



Tracking the effect of temperature in marine demersal fish communities

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ABSTRACT

Under current levels of global warming most demersal species in the Northeast Atlantic are experiencing tropicalization, meridionalization or borealization of their distributions, leading to profound changes in demersal communities. We explore these changes using the Community Weighted Mean Temperature (CWMT), an index to link the thermal preference of demersal fish communities and temperature. The CWMT is calculated as the summation of the mean temperature of each fish species distribution weighted by its relative abundance in the community. The relative abundance is based on the community composition data obtained by the International Bottom Trawl Surveys (IBTS) in the Southern Bay of Biscay between 1983 and 2015. Our analyses show that the CWMT responds to the actual temperature of the water column reproducing its space–time trends in the study area: (i) an increase from SW to NE, towards the inner Bay of Biscay, (ii) a decrease with depth, except in the SW area characterized by an intense upwelling, (iii) a general increase along the time series. Applying a k-means classification to the CWMT data we identified warm-, temperate- and cold-communities over the shelf and slope and their spatial changes in the last decades. The area occupied by warm communities has expanded 268.4 km²/yr since the 80 s, while the cold communities have retracted at a speed of −155.4 km²/yr. The CWMT was able to capture the community dynamics in relation to environmental temperature at different temporal and spatial scales, highlighting the potential of this index to explore and anticipate the effects of climate change in demersal communities under different scenarios of global warming.

1. Introduction

Global warming is modifying species distributions at an unprecedented rate in marine environments (Cheung et al., 2009; Burrows et al., 2011), as it challenges species to cope with increasing temperatures. Among the most commonly described changes, the abundance distribution and ranges of marine species are shifting toward higher latitudes, causing tropicalization (Horta e Costa et al., 2014), meridionalization (Punzón et al., 2016) and borealization (Fossheim et al., 2015) in the ecosystems, which become increasingly dominated by species with warmer affinities (Tasker, 2008; Lenoir et al., 2011; Simpson et al., 2011). Species ranges can also shift toward higher depths, due to physical constraints such as substrate types (Dulvy et al., 2008; Hofstede et al., 2010; Punzón et al., 2016), providing that tracking their preferred

temperature niche is among the first consequences of the increasing seawater temperatures. Indeed, 80% of the observed changes in marine species distributions are consistent with the expected impact of global warming, and phenological changes also comply (in over 75% of the reported cases) with the altered climate seasonality (Poloczanska et al., 2013). In addition to these responses, resilience mechanisms such as phenological plasticity and adaptation capabilities, could counterbalance the effect of global warming at the population level, decreasing the risk of local extinctions (Simpson et al., 2011).

Although species are the common unit of study in most climate change studies, the cumulative effect of these changes in species distributions can also be reflected in the fish assemblages and communities (Lucey and Nye, 2010; Kleisner et al., 2016), which may be displaced from their original distribution ranges (Fossheim et al., 2015). An early

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index to characterize these displacements was the Preferred Temperature of the Community (PTC), calculated by weighting the species preferred temperature by their annual abundance (Collie et al., 2008). Based on the most numerous species in the community, the PTC was able to characterize shifts in the communities towards species with warmer affinities, mirroring the increasing water temperature in the ecosystems (Collie et al., 2008; Lucey and Nye, 2010). However, the PTC was built upon 19% of the community richness (Collie et al., 2008), and thus these promising results might be over-conservative. In fact, first sightings of species outside their usual geographical range can be considered an early indication of climate-related shifts (Fogarty et al., 2017) and rare species can significantly contribute to changing the community functioning. Shortly afterwards, Cheung et al. (2013) developed the Mean Temperature of the Catch (MTC), calculated by weighting the preferred temperature of all exploited species by their annual catch. This index revealed the relationship between the structure of the commercial catches and the changes in Sea Surface Temperature (SST) in several large marine ecosystems (Cheung et al., 2013). However, issues related to resources accessibility, fleet targets, fisheries regulations and management or misreporting (Pauly et al., 2013; Payne, 2013; Pauly and Zeller, 2016) remained unaddressed with this index, hampering its ecological interpretation. More recently, Peristeraki et al. (2019) analyzed the spatial and inter-annual patterns of MTC of demersal assemblages from bottom trawl surveys along the northern Mediterranean, but without temporal trends in most part of the area. These authors concluded that the recent bottom temperature increases observed in the Mediterranean have not caused an immediate response in the structure of their demersal and benthic communities.

Building on these, we analyze the Community Weighted Mean Temperature (CWMT), an index to track the effect of warming in fish communities. CWMT is based on all fish species in the community and calculated through weighting the mean temperature of their distributions by their abundance. We will assess its performance in the Southern Bay of Biscay using 32 years of data from International Bottom Trawl Surveys in the area (1983–2015). The study area is located amidst the warm- and cold- temperate biogeographical regions in the Northeast Atlantic and thus characterized by a high biodiversity (Lavín et al., 2006). Species-specific responses to the increasing water temperatures (González-Pola et al., 2005; Gómez-Gesteira et al., 2008), have been recently documented in the area, with a generalized increase in the frequencies of occurrence and abundances of species with warmer affinities and a shift of the species centers of gravity towards deeper areas in the last decades (Punzón et al., 2016). In addition the southern Bay of Biscay is characterized by a pronounced spatial and seasonal variability (Gil, 2008), including the seasonal influence of the Iberian coastal

upwelling, stronger in the western area, and the strength of the Poleward Current in intermediate waters. This heterogeneous oceanography offers the perfect setting to explore how CWMT vary at different spatial scales and along the space–time continuum according to interannual variation of the regional hydrography and/or the observed long-term warming. Finally, we explore a method to evaluate the speed of these changes with CWMT.

