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Variability in biomass trends of European eel continental life stages and the influence of environmental and anthropogenic factors at a multi-country scale (France, Spain, Portugal)

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List of abbreviations

AIC Akaike Information Criterion
AR AutoRegression
ARIMA Auto Regressive Integrated Moving Average
CITES Convention of International Trade in Endangered Species
DFA Dynamic Factor Analysis
EA East Atlantic pattern
EDA Eel Density Analysis
EIFAAC European Inland Fisheries Aquaculture Advisory Commission
EMP Eel Management Plan
EMU Eel Management Unit
EU European Union
GAM Generalized Additive Models
GFCM General Fisheries Council of the Mediterranean
GLM Generalized Linear Model
ICES International Council for the Exploration of the Sea
IUCN International Union for Conservation of Nature
MA Moving Average
NAO North Atlantic Oscillation
WEPA West Europe Pressure Anomaly
WFD Water Framework Directive
WGEEL Working Group on EEL
WKEMP3 Technical evaluation of EU Member States' Eel Regulation Progress

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1. Introduction

Spatial correlations in environmental conditions can synchronize the dynamics of distant populations that are sensitive to the same factors, a phenomenon named Moran effect (Moran, 1953). Since global change deeply modifies environmental conditions at a very large scale, it might enhance these effects leading to the synchronization of dynamics in spatially distant populations, including (sub)populations of widely distributed or migratory species like the European eel (Hansen et al. 2020). Studying these synchronies can help identify the factors driving population dynamics, particularly to distinguish natural and anthropogenic influences.

The European eel*, Anguilla anguilla* (Linnaeus, 1758), is a catadromous species (Tesch et Thorpe 2003) belonging to the Anguillidae family (Dekker 2003). Its reproduction occurs in the Sargasso Sea (Fig 1), then larvae (leptocephali) drift for 7 to 24 months with warm oceanic currents (Bonhommeau et al. 2010; Miller et al. 2019). This larval drift ends when they reach the coasts of the Atlantic Ocean, Baltic or Mediterranean Seas (Fig 1) (Dekker 2003; ICES 2022a). Despite its large continental distribution, the European eel is panmictic and is, thereby, a single population and stock (Palm et al. 2009; Als et al. 2011).

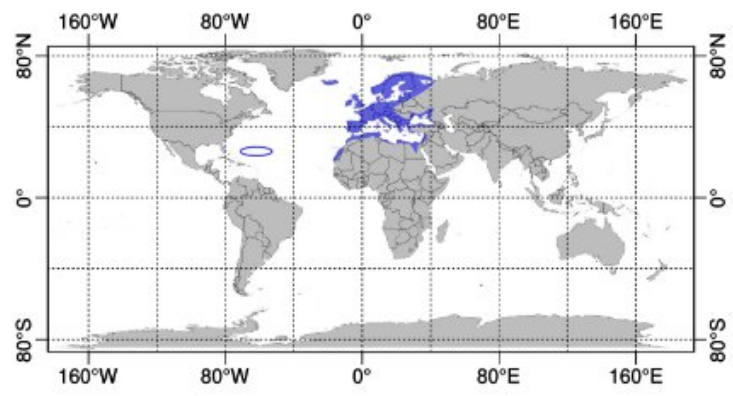

Figure 1: Continental distribution area (filled shape, Drouineau et al. 2018; modified) & Spawning ground (circle; Miller et al. 2015) of *Anguilla anguilla*

Leptocephali metamorphose into glass eels when they reach the continental shelf, after which they start an active migration towards continental waters, and settle in a wide range of habitats encompassing coastal, brackish and fresh waters from the north of Norway to the south of Morrocco (Tesch et Thorpe 2003; Jørgensen 2023). In these waters, glass eels grow; their pigmentation changes and they progressively become yellow eels (Tesch et Thorpe 2003) (Fig 2). Some eels never enter continental waters and grow in marine coastal waters (Arai et Chino 2012). A yellow eel can spend between 5 and 30 years in growth habitats before metamorphosing into a silver eel (Vollestad 1992; Durif et al. 2020; ICES 2022a). Silver eel corresponds to a prematured eel ready to start the 5,000 to 10,000 km long migration towards the Sargasso Sea (Béguer-Pon et al. 2015; Righton et al. 2016; Wright et al. 2022). The duration of the growth phase depends on the growth rate that is, among others, influenced by temperature food availability and quality and thus, latitude and habitat type (Sadler 1979; Tesch et Thorpe 2003; Durif et al. 2020; Jørgensen 2023). *Anguilla anguilla* is semelparous: the silver eels likely die after spawning (Wright et al. 2022; Jørgensen 2023).

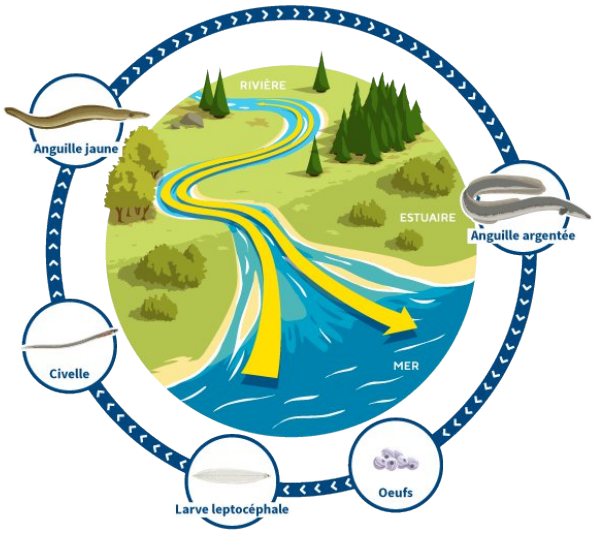

Figure 2: Life cycle of *Anguilla anguilla* (Agence française pour la biodiversité)

Because of its particular life cycle, *Anguilla anguilla* is sensitive to a wide range of environmental factors and anthropogenic pressures (Righton et al. 2016; Drouineau et al. 2018). First, climate change is inducing ocean modifications, which are believed to affect eel larvae drift and survival and therefore, recruitment. Among other, it leads to an increase of the sea temperature and a decrease of primary production on which the leptocephali depends to survive and grow (Knights 2003; Friedland et al. 2007; Bonhommeau et al. 2008a; Bonhommeau et al. 2008b). It also affects oceanic currents and thus, larvae transport (Knights 2003; Friedland et al. 2007). Moreover, climate change is suspected to affect the migration of silver eels. Indeed, changes in rainfalls affect the river discharge that triggers and accelerates the migration (Drouineau et al. 2017). Secondly, habitat fragmentation caused by physical barriers such as dams, can prevent glass eel and silver eels from migrating, reduce the amount of available habitats and cause moralities (Calles et al. 2010; Clavero et Hermoso 2015; Besson et al. 2016). Furthermore, the growing urbanization and modification of wetlands has led to a loss of growth-favourable habitats (Feunteun 2002). Eels face other threats in continental waters such as habitat degradation. Due to their type of reproduction, “capital breeding”, eels tend to accumulate contaminants as they grow which can subsequently impair the reproduction (Geeraerts et Belpaire 2010). Additionally, eels, in freshwater, are widely affected by an introduced swimbladder parasite, *Anguillicola crassus*, that is thought to impair migration success (Kirk 2003). Finally, *Anguilla anguilla* is targeted by recreational and professional fishing during all its life stages (Willem Dekker 2003; Righton et al. 2016). Moreover, the eel, especially glass eels, are victims of illegal fishing because of their market value (Stein et al. 2016; Alonso et Van Uhm 2023).

All those pressures have negatively impacted the abundance, survival and reproduction of the European eel through the years, resulting in the collapse of the population (Righton et al. 2021; Drouineau et al. 2018). Indeed, in 2023, the recruitment levels were around 90% less important compared to the levels observed between 1960 and 1979 (ICES 2024). For the yellow and silver eels, a decrease of abundance of at least 50% was observed for a period of 39 years (Pike et al., 2020). In light of this, the European eel was put on the Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) in 2007 which resulted in the ban of European eels import and export outside the European

Union (EU) (CITES 2022; ICES 2022b). Similarly, the International Union for Conservation of Nature (IUCN) put the European eel on the IUCN list of critically endangered species in 2008 (status unchanged since then - Freyhof et Kottelat 2008). Finally, the EU enforced the EU Council Regulation No 1100/2007, also called “Eel Regulation”, that stipulated that Member States should implement Eel Management Plans (EMPs) to: « reduce anthropogenic mortalities to permit with high probability the escapement to the sea of at least 40 % of the silver eel biomass relative to the best estimate of escapement that would have existed if no anthropogenic influences had impacted the stock. » (European Union, 2007). No short term mortality limit has been set, nor any deadline to achieve this objective. Within this framework, EMPs must include management measures following WGEEL advices to control the fishing landings and protect eels from any other threats. Most EMPs were effectively put in place around 2010.

In this context, France, Spain and Portugal have implemented national and/or regional EMPs in their Eel Management Units (EMUs) (Fig 3). In Spain, EMUs correspond to each of the 10 autonomous communities where eels can be observed (Gobierno de España 2010), with the EMU Minho that is managed jointly with Portugal (Estado Português 2010). In France, the division was based on the pre-existing 10 hydrographic basins defined for the management of migrating fish species (République Française 2010). Portugal is made up of a single Portuguese unit, and a transboundary EMU shared with Spain (Estado Português 2010). Theoretically, EMUs were created to be biologically and environmentally homogeneous areas so that the management measures would be efficient and consistent.

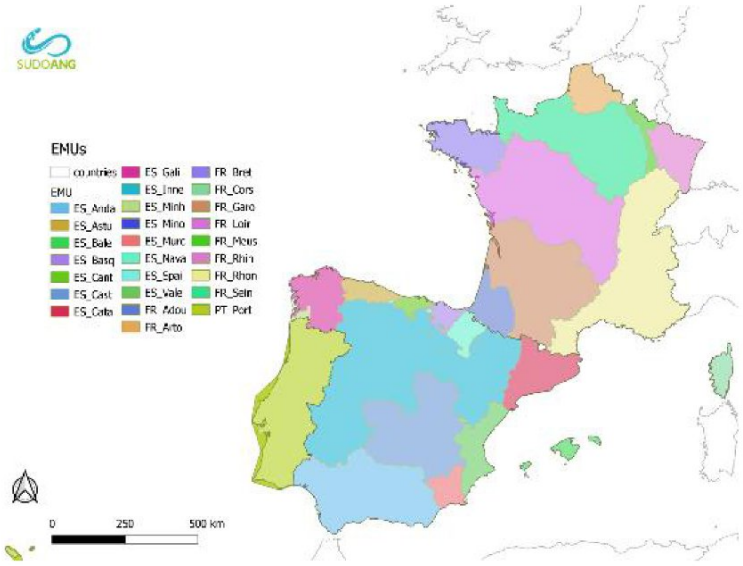

Figure 3: Eel Management Units (EMUs) for France, Spain and Portugal (Briand et al., 2022)

Species conservation measures vary among EMUs, especially fishery management. Fishery regulations can be daily and annual restrictions on the fishing period, on the number of ships/licenses, on the size, type and number of fishing gears and its meshes but also on the size of the eels. Glass eel quotas have also been enforced in France. Recreational fishing is forbidden or restricted in some areas. Some measures were also implemented to limit the impact of other threats. These include measures to restore the ecological continuity of the water stream, reduce turbine mortality and the impact of hydrological structures on migration. Secondly, efforts are made to restore and protect wetlands to counter the habitat loss caused by hydrological structures and urbanization. Finally, as part of the Water Framework Directive (WFD), work is being carried out to improve the biological and chemical water quality by

reducing contamination for example. Every three or four years, Member States have to report their progress in the implementation of their EMPs to the EU. According to the latest report of the ICES Workshop for the Technical evaluation of EU Member States' Eel Regulation Progress (WKEMP3), the escapement is far from the level asked by the European Regulation and is not increasing (ICES 2022b). Moreover, anthropogenic mortalities did not appear to have significantly declined (ICES 2022b). Therefore, the stock is still considered as depleted and the recovery will take a long time, especially considering the long life span of the European eel (Jørgensen 2023).

