



Modelling the temporal evolution of the food web in the Gironde estuary. Evolution of trophic controls by comparing two modelling approaches.

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Modelling the temporal evolution of the food web in the Gironde estuary. Evolution of trophic controls by comparing two modelling approaches.

Par: Marine GRENIER



Soutenu à Rennes le 16/09/2022

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Introduction

The effects of global changes on marine ecosystems are already largely visible across the world and they are expected to have dramatic consequences on fisheries (Du Pontavice *et al.*, 2020; Tittensor *et al.*, 2021). Estuaries and coastal areas are especially sensitive to these global changes (Hoegh-Guldberg and Bruno, 2010) since 60% of the world's human population were concentrated around these areas in the late 20th century (Goodland, 1995) and were expected to be 75% in 2025 (Bianchi, 2006). This phenomenon of littoralization makes them more and more exploited and contaminated (Budzinski *et al.*, 1997; Matthiessen and Law 2002). Moreover, while these ecosystems provide many important goods and services to human societies (they only represent 6% of the marine areas but they contribute 33% of the economic activity - Costanza *et al.*, 1997), they also support important ecosystem functions, numerous species and especially fish: refuge, nursery area and migratory routes (Elliott and Hemingway, 2002). Indeed, many marine fish species use estuaries as nursery areas during their early life stages, benefiting from enhanced growth and survival conditions (Beck *et al.*, 2001). Thus, a better understanding of the impact of global changes is critical to better manage and conserve these areas, the species that depend on them, and subsequently the sustainability of many marine fisheries.

However, the ecological functioning of estuaries is complex. On one hand, they are associated with high diversity and heritage values (due for instance to the occurrence of marine, freshwaters and amphihaline species - Elliott and Hemingway, 2002). However, on the other hand, because of their position at the interface between land and sea, they are submitted to multiple environmental stresses and oscillations at various scales such as tides or river flows. This high variability leads to a significant difficulty to disentangle the relative effects of anthropogenic and natural stresses known as 'the estuarine quality paradox' (Elliott and Quintino, 2007). In this context, it is necessary to clarify the link between biodiversity and ecological processes at the ecosystem scale in order to better understand the effects of global changes on the functioning and trajectory of estuarine ecosystems (Hillebrand and Matthiessen, 2009; Hering *et al.*, 2010; Sala and Knowlton, 2006). Since trophic interactions are key aspects in ecosystem functioning, food web modelling has become central to explore the consequences of environmental changes on marine ecosystems (Heymans *et al.* 2016). Food web modelling provides a quantitative framework that combines both aspects on species richness and community structure but also on underlying ecological processes such as energy flows between species (Thompson *et al.*, 2012). These models have proved to be useful to study estuarine ecosystems functioning (e.g., Monaco and Ulanowicz, 1997; Lobry *et al.*, 2008; Niquil *et al.*, 2012; Tecchio *et al.*, 2015).

The Gironde estuary is an emblematic case-study. It is one of the largest estuaries in Western Europe (Lobry *et al.*, 2003) and one of the most studied. In particular, the existence of a long-term scientific monitoring on both biotic and abiotic compartments (since 1979) allows the analysis of long-term evolutions (e.g., Lobry *et al.*, 2003; David *et al.*, 2005; David *et al.*, 2007; Lobry *et al.*, 2008; Chaalali *et al.*, 2013; Chevillot *et al.*, 2016; Chevillot *et al.*, 2019). It appears that the Gironde estuary has undergone drastic changes in its environmental conditions over the last thirty years (Chevillot *et al.*, 2019). These changes include an increase in water temperature and in the concentration of upstream sediments due to the displacement of the maximum turbidity zone, a migration of the upstream salinity limit toward Bordeaux and a decrease in the mean river flows (Sautour *et al.*, 2020). Such changes affect the species diversity (e.g., Chaalali *et al.*, 2013; Pasquaud *et al.*, 2012; Chevillot *et al.*, 2016), modify the interactions between the species (Chevillot *et al.*, 2019) and, finally, could affect the global resilience of the ecosystem (Holling, 1973; Barnosky *et al.*, 2012).

In more details, one of the main consequences of global changes is the progressive marinization of the Gironde estuary, i.e., an increase in the penetration of marine waters in the transitional area (Pasquaud *et al.*, 2012). This is mainly due to a progressive decrease in river flows caused by alterations in precipitation patterns, flow regulations and numerous upstream

withdrawals for large-scale corn cultivation (Chevillot *et al.*, 2016). Meanwhile, significant changes in the structure of its ecological communities have been documented at different trophic levels (Chaalali *et al.*, 2013), including zooplanktons (David *et al.*, 2005; Chaalali *et al.*, 2013), benthic communities (Quintin, 2014), crustaceans (Béguer, 2009) or fishes (Pasquaud *et al.*, 2012; Chevillot *et al.*, 2016). Among others, these changes include a significant increase in the relative abundance of marine fish juveniles in the estuary (Pasquaud *et al.*, 2012; Chevillot *et al.*, 2016) while the relative abundances of crustaceans have decreased. In addition, the species richness and relative abundance of benthic invertebrates have collapsed over the past decade (Chevillot *et al.*, 2019) while these species are, for instance, crucial in the diet of flatfish species (*e.g.*, Le Pape *et al.*, 2007). This potential prey limitation in nursery grounds is suspected to be one of the main causes of the oscillations of flatfish recruitment (Day *et al.*, 2020; Tableau *et al.*, 2019), and is a potential threat to the nursery function in the Gironde estuary (Chevillot *et al.*, 2019).

This makes us wonder if induced trophic consequences of these above-listed perturbations exist, especially in the context of global changes. To address this question, we will determine the main trophic controls and study their evolution in the Gironde estuary. This approach is expected to help us understand the cause and impact of the observed modifications on the functioning of the ecosystem.

This leads to specifically wonder **whether the observed changes of the trophic communities in the Gironde estuary can be explained by the trophic controls in the food webs or if they are rather linked to external forcing? Is there a threat for the nursery function?**

Previous works on the Gironde estuarine food web mainly consisted in comparing static pictures of the trophic network using the mass-balanced static food web model Ecopath (Lobry, 2004; Chevillot *et al.*, 2016). Indeed Chevillot *et al.* (2019) recently investigated changes in trophic controls in the Gironde estuary by implementing three Ecopath models on three periods separated by two previously documented regime shifts (Chevillot *et al.*, 2016). The existence of three distinct models allowed them to compare three “static pictures” of the ecosystem functioning over three stable periods. However this study did not describe the whole dynamics over the last decades and thus did not allow us to explore the potential causes of the shifts.

In our study, we first use Ecosim, the dynamic version of Ecopath in the Ecopath with Ecosim (EwE) suite (Christensen *et al.*, 2005). Still based on the mass-balance assumption, Ecosim allows the modelling of trophic flows dynamics within a food web while accounting for temporal variations of anthropogenic (fishing) or environmental (primary production and detritus) constraints. However, EwE, like any food web models, relies on the estimation of very large number of trophic flows over time, which is generally not directly possible given the amount of available data (a situation called under-determinacy). To address this lack of direct observations of trophic flow, Ecopath and Ecosim use additional sources of data and assumptions to specify the diet composition, consumption rates, production rates etc. to turn an underdetermined problem into a solvable overdetermined problem (Niquil *et al.*, 2012). In EwE, those values are assumed to be constant through time, though diet compositions may vary according to a tuning parameter called vulnerability. This parameter describes how consumption vary depending on prey and predator abundance. These assumptions are very strong and clearly do not account for the intrinsic stochasticity of natural systems (Planque *et al.*, 2014) and for the opportunistic nature of many trophic interactions (Shin and Cury, 2001).

Very recently, Chance and Necessity models have been proposed to address these issues (CaN - Planque and Mullan, 2020). This modelling framework enables us to implement more flexible non-deterministic trophic models, accounting for the intrinsic indeterminacy in nature while acknowledging the existence of physical and physiological laws that separate what is possible and what is impossible (Planque and Mullan, 2020).

In this context, we used both EwE and the R package implementing Chance and Necessity food web models (RCaN – [Drouineau et al., 2021](#)) to explore the effect of trophic controls on the dynamics of the Gironde estuarine food web, and more specifically, to investigate on the factors explaining the observed changes in the community. Moreover, the comparison between EwE and RCaN makes it possible to assess the robustness of EwE results and their sensitivity to EwE implicit assumptions and to detect alternative dynamics that are consistent with existing observations.

In this manuscript, I will first present the EwE and RCaN models I have implemented after a brief presentation of the two approaches.

The simulations will be analyzed and discussed. Specifically, I will study the food web trajectories simulated with RCaN using multivariate analysis to identify clusters of food web structures and potential time trends in the structure.

I will then compare the existing trophic controls in the different clusters.

Finally, I will discuss the insights of the analysis with respect to the evolution of the ecosystem and of its nursery function, and the benefit of comparing the two modelling approaches.

1. Materials and methods

1.1. The Gironde estuary

The Gironde estuary is located in the south-west of France (Figure 1). From a geographic view, it is formed by the confluence of the Dordogne and the Garonne Rivers and flows into the Bay of Biscay. From a hydrologic view, the upstream salinity limit is now located between the confluence and Bordeaux while the tidal movement can be detected up to 70km away.

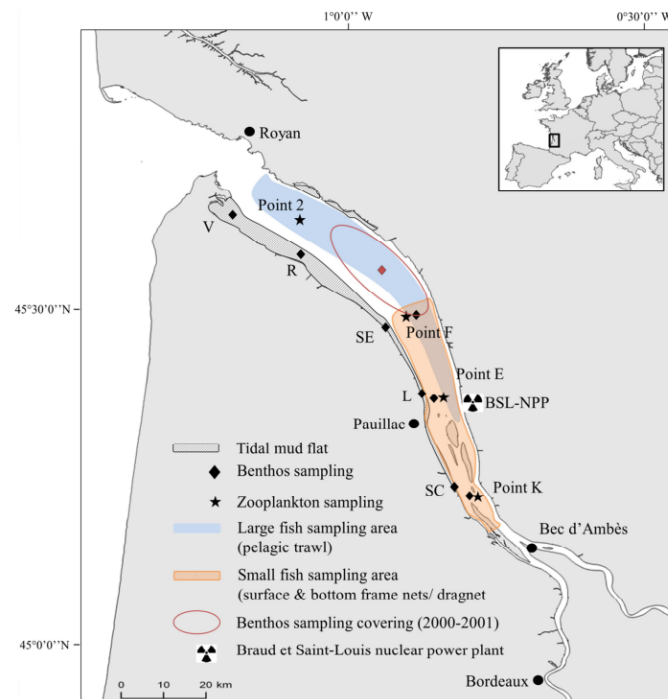


Figure 1 : Location of the Gironde estuary in France and location of all its sampling sites (source: Chevillot et al., 2016).

For the purpose of the present study and in accordance with previous modelling works, we will consider the part of the estuary located between the confluence (Bec d'Ambès) and the transversal limit of the sea. For simplicity, we will name this estuary “the Gironde estuary”. In this area, the estuary undergoes many anthropogenic pressures, such as commercial

fisheries, which mainly fish shrimps and yellow eels, and the influence of the Blayais Nuclear Power Plant (Centre Nucléaire de Production d'Electricité –CNPE- du Blayais) (Chevillot *et al.*, 2016). The latter removes water from the estuary to cool down its system while a warmer water is rejected a little downstream in the estuary. Numerous individuals from different fish and shrimp species can be trapped in the water intake which can induce various mortality levels (Boigontier and Mounié, 1984).

Several monitoring programs have been implemented to monitor the environmental consequences of this CNPE. These provide time series of biomasses and landings for various ecological groups and fish species.

In particular, the monitoring programs concerning fishes are:

- TRANSECT campaigns, which are carried out monthly near the CNPE to monitor small estuarine fauna since 1979.
- STURAT campaigns. Carried out every two months, they are designed to monitor the European sturgeon *Acipenser sturio* population of the estuary and are also adapted to the capture of large individuals.

Regarding zooplankton, since 1979 a regular monitoring of this community is carried out by means of two complementary observation programs:

- The environmental monitoring of the CNPE du Blayais.
- The monitoring operated by the Service d'Observation en Milieu LIToral (SOMILT) and conducted by the University of Bordeaux (David *et al.*, 2007, Chaalali *et al.*, 2013). Sampling is made monthly from April to November.

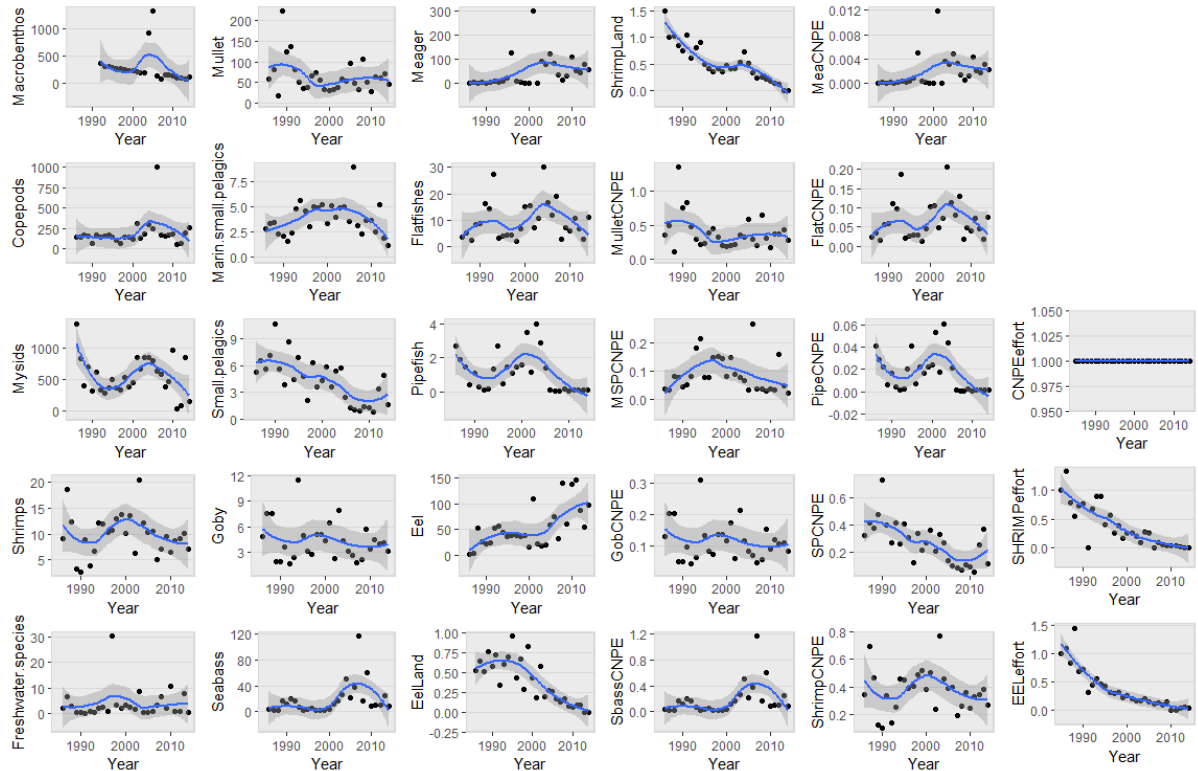
Finally, samplings of the benthic meio- and macrofauna were punctually implemented between 1991 and 2004 and are now completely included in the monitoring program of the power plant. These samplings are thus implemented 9 months a year in the intertidal and subtidal areas.

The estimation of the landings by the commercial fisheries is derived from the fishery monitoring of the Gironde estuary conducted since 1978 (this survey used to be included in the monitoring of the CNPE on the ichthyofauna). The catches per unit effort (CPUEs) are collected by métier and fishing area from a corpus of representative fishermen (Rochard, 1992).

The estimations of the mortality due to the CNPE are also available (Boigontier and Mounié, 1984).

As a summary, the following time series are available (Figure 2):

- Yearly estimated absolute biomasses (in $t.km^{-2}$) of the different species.
- Yearly catches of the shrimp and yellow eel fisheries in $t.km^{-2}.year^{-1}$.
- Yearly fishing efforts of these two commercial fisheries estimated from a yearly interview-based survey with a panel of commercial fishermen.
- The estimated quantity caught by the CNPE cooling system in $t.km^{-2}.year^{-1}$ per species.



SBass = Seabass; Gob = Goby; MSP = Marine small pelagic; SP = small pelagic; Pipe = Pipefish; Flat = Flatfish; Mea = Meager; Land = landings

Figure 2 : Time series of biomasses (in $t.km^{-2}$), landings (in $t.km^{-2}.year^{-1}$) and efforts (relative) of the various trophic compartments included in the models. Each point represents the value of this data at a time t . The blue line represents the LOESS smoothing and the shaded area is the confident interval (0.95).

1.2. The food web models

1.2.1. Ecopath and Ecosim

Ecopath is a mass-balanced static model that postulates that the food web is at a steady state (Christensen *et al.*, 2005). As such, it is generally applied to a stable period over a single year or a theoretical averaged year. Here, one of the models used during this study is the dynamic extension of Ecopath model, which is called Ecosim (Christensen *et al.*, 2005), to explore the dynamics of the food web over the last decades. Ecopath and Ecosim are among the most widely used food web models in fishery sciences (Ainsworth and Walters, 2015). Therefore, we will use Ecosim as implemented in the Ecopath with Ecosim (EwE) software, which facilitates the combined use of these two models (Christensen *et al.*, 2005).

For the rest of this manuscript, I will unduly use EwE to refer to our Ecosim trophic model.

1.2.1.1. Fundamental equations

The Ecopath model is based on two main equations that describe the mass conservation of any trophic group within the ecosystem (Christensen *et al.*, 2005):

$$P = M + F + OM + Bacc + (I - E) \quad (1)$$

With P the biomass production, M the natural mortality, F the fishery catches, OM the other mortality (predation), Bacc the biomass accumulation, I the immigration and E the emigration.

$$C = P + R + U \quad (2)$$

With C the consumption, R the respiration and U the unassimilated food.

Ecosim, which is the dynamic extension of Ecopath, is based on a differential equation of biomass production (Christensen *et al.*, 2005):

$$\frac{dB_i}{dt} = \left(\frac{P}{Q} \right)_i * \sum_j Q_{ji} - \sum_j Q_{ij} + I_i - (M_i + F_i + E_i) * B_i \quad (3)$$

With i representing a trophic group i and j a trophic group j, $(P/Q)_i$ the net growth yield, M_i the natural mortality, F_i the fishing mortality, E_i the emigration, I_i the immigration, $\sum_j Q_{ji}$ the total consumption of group i and $\sum_j Q_{ij}$ the predation by all predators on group i.

