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Mediterranean fish communities are struggling to adapt to global warming. Evidence from the western coast of Italy

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ABSTRACT

Climate change has significant impacts on marine ecosystems, resulting in disruptions in biological interactions, shifts in community composition, and changes in the physiology of fish and other marine organisms. In this study conducted in the central Mediterranean Sea, the mean temperature of the catch (MTC) was employed as an indicator to investigate the climatological factors influencing the fish community. The MTC, which utilizes species-preferred temperatures, was calculated using bottom temperature (BT) data weighted against scientific catches. The estimated MTC increasing rates were 0.01 °C year^{-1} for the entire community, 0.017 °C year^{-1} for the shelf break, and 0.004 °C year^{-1} for the continental slope assemblage. We found that MTC is increasing at a lower rate compared to BT, suggesting a progressive under-adaptation of the fish community that seems not fully able to keep up with the ongoing pace of warming. The study identified sea surface temperature and bottom temperature as key drivers of changes in fish community composition. Notably, the fish community composition exhibited drastic changes over the studied period, and we suggest that the MTC can be a useful index to monitor such changes within the context of the EU's climate change adaptation strategy.

1. Introduction

Climate change is rapidly changing the structure and functioning of marine ecosystems by acting at different levels of biological organization and interacting with fishing activities and other human stressors (Doney et al., 2011; Griffith et al., 2018). Asynchronous shifts in seasonal phenologies of predator and prey populations, biogeographic reorganizations, and loss of functionally important species can disrupt existing biological interactions (Doney et al., 2011). Studies on fish and other marine organisms showed how different components of climate change (e.g., global warming, ocean acidification) impact individuals at all life cycle stages (Pankhurst and Munday 2011; Holt and Jørgensen, 2015). Physiological changes occur in response to environmental variables such as temperature, dissolved oxygen, and carbon dioxide levels in the ocean (Pörtner and Peck, 2010; Heath et al., 2012). Such alterations in individual physiology could lead to changes in the mortality, growth, and reproduction rates of wild fish populations, as well as in their phenology and distribution (Anderson et al., 2013; McLean et al., 2018; Denechaud et al., 2020). In temperate waters, fish species respond to climate change by shifting their distribution poleward to find more suitable habitats (Perry et al., 2005; Dulvy et al., 2008; Lenoir et al., 2011; Engelhard et al., 2014). The presence of geographical barriers constrains this pattern in the semi-enclosed Mediterranean basin, and it is therefore expected that the colder north Mediterranean coast (e.g., Adriatic Sea, Gulf of Lions) will firstly act as refuges for cold-affinity species, then becoming a "cul de sac" that will drive those species towards local extinction in the next decades (Ben Rais Lasram et al., 2010).

How climate forcing will change the Mediterranean fish communities has been the focus of several studies that also investigated the possible "losers" and "winners" of environmental change under different warming climate scenarios (Albouy et al., 2012, 2013, 2014; Hattab et al., 2016; Moullec et al., 2019). The Mediterranean basin stands out as a climate change hotspot, representing one of the world's most vulnerable temperate regions due to its significant exposure to rapid warming processes (Giorgi and Lionello 2008; Tuel and Eltahir 2020). Consequently, the high marine biodiversity of the basin (Coll et al., 2010) is

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rapidly changing mostly due to an increased dominance of warm-affinity species (Cramer et al., 2018; Cavraro et al., 2023). This dominance is even increased by the occurrence of a large pool of non-indigenous invasive species of Indo-Pacific origin that have migrated through the Suez Canal (eg., Katsanevakis et al., 2016, Galil, 2023), and the decline of cold-affinity (temperate) species (Lejeusne et al., 2010; Azzurro et al., 2019). The Mediterranean Sea is one of the most exploited areas in the world, and most fish stocks are overexploited (Colloca et al., 2013, 2017; FAO 2022), making them particularly vulnerable to climate change (Moullec et al., 2019). Predicting the impacts of climatological factors on fisheries production is not trivial since each species has individual traits that govern responses to environmental changes (Brander 2010). One way to bypass the complexity of these interactions, which are mainly unknown, is to use indices that might inform about communities' response to climate change. The mean temperature of the catch (MTC) is an index proposed by Cheung et al. (2013) that helps to evaluate the effects of sea warming on fisheries catches and/or fish communities. MTC is driven by the preferred temperature range of the species, and it is weighted for the species' relative biomass. An increasing MTC indicates a progressive community shift in toward more thermophilous species, which might be related to a decrease in cold-affinity species (Tsikliras and Stergiou 2014). According to Cheung et al. (2013), the global MTC has increased at an average rate of 0.19 °C per decade, also showing a positive relation with the sea surface temperature (SST) in several large marine ecosystems. Studies carried out in the Mediterranean Sea, have shown contrasting MTC trends, from low or negligible temporal trends (Peristeraki et al., 2019) to clear MTC increasing (e.g., Keskin and Pauly 2014; Fortibuoni et al., 2015; Tsikliras et al., 2015) even at higher rates than the global average (Tsikliras and Stergiou 2014). However, most of these studies are based on Cheung's database of species' thermal preferences and did not explore the relationship occurring between MTC and other key environmental drivers. A possible drawback in applying Cheung's database is that it is based on sea surface temperature data (Cheung et al., 2013), and thus it does not consider the real thermal preferences of bottom-dwelling species, particularly for those living in the deep sea. In addition, this database includes a subsample of the species occurring in the Mediterranean Sea thus allowing to cover only a proportion of the catch biomass.

In this study, we estimated the MTC trend of the central Tyrrhenian Sea fish community, an area under high fishing pressure (Russo et al., 2019), to understand how it is reacting to the ongoing sea warming. We employed species abundance data derived from the international bottom trawl survey in the Mediterranean (MEDITS, Bertrand et al., 2002; Spedicato et al., 2019) building, therefore, a "survey-based MTC". This represents a relatively long ($n = 27$ years) fishery-independent time series acquired through a standardized sampling protocol and designed for monitoring demersal communities. We built a new species' thermal preferences dataset combining MEDITS species spatial distribution data and Copernicus bottom temperature data. The main objectives of the study were: i) to understand if and how the fish community is adapting to the water temperature increase; ii) to disentangle the effect of different climatic variables on MTC changes, and iii) to investigate the main changes in fish community composition over time.

2. Materials and methods

2.1. Study area

The study area covers the central-western coast of Italy (central Tyrrhenian Sea, Fig. 1). In this region, the continental shelf extends to a depth of 120–150 m and about 15–30 km from the coast. The boundary between the upper and middle slopes is around 400 and 500 m in depth (Carpine 1970; Relini et al., 1986). The temperature remains relatively constant around 13–14 °C at depths greater than 120–200 m (IFREMER, 1997). The Levantine intermediate water, a high salinity water layer, flows counterclockwise along the slope between depths of 250 and 700 m (Serravall and Cristofalo 1999).