These results call for further efforts to mitigate anthropogenic mortalities. However, the large distribution area, the complexity of the European eel life cycle and the diversity of pressures affecting the population impair the scientific assessment of the status of the species and of its threats, and makes it still difficult for the policymakers to implement efficient and well-coordinated conservation measures. More specifically, disentangling the effects of environmental drivers from the effects of anthropogenic pressures on the global population dynamic would be required to improve the integrated understanding of the species at local, regional and international levels. During the continental phase, individuals face various environmental and anthropogenic pressures and are managed in different way across EMUs. Therefore, we wonder whether the biomass trends of the yellow and silver eel stages vary across Europe and over time despite the overall decline in recruitment. Moreover, considering the potential for spatial synchrony of population dynamics driven by similar environmental fluctuations (Moran effect) it is crucial to investigate whether we observe synchronisms between spatial units. In this context, the objective is to compare the silver and yellow eels biomass dynamics between different areas, assuming that close spatial units should display similar abundance trends since their environmental conditions must be similar (1). Then, the second objective is to provide a better understanding of the species during its continental phase by looking at the link between biomass and habitat variables (2).

First, we will present the model that has been used to estimate the biomass of yellow and silver eels across the entire study area. Then, we will explain the methods identified to compare biomass trends among regions and test the link between biomass and habitat variables (Material and Methods section). Next, we will explore whether biomass trends are homogeneous among spatial units and examine the correlations between environmental/anthropogenic variables and biomass (Results section). Finally, we will discuss the results in light of our current knowledge of the European eel ecology and its current management, while highlighting the limitations of our analysis (Discussion section).

2. Materials and Methods

2.1 The data

The Interreg SUDOANG project (2018-2021) aimed to standardize, compile and improve the spatial coverage and quality of eel data, and the stock assessment methods in France, Spain and Portugal (Briand et al., 2022). In these countries, as in the rest of Europe, methods and data used to monitor and manage the species used to be highly heterogeneous. Therefore, standardization seemed necessary in order to improve the knowledge on eels and foster cooperation to make management more efficient. In this context, the Eel Density Analysis (EDA) model was used to estimate time series of yellow and silver eel biomass in each river segment of the hydrographic network of the three countries. Basically, EDA is a species distribution model that allows to extrapolate local abundance observations of yellow

and silver eels to non-sampled river segments based on spatial and environmental co-variables affecting (Briand et al., 2022).

Data used during the training period correspond to EDA results of the SUDOANG project, Here, we briefly describe the model and assumptions. Fish data come from electrofishing surveys that provide local abundances, length, age, weight and silvering of the eels sampled at various stations. Then, two different generalized additive models (GAMs) are fitted to predict, respectively, the presence/absence of eels ("Delta model") and their density ("Gamma model") (Fig 4). The combination of these two models provides estimates of biomass, abundance and density for all river segments in the three countries. For the "Delta model", wetted area, altitude, distance from Gibraltar, hydraulic density, downstream drainage water surface, fishing method, cumulated height of dams are used as predictors. The "Gamma model" uses the same variables except for the distance to the sea that is used instead of the wetted area and the density downstream drainage water surface used instead of the downstream drainage water surface (Briand et al., 2022). In addition, a year effect with area specific smoothers was integrated to describe the temporal trends in abundance. In a first version, a trend per ecoregion was used (i.e., s(year, ecoregion)) while a trend per EMU was used in a second version (i.e., s(year, EMU)). Ecoregions (Atlantic France, Cantabria, Atlantic Iberia, English Channel, Mediterranean Sea, Rhin-Meuse) refer to the regions defined by Drouineau et al. (2021) as groups of EMUs displaying similar environmental conditions for glass eels. The two versions correspond to two different scales of analysis: the finer scale of EMUs and the larger scale of ecoregions (EMUs are nested within an ecoregion). While ecoregions were built to be consistent with environmental conditions, EMUs were assumed to be also consistent with the scale of management and anthropogenic pressures. However, for some EMUs, the lack of electrofishing data impaired a reliable estimate of the year effect. In view of this, we removed the years and EMUs for which there were less than 25 fishing operations creating some gaps in the time series, leaving 11 EMUs from 1985 to 2016. On the other hand, all ecoregions were fitted over the period 1985 to 2018.

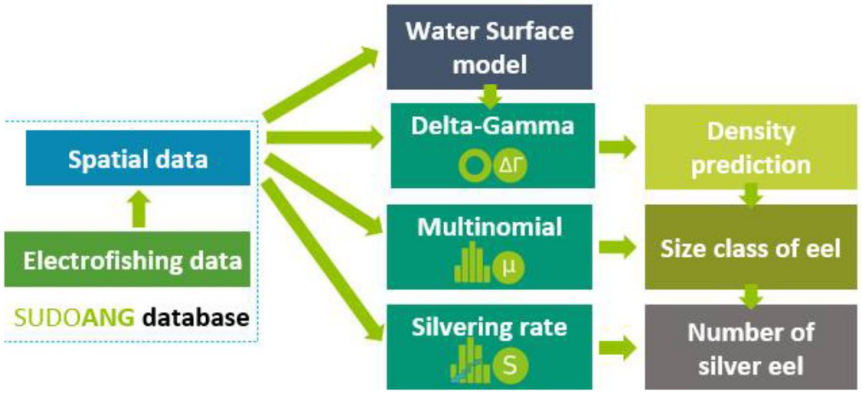

Figure 4: Modelling process of EDA (Briand et al., 2022)

2.2 Temporal trend analysis of yellow and silver eel biomass

A first objective was to explore whether the trends in biomass of yellow and silver eels are homogeneous among the different spatial units. Before the analysis, we formulated hypotheses on the evolution of yellow and silver eel biomasses based on the literature (tab 1). Specific statistical tests were then selected to validate these assumptions.

Table 1: Hypothesis for the temporal trends analysis of yellow and silver eel biomass

What we know	Hypotheses	
Depleted state of the stock and no sign of reconstitution (ICES, 2024)	Trends are, on average, decreasing over the whole time series and in all spatial units	H1
Yellow and silver eels time trends also depend on local environmental and anthropogenic factors (ICES 2022a)	Biomass trends vary among spatial unit at a given time step & depending on the year for a given spatial unit	H2
The correlation observed in the biomass trends of populations that are geographically separated is directly related to the correlation in the environmental noise they experience (Moran, 1953)	Close spatial units have similar biomass trends	H3
Continental environmental and anthropogenic factors affect the biomass of yellow and silver eels (Drouineau et al. 2018; Righton et al. 2016)	For all spatial units, recruitment does not fully explain biomass variations	H4

2.2.1 Is there a decrease in biomass in all spatial units ? Is the decrease homogeneous between the spatial units and trough time ? (H1 & H2)

To compare trends among regions, we carried out a **Dynamic Factor Analysis** (DFA). The DFA is a dimension-reduction technique used to extract common trends between several time series. It assumes that the set of time series can be summarized as a linear combination of M common trends (1) (Zuur et al. 2003):

$$y_{it} = z_{1t} * \alpha_{1t} + z_{2t} * \alpha_{2t} + \ldots. + z_{iM} * \alpha_{Mt} + \varepsilon_{it} \quad \text{with } \varepsilon_{it} \sim N(0, \sigma^2 V) \quad (1)$$

In the equation, y_{it} corresponds to the time series i at a given time t, α_{Mt} corresponds to the common trend M at a given time t, and ε_{it} are the residuals. z_{iM} represents the factor loadings, i.e. the weight of common trend M in series i. Therefore, the factor loading of a time series for a given common trend can be negative, indicating that the time series trend is the opposite of the common trend, while a positive factor would imply that the time series trend is similar to the common trend (Zuur et al. 2003).

Yellow and silver eel biomass time series were log-transformed before the analysis because we assumed that observations follow a log-normal distribution. Then, we carried out DFAs at the ecoregion (six ecoregions) and EMU scales (11 EMUs) using the corresponding versions of EDA.

In DFA, the number of common trends is set a priori, and the quality of fits with different trends is usually assessed using the Akaike Information Criterion (AIC). The AIC accounts for both the quality of the model fit and its number of parameters by penalizing overly complex ones (Buckland et al., 1997). However, it is important to notice that, in our case, the time series of biomass arised from GAMs, and as such, are already smoothed (it would be more correct to refer to pseudo-data, or pseudo-observations in our case). In this context observations are not independent and AIC can potentially overfit data and favour overly complex models with too many trends. Thus, we restricted DFA to two trends only for ecoregions (for 6 ecoregions) and three trends for EMUs (for 11 EMUs). We postulated a diagonal and equal covariance matrix for errors. With this method, we extracted common trends between our different time series thus summarizing the information of biomass trends and facilitating its analysis to, notably, see if there is a decrease in biomass in all spatial units. By comparing factor loadings among ecoregions or EMUs, we checked whether trends were similar.

The DFA allows to have a general overview of similarities among trends, but does not allow to detect differences in trends in specific years. To do so, we carried out a **double exponential smoothing**. The double exponential smoothing is a method based on the joint estimation of a local average value and local slope (Holt 1957). The local slope is denoted b_t (2 & 3) and can be seen as the slope of a local linear regression with the weights of point decreasing exponentially with time:

Level equation (Holt 1957): $l_t = \alpha * Biomass_t + (1-\alpha)*(l_{t-1} + b_{t-1})$ (2)

Trend equation (Holt 1957): $b_t = \beta*(l_t - l_{t-1}) + (1 - \beta)*b_{t-1}$ (3)

In the equation, l_t corresponds to the level (i.e. the average value), b_t represents the trend coefficients, α and β are smoothing parameters estimated to minimize the forecast error. Double exponential smoothing were carried out for each time series of silver eel biomass and yellow eel biomass, per ecoregion and then per EMU. The biomass time series tested will be, like the DFA, the log of yellow and silver eel biomass of six ecoregions and 11 EMUs. The analysis of the slope coefficients allowed to assess the evolution of the trend of the log of biomass through time and see if there is a decrease for most years. Moreover, their values can be quantitatively compared among spatial units at each time step making it easier to identify periods where the biomass trends are similar or different among them.

After estimating the annual trend coefficients per spatial unit, we wanted to compare their time series in their entirety so that spatial units with similar biomass trends during the studied time period might be grouped.

2.2.2 Are biomass trends similar between geographically close spatial units ? (H3)

A **clustering** aims at grouping data into separate similar sets, called clusters. The kmeans technique uses centroids around which data points are assigned according to their proximity with them (Euclidean distance). Then, the centroids are recalculated to be the mean of the points belonging to their cluster. This process is repeated until convergence (the clusters stay the same from one iteration to the next) (Lloyd 1982). We used this method on the local slopes (b_t) of the double exponential smoothing. This could not be done on the EMUs because there are only a few year for which we have data for all 11 of them.

The objective here is to detect patterns in the ecoregions that are grouped to get some clues about what could influence biomass variations. Are the grouped ecoregions geographically close or do they share similar anthropogenic pressures and/or environmental conditions ? Additionally, recruitment might explain part of the biomass trends and the differences or similarities observed among spatial units.

2.2.3 Does the recruitment fully explain silver and yellow eel biomass variations? (H4)

We explored the effect of recruitment variations on yellow and silver eel biomass. To do so, we used generalized linear models (Nelder et Wedderburn 1972).
We made the four following models :

$$\log(\text{silver eel biomass}_{t,i}) \sim \text{EMU} + \text{year} + \log(\text{glass eel biomass}_{t-6,i}) + \varepsilon$$
$$\log(\text{yellow eel biomass}_{t,i}) \sim \text{EMU} + \text{year} + \log(\text{glass eel biomass}_{t-1,i}) + \varepsilon$$

$$\log(\text{silver eel biomass}_{t,i}) \sim \text{ecoregion} + \text{year} + \log(\text{glass eel biomass}_{t-6,i}) + \varepsilon$$
$$\log(\text{yellow eel biomass}_{t,i}) \sim \text{ecoregion} + \text{year} + \log(\text{glass eel biomass}_{t-1,i}) + \varepsilon$$

In the equations, ε corresponds to the residuals with $\varepsilon \sim (0, \sigma^2 V)$*, t is the year and i the ecoregion*

.

Here, the variable eel biomass is quantitative and the variables year and EMU are qualitative. We chose to consider the year as a qualitative variable to better capture non-linear trends over time and avoid assuming that the effect of the year on biomass is linear. By observing the residuals per spatial area, we can identify the variability unexplained by the model and therefore, not explained by the recruitment. More specifically, it facilitates the identification of periods where the model overestimates or underestimates the biomass in specific EMUs or ecoregions and therefore, during which there might be other factors influencing the biomass variations.

After looking at the trends in yellow and silver eel biomasses over time and across the study area, we wondered what factors might influence these variations.

2.3 Analysis of correlations between environmental and anthropogenic variables and eel biomass

2.3.1 Environmental conditions

Temperature

As many fish species, the European eel growth is greatly affected by temperature, a key factor of metabolic reactions (Sadler 1979). Indirectly, temperature increases can also promote growth through a positive impact on the productivity of continental waters (Eppley, 1972) but have a negative impact on dissolved oxygen levels. Moreover, heatwaves can negatively impact species diversity and fish abundance (Cheung et al., 2021). Despite these challenges, eels may be more resilient to their impacts due to their non-monophagous diet and wide temperature tolerance (Tesch and Thorpe, 2003). In view of this, we postulated that temperature might affect eel biomass. Here, we collected annual average air temperature data over the period 1985-2018 and postulated that it was a good proxy of river temperature.