In particular, Q_{ij} denotes the predation of species j by species i. This predation is deterministic and based on the so-called “foraging area theory” (Christensen *et al.*, 2008). It postulates that predation varies with both the biomass of prey B_i and predator B_j , considering a parameter called vulnerability v_{ij} that describes the rate at which the prey becomes vulnerable to the predator, and a_{ij} the effective search rate of the predator:

$$Q_{ij} = \frac{a_{ij} * v_{ij} * B_i * B_j}{(2 * v_{ij} + a_{ij} + B_j)} \quad (4)$$

1.2.1.2. Application to the Gironde estuary

1.2.1.2.1. The trophic network and trophic groups characteristics

The first task when developing a food web model such as Ecopath or Ecosim is to describe the trophic network: its structure in terms of trophic groups and the characteristics of these trophic groups. One trophic group gathers one species or one group of species which have (almost) the same diet, (almost) the same biological parameters and are eaten by (almost) the same predators.

For the Gironde estuary case, we used an initial Ecopath food web model developed by Lobry *et al.* (2008) and taken over by Chevillot *et al.* (2019). This food-web model was initially based on 26 trophic groups, which were here rearranged in 17 trophic groups to simplify the model and limit computation time in the next step with RCaN.

Most trophic groups, which are Mysids, Suprabenthos, Shrimps, Freshwater species, Mullet, Goby, Flatfish, Pipefish, and Eel, were not modified. The compartment Detritus remains the same too.

A few trophic groups were pooled because of their similarities and because we considered they were not key species in the addressed ecological question:

- “Primary producers” regroups the former “Phytoplankton” and “Microphytobenthos” trophic groups because there is no way to know which groups the primary production comes from with the available data.
- “Macrobenthos” gathers the “Intertidal Macrobenthos” and “Subtidal Macrobenthos” trophic groups.

- “Copepods” gathers the “Microzooplankton” and “Mesozooplankton” trophic groups.

Conversely, we separated small pelagic into two groups since, in the context of marinization of the estuary, both groups are supposed to have contrasted dynamics:

- “Small pelagic” gathering “Shad” and “Smelt”.
- “Marine small pelagic” gathering “Anchovy” and “Sprat”.

Finally, a few minor species, which have both a small biomass and are associated with few flows, were removed from the model (Sturgeon, Ray, Whiting, and Birds).

The network also includes the two commercial fisheries (shrimp and yellow eel). Like in previous works, the CNPE is included in the model like a third fishery that would discard all catches.

All the modifications on the Ecopath model between Lobry (2008), Chevillot *et al.* (2019) and our study are available in appendix 1.

To run Ecosim, it is also required to provide some biological and ecological parameters that govern the dynamics of trophic groups:

- The different characteristics of each trophic groups (Appendix 2):
 - o The initial average biomass per unit area.
 - o The Production/Biomass (P/B), which represents the productivity of trophic groups.
 - o The Consumption/Biomass (Q/B), which represents the consumption rate of a predator.
 - o What is not assimilated (urine and feces).
- The diet matrix: the preys are in line and predators in column. The total consumption of a predator must be equal to one (Appendix 3).

These input data are used to balance the Ecopath model. When Ecopath is balanced, it can be used as input data for Ecosim simulations. With Ecopath, the different time series above (Figure 2) are used for the Ecosim part to transcribe the past variations. As for the trophic network, we used the Ecopath model of Lobry *et al.* (2008), and the subsequent modifications of Chevillot *et al.* (2019) to balance the new Ecopath model. Parameters were adjusted following our modifications in the trophic network using mainly weighted averages by biomasses. The group biomasses were set to the sum of the individual species biomasses.

1.2.1.2.2. Input data and general Ecosim calibration

Based on time series of fishing effort and eventually of environmental conditions (using the latter as forcing functions), Ecosim simulates the evolution of biomasses and catches (or landings) of the different trophic groups. As such, observed time series of catches and/or biomasses can be used to calibrate the model.

Here, we used the data provided by the monitoring programs described in section 1.1.

Ecosim assumes that trophic interactions among trophic groups are deterministic and depend on groups' vulnerabilities (equation 4). Generally, vulnerabilities are unknown and are commonly used as a tuning parameter. A numerical calibration is used to find the values that ensure the best fit of the model to the observed time-series of biomasses and catches (Christensen *et al.*, 2008). Therefore, fitting an Ecosim model generally consists in searching for the vulnerabilities of some trophic groups that maximize the fit between data and simulations. Since it is impossible to estimate vulnerabilities for all pairs of prey and predators, EwE provides a routine to quantify the sensitivity of the model to each vulnerability, and only the most sensitive vulnerabilities are estimated.

Here, we carried out a Stepwise Fitting Procedure (SFP), which is directly implemented in the EwE software ([Scott *et al.*, 2016](#)). This procedure consists in testing different calibrations with more or less parameters (fisheries, vulnerabilities and primary production anomalies). Two indices of fitting quality are associated with each calibration set: (1) the Sums of Squared (SS) between estimated biomasses, estimated landings and observations and (2) the Akaike Information Criterion (AIC) that accounts for the number of estimated parameters. Time series of biomasses are here used as “relative” biomasses since catchability of scientific survey is thought to be poorly known. The algorithm retains the lowest AIC, i.e., the calibration allowing the predicted biomass variations to be the closest to the observed ones. It is penalized by the number of estimated parameters (Appendix 4).

1.2.1.2.3. Calibration framework in our study

Since our aim is to explore which trophic control governs the food-web in this estuary and how it can explain changes observed in it, we built several hypotheses and carried out a calibration exercise based on each hypothesis:

- Hypothesis 1 (H1): Environmental changes in the Gironde estuary (especially through primary production and organic matter inputs) and internal food web dynamics explain the observed changes in community structure (hypothesis based on a bottom-up control).
- Hypothesis 2 (H2): Global changes modify the structure of fish communities, especially the relative abundance of marine juveniles due to marinization, which induce a cascade effect on preys (hypothesis based on a top-down control related to marine fish).
- Hypothesis 3 (H3): Global changes modify the structure of fish communities, especially the abundance of top-predators (considered here as the species which are in a trophic group with a trophic level higher than three), inducing a cascading effect on preys (hypothesis based on a top-down control related to top-predators).

The top-down control assumption is separated into two assumptions to explore whether the marinization, which leads to the increase in the relative abundance of marine juveniles, may have played a major role in the modifications of the estuarine ecosystem. However, as many marine juveniles are also top-predators (the proportion of marine juveniles on top-predators represents 55% of overlap), H2 and H3 are overlapping.

For each assumption, the biomasses of some trophic groups were forced. It means that trends in biomasses were not estimated within the model but imposed by the observed time series (i.e., these biomasses become input data and are not used in the calibration anymore). Implicitly, we thus supposed that variations of the biomasses of those species are caused by external factors and that they can subsequently affect the internal dynamics of the food web (top-down control since here we mostly forced the predators' biomasses). On the same rationale, we also added forcing functions that directly influence the time-trends of the primary producers or carbon input of the group detritus to mimic a potential environmental change that would have had a bottom-up control on the food web.

Note that the biomass of the Eel group is forced in all assumptions because this species has collapsed since the early 1980s for external reasons ([Drouineau *et al.*, 2018](#)).

All the hypotheses and their implementation in EwE are represented in the table 1.

Table 1 : Representation of the assumptions in EwE

Model	Forcing biomasses	Forcing functions (primary producers and detritus)	Note
H1	Eel	Both	Vulnerabilities are estimated for all trophic groups
H2	Marine fish and Eel	Both	Vulnerabilities are estimated only for other trophic groups
H3	Top-predators	Both	Vulnerabilities are adjusted only for other trophic groups

1.2.1.2.4. How to choose the best model

Comparing the fit among the different calibrations is not straightforward since biomass values for some species are forced in some assumptions while they are estimated in others. As such, we decided to compare the SS and AIC regarding only the trophic groups that are not forced in any of the calibration exercise. The trophic groups concerned are Macrobenthos, Mysids, Shrimps and Copepods.

The AIC is calculated as follows (Heymans *et al.*, 2016):

$$AIC = n * \log\left(\frac{\min SS}{n}\right) + 2 * k \quad (7)$$

With n the number of observations or time series values, minSS the minimum SS calculated by the algorithm and k the number of parameters estimated.

1.2.2. RCaN

1.2.2.1. General principles of RCaN models

A food web model based on the CaN approach was proposed by Planque and Mullon (2020) and the R package RCaN was developed to facilitate the implementation of such models (Drouineau *et al.*, 2021). For simplicity, we will call RCaN a CaN food web model. CaN approach acknowledged the stochasticity (Chance) of most ecological processes and the simultaneous existence of some physical and physiological rules (Necessities) delineating what is possible and what is not (e.g., gravity, mass conservation...). Like in EwE, a RCaN model is based on a hypothesis of mass conservation (first necessity) and trophic groups are connected through trophic flows. However, these flows assume that species' diet are largely opportunistic (chances), contrary to EwE in which the trophic interactions are deterministic and fixed. In addition to this, RCaN postulates that the dynamics of trophic groups are constrained by some physiological limits such as satiation, inertia, and refuge biomass (such necessities correspond to implicit constraints, see below). Finally, observation data can also be used to delineate what may have occurred (such necessities correspond to explicit and case specific constraints).

The constraints delimit the possible dynamics of the food web. Mathematically, providing that constraints are linear, it can be shown that they define a convex polytope, which includes all the possible trajectories of the food web (a trajectory is defined by all values of biomasses and flows for all time steps). Thus, the principle in a RCaN model is to sample random food web trajectories (Chance) inside the polytope of constraints (Necessities).

1.2.2.2. Fundamental equation

Unlike EwE, a RCaN model relies on only one fundamental equation:

$$B_{i,t+1} = e^{(-\mu_i)} * B_{i,t} + \frac{(1-e^{(-\mu_i)})}{\mu_i} * [\gamma_i * \sum_j \kappa_j F_{ji} - \sum_j F_{ij}] \quad (5)$$

With $B_{i,t}$ the biomass of trophic group i at time t , F_{ij} and F_{ji} the biomass flow between trophic groups i and j , μ other losses (natural mortality and metabolic losses), γ the potential assimilation efficiency, which represents the proportion of biomass ingested by the predator that is actually assimilated and κ the digestibility coefficient, which represents the ease with which a prey item can be digested.

Here, F_{ij} are stochastic and not determined by the foraging area theory like in EwE.

Planque and Mullon (2019) also proposed a set of standard implicit physiological constraints:

- The inertia, which limits the variations of biomass between the maximum rate of growth (ρ) and the maximum rate of mortality ($-\rho$): $e^{-\rho_i} * B_{i,t} \leq B_{i,t+1} \leq e^{\rho_i} * B_{i,t}$ with ρ_i the inertia of species i and $B_{i,t}$ the biomass of a species i at time t .
- Satiation, which is the maximum rate of consumption per unit of biomass of a predator (σ): $I_{i,t} \leq \sigma_i * B_{i,t}$ with $I_{i,t}$ the sum of incoming flows to species i at time t , σ_i the satiation of species i and $B_{i,t}$ the biomass at time t of species i .
- Refuge biomass, which stands for a threshold under which the species is not vulnerable to fisheries or predation. This value is considered fixed and does not depend on the relative biomasses of predators and preys as it is described in the foraging area theory.

1.2.2.3. Application to the Gironde estuary

1.2.2.3.1. The trophic network and trophic groups characteristics

Like in EwE, a RCaN food web is defined by trophic groups connected by (time-varying random) trophic flows. The “non-trophic flows” exists and refers to the migration fluxes between the inside and the outside of the delimited system or to the catches by fisheries. We used the same trophic groups as in the EwE application presented above and assumed that a trophic flow between two groups was possible only if the trophic interaction indeed exists in EwE.

Contrary to EwE, we assumed the existence of Meager and Freshwater species immigrations. The immigration is a specific type of flow in RCaN, which can contribute to a direct increase in the biomass of the group, without affecting any other group. Indeed, these species display rapid increase in their biomasses that are likely due to the arrival of external individuals during favorable years (warm years for Meager with species at the northern range of its distribution area; strong freshwater discharge for Freshwater species) rather than to the internal ecosystem dynamics.

RCaN allows the distinction between internal and external trophic groups. When a group is outside the system, its standing biomass is not modelled but it can still be connected to other groups by biomass flows. In the case of the Gironde estuary food web, the trophic groups that are considered outside the system are (Figure 3):

- All the fleets (Eel and Shrimp) and the CNPE.
- The primary producers and detritus, which are pooled into a single compartment because there is no need to separate them since we do not model their trajectories. They are at the basis of the trophic network and there are not input value available for both (like forcing functions in EwE).
- Eel is outside for the same reason as in EwE. Its dynamic does not depend on the food-web.

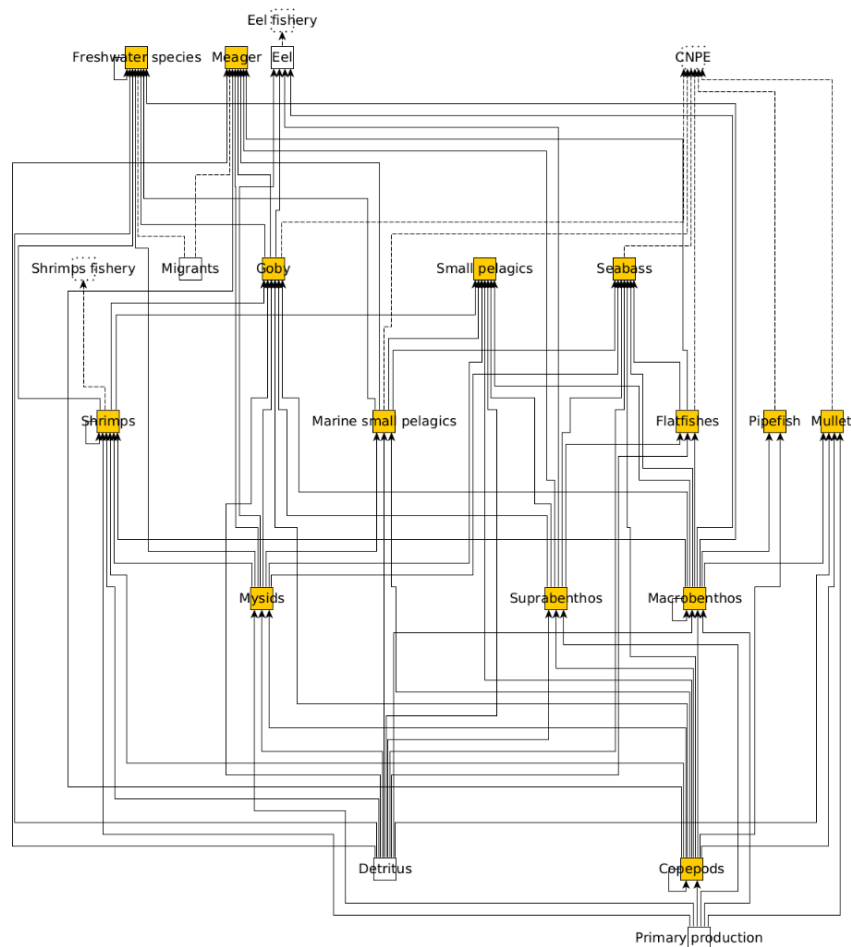


Figure 3 : Trophic network of the Gironde estuary. In yellow: the intern trophic groups, in white: the extern trophic groups with “migrants” regrouping Meager and Freshwater migration. Note that the migrant component exists only in RCaN. The other white components in solid lines are EwE trophic groups, which are always subject to forcing (forcing biomass for eel and forcing function for detritus and primary production). In dotted white: the fisheries, which are extern too. Solid arrows are trophic flows and dotted arrows are non-trophic flows (catches and migrations). Detritus and Primary Producers are merged into one large component in RCaN.

Similarly to EwE, it is also required to provide some parameters of species dynamics, that are related to the dynamics of trophic groups (both parameters of equation 5 and parameters of implicit constraints). A parallel exists with some parameters of EwE (Lindstrom *et al.*, 2017). To facilitate the comparison between the two models, we thus directly translated parameters

from EwE to parameters in RCaN (Appendix 5). It should be noted that there is no need to provide all these parameters for external groups, except potentially their digestibility factor if they constitute a prey in the system, since their biomass is not modelled (Drouineau *et al.*, 2021).

1.2.2.3.2. Explicit constraints: binding the model and time series

Contrary to EwE, a RCaN model is not calibrated on data. Indeed, rather than seeking the set of parameter values that ensure the best fit of predictions to observations, RCaN explores all the space of possible trajectories by uniformly sampling trajectories that satisfy all constraints. Constraints include implicit constraints and equation 5. In addition to those, observations can be used to define explicit constraints, e.g., by defining the range of plausible values for past biomasses of flow based on external estimations.

Here we used the same time-series used for EwE, which come from monitoring programs, to define such explicit constraints:

- Biomasses constraint: as in EwE, we assumed that time series of biomasses are good indices of the time trends, more precisely, good relative indices but that they provide poorer estimations of the absolute biomass since the catchabilities are uncertain. Therefore, we chose to define both informative constraints on relative biomasses time series, and less informative constraints on absolute values. The constraints are specified as:
 - o relative:

$$Bobs_t / \text{mean}(Bobs_{1986:2014}) * 0.1 \leq B_t / \text{mean}(B_{1986:2014}) \leq Bobs_t / \text{mean}(Bobs_{1986:2014}) * 2 \quad (6)$$

- o absolute:

$$Bobs_t * 0.2 \leq B_t \leq Bobs_t * 5 \quad (7)$$

- Catches of the “fisheries” constraints are separated into two different constraints:
 - CNPE: the literature provides an estimation of the mortality rate rather than absolute values of “catches”. Therefore, we wrote the constraints as:

$$\text{Flux to CNPE}_t \leq \text{mean} \left(\text{Flux obs to CNPE}_t / Bobs_t \right) * B_t \quad (8)$$
 - Commercial fisheries: the flows are constrained by the landings data. The variations are bounded by a wide confidence interval (twice the constraint explained): $\text{Landings}_t \leq 2 * \text{Landingsobs}_t \quad (9)$

The Eel group is considered to be external to the system. However, eels are important predators and, as such, we constrained the amount of predation. We assumed that the yearly sum of trophic flows towards Eel should be less than its biomass at year t in the observed time-series multiplied by its satiation. The satiation was calibrated the same way the other groups were, though it is not directly used in the model but just in this equation/constraint:

$$(\text{Goby} \rightarrow \text{Eel}) + (\text{Macrobenthos} \rightarrow \text{Eel}) + (\text{Mysids} \rightarrow \text{Eel}) + (\text{Shrimps} \rightarrow \text{Eel}) + (\text{Smallpelagics} \rightarrow \text{Eel}) + (\text{Suprabenthos} \rightarrow \text{Eel}) \leq \text{EelObserved} * \text{satiation} * 1.1 * 3 \quad (10)$$

with names of species representing the predicted biomass of the species, the arrow being equal to the transfer of biomass of Eel prey to Eel. We assumed a restricted variation of the biomass of 10 %. The 3 representing the confident interval.

