Environmental impact on fish communities in the global ocean : a mechanistic modeling approach

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Collège Doctoral du Languedoc-Roussillon

THÈSE

Pour obtenir le grade de

Docteur

Délivré par l'**UM2**

Préparée au sein de l'école doctorale **GAIA**
Et de l'unité de recherche **UMR 248 MARBEC**

Spécialité: **Écologie Communauté**

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Environmental impact on fish communities in the global ocean:

A mechanistic modeling approach

Soutenue le Le 7 mars 2016 devant le jury composé de

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Résumé

Les écosystèmes marins fournissent des services fondamentaux à l'humanité. Leur rôle dans le cycle du carbone contribue notamment à la régulation du climat, ils constituent par ailleurs une source importante de protéines animales à l'échelle planétaire. L'importance de ces services, la vulnérabilité avérée des écosystèmes marins au changement climatique et l'ampleur des changements attendus sont des injonctions pressantes à développer des moyens robustes pour mieux comprendre et prédire leur évolution. Dans cette perspective, cette thèse étudie l'impact de l'environnement sur la structure et le fonctionnement des écosystèmes marins, à l'aide d'un modèle du spectre de taille des communautés de poissons. Ce modèle est tout d'abord implémenté de manière adimensionnelle (0-D) idéalisée afin d'identifier les processus pertinents et d'analyser leurs rôles respectifs. Dans un second temps, le modèle est implémenté de manière tridimensionnelle (3-D) en résolvant les interactions spatiales dans les écosystèmes à l'aide du modèle APECOSM.

Le spectre de taille des communautés est la distribution de densité de biomasse en fonction de la taille des individus. Basés sur cette distribution, les modèles du spectre de taille permettent de représenter les propriétés des écosystèmes marins de façon mécaniste. Certaines variantes parmi ces modèles permettent une formulation fondée sur la représentation explicite de la diversité des traits d'histoire de vie au sein de la communauté. Dans cette thèse, un modèle du spectre de taille des communautés, structuré en tailles et en traits et basé sur la théorie DEB, est utilisé pour étudier théoriquement comment température et production primaire influencent les communautés de poissons.

Dans un premier temps, la réponse du spectre de communauté est étudiée à l'état stationnaire en 0-D, dans différentes configurations environnementales constantes. Quand la production primaire augmente ou quand la température diminue, le modèle révèle une dépendance variable des écosystèmes à leur environnement et caractérisée par quatre domaines de réponse distincts. Ces domaines sont liés au nombre de niveaux trophiques constituant les communautés, ils correspondent à différentes efficacités du transfert d'énergie des petits aux grands organismes. Nos résultats suggèrent que la sensibilité des écosystèmes aux changements environnementaux varie avec leur état environnemental.

Dans un second temps, la réponse 0-D du spectre de taille à des fluctuations environnementales est étudiée de manière dynamique, dans le cadre de cycles environnementaux

saisonniers. Le modèle révèle la propagation d'ondes le long des spectres. La propagation de ces ondes est contrôlée par deux processus: une advection de biomasse par la croissance des organismes et un transport de biomasse saltatoire lié à la prédation. À différentes latitudes, le transport de biomasse le long du spectre de taille des communautés est dominé par l'un ou l'autre de ces processus.

Afin de donner plus de pertinence à ces expériences adimensionnelles, le modèle est ensuite étudié le long d'un transect environnemental planétaire Nord-Sud idéalisé. Le modèle permet notamment d'expliquer les "lois de Bergmann", c.a.d. le fait que la taille des espèces augmente avec la latitude.

Finalement, le modèle a été incorporé à un modèle tridimensionnel des communautés marines (APECOSM) qui permet d'étudier la structuration 3-D de la biodiversité marine à l'échelle globale. Ce modèle est forcé avec des champs physiques et biogéochimiques climatologiques issus du modèle NEMO-PISCES. Le modèle permet d'estimer la biomasse totale de poissons dans les océans. De plus, il permet de décrire les caractéristiques des communautés de poisson dans différentes régions de l'océan global. Ce modèle est un pas vers une représentation mécaniste de l'impact de l'environnement sur la structure et les fonctions des écosystèmes marins dans l'océan prenant en compte le rôle fonctionnel de la biodiversité.

Abstract

Marine ecosystems provide fundamental services to humans. For instance, they contribute to the regulation of climate through the biological carbon pump and they are essential sources of food proteins worldwide. The importance of these services, the proven vulnerability of marine ecosystems to climate change and the magnitude of expected changes urge scientist to develop robust means to better understand and predict their potential evolution. In this perspective, this thesis investigates the impact of the environment on marine ecosystems' structure and function using a mechanistic trait-based community size-spectrum model for fish communities. The model is first implemented in a zero- dimensional idealized way (0-D) to identify the relevant processes and analyse their respective roles and interactions. In a second step, the model is implemented in a tridimensional way (3-D) and embedded into the APECOSM model to resolve the spatial ecosystem processes. This allows studying environmental impacts on the structure of global marine biodiversity.

The community size-spectrum is the distribution of biomass density as a function of individuals' size. It is a regular feature in marine ecosystems that community size-spectrum models exploit to model mechanistically marine ecosystems. In trait-based formulations, size-spectrum models account for the functional role of species diversity when deriving the community size-spectrum. In this thesis, a Dynamic energy Budget (DEB)-based trait-based community size-spectrum model is used to investigate theoretically how temperature and primary production influence the structure and functions of marine communities.

The response of the community spectrum is first investigated in 0-D at stationary state, in various constant environmental conditions. The model reveals a four domains response of fish communities to increasing resource levels and to decreasing temperature. These domains are related to the number of trophic levels sustained in the community, they correspond to different efficiencies of the transfer of energy from small to large organisms. Our results suggest that the sensitivity of ecosystems to environmental changes varies with the environmental state.

In a second step, the community response in 0-D is investigated dynamically, by forcing the model with different seasonal environmental cycles. The model reveals the propagation of waves along the fish community spectrum. Two processes control the propagation of

these waves: the growth-driven advection of biomass and the predation-driven saltation of biomass. At different latitudes the community level biomass transport along the spectrum is dominated by either of these two processes.

Following, in order to move toward more realistic situations, the model is studied along an idealized planet-wide North-South transect. Amongst other important characteristics, the model allows to explain the Bergmann's rules: the fact that larger species and larger individuals in the same species are found when latitude increases.

Finally, the model is embedded into the tridimensional ecosystem model APECOSM to study the global-scale 3-D structure of marine biodiversity. The model is forced with climatological physical and biogeochemical fields from the physics-biogeochemistry NEMO-PISCES model. The model provides estimates of the total fish biomass in the global ocean. It provides the characteristics of fish communities in the different ecosystems of the world ocean. This model is a step toward a mechanistic representation of the impact of the environment on the structure and function of marine ecosystems in the global ocean considering the functional role of biodiversity.

Remerciements

Les trois années et deux mois de cette thèse ont été une expérience grisante. Son accomplissement est néanmoins le fruit d'un effort soutenu qui a été facilité par la patience et le soutien de mon entourage.

Avant tout je tiens à remercier mon principal encadrant de thèse, Olivier Maury. Sans notre rencontre à l'Université du Cap (UCT) et sans sa confiance, je n'aurai jamais eu l'occasion de me lancer dans un tel projet. Il m'a permis une grande liberté dans cette recherche, me laissant largement autonome sur le traitement du sujet tout en suivant mon avancée avec intérêt. En toutes circonstances, il s'est rendu disponible et m'a aidé avec enthousiasme, pour surmonter les diverses difficultés scientifiques rencontrées, mais également pour m'aider à la préparation de conférences ou encore m'aider à la rédaction de ce mémoire. Olivier, je te remercie de m'avoir donné cette chance, d'avoir toujours été attentif au-delà du cadre académique et enfin pour tes encouragements jusqu'au terme de cette thèse.

J'aimerais aussi remercier d'autres intervenants importants durant ces années, à commencer par mon co-encadrant de thèse Jean-Christophe Poggiale. Il a toujours répondu à mes sollicitations et a apporté un regard extérieur précieux sur mes travaux en plus d'encouragements appréciés. Je tiens à remercier Olivier Aumont, membre du comité de thèse, qui par ses interventions m'a apporté une aide pertinente permettant de conforter le travail réalisé. Enfin, je remercie mon directeur de thèse, Philippe Cury, prompt à répondre à mes requêtes et qui a accepté de s'impliquer dans cette thèse malgré une collaboration à distance.

Je remercie également les membres du jury qui ont accepté de réviser et de discuter cette thèse: Uffe Høgsbro Thygesen, Éric Galbraith, Michel Loreau et David Mouillot. Ils ont donné de nombreux commentaires sur ce travail et ont suggéré autant de pistes à approfondir dans le futur, reconnaissant ainsi ce travail comme le jalon d'un parcours de recherche plus large. Je les remercie pour tout le temps qu'ils ont bien voulu investir dans cette révision et pour m'avoir fait l'honneur de s'intéresser à ce travail.

Cette thèse s'est déroulée en majeure partie à l'ICEMASA à UCT, dans la magnifique ville du Cap, me permettant de bénéficier d'un environnement idéal pour pouvoir de temps en temps m'échapper de mon bureau et profiter des beautés de la nature. Je re-

mercie Chris Reason, directeur du département d'océanographie de UCT pour avoir bien voulu m'accueillir durant tout ce temps. Je remercie également Francis Marsac, directeur de l'ICEMASA, pour m'avoir accepté comme membre de ce laboratoire. La fin de cette thèse s'est ensuite déroulée la ville méditerranéenne de Sète. J'ai une pensée particulière pour Ghislaine Ferard-Pouget qui m'a maintes fois proposé son aide afin de faciliter mon installation et pour me simplifier la vie lors des dernières semaines de rédactions. Je remercie également les administrateurs des structures de calcul intensif CORE et CAPARMOR dont le travail a indirectement contribué à l'aboutissement de cette thèse.

Enfin, merci à tous les collègues et amis qui m'ont accompagné durant ces trois ans et deux mois. First of all, thanks to the fellow PhD students of the "Square of hope and happiness", our beloved office, for all the fun times and sometimes heated debates: to our ancestor Majuto, to my office companion in every circumstances Obadias and his usefull flashlight to work late hours during the load sheddings crisis, to the irreplaceable Katherine and her efforts to take us out of campus from time to time, and to the newbies Daneeja and Majambo, keep the happiness! Un grand merci à Philippe, tout d'abord pour tout son travail sur le modèle APECOSM sans lequel je n'aurais pu aller aussi loin durant cette thèse, ainsi que pour son accueil et soutien avec Ainhoa au cours des derniers mois de rédaction. Un grand merci également à Laure, pour les bons moments passés au Cap et pour son assistance administrative et logistique essentielle. To my oldest friend in Cape Town, Ricardo, foreign PhD student like me and who has been a good adviser during this thesis with his one year extra experience, but more importantly, thanks to the delicious Peruvian dinners! Un merci particulier également à Bastien, qui du haut de sa position de postdoc a été un bon conseillé durant toutes nos sessions de mentorat à UCT pub. To Louis also, excellent adventure companion, thanks for the unforgettable moments! Une pensée particulière pour Vincent, pour ton aide technique au début de cette thèse mais surtout nos folles échappées sous-marines et expéditions à travers l'Afrique. Une pensée également pour Jeremy, les leçons de physique océanique et le reste... La liste est longue et j'oublie nécessairement des personnes, un grand merci à tous ceux avec qui j'ai partagé de bons moments et que j'ai surtout ennuyés au moins une fois à trop parler de mon sujet de thèse: Sarah, Fehmi, Lekraj, Elias, Yonss, Juliano, Xavier, George noel, Coralie, Alice, Adelaide, Marion, Rodrigue... Enfin, merci aux membres de la station Ifremer de Sète de m'avoir accueilli vers la fin de cette thèse, en particulier mes compagnons de bureau Camille et Jules, ainsi que les doctorants pour m'avoir confectionné un chapeau des plus coloré pour célébrer l'aboutissement de cette thèse.

Last but not least, thanks to Rama who has been an essential support during these three years and two months. Her unshakeable good humor is always resourcing and allows all difficulties to pass more smoothly. Thanks for your patience and thanks for investing yourself into this project with me, particularly reviewing many chapters of the thesis. Eish, now it is done !

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Part I

Résumé étendu

1 Contexte

Les océans et les écosystèmes marins fournissent de nombreux services à l'humanité. Ils contribuent aux quatre catégories de services écosystémiques identifiées lors de l'Évaluation des Écosystèmes pour le Millénaire en 2005 [1], c'est-à-dire: les services d'approvisionnement, de régulation, de soutiens et culturels. À titre d'exemple, les écosystèmes marins contribuent à la régulation du climat par leur rôle dans le cycle du carbone [2], ils contribuent également de façon significative à l'approvisionnement en protéines animales à l'échelle planétaire [3].

L'environnement contraint les écosystèmes marins et les services qu'ils fournissent. Les variations environnementales saisonnières influencent notamment le rendement et la qualité des captures de pêche [4]. À une échelle plus globale, la variabilité climatique affecte le cycle du carbone [5]. Avec l'intensification du changement climatique, la pollution ou encore la surexploitation des ressources halieutiques [6], les océans et les services essentiels qu'ils fournissent sont de plus en plus affectés, voire menacés. Il devient urgent de s'adapter aux effets induits par ces pressions environnementales, qu'ils soient en cours ou attendus. Pour y parvenir, **il est nécessaire de mieux comprendre les effets de l'environnement et du changement climatique sur les écosystèmes marins, notamment le rôle de la biodiversité [7, 8].**

Comprendre les effets de l'environnement et du changement climatique sur les écosystèmes marins est évidemment un énorme défi. Un très grand nombre de facteurs environnementaux interagissent de manière complexe [9, 10, 11]. **Ces effets peuvent être étudiés à différents niveaux d'organisation allant des individus, aux populations, espèces ou encore communautés.** Ces différents niveaux d'organisation sont liés les uns aux autres, des effets directs à un niveau d'organisation induisent des effets indirects à un autre niveau. Par exemple, un réchauffement de l'eau dans laquelle nagent des individus augmente directement leur métabolisme et leur taux d'activité [12, 13]. Au niveau de la communauté, en raison d'une différence de sensibilité au réchauffement entre les processus associés à l'assimilation de nourriture et ceux associés à la respiration [14], ce réchauffement induit indirectement une augmentation de la proportion d'espèces de petite taille et une diminution de la longueur des individus au même âge [15]. **Les effets de l'environnement peuvent être également étudiés à différentes échelles spatio-temporelles, allant du local au régional à l'océan global.** À différentes échelles, les mêmes facteurs environnementaux induisent différents effets. Par exemple, différentes espèces sont associées à différentes gammes optimales de températures. Au niveau local, ces différences expliquent l'alternance d'espèces dominantes, telle que des régimes chauds dominés par des anchois et des régimes froids dominés par des sardines dans le Nord-Ouest du Pacifique [16]. À l'échelle globale, le réchauffement des océans induit des changements dans la structure des écosystèmes, différentes espèces traquant ce

réchauffement à différentes vitesses [17].

Le changement climatique est un phénomène global, pour étudier ses effets sur les services fournis par les écosystèmes marins l'échelle globale est donc plus appropriée. Cependant, l'environnement affecte les individus localement. **Afin de comprendre comment les écosystèmes marins sont affectés par les perturbations environnementales, il est nécessaire de comprendre la propagation de ces perturbations d'un niveau d'organisation à un autre. Les interactions entre échelles spatiales doivent également être clarifiées.** C'est une tâche colossale que des modèles d'écosystèmes de plus en plus complexes permettent d'aborder [18].

Une grande variété de méthodes de modélisation existe pour représenter les écosystèmes marins, à différents niveaux d'organisation et à différentes échelles. Ces modèles représentent les bas niveaux trophiques avec des modèles biogéochimiques [19, 20], ils représentent les niveaux trophiques supérieurs en soulignant différents aspects, tels que l'histoire de vie des individus [21], ou la structure trophique des écosystèmes [22], entre autres [23, 24]. **Pour représenter la propagation des perturbations environnementales à travers les écosystèmes, des formulations dites "end-to-end" [25, 26] modélisent les écosystèmes marins en intégrant les processus du niveau physique jusqu'au niveau de la pêche en passant par toutes les composantes du vivant.** De telles formulations sont possibles grâce à l'augmentation des ressources en calcul et une meilleure compréhension de la complexité des écosystèmes.

Dans l'océan global quelques modèles du type "end-to-end" permettent d'estimer les effets du changement climatique sur les écosystèmes marins [27, 28, 29]. **Cependant, dans ces modèles globaux la représentation du rôle de la biodiversité sur le fonctionnement des écosystèmes reste un défi.** Alors que la biodiversité a lentement pris sa structure actuelle au cours des temps géologiques, elle est aujourd'hui menacée par la rapidité du changement climatique [30]. Afin d'obtenir des modèles valables des effets de l'environnement et du changement climatique sur les écosystèmes marins, ces modèles doivent prendre en compte les processus permettant l'émergence et la disparition de cette biodiversité. **Elle est habituellement agrégée au sein de groupes fonctionnels [27, 28] ou bien est explicitée par l'accumulation d'espèces [29].** Alors que dans le premier cas la biodiversité est représentée de façon grossière, dans le second cas, elle est associée à de nombreux paramètres souvent difficiles à estimer. **Une stratégie alternative consiste à caractériser cette biodiversité par la définition de traits fonctionnels**, des caractéristiques morphologiques ou physiologiques qui affectent les performances individuelles [31, 32]. Au lieu de considérer les caractéristiques taxinomiques des espèces, ces traits permettent de souligner le rôle fonctionnel occupé par une espèce.

Afin de mieux comprendre les effets de l'environnement et du changement climatique sur les écosystèmes marins, cette thèse étudie les effets des variations de ressource aux bas niveaux trophiques et les effets des variations de

température sur la structure des communautés de poissons. Pour y parvenir, cette étude est articulée autour du développement d'un modèle global des écosystèmes marins avec une représentation du rôle de la diversité d'espèces caractérisée par un trait fonctionnel: la longueur structurelle maximale atteinte par les individus d'une espèce.

2 Objectifs et résultats principaux

L'objectif principal de cette thèse est d'étudier les effets de l'environnement, essentiellement les effets de la ressource et température, sur la structure des communautés de poissons dans l'océan global, tout en considérant le rôle fonctionnel de la biodiversité.

Cet objectif général nécessite le développement d'un modèle de communauté prenant en compte le rôle fonctionnel de la biodiversité. Ce modèle doit être implémenté dans un contexte "end-to-end" à l'échelle de l'océan global. **Quatre objectifs intermédiaires sont traités pour y parvenir (voir Fig. I).** Les problématiques ainsi que les principaux résultats associés à ces objectifs intermédiaires sont présentés dans les quatre paragraphes suivants.

2.1 Détermination d'un cadre de modélisation adapté (OBJ1)

OBJ1: Quel cadre de modélisation permet la représentation des effets de l'environnement sur les communautés de poissons dans l'océan global, tout en permettant de prendre en compte le rôle fonctionnel de la biodiversité ?

De nombreux modèles sont disponibles pour représenter différents aspects des communautés de poissons [23, 24]. Le modèle adopté pour cette thèse doit être suffisamment générique pour être applicable dans tous les écosystèmes de l'océan global, des pôles à l'équateur et des régions oligotrophes à eutrophes. Il doit également rester prédictif dans des conditions environnementales inconnues, telles qu'elles peuvent arriver dans le futur. Ce modèle doit donc représenter les écosystèmes de manière mécaniste. Finalement, le modèle doit permettre la représentation des effets directs de l'environnement sur les individus tout en représentant les effets indirects au niveau de la population et communauté.

La longueur des individus s est un trait important pour expliquer la structure des communautés marines. Cette taille permet de décrire les relations de prédation entre proies et prédateurs [33, 34]. Elle permet de caractériser les propriétés physiologiques d'individus de différentes tailles, notamment leur croissance ou respiration [35, 36, 37].

Une conséquence remarquable de l'importance de la taille des individus pour la structuration des communautés est la régularité de la distribution de biomasse [38]. **Sur une échelle log-log, la densité de biomasse B en fonction de la longueur des indi-**

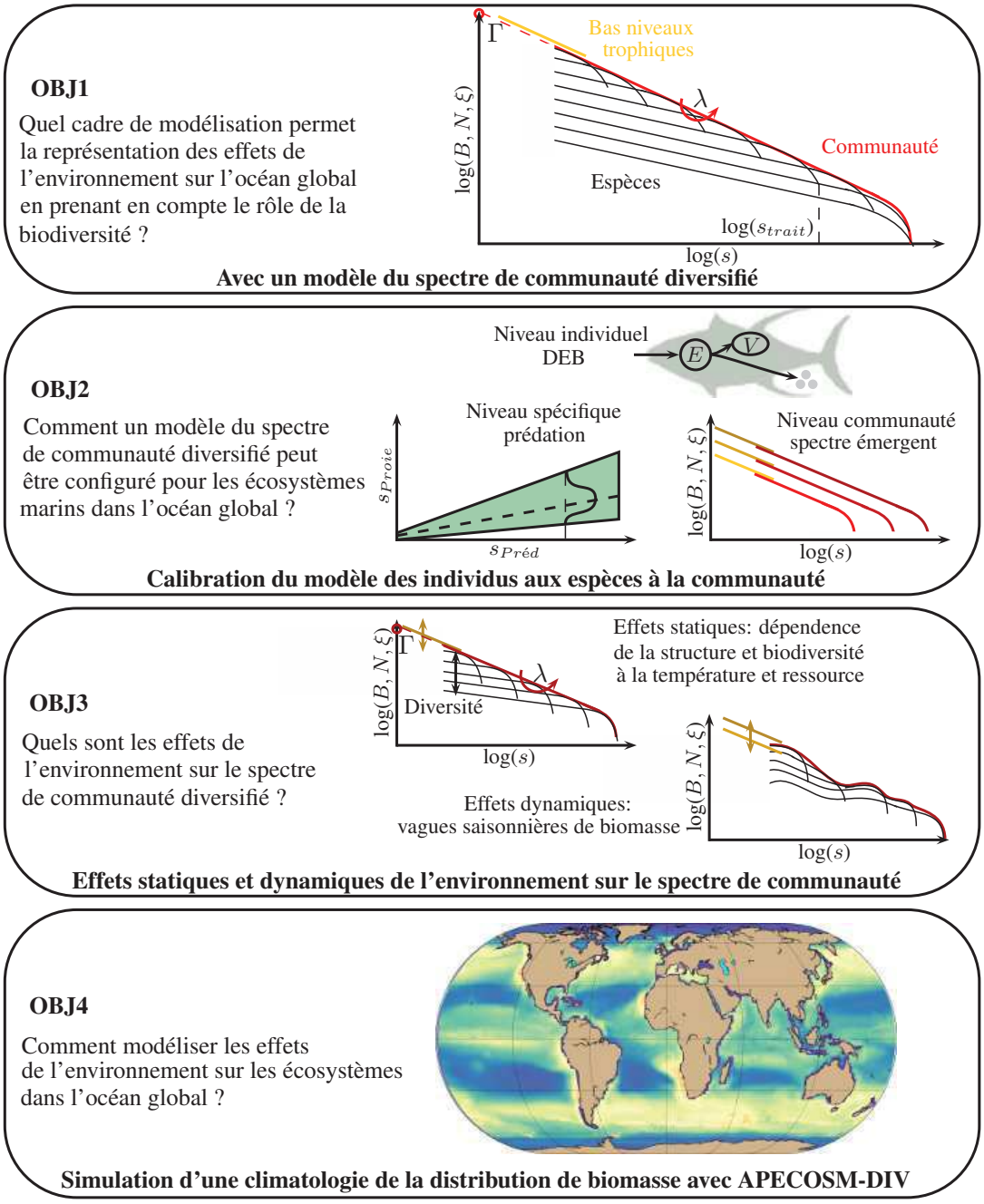


Figure I L'objectif de cette thèse est d'estimer les effets de l'environnement sur la structure des communautés de poissons dans l'océan global, tout en prenant en compte le rôle fonctionnel de la biodiversité. Quatre objectifs intermédiaires (OBJ) sont identifiés pour atteindre cet objectif principal.

vidus s est proche d'un spectre linéaire. Une telle régularité s'observe également pour la distribution de la densité d'abondance N ou de la densité d'énergie ξ. Ce spectre (voir OBJ1 Fig. I en rouge) est observé dans de nombreux écosystèmes et s'applique aussi bien aux communautés planctoniques [39, 40, 41] qu'aux communautés de poissons [42, 43]. Il permet de décrire l'état général des communautés avec deux indicateurs: une pente λ et un intercept Γ. Le premier exprime la contribution relative au sein de la communauté entre individus de petite et grande taille, il caractérise l'efficacité du transfert d'énergie le long de la chaîne trophique. Le second exprime l'abondance globale au sein de la communauté, les régions oligotrophes ont un faible intercept comparativement aux régions eutrophes [44].

Les modèles de spectre de communauté exploitent la forte structuration en taille des écosystèmes marins afin de modéliser de manière mécaniste les flux de biomasse entre les individus les plus petits et les individus les plus larges au sein de ces communautés [45, 46, 47, 48, 49]. Ils expliquent la régularité de la distribution de biomasse par un équilibre entre la prédation, la croissance et la respiration au niveau individuel, tous trois contrôlés par la taille des individus [50]. Diverses applications de ces modèles ont permis d'estimer l'impact de la pêche sur la distribution de biomasse dans les écosystèmes [34, 51, 52], elles ont permis d'étudier les effets de l'environnement [53] et du changement climatique [28] sur les propriétés du spectre de biomasse. **Des développements récents des modèles de spectre de communauté permettent désormais de prendre en compte le rôle fonctionnel de la biodiversité dans ces études [54, 55].** La diversité d'espèces y est représentée en désagrégeant le spectre de communauté en une série de spectres spécifiques différenciés par un trait s_{trait}, la longueur maximale que les individus d'une espèce peuvent atteindre (voir OBJ1 Fig. I en noir).

Les modèles de spectre de communauté caractérisent différents écosystèmes avec un cadre de modélisation unique. Ils expriment le rôle fonctionnel de la biodiversité et lient de façon mécaniste la physiologie des individus aux espèces à la communauté. Ainsi, **en réponse au premier objectif (OBJ1), les modèles de spectre de communauté diversifié s'avèrent particulièrement adaptés comme base pour l'étude des effets de l'environnement et du changement climatique sur les écosystèmes dans l'océan global [7].** Un modèle détaillé par Maury et Poggiale (2013) [55] a été choisit pour la suite de cette thèse, au niveau individuel, il a la particularité de résoudre précisément la physiologie avec la théorie du "Dynamic Energy Budget" (DEB) [56].

2.2 Modélisation de communautés de poissons avec un modèle de spectre de communauté diversifié (OBJ2)

OBJ2: Comment configurer le modèle du spectre de communauté diversifié afin de représenter les communautés de poissons et la propagation des effets de l'environnement des individus aux espèces aux communautés ?

Le modèle détaillé par Maury et Poggiale (2013) [55] doit être paramétré afin de ressembler à des communautés de poissons réelles. La physiologie au niveau individuel doit correspondre à ce qui est observé dans la nature. La sélection de proies par les prédateurs doit être conforme aux interactions observées dans la nature. De plus, des conditions environnementales distinctes dans différents écosystèmes devraient permettre l'émergence de spectres de communautés distincts.

Les modèles de spectre de communauté permettent la représentation des propriétés globales des écosystèmes avec peu de connaissances de la structure du réseau trophique. Cet avantage devient un inconvénient pour la calibration de ces modèles, il n'y a pas de formalisme particulier permettant de reproduire les caractéristiques d'écosystèmes donnés avec un modèle de spectre de communauté. **Dans cette thèse, le modèle est successivement paramétré aux différents niveaux d'organisation, au niveau individuel, spécifique et au niveau de la communauté (OBJ2 Fig. I).**

Au niveau individuel, le modèle est basé sur la théorie DEB. Cette théorie a été appliquée pour la modélisation de la physiologie d'individus appartenant à une grande diversité de taxon, dans l'environnement aquatique aussi bien que terrestre. Une liste de paramètres génériques en a été déduite [56]. Ici, les paramètres DEB génériques sont adaptés pour correspondre plus précisément à la physiologie d'espèces de poissons [57] (voir annexe). Les différences entre espèces caractérisées par le trait s_{trait} sont simplement exprimées par une proportionnalité des paramètres génériques avec s_{trait}.

Au niveau des espèces, les spectres spécifiques sont couplés les uns aux autres par la prédation. Cette prédation ignore l'identité des espèces et est uniquement caractérisée par la relation entre la taille des prédateurs $s_{Préd}$ et la taille de leurs proies potentielles s_{Proie}. Ainsi, les prédateurs de chaque espèce peuvent se nourrir sur n'importe quelle espèce du moment que la proie est à une taille adéquate. Les paramètres de la relation entre tailles des prédateurs et tailles des proies sont calibrés afin de reproduire des distributions de tailles de proies observées dans l'estomac de prédateurs [58] (Schéma de la distribution OBJ2 Fig. I).

Au niveau de la communauté enfin, la dynamique du spectre émerge de la somme des contributions spécifiques et leurs interactions. **Les effets de l'environnement au niveau individuel se propagent au niveau spécifique, puis à la communauté.** Les effets de l'environnement au niveau individuel sont dictés par le DEB, il s'agit essentiellement de l'effet des variations de nourriture disponible sur la physiologie, ainsi que l'effet de la température sur le métabolisme. Dans différents écosystèmes, des conditions environnementales différentes au niveau individuel induisent différentes propriétés des spectres de communauté. En particulier, dans des écosystèmes eutrophes un niveau de ressource élevé se traduit par un intercept élevé du spectre de biomasse aux bas niveaux trophiques (voir OBJ1 Fig. I en jaune), ce dernier va induire un intercept Γ élevé du spectre de la communauté de poissons. Inversement, dans des écosystèmes oligotrophes un niveau de

ressource bas induit un intercept Γ bas (voir OBJ2 Fig. I). **Les derniers paramètres du modèle sont calibrés afin de reproduire la variation de l'intercept du spectre de communauté dans des écosystèmes plus ou moins riches [44].**

En réponse au second objectif de cette thèse (OBJ2), trois étapes de calibration, des individus aux espèces à la communauté, permettent une représentation réaliste des communautés de poissons et permettent de reproduire des effets émergents de l'environnement sur les communautés.

2.3 Effets "locaux" de l'environnement sur le spectre de communauté diversifié (OBJ3)

OBJ3: Quels sont les effets de l'environnement sur le spectre de communauté diversifié ?

Une fois le cadre de modélisation identifié et le modèle configuré, les effets de l'environnement sur les propriétés du spectre de communauté sont étudiés. Ces effets sont étudiés localement, c'est-à-dire sur un spectre représentant une position ponctuelle de l'espace, ou encore un spectre moyen adimensionnel. Dans différents environnements, les propriétés du spectre de communauté diversifié sont peu connues, telles que les caractéristiques de la pente λ ou de l'intercept Γ, que ce soit dans des conditions environnementales statiques [41, 53] ou bien dynamiques [59, 53] (OBJ3 Fig. I). Les variations environnementales considérées ici se résument à des variations de la quantité de nourriture aux bas niveaux trophiques et des variations de température.

Dans un premier temps, les propriétés du spectre de communauté sont modélisées et comparées à différents niveaux constants de ressource et température. Ces niveaux sont sélectionnés afin de couvrir la gamme de conditions environnementales expérimentée par les communautés de poissons au sein de l'océan global. **Pour diverses combinaisons de ressource et température, différentes distributions de biomasse sont simulées.** Ces différentes distributions sont caractérisées par diverses pentes des spectres λ, divers intercepts Γ ou encore diverses tailles moyennes d'espèces (voir OBJ3 Fig. I). Le nombre de niveaux trophiques se développant au sein de ces communautés explique l'essentiel des variations. Ces résultats peuvent être résumés par la distinction de quatre domaines sur un diagramme de phase dans l'espace des niveaux de ressource et des températures (Fig. II). Ces quatre domaines, dit de collapse, régulier, de transition et saturé, sont indirectement associés à des spectres de communauté plus ou moins sensibles aux variations de leur environnement. Plus précisément, pour les quatre domaines les spectres de communauté sont respectivement très sensibles, sensibles, très sensibles de nouveau et insensibles. Maintenant, à différentes latitudes les écosystèmes marins sont caractérisés par différents niveaux moyens de ressource et température. Ainsi, en superposant au diagramme de phase les conditions environnementales moyennes rencontrées par les communautés de poissons le long d'une section allant du pôle Nord au

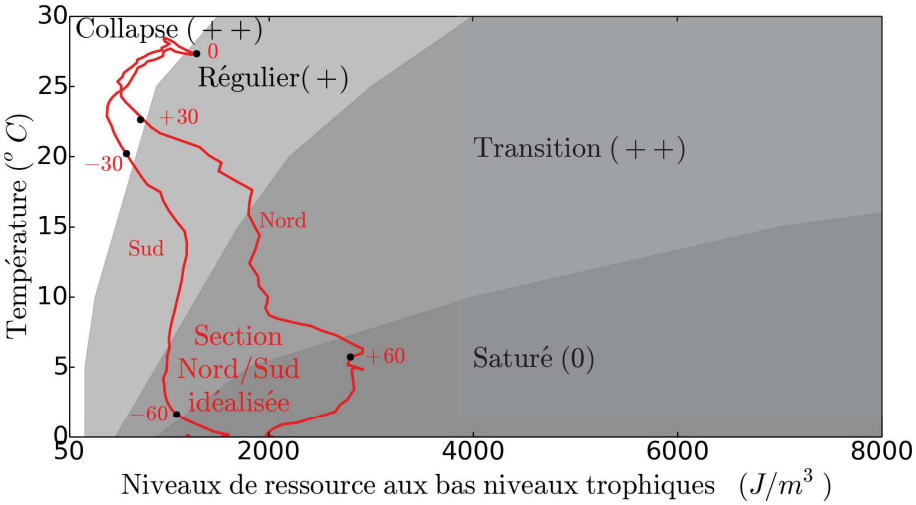


Figure II Diagramme de phase des communautés de poissons dans l'espace des niveaux de ressource et de température. Quatre domaines distincts peuvent être différenciés avec différentes propriétés des spectres de communauté diversifiés et différentes sensibilités aux perturbations environnementales (d'insensible 0 à très sensible ++). Les conditions environnementales moyennes rencontrées par les communautés de poissons le long d'une section allant du pôle Nord au pôle Sud permettent une estimation théorique de la sensibilité de ces communautés aux perturbations.

pôle Sud, cette étude permet une estimation théorique de la sensibilité des communautés de poissons à différentes latitudes (Fig. II en rouge). Globalement, les basses latitudes apparaissent particulièrement sensibles alors que les latitudes les plus hautes sont insensibles aux perturbations de leur environnement. D'après cette première expérience numérique, **le spectre de communauté diversifié est plus ou moins affecté par les perturbations environnementales dépendamment du nombre de niveaux trophiques qui le constitue.**

Dans un second temps, les propriétés du spectre de communauté diversifié sont modélisées et comparées dans des environnements variant saisonnièrement. Le modèle est forcé par des cycles de température et des cycles de ressource caractérisant différents écosystèmes à différentes latitudes de l'océan global. Le spectre de communauté est parcouru par des vagues de biomasse (voir OBJ3 Fig. I). **Dans ces environnements dynamiques, le modèle révèle deux processus principaux générant ces vagues et propageant le signal saisonnier des individus les plus petits aux individus les plus larges (voir illustration Fig.III): (1) l'advection de biomasse par la croissance en taille des individus; (2) le saut de biomasse entre classes de tailles s_{Proie} et $s_{Préd}$ par la prédation des individus les plus larges sur les individus les plus petits de la communauté.** La croissance des individus induit un transport de biomasse lent, la plupart des espèces de poissons atteignent

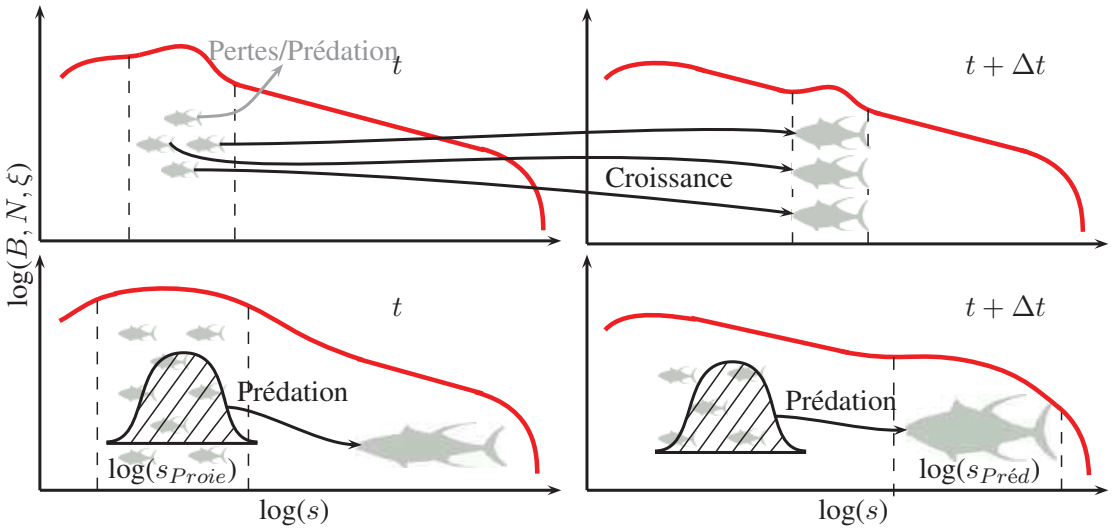


Figure III Entre deux pas de temps, deux processus principaux propagent le signal saisonnier le long du spectre de communauté diversifié: (1) l'advection de biomasse par la croissance en taille des individus (haut); le saut de biomasse entre classes de tailles s_{Proie} et $s_{Préd}$ par la prédation des individus les plus larges sur les individus les plus petits de la communauté (bas).

leur longueur maximale en plusieurs années. Inversement, le saut de biomasse induit un transport de biomasse rapide, la biomasse peut être transférée des individus les plus petits aux individus les plus larges en moins d'une année. D'après cette seconde expérience numérique, différentes espèces sont plus ou moins sensibles aux mêmes variations environnementales saisonnières, l'un ou l'autre des processus domine. **À différentes latitudes des pôles vers l'équateur, différentes sensibilités des espèces aux variations environnementales induisent la dominance de l'un ou l'autre des deux processus sur la dynamique du spectre de communauté diversifié.**

Ces expériences numériques locales permettent une meilleure compréhension des propriétés du modèle de spectre de communauté diversifié. **Ce troisième objectif (OBJ3) apporte quelques éléments de réponse sur les effets de l'environnement sur la structure des communautés de poissons dans l'océan global, que ce soit sur des spectres statiques ou dynamiques.**

2.4 Effets de l'environnement sur les écosystèmes de l'océan global (OBJ4)

OBJ4: Comment modéliser les effets de l'environnement sur les écosystèmes de l'océan global avec un modèle de spectre de communauté diversifié ?

Plusieurs modèles d'écosystèmes basés sur la représentation du spectre de communauté ont été implémentés, régionalement ou à l'échelle de l'océan global. Par exemple, ils ont été utilisés pour prédire la biomasse totale, la production ainsi que la structure des écosystèmes

dans l'océan global à partir de données de télédétection aux niveaux trophiques inférieurs [60, 61]. Forcés par des champs biogéochimiques, ils ont également été utilisés pour projeter l'effet dynamique du changement climatique et de la pêche dans différentes écorégions [28] ou à l'échelle de basins océaniques [62]. Cependant, ces méthodes peuvent être décrites comme la modélisation de spectres locaux en différents points d'une grille spatiale, c'est-à-dire qu'ils produisent des estimations spatiales, mais ils négligent le rôle des interactions entre régions. **Le modèle de communautés pélagiques APECOSM [27] considère explicitement les interactions spatiales, entre régions ainsi que le long de la colonne d'eau.** Il a notamment été couplé avec des modèles climatiques afin de projeter l'effet du changement climatique sur la structure des communautés pélagiques dans l'océan global [63].

Dans l'océan global, les modèles du spectre de communauté utilisés pour estimer l'impact du changement climatique adoptent une représentation simplifiée de la biodiversité. Au mieux, elle est agrégée au sein de groupes fonctionnels, par exemple épipélagique ou benthique [28], ou encore épipélagique, mésopélagique et migrants dans APECOSM [27]. **Pour mieux prendre en compte le rôle de la biodiversité, le modèle de spectre de communauté diversifié développé au fil de cette thèse est implémenté dans APECOSM.**

Le modèle APECOSM-DIV (DIVersifié) ainsi produit simule donc le flux de biomasse des individus les plus petits aux individus les plus larges dans trois communautés diversifiées (Fig.IV): épipélagiques, mésopélagiques et migrants. Il est forcé par le modèle couplé physique-biogéochimie NEMO-PISCES [20] qui fournit la ressource disponible aux bas niveaux trophiques (diatomées, microzooplancton, mésozooplancton et les particules inorganiques les plus larges), ainsi que la distribution de température dans l'océan global et le long de la colonne d'eau. NEMO-PISCES produit également la distribution d'oxygène et calcule la pénétration de la lumière le long de la colonne d'eau qui permettent de déterminer l'habitat tridimensionnel des communautés. Enfin NEMO [64] fournit les courants transportant la biomasse entre basins océaniques.

Le modèle APECOSM-DIV est utilisé pour simuler une climatologie d'un an de la distribution de biomasse de poisson dans l'océan global. Le réalisme de cette climatologie est estimé, notamment en comparant à d'autres modèles [60, 65, 66, 67, 61] les prédictions de la quantité totale de biomasse dans l'océan global. La moyenne annuelle de la distribution spatiale de biomasse au sein des trois communautés est également étudiée (Fig. V). Que ce soit pour les estimations de biomasse ou les distributions spatiales, **le modèle est en accord avec les références mais un effort important est nécessaire pour encore améliorer les prédictions**, notamment pour la représentation des écosystèmes aux hautes latitudes. À différentes latitudes, différentes conditions environnementales permettent l'émergence de spectres collapsés, réguliers, en transitions ou saturés (cf OBJ3), indépendamment pour chaque communauté pélagique. **En compara-**

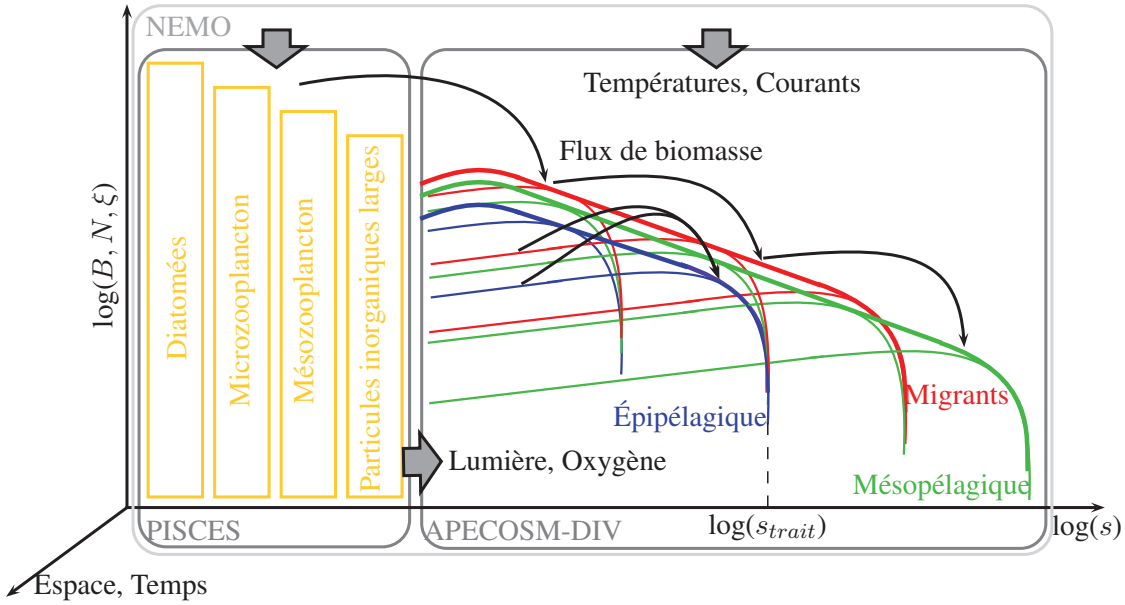


Figure IV Schéma du flux de biomasse des niveaux trophiques inférieurs, modélisés par NEMO-PISCES [20], aux niveaux trophiques supérieurs, modélisés par APECOSM-DIV, dans un environnement physique déterminé par NEMO [64].

ison à l'estimation théorique réalisée sur les spectres locaux (cf OBJ3, Fig.II), la simulation globale donne donc une estimation plus précise de la sensibilité aux perturbations environnementales des écosystèmes à différentes latitudes. La communauté mésopélagique, saturée à toutes les latitudes, apparaît insensible aux perturbations. La communauté des migrants apparaît insensible aux perturbations dans les basses latitudes et de plus en plus sensible vers les hautes latitudes. Enfin, la communauté épipélagique est similairement affectée par les perturbations environnementales à toutes les latitudes. Ces résultats restent des estimations préliminaires qui nécessitent plus d'études avant d'être confirmées.

