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Trophic amplification, an inter-model comparison study

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2. Introduction:

2.1 The ocean: a key element in the context of climate change

The ocean covers 71% of the earth's surface and contains almost all of the Earth's water. Three billion people depend directly or indirectly on marine and coastal biodiversity for their livelihoods (CBD 2010). Besides this food and water supply, it plays a crucial role as an attenuator in the current situation of global warming. It stores and redistributes enormous heat quantities, through the different ocean currents, around the Earth. Concretely, it absorbed near 93% of heat excesses and between 20 and 30% of the carbon dioxide induced by human greenhouse gas emissions to the atmosphere (Gattuso *et al.* 2015; IPCC 2019).

2.2 Climate change and its consequences on marine ecosystems

Human activity has disrupted the natural carbon cycle since the middle of the 19th century, with the release of huge quantities of greenhouse gases into the atmosphere (Pachauri *et al.* 2015), consequently affecting the Earth's climate and ocean (Bindoff *et al.* 2019). As a result, the ocean is becoming warmer, acidifying and reducing in oxygen content relative to pre-industrial levels, and these global changes are expected to intensify over the 21st century (Gattuso *et al.* 2015; Pachauri *et al.* 2015). The ocean has grown considerably warmer, from the surface of the sea to its deeper layers, even below 2000m; notably, from 1971 to 2010, ocean temperatures increased from the surface to a depth of 75m, at a rate of +0.11°C per decade (Stocker *et al.* 2013; IPCC 2019). Concerning ocean surface water acidification, pH declined by 0.11 in the 2010s relatively to 1870-1899 (Bopp *et al.* 2013; Gattuso *et al.* 2015). According to the latest IPCC report (2019), oxygen content in the open ocean decreased by 0.5–3.3% over the period of 1970–2010 and oxygen minimum zones expanded by a range of 3–8%, especially in the tropical regions.

In order to explore and predict the future climate over the 21st century, projections are made using Earth System Models (ESMs), which are developed to project future changes in climate and ocean properties under different scenarios of greenhouse gas emissions.

As a result of these changes in physical and chemical properties, major changes have already been observed in marine life at different ecological scales (Poloczanska *et al.* 2016; Bindoff *et al.* 2019; Lotze *et al.* 2019).

Phytoplankton, which accounts for 90% of primary oceanic production, plays an essential role in marine food web and will be particularly affected by climate change as its biomass and productivity are mainly driven by nutrient availability, light limitations and temperature (Steinacher *et al.* 2010). Simulations of primary production based on Earth System Models (ESMs) project an overall decrease in net primary production (NPP) at the global scale during the 21st century (Bopp *et al.* 2013; Cabré *et al.* 2015; Laufkötter *et al.* 2015). However, this global decrease in primary production masks a large spatial variability. Indeed, ocean NPP is expected to decrease in the low-latitude regions and increase in high latitudes. The NPP decreases in intertropical regions are largely due to the increase in stratification induced by significant temperature increases and changes in nutrient availability;

whereas the NPP increases at high latitudes is mostly linked to the rise of iron input and light intensity (Bopp *et al.* 2013; Cabré *et al.* 2015; Laufkötter *et al.* 2015).

Climate change affects the structure and functioning of ecosystems. Increased ocean temperature directly impact the physiological functions of marine organisms leading to modifications in body function, growth rates, maximum body size and reproductive rates (Pörtner & Peck 2010; Kroeker *et al.* 2013; Deutsch *et al.* 2015; Poloczanska *et al.* 2016).

In addition, shifts in species distribution and time events linked to climate change (e.g., in temperature, O₂ concentration and pH) may interact and amplify marine ecosystems' responses. Generally, these shifts are associated with either an expansion of populations toward higher latitudes or a decrease of populations at the southern boundary of its species range, or the combination of the two processes (Poloczanska *et al.* 2016). Differential responses to climate change across marine species and populations show a reorganization of species assemblages with changes in community structure and trophic interactions (Pinsky *et al.* 2020). At the same time, it has been observed that some marine populations change their biological timing events by bringing them forward in the year to adapt to changing conditions (Poloczanska *et al.* 2016).

2.3 Climate change and trophic amplification

Changes at low trophic levels may affect higher levels trophic biomass in larger proportions, through a process known as trophic amplification. This process describes the propagation of the climate signal from primary producers to higher trophic levels, causing biomass to decline (or increase) along the whole food web. In other words, trophic amplification determines the consequences of climate-induced relative changes of NPP for the higher trophic levels.

The trophic amplification of primary production changes has been previously shown between phytoplankton and zooplankton using different planktonic food web models and different ESMs (Chust *et al.* 2014; Stock *et al.* 2014; Kwiatkowski *et al.* 2018). At global scale, a projected increase in sea surface temperature (SST) of $2.29 \pm 0.05^\circ\text{C}$ may lead to a reduction in phytoplankton biomass of 6% while its predator (zooplankton biomass) would decrease by 11%, regarding 1980–2000 period to 2080–2100 (Chust *et al.* 2014).. This latter example suggests that trophic amplification may be driven through a bottom-up control. Study on trophic amplification at low trophic levels highlighted that negative amplification (i.e. where prey and predators decline) is the major response (with 47% of ocean surface) and prevails in the tropical oceans; whilst positive trophic amplification prevails in the Arctic and Antarctic oceans (Chust *et al.* 2014).

Despite this ecological process having been studied for low trophic levels, the effects of climate change on marine trophic amplification for high trophic levels have been scarcely explored, except through regional scale studies (e.g. Kirby & Beaugrand 2009) or global observations (Lotze *et al.* 2019). The latter highlighted that environmental change and mainly temperature drives trophodynamics, and therefore trophic amplification.

2.4 Marine Ecosystem modelling

Over the last few decades, a wide range of marine ecosystem models (MEMs) have been developed to improve our understanding of marine ecosystem functioning. These models have been developed to answer a broad variety of fundamental and applied questions mainly related to the effects of fishing and climate change. All of these ecosystem models differ from each other especially by the way they represent the biota, by the underlying ecological processes, the interactions with environment and by their complexity level.

Fish-MIP : Fisheries and marine ecosystem model Intercomparison Project

In order to better understand marine ecosystem functioning and forecast the long-term impacts of climate change and fisheries on marine ecosystems, a group of more than 40 global and regional marine ecosystem modelers created a network called Fish-MIP (Fisheries and Marine Ecosystem Model Intercomparison Project, <https://www.isimip.org/about/marine-ecosystems-fisheries/> ; Tittensor *et al.* 2018). Its power lies in the inclusion of a combination of different, published marine ecosystem models, based on different ecosystem modelling approaches (from population-based to functional traits- and size-based structure). Based on a standardised protocol, simulation experiments were developed to assess the effects of climate change on projected future changes in marine animals' abundance at global scale (Tittensor *et al.* 2018; Bindoff *et al.* 2019; Bryndum-Buchholz *et al.* 2019; Lotze *et al.* 2019). Projections estimate that total marine animal biomass would decrease by $4.3 \pm 2.0\%$ (95% confident intervals) and $15.0 \pm 5.9\%$ by 2090–2099 relative to 1990–1999, under RCP2.6 and RCP8.5, respectively (Bindoff *et al.* 2019; Lotze *et al.* 2019).

In addition to the Fish-MIP models, the EcoTroph model (Gascuel 2005; Gascuel & Pauly 2009; Gascuel *et al.* 2011), has recently joined this intercomparison project.

2.5 The Consequences of trophic amplification

By definition, this ecological process implies that biomass of higher trophic levels will be more positively or negatively impacted by climate change and global warming. That expectation raises various ecological and economical challenges. Shifting and/or decreasing biomass of species at high trophic levels induced by climate change disturbs the functioning and structure of ecosystems by changing the prey/predators relationships and trophic processes such as top-down control of predators on prey (Litzow & Ciannelli 2007; Cheung *et al.* 2009; Jochum *et al.* 2012 ; Beaugrand & Kirby 2018). Trophic amplification could also disrupt fishing activity as fisheries mostly target predator species, which are found at a high trophic level. It could indirectly lead to a decrease in potential catches on both the local and global scale.

2.6 Internship Objectives

In this study, we have considered five marine ecosystem models: four from Fish -MIP and EcoTroph. They vary by the ways of representing the food web, or by the way they integrate temperature, which lead us to think that there will be differences in the response of each model (e.g biomass projection) and hence in trophic amplification projections (Bopp *et al.* 2013). Nevertheless, by their heterogeneity, reflecting the diversity of model structures, parameterizations, scopes and purposes, the ensemble is more likely to include a greater number of relevant processes in the ocean than any single model for analysing trophic amplification process (Lotze *et al.* 2019). In that sense, the set of considered models reflect, at least partially, the uncertainty we face regarding the impact of climate change on ecosystem functioning, and more specifically on the trophic amplification.

The objective of the study was to explore how climate change may affect the marine food web through the trophic amplification process during the 21st century on a global scale. Thus, based on the outputs of the five marine ecosystem models and according to two greenhouse gas emission scenarios, the question we raised was: what are the expected repercussions/consequences of primary production changes on biomass along the food web?

In order to answer this question, I focused firstly on the spatial distribution and temporal dynamics of the trophic amplification process. When, where and how is it expected to occur? Are the projection of the five considered marine ecosystem models consistent from that point of view? This analysis demonstrated that trophic amplification does not occur everywhere, suggesting more complex patterns in the propagation of the NPP signal along the food web. Therefore, in a second part of the study, various categories of trophic amplification were considered and quantitative analysis conducted on order to answer the question: what is the link between trophic amplification types and changing environmental condition (ocean warming)? For this stage, I used the same output that in first stage. Finally, I studied trophic amplification by breaking it down along the food web and tried to identify which part, of food web, is the most affected by this phenomenon. To do so, I only utilised output of EcoTroph marine ecosystem model using both production and biomass data for each size class available. These three stages of analysis were examined all over two greenhouse gas emission scenarios.

3. Materials & Method

3.1 Two earth system models used

Two Earth system models (ESMs) have be used in our study, based on the Coupled Model Inter-comparison Project Phase 5 (CMIP5). The CMIP5 aims to bring together and compare models to better understand the impacts and consequences of climate change (Taylor *et al.* 2012).The two Earth System Models that we used are IPSL-CM5A-LR (referred in the report as IPSL) and GFDL-ESM2M (GFDL). They were respectively developed by the French Pierre Simon Laplace Institute (Dufresne *et al.* 2013) and by the Laboratory of Geophysical Fluid Dynamics at the US National Oceanic and Atmospheric Observing Agency (NOAA) (Dunne *et al.* 2012), respectively. These models integrate the interactions between the atmosphere,

ocean, land, ice and biosphere to estimate the state of regional and global climate under a wide variety of conditions (Bopp *et al.* 2013).

Two parameters were considered in our study: the sea surface temperature (SST, in °C) and the net primary production (NPP, in tons.year⁻¹), both provided each year from 1950 to 2099 by ESMs, according to two contrasted greenhouse gases emissions scenarios, RCP2.6 and RCP8.5. (RCP, Representative Concentration Pathways, https://sedac.ciesin.columbia.edu/ddc/ar5_scenario_process/RCPs.html). RCPs are based on the possible range of radiative forcing values by the end of the 21st century. RCP2.6 is the “strong mitigation” scenario in which the reduction of emission is projected to keep global mean atmosphere temperature 2°C while RCP8.5 is the “no mitigation policy” scenario in which greenhouse gas concentration will continue to rise throughout the 21st century. In CMIP5, GFDL and IPSL are referred to: low and high evolution models respectively (Lotze *et al.* 2019) Hence, IPSL predicts larger changes (positive and negative) in NPP and SST than GFDL for both RCPs (Fig 1.)

