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Aurore Maureaud

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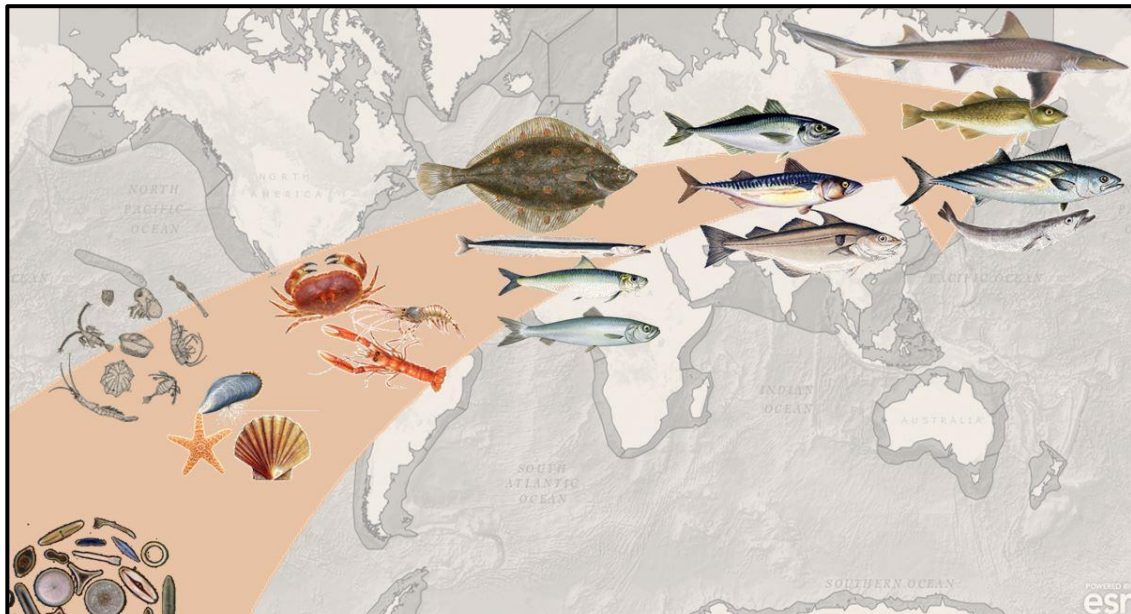
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Fishing and climate change impacts on the trophic functioning of marine ecosystems: a worldwide meta-analysis of the past changes in transfer efficiency and kinetics

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Résumé en français du travail de recherche

Le besoin de mettre en place une approche écosystémique des pêches s'accompagne tout d'abord d'une meilleure compréhension des systèmes marins. Le fonctionnement des réseaux trophiques à une échelle globale est très largement suspecté d'être impacté par la pêche et d'autres impacts anthropiques, tels que le changement climatique. Le développement de nombreux modèles écosystémiques et d'indices d'impacts humains sur les écosystèmes a initié des questionnements théoriques sur des paramètres de fonctionnement trophique des écosystèmes. C'est le cas par exemple de deux paramètres caractérisant les flux de biomasse : l'efficacité de transfert traduisant la productivité du réseau trophique et la vitesse de transfert, ou cinétique, inversement proportionnelle au temps nécessaire à la biomasse pour monter dans le réseau trophique. De par leur nature théorique, il est difficile de les estimer alors que leur variabilité temporelle, géographique et trophique est discutée dans la littérature scientifique. Ces deux paramètres sont donc susceptibles de changer notre vision du fonctionnement de l'écosystème mais ils sont très souvent considérés constants dans la pratique. L'objet de cette étude est d'étudier la variabilité de ces deux paramètres à une échelle mondiale depuis 1950.

Le deuxième objectif de ce travail de recherche est de rechercher les potentiels effets de stress tels que la pêche et le changement climatique sur ces paramètres. Selon la théorie écologique d'Odum, l'effet d'un stress sur l'écosystème s'opère à différentes échelles. Ici, on s'intéresse plus particulièrement aux assemblages spécifiques et aux impacts sur les communautés marines, modifiant ainsi l'ensemble de la chaîne trophique. Une perturbation conduirait théoriquement à une perte de productivité des écosystèmes, alors que les transferts énergétiques s'en trouveraient plus rapides. Cette hypothèse de recherche est testée sur l'ensemble de Large Marine Ecosystem pour lesquels on possède les captures de pêche reconstruites par le projet Sea Around Us de 1950 à 2010.

A partir de formules empiriques et des traits d'histoire de vie des espèces marines, deux indices de fonctionnement trophiques ont été créés. Ces indices sont construits à partir des spectres trophiques, selon une approche similaire à celle développée dans le modèle EcoTroph. Dans cette étude, le spectre construit des espèces est pondéré par les captures : le spectre construit à partir des données de capture est donc considéré comme représentatif du spectre construit à partir de données de biomasse. Les données par espèces se retrouvent groupées par classe trophique. Plusieurs tests ont été réalisés afin d'explorer le meilleur moyen d'étudier la variabilité de l'efficacité et de la vitesse de transfert. Chaque indice a été imaginé à partir de sa signification écologique pour le fonctionnement du réseau trophique :

- L'indice d'efficacité cumulée (*Efficiency Cumulated Index*, ECI) résulte d'un produit des proportions de production transmise d'une classe trophique à une autre, cumulant ainsi la proportion de production sur l'ensemble du réseau trophique
- L'indice de temps cumulé (*Time Cumulated Index*, TCI) : le temps est considéré inverse à la vitesse de transfert. Le temps nécessaire pour franchir le réseau trophique résulte de la somme du temps de transfert de l'ensemble des classes trophiques.

Les premiers résultats de l'étude montrent une variabilité assez importante de ces deux indices au cours du temps pour l'ensemble des *Large Marine Ecosystem*. Au sein de ces unités écosystémiques très différentes, les indices n'évoluent pas de la même manière ni au même moment. Cependant, il est possible d'identifier des types d'évolution par des méthodes statistiques et de modélisation, indiquant et regroupant ainsi les écosystèmes par évolution de leurs indices. 22 LME présentent une efficacité en diminution depuis 1950, donc une productivité en nette diminution. 53 LME démontrent une diminution du temps de transfert dans le réseau trophique, donc des transferts plus rapides. La tendance mondiale est donc une évolution vers des écosystèmes plus productifs et aux transferts plus rapides.

Ces tendances vont donc à l'inverse de l'hypothèse de recherche de départ. Il était donc essentiel d'explorer les raisons de ces variations en regardant les assemblages spécifiques depuis 1950 par classes trophiques, expliquant les variations progressives des indices. Ce travail a été mené pour 6 écosystèmes très différents de par leur nature, régime d'exploitation et assemblages spécifiques : le courant de Californie, le courant du Humboldt, le Golfe du Mexique, le courant des Canaries, la mer du Nord et la mer Est du Japon. A chaque écosystème correspond une histoire qui lui est propre. Par exemple, les écosystèmes upwellings sont énormément influencés par les conditions climatiques et les alternances d'abondance d'espèces de petits pélagiques et sont des écosystèmes moins impactés par le changement climatique. La mer du Nord, très largement surexploitée déjà en 1950, présente des changements d'espèces cumulés sur plusieurs classes trophiques induisant une diminution d'efficacité de 10 à 20%. De plus, c'est un écosystème plus touché par le réchauffement de l'océan, ce qui peut être lié au fait que c'est une mer peu ouverte sur la pleine mer.

La suite du travail consiste à l'identification des facteurs qui induisent ces changements. Deux phénomènes sont donc testés à travers plusieurs paramètres et indices : le changement climatique (température de surface, production primaire, disponibilité en oxygène) et la pêche (niveau trophique moyen 'MTL', production primaire requise pour soutenir les pêcheries 'PPR', indice de perte de production secondaire 'Lindex', Fishing in Balance 'FIB' et le pourcentage de stocks surexploités et collapsés à partir de la méthode de Stock Status Plot). Ces paramètres sont donc tout d'abord testés dans l'Analyse en Composantes Principales et la Classification Ascendante Hiérarchique des deux indices pour catégoriser les classes et les types de tendances. De plus, lors de la DFA (Dynamic Factor Analysis), ces paramètres sont testés de par leur évolution de tendance mondiale sur les écosystèmes. En effet, ces deux méthodes ne permettent pas le même test des facteurs explicatifs potentiels et ont donc leur intérêt à être combinées dans cette étude.

Les méthodes statistiques mises en place permettent de mettre en évidence une influence importante de la pêche sur certains écosystèmes, montrant également une diminution de l'efficacité de transfert au cours du temps. De plus, ces écosystèmes sont également caractérisés par une proportion de poissons constante ou en augmentation au cours du temps. L'augmentation de céphalopodes et de crevettes observée induirait donc des écosystèmes dont l'efficacité augmente et le temps de transfert diminue. Comme cette tendance concerne une grande partie des écosystèmes, il est essentiel d'explorer cette variable. D'autre part, les écosystèmes les plus surexploités ne montrent pas systématiquement une baisse de productivité dans les hauts niveaux trophiques. Quant à l'impact du réchauffement climatique, il s'agit d'un changement beaucoup plus fin. Il n'est pas directement démontré une tendance claire sur l'efficacité et le temps de transfert par le

changement climatique. Cependant, les variations observées sont non négligeables et affectent tous les écosystèmes, réagissant de manière mondiale à une tendance de réchauffement. La pêche semble cependant être la force majeure affectant les écosystèmes depuis 1950.

Les résultats obtenus mettent en évidence deux résultats importants. Tout d'abord, les écosystèmes présentant une diminution de l'indice d'efficacité ECI montrent également une absence de biais de stratégies de pêche. En effet, ces écosystèmes n'ont pas subi de développement de pêcheries de crustacés et céphalopodes pouvant fortement influencer les résultats des indices. De plus, les écosystèmes pour lesquels l'indice de temps TCI présente la plus forte diminution suggère une sélection des espèces à durée de vie courte depuis 1950. En effet, ces écosystèmes peuvent être identifiés comme ayant subi des effets importants de la pêche et montrés comme étant des LMEs où des effets de 'Fishing Down Marine Food Webs' et 'Fishing Through Marine Food Webs' ont déjà été mis en évidence. Ces écosystèmes présentent bien une diminution du niveau trophique moyen mais qui n'est pas dû à un développement de la pêche. Les indices explicatifs utilisés suggèrent une diminution de l'abondance des top-prédateurs par la pêche, menant à la sélection des espèces à durée de vie courte, comme dans les écosystèmes Nord-Américains.

Le changement climatique peut aussi générer des effets sur les écosystèmes indirects en agissant sur la pêche, les habitats et les abondances. De plus, la variabilité sur les paramètres de croissance, résultant de la variabilité individuelle, ou les effets démographiques internes à chacune des populations, ne sont pas inclus ici.

De manière globale, les espèces identifiées comme redondantes dans les changements sont les céphalopodes, qui de par une faible augmentation de proportion dans les captures peuvent influencer de manière non négligeable les indices, et donc le fonctionnement trophique. En effet, ces espèces à vie courte présentent des temps de transfert très rapides et une forte efficacité de transfert. Il est d'autant plus intéressant de noter que leur récente émergence dans plusieurs écosystèmes est suspectée d'être générée par la surpêche des compétiteurs pour les mêmes sources alimentaires et le changement climatique. Les petits pélagiques sont eux aussi de grande importance dans l'évolution des indices et influencent de manière importante le fonctionnement trophique : anchois du Pérou, sardine japonaise et californienne... De plus, la surexploitation de la morue et des thonidés se retrouve dans plusieurs écosystèmes. Le développement de la pêche aux crustacés est aussi mis en cause dans la variabilité temporelle des indices.

De par une démonstration d'importantes variations temporelles, écosystémiques et trophiques de l'efficacité et de la vitesse de transfert, cette étude constitue une base importante pour de futurs travaux de recherche. C'est le cas notamment de la modélisation trophique et du modèle EcoTroph dans lequel il apparaît à présent nécessaire d'inclure la variabilité de l'efficacité et de la vitesse de transfert pour réaliser des scénarios de changement climatique de production des écosystèmes. De même, la mise en place d'indices de pression de pêche, et d'évolution de biodiversité nécessite parfois le calcul de la variabilité de ces paramètres. L'utilisation de tels indices se développe et se répand dans la gestion opérationnelle d'où la nécessité de développer des indices écosystémiques plus cohérents.

List of abbreviations

AHC: Ascending Hierarchical Classification

DFA: Dynamic Factor Analysis

ECI: Efficiency Cumulated Index

ENSO: El Niño Southern Oscillation

FIB: Fishing in Balance

GFDL: Geophysic Fluid Dynamic Laboratory

IPSL: Institut Pierre Simon Laplace

LME(s): Large Marine Ecosystem(s)

MPI: Max Plank Institute

MTL: Mean Trophic Level

TCI: Time Cumulated Index

TE: Transfer Efficiency

TL: Trophic Level

PCA: Principle Component Analysis

PP: Primary Production

PPR: Primary Production Required for fisheries index

PPR/PP: Primary Production Required for fisheries divided by the Primary Production (%)

SAU: Sea Around Us

SSP: Stock Status Plot (%)

SST: Sea Surface Temperature

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1. Introduction and context of the study

Since there is a growing awareness on human-induced impacts on ecosystems, the idea that we need to develop sustainable management for marine systems expanded. The necessity to implement an ecosystem-based management for marine activities is now recognized worldwide, by the scientific community and international agencies (Garcia and Cochrane, 2005). Its importance cannot be neglected and has been discussed during worldwide summits like in Reykjavik (2008), and through the MSFD (Marine Strategies Framework Directive). The 1995 FAO Code of Conduct for Responsible Fisheries already advocated for an Ecosystem Approach of Fisheries (EAF) (Garcia and Cochrane, 2005) represented a key step in management considerations. EAF is especially enhancing the development of marine ecosystem indices for measuring human-induced impacts on ecosystems (Cury et al., 2005; Pauly and Watson, 2005), ecosystem resilience, or biodiversity loss in the context of conservation objectives (Collen and Nicholson, 2014).

The ecosystem approach is still under development and needs a better knowledge of ecosystems functioning (Rombouts et al., 2013) and human-induced impacts on ecosystems (Vitousek, 1997). Assessing our impacts on marine systems is a key step to anticipate and define management tools that allow ecological integrity of ecosystems, economics viability and social fairness. Numerous pressures are known such as fisheries activities on targeted or non-targeted species (Myers and Worm, 2005), destruction of essential habitats, pollution, intense activities on the coastal areas, invasive species and climate change (Halpern et al., 2008; Sherman, 2015).

1.1 Marine ecosystems as ecological units

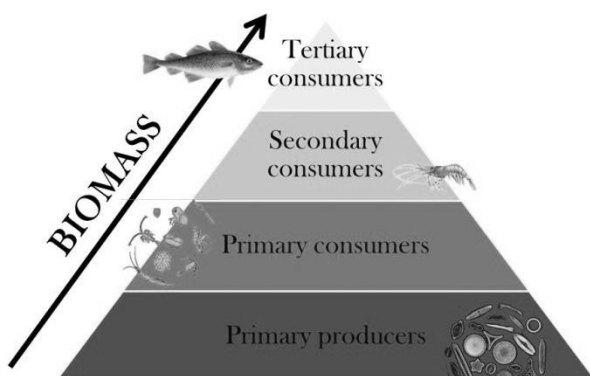


Figure 1: Pyramid of marine food webs with the decreasing biomass flow from low trophic levels to high trophic levels – adapted from (Lindeman, 1942)

Following Eugene P. Odum definition, an ecosystem can be defined as “a unit of biological organization made up of all of the organisms in a given area [...] interacting with the physical environment so that a flow of energy lead to characteristic trophic structure and material cycles within the system” (Odum, 1969).

In the current study, we will focus on the flow of biomass, decreasing with the rising trophic level in the food web (Figure 1). The progressive decrease results from all the loss by metabolism and mortalities (Gascuel et al., 2008). The ecosystem is naturally changing, evolving and demonstrating community successions that are responsible for general ecosystem trends and functioning (Odum, 1969). The biomass flow characteristics emerge from the combination of each species characteristics. Then, through energy flows and all the links between species, it is possible to examine the ecosystem functioning and structure.

The trophic level (TL) – initiated by (Lindeman, 1942) – is a non-unit value that determines the place of a species within the food web from its diet (Christensen and Pauly, 1992; Pauly

and Watson, 2005). It expresses the trophic complexity and structure of species assemblages and their trophic relationships in the ecosystems (Gascuel et al., 2008).

Therefore, a coherent consideration of marine systems as delimited ecological units is crucial to study them. One approach that has been developed is the Large Marine Ecosystems concept (Sherman, 1991). It has been largely investigated in science for meta-analysis on fisheries impacts and production potential (Britten et al., 2016; Brotz et al., 2012; Swartz et al., 2010), climate change impacts (Belkin, 2009; Blanchard et al., 2012; Cheung et al., 2013) and ecosystem functioning (Mcowen et al., 2015). This geographical division is already used for ecosystem-based management projects (Sherman, 2015).

1.2 Stress and trends expected on ecosystems

Nowadays, there is strong evidence that high level stress caused by human activities has an impact on ecosystems. More particularly, it is the case for climate change and intense fishing activities. The development of fisheries since the 50s from the North Atlantic and Pacific Ocean to the Southern Hemisphere led to a large worldwide expansion of fishing pressure and catches (Swartz et al., 2010; Worm et al., 2009). Fisheries intensively developed, inducing a decline in predators' biomass (Myers and Worm, 2003; Tremblay-Boyer et al., 2011), overexploitation and fish stocks collapse (Worm et al., 2009), and degradation of marine habitat (Kaiser et al., 2002; Vitousek, 1997). For several decades now, global and worldwide fisheries landings have been declining (Pauly and Zeller, 2015). Indeed, by the intensification and the diversification of fishing activities, the worldwide fisheries catch reached a maximum and fell off since the 90s (Pauly and Zeller, 2015). The highly dependent communities from fisheries are now threatened (Golden et al., 2016) and demonstrate the need for a better management. Nowadays, a large number of marine ecosystems can be identified as modified and driven by fishing activities, where fisheries might be the most important driving force of the ecosystem production (Mcowen et al., 2015). After threatening species dynamics, populations and small areas, fisheries are now recognized as a large-scale food web source of change (Daskalov et al., 2007; Palomares and Pauly, 1998).

Furthermore, climate variability and environment are also structuring the ecosystem functioning (Mcowen et al., 2015). Since a few decades, marine species have to face a change of a new nature. Climate change is expected to modify all the ecosystems structure and functionalities (Hoegh-Guldberg and Bruno, 2010) by a general warming (Belkin, 2009). It is responsible for changes in marine species' size and growth (Cheung et al., 2012) and in populations habitat by tropicalization (Cheung et al., 2013). Through several models, significant species migrations and invasions have been proved to already take place in the oceans (Perry et al., 2005; Pinsky et al., 2013). They are expected to amplify in the near future (Cheung et al., 2009) and to modify the fisheries catch potential at a worldwide scale (Blanchard et al., 2012; Cheung et al., 2016). Climate change scenarios help to explore future impacts of climate change on marine ecosystems production (Barange et al., 2014; Cheung et al., 2010).

It has already been highlighted that global warming is modifying fisheries catch at a large scale, in relation with tropical species migrations (Cheung et al., 2013). Climate change and fishing activities are both in synergy and modify ecosystem (Kirby et al., 2009). Combined together, these two stresses are questioned in this study as they might be responsible for

changes in ecosystem structure and functioning. For that purpose, understanding theory on the ecosystem natural development (Odum, 1969) and response to stresses (Odum, 1985) is essential. As such, anthropogenic disturbances may cause temporary or permanent changes in communities and affect the ecosystem.

“When stress is detectable at the ecosystem level, there is real cause for alarm, for it may signal a breakdown in homeostasis” (Odum, 1985)

As the level of complexity of the ecosystem is increasing during maturation, the system would accumulate more energy through an increasing efficiency (Saint-Béat et al., 2015) and slower biomass flow transfers (Gascuel et al., 2008). Stress is suspected for altering the productivity and stability of marine ecosystems and may induce a return to a less mature system. **Stress duration and intensity are expected to induce less stable and less productive ecosystems through faster biomass transfers and reduced transfer efficiencies.** This will constitute the research hypothesis of our work and will be tested on Large Marine Ecosystems from 1950 to 2010. In fact, such stresses are in theory expected to modify the ecosystem at a global scale through several mechanisms. A stress modifies the metabolism at an individual scale and can enhance a higher respiration rate in order to maintain survival of the marine species (Table 1). Then, in the metabolic balance, the conversion rate of food into growth may decline. At the community level, stresses are causing natural selection of short-living species with fast but potentially less efficient energy transfers. The reduced abundance of top-predators is caused by lower energy availability in the top of the food web and may induce a reduced overall productivity (Odum, 1985).

Table 1 : Trends expected on individuals/populations/communities generated by stress (adapted from Odum, 1985)

Impact of a stress on individuals	Impact of stress on populations	Impact of stress on communities
<ul style="list-style-type: none"> → Allocation of energy to survival and not to growth → Metabolism modified: less production, more respiration loss → Lifespan reduced → Size of organisms decreased 	<ul style="list-style-type: none"> → Size and age-structures modified → Relationship stock-recruitment modified → Change in spatial distribution → Higher mean productivity 	<ul style="list-style-type: none"> → Change in species assemblages → Shorter trophic chain → Selection of short-living species → Decline of top-predators abundance → Species diversity decreased

In this approach, we focus on the **community level** that expresses major changes in the ecosystem by succession of species through time series. Evidence for variations within the individual metabolism and growth and within populations have been highlighted in the scientific literature (Britten et al., 2016; Sumaila et al., 2011), but will not be considered here. The focus on the community level is useful to look for trophic interactions and ecosystem functioning variability in terms of energy flows (Rombouts et al., 2013). The present research work focuses on how changes in species assemblages induced by fishing or climate change stresses modify the global functioning of marine ecosystems worldwide.

1.3 Theoretical parameters in ecology of the trophic ecosystem functioning

In order to examine the impact of intense stress, two parameters are being investigated. They both characterize the biomass flow within food webs from phytoplankton to top-predators. The first parameter, the **trophic transfer efficiency** (TE), is related to the ecosystem productivity. It represents the rate of biomass that is transferred in the food web

from one trophic level to the next. So, it results from the opposite of all the biomass loss that can occur during metabolism and the species life cycle (respiration, excretion, fishing, natural mortality other than predation). The second parameter is **the speed of the biomass flow**, also called kinetics, inversely proportional to the time necessary for a unit of biomass to cross the food web from one trophic level to the next.

- *The trophic transfer efficiency can be considered as an “indicator of the system status and condition” (Libralato et al., 2004)*

The concept of trophic transfer efficiency is largely used in ecosystem modelling, and discussed in the scientific literature. The trophic transfer efficiency is often fixed for the whole ecosystem: “Since (Lindeman, 1942), it has often been assumed that trophic transfer efficiencies in ecosystems vary around 10%” (Christensen et al., 1993). Several definitions of the transfer efficiency exist such as per trophic level “efficiency at which energy was passed from one trophic level to the next” (Lindeman, 1942), “proportion of prey production that is converted to predator production” (Jennings et al., 2002), or for the entire food web “transfer of energy from phytoplankton to progressively larger animals” (Barnes et al., 2010). Assumptions are made: “Transfer efficiency from mesozooplankton to fishes is also probably higher in less productive and clear oceanic waters than in more productive and turbid shelf and coastal waters” (Irigoien et al., 2014).

In theoretical ecology, the TE is expected to vary with the period of time (Libralato et al., 2004) and the type of ecosystem considered (Pauly and Christensen, 1995). Depending on which species or which part of the food web, the transfer efficiency might be variable: some species are more efficient than others (Straile, 1997). The food web efficiency could be a decreasing function of the trophic level (Christensen et al., 1993) or the species size (Jennings et al., 2002). However, even if we know a lot about this parameter in theory, in practice it is usually considered as a constant such as in ecosystem models (Tremblay-Boyer et al., 2011) or in ecosystem indicators calculation (Chassot et al., 2010; Christensen, 2000; Pauly and Christensen, 1995). The parameter variability is not enough explored. Here we will reconsider the models’ assumptions in order to see if the TE actually varies over the time-series and between geographical locations. The variability of the TE across trophic levels is also very few explored and calculated (Libralato et al., 2008) and will be investigated here. As the TE is increasing with the ecosystem development, **the impact of stress would tend to abate the overall efficiency of the food web** (Odum, 1985). The loss of complexity and return to a less mature system would disrupt the productivity.

- *“Flow kinetics is a key characteristic, partly determining the ecosystem’s response to human disturbances such as fishing pressure” (Gascuel et al., 2008)*

The kinetics traduces the speed of the trophic flow from one trophic level to the next, according to predation. This parameter, as a characteristic of the general biomass decreasing flow within the food web, is just as important and informative of the ecosystem functioning. “Quantifying flow kinetics appears as a key step in our understanding of ecosystems dynamics” (Gascuel et al., 2008). The speed of flows is the reverse of the time required to go up the food web (Figure 2). It is related to the life expectancy of organisms in its trophic class (Gascuel et al., 2011).

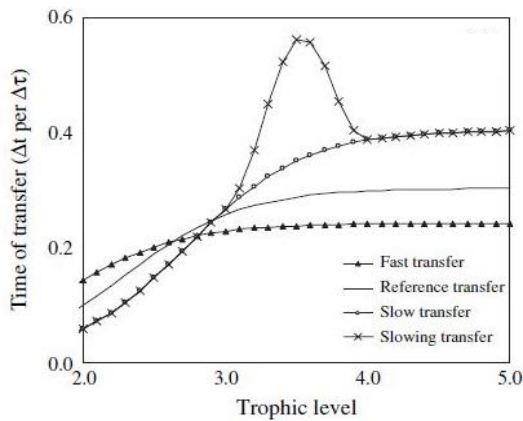


Figure 2 : Time of transfer in the food web per trophic level for various theoretical kinetics/speeds of biomass flow (from Gascuel et al., 2005)

Following a steady-state hypothesis, the residence time may be accessed as the reverse of Production/Biomass ratio for a species, an ecosystem compartment or the entire food web (Gascuel et al., 2011; Schramski et al., 2015). This approach of the time, also developed in the EcoTroph model (Gascuel and Pauly, 2009) is considered here. The residence time of biomass particles is sensitive to ecosystems and temporal variability. For instance, the residence time in the food web is longer for coral reefs than for upwelling systems (Christensen et al., 1993). The residence time of carbon particles in a trophic compartment can raise with producer body mass (Schramski et al., 2015) and during the ecosystem development (Fath et al., 2004).

Fishing pressure would boost the speed in the ecosystem due to the reduction in life expectancy of exploited species and the selection of short-living species characterized by fast turn-over. **This return to a less mature system would shorten the residence time of the biomass particles in the system.** Climate change and elevating sea surface temperature are also expected to shorten this time of biomass transfer.

1.4 Research questions

Basically, the trophic transfer efficiency and the kinetics depend on the ecosystem structure and assemblages and from all species properties. Then, stress like climate change and fisheries are suspected to modify these parameters through – among other modifications – **different species assemblages** in the ecosystem. We developed here a way to assess the transfer efficiency and kinetics and to study their trends over time series. The purpose is to identify and possibly explain their variations depending on the fishing activities and climate change. As described by (Worm and Duffy, 2003), we are interested in two of the three aspects of the ecosystem: the **quantity through the trophic transfer efficiency** and the **temporal stability, through the speed of biomass flows/residence time of biomass in the food web**. Indeed, the quality of the ecosystem is not assessed here.

Studying the variability of theoretical functioning parameters allow to explore the following research questions:

Did changes in species assemblages, induced since 1950 by climate change and fishing pressure, modify the two major parameters of the food web functioning : the trophic transfer efficiency and the trophic kinetics ?

More specifically, this implies to answer the following sub-questions:

- Are we able to identify such changes at the Large Marine Ecosystem scale using available data?
- What are the main patterns of these changes?
- Are they related to climate change and/or fishing pressure?
- Do they express – as in Odum ecological theory – variations leading to less productive and less stable marine food webs?

2. Method

2.1 Data, scale of the study

2.1.1 Sea Around Us catch database: worldwide marine ecosystems data

The database used for marine food webs species composition is the Sea Around Us (SAU) Project fisheries catch data (Pauly and Zeller, 2015). This catch data has been reconstructed starting in 1950 and until 2010 taking into account FAO declarations, small-scale fisheries, recreational fisheries, fisheries discards and illegal fishing or false declarations in order to get a better approach of the real impact of catch (Pauly and Zeller, 2015). Using catch data and not biomass or abundance information on species has two consequences. First, we consider only the exploited part of the ecosystem. For high trophic levels, most species are or can be fished and this exploited part of the biomass can be assumed very close (or similar) of the total biomass. In contrast, this is clearly not the case for low-trophic level species such as phytoplankton and zooplankton. Their influence cannot be studied here. This hypothesis has been tested on the North Sea ecosystem (Appendix II) thanks to the Ecopath model built by (Mackinson and Daskalov, 2007). It looks that biomass and catch give the same results, except for the low trophic-level species, as expected. Secondly, we do not consider changes induced by fishing strategies. We will discuss this assumption in the last part of this work, in light of our results.

In the objective of reducing the number of species for each ecosystem and to avoid bias linked to rare and poorly registered species, we selected only the species groups from the SAU data that represented at least 0.1% of the total catches at least one year between 1950 and 2010. For the North Sea, it divided the number of species by 2 (sensitivity analysis, Appendix II). This method is often used at a global scale and is assumed to well represent the ecosystem communities (Worm et al., 2009). This limit also allowed to get at least 95% of the catches every year for all the ecosystems.

All the trophic levels for taxonomic groups were also taken from the SAU Project. They were calculated from the most precise data available on FishBase (Froese and Pauly, 2016) and SeaLifeBase (Palomares and Pauly, 2016) for all the groups. The Sea Around Us dataset includes 2557 taxonomic groups. These groups can represent one species, one genus, one family, one order or one class.

2.1.2 Geographical scale: Large Marine Ecosystems

The spatial fisheries catch reconstruction from the SAU Project allows an ecosystem approach through the Large Marine Ecosystems (LMEs), ecosystem units defined by Sherman (1991). Nowadays, we count 66 LMEs (but 2 were taken out considering missing data for the Arctic and Antarctic Oceans). They correspond to coherent ecosystems defined by the bathymetry, the productivity, species assemblages and coastal areas limits (see the Large Marine Ecosystem official map in Appendix I). Coastal areas concentrate at least 80 to 90% of the total worldwide catch (Christensen et al., 2008): these ecosystems are representative of the major fisheries catch.

An extensive analysis is developed for 6 LMEs (Figure 3). They are diverse in their functioning, fisheries, habitat and nature: the North Sea (Europe), the California Current

(USA), the Humboldt Current (South American upwelling ecosystem), the Gulf of Mexico, the Canary Current (Western Africa) and the Sea of Japan (Asia). Here, the purpose is to deeply analyze past changes in efficiency and speed of flows and their causes through various marine species assemblages since 1950.

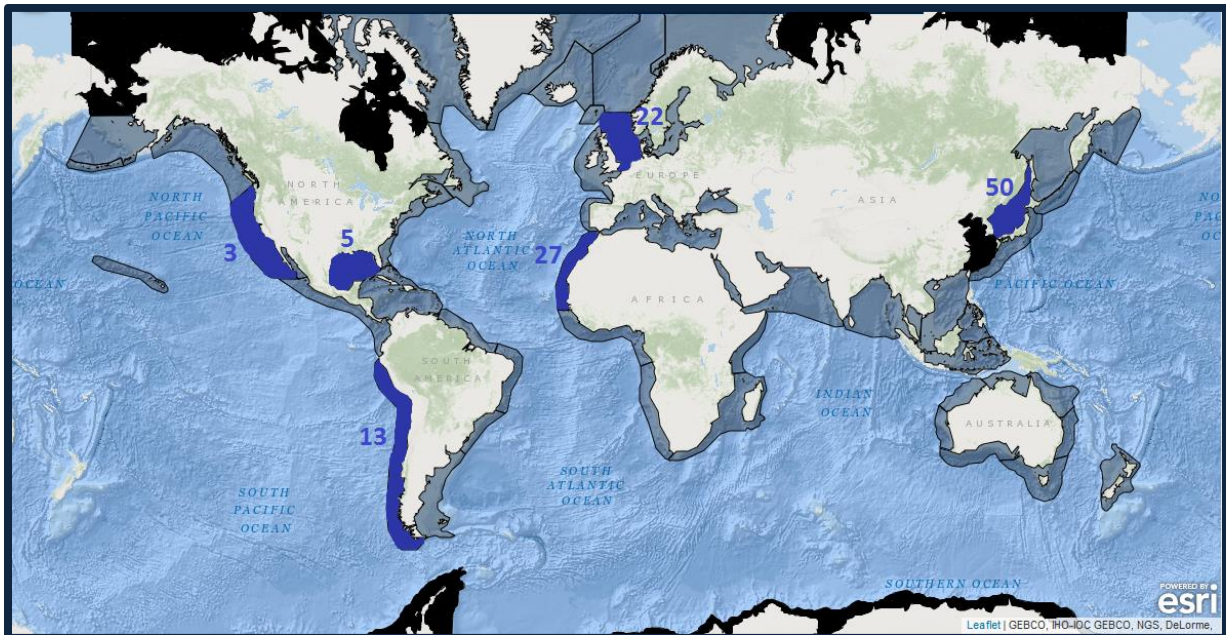


Figure 3 : Worldwide map with the Large Marine Ecosystems boundaries from <http://www.seaaroundus.org/> where are noticed the official LME number for the 6 chosen ecosystems (in blue) for the study (3: California Current, 5: Gulf of Mexico, 13: Humboldt Current, 22: North Sea, 27: Canary Current, 50: Sea of Japan) – the omitted LMEs in black.

A second statistical approach is led to test explicative factors for temporal variations in efficiency and speed, potentially affected by stress. The quantitative analysis is conducted on 56 of the 66 Large Marine Ecosystems, in order to include the ecosystems with the best data available (catch, climate data). Following Chassot et al., 2010, poorly documented LMEs were taken out: East China Sea, Yellow Sea, Chukchi Sea, Beaufort Sea, East Siberian Sea, Laptev Sea, Kara Sea, Antarctic, Hudson Bay and the Central Arctic Ocean (Figure 3).

2.1.3 Estimation of species parameters for all the Sea Around Us groups

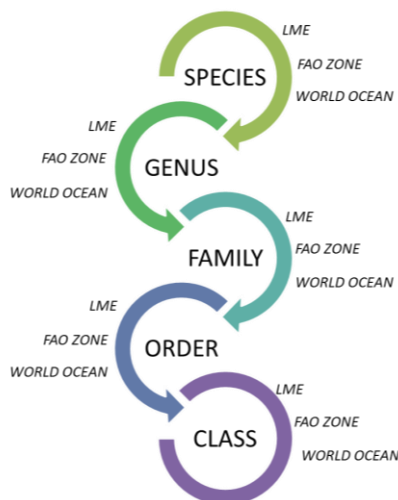


Figure 4 : Geographical and taxonomic scales included in the parameters estimation methodology

Using SAU database and the LMEs, the following species parameters have been estimated: the von Bertalanffy growth coefficient, weight and length, varying with the geographical locations. Two large databases are used to get these ecological parameters: FishBase (Froese and Pauly, 2016) and EcoBase (Colléter et al., 2015). FishBase regroups ecological parameters for fish species. If the population traits are not available for the smallest geographical scale, we can focus on a larger one (Figure 4). If no parameter is available for the species, we will first look at other species geographically close from the same genus. If none parameters can be found, a larger taxonomic scale is used.