2. Material and methods.

2.1. Study area and fish community data.

The study area is set on the Southern Bay of Biscay, a shelf sea on the Northeast Atlantic covering an approximate area of 20000 km² (Fig. 1). This area is characterised by a narrow continental shelf and a steep slope, and scattered by geographic features such as capes, estuaries and canyons, which configure a highly heterogeneous environment. Nevertheless, there is an apparent gradient in ocean exposure from Southwest to Northeast, which can be seen, for example, in the higher temperatures towards the inner Bay of Biscay (Tasker, 2008). During the spring and summer, the easterly winds favor coastal upwelling along the Cantabrian coast (Gil, 2008). These winds are more persistent and continuous in time on the Northwest coast (Galicia Waters) that on the northern slope of the Bay of Biscay, resulting in a decrease of the strength of the upwelling from the Southwest to the Northeast (Llope et al., 2006).

During the last decades warming trends have been identified both in the surface waters (Gómez-Gesteira et al., 2008; Tasker, 2008) and while upwelling intensity has generally increased, the number of days under upwelling conditions has decreased (Alvarez et al., 2011). These trends in water temperature and upwelling intensity have contrasting effects on the phytoplankton communities, whose productivity in the Southern Bay of Biscay has remained stable over the last decades (Otero et al., 2018; Beca-Carretero et al., 2019). However, the extension of primary productivity projection patterns to higher trophic levels need to be undertaken with caution (Chust et al., 2014).

The benthic-demersal fish community has been sampled every autumn from 1983 to 2015 (except in 1987) by the Instituto Español de Oceanografía (IEO) using the ICES standardized methodology for International Bottom Trawl Surveys (ICES, 2017). These surveys followed a random sampling scheme stratified to the area, with three bathymetric depth strata (70–120, 121–200, 201–500) and five geographical sectors delimited by the main geographical features: for Galician waters the geographical sectors are Miño River- Cape Finisterre (MF) and C. Finisterre- C. Estaca (FE); for Cantabrian Sea the geographical sectors are C. Estaca-C. Peñas (EP); C. Peñas-C. Ajo (PA); and C. Ajo-Bidasoa River

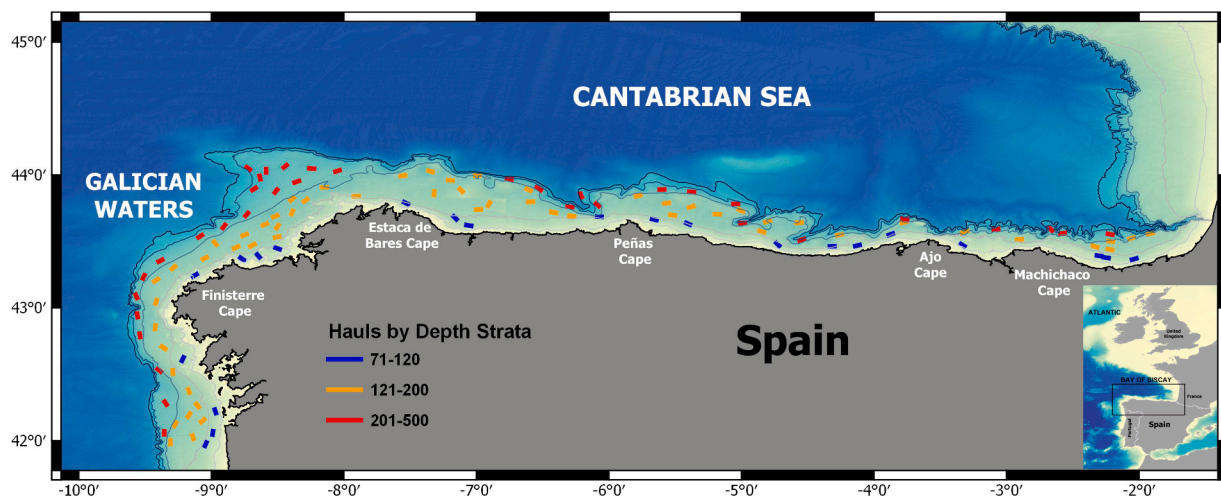


Fig. 1. Samples in the study area by depth strata and year (1983–2015).

(AB) (Fig. 1). The sampling unit consists on bottom trawls of 30 min at 3 knots, using a standard ‘baca’ 44/60 otter trawl gear with 10 mm cod-end mesh size. The mean horizontal and vertical opening of the net is 18.9 and 2.0 m, respectively. After each haul all fish species are identified, weighted, counted and measured. All fish species in the community were used in subsequent analysis, except for those few species which were ambiguously identified along the time series (family Gobiidae and Myctophidae) and those whose occurrence was considered incidental (further details in Punzón et al., 2016). Thus, the whole community comprised 69 fish species, most of them typically demersal (71%), but also including few species which are considered benthic with high vertical mobility (16%) and few which are characterized as pelagic (13%).

2.2. Temperature of the water.

Temperature data for the water column was obtained from the ocean physics reanalysis product “Atlantic-Iberian Iberian Biscay Irish- Ocean Physics Reanalysis”, generated and provided by the CMEMS IBI-MFC (see Sotillo et al., 2015 for a detailed description). The model provided monthly means of temperature for 50 different depths, between 0.5 and 5698 m depth for the period 2002–2015 with a high spatial resolution ($0.028^\circ \times 0.028^\circ$). Since the fish community is always sampled in early autumn (September–October) a mean value for the previous 5 months (June–October) was calculated for each depth in gridded layers of 5×5 nm resolution. This temporal window was selected because it features a season with stable environmental conditions (e.g. temperature and upwelling) previous to the survey. Subsequently, we computed the Mean Temperature of the Water Column Temperature (MTW) and the delta temperature (Δ MTW; difference between maximum and minimum temperature of the water column) of the first 1000 m, based on set of 17 depths. Computing an integrated value of temperature for the whole water column, the MTW accounted for the main oceanographic features conferring spatial variability to the system. Although initially we tried the bottom temperature following previous works on fish distribution (González-Irusta and Wright, 2017; Morato, et al., 2020), in our study are this value fails to capture the well described longitudinal gradients in the water column present in the area (Llope et al., 2006), gradient which is mirror by the demersal fish community (Serrano et al., 2011), reason why in this work we used the MTW and the Δ MTW.