We also assumed that the immigration of Meager or Freshwater species cannot be greater than 100 times the standing biomasses predicted by the model, to avoid incredibly large increases (and postulating that the carrying capacity of the ecosystem is not infinite).

All these constraints are listed in the appendix 6.

1.2.2.3.3. Sampling food web time trajectories

The sampling is achieved using a MCMC algorithm that generates uniformly distributed trajectories within the so-defined polytope satisfying the constraints. We decided to use ten chains and, in each chain, the algorithm is forced to sample 150 trajectories. To properly space the RCaN outputs, a thinning of 2,000 is used. This provides us 1,500 samplings, which is enough for the analysis of the results. The R package and a graphical interface allow us to automate this step.

As such, RCaN generates samples of possible trajectories: each iteration of the MCMC algorithm is a set of biomasses and flows for all time step satisfying all the constraints.

1.2.2.3.4. The analysis of this model

To analyze the outputs of the RCaN model, a scaled principal component analysis (PCA) on the simulated trajectories of the food web was carried out. The PCA variables are the log-transformed biomasses of the trophic groups, and each individual corresponds to the state of the food web in a given year in a given iteration of the MCMC. Thus, the number of columns in the table corresponds to the number of internal trophic groups and the number of rows is the product of the number of years and the number of MCMC iterations. Then, a hierarchical clustering (Euclidean distance, Ward method) based on the coordinates of the PCA was carried out to detect typologies of food-web structure (Sivel et al., 2021) and potentially the existence of temporal patterns. Since it turns out that resulting clusters indeed correspond to groups of years, we then defined periods as groups of years belonging to the same cluster.

For each cluster, we calculated the percentage of accuracy, which represents the proportion of years in the attributed cluster:

$$Accuracy = \frac{\sum \text{dots in the attributed cluster}}{\text{number of years in the cluster}} / 500 * 100 \quad (11)$$

500 being the maximum number of points in each year per cluster.

To check the existence of specific trophic controls in each cluster, we used graphical diagnoses provided by the package RCaN, such as the function *ggTopDownBottomUp*. This function displays a graph showing how the growth of a species (measured as $\frac{B_{t+1}}{B_t}$) is correlated either to the amount of feeding (we call feeding the sum of incoming trophic flows in time step t) or to the amount of predation (we call predation the sum of outgoing flows at time t). For each iteration, *ggTopDownBottomUp* computes the correlation between growth and feeding and between growth and predation for all the years within the considered period. Then, *ggTopDownBottomUp* produces histograms of correlation coefficients values estimated in the different iterations. Strong positive correlations between growth and feeding suggest a bottom-up control while strong negative correlations between growth and predations suggest a top-down control.

This will allow us to observe if there is a variation of the trophic controls in the estuary among the different periods (Sivel et al., 2021).

Here are some other functions which can help us to better understand the changes in trophic control in this ecosystem:

- *ggGrowth*, which displays pairs plots of biomass (x-axis) and growth (y-axis) and shows how the growth of a population evolves according to its biomass. It can for example be

used to detect emerging limitations in the capacity of the estuary when growth decreases with biomass.

- *ggSatiation*, which shows if the incoming fluxes (feeding) (y-axis) depend on the biomass of the species (x-axis). This could be used to detect if there is a competition on the resources. For example, a rise of the biomass combined with a decrease in the fluxes shows us that an increase in the biomass could lead to a competition for the resources.
- *ggTrophicRelation*, which displays how much the incoming fluxes (y-axis) depend on the biomass of the prey (x-axis). For example, if the biomass of a prey rises and the fluxes to its predator rise too, there is a bottom-up control. Thus, this will show us if a bottom-up control governs the trophic relation and which prey implies this control.

Given our initial questions about the role of marine juveniles on the changes discovered and on the possible risk of trophic limitation in the estuary (Chevillot *et al.*, 2019); we chose to focus on Flatfish and Macrobenthos groups.

1.3. Comparison between EwE and RCaN

To compare the two models, we projected EwE outputs (biomasses per year) in the PCA planes and in the clustering of RCaN. For this PCA, we used the relative biomass to observe if both models predict the same trend. This allowed us to observe if a CaN model, which is non-deterministic, could match the same trajectories as EwE, a deterministic model. This will show us if the three different results of EwE follow the same trends as RCaN. Thus, if the EwE results are in the same cluster as RCaN.

2. Results

2.1. First approach: EwE

For this part, the SFP provided us the matrix of vulnerability and allows us to calibrate the different models. Thus, the biomasses and fluxes of each model could be estimated.

2.1.1. Visual fit to data

As explained earlier, here, we focused on the four trophic groups whose biomasses were never forced in any of the calibration exercise: Shrimps, Copepods, Mysids and Macrobenthos.

For Shrimps, we observed a better visual fit with assumptions H2 and H3 than with H1, in which time shifts peaks are visible. For example, H1 predicted the biomass peak earlier (in 1988) compared to the actual biomass peak observed in 1990. Underestimations (e.g., in the late 1990s) or overestimations of the biomass (e.g., in the 2000s and 2010s) for H1 are visible too (Figure 4). While different, it is not possible to detect any obvious systematic patterns on the fits H2 and H3 though H3 simulations seem slightly closer to observed data (Figure 4).

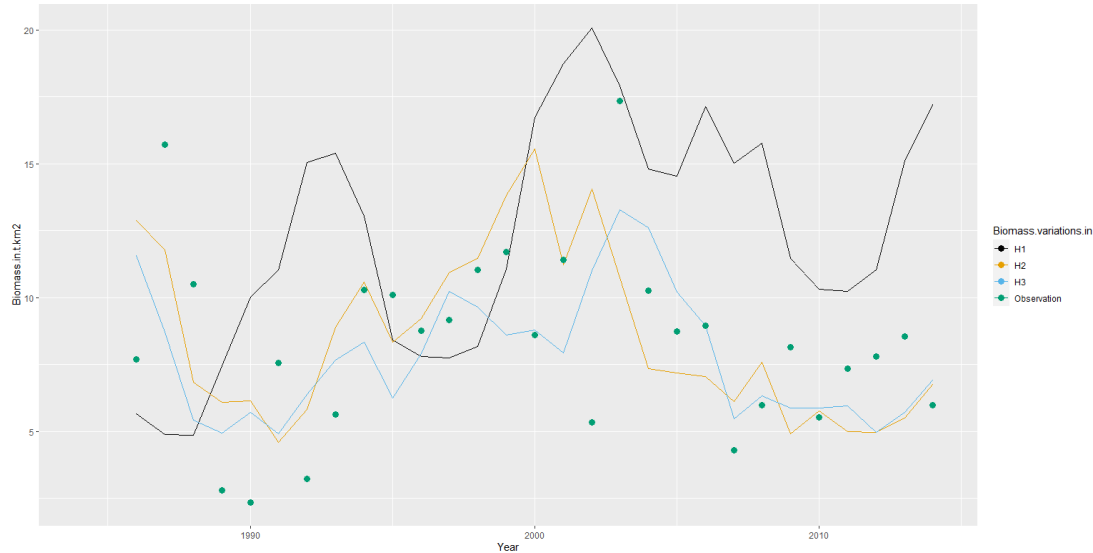


Figure 4 : Fitting the predicted Shrimps biomasses of H1, H2 and H3 to the observed biomasses.

For Copepods, the visual difference is difficult to perceive between the three assumptions. Especially between H1 and H2 of which the variations are quasi-similar (Figure 5). The three assumptions remain stable over time, whereas the observed biomass varies a little around 200t (Figure 5). H3 is slightly different from the other two hypotheses. With this visual, it is thus difficult to determine which assumption better fits the observed biomasses.

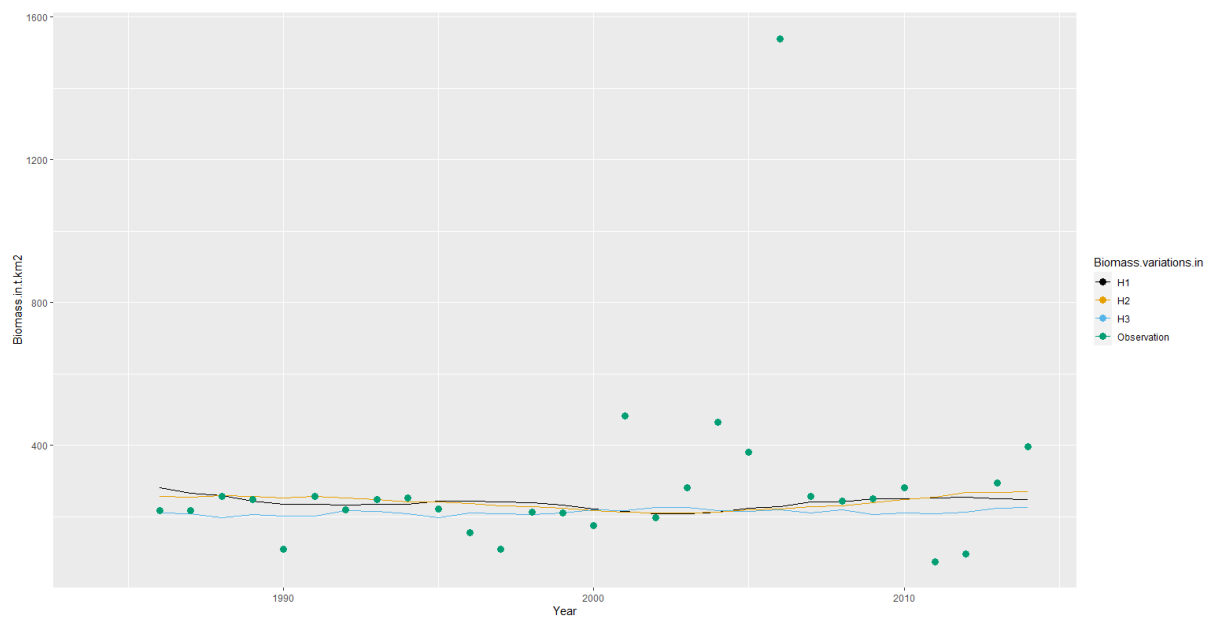


Figure 5: Fitting the predicted Copepods biomasses of H1, H2 and H3 to the observed biomasses.

For Mysids, the three assumptions, especially H1, do not follow the beginning of the time series. It is only between 1995 and 2010 that the three assumptions follow the trend of the time series. Between these years, calibration H2 provides a better fit to the data (Figure 6). After 2010, the predicted biomasses of the three assumptions are far above or below the observed ones.

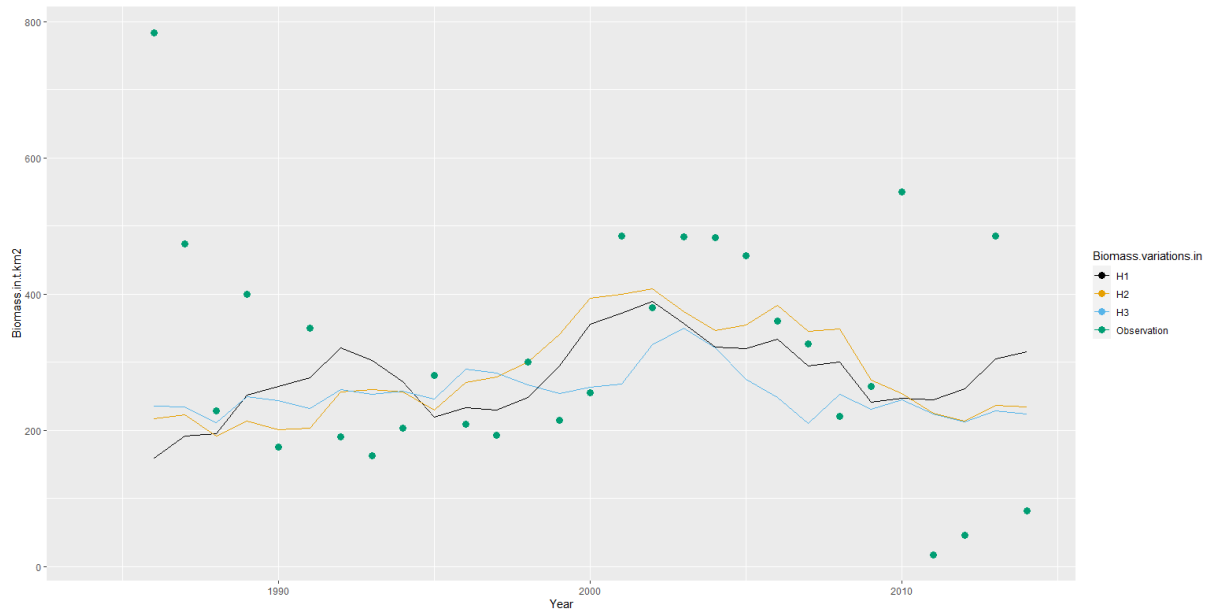


Figure 6 : Fitting the predicted Mysids biomasses of H1, H2 and H3 to the observed biomasses.

For Macroenthos, before 1999, the three assumptions lead to light underestimations and after this year, to light overestimations. H1 is the assumption where the variations are the most shifted compared to the two other calibrations. H3 better fits the observed biomass and its variations. H2 is an in-between (Figure 7).

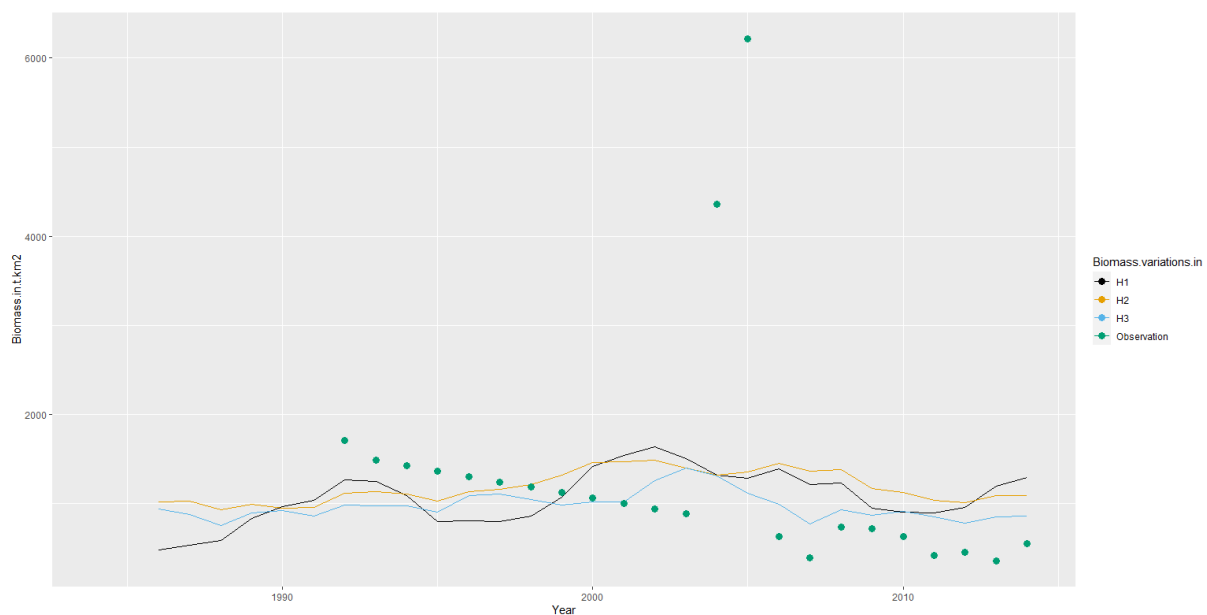


Figure 7 : Fitting the predicted Macroenthos biomasses of H1, H2 and H3 to the observed biomasses.

The results of the visual assessment show us that calibration H3 tends to better fit the data, followed by H2. This suggests that forcing biomass of top predators (or marine juveniles) is more informative than just forcing the primary production or the detritus input.

2.1.2. The AIC

The SS and the AIC were computed for each trophic calibration, accounting only for the four common trophic groups to have a comparable dataset among exercises. Consistently with the visual analysis of the fits, calibration 3 provides the lowest AIC while calibration 1 provides the poorest (Table 2). Differences in AIC among calibrations are greater than two, suggesting that the quality of the calibrations is significantly different.

Table 2: AIC and SS modelling with EwE. The asterisk is on the global SS and AIC of each model, which is shown as an indication.

Calibration	SS	AIC	SS of the common trophic groups	AIC of the common trophic groups
1	502.6	-174.3	48.8	-11.2
2	198.7	-506.3	40.3	-22.6
3	85.54	-645.8	35.8	-35.8

2.2. Second approach: RCaN

For the RCaN part, the series of biomasses and fluxes is provided by the sampling routine of RCaN. All the trajectories are sampled inside the polytope of constraints.

2.2.1. Biomass variations of the four common trophic groups of EwE

A quick overview of the results is shown in this section. It focuses on the variations of the four same trophic groups as EwE in order to compare them.

For the Copepod groups, huge differences between each trajectory can be observed. For example, in 2006 the biggest biomass predicted is five times bigger than the smallest one. There are remarkable points such as a diminution in the late 1980s, 1996 and after 2010 (divided by 2) and a huge augmentation in 2000, 2005 and 2012 (3 or 10 times) (Figure 8).

