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# Impact of large-scale oceanic variability on Adriatic fisheries evidenced through the 'mean temperature of the catch' approach

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Climate change is significantly impacting marine ecosystems, altering their structure and functioning by influencing all levels of organization. The effects of global warming alter the productivity of marine fish populations and cause shifts in their geographical distribution towards higher latitudes, altogether affecting resource availability for fisheries. The mean temperature of the catch (MTC) is an index used to assess the effect of climate warming on fisheries. MTC is calculated based on the preferred temperature of exploited species, weighted by their annual catch. In our study, we calculated the MTC for Adriatic Sea fishery landings over five decades (1970-2020) to evaluate the response of the local fish community to warming. Our results show that after an initial decreasing trend until the late 1980s at a rate of 0.48°C per decade, the MTC subsequently increased at a rate of 0.24°C per decade. The MTC trend correlated significantly with regional climate indices, such as the North Atlantic Oscillation (NAO) and the Atlantic Multidecadal Oscillation (AMO). Adriatic landings exhibit distinct temporal shifts in the ratio of warm-water to cold-water species, contrasting with patterns observed in other Mediterranean regions. Nevertheless, despite these fluctuations, the contribution of various warm-water species has increased over the last 15 years. Although this study suggests a lower increasing rate in the MTC in recent decades compared to other Mediterranean areas, it highlights that the Adriatic fish community is experiencing significant changes in relation to sea warming and demonstrates the MTC to be a useful indicator for changes in the Adriatic fish community composition.

KEYWORDS
**climate change, fisheries, mtc, thermal affinity, adriatic sea**

## 1 Introduction

Fishing and climate change represent the greatest pressures impacting marine ecosystems on a global scale (Costello et al., 2010; Worm and Lotze, 2021). Despite the implementation of various management measures and approaches, many fish populations worldwide remain overfished (Palomares et al., 2020; Britten et al., 2021). The unsustainable expansion of fishing effort is a primary driver of the significant decline in fish biomass (Watson et al., 2013), altering fish community structures (Stergiou and Tsikliras, 2011; Sguotti et al., 2022). Furthermore, fishing influences life history traits such as age and size at maturity, body size and growth rate (Ernande et al., 2004; Olsen et al., 2004; Sharpe and Hendry, 2009). Marine ecosystems are also under continuous pressure from ocean warming, which can alter species abundance, distribution and community structure, thereby influencing the composition of fisheries landings and its economic revenue (Cheung et al., 2013; Hollowed et al., 2013; Lam et al., 2016). The impacts of climate change and fishing interact in a number of ways and cannot be treated as separate issues. Climate effects may undermine the effectiveness of management measures, while fishing-induced changes can affect the sustainability, resilience and the adaptive capacity of marine ecosystems in response to climate change (Britten et al., 2017; Conradt et al., 2024).

Temperature plays a critical role in the physiology of marine organisms, making them highly sensitive to environmental variability (Little et al., 2020; Volkoff and Rønnestad, 2020). Each species has specific thermal preferences and tolerance limits that shapes their geographic distribution (Poloczanska et al., 2013; Little et al., 2020). Rising sea surface temperatures (SST) due to climate change have resulted in a poleward shift in the distribution of thermophilic species, allowing them to expand into areas that were previously not suitable for their thermal requirements (Perry et al., 2005; Cheung et al., 2009; Dimarchopoulou et al., 2022). In addition to such direct thermal effects, climate change has also been shown to impact marine ecosystems through increased stratification, disrupted nutrient dynamics and altering primary production (Doney et al., 2012; Powley et al., 2016). These processes directly influence marine productivity (Piroddi et al., 2017; Capuzzo et al., 2018). Consequently, warming and declines in primary productivity are forcing species to relocate in search of suitable habitats and food resources (du Pontavice et al., 2021; Sailley et al., 2025). However, when species have limited dispersal capabilities or lack suitable habitat, climate change may result also in localized extinctions (Perry et al., 2005; Pörtner and Knust, 2007). As a result, native species previously dominating their ecosystems may decline, thereby opening ecological niches that can be filled by warm-water species (Meyer et al., 2024).

The observed shift in species distribution has resulted in a phenomenon known as tropicalization of fish catches, characterized by an increasing dominance of warm-water species in the catches of temperate areas (Cheung et al., 2013; Zarzyczny et al., 2024). From a fisheries perspective, the tropicalization of catches poses serious challenges for fisheries as revenues may decline due to reduced landings of commercially important species (Zarzyczny et al., 2024), while landings of less commercially valuable species increase (Lam et al., 2016). Nevertheless, this effect is not universal as the emerge of new species can also create economic opportunities (Kleitou et al., 2022; Marchessaux et al., 2023; Frem et al., 2024). These shifts in species distribution and catch composition directly affect coastal communities, whose food security and economic sustainability depend on fisheries, making them socio-economically vulnerable to climate change (Cheung et al., 2013).

The mean temperature of the catch (MTC) is recognized as an index indicating the effects of climate change on shifts in the composition of fisheries landings (Cheung et al., 2013). An increasing MTC trend is indicative of a shift in catch composition towards warm-water species, likely driven by increased catches of warm-water species, reduced catches of cold-water species, or a combination of both factors (Cheung et al., 2013; Tsikliras and Stergiou, 2014). MTC is calculated from the average estimated temperature preference of exploited species, weighted by their annual catch in a specific area (Cheung et al., 2013). This index has been applied to assess the impact of warming in various ecosystems, including the Mediterranean (Tsikliras and Stergiou, 2014; Keskin and Pauly, 2014; Fortibuoni et al., 2015; Tsikliras et al., 2015; Peristeraki et al., 2019; Valente et al., 2023), the Atlantic Ocean (Auber et al., 2017; Leitão et al., 2018; Gianelli et al., 2019) and the Pacific Ocean (Liang et al., 2018; Dimarchopoulou et al., 2022).

