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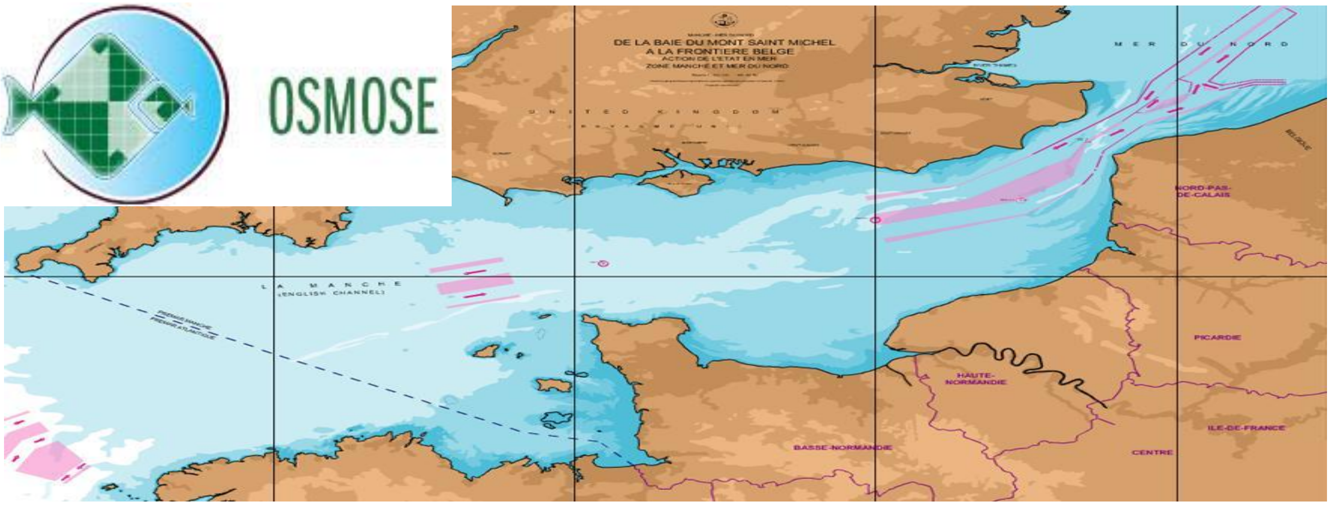
Relative importance of different mecanisms underlying fish response to climate change

Par : Mathieu GENU



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Résumé en Français du projet de recherche

Le changement climatique est un sujet qui soulève de plus en plus de question avec l'ampleur que ce phénomène prend. La libération dans l'atmosphère de gaz à effet de serre ne cesse d'augmenter avec l'accroissement démographique de l'homme. L'augmentation de température a lieu à la fois dans l'atmosphère mais aussi dans l'océan. Ainsi depuis presque trois décennies, dans un souci de connaître l'impact de ce changement climatique, le nombre d'études portant sur les effets du changement climatique sur les systèmes marins ne cesse d'augmenter. Il a été démontré que le changement climatique conduit à un déplacement de distribution des espèces vers les pôles. De plus, il a été montré que le changement climatique pouvait impacter les différents processus liés à la phénologie, comme la migration ou la reproduction. Ces processus sont étudiés à large échelle et donc seulement les effets macroscopiques du changement climatique sont identifiés. L'origine de ces changements proviennent de l'impact du changement climatique a plus fine échelle. En effet, la température intervient sur la physiologie d'un organisme, se répercutant sur les observations à l'échelle de la population et de la communauté. Cet effet direct de la température, est plus ou moins atténué lorsque l'on considère les interactions entre espèces, en effet, les relations entre espèces peuvent contribuer à amplifier ou atténuer les interactions entre les processus considérés comme la saison de reproduction, ou la croissance.

Deux types d'études peuvent se distinguer lorsque l'on veut regarder les effets du changement climatique.

- Des études faisant une analyse rétrospective de l'évolution passée d'un système marin ou d'une espèce, corrélée avec l'évolution passée de la température.

- D'autres études faisant des projections sur le futur état des systèmes marins.

Le premier type d'étude permet d'analyser les effets précis du changement climatique mais à une échelle régionale. Et le deuxième type d'étude correspond à des études à large échelle sans avoir d'informations précises sur les mécanismes gouvernant les changements observés.

Ainsi, dans le but de comprendre comment les processus régissent l'évolution du système marin, tout en intégrant les effets directs du changement climatique mais aussi les interactions entre espèces, Il est proposé de vérifier s'il existe des processus qui sont plus ou moins impactés par le changement climatique, et si oui lesquels interviennent le plus dans l'évolution du système. De plus, il est proposé projeter la situation écologique du système.

Pour cela, le modèle multispécifique, OSMOSE, a été utilisé, forcé par un modèle biogéochimique, le modèle ECOMARS-3D. Ce modèle a été appliqué à la zone Manche-Est, constituant une zone d'intérêt pour ces espèces à valeurs commerciales, mais également car cette zone constitue une zone de transition pour des espèces ayant différent type de distribution spatiale (boréale, méridionale). Le changement climatique a été projeté selon deux scenarios du GIEC et implanter dans un second modèle biogéochimique, le modèle ERSEM. Parmi ces scénarios, un scénario B1 prédisant une augmentation de la température de surface de 0.40°C par rapport aux années 2010 sur l'ensemble de la zone d'étude, et un scénario A2 prédisant une augmentation de 0.80°C pour 2040.

On considère dans cette étude que le changement climatique affecte seulement 4 processus, pour des raisons pratiques. Ainsi la production primaire, la saison de reproduction, la croissance et la distribution spatiale sont modifiés en fonction de la température. Pour la production primaire, les ratios sont calculés entre les sorties du modèle ERSEM pour les deux scénarios afin de modifier les données les sorties du modèle ECOMARS-3D servant d'entrée pour OSMOSE. Pour la saison de reproduction, il a été émis l'hypothèse que tous les poissons devaient cumuler 1630°C*jour durant leur gamétogénèse pour maturer, ainsi en fonction du scenario de changement climatique, la période de maturation est plus ou moins avancée, en fonction des espèces. Concernant la croissance, le modèle OSMOSE utilise la relation de Von Bertalanffy décrivant la croissance au cours du temps en fonction d'un paramètre K de croissance et L_∞ correspondant à la taille infinie. Ainsi une équation reliant la croissance à la température a été utilisée pour modifier le paramètre de croissance K. Enfin, pour la distribution spatiale, la distribution a été modifiée pour les espèces étant en limite de distribution au niveau de notre zone d'étude.

Les projections du changement climatique mettent en évidence que la saison de reproduction est le processus qui affecte le plus la biomasse, les captures et le niveau trophique dans la zone Manche-Est. La distribution a également un impact mais seulement sur la pente reliant l'abondance et la taille des individus du système. Les interactions entre espèces entrainent des effets synergiques et antagonistes entre les combinaisons des différents processus. Cette étude montre également que les résultats obtenus au niveau de la projection du système corroborent avec les précédentes études. C'est-à-dire une diminution de la biomasse des prédateurs du système, fragilisant la stabilité des interactions entre les différentes espèces. Ainsi, la compétition entre les espèces proies de ces prédateurs n'est plus régulée et favorise la prédominance d'espèces prédatrices de niveau intermédiaire de la chaîne trophique.

Cette étude constitue une première approche dans le but de déterminer l'importance relative des différents processus impactés par le changement climatique. Différents aspects de cette étude peuvent être améliorés, notamment, avec les données nécessaires, il serait par exemple possible d'améliorer le réalisme du processus de saison de reproduction. De plus, d'autres processus peuvent être impactés par le changement climatique, comme la mortalité larvaire non prise en compte dans l'étude et pouvant fortement contribué dans l'évolution du système.

Il serait intéressant par la suite d'étendre ce type d'étude à d'autres systèmes pour comparer l'impact du changement climatique sur ces différents processus et comparer l'importance des différents processus et constater si les observations de cette présente étude constituent une réalité générale.

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1 Introduction and context of the study

Global change constitutes a severe threat against marine ecosystems stability. These systems are composed of different species and of their interactions, between themselves but also with the environment. Perturbation of the environment might break ecosystem balance, and could affect the whole system through loss of species or outbreak of invasive species. Since humans have started to exploit marine resources, they have modified the system dynamics and have induced a decline of species abundance and richness (Hiddink and ter Hofstede, 2008; Portner and Knust, 2007). In parallel, with the global demographical expansion and the increasing use of fossil energy, human activity has developed more and more and has contributed to greenhouse gases release into the atmosphere, responsible of the global warming of atmosphere and the oceans. Climate change is a recognized threat for marine ecosystems (Hoegh-Guldberg and Bruno, 2010; Sumaila et al., 2011) but its effect on marine resources is more difficult to quantify and to anticipate than fishing effects, another anthropogenic pressure impacting them. Fishing pressure has indeed been analyzed for a longer period than the effects of climate change, and more information on the different effects of fishing pressure is nowadays available and partly used in management.

Since the beginning of the 1990's, research programs were launched to understand how climate change will affect marine system and anticipate the future organization of our oceans in the next 50 or 100 years ahead (Harley et al., 2006). This constitutes a very ambitious objective because the effects of climate change on marine systems are complex as they involve different abiotic variables (sea surface temperature, acidification of ocean, sea level rise) and can occur directly on species, but can also result from indirect effects of the perturbation of the abiotic and biotic environment in which species live.

1.1 Climate change affects marine system on multiple scales

Climate change is expected to modify different processes on species at the global scale. Shift in spatial distributions is a well-studied response of marine organisms to climate change, especially tractable for species in their limits of distribution. Thus, a shift of species distributions towards the pole of the planet is expected (Cheung et al., 2009). It is also expected to observe a modification in the timing of biological events, like season of reproduction or migration for some species. The phenology can be altered so the ecological event will occur earlier or later depending on how the increase of temperature modifies this event (Genner et al., 2010). Another impact of climate change would be the modification of growth and reproduction of fishes, in fact, the temperature will act as a stressor and will modify the balance of energy allocation to the reproduction and to the metabolic maintenance and growth (Pörtner et al., 2005).

The observed effects of climate change at a community or global scale mainly emerge from smaller scale impacts of temperature (Pörtner and Peck, 2010). Temperature drives the enzymatic reaction which occurs within an organism (metabolism impacting physiology) and indirectly drives the upper scale observations. Those impacts are dependent of the type of species, for example boreal species will not react as species with a wide range of distribution, the boreal species will be more affected than the second one. Therefore, each species will have its own range of reaction. (Rijnsdorp et al., 2009).

Effects of climate change at the species level are transmitted at upper scales notably due to interactions between species and because not all species have the same reaction facing climate change. The ecosystem is structured by predation interactions, resulting in bottom-up or top-down trophic controls, depending on the regions (Cury et al., 2008). Thus, relation between species can be reinforced by commensalism interactions for example when the system is subject to stressor, but in most of the cases, those relations are altered. For example climate change can induce a mismatch between a predator and its prey (Beaugrand et al., 2002) or can lead to the dominance of a species over other competitors.

1.2 Current state of knowledge on climate change

In the literature, plenty of studies evaluating the impact of climate change on marine ecosystems exist. Since the 1990's, the percentage of publications on climate change effect in the ecological field has constantly increased (Harley et al., 2006, Figure 1). Two types of studies can be distinguished, depending on the temporal period covered and the methodology used. Some studies consist in the analysis of the temperature increase over the past years correlated to a fluctuation of abundance, biomass, or distribution of species (Dulvy et al., 2008; Perry et al., 2005; Sims et al., 2004). The other type of studies consists in projections of future state of marine ecosystems based on scenarios of future temperature (Bentley et al., 2017; Cheung et al., 2009; Travers-Trolet et al., 2014).