Based on the European Fleet Register (accessed on 24/05/2023), Lazio's fishing fleet comprises 574 vessels. Most of the fleet (76%) is made up of artisanal fishing boats measuring less than 12 m and using a variety of fishing gear (e.g., trammel nets, gillnets, longlines) acting mainly on the continental shelf. A fleet of 86 trawlers exploits fishing grounds from 50 m to 700 m depth. The composition and structure of the fish community indicate the occurrence of three main species assemblages located respectively on the continental shelf, the shelf break, and the continental slope (Colloca et al., 2003, 2004), with also marked

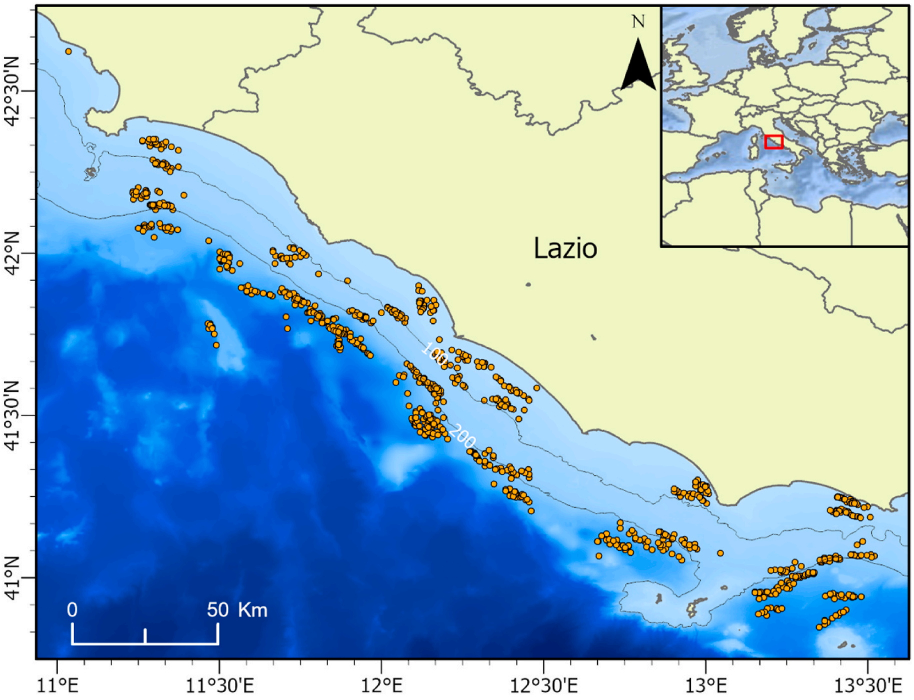

Fig. 1. Map of the investigated area showing the position of the trawl stations (orange dots). The bathymetric isolines of 100 m and 200m depth are shown.

changes between night and daylight (Carpentieri et al., 2005).

2.2. MEDITS trawl survey data

We obtained data on fish species abundances and locations of the surveys from the MEDITS programme. Started in 1994, the primary goal of MEDITS is to monitor the abundance and distribution of demersal species in EU Mediterranean waters. The MEDITS survey is generally conducted during late spring (May–June) to collect information on demersal fish and shellfish at depths ranging from 10 to 800 m. The survey uses a standardized trawl net (GOC 73) with a vertical opening of 2.5–3 m and a stretched mesh size of 20 mm in the cod-end. The net is designed to capture a broad range of species, including juvenile individuals of benthic to benthopelagic species. In the study area a total of 43 stations are sampled annually according to a standardized methodology (see Anonymous, 2017 for further details) (Fig. 1). For the purposes of this study, we extracted the biomass indices (kg km^{-2}) of fish species caught from 1994 to 2020 in a total of 1080 sampling stations. Species caught in less than 1% of hauls were considered occasional and removed from the dataset. Further details on the dataset used for the analyses can be found in Table S1.

2.3. Environmental data

For each haul, we extracted a series of 31 climatic covariates (Table S2 in supplementary materials) starting from daily-mean data of sea surface temperature (*SST*), bottom temperature (*BT*), and sea surface salinity (*SSS*) downloaded from the Mediterranean Sea Physics Reanalysis service of Copernicus Monitoring Environment Marine Service (Escudier et al., 2020) and covering the period 1994–2020. For the three variables, we calculated the average, minimum, and maximum value by quarter of the year (Q_1, Q_2, Q_3, Q_4). We also created a covariate of SST anomalies (*SSTa*) using the mean values of SST in the study area between 1987 and 2000 as a reference. Finally, the effect of large-scale climatic variability on MTC was analyzed using the winter NAO (North Atlantic Oscillation) and the AMO (Atlantic Multidecadal Oscillation) indices, both downloaded from the National Oceanic and Atmospheric Administration (NOAA, www.noaa.gov). The temporal trends in the mean SST, BT, and SSS, minimum and maximum SST, and BT per quarter of the year were estimated to understand their rate of change since 1994.

2.4. The mean temperature of the catch (MTC)

A new dataset of mean preferred temperatures (*TP*) of Mediterranean fish species was created using the whole MEDITS dataset, covering almost all the northern Mediterranean Sea in a depth range from 10 to 800 m. For this analysis, we focused exclusively on the initial period of the survey (1994–2000), during which BT conditions, especially in Q2 and Q3 when the survey took place, appeared relatively stable (Fig. 2). The *TPs* of each species were calculated using the following equation:

$$TP = \frac{\sum_i^n BT_i C_{j,i}}{\sum_i^n C_{j,i}} \tag{1}$$

where $C_{j,i}$ are the biomasses of species j in haul i, BT_i is the mean bottom temperature of the corresponding quarter of the year when and where the haul i was carried out (e.g., hauls sampled in May 2000 are associated with the mean bottom temperatures of the second quarter of 2000), and n is the total number of hauls. The list of the species for which the *TP* values were calculated (127 species, corresponding to about 97% of the MEDITS fish catch biomass) is shown in Table S3 of the supplementary materials. By comparing the preferred temperatures of the common species found in our and Cheung's dataset, we found that the former are substantially lower and with less variability than the latter (Fig. S1).

