Climate regime shifts and biodiversity redistribution in the Bay of Biscay

Guillem Chust*[1], Manuel González[1], Almudena Fontán[1], Marta Revilla[1], Paula Alvarez[1], María Santos[1], Unai Cotano[1], Marina Chifflet[1], Angel Borja[1,5], Iñigo Muxika[1], Yolanda Sagarminaga[1], Ainhoa Caballero[1], Iñaki de Santiago[1], Irati Epelde[1], Pedro Liria[1], Leire Ibaibarriaga[1], Roland Garnier[1], Javier Franco[1], Ernesto Villarino[1,3,4], Xabier Irigoien[1], José A. Fernandes-Salvador[1], Andrés Uriarte[1], Xabier Esteban[2], Dorleta Orue-Echevarria[2], Tiago Figueira[6], and Adolfo Uriarte[1]

[1] AZTI Marine Research, Basque Research and Technology Alliance (BRTA), Txatxarramendi Ugartea z/g, 48395 Sukarrieta, Spain

[2] Climate Change Foundation of Gipuzkoa – NATURKLIMA, Paseo Mikeletegi, 65 - Edif. B2, 20009 Donostia / San Sebastián, Spain

[3] Scripps Institution of Oceanography UC San Diego 9500 Gilman Dr 0218 La Jolla, CA 92093-0218

[4] College of Earth, Ocean and Atmospheric Sciences, Oregon State University, Corvallis, Oregon, USA, 97330

[5] King Abdulaziz University, Faculty of Marine Sciences, Jeddah, Saudi Arabia

[6] Humboldt-Universität zu Berlin, Thaer Institute for Agricultural and Horticultural Sciences, Invalidenstraße 42, 10099 Berlin, Germany

*Corresponding author: Guillem Chust. Email: gchust@azti.es. AZTI Marine Research, Basque Research and Technology Alliance (BRTA), Txatxarramendi Ugartea z/g, 48395 Sukarrieta, Spain

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ABSTRACT

Global ocean warming, wave extreme events, and accelerating sea-level rise are challenges that coastal communities must address to anticipate damages in coming decades. The objective of this study is to undertake a time-series analysis of climate change (CC) indicators within the Bay of Biscay, including the Basque coast. We used an integrated and flexible methodology, based on Generalized Additive Mixed Models, to detect trends on 19 indicators (including marine physics, chemistry, atmosphere, hydrology, geomorphology, biodiversity, and commercial species). The results of 87 long-term time series analysed (~512,000 observations), in the last four decades, indicate four groups of climate regime shifts: 1) A gradual shift associated with CC starting in the 1980s, with a warming of the sea surface down to 100 m depth in the bay (0.10-0.25 °C per decade), increase in air temperature and insolation. This warming may have impacted on benthic community redistribution in the Basque coast, favouring warm-water species relative to cold-water species. Weight at age for anchovy and sardine decreased in the last two decades. 2) Deepening of the winter mixed layer depth in the south-eastern bay that probably led to increases in nutrients, surface oxygen, and chlorophyll concentration. Current increases on chlorophyll and zooplankton (i.e., copepods) biomass are contrary to those expected under CC scenarios in the region. 3) Sea-level rise (1.5-3.5 cm per decade since 1990s), associated with CC. 4) Increase of extreme wave height events of 16.8 cm per decade in the south-eastern bay, probably related to stormy conditions in the last decade, with impacts on beach erosion. Estimating accurate rates of sea warming, sea-level rise, extreme events, and foreseeing the future pathways of marine productivity, are key to define the best adaptation measures to minimize negative CC impacts in the region.

INTRODUCTION

The effect of global warming on the oceans, the acidification, and the rise in mean sea level derived from climate change and greenhouse gases emissions are challenges that society must face promptly to avoid impacts in the coming decades. The Intergovernmental Panel on Climate Change (IPCC) Special Report on the Ocean and Cryosphere in a Changing Climate (SROCC) (IPCC, 2019), highlighted scenarios of global sea level rise higher than previous assessment reports (84 cm by 2100 in the RCP 8.5 scenario), and an ocean transition to unprecedented conditions, with an increase in temperatures, an increase in acidification, a decrease in oxygen and an alteration in primary production, impelling a global redistribution of life on Earth (Pecl et al., 2017). As a consequence, marine ecosystems are experiencing trophic changes, commercial fishes show body size reduction, poleward shifts and phenological alterations. In the near future, coastal cities and settlements may experience increasing damages from stormy weather, flooding, beach erosion, among other threats from global change (Gissi et al., 2021). However, there is a need to understand these changes at regional scales for proposing adaptation and mitigation measures (Kebede et al., 2018).

A better understanding of each one of these processes at specific regions requires access to consistent, high-quality, near real-time monitoring data on a series of climate, environmental and biological parameters (Miloslavich et al., 2018). Historical observations have been proven essential to detect and understand the recent evolution of climate and its consequences to the marine biogeochemical systems (Poloczanska et al., 2016). Marine monitoring includes the rigorous sampling of different physical, chemical and biological ecosystem components for a well-defined purpose (Borja and Elliott, 2013; McLusky and Elliott, 2004). For instance, most of national monitoring programmes on marine issues focus on short to mid-term temporal scales, such as weather forecast and emergency prevention, water quality, biological conservation, and fisheries stock assessment (Philippart et al., 2011). The collection of data from those programmes is valuable for other purposes such as the surveillance of climate change. However, local monitoring of climate change needs specific analysis of observations by identifying indicators of climate change, by integrating several observation programmes, and by using homogeneous and robust statistical and modelling tools. Furthermore, the interpretation of local trends should be evaluated within the context of regional and global trends to the correct attribution of the causes of variability. A key and priority step for developing a climate change marine observatory is to define potential indicators of climate change (EEA, 2017). There are in general two types of indicators, those describing the physical state of the climate system and its historical development, and those looking at future impact, risk and adaptation (GCOS, 2017). To select a potential climate change indicator to be monitored in a particular region, a set of criteria should be followed and applied to both data and variables. The U.S. Environmental Protection Agency (EPA, 2016), for instance, follows an established framework of criteria to identify time series of climate change indicators based on data reliability that present trends, known variability, and, more importantly, the relationship between the indicator and climate change should be supported by published and peer-reviewed science.

The marine ecosystems of the Bay of Biscay (North-eastern Atlantic) and its littoral have been extensively studied in relation to climate change, e.g., (Chust et al., 2011; Gimeno et al., 2011; Hemery et al., 2008; Le Marchand et al., 2020; Le Treut, 2018). However, this bay lacks of integrative and continuous surveillance connecting multiple observations from physics to biodiversity within the context of climate change, and covering from monitoring to future scenarios. The vulnerability of the coasts of the Bay of Biscay to the combination of extreme events and potential change in present climate regimes (de Santiago et al., 2021; Liria et al., 2011; Marcos et al., 2012) is increased by anthropogenic activities such as the urban and industrial discharges, water treatment, the exploitation of marine resources, tourism, marine traffic, oil spills, and the high human use of the marine space (Borja et al., 2019). The northern Spanish coast (i.e. Cantabrian coast, southern Bay of Biscay) is dominated by rocky substrata with vertical cliffs confining small estuaries and sandy beaches. At present, those estuaries and beaches are squeezed by urban settlements, industrial zones, and historical habitat degradation during the 20th century (Chust et al. 2009), and at risk of future flooding and erosion (Liria et al., 2011; Toimil et al., 2017; Valle et al., 2014). Coastal biotic communities have already changed according to sea warming rates, e.g. macroalgae (Casado-Amezúa et al., 2019), mammals and seabirds (Hemery et al., 2008). Similarly, commercial fish species in the bay, such as anchovy, mackerel, and tuna, are experiencing responses to sea warming with expected changes on latitudinal distribution and migration (Bruge et al., 2016; Caill-Milly et al., 2018; Chust et al., 2019; Erauskin-Extramiana et al., 2019a).

Implementing an integrated system for monitoring climate change and its effects through the selection of the main climate change indicators and their standardization would allow continuous monitoring of trends, and generation and validation of projection models. This is key to define the best adaptation criteria that must be carried out at specific coasts to face future threats such as flooding, and revise management actions on environmental conservation and local fisheries within the climate change context. The main objective of this study is the temporal trend analysis of physicochemical and biological variables in the Bay of Biscay, including specifically the Basque coast (northern Spanish coast, Fig. 1), within the context of ongoing climate change. The specific objectives are: 1) to define potential indicators of Climate Change (iCC) in the marine and coastal environment and identification of available time series, 2) to develop and apply the time-series analysis methodology based on Generalized Additive Mixed Models (GAMMs), and 3) to interpret the iCC trends within the context of climate change and other potential drivers. These specific objectives will enable in the future to develop and improve potential scenarios for impacts of climate change by means of downscaled models, as well as defining adaptation strategies.

MATERIAL AND METHODS

Monitoring programmes

At the Bay of Biscay, and in particular on the Basque coast, there are various monitoring programmes for physicochemical and biological variables with specific purposes: weather forecast and emergency prevention, hydrographic monitoring, water quality, biological conservation, fisheries stock assessment, and sustainable management of the coastal erosion. These programmes, together with earth observation monitoring programmes, collect multiple variables that we used here to derive the specific indicators for the marine climate change monitoring, as shown below.

Meteorological and hydrological observation networks in the coast

The national monitoring programme (AEMET, State Meteorological Agency, http://www.aemet.es/) provides daily atmospheric data of air temperature, sunshine duration and precipitation in Igeldo (Donostia-San Sebastián), and Hondarribia (Fig. 1). Data on daily river flow in five Basque estuaries are collected from the network of permanent stations of the Council of Gipuzkoa. The series of daily river flow exists since the 1990s. For each river, the gauging station considered is the nearest to the coast. Daily river flow from Adour river (Aquitaine, France, Fig. 1) is collected and provided by the French regional administration of Nouvelle-Aquitaine (DREAL, via Banque HYDRO).

Hydrographic surveys in the water column

The long-term monitoring programme *VARIACIONES* samples nearly monthly a section (D0-D1-D2-D3 stations) off the Pasaia coast (Fig. 1) through ship-based oceanographic surveys since 1986 (Valencia et al., 2019; Valencia et al., 2004). In this contribution, CTD (Conductivity, Temperature and Depth) profiles of temperature, salinity, oxygen, and chlorophyll concentration collected in station D2 (L-RF10) over 110 m water depth were used. Measurements at the D3 station (1986-2006) and Donostia-San Sebastián buoy (2007-2019) were also used to determine the Winter Mixed Layer Depth (WMLD). Until 1992, measurements of temperature and dissolved oxygen were performed at 0, 10, 20, 30, 50, 75 and 100 m depth with Martek Mark VIII hydrographic profiler. Niskin bottles were used for measurement of chlorophyll-a by spectrophotometry. Salinity was measured with induction salinometer KAHLSICO SR10, and dissolved oxygen via Winkler's method. Since 1993, continuous profiles with Sea-Bird CTD were used. For more information about the sampling procedure and instrumentation, see Fontan et al. (2008).

Oceanographic buoys

The Gascogne buoy (UK Met Office in cooperation with Meteo France; Fig. 1) acquires, among other ocean-meteorological variables, hourly wind intensity and direction data at 3 m of elevation above sea level through Marine Automatic Weather Station Network since 1998. This series is a representative historical source of information of climate conditions of central oceanic waters of the Bay of Biscay. We have analysed daily data of mean and maximum wind speed and wind components. The wave climate has been obtained from the Bilbao-Vizcaya offshore buoy (Fig. 1) providing hourly directional wave data from the year 1991 (Puertos del Estado, http://www.puertos.es/en-us). We computed daily mean variables of the significant wave height (Hs) and of the mean wave period for trends of daily (mean) Hs and wave power (Pw), and daily maximum Hs for trends of monthly extremes (90th percentile Hs).

Long-term monitoring of sea surface temperature at Aquarium of Donostia-San Sebastián

The Aquarium of Donostia-San Sebastián maintains a historical source of information on the Sea Surface Temperature (SST) in front of the Aquarium of the city (Basque coast) since 1946 (Goikoetxea et al., 2009; González et al., 2013; González et al., 2008). Measurement of water temperature at surface is on a daily basis in the morning at 10:00 am. In the 1960s and 1970s, there were frequent gaps, but since the 1980s it has been practically complete.

Open data from satellite platforms and reanalysis

Public open data acquired from satellite sensors corresponding to several Earth observation monitoring programmes and reanalysis have been used to extract information on sea temperature, sea level and chlorophyll concentration for the Bay of Biscay. For SST over the Bay of Biscay, we used satellite daily data distributed by NASA OBPG since 2003 to 2019, and the reanalysis-based NOAA Optimal Interpolation SST high resolution dataset within the spatial and temporal coverage of the anchovy stock assessment (see below; 1986-2019, in May, shelf of the Bay of Biscay). For sea level, we used daily grids (spatial resolution of 0.25º x 0.25º) computed by merging measurements of two altimeters on board different satellites depending on the date and with orbits close to Topex/Poseidon (NASA) and ERS-1 (ESA). This data set covered the period 1993-2019 and the Bay of Biscay. For surface chlorophyll-a concentration, we used daily data from MODIS-AQUA sensor with the OC5 bio-optical algorithm (Gohin et al., 2002) in the Bay of Biscay and in front of Donostia-San Sebastián between 2003 and 2019. This data is distributed by IFREMER/CERSAT.

Tide gauges

In the Bay of Biscay, coastal sea level data is acquired from tide gauges. Data available from the University of Hawaii Sea Level Center (Caldwell et al., 2015) at different locations: Brest (France, starting in 1846), Newlyn (United Kingdom, since 1915), and in Spain, A Coruña and Santander (hourly data since 1940s, 5-min data since 1990s), Gijón and Bilbao (5-min data since 1990s) (Fig. 1).

Coastal videometry

The morphological monitoring programme of the beaches of Gipuzkoa (eastern Basque coast) is based on coastal videometry systems (Davidson et al., 2007). Each beach has installed a KOSTASystem (www.kostasystem.com) station composed by 1 to 4 cameras allowing the view of the whole system (hard contours, beach and surf zone). Every 10 minutes, snapshots and time exposure (the average of 600 snapshots sampled at 1 Hz) images are stored. For the present study, a monthly representative image of low tide and high tide is selected for the Zarautz beach station (Fig. 1), since it has the longest dataset (2010-present). From these images, two indicators are derived: 1) the beach width (estimated as the distance between a baseline reference and the shoreline) at low and high tide, and 2) the intertidal and supralittoral beach areas.

Monitoring network of the ecological status in coastal systems

The monitoring network of the ecological status in estuarine and coastal systems generates data for the Basque Water Agency (URA) on biochemical properties of water and sediment and on benthic biodiversity (Borja et al., 2016). Here we have excluded estuarine stations and considered seasonal CTD measurements of dissolved oxygen in the water column and surface nutrients at 12 sampling stations along the Basque coast, on 35 m depth (Fig. 1), and at 3 stations located on 110 m depth (Fig. 1). Most of them were sampled since 1995.

Phytoplankton communities (species composition and abundance) were sampled in surface waters at the URA stations, every 3 months in most of years, since 2002. For this study, only the stations with almost no anthropogenic nutrient pressure were used (L-B20, L-L10, L-OK10) (Garmendia et al., 2013) and the 3 stations located on 110 m seafloor depth (Fig. 1). Rocky benthic communities were sampled every 3 years in 26 intertidal transects along the Basque coast, perpendicular to the shoreline. Semi-quantitative sampling of surface coverage (Braun-Blanquet, 1951) was carried out along the transects. Most of the transects started in 2002-2004. Soft-bottom macroinvertebrates were sampled with a van Veen grab to estimate abundance and biomass at all stations along the coast (Fig. 1). The sampling of most of the stations started in 1995. At each station, an annual sample was taken in winter, consisting of 3 replicates.

