



# Rising temperatures, falling fisheries: causes and consequences of crossing the tipping point in a small-pelagic community

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**Abstract** Global change has profound effects on marine species, communities, and ecosystems. Among these impacts, small pelagics have emerged as valuable indicators for detecting regime shifts in fish stocks. They exhibit swift responses to changes in ocean variables, including decreased abundances, accelerated juvenile growth rates, early maturation, and reduced adult sizes in warm waters. However, each pelagic species occupies a unique local ecological niche, that reflects the sum of all environmental

conditions. Consequently, their responses to environmental changes manifest in distinct ways. We explore here how global change affects small pelagics in the Madeira Archipelago (NE Atlantic Ocean) at (i) community level, by studying the effects of climate change over a 40-year (1980–2019) period on small pelagic landings, and (ii) population level, by studying the effects on the life-history traits of the two most abundant species, *Scomber colias* and *Trachurus picturatus*. Our study demonstrated that anomalies in

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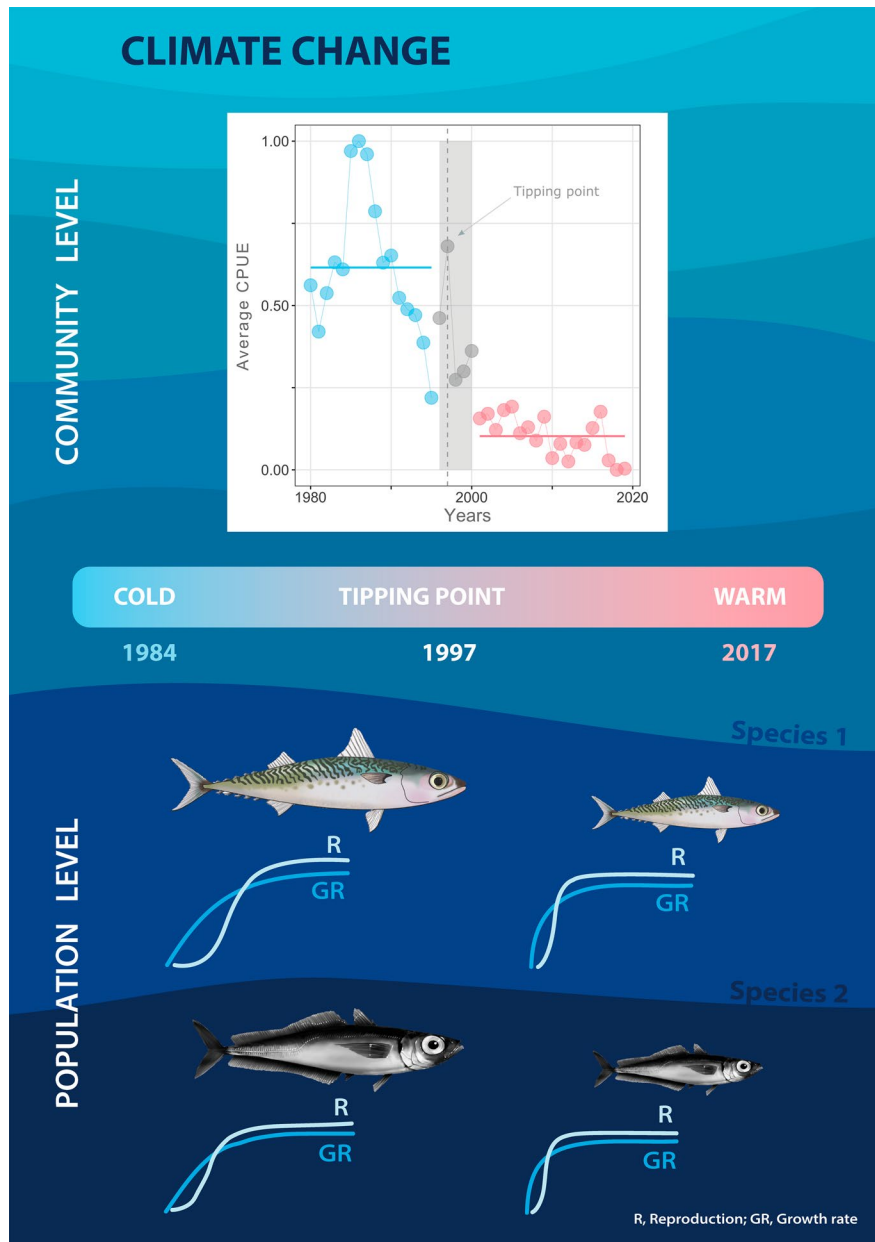
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the Sea Surface Temperature and the North Atlantic Oscillation caused a regime shift within the small pelagic community. Both environmental predictors explained 88.9% of the community landings oscillations. *S. colias* appears to exhibit a relatively more favorable adaptive response to climate change

compared to *T. picturatus*. Understanding the species-specific ecological responses of small pelagic fish to global change is crucial for effective management and conservation efforts in the face of ongoing environmental scenarios.

## Graphical abstract



**Keywords** Climate change · Marine resilience · Community regime shift · Critical transitions · Life-history traits · Atlantic Ocean

## Introduction

Climate change has significant implications for the primary productivity, growth, and distribution of marine species, as it causes reorganization of food webs, shifts in species distributions, and changes in yields of exploited species (Sumaila et al. 2011; Collins et al. 2013; Cheung et al. 2016; Boag et al. 2021). The impact of global warming on small and medium pelagic fish (SMPF) populations has been observed worldwide, leading to substantial shifts in their distribution and abundance (Sabatés et al. 2006; Schreiber 2012; Van Beveren et al. 2016). Furthermore, previous studies have documented variations in key life history traits of these fish stocks, such as age, growth, and the timing of size at first maturity (Otero and Hidalgo 2023). These variations are a result of the energy trade-off that SMPF undergoes, which involves allocating resources to growth, maintenance, or reproduction (McBride et al. 2015; Albo-Puigserver et al. 2021). SMPF responds quickly to environmental changes because of their plasticity in life-history parameters (Alheit et al. 2012). In warm waters, SMPF grow faster in the juvenile phase, mature earlier but attain smaller sizes as adults, following the temperature-size rule (TSR) (Atkinson et al. 2006). This pattern is a consequence of growth and reproduction trade-offs across temperatures, with more energy allocated to reproduction and fewer resources for growth (Brown et al. 2004; Wootton et al. 2022). Sea Surface Temperature (SST) seems to influence phenotypic flexibility, allowing populations to adjust their life history traits to maintain fitness under changing conditions (O’Dea et al. 2019). Phenotypic flexibility, which is the ability of an organism to change its phenotype in response to environmental conditions, allows populations to adapt and persist under rapid climate change (Chevin et al. 2013; Merilä and Hendry 2014).

Changes in environmental conditions resulting from climate change have significant impacts on the life history traits of SMPF. For instance, the European anchovy (*Engraulis encrasicolus*) in the Mediterranean Sea has shown a trend towards earlier spawning and reduced body size, which are responses attributed to rising sea temperatures (Palomera et al. 2007). Similarly, the distribution of the Atlantic mackerel

(*Scomber scombrus*) has shifted northwards, with changes in spawning times and growth rates observed in response to warmer waters (Jansen et al. 2012). In the California Current, the Pacific sardine (*Sardinops sagax*) has experienced changes in growth and reproductive timing linked to ocean temperature fluctuations (Checkley et al. 2009). These examples illustrate the broader pattern where SMPF exhibit plasticity in their life-history traits, adjusting their growth, maturation, and reproductive strategies to cope with changing thermal environments (Perry et al. 2005). Such phenotypic flexibility is crucial for their survival and persistence, as it enables these species to optimize their fitness in the face of rapid and ongoing climate change (Reed et al. 2011; Chevin et al. 2010). Understanding these responses is essential for managing fisheries and conserving marine biodiversity under future climate scenarios.