After calculating the *TP* for each species, we categorized them into

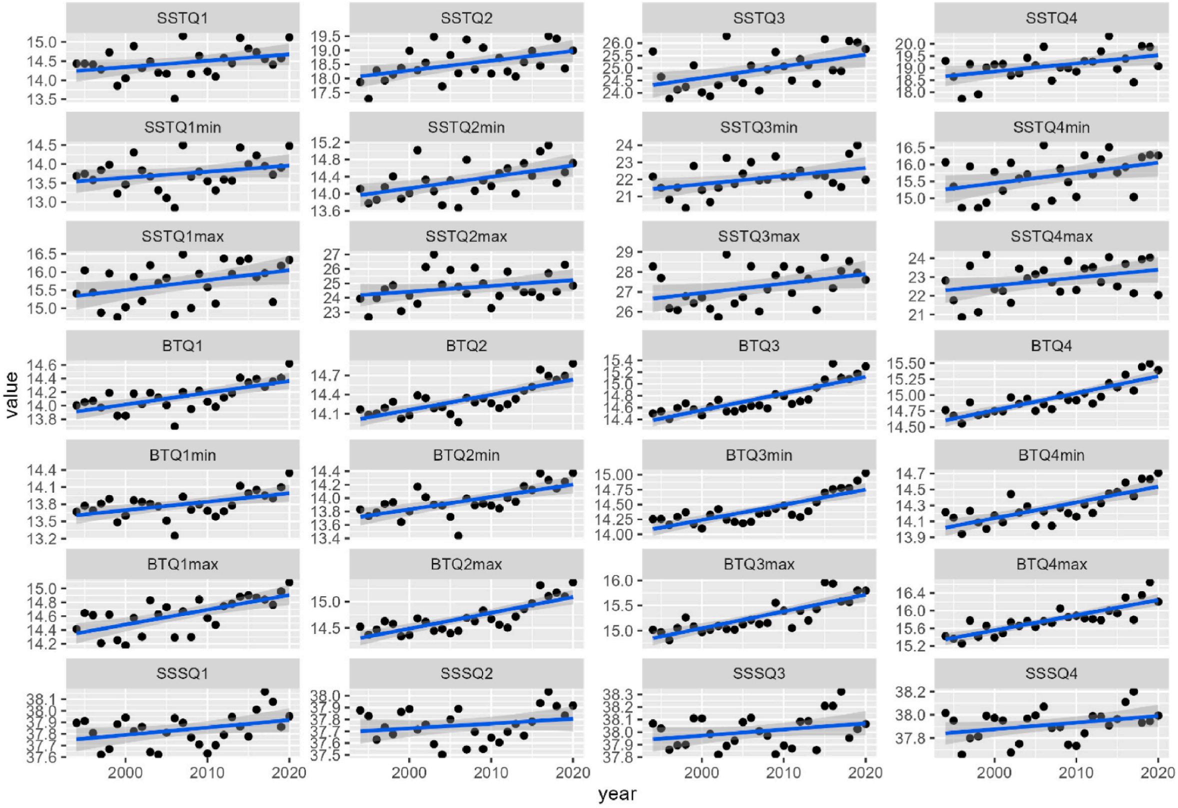

Fig. 2. Scatter plots of the covariates selected to describe the ongoing temporal trends. The blue line represents the trend of the linear regression while the grey shadow the confidence intervals of the model.

three groups based on quartiles derived from the inferred preferred temperature distribution. Species with a preferred temperature equal to or lower than the 25th percentile were classified as cold-affinity species, those falling between the 25th and 75th percentiles were classified as temperate-affinity species, and those with a preferred temperature higher than the 75th percentile were classified as warm-affinity species.

The new *TP* dataset was used to calculate MTC index per year as follows:

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

where $C_{i,yr}$ are the catches of species *i* for year *yr*, TP_i is the estimated temperature preference of species *i* and *n* is the total number of species in the annual catch.

2.5. Fish data analysis

We applied hierarchical cluster analysis and non-metric multidimensional scaling (nMDS), based on Bray-Curtis dissimilarity for classifying and ordinating trawl stations (Clarke and Warwick 1994) and thus identifying the main fish assemblages occurring in the investigated area. A square root transformation was applied to species abundance data (kg km^{-2}), followed by a Wisconsin double standardization (Legendre and Gallagher 2001). In this process, the species abundances were initially standardized by their maximum values, and then the hauls were standardized by the totals for each haul. This standardization approach is particularly suitable when significant variations in species abundance exist within the overall sample. Differences between assemblages were tested using the analysis of similarity randomization test (ANOSIM, Clarke, 1993).

Using the information derived from the cluster analysis, we estimated the MTC considering (1) the full fish community and (2) the major species assemblages detected. We used linear regression models to estimate the annual MTC rate of change and generalized additive models (GAMs, Wood, 2017) to investigate the effects of climatic covariates on MTC. We fitted GAMs through restricted maximum likelihood with a maximum of 2 covariates (among the covariates in Table S2), and having the general form:

$$MTC = \beta_0 + s(X_1) + s(X_2) + e$$

where MTC is the mean temperature of the catch, β is the intercept, *s* is the smoothing function of the corresponding independent variables X_1 and X_2, and *e* is a random error term.

First, we estimated the model using each covariate singularly. Then, the significant covariates were used to build different alternative models that included no more than two variables together because of the length of the time series ($n = 27$ years). To avoid overfitting, we set to 4 the number of knots for each smoothing term. Akaike Information Criterion corrected for small samples (AICc; Grueber et al., 2011) was used to select the best models. We assumed a Gaussian distribution for the response variable and models were also allowed to add extra penalty to each smoothing parameter estimation if needed.

GAMs were also applied to the aggregated abundance per year of the three groups of fish species with different TPs (warm, temperate, and cold) within each assemblage.

We used the ordination trajectory plot (Legendre and Legendre 2012; Rojas-Sandoval et al., 2012) to exemplify the overall change in the composition of the community over the entire sampling period and highlight the main species driving the changes. In such plots, the community composition at a given time is represented with dots. Hence, the distances between successive observations express the magnitude of the change in community composition for that time bin. To do so, we aggregated species abundances by year and applied nMDS on Bray-Curtis dissimilarity to display nMDS yearly scores as ‘sites’. Then, we created ‘species scores’ by calculating the Pearson correlation between the raw abundances and the annual scores.

Lastly, to investigate the fish community’s adaptation to the ongoing temperature trend, we examined the temporal changes in the observed differences between the mean bottom temperature (BT) of the second quartile (Q2) and the MTC of the entire fish community (Δ T).Ordination plot and dissimilarity measures were estimated through the *vegan* R package (Oksanen et al., 2019), while model fitting was performed via the *mgcv* R package (Wood 2017). All analyses were carried out in the R language environment (R Core Team 2014) via RStudio (v. 2023.06.0).

3. Results

3.1. Trends in environmental change

Our preliminary analysis showed a clear positive and significant trend for all the selected covariates (Fig. 2). The mean SST, according to the quarter of the year, rose between 0.015 and 0.047 °C year^{-1}, while BT has increased between 0.014 and 0.034 °C year^{-1} in the last 27 years. SSS increased up to 0.006 psμ year^{-1}. The strongest trends were found for minimum ($\beta = 0.0475$, $p < 0.001$), maximum ($\beta = 0.0471$, $p < 0.001$), and average ($\beta = 0.0469$, $p < 0.001$) SST of the third quarter. Table 1 shows the coefficient of all the 28 linear regressions.

3.2. Fish assemblages

A total of 195 fish species were recorded along the Latium coast during the study period. After removing rare species, we selected 127 fish species that were used for the classification and ordination of trawl survey stations. The dendrograms and nMDS (Fig. 3) identified 3 major groups of stations separated at 82% dissimilarity corresponding to the following fish assemblages: continental shelf (mean depth = 74.74 m),

Table 1

Coefficients of the temporal linear regressions describing the trends of the selected covariates in the study area. The variables include sea surface temperature (SST) in different quarters (Q1, Q2, Q3, and Q4), with minimum (min) and maximum (max) values, as well as bottom temperature (BT) in quarters Q1, Q2, Q3, and Q4, with minimum and maximum values. Additionally, the table includes the annual trend values for salinity (SSS) in quarters Q1, Q2, Q3, and Q4. The slope (Annual trend), the standard error (StdErr), test statistics (Tvalue), and p-value are reported.