Le modèle de spectre diversifié développé au fil de cette thèse est implémenté dans un modèle tridimensionnel de la structure des écosystèmes marins dans l'océan global, APECOSM [27]. Ce quatrième et dernier objectif (OBJ4) permet la simulation d'une climatologie de la distribution de biomasse de poissons dans l'océan global. **Les effets de l'environnement sur la structure des communautés sont comparés à différentes latitudes pour les communautés épipélagique, mésopélagique et les migrants.**

3 Conclusions et perspectives

Cette thèse décrit les étapes menant à l'implémentation d'un modèle mécaniste de la dynamique tridimensionnelle des communautés épipélagiques, mésopélagiques et migrantes à l'échelle de l'océan global: APECOSM-DIV.

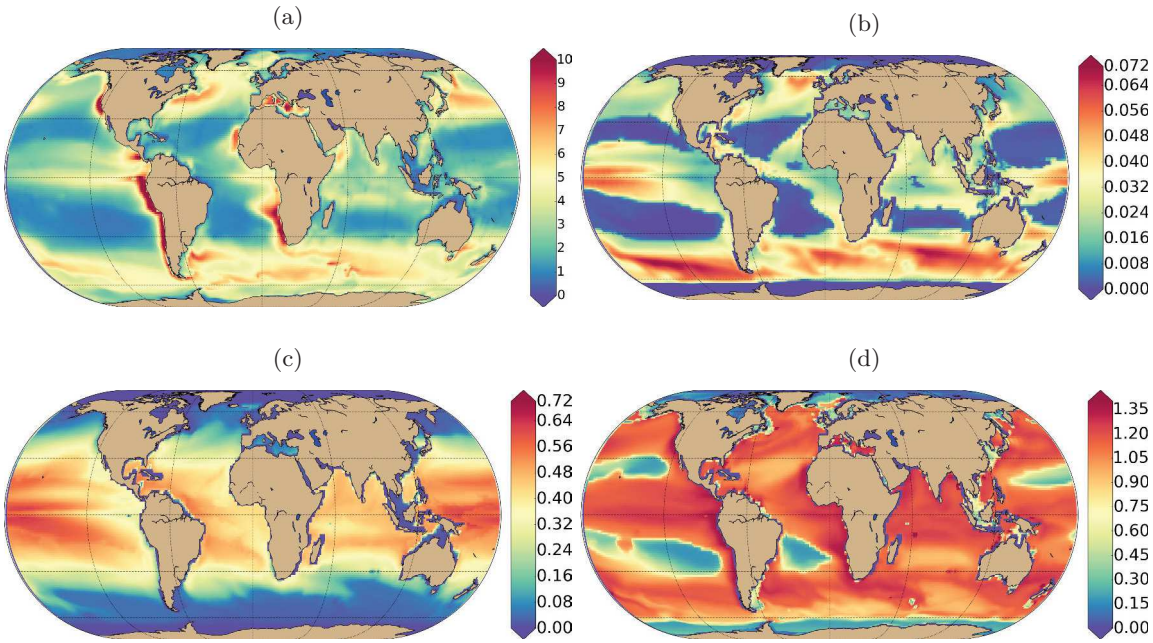


Figure V Estimations de la distribution de biomasse dans l'océan global (en gC/m^2), (a) à bas niveaux trophiques (d'après NEMO-PISCES), (b) pour la communauté épipélagique, (c) pour la communauté des migrants et (d) pour la communauté mésopélagique (d'après APECOSM-DIV).

Basé sur la modélisation du spectre de communauté, ce modèle permet la représentation du flux de biomasse des individus les plus petits aux individus les plus larges dans ces communautés de poissons. Basé sur la modélisation du spectre de communauté diversifié et construit sur la théorie DEB au niveau individuel, ce modèle permet une représentation mécaniste de la propagation des perturbations environnementales des individus aux espèces jusqu'à la communauté. Les espèces y sont différenciées en fonction d'un trait fonctionnel, leur longueur structurelle maximale. Ce modèle permet de mieux comprendre l'effet de l'environnement sur la diversité dans les écosystèmes à l'échelle planétaire, et inversement, permet d'estimer comment cette diversité influence la réponse des écosystèmes marins perturbés par leur environnement.

Cette approche est nouvelle parmi les modèles globaux d'écosystèmes marins. Elle est complémentaire aux modèles représentant les réseaux trophiques à l'échelle du globe [29]. Certes, la structure trophique des écosystèmes y est ignorée, mais **la formulation mécaniste du modèle ainsi que la représentation du rôle fonctionnel de la diversité permettent de projeter les propriétés des écosystèmes de l'océan global sans prescrire la structure spécifique de ces écosystèmes.** Ce modèle est également complémentaire à des modèles dits d'enveloppe bioclimatique [68]. Le modèle peut projeter de manière mécaniste l'évolution de la structure des écosystèmes en fonction de leurs interactions avec leur environnement. **Le modèle est, en revanche, inapproprié pour**

des applications où l'identité des espèces doit être considérée explicitement.

Maintenant, **en ce qui concerne l'étude des effets de l'environnement sur les communautés de poissons, dans cette thèse l'accent est mis sur l'étude de spectres diversifiés locaux (cf OBJ3)**. Avant de pouvoir comprendre les dynamiques complexes à l'échelle de l'océan global la compréhension locale du spectre de communauté est privilégiée. Les impacts statiques et dynamiques de l'environnement sur le spectre de communauté diversifié sont plus particulièrement évalués. **Il faut garder à l'esprit que les résultats détaillés reposent cependant sur différents choix et compromis et que des zones d'ombre subsistent autour du spectre de communauté et de sa modélisation.** Andersen et al. (2015) [69] classe ces zones d'ombre dans cinq catégories, des développements dans ces différentes directions risquent d'affecter les résultats:

1. **Pour les modèles d'écosystème, il est nécessaire de définir des processus de régulation** qui évitent la croissance illimitée des individus, évitent les oscillations parasites induites par les relations prédateur/proie et évitent l'exclusion d'espèces par compétition. **Dans cette thèse, cette régulation est exercée par l'agrégation des populations en bancs à partir d'une densité critique de biomasse** [**55**, **70**]. Des résultats plus ou moins différents peuvent être envisagés par le choix d'autres processus de régulation.
2. **La longueur maximale atteinte par les individus d'une espèce est choisie comme le principal trait fonctionnel affectant la physiologie des individus.** De nombreux autres traits peuvent être considérés et affecter les résultats, tels que par exemple différentes méthodes de reproduction [71]. **De plus, le modèle fait la supposition d'une diversité "infinie" et adopte une discrétisation continue de l'espace des traits fonctionnels.** Dans des écosystèmes réels cette diversité est finie et discontinue, les résultats de cette thèse peuvent représenter une limite théorique [72].
3. **Le modèle adopte une paramétrisation générique** pour les communautés de poissons, basée sur 28 paramètres. Cela permet de faire émerger de façon mécaniste les différences entre communautés des différences environnementales entre écosystèmes. Mais les résultats restent cependant **difficiles à valider empiriquement.** De plus, **le modèle permet l'émergence au mieux d'un système tritrophique**, on peut s'interroger sur la généralité des résultats avec plus de niveaux trophiques au sein de communautés.
4. **Le modèle repose sur quelques processus clef** qui permettent le transfert de biomasse d'un bout à l'autre du spectre de communauté. Cependant, **la représentation de processus additionnels pourrait affecter les résultats du modèle.** Par exemple, la modélisation de différentes techniques de reproduction peut fortement influencer les résultats dans un environnement saisonnier [73, 71].
5. Enfin, d'un point de vue numérique le modèle a été étudié en détail pour garantir

la conservation de biomasse des individus aux espèces à la communauté (voir à ce sujet l'annexe). Le schéma numérique adopté pour résoudre les équations du modèle, de type MUSCL [74], a été choisi pour permettre une résolution satisfaisante de la dynamique du spectre. Malgré cela **des méthodes numériques d'ordre supérieures peuvent encore être développées afin d'améliorer la confiance dans les prédictions du modèle.**

En plus de ces cinq catégories qui résument les zones d'ombre entourant les modèles du spectre de communauté, une sixième catégorie apparaît en lien avec cette thèse: **il est nécessaire de représenter de façon adéquate les effets de l'environnement des individus aux espèces au spectre de communauté diversifié.** Par exemple, les coefficients allométriques exprimant la sensibilité des processus associés à l'assimilation de nourriture et ceux associés à la respiration sont peu connus [15] alors qu'ils ont une forte influence sur les propriétés émergentes du spectre de communauté à diverses températures.

En résumé, les résultats concernant les effets de l'environnement obtenus avec le modèle local sont basés sur un certain nombre de choix et compromis qui sont amenés à évoluer. **Les résultats proposés par les simulations locales seront peut-être amenés à changer ainsi que les prédictions du modèle global APECOSM-DIV.** Malgré cela, le modèle global peut d'ores et déjà être appliqué pour étudier les effets de l'environnement sur les écosystèmes et services dans l'océan global. Il est certes difficile de vérifier empiriquement les prédictions du modèle, **mais sa nature mécaniste permet au moins de comprendre comment les perturbations environnementales peuvent se propager et affecter les écosystèmes de l'océan global.** Comme par exemple l'observation de différentes sensibilités à l'environnement entre communautés épipélagique, mésopélagique et migrants révélées par APECOSM-DIV à différentes latitudes (cf OBJ4).

Le modèle APECOSM-DIV peut ainsi être couplé avec des modèles climatiques pour estimer l'évolution interannuelle de la structure des écosystèmes marins, tout en prenant en compte le rôle de la diversité d'espèces [63]. Associé à un modèle spatial des effets de la pêche [75], il peut permettre d'étudier différents scénarios d'exploitation à l'échelle de l'océan global.

Les modèles des écosystèmes marins dans l'océan global deviennent possibles grâce à d'importantes ressources de calcul et grâce à une augmentation continue de la connaissance scientifique. Alors que la compréhension du rôle de la biodiversité à cette échelle globale est désormais un challenge important, il est tentant d'ajouter de plus en plus de détails taxinomiques et physiologiques dans ces modèles d'écosystème afin de modéliser les écosystèmes marins dans toute leur complexité. De par son caractère mécaniste, le modèle APECOSM-DIV adopte lui une représentation relativement simple des écosystèmes. Les simulations du modèle sont encore difficiles à comparer à des écosystèmes réels, mais malgré cela, je pense que cette approche mécaniste est la plus

adaptée pour comprendre significativement les effets de l'environnement et du changement climatique sur la structure des écosystèmes et sur les services qu'ils fournissent à l'humanité.

Part II

Manuscript

Chapter 1

Context and objectives

1.1 Context

1.1.1 Marine ecosystems services

Oceans and marine ecosystems provide many services to societies. They contribute to the four categories of ecosystem services identified by the Millennium Ecosystem Assessment in 2005 [1], namely: regulation, provision, support and cultural. For example, oceans and marine ecosystems contribute to the regulation of the climate through the biological carbon pump through which a fraction of the atmospheric carbon is exported to the sea floor and sequestered in the sediments [2]. They also regulate the water quality in coastal areas where microorganisms filter organic wastes produced inland before they reach the open ocean [76]. Furthermore, in the provision category, marine ecosystems have a key role in providing proteins to human populations worldwide [3].

The environment constrains marine ecosystems and the services that they provide. For instance, seasonal environmental variations influence the yield and quality of fisheries' catches [4]. In combination with fishing, inter-annual environmental variations can lead to fish stock collapses [77]. At a global scale, climate-driven variability affects the global carbon cycle [5].

Anthropogenic climate changes increasingly alter the environment, starting with the physical properties of the oceans [78]. **Climate change as well as other human induced pressures such as pollution, habitat degradation or over-exploitation of fish stocks [6] can durably alter marine ecosystems properties and the essential services they provide. Therefore, in order to adapt to ongoing and expected changes, it is a high priority to better understand how marine ecosystems and biodiversity may be impacted by these environmental perturbations [7, 8].**

1.1.2 Marine ecosystems and environment

Assessing the impacts of climate change and other environmental pressures on marine ecosystems is obviously a broad question. Many different environmental factors interacting in complex ways are described in the literature [9, 10, 11].

The environment impacts marine ecosystems at different organization levels, from individuals to populations, species or communities. These organization levels are linked, direct effects of the environment at an organization level induce indirect responses at another level. For instance, an increase of the water temperature affects directly the metabolisms of individuals swimming in it and enhances their activity rates [12, 13]. At the community level, the impact of warming on individuals induces an indirect increase of the proportion of small-sized species and a decreasing size at age [14]. This unintuitive response appears because various key processes related to food ingestion and respiration at the individuals level do not scale in the same way with temperature [15].

Moreover, the impact of environment on marine ecosystems can be analyzed at different spatio-temporal scales, from local to regional and global. At different scales, the same environmental factor can lead to different effects. For instance, species have different temperature ranges. At local scale, these distinct ranges can be used to explain the alternation of the dominance of species such as the succession of warm anchovy prone and cool sardines prone regimes in the western North Pacific [16]. This alternation is caused by different growth response to temperature during the early life stages. At global scale, ocean's warming shifts the spatial ranges of species that are tracking at different rates the poleward shift of their optimum environmental conditions. Thus, this leads to new species occurrences, new interactions and *in fine* new ecosystems' structures at local and regional scales [79, 17].

Note that the effect of temperature is only taken as an example here to show that the environment impacts ecosystems at different organization levels and scales. Many other environmental effects have been documented, involving stratification, ocean desoxygenation or acidification in the case of climate change.

Climate change is a global phenomenon. Therefore, in order to investigate its impact on marine ecosystems' services, the global scale is more appropriate. However, the environment directly affects individuals, locally. In order to better understand how marine ecosystems may be impacted by environmental perturbations, the propagation of these perturbations from individuals to populations to species and communities has to be understood. The interactions between spatial scales need to be unraveled. It is a colossal task that increasingly complex marine ecosystem models attempt to tackle [18].

1.1.3 Marine ecosystem models

In accordance with the large number of organization levels and scales at which marine ecosystems can be considered, a large variety of modeling techniques have been developed over the years. These models either focus on primary producers, such as bio-geochemical models [19, 80, 20], or higher trophic levels [23, 24]. They usually focus on different aspects of ecosystems. For instance, individual based models explicitly account for the representation of the life history of individuals [21], physiologically structured models link individual level processes to populations energetics [81], food web models focus on trophic interactions [22], or ecological niche models determine the probability of occurrence of species as a function of environmental variables [82, 68].

With the increase in computing resource and a better appreciation of the complexity of marine ecosystems, full models of ecosystems are now possible. These models represent marine ecosystems from the abiotic to the biotic components, from low to high trophic levels. These "end-to-end" formulations [25, 26] integrate several organization levels and scales and account for both environmental drivers and the impact of fishing on ecosystems. **In the global ocean, few "end-to-end" models are able to asses the impact of the environment and climate change on the services provided by marine ecosystems [27, 29].**

In global ecosystem models the representation of biodiversity is a challenge. Compared to the geological times over which biodiversity has been slowly taking its present structure, the rapidity of climate change is expected to have dramatic impacts on ecosystems' diversity [30]. Therefore, a proper representation of the processes driving ecosystem's dynamics and diversity is a prerequisite for good predictions of the impact of climate change on the services provided by marine ecosystems. So far, global ecosystems models either aggregate this biodiversity in functional groups [83, 27], or explicitly account for it assembling multitude of species [29]. On one hand, the specification of functional groups is a gross simplification of this biodiversity. On the other hand, the explicit representation of species implies a large number of parameters, many being difficult to estimate accurately. An alternative strategy consists in adopting a trait-based approach [31, 32]. Instead of accounting for the taxonomic characteristics of species, trait-based formulations account for the functional role of species that is summarized in functional traits. The traits can for example characterize the trophic interactions, such as foraging and vulnerability traits [84], energetic and physiological properties or habitat preferences.

In order to better understand and predict how the services provided by marine ecosystems are impacted by climate change, global ecosystem models are becoming technically possible. However, they adopt a simplified representations of the role of biodiversity which may limit their use for prediction. This thesis proposes an alternative approach. It is articulated around the

development of a global model of marine ecosystems including a trait-based representation of species biodiversity. The model is essentially used to asses the impact of resource and temperature variations on the structure of fish communities.

1.2 Objectives

As mentioned in the previous section, the aim of this thesis is to **assess the impact of the environment on the structure of fish communities in the global ocean while accounting for the functional role of biodiversity.** In order to reach this goal, a trait-based model for fish communities in the global ocean is developed. It is implemented in an "end-to-end" setting. The physical and biogeochemical characteristics of global marine ecosystems are considered as boundary conditions of the model. The impact of fishing on global marine ecosystems is not considered.

This overarching goal of the thesis has been decomposed into four intermediate objectives (see Fig. 1.1 for objectives list). This section summarizes these intermediate objectives and reveals how they contribute to the main goal. Each objective is detailed in the following chapters. Chapters are written in the form of scientific articles.

1.2.1 Determination of a modeling framework (OBJ1)

OBJ1: What modeling framework allows the representation of the impact of the environment on fish communities in the global ocean while accounting for the functional role of biodiversity ?

Many modeling techniques exist, the model needed to address the thesis' goal must apply in all ecosystems in the global ocean, using the same structure and parameters, from the pole to the equator and from oligotrophic to eutrophic regions. It must also keep predictive in the non-observed environmental conditions that might happen in the future. It must therefore explicit the key processes in a mechanistic way. Mechanistic models of populations and communities have to rest on individuals which constitute their lower invariant organization level. The model should therefore allow the representation of the direct impacts of environment at individuals level and represent the upscaling of these effects at the population and community levels.

In marine ecosystems body size s is an important structuring trait. It is measured in terms of individual's length, weight or volume that can be related to each other in marine ecosystems. Size constrains predatory relationships between preys and their predators [33, 34]. It also characterizes the physiology of individuals, for instance growth or respiration [35, 36, 37]. All along their life cycle fishes pass through several trophic levels which correlate well to their size [33, 85].

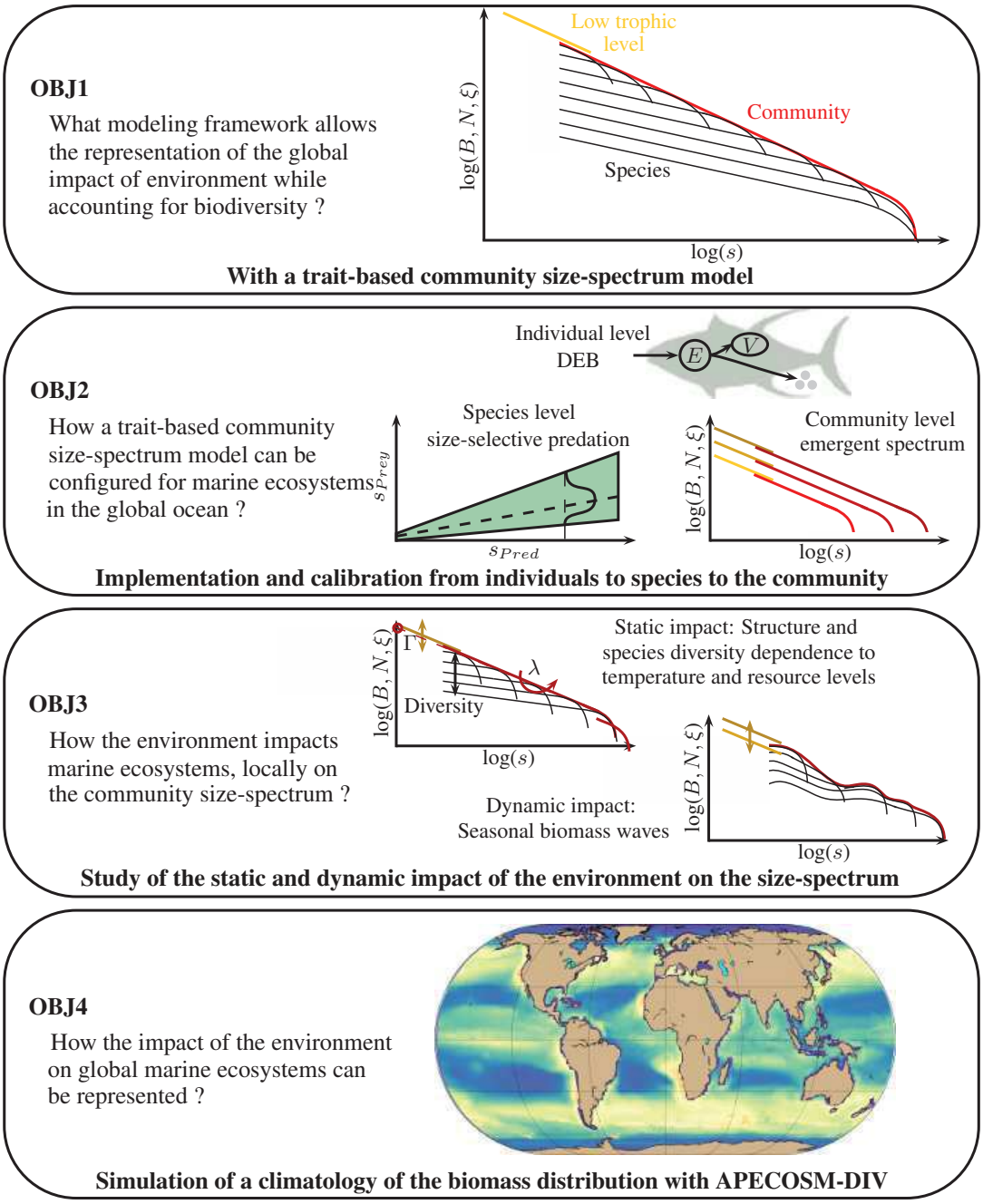


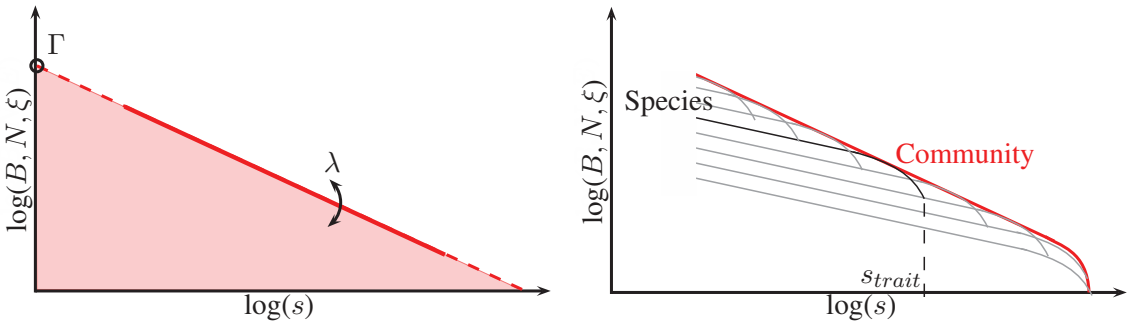
Figure 1.1 This thesis aims at assessing the impact of the environment on the structure of marine ecosystems in the global ocean while accounting for the functional role of biodiversity. Four intermediate objectives (OBJ) are identified to achieve this goal.

One of the striking consequence of the importance of body size in structuring marine ecosystems is the regularity of ecosystem biomass summed over logarithmically equal body size intervals[38]. On a log-log scale, the observed biomass density B plotted with respect to individual size is close to a linear spectrum. This regular biomass density size-spectrum corresponds to regular abundance density N or energy density ξ size-spectra. The regularity of the community size-spectrum (in term of biomass B, abundance N or energy ξ) has been observed in many ecosystems from plankton [39, 40, 41] to fish [42, 43]. The community size-spectrum (see illustration Fig. 1.2a) provides a simple representation of marine ecosystems. It aggregates complexity to keep only two emergent indicators: the slope λ and an the intercept Γ. The slope λ expresses the relative abundance of small and large individuals in the community. The intercept Γ refers to the abundance of a community, poor oligotrophic regions exhibit small values of their intercept compared to rich eutrophic environments [44].

Community size-spectrum models exploit the strong size-structure of marine ecosystems to represent mechanistically the biomass flow in marine ecosystems from small to large individuals [45, 46, 47, 48, 49]. They explain the regularity of the size-spectrum by a balance between individuals' size-dependent predation, growth and respiration [50]. Different variants of spectrum models exist [86, 87, 83, 88, 69], the biomass balance at the individual level remains the keystone of all methods.

Community size-spectrum models have been successfully applied to asses the impact of fishing on the biomass distribution in marine ecosystems [34, 51, 52]. They have been applied to asses the impact of the environment [53] and even climate change [28] on the spectrum features. Moreover, recent developments in community size-spectrum models allow the explicit consideration of the functional role of species diversity on the dynamic of the community size-spectrum [54, 55]. In these trait-based models, species diversity is represented through a disaggregation of the community size-spectrum into species size-spectra, each of them characterized by a single trait s_{trait}, their maximum structural length (see illustration Fig. 1.2b).

Community size-spectrum models characterize different ecosystems with a single framework. Trait-based community size-spectrum models link individuals' physiology to species and community responses. Furthermore, they represent the functional role of species diversity using maximum size as the most structuring functional trait. They appear to be suitable approaches to investigate the impact of environment and climate change on marine ecosystems in the global ocean [7]. **In response to the first objective (Fig. 1.1, OBJ1), a trait-based community size-spectrum model detailed in Maury and Poggiale (2013) [55] has been selected.** This model presents the particularity to resolve individuals' physiology with the Dynamic Energy Budget (DEB) theory [56].



(a) A slope λ and intercept Γ.

(b) A sum of trait-based species spectra.

Figure 1.2 The community size-spectrum in marine ecosystems: the distribution of biomass density B, abundance density N or energy density ξ as a function of individuals size s.

1.2.2 Configuration of the model (OBJ2)

OBJ2: How the trait-based community size-spectrum model can be configured to realistically represent fish communities and the impact of environment from individuals to species to communities ?

The trait-based community size-spectrum model must be parametrized to resemble real fish communities. For instance, the growth curves of individuals belonging to different trait-defined species should correspond to growth curves observed in the field. The selection of preys by predators should be conform to observed prey/predator interactions. Moreover, different environmental conditions in distinct ecosystems should allow the emergence of distinct community size-spectra.

Trait-based community size-spectrum models are flexible tools allowing the representation of marine ecosystems with little knowledge of the structure of food webs. However, **there is no formal calibration procedure in order to reproduce the characteristics of regional or global ecosystems with spectrum models. Taking advantage of the model structure integrating individual, population and community levels, the model parameters are estimated at the three organization levels (see Fig. 1.3).**

At individual level, the model is based on the DEB theory (Fig. 1.3). The DEB theory has been successfully applied to model the physiology of individuals belonging to a large variety of taxa, in the aquatic and terrestrial environments [56]. In this thesis, the generic parameters of the DEB are adapted to represent the physiology of fish species [57] (see appendix). These parameters are generic and scale with the trait s_{trait}.

At species level, the physiology of individuals belonging to distinct fish species of trait s_{trait} allows the determination of species size-spectra (Fig. 1.3). For different species, the species size-spectra represent the biomass density $B_{s_{trait}}$ (or abundance density $N_{s_{trait}}$ or energy density $\xi_{s_{trait}}$) distribution with respect to individual

size. This formalism is similar to the definition of the community size-spectrum, at specific level. The species spectra are coupled by size-selective predation where each species can potentially eat organisms of every species. The size-selective predation parameters are tuned to match empirical prey size distribution s_{Prey} in the stomach of predators of size s_{Pred} [58] (for distribution see scheme OBJ2 Fig. 1.1).

At the community level, the dynamics of the community size-spectrum emerges as the sum of each species contributions and interactions (Fig. 1.3). Thus, the model propagates environmental perturbations from individuals to species populations to the community. The physiology of individuals depends on their environment, especially the food available and the temperature of the water they swim into. It affects the dynamic of the species size-spectra which in their turn affect the community size-spectrum. In different environments, the emergent community size-spectrum changes and characterizes different ecosystems. For instance, food levels and temperatures characterizing eutrophic regions should lead to community size-spectra of rich ecosystems, with a high intercept Γ; food levels and temperatures characterizing oligotrophic regions should be associated with community spectra of poorer ecosystems, with a low intercept Γ. The last parameters of the model are tuned to reproduce variations of intercepts in both eutrophic and oligotrophic ecosystems in the global ocean.

In response to this second objective (Fig. 1.1, OBJ2), three configuration steps from individuals to species to the community allow the realistic representation of fish communities and the propagation of the impact of the environment across organization levels.

1.2.3 Local impact of environment on marine ecosystems (OBJ3)

OBJ3: How the environment impacts the community size-spectrum ?

Once the modeling framework selected and configured, the impact of the environment on the features of the community size-spectrum is investigated. Little is known about the properties of the community size-spectrum in different environments, whether the characteristics of the slope λ and intercept Γ in different static environments [41, 53], or the dynamic of the biomass distribution in a varying environment [59, 53]. The only known effect on the community size-spectrum is the impact of fishing which decreases the slope of the spectrum [43, 34, 89].

Here, the environment is only represented by variations of food resource and temperature. The resource corresponds to the food available to the smallest individuals of the fish spectrum. It is represented in the model by a low trophic level (LTL) biomass B_{LTL} (or abundance N_{LTL}, or energy ξ_{LTL}) spectrum (see representation Fig. 1.3) on which small fish feed by size-selective predation. The temperature increases or decreases the metabolic rates of individuals through the DEB theory. As previously noted, the variations of the environment impact the physiology of individuals and propagate up

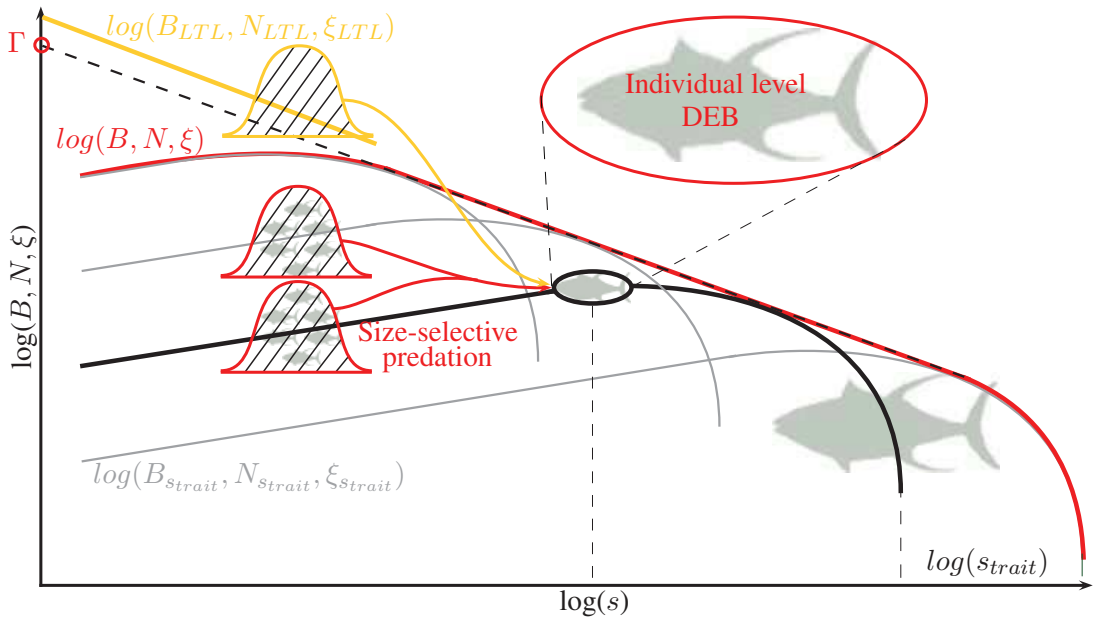


Figure 1.3 Configuration of the model from individuals to species to the community: configuration of the dynamic energy budget; configuration of the size-selective predation; configuration of the community level intercept.

to species and community levels.

First, the properties of the community size-spectrum are modeled and compared at distinct constant levels of temperature and/or resource. The trait-based community size-spectrum model is forced over a range of constant resource and temperature levels that can realistically be experienced by fish in the global ocean. For distinct combinations of resource and temperature, distinct patterns of the size s and trait s_{trait} distributions are identified. They are linked to the number of trophic levels in the modeled fish communities, which is an emergent feature determined by the environment. **In a temperature and resource level space, these distinct features can be summarized with a phase-diagram. Four domains appear clearly (see Fig. 1.4): collapse, regular, transition and saturation.** In the collapse, regular, transition and saturation domains, ecosystems are respectively very sensitive, slightly sensitive, very sensitive again, and insensitive to variations of their environment. At different latitudes, marine ecosystems are characterized by distinct mean resource and mean temperature levels. When superimposed on the phase diagram, the mean environmental conditions experienced by fish communities along an idealized planet-wide North-South transect provide a theoretical estimation of the sensitivity of these communities (see Fig. 1.4). For instance, high latitude communities appear insensitive while low latitude communities are very sensitive. **In these numerical experiments where the environment is kept "static", the species diversity response is responsible for this multi-domain environmental sensitivity of the community size-spectrum.**

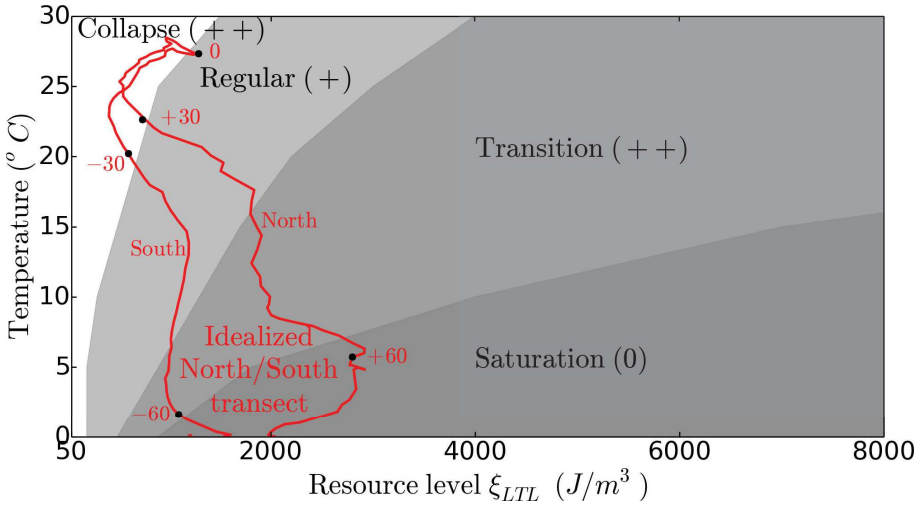


Figure 1.4 Phase-diagram of fish communities' state at different temperature and resource levels. Four distinct domains with distinct features of the biomass distribution as a function of individuals' sizes or traits. Four distinct domains with distinct sensitivities of modeled ecosystems to environmental variations of equal amplitude, from insensitive 0 to very sensitive ++. The mean environmental conditions experienced by fish communities along an idealized planet-wide North-South transect provides an estimate of the sensitivity of fish communities at distinct latitudes.

Second, the properties of the community size-spectrum are modeled and compared in distinct seasonal environments. The trait-based community size-spectrum model is forced by seasonal cycles of temperature and resource characterizing distinct ecosystems of the global ocean. Seasonal waves of biomass propagate across spectra. The dynamic properties of the community size-spectrum of fish communities is poorly documented [90, 53, 91]. **In a seasonal environment, the model reveals two distinct processes through which the environmental signal propagates from small to large individuals (see Fig. 1.5): (1) the advection of biomass along the size dimension due to individual growth and (2) the biomass saltation between prey and predator size classes, s_{Prey} and s_{Pred}, due to predator-prey interactions.** Individuals' growth induces a slow biomass transport from small to large size classes in fish communities as most species reach their maximal size after several years. On the contrary, the biomass saltation induces a fast biomass transport from small to large sizes since energy can be directly transferred from the smallest prey to the largest predator in less than a year. **The "dynamic" numerical experiments reveal that the specificity of species diversity to distinct ecosystems causes one or the other processes to dominate the propagation of environmental signal through communities.**

The "static" and "dynamic" local simulations performed provide a better understanding of the characteristics of the trait-based community size-

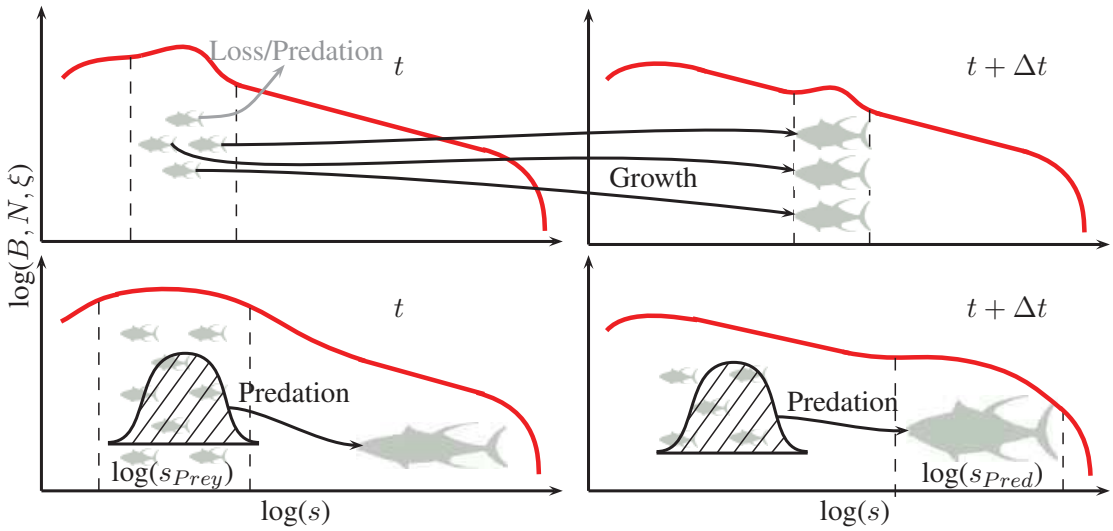


Figure 1.5 Modes of biomass propagation along the community size spectrum in a seasonal environment: top, the growth driven advection of biomass between two time steps; bottom, the saltation of biomass between sizes' class at two time steps.

spectrum model (Fig. 1.1, OBJ3). They provide insights about the functioning of fish communities in the global ocean and the functional role of diversity.

1.2.4 Global impact of environment on marine ecosystems (OBJ4)

OBJ4: How the impact of the environment on marine ecosystems can be represented in the global ocean with a trait-based community size-spectrum model ?

Different modeling approaches based on the representation of the community size-spectrum have been implemented from basin to global scales. For example, they have been used in order to predict from remote sensing data the potential biomass, production and size structure of global marine ecosystems [60, 61]. Forced with projected physical-biogeochemical fields from Earth-system models, they have been used to project the dynamic impact of climate change and fishing in large marine ecosystems [28], or ocean basins [62]. However, these approaches disregard the spatial interactions between different regional ecosystems and the vertical structure along the water column. The Apex Predators ECOSytem Model (APECOSM) [27] allows addressing these points. It is the only global tridimensional multi-communities size-spectrum model available to date. It has for instance been applied coupled with climate models to project the impact of climate change on the structure of global pelagic communities [63], or to analyze the climate-driven variability of marine ecosystems at basin-scale [92].

Community size-spectrum models used for predicting the impact of climate change on global marine ecosystems usually adopt a simplified representation of biodiversity. They

adopt a functional groups structure, for instance epipelagic and benthic communities [83], or in APECOSM, epipelagic, mesopelagic and migratory communities [27]. **In this thesis, the trait-based community size-spectrum model is implemented in APECOSM to produce the so-called APECOSM-DIV (DIVersified) model.** Including an explicit functional representation of the species diversity in the model is expected to enhance its realism. It is expected to help understanding how the environment is shaping the diversity structure of marine communities at the planetary scale and, conversely, how diversity influences the response of marine ecosystems to the environment.

The APECOSM-DIV model represents the biomass flow from small to large individuals in three trait-based fish communities: epipelagic, mesopelagic and migratory (Fig. 1.6). It is forced by the coupled physical biogeochemical model NEMO-PISCES [20] which provides resource (large diatoms, micro- and meso-zooplancton, large detritus) and temperatures fields, but also oxygen and light necessary to compute tridimensional habitat preferences of communities. The model NEMO [64] provides the currents that are transporting biomass across ocean basins.

A one year climatology of the biomass distribution in the global ocean is simulated. It provides global estimates of the total fish biomass in marine ecosystems. The model predicts the distribution of biomass in the global ocean for the epipelagic, mesopelagic and migratory communities. **These biomass estimations and distributions agree with references [60, 65, 66, 67, 61], but more work is necessary to properly represent marine ecosystems with APECOSM-DIV, especially toward higher latitudes.** Moreover, aggregated along a latitudinal transect, the characteristics

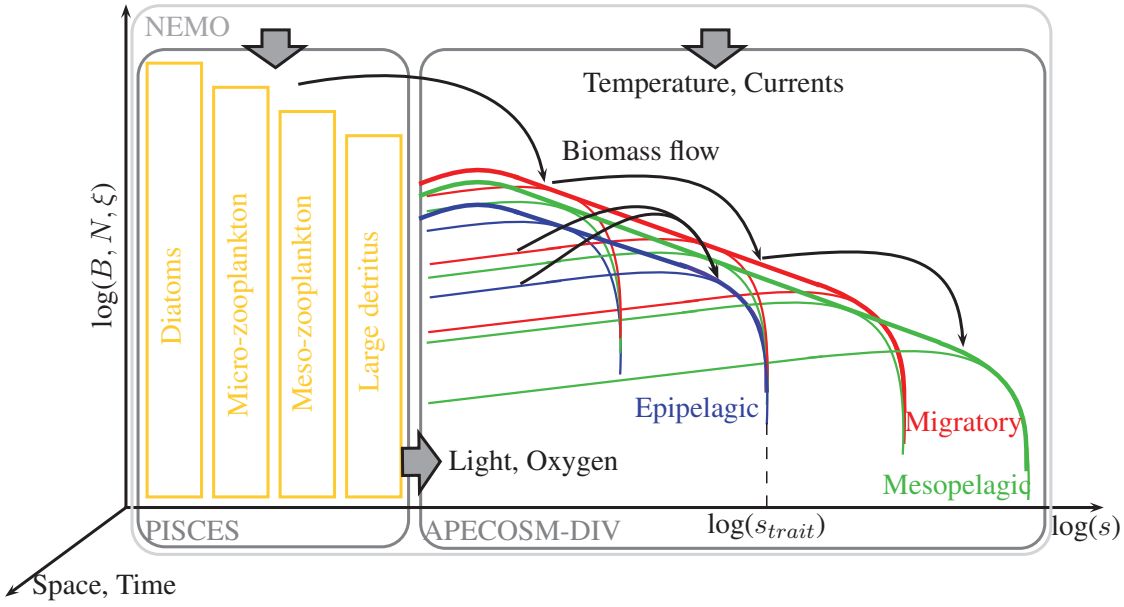


Figure 1.6 Biomass flow at low trophic levels, modeled by NEMO-PISCES [20], at high trophic levels, modeled by APECOSM-DIV, in a physical environment from NEMO [64].

of the three communities at different latitudes are described. Like in the idealized static study (cf OBJ3), at different latitudes the community size spectra show distinct features which correspond to four domains: collapse, regular, transition or saturation. However, the epipelagic, mesopelagic and migratory communities show distinct variations with latitude. Thus, **the global simulation provides finer estimates of the sensitivity of marine ecosystems to perturbations at different latitudes (compared to OBJ3 Fig. 1.4).** For instance, the mesopelagic community is at saturation at all latitudes, it appears always insensitive to the environment, the migratory community appears insensitive at low latitudes and sensitive toward high latitudes while the epipelagic community is similarly sensitive at all latitudes. These results are preliminary and require more analysis.

