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INTEGRATING KEY ECOSYSTEM COMPONENTS INTO STOCK ASSESSMENT MODELS FOR FISHERY MANAGEMENT

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“Sea belongs to no one, and for
that very reason everyone is
reponsable for It
”

~ Luis Sepúlveda

General Abstract

Small pelagic fishes, particularly European anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*), represent the ecological and economic backbone of the Adriatic Sea fisheries. Their short life cycles, central trophic role and sensitivity to environmental variability make them sentinel species for understanding the combined impacts of fishing pressure and climate change. Over the last decades, both species have undergone marked declines in mean body size and productivity, threatening ecosystem stability and fishery profitability. This PhD project aims to integrate environmental drivers into stock assessment models, thereby improving the robustness of scientific advice and supporting sustainable management of Adriatic small pelagic resources.

The research follows a multidisciplinary approach that combines two complementary methodologies: (i) Generalized Additive Models (GAMs), used to disentangle the effects of fishing and environmental variability on long-term trends in mean fish size; and (ii) Stock Synthesis (SS), employed to incorporate time-varying biological parameters and survey catchability functions directly linked to environmental covariates within population dynamics models. Together, these tools allow for a more realistic representation of the ecological processes that shaping stock dynamics and provide insight into adaptive management strategies under changing environmental conditions.

In Chapter 1, GAMs were applied to two decades of length frequency distribution data (2000–2021) collected from the harbors of Chioggia and Ancona, combined with environmental datasets (sea surface temperature, salinity, chlorophyll-a, Po River discharge) and fishing effort indices. Results suggest that fishing pressure and unmanaged exploitation are the main drivers of size decline in both anchovy and sardine. The temporal smoother, representing long-term cumulative impacts, captured the historical legacy of overfishing, while fleet size exerted clear size-selective effects. Environmental variables also contributed, with species-specific responses: Po River discharge and chlorophyll-a influenced anchovy size dynamics, while temperature affected sardine, particularly with lagged effects. However, these factors explained a smaller portion of variance compared to fishing-related drivers. This highlights the centrality of anthropogenic pressures, while also pointing to the role of ecosystem variability in modulating growth and recruitment success.

Chapter 2 extends the analysis through Stock Synthesis by explicitly embedding environmental covariates into anchovy stock assessment models. Using historical biological and fishery-independent survey data, SS models were parameterized to test the influence of sea surface temperature, Po runoff, chlorophyll-a and salinity on recruitment, growth and mortality. Results confirm that higher temperatures reduce size-at-age, while freshwater inflow modulates catchability and natural mortality, reinforcing the patterns detected by GAMs. These findings provide mechanistic

explanations for observed declines and underscore the need to account for environmental forcing in stock assessments to avoid biased estimates of stock status and reference points.

Chapter 3 presents a preliminary extension of this framework to sardine, thus an SS model including environmental variables was also developed for this stock. Also, the outcomes of this model have been compared with the results of the official sardine assessment run with the Stochastic Production Model in Continuous Time (SPiCT). The SS model successfully reproduced the main population trends identified by SPiCT—namely, a consistent decline in biomass and sustained overexploitation—while adding a higher level of biological realism by accounting for fleet-specific selectivity, recruitment variability, and environmentally driven growth patterns. Among the tested environmental linkages, chlorophyll-a in autumn and salinity in fall and spring emerged as the most influential factors on minimum length and catchability, suggesting that productivity and hydrological conditions play a measurable role in shaping sardine growth and availability to the fishery. These results, together with the diagnostic comparison among SS models, underscore the importance of maintaining multiple complementary approaches for complex, environmentally sensitive stocks such as sardine.

Overall, this thesis contributes to fisheries science by integrating flexible statistical approaches with structured population-dynamics models, enhancing the interpretation of long-term patterns and their consistency with biological processes. The combined use of GAMs and SS not only strengthens our understanding of how fishing and environmental variability interact to shape stock trajectories, but also provides a practical pathway for embedding environmental information into formal stock assessments in the Adriatic Sea. By aligning scientific outputs more closely with ecological reality, this work contributes to the ongoing shift toward ecosystem-informed fisheries management. Its implications extend beyond the Adriatic case study, offering transferable insights for other basins where environmental forcing and fishing pressure interact to determine the resilience of short-lived pelagic species.

Table of contents

GENERAL INTRODUCTION

Study area: Adriatic Sea

The Adriatic Sea is a long, narrow basin located in the central Mediterranean Sea, bordered by the Italian Peninsula to the west and the Balkan Peninsula to the east. It has a northwest-southeast orientation with different topography resulting in distinct environmental features: steep rocky shores dominate the eastern coastline, while the western side is primarily sandy and flat.

The Mediterranean basin is divided in Geographical Sub-Areas (GSAs), which have been established by the FAO General Fisheries Commission for the Mediterranean (GFCM) to facilitate the management of fisheries resources; the Adriatic Sea is split into two GSAs (Fig. 1). The northern and central Adriatic Sea is included in GSA 17; it is characterized by a wide continental shelf with shallow, eutrophic waters, generally not exceeding 100 m in depth, except in the Pomo/Jabuka Pits where depths can reach about 270 m. In contrast, the southern Adriatic Sea, which is comprised in GSA 18, is marked by a much narrower shelf and a steep continental slope, descending into a wide depression exceeding 1200 m in depth, which extends southwards to the Otranto Channel, the connection with the rest of the Mediterranean Sea (Artegiani et al., 1997a). Seasonal changes significantly influence the thermal dynamics of the whole basin, especially in coastal areas where bottom temperatures range from 7°C in winter to 27°C in summer. Deeper waters exhibit reduced thermal variability, with temperatures at 50 meters depth fluctuating between 10°C in winter and 18°C in summer (Russo et al., 2012).

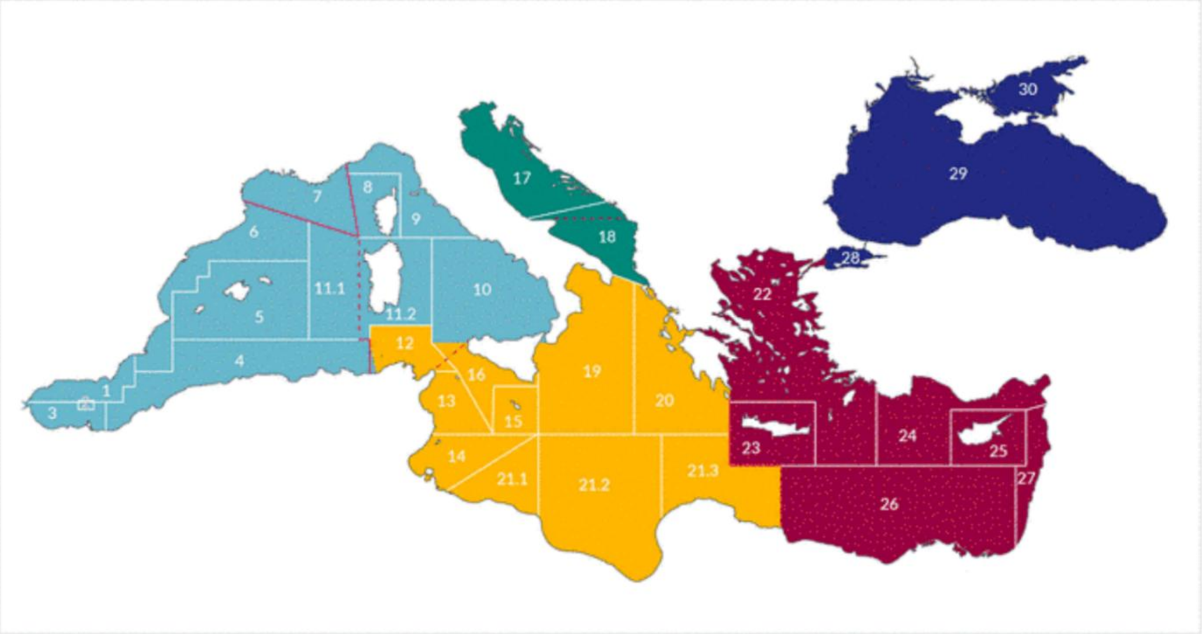

Figure 1 Map of the FAO-GFCM Geographical Sub-Areas (GSAs). GSAs 17 and 18 (green area) correspond to the Adriatic Sea. Source: FAO GFCM website (https://www.fao.org/gfcm/data/maps/gsas/en/).

A key feature of this basin is the substantial freshwater input from numerous rivers, that collectively contribute about 20% of the total river runoff into the Mediterranean Sea (Hopkins, 1999). Notably, the Po River provides nutrient-rich discharges that play a crucial role in sustaining high levels of productivity in the northern Adriatic Sea, making it one of the most biologically active regions in the Mediterranean Sea (Grilli et al., 2020; Sani et al., 2024). The Po River forms a buoyant, nutrient-rich coastal current that flows southward along the Italian coastline, enhancing primary production throughout the basin (Santojanni et al., 2006; Marini and Grilli, 2023).

The Adriatic's hydrodynamics are characterized by a general cyclonic circulation, with two primary currents: one moving northward along the Albanian-Croatian coast and the other flowing southward along the Italian coast. Seasonal cyclonic gyres also form within the northern, central, and southern sub-basins, influencing local circulation patterns (Artegiani et al., 1997b, Figure 2).

Sediment composition and benthic communities in the northern and central Adriatic Sea reflect the geological history and complex hydrodynamic patterns of the area. On the western side, fine well-sorted sands, terrigenous sediments, and muddy detrital bottoms dominate, due to the sediment input from the Po River and the alongshore currents that redistribute the material along the Italian coast. These regions provide excellent conditions for trawling, especially given the flat and dynamic substrate (Artegiani et al., 1979). Conversely, the eastern basin features relict sands and detrital bottoms, which support rich benthic biodiversity (Gamulin-Brida, 1967; Ott, 1992). Due to these favorable seabed conditions, particularly on the western side, the Adriatic Sea supports one of the most heavily exploited fishing grounds in the Mediterranean Sea (Eigaard et al., 2017).

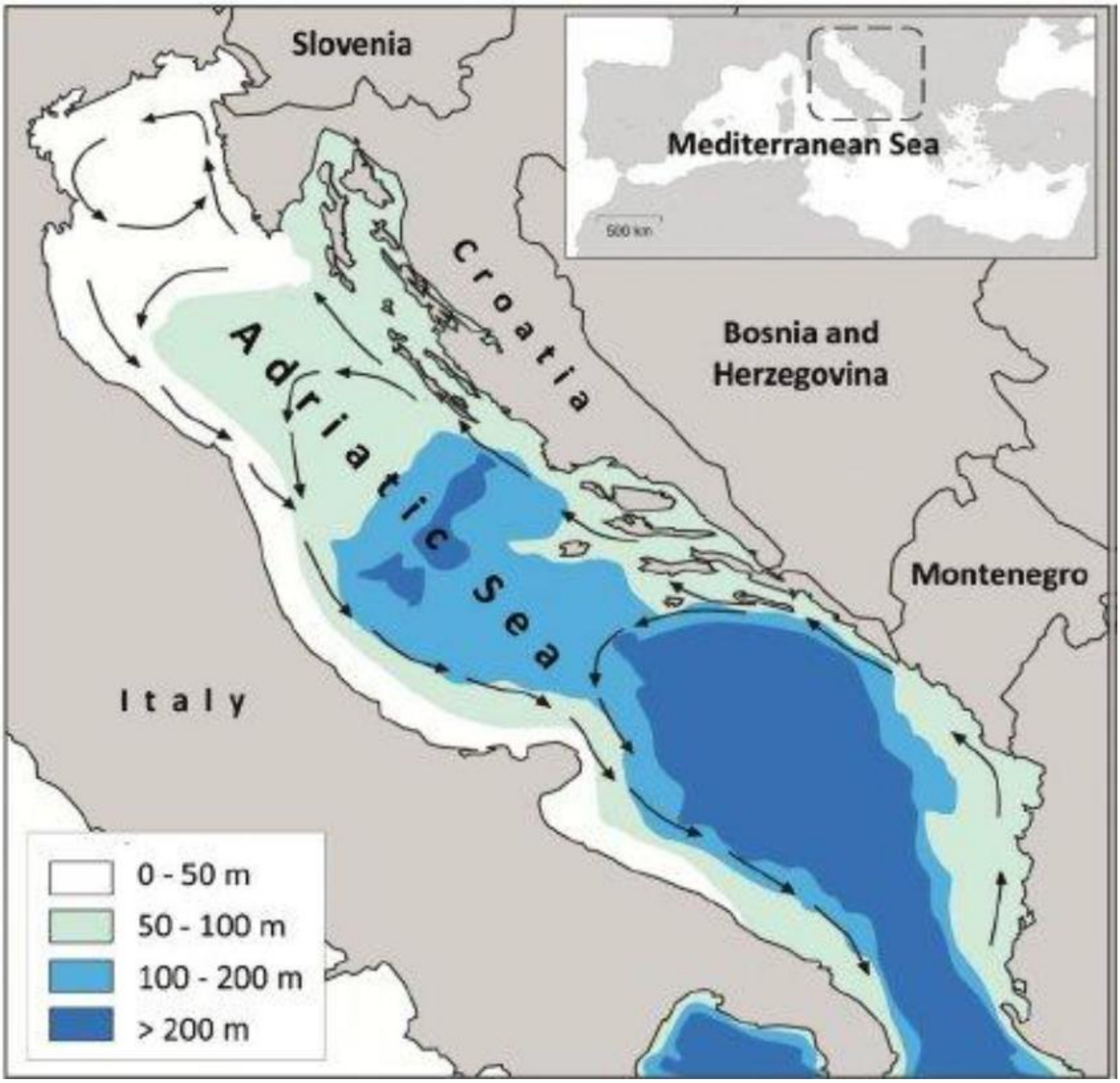

Figure 2 Map of the Adriatic Sea with bathymetry indication (see legend) and major currents (black arrows). Source: Gračan et al., 2014.

The Importance of Small Pelagic Fishes: Economic, Historical, and Ecological Perspective

History and economic importance of small pelagic species in the Adriatic Sea

Small pelagic fishes are the cornerstone of the Adriatic fishery and among the most important resources in the Mediterranean Sea. According to FAO (2023), the Mediterranean and Black Sea fisheries sector supports over 700,000 jobs and generates USD 7.8 billion in revenue from capture fisheries alone. While overall capture production has declined over the past decades, with notable drops during the COVID-19 pandemic, small pelagic species remain dominant in the catch composition, particularly sardine and anchovy in the Adriatic Sea, and anchovy in the Black Sea. Anchovy and sardine are among the most important commercial species in the Adriatic Sea and they are exploited by all the countries facing this basin. Anchovies are mainly target of the fishing activity occurring on the western side of the Adriatic Sea, whereas sardines are mainly caught on the eastern side of this basin and mainly by Croatia. The main gears exploiting these stocks are purse seiners with lights (*Lampara*) and pair trawlers (*Volante*). Purse seiners were introduced in the early 20th century but underwent rapid technological advancement in the post-World War II period, with the adoption of artificial light systems to attract fish schools (Lucchetti et al., 2018). This fishing technique was historically the backbone of small pelagic fisheries in the Adriatic, particularly before the expansion of pelagic trawling (Cingolani et al., 2001); nowadays, purse seine represents the main fishing gear for small pelagics in the eastern side of the Adriatic Sea. Purse seiners operate mostly at night, during calm weather and particularly in spring and summer, when fish aggregate near the surface (Lucchetti et al., 2018). From an ecological standpoint, purse seines are considered to have relatively limited environmental impact, as they do not interact with the seabed and generally produce low discard rates, thanks to the monospecific nature of pelagic aggregations and the gear's selectivity (Lucchetti et al., 2018; Sabatella et al., 2017). Despite their long history, *lampara* fleets have gradually declined in number due to rising operational costs, increasing competition, and stock decline driven by environmental conditions (Mannini and Massa, 2000; Sabatella et al., 2017). Pelagic trawlers became the main fishing method in the Adriatic Sea from the late 1970s onwards, especially in the northern and central regions of the western side of the basin (Cingolani et al., 1996; Coll et al., 2007). These trawl fisheries, often carried out by relatively large vessels, enable the exploitation of dispersed pelagic schools over broader areas and throughout most of the year (Coll and Libralato, 2012). The growth of this segment reflected broader trends of industrialization in fisheries, as well as the response to increasing market demand (Van Beveren et al., 2016).

Small pelagic fishery has historically supported the economies of most of the harbors facing on the Adriatic Sea, reaching its "golden era" in the 1970s and 1980s (Fortibuoni et al., 2017), and describing a decline trend in the recent decade as shown by Fig.3. This contraction has had severe consequences for profitability, reducing fleet revenues (Sabatella et al., 2017) and driving many vessels out of the sector.

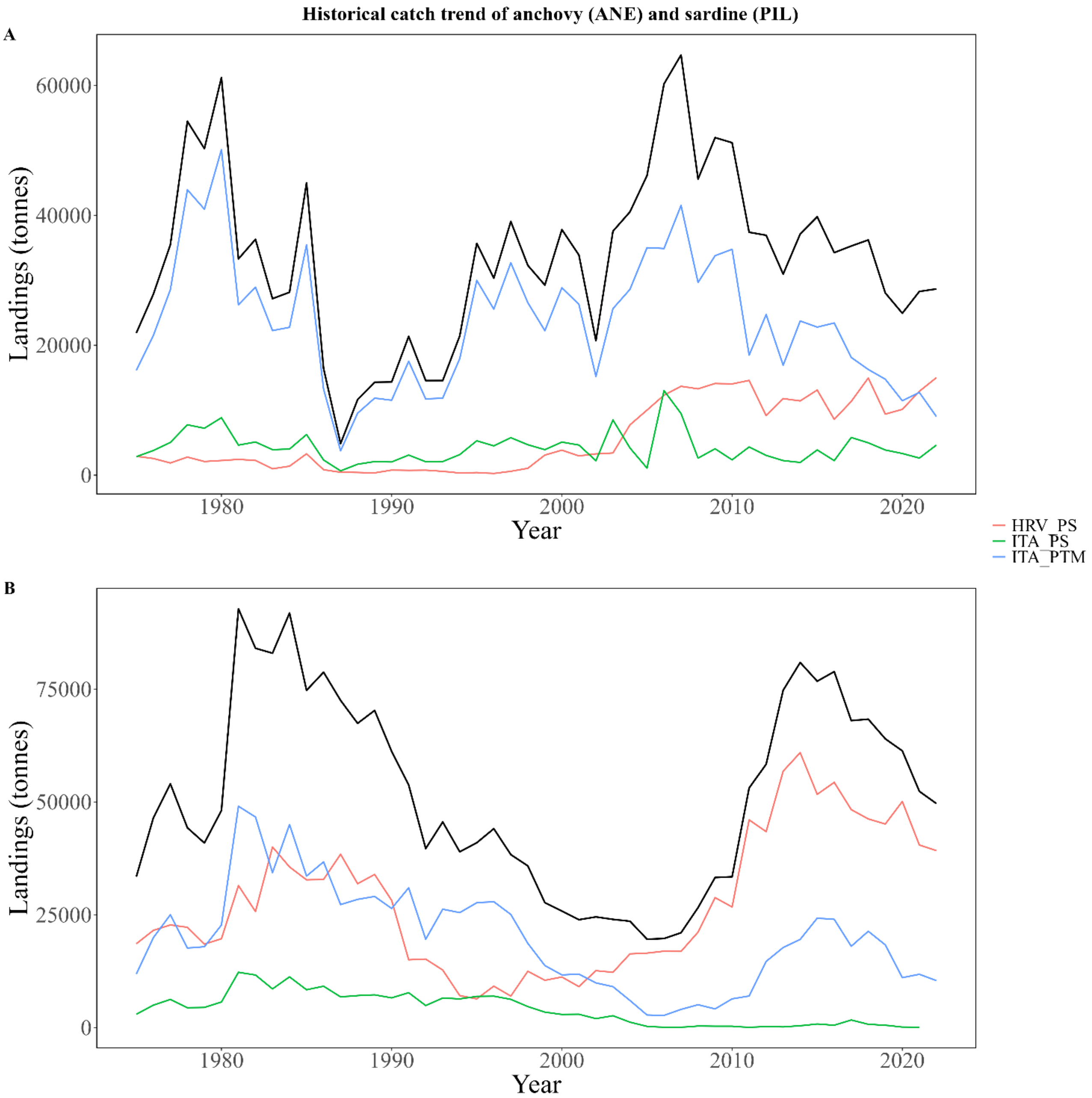

Fig. 3 Historical catch trend from Italian pelagic trawl (ITA_PTM), Italian purse seine (ITA_PS) and Croatian purse seine (HRVPS) for anchovy (A) and sardine (B). The black line rapresents the total landings. Source: FAO-FishstatJ (FAO, 2020) and RECFISH (RecFish, 2019) databases.

These dynamics were aggravated by historically weak management. Unlike in northern European seas, the Mediterranean countries effective controls were absent during the decades of expansion (Colloca et al., 2017; Carpi et al., 2017). Only in recent years, improvements have been obtained in management effectiveness. The proportion of overexploited stocks has dropped from 87% in 2013 to 52% in 2023, largely due to the efforts of the GFCM in implementing multiannual management plans, Fisheries Restricted Areas (FRAs), and technical measures such as spatial-temporal closures and gear restrictions (FAO, 2025). The Adriatic is at the forefront of these reforms, with two active management plans: one for small pelagics, which corresponds to the first management plan adopted in the Mediterranean Sea, and one for demersal fisheries. The management plan for small pelagics includes catch limits, effort limits, and fleet control mechanisms.

Nonetheless, the relevant efforts to reduce the fishing pressure on these stocks, the most recent assessments confirm that both anchovy and sardine are in overfishing with a positive sign for the anchovy stock, whose biomass is above its reference points (Table 1).

Table 1 Stock status of anchovy (ANE) and sardine (PIL) in the Adriatic Sea. Table reports: i) the estimated current levels of fishing mortality (F_{cur}) and spawning stock biomass (B_{cur}) by species, ii) the corresponding reference points for the fishing mortality, F_{tgt}, and for the biomass, B_{lim}, B_{pa} and B_{tgt}, and iii) the quantitative status expressed as the ratio between the current level and its corresponding reference point.

Species	Current levels		Reference points		Quantitative status		Reference
ANE	F_{cur}	0.84	F_{tgt}	0.81	F/F_{tgt}	1.04	Angelini et al., 2025
	B_{cur}	26,263	B_{pa}	21,400	B/B_{pa}	1.23	
			B_{lim}	16,200	B/B_{lim}	1.62	
PIL	F_{cur}	0.35	F_{tgt}	0.194	F/F_{tgt}	1.82	Čikeš Keč et al., 2025
	B_{cur}	72,230	B_{tgt}	228,577	B/B_{tgt}	0.32	
			B_{pa}	114,288	B/B_{pa}	0.63	
			B_{lim}	68,573	B/B_{lim}	1.05	

Ecological importance of small pelagics in the Adriatic Sea

Small pelagics represent key components of marine trophic dynamics (Piroddi et al., 2017; Navarro et al., 2017; Fanelli et al., 2023). Positioned at mid-trophic levels of the food chain, they are able to transfer energy from lower to higher trophic levels, 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). They are highly influenced by environmental changes, which make them important indicators of climate-induced environmental variability and fishing pressure (Carpi et al., 2015).

The general decline of the small pelagics fishery carries not only economic but also ecological implications. Anchovy and sardine are classic “wasp-waist” species, dominating intermediate trophic levels and funneling energy from plankton to predators such as tuna, seabirds, and cetaceans (Cury et al., 2000; Bakun, 2006; Checkley et al., 2009). Their fluctuations cascade through the ecosystem, affecting both predator abundance and plankton dynamics (Coll et al., 2007; Libralato et al., 2008). Anchovy, with a more flexible feeding strategy that alternates between filter feeding and active predation, can adapt to variable plankton availability (Bulgakova, 1993; Aldanondo et al., 2010), while sardine depends on larger, energy-rich prey and is expected to be more sensitive to environmental stress (Nikolioudakis et al., 2012; Borme et al., 2022; Fanelli et al., 2023). Their depletion therefore risks destabilizing the wider pelagic ecosystem, with consequences for biodiversity and fisheries beyond the species themselves.

Climate change further compounds these pressures. Rising sea surface temperatures have been linked to reduced growth and lower recruitment success (Brosset et al., 2017; Basilone et al., 2017). Altered riverine discharge, particularly from the Po, has changed nutrient availability and plankton productivity in the northern Adriatic Sea (Giani et al., 2012), undermining the survival of early life stages (Santojanni et al., 2006). Shifts in plankton phenology also create mismatches with spawning periods, further reducing recruitment (Morello and Arneri, 2009; Malavolti et al., 2021). Broader hydroclimatic changes, including increased stratification and circulation shifts, add additional uncertainty (Grbec et al., 2015; Otero and Hidalgo, 2023). These environmental drivers interact with fishing pressure, amplifying the vulnerability of small pelagics and reinforcing the trajectory of decline.

Target species

Anchovy in Adriatic Sea: stock and biology

Figure 4 *Engraulis encrasicolus*

Anchovy (*Engraulis encrasicolus*, Figure 4) is widely distributed across the Mediterranean Sea, the Black Sea, and the Eastern Atlantic coast, extending from the North Sea to South Africa (Fischer et al., 1987; Whitehead, 1990). This species is characterized by its short lifespan (around six years), early maturation, prolonged spawning period, and schooling behavior. As an euryhaline species, anchovy frequently inhabits estuaries and lagoons for feeding and spawning (Palomera et al., 2007; Morello and Arneri, 2009; Zorica et al., 2013; Pennino et al., 2020; Fanelli et al., 2023).

In the Adriatic Sea, anchovy populations are distributed throughout the basin but are rarely found below 100 meters in depth (Sinovčić, 1978). This species is a serial batch spawner, with spawning occurring from April to October, peaking in May-June and August-September (Regner, 1972; Sinovčić and Zorica, 2006; Morello and Arneri, 2009; Zorica et al., 2013). Anchovy larvae have been identified also in February and November, suggesting an extended spawning season. Major spawning sites are concentrated along the western Adriatic coast, from the Gulf of Trieste to the Gargano Peninsula, with additional areas identified near Vis, Biševo, and Palagruža Islands (Regner, 1996; Sinovčić, 2000a; Morello and Arneri, 2009).

Anchovy's reproductive success is closely linked to nutrient enrichment from freshwater inputs. In the northwest Mediterranean, spawning correlates positively with the freshwater flow of the Ebre River (Lloret et al., 2004; Pennino et al., 2020). Similarly, in the Adriatic Sea, the Po River plume has been found to enhance larval survival by stabilizing the water column and supporting vertical aggregations of food particles (Coombs et al., 2003). Studies have shown that increased river discharge and moderate wind stress promote higher phytoplankton and zooplankton biomass, boosting recruitment success (Santojanni et al., 2006). Variations in anchovy gonado-somatic indices also indicate that nutrient-rich riverine waters positively influence fertility (Zorica et al., 2013).

Anchovy eggs are found at temperatures ranging from 11.6°C to 28°C and salinities of 9.1–38.7 psu (Morello and Arneri, 2009). During the spawning season, eggs are distributed within the 200-meter depth zone of the Adriatic but are absent in deeper regions such as the Jabuka Pit and the southern

Adriatic Sea (Casavola et al., 1986; Gamulin and Hure, 1983). Adults migrate to coastal shallows for spawning and return offshore during winter, while juveniles typically remain nearshore until their first maturity (Sinovčić, 2000a; Marano, 2001).

Anchovy primarily feeds on mesozooplankton, undergoing ontogenetic dietary shifts. Studies in the Po Delta revealed a diet dominated by copepods, especially *Euterpina acutifrons* and *Oncaea* species. Feeding is predominantly diurnal, with some nocturnal activity observed (Borme et al., 2009; Morello and Arneri, 2009). This species exhibits schooling behavior: during the day, denser schools shift to deeper waters, while at night, smaller schools disperse near the surface (Azzali et al., 1985; Coombs et al., 1997; Borme et al., 2009).

Sardine in Adriatic Sea: stock and biology

The European sardine (*Sardina pilchardus*, Figure 5) distribution spans the Atlantic coast of Europe, from Portugal northward, as well as the Atlantic coast of North Africa and the Mediterranean coastal waters (Parrish et al., 1989). Similar to anchovies, European sardines are small-bodied, exhibit schooling behavior, and have an extended spawning period. They are also multiple spawners, which enhance their reproductive capacity (Morello and Arneri, 2009; Sinovčić et al., 2008). However, sardines have a slightly longer lifespan than anchovies, living up to eight years and reaching a maximum size of approximately 21 cm (Sinovčić, 2000b).

Figure 5 *Sardina pilchardus.*

In the Adriatic Sea, sardines are among the most abundant fish species, coexisting with anchovies. They are typically found at depths between 50 and 150 meters (Sinovčić, 2001). Sardine spawning occurs primarily from late autumn through early spring, peaking in December and January when water temperatures range from 9°C to 20°C, and salinity varies between 35.2 and 38.8 psu (Morello and Arneri, 2009). Eggs are distributed across the Adriatic continental shelf, although there are specific regions with higher reproductive intensity. For instance, surveys conducted in the mid-1980s identified the middle Adriatic as a critical spawning area. Additional significant zones include areas south of the Gargano Peninsula, which highlights the importance of the southern Adriatic for the species’ reproduction (Casavola et al., 1986). These spawning grounds are particularly notable near

Dugi Otok Island in the northern Adriatic and around mid-Dalmatian Islands in the southern Adriatic, extending offshore to Palagruža. In some years of intense reproduction, these areas may merge, and southern spawning zones may stretch along the Italian coast to Otranto (Piccinetti et al., 1981; Gamulin and Hure, 1983).

Sardine migrations involve movement from coastal areas to deeper offshore waters for feeding. In late winter and early spring, post-larvae and juveniles return to the coast, with smaller individuals often entering sheltered bays and estuaries such as the Krka River estuary, Novigrad Bay, Šibenik Bay and Kaštela Bay on the eastern coast, as well as the Gulf of Manfredonia on the western coast (Kačić et al., 1986; Sinovčić et al., 2008; Morello and Arneri, 2009;).

Several studies have highlighted the sardine's reliance on enriched primary and secondary production for reproductive success. For example, the Western Mediterranean Oscillation Index (WeMOI), which influences winds, river outflows, and sea surface temperature, has been positively linked to sardine reproductive success (Martín et al., 2012).

Unlike anchovies, sardines partially feed on phytoplankton and possess the ability to digest these cells. However, they derive most of their dietary needs from small zooplankton, as reported in studies also from other regions (Grbec et al., 2002; Van der Lingen et al., 2006; Nikolioudakis et al., 2012). Detailed dietary composition for Adriatic sardines remains limited.

Sardines exhibit schooling behavior from their juvenile stage, forming dense groups during the day at depths of 30–100 meters near the seabed. During the night, they disperse but remain within specific vertical zones. Echogram analyses have provided insights into the school shapes and densities, revealing that this behavior is consistent among juvenile and adult stages (Baltëza, 1985; Sinovčić, 2000b).

Climate change and Generalized Additive Model (GAM)

Environmental change and size reduction

Over the past several decades, climate change has emerged as one of the most significant forces driving ecological change in marine ecosystems. In the ocean, these shifts appear as rising surface and deep-water temperatures, stronger stratification, oxygen decline and altered nutrient dynamics, all of which directly affect productivity and trophic interactions (Grbec et al., 2015; Verri et al., 2024). Semi-enclosed basins, such as the Adriatic Sea, are especially vulnerable because their functioning depends heavily on riverine inputs and hydroclimatic variability, which are highly sensitive to climate shifts.

One of the most striking biological consequences of these changes is the reduction in body size observed across many marine ectotherms, including small pelagic fish such as anchovy and sardine. This trend is widely explained by the temperature–size rule, which predicts that warming reduces aerobic scope, favoring earlier maturation and smaller adult sizes (Lindmark et al., 2022). Evidence from northern ecosystems confirms these mechanisms: in the North Sea, a 1–2 °C increase over four decades produced a marked decline in asymptotic size for several exploited species, with measurable consequences for yield and long-term productivity (Baudron et al., 2014). At the global scale, projections suggest that maximum body size and biomass could decline by up to 24% by 2050 under climate warming scenarios (Cheung et al., 2013).

In the Mediterranean area, a basin-scale analysis confirmed that body condition and maximum size of small pelagic fish have declined in most subregions over recent decades (Brosset et al., 2017). For example, in the Gulf of Lions, a regime shift since the mid-2000s has led to a marked reduction in body condition, growth, and size-at-age of anchovy and sardine, accompanied by the disappearance of older individuals, suggesting bottom-up changes in plankton productivity rather than direct overfishing as the main driver (Van Beveren et al., 2014). More recently, long-term monitoring along the Spanish Mediterranean coast revealed consistent declines in life-history traits, including length-at-age, size at maturity and body condition, especially in the northern areas, with environmental variability and regional oceanographic conditions identified as key drivers (Albo-Puigserver et al., 2021). At the same time, comparative analyses across the basin demonstrated a strong negative correlation between temperature and body size, with anchovy and sardine showing average declines of about 3% per 1 °C of warming, highlighting their role as sentinel species of climate-driven changes in the Mediterranean Sea (Hattab et al., 2021). Also, in the Adriatic Sea, sardine and anchovy populations have shown strong reductions in body size and condition even when overall abundance remained relatively stable (Fig. 6).

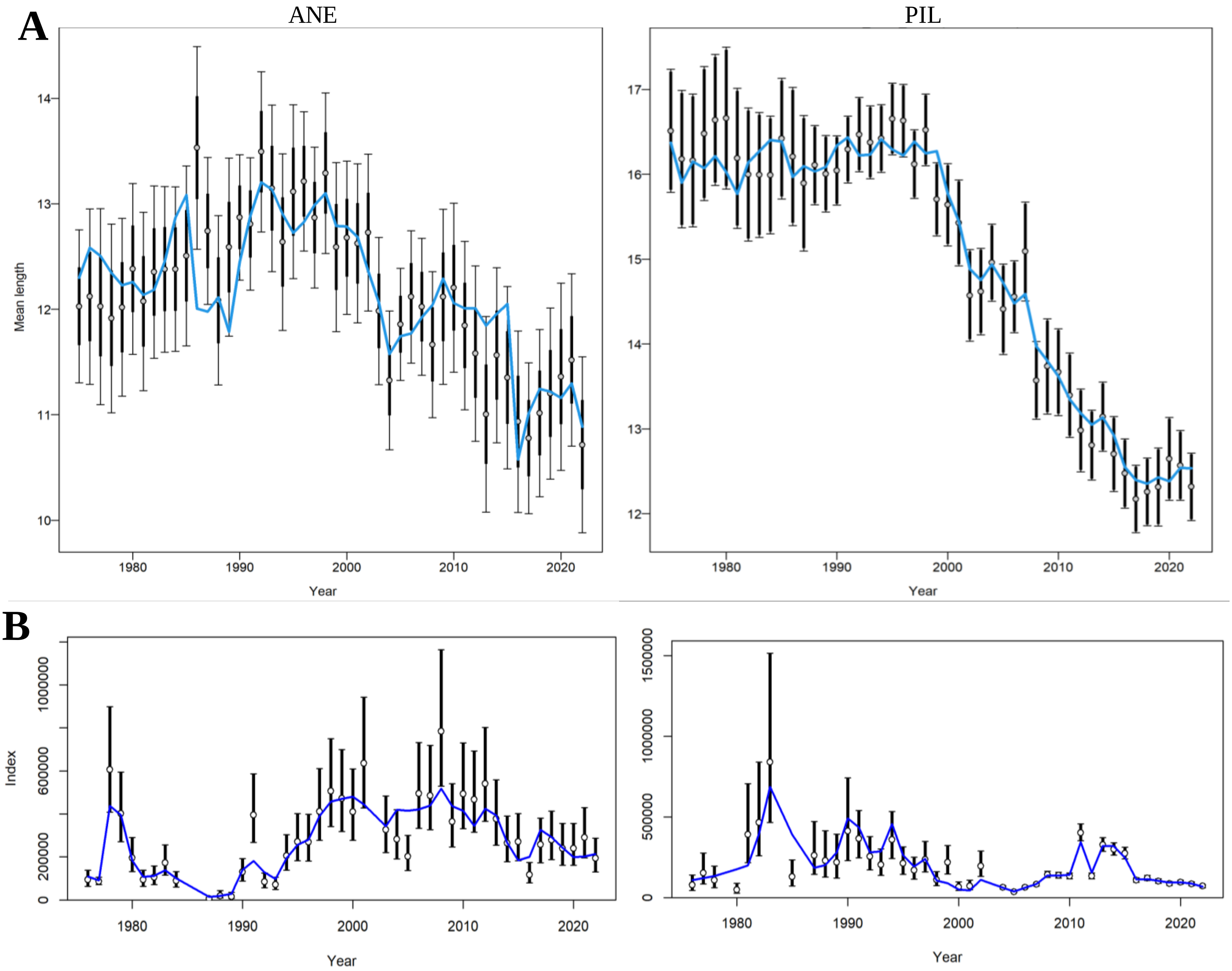

Figure 6 Historical trends in mean length (panels A) and abundance indices (panels B) for anchovy (left) and sardine (right) in the Adriatic Sea. Points represent estimates with confidence intervals (vertical bars), while blue lines indicate modelled trends fitting of the SS model detailed in Chapters 2 and 3.

This decoupling between biomass and size points to slower growth, truncated age structures, and shifts in recruitment success. Temperature contributes to these trends. On one side, elevated metabolic rates increase energetic demands. On the other hand, if prey availability does not scale accordingly, growth becomes suboptimal, resulting in smaller individuals and earlier reproduction (Takasuka et al., 2008; Giannoulaki et al., 2013). The vulnerability of early life stages magnifies these effects: even minor mismatches between spawning, larval hatching, and the seasonal timing of plankton blooms can drastically reduce recruitment success (Maynou et al., 2014; Fernández-Corredor et al., 2021).

Nutrient dynamics are key drivers in the Adriatic Sea. The northern part of the basin is strongly influenced by freshwater discharge, especially from the Po River, which contributes nearly half of the total freshwater input and nutrient load (Giani et al., 2012). While nutrient enrichment once fueled high productivity, river discharge and nutrient concentrations have declined in recent decades due to lower precipitation and stricter management of agricultural inputs. This shift has led to oligotrophication and reduced productivity at the base of the food web (Sani et al., 2024). Projections suggest that Po discharge could decline by another 35% by mid-century, with significant consequences for stratification and salinity regimes (Verri et al., 2024). These changes amplify the pressures on small pelagics, reducing prey availability and contributing to declining condition and size (Brosset et al., 2017).

Other climate-related processes, such as changes in large-scale circulation, also matter. In the past, events like the Eastern Mediterranean Transient (EMT) altered deep-water renewal and oxygenation in the Adriatic, reshaping plankton communities and fish dynamics (Grbec et al., 2015). More recently, short-term genetic studies of Adriatic anchovy have revealed shifts in population structure over just a few years, with larvae showing lower genetic diversity than adults (Ruggeri et al., 2016). These results point to uneven reproductive success and suggest that environmental stress is altering connectivity and resilience (Malavolti et al., 2021).

Taken together, the evidence shows that body size reduction in Adriatic small pelagics is the result of a multifactorial interplay between warming, hydrological variability, nutrient decline and fishing. These drivers act in nonlinear and sometimes unexpected ways, producing ecosystem responses that are difficult to predict (Van Beveren et al., 2014).

Generalized Additive Models (GAMs) as analytical tools

Generalized Additive Models (GAMs) are particularly well suited for evaluating the impact of environmental changes to biological mechanisms. They allow non-parametric, flexible relationships between environmental predictors (e.g., temperature, salinity, chlorophyll-a, freshwater inputs) and biological responses (e.g., abundance, recruitment, growth), making it possible to detect nonlinear effects, thresholds, and time lags (Wood, 2017).

In the Mediterranean basin, GAMs have already been applied successfully to small pelagic fish. Quattrocchi and Maynou (2017) used them to link sardine landings in the Northwestern Mediterranean to atmospheric indices, salinity and sea surface temperature, highlighting how certain hydrographic conditions favor productivity. Maynou et al. (2020) showed that rising Sea Surface Temperatures (SST) and declining chlorophyll-a concentrations were associated with contractions in anchovy spawning grounds and the increasing presence of thermophilic species such as *Sardinella aurita*. Domínguez-Bustos et al. (2023) further demonstrated the value of time-lagged analyses, showing that chlorophyll-a explained fluctuations in landings even years later, reflecting the delayed response of small pelagics to primary production.

Beyond descriptive applications, GAMs also serve as predictive tools. Pennino et al. (2020) combined GAM-based habitat models with climate projections to explore future changes in the distribution of sardines and anchovies in the Northwestern Mediterranean basins. Their models suggested contractions in distribution under pessimistic scenarios but identified potential climate refugia around river-influenced areas such as Rhône and Ebro. These insights highlight the importance of GAMs for anticipating future conditions and guiding adaptive management. Similar approaches have been applied outside the Mediterranean as well. In the Arabian Sea, Solanki et al. (2017) used GAMs with satellite-derived variables such as SST, chlorophyll, and sea surface height anomalies to predict fishery resource distributions, achieving strong correspondence with observed catches.

A major strength of GAMs lies in their ability to identify environmental thresholds—points beyond which recruitment or growth rapidly declines. This is especially relevant in semi-enclosed seas such as the Adriatic, where reduced deep-water ventilation or critical decreases in nutrient flux can trigger regime shifts in plankton and fish dynamics (Grbec et al., 2015). Incorporating lagged variables strengthens this capacity, allowing researchers to capture delayed responses such as recruitment failures linked to mismatches between spawning and plankton phenology (Schismenou et al., 2024).

By quantifying how environmental drivers affect fish condition and productivity, GAMs help managers design adaptive strategies that account for climate variability and uncertainty. As Pennino et al. (2020) emphasize, combining those models with fishery-independent surveys and climate projections allows the identification of priority habitats and potential refugia, making it possible to sustain small pelagic fisheries in the face of rapid change. In this sense, GAMs provide explanatory insight into the potential drivers of size reduction and allow powerful inference on the role of environmental and anthropogenic covariates under changing climatic conditions.

Fishery Management

What is a Stock Assessment?

A stock assessment is the scientific process by which the status of a fish population, defined as "*stock*" is estimated using available biological and fishery data. The primary goal is to quantify stock abundance and biomass at sea, as well as fishing mortality, in order to determine whether exploitation is sustainable. This information provides the scientific basis for management decisions on the examined stock.

Stock assessments rely on two main types of input: fishery-dependent and fishery-independent data. The former includes information derived from commercial fishing activity, such as catches, landings, effort data and length- or age-frequency distributions (Musick and Bonfil, 2005). The latter are collected through standardized scientific surveys that provide independent estimates of abundance, demographic structure and spatial distribution of populations at sea, thereby reducing biases introduced by fishing practices (Hoggarth et al., 2006; FAO, 2008). Ideally, both sources are integrated with life history traits (e.g., growth, natural mortality, maturity) to improve the robustness of assessment models.

In the Adriatic Sea, different types of fishery-independent surveys have been carried out. Early hydroacoustic applications for small pelagics date back to the 1950s (Kačić, 1972a; Vučetić and Kačić, 1973), with pilot campaigns in the 1970s laying the foundations for current biomass estimation protocols (Azzali and Levi, 1976; Azzali and Burczynski, 1977). Since 2009, the European countries facing on the Mediterranean Sea carry out standardized hydroacoustic surveys under the MEDiteranean International Acoustic Survey (MEDIAS) project, which is included in the EU Data Collection Framework (DCF; EU, 2017), allowing annual estimates of small pelagics', manly anchovy and sardine, abundance and distribution (Leonori et al., 2021). Other specific scientific surveys are carried out for demersal stocks, i.e. the GRUND survey (since 1982) and later the MEDITS trawl survey (since 1994) have provided long-term indices of abundance and biological samples (Bertrand et al., 2002), while the SOLEMON beam trawl survey has focused on flatfish resources (Grati et al., 2013).

Thus, the stock assessment of Adriatic resources is grounded in the combination of fishery-dependent commercial statistics and fishery-independent survey data, integrated into mathematical model, which reconstruct past dynamics and project future stock trajectories. In particular, integrated approaches and more advanced frameworks (e.g. Stock Synthesis) represent the direction in which modern stock assessment is moving, as they are designed to incorporate an increasing variety of data sources, including environmental drivers, thereby improving the capacity to explain variability in stock dynamics and provide more robust management advice (Maunder and Punt, 2013; Punt et al., 2021).

History of stock assessment models in Adriatic's small pelagic species

The management of small pelagic fish species in the Mediterranean Sea has undergone significant evolution in recent decades, moving toward more precautionary and science-based approaches. This shift reflects a growing recognition of both the ecological importance of these species in marine food webs and their socioeconomic relevance, particularly in the Adriatic Sea.

Early stock assessments in GSA 17 and GSA 18 were conducted separately and primarily relied on VPA models (Cingolani et al., 2004; 2005), particularly the Laurec-Shepherd tuning method (Laurec and Shepherd, 1983). These models provided deterministic reconstructions of fishing mortality and spawning stock biomass using catch-at-age data and were widely used until the early 2000s. To improve the estimation of recruitment and account for uncertainty in both catch and abundance indices, the Integrated Catch at Age (ICA) model (Patterson et al., 2001) was adopted for both species during the 2000s (Carpi et al. 2017), introducing a separability structure for fishing mortality and allowed for maximum likelihood fitting of observed data, thereby enhancing robustness over traditional VPA.

Following the 2014 benchmark, assessments of anchovy and sardine were consolidated across GSAs 17 and 18 to reflect biological and fishery connectivity (WGSASP, 2015a; 2015b). This marked a transition toward more integrated modeling approaches, such as the State-space Assessment Model (SAM; Nielsen and Berg, 2014), which was the accepted methodology for both stocks within the benchmark, and the 'assessment for all' (a4a; Scott et al., 2016), both belonging to the class of statistical catch-at-age models. These models are designed for flexibility in structural assumptions, e.g. time-varying selectivity.

The last assessment of anchovy is carried out using the SAM model wrapped in the R Fishery Library (FLR; Kell et al., 2007) (Angelini et al., 2025), which is a state-space model that explicitly separates process and observation error, improving the treatment of uncertainty in both recruitment and fishing mortality estimates. Indeed, in the last benchmark for sardine the Stochastic Production Model in Continuous Time (SPiCT; Pedersen and Berg, 2016) has been validated for the assessment of this stock (Čikeš Keč, 2025). SPiCT is a biomass-dynamic model suitable for data-limited contexts or situations where age structure is less reliable. This model is able to estimate biomass and harvest rates through a continuous-time surplus production framework.

Despite the relevant progresses occurred since the first stock evaluations, several issues remain unresolved. First, stock discrimination remains a scientific challenge. While morphometric and genetic studies have suggested population structuring in both species, the current management assumes a single shared stock for each species across GSAs 17 and 18, due to evidence of mixing and common exploitation (Ruggeri et al., 2013). Second, data gaps and quality issues—particularly in acoustic coverage and landings reporting—continue to affect the robustness of model outputs. The WGSASP has explicitly noted inconsistencies in MEDIAS indices for anchovy during low-coverage years (e.g., 2009–2012, 2021–2023) and urged improvements in CPUE standardization and survey effort (GFCM WGSASP, 2024).

New technologies and approaches: Stock Synthesis

Over the past few decades, fishery science has progressively embraced the necessity of incorporating environmental variability into the management of exploited stocks. The classic assumption of stationary productivity — where stock dynamics are solely dictated by fishing mortality and intrinsic biological processes — is increasingly challenged by evidence of ecosystem change, climate variability and the multifaceted influence of oceanographic drivers on recruitment, growth and spatial distribution of fish populations (Brander, 2007). In this context, Ecosystem-Based Fishery Management (EBFM, Pikitch et al., 2004) has emerged as a key pillar of modern fisheries governance, driving the development of new stock assessment models able to integrate species interaction and, on less extent, environmental information, such as temperature, salinity, river runoff, primary production, or climatic indices. The rationale is straightforward: for species whose productivity is environmentally driven, ignoring such variability may result in biased assessments and suboptimal management outcomes (Maunder and Watters, 2003; Schirripa et al., 2009).

Globally, several modeling frameworks have been developed or adapted to support EBFM. Age-structured statistical models such as Stock Synthesis (SS) (Methot and Wetzel, 2013) and Multifan-CL (Fournier et al., 1998) allow the incorporation of environmental variables as covariates affecting biological parameters. For example, in the eastern Bering Sea, ecosystem-linked models for walleye pollock included predator abundance and thermal regimes as modifiers of recruitment and natural mortality (Livingston and Methot, 1998). In the eastern Pacific, Pacific hake assessments incorporate ENSO-driven spatial dynamics across US and Canadian waters (Methot and Dorn, 1995). Similarly, in the Bay of Biscay, anchovy models routinely account for the timing of river plumes and upwelling events (Allain et al., 2001). Even in the Antarctic, models for krill explicitly integrate sea ice coverage and temperature to project plausible stock responses to climate-driven habitat change (Hill et al., 2013).

Efforts to understand the complexity of the Mediterranean small pelagic population dynamics include habitat modeling (e.g., GAMs, ENFA, MAXENT) for species-environment relationships

(Giannoulaki et al., 2013), and satellite-derived indices of chlorophyll and SST used to link environment to recruitment (Bonanno et al., 2016; Brosset et al., 2017). In the Strait of Sicily and North Aegean, habitat suitability models informed seasonal closures and acoustic survey design (Tugores et al., 2011). These studies underscore how fine-scale environmental monitoring and spatially explicit modeling can support adaptive, area-based management.

The challenge lies in ensuring these time series are ecologically meaningful, appropriately scaled (spatially and temporally) and robustly linked to demographic rates.

An influential study by Haltuch and Punt (2011) summarized several methodological routes for integrating environmental information into assessments:

1. Explanatory covariates in recruitment models (e.g., temperature effects on Beverton-Holt alpha or steepness);
2. Covariate-driven deviations (e.g., environmental modifiers for recruitment residuals);
3. State-space models, where both environment and biological dynamics evolve stochastically and simultaneously;
4. Scenario modeling, where projections of stock status depend on future environmental states.

Each of these strategies entails trade-offs in complexity, data requirements, and interpretability, but collectively they represent a maturing field aiming to make management more responsive and robust.

Among all platforms, Stock Synthesis is particularly suited to develop ecosystem-informed stock assessments for small pelagic species in the Adriatic Sea. These stocks are characterized by rapid population changes in response to environmental variability, which strongly influences recruitment success, growth, and overall stock productivity. Within SS, these dynamics can be explicitly modeled by linking environmental variables (e.g. riverine inputs, sea surface temperature anomalies, and chlorophyll-*a* concentrations) to key biological parameters, including recruitment, growth and natural mortality. Integrating such drivers into the assessment framework is crucial to capture interannual variability and improve the robustness of management advice. Recent advances, endorsed by the GFCM, have already demonstrated the feasibility of applying SS to anchovy with the incorporation of environmental covariates. In this context, SS allows parameters like recruitment or growth to vary as explicit functions of external time series (e.g., Po River discharge as an environmental index), thereby supporting scenario-based forecasting and enabling analysts to simulate future stock trajectories under different climatic and environmental conditions (Masnadi, 2023).

Unlike traditional models such as SAM, which relies on state-space methods applied to age-structured survey and catch data, or SPiCT, which uses a Bayesian surplus production approach suited for data-limited contexts, SS offers a more biologically detailed and flexible structure. As integrated age-structured assessment platform, it simulates the full life cycle of a population, allowing for time-varying parameters such as growth, selectivity, natural mortality and recruitment. These can be modeled as fixed, estimated, or environmentally driven processes, offering researchers the ability to test ecological hypotheses directly within the assessment framework (Methot and Wetzel, 2013; Carvalho et al., 2021).

In addition, SS brings together various biological and observational data types—such as catch, length and age compositions, abundance indices and tagging data—into a unified modeling framework capable of capturing complex population dynamics. A key advantage of SS lies in its capacity to integrate multiple fleets and survey sources, each with potentially distinct spatial-temporal dynamics and data types. This makes it particularly powerful for short-lived species like sardines and anchovies, whose populations are shaped by rapid turnover, high recruitment variability, and age-specific fishing pressure. Moreover, the model structure supports both estimation and projection, allowing it to be used not only for status determination but also as an operating model within Management Strategy Evaluation (MSE) frameworks.

Numerous international applications have demonstrated the value of SS in both data-rich and data-poor context, as well as in more complex settings. In the Bay of Biscay, SS was used to evaluate the sardine stock by integrating acoustic surveys, commercial length compositions, and biological samples to improve recruitment estimates and historical biomass reconstructions (ICES, 2022). In the Gulf of Mexico, Sagarese et al. (2021) applied SS to red grouper (*Epinephelus morio*), accounting for red tide-induced mortality events and improving the realism of natural mortality estimates. The flexibility of SS also enabled the incorporation of recruitment deviations linked to environmental anomalies in the assessments of Pacific sardine off the U.S. West Coast (Kuriyama et al., 2020), offering insight into ecosystem-linked harvest strategies. In the eastern Bering Sea and Gulf of Alaska, SS has been central to the assessment of groundfish stocks such as Pacific cod and pollock. These assessments have included area-specific dynamics, seasonal fishing behavior and environmental covariates such as predator consumption and bottom temperature, demonstrating SS's utility in ecosystem-informed fisheries management (Barbeaux et al., 2022). In these contexts, SS’s adaptability has supported the use of ensemble modeling approaches, combining multiple model configurations to improve robustness and accommodate structural uncertainty.

Within the Mediterranean context, SS has been more recently adopted but is already showing great potential. A number of demersal stocks are currently assed by SS, e.g. European hake (*Merluccius merluccius*), sole (*Solea solea*), red mullet (*Mullus barbatus*) and mantis shrips (*Squilla mantis*) in the Adriatic Sea, European hake and deep-water rose shrimp (*Parapeanaeus longirostris*) in the Strait of Sicily, red sea bream (*Pagellus bogaraveo*) in the northern and southern Alboran Sea. SS has been also implemented as the core engine for Management Strategy Evaluation (MSE) simulations conducted by the GFCM Working Group on MSE (GFCM WGMSE, 2024) for anchovy and sardine in the Adriatic Sea. In this role, SS has been used not only to reconstruct historical biomass and fishing mortality trends from data extending back to the 1970s, but also to simulate the long-term performance of alternative harvest control rules under different biological and environmental scenarios. The flexibility to test catch limits conditional on biomass thresholds—such as B_{lim}, B_{pa} and B_{MSY}—and evaluate probabilistic outcomes makes SS uniquely suited to supporting adaptive and precautionary management under uncertainty.

The growing preference for SS in Mediterranean and global stock assessments reflects a broader shift toward integrated and ecosystem-aware modeling frameworks. Its capacity to incorporate biologically realistic assumptions, handle multiple data streams, and serve as both an estimation and simulation tool has positioned it as an essential component of forward-looking fisheries governance. As challenges such as climate-driven productivity changes and spatial shifts in stock distribution become increasingly relevant, SS offers a comprehensive and credible tool for guiding sustainable management decisions.

AIM OF THE PROJECT

The overarching aim of this PhD project is to contribute to the advancement of Ecosystem-Based Fisheries Management (EBFM) approaches in the assessment and management of small pelagic fisheries, with a particular focus on the European anchovy (*Engraulis encrasicolus*) and European sardine (*Sardina pilchardus*) in the Adriatic Sea. These species, due to their short life cycles, ecological centrality and sensitivity to environmental change, serve as ideal case studies for exploring how environmental variability and anthropogenic pressures influence the biological and population dynamics of exploited marine resources.

In line with the principles of EBFM, this project adopts a multidisciplinary and integrated modeling framework. Two complementary analytical approaches are applied: (i) Generalized Additive Models (GAMs), used to investigate the long-term trends in size structure (Chapter 1), and (ii) Stock Synthesis (SS), used to incorporate environmental covariates into population dynamics models and assess their effects on key life-history processes (growth, recruitment and mortality), and stock status indicators, such as spawning stock biomass and exploitation levels.

The GAM component of the project (Chapter 1) supports and complements the SS analyses (Chapters 2 and 3) by independently evaluating the relationships between monthly weighted mean length and a range of environmental and anthropogenic covariates, including sea temperature, salinity, chlorophyll-a, Po River discharge, fishing effort, ecological processeses and socio-political changes. This approach allows for the exploration of delayed responses (0 to 12-month lags) and spatially explicit effects (e.g., port-specific environmental conditions), contributing to a broader understanding of the drivers shaping the size structure and dynamics of small pelagic stocks.

A complete application of this framework has been finalized for anchovy (Chapter 2). Using a suite of historical data sources, including length and age composition from commercial fisheries and acoustic surveys, the anchovy analysis has successfully integrated time-varying biological parameters and survey catchability linked to environmental variables—namely sea surface temperature (SST), Po River runoff, chlorophyll-a concentration and salinity. Multiple model variants were developed to evaluate the significance of these drivers, with results indicating that higher SST is associated with reduced mean length-at-age, while freshwater discharge from the Po River modulates mortality and catchability. These findings offer new insights into the environmental mechanisms underlying observed declines in anchovy size and productivity over recent decades.

In parallel, also a Stock Synthesis-based assessment has been developed for sardine (Chapter 3). This phase of the project inted to compare the outcomes between the SS model and the official stock assessment run in SPiCT, underlining pros and cons of the two methodologies. A secondary objective aimed to replicate and adapt the modeling strategy used for anchovy, considering species-specific ecological traits and data availability. We also investigated in greater depth the trade-offs among different diagnostics approaches for model selection, comparing performance of alternative SS configurations based on goodness-of-fit metrics (i.e., AIC), the internal consistency of parameter estimates, residual diagnostics and retrospective analyses. This multi-criteria evaluation aimed to balance statistical fit with biological plausibility, highlighting how some configurations may provide better numerical convergence but weaker ecological coherence, and vice versa. Together, these components form a coherent research project that not only advances methodological approaches to fish stock assessment under EBFM but also delivers practical insights for the sustainable management of Adriatic small pelagic fisheries under changing environmental conditions.

CHAPTER 1

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

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Abstract

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

1.1 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 tonnes) of fish captures in 2020-2021; of these, about 36% (81,930 tonnes) 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 observed in small pelagic species 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 (Fig. 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.

1.2 Materials and methods

1.2.1 Study area

The study area included the northern and central Adriatic Sea (Fig. 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).

