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Préface

Durant ces trois années de doctorat, j'ai réalisé de nombreux travaux au sein de multiples projets. J'ai ainsi pu participer aux projets TROPHIK (ANR-10-IED-0006-12), APPEAL (ANR-10-IED-0006-25), WINDSERV (ANR-10-IED-0006-34) et enfin SENSITROPH (Fondation de France). Ceci m'a permis de collaborer avec de nombreuses personnes dans de nombreux domaines scientifiques. Ces travaux m'ont permis de me former à de nouvelles approches mais également d'aborder de nouvelles thématiques, plus multidisciplinaires.

Le projet TROPHIK s'intéressait à l'étude des impacts du parc éolien en mer de Courseulles-sur-Mer grâce à des approches écosystémiques (rôle du parc éolien sur la structure et le fonctionnement des réseaux trophiques de la baie de Seine). Ayant réalisé mon stage de deuxième année de master durant ce projet, j'ai été dès ma première année de thèse, intégré à la réalisation de multiples études ayant fait l'objet de publications dans plusieurs journaux internationaux. J'ai ainsi été formé à l'utilisation de modèles de niche permettant de modéliser l'aire de répartition théorique de multiples espèces, et ai participé à la mise en place d'un papier méthodologique dans le journal « Ecological Informatics » (Ben Rais Lasram *et al.*, 2020). Ce papier présente une approche permettant de mieux modéliser l'aire de répartition d'espèces marines à une échelle locale. J'ai ensuite utilisé ces modèles pour aider à simuler l'effet du changement climatique sur des modèles trophiques, et ai ainsi pu participer à l'écriture d'un papier publié dans « Fisheries Oceanography » (Bourdaud *et al.*, 2021).

Le projet APPEAL cherche à développer une approche intégrée pour mesurer les effets des parcs éoliens flottants sur le fonctionnement des socio-écosystèmes côtiers. Grâce à ce dernier, j'ai pu encadrer une stagiaire en deuxième année de master (50%), Maud Thermes, avec qui nous avons écrit une étude qui devrait être soumise prochainement pour publication (Chapitre supplémentaire). Cette étude reprend les outils développés durant ma thèse et le projet TROPHIK, afin d'étudier les impacts de l'extraction de granulats marins et d'un nouveau parc éolien sur le fonctionnement du réseau trophique de la baie de Seine, en Manche.

Au-delà des travaux réalisés avec ces projets, j'ai également participé à des études interdisciplinaires en lien direct avec les résultats obtenus durant ma thèse. Ainsi, j'ai travaillé avec des mathématiciens du LMI de Rouen (Laboratoire de Mathématiques de l'INSA Rouen Normandie, UMR 3335 CNRS) et du LMNO de Caen (Laboratoire de Mathématiques Nicolas

Oresme, UMR 6139 CNRS), sur des méthodes d'optimisation des modèles trophiques que j'ai utilisé durant mon premier chapitre de thèse. J'ai également travaillé avec Daniel Kostic, philosophe des sciences, sur une présentation à un congrès de philosophie (Kostić, Niquil, Nogues "Perspectivism and verticalhorizontal explanatory modes in ecological networks" 3rd SURE annual workshop, 15-17 April 2021, Radboud University, The Netherlands) et un projet d'article s'intéressant au pouvoir explicatif des outils utilisés durant la thèse.

Mes collaborations ne s'arrêtent pas aux travaux de ma thèse, en effet je participe également au projet SENSITROPH, projet qui s'intéresse à la perception des rivages et des organismes qui les occupent, par les populations en Normandie. L'objectif de ce projet est de comprendre en quoi les organismes marins et côtiers ne sont pas seulement liés à l'homme pour des raisons alimentaires, mais touchent également à notre bien-être intérieur et existentiel. Il s'agit ainsi de définir de nouveaux liens entre l'homme et la nature au sein des réseaux trophiques des écosystèmes côtiers. Des travaux préliminaires au projet SENSITROPH m'ont permis de prendre en compte ces liens autres qu'alimentaires (Chapitre 3), mais ouvrent également à de futurs travaux au sein du projet. C'est pour cette raison que je dois réaliser un contrat post-doctoral de 6 mois, au sein de SENSITROPH, afin d'approfondir la question des relations homme-nature dans nos modèles écosystémiques, avant de chercher à partir dans un laboratoire étranger.

En parallèle du projet SENSITROPH, le projet WINDSERV développe des approches multi-modèles afin de prévoir les impacts des parcs éoliens en mer sur les écosystèmes et les services en découlant. Ma thèse partageant la thématique des services écosystémiques avec WINDSERV, j'ai pu travailler avec Yoann Baulaz, géographe ayant réalisé un contrat de post doctorat avec WINDSERV, durant mes travaux de thèse (Chapitre 3). Nous avons également posé les bases pour une collaboration future afin d'améliorer la quantification de la fourniture en services écosystémiques. Pour cela, nous souhaitons mettre en rapport des outils écosystémiques sur les flux de matière organique avec des études cartographiques.

Ma thèse s'intègre donc dans une suite de travaux qui ont commencé en 2014 avec la thèse d'Aurore Raoux, et qui continuent aujourd'hui et pour plusieurs années.

I Introduction

1 L'Anthropocène : Le défi de la multiplicité des impacts sur les écosystèmes marins.

1.1 L'Anthropocène et ses conséquences pour les écosystèmes

Tout au long de son histoire, la Terre a traversé de nombreuses époques géologiques, chacune caractérisée par leurs particularités biogéochimiques. La Terre a donc cheminé depuis l'Hadéen jusqu'à l'Holocène il y a à peu près 12000 ans. Cependant en 2000, Monsieur Paul Crutzen, vice-président du programme international sur la géosphère et la biosphère (IGBP en anglais), proposa que la terre eût quitté l'époque de l'Holocène et était entrée dans l'Anthropocène (Crutzen, 2002). Cette transition vers l'Anthropocène coïncide avec l'avènement de l'ère industrielle au milieu du 18^{ème} siècle, marqué par l'invention de la machine à vapeur en 1784 par James Watt. Cela suppose, qu'à partir de la révolution industrielle, dans les années 1800, la Terre entre dans une phase de changements drastiques par rapport à l'Holocène. Ces changements coïncident avec une importante augmentation de l'activité humaine sur Terre. Ceci se reflète dans le nom choisi pour l'époque, avec Anthro du grec *anthropos* qui veut dire « être humain » et cène du grec *kainos* qui veut dire « nouveau », relatif à l'époque géologique. Même si le point de départ exact de l'Anthropocène est encore débattu (ex. Steffen *et al.* 2015), les signes de son commencement sont indéniables et bien reconnus.

Le début de l'Anthropocène se caractérise par une modification importante de multiples indicateurs de la structure et du fonctionnement du système biogéochimique terrestre. Ces indicateurs sont très nombreux et témoignent de la grande diversité des effets de l'homme moderne sur la Terre. Ces indicateurs sont également corrélés à l'augmentation d'indices de l'activité humaine sur Terre. Ainsi, on observe depuis le 19^{ème} siècle, jusqu'à aujourd'hui : une importante augmentation de la population humaine sur Terre, une urbanisation toujours plus élevée, un accroissement continu du transport sur Terre (routier, aérien, maritime), une augmentation de l'utilisation de fertilisants pour l'agriculture, une augmentation de l'utilisation de l'eau mais également une augmentation d'un très grand nombre d'autres indices relatifs au développement des sociétés humaines. Ceci s'accompagne d'une modification importante des concentrations en gaz à effet de serre dans l'atmosphère, d'une augmentation de la température globale de la Terre, d'une augmentation des concentrations

en nutriments dans les eaux côtières et lacustres, d'une augmentation de l'utilisation des sols, de la dégradation des habitats, et des captures liées à la pêche ainsi que de nombreux autres indicateurs. Ces tendances indiquent que nous sommes entrés dans une phase de grande accélération. Il existe un grand nombre de preuves qui montrent que les changements dans la structure et le fonctionnement du système terrestre sont principalement dus aux activités humaines (Steffen *et al.*, 2015).

Avec un peu plus de 50% de la population mondiale vivant à moins de 200 kilomètres des côtes maritimes (Creel, 2003), cette grande transformation va fortement impacter les systèmes maritimes, depuis les estuaires, jusqu'aux côtes et aux océans. Les hommes ont ainsi impacté près de 87 à 90% de la surface globale des océans (Halpern *et al.*, 2015). On estime qu'en 2010, les populations de poissons avaient décliné de 38% par rapport aux années 1970 (Hutchings *et al.*, 2010), et que la surface en « habitat côtier exceptionnel » avait chuté de deux tiers (des habitats comme les mangroves, les herbiers marins, les récifs coraliens : Lotze *et al.* 2006). Cela a conduit à des pertes de biodiversité mondiale comparables aux précédentes grandes extinctions de masse sur terre (Ceballos *et al.*, 2015). Ceci est le résultat des nombreuses activités humaines et leurs effets sur les écosystèmes marins. La pêche est l'activité humaine principale qui impacte les écosystèmes marins (Jennings and Kaiser, 1998; Bell *et al.*, 2017). C'est pour cette raison que les captures des pêcheries mondiales sont souvent utilisées comme indicateur de l'activité humaine en mer. Mais la pêche n'est pas la seule activité humaine à fortement affecter les organismes des océans et des mers. Les systèmes marins sont également victimes de pollutions en tous genres, du transport maritime, de la bétonisation des côtes mais également des fonds marins, de l'aquaculture et d'un bon nombre d'autres activités (Griffiths *et al.*, 2005; Brander *et al.*, 2010). L'augmentation du nombre d'impacts sur les systèmes marins ne semble d'ailleurs pas prête de s'arrêter. On estime ainsi que la part de la population mondiale vivant près des côtes va augmenter dans le futur (Creel, 2003). De plus, de nombreux projets cherchent à « mieux exploiter le milieu marin » comme on peut le voir à travers les projets « Pavillon Bleu » (<https://www.pavillonbleu.org/>) ou encore « Plan bleu » (<https://planbleu.org/>) mais également le PPR « Océan et Climat » (Programme Prioritaire de Recherche piloté par le CNRS et l'Ifremer). Ceci peut être attribué à l'épuisement des ressources continentales, poussant l'homme à exploiter de nouveaux milieux, ici la mer (McCauley *et al.*, 2015). Ainsi, de nouvelles activités fleurissent dans tous les océans à travers

de grands projets d'énergie marine renouvelable (EMR, ex. Nachtane *et al.* 2018), des projets d'exploitation de minerais rares dans le fond des océans (Paulikas *et al.*, 2020; Mukherjee *et al.*, 2021) et bien d'autres.

Un autre élément vient se rajouter à cette multiplicité des activités humaines : le changement climatique. En effet, les activités humaines n'impactent pas uniquement les espèces à travers leurs actions directes (mortalité des espèces par capture, modification des cycles biologiques par la pollution, destruction des habitats par la bétonisation), elles les impactent aussi de manière indirecte. Les activités humaines émettent en effet des gaz à effet de serre, gaz qui ont un effet sur le climat et donc sur l'environnement. Ainsi, le changement climatique a une grande variété d'effets sur les espèces marines et donc sur les écosystèmes (Hoegh-Guldberg and Bruno, 2010). L'effet principal du changement climatique passe par une modification de la température atmosphérique, qui va elle-même modifier la température des eaux. Cette modification de la température des eaux a de nombreux effets sur les espèces marines. Une modification de la température des eaux peut modifier la distribution des espèces en fonction de leur préférence bioclimatique (Raitsos *et al.*, 2010; Hastings *et al.*, 2020), mais également modifier leur rythme physiologique (Brierley and Kingsford, 2009; Byrne, 2011). Cette modification des rythmes physiologiques des espèces peut être soit lié à une modification du métabolisme des espèces (effet de la température sur la cinétique métabolique des espèces) ou bien à un dérèglement des rythmes saisonniers des espèces, de par une modification des températures saisonnières. La température peut impacter d'autres paramètres environnementaux comme la densité des eaux, qui joue un rôle majeur dans la stratification verticale de la colonne d'eau (Capotondi *et al.*, 2012). La température des eaux agit aussi sur la solubilité de l'oxygène et donc sur sa concentration dans l'eau (Matear *et al.*, 2000). L'effet du changement climatique sur la chimie de l'eau ne s'arrête pas uniquement à la concentration en oxygène, le changement climatique peut également impacter d'autres paramètres. D'abord, les gaz à effet de serre responsables du changement climatique peuvent, comme l'oxygène, se dissoudre dans l'eau, modifiant ainsi le PH des eaux (Harrould-Kolieb and Herr, 2012). Cette modification de l'acidité des eaux peut avoir un impact important sur les organismes calcifiants, comme certaines espèces de phytoplanctons (Flynn *et al.*, 2012). Le changement climatique est également capable de modifier la salinité des eaux, à travers la fonte des glaces aux pôles, mais également à travers un changement des rythmes

pluviométriques (Durack and Wijffels, 2010). Toutes ces modifications environnementales ont/vont avoir un effet direct sur les espèces marines en plus des effets de chacune des activités humaines.

La multiplication des effets de l'homme sur les écosystèmes, que l'on appellera aussi facteurs de changement environnementaux (ou facteurs, de l'anglais « ecological drivers »), a un effet important sur l'environnement à travers des effets dits cumulés. Ainsi, plusieurs facteurs de changement peuvent interagir entre eux, ce qui peut avoir des conséquences importantes sur les écosystèmes (Crain *et al.*, 2008). Les modifications des écosystèmes peuvent donc être attribuées aux différents facteurs, mais également à leurs interactions. Les conséquences pour l'environnement sont potentiellement à même de durablement modifier notre relation avec les écosystèmes, se traduisant par une modification de la capacité des écosystèmes à fournir les services nécessaires au bien-être de l'homme (Montoya and Raffaelli, 2010). Les actions de l'homme sur les systèmes biologiques apparaissent ainsi comme l'une des plus sérieuses menaces à son propre bien être. Il est donc nécessaire de bien comprendre comment nous impactons notre environnement et comment nos actions peuvent se cumuler pour mener à de potentiels scénarios catastrophes (ex. Chagaris *et al.* 2015; Heymans and Tomczak 2016).

1.2 Le cumul d'impacts et les effets cumulés en résultant.

Le concept d'effet cumulé résultant du cumul de multiples facteurs de changement est un concept utilisé dans de nombreux domaines de la science. Ceci rend donc difficile la traçabilité d'une origine commune au concept. Les premières traces de la notion de cumul en écologie apparaissent dans les années 1970. Le cumul d'impacts est à ce moment déjà connu en médecine et est souvent cité en lien avec l'effet d'éléments toxiques sur la santé d'organismes (Dubos, 1964). Le cumul est donc très tôt apparenté aux potentiels risques liés à l'interaction de plusieurs éléments possiblement néfastes, pouvant agir ensemble vers la dégradation d'un système (en médecine et biologie : un organisme). De plus, le cumul d'impacts apparaît dès ses origines comme intrinsèquement lié à la notion de connectivité et à une vision intégrative des systèmes (Dubos, 1964) : pour étudier le cumul d'impacts, une vision plus globale est nécessaire, car on ne regarde pas uniquement l'effet de A sur X, mais également l'effet de B, C jusqu'à N sur X (Figure I - 1).

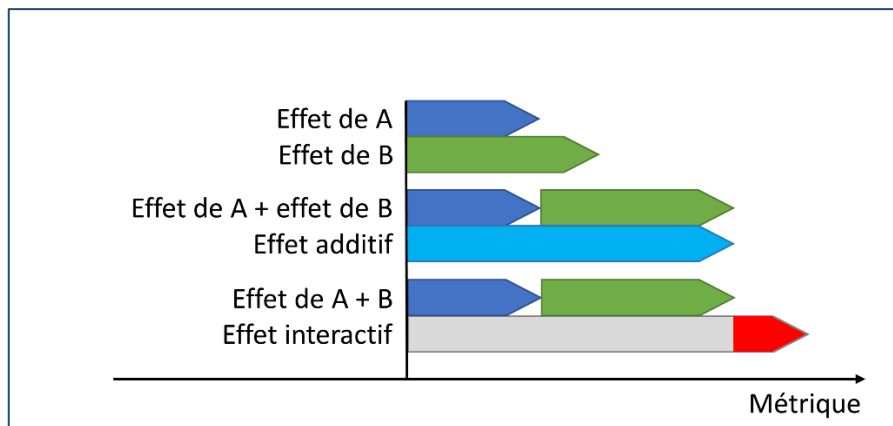


Figure I - 1 Effet additif et effet interactif du cumul de deux changements environnementaux (facteurs).

Les effets des changements environnementaux peuvent être quantifiés via une grande variété de métriques écologiques : structurels (biomasse, abondance ...) ou fonctionnels (indices de réseaux écologique).

La notion d'effet cumulé apparaît en écologie dans les années 1970, en Amérique du Nord, suite aux préoccupations du public face aux impacts environnementaux de la planification des territoires (Cobourn, 1989). Cette préoccupation a reçu un soutien institutionnel avec la promulgation de l'acte américain sur l'environnement (U.S. National Environmental Policy Act, or NEPA). C'est à la suite de la promulgation de la NEPA que l'évaluation des impacts environnementaux, dans le cadre de projets de planification, devient une pratique courante (Cocklin *et al.*, 1992a). C'est dans le cadre de la NEPA qu'en Amérique du Nord, dans les années 1970, les gestionnaires de l'environnement mettent en avant la notion de gestion et d'évaluation des effets cumulés. Ils mettent alors en évidence qu'un projet devrait être proposé en fonction de son emplacement et en relation avec les autres usages environnants, ceci afin de limiter les risques de pollution, de compétition ou d'autres interactions néfastes entre les différents usages (<https://www.iaia.org/index.php>). C'est donc le conseil pour la qualité de l'environnement (CEQ) qui, dans le cadre de la rédaction de directives pour l'évaluation des impacts environnementaux (environmental impact assessment ou EIA), cite pour une des premières fois la notion d'effet cumulé sur les écosystèmes. Les effets cumulés sont alors définis comme :

« Impact sur l'environnement qui résulte de l'effet incrémental d'une action lorsqu'elle est rajoutée à d'autres actions passées, présentes et raisonnablement prévisibles dans le futur, quelle que soit l'agence (fédérale ou non) ou la personne qui entreprend ces autres actions.

Les impacts cumulatifs peuvent résulter d'actions individuellement mineures, mais collectivement significatives, qui se déroulent sur une période donnée. » (CEQ, cité dans Cobourn 1989, p. 268)

Par la suite, c'est dans les années 1980 et 1990 que le concept de cumul d'impacts prend racine en écologie. Le concept d'évaluation des effets cumulés ou "cumulative effect assessment" en anglais (CEA), est donc d'abord utilisé à des fins pratiques pour la gestion des territoires, puis à des fins plus académiques pour la recherche scientifique. Alors que les gestionnaires sont plus perturbation-centrés, s'intéressant aux impacts des perturbations sur un système et sur les usages qui en résultent (ex. Spaling and Smit 1993), les chercheurs se concentrent davantage sur les effets et sur les mécanismes produisant ces effets (ex. Breitburg et al. 1998; Folt and Chen 1999). L'évaluation des effets cumulés étant encadrée par la loi américaine, puis canadienne (Canadian Environmental Assessment Research Council (CEARC) and U.S. National Research and (NRC), 1986; Canadian Environmental Assessment Research Council (CEARC), 1988), de nombreuses études ont été mises en place pour étudier le cumul d'impacts sur les écosystèmes terrestres (ex. Gillespie et al. 1980; Johnston et al. 1988; Ross 1990). Le concept a par la suite été exporté vers de nombreux autres pays, devenant une évidence dans beaucoup de programmes de planification (Commission for the Environment, 1981; Cooper and Sheate, 2002).

Très tôt, la communauté scientifique a mis en avant les nombreux risques pouvant découler du cumul d'impacts, ainsi que la grande complexité des mécanismes à l'origine des effets cumulés (Cocklin *et al.*, 1992a; Spaling, 1994). Ceci établit l'étude du cumul d'impacts comme l'une des priorités du 21^{ème} siècle (Schindler, 2001; Fleishman *et al.*, 2011). L'étude du cumul a donc fait l'objet de nombreuses études, d'une complexité toujours croissante (Hodgson and Halpern, 2019). À partir des années 1990, on met en place les premiers concepts et définitions des effets cumulés (Contant and Wiggins, 1991; Cocklin *et al.*, 1992a; Spaling and Smit, 1993). Les approches proposées ne sont pas exactement les mêmes mais elles suivent le même principe causal dans lequel :

- On définit en premier les effets à l'origine de l'effet cumulé sur un système (environnement ou espèce). Les sources à l'origine de ces effets pouvant provenir d'une seule ou de plusieurs activités humaines.

- Ensuite on caractérise les processus d'interactions entre les effets, à l'origine du cumul, indiquant que ces effets interagissent dans le temps et l'espace, d'une façon additive ou interactive.
- Puis on met en place une typologie des effets cumulés, indiquant que les effets cumulés peuvent être différenciés, en fonction de multiples paramètres (en fonction de l'effet combiné mais également en fonction du pas de temps, de l'échelle spatiale, des effets directs ou indirects...).

Le cumul d'impacts sur les écosystèmes est alors considéré comme l'accumulation de changements environnementaux à travers différentes voies. Comme les facteurs de changement, ces voies sont multiples et varient dans leur type, dans le temps et dans l'espace. Un changement peut alors suivre différentes voies et faire appel à des processus additifs ou bien interactifs (les effets cumulés, Figure 1 - 2). Alors que les processus additifs sont uniquement sommatifs (les effets des facteurs environnementaux peuvent être sommés pour caractériser l'effet combiné des facteurs), les interactions entre les facteurs peuvent conduire à des multiplications ou soustractions (appelées en ces débuts, effets synergiques ou multiplicatifs, l'accumulation des facteurs devient alors supérieure ou inférieure à l'effet additif). Très tôt, l'aspect spatio-temporel du cumul d'impacts est présenté comme jouant un rôle crucial dans les interactions entre les facteurs. Les voies d'interactions peuvent ainsi être caractérisées par des processus instantanés ou impliquer des délais. Elles peuvent également fonctionner à différentes échelles (locale, régionale ou mondiale) et impliquer des mouvements spatiaux.

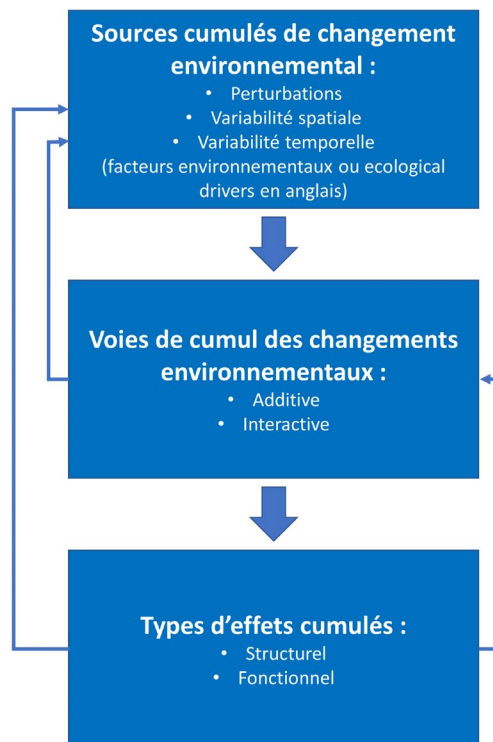


Figure I - 2 Le cadre théorique des effets cumulés.

Présenté dans Spaling (1994).

Néanmoins, même si les concepts sont mis en place et que l'on comprend vite l'ampleur potentielle du cumul d'impacts, que ce soit à l'échelle écologique ou spatio-temporelle, cette complexité n'est pas bien représentée dans les méthodes utilisées, et le cumul est très souvent supposé additif, sans tenir compte de l'aspect spatio-temporel (Shopley and Fuggle, 1984; Cocklin *et al.*, 1992b; Schultz, 2010).

Les travaux sur les effets cumulés se concentrent d'abord sur la réponse des organismes et de leur physiologie à la combinaison de plusieurs perturbations (voir Vinebrooke *et al.* (2004) ex. (Agawin *et al.*, 2000; Shatwell *et al.*, 2012; Schuback *et al.*, 2015)). Ces travaux à l'échelle de l'organisme sont réalisés avec des méthodes expérimentales en laboratoire ; mettant en œuvre des mésocosmes (Carpenter, 1996), ou sur le terrain, par le biais de prélèvements *in situ* (Diamond, 1983). Grace à ces méthodes, un processus biologique particulier est mesuré en présence d'une seule, puis d'une combinaison de perturbations. Ces expérimentations sont indispensables afin de comprendre comment plusieurs facteurs peuvent influencer les processus biologiques, mais les approches expérimentales sont souvent limitées à l'échelle des systèmes qu'elles peuvent étudier. Il est en effet compliqué

d'extrapoler les effets du cumul sur la physiologie d'une espèce, à l'échelle de l'écosystème complet, particulièrement en ce qui concerne les expérimentations *ex situ*. De plus, chaque approche possède des limites particulières au système qu'elle étudie, ainsi les expérimentations *in situ* et *ex situ* possèdent des limites différentes. Les expérimentations *ex situ* peuvent être limitées par leur difficulté à extrapoler les résultats des processus physiologiques ou de population, à l'échelle de la communauté. A contrario, les expérimentations *ex situ* peuvent avoir du mal à déterminer les origines des potentielles réponses de par leur impossibilité à isoler le système étudié. Néanmoins, l'approche expérimentale reste l'approche principalement utilisée et offre les premières informations sur les effets de combinaison de facteurs sur le vivant, même si cela est généralement fait à une échelle écologique réduite, et sans prendre nécessairement en compte une variabilité spatio-temporelle importante (Hodgson and Halpern, 2019). Les études expérimentales sont principalement utilisées à des fins de recherches académiques car elles cherchent à expliquer les mécanismes derrière le cumul, elles vont néanmoins servir de base pour une large variété de travaux, que ce soit à des fins appliquées ou non.

Parmi les approches qui bénéficient des informations obtenues par les approches expérimentales, on compte les modèles qualitatifs, qui rassemblent une large variété de méthodes (Smit and Spaling, 1995; Hodgson and Halpern, 2019). Les modèles qualitatifs ont largement été utilisés pour conceptualiser le cumul d'impacts ainsi que les potentiels effets du cumul à de larges échelles écosystémique (Smit and Spaling, 1995). Néanmoins, leur utilisation à des fins appliquées reste relativement limitée malgré leur fort potentiel (Justus, 2006). Les modèles qualitatifs regroupent des modèles d'analyses de réseaux et de « loop analysis » (Levins, 1974), des modèles matriciels (Carey *et al.*, 2014; Raoux *et al.*, 2018) ainsi que d'autres types d'approches (Dambacher *et al.*, 2007). Ces modèles peuvent modéliser les liens, de manière qualitative ou semi-quantitative, entre les composants d'un système mais également entre les composants du système et les facteurs de changement. Ces travaux utilisent largement le dire d'experts pour réaliser ces liens, ce qui permet ainsi d'établir les voies d'interactions pouvant conduire aux effets cumulés sans nécessairement les avoir quantifiés. C'est grâce à leur capacité à donner un aperçu des voies directes et indirectes pouvant conduire au cumul d'impacts que ces approches ont pu mettre en avant les potentiels risques du cumul d'impacts à l'échelle des écosystèmes (Reum *et al.*, 2015). Néanmoins, l'aspect

qualitatif de ces approches, leur permettant de plus aisément modéliser des systèmes manquant d'informations, est aussi leur principale limite. Les résultats qu'ils produisent sont en effet fortement liés aux informations partielles, voire subjectives, utilisées pour bâtir les modèles (généralement par dire d'experts). Leur principale limite reste néanmoins leur incapacité à prendre en compte la variabilité spatiale mais également leur impossibilité à tenir compte des effets non additifs, résultant d'interactions complexes entre les facteurs environnementaux.

Les études expérimentales servent également à la mise en place de méta-analyses permettant de déterminer de grandes tendances dans l'étude du cumul d'impacts. Les méta-analyses peuvent être utilisées pour cibler les interactions entre plusieurs facteurs spécifiques, comme le changement climatique et la pêche par exemple (Crain *et al.*, 2008). Les méta-analyses étant limitées par l'échelle des études qu'elles compilent, elles gardent souvent les limites de ces dernières, ce qui se traduit par des analyses très individu-centrées même s'il existe quelques travaux à l'échelle des communautés (Côté *et al.*, 2016). Cela peut également se traduire par une non-prise en compte de la variabilité spatio-temporelle. Une des utilités principales de ces approches est leur capacité à soulever les risques du cumul d'impacts. Ainsi, les métanalyses ont montré que les effets interactifs résultant de l'interaction de plusieurs facteurs environnementaux étaient plus importants que les effets additifs (Darling and Côté, 2008). Grâce au développement de l'outil informatique, les méta-analyses se sont développées au cours de 21^{ème} siècle. Il est par contre nécessaire de faire attention aux différentes typologies d'effets interactifs pouvant être utilisées dans les différents articles publiés. En effet, la typologie des effets interactifs peut varier, parfois même en gardant les mêmes noms, mais ne reflétant pas exactement les mêmes effets (exemples de différentes typologies d'effets cumulés Folt and Chen 1999; Crain *et al.* 2008; Piggott *et al.* 2015; Fu *et al.* 2018 ; Figure I - 3).

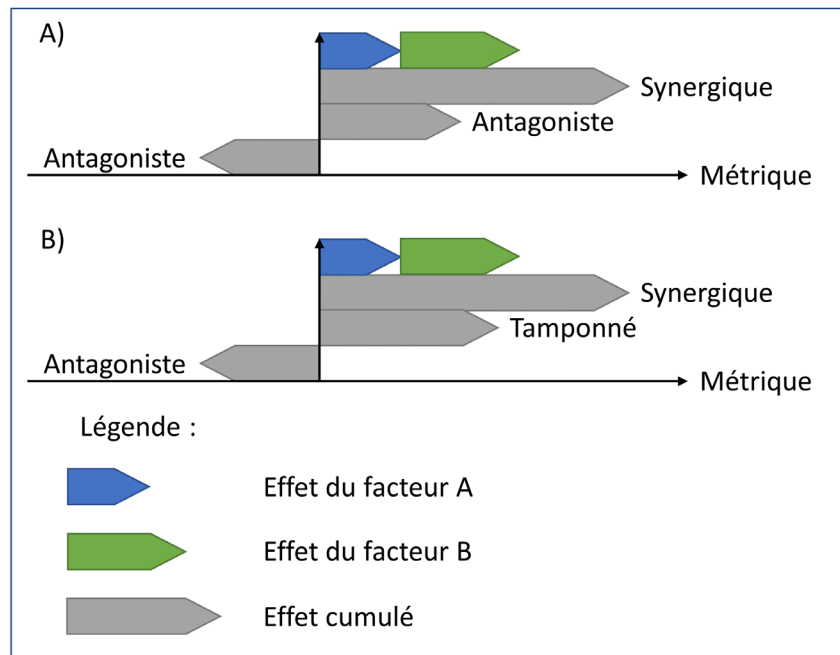


Figure 1 - 3 Évolution de la typologie des effets cumulés.

Les effets cumulés sont caractérisés différemment entre les auteurs : A) venant de Folt and Chen (1999) et Crain et al. (2008) ; et B) de Travers-Trolet et al. (2014) et Fu et al. (2018).

Un autre type d'approche ayant fortement permis de mettre en avant les potentiels risques du cumul d'impacts sont les approches cartographiques utilisant des systèmes d'informations géographiques (SIG). Il existe une très grande variété d'études faisant appel à cette approche (Halpern *et al.*, 2008b, 2015; Ban *et al.*, 2010; Clarke Murray *et al.*, 2015; Kotta *et al.*, 2020). Elles ont particulièrement été utilisées pour l'évaluation des effets cumulatifs à des fins d'aide à la décision et afin d'orienter la planification des territoires, qu'ils soient terrestres ou marins. Utilisant un système d'information géographique, ces méthodes cartographient les empreintes géographiques de plusieurs facteurs environnementaux afin de déterminer l'entendue de leur chevauchement. Ces approches peuvent également intégrer d'autres paramètres que les empreintes des facteurs : comme le type d'habitat et/ou la présence d'espèces (observée ou théorique à travers l'utilisation de modèles de distribution). Ceci va ainsi permettre de déterminer les habitats/espèces potentiellement les plus menacés par le cumul d'impacts ainsi que les zones pouvant nécessiter une protection particulière au vu des risques encourus. Le principal intérêt de ces approches est donc la prise en compte de la variabilité spatiale. Néanmoins, toutes approches spatialisées possèdent des limites qui peuvent être attribuées à la résolution spatiale utilisée ou bien à l'incertitude des données.

Une autre limite importante est celle attribuée à la quantité d'informations nécessaires pour la réalisation de cartographies ainsi qu'à l'utilisation importante des dires d'experts. Ainsi, le potentiel impact des facteurs sur les différents habitats et/ou espèces est défini en fonction d'études réalisés sur d'autres écosystèmes (information bibliographique) ou à travers du dire d'experts (Halpern *et al.*, 2007; Teck *et al.*, 2010). C'est également le cas des empreintes des facteurs environnementaux, qui sont pourtant fortement influencé par un grand nombre de paramètres écosystémiques, comme le déplacement des espèces, la variabilité spatiale des habitats et bien d'autres (Osenberg *et al.*, 1994; Fraterrigo and Rusak, 2008; Fraterrigo *et al.*, 2020). Mais la limite principale des approches cartographiques est la non prise en compte des interactions entre les facteurs (Ban *et al.*, 2010; Korpinen and Andersen, 2016). Ces approches sont généralement statiques, ne prenant donc pas en compte la variabilité temporelle du système ainsi que les évolutions futures possibles. Cependant, il existe des travaux prometteurs, même si peu nombreux, qui estiment ces évolutions et qui extrapolent des scénarios futurs (Afflerbach *et al.*, 2017; Andersen *et al.*, 2017). Malgré leurs limites, ces approches restent importantes pour sensibiliser la communauté scientifique à la prévalence des risques du cumul d'impacts (cf. Crain *et al.* 2008 et Halpern *et al.* 2008).

D'autres approches se distinguent par leur capacité à étudier le cumul de manière plus intégrée, il s'agit des modèles écosystémiques quantitatifs. Les modèles écosystémiques sont utilisés pour caractériser les écosystèmes dans toute leur complexité, en considérant les interactions inter et intra spécifiques. En écologie marine, on prend généralement en compte les interactions trophiques entre les espèces rassemblées en groupes écologiques/trophiques. Ces relations correspondent aux relations entre une proie et son prédateur. Des modèles trophiques caractérisant l'intégralité d'un écosystème, sont donc des modèles écosystémiques. Il existe un grand nombre de modèles écosystémiques qui peuvent simuler les écosystèmes marins à différents niveaux de complexité (Plagányi, 2007). En modélisant les interactions entre les espèces, ces modèles permettent de mettre en évidence les effets indirects des facteurs environnementaux sur le fonctionnement (flux de transfert au sein du système) et la structure (organisation des compartiments du système) des écosystèmes. C'est grâce à cette compétence qu'ils peuvent permettre une meilleure compréhension des mécanismes du cumul et prennent ainsi en compte les interactions entre facteurs environnementaux conduisant aux effets cumulés. C'est pour cette raison qu'ils sont

considérés comme indispensables pour une meilleure compréhension du cumul d'impacts (Kerr, 1982). Ces modèles ne permettent pas uniquement d'avoir une des visions les plus complexes des écosystèmes par rapport aux autres approches, ils peuvent également avoir une vision des écosystèmes explicites dans le temps et l'espace. Cependant, ces modèles sont également les plus compliqués à paramétrer. Ces modèles nécessitent en effet beaucoup de données sur le système étudié et les espèces qui y vivent, mais également des utilisateurs qualifiés et un temps important de mise en place mais aussi de calcul (Fulton *et al.*, 2004, 2011; Heymans *et al.*, 2016). Ces modèles sont également sujets à une forte incertitude autour des résultats obtenus et produisent une quantité d'informations importante qu'il peut être compliqué d'interpréter. Tout ceci rend ainsi la modélisation d'un grand nombre de facteurs compliqués, de par des raisons de faisabilité mais également de par la complexification de l'analyse des résultats. Les travaux mettant en place des modèles écosystémiques pour étudier le cumul d'impacts utilisent une large gamme d'approches (Fu *et al.*, 2018), telles que Osmose (Travers-Trolet *et al.*, 2014), Atlantis (Ortega-Cisneros *et al.*, 2018) ou encore *Ecopath with Ecosim* (Serpetti *et al.*, 2021).

Actuellement, ces travaux se concentrent principalement sur les effets du cumul d'impacts, sur la structure des systèmes étudiés, en utilisant des métriques basées sur les communautés, comme sur les biomasses des groupes écologiques des modèles. Néanmoins, à notre connaissance, il n'existe pas d'étude qui ait regardé l'effet du cumul d'impacts sur le fonctionnement global des écosystèmes. Pourtant, la communauté scientifique ainsi que les institutions ont depuis longtemps mis en avant le besoin d'étudier le fonctionnement des écosystèmes et leur évolution face aux impacts de l'homme (Balvanera *et al.*, 2005; de Jonge, 2007; Truchy *et al.*, 2015). C'est en regardant le fonctionnement des écosystèmes que l'on peut avoir une information sur les propriétés émergentes des écosystèmes comme la résilience écologique ou résistance face aux perturbations écosystémiques (Ulanowicz, 2004; Ulanowicz *et al.*, 2009; Saint-Béat *et al.*, 2015). Dans le contexte des changements globaux résultant des activités humaines, la question de la résilience des écosystèmes est cruciale pour déterminer la pérennité de la fourniture en services écosystémiques (Levin and Lubchenco, 2008; Montefalcone *et al.*, 2012; Oliver *et al.*, 2015). Ce sont en effet les fonctions écosystémiques qui permettent un bon approvisionnement en services écosystémiques (Peterson and Lubchenco, 1997; Costanza and Mageau, 1999; Costanza *et al.*, 2017), il convient

donc d'évaluer leurs sensibilités aux changements environnementaux ainsi que de prendre en compte leurs évolutions possibles dans le futur. Etudier le cumul d'impacts et son effet sur le fonctionnement des écosystèmes marins est donc crucial. Ainsi utiliser des modèles écosystémiques pour l'étude du cumul, c'est suivre les recommandations et les demandes de la communauté d'utiliser des outils toujours plus holistiques (Rombouts *et al.*, 2013; Fath *et al.*, 2019; Heymans *et al.*, 2020), et ainsi, garder une cohérence d'approche.

1.3 Approche fonctionnelle et gestion des écosystèmes

Les approches fonctionnelles sont des méthodes qui tentent de comprendre le fonctionnement des écosystèmes. Les termes « fonction » et « fonctionnement » ont reçu une importance particulière en écologie depuis les années 1960. Aujourd'hui ils sont principalement utilisés en relation avec les idées de : fonction des espèces, diversité fonctionnelle, fonctionnement des écosystèmes et fonction des écosystèmes. Le terme « fonction » en écologie joue donc plusieurs rôles. Pour différencier ces rôles, il faut se demander à quelle échelle ces termes sont-ils utilisés. Le terme « fonction » est dans toutes ces utilisations : synonyme d'actions qui se passent entre plusieurs éléments, de manière directionnelle et temporelle, comme une interaction. Comme toute action, elle est l'objet direct d'une relation causale (cause à effet), analogue à un procédé. Selon le niveau de complexité (l'échelle choisie), le « procédé » peut donc changer. A l'échelle d'un organisme vivant, on peut regarder la fonction de ses organes, ou alors avec une vision plus large, le fonctionnement de l'organisme lui-même, dépendant de tous les organes. En écologie, on regarde la fonction des organismes selon leurs relations avec les autres organismes d'un système (comme par exemple le rôle d'herbivore d'une espèce qui mange des plantes, la relation est donc alimentaire, et elle a lieu avec des plantes). En regardant à plus grande échelle, un observateur peut quantifier : la richesse des fonctions au sein d'un système (richesse fonctionnelle) ou bien le fonctionnement global du système (fonctionnement des écosystèmes). Le point de vue de l'observateur définit ainsi la fonction étudiée. L'échelle n'est pas seulement verticale (espèce -> communauté -> écosystème), elle peut également être horizontale (Figure I - 4). Ainsi, si l'observateur choisit de prendre le point de vue de l'humanité en lien avec son écosystème, il peut également voir la fonction du système et de ses composantes pour l'homme (fonction des écosystèmes pour l'homme, en lien avec la notion de services écosystémiques). Dans notre cas, si on décide de regarder le fonctionnement des

écosystèmes, on regarde ainsi les processus globaux qui soutiennent et définissent l'écosystème (Naeem *et al.*, 1999; Jax, 2005).

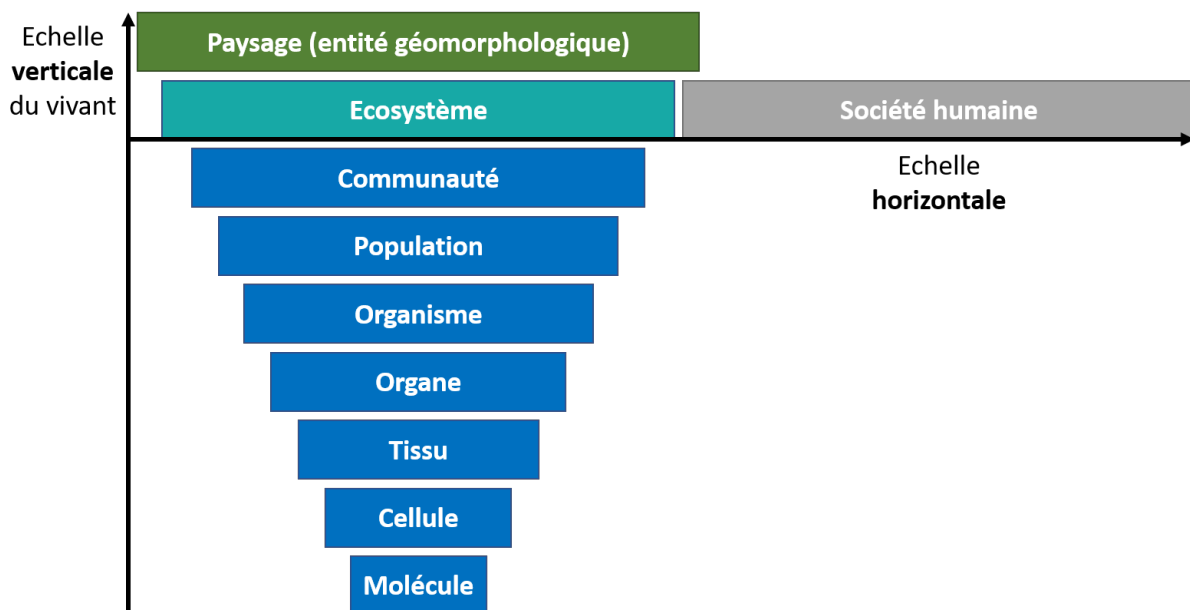


Figure I - 4 Echelle verticale et horizontale d'analyse du fonctionnement du vivant.

Inspiré de Odum and Barrett (1971).

En écologie marine, la recherche s'est concentrée sur les réseaux d'interactions trophiques entre les espèces, considérés comme clefs pour comprendre la dynamique, le maintien et le fonctionnement de ces systèmes complexes (Shurin *et al.*, 2006). Les réseaux trophiques utilisés pour étudier le fonctionnement des écosystèmes marins sont des réseaux qui représentent les interactions proie/prédateur d'un écosystème. L'unité de ces réseaux peut varier en fonction des approches mais les travaux utilisent généralement la matière organique ou le carbone organique comme unité d'énergie, qui circule entre des groupes trophiques, à travers les voies/flux trophiques (MacArthur, 1955). Les groupes trophiques, sont des groupes qui rassemblent des espèces pouvant partager la même écologie, les mêmes préférences trophiques (préférences alimentaires), des rythmes physiologiques équivalents, et même un habitat commun (c'est pour cela que l'on peut également les appeler groupes écologiques ou même fonctionnels) (Leguerrier *et al.*, 2003). Dans un modèle écosystémique, et donc dans un réseau trophique, les groupes trophiques correspondent à l'unité constituante du modèle, il s'agit des nœuds du modèle (Figure I - 5). Ces groupes peuvent être différenciés en fonction de leur niveau trophique, c'est-à-dire de leur position dans le réseau (Figure I - 5).

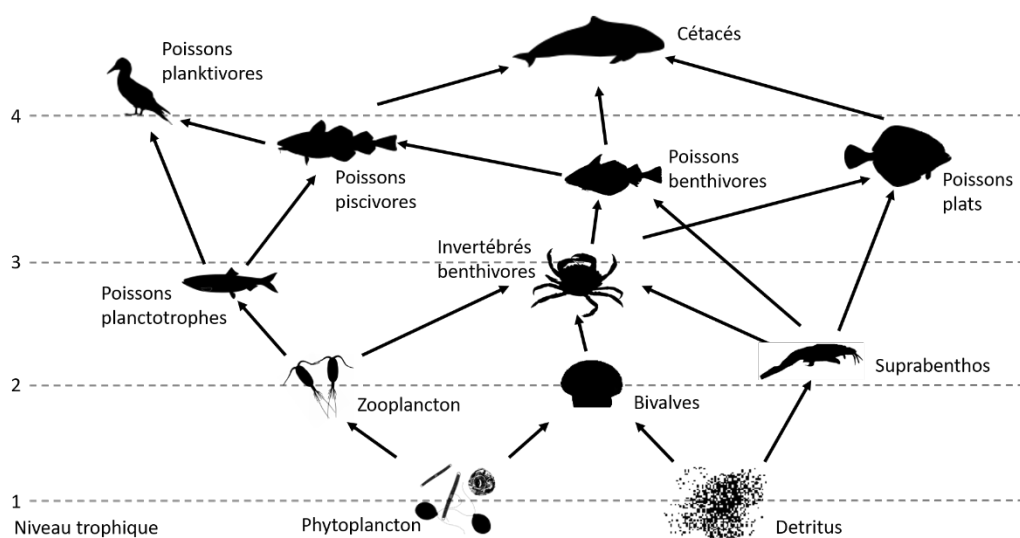


Figure I - 5 Schéma d'un réseau trophique.

Schéma organisé en fonction du niveau trophique des groupes.

Les approches écosystémiques sont particulièrement mises en avant ces dernières décennies car la gestion et la protection de la nature a évolué. Nous sommes passés d'une vision très espèce-centrée vers une vision plus écosystémique (Garcia *et al.*, 2003). Aujourd'hui on met en avant des approches plus environnementales et intégratives, qui prennent en compte l'intégralité des écosystèmes (Levin and Lubchenco, 2008; Buhl-Mortensen *et al.*, 2017; Fath *et al.*, 2019), car nos connaissances des écosystèmes ont évolué.

Comprendre le fonctionnement des écosystèmes a été et est toujours une question centrale pour les chercheurs en écologie. Les premiers travaux à s'intéresser à la notion de fonctionnement des écosystèmes remontent au début du 20^{ème} siècle. Ainsi, au début du 20^{ème} siècle, on étudie le fonctionnement des écosystèmes en utilisant des chaînes linéaires alimentaires (Lindeman, 1942). En utilisant des notions de thermodynamique, Lindeman (1942) utilise des chaînes trophiques (chaîne de Lindeman) pour expliquer les transferts d'énergies organiques au sein des écosystèmes. Ces approches ont permis de mieux comprendre l'organisation des systèmes vivants (Higashi *et al.*, 1989; France, 2014). Cependant, la communauté scientifique savait déjà que les écosystèmes et les interactions qui les dirigeaient étaient plus complexes que de simples chaînes. C'est avec la mise en évidence de l'importance de la complexité des écosystèmes comme propriété intrinsèque liée à leur stabilité, que les écosystèmes furent représentés comme des réseaux complexes d'interactions (MacArthur, 1955). En effet, MacArthur (1955) hypothèse que la stabilité des écosystèmes dépend de la multiplicité des voies trophiques qu'une unité d'énergie peut

emprunter en cas de perturbation. Ainsi, si le réseau trophique ne permet pas le bon acheminement de l'énergie aux différents groupes écologiques, le système s'effondrerait et ferait face à une modification catastrophique de sa dynamique, conduisant ainsi à un changement de son fonctionnement. D'autres auteurs ont mis en évidence l'importance de la « connectance » des systèmes pour leur maintien, c'est-à-dire à quel point les systèmes sont interconnectés (May, 1973). Même si la question de la relation entre complexité et stabilité des écosystème fait toujours l'objet d'un débat important (Pimm, 1984; Altena *et al.*, 2016; Jacquet *et al.*, 2016), May (1973) montra que, mathématiquement, la complexité avait tendance à déstabiliser les écosystèmes. Néanmoins il mit en évidence que des patrons stabilisants existaient dans la nature, indiquant donc que complexité et stabilité n'étaient pas obligatoirement corrélées. Néanmoins l'information de la connectivité d'un système reste importante dans une vision intégrative du fonctionnement des écosystèmes (voire (Altena *et al.*, 2016)). On montre également le rôle non négligeable de la détritivorie comme source d'énergie pour ces systèmes complexes (Wiegert and Owen, 1971). La production primaire n'apparaît ainsi plus comme la seule entrée d'énergie possible dans un système. Odum (1969) montre également que les systèmes ne sont pas statiques, mais qu'ils évoluent tout au long de leur développement, modifiant leur dynamique et leur fonctionnement vers un climax. Le recyclage au sein des écosystèmes est aussi présenté comme une fonction importante des systèmes (Finn, 1976).

Il devient ainsi évident que quantifier ces différentes propriétés de fonctionnement des écosystèmes est nécessaire pour caractériser le fonctionnement et l'organisation des écosystèmes. Ainsi une multitude d'indices fonctionnels sont mis en avant pour permettre de caractériser le fonctionnement des écosystèmes et en les reliant aux théories écologiques, pour déterminer l'état des écosystèmes et de leurs propriétés émergentes (propriétés inhérentes au fonctionnement de l'écosystème). Grâce à la modélisation des écosystèmes avec les modèles trophiques, la communauté scientifique peut calculer des indices comme l'efficacité de transfert trophique (trophic efficiency ou transfert efficiency, TE ; Lindeman 1942). Des indicateurs du recyclage de l'énergie dans un système, c'est à dire du passage de l'énergie dans des cycles, sont proposés comme le « Finn cycling index » (FCI ; Finn 1976). Le rapport détritivorie sur herbivorie voit le jour afin de pouvoir déterminer la part des sources d'énergies d'un système (D/H ; Kay *et al.* 1989). Les théories de l'information sont utilisées

pour développer des indices pour quantifier la diversité des voies de passages possibles de l'énergie dans un système (Rutledge *et al.*, 1976; Ulanowicz and Norden, 1990). Ainsi, en regardant l'incertitude autour des sources d'énergies d'un élément du système, il est possible de déterminer la richesse des flux d'un système. Des théories de l'information, on utilise également les notions issues de l'entropie à travers la mise en place d'un indice d'organisation : l'AMI ou « Average mutual information » qui utilise les équations de l'entropie conditionnelle d'un système pour quantifier les contraintes autour de l'organisation d'un système (Gallager, 1972; Rutledge *et al.*, 1976; Ulanowicz and Norden, 1990). C'est par le biais des théories de l'information que des indicateurs de la redondance des flux dans un système ou encore des indicateurs du développement d'un système vont être mis en place (Ulanowicz, 1986). Par d'autres indicateurs (ex Pauly *et al.* 1998; Latham 2006; Libralato 2013), le concept d'analyse des réseaux écologiques ou ENA (« ecological network analysis » en anglais) se développe et propose une large gamme d'indicateurs fonctionnels. Les indicateurs ENA sont donc dirigés par l'écologie des écosystèmes en analysant tous les flux (tout le réseau d'interactions) qui constitue la base du fonctionnement des écosystèmes marins. Il s'agit donc d'indices holistiques et intégratifs qui informent sur des propriétés des écosystèmes, impossibles à quantifier grâce à des observations des éléments isolés de l'écosystème.

Actuellement, la Directive Cadre « Stratégie pour le Milieu Marin » européenne (DCSMM) souligne le besoin urgent de développer, tester et valider des indicateurs de santé des écosystèmes (EC, 2008). Ces indicateurs doivent prendre en compte la structure, les fonctions et les processus des écosystèmes marins afin d'atteindre un bon état écologique (EC, 2017). Aujourd'hui, les indices ENA semblent donc idéalement placés pour aider les gestionnaires à la prise de décision en les informant sur l'état fonctionnel des écosystèmes, sur leur organisation et structure (Niquil *et al.*, 2014a; de la Vega *et al.*, 2018; Ulrike *et al.*, 2018; Safi *et al.*, 2019). Les capacités des indices ENA à caractériser une grande variabilité de processus fonctionnels en font des outils de choix pour la gestion intégrée des écosystèmes (Ecosystem-based management ou EBM ; voir Borja *et al.* 2010). Les indices ENA se montrent également très utiles grâce à leur capacité à étudier les écosystèmes à de multiples échelles, que ce soit en local ou bien à des échelles régionales. Les indices ENA peuvent ainsi être mis en œuvre pour des programmes de gestion à des échelles locales, mais également pour aider à de grands plans de gestion (Giebels *et al.*, 2013; Soma *et al.*, 2015). Grâce à cela, les indices

ENA ont été proposés à de nombreux programmes de stratégies générales de gestion. C'est pour cela que la convention OSPAR (coopération internationale sur la protection du milieu marin de l'Atlantique du Nord-Est) intègre les indices ENA dans sa liste d'indicateurs de santé des écosystèmes dérivés de modèles trophiques (Niquil *et al.*, 2014a). Néanmoins, afin de rendre les indicateurs ENA opérationnels, plusieurs travaux ont été réalisés afin de tester leur capacité à caractériser les effets d'une perturbation sur l'état de santé des écosystèmes (Baird *et al.*, 2012; Tecchio *et al.*, 2016; de la Vega *et al.*, 2018). Pour rendre ces indices opérationnels il convient donc d'innover dans leur utilisation et de multiplier leur utilisation en lien avec des thématiques demandées, comme en les utilisant dans le cadre d'études du cumul d'impacts.

1.4 Le cumul d'impacts sur le fonctionnement des écosystèmes.

Les indices ENA ont permis de mettre en évidence les effets des nombreuses activités de l'homme sur le fonctionnement et l'organisation de multiples écosystèmes marins, depuis les effets d'une extension portuaire (Tecchio *et al.*, 2016), jusqu'aux effets du changement climatique (Chaalali *et al.*, 2015), d'espèces invasives (Baird *et al.*, 2012) ou encore de la pêche (Libralato *et al.*, 2010). Même si certains travaux ont pu tester les effets de plusieurs facteurs environnementaux simultanément (Tomczak *et al.*, 2013; Heymans and Tomczak, 2016), aucun travail n'a jusqu'à présent utilisé les ENA pour étudier le cumul d'impacts. Or dans le but de développer les indices ENA afin de les rendre plus opérationnels, il est crucial de les tester en prenant en compte les potentiels effets cumulés pouvant résulter des interactions entre plusieurs facteurs (Heymans *et al.*, 2020). Ceci rejoint le fait qu'aujourd'hui, trop peu d'études ont travaillé sur les effets du cumul sur le fonctionnement des écosystèmes marins (Boyd and Hutchins, 2012). Le fonctionnement des écosystèmes jouant un rôle prépondérant dans l'approvisionnement en services écosystémiques, ignorer les potentiels effets du cumul d'impacts serait donc une erreur importante. Avec des effets cumulés pouvant varier entre les niveaux trophiques, le cumul d'impacts semble présenter un défi important pour la compréhension de l'organisation et du fonctionnement des écosystèmes.

De plus, même si l'étude écosystémique du cumul d'impacts commence à prendre racine dans différents travaux (Fu *et al.*, 2018; Ortega-Cisneros *et al.*, 2018; Serpetti *et al.*, 2021), l'étude des effets interactifs de manière spatialisée reste très limitée. C'est d'autant plus important que des études tendent à montrer que le cumul d'impacts est fortement corrélé à l'hétérogénéité des milieux (Boyd and Hutchins, 2012) et ainsi les impacts locaux dans des

écosystèmes côtiers très hétérogènes pourraient avoir des effets cumulés importants. Le changement climatique viendrait également exacerber ce risque, nécessitant donc sa prise en compte dans le cadre d'études d'impacts sur des environnements côtiers. C'est pour cela que, dans le cadre du développement éolien offshore sur les côtes françaises, il apparaît important d'étudier les potentiels risques des interactions entre les énergies marines renouvelables (EMR) et le changement climatique, ainsi qu'avec les autres pressions telles que la pêche.

2 Les études en baie de Seine.

La baie de Seine est un espace maritime situé au large de la Normandie, dans la partie nord de la France. Elle fait partie de la Manche (English Channel) et plus particulièrement de la Manche orientale. Entre la péninsule du Cotentin à son ouest (département de la Manche), la côte de Nacre à son sud (département du Calvados) et le Pays de Caux à son est (département de la Seine-Maritime). La baie forme un espace d'approximativement 5.000 km² (50 kilomètres de hauteur et 100 de largeur). On parlera également de la baie de Seine étendue (eBoS) qui possède comme limite nord la délimitation de la zone économique exclusive entre le France et le Royaume-Unis à son nord (ZEE) et couvre un espace d'approximativement 13.500 km² (Figure I - 6). Que ce soit la baie de Seine ou sa version étendue, il s'agit d'un espace maritime peu profond avec une moyenne de 30 et de 35 mètres de fond respectivement, et une profondeur maximale de 50 (BoS) et 71 (eBoS) mètres. Les principales structures morphodynamiques de la baie sont attribuées à l'activité du fleuve de la Seine, avec son estuaire situé au sud-est de la baie et les paléo-vallées du fleuve courant de l'embouchure jusqu'au nord-ouest de la baie étendue (zone les plus profondes de la zone eBoS). La Seine est la principale source en eau douce avec un débit moyen interannuel de 400 m³.s⁻¹, même s'il ne s'agit pas de l'unique source d'eau douce (on pourra également citer l'Orne ainsi que la Douve, la Taute, la Vire et l'Aure). La baie de Seine est un espace maritime fortement anthropisé et à forte valeur économique, patrimoniale et culturelle.

La baie de Seine a fait l'objet, depuis ces dernières années (2014 à aujourd'hui), de plusieurs travaux de modélisations s'intéressant aux potentiels impacts du futur parc éolien en mer de Courseulles-sur-Mer (aujourd'hui en cours de construction). Ces travaux s'inscrivent dans la continuité des travaux de thèse d'Aurore Raoux intitulée : « Approche écosystémique des Energies Marines Renouvelables étude des effets sur le réseau trophique de la

construction du parc éolien au large de Courseulles-sur-Mer et du cumul d'impacts. » (2014 à 2017). Ces différents travaux se sont toujours concentrés sur les potentiels effets du parc éolien afin de pouvoir soutenir le processus naissant en 2014, de développement de l'éolien offshore en France.

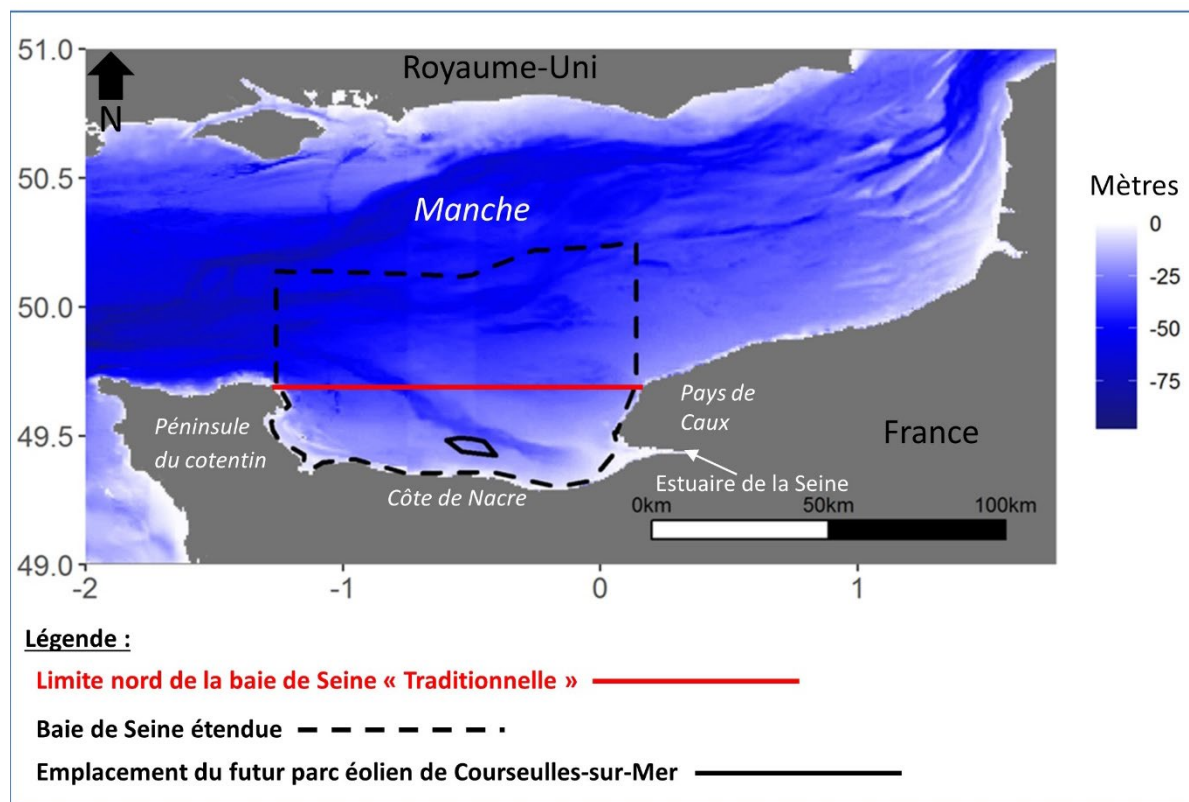


Figure I - 6 Carte de la baie de Seine et de la baie de Seine étendue.

2.1 Les caractéristiques de la baie de Seine

La baie de Seine fait l'objet d'un marnage dit semi-diurne pouvant atteindre en période de vives eaux jusqu'à 7 mètres. Le mouvement des masses d'eaux joue un rôle prépondérant dans la distribution sédimentaire marine. Ainsi, de par l'action de la marée, on observe un gradient sédimentaire côte large avec des sédiments plus grossiers au large de la baie (graviers ensablés) et des sédiments plus fins proche de la côte (sables fins et sables fins sablo-vaseux ; Larsonneur *et al.* 1982). Le trait côtier est composé d'une large variété de types sédimentaires, avec des sédiments vaso-sableux au niveau des baies et estuaires abrités, des plages sableuses et vaseuses ainsi que des zones avec du substrat rocheux. Ces différents types sédimentaires ont un impact important sur la structuration des communautés benthiques (Figure I - 7).

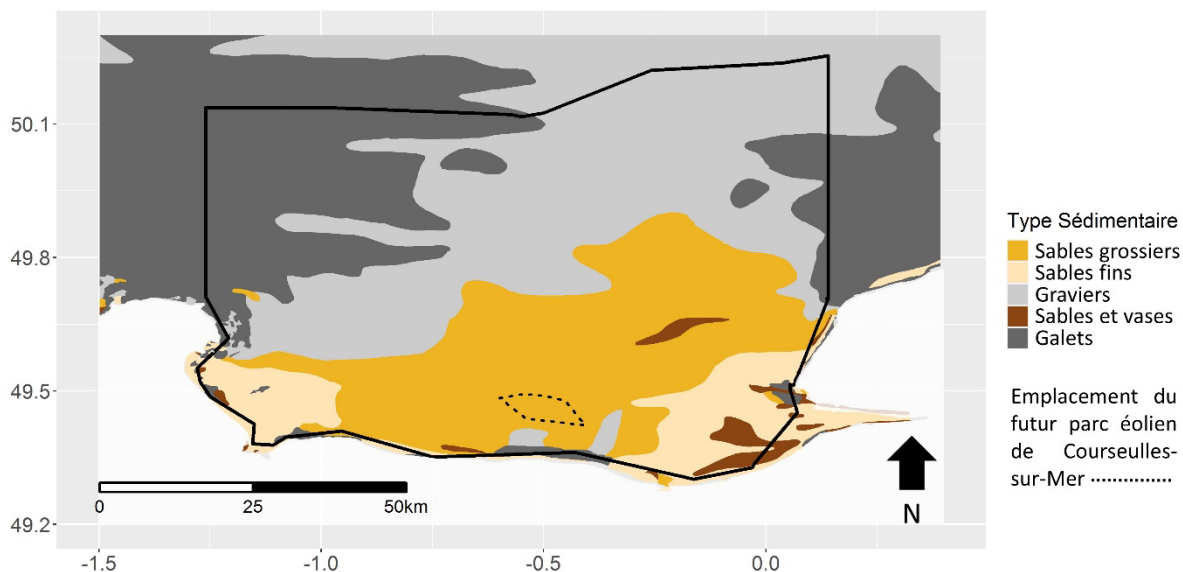


Figure 1 - 7 Carte des types sédimentaires de la baie de Seine étendue (modifiée d'après Larssonneur et al., 1982)

Plusieurs communautés sont identifiées par type sédimentaire au cours de plusieurs travaux, avec Gentil and Cabioch (1997) qui identifie six principales communautés et Baffreau et al. (2017) huit communautés. Dans Baffreau et al. (2017), on compte cinq communautés principales, et trois autres de moins grande importance pour un total de huit types de communautés benthiques : (1) La communauté de sable fin boueux d'*Abra alba* (espèce de bivalve dominante), on retrouve cet habitat principalement à l'embouchure des estuaires, dans la zone subtidale, que ce soit en zone occidentale ou orientale de la baie. (2) La communauté des boues sableuses de *Melinna palmata* (espèce de polychaete) cet habitat subtidal se retrouve principalement dans la partie orientale de la baie de Seine, de part et d'autre de l'embouchure de la Seine. (3) La communauté des sables fins et moyens à *Ophelia borealis* / *Nephtys cirrosa* (deux espèces de polychaete), se trouve sur des sables subtidaux fins et moyens dans la partie occidentale de la baie. (4) La communauté infralittorale de sédiments grossiers et mixtes à *Ophiothrix fragilis* (échinoderme), dans la partie centrale de la baie de Seine, est caractérisée par des sédiments graveleux avec de forts courants. Il s'agit de la communauté principale de la baie de Seine, occupant la plus forte surface, avec la plus forte biodiversité et aux fonctions importantes (Baffreau et al., 2017). (5) Communautés à fond dur, ces habitats possèdent une distribution non-homogène, mais on les trouve principalement dans la partie occidentale de la baie. (6) On trouve également des habitats sous condition de salinité variable au niveau des estuaires et principalement au niveau de l'estuaire de la Seine.

(7) Les communautés intertidales à fond mou, quant à elles, regroupent les différentes communautés qui subissent les aléas des marnages des côtes normandes. Enfin (8) les habitats particuliers regroupent ceux qui ne sont pas compris dans les catégories précédentes, comprenant des récifs de moules ainsi que des herbiers.

Les communautés de poissons quant à elles suivent un gradient côte large. Elles furent décrites par Vaz *et al.* (2007) grâce aux données de campagnes CGFS réalisées depuis 1988. Quatre communautés ont pu être définies avec : (1) La communauté du large comprenant des Tacauds (*Trisopterus luscus*) et des tops prédateurs éla-smobran-ches comme la petite roussette (*Scyliorhinus canicula*) ainsi que plusieurs espèces de raies (*raja undulata*). (2) La communauté intermédiaire comprenant des espèces pélagiques comme le maquereau (*Scomber scombrus*) ainsi que des espèces démersales comme le dragonnet (*Callionymus lyra*) ou le grondin (*Chelidonichthys lucerna*). On y retrouve également des Tacauds (*Trisopterus luscus*). Deux communautés côtières sont discernables, (3) une communauté homogène avec des céphalopodes comme des seiches et des calamars (*Sepia officinalis* et *Loligo sp*) ainsi que des espèces pélagiques comme la sardine (*Sardina pilchardus*) et des espèces démersales comme le rouget-barbet (*Mullus surmuletus*). Cette communauté est caractéristique des communautés benthiques associées aux sédiments de sable fin. A la différence de (4) la communauté hétérogène côtière qui préfère une gamme d'habitats benthiques plus hétérogènes (vivant sur des habitats variant de boues à des sables grossiers). Cette communauté se trouve principalement près de la côte, à proximité de grands estuaires de rivières. Cette communauté très diverse est principalement composée d'espèce de poissons plats (comme la sole *Solea solea*), ainsi que de Capelins (*Trisopterus minutus*).