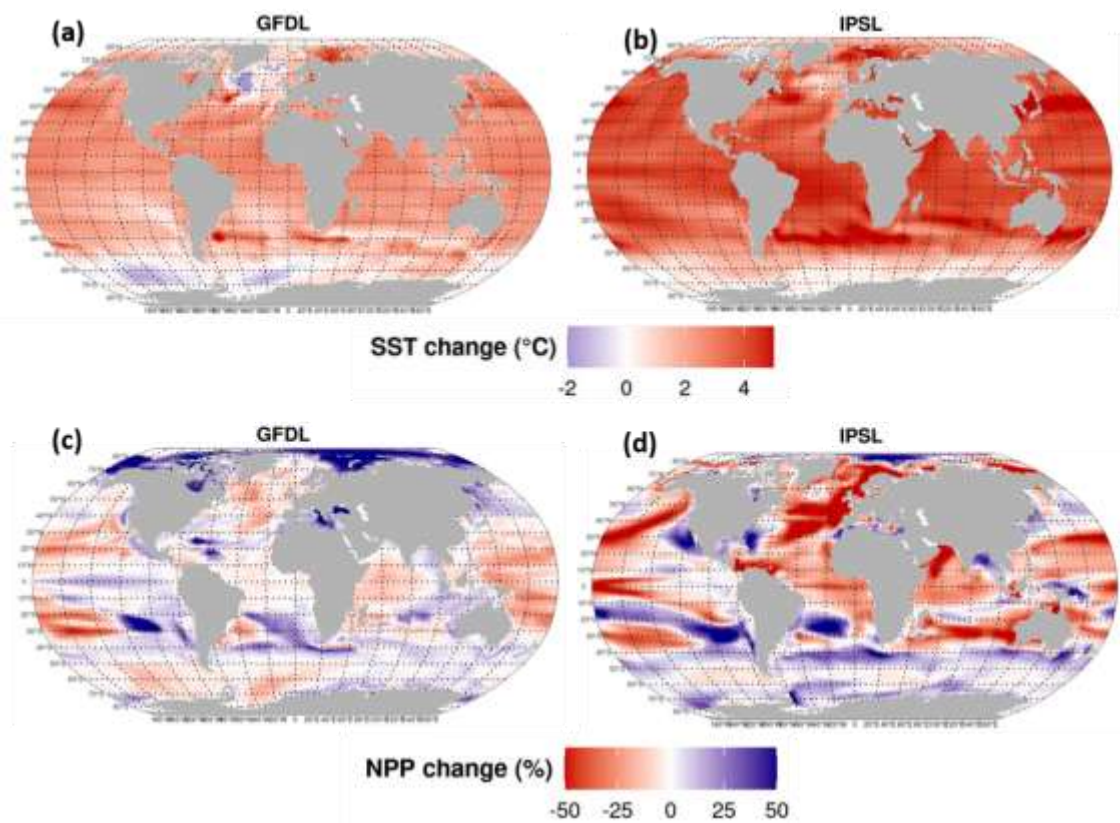


Fig. 1: Main outputs of the earth system models considered in the current study: mean changes in Sea surface temperature (a and b) and net primary production (c and d) in the 2090s relative to the reference period 1986-2005, under RCP8.5 and for the two models GFDL and IPSL.

3.2 The marine ecosystem models

In this study, we used the outputs of five marine ecosystem models (MEMs), which are DBEM, EcoOcean, Macroecological, Boats and EcoTroph, all of them forced by two ESMs and two greenhouse gas emissions scenarios. This gave us twenty ESM-MEM-RCP combinations to study.

The MEMs that we considered in the study vary widely in terms of how they represent food web or ecosystem components and the links between them. Ecosystem components can be represented by size classes (Macroecological, Boats), functional groups (EcoOcean), trophic levels (EcoTroph), or species groups (DBEM), whereas links can be represented by who-eats-whom networks, diet composition or energy transfer (Tittensor *et al.* 2018). Each MEMs are also characterised by their own ecological assumptions to represent the interactions with the environment and their responses to changing environmental conditions. Main features of the models are presented in Table1.

The responses of the MEMs that we considered are driven primarily by temperature and NPP, although oxygen, salinity and ocean advection are considered in a subset of models and play a secondary role (Cheung *et al.* 2009; Carozza *et al.* 2019). The projected changes of NPP are directly considered in all these MEMs, in rather similar ways, integrating either the change in phytoplankton biomass or the change in the production fuelling the food web. In contrast, the temperature effects all along the food web are integrated differently in the MEMs. For example, in EcoTroph, temperature directly influences the trophic transfer efficiency (Gascuel & Pauly 2009; du Pontavice *et al.* 2019). This latter being the fraction of energy transferred from one trophic level (TL) to the next and summarises all the losses in the food web at each TL. While in Boats and Macroecological, temperature directly influences natural mortality and growth rates (Carozza *et al.* 2019). This suggests differences in trophic amplification we will observe between MEMs might be due to the temperature effects and to the way it is represented within each MEM.

For this study, we work only with data from MEMs which run without fishing configuration; thus, our projections of climate change impacts are on a theoretical, unexploited global ecosystem.

Table 1. A taxonomy of marine ecosystem models taking part in the Fish-MIP project (modified from Tittensor *et al.* 2018; Lotze *et al.* 2019)

MEMs model	Brief model description	Defining features and key processes	Spatial and temporal scale and vertical resolution?	Taxonomic scope	Key reference
Species distribution models – statistical relationships between species and environment; focus on the role of habitat changes on population’s distribution					
DBEM	DBEM defines a bioclimatic envelope (niche) for each species and simulates changes in abundance and carrying capacity under a varying environment.	Carrying capacity is a function of the environment and species’ preferences for environment conditions (e.g, temperature, ice-coverage). Population dynamics are dependent of habitat suitability. Movement of adults is driven by a gradient of habitat suitability and density. Larval dispersal is dependent on current and predicted temperatures. Growth, reproduction, and mortality are dependent on oxygen, pH, and temperature.	1x1°; model outputs are annual average. Vertical dimension implicit through species niche preferences.	Fish and invertebrate species (primarily commercial).	Cheung <i>et al.</i> 2010
Trophodynamic models – structured based on species interactions and transfer of energy across trophic levels					
EcoOcean	EcoOcean is a global food web model based on the EwE framework designed to evaluate the impact of climate change and human pressure on marine ecosystems.	Running with atmosphere–ocean circulation model (COBALT); EwE food web model comprising a mass-balance component (Ecopath; input: biomass, production/biomass ratio, consumption/biomass ratio, diet composition, catches), a temporal dynamic predator-prey component (Ecosim), and a spatiotemporal dynamic component which is a function of grid cell specific habitat attributes i.e. pH, water depth, temperature, and bottom type (Ecospace)	Global model. Spatial resolution 1x1°and outputs are annual. Depth dimension is considered implicitly through food web interactions and habitat preference pattern.	All trophic levels and taxonomic groups included as biomass pools (51 groups).	Christensen <i>et al.</i> 2015
Size-based models – developed from food web, macroecological, and life history theory for exploration of community size spectra					

Macroecological	A static model size-structure model, which uses minimal inputs together with ecological and metabolic scaling theory to predict mean size composition and abundance of animals (including fish)	Provides a simple size-based characterization of marine ecosystems. Relies on estimates of predator–prey mass ratios, transfer efficiency and changing metabolic demands with body mass and temperature to predict body mass distributions and abundance of marine consumers from phytoplankton primary production and environmental temperature. Ignores non-phytoplankton production and animal movement.	Static equilibrium model, typically applied at scales from 1x1° grids to large marine ecosystems; forced with annual or monthly mean environmental variables. Single vertical (surface-integrated) layer.	180 body mass classes, Species are not resolved, only body mass classes.	Jennings & Collingridge 2015
Boats	Sized-structure model that combines size-based ecological theory and metabolic constraints to calculate the production of fish. This model is resolved across multiple size spectra.	Applies empirical parameterizations to describe phytoplankton community structure, trophic transfer of primary production from phytoplankton to fish, fish growth rate and natural mortality. Model parameters are calibrated against observed using a Monte Carlo technique. Explicitly models the evolution of effort and harvest. Recruitment is dependent on stock size and the environment. Simple life history features are resolved. Animal movement is not included. Predator-prey relationships are not resolved.	Flexible spatial scale; typically, global at 1x1°; monthly timestep; single vertical (surface-integrated) layer.	All commercial species represented by three groups, defined in terms of the asymptotic mass.	Carozza <i>et al.</i> 2016
Biomass flows model – developed from food web, account for transfer of energy across trophic levels (trophic spectra)					
EcoTroph	Global scale model representing the biomass flows from primary producers to top predators. Taking in account of metabolism to compute biomass by trophic level and can evaluate climate change impacts	Represents trophodynamics by the biomass flow across trophic levels, i.e., the ecosystem is represented by a continuous distribution of the biomass along trophic levels. Relies on estimates of trophic transfer efficiency for planktonic food web and for higher trophic levels and flow kinetic. These parameters are sensitive to temperature.	Global model. Typically applied at scales from 1x1° grids forced with annual mean environmental variables. Single vertical (surface-integrated) layer.	Species are not resolved, only trophic level classes.	(Gascuel & Pauly 2009; Gascuel <i>et al.</i> 2011)

3.3 Data exploitation:

A set of standardised outputs coming from these MEMs were produced for Fish-MIP and extracted from the related database (<https://www.isimip.org/protocol/>; except for EcoTroph whose outputs were produced independently of Fish-MIP):

- Total consumer biomass (Total animal biomass, in tons)
- Individuals larger than 10cm biomass (animal>10cm, in tons)
- Individuals larger than 30cm biomass (animal>30cm, in tons)

Biomass estimations for each category of outputs were available from 1971 to 2099 for RCP8.5 and RCP2.6 in a two-dimensional horizontal 1°×1° grid covering the global ocean.

To study trophic amplification across the food web, only with EcoTroph, we worked with three derived categories of biomass:

- The total consumer biomass conventionally defined here as the biomass of animals with trophic level between 2 and 5.5
- The prey biomass, conventionally defined here as the biomass of animals with trophic level between 2 and 3.1
- The predator biomass, conventionally defined here as the biomass of animals trophic level between 3.5 and 5.5

In EcoTroph, biomass was calculated for each trophic class of width $\Delta\tau = 0.1$ TL between TL=2 and TL=5.5 in each cell (two-dimensional horizontal 1×1° grid covering the global ocean), for the period 1971-2099 and for RCP8.5 and RCP2.6.

Then, in order to compare changes over time between the MEMs, ESMs and RCPs, we expressed changes in biomass relatively to a reference period using the reference period of the last IPCC report i.e. 1986-2005, was chosen. Hence, the relative change in biomass for cell i and year y is calculated as:

$$\text{Biomass change}_{y,i} = \frac{\text{Biomass}_{y,i} - \text{Biomass}_{1986-2005,i}}{\text{Biomass}_{1986-2005,i}}$$

With $\text{Biomass}_{y,i}$, the raw biomass for cell i and year y and $\text{Biomass}_{1986-2005,i}$ the mean annual biomass over the reference period 1986-2005.

We also calculated the net primary production change ΔNPP and the sea surface temperature change ΔSST for each cell i and year y of time as:

$$\text{Net Primary Production change}_{y,i} = \frac{\text{NPP}_{y,i} - \text{NPP}_{1986-2005,i}}{\text{NPP}_{1986-2005,i}}$$

$$\text{Sea Surface Temperature change}_{y,i} = \text{SST}_{y,i} - \text{SST}_{1986-2005,i}$$

With $NPP_{y,i}$ and $SST_{y,i}$, the raw net primary production and sea surface temperature for cell i and year y , respectively. $NPP_{1986-2005,i}$ and $SST_{1986-2005,i}$ the mean annual net primary production and sea surface temperature over the reference period 1986-2005, respectively.

3.4 Trophic amplification

Trophic amplification is the process by which climate induced changes in NPP propagate across the food web, with effects usually greater on high trophic levels than on the lower ones. Concretely, we study it by observing how a positive or negative change in NPP positively or negatively impacts the biomass at higher trophic levels.

For the first stage of my study, I worked on trophic amplification at global scale. For that purpose, we investigated the trophic amplification process by studying how the net primary production relative changes affect the total consumer biomass changes. In order to characterise and quantify this process, we defined a specific indicator named *Amplification index* as:

$$\text{Amplification index}_{y,i} = \frac{\text{Total consumer biomass change}_{y,i}}{\text{Net Primary Production change}_{y,i}} = \frac{tcb_{y,i} - tcb_{1986-2005,i}}{NPP_{y,i} - NPP_{1986-2005,i}} \times \frac{NPP_{1986-2005,i}}{tcb_{1986-2005,i}}$$

For each model and RCPs, this index was calculated in each $1^\circ \times 1^\circ$ grid cell i of the global ocean and for each year y between 1971 and 2099. With $tcb_{y,i}$, the raw Total consumer biomass for cell i and year y , $tcb_{1986-2005,i}$ the mean annual Total consumer biomass over the reference period 1986-2005 for cell i , $npp_{y,i}$, the raw net primary production for cell i and year y and $npp_{1986-2005,i}$ the mean annual net primary production over the reference period 1986-2005 for cell i .