Covariate	Annual trend (β)	StdErr	Tvalue	pvalue
SSTQ1	0.017	0.002	10.113	<0.001
SSTQ2	0.035	0.002	16.284	<0.001
SSTQ3	0.047	0.003	16.66	<0.001
SSTQ4	0.034	0.002	14.052	<0.001
SSTQ1min	0.016	0.002	8.194	<0.001
SSTQ2min	0.027	0.001	18.654	<0.001
SSTQ3min	0.048	0.004	11.831	<0.001
SSTQ4min	0.03	0.003	11.771	<0.001
SSTQ1max	0.027	0.002	12.22	<0.001
SSTQ2max	0.04	0.004	9.538	<0.001
SSTQ3max	0.047	0.004	13.089	<0.001
SSTQ4max	0.042	0.004	11.49	<0.001
BTQ1	0.017	0.001	13.445	<0.001
BTQ2	0.024	0.003	8.273	<0.001
BTQ3	0.028	0.007	4.111	<0.001
BTQ4	0.027	0.006	4.118	<0.001
BTQ1min	0.015	0.002	8.974	<0.001
BTQ2min	0.019	0.001	15.474	<0.001
BTQ3min	0.026	0.004	5.952	<0.001
BTQ4min	0.02	0.002	7.992	<0.001
BTQ1max	0.021	0.003	7.336	<0.001
BTQ2max	0.03	0.006	5.337	<0.001
BTQ3max	0.033	0.011	3.044	<0.01
BTQ4max	0.034	0.011	3.129	<0.01
SSSQ1	0.006	0.001	8.36	<0.001
SSSQ2	0.004	0.001	4.779	<0.001
SSSQ3	0.005	0.001	6.503	<0.001
SSSQ4	0.006	0.001	7.986	<0.001

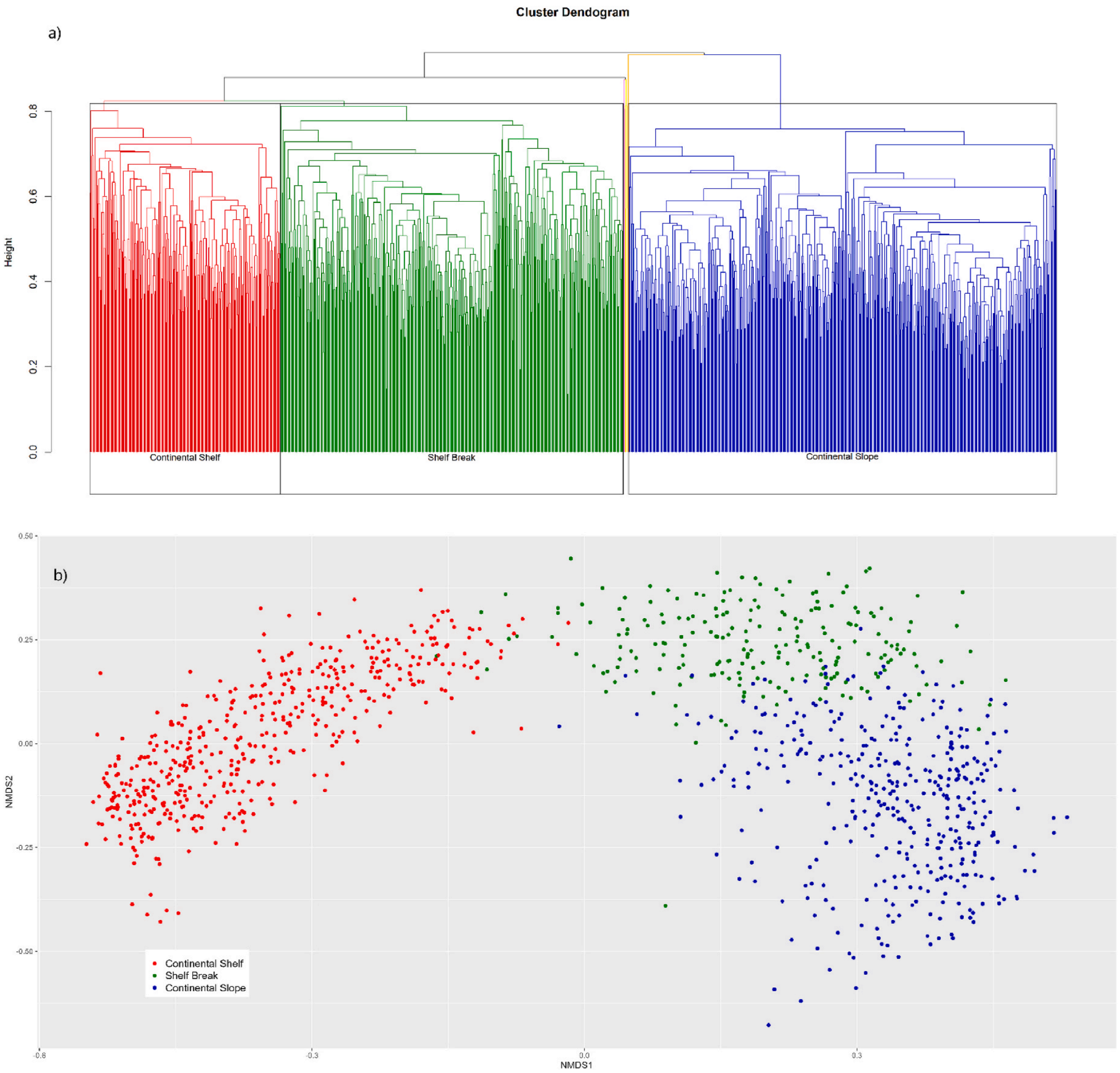

Fig. 3. Dendrogram (a) and NMDS ordination plot (b) of the 1080 trawl stations sampled in the period 1994–2020 using group-average clustering from Bray–Curtis similarity on square root transformed abundances of demersal fish in the central Tyrrhenian Sea. The three main assemblages are shown in different colors: red (continental shelf), green (shelf break), and blue (continental slope).

shelf break (mean depth = 167.1 m), and continental slope (mean depth = 474.24 m), which include 1074 out of 1080 stations. The remaining ones were discarded from the following analysis. The ANOSIM test confirmed significant differences between the three assemblages ($R = 0.75$, p-value <0.001). Table 2 shows the contributions in the percentage of the most abundant species of each assemblage. In the coastal shelf assemblage *Engraulis encrasicolus* (31.8%), *Sardina pilchardus* (14.4%), and *Mullus barbatus* (11.8%), accounted for nearly 60% of the total relative biomass. In the shelf break assemblage, the most abundant species were *Merluccius merluccius* (22.0%), *Glossanodon leioglossus* (20.5%), and *Lepidopus caudatus* (12.4%). On the continental slope, *Galeus melastomus* was the dominant species (31.2%) followed by *Lepidopus caudatus* (8.3%). Interestingly, *Merluccius merluccius* was the only species well represented in all three assemblages, highlighting its wide presence and importance across these communities.

3.3. MTC trend

A statistically significant increase in MTC was observed for the whole fish community (Fig. 4a), with an estimated increasing rate of 0.01 °C $year^{-1}$ (CI 95% [0.001, 0.019], $p < 0.05$). In contrast, the coastal shelf assemblage did not exhibit a significant MTC trend but only wide fluctuations from year to year (Fig. 4b). A pronounced increase in MTC was observed both in the shelf break (0.017 °C $year^{-1}$, CI 95% [0.011, 0.024], $p < 0.001$, Fig. 4c) and continental slope (0.004 °C $year^{1}$, CI 95% [0.001, 0.008], $p < 0.05$, Fig. 4d) assemblages.