SeaLifeBase, a similar database for non-fish species has been considered (Palomares and Pauly, 2016). However, because it is not enough complete, an estimation of P/B, P/Q and Q/B ratios is taken from EcoBase, repository for a large number of Ecopath with Ecosim models where these ratios have been collected (Colléter et al., 2015). These estimations are not as precise as for the fish species: no geographical precision and for large groups of species only (Table 2).

Table 2 : Estimation of parameters of interest per group of species from the Ecobase depository

Groups of species	Abalones, Clams, Mussels, Oysters, Sessile molluscs, Sea urchins, Starfish, Echinoderms, Cnidarians, Sea Cucumbers, Sea Snails, Shrimps, Lobsters, Crabs, Crustaceans, Squids, Octopuses, Cephalopods, Cuttlefishes, Cirripedes, Miscellaneous aquatic invertebrates, Miscellaneous crustaceans
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The growth parameters used such as the growth rate, the asymptotic length and weight are considered as constants over the whole time-period. The individual variability is not included. This methodology allowed us to get all the parameters for all the taxonomic groups selected from the SAU catch database for each LME. Because the taxonomic groups are not as precise all the time or because the parameters do not exist or are not reported into the database, a level of uncertainty and imprecision is existing. However, the methodology permitted to get the highest precision possible considering the taxonomic scale and level of the study.

2.2 Trophic-level based approaches: spectrum and indices

The trophic-level based approach was identified as adapted to answer the research question considering that species are not directly considered here but their trophic level by class. The variability of each trophic class by variations is the species assemblages, initiated by the TL classification of species (Gascuel et al., 2011) reflects the global variability. Then, from the species trophic level, we will transform the data into trophic class. Through this trophodynamic approach, partial transfer efficiency and speed of biomass flows are estimated.

2.2.1 Calculating ecological biomass flow parameters

The speed of flow of each species is identified as the ratio P/B, production by biomass (TL.year⁻¹) (Gascuel et al., 2008). Under equilibrium assumption, it is the total of mortalities noted Z, as the sum of the natural mortality and the fishing mortality (Allen, 1971) (Figure 5). Here, we only consider the natural mortality M. Thus, we analyze the changes in flow kinetics induced by changes in species assemblages occurring at each trophic level, independently of the level of fishing pressure. In other word, **the changes in species assemblages will be translated into changes in natural mortalities M per trophic class**, as a different mortality rate can be associated to each species. M delivers the residence time of a species in the ecosystem. For short time living species, the natural mortality and the speed of flow are high.

Numerous natural mortality empirical equations exist in order to calculate M directly from growth parameters. We tested some of them and led a sensitivity analysis to see if they actually influence the final results for the North Sea LME (Appendix II).

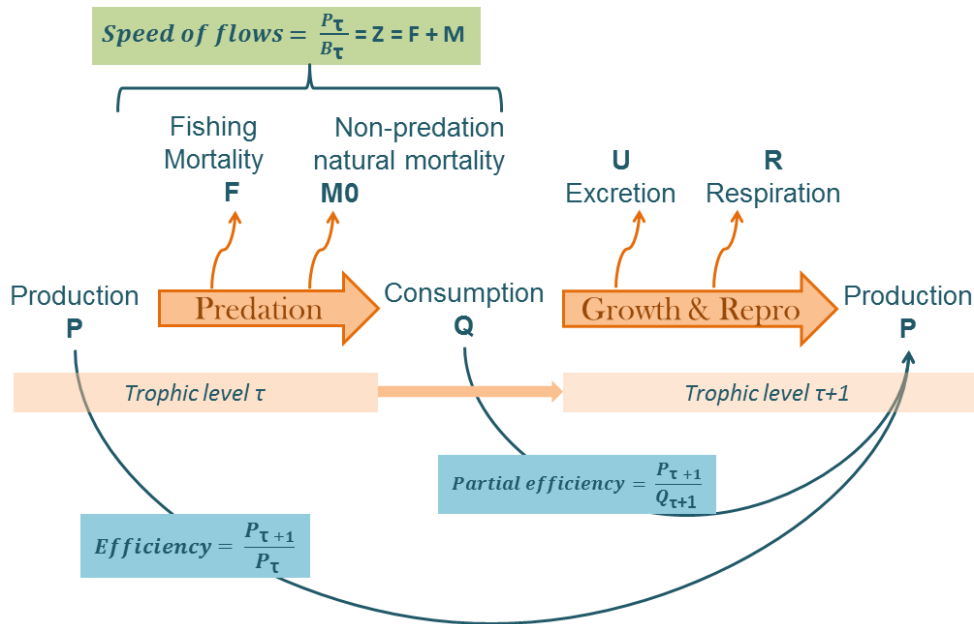


Figure 5 : Predation process with all the kind of loss occurring in the energy transmission between the prey and its predator (adapted from Gascuel et al., 2008)

The following equation initially fitted on FishBase data (Gascuel et al., 2008) has been selected as a reference one.

$$\frac{P}{B} = 1.06 \times e^{0,018 \times T} \times K^{0.75} \quad (1)$$

Where P/B is the speed of flows ($\text{TL} \cdot \text{year}^{-1}$), T in the temperature ($^{\circ}\text{C}$) and K von Bertalanffy growth coefficient (year^{-1})

The trophic transfer efficiency, as the ratio of two production rates between preys and predators (Figure 5), will not completely be assessed here. The ratio P/Q , Production by Consumption, is directly calculated from P/B ratio as following:

$$\left(\frac{P}{Q}\right)_\tau = \frac{(P/B)_\tau}{(Q/B)_\tau} = \frac{\text{speed of the biomass flow}}{\text{food consumption rate}} \quad (2)$$

For getting P/Q , the food consumption ratio Q/B was estimated using the following empirical equation (Palomares and Pauly, 1998):

$$\log\left(\frac{Q}{B}\right) = 7,964 - 0,204 \times \log(\text{Winf}) - 1,965 \times \frac{1000'}{T} + 0,083 \times A_R + 0,532 \times h + 0,398 \times d \quad (3)$$

Where Q/B is the food ingested relative to its biomass, Winf is the asymptotic weight from the Von Bertalanffy models (g), T is the water temperature ($^{\circ}\text{K}$), A_R is the aspect ratio of the caudal fin, $h=1$ if the species is herbivorous, $d=1$ if the species eats detritus

P/Q , being a partial trophic efficiency, is considered as the “gross food conversion efficiency” (Christensen et al., 1993). This ratio focusses on the effects that species composition might have on total losses related to respiration. So, it is strongly linked to the total transfer efficiency. Nevertheless, it should be noted that this partial efficiency does not consider the variability emerging from non-predation mortalities (Figure 4). In other words, the selection of

species with large predation mortalities (i.e. trophic dead-end species) caused by human-induced stresses will not be identified in our analysis.

It has been previously demonstrated that the respiration rates changes with time, especially with fishing activities and climate change (Cheung et al., 2012). The TE “depends on non-predation mortality, excretion and respiration” (Gascuel and Pauly, 2009) and it seems that respiration is the parameter that influences the most the efficiency (Christensen et al., 1993). Then, by looking into the various combinations of species assemblages per TL and trophic class, the partial efficiency variability will emerge from each species metabolic properties.

2.2.3 From species to the trophic class as units of study

P/B and P/Q parameters were estimated per trophic class using a trophic spectra approach following Gascuel et al., 2005. For that purpose, the R package EcoTroph was used (Coll  ter et al., 2013):

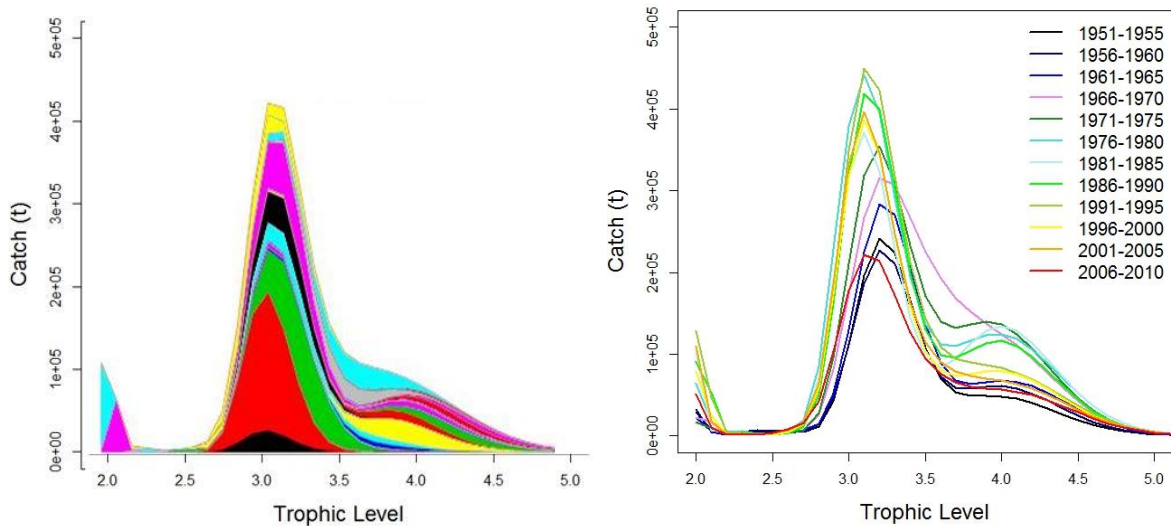


Figure 6 : Catch spectra for the North Sea – Left: Spectrum of the catches in 1990 per species (each color is a species) – Right: Spectrum of the catches from 1950 to 2010 every five years

A spectrum is the result of a transformation from the species data to trophic class data. From species catches and TL, a smooth function splits the value of interest through a log-normal distribution on the trophic levels. Thus, the value of interest is not distributed by species but by TL based on trophic class with a $\Delta\tau=0.1$ range. This trophic representation method of the ecosystem is useful to understand where the fisheries catch happen in the food web (Gascuel et al., 2005). For example, in the North Sea, catch are the most important in the trophic class 3.0-3.5 and changed over time (Figure 6). In order to study the time of residence of species in the ecosystem and the partial efficiency, we look at P/B and P/Q ratios spectra. For each trophic class $[\tau; \tau + \Delta\tau]$ mean P/B and P/Q ratios are calculated proportionally to the related catch amount of each species i :

$$\left(\frac{P}{B}\right)_{\tau} = \frac{\sum_i \left(\frac{P}{B}\right)_i \times Y_{i,\tau}}{\sum_i Y_{i,\tau}} \quad \text{and} \quad \left(\frac{P}{Q}\right)_{\tau} = \frac{\sum_i \left(\frac{P}{Q}\right)_i \times Y_{i,\tau}}{\sum_i Y_{i,\tau}} \quad (4)$$

Where Y are the catches, P/B the speed of flows and P/Q the partial efficiency of species.

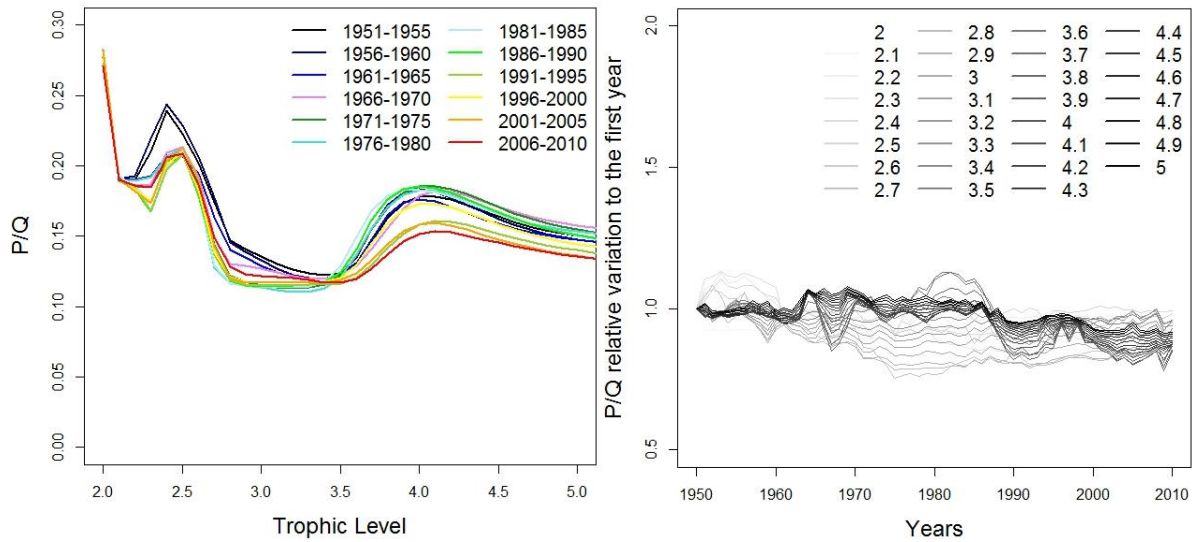


Figure 7 : Spectra for the North Sea – Left: P/Q spectrum per trophic level every 5 years – Right: relative P/Q values spectrum per year for each trophic class (step = 0.1), each value per year is divided by the P/Q (1950)

Then, for each ecosystem, we calculate the spectra of both parameters for which we can already observe temporal variations per trophic class (Figure 7). This data transformation is a key step in our trophodynamic approach to analyze the changes of parameters along the time-series at a global scale or by having a focus on certain parts of the ecosystem. Then, another transformation of the data into global ecosystem indices has been realized to lead the LME meta-analysis.

2.2.4 From parameters per trophic class to integrated ecosystem indices

P/Q is a ratio without unit. We create a cumulated index that allowed quantifying the proportion of production transferred to the top of the food web. Then, if this index is decreasing with time, it shows that high-TL species are having less food available and that the ecosystem lost in productivity.

- The **Efficiency Cumulated Index (ECI)** refers to the cumulated efficiency: from the multiplication in the index, the partial efficiency, just as in the food web, is progressively integrated from low trophic level parts of the food web to the top.

$$Efficiency\ Cumulated\ Index(y) = \frac{\prod_{\tau=2.0}^{\tau=b} \left(\frac{P}{Q}\right)_{\tau,y}^{\Delta\tau}}{\prod_{\tau=2.0}^{\tau=b} \left(\frac{P}{Q}\right)_{\tau,1950}^{\Delta\tau}} \quad (5)$$

$\Delta\tau$ is the trophic-level step used from one trophic level class to the upper one (here $\Delta\tau=0.1$). The coefficient b corresponds to the upper trophic level chosen (2.5/3.0/3.5/4.0/4.5).

- The **Time Cumulated Index (TCI)**, reversly proportionate to the speed of flows, refers to the time necessary to go up the food chain:

Regarding the speed of flows P/B, we developed another way to look at it based on the EcoTroph approach (Gascuel and Pauly, 2009). The inverse of this ratio captures the time necessary for the biomass to go along the food chain. Thus, we sum up all the times from all trophic levels and it indicates how long it takes to go to the top of the food chain from $TL=2.0$ to $TL=b$ as following:

$$\text{Time Cumulated Index (y)} = \frac{\sum_{\tau=2.0}^{\tau=b} \frac{\Delta\tau}{\left(\frac{P}{B}\right)_{\tau,y}}}{\sum_{\tau=2.0}^{\tau=b} \frac{\Delta\tau}{\left(\frac{P}{B}\right)_{\tau,1950}}} \quad (6)$$

This TCI can be interpreted as a factor of stability in the ecosystem, but this will be more discussed later. These indices are calculated relatively to the first year of the time series so we can see their relative variations over time, standardized the same way for all LMEs. **We calculate here the index from TL=2.0 to TL=4.0 as a reference.** Indeed, $b=4.0$ is an interesting limit because it shows how much of the biomass is available for top-predators in the ecosystem. We also tested different limits to search for the progressive index changes along the food chain.

2.3 Choice of explanatory parameters for fishing pressure and climate change

2.3.1 Fishing pressure measures

Because no access to reliable fishing effort data at this global LME scale is available yet from the SAU Project, several fishing pressures indices are investigated:

- Stock Status Plot (SSP), (Kleisner et al., 2013)

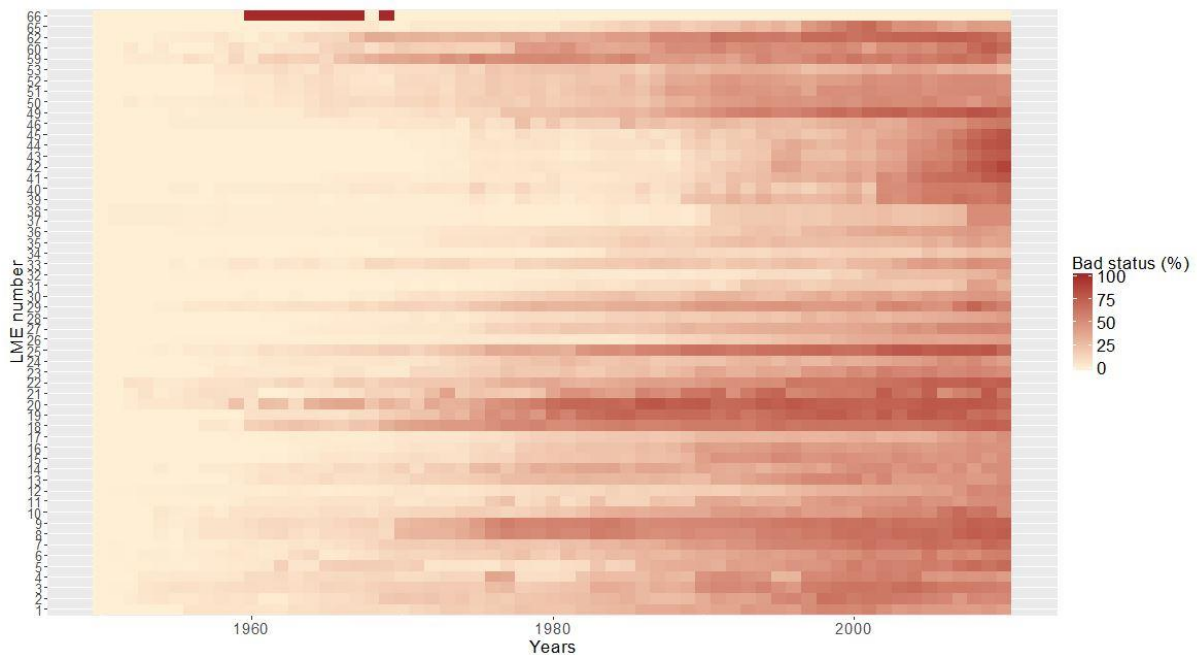


Figure 8 : Top – Time-series of the % of over-exploited and collapsed assessed stocks per Large Marine Ecosystem from 1950 to 2010

This index of fishing pressure is available for each LME on the SAU website, where the method of assessment is detailed (www.seaaroundus.org/). It measures the proportion in number of collapsed or overexploited stocks in each LME (Figure 8). This measure relies on two strong disputable hypotheses: the highest pick of catches in the time-series is considered as the maximum sustainable catches amount, while it can come from changes of fisheries strategy or fisheries management. Decreases in catch are assumed to be the result of over-exploitation of the related population.

- The Primary Production Required for fisheries (PPR) (Pauly and Christensen, 1995) is the amount of carbon needed to produce the catches:

$$PPR_k = \sum_{i=1}^n \left(\frac{Y_{ik}}{9} \right) \times \left(\frac{1}{TE_k} \right)^{\tau_i - 1} \quad (7)$$

Where PPR_k is in $t \text{ C.km}^{-2} \cdot \text{year}^{-1}$ and k is the LME, i the species, Y_{ik} the catch of species i in LME k , TE is the Transfer Efficiency, here assumed to be equal to 10% and τ the trophic level of the species.

The PPR value is not directly used, but the ratio PPR/PP (%) (where PP is the Primary Production) as the fishing pressure index. As a reference, a constant PP value is attributed to each LME from the Eppley correction observation data. However, the PPR/PP values (%) are extremely high for some ecosystems. This index should vary between 0 and 30-50% (Pauly and Christensen, 1995; Swartz et al., 2010), and our results show much higher variations (Appendix III). More particularly, PPR/PP is sensitive to the trophic transfer efficiency value used (Watson et al., 2014) and the primary production data (Cury et al., 2005). This led to a sensitivity analysis (Appendix III).

- L_{index} (Libralato et al., 2005)

$$L_{index,j,k} = - \frac{PPR_k \times TE^{\tau_c (k)-1}}{PP_k \times \ln(TE)} \quad (8)$$

Where k is the LME, PPR is the primary production required for fisheries, TE is the transfer efficiency, τ_c is the mean trophic level of catches per LME and PP is the primary production from Eppley.

Again the transfer efficiency value is considered as 10% per ecosystem as a reference value. L_{index} is constructed on a different way than the PPR, informing differently on the impact of fishing: it quantifies the loss in the secondary production in the ecosystem, due to fishing at the various trophic levels.

- The Mean Trophic Level (MTL), (Pauly, 1998) of catch informs on the mean food web level of the fisheries catch

$$MTL_{j,k} = \frac{\sum_{i=1}^n Y_{i,j,k} \times \tau_i}{\sum_{i=1}^n Y_{i,j,k}} \quad (9)$$

Where $MTL_{j,k}$ is the mean trophic level per year j and per LME k , $Y_{i,j,k}$ the catches per species, year and LME, τ_i is the trophic level per species i .

- Fishing in Balance (FIB) index, (Pauly, 2000) informs on the deployment of the fisheries on an ecosystem through an integrative construction relative to 1950:

$$FIB_{j,k} = \log_{10} \left(\frac{\sum_{i=1}^n Y_{i,j,k} \times 10^{\tau_i}}{\sum_{i=1}^n Y_{i,1950,k} \times 10^{\tau_i}} \right) \quad (10)$$

Where $FIB_{j,k}$ is the index per year j and per LME k , $Y_{i,j,k}$ the catches per species, year and LME, τ_i is the trophic level per species i .

2.3.2 Climate change data

Several sources of climate data have been considered, from satellite observations to models. As observations, the Eppley data (sbir.nasa.gov) have been used (as aggregated per Large Marine Ecosystems) for mean values over the observed time-series in order to get the best climate information. For the variation of the values from 1950 to 2010, GFDL model data was used (Geophysical Fluid Dynamics Laboratory, NOAA, www.gfdl.noaa.gov).

2.3.3 Other explanatory variables

Along the study, it appeared interesting to include as well other explanatory variables that inform differently on the ecosystem functioning: the proportion of fish, cephalopods and shrimps species in the catches, calculated all from the SAU database (Appendix III).

2.4 Statistical analysis of the index variations

2.4.1 Dynamic Factor Analysis

The Dynamic Factor Analysis (DFA) has been conducted in the following purpose: showing the relationship of the ecosystems time-series to temporal covariates trends. It is a multivariate time-series analysis, and it helps to put in light the major trends in the ecosystems. The DFA allows studying the correlation to the worldwide temporal trend in fishing pressure and climate change.

Using the MARSS R package (Holmes et al., 2013), several models were tested on the ECI only. Already used for LMEs meta-analysis with SAU data (Mcowen et al., 2015) and for other fisheries and marine species temporal trends (Mills et al., 2013; Zuur et al., 2003; Zuur and Pierce, 2004), this method was selected here in order to identify the major trends in the ECI common to all LMEs, and to include explanatory variables as additional trends. From the 1950-2010 time-series, we analyzed the temporal variations on the 56 LMEs. The DFA tests m common trends within the time-series and can contain covariate effects. Basically, the observations (ECI_t) are considered as a linear combination of m trends (x), explanatory covariates (d) and noise (v). The model is constructed in the following way:

$$ECI_t = Zx_t + a + Dd_t + v_t \quad (11)$$

Where ECI_t are the observations at year t , Z the factor loadings, x_t the matrix of m trends, a the offsets, D the matrix containing the covariates effects on the observations, d_t the covariates matrix at year t , v_t the observations errors at year t as the noise component. This noise follows a multivariate normal distribution, centered on 0, with various possible variances and covariance relationships. The matrix of variance needs to be tested with several options during the model run (Zuur et al., 2003).

We tested several models, and selected the best one/ones by their corrected Akaike's information criteria (AICc), distinguishing the model getting the best number of trends and the best covariates to fit the ecosystem time-series. In order to restrict the test of models, we set the common trends from 2 to 5. The data was standardized by the mean on the time-series and the standard deviation (Appendix VII, Fig.1). Regarding the noise component, we choose to test a "diagonal and unequal" variance matrix: the ecosystems have unequal variance and no covariance (considering that LMEs have the same variance is not realistic). The covariates added to the model are mean of all ecosystem trends per year. Because we do not add the proper ecosystem covariate but the global worldwide signal, the model answers to the question: **are the LMEs correlated / influenced by the worldwide temporal signal in fishing pressure and climate change?** Five covariates have been tested separately into the Dynamic Factor Analysis (DFA) model. Then, two covariates were selected for a model incorporating climate change effects and fishing pressure effects.

2.4.2 Principle Component Analysis and Ascending Hierarchical Classification

For ECI and TCI, we performed a Principle Component Analysis (PCA) and a classification (using the R package FactomineR, Lê et al., 2008) to identify the major trends in the LMEs, to classify LMEs from their temporal variations and to explain specifically the temporal variations by explanatory variables. This analysis especially allows demonstrating the correlation between the trends and covariates per ecosystems type. We used the 56 selected LMEs as the statistical individuals and the 61 years as the explanatory variables. This method has already been used in statistical ecology (Beaugrand et al., 2003) and provides a global overview of the systems whose dimensions do not help to select major trends directly. We add in the PCA supplementary variables (details for the variables and modalities in Appendix IV). As the ecosystems are the statistical individuals, we are able to include the supplementary variables as properties of each ecosystem, presenting various fishing regimes and climate change intensities. Each variable is tested either based on absolute values or using relative to 1950 values. All the quantitative variables were also tested with simple modalities as qualitative variables in order to emphasize all simple and complex effects existing for the ECI and TCI indices. These supplementary variables help to understand the Ascending Hierarchical Classification (AHC) and qualify each cluster by the LMEs characteristics.

3. Results

3.1 ECI and TCI for the 6 Large Marine Ecosystems: analysis of the species assemblages

All of these 6 LMEs present different patterns and various intensities. The ECI and TCI variations help to understand changes over time in the species assemblages from low to high trophic classes. The selected LMEs provide a global picture of index changes since 1950 (Figure 9) and species assemblages. The temporal variations of species per trophic class are presented in the Appendix V and were used to analyze the following results.

- *California Current*

This ecosystem is by far the one where highest changes in the studies indices are observed. From the trophic class 2.5-3.0, there is a clear succession of anchovies and pilchard abundances due to changes in upwelling intensity and El Niño Southern Oscillation (ENSO) events (Lindegren et al., 2013). The **Californian anchovy** (*Engraulis mordax*, $TL=2.96$) has been abundant between the 70s and the 90s. The Californian anchovy is a more efficient species but generates slower biomass transfers compared to the **South American pilchard** (*Sardinops sagax*, $TL=2.84$), inducing a decrease in TCI since the 70s.

The species assemblages between trophic levels 3.5 and 4.0 also show some major changes associated with an abundance increase in the **Pacific jack mackerel** (*Trachurus symmetricus*, $TL=3.57$) and the **Californian squid** (*Loligo opalescens*, $TL=3.88$). The squid is a more efficient species with way faster biomass transfers. The squid abundance in the catches has increased up to 50% in the recent years (in the trophic class 3.5 to 4.0), while it was almost absent in the 50s. Concerning top predators, there is a clear transition from **Tuna species** (*Thunnus albacares*, *Thunnus obesus*, *Thunnus alalunga*, $TL>4.2$) to the **North Pacific hake** (*Merluccius productus*, $TL=4.35$), and the **Jumbo flying squid** (*Dosidicus gigas*, $TL=4.14$) since the 90s.

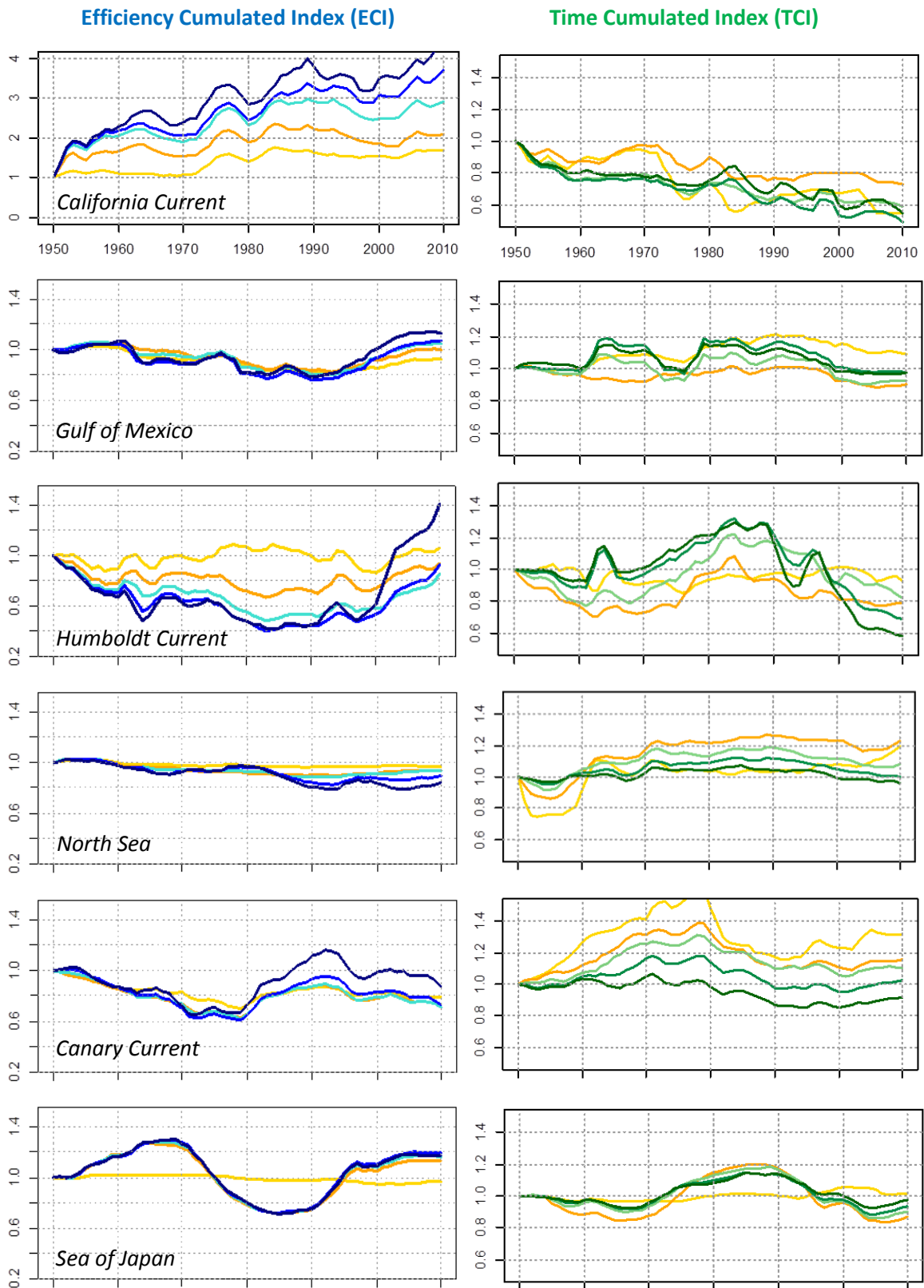
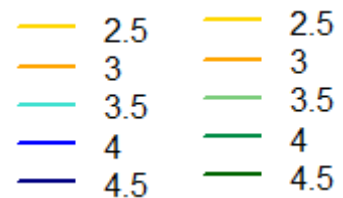


Figure 9 : ECI (left) and TCI (right) for the 6 Large Marine Ecosystems cumulated to the highest trophic level progressively (from TLmax=2.5 to TLmax=4.5)



- *Gulf of Mexico*

In the Gulf of Mexico, the majority of fisheries target low-trophic level species (MTL usually below 3.0) such as the **Gulf menhaden** (*Brevoortia patronus*, $TL=2.19$). The changes observed in the two low trophic-level species since 1950 explains the small reduction of ECI until the 90s when the **American cupped oyster** (*Crassostrea virginica*, $TL=2.0$) increased. The oyster induces the ECI rise on the recent years due to its higher P/Q ratio (0.263) compared to the **Gulf menhaden** (P/Q=0.022). The TCI is showing an opposite trend, since the oyster exhibits a very high speed of flows ($P/B=2.56y^{-1}$), inducing a decrease in the TCI on the recent years. These two species represent the large majority of the catch in the ecosystem (up to 1million tons for the Gulf Menhaden and 250.000 tons for the oyster in the mid-80s).

Changes in **Prawns** ($TL=2.65$) and **Mulletts** ($TL=2.53$) abundance explain the variations in the indices: when Mulletts represent a higher proportion of the catch then the ECI is decreasing and the TCI is increasing, as Mulletts are less efficient and less rapid for biomass flows. The important variations observed in the TCI since the $TL>3.0$ is induced by the variations in the catches of 'the Marine fishes neii', as the non-identified fish groups and the '**Decapoda**' ($TL=3.43$), inducing the drop of the TCI index (before the 80s). As these taxonomic groups are including a lot of different species, it remains challenging to analyze. On upper trophic class, there is a higher proportion of sea basses and groupers in the catches contributing to the low ECI and high TCI on the 70s-90s period.

- *Humboldt Current*

The majority of catches belongs to trophic levels between 2.5 and 3.0 and due to the dominance of the pelagic fishery in this upwelling ecosystem. The **Peruvian Anchoveta** (*Engraulis ringens*, $TL=2.7$) and the **South American Pilchard** (*Sardinops sagax*, $TL=2.84$) are dominating the catches. The Humboldt Current is dominated by environmental changing conditions through ENSO events. They induce high abundances in sardine when the temperature is higher. On the opposite, the anchovy is abundant out of these high-temperature regimes (Alheit and Niquen, 2004). This accounts for the succession in catches between the two species. The anchovy and sardine have different characteristics: the **Peruvian Anchoveta** is two times more efficient and induce faster transfers in the ecosystem than the **South American Pilchard**. Therefore, when an ENSO event happens, the ECI of the Humboldt Current increases, the ecosystem is more productive and the TCI is lower. The **Chilean Jack Mackerel** (*Trachurus murphyi*, $TL=3.33$) – one of the main predator of the anchovy (Alheit and Niquen, 2004) – appears to be highly fished since the mid-70s. This species is responsible for a decrease in the ECI and an elevation in the TCI, as we can see on the index results cumulated until $TL=3.5$.