Scientific surveys for fish stock assessment

Three monitoring programmes for fish stock assessment in the Bay of Biscay were used for deriving indicators for European anchovy (*Engraulis encrasicolus*), European sardine (*Sardina pilchardus*), and zooplankton (specifically copepods): 1) BIOMAN surveys (BIOMass of ANchovy) (Erauskin-Extramiana et al., 2019a; Santos et al., 2018) on anchovy spawning. Egg abundance and weight-at-age of adult anchovy data and zooplankton biomass have been collected annually during these surveys, between 1989 and 2019. Surveys were carried out between May and the first half of June, to coincide with the peak of the spawning period. The area covered by BIOMAN was the wide French continental shelf, and the narrow Spanish shelf (Fig. 1), which corresponds to the main spawning area of anchovy. In average, 500 annual samples are collected from the surface to 100 m depth or 5 m above the bottom in shallower waters. Zooplankton samples were processed for taxonomic identification and size distribution estimation using image analysis with the software ZooImage (www.sciviews.org/Zooimage) (Bachiller and Fernandes, 2011; Fernandes et al., 2008). In particular, copepod biomass was estimated. 2) JUVENA surveys on juvenile anchovy (Boyra et al., 2013). Anchovy juveniles were sampled since 2003 in September. Randomly sampled juvenile specimens were measured to the nearest mm for standard length (SL) to determine the length-frequency distribution in 0.5 cm length classes (Aldanondo et al., 2016). Juvenile length was transformed to weight according to a size-length allometric relationship ($\text{weight} = 0.0027(\text{length})^{3.3066}$). 3) The monitoring programme PELGAS in the Bay of Biscay is an integrated ecosystem survey conducted by Ifremer (Doray et al., 2018; ICES, 2020; Véron et al., 2020), which was used for deriving indicators for weight-at-age of sardine from 2000 to 2019.

Defining climate change indicators for the study area

The objective of this study is to identify useful iCC from measured variables for the Bay of Biscay and the Basque coast; therefore, we do not limit to climate indicators, but include those variables that may vary with climate change such as chemical, geomorphological and biotic. To define the iCC in the marine environment, we have selected some of the criteria used by U.S. Environmental Protection Agency (EPA, 2016): 1) data available to show trends over time, 2) data consist of actual measurements, 3) data representative of the region, 4) data credible, reliable, peer-reviewed and published, 5) sources of variability and uncertainty available, 6) the relationship between the indicator and climate change is supported by published, peer-reviewed science and data, and 7) data and analysis are founded on scientifically objective and transparent methods.

In order to monitor and analyse the evolution of physicochemical and biological iCC in the marine environment of the Bay of Biscay, we have preselected 19 indicators of climate change based on the abovementioned criteria and for which there is a monitoring programme that provides periodic and continuous sampling mentioned above. For each of the indicators, a description has been made that justifies its inclusion *a priori* as an iCC in the following sections of the corresponding indicators. They are grouped in four main categories: 1) Physical and chemical marine indicators (sea temperature, salinity, water column stratification, sea level, wave energy and height, oxygen, nutrients), 2) Atmospheric and hydrological indicators (air temperature, insolation, wind, precipitation, river flow), 3) Geomorphologic indicators (coastline, intertidal and subtidal beach area), and 4) Biotic indicators (phytoplankton, zooplankton, rocky- and soft-bottom benthic communities, fish). The time series analysed are summarised in Table 1. The potential relation between local iCC and climate change is described at Supplementary Material 1 (SM 1). The method of measurement (instrumentation, sensor) for each iCC are summarised at Supplementary Material 2 (SM 2).

Time series statistical methods

Traditionally, time series methods decompose the temporal data into the following components: cyclical fluctuation, trend, and random error (Mudelsee, 2019). The most adequate statistical method for time series analysis depends on: 1) Regularity of the data. The classic methods of time series analysis usually assume that the data are regular through time. However, sampling often result in irregular time series. It is therefore necessary to use time series analysis methods adapted for irregular data such as Generalized Additive Models (GAMs) (Simpson, 2018). 2) Type of series: univariate or multivariate. A data series measured at a single spatial point can be defined as univariate and is the simplest case. An indicator (e.g., salinity) can be measured at several stations or depths simultaneously, and therefore we are in the case of multivariate series. In this case, we can estimate the general trend of the variable taking into account each station or depth as a random effect, and the year and seasonality as fixed effects, using mixed effects models (Zuur et al., 2009). 3) Objective of the study (average, extremes, seasonality). The simplest case is when the objective is to study changes in the mean values of the variable. To address extreme events, an appropriate metric needs to be defined (e.g., intensity, duration or frequency of the event) before the trend analysis. A complex case is the study of changes in seasonality, which in classical decomposition methods is assumed to be constant over the years.

Error distribution and autocorrelation in time series

If a random variable follows a Gaussian distribution and the observations are independent (no temporal autocorrelation), it is possible to apply linear methods such as linear regression to estimate the linear trend. Climatic and biological variables often have probability distributions that differ from Gaussian and observations may be autocorrelated, i.e., $X_{\mathrm{error}}(i)$ is positive, then $X_{\mathrm{error}}(i+1)$ is also probably positive. Both non-normality (non-Gaussian) and temporal autocorrelation in the error must be considered to correctly estimate uncertainty (Mudelsee, 2019), and the use of parametric methods may underestimate the error. In the case of an autocorrelated variable with irregular sampling that also presents a complex and unknown seasonal cycle (difficult to adjust to a predetermined model such as the sinusoidal one), methods based on GAMMs are a suitable alternative (Simpson, 2018). GAMMs provide a suitable tool that allows a statistical test to be carried out on the significance of each of the terms analysed (Dominici et al., 2002). For those reasons, we have used GAMMs to analyse the trend of iCCs.

GAMMs for analysing time series

A GAM generalizes a Generalized Linear Model (GLM) so that the linear predictor depends linearly on non-parametric smoothing regression functions, which allow the study of non-linear relationships between the response variable and the explanatory variables (Hastie and Tibshirani, 1990; Wood, 2006). As in GLMs, GAMs can model a wide range of probability distributions including Gaussian, binomial, Poisson and gamma distributions, among others. A GAMM goes a step further and allows the inclusion of random effects and spatio-temporal correlation structures.

To analyse the time-series of physicochemical and biological iCCs, we constructed GAMMs that included terms accounting for linear trends along time, cyclical fluctuations within the year and temporal correlation. In particular:

$$g(\mu_i^b) = \beta_0 + \beta_1 t + \boldsymbol{X_i\theta} + f(t) + f(x_{1i}) + \cdots + \boldsymbol{Z_i b} \,,$$

where $g(.)$ is a monotonic function, and μ_i^b is the mean of $y_i|\boldsymbol{b}$ that represents the iCC conditional on the vector of random effects $\boldsymbol{b}$ and follows an exponential family probability distribution (e.g. Gaussian, Poisson, binomial). On the right hand side, $\beta_0 + \beta_1 t$ represent the linear trend through the time, $f(t)$ is the seasonal component and $\boldsymbol{X_i\theta}$ y $f(x_{1i})$ represent other potential linear and non-linear relations with other variables. The term $\boldsymbol{b}$ is the vector of random effects representing the temporal correlation that follows a Gaussian distribution with mean zero and covariance matrix $\boldsymbol{\psi}$ (i.e. $\boldsymbol{b} \sim \boldsymbol{N}(\boldsymbol{0}, \boldsymbol{\psi})$).

The type of distribution was assumed according to the type of variable of iCC (e.g., Gaussian for temperature, and Poisson for the abundance of a species). To correctly estimate the trend and its confidence interval it is necessary to ensure that the residuals are not autocorrelated. So, the model was built in two steps. First, we constructed a model without correlation. Then, we checked if there was autocorrelation in the residuals, and if there is, we included random effects (Simpson, 2018).

A first model (model 1) included both the seasonality and the linear trend. The seasonal component was modelled with a smoothing term *s*, with a maximum of degrees of freedom of k=6 in order to avoid overfitting (Burnham and Anderson, 2002), and imposing cyclicality (bs="cc") to the variable so that the values of day 366 are joined with those of day 1 of the following year. The temporal trend component was modelled with a linear term of the variable Year in decimals to better reflect the precise date of observation throughout the period:

iCC ~ Year + s(Day, k = 6, bs = "cc") (model 1)

The next step was to check whether the residuals are autocorrelated with time. If this is the case, we built a new model (model 2) that includes the random effect of the year by fitting the residuals to an autoregressive model of order 1 to remove the temporal autocorrelation in the estimation of the linear trend by means of a GAMM. If the Akaike information criterion (AIC), as estimator of the error, of model 2 is lower than that of model 1, we therefore choose model 2 to estimate whether the linear trend term for the year is significant or not.

For those variables where data is available from different stations or depths, GAMMs are able to analyse several series by combining them in a single model to estimate the overall trend of the variable taking into account each station as a random effect.

The 95% confidence interval of the linear trend is estimated from the parametric coefficients (SE: Standard Error and β_1: slope, *n*: number of degrees of freedom) and the percentile of the *t*-Student distribution (*qt*) as follows:

$$\text{Upper confidence interval: } \beta_1 - qt(0.025, n\text{-}2) \times SE$$

$$\text{Lower confidence interval: } \beta_1 + qt(0.025, n\text{-}2) \times SE$$

Analysis of seasonal timing of life-cycles trends

The GAMM established in the previous section for analysing the mean, assumes that seasonality is constant over time. However, the seasonal timing of biological life cycles (i.e. phenology) can change with varying conditions such as warming. The study of the phenology of certain processes such as the spawning or migration of a species has been analysed using GAMMs incorporating interaction factors. GAMMs allow the characterization of seasonality and in turn include an interaction factor that allows the analysis of whether this pattern of seasonal timing (beginning, peak, end) varies over time (Erauskin-Extramiana et al., 2019a). Here, the study of the spring bloom of the total biomass of phytoplankton (Y) throughout the year and its variation over the years has been analysed using the following model: $Y \sim s(d, t)$, where d is the seasonality (day of year), t is the temporal variable (year) and s is a two-dimensional smoothing function representing the interaction between d and t.

Trend analysis on extreme events

The trend analysis of extreme events from monthly extreme values (high percentiles) of the indicators studied was undertaken using a GAMM adapted to a time series with monthly values. While the GAMM for trend analysis on mean values defines the seasonal component with a smoothing term (s) that depends on the day of the year, the GAMM for extremes fits the seasonal component with an s term that depends on the month of the year (Month) and the linear term of the variable Year in decimals. For instance, the case of the extreme waves of the buoy of Bilbao-Vizcaya has been modelled by means of Hs90, which is the monthly 90th percentile of the significant Hs, with k=6 is the maximum of degrees of freedom in the smoothing term.

Trend analysis of biotic communities

As a consequence of the latitudinal shift in populations resulting from the response to warming, the abundance in each latitude range (more specifically, in each thermal range) may vary. However, the movement of a species may be the result of other factors not related to climate change such as the exploitation of commercial species. Therefore, studying the response of a group of species (community) to warming is a more complete and reliable analysis strategy for attributing the causes. To this end, a methodology at community level was used to test whether changes in the composition of species in a community correspond to their thermal preferences, using the CTI, a measure of the average thermal affinity of ecological communities, weighted by the relative abundance (Devictor et al., 2008; Stuart-Smith et al., 2015):

$$CTI = \sum_{s=1}^{n} Temp.pref_s \times Relative.Abundance_s$$

where the number of species in the community is *n* and each species (*s*) has a temperature preference (*Temp.pref*) and a relative abundance (the species' abundance divided by the abundances of all species) in the community.

By comparing the inter-annual changes in CTI with local temperature trends, inferences of community tracking to warming can be made. The thermal preferences were determined for each species by matching occurrence records collected from OBIS (Ocean Biogeographic Information System; www.iobis.org) with annual means of GODAS local SST during the 1982−1999 period, Webb et al. (2020). Then, the midpoint between the 5th and 95th percentile of the temperature distribution occupied by each species was calculated, as a measure of central tendency of their realized thermal distribution (Stuart-Smith et al., 2015). Subsequently, CTI was calculated at each station using the thermal midpoint values for each species recorded weighted by their *log*(abundance + 1) (Stuart-Smith et al., 2015). We estimated the CTI per each time unit for time series of communities identified at species level: phytoplankton, hard- and soft-bottom benthos. The trend of CTI has been analysed with GAMMs in the case of phytoplankton, and with linear model for yearly benthos data.

Main approach and specificities

Each iCC has been measured with different metrics (e.g., mean, extreme events), platforms (e.g., tide gauge, satellite), stations, coverage (e.g., Bay of Biscay, fixed station), and conditions (e.g., depths) described in Table 1. Therefore, each time series dataset has been analysed with different types of GAMMs specified in Table 1.

The time-series analysis of sea level follows a distinct statistical approach in order to account for intrinsic variability (high frequency, astronomical, longer period, noise) and capture changes on the long-term variability or trend. Sea level and long-time series of sea temperature have been analysed with the Kolmogorov-Zurbenko Adaptive moving Averages (KZA) filter (Zurbenko et al., 1996) combined with GAMMs (or Linear Models (LMs) for annual data) specified in Table 1. In particular, the analysis of the historical long-time series of SST of the Aquarium of Donostia-San Sebastián in the period 1946-2019 has been undertaken in two steps: 1) a digital filter to remove the variability of period less than 1 year (Thompson, 1983) and a trend change analysis (Mudelsee, 2010), 2) if a break point is detected, the two corresponding periods where independently analysed with GAMMs to estimate the rate of change in each period. The analyses of the time series of the mean sea level of tide gauges of the Bay of Biscay have been carried out by means of 1) a filtering of the series with a digital filter (González and Fontán, 2013) to remove seasonal variability (period < 1 year); 2) mean values per year have been estimated, thus reducing the temporal autocorrelation between observations; and 3) the trend in the series has been estimated with a linear regression model. For comparison purposes, some time series have been also analysed at different time spans: from the beginning of the time series and from the sea warming period detected in the long time series of Aquarium of Donostia-San Sebastián.

A particular case was the analysis of the beach width that was estimated from the net distance in a direction significantly perpendicular to the coast, between each point (transect) of the coastline and the baseline. It has been calculated in both the high and low tide series. For each transect, a trend of accretion or erosion has been estimated from a GAM model with the year for the linear component and a smooth for the seasonal variability.

RESULTS

Atmospheric and hydrologic indicators

Air Temperature

The results of the time series are indicated in rates per decade (= dec^{-1}). The analysis of daily mean air temperature at two stations indicated warming from the beginning of the series to 2019 (0.195 ºC dec^{-1} since 1928 in Igeldo and 0.369 since 1970 in Hondarribia) and between 1980 and 2019 (0.31 and 0.25 ºC dec^{-1} in Igeldo ($p=0.056$) and Hondarribia ($p<0.0001$) (Table 1), respectively.

Sunshine hours

The results of the time series of the daily number of sunshine hours in Igeldo indicated an increase in the two periods: 1947-2019 (at a rate of 0.0462 ± 0.0156 h dec^{-1}, $p=0.0031$) and with larger rate in 1980-2019 (0.2615 ± 0.0387 h dec^{-1}, $p<0.0001$; i.e., 15 min more of daily sunshine per decade) (Table 1).

Wind

The analysis of the time series of the wind at the Gascogne buoy for the period 1998-2019 showed that wind speed has increased significantly, the daily mean at a rate of 0.249±0.087 m.s^{-1} dec^{-1} ($p<0.0043$) and the daily maximum at a rate of 0.363 ± 0.113 m.s^{-1} dec^{-1} ($p=0.0012$) (Table 1). The trends for the eastward and northward wind components were not significant.

