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Evidence of climate-driven regime shifts in Adriatic Sea fisheries

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Summary: Marine ecosystems can undergo abrupt changes due to the interaction between human activities and environmental drivers. These changes can result in a non-linear response, causing the system to shift to a different state, known as a regime shift. Such shifts imply changes in the structure, dynamics and functioning of ecosystems, ultimately impacting on the services they provide to humans. Additionally, such abrupt changes can have serious implications for the effectiveness of management measures, hindering the sustainable exploitation of marine resources and affecting their overall well-being. In our study, we adopted a multi-method approach to test for abrupt changes in Adriatic Sea fishery landings over five decades (1970–2020) and their potential connection with climate change. The ensemble of statistical changepoint analyses applied here identified that the fish community experienced an instability period during the 1990s under the influence of a changing climate, as indicated by significant correlations between fish landings and climate indices. Our study reveals important insights into the development of Adriatic Sea fishery landings under climate change and provides important knowledge for decision-making, sustainable fishery management and preserving the biodiversity and economic viability of the fishery.

Keywords: abrupt changes; instability; sea warming; fisheries; Adriatic ecosystem; changepoint; regime shifts.

Evidencia de cambios de régimen impulsados por el clima en la pesca del mar Adriático

Resumen: Los ecosistemas marinos pueden experimentar cambios bruscos debido a la interacción entre las actividades humanas y los factores ambientales. Estos cambios pueden provocar una respuesta no lineal, lo que lleva al sistema a un estado diferente, conocido como cambio de régimen. Estas modificaciones conllevan alteraciones en la estructura, dinámica y funcionamiento de los ecosistemas, lo que finalmente afecta los servicios que brindan a los seres humanos. Además, cambios tan abruptos pueden tener serias implicaciones en la efectividad de las medidas de gestión, dificultando la explotación sostenible de los recursos marinos y afectando el bienestar general. En nuestra investigación, hemos adoptado un enfoque de múltiples métodos para analizar los cambios bruscos en los desembarques pesqueros en el Mar Adriático a lo largo de cinco décadas (1970-2020) y su posible relación con el cambio climático. Los análisis estadísticos de puntos de cambio aplicados en este estudio identificaron que la comunidad de peces experimentó un período de inestabilidad en la década de los 90 bajo la influencia de un clima cambiante, como lo demuestran las correlaciones significativas entre los desembarques de peces y los índices climáticos. Nuestra investigación aporta información relevante sobre la evolución de los desembarques pesqueros en el mar Adriático en el contexto del cambio climático, ofreciendo valiosos conocimientos para la toma de decisiones orientadas a una gestión pesquera sostenible y la preservación de la biodiversidad y la viabilidad económica de la pesca.

Palabras clave: cambios bruscos; inestabilidad; pesca; ecosistema del Adriático; punto de cambio; cambios en el régimen.

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INTRODUCTION

The extensive exploitation of marine ecosystems from ancient Roman times to the present day, and particularly in the last century, has significantly shifted these ecosystems from their historical baseline characterized by richness, diversity and productivity (Lotze et al. 2006, Pauly 2009). Both land- and ocean-based human activities have altered the oceans through direct and indirect impacts (Halpern et al. 2008). Anthropogenic drivers associated with climate change are one of the main causes of large-scale changes in populations, communities and ecosystems, affecting the global biosphere in general (Rockström et al. 2009, Cheung et al. 2013, Marbà et al. 2015). The interplay of environmental drivers and human pressures may cause a change in the equilibrium state of an ecosystem, affecting its resilience and adaptive capacity in the face of external drivers (Scheffer and Carpenter 2003, Diekmann et al. 2012, Levin and Möllmann 2015).

The rapid reorganization of a system from a state that is quasi-stable state over time to one showing discontinuous dynamics is called a "regime shift" (Scheffer et al. 2001). Regime shifts alter the properties of ecosystems, leading to drastic changes in their structure, dynamics and internal feedbacks, and eventually affecting their specific ecosystem functioning. These phenomena may lead to significant alterations in the services that these ecosystems provide to the human population. Each regime is characterized by a set of governing processes, species compositions and relationships among species and external drivers (Scheffer et al. 2001, Levin and Möllmann 2015). Abrupt and catastrophic changes are expected to increase in strength and frequency following the synergetic effect of anthropogenic pressure and climate change, leading to a potential failure of management measures (Möllmann et al. 2015, Turner et al. 2020).

The Mediterranean Sea is considered as an ecosystem of particular importance due to its rich biodiversity and the unique habitats it offers (Bianchi and Morri 2000). This biodiversity spans multiple forms, including species richness (particularly in the western basin), a high number of endemic species (e.g. in the Adriatic), and the presence of unique and functionally important habitats such as seagrass meadows of the endemic *Posidonia oceanica*, vermetid reefs build by *Dendropoma petraeum*, coralligenous assemblages, and deep sea and pelagic habitats that support uniques species and ecosystems (Coll et al. 2010). Despite supporting human civilizations for millennia, this basin faces significant challenges and it is now recognized as one of the most impacted ecoregions in the world (Halpern et al. 2008, Coll et al. 2009a, Sartor et al. 2014).

Human populations have significantly altered the ecosystems of the Mediterranean through overexploitation, habitat modification, introduction of non-native species, pollution, eutrophication and climate change (Coll et al. 2009a, Marbà et al. 2015). Among these activities, fishing plays an essential role, contributing significantly to employment, economic well-being and food supply. However, the development of advanced fishing technologies, combined with an excessive fishing effort and growing demand for marine resources, has put intense pressure on Mediterranean marine ecosystems (Coll et al. 2009a, Maravelias et al. 2014). Overfishing is considered the main driver of change across the basin, affecting multiple dimensions of biodiversity (Coll et al. 2010). In heavily exploited regions such as the western Mediterranean and the Adriatic Sea, industrialized fishing has significantly reduced the abundance of top predators. This decline, along with the introduction of non-native species, has caused major shifts in species composition. Trawling has further degraded benthic habitats, especially seagrass beds and coralligenous assemblages, reducing both their structural complexity and their ecological functionality (Lotze et al. 2006, Coll et al. 2010).