The **Jumbo flying squid** (*Dosidicus gigas*, $TL=4.14$) has been emerging recently. It is fished since 2000s and enhanced the cephalopod proportion in the catches up to 15% (Appendix V). This species is driving the ECI in the high TLs. Some major changes in the catch assemblages happened: before the 70s, majority of the catch came from the **Pacific bonito** (*Sarda chiliensis*, $TL=4.49$) and the **South Pacific hake** (*Merluccius gayi gayi*, $TL=4.26$). Between the 70s and the 90s, *Merluccius* genus was preponderant in the catch composition. All these species have a lower P/Q and P/B which elucidates that the apparition of the **Jumbo flying squid** in the catches induced major changes in the ecosystem (ECI rise to 1.5

times the value in 1950 while TCI reduces to 60% of the value in 1950). The speed of flows for the jumbo flying squid is 6 times higher than for the other species and the partial efficiency and 2 to 4 times higher. His adaptive capacity ensures its resilience, which might not be the case for example of the **Chilean Jack Mackerel**, feeding on the variable source of Peruvian Anchoveta.

- *North Sea*

While the fishing pressure was already high in the North Sea LME in the early 50s, the PPR/PP intensified until the 70s (Appendix V) up to 60%. Because of overexploitation, the fisheries catch diminished since the 80s. The ECI cumulated until TL=4.0 shows a 20% reduction since the 1990s. Consequently, less biomass is available for top-predators like cods or tunas, for which the TL is higher than 4.0. However, the time necessary to go along the food web was prolonged in the 70s and then went back to the 50s values (2.5 years).

Sand lances (*Ammodytidae*, TL=3.11) replaced the **Atlantic herring** (*Clupea harengus*, TL=3.38) in pelagic fisheries in the 80s (Appendix V) which explains a slight elevation of the ECI values. It constitutes one of the major changes in this LME. Indeed, Sand Lances have a much higher P/B ratio: they induce faster energy transfers in the ecosystem which make the time index decreasing on the recent years. The increase and stabilization of the TCI in the 60-90s might be driven by the **European flounder** (*Platichthys flesus*, TL=3.32) and the **European plaice** (*Pleuronectes platessa*, TL=3.26) fisheries, species generating slower energy transfers.

The decrease in ECI since the mid-90s when the index is cumulated until 4.5 (top-predators) can be explained by the fact that **Whiting** (*Merlangius merlangus*, TL=4.36) and **Cod** (*Gadus morhua*, TL=4.09) are less abundant in the catches: those species are very efficient and their replacement in terms of catch by **saithe** (*Polliachus virens*, TL=4.31), the **Atlantic bonito** (*Sarda sarda*, TL=4.5) and the **Blue whiting** (*Micromesistius poutassou*, TL=4.13) modified the ECI. The North Sea is impacted by species changes at various trophic levels.

- *Canary Current*

The Canary Current LME presents a drop in the ECI and an increase in the TCI until the 80s. After that, the trends were reversed, showing that the ecosystem experienced some important changes in both indices. The higher proportion of the **Bonga shad** (*Ethmalosa fimbriata*, TL=2.5) since the 70s induced a fall of the ECI and an increase in the TCI, as this fish is less efficient and use more time to transfer biomass. It induced an elevated TCI to 1.5 times higher in the 80s than in 1950.

The important proportion of **Mackerels** (*Trachurus*, TL=3.69), in the 60s-70s induced a less elevated ECI and an increase in the TCI. In the 80s, the increase in octopus abundance and catch leads to more efficient and rapid transfers. The rise of ECI in the recent years (since the 90s) for TL<4.0 species is due to the **Largehead hairtail** (*Trichiurus lepturus*, TL=4.42) more efficient than **Tuna species** (*Thunnus alalunga*, *obesus*, *thynnus*, *albacares*, TL>4.2) and the **Senegalese hake** (*Merluccius senegalensis*, TL=4.5).

- *Sea of Japan*

The **Pacific sardine or pilchard** (*Sardinops sagax*, $TL=2.84$) is leading all the changes observed in the Sea of Japan ecosystem, even though some variations are noticeable in the fisheries catches for higher trophic class (Appendix V). This only species looks like driving all the ecosystem changes. The pilchard has been highly caught between the 70s and 2000s with a peak of catches reaching 908.000 tons in 1988. This species demonstrates a high decline of the ECI values and prolonged TCI, because all the other species in the trophic class are only non-fish species such as prawns and crabs, with higher P/Q and P/B ratios. Even though other assemblage's changes appear noticeable on the higher trophic levels, they do not influence the ECI and TCI variations.

Small pelagic species are structuring a lot the food web in upwelling ecosystems
 Decrease in abundance of top-predators modify the indices (tunas, cods)
 Cephalopods are suspected to influence the temporal variations

3.2 Worldwide signals in the Large Marine Ecosystems

3.2.1 Exploration of global changes

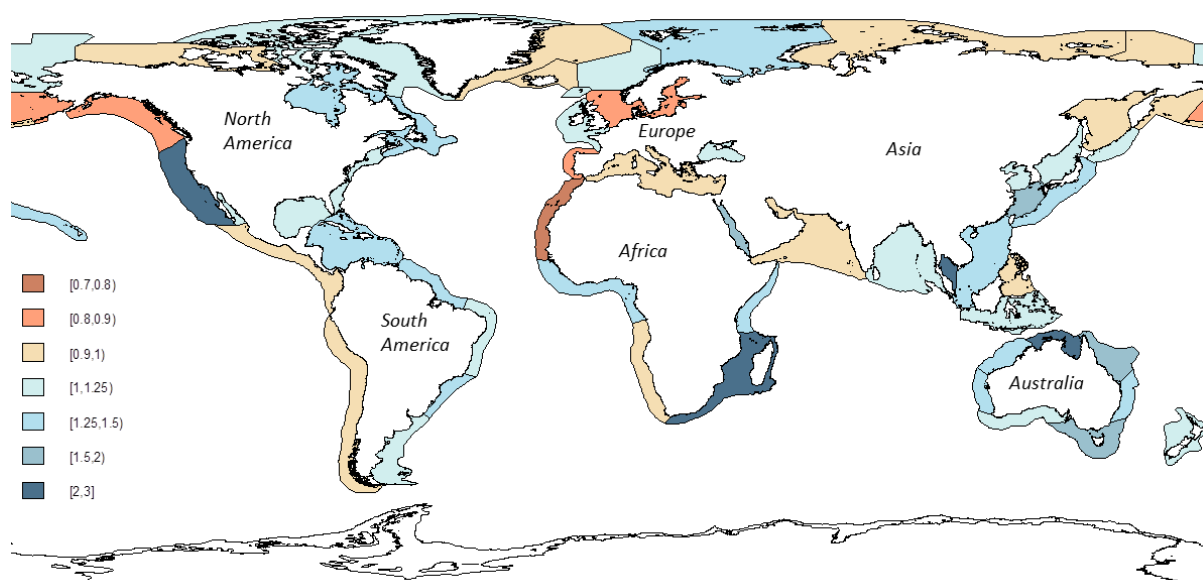


Figure 10 : Efficiency Cumulated Index relative to 1950 for all the Large Marine Ecosystems (ratio mean2005-2010/mean1950-1955)

This kind of meta-analysis at the LME scale helps to get a global overview of the marine ecosystems. 22 LMEs have experienced a decrease in the ECI (Figure 10), showing that these ecosystems are globally less productive in the recent years. Efficiency severely decreased especially in: the Canary Current (reduction of 20 to 30%), the Iberian Coastal, the North Sea, the Baltic Sea, the Gulf of Alaska and the East Bering Sea (10 to 20% fall in productivity). On the opposite, 42 LMEs have become more efficient. Four of them have an ECI more than 2 times higher in 2010 compared to 1950: the California Current, the Agulhas Current, the North Australian Shelf and the Gulf of Thailand (Figure 10).

These results are questioning our research hypothesis considering that the fishing pressure is very high for the majority of LMEs and has been so for a long time period since the 80s. Indeed, it would be expected to find a majority of decreasing ECI ecosystems.

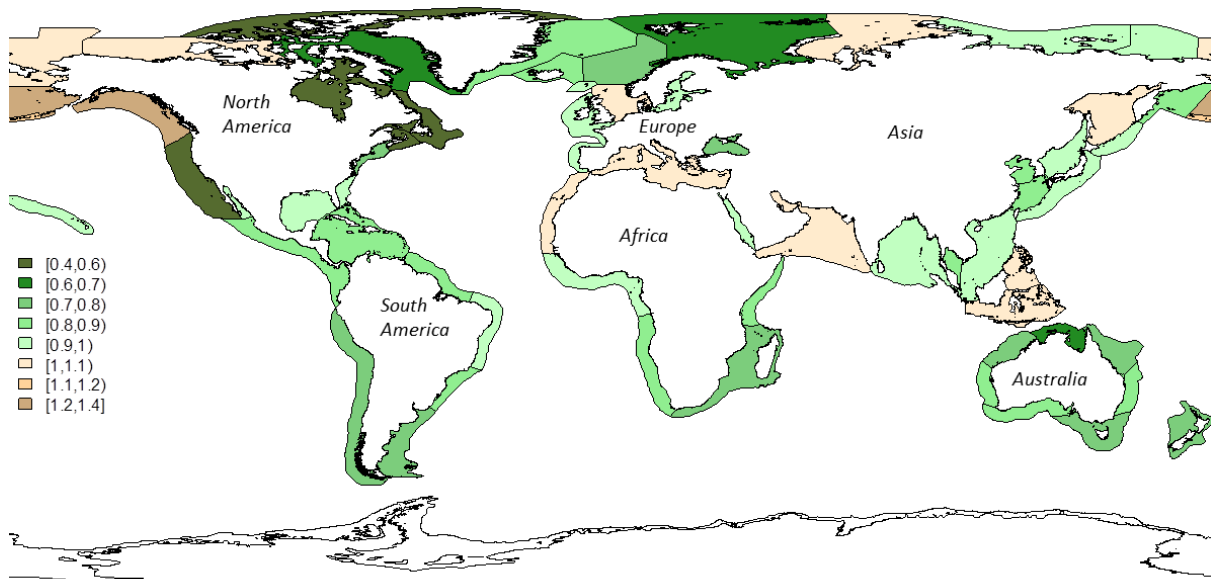


Figure 11 : Time Cumulated Index relative to 1950 for all the Large Marine Ecosystems (ratio mean2005-2010/mean1950-1955)

As for the Time Cumulated Index, 51 LMEs prove to have a lower TCI (Figure 11). This means that the majority of ecosystems are characterized by faster transfers due to the selection of short-living species at each TL. For example, the Humboldt Current has decreased his time index by 20 to 30%, which is a lot of change. Five LMEs drastically diminished from 40 to 60% in recent years compared to the value in 1950-1955: the California Current, the Scotian Shelf, the Newfoundland-Labrador, the Hudson Bay Complex and the North Greenland. However, 13 LMEs increased in TCI. It is the case for the North Sea: the time necessary to go to the top of the food web has gone up to 1.1 times the value in 1950-1955. Furthermore, for the LMEs demonstrating a lower ECI, a drop of TCI is expected. But we can see on the maps that this correlation between the low indices seems to be verified only for 9 LMEs including the Benguela Current and the Humboldt Current.

The time-series on the 56 selected Large Marine Ecosystems are presented in the Appendix VI, Fig.1 and Fig.2, which constitutes the base data for all the following quantitative analysis.

Large changes observed for the two indices: food web functioning changing
 Unsuspected increase in the Efficiency Cumulated Index for the majority of LMEs
 Faster biomass flow transfers in the LMEs

3.2.2 LMEs response to the worldwide temporal signal of stress

After standardization, the mean worldwide trends of each covariate since 1950 exhibit various patterns (Figure 12):

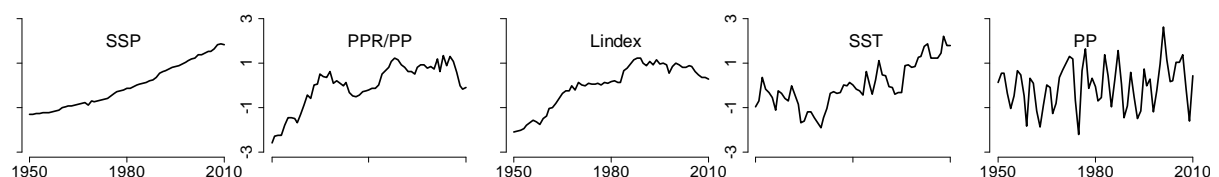


Figure 12 : Standardized covariates trends included in the Dynamic Factor Analysis after standardization from 1950 to 2010 – Left to right: Stock Status Plot, Primary Production Required for fisheries divided by the Primary Production, L_{index} as the loss of production, Sea Surface Temperature and the Primary Production

The fishing pressure trends have different shapes and then cannot be considered as equivalent covariates. The selection of the index that reflects the best the fishing pressure at the worldwide scale is very important. Concerning the climate variables, we can already expect the sea temperature to be selected because the primary production trend is fluctuating around 0.

Using a Dynamic Factor Analysis approach (DFA), more than 30 different models were tested and selected on several criteria. In order to work out the influence of the fishing pressure or the climate on the ecosystems, a model with two covariates should be selected. Only the models with all converged parameters are represented on Table 3. We limited the number of trends tested to 5. Considering that the covariates supplementary are trends as well, there is a number of 6 to 7 trends maximum for the 56 ecosystems. Based on AIC_c criteria, two fishing pressure indices are identified as the best resuming the data: L_{index} and the SSP (Stock Status Plot).

Table 3 : Results of the models tested with the Dynamic Factor Analysis ranked by a decreasing AIC_c – The models represented are the models that converged for all parameters until 2.000.000 iterations – The red ones represent the compared final models

Model n°	Number of covariates	Covariates	Trends	AIC _c
1	2	SST, Lindex	5	4651.113
2	2	SST, SSP	5	4686.164
3	1	Lindex	5	4696.434
4	1	SSP	5	4700.675
5	2	SST, SSP	4	4840.283
6	2	SST, Lindex	4	4895.749
7	1	PPR/PP	5	4772.623
8	1	SST	5	4813.059
9	0	No covariate	5	4856.684
10	1	SSP	4	4866.686
11	1	Lindex	4	4932.423
12	1	PPR/PP	4	4939.939
13	1	PP	5	4951.501
14	1	SST	4	5056.210
15	0	No covariate	4	5086.000
16	2	SST, SSP	3	5101.727
17	1	SSP	3	5115.427
18	1	PP	4	5165.015
19	2	SST, Lindex	3	5248.214
20	1	Lindex	3	5283.102
21	1	PPR/PP	3	5325.267
22	0	No covariate	3	5971.402
23	1	PP	3	6015.405
24	1	Lindex	2	6256.182

The addition of Primary Production covariate conducts to a higher AIC_c than when no covariates are added to the model. Then, with the two covariates, several numbers of trends were tested again (from 2 to 5). As the factor loadings are lower on the models n°1 and 2 (Table 3), a model with 2 covariates was selected and 4 trends (model n°5). The best model constructed with 4 trends is the one with SST and SSP. As the similar model with L_{index} demonstrates a different trend but is also a good model on the AIC_c criterion, we compared these two models. Indeed, we can observe that the variance matrix or error matrix presents various coefficients for the models (Figure 13). However, the variance that is not explained for some ecosystems is likely the same for the two models. The Gulf of California (LME 4), the Barents Sea (LME 20), the Arabian Sea (LME 32), the South China Sea (LME 36) and the Iceland Shelf and Sea (LME 59) are the ecosystems for which the models explain less of the data variability, as their coefficients in the noise matrix are the highest. On the opposite, the Asian ecosystems (n°49 to 53, Figure 13) are very well explained in the model, due to their similar trend closely linked to the trend n°2 (Appendix VIII, Fig.8). Globally, the noise

matrix confirms the selection of the model with the SSP covariate and not the L_{index} . The residual variance in the model is higher for the model 6 than for the model 5 for a majority of Large Marine Ecosystems.

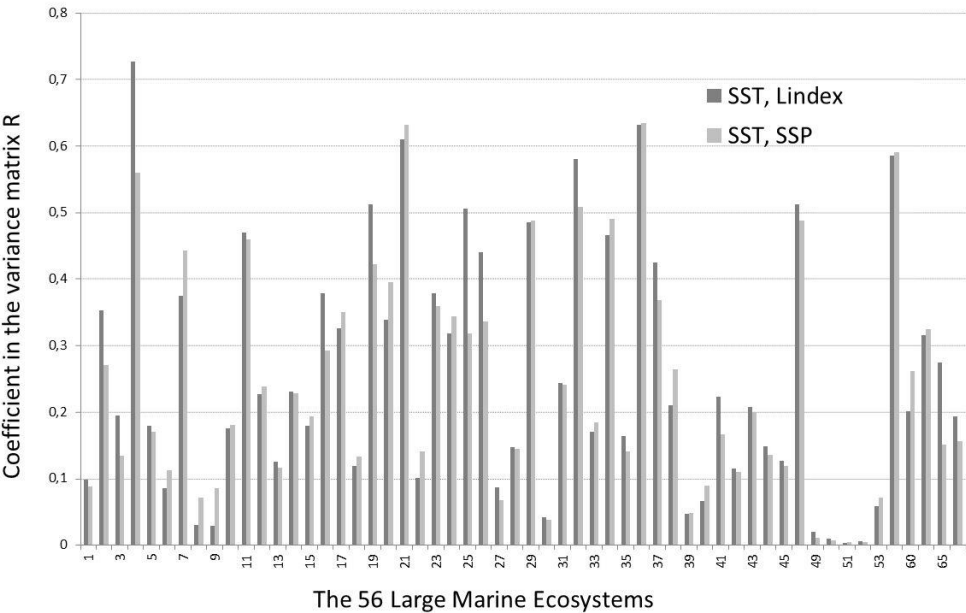


Figure 13 : Coefficients in the variance matrix R for each ecosystem for the two best models: 4 trends, 2 covariates (SST and L_{index} , SST and SSP)

All the enclosed ecosystems such as the Gulf of Mexico, the North Sea and the Mediterranean Sea are significantly affected by the worldwide increasing trend temperature. 32 Large Marine Ecosystems show a positive relationship with the Stock Status Plot covariate (Figure 14), indicating that 32 LMEs on the 56 studied present a significant increasing efficiency trend concordant with the worldwide increasing fishing overexploitation trend (Figure 12).

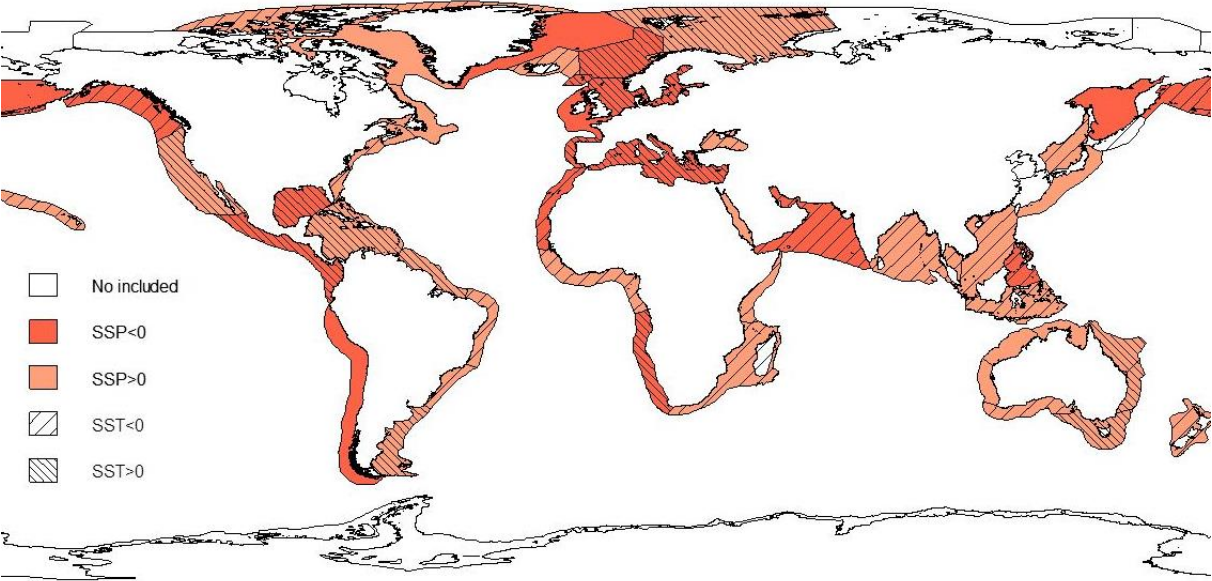


Figure 14 : Large Marine Ecosystems worldwide map with the SSP and SST covariate coefficients from the DFA with two covariates and 4 trends – if the coefficient associated to the covariate by the model belong to $]-0.5;0.5]$, it is considered as null

However, this positive correlation to the overexploitation trend is not completely linked to the ecosystem own properties: when the ecosystems are ranked by their increasing SSP, their covariate coefficient expressing the link to the worldwide trend do not express a particular pattern in terms of efficiency (Figure 15). The same remark can be made for the SST covariate. The importance of the second fluctuating trend in the DFA model (Appendix VIII) for Asian LMEs and the last generally increasing trend for Australian LMEs gives rise to complementary exploratory analysis on the reason of these similar geographical ECI trends (Appendix IX).

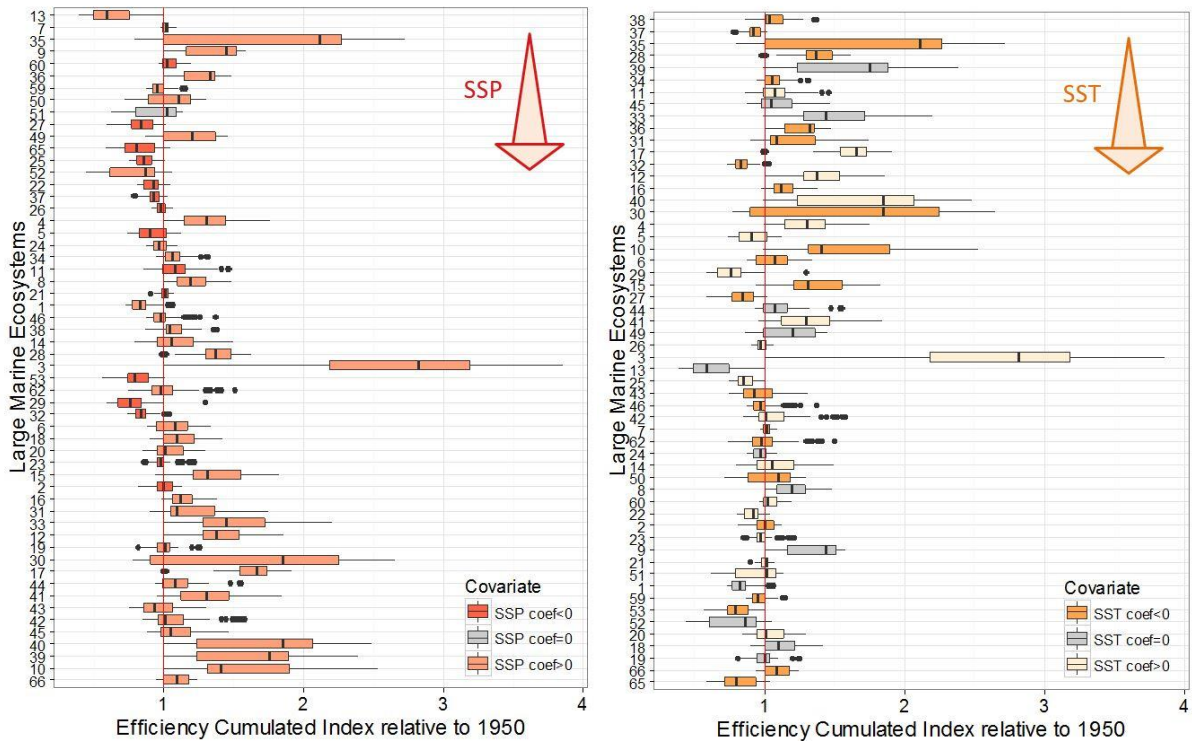


Figure 15: ECI relative to 1950 for the 56 LMEs with their covariate coefficient in colors from the DFA with two covariates and 4 trends – Left: Stock Status Plot covariate, LMEs ranked by increasing SSP value (mean on 2000-2010) – Right: Sea Surface Temperature covariate, LMEs ranked by increasing SST variation (mean on 2000-2010)

A majority of LMEs with a positive relationship of ECI to the worldwide fishing pressure trend
 An important impact of climate variability and fishing index on the efficiency trends
 The LMEs with the highest increase in stresses does show a particular pattern in ECI and covariate coefficient from the model – Need for a further exploration of the patterns

3.3 Efficiency Time Cumulated Indices correlation to ecosystem stresses covariates

3.3.1 Efficiency response to the ecosystem fishing and climate pressures

This analysis using a PCA was conducted on 55 LMEs only because the California Current was very isolated with high positive coordinates on the first axis of the PCA and was considered as a separate cluster. The factor map with the repartition of the LMEs (Figure 16) clearly shows that the ecosystems positively correlated to the first dimension are LMEs with increasing ECI (Insular Pacific-Hawaiian, Caribbean Sea, North Brazil Shelf...) and the ecosystems negatively correlated to the first dimension are ecosystems with a decreasing ECI (Aleutian Islands, Humboldt Current, Sea of Okhotsk, West Bering Sea...).

A shift of the year variables on the Dimension 2 shows an evolution pattern (Appendix VII) in the 70s. While the Dimension 1 in the PCA catches a high rate of inertia (65.95%) based on the LMEs signal, some supplementary variables are linked to this dimension (Appendix VII).

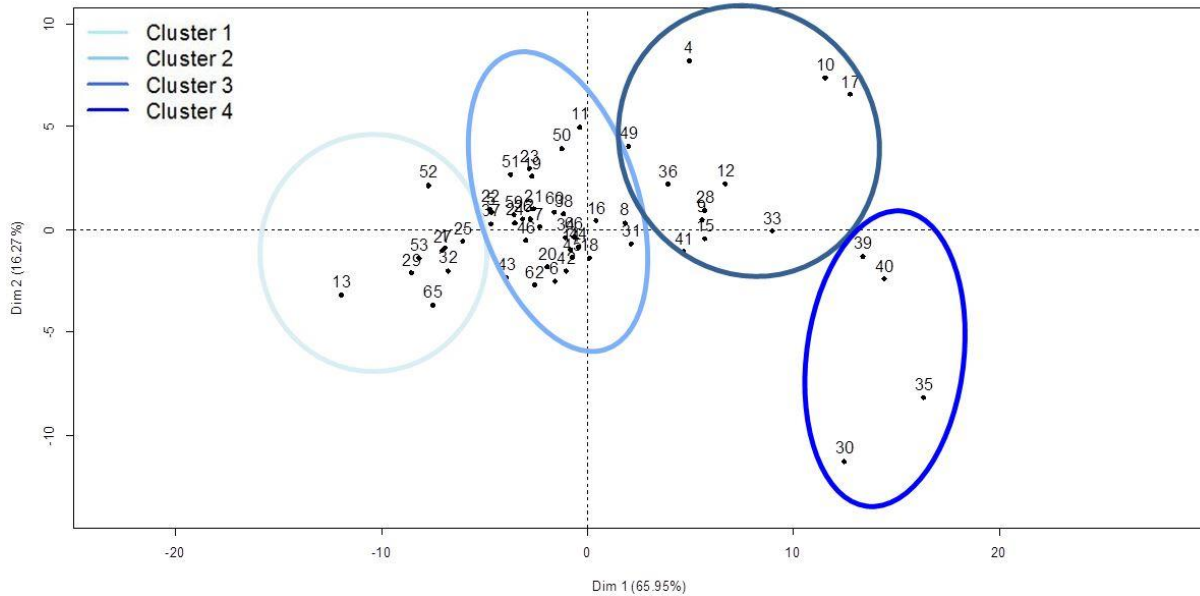


Figure 16 : Factor map from the Principle Component Analysis with the two first dimensions and the 3 Clusters from the Ascending Hierarchical Classification for the Efficiency Cumulated Index

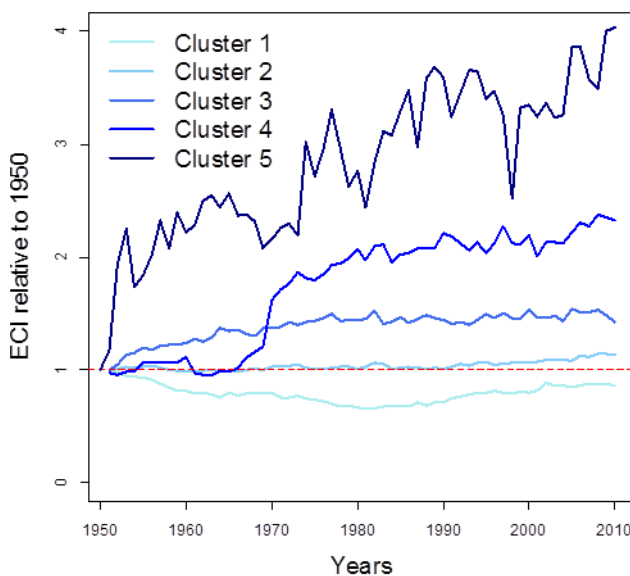


Figure 17 : Mean trends of the ECI relative to 1950 on the time-series for each Cluster resulting from the AHC

As we could expect from the PCA results, the AHC clusters correspond to the decreasing and increasing LMEs trends (Figure 17). The Cluster 1 represents the decreasing ECI LMEs, as the ones that become less efficient with time. The Cluster 2 includes ecosystems with a stable ECI. From the Cluster 3, the efficiency is increasing and following various shapes. The Cluster 3 and 4 are two groups increasing at various rates (until 1.5 the value of 1950 for Cluster 3 and up to 2 times the value of 1950 for Cluster 4). In the Cluster 4, LMEs are increasing starting in the 70s, illustrating the years shift in the PCA, dimension 2 (Appendix VIII). The Cluster 5 represents the California Current, highly increasing.

From AHC, ecosystems highlighting a decreasing efficiency (Cluster 1) can be characterized by a large fishing pressure (no LMEs with a low L_{index} and PPR/PP). 77% of the ecosystems in this cluster present a stock status plot in 2000-2010 between 25 and 50%, indicating a high percentage of overexploited and collapsed fish stocks (Table 4). Furthermore, this Cluster 1 is also characterized by an increasing proportion of fish species in the catches. On the opposite, all the LMEs in Cluster 4 include a high proportion of shrimp species (proportion between 5 and 40%).

Table 4 : Main results from the AHC on the 55 LMEs characterizing the ECI trends cluster - $p.value < 0.05$ ‘**’, $p.value < 0.01$ ‘***’, $p.value < 0.001$ ‘****’

Number of Cluster	Type of trend	Number of LMEs	Main significant modalities of the qualitative supplementary variables	% of LMEs concerned in the Cluster 1	p.value
1	↘	9	Upwelling ecosystems	33.33%	0.0032 **
			High mean SSP	77.78%	0.0329 *
			PPR/PP < 10%	0%	0.0111 *
			Proportion of fish species > 90%	88.89%	0.0039 **
			Proportion of fish species stagnating	66.67%	0.0299 *
2	→	32	LMEs with a high SSP on 2000-2010	29.03%	0.0161 *
3	↗	11	Tropical ecosystems	90.91%	0.0022 **
			Temperate ecosystems	0%	0.0357 *
4	↗	4	High proportion of shrimps > 5%	100%	0.0040 **
			Low recent L_{index}	75%	0.0496 *

The Cluster 1 demonstrates LMEs with a high fishing pressure (SSP, PPR/PP, L_{index} Figure 18 (c), (d), (e)) that stagnated over time (PPR/PP, L_{index}). The proportion of fish species is high and constant, on the opposite of low proportions of cephalopods and shrimps (Figure 18 (f)). The similarity between the Cluster 1 ecosystems means climatic trends and the worldwide trend do not highlight a particular effect of climate change on the ecosystem ECI.

Only covariates for whose the trend in the Cluster 1 differs from the worldwide trend are presented here

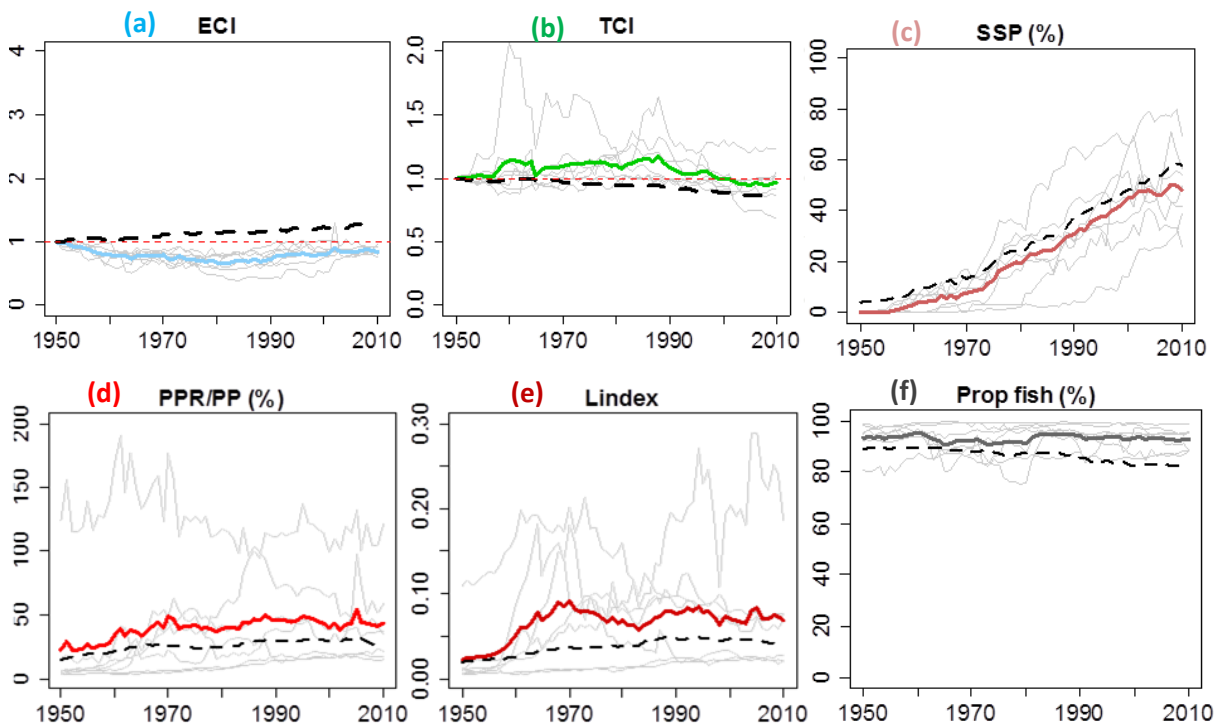


Figure 18 : Graphs of covariate trends for LMEs in the Cluster 1 from the AHC on 1950-2010 – on each graph, the dashed line is the worldwide trend, the plane colored line is the mean Cluster 1 trend and the grey lines are the individual LME trends (a) Efficiency Cumulated Index (ECI) trends for the Cluster 1 (b) Time Cumulated Index (TCI) trends (c) Stock Status Plot, % of overexploited and collapsed stocks (d) PPR/PP fishing pressure index in % (e) L_{index} loss of secondary production and (f) Proportion of fish species (%)

These results suggest two conclusions: ecosystems with a decreasing ECI are characterized by an important fishing activity, according to several fishing pressure indices. However, all LMEs with an intense fishing pressure do not systematically exhibit a decreasing ECI.