Precipitation

The analysis of the time series of rainfall in Igeldo and Hondarribia for the period 1980-2019 showed that trends in annual accumulated rainfall were no significant (Table 1). The analysis of extreme precipitation, defined as the number of days of the year with precipitation greater than the 75th percentile of the corresponding series (4.3 mm in both locations), showed that in Hondarribia there was a positive trend (5.42 days dec^{-1}, $p=0.0108$) whilst it was not significant in Igeldo ($p=0.1871$) (Table 1).

River Flow

The analysis of five eastern Basque rivers from the 1990s to 2019 showed that the trend of annual accumulated river flow is not significant in four of them (p-value>0.05) (Table 1). Only in the case of the Oiartzun river, the accumulated river flow showed a significant positive trend of 0.155 ± 0.057 m^3s^{-1} dec^{-1} in 1997-2019. In contrast, the trend of the river flow of the Adour (Aquitaine, France) showed a decrease of -0.066 ± 0.016 m^3s^{-1} dec^{-1} (i.e., -5% in 42 years). The analysis of the annual extreme events, those above 90th percentile, showed a significant positive trend for the five Basque rivers analysed (Table 1). In the case of the Adour, which has a mixed pluvio-nival regime (characterised by snow-melting), there was no significant trend in extreme events.

Physical and chemical marine indicators

Sea temperature

The filter and trend change analysis of the historical time series of SST of the Aquarium of Donostia-San Sebastián (1946-2019) identified a trend reversal in 1980 (Fig. 2). The analysis of trends in each of the periods with GAMMs provided the following estimates (Fig. 3, Table 1): 1) a decreasing trend at a rate of -0.22 ± 0.06 °C dec^{-1} from 1946 to 1980, and 2) an increasing trend in the most recent period (1980-2019) at a rate of 0.23 ± 0.04 °C dec^{-1} (Fig. 3, Table 1). The analysis of the time series of satellite-based SST of the Bay of Biscay for the period 2003-2019 indicated a significant increasing trend with a rate of 0.11 ± 0.04 °C dec^{-1} (p=0.00923) (Table 1). The analysis of reanalysis-based SST in May in the Bay of Biscay in the period 1986-2019 showed a significant increase with a rate of 0.25 ± 0.05 °C dec^{-1} (p=0.00923) (Table 1). The sea temperature in the water column (0-100 m depth) (from 1986 to 2019) at the L-RF10 (D2) station (Fig. 4) showed an increasing trend of 0.15 ± 0.04 °C dec^{-1} (Table 1).

Salinity

The time series of the salinity in the upper 100 m from 1986 to 2019 at the L-RF10 (D2) station (Fig. 5) has been analysed using the GAMMs. Two measures have been analysed: averaged over the upper 100 m and at discrete depths (0, 5, 10, 25, 50, 75 and 100 m). The results indicated that the integrated salinity in the 0-100 m depth column for the two periods (1986-2019 and 1993-2019) does not present any significant temporal trend (p=0.1620 and p=0.481, respectively) (Table 1), although in both cases the slopes are negative. The results of the analysis of salinity at discrete depths (i.e., where depth is considered a random effect) indicated that salinity has a significant negative trend (p=0.0095) of -0.029 per decade from 1993 to 2019 (Fig. 5, Table 1), and of -0.037 per decade (p<0.0001) from 1986 to 2019.

Thermocline, stratification and Winter Mixed Layer Depth (WMLD)

The depth of the thermocline has been analysed at station D2 through the depth of the 14 °C isotherm throughout the year and in the months in which it is present (April to mid-December) for the period 1993-2019. The use of a representative isotherm is a very extended method to represent the thermocline depth (Valencia et al., 2019). The maximum vertical gradients in the upper water column (0-100 m) temperature and density (1993-2019) can be considered proxies of the thermal and thermohaline stratification strengths, respectively. The trend analysis of the 14 ºC isotherm depth indicated a decrease (i.e., the isotherm deepens) of 5.04 ± 2.09 m dec^{-1} (p=0.0167) (Table 1, Fig. 6), whilst the depth of the 14 °C isotherm in the months in which it is present did not show any significant trend (p=0.3165). The indicators of thermal and thermohaline stratification did not show significant temporal trends (p>0.05; Table 1). The WMLD has been estimated as the maximum ML in winter (from January to March) for the period 1986-2019. The analysis of the WMLD time series showed a significant negative trend from 1986 to 2019 at a rate of -21.39 ± 9.94 m dec^{-1} (p=0.0391) (Table 1), but with high variability (WMLD in 1986 was -175 m and in 2019 was -150 m.

Dissolved oxygen

The analyses of dissolved oxygen concentration in the water column (at sea surface, 25 m and 100 m), sampled at the Basque coastal stations from 1995 to 2019 (from 2002 to 2019 for 100 m depth), have been carried out using the GAMMs, where the stations were treated as random effects. The results of the trend analysis indicated that dissolved oxygen concentration at sea surface and at 25 m increased significantly (p<0.0001) in the study period with rates of 0.144 ± 0.021 mg l^{-1} dec^{-1} and 0.090 ± 0.022 mg l^{-1} dec^{-1}, respectively (Table 1). In contrast, the dissolved oxygen concentration at 100 m depth has decreased -0.253 ± 0.062 mg l^{-1} dec^{-1} (p=0.0001) (Table 1).

Nutrients

The concentration of surface dissolved nutrients (NH_4, PO_4, NO_2, NO_3 and SiO_4) at the Basque coastal stations from 1995 to 2019 were analysed using GAMMs, with the set of stations as random effect. The results indicated that all the nutrients (except NO_2) increased significantly (p<0.05) their concentration in the period studied (from 0.013 µmol.l^{-1} $dec^{-1}$of PO_4, to 0.447 µmol.l^{-1} dec^{-1} of SiO_4) (Fig. S1, Table 1).

Sea level

The results of the time series of the mean sea level of 9 tide gauges in the Bay of Biscay indicated that mean sea level is rising significantly in all tide gauges, except for that of Gijón, which is not significant (Table 1). The rates of rise for the 8 significant series ranged from 1.25 ± 0.05 cm dec^{-1} (in Brest, 1846-2019) to 2.97 ± 0.33 cm dec^{-1} (in Bilbao, 1992-2019). In general, the highest rates correspond to the most recent periods (since the 1990s), as it can be seen by analysing the same Brest series from 1992 to 2019, and that the rate of increase is twice as high as for the entire period of the series: 2.48 ± 0.44 cm dec^{-1}. The mean sea level in the Bay of Biscay obtained with satellite sensors from 1993 to 2019 indicated that it is rising at a rate of 2.46±0.43 cm dec^{-1} (p<0.0001) (Table 1, Fig. 7). Between 2004 and 2013, there is a fairly constant period of deceleration of the rise, which is evident in the non-linear trend model.

Wave height and power

The GAMM analysis applied to the wave data obtained from the Bilbao-Vizcaya buoy shows no significant trends in the daily mean significant Hs and Pw, for the period 1991-2019 (Table 1). However, the analysis of extreme conditions indicates significant trends for the same period (Table 1). The GAMM applied to the monthly Hs90 shows a significant increase of 16.80 ± 8.03 cm dec^{-1} (p=0.037).

Geomorphologic indicators

Beach shoreline and area

The analysis of the Zarautz beach showed that the low tide shoreline is increasing by 1.72 m yr^{-1} towards the sea and the high tide shoreline is eroding by 0.45 m yr^{-1} towards the inland (Table 1). Therefore, the net balance was a loss of the supratidal beach (0.45 m yr^{-1}) and an increase of intertidal beach of 2.17 m yr^{-1}. In particular, the width of the intertidal beach in 2010 was 130.7 m on average, and 150.2 m in 2019. The time series analysis of the Zarautz beach area in the period 2010-2019 showed a non-significant trend of the supratidal area ($p=0.8436$), and a significant increase of intertidal area ($p=0.0023$) with a trend of 30,544 ± 9,793 m^2 per decade (Table 1).

Biotic indicators

Phytoplankton

Trend of phytoplankton indicators has been undertaken with and without logarithmic transformation (Table 2). Concerning the chlorophyll concentration at the D2 station for the period 1993-2019, the analysis showed no significant linear trend for the surface and 0-50 m integrated chlorophyll concentration (*log*-transformed and untransformed) (Table 2), and for the depth of the maximum chlorophyll concentration (Table 2). On the contrary, the analysis by depth as random effect showed a significant increase in the concentration of chlorophyll of 0.036 ± 0.010 µg l^{-1} dec^{-1}, $p=0.0004$, which was also significant in logarithmic scale (Table 2, Fig. 8).

The analysis of the surface chlorophyll concentration measured by satellite in the whole area of the Bay of Biscay showed an increasing trend of 0.054 ± 0.012 mg m^{-3} dec^{-1} ($p<0.0001$, n=5,903) in the period 2003-2019 (Table 2) (in logarithmic scale it was also significant). The trend analysis for the station in front of Donostia-San Sebastián was not significant ($p=0.2465$). The trend analysis of the seasonal timing of the satellite-based surface chlorophyll concentration (for the spring bloom) showed that the three indicators (beginning, peak and end of the bloom) did not have a significant trend (Table 2), although they all presented a negative rate that could suggest a slight advance in the year Table 2).

The trend analysis of total cell abundance in 2002–2019, using only the six stations with almost no anthropogenic nutrient pressure, showed a statistically significant increase ($p=0.0311$, n = 351) applying the log transformation, while the trend was not significant without log transformation (Table 2). The community, taking the above six stations together, involved 387 phytoplankton taxa; among them, it was possible to extract the thermal optimum of 174 species. The trend of the phytoplankton CTI from 2002 to 2019 was no significant (Table 2, Fig. 9).

Zooplankton

The analysis of the spring copepod biomass series of the Bay of Biscay in the period 1998-2019 indicated a positive and significant trend of 2.27 ± 0.51 mg/m3 dec^{-1}, $p<0.001$ (Fig. 10).

Hard-bottom benthos

The hard-bottom benthos community in the Basque coast is represented by 196 species; among them, it has been possible to extract the thermal optimum of 154 species. The trend analysis of this community showed a statistically significant increase of 0.27 ºC dec^{-1} ($p<0.001$) in the 2002-2019 period (Table 1, Fig. 9). This indicates that the community is changing, and that warm water species have significantly increased relative to colder water species. On the other hand, the CTI and the annual temperature of the Aquarium have no significant correlation ($p=0.081$).

Soft-bottom benthos

The soft-bottom benthic community integrates macroinvertebrates of 774 species; among them, it has been possible to extract the thermal optimum of 559 species. The results showed a significant increase in the CTI ($p<0.032$) over time, with a rate of change of 0.16 ºC dec^{-1} in the 2002-2019 period (Table 1, Fig. 9). There is a significant correlation ($p=0.038$) between the CTI and the warming of the sea surface of the area (in Donostia-San Sebastián Aquarium).

Fish

The analysis of annual mean weight at age of anchovy in the Bay of Biscay showed a general decrease (1.3-3.3 g dec^{-1}) for the three age classes (age 1-2 from BIOMAN survey and juveniles from JUVENA survey, Table 1) and particularly for recent years (Fig. 11). The break-point detection analysis has detected a change in trend in 2005 for ages 1 and 2; beyond this year, weight decreases substantially. A sharp decline starts in 2011 for all ages. The trend analysis of annual mean weight at age of sardine in the Bay of Biscay from PELGAS showed a general decrease (1.1-1.4 g dec^{-1}) for the six age classes (Table 1, Fig. 11).

DISCUSSION

Air and sea warming and redistribution of biotic communities

In the Basque coast at southeast of the Bay of Biscay, our analysis indicate that sea surface has been warming since the 1980s, after a cooling period from 1946 to 1980. Sea warming rates from 1980s onwards varied between 0.15 and 0.25 °C dec^{-1}, with the greater increase at the surface than in the upper 100 m. At the entire Bay of Biscay, the rate is slightly lower (0.10 °C dec^{-1}) in 2003-2019. As the heat content accumulated in the surface layers is transferred through the water column, a deepening of the 14 °C isotherm was also observed (Valencia et al., 2019), in agreement with the abovementioned trends. These rates of sea warming along the Basque coast and the Bay of Biscay confirm the trends detected in previous studies (Costoya et al., 2015; deCastro et al., 2009; Goikoetxea et al., 2009; González et al., 2008).

For subsurface waters, trends are more heterogeneous depending on the period, spatial domain and depth considered. For instance, Michel et al. (2009) found warming rates between 0.30 and 0.19 °C dec^{-1} from sea surface to 100 m depth for the period 1965-2003 for the whole Bay of Biscay. Costoya et al. (2014) found no significant trends for the top

100 m of the water column during 2004-2013 for the entire Bay of Biscay. Below the subsurface waters occurs the East North Atlantic Central Water (ENACW), with the core located between 27.1 and 27.2 kg m^{-3} (Pollard et al., 1996). González-Pola et al. (2005) found a warming trend of 0.32 °C dec^{-1} for the ENACW between 1991 and 2003. A maximum warming rate for ENACW of 0.30 °C dec^{-1} was found for the period 1975-2010 (Gómez-Gesteira et al., 2013). Unfortunately, the isopycnals 27.1 and 27.2 kg m^{-3} are rarely reached due to depth limitations in our measurements and, therefore, we cannot estimate warming trends for ENACW in the south-eastern Bay of Biscay.

In the Cantabrian Sea (southern part of the Bay of Biscay), the water column from the surface down to 1,000 m has been warming in the order of 0.20 °C dec^{-1} over the last few decades (1992-2009) (González-Pola et al., 2012). The sea warming of the Bay of Biscay observed would be associated with the warming of the northeast Atlantic, linked to the ocean-atmosphere interaction patterns, associated with global climate change (Drinkwater et al., 2014; Harris et al., 2014). It has been estimated that ocean has been storing 90% of the gained heat by the planet (Zanna et al., 2019). The warming rate of the sea surface along the Basque coast shelf and the entire bay is in the same order of that of the air (0.25-0.31 ºC dec^{-1}).

In the biotic component, the results of CTI increase indicated that the warming of the sea has consequences on the redistribution of intertidal benthic communities, increasing the relative abundance of warm water species with respect to that of cold-water species. The trend analysis of benthic communities showed a CTI increase of 0.16 ºC (soft-bottom) and 0.27 ºC (hard-bottom) dec^{-1} in the 2002-2019 period that is similar to the rate of warming of sea and air temperature in the area. In soft-bottom communities, there is a significant correlation between CTI and sea surface warming in the Aquarium, indicating that the community responds year-to-year to sea temperature variation, as it can correspond to species that have a short to medium lifespan (1-3 years) (van der Linden et al., 2016). On the other hand, the CTI of hard-bottom community and the annual temperature of the Aquarium showed no significant correlation. Given that many of these species have a life cycle longer than one year, e.g. bivalves and macroalgae can live more than 10 years (Montero-Serra et al., 2018), they would need several years to respond to the new conditions and, therefore, it is not surprising that there is no correlation between the annual observations of both variables. Therefore, we can conclude that warming of the sea and air in the area could partly explain the increase in the CTI of the two intertidal benthic communities favouring warm water species relative to colder water species. The lack of response in phytoplankton could be due to the higher biogeographic and dispersal ranges of plankton species relative to benthic communities (Chust et al., 2016), but also due to the limitations of the taxonomic identification at species level in long time series, e.g., Muñiz et al. (2020).