La baie de Seine est également un lieu de vie pour plusieurs espèces de mammifères marins comme des grands dauphins (*Tursiops truncatus*) ou bien des Marsouins (*Phocoena phocoena*) qui sont fréquemment observés par des bateaux au large ou bien retrouvés échoués sur les plages. Il existe aussi plusieurs colonies de phoques vivant dans la baie, comprenant des phoques veau-marins (*Phoca vitulina*) ainsi que des phoques gris (*Halichoerus grypus*). Enfin il existe également une grande variété d'oiseaux marins qui vivent à proximité et dans la baie de Seine (depuis des Fous de bassan *Morus bassanus*, jusqu'à des petits pingouins *Alca torda*). L'avifaune peut profiter des parcs de la réserve ornithologique du Gros

Banc et du parc naturel régional des marais du Cotentin et du Bessin (près de la baie des Veys) ainsi que la réserve naturelle de l'estuaire de la Seine.

2.2 Les activités humaines en baie de Seine.

La baie de Seine n'est pas qu'un lieu important pour les espèces marines, c'est également un espace important pour l'homme. En proximité directe avec l'une des voies de transport maritime la plus importante du monde (la Manche représenté 20% du trafic mondial en 2008 ; (Buléon and Shurmer-Smith (2021)), la baie de Seine fait partie des écosystèmes les plus anthropisés au monde (Halpern *et al.*, 2007, 2015). Le transport international croise les ferries qui font la jonction avec le Royaume-Uni et les nombreux navires de pêche pratiquant leur activité dans la baie. La pêche est en effet une activité primordiale pour beaucoup vivant en Normandie (Buléon and Shurmer-Smith, 2021). Il existe ainsi de nombreux ports de pêche d'importance nationale en proximité directe avec la baie. Les ports de Port-en-Bessin et de Grandcamp-Maisy se trouvant dans le périmètre de la baie de Seine étendue jusqu'à la délimitation de la ZEE, faisait partie des 10 plus importants ports de pêche en France de par le volume de capture réalisé. Port-en-Bessin est un port majeur de par son rôle principal dans la capture de coquilles Saint Jacques en France (1^{er} port en Europe pour la capture de la Coquilles ; <https://www.franceagrimer.fr/>). Même si la drague à la coquille Saint Jacques constitue une part importante des activités de pêche dans la baie de Seine, une grande variété de méthodes est également utilisée, comme des chaluts pélagiques et des chaluts de fond pour capturer les espèces démersales. On pratique également la pêche à la Senne, mais également la pêche au casier ainsi que d'autres outils de pêche. Ainsi, on capture dans la baie de Seine des espèces de poissons et de céphalopodes pélagiques (calamars, sardine ou maquereau), ainsi que des espèces de poissons et de céphalopodes démersales (seiche, sole ou encore turbot). L'aquaculture joue également un rôle important en baie de Seine, tout comme l'extraction de granulats marins ainsi que le tourisme. Par conséquent on observe que la baie de Seine accueille une large variété d'activités et d'usages. Une activité qui dispose d'un très fort potentiel en baie de Seine est la production d'énergie renouvelable (Buléon and Shurmer-Smith, 2021). La baie de Seine possède en effet un potentiel éolien très fort et c'est pour cette raison qu'elle a été choisie pour accueillir l'un des huit premiers parcs éoliens en mer de France, le parc de Courseulles-sur-Mer. Le potentiel éolien est si important qu'un second parc doit également être construit dans la baie, plus au large que celui de Courseulles-sur-Mer.

Alors que le projet du parc de Courseulles-sur-Mer est finalisé, le second est en cours de négociation avec les partenaires industriels (com. pers. Georges Safi, France Energie Marine). C'est pour cela que depuis quelques années, les potentiels impacts de l'éolien en mer en baie de Seine ont fait l'objet de plusieurs projets et travaux.

2.3 Les études d'impacts du parc éolien offshore de Courseulles-sur-Mer.

Le parc éolien offshore de Courseulles-sur-Mer est en construction au large de la ville du même nom dans le Calvados. Le parc s'étend sur une superficie de 70 km² et est composé de 64 éoliennes en mer monopieux, pour une puissance totale approximative de 450 mégawatts. La construction a commencé en hiver (mars) 2021 et la mise en service est estimée à 2024. La profondeur d'emplacement choisi pour l'installation du parc varie de 22 à 31 mètres, pour une hauteur maximale des éoliennes de 175 mètres et une longueur de pale de 73.5 mètres.

Les premiers travaux d'études d'impacts du parc éolien de Courseulles-sur-Mer ont commencé en 2011 au moment du premier appel d'offre le 11 juillet 2011. Ces premiers travaux mandatés par Eoliennes Offshore du Calvados (EOC) ont couvert une grande partie des compartiments écologiques grâce à de nombreuses missions d'acquisition de données en mer, réalisées par de multiples bureaux d'études. Néanmoins ces travaux ont été faits de manière fractionnée, ne regardant les effets du parc éolien sur les compartiments biologiques que, un à un, sans avoir une vision écosystémique des potentiels effets du parc. Il y avait donc un manque de prise en compte des interactions entre les différents composants de l'écosystème, interactions pourtant cruciales pour les écosystèmes marins. C'est pour pallier à ce manque, que la thèse de Aurore Raoux a été mise en place, se basant entre autres sur les données acquises dans ce cadre (Raoux, 2017). Cette thèse avait pour objectif d'utiliser des approches écosystémiques pour étudier les impacts potentiels du futur parc de Courseulles-sur-Mer en prenant en compte les interactions trophiques de l'écosystème. Pour cela, un modèle trophique, Ecopath, fut mis en place pour modéliser l'écosystème de la zone du futur parc de Courseulles-sur-Mer. Ecopath est une approche de modélisation trophique (Pauly *et al.*, 2000). Avec le programme *Ecopath with Ecosim* (EwE), Ecopath permet de modéliser les réseaux trophiques à l'équilibre, c'est à dire que tout ce qui rentre dans le système doit en ressortir. Avec une approche à l'équilibre, les variations de biomasses sont considérées comme négligeables par rapport aux variations des flux du système. Raoux *et al.* (2017) construisirent deux modèles Ecopath, un modèle avant l'installation du parc qui représentait l'état initial

avant construction du parc (BOWF ou Before offshore wind farm) et un modèle 30ans après l'installation du parc (modèle REEF). Ce dernier modélise le potentiel effet récif résultant de l'arrivée de substrat dur par les mats, les câbles et les enrochements dus à la construction du parc. Avec l'arrivée de ce substrat dur, Raoux *et al.* (2017) modélisent l'arrivée potentielle d'espèces bénéficiant de ce nouvel habitat. Pour créer le modèle REEF à partir du modèle BOWF, Raoux *et al.* (2017) utilisèrent Ecosim, la version dynamique dans le temps de Ecopath (Pauly *et al.*, 2000). Ecosim fut utilisé pour effectuer un forçage des biomasses des espèces profitant de l'effet récif, d'après des observations sur d'autres parcs éoliens en mer du Nord. Ce travail mit en évidence que : (1) l'effet récif ne bénéficierait pas uniquement aux espèces directement impactées par l'arrivée de substrat dur (comme les moules bivalves *Mytilus Edulis*), mais que des prédateurs supérieurs pourraient indirectement être attirés par l'augmentation de la biomasse de leurs proies dans le parc. Mais également (2) que l'effet récif pourrait être à l'origine d'une modification de l'écosystème, vers un système plus détritivore. La thèse d'Aurore Raoux ne regarda pas uniquement l'effet récif du parc éolien de Courseulles-sur-Mer, elle permit également de modéliser le potentiel effet réserve du parc (Raoux *et al.*, 2019). L'effet réserve, comme l'effet récif, sont considérés comme les effets principaux d'un parc éolien sur les écosystèmes marins et leur structure (Petersen and Malm, 2006; Langhamer, 2012; De Mesel *et al.*, 2015). Raoux *et al.* (2019) mirent ainsi en évidence les impacts potentiels de l'effet récif et réserve sur l'écosystème de Courseulles-sur-Mer grâce à une analyse des indices ENA. Ce travail permit (1) de voir que l'effet récif avait un effet plus structurant sur la communauté que l'effet réserve, et que (2) le parc éolien semblait avoir un effet bénéfique sur la résilience écologique du système. En définitive le dernier chapitre de thèse de Aurore Raoux, Raoux *et al.* (2018), a exploré le cumul d'impacts en utilisant un modèle qualitatif (modèle en digraphe orienté). Raoux *et al.* (2018) mirent en avant la nécessité de travailler sur les potentiels effets cumulés pouvant résulter du changement climatique en lien avec le parc éolien de Courseulles-sur-Mer. A la fin de la thèse d'Aurore Raoux et dans le prolongement de son travail, le projet TROPHIK (Approche écosystémique des EMR : modélisation du rôle des éoliennes offshore dans la modification du fonctionnement des réseaux trophiques côtiers et dans le cumul d'impacts ANR/FEM EMR-ITE ANR-10-IED-0006-12) débuta.

Ce projet avait pour objectif de continuer le développement d'approches écosystémiques des énergies marines renouvelables (EMR). TROPHIK avait plusieurs objectifs :

(1) d'abord il s'agissait de prendre en compte la dynamique spatio-temporelle de l'écosystème de la baie de Seine, (2) d'analyser la sensibilité de l'écosystème de la baie de Seine aux effets potentiels de la construction et de l'exploitation des éoliennes du parc de Courseulles-sur-Mer, mais également sa sensibilité aux effets du changement climatique, et enfin (3) de conduire une première approche quantitative de l'analyse du cumul d'impacts grâce à des indicateurs ENA. De nombreux travaux innovants furent développés durant le projet (Araignous *et al.*, 2019) :

- Un modèle trophique 2D de la baie de Seine étendue fut développé par Halouani *et al.* (2020) grâce à Ecospace de *Ecopath with Ecosim* (Walters *et al.*, 1999). Ce modèle permet d'explorer les effets spatiaux du parc éolien de Courseulles-sur-Mer et sert de base pour de nombreux travaux y compris pour cette thèse.
- Un nouveau modèle trophique à l'équilibre fut développé avec les résultats de Raoux *et al.* (2017). Ce nouveau modèle fut développé par Emma Araignous avec une approche linéaire inverse Monte Carlo en chaînes de Markov (Nogues *et al.*, 2020). Il mit également en œuvre des études isotopiques pour tester la validité des modèles trophiques de Courseulles-sur-Mer (Araignous *et al.*, 2019).
- Pour explorer les potentiels effets du changement climatique sur l'écosystème de la baie de Seine, des modèles de niche bioclimatiques furent mis en place (Ben Rais Lasram *et al.*, 2020). Les modèles de niche (ou Species Distribution Models) sont des approches corrélatives qui permettent d'identifier les conditions environnementales abiotiques propices à la pérennité de populations d'espèces, en identifiant leurs préférences environnementales. Lasram *et al.* (2020) développa une approche multi-algorithmes permettant de déterminer les préférences environnementales d'espèces marines, en prenant en compte un grand nombre de paramètres environnementaux.
- J'ai réalisé mon stage de deuxième année de master au sein du projet TROPHIK. Durant ce stage, j'ai utilisé le modèle LIM-MCMC du parc pour faire un premier test des effets du cumul d'impacts sur le réseau trophique de Courseulles-sur-Mer. J'ai cumulé l'effet récif du parc avec l'effet du changement climatique sur les aires de répartition en utilisant les résultats des modèles de niche.

- Les résultats des modèles de niche furent également intégrés au modèle Ecospace 2D de la baie de Seine étendue afin d'effectuer un premier test de l'impact du changement climatique sur l'écosystème de la zone (Bourdaud *et al.*, 2021).
- TROPHIK permet également de tester les potentiels effets d'une variation des rythmes de pêche sur les captures et les communautés de la baie de Seine grâce aux travaux du stage de deuxième année de master de Juliette Champagnat (Araignous *et al.*, 2019).
- Une table ronde fut également mise en place pour discuter des potentiels impacts du parc éolien sur les mammifères marins et des solutions pour les limiter (Araignous *et al.*, 2019).
- Enfin, le projet TROPHIK permet le développement d'outils pouvant effectuer une analyse spatialisée des indices ENA, en utilisant le modèle Ecospace de la baie de Seine étendue (Araignous *et al.*, 2019).

Le projet TROPHIK permet donc de développer plusieurs approches et outils innovants pour aider à une meilleure étude écosystémique des potentiels impacts d'un futur parc éolien. C'est dans la continuation du projet TROPHIK et à la suite des premières explorations des effets du cumul d'impacts en baie de Seine, que ma thèse débuta.

3 Objectifs de la thèse

A la suite des travaux de la thèse d'Aurore Raoux et des travaux réalisés durant le projet TROPHIK, ma thèse a pour objectif d'étudier les effets du cumul d'impacts sur l'écosystème de Courseulles-sur-Mer en utilisant des méthodes innovantes et en répondant aux questions de la communauté scientifique.

Cette thèse vise donc à combler les lacunes récurrentes concernant l'étude des effets cumulés, la communauté scientifique ayant démontré que les risques du cumul d'impacts sur les écosystèmes étaient importants et qu'il était temps de l'étudier en employant des approches écosystémiques pouvant quantifier les variations de la structure, de l'organisation et du fonctionnement des écosystèmes (Boyd and Hutchins, 2012; Gissi *et al.*, 2021). En regardant ces paramètres, l'objectif est d'avoir une idée de l'état des propriétés émergentes des écosystèmes, comme la résilience écologique (Rombouts *et al.* 2013; Heymans *et al.* 2020). Grâce à la mise en place de multiples modèles trophiques en baie de Seine, et dans le cadre du

projet TROPHIK, les bases nécessaires à la mise en place d'approches écosystémiques ont été posées avant le début de ces travaux, que ce soit en prenant compte la variabilité du vivant avec le modèle LIM ou en prenant en compte la variabilité spatio-temporelle de la baie avec le modèle 2D dynamique Ecospace. De plus, nous possédons les connaissances nécessaires pour modéliser de multiples facteurs environnementaux, comme l'effet d'un parc éolien, mais également l'effet du changement climatique sur la distribution des espèces ou encore l'effet de la variation de la pression de pêche.

En couplant les modèles trophiques de la baie avec nos connaissances des facteurs environnementaux risquant d'impacter l'écosystème, et en réalisant des analyses des indices ENA, l'objectif principal de cette thèse est donc de proposer une nouvelle méthode de quantification des effets de ces facteurs et de leur cumul sur le fonctionnement de l'écosystème de la baie, ainsi que sur sa résilience écologique et sur la production en services écosystémiques. Pour cela, les travaux de la thèse s'articulent autour de plusieurs points clefs. (1) Il est nécessaire d'étudier la sensibilité des indices écosystémiques ENA au cumul d'impacts, ainsi que leur capacité à quantifier et à caractériser les effets cumulés sur l'écosystème de la baie de Seine. Ensuite (2) il faut comprendre comment le cumul impacte le fonctionnement des écosystèmes. En définitive (3) il faut déterminer les conséquences pour l'homme et donc l'effet du cumul d'impacts sur la résilience de l'écosystème de la baie de Seine ainsi que sur sa capacité à fournir les services écosystémiques nécessaires au bien être humain. Pour répondre à ces objectifs autant théoriques qu'appliqués, la thèse se divise en 4 études, dans 3 chapitres distincts :

Le premier chapitre de thèse est composé d'un article qui vérifie la capacité des indices ENA à quantifier les effets cumulés de deux facteurs de changement : le changement climatique et le parc éolien de Courseulles-sur-Mer. Grâce à un modèle trophique linéaire inverse de Monte Carlo en chaîne de Markov de l'écosystème du parc éolien de Courseulles-sur-Mer, cette étude simule les effets du changement climatique sur les aires de répartition et la physiologie de plusieurs groupes trophiques, ainsi que l'effet récif éventuel du parc éolien de Courseulles-sur-Mer. Ces deux facteurs sont combinés dans plusieurs scénarios afin de tester les effets du cumul d'impacts à plusieurs niveaux trophiques, en impactant différents groupes écologiques avec les effets du changement climatique. Cette étude ne cherche pas uniquement à caractériser la sensibilité d'une liste d'indices ENA au cumul d'impacts, mais

également leur capacité à comprendre et à expliquer les mécanismes du cumul d'impacts. L'étude regarde également l'effet du cumul d'impacts sur la résilience de l'écosystème du parc et confirme une partie des résultats de Raoux *et al.* (2019), tout en allant plus loin dans l'analyse fonctionnelle de l'écosystème et de l'effet récif.

Le second chapitre de thèse, quant à lui, a pour objectif d'utiliser les indices de réseaux ENA pour évaluer le fonctionnement spatial de la baie de Seine et son évolution potentielle face aux effets éventuels des activités humaines. Pour cela, un modèle spatialisé et dynamique de la baie de Seine a été utilisé, Ecospace de *Ecopath with Ecosim*. Ce chapitre de thèse a fait l'objet de deux études :

Une première étude met en place la simulation des différents facteurs de changement sur le modèle spatialisé de la baie de Seine étendue. Les facteurs incluent : le changement climatique, le parc éolien de Courseulles-sur-Mer et enfin plusieurs scénarios de pêche liés au Brexit. Comme pour le chapitre précédent, des modèles de niche sont utilisés pour simuler les effets du changement climatique sur les aires de répartition et la physiologie des espèces et *in fine* des groupes trophiques. Des scénarios réalistes des effets du Brexit sur la pêche en Normandie sont produits avec des experts locaux des pêches normandes, et des résultats d'études précédentes permettent de simuler les effets récif et réserve du parc éolien de Courseulles-sur-Mer. Une étude fonctionnelle et spatialisée est réalisée pour mieux comprendre la baie de Seine et les différents effets de ces facteurs sont étudiés pour déterminer leurs impacts sur la résilience écosystémique de la baie de Seine.

La seconde étude de ce chapitre combine les différents facteurs modélisés lors de la partie précédente sur le même modèle spatialisé de la baie de Seine afin d'en déterminer leurs effets cumulés. Les effets cumulés sont cartographiés afin de déterminer les zones d'interactions des facteurs, le sens de ces interactions et leurs effets sur le fonctionnement écosystémique. Les mécanismes à l'origine de ces effets et des interactions des facteurs sont explorés en utilisant les indices ENA et leurs implications pour la résilience sont mises en avant afin de montrer l'intérêt d'étudier le cumul d'impacts avec des outils fonctionnels et spatialisés.

Enfin le troisième chapitre de thèse explore les conséquences du cumul du changement climatique et du parc éolien de Courseulles-sur-Mer sur la capacité de l'écosystème à fournir

plusieurs services écosystémiques. Toujours en se basant sur le modèle spatialisé de la baie de Seine, cette étude utilise des sorties fonctionnelles et personnalisées du modèle Ecospace de la Baie de Seine. Ce papier au potentiel plus appliqué que les précédents emploie une approche écosystémique, pour proposer une nouvelle méthode de quantification de la fourniture en services écosystémiques. Il propose également d'utiliser un indice ENA pour quantifier la fourniture en services écosystémiques et ce, afin de pouvoir quantifier des propriétés écosystémiques parfois difficiles à saisir avec des expérimentations sur le terrain. Cette partie présente donc une étude locale des évolutions possibles des relations homme-nature, des potentiels risques des changements environnementaux sur ces relations et utilise les résultats obtenus pour mettre en avant une initiative pour limiter ces pertes.

Au-delà des travaux réalisés dans le cadre de la thèse, ces trois années de doctorat m'auront également permis de participer à différents travaux de modélisation avec plusieurs personnes au sein des projets TROPHIK, APPEAL, WINDSERV et SENSITROPH. Parmi ces derniers le travail réalisé avec Maud Thermes a permis d'utiliser les méthodes et les outils développés durant cette thèse et le projet TROPHIK, afin de tirer profit des capacités des ENA dans l'étude des effets de la planification spatiale en baie de Seine. Ce travail bien qu'utilisant des approches très similaires à cette thèse, n'a pas été intégré dans le corps du texte, mais au vu de sa proximité avec cette thèse, autant d'un point de vue technique que spatial, a été ajouté en supplément de cette thèse.

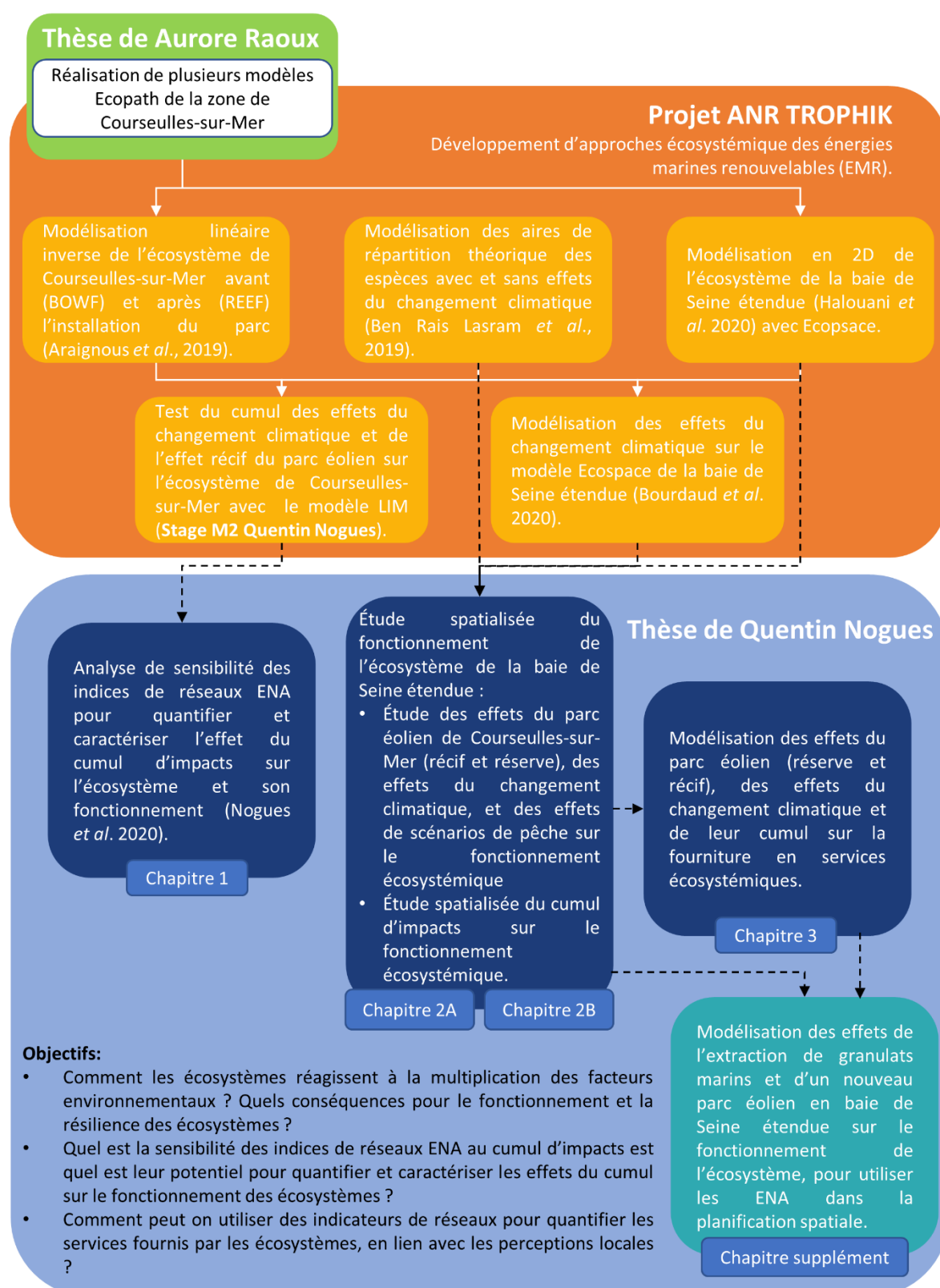


Figure I - 8 La thèse et son contexte scientifique.

II Chapitre 1 :

Cumulative effects of marine renewable energy and climate change on ecosystem properties: Sensitivity of ecological network analysis

Reprenant une partie de la méthodologie développée pour mon stage de deuxième année de master, qui étudiait pour la première fois la sensibilité des indices ENA au cumul d'impacts (travail intitulé : « Analyse de sensibilité du cumul de l'effet récif et de l'effet du changement climatique, sur différents indices ENA : le cas du parc éolien offshore de Courseulles-sur-Mer. »), ce premier chapitre de thèse cherche à caractériser l'utilité réelle des ENA dans des scénarios de cumul. Ce premier chapitre utilise la vision holistique des ENA de manière intégrative pour étudier l'effet récif potentiel des éoliennes de Courseulles-Sur-Mer et l'effet du changement climatique sur l'écosystème du parc.

Ce premier chapitre a fait l'objet de nombreuses modifications par rapport aux travaux réalisés pendant mon stage. La méthodologie a ainsi été modifiée et l'analyse des résultats a complètement été reprise. Les travaux de mon stage ont donc servi d'analyse préliminaire à ce premier chapitre, avec peu de similarités dans les messages de ces travaux. Nous avons gardé quelques messages importants déjà mis en avant durant mon stage : (1) Que les indices ENA étaient sensibles au cumul d'impacts, exposant des effets cumulés comme des effets synergiques, tamponnés ou antagonistes. (2) Qu'il était important de garder une vision intégrative et holistique des écosystèmes, en utilisant de multiples indices ENA complémentaires. En plus de ces points déjà mis en avant durant mon stage, ce chapitre apporte une vision réellement fonctionnelle du cumul d'impacts, jusque-là manquante.

Ce chapitre a ainsi fait l'objet d'une publication dans le journal international « Ecological Indicators » en 2020 :

Cumulative effects of marine renewable energy and climate change on ecosystem properties: Sensitivity of ecological network analysis

Quentin Nogues¹, Aurore Raoux^{1,2}, Emma Araignous^{1,3}, Aurélie Chaalali¹, Tarek Hattab^{4,5}, Boris Leroy⁶, Frida Ben Rais Lasram⁴, Valérie David⁷, François Le Loc'h⁸, Jean-Claude Dauvin², Nathalie Niquil¹.

Résumé :

Dans un monde de plus en plus anthropisé, où la multiplication des activités humaines ne cesse d'augmenter, il est nécessaire de comprendre les risques qu'encourent les écosystèmes marins et côtiers. En effet, avec la multitude de facteurs pouvant affecter les écosystèmes, le cumul d'impacts a le potentiel d'avoir des effets dramatiques sur le fonctionnement et l'organisation des écosystèmes. Des outils comme les indices d'analyse des réseaux écologiques (ENA) offrent l'opportunité d'étudier les effets du cumul sur le fonctionnement et l'organisation des écosystèmes. Malgré ce potentiel, les indices ENA n'ont jamais été testés dans l'optique d'étudier les effets cumulés résultant de la combinaison de plusieurs facteurs environnementaux. Cette étude remédie à ce besoin en étudiant les effets du cumul (1) du potentiel effet récif du parc éolien en mer de Courseulles-sur-Mer et (2) des effets du changement climatique sur les aires de répartition des espèces endémiques de la baie de Seine. Pour cela, un modèle trophique de l'écosystème du parc de Courseulles-sur-Mer a été mis en place afin de calculer et de tester une série d'indices ENA. Les effets de chacun des facteurs environnementaux sur le fonctionnement de l'écosystème furent étudiés isolément et de manière combinée. Séparément, l'effet récif du parc semble avoir un rôle structurant sur l'écosystème augmentant sa résilience, mais changeant son fonctionnement et donc sa réponse à d'autres perturbations. L'effet du changement climatique sur les aires de répartition quant à lui fut testé par groupe d'intérêt commercial et pour tous les groupes. L'écosystème apparaît aussi sensible aux effets du changement climatique sur le groupe des poissons mangeurs de benthos que sur tous les groupes d'intérêt commercial. Ceci met en évidence la forte vulnérabilité de l'écosystème à l'impact de son groupe Keystone. Quand les deux facteurs sont combinés, le cumul d'impacts semble avoir un effet important sur de multiples indices ENA, mettant en avant les risques des effets cumulés sur le fonctionnement des écosystèmes. Non seulement l'effet du cumul est visible sur de multiples indices ENA, mais le type d'effet cumulé varie entre les ENA, indiquant que le cumul d'impacts semble passer par différentes voies fonctionnelles. Il apparaît également clairement que l'effet structurant de l'effet récif joue un rôle prépondérant dans la naissance des effets cumulés interactifs comme les effets synergiques, antagonistes et tamponnés. En conclusion, il semble que les ENA offrent une nouvelle vision des processus et des mécanismes du cumul d'impacts, une vision fonctionnelle qui semble nécessaire pour comprendre les interactions de multiples facteurs

par écosystème donné. Comme il est difficile de prédire les potentiels effets structurants pouvant conduire à des effets cumulés ayant potentiellement un rôle important sur le fonctionnement des écosystèmes, il est donc nécessaire d'effectuer des études continues et approfondies du fonctionnement des écosystèmes.



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Cumulative effects of marine renewable energy and climate change on ecosystem properties: Sensitivity of ecological network analysis

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Cumulative Effects of Marine Renewable Energy and Climate Change on Ecosystem

Properties: Sensitivity of Ecological Network Analysis

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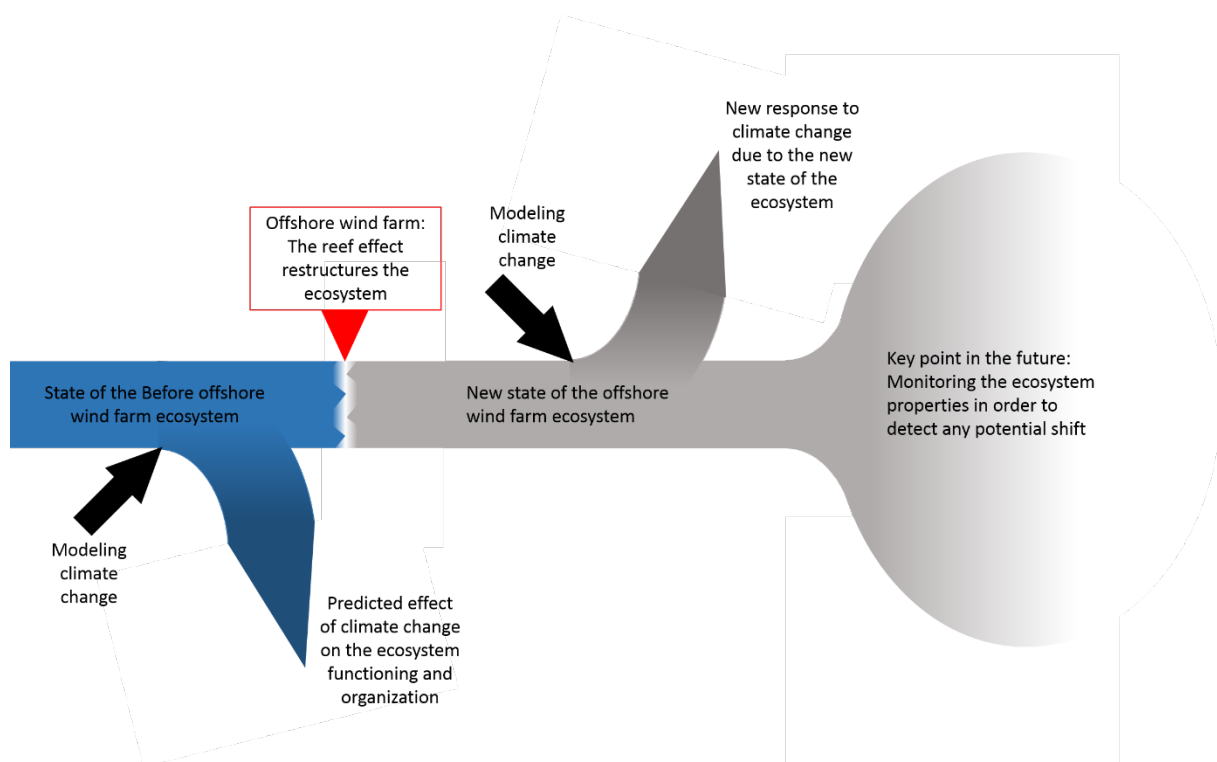
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Abstract:

In an increasingly anthropogenic world, the scientific community and managers have to take interactions between the drivers of ecosystems into consideration. Tools like ecological network analysis (ENA) indices offer the opportunity to study those interactions at the ecosystem level. However, ENA indices have never been used to test the incidence of cumulative drivers. The present study uses models combining the effects of (i) the reef caused by the future offshore wind farm of Courseulles-sur-Mer and (ii) climate change on species distribution, to test the response of multiple ENA indices. ENA indices proved sensitive to this cumulative impact, displaying a wide variety of cumulative effects. They were also very powerful to characterize the role of the cumulative impact on ecosystem functioning. These results demonstrate the capacity of ENA indices to describe and understand cumulative effects at the ecosystem scale. Using a sensitivity analysis approach, this study shows that ENA indices could be viable tools for managers. To help them in their tasks, the next step could be to link ecosystem services to ENA indices for a more practical use.

Key words: Cumulative impact, Linear inverse modeling, Marine Renewable Energies, Ecological Network Analysis, ENA food web.



Graphical abstract I

1 Introduction

The world is in constant evolution, and human activities have deeply changed the rate of this evolution (Halpern et al., 2008b). Due to constant human activity, ecosystem functioning can no longer be dissociated from the dynamics of anthropogenic activities (Vitousek et al., 1997). Although coastal ecosystems are already heavily stressed, they are going to be increasingly exploited owing to the ever-increasing human population and demand for resources (Halpern *et al.*, 2015). The English Channel – an epicontinental sea – is considered as one of the most anthropized marine ecosystems in the world (Halpern et al., 2008b; Dauvin, 2019). It is subjected to multiple anthropogenic drivers such as marine transport, fishing, sediment dredging and aggregate extraction (Dauvin et al., 2004; Dauvin, 2019). It is also a hotspot for the future development of an offshore wind farm (OWF) in France (Pezy et al., 2020; Raoux et al., 2017). The effects of OWFs on ecosystems are divided in two phases: (i) the construction phase and (ii) the operational phase. The construction phase is characterized by short-lasting heavy disturbance (extreme noise from pile driving and vessels, cable-trenching disturbance), while the operational phase is associated to long-lasting effects on the environment (Hammar *et al.*, 2014). One of the long-lasting effects of OWFs is the creation of new habitats and shelters for benthic and demersal species through the introduction of hard substrates in the surrounding soft substrate habitats (Wilhelmsson and Malm, 2008). The increased habitat heterogeneity can lead to changes in the abundance, biomass, and species richness of benthos and fish (Wilhelmsson *et al.*, 2006; Coates *et al.*, 2014), known as the reef effect. This reef effect is likely to be the main ecosystem effect of OWFs during the exploitation phase and can potentially affect the whole food web (Bergström *et al.*, 2013). Only the exploitation phase is considered in this study, and the construction phase is ignored (Petersen and Malm, 2006; Langhamer, 2012; De Mesel *et al.*, 2015).

To help managers and decision-makers in their sustainable development mission, it is a priority to understand how OWFs act on ecosystem dynamics, which is mainly driven by trophic interactions between species. Trophic network modeling can help to study those interactions. In a network, a stimulus on one part of the model can cascade throughout the network. Trophic network modeling is therefore an interesting tool to understand how drivers act on the whole ecosystem.

To analyze how food webs are affected by drivers, Ulanowicz (1997, 2004) used ecological network analysis (ENA) indices. ENA indices can assess properties like the size, function or organization of a network through multiple metrics related to ecological processes, such as omnivory, recycling, overhead of flows (Ulanowicz, 1986; Niquil *et al.*, 2012a; Heymans and Tomczak, 2016). These indices have been considered to be good potential indicators of the ecosystem health status and were thus cited by the OSPAR convention as promising indicators (Niquil *et al.*, 2014; De la Vega *et al.*, 2018; Safi *et al.*, 2019). They were subsequently employed to understand the effects of human activities (e.g., the extension of a harbor) on ecosystems (Tecchio *et al.*, 2016), or even to develop different management scenarios (Heymans and Tomczak, 2016; Tomczak *et al.*, 2013).

Raoux *et al.* (2017) explored a new way to look at the potential effects of OWFs through food web models and flow analysis. These authors implemented the Ecopath with Ecosim (EwE) approach (Polovina, 1984a; Christensen and Walters, 2004; Heymans *et al.*, 2011) to model the food web at a planned OWF (Courseulles-sur-mer, Bay of Seine, English Channel, France). One of their main results was that the total ecosystem activity, recycling, and the ecosystem maturity increased after OWF construction, due to the reef effect (Raoux *et al.*, 2017, 2019). Results also indicated an anticipated increase in detritivory flows and an increased benthic fish biomass after OWF construction.

However, one of the main weaknesses of impact studies is that they focus on a single ecosystemic driver (Raoux *et al.*, 2018), and ignore the other drivers of disturbance with long-lasting effects such as climate change (Hoegh-Guldberg and Bruno, 2010). The main issue when ignoring combined drivers is to miss cumulative effects that may alter the magnitude or direction of predicted changes (Breitburg *et al.*, 1998; Vinebrooke *et al.*, 2004; Fu *et al.*, 2018; Planque *et al.*, 2010). Hence, irrelevant or misleading recommendations can be issued when cumulative effects are not included (Halpern *et al.*, 2008).

We propose to investigate the cumulative effects of climate change and one OWF using ecological network analysis on a food web model. To do so, we transformed the Raoux *et al.* (2017) Ecopath model of the future Courseulles-sur-Mer OWF into a Linear inverse model (LIM). We coupled this OWF LIM model with niche models of the Courseulles-sur-Mer ecosystem (Ben Rais Lasram *et al.*, 2020) to study the effects of climate change on species. Several representative concentration pathway (IPCC 2014) scenarios were used to simulate

changes in the bioclimatic niches of 72 macrofauna species with dominant biomass within the trophic groups of the food web.

We used those scenarios combining the effects of climate change and the OWF to compute a series of ENA indices to study the effects of each driver separately and then of the combined drivers on the food web of Courseulles-sur-Mer. We explored the capacities of ENA indices to study cumulative effects. Finally, we discussed the advantages and weaknesses of a framework based on ENA indices to investigate cumulative impacts and provide management recommendations.

2 Materials and methods

2.1 Study area

This study is focused on the area of the future OWF of Courseulles-sur-Mer (Normandy, France), that will be located in the lower middle part of the Bay of Seine (Figure II - 1). The bay opens onto the English Channel in its northern part, its depth is relatively shallow with a mean of 30 m at the future OWF location. The OWF area will cover 50 km², and 64 offshore wind turbines are planned. The OWF will be built on coarse sand and sandy gravels harboring benthic communities of the Bay of Seine (Baffreau *et al.*, 2017).

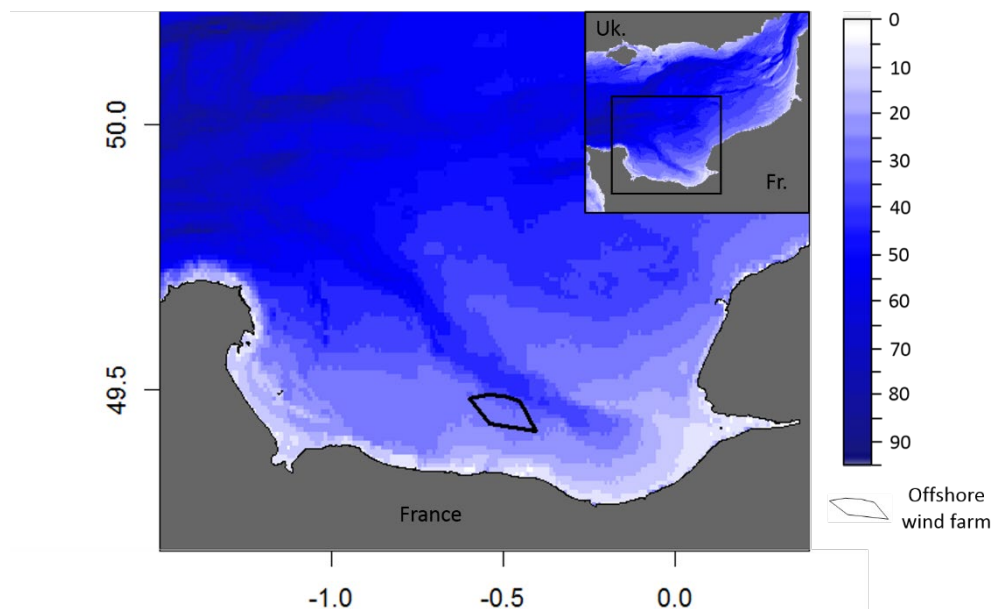


Figure II - 1 Localization of the future offshore wind farm of Courseulles-sur-Mer in the Bay of Seine.

2.2 Cumulative impact models

In order to test ENA indices in cumulative impact scenarios, we created trophic models based on two studies: (i) a trophic modeling of the expected reef effect caused by the future Courseulles-sur-Mer OWF (Raoux et al., 2017), and (ii) results from niche models simulating climate change (Ben Rais Lasram et al., 2020).

2.2.1 Wind farm effect on the food web

The construction of turbines and their associated scour protection creates new hard-substrate habitats and shelters such as artificial reefs. These new hard-substrate habitats increase habitat heterogeneity, leading to increased abundance, biomass, and species richness of the benthic macrofauna (e.g., the mussel (*Mytilus edulis*)) and of demersal fish (e.g., the pouting (*Trisopterus luscus*)) (Wilhelmsson et al., 2006; Coates et al., 2014; Raoux et al., 2017).

The reef effect of the future Courseulles-sur-Mer OWF was modeled using trophic network models quantifying the flows of energy between organisms, as described in Raoux et al. (2017). This trophic model was based on the Ecopath with Ecosim approach (Polovina, 1984a; Christensen and Walters, 2004). A first Ecopath model was built to model the ecosystem before the establishment of the OWF. Ecopath is a mass balance model, meaning that the sums of the inflows and outflows of the system are equal. It was used as a basis for an Ecosim model. Ecosim is a time dynamic model based on the mass balance Ecopath model (Pauly et al., 2000). It was used to model the reef effect of the future Courseulles-sur-Mer OWF and to create an Ecopath model 30 years from the OWF construction. Two Ecopath models were thus created: a baseline Ecopath model called BOWF (before offshore wind farm), and a model called REEF, based on the reef effect demonstrated to be the main long-term effect of the farm (Raoux et al., 2017). Both models were composed of the same 37 groups of species, with similar trophic interactions (Leguerrier et al., 2003).

While the Ecopath approach is a well acknowledged mass balance approach, it can be criticized for its limitations in the modeling of low-trophic-level groups – which are often subjected to high inter and intra year biomass variability – and because the method is based on a manual balancing procedure, which is not based on uncertainty evaluation of the input parameters. In order to take into account the uncertainty in the input parameters but also to define uncertainty in the outputs (flow values or ENA indices), another mass balance modeling

approach is more suitable, i.e., the LIM linear inverse models, Monte Carlo Markov Chain or LIM-MCMC (Van Oevelen *et al.*, 2010a; Niquil *et al.*, 2012b). Linear inverse modeling relies on a set of linear equalities and inequalities to estimate unknown flows in food webs. The equalities set the mass balance of the model, while the inequalities correspond to the confidence intervals of the measured flows. The Monte Carlo method is a sampling procedure used to determine the complete coverage of the range of possible solutions. Which means that while Ecopath only considers one value for each parameter/flow, LIM-MCMC integrates a range of values to represent the variability of living organisms (Meersche *et al.*, 2009; Niquil *et al.*, 2012; van Oevelen *et al.*, 2010). This variability is also very useful to compare models statistically.

We thus used the BOWF and REEF Ecopath models of Raoux *et al.* (2017) and transformed them into linear inverse models (LIMs). Four steps are necessary to create a LIM model, in which we determined:

- The topology of the network based on the possible flows
- The mass balance equations
- The constraints of the model
- The computing parameters (jump and iterations).

Because the two Ecopath models used the same topology, we based our topology on them. However, we had to reduce the number of biological groups to shorten the computation time. The number of groups decreased from 37 to 19 (Figure II - 2, Table A.1), and aggregation was based on the diet of each Ecopath group (Table A.1, A.3 & A.4; Leguerrier *et al.*, 2003). Keeping the same topology between the LIM BOWF model and the LIM REEF model allowed us to compare the results of the two models free of any structural bias (Table A.3 & A.4).

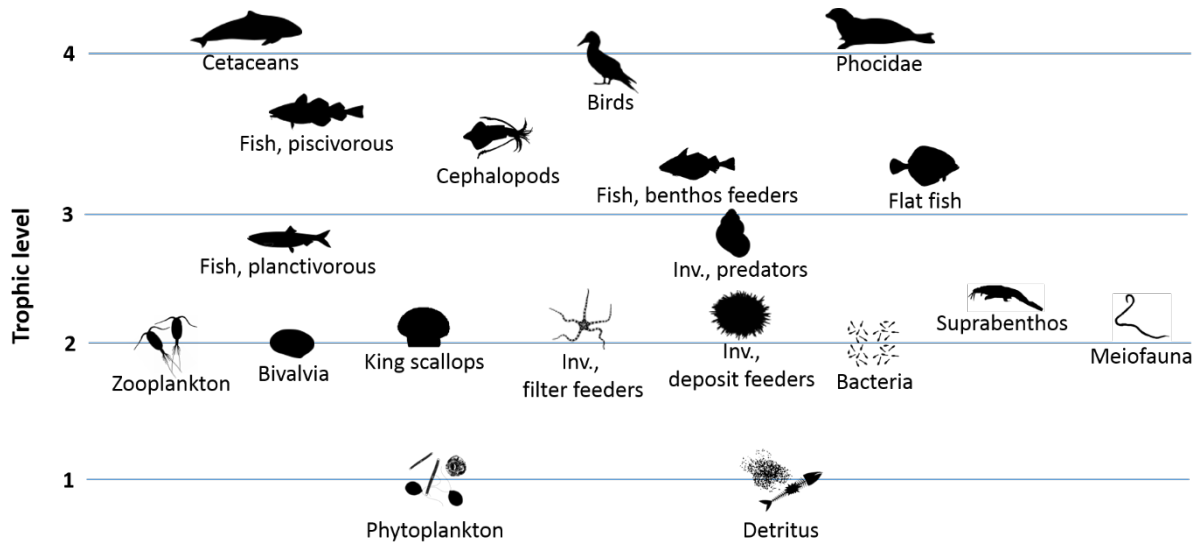


Figure II - 2 Functional groups of the Courseulles-sur-Mer ecosystem model organized according to their trophic level, based on the BOWF trophic levels.

We defined the mass balance equation for each group. In a mass balance equation, the input of a group is equal to its output. The input is the consumption of the group, while the output is the excretion, the respiration and the production of the group available for the system (predation).

$$\text{Production (P)} = \text{consumption (Q)} - \text{excretion (U)} - \text{respiration (R)}$$

Regarding the constraints of the model, we set minimum and maximum values for parameters such as the production to biomass ratio (P/B), the production to consumption ratio (P/Q), the respiration to consumption ratio (R/Q), and the excretion to consumption ratio (U/Q) (Table A.2). We used constraint values from the literature for some groups, while others were computed with the Ecopath values and pedigrees. Pedigrees were used to define the uncertainty around the Ecopath values to determine minimum and maximum values (Table A.2). When the Ecopath values were considered very reliable ('Fish, planktivorous', 'Fish, benthos feeders', 'Fish, piscivorous' and 'Flat fish'), the uncertainty around the P/B, P/Q and U/Q values was set to 10 %. The diet constraints were calculated with the same method for all groups of the models (BOWF and REEF). Finally, we added primary production values to drive the two LIM models: while the Ecopath model does not consider primary production values, the LIM model needs minimum and maximum values of potential primary production (Behrenfeld and Falkowski, 1997; Napoléon and Claquin, 2012).

The `xsample` function from the LIM package was used to compute the LIM models (van den Meersche et al., 2009). The LIM-MCMC model depends on two parameters for its computing: the jump and the number of iterations. With the equations and the constraints, the LIM MCMC model creates a polytope of solution that includes all the possible values for each flow of the system. The number of iterations indicates the number of solutions sampled in the space of solution. The mean distance between iterations is the jump. If the sampling goes outside the space of solution, it will bounce back (mirror technique) inside the space. A jump of 0.05 gC.m^{-2} and 500,000 iterations was chosen after testing the mean shifting value/variability of the biggest flows in order to properly sample solutions.

2.2.2 Climate change simulation

In order to assess cumulative impacts through a trophic modeling approach, we had to integrate the climate change effect in both LIM trophic models. To evaluate the effect of climate change, we used results from the niche models published in Ben Rais Lasram et al. (2020). Niche model algorithms are correlative approaches aimed at identifying the potential species niches by correlating species occurrences to environmental variables such as temperature, salinity or other parameters. Niche models were built with an ensemble modeling procedure combining different modeling techniques. Future climate change projections for 72 species of the Bay of Seine were based on the “business as usual” representative concentration pathway scenarios (Intergovernmental Panel on Climate Change, RCP 8.5) at the 2091-2100 time steps (Ben Rais Lasram et al., 2020).

The groups of the LIM trophic model were not all simulated in the niche model approach. Consequently, we focused on integrating the niche model results of the commercially exploited groups, which included 4 fish groups – Fish, benthos feeders (FBF); Flat Fish (FFI); Fish, Piscivorous (FPI); Fish, Planktivorous (FPL) – and 2 mollusk groups – Cephalopods (CEP); King Scallop (KSC). Those groups represented the groups impacted by climate change.

To integrate the results of the niche models into the trophic models, we linked the evolution of the suitability index of the niche models to biomass according to Chaalali et al. (2016). We used the evolution of the suitability index C to multiply the biomass of the species by $(1-C)$ to reflect the biomass changes:

$$C = \frac{P_{ref} - P_{rcp}}{P_{ref}}$$

where P_{ref} is the suitability index of the species in the current niche model and P_{rcp} the suitability index of the species in RCP 8.5.

As the production to biomass ratio (P/B) of fish is based on temperature (Lassalle *et al.*, 2011), the P/B ratios of all the fish groups impacted by climate change were modified following the temperature values of the RCP 8.5 scenarios (Table A.6). We used the temperature values corresponding to the habitats of each group (surface temperature for the pelagic groups, sub-surface temperature for the benthopelagic groups, and bottom temperature for the benthic and demersal groups). In a mass balanced condition, the P/B ratio of fish species is considered to be equal to the instantaneous coefficient of total mortality (Z) (Figure II - 3):

$$Z = M + F$$

where M is natural mortality and F is fishing mortality, and M is calculated from the empirical equation:

$$M = K^{0.65} \times L_{\infty}^{-0.279} \times T^{0.463}$$

where K is the curvature parameter of the von Bertalanffy growth function (VBGF), while L_{∞} is the asymptotic length and T the mean environmental temperature in °C depending of the depth.

We computed new P/B ratios by changing the temperature in the natural mortality equation (M) without changing fishing mortality (F) so as to be coherent. The evolution of natural mortality was then applied to the P/B ratio of each fish group. If natural mortality increased by 10 % for a fish species owing to the new temperature, we increased the P/B ratio of the species by 10 % in the climate change scenario.

We had to use different methods for the Mollusk groups. There was no equation connecting the P/B ratio with temperature for cephalopods. We therefore used the cephalopod feeding rate equation because of its link to temperature (O'Dor and Wells, 1987):

$$Feeding\ rate = 0.058 \times W^{0.79} \times 1.082^T$$

where W is the body mass in g and T is temperature in degrees Celsius.

We computed a new feeding rate for cephalopods with the niche model. The evolution of the feeding rate between the current and the future RCP 8.5 temperatures allowed us to estimate the P/B ratio of the cephalopod group. We used a food conversion rate of 30 % for cephalopods (Boyle and Rodhouse, 2005).

For king scallops, we used the growth rate equation (Laing, 1999). The equation was verified by comparing the temperature estimated from the RCP 8.5 scenarios with the temperature ranges applied in growth experiments (Laing, 2000; Chauvaud *et al.*, 2012). The temperature estimated with the RCP model was sustainable by *Pecten maximus in situ* and *ex situ* (15.3°C), and resulted in increased production:

$$\text{Growth rate} = 0.0199 \times T - 0.081$$

We thus changed the P/B ratio of the king scallop group according to the evolution of its growth rate between the current temperature and the future temperature under the RCP 8.5 scenario.

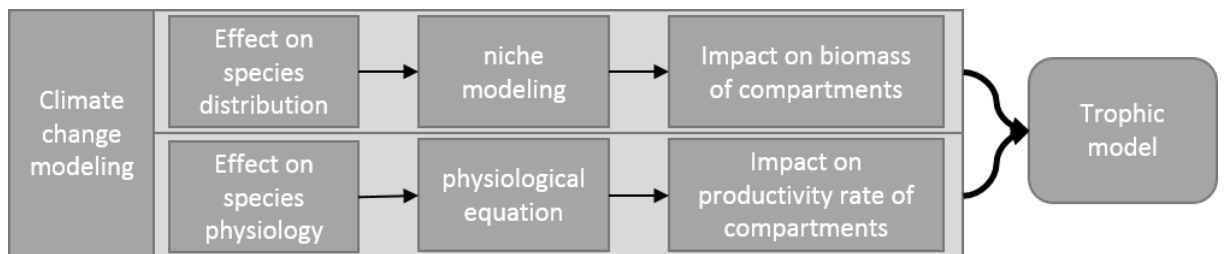


Figure II - 3 Schematic representation of the climate change modeling approach.

2.2.3 Ecological network analysis

With their 19 groups each, the LIM models contained a flow matrix of 144 flows. We computed multiple metrics to analyze the ecological properties of each model. We first computed the throughflow/activity of (i) each group (sum of all the inflows/outflows) (Table A.1), (ii) the import (IMP), and (iii) respiration (RES) to understand the effects of the climate change and of the OWF at the flow matrix level. We also computed ENA indices (Table II - 1).

ENA indices summarize the emergent properties of the ecosystem. A range of indices was chosen according to previous recommendations about their use by ecosystem managers (Fath *et al.*, 2019; Safi *et al.*, 2019).

Table II - 1 ENA indices computed with the LIM models results.

Name	Objective	Calculation	References
Total activity of the system or Total System Throughput (T..)	The total system throughput is equal to the sum of all the flows in the system. It is a network level indicator of the size and activity of the system.	$T_{..} = \sum_{i,j=1}^n T_{ij}$ where T_{ij} is the flow between groups j and i.	(Finn, 1976; Ulanowicz and Norden, 1990).
Average Mutual Information (AMI)	Average mutual information measures the organization of a network, the more web-like the system is, the lower the AMI should be.	$AMI = k \sum_{i=1}^{n+2} \sum_{j=0}^n \frac{T_{ij}}{T_{..}} \log_2 \frac{T_{ij} T_{..}}{T_i T_j}$	(Gallager, 1968; Latham, 2006)
Ascendency (A)	Ascendency is a measurement of the growth of the system, integrating its size (T..) and its organization (AMI).	$A = \sum_{i=1}^{n+2} \sum_{j=0}^n T_{ij} \log_2 \frac{T_{ij} T_{..}}{T_i T_j}$ $A = AMI \times T_{..}$	(Ulanowicz, 1980, 1986; Latham, 2006)
Development capacity (DC)	The total development capacity is the upper limit of ascendency, it represents the maximum development of the system.	$DC = \sum_{i=1}^{n+2} \sum_{j=0}^n T_{ij} \log_2 \frac{T_{ij}}{T_{..}}$	(Latham, 2006)
Overhead (R)	The overhead is the “reserve” of the system information and refers to the extent of parallel flows in the system	$R = DC - A$	(Ulanowicz et al., 2009; Ulanowicz and Norden, 1990)
Detritivory to herbivory ratio (D/H)	The detritivory to herbivory ratio is the ratio of detritus consumption (Detritivory) compared to the consumption of primary producers (Herbivory) in the ecosystem.	$D/H = \frac{(\sum DET)}{(\sum PP)}$ where <i>DET</i> is the flow of detritus consumption and <i>PP</i> the flow of consumption by primary producers	(Latham, 2006)
System omnivory (SOI)	The system omnivory index quantifies the distribution of trophic interactions among different trophic levels.	$OI_i = \sum_{j=1}^n [TL_j - (TL_i - 1)]^2 \times DC_{ij}$ $SOI = \frac{\sum_{i=1}^n [OI_i \times \log(Q_i)]}{\sum_{i=1}^n \log(Q_i)}$ where TL is the trophic level of i or j.	(Libralato, 2013)

Recycling index or Finn Cycling Index (FCI)	The recycling index is the fraction of energy recycled in the system.	$FCI = \frac{TST_c}{TST}$ where TST is the total system throughflow and TST_c the cycled total system throughflow.	(Odum, 1985)
Mean Trophic Level (MTL)	The mean trophic level is the mean trophic level of the network's groups. It is based on the groups' trophic levels. Its values can be 1 (primary producers and detritus), 2 (all consumers), and can reach > 4 (top predators).	$MTL = \frac{\sum_i TL_i \times B_i}{\sum_i B_i}$ where B is the biomass of i or j.	(Latham, 2006)

2.2.4 The different types of cumulative effects

Sixteen models were computed to test ENA indices in multiple scenarios. The models included:

- The reference BOWF model
- The REEF model
- The climate-change-only scenarios, based on the LIM BOWF model, with each of the selected groups impacted by the climate change effect and an extra model (BOWFTOT) combining all the groups impacted at once
- The cumulative impact scenarios, based on the LIM REEF model, with each of the selected groups impacted by the climate change effect and an extra model (REEFTOT) combining all the groups impacted at once.

Each model was named according to its initial model (BOWF or REEF) and to the name of the impacted group if impacted by climate change (Figure II - 4).

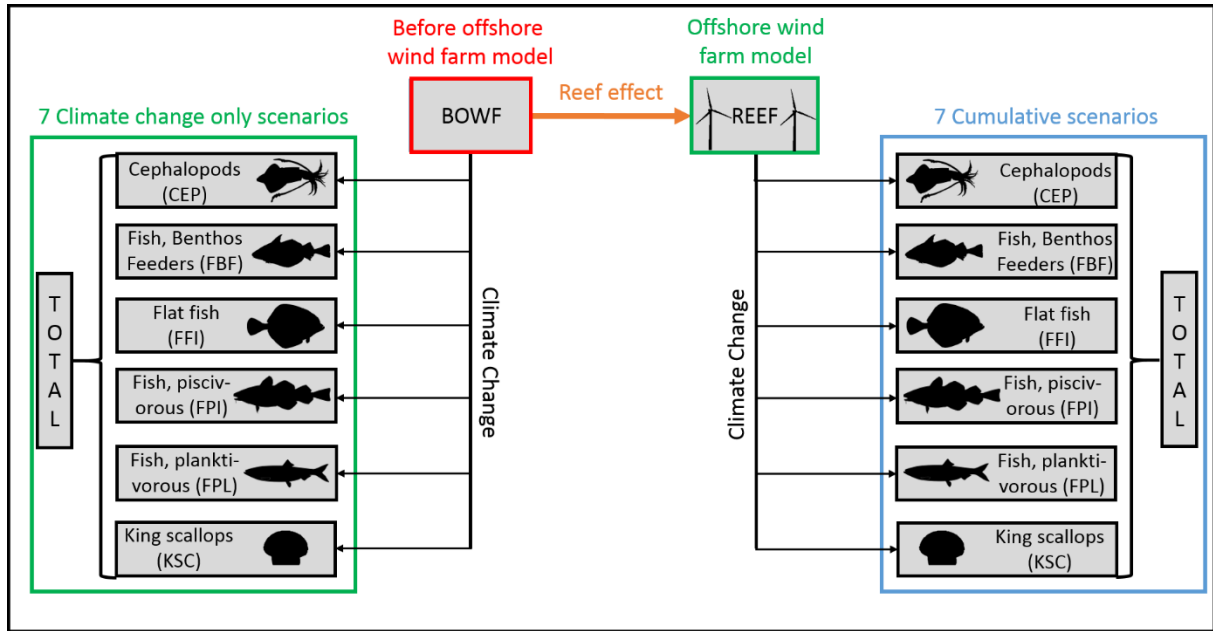


Figure II - 4 Modeling framework of the sixteen models all represented by gray boxes, with the initial BOWF model, single effect models including seven climate change scenarios and the REEF model, and the combined models including seven cumulative scenarios.

We followed this framework (Figure II - 4) to analyze the combined effects of climate change and of the reef effect depending on the impacted group. We used the same methodology as Fu et al. (2018) to characterize the combined effect on each ENA index and for each scenario.

First, we computed the relative index variation between the reference BOWF model and a single effect model (reef effect only or climate change only) for each ENA:

$$\Delta I_k^{sep} = \frac{I_k - I_c}{I_c}$$

where I_c is the index value of the reference model and I_k the index value of a single-effect model (reef only or CC only).

Then, we summed the variation (ΔI_k^{sep}) of each single effect in a same scenario to get the reef + climate change additive effect:

$$\sum \Delta I_k^{sep}$$

We also computed the cumulative effect as the variation between the initial BOWF model and the cumulative impact scenario (reef effect and climate change effect) for each ENA (ΔI_k^{cum}):

$$\Delta I_k^{cum} = \frac{I_k - I_c}{I_c}$$

To determine the combined effect, we compared the additive effect variation with the cumulative effect variation. If the two variations were equal, the effect was considered additive:

$$\Delta I_k^{cum} = \sum \Delta I_k^{sep}$$

If the additive effect variation was lower than the cumulative effect variation and both variations were positive or negative, the response was synergistic positive or negative:

$$\text{Synergistic positive: } \Delta I_k^{cum} > \sum \Delta I_k^{sep} > 0$$

$$\text{Synergistic negative: } \Delta I_k^{cum} < \sum \Delta I_k^{sep} < 0$$

If the additive effect variation was higher than the cumulative effect variation while both variations were positive or negative, the response was dampened positive or negative.

If the additive effect variation was opposite to the cumulative effect variation, the response was antagonistic. When the combined effect variation was positive, it was a positive antagonism, and *vice versa* for negative antagonism (Figure II - 5).

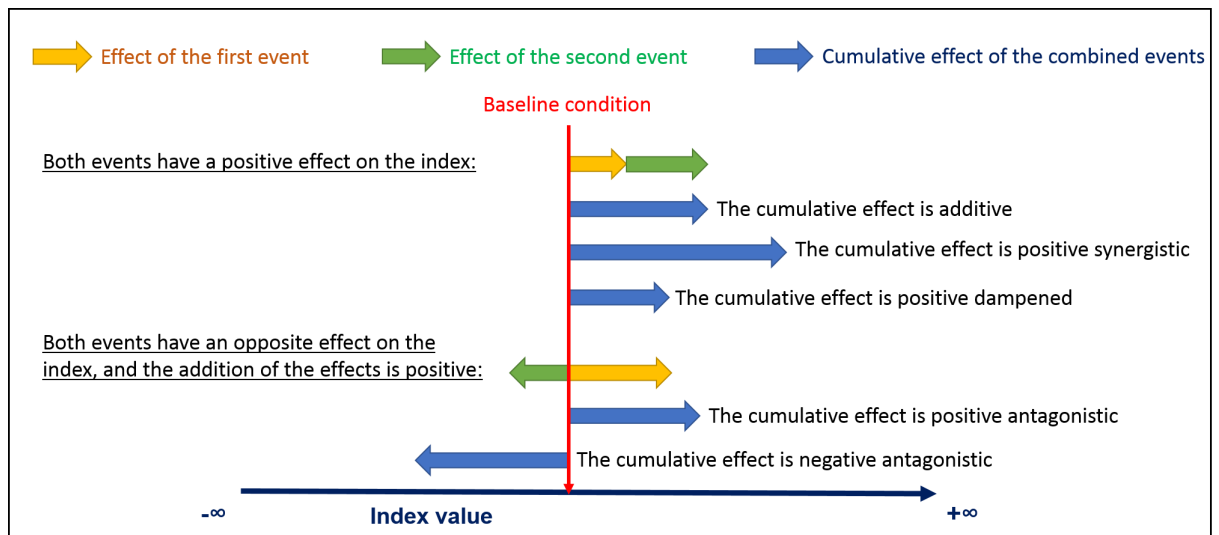


Figure II - 5 Different types of cumulative effects on the different index values (e.g., ENA index).

2.2.5 Statistical comparison

Indices were calculated for each solution of the LIM models (500,000 solutions quantifying each flow for each model). A previous study showed that parametric tests like Student's T-tests could identify differences even for tiny effects (Tecchio *et al.*, 2016). The non-parametric Cliff delta (Cliff, 1993) was chosen for its better suitability (Valérie Girardin & Justine Lequesne, pers. com., Laboratoire de Mathématiques Nicolas Oresme, Tecchio *et al.*, 2016). The same threshold as Romano *et al.* (2006) and MacBeth *et al.* (2012) was used considering the differences between the datasets: negligible if the Cliff delta ($|\partial\text{Cliff}|$) was < 0.147 , low if < 0.33 , medium if < 0.474 , or strong if > 0.474 .

The Cliff delta was used to compare single effect models ("reef only" and "climate change only" scenarios) to the initial reference BOWF model and to compare the REEF model with the cumulative impact scenarios (reef effect + climate change effect). This was applied to the throughflow/activity (input/output) of each group as well as on the ENA. The delta also allowed us to compare the additive effect variation (ΔI_k^{sep}) with the cumulative effect variation (ΔI_k^{cum}). If the difference was considered medium ($|\partial\text{Cliff}| < 0.33$), the cumulative effect was considered different than the additive effect. We determined the cumulative effect depending on the difference between the additive effect variation and the cumulative effect variation (Figure II - 5).

To reduce the number of models when describing the ENA indices, we used an average unweighted pair group method with arithmetic mean (UPGMA) based on Euclidean distance. The UPGMA compared all the different models according to their mean ENA values.

3 Results

3.1 Reef effect on the food web

When the reef effect of the offshore wind farm was modeled in the LIM model, it resulted in an increased activity of the benthic group and in a decreased activity of the pelagic group. The reef effect also resulted in increased detritus consumption, increased phytoplankton activity and increased import (Figure II - 6).

3.2 Effects of climate change on the food webs before offshore wind farm construction

When the BOWF models were impacted by the climate change scenarios, three groups displayed a strong increase in activity and 11 displayed a strong decrease in activity. Throughout the groups and scenarios, climate change had mainly a negative effect on group activity. Negative effects on activity can be divided into two types: (i) the direct effect of climate change on the targeted group (for instance, lower biomass of the cephalopod group in the cephalopod scenario leading to lower cephalopod activity), and (ii) the indirect / cascading effect of climate change on activity (lower biomass of the cephalopod group in the cephalopod scenario leading to lower cetaceous activity) (Figure II - 6).

3.3 Combined effects of climate change and of an offshore wind farm on the food web

When the offshore wind farm (REEF) models were impacted by the climate change scenarios, 8 groups showed a strong increase in activity and 13 a strong decrease in activity. The REEF scenarios displayed greater changes due to climate change than the BOWF scenarios (38 strong variations in total for the REEF scenarios *versus* 30 for the BOWF scenarios), with a relatively more positive effect on activity. Similarly, to the BOWF scenarios, the negative effects on activity were of two types: (i) the direct effects, and (ii) the indirect / cascading effects. While the direct effects of climate change appeared to be similar in the BOWF and

REEF scenarios, the indirect / cascading effects were mostly different. There were four similarities between the BOWF and REEF models among the twenty indirect effects of climate change: (i) the indirect increase in invertebrate predator activity in the total scenario and the “fish, benthos feeders” scenario, (ii) the indirect decrease in phocidae activity in the total scenario and in the “fish, piscivorous” scenario, (iii) the indirect decrease in cetaceous activity in the total scenario and in the “fish, piscivorous” scenario, and (iv) the indirect decrease in import in the total scenario and the “fish, benthos feeders” scenario (Figure II - 6).