Rainfalls

Rainfalls are a direct driver of river flow and level. High discharges are supposed to favour eel migration (Drouineau et al. 2017), it might also create disturbances in eels' rest areas and hiding places. Moreover, important rainfalls are responsible for runoff that might contribute to an arrival of contaminants in the water but it can also help dilute them (Costa et al., 2021), while promoting water oxygenation (Liu et al., 2020). Knowing this, we assumed that rainfalls might be correlated to the biomass, in a positive or negative way. Rainfalls data correspond to the average of the sum of daily rainfall in millimeters, and are available from 1985 to 2018.

Atmospheric pressure

High atmospheric pressure is associated with stable weather conditions, low wind and few clouds. Conversely, low atmospheric pressure is associated with higher winds, clouds and rainfalls (Barry et al. 2010). It is necessary to test whether the atmospheric pressure is correlated to the biomass because it is an integrated weather indicator that influences several other meteorological parameters potentially linked to biomass (Stenseth et al. 2002). The data for this indicator correspond to the annual average atmospheric pressure in pascal, and are available from 1985 to 2018.

Temperature, rainfalls and atmospheric pressure data were extracted from the website https://www.ecad.eu. Values were averaged per year and ecoregions.

Atmospheric pressure anomalies

The North Atlantic Oscillation (NAO) is the difference in atmospheric pressure at sea level between the Azores and Iceland. Similarly, the East Atlantic pattern (EA) is the difference of atmospheric pressures at sea level but its anomaly centers are moved southeast to the approximate nodal lines of the NAO (Barnston and Livezey 1987). The West Europe Pressure Anomaly (WEPA) is also a difference in atmospheric pressure but between the Canary Islands and Ireland (Castelle et al. 2017). When those indicators are positive, we observe warmer and wetter winters in northern Europe, while drier conditions prevail in the south (Hanna et Cropper 2017). When they are negative, westerly winds and storm tracks move south, increasing rainfalls over southern Europe (Castelle et al. 2017). Therefore, considering the assumptions made previously regarding the temperature and rainfalls, we could assume observing differences in direction of the correlation between the ecoregions of the south and north.

Unlike the previous three variables, which vary by ecoregion, the NAO, EA, and WEPA indices operate on a larger scale. Consequently, their time series are consistent across all ecoregions. The NAO and EA indices was retrieved from the Climate Prediction Center (https://www.cpc.ncep.noaa.gov/). Indices were averaged by year from 1960 to 2022. Annual WEPA data were downloaded from 1960 to 2016 (no values beyond 2016) (Castelle et al., 2017). Contrary to the previous variables, the indices are at a large spatial scale and therefore the same for all ecoregions.

2.3.2 Anthropogenic pressures

Landings

Landings data are only available from 2009 to 2018 and correspond to the sum of both yellow and silver eels. Because landings represent a biomass harvest but also depend on the biomass available, we assumed that they were positively correlated to the eel biomass in the short term. However, in the long term we might see that landings and biomass are negatively correlated. The annual data of landings arise from the database of the ICES/EIFFAC/GFCM Working Group on Eels (WGEEL).

Proportion of area occupied by "degraded areas"

Habitat degradation is thought to be an important pressure affecting eels (Geeraerts et Belpaire 2010). We used data on land usage arising from Corine Land Cover (CLC) as a proxy of the overall anthropogenic pressure in river basins. Data on the proportion "degraded areas", as defined by Girardin et al. (2009), were computed for the years 1990, 2000, 2006, 2012 and 2018 (years for which CLC data are available) . A high proportion of degraded habitat is thought to indicate a direct destruction of available habitats. It can also have indirect negative effects. For example, eels tend to accumulate contaminants as they grow which can subsequently impair the reproduction and their survival (Geeraerts et Belpaire 2010). An increase of the proportion can indicate a loss of wetlands and morphological changes in riverbeds and estuaries, which can create disturbances for eels due to their thigmotactic behavior (Tesch and Thorpe, 2003). Therefore, we expect to see that the proportion of "degraded areas" is negatively correlated to the biomass.

We assessed the correlation between biomass and anthropogenic/environmental variables in the short and long terms. Before the analysis, data of biomass and landings were log-transformed and scaled. All the environmental variables and the proportion of area occupied by "degraded areas" were scaled as well.

2.3.3 Pretreatment of the data for short term correlation tests

In order to measure the correlation between biomass and habitat variables on the short term, it was necessary to remove the autocorrelation in the time series, since autocorrelation

might bias correlation tests. To do so, we used the prewhitening method which allows to extract the high frequency signal using Box and Jenkins method (1976). It consists in fitting an Auto Regressive Integrated Moving Average (ARIMA) model to the data; and to use the residuals of those models to carry out the correlation analysis. ARIMA combine autoregression (AR), differencing (I) and moving average (MA) components which collectively help to capture the underlying patterns in the time series data. It means that the model effectively accounts for the dependencies of current values and past ones, thereby ensuring that the residuals primarily represent random noise and are deprived of autocorrelation.

2.3.4 Pretreatment of the data for long term correlation tests

In order to test long term correlations, it was necessary to smooth the time series to remove high frequency variation and to extract low frequency signals. To that end, a moving average (MA) model was used with a window of 5 years for every time series (Pyper and Peterman 1998), except the time series of landings for which we used a window of 4 years because its time period is smaller (10 years). The model calculates the average value of the data over the window period, providing series that are less influenced by annual variability. However, smoothing the time series increases autocorrelation and to compensate it, we adjusted the degree of freedom. To do so, we used the equation suggested by Pyper and Peterman (1998):

$$\frac{1}{N^*} \approx \frac{1}{N} + \frac{2}{N}\sum_{j=1}^{\infty} r_{xx}(j) \times r_{yy}(j) \qquad (4)$$

In this equation, N is the initial sample size, N* is the new number of independent observations, X and Y are the time series of biomass (X) and environmental and anthropogenic data (Y), r $r_{xx}\ (j)\ and\ r_{yy}(j)$ are the autocorrelation of the time series at the lag j. The autocorrelation is calculated as follows using the equation of Box-Jenkins (Box and Jenkins, 1976) modified by Chatfield (1989):

$$r_{xx}(j) = \frac{\sum_{t=1}^{N-j}(X_t - \overline{X})(X_{t+j} - \overline{X})}{\sum_{t=1}^{N}(X_t - \overline{X})^2} \qquad (5)$$

With $\overline{X}$, the biomass mean. For our analysis, we set the maximum lag to be one-fifth of the length of the time series as recommended by Pyper and Peterman (1998). It is important to note that the long term correlation was not done for the proportion of area occupied by "degraded areas" because the time series is not complete.

2.3.5 Correlation tests

After the pretreatment of the data, we used the correlation test of Pearson to determine short and long term correlations between biomass and environmental/anthropogenic variables (Bonhommeau, 2008). The Pearson coefficients obtained from the test measure the strength and direction of the linear relationship between two variables. A Pearson coefficient of 1 indicates a perfect positive linear relationship, 0 indicates no linear relationship and -1 indicates perfect negative linear relationship. In addition, we also carried out the non parametric correlation test of Spearman which evaluates the strength and direction of the association between two variables, releasing the linearity assumption. A Spearman correlation coefficient,

denoted ρ (rho), of 1 indicates a perfect positive correlation, 0 indicates no correlation and -1 indicates a perfect negative correlation.

3. Results

3.1 Temporal trend analysis of yellow and silver eel biomass

The visual inspection of the different time series of biomass per ecoregion confirm the overall decline in abundance. However, it suggests some slight variations depending on ecoregions and stages (Fig 5). The most important biomass is found in the ecoregions Iberian Coast and Mediterranean Sea for both stages. However, for the ecoregion North Sea the biomass is very low.

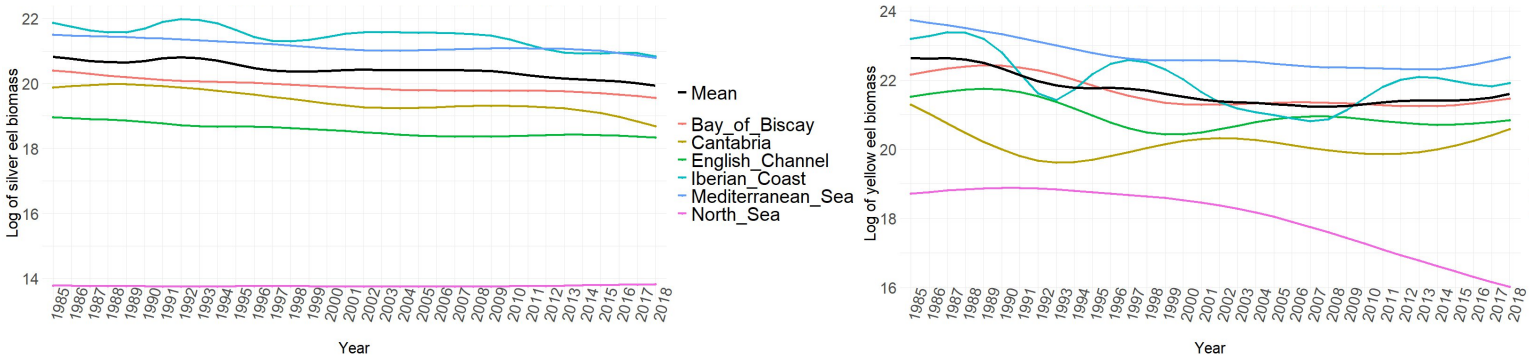

Figure 5: Temporal evolution of the log of biomass (left: silver eels / right: yellow eels) depending on the ecoregion

3.1.1 Is there a decrease in biomass in all spatial units ? (H1) Is the decrease homogeneous among spatial units and across years ? (H2) Are biomass trends similar between geographically close spatial units ? (H3)

As mentioned earlier, we fitted the DFA with two (ecoregions) or three (EMUs) common trends as a maximum. Finally, for both spatial scales, the model with two trends was kept since we saw that no EMU was significantly correlated to the third trend when added.

Yellow eels

The first common trend at the ecoregion scale is predominantly upward. The second one shows a downward pattern, turning upward after 2008 (Fig 6). We can see a first group of ecoregions (Mediterranean, Iberian Coast, English Channel and Bay of Biscay) negatively correlated to trend 1 and positively to trend 2, indicating an overall decline over the period and a roughly stable biomass in recent years. Cantabria is only positively correlated to trend 2, suggesting that the strong decrease tends to stop after 1990. North Sea is negatively correlated to both trends, suggesting an overall decline over the period (Fig 7). This indicates slight differences among EMUs despite the overall decline.

At the EMU scale, factor loadings are all negative for the first trend and slightly correlated to the second one, except for Meuse and Adour (Fig 8 & 9). Therefore, the trend of the other 9 EMUs corresponds to a strong decrease from 1985 to 2001, then an increase of biomass until 2007 and a decrease afterwards. The EMU Adour is strongly negatively correlated to trend 2 and sligthly to trend 1 indicating that the yellow eel biomass there increased until 1995, decreased until 2007 and is increasing since then. Conversely, the EMU

Meuse, strongly positively correlated with trend 2 and slightly with trend 1, exhibits the opposite trend to the EMU Adour.