As the MTW did not cover completely our study period, we obtained as well temperature profiles from the ocean reanalysis (ECMWF Ocean Reanalysis System 4, ORAS4) (Balmaseda et al., 2013). This reanalysis provides monthly temperature data at 42 pressure levels from 5 to 5000 m with higher vertical spacing towards the bottom (1959-present). However, the coarser spatial resolution of $1^\circ \times 1^\circ$ of this reanalysis would not allow for a detailed spatial analysis of temperature changes. The ORAS4 reanalysis has been systematically presented together with data from oceanographic sections in the Bay of Biscay for the study of hydrographic and circulation changes in the mid-latitudes of the Eastern North Atlantic (Somavilla et al., 2016, 2017). These previous comparisons serve as an important validation since gridded data sets are in general affected by factors such as contamination from model errors in ocean reanalysis data (Balmaseda et al., 2013), or the gap-filling strategy in climatological data (Cheng and Zhu, 2015). To assess low frequency temperature changes in the study, we calculated the annual average of temperature in the depth range between 300 and 600 m depth, excluding from this average the surface mixed layer depth affected by strong seasonality. The climatological maximum winter mixed layer in the area is within 250 m depth, and so we name this average temperature from hereinafter Temperature Below Winter Mixed Layer (TBWML).

2.3. The Community Weighted Mean Temperature (CWMT)

The Community Weighted Mean Temperature (CWMT) was calcu-

lated in each haul as,

$$CWMT_i = \sum T_{pref_s} * W_{si} / \sum W_{si}$$

where $CWMT_i$ is the Community Weighted Mean Temperature in haul i , the T_{pref_s} is the preferred temperature of species and W_{si} is the biomass in weight of specie s in the haul i .

The preferred temperature was calculated for each species by spatially weighting the mean water bottom temperature and the species probability of occurrence (Table Suppl. 1). The distribution ranges and probabilities of occurrence for all fish species were obtained from the bioclimatic envelope models developed by AQUAMAPS (Kaschner et al., 2016). Bottom temperature is commonly used to characterize the thermal preferences of demersal species because they tend to dwell close to the sea bottom, and because bottom temperatures are generally more conservative than temperatures measured elsewhere in the water column (Hiddink and Ter Hofstede, 2008). This approach, despite its simplicity, overcomes some of the limitations of previous indices based on the species preferred temperatures, such as the lack of information on the temperature affinities of each species in the scientific literature (as used in Collie et al., 2008). In addition, we considered the overall distribution range of each species, avoiding the bias of considering only the temperatures within the study area (as used in Lucey and Nye, 2010) and we used the water temperature at the sea bottom, which is more sensible for benthic-demersal communities, particularly when including deep species (Hiddink and Ter Hofstede, 2008). Nevertheless, these preferred temperatures should be considered a proxy for the temperature affinity of the species, rather than the optimum temperature on the species temperature.

Statistics of CMWT by depth range and geographical sector were estimated based on the CWMT by haul. The spatial distribution of this metric for the time period (2002–2015) to be compared with the information available for MWT and was calculated as the mean for each sample station. Using the spatial distribution of MWT and Community Weighted Mean Temperature (CWMT) between 2002 and 2015, we calculated the correlation between them. In order to represent the index (CWMT) at a finer resolution we used the Universal Kriging Analysis. The Universal kriging was computed using the function `autofitVario` from the package `automap` (Hiemstra et al., 2008) to compute the variogram and the function `krige` from the package `gstat` (Pebesma, 2004) to do the universal kriging, using depth as covariate.

To estimate the evolution in time of CWMT for the total area and by geographical sector a General Additive Models (GAMs; Hastie and Tibshirani, 1990) was performed. To analyze the trends in the spatial distribution over time, the CWMT by haul was classified using k-means algorithm to discriminate distinct geographical areas. K-means stores k centroids that it uses to define clusters.

The analysis were performed using R (R Development Core Team, 2018). The GAM was performed using the “`mgcv`” library without limiting the degrees of freedom of the smoothers and assuming a gaussian distribution (Wood, 2011), and the k-means classification was performed using “`classInt`” library (Bivand, 2018).

3. Results

The spatial pattern displayed by the Mean Temperature of the Water Column (MTW) over the continental shelf reflects the regional oceanography of the southern Bay of Biscay, generally increasing either in mean and/or maximum values from Southwest to Northeast, towards the inner Bay of Biscay (Suppl. Figs. 1 and 2a). Across the depth strata, the MTW decreased ($T^{70-120} = 14.32$, $T^{120-200} = 13.98$, $T^{200-500} = 13.82$) (Suppl. Fig. 2a), but aggregating the MTW data by depth stratum and geographical sector, this temperature decline with depth was only apparent in the Cantabrian Sea (inner Bay of Biscay), but not in the westernmost sectors (Suppl. Fig. 3). Based on the temperature of the water column, the ΔT^a (difference between maximum and minimum

water column temperature), is minimum in the shelf of the Galician waters, mainly in MF (Fig. 2b). Meanwhile in the Cantabrian Sea the ΔT^w has a pattern according with depth strata, minimum in the shallow strata and maximum in the deep one (Fig. 2b).

The median values of the Community Weighted Mean Temperature (CWMT) showed a similar trend to the observed in the MTW, with a generalized increase from the Southwest of the study area to the inner Bay of Biscay in the Northeast (Fig. 3a), with CWMT values significantly differing between Galician waters (MF and FE sectors) and the Cantabrian Sea (EP, PA and AB sectors). The CWMT also decreased across depth strata (CWMT₇₀₋₁₂₀ = 11.04, CWMT₁₂₀₋₂₀₀ = 8.06, CWMT₂₀₀₋₅₀₀ = 7.35) (Fig. 3b). Aggregating the results by geographical sector and depth strata (Fig. 3c), the CWMT patterns were geographically distinct; in Galician waters the changes in CWMT with depth were not clear, with no significant differences at all between the two deeper strata (120–200 and 200–500), while in the Cantabrian Sea differences in CWMT were significant along the depth gradient (Fig. 3c). Comparing the distributions of MTW and CWMT, the spatial patterns displayed by both metrics were quite similar (Fig. 2a, Fig. 4, and Suppl. Fig. 4). The Pearson correlation between CWMT and MTW was 0.372 (interval confidence = 0.29–0.44, $p = 2.2e-16$).