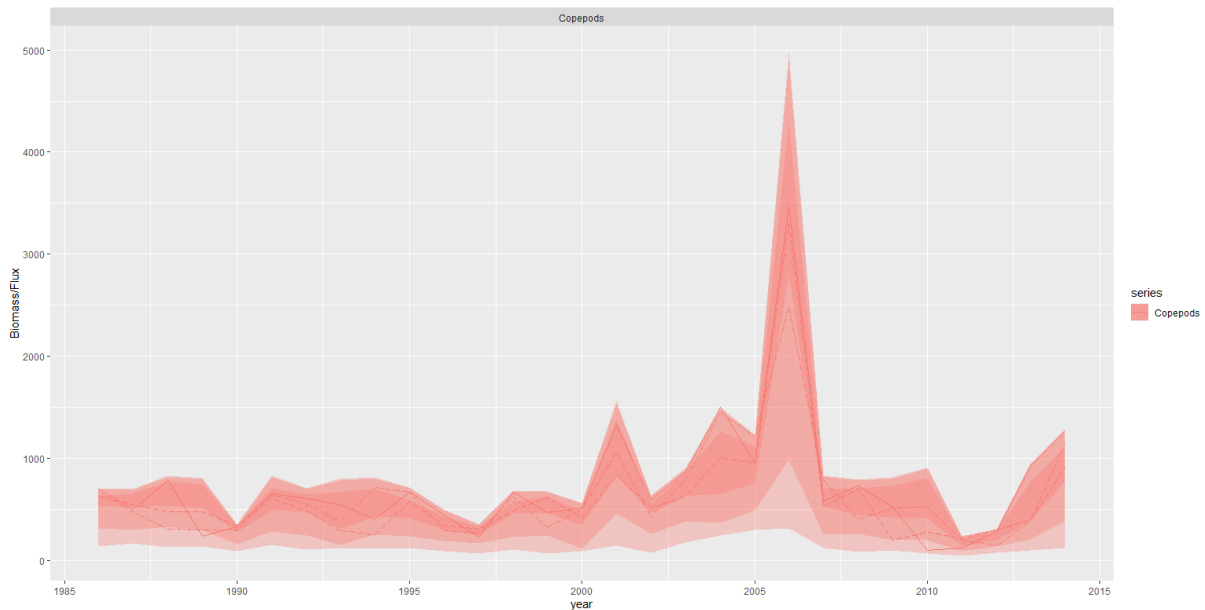


Figure 8: The different RCaN trajectories of the copepod biomass. The line corresponds to median of the MCMC simulation, and the ribbon corresponds to quantiles 2.5.

For the Macrobenthos groups, the first remarkable observation is that before 1992, the estimation of the biomass is very high (the biggest difference is 90 times bigger) compared to after 1992. The variations after 1992 look steady. The peak before 1992 is certainly mainly due to the lack of time series before this year. RCaN shows us the peak of biomass in 2005. The biomass of Macrobenthos is depleting through the years with an upturn in 2005 (Figure 9).

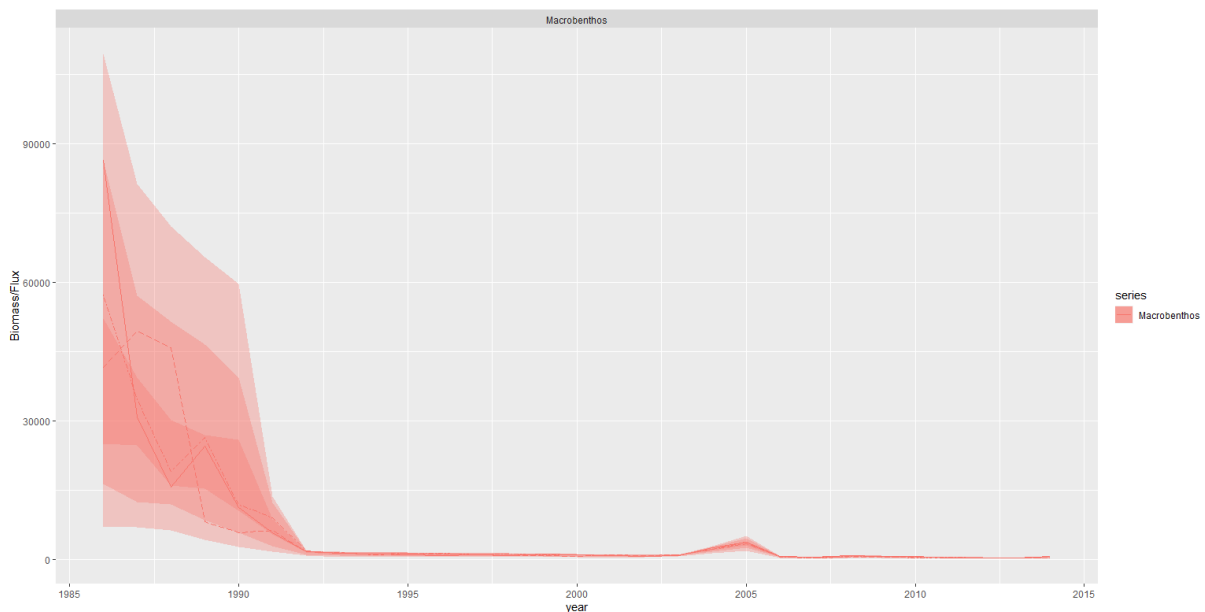


Figure 9: The different RCaN trajectories of the Macrobenthos biomass. The line corresponds to median of the MCMC simulation, and the ribbon corresponds to quantiles 2.5.

The variations of shrimp biomasses can also exhibit huge differences between each trajectory and each year (three times bigger or lower). The remarkable points are the huge decreases from 1988, the upturn between 1990 and 1992 and a second drop in 2001 followed by a huge peak (Figure 10).

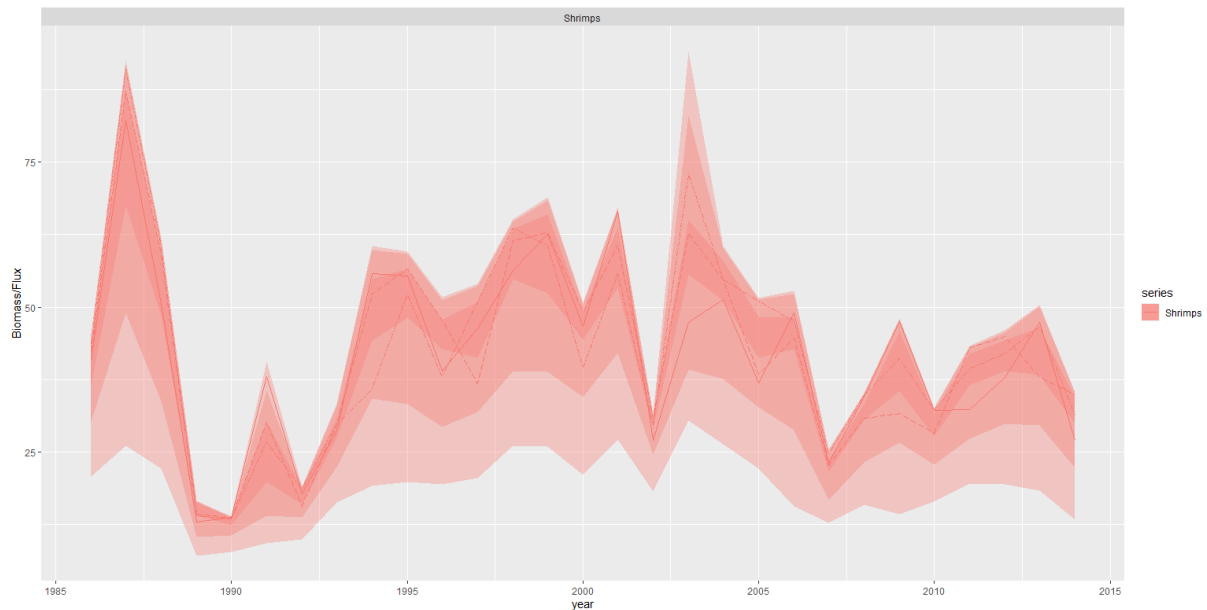


Figure 10 : The different RCaN trajectories of the Shrimps biomass. The line corresponds to median of the MCMC simulation, and the ribbon corresponds to quantiles 2.5.

As in the other groups, the variations are huge between each trajectory and year. Here there are remarkable points such as the depletion in the beginning of the simulation and the augmentation in 2000 followed by the diminution of the biomasses from 2006 to 2011 (Figure 11).

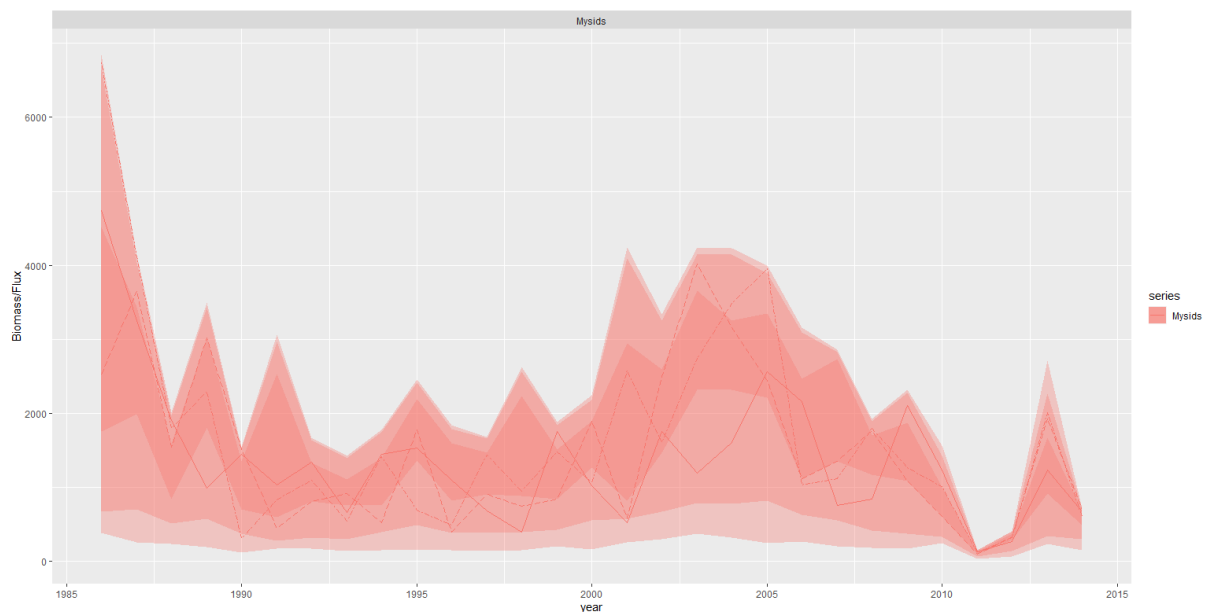


Figure 11: The different RCaN trajectories of the Mysids biomass. The line corresponds to median of the MCMC simulation, and the ribbon corresponds to quantiles 2.5.

Compared to EwE, the set of trajectories of RCaN better follows the variations of the observed biomass. In fact, the main peaks of biomasses are represented for all the trophic groups.

In general, the biomasses of the four groups are decreasing through the years, except for the Copepods, which are globally constant (not counting the 2006 peak).

Now, I will focus on the results proper to RCaN.

2.2.2. PCA results

The hierarchical clustering of the RCaN results allows us to gather RCaN trajectories in four clusters, which explain 70% of the inertia (Figure 12).

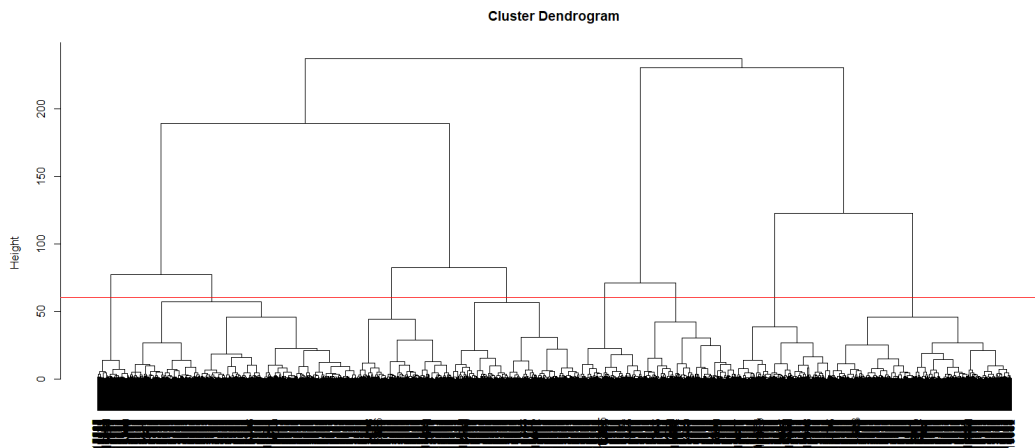


Figure 12 : The cluster dendrogram of RCaN trajectories. Red line represents the cut to separate the 4 clusters.

Figure 13 displays the individuals in the two first axis of the PCA (which represent 24.5% and 18.6% of the total inertia respectively while the three first axis represent 57.1%). Each dot stands for a year in an iteration of the MCMC chain. The color indicates the cluster to which the point following the above presented hierarchical clustering in the three PCA dimensions belongs.

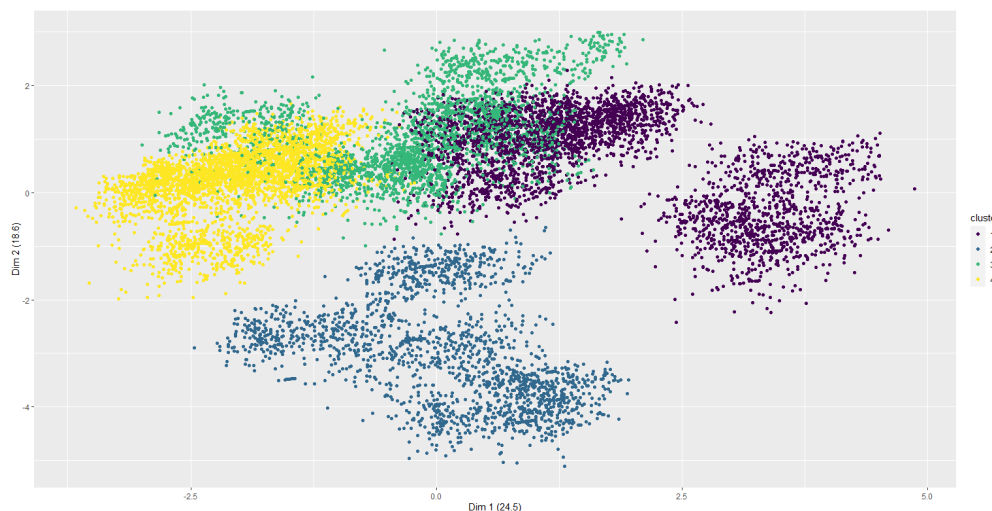


Figure 13 : PCA of the RCaN results. One dot represents a biomass of a species in a certain year and iteration of the MCMC chains. The ensemble is the entire trajectory that RCaN sampled. Colors stand for the clustering from the hierarchical clustering (Figure 12).

Clusters regroup consistent periods of years (Table 3). As such, the PCA and the hierarchical clustering put forward a temporal pattern in the structure of the food web with different (good) accuracy (Table 3).

Table 3 : The clusters, their time range and the accuracy of the grouping.

Cluster	Time range	Accuracy (%)
1	1986-1988	100
	1994-2000	81.5
2	1989-1993	99.98
3	2001-2006	94.6
4	2007-2014	98.5

As the first cluster is divided into two periods, we decided for the rest of the manuscript to rename the clusters according to their temporality:

- Cluster 1 (1986-1988): period 1
- Cluster 2 (1989-1993): period 2
- Cluster 1 (1994-2000): period 3
- Cluster 3 (2001-2006): period 4
- Cluster 4 (2007-2014): period 5

2.2.3. Identification of the trophic controls within each period

Here, the results are shown for the different above-highlighted periods on Flatfish and Macrobenthos but the results on all the species are displayed in appendix 7.

For Flatfish, during the first and the second period Growth and Feeding are strongly positively correlated, suggesting a bottom-up control. During the third period, the relation Growth-Predation becomes more visible, but the peak is far from being centered on one and thus the relationship is still not strongly negatively correlated compared to the Growth-Feeding relation (Figure 14; P1, P2 and P3). Therefore the trophic control seems mixed but mainly bottom-up. For the last two periods, the shift continues towards a more top-down control. The Growth-Predation relation is more and more negatively correlated, and the other relation is less and less positively correlated (Figure 14; P4 and P5). Thus, the Flatfish group (whose predators are Seabass and Meager) has progressively moved from a bottom-up control to a more top-down control.

For the Macrobenthos, the trophic control is mixed. Both relations are mixed during the first three periods so we cannot exactly conclude on the trophic control (Figure 14; P1, P2 and P3). However, from period four, the two relations are separated, and the peak of the Growth-Predation relation is near one. Thus, this relation is strongly negatively correlated, and the other relation is more laid out. Therefore, there is a predominance of a top-down control on the macrobenthos stock (Figure 14; P4). For the last period, both relations are not strongly correlated, each peak is in average of 0.5 (respectively negatively for the Growth-Predation and positively for the Growth-Feeding). We can conclude that the trophic control is mixed in the last period (Figure 14; P5).

Thus, there is a variation in the trophic control through time for both Flatfish and Macrobenthos. The trophic control for both groups tends to be a top-down control.