The Adriatic Sea, especially its northern sub-basin, is considered as one of coldest regions in the Mediterranean and has historically been inhabited by endemic species with cold- and temperate-water affinities (Pranovi et al., 2013). In the context of the ongoing warming trend in the Mediterranean, the northern Adriatic Sea could play an essential role as a sanctuary for cold water species. Due to its relatively cooler temperatures, this basin might offer a suitable environment for species that are less adapted to the increasingly warm conditions elsewhere in the Mediterranean (Ben Rais Lasram et al., 2010). Previous studies, based on Italian landings data, indicate a slower increase in the MTC in the Adriatic, with the northern basin even showing a negative trend, in contrast to the rising temperatures (Fortibuoni et al., 2015). However, being the shallowest Mediterranean sub-basin (mean depth ≈ 30 m), the northern Adriatic is also highly sensitive to climate change (Russo and Artegiani, 1996; Vilibić et al., 2019). As a consequence the basin is increasingly exposed to episodic hypoxia (Zennaro et al., 2024), harmful algal blooms (Zoffoli et al., 2025), enhanced stratification and salinity shifts due to seasonal heating and freshening by a substantial river inflow, and northward expansion of thermophilic species (Iveša et al., 2021). While the northern Adriatic could act as a refuge for cold-water species, rising temperatures have made other parts of the basin suitable habitats for certain thermophilic species of the Mediterranean that were previously uncommon or even absent (Dragičević et al., 2017). In addition to the process of "meridionalization", characterized by the northward expansion of native Mediterranean species (Azzurro, 2008), sea warming has also facilitated the introduction of non-indigenous, thermophilic species, due to the "tropicalization" process (Azzurro et al., 2019; Lipej et al., 2022). Furthermore, the basin has suffered a high rate of exploitation pressure, making its fish stocks vulnerable to other stressors, in particular climate change (Lotze et al., 2011; Moullec et al., 2019; Russo et al., 2019; Sumaila and Tai, 2020).

In this study we investigated the variation in the MTC pattern in Adriatic Sea fisheries landings to understand its relation to the ongoing sea warming over a five-decade time period. Furthermore, this study examined the influence of SST, the North Atlantic Oscillation NAO, and the Atlantic Multidecadal Oscillation (AMO) on the MTC, all of which have previously been recognized for affecting Mediterranean ecosystems (Conversi et al., 2010; Gordo et al., 2011; Tsikliras et al., 2019). By doing so, this study aims to evaluate whether shifts in the thermal structure of landings are occurring and to what extent regional and large-scale climate variability contributes to these patterns in the Adriatic basin. Furthermore, it evaluates the suitability of MTC as an indicator for monitoring climate-driven changes in fisheries in the context of climate adaptation.

# 2 Materials and methods

## 2.1 Study area

The Adriatic Sea is a semi-enclosed basin located between the Italian peninsula and the Balkans, with a major axis of 800 km and a mean width of 180 km (Russo and Artegiani, 1996). This basin is divided in three sub-basins: the Northern, Central and Southern, with depth increasing from north to south (Figure 1) (Artegiani et al., 1997). The northern sub-basin, being the shallowest, has a gently sloping seabed that gradually reaches 100 m and then dropping quickly to 200 m as it transitions into the central region (Orlic et al., 1992). The central sub-basin is characterized by two notable depressions known as the Jabuka (Pomo) Pits, reaching a depth of approximately 270 m (Russo and Artegiani, 1996). The southern sub-basin is characterized by a narrow continental shelf and a steep slope that leads down to the deepest point in the Adriatic, the South Adriatic Pit, with a maximum depth of 1223 m (Russo and Artegiani, 1996). The seabed then rises again at the Otranto Strait, where the Adriatic connects to the Ionian Sea (Orlic et al., 1992; Russo and Artegiani, 1996). For fisheries management purposes, the Adriatic is divided in two Geographical Sub-Areas (GSA): GSA17 and GSA18. GSA17 encompasses the Northern and Central Adriatic and is bordered by Croatia, Bosnia-Herzegovina, Italy and Slovenia. Meanwhile GSA 18, covers the Southern Adriatic, bordered by Albania and Montenegro to the east and the south-eastern Italian coast to the west (Farrugio et al., 2015).

## 2.2 MTC calculation

For our study, we used fisheries catch data for the Adriatic Sea covering 5 decades (1970 – 2020), encompassing both GSA 17 and GSA 18, obtained from the General Fisheries Commission for the Mediterranean (GFCM) database of fisheries production (https://www.fao.org/gfcm/data/capture-production). The database includes legal large- and small-scale catches, but excludes discarded catches, as well as illegal, unreported, recreational and sport fishing (GFCM, 2023). GFCM landing statistics are reported at mixed taxonomic resolutions depending on the Data Collection Framework (DCF) requirements and national practices; some landings are reported consistently at species level, whereas others are aggregated at higher levels (e.g., genus or family). Reporting resolution also changed through time, with several taxa reported at genus level for most of the series and only recently at species level. To ensure temporal consistency our analysis was restricted to taxa with data available for the entire study period. From an initial set of 27 taxonomic groups, 5 reported at the family level and 4 that included species from more than 1 family were excluded, leaving 18 taxa for analysis (Supplementary Table S1). For taxa aggregated at the genus-level, a mean temperature was calculated based on all the species within the given genus present in the fisheries landings. This approach was applied exclusively when species-level landings were unavailable, due to changes and inconsistencies in reporting resolution within the GFCM database over time. Integrating genus-level data in the analysis increased the proportion of the total analyzed landings in the study area. The species and genus level landing records represented between 79 - 94% of the total analyzed landings. Additionally, the MTC derived from both genus and species-level data showed a strong correlation with the MTC based only on species-level data (Supplementary Table S2).

Median temperature preferences (in °C) were obtained from two different sources (Supplementary Table S1):

a) The supplementary materials of Cheung et al. (2013), covering the majority of the records in our database, which includes data for 16 out of 18 analyzed taxa.
b) For species not covered in (a), temperature preferences were obtained from AquaMaps (Kaschner et al., 2019).

An annual MTC index was calculated based on the temperature preferences of the exploited taxa according to the following formula (Cheung et al., 2013):

$$MTC_{yr} = \frac{\sum_i^n T_i C_{i,yr}}{\sum_i^n C_{i,yr}}$$

where $C_{i,yr}$ represents the catches of taxon *i* for year *yr* in the study area, $T_i$ denotes the median temperature preference of taxon *i*, and *n* is the total number of taxa present in the annual catch.

In addition to the MTC we calculated the average assemblage temperature by calculating the mean preferred temperatures of all taxa included in the analysis. This measure was used as a threshold to classify the taxa into warm-water (thermophilous) and cold-water (psychrophilous) groups, depending on whether their preferred temperature was above or below the average (Tsikliras et al., 2015; Dimarchopoulou et al., 2022). Thermophilous species are thus characterized by a higher affinity for warmer waters, while psychrophilous species prefer colder environments.

We used linear regression analyses to assess temporal trends in MTC and SST. After visual inspection, MTC trend analysis was


FIGURE 1
Overview map of the Adriatic Sea located between Italy and the Balkan Peninsula. The inset map shows the position of the Adriatic Sea within the Mediterranean basin.

conducted using segmented linear regression, while simple linear regression was employed for SST.