In the last part of our study, focusing on EcoTroph we tried to analyse how trophic amplification intervenes within the food web, and which food web class is the most affected. At the same time, we noticed that trophic amplification is usually defined by comparing a biomass (the total consumer biomass in tons) and a flow of biomass (the NPP in $\text{tons} \cdot \text{an}^{-1}$). As with EcoTroph, we had easy access to both production and biomass values, for each trophic class of width $\Delta\tau = 0.1$ TL, we tried to identify what we called the “production amplification”, comparing changes in productions only, along the food web. To study it, we kept the same value of TL for grouping production into Prey production and Predator production. Hence, Predator production is the production between trophic level 3.5 and 5.5 and Prey biomass between trophic level 2 and 3.1. We then used the following partial indicators:

$$\text{Predator production amplification index}_{y,i} = \frac{\text{Pred_prod}_{y,i} - \text{Pred_prod}_{1986-2005,i}}{NPP_{y,i} - npp_{1986-2005,i}} \times \frac{NPP_{1986-2005,i}}{\text{Pred_prod}_{1986-2005,i}}$$

$$\text{Prey production amplification index}_{y,i} = \frac{\text{Prey_prod}_{y,i} - \text{Prey_prod}_{1986-2005,i}}{NPP_{y,i} - NPP_{1986-2005,i}} \times \frac{NPP_{1986-2005,i}}{\text{Prey_prod}_{1986-2005,i}}$$

$$\text{Predator to prey production amplification index}_{y,i} = \frac{\text{Pred_prod}_{y,i} - \text{Pred_prod}_{1986-2005,i}}{\text{Prey_prod}_{y,i} - \text{Prey_prod}_{1986-2005,i}} \times \frac{\text{Prey_prod}_{1986-2005,i}}{\text{Pred_prod}_{1986-2005,i}}$$

With : $Pred_Prod_{y,i}$, the raw Predators production for cell i and year y
 $Pred_Prod_{1986-2005,i}$ the mean annual Predators production over the reference period 1986-2005 for cell i .
 $npp_{y,i}$ and $npp_{1986-2005,i}$ as above for Amplification index
 $Prey_Prod_{y,i}$, the raw Preys production for cell i and year y
 $Prey_Prod_{1986-2005,i}$ the mean annual Preys production over the reference period 1986-2005 for cell i .

3.5 Trophic amplification range:

From our analysis, it appeared that an amplification of the NPP signal along the food web does not always occur. More complex patterns were observed. Therefore, we also characterised amplification by types. The processes of amplification in the ecosystem response were investigated by comparing the relative change of the consumer biomass to climate change, to the relative change of the NPP (Chust *et al.* 2014; Stock *et al.* 2014; Kwiatkowski *et al.* 2019) (Fig.2). Hence, the process is split into three main types: amplification, attenuation and inversion (Fig.2), reflecting situations where the change in biomass is respectively larger, smaller or opposite, compare to the NPP signal. In turn each of the groups encompasses two classes corresponding to positive or negative changes in biomass. We finally obtained six trophic amplification types associated with different values of the *Amplification index* (Fig.2).

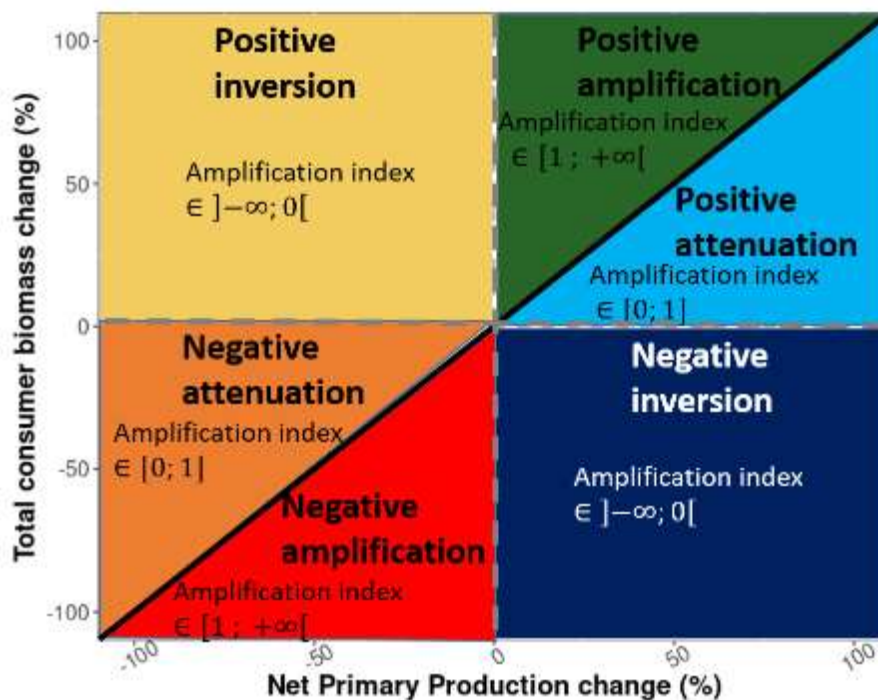


Fig. 2: Different types of trophic amplification associated with *Amplification index* range.
 Amplification types explicative scheme

3.6 Statistical Modelling approaches

We used statistical models to analyse our amplification index. The first one was used to analyse the spatial differences of trophic amplification between five ecosystem types at global scale, taking inter-MEM variability into account (see *SI Appendix, Fig.S1* for the considered ecosystem types). The second model aims to investigate the effect of ocean warming on trophic amplification. Preliminary analysis revealed that DBEM projections were too far from others models and did not allow the statistic models to fit correctly. Therefore, we developed the statistical models considering four MEMs only.

Statistical models are based on the outputs per 1°x 1° cell of the IPSL earth system model on average for the period 2090-2099. We separately analysed the regions where NPP is projected to increase or decrease to be able to ecologically interpret the trophic amplification estimates. Indeed, the Amplification index range is $]-\infty; +\infty[$ but the same estimates can have two ecological significations depending on the direction of change in NPP. For example, if Amplification index is greater than one:

- Either the relative changes in biomass and primary production are both positive with the change in biomass greater than the changes in primary production. In this case, the amplification can be induced by “improvement” of environmental conditions.
- Or the changes in biomass and primary production relative change are both negative, with the change in biomass more negative than the changes in primary production linked to “deterioration” of environmental conditions.

In addition, we remove data with NPP change within $[-1; 1]$ to avoid dealing with Amplification index extreme value.

We used a Generalised Additive Model (GAM) in which we integrated the effects of the variability induced by MEMs, the type of ecosystems (polar...), the interaction between MEMs and ecosystem types as well as a non-linear spatial component to integrate the residual spatial autocorrelation.

$$(1) Y_{i,m} = \beta MEM_m * \beta_1 ecosystem + te(latitude, longitude) + \varepsilon_i$$

Where $Y_{i,m}$ referred to the expected *Amplification index* mean value projected for the period 2090-2099 in cell i for model m , MEM was dummy variable for marine ecosystem model and ε_i corresponding to residuals. Concerning β and β_1 , they correspond to a vector of parameters as it estimates a specific β and β_1 for each model and ecosystem, respectively. The tensor, $te()$ allows us to integrate the residual spatial autocorrelation. A tensor is similar to a smooth ($s()$), it permits us to introduce a nonlinear relation of an explicative variable with the explained variable, but with two smoothing parameters, one for each variable.

To investigate the influence of warming ocean on trophic amplification, we also used a GAM in which we integrated the effects of the variability induced by MEMs, the relative change of sea surface temperature, the interaction between MEMs and relative change of sea surface temperature as well as a non-linear spatial component to integrate the residual spatial autocorrelation

$$(2) Y_{i,m} = \beta MEM_m + s(sst_change, by = MEM_m) + te(latitude, longitude) + \varepsilon_i$$

Where $Y_{i,m}$ referred to the expected *Amplification index* value in cell i for model m , MEM was dummy variable for marine ecosystem model and ε_i corresponding to residuals. Concerning β and $te()$, it is the same thing as for the above model. The smooth $s()$ in this model allows us to integrate a nonlinear response with only one smoothing parameter.

In the two models, the MEM variable was essential due to the high projection variability carried by them (explained in 2.2).

4. Results

4.1 Spatial and temporal trends of trophic amplification

Temporal trends in NPP and consumer biomass

Focusing firstly on global annual changes in response to ocean warming, we observe that total consumer biomass change is projected to decrease more and faster than NPP and this difference is enlarging over time, for almost every MEMs-ESMs configuration (except EcoOcean) and for both RCP2.6 and RCP8.5 (Fig.3). However, there is a difference in the magnitude of the response between ESMS and RCPs. IPSL projects higher values of relative change in total consumer biomass than GFDL: with over 2090s on RCP8.5, a decrease of -26.0% ($\pm 7.3SD$) and -11.4% ($\pm 6.0SD$) for IPSL and GFDL, respectively. Furthermore, regarding EcoOcean modelling, for the two RCPs, total consumer biomass relative change follows NPP changes over time with the same range of magnitude. We so do not expect a significant trophic amplification in this model.

Focusing, on IPSL-RCP8.5 projection configuration, we observe trophic amplification over the period 1971-2099 (Fig.3). It is marked $\Delta 1$ and $\Delta 2$ for Ecotroph model. Two things emerge from these deltas: firstly, that trophic amplification evolved over time ($\Delta 1 < \Delta 2$) and secondly, as expected and explained in 2.2, MEMs modelling project different magnitudes of trophic amplification with Macroecological and Boats proposing extreme values.

For IPSL and GFDL, we observe the same time trend evolution under RCP2.6 and RCP 8.5, yet, with a greater difference with RCP8.5 (end projection with RCP2.6 corresponding to mid-21st century RCP8.5 projection) and therefore a better contrast, allowing us to well observe the trophic amplification. This is why, for the rest of the results development, only outputs under RCP8.5 will be shown on figures.

Back to the definition of trophic amplification outlined in 1.3 and 2.4, there is trophic amplification, only if there is change at low trophic level, so here in NPP. Yet in GFDL projection configuration, the changes in NPP are much smaller than those of IPSL configuration; so, for the rest of development, we will not explicitly show figures with GFDL output, only referring to it in certain places.

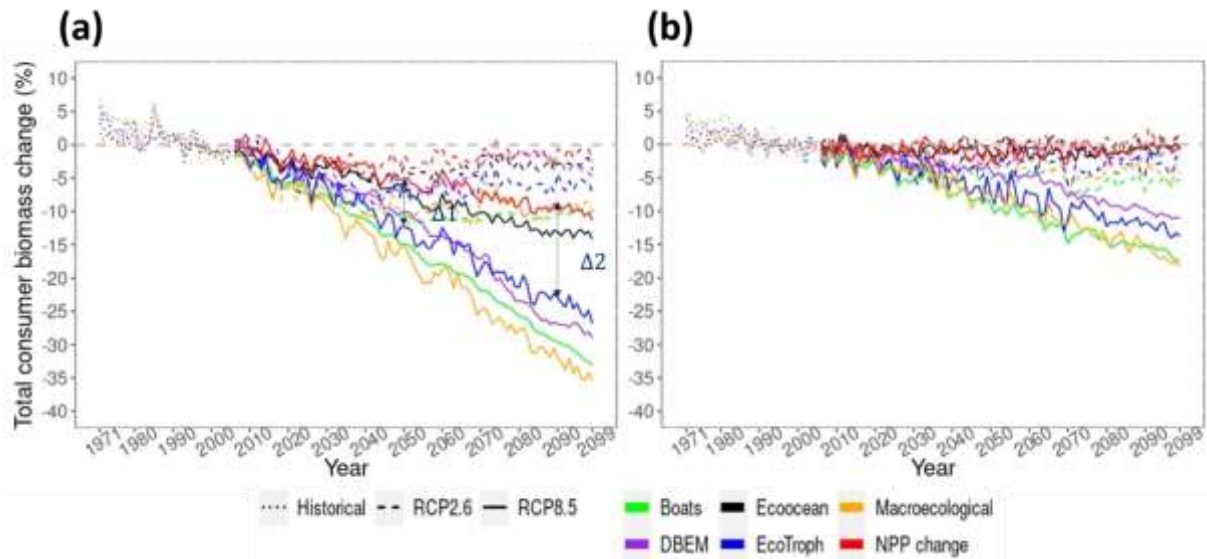


Fig. 3: Ensemble projections of global total consumer biomass in response to climate change.