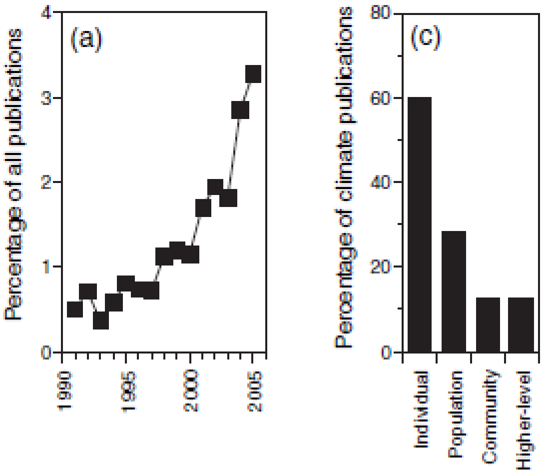

Figure 1: Importance of the climate change topic in the literature. On the left, percentage of publications on the effect of climate in the ecological field since 1990. On the right, the percentage of publications addressing the different levels of organization

The spatial coverage varies also among the published studies, from global distribution patterns of numerous species (e.g., Cheung et al., 2009) to local or regional analysis of particular species or functional group (e.g., Beaugrand et al., 2002; Dulvy et al., 2008; Perry et al., 2005; Wang, 2003).Some studies highlight the fact that to understand what can be seen at global scale, it is necessary to understand what is happening at a lower scale. Indeed, the different interactions between species can lead to antagonistic or synergistic effects of climate change (Poloczanska et al., 2013; Pörtner and Peck, 2010). In most cases, global studies reveal a shift of species distribution as being the effect of climate change. However, it is worth noting that for modeling studies projecting the possible future of marine systems, the other processes affected by climate change affect are not analyzed. In fact, those studies mainly use statistical habitat models for predicting a species distribution, and don't present nor take into account possible modification of life history traits of fishes.

So in today's studies, a trade-off has to be made between on one hand a large scale analysis but with a lesser understanding of the different mechanisms underlying the projections or on the other hand a regional scale analysis with a more detailed understanding of the processes occurring with the effect of climate change, but with a reliability limited to the studied area.

1.3 Interest of modelling approach to evaluate climate change effects

Conversely to statistical models for which extrapolation is not advised as statistical relationship may not remain valid out of their range of observed values, mechanistic models based on mathematical formulation of several processes allow projecting a potential situation for marine systems. In fact, these models can be used as virtual laboratories in making projections of future ecosystem state by considering different kinds of potential scenario. Knowing the different mechanisms modelled, conclusions can be made about how a stress such as ocean warming can impact the trophic system considered.

More recently, the projection of climate change have been done considering the effect on every compound of the marine system (Travers et al., 2009). Ecosystem models simulate the whole trophic web, from the low trophic levels (LTL), composed of primary and secondary producers (phytoplankton and zooplankton), to the high trophic levels (HTL) represented by the upper compartments in the food chain. The LTL model, with its fast dynamics, can be coupled to a physical model to project the variation of nutrient composition induced by climate change. This approach allows to simulate the effects of a stress, like climate change, on the whole marine system, and to consider the different interactions occurring both among the lower compartments of the food-web and interactions among species at the upper trophic levels. In this way, it improves the realism of the effects of the climate change on the marine system.

1.4 Aim of the current study

Until now, studies of the effects of climate change on marine ecosystems highlighted a shift in the spatial distribution of the species, particularly illustrated by the projection of habitat models under warming conditions. However, climate change affects marine systems on different scales and through different processes. Moreover the existing interactions between species complicate the analysis of the contribution of the processes affected by climate change. Habitat models do not allow to understand the underlying mechanisms or how climate change affect this spatial distribution process (including migration) and even less how other processes might be affected (Phenology, growth,..), with the subtlety that those processes will combined themselves to form the community response to climate change.

With this in mind, it is necessary to evaluate which processes contribute to the response of marine systems to climate change, and if those processes affect the system equally, or if certain processes are more preponderant than others in the manner the system evolves.

Given that, the present study proposes to use a multispecies model (OSMOSE) which represents a large part of the food web (from high to low trophic levels) in order to simulate the state of the ecosystem under two different scenarios of climate change proposed by the IPCC (Inter-Governmental panel on Climate Change). By modifying the different processes to simulate their evolution under climate change, this OSMOSE model is used to experiment which process affects the most the variation of different indicators of the marine system. This model also allows projecting the situation of the ecosystem under climate change scenarios and evaluating the behavior of the different species.

2 Modeling approach used for representing the English Channel ecosystem

The high trophic-level (HTL) model OSMOSE simulates the spatio-temporal dynamics of the fish community, by explicitly representing the interactions between fish individuals based on a size-based opportunistic predation. It is forced by the outputs of a biogeochemical model, which simulates the dynamics of the low-trophic levels (LTL). After presenting the main features of this model and its current application to eastern English Channel, we describe the climate change scenarios used in this study and how they impact the modeled ecosystem.

2.1 The high trophic-levels model : OSMOSE

The high trophic-levels model OSMOSE is a spatially-structured, multispecies, individual-based model (Shin and Cury, 2001, 2004; Travers et al., 2009). This model differs from other ecosystem models (e.g. Ecopath with Ecosim and Ecospace, (Pauly et al., 2000) notably by its hypothesis regarding the predation process. The diet of species is not fixed, but depends on local interactions between individuals, with predation occurring when a prey is at the same time at the same location than the predator (spatio-temporal co-occurrence) and if it can fit in the predator mouth gap (size adequacy). This model represents fish as super-individuals, meaning that organisms within super-individuals have the same state variables (belonging to the same species, size, age, location, trophic level). During a time step of 2-weeks, super-individuals move on the 2D grid, interact with other super-individuals and forcing prey fields following the opportunistic predation process and undergo several sources of mortality (predation, fishing, starvation, residual natural mortality), possibly growth depending of the amount of prey eaten and reproduce (Figure 2). The particular processes affected by climate change in this study are detailed below.

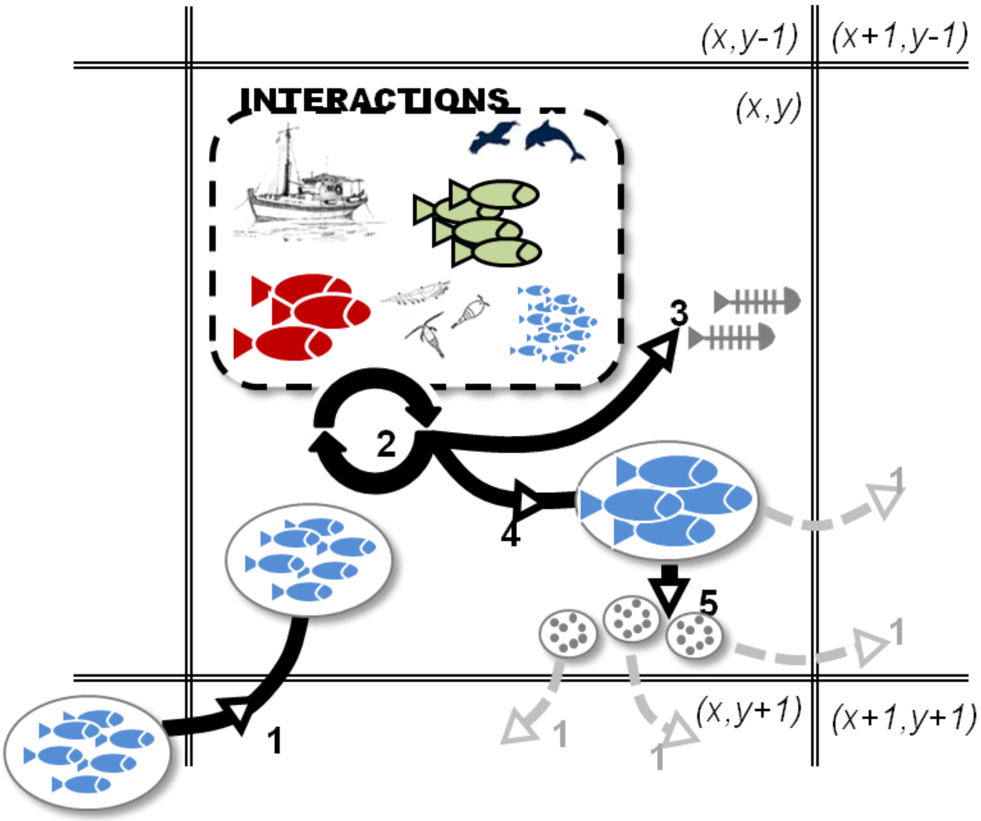

Figure 2: Processes constituting each time step within OSMOSE. Super-individuals move to a new cell of the grid (1), then the super-individual interacts with other compartments (other super-individuals and low-trophic level groups) and undergoes some mortalities, which both can modify its abundance(2), after that if the super-individual hasn't eaten enough its abundance decreases by starvation (3), otherwise the super-individual grows and the biomass increases (4), if the individuals are mature they can reproduce and lay eggs which will form new super-individuals (5). From Travers-Trolet et al., in prep.

2.2 Use of the models in the eastern English channel

The model was applied to the eastern English Channel (ICES area 7d – figure 2), for the period 2000-2009 (Travers-Trolet et al. in prep.).

The eastern English Channel is an epicontinental sea, representing a corridor between Atlantic sea and North sea. This sea constitute an habitat for different type of species, for boreal species coming from the north sea, for species with a large distribution range and for lusitanian species with their northern distribution reaching the eastern English channel. For this, this sea represents a model for experimental studies in evaluating the effect of climate change. Numerous of European economical species are represented in this sea, thus making the monitoring of this area a priority.

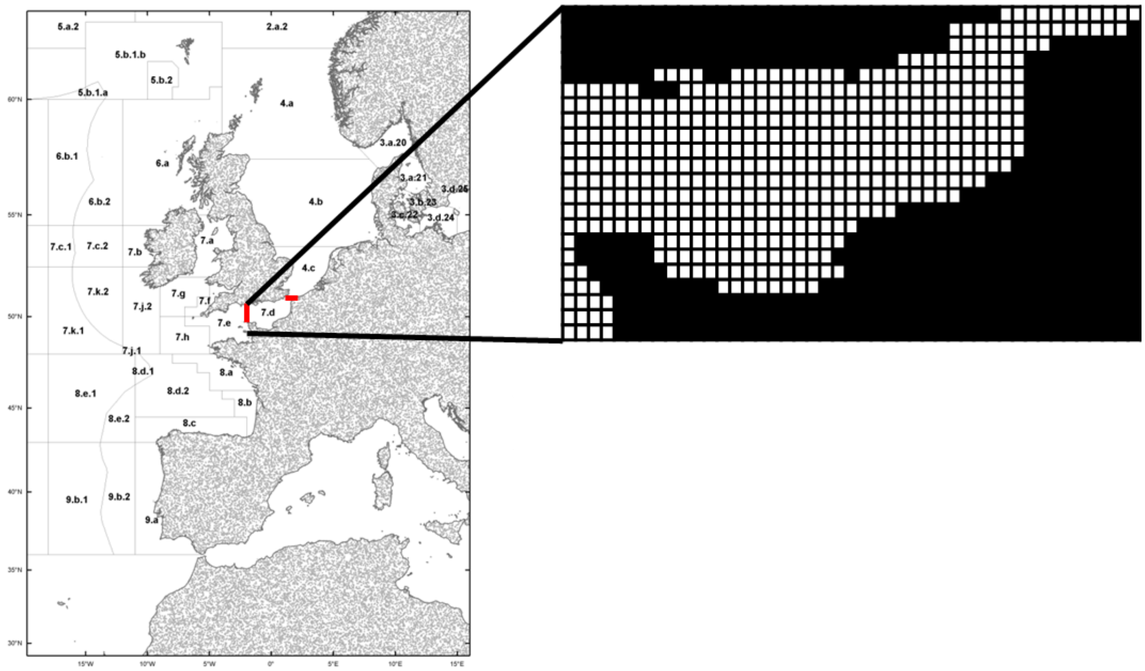

Figure 3 : Location of the study area(ICES area 7d) delimited in red on the map (source : ICES). The spatial resolution of the OSMOSE grid (0.6° x 0.6°) is presented on the right

14 species were explicitly modeled in this OSMOSE application, chosen for their representativeness in total yield, biomass and their trophic function in the system: cod, dragonet, horse mackerel, lesser spotted dogfish, herring, mackerel, plaice, poor cod, pouting, red mullet, sardine, sole, squids and whiting. Parameters for the OSMOSE model used in this study are the same as those used in Travers-Trolet et al (in prep) and are reported in appendix A.