## 2.3 Potential effects of climate change

To investigate the relationship with climate change, we related the MTC index to SST anomaly, calculated as deviations from the long-term mean, as well as to the NAO and AMO indices. These indices are commonly used as proxies for climate-driven variability in the Mediterranean ecosystem (Conversi et al., 2010; Gordo et al., 2011; Tsikliras et al., 2019). SST data for the Adriatic Sea were extracted from the NOAA ERSST v5 dataset (Huang et al., 2017) and averaged to obtain annual values for comparison with the MTC. To mitigate the influence of confounding factors, we used anomaly data rather than absolute temperature (Dimarchopoulou et al., 2022). The NAO index, which measures the difference in sea-level pressure between the Azores High and Icelandic Low over the North Atlantic (Hurrell et al., 2001), was obtained from the Earth System Research Laboratory (NOAA, https://www.esrl.noaa.gov/). Given that NAO variability is most pronounced during the winter months, its influence on surface temperature and precipitation is greater, the NAO winter index was calculated considering the pressure differences from December to March (Hurrell et al., 2001). Additionally, the mean annual values of AMO were also obtained from the Earth System Research Laboratory (NOAA, https://www.esrl.noaa.gov/). The AMO represents long-term SST variations over the Northern Hemisphere (0°–70°N) (Knight et al., 2006). These oscillations influence large-scale climate variability, including precipitation patterns, hurricane activity, and ocean circulation patterns and have been shown to affect marine productivity and ecosystem dynamics across the Northern Hemisphere (Nye et al., 2014).

Initially, we conducted Pearson correlation analysis to explore the relationship between MTC and climate indices including time lags of 0–4 years. To address the influence of autocorrelation, the modified Chelton method was employed (Pyper and Peterman, 1998). This method adjusts the effective degrees of freedom when positive autocorrelation is present in both time series. As a result, it calculates a critical value ($r_{crit}$) that must be exceeded by the correlation coefficient for it to be considered significant.

$$r_{crit} = \sqrt{\frac{t^2_{\alpha,N*-2}}{t^2_{\alpha,N*-2} + (N^* - 2)}}$$

where $r_{crit}$ is the critical correlation coefficient (two-sided test), $N^*$ is the effective sample size adjusted for autocorrelation and $t_{\alpha,\ N^*-2}$ is the critical value of the Student's $t$ distribution at significance level $\alpha = 0.05$.

Subsequently we conducted univariate and multivariate linear regression analysis of climate effects on MTC with SST anomaly, NAO and AMO as predictors. For each predictor, we first fitted linear regression models, including different lag structures, and evaluated residuals for normality, heteroscedasticity, and temporal autocorrelation. Residual autocorrelation was assessed using the Ljung–Box portmanteau test (lag = 10); for generalized least squares GLS models the test used normalized residuals with degrees of freedom adjusted by the number of ARMA parameters ($p$+$q$). To account for potential autocorrelation in the residuals, we fitted GLS models, incorporating autoregressive (AR) and autoregressive moving average (ARMA) correlation structures of different orders. Candidate models were compared using Akaike's Information Criterion (AIC), and the model with the lowest AIC was retained as the best representation of the data.

Additionally, we examined the temporal variation in the difference between mean sea surface temperature and the MTC of the fish community (ΔT) using linear regression, in order to explore how the community adapts in response to ongoing temperature trend. To address potential autocorrelation, we fitted GLS models with various correlation structures, including AR(1) and ARMA (p,q). Model fit was again compared using Akaike's Information Criterion (AIC), and the model with the lowest value was selected as the best fit.

All the analyses were conducted in R environment (version 4.2.1).

# 3 Results

## 3.1 MTC temporal trend

We found the trend of the MTC index for the Adriatic Sea to be best described by a segmented regression model indicating a declining trend of 0.48°C per decade until the late 1980s, followed by an increase of 0.23°C per decade since 1987 (Supplementary Table S3). The lowest MTC value occurred in 1987, after which it increased until peaking in 2006. Although the model estimates a positive slope after 1987, visual inspection of the time series suggests a slight downward tendency in recent years (Figure 2).

## 3.2 Assemblage composition

The assemblage average temperature used as a cut-off value to classify species as psychrophilous (cold-water) or thermophilous (warm-water) was determined to be 16.9 °C. Our study revealed that the ratio of psychrophilous to thermophilous species in the landings fluctuated during the study period (Figure 3). Cold-water species dominated for most of the study period, particularly from the 1980s to the early 2000s. However, since the 1990s, a noticeable increase in the proportion of the warm-water species was observed, balancing the abundance with that of cold-water species by the mid-1995 and surpassing them during the second half of 2000s. In the last decade, the ratio between cold- and warm-water species increased again, with psychrophilous species reestablishing their dominance in the landings (Figure 3).

## 3.3 Climate drivers of MTC

The univariate relationships between the MTC and climate indices (SST anomalies, NAO and AMO) were investigated using Pearson correlation analyses (Figure 4) and linear regression models (Table 1). Unlike SST anomalies, both NAO and AMO showed significant correlations with MTC.

SST anomalies exhibited a consistent increase of 0.028 °C per year ($p < 0.001$) (Supplementary Table S3), remaining negative until 1998 before shifting to positive values over the last two decades (Figure 2A). Linear regression indicated a significant positive effect of SST on MTC, explaining approximately 11.5% of its variability ($p < 0.01$). However, unlike NAO and AMO, including ARMA structure in the GLS model rendered the SST's effect non-significant ($p = 0.5409$), despite improving the model fit, as indicated by a reduction in AIC (Table 1).

The NAO, remained predominantly positive throughout the study period with occasional negative shifts (Figure 2B) and showed a significant negative correlation with MTC at zero lag ($p < 0.05$) (Figure 4B), confirmed by linear regression. Accounting for temporal autocorrelation using a generalized least squares (GLS) model incorporating an autoregressive moving average (ARMA) (3,2) structure improved the model fit, as indicated by a lower Akaike Information Criterion (AIC) value (Table 1).

The AMO demonstrated an increasing trend, transitioning to a positive phase by the late 1990s (Figure 2C). A significant positive correlation with MTC was identified at a two-year lag ($p < 0.05$) (Figure 4C). Linear regression indicated lagged AMO explained 14% of MTC variability ($p < 0.01$) (Table 1). As with NAO, incorporating an ARMA structure in the GLS model enhanced model fit, as indicated by a lower AIC (Table 1).