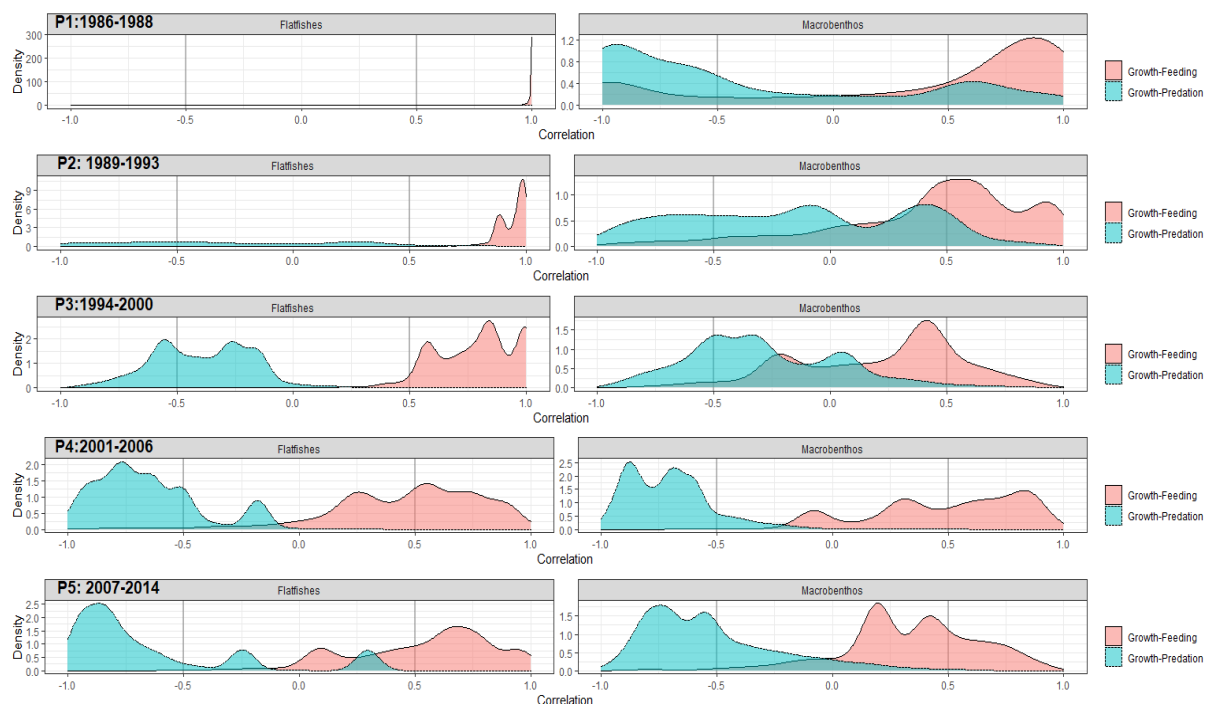


Figure 14 : Trophic control through the time by period: period (P1), period 2 (P2), period 3 (P3), period 4 (P4) and period 5 (P5). Growth-Feeding is used to detect bottom-up control and Growth-Predation to detect the top-down control.

Now that we have studied the temporal evolution of the trophic control inside the ecosystem (here presented only for these two trophic groups), we will focus on understanding these changes and in particular the evolution of the trophic relations between Macrobenthos and Flatfish but also the possible evolution of the trophic capacity limitation in the estuary.

2.2.4. The relations between prey and predators

2.2.4.1. Trophic controls on species growth rate

Figure 15 shows how the growth of Flatfish (i.e. B_{t+1} / B_t) varies with their biomass (at time t).

A decrease in growth is expected with an increase in biomass because the carrying and trophic capacity of the estuary is finite. The steeper the growth-decreased slope is, the more limited the capacity is. Here, the decrease in growth is not linear with the augmentation of the biomass. It varies a lot through the periods. In every period, an early drop around the low biomass (5-15 t) is observed. It is followed by a huge increase until a threshold (the growth is almost equal to 2 for all the periods). The biomass of the threshold varies according to the periods, but it is always before 20 t except for period four whose biomass is near 40 t. Beyond the threshold, the growth decreases more or less quickly according to the periods. The same pattern is repeated every two periods. In period four, the decrease in growth is slower and after the transition between the period four and five, the slope is steeper (Figure 15). It can indicate an emerging capacity limitation of this estuary.

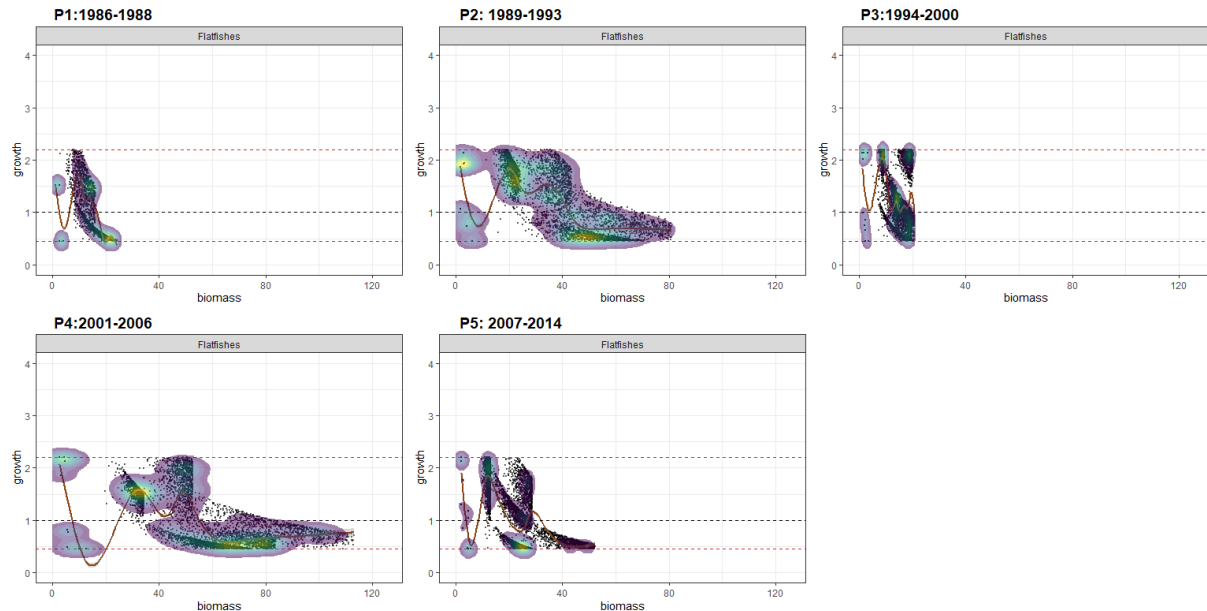


Figure 15 : The growth (biomass at $t+1$ divided by biomass at t) of Flatfish depending on their biomass (at time t) in stable period 1 (P1), 2 (P2), 3 (P3), 4 (P4) and 5 (P5). The red dotted lines represent the minimum and the maximum of the growth (resulting from the inertia constraint). The dot represents one biomass in a trajectory sampled. The color varies depending on the density of dots. The line is a smoother of the relationship growth~biomass.

Concerning Macrobenthos, the growth always decreases quickly with the augmentation of the biomass and the slope is increasingly steeper through time. The real difference is during period four when the growth rises with the augmentation of the biomass to a certain threshold (2200-2500 t of its biomass). Otherwise, the growth rate is quickly below one. Sometimes the growth is even steady despite the augmentation of the biomass. Period five has the steeper slope and the biomass does not rise as much as before (Figure 16). This shows us a real limitation in the capacity of the estuary for the Macrobenchos.

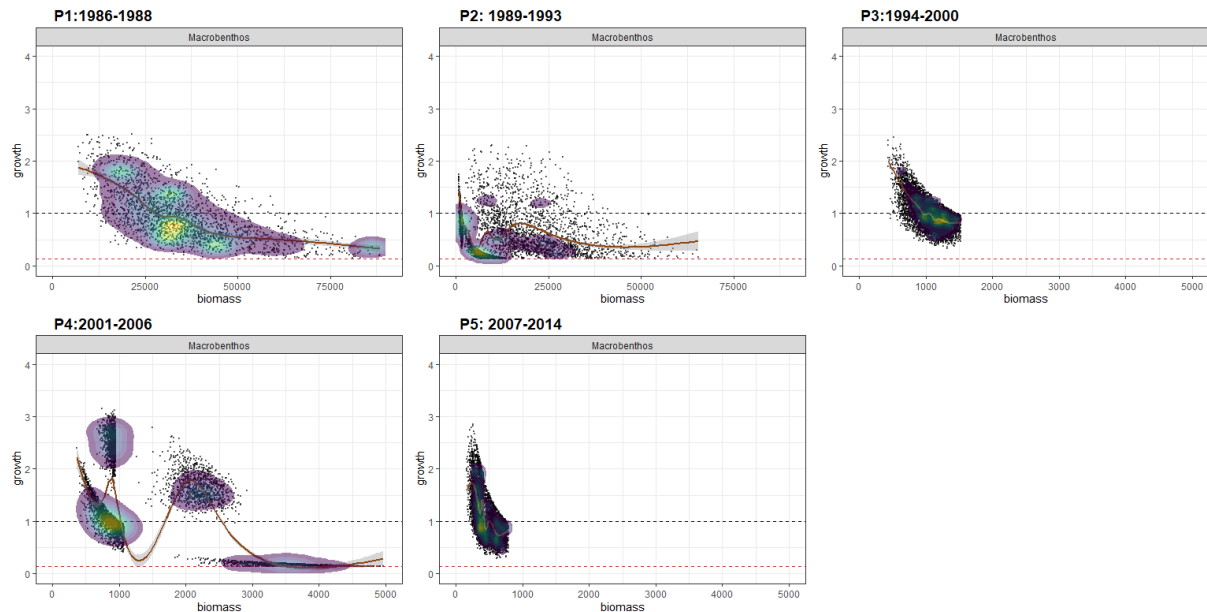


Figure 16 : The growth (biomass at t+1 divided by biomass at t) of Macrobenchos depending on their biomass (at time t) in stable period 1 (P1), 2 (P2), 3 (P3), 4 (P4) and 5 (P5). The red dotted lines represent the minimum and the maximum of the growth (resulting from the inertia constraint). The dot represents one biomass in a trajectory sampled. The color varies depending on the density of dots. The line is a smoother of the relationship growth~biomass. Note that the two first periods have not the same biomass range as the last three.

All these graphs highlight that whether it concerns the Macrobenchos or the Flatfish, there is an emerging capacity limitation of the estuary.

Now, we will focus on the trophic relations and observe if the emerging capacity limitation is partially due to a potential trophic limitation.

2.2.4.2. Trophic relations

Figure 17 shows how the predation flux from Macrobenthos to Flatfish at time t , varies with the biomass of Macrobenthos at time t . The scale of the x-axis is not the same according to the period. Indeed, the prey's biomasses simulated by the model are lower from the second period onward and especially very low at periods three and five. Therefore, the biomass of the Macrobenthos is depleting through the years. The patterns for each period are quite similar (except for the third and last one where it is a bit different and very condensed). There seems to be a positive relationship between prey biomass and the predation flow. The more prey there is, the more predation there is on that prey (Figure 17).

It indicates that the Macrobenthos group induces a bottom-up control on the Flatfish group.

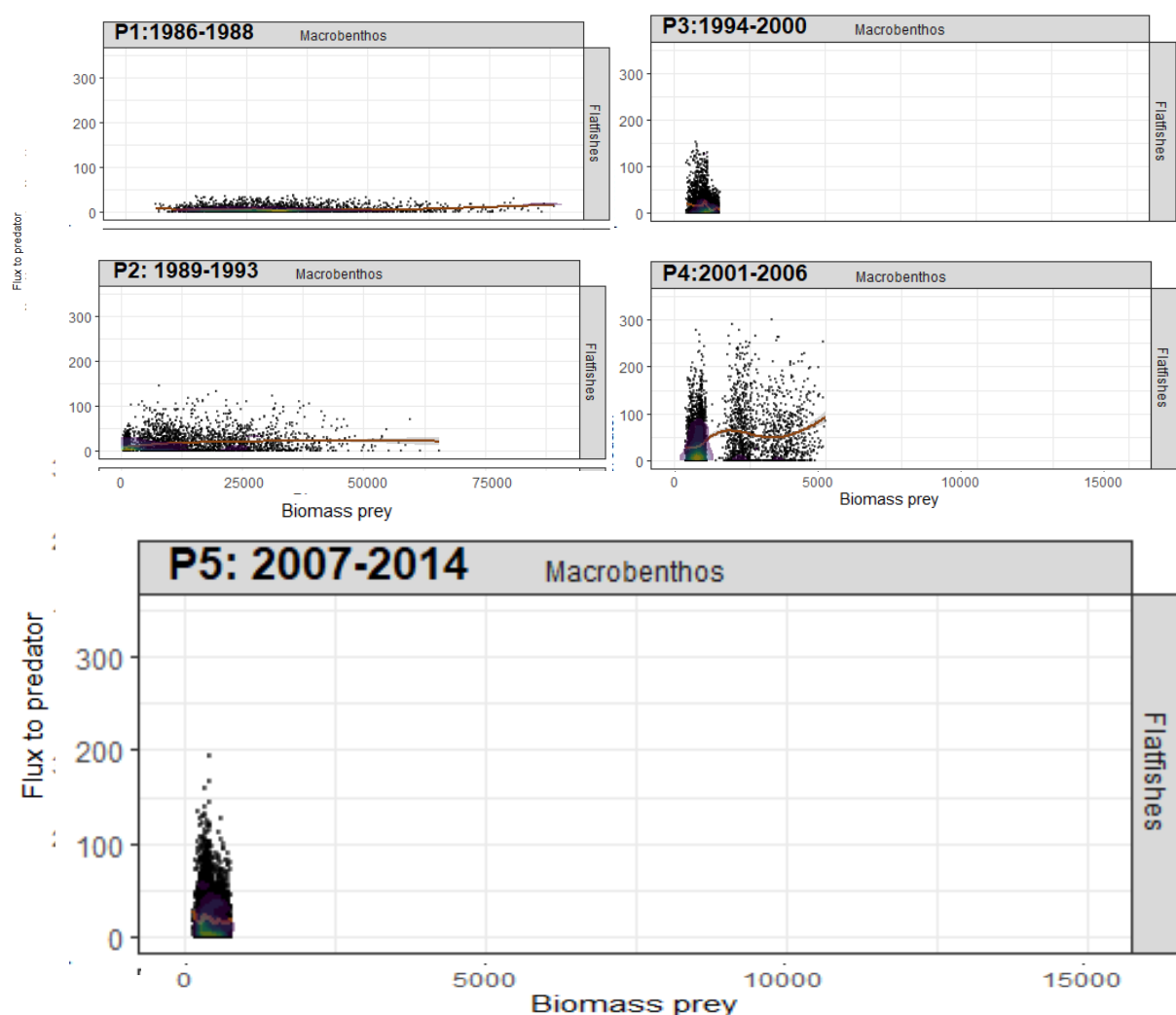


Figure 17 : Flux of Macrobenthos biomass to Flatfish depending on the Macrobenthos biomass in stable period 1 (P1), 2 (P2), 3 (P3), 4 (P4) and 5 (P5). The dot represents one biomass in a trajectory sampled. The color varies depending on the density of dots. The line represents the mean trajectory of the flux depending on the Macrobenthos biomass. Note that the two first periods have not the same biomass range as the last three.

Figure 18 aims at highlighting whether resources are limiting for Flatfishes.

For the two first periods, the flatfishes were not at their satiation capacity when the biomass rose. However, there is an evolution through the periods. The more we advance through the periods, the more they are at their satiation even if the biomass rises. It is from period three that the feeding flux is linear with the biomass and follows the maximum satiation. In the last period, the flux is less correlated to the maximum satiation, which matches the second depleting of Macrobenthos biomasses. This reinforces the idea that resources may become limiting for those species when their biomass is too high, at least in the early periods and the last one (Figure 18).

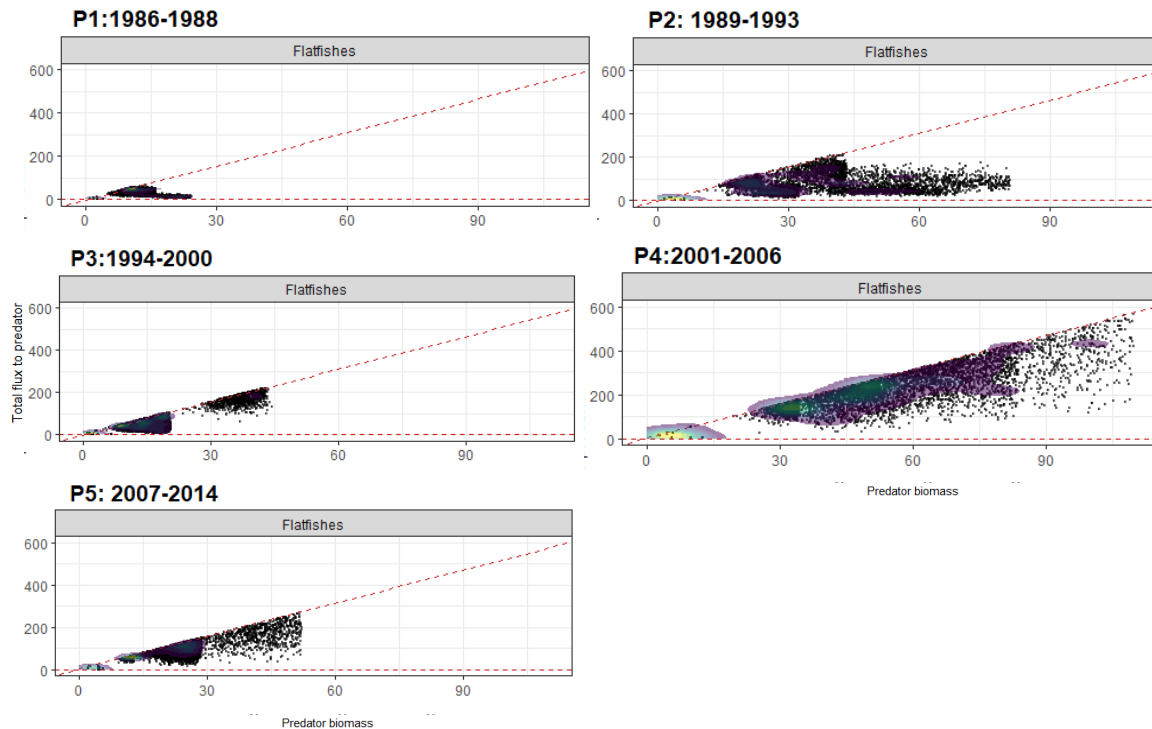


Figure 18 : The flux of prey to Flatfish depending on their biomass in in stable period 1 (P1), 2 (P2), 3 (P3), 4 (P4) and 5 (P5). The red dotted lines represent the satiation. The dot represents one biomass in a trajectory sampled. The color varies depending on the density of dots.

All these graphs provided by RCaN allow us to better understand the evolution of the trophic control. The evolution of the trophic control to a top-down control (or mixed) (Figure 14) and the global diminution of the biomass of the main prey of top-predators (Figure 8 to 11) occurred at the same time. This could explain the trophic limitation observed in figure 18 and the importance of the slight augmentation in Macrobenthos shown in figure 17.

Now that we have all the information given by RCaN, we can proceed to the comparison of the two models.

2.3. Comparison of the results from the two models

All the (relative) biomasses simulated by both RCaN, and EwE are displayed on the first plane of the PCA previously presented (Figure 19). The relative biomass at time t is the absolute biomass at time t divided by the mean absolute biomass of a sample. Results from EwE are projected as supplementary variables.

EwE trajectories are included in the possible set of RCaN trajectories. More precisely, simulations resulting from the calibration associated with H1 are projected in the center of the PCA plane whereas simulations associated with H3 are more off-centered and more located in the corresponding RCaN resulting plots. H2, being an intermediary, is in between of these two hypotheses in the PCA.