In response to diverse ecological and socioeconomic implications of the global fisheries crisis, and in order to preserve the sustainability of the marine ecosystems and the services that they provide to human populations, various management measures have been proposed and implemented (Mora et al. 2009). In the Mediterranean, management strategies have been guided by the Implementation Plan adopted during the World Summit on Sustainable Development, aiming to restore the depleted fish stocks to levels that can produce the maximum sustainable yield. However, the number of exploited species in the region far exceeds the number of stocks that are regularly assessed (GFCM 2023). Furthermore, the Common Fisheries Policy (CFP) has struggled to reduce the trend of exploitation to the required levels and to restore marine ecosystems. Though concrete progress has been made towards creating a more sustainable fishery sector, the Mediterranean ecosystem is facing various complex challenges which the CFP and fishery sector cannot address alone. The adverse effects of the fishing activities on the marine ecosystems, coupled with the poor status of the marine ecosystems, pose a direct threat to the sustainability of the fisheries resources (Colloca et al. 2017, European Commission 2023). As a consequence, many fish stocks are still assessed to be overfished and exceeding their biological limits, hindering restoration efforts (GFCM 2023).

In this study, we used a combination of approaches to identify abrupt changes as an indicator of regime shifts in the Adriatic Sea fish community and explored the influence of climate change, which is recognized as playing a crucial role in the dynamics of the Adriatic ecosystem (Coll et al. 2009b, Barausse et al. 2011). The Adriatic Sea is characterized by intense exploitation and significant anthropogenic influences such as fisheries, nutrient inputs and environmental factors. Over the years, there has been a notable shift in species composition and diversity, marked by a decline of formerly abundant species and the introduction of new ones, predominantly involving smaller organisms of lower trophic levels (Coll et al. 2009b, Lotze et al. 2011, Sguotti et al. 2022). The Adriatic Sea is a highly productive basin characterized by high species richness and a pronounced presence of endemic species (Fanelli et al. 2023), which makes it an ideal location for studies investigating the impact of climate conditions on marine populations.

MATERIALS AND METHODS

Data

One of the main challenges in the analysis of fish population dynamics is the lack of available long-term time-series data from scientific surveys. In the Mediterranean, the longest running scientific survey of fisheries resources is the Mediterranean International Bottom Trawl Survey (MEDITS), which provides field-based data from scientific surveys of fish stocks. However, MEDITS data are not publicly available (Vasilakopoulos et al. 2017). As a result, landing datasets have been commonly used as a proxy of fish abundance trends in previous studies in the basin (Barausse et al. 2011, Tzanatos et al. 2014, Vasilakopoulos et al. 2017). While landing data can offer useful insights, they come with inherent biases and show various limitations because of several factors influencing catches, such as changes in fishing effort, fishing regulations, data collection frameworks, reporting systems and market demands (Barausse et al. 2011). Despite these limitations, landing data remain a crucial component of any fisheries assessment (Pauly et al. 2013). They are often the best data available for many fisheries and, if properly conditioned, are expected to provide a generally suitable picture of the trends of exploited taxa (Froese et al. 2012).

In our analysis, limited by the lack of available time-series data from scientific surveys carried out in the basin, we used annual fish catches in the Adriatic Sea, expressed as live weight equivalent of landings, which have been routinely recorded since 1970 by the General Fisheries Commission for the Mediterranean (GFCM 2023). To define statistical subareas, the GFCM designates the Adriatic Sea within area 2.1, encompassing only the northern and central basins. The southern Adriatic basin, the coast of southeastern Italy and of Albania, is classified under area 2.2 (as the Ionian Sea). In order to provide an overview of the Adriatic Sea fishery production that is as comprehensive as possible, catch data from Albanian fisheries originally classified as from the Ionian Sea were incorporated into the Adriatic data set, as indicated in previous studies of the fishery dynamics in the Adriatic Sea (Mannini and Massa 2000). Unfortunately, this inclusion was not feasible for southeast Italy because area 2.2 encompasses both the southeastern Adriatic coast and the southern Ionian coast of Italy, making it impossible to distinguish the data from these two regions. To assess temporal variations in community composition, we aggregated yearly data for each Adriatic country into annual cumulative datasets. Our analysis was limited to taxa for which data were available throughout the entire period. In total, 27 taxa were analysed, of which 11 referred to the species level, 7 to the genus level and 5 to the family level, and the remaining 4 encompassed species from more than one family (Table S1).

External pressures

In our study we used sea surface temperature (SST), the North Atlantic Oscillation (NAO) and the Atlantic Multidecadal Oscillation (AMO) as indicators of climate change, as they have been shown to affect the Mediterranean Sea ecosystem in the past (Tsikliras et al. 2019, Alheit et al. 2019, Sguotti et al. 2022). SST data for Geographical Subareas (GSA) 17 and 18 were extracted from the NOAA ERSST v5 dataset (data.noaa.ersst.v5.html). The SST data (in °C) were averaged to annual values to make them comparable with the fisheries time series. Although this method may have led to the loss of specific details concerning extreme events in the Adriatic region, it enabled us to extract the main temperature trend over time (Sguotti et al. 2022). To minimize the effect of the confounding factors on the data, we used anomaly data instead of absolute temperature (https://www.ncei.noaa.gov/access/monitoring/dyk/anomalies-vs-temperature). NAO and AMO data were collected from the Earth System Research Laboratory (NOAA, https://www.esrl.noaa.gov/). The NAO index describes changes in strength of two atmospheric pressure patterns over the North Atlantic, a low near Iceland and a high near Azores. We used the NAO winter index, which is derived from the mean pressure difference between December and March as the NAO pattern is most pronounced during the winter months (Hurrell et al. 2001). The AMO index is based on the SST anomalies in the Atlantic Ocean's northern hemisphere. The AMO refers to long-term fluctuations in Atlantic SSTs, which are linked to coherent temperature variations across the northern hemisphere (0°–70°N) (Knight et al. 2006). Monthly AMO data were averaged to annual values as well.