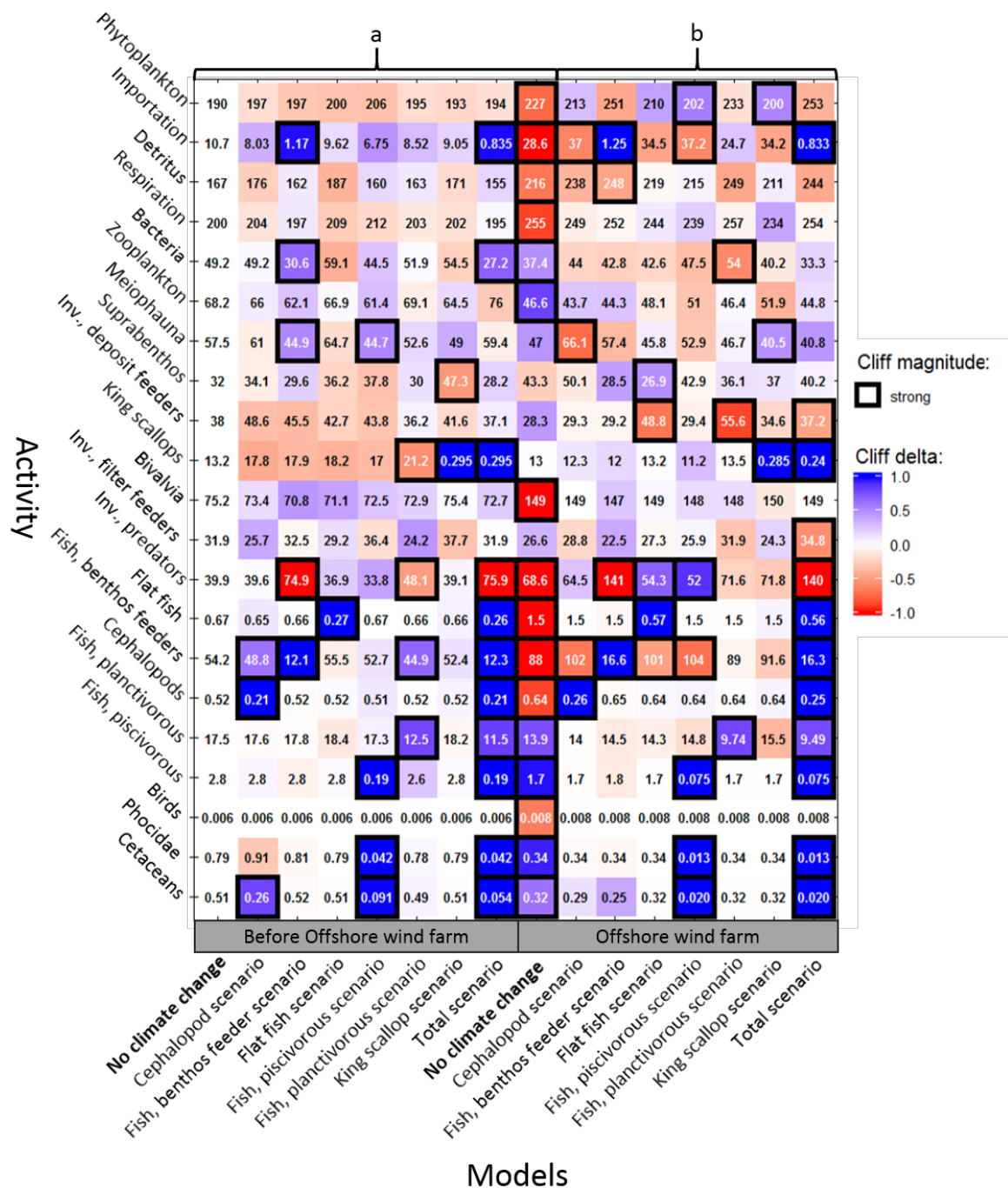


Figure II - 6 Variation of all the throughflow/activity (input/output) in $gC.m^2$ between: the BOWF model and the single effect models (reef effect or climate change effect, a group on the left), and between the REEF model and the cumulative models (reef effect + climate change effect, b group on the right).

Red, increased activity; blue, decreased activity; bold-bordered square, strong variation according to the cliff delta ($|\Delta\text{Cliff}| < 0.474$).

3.4 Changes in the structure and functioning of the food web

The flow matrices were used to compute the ENA indices. The UPGMA discriminated five groups of models. The models including the sole climate change effect and the BOWF model formed three groups (with two groups composed of only one model). The models including the reef + climate change effect formed two groups (Figure II - 7, A).

In both the BOWF and REEF scenarios, the “fish, benthos feeders” (FBF) scenario and the total (TOT) scenario showed differences with the rest of the climate change scenarios (Figure II - 7, B). Those models showed a greater number of strong differences ($|\partial\text{Cliff}| > 0.474$) with their respective reference model compared to the other scenarios. Four strong differences were observed under the BOWFTOT model compared to BOWF, six under BOWFFBF compared to BOWF, and three under REEFTOT and REEFFBF compared to REEF.

The climate change effects on the “fish, benthos feeders” (FBF) scenario and the total (TOT) scenario appeared as structuring as the REEF effect itself (Figure II - 7, A & B). The climate change effect strongly impacted ($|\partial\text{Cliff}| > 0.474$) four indices of the total scenario and six of the “fish, benthos feeders” scenario, while the reef effect strongly impacted six indices. The remaining climate change scenarios had little effect on the system (Figure II - 7, B).

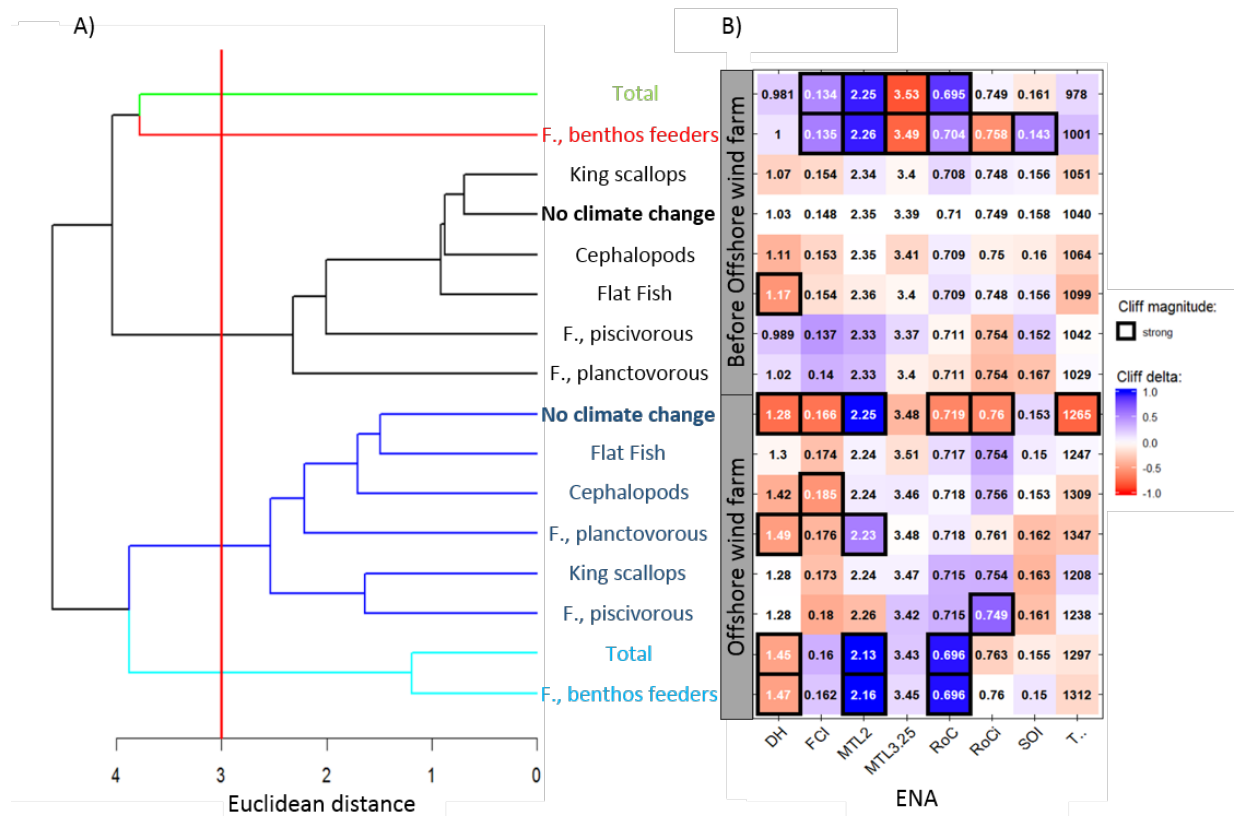


Figure II - 7 Effects of climate change and the offshore wind farm on ENA indices.

A) Following UPGMA to determine different groups of models, 5 groups were selected. B) The Cliff delta was used to compare the ENA results of: the BOWF model and the single effect models (reef effect or climate change effect), and between the REEF model and the cumulative models (reef effect + climate change effect).

3.5 Cumulative effects on ENA indices

The cumulative impact assessment showed a wide variety of cumulative effects – additional, synergetic, dampened, and antagonistic. Six of the seven scenarios showed at least one cumulative effect on their ENA ($0.33 < |\Delta \text{Cliff}|$). As for ENA indices, seven out of eight indices in total showed at least one cumulative effect ($\Delta \text{Iksep} \neq \Delta \text{Ikum}$) (Figure II - 8).

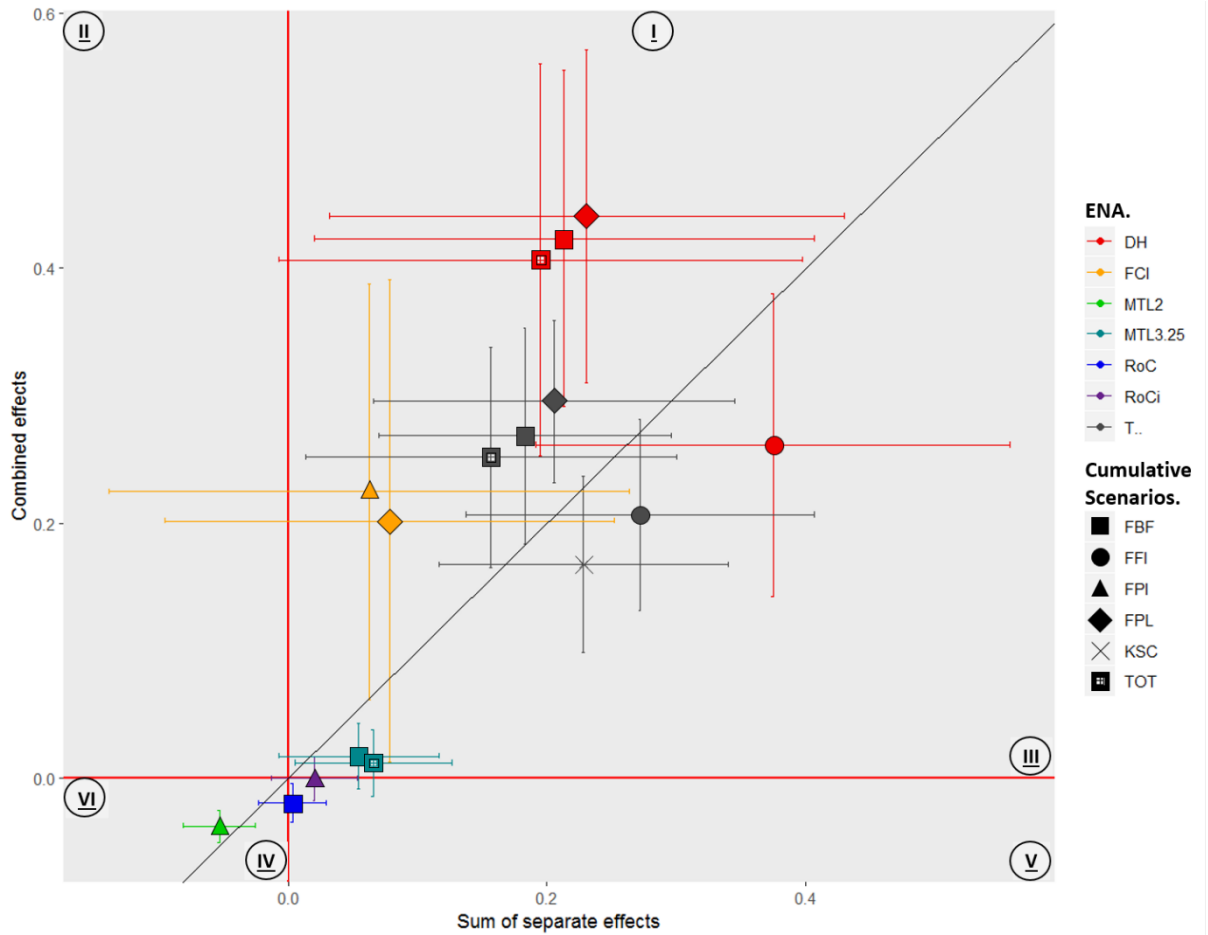


Figure II - 8 Cumulative effects of the different scenarios on multiple ENA indices (+/- SD).

Each cumulative effect is represented in a zone. Zone I, positive synergistic effect; zone II, positive antagonistic effect; zone III, positive dampened effect; zone IV, negative synergistic effect; zone V, negative antagonistic effect; and zone VI, negative dampened effect.

Most of the cumulative effects were additive ($\Delta k_{sep} = \Delta k_{cum}$) for all the results (all ENA indices for all models). Sixteen percent of the models showed a cumulative effect (Δk_{sep} different from Δk_{cum} with $|\partial Cliff| > 0.33$).

4 Discussion

This study assesses the cumulative impacts of climate change and an OWF on the Bay of the Seine food web, based on LIM models. Because of the complexity of modeling climate change in its full extent (Larocque *et al.*, 2011), this work was focused on the effect of climate change on the indigenous species of the bay, more particularly on commercially exploited species. That is why it is a sensitivity analysis of these cumulative impacts on ENA indices. First,

our sensitivity analysis revealed that each effect taken separately had an impact on the functioning and organization of the ecosystem. The “fish, benthos feeders” group appeared particularly sensitive to the two single effects. When the effects were combined, we observed significant cumulative effects on multiple ENA indices for multiple scenarios. Those significant cumulative effects led to unexpected effects on the ecosystem. Overall, ENA indices appeared sensitive to the cumulative impact.

4.1 The structuring role of the reef effect

The results of the REEF model seem to suggest a regime shifting towards a new stable state. An ecosystem shift is documented as a change at several trophic levels leading to ecosystem restructuring (Lees *et al.*, 2006; Andersen *et al.*, 2009). The restructuring of the system should be visible on the ecosystem structure but also on its functioning. The restructuring due to the reef effect was already predicted by Raoux *et al.* (2017; 2019) based on the evolution of the mean trophic level (MTL 2). We modeled a similar decrease in MTL 2 between the BOWF and REEF models. A decline in MTL 2 would explain a transition in the food web from long-lived high-trophic-level organisms like piscivorous fish towards short-lived low-trophic-level organisms such as invertebrates and planktivorous fish (Pauly *et al.*, 1998). In the reef effect case, the biomass of the higher trophic level was not reduced, whereas the biomass of low-trophic-level organisms increased. Like Raoux *et al.* (2017; 2019), we consider this change as a restructuring of the community towards a new stable state rather than an unsustainable alteration of the ecosystem (Holling, 1996). We improved over Raoux *et al.* (2017; 2019) by also observing a change in the ecosystem’s functioning. This change was noticeable through the different responses of the BOWF and REEF models to climate change. When we impacted the two models with the climate change scenarios, very few similarities between the BOWF response and the REEF response emerged. The differences in the cascading responses to climate change between the BOWF and REEF models may be explained by a shift in the system (Lees *et al.*, 2006; Andersen *et al.*, 2009). Our ENA results reflect a shift from a benthopelagic system towards a more benthic system. The system appeared more active with lower-trophic-level species relying less on herbivory and more on detritivory and recycling. Alongside the increase in redundant pathways, the system appeared more resistant to changes.

The ENA variations that we predicted between the BOWF model and the REEF model described a more resistant OWF system. Resistance is defined as the ability of a system to maintain its original state in a disturbed context as described by Holling (1996), and in accordance with ‘ecological resilience’ as described by Harrison (1979). Many ENA indices have been related to the notion of resistance. Lassalle et al. (2011) hypothesized that an increase in the detritivory to herbivory (D/H) rate was associated with a system more resistant to primary production variation. Recycling (FCI) may act as a buffer during disturbances and increase the resistance of the system (Saint-Béat et al., 2015). The overhead/redundancy of the flow (RoC and RoCi) may also act as a buffer during disturbances to maintain the system and thus increase its resistance (Ulanowicz and Norden, 1990). We predicted an increase of each of those indices (D/H, FCI, RoCi). Our results are less conflicting than the ones observed by Raoux et al. (2019) and describe a more coherent picture of the system, with benthic groups playing a key role in the resistance of ecosystems (Norling and Kautsky, 2007; Dame and Christian, 2007; Raoux et al. 2019; Wang et al. 2019).

The effect of climate change on the system also appeared to validate the more resistant state of the REEF model, especially on the “fish, benthos feeders” scenario (FBF). The BOWF model led to more changes in ENA indices than the REEF model: Its lower omnivory level (SOI) revealed a less complex system evolving from a web-like system towards a more linear system (Libralato, 2013). As the complexity of a system is an indicator of flexibility (Fagan, 1997b; Lobry *et al.*, 2008), we can expect a less stable and more vulnerable system. We also predicted that the system would lose part of its recycling capacity (FCI) and be less mature due to the lower redundancy of internal flows (RoCi) (Odum, 1969; Ulanowicz and Norden, 1990; Christensen, 1995; Ulanowicz, 2009). On the other hand, the only modeled effect of climate change on the “fish, benthos feeders” scenario of the REEF model was a higher detritivory to herbivory rate (D/H) of the system. As such, the reef effect seemed to increase the resistance of the system to climate change. However, one must not forget that these results depend on the way the climate change effect was modeled. The reef effect could also promote other effects of climate change, like the establishment of invasive species (Langhamer, 2012), but their study would need specific field experiments.

4.2 Role of the group impacted by climate change in the response of the ecosystem

Our analysis of the different ENA responses showed a pattern segregating the responses of the scenarios depending on the group impacted by climate change. The “fish, benthos feeders” (FBF) and the total (TOT) climate change scenarios showed important estimated changes in their structure and functioning, while the other climate change scenarios seemed close to their reference model. This happened in both the BOWF and REEF models. In both cases, the “fish, benthos feeders” (FBF) and the total (TOT) climate change scenarios impacted the “fish, benthos feeders” group (FBF). This leads us to think that the importance of the “fish, benthos feeders” group isn’t defined by the aggregating role of the reef effect (Reubens *et al.*, 2011), but rather by its position in the food web and thus its keystone-ness. The keystone-ness of a species defines its structuring role (Power *et al.*, 1996; Libralato, 2019) and is not an intrinsic property of any given species (Fauth, 1999). The fact that the “fish, benthos feeders” group maintained its role despite the shift in the regime of the system might be due to the central position of its trophic niche in both systems.

The “fish, benthos feeders” (FBF) group seemed to play two roles in both models: first, it regulated the “invertebrates, benthic predators” group (IPR), and second, it ramified the system through its high omnivory. This was predicted when the “fish, benthos feeders” were impacted by the climate change effect (Figure II - 7). The trophic niche of the “fish, benthos feeders” was thus claimed by the “invertebrate, benthic predators”, and consequently changed the functioning of the food web. This result was different when considering the ecosystem shift caused by the reef effect: the “invertebrate, benthic predators” seemed more capable to replace the “fish, benthos feeders” in their niche. This replacement seemed to be facilitated by the shift of the ecosystem towards a more benthic system, in which the invertebrate benthic predators might be more successful in filling the same trophic role as the fish benthos feeders. As such, the system seemed less altered by the effect of climate change on the “fish, benthos feeders” scenario in the offshore wind farm system. However, we should remain careful because changing communities can have wider effects on the ecosystem likely to go undetected by trophic modeling approaches (Fontaine *et al.*, 2011; Kéfi *et al.*, 2012, 2015). As such, it is necessary to monitor such keystone species to maintain the ecosystem properties before, during and after the exploitation of the offshore wind farm. Previous studies

have indeed already highlighted the advantages of monitoring keystone species (Payton et al., 2002; Libralato et al., 2006; Gelcich et al., 2010).

4.3 Understanding the mechanism behind the unexpected effect of the cumulative impact

Our scenarios show a wide variety of cumulative impacts, in line with previous studies that consider the additive effect to be the main type of combined effect in marine ecosystems, with a significant role of the cumulative impact on ecosystems (Crain et al., 2008). We evidenced synergetic and antagonistic effects, which proved the ability of ENA indices to reflect unexpected effects visible only when studying cumulative impacts (Jackson *et al.*, 2001; Przeslawski *et al.*, 2005). Cumulative impacts are often studied using community or population level metrics (Crain et al., 2008). By observing the same type of response with ENA, we demonstrate that cumulative effects are also significant at the functional level of the ecosystem. This is useful as it allows us to follow the properties of the ecosystem and its state in relation to the cumulated impact. Using functional metrics like ENA indicators might also help us better understand cumulative effects. This strengthens the importance of incorporating multiple scenarios of events in future ecological network analysis.

The strongest synergetic effect was predicted on the detritivory to herbivory (D/H) index of the “fish, benthos feeders” scenario (FBF). This synergistic effect seems to result from the shifting regime of the Courseulles-sur-Mer ecosystem. As the system shifted from a benthopelagic system to a more benthic system, the effect of climate change on the ecosystem functioning seemed to change (Figure II - 7). In the BOWF model, the climate change effect on the fish benthos feeders resulted in an increased activity of the invertebrate benthic predators. This higher invertebrate benthic predator activity did not lead to an increase in detritivory because the system was not producing enough benthic detritus. Yet, this changed with the reef effect. As a system becomes more benthic, it produces more benthic detritus (Norling and Kautsky, 2008, 2007; Raoux et al., 2017). This increase in benthic detritus became available to the invertebrate benthic predators, and increased the detritivory to herbivory rate of the system. Many invertebrate benthic predators are indeed also scavengers. This changing response of the ecosystem to climate change due to the regime shift induced this unexpected effect on the detritivory to herbivory rate. This higher detritus consumption with the higher detritivory to herbivory rate of the OWF ecosystem resulted in a synergistic effect, as predicted

by the “fish, benthos feeders” scenario (Table II - 2). An interaction between effects has already been shown to modify the effect of one or multiple events, e.g., in chemical reactions (Pelletier *et al.*, 2006) and physiological/ecological reactions (Przeslawski *et al.*, 2005; Christensen *et al.*, 2006). We observed it at the functional level of the ecosystem. Integrating the evolving interactions between effects in a shifting ecosystem could help us better anticipate these effects. For us to detect those shifts, monitoring the entire ecosystem using ecological network analysis is needed, using local and relevant data on all trophic levels (Araignous *et al.*, 2019).

While two effects can interact with each other toward a synergistic effect, they may also interact negatively, with a resulting antagonistic or dampened effect. This was mainly modelled for the detritivory to herbivory rate of the “flat fish” scenario (Table II - 2). When considered independently, the climate change effect and the reef effect increased the detritivory to herbivory rate. However, when the effects were combined, the cumulative effect on the detritivory to herbivory rate was dampened. This could be explained by the fact that the regime shift made the ecosystem impervious to the climate change effect. This mechanism of resistance has already been acknowledged at the physiological level or at the population level (Vinebrooke *et al.*, 2004). ENA proved able to do the same at the functional level of the ecosystem.

The regime shift due to the reef effect seemed to explain multiple cumulative effects. However, sometimes it was uncertain whether the cumulated effect resulted from the model structure or not. This was visible on the total overhead of the “fish, benthos feeders” scenarios. In this case, the dominating effect of climate change overcame the cumulative effect (Table II - 2). With the “fish, benthos feeders” group relying significantly on imports (like cetaceous, seals and birds), a reduction of its biomass will lower the import overhead. As the import overhead is a part of the total overhead (Ulanowicz and Norden, 1990), the total overhead will decrease even though the internal overhead remains unchanged. This could be the result of the model structure itself, as the dependency of the “fish, benthos feeders” group to import is mainly due to the reduced scale of the trophic model. Moreover, ENA indices are known to be potentially highly influenced by the model structure (Baird *et al.*, 2009; Johnson *et al.*, 2009). The lower import overhead could also be the sign of a more isolated system compared to the rest of the English Channel ecosystem (Baird and Ulanowicz, 1993).

Table II - 2 Representation of the different mechanisms of the cumulative effects based on the LIM model results.

Scenario	ENA index	Climate change effect alone	Reef effect alone	Combined effects	Type of cumulative effect	Mechanism
Fish, benthos feeders (FBF)	Detritivory to herbivory (D/H)	+	+	++++	Positive synergistic	Interaction between the two effects due to the regime shift caused by the reef effect.
Fish, piscivorous (FPI)	Internal relative overhead (RoCi)	+	+	-	Negative antagonistic	Interaction between the two effects due to the regime shift caused by the reef effect.
Flat fish (FFI)	Detritivory to herbivory (D/H)	+	+	+	Positive dampened	Resilience of the ecosystem to the climate change effect due to the regime shift caused by the reef effect.
Fish, benthos feeders (FBF)	Relative overhead (RoC)	-	++	--	Negative antagonistic	The climate change effect overpowers the reef effect.

4.4 Ecological network analysis indices: sensitive tools to manage the cumulative impact of the REEF and climate change effects.

Using a single ENA index to describe a changing system is not suitable to describe a changing ecosystem; a larger pool of indices is more adapted to reach an overall picture of the ecosystem organization and functioning (de la Vega *et al.*, 2018). The same is true for combined impacts, which make it possible to predict different types of cumulative effects for different parameters of the ecosystem. While an index can describe a synergetic effect of the combined reef and climate change effects, another index may describe an antagonistic effect. This point should be emphasized when working on a limited number of indices, as multiple indices can be impacted differently. Interactions between events thus appear to be radiative – not unidirectional –, i.e., different properties of an ecosystem can evolve in different ways. This emphasizes the need for complementary indices to provide a holistic view of the ecosystem

(Fath *et al.*, 2019; Safi *et al.*, 2019), especially while addressing the effect of cumulative impacts.

Ecological network analysis indices seem to be suitable for addressing a wide range of cumulative effects. Along with an integrative approach, this ability to study cumulative impacts in their overall diversity makes ENA indices the ideal ecological indicators necessary for the future of ecological science and management (de la Vega *et al.*, 2018; Fath *et al.*, 2019; Safi *et al.*, 2019). It is now time to implement those indices in more complex cumulative impact scenarios to describe the mechanisms behind cumulative impacts.

Acknowledgements

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III Chapitre 2A :

Spatialized ecological network analysis for ecosystem-based management: effects of climate change, marine renewable energy and fishing on ecosystem functioning in the Bay of Seine

Le second chapitre de la thèse se base, comme le premier chapitre, sur une partie des travaux réalisés durant le projet TROPHIK, avec l'objectif d'améliorer les méthodes de modélisation tout en prenant en compte le potentiel cumul d'impacts. C'est dans cet objectif que nous avons mis en place un cadre méthodologique basé sur le modèle Ecospace réalisé par Halouani et al. (2020). Ecospace est une approche de modélisation des réseaux trophiques spatialisés basé sur Ecopath, un modèle trophique à l'équilibre comme le LIM, couramment utilisé par la communauté scientifique dans un but de gestion des écosystèmes (Walters *et al.*, 1999; Pauly *et al.*, 2000). Le modèle Ecospace de Halouani et al. (2020) modélise l'écosystème de la baie de Seine étendue et enveloppe de nombreuses espèces, depuis les mammifères marins et les oiseaux jusqu'au zooplancton et phytoplancton. Grâce à ce modèle spatialisé de l'écosystème de la baie de Seine étendue et aux connaissances acquises de l'analyse du cumul d'impacts avec les indices ENA sur le modèle LIM de Courseulles-sur-Mer, les objectifs de ce chapitre sont les suivants. (1) Repenser les méthodes utilisées pour améliorer la modélisation des effets des facteurs sur l'écosystème de la baie de Seine étendue, en ajoutant la modélisation de l'effet récif du parc éolien par rapport à Halouani et al. (2020) et en améliorant la modélisation de l'effet du changement climatique sur l'écosystème par rapport à Bourdaud et al. (2021). (2) Proposer une étude spatialisée des effets des différents facteurs impactant la baie de Seine étendue, en utilisant des indicateurs écologiques holistiques et en regardant l'effet des facteurs sur le fonctionnement et l'organisation de l'écosystème de la baie. (3) Modéliser de nouveaux facteurs, comme des variations des régimes de pêche liées au Brexit ou bien l'effet de l'extraction de granulats marins ayant lieu en baie de Seine étendue. (4) Proposer une analyse spatialisée du cumul d'impacts et des mécanismes le régissant.

Pour réaliser ces multiples objectifs, ce chapitre a donc été divisé en trois parties, dont deux sont présentées dans le corps de la thèse et une troisième en supplément (**Chapitre supplémentaire**). La première partie de ce deuxième chapitre (de thèse), partie A, vise donc à mettre en place un cadre méthodologique pour permettre la réalisation des deux autres (partie B et supplément). Cette partie présente l'utilisation du modèle Ecospace de la baie de Seine étendue dans le but de modéliser séparément les effets de multiples facteurs environnementaux : le parc éolien de Courseulles-sur-Mer, le changement climatique et l'effet du Brexit sur les régimes de pêche. Pensée dès ses débuts pour pouvoir réaliser une analyse du cumul d'impacts, cette partie présente aussi des méthodologies complémentaires en

utilisant des outils basés sur des théories matures d'Ecopath with Ecosim (Pauly *et al.*, 2000; Christensen *et al.*, 2014). Une première analyse des effets séparés de chaque facteur est également présentée et est réalisée grâce à une analyse spatialisée des indices de réseaux écologiques ENA. Il s'agit de la première étude utilisant les indices de réseaux ENA de manière spatialisée, faisant de cette dernière une approche très novatrice.

C'est pour cette raison que cette première partie de ce second chapitre de thèse a été soumise au journal international « ICES Journal of Marine Science » en Juin 2021 :

Spatialized ecological network analysis for ecosystem-based management: effects of climate change, marine renewable energy and fishing on ecosystem functioning in the Bay of Seine

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Résumé :

Des outils écosystémiques, holistiques et spatialisés capables d'étudier les effets d'une grande variété de facteurs environnementaux sont nécessaires pour mettre en œuvre une bonne gestion et planification des écosystèmes marins. Dans ce chapitre, nous développons un outil permettant d'analyser les effets directs et indirects de plusieurs facteurs environnementaux, incluant le changement climatique, un parc éolien en mer et différents scénarios de pêche, sur le fonctionnement et l'organisation de l'écosystème côtier de la baie de Seine, en Manche. Avec des techniques de modélisation innovantes, nous avons utilisé un modèle trophique spatialisé, Ecospace, pour réaliser une analyse du réseau écologique de la baie de Seine. Les facteurs environnementaux furent modélisés grâce à différentes approches d'Ecopath with Ecosim, en couplage direct avec des modèles de niche, des résultats expérimentaux et des connaissances d'experts. Les indices de réseaux écologiques ENA mirent en évidence une structuration côte / large du fonctionnement de l'écosystème de la baie de Seine. Trois régions fonctionnelles ont été mises en évidence et ont été utilisées pour caractériser les effets des différents facteurs sur l'écosystème. L'effet du changement climatique apparaît comme l'effet le plus structurant sur le système, que ce soit entre les différentes régions intra-baie de Seine, qu'à l'échelle globale de la baie de Seine. Ceci montre qu'il est important de prendre en compte les potentiels effets du changement climatique, que ce soit à une échelle globale comme par exemple à l'échelle des côtes européennes, mais également à une échelle plus locale comme à l'échelle de la baie. En effet les différentes cinétiques de dérive des espèces vers le nord semblent avoir un effet important sur la structure locale des écosystèmes. La résilience de l'écosystème semble d'ailleurs impactée par cet effet, même s'il est important de garder à l'esprit que cette réponse est probablement spécifique à l'écosystème étudié (à cause de la structure initiale de l'écosystème et de l'effet spécifique du changement climatique dans l'écosystème étudié). *A contrario*, l'effet des changements des régimes de pêche liés au Brexit ne semble pas modifier le fonctionnement de l'écosystème de manière significative. En effet, les différents scénarios que nous avons testés pour déterminer les potentiels effets du Brexit avaient tous un effet négligeable sur le système. Enfin, l'effet combiné « réserve » et « récif » du parc éolien de Courseulles-sur-Mer continue de montrer leur rôle important sur la structure et la résilience de l'écosystème de Courseulles-sur-Mer. Le modèle nous montre également très bien l'effet attractif du parc, qui a aussi un rôle

structurant à l'extérieur du parc, réduisant la résilience du système dans la zone de débordement autour du parc. L'étude montre donc l'intérêt des indices ENA dans une analyse spatialisée des effets de différents facteurs sur l'écosystème. Ce travail s'inscrit également comme une première étape, qui sera suivie d'une étude des effets du cumul d'impacts sur le fonctionnement de l'écosystème.

Spatialized ecological network analysis for ecosystem-based management: effects of climate change, marine renewable energy and fishing on ecosystem functioning in the Bay of Seine

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Abstract

Integrative and spatialized tools for studying the effects of a wide variety of ecosystem drivers are needed to implement ecosystem-based management and marine spatial planning. We developed a tool for analyzing the direct and indirect effects of anthropic activities on the structure and functioning of coastal and marine ecosystems. Using innovative modeling techniques, we ran a spatially explicit model to carry out an ecological network analysis (ENA) of the effects of climate change, of an offshore wind farm and of multiple fishing scenarios on the Bay of Seine (eastern part of the English Channel) ecosystem. ENA indices described the effects of those different drivers in a holistic and spatial way. The spatial analysis of ecosystem properties revealed local and global patterns of modifications attributed to climate change, while the offshore wind farm resulted in localized changes in the ecosystem. This ability of ENA indicators to detect human-induced changes in ecosystem functioning at various spatial scales allows for a more integrative view of the effects of human activities on ecosystems. ENA indices could be used to link both local and global ecosystem changes, for a more cross-scale approach to ecosystem management.

Key words: Ecological network analysis, ENA, Ecospace, trophic structure, ecosystem functioning, climate change, Offshore wind farm, fishing effects, species distribution.

Highlights:

- Ecological network analysis describes the spatial effects of multiple environmental drivers on the functioning of the extended Bay of Seine ecosystem.
- Climate change effect on species distribution had strong structuring effects on the ecosystem.
- Two fishing scenarios linked to Brexit (increased and decreased fishing) were tested; they had limited effects on ecosystem functioning compared to the effects of climate change on species distribution.
- Ecological network analysis distinguished vulnerable areas that might require special attention in terms of ecological management.

1 Introduction

Marine ecosystems are crucial for human societies because they provide many services such as food provisioning, nutrient regulation, habitat maintenance and climate mitigation (Peterson and Lubchenco, 1997). Marine ecosystems are subject to pressures from human activities (Halpern *et al.*, 2008b) and their subsequent detrimental impacts. Anthropogenic pressure is predicted to keep on increasing in the next decades due to the growing human needs (MEA *et al.*, 2005). This is reflected in the expanding number of offshore wind farms (OWFs) to meet the need for greener energy. The environmental impacts of OWFs occur in three phases: i) during the construction phase impacts may be considered temporary, the same can be said of the ii) decommission phase while iii) during the operational phase impacts are longer lasting (Petersen and Malm, 2006). The most significant long-lasting impacts of the operational phase on the whole ecosystem functioning include the reef effect caused by the turbine structures and the reserve effect resulting from fishing closure (Raoux *et al.*, 2019; Degraer *et al.*, 2020). Direct anthropogenic activities are not the only driver of ecosystems: climate change (CC) may also have many hard to predict effects (Hoegh-Guldberg and Bruno, 2010; Poloczanska *et al.*, 2016; Winder and Sommer, 2012a). These effects include (among others) drifts in species distribution (Cheung *et al.*, 2009) and changing physiological rates (Brierley and Kingsford, 2009). Ecosystems are complex and interconnected. Unpredictable effects on several of their components could cascade through trophic chains and interactions, limit their resilience and thus facilitate regime shifts and ecosystem collapses (Levin and Lubchenco, 2008). In this situation, there is a growing need for integrative approaches to understand the sensitivity of such ecosystems to a wide variety of drivers.

The scientific community and the decision makers encourage the use of integrative approaches that can address an increasing complexity (Rombouts *et al.*, 2013) and number of anthropogenic pressures (de Jonge, 2007; Fath *et al.*, 2019; Rodriguez, 2017). Integrative approaches are holistic methods employed to understand the functioning of whole ecosystems. Integrative or ecosystem-based approaches are considered essential for adequate ecosystem-based management (Agardy *et al.*, 2011; Borja *et al.*, 2010; Buhl-Mortensen *et al.*, 2017) and have been highly advocated for sustainable management of marine and coastal environments (Langlet and Rayfuse, 2018).

Ecological network analysis (ENA) is promising because it is compatible with ecosystem-based management and offers a quantitative assessment of marine ecosystem functioning (Niquil *et al.*, 2014b; Safi *et al.*, 2019; Heymans *et al.*, 2020). ENAs depict the ecosystem as a network of interactions, where information can cascade from one part of the network to the other. Derived from different sciences including economics and thermodynamics (Wulff *et al.*, 1989), ENA indices can quantify emerging properties of ecosystems and monitor their evolution (Ulanowicz, 1986; Heymans and Tomczak, 2016; Borrett and Scharler, 2019). Using ENA to spatialize ecosystem models would make them more operational and help marine spatial planning (Le Tissier, 2020).

Ecospace is a well-known spatio-temporal trophic model derived from the Ecopath with Ecosim framework (Walters *et al.*, 1999; Christensen and Walters, 2004). It can help marine spatial planning initiatives by simulating the effects of environmental changes on food webs (e.g. Alexander *et al.*, 2016; Liqueste *et al.*, 2016). However, to our knowledge, no study has tested ENA in an Ecospace model. Combining ENA with Ecospace could give us a holistic view of the ecosystem under multiple schemes of environmental changes in order to link ecosystem-based management to marine spatial planning.

In this study, we propose to investigate the spatial effects of multiple drivers on the Bay of Seine (eastern part of the English Channel) ecosystem, using ENA indices. This work is based on the Ecospace model of Halouani *et al.* (2020) modified by Bourdaud *et al.* (2021). It represents the food web of the extended Bay of Seine (eBoS), and initially modeled the potential reserve effect of the future offshore wind farm (OWF) of Courseulles-sur-Mer (Halouani *et al.* 2020). It was also used to explore the potential effects of CC on species distribution (Bourdaud *et al.* 2021) by combining it with niche models (Ben Rais Lasram *et al.*, 2020).

Following these works, we integrated new approaches aimed at better forecasting the possible evolution of the Bay of Seine ecosystem. First, we added the reef effect to the potential impacts of the future OWF of Courseulles-sur-Mer. Secondly, we used the spatial-temporal framework module of *EwE* (Steenbeek *et al.*, 2013) to better model the likely effect of CC on species distribution in the Bay of Seine. Finally, we integrated fishing scenarios following the plausible effects of Brexit into the eBoS model. The spatial explanatory power of ENA indices was tested, both at a local scale inside the eBoS (OWF) and at a global scale across

eBoS (CC and fishing scenarios), using these scenarios. We explored the spatial variability of the ecosystem properties and determined three functional regions with similar properties in the eBoS. We also discussed the sensitivity of the ecosystem properties to the different drivers within each functional region. By doing so, we determined the potential risk that such changes in ecosystem properties occur. We also highlighted the sensitive areas of the ecosystems that may require special attention from decision makers in the future, especially in the implementation of new OWFs in the English Channel. Finally, we investigated ENA sensitivity and explanatory power as a spatial planning tool.

2 Materials and methods

2.1 Study area

The extended Bay of Seine Ecospace model covers the sea space from the Cotentin peninsula to Le Havre all the way up to the French-British delimitation of the Exclusive Economic Zones (Figure III - 1). It is a shallow coastal ecosystem open onto the English Channel, with a mean depth of 35 m varying from 5 m to around 70 m in the paleo-valley north-west of the eBoS. The eBoS covers 13,500 km²; the main sediment types include gravels, coarse sand, fine sand and muddy fine sand (Supplementary materials Figure SII - 1, Dauvin, 2015). Oceanographic features include the Seine estuary (south-east of the eBoS), and the Seine paleo valley (south-east to north-west of the eBoS) (Figure III - 1). The Bay of Seine and the English Channel in general are a highly anthropized ecosystem, with numerous activities including fishing, aggregate extraction, marine renewable energy, tourism, sea freight and more (Dauvin, 2015). Fishing is very important in the bay, and more particularly king scallop (*Pectens maximus*) dredging, but many other fishing techniques are also used. Fishing gears include trawls and nets targeting demersal fish, trawls targeting small pelagic fish, demersal fish and cephalopods, as well as other fishing gears (Supplementary materials Table S II - 1). The most harvested fish species include sole (*Solea solea*) and cod (*Gadus morhua*). The bay is also of great interest for renewable marine energy. The offshore wind farm of Courseulles-sur-Mer is currently being built (~ 50 km², 64 turbines), while other offshore wind farm projects of various sizes are under consideration in the bay.

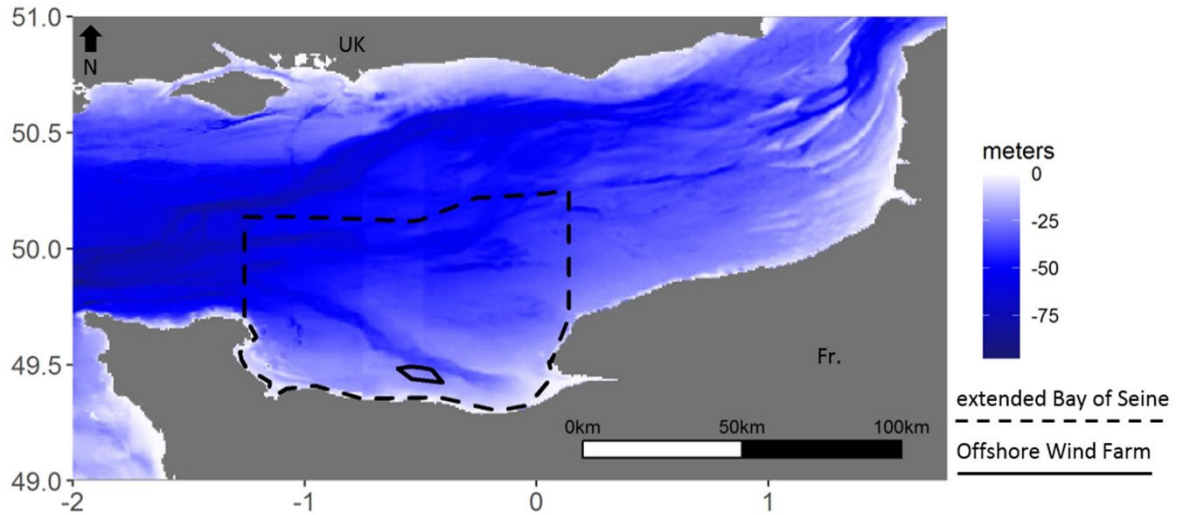


Figure III - 1 Map of the eastern English Channel, including the boundaries of the extended Bay of Seine Ecospace model and the localization of the offshore wind farm of Courseulles-sur-Mer.

2.2 Food web modeling

The eBoS model was built from Ecopath with Ecosim (EwE 6) software. EwE can model marine food webs through a static average representation (Ecopath), with a time dynamics (Ecosim) and spatio-temporally (Ecospace).

The basic Ecopath model is a balanced model where the production of a trophic group is considered equal to its consumption by the system (Polovina, 1984b; Pauly *et al.*, 2000). The production of each group of Ecopath follows the equation:

$$B_i \cdot (P/B)_i = \sum B_j \cdot (Q/B)_j \cdot DC_{ij} + Y_i + E_i + BA_i + B_i \cdot (P/B)_i \cdot (1 - EE_i) \quad (1)$$

Where B is the biomass of prey i or predator j, $(P/B)_i$ is the production of i *per* unit of biomass, $(Q/B)_j$ is the consumption of j *per* unit of biomass, DC_{ij} is the fraction of i in the diet of j, Y_i is the total fishery catch rate of i, E_i is the net migration rate of i, BA_i is the biomass accumulation rate of i and EE_i is the ecotrophic efficiency of i or the proportion of i's production utilized in the system.

The eBoS Ecopath model is composed of 40 living groups including a wide range of marine species – fish, invertebrates, birds and marine mammals – and 2 non-living groups –

detritus and fishing discards. Living groups include monospecific groups as well as multi-specific groups (Supplementary materials Table S II - 2). Multiple fishing techniques were modeled (trawling, nets, angling, traps, and other minor gears). A full description of the eBos model is available in *Halouani et al. (2020)*.

Ecosim is a time-dynamic version of Ecopath and considers biomass variation over time (Walters *et al.*, 1997; Christensen and Walters, 2004). Ecosim represents the biomass dynamics as:

$$dB_j/dt = \frac{g_j \cdot a_{ij} \cdot v_{ij} \cdot B_j \cdot B_i}{2 \cdot v_{ij} + a_{ij} \cdot B_j} - Z_j \cdot B_j \quad (2)$$

where B_j is predator j biomass, i the prey of j , g_j is the growth efficiency of j , v_{ij} is the prey vulnerability exchange rate, a_{ij} is the predator search rate, and Z_j is the total instantaneous mortality of j .

The eBoS Ecosim model was set to run from 2000 to 2015 and used 29 annual time series, including 21 time series of catches from the IFREMER database SACROIX (Système d'Information Halieutique, 2017) and 8 time series of biomass from multiple stock assessment campaigns. See Halouani *et al. (2020)* for more details.

Finally, Ecospace is a spatially explicit time-dynamic model based on Ecopath and Ecosim. In Ecospace, the spatial extent of the ecosystem is represented by a grid of cells and each cell is a time-dynamic trophic model based on Ecosim, with interconnections between cells (Walters *et al.*, 1999; Christensen *et al.*, 2014). The base map of the eBoS Ecospace model was made of 4,907 cells, with a resolution of $0.015^\circ \times 0.015^\circ$ each, identified depending on their row r and their column c (r, c). Input maps included a bathymetric map to define the model area, extracted from GEBCO (General Bathymetric Chart of the Oceans: <https://www.gebco.net/>) and a map of primary production from SeaWiFS representing the relative chlorophyll a concentration in the bay in 2000 (<https://podaac.jpl.nasa.gov/>). A habitat map was used to define species distributions in the initial model of Halouani *et al. (2020)*, but it was replaced with niche model suitability index maps in Bourdaud *et al. (2021)* (Supplementary materials Table S II - 3). These suitability index maps were computed using multi-algorithm niche models (Ben Rais Lasram *et al.*, 2020). Niche model algorithms are correlative approaches aimed at identifying the potential niches of species by correlating

species occurrences with environmental variables (h). The niche models developed by Ben Rais Lasram *et al.* (2020) used temperature and salinity variables as well as benthic habitat data: type of substrate, depth, slope, and orientation. All the modeling choices can be found in Ben Rais Lasram *et al.* (2020). Suitability index maps were employed as environmental driver maps for most of the groups of the model (Coll *et al.*, 2019). Some groups considered poorly modeled by the niche models were driven by other parameters, e.g. depth (Supplementary materials Table S II - 3). Monospecific niche model outputs were directly applied for monospecific trophic groups and merged according to the biomass of each species in multi-specific groups. The multi-specific trophic groups lacking data to model the distribution of all the species of the group were driven by the suitability index map of the dominant species of the group (Bourdaud *et al.*, 2021).

Environmental drivers (h) were used to compute the habitat capacity (C_{rcj}) of each trophic group j in each cell (r,c) of the eBoS Ecospace model and define suitable habitats for each group of the model (Christensen *et al.*, 2014). The habitat capacity drove the vulnerable prey densities (V_{ij}) as well as the vulnerability exchange rate (v_{ij}), the search rate (a_{ij}) and the predation rate (z_j) to set suitable environments for all the groups of the model according to their environmental preferences. The habitat capacity C_{rcj} ranged between 0 and 1 and was calculated for each cell as a function of a vector of habitat attributes (environmental drivers):

$$C_{rcj} = f_j(h_{r,c}) \quad (3)$$

$$V_{ij} = \frac{v_{ij} \cdot B_j}{2 \cdot v_{ij} + a_{ij} \cdot \frac{B_j}{C_{rcj}}} \quad (4)$$

Where B_j is the biomass of predator j, v_{ij} is the vulnerability exchange rate, and a_{ij} the search rate.

Multiple types of environmental drivers can define the habitat capacity of a species (water depth, temperature, or suitability index maps from niche models, Supplementary materials Table S II - 3), and each environmental driver is associated with a specific response curve. In the eBoS model, a linear response curve was associated to the niche model results to compute the habitat capacity of each species (see De Mutsert *et al.*, 2017). The suitability index

of the niche models varied between 0 (not suitable) and 1 (suitable), like the habitat capacity (Bourdaud *et al.*, 2021). Other response curves were built for the other groups (Supplementary materials Figure SII - 2 to Figure SII - 7).

The eBoS model simulated multiple scenarios and each scenario modeled one driver. In the first scenario, we modeled the potential long-term effects of the future OWF of Courseulles-sur-Mer. The second and third scenarios modeled the likely effects of CC on species distribution in the bay of Seine under the RCP8.5 forcing scenario of the IPCC (Intergovernmental Panel on Climate Change) that appears to be the most realistic one (Schwalm *et al.*, 2020). Finally, we built two fishing scenarios linked to the potential effects of Brexit: a “reduced fishing activities” scenario – F_red – and an “increasing fishing activities” scenario – F_inc (Figure III - 2).

ENA required working with a mass-balanced model. As such, we did not work in a temporal way and we only needed “snapshot” of trophic flows. Ecospace was used to create end maps of indices for each scenario (Figure III - 2) at a mass-balanced state.

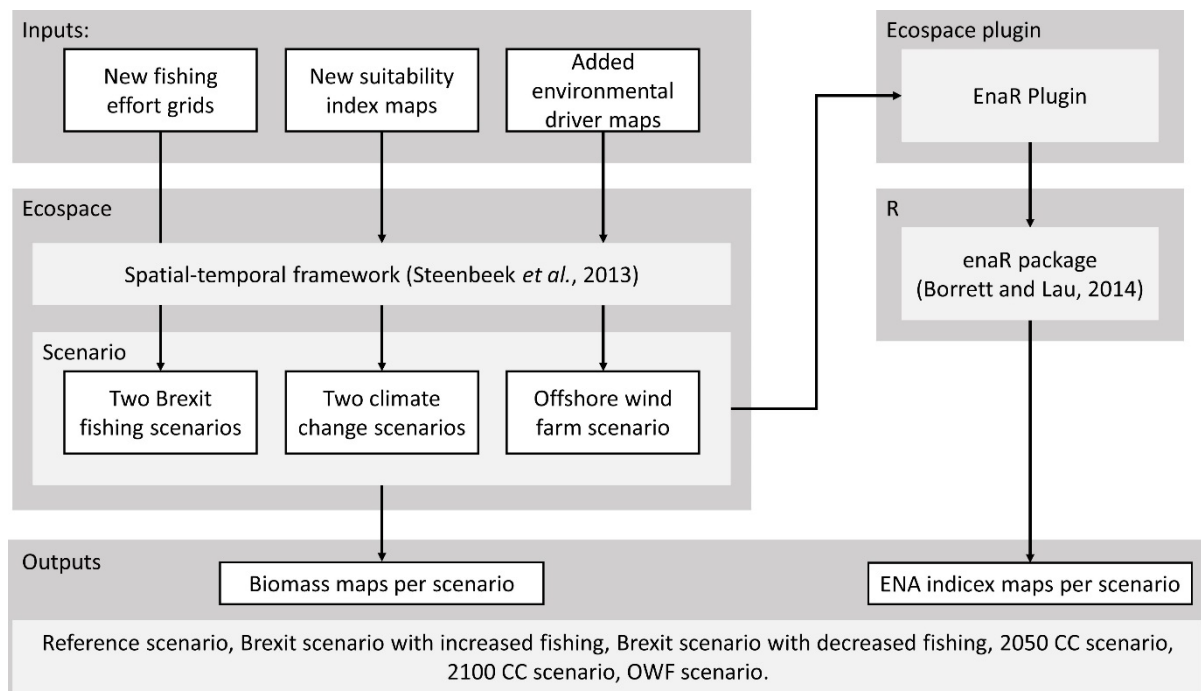


Figure III - 2 Modeling framework. eBoS, extended Bay of Seine; ENA, ecological network analysis; OWF, offshore wind farm; CC, climate change.

2.3 Effect of climate change on species distribution

In Bourdaud *et al.* (2021), a first set of suitability index maps was computed using niche models with climate parameters over the 2005 - 2012 period (Ben Rais Lasram *et al.*, 2020). It was defined as the initial environmental driver for 27 of the 40 living groups, from benthic invertebrates to piscivorous fish (Supplementary materials Table S II - 2). To model the effect of CC on the distribution and dynamics of eBoS species, two new sets of suitability index maps were computed with niche models, using climate projections under the IPPC “business as usual” scenario RCP 8.5 (Ben Rais Lasram *et al.*, 2020), but at different time intervals: one in 2050 (2041 - 2050) and one in 2100 (2091 - 2100). Using these new niche models, we determined the evolution of the suitability index of eBoS species under the effects of climate change. The suitability index defined the theoretical niche of the species, between the realized niche and the fundamental one (Soberón and Nakamura, 2009; Jiménez *et al.*, 2019). Considering the fundamental niche as the extent of geoclimatic parameters where species have a positive production rate (Hutchinson, 1957), we hypothesized that the production of the species would be lower close to the limit of the theoretical niche (lower suitability index), and higher in the center of the theoretical niche (higher suitability index). The niche models simulated how suitable the geoclimatic parameters were and their evolution by 2050 and 2100, following the IPPC “business as usual” scenario RCP 8.5.

Like the Ecospace model outputs, the niche model outputs used to model the effects of climate change were all validated by experts (pers. com. Jean-Claude Dauvin, Jean-Paul Robin and Éric Foucher), and the results were similar to those of other works on similar species in the English Channel (Rombouts *et al.*, 2013).

Averaged suitability index maps for each of the 27 groups were computed for the two climate change projections (2050 and 2100), and were introduced in Ecospace using the spatial-temporal framework of *EwE* (Steenbeek *et al.*, 2013) to model the effects of climate change. The spatial-temporal framework was used with the following protocol: all Ecospace scenarios were first started with the initial suitability index maps as environmental drivers computed from 2005 - 2012 climate parameters. After 20 years of spin-up used to reach stable biomass for each group, the suitability index maps of the CC niche models were introduced to replace the initial suitability index maps and to model the effect of CC on species distribution in the two CC scenarios. Subsequently, Ecospace scenarios were run until group biomass values

were considered stable and reached a balanced state, as required by ENA. The models were run for 55 years after the spin-up in each CC scenario. The results retrieved after stabilization were used to compute ENA indices.

By replacing the initial suitability index computed from 2005 - 2012 climate parameters with suitability index sets computed from the effects of climate change on climate parameters, we modified the environmental driver for each of the 27 groups, to reflect the effects of climate change in 2050 and in 2100. The aim was to reflect the impact of climate change on the biogeoclimatic niches of the trophic groups: as climate change modifies the environment, geoclimatic parameters become more or less suitable for the species of the trophic groups and modify habitat suitability (see Coll *et al.*, 2019). Following the foraging arena theory, if the habitat becomes more or less suitable for a group (according to niche models), then the habitat capacity changes accordingly and modifies the group dynamic in Ecospace (Walters *et al.*, 1999; Christensen *et al.*, 2014). If the suitability index of a group decreases between the reference niche model — computed from the 2005 - 2012 climatic parameters — and one of the climate change niche models — IPPC “business as usual” scenario RCP 8.5 —, the habitat capacity of the group is reduced (C_{rcj}). Consequently, the habitat is less suitable for the group j , consumption of i by j decreases (Christensen *et al.*, 2014; Coll *et al.*, 2019), and so does the production of j (Eq. 4). Therefore, the evolution of biomass distribution in the Ecospace model due to climate change depends both on the suitability index of the species (evolution of abiotic parameters) and on prey availability (biotic relationship between species), allowing for a more realistic simulation of the effects of climate change (see Bourdaud *et al.*, 2021).

Using the spatial-temporal framework of *EwE* (Steenbeek *et al.*, 2013), we produced end model results for the two CC time intervals rather than modeling the “continuous” impact of CC from the current period to the 2050 or 2100 horizon.

2.4 Fishing scenarios

To evaluate the significance of the effects of fishing on the ecosystem, we designed fishing scenarios related to the potential trends induced by Brexit on fishing. Two scenarios were built: one with a decreased fishing pressure (**F_dec**) and one with an increased fishing pressure (**F_inc**) in the eBoS.

- **F_dec** considered a decrease of the fishing activities in the area. Such a decrease would be the result of the closing of British fishing areas to French fishermen. Those areas are considered very rich in fish resources (<https://atlas-transmanche.certic.unicaen.fr/en/>), so it was speculated that fishermen would lose part of their income and could decide to stop or shift their activity. As France provides strong support to European fishing, French fishermen could be helped find other jobs, and this would limit French fishing in the area. By looking at the “fishing vessel activity” report of Caen by the Ifremer (Ifremer SIH, 2017), we supposed that medium-sized to small ships (< 12 m) would be more impacted. Such vessels mainly performed 3 fishing activities in the eBoS model (“pelagic and bottom trawls”, “bottom trawls”, “pelagic trawls”), as well as “other fishing gears”. To model the potential effects of this scenario, we approximated a 20% reduction of the “trawl” activities and a 5 % reduction of “other fishing gears”. Moreover, British fishermen would not be able to catch king scallops in French waters anymore, and in the absence of potential modifications of quotas, this would result in a lower fishing pressure in the area. The “dredge” gear activity would thus be reduced by 20 % based on British quotas on king scallops.
- **F_inc** considered an increase of fishing in the area resulting from the relocation of European fisheries from France, Belgium, The Netherlands or even Denmark inside the eBoS. As European fishermen would not have access to the United Kingdom waters, they would have to fish in other places, e.g. in the eBoS. King scallop fishing would still be reduced, as no new quotas are likely to be set to let other countries take up the UK’s vacant place, even though some French fishermen could benefit from it. In our scenario, this resulted in a 20 % increase of the “pelagic and bottom trawls”, the “bottom trawls” and the “pelagic trawls” activities, as well as a 5 % increase of “other fishing gears” activities based on the previous Brexit scenario.

Following the December 2020 negotiations between the European Union and the United Kingdom government, decisions on fishing have been postponed till 2026, making our scenarios still plausible to this day.

New fishing effort grids were built from the initial model of Halouani *et al.* (2020) and modified according to the desired scenario (Supplementary materials Table S II - 4 to Table S II - 6).

2.5 Offshore wind farm

The effects of OWFs on ecosystems have been extensively studied by the scientific community (Shields and Payne, 2014). They have been split into three main categories depending on the phase of life of the offshore wind farm: 1, construction; 2, routine operation; 3, decommission (Gill, 2005; Shields and Payne, 2014). While the construction and decommission phases are characterized by a strong and abrupt impact on the ecosystem, the operating phase is characterized by a long and structuring effect lasting as long as the park is operating (Gill, 2005; Petersen and Malm, 2006; Wilhelmsson *et al.*, 2006; Wilhelmsson and Malm, 2008). This study targets the two main structuring effects of the operating phase on the whole ecosystem: the reef effect and the reserve effect (Petersen and Malm, 2006; Raoux *et al.*, 2019; Degraer *et al.*, 2020).

To model these impacts, we used tools available in Ecospace and data from a previous Ecopath model of the Courseulles-sur-Mer OWF (Raoux *et al.*, 2017). Modeling the potential reserve effect induced by the OWF was straightforward and had been achieved by creating a marine protected area (MPA) in the simulations of Halouani *et al.* (2020). This was also done in many other works (Walters *et al.*, 1999; Le Quesne *et al.*, 2008; Abdou *et al.*, 2016). To do so, a map of the future OWF was added as a MPA in Ecospace. Only 15 % of the OWF surface was blocked for fishermen so as to accurately represent the OWF owners' proposal during the environmental impact assessment, to "optimize" the fishing area (Raoux *et al.*, 2018).

Due to the small footprint of the OWF foundation compared to the Ecospace cell resolution and because of our use of niche model results as environmental drivers of species distribution, modeling the reef effect was not possible by simply changing the habitats in the cells. We had to look at a previous model of the reef effect of the Courseulles-sur-Mer OWF (Raoux *et al.*, 2017). The observations on this Ecopath model were linked to the 70 km² farm in Ecospace (37 cells). In Raoux *et al.* (2017), the reef effect was modeled by forcing the biomass of 10 trophic groups. We did the same by creating new environmental maps for the same groups in the eBoS Ecospace model to represent the biomass variations caused by the reef effect (Supplementary materials Table S II - 7). The increased habitat suitability due to the reef effect would thus lead to a higher foraging capacity based on the foraging arenas theory (Walters *et al.*, 1997; Ahrens *et al.*, 2012). The new environmental maps were added using the spatial-temporal framework of Ecospace at the 2015 time step, before the CC simulations.

Similar structural sub-regions were used to characterize the effects of the OWF on the eBoS ecosystem (Halouani *et al.* 2020): the OWF area itself, the first two rows of cells surrounding the farm (spillover 1), the next two rows of cells surrounding the farm (spillover 2) and the rest of the eBoS model (Bay) (Supplementary materials Figure SII - 8).

2.6 Ecological network analysis

Ecological network analysis indices are holistic indices describing the functioning and organization of the food web. They are computed from flow matrices of the food web. ENA indices were computed for each cell of the Ecospace model with a beta Ecospace plugin: "EnaR" (Table III - 1). This plugin allows Ecospace to build SCOR files for each cell of the model at every time step. Based on the SCOR file, the ENA indices were calculated with the "enaR" R package (Borrett and Lau, 2014). ENA indices were calculated for the 4,907 cells of the Ecospace model in the extended Bay of Seine. They were computed for the initial reference current scenario, for the two CC scenarios, for the two fishing scenarios and for the OWF scenario.

Table III - 1 ENA indices computed with enaR from Ecospace SCOR files.

Name	Objective	Calculation	References
Relative redundancy of the flow (RDC)	The relative redundancy is the “reserve” of the system information and refers to the extent of parallel flows in the system relative to the total capacity of the system.	$\Phi_i = - \sum_{i,j=1}^n T_{ij} \log \left[\frac{T_{ij}^2}{T_i T_j} \right]$ Where Φ_i is the internal relative redundancy, T_{ij} the flow between i and j, T_i the sum of all the flows leaving i, T_j' the sum of all the flows leaving j. $RDC = \frac{\Phi_i}{DC}$ Where DC is the development capacity of the system.	(Ulanowicz and Norden, 1990; Christensen, 1995; Ulanowicz <i>et al.</i> , 2009)
Total flow diversity (H)	Flow diversity quantifies the diversity of flows passing through all the groups of the model.	$H = \sum_i \sum_j f_{ij} \log(f_{ij} Q_i)$ Where f_{ij} is the fraction of the total flow from j that passes through i, and Q_i is the probability that a unit of energy passes through i.	(Christensen, 1995)
Mean trophic efficiency / Mean transfer Efficiency (TE)	The mean trophic efficiency describes the mean percentage of production of one trophic level converted to production by the next trophic level. It is averaged for the entire trophic network.	Using Lindeman spine, the trophic efficiency for a trophic level tl was computed as: $TE_{tl} = \frac{T_{.tl+1}}{T_{.tl}} \times 100$ Where $T_{.tl}$ is the total outflow for trophic level tl, and $T_{.tl+1}$ is the total outflow for the next trophic level. The ‘mean trophic efficiency’ of the system is then derived from the geometric mean of the efficiencies of all trophic levels.	(Lindeman, 1942; Niquil <i>et al.</i> , 2014)
System omnivory index (SOI)	The system omnivory index quantifies the distribution of trophic interactions among different trophic levels. It is the mean omnivory index of all the groups.	$OI_i = \sum_{j=1}^n [TL_j - (TL_i - 1)]^2 \times DC_{ij}$ $SOI = \frac{\sum_{i=1}^n [OI_i \times \log(Q_i)]}{\sum_{i=1}^n \log(Q_i)}$ where TL is the trophic level of i or j.	(Libralato, 2013)
Recycling index or Finn Cycling Index (FCI)	The recycling index is the fraction of energy recycled in the system.	$FCI = \frac{TST_c}{TST}$ where TST is the total system throughflow, and TST_c the cycled total system throughflow.	(Finn, 1980)

Mean trophic level (MTL2)	The MTL2 is the mean trophic level of the network's groups, taking all level-2 consumers into account.	$MTL = \frac{\sum_i TL_i \times B_i}{\sum_i B_i}$ where B is the biomass of i or j.	(Latham, 2006)
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2.7 Statistical analysis

In order to better understand the effects of each scenario spatially, a K-means clustering analysis was carried out (MacQueen, 1967) on the ENA results of the current reference scenario. The “Elbow” method was used to determine the optimal value of the cluster based on multiple K values and their effects on the averaged distance between points (sum of the square).

A Cliff delta was used to test the significance of the differences between the ENA values of the reference scenario and those of the different scenarios modeling the effects of a driver. In previous works, the Cliff Delta (Cliff, 1993) proved useful to compare ENA results when large sample sizes and heteroscedasticity precluded the application of parametric statistical tests (Tecchio *et al.*, 2016; V. Girardin & J. Lequesne, pers. comm.). We employed the non-parametric Cliff Delta with the same threshold as Romano *et al.* (2006), who considered differences between datasets negligible if the Cliff Delta ($|\partial\text{Cliff}|$) was < 0.147 , low if $0.147 < |\partial\text{Cliff}| < 0.33$, medium if $0.33 < |\partial\text{Cliff}| < 0.474$, or strong if $|\partial\text{Cliff}| > 0.474$.

3 Results

3.1 Regionalization of the model

The ENA values of the reference scenario were higher near the coastline and especially near the Seine estuary south east of the eBoS model, for the 6 indices; they were lower in the deepest, most offshore part of the eBoS, north west of the eBoS model (Figure III - 3). While most of the indices followed this trend, the FCI obviously differed, with a pattern closer to the primary production pattern (Supplementary materials Figure SII - 9). Overall, this indicates that the flow diversity, the relative overhead, the mean trophic level and to a lesser extent recycling seemed to follow a coastline / open sea gradient.

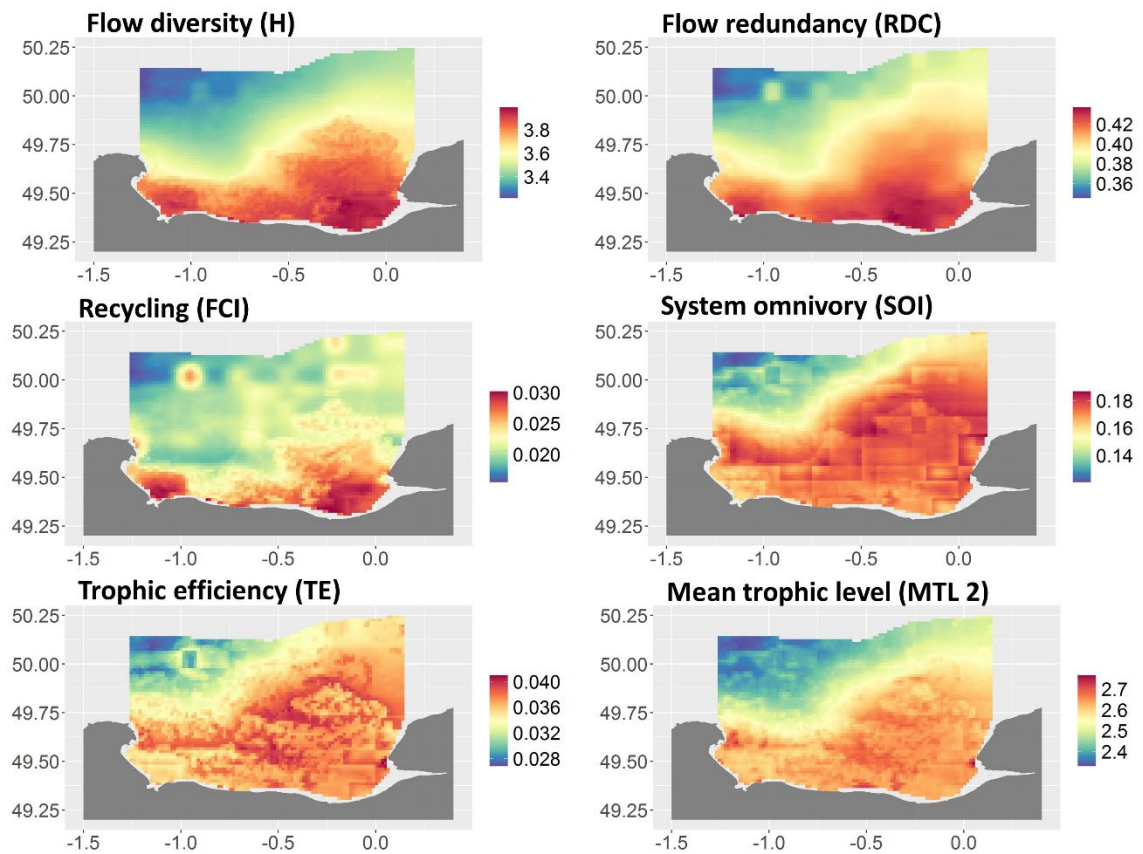


Figure III - 3 Maps of ecological network analysis indices for the reference scenario.