2.3 Plankton prey fields derived from ECOMARS-3D

The LTL model ECOMARS-3D is a coupled physical-biogeochemical model, which simulates the pelagic dynamics. This model is a 3-dimensional model, with a horizontal resolution of 4km x 4 km, and a vertical scale of 30 levels. The variation of phytoplankton's biomass (dinoflagellates and diatoms) is driven by the availability of nutrients (nitrogen, phosphorus and silicate) and impacts the zooplankton dynamics (micro- and mesozooplankton). Phytoplankton and zooplankton biomass simulated by this model over 2000-2009 were vertically integrated and averaged over 2 weeks to be used as forcing fields of the primary and secondary production within OSMOSE.

2.4 Selection of climate change scenarios

Two scenarios from the IPCC (Intergovernmental Panel on Climate Change) were used in this study (IPCC 2007). A first scenario, B1, corresponds to a modest release of carbon dioxide in the atmosphere, and a peak of greenhouse gas in 2040 corresponding to an increase of 1.8°C for 2090-2099 compared to 1980-1999 (dark blue, Figure 4). The other scenario, A2, projects a continuous increase of the release of greenhouse gas until 2100, which induces an increase of surface temperature of 3.4°C for 2090-2099 years compared to 1989-1999 (red on Figure 4). More recent scenarios have been released by IPCC, but were not used in this study as regional downscaling of these scenarios was not available (see below). However, some correspondences exist, and the moderate B1 scenario is comparable with the recent RCP4.5 scenario while the pessimistic scenario A2 corresponds to the more recent RCP8.5 scenario (IPCC 2014).

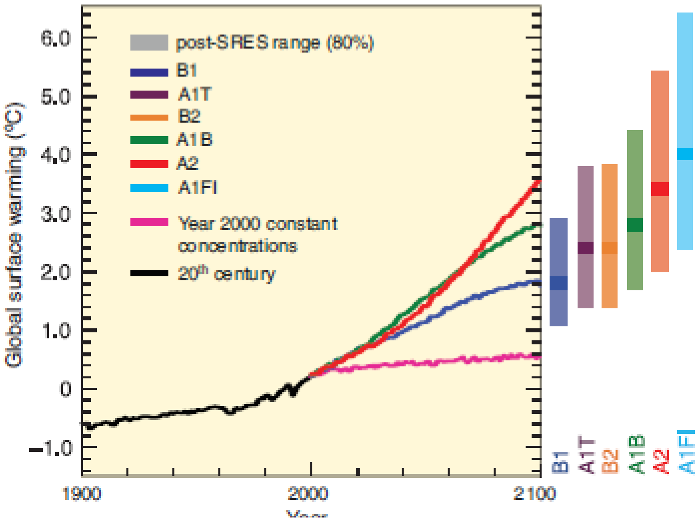

Figure 4 : Evolution of the global surface temperature from 1900 to 2100 under the different scenarios considered(IPCC, 2007)

2.5 Modeling the effects of climate change for the high trophic levels model

Climate change can impact the system at different levels, both at the basis of the trophic pyramid (primary and secondary production), and higher in the food web (on fish community). So, to simulate the effects of climate change it is necessary to implement the different IPCC scenarios to both models ECOMARS3D and OSMOSE. As no climatic run was available with the MARS3D framework, an existing projection of the low trophic community run with another biogeochemical model (ERSEM) was used instead. The POLCOMS-ERSEM model has been applied to the northeast Atlantic and used to simulate the plankton dynamics under B1 and A2 scenarios (Kay and Butenschön, 2016). For OSMOSE model, climate change impacts were inferred on the input parameters of the processes on which climate change could have an effect. In this study it was considered that climate change would modify the primary production, reproduction season, growth and spatial distribution (Figure 5).

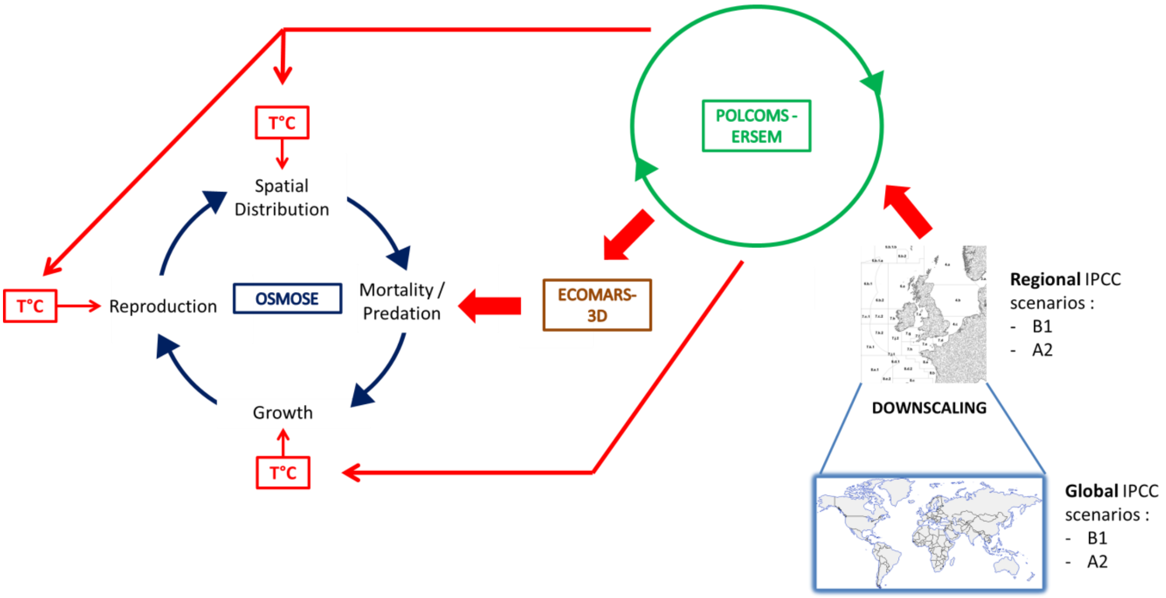

Figure 5 : Conceptual scheme of how global climate change scenarios affect the processes of a regional model

2.5.1 For primary and secondary production

The effect of climate change on primary and secondary productions comes from the ERSEM model. Due to the coarse resolution of the ERSEM model, we compute a global ratio of change for the plankton groups, corresponding to the ratio of the projected biomass of a functional group (averaged over space and the 2040-2049 period) over the biomass of the current state (2000-2009) simulated with the same model, i.e. ERSEM. This ratio of change (Table 1) is then applied to the biomass of the same functional group simulated by ECOMARS-3D at a finer resolution. The resulting projected prey fields are finally provided as input to OSMOSE. A preliminary analysis was made to exclude seasonal or spatial impacts on primary and secondary productions, and showed that spatial and seasonal fluctuations were negligible.

Table 1 : Percentage of change in SST and plankton functional group biomass over the area of interest (ICES 7d) for both scenarios (2040 -2049) compared to actual situation (2000-2009). (SST : Sea surface temperature, P4c : Dinoflagellates, P1c : Diatoms, Z4c : Mesozooplankton, Z5c : Microzooplankton)

	SST	P4c	P1c	Z4c	Z5c
B1	3,67%	2,07%	-0,94%	-1,93%	-1,83%
A2	6,53%	0,3%	-0,8%	2,46%	-2,39%

2.5.2 Effect of climate change on growth

In OSMOSE, the growth of fishes is determined by the quantity of prey they eat. It is considered that fishes have to cover the need in energy for metabolic maintenance, then the exceeding of energy is allocated to growth, so there is a threshold of predation efficiency (ξ_{crit}) to reach, for fishes to grow (equations 1 and 3). When the quantity of prey eaten is above the threshold, the growth process follows the Von Bertallanffy relation (equations 2 and 3)

$$\Delta L_{s,a} = L_{\infty s}\left(1-e^{-K_s \Delta t}\right)e^{-K_s\left(a-t_{0s}\right)} \; (eq.1)$$

$$\Delta L_{s,a,i,t'} = 0 \qquad \boldsymbol{if}\ \boldsymbol{\xi_i} < \boldsymbol{\xi_{crit}}\ (\text{eq.}2)$$

$$\Delta L_{s,a,i,t'} = \frac{2\Delta L_{s,a}}{1-\boldsymbol{\xi_{crit}}} \qquad \boldsymbol{if}\ \boldsymbol{\xi_i} < \boldsymbol{\xi_{crit}}\ (\text{eq.}3)$$

Climate change is expected to affect physiological rates of marine organisms, including growth rate. Therefore, we simulated the effect of climate change on the parameter K of the Von Bertalanfy growth model, by applying an equation previously used (Kielbassa et al. 2010). This equation (equation 4) relates the growth coefficient K to temperature, based on 4 parameters: $K_{opt,}$ the optimal growth coefficient, $T_{opt,}$ the temperature associated to the optimal growth coefficient, T_{min} and $T_{max,}$ respectively the minimal and maximal temperature that a species can endure.

$$\mathrm{K(T)} = \mathrm{K_{opt}} \times \frac{(\mathrm{T}-\mathrm{T_{min}})(\mathrm{T}-\mathrm{T_{max}})}{(\mathrm{T}-\mathrm{T_{min}})(\mathrm{T}-\mathrm{T_{min}})-(\mathrm{T}-\mathrm{T_{opt}})^2} \text{ (eq. 4)}$$

For each species, values of T_{opt}, T_{min} and T_{max} were first collected (Table 2) based on global presence records of each species. This was made using the GBIF and OBIS database, available online.

Table 2 : Values of Topt, Tmax and Tmin (in °C) for the 14 species of the model

Topt	**Tmax**	**Tmin**	**latin name**	**common name**
6,63	14,65	2,64	*Gadus morhua*	cod
14,86	17,77	6,32	*Callionymus lyra*	dragonet
7,13	15,07	2,99	*Clupea harengus*	herring
13,31	17,92	7,77	*Trachurus trachurus*	horse mackerel
12,97	16,85	8,52	*Scyliorhinus canicula*	lesser spotted dogfish
12,41	17,65	7,13	*Scomber scombrus*	mackerel
12,14	17,72	3,79	*Pleuronectes platessa*	plaice
12,01	16,51	5,79	*Trisopterus minutus*	poor cod
15,745	18,13	5,7	*Trisopterus luscus*	pouting
12,696	19,764	10,359	*Mullus surmuletus*	red mullet
18,791	26,956	8,448	*Sardina pilchardus*	sardine
16,34	18,76	6,73	*Solea solea*	sole
20,11	29,84	4,43	*Loligo sp*	squids
8,21	15,83	4,46	*Merlangius merlangus*	whiting

Then, we estimated the K_{opt} value of each species by reversing equation (1) and using the current growth coefficient (K_{curr}) corresponding to the parameter initially used in Osmose with the current temperature associated (T_{curr}) (equation 5).

$$\mathrm{K_{opt}} = \mathrm{K(T_{curr})} \times \frac{(\mathrm{T_{curr}}-\mathrm{T_{min}})(\mathrm{T_{curr}}-\mathrm{T_{max}})}{(\mathrm{T_{curr}}-\mathrm{T_{min}})(\mathrm{T_{curr}}-\mathrm{T_{min}})-(\mathrm{T_{curr}}-\mathrm{T_{opt}})^2} \text{ (eq. 5)}$$

The parameters of the von Bertalanffy growth model are not independent, and their relationship (equation 6) has been brought to light on a study on 84 species of fish from freshwater and marine water (Pauly, 1980).

$$\phi = \log_{10}(K) + 2\log_{10}(L_\infty) \text{ (eq. 6)}$$

Thus, we consider that the relationship between K and L_∞ remains the same under climate change. This allows us to determine the projected parameters L_∞ using equation 3 with the projected parameters K derived from equation (1), for both scenarios B1 and A2.