To assess the cumulative effects of the climate indices on MTC, we applied a set of multivariate linear regression models, incorporating different lag structures of the climate indices (Supplementary Table S4). Model comparison using AIC

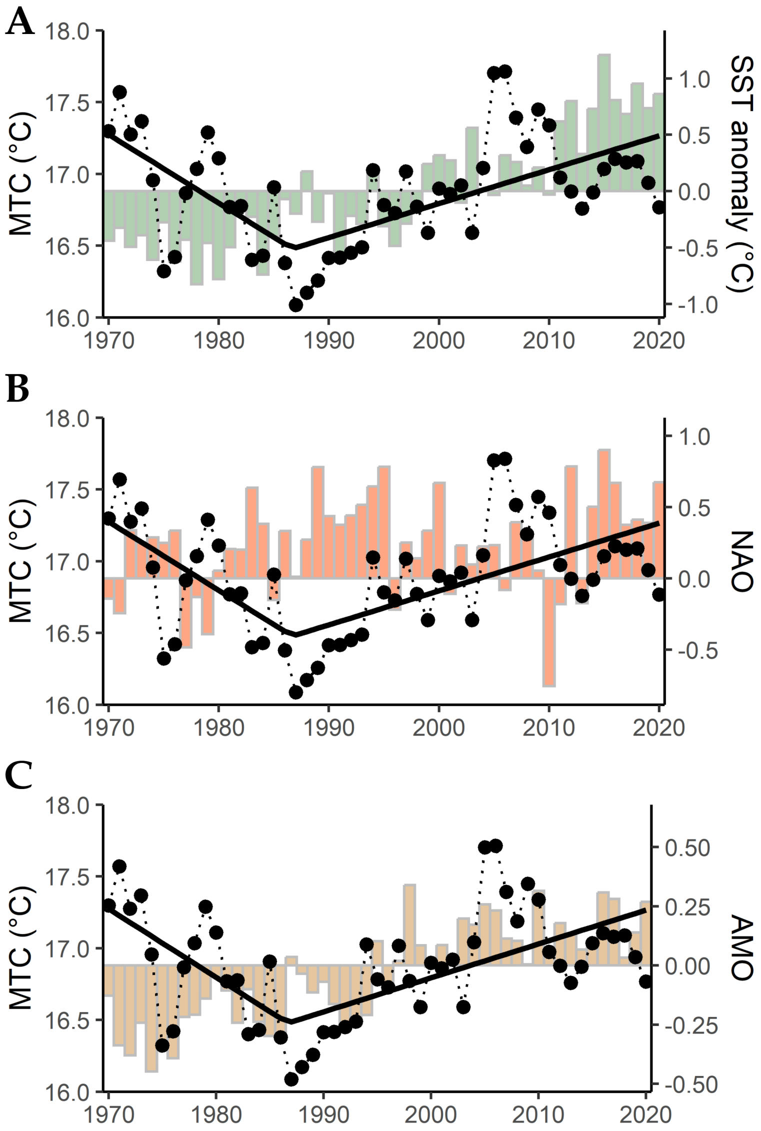


FIGURE 2
Temporal trend of the climate indicators: **(A)** Sea Surface Temperature (SST) anomaly, **(B)** North Atlantic Oscillation (NAO) and Atlantic Multidecadal Oscillation (AMO), overlaid by the MTC of the region.

identified the best performing model as including SST lagged by three years, NAO with no lag and AMO lagged by two years ($p < 0.001$), which explained approximately 32% of variability in the MTC index (Table 2). The results suggest that SST anomalies were not significantly related to MTC, AMO displayed a significantly positive relationship while NAO showed a significantly negative relationship. Residual diagnostics of this model revealed temporal autocorrelation, and therefore GLS models with autoregressive error structures were applied. Comparison of GLS models with different correlation structures (AR[1] and ARMA[p, q]) identified the ARMA (1,1) structure as the best-performing model, providing the lowest AIC and therefore the most adequate fit to the data (Supplementary Table S5). After accounting for autocorrelation, AMO remained a significant positive predictor, while NAO lost significance and SST remained non-significant (Table 2). These findings highlight the robust influence of AMO on MTC variability, whereas the role of NAO appears less consistent once autocorrelation is considered.

## 3.4 Difference between MTC and SST trends

To evaluate the changes of the fish landings to the ongoing SST trend (ΔT), we analyzed the difference between SST and MTC. A linear regression model fitted to the data showed that ΔT increased significantly ($R^2 = 0.36$, $p < 0.001$) at a rate of 0.024°C per year, indicating that the rate of increase of MTC was slower compared to the increase in SST during the study period (Figure 5). However, residual diagnostics revealed moderate positive autocorrelation. To

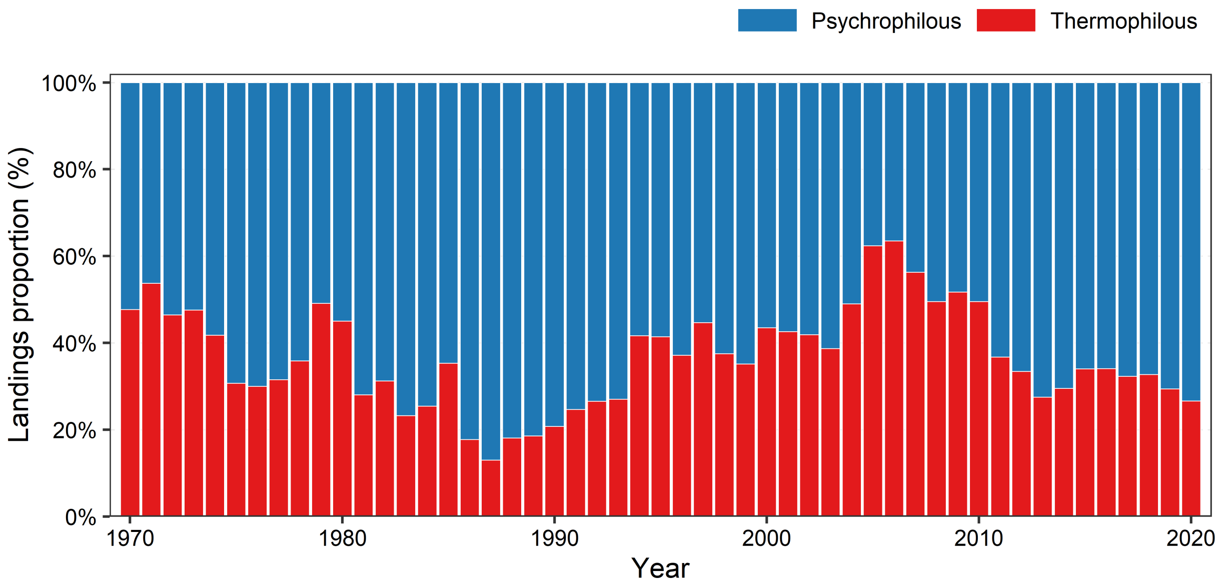


FIGURE 3
Landings proportion of psychrophilous (cold-water) and thermophilous (warm-water) species in the Adriatic Sea from 1970 to 2020.

address this, we fitted a generalized least squares model with an AR (1) correlation structure, which improved model fit by accounting for temporal dependence. After this correction, the trend remained significant, with ΔT increasing by ~0.026 °C per year ($p < 0.01$), thus reinforcing the robustness of the result.