The K-means clustering analysis associated to the “elbow” method determined three to four clusters. In order to simplify the analysis and because three clusters provided better spatial delimitation, we set it at three. The three clusters revealed a gradient from the coastline to the open sea (Figure III - 4). The clusters were named accordingly, with the most coastal cluster called “Coastal Bay of Seine”, the following one “Offshore Bay of Seine” and the last one “Central English Channel”.

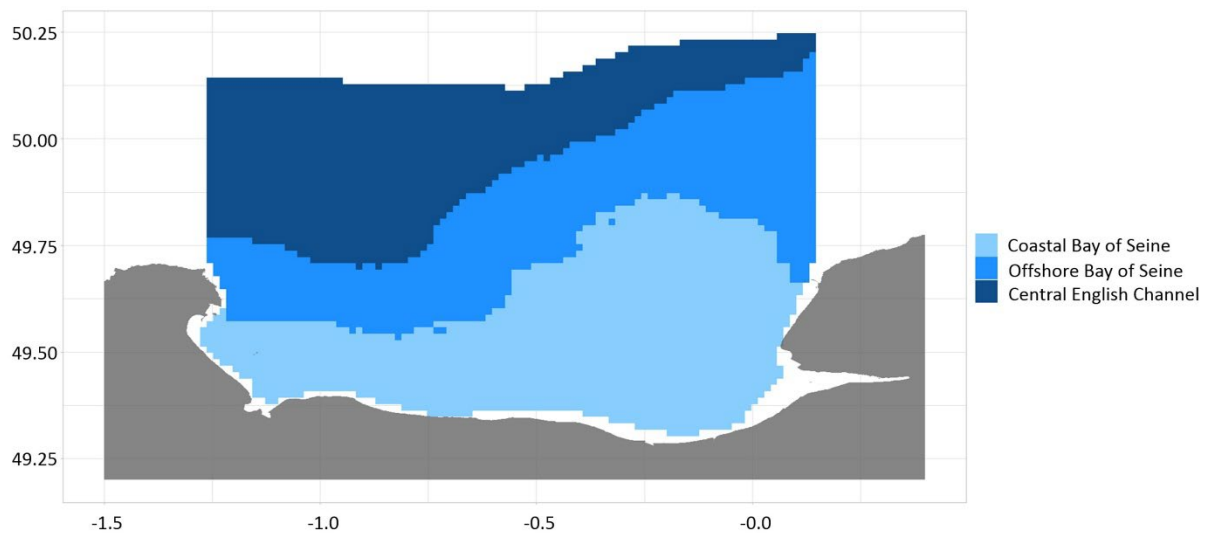


Figure III - 4 Regions with similar ecosystem properties and functioning determined using a K-means clustering analysis based on the ecological network analysis index values in the reference scenario.

3.2 Effects of climate change and fishing on the functioning and organization of the system

Climate change scenarios displayed much larger variation in their ENA indices than fishing scenarios did. The CC 2100 scenario was the one with the highest number of strong variations with the reference scenario ($|\Delta \text{Cliff}| > 0.474$, Figure III - 5). While fishing scenarios had logical effects on ENA indices, with opposite responses to the increased or decreased fishing pressure, CC scenarios had surprising effects. For example, the 2050 CC scenario increased the SOI of the Coastal Bay of Seine region, while the 2100 CC scenario greatly decreased it (Figure III - 5). This is linked to the different effects of climate change on the groups of the Ecospace model (Supplementary materials Figure SII - 10 to Figure SII - 12).

All but two indices displayed medium to strong variation in the 2100 CC scenario. Flow diversity (H) in the Central English Channel region and recycling (FCI) in the Offshore Bay of Seine region were the only indices displaying negligible variation compared to the reference scenario (Figure III - 5). In the 2050 CC scenario, six indices displayed negligible variation compared to the reference scenario, especially in the Offshore Bay of Seine (3 indices) and the Central English Channel (2 indices) (Figure III - 5). Variations due to the 2050 CC scenario were small or negligible. This difference between the 2050 and 2100 scenarios is linked to the

greater effect of climate change on the trophic group's habitat suitability in the 2100 scenario than in the 2050 scenario (Supplementary materials Figure SII - 11).

In general, the Coastal Bay of Seine region was the most sensitive area to CC (in both the 2050 and 2100 scenarios), with negligible variation of only one of its ecological indices, followed by the Central English Channel (3 indices) and finally the Offshore Bay of Seine (4 indices).

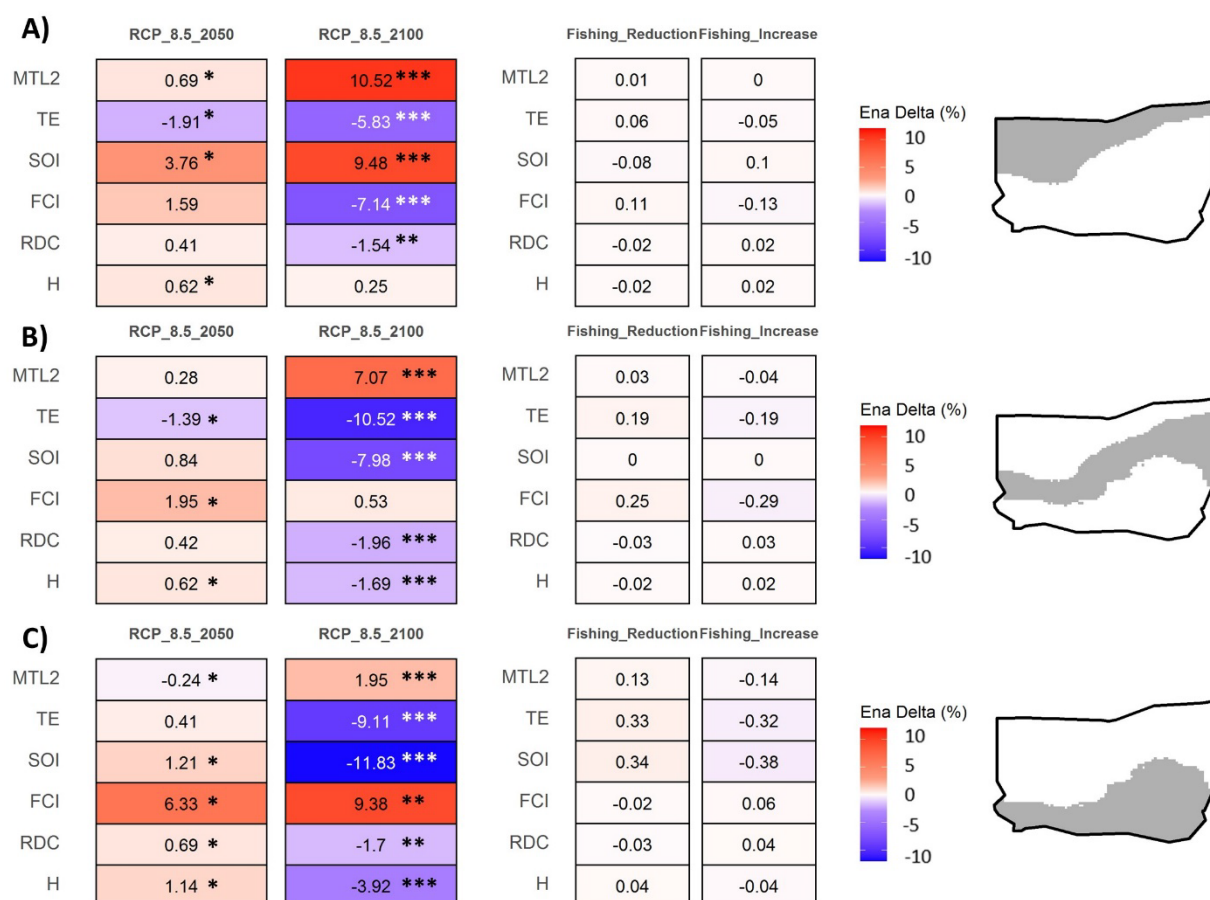


Figure III - 5 Variations between the reference scenario and the different CC scenarios (left columns) and Brexit scenarios (right columns).

Positive variations are in red boxes, and negative variations in blue boxes. A), variation in the Central English Channel region; B), variation in the Offshore Bay of Seine region; C), variation in the Coastal Bay of Seine region. Cliff Delta results: *** strong variation ($|\partial\text{Cliff}| > 0.474$); ** medium variation ($0.33 < |\partial\text{Cliff}| < 0.474$); * small variation ($0.147 < |\partial\text{Cliff}| < 0.33$); no *, negligible variation ($|\partial\text{Cliff}| < 0.147$).

3.3 Effect of the offshore wind farm on the system

The effect of the OWF was the most visible one on the SOI of the eBoS model, followed by the mean trophic level, trophic efficiency, flow diversity, the relative redundancy of the flows, and recycling. Spatially speaking, the effects were mainly localized within the OWF perimeter, where all the above-mentioned indices increased, except recycling that was slightly reduced compared to the reference scenario ($0.147 < |\partial \text{Cliff}| < 0.33$) (Figure III - 6). While recycling did not appear to be impacted by the OWF in the spillover regions, flow diversity, omnivory, trophic efficiency and the mean trophic level decreased. The spillover regions always resulted in a decreased metric, regardless of ENA indices, in diverse proportions. The rest of the bay of Seine did not show any significant variation between the OWF and reference scenarios, indicating that the OWF had a localized effect on the Bay of Seine ecosystem.

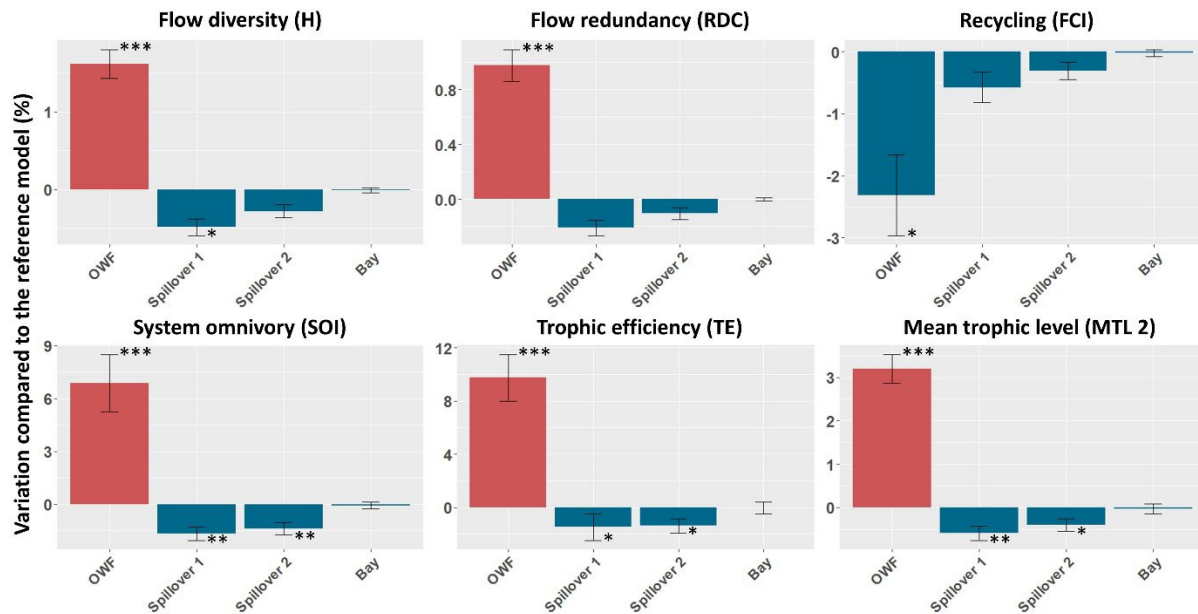


Figure III - 6 Variations between the reference and OWF scenarios for the OWF sub-region.

Regions include the spillover 1 region (first two rows of cells around the OWF), the spillover 2 region (next two rows of cells around the OWF) and the rest of the bay. All sub-regions are exclusive, with no overlapping. Red bars, positive variations; blue bars, negative variations. Cliff Delta variation: *** strong ($|\partial \text{Cliff}| > 0.474$); ** medium ($0.33 < |\partial \text{Cliff}| < 0.474$); * small ($0.147 < |\partial \text{Cliff}| < 0.33$); no *, negligible ($|\partial \text{Cliff}| < 0.147$).

4 Discussion

The modeling approach implemented in the present study improved the simulation of multiple drivers, using whole ecosystem approaches based on a single reference model. We did not represent the entire effect of CC, but rather tried to progressively improve the forecasting previously achieved in the Bay of Seine (Bourdaud *et al.*, 2021; Halouani *et al.*, 2020; Nogues *et al.*, 2020; Raoux *et al.*, 2019). Despite improvements such as modeling the reef effect of the OWF, modeling the effects of climate change on species physiology (through the habitat capacity), adding variability in the fishing regimes, there still remains limitations related to the great complexity of climate change and of its impacts on ecosystems (Hoegh-Guldberg and Bruno, 2010; Ainsworth *et al.*, 2011). Such limitations include the failure to account for the arrival of tropical non-indigenous species (NIS) in the eBoS (Cheung *et al.*, 2009; Weatherdon *et al.*, 2016). Modeling the inflow of non-indigenous species due to CC in an open system like the Bay of Seine is a very hard task. The results are often hypothetical and subject to many modeling hypotheses (Morin and Thuiller, 2009; Beaugrand *et al.*, 2018; Le Marchand *et al.*, 2020). Moreover, the arrival of non-indigenous species is often modeled with new trophic groups (Libralato *et al.*, 2015; Corrales *et al.*, 2018), which change the system aggregation. Comparing the system before and after the arrival of NIS using ecological network analysis becomes tricky, as some ENA indices are highly sensitive to the system aggregation (Johnson *et al.*, 2009). That is why we chose not to integrate such arrivals for the time being, even though NIS might have several effects on the food web structure (Libralato *et al.*, 2015; Kotta *et al.*, 2018).

Another important effect of CC on marine and coastal ecosystems is its potential impact on phytoplankton primary production (Winder and Sommer, 2012). So far, primary production models have not foreseen a clear trend of primary production in the Bay of Seine related to CC (Holt *et al.*, 2016). Moreover, turbidity is expected to be the main limiting factor of primary production in the Bay of Seine (Pascal Claquin, pers. com., UMR Borea), but the responses of current turbidity models are not consistent enough for us to predict potential primary production changes in the eBoS (Fettweis *et al.*, 2012; Capuzzo *et al.*, 2015; Wilson and Heath, 2019). We therefore focused on the effect of CC on the distribution and dynamics of local macro-organisms and its effects on the ecosystem functioning, as requested by the scientific community (Harley *et al.*, 2006a).

This study also aimed to build a framework for future studies on cumulative impacts using ENA indices. The methodology had to be simple in order to be compatible with complex cumulative assessment methods. Taking into account the uncertainty of the Ecospace model — through Monte Carlo analysis of the Ecopath pedigree — and the niche model results — through a sensitivity analysis of the niche model results — requires a large number of simulations. The long time needed to compute ENA maps and the large number of scenarios necessary for cumulative effect assessment (CEA) would make a study of uncertainty incompatible with CEA based on ENA indices. However, taking the uncertainty around the niche model results into account could represent a significant improvement for future works (Payne *et al.*, 2016), but will first require significant work to optimize the computation time of ENA indices.

4.1 Climate change and species distribution: consequences on food web functioning

The potential effects of CC on species distribution appear to have a strong structuring effect on the eBoS community in the different functional regions of the eBoS. These structural changes are clearly visible in the reduced trophic efficiency of nearly all the regions of the eBoS under both CC scenarios, except for the Coastal Bay of Seine region in the 2050 CC scenario. This implies that CC would reduce the efficiency of the ecosystem in the processing of energy through its trophic levels (Lindeman, 1942). Trophic efficiency is widely used to tackle the effects of multiple stressors, with a broad range of responses (Coll *et al.*, 2009; Niquil *et al.*, 2014c). Lower trophic efficiency can be linked to a possible ecosystem shift caused by invasive species (Baird *et al.*, 2012). Trophic efficiency in the present study seems to indicate a similar major modification of the ecosystem, regardless of the region, leading to lower efficiency and requiring a higher energy input to maintain medium to top trophic level species. This lower trophic efficiency is likely caused by the shift toward a more fish-based system (Supplementary materials Figure SII - 11), as fish allocate more energy to maintenance and thus have a lower trophic efficiency than smaller invertebrates (Gillooly *et al.*, 2001). Such a structuring effect of CC due to community shifts has already been observed and is expected to play a major role in the future evolution of marine ecosystems (Walther *et al.*, 2002; Parmesan, 2006).

The structuring effect of climate change in the 2100 RCP8.5 scenario seems to result from important community changes that lead to a lower resistance of the system to disturbances. Community changes are visible through the increased mean trophic level of the system and

coincide with decreased benthic invertebrate biomass as well as modified fish biomass (Supplementary materials Figure SII - 11). These predicted biomass changes in the English Channel could be the result of the high sensitivity of multiple benthic invertebrates species to CC (Rombouts *et al.*, 2012). They could also stem from the high vulnerability of low-trophic-level fish to changing climate conditions (McLean *et al.*, 2018), making them potentially highly sensitive to CC. Taken together, these modifications of the ecological community seem to result in losses of redundant trophic pathways, leading to a lower relative redundancy of the flow in the system. Such changes have been related to losses in the ability of the system to adequately respond to external pressure by reconfiguring itself (Odum, 1985; Ulanowicz, 1986). Losing this ability makes a system less resilient to stressors, as described by Heymans and Tomczak (2016). It is well known that invertebrates are going to be highly impacted by CC (Kendall *et al.*, 2004; Byrne, 2011). However, few studies have investigated the overall effect of community changes on ecosystem functioning. Our results support the idea that benthic communities could play a major role in the resilience of the eBoS ecosystem (Nogues *et al.*, 2020; Raoux *et al.*, 2019).

We predict that the effects of climate change at the 2100 horizon could result in important local variations of the system omnivory and recycling indices between the Coastal Bay of Seine and the Central English Channel regions. These variations could be attributed to the local shift of the ecological community within the eBoS. The decreased system omnivory index near the coast and its increase in the Central English Channel region could be explained by the northward movement of the more omnivorous fish group from the Coastal Bay of Seine region to the deeper Central English Channel waters (Supplementary materials Figure SII - 11). In a reverse trend, the expected decrease of invertebrate biomass values in the Central English Channel region can be opposed to the increase of these values in the Coastal Bay of Seine region (Supplementary materials Figure SII - 11). This is visible through the ENA, as recycling is predicted to increase in the Coastal Bay of Seine region and decrease in the Central English Channel region. Some studies have already pointed out the overall effect of changing species distribution on ecosystem functioning (Corrales *et al.*, 2018; Libralato *et al.*, 2015). The present study shows that effects on the ecosystem can also be local, leading to variable ecosystem properties at a regional scale.

Modifications of the ecosystem are smaller in the 2050 CC scenario than in the 2100 scenario. They are also different for many indices in each functional region of the model. Out of the six ENA indices for the three functional regions, only five out of eighteen cases had similar responses in the two CC scenarios. The limited number of proportional responses between the 2050 and 2100 scenarios is a potential sign of the non-linear effect of CC on ecosystems. While this is partly linked to the niche model themselves and to their predictions of species suitability experiencing a range drift related to the loss of suitable climatic conditions between 2050 and 2100, as observed in other studies (Ben Rais Lasram *et al.*, 2010; Albouy *et al.*, 2013; Hattab *et al.*, 2014), this might also be caused by the cascading effects on the system (Carpenter *et al.*, 1985).

Although CC effects in the 2050 scenario are less visible than in the 2100 scenario, local trends can still be outlined. While the model forecasts a decrease of the mean trophic level in the Coastal Bay of Seine region, an increased mean trophic level is expected in the Central English Channel region. This gradient can be explained by the increase of invertebrate biomass values in the most coastal region, increasing flow redundancy and recycling (Supplementary materials Figure SII - 12). In the more offshore Central English Channel region, a loss of invertebrate biomass results in a decreased invertebrate / fish ratio (Supplementary materials Figure SII - 12). This modification of the ecological communities is noticeable at the ecosystem level *via* a higher mean trophic level and a lower trophic efficiency. While the 2100 scenario appears to be impacted both globally (at the entire eBoS scale) and locally (inside the eBoS), the impact of CC seems more local in the 2050 scenario with no homogeneous effects at the entire eBoS scale. This is why it is crucial to take the effects of CC into account both globally and locally. Detecting such effects at the community level might be an issue for many local development actors as they prefer to use “tailor-made” solutions, specific to their case study, that may fail to detect holistic ecosystem changes (Hendriksen *et al.*, 2014). ENA showed that by using a spatialized model, they could characterize and understand the effects of CC on the ecosystem between functional regions (local effects) and across the whole eBoS (global effects). This represents a societal priority for us to be able to predict the evolution of marine ecosystems (Claudet *et al.*, 2020). Information about the local effect of CC could prompt local stakeholders to set up actions in the field of vulnerability and adaptation of the societal system (Charles, 2012) and to raise awareness at a local scale (Ireland and Clausen, 2019).

4.2 ENA indices in fishing scenarios

While the effects of CC on the ecosystem are not proportional between the 2050 and 2100 scenarios, with strong but sometimes completely different effects on some indices, fishing has negligible but proportional effects, opposite in the two Brexit scenarios (fishing increase / decrease). The trophic efficiency and the mean trophic level have already been used in many studies to describe the effect of fishing on the ecosystems (Libralato *et al.*, 2004, 2010; Coll *et al.*, 2009). On the other hand, the mean trophic level was popularized by Pauly *et al.* (1998) and his “Fishing down the marine food web” theory that depicts the mean trophic level as sensitive to the effect of fishing, i.e. decreasing with the fishing pressure due to the decreased predator biomass. The omnivory index was also promoted as a robust index to detect the effect of fishing (Fulton *et al.*, 2005). Despite the many items of evidence of their operational ability to describe the effects of fishing, ENA variations due to fishing were consistently considered negligible by the Cliff Delta. The little sensitivity of ENA indices to fishing scenarios might thus result from the little impact of the Brexit scenario on ecosystem functioning. The eBoS is a heavily anthropized ecosystem, with a strong fishing industry (Bul  on and Shurmer-Smith, 2021). Protecting the ecosystem from the effects of fishing might require ambitious management plans to truly help ecosystems recover (Dunford *et al.*, 2004).

4.3 Effect of the offshore wind farm on the extended bay of Seine

As observed by Halouani *et al.* (2020) who simulated the possible reserve effect in the case of fishery closing in the entire OWF area, it appears that the OWF could play the role of a “fish aggregating device”. The aggregating role of the OWF appears to have an important structuring effect on the ecosystem. The structuring role of the OWF is particularly prominent with the increased mean trophic level, trophic efficiency, omnivory and redundancy of the flows. The aggregating effect is also noticeable outside the OWF perimeter. Biomass outside the OWF appears lower in the OWF eBoS scenario than in the reference scenario. This decreased fish biomass is likely due to the agglomeration of the mobile fish groups inside the OWF area due to the higher suitability of the cells and to the higher prey density for fish groups inside the OWF. Agglomeration is well known and has been extensively studied (Bohnsack, 1989; Pickering and Whitmarsh, 1997; Smith *et al.*, 2015) and was also observed by Halouani *et al.* (2020) to be caused by the reserve effect only (Coll  ter *et al.*, 2014).

Inside the OWF perimeter, Ecospace predicted a similar structuring effect to the one forecasted in Nogues *et al.* (2020). This structuring effect is visible through the many important modifications of the ecosystem, which appears to shift toward a more demersal / benthic system (Supplementary materials Figure SII - 15). Similarly to the results of Raoux *et al.* (2019), the OWF could increase the relative redundancy of the flow. The OWF of the eBoS model may also increase the omnivory index of the system, as observed by Nogues *et al.* (2020). However, unlike previous studies, recycling is reduced by the OWF in our simulations. All these modifications – along with the increased trophic efficiency and the increased flow diversity – seem to be linked to an increased resistance of the system to disturbance. With the higher flow redundancy, the system has more in store against disturbances (Levin and Lubchenco, 2008), improving its ability to adapt and overcome stresses. The higher omnivory index also suggests that the system would be more resilient, as it makes it more flexible (Fagan, 1997b; Libralato, 2013). The heterogeneity brought by the hard substrate of the wind turbine structure to the sandy habitat surrounding the OWF seems to increase the flow diversity. Flow diversity can be interpreted as species diversity (Christensen, 1995). Therefore, an increase in habitat heterogeneity should also increase local diversity (Munguia *et al.*, 2011). These changes are all linked to the increase in benthic and demersal biomass (Supplementary materials Figure SII - 15), which tends to have an overall positive impact on the ecosystem of Courseulles-sur-Mer by making it more complex, efficient, diverse and resilient (Nogues *et al.* 2020).

Changes in the eBoS system are also visible outside the OWF area. Through the agglomeration of fish species in the OWF area, fish biomass may decrease in the vicinity of the OWF. Even though these biomass changes are small, they still have an effect on ENA indices and on the ecosystem. Decreased fish biomass and increased invertebrate biomass lead to a lower mean trophic level as well as a lower omnivory index of the system around the OWF (Supplementary materials Figure SII - 15). As trophic efficiency and flow diversity also appear to decrease, these results tend to indicate a simplification of the ecosystem around the OWF toward a less resilient state. However, because fishing could increase inside the OWF due to the reef effect (see above, Grossman *et al.*, 1997), fishing may also increase in the surrounding areas of the OWF, potentially affecting an already weakened system. This emphasizes the need for careful planning of fishing around and inside the OWF area and may require mitigation,

even in such a limited space. With these new insights into the spatial footprint of multiple drivers on the ecosystem, ENA indices demonstrate their usefulness to locate areas in need of careful ecological management (Safi *et al.*, 2019). ENA indices could be used to i) plan spatial management projects based on the responses of the ecosystem to drivers and ii) better maintain ecosystem sustainability (Curtin and Pallezo, 2010).

Conclusion

For the first time in ecological network analysis, the mapping of ENA indices provides insights into spatial ecosystem functioning. ENA indices further prove their usefulness and potential as tools for ecosystem management by helping us understand human-induced ecosystem changes. Therefore, they could be used to support marine spatial planning by highlighting areas of concern where the ecosystem could be more sensitive to perturbations. Their ability to detect the effects of localized and more global ecosystem drivers on ecosystem functioning could be used to link local and global ecosystem management initiatives. It is also important to note that these scenarios were built to test the ability of ENA indices to assess cumulative effects (Nogues *et al.*, in prep.). There is an increasing demand for studying the combined effects of climate change and other drivers at the whole ecosystem scale in order to predict ecosystem changes and elaborate management scenarios. This study sets the basis for such work: it provides tools for simulating the effects of multiple drivers, which then need to be combined, to determine the potential cumulative effects resulting from interactions between the different anthropogenic drivers.

Acknowledgements

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IV Chapitre 2B :

An ecosystem wide approach for assessing the spatialized cumulative effects of local and global changes on coastal ecosystem functioning

La seconde partie du deuxième chapitre de cette thèse, partie B, suit directement les travaux réalisés précédemment et se base sur le cadre méthodologique développé en première partie, pour étudier les effets du cumul d'impacts sur le fonctionnement de l'écosystème de la baie de Seine, de manière spatialisée. Dans cette partie, les facteurs préalablement modélisés en baie de Seine étendue comme : le changement climatique, le parc éolien de Courseulles-sur-Mer et les variations des activités de pêche par le Brexit ont été combinés en suivant un cadre méthodologique précis, dans le but d'étudier les effets du cumul d'impacts. Comme les simulations des variations des activités de pêche dues au Brexit n'avaient qu'un effet négligeable sur le système, les différents scénarios de pêches furent combinés ensemble. La pêche ne fut donc pas considérée directement dans l'étude du cumul, mais plutôt indirectement, ceci afin d'étudier le cumul du changement climatique et du parc éolien, tout en prenant en compte les potentielles variations possibles des rythmes de pêches. Ceci nous a permis de passer de 6 combinaisons de drivers, à deux combinaisons, chacune composée de 3 sous-combinaisons, réduisant grandement la complexité de l'analyse et améliorant la clarté du texte. Les deux combinaisons de cumul incluent :

- La combinaison de facteurs en 2050 : avec l'effet du changement climatique à l'horizon 2050, et l'effet du parc éolien (récif et réserve), couplés aux trois scénarios de pêche (3 jeux de données).
- La combinaison de facteurs en 2100 : avec l'effet du changement climatique à l'horizon 2100, l'effet du parc éolien (récif et réserve) couplés aux trois scénarios de pêche (3 jeux de données).

Pour caractériser les effets du cumul d'impacts, nous avons comparé la somme des effets séparés de chaque facteur étudié (effet additif), à leur effet combiné. Pour ce faire, nous avons donc directement utilisé les résultats de la première partie du deuxième chapitre de thèse pour déterminer l'effet additif des combinaisons de facteurs. Enfin, il ne faut pas uniquement comparer l'effet additif à l'effet combiné pour déterminer la typologie et le sens des effets cumulés, en effet il faut également regarder le sens de l'effet additif et combiné. Ainsi, la même méthodologie que le premier chapitre de thèse a été utilisée pour déterminer les effets cumulés :

- Si l'effet additif et l'effet combiné sont positifs et que l'effet combiné est supérieur à l'effet additif, l'effet cumulé est positif synergique. En revanche, si l'effet combiné est inférieur à l'effet additif, l'effet cumulé est tamponné positif.
- Si l'effet additif et l'effet combiné sont négatifs et que l'effet combiné est inférieur à l'effet additif, l'effet cumulé est synergique négatif. En revanche, si l'effet combiné est supérieur à l'effet additif, l'effet cumulé est tamponné négatif.
- Enfin, si l'effet additif et l'effet combiné sont opposés l'un à l'autre, l'effet cumulé est antagoniste. Lorsque l'effet combiné est positif, il est antagoniste positif, et si l'effet combiné est négatif, il est antagoniste négatif.

Ceci permet ainsi de caractériser l'effet cumulé par ensemble spatial, en fonction du scénario de référence (positif / négatif) et en comparant effet additif et combiné (synergique, antagoniste et tamponné). L'approche spatialisée rend cette détermination plus complexe car, la variabilité spatiale de l'écosystème ne va pas uniquement faire varier les effets additifs et combinés par cellule du modèle Ecospace, mais également la valeur du modèle de référence, pour chaque métrique étudiée. Néanmoins, ignorer cette complexité du cumul d'impacts, c'est potentiellement ignorer ses effets complexes sur les écosystèmes que les approches écosystémiques nous permettent d'étudier.

A travers une approche écosystémique et spatialisée du cumul d'impacts cette partie a pour objectifs : (1) De cartographier l'étendue « réelle » attendue des effets cumulés. (2) De continuer à caractériser l'effet du cumul sur le fonctionnement et l'organisation de l'écosystème de la baie de Seine pour une meilleure gestion des systèmes, à travers l'utilisation des indices de réseaux ENA. (3) D'explorer le rôle du cumul sur les propriétés émergentes des écosystèmes. (4) Enfin, de mieux comprendre les mécanismes d'interactions des facteurs environnementaux.

Cette seconde partie de deuxième chapitre de thèse va faire l'objet d'un envoi couplé avec la première partie du **second chapitre**, au journal international anglais « ICES Journal of Marine Science », annoncé lors de la soumission de l'article précédent :

An ecosystem approach to spatialized cumulative effect assessment of local and global changes on coastal ecosystem functioning

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Résumé :

Les écosystèmes marins sont de plus en plus impactés par les activités anthropiques. Avec près de la moitié de la population humaine vivant à moins de 200 kilomètres des côtes, les écosystèmes marins font face à un nombre toujours grandissant de facteurs anthropiques. Couplée aux effets grandissants du changement climatique, la grande quantité et diversité des facteurs anthropiques peuvent interagir de manière complexe, ce qui peut mener à des effets cumulés. Ces effets peuvent avoir des conséquences importantes sur les écosystèmes, ce qui nécessite d'étudier les mécanismes à l'origine de ces derniers, afin de mieux les anticiper. Il s'agit également d'intégrer ces effets dans les outils d'aide à la gestion des écosystèmes. C'est pour cette raison que nous avons utilisé une approche holistique (une analyse des réseaux écologiques ENA), couplée à un modèle de réseau alimentaire spatial (Ecospace) pour réaliser une étude écosystémique des effets cumulés du changement climatique, de l'opération d'un parc éolien offshore en fonction de multiples scénarios de pêche, sur le fonctionnement de l'écosystème de la baie de Seine étendue. L'utilisation d'une approche écosystémique pour cartographier les effets cumulés permet une meilleure caractérisation de l'empreinte spatiale du cumul d'impacts. Nous avons mis en évidence de nombreux types d'effets cumulés autour et dans la zone d'interaction des facteurs (le parc éolien), avec des emprises spatiales variant en fonction des propriétés écosystémiques. Cette étude démontre encore une fois l'intérêt des ENA pour étudier les mécanismes du cumul en explicitant : (1) le rôle important des effets structurants sur la formation d'effets cumulés à l'échelle de l'écosystème, (2) la capacité des ENA à présenter les différentes voies fonctionnelles d'interactions entre les facteurs et enfin (3) que les mécanismes produisant ces effets cumulés sont fortement spécifiques à l'écosystème, son organisation, son fonctionnement et sa structure. Ceci souligne donc le besoin de promouvoir davantage l'utilisation d'approches écosystémiques et fonctionnelles pour caractériser les mécanismes spécifiques aux écosystèmes pouvant conduire aux effets cumulés. Cela doit également être accompagné d'un suivi des écosystèmes afin de détecter les potentiels signes de restructuration pouvant induire ces effets cumulés.

**An ecosystem-wide approach for assessing the spatialized cumulative effects of local
and global changes on coastal ecosystem functioning**

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Abstract

Coastal ecosystems are subjected to an increasing number of anthropogenic drivers, from marine renewable energies to climate change. These drivers can interact in complex ways, which may lead to cumulative effects whose potential consequences on the ecosystems need to be addressed. We used a holistic approach — ecological network analysis (ENA) — coupled with a two-dimension food web model — Ecospace — to conduct an ecosystemic study of the cumulative effects of climate change plus the operation of an offshore wind farm depending on multiple fishing scenarios on ecosystem functioning in the extended Bay of Seine (English Channel). Mapped ENA indices showed that cumulative effects were not restricted to the wind farm, *i.e.*, to the area of the expected interactions. Cumulative effects varied both in space and among ecosystem properties, showing that ENA indices can distinguish between different cumulative pathways that modify ecosystem functioning in multiple ways. Cumulative effects seemed to be tied to the structuring effect of climate change, and differed under the 2050 and 2100 scenarios. Such changes resulted in stronger loss of ecosystem resilience under the 2100 scenario despite the benefits of the reef and reserve effects of the wind farm.

Key words: coastal ecology, ecological network analysis, cumulative effects, ecosystem functioning, resilience, combined drivers, climate change, offshore wind farm, fishing.

Highlights:

- Interactions between offshore wind farms and climate change can lead to a wide range of cumulative effects on ecosystems
- The structuring effects of climate change seem to have a preponderous role in the formation of cumulative effects
- Cumulative effects appear heterogeneous across space, over time and among ecosystem functional properties
- Under the 2050 scenario, the combined effects of climate change and the wind farm remain positive for ecological resilience
- Under the 2100 scenario, interactions between climate change and the wind farm change, reducing ecological resilience

1 Introduction

When multiple anthropogenic drivers — fishing and climate change among others — co-occur in an ecosystem, they often interact with each other to produce cumulative effects on the ecosystems (Folt and Chen, 1999; Vinebrooke *et al.*, 2004). Cumulative effects have been observed in many marine ecosystems (Crain *et al.*, 2008; Halpern and Fujita, 2013). They can result in different ecosystem changes than the sum of the individual drivers, depending on the type of interactive effect – synergistic, antagonistic or dampened. These interactive effects can occur at all the levels of biological organization, from single organisms to complex and interconnected systems (Stelzenmüller *et al.*, 2018). In ecosystems, cumulative effects result from complex interactions among ecosystem drivers and depend on ecosystem functioning (Breitburg *et al.*, 1998; Boyd and Hutchins, 2012). In a world subjected to intense human activities and climate change (IPCC, 2021), understanding the effect of each individual driver is not enough. Interactions among drivers must also be studied because they could represent a major threat for marine conservation and management (Willsteed *et al.*, 2017; Gissi *et al.*, 2021).

It is important to understand the full extent to which biotic and abiotic drivers affect ecosystems to properly manage marine resources (Rombouts *et al.*, 2013; Heymans *et al.*, 2020), and where these effects take place (Halpern and Fujita, 2013). The European marine spatial planning (MSP) directive (2014/89/EU) requests EU members to establish spatial planning processes to achieve ecological, economic and social development. Ecosystem-based management has been advocated as a key pillar for the sustainable management of marine and coastal environments (Langlet and Rayfuse, 2018). As a result, cumulative effects on the whole ecosystem functioning must be considered across space to manage ecosystems efficiently. This would ensure more accurate spatial zoning decisions and ecosystem-based management plans (Buhl-Mortensen *et al.*, 2017; Le Tissier, 2020). Unfortunately, time passed until cumulative effects were properly considered in strategic environmental impact assessment (Bidstrup *et al.*, 2016), and there is still an urgent need to further include them nowadays (Guşatu *et al.*, 2021).

When cumulative effects are considered, assessment studies of spatial cumulative impacts often fail to explore their complex nature because (i) interactions among drivers are

ignored, and cumulative effects are considered additive, and (ii) each driver is usually mapped using the expected footprint of an impact, without considering the specific response of habitat / community types to the tested drivers (Ban *et al.*, 2010; Halpern and Fujita, 2013; Kotta *et al.*, 2020; Guşatu *et al.*, 2021).

Mapping the expected environmental footprints of multiple anthropogenic drivers can help identify areas prone to cumulative impacts and possibly requiring thorough monitoring to limit cumulative effects; but using expert judgement does not allow for an accurate representation of the ecosystem processes that pilot interactions among drivers. Such complex processes depend on many ecosystem parameters (ecosystem heterogeneity, species tolerances & displacement, driver magnitude among others (D. Vinebrooke *et al.*, 2004; Boyd and Hutchins, 2012)), and may affect the spatial extent of cumulative effects and in turn the areas subjected to cumulative responses. The assessment of spatial cumulative effects would greatly benefit from ecosystem approaches taking the complexity of the food web into account to represent the mechanisms leading to cumulative effects (both direct and indirect). It would ensure a quantitative assessment of cumulative effects and their impacts on ecosystem functioning to monitor ecosystems more efficiently (Buhl-Mortensen *et al.*, 2017; Le Tissier, 2020). With their shared vision of ecosystems as networks of interactions, cumulative assessment methods and ecosystem approaches seem to fit together to build a coherent tool for marine management and zoning purposes.

Holistic ecological network analysis (ENA) indices can be used to link both ecosystem approaches and cumulative assessment. ENA indices are utilized to understand the functioning of a food web; they provide an integrative and holistic view of ecosystem functioning, organization and structure (Ulanowicz, 1986; Baird and Ulanowicz, 1993; Borrett and Scharler, 2019). ENA indices can be computed using food web modeling techniques and have been extensively promoted as promising tools for ecosystem-based management (Ulrike *et al.*, 2018; Fath *et al.*, 2019; Safi *et al.*, 2019). ENA indices have already been used to study the cumulative effects and the spatial effect of multiple individual anthropogenic drivers (Nogues *et al.*, 2020; Nogues *et al.*, submitted).

Ecopath with Ecosim (EwE) is a food web modeling suite that can explore cumulative impacts on ENA indices. The spatialized version of Ecopath – Ecospace – was used in Nogues *et al.* (submitted) to compute maps of ENA indices in order to understand the spatial

organization and functioning of the extended Bay of Seine ecosystem (eBoS, English Channel). Developed by Halouani *et al.* (2020) and modified by Bourdaud *et al.* (2021), the eBoS Ecospace model defines multiple functional regions of the eBoS ecosystem based on ENA indices (Nogues *et al.*, submitted). These regions were defined to explore the potential effects of individual drivers using ENA indices. These drivers included the potential effects of climate change (CC) on species distribution, the exploitation of the offshore wind farm (OWF) of Courseulles-sur-Mer (in the Bay of Seine) and multiple Brexit fishing scenarios.

In this study and based on the insights from Nogues *et al.* (submitted), we combined the different drivers previously modeled in the eBoS model to evaluate holistically how their effects could affect the organization and the functioning of the Bay of Seine ecosystem. We aimed to characterize the mechanisms that drive cumulative effects as well as the locations where ecosystem functioning was mostly impacted by cumulative effects. Finally, we studied the effects of the combined drivers on the resilience of the ecosystem.

2 Materials and methods

2.1 Study area

The extended Bay of Seine (eBoS) Ecospace model covers the coastal ecosystem of the Bay of Seine, from the Cotentin peninsula to Le Havre and from the French coastline to the Franco-British delimitation of the Exclusive Economic Zones (Figure IV - 1). It is a shallow coastal ecosystem open onto the English Channel in the north, with depth varying from 5 m to 70 m in the paleo-valley of the Seine (mean 35 m). It covers 13,500 km² and is mainly composed of gravel, coarse sand in the offshore part of the bay, while fine sand and muddy fine sand are located near the coast (Dauvin, 2015). The area is heavily anthropized and is home to many human activities including fishing, aggregate extraction, marine renewable energy, tourism, fret transport, and pleasure sailing among others (Dauvin, 2019).

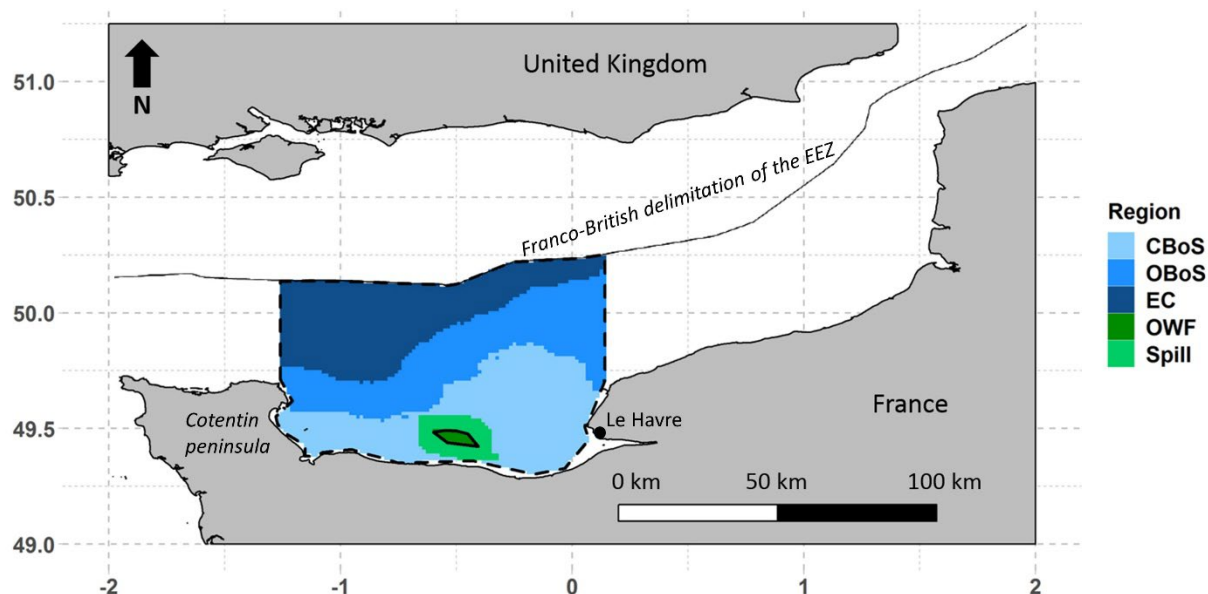


Figure IV - 1 Map of the eastern part of the English Channel and location of the eBoS Ecospace model.

The Ecospace model was divided into five regions. Three functional regions were built from network analysis (Nogues *et al.*, submitted): CBoS (Coastal Bay of Seine), OBoS (Offshore Bay of Seine), and EC (Central English Channel). Two structural regions were built around the OWF: OWF (Offshore wind farm) and Spill (Spillover region surrounding the OWF). All regions are exclusive.

2.2 Ecospace spatialized food web modeling

The eBoS food web was modeled with a modified version of Ecopath with Ecosim (*EwE* 6) software (Pauly *et al.*, 2000). This software can be used to model marine food webs in multiple ways: in a static way with Ecopath (Pauly *et al.*, 2000), in a time-dynamic way with Ecosim (Christensen and Walters, 2004), and spatially with Ecospace (Walters *et al.*, 1999; Christensen *et al.*, 2014). The *EwE* 6 version we used was specially modified to compute food web indices (Nogues *et al.*, submitted). Following Nogues *et al.* (submitted), this study is based on Halouani *et al.* (2020) to model the eBoS ecosystem.

The original eBoS Ecopath was composed of 42 groups, including 40 living groups with a wide variety of marine species – from phytoplankton and bacteria to bottlenose dolphins and sea birds – and 2 non-living groups, namely Detritus and Discards (Supplementary materials Table SIII - 1). This Ecopath model served as a basis to build an Ecosim time-dynamic model using 21 time series of catches (Système d'Information Halieutique, 2017) and 8 time series of biomass from multiple stock assessment surveys (2000 to 2015) (Halouani *et al.*, 2020). An

Ecospace model was later built to spatially model the eBoS ecosystem. The eBoS model map was composed of 4,907 cells, and each cell modeled a time-dynamic Ecosim food web and had a resolution of $0.015^{\circ} \times 0.015^{\circ}$. Species distributions inside the eBoS model were set using a depth map from the General Bathymetric Chart of the Oceans (GEBCO: <https://www.gebco.net/>) and a primary production map from SeaWiFS representing the relative chlorophyll a concentration in the bay in 2000 (<https://podaac.jpl.nasa.gov/>) and a set of environmental driver maps for 27 of the 40 trophic groups (Supplementary materials Table SIII - 1; Bourdaud *et al.*, 2021; Halouani *et al.*, 2020; Nogues *et al.*, submitted). Environmental driver maps were built from niche model suitability index maps computed by Ben Rais Lasram *et al.* (2020), and were used to define habitat suitability for the specified species (Christensen *et al.*, 2014), in the presence and in the absence of CC effects (Bourdaud *et al.*, 2021; Nogues *et al.*, submitted). Suitability index maps were species distribution model (SDM) outputs from Ben Rais Lasram *et al.* (2020), and were computed using 2005 – 2012 climate and habitat parameters (temperature, salinity, type of substrate, depth, seafloor slope, and orientation to the north). All the parameters of the eBoS model are available in Halouani *et al.* (2020), Bourdaud *et al.* (2021), and Nogues *et al.* (submitted).

2.3 Modeling of anthropogenic drivers: effects of climate change, fishing and the offshore wind farm of Courseulles-sur-Mer

In Nogues *et al.* (submitted), multiple anthropogenic drivers were modeled to determine their individual effects on the ecosystem. These drivers included climate change, the operation of an offshore wind farm and three Brexit fishing scenarios.

The spatio-temporal framework of *EwE* (Steenbeek *et al.*, 2013) was used to model the effect of CC. This Ecospace tool can modify Ecospace inputs over time, such as environmental driver maps and a wide variety of Ecospace parameters. In the present study, it was used to replace the initial suitability index maps computed from 2005 - 2012 climate parameters, using new suitability index maps taking the effects of CC on species distribution into account. Two new sets of suitability index maps were computed at two different horizons of the RCP 8.5 projection. One scenario represented the 2050 decade (2041 - 2050), while another represented the 2100 decade (2091 - 2100) (Nogues *et al.*, submitted, Figure IV - 2). By replacing the reference “current” suitability index maps with the “climate change” ones for 2050 and 2100, we changed habitat suitability for the eBoS trophic groups according to the

effect of CC on the suitability index. As such, these CC-induced changes in the environmental parameters affected the suitability indexes and the habitat suitability of the impacted groups. Following the foraging arena theory (Walters *et al.*, 1997, 1999), changes in habitat suitability affect consumption by the groups in the cells and modify their production and biomass (Christensen *et al.*, 2014).

The long-lasting effects of the future offshore wind farm of Courseulles-sur-Mer were modeled following Halouani *et al.* (2020) who first modeled the reserve effect of the OWF. We improved on Halouani *et al.* (2020) by modeling a limited closure of the farm following the owners' proposal to "optimize" fishing inside the farm (~15 %, Raoux *et al.*, 2018, 2019) and by modeling the potential reef effect of the OWF (Nogues *et al.*, submitted) based on a previous study that modeled the potential reef effect of the Courseulles-sur-Mer OWF (Raoux *et al.*, 2017). Using the spatial-temporal framework of *EwE* (Steenbeek *et al.*, 2013), biomass changes observed in Raoux *et al.* (2017) due to the reef effect were transposed to environmental driver maps to increase the habitat suitability of multiple benthic and demersal groups inside the OWF (Nogues *et al.*, submitted). Combined with 15% closure to fishing, the effects of the OWF included both the reef and the reserve effects, two effects considered as highly structuring on the ecosystems (Langhamer, 2012; De Mesel *et al.*, 2015).

Three fishing scenarios based on the potential effects of Brexit on fishing were used in this study (Nogues *et al.* submitted). They simulated the potential effect of changing fishing pressure on the eBoS ecosystem: one increased the overall fishing pressure (**F_inc**), another one decreased it (**F_dec**), and the last one did not change it (**F_ref**). For more details, see Nogues *et al.* (submitted) and Supplementary materials Table SII - 1 and Table SII - 2.

In Nogues *et al.* (submitted), each anthropogenic driver was modeled separately to determine their respective effects on the eBoS. In the present study, we created cumulative scenarios that combined those drivers to determine their cumulative effects on food-web functioning (Figure IV - 2). As the Brexit fishing scenarios had negligible effects on the ecosystem (Nogues *et al.*, submitted) and preliminary results showed little differences in the magnitude of the cumulative effects between fishing scenarios (Supplementary materials Figure SIII - 17 to Figure SIII - 32), we did not consider fishing scenarios explicitly in the assessment of cumulative effects. Instead, all fishing scenarios were combined for each CC scenario and with the OWF to build two main cumulative scenarios each composed of three

results (one *per* fishing scenario). These two cumulative scenarios were designed to study the cumulative effects of CC plus the OWF, while considering potential fishing variations in the eBoS. They were called “Combined 2050” and “Combined 2100”, with three suites of driver combinations *per* cumulative scenario:

- Combined 2050: CC 2050 + the OWF with each fishing scenario (F_ref, F_inc and F_red).
- Combined 2100: CC 2100 + the OWF with each fishing scenario (F_ref, F_inc and F_red).

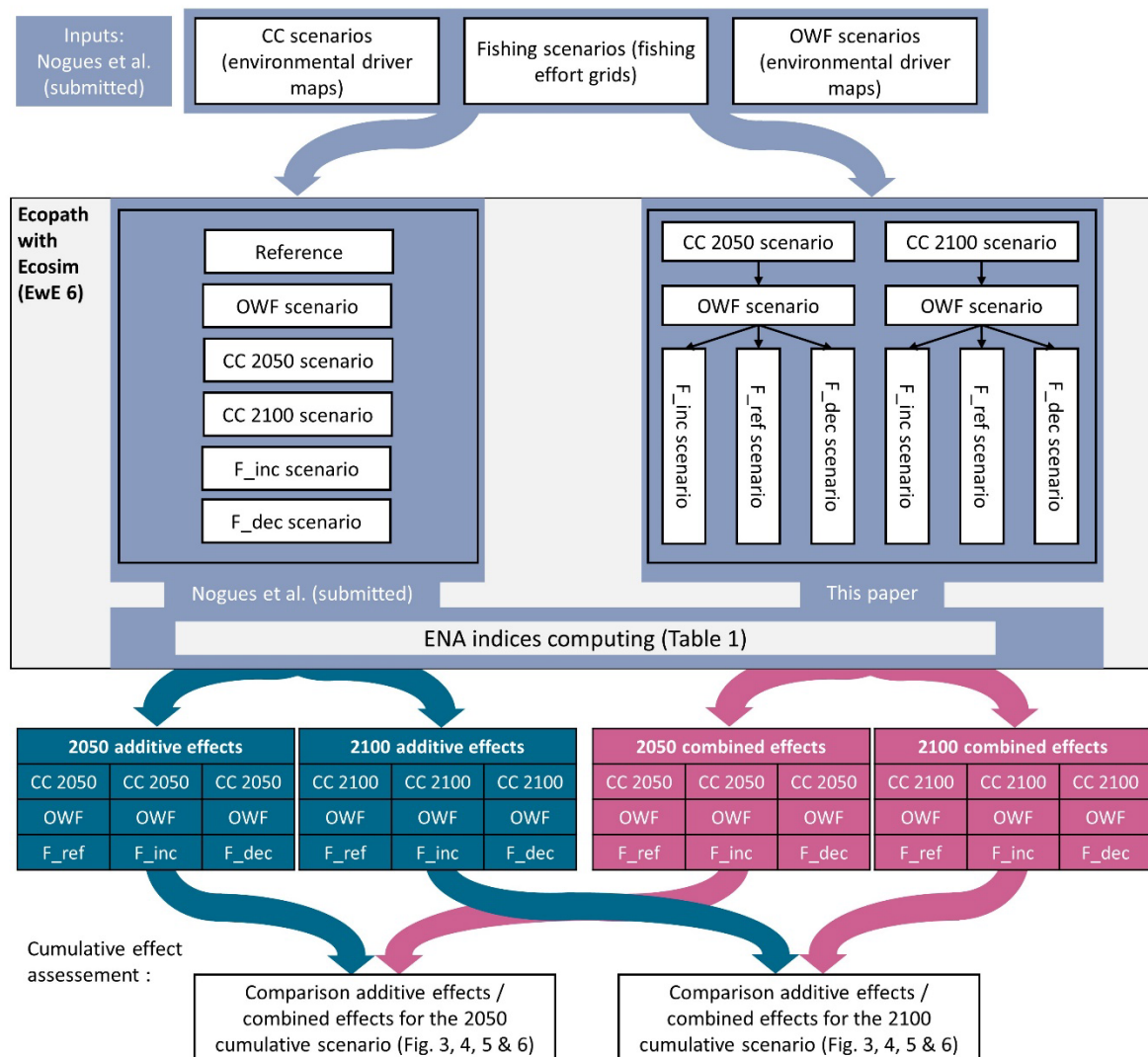


Figure IV - 2 Modeling framework

2.4 Ecological network analysis

The scenarios built in Nogues *et al.* (submitted) were used to compute maps of ENA indices using the “EnaR” Ecospace plugin (Nogues *et al.* (submitted)). This plugin available in a modified version of *EwE* 6 is used to create Scientific Committee for Ocean Research (SCOR) formatted files for each cell of the Ecospace model at each time step. SCOR files contain all the data needed to create maps of ENA indices using the R package “enaR” (Borrett and Lau, 2014). Each cell of the Ecospace model had ENA values that were used to build ENA maps using the same resolution as the Ecospace grid cell. We selected four ENA indices to describe and understand the functioning and organization of the food web (Table IV - 1), based on previous lists of ENA indices considered promising for ecosystem management due to their insights into ecosystem functioning and ecosystem resilience (Fath *et al.*, 2019; Safi *et al.*, 2019). Each cumulative scenario had three sets of ENA results – one *per* fishing scenario.

Table IV - 1 ENA indices computed with enaR from Ecospace SCOR files.

Name	Objective	Calculation	References
Relative flow redundancy (RDC)	Quantify the relative redundancy of the flows in the system.	$\Phi_i = - \sum_{i,j=1}^n T_{ij} \log \left[\frac{T_{ij}^2}{T_i T_j'} \right]$ Where Φ_i is the internal relative redundancy, T_{ij} the flow between i and j, T_i is the sum of all the flows leaving i, T_j' the sum of all the flows leaving j. $RDC = \frac{\Phi_i}{DC}$ Where DC is the development capacity of the system.	(Ulanowicz and Norden, 1990; Christensen, 1995)
System omnivory (SOI)	Determine the level of omnivory of the system, <i>i.e.</i> , to what extent the groups in the system consume multiple other groups.	$OI_i = \sum_{j=1}^n [TL_j - (TL_i - 1)]^2 \times DC_{ij}$ $SOI = \frac{\sum_{i=1}^n [OI_i \times \log(Q_i)]}{\sum_{i=1}^n \log(Q_i)}$ where TL is the trophic level of i or j.	(Libralato, 2013)
Finn cycling index (FCI)	Specify how much energy of the system passes through cycles.	$FCI = \frac{TST_c}{TST}$ where TST is the total system throughflow and TST_c the cycled total system throughflow.	(Finn, 1980)
Mean trophic level (MTL 2)	Quantify the mean trophic level of the system and thus the ecological community structure.	$MTL = \frac{\sum_i TL_i \times B_i}{\sum_i B_i}$ where B is the biomass of i or j.	(Latham, 2006)

2.5 Functional & structural regions of the extended Bay of Seine.

In Nogues *et al.* (submitted), the eBoS was divided into multiple regions to help distinguish the effects of the different drivers on the ecosystem. A K-means clustering analysis (MacQueen, 1967) was performed on the ENA results of the reference model (with anthropogenic drivers), to determine functional regions. Three regions with different properties of functioning were defined and used to describe the effects of each individual driver (Nogues *et al.*, submitted), and named “Coastal Bay of Seine” (CBoS), “Offshore Bay of

Seine” (OBoS) and “Central English Channel” (EC) from coast to offshore. These regions clearly depicted a coast-to-offshore gradient, with the most coastal region more resilient and complex and the farther regions less so.

We defined two other structural regions based on the OWF of Courseulles-sur-Mer inside the CBoS functional region and named them “Offshore wind farm” (OWF) and “Spillover region” (Spill). All the regions were mutually exclusive and allowed for a better understanding of cumulative effects within the eBoS (Figure IV - 1).

2.6 Assessment of cumulative effects

ENA indices can assess the cumulative effects on the ecosystem properties, as described in Nogues *et al.* (2020). The methodology of Travers-Trolet *et al.* (2014) and Fu *et al.* (2018) was applied to determine the type of cumulative effect. This method considers that cumulative effects can be synergistic, antagonistic or dampened. It also considers the direction of the effect on the studied index (positive or negative relative to the reference).

To determine cumulative effects, we computed the relative index change (delta) between the reference scenario and each independent driver (eq. 1, *e.g.*, the OWF alone or one of the CC scenarios (2050 or 2100) or one of the fishing scenarios) for all ENA indices.

$$\Delta I_s^{sep} = \frac{I_s - I_r}{I_r} \quad (1)$$

where I_r is the index value of the reference model and I_s the index value of a single-effect model (OWF only or CC only).

Then, we summed the ΔI_s^{sep} of each driver (CC, OWF and fishing) for each combination (F_red, F_inc, F_ref) in each cumulative scenario (cumulative 2050 and cumulative 2100, Figure IV - 2). This yielded three additive effects $\sum \Delta I_s^{sep}$ per cumulative scenario ($\sum \Delta I_s^{sep}$ F_red, the $\sum \Delta I_s^{sep}$ F_inc and the $\sum \Delta I_s^{sep}$ F_ref). To characterize cumulative effects, we compared the three additive effects ($\sum \Delta I_s^{sep}$ F_red & $\sum \Delta I_s^{sep}$ F_inc & $\sum \Delta I_s^{sep}$ F_ref) to the three corresponding combined effects (ΔI_c^{cum} F_red & ΔI_c^{cum} F_inc & ΔI_c^{cum} F_ref), (Figure IV - 3, eq. 2) for the 2050 and 2100 cumulative scenarios.

$$\Delta I_c^{cum} = \frac{I_c - I_r}{I_r} \quad (2)$$

where I_r is the index value of the reference model and I_c the index value of the combined drivers (CC effects + OWF effects + one fishing scenario).

2.7 Comparison of additive effects and combined effects

The cumulative effects under the 2050 and the 2100 cumulative scenarios were determined using two methods. First, the effects were determined for each region (functional and structural) of the eBoS (Figure IV - 1) by comparing the average additive effect ($\overline{\Delta I_s^{sep}}$ averaging each combination *per* cumulative scenario) with the average combined effect ($\overline{\Delta I_c^{cum}}$ averaging each combination *per* cumulative scenario) under each cumulative scenario, using barplots. If the two averaged effects ($\overline{\Delta I_s^{sep}}$ and $\overline{\Delta I_c^{cum}}$) were equal, we considered that no cumulative effect resulted from the combined drivers (Figure IV - 3, case 1). Otherwise, the OWF and CC were considered as interacting, leading to cumulative effects, despite potential variability in the fishing pressure (Figure IV - 3)

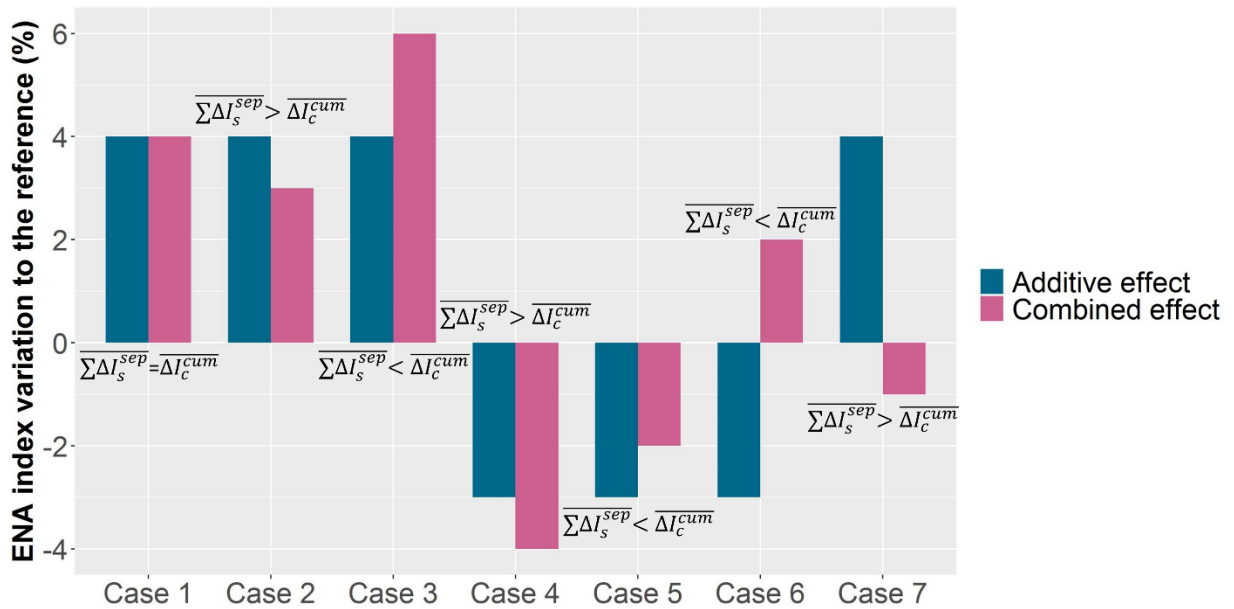


Figure IV - 3 Comparison of the additive and combined effects of drivers to determine the resulting cumulative effect of drivers on ENA indices.

Case 1: no cumulative effect; case 2: positive dampened; case 3: positive synergistic; case 4: negative synergistic; case 5: negative dampened; case 6: positive antagonistic; case 7: negative antagonistic.

The Cliff delta (Cliff, 1993) effect size metric was used to compare the three additive effects with the three combined effects for each cumulative scenario in each cell of the eBoS Ecospace model (4,907 comparisons). It was chosen because it is a non-parametric effect size metric that can be used to compare datasets with different treatments. Thus, we compared the three $\sum \Delta I_s^{sep}$ with the three ΔI_c^{cum} of each cumulative scenario. The Cliff delta determined if the difference between the three $\sum \Delta I_s^{sep}$ datasets and the three ΔI_c^{cum} datasets (*per* cumulative scenario) was large, medium, small or negligible. If the difference was considered large, based on the threshold given by Romano *et al.* (2006) ($| \partial \text{Cliff} | < 0.474$), then the cumulative effect was considered significant in the cell. This allowed a more precise discrimination of cumulative effects within the eBoS compared to the barplot, and a mapping of cumulative effects despite variability inside the regions and between the Brexit scenarios. Cumulative effects were determined using the same typology as the barplot method (Figure IV - 3).

3 Results

3.1 Cumulative effects in the eBoS regions

The graphical comparison of the additive and combined effects under the two cumulative scenarios (combined 2050 and combined 2100) showed that only the OWF appeared to be affected by cumulative effects. The average additive effect was an outlier to the average combined effect for the recycling index (FCI), the mean trophic level (MTL2) and relative flow redundancy (RDC), despite variability (i) inside the OWF sub-region as all cells had different values and (ii) among the three fishing scenarios within each cumulative scenario. Under the 2050 cumulative scenario, cumulative effects inside the OWF were always positive – positive synergistic for the FCI and positive dampened for the MTL2 and RDC. Under the 2100 cumulative scenario, cumulative effects within the OWF were similar to those under the 2050 cumulative scenario for FCI and MTL 2 – positive synergistic for the FCI and dampened positive for the MTL2 (Figure IV - 4). However, a negative cumulative effect – negative synergistic for relative redundancy (RDC, Figure IV - 4) – was found under the 2100 cumulative scenario that was not found under the 2050 cumulative scenario. Another region that seemed to exhibit a cumulative effect was the Spillover region under the 2050 cumulative scenario, for the system

omnivory (SOI). However, this effect was not as clear-cut as in the OWF region because there was greater variability within the region.

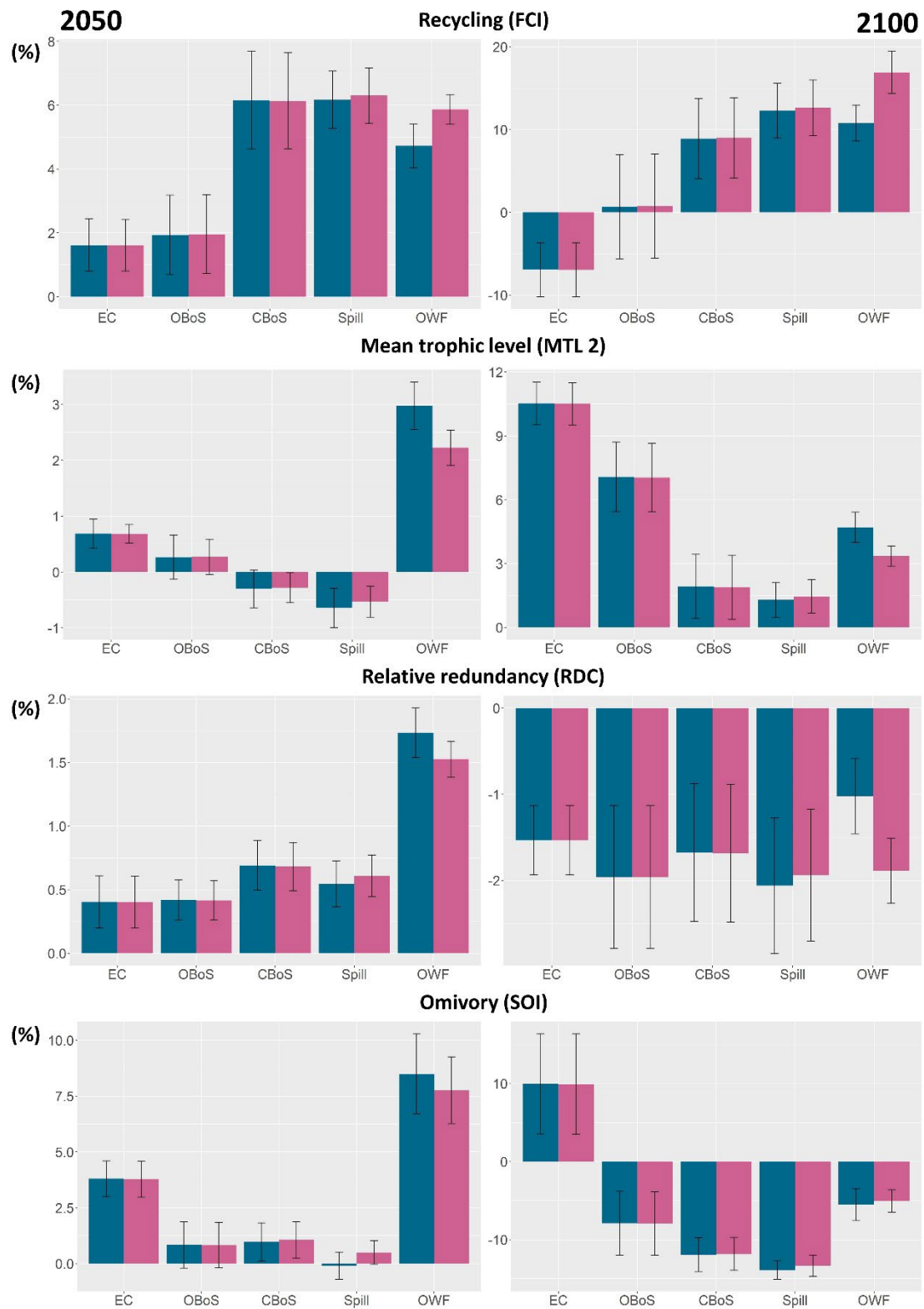


Figure IV - 4 Regional differences between the averaged additive effect (blue) and the averaged combined effect (red) under the two cumulative scenarios (2050 and 2100).