The shifts observed in the abundance and distribution of commercial small pelagic fish (SMPF) are primarily characterized by decreasing catch levels (Free et al. 2019; Schickele et al. 2021), and these trends may be further exacerbated by the ongoing effects of climate change (Shannon et al. 2009; Brochier et al. 2013). As a result, the management and long-term sustainability of SMPF have become crucial objectives to ensure the viability of this fishery resource (Taboada and Anadón 2016). As in economic terms, SMPF are highly valued for their meat, contributing to the seafood industry and supporting the livelihoods of fishers and related sectors (Hilborn et al. 2022). Hence, strategies have been considered to mitigate the impacts of climate change on SMPF populations (Gaines et al. 2018). Enhancing fisheries enforcement and management efforts are crucial steps associated with monitoring biomass trends (Pons et al. 2017; Hilborn et al. 2020). However, to maintain sustainable fisheries, integrated actions encompassing both climate change mitigation and proactive management reforms are essential (Gaines et al. 2018; Cheung et al. 2021). The consequences of landings decrease of SMPF are not only economic but to ecological ones since these species play a significant ecological role (Suca et al. 2018; Peck et al. 2021). They function as important energy transfer agents within the marine food web, serving as prey for marine mammals, seabirds, and larger fish species like tuna (Soudijn et al. 2021). Therefore, SMPF play a pivotal role in maintaining the overall balance and

functioning of the marine ecosystem (Costalago et al. 2012).

The NE Atlantic Ocean is recognized as a highly productive fishing region (Townsend et al. 2006). However, data on small pelagic fish stocks in this area are predominantly centered around the Baltic and North Sea, with limited information available for Atlantic oceanic archipelagos, such as the Azores, Madeira, and the Canaries. Among these regions, the Madeiran purse seine fishery holds significant importance (Vasconcelos et al. 2006, 2018). Four small pelagic species are targeted, namely *Scomber colias* Gmelin, 1789, *Trachurus picturatus* Bowdich, 1825, *Sardina pilchardus* Walbaum, 1792 and *Boops boops* Linnaeus, 1758 (Vasconcelos et al. 2018). These species have distribution ranges from the North Sea to the West African coast (Moreira et al. 2019; Martins et al. 2013; Caballero-Huertas et al. 2022), and they are esteemed for its taste, commonly consumed as fresh or canned fish (FAO 2018).

In response to a gradual decline in the abundance of *Trachurus picturatus* in the Madeiran waters, various management actions have been implemented over the past two decades to stabilize their exploitation levels. This decline in small pelagic fish populations is expected to impact their life-history traits. Analyzing life-history data becomes crucial in assessing the resilience of these species to fishing and climate change. The insights gained from such analyses can significantly contribute to enhancing integrative stock assessments, which take environmental factors into account, thereby leading to more effective and sustainable management strategies. The present study assesses the effects of climate change on small pelagic fish at two organizational levels: (i) at community level, through the study of temporal variations of the small pelagic community landings in Madeira throughout the last four decades (1980–2019) and how environmental predictors such as Sea Surface Temperature and North Atlantic Oscillation anomalies have influenced the oscillations of the small pelagic community, and (ii) at population level, by studying the effects on body size and life-history traits (growth, reproduction and mortality) of the two most abundant species, *Scomber colias* and *Trachurus picturatus* in the Madeira archipelago (NE Atlantic Ocean), over inter-generational timescales. The integration of both data series (landings and life-history traits) represents a novel perspective that deepens

our understanding of the impacts of climate change and sheds light on whether species are adapting their life-history traits to the new environmental conditions resulting from global change.

## Material and methods

### Study area

The Madeira archipelago, located around 874 km off Portugal and 500 km north of the Canary Islands, is affected by multiple coastal and oceanic currents (Caldeira et al. 2002). Between the Madeira archipelago (33° latitude) and the Portuguese mainland exclusive economic zone (38° N) there are seamounts jointly defined as the Madeira-Tore geologic complex (Morato et al. 2008). This complex promotes the occurrence of diverse benthic communities (Lobo et al. 2016) and provides spawning areas to benthopelagic species (Menezes et al. 2009).

### Pelagic community data

A long-time series of coastal and pelagic landings biomass of bogue (*Boops boops*), Atlantic chub mackerel (*Scomber colias*), sardine (*Sardina pilchardus*) and blue jack mackerel (*Trachurus picturatus*) caught around Madeira was obtained from the National Institute of Statistics (INE) with annual resolution from 1980 to 2019. These species are caught throughout the year by an artisanal purse-seine fleet which operates off the south coast of Madeira and near the Desertas Islands (Vasconcelos et al. 2018). The number of fishing days and active fishing vessels were used as measures of fishing effort (McCluskey and Lewison 2008; Martín et al. 2019). As some vessels ceased their activity in the last decades due to the support for the permanent immobilization of fishing vessels as part of the Small Pelagic Fishing Effort Adjustment Plan by the Government of Madeira (Decree No. 82/2009), the number of fishing days also decreased as a consequence. Since no significant relationship was found between the annual ratio of fishing days and the number of vessels over the period where data for fishing effort was available (2002–2017; Fig. S1), the fishing effort was averaged and extrapolated for the remaining years where data was unavailable. Catch per unit effort (CPUE) was then calculated for each species as

the biomass landings per fishing effort and averaged to obtain the Average CPUE, which was used in subsequent analyses. For environmental variables, Sea Surface Temperature (SST, °C) and North Atlantic Oscillation (NAO) Index were extracted from NASA and National Centers For Environmental Information (NOAA) databases, respectively, for the period within 1980–2019. Specifically, we used the GISS Surface Temperature Analysis (GISTEMP v4) software (GISTEMP-Team 2020; Lenssen et al. 2019) to obtain the annual average SST.

SST anomaly was calculated as the difference between the average SST over the 40-year study period and each annual average value. Positive SST anomaly scores are indicative of warm years whilst negative scores indicate cold years. As for the NAO index, the average annual value was collected based on the surface sea level pressure between the Sub-tropical area (Azores) and the Subpolar area. These values were then normalized between  $-1$  and  $1$ , and their anomalies calculated. NAO index oscillations reflect irregularities in temperature and precipitation. For instance, during a negative NAO phase, Southern Europe experiences wet conditions while Greenland tends to be dry, whereas the opposite pattern is observed during a positive NAO phase. Both environmental variables were obtained with a  $4 \times 4$  km spatial resolution.

#### *Climate change impacts and CPUE tipping point*

To synthesize the environmental information into a single variable, we performed an environmental Principal Component Analysis (PCA) using the *psych* R package (Revelle and Revelle 2015). The resulting principal component (Environmental PC) was standardized between 0 and 1. This step allowed us to visualize the relationship between the Environmental PC and the Average CPUE in two dimensions (Fig. 1b). Additionally, we also standardized the Average CPUE between 0 and 1 through min-max scaling. This process aids in comparing the two indicators.

To investigate the factors contributing to the oscillations observed in the Average CPUE, we employed a modeling approach using environmental variables (SST anomaly and the NAO anomaly). For this purpose, we fitted a set of General Additive Models (hereafter, GAM), with the Average CPUE as the

response variable and the SST anomaly and the NAO anomaly as the predictors, using the *mgcv* R package (Wood and Wood 2015). Multiple GAMs were fitted with different parameterizations of the variables, employing the Gaussian distribution as the default setting and applying the identity function link. The best-fitting model was selected based on the Akaike Information Criteria (AIC) (Burnham and Anderson 2002). GAMs were chosen for their ability to capture nonlinear trends and assume additive and stationary relationships between the response and predictor variables (Vasilakopoulos and Marshall 2015). Furthermore, we examined the proportion of deviance explained by the predictor variables. To assess this, we calculated three R-squared scores corresponding to models adjusted with only the SST anomaly, only the NAO anomaly, and a combination of both. Subsequently, we used the *modEvA* R package (Márcia Barbosa et al. 2013) to determine the variance explained by the environmental predictors individually and in combination.