Dimension 1 in the PCA from decreasing to increasing ECI
 The decreasing LMEs (Cluster 1) are characterized by a large fishing pressure
 Stable proportion of fish species in the Cluster 1 - No apparent effect of SST

3.3.2 Time index response to the ecosystem fishing pressure and climate

Just as for the ECI, 70.95% of the inertia is expressed through the Dimension 1 of the PCA. The LMEs with positive Dimension 1 coordinates such as Aleutian Islands, East Bering Sea, Sea of Okhotsk and the Gulf of Alaska are LMEs increasing in the TCI. LMEs with negative Dimension 1 coordinates are ecosystems with a decreasing TCI such as the California Current, North Australian Shelf, Barents Sea, and the Norwegian Sea (Figure 19). The Dimension 1 is correlated to several supplementary variables (Appendix VII).

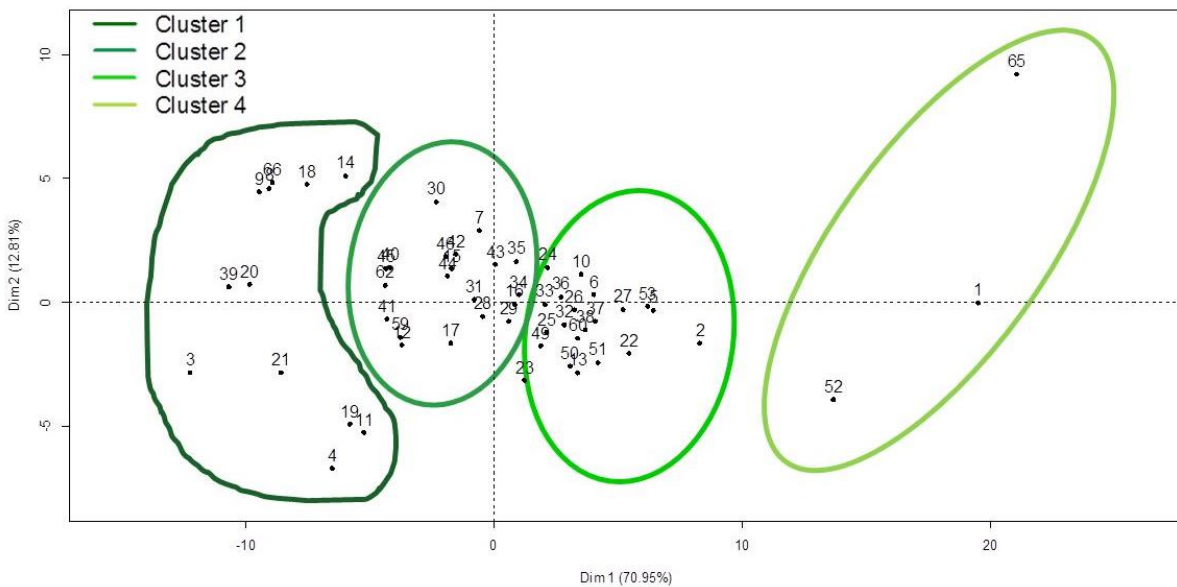


Figure 19 : Factor map from the Principle Component Analysis with the two first dimensions and the 4 Clusters from the AHC for the TCI

From the AHC, the first cluster (Figure 20) is characterized by a decreasing fishing pressure (Table 5) a high number of overexploited or collapsed stocks and a dropping mean trophic level. For 75% of the ecosystems in this Cluster, the proportion of cephalopods is low (between 0 and 1% and stable). 50% of them are polar ecosystems globally characterized by slow transfers. Concerning the second cluster, the ecosystems are clearly characterized by a low fishing pressure (PPR/PP, L_{index}) for more than 50% of the ecosystems in the cluster. The MTL is

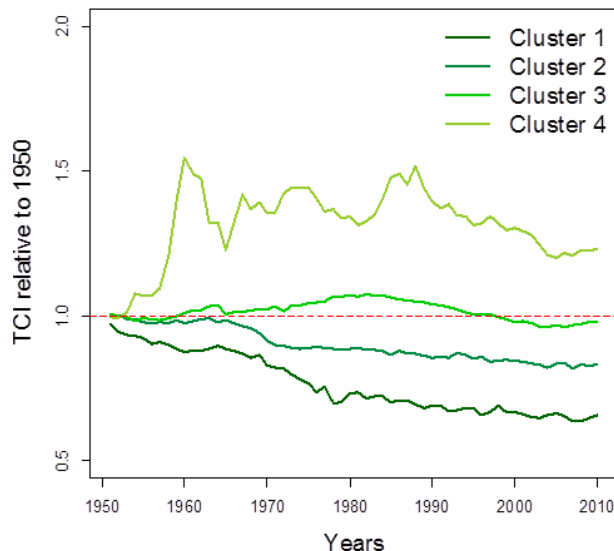


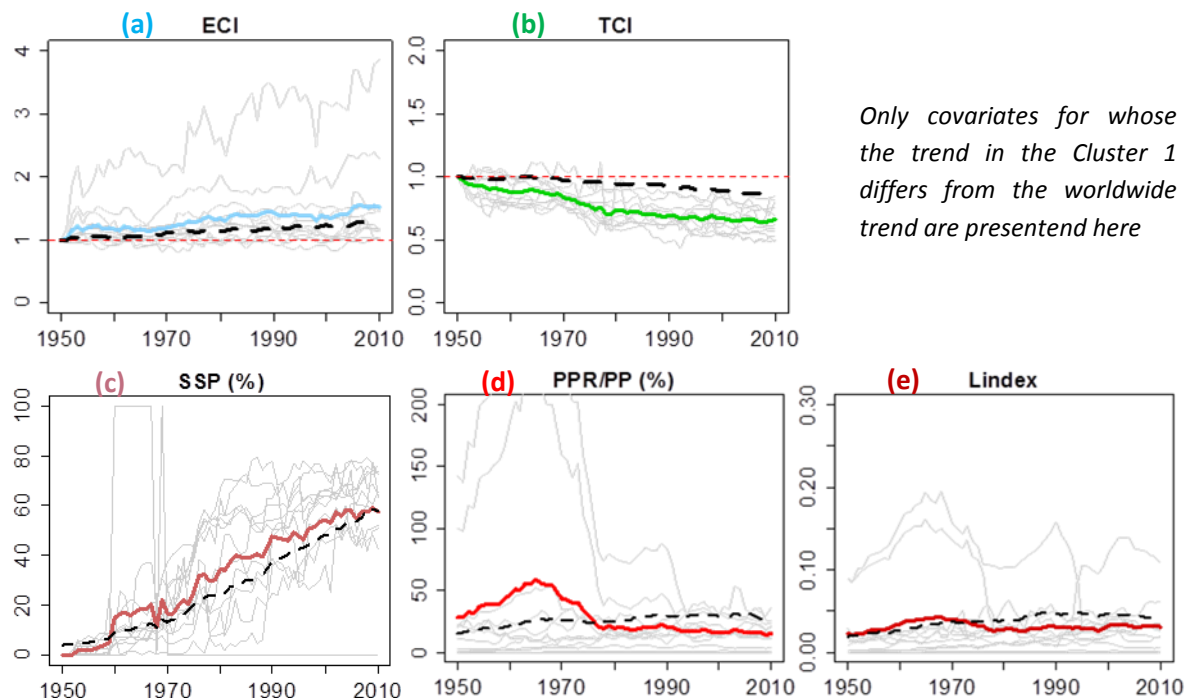
Figure 20 : Mean trends of the TCI relative to 1950 on the time-series per Cluster from the AHC

stable for 75% of the LMEs and 70% of the ecosystems are tropical. The Cluster 3 presents a stable trend and a high L_{index} .

Table 5 : Main results from the AHC on the 56 LMEs characterizing the clusters, complete results in Appendix VII
 - $p.value < 0.05$ ‘*’, $p.value < 0.01$ ‘**’, $p.value < 0.001$ ‘***’

Number of Cluster	Trend	Number of LMEs	Main significant modalities of the qualitative supplementary variables	% of concerned LMEs	p.value
1	↘	12	FIB decrease	33%	0.0013 **
			MTL decrease	83.33%	0.0032 **
			Recent mean PPR/PP: 10-25%	50%	0.0399 *
			Polar ecosystems	50%	0.0150 *
			Proportion of cephalopods 1-5%	16.67%	0.0229 *
2	↘	20	Mean PPR/PP <10%	65.00%	0.0010***
			MTL stable	75.00%	0.0114 *
			Proportion of cephalopods 1-5%	65.00%	0.0448 *
			Tropical ecosystems	70.00%	0.0183 *
3	→	21	Very high recent mean L_{index}	61.90%	0.0023 **
			SST increase >0.7°C	63.64%	0.0495 *
4	↗	3	Polar ecosystems	100.00%	0.0079 **

These covariates in the Cluster 1 emphasize again a high fishing pressure on the ecosystems, but also a decreasing Mean Trophic Level and a stagnating Fishing in Balance (Figure 21, (f) and (g)). Here major variations in the species proportions are noticeable: a reduction in fish species, a development of cephalopods and shrimps, possibly justifying the faster biomass flow speeds (Figure 21, (h), (i) and (j)). As for the ECI, climatic trends in the Cluster1 put in light that no particular trend in the Cluster is observable compared to the worldwide trend.



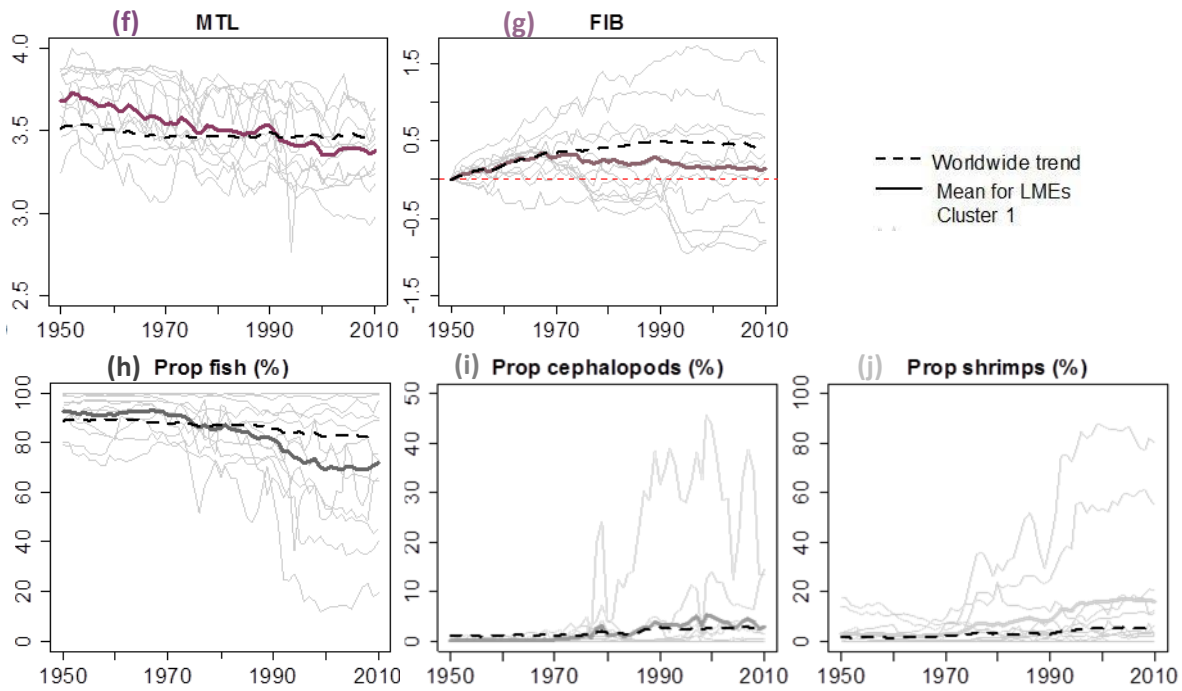


Figure 21 : Graphs of covariate trends for LMEs in the Cluster 1 from the AHC on 1950-2010 – on each graph, the dashed line is the worldwide trend, the plane colored line is the mean Cluster 1 trend and the grey lines are the individual LME trends (a) ECI trends (b) TCI trends (c) Stock Status Plot, % of overexploited and collapsed stocks (d) PPR/PP fishing pressure index in % (e) L_{index} loss of secondary production (f) Mean Trophic Level (g) Fishing in Balance index (h) Proportion of fish species (%) (i) Proportion of cephalopod species (%) (j) Proportion of shrimp species (%)

Faster transfers up the food web described by the Dimension 1 in the PCA
 Polar and North American ecosystems with a decreasing
 mean trophic level and faster biomass transfers
 Selection of short living species in the fisheries inducing faster transfers

3.4 Exploration of the relationship between the efficiency and the time index

The PCA on the ECI indicates that the ECI and the TCI are evolving on the opposite way: when the efficiency index ECI increases, the TCI tends to decrease, thus reflecting faster transfers (Figure 22). This result is not coherent to the research hypothesis as expected. Indeed, for a loss in efficiency, the time is expected to shorten, accelerating the speed of biomass flow. However, the addition of the TCI as a supplementary variable in the ECI PCA shows more ecosystems with a decreasing efficiency and an increasing TCI (33%). The TCI, as a relative value, is the best quantitative supplementary variable that best describing the Dimension1 as negatively correlated (-0.432, $p\text{-value}=9.69.10^{-4}$). The correlation coefficient between the two indices is indicating a negative but not perfect correlation as it is not close to 1. This relationship has been investigated even more with linear models and adjustment through *nls* but considering the bad quality of the residuals, the results will not be presented.

This is indicating that the ECI does not seem to react in the expected way: a majority of Large Marine Ecosystems are more efficient. However, the time index global decrease (faster biomass transfers) responds correctly to our research hypothesis: the majority of ecosystems present faster speeds of biomass flow.

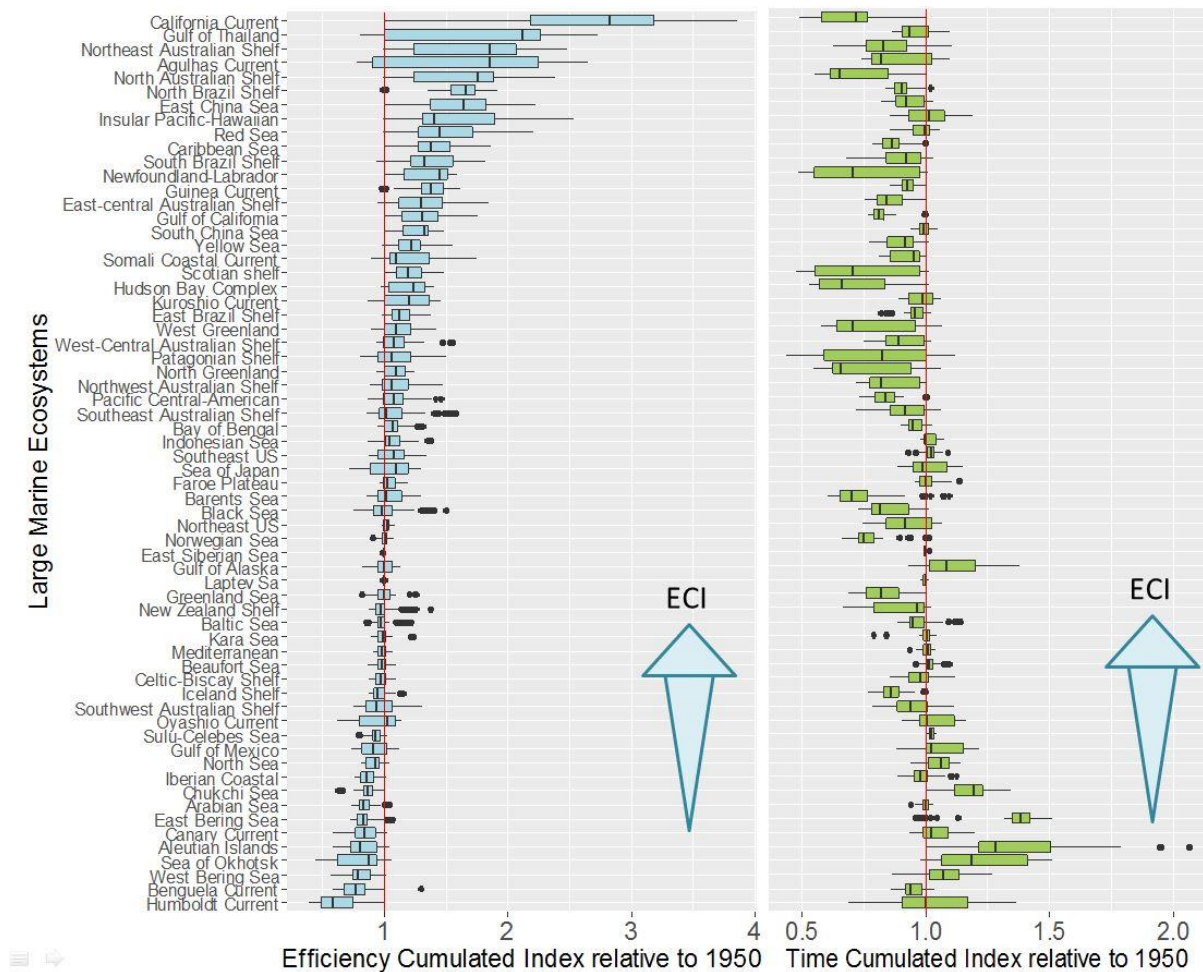


Figure 22 : Boxplots of the Large Marine Ecosystems ECI (left) and TCI (right) values relative to 1950 – the red line indicates the value 1, as the limit between a decreasing (below 1) and an increasing index (above 1) – the arrow indicates that LMEs are sorted by increasing ECI mean of all values on the times series

4. Discussion

4.1 A large meta-analysis to explore the productivity and stability of marine ecosystems

Exploring the biomass flow with the indices ECI and TCI is useful to understand the consequences of human impacts on the global functioning of marine ecosystems. The fact that there is a high removal of species – whatever the trophic class concerned – can importantly influence the indices, due to their integrative construction. As well, it is useful to picture the species composition through time. If one species finds its abundance decreasing, the importance of the other species at the same level will impact more the functioning and it will be captured in the index temporal variations.

The construction of both indices, after several tests aiming to capture the change in the TE and speed of flows, conducted us to choose ECI and TCI for several reasons: the need of community level approach to study energy flows and functioning (Rombouts et al., 2013), their integrative construction useful for analyzing the food web structure and their sensitivity to the change in the ecosystem (Noss, 1990).

Our results showed that the Large Marine Ecosystems tend to be more efficient in high latitudes and less efficient on low latitudes, which is expected from the trophic transfer

efficiency theory and calculation (Coll et al., 2008; Libralato et al., 2008). As well, the most efficient ecosystems, in term of transfer efficiency, are also demonstrating slow transfers and thus long time of biomass residence in the food web. This ambivalence is due to temperature, explaining that polar ecosystems generate rapid biomass transfers compared to tropical ecosystems (Schramski et al., 2015; Christensen et al., 1993). These reassuring results confirm that our index gives output close to other studies and assumptions.

The Efficiency Cumulated Index reflects, at least partially, the productivity of the ecosystem through the calculated ratio. Indeed, the transfer efficiency is strongly linked to the productivity of the food web, cumulated level by level (Lindeman, 1942). Our index captures the decreasing efficiency rate with rising trophic level in the food web, as the loss by respiration increase (Christensen et al., 1993; Lindeman, 1942). The index, from its cumulated nature, quantifies the rate of potential available energy for high trophic-level species. This is determinant to assess the productivity potential of ecosystems and of top-predators in marine ecosystems (Irigoien et al., 2014).

The Time Cumulated Index is assumed to be a factor of stability of the ecosystem. However, the link between the speed of biomass flows and the stability does not capture the whole ecosystem stability concept, as disrupted ecosystems can move forward to stable and unstable systems for a level of complexity (Kondoh, 2005). If an ecosystem has a time index that decreases drastically (faster biomass transfers), it can be considered as less complex and less mature, as the species assemblages are expected to be simplified (Gascuel et al., 2008). Here, we will consider that complexity and the high number of trophic links in the system brings stability: the loss of complexity can be linked to a less stabilized system (Polis, 1998). Stress is increasing natural instability by making the ecosystem facing potential harder conditions over long periods of time. The change in the speed of flow can be considered as a factor of stability/instability of the system changing from one trophic structure (that can be complex, characterized by slow biomass flow transfers) to another one, which is susceptible to be less complex (and may be characterized by faster biomass flow transfers and a different stability) (Gascuel et al., 2008). "Systems with greater (dynamic) complexity may permit species composition to remain unchanged when comparable simple models would predict species losses" (Pimm, 1984). The TCI constitutes one way to explore a part of the ecosystem stability/complexity concept, analyzing an emergent property (the speed of flow at a given trophic level) of species assemblages.

"Species-rich communities showed reduced variation in aggregate biomass (higher community stability) under a range of environmental conditions, including stress and disturbance" (Worm and Duffy, 2003). In a situation in which the stress duration and intensity is high, the change in the ecosystem functioning through these two indices express the change to a different system. As a result, the food web functioning properties are modified.

4.2 Pitfalls and potential improvements

In this study, some limits in the data and selective choice led to several sensitivity analyses, in order to evaluate the quality of the index results. For this reason, some points are questionable and improvable. As it has been tested on the North Sea ecosystem (Appendix II, Fig.1), the use of catch data does not reflect completely the changes in the ecosystem.

The fact that catch does not reflect abundance is an important debate in fisheries science (Pauly et al., 2013). However, its use to identify the major species in the food web at a worldwide scale and build the functioning indices weighted by their catch volume is necessary here and might reflect major changes (Heath, 2005), at least at the intermediate and high trophic levels. To build a complete food web meta-analysis on efficiency and speed of flows, all of the unfished species would have to be included. Phytoplankton is initiating all the biomass flow dynamics and bottom-up forcing in the ecosystem productivity (Mcowen et al., 2015). Because primary production in marine ecosystems is expected to be impacted by ocean warming (Sarmiento et al., 2004), it is essential to consider its implication in the ecosystem functioning to create future scenarios.

Concerning the assumption that catches are reflecting well the accessible biomass part in the ecosystem, species such as jellyfish or some cephalopods are problematic. Not all countries fish macro gelatinous species (but they are present in Asian ecosystems for example). However, they seem to influence food web functioning importantly (Robinson et al., 2014, 2015). In particular, macro gelatinous species influence strongly the ecosystem functioning, especially by competing with forage fish species (Robinson et al., 2014). With climate change and fishing, jellyfish populations expand in some LMEs (Brotz et al., 2012) and their sudden development and blooms can drive ecosystem shifts (Daskalov et al., 2007; Kirby et al., 2009). This species have a very important impact on the food web functioning: they can induce less efficient energy transfers and they are also considered as 'trophic dead-end species' (Robinson et al., 2015).

From the various sensitivity analyses developed in the study, one must be particularly discussed. The choice of the natural mortality equation has a significant impact on the indices results (Appendix II, Fig.3 and 4). The choice of the reference equation has been conducted with several tests and explorations. Indeed, the mostly used natural mortality formula is the one from Pauly, 1980, but has not been fitted for polar ecosystems for example and is more focused on tropical ones. It generates issues for calculation with negative temperature values. On the other hand, the Gislason natural mortality equation (Gislason et al., 2010) tends to be very dependent on the 'Common Length' parameter but is the less precise parameter estimated.

4.3 Evidence and causes for the variable ecosystem functioning

4.3.1 Consequent changes in the species assemblages

The six LMEs for which we studied the change in the species composition tend to present various fishing exploitation histories since 1950. The California Current, the Canary Current and the Humboldt Current are specific ecosystems, as they are upwelling areas largely driven by climate conditions. The North Sea showed some major changes at various trophic classes, where the fishing pressure is intense since the 50s and led to overexploitation of species such as *Gadus Morhua* (Cook et al., 1997). The Sea of Japan proves to be driven by small pelagic species. The Gulf of Mexico is also a highly fished ecosystem but where the catches are concentrated on low trophic levels. This ecosystem is influenced by the Gulf Menhaden catches (Robinson et al., 2015). The type of the ecosystem is likely to elucidate the high scale changes for the upwelling areas compared to the other three ecosystems, with less intense variations. Because of the strong bottom-up controls of the upwelling ecosystems driven by the primary productivity changes (Chavez, 2003), a high and intense

fishing activity will have less influence on the functioning of the ecosystem. However, on more enclosed and naturally less productive ecosystems as the Gulf of Mexico and the North Sea, fishing activities and climate change can drive major ecosystem changes (Perry et al., 2005; Robinson et al., 2015). The impact of climate change might be different depending on the ecosystems: rapid warming is observed for the North Sea and the Sea of Japan (Belkin, 2009). Climate change and fishing pressures are structuring the food web in the North Sea (Heath, 2005). All of these studied ecosystems, except the Canary Current, have been intensively overexploited since the 50s and showed low sustainability in the fisheries (Coll et al., 2008). However, they do not show the same variation patterns in terms of ECI and TCI.

Another possible line of thought is that in 4 of the 6 Large Marine Ecosystems, cephalopod species are growing in the catches (mainly octopuses and squids). Cephalopods fisheries are more or less developed depending on LMEs. For countries such as Japan, this fishery is of high importance (Bower and Ichii, 2005). The cephalopods' influence on the ecosystem cannot be neglected, because of their high efficiency and speed. Then, a small variation on the proportion in the catches can influence highly the indices. For example, in the Humboldt Current, even if the ecosystem expresses different regimes caused by the environment and ENSO events (Alheit and Niquen, 2004), the Jumbo flying squid (*Dosidicus gigas*) has a high influence on the ecosystem. This species development in this area is linked to climate change and to the declining abundance of competitors such as tunas (Alegre et al., 2014; Zeidberg and Robison, 2007). Once settled in its environment, *Dosidicus gigas* shows as variable diet and different adaptive strategies in face to changing environmental conditions (Tafur et al., 2010). Because of their high adaptability conditions, cephalopods may influence several ecosystems since their abundance is globally increasing (Doubleday et al., 2016).

4.3.2 Is the LME functioning driven by human-induced impacts?

- Impact of fishing pressure since 1950

The global fishing pressure has largely risen worldwide, but affects differently marine ecosystems through various fisheries histories (Worm et al., 2009). Defining a measure at the ecosystem scale remains challenging. Indeed, each fishing index we used reflects differently the fishing pressure in the ecosystem (Table 6). The combination of fishing indices is necessary to confront effects (Rombouts et al., 2013). Their variable trends (Appendix V, Fig.2 to 7) are expected (Cury et al., 2005)

As the percentage of overexploited and collapsed stocks is increasing almost for all ecosystems since 1950, the other indices are reacting differently for ecosystems (Appendix V, Fig.2 to 7). For example, in the North Sea, PPR/PP and L_{index} capture the decreasing fishing pressure on the recent years. The mean trophic level is more related to the fished species position in the food web (Table 6). As a result, it has various trends unrelated to the other indices and measures qualitative changes in fisheries more than an overall fishing pressure at ecosystem scale (Branch et al., 2010). Nevertheless, in order to detect 'fishing down the marine food webs' effects, a combined analysis of the mean trophic level and the Fishing In Balance is necessary (Christensen, 2000). This way, it distinguishes fishing effects on the food webs and development of fisheries through variable fisheries strategies. The loss of production L_{index} quantifies the impact of fishing removal on the food web, whereas PPR/PP is focused on quantifying the equivalent of primary production used in the ecosystem (Coll et al., 2008).

Table 6 : Synthesis of the fishing pressure measure and ecological explanations linked to the indices

Type of fishing pressure measure	Ecological meaning
Mean Trophic Level MTL	Mean level of the catches in the food web
Fishing in Balance FIB	Amount of Primary Production necessary to ensure the fishing production compared to the reference scale (i.e. a given year). FIB measures if losses in predator catches are compensated by preys catches equivalent to the predation release
Stock Status Plot (% of number of stocks overexploited and collapsed) SSP	Extent of the overexploitation and collapse in the ecosystem
Primary Production Required for fisheries (PPR/PP %)	Part of the primary production used to ensure the feeding (through the food web) and thus the production of all catches (fishing high TLs implies large PPR)
Loss of secondary production L_{index}	Index quantifying the cumulated loss in the food web caused by fisheries (inducing losses of predators when preys are fished; fishing low TLs implies large Lindex)

The main idea from the fishing pressure influence and correlation on the Large Marine Ecosystems is that L_{index} and PPR/PP tend to express an important fishing activity on the ecosystems with a loss of productivity, for which we expected an induced-impact from fisheries. On the opposite, faster kinetics are observed for a high fishing pressure (with a high proportion of stocks overexploited and collapsed and a significant PPR/PP). The impact of the mean trophic level might explain some part of the trends since low-trophic level species might induce faster kinetics and a shorter TCI in the food web.

- Impact of climate change

Even though the ocean warming is already detectable largely on ecosystems and has various influences (Belkin, 2009), the impact of an increasing sea surface temperature is not as clear as the fishing impact in our results. This can be explained by the fact that climate change and especially SST raise has indirect effects on the ecosystem functioning since the 70s-80s. Indeed, through climate change, the catch potential is changing, affecting the fishing activities through species migration, for example. Furthermore, the SST is influencing the parameters in the basis equations used in this study (equations (1) and (3)), such as the temperature and the Von Bertalanffy growth parameters. A high increase in the SST (>0.7°C) is observed for some increasing ECI ecosystems, not concordant with the hypothesis that ocean warming might induce a decrease in transfer efficiencies and thus a lower productivity on tropical ecosystems. Nevertheless, the worldwide increasing sea temperature trend has an important influence, that we were able to show through the Dynamic Factor Analysis. SST is often linked to SSP variable, which can put in light a common impact of climate change and fisheries (Kirby et al., 2009). The efficiency might be reduced in the food web with an increasing SST in tropical areas. The fact that it will grow in the coming years will also lead to restructuration of the food web and a decline in the fish production potential (Jennings et al., 2002). On the opposite, high-latitude areas gain in fish production, through marine species migrations searching for their preference habitat (Cheung et al., 2010). The impact of climate change is also linked to fisheries production and influences the catches, increasing in high latitudes and decreasing in lower latitudes (Cheung et al., 2013). Those changes influence the food web greatly.

- Conclusions on the drivers effect

From the Dynamic Factor Analysis, the relationships to the worldwide trend in terms of fishing pressure and climate change are demonstrating an effect on the transfer efficiencies and on ecosystem productivity (Table 7). The relationship with the covariate is not always the

one expected. We would expect a negative relationship between the ECI index and the two drivers, the fishing pressure or the sea surface temperature. However, this DFA model reflects more that all LMEs are greatly influenced by the covariates from their significant coefficients. It shows the variability among all ecosystems. It is a reminder that each ecosystem is reacting differently to stresses, due to their nature and specific food web structures. The fishing index is likely to have more impact than the SST covariate on a majority of ecosystems. All LMEs with an increasing efficiency index tend to be positively impacted by overexploitation, meaning that fisheries would enhance the productivity of ecosystems (Figure 15). This conclusion is not valid for the temperature, influencing various patterns depending on ecosystems.

From the PCA, losses in productivity are shown in several ecosystems, which are characterized by a large fishing pressure from several fishing indices. Conversely, a parallel analysis on the 10 most exploited ecosystems of the world tend to prove that they are not all characterized by a decrease in the cumulated transfer efficiency (Appendix X). Then, we were not able to demonstrate that an intense fishing activity necessarily leads to productivity losses in all ecosystems. However, the analysis of the supplementary variables reveals that such a loss in productivity is detectable when there is no bias from developing crustaceans and cephalopods fisheries. This may explain the global apparent increase in transfer efficiency. In other words, biases linked to changes which have occurred in fishing strategies might explain, at least partially, why we did not observe in the catch the trends we expected at the scale of the ecosystem's biomass. In addition, our ECI index only considers transfer losses due to respiration (and secondarily to excretion; see Figure 5), but it does not take into account changes in the mean non predation mortality, which might be a significant factor of the transfer efficiency variability. A larger proportion of trophic dead-end species, a well-known effect of overexploitation, might drastically change the efficiency of the whole food web. This effect cannot be highlighted by our parameters based on catch only.

Concerning the kinetics, faster transfers are enhanced by a decrease in the mean trophic level in some ecosystems. It could emphasize a potential 'Fishing Down the Marine Food web' effect (Pauly, 1998) of the LMEs in the Cluster 1 identified by the PCA. The FIB trend, concordant with the decrease in Mean Trophic Level, is not due to developing fisheries on low trophic level. The change of fisheries strategy is still a potential explanation, through various trophic levels, as a 'Fishing Through Marine Food Web' phenomena (Essington et al., 2006). The presence of North American and North Atlantic LMEs in this Cluster 1 – demonstrating the strongest increase in speed of flows – such as the California Current, the Scotian Shelf, the Newfoundland-Labrador Shelf, the Barents Sea and the West Greenland Shelf confirm some of these interpretations. Indeed, these ecosystems have supported intense overexploitation, an important decline of predatory species (Myers and Worm, 2005), and demonstrate consistent evidence for 'Fishing Down Marine Food Web', as showed by Essington et al., 2006. The collapse of Atlantic cod in the Scotian Shelf and Newfoundland-Labrador is a strong evidence and example of a decrease in the abundance of top-predators in the ecosystem, leading to a report of fishing effort on other species. Our analysis, through the Time Cumulated Index, puts well in light the selection of short living marine species on highly exploited ecosystems.

Table 7 : Main results from the modelling and statistical methods on the Efficiency Cumulated Index and the Time Cumulated Index

Type of quantitative analysis	Main ecological conclusions
Dynamic Factor Analysis	<ul style="list-style-type: none"> • 38 ecosystems with a combined relationship to SSP and SST Evidence for an important impact from both fisheries and climate change on the ECI Fisheries are not always producing decrease in ECI
Principal Component Analysis and Ascending Hierarchical Clustering	<ul style="list-style-type: none"> • ECI: some ecosystems with a loss of productivity and an intense fishing activity • TCI: selection of short-living species through intense marine species exploitation Fishing Down Marine Food Web / Fishing Through Marine Food Webs for North Atlantic ecosystems

The effect of climate change and fishing pressure are hardly resuming all the LMEs variations. This is due to the fact that each ecosystem has its own structure, climate variability and functioning depending on the species assemblages and biophysical environment. Then, the temperature and fishing pressure variables are probably not the only drivers that would influence the efficiency and the time indices. Indeed, it can be changed by factors such as pollution, invasive species (Daskalov et al., 2007) and eutrophication (Vitousek, 1997).