Principal component analysis and constrained clustering

In order to understand the common trends in the Adriatic Sea fisheries landings, we conducted a principal component analysis (PCA) and constrained clustering. PCA is one of the most common techniques used to reduce the dimensionality of a large data set because it allows the dataset to be simplified, while preserving as much information as possible. The aim of this multivariate analysis is to obtain a compact and accurate representation of the data that reduces statistically redundant components (Planque and Arneberg 2018). After decomposing the variability of the dataset, PCA provides a set of linearly uncorrelated variables known as principal components. These components are ranked according to their ability to explain the overall variation of the dataset, enabling comparison with system stressors (Möllmann and Diekmann 2012). PC1 and PC2 were extracted as long-term signals of the fish community change, capturing the main variability observed in the time series of all the analysed species.

Constrained clustering was performed on the principal components to identify groups of years with similar patterns by calculating the Euclidian distances between years. The number of significant clusters was determined through graphical interpretation of the constrained incremental sum of squares clustering (CONISS) broken stick method, along with CONISS cluster plots (Diekmann et al. 2012)

Correlation analysis

Pearson correlation analysis was employed to investigate the relationship between landings and climate indices. To mitigate the influence of autocorrelation, the significance of the correlation was adjusted using the “modified Chelton method” (Pyper and Peterman 1998). This method calculates the effective degrees of freedom which are fewer in the autocorrelated series; consequently, it yields a higher critical value (r_{crit}) that the correlation coefficient must exceed to be considered significant.

Changepoint identification

The presence of structural changes in the first principal component (PC1) was identified using different statistical change-point methods, each encompassing distinct statistical concepts. Consequently, changepoints identified in a time series may exhibit slight variation. Three R packages were utilized in our analysis: bcp, changepoint and STARS. Changepoints were considered valid only if detected by at least two methods with approximately the same timeframe (±1 year).

Bayesian changepoint analysis utilizes a Bayesian approach to calculate posterior probabilities of changes at any given point of the time series. The bcp function applies the Markov chain Monte Carlo method to estimate the probability that the mean values before and after a potential change point differ significally enough to be considered a real change rather than just random variation (Erdman and Emerson 2008). The second method was applied using the R-package changepoint, which identifies the points where the statistical properties of a time series change. The changepoints in the mean value of the PC1 time-series were tested using the cpt.mean function (Killick and Eckley 2014). Within the algorithm we used the Pruned Exact Linear Time method, which efficiently identifies the optimal number and location of changepoints in time-series data. Additionally, we employed the “Normal” test statistic and the Akaike information criterion as the penalty criterion, while setting a minimum segment length of 10 years to ensure a reasonable regime length (Möllmann et al. 2021).

Sequential t-test analysis of regime shifts (STARS) is based on a sequential t-test that can signal a possibility of a regime shift in real time. The STARS algorithm is designed to identify statistically significant changes in both the mean level and the magnitude of fluctuations in time-series data by applying modified two-sided Student t-tests. Additionally, it calculates a regime shift index (RSI) to examine the existence, timing and significance of abrupt changes in time-series data (Rodionov 2004).

R environment and packages

The analysis was completed using the R programming language and statistical environment (R Core Team 2024). For visualizations, we utilized the ggplot2 package. A comprehensive list of packages and functions employed in the analyses mentioned above is provided in Table S2.

RESULTS

Changes in the structure of Adriatic Sea fisheries landings

We investigated trends in fisheries landings of 27 taxa in the Adriatic Sea for the period 1970–2020 based on data obtained from the GFCM database to assess temporal changes in the fish community composition. The species composition of Adriatic Sea fishery landings, considered as indicative of marine population dynamics, demonstrates diverse patterns. Applying constrained clustering we identified a strong structural change in the fisheries landings of the Adriatic Sea (Fig. 1). We found that about half of the analysed taxa followed a decreasing trend, and cluster analysis revealed a sharp change in their landings in the early 1990s, i.e. between 1991 and 1992 (Fig. 1 A,