(a) Individual model projections of annual mean change in total consumer biomass for historical, RCP2.6 and RCP8.5 relative to 1986–2005, showing the spread across different ecosystem model with IPSL/ESMs combination.

(b) Same as (a), but with GFDL/ESMs combination.

Temporal trends in the Amplification index

Concerning evolution over time of our Amplification index, it varies until 2040s (Fig.4). This chaotic pattern is related to a small NPP signal over this period, with not clear changes and for many areas alternative increase and decrease in NPP. After that time, decrease in NPP become dominant and the amplification index stabilises. Depending on MEMs modelling except EcoOcean, the average of our Amplification index range is [2.4 ; 3.4] with value of 2.4, 1.4, 3.4, 3.0 and 2.5 for DBEM, EcoOcean, Macroecological, Boats and EcoTroph, respectively. We then have the confirmation that all MEMs, except EcoOcean, take into account the trophic amplification process, with a mean amplification index equal to 2.6 over the whole second half of the century. For the extreme modelling combination (IPSL-Macroecological-RCP8.5), total consumer biomass is expected to change 3.4 times more than the NPP. That means that the expected 10% decrease in NPP would lead to a 34% loss in the total biomass of consumers at global scale.

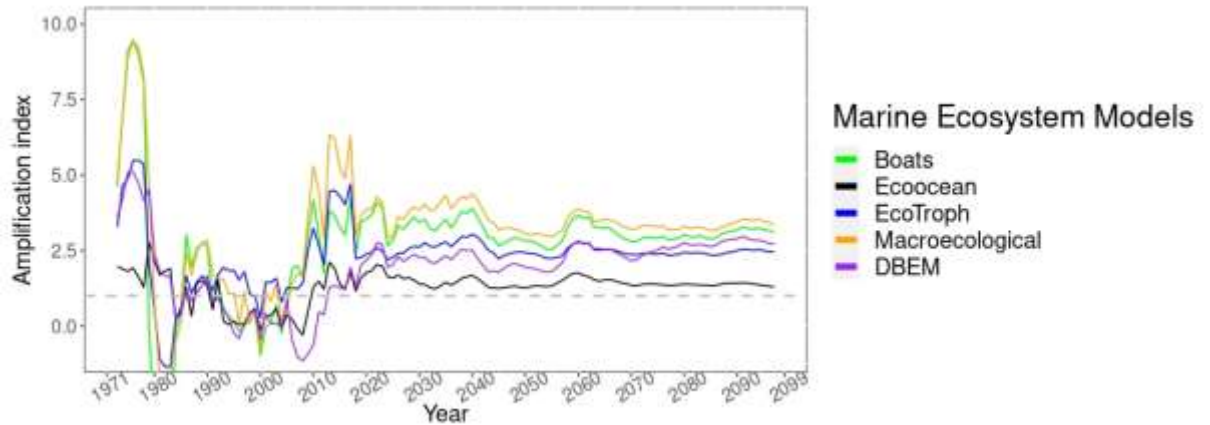


Fig. 4: Ensemble projections of Amplification index in response to climate change.

Individual model projections of rolling average of Amplification index for historical and RCP8.5 relative to 1986–2005, showing the magnitude of expected trophic amplification across different ecosystem model with IPSL ESM combination.

Spatial trends

Our results highlighted trophic amplification between net primary producer and the consumers at global scale. Nevertheless, associated to these trends, there is a spatial variability between ocean regions and between MEMs (Fig.5). Indeed, over the 2090 decade relatively to (1986-2005), each marine ecosystem model projects areas with positive and negative Amplification index but the magnitude of change varies widely between MEMs.

Globally, positive values of the amplification index dominate in almost all regions of the world ocean. This is especially true for Macroecological, Boats and EcoTroph whose patterns appear very similar. In contrast, EcoOcean exhibits mostly low amplification index, with few values higher than one (thus really related to an amplification situation), while DBEM shows extreme values, often very different from the ones of other MEMs.

Such MAPs are difficult to interpret and reveal the huge heterogeneity and complexity of the amplification process. Indeed, not only positive values of our index may correspond to both positive or negative amplifications, thus referring to very different situations, but more importantly, amplification does not occur everywhere. In large areas, the amplification index is between 0 and 1, thus traducing an attenuation process between NPP and consumer biomass changes, while in other areas it exhibits negative values, thus traducing an inversion of the signal between NPP and consumer biomass. Therefore, the amplification process at local scale has to be analysed based on distinct categories.

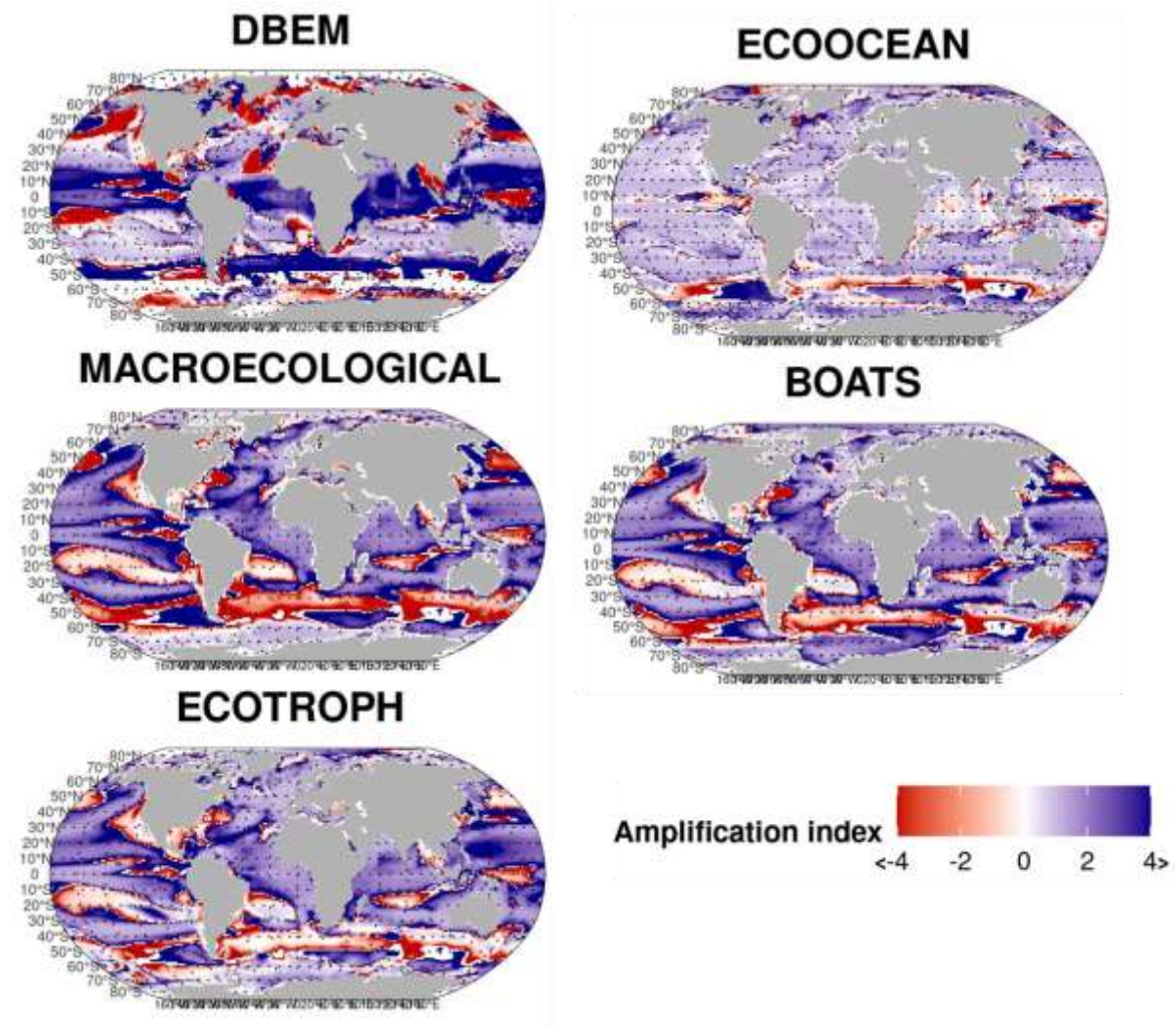


Fig. 5: Spatial patterns of projected Amplification index

Shown are global ensemble projections at a 1×1 degree resolution. Individual model projections of mean 2090s Amplification index under IPSL-RCP8.5 modelling. Values inferior to -4 and superior to 4 take scale extreme colours, explaining border effect.

4.2 Amplification types and ecological process

Amplification types

To interpret ecologically the trophic amplification process, we have categorised trophic amplification by types (Material & Method 2.5). Over the last decade compared to 1986-2005, the different MEMs project majority of negative amplification, with a covered surface of 35.5%, 30.0%, 56.4%, 51.8% and 50.6% for DBEM, EcoOcean, Macroecological, Boats and EcoTroph, respectively. (Fig.6). Negative amplification occurs in areas where ocean warming is high and in consequences NPP changes is strongly negative, due to water stratification increase (Fig.1 (d)). This leads to a loose even more important of total consumer biomass (*SI Appendix, Fig.S2*).

The second pattern we observed, in term of surface coverage, is the negative inversion. It corresponds to areas where total consumer biomass change is negative despite the fact NPP change is positive. This situation can be explained by temperature role: in these areas, an increase of water temperature conduct to an increase of NPP but this latter is not enough to compensate the effect of warming water on total consumer biomass and decreasing it by mainly affecting negatively trophic transfer efficiency and metabolism. The same mechanisms may explain positive attenuation where the increase in NPP is partly compensated temperature effects on the consumer biomass, which thus exhibit a smaller increase.

Positive amplification also appears in some areas where NPP increases. This is a situation rarely observed, only in polar region. It seems to be related either to areas such as Antarctic where a very small increases (if not a decrease) is expected in SST, or to the northern part of Arctic regions where it could be explained by a change in plankton communities.