4.3.3 Are these drivers leading to less productive and less stable ecosystems?

The Table 8 indicates various results on the relationship between the indices. Mainly, at the worldwide scale, LMEs food web functioning is characterized by more efficient and faster biomass flows. The most overexploited ecosystems do not systematically show a combined decreasing ECI and TCI (Appendix X, Fig.1). For a reduction of the ECI, we would expect the TCI to shorten as well. However, this relationship between the two indices has been tested in the PCA and AHC and proved to be wrong, and even the opposite.

Table 8 : Main results on the relationship between the Efficiency Cumulated Index and the Time Cumulated Index and effects on the Large Marine Ecosystems

	Increase in the Time Cumulated Index	Decrease in the Time Cumulated Index
Increase in the Efficiency Cumulated Index	+ / + 1 LME	+ / - 38 LMEs
Decrease in the Efficiency Cumulated Index	- / + 9 LMEs	- / - 8 LMEs

The analysis of the species assemblages highlights a significant transition to non-fish species such as cephalopods and crustaceans. As they are largely demonstrating high P/Q and P/B ratios, they induce an increase in the efficiency index and a decrease in the time index. They influence the ecosystem functioning to more productive and less stable ecosystems, which correspond to the main worldwide pattern (Table 8).

The very strong efficiency and high speed of flow for these species – and especially cephalopods – could justify that the ECI and TCI change in opposite ways. The LMEs with the highest increase in cephalopod proportions clearly show an increasing ECI and a decreasing TCI (Appendix X, Fig.2). The recent amplification of cephalopod proportions are caused for a part by climate change and fishing impacts (Doubleday et al., 2016). The high flexibility and plasticity of those species to various ecosystem conditions is high through their

adapting diets and high productivity (Pecl and Jackson, 2008). Nevertheless, they are sensitive to environmental variability and cooler temperatures are optimal for their development. *Dosidicus gigas*, despite its high development in the Humboldt Current, tends to show a preference for cool temperature and low productivity areas (Robinson et al., 2013). Then, cephalopods response to climate change remains uncertain, depending on the species (Pecl and Jackson, 2008). On some ecosystems, climate change scenarios suggest an increase of pelagic and demersal invertebrates (Ainsworth et al., 2011).

Another explanation was considered as the recent development of invertebrate fisheries in general (Anderson et al., 2011). If these fisheries developed but did not reflect the abundance of the marine species, this will bias our analysis, inducing an increase in ECI and a reduction of TCI.

The importance of the small pelagic fisheries in many ecosystems is driving both indices temporal variations, such as for upwelling, Asian LMEs and some Australian ecosystems. Indeed, even if some changes happen at several trophic classes in species assemblages, because the main catches are produced by small pelagic species, the spectrum is strongly driven by those species. As a result, it determinates the major variability in the efficiency and time indices (Appendix IX). For the Sea of Japan, *Sardinops sagax* represents up to 25% of the total catches in the ecosystem in 1988. This puts in light the importance of such species in the ecosystem functioning.

4.4 Perspectives

In the objective of exploring the totality of the variability of the transfer efficiency and the speed of flows, several options are possible. Including the population and individual variability in the equations through temperature and growth parameters variability would influence the final results. The marine populations growth (like the size) parameters are influenced by climate change for a part (Cheung et al., 2012) and by fishing activities (Shin et al., 2005). In the present research work, the parameters are considered constant along the time series in order to identify only the effects of marine community changes, which are already significant since 1950. The climatic relationship that puts in light warming consequences needs more investigation. The study of the trophic transfer efficiency might be more affected by climate change, when it is not estimated as a partial TE.

As a complementary analysis, leading the same methodology and exclude the non-fish species could be very interesting. Maybe our research hypothesis is only valid for fish species (as suggested by parameters values in Appendix V) and would demonstrate worldwide strong effects of fisheries and climate change on the fish communities functioning. However, such an analysis would be an incomplete food web approach. An exploration has been realized for the California Current (Appendix XI), and reveals a less intense trend for this LME, especially on the ECI.

It is worth noting that the scale chosen has a fundamental influence. The Large Marine Ecosystems do not include all the ecosystems, like many regions in the Indo-Pacific. For example, the units are sometimes large surface and contain several sub-systems. This is the case for the Humboldt Current, for which the upwelling area is not present on the whole West coast of South America. Another approach of ecosystem division could be explored, such as the 293 Marine Ecoregions of the World (MEOW), developed by Spalding et al., 2007. The

Humboldt Ecosystem would be divided into 7 Ecoregions. However, some other areas are similar like the North Sea ecosystem, which means that depending on the basis criteria to distinguish the ecosystems, the geographical division might differ.

This study is one of the first exploring the transfer efficiency variability and the speed of flows at a very large scale, in the objective of improving trophodynamic food web models. This work shows pretty well that considering these two theoretical parameters invariable in the models is ecologically wrong and can false the outputs, especially leading to an underestimate of the impacts of fishing on marine food webs. Even if the efficiency variability is studied as a portion of the real parameter, the two indices give strong evidence for their temporal, geographical and trophic variability.

This work could be used as well to improve indices calculation, where the trophic transfer efficiency is used a lot, like for the fishing indices (L_{index} , PPR/PP, FIB). The sensitivity analysis on the transfer efficiency values for the calculation of PPR/PP clearly showed a high sensitivity to this parameter (Appendix III, Fig.1). These pressure indices are more and more used in management planning and for biodiversity considerations (Collen and Nicholson, 2014). Therefore, their expanding use must drive a path for improved marine ecosystems assessment in terms of biodiversity, human-induced impacts and food web functioning, health and resilience of ecosystems.

In order to validate the analyzed variations in the ecosystem functioning, it would be also necessary to compare our indices results to other study and combine several functioning indicators to see if the same conclusions emerge from the data (Rombouts et al., 2013). This would add strength to the study. It would be really interesting to compare the results with other explorations of the trophic transfer efficiency or size-based transfer efficiency (Jennings et al., 2002). However, as the food webs are not structured in the same way for both approaches, it would be coherent to compare output from biomass production models. This could be the case using EcoTroph (Gascuel et al., 2005; Gascuel and Pauly, 2009) and size-based models (Jennings et al., 2002), where the trophic transfer efficiency would be variable with ecosystems, time and trophic levels.

Climate change will affect differently marine species in the coming years. For example, fast growth species are expected to respond strongly to climate change (Perry et al., 2005) and can be used as useful ecosystem response indicators (Pech and Jackson, 2008). Small pelagic species and cephalopods will possibly respond faster to environmental changing conditions, due to their life-history traits. Then, global warming consequences on the food web functioning needs further investigation, especially regarding the transfer efficiency, determinant in the productivity of marine ecosystems (Barange et al., 2014). More consideration of global warming on phytoplankton would be consistent for further research, as they affect greatly the ecosystem productivity (Barange et al., 2014). The rising climate change worldwide scenarios in oceans (Blanchard et al., 2012; Cheung et al., 2010) puts in light the need to integrate food web functioning variability to explore future changes and implications for productivity and catch potentials. Anticipation for future oceans production is essential in order to help threatened communities. Implementation of effective management remains harder in developing countries (Worm et al., 2009). Climate change might not beneficiate to developing countries communities and there is an urgent need to ensure worldwide food security (Béné et al., 2015; Golden et al., 2016).

5. Literature

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Appendix I: Large Marine Ecosystems official numbers and name, NOAA

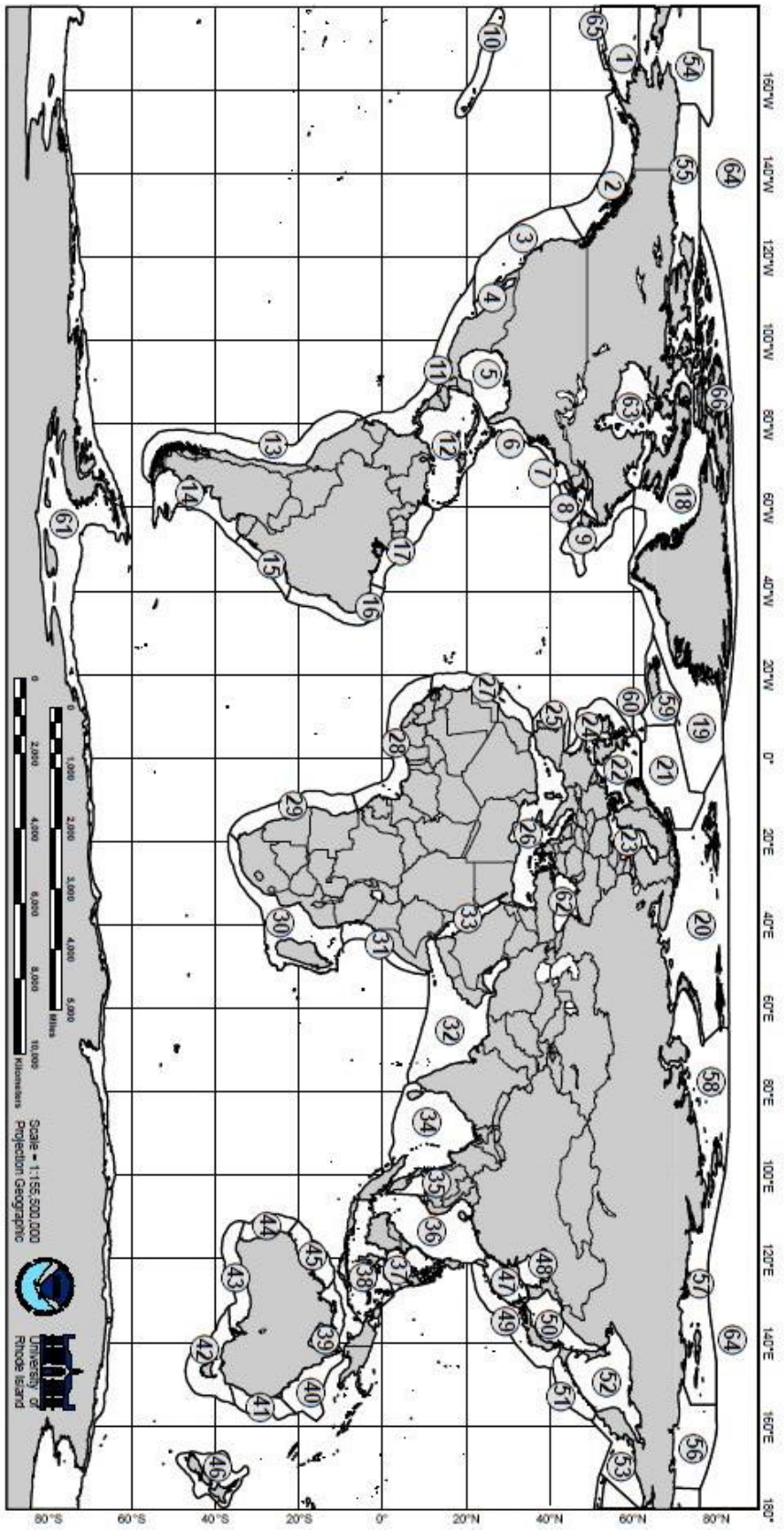
1. East Bering Sea
2. Gulf of Alaska
3. California Current
4. Gulf of California
5. Gulf of Mexico
6. Southeast U.S. Continental Shelf
7. Northeast U.S. Continental Shelf
8. Scotian Shelf
9. Newfoundland-Labrador Shelf
10. Insular Pacific-Hawaiian
11. Pacific Central-American
12. Caribbean Sea
13. Humboldt Current
14. Patagonian Shelf

15. South Brazil Shelf
16. East Brazil Shelf
17. North Brazil Shelf
18. Canadian Eastern Arctic - West Greenland
19. Greenland Sea
20. Barents Sea
21. Norwegian Sea
22. North Sea
23. Baltic Sea
24. Celtic-Biscay Shelf
25. Iberian Coastal
26. Mediterranean
27. Canary Current

28. Guinea Current
29. Benguela Current
30. Agulhas Current
31. Somali Coastal Current
32. Arabian Sea
33. Red Sea
34. Bay of Bengal
35. Gulf of Thailand
36. South China Sea
37. Sulu-Celebes Sea
38. Indonesian Sea
39. North Australian Shelf
40. Northeast Australian Shelf
41. East-Central Australian Shelf

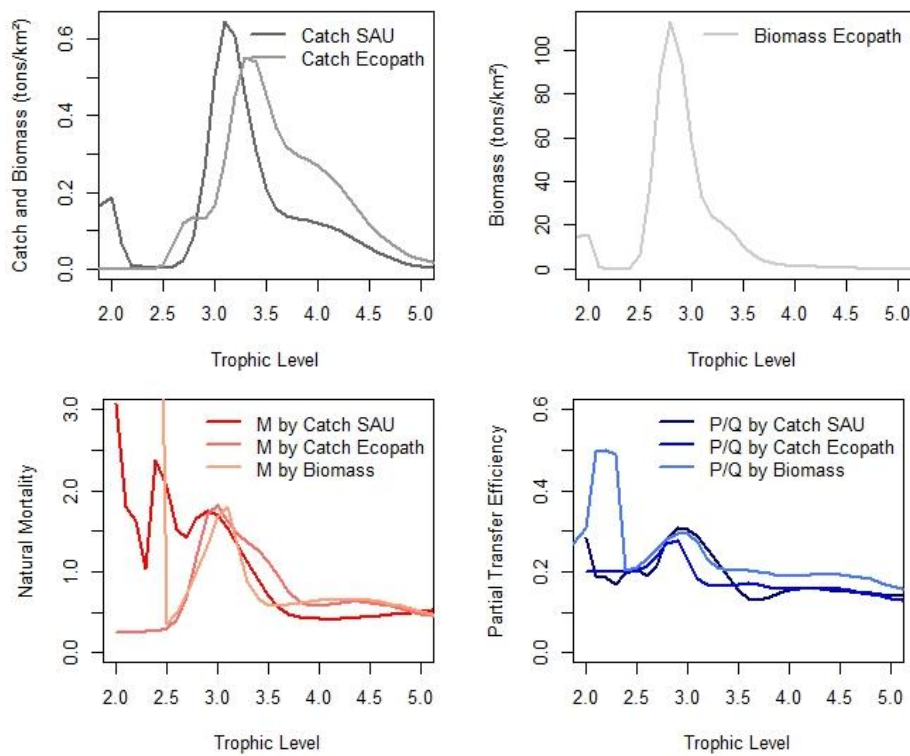
42. Southeast Australian Shelf
43. Southwest Australian Shelf
44. West-Central Australian Shelf
45. Northwest Australian Shelf
46. New Zealand Shelf
47. East China Sea
48. Yellow Sea
49. Kuroshio Current
50. Sea of Japan/East Sea
51. Oyashio Current
52. Sea of Okhotsk
53. West Bering Sea
54. Northern Bering-Chukchi Seas

55. Beaufort Sea
56. East Siberian Sea
57. Laptev Sea
58. Kara Sea
59. Iceland Shelf and Sea
60. Faroe Plateau
61. Antarctic
62. Black Sea
63. Hudson Bay Complex
64. Central Arctic Ocean
65. Aleutian Islands
66. Canadian High Arctic-North Greenland



Appendix II: Sensitivity analysis on the North Sea

Sensitivity to hypothesis concerning the catch and biomass in the ecosystem



App II, Fig. 1:

Catch SAU stands for the catch data from the Sea Around Us Project used in the study

Catch Ecopath stands for the catch data from the Ecopath model from Mackinson & Daskalov, 2007

Biomass stands for the biomass used from the Ecopath model from Mackinson & Daskalov, 2007

P/Q stands for the gross food conversion parameter, or here called the partial transfer efficiency

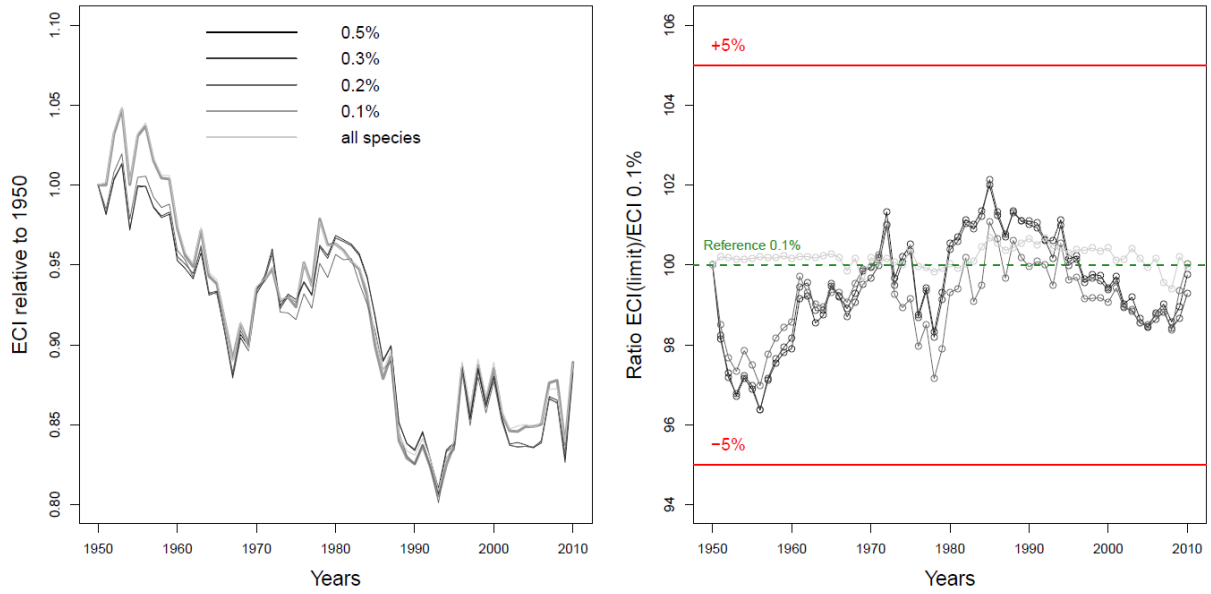
M stands for the natural mortality parameter

This sensitivity analysis on the North Sea is of great importance, showing that the spectra built with catch data is quite close to spectra from biomass data, directly traducing the abundance of species. However, this is likely to be valid only for high trophic level species from 2.5/3.0.

Sensitivity to taxonomic groups selection

A taxonomic group from the Sea Around Us database is selected if it represents at least 0.1% of the catches for the ecosystem at least one years on the time-series. Several limits have been tested and 0.1% allowed a reduction of the groups and ensure to keep at least 95% of the total catches for all ecosystems on all years.

Furthermore, the sensitivity of this choice has been tested on the index ECI (Efficiency Cumulated Index) output for the North Sea. Visually, it appears that all limits considered conduct to similar results and does not induce variations of more than +/-5% for all years.



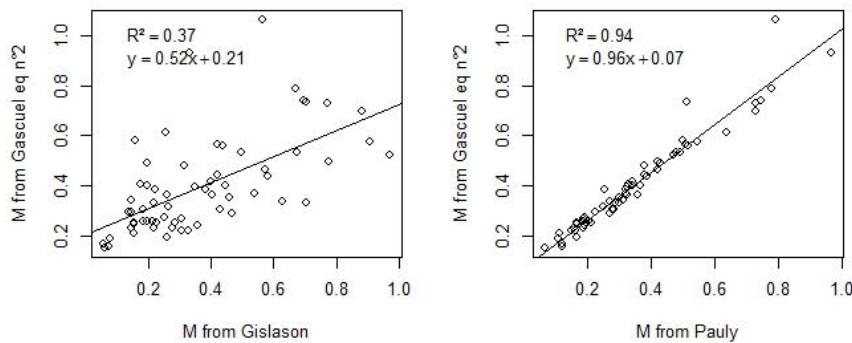
App II, Fig.2

Sensitivity to different options possible for the natural mortality empirical equation

Table with all the natural mortality equations tested *Pauly, 1980; Gislason, 2010; Gascuel et al., 2008, Gouffier in prep.*

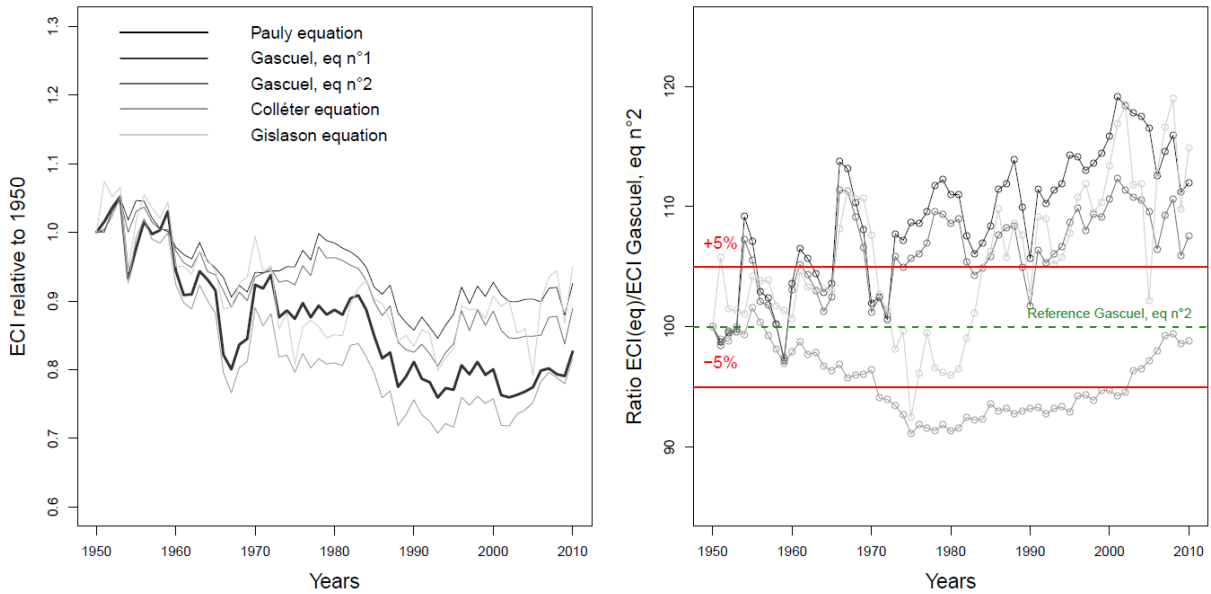
Natural mortality equation source	Equation
Pauly, 1980	$M = Linf^{0.279} \times K^{0.6543} \times T^{0.4634}$
Gislason, 2010	$\ln(M) = 0.55 - 1.61 \times \ln(L) + 1.44 \times \ln(Linf) + \ln(K)$
Gascuel, 2008 equation n°1	$\frac{P}{B} = 20,19 \times TL^{-1,72} \times e^{0,053 \times T}$
Gascuel, 2008 equation n°2	$\frac{P}{B} = 1.06 \times e^{0,018 \times T} \times K^{0.75}$
Gouffier et al., in prep.	$M = 34,36 \times TL^{-3,580} \times e^{0,024 \times SST}$

M is the natural mortality rate, *Linf* the asymptotic length from the Von Bertalanffy models (cm), *K* is the speed of growth (year⁻¹), *L* is the common length of the species (cm), *τ* is the trophic level and *T* is the mean annual temperature (°C)



App II, Fig.3

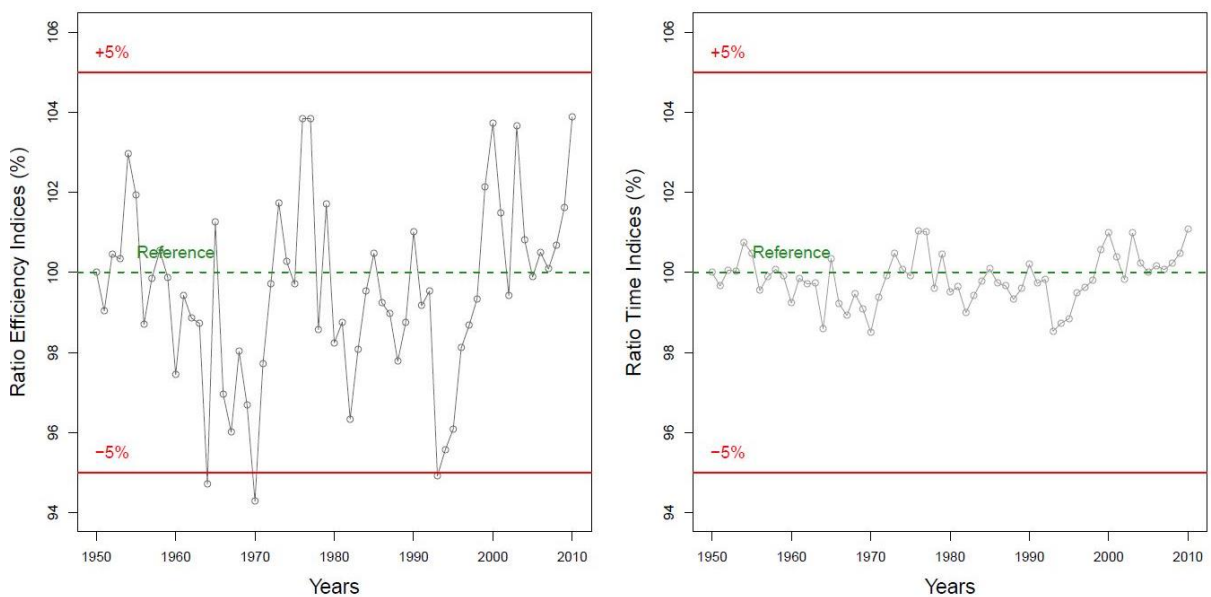
The equation of Gascuel et al., 2008, eq n°2 has been selected as a reference equation in the study. This equation is closely related to the equation from Pauly, 1980 and to the natural mortality from Gislason, 2010. Again, a sensitivity analysis was conducted on the North Sea Large Marine Ecosystem and shows that depending on the natural mortality equation chosen, the results vary in terms of final index output, as it is shown on the graphs below. The variation to the reference equation is higher than +/-5% and indicates sensitivity to that modelling choice.



App II, Fig.4

Sensitivity to the use of the temperature variability into the equations for P/B and Q/B

Another source of variability considered in the study is to put the sea surface temperature variations into the equations (1) and (3). However, this would have meant including a population variability in the study, focusing only on the community level. For the North Sea, a sensitivity to the inclusion of a varying temperature is significant for the ECI (Efficiency Cumulated Index) but not for the TCI (Time Cumulated Index). Then, this parameter influences the final data used for the statistical analysis. It was also found to have a very variable influence depending on the ecosystem chosen. Some demonstrates a much higher sensitivity to the temperature than the North Sea.



App II, Fig.5

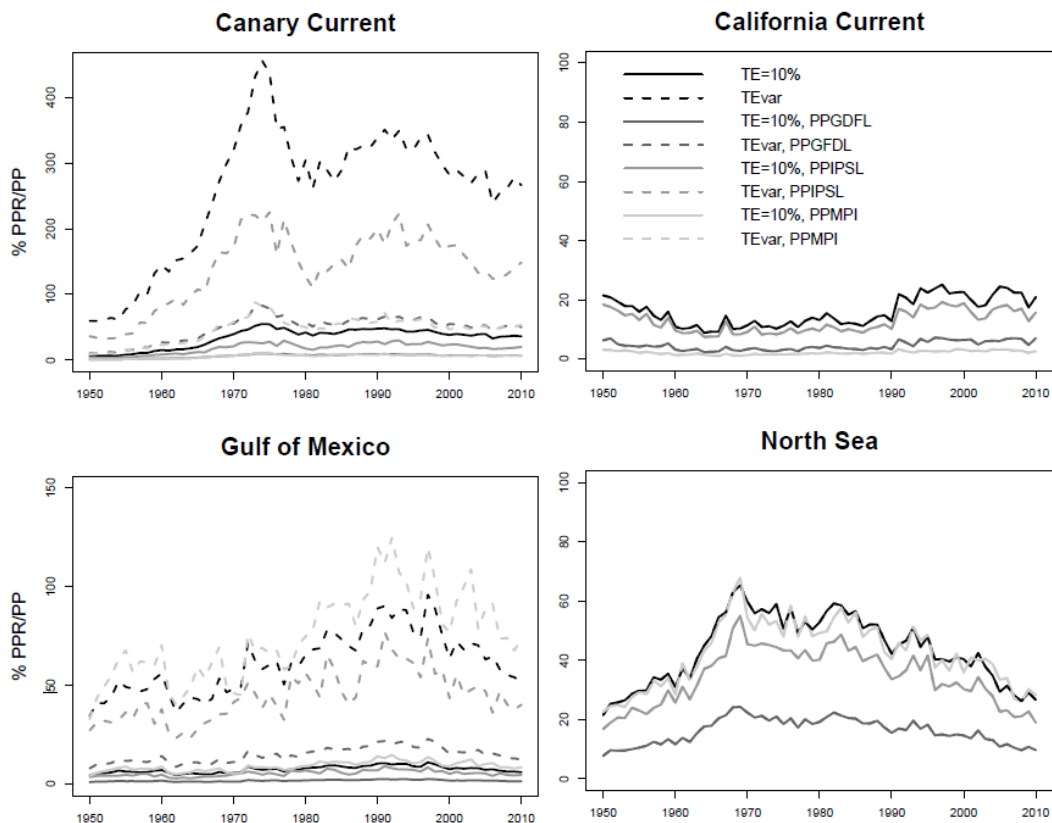
Appendix III: Sensitivity analysis on the fishing pressure calculation

A sensitivity analysis on the calculation of the Primary Production Required (index PPR/PP) for fisheries index (Christensen & Pauly, 1995) revealed necessary to justify our choice for 2 variables:

- The Trophic Transfer Efficiency, for which we do not have real values but only approximate values with the efficiency index. We considered TE=10% or variable from Chassot et al., 2010
- The primary production data from observation (Eppley) per Large Marine Ecosystem or variable coming from time-series reconstruction models (GFDL, IPSL, MPI)

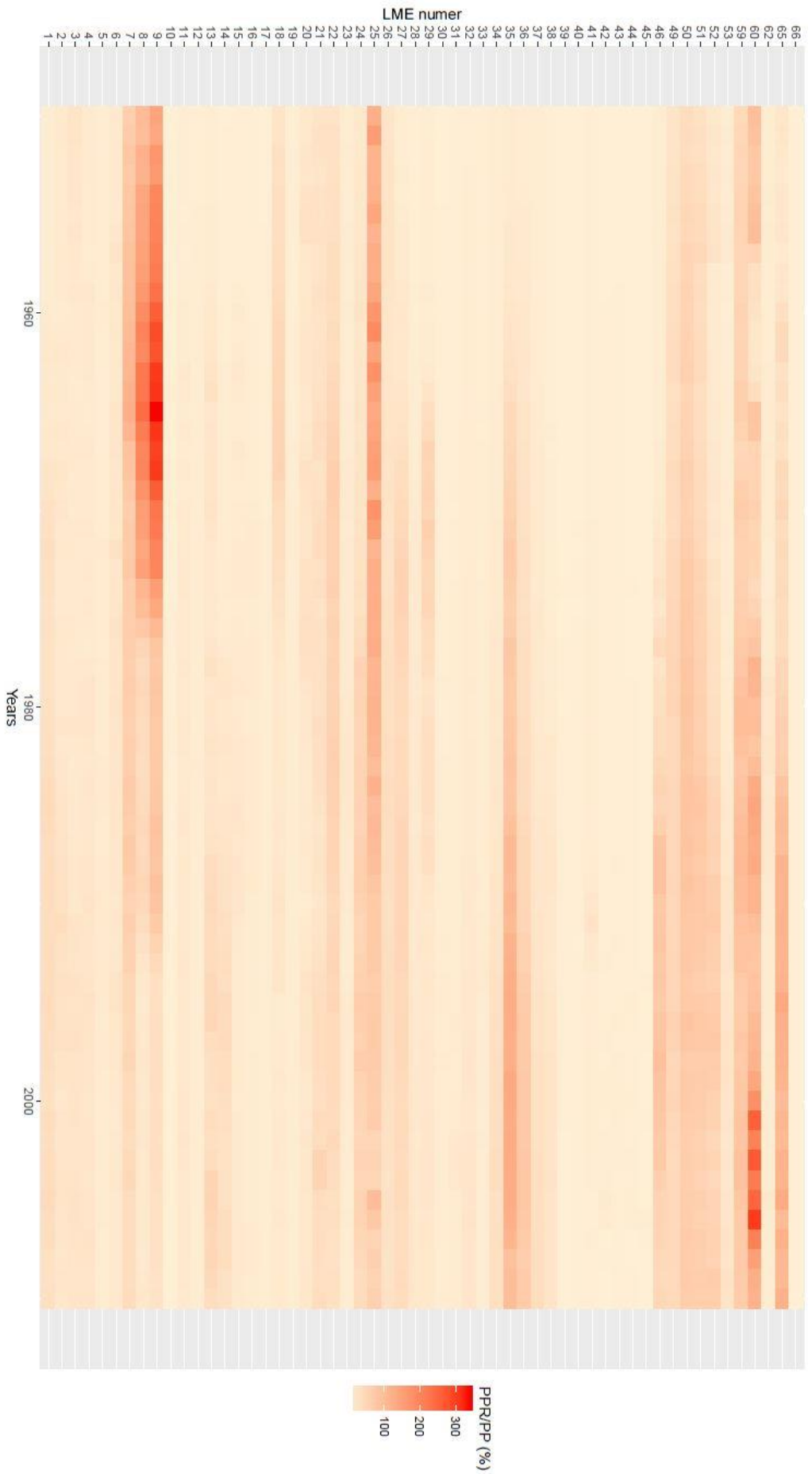
We tested all of these options in order to see how it affects the PPR/PP index:

Variability considered for the trophic transfer efficiency TE	Variability considered for the Primary Production PP	Name in the graphs legend
TE constant, TE=10%	Constant from Eppley	TE=10%
TE variable: 5% for tropical LMEs; 10% for temperate LMEs; 15% for polar LMEs	Constant from Eppley	TEvar
TE constant	Variable from the GFDL models (Geophysical Fluid Dynamic Laboratory)	TE=10%, PPGFDL
TE variable	Variable from the GFDL models	TEvar, PPGFDL
TE constant	Variable from the IPSL models (Institut Pierre Simon Laplace)	TE=10%, PPIPSL
TE variable	Variable from the IPSL models	TEvar, PPIPSL
TE constant	Variable from the MPI models (Max Plank Institute)	TE=10%, PPMPI
TE variable	Variable from the MPI models	TEvar, PPMPI