The fourth and last intermediate objective (Fig. 1.1, OBJ4) is tackled by implementing the trait-based community size-spectrum model into the spatially resolved global marine ecosystem model, APECOSM. The impact of the environment on the structure of marine ecosystems in the global ocean is briefly touched studying a one year climatology simulated with this spatially resolved trait based community size-spectrum model, APECOSM-DIV.

1.3 Thesis structure

The four intermediate objectives (Fig. 1.1) are discussed in detail in the four following chapters in the form of standalone papers. Each paper is related to one or two intermediate objectives (Fig. 1.7).

- **Paper I: Modelling the community size-spectrum, toward global ecosystem models.** This paper is a review of community size-spectrum models. It places size-spectrum models in the more general landscape of marine ecosystem models. It discusses their advantages and disadvantages. It underlines the benefit of using size-spectrum models to model marine ecosystems on large scales. This first paper justifies the choice of a trait-based community size-spectrum model to tackle the main problematic of the thesis (OBJ1).

- **Paper II: Effects of low trophic level biomass and temperature on fish communities: A modeling study.** This paper details the improvement, implementation an parametrization of the trait-based community size-spectrum model presented in Maury and Poggiale (2013) [55] in order to represent the impact of environment on fish communities. The environment is represented by the temperature and the level of resource available in low trophic levels. First, the configuration of the model is detailed (OBJ2). Second, the "static" characteristics of modeled fish communities forced with constant environmental conditions are investigated using a set of indicators developed for that purpose (OBJ3). This paper finally discusses the characteristics of fish communities along a latitudinal section of environmental conditions.

- **Paper III: Seasonal dynamics of the biomass spectrum along a latitudinal transect.** This paper investigates the dynamics of the community size-spectrum in the case of seasonal environment for ecosystems at different latitudes (OBJ3). The simulations reveal two processes through which environmental variability propagates through the community size-spectrum: the advection of biomass with the growing individuals and the biomass saltation from prey to predator size classes. At different latitudes, one or the other of these processes dominates.

- **Paper IV: Simulation of the biomass distribution of epipelagic, mesopelagic and migratory trait-based fish communities in the global ocean using APECOSM-DIV.** This paper presents the spatially resolved trait-based community size-spectrum model APECOSM-DIV. A one year climatology of the biomass distribution in the global ocean is discussed. Forced with physical and biogeochemical forcing, this fully mechanistic model allows simulating the characteristics of marine ecosystems in the global ocean (OBJ4).

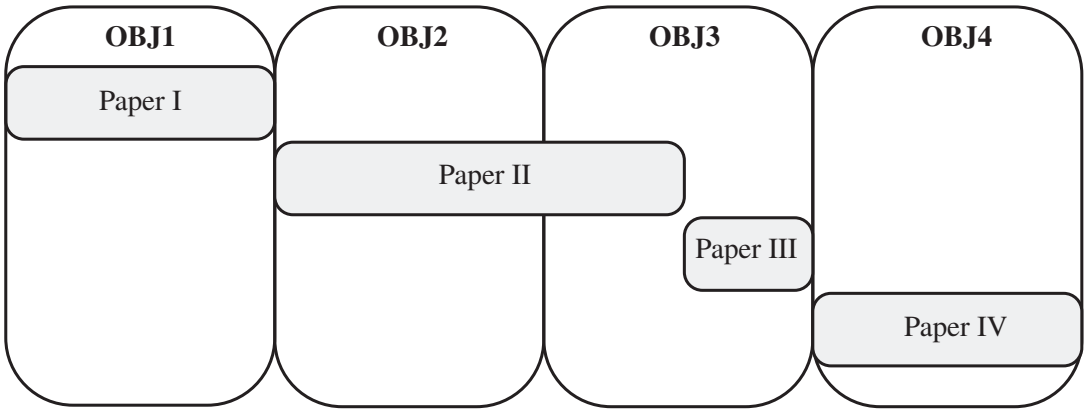


Figure 1.7 Structure of the thesis, four chapters in form of papers covering the four main objectives.

Chapter 2

Modelling the community size-spectrum, toward global ecosystem models

Modelling the community size-spectrum, toward global ecosystem models

Jérôme Guiet[1,2], Jean-Christophe Poggiale[3] and Olivier Maury[1,2]

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Abstract

The regularity of the community size-spectrum, i.e. the fact that the total ecosystem biomass contained in logarithmically equal body mass intervals remains constant, is a striking characteristics of marine ecosystems. Community size-spectrum models exploit this feature to represent marine ecosystems with two measures : the slope and the intercept of the community spectrum. Size-spectrum models have gain popularity over time to model the properties of fish communities, whether to investigate the impact of fishing, or embedded into end-to-end models to investigate the impact of climate. We review the main features and state of the art developments in the domain of continuous size-spectrum models. The community spectrum emerges from a balance between size-selective predation, growth and biomass dissipation. At the community level, this balance leads to steady or unsteady solutions depending on the parametrization of the size-selective predation. Further to these basic components, reproduction and various causes of mortality have been introduced in recent studies to increase the model's realism or simply close the mass budget of the spectrum. These processes also affect the stability of the spectrum. They can affect the predictions of the size-spectrum models. A few models have also introduced a representation of life-history traits in the community size-spectrum. This allows to account for the diversity of energy pathways in food webs and for the fact that metabolism is both size- and species-specific. The community-level metabolism therefore depends on the species composition of the community. The size-spectrum's regularity

at the community level can serve as a basis for building theories of marine ecosystems' functioning. It can also be used to compare the structure of communities in different ecosystems. The mechanistic nature of size-spectrum models as well as their simple and aggregated representation of complex systems make them good candidates for global and long term simulations. For instance, for projecting marine ecosystem's states under various climate change scenarios.

Keywords: Marine Ecosystem Model, Community size-spectrum, End-to-End model, Trait-based model, Climate Change

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Introduction

Marine ecosystems encompass many physical, chemical and biological interactions. Various types of ecosystem models have been developed over the years, each focusing on different aspects of these ecosystems. For instance, food web models focus on trophic interactions between populations or functional groups (Yodzis (1998); Pauly *et al.* (2000); Fulton *et al.* (2004)), physiologically structured models link individual level processes to populations energetics (Metz & Diekmann (1986); De Roos & Persson (2001)) or spatially explicit population models focus on distributions and movements (Lehodey *et al.* (2008); Dueri *et al.* (2014)). Marine ecosystem models have been set up at very different scales, from plankton to whales, from bays to oceans, and from days to centuries (Plagányi (2007)). Formally, these models can be continuous or discrete, Lagrangian or Eulerian, individual based or formulated at the population level with an age or size structure, multi-agent systems or deterministic differential equations (Tuljapurkar & Caswell (1997); Kot (2001)). Such a variety of focus, scales and formalisms reflects the complexity of marine ecosystems and the diversity of modelling objectives, but also the lack of a single unifying ecosystem dynamic theory.

In this context, modellers are facing a difficult challenge when they study ecosystem responses to climate or fishing. They have to find ways to integrate processes taking place within distinct spatio-temporal scales at different organization levels, keeping the number of model components and processes considered in a manageable domain of complexity. A promising direction to keep marine ecosystem models tractable is the one taken by size-based models that project ecosystems complexity and dynamics along organisms size (Jennings & Brander (2010)).

Sheldon *et al.* (1972) first made the observation that ecosystem biomass remains approximately constant when summed within logarithmically equal body mass intervals, from bacteria to whales. It triggered the definition of the size-spectrum, the distribution of biomass or abundance as a function of individuals' size or mass on a log-log scale. The observation ofSheldon *et al.* (1972) inspired several pioneering studies that have set the bases needed for developing a quantitative theory of ecosystem size-spectrum (e.g. Kerr (1974); Platt & Denman (1977, 1978); Silvert & Platt (1978, 1980); Dickie *et al.* (1987); Moloney & Field (1991); Thiebaux & Dickie (1993)). In the meantime empirical observations of this spectrum multiplied for plankton communities (Sprules & Munawar (1986); Heath (1995); San Martin *et al.*

(2006)) as well as fish communities (Rice & Gislason (1996); Bianchi *et al.* (2000)). Recently, the spectrum theory has experienced a rejuvenated and growing interest for modelling energy flux and ecosystems dynamics at higher trophic levels while keeping a reasonable model complexity (e.g. Shin & Cury (2001); Arino *et al.* (2004); Benoît & Rochet (2004); Andersen & Beyer (2006); Hall *et al.* (2006); Pope *et al.* (2006); Baird & Suthers (2007); Maury *et al.* (2007a); Blanchard *et al.* (2009); Datta *et al.* (2010); Hartvig *et al.* (2011); Poulin & Franks (2010); Maury & Poggiale (2013)).

In the present review we discuss the use of community size-spectrum models for representing aquatic ecosystems. We underline the main features of the size-spectrum representation and its central mechanisms : the balance between growth, maintenance and size-selective predation. We describe the latest improvements of spectrum models and discuss their advantages and disadvantages. Finally, we review the modern challenges and potential applications of the size-spectrum approach, for the management of fisheries (Blanchard *et al.* (2012); Law *et al.* (2012); Merino *et al.* (2012)) or in the perspective of « end-to-end » modelling (Travers *et al.* (2007); Rose *et al.* (2010); Maury (2010)).

1. Modelling the community size-spectrum

1.1. Size structure and community size-spectrum in marine ecosystems

Size is a major structuring trait of aquatic ecosystems and fish communities. Size heavily influences organisms' movement (Bainbridge (1958); Ware (1978)), predation (Cohen *et al.* (1993); Lundvall *et al.* (1999); Scharf *et al.* (2000)), growth, mortality and reproduction (Peters (1986); Marquet *et al.* (2005); Woodward *et al.* (2005)). All along their life cycle fishes pass through several trophic levels that are well correlated to their size (Jennings *et al.* (2001); Trebilco *et al.* (2013)).

The size structuration of marine ecosystems is manifest at the community level, with the emergence of the community size-spectrum. Defined as the biomass density distribution B, or abundance density N, or energy density E, as a function of individuals length l, or weight w, or volume v, in a log-log space, it first has been pointed out by Sheldon *et al.* (1972). The biomass B (or N, or E) is a density with respect to individual length l (or w, or v). The community size-spectrum summarizes complex biological and ecological processes with a simple distribution. Linear or quasi-linear in logarithmic scale, it can be characterized by its slope λ and intercept Γ (Fig. 1).

The slope λ of the community size-spectrum can take different values depending of the quantities considered (B or N or E versus l or w or v see Table 1). But it is considered as an invariant property of unexploited ecosystems emerging from the scaling of individual level processes. Variations around the linear slope can be used as indicators of marine ecosystems health. For instance, departure from a linear shape is a robust measure to detect the impact of fishing (Bianchi *et al.* (2000); Shin & Cury (2001); Fulton *et al.* (2004)). It can also be impacted by environmental variations, so far most known effects of the environment concern plankton communities (San Martin *et al.* (2006)).

The intercept Γ ultimately refers to the level of richness of an ecosystem. It is a stronger indicator of the impact of the environment. For example, poor oligotrophic regions show small values of their intercept compared to rich eutrophic environments. This second property of the community size-spectrum links ecosystems total biomass to primary production over large scales (Boudreau & Dickie (1992)).

Empirical studies of freshwater ecosystems nuanced the linear spectra assumption with the observation of dome-shaped structures where levels of biomass deviate from the expected values (Boudreau & Dickie (1992); Sprules

& Goyke (1994)). Considered to be stable features Thiebaux & Dickie (1993) proposed that the domes correspond to different trophic groups.

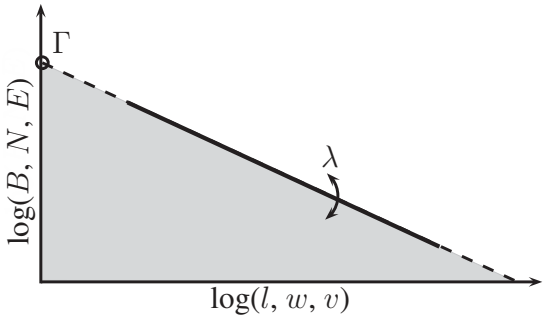


FIGURE 1: Linear community size-spectrum : λ, slope ; Γ, intercept.

TABLE 1: Slope λ values depending on ecosystems metrics (in bold, main values referred in the literature). Expressed as a multiple of $\alpha \simeq 1$.

	Biomass B	**Abundance N (B = Nw)**	**Energy E ($\mathbf{E \propto B}$)**
$\mathbf{w \propto v}$	$\boldsymbol{-\alpha}$	$\boldsymbol{-2\alpha}$	$-\alpha$
$\mathbf{l \propto v^{1/3}}$	-3α	-6α	$\boldsymbol{-3\alpha}$

1.2. Main mechanisms of biomass size distribution and flux

As a subset of physiologically structured models, the community size-spectrum models link the biomass size-distribution B (or N, or E) of the community to s (l, w or v), with individual level processes. For doing so, they usually rely on the predation-driven biomass transfer from a prey of size s_j to a larger predator of size s_i (Fig. 2a). Biologic matter $P(s_i, s_j)$ (expressed in term of B, N or E) eaten by predators at s_i from preys at s_j is turned into growth of the predator $G(s_i) = \alpha P(s_i, s_j) - M(s_i)$, after removing maintenance needs $M(s_i)$, and accounting for the yield α of the conversion of preyed matter into predators tissues (Andersen & Beyer (2006); Maury *et al.* (2007a)). Predators s_i are also potential preys for larger predators of size s_k, thus propagating this individual based process from the smaller to the larger individuals in the community. Disregarding species, the community level biomass density

distribution B (or N or E) emerges summing the biomass density associated to all individuals at sizes s_i, s_j, s_k and so on along s.

Integrated at the community level, these individual level processes lead to a flux of abundance N from size s to size $s+\Delta s$ that is mediated by predation and growth (Fig. 2b). Predation p is controlled by a prey selection function Ω characterized by the mean predator-prey mass ratio s_i/s_j and the width of prey selectivity $S_{i,j}$, namely the range of prey of size s_j available to a predator of size s_i. Predation fuels maintenance m and growth g. The dynamics of the abundance distribution is usually represented combining and advection term representing growth and a sink term μ accounting for predation induced mortality and other types of mortality :

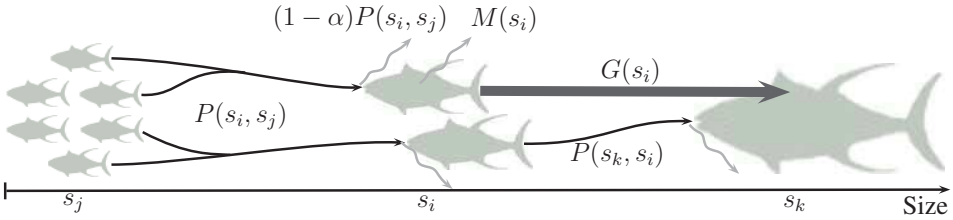
$$\frac{\partial N}{\partial t} = -\frac{\partial gN}{\partial s} - \mu N \tag{1}$$

This equation is well-known in population ecology as the McKendrick von Foerster equation (M'Kendrick (1925); Foerster (1959)), expressed in size instead of age. The McKendrick von Foerster equation is at the core of continuous community size-spectrum models (Arino *et al.* (2004); Benoît & Rochet (2004); Blanchard *et al.* (2009); Hartvig *et al.* (2011)). Other biological processes have been added to this equation, such as reproduction as boundary condition, or various types of mortalities such as disease, ageing, starvation or fishing. However, only the relationship between predation p, individual growth g and maintenance m explains the regularity of the spectrum.

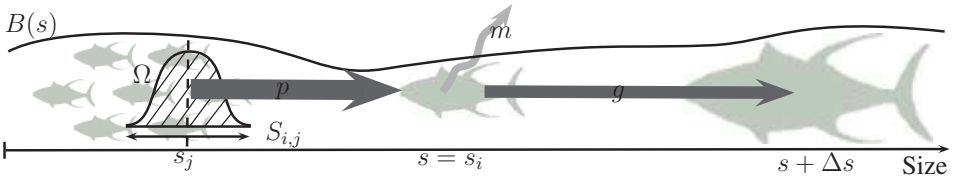
Based on the individual and community levels representations, two theoretical explanations are suggested to explain the regularity of the slope λ. They are labeled by Rossberg (2012) as the « oligotrophic » and the « eutrophic » regimes. In the « oligotrophic » regime, the encountered food compensates the metabolism and the slope is determined by the allometric exponents of encountered food (p) and metabolic requirement ($g + r$) (Andersen & Beyer (2006)). In the « eutrophic » regime, the food available is not limiting and the slope is determined by the balance between growth of predators (g) and the mortality they inflict on their prey (p) (Benoît & Rochet (2004))

Note that besides the continuous size-spectrum formulation (eq. 1) other formulations exist to compute the community size-spectrum. Also based on individual bioenergetics, they can be summarized as size resolved food webs, for plankton communities in particular (Moloney & Field (1991); Poulin & Franks (2010)), or size-resolved life history models (Shin & Cury (2001); Hall *et al.* (2006); Pope *et al.* (2006)). The first category accounts for the

predation-driven biomass transfer from preys to predators but doesn't account for individuals growth in size during life history. Individuals in a size class always remain in this size class. The second category represents explicitly the growth of populations or species, parametrized using empirically-derived life history traits (e.g. growth rates, fecundity, etc). It disregards mass and energy conservation. In this paper we focus on continuous size-spectrum models.



(a) Individual level processes.



(b) Community level processes.

FIGURE 2: Size selective predation drives the flow of energy in marine ecosystems at individual and community levels : black arrows represent biomass fluxe and grey arrows biomass dissipation.

1.3. More processes to realistically model marine ecosystems

Further to the basic biomass balance which accounts for individual's growth, respiration and death by predation, other processes have been introduced to increase the model's realism or close the mass budget (Fig. 3). These processes can impact the stability of community spectra (see section 2.1), they can be related to the slope λ, its intercept Γ, or affect the sensitivity of the spectrum to environment or fishing.

Arino *et al.* (2004) and Maury *et al.* (2007a) introduced reproduction in the boundary condition formulation at the smaller size end of the spectrum s_0 in fish communities (see Fig. 3). In Maury *et al.* (2007a), part of the biomass preyed is diverted from growth and maintenance to be invested into the reproduction of offspring that is re-injected into the size-spectrum at the

initial size s_0. With such a resource-dependent reproduction, the model links the intercept Γ to food-resources. Developments of trait based size-spectrum models (see section 1.5) completed this representation by considering that only adults larger than a species-dependent size threshold can contribute to reproduction (Hartvig *et al.* (2011); Maury & Poggiale (2013)). These formulations can be associated with a starvation mortality limiting the development on the community spectrum when maintenance, growth and/or reproduction needs can't be supported with available resources (Maury *et al.* (2007a)). Thus, community size-spectrum models can account for the tradeoff between reproduction, growth and development that individuals are facing when resources are limited.

Toward large size classes s_∞, senescence mortality or predation by super predators out of the spectrum are used to close it (Fig. 3). In spectrum models it avoids the unrealistic case of unbounded spectra since the range of sizes in real ecosystems are obviously bounded. Introduced for their ecological realism these processes are independent of life histories except for the DEB-derived ageing mortality in Maury & Poggiale (2013). They may have a strong impact on community size-spectra slopes λ and intercepts Γ. Besides a mortality to close the spectrum, a background mortality accounting for disease or other hazard source can be distributed throughout the spectrum. It has been shown to enhance solution's stability (Plank (2012)).

Maury & Poggiale (2013) used the Dynamic Energy Budget theory (DEB, Kooijman (2010)) to fully account for individual's physiology in a community size-spectrum model. It introduces the role of reserves on community dynamic. The introduction of these reserves provides a buffer to perturbations when investigating the sensitivity of marine ecosystems to the environment.

Figure 3, illustrates how reproduction, starvation and senescence (with or without background mortality such as disease) complete the community size-spectra theory. In the case of fish communities, these processes can be complemented by the addition of fishing as external stressor. An external size-selective mortality term is usually directly introduced in the governing equation 1 (Benoît & Rochet (2004); Blanchard *et al.* (2009)) to account for fishing.

1.4. Boundaries in community size-spectrum models

In marine ecosystems the regular biomass distribution of the spectrum (Fig. 1) spans up to 20 orders of magnitude in size from bacteria to fish. Over such a wide size range, organisms display many different reproduction

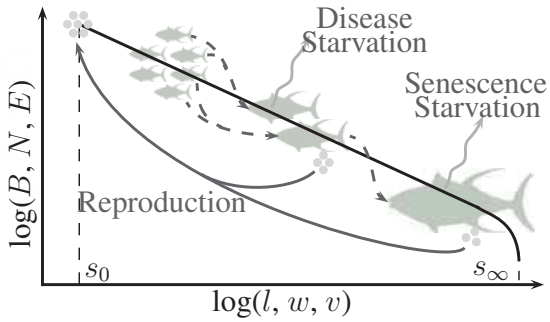


FIGURE 3: Additional processes of the community size-spectrum besides predation-driven growth : black arrows represent biomass fluxes in the community and grey arrows represent dissipation and losses.

strategies and feeding modes. Most recent studies in community size-spectrum modelling focus on fish communities with an external primary production pool or spectrum serving as a food source for small fish sizes. This primary production pool or spectrum (see Fig. 4) constrains the intercept Γ of the ecosystem spectrum and the total fish biomass. It sets the amount of resource available to consumers and indirectly fuels the reproduction which defines the initial biomass level of fish. The slope of the primary production's spectrum λ is usually fixed at a constant theoretical value (cf Table 1), though variations of the relative biomass of small and large primary producers have been shown to impact the production of fish communities.

The biomass spectrum exhibits a regular shape across ecosystems, and different intercepts at distinct primary production levels or at distinct temperature. Because it controls chemical reactions, temperature controls metabolic rates which underpin maintenance, growth or reproduction (Clarke & Johnston (1999); Kooijman (2010)) as well as the functional responses to food density (Rall *et al.* (2012)). Maury *et al.* (2007a) used the Arrhenius equation to correct ingestion, maintenance and background mortality. This leads the spectrum intercept to decrease with warming (Maury *et al.* (2007b)). Other community size-spectrum models use a similar formulation to investigate the impact of climate change on fish production (Blanchard *et al.* (2012); Merino *et al.* (2012); Woodworth-Jefcoats *et al.* (2013)) or the role of temperature on trophic cascades (Andersen & Pedersen (2009)). Fish communities have been shown to be less sensitive to temperature than to primary production (Blanchard *et al.* (2012)).

1.5. Representation of diversity with the size-spectrum

Unlike species-based models, size-spectrum models disregard metabolic and physiological differences of the individuals having the same size. However, a sardine and a juvenile tuna are obviously very different despite their same size. The only dimension of biodiversity that is considered in standard size-spectrum models is body size, disregarding any other dimension possibly important in a functional perspective.

To overcome this weakness, some community size-spectrum formulations adopt a mixed compartment based and spectrum based approach, to represent functional groups diversity (Fig. 4). For instance, Blanchard *et al.* (2009) couples two community size-spectra, parametrized to represent pelagic and benthic communities, and interacting through size selective predation but also through the recycling of dead organic matter. This detrital pathway aliments benthic communities and is slow compared to the main energy pathway between the pelagic community and the primary producers. Accounting for non predatory interactions in marine ecosystems, the approach revealed that ecosystem's resilience and function depends on the coupling's strength (Blanchard *et al.* (2011)). Also accounting for functional groups diversity and for differences in energy pathways, the ecosystem model APECOSM (Maury (2010)) focuses on the interaction between epipelagic, mesopelagic and migratory communities in the water column. The three spectra are linked through size-selective predation and they account for the biomass export to the deep sea by the diurnal cycle of migratory organisms.

However, even in compartment-based size-spectrum formulations, the functional role of biodiversity remains largely eluded as they do not resolve the metabolic differences of distinct species of the same size. To fill this gap, the most recent developments in community size-spectrum models attempt to account mechanistically for the role of species diversity with the introduction of trait-based formulations (Hartvig *et al.* (2011); Maury & Poggiale (2013)). These formulations resolve the biomass advection (eq. 1) not at the community level but at the level of trait defined species. Instead of solving a single community spectrum, they solve the McKenrick von Foerster equation for a potentially large set of functionally different species. The community dynamics emerges as the sum of each species contributions and interactions (Fig. 4). Transposing at the species level the general and simple parametrization of original size-spectrum formulated at the community level, trait-based approaches differentiate species by their maturation size s_{mat} (Hartvig *et al.* (2011)) or by their maximum length s_{max} (Maury & Poggiale (2013)). Both

measures are indeed scaling with metabolism in a number of ways (e.g. Kooijman (2010)). The species spectra are coupled by the size-selective predation so that each species can potentially eat organisms of every species. Considering a diversity of traits allows multiple energy pathways and it impacts the stability of the community spectrum (Zhang *et al.* (2013)). It also allows to represent trade-offs between species spectra when perturbed by environment or fishing. Note that to ensure the coexistence between species spectra, a random coupling between predator and prey species had to be introduced (Hartvig *et al.* (2011)), or the inclusion of schooling that prevents small species to be fully depleted by large predator species (Maury & Poggiale (2013)). The definition of additional traits such as habitat traits may be the next step to model species-diversified communities maintaining the coexistence (Hartvig & Andersen (2013)).

Finally, some approaches go beyond generic trait-based representations by parameterizing explicitly species spectra to represent a particular set of species in a given ecosystem (see the model Mizer, Scott *et al.* (2014)). These models are better suited than the trait-based model for studies where a level of taxonomic identity is required.

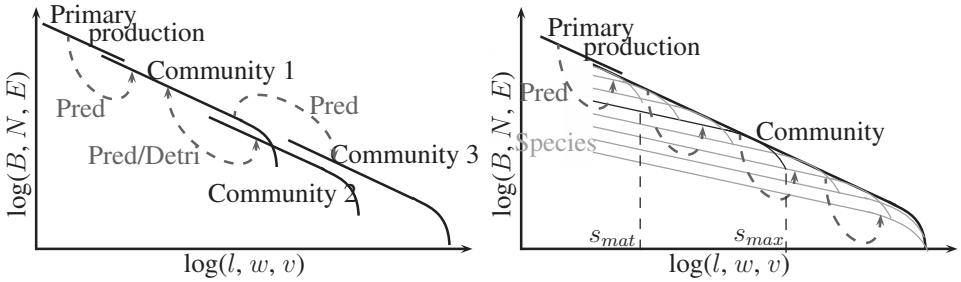


FIGURE 4: Representation of diversity with community size-spectrum models : functional community diversity (left) ; trait-based community spectrum (right).

2. Properties of community size-spectrum models

2.1. Stability

Continuous models of community size-spectra account for the dependence of individuals growth to prey density. This property is a major benefit of the method compared to size resolved food webs or life history models. While averaged at the ecosystem scale, empirical community spectra appear close to a stable steady state. This property is however usually not obtained using size-spectrum models that often exhibit transient or oscillating solutions (Arino *et al.* (2004); Benoît & Rochet (2004)), as illustrated figure 5. These oscillations correspond to a well known characteristic of predator-prey models (Lotka (1925); Volterra (1928)). Such oscillations have however not been documented empirically in actual marine ecosystems, though it is possible that, convoluted with the effects of environmental variability at different frequency, they might underpin unexplained fluctuations of marine fish stocks.

To investigate these oscillations, Law *et al.* (2008) as well as Datta *et al.* (2010) developed an individual-centered stochastic model of the predation and growth process. In order to better account for the randomness of predatory interactions, this so called jump-growth model allows two predators of a same size s_i to grow differently when then each ingest a prey of size $s_j < s_i$. A cohort of predators at s will be spread on $[s + \Delta s - \delta_1, s + \Delta s + \delta_1]$ after growth (δ_1 illustrates the variability of growth due to the variability of the predation success). The McKendrick von Foerster equation (eq. 1) is a first order approximation of the jump growth model. Valid close to the steady state, the equation loses its correctness for non-equilibrium solutions (Datta *et al.* (2010)). The addition of a diffusion term accounting for the cohort spread is suggested to be a better second order approximation of the jump-growth equation in this case (Benoît & Rochet (2004); Datta *et al.* (2010)), and it also tends to stabilize the modelled spectra.

In reality, various processes are susceptible to stabilize community size-spectra. First, Plank & Law (2011) and Plank (2012) show using the jump-growth model that decreasing the predator-prey size ratio s_i/s_j and widening prey selectivity $S_{i,j}$ have important stabilizing roles. A small, close to unity, predator-prey size ratio s_i/s_j is stabilizing. Disregarding the shape of the selectivity function (a gaussian curve or the convolution of two sigmoidal curves for instance), a spread selectivity (large $S_{i,j}$) also stabilizes the size-spectrum. Ecologically, it implies that increased connectance (selectivity width) and increased food chain length (small predator-prey size ratio) enhance stability.

Second, some density-independent processes have also been shown to be stabilizing. Capitán & Delius (2010) used an approach similar to the jump-growth formulation to demonstrate the stabilizing role of maintenance respiration and continuous reproduction. Finally, the introduction of biodiversity in size-spectrum models (Zhang *et al.* (2013), see section 1.5) appears to be stabilizing as well. Trait-based size-spectrum models allow to represent the diversity of size-dependent growth rates of individuals belonging to different species. Individuals in the same food environment do not grow at the same speed because they do not all belong to the same species. Like in the jump-growth model, they therefore lead to a dispersion phenomenon along the size dimension.

The inclusion of traits is however not sufficient to fully stabilize size-spectrum models (e.g. Zhang *et al.* (2013)) and the potential stabilizing role of other stabilizing processes have to be investigated. In this perspective, Maury & Poggiale (2013) proposed that schooling could exert such a stabilizing effect on the community size-spectrum. According to Maury (2016), schools are indeed density-dependent and they only appear when populations are abundant, increasing the predatory mortality and limiting individuals growth. This density-dependent phenomena would strongly stabilize marine ecosystems and the associated size-spectrum.

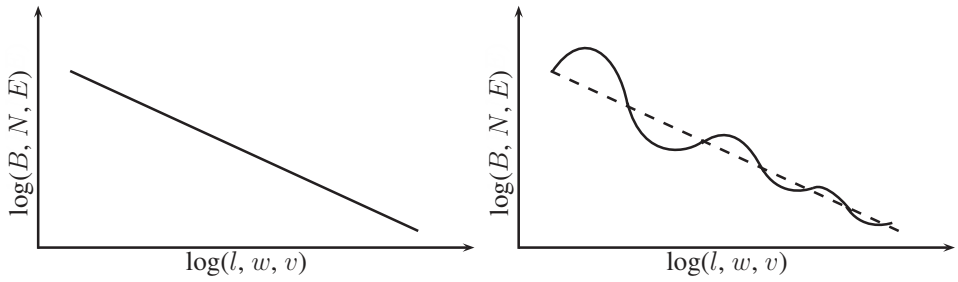


FIGURE 5: Dynamic of the community size-spectrum : steady spectrum (left) ; oscillating solutions (right).

2.2. Dynamic

Besides dynamic oscillations exhibited by unstable spectra, the dynamic response to perturbations of the community size-spectrum is overlooked.

In Pope *et al.* (1994), this dynamic is described as large waves of biomass propagating from small to large individuals while fading (see Fig. 5

right for illustration). The waves represent seasonal variations or resource which propagate up the size-spectrum. In this study they don't study the mechanisms of this dynamic but assume it to determine the environment in which individuals develop. Zhou (2006) formalizes the dynamic response of the perturbed dynamic size-spectrum. It is described by the propagation of waves driven by individuals growth, dumped by mortalities and spreading while they propagate away from the source. Maury *et al.* (2007b) on their side investigate the dynamic of the spectrum in upper trophic levels when forced by oscillations of resource or temperature. Waves of biomass propagate through the spectrum but amplify up to a resonant range before they fade. It is explained by different characteristic times (the time to reach a given size) between small individuals which grow and die quickly compared to large individuals. At different sizes individuals track the oscillations of resource more or less closely.

These different models of the dynamic of the size-spectrum however rely on the community level spectrum representation. They disregard the important role of species diversity. Different species with different growth speed and different sensitivities to variations of their environment will propagate perturbations differently. While clear waves propagation may be observed along species spectra, at the community level the signal may not be as clear since species waves could be out of phase or cancel each other.

Trait-based size-spectrum models could provide information on the dynamic of communities. Note that the analysis of the dynamic of the size-spectrum should be accompanied by the improvement of the numerical schemes used to solve the dynamic of size-spectra. They should avoid an excessive numerical diffusion.

2.3. Advantages and disadvantages of the size-spectrum formulation

With size-spectrum models, the complexity of aquatic ecosystems is aggregated using organism's size as the only structuring trait, and eventually species' size with trait based formulations. They disregard the role of taxonomic diversity on life history or behavior. On the other side, food web models or other specifically disaggregated approaches (e.g. Plagányi (2007)) are structured according to taxonomic identity or functional groups. They allow the explicit representation of the role biodiversity. In this context, size-spectrum models have both advantages and disadvantages.

On the advantages side, size-spectrum models focus on emergent properties at the level of ecosystems. They rest on synthetic parametrization of a few

key governing processes and avoid the caveat of over-parametrization that is associated to the explicit representation of specific traits and intra-specific interactions that species-based food web models require. Synthesizing the complexity of marine ecosystems at the specific level, they are convenient for large scale studies to analyze the impacts of climate and/or fishing on ecosystems biomass (Blanchard *et al.* (2012); Woodworth-Jefcoats *et al.* (2013); Lefort *et al.* (2015); Mézo *et al.* (2016)). Moreover, while the empirical determination of all the interactions or energy pathways in marine ecosystems would be a colossal task, the easily measured biomass size-spectrum provides a consistent starting point to develop theories of the functioning of marine ecosystems. In a nutshell, community size-spectrum models allow to override the gaps of our empirical knowledge at the species level.

On the disadvantages side, size-spectrum models are expressed at the community level. They are obviously not appropriate to address species-specific dynamics, though they have sometimes been used to provide the biotic environment in which target species evolve (Maury (2010)). Community size-spectrum models generally disregard the role of taxonomic diversity, though recent developments attempt to tackle this issue (Andersen & Beyer (2006); Hartvig *et al.* (2011); Maury & Poggiale (2013)) as reviewed chapter 1.5. It makes them especially difficult to compare to observations. Finally the regularity of the community size-spectrum appears over large spatial and temporal scales. This make it difficult to use it to reproduce local systems where imports and exports are important.

3. Modelling marine ecosystems with the community size-spectrum

3.1. Functioning of the community size-spectrum

Using the community size-spectrum as benchmark, Maury *et al.* (2007b) investigates the impact of primary production and temperature variations on the intercept of consumer spectra an show that they are non-linearly related. Under constant or oscillating forcing, they derive the properties of the biomass flux. The community size-spectrum theory can be used to globally quantify the biomass production, dissipation and loss in marine ecosystems. It provides estimates of the evolution of marine ecosystems in a changing environment from bioenergetic considerations.

Linking the energy balance at individual level to the dynamic of communities with the so-called equilibrium size-spectrum theory (Andersen & Beyer (2006)), important ecological properties can also be derived from the spectrum features. For example Andersen & Pedersen (2009) relates trophic and average individual growth efficiencies to the spectrum slope λ. Fishing impacts the steepness of the spectrum and thus the trophic efficiency. With the same equilibrium theory Andersen *et al.* (2009) uses the biomass spectrum to demonstrate the links between growth, predation and fish production. Andersen *et al.* (2008) investigates the benefit for fish to produce many small eggs as reproductive strategy.

Thanks to their species-based structure, trait-based formulations allow to investigate population interactions and the functional role of specific diversity. In this perspective, Hartvig & Andersen (2013) analyze the coexistence between species and linked it to maturation sizes and predator-prey mass ratios. Depending on these parameters, the relationship between two species will be dominated by their competition or a state of « trophic ladder » where the second species develop based on the first one. With trait-based size spectrum models other traits can be considered to test the conditions of species coexistence.

Finally, extending the biomass distribution function of size s to the biomass distribution function of trait s_{max}, Reuman *et al.* (2014) developed a diversity spectrum of the species distribution in a spatially delineated assemblage. The community spectrum striking characteristic of regularity could therefore be extended to characterize species abundance distributions thus opening new perspectives for the study and modelling of marine ecosystems. Still on the subject of the characterization of the species distribution, Maury & Poggiale (2013) developed a function, $\Phi_s^{s_{max}}$, which expresses the relative

contribution of each trait to the total energy content of the ecosystem. Since different species do not have the same metabolic parameters, it characterizes the differences of energy flow along the size s dimension. The trait distribution can be used as a metric of ecosystem biodiversity.

3.2. Impact of fishing on the community size-spectrum

It is recognized that fishing activities target the largest organisms in marine ecosystems and alter the slope of the community size-spectrum λ, which has been shown to be a consistent indicator of fishing pressure (Bianchi *et al.* (2000); Fulton *et al.* (2004); Shin *et al.* (2005)). Its departure from the theoretical value without fishing (see Table 1) allows estimating the exploitation level of the system considered (Jennings & Blanchard (2004)). However, with a size-spectrum model Andersen & Pedersen (2009) give a broader description. Fishing depletes larger individuals and induces trophic cascades up and down in trophic levels. Observations of variation of the slope λ could actually correspond to the fitting of the spectrum on one oscillation along the cascade.

Fishing being often size-selective, community size-spectrum models provide a tool to test how fishing impacts ecosystems. For example, recent studies suggest that spreading the fishing pressure over large portions of ecosystems, in term of size or species, may be ecologically less destructive than the highly selective fishing patterns that usually prevail. With their simple structure, size-spectrum models have been used to quantify the differences of both fishing approaches. Law *et al.* (2012) concluded that a spread fishing pressure increases productivity. In the same spirit, Rochet & Benoît (2012) used the stability properties of the community spectrum to investigate how the distinct fishing strategies impact the dynamic of the spectrum. Fishing globally amplifies oscillations and spread fishing mitigates them compared to selective fishing.

The community size-spectrum reflects the impact of fishing. Spectrum models have been used to measure the sensitivity of indicators of ecosystems to different fishing strategies, in term of intensity and selectivity (Houle *et al.* (2012)). No single indicator emerges as superior in all respects, so multiple complementary indicators are suggested for community monitoring. Trait-based size-spectrum models also allow to measure the impact of fishing on species composition. Most variability in the relative abundance of large fish is caused by shifts in the relative abundance of species (Shephard *et al.* (2012)).

3.3. Ecosystem study with the community size-spectrum

Size-spectrum models can provide useful insights on the characteristics of ecosystems when the functional role of individuals and species is of bigger interest than their identity.

Over the last decade marine ecosystem models have adopted more integrative approaches linking ocean's physics to bio-geochemical cycles and fisheries. Community size-spectrum models present advantages in this « end-to-end » perspective (Travers *et al.* (2007); Rose *et al.* (2010)). First they allow compact representations of global-scale ecosystems at a reduced computational cost. Second, thanks to their mechanistic formulation, they adapt to various regional ecosystems configurations without the need for region-specific parametrization and allow projections of ecosystem states in future conditions without prescribing the food web structure. This is especially valuable for studying climate change impacts that are expected to trigger changes in oceans with no-analogues in the past. Coupled climate, biogeochemical, fish spectrum models are already applied to investigate the impact of climate, temperature and primary production, on fish production. Using such models, few studies attempted to investigate the convoluted effects of climate and fishing on large marine ecosystems (Blanchard *et al.* (2012)), or in the pacific (Woodworth-Jefcoats *et al.* (2013)). Coupled with a bioeconomic model, a spectrum model was also applied to investigate the conditions that would allow fisheries and aquaculture to sustain current and increased fish consumption rates (Merino *et al.* (2012)). Community size-spectrum models are tools to asses the impact of climate change on marine ecosystems services.

The APECOSM model Maury (2010) embed a continuous size-spectrum model of interactive epipelagic, mesopelagic and migratory communities into a spatially resolved advection-diffusion model accounting for the tridimensional transport of biomass by ocean currents and active swimming. APECOSM also considers the effects of food, temperature, oxygen and light on the behavior of individuals. The model has been applied to investigate the bottom-up forcing of climate on fish communities (Lefort *et al.* (2015)). Forced with a pre-industrial physical and biogeochemical environment the model has been applied to investigate the variability of the biomass spectrum at different individual's size (Mézo *et al.* (2016)). It offers a strong basis for developing scenarios of the evolution of fish abundance in oceanic ecosystems.

Conclusion and perspectives

A wide range of marine ecosystem's models have been developed over the years and are presently available to the scientific community. Given the number of possible ways to look at the complexity of marine ecosystems, various objective-specific approach coexist, all with advantages and disadvantages (Plagányi (2007)).

Continuous community size-spectrum models provide simple mechanistic representations of marine ecosystems (Benoît & Rochet (2004); Andersen & Beyer (2006); Maury *et al.* (2007a)). They reduce the complexity of food webs and suggest the spectrum' slope and intercept are useful for characterizing ecosystems' state. Size-spectrum models are valid over large regions, in ecosystems where body size is the main driver of individuals' physiology and interactions, such as in pelagic ecosystems. The method may be inappropriate in small regions, where energy import and export from neighboring systems dominate.

The theory behind the community size-spectrum is now sufficiently developed to use size-spectrum models for testing ecological assumptions, for example regarding the impact of fishing (Houle *et al.* (2012); Rochet & Benoît (2012)), the efficiency of reproduction strategies (Andersen *et al.* (2008)) or the impacts of environmental variability at various frequencies (Mézo *et al.* (2016)). It is sufficiently developed to use size-spectrum models to asses the effects of climate change on marine ecosystem services (Blanchard *et al.* (2012); Merino *et al.* (2012); Woodworth-Jefcoats *et al.* (2013)). The recent recognition that the structure of species diversity in communities exerts a strong influence on ecosystems' functioning, sensitivity to perturbations, and resilience (Blanchard *et al.* (2011)), have spurred the development of trait-based models of community spectrum (Hartvig *et al.* (2011); Maury & Poggiale (2013)). However, despite this ongoing complexification of models, few comparisons to empirical data have been conducted to date. The development of a size-based theory of marine ecosystems would certainly benefit from a better empirical validation. It may become possible with the recent determination of size-spectrum based food web models (Scott *et al.* (2014)).

The size-spectrum models provide a baseline of ecosystems states and allow deconvoluting the effects of natural drivers from human induced perturbations and changes. Comparing theoretical spectrum values with empirical size-spectra provides insights on the health of ecosystems (Rice & Gislason (1996); Bianchi *et al.* (2000)). Size-spectrum models also provide tools to investigate

in silico how environmental drivers alter the biomass flux from primary production to upper trophic levels (Maury *et al.* (2007b)). Embedded into « end-to-end » approaches, the mechanistic basis of size-spectrum models is well adapted to long-term projections of ecosystems to investigate oceans' future in different environmental and fishing context (Lefort *et al.* (2015)).