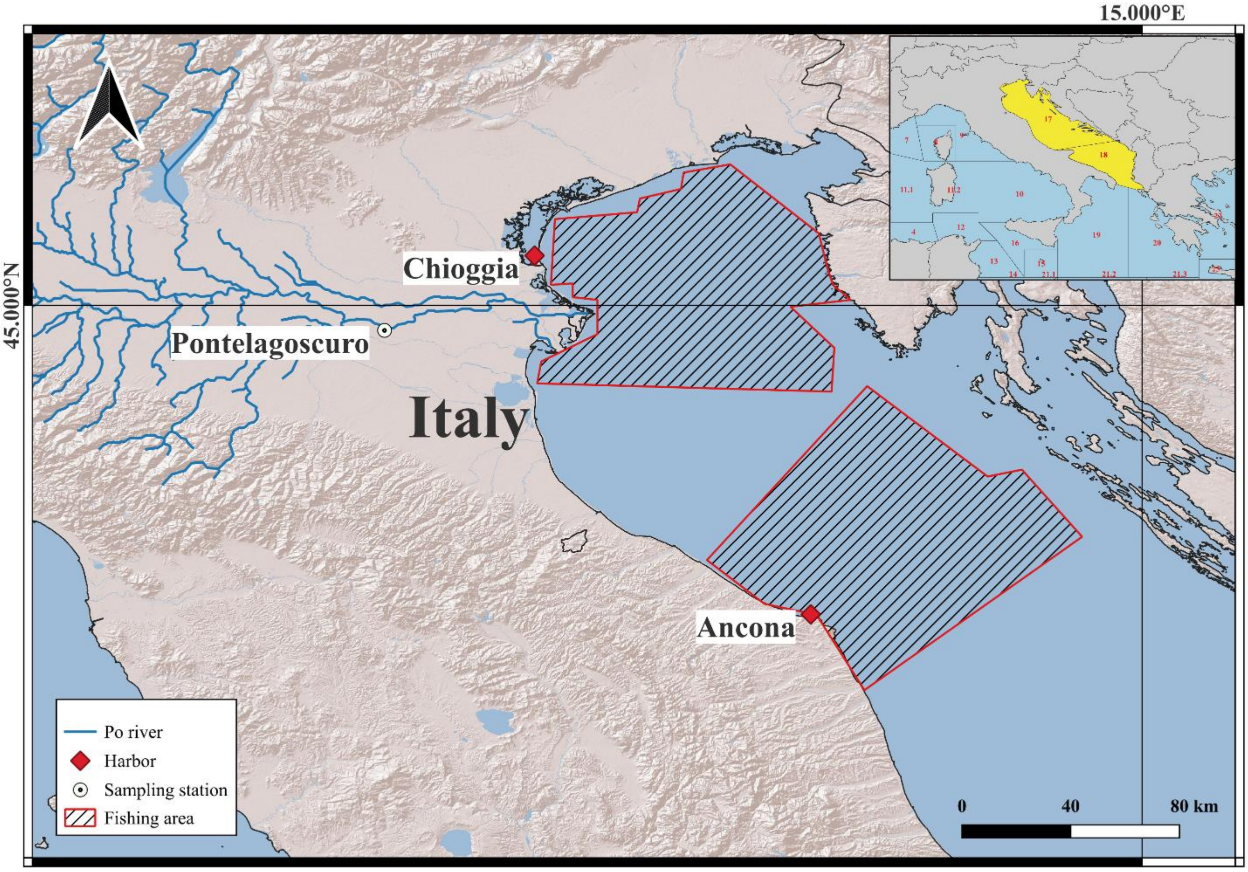

Figure 1 Map of the study area including the location of the selected harbors, Chioggia and Ancona, and the corresponding fishing grounds georeferenced using QGIS v.3.20.0 (www.qgis.org). The location of Pontelagoscuro station is highlighted in the map. Mediterranean Geographical Sub-Areas (GSAs) are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

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.

1.2.2 Data

1.2.2.1 Dependent variable

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

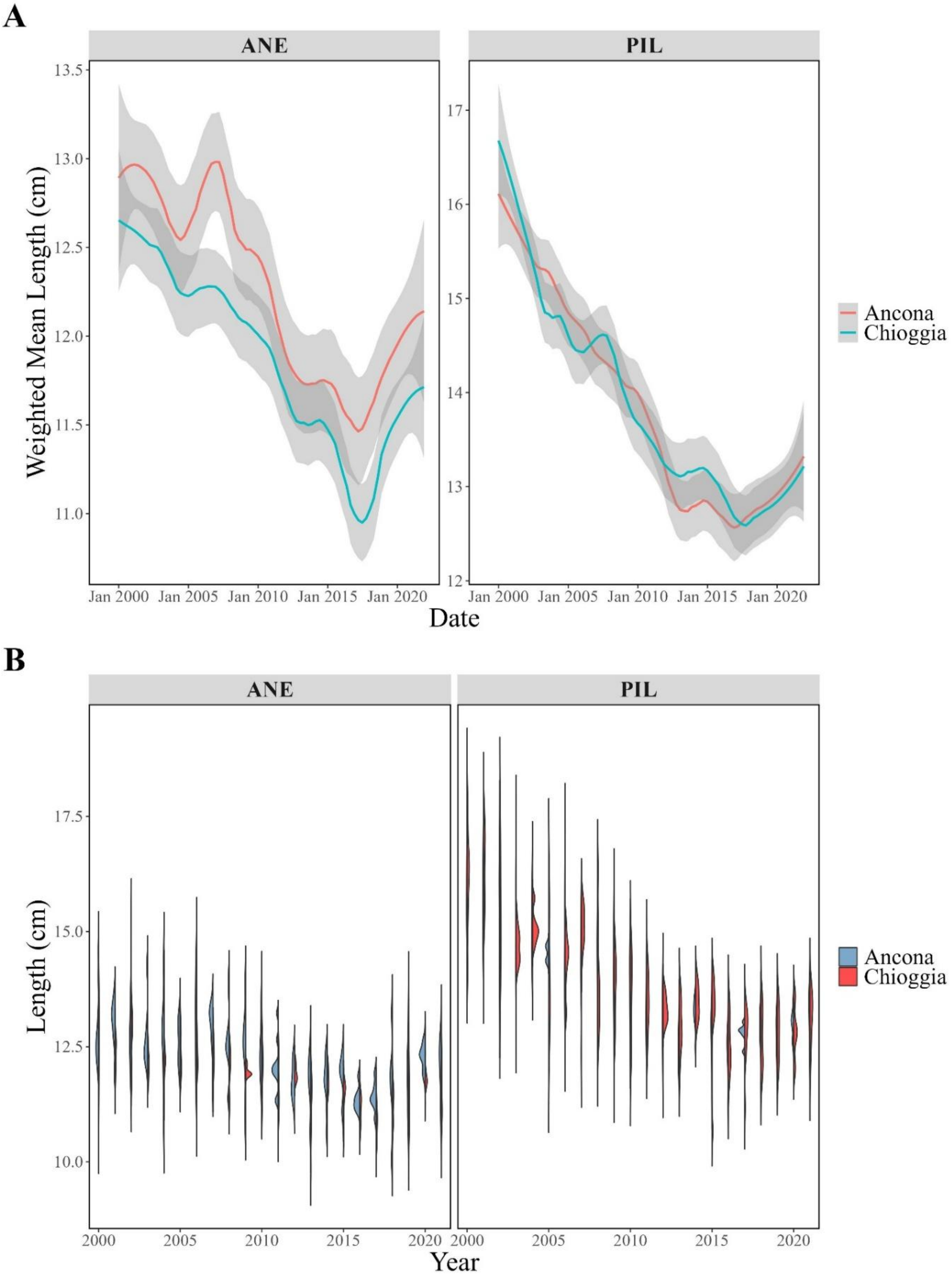

Figure 2 (A) Long-term trends in weighted Mean Length of anchovy (ANE, left) and sardine (PIL, right) from January 2000 to December 2021. Colored lines represent smoothed estimates by harbor (Ancona, orange line; Chioggia light green line) with 95% confidence intervals shown in grey. (B) Violin plots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

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 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 shown in Equation 1.

$$wML = \frac{\sum_{i=1}^{k} N_i \, L_i}{\sum_{1=1}^{k} N_i} \, (Eq. 1)$$

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 Figure S2 for anchovy and Figure S3 for sardine.

1.2.3 Covariates

1.2.3.1 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 (Fig. 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.

1.2.3.2 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 (Fig. 1) were obtained via the Regional Open Data Portal (RODP, 2024), provided by the Agenzia Regionale Prevenzione Ambiente Energia Emilia- Romagna (ARPAE-ER).

1.2.3.3 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.

1.2.4 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 (Winklin, 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 shown in Equation 2.

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

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 *FWDselec*t 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.

$$RMSE = \sqrt{\frac{1}{n}\sum_{i=1}^{n}(\hat{y_i} - y_i)^2} \quad (Eq. 3)$$

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.

1.3 Results

1.3.1 Environmental variables assessment

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 *Chl-a* and *Sal* between Ancona and Chioggia, supporting the inclusion of spatially stratified smoothers for these variables (Fig. S5).

1.3.2 Influence of covariates on wML

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.

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

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

	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	0.73
	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	0.75
	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	0.73
	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	0.73
	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	0.76
	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	0.70

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.

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	

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 (Fig. 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 (Fig. S7 and S8). In addition, the comparison between observed and predicted values on the independent test dataset (Fig. S9) confirmed that the models achieved consistent predictive performance, providing a reliable assessment of their predictive skill.

1.3.2.1 Anchovy

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

$$wML\_ANE \sim s(Time) + s(Fleet,\ by = Harbor) + ti(Time,\ Fleet,\ by = Harbor) + s(Po) + s(Chl\text{-}a,\ by = Harbor) + Harbor \quad (Eq.\ 4)$$

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.

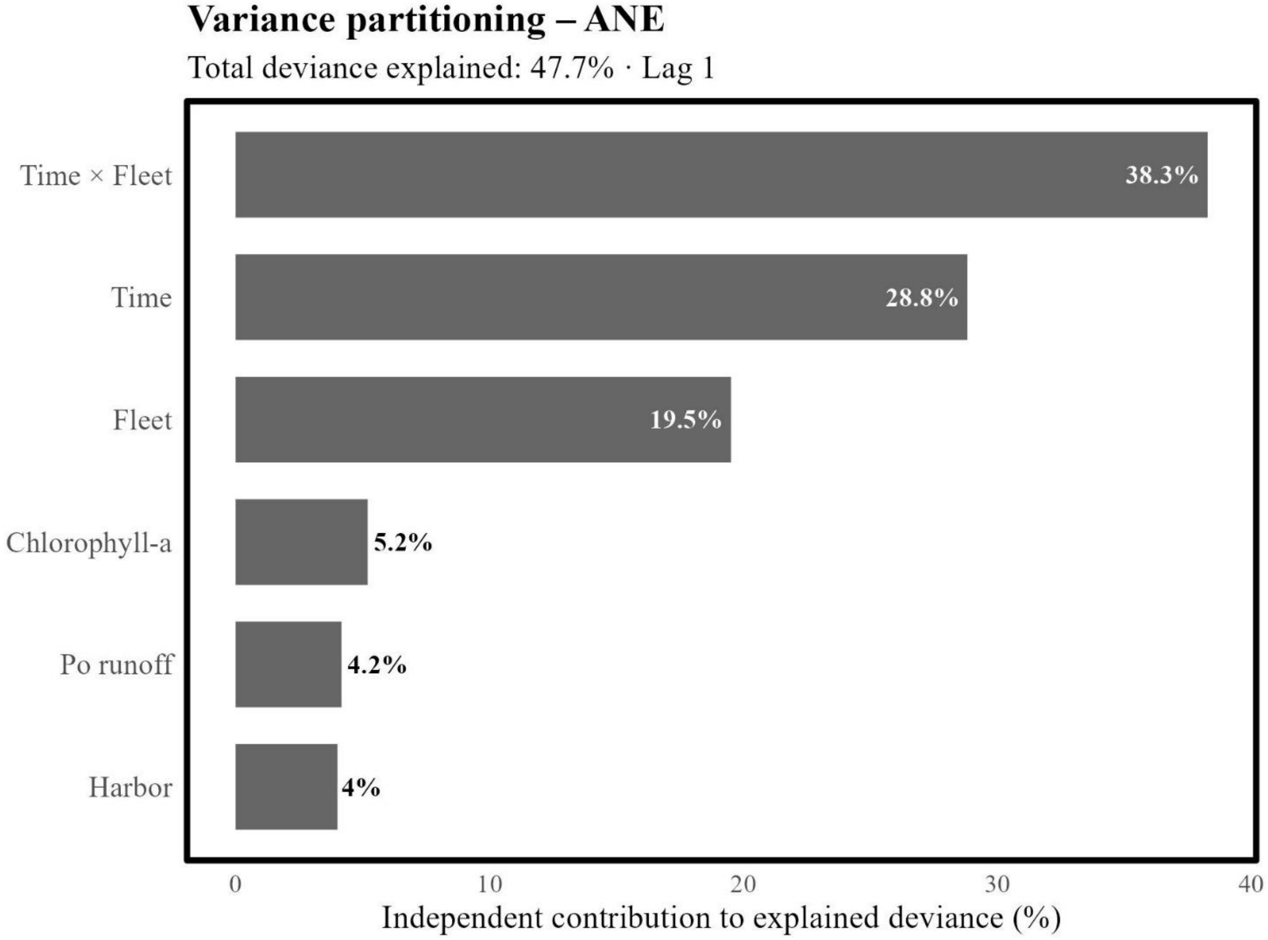

Figure 3 Variance partitioning of deviance for the best GAM model of anchovy (ANE). Bars represent the independent contribution of each predictor to the total deviance explained (47.7%), as estimated through hierarchical partitioning of deviance. Percentage values for each predictor are displayed.

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* (Fig. 4, top panels) revealed marked spatiotemporal contrasts between harbors.

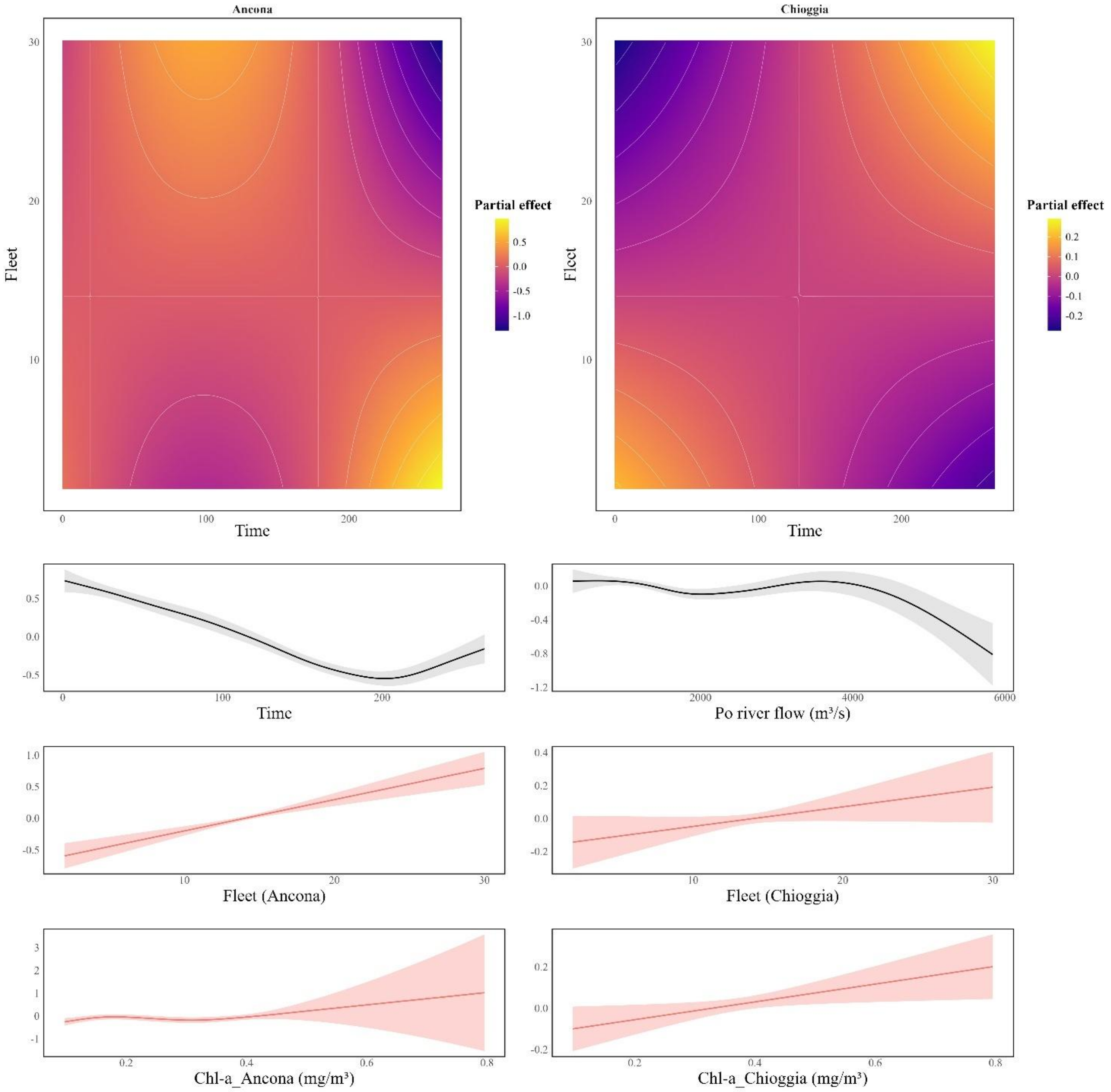

Figure 4 Partial effect plots for the best-fitting GAM explaining *wML* of anchovy including the interaction between *Time* and Fleet, temporal proxy (*Time*) and key covariates. Shaded areas represent 95% confidence intervals. Covariates stratified by *Harbor* are indicated in red to distinguish their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

In Ancona, the interaction surface 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 (Fig. 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 (Fig. 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 (Fig. 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* (Fig. 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.

1.3.2.2 Sardine

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

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

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 (Fig. 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.

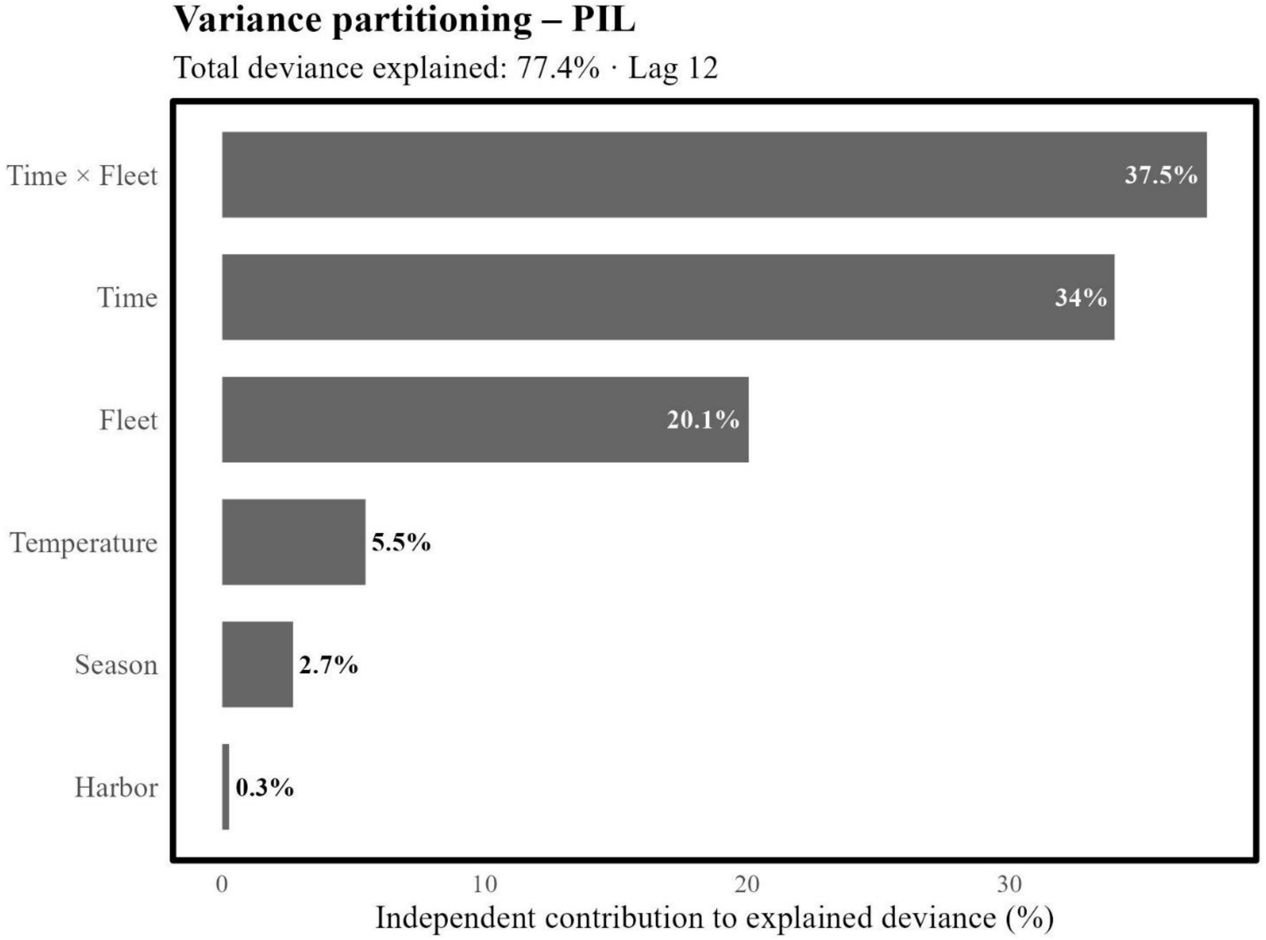

Figure 5 Variance partitioning of deviance for the best GAM model of sardine (PIL). Bars represent the independent contribution of each predictor to the total deviance explained (77.4%), as estimated through hierarchical partitioning of deviance. Percentage values for each predictor are displayed.

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 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 (Fig. S3).

Figure 6 visually summarized the partial effects of the covariates included in the final sardine model.

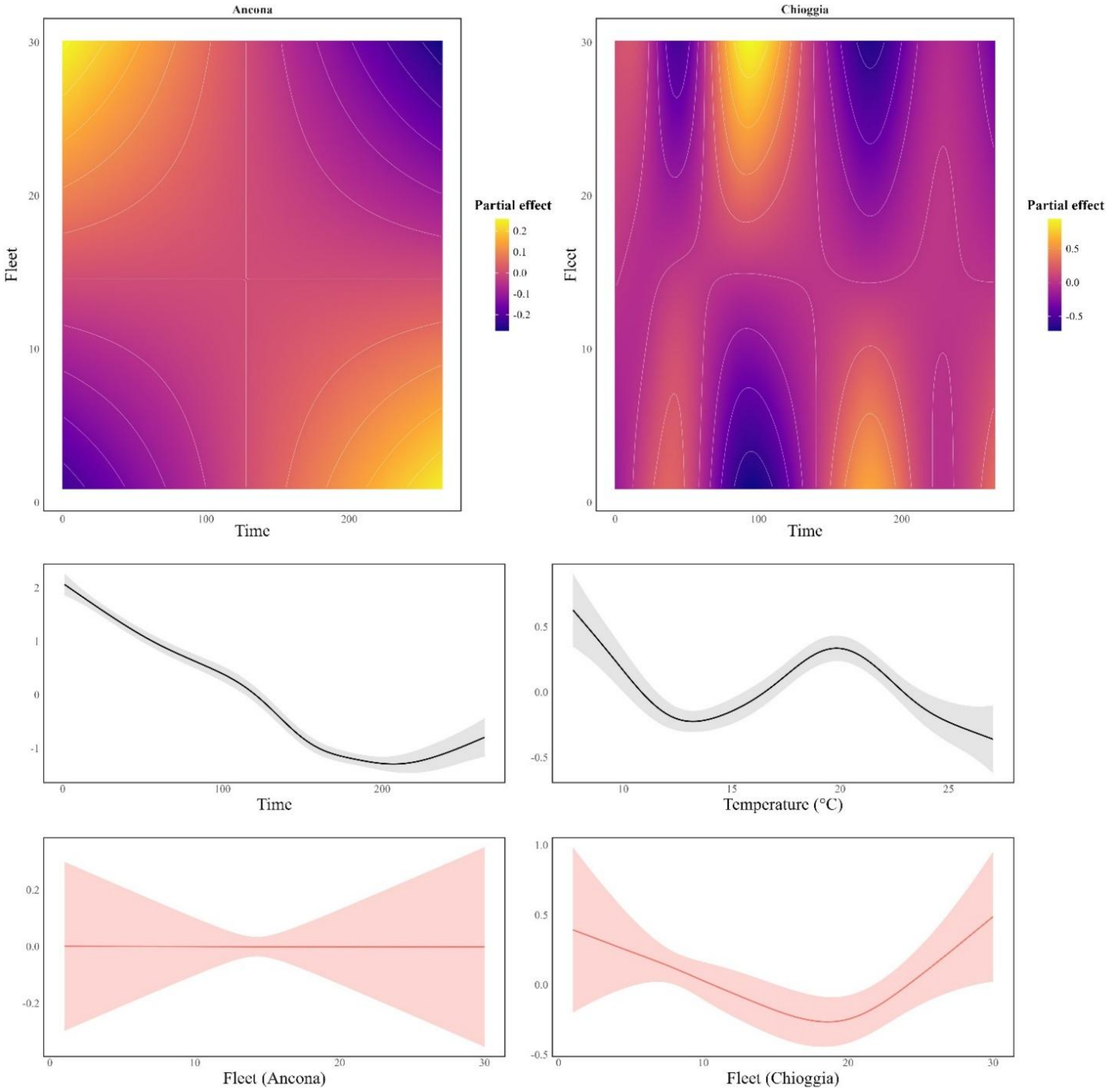

Figure 6 Partial effect plots for the best-fitting GAM explaining *wML* of sardine including the interaction between *Time* and Fleet, temporal proxy (*Time*) and key covariates. Shaded areas represent 95% confidence intervals. Covariates stratified by *Harbor* are indicated in red to distinguish their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

The interaction between *Time* and *Fleet* (Fig. 6, top panels) revealed distinct temporal and spatial dynamics in the relationship between fishing activity and sardine size. 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 (Fig. 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* (Fig. 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 (Fig. 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 (Fig. 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.

1.4 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).

1.4.1 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 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).

1.4.2 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 (Fig. 4, middle panels). While this trend may initially appear counterintuitive, a better look on the interaction between *Fleet* and *Time* (Fig. 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 (Fig. S1).

For sardine, the relationship between *wML* and fleet size differed between the two harbors and appeared more complex (Fig. 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 (Fig. 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.

1.4.3 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.

1.4.3.1 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 utilise moderately turbid coastal areas as temporary refuge habitats. Drake et al. (2007) and Costalago (2015) noted this behaviour, 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 (Fig. 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 (Fig. 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.

1.4.3.2 Sardine

In our model, temperature was selected showing a sigmoidal response that indicates the existence of an optimal thermal window (Fig. 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 favour 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.

1.4.4 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 (Fig. S1), indicating a contraction of the fishery sector. According to the FAO (2023), Italy remains among the top contributors to capture small pelagics species in the Mediterranean Sea; 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 disincentivizing 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; 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 stabilisation, suggesting that such measures may be beginning to reverse previous declines.

1.5 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.

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Supplementary material

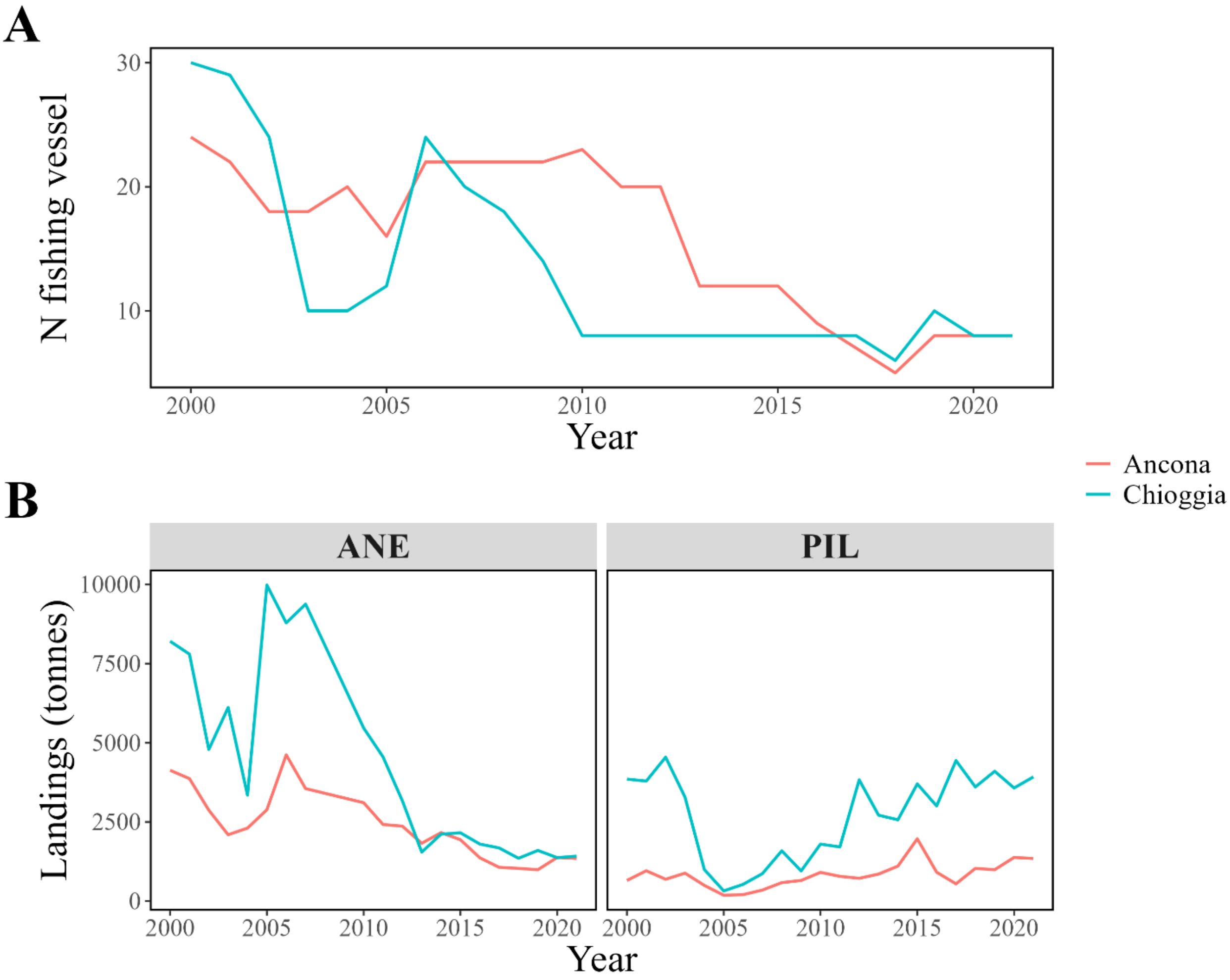
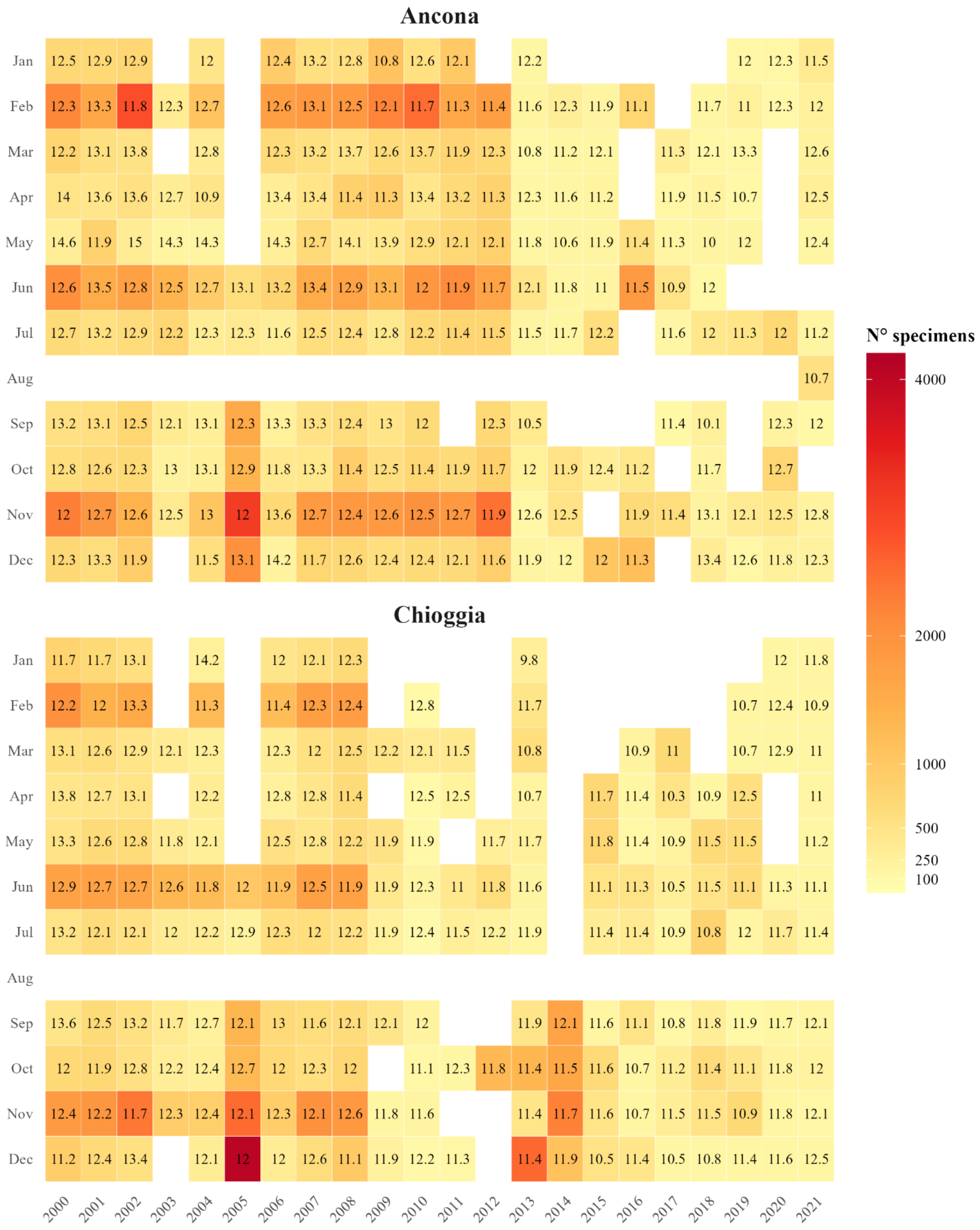


Figure S1 (A) Temporal trends in the number of fishing vessels and (B) annual landings of anchovy (ANE) and sardine (PIL) from Ancona (orange) and Chioggia (light green) harbors.



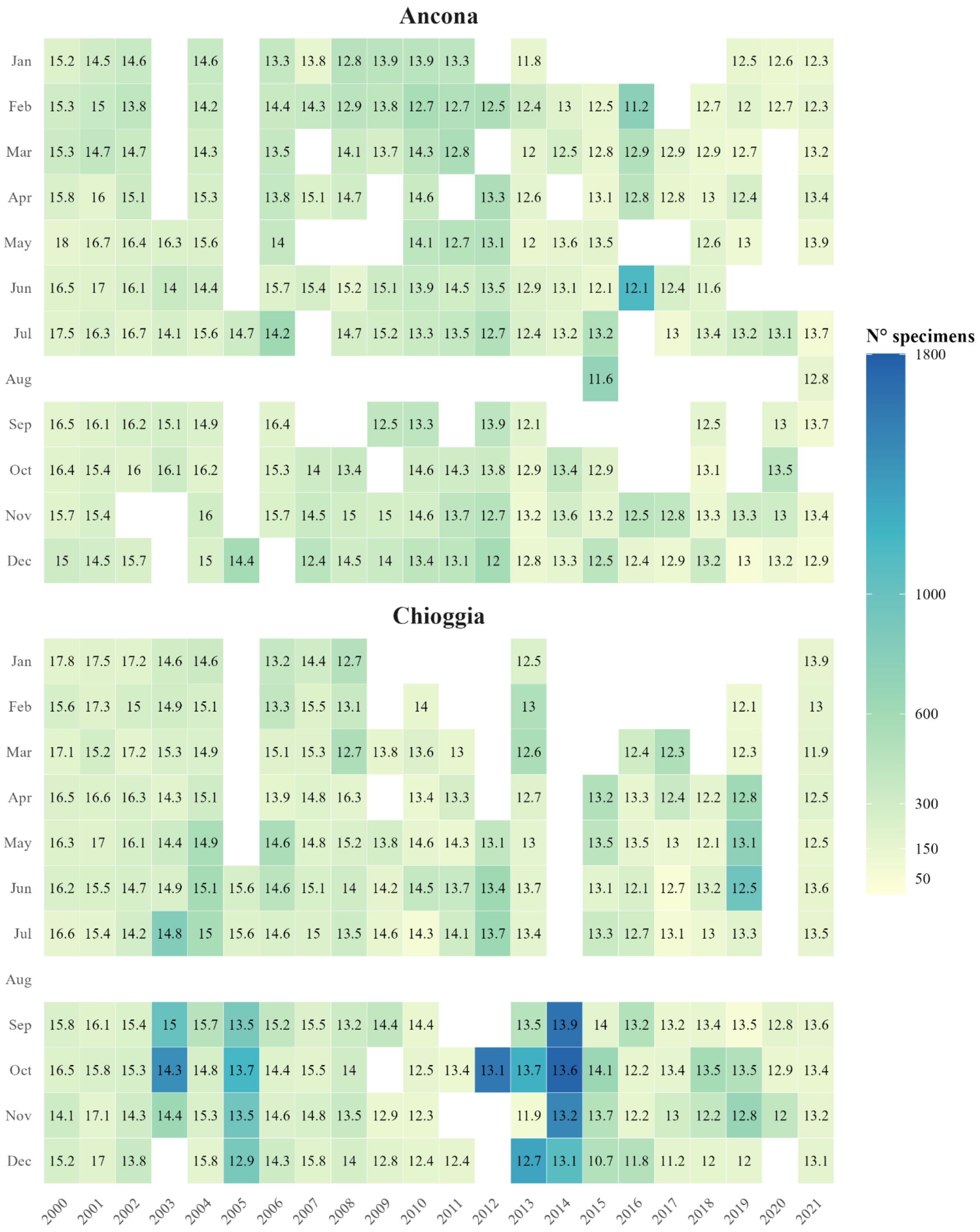
Ancona

	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021
Jan	12.5	12.9	12.9		12		12.4	13.2	12.8	10.8	12.6	12.1		12.2						12	12.3	11.5
Feb	12.3	13.3	11.8	12.3	12.7		12.6	13.1	12.5	12.1	11.7	11.3	11.4	11.6	12.3	11.9	11.1		11.7	11	12.3	12
Mar	12.2	13.1	13.8		12.8		12.3	13.2	13.7	12.6	13.7	11.9	12.3	10.8	11.2	12.1		11.3	12.1	13.3		12.6
Apr	14	13.6	13.6	12.7	10.9		13.4	13.4	11.4	11.3	13.4	13.2	11.3	12.3	11.6	11.2		11.9	11.5	10.7		12.5
May	14.6	11.9	15	14.3	14.3		14.3	12.7	14.1	13.9	12.9	12.1	12.1	11.8	10.6	11.9	11.4	11.3	10	12		12.4
Jun	12.6	13.5	12.8	12.5	12.7	13.1	13.2	13.4	12.9	13.1	12	11.9	11.7	12.1	11.8	11	11.5	10.9	12			
Jul	12.7	13.2	12.9	12.2	12.3	12.3	11.6	12.5	12.4	12.8	12.2	11.4	11.5	11.5	11.7	12.2		11.6	12	11.3	12	11.2
Aug																						10.7
Sep	13.2	13.1	12.5	12.1	13.1	12.3	13.3	13.3	12.4	13	12		12.3	10.5				11.4	10.1		12.3	12
Oct	12.8	12.6	12.3	13	13.1	12.9	11.8	13.3	11.4	12.5	11.4	11.9	11.7	12	11.9	12.4	11.2		11.7		12.7	
Nov	12	12.7	12.6	12.5	13	12	13.6	12.7	12.4	12.6	12.5	12.7	11.9	12.6	12.5		11.9	11.4	13.1	12.1	12.5	12.8
Dec	12.3	13.3	11.9		11.5	13.1	14.2	11.7	12.6	12.4	12.4	12.1	11.6	11.9	12	12	11.3		13.4	12.6	11.8	12.3

Chioggia

	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021
Jan	11.7	11.7	13.1		14.2		12	12.1	12.3					9.8							12	11.8
Feb	12.2	12	13.3		11.3		11.4	12.3	12.4		12.8			11.7						10.7	12.4	10.9
Mar	13.1	12.6	12.9	12.1	12.3		12.3	12	12.5	12.2	12.1	11.5		10.8			10.9	11		10.7	12.9	11
Apr	13.8	12.7	13.1		12.2		12.8	12.8	11.4		12.5	12.5		10.7		11.7	11.4	10.3	10.9	12.5		11
May	13.3	12.6	12.8	11.8	12.1		12.5	12.8	12.2	11.9	11.9		11.7	11.7		11.8	11.4	10.9	11.5	11.5		11.2
Jun	12.9	12.7	12.7	12.6	11.8	12	11.9	12.5	11.9	11.9	12.3	11	11.8	11.6		11.1	11.3	10.5	11.5	11.1	11.3	11.1
Jul	13.2	12.1	12.1	12	12.2	12.9	12.3	12	12.2	11.9	12.4	11.5	12.2	11.9		11.4	11.4	10.9	10.8	12	11.7	11.4
Aug																						
Sep	13.6	12.5	13.2	11.7	12.7	12.1	13	11.6	12.1	12.1	12			11.9	12.1	11.6	11.1	10.8	11.8	11.9	11.7	12.1
Oct	12	11.9	12.8	12.2	12.4	12.7	12	12.3	12		11.1	12.3	11.8	11.4	11.5	11.6	10.7	11.2	11.4	11.1	11.8	12
Nov	12.4	12.2	11.7	12.3	12.4	12.1	12.3	12.1	12.6	11.8	11.6			11.4	11.7	11.6	10.7	11.5	11.5	10.9	11.8	12.1
Dec	11.2	12.4	13.4		12.1	12	12	12.6	11.1	11.9	12.2	11.3		11.4	11.9	10.5	11.4	10.5	10.8	11.4	11.6	12.5

Fig. S2 Monthly and annual distribution of the weighted mean length (*wML*, numbers within cells) and the number of specimens examined (color scale) of anchovy in the ports of Ancona and Chioggia. Warmer colors indicates a higher number of measured specimens.



Ancona

	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021
Jan	15.2	14.5	14.6		14.6		13.3	13.8	12.8	13.9	13.9	13.3		11.8						12.5	12.6	12.3
Feb	15.3	15	13.8		14.2		14.4	14.3	12.9	13.8	12.7	12.7	12.5	12.4	13	12.5	11.2		12.7	12	12.7	12.3
Mar	15.3	14.7	14.7		14.3		13.5		14.1	13.7	14.3	12.8		12	12.5	12.8	12.9	12.9	12.9	12.7		13.2
Apr	15.8	16	15.1		15.3		13.8	15.1	14.7		14.6		13.3	12.6		13.1	12.8	12.8	13	12.4		13.4
May	18	16.7	16.4	16.3	15.6		14				14.1	12.7	13.1	12	13.6	13.5			12.6	13		13.9
Jun	16.5	17	16.1	14	14.4		15.7	15.4	15.2	15.1	13.9	14.5	13.5	12.9	13.1	12.1	12.1	12.4	11.6			
Jul	17.5	16.3	16.7	14.1	15.6	14.7	14.2		14.7	15.2	13.3	13.5	12.7	12.4	13.2	13.2		13	13.4	13.2	13.1	13.7
Aug																11.6						12.8
Sep	16.5	16.1	16.2	15.1	14.9		16.4			12.5	13.3		13.9	12.1					12.5		13	13.7
Oct	16.4	15.4	16	16.1	16.2		15.3	14	13.4		14.6	14.3	13.8	12.9	13.4	12.9			13.1		13.5	
Nov	15.7	15.4			16		15.7	14.5	15	15	14.6	13.7	12.7	13.2	13.6	13.2	12.5	12.8	13.3	13.3	13	13.4
Dec	15	14.5	15.7		15	14.4		12.4	14.5	14	13.4	13.1	12	12.8	13.3	12.5	12.4	12.9	13.2	13	13.2	12.9

Chioggia

	2000	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019	2020	2021
Jan	17.8	17.5	17.2	14.6	14.6		13.2	14.4	12.7					12.5								13.9
Feb	15.6	17.3	15	14.9	15.1		13.3	15.5	13.1		14			13						12.1		13
Mar	17.1	15.2	17.2	15.3	14.9		15.1	15.3	12.7	13.8	13.6	13		12.6			12.4	12.3		12.3		11.9
Apr	16.5	16.6	16.3	14.3	15.1		13.9	14.8	16.3		13.4	13.3		12.7		13.2	13.3	12.4	12.2	12.8		12.5
May	16.3	17	16.1	14.4	14.9		14.6	14.8	15.2	13.8	14.6	14.3	13.1	13		13.5	13.5	13	12.1	13.1		12.5
Jun	16.2	15.5	14.7	14.9	15.1	15.6	14.6	15.1	14	14.2	14.5	13.7	13.4	13.7		13.1	12.1	12.7	13.2	12.5		13.6
Jul	16.6	15.4	14.2	14.8	15	15.6	14.6	15	13.5	14.6	14.3	14.1	13.7	13.4		13.3	12.7	13.1	13	13.3		13.5
Aug																						
Sep	15.8	16.1	15.4	15	15.7	13.5	15.2	15.5	13.2	14.4	14.4			13.5	13.9	14	13.2	13.2	13.4	13.5	12.8	13.6
Oct	16.5	15.8	15.3	14.3	14.8	13.7	14.4	15.5	14		12.5	13.4	13.1	13.7	13.6	14.1	12.2	13.4	13.5	13.5	12.9	13.4
Nov	14.1	17.1	14.3	14.4	15.3	13.5	14.6	14.8	13.5	12.9	12.3			11.9	13.2	13.7	12.2	13	12.2	12.8	12	13.2
Dec	15.2	17	13.8		15.8	12.9	14.3	15.8	14	12.8	12.4	12.4		12.7	13.1	10.7	11.8	11.2	12	12		13.1

Fig. S3 Monthly and annual distribution of the weighted mean length (*wML*, numbers within cells) and the number of specimens examined (color scale) of sardine in the ports of Ancona and Chioggia. Warmer colors indicates a higher number of measured specimens.

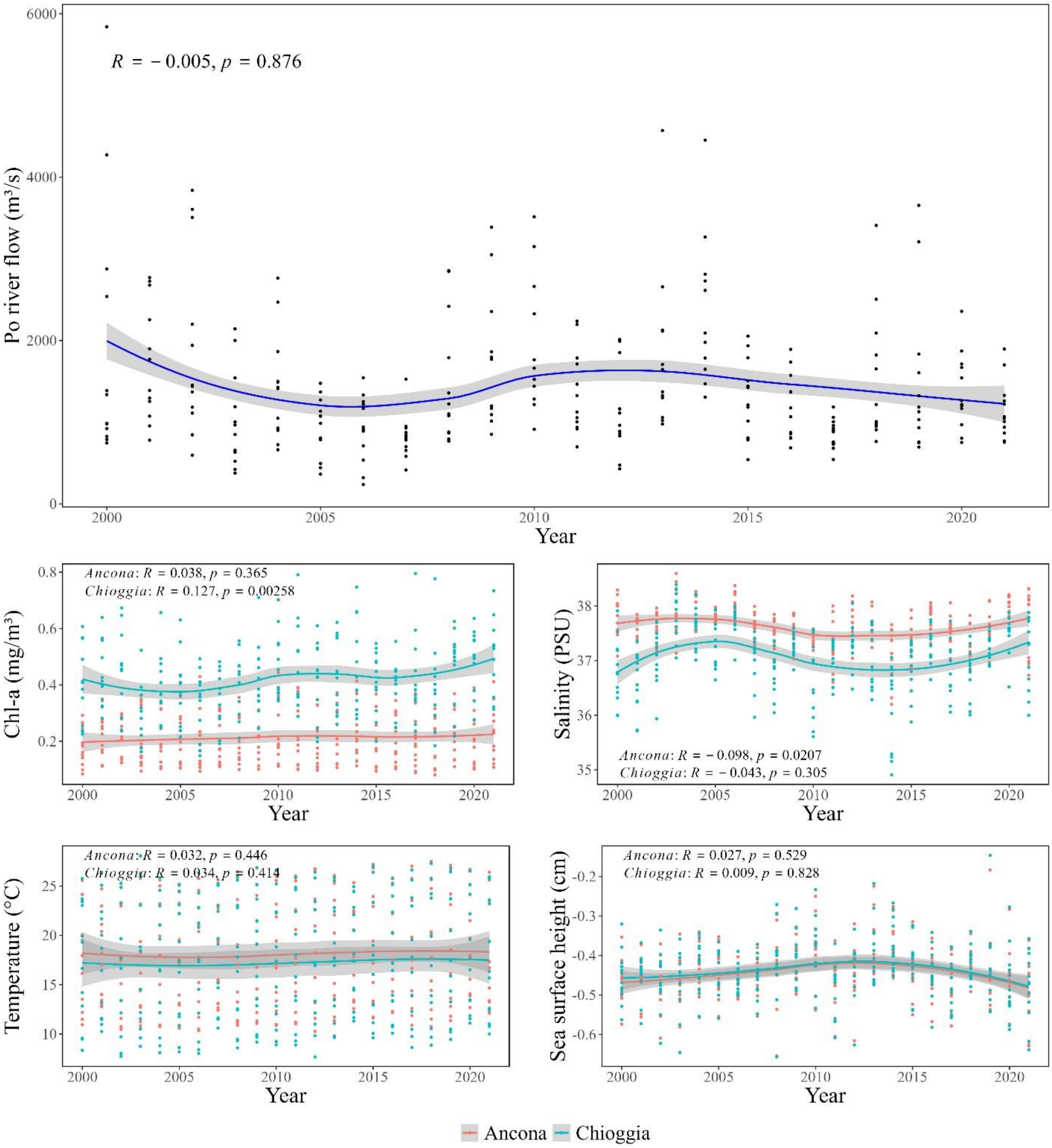


Figure S4 Temporal trends of the environmental variables. Linear regression lines, correlation coefficients (R), and significance levels (p-values) are displayed.

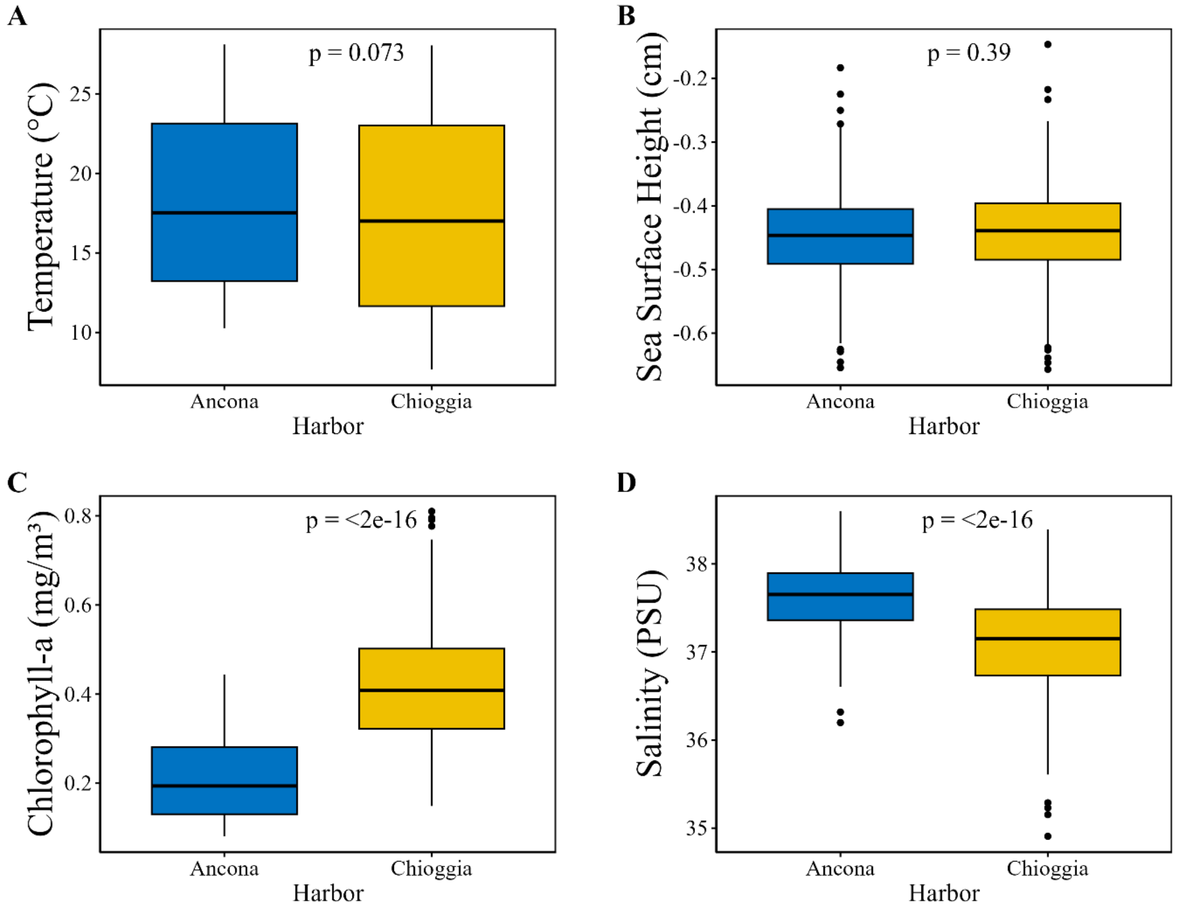


Figure S5 T-test boxplot for (A) temperature, (B) Sea Surface Height, (C) chlorophyll-a concentration and (D) salinity that shows spatial differences between Ancona (blue) and Chioggia (yellow). P-values are shown.

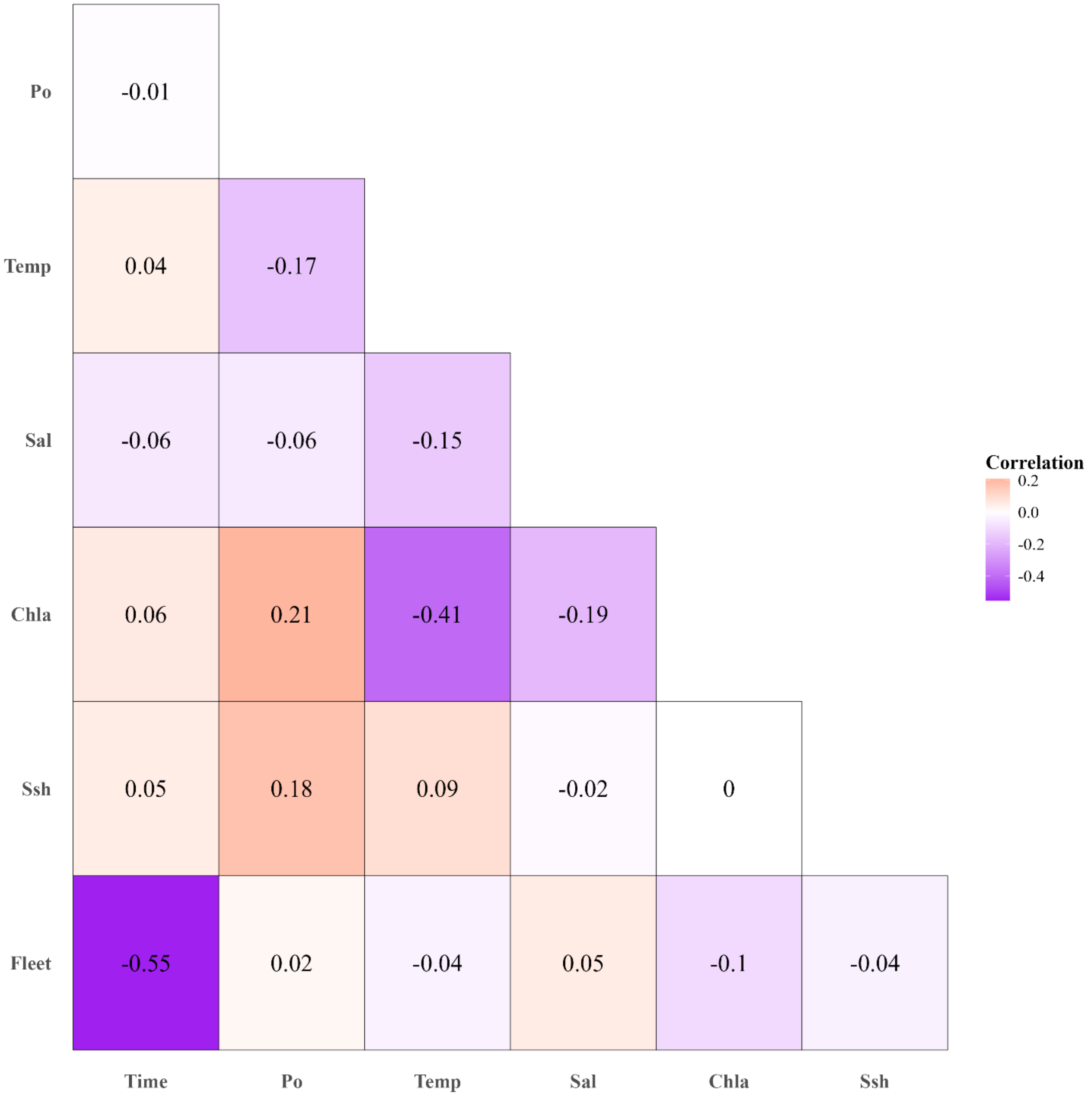


Figure S6 Kendall's rank correlation matrix among temporal, environmental, and anthropogenic variables used in the GAM analysis. Color scale represents the strength and direction of correlations, from negative (purple) to positive (orange) values. Correlation coefficients above 0.49 (in absolute value) are considered significant.