In previous studies, the sea warming of the Bay of Biscay seems to also induce changes in fish biology such as the earlier anchovy spawning (Erauskin-Extramiana et al., 2019a) and the arrival of albacore tuna juveniles during their trophic migration (Chust et al., 2019). Our analysis on the anchovy (1987-2019) and sardine (2000-2019) indicated that weight at age has decreased in all the analysed periods and specially in the last 15 years, in agreement with recent analysis of these traits (Doray et al., 2018; Escribano et al., 2019; Véron et al., 2020). It is well established that body size of marine ectotherm individuals is inversely related to the sea temperature (Atkinson, 1994; Gardner et al., 2011; Huss et al., 2019; Pauly and Cheung, 2018). However, the size (length or weight) of fish individuals may be further conditioned by population size and density (Rose et al., 2001), food availability of the species (Ljungström et al., 2020), fishing exploitation -including positive effects of fishery closure- (Barnett et al., 2017), and toxic effects of crude oil spill (Carls et al., 1999). Size reduction in sardine has been associated with the increased survival rate of younger individuals leading to (density-dependent) competition for food in spawning areas (Doray et al., 2018), or to the condition factor (Véron et al., 2020). In support to the warming effect hypothesis, rather than on the density-dependent effect, both anchovy and sardine have shown a declining trend in mean weight for different stock biomass trends (increasing for anchovy and decreasing for sardine) (ICES, 2018). Moreover, the anchovy size reduction has continued during the fishing closure (2005-2010). On the other hand, our estimates of size reduction are probably larger than what we could expect from only sea temperature effect. Other drivers such as the Prestige oil spill, occurred in November 2002, should be considered in the analysis. The consequences of oil spills including counteracting drivers as toxic negative effects and fishery closure positive effects have been shown in other regions (van der Ham and de Mutsert, 2014). However, the lack of historical data preceding the Prestige disaster could not allow to state conclusions on whether oil spill histopathology in fish liver were related or not to oil spill (Marigómez et al., 2006). Due to these reasons and taking into account that parallel changes have happened in small pelagic fishes in the Mediterranean sea linked probably to food quality and availability (Saraux et al., 2019; Van Beveren et al., 2014), lead us to preliminary conclude that a direct effect of the sea warming could only partially explain the size reduction of these small pelagic fish in the Bay of Biscay, and that other ecosystem trophodynamic mechanisms and anthropogenic activities might be playing a role as well, though confirmation would require further research.

Changes in the water column, salinity, oxygen, nutrients, and plankton

Our analysis showed that the trends in the degree of thermal and thermohaline stratification in the Basque coastal shelf were not significant. During the seasonal cycle, stratification reaches its maximum in August and shows a maximum degree of variability at this time. Thereafter, the strength of stratification starts to decrease until the column is mixed and homogenised. Due to the large intra-annual variability of stratification (not resolved through monthly sampling), it is not possible to establish consistent trends for this variable (González-Pola et al., 2012*)*. In relation to the WMLD, our study showed that the thickness of the winter mixed layer in the south-eastern Bay of Biscay is increasing at a rate of 21 m dec^{-1} since 1986, which confirms the trend of previous studies (Valencia et al., 2019; Fontán et al., 2020). The processes contributing to the deep mixing are: 1) the extraordinary events of 2005 and 2006 that were related to cold and dry winters, 2) the event of 2009 that was induced by cyclone Klaus, 3) the event of 2016 that was due to extraordinary downwelling, and 4) the episode of 2018 induced by anomalously cold winter (Valencia et al., 2019). Somavilla Cabrillo et al. (2011) concluded that the heat accumulated in the subsurface levels in recent decades had favoured the development of very deep mixing layers in extremely cold winters, as in 2005 and 2006. Deep mixing events contribute to the integration of previously accumulated surface thermal and hydric anomalies at depth levels that are usually isolated from the effect of the atmosphere, i.e. ENACW (Somavilla et al., 2009). Additionally, the increase of the mixing layer in winter can be associated with higher concentrations of nitrate and chlorophyll in spring (González-Gil et al., 2018). Valencia and Franco (2004) estimated that, for every 30 m of winter mixing layer, the available nitrate concentration increases by 1 µmol l^{-1} in the water column. This is in agreement with the slight increase detected since 1995 in the concentration of nutrients at sea surface along the Basque coast, mainly nitrate and silicate, and may be with the increase in the concentration of dissolved oxygen at 0 m and 25 m depth that could have resulted from higher rates of primary production in the photic layer.

On the other hand, river flows and precipitation showed a predominance of positive anomalies (Fontán et al., 2020) and an increase in extreme events. Therefore, we also conclude that two processes (deepening of the winter mixing layer and the increase in the continental contributions extremes) could explain the increase in the concentration of nutrients and, perhaps oxygen derived from phytoplankton production, at the sea surface of Basque coast. Further analysis is needed to differentiate the relative contribution of the two processes.

The annual salinity cycle is also affected by different processes such as the advective transport and large-scale interannual variations and by local variability in the precipitation-evaporation balance. The propagation of low salinity anomalies and the local precipitation extremes could explain the decreasing trend on salinity in the water column (0 to 100 m) at the station off Pasaia (D2) from 1993 to 2019. Due to depth limitations of our measurements, it is therefore difficult to associate the decrease in salinity in D2 with global-scale processes related to climate change, such as the expected decrease in salinity in the high latitudes of the North Atlantic (Bindoff et al. 2019).

The vertical structure of the water column and chemical composition are key to understand the seasonal and intensity of phytoplankton blooms (Brody and Lozier, 2015). A slight increase of chlorophyll concentration was detected in the 1993-2019 series off the Basque coast (station D2) when the analysis takes into account all the observations by depth. On the scale of the Bay of Biscay, with satellite data, an increase in surface chlorophyll concentration has also been detected in the period 2003-2019. These increases could be responding to changes in ocean-meteorological processes, such as the deepening of the winter mixed layer that would increase the magnitude of the spring phytoplankton blooms. Several ocean-meteorological factors (mainly the winter mixed layer, river inputs and solar radiation) are known to modulate the seasonal cycle and intensity of phytoplankton blooms (Smayda, 1997), and therefore their integrated study would allow us to better understand the observed trends.

In the North Atlantic, contrasting trends in phytoplankton have been observed. A decline in chlorophyll has been observed by remote sensing (Boyce et al., 2014), although this could be due to a physiological adaptation to thermal stratification, rather than a decline in the overall primary production (Behrenfeld et al., 2016). Other authors indicate that chlorophyll in the North Atlantic has increased over several decades, analysing data from the Continuous Plankton Recorder (McQuatters-Gollop et al., 2011). In contrast, water transparency in high latitude coastal seas may have decreased over the 20th century in response to climate change, resulting in decreased primary production and delayed spring bloom (Opdal et al., 2019).

The increase detected in chlorophyll concentration in the bay could be responsible to fuel the increase in spring copepod biomass in the last two decades. These increases in phytoplankton and copepods are contrary to those expected by climate change in the north-eastern Atlantic by the end of the century with slight decreases (Erauskin-Extramiana et al., 2019a) due to higher water column thermal stratification (Bindoff et al., 2019). However, this process is under debate by certain authors (Dave and Lozier, 2013) as explained above. Moreover, in the Bay of Biscay, primary production projections still show a large uncertainty (Holt et al., 2014).

Sea level rise and acceleration

All series analysed at different stations on the coast (tide gauges) and at sea (remote sensors) indicated that the mean sea level in the Bay of Biscay is rising at a rate of between 1.5 and 3.5 cm dec^{-1} (on average 2.5 cm dec^{-1}) since the 1990s, in agreement with previous studies (Caballero et al., 2008; Chust et al., 2009; González et al., 2011; Marcos et al., 2007), and with the estimates from other types of measurements such as paleo-ecological records (Leorri and Cearreta, 2009); see also a review in (Chust et al., 2011). This rate is slightly lower than the global rate over the same period (3.2-3.6 cm dec^{-1}) (Oppenheimer et al., 2019), but it is similar to the rates observed for the subpolar North Atlantic (2.3 ± 0.6 and 2.6 ± 0.7 cm dec^{-1}, respectively) for the 1993-2015 period (Dangendorf et al., 2019). The lower rate observed in the area than that of global is mainly due to a lower barystatic contribution in the subpolar North Atlantic than in other basins (e.g., northwest Pacific, south Atlantic) due to its proximity to the Greenland ice sheet (Frederikse et al., 2020); according to these authors, the main contributor to the sea level budget in the subpolar North Atlantic is the steric one. It can therefore be concluded that the updated rise detected in the coast and the Bay of Biscay is consistent with the regional sea level rise and slightly lower than the global sea level.

The analysis of the series studied also confirms that the rise in sea level is accelerating in the area in line with global studies (Dangendorf et al., 2019; Nerem et al., 2018; Woppelmann et al., 2006). Sea level rise can have future consequences on coastal flooding, beach erosion and intensified storm damage to the coast (Chust et al., 2011; Liria et al., 2011). The present time series of videometry-based beach erosion in the Basque coast is, however, too short to quantify the relative contribution of sea level rise with respect to wave events in eroding beach coastline.

Increase of extreme wave and wind events, and sandy coastal erosion

Over the last 30 years, no significant trends have been found in the hourly time series of the wave variables obtained from the Bilbao-Vizcaya buoy (Hs, Pw, and wave period), whilst monthly extreme wave height (the 90th percentile of the Hs) increased significantly by 27 cm dec^{-1}. This increase is larger than the increase obtained in the earlier studies based on satellite results and on reanalysis data. In particular, the global satellite study of Young and Ribal (2019) indicated an increase of 8 cm dec^{-1} (for the period 1985-2018) and the reanalysis study of Dodet et al. (2010) up to 20 cm dec^{-1} in the Bay of Biscay, with no-significant trends in the Basque coast (for the period 1953-2009). In line with the increase in extreme waves, the maximum daily wind speed at the station located in the central part of the Bay of Biscay has increased significantly by 0.36±0.11 m s^{-1} dec^{-1} in the period 1998-2019. These trends, however, cannot be directly attributed (nor rejected) to climate change. The attribution or rejection of observed changes to climate change effects is a complex task due to the limited time period of buoy measurements and the limited spatial scale of the analysis. In addition, few studies have observed a correlation between changes in mean and extreme wave regimes and changes in atmospheric variables attributed to climate change. These include global studies by (1) Reguero et al. (2019) relating ocean surface warming to an increase in mean wave power from reanalysis data, and (2) Meucci et al. (2020) showing a change in the extreme regime obtained with numerical models from climate projections. However, none of these studies have shown significant trend changes in our study area.

A possible consequence of the increase in extreme waves, and in particular of certain extreme events (e.g., the sequence of storms in the winter of 2013-2014), is the significant recession of the high tide shoreline and the resulting reduction of the supratidal area observed on the beach of Zarautz since observations (2010-2019). The studied indicators showed a decrease trend of the supratidal area and an increase in intertidal area on Zarautz beach during the period analysed (2010-2019). However, this might be more consistent with a trend towards a more dissipative beach profile over the cycle analysed than a retreat of the beach profile. These changes are hence consistent with the increasing wave energy data observed in recent years in this study and in previous studies (Castelle et al., 2018). In this line, the sequence of storms in winter 2013-2014 caused the most severe erosion recorded in the last 60 years on most of the beaches of the European Atlantic coast (Burvingt et al., 2017) and four years after the events, many of these beaches were still recovering (Dodet et al., 2019), as may be occurring on the beach of Zarautz. However, the series analysed is too short to represent larger scale trends, although it provides relevant data regarding the natural variability of the beach and constitutes a basis for future monitoring within the context of climate change. Furthermore, while beach erosion processes can occur on timescales ranging from hours to days (Van Rijn et al., 2003), recovery can take months (Birkemeier, 1979; Phillips et al., 2017; Wang et al., 2006), years (Castelle et al., 2017; Corbella and Stretch, 2012), or decades (Houser et al., 2015; McLean and Shen, 2006). Therefore, the variability of the analysed signal is due to the superposition of processes of different nature and time scale and is not attributable to a single process.

Extreme waves and stormy weather can also shape marine communities and affect population mortality. For instance, dramatic effects on the reduction of biomass and cover of the canopy-forming subtidal macroalgae *Gelidium corneum* have been described in the Basque coast associated with wave height (Borja et al., 2016). Extreme wind events and associated wave height caused mass-mortality events in seabirds such as the common guillemot *Uria aalge* (Louzao et al., 2019).

Gaps in the current monitoring and next steps

In the south-eastern Bay of Biscay, we identified three main gaps on climate change indicators: 1) lack of continuous (i.e., ≤ week) observations for chlorophyll concentration, vertical water column structure, and nutrients that determine phytoplankton spring blooms. Phytoplankton biomass, its physical drivers and the future scenarios are the most uncertain trends within the current monitoring of marine iCCs. Current ship-based observations provide reliable data in the Basque coastal shelf but limited by temporal resolution (monthly) and spatial scales. Remote sensing can fill the temporal gap but is limited covering only the sea surface and it is influenced by particulate and dissolved organic matter in the coast (Novoa et al., 2011). Autonomous platforms equipped with biogeochemical sensors would allow for the observation of marine biogeochemical processes and ecosystem dynamics, covering a wide range of spatial and temporal scales (Chai et al., 2020). 2) Lack of continuous deep measurements in the water column. Our continuous measurements reach depths of 100 m at the D2 station. There are additional measurements at the Donostia-San Sebastián buoy at discrete depths of 10, 20, 30, 50, 75, 100 and 200 m and additional measurements during surveys at specific periods of the year. However, continuous deep measurements at deeper levels, namely ENACW, Mediterranean water, are required in order to quantify trends at those levels. 3) lack of high-accuracy pH measurements to determine regional acidification; ocean acidification (i.e. decrease in pH), which is due to the direct effect of the increase in atmospheric CO_2 concentration (Doney et al., 2009) might have important impacts on marine fauna (Hendriks et al., 2010; Melzner et al., 2020), with a greater incidence on calcifying organisms such as shells of molluscs and animal skeletons (Kroeker et al., 2010), and calcareous macroalgae, which are very abundant in the area (Borja et al., 2004), and can produce significant changes in community structure (Sunday et al., 2017). Although there are some measurements at different locations in the Bay of Biscay (Tilbrook et al., 2019), in particular in the Galician upwelling system (Padin et al., 2020), there is no continuous monitoring with regular pH measurements, as far as we know.

GAMMs provided a suitable tool for analysing time series trends in the case of autocorrelated variables, with irregular sampling, and with complex and not previously known seasonal cycle. Moreover, GAMM has been proven a flexible method due to its capacity to adapt to the type of data and variable required including the analysis of phenological changes and time series measured at different locations. The current marine climate change monitoring in the Bay of Biscay needs further analysis to improve the understanding of the potential causes of the observed trends, including climate change, natural variability of the oceanic climate, anthropogenic causes (e.g., fishing, pollution, transformation of habitats). This requires specific analysis based on, for instance, statistical models to quantify the relationship between the processes and indicators measured. New methodological frameworks of attribution detection are useful to identify the causes of species phenological changes and distribution shifts (Chust et al., 2019; Erauskin-Extramiana et al., 2019b).

The integration of several observation programmes and the use of homogeneous and robust statistical and modelling tools have allowed us to detect 57 significant trends out of 87 analysed time series of physical, chemical and biological variables, including ~512,000 observations. The continuous surveillance of climate change in the Bay of Biscay, including the Basque coast, together with the generation and validation of regionalised projection models, can provide the basis for defining the adaptation criteria to be undertaken on the local societies and sectors such as coastal settlements, tourism, maritime transport, marine-based food chain, and fisherman.