Acknowledgment

This study was supported by the ANR project MACROES (MACRoscope for Oceanic Earth System ANR-09-CEP-003)

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Chapter 3

Effects of low trophic level biomass and temperature on fish communities: A modeling study

Effects of low trophic level biomass and temperature on fish communities: A modeling study

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Abstract

Physical and bio-geochemical changes of the oceans have complex influences on fish communities. Variations of resource and temperature affect metabolic rates at the individual level, biomass fluxes at the population level, and trophic structure, diversity, at the community level. We use a Dynamic Energy Budget-, trait-based model of the community size-spectrum to assess the effects of low trophic level's biomass and temperature on communities at steady state. First, we look at them separately in idealized simulations, varying one of the stressors while the second remains constant. A multi-domain response is observed. Linked to the number of trophic levels sustained in the consumers's community, the regimes highlighted present similar properties when low trophic level's biomass is increased, or temperature decreased. These domains correspond to different efficiencies of the transfer of energy from small to large individuals. They are characterized by different sensitivities of fish communities to environmental changes. Moreover, differences in the scaling of individuals' metabolism and prey assimilation with temperature lead to a shrinking of fish communities with warming. In a second steps, we look at the impact of simultaneous variations of stressors along a realistic mean latitudinal gradient of low trophic level's biomass and temperature. The model explains known observed features of global marine ecosystems such as the Bergmann's rule, namely the fact that larger species compose fish communities when latitude increases. The structure, diversity and metabolic properties of fish communities obtained with the model at different latitudes are interpreted in light of the different regimes characterized in the idealized experiments. From the equator to the poles, the structure of consumer's communities is predicted to be heterogeneous, with variable sensitivities to environmental changes.

Keywords : Community size-spectrum ; Dynamic Energy Budget ; Biodiversity ; Bergmann's rule ; Trait based model ; Marine ecosystem model ; Impact of the environment ; Latitudinal gradient ; Ecosystem regimes.

Introduction

Climate driven physical and bio-geochemical changes (Bindoff *et al.* (2007); Doney *et al.* (2012)) impact marine ecosystems properties in a number of ways. They affect individuals directly, modifying their access to resources through increased stratification (Sarmiento *et al.* (2004); Bopp *et al.* (2013)) or their metabolism through temperature changes (Gillooly *et al.* (2001); Clarke & Fraser (2004)), acidification (Fabry *et al.* (2008)) or de-oxygenation (Pörtner & Knust (2007)). These direct effects at the individual level propagate to the community level through alterations of the energy transfer across trophic and organization levels. For example, climate changes have been shown to induce a global body size shrinking (Daufresne *et al.* (2009); Sheridan & Bickford (2011)). It will also lead to changes in fish production (Blanchard *et al.* (2012); Lefort *et al.* (2015)) or biodiversity (Cheung *et al.* (2009)). These indirect responses modify the services provided by marine ecosystems. Fisheries are expected to be particularly affected and the consequences in terms of food security and economic profitability are major issues (Brander (2007); Jennings & Brander (2010)). In this context, understanding the intricate response of fish communities to environmental changes is an urgent challenge (Rice & Garcia (2011); Merino *et al.* (2012)).

However, investigating and modeling environmental effects on fish communities is a difficult task since many processes interact, from the individual to the community level. Because of our limited knowledge, any attempt to model the response of fish communities to environmental changes usually implies pragmatic compromises depending on the organization levels and scales into focus. For example, some approaches fully account for individual life history as well as intra- and inter-specific interactions on local scales with individuals based models (Grimm (1999); Shin & Cury (2001)), while other only model target species and their evolution in a changing environment (Lehodey *et al.* (2008); Dueri *et al.* (2014)). Some approaches focus on the species probability of occurrence as a function of given environmental variables with ecological niche models (Peterson (2003); Cheung *et al.* (2009)), other disregard species differences and only derive the ecosystem size-spectrum (Maury *et al.* (2007); Blanchard *et al.* (2009, 2012); Woodworth-Jefcoats *et al.* (2013)). Body size plays a dominant role in fish communities. It structures individual's life history and trophic interactions. Recent studies use both body size and populations maximum (or maturity) size as structuring variables to integrate through organization levels and account for the influence of functional biodiversity on community dynamics. These trait-based size-spectrum models link individual's bio-energetic to the emergent response of communities (Andersen & Beyer (2006); Hartvig *et al.* (2011); Maury & Poggiale (2013)). Similarly to physiologically structured populations models (Metz & Diekmann (1986); De Roos & Persson (2001, 2013)) this approach accounts for environmental signals impacts across organization levels.

In this paper we use the trait-based size-spectrum model presented in Maury & Poggiale (2013) to investigate the impact of the environment on fish communities. We focus on two major factors affected by climate change, the impact of low trophic level's biomass and temperature. In the first section we summarize the model, especially how it links individual's bio-energetic and trait diversity to community dynamics. The way environmental effects are introduced is described. To analyze environmental impacts, indicators of the ecosystem state are derived. They characterize ecosystems in terms of structure, metabolism and trait diversity. The estimation of the model's parameters is presented. In a second section we use this framework to analyze how the characteristics of fish communities are linked to the environment. The effects of food in low trophic levels and temperature are first being considered independently, before focusing on their combined impacts. Distinct domains are observed over different low trophic level's biomass and temperature ranges. To bring realism into our idealized study the structure of marine ecosystems is then investigated along a latitudinal gradient representative of mean temperature and low trophic level's biomass co-variations from South to North poles. Finally, the third section discusses the use of our mechanistic approach to explain features of global marine ecosystems. It agrees especially with Bergmann's rule. From this base, the potential impact of environment on global fish biomass is discussed. The distinct domains when changing food in low trophic levels and temperature will lead to different sensitivities of fish communities to environment variations.

1 Method

1.1 The individual based community model

1.1.1 Individual level : the Dynamic Energy Budget theory (DEB)

Maury & Poggiale (2013) base their model on a reduced formulation of the DEB theory (Kooijman (2000, 2010); Nisbet *et al.* (2000); Sousa *et al.* (2010)) to represent the energetics of individuals with two state variables : reserve's energy E (J) ; structural volume V (cm^3), linked to structural length L by $V = (\delta L)^3$, with δ being a constant parameter characterizing the shape of organisms. These primary variables interact together through energy flux $\dot{p}$ (illustration Fig. 1a with flux Tab. 1). The life history of an individual is thus entirely derived from the dynamics of the state variables that is fully determined by : the quantity of food available, expressed by an ingested energy $\dot{p}_X$ that is determined by the scaled Holling type II functional response f_V (see Appendix A) ; the body temperature T, that increases or reduces metabolic rates (see T_{cor}, section 1.2.2).

In the DEB theory, most processes scale with the maximum structural volume V_m that a population can reach in a favorable environment. An infinite number of species can therefore be represented with a same set of generic parameters (see DEB parameters Tab. 4). It disregards other dimensions of species diversity since two individuals of different species with the same trait V_m will be considered as functionally identical. But it allows the modeling of the main life history characteristics of the full range of species in an ecosystem keeping the model complexity tractable.

This formulation provides a trait-dependent representation of life history based on individual's food- and temperature-dependent metabolism.

TABLE 1 – DEB energy flux as a function of primary DEB parameters, the energy reserve E, the structural volume V, for an individual of a given trait V_m (Kooijman (2000, 2010)). T_{cor} expresses the temperature correction of metabolic activity.

Eq. No.	**Metabolic process**	**Energy flux (in J/s)**
T1.a	Ingestion	$\dot{p}_X^{V_m} = \{\dot{p}_{Xm}^{V_m}\} f_V^{V_m} V^{2/3} T_{cor}$
T1.b	Assimilation	$\dot{p}_A^{V_m} = \kappa_X \dot{p}_X^{V_m} = \{\dot{p}_{Am}^{V_m}\} f_V^{V_m} V^{2/3} T_{cor}$
T1.c	Catabolism	$\dot{p}_C^{V_m} = \frac{f_V^{V_m}[E_m]}{[E_G]+\kappa f_V^{V_m}[E_m]} \left([E_G]\nu V^{2/3} + [\dot{p}_M]V\right) T_{cor}$
T1.d	Reserve growth	$\dot{p}_E^{V_m} = \dot{p}_A^{V_m} - \dot{p}_C^{V_m}$
T1.e	Structural maintenance	$\dot{p}_M^{V_m} = [\dot{p}_M] V T_{cor}$
T1.f	Structural growth	$\dot{p}_G^{V_m} = \kappa \dot{p}_C^{V_m} - \dot{p}_M^{V_m}$
T1.g	Maturity maintenance	$\dot{p}_J^{V_m} = \frac{1-\kappa}{\kappa} [\dot{p}_M] min\left(V, V_p^{V_m}\right) T_{cor}$
T1.h	Reproduction	$\dot{p}_R^{V_m} = (1-\kappa)\, \dot{p}_C^{V_m} - \dot{p}_J^{V_m}$

1.1.2 Population level : the population spectrum

From the DEB representation a population can be defined as a density of individuals' abundance in the state-space determined by the state variables E and V, for a single trait V_m. In Maury & Poggiale (2013), the reserves dimension E is simplified assuming that their dynamics are fast compared to the dynamics of structural volumes V and individual's mortalities. The reserves taken at equilibrium E^* the dynamic of individuals' abundance in this population, in a cubic meter of ocean water, $N_{V,t}^{V_m}$, writes

$$\frac{\partial N_{V,t}^{V_m}}{\partial t} = -\frac{\partial(\dot{\gamma}_{V,t}^{V_m} N_{V,t}^{V_m})}{\partial V} - M_{V,t}^{V_m} \quad \text{on} \quad \Omega =]V_b, V_m] \tag{1}$$

between a birth volume V_b and V_m. $M_{V,t}^{V_m}$ accounts for mortalities. $\dot{\gamma}_{V,t}^{V_m}$ is a structural growth rate.

Note that individual's physiology uses the energy currency while the population representation uses the abundance currency. Both are linked since for any individual the energy content ξ_{ind} is linked to

structural volume V and reserve's energy at equilibrium E^*, $\xi_{ind} = (E^* + d\psi V)$ (with d the density of biomass, ψ the energy content of biomass). The total energy of all individuals at t, V for V_m is $\xi_{V,t}^{V_m} = \xi_{ind} N_{V,t}^{V_m} = (E^* + d\psi V) N_{V,t}^{V_m}$ and the abundance advection (Eq. 1) can be represented by a flow of energy $\xi_{V,t}^{V_m}$.

The scaled functional response (T2.k, see Tab. 2), constraining individuals development, is established from the population level energy distribution. A size selective predation hypothesis determines the energy content of prey (T2.h) at structural volume V_{pr} available to a predator at a structural volume V_{Pr} (T2.f). The DEB then provides the rate of energy invested into growth (T1.f) to compute $\dot{\gamma}_{V_{Pr},t}^{V_m}$ (T2.l). Summing the rates of energies invested into reproduction (T1.h) by all mature individuals ($V_{Pr} > V_p = \alpha_p V_m$) in the population it provides the flux of offspring (T2.q) re-injected at birth $\dot{r}_t^{V_m}$:

$$\dot{\gamma}_{V_b,t}^{V_m} N_{V_b,t}^{V_m} = \dot{r}_t^{V_m} \quad \text{at} \quad V_b \tag{2}$$

Note that with such boundary condition the eggs and larval stages are neglected.

At the population level, the abundance density distribution governed by Eqs. 1 and 2 can be represented in a log-log space with a population size-spectrum (Fig. 1b). The population abundance $N_{V,t}^{V_m}$ decreases with increasing V because of energy dissipation at individual level (T1.e,g) and losses induced by mortalities : predation (T2.p,q) ; ageing, expressed from DEB (T2.o) ; disease (T2.n) proportional to a later described schooling probability (T2.g) ; starvation (T2.m).

Food and temperature conditions at individual level as well as the inter-individual predatory interactions fully determine the population density abundance distribution.

1.1.3 Community level : the aggregated community spectrum

At a given structural volume V, individuals from different trait-defined populations V_m have distinct life-history properties. For example at a same size, a sardine and a yellowfin tuna do not have the same growth, mortality, food requirements, etc. These differences shape the food web properties and constrain the response of communities to perturbations. To account for this diversity of traits, Maury & Poggiale (2013) extended the population spectrum model (Eqs. 1, 2 and Tab. 2) to a set of interacting population equations accounting for an « infinity » of asymptotic volumes V_m, from small to large populations over a trait range $[V_m^{min}, V_m^{max}]$:

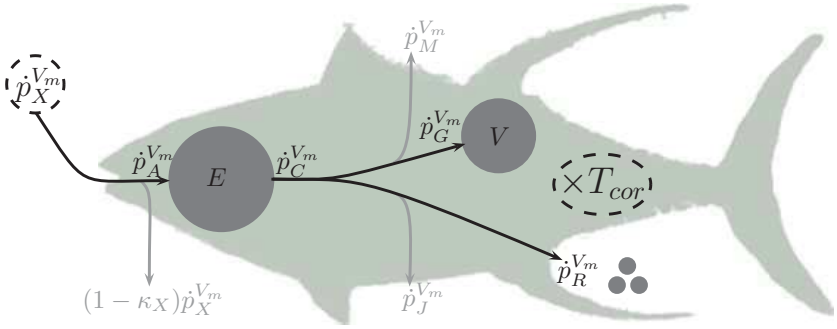
$$\forall V_m \in [V_m^{min}, V_m^{max}] \quad \begin{cases} \frac{\partial N_{V,t}^{V_m}}{\partial t} = -\frac{\partial(\gamma_{V,t}^{V_m} N_{V,t}^{V_m})}{\partial V} - (\dot{\lambda}_{V,t}^{V_m} + \dot{a}_{V,t}^{V_m} + \dot{d}_{V,t}^{V_m} + \dot{s}_{V,t}^{V_m}) N_{V,t}^{V_m} & \text{on} \quad \Omega =]V_b, V_m] \\ \gamma_{V_b,t}^{V_m} N_{V_b,t}^{V_m} = \dot{r}_t^{V_m} \end{cases} \tag{3}$$

Populations are linked to each other through predation since the food available to any predator of any population can come from prey in other populations ($p_{V,t}$ (T2.h)). In order to stabilize communities and maintain coexistence of small and large populations a schooling term is introduced (Maury & Poggiale (2013)). At each structural volume this schooling (T2.g) provides a threshold value below which prey are protected from predation. The coexistence is thus maintained avoiding the unrealistic depletion of smaller prey populations by predation (T2.i). This schooling term, which represents the level of aggregation of individuals into schools, is also assumed to be related to the prevalence of disease transmission and thus disease mortality (T2.n).

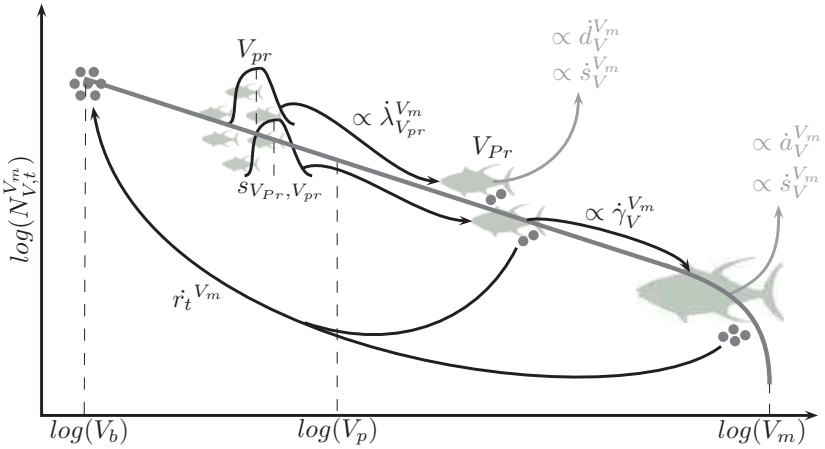
Emerging from populations, the community abundance size-spectrum $\mathrm{N}_{V,t}$ (Fig. 1c) is the integral :

$$\mathrm{N}_{V,t} = \int_{V_m^{min}}^{V_m^{max}} N_{V,t}^{V_m} dV_m \tag{4}$$

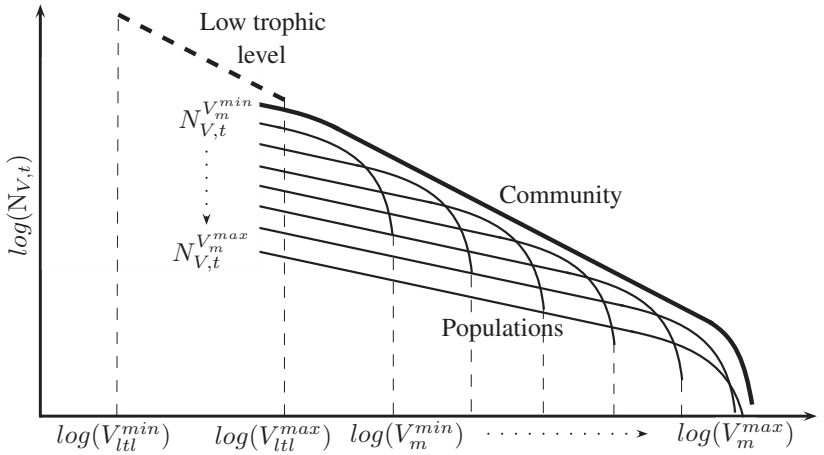
With this model (Eqs. 3, 4, Tabs. 1, 2) environmental conditions affecting individual level processes constrain the emergent communities properties.



(a) Individual : DEB state variables (compartments) and energy flux (arrows) involved in the bio-energetics of any individual of a species of maximum volume V_m.



(b) Population : population size-spectrum (black line) emerging form the advection of individuals along structural volumes driven by size selective predation and constrained by reproduction, energy losses, dissipation (arrows), for a population of individuals of maximum volume V_m.



(c) Community : community size-spectrum (black line) as integral of population spectra (thin black lines) of asymptotic volume $V_m \in [V_m^{min}, V_m^{max}]$, lower trophic level size-spectrum (dashed).

FIGURE 1 – Schematic representation of the model : the energy flows from individuals to populations to the community (black arrows) in balance with losses and dissipation (grey arrows) and shape the community size-spectrum. The environment impacts individuals through variations of food density and body temperature (dashed) and constrains the dynamic of the emerging community.

TABLE 2 – Summary of model's governing equations (Maury & Poggiale (2013)). T_{cor} express the temperature correction. $[x]^+ = x$ if $x > 0$, 0 else.

Eq.	Process	Equation
Consumers governing equations		
T2.a	Population dynamics equation ($\forall\ V_m$)	$\frac{\partial N_{V,t}^{V_m}}{\partial t} = -\frac{\partial(\gamma_{V,t}^{V_m} N_{V,t}^{V_m})}{\partial V} - (\dot{\lambda}_{V,t}^{V_m} + \dot{a}_{V,t}^{V_m} + \dot{d}_{V,t}^{V_m} + \dot{s}_{V,t}^{V_m}) N_{V,t}^{V_m}$
T2.b	Limit abundance flux (at $V = V_b$)	$\gamma_{V_b,t}^{V_m} N_{V_b,t}^{V_m} = \dot{r}_t^{V_m}$
T2.c	Community abundance distribution	$\mathrm{N}_{V,t} = \int_{V_m} N_{V,t}^{V_m} dV_m$
T2.d	Equivalence energy abundance	$\xi_{V,t}^{V_m} = (E^* + d\psi V) N_{V,t}^{V_m}$
T2.e	Reserve energy	$E^* = f_{V,t}^{V_m} [E_m^{V_m}] V$
Food encounter		
T2.f	Predator size selectivity on prey	$s_{V,U} = \frac{\left(1-\left(1+exp\left(\alpha_2\left(\rho_2-(\frac{V}{U})^{1/3}\right)\right)\right)^{-1}\right)}{\left(1+exp\left(\alpha_1\left(\rho_1-(\frac{V}{U})^{1/3}\right)\right)\right)}$
T2.g	Schooling probability	$ps_{V,t}^{V_m} = \frac{(V\xi_{V,t}^{V_m})^\beta}{s_{cr}^\beta + (V\xi_{V,t}^{V_m})^\beta}$
Predation		
T2.h	Energy content of available prey	$p_{V,t} = p_{V,t}^C + p_{V,t}^{LTL}$
T2.i	Prey density of consumers	$p_{V,t}^C = \int_{U=V_b}^{V_m^{max}} s_{V,U} \left(\int_{V_m=U}^{V_m^{max}} ps_{U,t}^{V_m} \xi_{U,t}^{V_m} dV_m \right) dU$
T2.j	Prey density of producers	$p_{V,t}^{LTL} = \int_{U=V_{ltl}^{min}}^{U=V_{ltl}^{max}} s_{V,U} \xi_{U,t}^{ltl} dU$
T2.k	Holling type II functional response	$f_{V,t}^{V_m} = \frac{p_{V,t}}{C' V_m^{1/3} V^{-1/3} T_{cor}^{-q} + p_{V,t}}$
Growth		
T2.l	Instantaneous growth rate	$\dot{\gamma}_{V,t}^{V_m} = \frac{[\dot{p}_G^{V_m}]^+}{[E_G]}$
Mortality		
T2.m	Starvation mortality coefficient	$\dot{s}_{V,t}^{V_m} = \frac{N_{V,t}^{V_m}}{\xi_{V,t}^{V_m}} \left([-\dot{p}_G^{V_m}]^+ + [-\dot{p}_R^{V_m}]^+ \right)$
T2.n	Disease mortality coefficient	$\dot{d}_{V,t}^{V_m} = D\ ps_{V,t}^{V_m} T_{cor}$
T2.o	Ageing mortality coefficient	$\dot{a}_{V,t}^{V_m} = \frac{\ddot{h}_a}{V_t} \int_{t_1=0}^{t_1=t} V_{t_1} dt_1 - V_b t + \frac{[\dot{p}_M]}{[E_G]} \int_{t_1=0}^{t_1=t} \int_{t_2=0}^{t_2=t_1} V_{t_2} dt_2 dt_1$
T2.p	Predation mortality coefficient	$\dot{\lambda}_{V,t}^{V_m} = \frac{ps_{V,t}^{V_m}}{\kappa_X} \int_{V_m=V_b}^{V_m^{max}} \int_{U=V_b}^{V_m} \left(\frac{\{\dot{p}_{Am}\} \xi_{U,t}^{V_m} U^{-1/3} s_{V,U} f_{V,t}^{V_m}}{p_{U,t}(d\psi + E^*/V)} \right) dU dV_m$
Reproduction		
T2.q	Reproductive input	$\dot{r}_t^{V_m} = (1 - M_{egg}) \phi \kappa_R \int_{V_p}^{V_m} N_{V,t}^{V_m} [\dot{p}_R^{V_m}]^+ dV$
Temperature		
T2.r	Arrhenius correction	$\dot{\rho}(T) = \dot{\rho}(T_{ref}) exp\left(\frac{T_A}{T_{ref}} - \frac{T_A}{T}\right) = \dot{\rho}(T_{ref}) T_{cor}$

1.2 Environmental drivers

1.2.1 Low trophic level's biomass (LTL)

For the fish community the low trophic level provides food to small individuals that are themselves eaten by larger individuals and so on. Perturbations propagate up the trophic chain and alter the community properties. In the model, the low trophic level is represented using a constant slope log-log size-spectrum over the range $[V_{ltl}^{min}, V_{ltl}^{max}]$. Small individuals feed on this spectrum through size selective predation (T2.f,j). In the present paper we focus on higher trophic levels properties. Therefore we disregard the effect of predation mortality exerted on this food resource and keep the low trophic level's total biomass p_{cc} constant during simulation.

1.2.2 Temperature (T)

For most marine fish water temperature has a direct influence on metabolic processes (Gillooly *et al.* (2001); Clarke & Fraser (2004)). In the model, the explicit representation of energy fluxes $\dot{p}$ at the individual level with DEB (Fig. 1a) is well suited to correct metabolism with temperature effect. It is introduced by a flux correction T_{cor} (Tab. 1). This correction T_{cor} follows an Arrhenius relationship (T2.r, Kooijman (2000, 2010)), increasing or decreasing $\dot{p}$ for a temperature T compared to a reference value $\dot{p}_{ref}$ at reference temperature T_{ref}. Other metabolism related processes such as ageing (T2.o) and disease (T2.n) are also corrected with T_{cor}. For the feeding rate, differences of scaling with temperature between handling time and attack rate have been suggested across biota (Rall *et al.* (2012); Englund *et al.* (2011)). In the model, the handling time is chosen to scale with T_{cor} while the attack rate scales with T_{cor}^{q} (T2.k, see Appendix B). This difference induces a dependence on temperature of the half saturation constant in the scale functional response (T2.k). All model parameters are determined at T_{ref} and the impact of temperature on fish communities is investigated modeling constant T levels with a constant T_{cor} correction.

1.3 Ecosystems indicators

1.3.1 Structure

We developed a set of indicators to investigate quantitatively how low trophic level's biomass and temperature impact the properties of ecosystems, from individuals to populations to communities. Note that for the modeled ecosystems indicators have constant values since the model converges toward a stable steady state solution for every environmental forcing considered.

On a log-log scale, the community spectrum $\mathrm{N}_{V,t}$ (Fig. 1c) is known to display a quasi-linear shape that can be characterized by its slope S_C, and its intercept (Fulton *et al.* (2004); Shin *et al.* (2005)). This last relates to the total energy ξ_t^{tot} in the modeled community.

$$\xi_t^{tot} = \int_{V_m} \int_{V} \xi_{V,t}^{V_m} \, dV \, dV_m \tag{5}$$

The abundance size distribution $\mathrm{N}_{V,t}$ is used to compute the cut-off frequency of maximum structural size in the community. It is defined as the length at which the abundance density ratio between two successive structural sizes class is less than 1/10 (Lefort *et al.* (2015)). We can compute trophic levels extracting $D_{V_{Pr},V_{pr}}$, the fraction of prey of size V_{pr} in the diet of predators of size V_{Pr} :

$$TL_{V_{Pr},t} = 1 + \sum_{V_{pr}} D_{V_{Pr},V_{pr}} TL_{V_{pr},t} \tag{6}$$

We therefore use four indicators to characterize the community structure :

— ξ_t^{tot} (T3.a) : The total amount of energy in the modeled community.

— S_C (T3.b) : The community size-spectrum slope. It describes the relative abundance of small and large individuals in the community. It is usually assumed to be approximately constant with a value around -2 for an abundance spectrum function of size (Benoît & Rochet (2004); Andersen & Beyer (2006)).

— L_{cut} (T3.c) : The cut-off frequency of maximum structural size. It is a simple indicator of the maximum size of the species sustained in the community.
— $TL_{max,t}$ (T3.d) : The trophic level $TL_{V_{Pr},t}$ of individuals in the larger size class sustained in the community. It characterizes the trophic chain length.

Some of these indicators are represented schematically in figure 2 and all are detailed table 3.

1.3.2 Diversity

While the size distribution characterizes the structure, the trait distribution of populations (Fig. 1c) characterizes the diversity in the community. Every population spectrum $N_{V,t}^{V_m}$ in the range $[V_m^{min}, V_m^{max}]$ contributes to the community size-spectrum $\mathrm{N}_{V,t}$. This contribution can be described at every individuals structural size by the $\Phi_{V,t}^{V_m}$ function (Maury & Poggiale (2013)) :

$$N_{V,t}^{V_m} = \Phi_{V,t}^{V_m} \mathrm{N}_{V,t} \qquad \text{and} \qquad \int_{V_m^{min}}^{V_m^{max}} \Phi_{V,t}^{V_m} dV_m = 1 \tag{7}$$

We developed an indicator of diversity based on this function and a « map » of trait diversity characterizing the modeled communities (Fig. 2). The « map » represents the maximum length L_m at the 5^{th} ($L_m(\Phi_{V,t}^{5\%})$), 50^{th} ($L_m(\Phi_{V,t}^{50\%})$) and 95^{th} ($L_m(\Phi_{V,t}^{95\%})$) percentiles of the $\Phi_{V,t}^{V_m}$ distribution as a function of L.

We therefore use two indicators of the community diversity :
— $\overline{\overline{L}}_m$ (T3.e) : The geometric mean of species maximum lengths. It determines the kind of species contributing to the community, small or large.
— $\overline{\Delta L}_m$ (T3.f) : The mean community trait diversity is defined as the mean value of the maximum sizes spread $\overline{(L_m(\Phi_{V,t}^{95\%}) - L_m(\Phi_{V,t}^{5\%}))}$ over the diversity « map ». It describes the functional diversity of energy pathways. When it is small, the energy flows in the community is carried by few species. When it is large, the populations provide a wide range of alternative energy pathways.

These indicators are represented schematically in figure 2.

1.3.3 Metabolism

Our model links the metabolism of individuals to the community. At the individual level, the DEB theory explicitly provides attributes of metabolism :
— consumption $\dot{p}_X^{V_m} = \dot{p}_{X,LTL}^{V_m} + \dot{p}_{X,C}^{V_m}$ (T1.a), where $\dot{p}_{X,LTL}^{V_m}$ is the energy ingested from the low trophic level and $\dot{p}_{X,C}^{V_m}$ is the energy ingested from other fish in the community.
— production $\dot{p}_E^{V_m} + \dot{p}_G^{V_m}$ (T1.d,f) by transformation of energy into organic matter in reserves or structure.

Knowing the abundance distribution $N_{V,t}^{V_m}$ we compute the community level consumption on low trophic level's biomass, $\dot{P}_{LTL,t}$, and production $\dot{P}_{Prod,t}$:

$$\dot{P}_{LTL,t} = \int_{V_m} \int_{V} \dot{p}_{X,LTL}^{V_m} N_{V,t}^{V_m} dV dV_m \qquad \dot{P}_{Prod,t} = \int_{V_m} \int_{V} \left(\dot{p}_E^{V_m} + \dot{p}_G^{V_m} \right) N_{V,t}^{V_m} dV dV_m \tag{8}$$

We therefore use two indicators to characterize the metabolism at the community level :
— $R^{Prod} = \dot{P}_{Prod,t} / \dot{P}_{LTL,t}$ (T3.g) : The efficiency of the community to transform the resource preyed on low trophic level into fish biomass.
— $t_{res} = \xi_t^{tot} / \dot{P}_{LTL,t}$ (T3.h) : At steady state, the energy preyed on the lower trophic level balances dissipation and losses (Appendix D). This energy consumed characterizes the residence time, the mean time spent by energy in the community. It is an indication of the speed of the energy flow in the community.

Table 3 summarizes all the community indicators of structure, diversity and metabolism.

TABLE 3 – Summary of model's indicators for stucture, diversity and metabolism. These are constant values for every environmental forcing considered.

Eq.	Indicator	Equation
Structure		
T3.a	Total energy	$\xi_t^{tot} = \int\limits_{V_m} \int\limits_{V} \xi_{V,t}^{V_m} dV dV_m$
T3.b	Spectrum slope	S_C
T3.c	Cut-off frequency of structural size	$L_{cut} \propto V_{cut}^{1/3}$ the length class where $\mathrm{N}_{V_{cut},t} < 10\ \mathrm{N}_{V_{cut}-\Delta V,t}$
T3.d	Maximum trophic level	$TL_{max} = max(TL_{V_{Pr},t})$ with $TL_{V_{Pr},t} = 1 + \sum_{V_{pr}} D_{V_{Pr},V_{pr}} TL_{V_{Pr},t}$
Diversity		
T3.e	Mean population trait	$\overline{\overline{L}}_m = exp\left(\frac{\int\limits_{L_m} \int\limits_{L} ln(L_m) N_{L,t}^{L_m} dL dL_m}{\int\limits_{L_m} \int\limits_{L} N_{L,t}^{L_m} dL dL_m} \right)$ with $L_m = \frac{V_m^{1/3}}{\delta}$
T3.f	Mean population trait diversity	$\overline{\Delta L}_m = \frac{\int\limits_{L_m} \int\limits_{L} (L_m(\Phi_{t,L}^{95\%}) - L_m(\Phi_{t,L}^{5\%})) dL dL_m}{\int\limits_{L_m} \int\limits_{L} dL dL_m}$ with $L_m = \frac{V_m^{1/3}}{\delta}$
Metabolism		
T3.g	Production efficiency	$R^{Prod} = \frac{\dot{P}_{Prod,t}}{\dot{P}_{LTL,t}} = \frac{\int\limits_{V_m} \int\limits_{V} \left(\dot{p}_E^{V_m} + \dot{p}_G^{V_m} \right) N_{V,t}^{V_m} dV dV_m}{\int\limits_{V_m} \int\limits_{V} \dot{p}_{X,LTL}^{V_m} N_{V,t}^{V_m} dV dV_m}$
T3.h	Residence time	$t_{res} = \frac{\xi_t^{tot}}{\dot{P}_{LTL,t}} = \frac{\int\limits_{V_m} \int\limits_{V} \xi_{V,t}^{V_m} dV dV_m}{\int\limits_{V_m} \int\limits_{V} \dot{p}_{X,LTL}^{V_m} N_{V,t}^{V_m} dV dV_m}$

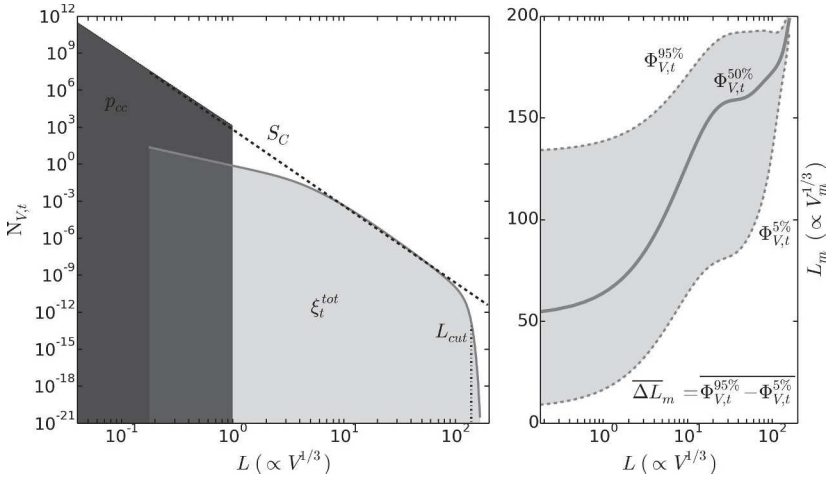


FIGURE 2 – Schematic representation of indicators : left, low trophic level abundance size-spectrum (black), community abundance size-spectrum (grey) and associated indicators, slope S_C, cut-off frequency L_{cut} and total energy ξ_t^{tot} ; right, diversity map (grey) and mean trait diversity $\overline{\Delta L}_m$.

1.4 Simulations

1.4.1 Numerical setting

The indicators are compared on the solutions of the model forced with constant foods in low trophic levels and temperatures. The system of governing equations table 2 is solved for a set of trait-based populations using an explicit donor-cell finite volume algorithm on a discretization of k_V structural volumes to approximate the advection term (T2.a). The discretization is non uniform, with increasing resolution toward the smallest size classes for computational performances. It ranges from $L^{min} = 0.1\ cm$ for eggs to $L^{max} = 2\ m$. The traits L_m ($\propto V_m^{1/3}$) are chosen in the the same size range with an irregular discretization of k_{V_m} populations. The numerical simulations run with a daily time step and start from an arbitrary residual initial state. They are run until the system reaches a stable steady solution.

Representative ranges of variability for food p_{cc} and temperature T are inferred from a realistic climatological simulation of the coupled NEMO-PISCES physics-biogeochemistry model (Aumont *et al.* (2015)). For that purpose, phytoplankton and zooplankton biomass concentration on a 1° grid are converted into energy content distributions. Pulled together they are associated to a size range $[L_{ltl}^{min}, L_{ltl}^{max}]$ and averaged over longitudes to provide mean latitudinal distributions of low trophic level's biomass. From these we keep the annual mean and monthly variability represented by the 5^{th} and 95^{th} percentiles (Fig. 3). Similarly realistic temperature values have been derived from the spatial and time distributions of sea surface temperatures in the NEMO-PISCES model, averaged in longitude, keeping the mean annual value and variability between the 5^{th} and 95^{th} percentiles of the latitudinal distributions (Fig. 3).

1.4.2 Parameters

The mechanistic bases of the model allow a reduced number of parameters but nevertheless requires a careful choice of these parameters (Tab. 4).

At the individual level, we used DEB parameters adapted from the generic ones (Kooijman (2010)) to better account for fish communities (Appendix D, Kooijman & Lika (2014)). The temperature correction of these DEB parameters is based on an Arrhenius temperature of $8000°K$. This correction is consistent with a mean value $Q_{10} = 2.36$ of the van't Hoff coefficient within species for teleost fishes compiled in Clarke & Johnston (1999). Since our analysis focuses on large scale environmental effects, especially across latitudes, we modified this Arrhenius temperature to better represent the impact of temperature. According to the evolutionary trade-off hypothesis on large scale the resting metabolic rate of species at normal living temperature is corrected according to $T_A = 5370°K$ ($Q_{10} = 1.83$) (Clarke & Fraser (2004)).

At the population level the size selective predation is the main constrain on energy transfer between size class. It is parametrized so that the modeled distribution of prey size L_{pr} ($\propto V_{pr}^{1/3}$) in the stomach of predators of size L_{Pr} ($\propto V_{Pr}^{1/3}$) matches empirical observations taken from Scharf *et al.* (2000). For that purpose, the parameters α_1, α_2, γ_1 and γ_2 of the size selectivity function (T2.f) are tuned so that the mean, 5^{th} and 95^{th} percentiles of the modeled prey distributions in predators stomach match the mean, 5^{th} and 95^{th} of the prey distribution derived from data (Fig. 4).

Last free parameters of the model, the disease mortality rate D, the ageing acceleration $\ddot{h}_a$, the constant of the functional response C' and s_{cr} the biomass density threshold above which the probability of schooling is larger than 0.5, are tuned to obtain realistic levels of biomass in modeled communities. They are determined over the wider range of realistic low trophic level's biomasses $p_{cc} \in [50\ J/m^3, 8000\ J/m^3]$ at an associated environmental temperature $T = 5°C$ (Fig. 3). The criteria for their determination are that, with a single set $(D, \ddot{h}_a, C', s_{cr})$: at the lowest level $50\ J/m^3$, the community spectrum characterizes a poor ecosystem, with few traits sustained ; at the highest level $8000\ J/m^3$, the community spectrum is completely developed, with all traits sustained ; at intermediate level $1200\ J/m^3$, the community spectrum is partially developed. In addition, according to the spectrum theory the biomass distribution in logarithmically equal particles size pools from « plankton to whales » is constant (Sheldon *et al.* (1972)). It implies the alignment of fish community and low trophic level size-spectra. This last criteria is enforced at intermediate level $1200\ J/m^3$ with the same set $(D, \ddot{h}_a, C', s_{cr})$. Figure 5 illustrates the obtained spectra.

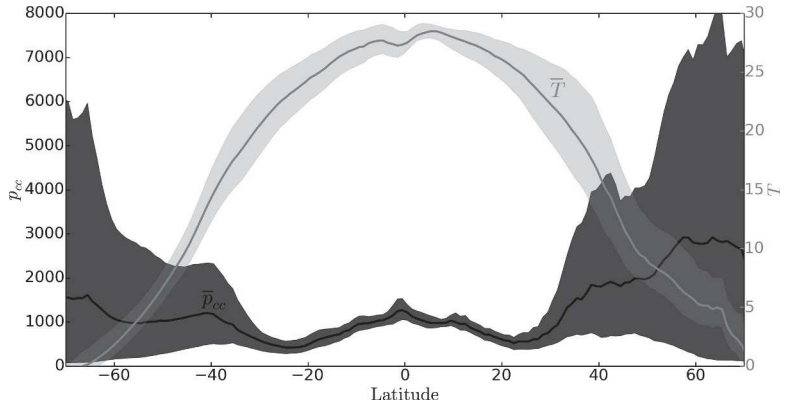


FIGURE 3 – Latitudinal distribution of the environmental conditions used to force the model : annual mean and monthly variability of total low trophic level's biomass p_{cc} (black) ; annual mean and monthly variability of sea surface temperature T (grey).

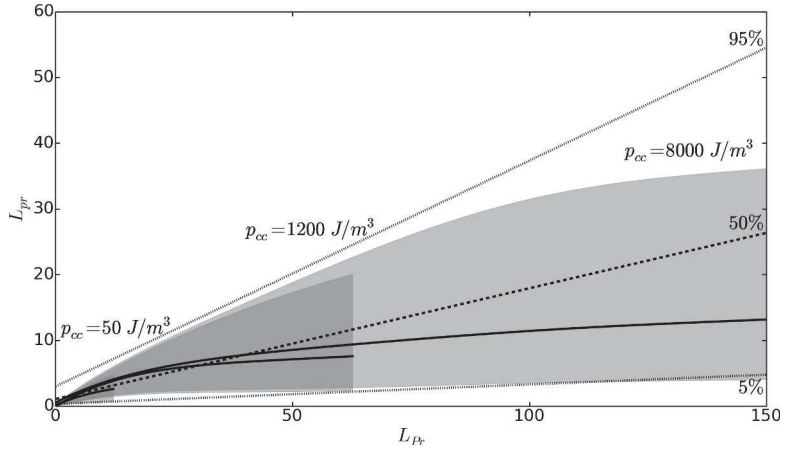


FIGURE 4 – Prey size distribution in the stomach of predators : as derived from empirical data (·· percentiles and –– mean) ; as modeled at various low trophic level's biomasses $p_{cc} = 50,\ 1200,\ 8000\ J/m^3$ at $T = 5°C$ (grey domains with ▬ mean).

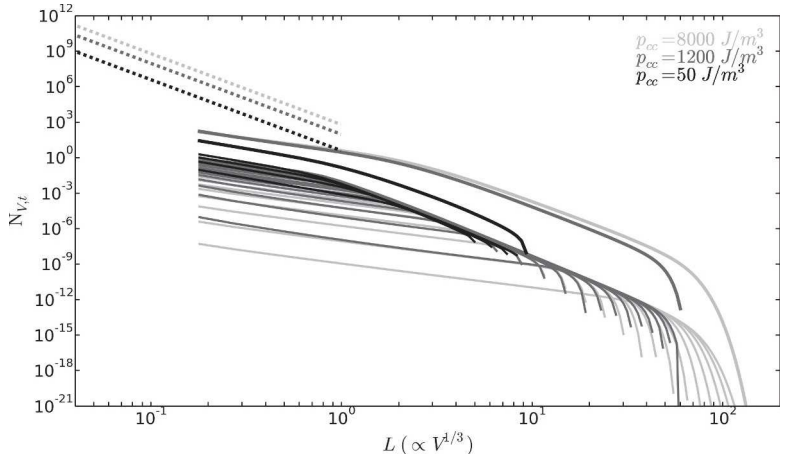


FIGURE 5 – Low trophic level (dashed), community (thick line) and populations (thin lines) size-spectra function of individual sizes L ($\propto V^{1/3}$) at different $p_{cc} = 50,\ 1200,\ 8000\ J/m^3$ and at $T = 5°C$ for a single set $(D, \ddot{h}_a, C', s_{cr})$.

TABLE 4 – Summary of model's parameters used for numerical simulation, values and references.