The standard deviation for the cumulative scenario was calculated with the values of all the cells of the given region, for all the combinations of drivers (F_ref, F_inc and F_red), and was pictured with error bars. Error bars show the standard deviations within the regions and among the driver combinations under each cumulative scenario.

3.2 Spatial cumulative effects

The OWF region consistently displayed most of the cumulative effects in the eBoS, but results at the cell level showed that cumulative effects could also occur elsewhere (Figure IV - 5 & Figure IV - 6). The OWF region displayed uniform cumulative effects. The Spillover region showed intra-regional variability of cumulative effects, especially under the 2050 scenario, with a uniform positive synergistic effect on the FCI and RDC, but heterogeneous effects on the SOI – positive synergistic, positive antagonistic and negative dampened effects all mixed together across the region (Figure IV - 5). Under the 2100 scenario, cumulative effects were more homogeneous across the region. This trend was not just visible at the regional scale: cumulative effects were altogether more homogeneous under the 2100 scenario than under the 2050 scenario (Figure IV - 5 & Figure IV - 6).

The interactions between the drivers of the two scenarios varied according to ENA indices (Figure IV - 5 & Figure IV - 6). Both scenarios displayed a similar positive synergistic effect within and around the OWF for the FCI, but the SOI and RDC had different interactions under each scenario, with positive cumulative effects under the 2050 scenario and negative ones under the 2100 scenario. The effects under the 2100 scenario were also higher than the effects under the 2050 scenario: cumulative effects had a 5 % positive synergistic effect on the FCI in the OWF sub-region under the 2100 scenario, *versus* a 2% synergistic increase of the FCI under the 2050 scenario (Figure IV - 5 & Figure IV - 6).

Overall, cumulative effects were closely spatially linked with the OWF, with varying sensitivity of the indices and scenarios. MTL2 was the only index that displayed cumulative effects far outside the OWF region, in all the regions of the model. Even though a lot of cells showed cumulative effects, similar cumulative effects were mixed (positive synergistic with positive dampened, negative synergistic with negative dampened), resulting in the absence of cumulative effects visible at the regional scale (Figure IV - 4) despite the large scale of the effects.

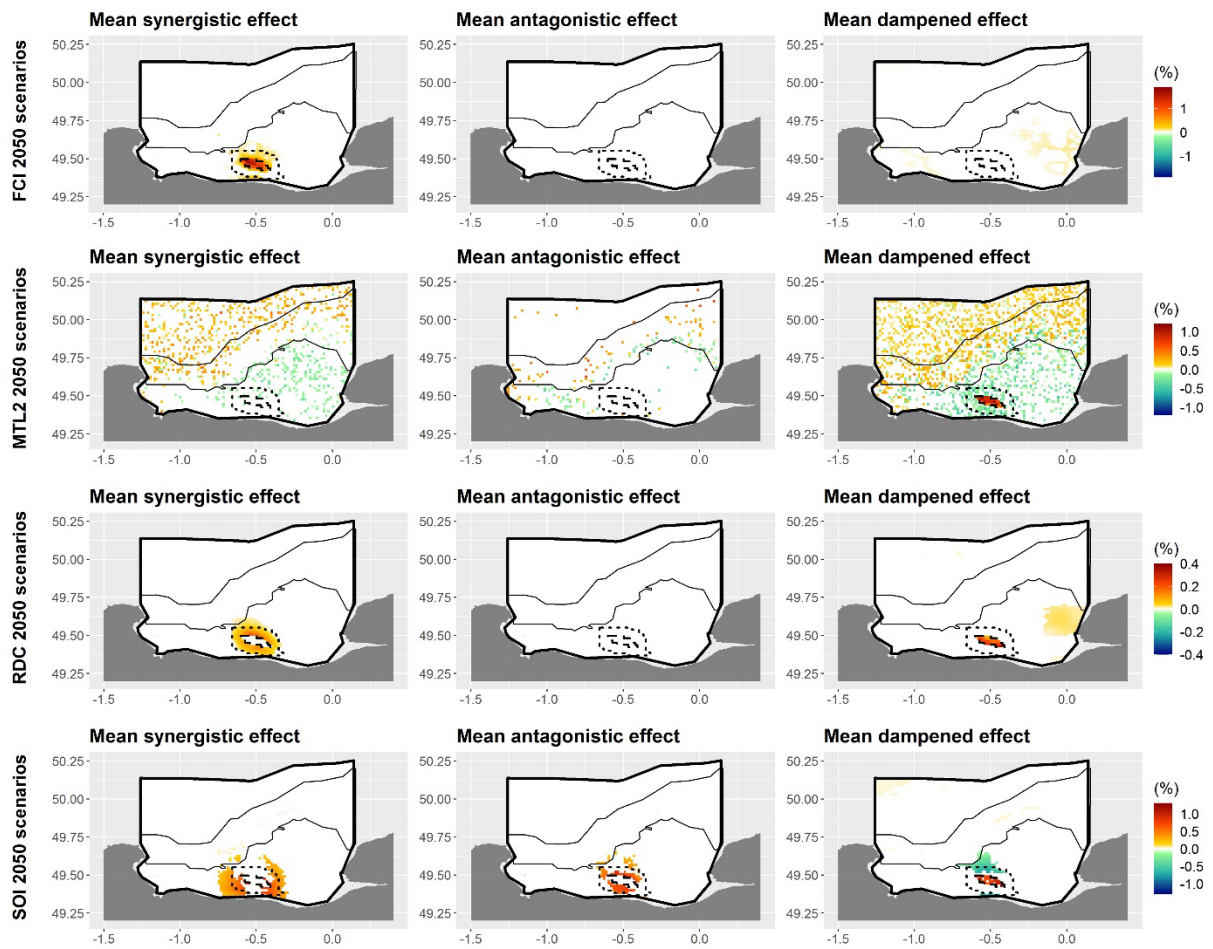


Figure IV - 5 Strong cumulative effects under the 2050 cumulative scenario according to the Cliff delta metric.

The averaged cumulative effects were mapped when the difference between the additive effect and the combined effect was considered large by the Cliff delta. Maps were sorted *per row* (ENA indices) and *per column* (cumulative effect). Warm colors, positive cumulative effects relative to the reference model; cold colors, negative cumulative effects relative to the reference model. Dashed line, OWF; dotted line, spillover region; full line, functional region.

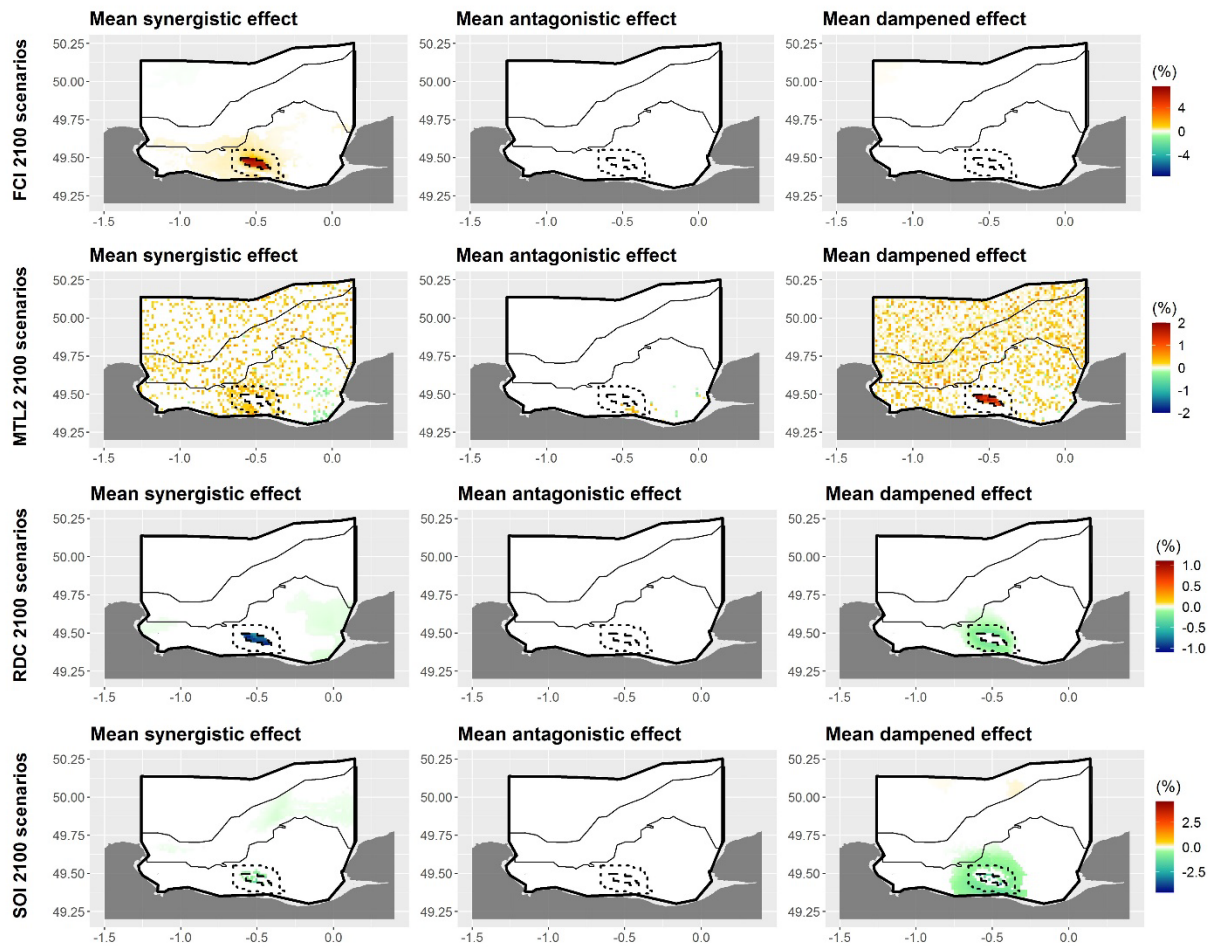


Figure IV - 6 Strong cumulative effects under the 2100 cumulative scenario according to the Cliff delta metric.

The averaged cumulative effects were mapped when the difference between the additive effect and the combined effect was considered large by the Cliff delta. Maps were sorted *per row* (ENA indices) and *per column* (cumulative effect). Warm colors, positive cumulative effects relative to the reference model; cold colors, negative cumulative effects relative to the reference model. Dashed line, OWF; dotted line, spillover region; full line, functional region.

4 Discussion

This study proposes an innovative method to characterize cumulative effects on whole ecosystem functioning using holistic indices, while taking the limitations of the approach into account. First, we did not account for the explicit role of fishing. Understanding the cumulative interactions between fishing and climate change is indeed a priority for many people, and is required to tackle future hazards to ecosystems (Gissi *et al.*, 2021). Unfortunately, our fishing scenarios did not enable us to do so directly, but rather through the consideration of fishing

variability. Another limitation of the approach is that the adaptation of species diet was not considered. In Ecospace, diets can vary depending on prey availability, and predators keep the same prey as the one defined in the Ecopath base model. Thus, new prey cannot be added from the pool of Ecopath's prey. Ecospace does not only inherit Ecopath diets but also other limitations discussed in Christensen and Walters (2004) and Ainsworth and Walters (2015). CC modeling would greatly benefit from the ability to take species adaptation into account (Hoffmann and Sgró, 2011).

Moreover, this model has the same limitations as those stated in Nogues *et al.* (submitted), who used the same model. For example, the simulations did not consider the arrival of non-indigenous species or the variability of the species distribution models, due to methodological reasons. Despite these limitations, studying cumulative effects on whole ecosystem functioning remains a priority often overlooked when studying cumulative effects using ecosystem approaches, even though such ecosystem approaches are increasingly used (Gissi *et al.*, 2021).

4.1 Mapping of cumulative effects using ecosystem approaches

Cumulative effects mainly occurred within the OWF region, highlighting the importance of the interactions between global (climate change) and local (OWF) drivers. This was mainly visible in the OWF region, where the largest differences between the additive and combined effects were observed. Multiple ecosystem indices showed this, including the recycling (FCI), the mean trophic level of the consumers (MTL 2) and the relative redundancy of the flows (RDC). This further confirmed the importance of considering larger-scale drivers like climate change when assessing the environmental impact of local strategic activities (Willstead *et al.*, 2017) because local and global drivers may interact with each other and can have unsuspected effects on the local system (Brown *et al.*, 2013). Furthermore, the OWF attracted fishermen: the highest fish biomass observed in the OWF region (Nogues *et al.*, submitted) indicated that the cumulative effects across the OWF region were not only the result of CC and the OWF, but also of fishing aggregated by the OWF. Thus, the overall heterogeneity of the eBoS ecosystem will be increased by the OWF, hence a more heterogeneous response of the eBoS to CC due to cumulative effects.

Cumulative effects were important across the OWF region, but it was not the only region with noticeable interactions among drivers. Cumulative effects were also visible in multiple cells outside the OWF region, such as in the spillover region surrounding the farm and other regions of the eBoS ecosystem. Moreover, the extent of these effects differed among ENA indices, with heterogeneous cumulative effects inside and outside the OWF region. The varying cumulative effects *per* ENA index, already observed by Nogues *et al.* (2020), indicated that cumulative effects can differ depending on the ecosystem property, and that interactions among drivers can occur through multiple cumulative pathways (Spaling, 1994). A cumulative impact may affect differently each species of an ecosystem (Fu *et al.*, 2018; Ortega-Cisneros *et al.*, 2018), and the same goes for ecosystem properties (*e.g.*, recycling, omnivory and flow redundancy). However, while cumulative effects may impact species through a single pathway (*e.g.*, higher prey biomass due to cumulative effects resulting in a higher predator biomass), such changes may pass through multiple pathways interacting with each another as regards ecosystem properties, toward a larger systemic change. For example, cumulative effects on flow redundancy may be linked to simultaneous changes at multiple trophic levels. As habitat and ecological communities are not homogeneous in space and ecological responses to drivers differ (Schiel *et al.*, 2014; Epstein and Smale, 2018), such coordination may vary across space. Therefore, ecosystem responses to multiple drivers should not be generalized: two given drivers may interact differently in different ecosystems (Cocklin *et al.*, 1992a; Gissi *et al.*, 2021), and may not interact uniformly within a given ecosystem. Current cumulative assessment works often overlook such variability (Ban *et al.*, 2010; Halpern and Fujita, 2013; Kotta *et al.*, 2020). Therefore, ecosystem approaches should be promoted to model these structures and properly assess the multiple effects of combined drivers on the ecosystem. This could also greatly help the mapping of the potential interactions between two large-scale drivers like fishing and CC because they may have complex spatial patterns of cumulative effects depending on ecosystem heterogeneity that conventional cumulative effect assessment may not be able to grasp.

4.2 Cumulative effects and climate change

Ecosystem approaches also benefit from their ability to detect potential ecosystem restructuring, which plays a key role on cumulative effects at the ecosystem level. Drivers themselves can indeed restructure the food web by changing the ecological community and

through trophic cascading (Tomczak *et al.*, 2013; Heymans and Tomczak, 2016). This is due to the structuring power of some drivers on the ecosystem and may be one of the main processes leading to cumulative effects at the ecosystem level of organization, as observed in Nogues *et al.* (2020) and Niiranen *et al.* (2013). This was visible on recycling under both CC cumulative scenarios. Taken separately, the OWF reduced system recycling, while climate change increased it with varying intensities under the two 2050 and 2100 cumulative scenarios. When combined, CC and the OWF resulted in a synergistic increase of recycling under both cumulative scenarios (2050 and 2100). Therefore, the effect of the OWF may change under the influence of CC. CC is already known to restructure food webs (Montoya and Raffaelli, 2010; Walther, 2010) due to varying velocities of species drift (Van Der Putten *et al.*, 2010; Brose *et al.*, 2012). Such restructuring of the system can change energy distribution in the food web through trophic cascades (Carpenter *et al.*, 1985), and modify the effect of the OWF on recycling and lead to a positive synergistic effect. Ecosystems need to be monitored using holistic indices (Tomczak *et al.*, 2013) to detect potential ecosystem restructuring (Rilov *et al.*, 2020). Our results show that ignoring the plasticity of ecosystems to drivers and their effects on species interactions may hinder the detection of cumulative effects on ecosystem functioning.

A driver effect on the ecosystem may also change over time, especially in the case of CC and its effect on species distribution (Martinez-Meyer, 2005). As the magnitude of the effect of CC on the ecosystem changed over time, the role of CC in the cumulative effect with the OWF changed too. This was visible through the different cumulative effects of the two cumulative scenarios on omnivory and flow redundancy. The effect was also distinguishable on the mean trophic level of the OWF region: while both cumulative scenarios displayed the same positive dampened effect on the mean trophic level, they resulted in different interactions between CC and the OWF. Under the 2050 cumulative scenario, the dampened positive effect resulted from the aggregation of fish by the OWF that mitigated the negative effect of CC on the mean trophic level (Supplementary materials Figure SIII - 5); under the 2100 cumulative scenario, the effect of CC on the ecosystem structure limited the aggregating effect of the OWF on the mean trophic level (Supplementary materials Figure SIII - 6 & Figure SIII - 8). Thus, the dampened effect resulted from the aggregating effect of the OWF (Halouani *et al.*, 2020) under the 2050 scenario, while it resulted from the changed community structure across

the entire eBoS under the 2100 scenario (Fulton, 2011; Pinsky *et al.*, 2013; Kleisner *et al.*, 2016). Climate change may indeed produce “winners” and “losers”, and modify ecosystem structures up to a point where interactions among drivers may change. Therefore, cumulative effects should not be considered consistent over time because drivers like CC may change, so that continuous monitoring of ecosystems is required (Cocklin *et al.*, 1992a; Spaling, 1994).

Climate change seems to have a preponderant role in the formation cumulative effects, especially under the 2100 scenario compared to the 2050 scenario. For many ENA indices, the direction of cumulative effects nearly always followed the direction of CC rather than the direction of the OWF. The only exceptions occurred under the 2050 cumulative scenario, when the effects of CC were weaker because ecosystem properties were less impacted by CC than in 2100 (Nogues *et al.*, submitted). This was visible for the negative dampened effect on the omnivory of the spillover region and for the positive dampened effect on the mean trophic level of the OWF region. This can be explained by the fact that CC under the 2050 scenario had limited or no effect compared to the effects of the OWF (Supplementary materials Figure SIII - 5 & Figure SIII - 13). In the other cases, interactions among drivers acted in the same direction as CC did, with cumulative effects varying from synergistic to dampened along with limited antagonistic effects, despite the variability among the different Brexit fishing scenarios. Such results remain difficult to compare to meta-analyses of cumulative impacts (*e.g.*, Hodgson and Halpern, 2019) because we used a new method to characterize combined effects. However, our results are in line with the idea that the interactions of multiple drivers are often non-additive (Darling and Côté, 2008). Overall, the fact that CC appeared to be the preponderous effect compared to the OWF, resulting in cumulative effects closer to the effect of CC than to the effect of the OWF, further emphasized the need to consider the effect of CC in cumulative impact assessment and to better understand its potential structuring effects on species interactions (Wernberg *et al.*, 2012).

The increasing effect of CC on the ecosystem between the 2050 and the 2100 scenarios impacted the ecosystem’s resilience. Under the 2050 scenario, the combined drivers increased recycling, mean trophic level, omnivory and relative redundancy of the flow, indicating a more resilient system to potential future disturbances. Higher system omnivory and relative flow redundancy could indeed be beneficial to the system’s resilience, indicating an increased flexibility of the system. The complexity associated to the system omnivory has been linked to

the system flexibility, which makes the ecosystem more resilient to disturbances (Fagan, 1997a; Lobry *et al.*, 2008). Relative flow redundancy is also associated to ecological resilience because flow redundancy can act as a reserve to be used when the system is perturbed, and makes it more resistant to disturbances (Ulanowicz *et al.*, 2009). Recycling can further improve ecosystem resilience, acting as a buffer to perturbation further indicating that the OWF could limit the effect of CC on the ecosystem's resilience in the spillover region (Saint-Béat *et al.*, 2015). The increased resilience of the system due to the OWF and its interaction with CC is again in line with the idea that the habitat heterogeneity brought by the OWF can improve ecosystem resilience (Munguia *et al.*, 2011). However, with a strong effect of CC, this can only be true until CC restructures the system to a point where the OWF will potentially not have any effect on the ecosystem's resilience. Under the 2100 scenario, the lower system omnivory and the lower relative redundancy constitute signs of a lower ecological resilience compared to the 2050 scenario. The combined effect of the two drivers impairs the system's resilience under the 2100 scenario. This needs to be considered carefully as Ecospace – like Ecopath – does not take the potential adaptability of species into account, but follows trends of the relationship between CC and ecosystem resilience at different levels of organization (Harley *et al.*, 2006a; Côté and Darling, 2010; Wernberg *et al.*, 2011).

Conclusion

Using ENA indices to study cumulative effects on ecosystem functioning provides new insights into the functional pathways of cumulative effects. Such pathways seem inherently ecosystem-dependent, driver-dependent but more importantly effect-dependent. This is emphasized by the effect of climate change on species distribution: the location of the ecosystem and the differential sensitivity levels of the different species are unique to each case study. As such, the resulting structuring effect is specific to the community assemblage of the ecosystem. Thus, interactions among drivers can be highly dependent on the studied system. This was previously theorized by Cocklin *et al.* (1992) and Spaling (1994), and shows that such studies should be encouraged all around the world to explore the wide variability of functional mechanisms that could lead to cumulative effects (Gissi *et al.*, 2021). The functional study of systems and of the drivers impacting them could allow us to better grasp the complexity of cumulative ecosystem pathways and better guide ecosystem monitoring and management to favor ecosystem properties like ecological resilience to disturbances.

Acknowledgements

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V Chapitre 3 :

An ecosystem approach based on ecological network analysis to quantify ecosystem services supply in scenarios combining climate change and an offshore wind farm

Le dernier chapitre de cette thèse s'intéresse aux effets du cumul d'impacts sur la fourniture en services écosystémiques et au lien entre les indices de l'analyse des réseaux écologiques (ENA) et les services écosystémiques (SE). Aujourd'hui, la quantification de la fourniture en services écosystémiques est souvent faite avec des données aux sources hétéroclites (Böhnke-Henrichs *et al.*, 2013; Benzeev *et al.*, 2017; Newton *et al.*, 2018; Chen *et al.*, 2020). Il est également complexe de prédire l'évolution, pour un écosystème marin donné, de la fourniture en SE (de Groot *et al.*, 2010; Montoya and Raffaelli, 2010). De plus, la multiplication d'indicateurs de fourniture en service se fait souvent en ignorant les interconnexions des systèmes fournissant ces SE (Hummel *et al.*, 2019). Or il est nécessaire de prendre en compte la connectivité des systèmes vivants pour déterminer leur potentielle évolution dans le futur, de par les effets du changement climatique ou bien des effets des nombreuses activités humaines. Cette déconnexion des systèmes n'a pas uniquement lieu dans la prise en compte des systèmes biologiques, mais également entre les différents services (Duncan *et al.*, 2015). On cherche ainsi à caractériser une grande variété de services en utilisant des métriques spécifiques à chaque service. Cette « hyper taxonomisation » des services, mais également des processus les produisant, a pour objectif de standardiser les approches de quantification des services, mais a pour conséquence une représentation biaisée des systèmes les fournissant et donc des mécanismes sous-jacents régissant la dynamique de la fourniture des services écosystémiques. De plus, de nombreux services tendent à être ignorés, car ils sont difficiles à quantifier ou qu'il n'y a pas de consensus sur leur définition ou même leur rôle dans le cadre théorique des SE (Haines-Young and Potschin, 2018). Un de ces services est le SE de contrôle trophique / maintien écologique / d'assurance des écosystèmes apporté par le fonctionnement intrinsèque de l'écosystème (Baumgärtner and Strunz, 2011; Böhnke-Henrichs *et al.*, 2013; Peled *et al.*, 2020). En écologie fonctionnelle, on parle de résilience écologique ou de résistance des écosystèmes face aux perturbations. Les analyses des réseaux écologiques ont d'ailleurs souvent été utilisés pour caractériser cette propriété émergente des écosystèmes (Ulanowicz *et al.*, 2009; Saint-Béat *et al.*, 2015), ainsi que pour la quantifier. Néanmoins, les théories d'écologie fonctionnelle ont rarement été utilisées dans le cadre théorique des SE, pour quantifier ou aider à quantifier un service.

C'est pour répondre à ces différentes problématiques que nous avons décidé d'utiliser nos méthodes écosystémiques dans le but de quantifier la fourniture en services

écosystémiques en baie de Seine étendue. En effet, nos approches pouvant caractériser le fonctionnement et l'activité des systèmes écologiques et de leurs composantes, elles permettent de quantifier le rôle potentiel et actuel de l'écosystème dans la fourniture en services écosystémiques. De plus elles peuvent déterminer l'évolution de la fourniture des SE en fonction des effets du changement climatique sur les aires de répartition des espèces ainsi les effets récif et réserve du parc éolien en mer de Courseulles-sur-Mer.

Ce chapitre va faire l'objet d'une soumission au journal anglais « Science of the Total Environment » car il tente de combler le vide entre écosystème et socio-écosystème, sans ignorer leur complexité et leurs particularités inhérentes.

An ecosystem approach based on ecological network analysis to quantify ecosystem services supply in scenarios combining climate change and an offshore wind farm

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Résumé :

Les écosystèmes marins apportent un grand nombre de services écosystémiques (SE) à l'humanité partout dans le monde. Ces services sont d'une grande valeur, que ce soit économique ou non, et soutiennent le bien-être de millions de personnes. Néanmoins, l'exploitation de ces services telle qu'elle est faite aujourd'hui, nuit aux écosystèmes, ce qui provoque des changements du fonctionnement, de la structure et de l'organisation de ces derniers. Ces changements peuvent avoir un effet sur la fourniture en SE, se retournant ainsi contre l'homme. Pour mieux prédire ces changements et les anticiper, nous avons utilisé une approche écosystémique avec des indices holistiques pour prévoir les potentiels effets du changement climatique sur les aires de répartition des espèces et les effets récif et réserve du parc éolien de Courseulles-sur-Mer sur la fourniture de trois SE : (1) la fourniture en nourriture par le prélèvement dans le milieu naturel (pêche), (2) la résilience de l'écosystème face à des perturbations, et enfin (3) la dynamique des espèces patrimoniales de la baie comme les phoques, les cétacés et les oiseaux marins. Nos résultats indiquent que le changement climatique aura un impact sur la fourniture en nourriture par la pêche, ce qui pourrait avoir des répercussions importantes pour le tissu socio-culturel normand. Ceci nous montre la forte interdépendance des SE les uns avec les autres, avec l'indicateur de fourniture d'un SE relié à de nombreux autres, comme une passerelle entre l'écosystème et le sociosystème, chacun mû selon sa propre dynamique. Nos résultats montrent également que le parc éolien, à travers l'effet récif et réserve, semble améliorer l'apport des trois SE étudiés. C'est aussi le cas lorsqu'il est couplé avec le changement climatique, malgré l'impact important de ce dernier considéré seul. Cet effet cumulé reste néanmoins très local mais pourrait donner des pistes pour les acteurs de la gestion des écosystèmes, afin d'agir localement pour limiter les potentielles pertes en SE, dues au changement climatique. Globalement, on montre que nos approches écosystémiques permettent d'avoir une vision plus intégrée de l'approvisionnement en SE. Cette vision est en accord avec la gestion écosystémique des milieux et est ainsi cohérente avec les demandes de la communauté scientifique ainsi qu'avec les besoins des gestionnaires.

An ecosystem approach based on ecological network analysis to quantify ecosystem services supply in scenarios combining climate change and an offshore wind farm

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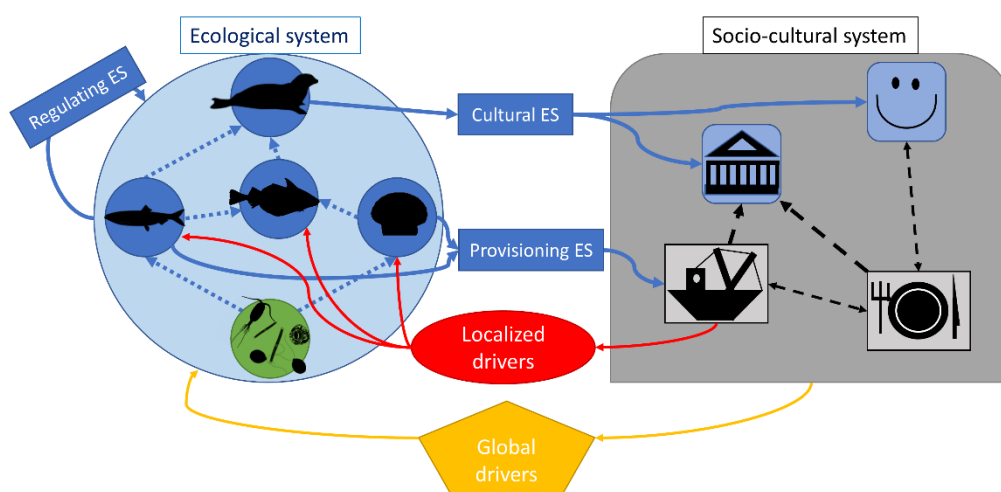
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Abstract

Coastal ecosystems provide a wide range of valuable ecosystem services for human well-being. Such services depend on the functioning and structure of ecosystems. Unfortunately, ecosystems are threatened by humans, directly impairing their ability to provide such services. To predict potential changes in services supply, we used a food web model alongside holistic ecological indicators to forecast the impact of climate change effects on species distribution and of the operation of the Courseulles-sur-Mer offshore wind farm in the Bay of Seine (English Channel). Three services were studied, food production from fishing, top predator production for cultural purposes and the trophic regulation of the ecosystem. The Bay of Seine system appeared vulnerable to the effects of climate change which may have important consequences on food production. Such changes may lead to impacts on other beneficiaries than fishermen, and could percolate on the entire social-ecological system. The offshore wind farm of Courseulles-sur-Mer seems to increase services supply as well as limit the impact of climate change locally, potentially giving keys for stakeholders to help mitigate its effects at the local scale. Such ecosystemic approach thus enables for a more integrative view of ES supply, through the characterization of the entire system functioning.

Key words: Ecosystem services, ecosystemic approach, holistic indices, Ecological network analysis, climate change, offshore wind farm, ecosystem functioning, social-system, Bay of Seine, English Channel.



Graphical abstract II

1 Introduction

Marine and coastal ecosystems are of great importance for societies around the world as they provide many ecosystem services (ES) of high values (Martínez *et al.*, 2007; Galparsoro *et al.*, 2012). Unfortunately, these ecosystems are highly threatened by anthropic activities. Indeed, more than half of all humans on earth live close to the coastline (Kennish, 2002; UNEP, 2012), which generate an immense pressure on coastal and marine ecosystems, through fishing or habitat destruction, among others. Such pressures may threaten the supply of ES and thus change our relationship with nature (MEA *et al.*, 2005; Worm *et al.*, 2006). Moreover, multiple ecosystem changes may lead to unsuspected cumulative effects on the ecosystems and thus on ES supply (Singh *et al.*, 2017). The ever increasing impacts of climate change (CC) will inevitably lead to structuring effects on the ecosystems (Richardson, 2008; Brose *et al.*, 2012), that may also indefinitely change ES supply (Montoya and Raffaelli, 2010). The same changes may come from the many other human activities in coastal systems, like the growing development of marine energies. In order to better manage such changes, we must first be able to adequately quantify the supply of ES (de Groot *et al.*, 2010), as well as their evolution in the face of changes resulting from anthropic drivers like CC, fishing, and marine renewable energies among others (driver as something that drivers ecosystem changes). We need to develop holistic approaches that can properly model the effects of a wide range of drivers on the whole ecosystem, its structure, organization and more importantly for ES, its functioning (De Groot, R.S., 1992; Hein *et al.*, 2006; Duncan *et al.*, 2015).

The representation of marine and coastal ecosystems as interconnected systems is crucial and necessary to correctly model them (Shurin *et al.*, 2006), with changes in one part of the system often cascading to result in changes at the whole system level. This is why, during the last years, the scientific community has emphasized the use of ecosystemic approaches in order to characterize the effects of ecological drivers on whole ecosystems (Rombouts *et al.*, 2013; Heymans *et al.*, 2020), to allow ecosystem-based management. Ecosystem-based management has been described as the solution needed to enable a sustainable exploitation of marine ecosystems (Gregory *et al.*, 2013; Buhl-Mortensen *et al.*, 2017). In an ecosystem services framework, it means to better maintain the supply of a wide range of ES (Beaumont *et al.*, 2007). Indeed, the supply of ES depends on the functioning of the entire ecosystem, and many ecological groups may play a significant role for the supply of ES, across a wide range of

scales (Kremen, 2005). Using ecosystem approaches to quantify ES combines multiple benefits: they follow the requirement from stakeholders to use ecosystem-based approach and they take into consideration the interconnectivity of marine and coastal ecosystems in order to adequately predict the potential changes of ecosystem functioning and thus of ES supply.

Food web models can quantify many aspects of coastal and marine ecosystems, from structural information like the biomass of each compartment to, in our case, more informative functional information like energy flows between ecological trophic groups or their production. This understanding of the ecosystem pathways of energy provides knowledge about the ecosystem functioning that can be used to quantify the supply of ES through ecological functions. Food web models can quantify the secondary production of any ecological group in an ecosystem and thus the effective activity of such group in providing a said ES (Beaumont *et al.*, 2007; Duncan *et al.*, 2015). This could be used to quantify both the potential and the actual supplies of ES (Bastian *et al.*, 2012). Moreover, other information than group production can also be quantified using ecological network analysis (ENA). With ENA, more complex information relying on the trophic pathways of the entire food web can be computed, in order to better understand the functioning properties and process that occur in a system (Ulanowicz, 1986). ENA can measure complex properties like the recycling of the system with the Finn Cycling index (FCI; Finn, 1976), the system omnivory (SOI; Libralato, 2013) or the redundancy of internal trophic pathways in the system (RDC; Ulanowicz and Norden, 1990). Ecological properties can be linked to emerging properties of ecosystems like maturity or ecological resilience (Christensen, 1995; Bondavalli *et al.*, 2006; Saint-Béat *et al.*, 2015). This means that ENA can quantify both simple ecological functions like secondary production, and more complex ones, in a holistic way. Food web models could thus help assess a wide variety of ES, while keeping an integrative view of ecosystems and consider their inherent complexity.

In this paper, we used Ecospace, a spatial food web modeling approach, in order to quantify the supply of multiple ES in the extended Bay of Seine (eBoS) in the English Channel. This work was not made to extensively quantify each ES supplied by the eBoS ecosystem. Rather, it was made to show the potential of food web models to quantify ES supply using functional model outputs. One service from each category of ES of the CICES (*Common International Classification of Ecosystem Services*) was chosen in this work (Haines-Young and Potschin, 2018), each depending on different biotic process and using different outputs of the

eBoS Ecospace food web model. We first selected the most suitable indices to quantify the actual supply of each of these ES and mapped them to characterize the ability of the eBoS to provide the selected ES. In a second step, we identified which of the functional regions of the eBoS played key roles in ES supply. Then we used insights from previous works on the eBoS to model the potential effects of CC and of an offshore wind farm (OWF) on the supply of the selected ES. Furthermore, we combined CC and the OWF to determine their cumulative effects on the selected services. Finally, we discussed the utility of food web models in quantifying ES, their benefits and especially their ability to bring an environmental view to the ES framework.

2 Materials and methods

2.1 Study area

The extended Bay of Seine is a sea space enclosed between the Cotentin peninsula in its west and the 'Pays de Caux' in its east. South of the eBoS is the Calvados Department Coastline in France and north the French-British delimitation of the Exclusive Economic Zones (Figure V - 1). It is a shallow coastal system open in its north to the English Channel, with a mean depth of 35 m. Notable geomorphologic features include the Seine estuary south-east of the eBoS and the Seine estuary paleo-valley north-west of it (Dauvin, 2015). The eBoS ecosystem, inside the English Channel, with a ship entering or leaving it every ~ 10 minutes, making it one of the busiest shipping lane in the world and representing 20% of the global maritime transport (Bul  on and Shurmer-Smith, 2021). The coastlines of the eBoS are densely populated with densities often reaching 500 inhabitants/km², resulting in a significant volume of people living in close proximity of the eBoS and benefiting from its ES. The eBoS is home to a wide variety of anthropic activities (Dauvin *et al.*, 2020; Bul  on and Shurmer-Smith, 2021). The Normandy coastline is an important place for tourism: mainly recreational above all (marinas, seaside resorts, "blue flag" label, sailing, *etc.*), historical and cultural (World War II landing beaches being classified as a UNESCO World Heritage Site, Viking invasions, museums and maritime heritage, *etc.*), and finally natural (animal watching, hiking, coastal paths, *etc.*). Fishing also plays an essential role in the eBoS, including on-foot fishing. Several fishing ports are located in direct proximity of the eBoS, with the fishing port of "Port-en-Bessin" being the first port in France for king scallops fishing (more than 15,000 tons of annual catch in Normandy) and the fourth most earning fish market in France in 2016 (Bul  on and Shurmer-Smith, 2021). Aquaculture activities (mussels and oysters) are also important on the Normandy coastline.

The eBoS sea space has important marine renewable energy perspectives (one of the largest in Europe) with two OWF under construction, Courseulles-sur-Mer (~ 50 km², 64 turbines) and Fécamp (~60 km², 71 turbines), just outside of the eBoS, in its east. A third and fourth OWF in the eBoS are also in discussion. Thus, the eBoS plays a key role for many people and activities. This is the reason why we need to understand its ability to provide ES, and how it may evolve in response to human activities.

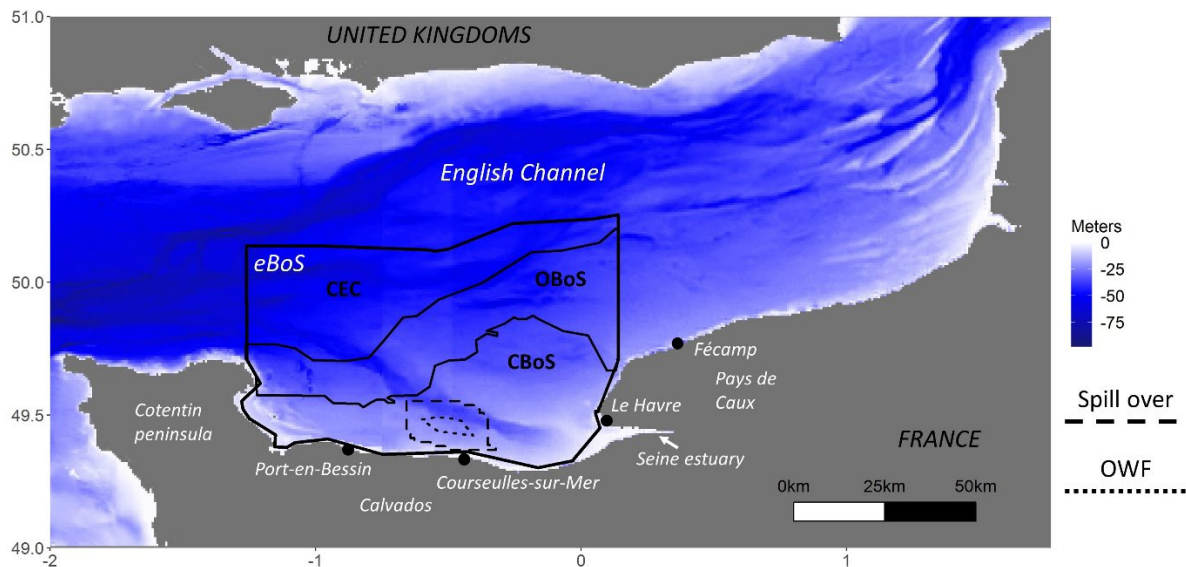


Figure V - 1 Map of the extended Bay of Seine (eBoS) within the English Channel.

The eBoS model is mapped with a continuous line and includes the coastal system of the Bay of Seine from 5 meters depth to the France/UK Exclusive Economic Zone delimitation. The offshore wind farm (OWF) of Courseulles-sur-Mer is mapped with a dotted line, and the spillover region around the park in a dashed line. Inside of the eBoS we mapped the functional regions of the ecosystem determined by Nogues et al. (submitted): the Central English Channel (CEC), the Offshore Bay of Seine (OBoS) and the Coastal Bay of Seine (CBoS).

2.2 Spatial food web modeling of the eBoS using Ecospace.

Food web models are network models that represent prey-predator interactions in order to quantify the pathways of energy between the different species/trophic groups of an ecosystem. They are composed of nodes and edges, with nodes representing ecological groups, i.e. one or multiple species with similar ecology and trophic sources (Gauzens *et al.*, 2015). Edges are flows of energy between the different nodes and represent prey-predator interactions. Food web models have been created in order to determine unknowns in

ecosystems which are hard to quantify *in situ*. There are multiple approaches to model food webs, which may be static (steady-state model) or dynamic in time and even space. In this study we used a spatio-temporal dynamic model based on a steady state one: Ecospace, from *Ecopath with Ecosim* (EwE).

The food web of the eBoS was modeled in a series of works and using multiple approaches in order to perform ecosystemic studies of multiple anthropic activities. First, Raoux *et al.* (2017) used trophic models to simulate the potential long lasting effects of the Courseulles-sur-Mer OWF on the ecosystem. This study was the basis for multiple modeling approaches including the Ecospace model of the eBoS used in this study. A full description of the EwE framework used to build Ecospace models is available in Pauly *et al.* (2000).

The Ecospace model of the eBoS was developed by Halouani *et al.* (2020) to perform a sensitivity analysis of the potential reserve effect that could be caused by the Courseulles-sur-Mer OWF. The eBoS Ecospace model latter became the basis for multiple other works. The model was then modified by Bourdaud *et al.* (2021) in order to model the potential effects of CC on species distributions on the eBoS food web. Nogues *et al.* (submitted) improved on it in order to model multiple ecological drivers, including the effects of CC, reserve and reef effects of the Courseulles-sur-Mer OWF and the potential effects of Brexit on fishing. The Ecospace model then became the basis for a cumulative effect assessment work in (Nogues *et al.*, written).

The eBoS Ecopath, Ecosim and Ecospace models are composed of 42 groups, including 40 living groups and 2 non-living groups. Living groups include a large spectrum of marine species from planktivorous species to marine mammals and seabirds. The Ecosim time dynamic model was set up using 29 time series stretching from 2000 to 2015. Time series include 21 time series of catches from the IFREMER database SACROIX (Système d'Information Halieutique, 2017) and 8 time series of biomass from multiple surveys. The Ecospace spatial model of the eBoS was composed of 4907 cells, each cell modeling a time dynamic Ecosim food web model and having a resolution of 0.015° x 0.015°. Species distribution in each of the Ecospace cell was set using multiple environmental driver maps. Environmental driver maps include depth map from GEBCO (General Bathymetric Chart of the Oceans: <https://www.gebco.net/>) as well as a primary production map from SeaWiFS representing the relative chlorophyll a concentration in the bay in 2000 (<https://podaac.jpl.nasa.gov/>). Following

Bourdaud *et al.* (2021), species distribution models (SDM) were used to drive the distribution of 27 of the 40 ecological groups. Environmental driver maps were built from species distribution model suitability index maps (Christensen *et al.*, 2014; Coll *et al.*, 2019). Species distribution models used temperature and salinity as well as benthic habitat data for benthic species like: type of substrate, bathymetry, the slope and the orientation (Ben Rais Lasram *et al.*, 2020). When ecological groups were composed of only one species, SDM outputs were directly applied to drive the group distribution while groups composed of multiple species were driven according to the weighted suitability index maps of each species, based on their biomass. For more details on the model, see Halouani *et al.* (2020) and Nogues *et al.* (submitted).

2.3 Ecological drivers modeling

Modeling the effects of CC and of the Courseulles-sur-Mer OWF on the food web of the eBoS was made using multiple data sources that were introduced in Ecospace using built-in tools.

The first to employ SDM suitability index maps as species environmental driver to define species distribution were Bourdaud *et al.* (2021) in order to be able to use SDM models to simulate the effect of CC on species distribution. Indeed, while the initial distribution of species was driven by suitability index maps computed using current climatic parameters (2012 to 2015), SDM were also run with climatic parameters from forcing scenarios of the IPCC (Intergovernmental Panel on Climate Change, (Ben Rais Lasram *et al.*, 2020)). We tested multiple scenarios and favored the RCP 8.5 scenario at the 2050 horizon because we considered it as more realistic (Schwalm *et al.*, 2020). To introduce suitability index maps in the Ecospace model, we used the Spatial-Temporal framework of *EwE* 6 (Steenbeek *et al.*, 2013). This allowed us to replace the reference suitability index maps with the CC suitability index maps as environmental drivers, thus changing the habitat suitability for each species according to the expected effect of CC on the species distribution. By changing the habitat suitability, and following the foraging arenas theory (Walters *et al.*, 1997; Ahrens *et al.*, 2012), this changed the habitat capacity of the species and thus altered multiple predation parameters and *in fine* the species vulnerability to predation, its consumption and thus its production (Christensen *et al.*, 2014). CC modeling is explained in detail in Nogues *et al.* (submitted).

To model the potential effects of the Courseulles-sur-Mer OWF, data from previous works on the potential impacts of the Courseulles-sur-Mer OWF were introduced in Ecospace with built-in tools. In this work we decided to model the long lasting and structuring effects of the OWF on the ecosystem, thus we focused on the impact of the operational phase of the OWF (Elmer *et al.*, 2006; Koeller *et al.*, 2006; Bergström *et al.*, 2013). Multiple sources state that the most relevant long lasting effects of the OWF on its environment are the reef effect caused by the arrival of new hard substrate as well as the reserve effect caused by the closing of fishing activities within the OWF area (Langhamer, 2012; De Mesel *et al.*, 2015; Degraer *et al.*, 2020). The reserve effect of the OWF was already modeled by Halouani *et al.* (2020), and we used the same method. Fifteen percent of the OWF total surface was set as an MPA as to correctly represent the OWF owners' proposal to "optimize" fishing (Raoux *et al.*, 2018), representing 6 out of the 37 cells of the OWF. To model the potential reef effect caused by the OWF, results from Raoux *et al.*, (2017) which model the Courseulles-sur-Mer OWF reef effect with Ecopath were used. In Raoux *et al.* (2017), multiple groups biomasses were forced as they appeared to be benefiting from the reef effect of the OWF in other parks in Europe. The same benefiting effects on the same ecological groups were model in the eBoS Ecospace model using new environmental driver maps, which mirror the forcing used by Raoux *et al.* (2017). Thus, the habitats of the OWF were made more suitable for the species considered attracted by the OWF reef effect. OWF modeling is explained in detail in Nogues *et al.* (submitted).

2.4 Ecosystem services quantification

To quantify ecosystem services supply we followed the ES cascade framework (Haines-Young and Potschin, 2010; Potschin-Young *et al.*, 2018) and considered ES supply to be the result of ecosystem functions which determine the "capacity of ecosystems to provide goods and services that satisfy human needs, directly and indirectly" (de Groot, 1992).

As food web models can be used to quantify ecosystem functioning, ES supply quantification was made using a wide range of Ecospace outputs, including standard outputs from Ecospace and enaR plug-in outputs (Nogues *et al.*, submitted). Because we did not try to make an exhaustive quantification of ES supply, we choose to quantify a limited number of services, but using a wide variety of outputs. This was made in order to give insights on how food web models could be used to quantify ES supply.

Because of the use of food web model, ES quantification could only be done on ES relying on the biotic sphere. ES were chosen based on the author appreciation but represent ES of great importance in the eBoS but also in many ecosystems around the world and include:

- A provisioning ES -> Food provisioning from fishing (CICES 1.1.3.1): this ES considered food production from fishing commercial activities in the eBoS. This ES was chosen due to the high importance of fishing in the eBoS and include fish and invertebrate fishing. We didn't take into consideration food provisioning from aquaculture like shellfish farming as, in the eBoS model, the intertidal zones were not modeled, impairing our capacity to model shellfish farming in the area and its interaction with the eBoS ecosystem.
- A regulating ES -> Ecological resilience based on food web functioning ("Biological control"; (Böhnke-Henrichs *et al.*, 2013) and "Biological and Natural insurance"; (Baumgärtner and Strunz, 2011; Peled *et al.*, 2020)): this ES is linked to the ecological resilience emerging property. Emerging properties are ecosystem properties inherently linked to the ecosystem functioning which occur as a consequence of it. In food webs, and in interaction networks in general, some network properties can be stabilizing. These stabilizing effects in ecosystems can be linked to the 'ecological resilience' which determines the ability of an ecosystem to maintain its original state in the context of external changes (Holling, 1996; Saint-Béat *et al.*, 2015). In ecosystems, ecological resilience plays a key role in the maintenance of ecosystems structure and functioning, which *in fine* has a key role in ES supply (Daily *et al.*, 1997; Biggs *et al.*, 2012). Regulation ES thus plays the role of feedback on ES supply, supporting all the other ES.
- A cultural ES -> Flagship species (CICES 3.1.1.1; 3.1.2.4; 3.2.2.1 and 3.2.1.3): this ES represents the role of flagship marine species for human wellbeing through aesthetic value but also through spiritual, imaginary, relational and intrinsic values among others.

To quantify ES supply, we looked at the state and dynamic of ecosystem functions, and more precisely at the functions responsible for the provisioning of each of them. This functional approach is thus based on flows between ecological groups rather than biomass (i.e. production). We also looked at the requirements made by Boerema *et al.* (2017) to coherently define what we were quantifying. Following their remarks, we decided to quantify the actual

supply of ES when possible, and the potential supply of ES if not. While for the provisioning services, quantifying the actual supply is relatively straightforward, for the regulating ES and the cultural one, delimitations are not as clearly outlined. On one hand the potential supply of ES refers to the capacity of the system to produce such service while the actual supply of ES defines the part actually used for the well-being of human population (Bastian *et al.*, 2012). ES supply quantification was made based on previously published literature on ES but also on other ecosystemic studies:

- For the food provisioning ES: we used capture flows computed from Ecospace for the Fish and the invertebrate groups that we combined to quantify the actual supply of the ES (in t/km²/year). Using Landings as an indicator of ES supply has been suggested in multiple previous works (Böhnke-Henrichs *et al.*, 2013; Olander *et al.*, 2018; Weijerman *et al.*, 2018). Landings quantify the actual supply of ES as Ecospace gravitational fishing model takes into account many parameters for achieving fishing: availability of the targeted groups, catchability, price and distance to port for each gear type and depending on fleet activity (Walters *et al.*, 1999). This is opposed to the targeted groups production which is more of an indicator of the potential supply of ES as it doesn't consider the ability of human to get access to the groups, i.e. to fish the targeted groups.
- For the ecological resilience ES: we used ENA indices (no unit). Following the recently developed theory of information, MacArthur (1955) used species diversity and trophic pathways (flows) diversity to quantify ecosystem stability. While species diversity has been extensively used and linked to ecosystem resilience (Stachowicz *et al.*, 2007; Levin and Lubchenco, 2008), flow diversity was only considered after Rutledge *et al.* (1976) re-interpretation of MacArthur's (1955) ideas in terms of conditional probabilities. Flow diversity became the usual measure of the uncertainty surrounding energy inputs (the higher the uncertainty, the more diverse the trophic sources for a group are). Ulanowicz and Norden (1990), were also inspired by the theory of information to define the ascendancy and the overhead of trophic networks as estimations of the development and ecological resilience/resistance of ecosystems. In Ulanowicz and Norden (1990), ecosystem resilience is measured by the overhead of trophic pathways. Since the overhead and the ascendancy share the same upper limit, the development

capacity (uncertainty around the energy inputs times the total system throughflow), this means that the relative redundancy (overhead of the internal flows on the development capacity) can only vary between 0 and 1. A relative redundancy close to 0 indicates a very constrained system (i.e., a low uncertainty around the origin of the trophic input, more akin to a food chain), while close to 1 indicates a redundant system (i.e., a high uncertainty around the origin of the trophic input indicate redundant trophic pathways and thus a high flow diversity). Following ecological theory studies (Odum, 1953), the redundancy of internal trophic pathways thus seems to be a good measure of the actual ecosystem resilience, and thus of ES supply by the ecosystem (Biggs *et al.*, 2012), while the potential ecosystem resilience is the development capacity.

- For the flagship species ES: we used the summed production of multiple top predator compartments (i.e. Marine mammals and Birds in t/km²/year). We selected these compartments based on preliminary results from current research studying humans and biodiversity relationships where cultural attachment on sea ecosystems (biodiversity, landscapes and places) are investigating by ethnographic inquiry and quantitative survey (Sensitroph project, unpublished). While the actual and potential supply of provisioning ES depends on the ability of human to interact (by fishing) with the targeted groups, in the case of cultural services it is less tangible. One can hardly quantify the part of the groups of interest that are observed by human and what benefits are acquired from the encountered (Blicharska *et al.*, 2017). Quantifying the production of the ecological groups of interest thus cannot be considered as the actual supply of the ES, but is more closely related to the potential one, with the actual one being more than likely only a part of the potential supply.

ES supply indicators were computed from the reference scenario without any ecological driver effects, but also from each scenario with one ecological driver effect and from the scenario combining both ecological drivers. This was made to get an overview of the area producing ES, but also to determine the effects of CC and of the OWF on the ES supply as well the potential cumulative effects of the OWF and CC on ES supply.

2.5 Mapping and evolution of ES supply in the eBoS.

Indicators made to quantify the supply of each ES were mapped for each scenario tested in the eBoS. To better analyze the evolution of ES supply in the eBoS, we regionalized the eBoS based on previously determined functional regions and structural sub-regions (Figure V - 1, Nogues *et al.* submitted).

To help determine if the effect of each driver (CC and OWF) were significant on the ES supply, a Cliff's delta was made between all the cells of the reference Ecospace scenario and the scenarios modeling the individual effects of each driver, for each region of the model. The Cliff's delta is a non-parametric effect size metric that quantifies the amount of difference between two groups of observations, whatever their size (Cliff, 1993; see Tecchio *et al.*, 2016). It was previously used to compare ENA values inside the eBoS (Nogues *et al.*, 2021).

To characterize the cumulative effects of CC and the OWF on the ES supply, the individual effects (ΔI_s^{sep}) of each driver were summed to determine the additive effect of both CC and the OWF ($\sum \Delta I_s^{sep}$).

$$\Delta I_s^{sep} = \frac{I_s - I_r}{I_r} \quad (1)$$

where I_r is the index value of the reference model and I_s the index value of a single-effect model (OWF only or CC only).

$$\Delta I_c^{cum} = \frac{I_c - I_r}{I_r} \quad (2)$$

where I_r is the index value of the reference model and I_c the index value of the combined drivers (CC effects with the OWF effects).

The additive effect ($\sum \Delta I_s^{sep}$) was then compared to the combined effect (ΔI_c^{cum}) of both drivers to determine the cumulative effects resulting from the interaction of CC and of the OWF on the ES supply (Figure V - 2). This was made for each functional and structural region of the eBoS. In order to determine if the cumulative effect was relevant on the said supply of ES, a Cliff's delta was made to compare the additive effect to the combined one, for each region and ES supply indicator.

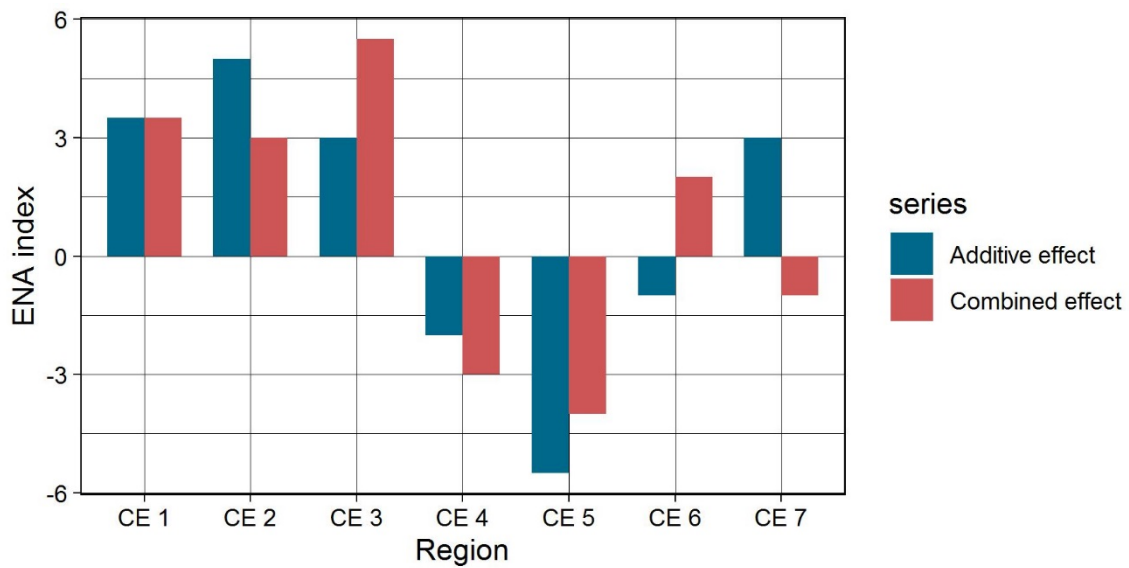


Figure V - 2 A typology of potential cumulative effects (CE) resulting from the interactions of multiple ecological drivers.

Cumulative effects are determined by comparing the additive effect (sum of the individual effects of each driver; in blue) to the combined effect of both driver (in red). CE 1 is additive with no driver interactions; CE 2 is positive dampened; CE 3 is positive synergistic; CE 4 is negative synergistic; CE 5 is negative dampened; CE 6 is positive antagonistic; CE 7 is negative antagonistic.

3 Results

The ES supply indicators were mapped for the eBoS and show a higher supply for all indicators in the most coastal part of the study area, i.e. the Coastal Bay of Seine. We observe a decreasing intensity of the supply of the 3 ES, following a gradient from the coast to the open sea (Figure V - 3).

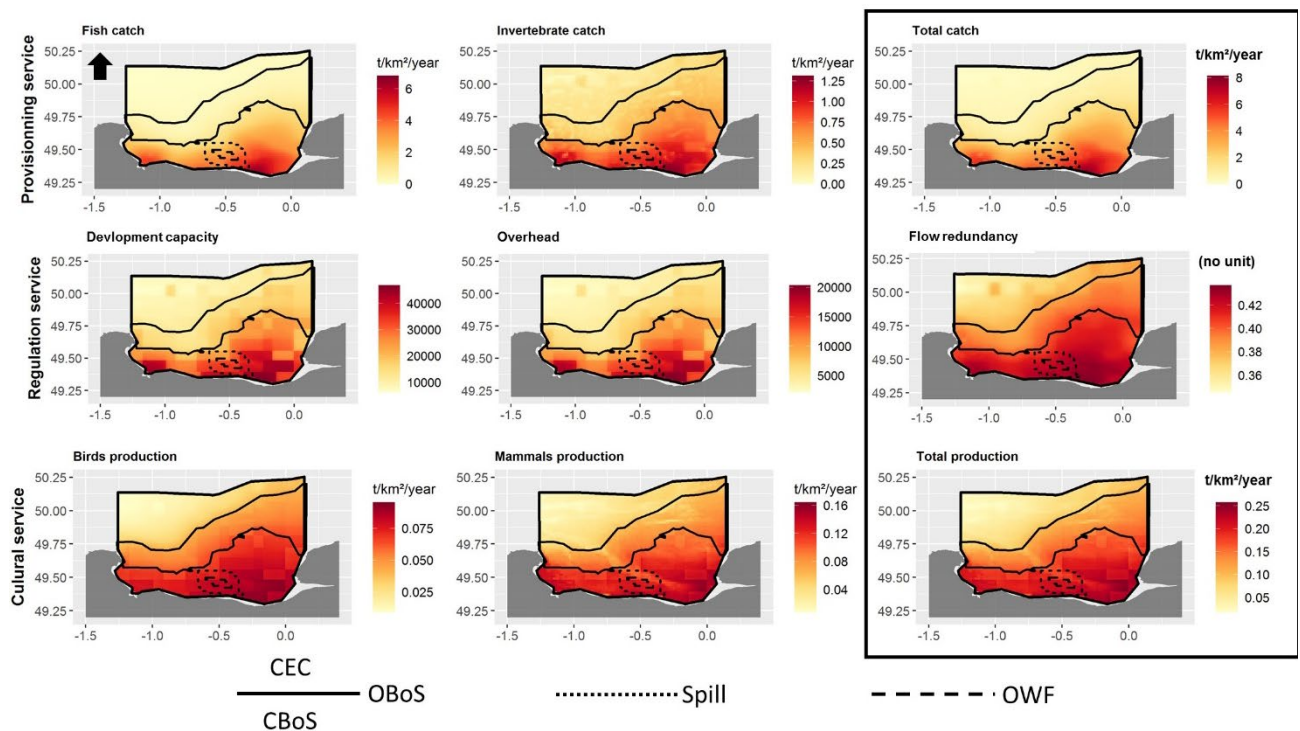


Figure V - 3 Indicators of Ecosystem services supply in the extended Bay of Seine model.

The three indicators (each line) are mapped in the black rectangle on the right and the components of each indicator are mapped left of it. The regions and sub-regions of the model are also mapped with: the dotted line mapping the OWF, the dotted one the spillover region and the continuous line each functional region of the eBoS (CBoS, OBoS, CEC).

Looking at the effect of CC on the ES supply, the provisioning ES (total catch) seems to be the most impacted with around 30 % loss in the CEC region to approximately 9 % in the Coastal Bay of Seine region (Figure V - 4). This appeared to be mainly linked to the loss of invertebrate catches while fish catches didn't display any major evolution due to CC. The other ES supplies are less impacted but we notice an increase in the regulation ES for the most coastal region, with high local increase in resilience (RDC) as visible in the OWF sub-region. Finally, the cultural ES present limited changes due to CC, with very localized increase spotted in the OWF sub-region (Figure V - 4).

Region	Provisioning service			Cultural service			Regulation service		
	Fish	Invertebrates	Total	Birds	Mammals	Total	Dev. capacity	Overhead	Redundancy
EC	-0.89	-52.64***	-28.93***	7.28	0.92	3.56	1.67	2.12	0.41
OBoS	-0.42	-53.12***	-20.61**	2.26	0.39	1.15	1.97	2.41	0.42
CBoS	1.75	-45.55***	-8.52	0.19	0.45	0.35	2.17	2.91	0.69*
Spill	-1.17	-48.28***	-10.99*	-0.21	1.75	0.97	2.02	2.75	0.69*
OWF	-1.81	-48.64***	-11.75**	-0.20	1.78**	1.00**	2.11*	2.88**	0.75***

Figure V - 4 Climate change effects in 2050 on the ecosystem services supply indicators (in percent).

Effects of CC were computed per functional and structural regions of the eBoS. To determine if the effect is important or not, Cliff's deltas were realized with variation considered: *** strong ($|\partial\text{Cliff}| > 0.474$); ** medium ($0.33 < |\partial\text{Cliff}| < 0.474$); * small ($0.147 < |\partial\text{Cliff}| < 0.33$); nothing, negligible ($|\partial\text{Cliff}| < 0.147$). Colors were plotted only on the indicators with a $|\partial\text{Cliff}| > 0.147$, with blue indicating a decrease and red an increase.

The potential reserve and reef effects of the future OWF of Courseulles-sur-Mer have strong impacts on the ES supply (Figure V - 5). All the ES were affected, with large variations compare to the reference scenario. In this case both the reserve and reef effects of the OWF appeared to increase ES supply.

Region	Provisioning service			Cultural service			Regulation service		
	Fish	Invertebrate	Total	Birds	Mammals	Total	Dev. capacity	Overhead	Redundancy
CBoS	-0.21	0.04	-0.16	-0.35	-0.21	-0.26	0.03	0.03	0.00
Spill	-6.96	-0.76	-5.67	-1.07	-2.60	-2.00	-0.35	-0.49	-0.15
OWF	65.63***	2.04***	52.12***	66.45***	4.02***	28.65***	2.38*	3.39**	0.98***

Figure V - 5 Offshore wind farm effects on the ecosystem services supply indicators (in percent).

Effects of the OWF were computed for the Coastal Bay of Seine functional region and for the structural sub-regions of the eBoS. To determine if the effects are important or not, Cliff's deltas were realized with variation considered: *** strong ($|\partial\text{Cliff}| > 0.474$); ** medium ($0.33 < |\partial\text{Cliff}| < 0.474$); * small ($0.147 < |\partial\text{Cliff}| < 0.33$); nothing, negligible ($|\partial\text{Cliff}| < 0.147$). Colors were plotted only on the indicators with a $|\partial\text{Cliff}| > 0.147$, with blue indicating a decrease and red an increase.

When both ecological drivers are combined, multiple cumulative effects appeared in close proximity to the OWF of Courseulles-sur-Mer (Figure V - 6). Despite the high variability of catches inside the OWF sub-region due to the reserve effect being applied for 6 of the 37 Ecospace cells of the park, a positive dampened effect can be seen on the provisioning ES supply in the OWF. The regulating ES had cumulative effects, but unlike the provisioning one, it was not only limited to the OWF as a small cumulative effect was also visible in the spillover region of the OWF, resulting in a positive synergistic effect. Inside the OWF, the regulating ES

also experienced a positive dampened effect, like the provisioning ES. Finally, the cultural ES showed a positive synergistic effect of the combined CC and reef end reserve effects in the OWF (Figure V - 6).