## 4 Discussion

In this study we investigated the variation in the MTC of the Adriatic Sea fisheries in relation to climatic variability, over a five-decade period. The Adriatic has experienced a significant warming

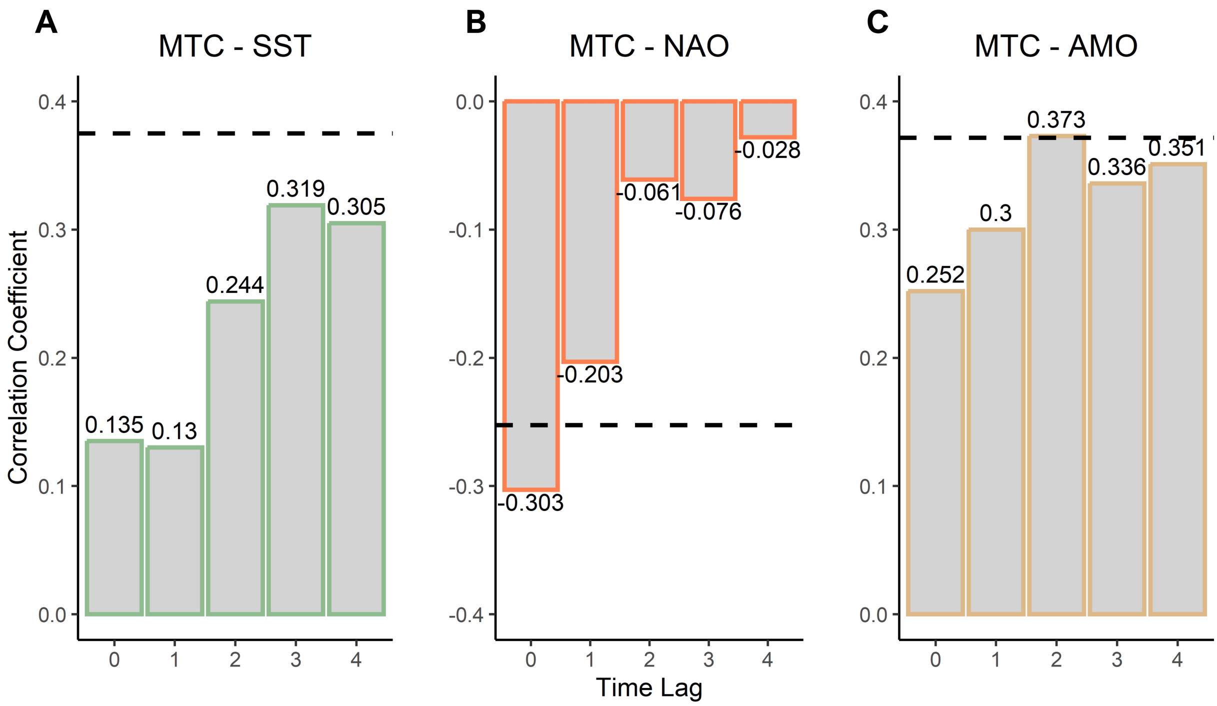


FIGURE 4
Bar plot of the cross correlation of the MTC time series with the Sea Surface Temperature anomaly **(A)**, North Atlantic Oscillation **(B)** and Atlantic Multidecadal Oscillation **(C)** at time lags of 0–4 years. Horizontal dashed line indicates the significance level at $p < 0.05$.

TABLE 1 Output of linear regression and generalized least squares models of the mean temperature of the catch (MTC) with the climate indices, respectively; sea surface temperature anomaly (SST), North Atlantic Oscillation (NAO) and Atlantic Multidecadal Oscillation (AMO).

| Model | Estimate | SE | t - value | p - value | Adjusted $R^2$ | AIC | ARMA order |
|---|---|---|---|---|---|---|---|
| Linear reg. (SST lag-3) | 0.2961 | 0.1113 | 2.689 | 0.0099 ** | 0.115 | 40.2920 | – |
| Linear reg. (NAO) | -0.3355 | 0.1506 | -2.227 | 0.0305 * | 0.073 | 53.9905 | – |
| Linear reg. (AMO lag-2) | 0.7382 | 0.2447 | 3.017 | 0.0041 ** | 0.14 | 39.8004 | – |
| GLS (SST lag-3) | 0.0547 | 0.0888 | 0.616 | 0.5409 | – | 15.8394 | ARMA (p=1, q=1) |
| GLS (NAO) | -0.1732 | 0.0723 | -2.396 | 0.0204 * | – | 18.5534 | ARMA (p=3, q=2) |
| GLS (AMO lag-2) | 0.4038 | 0.2059 | 1.961 | 0.05 * | – | 9.6924 | ARMA (p=1, q=1) |

GLS models account for autocorrelation using ARMA structures, specified as (p, q) order. Asterisks indicate significance levels: *$p$ < 0.05, **$p$ < 0.01 and ***$p$ < 0.001.

trend, with consequences observed across various levels of ecosystem organisation (Lotze et al., 2011; Piroddi et al., 2017). Our results indicate that the MTC exhibits two distinct trends over the study period: an initial decreasing trend, with a rate of change of (-0.048)°C per year observed during the first two decades, followed by a more gradual increasing trend at 0.024°C per year for the subsequent decades. Additionally, our findings show that the landings have undergone continuous shifts in species composition driven by climate change, with warm and cold-water species alternating during different periods. Although this study suggests a lower increasing rate in the MTC in recent decades compared to other Mediterranean areas (Tsikliras and Stergiou, 2014; Tsikliras et al., 2015; Fortibuoni et al., 2015), it highlights that the Adriatic fish community is experiencing significant changes in relation to sea warming.

Thermal conditions in the Adriatic basin reveal a significant warming trend, as indicated by SST anomalies (Supplementary Table S3). Following an initial cooling phase in the first decade, SST showed an increasing trend over the subsequent decades (Figure 2A). This pattern aligns with broader trends observed in many large marine ecosystems (LMEs) of the North Atlantic, which experienced accelerated warming around the 1980s after a preceding cooling phase (Belkin, 2009). The SST in the Adriatic basin increased by 1.37°C overall, at a rate of 0.028 °C per year, which is lower than the observed average Mediterranean rate of 0.035°C (Pastor et al., 2020). The differences are even more pronounced when compared to other Mediterranean regions, such as Levantine-Aegean region, which shows a warming trend of 0.048 °C per year (Pisano et al., 2020).