2.5.3 Effect of climate change on reproduction seasonnality

Osmose have a seasonality parameter that quantifies the percentage of reproduction intensity for each time step. The number of eggs laid depends of the sex ratio, the relative fecundity of the species expressed in number of egg per grams of biomass, the total biomass of the species and the seasonality parameter (eq.7)

$$Neggs_{s,t} = Ratio_{sex} \times RF \times SSB_{s,t} \times seasonality \text{ (eq.7)}$$

We change this seasonality parameter for each species to simulate the effect of climate change. To do so, we considered that the gametogenesis requires a certain amount of degree*day to be completed to start the spawning period, meaning that the gametogenesis will be completed when the sum of the temperature during each day reaches a specific threshold. It has been previously showed for spring-spawning species that 1630 degree*day are needed for achieving gametogenesis (Lange and Greve, 1997). As no information was available for other spawning seasons, we applied this value to all species.

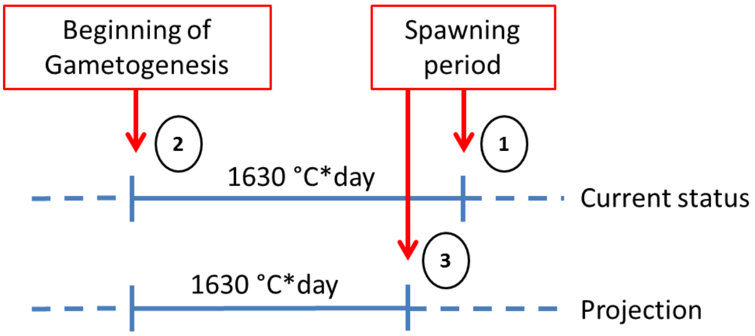

Figure 6 : Steps of modelling the effect of climate change on the reproduction season. Starting from the current spawning period (1), computing the sum of degree x days backward allows to find the beginning of the gametogenesis (2), and finally to project the new spawning period for B1 and A2 (3)

Based on the spawning period initially parameterized in Osmose, we determine the beginning of gametogenesis by summing 1630°C*day backwards from the spawning time, with daily temperatures provided by the 2000-2009 outputs of ERSEM model. Then, using this time the projected daily temperatures for 2040-2049 under B1 and A2 scenarios, we sum 1630°C*day forwards from the beginning of gametogenesis (Figure 6). Climate warming induces an earlier spawning period (Table 3), different for each species as their reproduction seasonality is different. The duration of the spawning period was not modified.

Table 3: Number of days of which the reproduction season is advanced for the species modelled in OSMOSE, according to the two climate scenarios considered

	scenario B1	scenario A2
lesser spotted dogfish	5	7
red mullet	5	8
mackerel	5	7
herring	5	9
sardine	3	7
squids	5	9
pouting	11	15
whiting	12	16
poor cod	12	16
cod	10	16
dragonet	8	11
sole	10	13
plaice	6	11
horse mackerel	8	10

Because the time step of OSMOSE is 15 days and our delay in spawning is smaller than 15 days for some species, we displaced the percentage of eggs laid for one step on the previous one with a ratio corresponding to the number of days of delay divided by 15 days.

2.5.4 Effect of climate change on species spatial distribution

The spatial distribution is different for each species, but also, it is different for a single species depending on the season and the age. The maps of spatial distributions are presented appendix B.

To modify the spatial distribution of species, it was considered that the distribution of species follow the hierarchical concept of distribution, i.e. their distribution is driven by both large scale filter and smaller scale filter (Hattab et al., 2014). Temperature classically acts as a large scale filter and drives the global distribution area of a species. Small scale filters are based on bathymetry and sediment types for instance, and drive the local distribution of populations. While climate change will affect the former, there is no clear evidence on how it will affect the latter. Therefore, we consider that only species with a southern boundary of distribution situated near the eastern English Channel will have their distribution modified (large scale filter). To identify the species which have to have their spatial distribution modified, we used the presence record data, previously used for the growth process, to evaluate if the eastern English Channel corresponds to their limit of distribution. In our study it is the case for 3 species, Cod, Herring and Whiting. To modify their distribution, we determined the maximum temperature they can tolerate in winter and summer from the presence record data. We used the first centile of the frequency of distribution to remove the occurrence beyond the area of distribution. Then we verified that they confirm the distribution maps used for the 2000-2009 years. Then we used these temperatures as isocline on the maps of future temperature for the two scenarios to define the future distribution for the 3 species (Figure 7, appendix C).

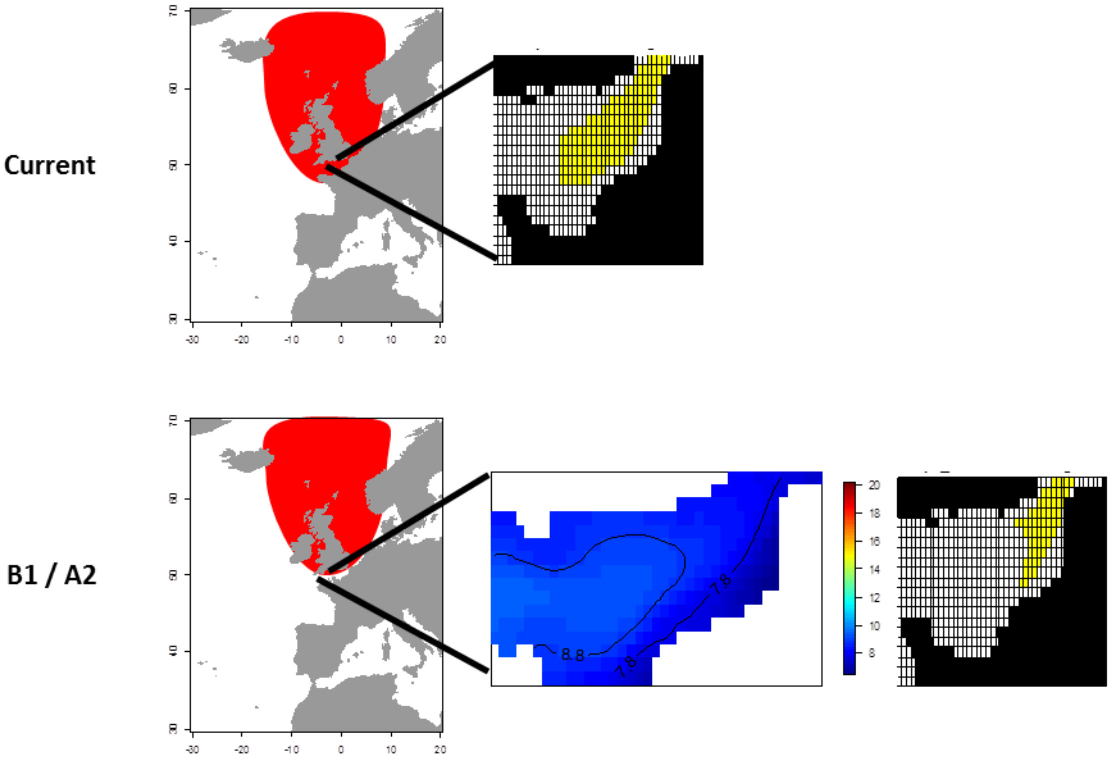

Figure 7 : Method used for projecting species distribution under climate change. On the top, current spatial distribution (yellow area) resulting from large scale filter driven by temperature (red area) and small scale filters (not shown). On the bottom, projection of the species distribution, using temperature isoclines to cut the current distribution.

2.6 Simulation plan and indicators used

To identify the separate and combined effects of each process subject to climate change, we use OSMOSE as a virtual laboratory and simulated all combinations of changes of the different processes. For each climate change scenario a full factorial design was realized (with 4 processes, this leads to 4^2 simulations). However, the reference simulation (i.e. none process affected) is the same for the two scenarios, thus a total of $2 \times 4^2 - 1 = 31$ simulations were run (Table 4). For each simulation, 30 replicates were launched to have statistic reliability because of the stochasticity of the model. Simulations were launched for 120 years, and only the 20 last ones were kept and averaged to have stabilized situation for the projection.

The relative importance of the processes in the overall response of the fish community to climate change was assessed by analyzing different indicators. First, species biomass was analyzed to better understand the direct effect of each process. Global indicators were also used to have an integrated view of climate change effects. Total biomass and total yields inform on the global state and functioning of the system. The mean trophic level, computed from the individual trophic levels weighted by their biomass (Travers et al., 2010), gives information of the trophic structure of the system and is sensitive to variations of key functional groups such as top predators. The size spectrum was also considered to characterize the evolution of the size of fishes in the system. The corresponding indicator is the slope of the linear adjustment between the logarithm of abundance versus the logarithm of the size.

Table 4 : Combinations of the processes affected (cross) or not (empty cell) by climate change, for the two scenarios B1 and A2.

		(ref)	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
B1	Primary production		X		X		X		X		X		X		X		X
	Reproduction Season			X	X			X	X			X	X			X	X
	Growth					X	X	X	X					X	X	X	X
	Spatial Distribution									X	X	X	X	X	X	X	X
A2	Primary production		X		X		X		X		X		X		X		X
	Reproduction Season			X	X			X	X			X	X			X	X
	Growth					X	X	X	X					X	X	X	X
	Spatial Distribution									X	X	X	X	X	X	X	X

The relative contribution of each process was analyzed for these four global indicators (biomass, yield, mean trophic level slope of size spectrum) using sensitivity indices based on variance (Faivre et al. 2013). The sum of square resulting from an ANOVA run for each indicator was used to derive sensitivity indices For each process. The first order index corresponding to the effect of a process alone is computed as the ratio between the sum of square of the factor alone over the sum of the sums of square. The second-order index is computed as the sum of square of the interaction of the processes, considering interaction for second order but also third and fourth order.

The biomass was also used in combination with species trophic levels and diet to characterize the projected system in 2040 years. Diet corresponds to the biomass of prey eaten by each species for each step of a simulation, and can vary through time as it emerges from local opportunistic predation interactions. In the results, only the mean diet over space and season was presented.

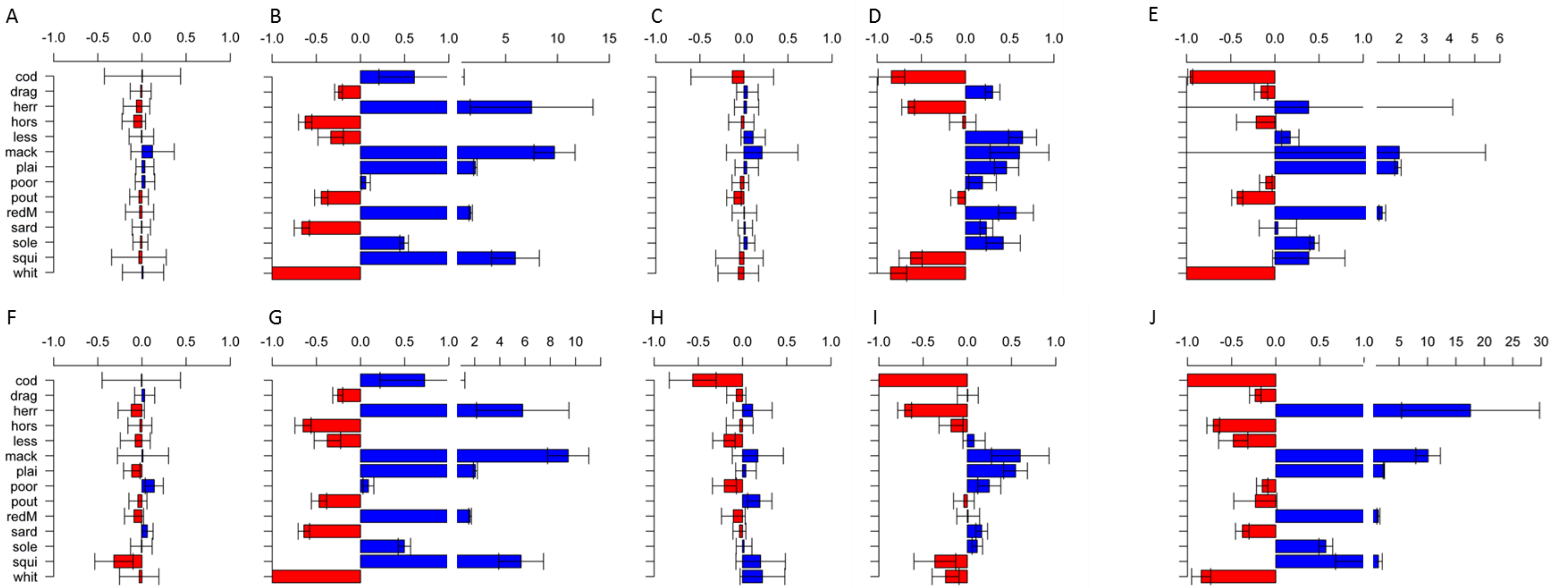

Figure 8 : Relative change of biomass of the 14 species considered, when considering separate effects of the four processes studied (panels A-D for scenario B1, panels F-I for scenario A2) and combined effects of all processes simulated together (panel Efor scenario B1, panel J for scenario A2) Species biomass is expressed relatively to reference biomass using (B-B$_{ref}$)/B$_{ref}$

3 Results

3.1 Relative importance of the different processes under climate change

3.1.1 Effects at the species biomass level

Relative change of biomass of each species induced by the separate effects of each process studied is presented for both scenarios (Figure 8A-D for B1, Figure 8F-I for A2) and compared to the results obtained when all processes are modified simultaneously (Figure 8E and J).