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REFERENCES

Aldanondo N, Cotano U, Goikoetxea N, Boyra G, Ibaibarriaga L, Irigoien X. Interannual differences in growth and hatch-date distributions of early juvenile European anchovy in the Bay of Biscay: implications for recruitment. Fisheries Oceanography 2016; 25: 147-163.

Atkinson D. Temperature and Organism Size: A Biological Law for Ectotherms?: Academic Press, 1994.

Bachiller E, Fernandes JA. Zooplankton Image Analysis Manual: Automated identification by means of scanner and digital camera as imaging devices. Revista de Investigación Marina 2011; 18(2): 16-37.

Barnett LAK, Branch TA, Ranasinghe RA, Essington TE. Old-Growth Fishes Become Scarce under Fishing. Current Biology 2017; 27: 2843-2848.e2.

Behrenfeld MJ, O'Malley RT, Boss ES, Westberry TK, Graff JR, Halsey KH, et al. Revaluating ocean warming impacts on global phytoplankton. Nature Climate Change 2016; 6: 323-330.

Bindoff NL, Cheung WWL, Kairo JG, Arístegui J, Guinder VA, Hallberg R, et al. Changing Ocean, Marine Ecosystems, and Dependent Communities. In: IPCC Special Report on the Ocean and Cryosphere in a Changing Climate [H.-O. Pörtner, D.C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama, N.M. Weyer (eds.)]. In press. 2019.

Birkemeier WA. The effects of the 19 December 1977 coastal storm on beaches in North Carolina and New Jersey. shore beach 1979; 47: 7-15.

Borja A, Aguirrezabalaga F, Martínez J, Sola JC, García-Arberas L, Gorostiaga JM. Benthic communities, biogeography and resources management. Borja, A. and Collins, M. (Eds.). Oceanography and Marine Environment of the Basque Country, Elsevier Oceanography Series 2004; 70: 455-492.

Borja A, Amouroux D, Anschutz P, Gómez-Gesteira M, Uyarra MC, Valdés L. Chapter 5: The Bay of Biscay. Editor Charles Sheppard. World Seas: an environmental evaluation. Volume I: Europe, The Americas and West Africa. Second Edition, Academic Press, Elsevier, London: 113-152., 2019.

Borja Á, Chust G, Rodríguez JG, Bald J, Belzunce-Segarra MJ, Franco J, et al. 'The past is the future of the present': Learning from long-time series of marine monitoring. Science of The Total Environment 2016; 566–567: 698-711.

Borja Á, Elliott M. Marine monitoring during an economic crisis: The cure is worse than the disease. Marine Pollution Bulletin 2013; 68: 1-3.

Boyce DG, Dowd M, Lewis MR, Worm B. Estimating global chlorophyll changes over the past century. Progress in Oceanography 2014; 122: 163-173.

Boyra G, Martínez U, Cotano U, Santos M, Irigoien X, Uriarte A. Acoustic surveys for juvenile anchovy in the Bay of Biscay: abundance estimate as an indicator of the next year's recruitment and spatial distribution patterns. ICES Journal of Marine Science 2013; 70: 1354-1368.

Braun-Blanquet J. Pflanzensoziologie. Grundzüge der Vegetationskunde. Wien: 2nd. ed. Springer, 1951.

Brody SR, Lozier MS. Characterizing upper-ocean mixing and its effect on the spring phytoplankton bloom with in situ data. Ices Journal of Marine Science 2015; 72: 1961-1970.

Bruge A, Alvarez P, Fontán A, Cotano U, Chust G. Thermal Niche Tracking and Future Distribution of Atlantic Mackerel Spawning in response to Ocean Warming. Frontiers in Marine Science 2016; 3: 86.

Burnham KP, Anderson DR. Model selection and multi-model inference: A practical information-theoretic approach: Springer, 2002.

Burvingt O, Masselink G, Russell P, Scott T. Classification of beach response to extreme storms. Geomorphology 2017; 295: 722-737.

Caballero A, Pascual A, Dibarboure G, Espino M. Sea level and Eddy Kinetic Energy variability in the Bay of Biscay, inferred from satellite altimeter data. Journal of Marine Systems 2008; 72: 116-134.

Caill-Milly N, Morandeau G, Castège I, Sanchez F, Lissardy M, Chust G, et al. Les ressources exploitées par la pêche et la conchyliculture. In: Le Treut Hd, editor. AcclimaTerra. Anticiper les changements climatiques en Nouvelle-Aquitaine. Pour agir dans les territoires. 488 pp. Éditions Région Nouvelle-Aquitaine, France, 2018, pp. 201-222.

Caldwell PC, Merrifield MA, Thompson PR. Sea level measured by tide gauges from global oceans - the Joint Archive for Sea Level holdings (NCEI Accession 0019568), Version 5.5, NOAA National Centers for Environmental Information, Dataset, 2015.

Carls MG, Rice SD, Hose JE. Sensitivity of fish embryos to weathered crude oil: Part I. Low-level exposure during incubation causes malformations, genetic damage, and mortality in larval pacific herring (Clupea pallasi). Environmental Toxicology and Chemistry 1999; 18: 481-493.

Casado-Amezúa P, Araújo R, Bárbara I, Bermejo R, Borja Á, Díez I, et al. Distributional shifts of canopy-forming seaweeds from the Atlantic coast of Southern Europe. Biodiversity and Conservation 2019; 28: 1151-1172.

Castelle B, Bujan S, Ferreira S, Dodet G. Foredune morphological changes and beach recovery from the extreme 2013/2014 winter at a high-energy sandy coast. Marine Geology 2017; 385: 41-55.

Castelle B, Dodet G, Masselink G, Scott T. Increased winter-mean wave height, variability, and periodicity in the Northeast Atlantic over 1949–2017. Geophysical Research Letters 2018; 45: 3586-3596.

Corbella S, Stretch DD. Shoreline recovery from storms on the east coast of Southern Africa. Natural Hazards & Earth System Sciences 2012; 12.

Costoya X, deCastro M, Gómez-Gesteira M, Santos F. Mixed Layer Depth Trends in the Bay of Biscay over the Period 1975–2010. PloS one 2014; 9: e99321.

Costoya X, deCastro M, Gómez-Gesteira M, Santos F. Changes in sea surface temperature seasonality in the Bay of Biscay over the last decades (1982–2014). Journal of Marine Systems 2015; 150: 91-101.

Chai F, Johnson KS, Claustre H, Xing X, Wang Y, Boss E, et al. Monitoring ocean biogeochemistry with autonomous platforms. Nature Reviews Earth & Environment 2020; 1: 315-326.

Chust G, Borja Á, Caballero A, Irigoien X, Sáenz J, Moncho R, et al. Climate change impacts on coastal and pelagic environments in the southeastern Bay of Biscay. Climate Research 2011; 48: 307–332.

Chust G, Borja Á, Liria P, Galparsoro I, Marcos M, Caballero A, et al. Human impacts overwhelm the effects of sea-level rise on Basque coastal habitats (N Spain) between 1954 and 2004. Estuarine, Coastal and Shelf Science 2009; 84: 453-462.

Chust G, Goikoetxea N, Ibaibarriaga L, Sagarminaga Y, Arregui I, Fontán A, et al. Earlier migration and distribution changes of albacore in the Northeast Atlantic. Fisheries Oceanography 2019; 28: 505-516.

Chust G, Villarino E, Chenuil A, Irigoien X, Bizsel N, Bode A, et al. Dispersal similarly shapes both population genetics and community patterns in the marine realm. Scientific Reports 2016; 6: 28730.

Dangendorf S, Hay C, Calafat F, Marcos M, Piecuch C, Berk K, et al. Persistent acceleration in global sea-level rise since the 1960s. Nature Climate Change 2019; 9.

Dave AC, Lozier MS. Examining the global record of interannual variability in stratification and marine productivity in the low-latitude and mid-latitude ocean. Journal of Geophysical Research: Oceans 2013; 118: 3114-3127.

Davidson M, Van Koningsveld M, de Kruif A, Rawson J, Holman R, Lamberti A, et al. The CoastView project: Developing video-derived Coastal State Indicators in support of coastal zone management. Coastal Engineering 2007; 54: 463-475.

de Santiago I, Camus P, González M, Liria P, Epelde I, Chust G, et al. Impact of climate change on beach erosion in the Basque Coast (NE Spain). Coastal Engineering 2021; 167: 103916.

deCastro M, Gómez-Gesteira M, Alvarez I, Gesteira JLG. Present warming within the context of cooling-warming cycles observed since 1854 in the Bay of Biscay. Continental Shelf Research. 100 Years of Research within the Bay of Biscay - XI International Symposium on Oceanography of the Bay of Biscay 2009; 29: 1053-1059.

Devictor V, Julliard R, Couvet D, Jiguet F. Birds are tracking climate warming, but not fast enough. Proceedings of the Royal Society B: Biological Sciences 2008; 275: 2743-2748.

Dodet G, Bertin X, Taborda R. Wave climate variability in the North-East Atlantic Ocean over the last six decades. Ocean Modelling 2010; 31: 120-131.

Dodet G, Castelle B, Masselink G, Scott T, Davidson M, Floc'h F, et al. Beach recovery from extreme storm activity during the 2013–14 winter along the Atlantic coast of Europe. Earth Surface Processes and Landforms 2019; 44: 393-401.

Dominici F, McDermott A, Zeger SL, Samet JM. On the Use of Generalized Additive Models in Time-Series Studies of Air Pollution and Health. American Journal of Epidemiology 2002; 156: 193-203.

Doney SC, Fabry VJ, Feely RA, Kleypas JA. Ocean Acidification: The Other CO2 Problem. Annual Review of Marine Science 2009; 1: 169-192.

Doray M, Petitgas P, Huret M, Duhamel E, Romagnan JB, Authier M, et al. Monitoring small pelagic fish in the Bay of Biscay ecosystem, using indicators from an integrated survey. Progress in Oceanography 2018; 166: 168-188.

Drinkwater KF, Miles M, Medhaug I, Otterå OH, Kristiansen T, Sundby S, et al. The Atlantic Multidecadal Oscillation: Its manifestations and impacts with special emphasis on the Atlantic region north of 60°N. Journal of Marine Systems 2014; 133: 117-130.

EEA. Climate change, impacts and vulnerability in Europe 2016. An indicator-based report. EEA Report No 1, 2017, pp. 424.

EPA. Climate Change Indicators in the United States. Technical Documentation Overview. US Environmental Protection Agency. 15pp, 2016.

Erauskin-Extramiana M, Alvarez P, Arrizabalaga H, Ibaibarriaga L, Uriarte A, Cotano U, et al. Historical trends and future distribution of anchovy spawning in the Bay of Biscay. Deep Sea Research Part II: Topical Studies in Oceanography 2019a; 159: 169-182.

Erauskin-Extramiana M, Arrizabalaga H, Cabré A, Coelho R, Rosa D, Ibaibarriaga L, et al. Are shifts in species distribution triggered by climate change? A swordfish case study. Deep Sea Research Part II: Topical Studies in Oceanography 2019b: In Press - Available online 13 October 2019, 104666.

Escribano A, Aldanondo N, Cotano U, Boyra G, Urtizberea A. Size- and density-dependent overwinter mortality of anchovy juveniles in the Bay of Biscay. Continental Shelf Research 2019; 183: 28-37.

Fernandes JA, Irigoien X, Boyra G, Lozano JA, Inza I. Optimizing the number of classes in automated zooplankton classification. Journal of Plankton Research 2008; 31: 19-29.

Fontan A, Valencia V, Borja A, Goikoetxea N. Oceano-meteorological conditions and coupling in the southeastern Bay of Biscay, for the period 2001-2005: A comparison with the past two decades. Journal of Marine Systems 2008; 72: 167-177.

Frederikse T, Landerer F, Caron L, Adhikari S, Parkes D, Humphrey VW, et al. The causes of sea-level rise since 1900. Nature 2020; 584: 393-397.

Gardner JL, Peters A, Kearney MR, Joseph L, Heinsohn R. Declining body size: a third universal response to warming? Trends in Ecology & Evolution 2011; 26: 285-291.

Garmendia M, Revilla M, Zarauz L. Testing the usefulness of a simple automatic method for particles abundance and size determination to derive cost-effective biological indicators in large monitoring networks. Hydrobiologia 2013; 704: 231-252.

GCOS. Indicators of Climate Change. Outcome of a meeting. Technical Report, 206. WMO, Geneva, Switzerland, 3 February 2017. Available at https://library.wmo.int/opac/doc_num.php?explnum_id=3418, 2017.

Gimeno L, Trigo RM, Gómez-Gesteira M. Regional climate change in the NW Iberian Peninsula. Climate Research 2011; 48: 105-108.

Gissi E, Manea E, Mazaris AD, Fraschetti S, Almpanidou V, Bevilacqua S, et al. A review of the combined effects of climate change and other local human stressors on the marine environment. Science of the Total Environment 2021; 755: 142564.

Gohin F, Druon JN, Lampert L. A five channel chlorophyll concentration algorithm applied to SeaWiFS data processed by SeaDAS in coastal waters. International Journal of Remote Sensing 2002; 23: 1639-1661.

Goikoetxea N, Borja Á, Fontán A, González M, Valencia V. Trends and anomalies in sea-surface temperature, observed over the last 60 years, within the southeastern Bay of Biscay. Continental Shelf Research, 100 Years of Research within the Bay of Biscay - XI International Symposium on Oceanography of the Bay of Biscay 2009; 29: 1060-1069.

Gómez-Gesteira M, deCastro M, Santos F, Álvarez I, Costoya X. Changes in ENACW observed in the Bay of Biscay over the period 1975-2010. Continental Shelf Research 2013; 65C: 73-80.

González-Gil R, González Taboada F, Cáceres C, Largier JL, Anadón R. Winter-mixing preconditioning of the spring phytoplankton bloom in the Bay of Biscay. Limnology and Oceanography 2018; 63: 1264-1282.

González-Pola C, Lavín A, Díaz del Rio G, Cabanas JM, Ruiz-Villarreal M, Somavilla R, et al. Hidrografía y circulación. En: Cambio climático y oceanográfico en el Atlántico del norte de España. Inst. Español de Oceanografía. 69-98 pp. 2012.

González-Pola C, Lavín A, Vargas-Yáñez M. Intense warming and salinity modification of intermediate water masses in the southeastern corner of the Bay of Biscay for the period 1992–2003. Journal of Geophysical Research: Oceans 2005; 110.

González M, Fontán A. Filtros digitales para suprimir la variabilidad estacional y plurianual en series climáticas de datos. Revista de Investigación Marina, AZTI-Tecnalia 2013; 20: 71-76.

González M, Fontán A, Esnaola G, Collins M. Abrupt changes, multidecadal variability and long-term trends in sea surface temperature and sea level datasets within the southeastern Bay of Biscay. Journal of Marine Systems 2013; 109-110: S144-S152.

González M, Fontán A, Esnaola G, Valencia V. Variaciones multidecadales notables en la temperatura atmosférica, temperatura superficial y nivel del mar en el sudeste del golfo de Vizcaya, detectadas mediante filtros “Kolmogorov-Zurbenko”. RIM 2011; 17: 1-15.

González M, Mader J, Fontán A, Uriarte A, Ferrer L. Análisis de la tendencia de la temperatura superficial del agua del mar en Donostia-San Sebastián a partir del estudio de la serie del Aquarium (1946-2007). Revista de Investigación Marina 2008; 4: 7.

Harris V, Edwards M, Olhede SC. Multidecadal Atlantic climate variability and its impact on marine pelagic communities. Journal of Marine Systems 2014; 133: 55-69.

Hastie T, Tibshirani R. Generalized additive models, volume 43 of Monographs on Statistics and Applied Probability. London: Chapman & Hall, 1990.