Beyond local warming, large-scale climate oscillations, particularly NAO and AMO, are major drivers of change in the Mediterranean marine environment (Conversi et al., 2010; Gordo et al., 2011; Alheit et al., 2014). These climate drivers alter sea temperature, salinity and circulation patterns, which in turn influence productivity, distribution and reshape community structures (Van Beveren et al., 2016; Valente et al., 2023; Sanz-Martín et al., 2024). Periods of high NAO or shifts in the AMO have been associated with evident changes in fish populations and landings across the region. For instance, NAO variability has been linked to small pelagic dynamics including the late-1980s anchovy collapse in the Adriatic (Santojanni et al., 2006) and sardine declines in the northwestern Mediterranean (Gordo et al., 2011). Small pelagics also exhibit long-term fluctuations aligned with warm and cool phases of the AMO, with warm phases favoring anchovy increases in central/eastern Mediterranean sub-regions, while having an opposite effect on the western basin (Alheit et al., 2014; Tsikliras et al., 2019). Climate signals extend to demersal resources as well: landings of deep-water rose shrimp in the Catalan Sea covary with NAO (Maynou, 2008), while European hake recruitment in the Ligurian Sea shows a negative correlation

TABLE 2 Multiple linear regression and Generalized Least Squares (ARMA (p=1, q=1) models of the mean of the mean temperature of the catch (MTC) with sea surface temperature anomaly (SST), North Atlantic Oscillation (NAO) and Atlantic Multidecadal Oscillation (AMO).

| | Estimate | SE | *t* - value | p - value | Adjusted $R^2$ | AIC |
|---|---|---|---|---|---|---|
| Multivariate Model | | | | 0.000625 | 0.2753 | 32.8078 |
| SST (lag 3) | 0.158 | 0.1371 | 1.152 | 0.255534 | | |
| AMO (lag 2) | 0.6677 | 0.3072 | 2.174 | 0.03515 * | | |
| NAO | -0.4054 | 0.1381 | -2.936 | 0.00527 ** | | |
| GLS ARMA (p=1, q=1) | | | | – | – | 19.0872 |
| SST (lag 3) | 0.0853 | 0.0982 | 0.0982 | 0.3894 | | |
| AMO (lag 2) | 0.4841 | 0.2327 | 2.0809 | 0.0433 * | | |
| NAO | -0.1218 | 0.0903 | -1.3486 | 0.1844 | | |

Asterisks indicate significance levels: *$p$ < 0.05, **$p$ < 0.01 and ***$p$ < 0.001.

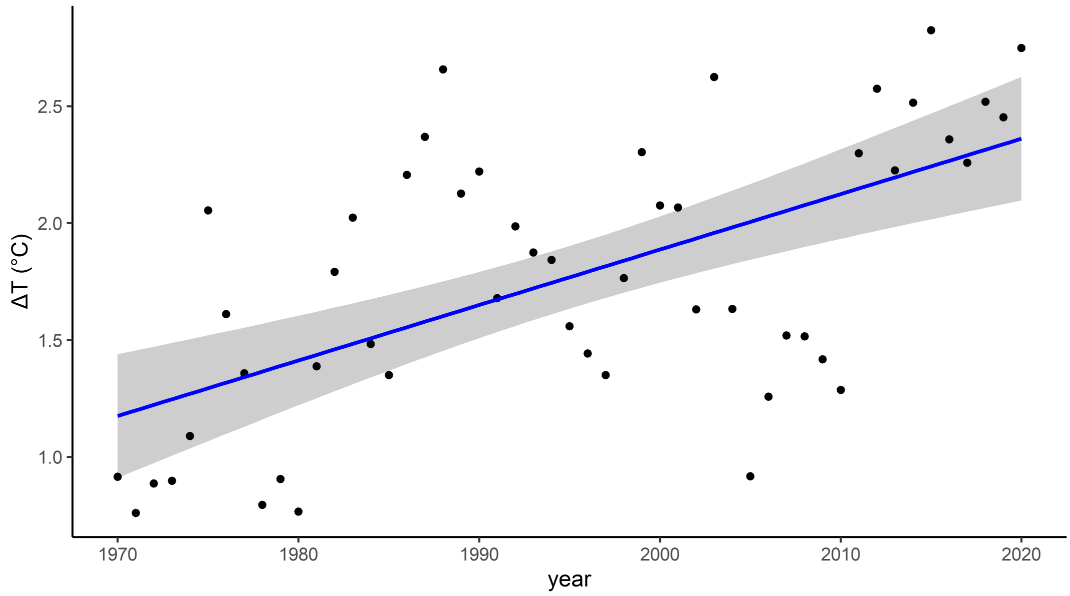


FIGURE 5
Linear regression showing the relationship between ΔT (the difference between MTC and mean SST) and year. The shaded gray area represents the 95% confidence interval.

(Abella et al., 2008). Beyond the Mediterranean, positive NAO years in the Black Sea have influenced fish productivity by limiting food availability and altering trophic dynamics (Llope et al., 2011). More broadly across the Northeast Atlantic, the NAO's ecological impact on plankton dynamics and fish stocks is well established (Stige et al., 2006; Blöcker et al., 2023). Consequently, climate driven population variability translates into fluctuations in fisheries performance, affecting both total catches and the relative availability of target species (Tsikliras et al., 2019).

Marine ecosystems are composed of various species that often exhibit delayed responses to environmental changes, potentially leading to varying time scales in the system's response to driver variations (deYoung et al., 2008; Kuczynski et al., 2017). Accordingly, we tested whether Adriatic MTC co-varies with these indices at different time lags. The MTC trend observed here showed significant correlations with NAO and AMO (Figure 4). Specifically, a positive correlation was found with the AMO at lag 2, while a negative correlation was observed with NAO at lag-0. As confirmed by previous studies, our findings reinforce that substantial changes in the Adriatic Sea fish community composition are significantly influenced by hemispheric climate variability (Barausse et al., 2011). The lagged response of the MTC to climate indices suggests that sea warming affects the fish community indirectly, likely through trophic interactions or biological processes that take time to manifest, thereby introducing delays in response times (Auber et al., 2017).

In our analyses, after testing correlations and fitting univariate linear models between MTC and each climate index, we fitted a multivariate linear regression model with SST, NAO, and AMO as predictors to explain variations in the MTC. When dealing with time-series data, it is critical to address autocorrelation in the regression residuals, otherwise, the non-independence of observations can overestimate the significance of predictor effects and lead to false detection of significant relationships if unaccounted for, thereby violating linear model assumptions (Hefley et al., 2017). The consideration of temporal autocorrelation has the capacity to modify the perceived relationship. For instance, the implementation of serial correlation correction in the Greek Seas resulted in a shift of the peak correlation between MTC and SST to a one- to two-year lag (Tsikliras et al., 2015). By incorporating multiple climate indices in one model and ensuring the residuals are independent, we obtain a robust assessment of climate impacts on the fish community. Notably, under these refined modeling conditions, the NAO's effect on MTC was no longer significant in our results.