Under scenario B1, increase of primary production doesn't have an impact on biomass for any species (Figure 8, Figure 8A). A similar result is obtained when modifying only the growth process, with no change of species biomass (Figure 8C). Conversely, the separate effect of earlier reproduction seasons impacts all species, but in different directions (Figure 8B). Some species show a biomass decline compared to the reference situation, such as whiting which completely died out, or horse mackerel and sardine which have their biomass more than halved, and dragonet, lesser spotted dogfish, and pouting which also have a decreased biomass. For the other species, earlier reproduction seasons have a positive effect: species like herring, mackerel and squids have their biomass which is more than 6 times higher than reference, plaice and red mullet have their biomass more than tripled, and sole, cod and poor cod display a moderate increase of biomass. For the last process simulated separately, i.e. spatial distribution, four species have their biomass more than halved (cod, herring, squids and whiting), while the others have their biomass which increase (Figure 8D). Furthermore the range of variation of biomass is higher for the reproduction season process than for the other processes.

When considering change of all processes simultaneously (Figure 8E) , whiting goes extinct, cod biomass is divided by 10, and dragonet, horse mackerel, pouting and poor cod present a slight decrease of biomass compared to the reference situation. Herring and mackerel have their biomass which increases in average but with a lot of variability among the replicates, leading to high uncertainty regarding this pattern. The biomass of plaice and red mullet more than tripled compared to the reference situation. Lesser spotted dogfish and squids have also their biomass which increases but to a lesser extent. For sardine, simulating changes of all processes simultaneously does not seem to affect its biomass. For most species, the change of biomass observed when all process are modified is similar to the changes observed when only the reproduction season is changed, except for cod (decreasing biomass when all processes are considered versus increasing biomass when only change of reproduction season is modeled) and to a lesser extent for lesser spotted dogfish, poor cod and sardine.

Results obtained for the scenario A2 are at first glance similar to B1 results, but some differences are to be pointed out. First, the higher increase of primary production under A2 compared to B1 leads to change of biomass for some species: plaice and squids decrease in biomass while poor cod increases (Figure 8F). Similarly, modifying the growth process separately under A2 leads this time to changes of some species biomass: cod, lesser spotted dogfish and poor cod biomasses decrease, while the biomass of pouting increases (Figure 8H). For reproduction season, the directions but also the values of variation are very similar to those obtained under B1 scenario (Figure 8G). The spatial distribution process for

A2 causes the extinction of cod, and the decrease of biomass of other species such as herring, horse mackerel, squids and whiting. Even if their biomass was affected by the moderate B1 scenario, dragonet, lesser spotted dogfish, pouting and red mullet biomass does not change under the stronger A2 scenario (Figure 8I).

The simulation of climate change impacts on all processes simultaneously leads to cod extinction, and very low level of whiting biomass (Figure 8J). Compared to B1, two additional species have a decreasing biomass, sardine and lesser spotted dogfish. Moreover, the biomass of herring and mackerel is respectively multiplied by nearly 16 and 11. Biomass of plaice, red mullet, sole and squids increases, similarly to B1. Globally, the patterns of species biomass change are similar for B1 and A2 scenario, but with higher amplitudes of change under A2 scenarios.

3.1.2 Sensitivity of the model

The relative contribution of each process on four indicators (total biomass, total yield, slope of the size spectrum and mean trophic level) is presented in Figure 9.

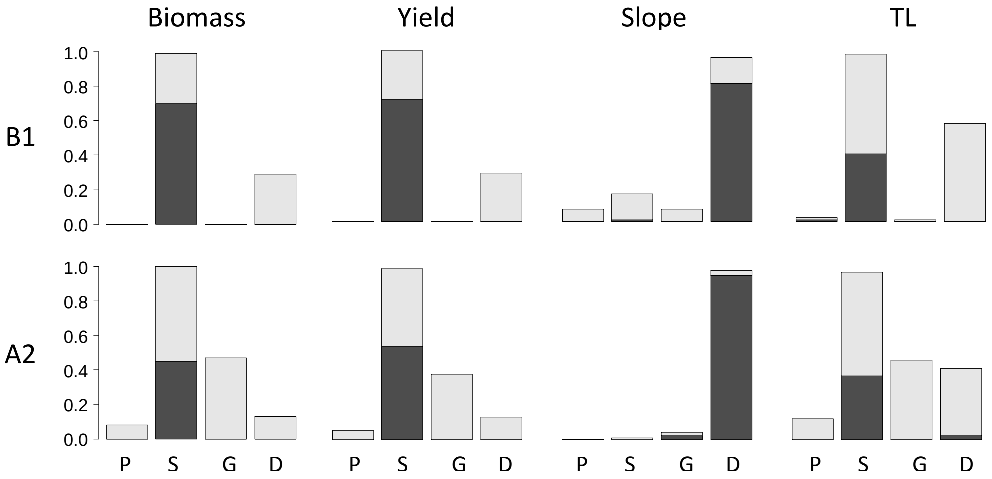

Figure 9 : Sensitivity index of the four processes (P : Primary production, S : reproduction season, G : Growth, D : Spatial distribution) on four different indicators for the two scenarios (first row: B1; second row: A2). Dark grey bars represent first order indices and light grey bars represent second order indices, i.e. from the interaction of the process of interest with other ones

For B1 scenario, the relative contribution of the different processes is similar for the total biomass and the total yield. These indicators are mostly affected by the reproduction season, as illustrated by its first order contribution of 0.70 and a total contribution reaching 0.99 when interactions are included (the main interaction being between reproduction season and distribution). Primary production and growth do not contribute to biomass and yield changes. For the mean trophic level, the same pattern is globally observed, but with a lower contribution of reproduction season alone (first order index) and higher contribution of the interaction between total index of reproduction season and spatial distribution. The slope indicator is impacted differently by the four processes than the other indicators. The spatial distribution has a first order index of 0.80 and all the processes have an effect on slope change through interactions with other processes (second-order index between 0.07 and 0.15).

For A2 scenario, it can be noticed that for the biomass and yield indicators, there is a decline of the first order contribution of the reproduction season (0.45 and 0.54 respectively) counterbalanced by an increase of the relative contribution of interacting processes than for B1. The second order contribution of growth reaches 0.54 and 0.45 for biomass and yield respectively, while it was null for B1. Primary production also contributes through interactions with other processes to change in biomass and yield for A2 but it does not exceed 0.08 for biomass and 0.05 for yield. For spatial distribution the second order contribution decreases down to 0.13 for biomass and yield. Moreover, for the trophic level, the same pattern occurs as for biomass and yield, but with only a slight decline of first order contribution of reproduction season, while we see a similar increase of second order contributions of all other processes. For the slope indicator an opposite evolution than the other 3 indicators can be observed. We note a general decrease in second order contributions of all processes and an increase of the first order contribution for season reproduction, growth and spatial distribution, with first order contribution of distribution reaching 0.95 while other processes contribution remains below 0.1 (Figure 9).

3.2 Projection of the future eastern English Channel system

3.2.1 Changes of species biomass

The projection of the system under both climate change scenarios induces the loss of predatory species, cod and whiting, which are at their southern limit of distribution in the eastern English Channel. This decline is not a general pattern for all the species with a cold temperature affinity, as illustrated by herring, which has a northern distribution and does not seem to be negatively impacted by climate change, as it displays an increase of biomass. For the species with a warm water affinity, different reactions are also encountered: some will have their biomass which increases, such as the highly commercial red mullet, but on the other hand, some species do not seem to be impacted by climate change. This is the case for sardine whose biomass does not change for B1 scenario and even decline on the A2 scenario. It has to be noticed that flatfish always have their biomass which increases for both scenarios (Figure 8E, J).

3.2.2 Dynamic of the system

The relationship between abundance versus size of all modelled individuals of the system is represented for the current situation and for the two scenarios B1 and A2 (Figure 10). It shows that climate change modifies the distribution in size of individuals, with both a decrease of the number of large fishes and an increase of small size fishes (Figure 10).

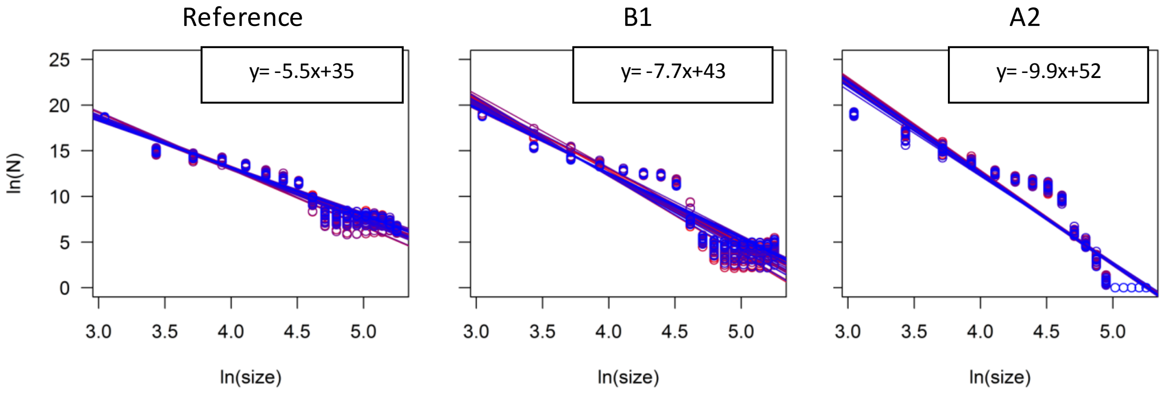

Figure 10 : Relationship between abundance (N) and length (size), both represented in natural logarithm.The linear regression is represented for each of the 30 replicates, but he equation represents the mean linear adjustment over the 30 replicates.

This modification of abundance distribution over size classes induces a steepening slope of the size spectrum. The slope decreases apparently linearly as temperature increases (from 12.99°C in average in the reference situation to 13.39°C for B1 and 13.79°C for A2),but the limited number of scenarios does not allow us to test for it. It is also worth noting that climate change induces an amplification of the oscillations of the size spectrum around the linear regression (Figure 10).

The trophic structure of the 14 modeled species is represented for the B1 and A2 scenario and the reference situation (Figure 11).