To identify the critical point at which the temporal original average CPUE experienced a substantial decline, we employed the *strucchange* R package (Zeileis et al. 2015) to determine the tipping point and the transition period in the trend for Average CPUE. The identification of the tipping point was based on minimizing the residual sum of squares, enabling us to identify a significant shift in the trends (Zeileis et al. 2002, 2003). This analysis allowed us to classify the periods before and after the tipping point occurred. For the determination of the transition periods, we considered the 95% confidence interval of the tipping point (Zeileis et al. 2002).

#### *Effects of ocean warming at population level*

The life history of *S. colias* and *T. picturatus* was selected as a case study to examine the potential impacts of warming, considering that these species had the highest contribution to the small pelagic Average CPUE in Madeira from 1980 to 2019 (Fig. S2). Two types of sampling were conducted over a period of 33 years (1984–2017) to gather data on *S. colias* and *T. picturatus*: (i) Auction samples - these samples were collected monthly from 2002 to 2017 to analyze the body size and mortality of landed fish. Data from before 2002 were not available, and only the total length (TL, in centimeters) and total

sample weight of the individuals were recorded; (ii) Laboratory samples - these samples were collected monthly from 1984 to 1991 and from 2002 to 2017 to estimate the life history of the species. The fish were processed while still fresh, and their size (total length, TL, measured to the nearest 0.1 cm) and weight (total weight, TW, and eviscerated weight, EW, measured to the nearest 0.01 g) were recorded. The gonads were removed and weighed (GW) with a precision of 0.01 g. The maturity stage of the fish was determined through visual inspection, following the five-stage maturity scale (I - immature, II - developing, III - spawning capable, IV - regressing, and V - regenerating) proposed by Brown-Peterson et al. (2011). This analysis included data collected between 1984 and 2017. Maturity stages recorded prior to 2011 were adapted to align with the referenced maturity scale. Additionally, the *sagitta* otoliths were carefully removed, washed, and stored in labeled vials for further aging studies. The fish were aged by a single reader using standard aging techniques (Vitale et al. 2019).

To investigate the impact of ocean warming at the population level, two distinct periods were identified based on the tipping point and the corresponding transition period (see results section "CPUE declines as a response to climate change" and Fig. 1a). The first period (P1) spans from 1984 to 1995 and is characterized by a cold state, with an average SST of 19.81C. The second period (P2) covers the years 2002 to 2017 and represents a warm state, with an average SST of 20.46C.

To compare the laboratory-length frequency distributions among the identified periods, a two-sample Kolmogorov–Smirnov (K–S) test was performed using the *stats* R package (R Core Team 2023). To address the uncertainty associated with the asymptotic distributions of K–S test statistics under the null hypothesis, Monte Carlo simulations were conducted using the *ks.boot()* function from the *Matching* R package (Sekhon 2020). This approach involved running 100,000 simulations and allowed for the consideration of ties, which is not possible in the traditional K–S test. Furthermore, to assess the differences in average lengths between the two periods, the Mann–Whitney U test was used within the *stats* R package.

A total of 4154 otoliths from *S. colias* and 2542 otoliths from *T. picturatus* were used for growth

parameter estimation during P2 (2002–2017). Unfortunately, no age data were available for P1, except for previously published studies (Lorenzo Nespereira et al. 1995; Carvalho et al. 2002; Vasconcelos et al. 2006). To estimate the growth parameters, the von Bertalanffy growth model was fitted to the data of females and males from P2 using the *FSA* R package (Ogle et al. 2022). Years used for this estimation were selected based on the following criteria: (i) similar maximum lengths, (ii) similar mean lengths at age, and (iii) better data convergence (see Figs. S3 and S4). The starting parameters for the model were determined using a Ford-Walford plot, and the estimation of the growth parameters asymptotic length ( $L_{inf}$ , cm), brody growth coefficient ( $k$ , year<sup>-1</sup>), and theoretical age at which length is zero ( $t_0$ , year), was carried out using Gauss-Newton's algorithm for non-linear least-square procedure. Confidence intervals for the growth parameters were calculated through bootstrapping with 1000 iterations. To compare the growth parameters between sexes, the Akaike's Information Criterion (AIC) was used (Sakamoto et al. 1986). Multiple models were constructed by fixing one or two parameters and comparing their AIC values. The model with the lowest AIC value was considered the best model. The  $\Delta$ AIC value, which represents the difference between the AIC value of each model and the lowest observed AIC value, was also calculated and used to confirm the optimal model. Once the optimal model was identified, differences in growth between sexes were evaluated using this model.

To estimate mortality, the length compositions of landings were analyzed for P2. The length-frequency distributions from the auction samples were amplified to account for each vessel, day, and month. By summing the monthly length compositions, annual length compositions were obtained. To estimate annual age

**Table 1** Synthesis of the scores (average  $\pm$  standard error) of the variables during the cold period (Period 1, before the transition) and the warm period (Period 2, after the transition)

Variables	Period 1	Period 2
SST anomaly	-0.29 $\pm$ 0.12	0.35 $\pm$ 0.007
SST average	19.81 $\pm$ 0.12	20.46 $\pm$ 0.07
NAO anomaly	0.06 $\pm$ 0.03	-0.04 $\pm$ 0.05
Average CPUE	2.81 $\pm$ 0.20	0.91 $\pm$ 0.05

distributions, the annual-age length keys derived from laboratory samples were multiplied by the estimated annual landings' length composition. The methodology for this process is detailed in Vasconcelos et al. (2011). The total instantaneous mortality rate ( $Z$ ) was estimated based on this age distribution using the age catch curve analysis method (Beverton and Holt 1957), considering exclusively fully recruited ages (Ricker 1975). The same periods selected for the estimation of growth parameters were used in this analysis. The total mortality ( $Z$ ) was calculated by employing linear regression analysis with the *fishmethods* R package (Nelson and Nelson 2022). Natural mortality ( $M$ ) was estimated for each period using Pauly's method (Pauly 1980). Fishing mortality ( $F$ ) was then estimated by subtracting natural mortality ( $M$ ) from total mortality ( $Z$ ), following the equation  $F = Z - M$ .

The reproductive activity of each population was assessed by analyzing the gonadosomatic index (GSI) and size at first maturity ( $L_{50}$ ). The monthly changes in GSI were calculated separately for females and males using the following equation (King 2013):

$$GSI = 100 * \frac{GW}{EW} \tag{1}$$

where GW and EW are gonad weight and eviscerated weight, respectively. The null hypothesis of equal monthly GSI means before (P1) and after (P2) the transition period was tested using the Mann-Whitney U test in the *stats* R package (R Core Team 2023).