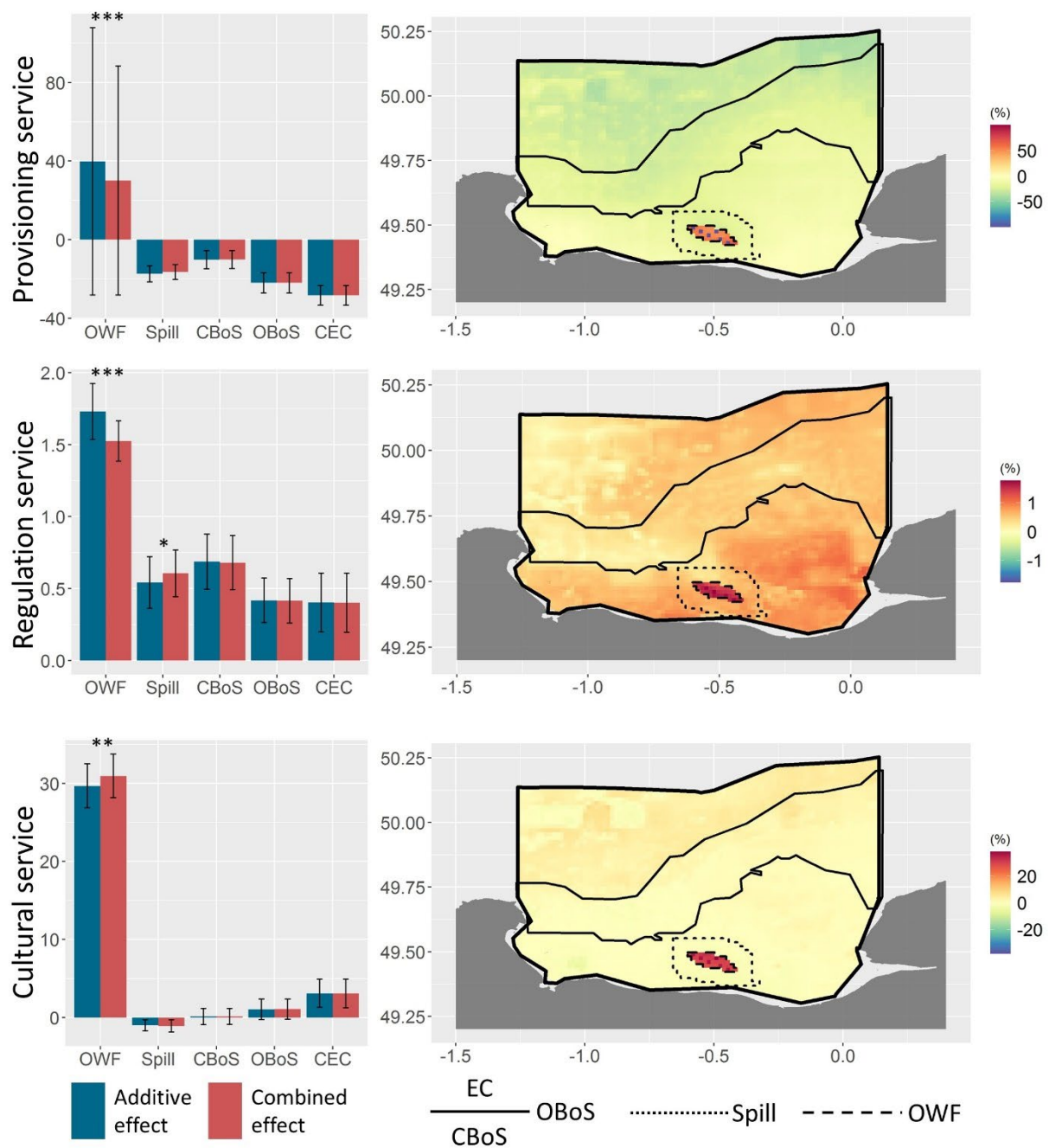


Figure V - 6 Cumulative effects of climate change and of the offshore wind farm on the ecosystem services supply.

Bar charts compare the additive effects to the combine effects of both CC and of the OWF while the map plot combine the effects of both drivers on the eBoS. Error bar display the standard deviation. To determine if cumulative effects were considered important or not, Cliff's deltas were realized with variation considered: *** strong ($|\partial \text{Cliff}| > 0.474$); ** medium ($0.33 < |\partial \text{Cliff}| < 0.474$); * small ($0.147 < |\partial \text{Cliff}| < 0.33$); nothing, negligible ($|\partial \text{Cliff}| < 0.147$).

4 Discussion

Up to our knowledge, this study constitutes the first attempt to show the usefulness of food web models to quantify the supply of a range of ES by considering the functioning of the food web, through both holistic and functional indices. However, this comes with limitations that are worth to be kept in mind. They come from the wide range of CC effects or OWF effects. One can hardly model the full extent of these effects, especially since they are still under debate amongst the scientific community (e.g. Harley *et al.*, 2006; Dannheim *et al.*, 2020). Further, this paper is based on the previous studies of the eBoS that did not aim at modeling the full extent of the effects of CC and the OWF but rather, to model their main and most structuring effects on the food web and then to gradually improve, step by step, their simulation. We thus benefit from the improvements on the OWF simulation from Halouani *et al.* (2020) and on CC simulation from Bourdaud *et al.* (2021), as presented in Nogues *et al.* (submitted).

4.1 Food web model: toward a more ecosystem-based approach of ecosystem services

Using food web modeling for ES quantification was made to have an integrative view of ES supply, often missed in ES quantification (García-Onetti *et al.*, 2018). In the literature, ecological functions such as primary production or secondary production play a key role in supplying ES (Armoškaitė *et al.*, 2020; Martinetto *et al.*, 2020). However, through the increased subdivision of ES and the ecological functions they are relying on (see Hummel *et al.*, 2019), one may disconnect processes, thus ignoring their inherent connections. In the food web modeling framework, such functions are all linked thus forming a continuum. Outputs often used to quantify ES supply ignore such connections and goes against the very idea of ecosystemic approaches, which makes them unable to correctly identify the potential changes in ES supply when environmental changes occur. In food web models, such functions are highly intertwined. ES quantification requires to consider such relations, otherwise the advances made using ecosystemic approaches will be ignored (de Groot *et al.*, 2010). It also means that one group may, through the connections within the system, play a role in the supply of multiple ES (Duncan *et al.*, 2015). This emphasizes the fact that the maintenance of one ES passes

though the maintenance of multiple others, promoting ecosystem-based approaches as the only tools able to have such holistic vision of ES supply.

ES may also depend upon ecosystem level processes, and hence their quantification should be made using holistic approaches. This is the case of the food web resilience, which can depend on the multiplicity of pathways an energy increment can pass through, in case of perturbation, allowing its sustain conveyance towards other ecological groups (Contanza and Mageau, 1999; Saint-Béat *et al.*, 2015). Other ES are likely to depend on such ecosystem processes (Kremen, 2005). While these ES further promote the need for ecosystem-based approach in the ES framework, they also can only be quantified using holistic approaches (Fath, 2015; Borrett and Scharler, 2019). Their quantification, using the wide range of information given by food web models could enable for a broader approach on ES. One could use a food web model to rank the role of biological groups or species in their ability to supply on ES, through knowledge on their functional importance (Balvanera *et al.*, 2005). Habitat parameters could be added in the quantification process to get a grasp on ES depending on both biotic and abiotic parameters, like carbon sequestration (Carss *et al.*, 2020). We believe that food web models could open ways to study a wider range of ES, using more integrative and holistic approaches and with better forecasting power to future changes (de Groot *et al.*, 2010; Müller *et al.*, 2010).

4.2 Climate change effect on the ecosystem services supply of the eBoS

Climate change appears to have a significant effect on ES supply. With losses reaching up to 30% for the supply of the provisioning ES, CC seems to have a major impact on the food production of the eBoS. This appears to be mainly due to losses in invertebrate catches, attributed to the important decrease of King Scallops (*Pectens maximus*). This potentially high impact of CC on this particular species of shellfish was already pointed out in Rombouts *et al.* (2012) and Lavaud (2014). This would result from the expected Northward drift of many cold water species due to the expected increase in water temperature (e.g. Nye *et al.*, 2009; Kleisner *et al.*, 2016, 2017).

Since shellfish and more particularly King scallops play a key economic role in Normandy, CC may have dramatic consequences on the socio-economic and socio-cultural sector. King scallops represent ~40% of the seafood sales at the Port-en-Bessin fish market (both in value

and tonnage, Buléon and Shurmer-Smith, 2021), making it one of the most valuable species in the eBoS, both at a monetary and cultural level. The evolving supply of the food provisioning ES, linked to the changing rate between fish and invertebrate capture due to CC will thus have a major impact on fishing fleets which will necessarily have to evolve. In a political context (Brexit) where the areas and quotas dedicated to fishing are already restricted, one can only assume that this will have a major effect on Normandy economy and socio-cultural fabric, together with recent effects of the Covid. The whole fishing sector (fishmongers, shipyards, fish processing industries) may not be able to resist to such an evolution. Fishing (in particular king scallop fishing) also plays an essential part in tourism industry, including local gastronomy and restaurants. The economic activities and socio-cultural practices will thus have to either evolve at a forced march, or perish. The indicator of the supply of the food provisioning ES is therefore linked to many beneficiaries. The provisioning indicator also reflects the supply of other ES than just food provisioning. Here, the provisioning indicator is thus more akin to a link between two different systems, the social and the ecological system, where one perturbation in the ecosystem can cascade throughout the social system (Haraldsson *et al.*, 2020; Niquil *et al.*, 2021). CC could also impacts fish quality and availability, but we didn't consider such aspects in this study (see Pauly *et al.*, 1998; Bourdaud *et al.*, 2021)

One potentially light positive effect of CC on the eBoS is the possible increase in the ecological resilience of the food web. This is visible as the supply of the regulating ES increases in the coastal zone of the eBoS. While significant, the increase remains small. However, small changes in the relative redundancy of a system can indicate important changes in the ecosystem organization and functioning (e.g. Tomczak *et al.*, 2013). In the eBoS model, the increase resilience is not linked to the potential arrival of non indigenous species which can elevate local diversity (Worm and Lotze, 2009), and thus resilience (Stachowicz *et al.*, 2002, 2007; Levin and Lubchenco, 2008), as NIS species were not modeled. In this case the resilience increase is likely the result of a food web reorganization. This effect is however very localized and cannot be generalized for other systems as it depends on the organization and functioning of the initial system. Similar effects in other ecosystems could thus result in different changes. It must also be acknowledged that CC modeling is subject to many uncertainties and thus require a careful analysis (see Nogues *et al.*, submitted).

4.3 Offshore wind farm effect on ecosystem services supply in the eBoS

The OWF of Courseulles-sur-Mer reef and reserve effects seem to have a positive effect on the ES supply in the eBoS, for all of the studied ES. This finding confirms the results obtained in several previous studies that showed that not only fishermen could benefit of the OWF despite losses in fishing areas (Halouani *et al.*, 2020) but the OWF also has a positive effect on the food web resilience (Raoux *et al.*, 2019; Nogues *et al.*, 2021). Furthermore, the OWF reef and reserve effects appears to have a positive effect on the species of aesthetic/spiritual/imaginary/relational interest, like birds and marine mammals (Busch *et al.*, 2010). This must however be taken carefully. Indeed, one of the limitations of our approach is that the OWF effect on the ecosystem was limited to the expected main effect of the OWF on the ecosystem i.e. the reef and reserve effects. However, the OWF can have other important effects on birds and marine mammals that may not be as structuring as the reef and reserve effects for the entire system. On one hand, several studies have pointed out the potential negative effects of OWFs on such species like the dislocation or collision effects of OWF on seabird species (Camphuysen *et al.*, 2004; Blew *et al.*, 2008; Furness *et al.*, 2013) or their effects on migratory species (Masden *et al.*, 2009), as well as the potential effects of underwater noise of wind turbines on marine mammals feeding behavior (Carstensen *et al.*, 2006). On the other, studies have shown positive effects of the OWF on these species, with some displaying an attractive effect of wind turbines on some marine seabird species (Petersen and Fox, 2007), while other have described a similar attraction of marine mammals (Scheidat *et al.*, 2011) or no effects at all (Tougaard *et al.*, 2006; Edrén *et al.*, 2010). Furthermore, some pointed out the potential adaptive power of such species to environmental changes, which may limit the negative effects of the OWF (Tyack, 2008). One must also consider the OWF specifications, its cycle of operation, its emplacement, as well as the specificities of the ecosystem itself. Indeed, the OWF of Courseulles-sur-Mer was designed to be optimized for fishing activities, through increasing distances between wind turbines, which may benefit some species of birds and marine mammals (May *et al.*, 2015). Overall, the reef and reserve effects of the OWF of Courseulles-sur-Mer may benefit such species by increasing their prey densities in the OWF (Lindeboom *et al.*, 2011).

4.4 The combined effects of both drivers

Combining the effects of the OWF and of CC resulted in significant cumulative effects on each indicator of ES supply. Despite the effects of CC, the OWF seems to be able to limit the losses of the provisioning and regulating ES, while improving the supply of the cultural one. All of this happened in close proximity to the OWF, where driver interactions were the strongest, but with different ranges between the indicators. As such the ENA based indicator showed small cumulative effects around the OWF while the community-based indicators mainly had them within the farm. These observations go alongside previous works indicating that cumulative effects happen often when two or more ecological drivers interact with each other (Darling and Côté, 2008); and that the spatial extent of cumulative effects can vary depending on the studied property, with some capable of showing effects outside of the expected zone of drivers interaction (Nogues *et al.* written). Marine protected areas and artificial reef have already demonstrated their ability to increase ES supply (Qin *et al.*, 2011; Leenhardt *et al.*, 2015; Ramos *et al.*, 2019). We demonstrate that, in Courseulles-sur-Mer, the reef and reserve effects seem to be able to keep this ability despite the effects of climate change, and thus are able to limit the losses from CC. As these effects remain limited in space, this could emphasize the need for ambitious ecological management plans at the local scale (Charles, 2012), as to limit the impact of CC on ES supply and thus on human wellbeing.

limits and perspectives

This study shows that food web models are useful modeling tools in the ES framework, for mapping and quantifying ES supply and their evolution in the face of environmental changes. The potential limitations all models may present are to be overcome, since models are constantly improving to reach a better understanding of reality. Thus, CC modeling can be through the use of coupled model approaches which combine different models (e.g. biogeochemical models could help modeling the effects of CC on low trophic levels). Simulations of the effects of OWF on the megafauna might also be improved by introducing zones of lower suitability around the turbines, thus enabling a better simulation of the future.

The cultural ES category has often been back sided (Blicharska *et al.*, 2017). Such an omission may be explained by the oversimplification of the attachment of humans to the natural world and the fracture in sciences between nature and culture. Thus, a large body of

literature produced by human and social sciences, studying for decades the links between human societies and their material environment has not been mobilized enough by ES studies, compared to the biophysical literature (Liu *et al.*, 2007). Yet, integrating social sciences into ecological research has become a top issue in the ES scientific community (Redman *et al.*, 2004; Collins *et al.*, 2011).

Considering food web models and their ability to study interactions at the ecosystem scale should bring the different disciplines together. As such, by appropriately understanding human attachments to nature, and by connecting scientific fields and using holistic approaches such as food web models, we could better link human well-being with nature and its evolution. The cultural construct is directly related to the sea ecosystem, intertwined through multiple ES, rather than compartmentalized (Mongruel *et al.*, 2019). For example, food production has fostered development of rich fishing cultures, that vary by location, in terms of fished species but also of local communities, boats and other technologies, physical port characteristics, fish markets, and, obviously, culinary practices. The present study has shown a potential collapse of scallop populations under CC effects. If the consequences on the provisioning ES are clear, it will also have repercussions on the whole social system, since scallop fishing in a way shapes the coastal Normandy's identity. Strong link between cultural and other categories of ES are revealed here, which are often underestimated (Blicharska *et al.*, 2017).

The pace of coastal human life is pulsed by the sea ecosystem (tides, seasons, storms). Experiences with the sea shapes individual thought patterns and develop their creative and imaginative capacities, as well as their social values. These inter-woven relationships have been described and studied in Humanities and Social sciences and should be further integrated in ES studies. We thus hope that through the new insights given by ecosystem approaches, we can better link both the ecological systems and the cultural ones.

VI Discussion générale

Cette discussion a pour objectif de reprendre les avancées faites durant ces trois années de thèse, mais également d'apporter de nouvelles idées afin d'aller plus loin dans l'analyse des écosystèmes, du cumul d'impacts, des effets du changement climatique sur les écosystèmes et des connexions entre « humanités » et écosystèmes. Nous cherchons également à adresser les limites mises en avant durant la thèse et à proposer des méthodes alternatives pour pallier à ces dernières. Enfin, il est question de l'après thèse et des avancements pouvant être fait pour faire progresser les connaissances scientifiques sur les sujets évoqués durant la thèse. Cette discussion se base sur une partie des travaux ayant été faits durant celle-ci et n'ayant pas fait l'objet d'un chapitre ou n'étant pas destinés à être publiés, ainsi que sur des développements plus récents.

1 Les innovations de la thèse : des approches nouvelles pour une étude fonctionnelle des systèmes vivants.

Les demandes de la communauté scientifique d'utiliser des approches écosystémiques pour étudier les effets de l'homme sur les écosystèmes sont de plus en plus nombreuses (Kremen, 2005; Rombouts *et al.*, 2013; Heymans *et al.*, 2020). Elles sont faites dans de nombreux cadres : que ce soit pour l'aide à la gestion des écosystèmes (Apitz *et al.*, 2006; Farber *et al.*, 2006; Jennings *et al.*, 2014) ou pour l'étude théorique du cumul d'impacts (Travers-Trolet *et al.*, 2014; Fu *et al.*, 2018; Ortega-Cisneros *et al.*, 2018). Cette demande pressante se fait au moment où les effets de l'homme sur les systèmes terrestres et aquatiques sont de plus en plus manifestes (IPCC, 2021). Cette grande accélération, qui a déjà commencé depuis plusieurs années, sera sans doute l'un des défis les plus importants pour l'humanité. Cette dernière ne pourra pas vivre normalement sans des écosystèmes terrestres et aquatiques en bonne santé. L'humanité a besoin de ces écosystèmes, qui jouent de multiples rôles cruciaux pour son bien-être et son développement (Peterson and Lubchenco, 1997; Newton *et al.*, 2018; Olander *et al.*, 2018). Les approches écosystémiques nous ont montré que pour les préserver des changements induits par les activités humaines et par le changement climatique, il ne faut pas ignorer leur complexité, sans quoi nous manquerions de comprendre les mécanismes qui régissent leur dynamique (Kay and Schneider, 1995). Ainsi il est nécessaire, pour les décennies à venir, de continuer à développer des approches intégratives, holistiques et écosystémiques qui puissent répondre aux demandes variées de la communauté

scientifique et de la communauté des gestionnaires des écosystèmes. En effet, il n'existe pas de méthode omnipotente et universelle qui puissent répondre à toutes les demandes de ces communautés. C'est pour cela qu'il est important d'explorer des approches toujours plus variées, dans l'espoir de pouvoir en tirer de nouvelles connaissances sur les mécanismes écosystémiques.

Cette thèse vise donc à répondre à différentes problématiques en utilisant de nouvelles approches au sein de différents cadres thématiques comme : le cumul d'impacts, le fonctionnement et la résilience des écosystèmes, la planification spatiale des territoires et les services écosystémiques.

En utilisant des indices ENA pour étudier les effets du cumul d'impacts sur le fonctionnement et l'organisation des écosystèmes (**chapitre 1 et chapitre 2B**), nous avons pu, pour la première fois, utiliser une approche intégrative d'analyse fonctionnelle des écosystèmes dans un contexte d'évaluation des effets du cumul d'impacts. Ainsi, nous avons pu réaliser, comme demandé par la communauté scientifique (Boyd and Hutchins, 2012; Gissi *et al.*, 2021), une analyse plus fonctionnelle des effets cumulés sur les écosystèmes. Malgré les références au cumul d'impacts dans des travaux d'analyse des réseaux écologiques (Tomczak *et al.*, 2013; Heymans and Tomczak, 2016), c'est la première fois que les indices ENA sont utilisés pour cela. Nous avons montré la grande complexité des processus interactifs menant à des effets cumulés sur le fonctionnement des écosystèmes (**chapitre 1 et chapitre 2B**). Les mécanismes produisant ce cumul apparaissent comme nombreux et semblent très spécifiques à l'écosystème étudié et à son fonctionnement, mais également aux effets des différents facteurs de changement environnementaux sur les écosystèmes. Comparé aux analyses plus structurelles sur le cumul d'impacts (Travers-Trolet *et al.*, 2014; Fu *et al.*, 2018), une analyse fonctionnelle du cumul nous permet de déterminer les effets sur les grands processus écosystémiques qui jouent un rôle important dans le maintien des systèmes, mais également d'avoir une vision plus large et intégrative.

Grâce à l'analyse spatialisée des indices ENA et à la vision fonctionnelle spatialisée qu'ils nous offrent de l'écosystème (**Chapitre 2A**), nous avons une vision plus appliquée, pouvant permettre une meilleure planification de l'espace marin côtier (**Chapitre 2A et chapitre 3**). En effet, grâce à ces approches, on peut définir des espaces d'importance stratégique pour les

territoires (**Chapitre 2A et Chapitre 3**), mais aussi délimiter des espaces potentiellement à risque et nécessitant une attention toute particulière (**Chapitre 2A**). En regardant le fonctionnement des écosystèmes, nous avons également pu donner des pistes sur de possibles actions de mitigation des effets du changement climatique à une échelle plus locale (**Chapitre 3**), chose souvent mise en avant par rapport à une gestion uniquement globale de ces effets (Engel, 2006; Ireland and Clausen, 2019). Ces actions locales étant fortement liées aux spécificités régionales des écosystèmes, elles sont difficilement généralisables à différents écosystèmes, de par leurs différences structurelles et fonctionnelles. Il est donc nécessaire de développer des outils capables d'extrapoler des scénarios de changement des écosystèmes, tout en prenant en compte les spécificités fonctionnelles locales des écosystèmes, afin de pouvoir tester de telles solutions de mitigation. C'est une innovation importante pour permettre une gestion plus spécifique des territoires locaux, pouvant s'intégrer dans une plus grande dynamique, comme par exemple à l'échelle d'une façade entière. Les indices ENA peuvent en effet être utilisés pour caractériser des modifications localisées des écosystèmes, mais aussi des modifications à de plus larges échelles géographiques (van Leeuwen *et al.* 2014; Oakley *et al.* 2018). L'interopérabilité spatiale des indices ENA en fait des outils idéaux pour relier les initiatives de gestion locale aux grands plans de gestion, en cherchant à plusieurs échelles un objectif commun de management des écosystèmes.

2 Les limites des travaux de modélisation et les modifications possibles.

Tout expérimentateur doit être conscient des limites de son travail, surtout quand il s'agit de modéliser des systèmes aussi complexes que les écosystèmes (Hipsey *et al.*, 2020). Il est important d'identifier les limites de ses travaux afin de mieux interpréter les résultats dans le contexte approprié. Cela donne également un aperçu des améliorations possibles et nécessaires pour mieux développer les approches et les méthodes de modélisation des écosystèmes, pour rendre la communauté des modélisateurs écologues plus efficace. Il existe différents types de limites en modélisation (Hawkins and Sutton, 2009), limites qui peuvent être partitionnées en : (1) limites associées à l'incertitude autour de la variabilité du vivant (comme par exemple en fonction de la plasticité alimentaire de certaines espèces), (2) limites autour de l'incertitude des scénarios modélisés (comme par exemple autour des scénarios de

changement climatique et de la variabilité des modèles de circulation), et enfin (3) des limites autour des méthodes de modélisation (comme par exemple entre Ecopath et le LIM).

Dans cette partie nous allons principalement aborder les limites associées à la modélisation des facteurs anthropiques comme le changement climatique et le parc éolien de Courseulles-sur-Mer. Nous n'aborderons pas les limites associées à la modélisation de l'écosystème avec des approches de modélisation différentes. En effet, les modèles Ecopath et LIM à la base des différents chapitres de cette thèse furent validés préalablement à travers : des analyses isotopiques et des comparaisons avec des données expérimentales (Araignous *et al.*, 2019). Seul le modèle Ecospace de Halouani *et al.* (2020) n'a pas été validé au vu des difficultés de réaliser un tel objectif (Halouani *et al.*, 2020). Néanmoins, des dires d'experts furent utilisés pour valider les sorties du modèle Ecospace, ainsi que des modèles de niche utilisés pour forcer la distribution des espèces dans le modèle Ecospace de la baie de Seine étendue (com. pers. Jean-Claude Dauvin, Jean-Paul Robin et Éric Foucher).

2.1 Les limites de la modélisation du changement climatique

Modéliser les effets du changement climatique avec des modèles écosystémiques s'accompagne inévitablement d'un grand nombre de limites liées à la complexité et à l'incertitude autour des effets du changement climatique sur les écosystèmes. Modéliser les évolutions possibles de ces systèmes complexes, dont les dynamiques peuvent être mal comprises, nécessite donc souvent de mettre en place de fortes hypothèses sur les conséquences du changement climatique (modification de la température, de l'oxygénation, de l'acidité de l'eau ...) et de leurs effets sur le vivant (Kendall *et al.*, 2004; Araújo and Luoto, 2007; Holt *et al.*, 2016; Payne *et al.*, 2016). Il appartient donc au modélisateur de faire des choix sur la démarche méthodologique, tout en considérant les limites de cette dernière. Ainsi, dès le **premier chapitre** de thèse, plusieurs limites ont été soulevées suite à la modélisation des effets du changement climatique avec la méthode de Chaalali *et al.* (2016) :

- (1) Tout d'abord, l'hypothèse principale faite pour modéliser l'effet du changement climatique dans le **premier chapitre** est que les biomasses des espèces de la baie suivent l'évolution de leur niche théorique. En effet, on considère l'évolution de la biomasse des espèces comme étant proportionnelle à l'évolution de l'indice de confort (suitability index des modèles de niche) qui modélise la niche théorique des espèces

(entre la niche potentielle et la niche réelle, Figure VI - 1 : Jiménez-Valverde *et al.* 2008; Soberón and Nakamura 2009; Jiménez *et al.* 2019). Ce forçage est donc critiquable car la biomasse des espèces suit la niche réalisée des espèces, niche qui ne dépend pas uniquement des paramètres environnementaux comme la température, la salinité et la typologie du sédiment (paramètres sédimentaires à voir dans le **chapitre 1**), mais qui dépend aussi de paramètres biotiques comme : les interactions trophiques, la compétition, le parasitisme, les maladies, les traits d'histoire de vie des espèces et de bien d'autres paramètres (Jackson and Overpeck, 2000; Prinzing *et al.*, 2002; Hirzel and Le Lay, 2008; Pearman *et al.*, 2008). Ici, il s'agit donc d'une limite de mon approche associée aux scénarios réalisés, et à la méthode de modélisation choisie.

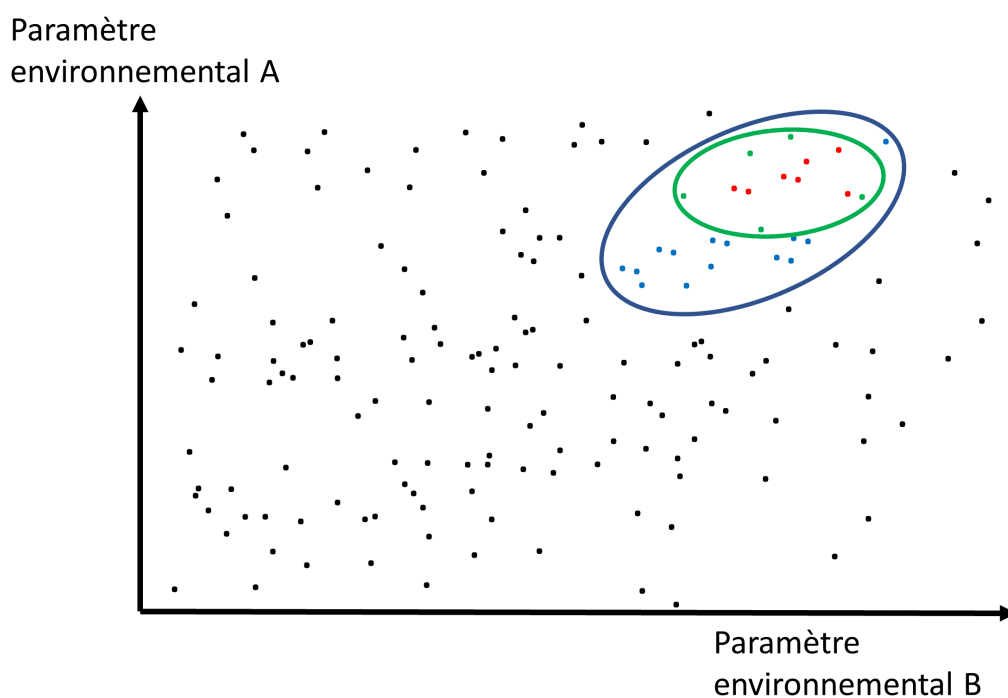


Figure VI - 1 Schéma représentant les différents types de niche écologique d'une espèce dans un espace de paramètres géoclimatiques composé de deux paramètres (A et B).

Le nuage de points représente l'espace des conditions géoclimatiques possibles. La niche fondamentale est représentée par l'ellipse bleue. Les points dans l'ellipse bleue représentent la niche potentielle ou existante. La niche théorique est représentée par l'ellipse verte et les points à l'intérieur. La niche réalisée est représentée par les points rouges.

- (2) Les effets du changement climatique ont été modélisés sur un nombre réduit de groupes écologiques. Ceci a permis une analyse de sensibilité détaillée des effets du changement climatique sur différents compartiments ciblés (voire **Chapitre 1**). Néanmoins, cette approche ne permet pas de caractériser l'effet potentiel du changement climatique sur l'intégralité de l'écosystème, et particulièrement, les effets induits par les différentes cinétiques de déplacement des espèces vers le nord. En effet, à l'échelle de tout un écosystème, cet effet a un rôle particulièrement important sur les interactions formant la structure des écosystèmes. De plus, cet effet est très spécifique au système étudié, car dépendant des différentes préférences environnementales des espèces de l'écosystème (Araújo and Luoto, 2007; Schiel *et al.*, 2014). Il s'agit donc d'une limite attribuée au scénario modélisé.
- (3) Pour des soucis de praticité et de temps de calcul, les résultats des modèles de niche ont été moyennés pour forcer les biomasses. Ce faisant, on moyenne les résultats des différents modèles de circulation généraux utilisés pour projeter l'effet du changement climatique sur les paramètres climatiques, ainsi que les résultats des différents algorithmes de modèles de niche utilisés pour corréliser les paramètres géoclimatiques à la distribution des espèces (Ben Rais Lasram *et al.*, 2020). On ne prend donc pas en compte la variabilité des résultats des modèles de niche, et donc l'incertitude autour des résultats. Néanmoins, Bourdaud *et al.* (2021) qui a pris en compte cette variabilité (mais sans pouvoir calculer des indices ENA), montre que les tendances restent les mêmes entre les différents résultats des modèles, indiquant qu'une analyse autour de la moyenne est représentative des résultats des modèles de niche.
- (4) Finalement une autre limite importante de la modélisation des effets du changement climatique dans le **premier chapitre de thèse** est la non prise en compte de l'arrivée d'espèces non-indigènes (espèces dites NIS). Effectivement, si les effets du changement climatique sur les aires de répartition des espèces sont censés pousser les espèces de la baie vers le nord, alors qu'en est-il des espèces au sud de la baie ? On s'attend donc à une dérive des espèces vers le nord, qu'elles soient des espèces tempérées, subtropicales ou tropicales, poussant graduellement à un grand remplacement des communautés dû au changement climatique (Perry *et al.*, 2005; Comte and Grenouillet, 2013; Vanderwal *et al.*, 2013). Néanmoins, durant la réalisation

du **premier chapitre** de thèse, aucun travail n'avait été fait pour étudier l'arrivée potentielle d'espèces NIS en baie de Seine à cause des effets du changement climatique.

On voit donc que les limites autour de la modélisation des effets du changement climatique sont majoritairement liées aux scénarios et aux méthodes associées à la simulation de ces scénarios. C'est dans l'objectif de combler ces limites, que pour le **second chapitre** de thèse, j'ai utilisé de nouvelles méthodes compatibles avec l'approche *Ecopath with Ecosim*, pour améliorer la modélisation des scénarios de changement climatique sur le modèle Ecospace de la baie de Seine étendue. Tout d'abord, c'est grâce aux travaux de Bourdaud et al. (2021) que les effets du changement climatique purent être modélisés sur tous les groupes écologiques de la baie de Seine étendue. Néanmoins, Bourdaud *et al.* (2021) utilise la même approche que Chaalali *et al.* (2016) et Nogues *et al.* (2020).

Différentes méthodes ont été mises en place durant la thèse pour pallier aux limites de l'approche de Chaalali *et al.* (2016). L'objectif de ces méthodes était de ne plus forcer directement la biomasse des espèces avec les résultats des modèles de niche, pour ne plus relier la niche théorique des espèces à leur biomasse. Pour cela nous avons cherché à relier les résultats des modèles de niche aux rythmes physiologiques des espèces (Gillooly *et al.*, 2001). Sachant que les espèces tendent à avoir un taux de croissance positif dans leur niche fondamentale (Hutchinson, 1957), nous avons fait l'hypothèse que les espèces produisent le plus au centre de leur niche fondamentale (optimum des paramètres géoclimatiques). Au contraire, plus les espèces se trouvent aux limites de leur niche fondamentale, alors moins elles sont productives. En théorisant que la niche théorique calculée par les modèles de niche se rapproche de la niche fondamentale (Soberón and Nakamura 2009; Jiménez *et al.* 2019), on peut donc relier l'indice de confort à la production des espèces, et non plus à leur biomasse. Ainsi si l'indice de confort diminue suite à une modification des paramètres géoclimatiques, du fait du changement climatique, alors c'est que les paramètres géoclimatiques de l'environnement deviennent de moins en moins appropriés aux espèces, et donc que leur production diminue. L'avantage de cette approche c'est que, si on ne force pas la biomasse mais juste la production des espèces, alors les interactions biotiques peuvent jouer un rôle dans la dynamique des biomasses des espèces. Ainsi, si une espèce voit son indice de confort diminuer, mais que la disponibilité de ses proies augmente, alors elle peut théoriquement

conserver une biomasse importante, en augmentant sa consommation (plus de proies, plus d'opportunités de consommer). En prenant en compte les relations biotiques, on se rapproche donc un peu plus d'une estimation de la niche réelle (Davis *et al.*, 1998). Cette même niche réelle peut avoir une forme complexe, ce qui peut éloigner le centre de la niche réelle du centre de la niche fondamentale (et donc de la niche théorique dans notre hypothèse). Cet éloignement émane de processus comme les interactions biotiques.

Dans Ecospace, la méthode la plus adaptée pour modifier la production d'un groupe trophique en fonction de l'indice de confort consiste à relier l'indice de confort des espèces qui le composent à la capacité des habitats d'Ecospace (Habitat capacity, voir **Chapitre 2 A** ou Christensen *et al.* 2014). La capacité des habitats est un indice calculé à partir des cartes environnementales (environmental drivers) et est utilisée dans Ecospace pour paramétrer la distribution des groupes écologiques dans le modèle. Cette capacité, à l'origine des théories sur les « foraging arenas », joue sur les paramètres de prédation des espèces et donc sur leur consommation, qui *in fine* influence la production en fonction de l'habitat (Christensen *et al.* 2014). Le problème est que la version standard d'Ecospace ne permet pas de modifier la capacité des habitats, par rapport à un point de référence. Il est donc impossible de changer cette capacité pour refléter les effets du changement climatique sur la convenance des habitats pour les groupes écologiques, par rapport au modèle « current » représentant l'écosystème actuel. Pour contourner cette limitation, nous avons commencé par modifier les modèles Ecopath à la base des modèles Ecospace, pour refléter les effets des modifications des indices de confort sur les rythmes physiologiques des groupes. Ce processus extrêmement fastidieux fut abandonné courant 2020, car nous avons eu accès à la spatial-temporal dataframe de la nouvelle version pro d'*Ecopath with Ecosim* (Steenbeek *et al.* 2013). Cet outil d'Ecospace permet d'intégrer dans le temps, des modifications des entrées d'Ecospace. Ainsi en utilisant des cartes d'indices de confort sans effet du changement climatique en entrée d'Ecospace (environmental driver), puis en intégrant des cartes d'indice de confort avec effet du changement climatique avec la spatial-temporal dataframe (comme nouvelles cartes d'environnemental driver), on peut simuler l'effet du changement climatique sur la convenance des habitats des groupes écologiques. Ainsi, les modèles de niche ne viennent pas directement forcer la biomasse des groupes (voir Christensen *et al.* 2014 ; Coll *et al.* 2016),

mais jouent sur la consommation et la production des groupes, éliminant la relation entre la biomasse et l'indice de confort utilisée dans le **premier chapitre**.

La dernière limite à résoudre, suite au **premier chapitre de thèse**, était l'arrivée d'espèces NIS dans le modèle depuis des écosystèmes plus au sud. Pour explorer ce point, 211 nouveaux modèles de niche furent réalisés en utilisant les mêmes approches développées durant le projet TROPHIK (Ben Rais Lasram *et al.*, 2020), d'après une liste d'espèces fournie par Le Marchand *et al.* (2020). Ces modèles avaient pour objectif d'extrapoler l'effet du changement climatique sur les aires de répartition de 211 espèces des côtes méditerranéennes et africaines en utilisant la projection RCP 8.5 de l'IPCC, avec 3 modèles de circulation générale (General Circulation Model ou GCM). Les 211 espèces ont été choisies en collaboration avec Marie Le Marchand qui étudiait l'arrivée de potentielles espèces NIS depuis les côtes africaines et méditerranéennes en golfe de Gascogne (Le Marchand, 2020). Ces 211 espèces ont donc été sélectionnées à cause de leur forte probabilité d'arriver sur les côtes françaises. En moyenne, les résultats des modèles de niche indiquèrent qu'avec l'effet du changement climatique seulement 11 des 211 espèces présentaient une augmentation de leur indice de confort dans la baie de Seine. Sur ces 11, seulement une espèce présentait une augmentation de son indice de confort supérieure à 5% (*Lagocephalus lagocephalus*).

Comment expliquer qu'une seule espèce n'a présenté une augmentation importante de son indice de confort dans la baie de Seine ? Cela peut être attribué au fait que le changement climatique ne réunit pas les conditions nécessaires pour que d'autres espèces voient leur aire de répartition arriver dans baie de Seine ou bien, que les modèles de circulation utilisés pour estimer l'évolution des paramètres climatiques ne sont pas adaptés. En effet, pour estimer l'évolution des paramètres climatiques dans le futur, on a utilisé plusieurs modèles de circulation générale. Ceux issus du CMIP5 (Coupled Model Intercomparison Project Phase 5) (Taylor *et al.*, 2012) comprennent : ESM2G (Geophysical Fluid Dynamics Laboratory; NOAA), CM5A-MR (Institut Pierre-Simon-Laplace) et ESM-MR (Max-Planck-Institut für Meteorologie). Ils permettent d'estimer les évolutions possibles des paramètres climatiques, utilisés pour estimer le changement des aires de répartition des espèces en fonction de leurs courbes de réponses. Pour estimer les évolutions possibles des paramètres climatiques, les modèles de circulation prennent en compte de nombreux mécanismes globaux (activité volcanique, cycle du carbone, couverture glaciaire et autres). Les modèles de circulation prenant en compte des

paramètres différents (Taylor *et al.*, 2012), ils peuvent avoir des réponses différentes en fonction de l'environnement, par exemple pour des zones complexes comme les côtes (Fernández *et al.*, 2015). Des modèles de circulation plus adaptés aux milieux côtiers pourraient ainsi être nécessaires pour mieux simuler les évolutions climatiques dans ces habitats et ainsi mieux modéliser les évolutions des distributions des espèces.

Parmi les 11 espèces présentant une augmentation de leur indice de confort, 10 possédaient déjà un indice de confort supérieur à 90 % dans la baie de Seine, sans effet du changement climatique, alors même qu'elles ne sont pas présentes actuellement dans la baie. Ainsi, comme beaucoup des espèces choisies possédaient déjà un indice de confort élevé dans la baie de Seine, comment choisir les espèces à intégrer dans le modèle pour simuler l'arrivée d'espèce NIS ? Et quelle biomasse faire arriver dans le modèle ? Si les modèles de niche prédisent que ces espèces doivent, théoriquement, déjà être dans la baie de Seine, alors c'est que les modèles de niche ne prennent pas en compte des paramètres limitant l'arrivée de ces espèces. Il existe plusieurs paramètres qui peuvent expliquer cette situation :

- Des paramètres abiotiques : Certains paramètres comme la turbidité, l'acidité et le taux en oxygène dissous n'ont pas été pris en compte dans les modèles de niche utilisés pour tester l'arrivée d'espèces NIS durant ma thèse (Ben Rais Lasram *et al.*, 2020). Ne pas prendre en compte des paramètres pouvant avoir un rôle important dans la distribution des espèces peut avoir un effet négatif sur les capacités prédictives des modèles de niche. Néanmoins, au vu des espèces et des paramètres environnementaux de la baie, ainsi que des effets du changement climatique sur ces paramètres, ceci ne semble pas pouvoir expliquer pourquoi, sur 211 espèces, seulement 1 présente une véritable augmentation de son indice de confort dans la zone.
- Les stades juvéniles : Les modèles de niche ne prenant pas explicitement en compte les stades juvéniles, des espèces pourraient apparaître comme adaptées aux conditions géoclimatiques de la zone, mais leur stade juvénile ne le serait pas (Le Marchand *et al.*, 2020), entravant leur cycle de vie dans l'habitat (Hijuelos *et al.*, 2016).
- Les traits fonctionnels : parmi les 211 espèces testés, certaines aujourd'hui absentes de la baie de Seine, comme le poulpe (*Octopus vulgaris*), habitaient la baie dans le passé

(Rees and Lumby, 1954). Suite à des changements environnementaux (modification des conditions géoclimatiques, changement des pressions de pêche ou autre), ces espèces ont disparu de la baie de Seine. La question de leur retour dépend alors de leur capacité à se réimplanter dans l'écosystème de la baie et à trouver une « place » dans l'écosystème. Si elles sont bloquées par des barrières x ou y , il faut pouvoir les identifier et estimer leurs potentielles évolutions. Ces barrières peuvent être multiples : il peut s'agir des capacités adaptatives des espèces (plasticité de sa niche écologique), des relations biotiques avec les autres espèces de l'environnement d'arrivée (compétition avec d'autres, disponibilité en ressources dans l'écosystème) ou bien de l'environnement de départ (symbiose, mutualisme, commensalisme). Déterminer la place à donner à une espèce dans un nouvel habitat constitue l'une des problématiques principales de la modélisation de l'arrivée d'espèces NIS. En prenant en compte les traits fonctionnels des espèces, des méthodes ont permis de caractériser le potentiel d'une ou de plusieurs espèces à s'implanter ou se réimplanter dans un milieu (Albouy *et al.*, 2011; Willis *et al.*, 2015), mais également de définir son rôle dans l'écosystème et donc dans le réseau trophique (Albouy *et al.*, 2011; Green and Côté, 2014; Nagelkerke *et al.*, 2018).

Modéliser l'arrivée d'espèces NIS est d'autant plus problématique que les modèles trophiques définissent les interactions trophiques entre les espèces, moteur de la dynamique des systèmes, en paramétrant la matrice des régimes alimentaires grâce à des données *in situ* ou bibliographiques. Pour cela, il faut savoir quelles espèces pourraient être consommées par les espèces NIS, mais également quelles espèces pourraient les consommer (Albouy *et al.*, 2011). De plus ceci doit être fait *a priori* et donc sans information sur la zone d'intérêt.

Déterminer la matrice des régimes alimentaires n'est pas la seule problématique, en effet il faut pouvoir déterminer une biomasse initiale pour les espèces NIS dans le nouvel habitat, ainsi que son évolution dans l'habitat (Langseth *et al.*, 2012). Déterminer la dynamique de cette biomasse est donc également un défi en soit, car cette dynamique est intrinsèquement liée aux relations proies/prédateurs et à la vulnérabilité des proies aux prédateurs et *vice versa* (Corrales *et al.*, 2017). Pour bien faire, il faut tester différents scénarios de vulnérabilité proies/prédateurs, ce qui peut rajouter beaucoup d'incertitudes et surtout, nécessiter la mise en place d'un grand nombre de modèles. Or, étudier le cumul d'impacts est

déjà une tâche complexe, qui nécessite un nombre important de scénarios en soi, pour déterminer les effets séparés, les effets combinés et *in fine* les effets cumulés de multiples facteurs anthropiques. C'est pour cette raison que, malgré les limites associées à la non modélisation des espèces NIS (Le Marchand *et al.*, 2020), nous avons décidé de ne pas les prendre en compte durant cette thèse et plutôt de s'y concentrer en perspective.

2.2 Les limites de la modélisation des effets d'un parc éolien.

Les parcs éoliens en mer peuvent engendrer une grande variété d'effets pouvant affecter les organismes marins. Ces effets peuvent être départagés en fonction de la phase d'exploitation du parc, avec trois grandes phases ayant été déterminées dans la littérature : la phase de construction, la phase d'opération et la phase de démantèlement (Koeller *et al.*, 2006; Inger *et al.*, 2009; Riefolo *et al.*, 2016). Chacune de ces phases est associée à différents effets, plus ou moins forts, et affectant une partie plus ou moins importante de l'écosystème. De nombreuses études ont énuméré ces effets (Inger *et al.*, 2009; Masden *et al.*, 2009; Lindeboom *et al.*, 2011; Raoux *et al.*, 2017), néanmoins il n'y a pas de véritable consensus sur la phase la plus dangereuse pour les écosystèmes (Shields and Payne, 2014). Cependant, plusieurs travaux établissent que la phase d'opération du parc, la phase la plus longue, comme la plus structurante sur les écosystèmes et impactant une grande variété d'espèces (Petersen and Malm, 2006; Langhamer, 2012; Dannheim *et al.*, 2020; Degraer *et al.*, 2020). Parmi ces effets, on peut citer l'effet récif et l'effet réserve potentiels de la phase opérationnelle. C'est pour cette raison que ces derniers furent modélisés par Aurore Raoux durant sa thèse sur une étude écosystémique des impacts du futur parc éolien de Courseulles-sur-Mer. Les effets réserve et récif ont été modélisés durant la totalité de cette thèse et leurs effets structurants sur le système de Courseulles-sur-Mer apparaissent comme moteur du cumul d'impacts et des effets cumulés (**Chapitre 1**). A l'échelle écosystémique, les effets récif et réserve d'un parc éolien jouent donc un rôle prépondérant sur le fonctionnement de l'écosystème.

Néanmoins, si l'intérêt d'un expérimentateur est d'étudier les effets du parc à plusieurs niveaux d'organisation, comme par exemple pour étudier ses effets sur un groupe écologique en particulier ainsi que sur tout le système, alors les effets les plus importants du parc peuvent changer en relation avec le point de vue de l'expérimentateur. Ainsi, dans le **troisième chapitre** de thèse, on a regardé les effets du parc de Courseulles-sur-Mer sur la résilience de

l'écosystème et sur des espèces patrimoniales comme les oiseaux marins. Tandis que l'effet le plus important du parc sur la résilience écosystémique semble être l'effet réserve et surtout récif du parc (Raoux *et al.*, 2019; Wang *et al.*, 2019; Nogues *et al.*, 2020), les effets les plus importants du parc sur les oiseaux marins sont : le risque d'impact et l'évitement de la zone par certaines espèces d'oiseaux (Camphuysen *et al.*, 2004; Blew *et al.*, 2008; Furness *et al.*, 2013). Pour analyser le rôle du parc éolien sur la fourniture en services écosystémiques pour l'homme, il faut donc modéliser les effets du parc aux niveaux d'organisation qui nous intéressent : à l'échelle de l'écosystème mais aussi des groupes écologiques d'intérêts. Même si les résultats obtenus durant le **troisième chapitre** de la thèse suivent certaines observations (Lindeboom *et al.*, 2011; Scheidat *et al.*, 2011), il est important d'adapter les modèles et les scénarios de modélisation afin de rendre nos scénarios plus réalistes et donc plus opérationnels. Les travaux récents réalisés sur le sujet nous montrent que des méthodes existent et qu'elles sont parfaitement adaptables à notre cas d'étude (Serpetti *et al.*, 2021). C'est donc une piste d'amélioration du modèle possible pour la suite des travaux en baie de Seine mais également sur d'autres systèmes. Tous ces effets pourraient également être repris afin de tester les effets de la multiplication des parcs éoliens en baie de Seine étendue, sur l'écosystème et sa fourniture en services écosystémiques (voir **chapitre supplémentaire**).

Une autre limite mise en avant par la modélisation des effets du parc éolien de Courseulles-sur-Mer est la différence de réponse entre le LIM du **premier chapitre** de thèse et le modèle Ecospace du **deuxième chapitre** de thèse. La différence la plus importante concerne l'effet du parc éolien sur le recyclage de l'écosystème (Finn Cycling Index), avec le modèle LIM indiquant une augmentation du recyclage et le modèle Ecospace, une réduction du recyclage. Cette différence est due à la différence de fonctionnement des deux approches, à leur emprise spatiale différente, ainsi qu'aux différents effets modélisés entre le modèle LIM et le modèle Ecospace. Ainsi, le LIM ne modélise que l'effet récif alors que Ecospace mesure également l'effet réserve induit par le parc éolien sur les activités de pêche. Les modèles ne prennent également pas en compte la même emprise spatiale, avec le modèle LIM représentant uniquement le système du parc éolien, alors qu'Ecospace prend en compte l'intégralité de la baie de Seine étendue. Cette différence d'échelle joue un rôle important sur la modélisation des interactions entre l'écosystème du parc et le reste de la baie. Dans le modèle Ecospace, le parc est modélisé dans le continuum de la baie de Seine étendue, les arrivées d'espèces

bénéficiant de l'effet récif et réserve dépendent donc de l'écosystème environnant et des échanges avec le reste de la baie. *A contrario*, dans le modèle LIM, les biomasses des espèces bénéficiant de l'effet récif ont été forcées grâce à des observations faites sur d'autres parcs éoliens en mer du Nord, recroisées avec les experts de l'écosystème local (Raoux *et al.*, 2017). L'effet récif et réserve dans le modèle Ecospace s'apparente donc plus à un effet agrégatif du parc sur des espèces de la baie. Cela se traduit par une augmentation plus faible de la biomasse des bivalves dans le modèle Ecospace que dans le modèle LIM, et par une plus grande augmentation de la biomasse de poissons mangeurs de benthos dans le modèle Ecospace par rapport au modèle LIM (poissons plats et autres poissons consommateurs de benthos, Table SII - 6 & Figure SII - 14 , **chapitre 2A**, Raoux *et al.* 2017). Une façon de rendre les résultats plus homogènes entre les deux approches serait de forcer la biomasse des bivalves dans le modèle Ecospace en fonction des observations faites chez Raoux *et al.* (2017) en utilisant des plugins d'*Ecopath with Ecosim* comme le plugin « Biomass emitter ». Un plugin est une extension du logiciel *EwE* qui permet d'ajouter des fonctionnalités. Dans le cas de « Biomass emitter », c'est un plugin qui permet de forcer une biomasse dans des cellules du modèle spatialisé Ecospace. On pourrait l'utiliser afin de forcer la biomasse des bivalves dans la zone du parc pour atteindre les biomasses attendues dans Raoux *et al.* (2017).

Identifier les limites des approches utilisées permet ainsi de proposer des améliorations pour les travaux à venir. Néanmoins, certaines améliorations peuvent nécessiter de repenser nos approches depuis leurs fondations, afin d'améliorer la modélisation des écosystèmes en l'intégrant au sein d'un cadre méthodologique plus large, pour se tourner vers une modélisation globale des systèmes.

3 Recommandations et perspectives.

3.1 Les combinaisons d'approches.

Pour prendre en compte une plus grande variété d'effets de facteurs anthropiques complexes comme le changement climatique, il est nécessaire d'utiliser des outils capables de nous aider à mieux comprendre les effets des modifications de l'environnement sur les écosystèmes. En couplant un modèle trophique avec des modèles de niches nous avons pu prendre en compte les effets du changement de paramètres géoclimatiques sur les aires de répartition d'espèces de la baie de Seine. En utilisant d'autres approches spécialisées dans la

simulation de différents processus environnementaux, on pourrait améliorer la prise en compte des effets du changement climatique. Une approche combinée utilise donc différents outils pour comprendre les modifications des écosystèmes. Il est également possible de lier entre elles différentes méthodes de modélisation environnementales, afin de prendre en compte les interactions entre les systèmes anthropologiques, géochimiques et climatiques avec les écosystèmes (voire Shin and Cury 2004; Fulton *et al.* 2007; Maury *et al.* 2007), afin de mettre en place une modélisation globale des systèmes (Fulton, 2010). Ces approches dites end-to-end se différencient du reste des approches combinées car elles associent environnement et écosystème et prennent en compte les liens bilatéraux entre les deux systèmes. Prendre en compte ces liens bilatéraux entre écosystème et environnement peut être très complexe et très lourd à calculer. De ce fait, beaucoup d'études modélisent uniquement des interactions à sens unique, de l'environnement à l'écosystème (fonctions de forçage), en ignorant les rétroactions potentielles, ce qui s'apparente à une approche combinée plus « classique » (exemple Lefort *et al.* 2015)

Avec le couplage de différents outils, nous pourrions inclure les effets potentiels du changement climatique sur les rythmes biogéochimiques de la baie de Seine et ainsi prédire l'évolution possible de la production primaire et ses effets sur l'écosystème (Vichi *et al.*, 2007; Butenschön *et al.*, 2016; van Der Molen *et al.*, 2017). On pourrait également parfaire la modélisation d'autres facteurs, comme l'effet du parc éolien de Courseulles-sur-Mer, en utilisant des modèles hydrodynamiques pour déterminer l'effet du parc éolien sur des espèces de poissons en baie de Seine (Bednarek *et al.*, 2020), ainsi que les effets du parc sur la structure sédimentaire local (Jones *et al.*, 2020). Il existe déjà plusieurs types de modèles qui pourraient potentiellement être utilisés avec le modèle Ecospace de la baie de Seine. Des modèles biogéochimiques comme ERSEM (van Der Molen *et al.*, 2017), ERSEM II (Baretta-Bekker *et al.*, 1997; Ebenhöh *et al.*, 1997; Fulton *et al.*, 2004) et PISCES (Aumont *et al.*, 2015) pourraient être couplés de différentes façons avec le modèle Ecospace de la baie de Seine étendue, afin de permettre une meilleure prise en compte des effets du changement climatique sur les bas niveaux trophiques de l'écosystème. Ce couplage pourrait être fait en forçant le modèle Ecospace avec des sorties de modèles biogéochimiques (Bauer *et al.*, 2019). Ceci permettrait de prendre en compte les potentiels effets bottom-up du changement climatique, en plus des effets sur la distribution des espèces, et ainsi voir les interactions entre les deux effets.

Le couplage de modèles présente de nombreux avantages pour modéliser la dynamique des systèmes côtiers et marins ; néanmoins, il convient de bien prendre en compte les limites pouvant apparaître d'un tel couplage. En effet, comme nous avons pu le voir durant cette thèse, chaque modèle complémentaire rajouté au cadre méthodologique apporte son lot d'incertitudes et de complexités. Cette incertitude et cette complexité rendent l'interprétation des résultats de plus en plus complexe, défi d'autant plus important dans le cadre de l'étude des effets cumulés de plusieurs facteurs de changements écosystémiques. Les résultats obtenus sont donc souvent utilisés pour estimer des tendances plutôt qu'à des fins tactiques, dans le but d'obtenir des valeurs absolues, associées au changement des écosystèmes (Fulton, 2010). Comme dans nos travaux de thèse, les contraintes méthodologiques d'une approche combinée (temps de calcul, puissance de calcul nécessaire, complexité d'analyse) entrent en conflit avec la masse d'informations disponibles, ce qui nécessite de faire des concessions sur la densité d'informations prises en compte lors de l'interprétation. Cela a été particulièrement visible durant les travaux de thèse avec la difficulté d'utiliser l'incertitude autour des résultats des modèles de niche, au vu du temps important de calcul des indices ENA, et du fait qu'Ecospace ne permet pas de prendre en compte de manière explicite l'incertitude autour des cartes environnementales. De plus, la complexité grandissante induite par l'ajout de nouvelles approches de modélisation peut nuire à la compréhension des résultats. C'est d'autant plus important que l'étude du cumul d'impacts apporte son lot de complexité, qui peut également nuire à la compréhension des processus. L'une des façons de simplifier les approches pour faciliter leur compréhension est d'alléger la méthode. Cela peut passer par une simplification du modèle écosystémique, comme par exemple en réduisant le nombre de groupes écologiques (modification de l'agrégation des espèces du réseau trophique), tout en essayant de garder un maximum d'information structurelle sur les écosystèmes.

Le choix d'agrégation est d'autant plus important qu'il a été démontré que des modèles mettant en avant des parties spécifiques des réseaux trophiques, par exemple un groupe d'organismes spécifiques, à travers une structuration asymétrique des réseaux, peuvent présenter des propriétés fonctionnelles nettement différentes de modèles qui ont une structure plus homogène (Pinnegar *et al.*, 2005). Par exemple, des modèles agrégés de manière à mettre l'accent sur les invertébrés benthiques, étaient bien plus résilients aux changements environnementaux que des modèles mettant l'accent sur les poissons (Pinnegar *et al.*, 2005).

En préparant une agrégation fonctionnelle homogène, on peut ainsi réduire la complexité des systèmes et simplifier l'utilisation d'approches couplant plusieurs méthodes. Une grande variété d'approches peuvent être adoptées pour définir les groupes écologiques d'un modèle (Pauly *et al.*, 2000; Shin and Cury, 2001; Fulton *et al.*, 2005; Maury *et al.*, 2007). Les composantes écologiques de nombreux modèles sont des groupes écologiques/fonctionnels, partageant une écologie et des interactions trophiques similaires, comme dans les modèles linéaires inverses LIM ou bien les modèles *Ecopath with Ecosim*. Néanmoins, ces groupes écologiques sont souvent mélangés à des groupes définis au niveau de l'espèce ou même du stock (groupe des coquilles Saint-Jacques dans **le premier chapitre** de thèse). Ce mélange peut jouer en faveur d'un déséquilibre du modèle, vers une partie du réseau trophique (pour la coquille Saint Jacques, les invertébrés filtreurs). Néanmoins, agréger les groupes de cette manière possède également l'avantage de pouvoir répondre à des questions de gestion locale des ressources d'intérêt commercial ou pour la conservation d'espèces particulières.

Pour pallier à cette limite, nous avons donc besoin d'une nouvelle méthode d'agrégation des modèles écologiques, qui puisse prendre en compte la spécificité fonctionnelle des espèces, tout en évitant un déséquilibre. En définissant une nouvelle méthode de d'agrégation des modèles écosystémiques, interopérable entre différents écosystèmes côtiers et en encourageant l'utilisation d'une typologie et d'un niveau d'organisation commun, on pourrait ainsi faciliter la comparaison des résultats des modèles, afin d'en extraire les grandes tendances et les grands mécanismes clefs qui entraînent des changements dans les écosystèmes. Dans le cadre spécifique de l'étude du cumul d'impacts, où nous avons vu que ce dernier était fortement dépendant du fonctionnement des systèmes et des facteurs de changement, on pourrait ainsi mettre en avant les grands mécanismes conduisant aux effets cumulés et les comparer entre des modèles partageant une agrégation homogène. Pour recentrer cette agrégation sur les informations fonctionnelles des espèces, nous proposons de se baser sur les traits fonctionnels des espèces (Barton *et al.*, 2013; Stuart-Smith *et al.*, 2013; Willis *et al.*, 2015; Frainer *et al.*, 2017; McLean *et al.*, 2018), afin de grouper les espèces selon différents paramètres prédéfinis *a priori*.

3.2 Groupes écologiques et traits fonctionnels

Baser les groupes écologiques d'un modèle écosystémique sur les traits fonctionnels des espèces peut être fait en fonction des paramètres de leur cycle de vie comme : leur méthode de reproduction, leur habitat (profondeur, type de sédiment ...), leurs relations trophiques (mode d'alimentation) (Table VI - 1). Les groupes seraient alors formés à l'aide d'outils statistiques de groupement afin de regrouper les espèces en fonction de leurs similarités de traits fonctionnels. L'autre avantage de cette approche est que les facteurs anthropiques pouvant impacter l'écosystème pourraient être directement considérés lors de l'agrégation du modèle écosystémique. Ainsi, on peut prendre en compte les préférences thermiques et halines des espèces dans le cas de la simulation des effets du changement climatique, ou la préférence d'habitat des espèces dans le cas de l'étude des effets d'un parc éolien (Table VI - 1). D'autres traits pourraient également être pris en compte afin d'aider à la simulation d'autres facteurs de changement, comme par exemple la sensibilité sonore des espèces lors de l'étude des effets du bruit des activités anthropiques sur l'écosystème (Rakogospic and Picciulin, 2018). En effet, il est important de prendre en compte les implications, les objectifs et les méthodes d'un modèle dès sa mise en place (FAO, 2008). En intégrant ces objectifs dès la définition des groupes écologiques, on permet ainsi de faciliter leur prise en compte dans l'analyse des résultats. De plus, en utilisant une telle approche, on rend les modèles écosystémiques compatibles avec d'autres approches basées sur les traits fonctionnels comme l'évaluation de la vulnérabilité des espèces aux changements climatiques basée sur ces derniers ('Trait-based Vulnerability Assessment' ou VTA). Les approches VTA sont apparentées aux modèles de niche SDM (Species Distribution Models) et peuvent être utilisées en complément, dans l'objectif d'estimer les potentiels effets du changement climatique sur la distribution et le déplacement des espèces (Willis *et al.*, 2015).

Les approches VTA permettent d'évaluer la vulnérabilité des espèces aux effets potentiels du changement climatique sur la base des connaissances disponibles sur leur écologie et leur cycle de vie (traits fonctionnels). Elles identifient les traits qui sont présumés comme détritimentaires face aux impacts potentiels du changement climatique (exemple Gardali *et al.* 2012; Foden *et al.* 2013). Pour ce faire, ces approches prennent en compte : l'exposition aux changements climatiques, la sensibilité aux changements climatiques et les capacités d'adaptation à ces changements (Rowland *et al.*, 2011). En considérant les traits

fonctionnels des espèces, cela permet d'avoir une information, selon les connaissances bibliographiques ou des experts, sur la sensibilité aux changements climatiques ainsi que sur les capacités adaptatives des espèces. Ces approches peuvent également prendre en compte des paramètres extérieurs qui pourraient influencer la capacité d'adaptation d'une espèce (empêchement de la dispersion en raison de barrières environnementales). Couplé avec des approches comme les modèles de niche, on peut ainsi avoir des informations sur les espèces les plus aptes à se déplacer vers de nouveaux habitats et ainsi modéliser l'arrivée potentielle d'espèces NIS dans des modèles écosystémiques, en fonction de leurs traits fonctionnels. En effet, les modèles de niche SDM ne prennent pas en compte les capacités de dispersion et d'adaptation des espèces, mais en couplant SDM et VTA, elles le peuvent (exemple Early and Sax 2011; Barbet-Massin *et al.* 2012).

En lien direct avec des modèles écosystémiques structurés selon les traits fonctionnels, le couple SDM VTA pourrait permettre d'estimer l'arrivée potentielle de groupes fonctionnels, à partir des modifications de l'écosystème. En considérant le changement climatique dès la construction du modèle, il est possible de prendre en compte les préférences climatiques dans la formation des groupes fonctionnels et donc avoir différents groupes par préférence climatique. Ainsi, on peut considérer l'arrivée d'un groupe fonctionnel NIS, par rapport au départ d'un groupe fonctionnel similaire endémique et partageant les mêmes traits fonctionnels (à l'exception de la préférence climatique). De cette manière, on prend en compte la libération des niches écologiques dans le processus d'arrivée de groupes NIS (Figure VI - 2). Par conséquent, en considérant, dès la mise en place de la typologie d'un modèle, les traits fonctionnels qui pourraient optimiser la modélisation d'un facteur de changement comme le changement climatique, on optimise la méthodologie.

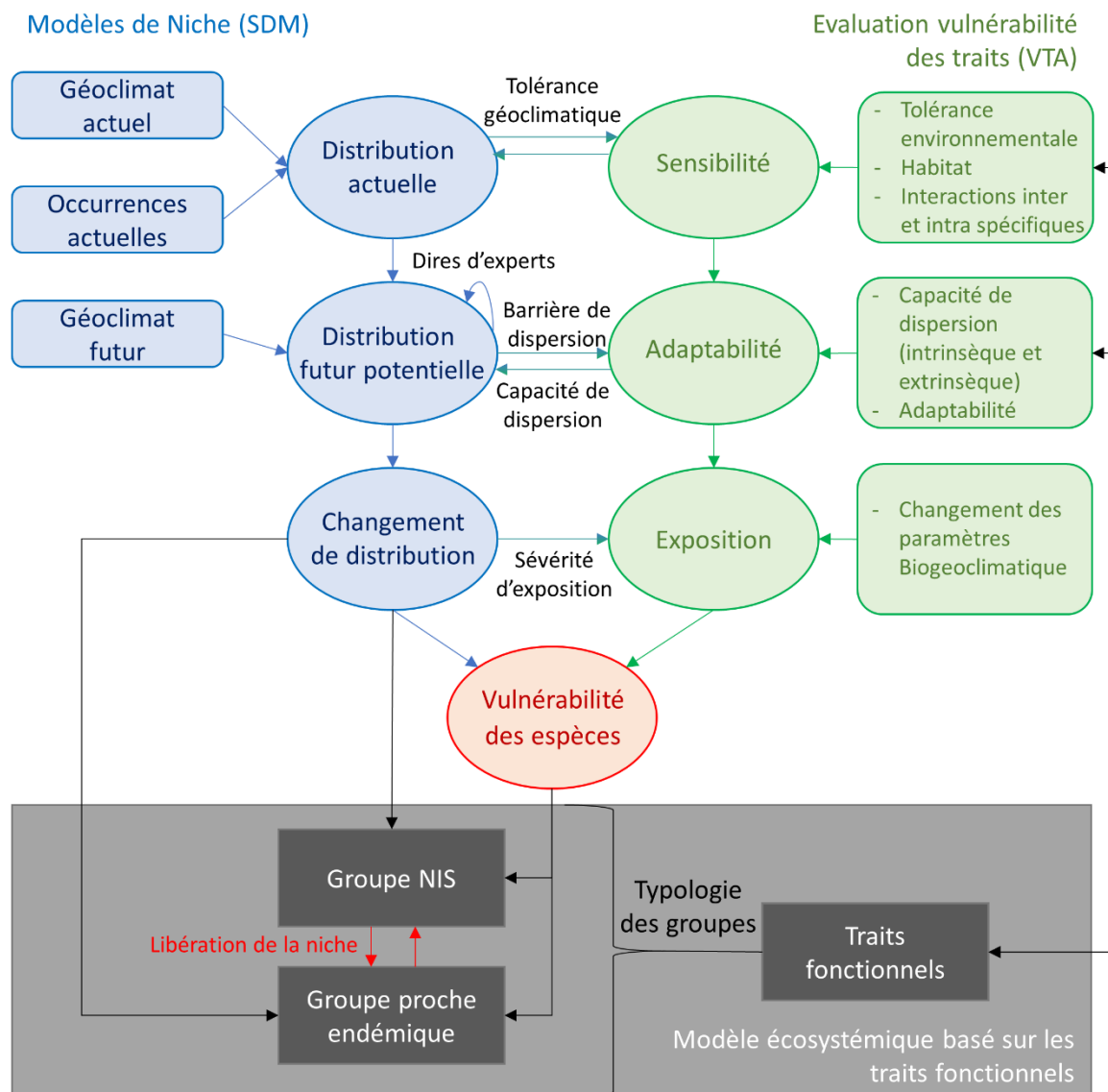


Figure VI - 2 Schéma d'un cadre de modélisation écosystémique, basé sur les traits fonctionnels.

L'approche couple : un modèle écosystémique basé sur les traits fonctionnels, avec un modèle de niche et un modèle d'évaluation de la vulnérabilité des traits fonctionnels, pour simuler l'arrivée d'espèces NIS dans le modèle écosystémique.

3.3 Traits fonctionnels et relation avec l'anthroposphère.

Pour prendre en compte les relations avec l'anthroposphère, un trait d'intérêt anthropique pourrait être pris en compte, en parallèle aux traits fonctionnels (Table VI - 1), dès la mise en place des groupes fonctionnels. En considérant les groupes fonctionnels du modèle en fonction de leurs relations avec l'homme, on facilite la mise en place de relations entre

l'écosystème et le sociosystème. De cette manière, on limite une sur-agrégation du modèle causée par les groupes d'intérêt économique ou culturel, comme dans le cas de la coquille Saint Jacques, tout en considérant les spécificités des interactions entre homme et nature (**chapitre 3**). Une telle structuration pourrait également permettre de tenir compte des interactions autres que liées à la pêche, afin de considérer dès la formation du modèle les liens divers et variés entre écosystèmes et sociosystèmes. Ainsi en considérant l'intérêt culturel ou le pouvoir de régulation de certaines espèces sur les cycles environnementaux (ex. capacité des bivalves à limiter l'érosion des plages (Gracia *et al.*, 2018), à servir de puits de carbone (Aubin *et al.*, 2018)), on facilite la mise en place de liens entre les deux systèmes. Il est important d'intégrer de nouveaux liens entre les systèmes écologiques et les systèmes sociaux, car il a été démontré que la pêche n'est pas la seule relation entre ces deux entités, et que d'autres connexions peuvent jouer un rôle tout aussi important (exemple Gregr *et al.* 2020). En considérant ces autres liens, on peut, face à des changements écosystémiques, mettre en avant les compromis entre les différents services écosystémiques (Lamarque *et al.*, 2011). En effet, optimiser la fourniture d'un service peut conduire à une chute de l'approvisionnement d'une multitude d'autres services (Ring *et al.*, 2010). C'est souvent le cas quand on cherchait à optimiser un service d'approvisionnement face à des services culturels et de régulations (Pretty *et al.*, 2006). C'est aussi important pour montrer à quel point un changement écosystémique s'accompagne d'une réduction de fourniture d'une multitude de services écosystémiques (Carpenter *et al.*, 2006). Tout ceci permet d'avoir une vision plus intégrative des socio-écosystèmes, afin d'anticiper les possibles évolutions de ces systèmes face aux changements environnementaux.