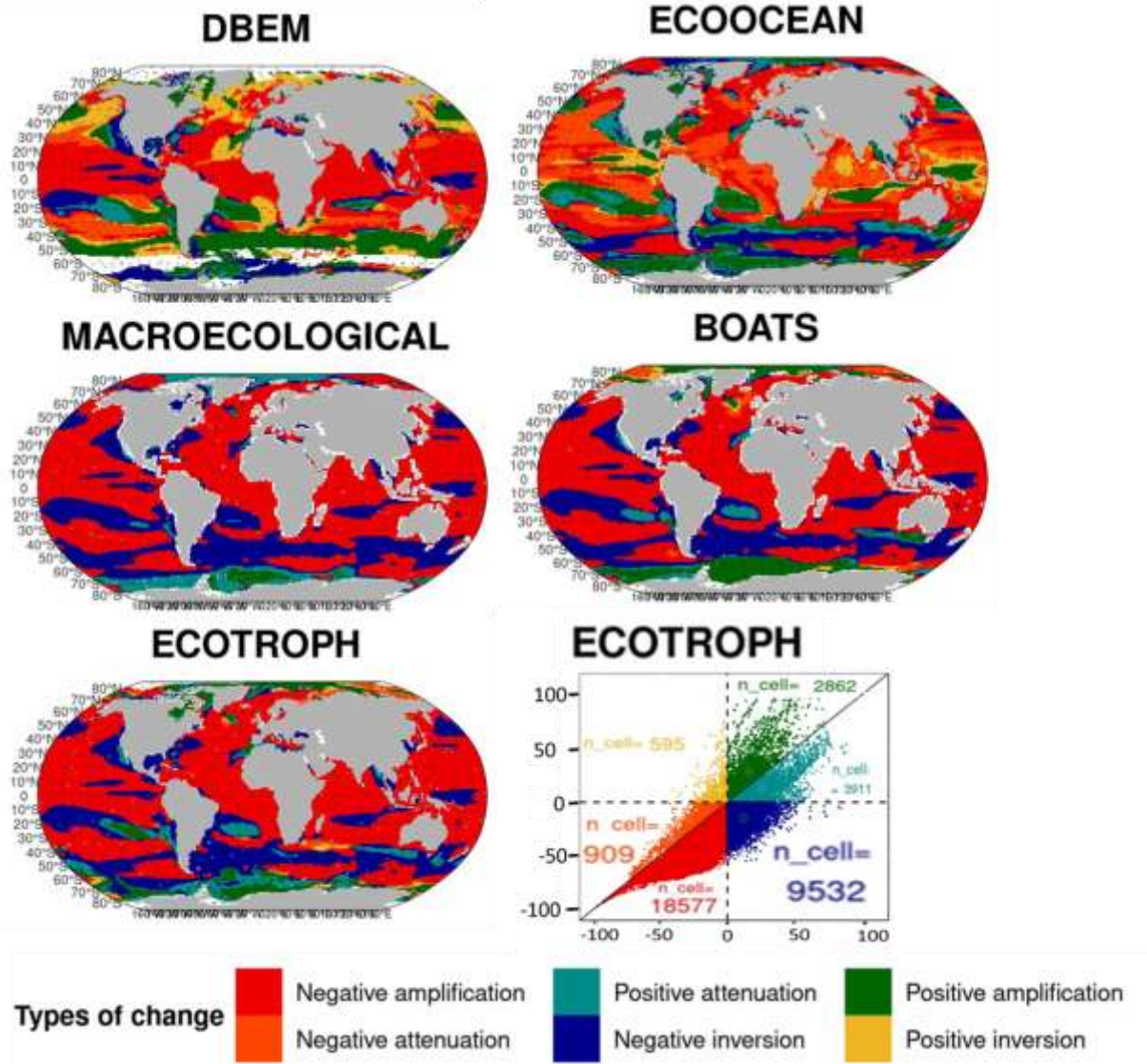


Fig. 6: Spatial patterns of trophic amplification types
 Shown are global ensemble projections at a 1 × 1 degree resolution. Individual model projections of mean 2090s amplification types under IPSL-RCP8.5 modelling; and for EcoTroph, plot counting mean cell number by type over 2090s.

In addition, it appears from this categorisation of trophic amplification that Boats, EcoTroph and Macroecological are in strong agreement. Taking EcoTroph example (Fig.6), cells with a negative change in NPP represent 55% of ocean surface over 2090 decade and in this 55%, negative amplification occurs at 92%. While when NPP change is positive, there is a better distribution between amplification types with 58%, 24% and 18% for negative inversion, positive attenuation and positive amplification, respectively. This last characteristic strengthens the predominance of negative amplification.

Complementary to this spatial approach, over time, negative amplification prevails in all MEMs projections (*SI Appendix Fig.S3*). This shift towards negative amplification happens between 2030 and 2040. For three of the five models considered, this shift to negative amplification is continuous and alarming, leading to the situation above (Fig.6), which give us both confidence in spatial and temporal results.

Spatial pattern

A statistical approach allows us to better understand how each MEM spatially integrates trophic amplification. As explained in 2.6, we analysed separately regions where NPP is projected to increase and decrease. As this is by far the dominant situation, we only present here the model for areas where NPP is predicted to decrease by 2090s. This model explains 24.9% of the deviance permits us to rule that MEMs are rather in agreement as to the projection of the trophic amplification process (Fig.7). By 2090, it is estimated that ecosystems except Antarctic will have a Amplification value superior to one, corresponding to a change in biomass and in primary production both negative with change in biomass larger than the changes in primary production. For example, temperate ecosystem is expected to reach a mean Amplification index value of 3.5. In contrast, it is projected that Antarctic ecosystem has a negative inversion translating a gain in consumers biomass and a loose in primary production.

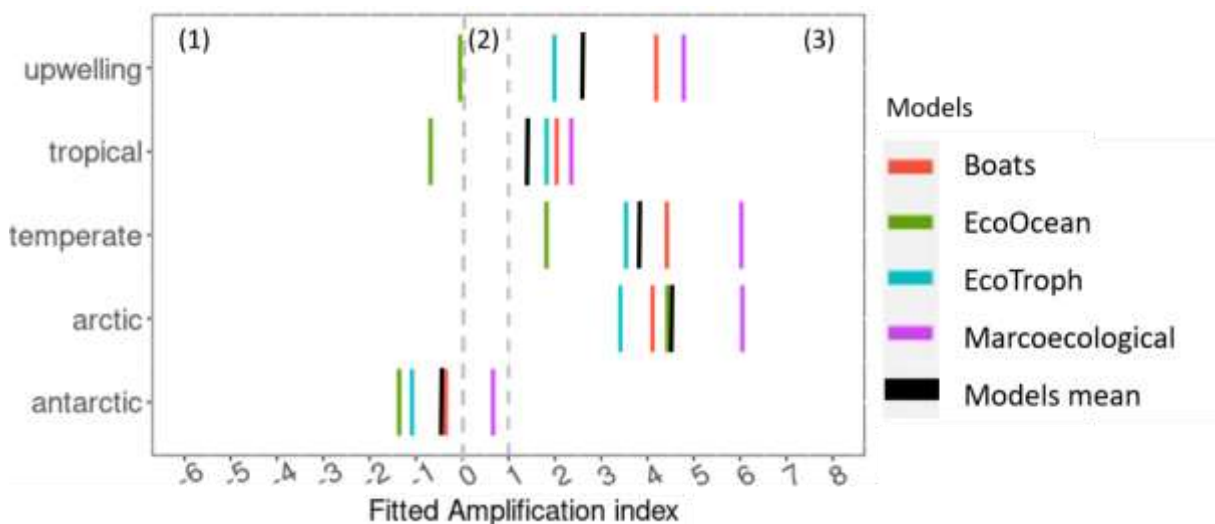


Fig. 7: Spatial differences of Amplification index between five ecosystem types at global scale taking into the inter-MEM variability

GAM model corresponding to equation 1 in 2.6. (1), (2) and (3) corresponding to positive inversion, negative attenuation and negative amplification, respectively. Dashed lines separate trophic amplification types.

Ecological process

To identify how a changing environment affects trophic amplification in each MEM, we developed a second statistic approach and tried to identify how sea temperature drives our Amplification index in MEMs. The statistical model explains 23.8% of deviance. The model allows us to say that MEMs does significantly predict different magnitudes of trophic amplification regarding a specific value of temperature change, and more generally regarding ocean warming (Fig.8). SST increase tends to drive trophic amplification to negative amplification type, while a small increase in increase in SST can lead to negative attenuation or (rarely) to positive inversion processes (Fig.8). It also emerges that Macroecological, Boats and EcoTroph, react similarly to temperature change.

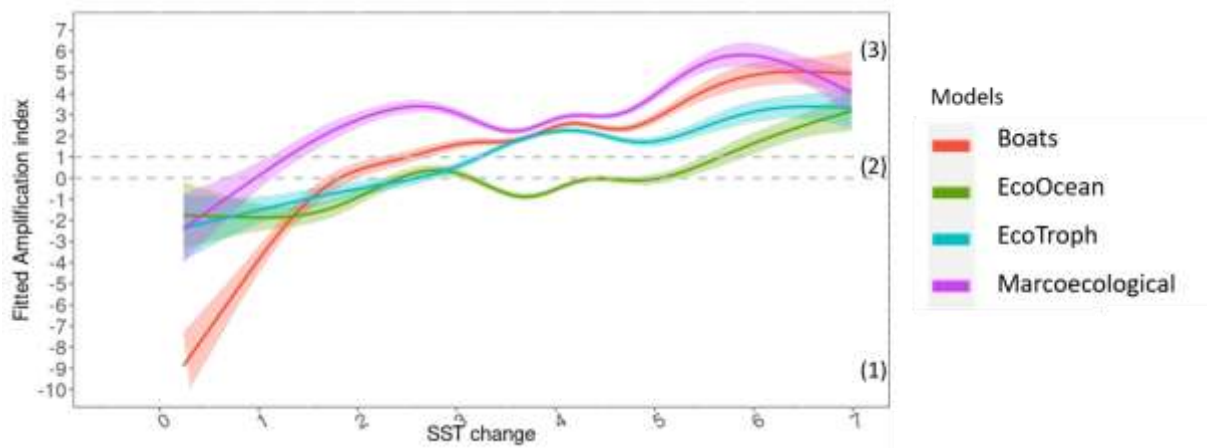


Fig. 8: MEMs Amplification index response to changing environment : SST increase

GAM model corresponding to equation 2 in 2.6

(1), (2) and (3) corresponding to positive inversion, negative attenuation and negative amplification, respectively. Dashed lines separate trophic amplification types.

Variability and uncertainties associated to trophic amplification type:

Analyses of amplification type over 2090s by each model highlight global agreement on prediction, with the exception of polar waters and specific areas such as off the coast of Brazil or in the North Atlantic Ocean (Fig.9a). Regarding the percentage of agreement between models two by two, confirms that Boats, EcoTroph and Macroecological highly agree one with each other, with more than 70% of agreement. Whereas, EcoOcean and DBEM do not specially agree together (30.9%) or compared to the three above (around 30%). Therefore, agreement is observed between MEMs reposing on ecosystem functioning by a flux: Boats, EcoTroph and Macroecological (Fig.9b). Within these models, and despite the diversity of models structures, we obtain at minima 70% agreement, which allow us to have high confidence of our result and notably in the future spatial distribution of trophic amplification types and on their consequences

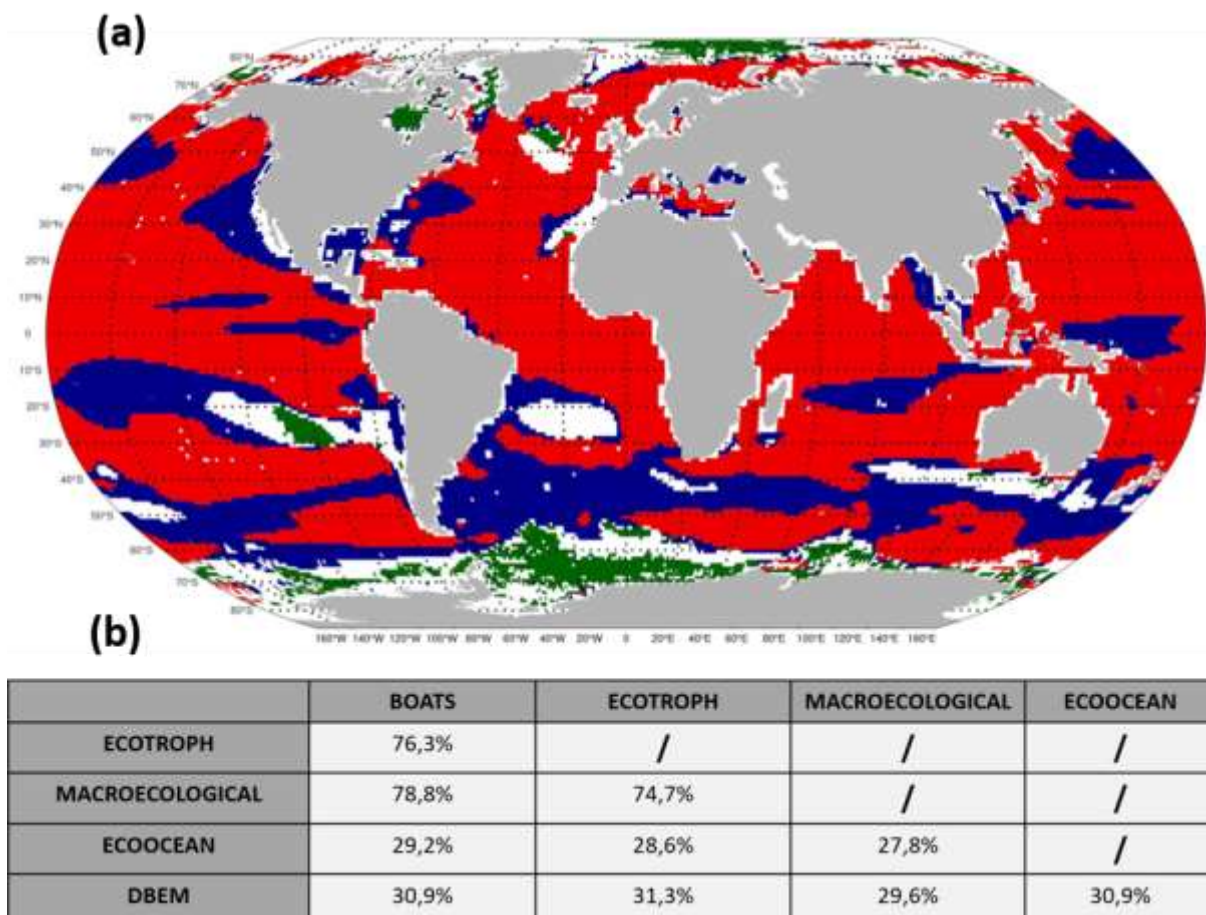


Fig. 9: models intercomparaison over 2090s regarding 1986_2005 reference time

(a) Intercomparison of amplification type projections from five MEMs under the IPSL-RCP8.5 configuration. With red corresponding to 3 or more models agreement for Negative amplification, blue corresponding to 3 or more models agreement for Negative inversion, green to 3 or more models agreement for Positive amplification and white corresponding to less than 3 model agreement. (b) Two-by-two model intercomparaison of amplification type projections under the IPSL-RCP8.5 configuration