For each species and period, the size at which 50% of individuals are mature ( $L_{50}$ ) was estimated for females and males. The proportion of mature individuals (P) per size class (L) was defined as those with maturity stages II to V. Only maturity data

**Table 2** Von Bertalanffy growth parameters (VBGP) estimated using the direct otolith reading and back-calculation methods for *Scomber colias* and *Trachurus picturatus*

from the Madeira archipelago (NE Atlantic Ocean) for the sampled periods of P1 (1984–1991) and P2 (2002–2017). \*\* denote significant differences

Method	Period	n	<i>Scomber colias</i>			
			VBGP	VBGP-value	SE	P-value
Back-calculation (Canary Islands, Lorenzo Nespereira et al. 1995)	1	658	$L_{inf}$	49.20	–	–
			$k$	0.210	–	–
			$t_0$	-1.400	–	–
Direct Otolith Aging (Azores, Carvalho et al. 2002))	1	349	$L_{inf}$	57.52	–	–
			$k$	0.201	–	–
			$t_0$	-1.093	–	–

Method	Period	n	Females				Males			
			VBP	VBP-value	SE	P	n	VBP-value	SE	P
Direct Otolith Aging (FSA R package)	2	2048	$L_{inf}$	40.92	1.464	<0.001**	2106	40.80	1.791	<0.001**
			$k$	0.317	0.039	<0.001**	0.283	0.041	<0.001**	
			$t_0$	-1.844	0.198	<0.001**	-2.212	0.242	<0.001**	

Method	Period	n	<i>Trachurus picturatus</i>							
			Females				Males			
			VBP	VBP-value	SE	P	n	VBP-value	SE	P
Direct Otolith Aging (software Statistica 6.0, Vasconcelos et al. 2006)	1	295	$L_{inf}$	49.78	–	–	248	39.57	–	–
			$k$	0.114	–	–	0.194	–	–	
			$t_0$	-3.052	–	–	-2.563	–	–	
Direct Otolith Aging (FSA R package)	2	1434	$L_{inf}$	29.01	1.249	<0.001**	1108	27.30	0.813	<0.001**
			$k$	0.295	0.057	<0.001**	0.403	0.066	<0.001**	
			$t_0$	-3.473	0.510	<0.001**	-2.703	0.376	<0.001**	

$L_{inf}$  represents the asymptotic length (cm),  $k$  is the Brody growth coefficient ( $year^{-1}$ ),  $t_0$  is the theoretical age at which length is zero (year), n is the number of individuals, and SE indicates the standard error

corresponding to the reproduction period of each species was used in the determination of  $L_{50}$ . This parameter was obtained by fitting logistic ogives to the proportion of sexually mature individuals using non-linear least squares analysis (Jennings et al. 2001), as follows:

$$P = \frac{100}{1 + e^{-b(L-L_{50})}} \quad (2)$$

## Results

CPUE declines as a response to climate change

The environmental dimension was found to have a significant impact on the Average CPUE. The anomalies in SST and NAO accounted for 88.9% of the variance in the Average CPUE, with both variables showing a significant effect (GAM model;  $p < 0.001$  for SST anomaly and  $p = 0.007$  for NAO anomaly). Variance partitioning analysis revealed that the SST anomaly explained 61.8% of the variance, the NAO anomaly explained 27.8% of the variance, the intersection between the two environmental factors accounted for -15.1% of the variance, and the remaining unexplained variance was 25.5%. Additionally, the environmental principal component (Environmental PC) explained 63.8% of the variance.

The tipping point for the Average CPUE occurred in 1997, with a transition period spanning from 1996 to 2000 (Fig. 1a). The first period (P1), from

1980 to the onset of the respective transition period, was characterized by high average CPUE values, positive NAO anomalies, negative SST anomalies, and lower SST averages, referred to as the cold period (Table 1). The second period (P2) extended from the end of the respective transition period to 2019 and exhibited low average CPUE values, negative NAO anomalies, positive SST anomalies, and higher SST averages, referred to as the warm period (Table 1). Furthermore, our analysis revealed that the identified periods in the Average CPUE could be explained by the environmental variables (Fig. 1b).

Higher growth rate, smaller body size and higher natural mortality at warmer temperatures

A total of 38,056 specimens of *S. colias* (25.76  $\pm$  4.83, range 10.0–51.0 cm TL) and 43,602 of *T. picturatus* (19.97  $\pm$  3.30, 10.0–44.0 cm TL) were

**Table 4** The estimated values of size at first maturity ( $L_{50}$ , cm TL) for female (F), male (M), and total (T) individuals of *Scomber colias* and *Trachurus picturatus* from Madeira archipelago (NE Atlantic Ocean) for the sampled periods P1 (1984–1991) and P2 (2002–2017)

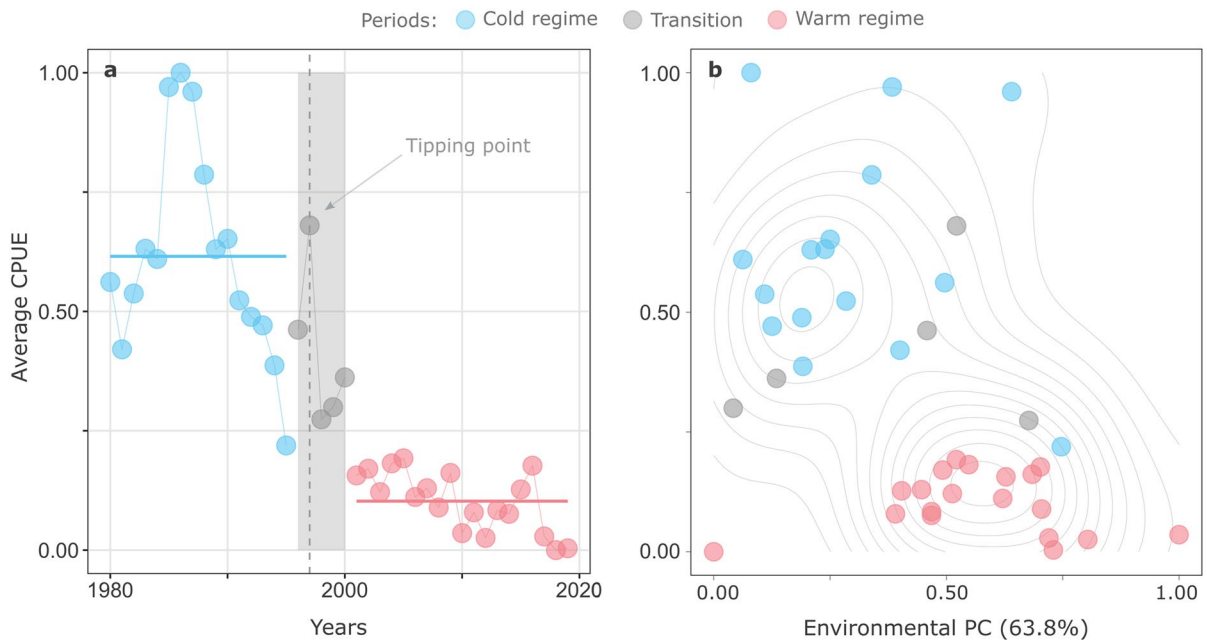
Species		Period 1	Period 2
<i>S. colias</i>	Females	21.99 ( $r^2 = 0.93$ )	18.32 ( $r^2 = 0.96$ )
	Males	20.33 ( $r^2 = 0.98$ )	17.52 ( $r^2 = 0.99$ )
	Total	19.18 ( $r^2 = 0.99$ )	17.96 ( $r^2 = 0.99$ )
<i>T. picturatus</i>	Females	19.04 ( $r^2 = 0.96$ )	17.19 ( $r^2 = 0.98$ )
	Males	18.99 ( $r^2 = 0.97$ )	16.52 ( $r^2 = 0.99$ )
	Total	19.03 ( $r^2 = 0.98$ )	16.50 ( $r^2 = 0.96$ )

**Table 3** Estimated values of total instantaneous mortality (Z, in years), natural mortality (M, in years), and fishing mortality (F, in years) for *Scomber colias* and *Trachurus picturatus* from

Species	Period	SST	Sex	Z $\pm$ SE	M	F
<i>S. colias</i>	1 (Lorenzo Nespereira et al. 1995)	19.81	Total	–	0.477	–
	1 (Carvalho et al. 2002)		Total	–	0.444	–
	2	20.46	Females	1.368 $\pm$ 0.335	0.668	0.700
			Males	1.118 $\pm$ 0.241	0.621	0.497
<i>T. picturatus</i>	1 (Vasconcelos et al. 2006)	19.81	Females	–	0.319	–
			Males	–	0.484	–
	2	20.46	Females	1.563 $\pm$ 0.279	0.701	0.862
			Males	1.522 $\pm$ 0.211	0.875	0.647

SST represents the average Sea Surface Temperature (C). SE indicates the standard error.