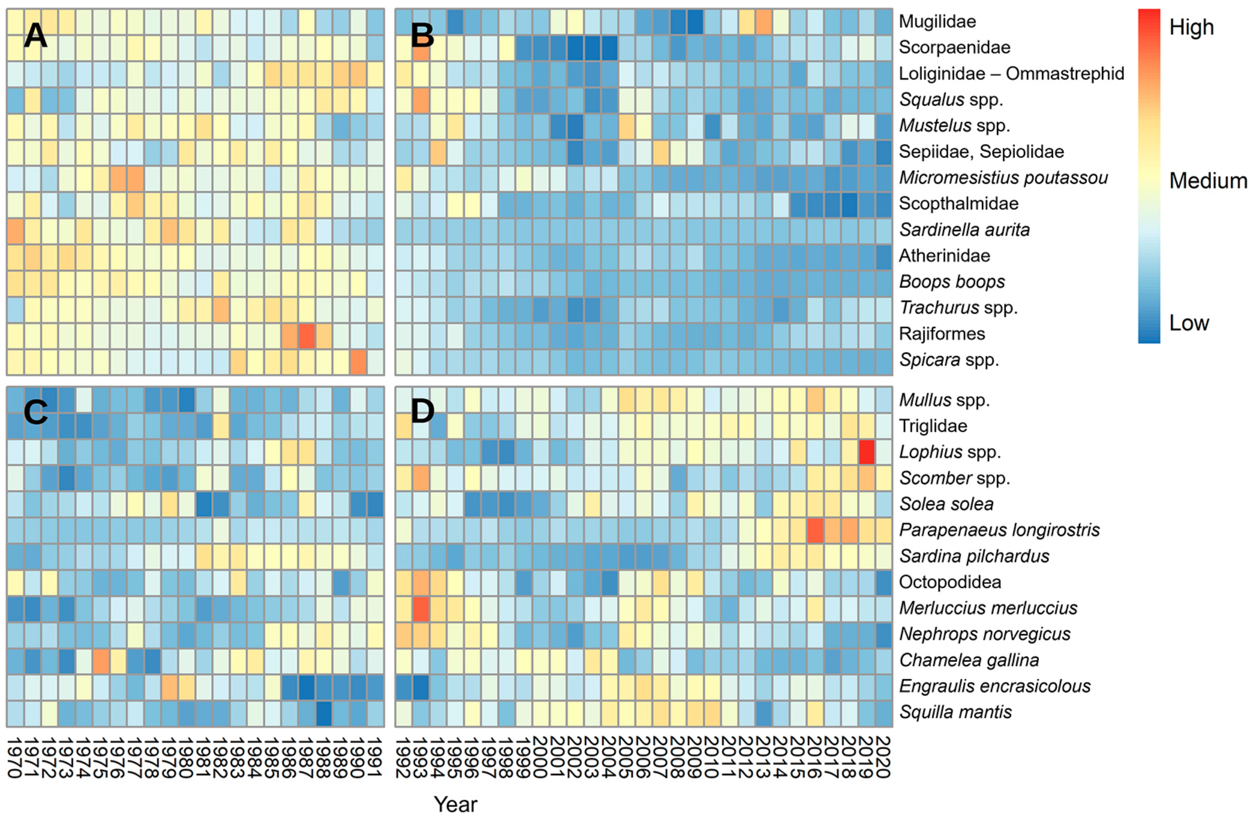

Fig. 1. – Changes in the structure of Adriatic Sea fisheries landings. Heatmap of temporal development of relative landings of 27 taxonomic categories; labels (A-D), taxonomic categories order and breaks in the heatmap are according to constrained clustering (see Fig. 2)

B). A second cluster of the landed fish community displayed a more variable but mostly increasing trend during the study period (Fig. 1 C, D).

During our study period, the overall landings of the Adriatic countries reached a peak in 1982 but thereafter experienced a sharp decline that persisted until the mid-1990s. Subsequently, the Adriatic fishery showed small perturbations, and a gradual increase in landings reached a second peak in the mid-2010s (Fig. S1). It is important to mention that the trend of overall landings is primarily influenced by the landings of the small pelagics. These species make the highest contribution to the total yearly landings, accounting for 38% to 70.7% of the total. The contribution of the demersal share in the total landings showed less variation during the study period, accounting for 8% to 18 % of the total.

In the second step of our analysis, we conducted a PCA to identify the dominating modes of variability in the matrix of Adriatic fisheries landings (Fig. 2). The first two principal components (PC 1 and 2) explained 37% and 14% of the total variance, respectively. A PCA biplot further demonstrated the divide in Adriatic fisheries landings between the periods before and after the early 1990s (Fig. 2A; years in blue and red identified by constrained cluster analysis). PC1 represented the temporal development of cluster 1, of which red mullet, gurnard, bogue, skates and rays, and horse mackerels were indicative species (Fig. 2B). PC1 was characterized by a relatively stable state until 1990 and a rapid change afterwards towards a more stable situation from the early 2000s (Fig. 2B). In contrast, PC2 demonstrated a linear change in a group of species characterized by hake, Norway lobster, octopuses and mackerels (Fig. 2C) until the early

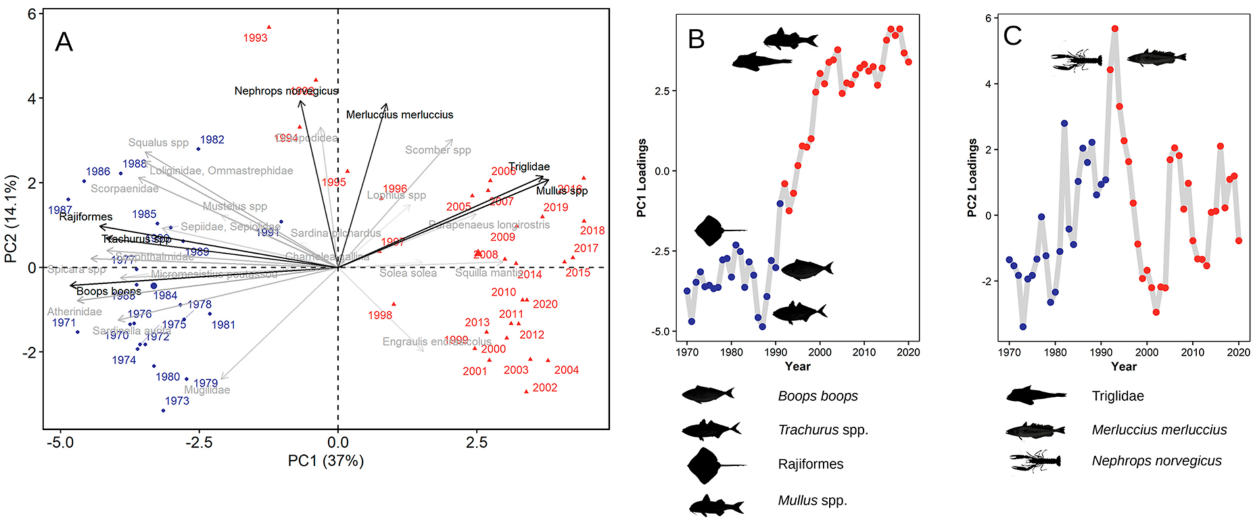

Fig. 2. – Principal Component Analysis of Adriatic Sea fisheries landings. (A) Biplot of principal component (PC)1 and PC2 loadings with the respective explained variance in brackets. (B) Time-series of PC1 and (C) of PC2 scores. Point color indicates the phases identified by a constrained cluster analysis. Arrows in (A) and fish icons in (B) and (C) represent the most important species in each temporal cluster.

1990s. The temporal development of PC2 was reversed until the early 2000s and quite variable towards the end of the study period.