4.3 Trophic amplification behavior across food web

By focussing on EcoTroph, we can follow biomass or production along the food web. We firstly break the signal by preys and predators production (Fig.10a) in order to visual which class of food web is more impacted. From 2030s, the differences in production change accentuate between NPP and each size class, showing that climate change and ocean warming are affecting production with a trophic amplification process which affect the various trophic levels all along the food web. With predators appearing to be the part of the food web undergoing the greater effects. Near 2100 and under the IPSL-RCP8.5 combination, predators will lose near 23% of their production against 15% for preys production for a loose of 11% in net primary production. It can be noticed that biomass of predator is projected to decrease even more, reaching a -30% decline at the end of the century.

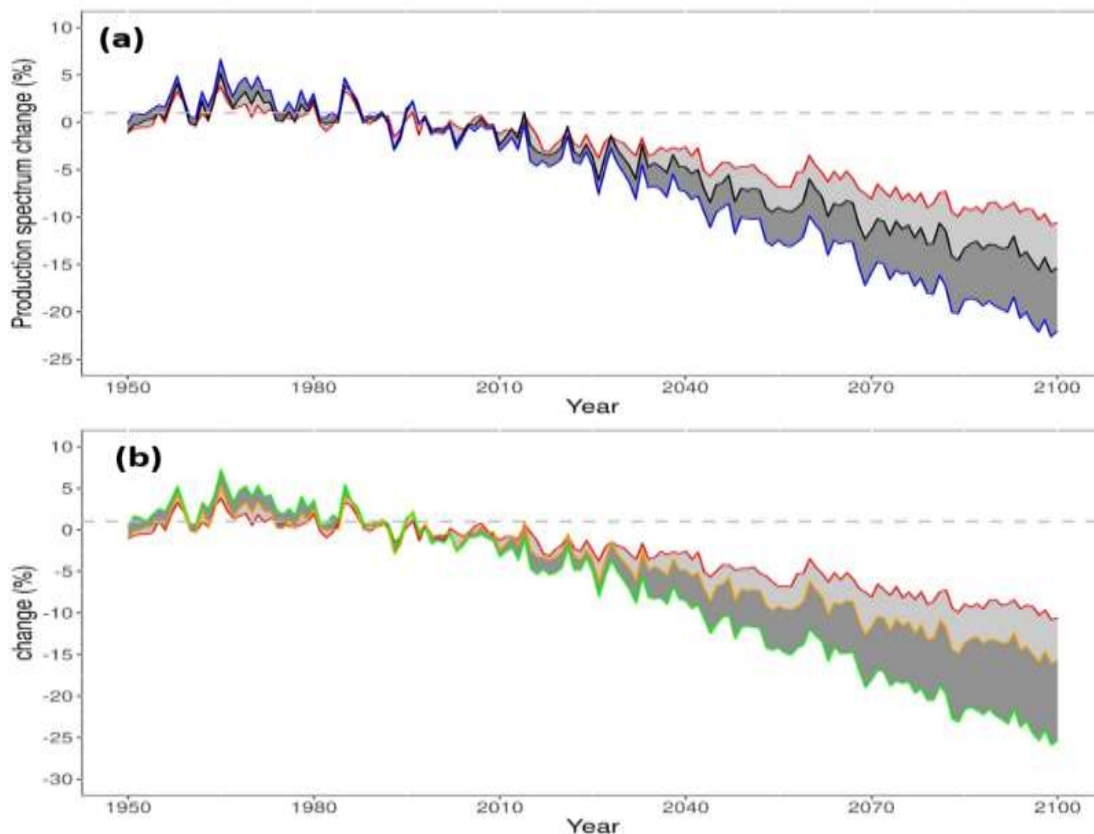


Fig.

10: Climate change signal propagation across food web under IPSL-RCP8.5 modelling

(a) EcoTroph projections of mean annual change in NPP, prey production and predator production relative to 1986–2005, in red, black and blue, respectively. Shade areas materialising the increase of climate signal along food web and over time.

(b) EcoTroph projections of mean annual change in NPP, total consumer production and total consumer biomass relative to 1986–2005, in red, orange and green, respectively. Shade areas materialising the increase of each “sub-amplification” process

In the case of EcoTroph, the amplification of production losses, can be linked to the climate-induced decrease in the trophic efficiency (TE). Indeed the EcoTroph TE parameter depends directly from SST and in an ocean warming context TE decreases. This latter explaining the greater loss of production in the upper classes of the food web

Secondly, we try to identify which of “production amplification” and production to biomass conversion affect more the total consumer biomass (Fig.10b). Production to biomass conversion, associates to kinetic and metabolism, is more affecting total consumer biomass change than the change of production between NPP and total consumers. By 2100 and under IPSL-RCP8.5 combination, NPP production, total consumer production and total consumer biomass changes are projected to decrease by 11%, 16% and 26%, respectively, indicating the major role played by the metabolism in trophic amplification with more than 50% of explanation (highlighted by a shade area larger on Fig.10b).

Breaking down Amplification index allow to identify trophic amplification behaviour along the food web. It appears by the construction of EcoTroph model that trophic amplification is the same between each food web class (Fig.11); notably because in this model, trophic transfer efficiency is assumed to be the same for all trophic class of the food web. Nevertheless, from the first to the last link in the food web, trophic amplification process have a multiplicative effect, confirming that predator are the more affected by climate change, with a index value of 1.45,1.45 and 2.1 for prey production amplification index, predator to prey production amplification index and predator production amplification index, respectively.

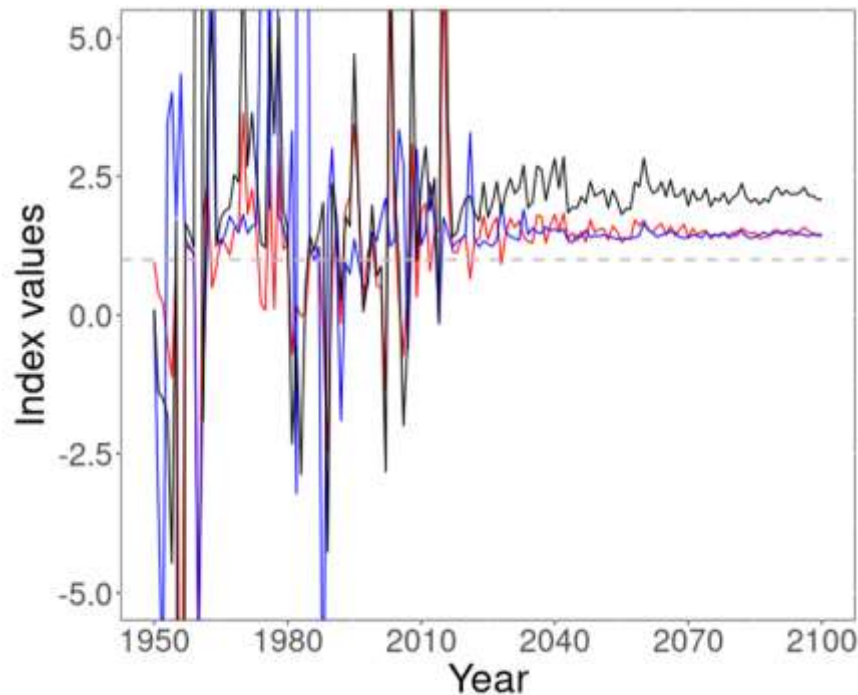


Fig. 11: Breaking down trophic amplification process over time with EcoTroph MEM through the food web under IPSL-RCP8.5 combination

With in red : Prey production amplification index, in blue : Predator to prey production amplification index and in black Predator production amplification index

5. Discussion :

Main limitations of the inter-model comparison

In our study, we highlighted high agreement between three models: two are sized-based and one is based on trophic levels biomass flow. This point out the high link between size and trophic level. Romanuk *et al.*, (2011) found a linear relation between trophic level and size of all fish species with an r^2 of 0.19, as follow, which confirm our results.

$$y = 10^{(\log_{10}(x)-0.442)/0.065)}$$

With y: length in centimetre and x: trophic level.

Nevertheless, a recent study (Keppeler *et al.* 2020) highlights the complexity of the relation: they find no relation between trophic level and body when including all species, but only a positive relation for carnivorous species. This underscores that linear positive relation between trophic level and body size is more complex, which is something to keep in mind for future studies and for interpreting our results.

We used two Earths Systems Models that propose very different outputs due to their own assumptions and structure, with IPSL projecting larger changes in NPP and SST under RCP85 scenario, compared to GFDL. If we assume that this inter-ESM projection reflects the uncertainty of climate change projections, we therefore have difficulties to rule about what will happen in the future of our oceans concerning NPP and the trophic amplification.

The variability in our results can mainly be attributed to uncertainties from NPP and SST projection, incomplete understanding of fundamental processes, internal climate variability, and divergent carbon emission scenarios (Frölicher *et al.* 2016). Regarding NPP projections, Earth System Model is mostly responsible for its associated uncertainties. Indeed, ESM handles more than half of the NPP projections uncertainty through nearly the entire 21st century (Frölicher *et al.* 2016). Concerning SST, it is greenhouse gas emission scenario uncertainty that carries most of projection variability (Frölicher *et al.* 2016).

We only tried to estimate and visualise trophic amplification process and magnitude by using two variables (SST and NPP), but without taking into account other forcing variables as acidification, deoxygenation and extreme oceanic events (e.g., heat waves). These latter, being expected to take part of driving future changes in marine ecosystems and likely exacerbate the projected changes (IPCC 2014).

Finally, in our study, we do not consider fishing effects...As it is the major process that affects oceans biomass, the results expressed in this report could be accentuated in reality.

Major Result

In spite of these delicate points, the conclusions of our analysis allow us to say that under IPSL and “no-mitigation policies” pathway, we could expect at global scale a decrease in biomass much more important than the NPP decrease throughout the 21st century. This result is reflecting a global trophic negative amplification process. Some ecosystems (tropical, temperate, upwelling and arctic) are expected to be more affected by this trophic amplification process.

Associated to time series trend, a spatial variability of trophic amplification appears, revealing the existence of other possible types of amplification processes along the food web (Fig.7). By inter-comparing Marine Ecosystem Model, we attempt at global scale a trophic amplification (Amplification index) of 2.7 (± 0.75 SD) magnitude under IPSL-RCP8.5 combination for 2090 decade over reference period (1986_2005). The stabilisation of this later near 2040 (Fig.4), raise interrogation about trophic amplification functioning and the possible change threshold value of temperature. This threshold temperature role been already discuss (Kirby & Beaugrand 2009).

Finally, by breaking down, with EcoTroph, trophic amplification signal differentiating effect on biomass and production, thought the food web, we identify that higher trophic level is more impacted by this process. We also identify the pathways by which trophic amplification propagates through the food web. Notably, we have been able to differentiate the effect of metabolic change and the effect of what we call "production amplification" on what it is common call trophic amplification. This “production amplification” reflecting the behaviour of trophic transfer efficiency. Both component of trophic amplification have been largely analyse through EcoTroph in response of climate change and warming ocean (du Pontavice *et al.* 2019), showing both negatively affected by SST increases which support our results.