Hemery G, D'Amico F, Castege I, Dupont B, D'Elbee J, Lalanne Y, et al. Detecting the impact of oceano-climatic changes on marine ecosystems using a multivariate index: The case of the Bay of Biscay (North Atlantic-European Ocean). Global Change Biology 2008; 14: 27-38.

Hendriks IE, Duarte CM, Álvarez M. Vulnerability of marine biodiversity to ocean acidification: A meta-analysis. Estuarine, Coastal and Shelf Science 2010; 86: 157-164.

Holt J, Icarus Allen J, Anderson TR, Brewin R, Butenschön M, Harle J, et al. Challenges in integrative approaches to modelling the marine ecosystems of the North Atlantic: Physics to fish and coasts to ocean. Progress in Oceanography 2014; 129, Part B: 285-313.

Houser C, Wernette P, Rentschlar E, Jones H, Hammond B, Trimble S. Post-storm beach and dune recovery: Implications for barrier island resilience. Geomorphology 2015; 234: 54-63.

Huss M, Lindmark M, Jacobson P, van Dorst RM, Gårdmark A. Experimental evidence of gradual size-dependent shifts in body size and growth of fish in response to warming. Global Change Biology 2019; 25: 2285-2295.

ICES. Report of the Working Group on Southern Horse Mackerel, Anchovy and Sardine (WGHANSA), 26-30 June 2018, Lisbon, Portugal. ICES CM 2018/ACOM:17, 2018, pp. 639

ICES. Working Group on Acoustic and Egg Surveys for Sardine and Anchovy in ICES areas 7, 8 and 9. ICES Scientific Reports. 2:44, 2020, pp. 490.

IPCC. Summary for Policymakers. In: IPCC Special Report on the Ocean and Cryosphere in a Changing Climate. H.-O. Pörtner, D.C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama, N.M. Weyer (eds.). In press., 2019.

Kebede AS, Nicholls RJ, Allan A, Arto I, Cazcarro I, Fernandes JA, et al. Applying the global RCP–SSP–SPA scenario framework at sub-national scale: A multi-scale and participatory scenario approach. Science of The Total Environment 2018; 635: 659-672.

Kroeker KJ, Kordas RL, Crim RN, Singh GG. Meta-analysis reveals negative yet variable effects of ocean acidification on marine organisms. Ecology Letters 2010; 13: 1419-1434.

Le Marchand M, Hattab T, Niquil N, Albouy C, Le Loc’ h F, Lasram FBR. Climate change in the Bay of Biscay: Changes in spatial biodiversity patterns could be driven by the arrivals of southern species. Marine Ecology Progress Series 2020; 647: 17-31.

Le Treut Hd. AcclimaTerra. Anticiper les changements climatiques en Nouvelle-Aquitaine. Pour agir dans les territoires. Éditions Région Nouvelle-Aquitaine, 2018.

Leorri E, Cearreta A. Recent sea-level changes in the southern Bay of Biscay: transfer function reconstructions from salt-marshes compared with instrumental data. Scientia Marina 2009; 73: 287-296.

Liria P, Chust G, Epelde I, Caballero A. Extreme Wave Flood-Risk Mapping Within the Basque Coast. Journal of Coastal Research 2011: 225-229.

Ljungström G, Claireaux M, Fiksen Ø, Jørgensen C. Body size adaptions under climate change: zooplankton community more important than temperature or food abundance in model of a zooplanktivorous fish. Marine Ecology Progress Series 2020; 636: 1-18.

Louzao M, Gallagher R, García-Barón I, Chust G, Intxausti I, Albisu J, et al. Threshold responses in bird mortality driven by extreme wind events. Ecological Indicators 2019; 99: 183-192.

Marcos M, Chust G, Jordà G, Caballero A. Effect of sea level extremes on the western Basque coast during the 21st century. Climate Research 2012; 51: 237-248.

Marcos M, Woepelmann G, Bosch W, Savcenko R. Decadal sea level trends in the Bay of Biscay from tide gauges, GPS and TOPEX. Journal of Marine Systems 2007; 68: 529-536.

Marigómez I, Soto M, Cancio I, Orbea A, Garmendia L, Cajaraville MP. Cell and tissue biomarkers in mussel, and histopathology in hake and anchovy from Bay of Biscay after the Prestige oil spill (Monitoring Campaign 2003). Marine Pollution Bulletin 2006; 53: 287-304.

McLean R, Shen J-S. From foreshore to foredune: foredune development over the last 30 years at Moruya Beach, New South Wales, Australia. Journal of Coastal Research 2006; 22: 28-36.

McLusky DS, Elliott M. The estuarine ecosystem: ecology, threats and management. Oxford University Press, New York 2004: 224.

Melzner F, Mark FC, Seibel BA, Tomanek L. Ocean Acidification and Coastal Marine Invertebrates: Tracking CO2 Effects from Seawater to the Cell. Annual Review of Marine Science 2020; 12: 499-523.

Meucci A, Young IR, Hemer M, Kirezci E, Ranasinghe R. Projected 21st century changes in extreme wind-wave events. Science Advances 2020; 6: eaaz7295.

Michel S, Vandermeirsch F, Lorance P. Evolution of upper layer temperature in the Bay of Biscay during the last 40 years. Aquatic Living Resources 2009; 22: 447-461.

Miloslavich P, Bax NJ, Simmons SE, Klein E, Appeltans W, Aburto-Oropeza O, et al. Essential ocean variables for global sustained observations of biodiversity and ecosystem changes. Global Change Biology 2018; 24: 2416-2433.

Montero-Serra I, Linares C, Doak DF, Ledoux JB, Garrabou J. Strong linkages between depth, longevity and demographic stability across marine sessile species. Proceedings of the Royal Society B: Biological Sciences 2018; 285.

Mudelsee M. Climate time series analysis. Classical statistical and bootstrap methods. 2nd ed. 10.1007/978-3-319-04450-7, 2010.

Mudelsee M. Trend analysis of climate time series: A review of methods. Earth-Science Reviews 2019; 190: 310-322.

Muñiz O, Rodríguez JG, Revilla M, Laza-Martínez A, Seoane S, Franco J. Inhomogeneity detection in phytoplankton time series using multivariate analyses. Oceanologia 2020; 62: 243-254.

Nerem RS, Beckley BD, Fasullo JT, Hamlington BD, Masters D, Mitchum GT. Climate-change–driven accelerated sea-level rise detected in the altimeter era. Proceedings of the National Academy of Sciences 2018; 115: 2022-2025.

Novoa S, Chust G, Valencia V, Froidefond J-M, Morichon D. Estimation of chlorophyll-a concentration in waters over the continental shelf of the Bay of Biscay: a comparison of remote sensing algorithms. International Journal of Remote Sensing 2011; 32: 8349-8371.

Opdal AF, Lindemann C, Aksnes DL. Centennial decline in North Sea water clarity causes strong delay in phytoplankton bloom timing. Global Change Biology 2019; 25: 3946-3953.

Oppenheimer M, Glavovic BC, Hinkel J, Wal Rvd, Magnan AK, Abd-Elgawad A, et al. Sea Level Rise and Implications for Low-Lying Islands, Coasts and Communities. In: IPCC Special Report on the Ocean and Cryosphere in a Changing Climate [H.-O. Pörtner, D.C. Roberts, V. Masson-Delmotte, P. Zhai, M. Tignor, E. Poloczanska, K. Mintenbeck, A. Alegría, M. Nicolai, A. Okem, J. Petzold, B. Rama, N.M. Weyer (eds.)]. In press., 2019.

Padin XA, Velo A, Pérez FF. ARIOS: a database for ocean acidification assessment in the Iberian upwelling system (1976–2018). Earth Syst. Sci. Data 2020; 12: 2647-2663.

Pauly D, Cheung WWL. Sound physiological knowledge and principles in modeling shrinking of fishes under climate change. Global Change Biology 2018; 24: e15-e26.

Pecl GT, Araújo MB, Bell JD, Blanchard J, Bonebrake TC, Chen I-C, et al. Biodiversity redistribution under climate change: Impacts on ecosystems and human well-being. Science 2017; 355: eaai9214.

Philippart C, Anadón R, Danovaro R, Dippner J, Drinkwater K, Hawkins S, et al. Impacts of climate change on European marine ecosystems: Observations, expectations and indicators. Journal of Experimental Marine Biology and Ecology - J EXP MAR BIOL ECOL 2011; 400: 52-69.

Phillips MS, Harley MD, Turner IL, Splinter KD, Cox RJ. Shoreline recovery on wave-dominated sandy coastlines: the role of sandbar morphodynamics and nearshore wave parameters. Marine Geology 2017; 385: 146-159.

Poloczanska ES, Burrows MT, Brown CJ, Garcia Molinos J, Halpern BS, Hoegh-Guldberg O, et al. Responses of marine organisms to climate change across oceans. Frontiers in Marine Science 2016; 3.

Pollard RT, Grifftths MJ, Cunningham SA, Read JF, Pérez FF, Ríos AF. Vivaldi 1991 - A study of the formation, circulation and ventilation of Eastern North Atlantic Central Water. Progress in Oceanography 1996; 37: 167-192.

Reguero BG, Losada IJ, Méndez FJ. A recent increase in global wave power as a consequence of oceanic warming. Nature Communications 2019; 10: 205.

Rose KA, Cowan Jr JH, Winemiller KO, Myers RA, Hilborn R. Compensatory density dependence in fish populations: importance, controversy, understanding and prognosis. Fish and Fisheries 2001; 2: 293-327.

Santos M, Uriarte A, Boyra G, Ibaibarriaga L. Anchovy DEPM surveys 2003-2012 in the Bay of Biscay (Subarea 8): BIOMAN survey series. In Massé, J., Uriarte, A., Angélico, M. M., and Carrera, P. (Eds.). Pelagic survey series for sardine and anchovy in ICES subareas 8 and 9 -Towards an ecosystem approach. ICES Cooperative Research Report No. 332. 268 pp., 2018.

Saraux C, Van Beveren E, Brosset P, Queiros Q, Bourdeix J-H, Dutto G, et al. Small pelagic fish dynamics: A review of mechanisms in the Gulf of Lions. Deep Sea Research Part II: Topical Studies in Oceanography 2019; 159: 52-61.

Simpson GL. Modelling Palaeoecological Time Series Using Generalised Additive Models. Frontiers in Ecology and Evolution 2018; 6.

Smayda TJ. What is a bloom? A commentary. Limnology and Oceanography 1997; 42: 1132-1136.

Somavilla Cabrillo R, González-Pola C, Ruiz-Villarreal M, Lavín Montero A. Mixed layer depth (MLD) variability in the southern Bay of Biscay. Deepening of winter MLDs concurrent with generalized upper water warming trends? Ocean Dynamics 2011; 61: 1215.

Somavilla R, González-Pola C, Rodriguez C, Josey SA, Sánchez RF, Lavín A. Large changes in the hydrographic structure of the Bay of Biscay after the extreme mixing of winter 2005. Journal of Geophysical Research: Oceans 2009; 114.

Stuart-Smith RD, Edgar GJ, Barrett NS, Kininmonth SJ, Bates AE. Thermal biases and vulnerability to warming in the world's marine fauna. Nature 2015; 528: 88-92.

Sunday JM, Fabricius KE, Kroeker KJ, Anderson KM, Brown NE, Barry JP, et al. Ocean acidification can mediate biodiversity shifts by changing biogenic habitat. Nature Climate Change 2017; 7: 81-85.

Thompson RORY. Low-Pass Filters to Suppress Inertial and Tidal Frequencies. Journal of Physical Oceanography 1983; 13: 1077-1083.

Tilbrook B, Jewett EB, DeGrandpre MD, Hernandez-Ayon JM, Feely RA, Gledhill DK, et al. An Enhanced Ocean Acidification Observing Network: From People to Technology to Data Synthesis and Information Exchange. Frontiers in Marine Science 2019; 6.

Toimil A, Losada IJ, Camus P, Díaz-Simal P. Managing coastal erosion under climate change at the regional scale. Coastal Engineering 2017; 128: 106-122.

Valencia V, Fontán A, Goikoetxea N, Chifflet M, González M, López A. Long-term evolution of the stratification, winter mixing and θ-S signature of upper water masses in the southeastern Bay of Biscay. Continental Shelf Research 2019; 181: 124-134.

Valencia V, Franco J. Main characteristics of the water masses. Borja, A. and Collins, M. (Eds.) Oceanography and Marine Environment of the Basque Country, Elsevier Oceanography Series 2004; 70: 197-232.

Valencia V, Franco J, Borja A, Fontán A. Hydrography of the southeastern Bay of Biscay. Borja, A. and Collins, M. (Eds.) Oceanography and Marine Environment of the Basque Country, Elsevier Oceanography Series 2004; 70: 159-194.

Valle M, Chust G, del Campo A, Wisz MS, Olsen SM, Garmendia JM, et al. Projecting future distribution of the seagrass *Zostera noltii* under global warming and sea level rise. Biological conservation 2014; 170: 74-85.

Van Beveren E, Bonhommeau S, Fromentin J-M, Bigot J-L, Bourdeix J-H, Brosset P, et al. Rapid changes in growth, condition, size and age of small pelagic fish in the Mediterranean. Marine Biology 2014; 161: 1809-1822.

van der Ham JL, de Mutsert K. Abundance and Size of Gulf Shrimp in Louisiana's Coastal Estuaries following the Deepwater Horizon Oil Spill. Plos One 2014; 9: e108884.

van der Linden P, Borja A, Rodríquez JG, Muxika I, Galparsoro I, Patrício J, et al. Spatial and temporal response of multiple trait-based indices to natural- and anthropogenic seafloor disturbance (effluents). Ecological Indicators 2016; 69: 617-628.

Van Rijn LC, Walstra DJR, Grasmeijer B, Sutherland J, Pan S, Sierra JP. The predictability of cross-shore bed evolution of sandy beaches at the time scale of storms and seasons using process-based profile models. Coastal Engineering 2003; 47: 295-327.

Véron M, Duhamel E, Bertignac M, Pawlowski L, Huret M. Major changes in sardine growth and body condition in the Bay of Biscay between 2003 and 2016: Temporal trends and drivers. Progress in Oceanography 2020; 182: 102274.

Wang P, Kirby JH, Haber JD, Horwitz MH, Knorr PO, Krock JR. Morphological and sedimentological impacts of Hurricane Ivan and immediate poststorm beach recovery along the northwestern Florida barrier-island coasts. Journal of Coastal Research 2006; 22: 1382-1402.

Webb TJ, Lines A, Howarth LM. Occupancy-derived thermal affinities reflect known physiological thermal limits of marine species. Ecology and Evolution 2020; n/a.

Wood SN. Generalized Additive Models: An Introduction with R: Chapman and Hall/CRC., 2006.

Woppelmann G, Pouvreau N, Simon B. Brest sea level record: a time series construction back to the early eighteenth century. Ocean Dynamics 2006; 56: 487-497.

Zanna L, Khatiwala S, Gregory JM, Ison J, Heimbach P. Global reconstruction of historical ocean heat storage and transport. Proceedings of the National Academy of Sciences 2019; 116: 1126-1131.

Zurbenko I, Porter PS, Gui R, Rao ST, Ku JY, Eskridge RE. Detecting Discontinuities in Time Series of Upper-Air Data: Development and Demonstration of an Adaptive Filter Technique. Journal of Climate 1996; 9: 3548-3560.

Zuur AF, Ieno EN, Walker NJ. Mixed effects models and extensions in ecology with R. New York: Springer Science, 2009.