The annual trend for CWMT for all area (Fig. 5b) is according to annual trend of the TBWML (Fig. 5a), in neither of the two series was temporal autocorrelation identified. The Pearson correlation between time series was 0.613 (interval confidence = 0.339–0.794, $p < 0.001$). Our analysis revealed a clear temporal pattern in the CWMT (CWMT ~ year, $p < 2e-16$) (Fig. 5b), but heterogeneous among geographic sectors (Fig. 6), with an annual rate of increase of the CWMT of 0.04 °C/yr. Sectors in the west displayed lower, but more fluctuating patterns

compared to sectors in the east, with the patterns at MF, FE and EP temporally asynchronized from mid 90 s with AB pattern. The Pearson correlation between the CWMT of western area (sectors MF and FE) with TBWML of the western areas was 0.522 (interval confidence = 0.212–0.78, $p < 0.001$); and between CWMT of northeastern area and the TBWML from this area was 0.5918 (interval confidence = 0.30–0.78, $p = 0.0003601$).

We identify the species involved in the observed temporal trend, based on their percentage contribution to the CWMT (Fig. 5c). The proportion of the species with cooler preferred temperatures decreased over the time, particularly blue whiting (*Micromesistius poutassou*), which despite its high interannual variability it is one of the dominant species in the community. On the other hand, the number of species with warmer preferred temperatures, with a pool of species including *Scyliorhinus canicula*, *Pagellus acarne* and *Lepidorhombus whiffiagonis*, seems to be increasing over time (Fig. 5b). The exceptional increases of CWMT in 1994 and 2008 were caused by different communities (Fig. 5). The first peak was related to the increase in the abundance of few species with warmer preferred temperatures, particularly *Macroramphosus scolopax* and *Trachurus trachurus*, while the second one was caused by a steep decrease in *M. poutassou* and a generalized gain in abundance of species with warmer preferred temperatures (Fig. 5).

In the temporal trends of the CWMT by geographic sector, we observed that the generalized increase identified for the whole study area varied among regions, the geographical sectors of inner Bay of Biscay (PA and AB) displaying a more stable increase, while Galician waters sectors (MF and FE) displayed higher rates of increment and higher variability (Fig. 6). The peaks of CWMT in 1994 and 2008 corresponded with high values of CWMT in Galician waters, when the

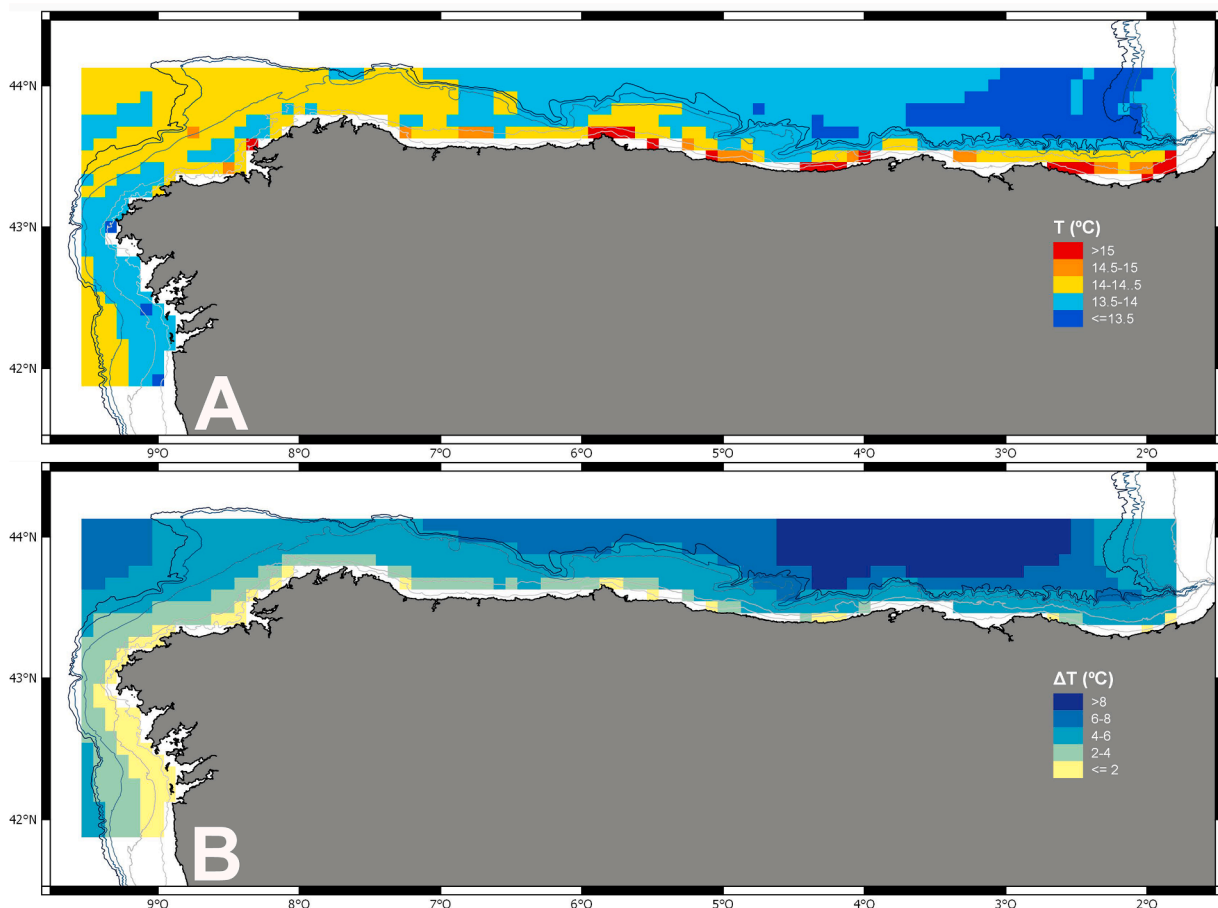


Fig. 2. Spatial distribution of the Mean Temperature of the Water column (MTW) (A) and increment (difference between maximum and minimum water column temperature) of MTW over the period 2002–2015 (B).