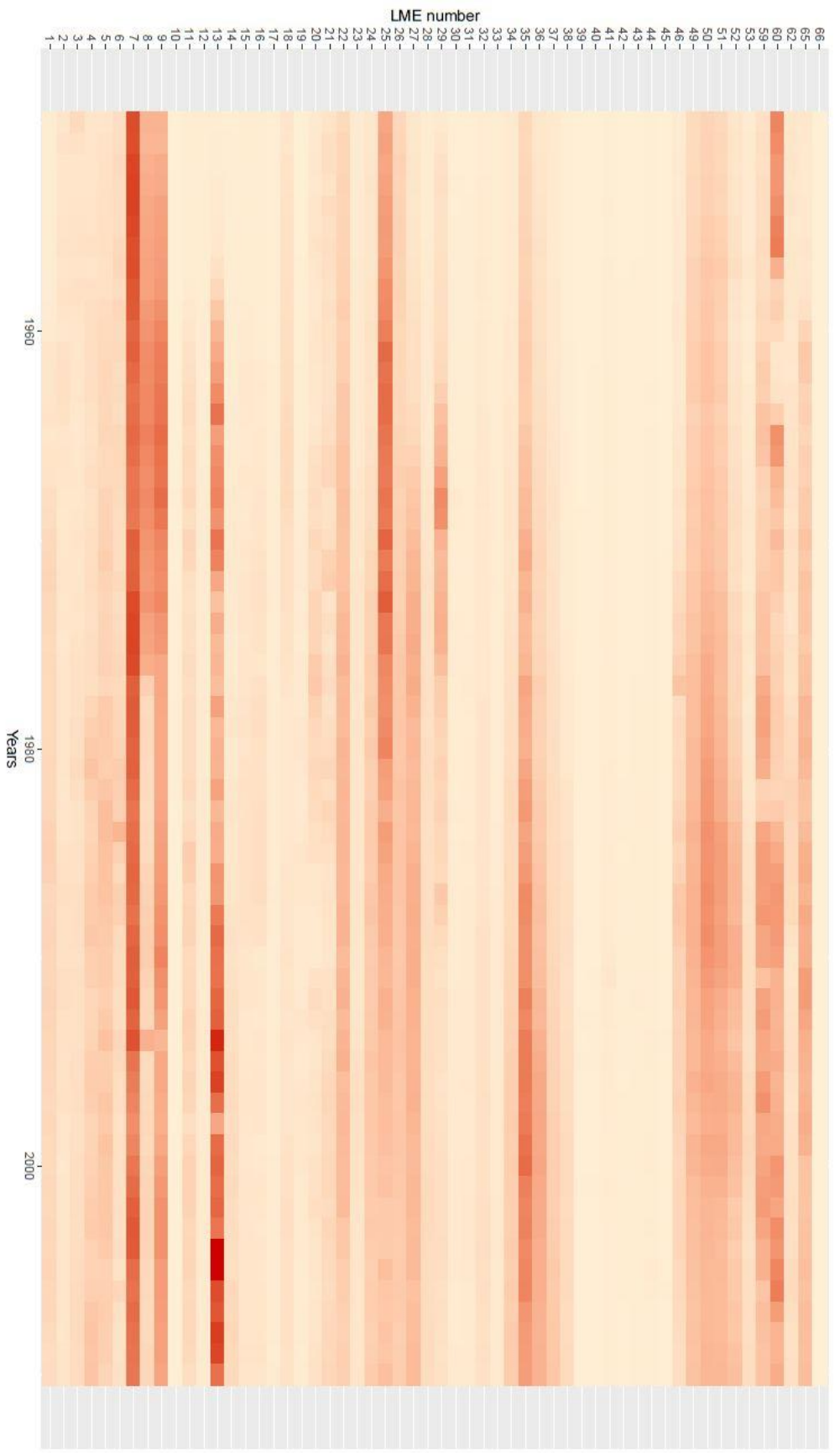


App III, Fig.1

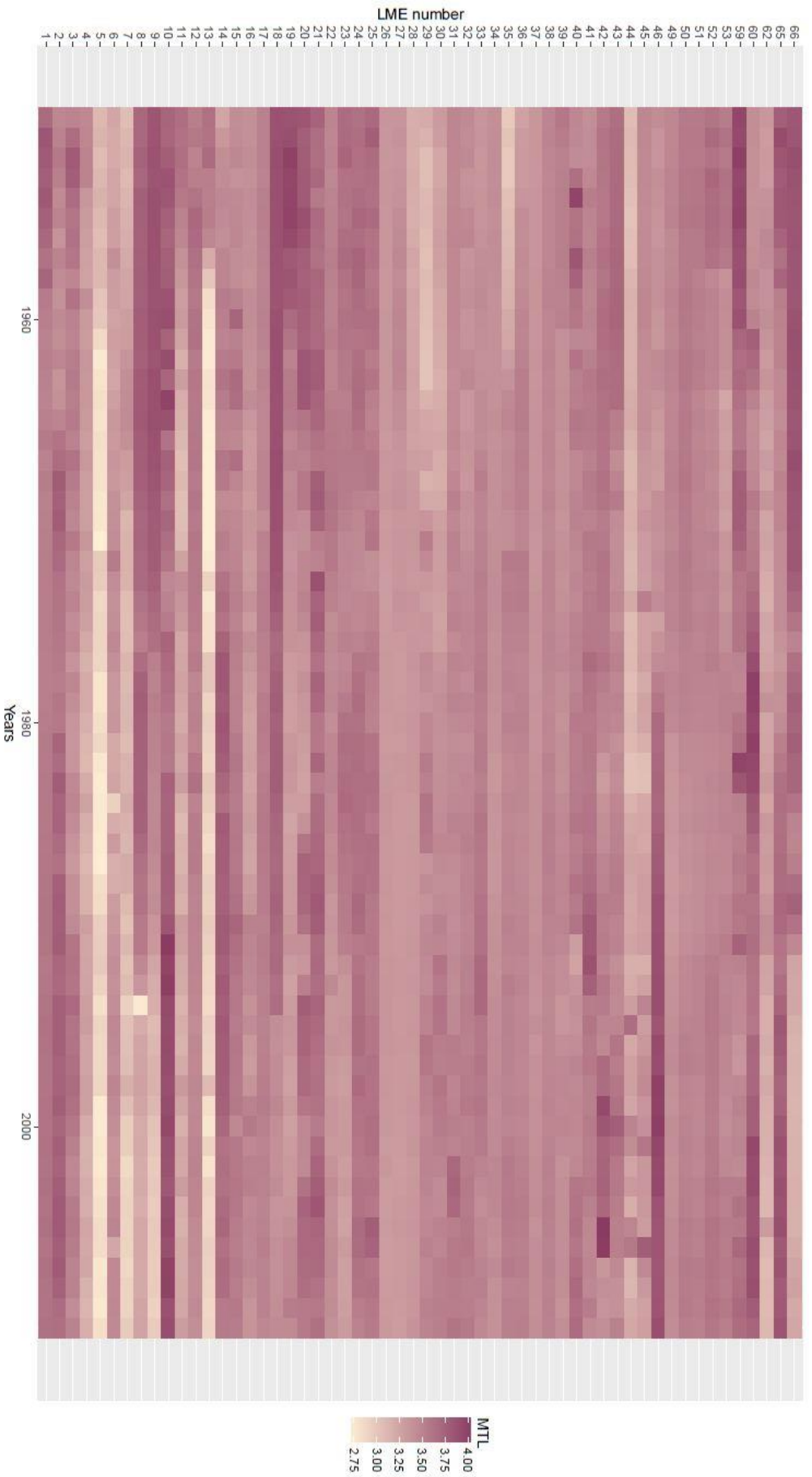
This analysis highlights the fact that the chosen primary production model influences a lot the final value of the index. It was then preferable choosing the best data, being the observation from Eppley, but as a constant on the time-series. TE changes as well the PPR considerably for the Canary Current, from less than a 100% to more than 400% when Eppley data is selected. This analysis shows the importance of choosing the right TE per LME and not just as polar/temperate/tropical, which is not yet possible in this study.



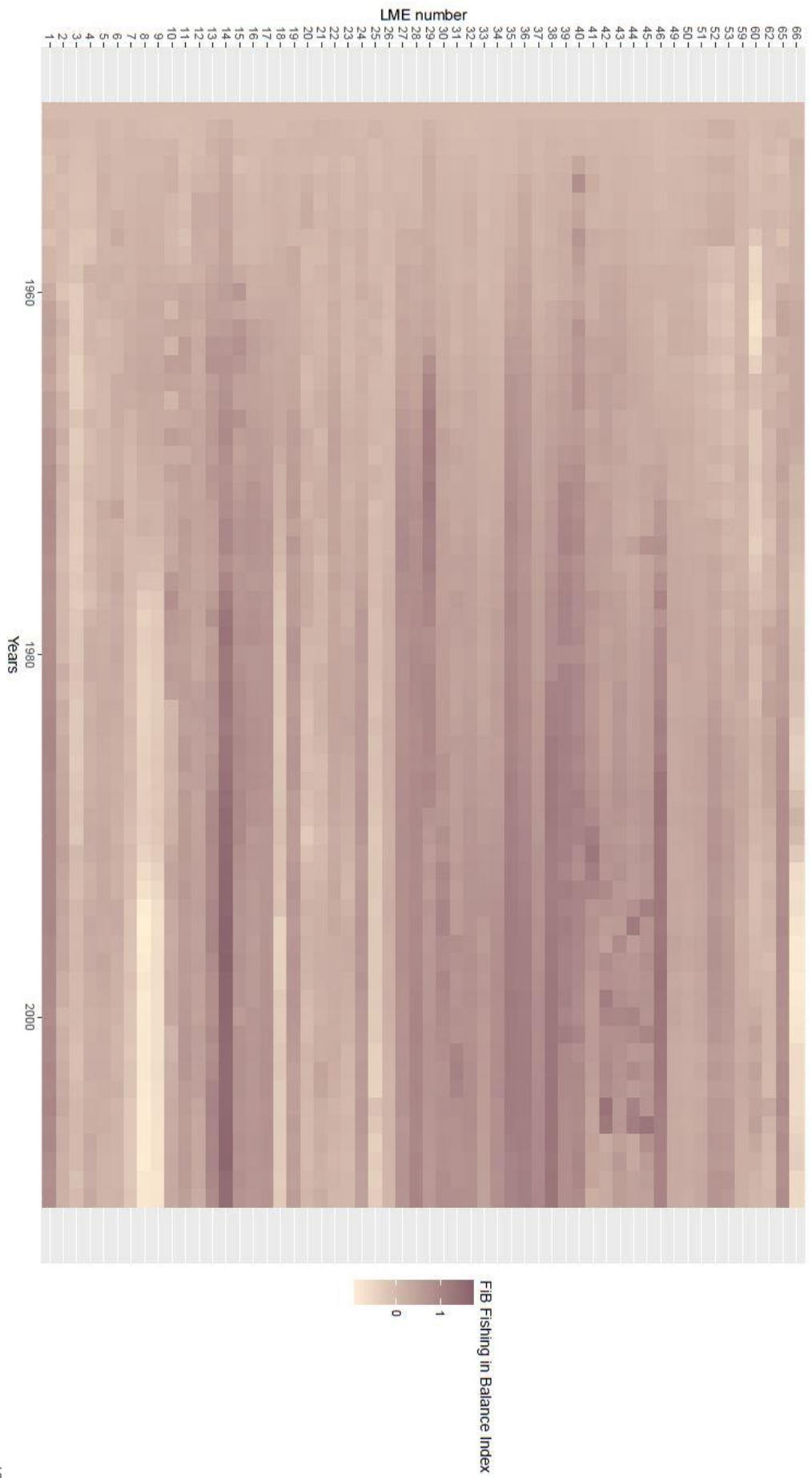
App III, Fig.2



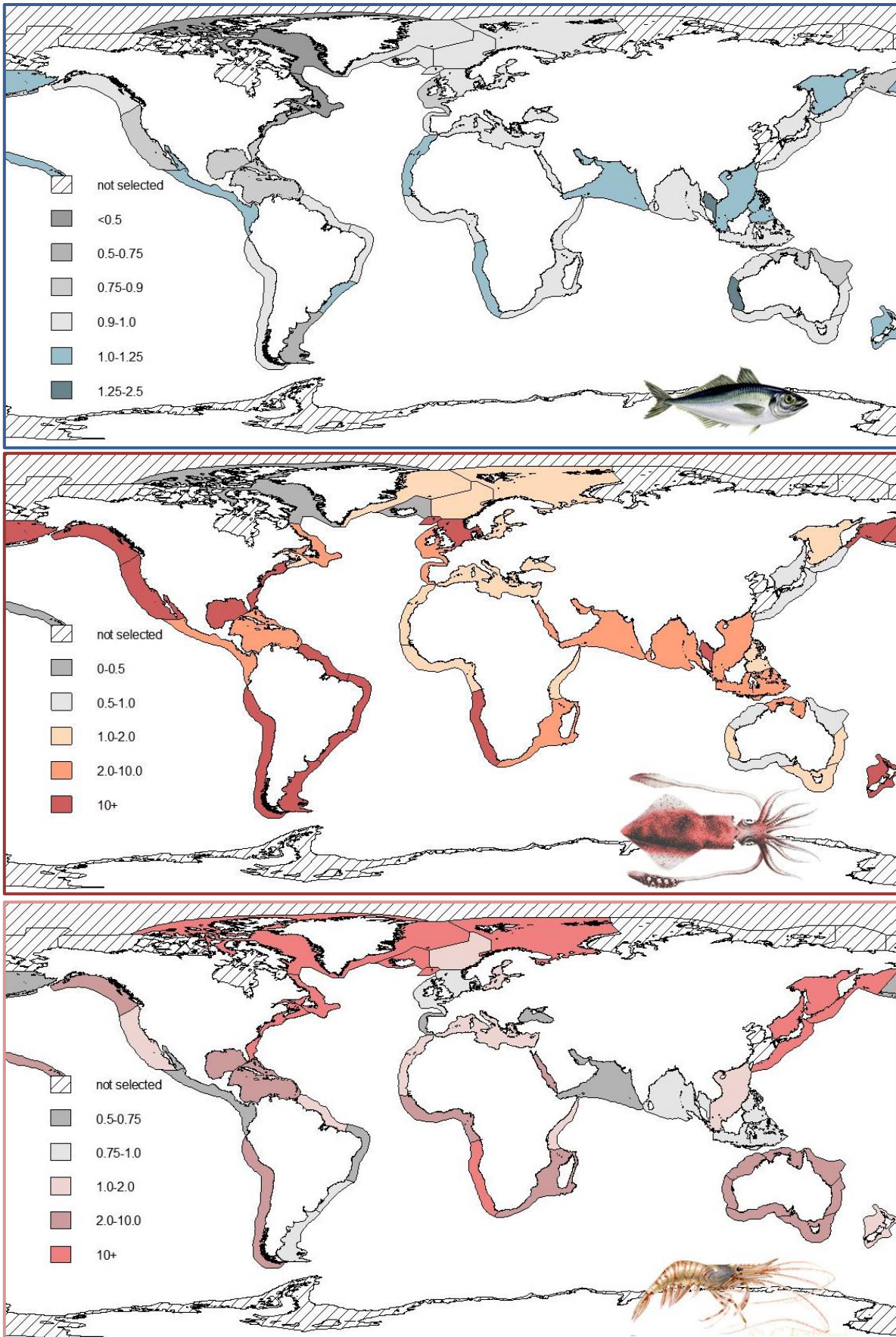
App III, Fig.3



App III, Fig.4



App III, Fig.5



App III, Fig. 6, 7 and 8: Worldwide maps of the relative proportion of fish, cephalopods and shrimps for all the Large Marine Ecosystems ratio (mean of the proportion (1950-1955)/mean of the proportion (2005-2010))

Appendix IV: Supplementary variables for the PCA and AHC

Each variable is tested as a simple value or as a relative value to 1950. The first one gives information on the global mean situation of the LME (the level of primary production, sea surface temperature and fishing pressure) and the second one indicates the increase or decrease of the variable. Indeed, it is interesting to test the influence of the mean fishing pressure on the time-series but also the global trend (increasing or decreasing).

Variable	Type	Definition
Habitat	Qualitative	LME ' polar ', ' temperate ' or ' tropical '
Mean Temperature as SST	Quantitative	Mean SST from Eppley temperature for each LME
Mean Temperature as SST	Qualitative	<u>Range of SST:</u> SST < 8°C ' cold ' 8°C ≤ SST < 16°C ' medium ' SST > 16°C ' hot '
Mean Primary Production PP	Quantitative	Mean PP from Eppley production data for each LME
Mean Primary Production PP	Qualitative	<u>Range of PP:</u> PP < 500mgC.m ⁻² .day ⁻¹ ' low PP ' 500mg ≤ PP < 1000mgC.m ⁻² .day ⁻¹ ' moderate PP ' PP > 1000mgC.m ⁻² .day ⁻¹ ' high PP '
Mean Stock Status Plot SSP	Quantitative	Mean % of Overexploited + Collapsed number of assessed stocks
Mean Stock Status Plot SSP	Qualitative	<u>Range of SSP:</u> SSP < 25% ' moderate SSP ' 25% ≤ SSP < 50% ' high SSP ' SSP > 50% ' very high SSP '
Mean Lindex Lindex	Quantitative	Mean Lindex value on the time series for each LME
Mean Lindex Lindex	Qualitative	<u>Range of Lindex:</u> Lindex < 0.01 ' low Lindex ' 0.01 ≤ Lindex < 0.05 ' med Lindex ' 0.05 ≤ Lindex ' high Lindex '
Mean Lindex relative to the values in 1950 Lindex relative to 1950	Quantitative	Mean Lindex relative value
Mean Lindex relative to the values in 1950 Lindex relative to 1950	Qualitative	<u>Range of Lindex relative:</u> Lindex < 0.99 ' Lindex decrease ' 0.99 ≤ Lindex < 1.1 ' Lindex stable ' 1.1 ≤ Lindex ' Lindex increase '
Mean Primary Production Required for fisheries index PPR/PP	Quantitative	Mean PPR index value on the time series for each LME
Mean Primary Production Required for fisheries index PPR/PP	Qualitative	<u>Range of PPR:</u> PPR/PP < 10% ' <10% ' 10% ≤ PPR/PP < 25% ' 10-25% ' 25% ≤ PPR/PP < 50% ' 25-50% ' 50% ≤ PPR/PP ' >50% '
Mean PPR index relative to the values in 1950 PPR/PP relative to 1950	Quantitative	Mean PPR index relative values
Mean PPR index relative to the values in 1950 PPR/PP relative to 1950	Qualitative	<u>Range of PPR relative:</u> PPR < 0.99 ' PPR/PP decrease ' 0.99 ≤ PPR < 1.1 ' PPR/PP stable ' 1.1 ≤ PPR ' PPR/PP increase '
PPR index as a mean on the last 10 years PPR/PP 2000s	Quantitative	Mean of the fishing index on 2000-2010
PPR index as a mean on the last 10 years PPR/PP 2000s	Qualitative	<u>Range of PPR:</u> PPR < 10% ' PPR/PP 2000s <10% ' 10% ≤ PPR < 25% ' PPR/PP 2000s 10-25% ' 25% ≤ PPR < 50% ' PPR/PP 2000s 25-50% ' 50% ≤ PPR ' PPR/PP 2000s >50% '
Lindex as a mean on the last 10 years Lindex 2000s	Quantitative	Mean of the fishing index on 2000-2010
Lindex as a mean on the last 10 years Lindex 2000s	Qualitative	<u>Range of Lindex:</u> Lindex < 0.01 ' low Lindex 2000s ' 0.01 ≤ Lindex < 0.05 ' high Lindex 2000s ' 0.05 ≤ Lindex ' very high Lindex 2000s '
SSP as a mean on the last 10 years SSP 2000s	Quantitative	Mean of the fishing index on 2000-2010
SSP index as a mean on the last 10 years SSP 2000s	Qualitative	<u>Range of SSP:</u> SSP < 25% ' SSP 2000s <25% ' 25% ≤ SSP < 50% ' SSP 2000s 25-50% ' 50% ≤ SSP < 75% ' SSP 2000s 50-75% ' 75% ≤ SSP ' SSP 2000s >75% '

Mean proportion of fish species in % Prop fish	Quantitative	Mean proportion in %
Mean proportion of fish species Prop fish	Qualitative	<u>Range of proportion values:</u> prop<80% ' Prop fish:<80% ' 80%<=prop<90% ' Prop fish:80%-90% ' Prop >90% ' Prop fish:>90% '
Mean proportion of shrimps species in % Prop shrimp	Quantitative	Mean proportion in %
Mean proportion of shrimps species in % Prop shrimp	Qualitative	<u>Range of proportion values:</u> prop<1% ' Prop shrimp:0%-1% ' 1%<=prop<5% ' Prop shrimp:1%-5% ' Prop >5% ' Prop shrimp:5%-40% '
Mean proportion of cephalopods species in % Prop cephalopods	Quantitative	Mean proportion in %
Mean proportion of cephalopods species Prop cephalopods	Qualitative	<u>Range of proportion values:</u> prop<1% ' prop cephalopods:0%-1% ' 1%<=prop<5% ' prop cephalopods:1%-5% ' Prop >5% ' prop cephalopods:5%-40% '
Mean proportion relative to 1950 Prop fish relative to 1950	Quantitative	Mean relative value
Mean proportion relative to 1950 Prop fish relative to 1950	Qualitative	<u>Range of proportion relative values:</u> prop<0.99 ' Prop fish decrease ' 0.99<=prop<1.1 ' Prop fish stable ' Prop >1.1 ' Prop fish increase '
Mean proportion relative to 1950 Prop shrimp relative to 1950	Quantitative	Mean relative value
Mean proportion relative to 1950 Prop shrimp relative to 1950	Qualitative	<u>Range of proportion relative values:</u> prop<0.99 ' Prop shrimp decrease ' 0.99<=prop<1.1 ' Prop shrimp stable ' Prop >1.1 ' Prop shrimp increase '
Mean proportion relative to 1950 Prop cephalopods relative to 1950	Quantitative	Mean relative value
Mean proportion relative to 1950 Prop cephalopods relative to 1950	Qualitative	<u>Range of proportion relative values:</u> prop<0.99 ' prop cephalopods decrease ' 0.99<=prop<1.1 ' prop cephalopods stable ' Prop >1.1 ' prop cephalopods increase '
Mean O2 relative to 1950 O2 relative to 1950	Quantitative	Mean relative value
Mean O2 relative to 1950 O2 relative to 1950	Qualitative	<u>Range O2 relative value:</u> O2<0.995 ' O2 decrease ' 0.995<=O2<1.005 ' O2 stable ' 1.005<O2 ' O2 increase '
Mean Mean trophic level MTL	Quantitative	Mean value
Mean Mean trophic level MTL	Qualitative	<u>Range MTL value:</u> MTL<3.40 ' low MTL ' 3.40<=MTL<3.60 ' medium MTL ' 3.60<=MTL ' high MTL '
Mean Mean trophic level relative to 1950 MTL relative to 1950	Quantitative	Mean relative value
Mean trophic level relative to 1950 MTL relative to 1950	Qualitative	<u>Range relative MTL:</u> MTL<0.99 ' MTL decrease ' 0.99<=MTL<1.1 ' MTL stable ' 1.1<MTL ' MTL increase '
Mean FIB relative to 1950 FIB relative to 1950	Quantitative	Mean relative value
Mean FIB relative to 1950 FIB relative to 1950	Qualitative	<u>Range of FIB relative value:</u> FIB<-0.1 ' FIB decrease ' -0.1<=FIB<0.1 ' FIB stable ' 0.1<= FIB ' FIB increase '

- ✓ Mean variable between 1950-2010: global fishing pressure amount
- ✓ Class of the mean variable: fishing pressure is 'low', 'moderate', 'high'
- ✓ Mean variable relative to 1950: the fishing pressure has increased (>1)/decreased(<1)/been stable(=1)
- ✓ Class of the relative variable: fishing pressure is 'decreasing', 'stable', 'increasing'

Appendix V: the 6 Large Marine Ecosystems complementary data

App V Fig. 1: For the 6 Large Marine Ecosystems studied in details, the following graphs are showing the major changes in species proportions for each trophic class per 0.5 trophic level step from $\tau = 2.0$ to 4.5. Then, these graphs are useful for analyzing all the variations in the ECI (Efficiency Cumulated Index) and the TCI (Time Cumulated Index).

The number per row indicated to official Large Marine Ecosystem number as following:

3: California Current

5: Gulf of Mexico

13: Humboldt Current

22: North Sea

27: Canary Current

50: Sea of Japan

All the graphs represent the percentage of species per year and per trophic class studied.

2,0 ≤ τ < 2,5

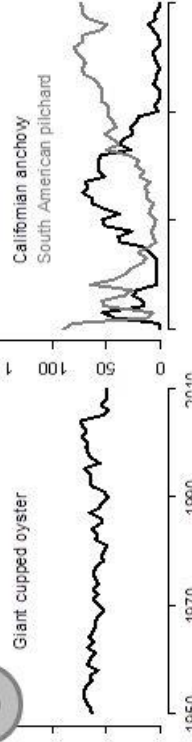
2,5 ≤ τ < 3,0

3,0 ≤ τ < 3,5

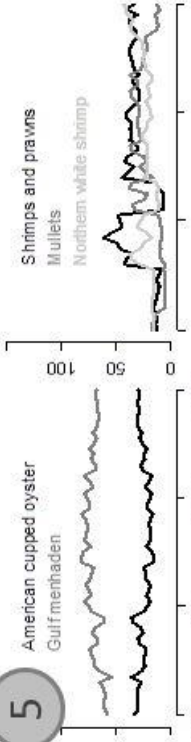
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4,0 ≤ τ < 4,5

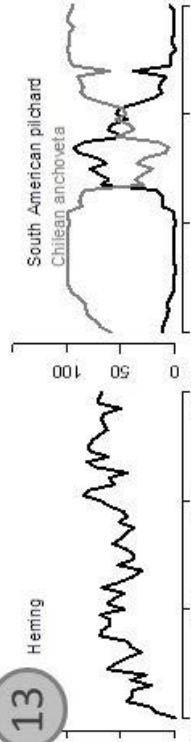
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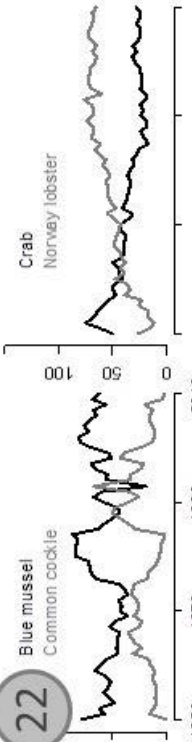
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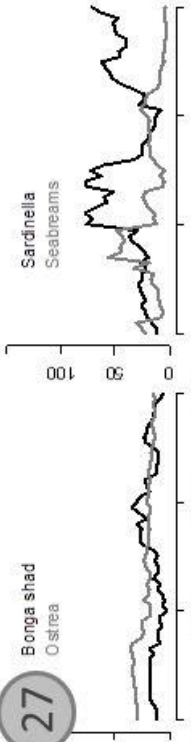
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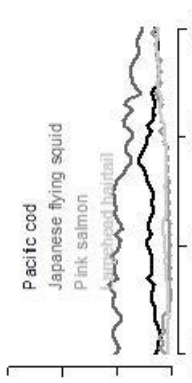
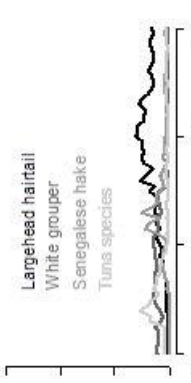
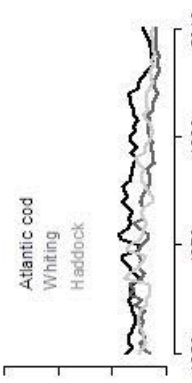
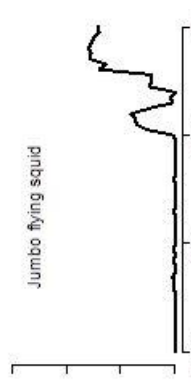
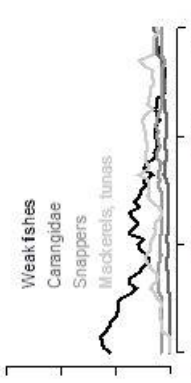
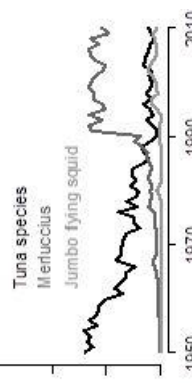
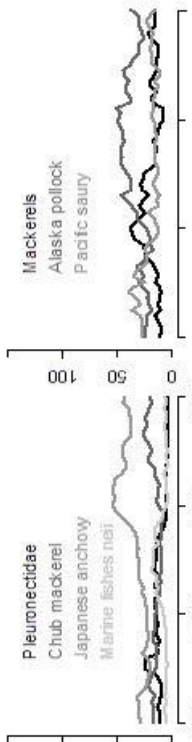
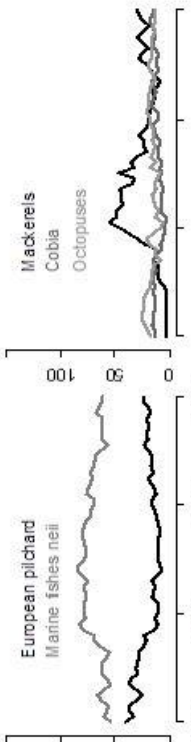
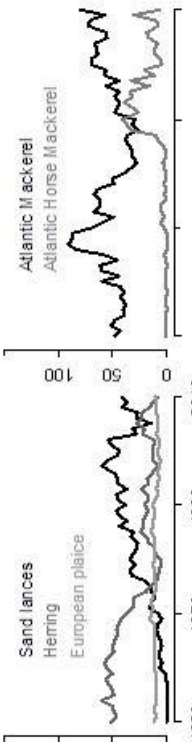
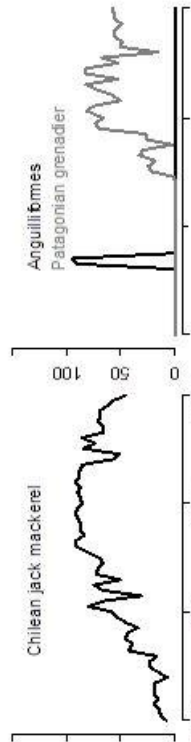
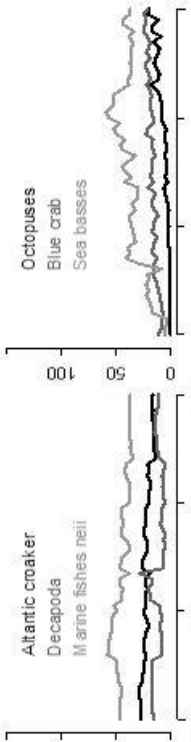
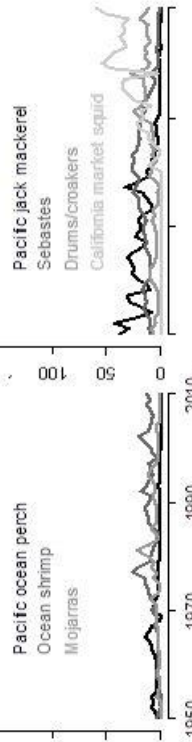
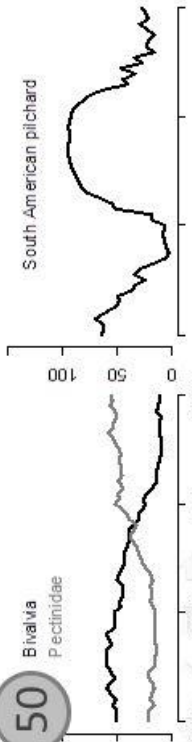
22



27



50



3. The California Current

Common name	Scientific name	Trophic level	P/B ratio	P/Q ratio
Californian anchovy	<i>Engraulis mordax</i>	2.96	0.6479	0.0543
South American pilchard	<i>Sardinops sagax</i>	2.84	0.9131	0.0349
Pacific Jack Mackerel	<i>Trachurus symmetricus</i>	3.57	0.4020	0.0579
California squid	<i>Loligo opalescens</i>	3.88	3.0456	0.2253
North Pacific Hake	<i>Merluccius productus</i>	4.35	0.4685	0.1007
Jumbo flying squid	<i>Dosidicus gigas</i>	4.14	3.0456	0.2253
Bigeye tuna	<i>Thunnus obesus</i>	4.49	0.4308	0.0709
Albacore tuna	<i>Thunnus alalunga</i>	4.30	0.4242	0.0488
Yellowfin tuna	<i>Thunnus albacares</i>	4.41	0.6068	0.0679

5. The Gulf of Mexico

Common name	Scientific name	Trophic level	P/B ratio	P/Q ratio
Gulf menhaden	<i>Brevoortia patronus</i>	2.19	0.8399	0.0227
American cupped oyster	<i>Crassostrea virginica</i>	2.0	2.56	0.2627
Shrimps and prawns	<i>Mugilidae</i>	2.65	3.3304	0.2082
Mulletts		2.53	0.5556	0.0074
Decapodes	<i>Decapoda</i>	3.43	2.8446	0.2055

13. The Humboldt Current

Common name	Scientific name	Trophic level	P/B ratio	P/Q ratio
Peruvian anchoveta	<i>Engraulis ringens</i>	2.7	1.9209	0.0703
South American pilchard	<i>Sardinops sagax</i>	2.84	0.7334	0.0298
Chilean Jack mackerel	<i>Trachurus murphyi</i>	3.33	0.2482	0.0807
Jumbo Flying squid	<i>Dosidicus gigas</i>	4.14	3.0456	0.2253
Pacific bonito	<i>Sarda chiliensis</i>	4.49	0.5104	0.0649
South Pacific hake	<i>Merluccius gayi gayi</i>	4.26	0.4434	0.1087
-	<i>Merluccius</i>	4.27	0.3478	0.1035

22. The North Sea

Common name	Scientific name	Trophic level	P/B ratio	P/Q ratio
Sand lances	<i>Ammodytidae</i>	3.11	0.7464	0.1251
Atlantic herring	<i>Clupea harengus</i>	3.38	0.5744	0.1157
European flounder	<i>Platichthys flesus</i>	3.32	0.5021	0.1606
European plaice	<i>Pleuronectes platessa</i>	3.26	0.3400	0.1027
Whiting	<i>Merlangius merlangus</i>	4.36	0.5093	0.1676
Cod	<i>Gadus morhua</i>	4.09	0.3944	0.2127
Saithe	<i>Pollachius virens</i>	4.31	0.2766	0.1319
Atlantic bonito	<i>Sarda sarda</i>	4.5	0.7520	0.1161
Blue whiting	<i>Micromesistius poutassou</i>	4.13	0.4761	0.1263