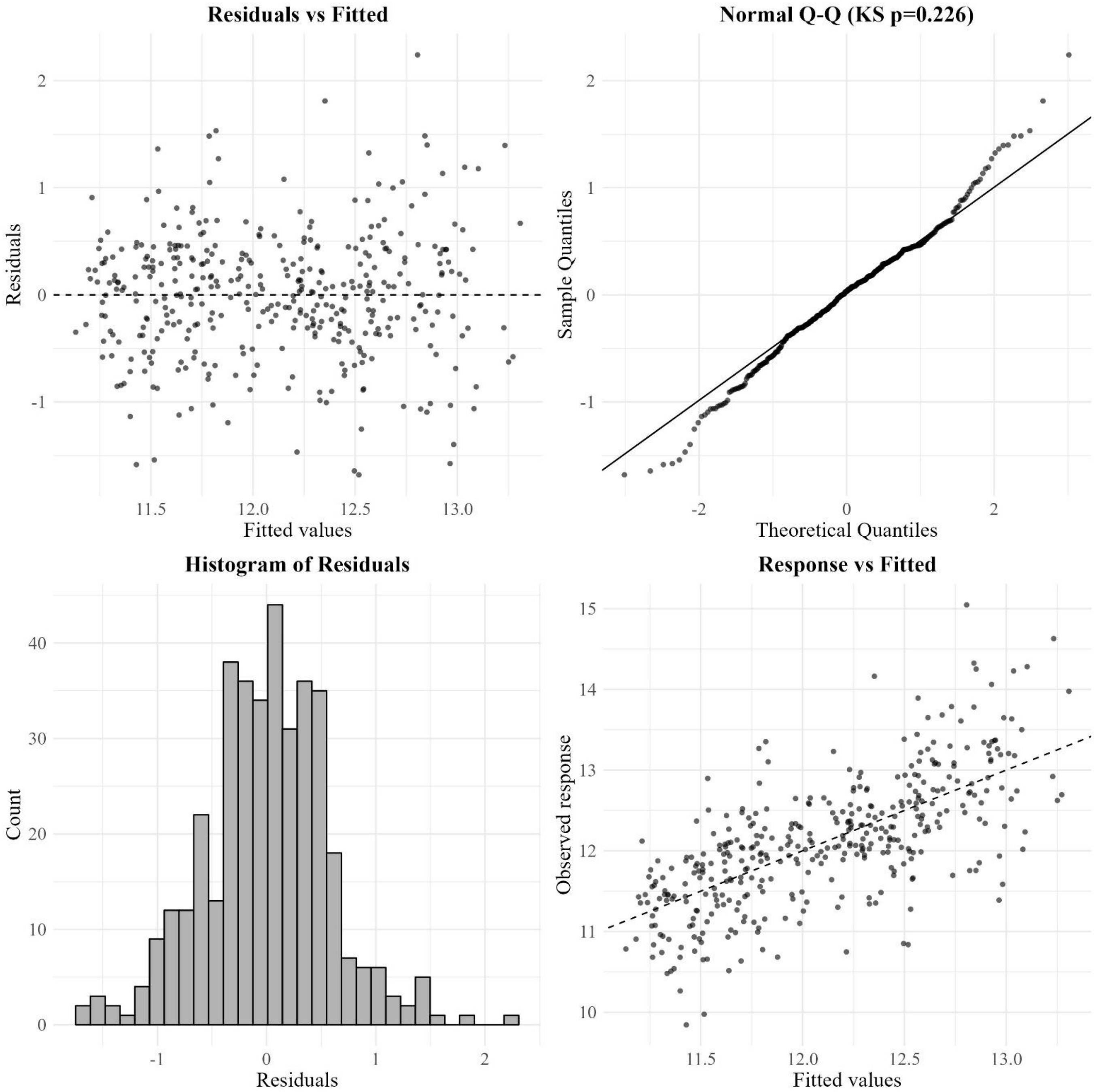


Figure S7. GAM diagnostic for anchovy

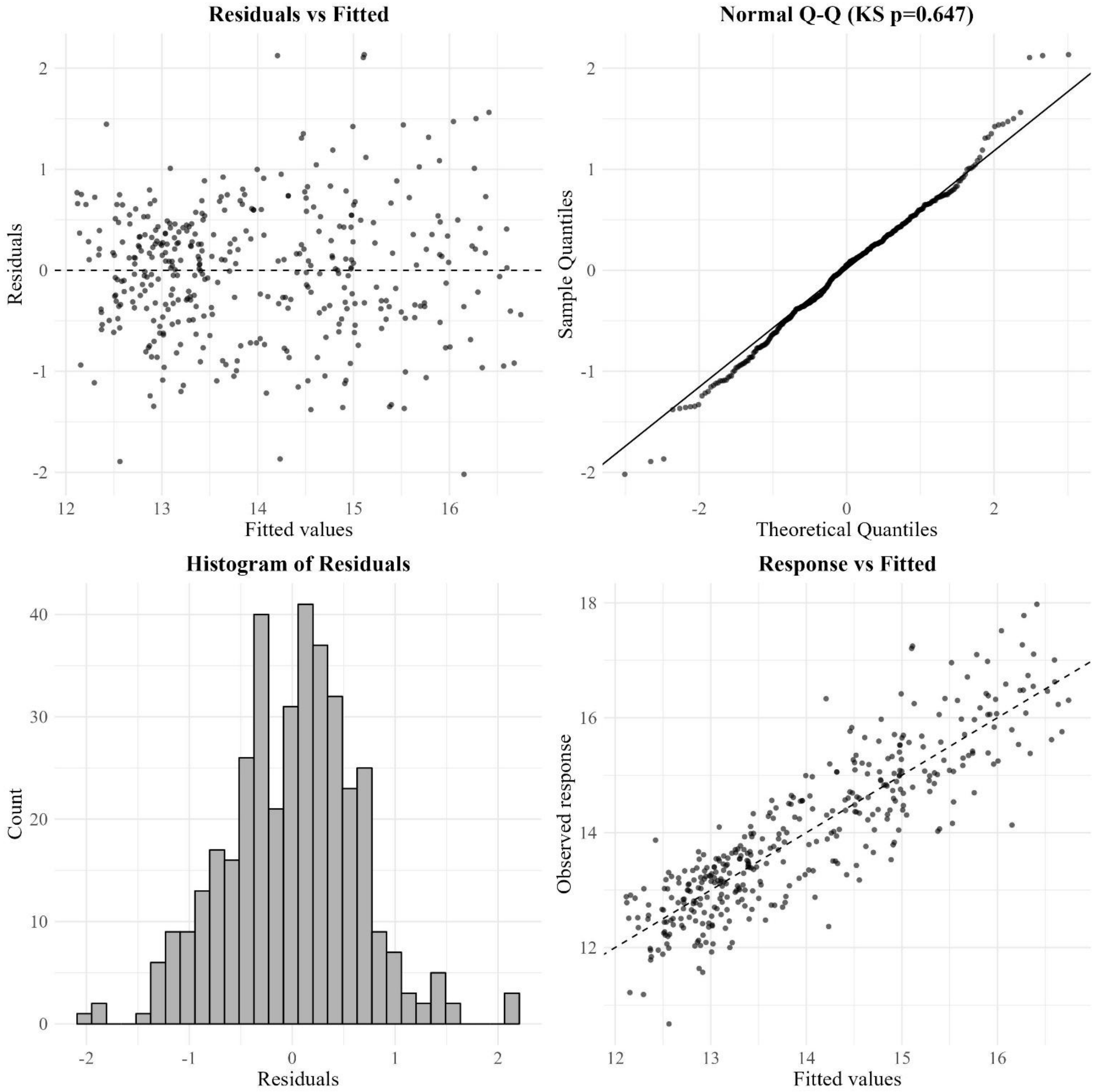


Figure S8 GAM diagnostic for sardines

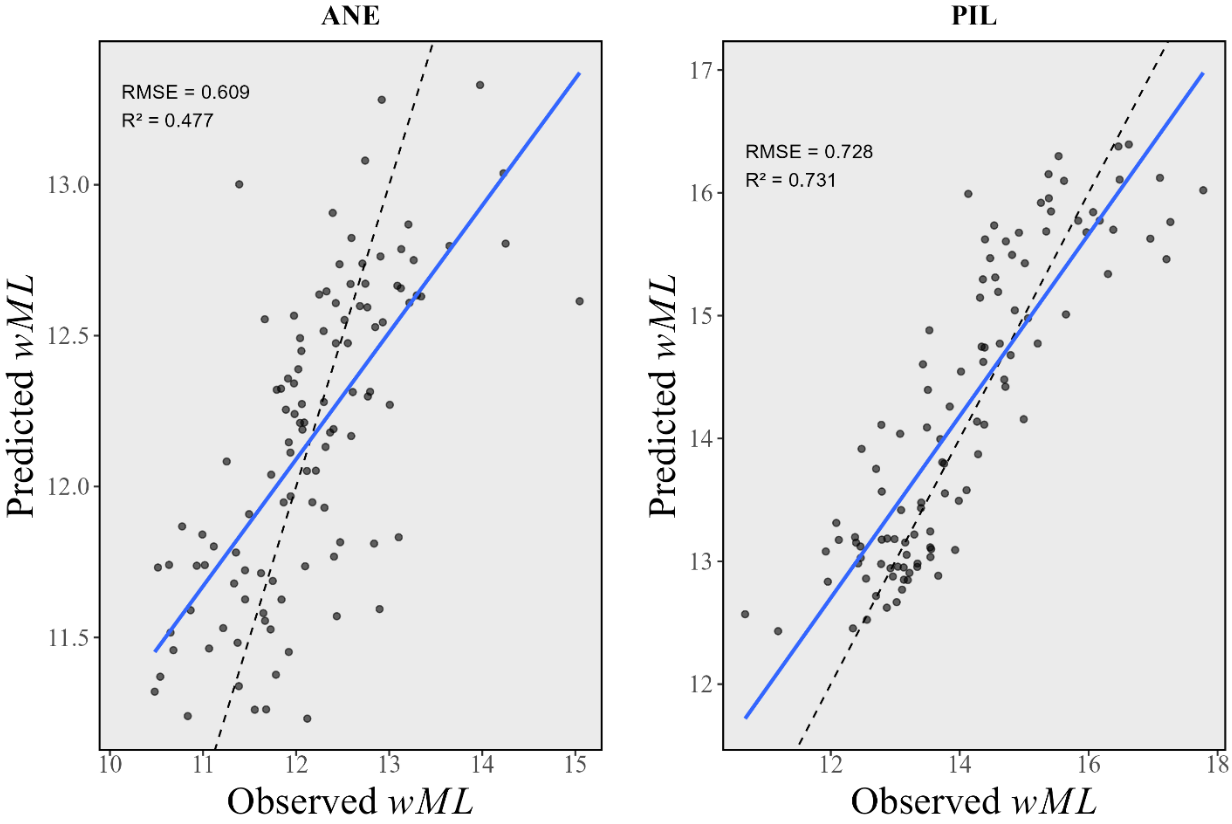


Fig. S9 Observed versus predicted weighted mean length (wML) for anchovy (ANE, left panel) and sardine (PIL, right panel) from the best GAM models. The solid line represents the fitted linear regression, while the dashed line is the 'fitting of the observed data. Model performance is summarized by root mean squared error (RMSE) and coefficient of determination (R²).

Table S1 Results of variable selection procedure for GAMs applied to anchovy (ANE) and sardine (PIL). Each row represents a model tested at different temporal lags (0–12 months) for environmental and anthropogenic predictors. The column *Factors* lists the covariates included in each model, and the corresponding Akaike Information Criterion (AIC) values are reported and ranked by lowest to highest for each lag. Lower AIC values indicate better model performance.

	ANE		PIL	
Lag	**Factors**	**AIC**	**Factors**	**AIC**
0	Time, Harbor, Fleet, Ssh, Temp	531.884	Time, Temp, Fleet, Season, Po, Sal, Chla	572.835
	Time, Harbor, Fleet, Ssh, Temp, Po	533.323	Time, Temp, Fleet, Season, Po	573.636
	Time, Harbor, Fleet, Ssh, Temp, Po, Season	534.844	Time, Temp, Fleet, Season, Po, Sal	573.679
	Time, Harbor, Fleet, Season	534.875	Time, Temp, Fleet, Season	574.393
	Time, Harbor, Fleet	535.059	Time, Temp, Fleet	583.032
	Time, Harbor	541.692	Time, Temp	591.910
	Time	567.281	Time	633.629
1	Time, Harbor, Fleet, Chla, Po	516.205	Time, Season, Fleet, Po, Chla, Harbor	560.786
	Time, Harbor, Fleet, Chla, Po, Temp	516.482	Time, Season, Fleet, Po, Chla, Harbor, Sal	562.017
	Time, Harbor, Fleet, Chla, Po, Temp, Sal	518.328	Time, Season, Fleet, Temp, Chla	564.186
	Time, Harbor, Fleet	518.656	Time, Season, Fleet, Temp	564.770
	Time, Harbor, Fleet, Chla	520.380	Time, Season, Fleet	569.553
	Time, Harbor	541.692	Time, Season	602.062
	Time	567.281	Time	633.629
2	Time, Harbor, Po, Fleet, Temp, Ssh, Sal	505.188	Time, Season, Fleet, Po, Sal	554.608
	Time, Harbor, Po, Fleet, Temp, Ssh	507.239	Time, Season, Fleet, Po, Sal, Chla	554.853
	Time, Harbor, Po, Fleet, Temp	507.411	Time, Season, Fleet, Po, Sal, Harbor, Temp	555.404
	Time, Harbor, Po, Fleet	509.389	Time, Season, Fleet, Po	556.390
	Time, Harbor, Po	538.588	Time, Season, Fleet	561.178
	Time, Harbor	541.692	Time, Season	602.062
	Time	567.281	Time	633.629
3	Time, Harbor, Fleet, Chla, Temp, Ssh	513.265	Time, Season, Fleet, Chla, Sal, Po	562.569
	Time, Harbor, Fleet, Chla, Temp, Ssh, Po	513.728	Time, Season, Fleet, Chla, Sal	563.491
	Time, Harbor, Fleet, Chla, Temp	513.920	Time, Season, Fleet, Chla, Sal, Po, Temp	564.397
	Time, Harbor, Fleet, Chla	518.942	Time, Season, Fleet, Chla	565.043
	Time, Harbor, Fleet	519.910	Time, Season, Fleet	567.671
	Time, Harbor	541.692	Time, Season	602.062
	Time	567.281	Time	633.629
4	Time, Fleet, Ssh, Harbor, Temp, Sal	484.653	Time, Season, Fleet	567.091
	Time, Fleet, Ssh, Harbor, Temp	485.274	Time, Season, Fleet, Temp	567.522
	Time, Fleet, Ssh, Harbor	485.278	Time, Season, Fleet, Temp, Chla	568.320
	Time, Fleet, Ssh, Harbor, Temp, Sal, Po	486.521	Time, Season, Fleet, Temp, Chla, Po	568.981
	Time, Fleet, Ssh	508.048	Time, Season, Fleet, Temp, Chla, Ssh, Sal	571.284
	Time, Fleet	517.371	Time, Season	602.062
	Time	567.281	Time	633.629
5	Time, Fleet, Harbor, Sal	498.104	Time, Temp, Fleet, Season, Sal	541.621
	Time, Fleet, Harbor	499.348	Time, Temp, Fleet, Season, Sal, Ssh	542.041
	Time, Fleet, Chla, Sal, Temp	502.709	Time, Temp, Fleet, Season, Sal, Ssh, Chla	542.350

	Time, Fleet, Chla, Sal, Temp, Season	502.977	Time, Temp, Fleet, Season	543.639
	Time, Fleet, Chla, Sal, Temp, Season, Ssh	503.952	Time, Temp, Fleet	555.890
	Time, Fleet	520.846	Time, Temp	601.076
	Time	567.281	Time	633.629
6	Time, Fleet, Sal, Harbor, Season	512.285	Time, Temp, Fleet, Po, Sal, Chla	539.038
	Time, Fleet, Sal, Harbor	512.364	Time, Temp, Fleet, Po, Sal, Chla, Harbor	539.895
	Time, Fleet, Sal, Harbor, Season, Po	513.592	Time, Temp, Fleet, Po, Sal	540.302
	Time, Fleet, Sal, Harbor, Season, Po, Ssh	514.484	Time, Temp, Fleet, Po	544.626
	Time, Fleet, Sal	523.391	Time, Temp, Fleet	551.010
	Time, Fleet	529.779	Time, Temp	584.316
	Time	567.281	Time	633.629
7	Time, Fleet, Harbor, Season, Ssh	502.052	Time, Season, Fleet, Po, Chla, Temp	567.199
	Time, Fleet, Harbor, Season	503.958	Time, Season, Fleet, Po, Chla, Temp, Harbor	568.645
	Time, Fleet, Harbor, Temp, Ssh, Chla, Season	504.867	Time, Season, Fleet, Po, Chla	571.775
	Time, Fleet, Harbor	508.611	Time, Season, Fleet, Po	574.768
	Time, Fleet, Harbor, Po, Ssh, Chla	511.871	Time, Season, Fleet	575.310
	Time, Fleet	526.938	Time, Season	602.062
	Time	567.281	Time	633.629
8	Time, Fleet, Chla, Harbor, Season, Po, Ssh	479.331	Time, Season, Temp, Fleet, Chla, Harbor, Sal	580.845
	Time, Fleet, Chla, Harbor, Season	479.521	Time, Season, Temp, Fleet, Chla, Harbor	581.113
	Time, Fleet, Chla, Harbor, Season, Po	479.600	Time, Season, Temp, Fleet	581.970
	Time, Fleet, Chla, Harbor	481.414	Time, Season, Temp, Fleet, Chla	582.151
	Time, Fleet, Chla	495.028	Time, Season, Temp	599.863
	Time, Fleet	518.650	Time, Season	602.062
	Time	567.281	Time	633.629
9	Time, Fleet, Chla, Temp, Harbor, Po, Season	484.231	Time, Fleet, Sal, Temp, Season, Chla	557.459
	Time, Fleet, Chla, Temp, Sal, Po	485.654	Time, Fleet, Sal, Temp, Season, Chla, Ssh	558.350
	Time, Fleet, Chla, Temp	486.880	Time, Fleet, Sal, Temp, Ssh	565.993
	Time, Fleet, Chla	489.006	Time, Fleet, Sal, Temp	570.342
	Time, Fleet, Chla, Temp, Season	489.197	Time, Fleet, Season	570.505
	Time, Fleet	509.420	Time, Fleet	590.337
	Time	567.281	Time	633.629
10	Time, Fleet, Ssh, Harbor, Chla, Temp	494.855	Time, Season, Fleet, Temp	548.685
	Time, Fleet, Ssh, Harbor, Chla, Temp, Sal	496.737	Time, Po, Fleet, Temp, Sal, Season	550.864
	Time, Fleet, Po, Harbor	499.166	Time, Po, Fleet, Temp, Sal, Season, Harbor	552.745
	Time, Fleet, Po, Harbor, Chla	499.577	Time, Season, Fleet	559.195
	Time, Fleet, Po	517.870	Time, Harbor, Fleet, Temp, Sal	563.982
	Time, Fleet	526.479	Time, Season	602.062
	Time	567.281	Time	633.629
11	Time, Harbor, Po, Fleet, Temp	502.752	Time, Temp, Fleet, Season	549.402
	Time, Harbor, Po, Fleet	505.549	Time, Temp, Fleet	550.201
	Time, Harbor, Po, Fleet, Temp, Season	507.147	Time, Temp, Fleet, Season, Po	550.837
	Time, Harbor, Po, Fleet, Temp, Season, Sal	508.951	Time, Temp, Fleet, Season, Po, Sal	552.571
	Time, Harbor, Po	527.247	Time, Temp, Fleet, Season, Po, Sal, Chla	554.254
	Time, Harbor	541.692	Time, Temp	592.606
	Time	567.281	Time	633.629

12	Time, Chla, Harbor, Fleet, Temp, Ssh, Sal	531.598	Time, Temp, Season, Harbor, Fleet	578.739
	Time, Chla, Harbor, Sal, Temp	533.296	Time, Temp, Season, Harbor, Fleet, Po	579.612
	Time, Chla, Harbor, Sal	534.475	Time, Temp, Season, Harbor, Fleet, Po, Sal	581.306
	Time, Chla, Harbor, Fleet, Temp, Po	535.294	Time, Temp, Season, Po	586.487
	Time, Chla, Harbor	536.997	Time, Temp, Season	587.408
	Time, Chla	547.527	Time, Temp	593.876
	Time	567.281	Time	633.629

References

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

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. https://doi.org/10.3389/fmars.2021.570354.

Aldanondo, N., Cotano, U., Tiepolo, M., Boytra, G., 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(3): 196-208. https://doi.org/10.1111/j.1365-2419.2010.00537.x.

Andersen, K.H., Brander, K. (2009). Expected rate of fisheries-induced evolution is slow. PNAS. 106(28): 11657-11660. https://doi.org/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, 1–16. https://doi.org/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. https://www.fao.org/gfcm/data/safs/en. [Accessed July 2024]

Aragão, L., Mentaschi, L., Pinardi, N., Verri, G., Senatore, A., Di Sabatino, S. (2024). The freshwater discharge into the Adriatic Sea revisited. Front. Clim. 6, 1–18. https://doi.org/10.3389/fclim.2024.1368456.

Azzurro, E., Moschella, P., Maynou, F. (2011). Tracking signals of change in Mediterranean fish diversity based on local ecological knowledge. PLoSONE. 6(9): e24885. https://doi.org/10.1371/journal.pone.0024885.

Bakun, A. (2006). Wasp-waist populations and marine ecosystem dynamics: Navigating the "predator pit" topographies. Prog. Oceanogr. 68(2–4): 271–288. https://doi.org/10.1016/j.pocean.2006.02.004.

Barange, M., Bahri, T., Beveridge, M.C.M., Cochrane, K.L., Funge-Smith, S., Poulain, F. (2018). Impacts of climate change on fisheries and aquaculture. Synthesis of current knowledge, adaptation and mitigation options. FAO, FAO Fisheries and Aquaculture Technical Paper No. 627. Rome, Italy. 654 pp.

Barausse, A., Duci, A., Mazzoldi, C., Artioli, Y., Palmeri, L. (2009). Trophic network model of the Northern Adriatic Sea: analysis of an exploited and eutrophic ecosystem. Estuar. Coast. Shelf S. 83(4): 577–590. https://doi.org/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(3):504-516. http://dx.doi.org/10.12681/mms.2059.

Baudron, A.R., Needle, C.L., Rijnsdrop, A.D., Marshall, C.T. (2014). Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes. Glob. Change Biol. 20(4): 1023-1031. https://doi.org/10.1111/gcb.12514.

Bigelow, K.A., Boggs, C.H., He, X. (1999). Environmental effects on swordfish and blue shark catch rates in the US North Pacific longline fishery. Fish. Oceanogr. 8(3): 178 – 198. https://doi.org/10.1046/j.1365-2419.1999.00105.x.

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. https://doi.org/10.3354/meps11275.

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. http://dx.doi.org/10.1098/rsos.160202.

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. https://doi.org/10.1016/j.pocean.2016.12.002.

Bulgakova, Y.V. (1993). Daily feeding dynamics of the Black Sea anchovy, Engraulis encrasicholus. J. Ichthyol. 33(7):78-88.

Burnham, K.P., Anderson, D.R. (2002) Model Selection and Multimodel Inference. A practical information-theoretic approach. 2nd edn. New York: Springer-Verlag Inc.

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(6): 521–532. https://doi.org/10.1111/fog.12126.

Carpi, P., Scarcella, G., 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. https://doi.org/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. https://www.fao.org/gfcm/data/safs/en. [Accessed July 2024].

Cingolani, N., Giannetti, G., Arneri, E. (1996). Anchovy fisheries in the Adriatic Sea. Sci. Mar. 60: 269–277.

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 Technical Documents. 3: 39-52.

Coll, M., Santojanni, A., Palomera, I., Tudela, S., 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. https://doi.org/10.1016/j.jmarsys.2006.10.002.

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

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. https://doi.org/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 and Fish. 14(1): 89-109. https://doi.org/10.1111/j.1467-2979.2011.00453.x.

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

Copernicus Marine Environment Monitoring Service (2024). 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. https://doi.org/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(2): 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(3): 603–618. https://doi.org/10.1006/jmsc.2000.0712.

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

Drake, P., Borlán, A. González-Ortegón, E. Baldó, F., Vilas, C., 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(6):1689-1709. https://doi.org/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., Arneri, E. (2007). An observing system for the collection of fishery and oceanographic data. Ocean Sci. 3: 189-203. https://doi.org/10.5194/os-3-189-2007.

Food and Agriculture Organization (2023). The State of Mediterranean and Black Sea Fisheries 2023 – Special edition. FAO, General Fisheries Commission for the Mediterranean. Rome. 2023. https://doi.org/10.4060/cc8888en.

Food and Agriculture Organization (2025). Number of Fishing Vessels: Fishing Effort Indicator. https://www.fao.org/cwp-on-fishery-statistics/handbook/capture-fisheries-statistics/fishing-effort/en/. [Accessed January 28, 2025].

Fernández-Corredor, E., Albo-Puigserver, M., Pennino, M.G., Bellido, J.M., 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. https://doi.org/10.1016/j.rsma.2020.101606.

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

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

Giani, M., Djakovac, T., Degobbis, D., Cozzi, S., Solidoro, C., Umani, S.F. (2012). Recent changes in the marine ecosystems of the northern Adriatic Sea. Estuar. Coast. Shelf S. 115:1-13. https://doi.org/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(2):69-89. https://doi.org/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(8): e0219671. https://doi.org/10.1371/journal.pone.0219671.

Grbec, B., Morović, M., Matić, F., Ninćević Gladan, Ž., Marasović, I., Vidjak, O., et al. (2015). Climate regime shifts and multi-decadal variability of the Adriatic Sea pelagic ecosystem. Acta Adriat. 56(1): 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(1):11609. https://doi.org/10.1038/s41598-019-47201-9.

Heino, M., Pauli, B.D., Dieckmann, U. (2015). Fisheries-Induced Evolution. Annu. Rev. Ecol. Evol. S. 46: 461-480. https://doi.org/10.1146/annurev-ecolsys-112414-054339.

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(4):800-811. https://doi.org/10.12681/mms.26525.

Hilborn, R., Walters, C.J. (1992). Quantitative fisheries stock assessment: Choice, dynamics and uncertainty. Rev Fish Biol Fisheries 2, 177–178 (1992). https://doi.org/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., Tibshirani, R. (2023). An introduction to statistical learning with applications in R. 2ed. Springer, New York, NY.

Jennings, S., Greenstreet, S.P.R., 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(3): 617-627. https://doi.org/10.1046/j.1365-2656.1999.00312.x.

Lai, J., Tang, J., Li, T., Zhang, A., Mao, L. (2024). Evaluating the relative importance of predictors in Generalized Additive Models using the gam.hp R package. Plant Divers. 46(4):542-546. https://doi.org/10.1016/j.pld.2024.06.002.

Law, R. (2000). Fishing, selection, and phenotypic evolution. ICES J. Mar. Sci. 57(3): 659–668. https://doi.org/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(4):751-768. https://doi.org/10.12681/mms.26001.

Lima, A.R.A., Baltazar-Soarez, M., Garrido, S., Riveiro, I., Carrera, P., Piecho-Santos, M.A. et al. 82022). 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. https://doi.org/10.1016/j.scitotenv.2021.150167.

Lindmark, M., Audzijonyte, A., Blanchard, J.L., 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. https://doi.org/10.1111/gcb.16341.

Lleonart, J., Maynou, F. (2003). Fish stock assessments in the Mediterranean: state of the art. Sci. Mar., 67(1): 37-49. https://doi.org/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. https://doi.org/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(4): 843–857. https://doi.org/10.12681/mms.25990.

Marini, M., Grilli, F. (2023). The role of Nitrogen and Phosphorus in eutrophication of the Northern Adriatic Sea: History and future scenarios. Appl Sci. 13(16): 9267. https://doi.org/10.3390/app13169267.

Maunder, M.N., Punt, A.E. (2004). Standardizing catch and effort data: a review of recent approaches. Fish. Res. 70:141-159. https://doi.org/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(32): eadg8304. https://doi.org/10.1126/sciadv.adg8304.

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

Mozetič, P., Francé, J., Kogovšek, T., Talaber, I., 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., 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(3): 325-333. https://doi.org/18048/2020.00.24.

Otero, J., 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. https://doi.org/10.1093/icesjms/fsad072.

Palomera, I., Olivar, M.P., Salat, J., Sabatés, A., Coll, M., García, A., Morales-Nin, B. (2007). Small pelagic fish in the NW Mediterranean Sea: An ecological review. Prog. Oceanogr. 74(2–3): 377–396. https://doi.org/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. https://doi.org/10.1007/BF00043521.

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

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

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

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

Penna, N., Capellacci, S., 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(3-4): 321-326. https://doi.org/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: 1–20. https://doi.org/10.3389/fmars.2020.00622.

Piet, G.J., Quirijns F.J., Robinson, L., Greenstreet S.P.R. (2006). Potential pressure indicators for fishing and their data requirements. ICES J. Mar. Sci. 64(1): 110-121. https://doi.org/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. https://doi.org/10.1126/science.1098222.

Pinardi, N., Zavatarelli, M., Arneri, E., Crise, A., Ravaioli, M. (2004). "The physical, sedimentary and ecological structure and variability of shelf areas in the Mediterranean Sea" in The Global Coastal Ocean, ed. RR. Robinson and K.H. Brink (Cambridge: Harvard University press), 14(32): 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. https://doi.org/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. Marine Syst. 79(3-4): 403-417. https://doi.org/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. https://doi.org/10.1007/s11160-025-09949-4.

Regional Open Data Portal (2024). 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. https://doi.org/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. 4:371. https://doi.org/10.3389/fmars.2017.00371.

Sainmont, J., Andersen, K., Varpe, Ø., Visser, A. (2014). Capital versus Income Breeding in a Seasonal Environment. Am. Nat. 184: 466-476. https://doi.org/10.1086/677926.

Salini, R., Tora, S., Filipponi, F., Conte, A., Giansante, C., Ippoliti, C. (2024). Analyzing trend and heatwaves of 15 years of Sea Surface Temperature Variations along the Italian Adriatic Coast. Vet. Ital. 60(4). https://doi.org/10.12834/VetIt.3583.27524.2.

Sani, T.; Marini, M.; Campanelli, A.; Machado Toffolo, M.; Goffredo, S.; Grilli, F. (2024). Evolution of freshwater runoff in the Western Adriatic Sea over the last century. Environments 11(1): 22. https://doi.org/10.3390/environments11010022.

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(1):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(4): 603-617. https://doi.org/10.3989/scimar.2005.69n4603.

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

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(1): 212–225. https://doi.org/10.1111/faf.12515.

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(4):362-372. https://doi.org/10.1111/fog.12158.

Schismenou, E., Chatzifotis, S., Tsiaras, K., 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. https://doi.org/10.1111/jfb.15872.

Sestelo, M., Villanueva, N.M., Meira-Machado, L., Roca-Pardinas, J. (2016). FWDselect: An R Package for Variable Selection in Regression Models. The R Journal. 8(1):132-148. https://doi.org/10.32614/RJ-2016-009.

Sharpe, D.M.T., Hendry, A.P. (2009). SYNTHESIS: Life history change in commercially exploited fish stocks: an analysis of trends across studies. Evol. Appl. 2(3): 260-275. https://doi.org/10.1111/j.1752-4571.2009.00080.x.

Solanki, H.U., Bhatpuria, D., 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(1): 30:43. http://dx.doi.org/10.1080/10106049.2015.1120357.

Swain, D.P., Sinclair, A.F., Hanson, M.K. (2007). Evolutionary response to size-selective mortality in an exploited fish population. Proc. R. Soc. B. 274: 1015-1022. https://doi.org/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(2): jeb244984. https://doi.org/10.1242/jeb.244984.

Trenkel, V.M. (2018). How to provide scientific advice for ecosystem-based management now. Fish Fish. 19(2): 390-398. https://doi.org/10.1111/faf.12263.

Tsagarakis, K., Palialexis, A., Vassilopoulou V. (2014). Mediterranean fishery discards: review of the existing knowledge. ICES J. Mar. Sci. 71(5): 1219–1234. https://doi.org/10.1093/icesjms/fst074.

Tsikliras, A.C., Dinouli, A., Tsiros, V-Z., Tsalkou, E. (2015) The Mediterranean and Black Sea fisheries at risk from overexploitation. PLoS ONE. 10(3): e0121188. https://doi.org/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. https://doi.org/10.3354/meps09366.

Tzanatos, E., Raitsos, D.E., Triantafyllou, G., Somarakis S., Tsonis A.A. (2014). Indications of a climate effect on Mediterranean fisheries. Climatic Change. 122: 41–54. https://doi.org/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. https://doi.org/10.1007/s00227-014-2463-1.

Van Beveren, E., Fromentin, J., Rouyer, T., Bonhommeau, S., Brosset, P., Saraux, C. (2016). The fisheries history of small pelagiscs in the Northern Mediterranean. ICES J. Mar. Sci. 73(6): 1474–1484. https://doi.org/10.1093/icesjms/fsw023.

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

Villasante S., Sumaila U. R. (2010). Estimating the effects of technological efficiency on the European fishing fleet. Mar. Pol. 34(3): 720-722. https://doi.org/10.1016/j.marpol.2009.11.008.

Wicklin, R. (2023). How to Interpret Spearman and Kendall Correlation Coefficients. SAS Blogs, April 5. https://blogs.sas.com/content/iml/2023/04/05/interpret-spearman-kendall-corr.html.

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. https://doi.org/10.3389/fmars.2021.609432.

CHAPTER 2

~ Incorporating key environmental drivers in European anchovy (E*ngraulis encrasicolus*) stock assessment model in the Adriatic Sea

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Abstract

Recent advancements in integrated single-species models allow for the inclusion of environmental drivers in stock assessment models, improving stock evaluation and better explaining fish population dynamics. This study applies Stock Synthesis (SS) to assess the European anchovy (*Engraulis encrasicolus*) stock in the Adriatic Sea, allowing for time-varying growth, recruitment, mortality, and survey catchability. These processes were linked to sea surface temperature (SST), river runoff, chlorophyll-a concentration, and salinity. Model selection, based on AIC and parameter significance, revealed that higher SST is significantly associated with reduced mean length-at-age. Two-variable models further revealed that SST strongly influences growth, while freshwater input modulates mortality at age one and survey catchability. Integrating these environmental factors reduced unexplained recruitment variability and improved model fit to length- and age-composition data, enhancing stock status estimates such as spawning biomass and fishing mortality. Diagnostic evaluations indicate that the integration of environmental covariates, despite inherent challenges associated with data quality, offers valuable insights into the observed declines in anchovy size and recruitment. The findings emphasize the importance of environmental conditions — particularly temperature and freshwater discharge — in driving life-history traits and population dynamics.

Keywords: European anchovy, Adriatic Sea, ecosystem-based fishery management, stock assessment, Stock Synthesis

2.1 Introduction

Fishery production in the Mediterranean and Black Seas amounted to nearly 2 million tonnes in 2021, with capture fisheries contributing 1,063,000 tonnes and generating a total revenue 7.8 billion USD. Although those production levels have doubled since the 1970s, they fluctuate markedly and show a general declining trend (i.e., the total revenue has increased only 1.3% since 2020). Overfishing appears to be one of the primary drivers of the current low production in the area, since 58% of commercial fish stocks are considered overfished. Although the percentage is high, it represents a notable improvement compared to the 73% estimated in 2020 (FAO 2023).

The Adriatic Sea is among the most heavily exploited basins in the Mediterranean Sea (Micheli et al. 2013, Eigaard et al. 2017) and supports two of the most commercially important fish stocks in the basin: European anchovy (*Engraulis encrasicolus*) and sardine (*Sardina pilchardus*). The decline in small pelagic stocks in the Adriatic Sea has significant socio-economic consequences for local fisheries, as these species represent 67.5% of the total landings in the region (FAO, 2023). Fluctuations in the abundance of these stocks affect economics and the marine ecosystem, since they support major fisheries and serve as a vital trophic link between primary producers and top predators (Palomera et al. 2007, Coll et al. 2008, Navarro et al. 2009, 2017, Gómez-Campos et al. 2011, Piroddi et al. 2017, Fanelli et al. 2023). Regional efforts to address the state of these stocks have a long history. It begun with annual analytical assessments since the 1990s (e.g., Arneri 1994; Cingolani et al. 1996; Angelini et al. 2024) under the framework of the General Fisheries Commission for the Mediterranean (GFCM), the Regional Fisheries Management Organization (RFMO) of Food and Agriculture Organization (FAO), responsible for providing scientific advice for the management of fish stocks in the Mediterranean and Black Seas. Building on these longstanding regional efforts, the anchovy stock in the Adriatic Sea is currently assessed using a catch-at-age model (Angelini et al. 2024) based on FLSAM, the State-space Assessment Model (SAM) (Nielsen and Berg 2014; Payne 2022) included in the Fisheries Library in R (Kell et al. 2007). This assessment method has been selected as the best for this stock since the benchmark run in 2015 (GFCM 2015). However, the complexity of the input data for this stock, e.g. i) different time series of survey index occurring in different periods (early and late summer), ii) possible uncertainties about aggregating age data from multiple countries, causes stock assessments to often fail to capture the high variability in population dynamics that is characteristic of this stock (GFCM 2024). Moreover, FLSAM does not adequately explain the observed decline in catch, biomass, and mean length, despite the ongoing crisis in the fishery, which has been driven by both management regulations and reduced stock productivity (Palomera et al. 2007, Scientific Technical and Economic Committee for Fisheries [STECF] 2015, 2023, Ramirez et al. 2018, FAO 2023). This crisis is closely linked to the reduction in the average size of anchovy, which has made their sale less profitable. As a result, fewer fishermen are willing to work on fishing vessels, leading to a decline in the number of active boats in this sector.

Considering all these aspects and the importance of the small pelagic fishery in the Adriatic Sea, the GFCM (Rec. GFCM/37/2013/1) adopted the first multi-annual management plan in 2013, which aimed to minimize the risk of stock collapse while promoting sustainable and relatively stable fisheries. The management plan has been updated based on the outcomes of stock assessments, including for the last GFCM Recommendation (Rec. GFCM/44/2021/20). This plan introduced measures to regulate fishing effort, set catch limits, and protect essential fish habitat, i.e. nursery and spawning grounds. In recent years, these measures, together with the decrease of the profitability of the small pelagic fishing sector, have contributed to improvements in the status of the anchovy stock. In fact, the most recent stock assessment reports an increase of the spawning stock biomass, which now exceeds both the limit and the upper stock reference points. At the same time, fishing mortality (F) is close to the target value of 0.81, corresponding to the exploitation level (E = 0.4) as proposed by Patterson (1992) (Angelini et al. 2024).

However, fishing is not the only factor influencing the dynamics of the anchovy stock, which is also strongly impacted by the environmental effects due to climate change over the last decade (Pennino et al. 2020). The northern-central part of Adriatic Sea, which is included in the GFCM Geographical Sub-Area (GSA) 17 (Fig. 1) is characterized by shallow waters with low salinity and low temperatures (Raicich 1996).

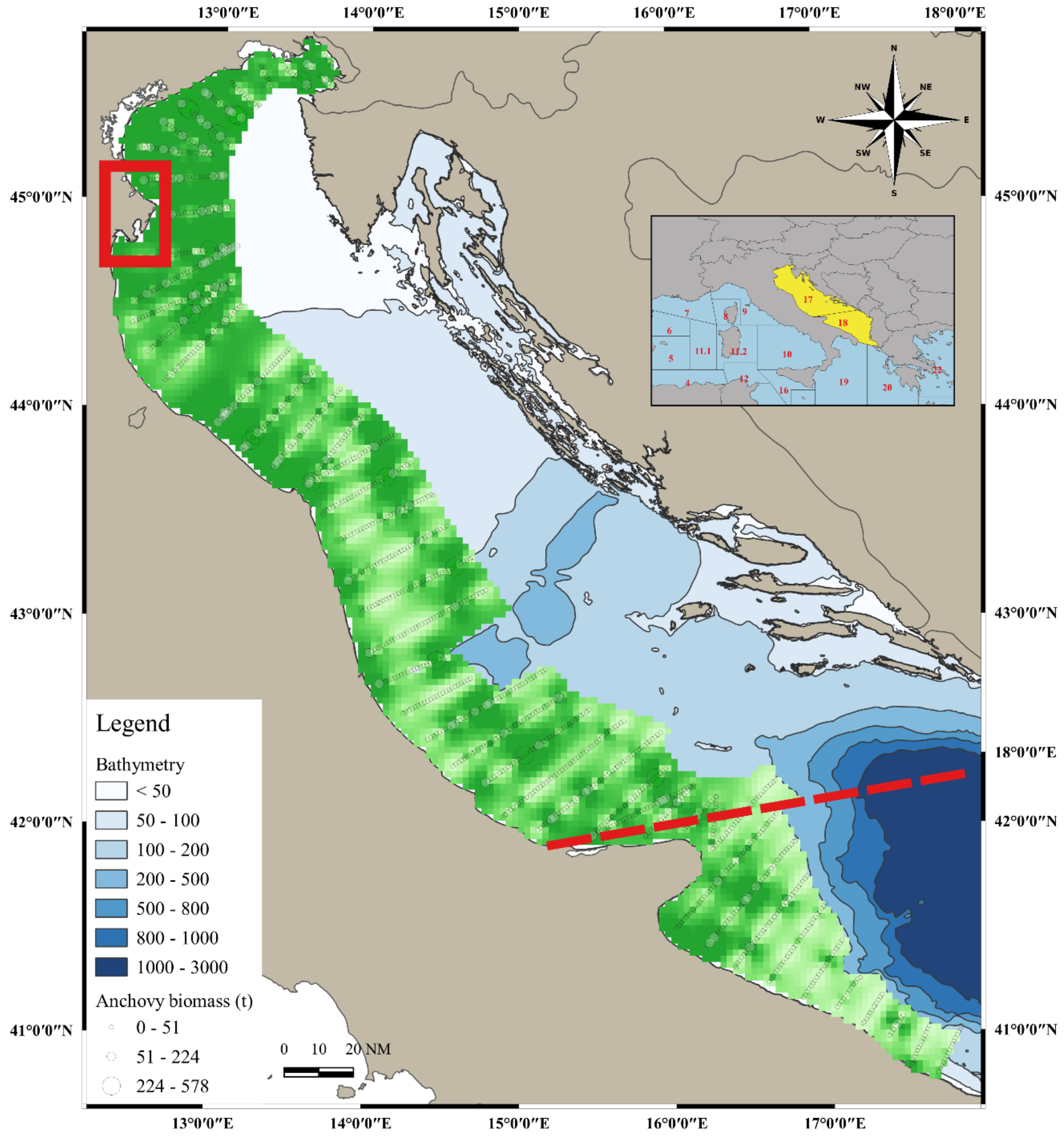

Figure 1 Map of the study area. The green area represents the distribution of anchovy biomass in the Western part of the Adriatic Sea in 2019 assessed by the acoustic survey MEDIAS; darker green areas denote higher anchovy biomass (Fanelli et al., 2023). The red dashed line is the boundary between GSA 17 (Northern-Central Adriatic Sea) and GSA 18 (Southern Adriatic Sea). The solid red square shows the location of Po Delta.

It is heavily influenced by freshwater input from the Po River. Climate change, through rising temperatures and decreasing precipitation, is significantly altering the magnitude and temperature of freshwater flow from the Po River (Cozzi and Giani 2011, Grilli et al. 2020, Sani et al. 2024). Anchovy rely heavily on the Po River–sea continuum; therefore, changes in river discharge can alter zooplankton abundance and disrupt water column stratification, both of which are critical to feeding and reproductive success (Morello and Arneri, 2009, Santojanni et al. 2006, Malavolti et al. 2018, Marini et al. 2023). Moreover, prolonged droughts and intense floods, which have occurred more often during the last decade (Kaniewski et al. 2021), can delay spawning, reduce recruitment success, and slow growth rates (e.g., Palomera et al. 2007, Martin et al. 2008, Giannoulaki et al. 2013, Peck et al. 2013, Van Beveren et al. 2014, Basilone et al. 2017, Brosset et al. 2017, Coll et al. 2019, De Felice et al. 2021, Palermino et al. 2024). Despite the increasing number of hypotheses related the role of environmental drivers, these factors have not yet been directly incorporated into most stock assessments. Several studies suggest that assessment approaches must be updated to keep pace with rapid ecosystem changes that are driving shifts in resource dynamics (Zorica et al. 2013, Pikitch et al. 2014, Carpi et al. 2015a, Punt et al. 2016, Ortega et al. 2024). This highlights the need to move beyond traditional assessment methods and adopting models that account for broader ecological interactions (Hilborn 2011). The Ecosystem-Based Fisheries Management (EBFM) approach is rapidly gaining ground worldwide (Pikitch et al. 2004, Arkema et al. 2006, Smith et al. 2007, Cowan et al. 2012, Patrick and Link 2015, Trenkel 2018, Halpern et al. 2019). EBFM tools range from multi-species assessment methods that include species interactions and predation (e.g., CEATTLE, Holsman et al. 2015; MICE, Angelini et al. 2016), to comprehensive ecosystem models such as ATLANTIS (Fulton and Smith 2004) and Ecopath (Christensen and Walters 2004). Even more complex EBFM approaches involve integrating ecological, social, and economic objectives to maintain ecosystem integrity while supporting sustainable fisheries (see Karnauskas et al. 2021). The potential benefits of EBFM are most apparent in regions where Single Species Assessment Methods (SSAM) has been effective and scientific advice is followed (Murawski et al. 2010, Patrick and Link, 2015; Melnychuck et al. 2017, Hilborn et al. 2020), indicating that integrating ecosystem considerations into stock assessments can address deficiencies and improve fisheries management outcomes (Karnauskas et al. 2021).In this study, we propose an initial step towards developing a single species stock assessment framework to support the transition of Adriatic small pelagic fisheries from traditional management to an EBFM approach. This direction is consistent with international recommendations, as major organizations advocate the integration of ecosystemic and climate considerations into stock assessments (FAO, 2003; Marine Strategy Framework Directive, 2008). In particular, we explore the potential of the integrated catch at age stock assessment method Stock Synthesis (SS; Methot and Wetzel 2013; Methot et al. 2020) to incorporate environmental drivers, allowing linked parameters to vary over time. At the same time, we aim to address some of the limitations of SAM by taking advantage of the flexible structure of SS, which supports the modeling of key biological processes—such as growth, selectivity, and recruitment—even when data are limited or incomplete. SS also offer a finer control over biological settings and data weighting, for example through the definition of multiple fleets with independent specifications Moreover, unlike SAM—which is strictly age-structured and relies on empirical weights-at-age—SS can estimate population dynamics parameters (e.g., growth) and the associated uncertainty in length-at-age directly within the model. These estimates are informed by a variety of data types, typically survey indices, age composition, and length composition data. This feature is particularly relevant for Adriatic anchovy, whose growth is strongly influenced by environmental variability and has been affected by changes in Age–Length Key (ALK) methodology. In conclusion, SS provides a more integrated and versatile framework than SAM, and its ability to combine diverse data sources while capturing the complexities of fish population dynamics has made it a powerful tool for stock assessment. Here, we describe how SS was tailored to the characteristics of European anchovy in the Adriatic Sea, detailing the data sources and model structure, as well as findings from fitting a range of models. We discuss the challenges encountered during model development and validation, as well as the implications of our findings for the sustainable management of anchovy fisheries in the region. Overall, our research represents a critical step towards establishing a robust stock assessment framework for European anchovy in the Adriatic Sea.

2.2 Materials and Methods

2.2.1 Data selection

Given the long history of exploitation of the anchovy and sardine stocks in the Adriatic Sea, we investigated how the anchovy population in the Adriatic Sea has changed from the 1970s to the present, using the most representative available data. However, this presents a significant challenge. Data collection in the Adriatic basin prior to the establishment of the European Union (EU) in the 2000s was complex, as individual countries were responsible for developing their own monitoring protocols. Over the years, various efforts have been made to standardize data collection protocols, culminating in the establishment of the Data Collection Framework (DCF) during the 2000s (Council Regulation 199/2008), which set guidelines for fisheries data collection across EU member states.

Italy has participated in the DCF since its inception in 2002, while Slovenia and Croatia joined in 2005 and 2013, respectively. Although Montenegro and Albania are not EU members, they have adopted data collection methods in line with the DCF, with their data made available through regional initiatives such as the FAO AdriaMed project (https://www.faoadriamed.org/) and GFCM working groups. The DCF mandates that member countries provide data, such as landings, Length Frequency Distributions (LFDs), Catch-At-Age (CAA), length- weight parameters and ALKs for commercial fleets, on a seasonal basis and categorized by gear type (except for ALKs), and GSA, and survey data as abundance and biomass per length class and age class.

Historical data are often managed by institutions rather than in open-access databases, making collaboration essential for access and integration. In addition, these historical data are frequently aggregated by gear type and reported on an annual basis, necessitating assumptions or, in some cases, the exclusion of certain data types from analyses.

Age determination in the Adriatic Sea poses a particular challenge due to the multiple revisions in age reading protocols over time. These changes have made older ALKs, specifically before 2015, not fully comparable with more recent ones, leading to mismatches in model outputs due to differences in age assumptions. The most recent age revision, completed in 2020 (Uriarte et al. 2020), led to updated growth parameters (used as initial values for estimated parameters in Table 1), and established new criteria for the construction of ALKs. In particular, for anchovy - a species that spawns in mid-year (around July) - the standard biological calendar conflicted with the calendar-year-based assessment framework (January 1st). To resolve this, two types of ALKs were introduced: a yearly ALK related to the full year, and two semester-based ALKs to better account for within-year age transitions (i.e., age-0 individual do not occur during the first semester). However, the revised protocol was not retroactively applied to all historical otoliths, which include larger specimens than those currently observed in the assessment. In addition, a reduction in the estimated lengths and ages of anchovies has been observed over the last decade, effectively halving the estimated life expectancy of the population.

This shift in age structure due to the inconsistency in ageing protocols causes the model to interpret the absence of older individuals as increased fishery mortality, which in turn influences the estimation of growth parameters. In addition, the adoption of the most recent ageing protocol in 2020 limits the available time series to a shorter and more recent period (covering 2017–2022 at most), thereby limiting the ability to capture long-term population trends.

For these reasons, in this study we used only the ALKs for years for which direct age readings were available, following the pre-2020 protocol to ensure consistency across the dataset and extend the time series. ALKs derived from commercial data were analyzed accounting for commercial fleet selectivity, while ALKs derived from scientific surveys were analyzed accounting for survey selectivity. Specifically, this approach covers the period from 1977 to 2015 for commercial fleets and from 2009 to 2014 for surveys. Furthermore, the use of these ALKs allows for the inclusion of age 6 as a plausible maximum age for anchovy, consistent with historical growth and longevity patterns (Sinovcic 2000).

Another challenge in data processing arises from the use of imputed data in some ALKs, where missing age information for certain length classes was filled using data from previous years. While this approach mitigates gaps in the age composition dataset, it also introduces potential inconsistencies. Thus, no imputed data were used for this paper.

2.2.1.1 Commercial data

An in-depth examination of the available data was conducted to select data for use in the assessment. Historical landings data (1975 – 2001) for Italy were obtained from the GFCM stock assessment conducted during 2019 (Angelini et al. 2019), whereas Croatian information is from the RECFISH project (RecFish 2019). Catch data for Albania, Slovenia, and Montenegro were obtained from FAO-FishStatJ (FAO 2020). The analysis of catch data have revealed that most of the anchovy are landed by Italy, which includes the western parts of GSAs 17 and 18 (Fig. 2), using two gears: pelagic trawls (or '*Volante*'; PTM) and purse seines (or "*Lampara*", PS). PTM is the main gear used to catch pelagic species in the north-western side of the Adriatic Sea, whereas PS is mainly used in the whole eastern side, and partly in the central and southern area of the Italian side.

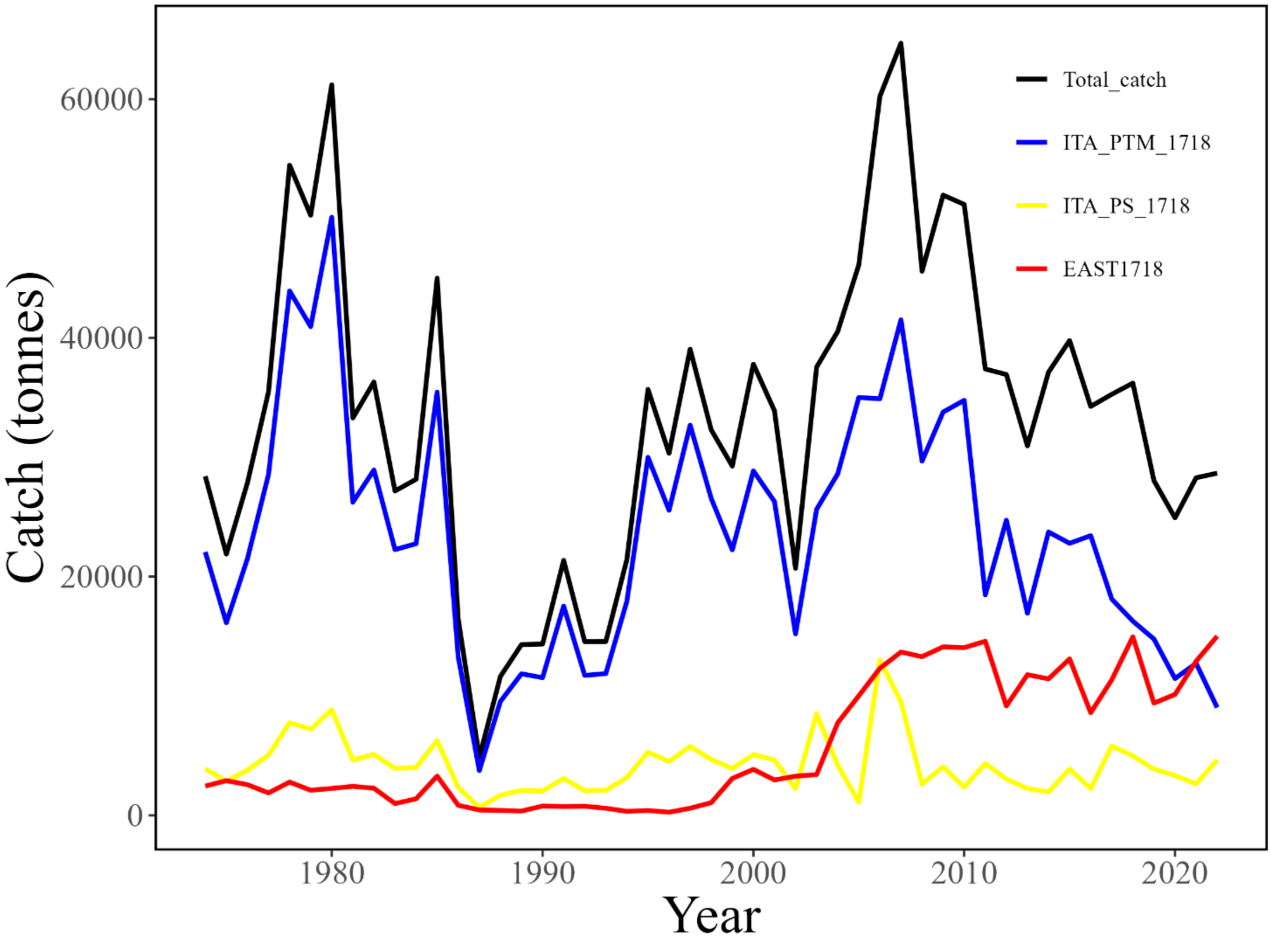

Figure 2 Commercial landings of anchovy in the Adriatic Sea by fleet (the blue line represents the Italian PTM landings in GSAs 17 and 18 – ITA_PTM_1718; the yellow line shows the Italian PS landings from GSAs 17 and 18 – ITA_PS_1718; the red line groups the landings from Croatia, Montenegro, Albania and Slovenia – EAST1718; the black line represents the total landings) from 1975 to 2022.

Previous analyses found no significant differences in age and length distributions between the GSAs, as the majority of the stock is concentrated in the Northern-Central part of the Adriatic Sea (unpublished data). Thus, two fleets were created for Italy: ITA PTM 1718 and ITA PS 1718. The catches by Montenegro, Slovenia and Albania were combined with those of Croatia into a single fleet, EAST 1718, given the low landings and the use of the same gears in the eastern area of this basin.

2.2.1.2 Survey data

The sampling design of the acoustic surveys for pelagic species in the Mediterranean Sea was standardized since 2009 under the EU MEDiterranean International Acoustic Surveys (MEDIAS) project (MEDIAS Handbook 2024, Leonori et al. 2021). Specifically, Italy conducted its acoustic surveys under the ECHOADRI project starting in 1976, while Croatia began its surveys in 2003 under the PELMON project and joined the MEDIAS in 2013 (Leonori et al. 2021).

As a result, two teams and two vessels have operated in the Adriatic basin: the Croatian team covering Croatian waters and the Italian team surveying Italian and Slovenian waters (GSA 17), as well as southern Italy, Montenegro and Albania (GSA 18). The acoustic surveys in GSA 17 were typically conducted at the end of summer, mainly during September, except in GSA 18, which was surveyed between June and July. However, starting in 2015, Italy shifted its MEDIAS survey in GSA 17 to early summer (June and July) to sample during the anchovy spawning season, as required by the MEDIAS program (MEDIAS Handbook, 2024). As a result, the MEDIAS information was divided into four abundance indexes for the most recent anchovy benchmark assessment (Angelini et al. 2019). Figure 3 shows that the majority of the anchovy population is concentrated on the western side of the Adriatic Sea.