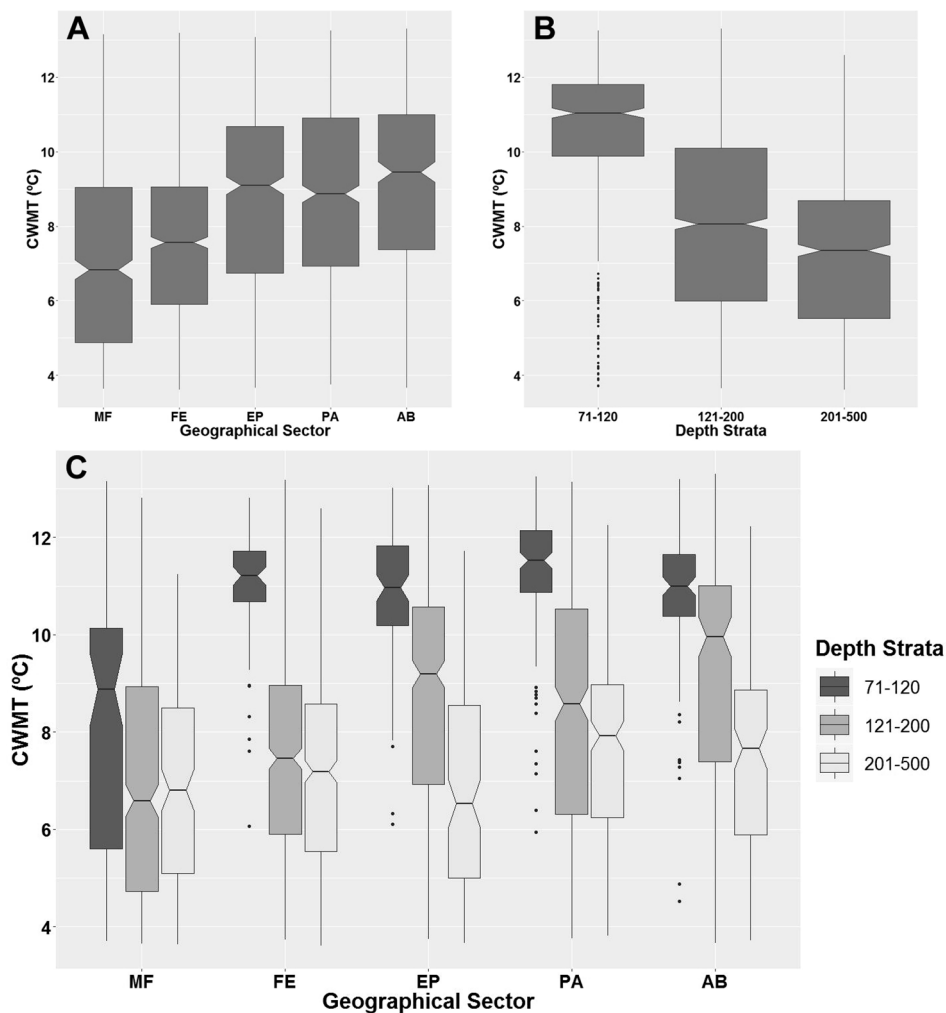


Fig. 3. CWMT by geographical sector (A), by depth strata (B) and by geographical sector and depth strata combined (C). The boxes represent the interquartile range (IQR), the line is the median and the notches are its confidence interval. The lines of the whiskers extend 1.5 IQR and outliers are identified as points beyond the whiskers.

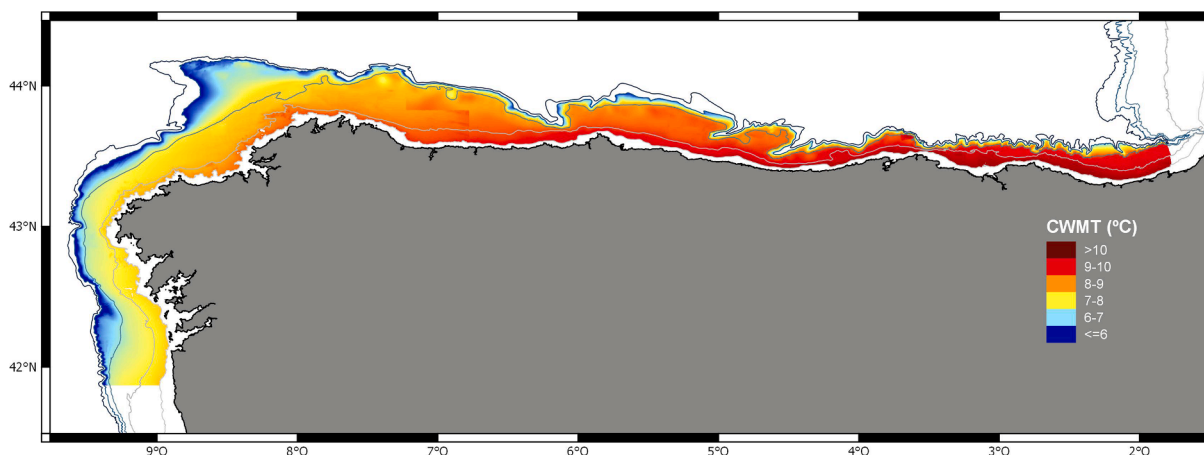


Fig. 4. Spatial distribution of the CWMT between 2002 and 2015.

CWMT was quite homogeneous between regions (i.e. 8–9 °C on average). On the other hand, CWMT strongly varied between geographic sectors (by approximately 5 °C), reflecting the steep CWMT gradient from the Southwest (Galician waters) to the Northeast (inner Bay of Biscay).