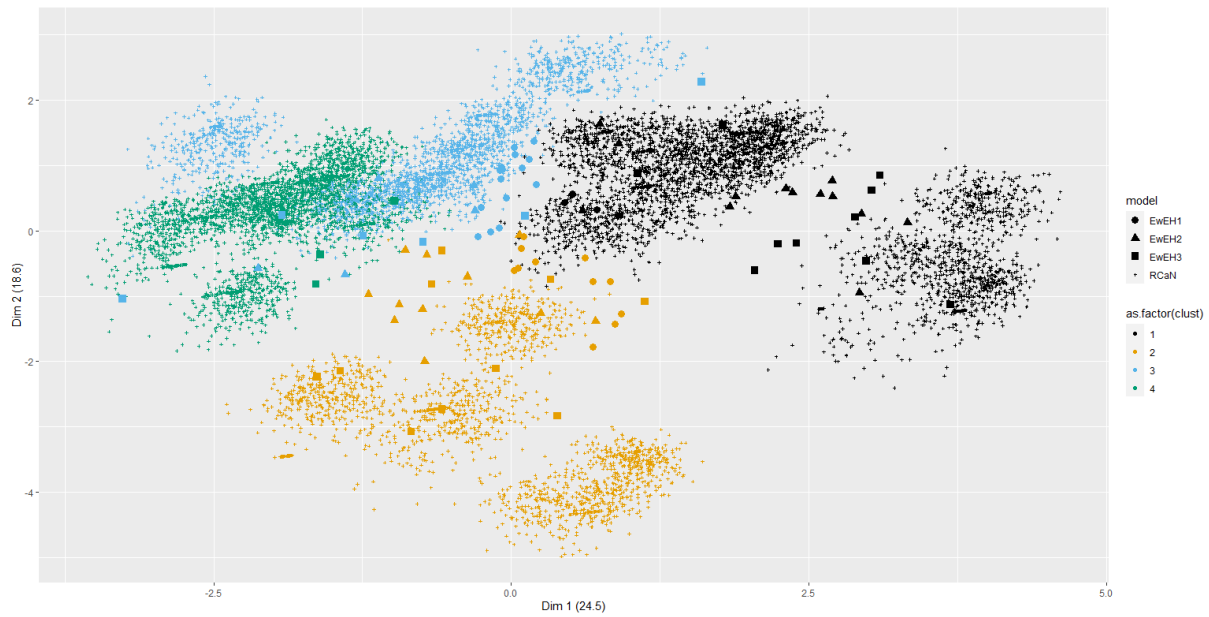


Figure 19 : PCA of the relative biomasses resulting from RCaN and EwE. One dot represents a biomass of a species in a certain year and iteration of the MCMC chains for RCaN and represents a biomass of a species in a certain year and model for EwE. Colors stand for the time periods resulting from the hierarchical clustering as for the previous PCA.

EwE results are thus consistent with RCaN trajectories.

3. Discussion

In this analysis, we focused on the evolution of the Gironde estuary ecosystem and particularly the evolution of the trophic controls inside this ecosystem using an original approach combining two food-web models: EwE and RCaN. This work aims at going further previous analyses that had documented an augmentation of marine fishes and a collapse in the benthic macrofauna after the 2000s (Pasquaud *et al.*, 2012; Chaalali *et al.*, 2013; Chevillot *et al.*, 2019). The models confirmed both observations, but they also provided new insights on their causes.

A few years ago, Chevillot *et al.* (2019) highlighted the existence of two regime shifts in the Gironde estuary, with stable periods between these shifts (Chevillot *et al.*, 2016). The two shifts discovered by them took place around 1989 and 2002, while in my study we discovered four shifts, which happened in 1988, 1993, 2001 and 2006. Our results are rather consistent (although we observe five stable periods instead of 3) with very timely shifts occurring almost at the same time. Our results confirm that the estuary has progressively changed with a first period dominated by preys like benthic macro fauna towards a latest period dominated by predators such as marine juvenile fish (Pronier and Rochard, 1998; David *et al.*, 2005; Chaalali *et al.*, 2013; Bachelet and Leconte, 2015; Chevillot *et al.*, 2016).

The trophic control in this estuary has been studied since the 2000s with Lobry *et al.* (2008), who stated that the trophic control was dominated by a bottom-up control. Then, Chevillot *et al.* (2019) compared the functioning of the ecosystem using three “static” pictures of stable periods (corresponding to the in-between of the abrupt shifts) provided by Ecopath. They suggested that top-down control might become more important, because of the potential trophic cascades induced by the increase in the number of predators and a decrease in the number of their preys. The use of dynamic food web models allowed us to go further and to explore the drivers of the changes over the full study-period. Indeed, EwE results suggest that the past dynamics of the food web in the estuary was mainly driven by the dynamics of top-predators (including marine juveniles) biomass, confirming a top-down control. The increase in the relative abundance of top predators in the Gironde estuary is not explained in our analysis, but is likely due to environmental changes: the marinization (Pasquaud *et al.*, 2012; Chaalali *et al.*, 2013; Chevillot *et al.*, 2016) of the estuary has probably improved its suitability for marine juveniles (Chevillot *et al.*, 2019), while the decline in diadromous fish (Pronier and Rochard, 1998; Rougier *et al.*, 2012; Chevillot *et al.*, 2016) populations have limited the competition.

RCaN provided additional insight on the temporal changes of trophic controls over time. It suggests a progressive shift from a bottom-up control towards a top-down control and that, in the last period, there are more top-down (or mixed) controls for most of the groups. This might be explained by a cascade effect from top-predators and marine juveniles to the lowest trophic levels, as suggested by Chevillot *et al.* (2019).

Chevillot *et al.* (2019) suggested that the simultaneous increase in marine juveniles and decrease in their prey might jeopardize the nursery function of the estuary. We explored this assumption by focusing on Flatfishes and Macrobenthos. Using RCaN, we observed that the biomass of the Macrobenthos varies a lot during stable periods and the decrease of the growth gets stronger through time, so the growth rate is more quickly below one. The situation appears threatening in the latest time period with a faster declining rate. This explains the overall collapse over the years.

We also observed that while flatfishes were far from satiation at the beginning of the studied periods, they progressively reached the satiation despite the decrease in Macrobenthos biomass. This might be due to the progressive decline in some Flatfishes competitors such as diadromous fishes (Pronier and Rochard, 1998; Rougier *et al.*, 2012; Chevillot *et al.*, 2016). However, from 2001 and especially after 2007, flatfishes are increasingly far from reaching

their maximum satiation and this might be a sign of trophic capacity limitation: as such, and as suggested by Chevillot et al. (2019), macrobenthos could be a limiting factor for the growth of marine juveniles.

This study does not enable us to determine the key factors for these changes, and especially to disentangle between changes in environmental conditions and anthropogenic pressures. However, it might be possible in the future to explore the correlation or synchrony of environmental variables with the growth rates and the transitions periods depicted by RCaN.

The risk of trophic limitation for marine juveniles in estuaries is an important question in fishery sciences. While some scientists argue that the carrying capacity of nurseries is almost never reached (Van der Veer et al., 2000; Vinagre et al., 2008) and that juveniles are not affected by the lack of resources (Diaz et al., 2011; Selleslagh et al., 2012), others have observed that food resources can be limiting (van der Veer, 1993; Nash and Geffen, 2000; Nash et al., 2007; Le Pape and Bonhommeau 2015). Our results tend to support the latter point of view with a seemingly risk of trophic limitation in the Gironde estuary. The impact on population dynamics still needs to be investigated.

Here, we chose to use two food web models: EwE and RCaN. While EwE has proved to be useful to detect the overall top-down control in the ecosystem, it requires to compare three calibration exercises based on three predetermined scientific assumptions. The PCA suggested that H3 predicted a trajectory rather consistent with RCaN simulations, and as such, that H3 is the more consistent with the biological constraints that were implemented in RCaN. Given the differences among H1, H2 and H3, it also showed that with an appropriate calibration, EwE can provide time trajectories that are consistent with RCaN simulations. However EwE is very sensitive to pre-established assumptions and unsuitable assumptions can lead to biased results. As such, while RCaN provides high dimensional results that are more complex to analyze, the model appears more flexible. The “Chance” paradigm allows us to handle unpredictable events: here the model was able to cope with the marinization process without forcing any biomass (while we had to force top-predator biomass in EwE) and without explicitly modelling changes in the salinity in the estuary. Moreover, instead of focusing on a single “optimal” trajectory, the exploration of a “space” of possible trajectories allows to get a large range of indicators (for example, a distribution of correlation coefficient between growth and feeding or growth and predation in diagram ggTopDownBottomUp), instead of a single estimation based on a single trajectory. This is likely to be more robust given the intrinsic stochasticity of nature.

Overall, this tends to confirm the rationales behind the linear inverse modelling (LIM) and the chance and necessity approaches. Focusing on a single trajectory requires adding extra-assumptions that might lead to biased results if the assumptions are incorrect. Moreover, ignoring the stochasticity of nature might give overconfident results. As such, CaN and LIM postulate that it is more cautious to explore the range of possible states or trajectories of a system instead of looking for the optimal one.

This study over such a large period of time was enabled by the long-term scientific monitoring of the Gironde estuary. Of course, data are not perfect. They are collected in a limited area of the estuary, and while most of them are collected monthly, the surveys only last a few days and might miss peaks of abundance (e.g., peak of migration of diadromous fishes). Moreover, some species may be less well sampled than others. Nevertheless, the consistency in the sampling protocols and the monthly surveys should ensure that long-term trends are well detected. Moreover, the existence of two different fish surveys with two different fishing gears allow to have a good coverage of all species (if a fish species was not well caught by a survey,

it was well caught by the other). The spatial limitation of the survey might be more problematic and some of our results might be biased by changes in the spatial distribution of fishes.

Given those uncertainties, we used very large bounds in RCaN constraints. However, as in most food web models, uncertainties remain on the estimation of absolute biomass due to uncertainties on the catchability of fishing gears. Here, we did three different RCaN models with three scenarios (one with an overestimation of the catchability, one with an underestimation and one more centered which was presented here). This allowed us to see that while uncertainties in catchability lead to very contrasted absolute biomass, the time trends were very consistent among scenarios.

Interestingly, EwE and RCaN are based on very similar parameters, and as such, it was possible to use a “translation” in these parameters to facilitate the comparison (Appendix 5). However, estimating those parameters is not straightforward; thus, it is not possible in every ecosystem and particularly in data-poor ecosystems. That is why we also calculated RCaN parameters based on simpler allometric relationships following Lindstrom *et al.* (2017). While parameters were slightly different, they remain in the same range of values (Appendix 8).

Finally, to go further, it might be interesting to look at the transition periods to better understand the inter-periods evolution. We began to focus on it but because of the lack of time, this will be presented as an opening. It seems that most of the overall evolutions have occurred in those limited number of transitions years, so it would be interesting in the future to explore whether they correspond to specific environmental conditions or external events.

Conclusion

Global changes have an impact on the marine ecosystem and on fisheries (Du Pontavice *et al.*, 2020; Tittensor *et al.*, 2021). Estuaries and coastal areas are especially sensitive to these global changes (Hoegh-Guldberg and Bruno, 2010). The management of estuaries is complex because these ecosystems provide many important goods and services to human societies and support important ecosystem functions for numerous species: refuges, nursery areas and migratory routes (Elliott and Hemingway, 2002). Thus, a better understanding of the impact of global changes is critical to better manage and conserve these areas, the species that depend on them, and subsequently the sustainability of many marine fisheries. Since trophic interactions are key aspects in ecosystem functioning, food web modelling has become central to explore the consequences of environmental changes on marine ecosystems (Heymans *et al.* 2016). Here, I have worked on the trophic network of the Gironde estuary and studied the trophic control(s). More precisely, I have focused on the following questions: **can the observed changes of the trophic communities in the Gironde estuary be explained by the trophic controls in the food webs or are they rather linked to external forcing? Is there a threat for the nursery function?**

Using trophic food web models, we observed that the past dynamics of the food web in the estuary was mainly driven by the dynamics of top-predators and marine juvenile biomasses through a top-down control. Compared to previous studies, we highlighted new shifts over the studied period. We have also shown how the top-down control has progressively increased over time and highlighted signs of trophic limitation in the most recent period.

Thus, our results confirm that the estuary has progressively changed with a first period dominated by preys like benthic macro fauna towards a latest period dominated by predators such as marine juvenile fish (Pronier and Rochard, 1998; David *et al.*, 2005; Chaalali *et al.*, 2013; Bachelet and Leconte, 2015; Chevallot *et al.*, 2016).

Our study was based on the use of two food web models. They have proved to be complementary, each one having pros and cons. The most recent model, RCaN, provides high dimensional results that are more complex to analyze but the model appears more flexible. Moreover, the exploration of possible trajectories instead of focusing on a single trajectory is likely to be more robust.

The observed variations of the trophic communities are mainly explained by the changes in the environmental conditions such as the marinization (Pasquaud *et al.*, 2012; Chaalali *et al.*, 2013; Chevallot *et al.*, 2016) of the estuary, which has probably improved its suitability for marine juveniles (Chevallot *et al.*, 2019). Our results tend to support the point of view that the trophic resources are limiting for the juveniles (van der Veer, 1993; Nash and Geffen, 2000; Nash *et al.*, 2007; Le Pape and Bonhommeau 2015) in the Gironde estuary. Its nursery function is in danger.

To go further, it might be interesting to look at the transition periods to better understand the inter-periods evolution because it seems that most of the overall evolutions have occurred in those limited number of transitions years. Therefore, it would be interesting in the future to explore whether they correspond to specific environmental conditions or external events.

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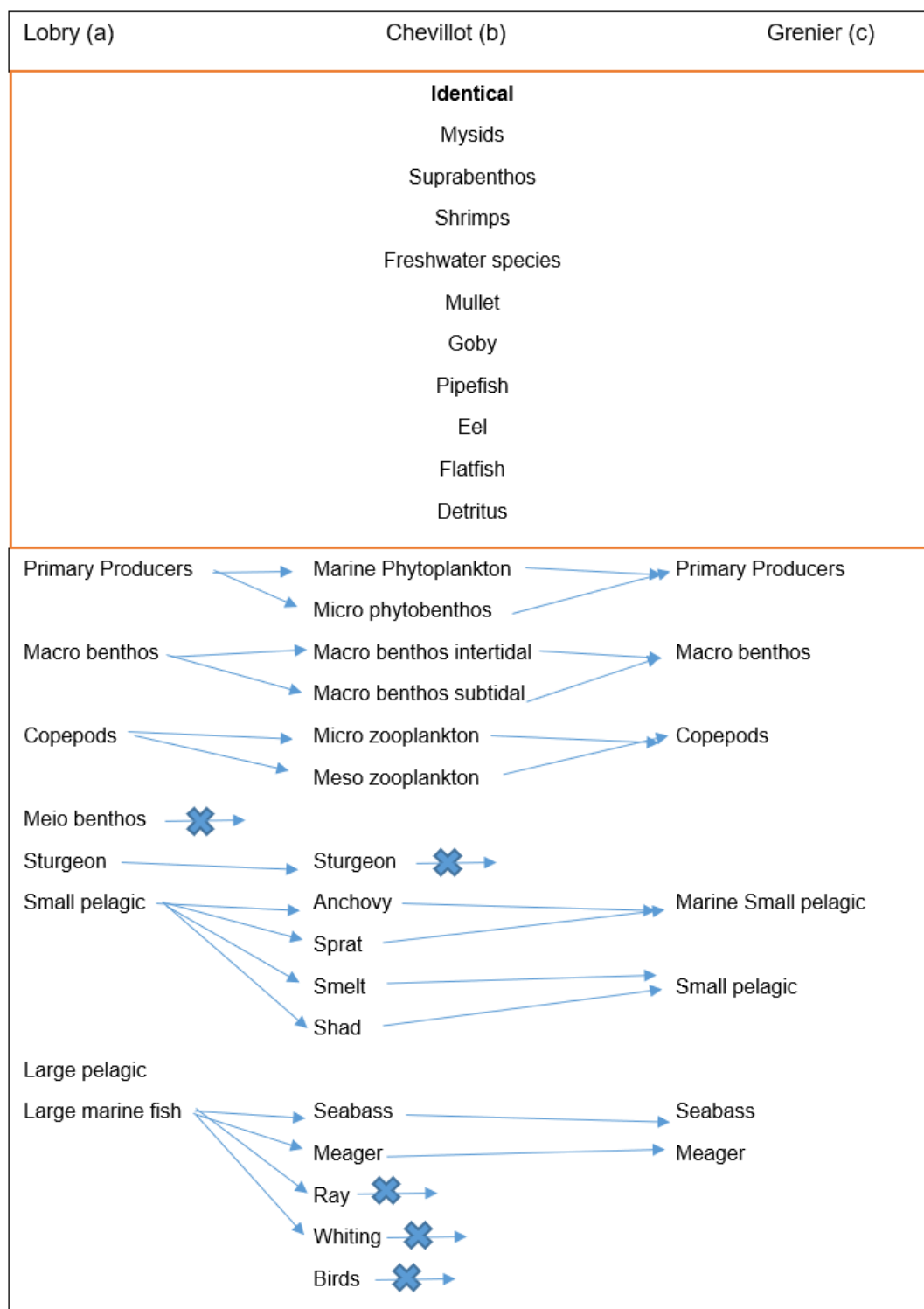
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Appendix

Appendix 1: Transition between different Ecopath models. Lobry (2008) (a), Chevillot *et al.* (2019) (b) and this study (c)



Appendix 2 : The different trophic groups and the detritus of the Ecopath model and their characteristics

Define groups... Edit multi-stanza...										
	Group name	Hab area (proportion)	Biomass in habitat area (t/km ²)	Production / biomass (/year)	Consumption / biomass (/year)	Ecotrophic Efficiency	Other mortality	Production / consumption	Unassim. consumption	Detritus import (t/km ² /year)
1	Primary producers	1,000	1673	80,12						
2	Macrobenthos	1,000	1330	6,534	23,90				0,400	
3	Copepods	1,000	247,5	106,3	210,0				0,400	
4	Mysids	1,000	318,0	9,500	92,83				0,200	
5	Suprabenthos	1,000	74,80	3,500	8,300				0,200	
6	Shrimps	1,000	17,56	7,300	25,00				0,200	
7	Freshwater species	1,000	5,700	0,590	5,900				0,200	
8	Mullet	1,000	24,50	3,470	7,220				0,200	
9	Small pelagics	1,000	5,680	2,105	7,850				0,200	
10	Marin small pelagics	1,000	4,760	3,750	12,00				0,200	
11	Goby	1,000	6,700	3,200	9,000				0,200	
12	Seabass	1,000	3,500	1,240	7,000				0,200	
13	Meager	1,000	0,900	2,010	3,000				0,200	
14	Flatfishes	1,000	7,300	1,200	5,200				0,200	
15	Pipefish	1,000	3,280	1,260	9,000				0,200	
16	Eel	1,000	8,300	0,590	3,000				0,200	
17	Detritus	1,000	209923							160193

Appendix 3 : Ecopath diet matrix

Prey \ predator	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
1 Primary producers	0,177	0,140	0,200	0,400	0,0170		0,350								
2 Macrobenthos	0,0870				0,170	0,770	0,00600	0,00600		0,01000	0,0200		0,330	0,280	0,0200
3 Copepods	0,0300	0,0330	0,760	0,200	0,220		0,294	0,602	0,493	0,580	0,0800	0,0420		0,720	
4 Mysids					0,160	0,01000		0,0290	0,316	0,130	0,140	0,340			0,0800
5 Suprabenthos								0,0920		0,160	0,290	0,250	0,400		0,550
6 Shrimps					0,01000	0,0700		0,0295		0,0200	0,310	0,300	0,0900		0,229
7 Freshwater species						0,01000									
8 Mulet															
9 Small pelagics												0,01000			0,0135
10 Marin small pelagics						0,01000		0,0630			0,0550	0,0150			
11 Goby						0,0300					0,0250	0,0230			0,0134
12 Seabass															
13 Meager															
14 Flatfishes											0,0200	0,01000			
15 Pipefish															
16 Eel															
17 Detritus	0,706	0,827	0,0400	0,400	0,423	0,100	0,350	0,179	0,191	0,100	0,0600	0,01000	0,180		0,0940
Import	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000
Sum	1,000	1,000	1,000	1,000	1,000	1,000	1,000	1,000	1,000	1,000	1,000	1,000	1,000	1,000	1,000
(1 - Sum)	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000	0,000

Appendix 4 : Example of the Stepwise Fitting Procedure: Assumption 2 (top-down control regarding the marine fish juveniles).