**Fig. 1** Trends in average catch per unit effort (CPUE) over the 40-year study period, with a tipping point indicated by a vertical dashed line and a dark grey area representing the transition

sampled between 2002 and 2017 for length-frequency estimation of the auction samples obtained via purse seine fishery. The laboratory sample included a total of 17,609 *S. colias* ( $28.74 \pm 5.05$ , 13.5–48.0 cm TL), with 4655 from P1 (18.0–48.0 cm TL) and 12,954 from P2 (13.0–45.7 cm TL), and 17,333 *T. picturatus* ( $22.63 \pm 4.21$ , 11.0–47.0 cm TL), with 6310 from P1 (24.25  $\pm$  5.10, 13.0–47.0 cm TL) and 11,023 from P2 (21.70  $\pm$  3.26, 11.0–41.7 cm TL). These samples were used to obtain biological parameters to analyse the effects of temperature increase on the biological parameters (see Table S1).

Temperature-driven body-size changes were observed in the laboratory length-frequency distributions (Fig. 2) (Kolmogorov–Smirnov test: *S. colias*:  $Z = 0.89394$ ,  $p < 0.001$ ; *T. picturatus*:  $Z = 0.8$ ,  $p < 0.001$ ) samples, showing a decrease in the average lengths (Mann–Whitney U test: *S. colias*,  $W = 173,618,454$ ,  $p < 0.001$ ; *T. picturatus*,  $W = 44,641,614$ ,  $p < 0.01$ ). In P2, individuals of *S. colias* and *T. picturatus* were aged from 0 to 5 years. Among *S. colias*, 66% of individuals were aged 2 and 3 years old, while among *T. picturatus*, 72% of individuals were aged 1 and 2 years. Age-length keys using

period from 1996 to 2000 (a). The relationship between Average CPUE and the Environmental PC is shown in (b)

data from direct readings are represented in Tables S2 and S3. For both species, higher temperatures led to an increase in the brody growth coefficient ( $k$ ) and a decrease in the asymptotic length (Table 2, Fig. S5). Two models were selected for comparing the growth curves of females and males in P2. The selection of these models was based on the AIC and  $\Delta AIC$  values (Tables S4 and S5). For *S. colias*, one variable ( $L_{inf}$ ) was fixed, resulting in an AIC of 21,703.87 ( $\Delta AIC = 0$ ). For *T. picturatus*, two variables ( $L_{inf}$  and  $k$ ) were fixed, resulting in an AIC of 11,044.00 ( $\Delta AIC = 0$ ).

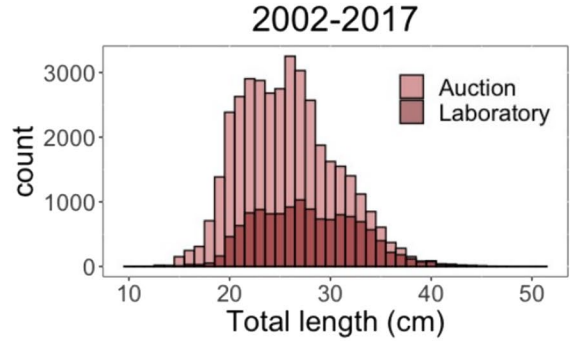
Natural mortality also showed clear temperature sensitivity, with a significant increase of around 40% from P1 ( $M$  between 0.444 to 0.477 year) to P2 ( $M$  between 0.621 to 0.668) for *S. colias* (Table 3). For *T. picturatus*, natural mortality doubled from P1 ( $M$  between 0.319 to 0.484) to P2 ( $M$  values between 0.701 to 0.875).

Early maturity and long premature ages at warm temperatures

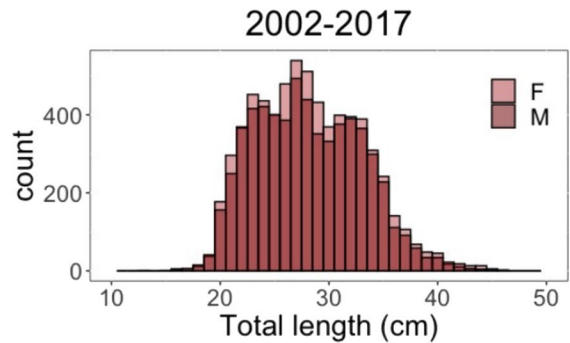
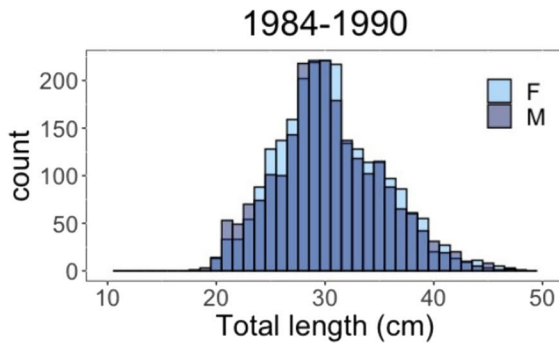
The gonadosomatic index (GSI) values for both *S. colias* and *T. picturatus* (Fig. 3) reached their highest

*Scomber colias*

Auction vs. Laboratory

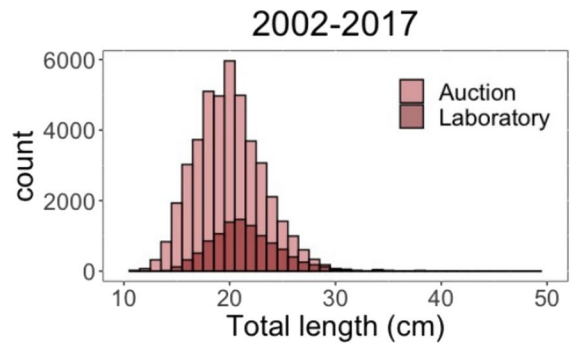


Laboratory

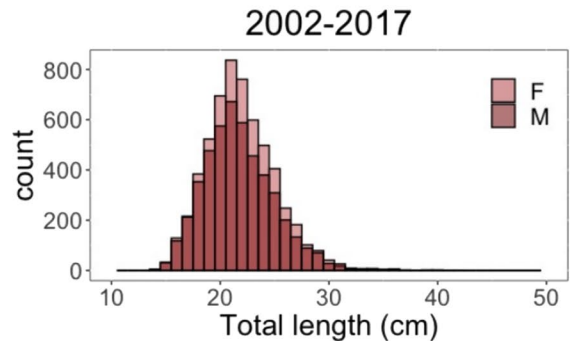
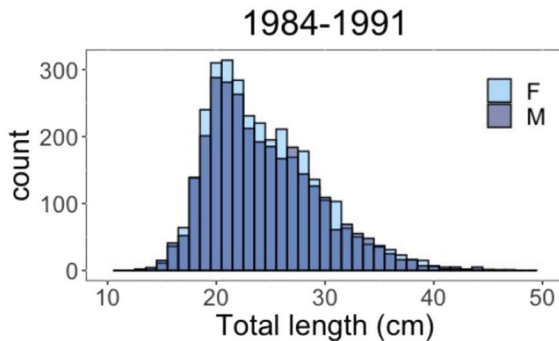