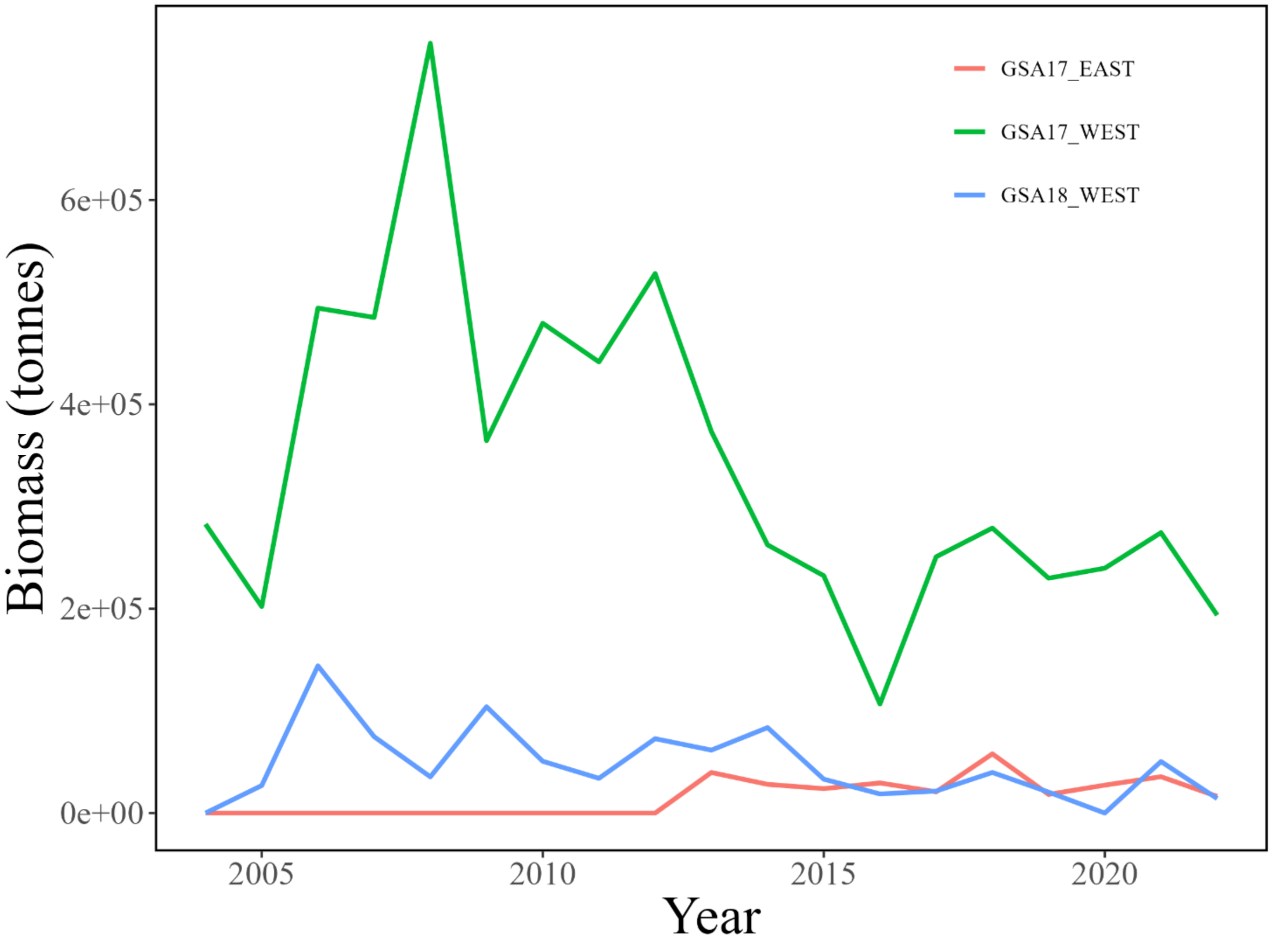

Figure 3 Biomass indexes for the acoustic survey MEDIAS collected in various areas of the Adriatic Sea: Eastern GSA 17 (GSA 17_EAST, red line, since 2013), Western GSA 17 (GSA 17_WEST, green line) and Western GSA 18 (GSA 18-WEST blue line).

Thus, the GSA 17 WEST survey (hereafter referred to as MEDIAS ITA) provides the most consistent and longest time series, encompassing the majority of the anchovy population in the Adriatic Sea. Therefore, only this index was used in this study when fitting the population dynamics model.

The discrepancy in survey timing between past and recent Western GSA 17 biomass indexes has led to marked changes in survey-based estimates of population age structure. In particular, age-0 individuals are present in very low abundance and biomass in the Italian surveys conducted during June and July, as most of the cohort has not yet fully recruited to the population at that time (Fig. 4). Hence, the variation in survey timing necessitated several assumptions and a thorough examination of the length and age data. According to ICES guidelines (ICES 2021a), survey selectivity should ideally be assumed to be logistic and temporally invariant when applying stock assessment methods, but this was not feasible in this case due to the profound impact of the shift in the timing of the survey on age composition (Fig. 4).

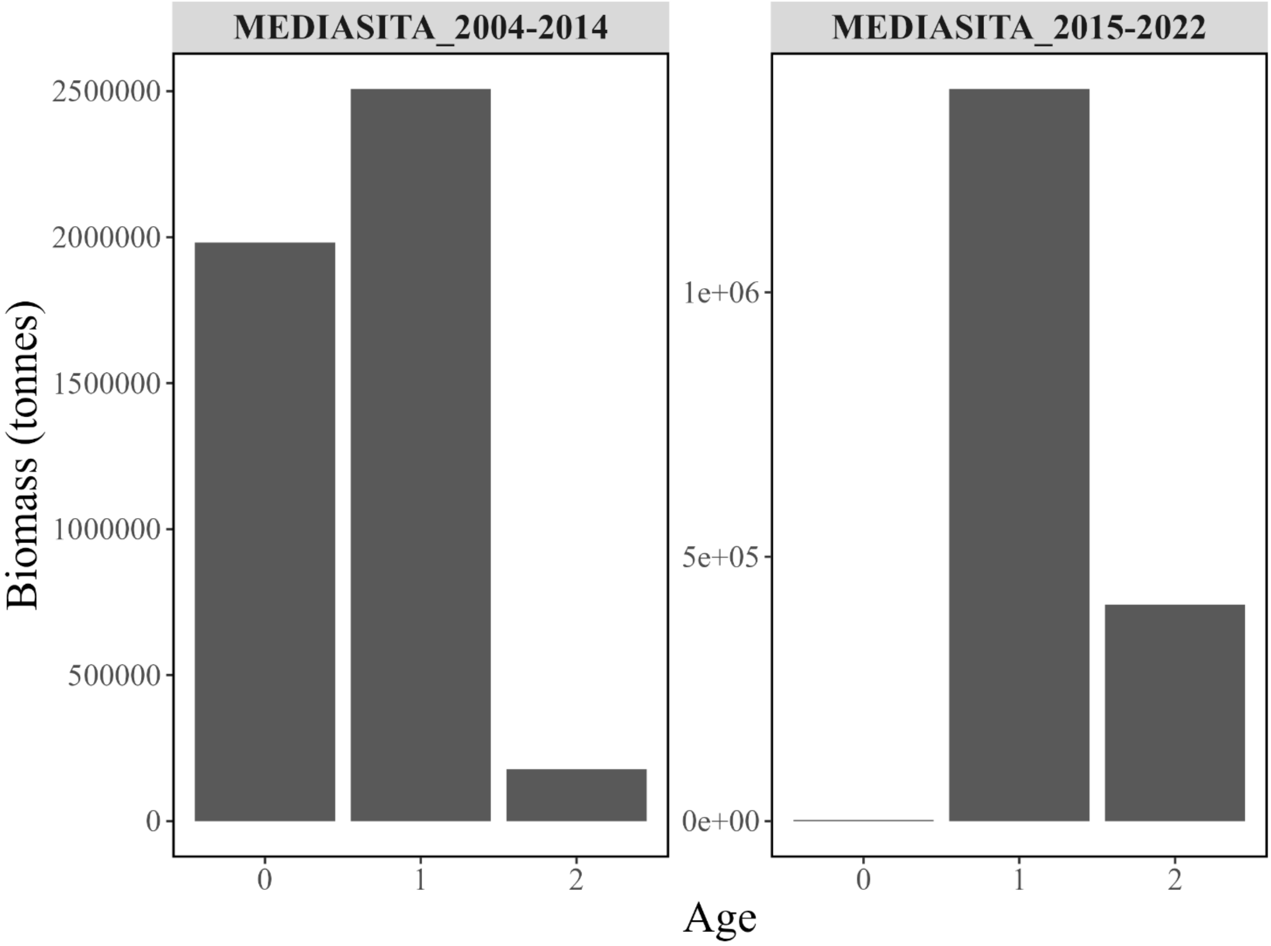

Figure 4 Average age-compositions for the MEDIAS ITA survey for the years 2004-2014 (left) and 2015-2022 (right). These biomass-at-age data were obtained from the official DCF database and processed using the recent ALK protocol. Since the MEDIAS ALKs from this protocol has been applied backwards for the most recent stock assessment (Angelini et al. 2024), the data before and after 2015 are directly comparable.

Various model variants were explored to identify the best way to account for the time shift, resulting in the division of the MEDIAS ITA index into two distinct survey indices (MEDIASITAsep and MEDIASITAjun).

2.2.1.3 Environmental data

According to Fernandez-Corredor et al. (2021), Sea Surface Temperature (SST), chlorophyll-a concentration (chl-a) and salinity (so) seem to be the key environmental variables that drive recruitment and growth of small pelagic species in the Mediterranean Sea. However, the Adriatic Sea is different from the other basins in the area. It is a narrow sea with a shallow northern shelf (average depth 35 m), with a primary production cycle that is influenced by the riverine discharge of land-derived nutrients (Revelante and Gilmartin 1992, Zavatarelli et al. 1998). Several studies highlight the importance of river input on the reproductive success of Adriatic anchovy, since it seems that river input determines the distribution of chlorophyll and salinity (e.g., Santojanni et al. 2006, Zorica et al. 2013, Malavolti et al. 2018, Mandic et al. 2019). The outflow of the Po River is a main cause of eutrophication, which occurs periodically along the Italian coast (Penna et al. 2004), forcing the general circulation to turn southward along the western coast forming the Western Adriatic Current (WAC) (Artegiani et al. 1997, Marini et al. 2008), and contributes to create a north-south trophic gradient, with a considerably higher chl-a concentration in the northern sub-basin (Fig. 5, top-right panel).

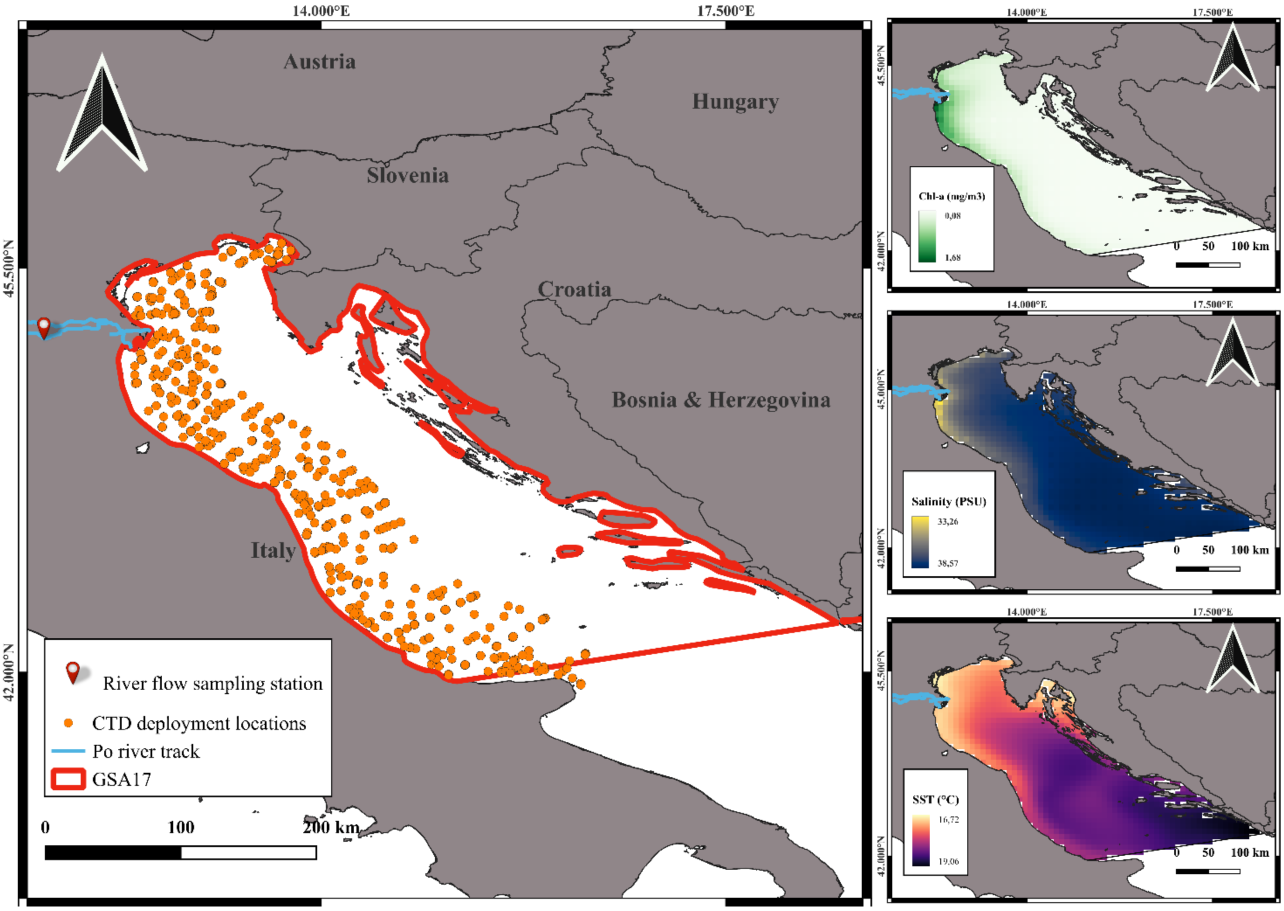

Figure 5 Map of the monthly aggregated distributions of the selected environmental variables in the Adriatic Sea downloaded from Copernicus: a) chl-a concentration (bottom-left panel) available since 1999, b) salinity (bottom-center panel) available since 1987, c) and SST (bottom-right panel) available since 1981. The top panel shows the deployment location of CTD devices. These maps were created using QGIS 3.32.3.

Changes in seasonal averages of these variables occurred in the last decade are shown by Grilli et al. (2020), which reports an increase of the SST by + 0.36% year-a over four decades, an important decrease of the annual mean flow of the Po river, strictly connected to the general increase of salinity in the basin and a fluctuating trend of chl-a, decreasing in autumn and increasing in spring.

An *ex-ante* investigation of the spatial and temporal distribution of the selected variables was carried out. Daily data for these variables were extracted from the Copernicus Marine Environment Monitoring Service (https://marine.copernicus.eu), an open-source platform that provides up-to-date modeled environmental data for all of the world's oceans. The resulting dataset spans GSA17 (referred to as the "GSA17 dataset"). CTD deployment locations (indicated by orange dots in Figure 5, left panel), monitored during the MEDIAS survey, were used to spatially constrain the broader GSA17 dataset and better match the habitat preferences of anchovies (Fig. 1). Only data points within a 1 km buffer zone surrounding each CTD deployment location were included in analyses, resulting in a filtered database.

A spatial analysis was not needed for river runoff, since the daily river runoff data for the Po River have been collected since 1975 at the Pontelagoscuro station (Fig. 5, red point in left panel) and were made available by the Agenzia Regionale per la Prevenzione, l'Ambiente e l'Energia dell´Emilia-Romagna (ARPAE) website (https://www.arpae.it/it). Santojanni et al. (2006) highlighted the critical role of autumn river runoff in influencing anchovy recruitment, suggesting that timing is a key factor to consider in stock assessments. Building on this insight, we considered seasonal as well as annual environmental variables in the stock assessment analyses to better capture their potential influence on anchovy stock dynamics. Thus, we considered seasonal and annual environmental variables for SST, chl-a, salinity, and river runoff.

A Mann-Whitney U test for spatial differences and a Mann-Kendall test for temporal trends were used to evaluate spatial and temporal differences while Spearman’s correlation implemented in 'corrplot' R package (Wei et al. 2017) was used to examine the relationships among environmental variables on annual and seasonal time scales.

2.2.2 Stock Assessment

The stock assessment, conducted using Stock Synthesis (SS), was based on a length and age-structured population dynamics model with a single sex and a single spatial area. The model includes three commercial fishing fleets and two fishery-independent survey indices, and operates on an annual time step. The spawning month was set as the middle of the year (Carpi et al. 2015b), with the settlement month assumed to be February (Morello and Arneri 2009). The model spans 1975 to 2022, but the years with data for each data source differs (Fig. 6).

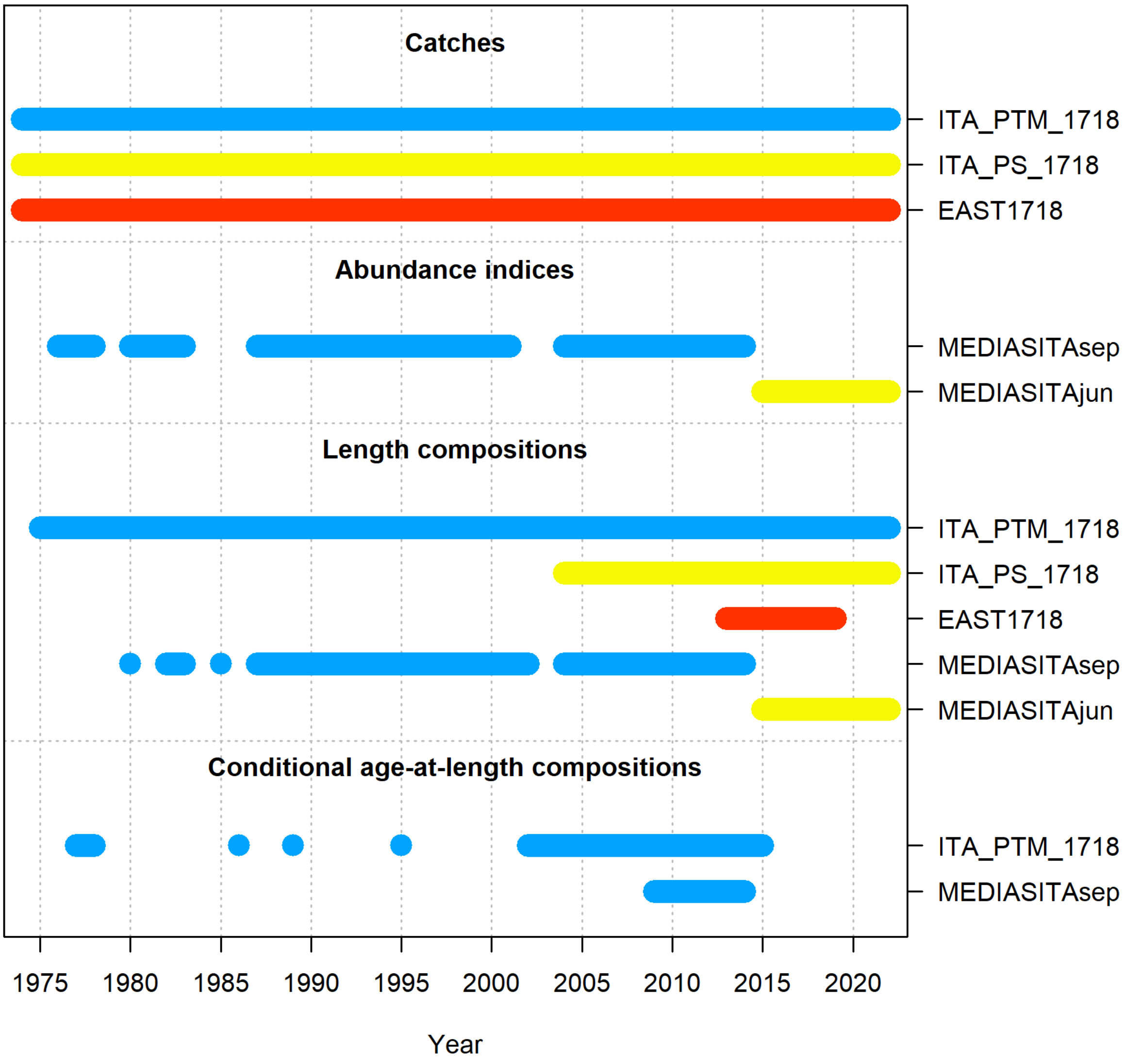

Figure 6 Summary of the data used in the SS models.

Table 1 lists the parameters of the population dynamics model and their treatment in the model fitting process.

Table 2 Stock Synthesis parameters. The column “Pre-specified / Initial Value (s)” lists the values for the parameters that are pre-specified and the initial values for those parameters when they were estimated.

Parameter	Treatment	Pre-specified / Initial Value (s)	Source
Biological parameters			
Natural mortality (yr^{-1})	Pre-specified for ages 0, 1, 2, 3, 4, 5	2.36, 1.1, 0.81, 0.69, 0.64, 0.61	Gislason et al. 2010
Growth			
Von Bertalaffy function			
L_{min} (cm)	Estimated	7.5	
L_{inf} (cm)	Estimated	19.4	Sinovčić, 2000
□ (yr^{-1})	Estimated	0.57	Sinovčić, 2000
CV young	Estimated	0.4	
CV old	Estimated	0.25	
Maturity			
Size-at-50%-maturity	Pre-specified	6	Sinovčić, 2000
Maturity slope	Pre-specified	-0.61	Thorson et al. 2023
Recruitment			
$\ln R_0$	Estimated	20.49	
B-H steepness (h)	Pre-specified	0.78	Thorson et al. 2023
σ_R	Pre-specified	0.5	Kuriyama et al. 2020
Recruitment deviations	Estimated	1976 - 2020	
Catchability			
MEDIASITAsep	Estimated	2.47	
MEDIASITAjun	Estimated	1.45	
Fishery mortality	Estimated (Hybrid F method)		
Fishery selectivity			

ITA PTM 1718			
Size-at-inflection (cm)	Estimated	11 (time varying 1989-2016)	
Selectivity width (cm)	Estimated	2	
ITA PS 1718			
Size-at-inflection (cm)	Estimated	13	
Selectivity width (cm)	Estimated	1 (time varying 2008 – 2022)	
EAST 1718	Same as for ITA PS 1718		
Survey selectivity			
MEDIASITAsep			
Size-at-inflection (cm)	Estimated	9 (time-varying 1976 – 2001)	
Selectivity width (cm)	Estimated	1	
MEDIASITAjun			
Size-at-inflection (cm)	Estimated	11	
Selectivity width (cm)	Estimated	2	

The pre-specified values for parameters related to maturity, natural mortality and recruitment were derived from biological data collected during field surveys and summarized in Stock Assessment Forms (SAFs) and literature reviews specific to anchovy in the Adriatic Sea and globally (e.g. Morello and Arneri 2009, Kuriyama et al. 2020, Thorson et al. 2023, Angelini et al. 2024). The stock-recruitment relationship was assumed to be of the Beverton-Holt form, with the “steepness” parameter set based on the meta-analysis by Thorson et al. (2023) and the extent of variation in recruitment about the stock-recruitment relationship set based on the results of assessments for other anchovy stocks (e.g., Angelini et al. 2024, Kuriyama et al. 2020). Parameters related to growth, survey catchability, and fishery/survey selectivity were estimated, with fishery and survey selectivity assumed to be asymptotic (logistic) functions of size. The size-at-inflection for the ITA PTM 1718 (pelagic trawl) fishery and the width at 95% selection for the ITA PS 1718 (purse seine) fishery were allowed to vary over time to account for the changing operational and regulatory factors that influence these fleets. The size-at-inflection for the MEDIASITAsep survey was assumed to be time-varying for the years prior to 2009, when the DCF program began. The difference in the size at inflection between the MEDIASITAsep and MEDIASITAjun surveys reflects the shift in survey timing from

September to June. This change resulted in a size distribution shifted towards larger individuals in the June survey, as smaller individuals (particularly age-0) are less detectable at that time.

The stage-1 effective sample sizes, which represent the initial assumed precision of the composition data prior to iterative reweighting or estimation (Francis 2011, Thorson et al. 2017), for the survey length data were set to the number of hauls, for the commercial length data to the number of sampling events, and for the survey age-composition data to the number of otoliths read. Biomass index geostatistical CVs (Walline 2007, Leonori et al. 2021) were only available for the time interval 2018-2022; the average value among these years was assumed appropriate for the years from 2002 to 2017. The biomass index CVs for 1976 to 1989 were assumed to be 0.3 and those for 1990 to 2001 to be 0.2, reflecting lower uncertainty with the more recent data. The standard errors of the logs (SELs) for the landings data collected during the DCF years were set to 0.1, while they were set to 0.15 for the years before the implementation of the DCF. The SELs of the early initial catches were set to 0.2. Pre-specification of SEL and CVs was adopted to account for the differences in monitoring protocols between countries prior to the establishment of the DCF.

Multiple runs of SS were conducted, and the 'r4ss' R package (Taylor et al. 2021) was used to evaluate how well the model fitted the data. Sensitivity analyses were performed using the 'Stock Assessment Continuum Tool' (SS-DL tool) shiny app (Cope 2020) to identify key parameters driving model outcomes and to assess the robustness of model predictions to varying assumptions and data inputs. Diagnostic analysis was performed using 'ss3diags' R package (Carvalho et al. 2021) to evaluate whether the SS configuration can address the data-related issues raised in the official assessment and to explore the influence of environmental variables on model predictive skills. We reported the adjusted MASE values as indicators of model predictive skill, following the approach of Kapur et al. (2025). SS allows model parameters (e.g., unfished recruitment, natural mortality, survey catchability, and the parameters of the growth curve) to be related to environmental variables. In this study, environmental variables were linked to model parameters according to:

$$\boldsymbol{P_y = P_{base} e^{\alpha E y}} \ \textbf{(1)}$$

$$\boldsymbol{P_y = P_{base} + \alpha E_y} \ \textbf{(2)}$$

where, P_y is the parameter value for year y, P_{base} is the base value of the parameter, α is the "link" parameter, and E_y is the environmental index value for year y (Z-scored). Because some environmental variables are not available for the entire period considered in the assessment, E_y was assumed to be 0 (i.e., average) for the years with no environmental data.

We developed a set of candidate models that incorporated one and two environmental variables. These models were designed to address key concerns raised during the most recent stock assessment meetings, specifically the observed reduction in fish size, a decline in biomass despite reduced fishing effort, and two periods of very low recruitment (GFCM 2022). The aim of the model was to explore whether environmental factors could capture these patterns. We therefore explored the influence of environmental variables on natural mortality at age 1 (M_1), the parameters of the Von Bertalanffy growth curve (L_{inf} and κ), and the mean length at age 0 (L_{min}) to better understand their role in the observed decline in size, biomass and recruitment. In addition, we assessed the potential impact of environmental conditions on anchovy distribution by analyzing their influence on survey catchability (q). All these parameters were linked to the environmental variables using Equation 1, while for the logarithms of average recruitment regime switch (*regime*) were used Equation 2. This parameterization guarantees positivity of the parameters and ensures that variations in environmental variables translate proportionally into changes in the linked parameters (e.g., a 10% increase in an environmental variable results in an exponential 0.1·alpha adjustment). A Two-Tailed Z-test was applied to the estimated link parameters (α in Equations 1 and 2) to assess their significance (p-values < 0.05). The difference in the objective function between the null (no environmental drivers) model and each candidate model with an environmental variable (ΔObj) was computed, with a value of 1.92 or greater indicating a notable improvement in fit when one environmental parameter was included in the population model. Models were then ranked according to their Akaike Information Criterion (AIC) values, where lower AIC values indicate a better fit.

2.3 Results

2.3.1 Environmental data

Four environmental time-series were included in our analyses (SST 1981-2022; chl-a 1999-2022; so 1987-2022 and river runoff 1975-2022). Statistical tests (Tab S.1 and S.2) evaluated temporal trends and spatial patterns in these indexes. Based on these results and considering the anchovy spawning season (spring through fall), we decided to investigate the effects of chl-a, salinity, and river runoff during spring, summer, autumn, and annually (i.e., 12 indices). These three variables are highly correlated (Fig. S.1), suggesting that river runoff plays a key role in driving chlorophyll-a concentration and shaping salinity dynamics. Consequently, the information from the filtered database was used in the stock assessment to focus on spatially constrained environmental factors. In contrast, SST exhibited a strong increasing trend over time, both at the seasonal and annual scale (Fig. S.2), and has a weaker correlation with the other variables (except for seasonal chl-a, Fig. S.1), suggesting that temperature might influence the anchovy population in the study area independently of other factors. Therefore, we included the annual SST indices from the filtered and GSA17 databases in the set of candidate models. Although the only difference between these two SST indices is their geographic origin, this distinction is important because anchovies are spread throughout the basin; we therefore assessed whether temperature influences anchovy stocks locally or throughout the entire Adriatic basin by considering SST globally and locally in the candidate models.
The final set of 14 environmental variables are listed in Table S.3.

2.3.2 Stock assessment

2.3.2.1 Model selection

2.3.2.1.1 Single-variable model

Table 2 lists all of the single-variable models explored (N = 84; 6 parameters x 14 environmental variables).

Table 3 Ranked comparison of the single-variable models. The null model had an objective function value of 2144.62 and an ΔAIC of 332.52. **Δ**Obj is the difference in the objective function value at its global minimum (negative log-likelihood plus summed logs of penalty terms) between the null and each alternative model. Link values that are significant at $p < 0.05$ are underlined.

Model No	ΔAIC	Enviromental variable	Parameter	ΔObj	Link value	Model No	ΔAIC	Enviromental variable	Parameter	ΔObj	Link value
4	0.00	SST	L_{min}	167.26	-0.0384	79	326.18	sosum	*Linf*	4.17	0.0062
7	47.82	SSTfil	L_{inf}	143.35	-0.0464	31	327.06	chlfall	L_{inf}	3.73	-0.0037
8	59.54	SSTfil	κ	137.49	-0.1085	34	327.06	chlfall	L_{min}	3.73	-0.0037
1	71.70	SST	L_{inf}	131.41	-0.0499	24	327.32	rivspr	M_1	3.60	0.0704
2	75.28	SST	κ	129.62	-0.1182	25	327.92	rivy	L_{inf}	3.30	-0.0055
10	79.66	SSTfil	L_{min}	127.43	-0.0293	64	328.32	soy	L_{min}	3.10	0.0030
57	261.92	sospr	q	36.30	-0.0586	42	328.82	chlspr	M_1	2.85	0.0456
16	263.82	rivfall	L_{min}	35.35	-0.0157	55	328.90	sospr	L_{inf}	2.81	-0.0051
20	272.88	rivspr	κ	30.82	0.0370	56	330.44	sospr	κ	2.04	-0.0090
40	276.46	chlspr	L_{min}	29.03	-0.0078	45	330.54	chly	q	1.99	0.0129
46	284.50	chly	L_{min}	25.01	-0.0077	59	330.72	sospr	*regime*	1.90	0.1456
19	285.54	rivspr	L_{inf}	24.49	0.0159	44	331.96	chly	κ	1.28	-0.0061
21	291.48	rivspr	q	21.52	0.0436	26	332.10	rivy	κ	1.21	-0.0067
6	291.62	SST	M_1	21.45	-0.2721	15	332.14	rivfall	q	1.19	0.0141
36	296.24	chlfall	M_1	19.14	0.1520	71	332.18	rivsum	*regime*	1.17	0.1180
32	297.68	chlfall	κ	18.42	0.0334	9	332.24	SSTfil	q	1.14	0.0180
12	301.48	SSTfil	M_1	16.52	-0.2082	43	332.48	chly	L_{inf}	1.02	-0.0026
33	303.32	chlfall	q	15.60	0.0401	11	332.60	SSTfil	*regime*	0.96	0.1064
18	303.88	rivfall	M_1	15.32	0.2014	5	332.80	SST	*regime*	0.86	0.1021
60	304.06	sospr	M_1	15.23	-0.1318	22	333.14	rivspr	L_{min}	0.69	0.0013
13	306.06	rivfall	L_{inf}	14.23	-0.0160	62	333.18	soy	κ	0.67	0.0045
78	307.04	chlsum	M_1	13.74	0.1252	65	333.50	soy	*regime*	0.51	0.0748
67	308.40	rivsum	L_{inf}	13.06	-0.0127	61	333.62	soy	L_{inf}	0.45	0.0016
66	309.92	soy	M_1	12.30	-0.1257	73	333.74	chlsum	L_{inf}	0.39	0.0014
28	310.82	rivy	L_{min}	11.85	-0.0068	47	333.76	chly	*regime*	0.38	-0.0676
63	312.34	soy	q	11.09	-0.0322	77	333.78	chlsum	*regime*	0.37	-0.0691
48	314.66	chly	M_1	9.93	0.1178	41	333.80	chlspr	*regime*	0.36	-0.0639
14	314.70	rivfall	κ	9.91	-0.0283	58	333.86	sospr	L_{min}	0.33	0.0007
75	316.36	chlsum	q	9.08	0.0264	37	333.90	chlspr	L_{inf}	0.31	0.0008
82	316.36	sosum	L_{min}	9.08	0.0055	38	333.94	chlspr	κ	0.29	0.0014
50	316.48	sofall	κ	9.02	0.0215	51	333.96	sofall	q	0.28	-0.0059

49	318.04	sofall	L_{inf}	8.24	0.0099	70	334.00	rivsum	L_{min}	0.26	0.0006
30	320.36	rivy	M_1	7.08	0.1030	74	334.02	chlsum	κ	0.25	0.0014
84	320.36	sosum	M_1	7.08	-0.0904	83	334.14	sosum	*regime*	0.19	0.0457
72	320.56	rivsum	M_1	6.98	0.1209	39	334.18	chlspr	q	0.17	-0.0030
52	320.74	sofall	L_{min}	6.89	0.0050	35	334.30	chlfall	*regime*	0.11	0.0340
76	321.86	chlsum	L_{min}	6.33	-0.0046	17	334.34	rivfall	*regime*	0.09	-0.0314
27	322.00	rivy	q	6.26	0.0244	23	334.50	rivspr	*regime*	0.01	-0.0084
68	323.36	rivsum	κ	5.58	-0.0178	29	334.50	rivy	*regime*	0.01	0.0070
54	323.44	sofall	M_1	5.54	-0.1063	69	334.50	rivsum	q	0.01	0.0013
3	324.14	SST	q	5.19	0.0415	81	334.50	sosum	q	0.01	-0.0009
80	325.20	sosum	κ	4.66	0.0135	53	334.52	sofall	*regime*	0.00	-0.0014

Fifty-nine of the models led to fits that improved on the null model in terms of AIC and all but eight of these led to values for the link parameter that differed from 0 at $p < 0.05$. One model (4; L_{min} related to SST) had the lowest AIC (a ΔAIC of 332.52 from the null model and of 47.82 from the next best model (model 7: L_{inf} related to SSTfil). The AIC weight for the best model was essentially 1. Five models (1, 2, 7, 8 and 10) had ΔAIC values within 100 units of model 4. All of the six best models related SST to growth parameters (L_{inf}, κ, and L_{min}). The best models involving natural mortality, survey catchability and expected recruitment were 6, 57, and 59, although they were far inferior to the six best models in terms of ΔAIC. Models with covariates other than SST were represented in a second tier of models 100 < ΔAIC < 280. In particular, salinity in spring appears in model 57, autumnal and spring runoff in model 16 and 20, respectively and chl-a in spring in model 40. The remaining eight environmental covariates are only found in models with ΔAIC > 280.

Table 3 lists the components of the objective function for the null model (0) and the three-best single-variable models (4, 7 and 8), highlighting that incorporating time-varying biological parameters linked to temperature improves the fit to the age- and length-composition data, although at the expense of somewhat poorer fits to the index data.

Table 3 Values of the components of the objective function (negative log-likelihood plus summed logs of penalty terms) for the null model and the three best single-variable models. The value in parenthesis is the number of parameters.

Component	Model No (number of parameters)			
	Null (142)	4 (143)	7 (143)	8 (143)
Catches	0.00	0.17	0.79	0.88
Index data	139.66	150.67	160.00	160.62
Length data	531.91	478.34	442.63	448.65
Age data	1408.90	1299.60	1336.34	1335.91
Recruitment	17.13	3.70	13.92	13.03
Other penalties	47.01	44.87	47.60	48.05
Total	2144.62	1977.36	2001.27	2007.13

Allowing for environmental variables reduced the estimated variability in unexplained recruitment about the stock-recruitment relationship. Table S.4 provides an overview of the model diagnostics for the best models (unpublished data for other selected models shows similar results). The goodness-of-fit runs tests (Winker et al. 2018) did not generally indicate any systematic patterns, trends, or temporal variation in the fits to the data, except for model 10 (EAST1718 mean length data). Outlier analysis revealed that a few data points in the ITA_PTM1718 and ITA_PS_1718 mean length data sets exceeded the 3σ threshold. The Root Mean Square Error (RMSE, Carvalho et al. 2017) values for the mean length data for the commercial fleets were low (< 10% deviation). RMSE box plots indicated that the greatest deviations occurred between 1987 and the early 2000s for all models. The MEDIASITAsep index had the largest discrepancy (RMSE > 5%). This issue was also evident in the abundance index results, where the RMSE exceeded 50% for the MEDIASITAsep index. The retrospective analyses indicate robust model accuracy, as all models exhibited Mohn's Rho (ρ_M, Mohn 1999) values within the recommended range for short-lived species (-0.22 to 0.30; Hurtado-Ferro et al. 2015). However, there is an indication that spawning stock biomass (SSB) may be somewhat overestimated due to a systematic positive bias. Predictive performance was assessed using forecast bias (ρ_F, Brooks and Legault 2016) and hindcast cross-validation (Hcxval, Kell et al. 2016), with the predictive error quantified by the Mean Absolute Scaled Error (MASE, Hyndman and Koehler 2006). The forecast bias analysis did not reveal any undesirable patterns, as the values fell within the established range. However, a MASE score above 1 indicates that the models exhibit poor predictive skills, especially for survey indexes.

The values for the link parameters for the best six models were all negative, indicating that increasing SST has led to lower length-at-age (Fig. 7, bottom right panel), with this effect greatest for model 4 (an 4.18% reduction in the mean length of age - 1 fish between 2012 and 2022) and least for model 7 (1.32% reduction in mean length at age from 2012 to 2019).

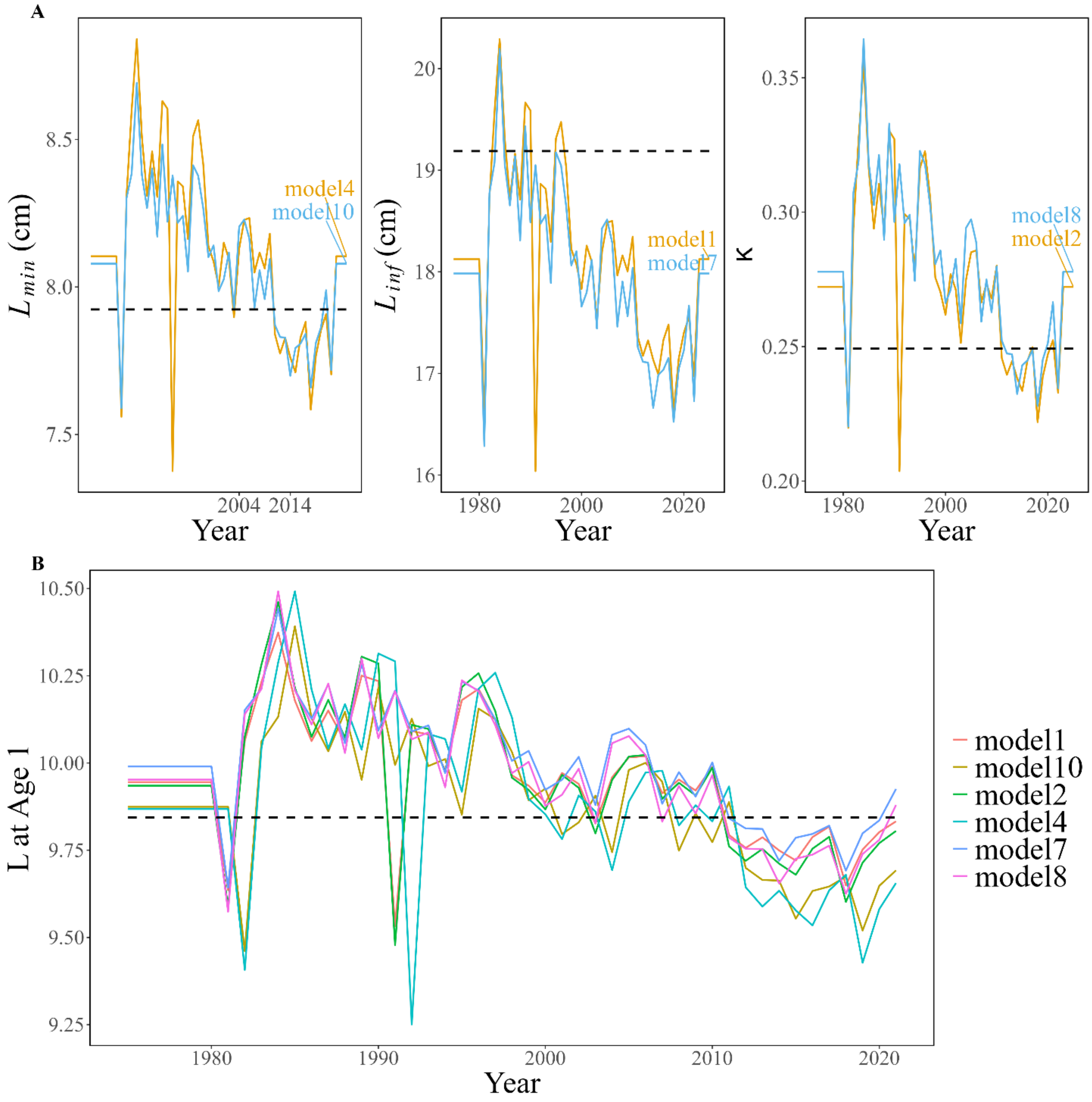

Figure 7 Growth parameters for the six best single-variable models and the null model (dashed black line). Panel A: the top-left, top-center and top-right plots respectively show time-trajectories of L_{min}, L_{inf} and κ, highlighting differences between the two temperature databases. Panel B shows the time-trajectory of mean length-at-age 1 for the best single-variable models.

2.3.2.1.2 Two- variable models

Table 4 shows a subset of the 150 possible two-variable models, obtained by combining factors from the six best single-variable models with 14 of the mortality-related models and 11 of the survey catchability-related models identified in the single-variable analysis.

Table 4 Ranked comparison of the two-variable models. The null model had an objective function value of 2144.62 and an ΔAIC of 332.52. **Δ**Obj is the difference in the objective function value at its global minimum (negative log-likelihood plus summed logs of penalty terms) between the null and each alternative model. Link values that are significant at $p < 0.05$ are underlined. The first environmental variable is linked to the first parameter and the second environmental variable to the second parameter.

Model No	ΔAIC	Environmental variables		Parameters		ΔObj	Link value	
101	0.00	SST	SST	L_{min}	q	211.09	-0.0441	0.0958
100	1.86	SST	rivspr	L_{min}	q	210.16	-0.0410	0.0431
99	3.42	SST	sospr	L_{min}	q	209.38	-0.0392	-0.0520
92	6.98	SST	rivy	L_{min}	M_1	207.60	-0.0438	0.1914
88	19.98	SST	rivfall	L_{min}	M_1	201.10	-0.0411	0.2230
124	20.64	SSTfil	sospr	L_{inf}	q	200.77	-0.0494	-0.0675
97	24.16	SST	chlspr	L_{min}	M_1	199.01	-0.0440	0.1277
93	26.08	SST	chly	L_{min}	M_1	198.05	-0.0419	0.1648
98	27.54	SST	sofall	L_{min}	M_1	197.32	-0.0430	-0.2016
91	28.14	SST	soy	L_{min}	M_1	197.02	-0.0413	-0.1633
96	28.76	SST	rivspr	L_{min}	M_1	196.71	-0.0425	0.1511
102	29.00	SST	chlfall	L_{min}	q	196.59	-0.0394	0.0391
95	29.06	SST	sosum	L_{min}	M_1	196.56	-0.0421	-0.1479
149	31.40	SSTfil	sospr	κ	q	195.39	-0.1189	-0.0663
103	34.68	SST	SSTfil	L_{min}	q	193.75	-0.0427	0.0719
105	45.76	SST	soy	L_{min}	q	188.21	-0.0396	-0.0355
90	47.38	SST	chlsum	L_{min}	M_1	187.40	-0.0393	0.1206
108	48.42	SST	rivy	L_{min}	q	186.88	-0.0401	0.0316
174	52.14	SSTfil	sospr	L_{min}	q	185.02	-0.0319	-0.0637
89	52.80	SST	sospr	L_{min}	M_1	184.69	-0.0386	-0.1135
94	54.68	SST	rivsum	L_{min}	M_1	183.75	-0.0398	0.1385
126	54.94	SSTfil	SST	L_{inf}	q	183.62	-0.0510	0.1024
87	54.96	SST	chlfall	L_{min}	M_1	183.61	-0.0379	0.1105
151	55.06	SSTfil	SST	κ	q	183.56	-0.1293	0.1094
226	66.00	SST	SST	κ	q	178.09	-0.1385	0.1077
162	105.36	SSTfil	chlfall	L_{min}	M_1	158.41	-0.0304	0.1504
138	105.50	SSTfil	rivfall	κ	M_1	158.34	-0.1108	0.2305
123	107.14	SSTfil	sofall	L_{inf}	M_1	157.52	-0.0487	-0.1881
180	107.68	SSTfil	soy	L_{min}	q	157.25	-0.0315	-0.0456
121	108.10	SSTfil	rivspr	L_{inf}	M_1	157.04	-0.0482	0.1476
132	108.26	SSTfil	chlsum	L_{inf}	q	156.96	-0.0483	0.0320
122	109.06	SSTfil	chlspr	L_{inf}	M_1	156.56	-0.0495	0.1132
203	110.30	SST	SSTfil	L_{inf}	q	155.94	-0.0520	0.0733
145	110.76	SSTfil	sosum	κ	M_1	155.71	-0.1133	-0.1410
230	111.56	SST	soy	κ	q	155.31	-0.1241	-0.0432
158	112.22	SSTfil	rivy	κ	q	154.98	-0.1115	0.0357
147	112.46	SSTfil	chlspr	κ	M_1	154.86	-0.1166	0.1138
148	112.82	SSTfil	sofall	κ	M_1	154.68	-0.1161	-0.1979
205	113.38	SST	soy	L_{inf}	q	154.40	-0.0502	-0.0416
178	113.40	SSTfil	SSTfil	L_{min}	q	154.39	-0.0333	0.0790
216	113.50	SST	soy	κ	M_1	154.34	-0.1228	-0.1731
212	113.90	SST	chlfall	κ	M_1	154.14	-0.1216	0.1601
187	114.46	SST	chlfall	L_{inf}	M_1	153.86	-0.0521	0.1705
227	114.94	SST	chlfall	κ	q	153.62	-0.1215	0.0425
146	115.56	SSTfil	rivspr	κ	M_1	153.31	-0.1151	0.1424
157	116.92	SSTfil	chlsum	κ	q	152.63	-0.1100	0.0308
202	117.18	SST	chlfall	L_{inf}	q	152.50	-0.0514	0.0434
119	118.46	SSTfil	rivsum	L_{inf}	M_1	151.86	-0.0478	0.1477
213	119.00	SST	rivfall	κ	M_1	151.59	-0.1204	0.2327
217	119.32	SST	rivy	κ	M_1	151.43	-0.1252	0.1715

107	66.20	SST	chlsum	L_{min}	q	177.99	-0.0384	0.0218	190	121.08	SST	chlsum	L_{inf}	M_1	150.55	-0.0521	0.1566
125	68.80	SSTfil	rivspr	L_{inf}	q	176.69	-0.0473	0.0496	215	121.98	SST	chlsum	κ	M_1	150.10	-0.1206	0.1530
167	69.18	SSTfil	rivy	L_{min}	M_1	176.50	-0.0357	0.2070	131	122.12	SSTfil	sofall	L_{inf}	q	150.03	-0.0474	-0.0259
153	69.82	SSTfil	SSTfil	κ	q	176.18	-0.1310	0.0972	188	122.30	SST	rivfall	L_{inf}	M_1	149.94	-0.0514	0.2372
128	70.52	SSTfil	SSTfil	L_{inf}	q	175.83	-0.0513	0.0882	192	122.52	SST	rivy	L_{inf}	M_1	149.83	-0.0504	0.1675
224	71.04	SST	sospr	κ	q	175.57	-0.1235	-0.0597	220	122.82	SST	sosum	κ	M_1	149.68	-0.1231	-0.1435
118	71.30	SSTfil	chly	L_{inf}	M_1	175.44	-0.0496	0.2888	191	123.78	SST	soy	L_{inf}	M_1	149.20	-0.0519	-0.1672
166	71.50	SSTfil	soy	L_{min}	M_1	175.34	-0.0344	-0.1995	183	124.32	SSTfil	rivy	L_{min}	q	148.93	-0.0312	0.0362
168	72.98	SSTfil	chly	L_{min}	M_1	174.60	-0.0350	0.2123	169	124.40	SSTfil	rivsum	L_{min}	M_1	148.89	-0.0313	0.1537
199	73.08	SST	sospr	L_{inf}	q	174.55	-0.0503	-0.0597	134	124.92	SSTfil	sosum	L_{inf}	q	148.63	-0.0473	-0.0187
130	74.48	SSTfil	soy	L_{inf}	q	173.85	-0.0487	-0.0483	144	125.08	SSTfil	rivsum	κ	M_1	148.55	-0.1100	0.1450
150	77.80	SSTfil	rivspr	κ	q	172.19	-0.1118	0.0491	195	125.24	SST	sosum	L_{inf}	M_1	148.47	-0.0502	-0.1405
201	78.56	SST	SST	L_{inf}	q	171.81	-0.0564	0.1009	214	125.92	SST	sospr	κ	M_1	148.13	-0.1196	-0.1376
143	78.74	SSTfil	chly	κ	M_1	171.72	-0.1230	0.2563	189	126.24	SST	sospr	L_{inf}	M_1	147.97	-0.0492	-0.1399
104	79.10	SST	chlspr	L_{min}	q	171.54	-0.0394	0.0115	198	128.06	SST	sofall	L_{inf}	M_1	147.06	-0.0508	-0.1974
106	79.10	SST	sofall	L_{min}	q	171.54	-0.0391	-0.0179	233	128.10	SST	rivy	κ	q	147.04	-0.1213	0.0348
175	79.48	SSTfil	rivspr	L_{min}	q	171.35	-0.0319	0.0486	222	129.76	SST	chlspr	κ	M_1	146.21	-0.1263	0.1123
163	80.72	SSTfil	rivfall	L_{min}	M_1	170.73	-0.0330	0.2459	208	129.96	SST	rivy	L_{inf}	q	146.11	-0.0514	0.0343
155	82.10	SSTfil	soy	κ	q	170.04	-0.1171	-0.0492	223	130.08	SST	sofall	κ	M_1	146.05	-0.1228	-0.1855
112	82.46	SSTfil	chlfall	L_{inf}	M_1	169.86	-0.0484	0.1843	197	130.52	SST	chlspr	L_{inf}	M_1	145.83	-0.0508	0.1067
109	83.36	SST	sosum	L_{min}	q	169.41	-0.0388	-0.0103	156	134.24	SSTfil	sofall	κ	q	143.97	-0.1116	-0.0252
85	84.46	SST	SST	L_{min}	M_1	168.86	-0.0403	0.0717	182	134.24	SSTfil	chlsum	L_{min}	q	143.97	-0.0300	0.0290
86	86.48	SST	SSTfil	L_{min}	M_1	167.85	-0.0395	0.0399	110	134.72	SSTfil	SST	L_{inf}	M_1	143.73	-0.0457	-0.0479
137	88.32	SSTfil	chlfall	κ	M_1	166.93	-0.1123	0.1775	111	135.32	SSTfil	SSTfil	L_{inf}	M_1	143.43	-0.0461	-0.0191
127	88.74	SSTfil	chlfall	L_{inf}	q	166.72	-0.0473	0.0444	221	135.36	SST	rivspr	κ	M_1	143.41	-0.1246	0.1339
116	89.12	SSTfil	soy	L_{inf}	M_1	166.53	-0.0476	-0.1869	129	135.74	SSTfil	chlspr	L_{inf}	q	143.22	-0.0478	0.0093
115	89.44	SSTfil	chlsum	L_{inf}	M_1	166.37	-0.0473	0.1816	159	135.78	SSTfil	sosum	κ	q	143.20	-0.1117	-0.0197
114	89.86	SSTfil	sospr	L_{inf}	M_1	166.16	-0.0475	-0.1660	196	136.08	SST	rivspr	L_{inf}	M_1	143.05	-0.0502	0.1263
164	90.80	SSTfil	sospr	L_{min}	M_1	165.69	-0.0322	-0.1649	207	137.82	SST	chlsum	L_{inf}	q	142.18	-0.0507	0.0278
141	92.04	SSTfil	soy	κ	M_1	165.07	-0.1144	-0.1822	194	137.88	SST	rivsum	L_{inf}	M_1	142.15	-0.0497	0.1475
170	93.00	SSTfil	sosum	L_{min}	M_1	164.59	-0.0338	-0.1609	219	139.48	SST	rivsum	κ	M_1	141.35	-0.1203	0.1497
165	93.60	SSTfil	chlsum	L_{min}	M_1	164.29	-0.0324	0.1627	232	140.52	SST	chlsum	κ	q	140.83	-0.1183	0.0266
113	96.10	SSTfil	rivfall	L_{inf}	M_1	163.04	-0.0466	0.2522	154	143.18	SSTfil	chlspr	κ	q	139.50	-0.1099	0.0100
225	96.58	SST	rivspr	κ	q	162.80	-0.1216	0.0475	135	146.74	SSTfil	SST	κ	M_1	137.72	-0.1068	-0.0352
173	97.02	SSTfil	sofall	L_{min}	M_1	162.58	-0.0342	-0.2139	136	147.12	SSTfil	SSTfil	κ	M_1	137.53	-0.1078	-0.0134
200	97.32	SST	rivspr	L_{inf}	q	162.43	-0.0501	0.0475	206	152.16	SST	sofall	L_{inf}	q	135.01	-0.0500	-0.0190
176	97.62	SSTfil	SST	L_{min}	q	162.28	-0.0335	0.0913	231	153.04	SST	sofall	κ	q	134.57	-0.1205	-0.0207

152	98.56	SSTfil	chlfall	κ	q	161.81	-0.1111	0.0439	209	153.16	SST	sosum	L_{inf}	q	134.51	-0.0500	-0.0143
140	98.92	SSTfil	chlsum	κ	M_1	161.63	-0.1121	0.1644	181	153.64	SSTfil	sofall	L_{min}	q	134.27	-0.0304	-0.0246
117	98.98	SSTfil	rivy	L_{inf}	M_1	161.60	-0.0479	0.1835	234	154.06	SST	sosum	κ	q	134.06	-0.1207	-0.0158
228	99.80	SST	SSTfil	κ	q	161.19	-0.1346	0.0834	204	155.92	SST	chlspr	L_{inf}	q	133.13	-0.0492	0.0093
177	100.54	SSTfil	chlfall	L_{min}	q	160.82	-0.0309	0.0447	229	156.66	SST	chlspr	κ	q	132.76	-0.1202	0.0105
139	100.94	SSTfil	sospr	κ	M_1	160.62	-0.1119	-0.1563	186	159.32	SST	SSTfil	L_{inf}	M_1	131.43	-0.0486	-0.0310
171	101.40	SSTfil	rivspr	L_{min}	M_1	160.39	-0.0338	0.1589	184	160.22	SSTfil	sosum	L_{min}	q	130.98	-0.0300	-0.0144
120	103.12	SSTfil	sosum	L_{inf}	M_1	159.53	-0.0473	-0.1474	185	160.54	SST	SST	L_{inf}	M_1	130.82	-0.0479	-0.0560
218	103.22	SST	chly	κ	M_1	159.48	-0.1281	0.2211	179	161.52	SSTfil	chlspr	L_{min}	q	130.33	-0.0299	0.0105
133	103.68	SSTfil	rivy	L_{inf}	q	159.25	-0.0470	0.0350	210	162.46	SST	SST	κ	M_1	129.86	-0.1163	-0.0346
172	104.12	SSTfil	chlspr	L_{min}	M_1	159.03	-0.0343	0.1226	211	162.60	SST	SSTfil	κ	M_1	129.79	-0.1168	-0.0256
142	104.84	SSTfil	rivy	κ	M_1	158.67	-0.1153	0.1735	160	166.46	SSTfil	SST	L_{min}	M_1	127.86	-0.0302	0.0396
193	105.10	SST	chly	L_{inf}	M_1	158.54	-0.0539	0.2221	161	167.10	SSTfil	SSTfil	L_{min}	M_1	127.54	-0.0297	0.0175

All 150 models had lower AIC values than the null model, and all but eleven also had link parameter estimates significantly different from zero ($p < 0.05$). One model—model 101, which relates $L_{\min}$ and q to SST—led to the lowest AIC overall, improving on the null model by 418.18 units, and the next-best model (model 100, where $L_{\min}$ is linked to SST and q is linked to river runoff in spring) by 1.86 units. The AIC weight for model 101 was effectively 1. Three other models (92, 100 and 99) had ΔAIC values within 10 units of model 101. All four of the top models linked SST to $L_{\min}$, while annual runoff was linked to M_1 in model 92, spring river runoff to q in model 100 and spring salinity to q in model 99. The best-performing models that linked the other growth parameters to SST were models 199 ($L_{\inf}$) and 226 (κ). The best models that included SSTfil were 124 ($L_{\inf}$), 149 (κ), and 174 ($L_{\min}$), with q linked to spring salinity. However, these models had much poorer fits than the best four models as indicated by ΔAIC values greater than 20. In this second tier, chlorophyll-a first appears in model 97, where it is linked to M_1.

Including two environmental covariates in the model led to noticeable improvements for several diagnostic metrics. This is most noticeable for model 101, which led to better fits to the index, age-composition and length-composition data (Tab. 5), as well as having lower estimated variability in recruitment.

Table 5 Values of the components of the objective function (negative log-likelihood plus summed logs of penalty terms) for the null model and the three best two-variable models. The value in parenthesis is the number of parameters.