Start

Basic input

Definition of fleets

Landings

Discards

Time series

Stepwise fitting

Fitting parameters

Search by:

Predator

Predator/Prey

No. vars to estimate:

15

Anomaly shape:

1: Chloro

Spline point step size:

1

Absolute Biomass enabled in Baseline iterations

Time series...

Fitting iterations

	Name	Enabled	K	# Vs	# spline	SS	AIC	AICc	State	Elapsed
92	Fishing and 6v + 3pp	<input checked="" type="checkbox"/>	14	6	8	209.9	-477.7	-477.0	OK	00:00:41.88
93	Fishing and 6v + 5pp	<input checked="" type="checkbox"/>	15	6	9	205.3	-487.5	-486.7	OK	00:01:10.55
94	Fishing and 7v + 2pp	<input checked="" type="checkbox"/>	9	7	2	221.1	-460.0	-459.7	OK	00:00:49.84
95	Fishing and 7v + 3pp	<input checked="" type="checkbox"/>	10	7	3	210.2	-485.3	-484.9	OK	00:00:49.36
96	Fishing and 7v + 4pp	<input checked="" type="checkbox"/>	11	7	4	210.1	-483.4	-483.0	OK	00:01:33.16
97	Fishing and 7v + 5pp	<input checked="" type="checkbox"/>	12	7	5	209.7	-482.2	-481.7	OK	00:01:18.89
98	Fishing and 7v + 6pp	<input checked="" type="checkbox"/>	13	7	6	210.6	-478.0	-477.4	OK	00:01:05.27
99	Fishing and 7v + 7pp	<input checked="" type="checkbox"/>	14	7	7	209.5	-478.7	-478.0	OK	00:01:48.09
100	Fishing and 7v + 8pp	<input checked="" type="checkbox"/>	15	7	8	209.2	-477.3	-476.5	OK	00:00:56.31
101	Fishing and 8v + 2pp	<input checked="" type="checkbox"/>	10	8	2	218.5	-464.4	-464.1	OK	00:01:31.12
102	Fishing and 8v + 3pp	<input checked="" type="checkbox"/>	11	8	3	208.7	-486.9	-486.5	OK	00:00:50.97
103	Fishing and 8v + 4pp	<input checked="" type="checkbox"/>	12	8	4	205.5	-493.1	-492.6	OK	00:01:12.12
104	Fishing and 8v + 5pp	<input checked="" type="checkbox"/>	13	8	5	205.7	-490.5	-489.9	OK	00:01:24.82
105	Fishing and 8v + 6pp	<input checked="" type="checkbox"/>	14	8	6	205.9	-488.0	-487.3	OK	00:01:32.15
106	Fishing and 8v + 7pp	<input checked="" type="checkbox"/>	15	8	7	202.8	-494.0	-493.2	OK	00:01:16.37
107	Fishing and 9v + 2pp	<input checked="" type="checkbox"/>	11	9	2	217.3	-465.3	-464.9	OK	00:00:59.69
108	Fishing and 9v + 3pp	<input checked="" type="checkbox"/>	12	9	3	206.0	-492.0	-491.5	OK	00:01:01.90
109	Fishing and 9v + 4pp	<input checked="" type="checkbox"/>	13	9	4	204.3	-494.3	-493.7	OK	00:00:59.68
110	Fishing and 9v + 5pp	<input checked="" type="checkbox"/>	14	9	5	204.5	-491.6	-490.9	OK	00:01:37.72
111	Fishing and 9v + 6pp	<input checked="" type="checkbox"/>	15	9	6	203.8	-491.4	-490.6	OK	00:00:54.42
112	Fishing and 10v + 2pp	<input checked="" type="checkbox"/>	12	10	2	210.1	-481.3	-480.8	OK	00:00:52.26
113	Fishing and 10v + 3pp	<input checked="" type="checkbox"/>	13	10	3	199.8	-506.2	-505.7	OK	00:01:15.21
114	Fishing and 10v + 4pp	<input checked="" type="checkbox"/>	14	10	4	198.7	-507.0	-506.3	OK	00:01:40.83
115	Fishing and 10v + 5pp	<input checked="" type="checkbox"/>	15	10	5	197.9	-507.0	-506.2	OK	00:01:32.27
116	Fishing and 11v + 2pp	<input checked="" type="checkbox"/>	13	11	2	209.4	-481.0	-480.4	OK	00:01:08.74
117	Fishing and 11v + 3pp	<input checked="" type="checkbox"/>	14	11	3	199.3	-505.4	-504.7	OK	00:01:15.90
118	Fishing and 11v + 4pp	<input checked="" type="checkbox"/>	15	11	4	198.6	-505.2	-504.4	OK	00:02:11.76
119	Fishing and 12v + 2pp	<input checked="" type="checkbox"/>	14	12	2	208.8	-480.4	-479.7	OK	00:00:48.96
120	Fishing and 12v + 3pp	<input checked="" type="checkbox"/>	15	12	3	199.6	-502.5	-501.7	OK	00:00:51.56
121	Fishing and 13v + 2pp	<input checked="" type="checkbox"/>	15	13	2	208.7	-478.5	-477.7	OK	00:01:15.76
122	Baseline	<input checked="" type="checkbox"/>	0	0	0	581.3	41.67	41.67	OK	00:00:05.90
123	Baseline and 1v	<input checked="" type="checkbox"/>	1	1	0	541.1	5.080	5.080	OK	00:00:14.60
124	Baseline and 2v	<input checked="" type="checkbox"/>	2	2	0	476.2	-61.63	-61.63	OK	00:00:19.57
125	Baseline and 3v	<input checked="" type="checkbox"/>	3	3	0	465.5	-71.88	-71.86	OK	00:00:18.65
126	Baseline and 4v	<input checked="" type="checkbox"/>	4	4	0	454.6	-82.55	-82.50	OK	00:00:22.76
127	Baseline and 5v	<input checked="" type="checkbox"/>	5	5	0	444.5	-92.64	-92.56	OK	00:00:27.44
128	Baseline and 6v	<input checked="" type="checkbox"/>	6	6	0	437.4	-99.22	-99.11	OK	00:00:27.53
129	Baseline and 7v	<input checked="" type="checkbox"/>	7	7	0	431.8	-104.1	-104.0	OK	00:00:32.58
130	Baseline and 8v	<input checked="" type="checkbox"/>	8	8	0	417.2	-120.6	-120.3	OK	00:00:38.46
131	Baseline and 9v	<input checked="" type="checkbox"/>	9	9	0	413.0	-124.0	-123.7	OK	00:00:41.66
132	Baseline and 10v	<input checked="" type="checkbox"/>	10	10	0	408.5	-127.7	-127.4	OK	00:00:48.02

All

None

Baseline

Fishing

Vulnerability

Anomaly

Vulnerability and anomaly

Apply

Appendix 5 : Table of the correspondence between Ecopath with Ecosim and RCan parameters

PARAMETER	MEANING	FORMULA	EWE	WHY
SATIATION (σ)	Maximum consumption rate per unit biomass of a predator	$\sigma = \frac{1}{\gamma \kappa} f_j a_j M^{0,25}$ (Yodzis and Innes, 1992) <i>M</i> : average weight of an individual (kg) <i>γ</i> : the potential assimilation efficiency <i>κ</i> : the digestibility factor of a prey <i>f_j</i> : fractional quantity <i>a_j</i> : a constant taken from Yodzis and Innes (1992) (kg(kg.year) ⁻¹ kg ^{0.25})	Q/B	Max consumption rate per unit of biomass in EwE
INERTIA (ρ)	Limits biomass variations between maximum growth rate and maximum mortality rate Lower limit: e ^{-P}	$r_{max} = e^{as} e^{-bs/kT} M^{-0,25}$ $\rho = r_{max} . d$ (Savage <i>et al.</i> , 2004) <i>M</i> : average weight of an individual (μg) <i>k</i> : Boltzmann's constant (8.62.10 ⁻⁵ eV.K ⁻¹) <i>T</i> : the temperature of the body (K)	Log(1+ P/B)	In EwE : Bfinal/Binitial = 1+(P/B) In RCan : Bfinal/Binitial <= exp(inertie)

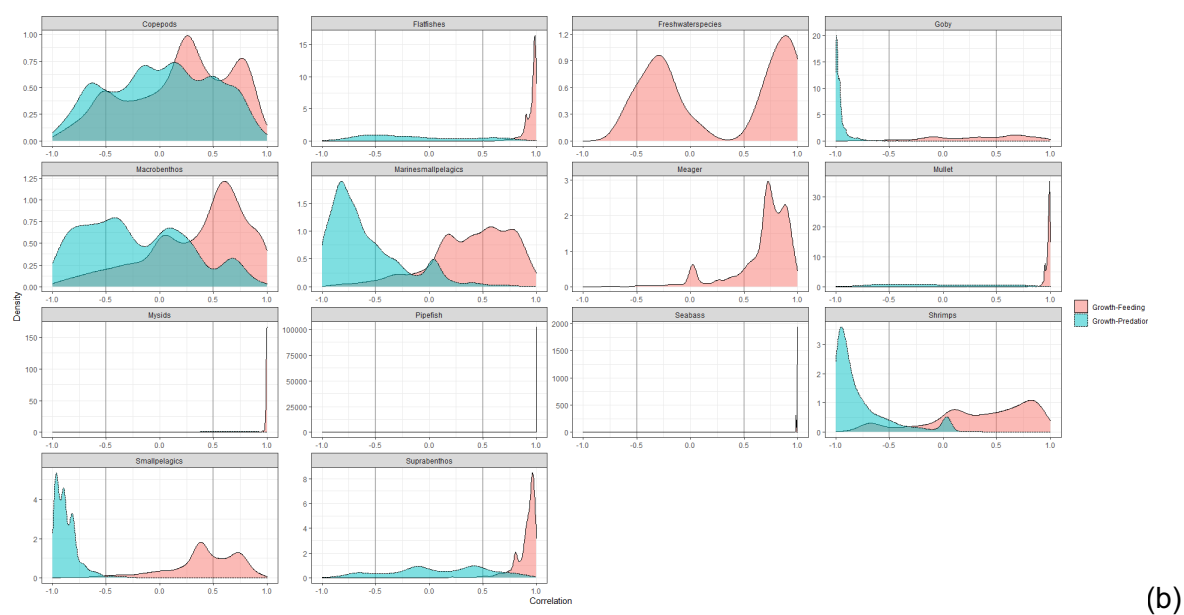
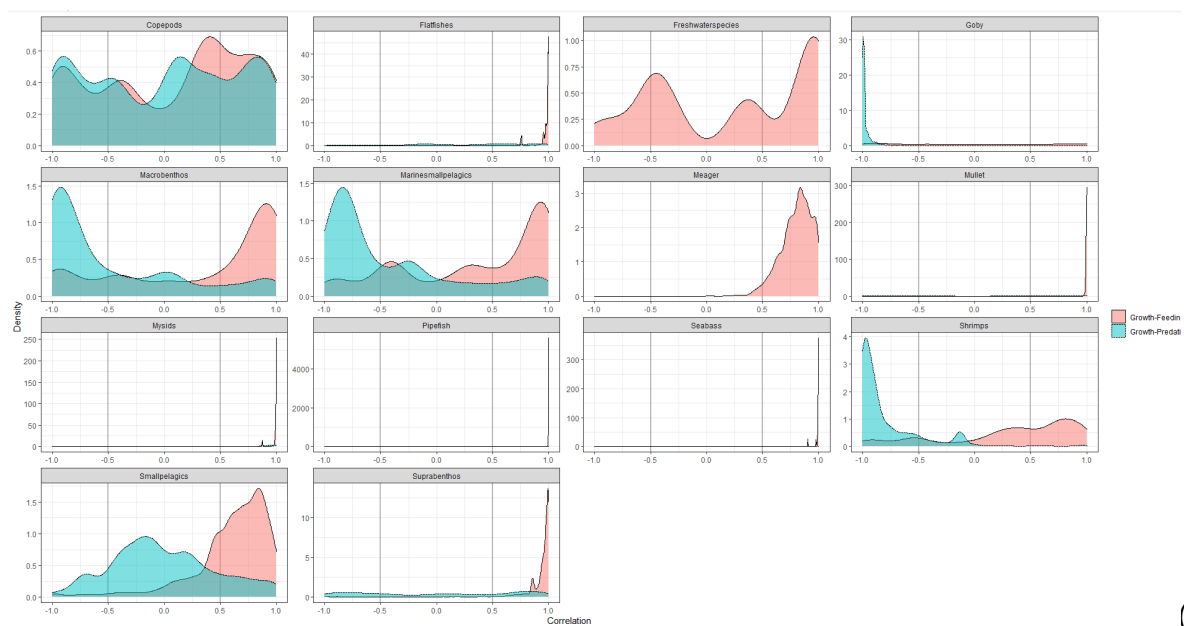
	Upper limit: e^p	<p>as and bs: a constant taken from Savage et al (2004)</p> <p>d: the number of days the species actually grows</p> <hr/> $\rho = f_r a_r M^{-0,25}$ <p>(Yodzis and Innes, 1992)</p> <p>M : poids moyen d'un individu (kg)</p> <p>f_r : quantité fractionnée (0.1)</p> <p>a_r : une constante prise de Yodzis et Innes (1992) (kg(kg.year)⁻¹ kg^{0.25})</p> <hr/>		
OTHER LOSSES (μ)	A coefficient that accounts for losses other than predation and fishing	<p>μ</p> <hr/> $= 3 (e^{a_{bmr}} e^{(b_{bmr}/T)*1000} M^{0,75})$ <p>(Gillooly et al, 2001)</p> <p>M: average weight of an individual (g)</p> <p>T: body temperature (K)</p> <p>a_{bmr} and b_{bmr}: a constant taken from Gillooly et al (2001)</p> <hr/> $\mu = a_T M^{-0,25}$ <p>(Yodzis and Innes, 1992)</p> <p>M : average weight of an individual (kg)</p> <p>a_t : a constant taken from Yodzis and Innes (1992) (kg(kg.year)⁻¹ kg^{0.25})</p> <hr/> $\mu = 3 (BMR_{Mak} * 2^{\frac{T_{EG}-T_M}{10}})$ <p>(Makarieva et al., 2008)</p> <p>T_{EG} : Water temperature of the Gironde estuary</p> <p>T_M: Ambient temperature when BMR was measured</p> <p>BMR_{Mak} : a constant taken from Makarieva et al (2008)</p> <hr/>	P/B*(1-EE) EE: ecotrophic efficiency	Considered as natural mortality in EwE
THE ASSIMILATION EFFICIENCY POTENTIAL (γ)	The proportion of biomass ingested by the predator that is actually assimilated	$\gamma = AbE / \kappa$	X	X
THE COEFFICIENT OF DIGESTIBILITY OF A PREY (κ)	Represents the ease with which a prey item can be digested	X	X	We will take those of the literature (we assume that this