Variable	Designation	Unit	Value	Ref
Individual's DEB				
E / E^*	Energy of the reserve/ at equilibrium	J	–	Maury & Poggiale (2013)
V / L	Structural volume/length	cm^3/cm	$\begin{cases} V = (\delta L)^3 \\ \delta = 0.2466 \end{cases}$	Maury & Poggiale (2013)
V_m / L_m	Maximum structural volume/length	cm^3/cm	$V_m = (\delta L_m)^3$	Kooijman (2010)
V_p	Puberty structural volume	cm^3	$\begin{cases} V_p = \alpha_p V_m \\ \alpha_p = 0.125 \end{cases}$	Kooijman & Lika (2014)
$\{\dot{p}_{A_m}^{V_m}\}$	Maximum surface-specific assimilation rate	$J\ cm^{-2} d^{-1}$	$\begin{cases} \alpha_{\{\dot{p}_{Am}\}} V_m^{1/3} \\ \alpha_{\{\dot{p}_{Am}\}} = 31.25 \end{cases}$	Section 3.2.2
$[E_m^{V_m}]$	Maximum reserve density	$J\ cm^{-3}$	$\begin{cases} \alpha_{[E_m]} V_m^{1/3} \\ \alpha_{[E_m]} = 312.5 \end{cases}$	Section 3.2.2
ν	Energy conductance $\{\dot{p}_{A_m}^{V_m}\}/[E_m^{V_m}]$	$cm\ d^{-1}$	0.1	Section 3.2.2
$[\dot{p}_M]$	Maintenance rate	$J\ m^{-3} d^{-1}$	25.	Kooijman & Lika (2014)
$[E_G]$	Volume specific cost of growth	$J\ cm^{-3}$	5691.	Section 3.2.2
κ_X	Assimilation efficiency	–	0.8	Maury & Poggiale (2013)
κ	Energy fraction allocated to growth and maintenance	–	0.8	Maury & Poggiale (2013)
κ_R	Energy fraction of gonads turned into eggs	–	0.95	Kooijman (2010)
$\ddot{h}_a$	Ageing acceleration	d^{-2}	$45.\ 10^{-8}$	Section 1.4.2
Community's biology				
C'	Specific searching rate of the functional response	$J\ d^{-1}$	3.5	Section 1.4.2
D	Maximum mortality rate due to disease	d^{-1}	0.4	Section 1.4.2
M_{egg}	Fraction of spawned eggs not fertilized	–	0.8	–
φ	Sex-ratio (Mean proportion of female)	–	0.5	–
d	Density of biomass	$g\ cm^{-3}$	1.	–
ψ	Energy content of biomass	$J\ g^{-1}$	4552.	Section 3.2.2
Predation				
(ρ_1, ρ_2)	Mean mini/maxi ratio predator over prey lengths	–	(2.5, 10.)	Section 1.4.2
(α_1, α_2)	Variability mini/maxi ratio predator over prey lengths	–	(5., 0.08)	Section 1.4.2
Schooling				
β	Shape of the schooling probability function	–	2.	Section 1.4.2
s_{cr}	Schooling probability threshold	m^{-6}	0.005	Section 1.4.2
Environment				
p_{cc}	Primary production carrying capacity	$J\ m^{-3}$	–	Section 1.4.1
T	Temperature	$°K/°C$	$°K =° C + 273.15$	Section 1.4.1
T_A	Mean Arrhenius temperature	$°K$	5370.	Section 1.4.2
T_{ref}	Reference temperature of biological parameters	$°K$	293.15	Section 1.4.2
Numerical parameters				
$[L^{min}, L^{max}]$	Consumers size range ($L_{min} = L_b$)	cm	$[0.1, 200.]$	Section 1.4.1
$[L_{ltl}^{min}, L_{ltl}^{max}]$	Primary producers size range	cm	$[0.001, 1.]$	Section 1.4.1
k_{V_m}	Number of trait discretizations	–	98	Section 1.4.1
k_V	Number of volume discretizations	–	100	Section 1.4.1
Δt	Time step	d	1	Section 1.4.1

2 Results

2.1 Separate low trophic level's biomass and temperature impact

2.1.1 A multi-domain response

The effects of low trophic level's biomasses are observed over the range $p_{cc} \in [50\ J/m^3, 8000\ J/m^3]$ keeping temperature constant $T = 5°C$. The effects of temperature are observed over the range $T \in [0°C, 30°C]$ keeping the low trophic level's biomass constant $p_{cc} = 3000\ J/m^3$ (based on Fig. 3). Indicators reveal that the emerging community level responses are consistent for both set of experiments (Fig. 6), with four distinct domains of community structure and function.

Collapse

A collapsed domain characterized by a minimal total community biomass ξ_t^{tot} at low p_{cc}, or high T. In this regime communities are constituted of small individuals (L_{cut}) exclusively feeding on the low trophic level spectra ($TL_{max} \simeq 2$). These communities are constituted of small species of primary consumers populations.

Within the collapsed domain, increasing p_{cc} or decreasing T leads to a slow increase of the maximum size of individuals (L_{cut} increases) and the development of consumer populations ($\overline{\overline{L}}_m$ increases) without interactions within and between them since individuals exclusively feed on resource ($TL_{max} \simeq 2$). There is no intra-community predation and no resource competition ; the low trophic level's biomass is *ad libitum*. While larger populations develop small individuals become dominant since every populations has individuals in small size class, but only larger populations bring individuals in larger size class (S_C decreases). The trait diversity ($\overline{\Delta L}_m$) is minimal because of a reduced range of species supported.

Note that the collapse domain is not visible over the range of temperatures explored figure 6. It appears at very low constant biomass p_{cc} (see distributions Fig. 7 at $p_{cc} = 200\ J/m^3$).

Regular

Within the regular domain, the variation of fish production (R^{Prod}) is attenuated compared to the collapse domain. Communities include primary consumers but with larger individuals (L_{cut}) and species ($\overline{\overline{L}}_m$) preying up to half of their diet on fish, their trophic levels increase ($2 < TL_{max} < 2.5$).

With larger individuals in the community, intra-community predation starts exerting a top-down pressure on small size classes. The relative abundance of small and large individuals remains seemingly constant (small S_C variation) when environmental conditions vary. This is a consequence of the intra-community predation which harvest preferentially the most abundant small species that are forming schools, to the benefit of larger ones. In the regular domain with intra-community predation, the total fish biomass ξ_t^{tot} is less sensitive to variations than in the collapsed regime.

Transition

Increasing food or decreasing temperature within the transition domain leads to greater variations of the total community biomass ξ_t^{tot} than within the regular domain. Very large individuals can be supported (L_{cut}). Secondary consumers develop for which more than half of the diet comes from fish consumers ($2.5 < TL_{max}$).

In this regime, individuals from large species feed on resource at low trophic level when they are small and mainly on the fish community when they grow bigger. With this ontogenetic diet shift and apparition of secondary consumer the fish community is now significantly providing food for its own development, enhancing the predation pressure on smaller size class. The schooling ensures the coexistence between large and small species and avoids the unrealistic complete depletion of small populations. With low trophic level's biomass or temperature variations the relative abundance of large against small species fixed by schooling changes (S_C increases, decreases). The trait diversity is enhanced ($\overline{\Delta L}_m$), the food web includes more functional species from small to large. With secondary consumer in the community a large portion of the energy preyed on resource is used for the development of more than one individual.

Compared to the previous domains it enhances the community development (L_{cut} increases sharply) and efficiency to transform resource into biomass (R^{Prod} is enhanced).

Saturation

Within the saturation domain, communities reach their maximum biomass level ξ_t^{tot}. Fish production (R^{Prod}) becomes independent of food or temperature variations. A tri-trophic system, primary producers, primary consumers and secondary consumers is established ($TL_{max} \simeq 3$).

The community size-spectrum is fully developed and the functional response is saturated for all populations. An optimal balance between bottom-up energy supply, top-down predation pressure, energy dissipation and losses maintains the full community. The length of the largest individuals (L_{cut}) as well as the mean species size ($\overline{\overline{L}}_m$) reach their maximum. Coexistence allows the presence of a large range of species, the trait diversity ($\overline{\Delta L}_m$) is maximum. Some indicators are not completely fixed however and reveal a slight structural reorganization of the community (S_C). The scaled functional response converges toward unity at food densities depending on the species considered. At a given food density or temperature, smaller species are closer to satiation ($f_V^{Vm} \propto V_m^{-1/3}$, T2.k). When resource increases or temperature decreases, the largest species are the last to reach saturation. They slowly increase their dominance over the community and slowly modify its structure.

Note that the saturation domain is not fully visible over the range of temperatures explored figure 6. It appears more clearly at very high food levels p_{cc} (see distributions Fig. 7 at $p_{cc} = 8000\ J/m^3$).

2.1.2 Impact of low trophic level's biomass

The community develops non linearly when the biomass of low trophic levels increases (Fig. 6a). In the framework of the DEB theory, the individual costs of maintenance are constant at individual level at a given structural volume V (T1.e,g, reproduction overhead). An increase in food availability (p_{cc}) thus releases more energy for growth. It allows populations to develop larger individuals (L_{cut} increases) and communities to sustain larger species ($\overline{\overline{L}}_m$ increases). The associated trait diversity increases ($\overline{\Delta L}_m$).

The biomass increase is faster than low trophic level's biomass increase in the collapsed domain, tends to become proportional ($\propto p_{cc}^{+1}$) in the regular domain and is faster again in the transition domain before reaching a plateau ($\propto p_{cc}^{0}$) at saturation.

The residence time of energy preyed upon low trophic levels also follows this multi-domain dependence. At a given structural volume and scaled functional response, individuals of larger species grow faster. With increasing low trophic level's biomass, larger species are sustained, the flow of energy is enhanced, and the residence time t_{res} globally decreases.

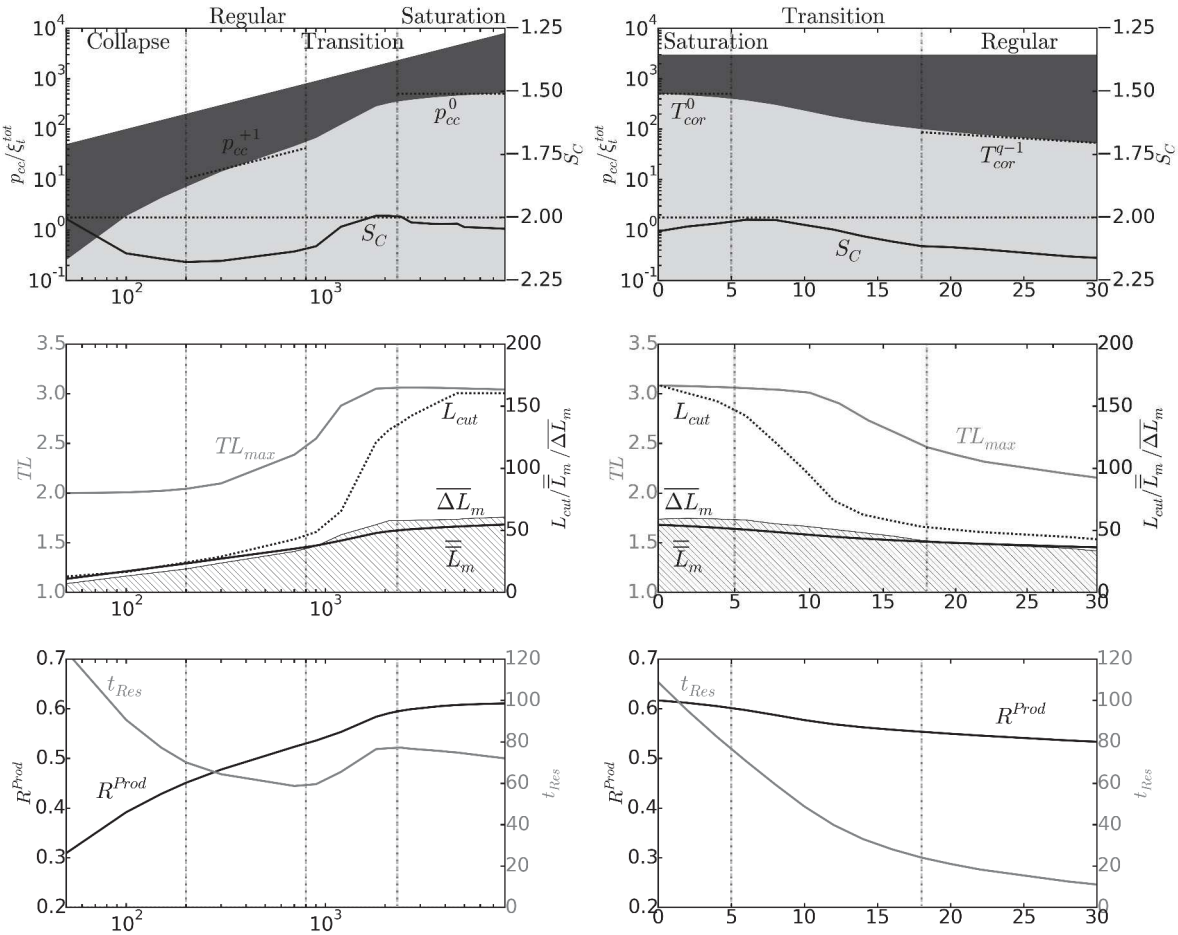
In the meantime with the increase of the community size span and the elongation of the trophic chain a unit of energy preyed on the resource supports more and more trophic levels. It induces an implicit increase of the residence time which mitigates the global t_{res} decrease and explains its different slopes in each domain. Note that in the transition domain this increase actually dominates the global enhancement of the energy flow, t_{res} jumps. These distinct characteristics of the energy flow have consequences on the sensitivity of communities to perturbations.

2.1.3 Impact of temperature

The community shrinks non linearly when temperature increases (Fig. 6b). It is the combined effect of metabolism and attack rate (Appendix B) that scale differently with temperature. Warming mostly enhances the speed of the energy flux through the community (t_{res} constantly decreases). But assimilation ($\propto T_{cor}^q$ or T_{cor}) and metabolism ($\propto T_{cor}$) have a different sensitivity to warming, the first increasing less quickly than the second ($q < 1$). Under warming condition, because of this asymmetry, the energy assimilated by larger species becomes insufficient to pay their maintenance costs. The largest species collapse progressively, the maximum individuals size (L_{cut}), mean population size ($\overline{\overline{L}}_m$) and trait diversity ($\overline{\Delta L}_m$) decrease.

At equilibrium, the community can be looked at as an open system with the food ingested from the resource strictly balanced by the community level losses and dissipation (Appendix C). When all the

individuals in a community can access enough food to be at satiation, feeding becomes proportional to ingestion time which depends on T_{cor} (Appendix B). The metabolism also scales with T_{cor}. The temperature induced variations of ingestion on low trophic levels are balanced by the same variations of losses and dissipation. The community is globally unaffected by temperature. In the saturation domain at colder temperatures the fish total biomass is invariant ($\propto T_{cor}^{0}$). When populations start to become food limited, this balance breaks. Metabolism still scales with T_{cor} but ingestion scales between T_{cor}^{q} and T_{cor} (Appendix B). The energy entering the community ($\propto T_{cor}^{q}$, T_{cor}) is smaller or equal to the dissipation and loss ($\propto T_{cor}$). The community loses energy and shrinks with warming in the transition and regular domains. Ultimately, all individuals are food limited. The ingestion is limited by the attack rate, which scales with T_{cor}^{q}, and the metabolism scales with T_{cor} so that the fish total biomass decreases proportionally to $T_{cor}^{(q-1)}$ at warm temperatures.



(a) Lower trophic level's biomass $p_{cc} \in [50\ J/m^3, 8000\ J/m^3]$.

(b) Temperature $T \in [0°C, 30°C]$.

FIGURE 6 – Multi-domain responses of the community level indicators, from top to bottom : total energy of low trophic level p_{cc} (black) and community ξ_t^{tot} (grey) spectra, community slope S_C (black line) ; middle, maximum trophic level TL_{max} (grey line), cut-off length L_{cut} (dashed line), mean species lengths $\overline{\overline{L}}_m$ (black line) and mean trait diversity $\overline{\Delta L}_m$ (hatched) ; bottom, biomass production efficiency R^{Prod} (black line), residence time (grey line).

2.2 Combined low trophic level's biomass and temperature impact

2.2.1 Phase diagram

In this section we investigate the separate effects of low trophic level's biomass and temperature over the ranges $p_{cc} \in [50\ J/m^3, 8000\ J/m^3]$ and $T \in [0°C, 30°C]$ at respectively distinct constant temperatures T and distinct constant biomasses p_{cc}. The multi-domain response is maintained but is shifted and attenuated (Fig. 7).

At various constant temperatures, the domains succession when at various resource levels is modified (Fig. 7a) : in cold waters, the domains transitions occur earlier in these more productive communities ; in warmer waters, the domains cover wider food ranges in these less productive communities. It implies that cold waters communities can sustain larger individuals at lower food levels than they would in warm waters. Structure and diversity transitions between domains are sharper in cold than in warm waters. At different food levels the domains succession with temperature has similar characteristics (Fig. 7b). Oligotrophic ecosystems display an earlier community shrinking and have sharper domain's transitions.

Figure 7c summarizes the combined influences of food and temperature with a phase diagram. It represents the different domain transitions and the different width of these domains as a function of food biomass (p_{cc}) and temperature (T). Different areas are dominated by primary or secondary consumers and have different properties. On this figure the mean environmental conditions $[\overline{p}_{cc}, \overline{T}]$ along the latitudinal gradient figure 3 are superimposed. Different latitudes of the northern and southern hemisphere fall into different domains and thus exhibit different sensitivities to perturbations.

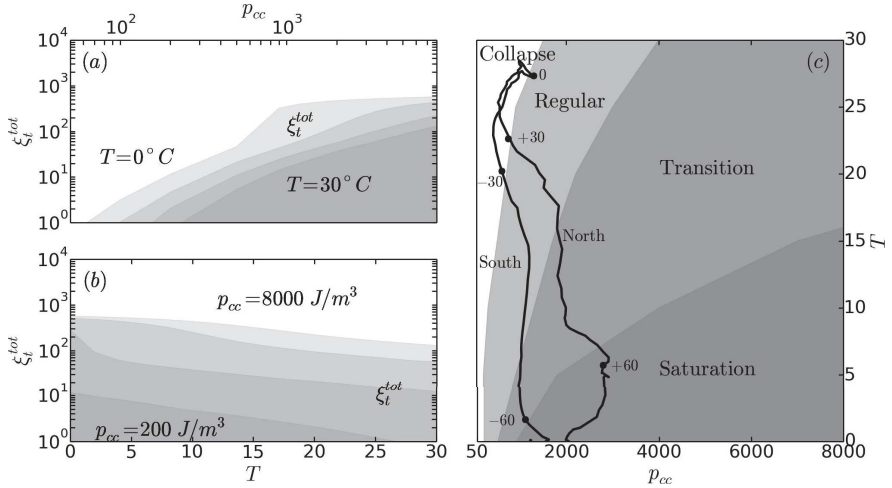


FIGURE 7 – Combined impact of low trophic level's biomass and temperature : (a) total energy in the community over the range $p_{cc} \in [50\ J/m^3, 8000\ J/m^3]$ at various constant temperature levels $T \in [0°, 30°]$; (b) total energy in the community over the range $T \in [0°, 30°]$ at various constant low trophic level's biomasses $p_{cc} \in [200\ J/m^3, 8000\ J/m^3]$; (c) phase diagram of the four domains at distinct environmental conditions with mean environmental conditions along the realistic latitudinal gradient in figure 3 (black line).

2.2.2 Latitudinal gradient

To asses the realism of our idealized study, the combined effect of low trophic level's biomass and temperature is simulated along a mean latitudinal gradient (see Fig. 3). Figure 8 illustrates the obtained indicators.

From low to mid-latitudes, the total biomass ξ_t^{tot} follows the resource p_{cc}. Communities are dominated by small and medium species of primary consumers ($TL_{max} \approx 2$). Moving towards higher latitudes, colder temperatures reduce maintenance costs and allow the development of larger individuals (L_{cut} increases) as well as larger species ($\overline{\overline{L}}_m$ increases). It enhances the fish biomass supported and indicators change

like in the transition domain defined previously. Secondary consumers develop, TL_{max} and S_C increases. Finally abundant food-saturated populations become dominant at high latitude.

From the equator to the poles, modeled communities transform from small (small $\overline{\overline{L}}_m$), fast living (small t_{res}) species to large (large $\overline{\overline{L}}_m$) slow living (large t_{res}) species. When larger populations are sustained, more species coexist because of schooling, the trait diversity increases up to a plateau at higher latitudes ($\overline{\Delta L}_m$).

The mean species length values respect a realistic range illustrated by measurement detailed in Fisher *et al.* (2010).

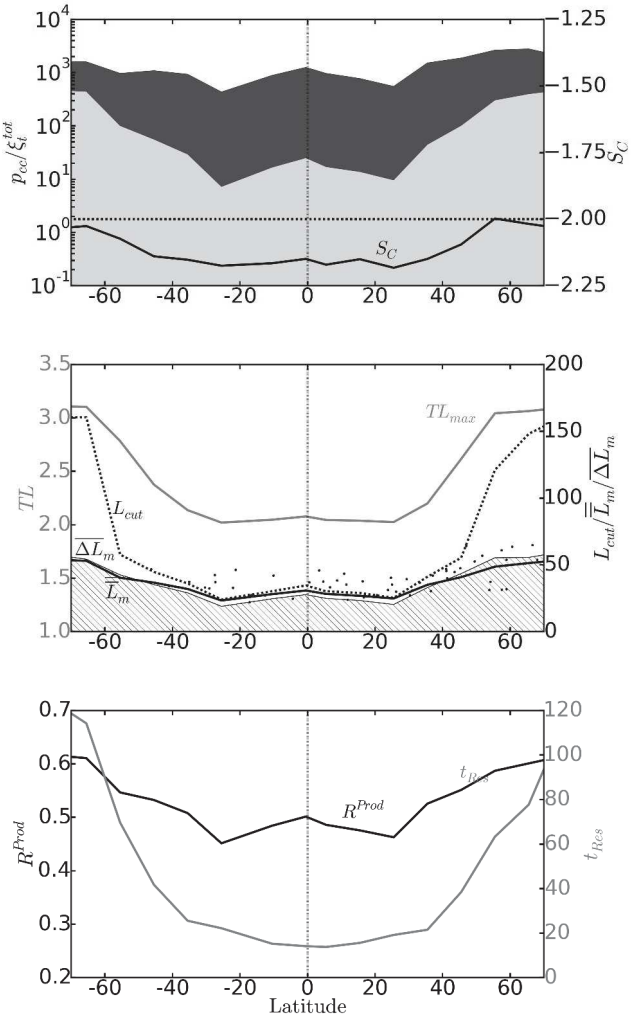


FIGURE 8 – Variations of the indicators of the community size-spectrum with low trophic level's biomass and temperature found in average along a latitudinal axis. From top to bottom : total energy of the lower trophic level p_{cc} (black) and community ξ_t^{tot} (grey) spectra, community slope S_C (black line) ; middle, maximum trophic level TL_{max} (grey line), cut-off length L_{cut} (dashed line), mean species lengths $\overline{\overline{L}}_m$ (black line) compared to observations (black dots) and mean trait diversity $\overline{\Delta L}_m$ (hatched) ; bottom, biomass production efficiency R^{Prod} (black line), residence time (grey line).

3 Discussion

3.1 Latitudinal gradients

3.1.1 The population size gradient

Integrating individual bioenergetics and trophic interactions, the model predicts that the average species size in fish communities $\overline{\overline{L}}_m$ increase with latitude (Fig. 8). This distribution is known as the Bergmann rule (Blackburn *et al.* (1999)), one of the most widespread biogeographical pattern. Initially related to endotherms, the pattern has also been documented for ectotherms (Lindsey (1966)).

There is still no clear explanation to this universal pattern and different physiological or ecological processes have been proposed to explain it (Blackburn *et al.* (1999)). High latitude ecosystems are characterized by high primary production levels (Fig. 3). Here high latitudes can therefore support bigger consumer populations (cf Fig. 6a). Towards low latitude ecosystems are characterized by warmer temperatures. From the rich and cold pole to the poor and warm equator ecosystems the warming decreases the attack rate of predators compared to their ingestion. Low latitudes favor the survival of smaller populations (cf Fig. 6b). With the present bio-energetic formulation the latitudinal distribution emerges from a balance between resource available and the capacity of fish to capture sufficient food.

The model predicts mean species lengths $\overline{\overline{L}}_m$ in the communities in the same range of measurements of geometric mean maximum lengths compiled by Fisher *et al.* (2010). However other processes should also play a role on this distribution. We disregard the role of seasonality in the model and while at low latitude seasonal variations are small, at high latitude ecosystems are characterized by strong variations of their drivers (Fig. 3). Kooijman (2010) explains that large amplitude variations of primary producers supply in high latitudes ecosystems split the year into good and bad seasons. Bad seasons of poor food supply reduce populations, starting with the small species that have less reserves. Good seasons boost the development of the surviving individuals enhancing the flux of energy toward larger populations. Seasonality affect mid- to high latitude ecosystem properties.

From bio-energetic considerations the model can account for Bergmann's rule, this shape remaining consistent with variations of model parameters. Other processes may play a role in structuring the mean species size gradient, seasonality, but also spatial interactions, evolution.

3.1.2 The trait diversity gradient

The mean community trait diversity $\overline{\Delta L}_m$ increases with latitude (Fig. 8). It represents the increase with latitude of the diversity of species sizes in communities. This is in agreement with the observation of an increased variability in species length as richness declines, when latitudes increases (Fisher *et al.* (2010)).

The model cannot calculate species richness. But considering functional trait-diversity allows accounting for the diversity of energy pathways in the community. Rich and cold ecosystems allow the maintenance of large species coexisting with small ones. They are characterized by a high trait diversity. In these ecosystems the energy from producers can follow many different routes when it is consumed and moves up the food-web. At low latitudes, the shrinking of the fish community reduces the range of possibilities. With less trait diversity, these ecosystems offer less potential energy pathways. The diversity of energy pathways may impact the sensitivity of fish communities to environmental perturbations.

3.1.3 The maximum trophic level gradient

The maximum trophic level reached by communities at different latitudes is related to the maximum size of the individuals. Like the cut-off frequency of maximal structural size L_{cut}, the maximum trophic level TL_{max} increases with latitude (Fig. 8).

The maximum trophic level increases sharply with latitude. Poor low latitude ecosystems of primary consumer ($TL_{max} \simeq 2$), which are mostly driven by bottom-up forcing, are especially sensitive to resource variations (cf Fig. 6a). Richer mid- to high latitude ecosystems support secondary consumers ($TL_{max} > 2$) exerting a top-down predation on primary consumers. High latitude saturated ecosystems ($TL_{max} \simeq 3$) are essentially controlled top-down. The changes of the maximum trophic level in the fish community

with lattitude that we predict are linked to the multi-stage response of communities to low trophic level's biomass and temperature (Fig. 6). This suggests different sensitivity of communities to the environment at different latitudes. The phase diagram figure 7c summarizes this effect. For example, when low trophic levels biomass increases (shift to the right of environmental conditions), from the equator to mid-latitudes ($+/-60°$), the fish community shifts through collapse, regular and transition domains, indicating a possible amplification of fish production compared to less sensitive saturated higher latitude ecosystems (Lefort *et al.* (2015)). With increasing temperature (upward shift of environmental conditions) from the pole to the equator, the fish community is shrinking (Daufresne *et al.* (2009)). This is accompanied by a stronger drop of fish biomass at high latitudes ($+/-60°$), when the fish community shifts from saturation to transition, compared to low latitudes ($+/-30°$), when it shifts from regular to the collapse domain.

3.2 Multi-stage response of fish production

3.2.1 Dependence on low trophic level's biomass

While fish biomass is often considered to be proportionally related to primary production (Ware & Thomson (2005); Frank *et al.* (2006); Blanchard *et al.* (2012)), our results suggest a more complex multi-domain dependence (Fig 6a). They corroborate other observations supporting the idea that primary production is an imperfect predictor of fish production (Friedland *et al.* (2012)).

We identify four domains : collapse, regular, transition and saturation. In each of these small-sized species survive and dominate larger size species because of their higher reproductive output. With increasing low trophic level's biomass, larger and larger species can be sustained and trigger changes of domains, each characterized by specific types of interactions between primary producers, primary consumers and secondary consumers. Allowed by the explicit trait diversity representation in our model, our results underline the influence of trophic interactions on the link between primary production and fish biomass.

It should be noted that the tri-trophic structure appearing is directly linked to the definition of the size selectivity for predation in the model (Fig 4), especially the mean predator-prey mass ratio. A reduction of this ratio would increase the length of the trophic chain. We also tested (not shown) the relationship between low trophic levels biomass and fish biomass in a community reaching a trophic level of 4.5 and we obtained the same succession of domains.

The multi-domain response of fish community strongly depends on the coexistence of small and large species. In tri-trophic systems the onset of intra-community predation has been shown to limit the coexistence of primary consumers with secondary ones (Mylius *et al.* (2001)). A property which questions the commonness of omnivory and coexistence in marine ecosystems. Here, the density dependent schooling protecting small populations from depletion by predation permits this coexistence. Other models use alternative stabilizing factors such as additional resources, differential resource edibility or spatial and temporal refugees (Amarasekare (2007); Janssen *et al.* (2007)).Hartvig & Andersen (2013) justifies the existence of such trophic ladder state by a relationship between the ratio of sizes at maturation (or here maximum size) and the predator-prey mass ratio of interacting species.

Finally, the enhancement of fish biomass with increasing food in low tropic levels in the transition domain is limited and reaches saturation. It may be a limit of the model definition on a finite range of individuals $L < L^{max}$ and species $L_m < L_m^{max}$ lengths. Also note that Jennings & Brander (2010) refer to a weakness of the size-spectrum representation which breaks down in the larger size class because of the non linear relationship between trophic levels and body size for increasing species size. For example filter feeding sharks and whales feed down the food chain. The formulation of the model with size selective predation may not completely hold at high levels of low trophic level's biomass.

3.2.2 Dependence on temperature

The enhancement of the energy flux and respiration with warming increases the energy demand on resource and depending on the resource availability, shifts in community properties can occur (Petchey *et al.* (2010); O'Connor *et al.* (2009); Brose *et al.* (2012)). Here, we show that temperature changes lead

to a multi-domain response of communities similar to their response to primary production changes. Warming at constant low trophic level biomass induces an emergent shrinking of the community (Fig 6b).

Both theoretical and empirical studies have shown that warming favors small species and lower trophic levels (Petchey *et al.* (2008, 2010)) over large bodied species in communities (Daufresne *et al.* (2009); Brose *et al.* (2012)). Here, this trend is reproduced and attributed to a difference of scaling with temperature of the energy assimilation that is scaling between T_{cor}^{q} and T_{cor} and energy dissipation that is scaling with T_{cor}. The generality of such scaling difference is discussed and empirically demonstrated in Rall *et al.* (2012). They suggest a universal dependence to temperature of attack rate and handling time, both defining the temperature-dependence of assimilation through the functional response (see Appendix B) and metabolism. Their empirical study corroborates our theoretical predictions that feeding increases at a lower rate than metabolism when temperature increases. However, they underline different scaling relationships between attack rate and handling time, the latter being less sensitive. In a nutshell, they suggest that handling time ($\propto T_{cor}^{-}p$) is less dependent to warming than attack rate ($\propto T_{cor}^{q}$) which is itself less dependent than metabolism ($\propto T_{cor}$) : $-p < q < 1$. Englund *et al.* (2011) document a higher temperature-dependence of handling time than attack rate for fish : $q < -p$. In our model, to maintain theoretical consistency with the DEB theory at the individual level, handling time is assumed to scale like the metabolism : $q < -p = 1$. As explained in appendix B, ingestion scales as T_{cor}^{q} at low food density and as T_{cor}^{p} at high food density. Qualitatively, the behaviour of the model would be modified as follows if we could modify the relationship between $-p$ and q :

— $q = -p = 1$: no dependence of the model to temperature, ingestion changes balance dissipation changes in any case.

— $-p < q = 1$: with warming the ingestion increases less quickly than dissipation at high food density and at the same rate at low food density. The community shrinks and tends toward poor insensitive ecosystems.

— $-p < q < 1$: with warming the ingestion increases less quickly than dissipation at high and low food densities. The community shrinks continuously.

Changes in the community structure due to warming are expected to impact the community characteristics. For example Petchey *et al.* (2010) shows that the relative dependence of handling time and attack rate to warming can affect the connectance of food webs. The different scaling of processes with warming such as the use of the Arrhenius equation for the temperature dependence of consumption remains an ongoing question. In this perspective, Englund *et al.* (2011) even questions the validity of the Arrhenius relationship. A better empirical verification remains necessary to properly asses our predictions regarding the impact of temperature on fish communities. This would go beyond the scope of the present work however.

In the model, the impact of temperature on fish production is weaker than the impact of low trophic level's biomass (Fig. 7b). But in real ecosystems, the sensitivity to temperature variations would be intensified by the impact of temperature on low trophic levels. The dependence of marine ecosystems to temperature is therefore complex and we can expect fish community response to temperature and low trophic level's biomass variations to vary strongly with latitude (Brander (2007); Sarmiento *et al.* (2004)).

Conclusion

The present study investigates the response of fish communities to low trophic level's biomass and temperature changes using a mechanistic DEB- and trait- based size-spectrum model (Maury & Poggiale (2013)). Parameterized for a generic fish community, the model is studied in a realistic range of environmental conditions extracted from the outputs of a global physics and biochemistry model along a mean latitudinal gradient. The model provides an explanation to the well-known Bergmann rule, i.e. the fact that larger species appear when latitude increases (Blackburn *et al.* (1999); Fisher *et al.* (2010)). Our results support the idea that bio-energetic and trophic processus strongly determine the structural and functional properties of communities. Moreover the model allows to disentangle the impact of primary production from the impact of temperature on marine ecosystem's structure and function. We show that trophic interactions and the different metabolism of small and large species lead to a multi-domain response of communities to the environment.

We use a model that includes both individual's metabolism and predator-prey interactions to study the emergent structure, diversity and metabolism at the population and community levels. It doesn't explicit any particular species. It rest on the idea that communities include functionally redundant populations. It is useful for studying the impact of climate change at the community level. There is still a lot of room for improving our understanding of the structure of communities in variable environments. In this perspective the present spectrum based approach provides a sound basis to investigate the effects of important structuring processes such as seasonality. It also provides a sound starting point to build realistic representation and investigate the sensitivity of marine ecosystems to environmental changes over large scales, along other methods (Cheung *et al.* (2010); Blanchard *et al.* (2012); Brander (2010); Lefort *et al.* (2015)). Adding more realism to our idealized study would involve considering the effects of other stressors such as acidification (Fabry *et al.* (2008)) and oxygen limitation (Pörtner & Knust (2007)), or constraints such as thermal ranges (Englund *et al.* (2011)). It would also require considering spatial interactions explicitly.

Acknowledgment

This study was supported by the ANR project MACROES (MACRoscope for Oceanic Earth System ANR-09-CEP-003)

Appendix A : Functional response formulation

At a given time step t, for an individual of structural volume V, trait maximal volume V_m, the scaled functional response $f_V^{V_m}$ is a key component of the model. It constrains the food assimilation $\dot{p}_A^{V_m}$ and introduces the role of trait diversity in feeding interactions :

$$\dot{p}_A^{V_m} = f_V^{V_m} \dot{p}_{Am_{max}}^{V_m} = f_V^{V_m} \{\dot{p}_{Am}^{V_m}\} V^{2/3} = f_V^{V_m} \alpha_{\{\dot{p}_{Am}\}} V_m^{1/3} V^{2/3} \tag{9}$$

where $\dot{p}_{Am_{max}}^{V_m}$ is the maximum food assimilation rate.

We use a Holling type II formulation for the functional response (Holling (1959)) where the feeding is characterized by the capacity of the individual to : first, process food, limited by the handling time $h_V^{V_m}$; second, search and find food, limited by the attack rate $a_V^{V_m}$.

$$f_V^{V_m} = \frac{p_V}{\frac{1.}{h_V^{V_m} a_V^{V_m}} + p_V} \tag{10}$$

for a density of available prey p_V .

The handling time is directly linked to the maximum assimilation rate $\dot{p}_{Am_{max}}^{V_m}$:

$$h_V^{V_m} = \frac{1.}{\dot{p}_{Am_{max}}^{V_m}} = \frac{1.}{\alpha_{\{\dot{p}_{Am}\}} V_m^{1/3} V^{2/3}} \tag{11}$$

The attack rate is the product of individuals swimming speed, proportional to individuals length $L \propto V^{1/3}$, and the cross section of the capturing apparatus, proportional to $V^{2/3}$:

$$a_V^{V_m} = C V^{1/3} V^{2/3} = CV \tag{12}$$

volume specific with C a dimensionless constant.

The functional response can be written :

$$f_V^{V_m} = \frac{p_V}{\frac{\alpha_{\{\dot{p}_{Am}\}} V_m^{1/3} V^{2/3}}{CV} + p_V} = \frac{p_V}{C' V_m^{1/3} V^{-1/3} + p_V} \tag{13}$$

with C' a semi-saturation constant $\propto C^{-1} \alpha_{\{\dot{p}_{Am}\}}$.

Appendix B : Temperature dependence

The processes related to food assimilation are temperature dependent : the maximum food assimilation $\dot{p}_{Am_{max}}^{V_m}$; the handling time $h_V^{V_m} = (\dot{p}_{Am_{max}}^{V_m})^{-1}$; the attack rate $a_V^{V_m}$. With a correction of the metabolism according to the Arrhenius relationship T_{cor} these processes have been shown to present different scaling properties with temperature (Englund *et al.* (2011); Rall *et al.* (2012)), lets say T_{cor}^{-p} for handling time, T_{cor}^{q} for attack rate. Little is known about these scaling but in a meta-analysis Rall *et al.* (2012) tend to support a universal scaling across taxa, with handling time and attack rate less dependent than metabolism. In mathematical term $-p$, $q < 1$.

With temperature correction the scaled functional response writes :

$$f_V^{V_m} = \frac{p_V}{\frac{\alpha_{\{\dot{p}_{Am}\}} V_m^{1/3} V^{2/3} T_{cor}^{p}}{CV T_{cor}^{q}} + p_V} = \frac{p_V}{C' V_m^{1/3} V^{-1/3} T_{cor}^{p-q} + p_V} \tag{14}$$

and the food ingestion :

$$\dot{p}_A^{V_m} = f_V^{V_m} \dot{p}_{Am_{max}}^{V_m} T_{cor}^{p} \tag{15}$$

If we merge equations 14 and 15 : at high food density, $p_V \gg C' V_m^{1/3} V^{-1/3} T_{cor}^{p-q}$, $f \approx 1$, the assimilation scales with T_{cor}^{p} ; at low food density $p_V \ll C' V_m^{1/3} V^{-1/3} T_{cor}^{p-q}$, the sensitivity of the scale functional response to temperature matters, the assimilation scales with $T_{cor}^{-p+q} T_{cor}^{p} = T_{cor}^{q}$. At saturation the limiting process is the maximum ingestion. At low food density the limiting process is the attack rate.

The determination of the scaling factors p and q for the modeling of fish communities is a challenge. Rall *et al.* (2012) estimated generic values in a meta-analysis (in term of activation energy), the attack rate scaling being higher than ingestion ($-p < q$). Nevertheless looking at the values for fish communities in a meta-analysis of Englund *et al.* (2011) the opposite relationship is observed for this specific taxa ($q < -p$). In the present model we therefore choose a value of $-p = 1$ to keep consistency within the DEB an $q < -p = 1$. For the attack rate the value of $q = 1/3$ has been chosen from bio-mechanic considerations.

The determination of the temperature dependence of feeding in the model is a key component and obviously more efforts are necessary for a realistic representation. The present choice at least agrees with the observation that feeding increases less strongly with temperature than metabolism (Rall *et al.* (2012)). It supports the conclusion that consumers biomass should decrease with warming (Rall *et al.* (2010)).

Appendix C : Community level energy balance

The community spectrum can be visualized as a closed compartment which draws its resource from the lower trophic level, through size selective predation, and looses it through individual level dissipation, disease or ageing mortality, growth overhead or fecundation loss (see Fig.9). The model being energy balanced from individuals to the community, at stationary steady state the input of energy $\dot{P}_{in} = \dot{P}_{PP,t}$ rigorously balances the output $\dot{P}_{out} = \dot{P}_{Dissip,t} + \dot{P}_{Loss,t}$, $\dot{P}_{in} = \dot{P}_{out}$.

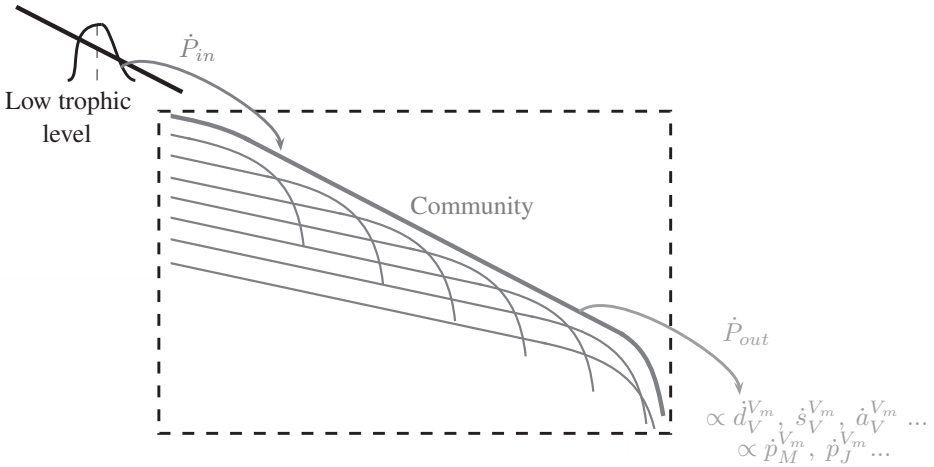


FIGURE 9 – Community level energy balance at stationary steady state.

Appendix D : DEB fish parameters

In Kooijman (2010) a set of generic DEB parameters are provided. While the present model in its initial formulation used these values (Maury & Poggiale (2013)), we here adapted them to better account for fish communities.

— **Volume specific cost of growth** $[E_G]$ **:** The ash-free-dry-weight of fish is taken higher $d_{V_{dry}} = 0.2\ g\ cm^{-3}$ (against $d_{V_{dry}} = 0.1\ g\ cm^{-3}$ for the generic parameters) for a wet mass at $d_{V_{wet}} = 1\ g\ cm^{-3}$ (Lika *et al.* (2011)). With a chemical potential for structure of $\mu_V = 560\ kJ\ Cmol^{-1}$, a growth efficiency of $\kappa_G = 0.8$ and a dry molecular weight for structure taken $w_{V_{dry}} = 24.6\ g\ C-mol^{-1}$:

$$[E_G] = \frac{\mu_V \frac{d_{V_{dry}}}{w_V}}{\kappa_G} = 5691\ J\ cm^{-3} \tag{16}$$

— **Energy content of biomass** Ψ **:** We assumed identical chemical potentials for structure and reserve, $\mu_E = \mu_V = 560\ kJ\ Cmol^{-1}$, identical molecular weights for structure and reserve $w_{E_{dry}} =$

$w_{V_{dry}} = 24.6\ g\ C - mol^{-1}$, $w_{E_{wet}} = w_{V_{wet}} = w_{*_{dry}}/0.2$:

$$\Psi = \frac{\mu_*}{w_{*_{wet}}} = 4552J\ g^{-1} \tag{17}$$

Kooijman & Lika (2014) compile the DEB parameters specific of fish communities, it allows to adapt few generic parameters.

— **Somatic maintenance rate** $[\dot{p}_M] = 25\ J\ d^{-1}cm^{-3}$ **:** Due to this modification the **maximum surface-specific assimilation rate** becomes proportional to $\alpha_{\{\dot{p}_{Am}\}} = 31.25\ J\ cm^{-3}\ d^{-1}$.

— **The structural volume at puberty** $V_p = \alpha_p V_m$**,** $\alpha_p = 0.125$ **:** For all fish it is estimated that $L_p = 0.5L_m$, $V_p = 0.125V_m$.

The **maximum reserve density** has been corrected to better fit empirical growth curves, $\alpha_{[E_m]} = 312.5\ J\ cm^{-4}$ which induces an **energy conductance** $\nu = 0.1$.

