. (2017). Key economic characteristics of Italian trawl fisheries and management challenges. *Front. Mar. Sci.* 4. doi: 10.3389/fmars.2017.00371

Sainmont, J., Andersen, K., Varpe, Ø., and Visser, A. (2014). Capital versus income breeding in a seasonal environment. *Am. Nat.* 184, 466–476. doi: 10.1086/677926

Salini, R., Tora, S., Filipponi, F., Conte, A., Giansante, C., and Ippoliti, C. (2024). Analyzing trend and heatwaves of 15 years of Sea Surface Temperature Variations along the Italian Adriatic Coast. *Vet. Ital.* 60. doi: 10.12834/VetIt.3583.27524.2

Sani, T., Marini, M., Campanelli, A., MaChado Toffolo, M., Goffredo, S., and Grilli, F. (2024). Evolution of freshwater runoff in the Western Adriatic Sea over the last century. *Environments* 11, 22. doi: 10.3390/environments11010022

Santojanni, A., Arneri, E., Bernardini, V., Cingolani, N., Di Marco, M., and Russo, A. (2006). Effects of environmental variables on recruitment of anchovy in the Adriatic Sea. *Clim. Res.* 31, 181–193. doi: 10.3354/cr031181

Santojanni, A., Cingolani, N., Arneri, E., Giannetti, G., Belardinelli, A., Donato, F., et al. (2002). Calculation of small pelagic catch per unit of fishing effort in the Adriatic Sea. *Biol. Mar. Medit.* 9, 89–95.

Santojanni, A., Cingolani, N., Arneri, E., Kirkwood, G., Belardinelli, A., Giannetti, G., et al. (2005). Stock assessment of sardine (Sardina pilchardus, WALB.) in the Adriatic Sea, with an estimate of discards. *Sci. Mar.* 69, 603–617. doi: 10.3989/scimar.2005.69n4603

Schickele, A., Goberville, E., Leroy, B., Beaugrand, G., Hattab, T., Francour, P., et al. (2020). European small pelagic fish distribution under global change scenarios. *Fish Fish.* 22, 212–225. doi: 10.1111/faf.12515

Schismenou, E., Chatzifotis, S., Tsiaras, K., and Somarakis, S. (2024). Anchovy and sardine condition and energy content in the North Aegean Sea (eastern Mediterranean) in relation to their contrasting reproductive strategies. *J. Fis Biol.* 105, 1178–1188. doi: 10.1111/jfb.15872

Schismenou, E., Palmer, M., Giannoulaki, M., Alvarez, I., Tsiaras, K., Triantafyllou, G., et al. (2016). Seasonal changes in otolith increment width trajectories and the effect of temperature on the daily growth rate of young sardines. *Fish. Oceanogr.* 25, 362–372. doi: 10.1111/fog.12158

Sestelo, M., Villanueva, N. M., Meira-MaChado, L., and Roca-Pardinas, J. (2016). FWDselect: an R package for variable selection in regression models. *R J.* 8, 132–148. doi: 10.32614/RJ-2016-009

Sharpe, D. M. T., and Hendry, A. P. (2009). SYNTHESIS: Life history change in commercially exploited fish stocks: an analysis of trends across studies. *Evol. Appl.* 2, 260–275. doi: 10.1111/j.1752-4571.2009.00080.x

Solanki, H. U., Bhatpuria, D., and Chauhan, P. (2017). Applications of generalized additive model (GAM) to satellite-derived variables and fishery data for prediction of fishery resources distributions in the Arabian Sea. *Geocarto Int.* 32, 43. doi: 10.1080/10106049.2015.1120357

Swain, D. P., Sinclair, A. F., and Hanson, M. K. (2007). Evolutionary response to size-selective mortality in an exploited fish population. *Proc. R. Soc B.* 274, 1015–1022. doi: 10.1098/rspb.2006.0275

Thoral, E., Roussel, D., Gasset, E., Dutto, G., Queiros, Q., McKenzie, D. J., et al. (2023). Temperature-dependent metabolic consequences of food deprivation in the European sardine. *J. Exp. Biol.* 226, jeb244984. doi: 10.1242/jeb.244984

Trenkel, V. M. (2018). How to provide scientific advice for ecosystem-based management now. *Fish Fish.* 19, 390–398. doi: 10.1111/faf.12263

Tsagarakis, K., Palialexis, A., and Vassilopoulou, V. (2014). Mediterranean fishery discards: review of the existing knowledge. *ICES J. Mar. Sci.* 71, 1219–1234. doi: 10.1093/icesjms/fst074

Tsikliras, A. C., Dinouli, A., Tsiros, V.-Z., and Tsalkou, E. (2015). The Mediterranean and Black Sea fisheries at risk from overexploitation. *PloS One* 10, e0121188. doi: 10.1371/journal.pone.0121188

Tugores, M. P., Giannoulaki, M., Iglesias, M., Bonanno, A., Tičina, V., Leonori, I., et al. (2011). Habitat suitability modelling for sardine Sardina pilchardus in a highly diverse ecosystem: the Mediterranean Sea. *Mar. Ecol. Prog. Ser.* 443, 181–205. doi: 10.3354/meps09366

Tzanatos, E., Raitsos, D. E., Triantafyllou, G., Somarakis, S., and Tsonis, A. A. (2014). Indications of a climate effect on Mediterranean fisheries. *Climatic Change.* 122, 41–54. doi: 10.1007/s10584-013-0972-4

Van Beveren, E., Bonhommeau, S., Fromentin, J. M., Bigot, J.-L., Bourdeix, J.-H., Borsset, P., et al. (2014). Rapid changes in growth, condition, size and age of small pelagic fish in the Mediterranean. *Mar. Biol.* 161, 1809–1822. doi: 10.1007/s00227-014-2463-1

Van Beveren, E., Fromentin, J., Rouyer, T., Bonhommeau, S., Brosset, P., and Saraux, C. (2016). The fisheries history of small pelagiscs in the Northern Mediterranean. *ICES J. Mar. Sci.* 73, 1474–1484. doi: 10.1093/icesjms/fsw023

Varpe, Ø., Jørgensen, C., Tarling, G., and Fiksen, Ø. (2009). The adaptive value of energy storage and capital breeding in seasonal environments. *Oikos.* 118, 363–370. doi: 10.1111/J.1600-0706.2008.17036.X

Villasante, S., and Sumaila, U. R. (2010). Estimating the effects of technological efficiency on the European fishing fleet. *Mar. Pol.* 34, 720–722. doi: 10.1016/j.marpol.2009.11.008

Wicklin, R. (2023). *How to interpret spearman and kendall correlation coefficients* (SAS Blogs). Available online at: https://blogs.sas.com/content/iml/2023/04/05/interpret-spearman-kendall-corr.html (Accessed July 2024).

Wood, S. N. (2017). *Generalized additive models: an introduction with R* (Chapman and Hall: CRC press).

Zorica, B., Ezgeta-Balić, D., Vidjak, O., Vuletin, V., Šestanović, M., Isajlović, I., et al. (2021). Diet composition and isotopic analysis of nine important fisheries resources in the Eastern Adriatic Sea (Mediterranean). *Front. Mar. Sci.* 8. doi: 10.3389/fmars.2021.609432