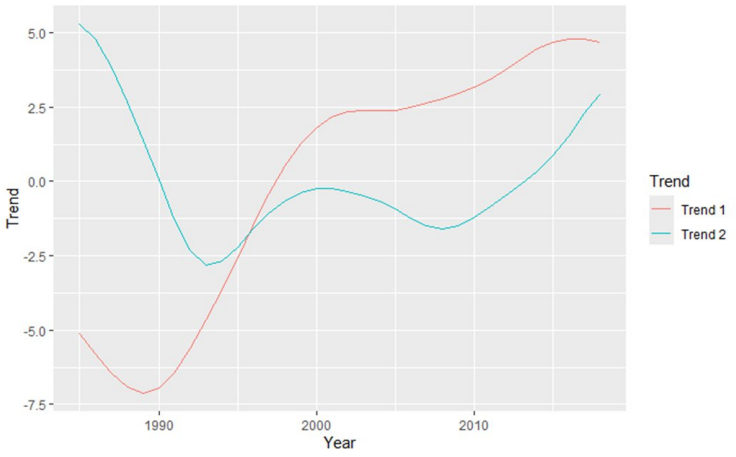

Figure 6: Common trends for the log of yellow eels biomass at the ecoregion scale obtained by the DFA model

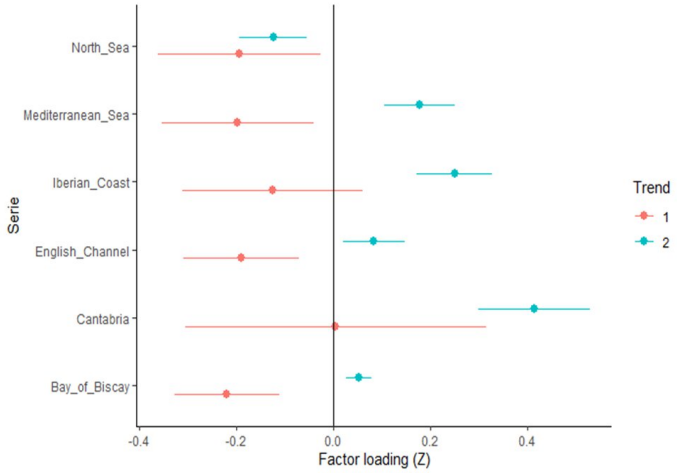

Figure 7: Factor loadings for the log of yellow eels biomass at the ecoregion scale obtained by the DFA model

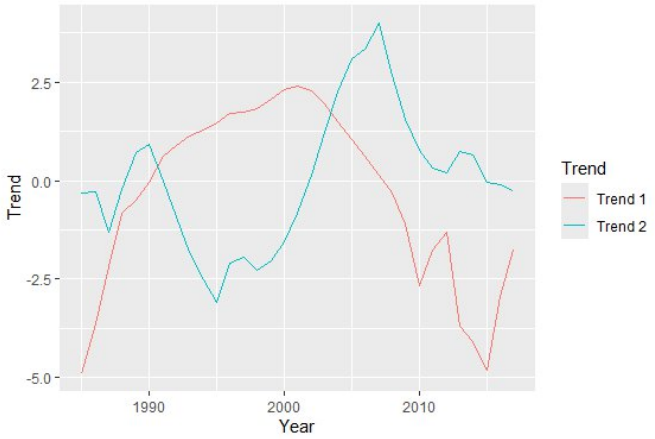

Figure 8: Common trends for the log of yellow eels biomass at the EMU scale obtained by the DFA model

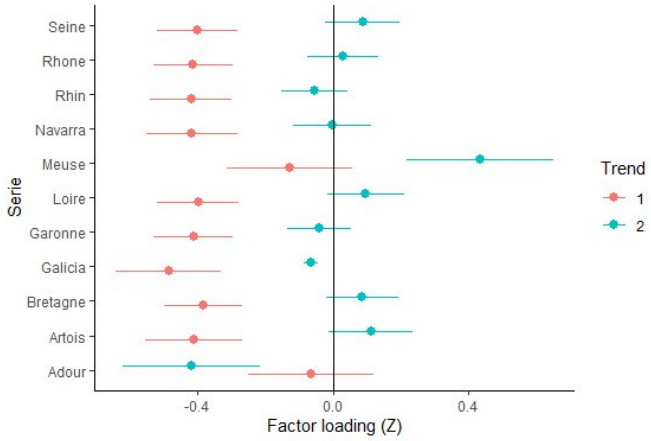

Figure 9: Factor loadings for the log of yellow eels biomass at the EMU scale obtained by the DFA model

Silver eels

The first common trend for silver eels at the ecoregion scale is predominantly upwards. The second one shows an alternating increase and decrease of biomass until 2005, and an increase afterwards (Fig 10). A first group (Mediterranean, Cantabria, English Channel and Bay of Biscay) is negatively correlated to trend 1 and positively to trend 2. Therefore, the trend of these four ecoregions correspond to a sharp decline for most years especially the last ones. The Iberian coast shows a weaker decline in the early years compared to other ecoregions, being negatively correlated to trends 1 and 2. Similarly, the North Sea, with positive factor loadings for both trends, has a weaker decline in the first years but also an increase in the later years (Fig 11).

At the EMU scale, the first trend shows a strong decrease of biomass until 2002, then a strong increase until 2015 and a decrease afterwards. The second trend shows an increase of biomass until 1995, a decrease until 2007 and an increase afterwards (Fig 12). When observing the factor loadings, two groups can be identified. The first one (Seine, Rhône, Loire,

Bretagne and Artois) is negatively correlated to both trends, corresponding to a strong decrease of biomass for most years except between 2004 and 2014. The second group (Rhin, Garonne, Navarra and Galicia) is negatively correlated to trend 1 and not correlated to trend 2, suggesting a strong decrease of biomass for most years except between 2002 and 2015. The EMU Adour is positively correlated to trend 2 and not to the other while the EMU Meuse is strongly negatively correlated to the second trend and slightly negatively correlated to the other (Fig 13). This suggests that the difference between these EMUs seems to be similar between the two stages.

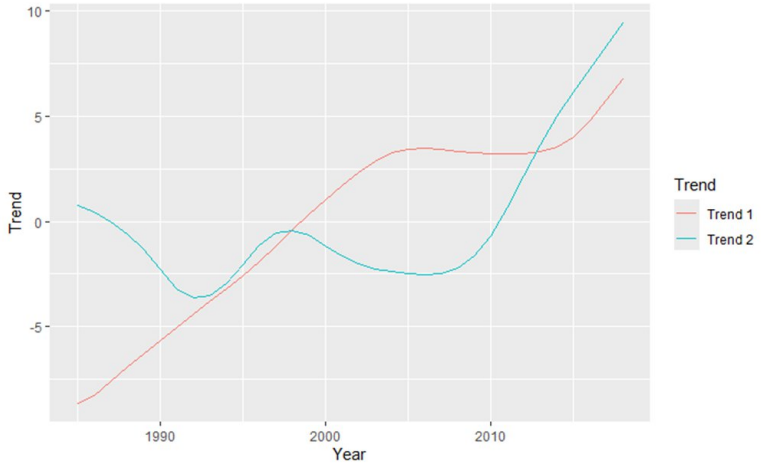

Figure 10: Common trends for the log of silver eels biomass at the ecoregion scale obtained by the DFA model

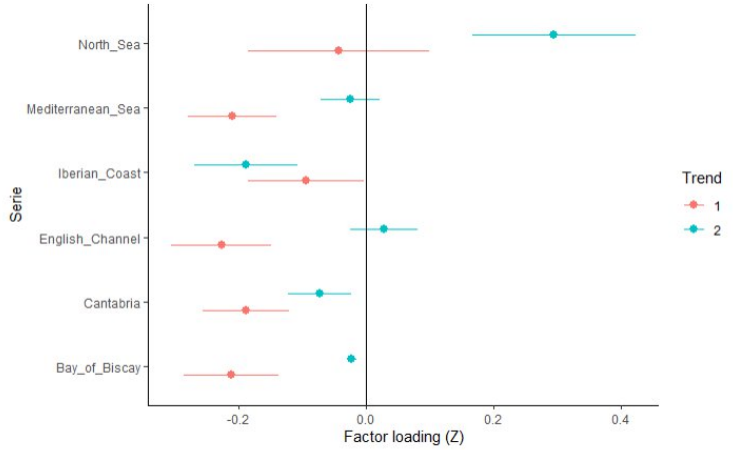

Figure 11: Factor loadings for the log of silver eels biomass at the ecoregion scale obtained by the DFA model

Figure 12: Common trends for the log of silver eels biomass at the EMU scale obtained by the DFA model

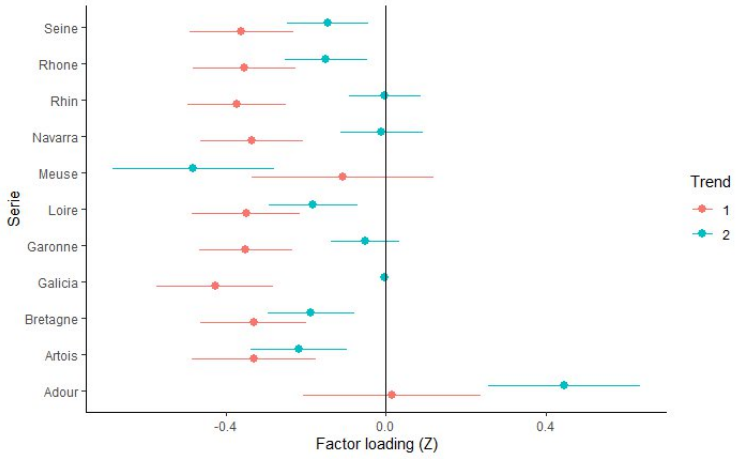

Figure 13: Factor loadings for the log of silver eels biomass at the EMU scale obtained by the DFA model

At both scales and for both stages, we observe local trend variations or atypical spatial units for which the importance of the decline and its duration is slightly different from the others (e.g., North Sea, Adour and Meuse for both stages, Cantabria for yellow eels and Iberian coast for silver eels for the ecoregion scale). Additionally, groups were highlighted by the analysis:

- at the ecoregion scale: Mediterranean, English Channel and Bay of Biscay had very similar trends for both stages
- at the EMU scale: Seine, Rhône, Loire, Bretagne, Artois, Rhin, Garonne, Navarra and Galicia for both stages

To identify more precisely periods of heterogeneities in trends among spatial units, we analyse the local slopes (b_t) arising from the double exponential smoothing. For yellow eels, the Bay of Biscay and English Channel show similar annual biomass variation (local slopes) which appears to be in opposition to the Cantabria in terms of direction (Fig 14). Compared to these three ecoregions, the Mediterranean Sea exhibits lower variations overall, except for the last three years. However, the direction of the biomass trend of this ecoregion is similar to Cantabria's until 1993 and from 2003 to 2008. The North Sea is particularly distinct from 2000 onwards, with a significant downward trend. Similar to silver eels, the Iberian Coast almost consistently differs from all other regions in both the importance and direction of biomass variations.

For silver eels, the local slope values for Cantabria, the Mediterranean Sea, Bay of Biscay, English Channel, and North Sea similar and very low (Fig 14). However, during the first 10 years, the Mediterranean Sea, Bay of Biscay, and English Channel exhibit significant negative slopes, while Cantabria shows significant positive slopes for the first 5 years. The Iberian Coast remains distinct from these spatial units when looking at the importance and direction of biomass variations, with occasional brief alignments with other ecoregions.

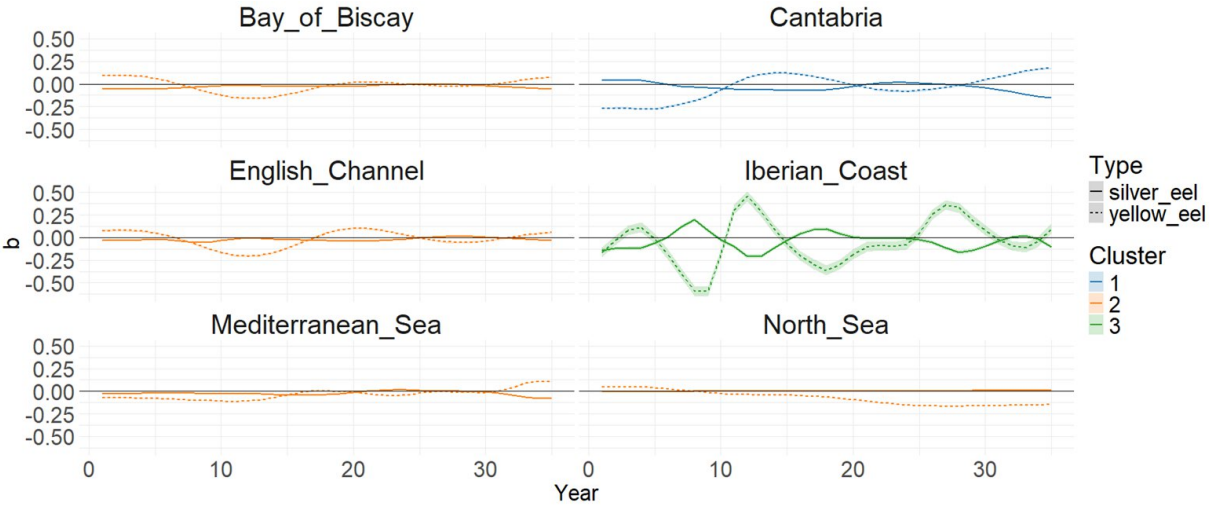

Figure 14: Double exponential smoothing on eel biomass logs: local slope b for each year from 1985 to 2018 and for each ecoregion (fixed scale)