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Chapter 4

Seasonal dynamic of the biomass spectrum along a latitudinal cline

Seasonal dynamics of the biomass spectrum along a latitudinal transect

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Abstract

The community biomass density size-spectrum, namely the density of biomass distribution as a function of individuals' body size, is a strong characteristic of marine ecosystems. It is observed empirically in a wide range of ecosystems and well explained theoretically. However, most studies focus on temporally or spatially averaged spectra and little is known about its dynamics. We investigate the impact of seasonality on the community spectrum dynamics using a Dynamic Energy Budget-, trait-based size-spectrum model. In order to account for the large range of seasonal patterns that can be experienced in marine ecosystems worldwide, the model is forced by seasonal variations of temperature and low trophic level biomass at different spatial positions along an average latitudinal transect. In these numerical experiments, two main processes characterize the seasonal dynamic of the modeled community spectra. First, the slow propagation of cohorts along the spectrum driven by the growth of batch of individuals. Second, the fast propagation of a seasonal wave of biomass from small to large individuals driven by predator-prey interactions. Depending on the intensity of the seasonal variations of resource and depending on the temperature at different latitudes, the dynamics of species spectra is dominated by either one or the other process. Highly seasonal high latitude ecosystems are dominated by a strong pulse of growing recruits in small sizes and an annual biomass wave across the spectrum. Low latitude ecosystems are dominated by the sole propagation of growing cohorts across the spectrum. In mid-latitude ecosystems, both processes overlap up to mid-size (30 cm long individuals) and the biomass wave dominates toward larger individuals. These dynamics at the community level reveal different flows of biomass across communities a different latitudes, from a fast one dominated by size-selective predation to a slow one constrained by individuals' growth. Finally, looking at the latitudinal distribution of communities' indicators of structure, the model explains the link between environment and seasonal variability of community size-spectra along latitudes.

Keywords : Seasonality ; Cohorts ; Succession ; Community size-spectrum ; Biodiversity ; Trait based model ; Marine ecosystem model ; Impact of the environment ; Latitudinal gradient ; Biomass flux.

Introduction

The community biomass density spectrum, namely the biomass density distribution as a function of individuals' size (weight, volume or mass) on a log-log scale, is an important emergent property to characterize aquatic ecosystems (Sheldon *et al.* (1972); Kerr & Dickie (2001)). The spectrum aggregates the complexity of ecosystems into two emergent synthetic measures : the slope that relates to the efficiency of the biomass flow from small to large individuals and the intercept that is linked to the total biomass of the community. These measures can be used as indicators of ecosystems' states (Fulton *et al.* (2004); Jennings & Brander (2010)).

The community biomass spectrum has been documented in both marine and freshwater ecosystems, for plankton and fish communities (Boudreau & Dickie (1992); Sprules & Goyke (1994); Heath (1995); Rice & Gislason (1996); Bianchi *et al.* (2000); San Martin *et al.* (2006); Tarling *et al.* (2012)). More and increasingly precise measures can be expected with the development of modern size-resolving observation technologies (Pollom & Rose (2015)). Moreover, many models of the spectrum have been developed (Andersen *et al.* (2015); Guiet *et al.* (2016b)). They are usually based on few key processes including growth, respiration and predation, as well as secondary processes such as reproduction or mortalities. A few of these models can account for the functional role of species diversity. Measured and modeled biomass spectra are often spatial or temporal averages of ecosystems' state disregarding the propagation of perturbations through the spectrum. Average biomass spectra account for the average energy flux underlying biomass distribution in aquatic communities but they overlook the dynamical properties of the spectrum and the biological and ecological processes involved.

The propagation of perturbations through the spectrum has been looked at in early models of the biomass spectrum (Silvert & Platt (1978)). However it has been overlooked since then, with most recent studies of the dynamic of the spectrum focused on the conditions of its stability (Datta *et al.* (2011)). This stability relates to characteristics of predation (Plank (2012)) or species diversity (Zhang *et al.* (2013)). To our knowledge, few studies analyzed how the spectrum is dynamically impacted by perturbations. Zhou (2006) formalized the response to perturbations as the propagation of waves driven by growth, dumped by mortalities and spreading while propagating away from their source. Maury *et al.* (2007b) investigated how oscillations of resource and temperature affect the community biomass spectrum. Waves of biomass propagate through the spectrum and amplify up to a resonant size before they fade. They tested different amplitudes and periods of oscillations and revealed an indirect link between the frequency of environmental variability and the resonant size range. Maury & Poggiale (2013) extended this study accounting for species functional diversity using a trait-based approach. More recently, Le Mézo *et al.* (2016) used the ecosystem model APECOSM (Maury (2010)) to study how various modes of environmental variability propagate in North Atlantic and North Pacific ecosystems.

In this paper, we use a size-spectrum model tuned for upper trophic levels (Maury & Poggiale (2013); Guiet *et al.* (2016a)) to investigate the impact of seasonality on the dynamic of the community spectrum. We focus on the impact of seasonality because few empirical studies allow the discussion of the results (Hargrave *et al.* (1985); Sprules *et al.* (1991); Gaedke (1992); Pope *et al.* (1994); Heath (1995); Tarling *et al.* (2012)). Since seasonality impacts both temperature and the resources available to predators with different timing and amplitude along latitudes (Cullen *et al.* (2002)), we compare simulated spectra along latitudes from the South to the North pole.

In a first section we describe the theoretical framework adopted in our study. We describe the main features of the model and explain how seasonality is represented. We focus on the impact of seasonal variations of the resource in low trophic levels and seasonal variations of water temperature. In a second section, the simulated dynamics of the community spectrum forced with seasonal variations of food resources and temperature is described. Two main processes of biomass propagation explain the dynamics of the spectrum : growth driven cohort propagation for small sizes ; predation-driven saltation of biomass for large sizes. The relative importance of the two processes vary across latitudes. The seasonality induces different patterns of community structure at different latitudes. These patterns constrain the different modes of biomass propagation through the spectrum and *in fine* affect the environmental sensitivity of ecosystems along latitudes. Finally we discuss the results obtained.

1 Method

1.1 Model

We use the mechanistic Dynamic Energy Budget (DEB, Kooijman (2010)), trait-based, continuous biomass spectrum model described in detail in Maury & Poggiale (2013) and parametrized for fish communities in Guiet *et al.* (2016a). The model allows the representation of the community level dynamics from the individual level response to environmental perturbations (Fig. 1).

The energetics and life history of individuals is determined by the dynamics of reserve E and structural volume $V \propto L^3$ according to the DEB theory. The DEB also prescribes the allocation of energy to respiration, maturation and reproduction. It is constrained by food density Γ and water temperature T encountered by individuals during their life time. The DEB allows the calculation of the growth and eggs production of individuals. We parametrized the individual level to represent fishes. Different fish species can be parametrized with the same reduced set of parameters by scaling generic parameters with maximum structural size L_m (see appendix A for the list of parameters of the model).

At the population level, the biomass density $\xi_{L,t}^{L_m}$ of individuals of a given trait defined species L_m can be represented as a function of their length $L \in [L_b, L_m]$ with a biomass density spectrum. Each species of trait $L_m \in [L_m^{min}, L_m^{max}]$, the range of specific traits of the community, can be represented with a distinct species spectrum. Predators are opportunists, their prey can belong to any species and is calculated using the size-selectivity predation function Ω. Prey biomass and water temperature affect individuals' life histories and the dynamics of the population $\xi_{L,t}^{L_m}$. Part of the energy allocated to reproduction is re-injected as eggs at a birth size L_b and constrains the intercept of the population biomass spectrum. The energy allocated to growth allows the advection of biomass through sizes.

At the community level, the biomass density distribution $\xi_{L,t}$ as a function of $L \in [L^b, L_m^{max}]$ emerges as the integral of trait-defined populations spectra in the trait space $[L_m^{min}, L_m^{max}]$:

$$\xi_{L,t} = \int_{L_m^{min}}^{L_m^{max}} \xi_{L,t}^{L_m} dL_m \tag{1}$$

Few additional processes complete the definition of the model. These include ageing, schooling and disease mortalities. See Maury & Poggiale (2013) or Guiet *et al.* (2016a) for a detailed description of the model. Figure 1 represents schematically the model ; the parameters are summarized in appendix A.

To represent the impact of seasonality we focus on two stressors. First the water temperature which increases the metabolism of individuals when warming and decreases it when cooling (Clarke & Fraser (2004)). Temperature is accounted for by correcting all energy fluxes at the individual level (see Fig. 1) with an Arrhenius function (Kooijman (2010)). The correction also concerns the feeding rate at individual level and other processes such as disease and ageing mortalities (see Guiet *et al.* (2016a)). Temperature affects all individuals in the modeled community. Second, we represent the variation of the Low Trophic Level biomass ξ_{LTL} that is fed upon by the smallest organisms in the fish community. Represented by a spectrum (Fig. 1), the contribution of low trophic level prey to the diet decreases down to zero when predators' size increases. The low trophic level spectrum is a boundary condition providing the energy for the development of the smallest individuals that are themselves eaten by larger individuals and so on. The low trophic level spectrum is submitted to predation pressure. However, in the present paper we focus on high trophic levels and disregard the mortality induced by predation on the low trophic level spectrum.

The model is used to compute the fish community spectrum forced with different seasonal cycles of low trophic level biomass ξ_{LTL} and temperature T. The numerical scheme adopted to solve the advection of abundance along the spectrum (Table 2, T2.a in Guiet *et al.* (2016a)) is a finite volume approximation with piecewise linear reconstruction and slope limiter (LeVeque (1996)). It is solved on a range of structural size from $L_b = 0.1\ cm$ where reproduction provides the initial level of abundance of populations, to a maximum length of $L_m^{max} = 200\ cm$, on a non uniform discretization of 100 structural length. The traits are chosen in the same size range $[L_m^{min}, L_m^{max}] = [0.1\ cm, 200\ cm]$ with an irregular arbitratry discretization including 77 species. The non regular discretizations have been used to account for the large variation of size over 3 orders of magnitude from L^{min} to L^{max}, keeping a reasonable

computation time. The model is ran with a daily time step for 100 years. Starting from an arbitrary initial state, 100 years allowed every simulation to reach a stationary seasonal cycle.

Finally, in order to simplify the analyze of the large amount of data produced by the model, we use a set indicators to describe the community size-spectrum (see detail in appendix B) : ξ_{tot}, the total amount of energy in the community ; S_C, the slope of the community size spectrum ; TL_{max}, the maximum trophic level sustained in the community ; $\overline{L}_m$, the geometric mean of species maximum length. We compute the mean values of indicators as well as their variability range taking the 5^{th} and 95^{th} percentile of their seasonal distribution.

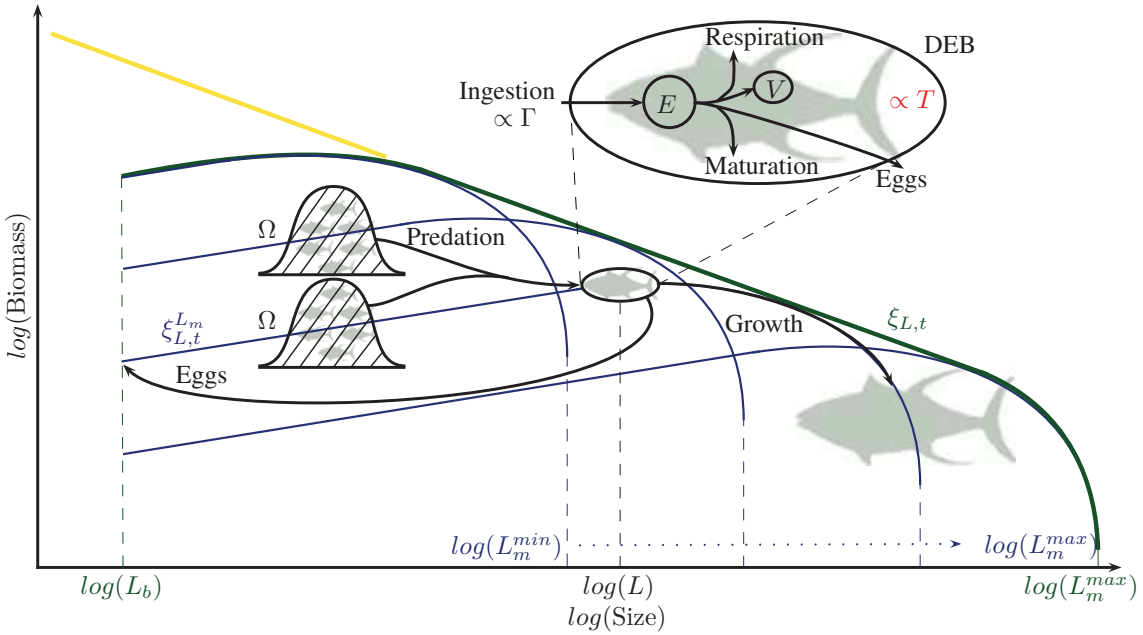

FIGURE 1 – Schematic representation of the community biomass spectrum $\xi_{L,t}$ (green line) as a sum of population spectra $\xi_{L,t}^{L_m}$ (blue lines) emerging from the individual level DEB energy fluxes driven by size selective predation (black). Low trophic level resource spectrum (yellow line).

1.2 Seasonal forcing

Seasonality impacts physical and ecological processes. Across latitudes, it is linked to the timing, amplitude and duration of low trophic level's blooms. It determines the mean value and amplitude of water temperature oscillations.

In order to force the model with seasonal cycles of low trophic level biomass ξ_{LTL} and temperature T along a representative latitudinal section, we use a climatological simulation of the coupled NEMO-PISCES physics-biogeochemistry model (Aumont *et al.* (2015)). Phytoplankton and zooplankton biomass concentrations simulated on a 1° grid are converted into biomass time series that are averaged over longitudes to calculate the average latitudinal distribution of resources. Similarly, realistic temperature values have been derived from simulated sea surface temperature fields from the NEMO-PISCES model. See figure 2 for the properties of the latitudinal distribution of low trophic level biomass ξ_{LTL} and temperature T used to seasonally force the model.

Note that a first-order classification of ecological biomes recognizes four typical categories, polar, westerlies, trades and coastal biomes (Cullen *et al.* (2002); Longhurst (2010)). Along the latitudinal distribution, and according to this classification, we will specifically focus on the impact of seasonality at three virtual stations representative of three of these biomes : polar, 65° N, with a strong productive summer, the good season, and a poor winter, the bad season ; westerlies, 45° N, with a more regular resource supply but poorer conditions and large temperature oscillations ; trades, 5° N, with constant poor resources and dampened temperature variation. See figure 2 for the detail of the seasonal forcing

used at the three stations.

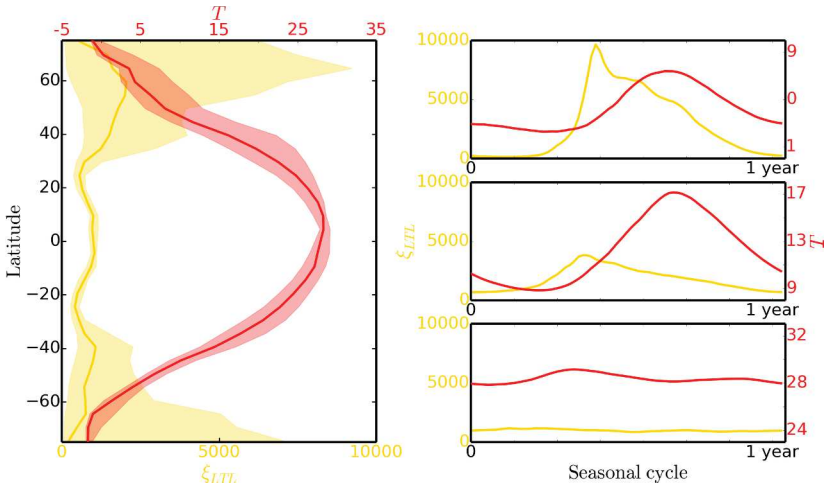

FIGURE 2 – Low trophic level biomass ξ_{LTL} (yellow) and temperature T (red) variations along latitudes : left, mean seasonal values (line) and variation along latitudes ; right, seasonal cycle of resource and temperature at three virtual stations, polar (65° N), westerlies (45° N), trades (5° N).

2 Results

2.1 The seasonal community size-spectrum

The modeled community level biomass density distribution $\xi_{L,t}$ is globally a dome shaped log-log decreasing biomass spectrum (see Fig. 3 at the polar virtual station). It is curved in small size classes where it overlaps with the resource, then quasi-linear before tumbling down in large size classes where ageing mortality dominates and closes the distribution. Aligned with the resource spectrum, this distribution is consistent with the observation of a constant biomass in logarithmically equal body size intervals (Sheldon *et al.* (1972)).

At the population level, population spectra $\xi_{L,t}^{L_m}$ inform about the community structure. Reaching distinct maximum lengths L_m and developing from distinct levels of biomass at birth L_b, these spectra account for the diversity of energy pathways within the community. The species spectra are traversed by waves that propagate from small to large individuals' size. Triggered by the seasonality of the environment, these waves correspond to growing yearly cohorts. For larger species, these cohorts can be followed for several generations (up to four for the largest species) before vanishing at large body sizes.

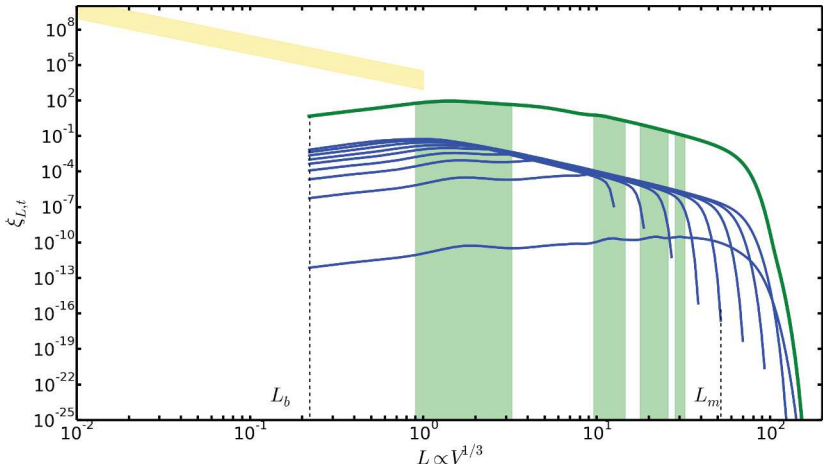

FIGURE 3 – Community biomass spectrum $\xi_{L,t}$ function of individual sizes L at the polar virtual station : low trophic level spectrum range of variation (yellow shading), community (green) and populations (blue) biomass spectra, yearly cohorts (green shading).

2.2 A growth driven advection

Cohorts propagate along the species spectra due to individuals' growth. The propagating cohorts are initiated at the peak of low trophic level biomass and move from small to large individuals at different velocities (growth rates) depending on the environment and the species considered. Figure 4 (left) illustrates the growth in size ΔL of cohorts over a year as a function of species maximum length L_m, at different latitudes. The growth is measured from the pics of the seasonal bloom at each latitude.

Cohorts grow faster along the spectra of large species because they have a higher maximum surface specific assimilation rate (the maximum surface specific assimilation rate is proportional to the maximum structural length of the species in the DEB theory) that allows more energy for structural growth. They also grow faster in warm low latitude ecosystems because the growth rate is proportional to the Arrhenius function of temperature (Clarke & Fraser (2004); Kooijman (2010)). The velocity of cohorts' propagation is therefore strongly correlated with water temperature at different latitudes. When divided by the temperature correction T_{cor}, the propagation velocity of cohorts at different latitudes falls into a similar range (Fig 4, right). Whether in poor low-latitude or rich high-latitude ecosystems, the propagation of biomass by growth is strongly constrained by the impact of temperature on individuals' metabolism.

Note that towards small species' lengths the growth difference between latitudes is not measured or breaks (Fig. 4). The cohorts are not clearly visible compared to another biomass wave (see next

section). Moreover, towards large species's lengths the maximum length represented figure 4 decreases with decreasing latitudes. Towards low latitudes smaller and smaller species are sustained in modeled communities (see Guiet *et al.* (2016a)).

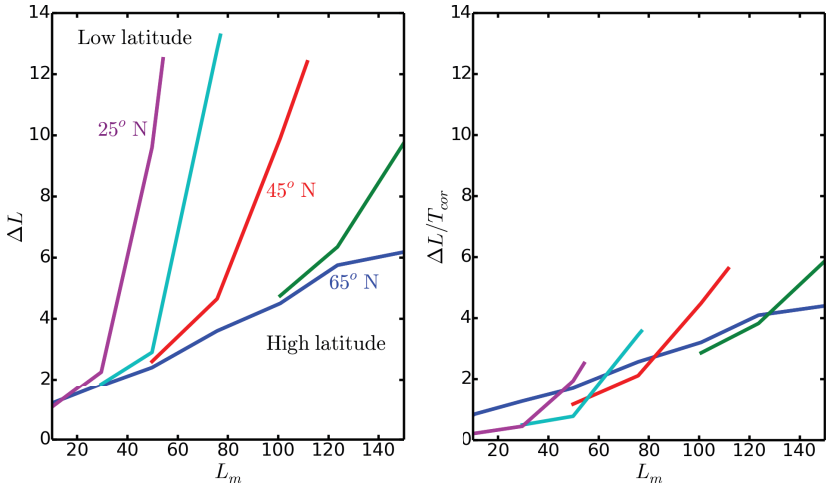

FIGURE 4 – Growth in size ΔL of cohorts over a yearly seasonal cycle as a function of species maximum length L_m : left, at different latitudes ; right, at different latitudes removing the effect of the temperature correction T_{cor} on the growth.

At the community level, cohorts' growth induces the formation of a biomass' wave. Figure 5 (left) illustrates the effects of this wave on the seasonal variation of the community biomass $\xi_{L,t}/\overline{\xi}_{L,t}$ (where $\overline{\xi}_{L,t}$ is the yearly average) at different sizes L (at the polar station). It is superimposed on the seasonal variation of resource (cf ξ_{LTL} Fig. 3) at the same location. The good season is in black and the bad one in white. Small individuals in the spectrum pic simultaneously with the low trophic level biomass. Then, integrating the propagation of all species level cohorts, the wave propagates with average individual's growth. The wave is strongly attenuated for larger individuals. The attenuated growth-driven biomass wave fades against a second pic of biomass, which forms during the good season and progressively dominates the annual biomass variation at larger sizes (see the formation of this second pic at $L = 7\ cm$).

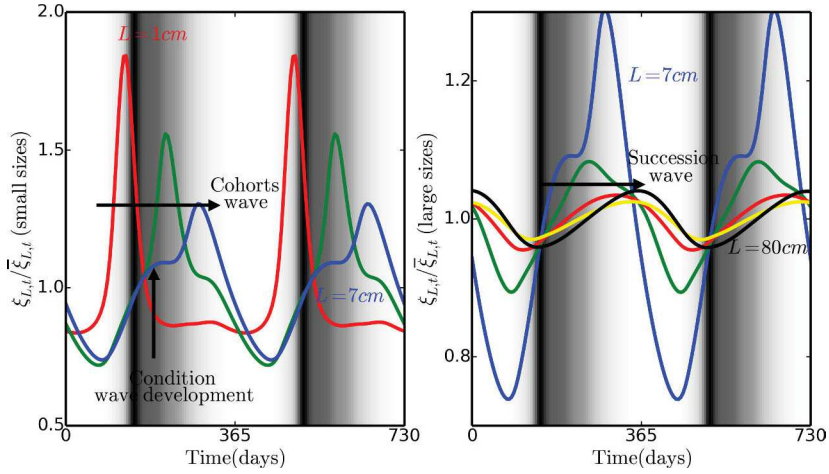

FIGURE 5 – Seasonal variation of the total biomass $\xi_{L,t}/\overline{\xi}_{L,t}$ at different sizes L along the spectrum (curves) superimposed with the resource seasonal cycle (grey shading) : left, in small size class, L = 1., 4., 7 cm, dominated by the cohorts wave ; right, in large size class, L = 7., 10., 20., 40., 80. cm, dominated by the sucession wave.

2.3 A predation driven biomass saltation

Besides the effect of the growth of species-specific cohorts, a second wave of community biomass propagates along the community spectrum figure 5 (right). It results from a second driving mechanism of the spectrum's dynamic. This wave reaches the largest individuals within a year, much faster than growth would allow. In a season, the wave propagates from 7 up to 80 cm long individuals in the polar virtual station.

The model explicitly computes the biomass allocated to the reserve compartment E (the model accounts for the dynamic of the body condition of individuals) and the accumulation of structural biomass due to growing individuals within each size class. During the pic of biomass in the good season, small individuals feeding on the low trophic level spectrum build reserve and accumulate biomass with the surplus of resource available. The accumulated biomass in these primary consumers initiates a predation driven succession up to the biggest individuals in the community. Secondary consumers prey on the surplus of primary consumers. In turn, they improve their condition and biomass. During the bad season the predation pressure is maintained and depletes the primary consumers' biomass, generating the wave-like signal. Larger individuals reach their annual biomass maximum during the bad season (see Fig. 5 (right)).

At the individual level, the allocation of ingested food into reserves depends on the functional response, which is linked to prey density and temperature. This allocation varies between species and ecosystems, impacting the intensity of the succession wave.

2.4 Impact of the environment on the dynamic of the community

We have identified two dominant driving processes of the community biomass spectrum dynamics : the growth driven advection and the predation driven biomass saltation. The speed of the first one depends on water temperature and food availability while the intensity of the second one depends mostly on the level of satiation at the community level. Besides growth and reserve, a third portion of the ingested food is invested into reproduction, which also impacts the dynamics. We investigate environmental impacts on the dynamics of the community biomass spectrum by comparing three virtual stations along latitudes (cf Fig. 2). Figure 6 represents the seasonal variation of the total biomass $\xi_{L,t}/\overline{\xi}_{L,t}$ at different sizes L as a function of time t for the three stations.

The polar virtual station is characterized by globally cold temperatures and highly seasonal resource variations (cf Fig. 2). During the low trophic level bloom, small individuals are satiated. The food ingested is allocated to growth, reproduction reaches its maximum and the surplus is stored into reserves. Energy quickly accumulates in the small size classes. It initiates the succession wave that propagates toward larger individuals during the bad season (see Fig 6 (left)). In the meantime, the low trophic level bloom triggers a wave of recruits which grow as well. The wave can be followed for a few years at the small individuals' sizes.

Conversely, the trade winds virtual station is characterized by globally warm temperatures and a poor and constant low trophic level biomass (cf Fig. 2). The resource being scarce, small individuals allocate mostly the preyed food to growth and reproduction. Allocation to reserve is negligible but not really necessary since the resource remains constant. In accordance with the resource stability, the flux of energy in the community is constant, dominated by growth. There is no succession wave since there is no intra-community predation in this ecosystem dominated by smaller primary consumer species. Temperature oscillations induce variations of the reproduction flux and trigger the cohort waves. Driven by growth, figure 6 (right) we can see two cohorts triggered yearly because of the bimodal temperature distribution. This dynamics is the visible part of a constant growth-driven flux of biomass, which maintains the community.

Between high and low latitudes, the westerlies virtual station represents an intermediate dynamics. The station is most of the time in medium temperatures and low trophic level resources oscillate but always maintain a minimum level. Small or large species are more or less sensitive to the resource oscillations. In the model, small species reach satiation at lower food density. At medium level of low trophic level biomass, they allocate more energy to reserves than larger species. The succession wave is therefore stronger for small species. At medium level of low trophic level biomass, large species can become food limited. The oscillations of the resource affect the growth and reproduction and little

energy can be allocated to reserves. The succession wave is therefore weak and large species biomass propagation is dominated by growth. Therefore at mid-latitude, figure 6 (middle), the dynamic of the biomass spectrum appears as a combination of a growth driven wave, like in the low latitude station, and a condition wave like in the high latitude station. Note that this combination is valid for small to medium individuals' sizes (up to 30/40 cm). However, the dynamics at small sizes has an important impact on the emerging community biomass spectrum. In this mid-latitude ecosystem, two main energy pathways compete because of species diversity with both small and large species represented in the community.

Note that for the largest sizes, the spectrum is subject to strong variations at every station. At these sizes the spectrum is collapsing and the distribution is very sensitive to slight variations.

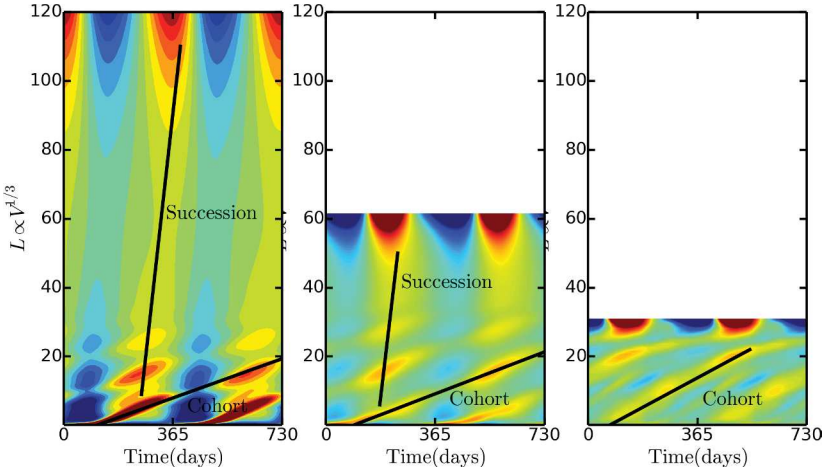

FIGURE 6 – Seasonal variation of the normalized community biomass spectrum $\xi_{L,t}/\overline{\xi}_{L,t}$ along size class, at the three virtual stations : left, polar ; middle, westerlies ; right, trades. Waves propagate from small to large individuals at different speeds, in red their positive pic, blue negative pic (on the same colors range).

2.5 Impact of seasonality on communities along latitudes

From the pole to the equator, the resource available to fish communities and its seasonal variability are globally decreasing. Conversely, temperatures are globally increasing (cf Fig. 2). Different sensitivities of large and small species to these gradients affect the mechanisms of the energy transfer that sustains the community biomass spectrum and drives its dynamics. Figure 7 synthesizes the effects of these differences on the characteristics of the community spectrum along a latitudinal transect from South to North poles (see appendix B for the description of the indicators represented).

First, the mean latitudinal distributions of the different indicators resemble qualitatively those obtained in static studies of the impact of the environment on the community size-spectrum (Guiet *et al.* (2016a)). At low latitudes, poor constant resources and high turnover rates allow the survival of the small species that are able to fulfill their maintenance needs with the scarce food available. At high latitudes, large resources and slow turnover rates sustain large species. Therefore, when latitude increases, the mean species length $\overline{L}_m$ increases. While larger species are sustained, larger individuals also subsist. Correlated with individuals' size, the length of the trophic chain TL_{max} follows this increase. Low latitude ecosystems are dominated by primary consumers feeding mostly on the low trophic level biomass spectrum. High latitude ecosystems are constituted of primary consumers and secondary consumers feeding on the small individuals of the community. Globally, high latitude ecosystems maintain larger biomasses ξ_{tot} and communities have softer slopes S_C (around the theoretical value -2) because of the top down pressure of secondary consumers.

Second, the situations are very different regarding the seasonality of communities at different latitudes. At low latitudes ($\pm\ 25^o$), the resource supply is constant and only temperatures oscillate slightly (Fig. 2). This corresponds to the trades station. The small amplitude growth driven cohorts triggered by the temperature oscillations only affect the slope S_C of the short spectrum. At mid-latitude (between

$\pm$ 25^o and $\pm$ 55^o), the resource at low trophic level is higher and starts exhibiting seasonal oscillations. This corresponds to the westerlies virtual station. Over the seasonal cycle, for different species the dynamics is either dominated by the succession wave or by the cohorts wave. When latitude increases further, the length of the spectrum increases and the oscillations of the spectrum induced by the propagating cohorts is balanced by the biomass redistribution due to the succession wave. The oscillations of the slope S_C are dampened. The variations of the low trophic level biomass ξ_{LTL} affect the length of the trophic chain TL_{max} since mid-size individuals can feed alternately on the abundant low trophic level resources or on the fish community. At high latitude (above $\pm$ 55^o), the resource varies from very poor to very rich within a season and temperatures are always cold. This corresponds to our polar station. The ecosystem supports large species and the succession wave is the primary process through which environmental seasonality propagates through the community. The slope S_C steepens during the good season and becomes softer during the bad season. Strong pulses of newborns cohorts are also triggered yearly but they attenuate quickly in small size class. At high latitude it affects the community mean species length $\overline{L}_m$. Finally, the trophic chain length TL_{max} varies with resource oscillations, and this phenomenon amplifies when latitude increases.

Globally, the biomass of the community ξ_{tot} remains remarkably constant compared to the strong variations of the resource. In the simulations, seasonality is indeed mostly impacting the structure of the communities but not their total biomass.

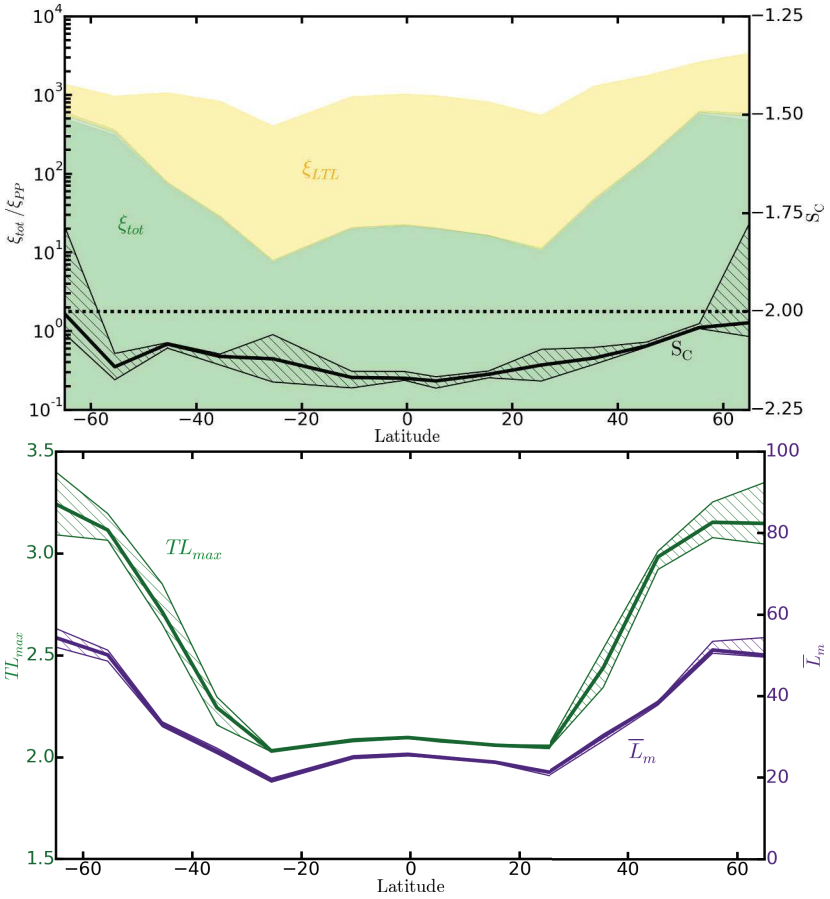

FIGURE 7 – Indicators of the community sise spectrum along latitudes from the South to North pole (see appendix B) : Total biomass in the resource spectrum ξ_{LTL} compared to the total biomass in the modeled fish community ξ_{tot} ; community slope S_C around the -2 reference value ; maximum trophic level reached by the community TL_{max} ; mean species length $\overline{L}_m$. Mean value (line) and variability of indicators over a season (dashed).

3 Discussion

3.1 Modeling the dynamic of the community size-spectrum

A large panel of community size-spectrum models have been developed (Andersen *et al.* (2015); Guiet *et al.* (2016b)). However, most studies have focused on stationary solutions and most have ignored their dynamical properties. Community size-spectrum models are indeed often prone to unrealistic dynamical instabilities (Datta *et al.* (2011)), which compromise the study of their dynamics. The stability of modeled community spectra can be improved with a wise parameterization of the size-selective predation Ω (Plank (2012)) or with alternative formulation of the governing flux equation (Datta *et al.* (2011)). The representation of trait-based diversity also improves this stability (Zhang *et al.* (2013)).

Our trait-based model also includes a density-dependent process, the schooling (Maury & Poggiale (2013)), which plays a strong stabilizing role (Maury (2016)). At different individuals' size, schooling protects preys from predation below a threshold value. It avoids their unrealistic exhaustion by predators and dampens the spectrum oscillations while maintaining the coexistence between species. In marine ecosystems, schooling is likely not the only important density-dependent phenomenon, other feedback such as spatial effects may be important. For example large and mobile top predators exert a strong top-down control on preys and spatially dampen the oscillations exhibited by lower trophic levels (Moloney *et al.* (2010)).

Therefore, in addition to the trait-based formulation, the stabilizing role of schooling allows interpretable unsteady solutions, but the results have to be discussed in light of this assumption.

3.2 The community spectrum and cohorts

At the community level, observed community spectra often appear as a succession of dome shaped structures along the size dimension (Boudreau & Dickie (1992); Sprules & Stockwell (1995); Tarling *et al.* (2012)). These domes are stable features. Thiebaux & Dickie (1993) proposed that they correspond to different trophic groups. They also recognized that periodic oscillations around these main features may arise. Our model produces such domes-like structure for the fish community, and the growing species cohorts contribute to its oscillations.

The cohorts propagating along the species-spectra include all the same age individuals growing in size and carrying with them their biomass. For certain species, these bumps of biomass can be an order of magnitude higher than the base spectrum (see the large species in Fig. 3). The propagation of cohorts along biomass size-spectra has been measured in few ecosystems, mostly on plankton communities. The successive sampling of ecosystems spectra has allowed the observation of traveling biomass bumps along the spectrum (Edvardsen *et al.* (2002); Tarling *et al.* (2012)). Put together, successive sampling scheme have allowed reconstructing the propagation of cohorts. For instance Hargrave *et al.* (1985) followed a copepods cohort over 8 months. They could actually identify three successive cohorts over the study period, each of them growing at different speeds depending on the environmental temperature. Another example, Zhou (2006) developed a method to derive the growth speed of populations from the comparison of two community size spectra taken at different seasons.

Here a clear signal is associated with the growth of cohorts in the small size classes (up to 30 cm). In high latitudes, the community level signal triggered by the seasonal bloom at low trophic level fades strongly with increasing sizes (see Fig. 5 left). This is mostly due to mortality, especially when young growing individuals start forming schools that expose them to predation. Also the different growth rates of species spread the cohort. Toward large sizes, oscillations are filtered out. In low latitudes ecosystems, the seasonal oscillations of temperature generate cohorts even when the resource is constant. Without predators, these cohorts are less attenuated and travel up to the larger individuals of the community. As long as they concern small individuals, the observation of traveling cohorts along the modeled community spectra does not contradict observations.

The observation of the traveling cohorts is an indicator of the contribution of growing individuals in the biomass flux from small to large individuals in different ecosystems.

3.3 The community spectrum and biomass saltation

At the community level, the propagation of the succession wave relies on the transfer of biomass from prey to predators. Increased prey density benefits larger predators that in turn increase their biomass. Because of their resource impoverishment and because of the predation pressure that prey undergo, prey biomass decreases and their predators start losing biomass as well when the biomass of prey is depleted. Explicit interactions between resource, primary consumers and secondary consumers in the model allow this signal to propagate. This process is initiated by the seasonal bloom. It can be seen as a big annual wave of biomass which travels from small to large individuals.

Borrowed from Pope *et al.* (1994), the annual wave picture as been used to illustrate this seasonal biomass propagation from plankton to fish. However, it relies on processes that are changing with individuals' size. For small individuals, the wave varies with the generation time of the species dominant at different sizes (Gaedke (1993)). For the small species, the generation time is shorter than the season. Thus, in plankton communities, the seasonal bloom first benefits to the small species that can grow and reproduce within a few months. Their larger predators, with a longer generation time, take advantage of the development of their prey and grow and reproduce with a delay, thus propagating the biomass wave in small sizes class (Gaedke (1993); Heath (1995)). For large individuals on the other hand, the generation time largely exceeds the duration of the season. Individuals do not contribute to the biomass wave by growing and reproducing but with changes of their condition and accumulation of biomass due to growth in each size class. In highly seasonal environments, reserve accumulation is an important factor of individuals' survival during the bad season (Mogensen & Post (2012)). The seasonal bloom allows primary consumers to develop their reserve in anticipation of the coming resource shortage. Secondary consumers also exploit this accumulation of biomass to develop their reserves, with a delay. Individuals of larger secondary consumer species are indeed away from satiation at the beginning of the low trophic level bloom. When their prey density increases, they first allocate the energy to growth and reproduction before starting accumulating reserves when their prey density is sufficient. This seasonal annual wave from small to large individuals affects the slope of the community spectrum. It is steeper during the seasonal bloom when the small individuals of small species are the quickest to take advantage of the surplus of resource, and is it shallower during the bad season when small individuals follow the depletion of the resource while the larger individuals are not impacted strongly (Tarling *et al.* (2012)).

Note that in our simulations the succession wave doesn't initiate exactly in the smallest size classes but rather at intermediate sizes. For the smallest sizes, the increase of condition is combined with an accumulation of biomass due to the growth of individuals. This accumulation occurs around a resonant size range which depends on the frequency of the resource oscillations that is one year in our case (see Maury & Poggiale (2013)).

The biomass condition wave represents a second flux of seasonal propagation of biomass from small to large individuals in fish communities. Faster than individuals' growth at large body size, this flux is responsible for the export of seasonal low trophic level productivity toward large individuals. Considering its role on the seasonal cycles of individuals condition could be used to optimize fisheries' productivity (Mello & Rose (2005)).

3.4 Reproduction and dynamics

We haven't mentioned yet the role of reproduction on the community size-spectrum. It is, however, a central process. Fish are highly fecund and spawning is a metabolically demanding activity. Although many reproduction strategies exist, they can be summarized in two main categories (McBride *et al.* (2015)) : capital breeding and income breeding. For capital breeders, the reproductive output comes largely from the energy acquired and stored during earlier periods of food abundance. Conversely, the reproduction of income breeders is directly supported by the energy acquired.

In high latitudes, strong seasonal fluctuations promote capital breeders, whereas at low latitudes more constant conditions promote income breeders (Sainmont *et al.* (2014)). In our model, at the individual level the DEB theory is simplified using the assumption of a continuous spawning of mature individuals. Therefore, the model only represents an income breeding strategy. Thus, while the model is adapted for the representation of the dynamic of the spectrum at low latitudes, this might lead to bias in high latitudes.

At low latitudes, resource levels are constant but most species are food-limited. When a surplus of resources is available, little goes to reserves to the benefit of growth and reproduction, both being proportional in the model. Resource variations are therefore directly impacting eggs production. Temperature also directly impacts the flux of energy invested into reproduction. These variations then propagate through growth. At low latitudes, the dynamics of the spectrum depends on the direct impact of environment on reproduction.

In higher latitudes, species experience higher food densities but on a shorter period. The surplus of energy during the good season fuels the reserves but also directly the eggs production. In the model, there is a direct spawning in accordance with an income breeding strategy. During the bad season, primary consumers lack resources, their spawning interrupts while larger secondary consumers are maintained later in the season by the succession wave, they maintain the eggs production. However, the growth potential of these newborns is very limited since the resources are lacking for small size classes. The eggs accumulate and those that didn't die by starvation or predation grow during the following good season, triggering the seasonal cohort. Thus, at high latitude, the model indirectly accounts for a capital like breeding strategy and generates a temporal decoupling between the energy acquired for reproduction and larval growth the following season. The implementation of capital spawning in the model would however lead to stronger seasonal cohorts since the mortality undergone by larvae during the bad season would be avoided by storing biomass in the reproduction buffer.

The simplification of reproduction in the model is likely to affect our results at high latitude. However, it doesn't put into question the interactions between the growth of cohorts and the succession wave.