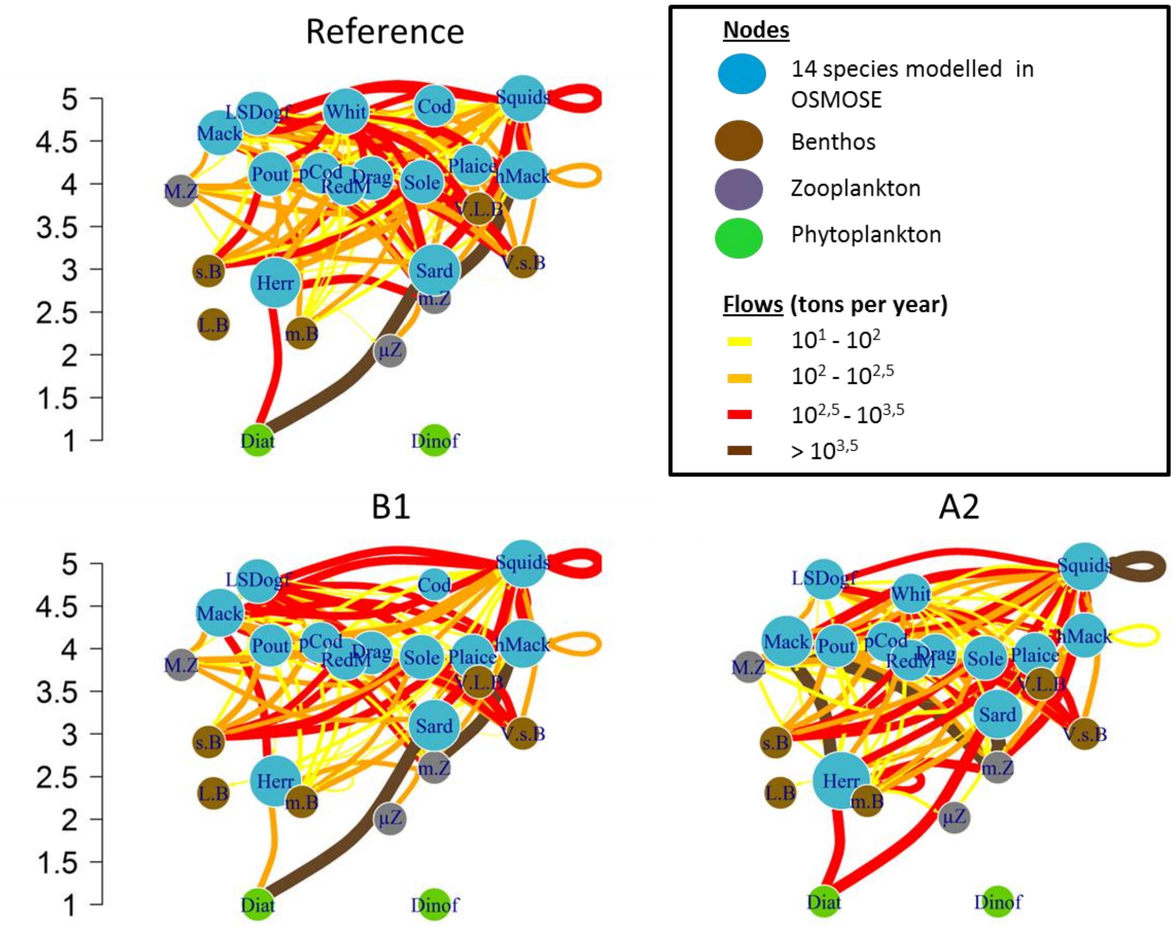

Figure 11 : Representation of the trophic structure of the 14 modeled species for the reference situation, B1 and A2 scenario, distributed on the y axis according to their mean trophic level. The size of nodes is proportional to the logarithm base 10 of the species biomass for the 14 species explicitly modelled in OSMOSE (blue nodes) and does not vary for the other nodes. Weak trophic links (smaller than 10 tons per year) are not represented for clarity. (LSDog : Lesser Spotted Dogfish, Whit : Whiting, RedM : Red Mullet, Pout : Pouting, PCod : Poor Cod, Mack : Mackerel, Drag : Dragonnet, HMack : Horse Mackerel, Sard : Sardine, Herr : Herring, M.Z : MacroZooplankton, m.Z : Mesozooplankton, µZ : Microzoolpankton, V.L.B : Very Large Benthos, L.B : Large Benthos, m.B : Medium Benthos, s.B : Small Benthos, V.s.B : Very small Benthos, Diat : Diatoms, Dinof : Dinoflagellates)

For the reference situation 3 groups of species can be identified according to their trophic levels. The first one, characterized by a trophic level between 4.5 and 5, regroups squids, cod, whiting, lesser spotted dogfish and mackerel. The second group, with a trophic level around 4 is composed of pouting, poor cod, red mullet, dragonet, sole, plaice and horse mackerel, and finally there is a third group of a trophic level of 3 with herring and sardine. Those groups are affected by climate change, in fact, for B1 scenario, the latter group (plankton feeders) is split with herring having its trophic level dropping down to 2.5 and sardine TL slightly increasing up to 3.1 while the other groups don't change much. For A2 scenario, additionally to the plankton feeders split described previously, we can note a modification for the mackerel which joins the group of the trophic level of 3 (Figure 11).

Concerning the flows between the different nodes, we can see that for the reference situation, the biggest trophic flows are directed to sardine and horse mackerel and come from microzooplankton for both species, but also from diatoms for sardine. Both species are highly predated by squids. Moreover, several important flows end up at the whiting node, characterizing it as an opportunistic predator strongly entangled within the food web.

Under scenario B1, the flows from plankton to sardine and horse mackerel remain similar to the reference situation, and the flows originated from small benthos and very small benthos increase. The extinction of whiting and diminution of the cod population result in an increase of fluxes towards the remaining predators, namely squids and lesser spotted dogfish, as well as mackerel to a smaller extent. Indeed, for B1 (but also A2), a shift in the diet of mackerel can be observed, with a bigger consumption of small herring under climate change scenarios. For the A2 scenario, the food web seems to be dragged down due both to the diminution of species trophic levels (notably herring and mackerel) and to the biomass diminution (or even extinction for cod) of the higher trophic level (whiting and lesser spotted dogfish).In this scenario, the phytoplankton flux goes more to herring and less to sardine, and the bulk of biomass appears to be around trophic level 4. Finally, the trophic links going to squids are more numerous and important, as it constitutes the main predator in this ecosystem configuration.

4 Discussion

4.1 Relative importance of the different processes affected by climate change

This study reveals that for the eastern English Channel, the reproduction season is the process which impacts the most the global dynamic of fishes under climate change scenario. First, at the species level, season reproduction is the process that, taken alone, induced the highest amplitude of variation of biomass both for B1 and A2. Indeed, even under the moderate B1 scenarios, simulating earlier reproduction seasons led to extinction and strong decreases of some species biomass while other were more than doubled. The prevalence of the reproduction season effect was also tractable when all processes were simulated simultaneously: the patterns of change of species biomass were very similar to the one obtained with only the reproduction season modified. Second, at a more integrated level, reproduction seasonality appears also to be the main driver of the overall community response to climate change. The relative contribution of the processes shows that for biomass, yield and trophic level, reproduction season is the most important process. This process reaches a minimum of 0.97 for the biomass, yield and trophic level indicator. It is also, among the four processes considered, the one that have a notable contribution of first order.

The effect of season reproduction on biomass based indicators is clearly revealed, but for the slope indicator which describes the size spectrum of the system, it is the spatial distribution process which contributes the most. It can be expected that the slope will be impacted by the same processes as for the trophic level indicator, because trophic systems are sized structured. In fact, species from the bottom part of the foodweb are generally small sized species and reciprocally, species of the top part of the food chain are large species. It can be seen that processes have a different contribution for TL than for biomass and yield. This can be explained by the effect of spatial distribution on cod, which is a large fish, i.e. the main contributor of the highest size classes of the size spectrum. Therefore, the decrease of cod biomass is well captured by the slope of the size spectrum which becomes steeper.

It is recognized that climate change will affect several processes at different scales, for instance via O_2 saturation inducing a lower metabolic performance (Pörtner and Peck, 2010) and phenology perturbations of fish larval dynamics (Genner et al., 2010). Still, projections of climate change impacts on fish community mostly focus on changes in spatial distribution (e.g., Cheung et al., 2009) and generally do not take into account interactions between species. Here we studied the effects of climate change at a regional scale, and we showed that interactions between species constitute an important factor that distorts the direct effects of climate changes. For example, when considering the spatial distribution process only, we saw that by changing the distribution of only three northern species over the 14 explicitly modelled, it affects directly these species but also modifies other species biomass indirectly by the release of predation pressure.

The conclusions obtained here on the relative effects of the four processes studied are of course to be put in relation to the main features of the study area, a coastal shelf sea highly supported by benthic resources (Giraldo et al., 2017). In fact, the same analysis in another ecosystem could lead to different conclusions regarding the relative impact of the different processes. For example, climate change induced a small amplitude of variation of primary and secondary production in the eastern English channel (+ or – 2 %), which had no or very limited impacts on the fish community. In other areas this process could have a bigger role in the projection of climate change effects on ecosystems, such as in upwelling areas where the whole marine system is governed by bottom-up control (Bakun, 1990).

4.2 Consistency of the results under different climate change scenarios

Climate change effects do not seem to vary linearly with global warming. Indeed, at the species level, effects of the different processes taken alone have the same amplitude for B1 as for A2, while we would expect bigger changes for A2. However, when all processes are simulated at the same time, amplitude of species biomass changes appears to be larger for A2, i.e. under warmer conditions. At the global level, reproduction season considered alone (i.e. first-order index) contributes more to the biomass indicators in the B1 scenario than for the A2 scenario, It was also shown that for the A2 scenario, the interactions of the different processes have a larger contribution in the variation of biomass, yield and mean trophic level.

These observations can emerge from the combination of the different processes directly on the species modelled, but they can also be explained by the interactions existing between species. The simulated decline of cod and whiting biomass can induce, through a top-down effect, an increase of their prey biomass. Most likely, The importance of interactions when projecting ecosystem state under climate change has been emphasized by (Kordas et al., 2011), who pointed out that indirect effects of climate change will be greater than direct effects at the community level

The increasing contribution of interacting processes for A2 suggests that under pessimistic scenarios of global warming, several processes have to be considered because of the high impact of their possible interactions. Thus, uncertainty of the projections probably increases with the increasing simulated future temperature, as the environment gets further away from the current situation and as interactions occur leading to non-linearity of the system. The ability to predict the future situation of the system is therefore less reliable under the pessimistic scenarios than for moderate ones (Christensen et al., 2006).

4.3 Ecosystem status for 2050

Our study corroborates previous observations made on marine system subject to climate change. In fact, we showed that top predators are the species which endure the most the effects of climate change, with a clear decline of their biomass. The sensitivity of this functional group is well known and was observed in other studies(Genner et al., 2010; Kordas et al., 2011). Our system is governed by two main predators, cod and whiting, which are opportunistic predators eating whatever prey they encounter, including a lot of other fishes. The decline of their biomass has a detrimental impact on the stability of the whole system, because the competition between the prey of cod and whiting is no more regulated and this could lead to the dominance of one species and the collapse of its competitors (Pörtner and Peck, 2010).

It was shown that larger individuals tend to disappear for the benefit of smaller ones, a phenomenon that increases with increasing temperature. Most likely larger individuals belong to large species of the modeled system, such as cod or lesser spotted dogfish, while smaller individuals may be issued from small species but also from young and non-mature individuals of large species. Therefore, the smaller species seem to be able to endure the climate change better than the larger ones (Genner et al., 2010). Climate change appears to be a stronger stressor for species which have a slower reproductive rate and which have long lifespan, i.e. those representing the K-strategy species. On the other side smaller species which have a high reproductive rate and which live only few years, are more likely to taking the hit and endure the effect of climate change (Perry et al., 2005; Pörtner and Farrell, 2008)

4.4 Limits of the approach

To assess the climate change effect on the four processes considered, some hypotheses were made to model the mechanisms driven by temperature.

First, the primary production comes from the ECOMARS-3D model but phytoplankton and zooplankton biomasses were homogeneously scaled following their evolution simulated by the ERSEM model forced by the two scenarios of warming prediction (B1 and A2). This was done because no climate projection existed for the ECOMARS-3D model and because the too coarse spatial resolution of the ERSEM model prevents it to be used directly as an input of the OSMOSE model. Thus, it could lead to an underestimation of the effect of the primary production, and then this process could have a more preponderant effect in the evolution of the system.

Second, it was chosen to simulate the effects of climate change on the different processes by modifying the related input parameters. Because the current study constitutes a first approach, we used this pragmatic method to simplify the modelling process and considered that the formulation of the different processes would not change, which allows not to calibrate the model again. Under highly different conditions of temperature, we could expect that the formulation of some processes would change, but how it will change remains uncertain. Bioenergetics models such as the DEB (Dynamic, energy budget,(Kooijman, 2000) could be used to explore new formulation of some processes.