Component	Model No (number of parameters)			
	Null (142)	100 (144)	101 (144)	99 (144)
Catches	0.00	0.59	0.76	0.36
Index data	139.66	126.51	140.84	141.24
Length data	531.91	483.23	457.66	463.37
Age data	1408.90	1275.71	1294.44	1281.55
Recruitment	17.13	3.19	2.00	3.70
Other penalties	47.01	45.23	37.83	45.03
Total	2144.62	1934.46	1933.53	1935.24

However, these improvements came at the expense of accurately matching recent catch data—especially for the EAST1718 fleet—resulting in a marked increase in estimated fishery mortality (Fig. 8).

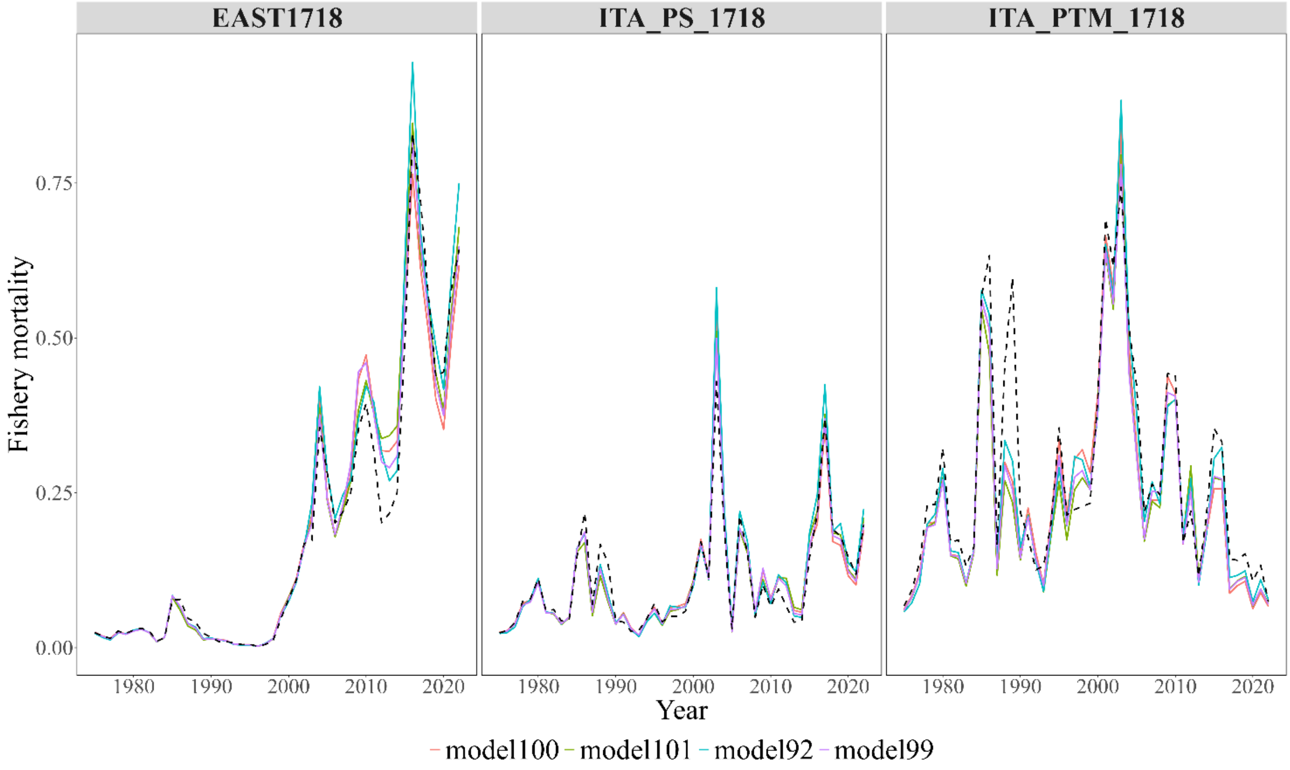

Figure 8 Comparison of fully-selected fishing mortality for the two-variable models for each commercial fleet. The black dashed line denotes the outcomes of the null model.

The other best two-variable models had better fits to the age-composition and length-composition data, as well as lower estimated variability in recruitment, but poorer fits to the index data. Table S.5 presents the diagnostic analysis for the two-variable models. The results indicate a modest improvement in the goodness-of-fit for the commercial mean lengths, with the retrospective and forecast metrics displaying performance comparable to that of the single-variable models. However, predictive skill, as quantified by Hcxval, is poorer than for the one-variable models.

The negative correlation between L_{min} and SST was maintained in the two-variable models, confirming that an increase in SST leads to lower mean lengths-at-age. Models 101 leads to higher survey catchability over time owing to increasing temperature, while mortality at age 1 drops under reduced freshwater input (model 92). Finally, the ability of the survey to detect anchovy is found to be lower owing the effects of higher salinity and lower river inflow rates during spring (model 99 and 100) (Fig. 9).

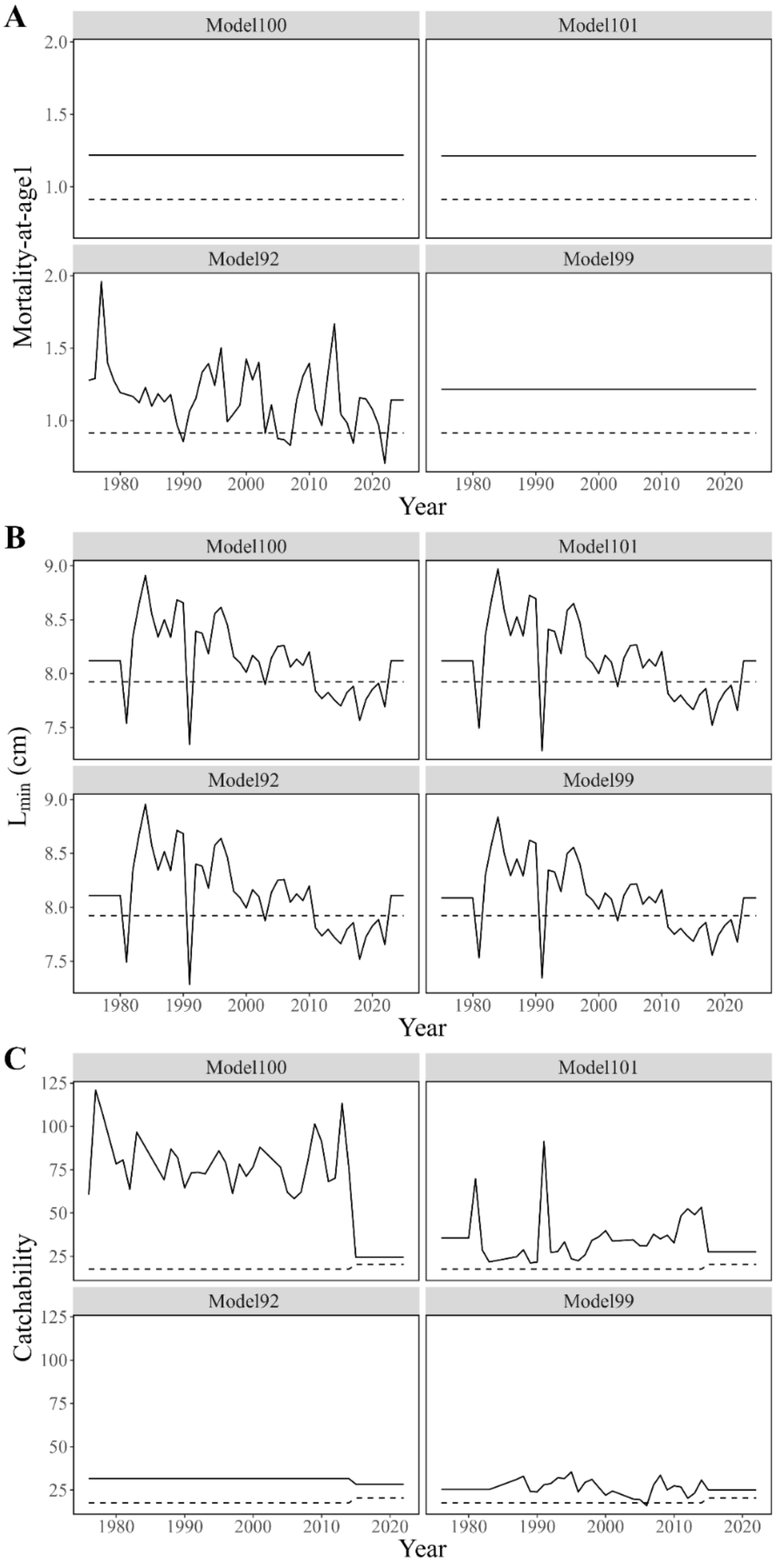

Figure 9 Comparison of parameters among the null (dashed line) and four best two-variable models (solid lines). (A) Time-varying M1, linked to annual river runoff in model 92 (bottom-right sub-panel - constant in the other models. (B) Time variation of L_{min}, linked to SST. (C) Time-varying survey q, linked to SST (model 101, top-left), SSTfil (model 103, top-right), and spring salinity (model 99, bottom-right). The abrupt change after 2015 in model 92 reflects different catchability settings for the MEDIASITAjun survey.

2.3.2.2 Impacts on management quantities

Figure 10 shows time-trajectories of estimated spawning stock biomass, fully-selected fishing mortality and recruitment (age-0 abundance) for the null model, the six best single-variable models and the four best two-variable models. All of the models estimate similar trends in these variables. The null model estimates a slightly lower spawning biomass compared to the other models, particularly for recent years (Fig. 10, top panel). Recruitment estimates for all of the two-variable models, as well as for single-variable models 4 and 10, are on average higher than those from the null model. In contrast, the recruitment levels for the remaining single-variable models are either comparable to or lower than from the null model (Fig. 10, central panel). As expected, the pattern of fully-selected fishing mortality is essentially the mirror image of that for spawning stock biomass (Fig. 10, bottom panel).

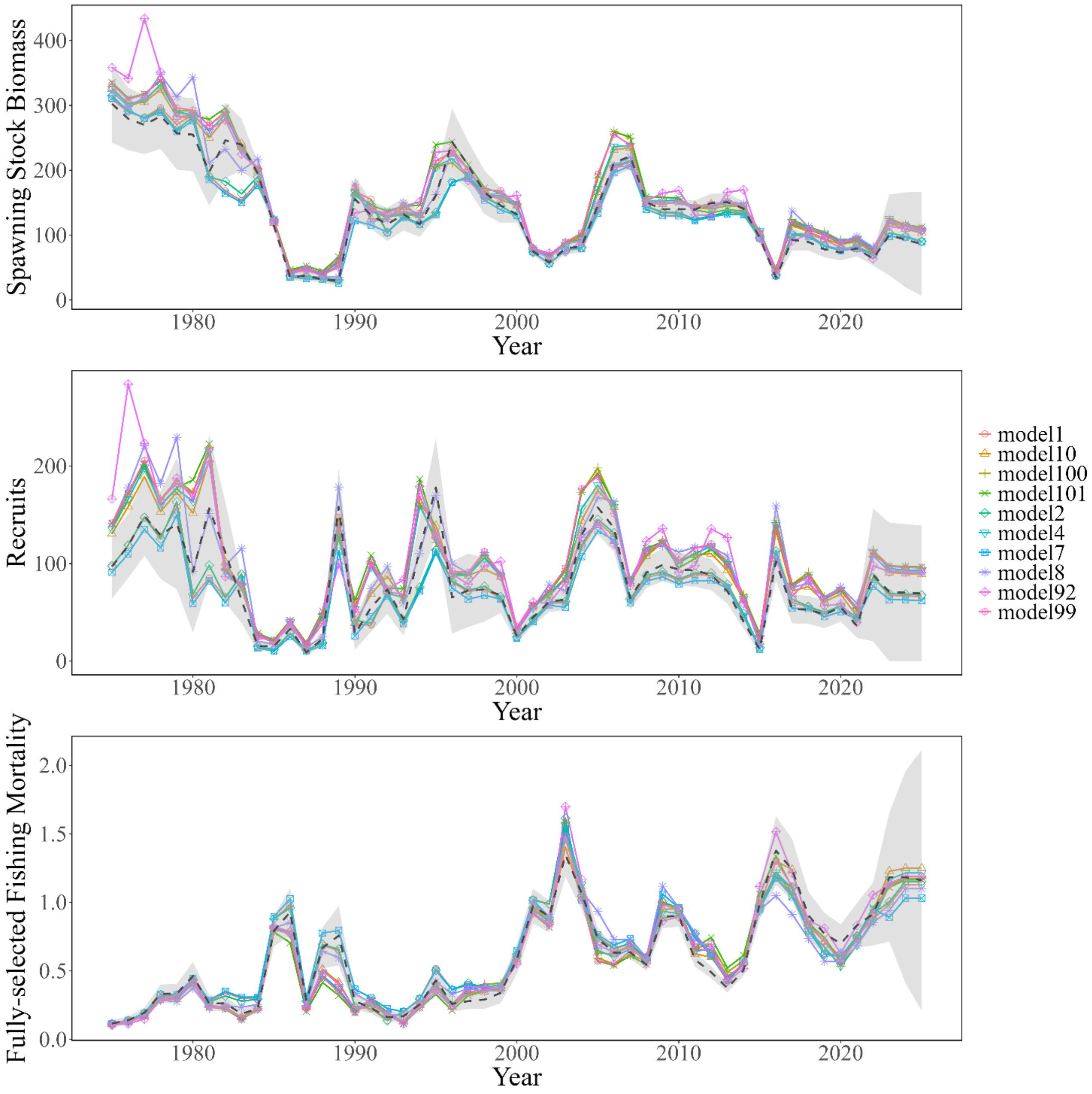

Figure 9 Comparison of parameters among the null (dashed line) and four best two-variable models (solid lines). (A) Time-varying M1, linked to annual river runoff in model 92 (bottom-right sub-panel - constant in the other models. (B) Time variation of L_{min}, linked to SST. (C) Time-varying survey q, linked to SST (model 101, top-left), SSTfil (model 103, top-right), and spring salinity (model 99, bottom-right). The abrupt change after 2015 in model 92 reflects different catchability settings for the MEDIASITAjun survey. Gray area rapresent 95% CI.

2.4 Discussion

This study represents the first attempt in the Mediterranean Sea to develop an environmentally-informed assessment model. Specifically, we explored links between environmental variables and key process, such as growth and recruitment, making use of the environmental linkage functionality provided by Stock Synthesis. This feature is particularly advantageous for Adriatic anchovy, whose growth is strongly influenced by environmental variability and is expected to be further affected by climate change in this region. In addition, we addressed several limitations highlighted in the official SAM assessment of the European anchovy in the Adriatic Sea, including gaps in data time series, trends over time in biological parameters, challenges creating consistent age structures due to changes in otolith reading protocols, and the change to the timing of the survey. Considerable effort went into refining the dataset used for model fitting, ultimately providing a comprehensive and robust basis for the analysis. By exploiting the flexibility of the SS framework—which allows for the estimation of growth parameters from length- and age-data while accounting for environmental influences—we were able to create a single, coherent modeling approach.

2.4.1 Environmental drivers of the anchovy stock in Adriatic Sea

Our findings demonstrate using single- and two-variable models that temperature is the predominant driver of growth for anchovy in the Adriatic Sea, with a significant negative relationship between SST and the parameters of the growth curve indicating that higher temperatures are associated with reduced mean length-at-age. The best-performing model (4) identifies SST as a key factor contributing to the decrease in length-at-age 0, while the second-best model (7), which incorporates locally measured SST, reinforces the notion that temperature exerts a significant influence on anchovy life-history traits, particularly maximum length. These findings align with numerous studies that have investigated the effect of SST on anchovy populations (e.g., Giannoulaki et al. 2013, Maynou et al. 2014, Mandic et al. 2019 for eggs and larvae; Vilibic et al. 2016, Basilone et al. 2017, Patti et al. 2020, Hattab et al. 2021, for juveniles and adults), which highlight the role rising temperature plays for reproductive triggers, gonad maturation, and egg survival. Anchovy, being a cooler water species, typically thrive in mixed water conditions, such as those created by wind mixing, upwelling, and river runoff, often in low-temperature waters (Bellido et al. 2008, Quattrocchi et al. 2016). Given that temperature rise could be driving changes in anchovy growth, it is evident that such warming could be affecting their traditional habitats, thereby compromising survival. Pennino et al. (2020) reported that climate change is expected to reduce freshwater input, dramatically shrinking anchovy habitat by 2050. In addition, increased temperatures exacerbate water hypoxia, which ultimately reduces fish growth. This phenomenon is well documented in the Baltic Sea, where rising temperatures have led to hypoxic conditions that threaten Baltic cod (*Gadus morhua*) populations (ICES WGBFAS, 2019). Temperature increases also influence the broader ecosystem by triggering algal blooms, leading to habitat contraction, and enhancing predation on cod recruits by proliferating warm-water species, all of which contribute to a reduction in individual growth and result in smaller-sized fish (Casini et al. 2009, 2016, Bartolino et al. 2017). Moreover, intensive fisheries that preferentially target larger individuals further intensify these environmental cascades by imposing strong selective pressures on populations (Svedang and Hornborg 2014). Our results appear to indicate that temperature may be driving a similar, albeit less severe, phenomenon in the anchovy population of the Adriatic Sea in accordance with Hattab et al. (2021). Consequently, incorporating SST into the anchovy stock assessment could provide valuable insights into its effects, also improving our understanding and informing management strategies.

Other notable findings emerged from the models that included other environmental variables; springtime chl-a and autumn river runoff may both contribute to a decrease in L_{min} (models 40 and 16, respectively, see Table 2 and Fig.S.2B for seasonal trends). These results may reflect the interplay among Po River discharge, temperature, and chl-a concentration, with freshwater input closely linked to nutrient distribution and temperature modulating phytoplankton cycles—factors that together might interact to reduce L_{min} (Santojanni et al. 2006, Malavolti et al. 2018, Fernandez-Corredor et al. 2021, Marini et al. 2023). Finally, model 57 introduces an interesting hypothesis related to the potential effect of salinity on survey catchability. Anchovy populations are strongly influenced by freshwater inflows and tend to favor low-salinity habitats (threshold = 37.86 ppm, Maynou et al. 2014). An increase in salinity (see Fig. S.2A and Fig. S.2B for the annual seasonal trends, both bottom left panel)—due to reduced freshwater inputs and heightened evaporation from rising temperatures—may lead to seasonal shifts in anchovy distribution (Pennino et al. 2020), altering both distribution and the availability of resources within traditional habitats, impacting on the fishery economics (i.e., a reduction in catch, Carpi et al. 2015a, Bonanno et al. 2016, Quattrocchi et al. 2016). In addition, variation in salinity within anchovy habitats may push the species into new areas, affecting survey catchability. This mirrors findings for the walleye pollock (*Gadus chalcogrammus*) fishery in the Gulf of Alaska, where climate-driven shifts in spawn timing influenced survey availability and led to discrepancies in biomass estimates (Walters and Maguire 1996, Langseth et al. 2016, Gruss et al. 2023, Rogers et al. 2024). This phenomenon could have important implications for stock assessments and fishery management.

Incorporating a second environmental variable into the model reveals an effect on survey catchability. However, temperature primarily influences length at age 0, which in turn affects survey catchability in the top two-variable model (101). Notably, rising temperatures tend to increase survey catchability—a result consistent with the MEDIAS protocol, since the survey is conducted during the anchovy spawning period (June-September). In contrast, model 99 and 100 incorporates the synergy between SST, salinity and river inflow rates in spring, with one variable affecting growth and the other influencing survey catchability; nevertheless, the effect of temperature remains dominant. In addition, annual river runoff, which has a declining trend (Fig. S.2B, top right panel), appears to be positively associated with reduced mortality at age 1 (see Fig.9), underscoring the crucial role of freshwater input to nutrient supply. Reduced water turbulence and lower phytoplankton concentrations associated with diminished runoff may enhance survival of anchovy recruits (Basilone et al. 2017, Brosset et al. 2017).

2.4.2 Impacts for fisheries management

The application of a single, coherent framework able to integrate a wide range of information (i.e. length and age composition) can improve the accuracy and robustness of stock assessments compared to methods that rely on only a subset of the available data. Importantly, SS also allows the inclusion of environmental variables as potential drivers of key population dynamics parameters, such as recruitment, natural mortality, and growth. This capacity makes SS particularly suitable for exploring alternative hypotheses about the factors influencing anchovy dynamics, including the effects of environmental variability on stock productivity. By adopting a more holistic modeling approach, SS contributes to a deeper understanding of population processes and strengthens the scientific basis for fisheries management in the Adriatic Sea. In this context, our primary objective is not merely to optimize model performance, but to identify the most influential environmental effects on the biological and fishery traits of anchovy. At the same time, we address several concerns raised in the last GFCM stock assessment working groups meetings, which are further described in this study, such as the need for consistent catch-at-age data and reliable growth parameters for Adriatic anchovy. Considering these issues, assessment frameworks such as SS represent good candidates to replace more rigid methods like SAM, the current official assessment model. An additional advantage of SS is the ability to define multiple fleets or areas and treat their related data independently. This feature is particularly relevant for Adriatic anchovy, a stock exploited by multiple gears and countries, as it enables finer control over data distribution, temporal coverage, and weighting, while also allowing distinct biological and fishery settings to be specified for each fleet or area. In turn, this facilitates the provision of more targeted and robust management advice.

As a key bottom-up driver in the pelagic food web, anchovies are particularly sensible to ecological change. Adopting an environmentally-informed approach in their assessment might provide a more robust explanations for population fluctuations, as highlighted by several studies in the Adriatic Sea (e.g., Palomera et al. 2007, Martin et al. 2008, Van Beveren et al. 2014, Brosset et al. 2017, Coll et al. 2019, Fanelli et al. 2023). Some regions have already incorporated climate-driven factors into their stock assessments. For example, management of Pacific sardine (*Sardinops sagax*) off the U.S. West Coast is based on a climate-aware harvest control rule that links E_{MSY} (the exploitation rate corresponding to MSY) to SST (Pacific Fishery Management Council 1998). Nonetheless, concerns regarding the robustness of this approach have been raised (e.g., Myers 1998, MacClatchie et al. 2010, Lindegren and Checkley 2013, Zwolinski and Demer 2019, Free et al. 2023), prompting some authors to advocate for climate-enhanced stock assessments that utilize Earth System Model projections (e.g., Holsman et al. 2020, Reum et al. 2020, Szuwalski et al. 2021, Punt et al. 2021, Whitehouse et al. 2021).

We show how the stock assessment for European anchovy in the Adriatic Sea responds to environmental variables related to key parameters. Our results indicate that temperature is a promising candidate for future assessments, as its inclusion significantly improved model fit—especially when linked to growth parameters. An additional enhancement involves incorporating a secondary link from SST to survey catchability. While the resulting link values are generally below 0.1, implying that a one standard deviation change in the environmental variable translates to less than a 10% change in the linked parameter, the linkage should not be ignored. In fact, as shown in Figure 10, there are several periods where environmentally informed models yield estimates of key model outputs (e.g., recruitment, SSB, and fishing mortality) that fall outside the 95% confidence intervals of the null model. Such departures are not merely statistical curiosities; they may have important implications for management advice. For example, the majority of models that incorporate environmental links suggest higher levels of fully-selected fishing mortality compared to the null model during the late 2000s and early 2010s (Fig. 10, bottom panel), a period of low spawning biomass and increased uncertainty in fishing mortality estimates. This divergence could imply that, had environmental indicators been considered, a more precautionary approach might have been justified. Crucially, environmentally informed models also tend to better capture the dynamics related to major recruitment failures, such as those observed in 1987 and 2002. In both cases, the deviations from the confidence bounds from the null model suggest that the inclusion of environmental information can help to anticipate or more accurately quantify extreme events in stock productivity. Similarly, recruitment estimates from the two-variable models tend to be consistently higher than those from single and null models. While this pattern may partly reflect the inherent difficulties in estimating recruitment (Hsu et al. 2024) and the inconsistencies in data collection that undermine model robustness (Silva et al. 2024), it also suggests that environmentally based models may offer improved responsiveness to shifts in population dynamics under changing oceanographic conditions. This capability is particularly valuable for short-lived species such as anchovy, which are highly responsive to environmental variability.

Beyond their statistical contribution, the inclusion of environmental covariates also responds to concerns raised by stakeholders about considering drivers other than fishing pressure in the assessment process. As reported from Sagarese et al. (2020), incorporating environmental information can help management move from a primarily reactive approach to a more proactive stance, in which potential ecological shifts are anticipated and addressed in advance. Even if the overall model fit does not change dramatically when environmental variables are included, accounting for ecological influences can increase awareness of the role of ecosystem dynamics in shaping a dynamic management of the marine resources.

Although the integration of environmental drivers can enhance understanding of the interplay between natural stock dynamics, fishery pressure, and ecological variability, it also introduces additional layers of complexity that must be carefully considered. In particular, time-varying growth parameters can alter the estimation of spawning stock biomass, recruitment, and fishing mortality, leading to divergent management outputs (Pitcher et al. 2009, Marshall et al. 2019). When these parameters are linked to environmental variability, such as increasing SST, the implications for stock assessment and management become more complex and uncertain. In this context, while future research could explore the integration of environmental variables into the derivation of reference points, such integration must be approached with appropriate caution. Reference points derived from long-term simulations depend heavily on assumptions about future environmental conditions, and choices such as using recent historical values versus projected trends can lead to substantially different outcomes. This is particularly critical in models with limited forecast skill, as is the case here, which increases the uncertainty of long-term management advice. However, exploring alternative reference points would be particularly beneficial for the anchovy population of the Adriatic Sea given that the official reference points for the fishing mortality are currently based on Patterson (1992). The reference points could be updated using the outputs from Stock Synthesis based on the guidelines provided by ICES (2021a).

2.4.3 Model diagnostics and implementation

The diagnostics (Table S.4 and S.5) indicate that the additional complexity introduced with environmental variables and time-varying parameters does not necessarily undermine model robustness, but it does not enhance it much either. The implementation of environmental links is relatively simple in Stock Synthesis, but the only available way the influence of covariates on biological parameters is modelled as a linear estimated effect on length. As such, the approach to including environmental covariates assumes a stationary relationship between environmental drivers and biological processes. Thus, there is no ability to test whether the relationships between covariates and model parameters has changed over time (i.e., non-stationarity), which can be highly relevant in rapidly changing ecosystems such as the Adriatic Sea. It is important to consider the limitations highlighted by the diagnostic analyses, particularly in view of the possibility to derive reference points. For example, the model appears to have overfit the historical survey index (MEDIASITAsep, Fig. S.3 and S.5A), leading to significant deviations of the residuals from the median, with RMSE values exceeding 30% (Tables S.4 and S.5), and hindcast skill that are limited (see Fig. S.4 and S.5B, MASE > 1). This issue is further exacerbated in the two-variable models, where MASE values exceed 2 (e.g., model 92, Table S.5). The poor performance under MASE for the survey data is likely related to short length of the time-series.

2.4.4 Future work and caveats

Our current approach does not account for the fact that the temporal coverage of most environmental variables is shorter than the model time series. This leads to the unrealistic assumption that environmental effects are negligible during the years for which data are missing. Future work should consider treating the biological parameters as time-varying with an environmental covariate taken as an index of how the biological parameter differs from its expected value (Crone et al., 2019). However, it would require a method to assess to magnitude of the variance of the relationship (Punt, 2023). We did not explore models involving three or more environmental covariates. Future work could test more complex models to investigate potential interactions among variables and assess whether such models improve predictive skill.

Future stock assessments should allow for time-varying growth because this study shows that environmental variations may significantly influence growth, leading to shifts in the population dynamics of this stock. In addition, future work could consider a finer time-step given, the use of seasonal data is advised (ICES 2021b) and this may enhance the capacity to estimate growth parameters.

Another important direction for further research is the development of a spatially explicit population dynamics model to address the data differences between the western and eastern Adriatic basins while accounting for anchovy behavior and spatially varying oceanographic conditions. Although, some spawning is reported in Croatia, the Italian coast remains the main spawning ground for anchovies, whereas they are more involved in foraging in eastern coast (Morello and Arneri 2009). This behavioral and environmental divergence supports a two-area approach that distinguishes between these regions, thereby capturing the spatial heterogeneity in anchovy behavior and environmental conditions more effectively. However, the paucity of data on movement will prove challenging. Assessing how anchovy respond to environmental variability across distinct areas could, however, provide critical insights for implementing more effective, ecosystem-based fisheries management strategies.

While the environmental indices included in the stock assessment model variants were selected based on previous work, the data quality issues identified in this study - particularly inconsistencies in age-slicing due to the use of different ALKs may be influencing the perceived trends in the anchovy population. As a result, environmental covariates could, in some cases, act as indirect proxies rather than directly capturing true drivers of population dynamics. This highlights a potential risk of overfitting when linking environmental variables to model parameters, particularly given that these covariates are derived from hypotheses rather than definitive evidence. Strengthening the quality and consistency of stock assessment data should be a key priority to support the transition to an environmental-driven approach. Addressing these data challenges would not only improve model accuracy but also ensure that environmental influences are correctly interpreted.

Notwithstanding that some aspects of this work require future improvements; this study provides a good example of how to integrate key ecosystem components into stock assessment models useful for fisheries management. The status of the Adriatic anchovy stock in terms of the trend estimated by SS is quite comparable to that obtained by the official model; however, SS and FLSAM are based on quite different methodologies. The ability of the SS model to include non-continuous time series of input data facilitates the use of a wide range of information, including more historical data. Incorporating more historical information allows for more realistic evaluations of stock status (Lotze and Milewski 2004; Myers and Worm 2005) and helps in determining more precise reference points, in particular for biomass (van Deurs et al. 2020). This aspect would be particularly beneficial for future assessments of this stock. Moreover, SS is a stock assessment method that allows for the inclusion of other types of information beyond those related to fishery activity and scientific surveys, such as environmental variables and mortality due to predation. In this study, only the relationships between some environmental variables and biological aspects were investigated, but in the future, predation from other species, e.g., large pelagic species, could also be examined. In a context where climate change significantly impacts ecosystem dynamics and fishing effort has notably decreased, incorporating variables beyond fishing activity and scientific surveys into stock assessment models can enhance the robustness of the results and better address the concerns of stakeholders and fishers. Therefore, the approach developed in this study represents a significant advancement in the development of an environmentally comprehensive stock assessment models moving towards a promising strategy for more effective management of fishery resources in a changing ecosystem.

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Supplementary material

Table S.1. Results of the Mann–Kendall trend test for the environmental variables. The table shows the mean, standard deviation (SD), Kendall's tau coefficient, and the p-value for each variable (Chl-a, runoff, salinity, SST for the GSA17 dataset and SSTfil for the filtered dataset) computed for annual and seasonal (Autumn, Spring, Summer, Winter) time series. An asterisk (*) indicates significance at $p < 0.05$.

Variable	Period	Mean	SD	Tau	p_value
Chl-a (mg/m^3)	Annual	0.32	0.03	0.26	0.078
	Autumn	0.35	0.03	0.11	0.117*
	Spring	0.33	0.06	0.11	0.117*
	Summer	0.17	0.03	0.11	0.117*
	Winter	0.42	0.05	0.11	0.117*
Runoff (m^3/s)	Annual	1499.80	396.85	-0.27	0.007*
	Autumn	1799.25	838.78	-0.16	0.001*
	Spring	1757.07	680.62	-0.16	0.001*
	Summer	1074.94	394.39	-0.16	0.001*
	Winter	1367.93	515.63	-0.16	0.001*
Salinity (PSU)	Annual	37.27	0.30	0.26	0.026*
	Autumn	37.48	0.32	0.17	0.002*
	Spring	36.94	0.29	0.17	0.002*
	Summer	37.19	0.46	0.17	0.002*
	Winter	37.46	0.30	0.17	0.002*
SST (°C)	Annual	18.37	0.66	0.59	0.000*
	Autumn	17.54	0.65	0.17	0.001*
	Spring	18.10	0.99	0.17	0.001*
	Summer	24.50	0.82	0.17	0.001*
	Winter	12.97	0.56	0.17	0.001*
SSTfil (°C)	Annual	17.66	0.61	0.60	0.000*
	Autumn	16.55	0.62	0.13	0.012*
	Spring	17.93	1.10	0.13	0.012*
	Summer	24.71	0.83	0.13	0.012*
	Winter	11.26	0.66	0.13	0.012*

Table S.2 Results of the Mann–Whitney U test comparing the filtered and GSA17 datasets for three of the four environmental variables. The table lists the mean, standard deviation (SD), test statistic (W) and p-value for Sea Surface Temperature (SST), Chlorophyll-a (Chl-a) and salinity, highlighting statistically significant differences between the two datasets.

Variable	Dataset	Mean	SD	W	p_value
SST (°C)	Filtered	17.66	0.61	383	3.90E-06
	GSA17	18.37	0.66		
Chl-a (mg/m3)	Filtered	0.32	0.03	576	6.20E-14
	GSA17	0.17	0.01		
Salinity (PSU)	Filtered	37.27	0.30	32	1.98E-16
	GSA17	38.01	0.21		

Table S.3 Environmental variables with their corresponding time scales, data sources, and acronyms.

Environmental variable	Time-scale	Database	Acronym
Sea Surface Temperature	Annual	GSA17	SST
		filtered	SSTfil
Chlorophyll -a concentration	Annual	filtered	chly
	Spring		chlspr
	Summer		chlsum
	Fall		chlfall
River runoff	Annual	filtered	rivy
	Spring		rivspr
	Summer		rivsum
	Fall		rivfall
Salinity	Annual	filtered	soy
	Spring		sospr
	Summer		sosum
	Fall		sofall

Table S.4 Summary of runs test, the residual standard deviation, Mohn’s rho based on retrospective analysis, retrospective forecasts and the HCxval model diagnostic for the null model and best six single-variable models. P-values with (*) are significant (p-value < 0.05) and indicate a non-random distribution of residuals. Five peels were applied (2017 – 2021) for the retrospective and forecast analyses.

Diagnostic	**Statistic**	**Quantity**	**Null model**	**Model 1**	**Model 10**	**Model 2**	**Model 4**	**Model 7**	**Model 8**
Runs test	p-value	MEDIASITAsep_cpue	0.200	0.200	0.189	0.200	0.221	0.200	0.432
Runs test	p-value	MEDIASITAjun_cpue	0.968	0.968	0.937	0.968	0.937	0.968	0.968
Runs test	p-value	ITA_PTM_1718_len	0.625	0.520	0.344	0.520	0.295	0.544	0.315
Runs test	p-value	ITA_PS_1718_len	0.136	0.411	0.449	0.411	0.449	0.411	0.136
Runs test	p-value	EAST1718_len	0.560	0.113	0.020*	0.113	0.113	0.113	0.113
Runs test	p-value	MEDIASITAsep_len	0.340	0.765	0.062	0.765	0.062	0.763	0.691
Runs test	p-value	MEDIASITAjun_len	0.860	0.848	0.848	0.848	0.848	0.848	0.848
Residual StdDev	RMSE	MEDIASITAsep_cpue	50.2	50.2	50.0	50.3	49.0	51.7	48.1
Residual StdDev	RMSE	MEDIASITAjun_cpue	12.3	7.5	7.4	7.2	7.4	7.0	6.1
Residual StdDev	RMSE	ITA_PTM_1718_len	3.4	3.0	3.0	3.0	2.9	3.0	3.5
Residual StdDev	RMSE	ITA_PS_1718_len	3.7	3.8	3.6	3.8	3.7	3.6	4.7
Residual StdDev	RMSE	EAST1718_len	2.4	1.8	2.0	1.9	1.9	1.8	1.9
Residual StdDev	RMSE	MEDIASITAsep_len	8.0	7.4	7.4	7.3	7.4	7.1	7.3
Residual StdDev	RMSE	MEDIASITAjun_len	2.3	2.3	2.2	2.2	2.1	2.5	2.6
Retrospective analysis	ρ_M	SSB_peels combined	0.057	0.026	0.051	0.035	0.080	0.033	0.051
Retrospective forecasts	ρ_F	SSB_peels combined	0.075	0.109	0.124	0.110	0.139	0.124	0.133
Retrospective analysis	ρ_M	F_peels combined	-0.095	-0.038	-0.065	-0.048	-0.078	-0.046	-0.073
Retrospective forecasts	ρ_F	F_peels combined	-0.119	-0.119	-0.132	-0.127	-0.123	-0.128	-0.146
Hcxval	MASE.adj	MEDIASITAjun_cpue	1.259	1.072	1.684	1.060	1.837	1.117	1.283
Hcxval	MASE.adj	ITA_PTM_1718_len	0.288	0.264	0.332	0.270	0.354	0.246	0.245
Hcxval	MASE.adj	ITA_PS_1718_len	0.263	0.227	0.269	0.236	0.268	0.230	0.236
Hcxval	MASE.adj	EAST1718_len	0.207	0.256	0.218	0.262	0.235	0.232	0.232
Hcxval	MASE.adj	MEDIASITAjun_len	0.246	0.246	0.240	0.247	0.230	0.268	0.274

Table S.5 Summary of runs test, the residual standard deviation, Mohn's rho based on retrospective analysis, retrospective forecasts and the HCxval model diagnostic for the null model and four best two-variable models. P-values with (*) are significant (p-value < 0.05) and indicate a non-random distribution of residuals. Five peels were applied (2017 – 2021) for the retrospective and forecast analyses.

Diagnostic	**Statistic**	**Quantity**	**Null model**	**Model 100**	**Model 101**	**Model 92**	**Model 99**
Runs test	p-value	MEDIASITAsep_cpue	0.200	0.448	0.257	0.448	0.536
Runs test	p-value	MEDIASjun_cpue	0.968	0.937	0.937	0.937	0.937
Runs test	p-value	ITA_PTM_1718_len	0.625	0.284	0.284	0.280	0.284
Runs test	p-value	ITA_PS_1718_len	0.136	0.449	0.449	0.449	0.449
Runs test	p-value	EAST1718_len	0.560	0.113	0.113	0.113	0.113
Runs test	p-value	MEDIASITAsep_len	0.340	0.062	0.062	0.430	0.216
Runs test	p-value	MEDIASjun_len	0.860	0.848	0.848	0.848	0.848
Residual StdDev	RMSE	MEDIASITAsep_cpue	50.2	47.0	49.8	48.5	49.0
Residual StdDev	RMSE	MEDIASjun_cpue	12.3	6.9	7.0	8.6	7.6
Residual StdDev	RMSE	ITA_PTM_1718_len	3.4	2.8	2.7	2.7	2.9
Residual StdDev	RMSE	ITA_PS_1718_len	3.7	3.4	3.3	3.6	3.3
Residual StdDev	RMSE	EAST1718_len	2.4	1.8	1.8	2.0	1.9
Residual StdDev	RMSE	MEDIASITAsep_len	8.0	7.7	7.1	6.8	6.7
Residual StdDev	RMSE	MEDIASjun_len	2.3	2.1	2.1	2.1	2.0
Retrospective analysis	ρ_M	SSB_peels combined	0.057	0.1329	0.0637	0.0751	0.0460
Retrospective forecasts	ρ_F	SSB_peels combined	0.075	0.1825	0.1294	0.2179	0.1083
Retrospective analysis	ρ_M	F_peels combined	-0.095	-0.0925	-0.0772	-0.0994	-0.0578
Retrospective forecasts	ρ_F	F_peels combined	-0.119	-0.1430	-0.1569	-0.2047	-0.1206
Hcxval	MASE.adj	MEDIASjun_cpue	1.259	1.8299	1.8323	2.6248	1.8124
Hcxval	MASE.adj	ITA_PTM_1718_len	0.288	0.3453	0.3605	0.3800	0.3436
Hcxval	MASE.adj	ITA_PS_1718_len	0.263	0.2583	0.2538	0.2616	0.2678
Hcxval	MASE.adj	EAST1718_len	0.207	0.1824	0.2262	0.2442	0.2186
Hcxval	MASE.adj	MEDIASjun_len	0.246	0.2583	0.2568	0.2608	0.2496

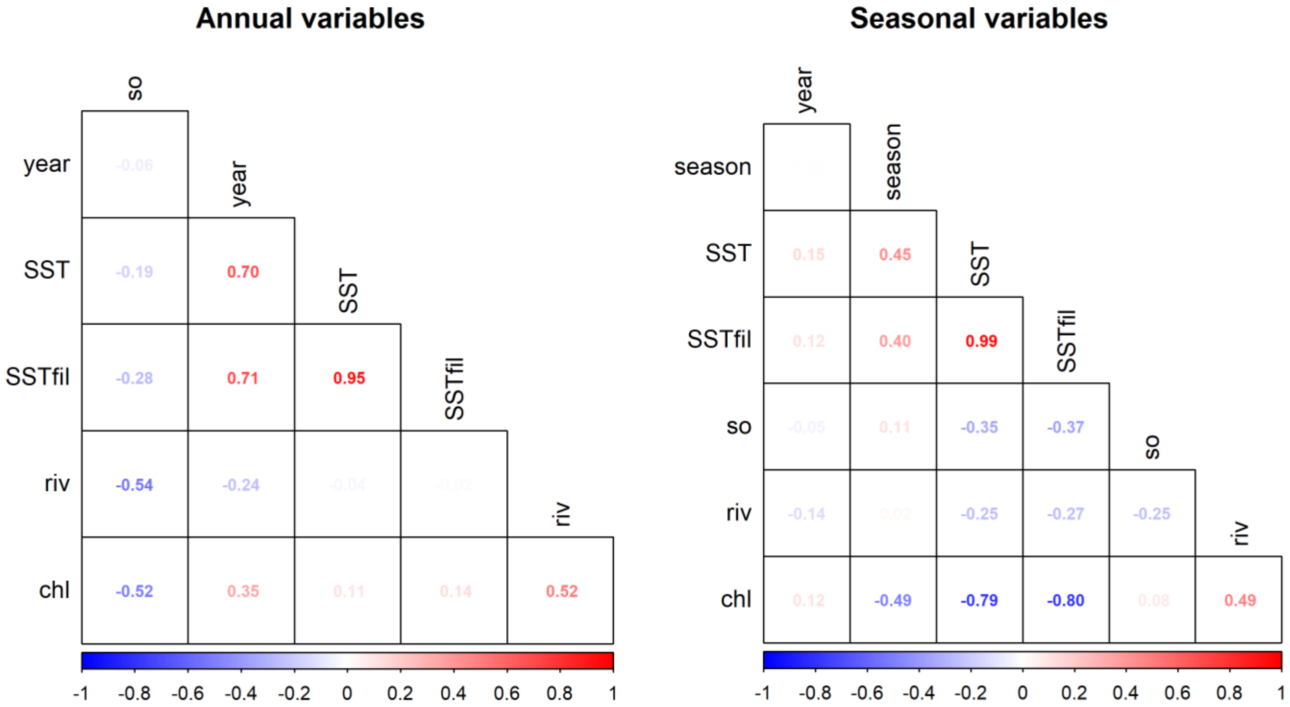

Figure S.1 Correlation matrices for annual (left) and seasonal (right) environmental variables. The strength and direction of correlations are represented by color intensity (red for positive correlations, blue for negative correlations) and the corresponding correlation coefficients. Annual variables capture trends over entire years, while seasonal variables account for intra-annual variability.

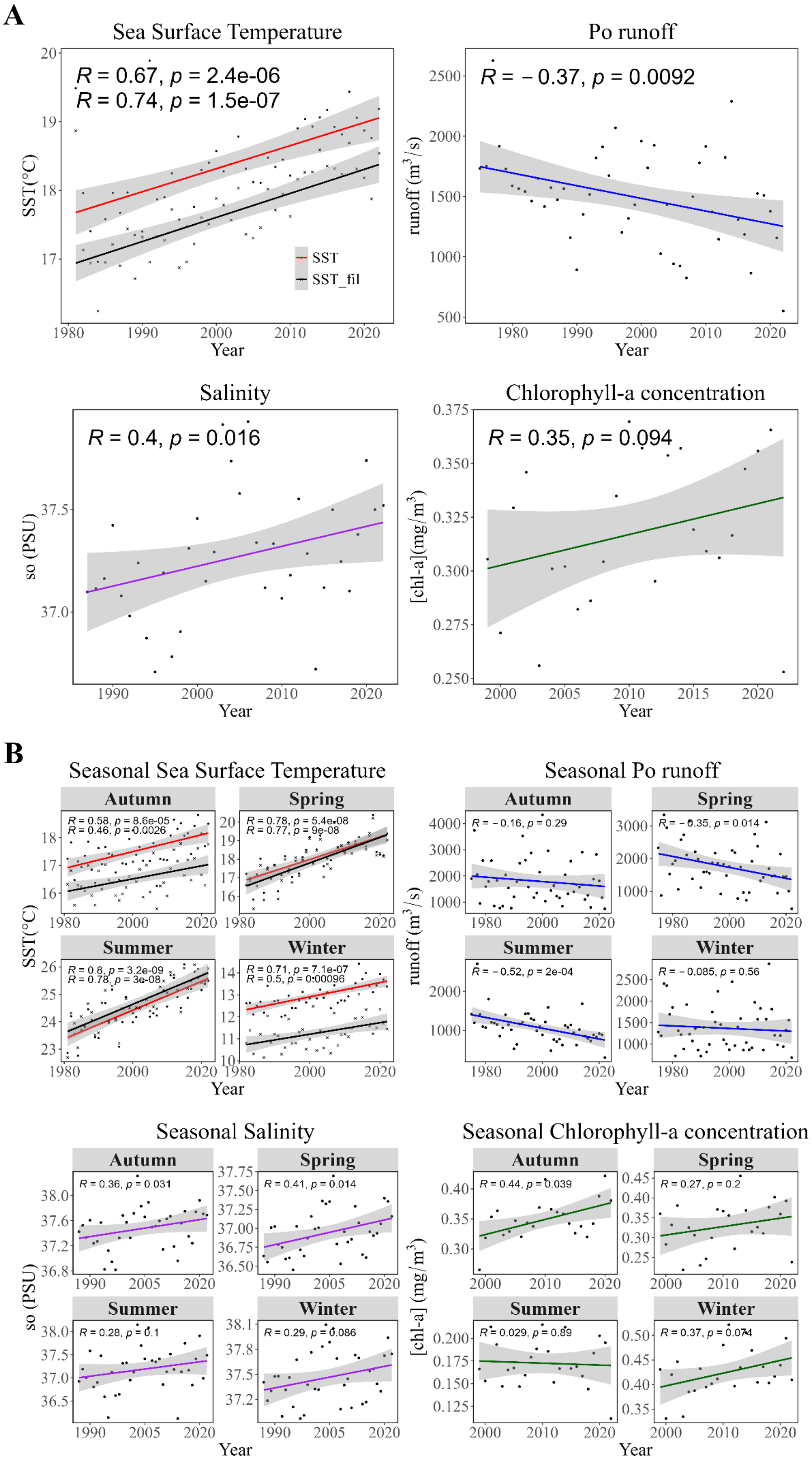

Figure S.2 (A) Annual trends in SST (red: whole basin; black: filtered), Po River runoff (blue), chlorophyll-a concentration (green), and salinity (purple). (B) Seasonal trends for SST, salinity, and chlorophyll-a. Linear regression lines, correlation coefficients (R), and significance levels (p-values) are displayed.

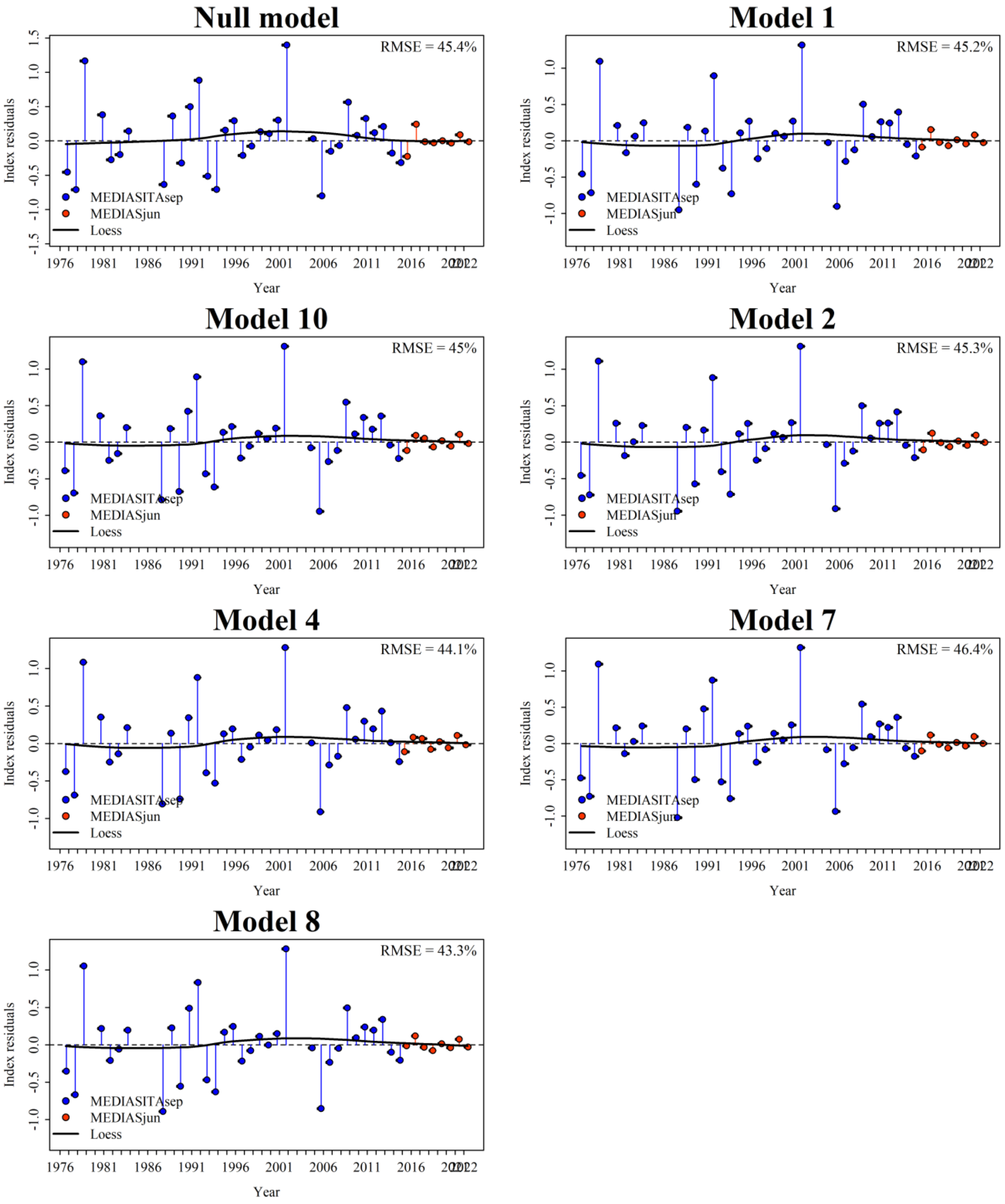

Figure S.3 RMSE plots for the survey index for the single variable models.

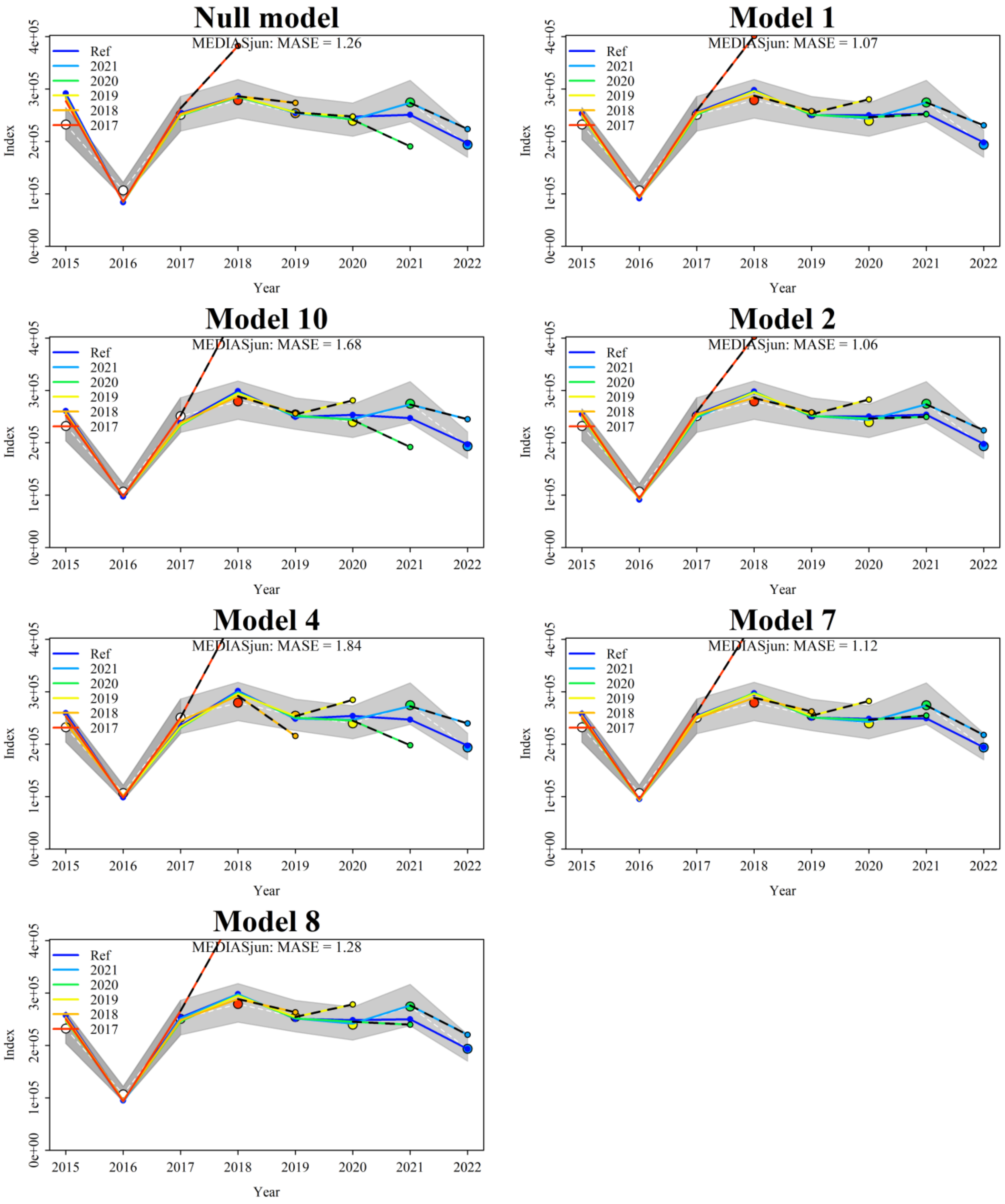

Figure S.4 MASE results for the survey index for the single variable models.

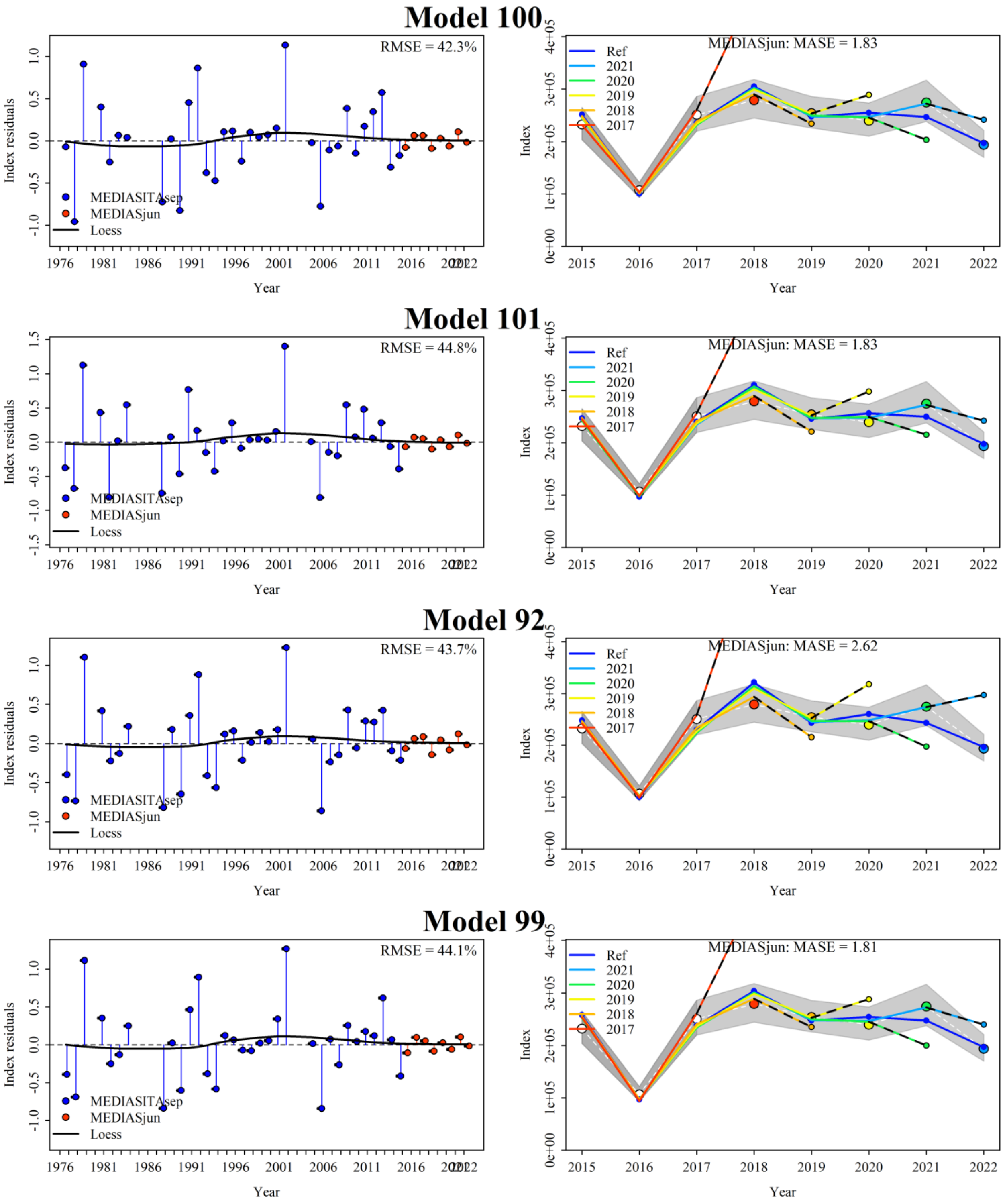

Figure S.5 RMSE (left panel) and MASE (right panel) for the survey index for the two-variable models.