Even if we scarcely talk about it in the development, the RCPs chosen for modelling change a lot the projections. Greenhouse gas scenario emission RCP2.6 projecting far less loose concerning NPP and total consumer biomass (Fig.1); with a 2090s multimodal mean total consumer biomass relative change over reference period (1986_2005) of -6.3% ($\pm 3.1\%$ Standard Deviation) and -26% ($\pm 7.3\%$ SD) under IPSL RCP2.6 and RCP8.5, respectively.

However, our results suggested that the same amplification coefficient will apply in the two scenarios. On average, the 2.6 multiplicative effect is observed as soon as in 2030 in the RCP8.5 (Fig. 4), at a time period where the two RCP scenario are very similar. Of course, at the end of century, the decrease in consumer or predator biomass is projected to be bigger in RCP8.5 than in RCP2.6; with more disastrous consequences on biomass by moving up the food web.

An interpretation of the Trophic amplification process

By this study, we have quite well interrogated and understood the functioning of trophic amplification process, which can be resumed in a scheme (Fig.12). Concretely, in response to climate change and ocean warming, NPP change fluctuates positively or negatively across time and space depending on specific conditions. This effect mechanically translates to the upper trophic levels, leading to the same reduction in production at every levels.

In addition, the effect of temperature, is affecting trophic efficiency (TE) which measures the part of production transferred from one trophic level to the next (higher). The more the ocean temperature rises, the more organisms require energy and thus, less energy is available to convert into matter, or more precisely, into biomass. Therefore TE of all intermediate and high trophic level is negatively impacted by SST increase (du Pontavice *et al.* 2019). This effect is multiplicative by rising all along the food web, thus inducing negative amplification, negative inversion or positive attenuation (depending of the change occurring in NPP).

In some ecosystems (especially in polar regions) changes in plankton communities may lead to an increase in the transfer efficiency at low trophic levels (Stock *et al.* 2017; du Pontavice *et al.* 2019). This process is for instance observed in the Cobalt model (Stock *et al.* 2017), whose outputs are used in our EcoTroph simulations. In such (rare) cases, and providing this effect compensate for the changes in kinetics and in the TE occurring at higher trophic levels, positive amplification or positive inversion and negative attenuation can be observed.

Finally, climate change through temperature change also affects the species composition and the life expectancy of organisms, leading to faster trophic transfer along the food web (kinetic effect). This process also adds to the previous one and explains why the decrease in biomass is larger than the decrease in production. In other words, kinetic is the parameter which allow to convert production into biomass (Gascuel *et al.* 2005), and faster transfers induced by warmer temperatures implies that each unit of biomass stays shorter at each trophic level, thus leading to less biomass.

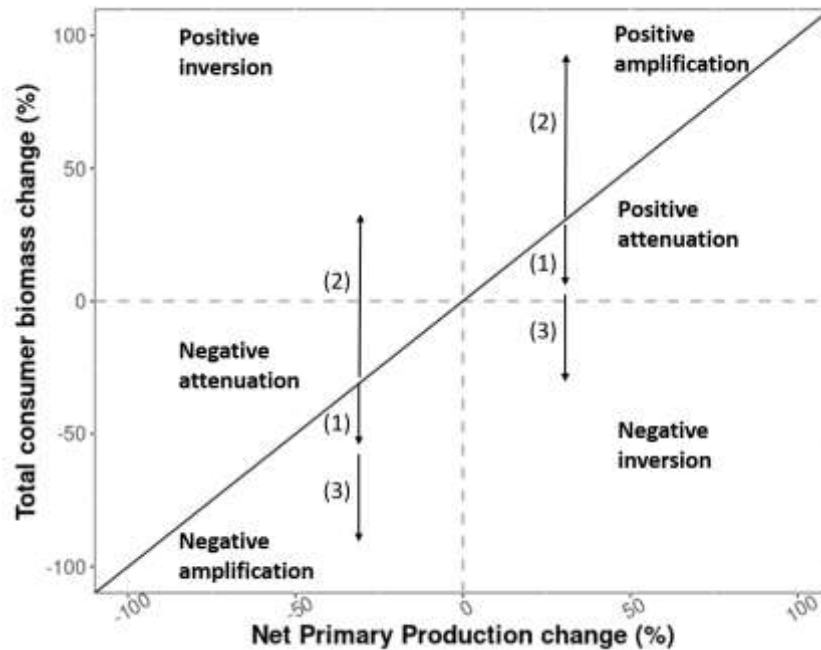


Fig. 12: Hypothesis of trophic amplification functioning

With black solid line representing theoretical situations where changes in total consumer biomass and NPP are the same, in response of ocean warming. (1) The first black arrow is representing the temperature effects on transfer efficiency. In some ecosystems, an increase in the TE of low trophic levels is projected in the Cobalt model considered in EcoTroph, leading to situations referred by arrow (2). and (3) the third black arrow is representing the kinetic (metabolism) affected by the temperature increasing.

Negative attenuation, positive inversion and positive amplification occurs only if the phenomenon materialized by the arrow (2) more or less compensates the phenomena represented by the arrows (1 and 3).

Having a better understanding on how trophic amplification applies along the food web permits us to better detect and understand the reasons for different responses and process integration between MEMs. As shown in Table 1, all models considered in this study differ in whether or not they incorporate trophic interactions or even the assumptions on which they are based. However, some MEMs share certain common points: for example, in Boats, Macroecological and EcoTroph temperatures do not influence not exactly the same parameters, but influence the same key process : metabolism and trophic transfer efficiency (Gascuel & Pauly 2009; Gascuel *et al.* 2011; Jennings & Collingridge 2015; Carozza *et al.* 2016). This explains why they considerably agree on trophic amplification patterns and magnitude.

Concerning DBEM, has similar temporal trend as the three models mentioned above, but it differs somewhat with regards to spatial patterns. Concerning spatial projection differences, we can link these to the fact that DBEM is a niche model and only accounts for species distribution in response to climate change. For the temporal aspect, in DBEM, SST also influences metabolism, this latter characteristic justifying, in part, the similarities on temporal trend. Finally, in EcoOcean trophic amplification is scarcely taken into account, because SST intervenes only on climates model determining species distribution over space (SST affects

the forcing variable of EcoOcean) , but not directly on the trophic transfer between boxes, nor on transfer efficiency or metabolism (Christensen *et al.* 2015).

Potential consequences of the trophic amplification

Some studies have focused on the issue of trophic amplification at low trophic levels (study of the dependence of zooplankton on phytoplacton) (Chust *et al.* 2014; Stock *et al.* 2014; Kwiatkowski *et al.* 2019); Others tackle this process by studying it in a specific food chain in an ecosystem (Kirby & Beaugrand 2009). The current study fits into this research theme by bringing other elements of response than the above studies and is complementary to the studies carried out recently. By using data from Fish-MIP, which until now has been only used to show that there is a difference in biomass change depending on the level in the food web (Lotze *et al.* 2019), I have been able to focus on the process of trophic amplification by qualifying and quantifying it. This approach was developed on a model intercomparison basis.

The novelty of my study is that I have also broken down the trophic amplification signal by trophic classes, allowing me to analyse which part of the food web is the most affected by this phenomenon, and by which pathways. Contrary to the Fish MIP study, which is only based on biomass evolution, (Lotze *et al.* 2019), we show that taking into account production change in response to climate change, provides complementary insight on trophic amplification and on its consequences. du Pontavice *et al.* (in prep) have shown that total consumer production is significantly impacted by climate change, and in our study, we completed this fact, visualising that production, at each stage of food web, is consistently impacted by climate change and so on, translating the trophic amplification process.

Changes in production are directly related to future catch possibility. Generally, we misconcept that catch potential is linked to the biomass present in oceans, whereas in reality it depends on production and more precisely on the exploitable production. Production in response to SST increases is expected to decrease less than biomass, but more in the upper part of the food web. Fisheries at global scale mostly target high value fishes, often corresponding to predator with higher trophic level. Currently it is considered that almost all species with a trophic level above 3.5 are targeted (Branch *et al.* 2010). As a result, trophic amplification associated with climate change is expected to severely affect the world potential catch during the 21st century.

Furthermore, knowing that this trophic amplification deteriorates the trophic structure of marine ecosystems, by affecting strongly higher trophic level classes, concerns about these consequences emerged. In particular, trophic relation degradation can be characterised by trophic cascades due to decrease of predator biomass. Indeed, several studies have shown that the depletion of top predators can have important repercussions on the structure and functioning of marine ecosystems (Heithaus & *et al.* 2008; Baum & Worm 2009; Ferretti *et al.* 2010; Estes *et al.* 2016). For example, depletion in apex predator, can leads to outbreak of mesopredators, driving to the increase of predation on smaller prey associated with a decrease of species number (Ritchie & Johnson 2009). More generally, this depletion can also modified the stability of marine ecosystems (Rooney *et al.* 2006; Britten *et al.* 2014). Thus, global changes in marine ecosystems leads to an alteration of biodiversity and abundance of

marine life. Ecosystem structure change are expected to induce a reorganization of marine biodiversity whose magnitude would depend on the intensity of the changes in ocean conditions (Tittensor *et al.* 2010; Beaugrand *et al.* 2015; Jones & Cheung 2015).

The crucial role played by the greenhouse gas emission scenario highlights the importance of working to reduce our greenhouse gas emissions, as it will play an essential role in ocean future and indirectly in our becoming as we depend a lot of oceans capacities and resources (Selig *et al.* 2019).

Finally, in order to improve knowledge of this process, it would be interesting to compare the results from the EcoTroph analysis with Fish-MIP accounting models in order to have more certitude on the behaviour of this phenomenon through the food web. It would also be desirable to be able to quantify trophic amplification's ecological consequences and impacts on fisheries using, for example, simulation and fishing scenarios models.

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7. Appendix:

Supplementary Information for

Trophic amplification, an inter-model comparison study

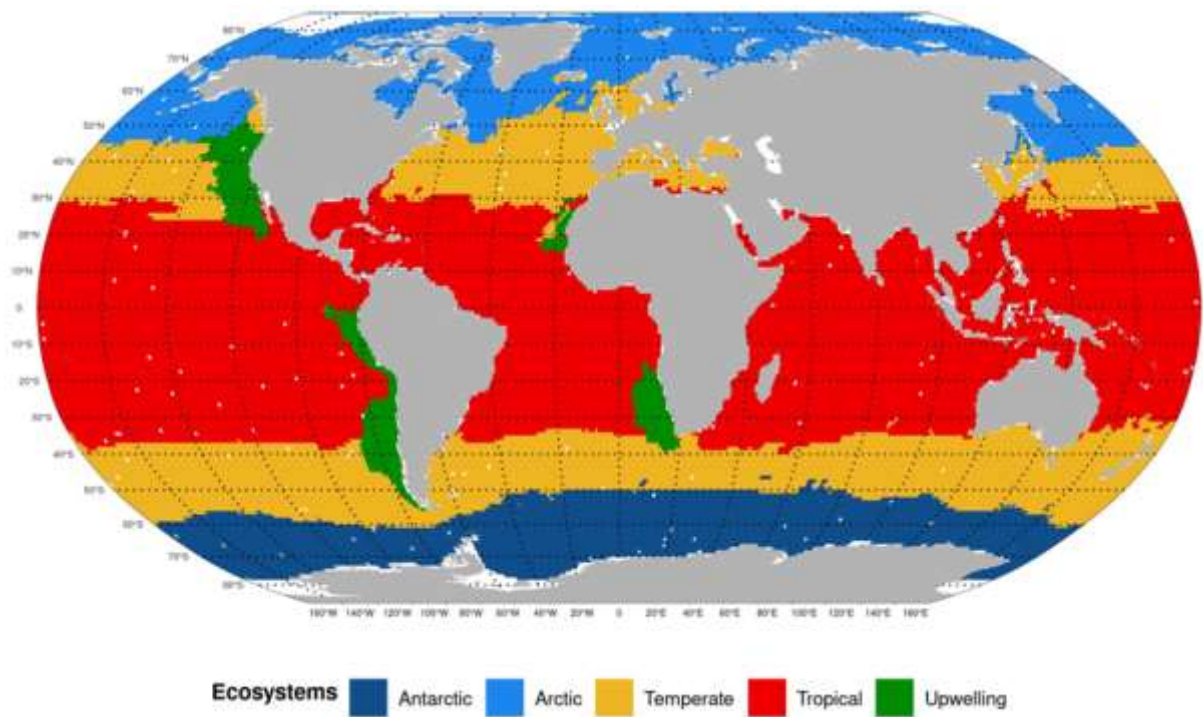


Fig. S1: Ecosystem definition : from (du Pontavice et al in prep).