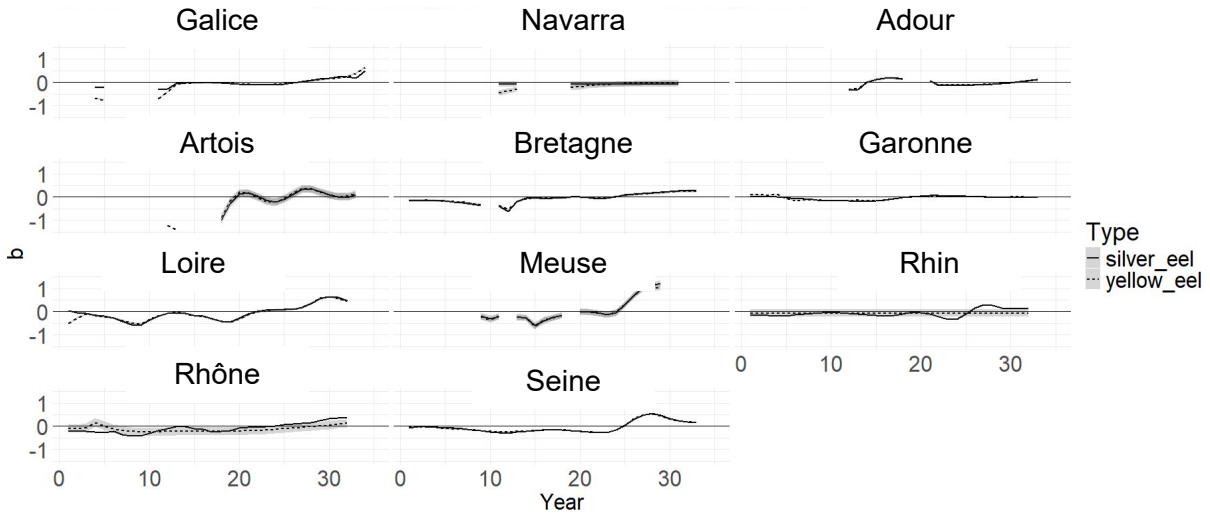

Figure 15: Double exponential smoothing on eel biomass logs: local slope b for each year from 1985 to 2018 and for each EMU (fixed scale)

Figures 14 and 15 show that the values of local slope (b) can vary depending on years but also spatial units. This suggests that for some periods, trends in biomass do not have the same importance (e.g., slight or sharp decline or increase) and/or direction (e.g., decline or increase) among spatial units. This result highlights the existence of periods of slight heterogeneities in biomass trends between spatial units for both silver and yellow eels.

Results of the DFA and double exponential smoothing show that Bay of Biscay and the English Channel, which are geographically close, have fairly similar trends. The same applies to the four EMUs Seine, Loire, Bretagne, Artois and the three EMUs Garonne, Navarra and Galicia. On the contrary, the Iberian Coast and Cantabria display distinct trends, despite being geographically close. Similarly, the EMU Adour has a very different trend from the EMUs Navarre and Garonne (respectively, the Meuse from the EMU Rhin).

Some spatially close areas display similar trends, suggesting a potential synchronism by environmental conditions because we assume that environmental conditions are similar between geographically close spatial units. However, distinct trends observed for geographically close areas are also noticed, questioning the assumption of similar environmental conditions between nearby units or indicating the effect of other factors on biomass dynamics.

Considering that the recruitment is also displaying an overall declining trend in Europe with high similarities and little variations among spatial units, it could partly explain the biomass trends. Therefore to check whether those similarities could be explained by a common trend in recruitment, we analyse the relationship between glass eel biomass and silver and yellow eel biomass.

3.1.2 Does the recruitment fully explain silver and yellow eel biomass variations? (H4)

A visual inspection of the residuals confirm that the assumptions of the GLM were satisfied (Annexe I). We observe a significant effect on eel biomass of the variable glass eel biomass (Annexe II). This confirms that a part of the trends in silver eel and yellow eel biomass can be explained by variations in recruitment. However, by analysing the residuals of the model per areas (Fig 16 & 17), we notice some temporal patterns (e.g. increasing trend of residuals in Bay of Biscay for silver eel, and on the other hand, a decreasing trend for yellow eel in the same area). This suggests that the “conversion rate” from glass eel to yellow and silver eel vary through time and areas, suggesting a potential effect of other anthropogenic or environmental factors.

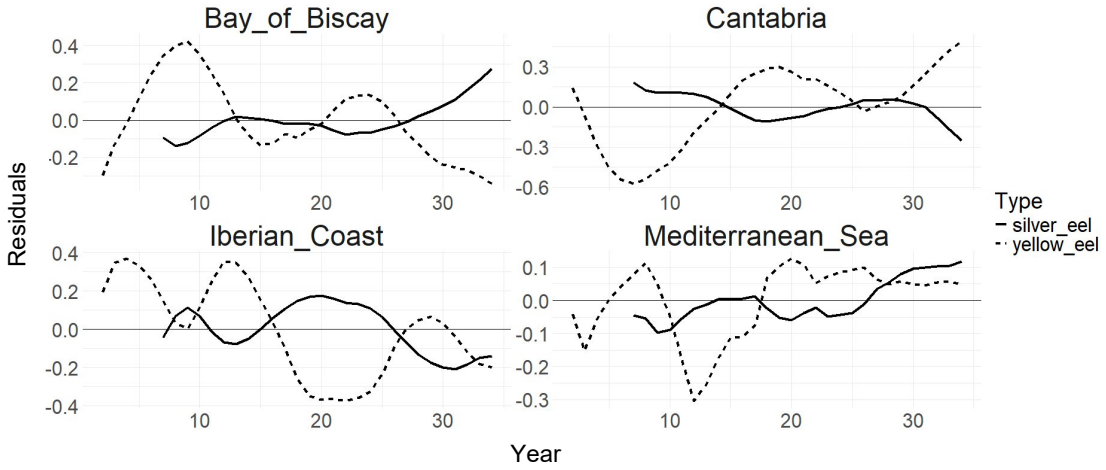

Figure 16: Residuals of the model log(Biomass) ~ Spatial unit + Year + Recruitment + ε over time (1985-2018) and for each ecoregion

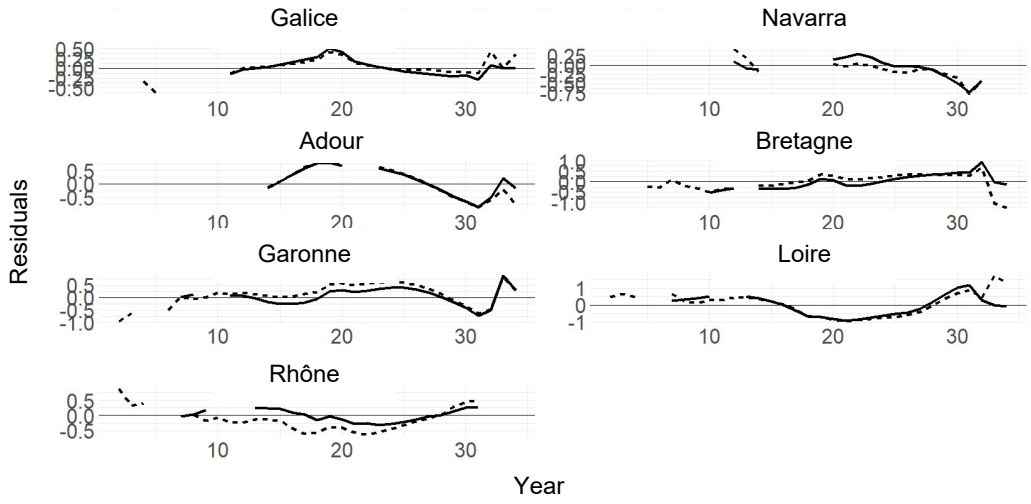

Figure 17: Residuals of the model log(Biomass) ~ Spatial unit + Year + Recruitment + ε over time (1985-2018) and for each EMU

According to these results, there could be environmental and anthropogenic factors influencing eel biomass in continental waters, which would explain the differences in temporal and spatial biomass trends. It is therefore of great interest to identify the environmental and anthropogenic factors that might be connected to the biomass of yellow and silver eels.

3.2 Analysis of correlations between environmental and anthropogenic variables and eel biomass

3.2.1 No correlation between silver and yellow eel biomass and atmospheric pressure or landings

Whatever the time scale (short term or long term) or the correlation test (Pearson or Spearman), we do not observe any significant correlations between biomass and atmospheric pressure or landings or proportion of “degraded area” (Annexe III & IV).

3.2.2 Correlation between silver and yellow eel biomass and temperature and rainfalls (local environmental factors)

We do not observe any significant linear relationship (Pearson test) between biomass and temperature or rainfalls (Annexe IV) but we do see significant correlations with the Spearman test.

There is a negative correlation between temperature and biomass on the short term only for yellow eels for the ecoregion North Sea (tab 2). Moreover, we observe a negative correlation on the long term for the ecoregion with the highest average temperatures only for silver eels: Mediterranean, Cantabria and Iberian Coast (Annexe V and tab 2).

Table 2: Results of the Spearman correlation test for the variable temperature

Ecoregions		Bay of Biscay	Iberian Coast	Cantabria	English Channel	Mediterranean	North Sea
Yellow eels	Short term						↘ *
Silver eels							
Yellow eels	Long term						
Silver eels			↘ *	↘ *		↘ *	

p-value < 0.001 (***), p-value < 0.01 (**), p-value < 0.05 (*)
Arrow direction and color indicate correlation: red downward for negative, green upward for positive

We observe significant negative correlation between rainfalls and biomass on the short term for silver eels only and for the ecoregion with the most important rainfalls: Cantabria (tab 3 and Annexe VI).

Table 3: Results of the Spearman correlation test for the variable rainfalls

Ecoregions		Bay of Biscay	Iberian Coast	Cantabria	English Channel	Mediterranean	North Sea
Yellow eels	Short term						
Silver eels				↘ *			
Yellow eels	Long term						
Silver eels							

p-value < 0.001 (***), p-value < 0.01 (**), p-value < 0.05 (*)
Arrow direction and color indicate correlation: red downward for negative, green upward for positive

3.2.3 Correlation between silver and yellow eel biomass and atmospheric pressure anomalies (large scale environmental factors)

Correlations between climate indices (NAO, WEPA, EA) and eel biomass vary significantly depending on the eel stage (yellow or silver), the temporal scale (long term or short term), and the spatial scale (northern or southern ecoregions):

- On the short term, the yellow eel biomass has a positive linear relationship with the WEPA for one ecoregion: the Bay of Biscay (Annexe IV), but it is negatively correlated

to the same indicator for the ecoregion Iberian Coast (tab 5). Moreover, it is negatively correlated and has a negative linear relationship with the NAO for one ecoregion in the north (English Channel) (Annexe IV and tab 4). For the silver eel biomass, we observe a negative correlation to the EA for one ecoregion in the north (English Channel) but no significant correlation for southern ecoregions (tab 6).

- On the long term, the yellow eel biomass is positively correlated and has a positive linear relationship with the WEPA for one ecoregion in the south (Iberian Coast). It is the same for silver eels but for one ecoregion in the north (North Sea) (Annexe IV and tab 5). On the other end, we observe no significant correlation with the yellow eel biomass for Northern ecoregions but a negative correlation between the silver eel biomass and EA for one ecoregion in the south (Iberian Coast) (tab 6).

Therefore, dry conditions and elevated temperature in summer are positively linked to yellow eel biomass in the long term but negatively to silver eel biomass. In the north, warmer and wetter winters, are positively linked to silver eel biomass in the long term. However, in the short term, dry conditions and elevated temperature are negatively linked to yellow eel biomass and warm and wet winters are negatively correlated to silver eel biomass, aligning with correlation results for the rainfalls variables.

Table 4: Results of the Spearman correlation test for the variable NAO

Ecoregions		Bay of Biscay	Iberian Coast	Cantabria	English Channel	Mediterranean	North Sea
Yellow eels	Short term				 *		
Silver eels							
Yellow eels	Long term						
Silver eels							

p-value < 0.001 (***), p-value < 0.01 (**), p-value < 0.05 (*)
Arrow direction and color indicate correlation: red downward for negative, green upward for positive

Table 5: Results of the Spearman correlation test for the variable WEPA

Ecoregions		Bay of Biscay	Iberian Coast	Cantabria	English Channel	Mediterranean	North Sea
Yellow eels	Short term		 *				
Silver eels							
Yellow eels	Long term		 *				
Silver eels							 *

p-value < 0.001 (***), p-value < 0.01 (**), p-value < 0.05 (*)
Arrow direction and color indicate correlation: red downward for negative, green upward for positive

Table 6: Results of the Spearman correlation test for the variable EA

Ecoregions		Bay of Biscay	Iberian Coast	Cantabria	English Channel	Mediterranean	North Sea
Yellow eels	Short term						
Silver eels					 *		
Yellow eels	Long term						
Silver eels			 *				

p-value < 0.001 (***), p-value < 0.01 (**), p-value < 0.05 (*)
Arrow direction and color indicate correlation: red downward for negative, green upward for positive

4. Discussion

Our study aimed to identify (i) potential spatial heterogeneities in European yellow and silver eel biomass trends, and (ii) the link between environmental and anthropogenic factors and the global biomass dynamics of the European eel (*Anguilla anguilla*) at different life stages (yellow and silver) over space and time.