To analyze the spatio-temporal trends of the CWMT, we classified CWMT by haul in three groups by the k-mean method. The CWMT range by groups was: Cold ≤ 6.64 °C; $6.64 < \text{Temperate} \leq 9.58$; Warm > 9.58 . In [Suppl. Fig. 5](#) we show the spatial distribution of the community types for all time series, where the warm community is in the littoral area of

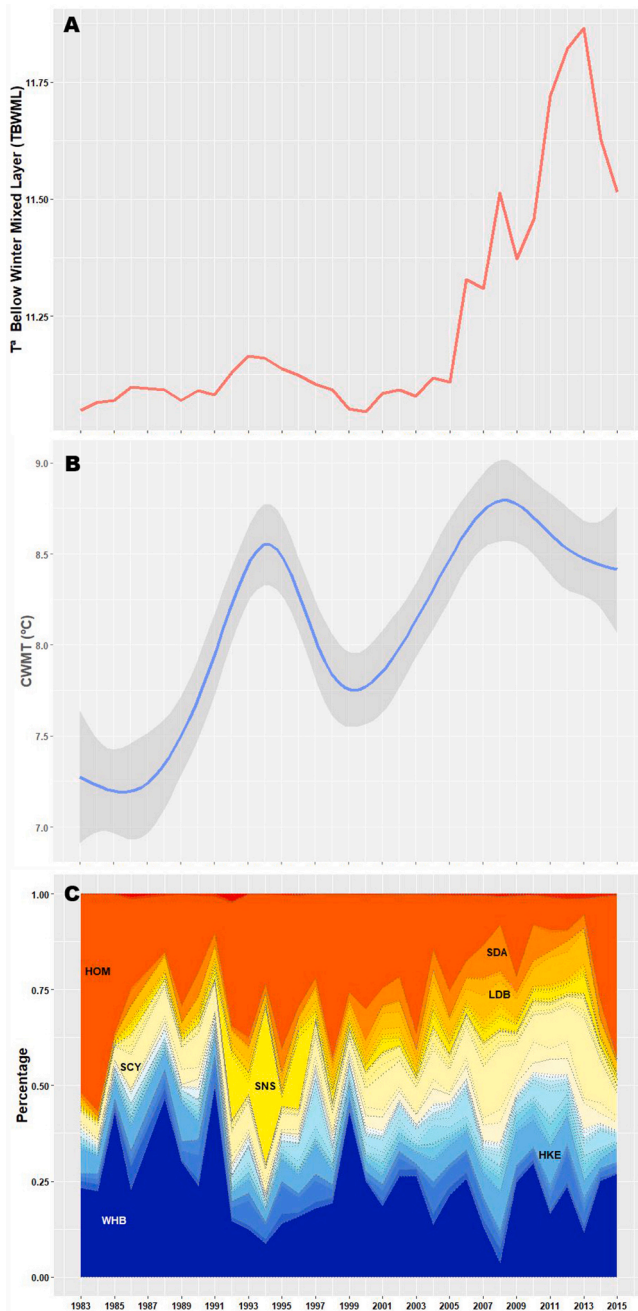


Fig. 5. Annual Temperature Winter Bellow Mixed Layer (TBWML) (A), annual changes in CWMT (results of the Generalized Additive Model) (B) and relative abundances of the different fish species in the community annually (C). The color of each species reflects the mean temperature of the species, with blue being the coolest and red the warmest (see Table Suppl. 1). Species code: *Micromesistius poutassou* (WHB), *Scyliorhinus canicula* (SCY), *Merluccius merluccius* (HKE), *Trachurus trachurus* (HOM), *Macroramphosus scolopax* (SNS), *Pagellus acarne* (SDA), *Lepidorhombus boscii* (LDB).

the Cantabrian Sea geographical sectors and scarcely in the north of Galician waters. In Galician waters geographical sectors the temperate community is the most important. Spatial interpolation was estimated for every year from data by haul, and every cell was classified to estimate the occupied area by CWMT range groups. In Fig. 7 we show the trend by CWMT range groups. The trend for warm and cold CWMT groups were significant (warm, $p = 0.0013$; cold, $p = 0.0014$). The slope for Warm CWMT group was 268.41 km^2 per year, and for Cold group was -155.39 km^2 per year.

4. Discussion

The Community Weighted Mean Temperature (CWMT) showed a good agreement with the Mean Temperature of the Water Column (MTW) and Temperature Below Winter Mixed Layer (TBWML), reproducing its space–time trends in the study area, i.e. (1) an increase from the southwest to the northeast (towards the inner Bay of Biscay); (2) a decrease with depth (except in the Southwestern area, characterized by intense upwelling); (3) a general increase over the time series; (4) temporal fluctuations declined when moving from SW to NE regions; and (5) from mid 90 s, a higher synchrony in the 3 most western sectors which contrast with the asynchrony observed with the eastern sectors (PA and AB). The Mean Temperature of the Water Column (MTW) was able to capture the main space–time patterns in sea temperature described for the southern Bay of Biscay, such as the increasing temperature values towards the inner Bay of Biscay (from SW to NE) and decrease with the depth. This gradient mirrors the regional oceanography, as it matches the decrease in upwelling intensity (from SW to NE) and the increase in water stratification following the same direction (Valdés et al., 2007; Gil, 2008). Indeed, the westernmost sectors of the study area, with similar MTW values across depth strata, show a temperature profile characteristic of upwelling ecosystems (Chavez and Messié, 2009) with a well-mixed water column and lacking a temperature gradient in depth (Bode et al., 2009). In the area, we also find a generalized increment along the time series on sea surface and intermediate water temperatures (González-Pola et al., 2005; Gómez-Gesteira et al., 2008; Tasker, 2008). This suggests that the CWMT responds to the temperature of the water column as a combination of the thermal niches (sensu Magnuson et al., 1979) of the species that constitute the fish community. In fact, temperature can be considered as one of the multiple dimensions of a species niche, understanding the niche as a multidimensional combination of both biotic and abiotic variables which provide an appropriate environment for a given species (Hutchinson, 1978). With temperature displaying marked spatial gradients in latitude, longitude and depth, the thermal niche arises as a fundamental factor in the distribution of fish species (Pörtner and Peck, 2010; Righton et al., 2010; Bruge et al., 2016; Kleisner et al., 2017).