References

Angelini S, Hillary R, Morello EB et al. An Ecosystem Model of Intermediate Complexity to test management options for fisheries: A case study. Ecol Model. 2016;319:218-232. https://doi.org/10.1016/j.ecolmodel.2015.07.031.

Angelini S, Arneri E, Belardinelli A et al. Stock Assessment Form Small Pelagics Anchovy GSA 17 and 18. 2019. https://www.fao.org/gfcm/data/safs/en.

Angelini S, Biagiotti I, Bratina P et al. Stock Assessment Form Small Pelagics Anchovy GSA 17 and 18. 2024. https://www.fao.org/gfcm/data/safs/en.

Arkema KK, Abramson SC, Dewsbury BM. Marine ecosystem-based management: from characterization to implementation. Front Ecol Environ. 2006;4(10):525-532. https://doi.org/10.1890/1540-9295(2006)4[525:MEMFCT]2.0.CO;2.

Arneri, E. Fisheries resources assessment and management in the Adriatic and Ionian Seas. FAO-GFCM 3rd Technical Consultation on Stock Assessment in the Central Mediterranean, Tunis 8-12 November 1994. FAO Fish. Rep. 1994; 533: 7-20. https://www.fao.org/gfcm/meetings/info/en/c/295626/.

Artegiani A, Paschini E, Russo A et al. The Adriatic Sea General Circulation. Part II:Baroclinic Circulation Structure. J Phys Ocenogr. 1997;27 (8):1515-1532. doi: https://doi.org/10.1175/1520-0485(1997)027<1515:TASGCP>2.0.CO.

Bartolino V, Tian H, Bergstrom U et al. Spatio-temporal dynamics of a fish predator: Density-dependent and hydrographic effects on Baltic Sea cod population. Plos One. 2017;12(2). e0172004. https://doi.org/10.1371/journal.pone.0172004.

Basilone G, Mangano S, Pulizzi, M et al. European anchovy (Engraulis encrasicolus) age structure and growth rate in two contrasted areas of the Mediterranean Sea: the paradox of faster growth in oligotrophic seas. Mediterr Mar. Sci. 2017;18(3):504-516. https://doi.org/10.12681/mms.2059.

Bellido JM, Brown AM, Valavanis VD et al. Identifying essential fish habitat for small pelagic species in Spanish Mediterranean waters. Hydrobiologia. 2008; 612:171–184. http://dx.doi.org/10.1007/s10750-008-9481-2.

Bonanno A, Barra M, Basilone G et al. Environmental processes driving anchovy and sardine distribution in a highly variable environment: the role of the coastal structure and riverine input. Fish Oceanogr. 2016; 25:471–490. http://dx.doi.org/10.1111/fog.12166.

Brooks EN, Legault CM. Retrospective forecasting — evaluating performance of stock projections for New England groundfish stocks. Can J Fish Aquat. Sci. 2016; 73:935–950. https://doi.org/10.1139/cjfas-2015-0163.

Brosset P, Fromentin JM, Van Beveren E et al. Spatio-temporal patterns and environmental controls of small pelagic fish body condition from contrasted Mediterranean areas. Prog Oceanogr. 2017; 151, 149-162. https://doi.org/10.1016/j.pocean.2016.12.002

Carpi P, Martinelli M, Belardinelli A et al. Coupling an oceanographic model to a Fishery Observing System through mixed models: the importance of fronts for anchovy in the Adriatic Sea. Fish Oceanogr. 2015a;24(6), 521-532. https://doi.org/10.1111/fog.12126.

Carpi P, Santojanni A, Donato F et al. A joint stock assessment for the anchovy stock of the northern and central Adriatic Sea: comparison of two catch-at-age models. Sci. Mar. 2015b:79(1), 57-70. http://dx.doi.org/10.3989/scimar.03903.29A.

Carvalho F, Punt AE, Chang Y-J et al. Can diagnostic tests help identify model misspecification in integrated stock assessments? Fish Res. 2017;192:28–40. https://doi.org/10.1016/j.fishres.2016.09.018.

Carvalho F, Winker H, Courtney D et al. A cookbook for using model diagnostics in integrated stock assessments. Fish Res. 2021;240:105959. https://doi.org/10.1016/j.fishres.2021.105959.

Casini M, Hjelm J, Molinero J et al. Trophic cascades promote threshold-like shifts in pelagic marine ecosystems, Proc Natl Acad Sci. U.S.A. 2009;106 (1) 197-202. https://doi.org/10.1073/pnas.0806649105.

Casini M. Hypoxicareas, density-dependence and food limitation drive the body condition of a heavily exploited marine fish predator. R Soc. 2016;3:160416. http://dx.doi.org/10.1098/rsos.160416.

Christensen V, Walters CJ. Ecopath with Ecosim: methods, capabilities and limitations. Ecol Model. 2004;172:109–139. https://doi.org/10.1016/j.ecolmodel.2003.09.003.

Cingolani N, Giannetti G, Arneri E. Anchovy fisheries in the Adriatic Sea. Sci Mar. 1996;60 (2): 269:277.

Coll M, Palomera I, Tudela S et al. Food-web dynamics in the South Catalan Sea ecosystem (NW Mediterranean) for 1978–2003. Ecol Model. 2008; 217(1-2):95-116. https://doi.org/10.1016/j.ecolmodel.2008.06.013.

Coll M, Albo-Puigserver M, Navarro J et al. Who is to blame? Plausible pressures on small pelagic fish population changes in the NW Mediterranean Sea. Mar Ecol Prog Ser. 2019; 617-618, 277-294. https://doi.org/10.3354/meps12591.

Cope JM. The Stock Synthesis Data-limited Tool (SS-DL tool). 2020. https://github.com/shcaba/SS-DL-tool#the-stock-synthesis-data-limited-tool-ss-dl-tool.

Cowan JH, Rice JC, Walters CJ et al. Challenges for implementing an ecosystem approach to fisheries management. Mar Coast Fish. 2012;4(1):496-510. https://doi.org/10.1080/19425120.2012.690825.

Cozzi S, Giani M. River water and nutrient discharges in the Northern Adriatic Sea: Current importance and long term changes. Cont Shelf Res. 2011;31:1881-1893. https://doi.org/10.1016/j.csr.2011.08.010.

Crone PR, Maunder MN, Lee HH et al. Good practices for including environmental data to inform spawner-recruit dynamics in integrated stock assessments: small pelagic species case study. Fish. Res. 2019;217: 122–132. https://doi.org/10.1016/j.fishres.2018.12.026.

De Felice A, Iglesias M, Saraux C et al. Environmental drivers influencing the abundance of round sardinella (Sardinella aurita) and European sprat (Sprattus sprattus) in different areas of the Mediterranean Sea. Medit. Mar. Sci. 2021;22(4): 812-826. https://doi.org/10.12681/mms.25933.

Eigaard OR, Bastardie F, Hintzen NT et al. The footprint of bottom trawling in European waters: distribution, intensity, and seabed integrity. ICES J Mar Sci. 2017;74(3):847-865. https://doi.org/10.1093/icesjms/fsw194.

Fanelli E, Da Ros Z, Menicucci S et al. The pelagic food web of the Western Adriatic Sea: a focus on the role of small pelagics. Sci Rep. 2023;13:14554. https://doi.org/10.1038/s41598-023-40665-w.

Fernandez-Corredor E, Albo-Puigserver M, Pennino MG et al. 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. in Mar Sci Ser. 2021;41(128):101-606. https://doi.org/10.1016/j.rsma.2020.101606.

Food and Agriculture Organization of the United Nations (FAO). The ecosystem approach to marine capture fisheries. FAO Technical Guidelines for Responsible Fisheries. 2003;4(2):112 pp.

Food and Agriculture Organization of the United Nations (FAO). The State of Mediterranean and Black Sea Fisheries 2023 – Special edition. General Fisheries Commission for the Mediterranean. Rome. 2023. https://doi.org/10.4060/cc8888en.

Food and Agriculture Organization of the United Nations (FAO) - Fisheries Division, Statistics and Information Branch. FishStatJ: Universal software for fishery statistical time series. Copyright 2020.

Francis RC. Data weighting in statistical fisheries stock assessment models. Can. J. Fish. Aquat. Sci. 2011;68:1124-1138. https://doi.org/10.1139/f2011-025.

Free CM, Anderson SC, Hellmers EA et al. Impact of the 2014–2016 marine heatwave on US and Canada West Coast fisheries: Surprises and lessons from key case studies. Fish Fish. 2023;24(4):652-674. https://doi.org/10.1111/faf.12753.

Fulton EA, Smith ADM. Lessons learnt from the comparison of three ecosystem models for Port Philip Bay, Australia. In: Shannon LJ, Cochrane KL, Pillar SC (Eds.), Ecosystem approaches to fisheries in the Southern Benguela, Afr J Mar Sci. 2004;26:219–243. https://doi.org/10.2989/18142320409504059

General Fisheries Commission for the Mediterranean (GFCM). Scientific Advisory Committee on Fisheries (SAC). Report of the Working Group on Stock Assessment of Small Pelagic Species (WGSASP). Rome, Italy, 23 November – 28 November 2015. https://www.fao.org/gfcm/technical-meetings/en/.

General Fisheries Commission for the Mediterranean (GFCM). Scientific Advisor Committee on Fisheries (SAC). Report of the Subregional Committee for the Adriatic Sea (SRC-AS). Online, 17-20 May 2022. https://www.fao.org/gfcm/technical-meetings/detail/en/c/1539830/.

General Fisheries Commission for the Mediterranean (GFCM). Working Group on Stock Assessment of Small Pelagic Species (WGSASP) session on small pelagic species in the Adriatic Sea (GSAs 17–18). Online, 6 May- 8 May 2024. https://www.fao.org/gfcm/technical-meetings/detail/en/c/1696873/.

Giannoulaki M, Iglesias M, Tugores MP et al. Characterizing the potential habitat of European anchovy Engraulis encrasicolus in the Mediterranean Sea, at different life stages. Fish. Oceanogr. 2013; 22: 69–89. https://doi.org/10.1111/fog.12005

Gislason H, Daan N, Rice JC et al. Size, growth, temperature and the natural mortality of marine fish. Fish. Fish. 2010;11(2):149-158. https://doi.org/10.1111/j.1467-2979.2009.00350.x.

Gomez-Campos E, Borrell A, Cardona L et al. Overfishing of small pelagic fishes increases trophic overlap between immature and mature striped dolphins in the Mediterranean Sea. Plos One. 2011; 6(9): e24554. https://doi.org/10.1371/journal.pone.0024554.

Grilli F, Accoroni S, Acri F, et al. Seasonal and Interannual Trends of Oceanographic Parameters over 40 Years in the Northern Adriatic Sea in Relation to Nutrient Loadings Using the EMODnet Chemistry Data Portal. Water. 2020; 12(8): 2280. https://doi.org/10.3390/w12082280.

Gruss A, McKenzie JR, Lindegren M et al. Supporting a stock assessment with spatio-temporal models fitted to fisheries-dependent data. Fish Res. 2023; 262:106649. https://doi.org/10.1016/j.fishres.2023.106649.

Halpern BS, Frazier M, Afflerbach J et al. Recent pace of change in human impact on the world's ocean. Sci Rep. 2019; 9(1):11609. https://doi.org/10.1038/s41598-019-47201-9.

Hattab T, Gucu A, Ventero A, et al. Temperature strongly correlates with regional patterns of body size variation in Mediterranean small pelagic fish species. Mediterranean Marine Science, 2021;22(4):800-811. https://doi.org/10.12681/mms.26525.

Hilborn R. Future directions in ecosystem based fisheries management: a personal perspective. Fish Res. 2011;108(2-3):235-239. https://doi.org/10.1016/j.fishres.2010.12.030.

Hilborn R, Amoroso RO, Anderson CM et al. Effective fisheries management instrumental in improving fish stock status. P Natl A Sci USA. 2020; 117(4):2218-2224. https://doi.org/10.1073/pnas.1909726116

Holsman, KK, Ianelli J, Aydin K et al. A comparison of fisheries biological reference points estimated from temperature-specific multi-species and single-species climate-enhanced stock assessment models. Deep Sea Res. II. 2015. https://doi.org/10.1016/j.dsr2.2015.08.001.

Holsman KK, Haynie AC, Hollowed AB et al. Ecosystem-based fisheries management forestalls climate-driven collapse. Nat Commun. 2020;11:4579. https://doi.org/10.1038/s41467-020-18300-3.

Hsu J, Chang Y-J, Brodziak J et al. On the probable distribution of stock-recruitment resilience of Pacific saury (Cololabis saira) in the Northwest Pacific Ocean. ICES J Mar Sci. 2024:81 (4):748–759. https://doi.org/10.1093/icesjms/fsae030.

Hurtado-Ferro F, Szuwalski CS, Valero JL et al. Looking in the rear-view mirror: bias and retrospective patterns in integrated, age-structured stock assessment models. ICES J Mar Sci. 2015; 72:99–110. https://doi.org/10.1093/icesjms/fsu198.

Hyndman RJ, Koehler AB. Another look at measures of forecast accuracy. Int. J. Forecasting. 2006; 22(4):679–688. https://doi.org/10.1016/j.ijforecast.2006.03.001.

International Council for the Exploration of the Sea (ICES) - áaltic Fisheries Assessment Working Group (WGBFAS). ICES Scientific Report. 2019. Report. https://doi.org/10.17895/ices.pub.5949.

International Council for the Exploration of the Sea (ICES). ICES fisheries management reference points for category 1 and 2 stocks; Technical Guidelines. In Report of the ICES Advisory Committee. ICES Advice 2021a, Section 16.4.3.1. https://doi.org/10.17895/ices.advice.7891.

International Council for the Exploration of the Sea (ICES). Workshop on Data-Limited Stocks of Short-Lived Species (WKDLSSLS3). ICES Scientific Reports. 2021b; 3:86. 60 pp. https://doi.org/10.17895/ices.pub.8145.

Kaniewski D, Marriner N, Cheddadi R et al. Coastal submersions in the north-eastern Adriatic during the last 5200 years. Global Planet. Change. 2021;204:103570. https://doi.org/10.1016/j.gloplacha.2021.103570.

Kapur SM, Ducharme-Barth N, Oshima et al. Good practices, trade-offs, and precautions for model diagnostics in integrated stock assessments. Fish Res. 2025;281:107206. https://doi.org/10.1016/j.fishres.2024.107206.

Karnauskas KB, Zhang L, Emanuel KA. The feedback of cold wakes on tropical cyclones. Geophys Res Lett. 2021;48(7):e2020GL091676. https://doi.org/10.1029/2020GL091676.

Kell LT, Mosqueira I, Grosjean P et al. FLR: an open-source framework for the evaluation and development of management strategies. ICES J Mar Sci. 2007;64 (4):640–646. https://doi.org/10.1093/icesjms/fsm012.

Kell LT, Kimoto A, Kitakado T. Evaluation of the prediction skill of stock assessment using hindcasting. Fish Res. 2016;183:119–127. https://doi.org/10.1016/j.fishres.2016.05.017.

Kuriyama PT, Zwolinski JP, Hill KT et al. Assessment of the Pacific sardine resource in 2020 for US management in 2020-2021. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-SWFSC-628. 2020.

Langseth BJ, Schueller AM, Shertzer KW et al. Management implications of temporally and spatially varying catchability for the Gulf of Mexico menhaden fishery. Fish Res. 2016;181:186–197. https://doi.org/10.1016/j.fishres.2016.04.013.

Leonori I, Ticina V, Giannoulaki M et al. History of hydroacoustic surveys on small pelagic fish species in the European Mediterranean Sea. Mediterr Mar Sci. 2021;22(4):751-768. https://doi.org/10.12681/mms.26001.

Lindegren M, Checkley DM. Temperature dependence of Pacific sardine (Sardinops sagax) recruitment in the California current Ecosystem revisited and revised. Can J Fish Aquat. Sci. 2013;70:245–252. https://doi.org/10.1139/cjfas-2012-0211.

Lotze, H.K., Milewski, I. Two centuries of multiple human impacts and successive changes in a north Atlantic food web. Ecol. Appl. 2004;14(5):1428-1447. https://doi.org/10.1890/03-5027.

Malavolti S, De Felice A, Costantini I et al. Distribution of Engraulis encrasicolus eggs and larvae in relation to coastal oceanographic conditions (the South-western Adriatic Sea case study). Mediterr Mar Sci. 2018;19(1):180-192. http://dx.doi.org/10.12681/mms.14402.

Mandic M, Pestoric B, Markovic O et al. Plankton community of trafficked ports as a baseline reference for Non Indigenous Species arrivals. Case study of the Port of Bar (South Adriatic Sea). Mediterr Mar Sci. 2019;20(4):718-726. http://dx.doi.org/10.12681/mms.19135.

Marine Strategy Framework Directive. MSFD 2008/56/EC of the European Parliament and of the Council of 17 June 2008 establishing a framework for community action in the field of marine environmental policy. Official Journal of the European Union. 2008; 176, 1–7.

Marini M, Burt JH, Campanelli A et al. Seasonal variability and Po River plume influence on biochemical properties along western Adriatic coast. J Geophys Res. 2008;113. https://doi.org/10.1029/2007JC004370.

Marini M, Grilli F. The Role of Nitrogen and Phosphorus in Eutrophication of the Northern Adriatic Sea:History and Future Scenarios. Appl Sci. 2023;13(16):9267. https://doi.org/10.3390/app13169267.

Marshall KN, Koehn LE, Levin PS et al. Inclusion of ecosystem information in US fish stock assessments suggests progress toward ecosystem-based fisheries management. ICES J Mar Sci. 2019;76(1):1–9. https://doi.org/10.1093/icesjms/fsy152.

Martin P, Bahamon N, Sabates A et al. European anchovy (Engraulis encrasicolus) landings and environmental conditions on the Catalan Coast (NW Mediterranean) during 2000–2005. Hydrobiologia 2008, 612:185-199. https://doi.org/10.1007/s10750-008-9482-1.

Maynou F, Sabates A, Salat J. Clues from the recent past to assess recruitment of Mediterranean small pelagic fishes under sea warming scenarios. Clim Change. 2014;126:175–188. http://dx.doi.org/10.1007/s10584-014-1194-0.

MacClatchie S, Goericke R, Auad G. Re-assessment of the stock-recruit and temperature-recruit relationships for Pacific sardine (Sardinops sagax). Can J Fish Aquat. Sci. 2010;67:1782–1790. https://doi.org/10.1139/F10-101.

Mediterranean International Acoustic Surveys (MEDIAS). MEDIAS handbook. Common protocol for the Pan-MEditerranean Acoustic Survey (MEDIAS), April 2024:17 pp https://www.medias-project.eu/index.php/medias-handbook. [Access January 2023].

Methot RD, Wetzel CR. Stock Synthesis: A biological and statistical framework for fish stock assessment and fishery management. Fish Res. 2013;142:86-99. https://doi.org/10.1016/j.fishres.2012.10.012.

Methot, RD, Wetzel CR, Taylor IG et al. Stock Synthesis User Manual Version 3.30.15. U.S. Department of Commerce, NOAA Processed Report NMFS. 2020. https://doi.org/10.25923/5wpn-qt71.

Melnychuk MC, Peterson E, Elliott M et al. Fisheries management impacts on target species status. P Natl A Sci USA. 2017;114(1):178-183. https://doi.org/10.1073/pnas.1609915114.

Micheli F, Halpern BS, Wallbridge S et al. Cumulative Human Impacts on Mediterranean and Black Sea Marine Ecosystems: Assessing Current Pressures and Opportunities. PLoS ONE. 2013;8(12): e79889. https://doi.org/10.1371/journal.pone.0079889.

Mohn R. The retrospective problem in sequential population analysis: An investigation using cod fishery and simulated data. ICES J Mar Sci.1999;56:473–488. https://doi.org/10.1006/jmsc.1999.0481.

Morello EB, Arneri E. Anchovy and Sardine in the Adriatic Sea — An Ecological Review. Oceanogr Mar Biol. 2009;47:209-256. https://doi.org/10.1201/9781420094220.ch5.

Murawski SA, Steele JH, Taylor P et al. Why compare marine ecosystems?. ICES J Mar Sci. 2010;67(1):1-9. https://doi.org/10.1093/icesjms/fsp221.

Myers RAM. When do environment-recruitment correlations work? Rev. Fish Biol Fish. 1998;8:285–305. https://api.semanticscholar.org/CorpusID:44009003.

Myers RAM, Worm B. Extinction, survival or recovery of large predatory fishes. Philos. Trans. R. Soc. Lond. B. Biol. Sci. 2005;360(1453):13-20. https://doi.org/10.1098/rstb.2004.1573.

Navarro E, Caputo L, Marce R et al. Ecological classification of a set of Mediterranean reservoirs applying the EU Water Framework Directive: A reasonable compromise between science and management. Lake Reserv Manage. 2009;25(4):364-376. https://doi.org/10.1080/07438140903238567.

Navarro J, Saez-Liante R, Albo-Puigserver M et al. Feeding strategies and ecological roles of three predatory pelagic fish in the western Mediterranean Sea. Deep Sea Res II. 2017;140:9-17. https://doi.org/10.1016/j.dsr2.2016.06.009.

Nielsen AN Berg CW. Estimation of time-varying selectivity in stock assessments using state-space models. Fish Res. 2014;158:96-101. https://doi.org/10.1016/j.fishres.2014.01.014.

Ortega-Cisneros K, de Moor CL, Cochrane K. Linking the movement of South African sardine and anchovy to environmental variables using a model of intermediate complexity. Fish Res. 2024;275:107001. https://doi.org/10.1016/j.fishres.2024.107001.

Pacific Fishery Management Council (PFMC). Amendment 8 (to the Northern Anchovy Fishery Management Plan) Incorporating a Name Change to: the Coastal Pelagic Species Fishery Management Plan. 1998. https://www.pcouncil.org/fishery-management-plan-and-amendments/. [Access January 2023]

Palermino A, De Felice A, Canduci G, et al. Modeling of the habitat suitability of European sprat (Sprattus sprattus, L.) in the Adriatic Sea under several climate change scenarios. Front. Mar. Sci. 2024;11:1383063. http://dx.doi.org/10.3389/fmars.2024.1383063.

Palomera I, Olivar MP, Salat J et al. Small pelagic fish in the NW Mediterranean Sea: an ecological review. Prog Oceanogr. 2007;74(2-3):377-396. https://doi.org/10.1016/j.pocean.2007.04.012.

Patrick WS, Link JS. Myths that continue to impede progress in ecosystem-based fisheries management. Fisheries. 2015;40(4):155-160. https://doi.org/10.1080/03632415.2015.1024308.

Patterson K. Fisheries for small pelagic species: an empirical approach to management targets. Rev Fish Biol FIsher. 1992;2:321-338. https://doi.org/10.1007/BF00043521.

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

Payne M. FLSAM: An Implementation of the State-Space Assessment Model for FLR. R package version 2.1.1. 2022. https://github.com/flr/FLSAM.

Peck MA, Reglero P, Takahashi M, et al. Life cycle ecophysiology of small pelagic fish and climate-driven changes in populations. Prog. Oceanogr. 2013;116:220–245. http://dx.doi.org/10.1016/j.pocean.2013.05.012.

Penna N, Capellacci S, Ricci F. The influence of the Po River discharge on phytoplankton bloom dynamics along the coastline of Pesaro (Italy) in the Adriatic Sea. Mar Pollut Bull. 2004;38(3-4):321-326. https://doi.org/10.1016/j.marpolbul.2003.08.007.

Pennino MG, Coll M, Albo-Puigserver M et al. Current and Future Influence of Environmental Factors on Small Pelagic Fish Distributions in the Northwestern Mediterranean Sea. Front Mar Sci. 2020;7:622. https://doi.org/10.3389/fmars.2020.00622.

Pikitch EK, Santora C, Babcock EA et al. Ecosystem based fishery management. Science. 2004;305:346–347. https:/doi.org/10.1126/science.109822.

Pikitch EK, Rountos KJ, Essington TE et al. The global contribution of forage fish to marine fisheries and ecosystems. Fish Fish. 2014;15(1):43-64. https://doi.org/10.1111/faf.12004.

Piroddi C, Coll M, Liquete C et al. Historical changes of the Mediterranean Sea ecosystem: modelling the role and impact of primary productivity and fisheries changes over time. Sci. Rep. 2017;7(1):44491. https://doi.org/10.1038/srep44491.

Pitcher TJ, Kalikoski D, Short K et al. An evaluation of progress in implementing ecosystem-based management of fisheries in 33 countries. Mar Policy. 2009;33(2):223-232. https://doi.org/10.1016/j.marpol.2008.06.002.

Punt AE, Butterworth DS, de Moor CL et al. Management strategy evaluation: best practices. Fish Fish. 2016;17(2):303-334. https://doi.org/10.1111/faf.12104.

Punt AE, Dalton MG, Cheng W et al. Evaluating the impact of climate and demographic variation on future prospects for fish stocks: an application for northern rock sole in Alaska. Deep Sea Res II. 2021;189–190. https://doi.org/10.1016/j.dsr2.2021.104951.

Punt AE. Those who fail to learn from history are condemned to repeat it: A perspective on current stock assessment good practices and the consequences of not following them. Fish. Res. 2023;261: 106642. https://doi.org/10.1016/j.fishres.2023.106642.

Quattrocchi F, Mamouridis V, Maynou, F. Occurrence of adult anchovy in Catalonia (NW Mediterranean) in relation to sea surface conditions. Sci. Mar. 2016;80 (457). http://dx.doi.org/10.3989/scimar.04413.24a.

Raicich, F. On the fresh water balance of the Adriatic Sea. J Marine Syst. 1996;9:305–319. https://doi.org/10.1016/S0924-7963(96)00042-5.

Ramirez F, Coll M, Navarro J et al. Spatial congruence between multiple stressors in the Mediterranean Sea may reduce its resilience to climate impacts. Sci Rep 2018;8(1):14871. https://doi.org/10.1038/s41598-018-33237-w.

RECovery of FISHeries historical time series for Mediterranean and Black Sea stock assessment (RECFISH). Framework Contract for the Provision of Scientific Advice for the Mediterranean and the Black Seas, EASME/EMFF/2016/032 Specific Contract Nr. 01. 2019. https://cinea.ec.europa.eu/publications/.

Reum JCP, Blanchard JL, Holsman KK et al. Ensemble projections of future climate change impacts on the Eastern Bering Sea food web using a multispecies size spectrum model. Front Mar Sci. 2020;7:124. https://doi.org/10.3389/fmars.2020.00124.

Revelante N Gilmartin M. The lateral advection of particulate organic matter from the Po delta region during summer stratification, and its implications for the northern Adriatic. Estuar COast Shelf S. 1992;35(2):191-212. https://doi.org/10.1016/S0272-7714(05)80113-1.

Rogers LA, Monnaham CC, Williams K et al. Climate-driven c hang es in the timing of spawning and the availability of walleye pollock (Gadus chalcogrammus) to assessment surveys in the Gulf of Alaska. ICES J Mar Sci. 2024:1–13. https://doi.org/10.1093/icesjms/fsae005.

Sagarese SR, Vaughan NR, Walter III JF, Karnauskas M. Enhancing single-species stock assessments with diverse ecosystem perspectives: a case study for Gulf of Mexico red grouper (Epinephelus morio) and red tides. Can J. Fish. Aquat. Sci. 2021;78:1168-1180. https://doi.org/10.1139/cjfas-2020-0257.

Sani T, Marini M, Campanelli A et al. Evolution of Freshwater Runoff in the Western Adriatic Sea over the Last Century. Environments. 2024;11(1):22. https://doi.org/10.3390/environments11010022.

Santojanni A, Arneri E, Bernardini V et al. Effects of environmental variables on recruitment of anchovy in the Adriatic Sea. Clim Res. 2006;31(2-3):181-193. https://doi.org/10.3354/cr031181.

Scientific, Technical and Economic Committee for Fisheries (STECF) – Small pelagic stocks in the Adriatic Sea. Mediterranean assessments part 1 (STECF-15-14). 2015. Publications Office of the European Union, Luxembourg, EUR 27492 EN, JRC 97707, 52 pp. https://doi.org/10.2788/763217.

Scientific Technical and Economic Committee for Fisheries (STECF) – Stock Assessments in the Adriatic, Ionian and Aegean Seas and Strait of Sicily (STECF-23-12), Mannini A, Ligas A and Kupschus S editor(s), Publications Office of the European Union, Luxembourg, 2023, https://doi.org/10.2760/194583.

Silva MI, Martins R, Sequeria V et al. Struggling with fish age, a comparison of otolith preparation techniques to unravel age and growth of boarfish, Capros aper (Linnaeus, 1758). Nature. 2024;14:20282. https://doi.org/10.1038/s41598-024-71209-5.

Sinovcic G. Anchovy, Engraulis encrasicolus (Linnaeus, 1758): biology, population dynamics and fisheries case study. Acta Adriat, 2000;41(1):1-54.

Smith ADM, Fulton EJ, Hobday AJ et al. Scientific tools to support the practical implementation of ecosystem-based fisheries management. ICES J Mar. Sci. 2007;64:633–639. https://doi.org/10.1093/icesjms/fsm041.

Svedang H, Hornborg S. Selective fishing induces density-dependent growth. Nat Commun. 2014;12:5-4152. https://doi.org/10.1038/ncomms5152.

Szuwalski C, Cheng W, Foy R et al. Climate change and the future productivity and distribution of crab in the Bering Sea. ICES J Mar Sci. 2021;78:502–515. https://doi.org/10.1093/icesjms/fsaa140.

Taylor IG, Doering KL, Johnson KF et al. Beyond visualizing catch-at-age models: Lessons learned from the r4ss package about software to support stock assessments, Fish Res. 2021;239:105924. https://doi.org/10.1016/j.fishres.2021.105924.

Thorson JT, Johnson KF, Methot RD et al. Model-based estimates of effective sample size in stock assessment models using the Dirichlet-multinomial distribution. Fish. Res. 2017;192:84–93. https://doi.org/10.1016/j.fishres.2016.06.005.

Thorson JT, Maureaud AA, Frelat R et al. Identifying direct and indirect associations among traits by merging phylogenetic comparative methods and structural equation models. Methods Ecol Evol. 2023. https://doi.org/10.1111/2041-210X.14076.

Trenkel VM. How to provide scientific advice for ecosystem-based management now. Fish Fish. 2018;19(2):390-398. https://doi.org/10.1111/faf.12263.

Uriarte A, Rico I, Ibaibarriaga L. Technical support towards the development of the assessment of anchovy and sardine in the Adriatic Sea - Intermediate Report. Report confidential delivered to the Food and Agriculture Organization of the United Nations (FAO). 2020;121. https://www.fao.org/gfcm/technical-meetings/detail/en/c/1542569/.

Van Beveren E, Bonhommeau S, Fromentin JM et al. Rapid changes in growth, condition, size and age of small pelagic fish in the Mediterranean. Mar Biol. 2014, 161. 1809-1822. https://doi.org/10.1007/s00227-014-2463-1.

Van Deurs M, Brooks ME, Lindegren M. Biomass limit reference points are sensitive to estimation method, timeseries length and stock development. Fish Fish. 2021;22(1),18-30. https://doi.org/10.1111/faf.12503.

Vilibic I, Sepic J, Zorica B et al. Hydrographic conditions driving sardine and anchovy populations in a land-locked sea. Mediterr Mar Sci. 2016;17:1. http://dx.doi.org/10.12681/mms.1120.

Walline PD. Geostatistical simulations of eastern Bering Sea walleye pollock spatial distributions, to estimate sampling precision. ICES Journal of Marine Science, 2007;64:559-569. https://doi.org/10.1093/icesjms/fsl045.

Walters C, Maguire JJ. Lessons for stock assessment from the northern cod collapse. Rev Fish Biol Fisher. 1996;6(2):125–137. https://doi.org/10.1007/BF00182340.

Wei T, Simko V, Levy M et al. Package ‘corrplot’. Statistician. 2017;56:316–324. https://github.com/taiyun/corrplot.

Whitehouse GA, Aydin KY, Hollowed AB et al. Bottom-up impacts of forecasted climate change on the eastern Bering Sea food web. Front Mar Sci. 2021;8, 624301. https://doi.org/10.3389/fmars.2021.624301.

Winker H, Carvalho F, Kapur M. JABBA: Just Another Bayesian Biomass Assessment. Fish Res. 2018;204:275–288. https://doi.org/10.1016/j.fishres.2018.03.010.

Zavatarelli M, Raicich F, Bregant D et al. Climatological biogeochemical characteristic of the Adriatic Sea. J Marine Syst. 1998;18:227-263. https://doi.org/10.1016/S0924-7963(98)00014-1.

Zorica B, Vilibic I, Kec VC et al. Environmental conditions conducive to anchovy (Engraulis encrasicolus) spawning in the Adriatic Sea. Fish Oceanogr. 2013;22(1):32-40. https://doi.org/10.1111/fog.12002.

CHAPTER 3

~ Stock Synthesis vs SPiCT: a preliminary study on European sardine (*Sardina pilchardus*) including an environmental perspective

3.1 Introduction

Sardine of the Adriatic Sea has long been central to small pelagic fisheries in the Mediterranean Sea, supporting fishery's economy of coastal communities in both Italy and Croatia (FAO, 2023). Together with anchovy, it dominates the pelagic ecosystem of the basin, displaying strong interannual fluctuations driven by recruitment variability, environmental conditions and fishing pressure (Cingolani and Santojanni, 2003; Carpi et al., 2015; Pennino et al., 2020; Palermino et al., 2024).

Systematic stock assessments of this species began in early 2000s, with VPA and cohort-based models applied to Italian national fishery data. These early efforts, which were carried out under the FAO-GFCM framework, provided the first biomass and fishing mortality estimates, highlighting the high sensitivity to assumptions about recruitment and discards (Santojanni et al., 2005).

The launch of the FAO Regional Project AdriaMed in 1999, which was aimed in promoting scientific cooperation among the Adriatic countries, strengthened regional cooperation through harmonized sampling protocols and otoliths' age-reading, and favoring joint acoustic surveys for small pelagics, whereas other activities were implemented for the demersal stocks. Thanks to the support by the FAO AdriaMed project, the stock assessment of small pelagics improved substantially over the years. Up to 2013, assessments were carried out separately for GSA 17 and GSA 18, whereas since 2014 onward, in light of genetic and fisheries evidence of a single shared stock, sardine in GSAs 17–18 has been assessed jointly (GFCM WGSASP, 2014; Čikeš-Keč et al., 2024).

In 2014, the first sardine benchmark represented an important milestone: different stock assessment models were tested and compared, defining the FLSAM, the State-space Assessment Model (SAM) (Nielsen and Berg 2014; Payne, 2022) wrapped into the Fisheries Library in R (Kell et al. 2007), the best assessment methodology for this stock. Also, for the first time the estimated reference points have been fixed to be used for future evaluations and until the next benchmark (Carpi et al., 2014). During the following evaluations, several issues and shortcomings related to input data and assumptions, biological parameters, and issues related to the configuration of assessment models were identified. Consequently, a new benchmark has begun in 2018, but due to a number of uncertainties in the assessment mainly related to issues in the catch-at-age, this meeting ended providing only a quantitative assessment performed using a4a (Čikeš-Keč et al., 2021). The last and finalized sardine benchmark occurred in 2023, when the Stochastic Production Model in Continuous Time (SPiCT; Pedersen and Berg, 2016) model was introduced as a pragmatic alternative, requiring only catch data and biomass indices (Čikeš-Keč et al., 2024).

SPiCT is a state–space biomass dynamic model that extends classical surplus production theory by modelling aggregated biomass growth under density dependence and including both process and observation error (Pedersen and Berg, 2017). It assumes that population dynamics can be represented without explicit age or size structure and that biomass and fishing mortality evolve as latent states in continuous time. These assumptions make SPiCT especially suitable for data-limited or data-moderate stocks, where only catches and abundance indices are available, but age or length data are scarce or uncertain. In the Adriatic Sea, for example, SPiCT has been applied to small pelagic species, such as sprat and horse mackerel, providing MSY-based reference points in situations where conventional age-structured assessments were not feasible (Angelini et al., 2021). One of the main strengths of the model is its ability to handle time series with missing years, except for catch, and still produce reliable indicators such as B/B_{MSY} and F/F_{MSY}. These indicators are expressed as relative ratios, which makes them straightforward to interpret in a management context (e.g., values above or below 1 immediately signal overfishing or stock depletion). Comparative studies have shown that SPiCT often produces more precautionary results than simpler surplus production approaches and has therefore been endorsed by ICES for data-limited assessments (Bouch et al., 2021).

Despite these advantages, SPiCT also faces limitations. The model can be sensitive to the specification of priors and requires sufficient data contrast to reliably estimate key parameters such as intrinsic growth rate and carrying capacity (Cousido-Rocha et al., 2022). Its simplified structure does not capture recruitment lags, selectivity changes, or environmental drivers, which may reduce realism in some contexts. However, recent simulation studies and methodological reviews have shown that many of these weaknesses can be mitigated by following good practices, such as ensuring sufficient time series length (≥15 years), careful preparation of catch and index data, robust CPUE standardization and systematic diagnostic checks (convergence, residuals, retrospective and hindcasting analyses), which all substantially increase the reliability of SPiCT outputs (Kokkalis et al., 2024). Nevertheless, in the case of sardines in the Adriatic Sea, these recommendations are difficult to apply in practice. The available survey indexes show inconsistencies across the time series, and unresolved issues in ageing protocols have limited the reliability of biological inputs. As acknowledged during the 2023 sardine benchmark, there is still a need for improved age data, better integration of survey indices, and possibly the adoption of more complex models such as Stock Synthesis in future assessments (GFCM WGSASP, 2025). In this context, SS has been identified by experts as a potential alternative for the assessment of small pelagic stocks, owing to its flexibility and its capacity to partition data by fleet and area, apply alternative weighting schemes, and incorporate time-varying biological parameters.

In this chapter, it will be described the stock assessment model for the European sardine in the Adriatic Sea using the SS framework. This model follows the same approach already applied to anchovy (Chapter 2), and it is used also to study how environmental variability can influence sardine population dynamics. In particular, the analysis looks at changes in growth parameters (L_{min}, L_{inf}, κ) and survey catchability (q). For this purpose, the model includes time-varying biological parameters linked to important environmental covariates, such as sea surface temperature (SST), chlorophyll-a (chl-a), salinity (so) and Po River runoff (riv). These variables were tested with different time lags and spatial scales in GAM, as explained in Chapter 1.

A second objective of the chapter is to compare SS outputs with the official sardine assessment developed by SPiCT (Čikeš Keč et al., 2025), thus evaluating differences between the two approaches and to explore whether a more flexible integrated, age-structured model can provide a detailed understanding of sardine dynamics and more robust scientific support for the management of this stock in the Adriatic Sea.

3.2 Model structure

3.2.1 Input data and settings

The stock assessment model for the Adriatic sardine was developed within the Stock Synthesis v3.30 framework, integrating commercial information, survey and environmental data collected between 2004 and 2022. The input dataset included complete catch time series, length- and age-composition data, acoustic biomass indices, biological parameters and environmental covariates. Italian and Croatian data were mainly obtained from the Data Collection Framework (DCF), including also the acoustic surveys MEDIAS and PELMON (Fig. 1).

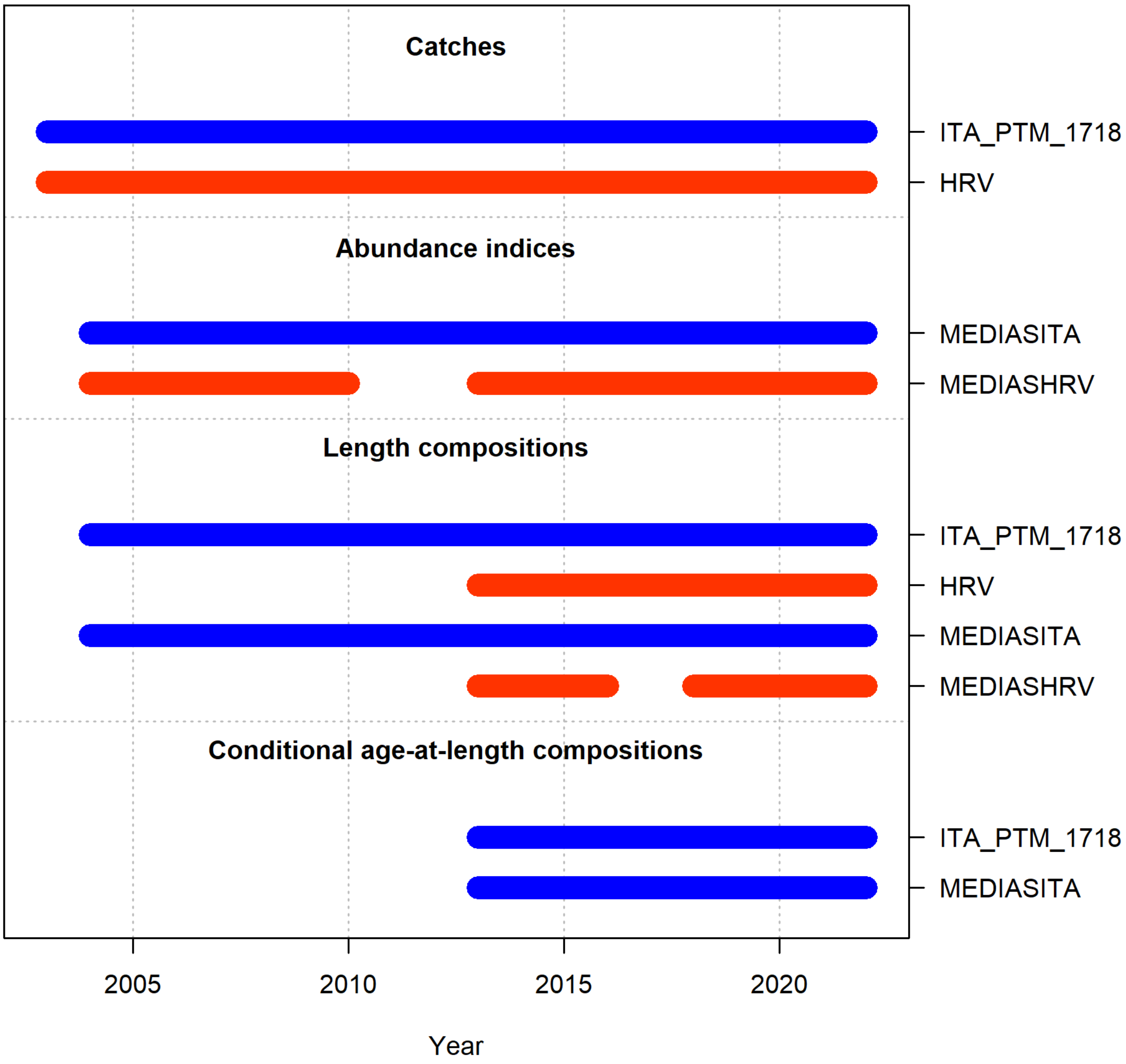

Figure 1 Data input for the sardine SS model.

3.2.2.1 Commercial data

Commercial data, covered the period 2004–2022 for Italy (ITA) and 2013–2022 for Croatia (HRV), were obtained from official DG-MARE sources. However, since SS requires complete catch series for all fleets across the entire time frame, Croatian catch prior 2013 were integrating from the RECFISH (2019) database, ensuring continuity of the total catch series across fleets and years. Comparisons across gears and GSAs were conducted to define the fleet structure used in the model. The Italian purse seine fishery (ITA_PS1718), together with the fisheries of Slovenia (SVN), Albania (ALB) and Montenegro (MNE), have a negligible impact on the sardine stock, contributing only marginal to total landings; therefore, the corresponding data were excluded from the analysis. Finally, sardines in Croatia are only fished by purse seine (Fig. 2).

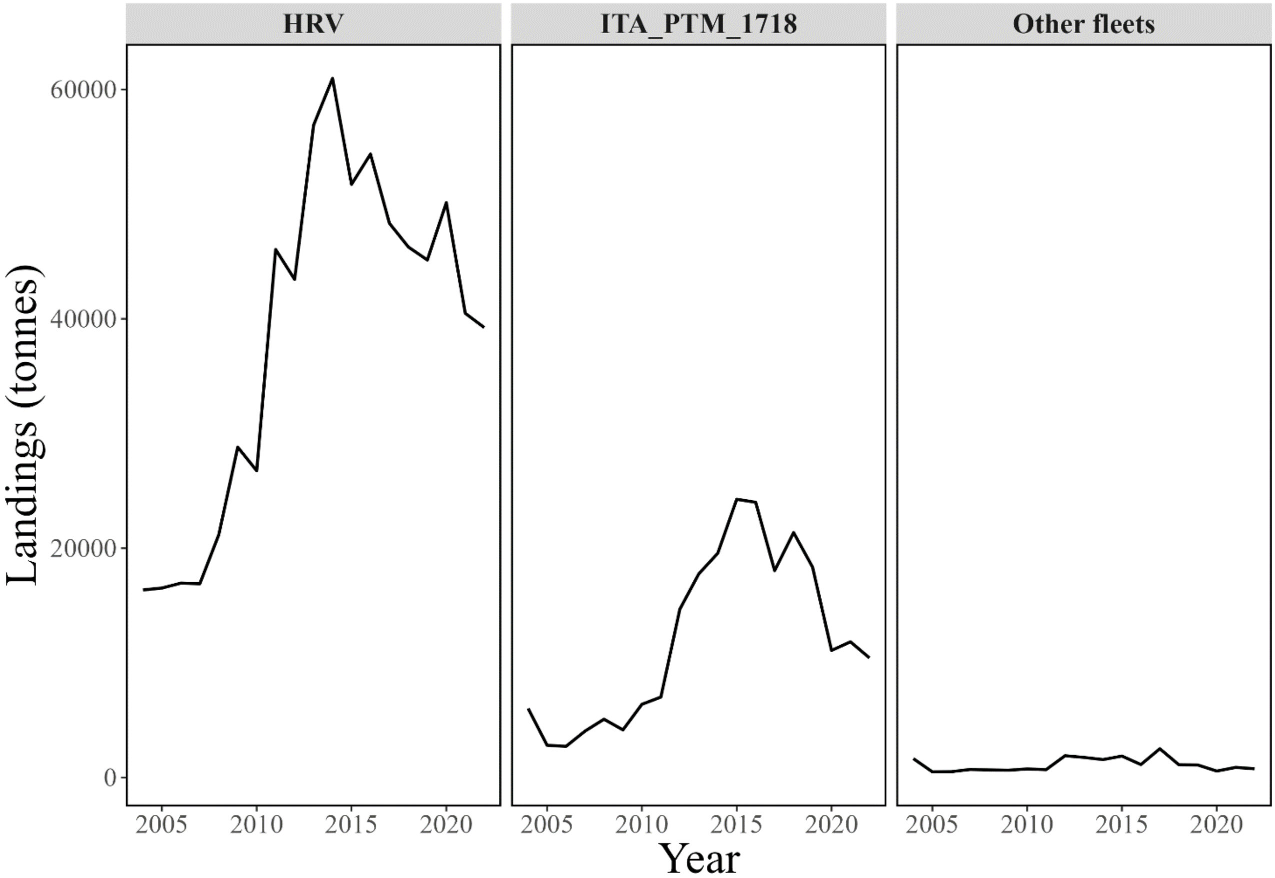

Figure 2 Sardine landings by fleet: Croatia purse seine (HRV), Italian pelagic trawl (ITA_PTM_1718) and the aggregate group ITA_PS1718, MNE, SVN and ALB.

Commercial Length Frequency Distributions (LFDs) and Age-Length Keys (ALKs) are included in the model split into two commercial fleets: Italian pelagic trawl (ITAPTM_1718) and Croatian purse seine (HRV). Regarding ALKs, only those derived from the Italian commercial data were used, as they have been provided on a semiannual basis since 2002. Although these ALKs are technically pooled between GSA 17 and GSA 18, the contribution from GSA 18 is very limited and does not compromise their representativeness for GSA 17, which is the focus area of this model. During the GFCM WGSASP benchmark meetings (2023), a thorough review of sardine ageing procedures revealed that the ageing protocol adopted in 2015—which followed the same scheme used for anchovy—was not biologically appropriate for sardine. The anchovy protocol divides the year into two semesters based on its summer spawning season (May–July), while sardine spawns in winter (December–March). Applying the same semester-based system caused systematic biases in age assignment, most notably the artificial disappearance of age-0 fish from Italian MEDIAS data after 2015. This occurred because individuals of 7–8 cm caught in the first semester were automatically classified as age 1, even though they had not yet formed their first winter ring. To address this issue, the ageing criteria were revised in 2023 under the GFCM benchmark process. The new protocol specifies that age 1 should only be assigned when the first annulus (winter ring) is clearly visible, and that the date of spawning must be accounted for when determining growth increments. Following these recommendations, the Italian ALKs were retrospectively recalculated on an annual basis back to 2013 to ensure internal consistency and alignment with the corrected biological interpretation. Conversely, the ALKs used to convert length data before 2013 were obtained from pooled 2013–2015 data across GSA 17 and 18, also on a semiannual basis, and are not considered biologically valid for use in SS.

3.2.2.2 Survey data

Acoustic surveys targeting small pelagic fish in the Adriatic Sea have been regularly conducted since the late 1970s and currently operate under the MEDIAS framework (Leonori et al., 2021), covering both GSA 17 and GSA 18. Four main surveys were carried out: West GSA 17, West GSA 18, East GSA 17 and East GSA 18. The Italian surveys in the western Adriatic Sea (West GSA 17 and 18) have evolved from the historical ECHOADRI program (1976–2008) to the MEDIAS framework since 2009 and they are performed by the Italian acoustic team. West GSA 17 survey cover the Northern and Central Adriatic Sea, initially performed in September (2004–2014) and since 2015 shifted to June–July to better match the seasonal distribution of pelagic species. West GSA 18 survey, focusing on the southern Adriatic Sea, is also carried out in summer, with some temporal gaps (notably in 2020 and 2023). The eastern Adriatic area was initially monitored through the Croatian national program PELMON (2003-2010), which since 2013 was included in the MEDIAS framework. The survey in the eastern side of GSA 18 is run by the Italian MEDIAS team together with colleagues from

Montenegro and Albania; it was conducted jointly with Montenegro and Albania since 2008, except for some years (2009, 2017-2022). The eastern surveys are generally performed in late summer (August–September for East GSA 17 and July–August for East GSA 18), though coverage has been irregular in some years due to logistical constraints and the COVID-19 pandemic. All surveys adopt standardized MEDIAS protocols (MEDIAS handbook, 2024), with parallel transects perpendicular to the coastline, SIMRAD EK60 or EK80 echosounders, and biological sampling through pelagic trawl hauls for length, age and maturity data. The resulting indices provide estimates of sardine abundance and biomass across the Adriatic Sea, with GSA 17 representing the core area of stock distribution and biomass concentration. For this reason, and given the consistency and continuity of the available data, only two fleets were considered in the SS model development, corresponding to the Italian MEDIAS carried out in GSA 17 only and the Croatian acoustic survey (hereafter MEDIASITA and MEDIASHRV, respectively, Fig. 3).

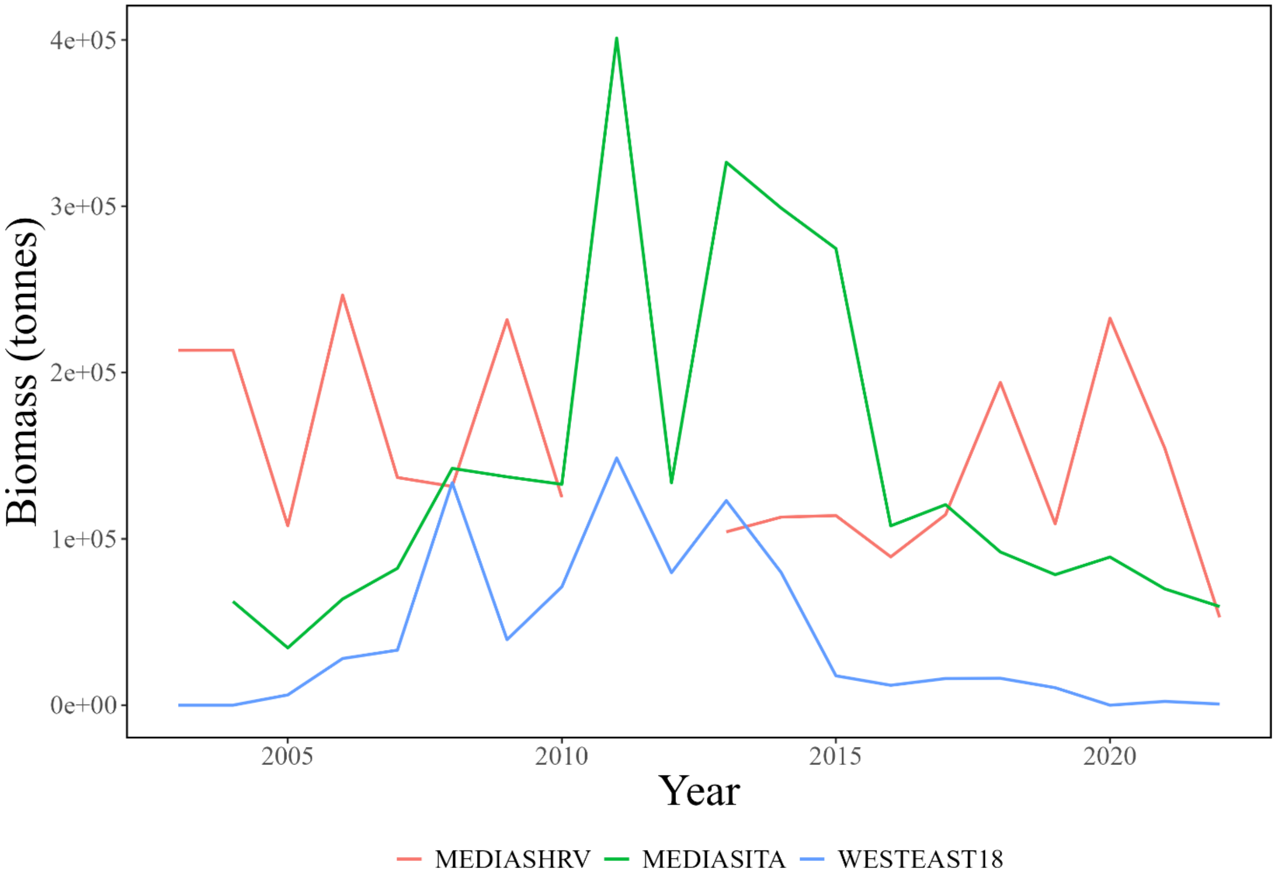

Figure 3 Biomass index for PELMON data from 2003 to 2010 and Croatian MEDIAS data from 2013 to 2022 (MEDIASHRV, red line); Italian MEDIAS data from 2004 to 2022 (MEDIASITA, green line) and aggregated MEDIAS index for Western and Eastern GSA 18 (blue line). Data source: Stock Assessment Form (SAF) 2023 (Čikeš Keč et al., 2023).

Since 2015 the Italian MEDIAS survey has been shifted from September to June/July. However, this change did not significantly affect the age distribution of sardines (Fig. 4) and thus this survey was retained as a single fleet.

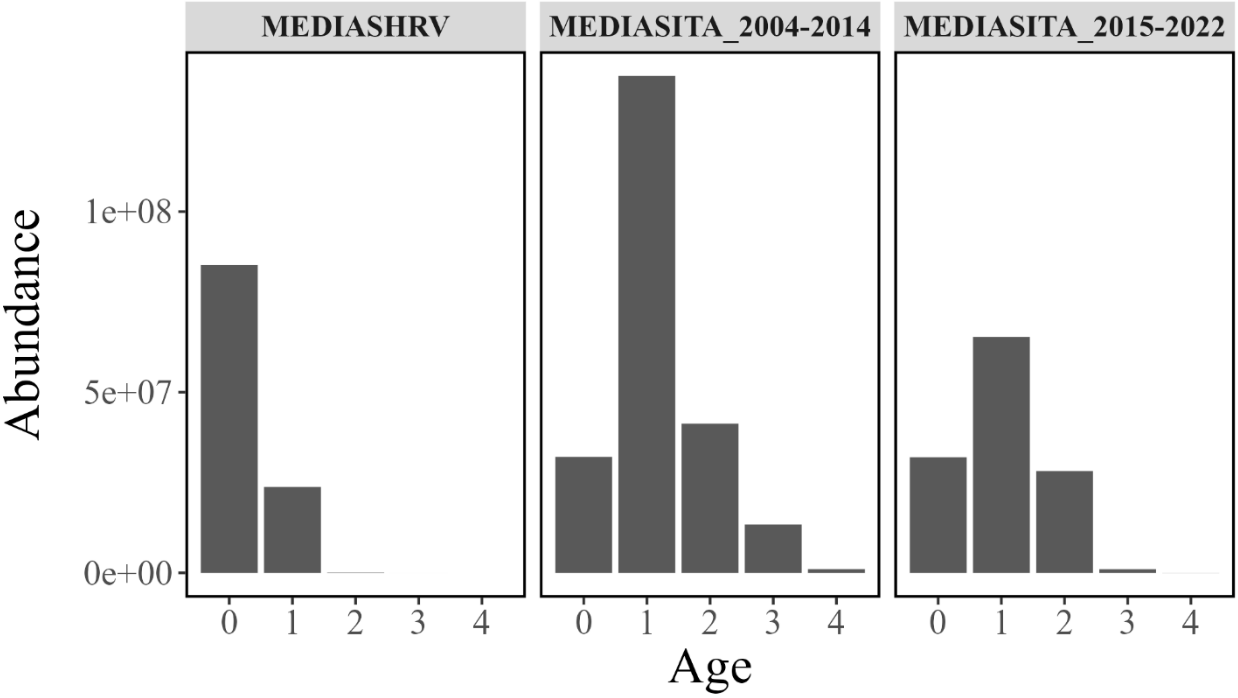

Figure 4 Mean age composition of sardine derived from acoustic surveys. The Croatian survey (MEDIASHRV, left panel) shows a dominance of age-0 individuals, while the Italian survey is presented separately for 2004–2014 (MEDIASITA_2004-2014, middle panel) and 2015–2022 (MEDIASITA_2015-2022, right panel), due to the change in survey period from September to June since 2015. In both cases, age-1 individuals are a consistent bulk of sardine abundance in the Italian waters.