Results of GAMs for the full fish community showed that the best model (66% of explained deviance, Table 3) of MTC response to environmental variability included the minimum bottom temperature of the second quarter (BTQ2min) and the mean sea surface salinity of the second quarter (SSSQ2). MTC increases almost linearly with these two predictors (Fig. 5a and b). For the shelf break assemblage, the best GAM model (76% of explained deviance, Table 3) incorporated two predictors: the minimum sea surface temperature of the third quarter (SSTQ3min) and the minimum bottom temperature of the third quarter (BTQ3min). SSTQ3min positively affected MTC until about 23 °C where it leveled off with greater uncertainty (Fig. 5c). Conversely, the BTQ3min began to positively influence MTC from about 14 °C (Fig. 5d). Lastly, for the slope assemblage, the most suitable GAM model (56% of explained deviance, Table 3) showed a significant effect of the mean surface sea temperature (SSTQ3min) and the maximum bottom temperature of the third quarter (BTQ3max) on the MTC. The former starts

Table 2
Percentage contribution of typifying species (over 2% of the total biomass) for the three major demersal assemblages identified in the trawl surveys carried out between 1994 and 2020 in the central Tyrrhenian Sea.

Species	Continental Shelf	Shelf break	Continental Slope
Engraulis encrasicolus	31.76	4.71	
Sardina pilchardus	14.4		
Mullus barbatus	11.85	5.73	
Merluccius merluccius	6.89	22.06	7.49
Trachurus trachurus	4.64	3.52	
Pagellus erythrinus	3.76		
Pagellus acarne	3.28		
Spicara flexuosa	2.84		
Chlorophthalmus agassizi			4.5
Conger conger			2.64
Etmopterus spinax			2.5
Micromesistius poutassou			2.1
Argentina sphyraena		3.77	
Gadiculus argenteus			6.38
Galeus melastomus			31.23
Glossanodon leioglossus		20.56	
Lepidopus caudatus		12.45	8.32
Macroramphosus scolopax		5.8	
Nezumia sclerorhynchus			5.33
Phycis blennoides			7.74

having an increasingly significant effect after 22.5 °C (Fig. 5e), while the second shows a constant positive linear effect on the MTC (Fig. 5f).

The difference (Δ T) between BTQ2 and MTC was analyzed to understand the fish community's adaptation to the ongoing temperature trend. Δ T was significant and increased during the study period ($R^2 = 0.33$, $p < 0.01$) at a rate of 0.013 °C $year^{-1}$ (CI 95% [0.005, 0.021], $p < 0.001$, Fig. 6) showing that MTC increased at a slower rate compared to bottom temperature in the period 1994–2020.

3.4. *Temporal changes in fish community composition and distribution*

The non-metric multidimensional scaling of Bray-Curtis dissimilarities from 27 yearly-aggregated samples of the fish community is presented in Fig. 7. The trajectory of the fish community over time highlights changes in composition that were not very pronounced until 2016 when the community composition started to drastically diverge from the original one mainly along the first axis of the nMDS. Species scores associated with temporal patterns in the community composition show that warm-affinity species such as *M. barbatus*, *Sardinella aurita,* and *Pagellus acarne* increased in recent years (2019–2020) when the community composition has changed the most. Additionally, other temperate species with temperature preference near the warm-affinity thermal threshold, such as *Boops boops* and *E. encrasicolus*, are similarly associated with this period.

The composition of the three fish assemblages changed following the temporal changes in the abundance of species with different preferential temperatures: warm, temperate, and cold (Fig. 8). In the continental shelf assemblage, there was an increase in warm and temperate species, though this latter seemed mostly driven by outlier data in 2020 when the survey was carried out in October–November, a period of the year with lower coastal temperature if compared with the usual survey period (Fig. 8a). In the shelf-break assemblage, there was a reduction of cold species with a parallel increasing trend of warm species, which therefore seem to have deepened their distribution range (Fig. 8b). Finally, in the continental slope assemblage there was an increase in warm and temperate species, while the cold ones did not show any clear pattern (Fig. 8c). The results of the significant GAMs are reported in Table 4.

Table 3
Analysis of deviance for the best GAM models applied to the mean temperature of the catch (MTC) of the 3 significant groups. The table shows the estimated degrees of freedom for all parameter estimates (DF), the F-tests on smooth terms (F-statistic), and the p-values for the null hypotheses that each smooth term is zero. The values in percentage represent the total deviance explained by the model.

Model	Parameters	DF	F-statistic	p-value
Full community ~66%	s(BTQ2min)	1.842	4.729	<0.01
	s(SSSQ2)	1.188	1.680	<0.01
Shelf break assemblage ~76%	s (SSTQ3min)	1.529	1.721	<0.05
	s(BTQ3min)	2.824	12.525	<2e-6
Continental slope assemblage ~56%	s (SSTQ3min)	2.270	3.605	<0.01
	s(BTQ3max)	1.044	1.157	<0.05

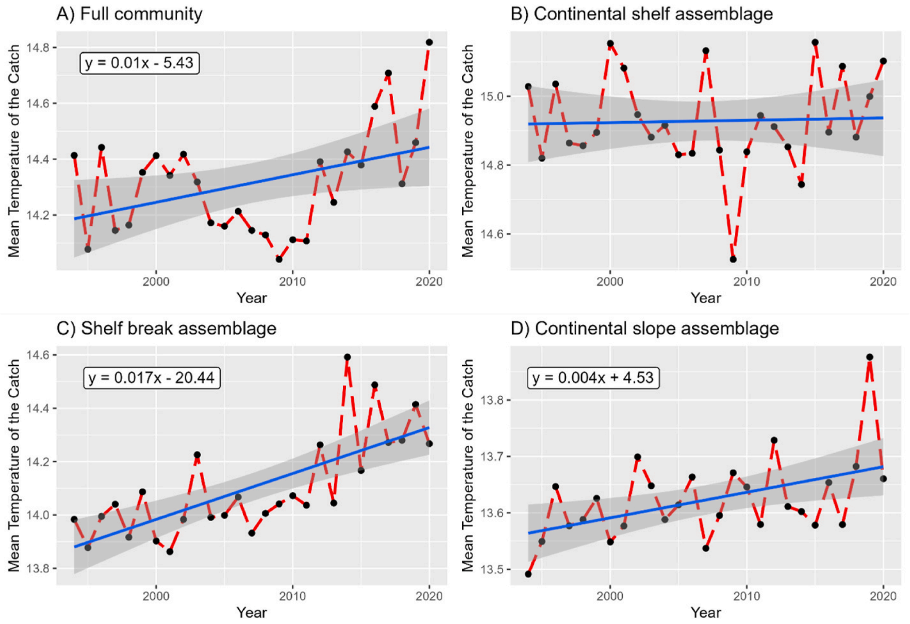

Fig. 4. The mean temperature of the catch for central Tyrrhenian Sea. The blue line represents the trend of the linear regression while the grey shadow is the confidence intervals of the model.