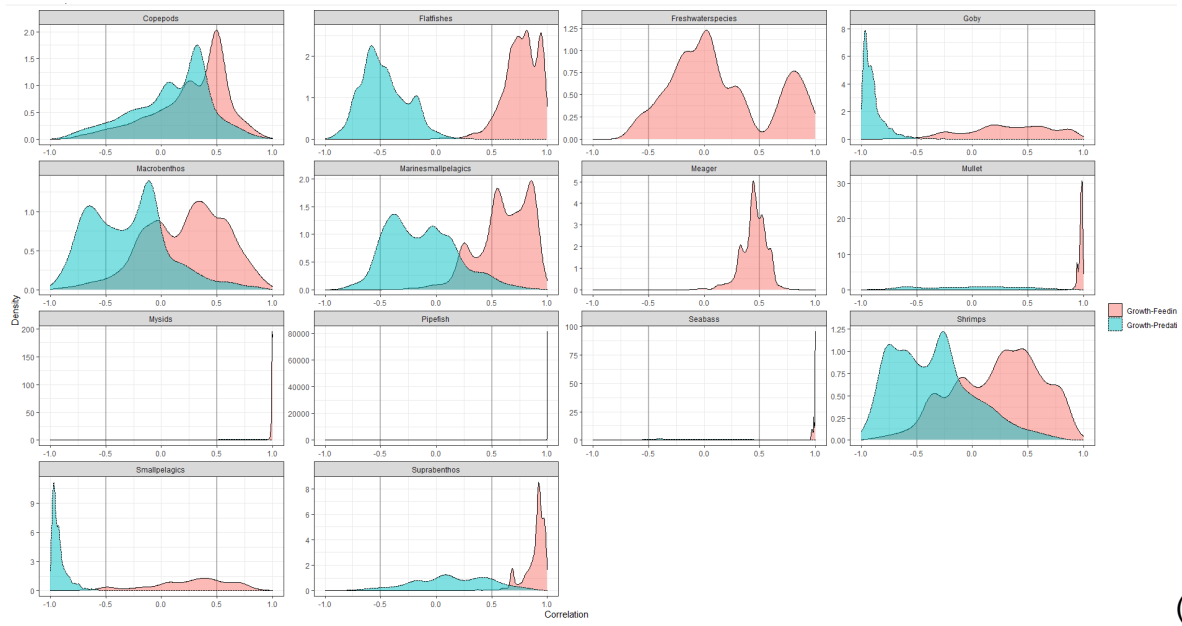
RelSPSup	$\text{Smallpelagics}/\text{mean}(\text{Smallpelagics}) \leq 2 * \text{SmallpelagicsTS}/\text{mean}(\text{SmallpelagicsTS})$	1986: 2014	1
RelGoInf	$\text{GobyTS} * 0.1 / \text{mean}(\text{GobyTS}) \leq \text{Goby} / \text{mean}(\text{Goby})$	1986: 2014	1
RelBoSup	$\text{Goby} / \text{mean}(\text{Goby}) \leq 2 * \text{GobyTS} / \text{mean}(\text{GobyTS})$	1986: 2014	1
RelSeInf	$\text{SeabassTS} * 0.1 / \text{mean}(\text{SeabassTS}) \leq \text{Seabass} / \text{mean}(\text{Seabass})$	1986: 2014	1
RelSeSup	$\text{Seabass} / \text{mean}(\text{Seabass}) \leq \text{SeabassTS} * 2 / \text{mean}(\text{SeabassTS})$	1986: 2014	1
RelMeInf	$\text{MeagerTS} * 0.1 / \text{mean}(\text{MeagerTS}) \leq \text{Meager} / \text{mean}(\text{Meager})$	1986: 2014	1
RelMeSup	$\text{Meager} / \text{mean}(\text{Meager}) \leq \text{MeagerTS} * 2 / \text{mean}(\text{MeagerTS})$	1986: 2014	1
RelFIInf	$\text{FlatfishesTS} * 0.1 / \text{mean}(\text{FlatfishesTS}) \leq \text{Flatfishes} / \text{mean}(\text{Flatfishes})$	1986: 2014	1
RelFISup	$\text{Flatfishes} / \text{mean}(\text{Flatfishes}) \leq \text{FlatfishesTS} * 2 / \text{mean}(\text{FlatfishesTS})$	1986: 2014	1
RelPiInf	$\text{PipefishTS} * 0.1 / \text{mean}(\text{PipefishTS}) \leq \text{Pipefish} / \text{mean}(\text{Pipefish})$	1986: 2014	1
RelPISup	$\text{Pipefish} / \text{mean}(\text{Pipefish}) \leq \text{PipefishTS} * 2 / \text{mean}(\text{PipefishTS})$	1986: 2014	1
RelCoInf	$0.1 * \text{CopepodsTS} / \text{mean}(\text{CopepodsTS}) \leq \text{Copepods} / \text{mean}(\text{Copepods})$	1986: 2014	1
RelCoSup	$\text{Copepods} / \text{mean}(\text{Copepods}) \leq 2 * \text{CopepodsTS} / \text{mean}(\text{CopepodsTS})$	1986: 2014	1
RelSBInInf	$0.1 * \text{SuprabenthosTS} / \text{mean}(\text{SuprabenthosTS}) \leq \text{Suprabenthos} / \text{mean}(\text{Suprabenthos})$	1986: 2014	1
RelSBSup	$\text{Suprabenthos} / \text{mean}(\text{Suprabenthos}) \leq 2 * \text{SuprabenthosTS} / \text{mean}(\text{SuprabenthosTS})$	1986: 2014	1
AbsMBSup	$(\text{Macrobenthos}) \leq 5 * (\text{MacrobenthosTS})$	1986: 2014	1
AbsCoSup	$(\text{Copepods}) \leq 5 * (\text{CopepodsTS})$	1986: 2014	1
AbsMySup	$(\text{Mysids}) \leq (\text{MysidsTS}) * 5$	1986: 2014	1
AbsShSup	$(\text{Shrimps}) \leq 5 * (\text{ShrimpsTS})$	1986: 2014	1
AbsFrSup	$(\text{Freshwaterspecies}) \leq 5 * (\text{FreshwaterspeciesTS})$	1986: 2014	1
AbsMuSup	$(\text{Mullet}) \leq 5 * (\text{MulletTS})$	1986: 2014	1
AbsMPSup	$(\text{Marinesmallpelagics}) \leq (\text{MarinesmallpelagicsTS}) * 5$	1986: 2014	1
AbsSPSup	$(\text{Smallpelagics}) \leq 5 * (\text{SmallpelagicsTS})$	1986: 2014	1
AbsGoSup	$(\text{Goby}) \leq 5 * (\text{GobyTS})$	1986: 2014	1
AbsSeSup	$(\text{Seabass}) \leq 5 * (\text{SeabassTS})$	1986: 2014	1

AbsMeSup	$(\text{Meager}) \leq 5 * (\text{MeagerTS})$	1986: 2014	1
AbsFISup	$(\text{Flatfishes}) \leq 5 * (\text{FlatfishesTS})$	1986: 2014	1
AbsPiSup	$(\text{Pipefish}) \leq (\text{PipefishTS}) * 5$	1986: 2014	1
AbsSBSup	$(\text{Suprabenthos}) \leq 5 * (\text{SuprabenthosTS})$	1986: 2014	1
AbsMBInf	$0.2 * (\text{MacrobenthosTS}) \leq (\text{Macrobenthos})$	1986: 2014	1
AbsCoInf	$(\text{CopepodsTS}) * 0.2 \leq (\text{Copepods})$	1986: 2014	1
AbsMyInf	$(\text{MysidsTS}) * 0.2 \leq (\text{Mysids})$	1986: 2014	1
AbsShInf	$(\text{ShrimpsTS}) * 0.2 \leq (\text{Shrimps})$	1986: 2014	1
AbsFrInf	$(\text{FreshwaterspeciesTS}) * 0.2 \leq (\text{Freshwaterspecies})$	1986: 2014	1
AbsMuInf	$(\text{MulletTS}) * 0.2 \leq (\text{Mullet})$	1986: 2014	1
AbsMPInf	$(\text{MarinesmallpelagicsTS}) * 0.2 \leq (\text{Marinesmallpelagics})$	1986: 2014	1
AbsSPInf	$(\text{SmallpelagicsTS}) * 0.2 \leq (\text{Smallpelagics})$	1986: 2014	1
AbsGoInf	$(\text{GobyTS}) * 0.2 \leq (\text{Goby})$	1986: 2014	1
AbsSeInf	$(\text{SeabassTS}) * 0.2 \leq (\text{Seabass})$	1986: 2014	1
AbsMeInf	$(\text{MeagerTS}) * 0.2 \leq (\text{Meager})$	1986: 2014	1
AbsFIInf	$(\text{FlatfishesTS}) * 0.2 \leq (\text{Flatfishes})$	1986: 2014	1
AbsPiOnf	$(\text{PipefishTS}) * 0.2 \leq (\text{Pipefish})$	1986: 2014	1
AbsSBInf	$(\text{SuprabenthosTS}) * 0.2 \leq (\text{Suprabenthos})$	1986: 2014	1
CNPMuSup	$\text{Mullet_CNPE} \leq 2 * \text{mean}(\text{MulletCNPETS} / \text{MulletTS}) * \text{Mullet}$	1986: 2014	1
CNPFISup	$\text{Flatfishes_CNPE} \leq 2 * \text{mean}(\text{FlatCNPETS} / \text{FlatfishesTS}) * \text{Flatfishes}$	1986: 2014	1
CNPGoSup	$\text{Goby_CNPE} \leq 2 * \text{mean}(\text{GobyTS} / \text{GobCNPETS}) * \text{Goby}$	1986: 2014	1
CNPMPSup	$\text{Marinesmallpelagics_CNPE} \leq 2 * \text{mean}(\text{MSPCNPETS} / \text{MarinesmallpelagicsTS}) * \text{Marinesmallpelagics}$	1986: 2014	1
CNPPISup	$\text{Pipefish_CNPE} \leq 2 * \text{mean}(\text{PipeCNPETS} / \text{PipefishTS}) * \text{Pipefish}$	1986: 2014	1
CNPSeSup	$\text{Seabass_CNPE} \leq 2 * \text{mean}(\text{SbassCNPETS} / \text{SeabassTS}) * \text{Seabass}$	1986: 2014	1
LANShSup	$\text{Shrimps_FishingShrimps} \leq 2 * \text{ShrimpLandTS}$	1986: 2014	1

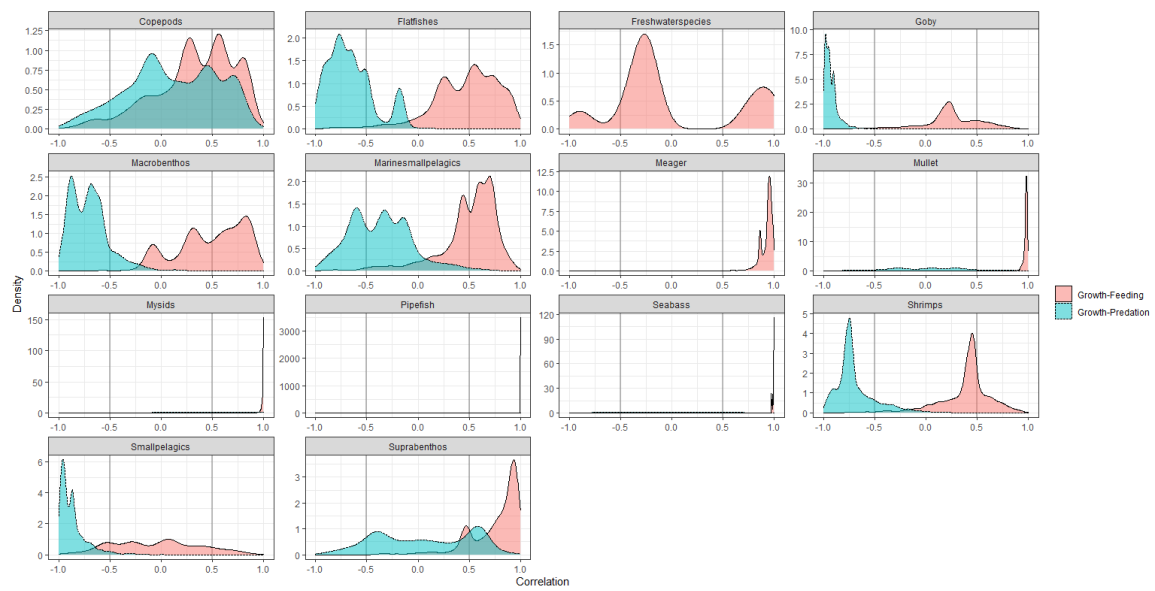
CNPShSup	$\text{Shrimps_CNPE} \leq 2 * \text{mean}(\text{ShrimpCNPETS} / \text{ShrimpsTS}) * \text{Shrimps}$	1986: 2014	1
CNPSPSup	$\text{Smallpelagics_CNPE} \leq 2 * \text{mean}(\text{SPCNPETS} / \text{SmallpelagicsTS}) * \text{Smallpelagics}$	1986: 2014	1
MigrationMeagerSup	$\text{MigrationMeager} \leq 100 * \text{Meager}$	1986: 2014	1
MigrationFreshwaterSup	$\text{MigrationFreshwater} \leq 100 * \text{Freshwaterspecies}$	1986: 2014	1
EelSatiation	$\text{Goby_Eel} + \text{Macrobenthos_Eel} + \text{Mysids_Eel} + \text{Shrimps_Eel} + \text{Smallpelagics_Eel} + \text{Suprabenthos_Eel} \leq \text{EelTS} * 1.1 * 3$	1986: 2014	1

Appendix 7 : Trophic control through the time of the whole ecosystem: period 1 (a), 2 (b), 3 (c), 4 (d) and 5 (e).

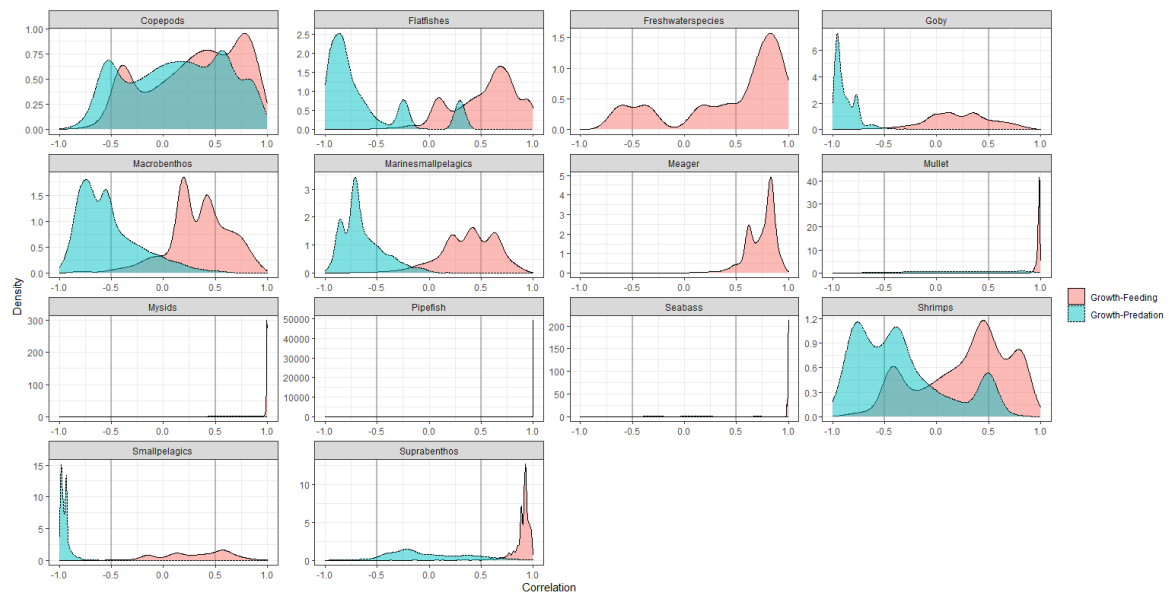





(c)



(d)



(e)

	Diplôme : Spécialité : Ingénieur Agronome Spécialisation / option : Sciences Halieutiques et Aquacoles (REA) Enseignant référent : Olivier Le Pape	
	Auteur(s) : Marine Grenier Date de naissance : 27/09/1999	Organisme d'accueil : INRAE Adresse : 50 avenue de Verdun, 33612 Cestas
	Nb pages : 57 Annexe(s) : 7	Maître de stage : Jérémy Lobry et Hilaire Drouineau
	Année de soutenance : 2022	
Titre français : Modélisation de l'évolution temporelle du réseau trophique de l'estuaire de la Gironde. Evolution des contrôles trophiques par la comparaison de deux approches de modélisation. Titre anglais: Modelling the temporal evolution of the food web in the Gironde estuary. Evolution of trophic controls by comparing two modelling approaches.		
<p>Résumé :</p> <p>De nombreux changements dans les communautés écologiques ont été observés en même temps que l'évolution des conditions environnementales dans l'estuaire de la Gironde. Cet estuaire est une zone de reproduction, de refuge et de couloir migratoire pour de nombreuses espèces dont celles d'intérêt halieutique, il est donc important de s'intéresser à son évolution. Les relations trophiques représentant un aspect primordial dans le fonctionnement d'un écosystème, l'utilisation des modèles trophiques est donc devenue centrale pour l'exploration des conséquences des changements globaux sur les écosystèmes marins. Pour décrire et comprendre les évolutions passées du réseau trophique estuarien, nous avons donc utilisé la modélisation de son réseau trophique et particulièrement, nous avons étudié l'évolution des contrôles trophiques au sein de cet estuaire. Grâce à notre étude nous pouvons étudier les possibles causes de ces changements observés qu'ils soient internes ou externes au réseau trophique. Pour ce faire, deux approches de modélisations trophodynamiques différentes sont utilisées : le modèle Ecopath combiné à sa version dynamique Ecosim (EwE) et le modèle de Chance et Nécessité (CaN). EwE étant le modèle le plus utilisé à travers le monde et CaN, étant une nouvelle approche de modélisation prenant en compte une partie aléatoire dans la détermination des flux entre compartiments. Un parallèle est fait entre les différents paramètres pour que les deux modèles soient comparables. Les deux modèles nous ont tous les deux montrés que le contrôle trophique expliquant les variations passées est le contrôle bottom-up. De plus, RCaN a servi à mieux comprendre ces variations passées. La comparaison des deux modèles nous montre l'importance de la stochasticité dans l'écologie et surtout que ces deux modèles, reposant sur des principes différents, sont en accord.</p>		
<p>Abstract:</p> <p>Many changes in ecological communities have been observed along with the evolution of environmental conditions in the Gironde estuary. This estuary is a nursery area, refuge area and migratory route for many species including species of fisheries interest, so it is important to focus on its evolution. Trophic relations being an essential aspect in the functioning of an ecosystem, the use of trophic models has become central to explore the consequences of global changes on marine ecosystems. To describe and understand the past evolution of the estuarine food web, we used food web modelling and, in particular, we studied the evolution of trophic controls within this estuary. Thanks to our study, we can study the possible causes of these observed changes whether they are internal or external to the food web. To do so, two different modelling approaches and thus, two different trophodynamic models are used: the Ecopath model combined with its dynamic version Ecosim (EwE) and the Chance and Necessity model (CaN). EwE being the most worldwide model used and CaN, a new modelling approach considering a random part in the determination of fluxes between trophic groups. A parallel is made between the different parameters to have the two models comparable. Both models showed us that the trophic control explaining the past variations is the bottom-up control. Moreover, RCaN was used to better understand these past variations. The comparison of the two models shows us the importance of stochasticity in ecology and especially that these two models, based on different principles, agree.</p>		
Mots-clés : modélisation trophique, estuaire de la Gironde, écosystème, Ecopath, Ecosim, EwE, CaN, RCaN. Key Words: trophic modelling, Gironde estuary, ecosystem, Ecopath, Ecosim, EwE, CaN, RCaN.		