Abrupt changes and regimes in the Adriatic fish community

Next, we applied an ensemble of statistical changepoint analyses to PC1 (the main mode of variability in the data) to test for abrupt changes as indications of a regime shift in Adriatic fisheries landings. The application of the three methods, each representing a different statistical philosophy, allowed us gain a better understanding of non-linear dynamics in the landings data set, potentially representing regime changes in the fish community (Fig. 3). First, the analysis with the algorithm of the changepoint package discerned three periods (indicated by horizontal lines in Fig. 3): 1970–1988, 1989–1999 and 2000–2020. High probabilities of change derived from the Bayesian changepoint analysis supported the existence of an unstable intermediate period (basically representing the 1990s). This period of instability was also indicated by the STARS algorithm, which demonstrates abrupt changes through high RSI values in 1991 and 1999.

Eventually, both STARS and the Bayesian approach indicated instability and potentially an abrupt change in the mid-2010s. The Bayesian method identified an abrupt change in 2014, albeit with lower posterior probability than the earlier changes, while the STARS method revealed several fluctuations of the RSI during the period 2015–2020 (Fig. 3).

The succession among the three identified stages of the Adriatic Sea fish community evolution showed significant changes. The demersal community showed a continuous decline of large, slow-growing predators over the entire time series, accompanied by an increase in smaller-bodied species. Initially, the hake and Norway lobster populations dominated the second phase, reaching their peak levels and decreasing again during the 1990s. Later, another shift took place in 1999, marked by the continuous increase in species such as gurnard and mullets.

Regarding the pelagic fish, the first phase was characterized by the collapse of the anchovy stock in the late 1980s, and the sardine population reached its lowest levels during the 1990s. While anchovy and sardines remained at their lowest levels, mackerels continued their increasing trend but decreased after the year 2000. The fluctuations of anchovy and sardine persisted in the last two decades, with anchovy fluctuating between similar levels before again reaching low levels comparable to those observed at the beginning of the time series, while sardine showed a sharp increase (Fig. S1).

Trends in climate indices and their relationship with fisheries landings

In the dynamics of fish communities in the Adriatic Sea, it is imperative to consider the broader context of environmental factors (Coll et al. 2009b, Barausse et al. 2011, Sguotti et al. 2022). These factors likely play a pivotal role in shaping the trends we have observed. Hence, we conducted a correlation analysis of the landings of each species/group and PC1 (considered as the fish community indicator) with SST and the climate indices NAO and AMO. Our analysis showed that SST in the Adriatic was constantly rising during the study period (Fig. 4). The mean SST showed a constant increase with an amplitude of change of about 2°C and an increasing rate of 0.03°C/year (Fig. 4A). Correlation analysis revealed that 17 of the 27 taxa were correlated with SST anomalies, 11 negatively and 6 positively (p<0.05) (Fig. 4D). All correlations were tested for a two-year time lag (Table S3).

The AMO demonstrated upward trends, with its transition from a negative to positive phase noted around the year 2000 (Fig. 4B). Similarly to SST, the landing trend of the majority of the analysed taxa exhibited significant correlations with the AMO. Of the 27 taxa examined, negative correlations were observed in 13 cases and positive correlations in 6 cases (Fig. 4E). Similarly, the NAO index exhibited a consistent increasing trend throughout the time series, predominantly characterized by positive phases occasionally interrupted by sporadic negative shifts (Fig 4C). Correlation analysis revealed that 10 taxa were significantly correlated (p<0.05) with NAO. Positive and negative correlations were observed in 5 cases each (Fig. 4F). When abiotic factors were correlated with the community signals, SST and the AMO

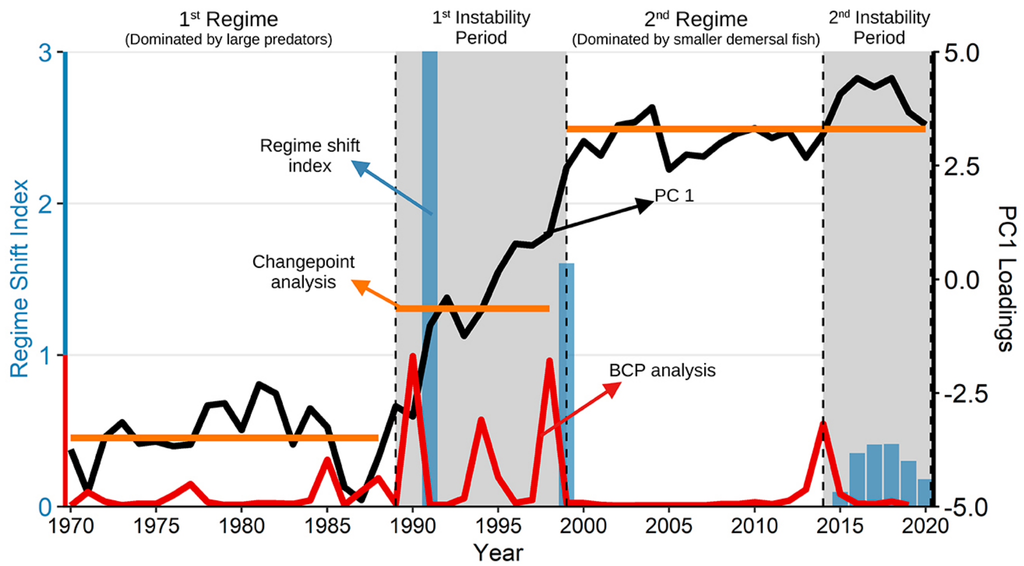

Fig. 3. – Abrupt shifts in Adriatic Sea fisheries landings identified by multiple changepoint analyses. The black line represents the main mode of temporal variation in the fish community (PC1; see Fig. 2); the red line represents the probability of change derived by Bayesian changepont analysis (BCP); horizontal orange lines indicate regimes identified by the changepoint package; light blue bars indicate the regime shift index values calculated with the STARS package; grey areas represent the ensemble interpretation of regimes and instability periods.