The MTC has been demonstrated to exhibit a positive correlation with the AMO in the basin, particularly in the central and eastern sub-basins, whereas the NAO did not show a significant correlation (Tsikliras et al., 2015). The influence of the NAO on Mediterranean ecosystems varies from west to east, with studies reporting more pronounced signals in the western Mediterranean and weaker or inconsistent in the central and eastern sub-basins (Tsikliras et al., 2019). This geographic heterogeneity may explain why the NAO effect on MTC did not remain significant once temporal autocorrelation was accounted for, whereas the AMO signal persisted as a significant driver. Although the NAO index is an important driver of atmospheric circulation in the Mediterranean, the consequences of its influence on fish populations should be interpreted with caution due to regional differences (Grbec et al., 2002; Gordo et al., 2011; Tsikliras et al., 2019).

We found the Adriatic Sea to exhibit alternating changes in the trend of the ratio between psychrophilous and thermophilous species over different time periods. This variability contrasts with patterns observed in other Mediterranean regions, where a tropicalization of catches in response to ocean warming has been observed (Tsikliras and Stergiou, 2014; Tsikliras et al., 2015). The northern sub-basin of the Adriatic Sea, being one of the coldest areas of the Mediterranean, may serve as a refuge for cold-water species. However, given its shallow depth and vulnerability to sea warming, this basin could eventually become a trap from which these species cannot escape (Ben Rais Lasram et al., 2010; Vilibić et al., 2019; Iveša et al., 2021; Zennaro et al., 2024). Additionally, the Adriatic Sea hosts an endemic community composed of cold- and temperate- affinity species (Fortibuoni et al., 2017). Under these relatively cold conditions, the ongoing warming, is expected, at least initially, to have a positive effect also on the biological cycle of these endemic species, potentially increasing their production (Pranovi et al., 2016; Fortibuoni et al., 2017). Consequently, this dynamic may contribute to the variability and lower rate of increase in MTC in the Adriatic compared to rest of the Mediterranean. However, the continued rise in sea temperature may eventually surpass the thermal tolerances of these endemic species, leading to negative long-term consequences (Fortibuoni et al., 2017). The observed decline in thermophilic catches may be attributed also to the trajectories of other taxa. It has been observed that certain cold water-species or groups, such as sardine, have increased their landings, thereby reducing the proportion of warm-water species in the total catch (Supplementary Figure S1). Despite these fluctuations, the contribution of various thermophilous species has increased over the last 15 years. Our analysis indicates that warm-water species, such as *Mullus* spp., *Parapenaeus longirostris*, *Lophius* spp. and *Scomber* spp. have increased significantly, particularly in recent decades.

Interpreting these dynamics requires acknowledging data constrains. In regions like the Adriatic Sea, where publicly available survey data do not cover the entire basin, catch data serve as a reliable indicator for detecting the influence of climate change in fisheries (Cheung et al., 2013; Tsikliras and Stergiou, 2014). Although scientific surveys, like the Mediterranean International Bottom Trawl Survey (MEDITS), have been conducted for years (Vasilakopoulos et al., 2017), their data were not publicly accessible until recently. Even now, only part of the dataset for EU member states has been released, while data from non-EU countries remain unavailable, making these sources unsuitable for our basin-wide analysis, which includes both EU and non-EU countries. Nonetheless, previous studies found no significant difference in the rate of change in MTC between scientific survey data and catch data (Cheung et al., 2013; Fortibuoni et al., 2015), further supporting the use of fishery dependent data to detect the effects of climate change on fisheries (Sguotti et al., 2022; McDonald et al., 2025). An additional potential limitation resides in the absence of fishing effort data analogous to the landings dataset. While the Adriatic Sea is exploited by several countries, the absence of effort data specifically for Croatia, which is major contributor to regional landings due to its substantial fishing fleet, creates a significant gap in the available data. The latest available data on Croatian fishing vessels are from 2013 (https://www.fao.org/gfcm/data/fleet/register) the year when the country joined the European Union. Because of this, fishing effort information cannot be used to adjust landings or to calculate reliable indicators such as landings per unit effort over the whole study period. Furthermore, landing data are also influenced by additional factors such as illegal, unregulated and unreported (IUU) practices as well as discarding practices and market demand (Barausse et al., 2011; Piroddi et al., 2015), biasing our ability to understand climate impact on fisheries. However, if conditioned properly, landings data are expected to provide an adequate picture of the main trends of exploited taxa (Froese et al., 2012).

Furthermore, our analysis relied on a reduced taxonomic dataset, reflecting limitations of the fisheries statistics in the Adriatic (Carpi et al., 2017). Prior to the implementation of the DCF (GFCM, 2014), fisheries data collection faced significant challenges due to social, political and historical factors (Carpi et al., 2017). As a result, the data collection system was poorly structured, leading to over-aggregation of the catches and complicating the development of species-specific studies. Nevertheless, the retained taxa represent the majority of total analysed landings. To increase the amount of data available for our analysis, genus-level data were also incorporated where species level data were unavailable. The MTC calculated using both genus- and species-level data showed a strong correlation with the MTC derived exclusively from species-level data (Supplementary Table S2). Even though the MTC signal may be stronger when catches are analysed at finer taxonomic resolution, analyses based on aggregated taxa remain informative and capture the overall temporal trends, albeit with a persistent bias (Lin et al., 2021; Dimarchopoulou et al., 2022). To obtain a more comprehensive understanding of climate-induced changes in fish populations and fisheries catches, the MTC should be used in complement with other approaches, such as analyses of species distribution shifts and the examination of life-history traits (Dimarchopoulou et al., 2022).

Interpreting the MTC requires caution as it is not always straightforward and it might be influenced by other anthropogenic and environmental factors (Alajmi et al., 2024). Assigning each species a single temperature preference overlooks the potential importance of intraspecific variation, which contributes to population resilience under changing environmental conditions. In response to thermal pressures, populations may exhibit greater plasticity or adaptive capacity than assumed when each species is attributed a fixed temperature preference (Tsimara et al., 2021). The use of highly aggregated indicators, such as MTC, and analyses at large spatial scales, can reveal general patterns but may may mask important local or regional patterns (Pranovi et al., 2016). Although ongoing sea warming and the northward spread of warm-affinity biota would be expected to increase the abundance of thermophilic species, the possible effect of other drivers should be further explored (Pranovi et al., 2016; Lavin et al., 2023). In the northern Adriatic, for instance, heavy exploitation has been identified as the primary driver of steep declines in warm-adapted fish populations (e.g. sharks and European hake), overwhelming any climate-driven increases (Barausse et al., 2014; JRC, 2023).