*Trachurus picturatus*

Auction vs. Laboratory

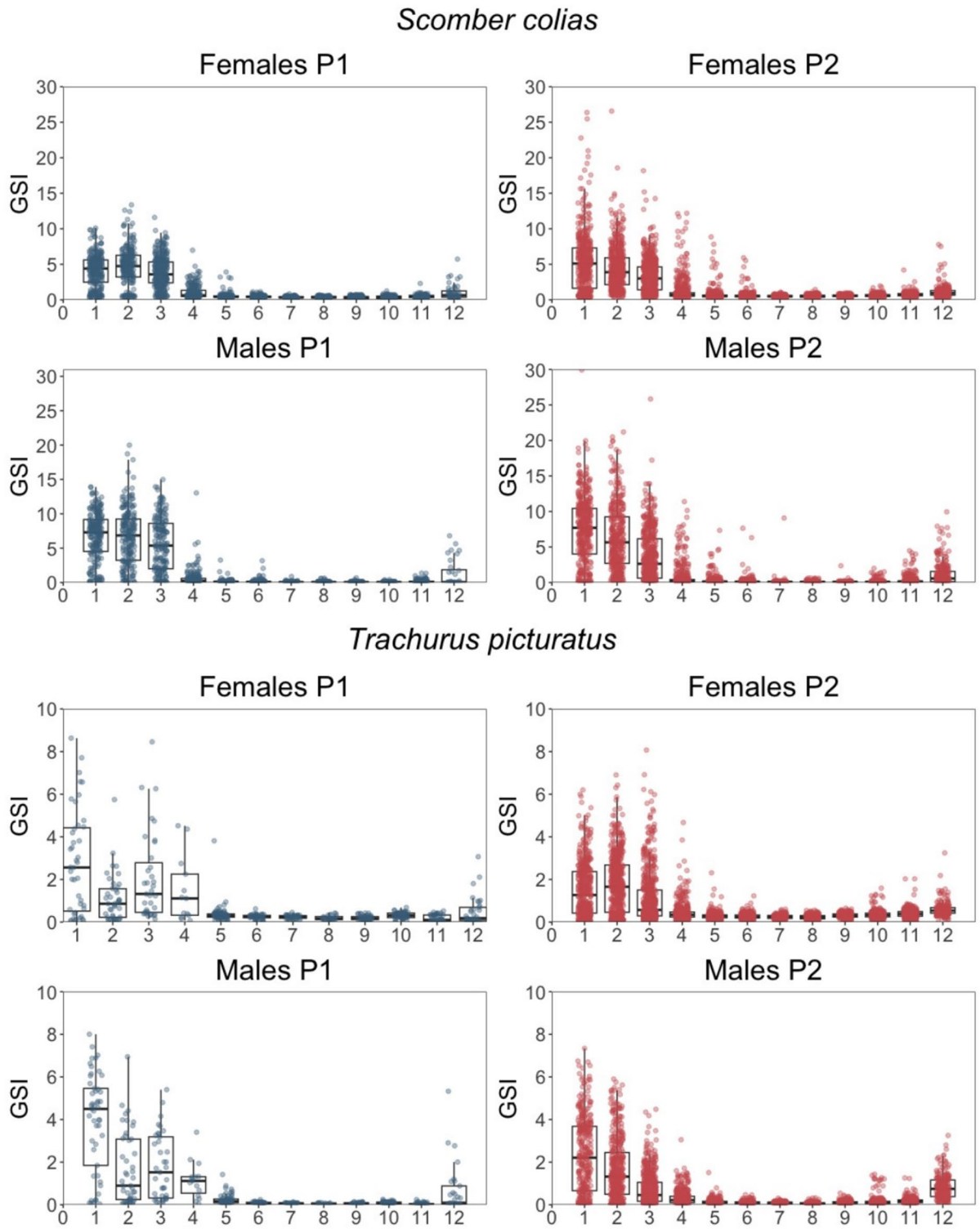


Laboratory



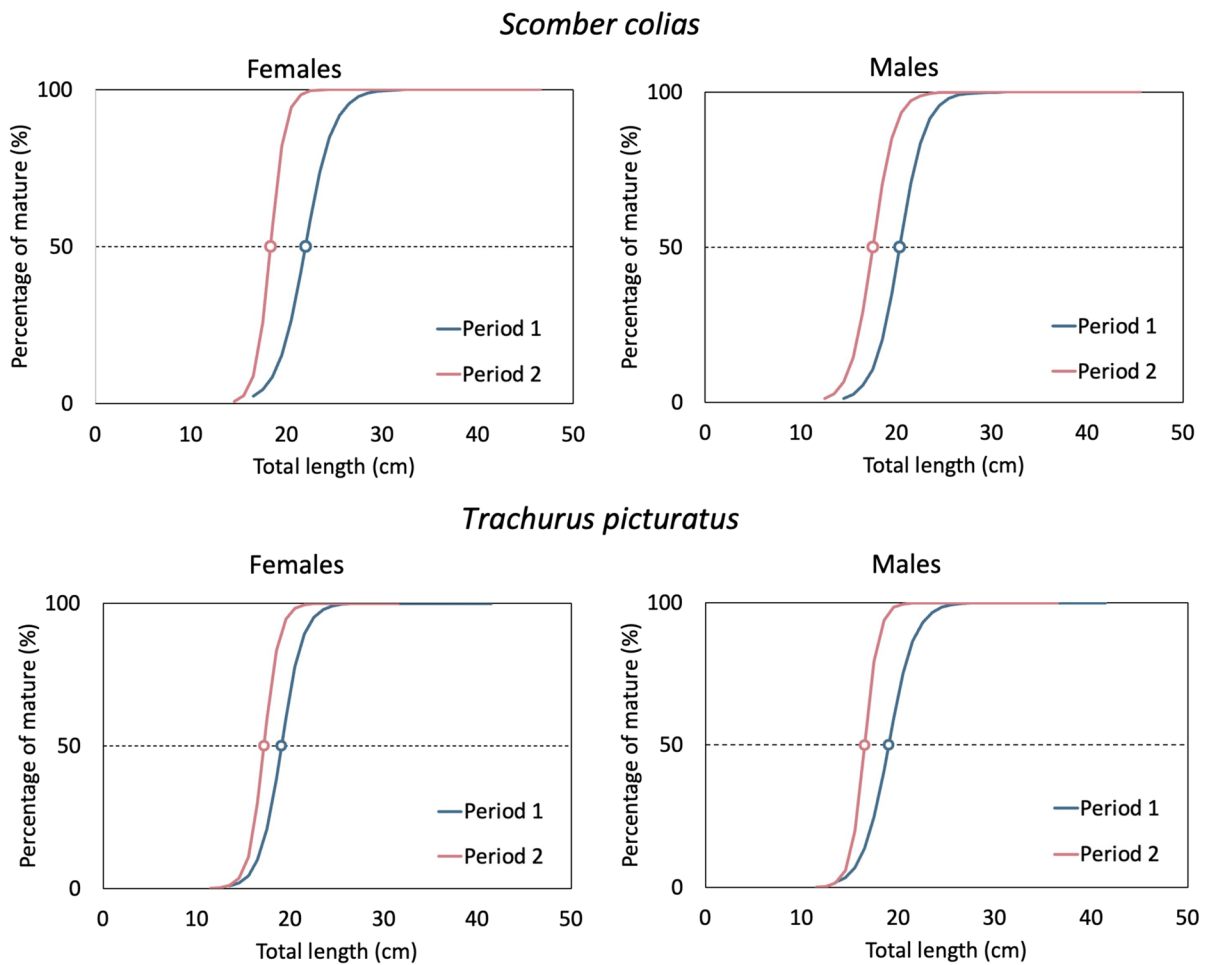
**Fig. 2** Length frequency distributions of the auction and laboratory samples for females (F) and males (M) of *Scomber colias* and *Trachurus picturatus* caught by the purse-seine fleet

off Madeira archipelago (NE Atlantic Ocean) in P1 (1984–1991) and P2 (2002–2017). Colors indicate the colder (blue) and warmer (red) periods



**Fig. 3** Monthly evolution of the gonadosomatic index per sex and period of *Scomber colias* and *Trachurus picturatus* from Madeira archipelago (NE Atlantic Ocean) sampled in P1