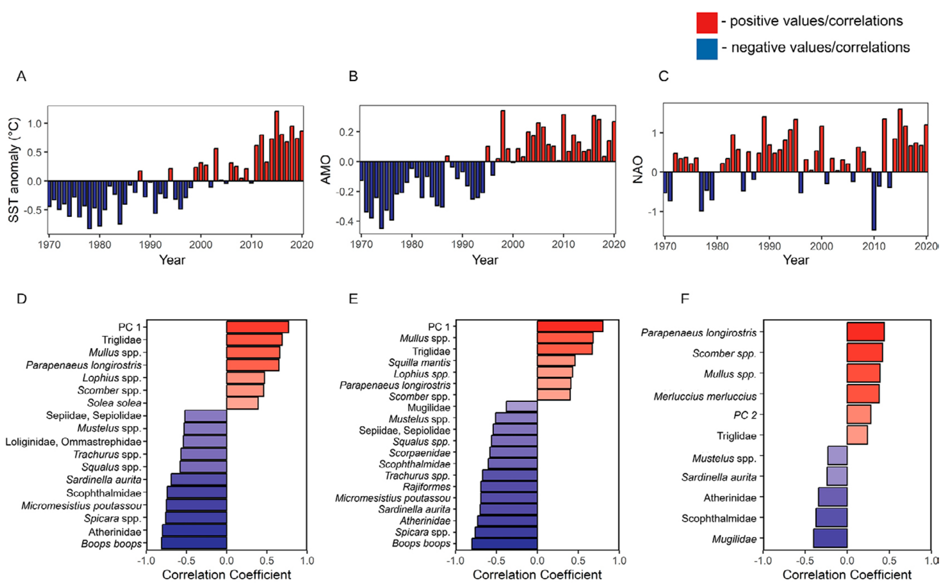

Fig. 4. – Temporal development of climate indicators. (A) Sea surface temperature (SST) anomaly, (B) Atlantic Multidecadal Oscillation (AMO) and (C) North Atlantic Oscillation (NAO). (D–F) Bar plots showing significant correlations (p<0.05) of the studied taxa with SST, AMO and NAO, respectively.

displayed highly significant positive correlations with PC1, whereas the NAO exhibited a positive correlation with PC2 (Fig. 4 D, E, F).

DISCUSSION

The objective of this study was to investigate abrupt shifts in Adriatic Sea fisheries landings over five decades as indications of a potential regime shift in the local fish community, in addition to assessing the importance of climate change for the observed changes. The combination of multivariate statistical analysis including principal component and cluster analysis, correlation analysis, and especially a multi-model changepoint analysis, revealed important insights into the stability of the fish community and the role of ocean warming. Specifically, we found two abrupt changes in the early and late 1990s, a transition period separating two quasi-stable states characterized by different species compositions. The first state was mostly dominated by large-sized and late-maturing predators, i.e. sharks and rays, while the second was characterized by an increase in small-sized and early-maturing species, i.e. gurnards and red mullets. Our study corroborates previous reports on regime shifts in the Mediterranean Sea and especially the Adriatic (Barausse et al. 2011, Vasilakopoulos et al. 2017, Sguotti et al. 2022), but adds a broader understanding of potential non-linear dynamics in the local fish community.

We based our analysis of potential abrupt changes in the Mediterranean fish community on a single data set covering 50 years of fisheries landings. Analysing landings instead of results from scientific surveys (because the latter are often not available) is problematic because they do not necessarily reflect the abundance or biomass of the species' populations and may additionally affect them (Pauly et al. 2013). Landings data are usually influenced by factors such as fishing effort, unreported landings, discarding practices and market demands (Barausse et al. 2011, Piroddi et al. 2015). However, landings are expected to provide a generally suitable picture of the trends of exploited taxa if conditioned properly (Froese et al. 2012).

Among the influencing factors, discarding and illegal, unregulated and unreported (IUU) fishing activities pose significant limitations. These practices are widespread in the Mediterranean and lead to substantial underestimation of the impact of fisheries on stock biomass, biasing our ability to understand fisheries impact and thereby complicating the design and implementation of effective management strategies (Coll et al. 2014, Tsagarakis et al. 2014). For instance, estimates indicate that IUU catches, including discards, account for more than 38% of the total fish removals in the Mediterranean, with average values exceeding 40% in southern regions. The reported estimates vary significantly, ranging from 35% in Greece and 63% in Turkey to more than five times the reported catch in Corsica and 2.3 times the reported catch in the Balearic Islands (Coll et al. 2014). These considerations suggest that, in addition to reported landings, the inclusion of estimates of IUU catches and discards would contribute to a more comprehensive understanding of community dynamics.

Despite these limitations, reconstructed FAO landings in the Mediterranean Sea, considering the potential biases, showed that the overall pattern of the reconstructed data aligns with official statistical trends (Pauly et al. 2014, Piroddi et al. 2015). Consequently, the FAO landing dataset has been used as a source of data in several studies focused on the dynamics of fish populations in the Mediterranean (Barausse et al. 2011, Tzanatos et al. 2014, Vasilakopoulos et al. 2017).

Another possible limitation resides in the lack of fishing effort data comparable with the landings dataset. While the Adriatic Sea is exploited by several countries, the absence of effort data specifically for Croatia, one of the major contributors to regional landings due to its large fishing fleet, creates a significant gap. Available data on Croatian vessel activity dates back only to 2013 (https://www.fao.org/gfcm/data/fleet/register), coinciding with its accession to the European Union, and therefore does not reflect the actual start of fishing operations. This limitation makes it impossible to use fishing effort data to correct landings and to apply more reliable proxies, such as landings per unit effort, over the entire study period. Consequently, we rely on landings data as a proxy for assessing population trends.