Although SST has been widely used as a driver in community-level studies within fisheries science (Cheung et al., 2013; Tsikliras et al., 2015), indicating a clear relationship with the assemblage distribution (Pranovi et al., 2016; Espasandín et al., 2025), it also carries an inherent limitation. Fish species occupy different layers of the water column, which may be affected differently by ocean warming (Liang et al., 2018). However, recent evidence suggests that warming signals can penetrate rapidly through the water column, reorganizing demersal communities even at depth (Emblemsvåg et al., 2022). These changes can also propagate through the food-web, influencing community structure even in the absence of immediate direct effects (Doney et al., 2012). In this study, SST is therefore not treated as a direct driver of species abundance but rather as a proxy for ocean warming affecting a community-level indicator, such as the MTC (Cheung et al., 2013; Tsikliras et al., 2015). Additional climate proxies that could be explored in the future analysis include the Mediterranean Oscillation (MO), the Adriatic–Ionian bimodal oscillating system (BiOS), the East Atlantic (EA) pattern and Eastern Mediterranean Transient (EMT), all of which have been shown to influence hydrographic and ecological variability across the Mediterranean basin (Grbec et al., 2015; Patti et al., 2025).

Another important limitation relates to the exclusion of thermophilous non-indigenous species (NIS), whose landings are not yet officially recorded by local authorities (Azzurro et al., 2019), even though some, such as the blue crab (*Callinectes sapidus*) have become increasingly present in fish markets (Frem et al., 2024). Consequently, the observed MTC variability in the Adriatic reflects exclusively shifts within native population. This implies that our MTC estimates are likely conservative, as the inclusion of additional warm-affinity species would further increase the MTC. The Mediterranean Sea is one of the world's most invaded marine regions, currently hosting more than 1000 NIS, of which approximately 200 are fish species (Zenetos et al., 2022; Galanidi et al., 2023; Tiralongo et al., 2023). This issue is of particular relevance also in the Adriatic Sea, where an increasing number of NIS has been documented (Kamberi et al., 2022; Lipej et al., 2022). Recent local ecological knowledge collected from fishers indicates that the frequency, geographical distribution and seasonal occurrence of NIS have increased over the past two decades, particularly in the northern Adriatic, which is considered a regional hotspot for biological invasions (Marchini et al., 2015; Azzurro et al., 2019).

Climate-driven changes in the thermal composition of fish assemblages reflect not only a shift toward tropicalization and meridionalization of catches, but also indicate deeper ecological consequences for ecosystem functioning. NIS are considered to be one of the most important drivers to local biodiversity loss, affecting ecosystem functioning by altering trophic pathways, affecting keystone species, disrupting ecological processes and modifying habitat structure (Katsanevakis et al., 2014; Gallardo et al., 2016). However, despite this climate-driven trend, ecological responses in natural systems are not linear or easily predictable (Turner et al., 2020). In semi-enclosed basins, such as the Adriatic Sea, community restructuring is not driven not only by rising temperatures, but also by the availability of suitable ecological niches (Libralato et al., 2015). As native and non-native species increasingly overlap in space and time, leading to direct competition, the invasion success depend on both thermal tolerance and ecological interactions, including competition, predation, and trophic dependencies (Libralato et al., 2015; Karachle et al., 2022; Vivó-Pons et al., 2023). Consequently, only a limited number of successful invaders occupy ecological niches similar to those of native species (Libralato et al., 2015).

These ecological shifts inevitably cascade into the socio-economic dimension of fisheries. The arrival of thermophilic NIS could modify food web structure and influence fisheries profitability (Hollowed et al., 2013; Lam et al., 2016). Declines in traditional species may reduce economic yields arriving from long term-consolidated markets, while the increase of warm-affinity or NIS may introduce species of lower commercial value or with uncertain market demand (Lam et al., 2016; Kleitou et al., 2022). NIS pose increasing risks to both small-scale and industrial fisheries, affecting coastal small-scale fleets as well as small pelagic and demersal fisheries (Hidalgo et al., 2022; Marchessaux et al., 2023). Although they are associated with numerous adverse ecological effects, these species are also being exploited as emerging fishery resources (Hidalgo et al., 2022; Kleitou et al., 2022). The growing awareness and acceptance of these species by consumers and fishers may facilitate their commercialization, raise market demand and ultimately lead to increased targeted catches (Kleitou et al., 2022; Minasidis et al., 2023; Frem et al., 2024).

These dynamics call for climate aware and adaptive policies. Temperature sensitive indicators such as MTC, can help track fish assemblages to warming (Cheung et al., 2013), although this matter should be analysed with caution since the catch composition could be influenced by other environmental and anthropogenic factors (Tsikliras et al., 2015; Espasandín et al., 2025). Furthermore, fisheries management should implement a proactive approach and take advantage of the positive contribution of NIS by supporting market innovation to responsibly valorize the catches of new species that fishers already perceive as beneficial (Kleitou et al., 2022).

In conclusion, our results demonstrate that the MTC is a valuable index for investigating the effects of climate change on the marine community and fisheries of the Adriatic Sea. This study reveals that fluctuations in the MTC are linked to the variability of large oceanic indices. Given the current dynamics, continued sea warming will divide the species in "winners" and "losers" (Moullec et al., 2019). While some warm-water species may benefit from changing environmental conditions, cold-water species will struggle to persists in their traditional habitats as their thermal tolerances are exceeded, leading to climate induced local extinctions (Cheung and Pauly, 2016). Consequently, the catch composition is expected to shift, with warm-water species becoming increasingly dominant, as observed in many temperate and cold regions of the world (Fodrie et al., 2010; Tsikliras et al., 2015; Dimarchopoulou et al., 2022). Incorporating MTC into the monitoring of climate change effects on marine ecosystems could provide an early warning indicator of climate-driven community shifts and supports adaptive fisheries management, protect the native fish populations and mitigate potential damage.

## Data availability statement

Publicly available datasets were analyzed in this study. These data can be accessed at: https://www.fao.org/gfcm/data/capture-production.

## Author contributions

EK: Formal Analysis, Writing – original draft, Data curation, Visualization, Conceptualization, Methodology, Investigation. EH: Supervision, Investigation, Writing – review & editing. CM: Writing – review & editing, Project administration, Supervision, Conceptualization, Methodology.

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## Conflict of interest

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

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## Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2025.1719738/full#supplementary-material

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