Finally, while for some well-studied species experimental studies exist and can be used to inform how parameters vary with temperature, this is not the case for all species modelled in OSMOSE. When only few or even none studies exist, it is difficult to set the parameter values corresponding to the climate predictions, such as for reproduction season, the way the timing of maturation is modified by climate change is complex, and need to approximated until more information are available. So some hypotheses were required for defining the values of certain parameters, and this may lead to some uncertainty regarding the conclusions made.

4.5 Conclusion and perspectives

This study brings out that among the four processes tested, the reproduction season contributes the most to the overall effect of climate change on the eastern English Channel ecosystem. The interactions between species lead to synergistic or antagonistic combinations of the different processes, refuting the classical null hypothesis of having cumulative effects of those processes, this kind of interaction with the climate change was also demonstrated in other studies (Christensen et al., 2006; Crain et al., 2008; Darling et al., 2010). It also highlights that the system is reshaped, with a clear decline of predators which are constituted by northern species. This tends to weaken the system structure, with no more regulation of the competition between secondary consumers.

This approach constitutes a first approach to understand the plausible projection of marine system situation for the future, considering multiple processes affected, under climate change scenarios at a regional scale. It clearly shows that considering only spatial distributions changes as it is mostly the case nowadays is not sufficient to estimate the possible future of a fish community under climate change. Nonetheless, several assumptions made could be improved to investigate deeper the first results obtained here.

Higher confidence in the results would require the consideration of uncertainty regarding how some parameters values were modified. Multiple values of a single parameter could be simulated to evaluate the way it affects the projection made. Such as for the growth process, the L_∞ value was derived from the value of K previously calculated with the equation formulating K with the temperature. A different way to change the value of L_∞, including no change of this parameter, could be tested to assess the effects on projections and the relative importance of growth for the simulated patterns. In this study climate change effects were considered to impact only four processes, but they must not be the only ones. As empirical studies increase, more information will probably become available and will allow to include other processes that are affected by climate change. Among those, it would be interesting to assess the effects of a reduced size at maturity, a change of fecundity (eggs number), modification of survival rates at different stages, including the critical larval stage.

This approach could be applied to another area and/or with another ecosystem model, in order to understand how specificities from an area impact the projection and see if the processes impacted by climate change have the same relative importance from an area to another. It would be interested to see if bottom-up controlled upwellings are more sensitive to primary production variations induced by climate change, and if other shelf sea ecosystems orientated along a north-sea axis (such as in the North Sea) are more sensitive to change in species distribution.

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Appendix A: Input parameters of OSMOSE for the 14 fish species modelled explicitly. L_∞, K, and t_0 are the parameters of the von Bertalanff growth model, with a linear growth before the threshold age a_{th} and a growth following the von Bertalanffy model after a_{th}; c is Fulton's condition factor and b the exponent of the L-W allometric relationship; L_{mat} is length at maturity and φ is relative fecundity; a_{max} is longevity; F is the annual fishing mortality rate and a_{rec} is age of recruitment; M_{oth} is an additional mortality rate (resulting from predation by other species of the ecosystem that are not explicitly modelled); $M_{\xi\ max}$ is the maximum starvation mortality rate, M_L is the larval mortality rate applied to the first life stage; ξ_{crit} is the critical predation efficiency corresponding to maintenance requirements+ predation param. Values reported in the table come from literature (references in Appendix 1) except from Moth, F and ML which come from calibration.

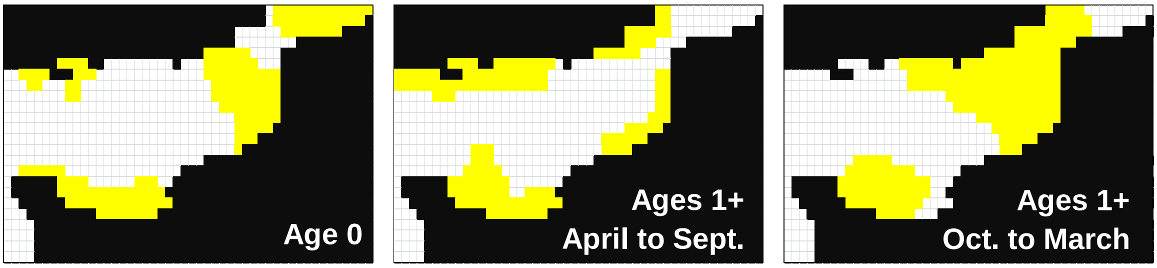
	GROWTH AND CONDITION						REPRODUCTION		SURVIVAL						PREDATION			
Species	L_∞	K	t_0	a_{th}	c	b	L_{mat}	φ	a_{max}	F	a_{rec}	M_{oth}	$M_{\xi\ max}$	M_L	Min size ratio	Max size ratio	ξ_{crit}	max ingestion rate
	cm	*y^{-1}*	*y*	*y*	*$g.cm^{-3}$*		*cm*	*$eggs.g^{-1}$*	*y*	*y^{-1}*	*y*	*y^{-1}*	*y^{-1}*	*$month^{-1}$*				*$g.g^{-1}$*
Lesserspotteddogfish	87.4	0.118	-1.09	0.5	0.00308	3.029	57	0.14	10	0.09	4	0.087	0.3	4.29	50	3	0.57	3.5
Redmullet	53.3	0.18	-1.23	1	0.00716	3.178	16.7	500	11	0.194	0.4	0	0.3	13.01	125	10	0.57	3.5
Pouting	37.6	0.46	-0.77	0.5	0.00657	3.202	23	620	4	0.106	1	0.12	0.3	6.69	50	3.5	0.57	3.5
Whiting	40.2	0.63	-0.37	1	0.00621	3.103	20	797	20	0.122	1	0.405	0.3	17.03	30	1.5	0.57	3.5
Poor cod	22.2	0.462	-0.679	0.5	0.0092	3.026	13	100	3	0	1	0.085	0.3	4.73	50	3.5	0.57	3.5
Cod	103.9	0.19	-0.1	0.5	0.00835	3.053	56	800	25	0.219	1	0	0.3	21.95	50 / 20*	2.3 / 1.8*	0.57	3.5
Dragonet	28.3	0.471	-0.443	0.5	0.0262	2.442	17.4	255	6	0	1	0.148	0.3	2.58	125	10	0.57	3.5
Sole	37.3	0.35	-1.61	0.5	0.00391	3.264	29	482	20	0.187	1.5	0	0.3	7.4	125	10	0.57	3.5
Plaice	71.7	0.23	-0.83	0.5	0.0103	3.017	27	255	15	0.44	1	0	0.3	13.52	125	5	0.57	3.5
Horse mackerel	39.2	0.18	-1.515	1	0.0054	3.114	22	1655	15	0.052	0.5	0	0.3	3.52	100	2.5	0.57	3.5
Mackerel	42	0.24	-2.07	1	0.00338	3.241	29	1070	17	0.142	0.5	0	0.3	7.94	100	2.5	0.57	3.5
Herring	29.2	0.37	-0.67	0.5	0.00503	3.1	25	458	11	0.156	1.5	0.008	0.3	1.24	1000	5	0.57	2
Sardine	24.6	0.79	-0.22	0.5	0.00594	3.077	15	2228	15	0.03	0.5	0.216	0.3	14.07	1000	5	0.57	3.5
Squids	50	2	0.5	0.7	0.25	2.27	30	50	2	0.036	0.5	0.298	0.3	7.97	20	1.5	0.57	3.5

*12cm threshold for morue

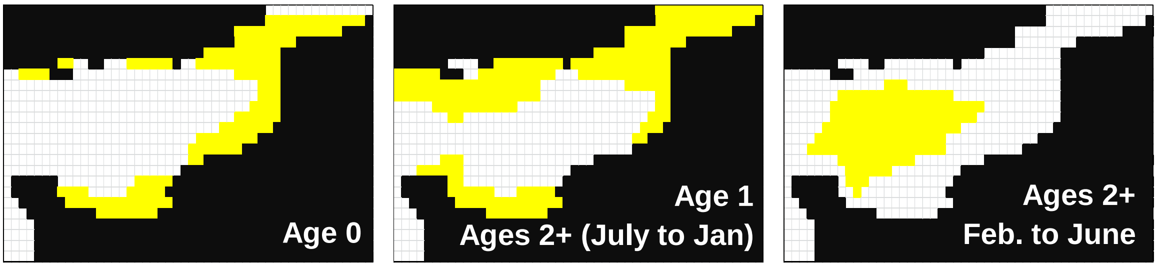
Appendix B :