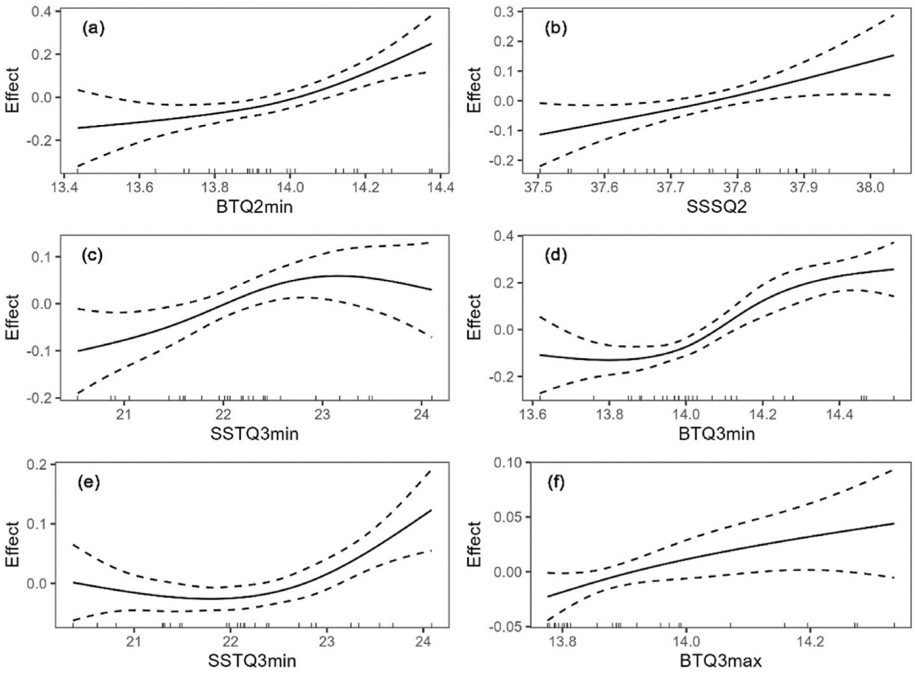

Fig. 5. [black and white]. GAM-derived significant effects of the covariates relative to the 3 best models on MTC. Figures *a* and *b* are relative to the full community model; *c* and *d* to the shelf break assemblage model; *e* and *f* represent the effects of the best slope assemblage model. Further details can be found in the text.

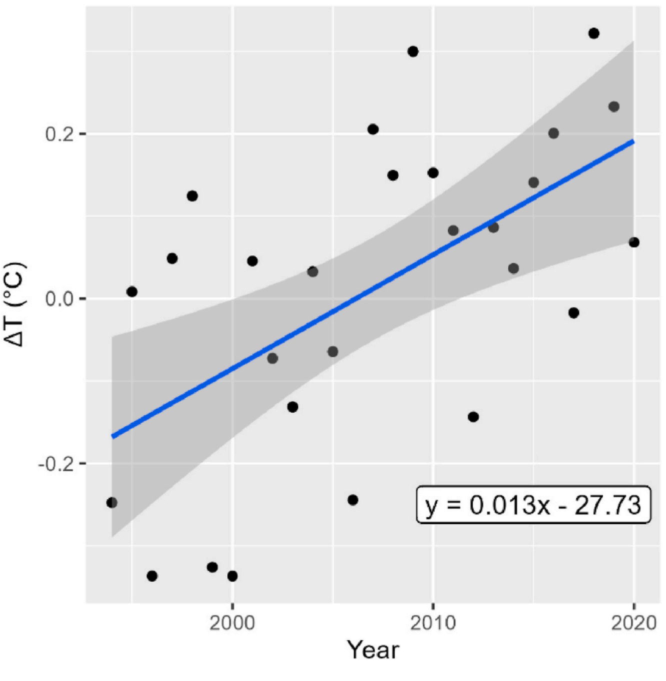

Fig. 6. [black and white]: Linear regression analysis showing the relationship between Δ T (difference between MTC and the mean bottom temperature of Q2) and year. The shaded area represents the 95% confidence interval.

4. Discussion

This study investigated temporal variation in the environmental conditions and the related community changes in the Central Mediterranean Sea demersal fish assemblages over the past 27 years. We showed that the warming trend in the study area was in line with previous studies in the Mediterranean basin (IPCC et al., 2022, Von Schuckmann et al., 2018; García-Monteiro et al., 2021). We found that warming rates accelerate throughout the year from winter to summer. In the summer season, the rate of increase in mean SST and mean BT was respectively 0.047 °C year^{-1} and 0.028 °C year^{-1}. García-Monteiro et al. (2021) highlighted a 0.04 ± 0.001 °C year^{-1} average increase in the Mediterranean Sea's SST during the period 2003–2019. The authors also investigated the spatial variability of SST over the sub-basins of the Mediterranean Sea and calculated warming trends ranging between 0.02 °C year^{1} in the Alboran Sea and 0.07 °C year^{-1} in the Aegean Sea. The Ligurian and Tyrrhenian Sea showed a progressive increase in SST trend up to 0.12 °C year^{-1} in 2010–2019 (García-Monteiro et al., 2021), which is overall the highest trend observed at the Mediterranean scale.

In relation to this sea warming trend, we found a significant increase in MTC and a shift in the fish community composition in the study area, with a trend towards an increase of thermophilous (warm-affinity) species. The GAM analysis revealed that sea surface temperature (SST) and bottom temperature (BT) during the third quarter of the year, as well as the sea surface salinity (SSS) of the second quarter, were the most important predictors of MTC changes. These findings are in contrast with the recent study of Peristeraki et al. (2019), which did not underline any significant MTC temporal trend along the western coasts of Italy using the MEDITS trawl survey data for the period 1994–2016. The reason for the different patterns in MTC between the two studies is not easy to explain. It could be linked to differences in various methodological aspects, such as the time series and the geographical area considered for the analyses as well as the use of different data sets of fish thermal preferences. For instance, considering the three predominant species in the survey -*E. encrasicolus*, *M. merluccius,* and *G. melastomus*-we determined their respective preferred temperatures to be 14.8 °C, 13.9 °C, and 13.8 °C. In contrast, Cheung's estimates indicated median preferred temperatures of 19 °C, 18 °C, and 17 °C for the same species. In our study we observed that the rate of change in the composition of the fish community was not constant during the investigated period, but, instead, a main shift toward thermophilous species occurred in 2016, the last year of the dataset used by Peristeraki and colleagues. Additionally, in our MTC estimates, we combined species spatial abundance data collected by trawl surveys (MEDITS) with Copernicus bottom temperature (BT) data to obtain a new ad-hoc dataset of thermal preferences for Mediterranean fish species. It is most likely that the new dataset provides more realistic estimates of the