4.1 Assessing spatial biomass trend patterns

Despite a generalized decrease, we identified slight spatial differences in biomass trends especially between southern and northern regions. Distinct trends observed for geographically close areas might be explained by different environmental conditions even if they are geographically close or by a possible influence of anthropogenic activities that would differ among ecoregions. On the other hand, spatial synchronism in biomass trends for geographically close spatial units were more often observed. It suggests that the environment might affect the biomass because they have similar environmental conditions. This result is consistent with the Moran effect, which postulates that the correlation in biomass trends of spatially separated populations is the same as the correlation in their environmental noise (Moran 1953). For instance, there is spatial synchrony in annual phytoplankton blooms, with studies showing this synchrony is driven by sea surface temperature and predators (Sheppard et al. 2019).

However there are limits to consider when looking at the trend analysis. Indeed, the pseudo-observed data generated by the EDA model have inherent measurement uncertainties associated with sampling, uncertainties stemming from the modeling process as well as limitations because of the model's specific assumptions. For instance, the EDA model for the ecoregion Iberian Coast was runned with very few observed data. For the ecoregion North Sea, the observed data were often zero. Therefore, the model’s outputs for these two areas should be considered with caution. On the other hand, in the model, the only spatial variables considered are the distance to Gibraltar and the EMUs or ecoregions. This ensures that nothing in the model forces neighboring spatial units to exhibit the same trends, as well as indicating that the observed similarities or differences are not forced by the model's design.

Additionally, it is important to note that our study has focused on only a portion of the species distribution range (Dekker 2003; Drouineau et al; 2018). Expanding the study to cover the entire continental distribution range of the species could reveal patterns undetected in the current analysis or further validate spatial synchronism in biomass trends for geographically close spatial units.

4.2 Assessing the link between biomass variables and habitat factors

When only one out of 12 correlation tests is significant, such as the result for temperature or precipitation on the short term, the reliability of this result can be questioned. Indeed, conducting multiple tests increases the probability of finding a significant result by chance, known as the problem of multiple comparisons. Without correction, a p-value threshold of 0.05 means there is a 5% chance of a false positive for each test. With 12 tests, this probability nears 8.3% if only one test is significant. Therefore, applying corrections to the p-value threshold would have improved the reliability of our results. Moreover, it is important to

note that this approach is a correlative study based on the link between two variables, but does not imply causality.

4.2.1 Temperature

It is important to note that, for the test, we assumed that in the absence of available water temperature data, air temperature could be used as a proxy.

Despite the annual temperature average never exceeding the optimal temperature for growth (22-23 °C) (Sadler 1979) (Annexe V), we observe a negative link between biomass and temperature on the long term for southern ecoregions. The summer temperatures in these regions can rise significantly high, and many rivers dry up during this season reducing eels' habitat (Vicente-Serrano et al. 2014). Moreover, this result is consistent with the negative impact of heat waves on food abundance (Cheung et al., 2021), which affects yellow eels and subsequently impacts silver eels that, although they do not feed, derive from yellow eels. High temperatures can also reduce their resilience to sudden temperature increases that potentially causes thermal stress and diminish dissolved oxygen levels, which is detrimental to eel survival and growth.

4.2.2 Rainfalls

We only observe one significant correlation for this variable. Assuming this output is reliable (see previously), it suggests that the negative link is significant only for this ecoregion. In this case, the negative impacts of rainfall on the eels' environment, such as contamination from runoff and habitat disturbance, might outweigh the positive effects like water oxygenation. Therefore, significant negative impacts on the eels' environment likely occur only with heavy rainfall; otherwise, the negative effects might not be substantial enough to affect them.

4.2.3 Atmospheric pressure anomalies

In the long term, for yellow eels, the positive impact of increased temperature on their growth and the productivity of their habitat may outweigh negative effects, such as lower dissolved oxygen levels. Conversely, for rainfall, the negative impacts of increased water levels and flow might outweigh the positive effects for yellow eels, but not for silver eels.

In contrast, the short term relationship between environmental conditions and eel biomass is opposite to the long term trends. For yellow eels, inter-annual temperature increases and low rainfall might be detrimental to their growth for the previously explained reasons. For silver eels, heavy rainfall is negatively correlated with biomass in the short term which is consistent with the correlation test results for the rainfall variable.

4.2.4 Atmospheric pressure

The lack of significant correlations could be due to the insufficient influence of atmospheric pressure on environmental conditions that impact eel biomass, such as water temperature, oxygen levels, and food availability. Alternatively, it could be that there are multiple potential effects, all indirect, which ultimately obscure any clear relationship.

4.2.5 Landings

Despite fishing being partly responsible for the collapse of the yellow and silver eel biomass (Dekker and Sjöberg 2013), we did not observe a significant link between biomass and landings on the long term. The time period available of landings data is short (10 years),

which might not be sufficient for the statistical tests to pick up a significant correlation. This is especially true for the long term correlation test considering that the MA model was adjusted with a window of 4 years. Moreover, in recent years, fishing restrictions were stricter than in the first years. Therefore, the fishing pressure is less important for the studied time period which might explain why no link between biomass and landings is identified. Finally, the correlation was tested at the ecoregion scale instead of the EMU scale, even though fishing restrictions are specific to each EMU. Therefore, testing the correlation at the EMU scale would have been more coherent, but was complicated due to gaps in most time series.

4.2.6 Proportion of area occupied by "degraded areas"

Despite what was expected (a negative correlation), there is no significant correlation between this variable and both silver and yellow eel biomass. Similarly to the previous variable, this result might be explained by the lack of data.

4.3 Perspectives

Some of our work has been limited by a lack of data quality and availability. This highlights the need for detailed and accurate data of biomass, environmental conditions and anthropogenic factors in order to better understand biomass trends and the link between eel biomass and environmental/anthropogenic variables. This is especially complex for eels given its widespread distribution in spatially fragmented rivers units and calls for higher coordination in data collection among countries and regions. Among the tested anthropogenic factors, no significant correlation between biomass and these habitat factors was detected. To enhance our understanding of the effects of anthropogenic pressures, it would be important to test the correlation between biomass and other variables. For instance, since European eel is facing contamination issue (Geeraerts et Belpaire 2010), it would be interesting to look at chemical and biological water quality data, if such data become available in the future. The Water Framework Directive (WFD) offers a promising prospect, as additional data will be collected in the future despite the current data series being too short (Michon et al. 2018).

Moreover, our study mainly focuses on bottom-up assumptions. It would be interesting to assess the link between eel predators biomass, such as catfish or birds, and eel biomass (Engström 2001; Martino et al. 2011; Westerberg et al. 2021).

4.3.1 Climate change context

In the context of climate change, an increase of temperature and heat waves occurrences is expected, as well as more extreme meteorological conditions impacting rainfalls with some regions experiencing prolonged periods of drought, while others may see increased rainfall and storms (Cheung et al. 2021; Hansen et al. 2020). Given that the temperature appears to be negatively correlated to the silver eels biomass and temperatures are rising in Europe, especially in southern regions, the challenges faced by the European eel could be exacerbated, hindering recovery efforts, despite the fact that the eel is a species with of tropical origin and with great adaptive capacities (Tesch et Thrope 2003). Moreover, we can wonder about the intensity of the effect of temperature change on others species with more restrictive temperature tolerance.

4.3.2 Management implications

Based on the findings of this study, several future directions can be considered to enhance the understanding and management of European eel. First, to improve the accuracy and reliability of biomass predictions by the ICES and given the observed differences in

biomass trends between northern and southern regions, it may be beneficial to develop separate prediction models for each region similarly to what has been done for glass eels.

Then, considering negative link between temperature, precipitation and biomass, more stringent measures may be implemented to reduce anthropogenic pressures in areas where temperatures and precipitation patterns are most extreme, as it is not possible to control these environmental variables. This calls for a more localized management approach, while enhancing significant cooperation across different regions as the European eel represents one single stock (Palm et al. 2009; Als et al. 2011).

5. Conclusion

Due to its complex life cycle, the European eel is exposed to various environmental conditions and anthropogenic pressures (fishing and poaching, parasitism, climate change, habitat fragmentation and degradation), making complex to understand the main drivers of the current decline and to prioritize restoration actions. Despite management measures put in place to stem the decline, there is no sign of recovery to date. To improve the understanding of the species at all levels and improve the management, our study aimed to explore spatial heterogeneities in European yellow and silver eel biomass trends and the relationships between these trends and various environmental and anthropogenic factors.

Trend analysis confirmed a general decline in eel biomass with punctual spatial heterogeneities. These analysis also revealed that geographically proximate regions typically exhibit biomass synchronism, suggesting an influence of environmental factors, consistent with the Moran effect. Our correlation analysis further indicated that while the overall decline in eel recruitment significantly explains the global biomass reduction, specific environmental factors such as temperature, precipitation and pressure anomalies might be linked to biomass trends, supporting the theory that the environmental conditions in eel continental distribution area may affect the biomass of both silver and yellow eels.

For instance, we observed a negative long term correlation between biomass and temperature in southern ecoregions. In the context of climate change, rising temperatures along with more extreme weather patterns affecting rainfalls are expected. Challenges for the conservation of the European eel could be intensified, impeding recovery efforts. This calls for a more localized management approach, while enhancing significant cooperation across different regions to implement efficient and well-coordinated conservation measures and finally stem the decline.