Table VI - 1 Exemple de traits fonctionnels pouvant être utilisés pour définir des groupes fonctionnels.

Exemples des traits fonctionnels	Catégorie	type
Taille maximale	Histoire de vie	Quantitatif ou Qualitatif
Age de maturité	Histoire de vie	Quantitatif ou Qualitatif
Fécondité	Histoire de vie	Quantitatif ou Qualitatif
Comportement parental	Histoire de vie	Qualitatif
Comportement de groupe	Histoire de vie	Qualitatif
Méthode de nutrition	Ecologie Trophique	Qualitatif
Groupe trophique	Ecologie Trophique	Qualitatif
Type de proie	Ecologie Trophique	Quantitatif ou Qualitatif
Position dans la colonne d'eau	Habitat	Quantitatif ou Qualitatif
Préférence d'habitat	Habitat	Qualitatif
Préférence de température	Habitat	Quantitatif ou Qualitatif
Préférence de salinité	Habitat	Quantitatif ou Qualitatif
Intérêt pour service d'approvisionnement	Lien anthropique	Qualitatif
Intérêt pour service de support	Lien anthropique	Qualitatif
Intérêt pour service culturel	Lien anthropique	Qualitatif

3.4 Vers les socio-écosystèmes.

Pour considérer un socio-écosystème, il est nécessaire de bien comprendre les dynamiques de chaque sous-système ainsi que leurs connexions, dans les deux sens. Améliorer la prise en compte des relations de l'écosystème vers le sociosystème n'est donc pas la seule priorité des modélisateurs écosystémiques. En effet il est impératif de prendre en compte les rétroactions possibles du sociosystème vers l'écosystème, en fonction de son évolution, ainsi que les incertitudes possibles dans ces rétroactions. Les modèles socio-écologiques cherchent à répondre à ces questions, ils cherchent à déterminer la résilience des systèmes socio-écologiques (Schlüter *et al.*, 2012), en regardant par exemple les réponses des écosystèmes aux changements environnementaux et le rôle des institutions dans la gestion de l'utilisation des ressources naturelles (voire Kellner *et al.* 2010; Pahl-Wostl *et al.* 2011; Biggs *et al.* 2012). Pour saisir la dynamique et le fonctionnement de ces systèmes socio-écologiques, des travaux interdisciplinaires sont nécessaires afin de bien définir chaque sous-système (écologique et social) ainsi que leurs interactions, dans toute leur diversité.

La communication n'est pas uniquement nécessaire entre les disciplines, mais également entre les acteurs locaux et les expérimentateurs (écologues et sociologues), pour demander leur avis, et ainsi permettre un transfert transversal de l'information. En effet, l'une des recommandations de la communauté scientifique est d'apprendre à dialoguer avec ces

acteur et de prendre en compte leurs connaissances (2021 AMEMR congress), afin de comprendre les mécanismes qui dirigent la dynamique des sociaux-écosystèmes (Villamor *et al.*, 2014). Dans la même lignée que les sciences participatives, il est aujourd’hui important de considérer de nouvelles sources d’informations, afin d’acquérir une information plus locale et spécifique sur les systèmes étudiés (Palomo *et al.*, 2011). Cela passe par la mise en place de scénarios avec les partis prenants de l’exploitation et de la gestion des écosystèmes, afin de rendre les modèles écosystémiques plus opérationnels (Luz, 2000; McBride *et al.*, 2017; Steenbeek *et al.*, 2020). C’est ainsi que l’on pourra mieux comprendre et intégrer les rétroactions entre sociosystème et écosystème et que l’on pourra mieux intégrer nos travaux dans la dynamique des systèmes.

Parmi les relations trop peu explorées dans la littérature, on peut citer les relations culturelles entre homme et nature (Blicharska *et al.*, 2017). En effet, les liens culturels sont peu considérés au profit des liens plus économiques et monétaires (Milcu *et al.*, 2013). Cette partie des relations est certes plus facile à quantifier pour les gestionnaires des écosystèmes (Boyd and Banzhaf, 2007; Weber, 2007), mais oublier les autres types de relations reste une limite importante. Il est donc nécessaire d’aller au-delà du physique, vers des liens plus imaginaires, qui jouent néanmoins des rôles cruciaux pour le bien être humain (Daniel *et al.*, 2012), mais également pour l’économie (Gegr *et al.*, 2020). Il est également important d’identifier la résilience de ces liens face aux grands changements des écosystèmes, comme pour les relations plus matérielles, afin de saisir leur pérennité face aux changements écosystémiques. Pour ce faire, il faut donc pouvoir quantifier ces relations et leurs accroches avec les écosystèmes, afin de prédire leurs évolutions. La perception des populations locales étant intrinsèque aux liens entre cultures et écosystèmes (Daniel *et al.*, 2012), prendre en compte ces perceptions peut aider à la prise de décision, en cas de compromis entre services culturels et services d’approvisionnements ou de régulations.

Comme pour les mécanismes d’interactions des facteurs de changement, lors de l’étude du cumul d’impacts, les relations homme nature sont très spécifiques aux écosystèmes et aux populations. C’est donc à une échelle plus locale, que ces études doivent être réalisées, en mobilisant les connaissances locales, pour rapprocher les problématiques scientifiques aux problématiques humaines.

4 Conclusion générale

La multiplication des activités anthropiques a un effet indéniable sur le fonctionnement des écosystèmes marins et côtiers. Cette thèse apporte de nouveaux outils pour étudier les effets du cumul d'impacts sur le fonctionnement et l'organisation des écosystèmes. Ces modifications du fonctionnement des écosystèmes ont un effet important sur leur résilience, partout dans le monde, et avec des dynamiques différentes selon les écosystèmes. Avec cette thèse, nous avons montré qu'il est possible de quantifier, en 0 et 2 dimensions, l'effet des interactions entre plusieurs facteurs de changement, sur le fonctionnement et la résilience des écosystèmes. Caractériser les effets du cumul d'impacts sur la résilience écologique est crucial dans un contexte de changement global. La résilience des écosystèmes est en effet un indicateur des potentielles modifications des relations entre les sociétés et les écosystèmes (Levin and Lubchenco, 2008), face à de potentiels changements environnementaux.

Nous avons montré que les interactions entre les facteurs anthropiques font appel à des mécanismes complexes et multiples, conduisant les écosystèmes vers des changements hétérogènes de leurs propriétés fonctionnelles, que seuls, les outils holistiques et fonctionnels peuvent identifier. Nous avons mis en avant que, parmi ces mécanismes, les effets structurants de facteurs de changements écosystémiques avaient un rôle particulier dans le cumul d'impacts. Ainsi, les effets structurants du parc éolien (**Chapitre 1**), ou du changement climatique (**Chapitre 1**), jouent des rôles déterminants dans la formation d'effets cumulés, à différentes échelles, spatiales et temporelles. Face aux enjeux du changement climatique et à l'intensification de ses effets sur les écosystèmes côtiers, il est urgent d'identifier les potentielles sources de restructurations des écosystèmes. C'est particulièrement important, car l'effet du changement climatique sur la distribution des espèces semble avoir des effets fonctionnels très spécifiques sur les écosystèmes, à cause des différentes réponses des espèces à ce dernier.

Face à la complexité des impacts du changement climatique sur les réseaux écologiques et aussi à celle des interactions entre les facteurs de changements, il est nécessaire d'effectuer des études locales du fonctionnement des écosystèmes. Ainsi, nos travaux montrent que les particularités fonctionnelles, structurelles et spatiales des écosystèmes doivent être mises en avant lors d'études du cumul des activités humaines. Par conséquent, prédire les interactions

entre le changement climatique et les activités humaines à l'échelle globale ne permet pas de répondre aux défis locaux. Il faut que ces études soient faites au cas par cas et que les informations soient mises en commun afin de mettre en avant les grands mécanismes du cumul d'impacts. Ainsi, on pourra plus facilement anticiper les évolutions possibles des écosystèmes et mettre en place des plans de gestion ciblés, dans le but de limiter les changements écosystémiques à risque.

Que ce soit pour quantifier les effets du changement climatique ou bien les services écosystémiques rendus par l'écosystème à l'homme, avoir une vision locale apporte des informations importantes pour les gestionnaires. On voit souvent le changement climatique comme une menace uniforme, mais ce dernier risque d'avoir des impacts locaux spécifiques. Face à ce défi, il est donc important de repenser l'étude des écosystèmes et d'intégrer pleinement les relations entre l'humanité et les écosystèmes. Cela passe par la quantification de nouveaux liens entre l'homme et la nature et par l'évaluation de leur pérennité face aux changements écosystémiques. Ainsi, l'impact de l'homme ne se limite pas uniquement aux poissons ou aux huîtres que l'on mange, les changements écosystémiques sont bien plus divers et profonds.

L'ensemble des résultats et des méthodes développés durant cette thèse montrent que beaucoup de travail reste à faire et qu'il est nécessaire d'étudier le fonctionnement des écosystèmes et socio-écosystèmes face au cumul d'impacts, pour mettre en avant les grands mécanismes de ces changements. Au-delà des apports théoriques pour la communauté scientifique, cette thèse montre que nos approches pourraient apporter des informations cruciales aux gestionnaires et aux décideurs, afin d'aider à la mise en place de stratégies de développement durable, adaptées aux enjeux locaux. Cette thèse ouvre ainsi des perspectives dans l'objectif de continuer à développer la recherche écologique théorique et appliquée.

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VII Chapitre supplémentaire:

Spatial modelling of anthropogenic activities and their
combined effects on the Bay of Seine (English
Channel) trophic web

Spatial modelling of anthropogenic activities and their combined effects on the Bay of Seine (English Channel) trophic web

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Abstract:

With the growing human population near the coastlines of the world, the number of anthropogenic activities is increasing. Through marine renewable energies and the constant need for marine aggregate for construction, the multiplication of activities can have serious consequences for ecosystems. In this study, we used an innovative ecosystem approach combining a spatialized trophic model (Ecospace), coupled with holistic network indices (Ecological Network Analysis or ENA) to perform a study of the potential reserve effect of an offshore wind farm, alongside the effects of marine aggregate extraction in the extended bay of Seine, in the English Channel. We determined the effects of both of these drivers separated and combined, on the ecosystem functioning, the ecosystem resilience, and the ecosystem maturity. Our results distinguished between the positive reserve effect of the offshore wind farm on the ecosystem resilience and maturity, and the negative aggregate extraction effect on the same two emerging properties. The effects of both drivers remained localized and thus, the scenarios combining them both displayed little mitigating effects of the offshore wind farm reserve effect on to the aggregate extraction area. This study shows the great potential of ENA indices for marine spatial planning and pave the way for future studies using ENA for spatial planning.

Key words: Ecological network analysis, bay of Seine, reserve effect, aggregate extraction, marine spatial planning.

1 Introduction

The exhaustion of terrestrial resources forces human to turn to the sea in the search of new sources of energy and materials. One example is the increase of marine aggregate extractions (Le Bot et al., 2010; Lozach, 2011; Dauvin, 2019). This practice is well developed in some countries, such as Netherlands, Belgium or United Kingdom (Cooper et al., 2008; ICES, 2016). In Great Britain, 15% of the production of aggregate extraction comes from marine extraction; in France, it only represents 2% of the aggregate production. But this technique is expanding, indeed, research permits have been filed, representing areas of 400 km² in the French territories (Ifremer.fr). In France, concerns have arisen regarding their possible expansion as French waters are already facing many anthropogenic activities. Indeed, areas such as the English Channel are highly exploited as it already hosts active aggregate extractions, sediment deposit, fisheries, tourism, leisure activities, aquaculture, future offshore wind farms (OWF), among others (Halpern et al., 2008; Raoux et al., 2018).

Extraction of marine aggregate consists in collecting sediments and water mixture from the seabed that are then separated at sea or at land to keep only the wanted aggregates. This process has been described to have physical, chemical and biological impacts on the ecosystem (ICES 2016, Sutton and Boyd, 2009). Marine aggregate extraction affects the composition of the substrate by removing the upper layers, changing the topography and thus modifying the sediment composition by releasing finer particles in the water column, then redepositing at the surface of the seabed (Dauvin, 2019). This release of finer particles and water creates a plume which increases the local turbidity. It is known that benthic organisms are strongly influenced by hydrodynamics and sediment types (McLusky and Elliot, 2004; Pesch, 2007). As a result, perturbations of these physical characteristics will most likely cause changes in the benthic community structure and functioning ICES 2016 case study of Buiten Ratel (ICES, 2016). Decreases in benthic species diversity, abundance and biomass following aggregate extraction were described in several studies (Boyd and Rees, 2003; Desprez, 2000 and Robinson, 2005). Other works were also made on the recovery time of ecosystems impacted by aggregate extraction and showed that given enough time, ecosystems could fully recover (Cooper *et al.*, 2008; Foden *et al.*, 2009).

Another increasing anthropogenic activity that marine ecosystems must face is the development of marine renewable energies and the implementation of OWF (Raoux et al., 2017, 2019). Several research studies have been performed regarding the effect of OWF on marine ecosystems. One of the main effects is the destruction of soft bottom substrate for the creation of new hard substrates (Petersen and Malm, 2006; Langhamer 2012; Degraer et al., 2020). This is described as the “reef effect”. The new hard substrate, built for supporting turbines, can lead to an increase in biodiversity, abundance and biomass of some fish and benthic species, it creates a shift from fine sediment biodiversity to hard substrate biodiversity (Coates et al., 2011; Lindeboom et al., 2014; Degraer et al., 2020). This is not the only effect that OWF will have. Indeed, around turbines, all human activities are often forbidden. This can lead to a “reserve effect” : closing a zone to fisheries can results in an increase in species biomass and diversity (Halouani *et al.*, 2020).

With the increasing stresses that marine ecosystems are facing, it seems fundamental to assess how they could be impacted. Ecosystemic approaches seem best suited for such role as they can adequately represent cascading effect in the system (Fulton *et al.*, 2011). They have also been promoted for their compatibility with Ecosystem-based management (Safi *et al.*, 2019) and have been often advocated in the recent years (Rodriguez, 2017; Fath *et al.*, 2019). One such promising ecosystem approach is the Ecological Network Analysis (ENA). Popularised by Ulanowicz (1986), ENA indices are holistic indices able to quantify multiple whole ecosystem properties. Coupled with trophic modelling approaches like Ecopath with Ecosim (EwE) (Christensen and Walters, 2004; Polovina, 1984; Walters et al., 1999), ENAs allow to evaluate the structure, organisation and functioning of the trophic network in the ecosystem (Ulanowicz, 1997, 2004). Those holistic indices are used to describe trophic network properties such as, recycling, omnivory or redundancy (Heymans et al., 2016; Heymans and Tomczak, 2016; Niquil et al., 2012), allowing to characterize emergent properties of the system. Recent works applied the EwE approach in order to compute ENA indices (Nogues et al. submitted).

Our aim in this study was to test the effect of marine aggregate extraction and the “reserve” effect of a future fourth OWF on the trophic web functioning in the Bay of Seine, as well as the cumulated impact of these two activities. To do so, we used a published spatialized food web model, the Ecospace model of the extended bay of Seine (Halouani *et al.*, 2020), to compute ENA indices (Nogues et al. submitted). We compared the values of ENA indices

between our anthropogenic scenario and a reference one and described the potential effects of those two activities on ecosystem functioning. It is the first time that those two anthropogenic activities were tested together in order to observe possible unexpected interactions between them. We further promote the use of ENA indices for spatial planning purposes.

2 Material and Methods

2.1 Study area

The extended Bay of Seine is located in-between the northern-west French coast and the eastern English Channel (Figure VII - 1). Tidal currents vary from 1 to 2 knots and are weaker in the eastern part of the bay (Dauvin, 2019). These currents play an important role in distributing sediments. The majority of the bay is composed of sandy gravels habitats (Dauvin, 2015). Those gravels are in the paleovalley called the Paleoseine and can reach several meters depth (Lozach 2011). But near the Seine estuary, patches of fine sand and shallow muddy sand are found (Dauvin, 2015, 2019), several gradients of sediments are observed in the Bay of Seine from fine to coarse sediment with the distance from the coast (Maer et al., 2006). It is possible to describe benthic communities based on the sediment gradient (Foveau, 2009, EUNIS classification). This classification and the work field (Foveau 2009, Lozach 2011) allow to have a good idea about the benthic species composition and distribution. For example, near the Seine estuary, the *Abra alba* – *Lagis koreni* muddy sand habitat covered about 400 km². In the centre and northern part of the bay, the habitat is described has circalittoral pebbles mixed with more or less sand and gravel. In these habitats, high abundances of bivalves such as *Glycymeris glycymeris* and *Polititapes rhomboids* have been described and patches characterized by very high abundances (> 1,000 ind.m⁻²) of the ophiurid *Ophiotrix fragilis* are found (Dauvin, 2015).

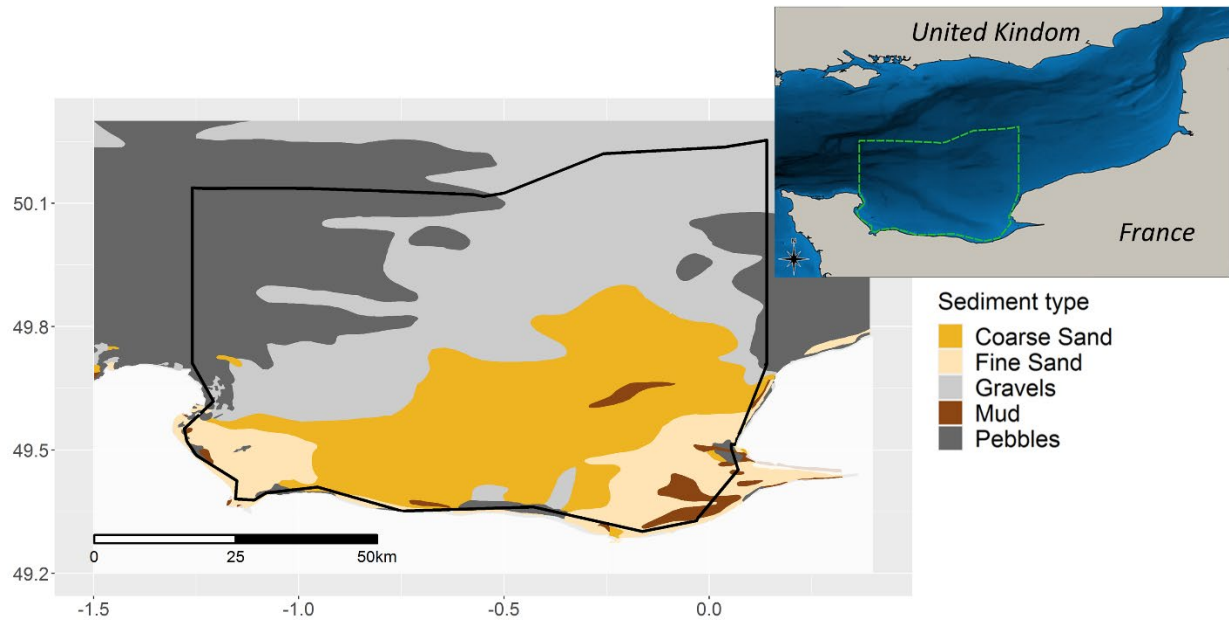


Figure VII - 1 Sedimentary map of the extended bay of Seine in the eastern English Channel (modified from Larssonneur et al. 1982).

2.2 Modelling anthropogenic activities

2.2.1 The Ecospace approach

In order to test the impact of marine aggregate extraction and the “reserve” effect of an offshore wind farm, we computed ENA indices (Table VII - 1) using Ecospace (Ecopath with Ecosim software 6.6). Ecospace is the spatio-temporally based model of EwE. We used the Ecospace model developed by Halouani et al. (2020) composed of 42 trophic groups (Supplementary materials Table SIV - 1) and completed by Bourdaud et al. (2021). Ecospace first required the building of static zero-dimensional mass-balanced Ecopath model (Polovina, 1984b; Pauly *et al.*, 2000) and its temporally dynamic module: Ecosim (Walters *et al.*, 1997).

The Ecopath model is based on two main equations to describe the trophic interactions among between functional groups. The first equation describes the production (Eq. 1).

$$\left(\frac{P}{B}\right)_i \cdot B_i = \sum_{Pred_j=1}^n \left(\frac{Q}{B}\right)_j \cdot B_j \cdot DC_{ij} + E_i + Y_i + BA_i + \left(\frac{P}{B}\right)_i \cdot B_i \cdot (1 - EE_i) \text{ (eq.1)}$$

Where $\left(\frac{P}{B}\right)_i \cdot B_i$ is the production; $\sum_{Pred_j=1}^n \left(\frac{Q}{B}\right)_j \cdot B_j \cdot DC_{ij}$ is the predation mortality; E_i is the catches; Y_i is the net migration; BA_i is the biomass accumulation and $\left(\frac{P}{B}\right)_i \cdot B_i \cdot (1 - EE_i)$ is the other mortality. Each compartment must respect:

$$\left(\frac{Q}{B}\right)_i \cdot B_i = \left(\frac{P}{B}\right)_i \cdot B_i + R_i + UN_i \text{ (eq.2)}$$

Where $\left(\frac{Q}{B}\right)_i \cdot B_i$ is the consumption; $\left(\frac{P}{B}\right)_i \cdot B_i$ is the production; R_i is the respiration and UN_i is the unassimilated food.

The mass-balance assumption of Ecopath allows the estimation of unknown flows and biomasses based on the knowledge of others.

Once these two master equations are respected, Ecopath can be used to assess the ecosystem structure and the trophic relationships (Figure 2) (Christensen, and Walters, 2004). The Ecosim model is used to represent the temporal dynamics of whole ecosystems. It is based on a system of differential equations for biomasses dynamics derived from the linear equations used to described trophic fluxes (Ecopath) (Walters et al, 1997; 2000; Christensen and Walters, 2004). The biomass dynamic equation is:

$$\frac{dB_i}{dt} = g_i \Sigma_j Q_{ij} - \Sigma_j Q_{ij} + I_i - (MO_i + F_i + e_i)B_i \text{ (eq.3)}$$

Where $g_i \Sigma_j Q_{ij}$ is the production term and $\Sigma_j Q_{ij}$ the predation one. g_i is the net growth efficiency, Q_{ji} is the consumption rate of the group i on a group j , Q_{ij} the cumulated predation undergone by i , I_i the immigration rate, MO_i the non-predation natural mortality, F_i the fishing mortality and e_i the emigration rate.

The second equation defines the consumption of a predator j on its prey i for each time step (Walters et al., 1997):

$$Q_{ij} = \frac{a_{ij}v_{ij}B_iB_j}{2v_{ij}+a_{ij}B_j} \text{ (eq.4)}$$

Where v_{ij} is the exchange rate between vulnerable and an invulnerable component, B_i is the biomass of the prey and B_j is the biomass of the predator. The a_{ij} term represents the effective search rate of predator j for prey i (Walters et al, 1997).

Ecosim is based on the foraging arena theory (Walters and Martell, 2004). Predator-prey relationships are describe using vulnerability exchange rates (Walters et al, 1997). The value of exchange rates between vulnerable and an invulnerable components determines if the control is top-down or bottom-up (Walters et al., 1999).. Our Ecosim model was fitted for the

period 2000 – 2015, using multiple catches and biomass time series (more details are available in Halouani et al. 2020).

The Ecospace model (Walters et al., 2000) was then derived from the Ecopath and the Ecosim models. It was a time dynamic and spatially-explicit model. It replicates Ecosim dynamic over a spatial grid of homogeneous sized cells (4907 cells for the extended Bay of Seine). The base map of our Bay of Seine Ecospace model consisted of a raster grid map of 70 rows and 101 columns, each cell is 0.015° side (≈ 1.6 km), and was defined using a bathymetric map from the GEBCO (GEBCO Compilation Group, 2020). Primary production in the model was defined using a Chlorophyll a map extracted from SeaWiFS (NASA Goddard Space Flight Center, Ocean Biology Processing Group, 2014).). In each cell, Eq 1 and 2 are solved along with delay-difference accounting for split pools. As a result, biomasses and consumption rate are determined by the trophic interactions inherited from Ecopath and through Ecosim differential equations (Walters et al., 1997, 2000). Species distribution is driven by the habitat capacity (Christensen et al. 2014) that is computed using an environmental driver map for each trophic compartment and can be linked to multiple parameters. To drive the distribution of our trophic compartment, we use results from Species Distribution Models (SDM) maps as environmental drivers. The cells were linked through spatial variations of organisms, movement, production and fishing effort. In our model, six fishing fleets were modelled. They are able to fish on the entire extent of the model and depended on a gravity model which influenced the fishing effort depending on multiple fishing related parameters (Walters *et al.*, 1999). It is also possible to close areas from fisheries to model MPAs. This type of modelling allows making predictions of mesoscale spatial pattern (Walters et al., 2000). As we used the Ecospace trophic model developed by Halouani et al (2020), layer information and input parameters used have already been set. All the model information can be found in Nogues et al.; Halouani et al. 2020, Bourdaud et al. 2021 and Nogues et al. submitted.

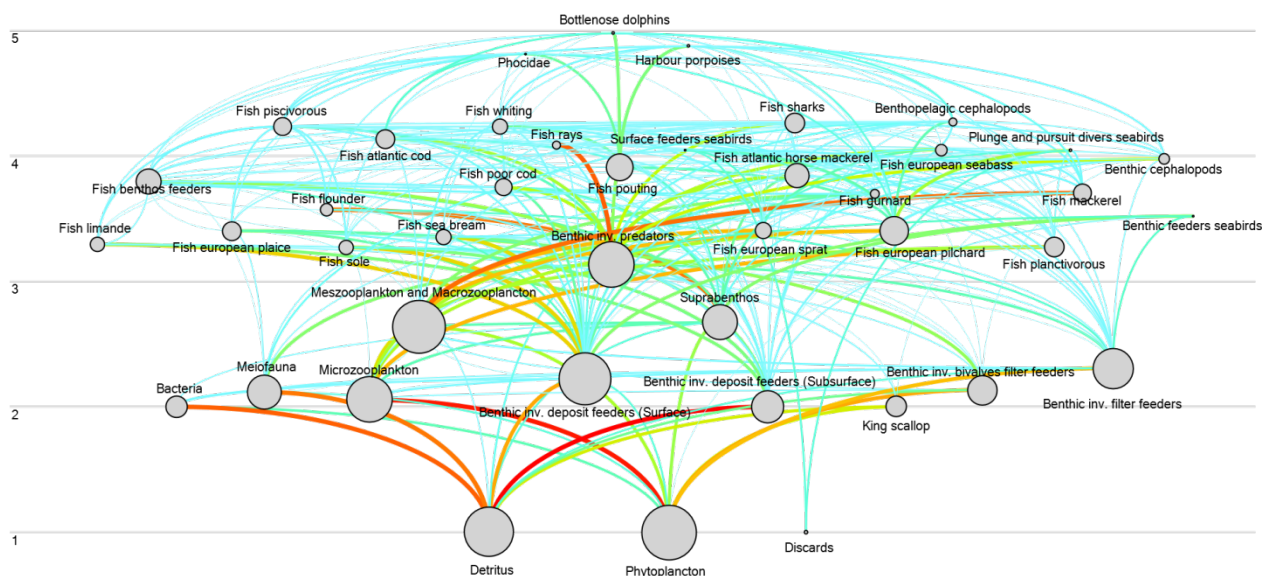


Figure VII - 2 Trophic food web of the extended Bay of Seine Ecospace model.

This figure shows the web with which our Ecospace model will run and the complexity of the flows that interact in this web. The number on the left represents the trophic level and the circles are the different trophic groups composing our model.

2.2.2 Marine aggregate extraction

In order to evaluate the effect of marine aggregate extraction on the food web, it was first necessary to quantify how extraction impacted the trophic groups. Many studies agreed on the decrease in species diversity, abundance and biomass caused by aggregate extraction (Boyd et al., 2004; Desprez et al., 2014; Robinson 2005). But they also observed recovery following aggregation. This has led us to make several assumptions: first, all benthic invertebrates species are impacted by extraction as it consists in the removal of their habitat. Then, after cessation of extraction, a recolonization is performed by mobile opportunistic species; carnivorous and necrophagic ones (Boyd et al., 2004; Desprez 2000; Cooper et al. 2008). As the model does not allow us to act on specific species, we used the results of the knowledge synthesis performed by Desprez et al. (2014). This synthesis resumed field work and literature knowledge in the experimental extraction sites in Dieppe and in the Bay of Seine. The main results were a decrease of 90% of the biomass and abundance and from 60% to 80% of the number of species, followed by a rapid recolonization of such community of mobile sediments. From the expertise of J.C. Dauvin and scientific reports (GIE-GMO: BEMACE 1 et 2), we assumed that a decrease of 90% in biomass could be applied to the group Bivalves mainly

dominated by the dog cockle *Glycymeris glycymeris*, the banded carpet shell *Polititapes rhomboides*, and the blunt tellin *Arcopagia crassa*. This group represents around 90% of the whole species biomass in the northern part of the Bay of Seine on the GIE GMO aggregate extraction site (Lozach & Dauvin, 2012), these large bivalves will highly suffer from marine aggregate extraction. Moreover, the extraction will change the sediment type : by removing the upper layer of sediments and resuspending fine particles. As a consequence, large bivalves such as *G. glycymeris*, *P. rhomboides* and *A. crassa* will not be able to colonize fine sediment. On the contrary, annelids and mobile crustaceans will be able to survive in the extracted zone and present in new habitat types. In order to model the arrival of predators and necrophagic species, a 20% increase in the benthic Invertebrates Predators group biomass was applied in Ecospace. Due to regulation applied to marine aggregate extraction in France, the extraction only occurs a few hours a year in each site. As we didn't have the tools to model the effect of aggregate extraction during such specific time period, the Invertebrates Filter Feeders and Invertebrates Deposit Feeders groups were not modified. Indeed, even if they are impacted by extraction, abundant species such as the sessile cirriped *Balanus crenatus* and polychaete worms *Spirobranchus triqueter* have high recolonization rates and are able to colonize pebbles and gravel, have high recolonization rates (Boyd and Rees, 2003; Boyd et al., 2004). So, in order to balance their decrease and their recolonization, we chose to not change their biomass. Two scenarios were developed: a first one, called ACT (actual), simulating extraction in the two zones that are nowadays exploited in the Bay of Seine (Figure VII - 3): these zones are called zone C and zone Baie de Seine, which we have called zone B. The second scenario named TOT, (total), as it simulates aggregates extraction in zones C, B and in two more zones which are not in activity but have been granted to extraction. Those two zones are called A and GH ("Granulats du Havre"). Those areas can be seen in Figure VII - 3.

2.2.3 Offshore Wind Farm (OWF)

The second anthropogenic impact studied was the implementation of an OWF. The position of the fourth OWF in the Bay of Seine has not yet been established. In order to decide where to put it in our model, discussions have been organized with M. Antonin GIMARD (project manager at the Office Français de la Biodiversité). He is working as support for the French Ministry of Ecological Transition on planning and managing industrial marine project in the Eastern English Channel and, as a consequence, he is involved in the public debate

regarding the new OWF project. Thanks to his expertise and the Planning of Renewable Marine Energies maps developed by the Cerema and the French government for public debate (<https://cerema.maps.arcgis.com/apps/MapJournal/index.html?appid=199c7945c2154a24bfd8a28ee3bbd254>), we were able to establish all the constraints and decide on a probable location of the future OWF (Figure VII - 3) targeted by a new project (names AO4). As the bay of Seine is highly exploited, the restrictions for the position were numerous: the administrative lines, the defence and security marine zones, the regulation due to fisheries, and finally there restrictions related to ecological factors such as the presence of birds and marine mammals. This has led us to decide on a location in the west part of the bay (Figure VII - 3). and more close to high bird densities. A concession of 300 km² has been explored. It seems likely that only 150 km² will be used for turbines, but at this level of definition of the project, this assumption isn't guaranteed, so the "maximum probable effect" has been kept. For our study, we focused on the "reserve" effect of OWF. We established two scenarios: a 150 km² one (called 150) and a 300 km² one (called 300) in order to test the two possible outcomes of the project. To model the reserve effect, we have closed fisheries in those zones and did not change anything else.

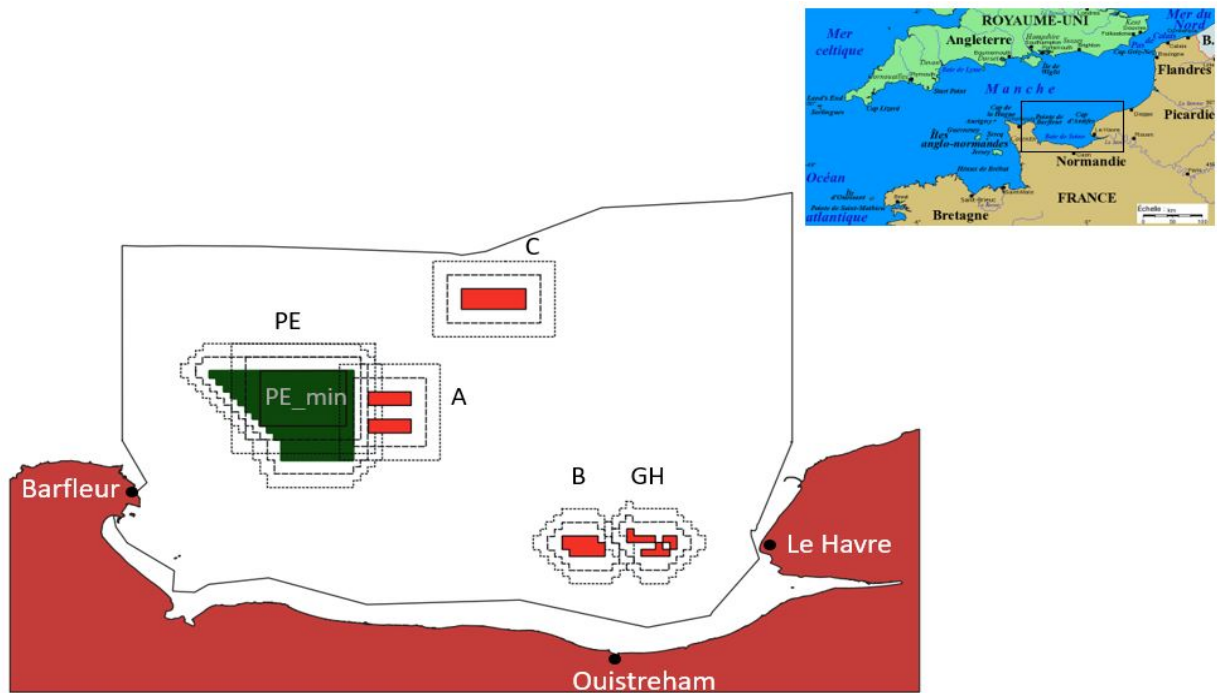


Figure VII - 3 Study area of the extended Bay of Seine and the anthropogenic activities area investigated.

In brown are the marine aggregate extraction zones and in green the location that has been chosen for the offshore wind farm. Zones A, B, C and GH are the marine aggregate extraction zones with their respective spillover zones Sp_1 and Sp_2 in dotted lines. Sp_1 is the closest to the zone of extraction. The PE polygon represent the offshore wind farm for the 300 km² scenario and the PEmin inside is the one for the 150 km² scenario. Their associated spillovers are also presented in dotted lines with the Sp_1 being the closest to the OWF zone.

2.3 Ecological Network Analysis (ENA)

Fath et al. (2007) define ENA as “a systems-oriented methodology to analyse within system interactions used to identify holistic properties that are otherwise not evident from the direct observations”. ENA indices were computed in order to define emergent properties of the system. For our study, four ENA indices were selected based on recommendations developed for management policy (Fath et al., 2019; Safi et al., 2019). Our four ENA indices are the Detritivory on Herbivory ratio (D/H); the Finn’s Cycling Index (FCI); the System Omnivory Index (SOI) and the Mean Trophic Level II (MTL2) (Table VII - 1). ENA indices were computed in every Ecospace cell for the 75 years using the EnaR ecospace plugin from Nogues et al. (submitted). The Ecospace enaR plugin allowed us to compute SCOR files for each cells of the eBoS model, containing the complete flow matrix. We then used the “enaR” R package package

(Borrett and Lau, 2014) to compute each of our ENA indices per cell. This allowed us to map ENA indices values of the entire eBoS. Then a comparison of the ENA indices value was made between the different scenarios. Depending on how they evolved with the scenarios, it was possible to deduce how the system has changed with perturbations. ENA indices calculations were done with the enaR package (Lau et al., 2017) using the software R studio 3.6.1.

Table VII - 1 ENA indices chosen to evaluate impact of anthropogenic activities in the extended Bay of Seine. Adapted from Nogues et al. (2020).

Indices	Equation	Meaning
The Detritivory on Herbivory (D/H) ratio ((Latham, 2006)	$D/H = \frac{\sum DET}{\sum PP}$ DET is the flows of consumption of Detritus and PP the consumption flows of primary producers	Ratio of detritus consumption (Detritivory) compared to the consumption of primary producers (Herbivory) in the ecosystem.
Finn's Cycling Index (FCI) (Odum, 1985)	$FCI = \frac{TST_c}{TST}$ TST_c is the cycled Total system throughflow and TST corresponds the Total system throughflow.	The recycling index represents the fraction of energy/matter recycled in the system.
System Omnivory Index (SOI) (Libralato, 2013)	$SOI = \frac{\sum_{i=1}^n [OI_i \times \log Q_i]}{\sum_{i=1}^n \log Q_i}$ OI being the omnivory index and Q_i the consumer food intake. SOI is the average omnivory index weighted by the consumer food intake.	The system omnivory index quantifies the distribution of trophic interactions among different trophic levels.
Mean Trophic Level (Latham, 2006)	$MTL = \frac{\sum_i TL_i \times B_i}{\sum_i B_i}$ B is the biomass and TL the trophic level of the compartments i.	The MTL is the mean trophic level of the system's compartment. It varies between 1 (primary producers); 2 (all consumers); up to 4 (top predators). MTL2 takes into account all consumers.

2.4 Combined effects

Another purpose of our work was to study the effect of the combination of marine aggregate extraction and the “reserve” effect linked with OWF. To do so, a fifth scenario was elaborated. It was named CUMUL. This scenario combined the TOT marine aggregate one and

the 300 OWF one. Combined effects of fisheries and climate change have been described by Fu et al. (2018). They demonstrated that, even if in literature the combined effect of stressors is usually seen as simply the addition of the two effects, this is not always the case and multiple activities can act together in synergetic and antagonistic ways (Crain et al., 2008). In a previous study, Nogues et al. (2020) analysed the potential combined effects (i.e synergism dampening, or antagonism) between different anthropic impacts in the Bay of Seine to describe ecosystem status through ENA indices.

In order to measure those combined effects, the relative index variation between the referential model without any activities (CURRENT) and a single effect model (TOT or 300) was first computed, for each ENA.

$$\Delta I_k^{sep} = \frac{I_k - I_c}{I_c}$$

I_c is the index value of the reference model and I_k the one of a single effect model.

Then, the variation (ΔI_k^{sep}) of TOT and 300 scenarios was summed in order to get the additive effect:

$$\sum \Delta I_k^{sep}$$

In order to get the cumulative effect, the variation between the CURRENT model and the CUMUL scenario was computed for each ENA:

$$\Delta I_{cum} = \frac{I_k - I_c}{I_c}$$

To evaluate the cumulative effect, we compared the value of the cumulative effect ΔI_{cum} and the additive one $\sum \Delta I_k^{sep}$.

The six different combined effects that derived from those calculations are:

- Positive synergism: $\Delta I_{cum} > \sum \Delta I_k^{sep} > 0$
- Negative synergism: $\Delta I_{cum} < \sum \Delta I_k^{sep} < 0$

Synergism describes a situation where: the combination of stressors is greater than the addition of those stressors.

- Positive antagonism: $\Delta I_{cum} > \Sigma \Delta I_{ksep} < 0$
- Negative antagonism: $\Delta I_{cum} < \Sigma \Delta I_{ksep} > 0$

Antagonism describes a situation where the two types of effect act in opposite directions.

- Positive dampened: $\Delta I_{cum} < \Sigma \Delta I_{ksep}$ with ΔI_{cum} and $\Sigma \Delta I_{ksep} > 0$
- Negative dampened: $\Delta I_{cum} > \Sigma \Delta I_{ksep}$ with ΔI_{cum} and $\Sigma \Delta I_{ksep} < 0$

Dampened effects occur when the additive effect is higher than the cumulative one. But it is described as a less positive or less negative effect than additive one.

- Positive dampening: $\Sigma \Delta I_{ksep} > \Delta I_{cum} > 0$
- Negative dampening: $\Sigma \Delta I_{ksep} < \Delta I_{cum} < 0$

3 Results

3.1 Impact of marine aggregate extraction and offshore wind farm scenarios on ENA indices.

3.1.1 Finn Cycling Index

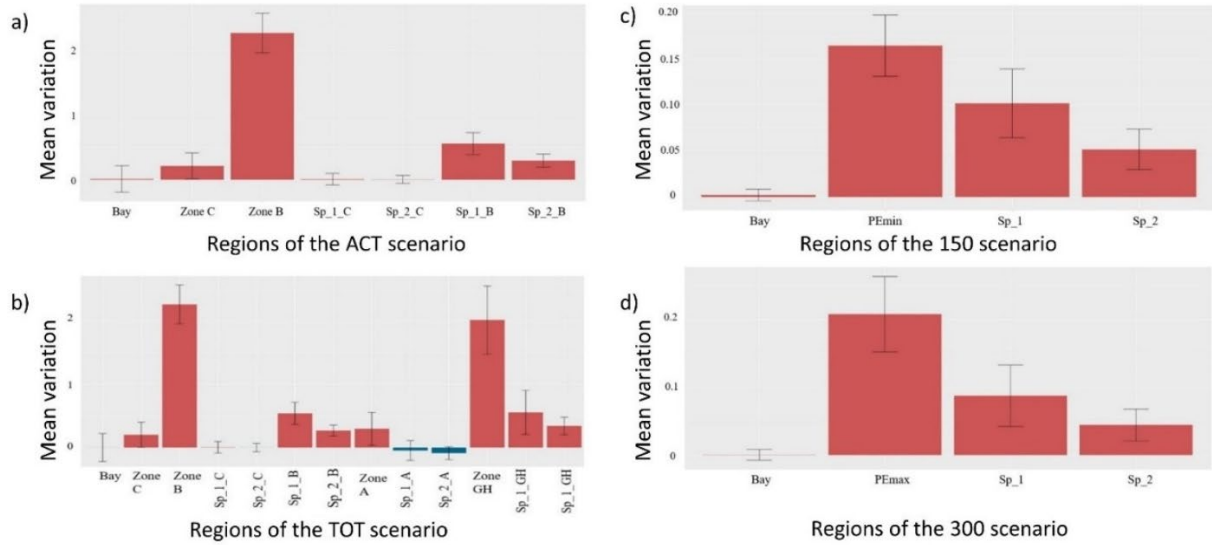


Figure VII - 4 Histograms showing the evolution the FCI index when the system is facing each of the scenarios that we described.

The value of this index, is, for each scenario, compared to the value of this index in the CURRENT state, without any perturbations

The result of the histograms showed that for marine aggregate extraction, the FCI increased in zone B and its spillovers for the two scenarios, and in zone GH and its spillovers, for the TOT scenario (Figure VII - 4). It also showed an increase in FCI values in the OWF area, but those values were smaller than in aggregate extraction scenarios. The spillover regions were also affected and exhibited an increase in FCI. For the four scenarios, the changes seemed to be more important in the closer spillover zone (sp_1) and decrease in the second one. For the two different types of perturbations applied; the recycling of the system was seen to increase.

3.1.2 System Omnivory Index

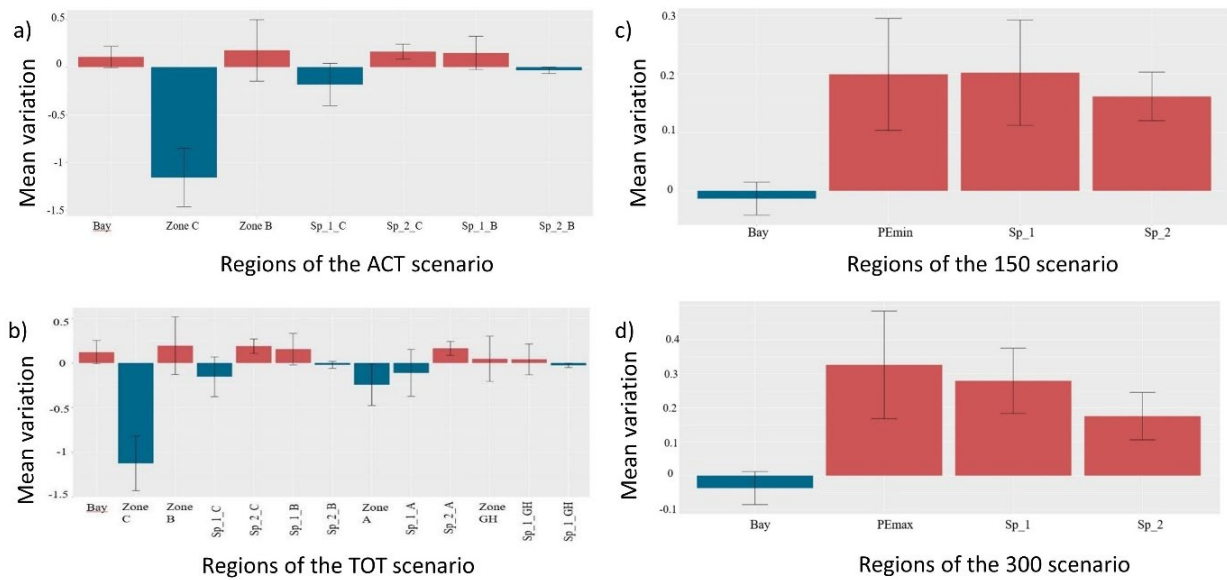


Figure VII - 5 Histograms showing the evolution the SOI index when the system is facing each of the scenarios that we described.

The value of this index, is, for each scenario, compared to the value of this index in the CURRENT state, without any perturbations.

The result for the SOI index (Figure VII - 5) exhibited a noticeable decrease in this index for marine aggregate scenarios in zone C. For OWF scenarios, the SOI increase inside (PEmin and PEmin) and around the offshore wind farm (Sp_1 and Sp_2). Unlike the effect of the OWF, aggregate extraction seems to decrease the omnivory, especially in zone A and C (Figure VII - 5).

3.1.3 Other ENA indices: D/H and MTL2

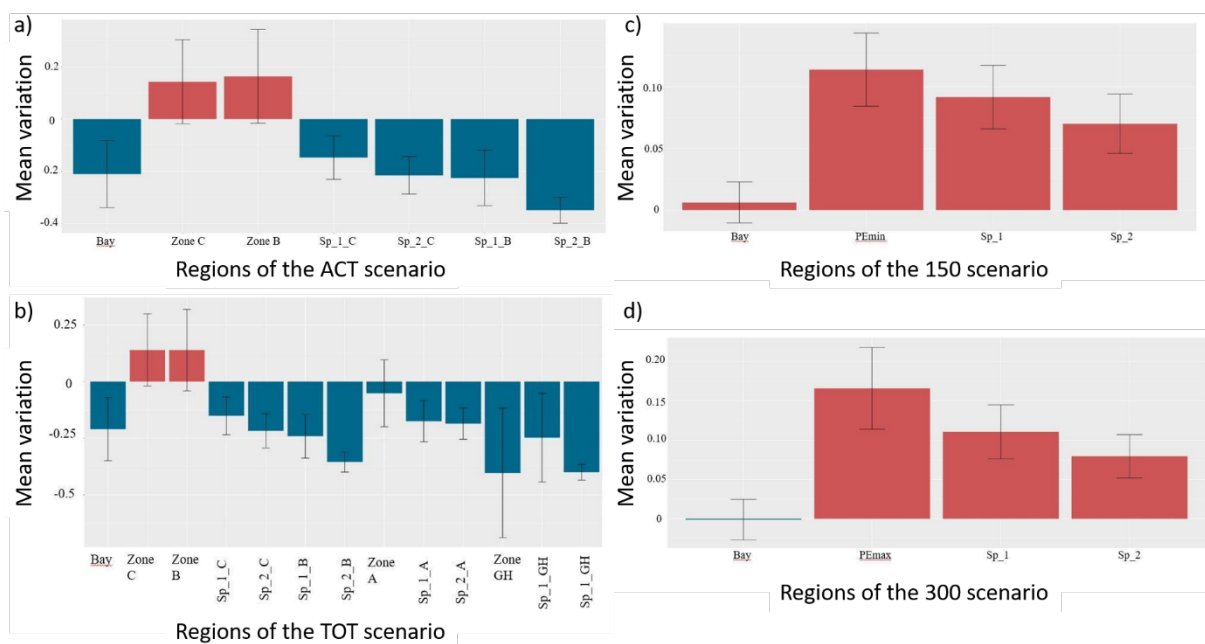


Figure VII - 6 Histograms showing the evolution the D/H index when the system is facing each of the scenarios that we described.

The value of this index, is, for each scenario, compared to the value of this index in the CURRENT state, without any perturbations.

While the impacts of marine aggregate extraction were mainly localized inside of the extraction area, other indices displayed impact at the whole model level. This was the case for the D/H ratio. Unlike aggregate extraction however, the OWF had constraint effects, with a localized increase of the D/H inside of the OWF area (Figure VII - 6).

For marine aggregate extraction and OWF, the MTL2 changed in the whole model (Figure VII - 7). But these changes seemed more important inside areas of anthropic activities. Moreover, in OWF the MTL2 seemed to increase whereas in aggregate extraction areas A and C it displayed a lessening.

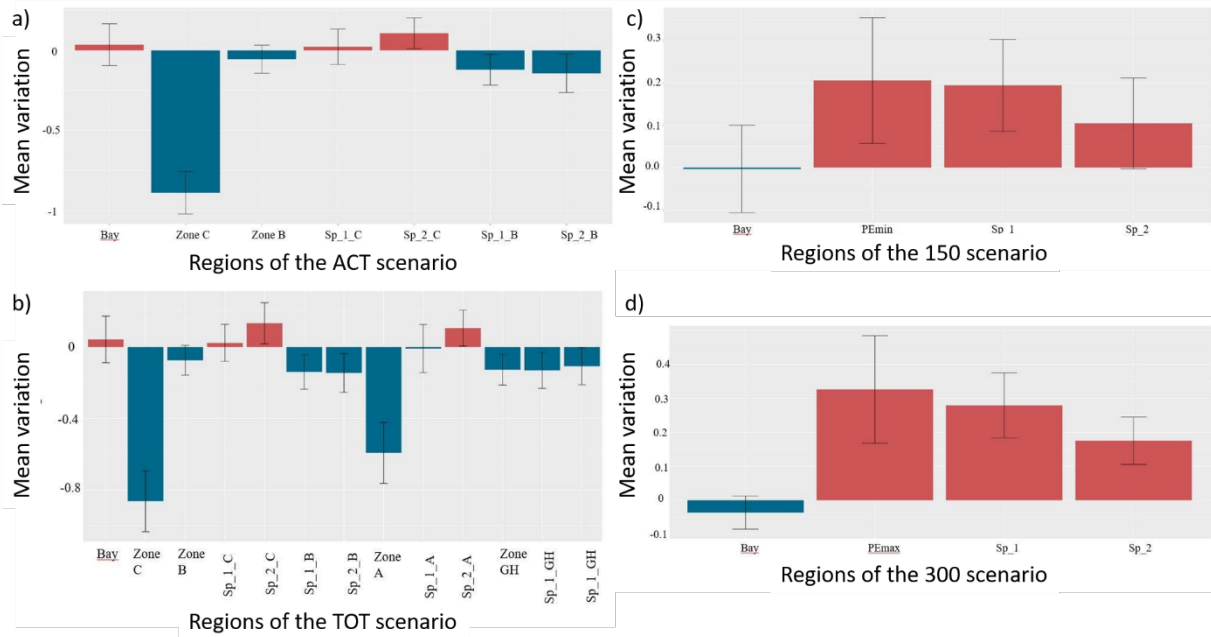


Figure VII - 7 Histograms showing the evolution the MTL2 index when the system is facing each of the scenarios that we described.

The value of this index, is, for each scenario, compared to the value of this index in the CURRENT state, without any perturbations.

3.2 Study of combined effect of TOT and 300

3.2.1 Finn's Cycling Index

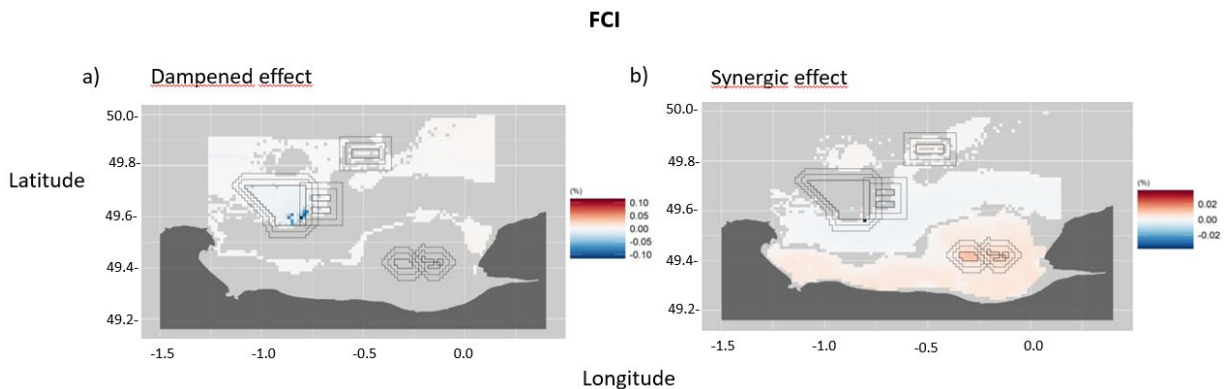


Figure VII - 8 Maps representing the combined effect of marine aggregate extraction and offshore wind farm on the FCI.

In a) the blue colour shows a positive dampened effect. The red one is for negative dampened effect. Cells that are transparent are cells where no dampened effect happened; In b) it is the synergic effect that is represented. In blue, negative synergic effect and in red positive one. When no synergic effect was detected, the cells remain transparent.

Cumulative effects on the recycling appear very limited, with only limited hotspot of negative dampened effects and a small positive synergetic effect in the south of the extended Bay of Seine (Figure VII - 8).

3.2.2 System Omnivory Index

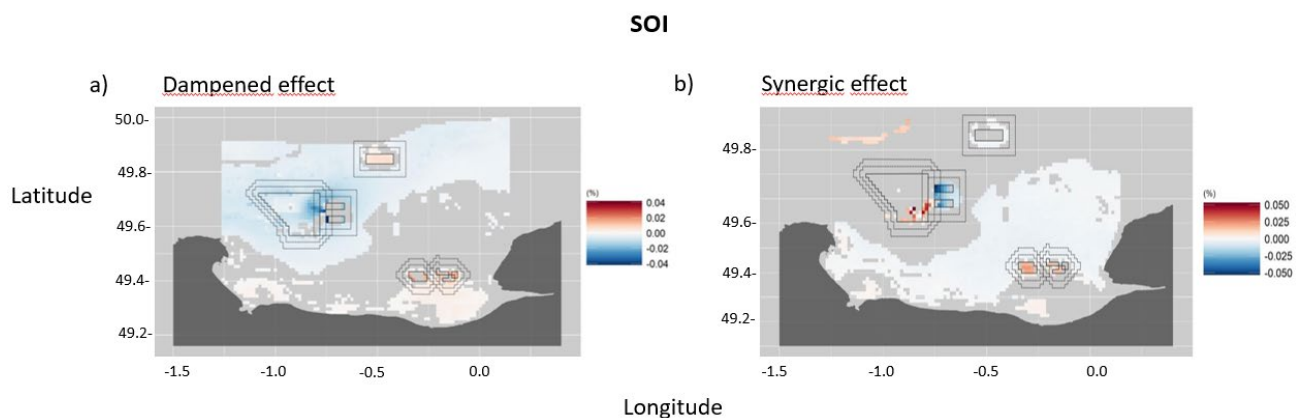


Figure VII - 9 Maps representing the combined effect of marine aggregate extraction and offshore wind farm on the SOI.

In a) the blue colour shows a positive dampened effect. The red one is for negative dampened effect. Cells that are transparent are cells where no dampened effect happened; In b) it is the synergic effect that is represented. In blue, negative synergic effect and in red positive one. When no synergic effect was detected, the cells remain transparent.

When tested for System Omnivory Index, there was nearly no antagonism effects detected between the combined scenario and the additive one. The dampened and synergism effects are location-dependent. Indeed, dampened effects were observed in most of the wind farm and in zone C (Figure VII - 9). Only a few cells in A, B and GH exhibit it. In these cells, the variations in the additive scenario were higher than in the cumulative one. Synergism was observed in zones B, GH, A and a few cells of the wind farm (Figure VII - 9). In such cases, the variations of the additive scenario were lower than in the combined one.

4 Discussion

Our work shows, to our knowledge for the first time, that ENA indices can be used to test the functional responses of the marine ecosystem to aggregate extraction, the reserve effect of an OWF (Offshore Wind Farm) and the combination of these two.

4.1 Marine aggregate extraction impact on the Bay of Seine trophic web

The results showed that the effect on recycling in the system in case of marine aggregate extraction was location-dependent. This spatialisation seems to be explained by the difference in ecological assemblages characterizing areas A and C on one hand, and B and GH on another hand (Figure VII - 4). In marine aggregate extraction scenarios ACT and TOT, the increase in recycling (FCI) and detritivory over herbivory (D/H) in zones B and GH can be explained by the potential arrival of detritivorous species. This result is coherent with experimental studies (Boyd and Rees, 2003), and shows that our methods are capable of detecting what was observed in Desprez (2000), who observed the colonization of detritivores species such as *Galathea* spp. following aggregate extraction. Some of these opportunistic species colonized the new sediment type and benefited from the detritus left by extraction and deposition from the plume. This arrival of detritivores induced a change in the trophic dynamic, as it relied more on detritus than on primary production.

With marine aggregate extraction scenarios, a decrease in omnivory (SOI) and mean trophic level (MTL2) were observed. The effects of marine aggregate extraction on omnivory also appeared to be structured by the ecological assemblage of each extraction area, with different responses in each region: a variation of -1.2 in zone C and one of 0.2 in zone B (Figure VII - 5). This decrease can be explained by the loss of middle trophic level species, such as the European plaice (*Pleuronectes platessa*), while for Sea bream (*Spondylus cantharus*), an increase in biomass was observed. This can be explained by the ability of those species to change their diet composition. Desprez et al., 2014 have shown that, during extraction, Bream species ate mainly *Galathea* species and *Pisidia* species, which recolonized rapidly extraction zones. Species like the plaice *Pleuronectes platessa* on the other hand feeds more on bivalves, highly impacted by aggregate extraction, which could explain its decreases in marine aggregate extraction areas. It seems that the lower MTL2 is the result of a loss of fish compartments, due to the lower prey density. The SOI reduction, that describes the system complexity, illustrates the change in system composition. Compartments are less diverse in species compositions, as only the ones that can adapt to the stress remain in the zone.

4.2 Offshore Wind Farm, the reserve effect

In our simulations, the “reserve” effect tested has led to an increase in recycling (FCI). A similar increase of FCI and detritivory on herbivory have been found for the OWF 150 and the OWF 300 (Figure VII - 4 & Figure VII - 6). It seems that it is the higher Invertebrates filter feeder biomass that intensified the recycling efficiency of the system, as filter feeders play a key role in recycling (Raoux et al., 2019; Nogues et al., 2020). The omnivory and the mean trophic level also increased in both OWF scenarios. The majority of fishes and high trophic level compartments such as birds and Phocidae in the wind farm area had shown an increase in their biomasses. The absence of fisheries induced an arrival of predators in middle and high trophic levels. This result in a higher MTL2 as already observed when adding a new MPA (Libralato et al., 2010; Valls et al., 2012). The higher abundance and diversity of preys offer new feeding opportunities for predators, increasing the omnivory of the system. The positive effect of MPA on the SOI was already observed and shows how protected system gain in complexity (Libralato *et al.*, 2010).

4.3 Ecological Network Analysis

The link between ENA and ecosystem properties is not always straightforward. That is why it is important to confront our work with the different existing theories. It is also very important to consider multiple ENA indices in order to properly explain the evolution of ecosystems and to determine their effects on the system emerging properties (Niquil et al., 2014).

ENA on the ecosystem seems to indicate an increased stress level due to the effect of marine aggregate extraction. With the loss of a whole compartment in marine aggregate scenarios (i.e., Bivalves) disequilibrium and a reorganization of the trophic web resulted in a stress, visible through a higher recycling (FCI) but also a lower system omnivory (SOI) and mean trophic level (MTL2). The more consequent impact is seen in zone C and A as Bivalves represents a major part of the total biomass, resulting in higher impact in such areas due to their loss. An increase in recycling (FCI) has been described as a consequence of stress endured by an ecosystem (Wulf and Ulanowicz, 1989). The stressed state of zone C and A can also be supported by the lower SOI and MTL2 which are two indices describing system complexity (Safi

et al, 2019). The ENA indices show here that the changes in the system induce stress and a loss of complexity.

The OWF seems to have an opposite effect on the system complexity than the marine aggregate extraction. In the case of OWF scenarios, all ENA indices seem to increase in the presence of the reserve effect, resulting in a higher FCI, D/H, MTL2 and SOI. Sumalia et al. (2000) explained that reserve areas with no finshing are expected to help ecosystem maturation toward a less perturbed system. This is visible in the OWF area through the higher SOI and the higher MTL2. Lobry et al. (2008) described the SOI as an indicator of maturity, as ecosystem tends to become more complex with time (Odum,1985). The mean trophic level (MTL 2) is also expected to increase in more mature system (Pauly et al., 1998). In ENA theories, ecosystem tend toward a climax (e.g. a more mature state), and the increase in mean trophic level and in omnivory tend to depict such evolution. The system also appears to be more resilient, as the FCI and D/H can act as a buffer against perturbations (Saint-Béat et al., 2015). The reserve effect of the OWF thus appears to improve the ecosystem complexity and resilience.

4.4 Combined effects

When both activities are combined, the OWF doesn't seem to be able to mitigate the effects of marine aggregate extraction on the ecosystem functioning. This is visible even through relatively small cumulative effects arise from the combined TOT and OWF 300 scenario. Negative synergetic effects on the omnivory of the aggregate extraction area A seems to indicate that the OWF further increase the impact of aggregate extraction. This is opposed by a positive synergism on the omnivory of the OWF 300 area, with some area of the OWF benefiting from the aggregate extraction. Moreover, the positive dampened effect on both the omnivory and recycling of the OWF area close to the zone A seem to indicate that aggregate extraction reduces the effect of the OWF reserve effect on the system recycling and omnivory. The reserve effect thus appeared to have no mitigating power over the adjacent aggregate extraction zone (Dunford *et al.*, 2004; Levrel *et al.*, 2012), but rather a negative effect on the omnivory of zone A. This might be due to the increase fishing pressure resulting from the spillover of the OWF reserve effect (Colléter *et al.*, 2014; Halouani *et al.*, 2020). The interaction between the increase of fishing pressure and the aggregate extraction impacted even more

the ecosystem, reducing the omnivory of the system, and thus its complexity (Libralato, 2013), resulting in a more vulnerable system (Fagan, 1997a; Saint-Béat *et al.*, 2015). Studying the interactions between anthropic activities in our case shows the interest of building combined driver scenarios, as demonstrated in Nogues *et al.* (2020). As driver interactions can lead to unpredictable and undesirable effects, they should be considered thoroughly in planification work (Pine *et al.*, 2009).

The other extraction area showed small cumulative effects while not close to the OWF. There cumulative effects are visible on the omnivory and the recycling of zone B and GH. This shows that cumulative effects between localized effects can arise outside of the suspected area of influence of a driver (Nogues *et al.* written). Indeed, throughout ecosystemic studies on the effects of the future OWF of Courseulles-sur-Mer, the influence of an OWF was often considered limited in space (Halouani *et al.* 2020). This is interesting because current studies of spatialized cumulative effects don't seem to reliably take into account the possible far stretching effects of localized drivers, such as marine protected areas (Ban *et al.*, 2010; Kotta *et al.*, 2020). With ecosystemic approaches like Ecospace we can take into consideration the multiple pathways of interactions generated by drivers, both spatially and not spatially. This is why ecosystemic approaches appear to better grasp the full extent of cumulative effects, which might be underestimated in current studies (Nogues *et al.* written).

4.5 Interest for management of ecosystems

This work has estimated how the Bay of Seine may be impacted by marine aggregate extraction if all the concessions are exploited. It has also studied the impact of the reserve effect over time within an OWF. The Ecospace model is an interesting tool for anticipating impact of anthropogenic stress and to model spatially the ecosystem functioning. As it has been shown by Fath *et al.* (2019) and Safi *et al.* (2019), the ENA indices are good potential tools to help decisions makers regarding management policies as they can help understanding changes in ecosystem functioning (de la Vega *et al.*, 2018). Indeed, in order to start a reflexion regarding conservation in an ecosystem, it seems important to first understand how it works and how it will be affected by stresses. Here we have used indices advised by Fath *et al.* (2019) (D/H, FCI and MTL 2) and Safi *et al.* (2019) (D/H, FCI and SOI), and it allowed us to study emergent properties of the system when applying our scenarios. The new methodology

applied here for combined effect is also interesting to take into account and underline the fact that numerical experiments should not study effects individually (Crain et al., 2008; Halpern et al., 2008). As the Bay of Seine is facing many anthropogenic activities, testing how they interact with each other seems a good way to evaluate the health of the ecosystem linked with possible decisions of spatial planning. Here we have seen that recycling efficiency may increase if adding a new OWF. MPA have also been shown to favor the arrival of marine mammals (Raoux et al., 2018), which is coherent with our scenarios on expected Phocidae biomass.

Our results support the use of ENA indices for spatial planning initiatives. For example, when looking for ways to protect the resilience of ecosystems or their ability to furnish services (bioturbation...), there are few data available (Van der Biest et al. 2020). Moreover, combined effects should thoroughly be looked at in such spatial planning initiative as they may produce unexpected changes that could impact ecosystem services (Raymond et al., 2013). Overall, this makes ENA indices relevant tools for an integrative approach to spatial planning. But even without looking at services, ENA indices give a good vision of the potential impacts of anthropogenic activities. They could be used in conservation as they are a way to anticipate how the system will evolve, and adapt to management policies.

5 limits and perspectives

In this work, we continue to use a new method developed by Nogues et al. (2020) which combine Ecospace modelling with Ecological Network Analysis. The use of ENA indices in Ecospace modelling is new, but we shouldn't ignore the potential limits of our approach. Only being able to simulate aggregate extraction year long leads to unrealistic estimation of marine aggregate extraction. Indeed, extraction only occurs a few times a year while in the model we had to apply extraction during the whole year. This is also the case for the impact of aggregate extraction on other trophic groups, which only occur during limited time period, as the increase turbidity due to extraction can limit marine bird predation (Cook and Burton, 2010). Aggregate extraction isn't the only pressure we could better model. To go further, it would be interesting to also test the "reef effect" caused by the OWF (Raoux et al., 2017 ; 2019), as modelled in Nogues et al. (submitted), and combine both model together to achieve a more complete study of marine planification in the bay of Seine.

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VIII Annexes

Supplementary materials I.

Table SI - 1 Ecopath groups from Raoux et al. (2017) compared to LIM groups.