TABLE LEGENDS

Table 1. Indicators of Climate Change (iCC) and time series analysis. CTI: Community Temperature Index. BoB: Bay of Biscay. LM: Linear Model. GAMM: Generalized Additive Mixed Model; MNES: Monitoring Network of the Ecological Status; St: station; Basque: Bq; Bilbao-V: Bilbao-Vizcaya. In all GAMMs, fixed effects are a linear term of the variable Year in decimals and a seasonal component of the variable day of the year (Day) fitted with a smoothing term (s, with a maximum of degrees of freedom of k=6), and imposing cyclicality (bs="cc"), whilst random effects (REff) are indicated in the corresponding time series.

Table 2. Time series trends in phytoplankton indicators (with and without logarithmic transformation). BoB: Bay of Biscay. LM: Linear Model. GAMM: Generalized Additive Mixed Model; MNES: Monitoring Network of the Ecological Status; St: station; Basque: Bq; Bilbao-V: Bilbao-Vizcaya. In all GAMMs, fixed effects are a linear term of the variable Year in decimals and a seasonal component of the variable day of the year (Day) fitted with a smoothing term (s, with a maximum of degrees of freedom of k=6), and imposing cyclicality (bs="cc"), whilst random effects (REff) are indicated in the corresponding time series.

FIGURES

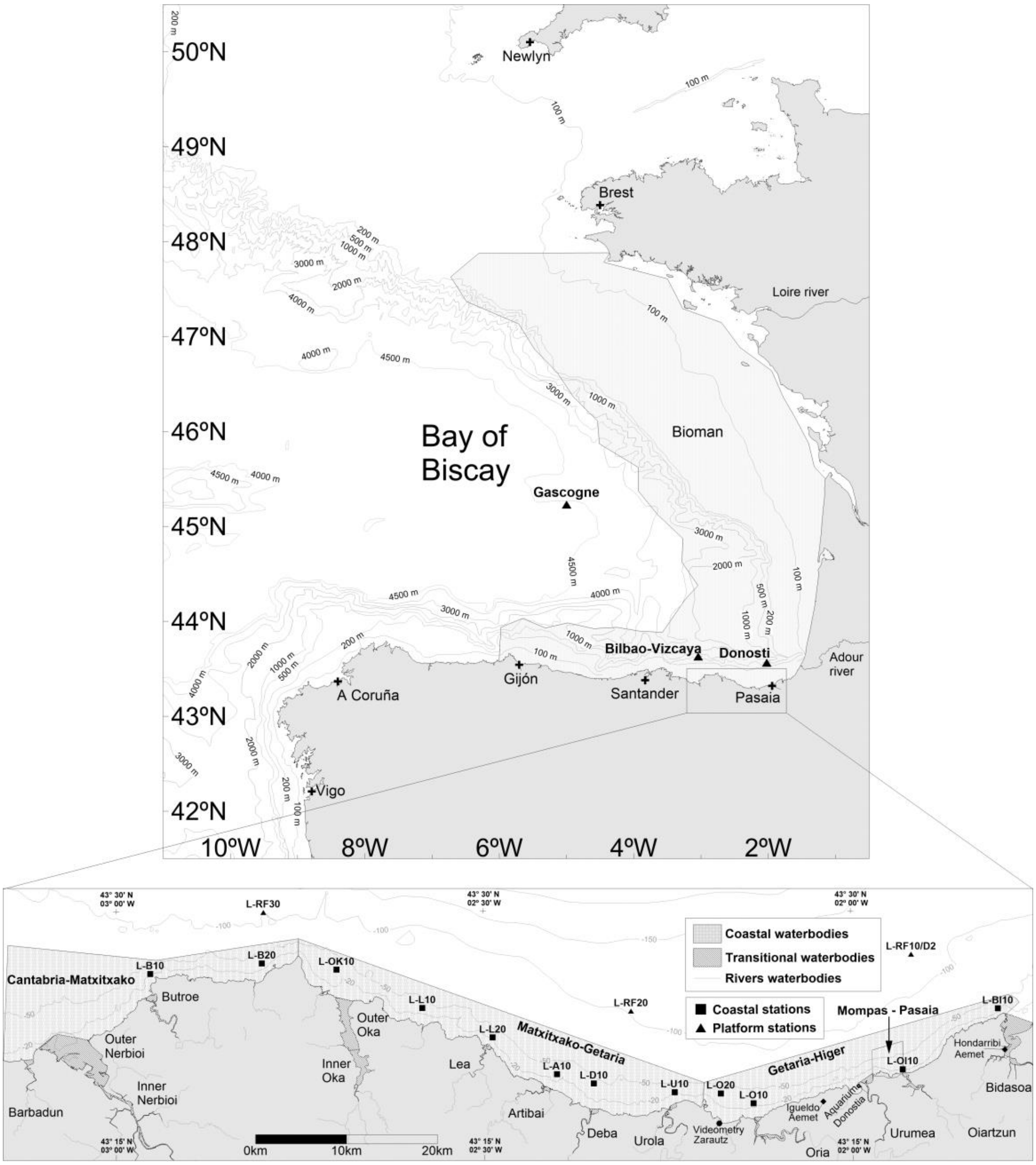

Fig. 1 Study area: The Bay of Biscay (above); and the Basque Country coast (below), with the locations of the monitoring programmes (see text), and main geographical features (isobaths and rivers).

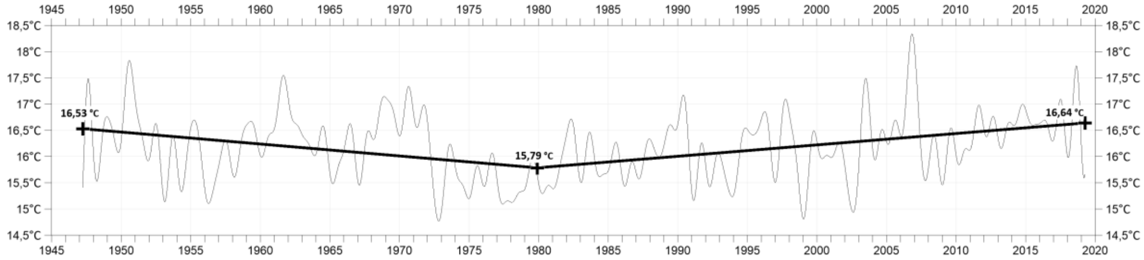

Fig. 2. Time series with low-pass filtered data (>1 year) of Sea Surface Temperature (SST) of the Donostia-San Sebastián Aquarium from 1946 to 2019.

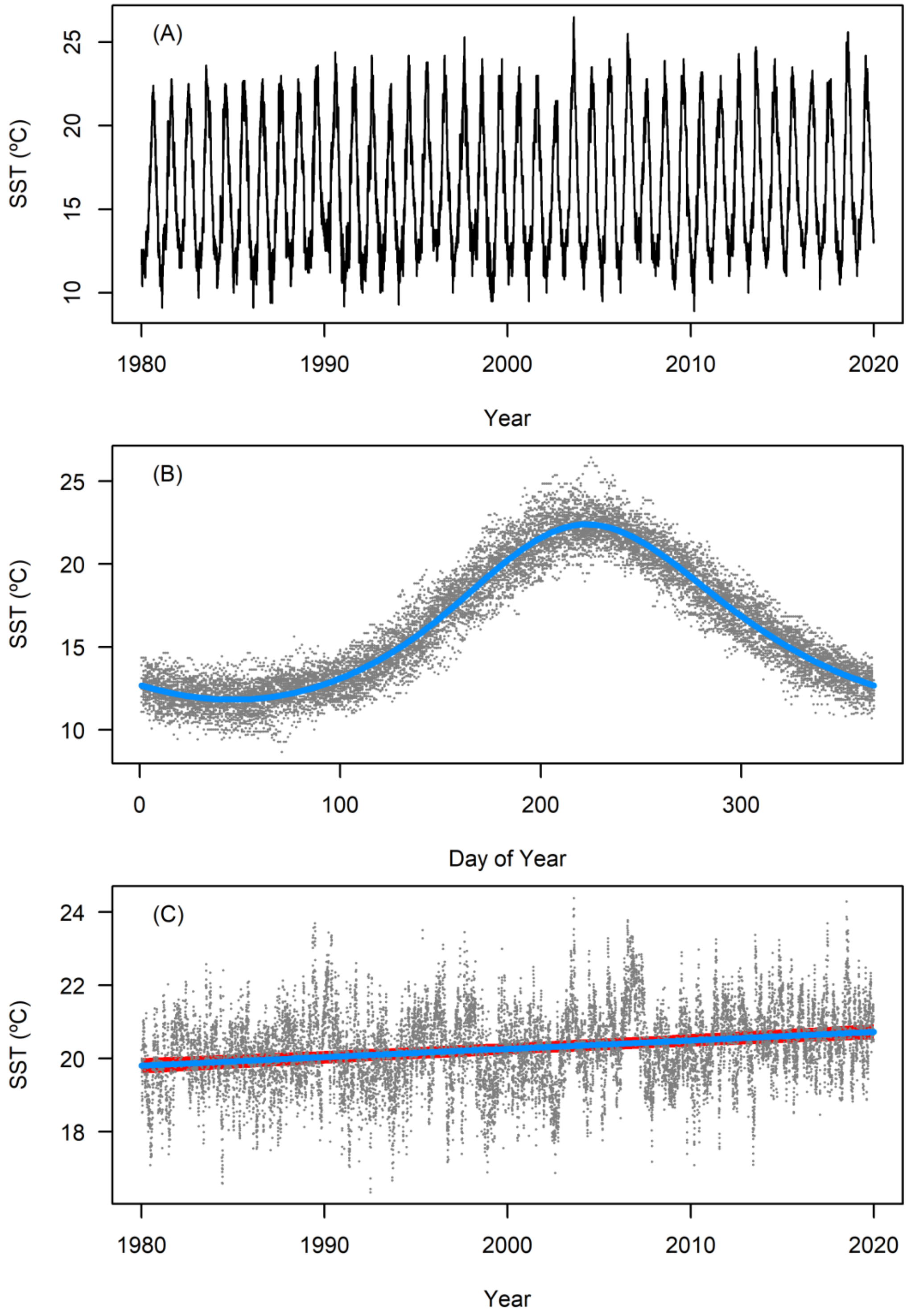

Fig. 3. Analysis of Sea Surface Temperature (SST) of the Donostia-San Sebastián Aquarium in the period 1980-2019 with GAMMs: decomposition into seasonal component and trend. A) Original data of the time series; B) Partial residuals throughout the year (points) and seasonal component of the model (blue line). C) Partial residuals of the time series after removing the seasonal component (i.e., deseasonalized, grey points) and the linear trend component of the model (blue line with red confidence interval). The partial residuals have been scaled up by adding the average SST of the whole series.

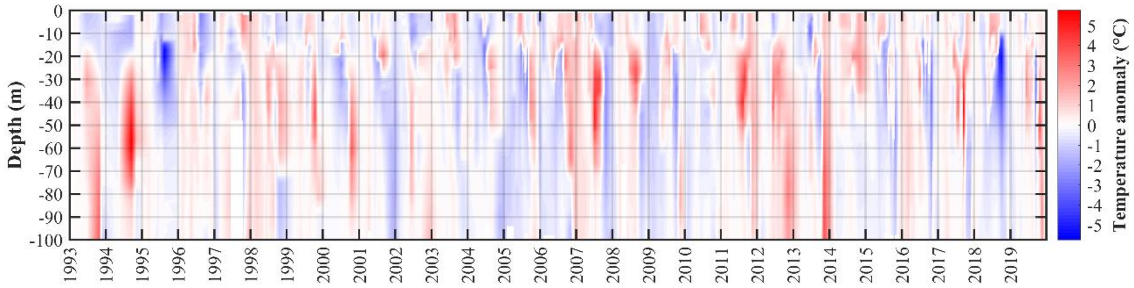

Fig. 4 Time-depth temperature anomalies for the hydrographic station D2 (1993-2019).

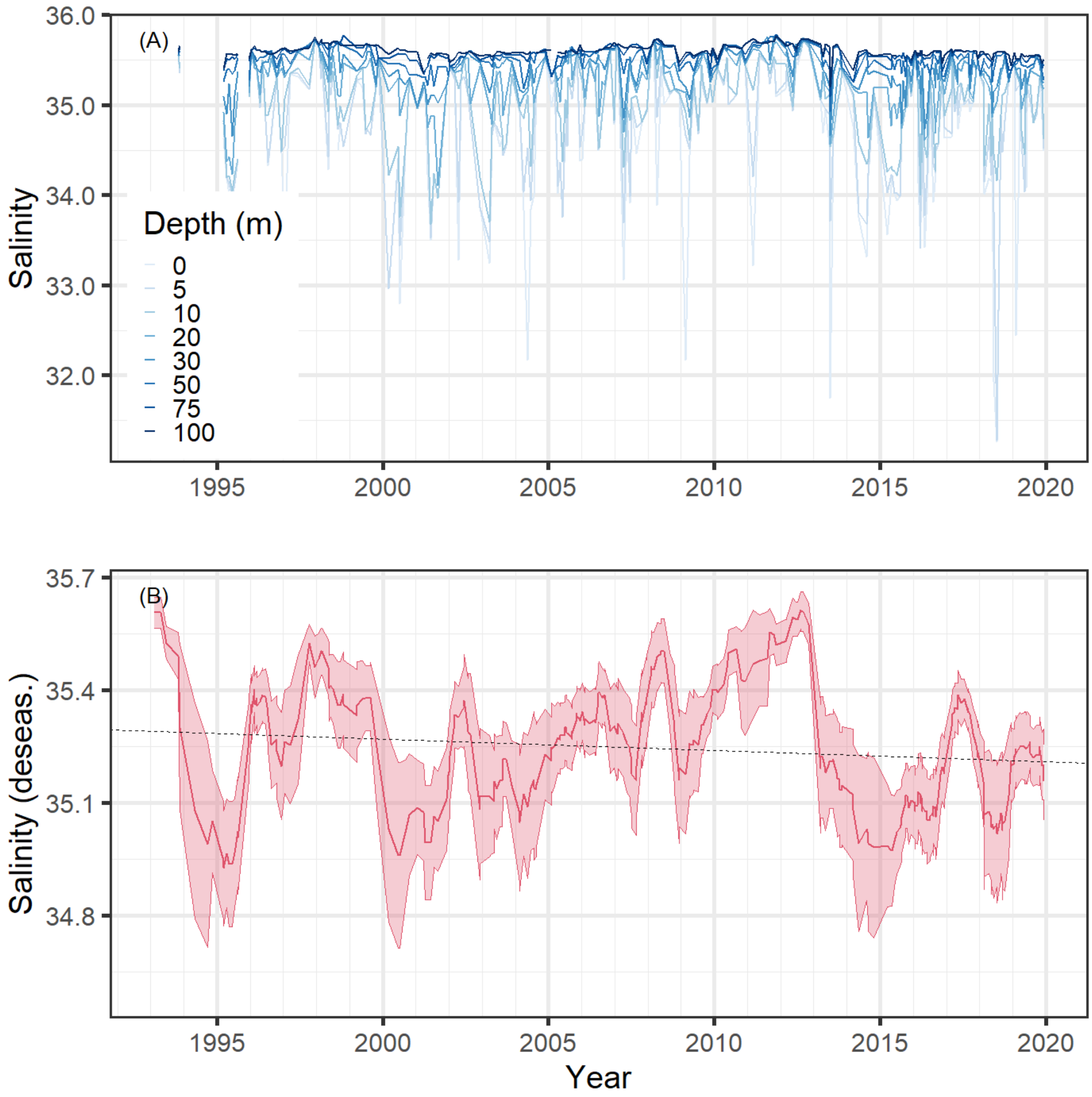

Fig. 5. Salinity at discrete depths (0, 5, 10, 25, 50, 75 and 100 m) at the D2 station. A) Original data at discrete depths; B) Annual moving average of partial residuals of the time series after removing the seasonal component (red line with its confidence interval in red shading) and the linear trend component of the model (dashed black line). The partial residuals have been scaled up by adding the average salinity of the whole series.