The spatial variability in CWMT observed in the present study should be expected. Changes in the structure of fish and invertebrate communities along the West-East axis of the Southern Bay of Biscay had been described in previous studies (Sánchez and Serrano, 2003; Serrano et al., 2006; Serrano et al., 2011), particularly an increase in biodiversity towards the Cantabrian Sea (central and eastern study area). In addition, the decrease in CWMT along the depth gradient in the Cantabrian Sea is paralleled by a clear succession of the fish and invertebrate communities (Sánchez and Serrano, 2003; Serrano et al., 2011). Though, in the westernmost sectors (Galician waters), where CWMT values remain constant along the depth gradient, this in-depth structure of the fish communities is not so apparent (Fariña et al., 1997) and can only be acknowledged if considering fish and invertebrate fauna together (Serrano et al., 2008). The strong agreement between CWMT and the community variability described in the aforementioned studies, suggests that longitude and depth are proxies for the spatial temperature gradients, notwithstanding the additive effect of other local environmental factors along these geographical variables and/or the spatial autocorrelation of the community structure (Currie, 2007). The long-term increment in CWMT indicates that the fish community is increasingly dominated by the species with warmer affinities, reflecting the increase in abundance and frequency of occurrence of temperate species with Lusitanian affinities (Punzón et al., 2016), and supporting the meridionalization hypothesis for this ecosystem, when an increase in the abundance of native fauna with southern affinities. The increase in CWMT over time is more evident in the inner part of the Bay of Biscay than in the SW zone. This may be related to the dampening effect of the upwelling on ocean warming, particularly in coastal areas (Santos et al., 2012). Indeed, SST warming in the SW area has been estimated as of

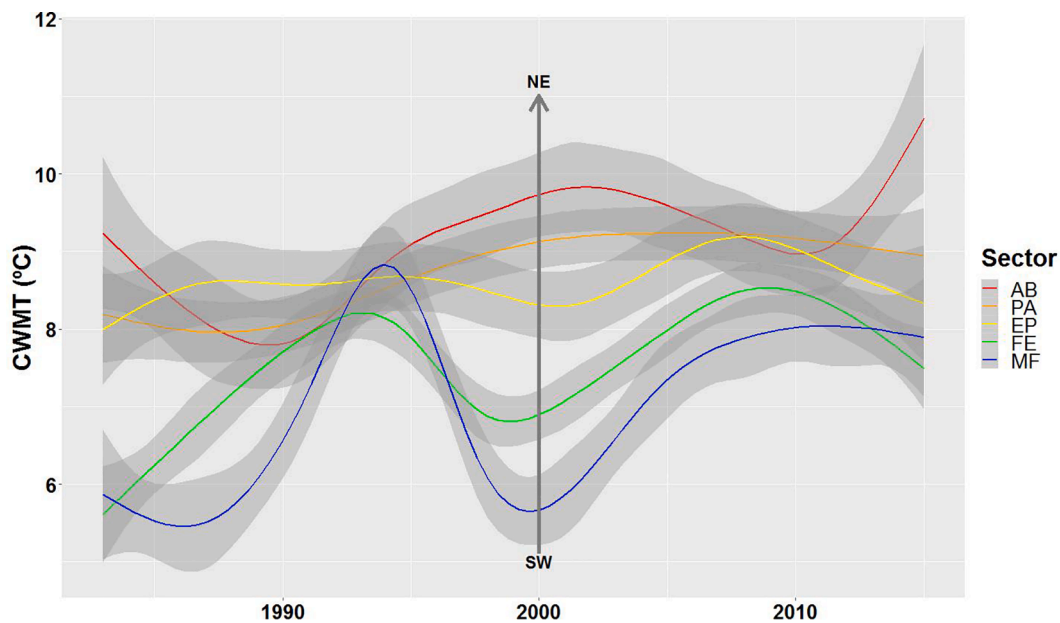


Fig. 6. Variability in the annual changes in CWMT represented by geographical sector (results from the Generalized Additive Model).