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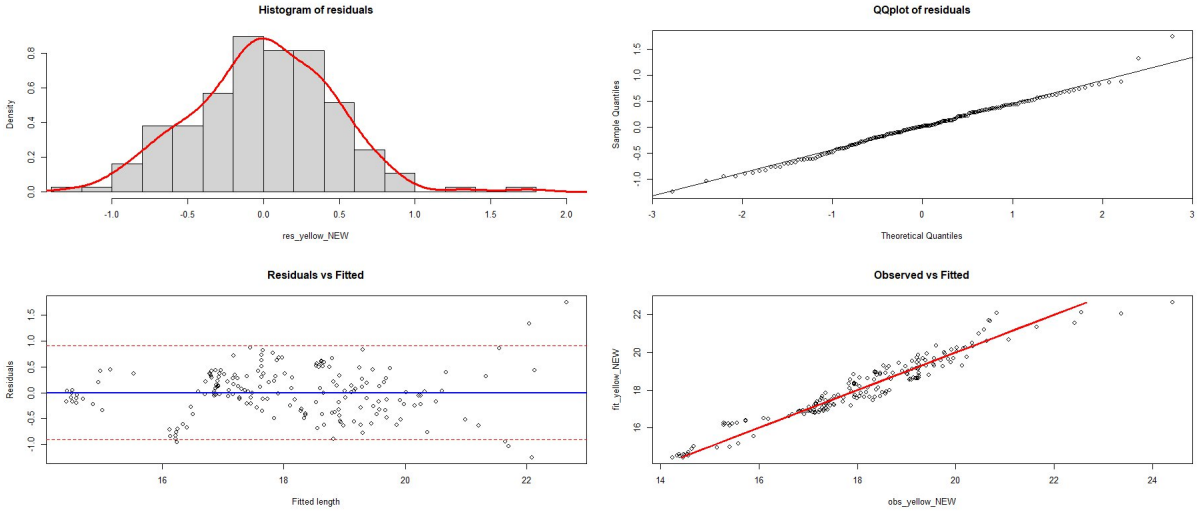
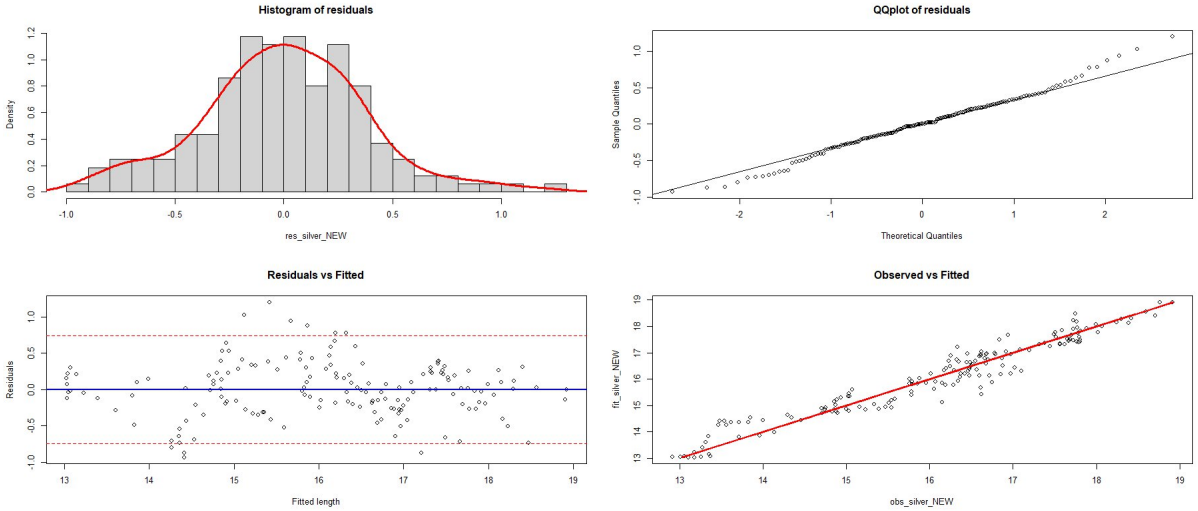
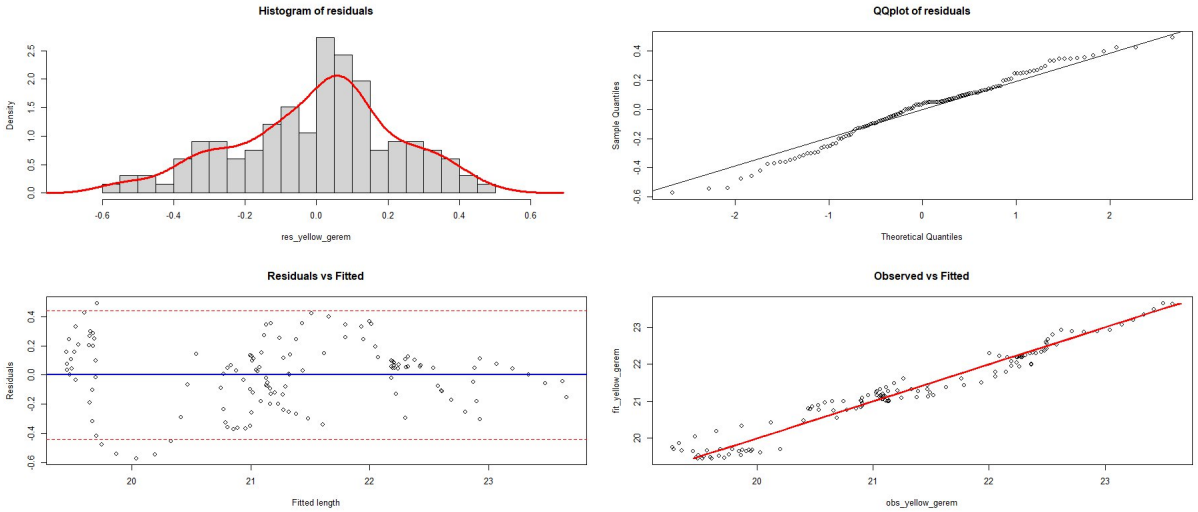
Annexe I : Residuals of the GLMs



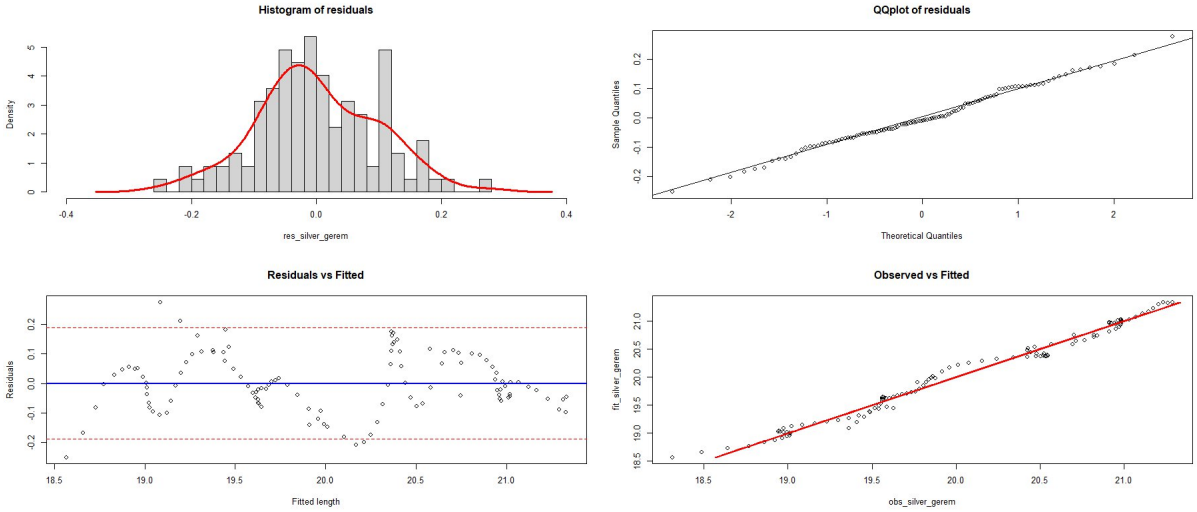
Residuals of the GLM : log(yellow eel biomass$_t$) ~ EMU + log(glass eel biomass$_{t-1}$) + year + ε



Residuals of the GLM log(silver eel biomass$_t$) ~ EMU + log(glass eel biomass$_{t-6}$) + year + ε



Residuals of the GLM : log(yellow eel biomass$_t$) ~ ecoregion + log(glass eel biomass$_{t-1}$) + year + ε



Residuals of the GLM log(silver eel biomass$_t$) ~ ecoregion + log(glass eel biomass$_{t-6}$) + year + ε

Annexe II : Anovas of the GLMs

```
Analysis of Deviance Table (Type III tests)

Response: log(bsilver)
Error estimate based on Pearson residuals

            Sum Sq Df  F values    Pr(>F)
ecoregion   55.561  3 1425.5875 < 2.2e-16 ***
log(bglass)  0.090  1    6.9534   0.01005 *
year         1.133 27    3.2302 2.622e-05 ***
Residuals    1.039 80
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

```
Analysis of Deviance Table (Type III tests)

Response: log(byellow)
Error estimate based on Pearson residuals

            Sum Sq Df F values    Pr(>F)
ecoregion   116.618  3 556.1730 < 2.2e-16 ***
log(bglass)   1.018  1  14.5698 0.0002405 ***
year         10.796 32   4.8269   1.2e-09 ***
Residuals     6.640 95
---
```

Anovas of the GLMs log(silver eel biomass$_t$) ~ ecoregion + log(glass eel biomass$_{t-6}$) + year + ε (left) and log(yellow eel biomass$_t$) ~ ecoregion + log(glass eel biomass$_{t-1}$) + year + ε (right)

```
Analysis of Deviance Table (Type III tests)

Response: log(bsilver)
Error estimate based on Pearson residuals

             Sum Sq  Df F values    Pr(>F)
ug          216.624   6 201.0091 < 2.2e-16 ***
log(bglass)   0.377   1   2.0962    0.1501
year         31.755  26   6.7999 3.974e-14 ***
Residuals    22.991 128
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1
```

```
Analysis of Deviance Table (Type III tests)