4 Conclusion

We have used a trait-based community size-spectrum model to investigate the effects of seasonality in marine ecosystems. Compared to more usual biomass spectrum models (Benoît & Rochet (2004); Maury *et al.* (2007a); Blanchard *et al.* (2009)), the present trait-based formulation accounts for the diversity of life histories by distinguishing functional species on the basis of their maximal structural length. Our model captures the fact that a sardine and a juvenile tuna of the same size have very different egg productions and growth rates. Moreover, while other trait-based spectrum models have been developed (Andersen & Beyer (2006); Hartvig *et al.* (2011)), the present model is fully based on the DEB theory. It allows an explicit consideration of the environmentally driven reserve dynamics and a rigorous derivation of the inter-specific scaling rules that we use in the trait-based formulation.

The model suggests that two distinct mechanisms drive the biomass flux through the size-spectrum : the growth of cohorts on the one hand and biomass saltation from prey to predators on the other hand. The relative importance of these processes changes with latitude. The response of the community size-spectrum to environmental seasonality is therefore also latitude-dependent. Our study proposes an in-depth elucidation of the role and interaction of these processes involved in the propagation of environmental variability in marine ecosystems. Important questions remain and will be tackled in our future works. These include the following examples. Does seasonality affect the efficiency of the energy transfer from low trophic levels to the larger predators ? Are ecosystems reaching lower or higher levels of biomass when forced seasonally compared to ecosystems forced with constant mean values ? More generally, how disturbance affect productivity in marine ecosystems ?

Acknowledgment

This study was supported by the ANR project MACROES (MACRoscope for Oceanic Earth System ANR-09-CEP-003)

Appendix A : Parameters of the model

Variable	Designation	Unit	Value
Individual's DEB			
E / E^*	Energy of the reserve/ at equilibrium	J	–
V / L	Structural volume/length	cm^3/cm	$\begin{cases} V = (\delta L)^3 \\ \delta = 0.2275 \end{cases}$
V_m / L_m	Maximum structural volume/length	cm^3/cm	$V_m = (\delta L_m)^3$
V_p	Puberty structural volume	cm^3	$\begin{cases} V_p = \alpha_p V_m \\ \alpha_p = 0.125 \end{cases}$
$\{\dot{p}_{A_m}^{V_m}\}$	Maximum surface-specific assimilation rate	$J\ cm^{-2} d^{-1}$	$\begin{cases} \alpha_{\{\dot{p}_{Am}\}} V_m^{1/3} \\ \alpha_{\{\dot{p}_{Am}\}} = 31.25 \end{cases}$
$[E_m^{V_m}]$	Maximum reserve density	$J\ cm^{-3}$	$\begin{cases} \alpha_{[E_m]} V_m^{1/3} \\ \alpha_{[E_m]} = 312.5 \end{cases}$
ν	Energy conductance $\{\dot{p}_{A_m}^{V_m}\}/[E_m^{V_m}]$	$cm\ d^{-1}$	0.1
$[\dot{p}_M]$	Maintenance rate	$J\ m^{-3} d^{-1}$	25.
$[E_G]$	Volume specific cost of growth	$J\ cm^{-3}$	5691.
κ_X	Assimilation efficiency	–	0.8
κ	Energy fraction allocated to growth and maintenance	–	0.8
κ_R	Energy fraction of gonads turned into eggs	–	0.95
$\ddot{h}_a$	Ageing acceleration	d^{-2}	43. 10^{-8}
Community's biology			
C'	Specific searching rate of the functional response	$J\ d^{-1}$	3.5
D	Maximum mortality rate due to disease	d^{-1}	0.34
M_{egg}	Fraction of spawned eggs not fertilized	–	0.2
φ	Sex-ratio (Mean proportion of female)	–	0.5
d	Density of biomass	$g\ cm^{-3}$	1.
ψ	Energy content of biomass	$J\ g^{-1}$	4552.
Predation			
(ρ_1, ρ_2)	Mean mini/maxi ratio predator over prey lengths	–	(2.5, 10.)
(α_1, α_2)	Variability mini/maxi ratio predator over prey lengths	–	(5., 0.08)
Schooling			
β	Shape of the schooling probability function	–	2.
s_{cr}	Schooling probability threshold	m^{-6}	0.005
Environment			
ξ_{PP}	Primary production carrying capacity	$J\ m^{-3}$	–
T	Temperature	$^\circ K / ^\circ C$	$^\circ K =^\circ C + 273.15$
T_A	Mean Arrhenius temperature	$^\circ K$	5370.
T_{ref}	Reference temperature of biological parameters	$^\circ K$	293.15
Numerical parameters			
$[L_b, L^{max}]$	Consumers size range	cm	$[0.1, 200.]$
$[L_m^{min}, L_m^{max}]$	Species traits size range	cm	$[0.1, 200.]$
k_{V_m}	Number of trait discretizations	–	77
k_V	Number of volume discretizations	–	100
Δt	Time step	d	1

Appendix B : Indicators of the community biomass spectrum

We developed a set of indicators to investigate quantitatively how low trophic level's biomass and temperature impact the properties of ecosystems. These indicators are time dependent because of the unsteady nature of simulations.

On a log-log scale, the community spectrum $\xi_{L,t}$ is known to display a quasi-linear shape that can be characterized by its slope S_C, and its intercept (Fulton *et al.* (2004); Shin *et al.* (2005)). This last relates to the total energy ξ_{tot} in the modeled community.

$$\xi_{tot} = \int_{L_m} \int_{L} \xi_{L,t}^{L_m} dL dL_m \tag{2}$$

We can compute trophic levels extracting $D_{L_{Pr},L_{pr}}$, the fraction of prey of size L_{pr} in the diet of predators of size L_{Pr} :

$$TL_{L_{Pr}} = 1 + \sum_{L_{pr}} D_{L_{Pr},L_{pr}} TL_{L_{pr}} \tag{3}$$

While the size distribution characterizes the structure, the trait distribution of populations characterizes the diversity in the community. Every population spectrum $\xi_{L,t}^{L_m}$ in the range $[L_m^{min}, L_m^{max}]$ contributes to the community size-spectrum $\xi_{L,t}$. The biomass distribution can be used to derive the abundance distribution $N_{V,t}^{L_m}$, $\xi_{L,t}^{L_m} = (E^* + d\psi V) N_{V,t}^{L_m}$ where $E^* = f[E_m^{V_m}]$ is the reserve's energy at equilibrium, d the density of biomass, ψ the energy content of biomass and the structural volume $V = (\delta L)^3$. We compute the geometric mean species length from the abundance distributions :

$$\overline{L}_m = exp\left(\frac{\int_{L_m} \int_{L} ln(L_m) N_{L,t}^{L_m} dL dL_m}{\int_{L_m} \int_{L} N_{L,t}^{L_m} dL dL_m} \right) \tag{4}$$

We therefore use four indicators to characterize the community structure :

— ξ_{tot} (T1) : The total amount of energy in the modeled community.

— S_C (T2) : The community size-spectrum slope. It describes the relative abundance of small and large individuals in the community. It is usually assumed to be approximately constant with a value around -2 for an abundance spectrum function of size (Benoît & Rochet (2004); Andersen & Beyer (2006)).

— TL_{max} (T3) : The trophic level $TL_{L_{Pr}}$ of individuals in the larger size class sustained in the community. It characterizes the trophic chain length.

— $\overline{L}_m$ (T4) : The geometric mean of species maximum lengths. It determines the kind of species contributing to the community, small or large.

TABLE 1 – Summary of model's indicators. These are time dependent values, we extract the mean and variatiblity.

Eq.	Indicator	Equation
Structure		
T1	Total energy	$\xi_{tot} = \int_{L_m} \int_{L} \xi_{L,t}^{L_m} dL dL_m$
T2	Spectrum slope	S_C
T3	Maximum trophic level	$TL_{max} = max(TL_{L_{Pr}})$ with $TL_{L_{Pr}} = 1 + \sum_{L_{pr}} D_{L_{Pr},L_{pr}} TL_{L_{Pr}}$
T4	Mean population trait	$\overline{L}_m = exp\left(\frac{\int_{L_m} \int_{L} ln(L_m) N_{L,t}^{L_m} dL dL_m}{\int_{L_m} \int_{L} N_{L,t}^{L_m} dL dL_m} \right)$ with $N_{L,t}^{L_m} = \frac{\xi_{V,t}^{L_m}}{(E^* + d\psi V)}$

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Chapter 5

Simulation of the biomass distribution of epipelagic, mesopelagic and migratory fish communities in the global ocean using APECOSM-DIV

Simulation of the biomass distribution of epipelagic, mesopelagic and migratory trait-based fish communities in the global ocean using APECOSM-DIV.

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Abstract

The services provided by marine ecosystems in the global ocean are affected by anthropogenic environmental changes. Global ecosystem models become valuable tools in order to estimate their possible evolution. However, the representation of the role of biodiversity in these global ecosystem models is simplified. We present the APECOSM-DIV model, an ecosystem model for upper trophic levels based on the community biomass density size-spectrum theory. The model represents the biomass distribution in pelagic ecosystems adopting a trait-based approach to account for the functional role of species diversity. Species are only differentiated according to the maximum length individuals can theoretically reach at satiation. It neglects the role of taxonomic diversity but accounts for a key component of functional diversity in term of metabolism. The model is forced by physical and biogeochemical tridimensional fields from the NEMO-PISCES coupled model in order to compute a one year climatology of the tridimensional biomass distribution of epipelagic, mesopelagic and migratory communities in the global ocean. The climatology allows the computation of global estimates of the total fish biomass in the global ocean. Averaged in time and aggregated along a latitudinal transect, the characteristics of the three communities at different latitudes are described. These preliminary results must be seen as the initial steps of an ongoing effort to model mechanistically global marine ecosystems with trait-based representation of the role of biodiversity.

Keywords : High trophic level model ; Pelagic communities ; Marine ecosystem model ; Global ocean ; Biodiversity ; Trait based model ; Impact of the environment ; Climate change.

1 Introduction

Marine ecosystems in the global ocean provide essential services to humans. Most of them are affected by anthropogenic environmental changes, for instance through climate changes, fishing or pollution (Halpern *et al.* (2008)). Global environmental changes are expected to amplify in the coming years, with unknown effects on biodiversity (Munday *et al.* (2013)) and the important services that marine ecosystems provide. For example, the regulation of climate through the export of carbon to deep sea sediments (Smith *et al.* (2009)) or the provision of animal proteins to human societies (Brander (2007); Jennings & Brander (2010)). In order to estimate globally these impacts, and devise adaptation strategies, global marine ecosystem models are developed (Cheung *et al.* (2009); Jennings *et al.* (2008); Maury (2010); Christensen *et al.* (2015)).

These models account for all the components constituting marine ecosystems, including physics of the oceans, biogeochemistry and their living component. The different components are often represented independently, or coupled together in the most integrated approaches. While the physics and biogeochemistry have been modeled at the global scale for several decades, generic models of the living part of the oceans remain a challenge (Jennings & Brander (2010)). Different approaches exist, focusing on different organization levels from individuals to species to communities. For example, food web models represent marine ecosystems and their diversity with inter-connected species or functional groups compartments (Christensen *et al.* (2015)). Bioclimate envelope models correlate the distribution of species with key environmental factors (Cheung *et al.* (2009)). Size-based models extrapolate the biomass distribution of high trophic levels in marine ecosystems from the features of the low trophic levels (Jennings *et al.* (2008)). Furthermore, global size-spectrum models account for the dynamic of this biomass distribution across ecosystems from individual level physiological considerations (Maury (2010)).

Overall, these models provide precious insights on the evolution of the biomass and the structure of ecosystems in the global ocean (Cheung *et al.* (2010); Jennings & Collingridge (2015); Lefort *et al.* (2015); Le Mézo *et al.* (2016)). However, the effects of biological diversity are usually poorly accounted for in global ecosystem models, which are adopting either an aggregated functional groups structure (Maury (2010)) or explicitly accounted for assembling multitude of species (Christensen *et al.* (2015); Cheung *et al.* (2009)). While the specification of functional groups is a strong simplification, the explicit representation of species implies a large number of parameters that are obviously not equally known and associated to uncertainty ranges. A possible way forward may lie in trait-based approaches (Follows *et al.* (2007); Bruggeman & Kooijman (2007)), which substitute the explicit representation of species by the representation of their major functional traits.

Maximum length is a useful trait to differentiate the functional role of species. By species' maximum length, we mean the maximum length that an individual of a given species can theoretically reach at satiation. This trait can be used to differentiate the bioenergetic properties of individuals of same body length belonging to different species (Kooijman (2010)). It inspired the development of trait-based community size-spectrum models (Andersen & Beyer (2006); Hartvig *et al.* (2011); Maury & Poggiale (2013)). This category of models represents the size distribution of marine communities accounting for the functional role of species diversity. In this framework, a community is composed of a large number of functional species characterized by their maximum size. The community level distribution emerges from the sum of the species level distributions. The method presents the advantage of deriving the structure of communities from individuals' level bioenergetics, accounting for inter-specific diversity (Guiet *et al.* (2016b)). It is particularly adapted to represent the biomass flow over large spatio-temporal scales where taxonomic details are either irrelevant or unknown. Trait-based community size-spectrum models have already been used to study the response of marine ecosystems to resource variations, temperature or fishing pressure (Houle *et al.* (2012); Shephard *et al.* (2012); Guiet *et al.* (2016a)), in a stationary or dynamic environment (Guiet *et al.* (2016c)).

In this paper, we present the implementation of a trait-based community size spectrum model (Maury & Poggiale (2013); Guiet *et al.* (2016a)) in the spatially resolved environmentally-driven global ecosystem model, APECOSM (Maury (2010)). The resulting APECOSM-DIV model is forced by the coupled physic biogeochemistry model NEMO-PISCES (Aumont *et al.* (2015)) in order to produce a one year climatology of ecosystems' properties in the global ocean. This is the first attempt to represent the tridimensional dynamics of the biomass distribution in the global ocean with a spatially-explicit trait-

based community size-spectrum model. The model predicts the biomass distribution as well as the size and trait structure of three interactive fish communities : epipelagic, mesopelagic and migratory, which occupies the mesopelagic habitat during the day and migrates up to the epipelagic habitat at night. We first describe the main features of the model and then the general properties of the climatology. The model provides estimates of the total fish biomass in the global ocean. They are in the same magnitude than previous studies (Jennings & Collingridge (2015); Wilson *et al.* (2009); Tremblay-Boyer *et al.* (2011); Irigoien *et al.* (2014)). Averaged in time and aggregated along a latitudinal transect, the characteristics of the three modeled communities at different latitudes are described. In order to asses the role of the environment on the modeled community size-spectra, they are compared to an idealized study of the impact of environment on fish communities (Guiet *et al.* (2016a)). This simulation disregards the human impact on upper trophic levels and only represents the impact of environment on ecosystems' characteristics.

2 Method

2.1 Models

This paper analyzes a climatology of the biomass distribution at high trophic levels ($\xi_{HTL}(L, L_m)$) as a function of individuals' length L and species maximum length L_m, in the global ocean. For this purpose, we use the APECOSM-DIV model forced by physical and biogeochemical tridimensional fields from the NEMO-PISCES coupled model (Fig. 1).

NEMO : Ocean physics is computed by the NEMO model (Madec (2008)). To force APECOSM-DIV we use the zonal and meridional components of current velocity ($\overrightarrow{u}$, $\overrightarrow{v}$), which contribute to the transport of biological matter and temperature T, which impacts individual metabolism.

PISCES : Coupled with NEMO, the PISCES model (Aumont *et al.* (2015)) simulates the biogeochemical cycles of carbon and of the main nutrients (P, N, Fe, Si). It represents the spatio-temporal dynamic of low trophic levels in marine ecosystems and includes two sizes of phytoplankton (nanophytoplankton and diatoms), two sizes of zooplankton (microzooplankton and mesozooplankton) as well as two detritus compartments distinguished by their vertical sinking speed (small and large organic matter). To force APECOSM-DIV, we use the biomass of diatoms, microzooplankton, mezozooplankton and large organic matter. Altogether, these compartments serve as a source of food for higher trophic levels. From now on we will refer to it as low trophic levels biomass (ξ_{LTL}). Dioxygen concentration O_2 and light (photosynthetic available radiation PAR) are computed by PISCES. They are used in APECOSM-DIV for their role in the definition of habitat.

APECOSM : The Apex Predators ECOsystem Model (Maury (2010)) represents biomass fluxes from small ($L_{min} = 0.1$ cm) to large heterotrophic consumers ($L_{max} = 200$ cm). It is based on the biomass size-spectrum theory (Sheldon *et al.* (1972); Kerr & Dickie (2001); Maury *et al.* (2007)). In APECOSM, biomass fluxes through the ecosystem are controlled by size-selective predation. Small individuals in the modeled communities feed on the low trophic levels' biomass pool ξ_{LTL} while larger individuals feed on the consumers community itself according to a selectivity function of the predator-prey size ratio. Predation results in a loss of energy for preyed size classes and a gain for predating ones. Preyed biomass fuels growth, reproduction and maintenance needs of predators. At any given spatio-temporal position (x, y, z, t), low trophic levels $\xi_{LTL}(x, y, z, t)$, temperature $T(x, y, z, t)$ and light $PAR(x, y, z, t)$ influence the dynamics of consumer organisms $\xi_{HTL}(L, x, y, z, t)$. In APECOSM, three distinct communities interact along the water column (Maury (2010); Maury *et al.* (in prep.)) : epipelagic, migratory and mesopelagic. These communities are defined according to their vertical behavior. The epipelagic community is mainly found above the thermocline and in the euphotic layer during the day. The mesopelagic community lies below the euphotic layer, roughly between 200 m and 1000 m depth where its development is sustained by migratory organisms and particulate organic matter. The migratory community stays in dark waters (roughly between 200 and 1000 m) during the day and migrates upward to feed on the community during the night. The three communities are distributed according to a vertical advection-diffusion process depending on their specific habitat preferences ($f(PAR, O_2, T, \xi_{LTL})$). In the model, their trophic interactions are constrained by their vertical co-occurence. Both marine currents ($\overrightarrow{u}$, $\overrightarrow{v}$), passive transport, and length-dependent swimming, active transport, have an impact on the biomass spatial distribution.

APECOSM-DIV : APECOSM rests on a simplified trait-based parametrization to account for the taxonomic diversity of communities (Maury *et al.* (in prep.)). In particular, the distribution of traits is supposed to be in equilibrium with local environmental conditions anywhere in space and time, thus neglecting the complex delayed effects of environmental variability on community structure such as succession or cohorts propagation (Guiet *et al.* (2016b)). Also, the trait-based parametrization used in APECOSM does not allow for the spatial transport of the trait structure of communities. APECOSM-DIV extends APECOSM with the introduction of explicit trait-defined species (Fig. 1). It represents the biomass flow from small ($L_{min} = 0.1$ cm) to large individuals ($L_{max} = L_m$ cm) along species spectra characterized by maximum species lengths $L_m \in [0.1, 200]$ cm. Based on the trait-based size-spectrum model presented in Maury & Poggiale (2013), the approach still neglects the role of taxonomic diversity but accounts for a key component of functional diversity in term of metabolism. In the model, two individuals of same size but belonging to different species grow at different rates or invest a different

share of their food into reproduction. In the model, opportunistic size-selective predation still controls the biomass flux through size-structured trait defined species. The community level size distribution of biomass ($\xi_{HTL}(L)$) is the integral along the trait dimension of species contributions ($\xi_{HTL}(L, L_m)$). APECOSM-DIV embeds the trait-based size-spectrum model developed in Maury & Poggiale (2013) and calibrated in Guiet *et al.* (2016a) into APECOSM (Maury (2010)). Note that this formulation is fully based on the Dynamic Energy Budget theory (DEB, see Kooijman (2010)) and such improves the mechanistic consistency of APECOSM. In the DEB theory, ingested food is stored in reserves before being allocated to growth, maintenance and reproduction. APECOSM-DIV uses a simplified representation of the dynamics of reserves based on time scales separation (Maury & Poggiale (2013)). APECOSM-DIV is exactly similar to APECOSM in terms of the behavioral distinction between epipelagic, mesopelagic and migratory communities and their habitat-based horizontal and vertical movements.

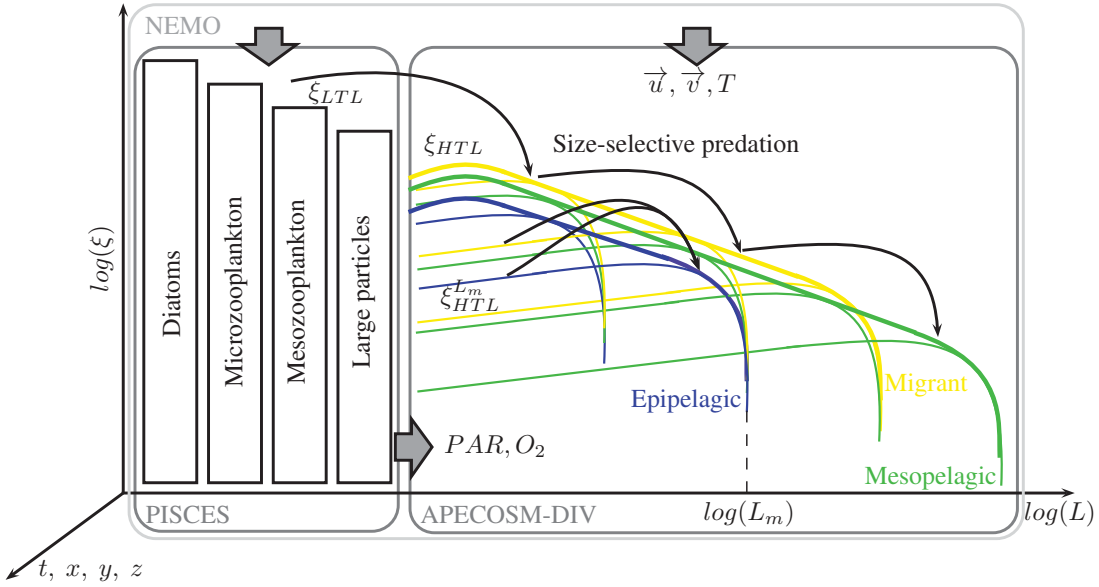

FIGURE 1 – Schematic representation of the size-structured biomass fluxes between the biogeochemical PISCES model (Aumont *et al.* (2015)) and APECOSM-DIV in a physical environment simulated with NEMO (Madec (2008)). Based on the schematic representation of APECOSM (Maury (2010)).

2.2 Simulation

In the present study, we use APECOSM-DIV in an « offline » configuration, i.e. it runs independently, forced by outputs of a NEMO-PISCES coupled dynamical simulation. The feedback of the upper trophic levels simulated by APECOSM-DIV on the lower trophic levels simulated by PISCES are therefore not represented. In particular, the predation pressure of upper trophic levels feeding on the resource ξ_{LTL} is not considered.

A one year climatology is produced for the global ocean on an ORCA2 grid Madec (2008). This means that our model has a mean spatial resolution of $2^o \times 2^o cos\phi$ (where ϕ is the latitude) with an enhanced resolution of 0.5^o at the equator. Interactions in the water column are solved on 37 vertical levels with a resolution decreasing with depth, from 10 m intervals over the first 100 m to 125 m intervals up to 1000 m. The model disregards the biomass below 1000 m.

APECOSM-DIV is parametrized using information at the individual, species and community levels. The parameters are tuned to represent generic fish communities and allow the full range of community spectra from collapsed to saturated over the full range of environmental conditions encountered in the global ocean (see Guiet *et al.* (2016a)). The three communities share the same parameters. They are only differentiated by their habitat preferences. The community size spectrum includes 100 size classes and 6 trait-defined species categories.

2.3 Analysis

Our simulation is a first attempt to predict the biomass distribution of epipelagic, mesopelagic and migratory communities in the global ocean, using a trait-based size-spectrum model accounting for the role of functional species characterized by their maximum length. We discuss these results knowing that improvements are still required. Although the model outputs monthly fields, all analysis presented here were performed on yearly means.

We first analyze the spatial distributions of predicted biomass. Biomass distributions are computed per community by integrating over individuals' size and maximum species length on a 1^o grid interpolation of the global ocean :

$$\xi_{HTL} = \int_{L^{min}}^{L^{max}} \int_{L_m^{min}}^{L_m^{max}} \xi_{HTL}(L, L_m) dL \; dL_m \tag{1}$$

The currency used in the model is energy density ξ_{HTL} per water volume, in J/m^3. For comparison with the predicted biomass distribution at lower trophic levels, it is converted in gC/m^3 dividing the predicted values by the value of biomass free energy, i.e. 474.6 $kJ/Cmol$ (Kooijman (2010); Maury *et al.* (2007)), and multiplying by the molar mass of carbon, i.e. 12 g/mol. The distribution along the water column is integrated to draw global biomass maps in gC/m^2. Furthermore, we also compute a global estimate of the total biomass integrated over the global ocean. The energy content per water volume, in J/m^3, is converted into wet weight dividing by the energy content of wet biomass, i.e. 4552 J/g (Guiet *et al.* (2016a)). Integrated spatially over the water column and over the globe, the model provides a global estimate of fish biomass, expressed in tons. In order to compare our global biomass estimates to other results, we extract the contribution of each communities. We also compute separately the contribution of ecosystems at low latitudes ($< \pm 40^o$) and high latitudes ($> \pm 40^o$). We finally extract the total biomass estimate over distinct size ranges. We calculate biomass over all the spectrum, $L \in [0.1, 200]$ cm, i.e. for individuals weighting between $w \in [1.5\ 10^{-5}\ g,\ 120kg]$ (because $w = d(\delta L)^3$, with $d = 1\ g/cm^3$ and $\delta = 0.2466$ a shape coefficient, see Guiet *et al.* (2016a)) and over a reduced range of the spectrum, $L \in [18.8, 87.4]$ cm, i.e. $w \in [100\ g, 10\ kg]$. We also calculate the full consumers' biomass, i.e. the full spectrum biomass plus the biomass of microzooplankton and mezozooplankton from the PISCES forcing, i.e. $L \in [0.002, 200.]$ cm.

In a second step, we analyze the global features of the modeled communities size-spectra, at each spatial position (x, y). The community size-spectrum displays a quasi-linear shape characterized by its slope λ (Fulton *et al.* (2004); Shin *et al.* (2005)). The slopes captures the relative abundance of small and large individuals in the community. It accounts for the efficiency of the energy transfer from small to large individuals. We also calculate the geometric mean maximum species length per community $\overline{L}_m$:

$$\overline{L}_m = exp\left(\frac{\int_{L_m} \int_{L} ln(L_m) N_{HTL}(L, L_m) dL dL_m}{\int_{L_m} \int_{L} N_{HTL}(L, L_m) dL dL_m} \right) \tag{2}$$

where $N_{HTL}(L, L_m)$ represents the abundance of individuals calculated from the biomass $\xi_{HTL}(L, L_m)$ (see Maury & Poggiale (2013); Guiet *et al.* (2016a)). The mean maximum species length characterizes the taxonomic structure of the community in terms of species size. In order to simplify the study of these features for the three communities in the global ocean, we focus on large scale patterns. The slopes λ and mean maximum species lengths $\overline{L}_m$ are aggregated along a mean North/South planetary section. In different ecosystems, at different latitudes, it reveals large scales differences between the global properties of communities.

3 Results

3.1 Biomass estimates

The APECOSM-DIV model provides estimates of the total biomass in the three communities. It provides global values of the biomass (Tab. 1) as well as estimates of the spatial distribution of this biomass (Fig. 2).

The total global biomass of consumers (including zooplankton) of body length ranging from 0.002 cm to 200 cm is estimated to be 9.4×10^9 tons with 3.7×10^9 tons of fish in size class 0.1 cm to 200 cm and just over $1. \times 10^9$ tons of fish in size class 18.8 cm to 87.4 cm (Tab. 1). This biomass is distributed with 2/3 in low latitudes while 1/3 is in high latitudes. Globally, the biomass in the epipelagic community represents a small portion, about 1%, while the migratory community represents about 25%. The mesopelagic community in deep cold waters represents the large majority of the biomass with about 3/4 of the total biomass estimates.

In high latitudes ($> \pm 40^o$), the cold and rich surface waters sustain a comparatively higher biomass of epipelagic species (3.4% of total), while the migratory community is depleted (only 6%) and the mesopelagic community still dominates (about 90%), feeding on sinking particles. In low latitudes ($< \pm 40^o$), the migratory and mesopelagic communities are both significantly high, with respectively about 30% and 70% of the total biomass. They maintain high levels of biomass despite the poorer environment.

The total biomass density distribution in gC/m^2 (Fig. 2) confirms the global trends estimated from the aggregated values (Tab. 1). In particular, the epipelagic community is neglectable compared to the migratory and the most abundant mesopelagic communities. Furthermore, the biomass of the epipelagic community is relative higher towards the poles. Finally, there is a higher relative biomass of migratory organism in equatorial waters and the mesopelagic biomass is evenly distributed globally. Looking at the regional patterns, the oligotrophic gyres in all oceans are clearly visible on the epipelagic community with almost no biomass. The food available to consumers is not sufficient to balance the increased dissipation due to warm waters. The migratory community that stay in cold waters during the day balances the dissipation. It therefore supports a higher biomass in the gyres. Finally, the mesopelagic community also accesses insufficient food and the gyres are particularly visible in the Pacific and South Atlantic. When compared to the resource distribution ξ_{LTL}, we observe mismatches of the biomass distribution, especially at higher trophic levels. This is particularly clear along the equatorial upwelling in the Pacific where the pic of biomass in the epipelagic and migratory communities is transported away from the pic of resource both sides of the equator. We observe the same phenomenon in western boundary currents where the biomass at high trophic levels pics far away from the low trophic level pic along the coast. The western side of the Pacific accumulates biomass despite the low trophic level resources compared to the eastern side. This relocation process is not visible deeper in the mesopelagic community. This decoupling induced by oceanic currents illustrates the importance of horizontal transport in the model. Finally, in polar waters all communities present low levels of biomass despite the high low trophic level's biomass. The representation of high latitudes ecosystems with the model is discussed in the last section.

Besides the global estimates of total fish biomass and the different spatial patterns between communities, we computed the biomass for different sizes ranges in order to compare our estimates to other results (Jennings *et al.* (2008); Wilson *et al.* (2009); Tremblay-Boyer *et al.* (2011); Irigoien *et al.* (2014); Jennings & Collingridge (2015)). The relative contribution of each community to the total biomass calculated for the full size range ($[0.1, 200]$ cm) is very similar when calculated for the reduced size range ($[18.8, 87.4]$ cm), except a slightly reduced proportion of epipelagic individuals. The epipelagic community is globally constituted of smaller species than the migratory and mesopelagic communities. When computing the total biomass for the reduced size range, the truncation of the small sizes induces a higher relative diminution of biomass for the epipelagic community.

3.2 Latitudinal section

The slopes λ and mean species length $\overline{L}_m$ provide information about the biomass distribution along respectively the size L and the species L_m dimensions. It complements biomass estimates to get a more complete picture of the spectrum characteristics in different regions of the global ocean. In order to simplify the analysis and to compare to idealized simulations (Guiet *et al.* (2016a)), we only look at the

TABLE 1 – Biomass estimates of the epipelagic (EP), migratory (MI) and mesopelagic (ME) communities : for the full biomass distribution ξ_{HTL} ; for the biomass distribution of individuals in the size range $[18.8, 87.4]$ cm ; for all consumers in upper trophic levels ξ_{HTL} and lower trophic levels (contribution of zooplankton in ξ_{LTL}). The biomass estimates are in the global ocean, at low latitudes (between 40^oS and 40^oN), at high latitudes (below 40^oS above 40^oN).

Size ranges	**Global ocean** ($\times 10^9$ **T**)			**Low latitudes** ($\times 10^9$ **T**)			**High latitudes** ($\times 10^9$ **T**)		
	EP	MI	ME	EP	MI	ME	EP	MI	ME
ξ_{HTL}	0.068	0.84	2.8	0.04	0.79	2.0	0.029	0.05	0.78
$L \in [0.1, 200]$ cm	(1.8%)	(23%)	(75.3%)	(1.3%)	(28%)	(70.7%)	(3.4%)	(6%)	(90.6%)
ξ_{HTL}	0.006	0.24	0.82	0.003	0.22	0.6	0.003	0.017	0.22
$L \in [18.8, 87.4]$ cm	(0.5%)	(22.5%)	(77%)	(0.4%)	(26.7%)	(72.9%)	(1.3%)	(7%)	(91.7%)
$\xi_{HTL} + \xi_{LTL}$		9.4			6.33			3.16	
$L \in [0.002, 200]$ cm									

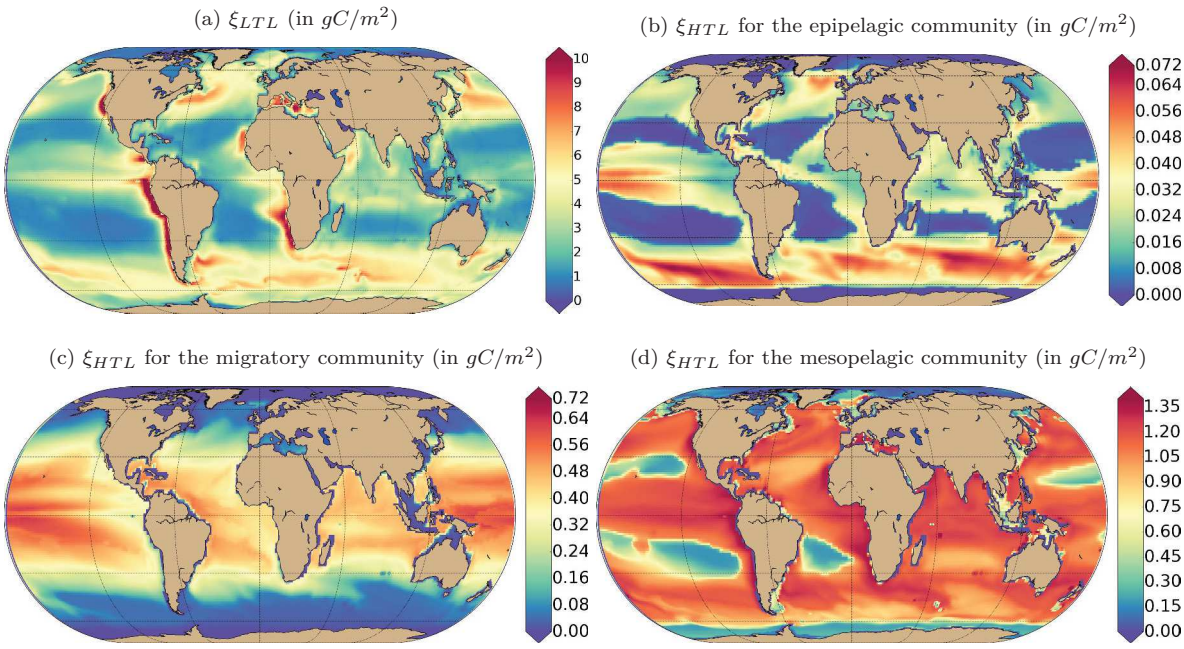

FIGURE 2 – Estimates of the biomass distribution accross oceans, (a) at low trophic levels (from NEMO-PISCES), (b) in the epipelagic community, (c) the migratory community and (d) the mesopelagic community (from APECOSM-DIV).

latitudinal differences between the three communities along a North/South planetary transect (Fig. 3). We look at the properties of the modeled ecosystems in high latitudes (around $> \pm 45^o$), mid-latitudes (between 45^o and 35^o) and low latitudes ($< \pm 35^o$).

In high latitudes, the rich and cold ecosystems are constituted of epipelagic and migratory communities dominated by small species while the mesopelagic community is dominated by large species (Fig. 3). In this region, the spectrum of the mesopelagic community is close to the theoretical value $\lambda = -3$ while both epipelagic and migratory communities are steeper. Guiet *et al.* (2016a) described the impact of the environment on the features of the community size-spectrum and identified four distinct domains for distinct levels of low trophic level biomass and temperature, namely collapsed, regular, transition and collapse domains (see their Fig. 6). In high latitudes, the epipelagic and migratory communities show features of communities in the collapsed or regular domains while the mesopelagic community is in the saturation domain (see summary Tab. 2). The epipelagic and migratory communities are dominated by small species of primary consumers while the mesopelagic community supports larger secondary consumers feeding on the primary consumers.

In mid-latitudes (between 45^o and 35^o), while the epipelagic community remains dominated by small primary consumers, the migratory community supports larger and larger individuals and the community slope becomes more and more soft. It is consistent with the development of secondary consumers in the migratory community. The epipelagic organisms remain in the collapsed or regular domain while the migratory individuals tend to show characteristics of communities in the transition domain (Tab. 2). Like at high latitude, the mesopelagic community remains constant and seems in the saturation domain.

In low latitudes ($< \pm 35^o$), the epipelagic community exhibits softer slopes while still dominated by small species. Compared to the idealized simulations (cf Fig. 6 in Guiet *et al.* (2016a)) this change of features indicates a shift toward fully collapsed communities. In the epipelagic community, only small species are sustained. Conversely, the mean species length of the migratory community reaches a plateau while the slope decreases slightly. These features indicate a saturated community with slight structural changes due to intra-community predation : larger species deplete the smaller ones to their benefit. Finally the mesopelagic community still presents the same constant properties of large species and shallow slopes. The mesopelagic community seems fully developed and in the saturation domain at all latitudes.

Large scale environmental features, in term of food access and temperature, constrain the latitude-dependent global characteristics of the different communities. In a nutshell, with decreasing latitude, the warming of surface waters and decrease in food abundance shift the epipelagic community from a regular state toward a collapsed domain. Conversely, with decreasing latitude the migratory community shifts from the collapsed/regular domain toward transitions and saturation domains. Finally, the mesopelagic community seems fully developed and saturated at all latitudes.

TABLE 2 – Domains associated to the community size-spectrum of the epipelagic (EP), migratory (MI) and mesopelagic (ME) communities according to the classification detailed in Guiet *et al.* (2016a) : collapse, regular, transition or saturation. The domains change between high, mid- and low latitudes.

Latitudes	EP	MI	ME
high	collapse/regular	regular	saturation
mid-	collapse/regular	transition	saturation
low	collapse	saturation	saturation

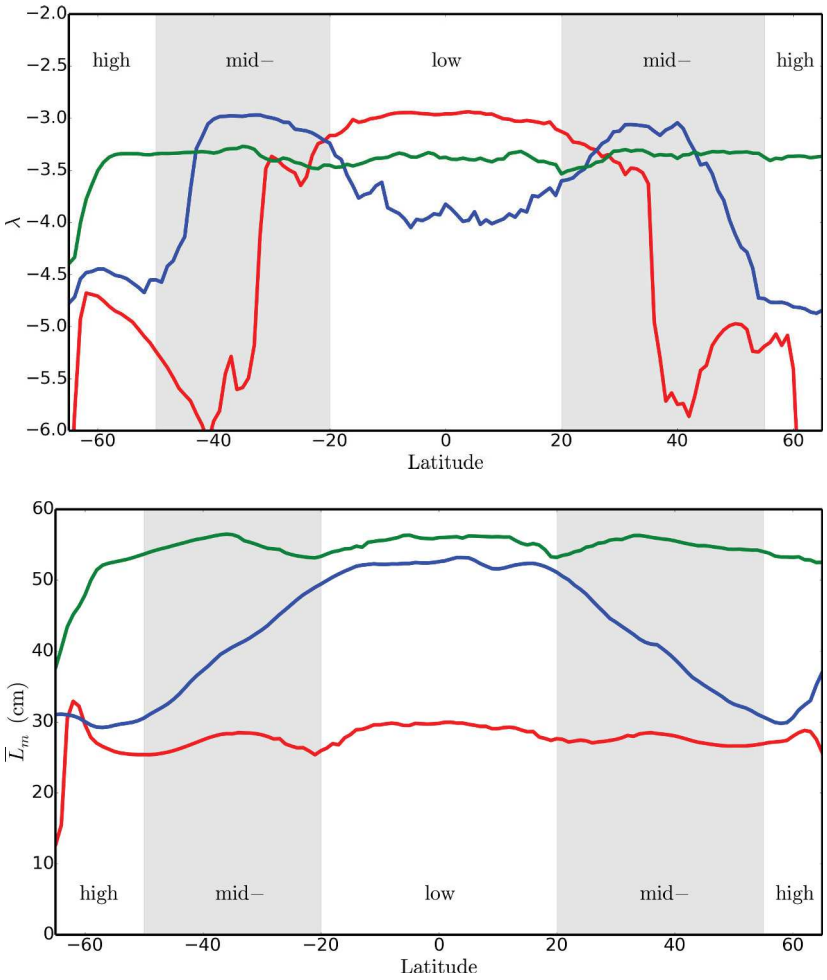

FIGURE 3 – Features of the community size-spectrum for epipelagic (red), mesopelagic (green) and migratory communities (blue) along a North/South planetary transect : top, distributions of slopes λ ; bottom, distributions of mean species lengths L_m.

4 Discussion

4.1 Biomass estimates

The model provides gross estimates of the total biomass in marine ecosystems. They fall into the same range of values than previously obtained using other approaches. For instance, in the range $w \in [100\ g, 10\ kg]$, it provides an estimate of 1.07 10^9 tons, a value consistent with Jennings & Collingridge (2015) who found a median biomass of 1.6 10^9 tons, with 50% uncertainty intervals of 0.6 10^9 to 3.5 10^9 tons. The estimate of Jennings & Collingridge (2015) is also determined from a method based on the properties of the size-spectrum. It predicts the total biomass in most regions of the global ocean from remote sensing data of resource and temperature (Jennings *et al.* (2008)). Similar estimates are therefore not surprising, they mainly indicate that both methods are based on consistent resource estimates and that our model properly accounts for the regularity of the biomass distribution from low to high trophic levels. Note that the global biomass estimates in Jennings & Collingridge (2015) are also compared to other formulations and are consistent with estimation of compartment based methods (Wilson *et al.* (2009); Tremblay-Boyer *et al.* (2011)). We don't explicitly discuss these values since they consider the biomass distribution on a larger size range than reproduced with the present model, but they are coherent with our results.

However, recent estimates suggest higher levels of total biomass in oceans. For instance, extrapolating acoustic observations of mesopelagic fishes in 40^o S to 40^o N region, Irigoien *et al.* (2014) proposes a global biomass estimate between 11. 10^9 and 15. 10^9 tons. Irigoien *et al.* (2014) also proposes model estimations between 2.3 10^9 and 71.2 10^9 tons for mesopelagic fishes only. Our model suggests that 2. 10^9 tons of mesopelagic fish are in the body length range $L \in [0.1, 200]$ cm and 0.6 10^9 tons for the range $L \in [18.8, 87.4]$ cm, or respectively 2.79 10^9 and 0.83 10^9 tons if we count the migratory community as part of the mesopelagic community. It is at best close from the lower limit estimated in (Irigoien *et al.* (2014)) or about one order of magnitude less if we consider their upper boundary. However, looking at the relative biomass of each community, the dominance of mesopelagic organisms and the small proportion of epipelagic fishes is consistent with their observations. The APECOSM-DIV model has the advantage of representing explicitly the mesopelagic community in its environment. Improving the mesopelagic biomass estimates may represent a first step for a calibration of the spatial simulation.

The spatial distribution of biomass for the three communities in the global ocean grossly matches the large scale patterns of low trophic level resource distribution for the epipelagic and mesopelagic communities, the later being more spread because of more constant conditions in deep waters. The migratory community also matches the resource but more toward low latitudes. However, a surprising result is a higher biomass toward low latitudes (2/3 in the area from 40^o S to 40^o N) while other methods conclude the opposite : higher biomass in the rich cold ecosystems at high latitudes (Jennings & Collingridge (2015)). Improvements of our predictions might be necessary in high latitudes, especially regarding the representation of day/night cycles that drive feeding. In polar ecosystems, the long nights in winter might cause excessive loss and dissipation since the epipelagic community is parametrized to only feed during the day. An excessive mortality of the epipelagic community during winter might explain our low biomass estimates in high latitudes but more investigations are necessary.