This approach is further supported by the generalist nature of fishing in the Adriatic, where vessels typically target multiple species. During the study period, the analysed species showed divergent trends; some increasing, some decreasing and others oscillating. These patterns cannot be fully explained by fishing effort alone, suggesting that landings also reflect underlying biological fluctuations (Barausse et al. 2011). Furthermore, historical trends in fishing capacity across Mediterranean EU countries, which increased throughout the 20th century before steadily declining after the 1980s–1990s (depending on the region), indicate that changes in landings cannot be attributed solely to fishing effort (Osio 2012, Cardinale et al. 2017).

Furthermore, our analyses were not directly based on raw landings data, but rather on the first principal component. This method normalized the data to ensure consistency across species with different abundances, reducing bias toward more heavily landed species, and captured the main variability in the community state. While this approach mitigates some of the biases inherent in the landings data, we advocate for the integration of complementary fishery-independent data from scientific surveys, such as MEDITS, to further strengthen the assessment of community dynamics.

Our analysis adds to the multitude of studies that report ecosystem regime changes during the late 1980s/early 1990s in the northern hemisphere (Möllmann and Diekmann 2012), which also appears to have been a crucial period of change in Mediterranean fish populations, as suggested by similar findings in the Northern Adriatic, the Aegean Sea and the Mediterranean basin in general (Conversi et al. 2010, Damalas et al. 2021, Sguotti et al. 2022). These substantial changes are likely caused by climatic dynamics, whose signature is a shift in the NAO and increased water temperature (Conversi et al. 2010, Barausse et al. 2011), as confirmed by our study.

In addition, our study confirms the occurrence of abrupt changes in the late 1990s. These shifts have also been identified by recent studies in the Mediterranean employing diverse datasets, techniques and approaches (Vasilakopoulos et al. 2017, Damalas et al. 2021, Sguotti et al. 2022). These shifts coincide with the warm phase of the AMO and the increase in water temperature (Fig. 3). The AMO phase shift is considered to have a positive effect on the increase in the anchovy population in central and eastern Mediterranean sub-regions (Tsikliras et al. 2019) (Fig. S1), which is an essential component of the marine ecosystems, occupying an important trophic role in the ecosystem, and its abundance could directly influence the majority of the biota in the ecosystem (Barausse et al. 2011).

Our correlation analysis revealed that most of the taxa displayed significative positive or negative relationships with climate change indicators. Specifically, a greater number of taxa exhibited a correlation with SST and the AMO than those demonstrating a correlation with the NAO. The influence of the NAO on Mediterranean ecosystems varies depending on their distance from the Atlantic, a stronger effect being observed in the western part of the basin than in the other sub-regions (Tsikliras et al. 2019).

Species showing positive correlation with all the environmental indices tended to be warm-affinity species such as red mullet, gurnard and deep water rose shrimp. An exception was the case of the *Scomber* spp, which, despite preferring colder waters, showed an increase in landings throughout the study period. This increase may be attributed to its distribution in the northern area of the basin, one of the coldest areas in the Mediterranean, which may act as a refuge for cold-water species (Fortibuoni et al. 2015). Cold-affinity species such as smelt, turbots, blue whiting and pickarels showed negative correlations with environmental indices. Elasmobranch species (*Mustelus* spp., *Squalus* spp. and Rajiformes) also exhibited a negative correlation with the environmental variability. As indicated by the time-series of the climate change indocators (Fig. 4 A, B, C), hydroclimatic changes have led to reduced productivity in the Adriatic ecosystem, with negative impacts on elasmobranch populations (Barausse et al. 2014). A negative correlation was also found for the warm-affinity species round sardinella, whose abundance also depends on life-history characteristics of the species (Guidetti et al. 2002).

Additionally, PC1 reflecting the community reorganization was found to be positively correlated with both SST and the AMO. Although fishing pressure (for which data are lacking) certainly has an important role in the dynamics of fished populations, our correlations highlight the well-established influence of warming on Mediterranean ecosystems (Barausse et al. 2011, Tzanatos et al. 2014, Vasilakopoulos et al. 2017).

The interaction between climate change and fishing pressure represents a critical challenge for the sustainability of marine ecosystems, resulting in an increase in the ecological stress and ecosystem variability. Intensive fishing reduces population abundance and truncates age structure, thereby increasing sensitivity to environmental fluctuations and inducing evolutionary changes in life-history traits such as age and size at maturity, body size and growth rate (Ernande et al. 2004, Sharpe and Hendry 2009). Simultaneously, climate change alters hydrographic and meteorological conditions, directly affecting fish physiology, distribution, growth and reproductive capacity, while indirectly reshaping ecosystem productivity and structure (Mackenzie et al. 2007, Cheung et al. 2010, Tzanatos et al. 2014). The resulting synergy between these pressures can undermine ecosystem stability and resilience, often leading to non-linear responses such as regime shifts, which challenge the effectiveness of conventional management strategies (Möllmann et al. 2015).

A major result of our study on potential non-linearities in the Adriatic fish community is the detection of periods that likely represent instabilities in the system. We found an important instability period with rapid changes in species composition during the 1990s, which separated quasi-stable periods in the landings before and after. A similar pattern was also observed in the Aegean Sea demersal community (Damalas et al. 2021). We additionally observed indications of an instability period at the end of the study period from 2015. The identification of these instabilities was possible due to the parallel use of multiple statistical changepoint analysis techniques, an approach that has been rarely followed in ecological applications (but see Pélissié et al. 2024).

The detection of these unstable periods on PC1 (representing the community change) was especially possible due to the use of the Bayesian approach to changepoints (i.e. bcp). This approach returns probabilities of change, and a sequence of such high probabilities is a characteristic of the 1990s (Möllmann and Diekmann 2012, Vasilakopoulos et al. 2017, Sguotti et al. 2022). The detection of instabilities is further supported by the STARS algorithm, which delineated the 1990s from the preceding and following periods based on high RSI values. A sequence of higher RSI values also indicates that the recent years of the time series represent unstable conditions, though such results of STARS need to be interpreted with caution since the algorithm tends to deliver false positives at the last cut-off window (Stirnimann et al. 2019). However, previous findings support a change in the community in the Adriatic Sea during the 2010s characterized by an increase in demersal species (Sguotti et al. 2022). A regime shift during the 2010s is also suggested for the Aegean demersal community, though the authors consider this finding with caution due to methodological limitations (Damalas et al. 2021).