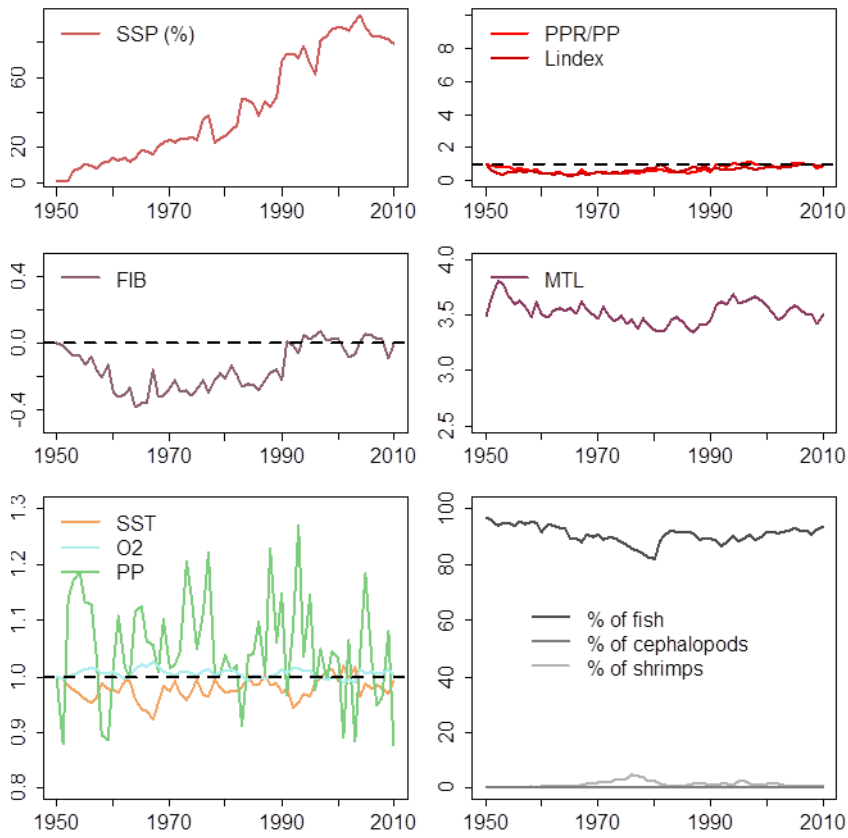
27. The Canary Current

Common name	Scientific name	Trophic level	P/B ratio	P/Q ratio
Bonga shad	<i>Ethmalosa fimbriata</i>	2.5	0.8758	0.0439
Mackerels	<i>Trachurus</i>	3.69	0.4703	0.0640
Largehead hairtail	<i>Trichiurus lepturus</i>	4.42	0.6161	0.1022
Albacore tuna	<i>Thunnus alalunga</i>	4.3	0.3833	0.0359
Bigeye tuna	<i>Thunnus obesus</i>	4.49	0.4700	0.0598
Atlantic Bluefin tuna	<i>Thunnus thynnus</i>	4.45	0.2676	0.0563
Yellowfin tuna	<i>Thunnus albacares</i>	4.41	0.4912	0.0442
Senegalese hake	<i>Merluccius senegalensis</i>	4.5	0.3385	0.0755

50. The Sea of Japan

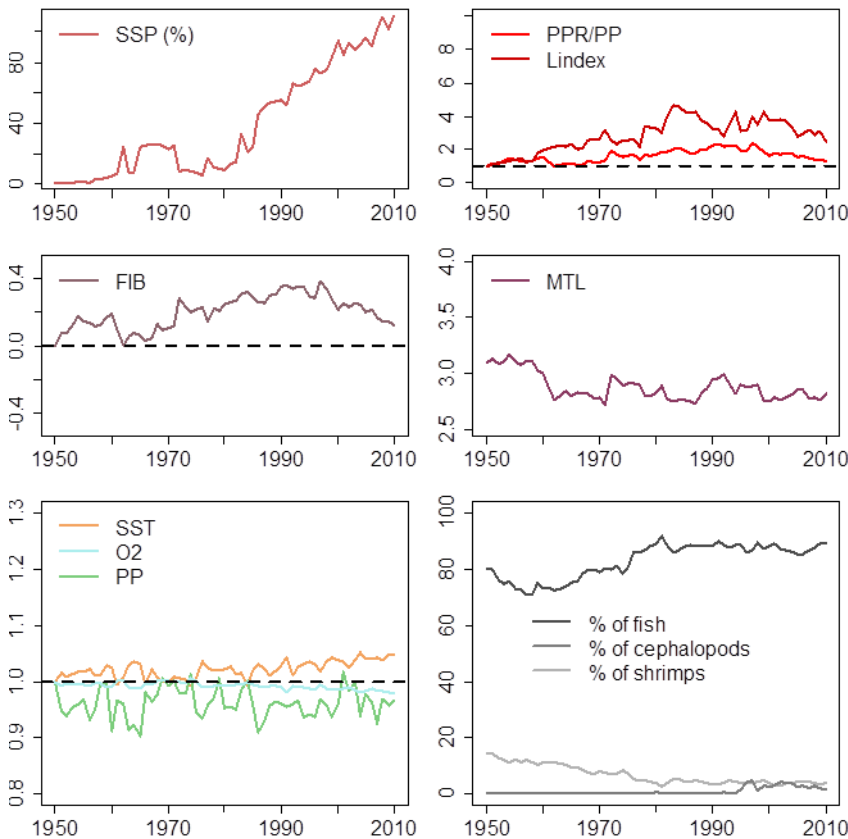
Common name	Scientific name	Trophic level	P/B ratio	P/Q ratio
Pacific sardine	<i>Sardinops sagax</i>	2.84	0.6976	0.0330

3. California Current supplementary variables



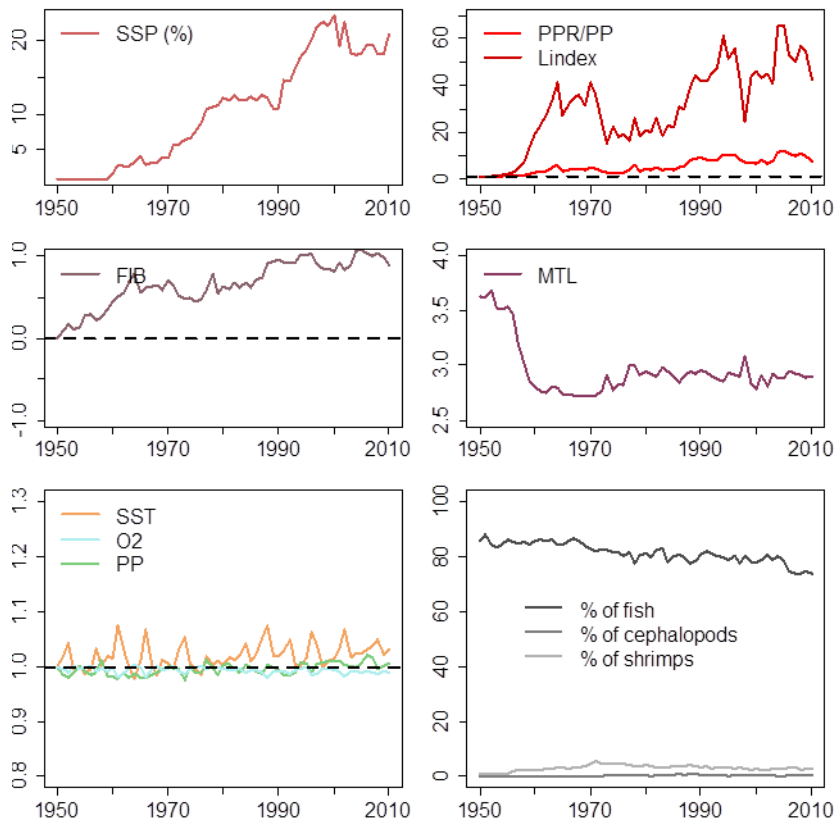
App V Fig 2

5. Gulf of Mexico



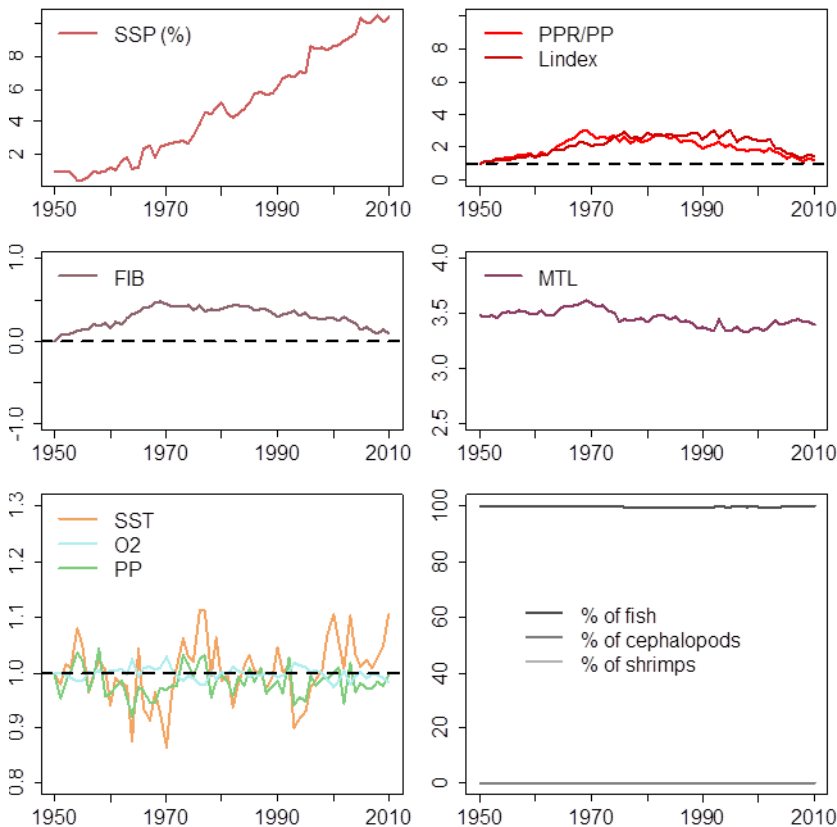
App V Fig 3

13. Humboldt Current



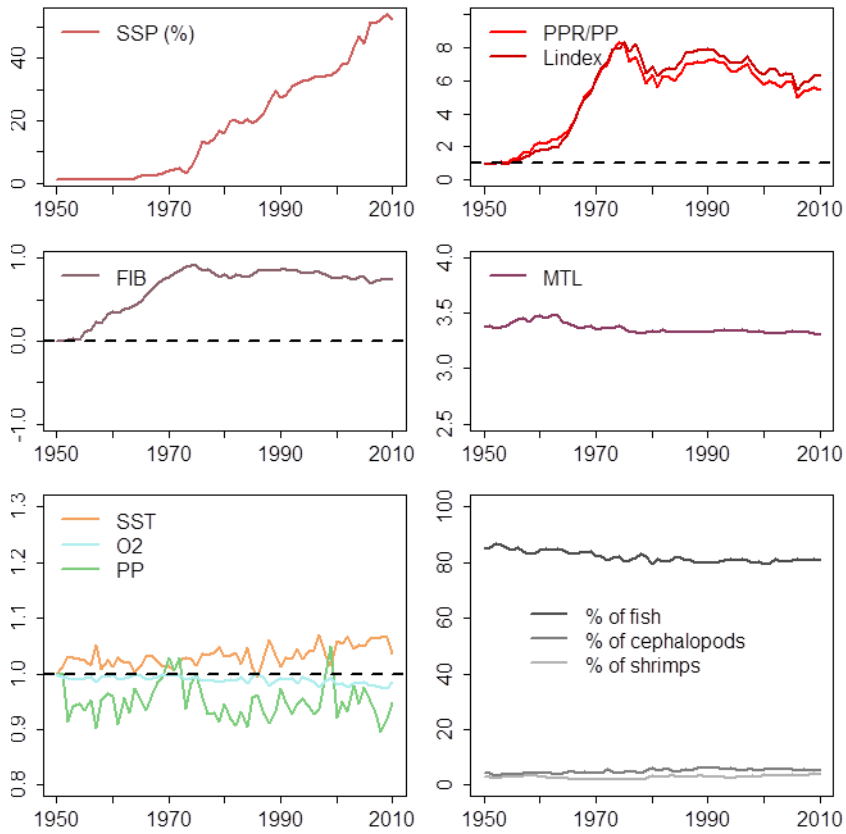
App V Fig 4

22. North Sea



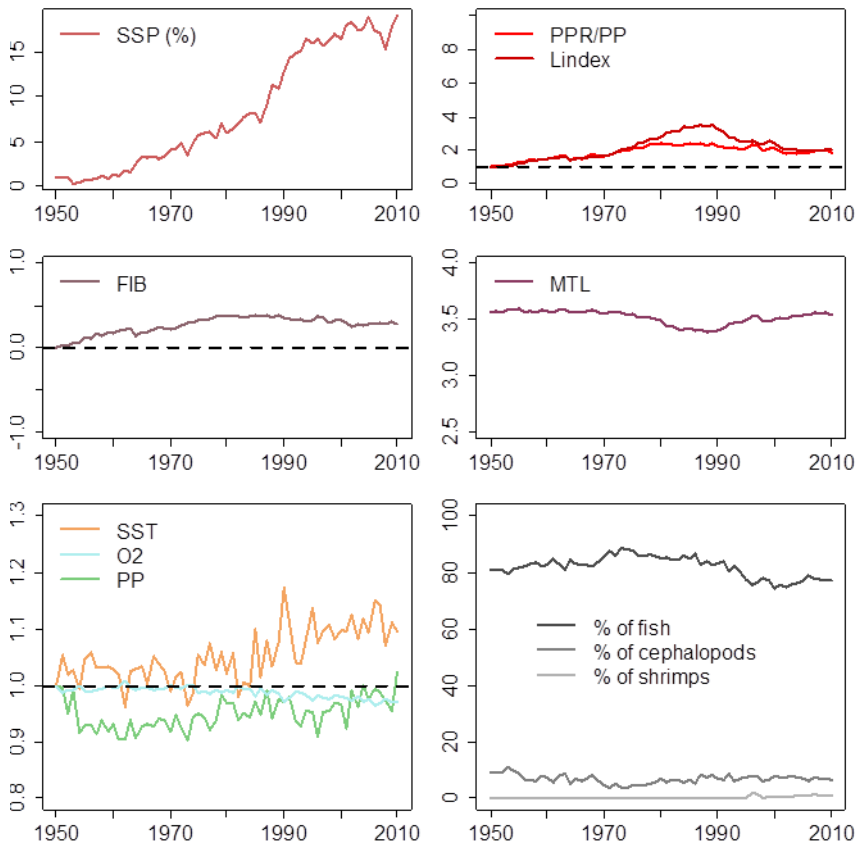
App V Fig 5

27. Canary Current



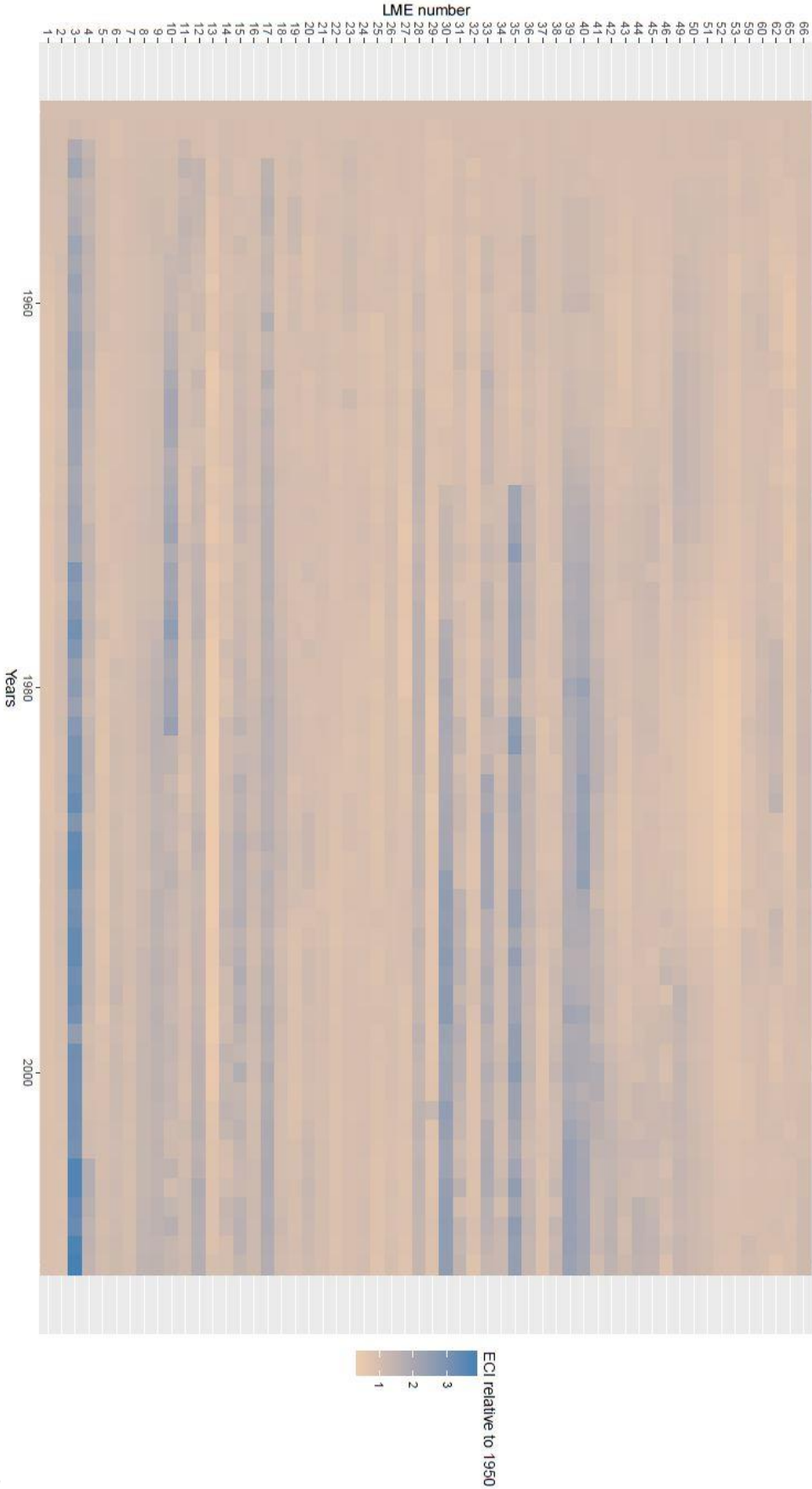
App V Fig 6

50. Sea of Japan

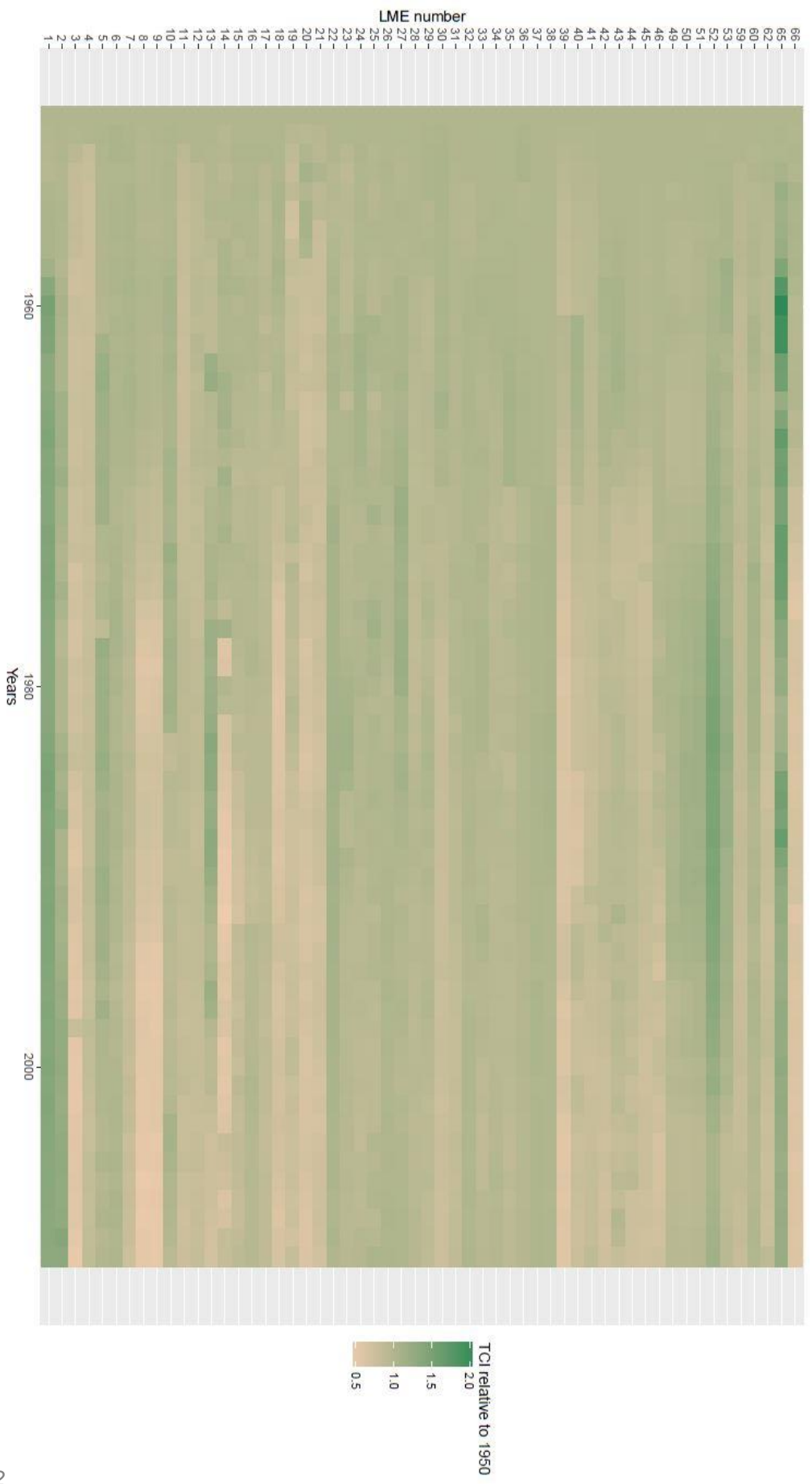


App V Fig 7

Appendix VI: Time series of ECI and TCI



App VI, Fig.1



App VI, Fig.2

Appendix VII: Principle Component Analysis and Ascending Hierarchical Classification complementary results

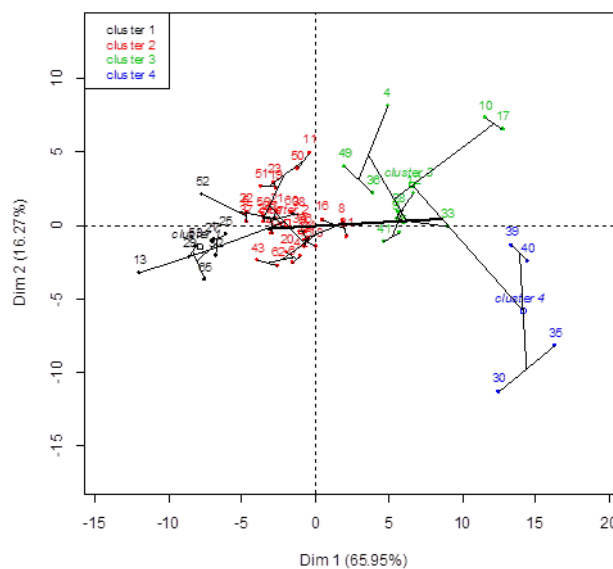
Results from the PCA on the ECI for supplementary variables

Type of quantitative variable	Dimension	Correlation	p.value
MTL relative to 1950	1	0.3491	8.99e-03**
TCI relative to 1950	1	-0.4327	9.69e-04***

Type of qualitative variable	Dimension	R ²	p.value
Habitat	1	0.3711	2.65e-05***
Prop shrimp	1	0.2762	3.08e-04***
Mean Lindex	1	0.2573	4.38e-04***
Mean Lindex 2000s	1	0.2520	5.26e-04***
TCI relative to 1950	1	0.1947	3.58e-03**
Mean PPR/PP	1	0.2197	5.16e-03**
PPR/PP 2000s	1	0.1870	1.37e-02*
Prop fish relative to 1950	1	0.1417	1.88e-02*
MTL relative to 1950	1	0.1364	2.98e-02*

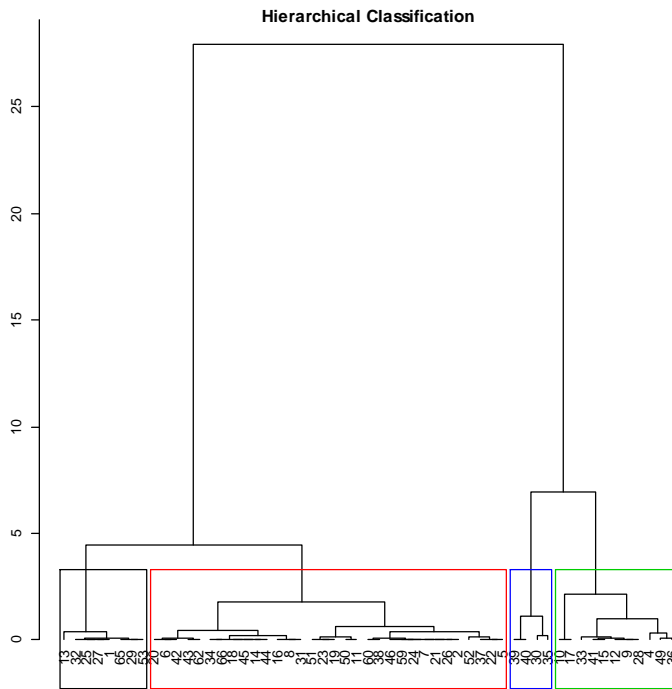
Qualitative category	Dimension	Estimate	p.value
Habitat: tropical	1	6.42	6.97e-06***
Low Lindex	1	4.69	8.66e-05***
Lindex 2000s: low	1	4.83	9.62e-05***
Prop shrimps: 5-40%	1	4.27	5.08e-04***
PPR/PP<10%	1	4.26	6.94e-04***
TCI decreasing	1	4.36	1.26e-03**
Last PPR<10%	1	4.08	1.67e-03**
Habitat: polar	1	-0.43	4.48e-02*
TCI increasing	1	-3.80	4.02e-02*
PPR/PP 2000s: 25-50%	1	-2.67	3.85e-02*
TCI stable	1	-0.56	3.11e-02*
PPR 10-25%	1	-2.30	3.06e-02*
MTL decreasing	1	-4.40	2.55e-02*
Lindex medium	1	-2.76	1.79e-02*
Habitat: upwelling	1	-6.37	8.74e-03**
Prop fish stable	1	-3.68	5.41e-03**
Prop shrimps 0-1%	1	-3.97	1.05e-03**

Ascending Hierarchical Clustering results for the Efficiency Cumulated Index

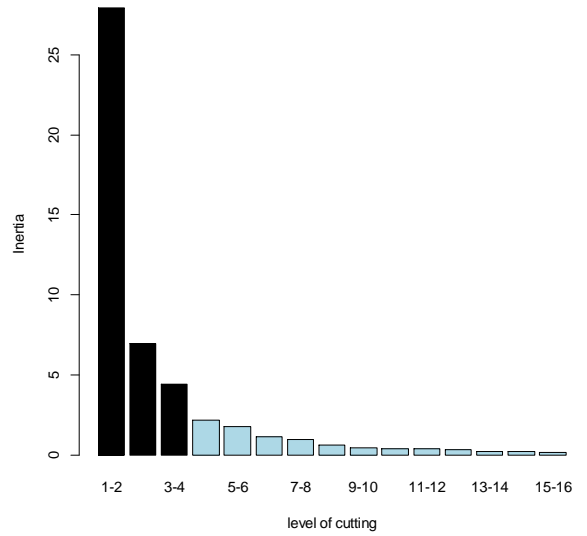


App VII, Fig. 1

Hierarchical Clustering



Inter-cluster inertia gains



App VII, Fig. 2

Results from the AHC on the ECI for the supplementary variables

Type of quantitative variable	Cluster	Mean in category	p.value
TCI relative to 1950	1	1.109	3.346e-05***
Prop fish	1	93.625	1.385e-04***
Lindex relative to 1950	1	7.215	2.075e-02*
Mean FIB	2	0.318	0.02984*
Mean FIB	4	0.750	1.357e-02*
PPR/PP relative to 1950	4	7.234	4.102e-02*

Qualitative category	Cluster	Cla/Mod	Mod/Cla	p.value	v.test
Habitat: upwelling	1	100	33.33	0.0032**	2.948
Prop fish >90%	1	33.33	88.89	0.0039**	2.878
Prop shrimp : 0-1%	1	35	77.78	0.0087**	2.624
TCI increase	1	75	33.33	0.0121*	2.510
Prop fish stable	1	33.33	66.67	0.0299*	2.172
SSP 2000s : 25-50%	1	29.17	77.78	0.0329*	2.133
Lindex low	1	0	0	0.0430*	-2.023
Habitat: tropical	1	3.70	11.11	0.0154*	-2.424
PPR/PP 2000s: <10%	1	0	0	0.0148*	-2.437
PPR/PP <10%	1	0	0	0.0111*	-2.539
TCI decreasing	1	5.56	22.22	0.0059**	-2.754
Habitat: temperate	2	92.31	38.71	0.0026**	3.009
SST decreasing	2	90.00	29.03	0.0196*	2.334
PP decreasing	2	75.00	48.39	0.0403*	2.051
PP increasing	2	35.00	22.58	0.0197*	-2.332
SST increasing	2	41.94	41.94	0.0168*	-2.392
Last SSP 25-50%	2	37.50	29.03	0.0161*	-2.407
Habitat: tropical	3	37.04	90.91	0.0022**	3.063
Habitat: temperate	3	0	0	0.0358*	-2.099
Prop shrimp 5-40%	4	26.67	100	0.0040**	2.878
Last Lindex low	4	21.43	75	0.0496*	1.963

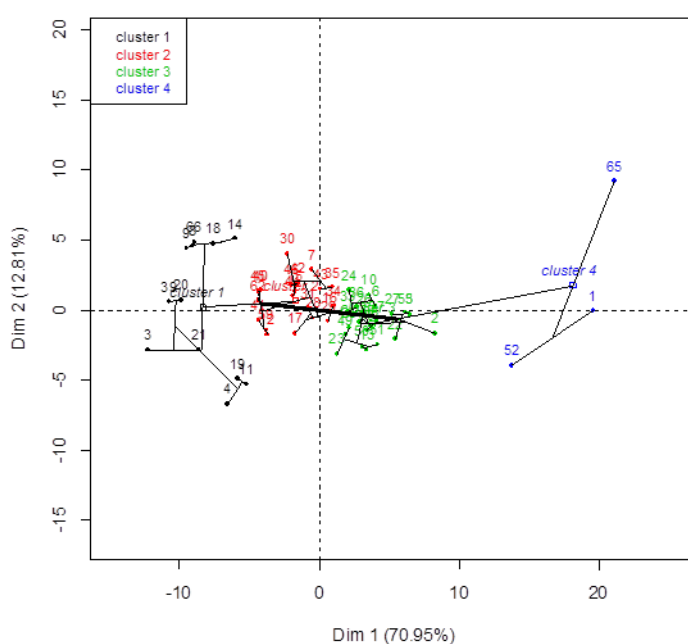
Results from the PCA on the TCI for the supplementary variables

Type of quantitative variable	Dimension	Correlation	p.value
PPR/PP 2000s	1	0.357	6.927e-03**
SST relative to 1950	1	0.306	2.175e-02*
Prop fish relative to 1950	1	0.283	3.432e-02*
SSP	1	-0.273	4.173e-02*
Prop shrimp	1	-0.343	9.623e-03**

Type of qualitative variable	Dimension	R ²	p.value
Mean FIB	1	0.2023	0.0025**
Mean SSP	1	0.1137	0.0111*
PPR/PP relative to 1950	1	0.1500	0.0135*
Lindex 2000s	1	0.1474	0.0146*
SSP 2000s	1	0.1713	0.0198*
Prop cephalopods relative to 1950	1	0.1338	0.0222*
PPR/PP 2000s	1	0.1594	0.0277*
Mean Prop fish	1	0.1219	0.0319*

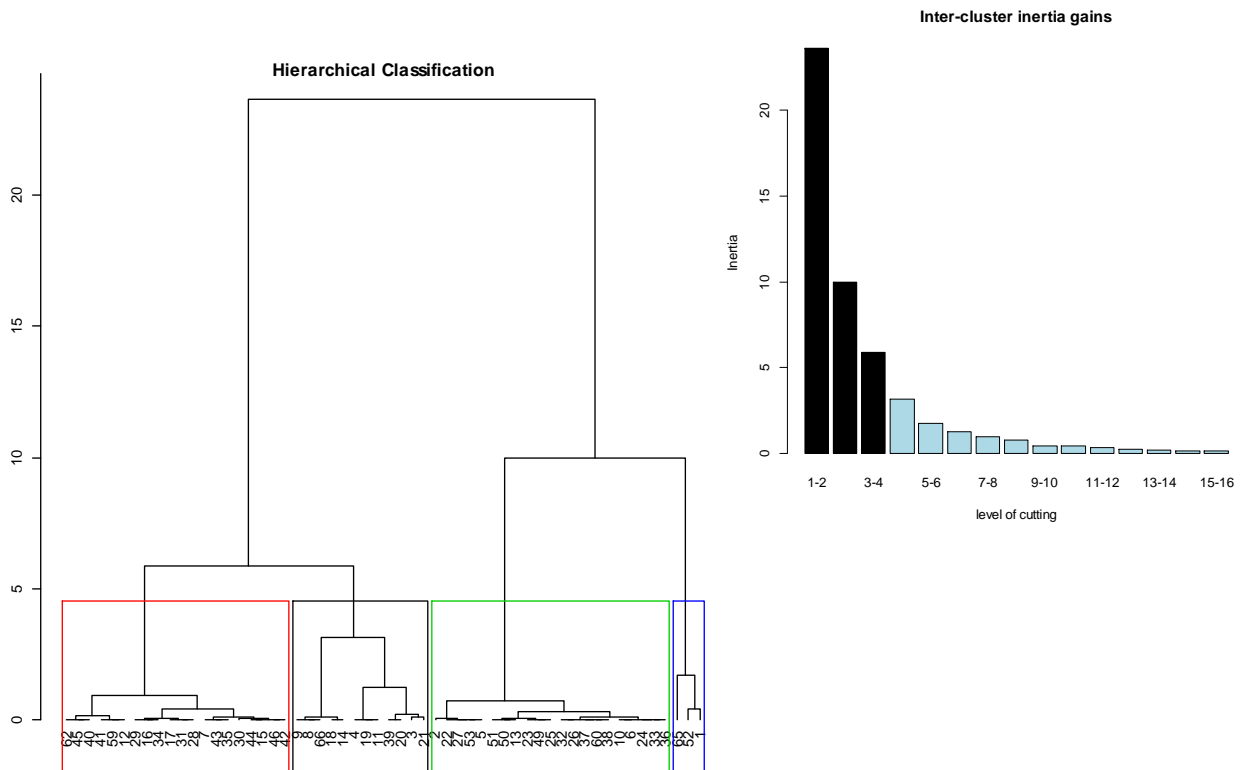
Qualitative category	Dimension	Estimate	p.value
FIB increase	1	4.87	0.0031**
PPR/PP increase	1	4.48	0.0041**
SSP 2000s: 25-50%	1	6.01	0.0042**
Lindex 2000s: very high	1	3.43	0.0065**
PPR/PP moderate	1	3.32	0.0111*
Prop fish: >90%	1	3.06	0.0137*
PPR/PP 2000s: >50%	1	4.01	0.0143*
SSP 2000s: 50-75%	1	1.44	0.0398*
O2 increase	1	-4.11	0.0450*
Lindex low	1	-2.82	0.0405*
Lindex 2000s low	1	-2.84	0.0395*
Prop cephalopods stable	1	-5.28	0.0178*
High	1	-2.32	0.0111*
PPR/PP decrease	1	-3.97	0.0063**
FIB decrease	1	-6.16	0.0012**