LFDs data for Italian and Croatian survey were retrieved from DG-MARE database. About ALKs, only the age data provided by the Italian team has been used and the same specifications described for commercial ageing data were applied, with the only exception that some age data were missing for certain length classes, so imputed data were used to fill the gap, introducing potential inconstancies. Thus, no imputed data were used in this model.

3.2.2.3 Environmental data

Following the anchovy setup, we evaluated Po River discharge, sea surface temperature (SST), chlorophyll-a (Chl-a) and salinity as environmental links in the sardine SS model. For each covariate, we tested both annual means and season-specific values after standardization (Z-scores) to ensure comparability across the timeseries. Because sardine spawns in winter, we aligned the covariate timing with key phases of reproduction and early life history between winter, spring and fall seasons.

To link each environmental covariate to the growth parameters (L_{min}, L_{inf}, and κ) and to catchability (q) in the sardine SS model, the following equation has been used:

$$P_y = P_{base} e^{\alpha E_y} \quad (1)$$

where, P_y is the parameter value for year y, P_{base} is the base value of the parameter, α is the "link" parameter, and E_y is the environmental index value for year y (Z-scored). Consistent with evidence from the anchovy analyses—where environmental effects on natural mortality at age 1 (M_1) and on recruitment regime were less influential than effects on growth and catchability—we did not test environmental links for M_1 or recruitment regime in sardine. Spatial differences (tested using Mann-Whitney U test), temporal trends (Mann-Kendall test applied), Spearman's correlation plot (implemented using '*corrplot*' R package, Wei and Simko, 2021) and relative tests results are shown in the Supplementary Material in Chapter 2.

3.2.2 Model setting

The Stock Synthesis model for the Adriatic sardine was configured as a single-area, single-sex, length and age-structured population dynamics model operating on an annual time step. Spawning was assumed to occur in January, consistent with the species' known reproductive timing in the Adriatic Sea while settlement was fixed in February (Morello and Arneri, 2009). Table 1 lists the parameters used to estimate the population dynamic of sardine. The pre-specified values for parameters related to maturity, natural mortality and recruitment were derived from biological data summarized in the official Stock Assessment Forms (SAFs) and literature reviews specific to sardine in the Adriatic Sea and globally (e.g. Morello and Arneri, 2009; Kuriyama et al., 2020; Čikeš Keč et al., 2021; Thorson et al., 2023). The stock-recruitment relationship was assumed to be of the Beverton-Holt form, with the steepness parameter set based on the meta-analysis by Thorson et al. (2023) and the extent of variation in recruitment about the stock-recruitment relationship set based on the results of assessments for other sardine stocks (e.g. Kuriyama et al..2020). Parameters related to growth, survey catchability, and fishery/survey selectivity were estimated, with fishery and survey selectivity assumed to be asymptotic (logistic) functions of size. Size-at-inflection for both the ITA PTM 1718 (pelagic trawl) fishery and the MEDIASITA survey were assumed to be time-varying for the years after 2009, when the DCF program began. On the other hand, for MEDIASHRV no time-varying option has been applied, in accordance with ICES (2021) guidelines.

Table 1 Stock Synthesis parameters. The column “Pre-specified / Initial Value (s)” lists the values of the parameters that are either pre-specified or serve as initial values for parameters to be estimated within the model.

Parameter	Treatment	Pre-specified / Initial Value (s)	Source
Biological parameters			
Natural mortality (yr^{-1})	Pre-specified for ages 0, 1, 2	1.06, 0.83, 0.69	Gislason et al., 2010
Growth			
Von Bertalaffy function			
L_{min} (cm)	Estimated	7.5	
L_{inf} (cm)	Estimated	19.4	Čikeš Keč et al., 2021
□ (yr^{-1})	Estimated	0.38	Čikeš Keč et al., 2021
CV young	Estimated	0.4	
CV old	Estimated	0.25	
Maturity			
Size-at-50%-maturity	Pre-specified	9	Sinovčić, 2000a
Maturity slope	Pre-specified	-1.5	Thorson et al., 2023
Recruitment			
$\ln R_0$	Estimated	9.97	
B-H steepness (h)	Pre-specified	0.78	Thorson et al., 2023
σ_R	Pre-specified	0.5	Kuriyama et al., 2020
Recruitment deviations	Estimated	2005 - 2021	
Catchability			
MEDIASITA	Estimated	1.2	
MEDIASHRV	Estimated	1.3	
Fishery mortality	Estimated (Hybrid F method)		
Fishery selectivity			
ITA PTM 1718			

Size-at-inflection (cm)	Estimated	13 (time varying 2009-2022)	
Selectivity width (cm)	Estimated	0.9	
HRV			
Size-at-inflection (cm)	Estimated	12	
Selectivity width (cm)	Estimated	0.8	
Survey selectivity			
MEDIASITA			
Size-at-inflection (cm)	Estimated	14 (time-varying 2009 – 2022)	
Selectivity width (cm)	Estimated	1.5	
MEDIASHRV			
Size-at-inflection (cm)	Estimated	12	
Selectivity width (cm)	Estimated	3.6	

Effective sample sizes (Francis, 2011; Thorson et al., 2017) for survey length data were set as the number of hauls, whereas for the commercial length data to the number of sampling events and for the survey age-composition data to the number of otoliths read. Biomass index geostatistical CVs (Walline, 2007; Leonori et al., 2021) for both surveys were only available for the time interval 2018–2022. The average value of 0.066 for MEDIASITA was assumed appropriate for the rest of the time series; while for the MEDIASHRV was assumed to be 0.1 as pragmatic approximation. This choice acknowledges the relatively uncertain quality of the early datasets (PELMON, 2004–2010) and the heterogeneous reporting during the initial MEDIAS years (2013–2017). The standard errors of the logs (SELs) for the landings data were set to 0.1 for the entire timeseries both fleets and initial catch. Model runs were implemented using the '*r4ss*' package (Taylor et al., 2021). Diagnostic checks included residual patterns, retrospective analyses and predictive skills were performed using the '*ss3diags*' package (Carvalho et al., 2021). The adjusted MASE values for hindcast cross evaluation (HCxvar) were used as indicators of model predictive skill, following the approach suggested by Kapur et al. (2025). Sensitivity analysis were carried out through the '*SS-DL continuum tool*' (Cope, 2020) to observed eventual differences in management quantities lead by environmental linkages.

3.3 Environmental Effects

A total of 48 single-variable models were evaluated, each linking an environmental covariate to a biological parameter (L_{min}, L_{inf}, κ) and catchability (q). Thirty-three models were selected, by the application of the Two-Tailed Z-test that has estimated link parameters (α in Equations 1) to assess their significance (p-values < 0.05). The Akaike Information Criterion (AIC) was used to rank models and shown in Table 2.

Table 2 Ranked comparison of the single-variable models. The null model had an objective function value of 2065.43 and an ΔAIC of 165.34. ΔObj is the difference in the objective function value at its global minimum (negative log-likelihood plus summed logs of penalty terms) between the null and each alternative model. Link values that are significant at $p < 0.05$ are underlined.

Model No	ΔAIC	Enviromental variable	Parameter	ΔObj	Link value	Model No	ΔAIC	Enviromental variable	Parameter	ΔObj	Link value
1	0.00	chlfall	L_{min}	83.67	$\underline{0.0212}$	9	160.14	chlwin	L_{min}	3.60	$\underline{0.0062}$
13	35.58	sofall	L_{min}	65.88	$\underline{0.0180}$	25	160.38	sstfall	L_{min}	3.48	-0.0046
17	63.88	sospr	L_{min}	51.73	$\underline{0.0187}$	23	160.58	sowin	κ	3.38	-0.0169
45	70.98	rivwin	L_{min}	48.18	$\underline{-0.0157}$	3	160.60	chlfall	κ	3.37	0.0174
41	73.52	rivspr	L_{min}	46.91	$\underline{-0.0176}$	36	162.48	sstwin	q	2.43	$\underline{-0.0096}$
16	88.82	sofall	q	39.26	$\underline{0.0343}$	31	162.66	sstspr	κ	2.34	0.0100
21	109.06	sowin	L_{min}	29.14	$\underline{0.0176}$	47	162.84	rivwin	κ	2.25	0.0058
20	120.78	sospr	q	23.28	$\underline{0.0274}$	34	162.96	sstwin	L_{inf}	2.19	$\underline{-0.0028}$
4	130.68	chlfall	q	18.33	$\underline{0.0211}$	37	163.12	rivfall	L_{min}	2.11	0.0013
24	133.56	sowin	q	16.89	$\underline{0.0284}$	43	163.30	rivspr	κ	2.02	0.0022
33	147.48	sstwin	L_{min}	9.93	$\underline{-0.0107}$	46	163.46	rivwin	L_{inf}	1.94	$\underline{0.0001}$
35	149.24	sstwin	κ	9.05	$\underline{-0.0330}$	42	163.52	rivspr	L_{inf}	1.91	$\underline{0.0001}$
12	151.34	chlwin	q	8.00	$\underline{0.0277}$	38	163.56	rivfall	L_{inf}	1.89	0.0002
10	151.84	chlwin	L_{inf}	7.75	$\underline{0.0227}$	39	163.58	rivfall	κ	1.88	0.0010
32	154.56	sstspr	q	6.39	$\underline{-0.0117}$	7	163.58	chlspr	κ	1.88	-0.0012
27	156.48	sstfall	κ	5.43	$\underline{-0.0311}$	26	163.62	sstfall	L_{inf}	1.86	$\underline{0.0000}$
29	156.74	sstspr	L_{min}	5.30	$\underline{-0.0050}$	14	163.64	sofall	L_{inf}	1.85	$\underline{0.0000}$
22	158.14	sowin	L_{inf}	4.60	$\underline{-0.0095}$	15	163.64	sofall	κ	1.85	$\underline{-0.0005}$
18	158.20	sospr	L_{inf}	4.57	$\underline{-0.0073}$	2	163.64	chlfall	L_{inf}	1.85	$\underline{0.0000}$
19	158.46	sospr	κ	4.44	$\underline{-0.0176}$	6	163.64	chlspr	L_{inf}	1.85	0.0001
11	159.34	chlwin	κ	4.00	$\underline{0.0322}$	28	165.28	sstfall	q	1.03	0.0060
5	159.46	chlspr	L_{min}	3.94	$\underline{-0.0039}$	44	165.68	rivspr	q	0.83	-0.0054
40	159.64	rivfall	q	3.85	$\underline{-0.0094}$	8	166.32	chlspr	q	0.51	0.0037
30	159.74	sstspr	L_{inf}	3.80	$\underline{0.0081}$	48	167.28	rivwin	q	0.03	0.0010

The best-fit models (AIC <80) reveal strong links between sardine L_{min} and environmental variability, with autumn chlorophyll-a (model 1) emerging as the main driver. Increased post-summer productivity likely enhances energy transfer through the planktonic food web, allowing juveniles to attain larger minimum sizes. Several studies have reported that sardine condition, growth and recruitment are positively associated with higher chlorophyll-a concentrations, which reflect food availability at the base of the food chain (Brosset et al., 2017; Pennino et al., 2020; Fernández-Corredor et al., 2021). Unlike anchovy, which may be constrained by visual feeding limitations at high chlorophyll levels, sardines' filter-feeding capacity allows it to exploit a broader spectrum of prey, making increased productivity largely beneficial (Palomera et al., 2007).

Salinity in autumn (model 13) and spring (model 17) also showed positive associations with sardine L_{min}, highlighting the importance of hydrographic stability for reproduction and early growth. Previous studies demonstrated that sardine spawning habitats are strongly conditioned by salinity, with stable regimes supporting buoyancy of eggs, larval survival and ultimately recruitment (Vilibic et al., 2016; Zorica et al., 2013).

By contrast, winter (model 45) and spring (model 41) river runoff displayed negative effects on L_{min}, pointing to the disruptive role of excessive freshwater inflow. In the Adriatic Sea, the Po River has long been recognized as a major driver of sardine dynamics, with moderate discharges enhancing frontal mixing and productivity, but excessive runoff reducing salinity, altering prey availability and lowering habitat suitability (Bonanno et al., 2016).

Long-term observations of the examined environmental variability (see Fig. S2 in Chapter 2) confirm that chl-a and salinity in the Adriatic Sea have been gradually rising, a trend that likely contributes to more favorable conditions for sardine, partially buffering the negative influence of warming (Fernández-Corredor et al., 2021). On the other hand, river runoff shows a declining trend, less marked in winter than in spring, but this change may have alleviated some of the negative impacts of freshwater input on sardine early growth.

These modeled associations resonate with empirical outputs from the base model, where L_{min} stabilized or slightly increased in recent years after a period of decline (Fig. 5).

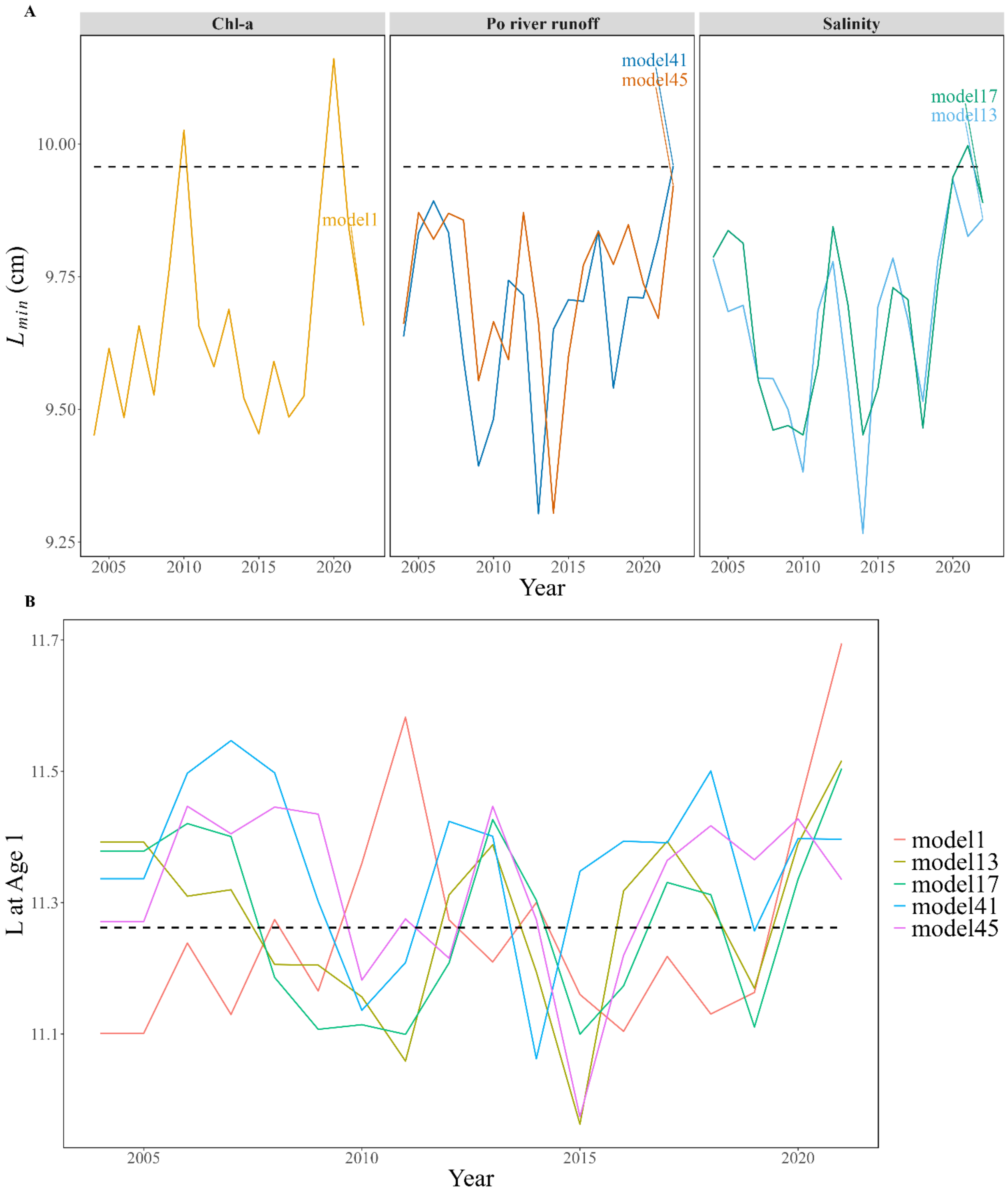

Figure 5 Time-trajectories of *Lmin* when linked to chl-a (panel A, left), Po river runoff (panel A, center) and salinity (panel A, right). Panel B shows the time-trajectory of mean length-at-age 1 in the best models.

The coherence between environmental trends — with chlorophyll-a and salinity all showing upward trajectories, while river runoff is declining — and the increasing of sardine size structure suggests that the recent halt in the decline of L_{min} might be environmentally mediated. Similar environmentally driven stabilizations in sardine growth and condition have been documented across the Mediterranean Sea, where the species is widely regarded as a sensitive bio-indicator of hydrographic and trophic variability (Katara et al., 2011; Caballero-Huertas et al., 2022).

Taken together, these findings indicate that the stabilization of sardine L_{min} in the Adriatic Sea cannot be attributed solely to changes in exploitation, but rather reflects a synergy between hydrographic forcing and trophic conditions. This fact is also confirmed from the comparison between the estimated manangement quatities (Fig.6), where, except for some deviation in 2010 or earlier, the introduction of environmental variables doesn’t change the estimated exploitation.

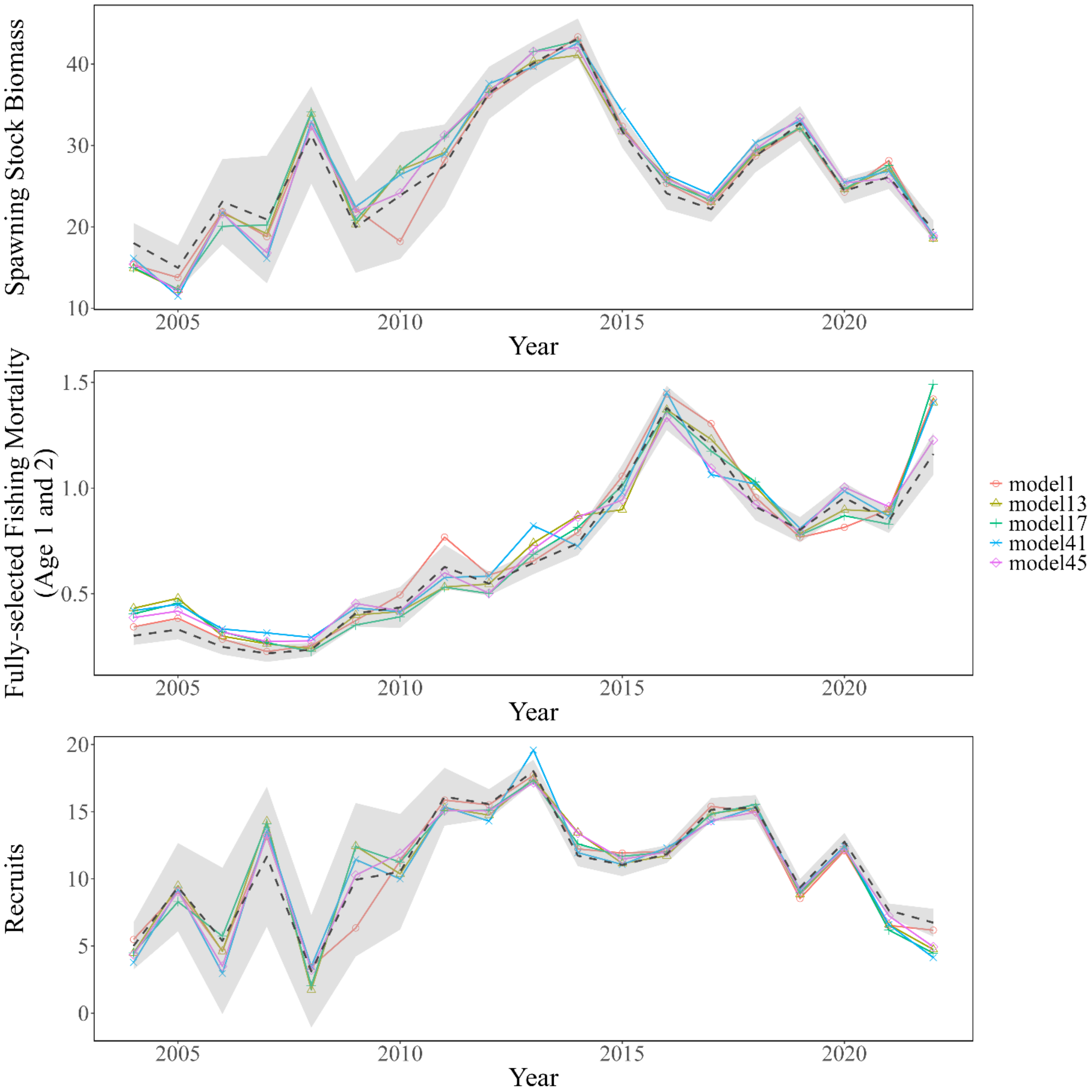

Figure 6 Spawning biomass (top panel), fully-selected fishing mortality (central panel) and recruitment (bottom panel) for the null model (dashed black line) and the five best single variable models. The gray shaded area is the asymptotic 95% confidence interval (CI) for the null model.

This aligns with the broader understanding that small pelagic population dynamics are shaped by environmental variability interacting with fishing pressure, a perspective central to ecosystem-based fisheries management in the face of climate change (Checkley et al., 2009; Coll et al., 2019).

3.3.1 Trade-off considering other diagnostics

In the present analysis on sardine, the integration of model diagnostics revealed insights that go beyond the AIC-driven approach previously applied to anchovy (Chapter 2). In the anchovy case study, model selection was essentially guided by the relative improvement in likelihood and the significance of estimated environmental linkages, in line with a pragmatic objective of identifying which covariates could most plausibly affect growth dynamics. This strategy offered a clear and operational selection criterion, but it also entailed limitations: potentially robust models with diagnostic strength but poorer AIC ranking were excluded a priori, restricting the exploration of alternative hypotheses.

The sardine exercise demonstrates how diagnostic evaluation can reframe the interpretation of environmental effects. Several models with suboptimal AIC nonetheless showed diagnostic strengths (Tab. 3).

Table 3 Summary of runs test, the residual standard deviation, Mohn's rho based on retrospective analysis, retrospective forecasts and the HCxval model diagnostic for the AIC <100 models. P-values in red are significant (p-value < 0.05) and indicate a non-random distribution of residuals. Five peels were applied (2017 – 2021) for the retrospective and forecast analyses. Green cells in residualStdDev, Retrospective and HCxval diagnostics mean better values than model 1.

Diagnostic (statistic)	IndexType	model1	model13	model16	model17	model41	model45
Runs test (p-value)	MEDIASITA_cpue	0.983	0.983	0.996	0.938	0.983	0.938
Runs test (p-value)	MEDIASHRV_cpue	0.230	0.230	0.898	0.261	0.752	0.924
Runs test (p-value)	ITA_PTM_1718_len	0.334	0.136	0.025	0.334	0.334	0.270
Runs test (p-value)	HRV_len	0.090	0.004	0.090	0.090	0.090	0.004
Runs test (p-value)	MEDIASITA_len	0.136	0.411	0.449	0.121	0.411	0.121
Runs test (p-value)	MEDIASHRV_len	0.374	0.374	0.374	0.374	0.374	0.374
Residual StdDev (RMSE)	MEDIASITA_cpue	13.4	14.1	11.7	13.7	14.0	13.9
Residual StdDev (RMSE)	MEDIASHRV_cpue	36.4	35.2	32.0	37.4	35.8	38
Residual StdDev (RMSE)	ITA_PTM_1718_len	2.2	2.2	2.5	2.2	2.3	2.2
Residual StdDev (RMSE)	HRV_len	2.9	2.7	2.6	2.6	2.7	2.5
Residual StdDev (RMSE)	MEDIASITA_len	3.9	3.9	3.8	3.7	3.7	4.1
Residual StdDev (RMSE)	MEDIASHRV_len	8.8	8.9	8.4	8.3	8.8	8.4
Retrospective analysis (Mohn's Rho)	SSB	0.256	0.172	0.171	0.203	0.340	0.453
Retrospective forecasts (Forecast bias)	SSB	1.317	1.225	1.248	1.291	1.748	1.899
Retrospective analysis (Mohn's Rho)	F	-0.179	-0.192	-0.158	-0.193	-0.155	-0.210
Retrospective forecasts (Forecast bias)	F	-0.395	-0.408	-0.363	-0.450	-0.389	-0.380
HCxval (MASE)	MEDIASITA_cpue	4.579	4.709	4.618	4.833	4.729	4.258
HCxval (MASE)	MEDIASHRV_cpue	1.768	1.833	1.959	1.850	1.928	1.924
HCxval (MASE)	ITA_PTM_1718_len	0.280	0.288	0.274	0.271	0.290	0.292
HCxval (MASE)	HRV_len	0.223	0.254	0.249	0.287	0.315	0.295
HCxval (MASE)	MEDIASITA_len	0.117	0.128	0.150	0.133	0.113	0.143
HCxval (MASE)	MEDIASHRV_len	0.906	0.944	0.853	0.880	0.968	0.939

For example, although model 17 ranks lower than model 1, it shows superior consistency and prediction skill, as indicated by retrospective and hindcast diagnostics. Another relevant case is model 16, which minimized retrospective bias and errors, but failed to meet the residual independence criterion, thus questioning its overall plausibility. However, this model emphasizes the role of catchability as a time-varying parameter, reintroducing a dimension already highlighted in the anchovy assessment (Chapter 2), where salinity affected distribution and fishing vulnerability. This resonates with findings from Maury et al. (2001), who demonstrated how hydrological factors such as salinity can modulate both habitat preferences and catchability. In this sense, the sardine diagnostics corroborate that catchability remains a parameter of ecological and management relevance, especially when distributional shifts influence the vulnerability of the stock to the fleets that monitor or exploit it.

These observations echo the trade-offs described by Kapur et al. (2025), who caution that no single diagnostic should dominate the evaluation of assessment models, and that conflicting signals are inevitable when multiple criteria are applied. Punt et al. (2024) further emphasize the necessity of capturing structural and process uncertainty when incorporating environmental drivers, given the risk that relationships may be temporally unstable or sensitive to scale. The sardine results exemplify this problem: models linking L_{min} to catchability respond well to certain diagnostics but not all, underlining the structural uncertainty inherent in environmental linkages. Crone et al. (2019) similarly noted that environmental covariates can improve explanatory power without necessarily improving all aspects of fit or management performance.

Taken together, these findings indicate that L_{min} is a particularly sensitive parameter to environmental forcing across both species. Importantly, the diagnostic analysis shows that models with different trade-offs—model 1 excelling in likelihood fit, model 17 in predictive diagnostics and model 16 in retrospective stability—should not be dismissed but rather considered jointly. Retaining multiple models that capture complementary aspects of fit and ecological plausibility aligns with the ensemble-oriented perspective advocated by Kapur et al. (2025) and Punt et al. (2024), ensuring that management advice reflects a balanced assessment of both statistical performance and ecological interpretability.

3.4 Output comparison

3.4.1 SPiCT configuration

SPiCT represents the accepted stock assessment model for the sardine stock since 2022. During the benchmark occurred between 2022 and 2023, the SPiCT model was tested under eight alternative scenarios, differing mainly in the time series of catches and biomass indices, as well as in the treatment of priors. Among these, Scenario 8 was selected as the benchmark model because it fulfilled all diagnostic requirements, providing the most robust fit (Čikeš Keč et al., 2023). The model was fitted using two main data sources: catches and a survey-based biomass index. The catch data consisted of official landings from 2000 onwards, reported annually in weight and aggregated across all national fleets exploiting the stock, namely purse seiners and pelagic trawlers operating in Italy, Croatia, Slovenia, Montenegro and Albania.

Survey information was derived from the four acoustic surveys carried out in the Adriatic Sea since 2003. However, some issues have been detected in the exploration of these indexes (Čikeš Keč et al., 2023), among them is aknowledged the Italian survey timing shift from September to June in 2015. A direct comparison of indices highlighted a lack of consistency between the two series (Fig 4.2.1.4), suggesting the use of two survey indices without combining them.

These discrepancies were not only methodological but also biological. Analyses of length composition and spatial distribution indicated that the Croatian survey effectively sampled two distinct zones, an inner and an outer area: while results from the outer area were broadly consistent with the Italian survey, the inclusion of the inner area generated biomass signals that diverged strongly from the Adriatic-wide pattern. In this context, the application of a joint index modelled with JARA (Just Another Red-list Assessment; Winker et al., 2020) provided a practical solution by integrating heterogeneous data sources into a single biomass trajectory, explicitly accounting for differences in coverage and uncertainty, and reducing noise in the input series (Čikeš Keč et al., 2023). The resulting composite index represented the main signal of relative biomass change for the stock, though its construction inevitably entailed a loss of spatial detail and dependence on methodological assumptions.

For SPiCT, the parameterization described in the official benchmark assessment (Čikeš Keč et al., 2023) is adopted to fit a Schaefer production function. Table 4 showed each parameter value, assuming a log-normal observation and process errors.

Table 4 Model parameters and priors used in the SPiCT benchmark assessment of Adriatic sardine. R prior refers to the intrinsic growth rate of the population. Catch error represents the assumed variability in reported catches. F error is the prior on fishing mortality variability. Process error accounts for the stochastic fluctuations in population dynamics. Observation error describes the variance associated with the biomass index observations. Bounding q is the prior on the catchability coefficient linking stock biomass to the survey index. BK_{frac} is the ratio between initial biomass (B) and carrying capacity K and it was left without a prior in the benchmark model, in order to be estimated among the different scenarios.

Parameter	**Mean**	**Variance**
R prior	0.4583	0.2554
Catch error	0.05	0.3
F error	4	0.5
Process error	0.2	0.5
Observation error	0.3	0.5
Bounding q	1	0.5
BK_{frac}	no prior	

3.4.2 SS vs SPiCT

In the present assessment, SS was applied to the Adriatic sardine stock and the results were compared with the official outputs obtained from SPiCT, leading to consistent and complementary results. The SS model, based on detailed length- and age-structured information, reconstructed stock dynamics showing a progressive decline in spawning biomass over the last decade, with fishing mortality generally increasing and overcoming the corresponding reference value in the last decade. Similarly, SPiCT results confirmed a pronounced biomass decline since 2011, with the lowest values in 2022, and fishing mortality consistently above sustainable thresholds.

Direct comparison of absolute reference points between SS and SPiCT is not straightforward, as the two models rely on different data inputs and methodologies. Accordingly, biomass and fishery mortality trajectories were compared only in relative terms, by scaling each estimate to its own target reference point (B/B_{tgt} and F/F_{tgt}). In the case of SPiCT, target reference points are only MSY-based (B_{MSY} and F_{MSY}), reflecting the simpler surplus production formulation of the model. In contrast, the integrated age-structured framework implemented in SS provides both MSY and non-MSY reference points. Although the use of the same type of target reference point would be recommended for comparative purposes, MSY-based reference points may result in a different—and potentially misleading—representation of stock status when applied to age-structured frameworks (Brooks et al., 2009). Thus, B_{40} and F_{40} were applied as target reference points for SS. These latter proxies are widely applied in official stock assessments and are generally regarded as robust indicators of sustainable exploitation within age-structured models (Mace, 1994; Legault and Brooks, 2013; ICES, 2017). An additional structural difference between the two approaches concerns biomass definitions. SPiCT provides estimates of total biomass (B) only, whereas SS estimates both total stock biomass (TSB) and spawning stock biomass (SSB). However, reference points in SS are defined exclusively on SSB. Consequently, the comparison shown in Fig. 7 reflects a necessary trade-off between maintaining internal consistency within each modelling framework and achieving comparability across two fundamentally different assessment methodologies.

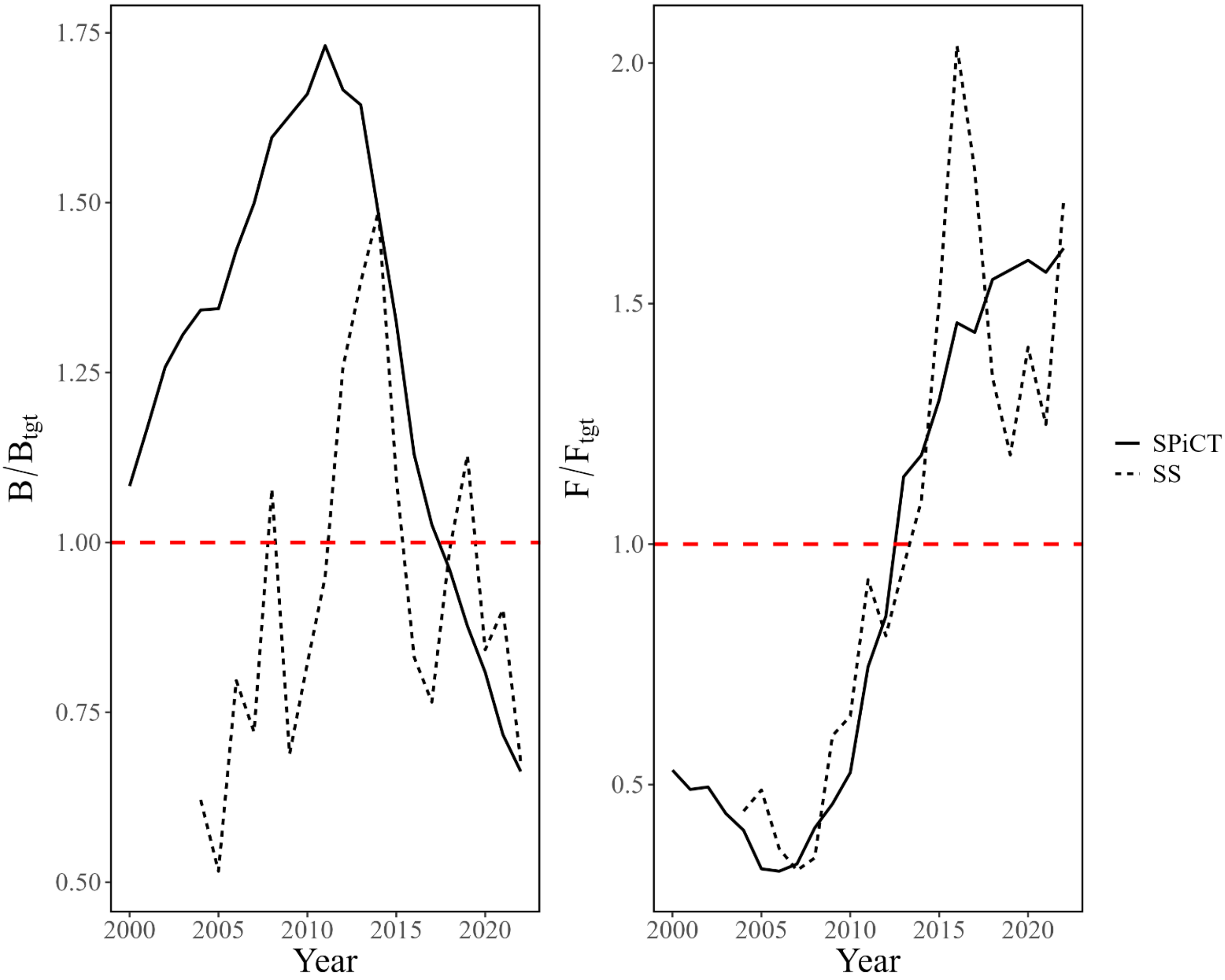

Figure 7 Comparison of the ratio between the estimated sardine stock biomass (B) and its corresponding reference point (B_{tgt}) (left panel) and the ratio between the estimated fishing mortality (F) and its reference point (F_{tgt}) (right panel) from SPiCT (solid line) and SS (dashed line).

A direct comparison of the reference points estimated by the two models (Table 5) reveals a strong convergence in relative terms, with both SS and SPiCT indicating fishing mortality above F_{tgt} and biomass below B_{tgt}. However, SS appears to provide a more pessimistic outlook, estimating lower current biomass relative to B_{tgt} and higher fishing mortality relative to F_{tgt} compared to SPiCT. This suggests that the integrated assessment may be more sensitive to the recent decline in recruitment and to the fleet-specific selectivity patterns, whereas the production model smooths variability over time. Taken together, the convergence in trends but divergence in magnitude highlights both the robustness of the overall diagnosis and the value of applying multiple modeling frameworks to the same stock.

Table 5 Reference point estimated by the two models.

Parameter	**SS**	**SPiCT**
Fishing mortality		
F_{cur}	1.16	0.32
F_{tgt}	0.68	0.218
F/F_{tgt}	1.71	1.47
Biomass		
B_{cur}	19616.7	153052
B_{tgt}	28992.2	231897
B/B_{tgt}	0.68	0.66

3.5 Conclusions

The comparative analysis between SS and SPiCT for the assessment of Adriatic sardine highlighted an overall convergence in the general trends, though with important differences in point estimates. Both models confirmed a decline in biomass starting from 2011 and fishing mortality levels consistently above sustainability thresholds, indicating a condition of overexploitation of the stock.

However, SPiCT, consistent with its simpler structure as a surplus production model, provided smoother and relatively less pessimistic estimates. This reflects its design as a data-limited tool that treats the stock as undifferentiated biomass, relying mainly on catch and abundance indices and equilibrium assumptions (Cousido-Rocha et al., 2022). By contrast, SS delivered a more severe diagnosis, reflecting its ability to integrate detailed information on age, length, fleet-specific selectivity and recruitment variability, as well as its capacity to incorporate conditional age-at-length data (Methot and Wetzel, 2013; Dichmont et al., 2016; Huynh et al., 2020).

These differences underscore the strengths and limitations of each approach: SPiCT offers parsimony and applicability when data are scarce (Bentley, 2015; Chrysafi and Kuparinen, 2016), while SS provides greater sensitivity and resolution, particularly important in fisheries such as the Adriatic sardine, where environmental drivers and fleet dynamics play a central role. Integrated, age- and length-structured models like SS have been shown to better account for growth variability, selectivity, and the so-called Rosa Lee effect, thereby reducing bias in biomass and mortality estimates (Taylor and Methot, 2013; McGarvey et al., 2024).

An additional advantage of SS is its potential to incorporate environmental covariates (e.g., SST, chlorophyll-a, salinity, Po River discharge) into the estimation of biological parameters and recruitment dynamics, offering a pathway toward ecosystem-informed stock assessments (Punt et al., 2020). However, in practice this capability remains relatively constrained compared with the flexibility of semi-parametric frameworks such as GAMs. As discussed in Chapter 1 and further explored in Section 4.4, both SS and GAM analyses revealed modest but coherent effects of environmental variability on fish length, though the type and timing of the selected covariates differed. In SS, weak associations emerged between growth parameters and variables, whereas GAMs captured comparable low-magnitude influences on mean length but with greater ability to represent non-linear and spatially varying responses.

As highlighted by Crone et al. (2019), integrated stock assessment models like SS can be viewed as structured analogues to GAMs, where environmental forcing is introduced either as structure—affecting the spawner–recruit relationship or growth— or as data, providing an index of recruitment. These approaches allow hypothesis testing within a mechanistic population-dynamics framework, but they are statistically more rigid and sensitive to assumptions such as bias correction and the partitioning of recruitment variability. Consequently, while SS offers a robust platform for evaluating population dynamics hypotheses, its capacity to detect complex, time-varying, or non-linear responses remains limited relative to the more flexible GAM framework.

Overall, the convergence of evidence from both modeling approaches suggests that environmental drivers play a secondary yet detectable role in shaping size dynamics, acting alongside fishing pressure and density-dependent processes. Nevertheless, this potential must be approached with caution: the relationships between environmental drivers and fish population dynamics are often uncertain, context-dependent, and prone to temporal breakdown, which can undermine their predictive power in a management setting if used uncritically (Planque et al., 2019; Punt et al.; 2024).

References

Angelini, S., Armelloni, E. N., Costantini, I., De Felice, A., Isajlović, I., Leonori, I., Manfredi, C., Masnadi, F., Scarcella, G., Tičina, V. (2021). Understanding the Dynamics of Ancillary Pelagic Species in the Adriatic Sea. Front. Mar. Sci. 8, 1–16. https://doi.org/10.3389/fmars.2021.728948.

Bentley, N. (2011) Data and time poverty in fishery estimation: potential approaches and solutions. ICES J. Mar. Sci. 72(1): 186-193. https://doi.org/10.1093/icesjms/fsu023.

Bonanno, A., Barra, M., Basilone, G., Genovese, S., Rumolo, P., Goncharov, S., Popov, S., Buongiorno, B., Nardelli, D., Iudicone, D., Procaccini, G., Aronica, S., Patti, B., Giacalone, G., Ferreri, R., Fontana, I., Tranchida, G., Mangano, S., Pulizzi, M., Garagano., A., Di Maria, A., Mazzola, S. (2016). Environmental processes driving anchovy and sardine distribution in a highly variable environment: the role of the coastal structure and riverine input. Fish Oceanogr. 25:471–490. http://dx.doi.org/10.1111/fog.12166.

Brooks, E.N., Powers, J.E., Corés, E. (2009) Analytical reference points for age-structured models: application to data-poor fisheries. ICES J. Mar. Sci. 67(1): 165-175. https://doi.org/10.1093/icesjms/fsp225.

Brosset, P., Fromentin, J.M., Van Beveren, E., Lloret, J., Marques, V., Basilone, G., Bonanno, A., Carpi, P., Donato, F., Čikeš Keč, V., De Felice, A., Ferreri, R., Gašparević, D., Giráldez, A., Gücü, A., Iglesias, M., Leonori, I., Palomera, I., Somarakis, S., Tičina, V., Torres, P., Ventero, A., Zorica, B., Ménard, F., Saraux, C. (2017). Spatio-temporal patterns and environmental controls of small pelagic fish body condition from contrasted Mediterranean areas. Prog. Oceanogr. 151:149–162. https://doi.org/10.1016/j.pocean.2016.12.002.

Caballero-Huertas, M., Vargas-Yánez, M., Frigola-Tepe, X., Viñas, J., Muñoz, M. (2022). Unravelling the drivers of variaiblity in body condition and reproduction of the European sardine along the Atlantic-Mediterranean transition. Mar. Environ. Res. 179:1056697. https://doi.org/10.1016/j.marenvres.2022.105697.

Carpi P., Angelini S., Belardinelli A., Biagiotti I., Campanella F., Canduci G., Cingolani N., Čikeš Keč V., Colella S., Croci C., De Felice A., Donato F., Leonori I., Martinelli M., Malavolti S., Modic T., Panfili M., Pengal P., Santojanni A., Ticina V., Vasapollo C., Zorica B., Arneri E. (2014). Sardine (Sardina pilchardus) – GSA 17 – Northern Adriatic Sea. Report of the Working Group on Stock Assessment of Small Pelagic Species (WGSASP). Bar, Montenegro, 28 January – 1 February 2014.

Carpi, P., Martinelli, M., Belardinelli, A., Russo, A., Arneri, E., Coluccelli, A., Sanotjanni, A. (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(6): 521–532. https://doi.org/10.1111/fog.12126.

Carvalho, F., Winker. H., Courtney, D., Kapur, M., Kell, L., Cardinale, M., Schirripa, M., Kitakado, T, Yemane, D., Pnier, K.R., Maunder, M.N., Taylor, I.G., Wetzel, C.R., Doering, K., Johnson, K.F., Methot, R.D. (2021). A cookbook for using model diagnostics in integrated stock assessments. Fish. Res. 240 :105959. https://doi.org/10.1016/j.fishres.2021.105959.

Checkley, D., Alheit, J., Oozeki, Y., Roy, C. (2009). Climate change and small pelagic fish. Cambridge University Press.

Čikeš Keč, V., Angelini S., Arneri E., Belardinelli A., Biagiotti I., Boscolo Palo G., Bratina P., Brunel T., Canduci G., Cacciamani R., Calì F., Colella S., Costantini I., De Felice A., Domenichetti F., Donato F., Gašparević D., Hintzen N., Ibaibarraga L., Juretic T., Kule M., Leonori I., Malavolti S., Martinelli M., Milone N., Modic T., Panfili M., Pesic A., Palluqi A., Santojanni A., Tesauro C., Tičina V. (2021). Stock Assessment Form Small Pelagics—Sardine—GSA 17 & 18. https://www.fao.org/gfcm/data/safs/en.

Čikeš Keč, V., Angelini, S., Biagiotti, I., Bratina, P., Caserta, V., Costantini, I., De Felice, A., Juretic, T., Kule, M., Leonori, I., Pesic, A., Santojanni, A., Joksimovic, A., Ramirez, J.G., Winker, H. (2023). Stock Assessment Form Small Pelagics—Sardine—GSA 17 & 18. https://www.fao.org/gfcm/data/safs/en.

Čikeš Keč, V., Angelini, S., Biagiotti, I., Bratina, P., De Felice, A., Juretic, T., Kule, M., Leonori, I., Pesic, A., Santojanni, A., Giannoulaki, M., Ramirez, J.G. (2024). Stock Assessment Form Small Pelagics—Sardine—GSA 17 & 18. https://www.fao.org/gfcm/data/safs/en.

Čikeš Keč, V., Angelini, S., Biagiotti, I., Bratina, P., De Felice, A., Juretic, T., et al., (2025). STock Assessment Results Small Pelagics—Sardine—GSA 17 & 18. https://gfcm.sharepoint.com/EG/_layouts/15/download.aspx?share=EeuQwV4VnWFAjhqZB6bKx50Bw5qo2sfJpt8DPzw9NJ5OQg.

Cingolani, N., Santojanni, A. (2003). Manual of the Recorder. AdriaMed Training Course on Data Collection and Biological Sampling System on Small Pelagics. AdriaMed Occasional Papers. No.6 (Rev.1). GCP/RER/010/ITA/OP-06-Rev.1, Termoli, 2003: 53 pp

Coll, M., Albo-Puigserver, M., Navarro, J., Palomera, I., Dambacher, J.M. (2019). Who is to blame? Plausible pressures on small pelagic fish population changes in the northwestern Mediterranean Sea. Mar. Ecol. Prog. Ser. 617-618:277-294. https://doi.org/10.3354/meps12591.

Cope, J.M. (2020). The stock synthesis data-limited tool (SS-DL tool). https://github.com/shcaba/SS-DL-tool#the-stock-synthesis-data-limited-tool-ss-dl-tool.

Cousido-Rocha, M., Pennino, M.G., Izquiredo, F., Paz, A., Lojo, D., Tifoura, A., Zanni, Y.M., Cerviño, S. (2022). Surplus production models: a practival review of recent approaches. Rev. Fish. Biol. Fisheries. 32:1085-1102. https://doi.org/10.1007/s11160-022-09731-w.

Crone, P.R., Maunder, M.N., Lee, H., Piner, K.R. (2019). Good practices for including environmental data to inform spawner-recruit dynamics in integrated stock assessments: Small pelagic species case study. Fish. Res. 217: 122-132. https://doi.org/10.1016/j.fishres.2018.12.026.

Chrysafi, A., Kuparinen, A. (2016). Assessing abundance of population with limited data: Lessons learned from data-poor fisheries stock assessment. Can. J. Mar. Sci. 24(1): 25-38. https://doi.org/10.1139/er-2015-0044.

Dichmont, C.M., Punt, A.E., Dowling, N., De Oliveira, J.A., Little, L.R., Sporcic, M., Fulton, E., Gorton, R., Klaer, N., Haddon, M., Smith, D. C. (2016). Is risk consistent across tier-based harvest control rule management systems? A comparison of four case-studies. Fish. Fish. 17(3), 731-747. https://doi.org/10.1111/faf.12142.

Fernández-Corredor, E., Albo-Puigserver, M., Pennino, M.G., Bellido, J.M., 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. https://doi.org/10.1016/j.rsma.2020.101606.

FAO (2023). The State of Mediterranean and Black Sea Fisheries 2023 – Special edition. General Fisheries Commission for the Mediterranean. Rome. https://doi.org/10.4060/cc8888en.

Francis, R.C. (2011). Data weighting in statistical fisheries stock assessment models. Can. J. Fish. Aquat. Sci. 68 :1124–38. https://doi.org/10.1139/f2011-025.

GFCM WGSASP (2014). Stock Assessment Form Small Pelagics—Sardine—GSA 17 & 18. https://www.fao.org/gfcm/data/safs/en.

GFCM WGSASP (2023). Data preparation meetings for a benchmark assessment of sardine in the Adriatic Sea. Session I, Online 1.-12 July; Session II, Rome 23-26 October; Session III, Online, 13-17 November. Report. https://www.fao.org/gfcm/technical-meetings/detail/en/c/1707867/.

GFCM WGSASP (2025). Session on small pelagic species in the Adriatic Sea. Online, 5-9 May. Report.

Gislason, H., Daan, N., Rice, J.C., Pope, J.G. (2010). Size, growth, temperature and the natural mortality of marine fish. Fish. Fish. 11(2):149-158. https://doi.org/10.1111/j.1467-2979.2009.00350.x.

Huynh, Q. C., Hordyk, A.R., Forrest, R.E., Porch, C.E., Anderson, S.C., Carruthers, T.R. (2020). The interim management procedure approach for assessed stocks: responsive management advice and lower assessment frequency. Fish. Fish. 21(3), 663-679. https://doi.org/10.1111/faf.12453.

ICES (2017). Techinical Guides – ICES fisheries management reference points for category 1 and 2 stocks. ICES Techincal Guidelines. Report. https://doi.org/10.17895/ices.pub.3036.

ICES (2021). ICES fish- eries management reference points for category 1 and 2 stocks. ICES Tecnical Guidelines Report. https://doi.org/10.17895/ices.advice.7891.

Kapur, M.S., Ducharme-Barth, N., Oshima, M., Carvalho, F. (2025). Good practices, trade-offs, and precautions for model diagnostics in integrated stock assessments. Fish. Res. 281: 1072206. https://doi.org/10.1016/j.fishres.2024.107206.

Katara, I., Pierce, G.J., Illian, J., Scott, B.E. (2011). Environmental drivers of the anchovy/sardine complex in the Eastern Mediterranean. Hydrobiologia 670, 49–65. https://doi.org/10.1007/s10750-011-0693-5.

Kell, L.T., Mosquiera I., Grosjean, P., Fromentin, J-M., Garcia, D., Hillary, R., Jardim, E., Mardle, S., Pastoors, M.A., Poos, J.J., Scott, F., Scott, R.D. (2007). FLR: an open-source framework for the evaluation and development of management strategies. ICES J. Mar, Sci. 64(4): 640-646. https://doi.org/10.1093/icesjms/fsm012.

Kokkalis, A., Berg, C. W., Kapur, M.S., Winker, H., Jacobsen, N.S., Taylor, M.H., Ichinokawa, M., Miyagawa, M., Medeiros-Leal, W., Nielsen, J.R., Mildenberger, T.K. (2024). Good practices for Surplus Production Models. Fish. Res. 275: 107010. https://doi.org/10.1016/j.fishres.2024.107010.

Kuriyama, P.T., Zwolinski, J.P., Hill, K.T., Crone, P.R. (2020). Assessment of the Pacific sardine resource in 2020 for US management in 2020-2021. U.S. Department of Commerce, NOAA Technical Memorandum NMFS-SWFSC-628.

Legault, C.M., Brooks, E.N. (2013). Can Stock-Recruitment Points determine which Spawning Potential Ration is the best proxy for Maximum Sustainable Yielad reference points? ICES J. Mar. Sci. 70: 1075-1080. https://doi.org/10.1093/icesjms/fst105.

Leonori, I., Tičina, V., Giannoulaki, M., Hattab, T., Iglesias, M., Bonanno, A., Costantini, I., Canduci, G., Machias, A., Ventero, A., Somarakis, S., Tsagarakis, K., Bogner, D., Barra, M., Basilone, G., Genovese, S., Juretić, T., Gašparević, D., De Felice, A. (2021). History of hydroacoustic surveys of small pelagic fish species in the European Mediterranean Sea. Mediterranean Marine Science, 22(4), 751–768. https://doi.org/10.12681/mms.26001.

Mace, P.M. (1994). Relationship between common biological reference points used as thresholds and targets of fisheries management strategies. Can. J. Fish. Aquat. Sci. 51: 110-122. https://doi.org/10.1139/f94-013.

Maury, O., Gascuel, D., Marsac, F., Fonteneau, A., Rosa, A.L.D. (2001). Hierarchical interpretation of nonlinear relationships linking yellowfin tuna (Thunnus albacares) distribution to the environment in the Atlantic Ocean. Canadian Journal of Fisheries and Aquatic Sciences, 58(3), 458-469. https://doi.org/10.1139/f00-261.

McGarvey, R., Methot, R.D., Punt, A.E., Matthews, J.M., Taylor, I.G., Feenstra, J.E., Doering, K. (2024). Performance gains from incorporating dynamic numbers by length-within-age in fishery assessment models. Fisheries Research, 276, 107039. https://doi.org/10.1016/j.fishres.2024.107039.

MEDIAS handbook (2024). Common protocol for the Pan-MEditerranean Acoustic Survey (MEDIAS). 17. https://www.medias-project.eu/index.php/medias-handbook. [Access January 2023]

Methot, R.D., Wetzel, C.R. (2013). Stock Synthesis: A biological and statistical framework for fish stock assessment and fishery management. Fish Res. 142:86-99. https://doi.org/10.1016/j.fishres.2012.10.012.

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

Nielsen, A., Berg, C.W. (2014). Estimatiuon of time-varying selectivity in stock assessment using state-space models. Fish. Res. 158:96-101. https://doi.org/10.1016/j.fishres.2014.01.014.

Palermino A, De Felice A, Canduci G, Biagiotti, I., Costantini, I., Centurelli, M., Menicucci, S., Gašparević, D., Tičina, V., Leonori, I. (2024). Modeling of the habitat suitability of European sprat (Sprattus sprattus, L.) in the Adriatic Sea under several climate change scenarios. Front. Mar. Sci. 11:1383063. http://dx.doi.org/10.3389/fmars.2024.1383063.

Palomera, I., Olivar, M.P., Salat, J., Sabatés, A., Coll, M., García, A., Morales-Nin, B. (2007). Small pelagic fish in the NW Mediterranean Sea: An ecological review. Prog. Oceanogr. 74(2–3): 377–396. https://doi.org/10.1016/j.pocean.2007.04.012.

Payne M. (2022). FLSAM: An Implementation of the State-Space Assessment Model for FLR. R package version 2.1.1. https://github.com /flr/FLSAM.Pedersen, M.W., Berg, C.W. (2016). A stochastic surplus production model in continuous time. Fish. Fish. 18(2): 226-243. https://doi.org/10.1111/faf.12174.

Pennino, M.G., Coll, M., Albo-Puigserver, M., Fernández-Corredor, E., Steenbeek, J., Giráldez, A., González, M., Esteban, A., Bellido, J.M. (2020). Current and future influence of environmental factors on small pelagic fish distributions in the Northwestern Mediterranean Sea. Front. Mar. Sci. 7: 1–20. https://doi.org/10.3389/fmars.2020.00622.

Planque, B., Mullon, C., Arneberg, P., Eide, A., Fromentin, J.M., Heymans, J.J., Hoel, A.H., Niiranen, S., Ottersen, G., Sandø, A.B., Sommerkorn, M., Thébaud, O., Thorvik, T. (2019). A participatory scenario method to explore the future of marine social-ecological systems. Fish. Fish. 20(3), 434-451. https://doi.org/10.1111/faf.12356.

Punt, A.E., Tuck, G.N., Day, J., Canales, C.M, Cope, J.M., de Moor, C.L., Oliveira, J.A.A., Dickey-Collas, M., Elvarsson, B.þ., Haltuch, M.A., Hamel, O.S., Hicks, A.C., Legault, C.M., Lynch, P.D., Wilberg, M.J. (2020). When are model-based stock assessments rejected for use in management and what happens then? Fish. Res. 224: 105465. https://doi.org/10.1016/j.fishres.2019.105465.

Punt A.E., Dalton, M.G., Adams, G.D., Barbeaux, S.J., Cheng, W., Hermann, A.J., Holsman, K.K, Hulson, P-J.F., Hurst, T.P., Rovellini, A. (2024). Capturing uncertainty when modelling environmental drivers of fish populations, with an illustrative application to Pacific Cod in the eastern Bering Sea. Fish. Res. 272: 106951. https://doi.org/10.1016/j.fishres.2024.106951.

Santojanni, A., Cingolani, N., Arneri, E., Kirkwood, G., Belardinelli, A., Giannetti, G., Colella, S., Donato, F., Barry, C. (2005). Stock assessment of sardine (Sardina pilchardus, WALB.) in the Adriatic Sea, with an estimate of discards. Sci. Mar. 69(4): 603-617. https://doi.org/10.3989/scimar.2005.69n4603.

Sinovčić, G. (2000a). Anchovy, Engraulis encrasicolus (LINNAEUS, 1758): biology, population dynamics and fisheries case study. Acta Adriatica. 41(1):3–53.

Taylor, I.G., Methot, R.D. (2013). Hiding or dead? A computationally efficient model of selective fisheries mortality. Fish. Res. 142: 75-85. https://doi.org/10.1016/j.fishres.2012.08.021.

Taylor, I.G., Doering, K.L., Johnson, K.F., Wetzel, C.R., Stewart, I.J. (2021). Beyond visualizing catch-at- age models: lessons learned from the r4ss package about software to support stock assessments. Fish. Res. 239 :105924. https://doi.org/10.1016/j.fishres.2021.105924.

Thorson, J.T., Johnson, K.F., Methot, R.D., Taylor, I.G. (2017). Model-based estimates of effective sample size in stock assessment models using the dirichlet-multinomial distribution. Fish. Res. 192 :84–93. https://doi.org/10.1016/j.fishres.2016.06.005.

Thorson, J.T., Maureaud, A.A., Frelat, R., Mérigot, B., Bigman, J.S., Friedman, S.T., Palomares, M-L.D., Pinsky, M.L., Price, S.A., Wainwright, P. (2023). Identifying direct and indirect associations among traits by merging phylogenetic comparative methods and structural equation models. Methods Ecol Evol. https://doi.org/10.1111/2041-210X.14076.

Vilibic, I., Čikeš Keč, V., Zorica, B., Šepić, J., Matijević, S., Džoić, T. (2016). Hydrographic conditions driving sardine and anchovy populations in a land-locked sea. Mediterr Mar Sci. 17:1. http://dx.doi.org/10.12681/mms.1120.