(1984–1991) and P2 (2002–2017). Numbers on the X-axis represent the months from January (1) to December (12). Colors indicate the colder (blue) and warmer (red) periods



**Fig. 4** Size maturity ogives estimated for females and males of *Scomber colias* and *Trachurus picturatus* from Madeira archipelago (NE Atlantic Ocean) sampled in P1 (1984–1991)

levels between December and April during P1. In P2 GSI values attained maximum values from December to March. Furthermore, an earlier rise in the GSI values was observed from November, in both sexes. In both periods, male gonads of *S. colias* exhibited higher GSI values from December to March compared to female gonads. From April, GSI indices sharply decreased until November, with female GSI consistently higher than male GSI. When comparing P1 and P2, GSI values estimated for *S. colias* were significantly higher in the warmer period (P2). However, no significant differences were observed in January (Mann–Whitney U test:  $W = 16,008$ ,  $p = 0.332$ ) and February ( $W = 40,340$ ,  $p = 0.1279$ ) for males, and in April (Females:  $W = 50,781$ ,  $p = 0.1842$ ;

and P2 (2002–2017).  $L_{50}$  values are represented as circles. Colors indicate the colder (blue) and warmer (red) periods

Males:  $W = 47,921$ ,  $p = 0.7418$ ) for both sexes. Male gonads of *T. picturatus* exhibited higher GSI values from December to February in P1, with a reduction to only two months in P2, from December to January. Throughout the rest of the year, female GSI values consistently surpassed those of males. GSI values were predominantly higher during the first semester of P1 and the second semester of P2 for both female and male individuals. However, no significant differences were observed in June (Females:  $W = 9802.5$ ,  $p = 0.6583$ ; Males:  $W = 5744.5$ ,  $p = 0.05516$ ), July (Females:  $W = 5291$ ,  $p = 0.9224$ ), and August (Females:  $W = 2487$ ,  $p = 0.07337$ ; Males:  $W = 1411$ ,  $p = 0.5965$ ). An earlier peak of spawning from February to January was also observed in *S. colias*.

Warmed populations matured at a smaller size (Table 4, Fig. 4). For *S. colias*, females showed a decrease in size at first maturity from 21.99 cm TL (1984–1991) to 18.32 cm TL (2002–2017), while for *T. picturatus*, the size decreased from 19.04 cm TL (P1) to 17.19 cm TL (P2). Similar patterns were observed in males, with *S. colias* decreasing from 20.33 cm TL (P1) to 17.52 cm TL (P2) and *T. picturatus* decreasing from 18.99 cm TL (P1) to 16.52 cm TL (P2). In *S. colias*, the smallest female and male measured 17.7 cm TL (maturity stage III) and 16.3 cm TL (maturity stage III), respectively, both from P2. For *T. picturatus*, the smallest female and male measured 13.0 cm TL (P1, maturity stage I).

## Discussion

Our research underscores the importance of incorporating landing data and life-history traits into climate change impact modeling on fish populations. Over the study period, the sea surface temperature (SST) anomaly exhibited distinct fluctuations characterized by three phases: a cold period (1980–1996), a warm period (2001–2019), and a transition period (1996–2000). A critical tipping point was observed in 1997, wherein the small pelagic community landings in Madeira experienced a significant decline, coinciding with a gradual and continuous increase in SST anomaly. This warming trend not only led to reduced landings but also triggered alterations in various life-history traits of the targeted species, including changes in maturity, growth, size, and mortality patterns. These findings highlight the far-reaching implications of climate change on fish populations and emphasize the need to consider both landing data and life-history traits when assessing its impacts.

### Climate change and landings

Research focusing on the impacts of climate change and fishing on fish stocks primarily focuses on intra-generational timescales (e.g. Rouyer et al. 2012; Tu et al. 2018; Morrongiello et al. 2021, ). However, there is a scarcity of information regarding the combined effects of ocean warming and fishing across inter-generational timescales (Wootton et al. 2021). Yet, ocean warming has been ongoing since the early 20th century (Tesi et al. 2021). Experimental studies

have provided evidence of a significant decline in recruitment when fish populations are exposed to warmer waters, resulting in severe consequences for future generations (Wootton et al. 2021, 2022). These findings also agree with previous research indicating that fishing selection can drive long-term changes in traits (Uusi-Heikkilä et al. 2015). Our model further predicted a strong association between the average catch per unit effort (CPUE) of small pelagic fish and the increase in sea surface temperature anomalies, particularly after the identified tipping point in 1997. The anomaly of SST and NAO index were identified as key drivers, with cold and warm regimes leading to substantial changes in the average CPUE of the small pelagic fishery.

Despite encountering limitations due to missing data on the number of fishing days during the colder period, we were able to address this issue by using the available data starting from 2002 to 2017. During this time, there was a degree of stability in the fishing effort per vessel, which allowed us to estimate values for the preceding years. Our findings have significant economic implications, and it is crucial to urgently implement adaptation strategies. Artisanal fisheries in Madeira relies on the exploitation of a limited number of fish species, mainly due to the geological and environmental characteristics of this archipelago. Among these species, SMPF hold the third position in importance, following tunas and tuna-like species, and the scabbardfishes (Hermida and Delgado 2016). The noticeable shift in the pelagic community towards smaller fish sizes, coupled with the depletion of the breeding population of these species, may lead to extended periods of population recovery, resulting in significant economic losses (Vasconcelos et al. 2018). This situation is also particularly concerning for isolated jurisdictions with limited connectivity to neighboring areas, as occurs in the archipelago of Madeira. Conventional management actions have typically focused on implementing gear restrictions, seasonal regulations, fishery closures, and capacity reductions to ensure sustainable exploitation levels (Worm et al. 2009). Inherent stock fluctuations due to environmental variables have been also considered in management approaches (Taboada and Anadón 2016). Extensive research has been conducted on the effects of ocean warming on small pelagic fish landings and productivity (Free et al. 2019; Pennino et al. 2020). Retrospective analysis of catch data and ocean

temperature is crucial for quantifying the impact of historical global warming (Britten et al. 2016). In addition, large-scale climate oscillations such as the North Atlantic Oscillation (NAO), Arctic Oscillation (AO), and East Atlantic (EA) have been found to be correlated with variations in SMPF landings (Castro-Gutiérrez et al. 2022). The NAO index, in particular, has been identified as a key factor in explaining the steady decrease in landings of the studied SMPF over four decades in Madeira. The effects of ocean warming and climate variations may have a more pronounced impact on coastal species, as their optimal sea surface temperature (SST) values may be exceeded in current and future environmental scenarios (Maynou et al. 2014). Consequently, a substantial climate-induced shift in the distributional range of SMPF to colder waters is expected (Jorda et al. 2020).

An imperative consideration pertains to the multi-specific characteristic of the SMPF stocks in Madeira. These stocks encompass a diverse assemblage of multiple species, where any managerial interventions directed towards one particular species may yield consequential effects on the remaining co-existing species (Rindorf 2013). An evident illustration of this phenomenon is the dissimilarity in the minimum legal size requirements between two species, namely, *Trachurus picturatus* (15 cm) and *Scomber colias* (20 cm), which has had a detrimental impact on the catch volumes of both species in the waters of Madeira. To address this issue and effectively manage these complex stocks, Madeira has implemented several measures, including a minimum mesh size of 16 mm, net size restrictions, and setting a fishing depth range of over 50 m (Portaria 1102-G/2000, 22th November). Furthermore, specific to *Trachurus picturatus*, an annual Total Allowable Catch (TAC) has been established, which undergoes yearly variations. Both targeted species, *Scomber colias* and *Trachurus picturatus*, exhibit a limited spawning season occurring from January to April. These measures are vital in ensuring sustainable management of the multispecies fishery in the region and warrant careful consideration in any further management decisions (Vasconcelos et al. 2012, 2017), and their vulnerability increases as they move to shallower waters during spawning.