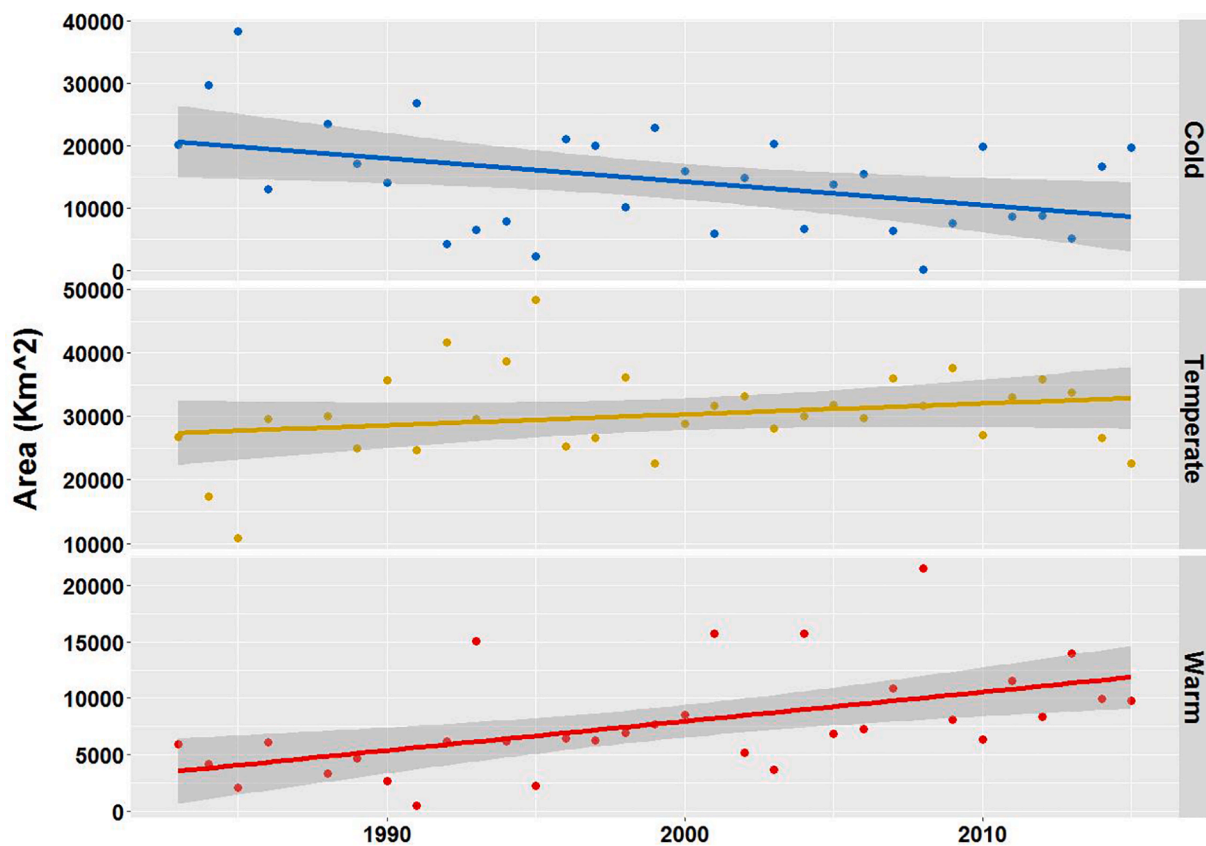


Fig. 7. Trends in the spatial occupation of the community types: warm ($p = 0.0013$, $r^2 = 0.3$, slope = 268.40937), temperate ($p = 0.1768$, $r^2 = 0.06$, slope = -121.34754) and cold ($p = 0.0144$, $r^2 = 0.18$, slope = -155.38934).

0.15 °C per decade (Gomez-Gesteira et al., 2011) while in the inner Bay of Biscay SST warming estimates reach 0.26 °C per decade (Goikoetxea et al., 2009).

Changes in fish communities tracking the increasing water temperature have been described using different indices in several large ecosystems (Collie et al., 2008; Lucey and Nye, 2010; Cheung et al., 2013;

Keskin and Pauly, 2014; Tsikliras and Stergiou, 2014; Vasilakopoulos et al., 2017). At a finer spatial scale, we demonstrate that the long-term increases in CWMT in the southern Bay of Biscay persist over sub-regional and local scales, although showing different degrees of variability. CWMT variability was least at the inner bay and increases towards the West, driven, mainly, by the variability in the abundance of

blue whiting (*M. poutassou*) which dominates the community when the CWMT reaches lower values. Blue whiting is a cold-water migratory species with a wide distribution in the Northeast Atlantic, whose abundance in the area is probably determined by its population dynamics over the whole Northeastern Atlantic rather than by the regional oceanography in the southern Bay of Biscay. On the other hand, the increase in CWMT over the time series responds to the increasing abundance of a pool of species with temperate and warm affinities (*S. canicula*, *L. bosci*, *P. acarne*, *C. aper*, *Raja clavata*, etc), rather than a unique species (Punzón et al., 2016). Despite the increasing abundance of these species, no distributional shifts were identified (Punzón et al., 2016). In particular, the dominant warm water species, horse mackerel (*T. trachurus*) also seem to decline over time, but the population distribution of this species ranges over an area much larger than our study site, and thus, its abundance might not be as influenced by the regional oceanography in the Southern Bay of Biscay. The distribution of this species in the study area also seems to be temporally stable, without significant changes in latitude, longitude or depth (Punzón et al., 2016). The exceptionally high CWMT of 1994 and 2008, could respond to oceanographic processes which improved the recruitment of some of these species. For instance, Sánchez and Serrano (2003) found that a moderate Poleward Current together with a high upwelling index favored good recruitment of hake (*Merluccius merluccius*) and possibly other demersal species of the Cantabrian Sea shelf.

The distribution pattern of three “communities” identified by CWMT, attributes the warm “communities” to the coastal inner Bay of Biscay, the temperate “communities” to the continental shelves and in the Galician coastal zone under the influence of the upwelling, and the cold “communities” to the shelf break and deep waters. Along the time series, we recorded an increase in the distribution area of the warm communities and a retraction of the cold communities in response to the increasing temperatures of the Southern Bay of Biscay. These trends provide further evidence for the phenomena of meridionalization of temperate ecosystems (Punzón et al., 2016), in line with the increasing proportion of species with temperate affinities in the landings of the North-East Atlantic large marine ecosystem (Cheung et al., 2013).

The benthic-demersal fish communities analyzed in the present study responded to the temperature at different spatio-temporal scales reflecting: (i) the observed warming trends in the water column; (ii) the local oceanographic processes; and (iii) their internal structure. Therefore, the CWMT proves to be a good indicator of changes in marine communities, reflecting both its spatial and temporal variability. In fact, the CWMT captured the community dynamics even in absence of species replacements or migration of new species into the Bay of Biscay, while these events have been commonly reported in cold-temperate fish communities subject to similar rates of warming (Perry et al., 2005; Collie et al., 2008; Hofstede et al., 2010). The biogeographic zone can be the key difference between these studies, as this study is set in a “warm-temperate province”, while previous studies took place in “cold-temperate provinces”, responding to the hypothesis of Hiddink and Ter Hofstede (2008), who suggested that changes in species richness would preferentially occur in temperate and cold latitudes, in relation to warmer latitudes. Therefore, we hypothesize the existence of a gradient in the rate of change of communities between “warm-provinces” and “cold provinces”, being faster at higher latitudes. CWMT could thus be a useful tool to further investigate this hypothesis and testing the performance of this index on a latitudinal range of marine ecosystems to test the generality of our findings. The rate of change of the communities in the Southern Bay of Biscay suffices to deeply impact the economic activities founded on benthic-demersal resources. This highlights the importance of predicting the evolution of the demersal ecosystem under different scenarios of climate change, with the aim to implement adaptation and mitigation tools.

Authors contribution

AP was the responsible of the conceptualization, formal analysis, writing - original draft and writing - review and editing investigation in collaboration with LLL, JMGI, MH, IP, AS, ET, RS, JP and EM. EM and FV were the responsible of project administration and funding acquisition. MB, SRP, OFZ, ET and RS were responsible of data curation and validation.

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.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.ecolind.2020.107142>.

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