Lesser spotted dogfish

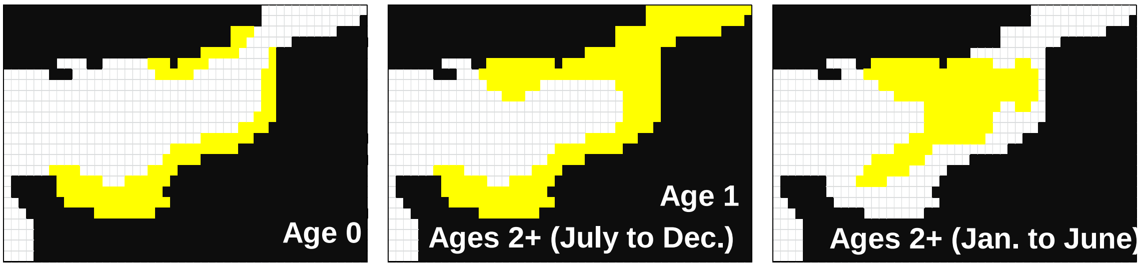
Red mullet



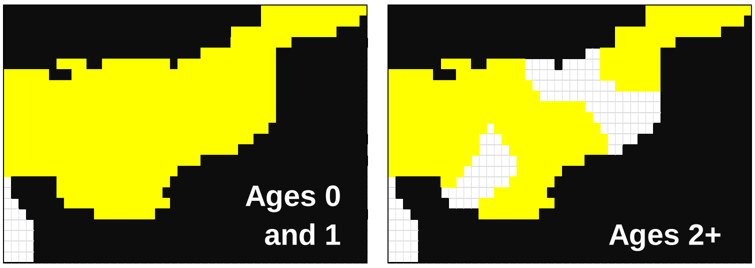
Pouting



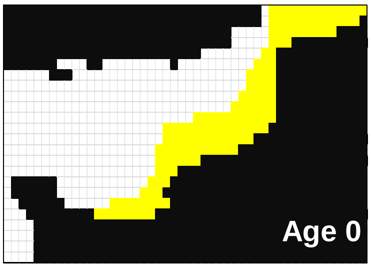
Whiting

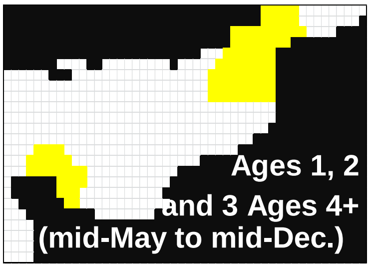


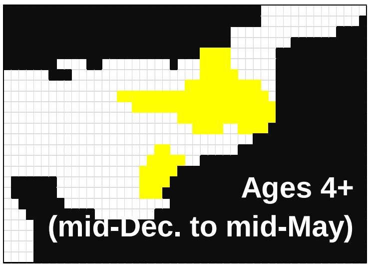
Poor cod



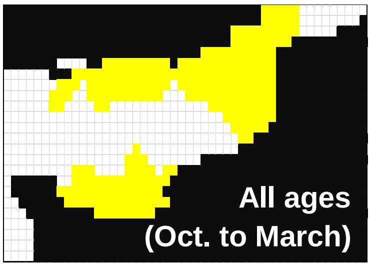
Cod

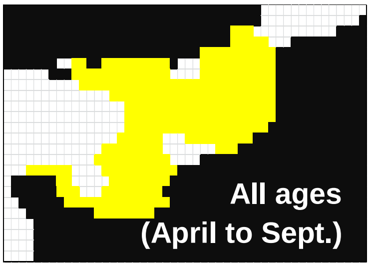




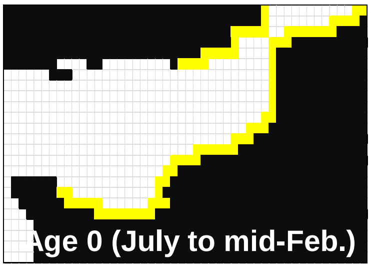


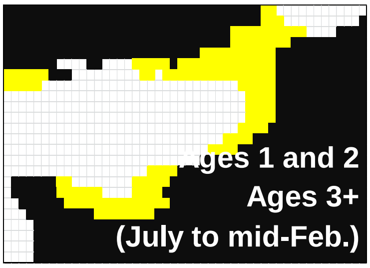
Dragonet

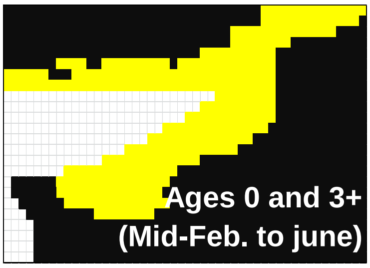




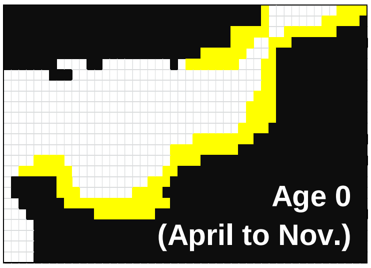
Sole

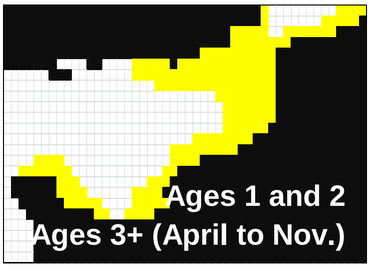


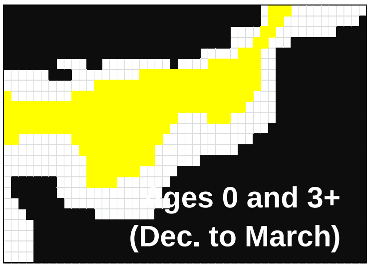




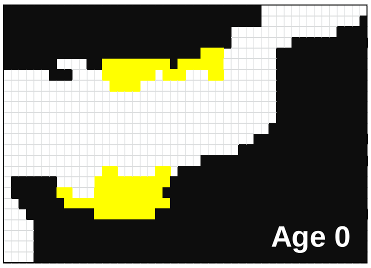
Plaice

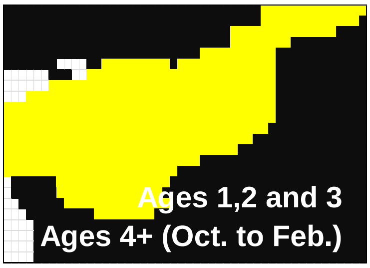


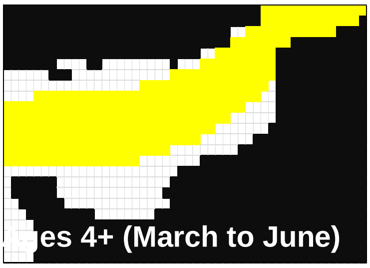




Horse mackerel *(ages 4+ from July to September : migration out of the area)*

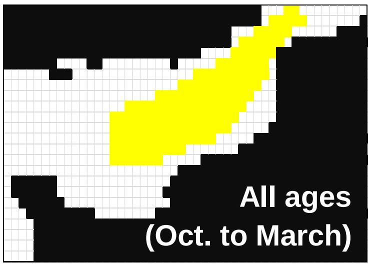




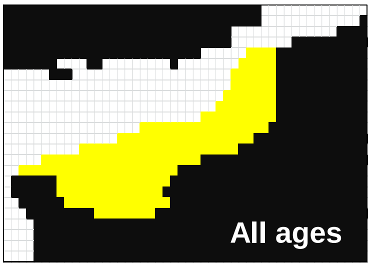


Mackerel

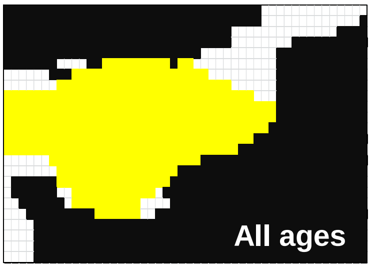
Herring *(All ages from April to September : migration out of the area)*



Sardine

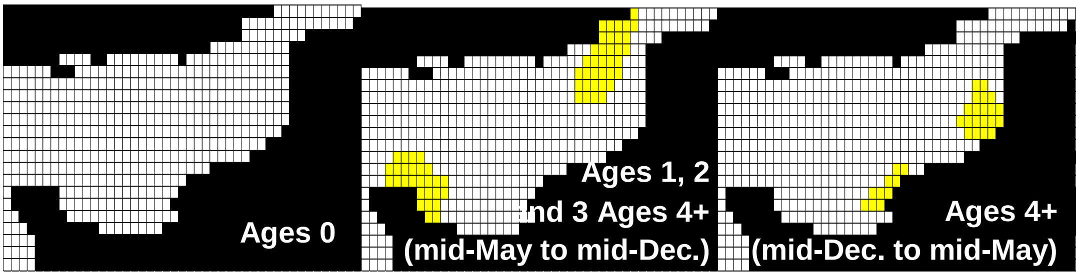


Squids

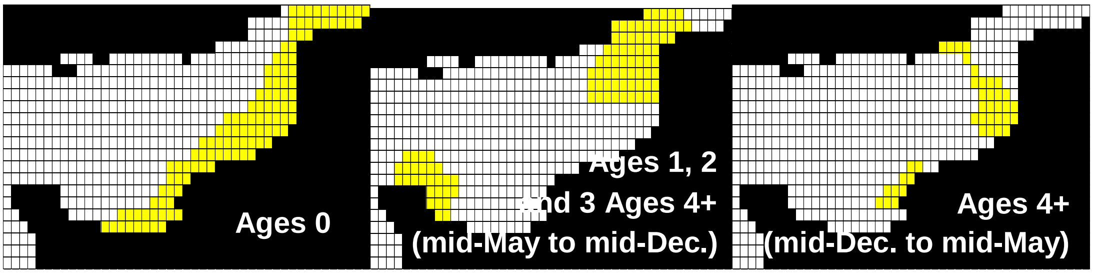


Appendix C : spatial distribution for the 3 species which are in limit of distribution in the eastern English Channel for the B1 and A2 scenario

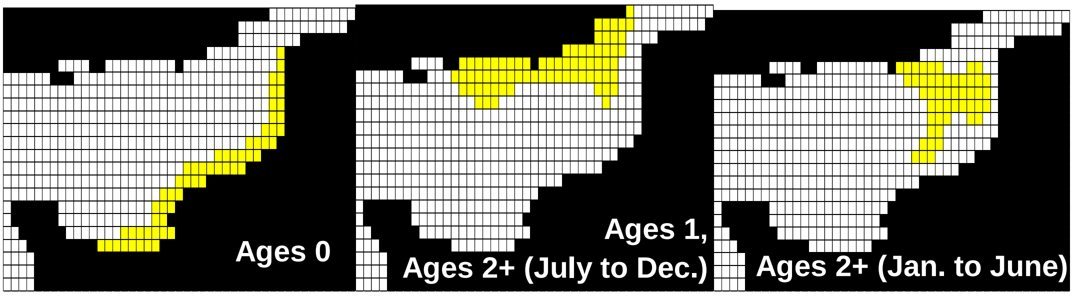
Cod A2



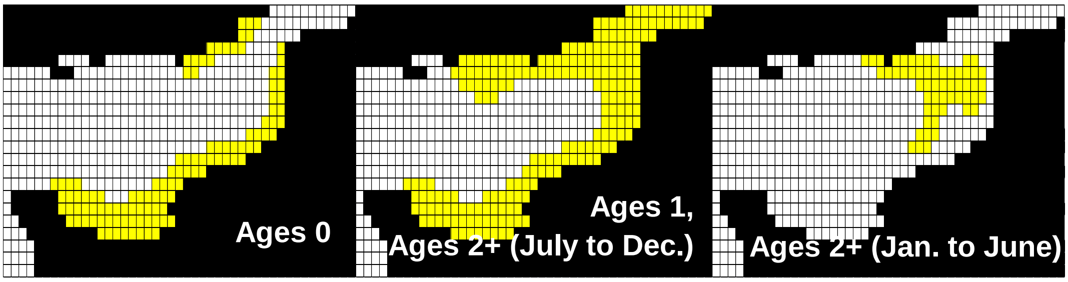
Cod B1



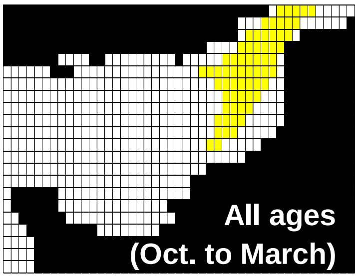
Whiting A2



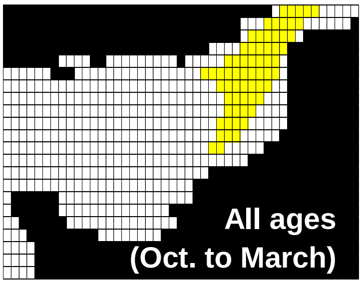
Whiting B1



Herring A2



Herring B1



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Titre français : Evaluation de l’importance relative des différents processus impactés par le changement climatique sur les commuauté de poissons

Titre anglais : Relative importance of different mecanisms underlying fish response to climate change

Les effets du changement climatique sur la stabilité des systèmes marins sont connus. L’augmentation de température entraine une redistribution spatiale des espèces vers les pôles de la planète. Il a également été démontré que la température pouvait influer les processus phénologique comme la migration ou la reproduction. Pour comprendre de manière précise comment le changement climatique affecte les divers processus qui régissent au sein des espèces, il est nécessaire de tenir compte des interactions entre les espèces du système en plus des effets directs du changement climatique. Ainsi, il est proposé dans cette étude d’utiliser un modèle multispécifique forcé par 2 scenarios de changement climatique provenant des prévisions du GIEC pour les années 2040 à 2049. Les effets directs du changement climatique sont supposés, dans cette étude, affecter 4 processus, la production primaire, la saison de reproduction, la croissance et la distribution spatiale. Les 2 scenarios de changement ont été régionalisés au site d’étude, correspondant à la Manche-Est. La projection de ces scenarios nous montre que la saison de reproduction est le paramètre qui influe le plus sur la biomasse du système mais également pour chaque espèce. Les interactions entre les espèces entrainent des interactions entre les 4 processus de type synergique ou antagoniste. Les projections du système pour les années 2040 corroborent les précédents résultats. Il est attendu de voir une diminution de l’abondance des ‘top-prédateurs’ et une augmentation de l’abondance de leur proies dû à la fragilisation que la perte prédateurs secondaire entraine.

Climate change affects marine systems stability, in particular temperature increase induces a shift of the fish spatial distribution polewards. Phenology of ecological processes, such as reproduction, migration seasons, and species physiology subject to temperature increase are also expected to change. The ecosystem response to climate change implying all these processes remains unknown and difficult to estimate due to the numerous interactions between species. To better understand the relative importance of the different processes affected by climate change, we use the multispecies model OSMOSE applied to the eastern English Channel and we simulated two climate scenarios for 2040-2049 from IPCC (B1 and A2). For this study, climate change is assumed to affect 4 main processes: the primary production, reproduction seasonality, growth and spatial distribution. Simulations followed a full factorial design in order to explore separate effects of each process as well as their combinations. The projections of IPCC scenarios on the system showed that reproduction seasonality is the process affecting the most total and species biomasses, while spatial distribution has a moderate effect of the different indicators studied. The interactions between species lead to antagonistic or synergistic combined effects of the different processes. When considering all processes simultaneously, the simulated state of the ecosystem in the 2040’s is characterized by a decrease of predators’ biomass weakening the system and leading to the prevalence of some intermediate-level predators.

Mots-clés : réchauffement océanique, OSMOSE, processus multiples, projections du GIEC

Key Words: Ocean warming, OSMOSE, multiple processes, IPCC projection