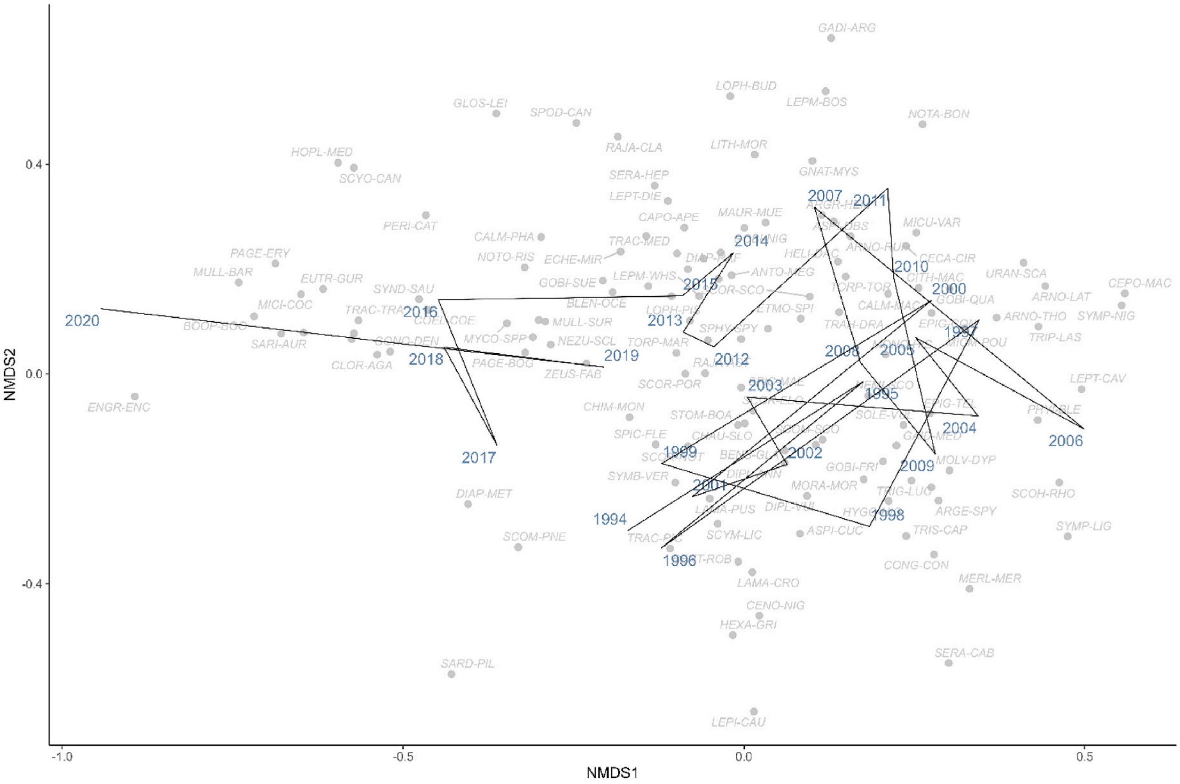

Fig. 7. [color]. Non-metric multidimensional scaling of Bray-Curtis dissimilarities from 27 yearly-aggregated samples of the fish community. The black line shows the temporal trajectory linking the yearly samples. Species labels are plotted using the coordinates of their correlations with each axis. Labels are reported in Table S3 along with the scientific names.

average thermal preferences of Mediterranean fish populations than the already existing database (Cheung et al., 2013), generally used in previous Mediterranean studies (e.g., Tsikliras and Stergiou 2014; Tsikliras et al., 2015; Fortibuoni et al., 2015; Peristeraki et al., 2019). The main caveat to our estimates is that MEDITS surveys are generally carried out from late spring to early summer, thus indicating the thermal fish preferences during this specific period of the year. Cheung's dataset was indeed inferred from worldwide fish distribution and based on average sea surface temperature data that are likely to overestimate the preferred temperature of bottom-dwelling and deep-sea species. Our choice was also dictated by the peculiar features of the semi-enclosed Mediterranean Sea with substantial differences in environmental conditions from the nearby Atlantic Ocean. As shown by many studies there are substantial intraspecific genetic divergences between Atlantic and Mediterranean fish populations (Bargelloni et al., 2003; Magoulas et al., 2006; Šegvić-Bubić et al., 2016), as well as differences in life history traits that can be likely due to the adaptation to the different environmental conditions (e.g., temperature and salinity) (Patarnello et al., 2007).

In our study, for the first time in the Mediterranean region, we considered differences in MTC among the main fish assemblages occurring from the coastal shelf to the middle slope in the 10–800 m depth range. This is particularly relevant in the Mediterranean Sea, where two completely different fish assemblages inhabit the shelf and the slope (Colloca et al., 2003, 2004). Therefore, any analysis involving the whole fish community could not be sensitive enough to detect the possible different responses of fish assemblages to climate forcing. Our findings indicate that although the MTC of the continental shelf fish assemblage did not show any trend, it was positively related to the ongoing warming for both the shelf break and the continental slope assemblages. The MTC increased at a rate of 0.017 °C year^{-1} in the shelf break community and 0.004 °C year^{-1} in the continental slope assemblages. Such differences were linked to the contrasting trend in abundance of species with different thermal preferences. In recent years, there has been a noticeable increase in warm affinity species in the coastal shelf and shelf break areas, with significant fluctuations observed on the continental slope. Conversely, cold affinity species have been found to be less abundant on the shelf and shelf break in recent years, while exhibiting substantial variability on the slope without any discernible trend. A deepening of fish assemblages (sensu Dulvy et al., 2008) is confirmed also by the increase of intermediate thermal preferences species (temperate) on the slope assemblage. For example, temperate species such as *L. caudatus*, *M. scolopax*, *Lophius budegassa*, and *G. argenteus* all exhibit a noticeable increase in their population abundances over time. Unexpectedly, the increase of warm species on the continental shelf was not counterbalanced by a decrease in temperate species. Therefore, an overall increase in relative fish biomass was observed in this assemblage. One plausible explanation could be attributed to the reduction in fishing fleet capacity observed in recent years (STECF, 2023). This decline in the number of fishing vessels might have counteracted the possible negative impacts of climate warming on temperate species. Further investigations would be therefore needed to understand how fishing activities and climate are driving fish dynamics in the continental shelf ecosystem. The MTC increasing rate that we found for the whole community (0.01 °C year^{-1}) was lower if compared to the one found in the Western and Central Mediterranean, which were 0.056 °C year^{-1} and 0.10 °C year^{-1}, respectively (Tsikliras and Stergiou 2014). It was, by contrast, more similar to what was highlighted by Fortibuoni et al. (2015). The authors detected an MTC increase of 0.012 °C year^{-1} and a significant effect of temperature. In Greek waters (East Mediterranean), the rate of increase of MTC applied on official catch statistics (landings) for the period 1970–2010 was much higher: 0.101 °C year^{-1} in the Aegean and 0.117 °C year^{-1} in the Ionian Sea (Tsikliras et al., 2015).