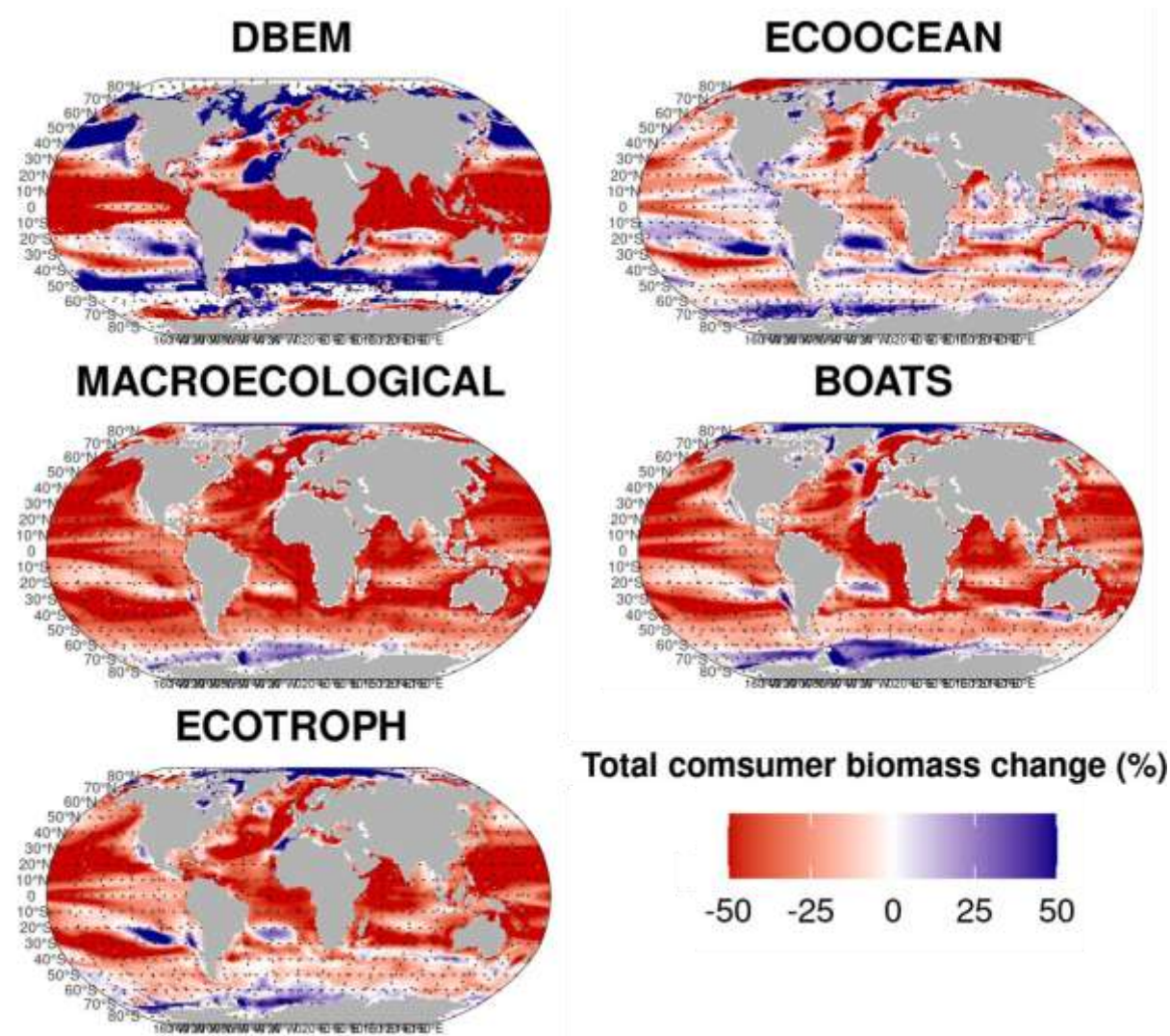


Fig.S2: Spatial patterns of projected total consumer biomass relative changes in percent Shown are global ensemble projections at a 1×1 degree resolution. Individual model projections of mean 2090s total consumer biomass relative change over reference period (1986_2005) under IPSL-RCP8.5 modelling.

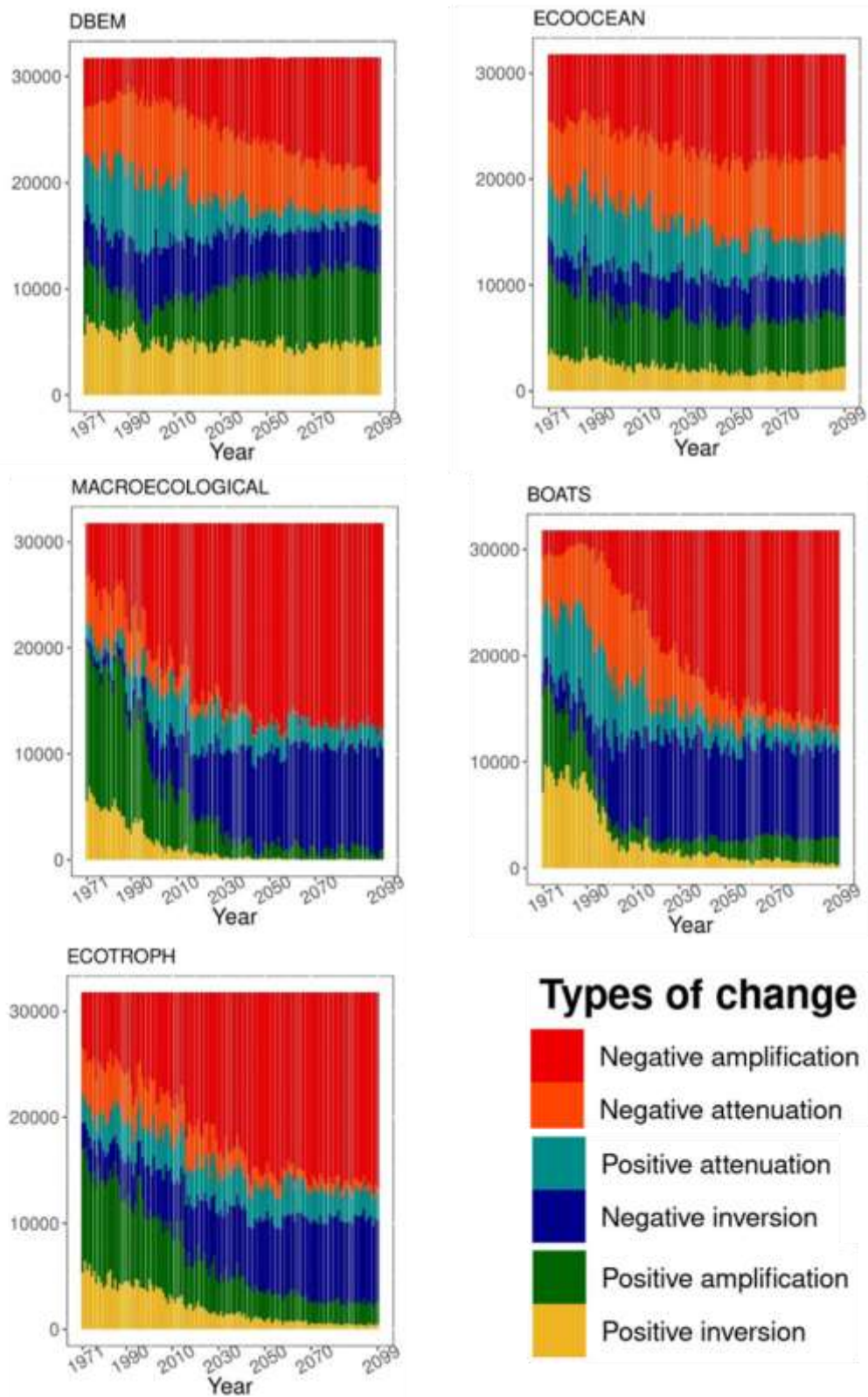


Fig.S3: Evolution of trophic amplification types
 Individual model projections of amplification types over time under IPSL-RCP8.5 modelling.

8. Appendix Bibliography:

du Pontavice et al, H. (in prep). Climate-induced decrease in biomass flow in marine food webs may severely affect predators.

 	Diplôme : Ingénieur agronome Spécialité : Halieutique Spécialisation / option : Sciences halieutiques et aquacoles, préparée à Agrocampus Ouest (REA) Enseignant référent : Le Pape Olivier
Auteur(s) : GUIBOURD de LUZINAIS Vianney Date de naissance* : 13/01/1997	Organisme d'accueil : UMR ESE Agrocampus Ouest Adresse : 65 rue de Saint Briec Rennes 35000
Nb pages : 30 Annexe(s) : 3	Maîtres de stage : Gascuel Didier et Du Pontavice Hubert (agrocampus-ouest) Co-maîtres de stage : REYGONDEAU Gabriel et BORNAREL Virginie (Université de Colombie Britannique) Collaboration : CHEUNG William (Université de Colombie Britannique)
Année de soutenance : 2020	
Titre français : L'amplification trophique, une étude basée sur une intercomparaison de modèles Titre anglais : Trophic amplification, an inter-model comparison study	
Résumé (1600 caractères maximum) : Le changement climatique est actuellement bien compris et évalué, mais ses conséquences sur l'océan mondial et sur les écosystèmes marins ne sont pas complètement établies. Dans cette étude, nous avons analysé comment le changement climatique pourrait affecter l'ensemble du réseau alimentaire par le biais du processus d'amplification trophique, qui reflète la propagation du changement de la NPP à travers le réseau trophique. Les effets des changements de la NPP sur la biomasse des producteurs et des prédateurs sont analysés en utilisant les sorties de cinq modèles écosystémiques marins, forcés avec deux modèles climatiques du système terrestre selon deux scénarios d'émission de gaz à effet de serre. A l'échelle globale du réseau alimentaire, basé sur une approche spatiale et temporelle, nous avons constaté que presque tous les modèles (sauf EcoOcean) rendent clairement compte du processus d'amplification trophique avec une amplification trophique négative globale moyenne de 2,7 ($\pm 0,75$ SD) dans les années 2090 sous RCP8.5. Néanmoins, la présence d'une variabilité spatiale non négligeable suggère la présence de différents types d'amplification et conséquences induites par différents changements environnementaux. La décomposition de l'amplification trophique à travers le réseau trophique a mis en évidence que les niveaux trophiques supérieurs seront plus touchés par ce processus. En ce qui concerne les deux scénarios d'émission de gaz à effet de serre pris en compte, nous avons noté des impacts significativement différents, ce qui souligne l'importance de réduire rapidement nos émissions de gaz à effet de serre.	
Abstract (1600 characters maximum) : Climate change is currently well assessed and understood, but its consequences on the world ocean and marine ecosystems are not fully established. In this study, we analysed how climate change may affect the entire food web through the trophic amplification process, which reflects the propagation of NPP changes through the food web. The effects of MPN changes on the biomass of producers and predators are analysed using the outputs of five marine ecosystem models, forced with two earth system climate models under two greenhouse gas emission scenarios. At the global food web scale, based on a spatial and temporal approach, we found that almost all models (except EcoOcean) clearly account trophic amplification process with a mean global negative trophic amplification of 2.7 (± 0.75 SD) in the 2090 decade under RCP8.5. Nevertheless, considerable spatial variability suggests different amplification types and consequences induced by different environmental changes. Breaking down trophic amplification across the food web indicates that higher trophic levels will be more affected by this process. For the two greenhouse gas emission scenarios considered, we have noted significantly different impacts, which underlines the importance of rapidly reducing our greenhouse gas emissions.	
Mots-clés : amplification trophique, impacts du changement climatique, réseaux trophiques marins, intercomparaison de modèles Key Words: trophic amplification, climate change impacts, marine food webs, model intercomparison	

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