4.2 Latitudinal transect

At distinct latitudes, for each community, the features of the biomass size-spectra allow the classification of marine ecosystems into four domains : collapse, regular, transition or saturation (Tab. 2).

The predicted properties of the three communities (Fig. 3) are difficult to confirm with empirical data. Indeed, while information about low trophic levels can be derived from satellite remote sensing and while fisheries data provide information about top predator species, mid-trophic levels are very poorly sampled. Like for any global marine ecosystem model, large programs such as acoustic observations of pelagic ecosystems (Handegard *et al.* (2013)) are needed for a better verification.

However, the mechanistic bases of APECOSM-DIV helps to better understand the functioning of large scale marine ecosystems as well as their sensitivity to environmental perturbations. For instance, according to Guiet *et al.* (2016a), the distinct structural domains that fish communities can exhibit correspond to distinct sensitivities to environmental perturbations. The most sensitive domains are the

collapse and transition domains, then the regular domain, while the saturation domain corresponds to insensitive ecosystems. Thus, the most abundant mesopelagic community, which we predict to be globally in the saturation domain, is insensitive to variations of the environment. Conversely, the epipelagic community, which we predict to be globally in the regular and collapsed domains, is strongly affected by environmental perturbations. Low latitude ecosystems are particularly sensitive. The migratory community, which we predict to globally belong to the regular, transition and saturation domains, will also be affected by variations of the environment, particularly in high to mid-latitudes.

Our results and assumptions about the latitude-dependent sensitivity of global marine ecosystem are still preliminary. They must be seen as the initial steps of an ongoing effort to model mechanistically global marine ecosystems with a trait-based community size-spectrum model. A lot remains necessary to improve and interpret the predictions of APECOSM-DIV. For instance, our first simulation failed to reproduce the empirical Bergmann's rule (Fisher *et al.* (2010)), namely the fact that mean species length in fish communities increases with increasing latitude, which was reproduced in the idealized simulations that we realized with a simplified version of the model (Guiet *et al.* (2016a)). The problem requires a finer tuning of the parameters. Indeed, the epipelagic community shifts from regular to collapsed domains when latitude decreases. A modification of the half saturation constant in the model (see Maury & Poggiale (2013); Guiet *et al.* (2016a)) would allow to change the response of the community to reproduce Bergmann's rule, at least in the epipelagic community. More analysis and tuning are necessary, which were not possible within this thesis framework given the computation time required to run the model.

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Chapter 6

Conclusion and perspectives

6.1 A new model for global marine ecosystems

In this thesis, we describe several steps leading to the implementation of a mechanistic model of the spatio-temporal dynamics of epipelagic, mesopelagic and migratory fish communities in the global ocean. Based on the community size-spectrum theory [38, 93], the model allows the representation of the biomass flow from small (0.1 cm) to large individuals (200 cm) in fish communities. Inspired by a trait-based representation of species diversity [48, 54, 55] and fully consistent with the DEB theory [56], the model allows the consideration of the functional role of biodiversity in a mechanistic way. Biodiversity is introduced by differentiating species according to their maximum structural length which is supposed to be continuous over the species size range $[0.1, 200]$ cm. The model represents the tridimensional interactions between communities in the global ocean.

This approach is novel in the landscape of global marine ecosystem models. It provides the first representation of interactive size and trait structured fish communities in a tridimensional environmentally forced setup. It is helpful to understand how the environment is shaping the diversity of marine communities at the planetary scale and, conversely, how diversity influences the response of marine ecosystems to the environment. This model in complementary to global food web models which represent ecosystems as an accumulation of species or functional groups [29]. It disregards the explicit taxonomic structure but accounts for the functional role of species diversity, without prescribing ecosystems' structure. This model is also complementary to bio-climate envelope models which project species spatial occurrence based on their environmental preferences [68]. This model disregards explicit taxonomic diversity, but it can project the evolution of marine ecosystems' structure in a changing climate. For instance, it reproduces changes in mean species length or changes in the efficiency of the energy transfer from small to large individuals in ecosystems. However, the model is not appropriate when the species

identity needs to be considered explicitly.

Community biomass size-spectrum models are already implemented to represent large scale ecosystems. They have been used to investigate the impact of climate change and exploitation on the global fish production in large marine ecosystems [28, 62]. They have been applied coupled with climate models to project the impact of climate change on the structure of global pelagic communities [63], or to analyze the climate-driven variability of marine ecosystems at basin-scale [92]. **However, the present formulation is the first one to represent the biomass distribution in global marine ecosystems accounting for the functional role of species diversity in a mechanistic and dynamic way.**

6.2 The local spectrum

In this thesis, the "static and dynamic" properties of the community size-spectrum are adimensionally investigated before implementing the global marine ecosystem model. The impact of the environment on modeled communities is studied to better understand the trait-based community size-spectrum model. Variations of the low trophic levels resources and variations of the temperature are considered. However, other aspects of community size-spectrum models are not fully addressed and would deserve specific analysis. They are summarized by Andersen et al. (2015) [69] as five categories of challenges and open issues in size-spectrum modeling: (1) density dependence, (2) life history traits and trade-offs, (3) calibration procedure, (4) closure of the community spectrum at large sizes and (5) numerical implementation. **Numerous progresses in the understanding of the community size-spectrum are still ongoing and might affect our results or lead to potential new developments.**

1. **First, food web models require some form of density dependent regulation to avoid unlimited population growth, spurious predator-prey oscillations or competitive exclusion.** Density dependence can be introduced in various ways [69]. Here, we assume that schooling is density-dependent and controls the availability of prey to predators [55, 70]. Without this assumption, small species are fully depleted by the large species in the community and spurious chaotic oscillations propagate in the community. Schooling allows the coexistence of species in the community and enables realistic results based on clear ecological processes. However, **the solutions of the model are probably dependent on the type of density-dependence introduced and the present results must therefore be seen as conditional to the schooling hypothesis.** For the sake of generality, other density dependent regulation processes could be tested in the model. For example, Hartvig et al. (2011) [54] developed a trait-based community size-spectrum model with a random species-specific interaction matrix linking

trait-defined species in a density-dependent way.

2. **Second, trait-based size-spectrum models assume that the most important trait is species' maximum length [54, 55]. However, many other traits characterize fish communities.** Thus the model could also account for other traits, for example differentiating reproduction strategies [71], activity traits to distinguish sedentary from active species or traits related to habitat preferences [72], like in APECOSM-DIV that differentiates three communities on the basis of their vertical habitat preference. The addition of new traits in the model would add complexity and limit the generality of the model, which is one of its main quality. However, more traits differentiation is a way to allow coexistence in species-rich size structured communities [94]. **Another possible development of the model related to traits concerns the distribution of the species maximum length along the trait dimension. The present formulation is based on the discretization of a continuous distribution, which accounts for an "infinite species diversity".** Compared to realistic food webs where the distribution of species is discontinuous, this continuous definition is a theoretical limit. In this perspective, Zhang et al. (2014) [72] use a simplified size-based food web model and show that the maximum trophic level reached in communities depends on the species richness, the upper limit being the solution of the "infinite diversity" model. The "infinite species diversity" hypothesis allows a practical simplification. It is likely valid over large spatial scales where a large number of species co-occur such as the global scale under study here.

3. **Third, while community size-spectrum models have been often used for theoretical studies with rough parameter estimates, the trait-based formulation allows using species data for parametrization.** Size-spectrum based food web models can even be developed to represent the biomass flow in particular ecosystems on local to regional scale, like the North Sea [95]. **In the present global approach, a generic parameterization for fish communities is selected.** It includes 28 parameters. It attributes local and regional differences of community structure to the sole impact of the environment and trade-offs between trait-defined species spectra. Nevertheless, while the individual level DEB parameters are supported empirically, the parametrization of the size-selective predation curves is more prone to critics. They are parametrized to reproduce empirical stomach contents but they only allow the development of primary and secondary consumers. The observed response to the environment of the "static and dynamic" community size-spectra is tightly linked to this tri-trophic structure. But what would happen with tertiary and even quaternary consumers ? Like in the case of the tri-trophic system, indirect effects on the slope of the community spectrum and the productivity of communities in different environments are expected. The

present results should therefore be reexamined in the case of longer trophic chain length.

4. **Fourth, while trait-based community size-spectrum models rely on few core processes to represent the biomass flow from small to large individuals, the representation of additional processes might impact the predictions of the models.** For example, Andersen et al. (2015) [69] underlines the need to understand theoretically the processes closing the community spectrum at large body sizes. Here, an arbitrary maximum species length $L_m = 200$ cm is selected and ageing mortality avoids the superabundance of large individuals. Both are determined mechanistically with the dynamic energy budget theory [56]. Reproduction also requires attention. Here it is represented by a constant flux of energy reinvested at the base of the spectrum. However, in seasonal ecosystems, recruitment success depends on species' ability to reproduce seasonally, for example to optimize food access to newborns [59, 71]. The consideration of discontinuous reproduction in trait-based community spectrum models is especially important to study the impact of environmental variability on communities. Environmental perturbations can induce mismatches between newborns and optimum environmental conditions, which affect the recruitment success [73]. Accounting explicitly for these cycles in our model would require the reserve and the reproduction buffer to be explicit. Both are in the DEB theory [56] but their representation has been simplified here because of the computational constraints of the global tridimensional implementation [55].
5. **Fifth, the last issue of size-spectrum models identified is their numerical implementation.** The model developed in this thesis has been carefully implemented numerically to ensure biomass conservation from individuals to species to communities (see appendix for details). Moreover it has been implemented with a finite volume approximation of the biomass flux along individuals' size, with piecewise linear reconstruction and slope limiter, MUSCL [74]. It provides less diffusive solutions than the standard semi-implicit upwind scheme at a reasonable computing cost. However, higher order schemes could be implemented to increase the confidence in the model predictions.

In addition to the five aforementioned categories, a sixth challenge is noteworthy. It corresponds to the challenge of properly representing the impacts of the environment on the trait-based community size-spectra. The first issue is the sensitivity to temperature. As described Chapter 3, individualss metabolism, handling time and attack rate follow different scaling rules with temperature [15, 96]. The response of fish communities to temperature changes with the dependence of these processes to temperature. The model would benefit from a better understanding of the scaling of these processes, especially handling time and attack rate. Regarding the impact of low

trophic levels resources, the pool of food supporting the community size spectrum is often represented by a resource spectrum. Its intercept is well correlated to the community spectrum in upper trophic levels. However, the slope of this spectrum, which influences the availability of low trophic level food to predators is overlooked. Changing the slope of the resource spectrum would directly affect primary consumers and the energy flow to the community size-spectrum. The present model could be used to investigate this effect. Finally, we haven't considered other environmental stressors such as oxygen or pH, despite their direct impact on individuals' physiology. Integrating their effect is needed to consistently address global changes in the ocean.

In summary, in this thesis a trait based community size-spectrum model has been implemented to investigate the impact of environment on the structure of fish communities. The model allows the identification of a multi-domain dependence of the community spectrum to stationary resources and temperature gradients (Chapter 3). Studied with seasonally varying forcings, the model allows the identification of the different processes responsible for the biomass flux through the spectrum (Chapter 4). **These results rely on assumptions and choices. Here six potential avenues to improve the model and maybe gain a better understanding of the impact of the environment on marine communities are listed.**

6.3 The global simulation

The model has been implemented in the tridimensional global ecosystem model APECOSM [27]. The resulting APECOSM-DIV model models mechanistically the biomass flow from small to large individuals' sizes for a continum of small to large species. It solves the spatial distribution of communities as well as the interactions along the water column between epipelagic, mesopelagic and migratory communities. One of the main characteristics of this model is that the structure of regional ecosystems is not prescribed *a priori* and emerges form the interactions of the generic structure of the model with the environment. **Many challenges are still associated with this model.**

The verification of its predictions is a major issue. Although the local simulations of the community size-spectrum are not formally assessed against empirical observations, the understanding of the mechanisms leading to the features of the community size-spectrum allows confidence in the results. Things are more difficult at the global scale because of the additional complexity induced by the interactions between communities as well as the spatial interactions and transport. An example is the modeling of Bergmann's rule along a latitudinal transect, namely the empirical observation that the proportion of larger species and larger individuals of the same species increases with latitude [97]. This pattern is reproduced with the adimensional simulations. However, the global simulation doesn't reproduce it. An important work remains to understand the global simulation

in depth, asses its realism and improve it. For that purpose, synoptic data characterizing fish communities at the scale of ocean's basins are necessary. But while information about lower trophic levels are available thanks to satellite remote sensing, while fisheries data provide information on exploited top predator species, mid-trophic levels are poorly sampled at these scales. Like for any global marine ecosystem model, large programs such as acoustic observations of pelagic ecosystems [98] would be needed. Modeling fishing pressure and comparing simulated fisheries catches with data [28, 99] can be done with the introduction of a fishing mortality in the model, uniformly along the spectrum to reproduced a balanced exploitation, or over distinct size classes [100], on the different communities. However this approach, which neglects the complex determinants of fishing effort distribution and catchability dynamics, is exposed to strong biases and uncertainties.

Identifying, understanding and incorporating in the model the key processes that are shaping global marine ecosystems is a long-term endeavour. For instance, while in APECOSM the export of biomass from epipelagic ecosystems to mesopelagic ecosystems by the migratory community is a key component for pelagic ecosystems, in shallow ecosystems the mechanism is inappropriate. In coastal shelf, Blanchard et al. [83, 28] thus couple the epipelagic community with benthic consumers feeding on sinking detritus. Moreover, the present formulation allows the consideration of the functional diversity of fish species only. The strong functional differences between crustaceans, jellies, squids and fish are therefore disregarded while they may have a strong impact on the dynamics of ecosystems, leading for example to the emergence of alternative food chains [101].

In order to study and eventually predict the impact of climate change on marine ecosystem services and biodiversity, the development of global marine ecosystem models is a major challenge. Despite the necessary improvements, the model developed in this thesis provides a mechanistic baseline which can already be used.

The model can be used to asses the impact of the environment on ecosystems. Studies examining historical observations and model projections agree on a basin wide warming and increased ocean stratification [78]. APECOSM-DIV responds to temperature and resource changes. It can be forced with climate change scenarios to asses the evolution of biodiversity in the global ocean. It can be used to test the assumption of a global shrinking of individuals [14] and estimate the variations of production at different latitudes [68]. Lefort et al. (2014) [63] undertook such a global scale study of climate change impacts using APECOSM. The predictions of the present model can be compared to their results to asses the effects of functional biodiversity on the total fish production in marine ecosystems.

The model can also be used to asses the combined impacts of environment and fishing. The living component of ecosystems is determined by the abiotic environ-

ment. But most marine ecosystems in the global ocean are also exploited. Associated with a spatially-explicit representation of fishing [75], the model is suitable to project the evolution of marine ecosystems under different climate change and exploitation scenarios [7, 61].

Models of global marine ecosystems are becoming possible with the progress of our understanding of ecosystems functioning and the improvements of computing power. It is tempting to keep on adding taxonomic or physiological details in these models. It is tempting to develop models that seem to reproduce global ecosystems by including too much of their complexity. Despite the apparent intricacy of APECOSM-DIV, one must realized that it actually adopts a rather simple representation of ecosystems functioning, while building on strong mechanistic basis and very few parameters. I believe that keeping the complexity of ecosystem models manageable is fundamental to produce meaningful predictions of the impact of the environment on marine ecosystems services in the coming century.

Appendix A

Individual level parameters and growth curves

In the model APECOSM-DIV, the bioenergetics at individual level is constrained by the Dynamic Energy Budget theory (DEB) [56]. The DEB parameters are tuned to represent fish individuals. While most DEB parameters are determined from physiological considerations [102, 57] (see chapter 3), few tuning steps allow the fitting of individuals' growth curves to empirical observations, it is detailed in this appendix.

DEB parameters and growth coefficients

According to the DEB theory [103], if food conditions are more or less constant, for ectotherms the estimated maximum volume can be determined by:

$$V_m = \left(\frac{\kappa f \{\dot{p}_{A_m}^{V_m}\}}{[\dot{p}_M]} \right)^3 \tag{A.1}$$

and the Von Bertalanffy growth coefficient equals:

$$\dot{r} = \frac{1}{3} \frac{[\dot{p}_M]}{\kappa f [E_m^{V_m}] + [E_G]} \tag{A.2}$$

with parameters detailed Table 3.4 and f the scaled functional response characterizing the level of satiation.

Equation A.2 can been expressed such that the growth coefficient $\dot{r}$ is a function of the maximum volume V_m, the somatic maintenance rate k_M and the energy conductance ν:

$$\dot{r} = \frac{1}{3} \frac{k_M}{\frac{V_m^{1/3} k_M}{\nu} + 1} \tag{A.3}$$

with $k_M = [\dot{p}_M]/[E_m^{V_m}]$ and $\nu = \{\dot{p}_{A_m}^{V_m}\}/[E_m^{V_m}]$.

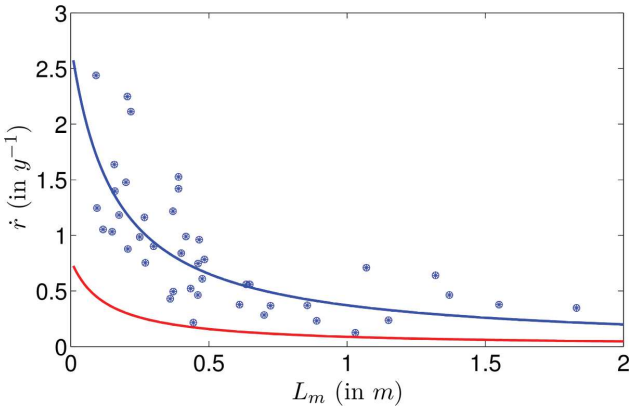

Figure A.1 Von Bertalanffy growth coefficients $\dot{r}$ as a function of species' maximum length L_m ($\propto V_m^{1/3}$): determined by the DEB relationship A.3 (curves) [103] and measured for fish species in the North Sea (blue dots) [104].

Paremeters' tuning

In order to reproduce empirical growth curves, the model can be tuned selecting the somatic maintenance rate k_M and the energy conductance ν that allow the best fit to empirical observations of the distribution of Von Bertalanffy coefficient $\dot{r}$, for different asymptotic volumes V_m (see Fig.A.1).

The generic DEB parameters [56] are convenient in order to represent the generic bioenergetics of any individual of any species. However, they may be inappropriate to respect the growth speed of fish. Figure A.1 illustrates the growth coefficients for distinct asymptotic sizes L_m ($\propto V_m^{1/3}$) with the generic DEB parameters, namely for $k_M = 0.0064285$ and $\nu = 0.02$ (red curve). Compared to reference growth coefficients characterizing the North Sea [104] (blue dots), the growth coefficients defined by the DEB are clearly inappropriate. When extracting the growth curves in APECOSM-DIV with the growth coefficients defined by the generic DEB parameters, the growth of individuals appears slower than what is expected from the reference data (see Fig. A.2, left).

Therefore, the somatic maintenance rate k_M and the energy conductance ν are tuned in APECOSM-DIV, namely $k_M = 0.08$ and $\nu = 0.1$ for the DEB parameters of fish [102, 57], such that the associated growth coefficients better fit the empirical reference (blue curve). The individuals' growth curves simulated by the model then respect the range of growth curves expected from the reference data (see Fig. A.2, right).

Note that in APECOSM-DIV the somatic maintenance rate k_M and the energy conductance ν are corrected for a single set of reference data, namely the North Sea [104]. For the tuning procedure, individuals are assumed close from satiation $f = 1$ and the growth coefficients are corrected with temperature according to the Arrhenius relationship [56]. Variations of growth coefficients in other ecosystems will be indirectly constrained by variations of the level of satiation and variations of the temperature.

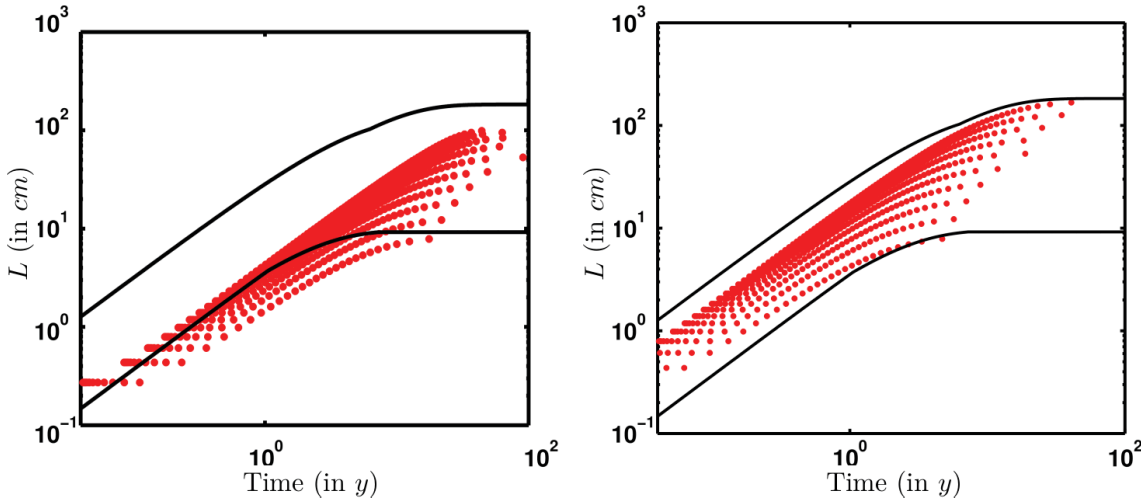

Figure A.2 Growth curves reproduced by the APECOSM-DIV model (red dots) compared to the lower and upper limits of the growth curves of species in the North Sea (black lines) [104]: left, growth curves with generic DEB parameters; right, growth curves with tuned DEB parameters.

Appendix B

Biomass conservation from individuals to species to the community

The model APECOSM-DIV links the bioenergetics at individual level to the biomass distribution at species and community levels. The flow of biomass B (or abundance N or energy ξ) between these organization levels has to be conserved for theoretical consistency. In order to ensure this conservation a correction term is necessary in the model of Maury and Poggiale (2013) [55], it is detailed in this appendix.

The species level

At individual level, according to the Dynamic Energy Budget theory (DEB) [56] and after few simplifications [55], the physiology of individuals is fully determined by the dynamic of their reserves E and structural volume V. For all individuals of a single species k, the dynamic of the abundance distribution $N^k_{V,E,t}$ can be written:

$$\frac{\partial N^k_{V,E,t}}{\partial t} = -\frac{\partial(\gamma^k_{V,E,t} N^k_{V,E,t})}{\partial V} - \frac{\partial(\eta^k_{V,E,t} N^k_{V,E,t})}{\partial E} - \mu^k_{V,E,t} N^k_{V,E,t} \tag{B.1}$$

In this formulation γ represents the structural growth, η the reserve energy "speed" and $\mu = Mage + Mdis + Mstarv + Mpred$ the mortalities, ageing, disease, starvation and predation.

This equation can be expressed in term of energy $\xi^k_{V,E,t}$ knowing the relationship between abundance and energy content [55]: $N^k_{V,E,t}(Vd\psi + E) = \xi^k_{V,E,t}$ where d is biomass density and ψ the energy content of biomass. Equation B.1 can be expressed:

$$\frac{\partial \frac{\xi^k_{V,E,t}}{Vd\psi+E}}{\partial t} = -\frac{\partial(\gamma^k_{V,E,t} \frac{\xi^k_{V,E,t}}{Vd\psi+E})}{\partial V} - \frac{\partial(\eta^k_{V,E,t} \frac{\xi^k_{V,E,t}}{Vd\psi+E})}{\partial E} - \mu^k_{V,E,t} \frac{\xi^k_{V,E,t}}{Vd\psi + E} \tag{B.2}$$

which develops:

$$\begin{aligned}\frac{\partial \xi^k_{V,E,t}}{\partial t} = &-\frac{\partial \gamma^k_{V,E,t}\xi^k_{V,E,t}}{\partial V} - \frac{\partial \eta^k_{V,E,t}\xi^k_{V,E,t}}{\partial E} - \mu^k_{V,E,t}\xi^k_{V,E,t} \\ &+ \frac{\xi^k_{V,E,t}}{(Vd\psi + E)}\left(\frac{\partial (Vd\psi + E)}{\partial t} + \gamma^k_{V,E,t}\frac{\partial (Vd\psi + E)}{\partial V} + \eta^k_{V,E,t}\frac{\partial (Vd\psi + E)}{\partial E}\right)\end{aligned} \tag{B.3}$$

According to the model presented in Maury and Poggiale (2013) [55], the dynamic of reserves is assumed fast compared to the growth and mortalities. It allows the simplification of the dynamic of reserves $\frac{\partial}{\partial E}$ in equations B.1 and B.3:

$$\frac{\partial N^k_{V,E^*,t}}{\partial t} = -\frac{\partial (\gamma^k_{V,E^*,t}N^k_{V,E^*,t})}{\partial V} - \mu^k_{V,E^*,t}N^k_{V,E^*,t} \tag{B.4}$$

and

$$\begin{aligned}\frac{\partial \xi^k_{V,E^*,t}}{\partial t} = &-\frac{\partial \gamma^k_{V,E^*,t}\xi^k_{V,E^*,t}}{\partial V} - \mu^k_{V,E^*,t}\xi^k_{V,E^*,t} \\ &+ \frac{\xi^k_{V,E^*,t}}{(Vd\psi + E^*)}\left(\frac{\partial (Vd\psi + E^*)}{\partial t} + \gamma^k_{V,E^*,t}\frac{\partial (Vd\psi + E^*)}{\partial V}\right)\end{aligned} \tag{B.5}$$

where E^* indicates reserves at equilibrium. Note that $E^* = f_{V,t}[E_m]V$ with $[E_m]$ the maximum reserve density and f the functional response [55].

In order to solve the governing equation B.5, we adopt an explicit discretization of the equation in flux conserving form:

$$\begin{aligned}\xi^k_{V,E^*,t+\Delta t} = &\ \xi^k_{V,E^*,t} \\ &+ \frac{\Delta t}{\Delta V}\left(\gamma^k_{V-1/2,E^*,t+\Delta t/2}\ \xi^k_{V-1/2,E^*,t+\Delta t/2} - \gamma^k_{V+1/2,E^*,t+\Delta t/2}\ \xi^k_{V+1/2,E^*,t+\Delta t/2}\right) \\ &+ \Delta t\frac{\xi^k_{V,E^*,t}}{(Vd\psi + E^*)}\left(\frac{\partial (Vd\psi + E^*)}{\partial t} + \gamma^k_{V,E^*,t}\frac{\partial (Vd\psi + E^*)}{\partial V}\right) \\ &- \Delta t\left(Mage^k_{V,E^*,t} + Mdis^k_{V,E^*,t} + Mstarv^k_{V,E^*,t} + Mpred^k_{V,E^*,t}\right)\xi^k_{V,E^*,t}\end{aligned} \tag{B.6}$$

From this point further the index E^* is removed from the equation for clarity.

The individual level

The advection equation B.6 is linked to the physiology of individuals defined by the DEB [55]. Any individual ingests a quantity of energy $Eing$ during Δt. This energy fuels

the metabolism during Δt:

$$\begin{aligned} Eing &= \Delta t \dot{p}_X \\ &= Eegest + EgthR + EgthV + Emaint + Emat + Efec + Erep + Estarv \end{aligned} \tag{B.7}$$

According to the DEB (see illustration Fig. B.1 and Table 3.1 for the description of the flux), the flow of ingested food $\dot{p}_X$ first balances $Eegest$, the preyed amount of energy not assimilated and lost:

$$Eegest^k = \Delta t(1 - \kappa_X)\dot{p}_X^k \tag{B.8}$$

It fuels $EgthR$, the energy invested into reserves:

$$EgthR^k = \Delta t(\dot{p}_A^k - \dot{p}_C^k) = \Delta t \frac{\partial E}{\partial t} \tag{B.9}$$

It also aliments $EgthV$, the energy invested into the structural growth of individuals:

$$EgthV^k = \Delta t(\dot{p}_G^k)^+ = \Delta t[E_G](\gamma^k)^+ \tag{B.10}$$

Part of the ingested energy is dissipated through maintenance $Emaint$ in order to maintain the structural volume:

$$Emaint^k = \Delta t \dot{p}_M^k \tag{B.11}$$

More energy is dissipated for maturation $Emat$:

$$Emat^k = \Delta t \dot{p}_J^k \tag{B.12}$$

When mature individuals allocate part of the ingested energy to reproduction, some is lost $Efec$:

$$Efec^k = \Delta t(1 - (1 - M_{egg})\phi\kappa_R)(\dot{p}_R^k)^+ \tag{B.13}$$

and some allows the production of eggs $Erep$:

$$Erep^k = \Delta t(1 - M_{egg})\phi\kappa_R(\dot{p}_R^k)^+ \tag{B.14}$$

Finally, in this individual level balance of energy, when the food ingested is not sufficient to fulfill the demand for growth and reproduction, individuals start starving $Estarv$ and loose energy:

$$Estarv^k = -\Delta t((\dot{p}_R^k)^- + (\dot{p}_G^k)^-) = -\Delta t((-\dot{p}_R^k)^+ + (-\dot{p}_G^k)^+) \tag{B.15}$$

The energy budget at individual level can be extrapolated at the specific level, considering not one but $N_{V,t}^k$ individuals of species k at a structural volume V. The energy ingested by $N_{V,t}^k$ individuals aliments their growth, reproduction, energy dissipation and

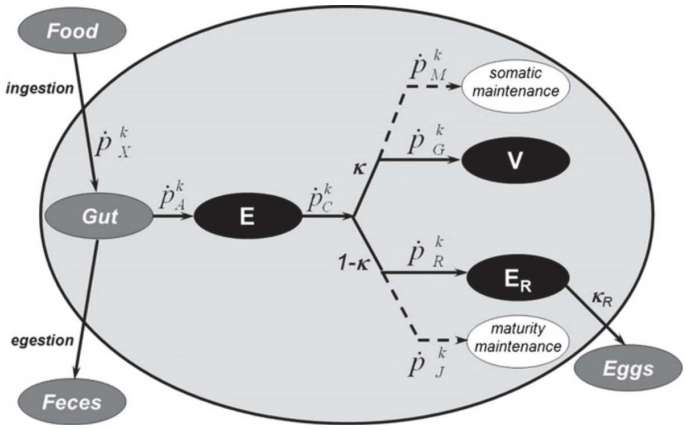

Figure B.1 States variables and energy flux involved in the bioenergetics of any individual in the framework of the DEB theory (taken from Maury and poggiale (2013) [55]).

losses.

$$\begin{aligned} N^k_{V,t} Eing^k_{V,t} &= N^k_{V,t}(Eegest^k_{V,t} + EgthR^k_{V,t} + EgthV^k_{V,t} + Emaint^k_{V,t} + \\ &\quad Emat^k_{V,t} + Efec^k_{V,t} + Erep^k_{V,t} + Estarv^k_{V,t}) \\ &= N^k_{V,t}(Edissip^k_{V,t} + Eloss^k_{V,t} + Egrowth^k_{V,t} + Erep^k_{V,t} + Estarv^k_{V,t}) \end{aligned} \tag{B.16}$$

where $Edissip = Emaint + Emat$ summarizes the energy dissipation, $Eloss = Eegest + Efec$ the energy loss and $Egrowth = EgthR + EgthV$ the growth of reserves and structure.

At community level, the total amount of energy preyed by all predators E_{tot} can be computed summing the energy ingested by all individuals (summing over all structural volumes V) of all species (summing over all species k):

$$E_{tot} = \int_k \int_V N^k_{V,t} Eing^k_{V,t} dV dk \tag{B.17}$$

It is equal to the total amount of energy preyed on the resource at low trophic level E_{LTL} and the total amount of energy preyed within the community by secondary consumers E_{CS}: $E_{tot} = E_{LTL} + E_{CS}$. The last term, E_{CS}, is equivalent to the predation mortality in the community:

$$\int_k \int_V N^k_{V,t} Eing^k_{V,t} dV dk = E_{LTL} + \Delta t \int_k \int_V Mpred^k_{V,t} \xi^k_{V,t} dV dk \tag{B.18}$$

The community level

The physiology of individuals is nested in the energy flux at species level, since it determines parameters such as structural growth and some mortalities [55]. In order to

identify the biomass budget from individuals to species to the community, equation B.6 is rewritten in its integral form:

$$\begin{aligned}\int_k \int_V \xi^k_{V,t+\Delta t} dV dk &= \int_k \int_V \xi^k_{V,t} dV dk \\ &+ \int_k \int_V \frac{\Delta t}{\Delta V} \left(\gamma^k_{V-1/2,t+\Delta t/2}\ \xi^k_{V-1/2,E^*,t+\Delta t/2} - \gamma^k_{V+1/2,t+\Delta t/2}\ \xi^k_{V+1/2,E^*,t+\Delta t/2} \right) dV dk \\ &+ \int_k \int_V \Delta t \frac{\xi^k_{V,t}}{(V d\psi + E^*)} \left(\frac{\partial (V d\psi + E^*)}{\partial t} + \gamma^k_{V,t} \frac{\partial (V d\psi + E^*)}{\partial V} \right) dV dk \\ &- \int_k \int_V \Delta t \left(Mage^k_{V,t} + Mdis^k_{V,t} + Mstarv^k_{V,t} + Mpred^k_{V,t} \right) \xi^k_{V,t} dV dk\end{aligned} \tag{B.19}$$

which becomes (V_b being a birth volume and V_d the maximum volume reached by species):

$$\begin{aligned}\int_k \int_V \xi^k_{V,t+\Delta t} dV dk &= \int_k \int_V \xi^k_{V,t} dV dk \\ &+ \Delta t \int_k \left(\gamma^k_{V_b,t+\Delta t/2} \xi^k_{V_b,t+\Delta t/2} - \gamma^k_{V_d,t+\Delta t/2} \xi^k_{V_d,t+\Delta t/2} \right) dk \\ &+ \Delta t \int_k \int_V \frac{\xi^k_{V,t}}{(V d\psi + E^*)} \left(\frac{\partial (V d\psi + E^*)}{\partial t} + \gamma^k_{V,t} \frac{\partial (V d\psi + E^*)}{\partial V} \right) dV dk \\ &- \Delta t \int_k \int_V \left(Mage^k_{V,t} + Mdis^k_{V,t} \right) \xi^k_{V,t} dV dk - \Delta t \int_k \int_V \left(Mstarv^k_{V,t} \right) \xi^k_{V,t} dV dk \\ &- \Delta t \int_k \int_V \left(Mpred^k_{V,t} \right) \xi^k_{V,t} dV dk\end{aligned} \tag{B.20}$$

The predation mortality can be replaced with equation B.18 and $\gamma^k_{Vd,t} = 0$, thus:

$$\begin{aligned}\int_k \int_V \xi^k_{V,t+\Delta t} dV dk &= \int_k \int_V \xi^k_{V,t} dV dk + \Delta t \int_k \gamma^k_{V_b,t+\Delta t/2} \xi^k_{V_b,t+\Delta t/2} dk \\ &+ \Delta t \int_k \int_V \frac{\xi^k_{V,t}}{(V d\psi + E^*)} \left(\frac{\partial (V d\psi + E^*)}{\partial t} + \gamma^k_{V,t} \frac{\partial (V d\psi + E^*}{\partial V} \right) dV dk \\ &- \Delta t \int_k \int_V \left(Mage^k_{V,t} + Mdis^k_{V,t} \right) \xi^k_{V,t} dV dk - \Delta t \int_k \int_V \left(Mstarv^k_{V,t} \right) \xi^k_{V,t} dV dk \\ &- \int_k \int_V N^k_{V,t} Eing^k_{V,t} dV dk + E_{LTL}\end{aligned} \tag{B.21}$$

or

$$\begin{aligned}\int_k\int_V \xi^k_{V,t+\Delta t}dVdk &= \int_k\int_V \xi^k_{V,t}dVdk + \Delta t\int_k \gamma^k_{V_b,t+\Delta t/2}\xi^k_{V_b,t+\Delta t/2}dk \\ &+ \Delta t\int_k\int_V \frac{\xi^k_{V,t}}{(Vd\psi+E^*)}\left(\frac{\partial(Vd\psi+E^*)}{\partial t}+\gamma^k_{V,t}\frac{\partial(Vd\psi+E^*)}{\partial V}\right)dVdk \\ &- \Delta t\int_k\int_V \left(Mage^k_{V,t}+Mdis^k_{V,t}\right)\xi^k_{V,t}dVdk - \Delta t\int_k\int_V \left(Mstarv^k_{V,t}\right)\xi^k_{V,t}dVdk \\ &- \int_k\int_V N^k_{V,t}(Edissip^k_{V,t}+Eloss^k_{V,t}+Egrowth^k_{V,t}+Erep^k_{V,t}+Estarv^k_{V,t})dVdk + E_{LTL}\end{aligned} \tag{B.22}$$

Between individual and species levels, the reproduction simplifies:

$$\begin{aligned}\int_k\int_V N^k_{V,t}(Erep^k_{V,t})dVdk &= \int_k\int_V N^k_{V,t}(\Delta t(1-M_{egg})\phi\kappa_R(\dot{p}^k_R)^+)dVdk \\ &= \Delta t\int_k\left((1-M_{egg})\phi\kappa_R\int_V N^k_{V,t}(\dot{p}^k_R)^+dV\right)dk \\ &= \Delta t\int_k \gamma^k_{V_b,t+\Delta t/2}\xi^k_{V_b,t+\Delta t/2}dk\end{aligned} \tag{B.23}$$

Between individual and species levels, the starvation simplifies:

$$\begin{aligned}\int_k\int_V N^k_{V,t}(Estarv^k_{V,t})dVdk &= -\int_k\int_V N^k_{V,t}(\Delta t((-\dot{p}^k_R)^+ + (-\dot{p}^k_G)^+))dVdk \\ &= -\Delta t\int_k\int_V \frac{N^k_{V,t}}{\xi^k_{V,t}}((-(\dot{p}^k_R)^+ - (\dot{p}^k_G)^+))\xi^k_{V,t}dVdk \\ &= -\Delta t\int_k\int_V \left(Mstarv^k_{V,t}\right)\xi^k_{V,t}dVdk\end{aligned} \tag{B.24}$$

The governing equation B.22 becomes:

$$\begin{aligned}\int_k\int_V \xi^k_{V,t+\Delta t}dVdk &= \int_k\int_V \xi^k_{V,t}dVdk + \Delta t\int_k\int_V \frac{\xi^k_{V,t}}{(Vd\psi+E^*)}\left(\frac{\partial(Vd\psi+E^*)}{\partial t}+\gamma^k_{V,t}\frac{\partial(Vd\psi+E^*)}{\partial V}\right)dVdk \\ &- \Delta t\int_k\int_V \left(Mage^k_{V,t}+Mdis^k_{V,t}\right)\xi^k_{V,t}dVdk \\ &- \int_k\int_V N^k_{V,t}(Edissip^k_{V,t}+Eloss^k_{V,t}+Egrowth^k_{V,t})dVdk + E_{LTL}\end{aligned} \tag{B.25}$$

At the community level, at equilibrium, the energy remains constant for all individuals and all species:

$$\int_k \int_V \xi^k_{V,t+\Delta t} dV dk - \int_k \int_V \xi^k_{V,t} dV dk = 0 \tag{B.26}$$

At equilibrium, according to equation B.25 the energy preyed on low trophic levels E_{LTL} is thus equivalent to:

$$\begin{aligned} E_{LTL} = &-\Delta t \int_k \int_V \frac{\xi^k_{V,t}}{(V d\psi + E^*)} \left(\frac{\partial (V d\psi + E^*)}{\partial t} + \gamma^k_{V,t} \frac{\partial (V d\psi + E^*)}{\partial V} \right) dV dk \\ &+ \Delta t \int_k \int_V \left(Mage^k_{V,t} + Mdis^k_{V,t} \right) \xi^k_{V,t} dV dk \\ &+ \int_k \int_V N^k_{V,t} (Edissip^k_{V,t} + Eloss^k_{V,t} + Egrowth^k_{V,t}) dV dk \end{aligned} \tag{B.27}$$

It compensates for the ageing and disease mortalities, the dissipation as well as energy losses. Note that other terms remain, at equilibrium and at the community level these term should be equivalent and cancel each others such that:

$$E_{LTL} = \Delta t \int_k \int_V \left(Mage^k_{V,t} + Mdis^k_{V,t} \right) \xi^k_{V,t} dV dk + \int_k \int_V N^k_{V,t} (Edissip^k_{V,t} + Eloss^k_{V,t}) dV dk \tag{B.28}$$

Therefore, it is necessary to verify the relationship:

$$\begin{aligned} \Delta t \int_k \int_V \frac{\xi^k_{V,t}}{(V d\psi + E^*)} \left(\frac{\partial (V d\psi + E^*)}{\partial t} + \gamma^k_{V,t} \frac{\partial (V d\psi + E^*)}{\partial V} \right) dV dk = \\ \int_k \int_V N^k_{V,t} (Egrowth^k_{V,t}) dV dk = \end{aligned} \tag{B.29}$$

or according to equations B.9 and B.10:

$$\begin{aligned} \Delta t \int_k \int_V \frac{\xi^k_{V,t}}{V(d\psi + V f_{V,t}[E_m]^k)} \left(\frac{\partial (V d\psi + E^*)}{\partial t} + \gamma^k_{V,t} \frac{\partial (V d\psi + E^*)}{\partial V} \right) dV dk = \\ \Delta t \int_k \int_V N^k_{V,t} \left(\frac{\partial E}{\partial t} + [E_G] (\gamma^k_{V,t})^+ \right) dV dk \end{aligned} \tag{B.30}$$

This equation expresses the link between reserves growth and structural growth at the individual level and their specific level terms. With $N^k_{V,t}(V d\psi + E^*) = \xi^k_{V,t}$ it can be written:

$$\int_k \int_V N^k_{V,t} \left(\frac{\partial (V d\psi + E^*)}{\partial t} + \gamma^k_{V,t} \frac{\partial (V d\psi + E^*)}{\partial V} - \frac{\partial E}{\partial t} - [E_G] (\gamma^k_{V,t})^+ \right) dV dk = 0 \tag{B.31}$$

or simplifying the derivatives

$$\int_k \int_V N_{V,t}^k \left(\frac{\partial E^*}{\partial t} + \gamma_{V,t}^k d\psi + \gamma_{V,t}^k \frac{\partial E^*}{\partial V} - \frac{\partial E}{\partial t} - [E_G](\gamma_{V,t}^k)^+ \right) dV dk = 0 \tag{B.32}$$

In equation B.32, the term:

$$\int_k \int_V N_{V,t}^k \left(\gamma_{V,t}^k d\psi - [E_G](\gamma_{V,t}^k)^+ \right) dV dk \tag{B.33}$$

expresses the structural growth efficiency. It is equivalent to a dissipation cost and can be introduced in equation B.28

To ensure the mass balance of the model from individuals to species to the community, a last term is left which should be zero:

$$\int_k \int_V N_{V,t}^k \left(\frac{\partial E^*}{\partial t} + \gamma_{V,t}^k \frac{\partial E^*}{\partial V} - \frac{\partial E}{\partial t} \right) dV dk = 0 \tag{B.34}$$

However, this term is not zero in the model.

Because of the simplification of the reserve dynamic assuming the fast reserve dynamics [55], the relationship equation B.34 is not verified. A correction term is necessary in the model to cancel this term in order to ensure the biomass conservation from individuals to species to the community.

List of Figures

I L'objectif de cette thèse est d'estimer les effets de l'environnement sur la structure des communautés de poissons dans l'océan global, tout en prenant en compte le rôle fonctionnel de la biodiversité. Quatre objectifs intermédiaires (OBJ) sont identifiés pour atteindre cet objectif principal. 6

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