Our results represent substantial evidence that fish communities of the central Tyrrhenian Sea progressively adapt to the increase in

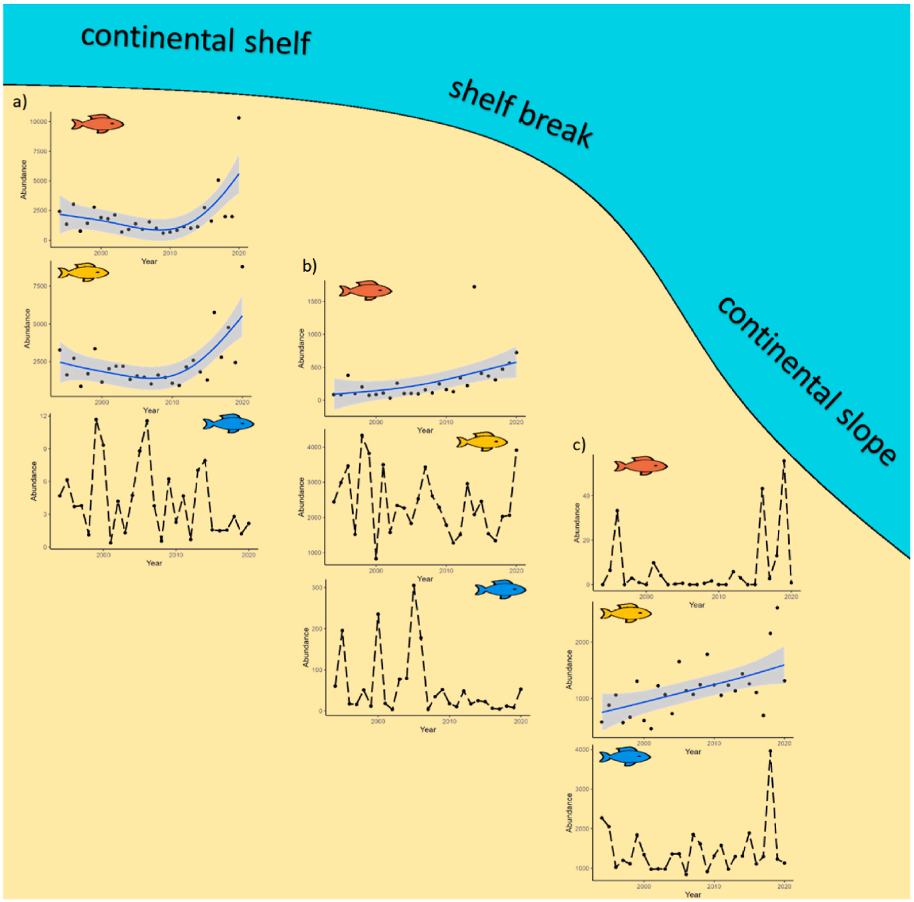

Fig. 8. Trend in abundance (kg km^{-2}) of fish with different thermal differences, namely: warm-affinity (red), temperate-affinity (yellow), and cold-affinity (blue) for the three fish assemblages on the continental shelf (a), shelf break (b), and continental slope (c) respectively. Plots showing significant trends are represented using the confidence intervals (grey shadow) of the associated Generalized Additive Models, whose results are shown in Table 4.

Table 4
Analysis of deviance for the significant temporal GAMs applied to the assemblage per group aggregated abundances. The values in percentage represent the total deviance explained by the model.

Model	DF	F-statistic	p-value
Warm affinity species (Continental shelf assemblage) ~51%	2.974	2.341	<0.01
Temperate affinity species (Continental shelf assemblage) ~53%	2.749	2.661	<0.01
Warm affinity species (Shelf break assemblage) ~31%	1.629	1.059	<0.01
Temperate affinity species (Continental slope assemblage) ~34%	0.925	1.361	<0.01

temperature through proportional changes in the abundance of species with different thermal preferences. However, we found that MTC is increasing at a lower rate compared to BT, suggesting a progressive under-adaptation of the fish community that seems not fully able to keep up with the ongoing pace of warming, While there are multiple possible explanations of this phenomenon, such as the genetic and physical limitations that can impair species adaptation (Rijnsdorp et al., 2009; Huang et al., 2021), it can be seen as an important wake-up call and a warning regarding the fish community's capacity to cope with the ongoing warming. We found that also salinity is increasing in the study area and was an important driver of MTC changes. Salinity is indeed a significant abiotic factor that plays a crucial role in regulating the behavior, physiological processes, evolutionary diversification, and geographical distribution of aquatic organisms, including fish (Boeuf and Payan 2001; Paiva et al., 2018; Velotta et al., 2022).

Salinity in the Mediterranean Sea is expected to increase in the future due to climate change as an effect of decreasing precipitations and increasing evaporation in the Mediterranean region (Soto-Navarro et al., 2020).

More research is needed to understand the resilience of Mediterranean fish communities to sea warming, and, in this regard, the key role played by functional biodiversity and compensatory dynamics in promoting stability in the face of environmental variability (Gonzalez and Loreau 2009; Loreau and de Mazancourt 2013). It is also still unclear the role of overfishing and how it interacts with climate change in altering the structure and functioning of fish communities in the Mediterranean Sea. Intensive fishing pressure can modify the structure of the food web as a result of shifts in predator-prey relationships (Kaiser et al., 2002), change the size structure of populations (Gislason 2002; Jennings and Dulvy 2005; Daan et al., 2005), and promote genetic selection toward faster growth rates and earlier maturity (Fromentin and Fonteneau 2001; Jørgensen et al., 2007). Moreover, the spatial distribution of target species may be affected by fishing practices (Ciannelli et al., 2013), and there can be unintended consequences on non-target species populations (Pranovi et al., 2001; Ordines et al., 2014). Additionally, fishing activities can lead to a reduction in habitat complexity and changes in the structure of the benthic community (Callaway et al., 2002), which can in turn affect fish abundance and distribution. In the Mediterranean Sea some important commercial fishes, such as hake (*Merluccius merluccius*), mackerel (*Scomber scombrus*), and blue whiting (*Micromesistius poutassou*), originate from the colder waters of the

Atlantic Ocean. These species have likely been impacted by the recent rise in sea temperatures in the region. Hake is experiencing overfishing in the entire Mediterranean basin (FAO, 2022), while both mackerel and blue whiting strongly declined at the very least in the last 20 years, becoming less profitable for local fisheries (Mazzoldi et al., 2014, Mir-Arguimbau et al., 2022). On the other hand, there is evidence of a positive effect of warming on warm-affinity species. An example is the deep-sea pink shrimp (*Parapenaeus longirostris*) which increased its abundance and expanded its northward distribution in the Tyrrhenian Sea in response to the increase in temperature (Colloca et al., 2014). Although our study was limited to a relatively small area in the western Mediterranean Sea, and further research is needed to determine to which extent our findings can be applied to other regions, it raises concerns about how pervasive changes induced by the current warming are. The impact on fisheries would need to be better explored from a socio-economic perspective, considering the important ongoing changes in landings composition.

Our findings show that MTC is a valuable and simple composite indicator to monitor the effects of climate change on marine communities and fisheries. As such, the MTC can be effective for monitoring the impact of warming waters on fishing communities, and it can be easily integrated into the framework of the EU's strategy for adaptation to climate change. The poor status and overexploitation of Mediterranean fish stocks should promote precautionary fishery management, also considering that climate change will likely shrink the maximum sustainable yield of commercial stocks, thus reducing the fishing opportunity in the next years (Free et al., 2019).

Authors contribution

Salvatore Valente: Data curation, Methodology, Software, Formal analysis, Visualization, Writing – Original Draft. Stefano Moro: Methodology, Writing – Review & Editing. Manfredi Di Lorenzo: Resources, Investigation, Writing – Review & Editing. Giacomo Milisenda: Resources, Investigation, Writing – Review & Editing. Luigi Maiorano: Supervision, Writing – Review & Editing. Francesco Colloca: Conceptualization, Methodology, Supervision, Writing – Review & Editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The authors do not have permission to share data.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marenvres.2023.106176.

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