Ascending Hierarchical Classification results for the Time Cumulated Index



App VII, Fig. 3

Hierarchical Clustering



App VII, Fig. 4

Results from the AHC on the TCI for the supplementary variables

Type of quantitative variable	Cluster	Mean in category	p.value
Mean SSP	1	31.84	5.910e-04***
Mean Prop Shrimp	1	8.49	2.517e-03**
Mean FIB	1	0.20	1.648e-02*
Mean MTL relative to 1950	1	0.96	1.443e-02*
Mean SST relative to 1950	1	0.90	9.512e-03**
Mean prop fish relative to 1950	1	0.90	2.382e-03**
Mean FIB	2	0.52	0.0151*
Mean MTL relative to 1950	2	1.02	0.0220*
Mean SSP	2	19.00	0.0268*

Qualitative category	Cluster	Cla/Mod	Mod/Cla	p.value	v.test
FIB decrease	1	100.00	33.33	0.0013**	3.206
SSP high	1	47.37	75.00	0.0015**	3.172
MTL decrease	1	40.00	83.33	0.0032**	3.944
PPR/PP decrease	1	80.00	33.33	0.0061**	2.741
SST decrease	1	54.54	50.00	0.0083**	2.640
Habitat: polar	1	50.00	50.00	0.0150*	2.432
Prop cephalopods 0-1%	1	34.62	75.00	0.0318*	2.146
Prop cephalopods stable	1	57.14	33.33	0.0350*	2.107
PPR/PP 2000s: 10-25%	1	42.86	50.00	0.0399*	2.054
SSP 2000s: 25-50%	1	8.33	16.67	0.0438*	-2.016
Prop cephalopods 1-5%	1	7.69	16.67	0.0229*	-2.275
PPR/PP increase	1	14.29	58.33	0.0036**	-2.912
FIB increase	1	12.77	50.00	0.0018**	-3.118
SSP moderate	1	8.11	25.00	0.0015**	-3.172
MTL stable	1	3.45	8.33	0.0007***	-3.375
PPR/PP <10%	2	65.00	65.00	0.0010***	3.282

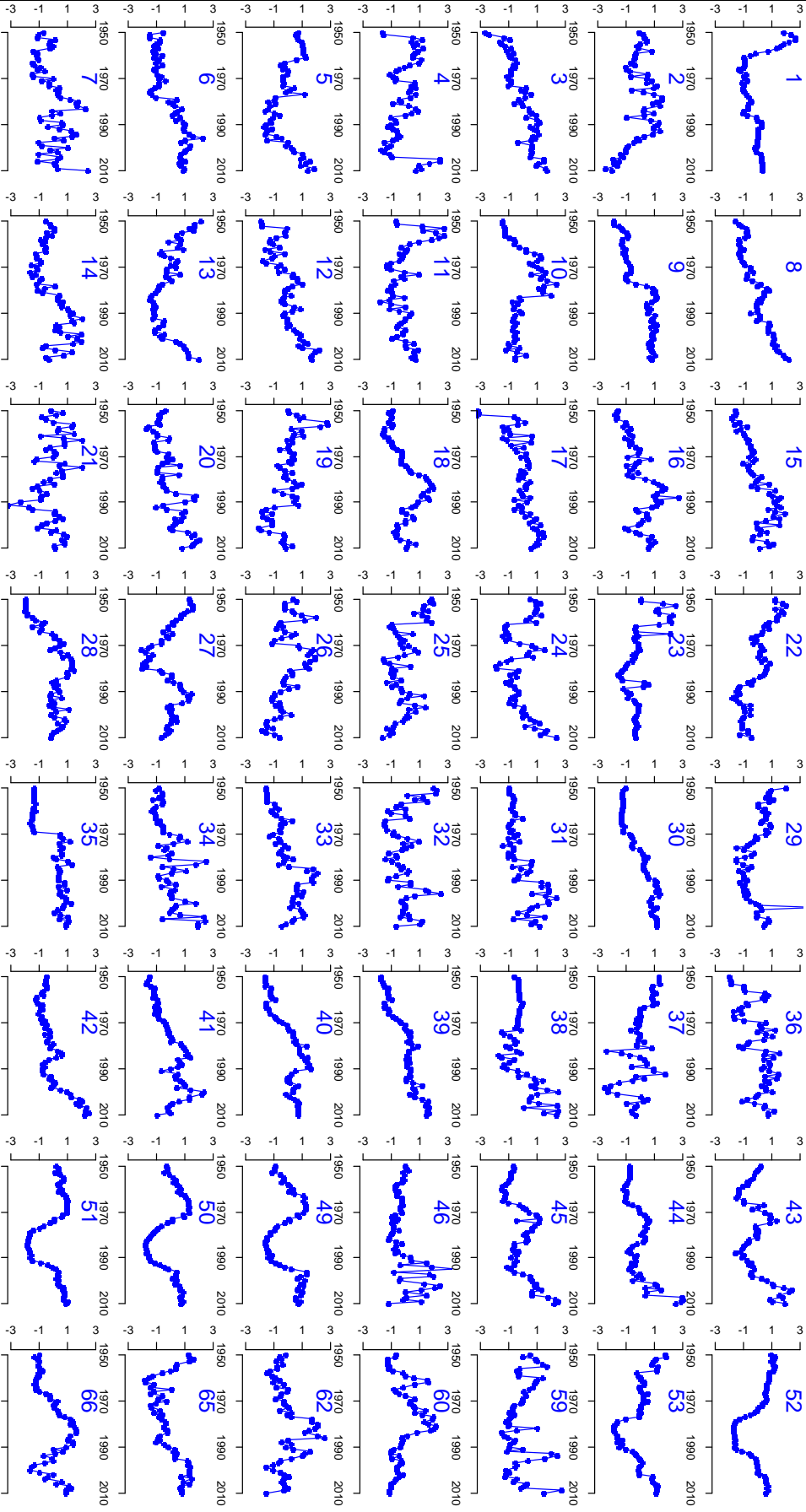
PPR/PP 2000s: <10%	2	63.16	60.00	0.0033***	2.942
Low Lindex	2	66.67	50.00	0.0056**	2.769
MTL stable	2	51.72	75.00	0.0114*	2.530
Lindex 2000s low	2	64.29	45.00	0.0151*	2.430
Habitat: tropical	2	51.85	70.00	0.0183*	2.360
Prop cephalopods 1-5%	2	50.00	65.00	0.0448*	2.009
Habitat: polar	2	8.33	5.00	0.0260*	-2.226
Lindex 2000s: very high	2	15.00	15.00	0.0173*	-2.380
MTL decrease	2	16.00	20.00	0.0066**	-2.718
Lindex 2000s: very high	3	65.00	61.90	0.0023**	3.052
Lindex high	3	62.50	47.62	0.0201*	2.325
PPR/PP <10%	3	20.00	19.05	0.0489*	-1.969
Lindex 2000s: low	3	14.29	9.52	0.0417*	-2.037
Lindex low	3	13.33	9.52	0.0255*	-2.234
SST increase >0.7°C	3	35.00	63.64	0.0495*	1.963
Habitat: polar	4	21.43	100.00	0.0079**	2.655

*p.value <0.05 ' * '*

*p.value <0.01 ' ** '*

*p.value <0.001 ' *** '*

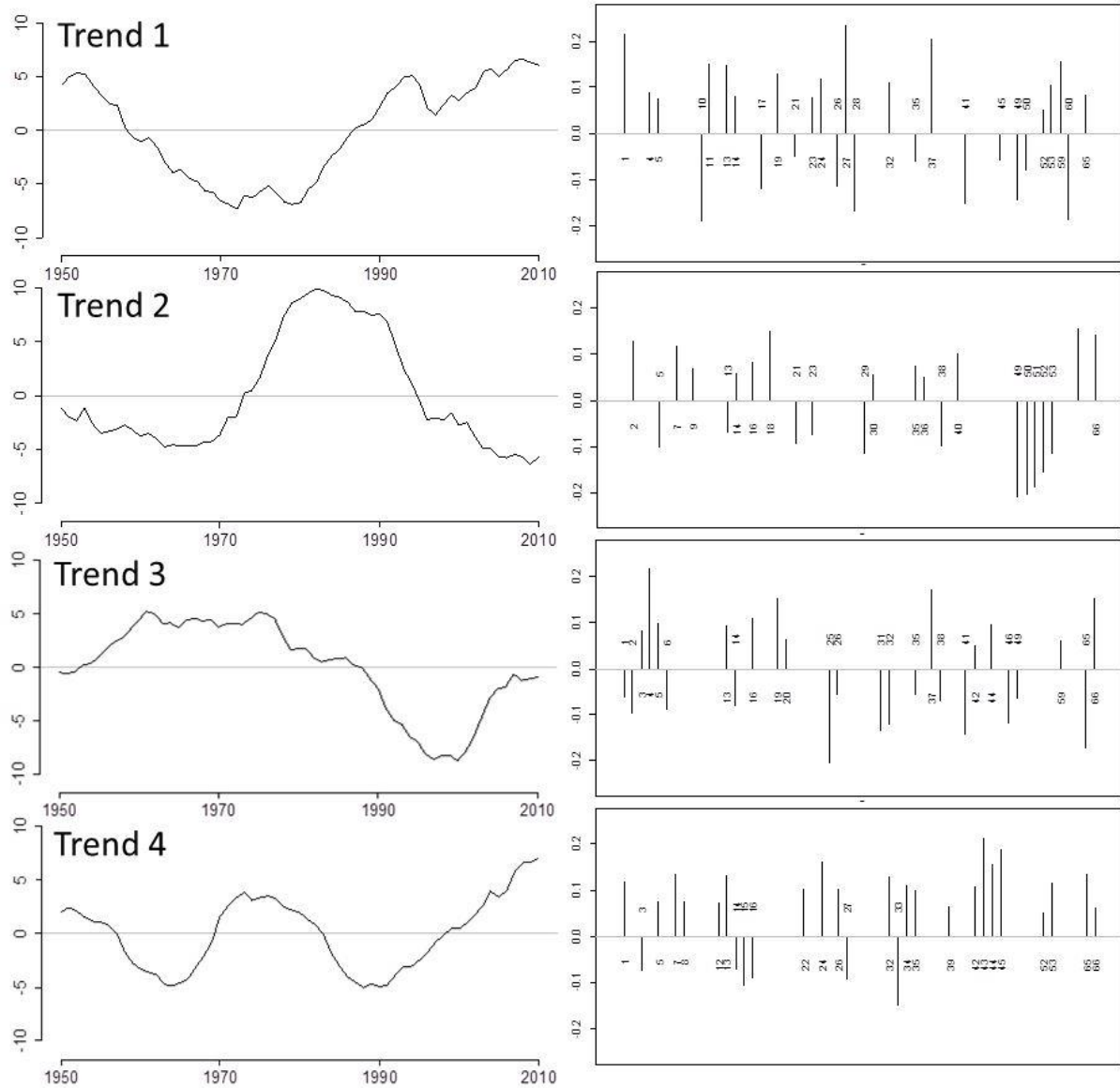
Appendix VIII: Dynamic Factor Analysis, Complementary results on the models



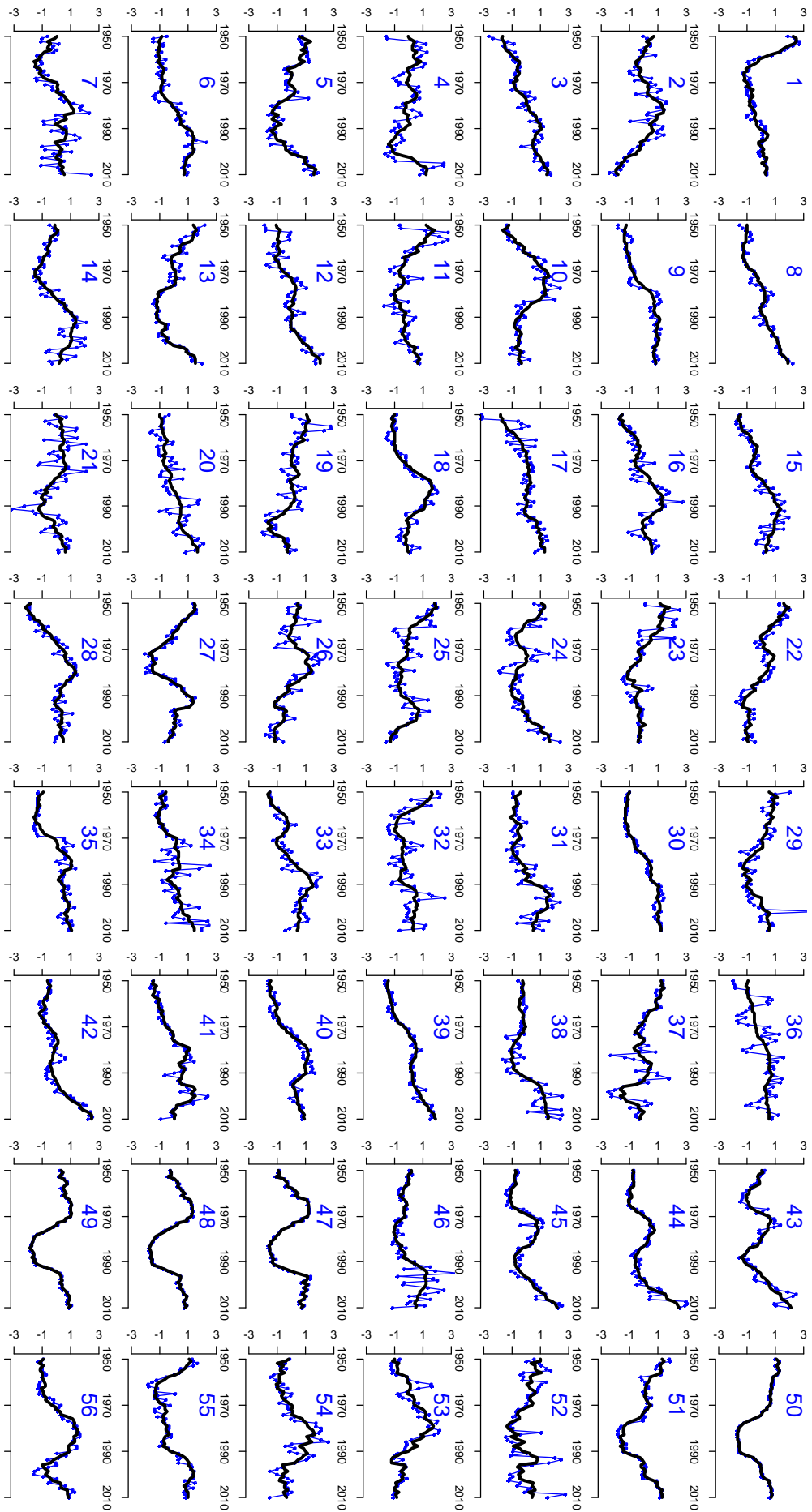
App VIII, Fig.1

The previous graph represents the time-series per LMEs for the standardized data as an input for the Dynamic Factor Analysis.

The following graphs are the results from the DFA for 4 trends and 2 covariates: the Sea Surface Temperature (SST) and the Stock Status Plot (SSP). The following graph shows the four trends on the left from the DFA output and the corresponding factor loadings for the 56 LMEs on the right. Then the last graph in this Appendix represents the fits per ecosystem obtained after the model run, including the covariates coefficients for the SST and SSP.



App VIII, Fig.2

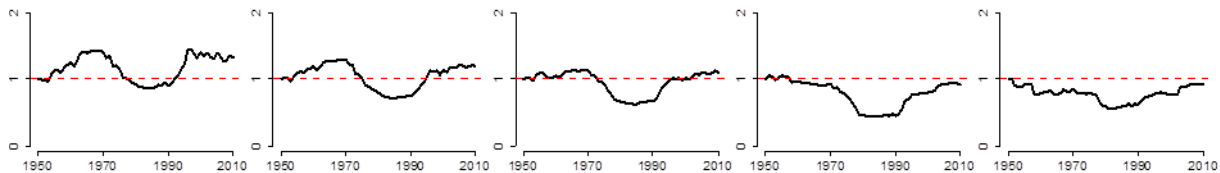


App VIII, Fig.3

Appendix IX: Complementary analysis: geographical efficiency types

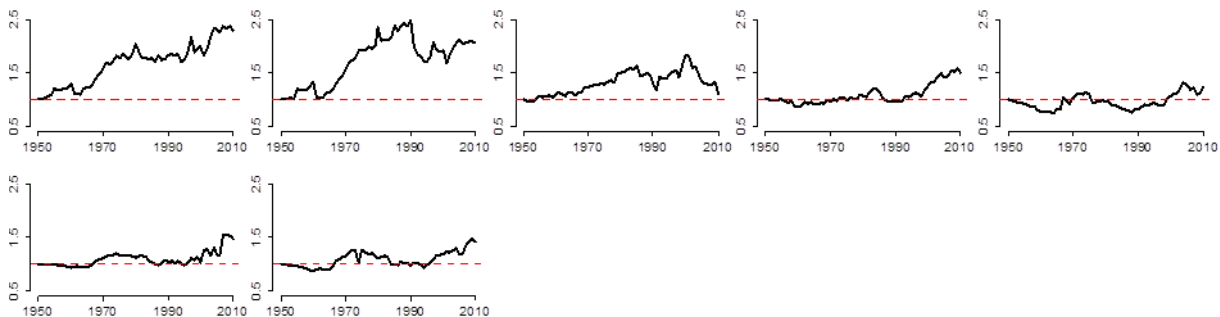
Two various types of evolution in the ECI have been identified in the Dynamic Factor Analysis linked to the geography of the Large Marine Ecosystems.

- The Asian ecosystems from 49 to 53 as (Kuroshio Current, Sea of Japan, Oyashio Current, Sea of Okhotsk and West Bering Sea)
- The Australian ecosystems from 39 to 45 (North Australian Shelf, Northeast Australian Shelf, East-Central Australian Shelf, Southeast Australian Shelf, Southwest Australian Shelf, West-central Australian Shelf, Northwest Australian Shelf).



App IX Fig.1: ECI time-series - relative to 1950 for the 5 Asian LMEs (49 to 53)

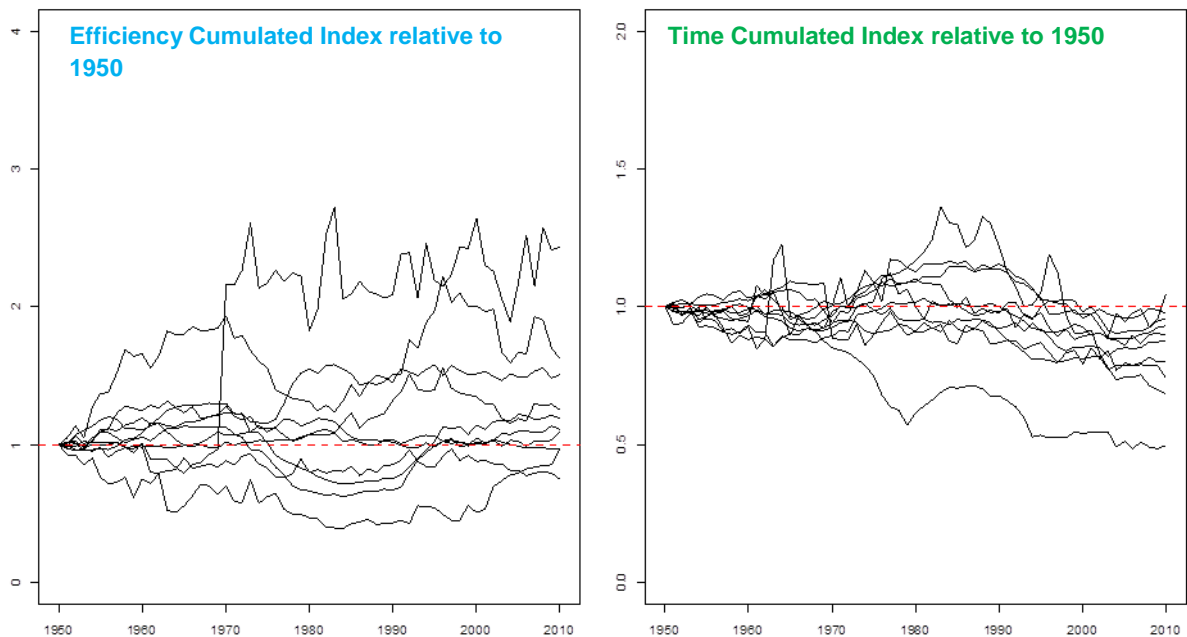
One species only is driving all the temporal changes as identified for the Sea of Japan LMEs in the species assemblage analysis. The pilchard *Sardinops sagax* species is driving the decrease in the Efficiency Cumulated Index in the 80s-2000s for the 5 ecosystems. This small pelagic species is identified as an important efficiency driver in other ecosystems such as the Humboldt Current and the California Current. However, in these other ecosystems, the efficiency is influenced by several trophic classes. *Sardinops sagax* has a trophic level of 2.84 so it influences the ecosystem functioning from the bottom part. Its low food conversion efficiency (0.033) and high speed ($0.6975y^{-1}$) explain the trends of the ECI in comparison to the other species in the same trophic class. The peak of catches of this species was in 1985 (nearly 13millions of tons at the worldwide scale, Sea Around Us data) and its abundance depends directly on the El Niño Southern Oscillation episodes.



App IX Fig.2: ECI times-series – relative to 1950 for the 6 Australian LMEs (39 to 45)

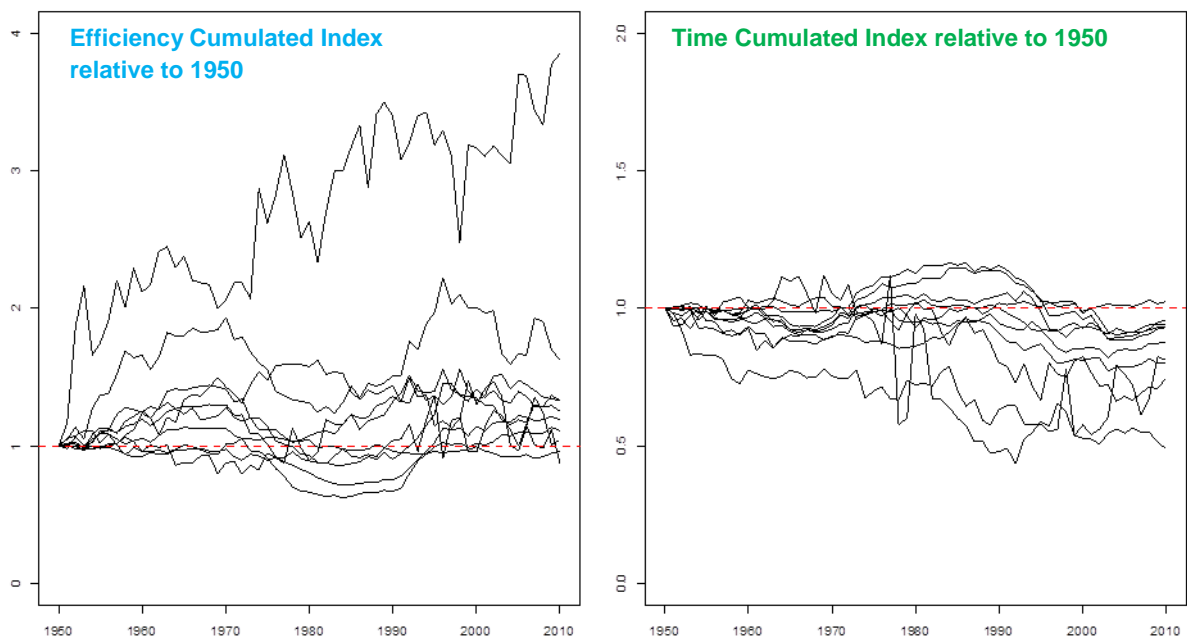
Concerning the Australian ecosystems, a global increasing efficiency is observed. Then, it was interesting its geographical similar trend. However, each ecosystem seems to present specific species assemblage variations on the times-series. Some are common but generally the increasing efficiency is due to many species. Still the shrimp's fishery was identified as driving an elevated ECI on the North Australian Shelf and the Northeast Australian Shelf. For the Southwest Australian Shelf and the Northwest Australian Shelf, *Sardinops sagax* was found again influencing largely the indices.

Appendix X: ECI and TCI for the most impacted LMEs through L_{index} , proportion of fish species and SST



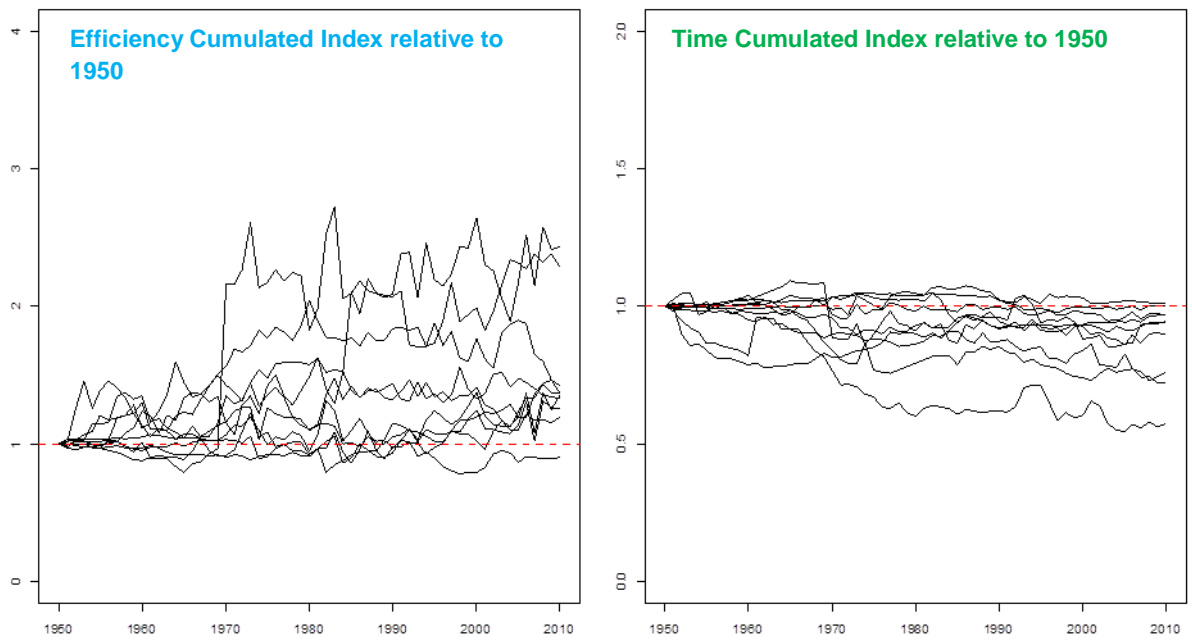
App. X Fig.1: ECI and TCI trends relative to 1950 for the 10 most exploited ecosystems (L_{index})

The upper graphs do not show any clear common trend for the most 10 exploited ecosystems. We took the example of the L_{index} fishing pressure but it is the same kind of results for the 4 other indices.



App. X Fig.2: ECI and TCI trends relative to 1950 for the 10 LMEs showing the highest increase in cephalopods proportion

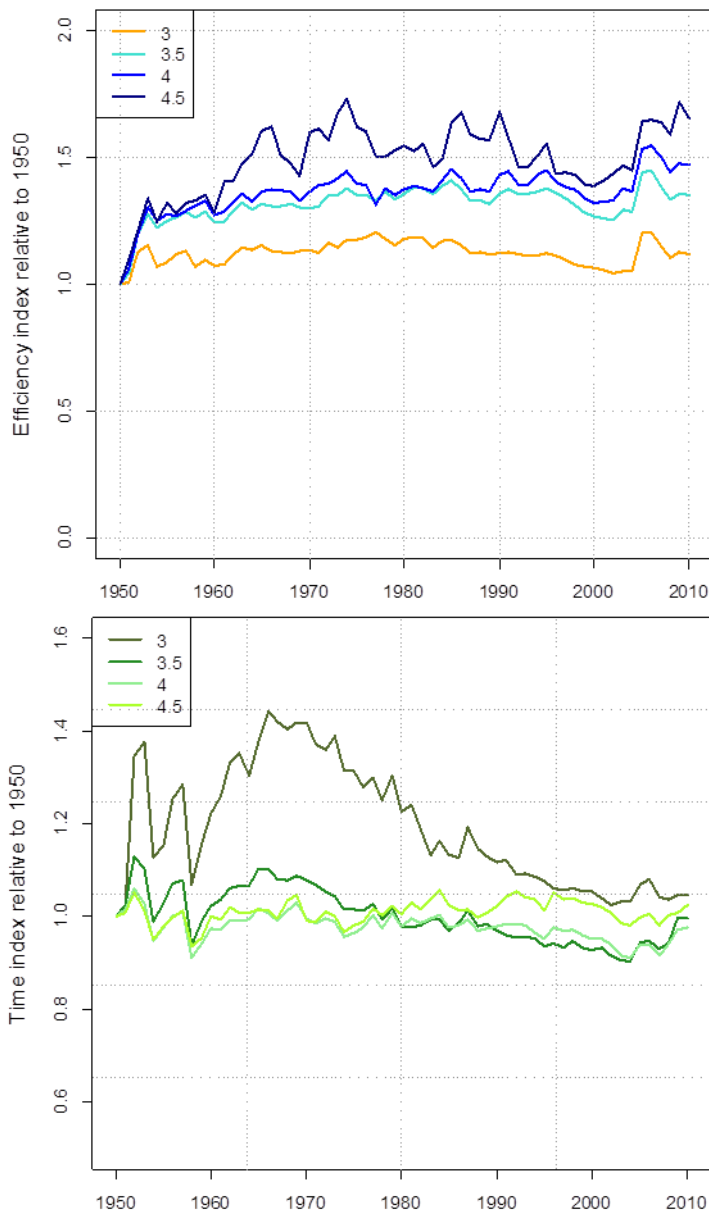
An increasing proportion of cephalopods species demonstrates a global increasing ECI trend and a decreasing TCI trend, which is concordant with the discussion ideas.



App. X Fig.3: ECI and TCI trends relative to 1950 for the ecosystems showing the highest increase in Sea Surface Temperature

As we were expecting the ECI to decrease and the TCI to increase with the SST and climate change, the exact opposite trends confirm that our study does not answer to climate change effect, for several possible reasons detailed in the discussion.

Appendix XI: Complementary analysis: indices with fish species only on the California Current



App XI, Fig.1: ECI (top) and TCI (bottom) relative to 1950 cumulated to different trophic-level limits from 3.0 to 4.5 for the California Current on fish species only

In order to test the hypothesis that the cephalopods, shrimps and other crustaceans might drive many changes and notably to more productive ecosystems with faster biomass transfers at a worldwide scale, a complementary analysis was conducted. As the California Current is suspected to be highly influenced by squids and the jumbo flying squid for its very high increasing efficiency, the indices were calculated without the non-fishes groups. However, the ECI and TCI were cumulated starting TL=2.5 because very few species

were influencing the indices. It appears that even without the cephalopods and other mollusks and crustaceans, the ECI of the California Current is still increasing on the time-series. Then, the non-fish species might influence a high part of the variability on this ecosystem, but it might not be all of it. The TCI is still decreasing a little but nothing compare to the very high decrease observed on the basis integrated index.



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Titre français : Impacts de la pêche et du changement climatique sur le fonctionnement trophique des écosystèmes marins : une méta-analyse mondiale des changements passés de l'efficacité et de la vitesse de transfert

Titre anglais : Fishing and climate change impacts on the trophic functioning of marine ecosystems: a worldwide meta-analysis of the past changes in transfer efficiency and kinetics

Résumé :

Le développement de la pêche à l'échelle mondiale et de divers impacts anthropiques tels que le changement climatique se sont accompagnés de changements d'abondances d'espèces, de composition spécifique et d'interactions trophiques. Ainsi, le fonctionnement des réseaux trophiques s'en trouve perturbé et ces impacts modifient la productivité, la stabilité et la résilience des écosystèmes marins. Cette étude trophique – utilisant des bases de données mondiales et les traits d'histoire de vie des espèces marines – teste l'hypothèse que la pêche et le changement climatique provoquent une perte de productivité et de stabilité, avec des effets négatifs sur les top-prédateurs. Nous avons analysé l'ensemble des Large Marine Ecosystem (LMEs) présentant des fonctionnements, des habitats, des régimes de pêche et de climat très variables. Le fonctionnement trophique est étudié à partir de deux paramètres : la vitesse de transfert et l'efficacité de transfert de 1950 à 2010. Deux indices construits à partir de ces deux paramètres théoriques ont été testés et validés : un indice d'efficacité cumulée (ECI) et un indice de temps de transfert cumulé (TCI). En fonction de l'écosystème étudié, plusieurs espèces sont identifiées comme responsables des changements. Ces indices ne sont pas stables au cours du temps mais ne suggèrent pas cependant une systématique évolution vers des écosystèmes moins productifs et aux temps de transfert plus rapides simultanément. A l'aide de plusieurs études quantitatives, le lien entre l'évolution de ces indices et les impacts anthropiques est étudié.

Abstract

The development of fisheries in the oceans, together with other natural and human drivers such as climate change, have led to changes in species abundance, composition, trophic interactions, and ultimately in the functioning of marine food webs such as their productivity, stability and resilience. Here, using a trophodynamic approach and global databases of catches and life history traits of marine species, we tested the hypothesis that human-induced ecological changes might have led to less productive and more unstable ecosystems, with potential adverse effects on top predators. We analyzed a set of Large Marine Ecosystems (LMEs) with contrasting trophic functioning, latitude, fishing and climate change intensities. We evaluated the changes of the speed of the biomass flow; surging up the food web from low to high trophic levels; and the trophic transfer efficiency, from 1950 to 2010. Two indices, based on these parameters, have been created, tested and validated to evaluate the ecosystem functioning changes since 1950 at the food web scale: the Time Cumulated Index (TCI) and the Efficiency Cumulated Index (ECI). Depending on the ecosystem, various species are identified as responsible of the changes. We show that those indices are not stable on the time-series and our results do not suggest simultaneously a global loss of productivity and faster speeds in the energetic transfers. Through several modelling and statistical techniques, the impact of fishing and climate change on the trophic functioning and the indices is explored.

Mots-clés : approche trophique, méta-analyse mondiale, Large Marine Ecosystem, efficacité de transfert, vitesse de transfert, fonctionnement des écosystèmes marins, changement climatique, impact de la pêche

Key Words: trophic-level based approach, global meta-analysis, Large Marine Ecosystem, transfer efficiency, kinetics, ecosystem functioning, climate change, fishing impacts