Walline. P.D. (2007). Geostatistical simulations of eastern Bering Sea wall- eye pollock spatial distributions, to estimate sampling precision. ICES J. Mar. Sci. 64 :559–69. https://doi.org/10.1093/icesjms/fsl045.

Wei, T., Simko, V. (2021). R package ‘corroplot': Visualization of a correlation Matrix (version 0.92). Avaiable from: https://github.com/taiyun/corrplot.

Winker, H., Pacoureau, N., Sherly, R. (2020). JARA: Just Another Red-list Assessment. https://github.com/henning-winker/JARA.

Zorica, B., Vilibic, I., Čikeš Keč, V., Šepić, J. (2013). Environmental conditions conducive to anchovy (Engraulis encrasicolus) spawning in the Adriatic Sea. Fish Oceanogr. 22(1):32-40. https://doi.org/10.1111/fog.12002.

GENERAL DISCUSSION

Novelty and integrative potential of the approach

This project aimed to connect environmental and anthropogenic drivers, traditionally investigated separately, demonstrating that the outputs of flexible statistical models can provide an evidence-based foundation for incorporating environmental covariates into population dynamics frameworks. In fact, correlative models such as Generalized Additive Models (GAMs) have been widely used to detect relationships between environmental variables and biological responses, while stock assessment models have focused primarily on fishing-related processes. Hence, the integration between GAM and SS achieved here is one of the most innovative elements of this work, and it offers a pathway for developing more realistic and adaptive stock assessments in the face of climate change.

GAMs were instrumental in identifying key environmental drivers, capturing non-linear and lagged effects that simple correlation analyses often overlook. The results highlighted the importance of Po River discharge and chlorophyll-a concentrations for anchovy, and of temperature and delayed productivity for sardine. These findings are consistent with global studies emphasizing the role of hydroclimatic forcing in shaping small pelagic populations (Bakun, 2006; Checkley et al., 2017; Yuniar et al., 2024). Translating these statistically derived signals into SS allowed the construction of models where environmental variability directly influences biological parameters such as growth, recruitment and mortality. This integration moves beyond traditional assumptions of stationarity, allowing key processes to vary dynamically in response to environmental conditions (Punt et al., 2020; McGarvey et al., 2024).

The methodological contribution of this study lies in the integration of GAM-based inference with Stock Synthesis outputs as a pragmatic analytical framework, rather than in demonstrating a dominant role of environmental forcing on small pelagic population dynamics. This approach allows environmental drivers to be evaluated explicitly alongside fishing pressure and management-related effects, without relying on fully coupled ecosystem models, which are often impractical in data-limited or unevenly monitored systems such as the Mediterranean Sea (Colloca et al., 2013; Piroddi et al., 2017). In the Adriatic Sea, the combined GAM and SS results indicate that fishing pressure and management regimes are the primary drivers of long-term variability in anchovy and sardine populations, while environmental covariates contribute more subtly by modulating biological processes such as growth and size structure. In this context, the inclusion of environmental information does not overturn the central role of exploitation dynamics, but helps reduce unexplained variability, improve model interpretability, and yield biologically coherent parameter estimates

(Huynh et al., 2020). By embedding environmental covariates within a management-focused assessment framework, this study contributes to the ongoing development of environmentally explicit or climate-informed stock assessment approaches, while also emphasizing that their added value depends on the relative strength of anthropogenic pressures in the system considered (Barange et al., 2018; Payne et al., 2022).

nAn important implication of this integrative framework concerns its relevance for Management Strategy Evaluation (MSE), which has long been recognized as a simulation-based approach specifically designed to evaluate the performance of management strategies under multiple and interacting sources of uncertainty (Punt et al., 2014). A core principle of MSE is the distinction between operating models (OMs), which aim to represent the plausible dynamics of the system to be managed, and estimation and management components, which are deliberately kept simple and transparent to ensure feasibility and interpretability (Rademeyer et al., 2007; Punt et al., 2014). Within this framework, complexity is not an end in itself but is introduced selectively to capture the key processes that may compromise management performance if ignored. In particular, for small pelagic fishes several studies have emphasized that strong environmental forcing, high recruitment variability and delayed responses in vital rates represent dominant sources of process uncertainty (Chavez et al., 2003; Cury et al., 2000; Plagányi, 2016). Recent syntheses further stress that such processes are most appropriately explored within operating models, even when assessment models and harvest control rules do not explicitly account for environmental drivers (Siple et al., 2021). The results of this thesis fit naturally within this perspective. By using GAMs to identify environmentally driven, non-linear and lagged effects on growth and size structure, this work provides an empirical basis for specifying how environmental variability can be translated into population dynamics within OMs. In particular, the lagged responses identified for sardine highlight a critical challenge for both assessment and management: changes in stock condition may reflect past environmental states rather than contemporary conditions. Such delays can generate a temporal mismatch between observed stock indicators and the underlying biological processes driving population dynamics, with important implications for projections and management performance. Similar concerns have been raised in the MSE literature, where delayed responses to environmental forcing have been shown to undermine the apparent effectiveness of management strategies if not explicitly represented in operating models (Hollowed et al., 2013; Essington et al., 2015). Explicitly accounting for lagged environmental effects within OMs is therefore essential to test the robustness of management procedures to delayed and cumulative responses, particularly for species such as sardine whose life-history traits make them especially sensitive to environmentally driven non-stationarity.

In conclusion, by coupling data-driven and process-based models, it provides a robust diagnostic–mechanistic pipeline: GAMs can identify which environmental variables have the greatest influence on stock dynamics, and these can subsequently be embedded in SS to test mechanistic hypotheses and improve projections. This approach not only improves the transparency of model construction but also strengthens the dialogue between statistical ecology and fisheries assessment. The Adriatic Sea, in this sense, becomes a natural laboratory—a microcosm where the benefits of methodological innovation and environmental awareness converge to produce tangible improvements in understanding and managing exploited populations.

Weaknesses, uncertainties and challenges

Despite its contributions, the study also reveals some weaknesses and challenges inherent to integrating environmental information into stock assessments. One of the main limitations concerns the proxy used for fishing pressure in the GAM models. Fleet size, although a practical index, cannot fully capture the multidimensional nature of fishing effort, which is influenced by gear efficiency, technological progress, targeting behavior and unreported catches (Hilborn et al., 2020). Therefore, the models may underestimate the true magnitude or temporal evolution of anthropogenic impacts. More accurate effort reconstructions, incorporating standardized effort data and vessel monitoring systems, would strengthen future analyses.

A second challenge relates to the spatial and temporal resolution of environmental data. The Adriatic Sea is a heterogeneous basin, with marked productivity gradients between the Italian and Croatian coasts. While the inclusion of variables such as Po River discharge and sea surface temperature was ecologically justified, coarse-resolution data can obscure fine-scale processes—such as retention fronts, mesoscale eddies or local upwelling—that influence larval transport and early survival (Grbec et al., 2015). Moreover, environmental variables often interact in non-linear and synergistic ways, complicating the identification of causal pathways. Modern GAM implementations can explicitly accommodate such complexity through multi-dimensional smoothers and interaction terms (e.g. tensor product splines), allowing flexible representation of joint effects (Planque et al., 2010; Wood, 2017). However, as model complexity increases, disentangling and interpreting these interactions in ecologically meaningful terms becomes increasingly challenging, particularly in observational studies where multiple drivers co-vary across space and time. In highly dynamic systems such as the Adriatic Sea, this limits the ability to unambiguously attribute observed patterns to specific environmental mechanisms, even when statistically robust interaction structures are supported by the data.From a modeling perspective, the use of a single-area SS structure represents another limitation. Anchovy and sardine stocks in the Adriatic are subject to distinct fishing regimes, productivity levels and management frameworks across national boundaries. Ignoring this spatial heterogeneity risks masking region-specific dynamics that could inform more targeted management interventions (Sinovčić et al., 2004; Zorica et al., 2016). The absence of spatial structure also restricts the model's ability to represent cross-border recruitment, differential growth and migration processes. Multi-area or spatially explicit SS models, though computationally more demanding, could address these gaps and enhance biological realism (Methot and Wetzel, 2013; McGarvey et al., 2024).

Uncertainty also arises from the limited length and consistency of the environmental time series available. Although satellite and reanalysis products have expanded dramatically in recent decades, long-term, high-frequency datasets remain scarce for the Adriatic. This constraint limits the ability to detect low-frequency climatic signals or to evaluate the persistence of relationships under changing baseline conditions (Báez et al., 2021). Additionally, while the inclusion of environmental covariates can improve explanatory power, it also increases model complexity and parameter uncertainty. Careful model selection and sensitivity testing are therefore essential to prevent overfitting and to ensure that environmental signals represent genuine causal effects rather than statistical artifacts.

Furthermore, an additional challenge concerns the risk of model misspecification when environmental covariates are incorporated into stock assessment models without prior ecological justification. Integrated assessment models are known to be sensitive to misspecified biological processes, time-varying parameters, and omitted drivers, which can propagate bias into estimates of stock status and management reference points (Punt et al., 2014). As emphasized by Carvalho et al. (2021), many apparent model deficiencies detected through diagnostics—such as retrospective patterns, conflicting likelihood components, or residual autocorrelation—often reflect underlying misspecification rather than deficiencies of the diagnostic tools themselves. By using GAMs as a preliminary diagnostic and variable-selection framework, this study shifts much of the complexity upstream, allowing environmental effects to be explored, screened and biologically interpreted before being translated into Stock Synthesis. Similar GAM-based approaches have been widely used to explore non-linear and lagged relationships between environmental and fishery drivers in small pelagic systems, but they also illustrate the risks of overfitting, autocorrelation and spurious inference when temporal structure and lag effects are not carefully addressed (Wood, 2017; Khoufi et al., 2025). In this context, GAMs serve not as end-point explanatory models, but as hypothesis-generating tools that inform the structure of subsequent mechanistic assessments. When environmental covariates are incorporated following this structured, hypothesis-driven pathway, standard diagnostics—such as likelihood component fits, residual patterns, convergence checks and retrospective analyses—remain appropriate and informative for evaluating model performance (Carvalho et al., 2021). The added value of the proposed framework therefore lies not in the development of an entirely new suite of diagnostic tools, but in reducing unexplained variability, improving interpretability, and minimizing the risk of compensatory misspecification. This perspective aligns with recent calls to prioritize transparent model development and biologically justified complexity, rather than indiscriminate model enrichment, as stock assessments move toward environmentally explicit formulations (Carvalho et al., 2021; Punt et al., 2024).Finally, while the combination of GAMs and SS provides a strong diagnostic and mechanistic framework, it still relies on the assumption that the relationships identified remain stable through time. In reality, climate change is inducing non-stationary dynamics: the same environmental anomaly may elicit different biological responses under altered baseline conditions (Cheung et al., 2013; Payne et al., 2022). This non-stationarity poses a fundamental challenge to all environment-based assessments, calling for more dynamic and adaptive modeling strategies capable of recalibrating relationships as systems evolve.

Future perspectives and paths forward

Despite these challenges, the project opens a wide range of future research and management opportunities. One immediate step involves improving the resolution and coverage of environmental and fishery data. Enhanced integration of in situ observations, satellite products and hydrodynamic models could provide more accurate representations of key variables such as primary productivity, temperature gradients and river plume dynamics. Harmonizing acoustic and biological data collection between Italian and Croatian monitoring programs would further allow a unified, basin-wide view of small pelagic dynamics—essential for transboundary management within the GFCM framework (FAO, 2023).

Methodologically, extending the Stock Synthesis framework to a multi-area or spatially explicit structure would be particularly valuable. This would allow explicit testing of spatial heterogeneity in growth, recruitment and selectivity, providing insights into how different subpopulations respond to both fishing and environmental pressures. Such models could also incorporate movement parameters or habitat suitability indices derived from GAM outputs, thereby creating a true feedback loop between statistical and mechanistic approaches (Punt et al., 2020; McGarvey et al., 2024). Coupling SS with regional climate models would further enable projections under alternative climate and management scenarios. Similar scenario-based approaches have been applied successfully in the North Pacific and Atlantic to test the resilience of key stocks to warming and acidification (Hollowed et al., 2013; Barange et al., 2018).

Beyond modeling, there is scope for developing decision-support tools that link biological and socioeconomic outcomes under environmental uncertainty. For instance, integrating economic data on fleet behavior and market prices with environmental indicators could help predict how environmental anomalies cascade into fisheries production and profitability (Castro-Gutiérrez et al., 2022). Such coupled human–natural models are increasingly recognized as essential components of climate-resilient management strategies (Hilborn et al., 2020; Payne et al., 2022).

In the longer term, this project underscores the potential of the Adriatic Sea as a "living laboratory" for climate-informed fisheries management. Its relatively small size, high productivity, and well-monitored stocks make it an ideal testing ground for methodological innovation. The integration of GAMs and SS shown here can serve as a transferable framework, adaptable to other semi-enclosed seas and data-rich ecosystems. By fostering collaboration among modelers, oceanographers, and managers, such initiatives can bridge the persistent gap between ecological knowledge and policy implementation.

Ultimately, this study demonstrates that fisheries assessment can no longer be conceived as a static, fish-centered exercise but must evolve into a dynamic, ecosystem-aware discipline. By embedding environmental knowledge into operational tools, we not only improve predictive accuracy but also cultivate a management paradigm that is precautionary, adaptive and resilient to change. The sustainability of small pelagic fisheries, in the Adriatic and beyond, will depend on our collective ability to embrace this transition—translating methodological innovation into meaningful conservation and governance outcomes in an ocean that is changing faster than ever before.

General references

Adriamed WGSASP (2015a). Stock Assessment Form Small Pelagics—Anchovy—GSA 17 & 18.

Adriamed WGSASP (2015b). Stock Assessment Form Small Pelagics—Sardine—GSA 17 & 18.

Albo-Puigserver, M., Pennino, M.G., Bellido, J.M., Colmenero, A.I., Girldez, A., Hidalgo, M., Ramirez, J.G., Steenbeek, J., Torres, P., Cousido-Rcha, M., Coll, M. (2021). Changes in Life History Traits of Small Pelagic Fish in the Western Mediterranean Sea. Front. Mar. Sci. 8. https://doi.org/10.3389/fmars.2021.570354.

Aldanondo, N., Cotano, U., Tiepolo, M., Boytra, G., 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(3): 196-208. https://doi.org/10.1111/j.1365-2419.2010.00537.x.

Allain, G., Petitgas, P., Lazure, P. (2001). The influence of mesoscale ocean processes on anchovy (Engraulis encrasicolus) recruitment in the Bay of Biscay estimated with a three-dimensional hydrodynamic model. Fisheries Oceanography. 10(2), 151-163.

Angelini, S., Biagiotti, I., Bratina, P., Čikeš Keč, V., De Felice, A., et al. (2025). STock Assessment Results Small Pelagics—Anchovy—GSA 17 & 18. https://gfcm.sharepoint.com/EG/_layouts/15/download.aspx?share=EU0UZA1NNnhPsKLnGPvBU7MBjwT1hQExd7hgsR0OxTQ7EQ.

Artegiani, A., Curzi P., Froglia, C., Lenaz, R., Tomadin, L., 1979. Primi risultati delle indagini sui fattori biologici, oceanografici e sedimentologici che condizionano la distribuzione degli Scampi (Nephrops norvegicus) in Adriatico. Atti Convegno Scientifico Nazionale P.F. Oceanografica e Fondi Marini, 1: 229–241.

Artegiani, A., Bregant, D., Paschini, E., Pinardi, N., Raicich, F., Russo, A. (1997a). The Adriatic Sea general circulation. Part I. Air-sea interactions and water mass structure. J. Phys. Oceanogr., 27:1492–1514.

Artegiani, A., Bregant, D., Paschini, E., Pinardi, N., Raicich, F., Russo, A. (1997b). The Adriatic Sea general circulation. Part II: Baroclinic Circulation Structure. J. Phys. Oceanogr., 27: 1515-1532.

Azzali, M., Levi, D. (1976). Il ruolo dell'automazione nelle tecniche di valutazione e gestione degli stocks pelagici. p. 141-179. In: Convegno Scientifico automazione e utilizzazione delle risorse. Milano, Italy, 23-24 November 1976.

Azzali, M., Burczynski, J. (1977). Quantitative Acoustic Estimation of Sardine Stock and Distribution in the Northern Adriatic Sea. Report to the Government of Italy. FAO/ITA/TF, FAO, No. 3, Rome, 53 pp.

Azzali, M., Buracchi, G., Conti, S., Gambetti, S., Luna, M. (1985). Relationship between the forms of pelagic fish distribution and nictemeral periods. A tentative model of behaviour. Oebalia. 11(2):471–488.

Azzali, M., De Felice, A., Luna, M., Cosimi, G., Parmiggiani, F. (2002). The state of the Adriatic Sea centered on the small pelagic fish populations. Mar. Ecol. 23 (1): 78–91. https://doi.org/10.1111/j.1439-0485.2002.tb00009.x.

Báez, J.C., Gimeno, L., Real, R. (2021). North Atlantic Oscillation and fisheries management during global climate change. Rev. Fish. Biol. Fish. 31:319-336. https://doi.org/10.1007/s11160-021-09645-z.

Bakun, A. (2006). Wasp-waist populations and marine ecosystem dynamics: Navigating the “predator pit” topographies. Prog. Oceanogr. 68(2–4): 271–288. https://doi.org/10.1016/j.pocean.2006.02.004.

Baltëza, B. (1985). On the structural characteristics of sardine schools (Sardina pilchardus, Walb.) along the Albanian coast in the winter period. FAO Fisheries Report. 342:161-163.

Barbeaux, S. J., Barnett, L., Connor, J., Nielson, J., Shotwell, S. K., Siddon, E., Spies, I. (2022). Assessment of the Pacific cod stock in the Eastern Bering Sea. Seattle: Alaska Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration.

Basilone, G., Mangano, S., Pulizzi, M., Fontana, I., Giacalone, G., Ferreri, R., Gargano, A., Aronica, S., Barra, M., Genovese, S., Rumolo, P., Mazzola, S., Bonanno, A. (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(3):504-516. http://dx.doi.org/10.12681/mms.2059.

Barange, M., Bahri, T., Beveridge, M.C.M., Cochrane, K.L., Funge-Smith, S., Poulain, F. (2018). Impacts of climate change on fisheries and aquaculture. Synthesis of current knowledge, adaptation and mitigation options. FAO Fisheries and Aquaculture Technical Paper No. 627. Rome, Italy. 654 pp.

Baudron, A.R., Needle, C.L., Rijnsdrop, A.D., Marshall, C.T. (2014). Warming temperatures and smaller body sizes: synchronous changes in growth of North Sea fishes. Glob. Change Biol. 20(4): 1023-1031. https://doi.org/10.1111/gcb.12514.

Bertrand J. A., Gil de Sola L., Papaconstantinou C., Relini G., Souplet A. (2002). The general specifications of the MEDITS surveys. Sci. Mar. 66 (2): 9-17.

Bonanno, A., Barra, M., Basilone, G., Genovese, S., Rumolo, P., Goncharov, S., Popov, S., Buongiorno, B., Nardelli, D., Iudicone, D., Procaccini, G., Aronica, S., Patti, B., Giacalone, G., Ferreri, R., Fontana, I., Tranchida, G., Mangano, S., Pulizzi, M., Garagano., A., Di Maria, A., Mazzola, S. (2016). Environmental processes driving anchovy and sardine distribution in a highly variable environment: the role of the coastal structure and riverine input. Fish Oceanogr. 25:471–490. http://dx.doi.org/10.1111/fog.12166.

Borme, D., Tirelli, V., Brandt, S., Fonda Umani, S., and Arneri, E. (2009). Diet of Engraulis encrasicolus in the northern Adriatic Sea (Mediterranean): ontogenetic changes and feeding selectivity. Marine Ecology Progress Series, 392:193–209.

Borme, D., Legovini, S., de Olazabal, A., Tirelli, V. (2022). Diet of Adult Sardine Sardina pilchardus in the Gulf of Trieste, Northern Adriatic Sea. J. Mar. Sci. Eng. 10(89: 1012. https://doi.org/10.3390/jmse10081012.

Brander, K.M. (2007). Global fish production and climate change. Proc. Nat. Acad. Sci. 104(50): 19709-14. https://doi.org/10.1073/pnas.0702059104.

Brosset, P., Fromentin, J.M., Van Beveren, E., Lloret, J., Marques, V., Basilone, G., Bonanno, A., Carpi, P., Donato, F., Čikeš Keč, V., De Felice, A., Ferreri, R., Gašparević, D., Giráldez, A., Gücü, A., Iglesias, M., Leonori, I., Palomera, I., Somarakis, S., Tičina, V., Torres, P., Ventero, A., Zorica, B., Ménard, F., Saraux, C. (2017). Spatio-temporal patterns and environmental controls of small pelagic fish body condition from contrasted Mediterranean areas. Prog. Oceanogr. 151:149–162. https://doi.org/10.1016/j.pocean.2016.12.002.

Bulgakova, Y.V. (1993). Daily feeding dynamics of the Black Sea anchovy, Engraulis encrasicholus. J. Ichthyol. 33(7):78-88.

Carpi, P., Martinelli, M., Belardinelli, A., Russo, A., Arneri, E., Coluccelli, A., Sanotjanni, A. (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(6): 521–532. https://doi.org/10.1111/fog.12126.

Carpi, P., Scarcella, G., 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. https://doi.org/10.3389/fmars.2017.00423.

Carvalho, F., Winker, H., Courtney, D., Kapur, M., Kell, L., Cardinale, M., Schirripa, M., Kitakado, T., Yemane, D., Piner, K.R., Maunder, M.N, Taylor, I., Wetzel, C.R., Doering, K., Johnson, K.F., Methot, R.D. (2021). A cookbook for using model diagnostic in integrated stock assessment. Fish. Res. 240: 105959. https://doi.org/10.1016/j.fishres.2021.105959.

Casavola, M., Marano, G., Furlan, L., Specchi, M., Piccinetti, C., and Piccinetti-Manfrin, G. (1986). Considérations sur la distribution des clupeiformes Engraulis encrasicolus et Sardina pilchardus en Adriatique. Technical report, FAO Fish. Rep. 345.

Castro-Gutiérrez, J., Cabrera-Castro, R., Czerwinski, I.A., Báez, J.C. (2022). Effect of climatic oscillation on small pelagic fihseries and its economic profit in the Gulf of Cadiz. Int. J. Biotec. 66:613-626. https://doi.org/10.1007/s00484-021-02223-9.

Chavez, F. P., Ryan, J., Lluch-Cota, S. E., Miguel Ñiquen, C. (2003). From anchovies to sardines and back: Multidecadal change in the Pacific Ocean. Science, 299(5604), 217–221. https://doi.org/10.1126/science.1075880.

Checkley, D., Alheit, J., Oozeki, Y., Roy, C. (2009). Climate change and small pelagic fish. Cambridge University Press.

Checkley, D.M., Asch, R.G., Rykaczewski, R.R. (2017). Climate, Anchovy, and Sardine. Ann. Rev. Mar. Sci. 9:469-93. https://doi.org/10.1146/annurev-marine-122414-033819.

Cheung, W.W., Watson, R., Pauly, D. (2013). Signature of ocean warming in global fisheries catch. Nature. 497(7449), 365-368. https://doi.org/10.1038/nature12156.

Čikeš Keč, V., Angelini, S., Biagiotti, I., Bratina, P., De Felice, A., Juretic, T., et al., (2025). STock Assessment Results Small Pelagics—Sardine—GSA 17 & 18. https://gfcm.sharepoint.com/EG/_layouts/15/download.aspx?share=EeuQwV4VnWFAjhqZB6bKx50Bw5qo2sfJpt8DPzw9NJ5OQg.

Cingolani, N., Giannetti, G., Arneri, E. (1996). Anchovy fisheries in the Adraitic Sea. Sci. Mar. 60(2): 269-277.

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 Technical Documents. 3: 39-52.

Cingolani, N., Karis, T., Sinovčić, G., Kapedani, E. (2004). Sardine (Sardina pilchardus, Walb.) stock assessment in the Adriatic Sea: 1975-2003. AdriaMed Occasional Paper.

Cingolani, N., Santojanni, A., Arneri, E., Berlardinelli, A., Colella, S., Donato, F., Giannetti, G., Sinovčić, G., Zorica, B., Marceta, B. (2005). Anchovy (Engraulis encrasicolus, L.) stock assessment in the Adriatic Sea: 1975-2004. AdriaMed Occasional Papers.

Coll, M., Santojanni, A., Palomera, I., Tudela, S., 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. https://doi.org/10.1016/j.jmarsys.2006.10.002.

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

Coll, M., Libralato, S. (2012). Contributions of food web modelling to the ecosystem approach to marine resource management in the Mediterranean Sea. Fish. Fish. 13:60-88. https://doi.org/10.1111/j.1467-2979.2011.00420.x.

Colloca, F., Cardinale, M., Maynou, F., Giannoulaki, M., Scarcella, G., Jenko, K., Bellido, J.M., Fiorentino, F. (2013). Rebuilding Mediterranean fisheries: a new paradigm for ecological sustainability. Fish. Fish. 14(1):89-109. https://doi.org/10.1111/j.1467-2979.2011.00453.x.

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

Coombs, S., Giovanardi, O., Conway, D., Manzueto, L., Halliday, N., and Barrett, C. (1997). The distribution of eggs and larvae of anchovy (Engraulis encrasicolus) in relation to hydrography and food availability in the outflow of the river Po. Acta Adriatica, 38(1):33–47.

Coombs, S., Giovanardi, O., Halliday, N., Franceschini, G., Conway, D., Manzueto, L., Barrett, C., and McFadzen, I. (2003). Wind mixing, food availability and mortality of anchovy larvae Engraulis encrasicolus in the northern Adriatic Sea. Marine Ecology Progress Series, 248:221–235.

Cury, P., Bakun, A., Crawford, R.J.M., Jarre, A., Quiñones, R.A., Shannon, L.J., Verheye, H.M. (2000). Small pelagics in upwelling systems: Patterns of interaction and structural changes in “wasp-waist” ecosystems. ICES J. Mar. Sci. 57(3): 603–618. https://doi.org/10.1006/jmsc.2000.0712.

Domínguez-Bustos, A.R., Castro-Gutiérrez, J., Gómez-Enri, J., Cabrera-Castro, R. (2023). Modelling relationships between fisheries landings and oceanographic variables: a case study in adjacent areas of Gibraltar Strat. Reg. Stud. Mar. Sci. 61:102895. https://doi.org/10.1016/j.rsma.2023.102895.

Eigaard, O.R., Bastardie, F., Hintzen, N.T., Buhl-Mortensen, L., Buhl-Mortensen, P., Catarino, R., Dinesen, G.E., Egekvist, J., Fock, H.O., Geitner, K., Gerritsen, H.D., González, M.M., Jonsson, P., Kavadas, S., Laffargue, P., Lundy, M., Gonzalez-Mirelis, G., Nielsen, R.J., Papadopoulou, N., Posen, P.E., Pulcinella, J., Russo, T., Sala, A., Silva, C., Smith, C.J., Vanelslander, B., Rijnsdorp, A.D. (2017). The footprint of bottom trawling in European waters: distribution, intensity, and seabed integrity. ICES J Mar Sci. 2017;74(3):847-865. https://doi.org/10.1093/icesjms/fsw194.

Essington, T. E., Moriarty, P. E., Froehlich, H. E., Hodgson, E. E., Koehn, L. E., Oken, K. L., Siple, M. C., & Stawitz, C. C. (2015). Fishing amplifies forage fish population collapses. Proceedings of the National Academy of Sciences, 112(21), 6648–6652. https://doi.org/10.1073/pnas.14220 20112.

EU (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.

Fanelli, E., Da Ros, Z., Menicucci, S., Malavolti, S., Biagiotti, I., Canduci, G., De Felice, A., Leonori, I. (2023) The pelagic food web of the Western Adriatic Sea: a focus on the role of small pelagics. Sci Rep.13:14554. https://doi.org/10.1038/s41598-023-40665-w.

Fernández-Corredor, E., Albo-Puigserver, M., Pennino, M.G., Bellido, J.M., 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. https://doi.org/10.1016/j.rsma.2020.101606.

Fischer, W. M., Bauchot, L., and Schneider, M. (1987). Fiches FAO d'identification des espèces pour les besoins de la pêche. (Révision 1). Méditerranée et mer Noire. Zone de pêche 37. Volume II. Vertébrés., volume 2:. Publication préparée par la FAO, résultat d'un accord entre la FAO et la Commission des Communautés Européennes (Projet GCP/INT/422/EEC) financée conjointement par ces deux organisations., Rome, FAO. 761- 1530 pp.

FAO (2008). Best practices in ecosystem modelling for informing an ecosystem approach to fisheries. FAO Fisheries Technical Guidelines for Responsible Fisheries. No. 4, Suppl. 2, Add. 1, Rome, FAO, 1–78.

FAO (2023). The State of Mediterranean and Black Sea Fisheries 2023 – Special edition. General Fisheries Commission for the Mediterranean. Rome. https://doi.org/10.4060/cc8888en.

FAO (2025). The State of Mediterranean and Black Sea Fisheries 2025. General Fisheries Commission for the Mediterranean. Rome. https://doi.org/10.4060/cd7701en.

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

Fournier, D.A., Hampton, J., Sibert, J.R. (1998). MULTIFAN-CL: a length-based, age- structured model for fisheries stock assessment, with application to South Pacific albacore, Thunnus alalonga. Can. J. Fish. Aquatic Sci. 55(9). https://doi.org/10.1139/f98-100.

Gamulin-Brida, H. (1967). The benthic fauna of the Adriatic Sea. In Barnes, H.B. (Ed.) Oceanogr. Mar. Biol. Ann. Rev. 5: 535-568.

Gamulin, T. and Hure, H. (1983). The spawning and spawning areas of pelagic fishes (Sardina pilchardus, Engraulis encrasicolus, Scomber scombrus, Sardinella aurita and Sprattus sprattus sprattus) in the Adriatic Sea. Acta Adriatica. 24:112–115.

GFCM WGMSE (2024). Working Group on Management Strategy Evaluation (WGMSE) on Adriatic Sea small pelagics. Session I: Online, 20-22 May 2024; Session II: Podgorica, Montenegro, 27 May 2024. Conclusion and raccomandations.

GFCM WGSASP (2024). Session on small pelagic species in the Adriatic Sea. Online, 6-8 May. Report.

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

Giannoulaki, M., Iglesias, M., Tugores, M.P., Bonanno, A., Patti, B., De Felice, A., Leonori, I., Bigot, J.L., Tičina, V., Pyrounaki, M.M., Tsagarakis, K., Machias, A., Somarakis, S., Schismenou, E., Quinci, E., Basilone, G., Cuttitta, A., Campanella, F., Miquel D. Oñate, J., Roos, D., Valvanis, V. (2013). Characterizing the potential habitat of European anchovy Engraulis encrasicolus in the Mediterranean Sea, at different life stages. Fish. Oceanogr. 22(2):69-89. https://doi.org/10.1111/fog.12005.

Grati, F., Scarcella G., Polidori P., Domenichetti F., Bolognini L., Gramolini R., Vasapollo C., Giovanardi O., Raicevich S., Celić I., Vrgoč N., Isajlovic I., Jenič A., Marčeta B., Fabi G. (2013). Multi-annual investigation of the spatial distributions of juvenile and adult sole (Solea solea, L.) in the Adriatic Sea (Northern Mediterranean). J. Sea Res. http://dx.doi.org/10.1016/j.seares.2013.05.001.

Grbec, B., Dulcic, J., Morovic, M. (2002). Long-term changes in landings of small pelagic fish in the eastern Adriatic - Possible influence of climate oscillations over the Northern Hemisphere. Clim. Res. 20:241–252. https://doi.org/10.3354/cr020241.

Grbec, B., Morović, M., Matić, F., Ninćević Gladan, Ž., Marasović, I., Vidjak, O., Bojanić, N., Čikeš Keč, V., Zorica, B., Kušplić, G., Matić-Skoko, S. (2015). Climate regime shifts and multi-decadal variability of the Adriatic Sea pelagic ecosystem. Acta Adriat. 56(1): 66.

Grilli, F., Accoroni, S., Acri, F., Aubry, F. B., Bergami, C., Cabrini, M., Campanelli, A., Giani, M., Guicciardi, S., Marini, M., Neri, F., Penna, A., Penna, P., Pugnetti, A., Ravaioli, M., Riminucci, F., Ricci, F., Totti, C., Viaroli, P., and Cozzi, S. (2020). Seasonal and interannual trends of oceanographic parameters over 40 years in the Northern Adriatic Sea in relation to nutrient loadings using the EMODnet chemistry data portal. Water. 12(8): 2280. https://doi.org/10.3390/w12082280.

Haltuch, M., Punt, A.E. (2011). The promises and pitfalls of including decadal- scale climate forcing of recruitment in groundfish stock assessment. Can. J. Fish. Aquatic. Sci. 68: 912-926. https://doi.org/10.1139/F2011-030.

Hattab, T., Gucu, A., Ventero, A., De Felice, A. Machias, A, Saraux, C., Gašparević, D., Basilone, G.; Costantini, I., Leonori, I., Bourdeix, J.-H., Iglesias, M., Barra, M., Giannoulaki, M., Ferreri. R., Ayoubi. S.E., Malavolti, S., Genovese, S., Somarakis, S., Juretić, T., Tičina, V., Certain, G. (2021). Temperature strongly correlates with regional patterns of body size variation in Mediterranean small pelagic fish species. Mediterr. Mar. Sci. 22(4):800-811. https://doi.org/10.12681/mms.26525.

Hilborn, R., Amoroso, R.O., Anderson, C.M., Baum, J.K., Branch, T.A., Costello, C., de Moor, C.L., Faraj, A., Hively, D., Jensen, O.P., Kurota, H., Little, L.R., Mace, P., McClanahan, T., Melnychuk, M.C., Minto, C., Osio, G.C., Parma, A.M., Pons, M., Segurado, S., Szuwalski, C.S., Wilson, J.R., Ye, Y. (2020). Effective fisheries management instrumental in improving fish stock status. P Natl A Sci USA. 117(4):2218-2224. https://doi.org/10.1073/pnas.1909726116.

Hill, S.L., Phillips, T., Atkinson, A. (2013). Potential climate effects on the habitat o Antartic krill in the Weddel Quadrant of the Southern Ocean. PLoSONE. 8(8): e72246. https://doi.org/10.1371/journal.pone.0072246.

Hoggarth, D.D., Abeyasekera, S., Arthur, R.I., Beddington, J.R., Burn, R.W., Halls, A.S., Kirkwood, G. P., McAllister, M.; Medley, P.; Mees, C.C.; Parkes, G.B.; Pilling, G.M.; Wakeford, R.C.; Welcomme, R.L. (2006). Stock assessment for fishery management – A framework guide to the stock assessment tools of the Fisheries Management Science Programme (FMSP). FAO Fish. Tech. Pap. No. 487. Rome, FAO: 261p.

Hollowed, A. B., Barange, M., Beamish, R., Brander, K., Cochrane, K., Drinkwater, K., Foreman, M., Hare, J., Holt, J., Ito, S-I., Kim, S., King, J., Loeng, H., MacKenzie, B., Mueter, F., Okey, T., Peck, M. A., Radchenko, V., Rice, J., Schirripa, M., Yatsu, A., and Yamanaka, Y. (2013). Projected impacts of climate change on marine fish and fisheries. ICES J. Mar. Sci. 70: 1023–1037. https://doi.org/10.1093/icesjms/fst081.

Hopkins T.S. (1999) Physical control of the eutrophic response in the Northern Adriatic Sea, illustrated by a nitrogen budget from ELNA data. Ann. Ist. Sup. Sanità. 35: 355 – 363.

ICES. 2022. Stock Annex: Sardine (Sardina pilchardus) in divisions 8.a–b and 8.d (Bay of Biscay). ICES Stock Annexes. 37 pp. https://doi.org/10.17895/ices.pub.18623198.

Kačić, I. (1972a). The behavior, distribution and quantity of sardines in the Bay of Kaštela. Acta Adriatica, 14 (1):33pp.

Kačić, I., Sinovčić, G., Alegría Hernández, V. (1986). Juvenile sardine along the eastern Adriatic coast - studies and protection -. Technical report, FAO Fish. Rep. 345.

Kell, L.T., Mosqueira, I., Grosjean, P., Fromentin, J-M., Garcia, D., Hillary, R., Jardim, E., Mardle, S., Pastoors, M.A., Poos, J.J., Scott, F., Scott, R.D. (2007). FLR: an open-source framework for the evaluation and development of management strategies. ICES J Mar Sci. 64 (4):640–646. https://doi.org/10.1093/icesjms/fsm012.

Khoufi, W., Belhoula, F., Jabeur, C. (2025). Antrohpogenic and environmental pressure on Sardina pilchardus stock. Euro-Mediterr. J. Environ. Integr. 10:543-554. https://doi.org/10.1007/s41207-024-00648-3.

Laurec, A., Shepherd, J.G. (1983). On the analysis of catch and effort data. J. Cons. Intern. Explor. Mer. 41: 81-84.

Leonori, I., Tičina, V., Giannoulaki, M., Hattab, T., Iglesias, M., Bonanno, A., Costantini, I., Canduci, G., Machias, A., Ventero, A., Somarakis, S., Tsagarakis, K., Bogner, D., Barra, M., Basilone, G., Genovese, S., Juretić, T., Gašparević, D., De Felice, A. (2021). History of hydroacoustic surveys on small pelagic fish species in the European Mediterranean Sea. Mediterr Mar Sci. 22(4):751-768. https://doi.org/10.12681/mms.26001.

Libralato, S., Coll, M., Tudela, S., Palomera, I., Pranovi, F. (2008). Novel index for quantification of ecosystem effects of fishing as removal of secondary production. Mar. Ecol. Prog. Ser. 355: 107-129. https://doi.org/10.3354/meps07224.

Lindmark, M., Audzijonyte, A., Blanchard, J.L., 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. https://doi.org/10.1111/gcb.16341.

Livingston P. A., Methot R. D. (1998). Incorporation of predation into a population assessment model of eastern Bering Sea walleye pollock. Fishery Stock Assessment Models, Alaska Sea Grant College Program, AK-SG-98-01.

Lloret, J., Palomera, I., Salat, J., and Sole, I. (2004). Impact of freshwater input and wind on landings of anchovy (Engraulis encrasicolus) and sardine (Sardina pilchardus) in shelf waters surrounding the Ebre (Ebro) River delta (north-western Mediterranean). Fisheries Oceanography, 13(2):102–110. https://doi.org/10.1046/j.1365-2419.2003.00279.x.

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. https://doi.org/10.1016/j.marpol.2018.09.031.

Malavolti, S., Ruggeri, P., Fioravanti, T., Tičina, V., Costantini, I., De Felice, A., Splendani, A., Gašparević, D., Caputo Barucchi, V., Leonori, I. (2021). Temporal and spatial genetic variation of Engraulis encrasicolus in the Adriatic Sea. Mediterr. Mar. Sci. 22(4): 843–857. https://doi.org/10.12681/mms.25990.

Mannini, P., Massa, F. (2000). Brief overview of Adriatci fisheries landings trends (1972-97). FAO-Technical report.

Marano, G. (2001). Small pelagic stock assessment (1984–1996). Techical Documents 3, 66–77, ADRIAMED.

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(16): 9267. https://doi.org/10.3390/app13169267.

Martín, P., Sabatés, A., Lloret, J., Martin-Vide, J. (2012). Climate modulation of fish populations: the role of the Western Mediterranean Oscillation (WeMO) in sardine (Sardina pilchardus) and anchovy

(Engraulis encrasicolus) production in the north-western Mediterranean. Clim. Change. 110(3-4): 925–939. https://doi.org/10.1007/s10584-011-0091-z.

Masnadi F. (2023). Evaluation and management of demersal stocks in the Adriatic: the case of common sole (Solea solea, L.,) in the Northern and Central Adriatic Sea. PhD Thesis dissertion.

Maunder, M.N., Watters, G.M. (2003). A General Framework for Integrating Environmental Time Series into Stock Assessment Models: Model Description, Simulation Testing, and Example. Fish. Bull. 101(1): 89–99.

Maunder, M.N, Punt, A.E. (2013). A review of integrated analysis in fisheries stock assessment. Fish. Res. 142: 61-74. https://doi.org/10.1016/j.fishres.2012.07.025.

Maynou F, Sabates A, Salat J. (2014). Clues from the recent past to assess recruitment of Mediterranean small pelagic fishes under sea warming scenarios. Clim Change. 126:175–188. http://dx.doi.org/10.1007/s10584-014-1194-0.

Maynou, F., Sabatés, A., & Raya, V. (2020). Changes in the spawning habitat of two small pelagic fish in the Northwestern Mediterranean. Fish. Ocean. 29(2), 201-213. https://doi.org/10.1111/fog.12464.

McGarvey, R., Methot, R.D., Punt, A.E., Matthews, J.M., Taylor, I.G., Feenstra, J.E., Doering, K. (2024). Performance gains from incorporating dynamic numbers by length-within-age in fishery assessment models. Fisheries Research, 276, 107039. https://doi.org/10.1016/j.fishres.2024.107039.

Methot, R. D., Dorn, M. W. (1995). Biology and fisheries of North Pacific hake (M. productus). In Hake: biology, fisheries and markets (pp. 389-414). Dordrecht: Springer Netherlands.

Methot, R.D., Wetzel, C.R. (2013). Stock Synthesis: A biological and statistical framework for fish stock assessment and fishery management. Fish Res. 142:86-99. https://doi.org/10.1016/j.fishres.2012.10.012.

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

Morello, E.B. (2010). SARDONE - Improving assessment and management of small pelagic species in the Mediterranean. Project final report (eu contract fp6-44294), CNR-ISMAR.

Musick, J.A., Bonfil, R. (2005) Management techniques for elasmobranch fisheries. FAO Fisheries Technical Paper, 474, 1-251.

Navarro, J., Saez-Liante, R., Albo-Puigserver, M., Coll, M., Palomera, I. (2017). Feeding strategies and ecological roles of three predatory pelagic fish in the western Mediterranean Sea. Deep Sea Res II. 140:9-17. https://doi.org/10.1016/j.dsr2.2016.06.009.

Nielsen, A.N., Berg, C.W. (2014). Estimation of time-varying selectivity in stock assessments using state-space models. Fish Res. 158:96-101. https://doi.org/10.1016/j.fishres.2014.01.014.

Nikolioudakis, N., Isari, S., Pitta, P., Somarakis, S. (2012). Diet of sardine Sardina pilchardus: an 'end-to-end' field study. Mar. Ecol. Prog. Ser. 453: 173:188. https://doi.org/10.3354/meps09656.

Otero, J., 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. https://doi.org/10.1093/icesjms/fsad072.

Ott, J.A. (1992). The Adriatic benthos: problems and perspectives, in: Colombo, G. et al. (Ed.) Marine Eutrophication and Population Dynamics: 25th European Marine Biology Symposium, Ferrara (Italy), 10-15 September 1990. International Symposium Series: 367-378.

Palomera, I., Olivar, M.P., Salat, J., Sabatés, A., Coll, M., García, A., Morales-Nin, B. (2007). Small pelagic fish in the NW Mediterranean Sea: An ecological review. Prog. Oceanogr. 74(2–3): 377–396. https://doi.org/10.1016/j.pocean.2007.04.012.

Parrish, R. H., Serra, R., Grant, W. (1989). The monotypic sardines, Sardina and Sardinops: their taxonomy, distribution, stock structure, and zoogeography. Can. J. Fish. Aquatic Sci. 46(11):2019–2036.

Patterson K., Cook R., Darby C., Gavaris S., Kell L., Lewy P., Mesnil B., Punt A., Restrepo V., Skagen D. W., Stefánsson G. (2001). Estimating uncertainty in fish stock assessment and forecasting. Fish Fish., 2(2): 125–157. https://doi.org/10.1046/j.1467-2960.2001.00042.x.

Payne, M.R., Danabasoglu, G., Keenlyside, N., Matei, D., Miesner, A.K., Yang, S., Yeager, S.G. (2022). Skilful decal-scale prediction of fish habitat and distribution shift. Nat. Commun. 13: 2660. https://doi.org/10.1038/s41467-022-30280-0.

Pedersen, M.W., Berg, C.W. (2016). A stochastic surplus production model in continuous time. Fish. Fish. 18(2): 226-243. https://doi.org/10.1111/faf.12174.

Pennino, M.G., Coll, M., Albo-Puigserver, M., Fernández-Corredor, E., Steenbeek, J., Giráldez, A., González, M., Esteban, A., Bellido, J.M. (2020). Current and future influence of environmental factors on small pelagic fish distributions in the Northwestern Mediterranean Sea. Front. Mar. Sci. 7: 1–20. https://doi.org/10.3389/fmars.2020.00622.

Piccinetti, C., Regner, S., and Specchi, M. (1981). Distribution des oeufs de sardine en Adriatique. Technical report, Rapport de la Commission Internationale pour la Mer Méditerranée. 27(5): 167-170.

Pikitch, E.K., Santora, C., Babcock, E.A., Bakun, A., Bonfil, R, Conover, D.O., Dayton, P., Fluharty, D., Heneman, B., Houde, E.D., Link, J., Livingston, P.A., Mangel, M., McAllister, M.K., Pope, J., Sainsbury, J. (2004). Ecosystem based fishery management. Science. 305:346–347. https://doi.org/10.1126/science.1098222.

Piroddi, C., Coll, M., Liquete, C., Macias, D., Greer, K., Buszowski, J., Steenbeek, J., Danovaro, R., Christensen, V. (2017). Historical changes of the Mediterranean Sea ecosystem: modelling the role and impact of primary productivity and fisheries changes over time. Sci. Rep. 7(1):44491. https://doi.org/10.1038/srep44491.

Plagányi, É. E. (2016). Using simulation evaluation to account for ecosystem considerations in fisheries management. In C. T. T. Edwards, and D. J. Dankel (Eds.), Management Science in Fisheries: An introduction to simulation-based methods. (298–318). Routledge.

Planque, B., Fromentin, J.M., Cury, P., Drinkwater, K.F., Jennings, S., Perry, R.I., Kifani, S. (2010). How does fishing alter marine populations and ecosystems sensitivity to climate? J. Marine Syst. 79(3-4): 403-417. https://doi.org/10.1016/j.jmarsys.2008.12.018.

Punt, A.E., Butterworth, D.S., de Moor, C.I., De Olivera, J.A.A, Haddon, M. (2014). Management strategy evaluation: best practices. Fish Fish., 17(2): 303-334. https://doi.org/10.1111/faf.12104.

Punt, A.E., Dalton, M.G., Cheng, W., Hermann, A.J., Holsman, K.K, Hurst, T.P., Ianelli, J.N., Kearney, K.A., McGalliard, C.R., Pilcher, D.J., Véron, M. (2021). Evaluating the impact of climate and demographic variation on future prospects for fish stocks: an application for northern rock sole in Alaska. Deep Sea Res II. 189–190. https://doi.org/10.1016/j.dsr2.2021.104951.

Punt, A.E., Dalton, M.G., Adams, G.D., Barbeaux, S.J., Cheng, W., Hermann, A.J., Holsman, K.K., Hulson, P-J. F., Hurst, T.P., Rovellini, A. (2024). Capturing uncertainty when modelling environmental drivers of fish populations, with an illustrative application to Pacific Cod in the eastern Bering Sea. Fish. Res. 272: 106951. https://doi.org/10.1016/j.fishres.2024.106951.

Quattrocchi, F., Maynou, F. (2017). Environmental drivers of sardine (Sardina pilchardus) in the Catalan Sea (NW Mediterranean Sea). Mar. Biol. Res. 13(9):1-12. https://doi.org/10.1080/17451000.2017.1331039.

Rademeyer, R.A., Plagányi, É.E., Butterworth, D.S. (2007) Tips and tricks in designing management procedures. ICES J. Mar. Sci. 64(2): 618– 625. https://doi.org/10.1093/icesjms/fsm050.

RECFISH (2019). Historical time series for Mediterranean and Black Sea stock assessment RECovery of FISHeries (RECFISH). Framework Contract for the Provision of Scientific Advice for the Mediterranean and the Black Seas, EASME/EMFF/2016/032 Specific Contract Nr. 01. https://cinea.ec.europa.eu/publications/.

Regner, S. (1972). Contribution to the study of the ecology of the planktonic phase in the life history of the anchovy in the central Adriatic. Acta Adriatica. 14(9):3—-43.

Regner, S. (1996). Effects of environmental changes on early stages and reproduction of anchovy in the Adriatic Sea. Scientia Marina. 60(2):167–177.

Ruggeri, P., Splendiani, A., Bonanomi, S., Arneri, E., Cingolani, N., Santojanni, A., Colella, S., Donato, F., Giovannotti, M., Barucchi, V. C. (2013). Searching for a stock structure in Sardina pilchardus from the Adriatic and Ionian seas using a microsatellite DNA-based approach. Scientia Marina, 77(4), 565-574. https://doi.org/10.3989/scimar.03843.26A.

Ruggeri, P., Splendani, A., Occhipinti, G., Fioravanti, T., Santojanni, A., Leonori, I., De Felice, A., Arneri, E., Procaccini, G., Catanaese, G., Tičina, V., Bonanno, A., Nisi Cerioni, P., Giovanotti, M., Grant W.S., Caputo Barucchi, V. (2016). Biocomplexity in populations of european anchovy in the Adriatic Sea. PLoSONE. 11(4): e0153061. https://doi.org/10.1371/journal.pone.0153061.

Russo, A., Carniel, S., Sclavo, M., and Krzelj, M. (2012). Climatology of the northern-central Adriatic Sea. In Wang, S.-Y.S. and Gillies R.R. (Ed.) Modern climatology, InTech. 177-212. https://doi.org/10.5772/34693.

Sabatella, E.C., Colloca, F., Coppola, G., Fiorentino, F., Gambino, M., Malvarosa, L., Sabatella, R. (2017) Key economic characteristics of Italian trawl fisheries and management challenges. Front. Mar. Sci. 4:371. https://doi.org/10.3389/fmars.2017.00371.

Sagarese, S.R., Vaughan, N.R., Walter III, J.F., Karnauskas, M. (2021) Enhancing single-species stock assessments with diverse ecosystem perspectives: a case study for Gulf of Mexico red grouper (Epinephelus morio) and red tides. Can J. Fish. Aquat. Sci. 78:1168-1180. https://doi.org/10.1139/cjfas-2020-0257.

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. In Environments - MDPI (Vol. 11, Issue 1). Multidisciplinary Digital Publishing Institute (MDPI). https://doi.org/10.3390/environments11010022.

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

Schickele, A., Goberville, E., Leroy, B., Beaugrand, G., Hattab, T., Francour, P., Raybaud, V. (2020). European small pelagic fish distribution under global change scenarios. Fish Fish. 22(1): 212–225. https://doi.org/10.1111/faf.12515.

Schirripa, M.J., Goodyear, P.C., Methot, R.M. (2009). Testing different methods of incorporating climate data into the assessment of US West Coast sablefish. ICES J. Mar. Sci. 66 (7): 1605-1613. https://doi.org/10.1093/icesjms/fsp043.

Schismenou, E., Chatzifotis, S., Tsiaras, K., 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. Fish Biol. 105:1178-1188. https://doi.org/10.1111/jfb.15872.

Scott, F., Jardim, E., Millar, C.P., Cerviño, S. (2016). An applied framework for incorporating multiple sources of uncertainty in fisheries stock assessments. PLoSONE. 11(5):e0154922. https://doi.org/10.1371/journal.pone.0154922.

Sinovčić, G. (1978). On the ecology of anchovy, Engraulis encrasicolus (L.), in the Central Adriatic. Acta Adriatica. 19(2):32.

Sinovčić, G. (2000a). Anchovy, Engraulis encrasicolus (LINNAEUS, 1758): biology, population dynamics and fisheries case study. Acta Adriatica. 41(1):3–53.

Sinovčić, G. (2000b). Responsible exploitation of the Sardine, Sardina pilchardus (Walb.), population in the coastal region of the Eastern Adriatic. Periodicum biologorum, 102(1):47–54.

Sinovčić, G. (2001). Biotic and abiotic factors influencing sardine, Sardina pilchardus (Walb.) abundance in the Croatian part of the Eastern Adriatic. Technical Documents 3: 82-86, AdriaMed Technical document, 3.

Sinovčić, G., Franičević, M., Zorica, B., Čikeš Keč, V. (2004). Length-weigth and length-length relationship for 10 pelagic fish species from Adriatic Sea (Croatia). J. Appl.Ichtyol. 20(2): 156-158. https://doi.org/10.1046/j.1439-0426.2003.00519.x.

Sinovčić, G., Zorica, B. (2006). Reproductive cycle and minimal length at sexual maturity of Engraulis encrasicolus (L.) in the Zrmaja River estuary (Adriatic Sea, Croatia). Est. Coast. Shelf Sci. 69:439–448. https://doi.org/10.1016/j.ecss.2006.04.003.

Sinovčić, G., Čikeš Keč, V., Zorica, B. (2008). Population structure, size at maturity and condition of sardine, Sardina pilchardus (Walb., 1792), in the nursery ground of the eastern Adriatic Sea (Krka River Estuary, Croatia). Estuar. Coast. Shelf. Sci. 76:739–744. https://doi.org/10.1016/j.ecss.2007.07.037.

Siple, M. C., Koehn, L. E., Johnson, K. F., Punt, A. E., Canales, T. M., Carpi, P., de Moor, C. L., De Oliveira, J.A. A., Gao, J., Jacobsen, N. S., Lam, M. E., Licandeo, R., Lindegren, M., Ma, S., Óskarsson, G. J., Sanchez Maroño, S., Smoliski, S., Surma, S., Tian, Y., Tommasi, D., Gutiérrez, M.T., Trenkel, V., Zador, S.G., Zimmermann, F. (2021). Considerations for management strategy evaluation for small pelagic fishes. Fish and Fisheries, 22(6), 1167-1186. https://doi.org/10.1111/faf.12579.

Solanki, H.U., Bhatpuria, D., 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(1): 30:43. http://dx.doi.org/10.1080/10106049.2015.1120357.

Takasuka, A., Oozeki, Y., Kubota, H. (2008). Multi-species regime shifts reflected in spawning temperature optima of small pelagic fish in the western North Pacific. Mar. Ecol. Prog. Ser. 360: 211-217. https://doi.org/10.3354/meps07407.

Tugores, M.P., Giannoulaki, M., Iglesias, M., Bonanno, A., Tičina, V., Leonori, I., Machias, A., Tsagarakis, K., Díaz, N., Giráldez, Patti, B., De Felice, A., Basilone, G., Valavanis, V. (2011). Habitat suitability modelling for sardine Sardina pilchardus in a highly diverse ecosystem: the Mediterranean Sea. Mar. Ecol. Prog. Ser. 443: 181-205. https://doi.org/10.3354/meps09366.

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. https://doi.org/10.1007/s00227-014-2463-1.

Van Beveren, E., Fromentin, J., Rouyer, T., Bonhommeau, S., Brosset, P., Saraux, C. (2016). The fisheries history of small pelagiscs in the Northern Mediterranean. ICES J. Mar. Sci. 73(6): 1474–1484. https://doi.org/10.1093/icesjms/fsw023.

Van der Lingen, C., Hutchings, L., and Field, J. (2006). Comparative trophodynamics of anchovy Engraulis encrasicolus and sardine Sardinops sagax in the southern Benguela: are species alternations between small pelagic fish trophodynamically mediated? Afr. J. Mar. Sci. 28(3-4):465–477. https://doi.org/10.2989/18142320609504199.

Verri, G., Furnari, L., Gunduz, M., Senatore, A., Santos da Costa, V., De Lorenzis, A., Fedele, G., Manco, L., Clementi, E., Coppini, G., Mercogliano, P., Mendicino, G., Pinardi, N. (2024). Climate projections of the Adriatic Sea: role of river release. Front. Clim. 6: 1368413. https://doi.org/10.3389/fclim.2024.1368413.

Vučetić, T., Kačić, I. (1973). Echosounder in fisheries: Relationship of small pelagic fish and zooplankton abundance in the central Adriatic. Pomorski zbornik, 11: 335-353.

Whitehead, P. (1990). Checklist of the fishes of the eastern tropical Atlantic (CLOFETA), volume 1, chapter Engraulididae, pages 228–229. JNICT, Lisbon; SEI, Paris; and UNESCO, Paris.

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

Yuniar, A., Zainuddin, M., Hidayat, R., Srioktoviana, S.K., Safruddin, Mustapha, M.A., Farhum, St.A. (2024). Review: The effect of climate change on the distribution pattern of small pelagic fish around the world. Biodiversitas. 25(8):3325-3341. https://doi.org/10.13057/biodiv/d250804.

Zorica, B., Vilibic, I., Čikeš Keč, V., Šepić, J. (2013). Environmental conditions conducive to anchovy (Engraulis encrasicolus) spawning in the Adriatic Sea. Fish Oceanogr. 22(1):32-40. https://doi.org/10.1111/fog.12002.

Zorica, B., Čikeš Keč, V., Vidjak, O., Mladineo, I., Ezgeta Balič, D. (2016). Feeding habits and helminth parasites of sardine (S. pilchardus) and anchovy (E. encrasicolus) in the Adriatic Sea. Mediterr. Mar. Sci. 17(1):216-229. https://doi.org/10.12681/mms.1467.

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Il viaggio a Seattle ha portato una serie di scompigli burocratici tragici che sono diventati comici, a causa del panico scaturito. E questo panico porta inevitabilmentead una chiamata da parte della mia compare **Rosaria**! La prima persona con cui ho parlato non appena messo piede nel famigerato Fano Marine Center, i cui ricordi durante la triennale e la magistrale non sono esattamente rosei, ma questa è un'altra storia. Ros, Ros, pensavi di esserti fatta amica una persona equilibrata e assennata e invece… Se non fosse per te, **Giulia** (terribile acquisto che forse è peggio di me, ma è per questo che ti adoro), **Mattia** detto **Mr. President** e il povero **Kevin** (eccellenza cinese che si è ritrovato in un gruppo di pazzoidi) credo che mi avrebbero trovata appesa all'asta dell'FMC… Vi amo, ragazzi, avete reso quelle interminabili ore di teaching week molto più affrontabili tra giochi dell'oca, battute e commenti mordaci. Grazie di esserci.

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GRAZIE

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