### Warming effects on life history traits

Both *S. colias* and *T. picturatus* exhibited similar responses to warming in their life history traits. These responses included a decrease in maturity size ( $L_{50}$ ), median size, and asymptotic length ( $L_{inf}$ ), as well as an increase in the growth coefficient ( $k$ ) and natural mortality. For *S. colias*, the spawning peak occurred one month earlier (January) in the warmer period. Although the overall spawning seasons remained similar between the cold (P1) and warm (P2) periods, mature individuals were observed beyond the typical spawning months during the warmer period (2002–2017), with some individuals exhibiting higher Gonadosomatic Index (GSI) values from October to June. The influence of warm temperatures on the life history traits of *S. colias* and *T. picturatus* includes accelerated development rates and earlier maturation (Forster and Hirst 2012; Wootton et al. 2022). Consequently, the earlier onset of reproductive allocation due to warm temperatures is expected to result in a redirection of energy away from growth (Audzijonyte et al. 2019; Verberk et al. 2021). During the warmer period, there was a notable decline in the asymptotic length of *S. colias* by 16.83% and *T. picturatus* by 42%, coinciding with an increase in the brody growth coefficient. These changes indicate that both species have responded to ocean warming by altering their life history traits. Interestingly, *S. colias* appears to exhibit a relatively more favorable adaptive response to ocean warming compared to *T. picturatus*, as evidenced by a lower increase in natural mortality and growth coefficient in *S. colias* compared to *T. picturatus*. Although both species have migratory patterns concerning spawning, feeding and ontogenetic behavior (Hernández and Ortega 2000; Sousa et al. 2005), better migratory feeding strategies (Perrotta et al. 1999) could lead to the dispersion of *S. colias* far from the coast of Madeira. It is known that a high presence of phenotypes could entail a better adaptive plasticity to environmental fluctuations (Ghalambor et al. 2007).

In addition to the direct physiological effects of increased temperature on species traits, it is crucial to consider the broader implications for fecundity and population dynamics, and also for marine ecosystems. Elevated temperatures can induce physiological stress in marine organisms, leading to altered reproductive patterns and reduced fecundity (Melzner et al. 2009).

For instance, thermal stress can disrupt the timing of reproductive events, such as spawning, and decrease the quality and quantity of gametes produced (Pottinger 2010). These disruptions in reproductive processes can have cascading effects on population dynamics, including changes in population size, age structure, and genetic diversity (Munday et al. 2017; Pérez-Ruzafa et al. 2018). Furthermore, increased temperature can influence the distribution and abundance of predators and competitors, leading to shifts in species interactions and community composition (Sunday et al. 2012; Pecl et al. 2017). Such ecological consequences of temperature-driven physiological changes are vital to consider in the context of long-term climate change impacts on marine ecosystems. Integrating these aspects into our understanding can provide more comprehensive insights into the adaptive capacities and vulnerabilities of marine species in a warming world. Moreover, climate change can significantly alter primary production, which forms the foundation of marine food webs and supports fisheries productivity (Palomera et al. 2007; Polovina et al. 2008; Chust et al. 2014). Changes in ocean temperature and circulation patterns can influence nutrient availability and phytoplankton growth, ultimately affecting the abundance and distribution of prey species for commercially important fish (Cushing 1990; Winder and Sommer 2012). Moreover, climate-induced shifts in species distributions and behavior can lead to changes in the spatial and temporal aggregation patterns of fish populations, impacting fishing effort and the success of catches (Cheung et al. 2009; Perry et al. 2010).

While this study primarily examines the direct physiological impacts of rising temperatures on small pelagic species, it's crucial to recognize the broader environmental context, including factors such as oceanic currents, fronts, upwelling events, and prey availability, all of which influence the habitat and ecological niche of these species. These environmental variables collectively shape primary production, nutrient availability, and prey distribution (e.g., Pérez-Ruzafa et al. 2024) thereby impacting the foraging behavior, reproductive success, and overall population dynamics of small pelagic fish. Understanding these complex interactions is essential for predicting and managing the effects of climate change on marine ecosystems and fisheries resources. Oceanic fronts and upwelling zones are known hotspots

of productivity and biodiversity, often serving as important foraging grounds and spawning areas for many marine species (van Ruth et al. 2010; Miller and Christodoulou 2014). Climate change can alter the intensity and spatial distribution of these oceanographic features, potentially impacting the availability of prey, larval recruitment, and overall ecosystem structure (Sydeman et al. 2014). While there may not be explicit evidence on the specific impacts of climate change on oceanic fronts and upwelling gradients in the context of the Madeira archipelago, it is reasonable to speculate that changes in ocean temperature and circulation patterns could affect the dynamics of these important oceanographic features. Further research investigating the response of oceanic fronts and upwelling systems to climate change in the context of the Madeira archipelago is warranted to better understand their potential influence on the ecology and fisheries of the region. Hence, understanding the multifaceted effects of climate change on primary productivity, species aggregation, and fisheries dynamics is crucial for developing effective management strategies to ensure the sustainability of marine resources in a changing environment.

Climate change significantly drives range shifts and local extinctions of species by exposing them to conditions beyond their normal tolerance levels (e.g., Wiens 2016). Predicting population responses under rapidly changing climate conditions is crucial as it can provide insights into species interactions and potential redistribution patterns (Burrows et al. 2019). Understanding the vulnerability or resilience of species to climate change is essential, and studying the mechanisms behind ecological responses can help identify species' capacities to cope with changing environments (Sandoval-Castillo et al. 2020). While some species may persist at the edge of their thermal tolerance limits, others may adjust to new conditions beyond their previous tolerance range (Sunday et al. 2011). Life-history traits exhibit plasticity, but the extent of this plasticity depends on environmental conditions (Ghalambor et al. 2015). Phenotypic flexibility can buffer against climate fluctuations, providing resilience in the face of climate change (Gibert et al. 2019; Gibbin et al. 2017b). In response to warmer temperatures, both *S. colias* and *T. picturatus* populations exhibited higher growth rates, smaller body sizes, increased natural mortality rates, and matured at smaller sizes compared to cold periods.

There is growing interest in understanding the interplay between plasticity and rapid acclimatization, particularly focusing on trans-generational effects (Gibbin et al. 2017a). Experimental studies in laboratory conditions have shown that at least three generations of exposure are needed for the accumulation of negative effects from parental conditioning (Shama et al. 2016). Resilient species experiencing ocean warming are expected to exhibit local adaptations, including plastic responses (Sandoval-Castillo et al. 2020). Our study is an initial step in investigating the persistence of plastic responses in small pelagic species and their capacity to cope with long-term climate change scenarios. We provide compelling evidence of the impact of environmental factors on small pelagic landings and their associated life-history traits. These findings are crucial for conducting vulnerability assessments in the face of climate change (Foden et al. 2019). Urgent action is required globally to develop tools and implement climate-adaptive fisheries reforms to enhance resilience to climate change (Free et al. 2020). These management policies will not only mitigate the effects of global warming on fisheries but also serve as catalysts for future sustainability (Gaines et al. 2018; Peck et al. 2021).

## Supplementary information

The online version contains supplementary material available at

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**Author contributions** Joana Vasconcelos: Conceptualization, Data curation, Statistical analysis, Methodology, Writing - Original draft preparation, Writing - Reviewing & Editing. Jose A. Sanabria-Fernandez: Data curation, Statistical analysis, Methodology. Victor M. Tuset: Validation, Writing - review & editing. Ricardo Sousa: Writing - Reviewing & Editing. Graça Faria: Data curation, Resources, Validation. Rodrigo Riera: Conceptualization, Supervision, Writing - Original draft, Writing - Reviewing & Editing.

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**Data availability** The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

## Declarations

**Conflict of interest** The authors have no conflict of interest to declare that are relevant to the content of this article.

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