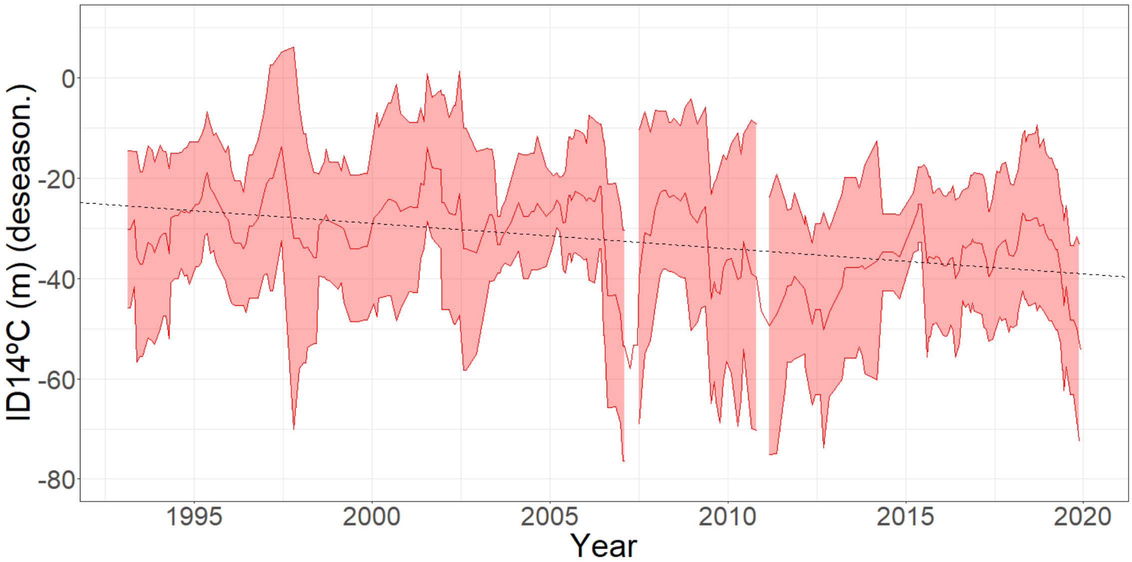

Fig. 6. Time series of the 14 °C Isotherm Depth (ID) (annual moving average of partial residuals for the linear trend component of the model in red line with its confidence interval in red shading) at station D2 in the period 1993-2019. The black dashed line represents the linear trend.

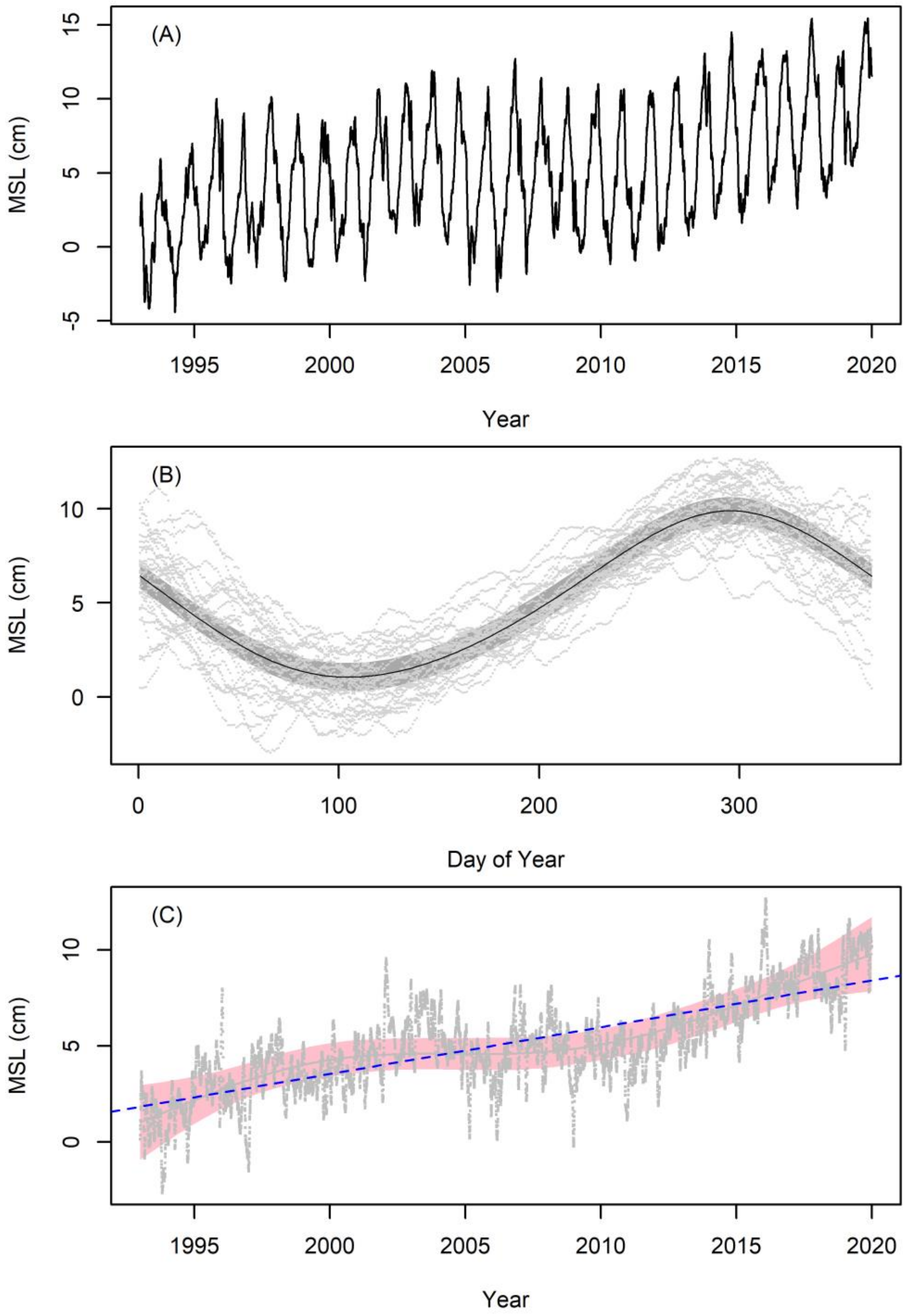

Fig. 7. Satellite-based mean sea level (MSL) in the Bay of Biscay from 1993 to 2019. A) Original data of the time series; B) Partial residuals throughout the year (grey points) and seasonal component of the model (black line with its confidence interval in grey shading). C) Partial residuals of the time series after removing the seasonal component (i.e. deseasonalised, grey points) and the linear trend component (blue dotted line), and non-linear time component (rose shade). The partial residuals have been scaled up by adding up the average of the MSL for the whole series.

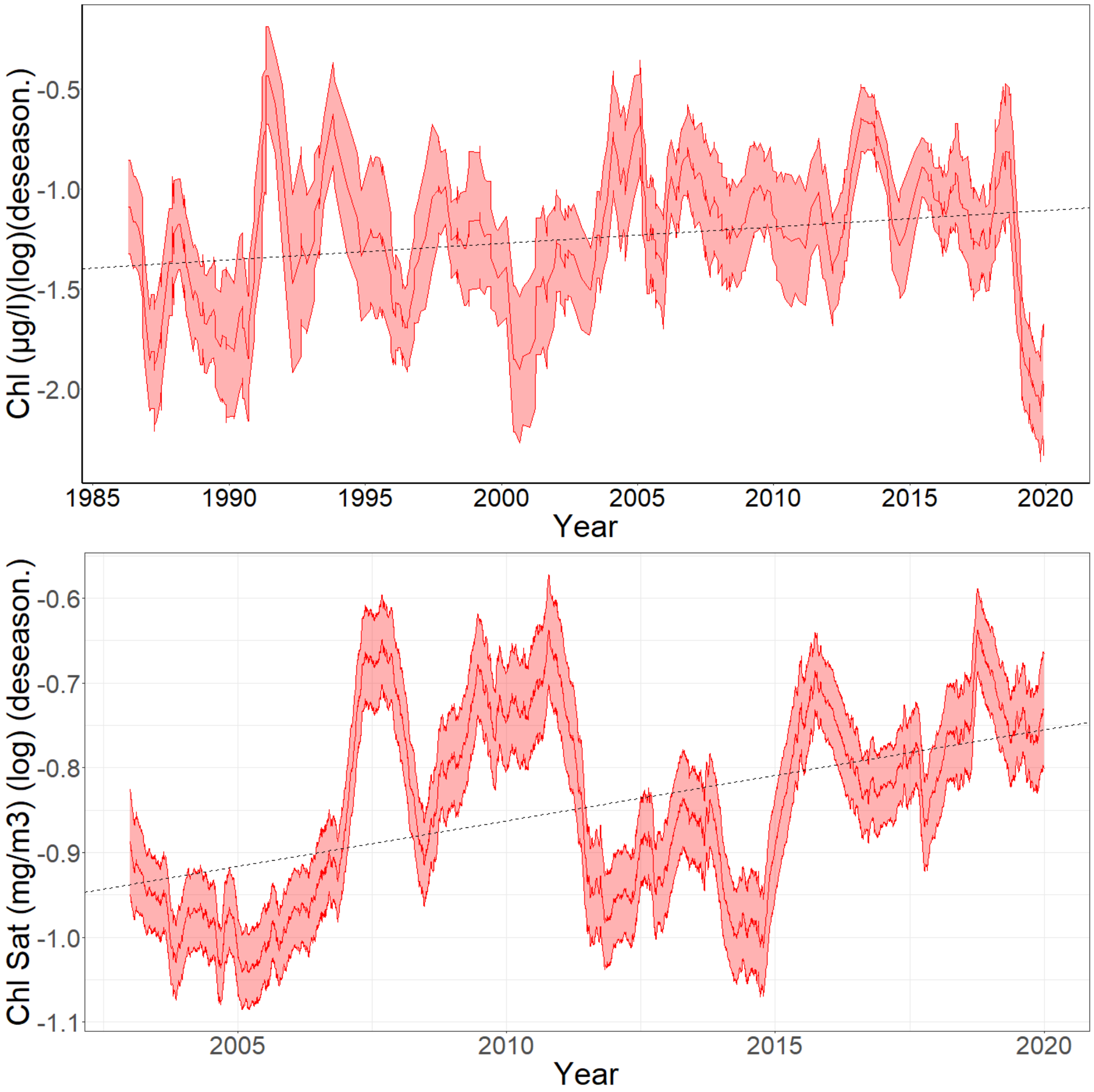

Fig. 8. Variation of the chlorophyll concentration and trend analysis in (A) the Basque coastal shelf (D2 station) for 1993-2019, and (B) over the Bay of Biscay (satellite data, at surface) for 2003-2019.

Fig. 9. Trends of Community Temperature Index on the Basque coastal shelf for phytoplankton, and intertidal soft- and hard-bottom benthic communities on the Basque coast. When significant, the relationship is fitted by a linear model (solid line), and smooth shadows with the 95% confidence level interval for predictions of a linear model. Soft-bottom benthos: slope=0.016, r^2=0.150, p-value=0.032; Hard-bottom benthos: slope=0.027, r^2=0.403, p-value=0.003.

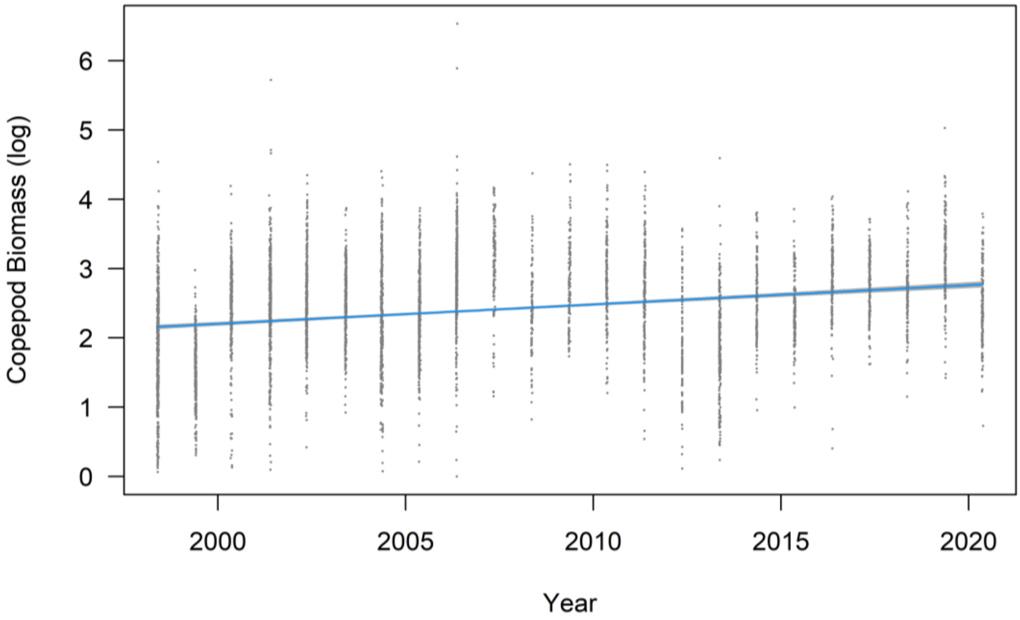

Fig. 10. Total spring copepod biomass from 1998 to 2019 for a fixed geographical and seasonally window (including the day of the year in the GAMM). Rate of change = 0.227 mg m^{-3} yr^{-1} ($p<0.0001$). Mean biomass = 13.55 mg m^{-3}. Partial residuals (grey points) of the time series for the linear trend component (blue line).

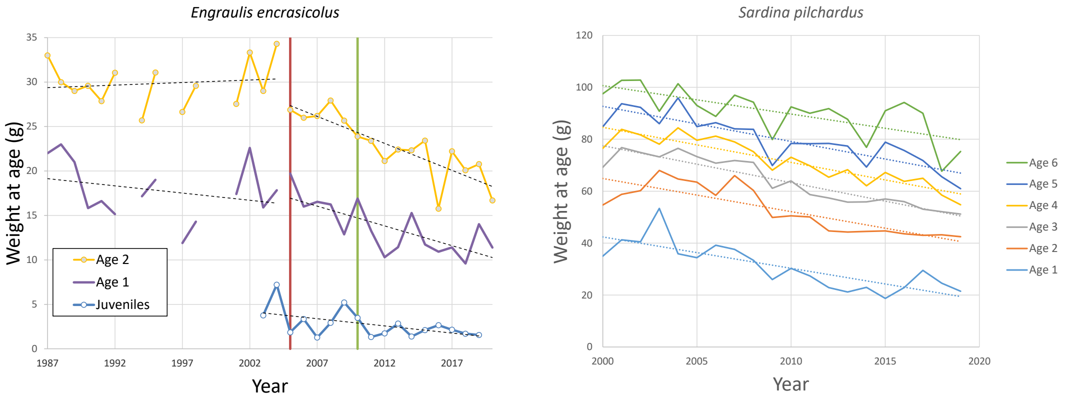

Fig. 11. Variability over time of the mean weight at age of the Bay of Biscay for anchovy and sardine. Anchovy data from Bioman – adults – and JUVENA – juveniles – surveys. Sardine data from PELGAS Survey of Ifremer, taken from: (Doray et al., 2018; ICES, 2020). For anchovy, the fishery was closed between 2005 and 2010 (vertical bars).