In the Adriatic, in addition to climate change and fishing, a variety of other environmental and anthropogenic drivers are likely to influence fish population dynamics. Habitat degradation, eutrophication from riverine inputs (notably the Po River), marine pollution and the introduction of non-indigenous species are all known to impact ecosystem structure and function in this region (Lotze et al. 2006, Coll et al. 2009b, Barausse et al. 2011). A notable example is the regime shift of the small pelagics in the late 1980s, attributed to the combined effects of overfishing, riverine inputs (and associated alternations in primary production), environmental variability, climate change and altered hydrographic conditions. An additional important factor was the increased anchovy mortality due to egg and larval predation by the purple-striped jelly (*Pelagia noctiluca*) (Conversi et al. 2010, Barausse et al. 2011). Given the critical trophic role that small pelagics play in the ecosystem, fluctuations in their biomass can propagate through the ecosystem, affecting a variety of marine organisms, including demersal communities (Barausse et al. 2011, Sguotti et al. 2022).

The late 1980s were also characterized by synchronous variability in the landings of different species across all Adriatic ports, decoupling landing patterns from local fishing effort, which alone cannot explain the observed changes (Conversi et al. 2010). Previous research highlights the occurrence of regime shifts not only in the Adriatic pelagic communities but also across several ecosystem components, including physical water properties, plankton and demersal communities, thus indicating that the ecosystem underwent general and profound abrupt changes (Barausse et al. 2011). Although the observed changes in the demersal communities are complex and not easy to explain, previous findings emphasized the important role of combined effects of climate change and fishing pressure in the development of new regimes within the basin (Sguotti et al. 2022). While the present study focuses on characterizing long-term shifts in the local fish community and exploring whether these reflected regime shifts are potentially linked to climate variability, evaluating the impact of additional drivers and their interacting mechanisms will require complementary analyses beyond the scope of this work.

The Adriatic marine community, like many other ecosystems such as the Baltic Sea, Black Sea and Northwest Atlantic (Möllmann and Diekmann 2012, Möllmann et al. 2015), appears to have reached a new structure characterized by a new species mix, as also noted in previous research (Barausse et al. 2011, Sguotti et al. 2022). While the long-term ecological and functional outcomes of such transitions, including their impact on ecosystem services, remain difficult to predict, the nature of regime shifts poses significant management challenges (Möllmann et al. 2015).

Regime shifts are particularly critical because they are often abrupt, occur without warning, and are driven by multiple interacting external pressures that erode systems' ability to tolerate disturbances without transforming to a qualitatively different state, recognized as resilience (Scheffer et al. 2001, Scheffer and Carpenter 2003). In the worst cases, these shifts can be irreversible, driving the ecosystem into new states governed by different feed-back mechanisms, leading to a potential failure of management measures. Understanding the drivers and pressures behind these changes is critical for informing early management responses (Levin and Möllmann 2015). Detecting early signals of such transitions is essential for implementing adaptive, ecosystem-based management approaches. Although further research is needed to fully assess the implications of these transitions, incorporating discontinuous dynamics into current management frameworks can help mitigate risks and enable more robust decision-making in the face of ongoing environmental variability (Conversi et al. 2010, Levin and Möllmann 2015, Möllmann et al. 2015).

In conclusion, our research provides strong evidence that the Adriatic Sea fish community has experienced abrupt regime shifts over the past five decades. Using a multi-model approach, we identified explicit non-linear dynamics with unstable periods of change separating quasi-stable regimes, at least partially in response to climate change. Our findings support the current body of knowledge and indicate the vulnerability of the Mediterranean fish community to environmental changes. Our results contribute important knowledge to be included in the decision-making process to support sustainable fishery management and preserve the biodiversity and economic viability of the Mediterranean Sea.

SUPPLEMENTARY MATERIAL

The following supplementary material is available through the online version of this article:

Table S1. Compilation of the taxa used for the analysis, along with their common names as coded in the FAO database and the corresponding groups (demersal fish, small pelagic fish, medium pelagic fish, cephalopods, crustaceans and bivalves).

Table S2. R packages and functions used in the analyses of the Adriatic Sea fish community.

Table S3. Relationship between the analysed taxa and environmental indices (SST, NAO and AMO), indicating the lag with the highest correlation coefficient ($p<0.05$). Non-significant results are denoted by an asterisk.

Fig. S1. Total landings (in tonnes) in the Adriatic during the studied time series (1970-2020).

Fig. S2. Temporal trends of the taxa landings (in tonnes) analysed. The smooth loess (blue line) is applied. Species are sorted according to their contribution to the PC 1.

Fig. S3. Constrained hierarchical cluster plot identifying two distinct clusters highlighted by red rectangles.

DATA AVAILABILITY

The fish landing data we used in this study are from the General Fisheries Commission for Mediterranean Database, available to download at: https://www.fao.org/gfcm/data/capture-production.

The temperature data are freely available from NOAA/ESRL PSD at https://psl.noaa.gov/data/gridded/data.noaa.ersst.v4.html.

The NAO and AMO data are freely available from Earth System Research Laboratory (NOAA, https://www.esrl.noaa.gov/)

DECLARATION OF COMPETING INTEREST

The authors of this article declare that they have no financial, professional or personal conflicts of interest that could have inappropriately influenced this work.

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AUTHORSHIP CONTRIBUTION STATEMENT

Elvis Kamberi: Conceptualization, Data Curation, Formal analysis, Investigation, Visualization, Methodology, Writing – original draft. **Edmond Hala:** Investigation, Supervision, Writing – review & editing. **Marco Kule:** Formal analysis, Writing – review & editing. **Christian Möllmann:** Conceptualization, Methodology, Supervision, Project Administration, Writing – review & editing.

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