Response: log(byellow)
Error estimate based on Pearson residuals

             Sum Sq  Df F values  Pr(>F)
ug          256.955   6 160.7862 < 2e-16 ***
log(bglass)   1.724   1   6.4737 0.01199 *
year        104.491  31  12.6550 < 2e-16 ***
Residuals    38.621 145
---
```

Anovas of the GLMs log(silver eel biomass$_t$) ~ EMU + log(glass eel biomass$_{t-6}$) + year + ε (left) and log(yellow eel biomass$_t$) ~ EMU + log(glass eel biomass$_{t-1}$) + year + ε (right)

Annexe III : Results of the Spearman correlation tests for the variables landings, atmospheric pressure and proportion of area occupied by "degraded areas"

Landings		Bay of Biscay	Iberian Coast	Cantabria	English Channel	Mediterranean	North Sea
Yellow eels	Short term correlation coefficient	0,62	-0,62	0,33	NA	-0,25	NA
	P value	0,06	0,06	0,35	NA	0,49	NA
Silver eels	Short term correlation coefficient	-0,21	0,59	-0,18	NA	0,24	NA
	P value	0,56	0,08	0,63	NA	0,51	NA
Yellow eels	Long term correlation coefficient	-0,57	0,46	-0,54	NA	0,14	NA
	P value	0,30	0,40	0,42	NA	0,78	NA
Silver eels	Long term correlation coefficient	-0,32	0,54	0,54	NA	-0,68	NA
	P value	0,63	0,39	0,42	NA	0,13	NA
Landings		Bay of Biscay	Iberian Coast	Cantabria	English Channel	Mediterranean	North Sea
Sliver and yellow eel biomass	Short term correlation coefficient	-0,41	-0,31	-0,24	NA	-0,21	NA
	P value	0,25	0,39	0,51	NA	0,56	NA
	Long term correlation coefficient	-0,71	0,82	-0,64	NA	0,07	NA
	P value	0,15	0,07	0,30	NA	0,89	NA
Atmospheric pressure		Bay of Biscay	Iberian Coast	Cantabria	English Channel	Mediterranean	North Sea
Yellow eels	Short term correlation coefficient	0,03	-0,22	-0,15	-0,05	0,05	-0,09
	P value	0,85	0,22	0,38	0,79	0,77	0,63
Silver eels	Short term correlation coefficient	0,02	0,11	0,02	0,12	-0,19	0,04
	P value	0,93	0,54	0,91	0,49	0,28	0,80
Yellow eels	Long term correlation coefficient	0,49	0,20	0,18	0,64	0,40	0,43
	P value	0,10	0,61	0,65	0,07	0,19	0,20
Silver eels	Long term correlation coefficient	0,34	0,57	0,04	0,36	0,07	-0,03
	P value	0,22	0,13	0,85	0,25	0,82	0,93
Proportion of area occupied by "degraded areas"		Bay of Biscay	Iberian Coast	Cantabria	English Channel	Mediterranean	North Sea
Yellow eels	Short term correlation coefficient	0,031	0,16	0,0079	-0,17	0,16	0,083
	P value	0,87	0,39	0,97	0,37	0,42	0,67
Silver eels	Short term correlation coefficient	-0,28	0,057	-0,33	-0,15	-0,036	-0,17
	P value	0,14	0,77	0,08	0,45	0,85	0,37

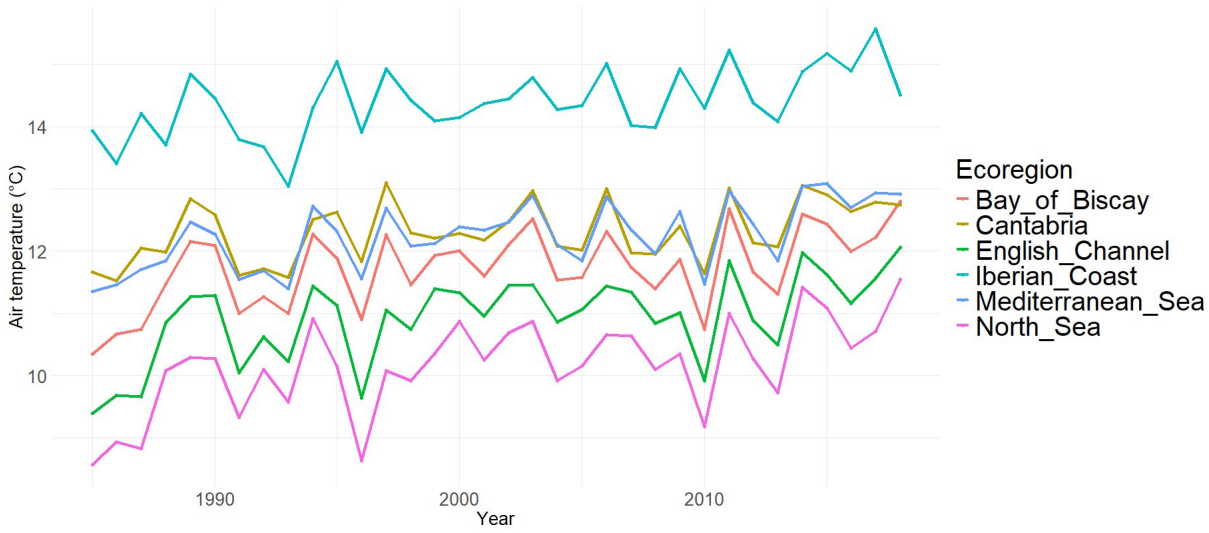
Annexe IV : Results of the Pearson correlation tests

Landings		Bay of Biscay	Iberian Coast	Cantabria	English Channel	Mediterranean	North Sea
Yellow eels	Short term correlation coefficient	0,54	-0,63	0,26	NA	0,06	NA
	P value	0,13	0,07	0,47	NA	0,86	NA
Silver eels	Short term correlation coefficient	-0,52	0,53	-0,07	NA	-0,11	NA
	P value	0,14	0,14	0,85	NA	0,76	NA
Yellow eels	Long term correlation coefficient	-0,44	0,34	-0,75	NA	0,24	NA
	P value	0,44	0,53	0,25	NA	0,63	NA
Silver eels	Long term correlation coefficient	-0,06	0,22	0,71	NA	-0,44	NA
	P value	0,92	0,72	0,28	NA	0,38	NA
Landings		Bay of Biscay	Iberian Coast	Cantabria	English Channel	Mediterranean	North Sea
Total Biomass	Short term correlation coefficient	-0,20	-0,23	-0,11	0,36	0,07	
	P value	0,58	0,52	0,76	0,30	0,84	
	Long term correlation coefficient	-0,57	0,75	-0,79	0,93	0,17	
	P value	0,30	0,18	0,21	0,12	0,73	
Proportion of area occupied by "degraded areas"		Bay of Biscay	Iberian Coast	Cantabria	English Channel	Mediterranean	North Sea
Yellow eels	Short term correlation coefficient	0,15	0,016	-0,077	-0,11	0,044	0,098
	P value	0,44	0,94	0,69	0,58	0,82	0,61
Silver eels	Short term correlation coefficient	-0,27	-0,0058	-0,3	-0,019	-0,017	-0,00066
	P value	0,16	0,98	0,13	0,92	0,93	0,1
EA		Bay of Biscay	Iberian Coast	Cantabria	English Channel	Mediterranean	North Sea
Yellow eels	Short term correlation coefficient	0,09	0,06	0,14	0,12	-0,07	0,09
	P value	0,60	0,73	0,44	0,48	0,69	0,62
Silver eels	Short term correlation coefficient	-0,06	0,00	-0,06	-0,10	0,12	0,00
	P value	0,72	0,99	0,74	0,56	0,50	0,99
Yellow eels	Long term correlation coefficient	-0,75	-0,31	0,31	-0,62	-0,68	-0,85
	P value	0,18	0,50	0,34	0,23	0,21	0,13
Silver eels	Long term correlation coefficient	-0,81	-0,88	-0,88	-0,73	-0,82	0,67
	P value	0,14	0,07	0,11	0,20	0,14	0,11
NAO		Bay of Biscay	Iberian Coast	Cantabria	English Channel	Mediterranean	North Sea
Yellow eels	Short term correlation coefficient	-0,06	-0,02	-0,09	-0,44	-0,06	0,10
	P value	0,73	0,92	0,60	*0,013	0,72	0,56
Silver eels	Short term correlation coefficient	-0,24	-0,05	-0,30	-0,24	-0,13	0,19
	P value	0,18	0,78	0,09	0,17	0,47	0,28
Yellow eels	Long term correlation coefficient	0,70	0,54	0,13	0,59	0,70	0,34
	P value	0,16	0,22	0,74	0,21	0,14	0,48
Silver eels	Long term correlation coefficient	0,54	0,32	0,52	0,64	0,55	0,26
	P value	0,25	0,48	0,28	0,18	0,25	0,53

WEPA		Bay of Biscay	Iberian Coast	Cantabria	English Channel	Mediterranean	North Sea
Yellow eels	Short term correlation coefficient	0,40	-0,06	-0,02	0,23	-0,04	0,31
	P value	*0,027	0,75	0,90	0,22	0,83	0,09
Silver eels	Short term correlation coefficient	-0,12	0,02	0,02	0,08	0,00	0,14
	P value	0,51	0,93	0,89	0,66	0,98	0,46
Yellow eels	Long term correlation coefficient	0,20	0,58	0,04	0,06	0,23	0,04
	P value	0,49	*0,047	0,90	0,84	0,42	0,90
Silver eels	Long term correlation coefficient	0,28	-0,24	0,24	0,35	0,29	0,60
	P value	0,33	0,41	0,42	0,22	0,32	*0,033
Temperature		Bay of Biscay	Iberian Coast	Cantabria	English Channel	Mediterranean	North Sea
Yellow eels	Short term correlation coefficient	-0,14	-0,30	0,08	-0,16	0,28	-0,15
	P value	0,44	0,09	0,65	0,35	0,12	0,39
Silver eels	Short term correlation coefficient	-0,26	-0,11	-0,15	-0,30	-0,28	0,08
	P value	0,14	0,52	0,41	0,09	0,11	0,63
Yellow eels	Long term correlation coefficient	-0,73	-0,35	0,17	-0,71	-0,78	-0,71
	P value	0,09	0,44	0,61	0,11	0,12	0,13
Silver eels	Long term correlation coefficient	-0,80	-0,90	-0,73	-0,77	-0,89	0,40
	P value	0,06	0,05	0,06	0,10	0,09	0,28
Precipitations		Bay of Biscay	Iberian Coast	Cantabria	English Channel	Mediterranean	North Sea
Yellow eels	Short term correlation coefficient	-0,09	0,11	0,31	0,17	0,23	-0,16
	P value	0,60	0,54	0,08	0,35	0,19	0,37
Silver eels	Short term correlation coefficient	-0,07	-0,04	-0,27	0,14	-0,20	0,32
	P value	0,71	0,82	0,12	0,44	0,27	0,07
Yellow eels	Long term correlation coefficient	-0,13	0,24	-0,44	-0,51	-0,28	0,61
	P value	0,77	0,42	0,26	0,17	0,33	0,13
Silver eels	Long term correlation coefficient	0,06	-0,27	-0,48	0,05	-0,12	-0,40
	P value	0,89	0,38	0,23	0,89	0,65	0,26
Atmospheric pressure		Bay of Biscay	Iberian Coast	Cantabria	English Channel	Mediterranean	North Sea
Yellow eels	Short term correlation coefficient	0,08	-0,18	-0,13	-0,04	-0,08	-0,15
	P value	0,66	0,31	0,45	0,82	0,64	0,39
Silver eels	Short term correlation coefficient	-0,03	0,19	-0,03	0,08	-0,06	-0,01
	P value	0,88	0,28	0,85	0,66	0,72	0,95
Yellow eels	Long term correlation coefficient	0,54	0,30	0,16	0,68	0,50	0,21
	P value	0,09	0,44	0,68	0,08	0,11	0,54
Silver eels	Long term correlation coefficient	0,34	0,46	0,17	0,33	0,36	0,13
	P value	0,24	0,25	0,45	0,30	0,23	0,73

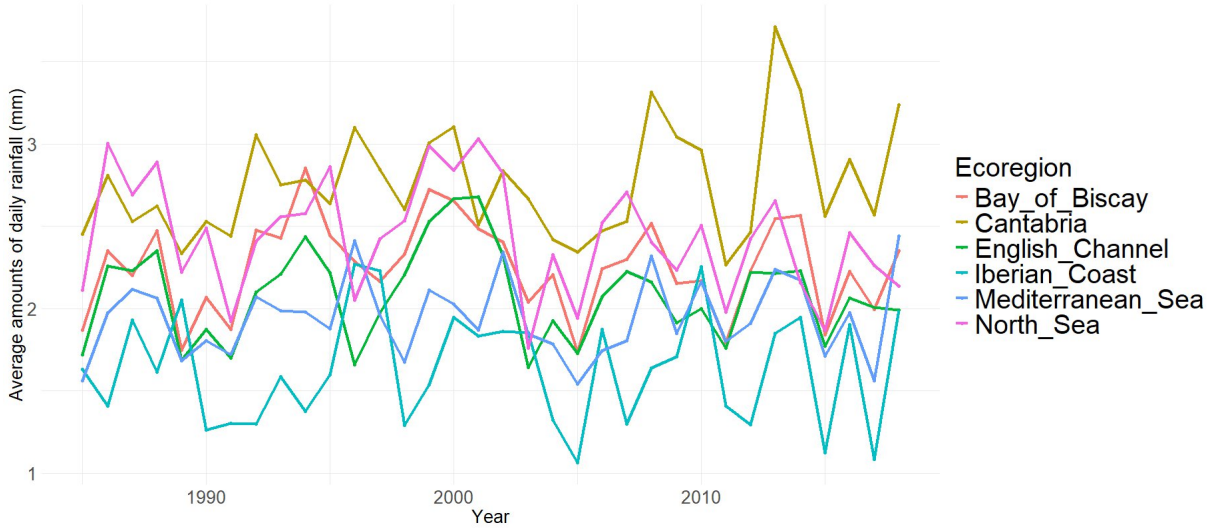
p-value < 0.001 (***), p-value < 0.01 (**), p-value < 0.05 (*)
Color indicates correlation: red for negative and green for positive

Annexe V : Annual average air temperature (°C) over 1985-2018 depending on the ecoregion



Annual average air temperature (°C) over 1985-2018 depending on the ecoregion

Annexe VI : The average of the sum of daily rainfall (mm) over 1985-2018 depending on the ecoregion



The average of the sum of daily rainfall (mm) over 1985-2018 depending on the ecoregion

Variabilité des tendances de la biomasse des stades continentaux de l'anguille européenne et influence des facteurs environnementaux et anthropiques à l'échelle de plusieurs pays (France, Espagne, Portugal)

L'anguille européenne (*Anguilla anguilla)* est une espèce catadrome et en raison de son cycle de vie complexe, l'espèce est exposée à diverses conditions environnementales et pressions anthropiques qui ont conduit à l'effondrement de la population. Malgré les mesures de gestion mises en place pour endiguer le déclin, il n'y a pas de signe de reconstitution du stock à ce jour. Il apparaît donc nécessaire d'améliorer les connaissances sur l'écologie de l'anguille européenne, notamment en démêlant les effets de l'environnement des effets anthropiques sur la biomasse des stades continentaux. Dans ce contexte, l'objectif du stage est (1) d'identifier de potentielles synchronies dans les dynamiques de biomasse d'anguilles jaunes et argentées entre différentes unités spatiales, et (2) d'étudier l'influence de l'habitat sur la biomasse d'anguilles jaunes et argentées en examinant le lien entre la biomasse et les variables environnementales et anthropiques. Les résultats montrent des similitudes dans les tendances de biomasse des anguilles jaunes et argentées entre des écorégions spatialement proches, suggérant un lien avec les conditions environnementales. Le test de corrélation a confirmé cela en montrant un lien entre la biomasse et la température, les précipitations. Cependant, des différences de tendances ont été observées entre certaines écorégions proches suggérant des liens possibles avec d'autres facteurs, notamment anthropiques, bien que ces derniers n'aient pas été mis en évidence par le test de corrélation. Compte tenu des résultats, les défis auxquels est confrontée l'anguille européenne seront potentiellement exacerbés avec le changement climatique. Cette analyse s'inscrit dans un projet plus large visant à mieux comprendre le fonctionnement de la dynamique de la population pour en optimiser l'évaluation et la gestion.
Mots-clés : Anguille européenne, biomasse, conditions environnementales, facteurs anthropiques, synchronisme spatial

Variability in biomass trends of European eel continental life stages and the influence of environmental and anthropogenic factors at a multi-country scale (France, Spain, Portugal)

The European eel (*Anguilla anguilla*) is a catadromous species and due to its complex life cycle, the species is exposed to various environmental conditions and anthropogenic pressures that have led to population collapse. Despite management measures put in place to stem the decline, there is no sign of recovery to date. It is therefore necessary to improve knowledge about the ecology of the European eel, in particular by separating the effects of the environment from anthropogenic effects on the biomass of continental stages. In this context, the objective of the internship is to (1) identify potential synchronies in the biomass dynamics of yellow and silver eels between different spatial units, and, (2) study the influence of habitat on the biomass of yellow and silver eels by examining the relationship between biomass and environmental and anthropogenic variables. Results show similarities in the biomass trends of yellow and silver eels between spatially close ecoregions, suggesting a link with environmental conditions. The correlation test confirmed this by showing a correlation between biomass and temperature, precipitation. However, differences in trends were observed between some close ecoregions suggesting possible links with other factors, including anthropogenic, although the latter were not evidenced by the correlation test. In view of the results, we expect the challenges faced by the European eel to be exacerbated with climate change. This analysis is part of a larger project to better understand how population dynamics work in order to optimize its evaluation and management.
Key Words: European eel, biomass, environmental conditions, anthropogenic factors, spatial synchronism