Ecopath compartments from Raoux et al. (2017)		LIM trophic compartments	LIM Symbol
1 Bottlenose dolphins	2 Harbour porpoises	1 Cetaceans	CET
3 Harbour seals	4 Grey seals	2 Phocidae	PHO
5 Plunge and pursuit, diverse seabirds	6 Surface feeders, seabirds	3 Birds	BIR
7 Benthopelagic cephalopods	8 Benthic cephalopods	4 Cephalopods	CEP
9 Fish, mackerel	10 Fish, European pilchard	5 Fish, planctivorous	FPL
11 Fish, European sprat	12 Fish, planctivorous		
13 Fish, atlantic horse mackerel			
14 Fish, European seabass	15 Fish, sharks and rays	6 Fish, benthos feeders	FBF
16 Fish, gurnard	17 Fish, pouting		
18 Fish, poor cod	19 Fish, benthos feeders		
20 Fish, sea bream	21 Fish, Atlantic cod	7 Fish, piscivorous	FPI
22 Fish, whiting	23 Fish, piscivorous		
24 Fish, sole	25 Fish, European plaice	8 Fish, flat fish	FFI
26 Fish, other flatfish	27 Benthic inv., predators	9 Invertebrates, predators	IPR
28 Benthic inv., filter feeders	29 Benthic inv., bivalves	10 Invertebrates, filter feeders	IFF
30 King scallop		11 Bivalvia	BIV
31 Benthic inv., deposit feeders		12 King scallops	KSC
32 Suprabenthos		13 Invertebrates, deposit feeders	IDF
33 Meiofauna		14 Suprabenthos	SUP
34 Zooplankton		15 Meiofauna (Nematodes)	NEM
35 Bacteria		16 Zooplankton	ZOO
36 Phytoplankton		17 Bacteria	BAC
37 Detritus		18 Phytoplankton	PHY
		19 Detritus	DET

Table SI - 2 Parameters of the LIM model.

Compartment	P/B min	max	P/Q min	max	R/Q min	max	U/Q min	max	Literature
CETaceans	0.04	0.12	-	-	-	-	-	-	Christensen et al. (2009)
PHOCidae	0.075	0.225	-	-	-	-	-	-	
BIRds	0.05	0.15	0.3	0.8	-	-	-	-	Saint-Béat (2012), Christensen et al. (2009)
CEPhalopods	1	3	0.1	0.4	-	-	-	-	Christensen et al, 2009
Fish, PLanktivorous	0.486	1.458	0.047	0.424	-	-	0.1	0.5	P/B, P/Q and U/Q generated using confidence intervals around standard Ecopath parameters (Christensen and Pauly, 1993), Leguerrier et al (2004)
Fish, Benthos Feeders	0.542	1.625	0.059	0.534	-	-	0.1	0.5	
Fish, Plscivorous	0.450	1.349	0.059	0.534	-	-	0.1	0.5	
Fish, Flat Fish	0.375	1.126	0.074	0.670	-	-	0.1	0.5	
Invertebrates, PRedators	1	5	0.05	0.3	-	-	0.12	0.28	Christensen and Pauly (1993), Brey (2001)
Invertebrates, Filter Feeders	1	5	0.05	0.3	-	-	0.18	0.42	
BIValvia	1	5	0.05	0.3	-	-	0.18	0.42	
King SCallops	1	5	0.05	0.3	-	-	0.18	0.42	
Invertebrates, Deposit Feeders	1	5	0.05	0.3	-	-	0.18	0.42	Brey (2001), Lobry et al. (2008), Lassalle et al. (2011)
SUPrabenthos	0.4	15	0.1	0.37	-	-	0.2	0.5	
Meiofauna (NEM)	10.1	35	0.05	0.4	-	-	0.13	0.3	Heip et al. (1990), Van Oevelen et al. (2006)
ZOOplankton			0.25	0.5	0.1	0.3	0.1	0.5	Vezina et al. (2000), Vézina and Savenkoff (1999)
BACteria	-	-	0.11	0.6	-	-	0.05	0.35	Del Giorgio and Cole (1998), Danovaro et al. (2008), Tortajada et al. (2012)
PHYtoplankton	-	-			0.05	0.3	0.05	0.5	Vezina et al. (2000), Vézina and Platt (1988), Vézina and Savenkoff (1999)

Table SI - 3 Diet matrix of the LIM before offshore wind farm model, including minimum and maximum values.

Prey \ Predator	CETaceans	PHOCIDA	BIRDS	CEPHALOPODS	Fish, Benthos Feeders	Fish, PLanktivorous	Fish, Piscivorous	Flat Fish	Invertebrates, Predators	Invertebrates, Filter Feeders	BIVALVIA	KING SCALLOPS	Invertebrates, Deposit Feeders	SUPERBENTHOS	MEIOFAUNA	ZOOPLANKTON	BACTERIA
IMPORT	0.05	0.05	0.00	0.00	0.00	-	-	-	-	-	-	-	-	-	-	-	-
	0.25	0.25	0.56	0.30	0.30	-	-	-	-	-	-	-	-	-	-	-	-
CEPHALOPODS	0.04	-	-	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-
	0.24	-	-	0.37	-	-	-	-	-	-	-	-	-	-	-	-	-
Fish, Feeder	0.25	0.33	0.00	0.00	0.00	-0.00	0.00	-	-	-	-	-	-	-	-	-	-
	0.45	0.53	0.36	0.42	0.36	-	0.33	0.31	-	-	-	-	-	-	-	-	-
Fish, PLanktivorous	0.08	0.00	0.36	0.00	0.00	0.50	-	-	-	-	-	-	-	-	-	-	-
	0.28	0.20	0.96	0.56	0.46	-	-	-	-	-	-	-	-	-	-	-	-
Fish, Piscivorous	0.08	0.20	-	0.00	0.00	-1.00	-	-	-	-	-	-	-	-	-	-	-
	0.28	0.40	-	0.34	0.32	-	-	-	-	-	-	-	-	-	-	-	-
Flat Fish	-	-	-	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	0.35	-	-	-	-	-	-	-	-	-	-	-	-	-
Invertebrates Predator	-	-	0.00	0.00	0.00	-0.00	0.00	-	-	-	-	-	-	-	-	-	-
	-	-	0.32	0.53	0.63	0.38	0.55	-	-	-	-	-	-	-	-	-	-
Invertebrates Filter Feeders	-	-	-	0.00	0.00	-0.00	0.00	0.00	-	-	-	-	-	-	-	-	-
	-	-	-	0.31	0.34	-0.31	0.31	0.50	-	-	-	-	-	-	-	-	-
BIVALVIA	-	-	-	0.00	0.00	-	0.00	-	-	-	-	-	-	-	-	-	-
	-	-	-	0.30	0.30	-	0.44	-	-	-	-	-	-	-	-	-	-
KING SCALLOPS	-	-	-	-0.00	0.00	-	0.00	-	-	-	-	-	-	-	-	-	-
	-	-	-	0.30	0.30	-	0.30	-	-	-	-	-	-	-	-	-	-
Invertebrates Deposit Feeder	-	-	-	-0.00	0.00	0.00	0.21	0.00	-	-	-	-	-	-	-	-	-
	-	-	-	-0.41	0.50	0.33	0.81	0.39	-	-	-	-	-	-	-	-	-
SUPERBENTHOS	-	-	-	-0.00	0.00	0.00	0.00	0.00	-	-	-	-	0.00	-	-	-	-
	-	-	-	0.33	0.48	0.31	0.33	0.45	-	-	-	-	0.35	-	-	-	-
MEIOFAUNA	-	-	-	-0.00	0.00	-	0.00	0.00	0.00	-	-	-0.00	-	-	-	-	-
	-	-	-	-0.38	0.30	-	0.35	0.60	0.15	-	-	-0.35	-	-	-	-	-
ZOOPLANKTON	-	0.00	0.00	-	0.00	0.50	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	-
	-	-0.12	0.31	-	0.30	1.00	0.31	0.31	0.31	0.20	0.20	0.20	0.35	0.70	0.35	0.10	-
BACTERIA	-	-	-	-	-	-	-	-	-	0.00	-	-	0.00	0.00	0.00	-	-
	-	-	-	-	-	-	-	-	-	-	-	-	0.40	0.35	0.35	-	-
PHYTOPLANKTON	-	-	-	-	-	0.00	-	-	0.60	0.55	0.55	0.00	0.05	0.00	0.83	-	-
	-	-	-	-	-	-	-	-	0.10	-	-	-	-	-	-	-	-
DETRITUS	-	-	-	-	-	-	-	-	0.80	0.75	0.75	0.45	0.65	0.45	1.00	-	-
	-	-	-	-	-	-	-	-	0.30	0.00	0.00	0.15	0.15	0.35	0.00	0.45	0.00
									0.70	0.42	0.20	0.35	0.35	0.95	0.45	1.00	0.17
									0.90								

Table SI - 4 Diet matrix of the LIM offshore wind farm model, including minimum and maximum values.

Prey\Predator	CETaceans	PHOCidae	BIRds	CEPhalopods	Fish, Benthos Feeders	Fish PLanktivorous	Fish, Plscivorous	Flat Fish	Invertebrates, PRedators	Invertebrates, Filter Feeders	BIValvia	King SCallops	Invertebrates, Deposit Feeders	SUPrabenthos	Meiofauna (NEM)	ZOOplankton	BACteria
IMPort	0.00	0.05	0.12	0.00	0.00	-	-	-	-	-	-	-	-	-	-	-	-
	0.19	0.25	0.72	0.34	0.45	-	-	-	-	-	-	-	-	-	-	-	-
CEPhalopods	0.03	-	-	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-
	0.23	-	-	0.38	-	-	-	-	-	-	-	-	-	-	-	-	-
Fish, Benthos Feeders	0.38	0.36	0.00	0.00	0.00	-	0.00	0.00	-	-	-	-	-	-	-	-	-
	0.46	0.56	0.34	0.49	0.38	-	0.43	0.31	-	-	-	-	-	-	-	-	-
Fish, PLanktivorous	0.00	0.00	0.23	0.00	0.00	-	0.36	-	-	-	-	-	-	-	-	-	-
	0.14	0.12	0.83	0.45	0.38	-	1.00	-	-	-	-	-	-	-	-	-	-
Fish, Plscivorous	0.16	0.26	-	0.00	-	-	0.00	-	-	-	-	-	-	-	-	-	-
	0.36	0.46	-	0.35	-	-	0.34	-	-	-	-	-	-	-	-	-	-
Flat Fish	-	-	-	0.00	-	-	-	-	-	-	-	-	-	-	-	-	-
	-	-	-	0.42	-	-	-	-	-	-	-	-	-	-	-	-	-
Invertebrates, PRedators	-	-	-	0.00	0.00	-	0.00	0.00	-	-	-	-	-	-	-	-	-
	-	-	-	0.47	0.55	-	0.40	0.48	-	-	-	-	-	-	-	-	-
Invertebrates, Filter Feeders	-	-	-	0.00	0.00	-	0.00	0.00	0.00	-	-	-	-	-	-	-	-
	-	-	-	0.32	0.38	-	0.32	0.31	0.57	-	-	-	-	-	-	-	-
BIValvia	-	-	-	0.00	0.00	-	-	0.08	0.00	-	-	-	-	-	-	-	-
	-	-	-	0.31	0.31	-	-	0.68	0.31	-	-	-	-	-	-	-	-
King SCallops	-	-	-	0.00	0.00	-	-	0.00	-	-	-	-	-	-	-	-	-
	-	-	-	0.10	0.10	-	-	0.30	-	-	-	-	-	-	-	-	-
Invertebrates, Deposit Feeders	-	-	-	0.00	0.00	-	0.00	0.03	0.00	-	-	-	-	-	-	-	-
	-	-	-	0.37	0.44	-	0.33	0.63	0.38	-	-	-	-	-	-	-	-
SUPrabenthos	-	-	-	0.00	0.00	-	0.00	0.00	0.00	-	-	-	-	0.00	-	-	-
	-	-	-	0.32	0.32	-	0.31	0.32	0.40	-	-	-	-	0.31	-	-	-
Meiofauna (NEM)	-	-	-	0.00	-	-	-	0.00	0.00	0.00	-	-	0.00	-	-	-	-
	-	-	-	0.38	-	-	-	0.36	0.50	0.16	-	-	0.36	-	-	-	-
ZOOplankton	-	-	-	-	-	0.53	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	-	-
	-	-	-	-	-	1.00	0.31	0.30	0.34	0.19	0.20	0.14	0.35	0.59	0.35	-	-
BACteria	-	-	-	-	-	-	-	-	-	0.00	-	-	0.00	0.00	0.00	-	-
	-	-	-	-	-	-	-	-	-	0.15	-	-	0.40	0.35	0.35	-	-
PHYtoplankton	-	-	-	-	-	0.00	-	-	-	0.48	0.52	0.60	0.00	0.04	0.00	0.78	0.09
	-	-	-	-	-	0.47	-	-	-	0.68	0.72	0.80	0.44	0.64	0.44	1.00	0.29
DETritus	-	-	-	-	-	-	-	-	0.00	0.12	0.19	0.16	0.35	0.01	0.46	0.00	0.71
	-	-	-	-	-	-	-	-	0.60	0.32	0.39	0.36	1.00	0.61	1.00	0.22	0.91

Table SI - 5 Biomass modifications caused by the climate change effect (RCP 8.5).

Compartment \ Biomass	BOWF	REEF	BOWF with RCP 8.5	REEF with RCP 8.5
CEP	1.98E-02	2.46E-02	6.60E-03	8.18E-03
FPL	5.92E+00	4.76E+00	2.53E+00	2.01E+00
FBF	3.20E+00	6.69E+00	6.25E-01	9.29E-01
FPI	2.68E-01	1.02E-01	1.81E-02	4.40E-03
FFI	7.85E-02	1.78E-01	3.07E-02	6.06E-02
KSC	7.70E-01	7.43E-01	3.31E-03	3.20E-03

Table SI - 6 P/B ratio modifications as a result of climate change effect modeled over the 2091-2100 period (RCP 8.5).

Group	Scientific name	P/B current	ecology	T° current	Linf	M	F	T° RCP 8,5	M RCP 8,5	P/B RCP 8,5
Fish, Benthos Feeders	<i>Mullus surmuletus</i>	1.42	Demersal	13.01	46.83	0.20	1.22	15.30	0.21	1.43
	<i>Mustelus mustelus</i>	0.37	Demersal	13.01	175.00	0.12	0.25	15.30	0.13	0.38
	<i>Labrus bergylta</i>	1.42	Demersal	13.01	59.45	0.19	1.23	15.30	0.20	1.43
	<i>Zeus faber</i>	0.86	Benthopelagic	13.01	69.30	0.25	0.61	15.40	0.26	0.87
	<i>Scyliorhinus canicula</i>	0.44	Demersal	13.01	81.25	0.22	0.22	15.30	0.23	0.45
	<i>Trigloporus lastoviza</i>	0.55	Demersal	13.01	39.50	0.77	-0.22	15.30	0.82	0.60
	<i>Scyliorhinus stellaris</i>	0.44	Demersal	13.01	-	-	-	15.30	-	0.45
	<i>Raja montagui</i>	0.44	Demersal	13.01	78.02	0.33	0.11	15.30	0.35	0.46
	<i>Callionymus lyra</i>	0.82	Demersal	13.01	21.25	0.92	-0.10	15.30	0.97	0.87
	<i>Dicentrarchus labrax</i>	0.54	Demersal	13.01	82.70	0.20	0.34	15.30	0.21	0.55
	<i>Trisopterus luscus</i>	1.32	Benthopelagic	13.01	41.00	0.79	0.53	15.40	0.83	1.36
	<i>Spondyllosoma cantharus</i>	0.58	Demersal	13.01	42.20	0.36	0.22	15.30	0.38	0.60
	<i>Trisopterus minutus</i>	1.50	Benthopelagic	13.01	22.00	0.71	0.79	15.40	0.75	1.54
	<i>Pollachius pollachius</i>	0.62	Benthopelagic	13.01	85.60	0.27	0.35	15.40	0.29	0.64
Fish, Piscivorous	<i>Gadus morhua</i>	1.20	Benthopelagic	13.01	123.67	0.18	1.02	15.40	0.19	1.21
	<i>Merlangius merlangus</i>	1.07	Benthopelagic	13.01	42.70	0.52	0.55	15.40	0.55	1.10
	<i>Limanda limanda</i>	1.14	Demersal	13.01	25.60	0.79	0.35	15.30	0.84	1.19
Flat Fish	<i>Platichthys flesus</i>	0.56	Demersal	13.01	40.80	0.49	0.07	15.30	0.51	0.58
	<i>Solea solea</i>	0.70	Demersal	13.01	42.40	0.44	0.26	15.30	0.46	0.72
	<i>Pleuronectes platessa</i>	0.85	Demersal	13.01	59.40	0.22	0.63	15.30	0.23	0.86
	<i>Clupea harengus</i>	0.75	Benthopelagic	13.01	33.10	0.50	0.25	15.40	0.53	0.78
Fish, Planctivorous	<i>Engraulis encrasicolus</i>	0.58	Pelagic	13.02	18.60	0.79	-0.21	15.40	0.84	0.63
	<i>Hyperoplus lanceolatus</i>	1.12	Benthopelagic	13.01	29.40	0.64	0.48	15.40	0.67	1.15
	<i>Ammodytes tobianus</i>	1.12	Benthopelagic	13.01	19.70	1.08	0.04	15.40	1.14	1.18
	<i>Scomber scombrus</i>	0.83	Pelagic	13.02	39.40	0.57	0.26	15.40	0.61	0.87
	<i>Trachurus trachurus</i>	0.55	Pelagic	13.02	40.20	0.37	0.18	15.40	0.39	0.57
	<i>Chelidonichthys lucernus</i>	0.55	Demersal	13.01	48.40	0.34	0.21	15.30	0.36	0.57
	<i>Sardina pilchardus</i>	0.99	Pelagic	13.02	19.50	0.64	0.35	15.40	0.68	1.03
	<i>Sprattus sprattus</i>	1.34	Pelagic	13.02	17.50	0.59	0.75	15.40	0.62	1.37

Table SI - 7 Keystoneness values for each compartment of the model as computed in Libralato et al. (2006).

<i>Compartments</i>	<i>Mean BOWF keystoneness</i>	<i>Mean BOWF biomass</i>	<i>Mean REEF keystoneness</i>	<i>Mean REEF biomass</i>
<i>FBF</i>	1.75E-01	3.19E+00	1.87E-01	6.69E+00
<i>BAC</i>	4.48E-02	7.50E-01	5.26E-02	7.70E-01
<i>IPR</i>	1.20E-02	2.94E+00	2.47E-02	3.01E+00
<i>PHY</i>	-1.82E-03	3.24E+00	4.16E-03	3.24E+00
<i>FPI</i>	-2.28E-02	2.68E-01	-8.60E-03	1.02E-01
<i>ZOO</i>	-4.53E-02	1.72E+00	-3.80E-02	1.79E+00
<i>PHO</i>	-1.77E-01	9.41E-04	-1.62E-01	2.76E-03
<i>NEM</i>	-1.97E-01	9.70E-01	-1.89E-01	1.06E+00
<i>CEP</i>	-3.06E-01	1.98E-02	-2.94E-01	2.47E-02
<i>DET</i>	-3.62E-01	1.90E+01	-3.57E-01	1.90E+01
<i>FPL</i>	-3.64E-01	5.92E+00	-3.57E-01	4.76E+00
<i>KSC</i>	-3.70E-01	7.70E-01	-3.61E-01	7.43E-01
<i>FFI</i>	-3.94E-01	7.86E-02	-3.85E-01	1.78E-01
<i>BIV</i>	-4.11E-01	1.95E+01	-4.53E-01	4.29E+01
<i>SUP</i>	-4.14E-01	2.00E+00	-4.06E-01	1.71E+00
<i>BIR</i>	-4.89E-01	1.70E-02	-4.75E-01	2.25E-02
<i>IFF</i>	-6.21E-01	3.12E+00	-6.18E-01	4.78E+00
<i>IDF</i>	-6.21E-01	3.57E+00	-6.16E-01	2.98E+00
<i>CET</i>	-6.61E-01	4.29E-04	-6.47E-01	1.51E-04

Supplementary materials II.

Figure SII - 1 Sediment type in the eBoS.

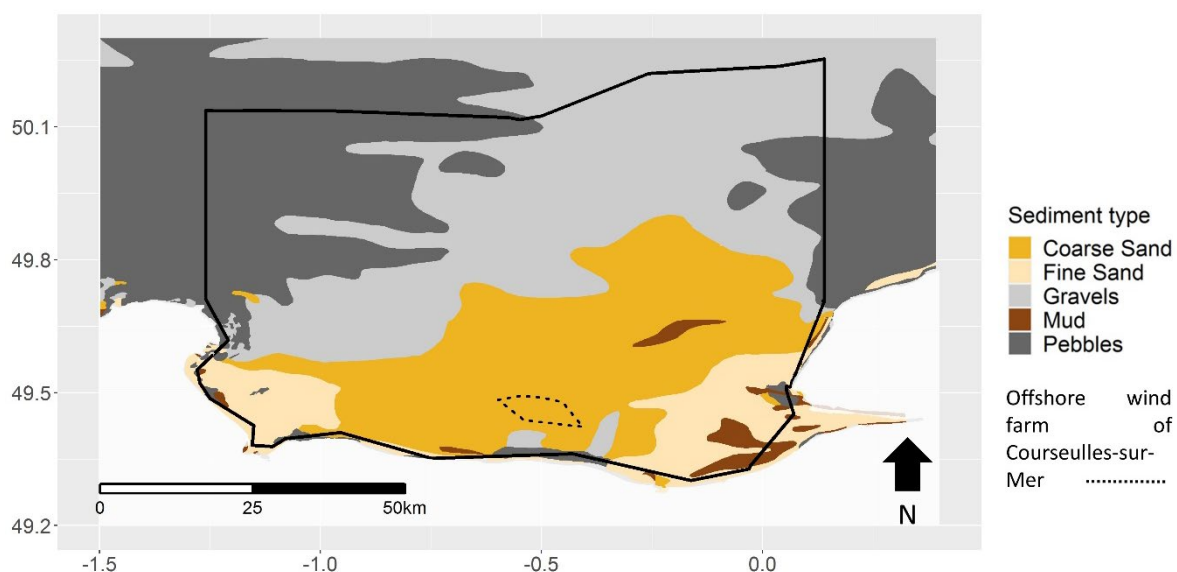


Table S II - 1 Absolute fishing landings of the eBoS model (t/km²/year).

Group name	Nets targeting demersal fish	Trawls targeting small pelagic fish	Trawls targeting demersal fish and cephalopods	Trawls targeting demersal fish	Other fishing gears	Dredge
Phytoplankton	0	0	0	0	0	0
Bacteria	0	0	0	0	0	0
Microzooplankton	0	0	0	0	0	0
Mesozooplankton and macrozooplankton	0	0	0	0	0	0
Meiofauna	0	0	0	0	0	0
Suprabenthos	0	0	0	0	0	0
Benthic inv. deposit feeders (Surface)	0	0	0	0	0	0
Benthic inv. deposit feeders (Subsurface)	0	0	0	0	0	0
King scallop	0.00037018	0	0.00082957	5.20E-05	0	0.3274384
Benthic inv. bivalves filter feeders	0	0	0	0	0	0
Benthic inv. filter feeders	0	0	0	0	0	0

Group name	Nets targeting demersal fish	Trawls targeting small pelagic fish	Trawls targeting demersal fish and cephalopods	Trawls targeting demersal fish	Other fishing gears	Dredge
Benthic inv. predators	0	0	0	0	0	0
Fish limande	0.00136914	8.20E-05	0.01360997	0.00010713	0.00083433	0
Fish flounder	0.00050364	1.83E-06	0.00117131	3.88E-06	9.69E-05	0
Fish European plaice	0.01160844	0.00063378	0.08738263	0.00046639	0.01348183	0
Fish sole	0.01994157	3.68E-05	0.02212876	6.84E-05	0.00728431	0
Fish sea bream	0.00010689	0.00089551	0.02305006	0.02742326	0.00043187	0
Fish benthos feeders	0.00216087	0.00035717	0.04413093	0.00041176	0.00157334	0
Fish planktivorous	0.00011777	0.05040085	0.00054509	3.65E-06	0.00105402	0
Fish piscivorous	0.00076925	0.00013645	0.01595292	0.00301107	0.00243441	0
Fish European sprat	0	0	0	0	0	0
Fish European pilchard	7.67E-06	0.3987412	0.00307695	0.00016376	6.11E-06	0
Fish poor cod	0	0	0	0	0	0
Fish pouting	0.00084178	0.00064293	0.079098	0.0030563	0.00331092	0
Fish gurnard	7.06E-05	0.00018195	0.02772665	0.00029845	0.00074049	0
Fish Atlantic horse mackerel	8.78E-05	0.02122579	0.00367715	0.00285164	0.00012468	0
Fish whiting	0.0002305	0.00101399	0.05385439	0.00033177	0.00144541	0
Fish Atlantic cod	0.01055186	0.00042124	0.03720592	0.00115248	0.00224472	0
Fish sharks	0.00890666	0.00078704	0.07944336	0.0044787	0.01426314	0
Fish rays	1.76E-05	3.11E-05	0.00204594	0.00026423	6.98E-05	0
Fish European seabass	0.00203618	0.00020811	0.01350535	0.00582477	0.00452945	0
Fish mackerel	0.00014466	0.05903089	0.03021581	0.00781924	0.00069502	0
Benthic cephalopods	9.75E-05	0	0.00060458	0	0.02756191	0
Benthopelagic cephalopods	8.97E-06	0.00034458	0.04951037	0.00069978	0.00103215	0
Surface feeders seabirds	0	0	0	0	0	0

Group name	Nets targeting demersal fish	Trawls targeting small pelagic fish	Trawls targeting demersal fish and cephalopods	Trawls targeting demersal fish	Other fishing gears	Dredge
Plunge and pursuit divers seabirds	0	0	0	0	0	0
Benthic feeders seabirds	0	0	0	0	0	0
Phocidae	0	0	0	0	0	0
Harbor porpoises	0	0	0	0	0	0
Bottlenose dolphins	0	0	0	0	0	0

Table S II - 2 Ecospace groups

Functional group id	Functional group	Ecology	Organism
1	Phytoplankton		
2	Bacteria		
3	Microzooplankton		
4	Mesozooplankton and macrozooplankton		
5	Meiofauna		
6	Suprabenthos		Invertebrate
7	Benthic inv. deposit feeders (surface)		Invertebrate
8	Benthic inv. deposit feeders (subsurface)		Invertebrate
9	King scallop	Benthic	Invertebrate
10	Benthic inv. bivalves filter feeders		Invertebrate
11	Benthic inv. filter feeders		Invertebrate
12	Benthic inv. predators		Invertebrate
13	Fish dab	Benthic	Fish
14	Fish flounder	Benthic	Fish
15	Fish European plaice	Benthic	Fish
16	Fish sole	Benthic	Fish
17	Fish sea bream	Demersal	Fish
18	Fish benthos feeders	Benthic	Fish
19	Fish planktivorous	Pelagic	Fish
20	Fish piscivorous	Benthopelagic	Fish
21	Fish European sprat	Pelagic	Fish
22	Fish European pilchard	Pelagic	Fish
23	Fish poor cod	Benthic	Fish
24	Fish pouting	Benthic	Fish
25	Fish gurnard	Benthic	Fish
26	Fish Atlantic horse mackerel	Benthopelagic	Fish

Functional group id	Functional group	Ecology	Organism
27	Fish whiting	Benthopelagic	Fish
28	Fish Atlantic cod	Demersal	Fish
29	Fish sharks	Demersal	Fish
30	Fish rays	Demersal	Fish
31	Fish European seabass	Demersal	Fish
32	Fish mackerel	Pelagic	Fish
33	Benthic cephalopods	Demersal	Invertebrate
34	Benthopelagic cephalopods	Benthopelagic	Invertebrate
35	Surface feeders seabirds		
36	Plunge and pursuit diverse seabirds		
37	Benthic feeders seabirds		
38	Phocidae		
39	Harbor porpoises		
40	Bottlenose dolphins		
41	Discards		
42	Detritus		

Table S II - 3 Ecospace environmental drivers

Group name	Environmental driver
Phytoplankton	Primary production map
Bacteria	Everywhere
Microzooplankton	Everywhere
Mesozooplankton and macrozooplankton	Everywhere
Meiofauna	Everywhere
Suprabenthos	Everywhere
Benthic inv. deposit feeders (Surface)	Suitability index map
Benthic inv. deposit feeders (Subsurface)	Suitability index map
King scallop	Suitability index map
Benthic inv. bivalves filter feeders	Suitability index map
Benthic inv. filter feeders	Suitability index map
Benthic inv. predators	Suitability index map
Fish dab	Suitability index map
Fish flounder	Suitability index map
Fish European plaice	Suitability index map
Fish sole	Suitability index map
Fish sea bream	Suitability index map
Fish benthos feeders	Suitability index map
Fish planktivorous	Suitability index map
Fish piscivorous	Suitability index map
Fish European sprat	Suitability index map
Fish European pilchard	Suitability index map
Fish poor cod	Suitability index map
Fish pouting	Suitability index map
Fish gurnard	Suitability index map
Fish Atlantic horse mackerel	Suitability index map
Fish whiting	Suitability index map
Fish Atlantic cod	Suitability index map
Fish sharks	Suitability index map
Fish rays	Suitability index map
Fish European seabass	Suitability index map
Fish mackerel	Suitability index map
Benthic cephalopods	Suitability index map
Benthopelagic cephalopods	Suitability index map
Surface feeders seabirds	Everywhere
Plunge and pursuit diverse seabirds	Everywhere
Benthic feeders seabirds	Depth dependent
Phocidae	Depth dependent
Harbor porpoises	Depth dependent
Bottlenose dolphins	Depth dependent
Discards	Everywhere
Detritus	Everywhere



Figure SII - 2 Response curve for phytoplankton driven by depth.



Figure SII - 3 Response curve for species with undefined habitats driven by depth.

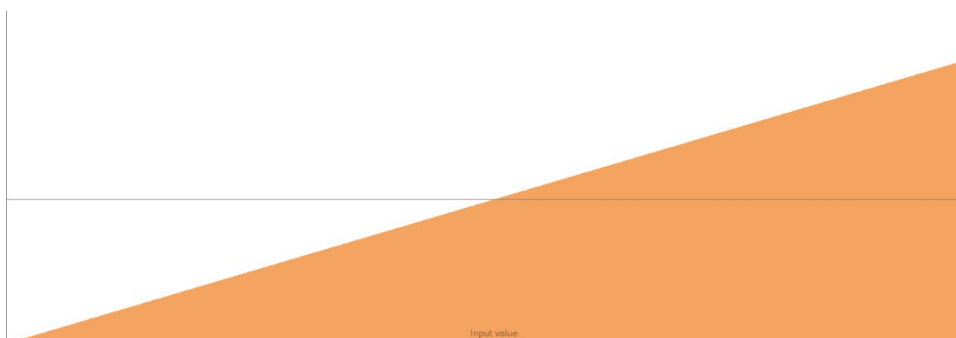


Figure SII - 4 Response curve for species driven by the suitability index map.

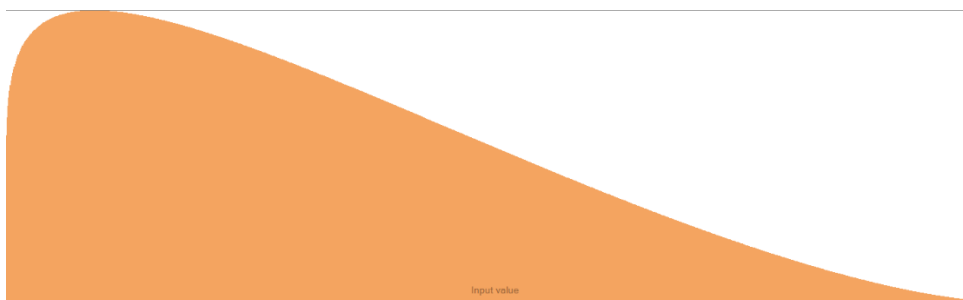


Figure SII - 5 Response curve for benthic feeding seabirds driven by depth.

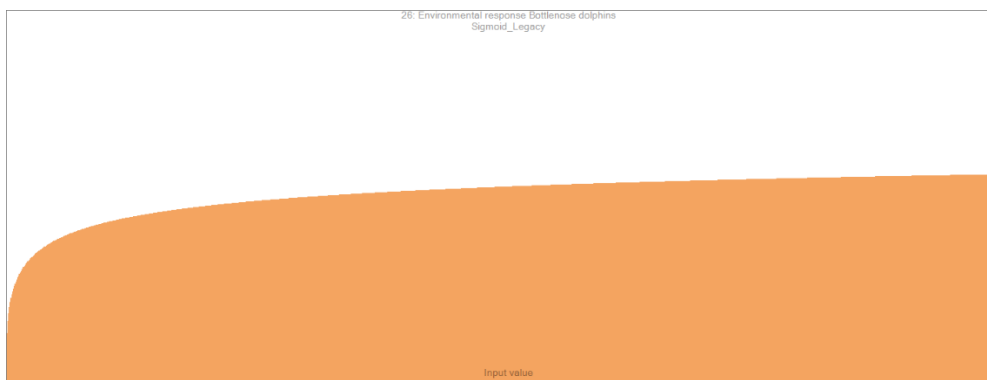


Figure SII - 6 Response curve for bottlenose dolphins driven by depth.

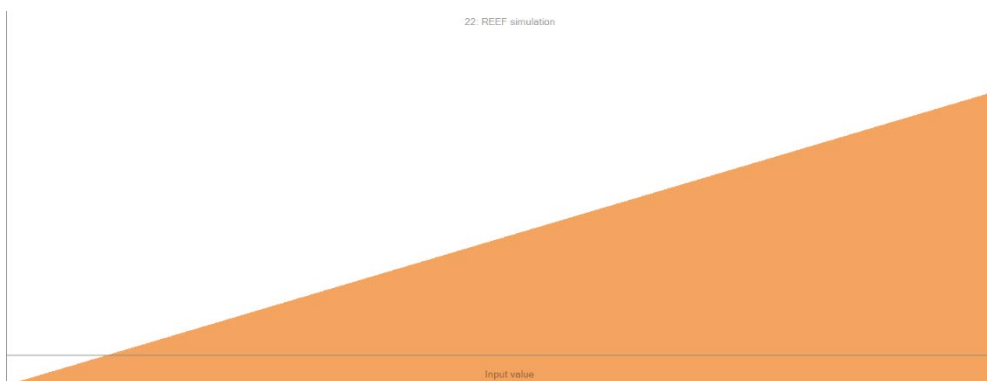


Figure SII - 7 Response curve for species impacted by the reef effect driven by the Ecospace reef factor.

Table S II - 4 Current fishing effort grid used in the reference scenario to set the value of the fishing effort.

Name	Nets targeting demersals and crustaceans	Pelagic and bottom trawls targeting small pelagic fish	Bottom trawls targeting demersals and cephalopods	Pelagic trawls targeting demersals	Other fishing gears	Dredge
2000	1.08	0.78	1.12	0.51	1.24	1.60
2001	1.08	0.78	1.12	0.51	1.24	1.60
[...]	1.08	0.78	1.12	0.51	1.24	1.60
	1.08	0.78	1.12	0.51	1.24	1.60
	1.08	0.78	1.12	0.51	1.24	1.60
	1.08	0.78	1.12	0.51	1.24	1.60
	1.08	0.78	1.12	0.51	1.24	1.60
	1.08	0.78	1.12	0.51	1.24	1.60
	1.08	0.78	1.12	0.51	1.24	1.60
	1.08	0.78	1.12	0.51	1.24	1.60
	1.08	0.78	1.12	0.51	1.24	1.60
2075	1.08	0.78	1.12	0.51	1.24	1.60

Table S II - 5 Brexit-linked decreased fishing effort grid used in the F_dec scenario to set fishing.

Name	Nets targeting demersals and crustaceans	Pelagic and bottom trawls targeting small pelagic fish	Bottom trawls targeting demersals and cephalopods	Pelagic trawls targeting demersals	Other fishing gears	Dredge
2000	1.08	0.63	0.90	0.41	1.18	1.28
2001	1.08	0.63	0.90	0.41	1.18	1.28
[...]	1.08	0.63	0.90	0.41	1.18	1.28
	1.08	0.63	0.90	0.41	1.18	1.28
	1.08	0.63	0.90	0.41	1.18	1.28
	1.08	0.63	0.90	0.41	1.18	1.28
	1.08	0.63	0.90	0.41	1.18	1.28
	1.08	0.63	0.90	0.41	1.18	1.28
	1.08	0.63	0.90	0.41	1.18	1.28
	1.08	0.63	0.90	0.41	1.18	1.28
	1.08	0.63	0.90	0.41	1.18	1.28
2075	1.08	0.63	0.90	0.41	1.18	1.28

Table S II - 6 Brexit-linked increased fishing effort grid used in the F_inc scenario to set fishing.

Name	Nets targeting demersals and crustaceans	Pelagic and bottom trawls targeting small pelagic fish	Bottom trawls targeting demersals and cephalopods	Pelagic trawls targeting demersals	Other fishing gears	Dredge
2000	1.08	0.94	1.35	0.61	1.30	1.36
2001	1.08	0.94	1.35	0.61	1.30	1.36
[...]	1.08	0.94	1.35	0.61	1.30	1.36
	1.08	0.94	1.35	0.61	1.30	1.36
	1.08	0.94	1.35	0.61	1.30	1.36
	1.08	0.94	1.35	0.61	1.30	1.36
	1.08	0.94	1.35	0.61	1.30	1.36
	1.08	0.94	1.35	0.61	1.30	1.36
	1.08	0.94	1.35	0.61	1.30	1.36
	1.08	0.94	1.35	0.61	1.30	1.36
	1.08	0.94	1.35	0.61	1.30	1.36
2075	1.08	0.94	1.35	0.61	1.30	1.36

Table S II - 7 Environmental drivers inside the OWF area for each specified group calculated according to Raoux et al. (2017) to model the reef effect inside the OWF of Courseulles-sur-Mer. The environmental driver value was set to 1 outside the OWF.

Raoux et al. (2017) groups	eBoS groups	Ecospace environmental driver inside the OWF
Surface feeders seabirds	Surface feeders seabirds	6.11
Fish Atlantic cod	Fish Atlantic cod	3.49
Fish whiting	Fish whiting	4.18
Fish pouting	Fish pouting	2.32
Fish benthos feeders	Fish benthos feeders	2.07
Fish sole	Fish sole	1.93
Other Flatfish	Fish flounder	4.37
	Fish dab	4.37
Benthic inv. predators	Benthic inv. predators	1.02
Benthic inv. filter feeders	Benthic inv. filter feeders	1.53
Benthic inv. bivalves	Benthic inv. bivalves	2.2

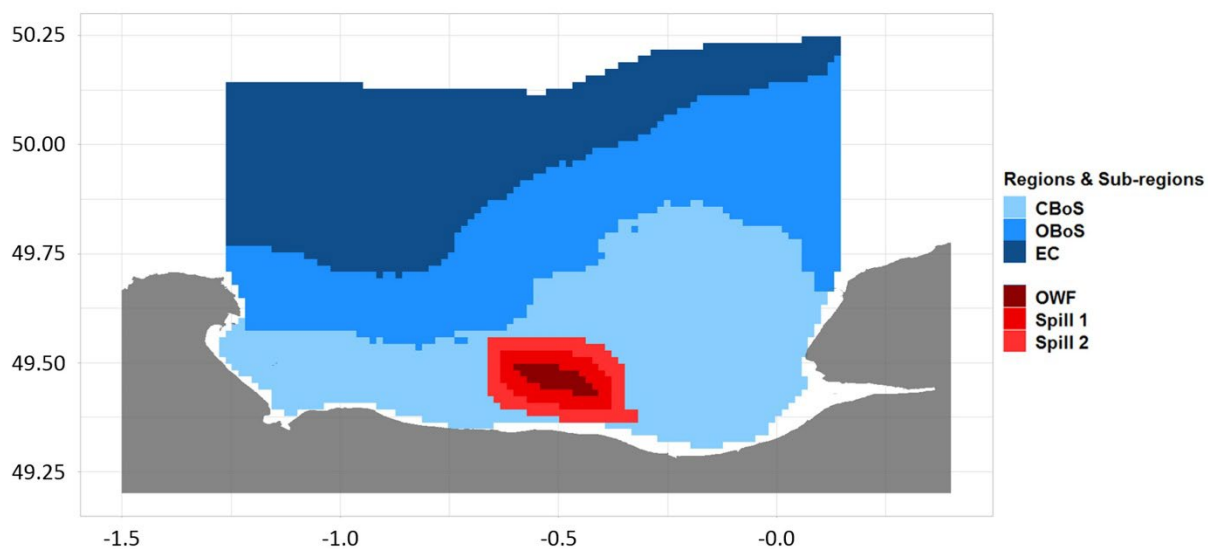


Figure SII - 8 All the regions and sub-regions of the extended Bay of Seine.

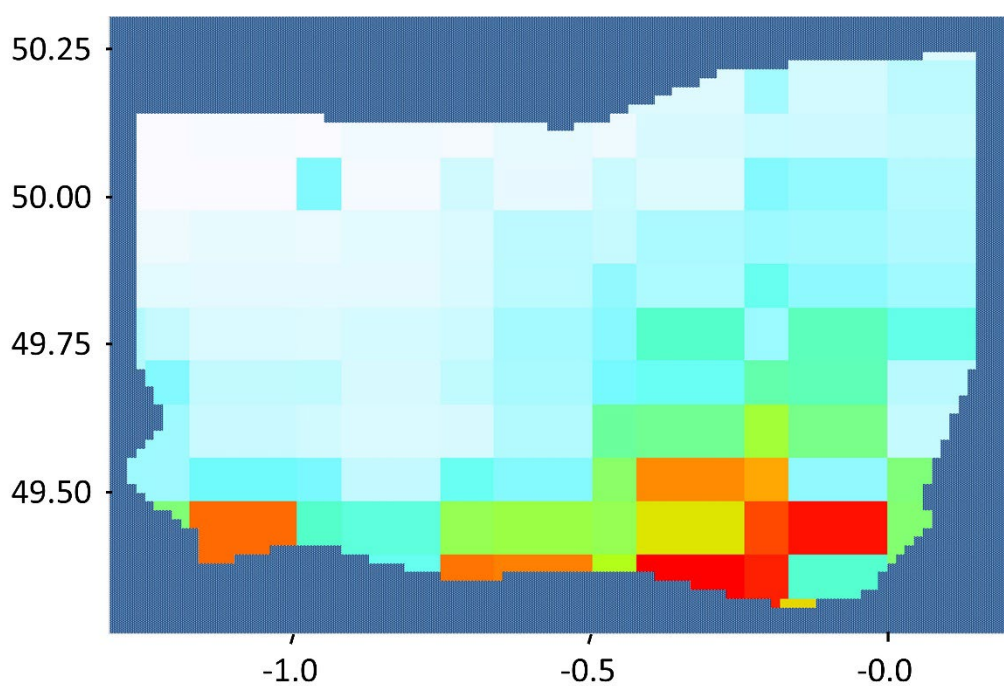


Figure SII - 9 Primary production map.

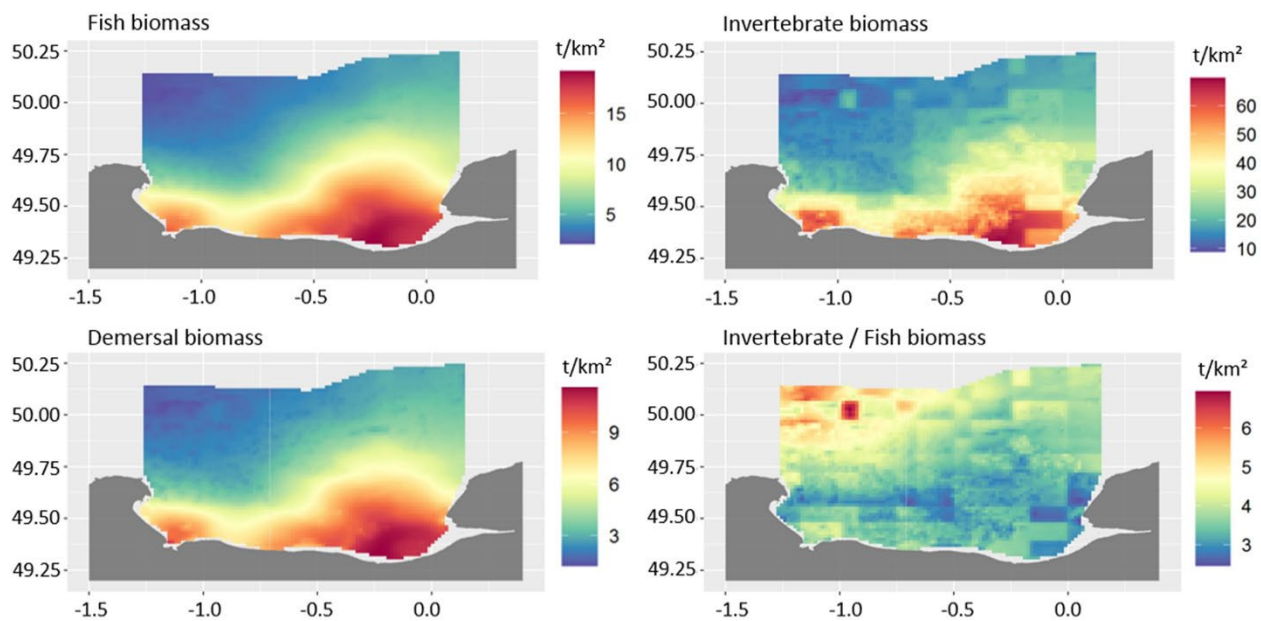


Figure SII - 10 Biomass of ecological groups in the reference scenario (wet weight).

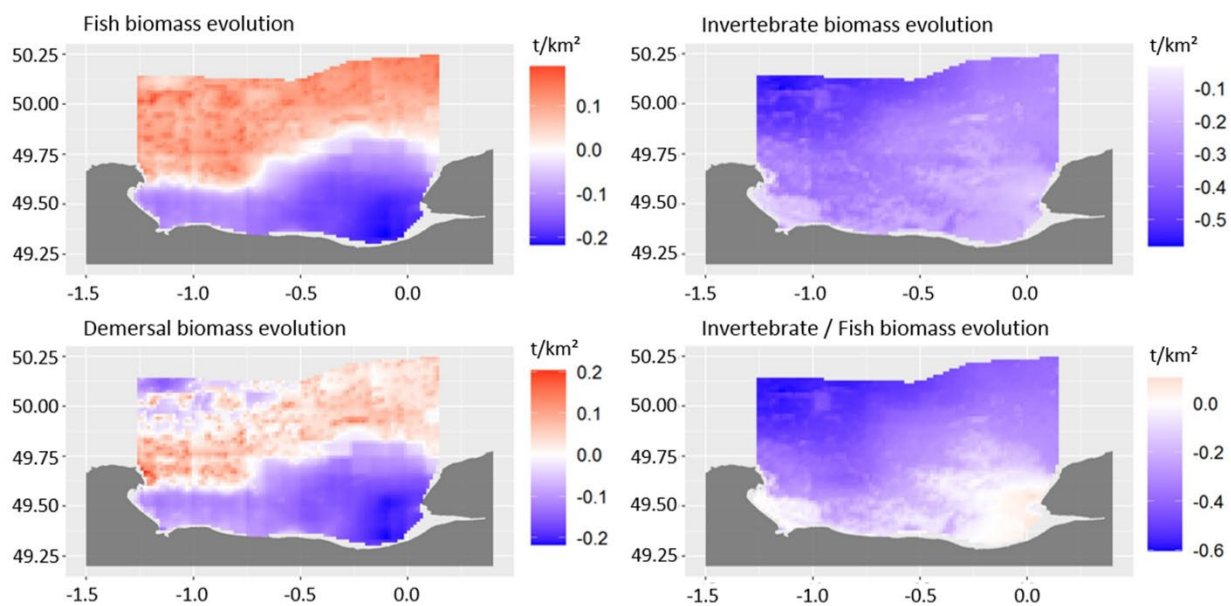


Figure SII - 11 Variation of ecological group rates between the reference and the 2100 climate change scenarios (wet weight).

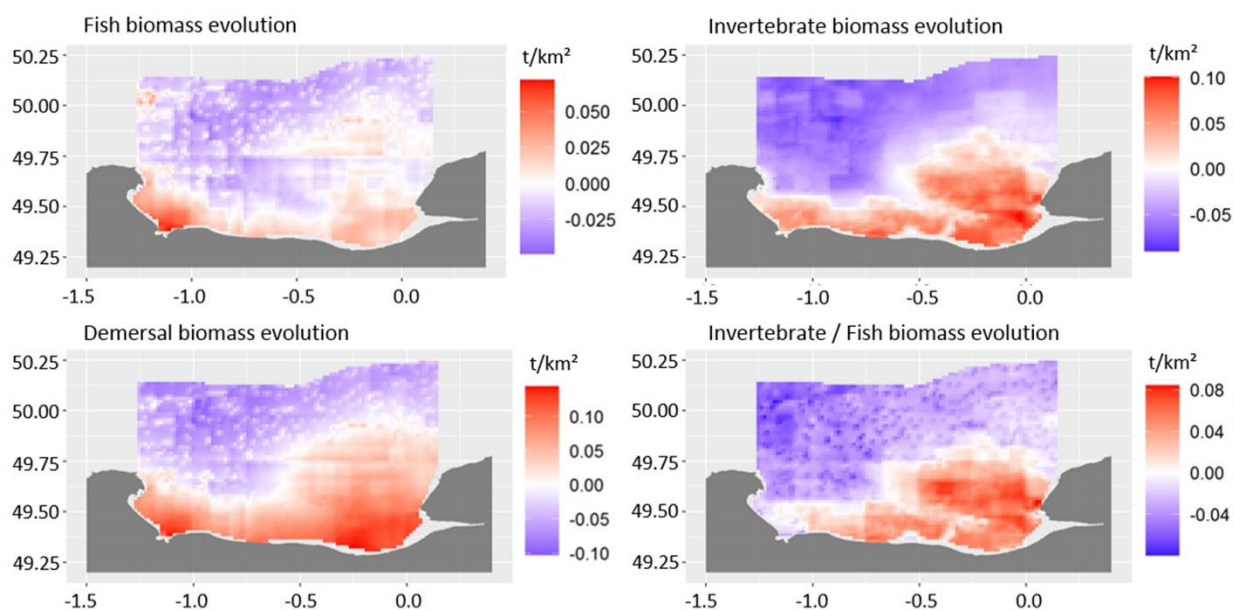


Figure SII - 12 Variation of ecological groups between the reference and the 2050 climate change scenarios (wet weight).

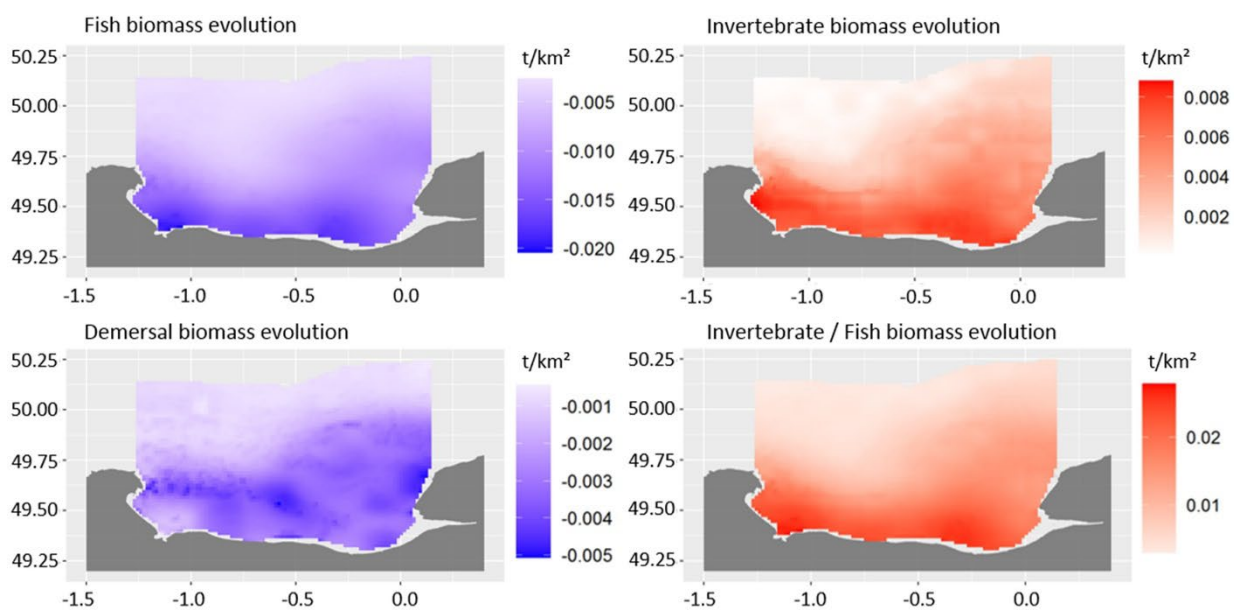


Figure SII - 13 Variation of ecological groups between the reference and the Fishing_inc brexit scenarios (wet weight).

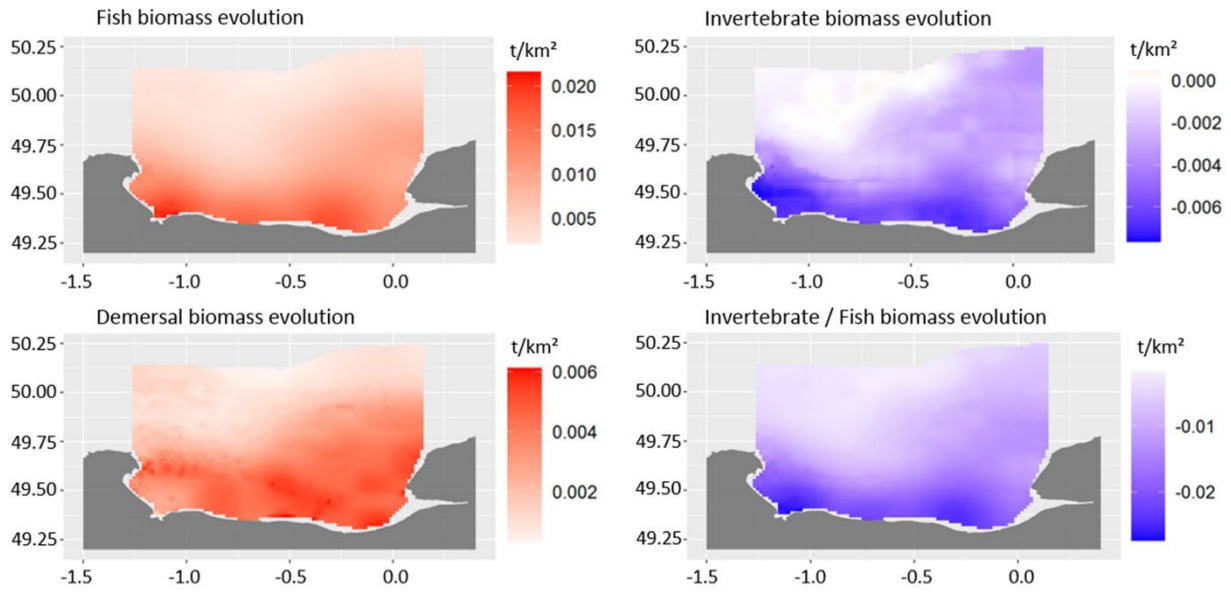


Figure SII - 14 Variation of ecological groups between the reference and the Fishing_red brexit scenarios (wet weight).

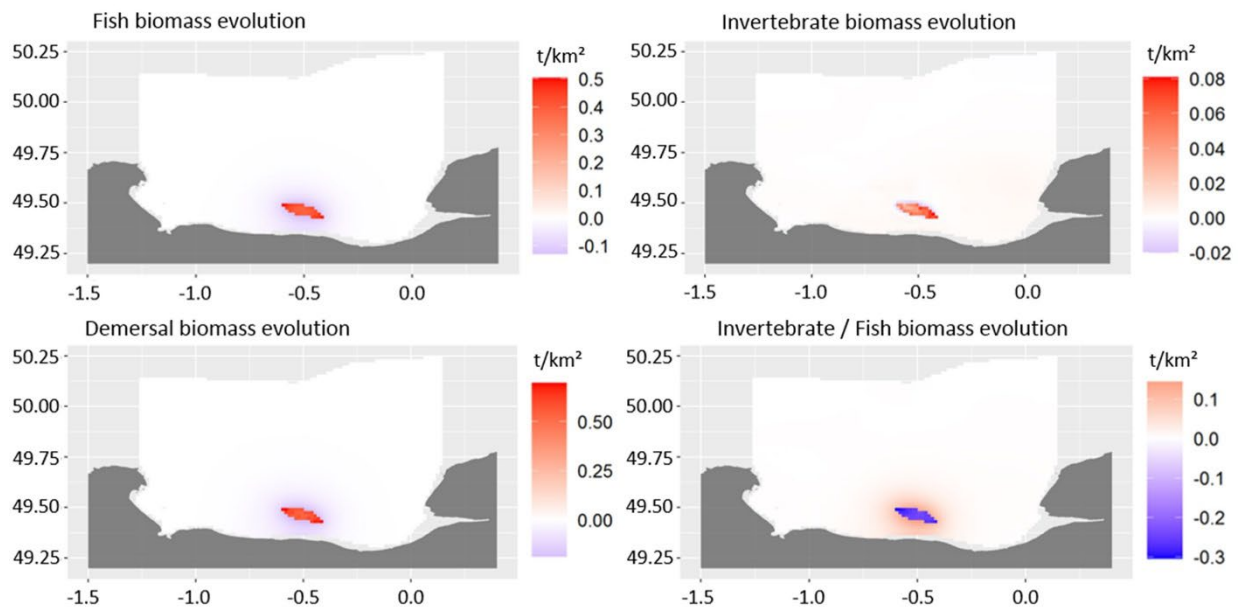


Figure SII - 15 Variation of ecological groups between the reference and the OWF scenarios (wet weight).

Supplementary materials III.

Table SIII - 1 Trophic groups of the eBoS Ecopath with Ecosim model.

Number of groups	Trophic groups	Environmental drivers
1	Phytoplankton	Primary production map
2	Bacteria	Everywhere
3	Microzooplankton	Everywhere
4	Mesozooplankton and macrozooplankton	Everywhere
5	Meiofauna	Everywhere
6	Suprabenthos	Everywhere
7	Benthic inv. deposit feeders (surface)	Suitability index map
8	Benthic inv. deposit feeders (subsurface)	Suitability index map
9	King scallop	Suitability index map
10	Benthic inv. bivalves filter feeders	Suitability index map
11	Benthic inv. filter feeders	Suitability index map
12	Benthic inv. predators	Suitability index map
13	Fish dab	Suitability index map
14	Fish flounder	Suitability index map
15	Fish European plaice	Suitability index map
16	Fish sole	Suitability index map
17	Fish sea bream	Suitability index map
18	Fish benthos feeders	Suitability index map
19	Fish planktivorous	Suitability index map
20	Fish piscivorous	Suitability index map
21	Fish European sprat	Suitability index map
22	Fish European pilchard	Suitability index map
23	Fish poor cod	Suitability index map
24	Fish pouting	Suitability index map
25	Fish gurnard	Suitability index map
26	Fish Atlantic horse mackerel	Suitability index map
27	Fish whiting	Suitability index map
28	Fish Atlantic cod	Suitability index map
29	Fish sharks	Suitability index map
30	Fish rays	Suitability index map
31	Fish European seabass	Suitability index map
32	Fish mackerel	Suitability index map
33	Benthic cephalopods	Suitability index map
34	Benthopelagic cephalopods	Suitability index map
35	Surface feeders seabirds	Everywhere
36	Plunge and pursuit diverse seabirds	Everywhere
37	Benthic feeders seabirds	Depth dependent
38	Phocidae	Depth dependent
39	Harbor porpoises	Depth dependent
40	Bottlenose dolphins	Depth dependent
41	Discards	Everywhere
42	Detritus	Everywhere

Table SIII - 2 Decreasing fishing effort scenario due to Brexit used in the *F_dec* scenario.

Name	Nets targeting demersals and crustaceans	Pelagic and bottom trawls targeting small pelagic fish	Bottom trawls targeting demersals and cephalopods	Pelagic trawls targeting demersals	Other fishing gears	Dredge
2000	1.08	0.63	0.90	0.41	1.18	1.28
2001	1.08	0.63	0.90	0.41	1.18	1.28
[...]	1.08	0.63	0.90	0.41	1.18	1.28
	1.08	0.63	0.90	0.41	1.18	1.28
	1.08	0.63	0.90	0.41	1.18	1.28
	1.08	0.63	0.90	0.41	1.18	1.28
	1.08	0.63	0.90	0.41	1.18	1.28
	1.08	0.63	0.90	0.41	1.18	1.28
	1.08	0.63	0.90	0.41	1.18	1.28
	1.08	0.63	0.90	0.41	1.18	1.28
	1.08	0.63	0.90	0.41	1.18	1.28
2075	1.08	0.63	0.90	0.41	1.18	1.28

Table SIII - 3. Increasing fishing effort scenario due to Brexit used in the *F_inc* scenario.

Name	Nets targeting demersals and crustaceans	Pelagic and bottom trawls targeting small pelagic fish	Bottom trawls targeting demersals and cephalopods	Pelagic trawls targeting demersals	Other fishing gears	Dredge
2000	1.08	0.94	1.35	0.61	1.30	1.36
2001	1.08	0.94	1.35	0.61	1.30	1.36
[...]	1.08	0.94	1.35	0.61	1.30	1.36
	1.08	0.94	1.35	0.61	1.30	1.36
	1.08	0.94	1.35	0.61	1.30	1.36
	1.08	0.94	1.35	0.61	1.30	1.36
	1.08	0.94	1.35	0.61	1.30	1.36
	1.08	0.94	1.35	0.61	1.30	1.36
	1.08	0.94	1.35	0.61	1.30	1.36
	1.08	0.94	1.35	0.61	1.30	1.36
	1.08	0.94	1.35	0.61	1.30	1.36
2075	1.08	0.94	1.35	0.61	1.30	1.36

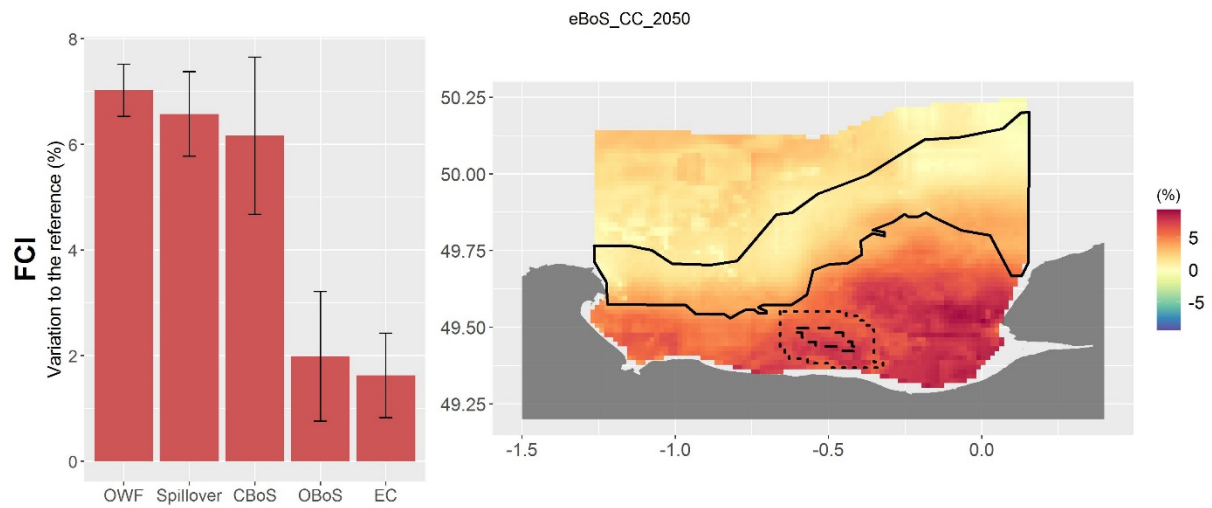


Figure SIII - 1 RCP 8.5 2050 climate change scenario effect on recycling (FCI).

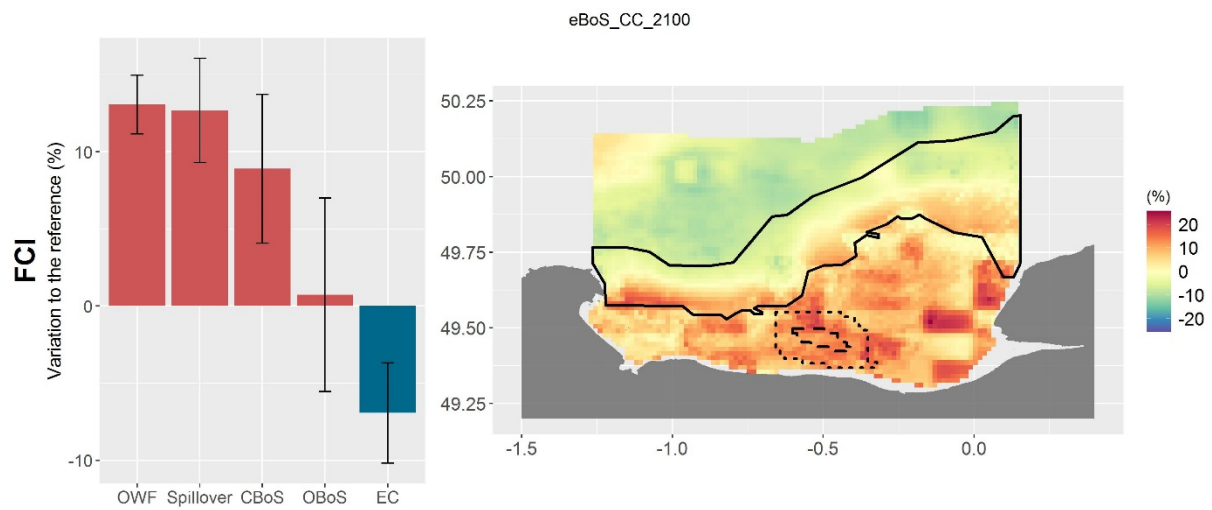


Figure SIII - 2 RCP 8.5 2100 climate change scenario effect on recycling (FCI).

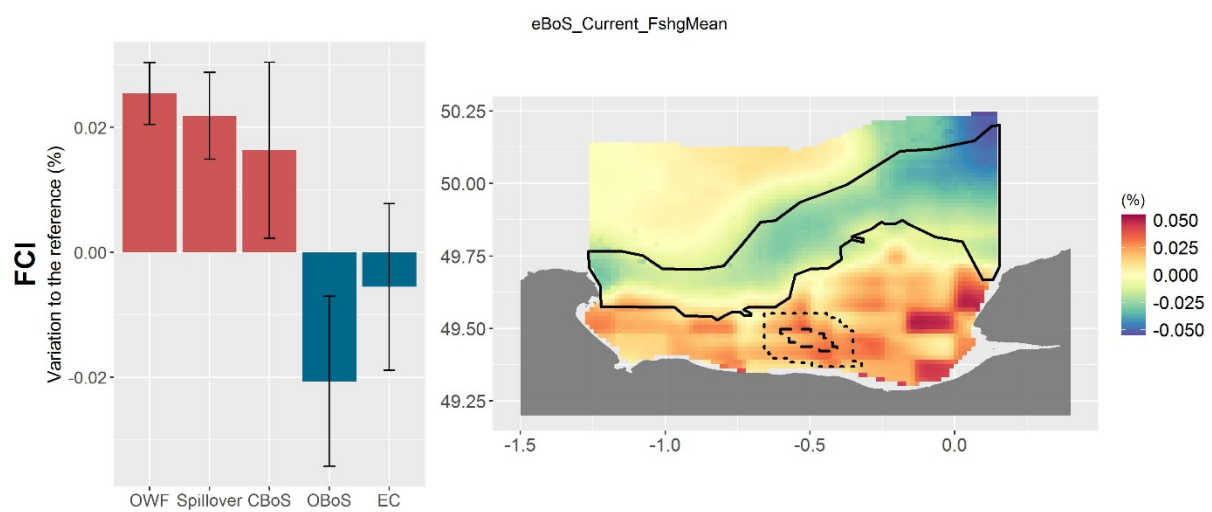


Figure SIII - 3 Averaged Brexit scenario effect on recycling (FCI).

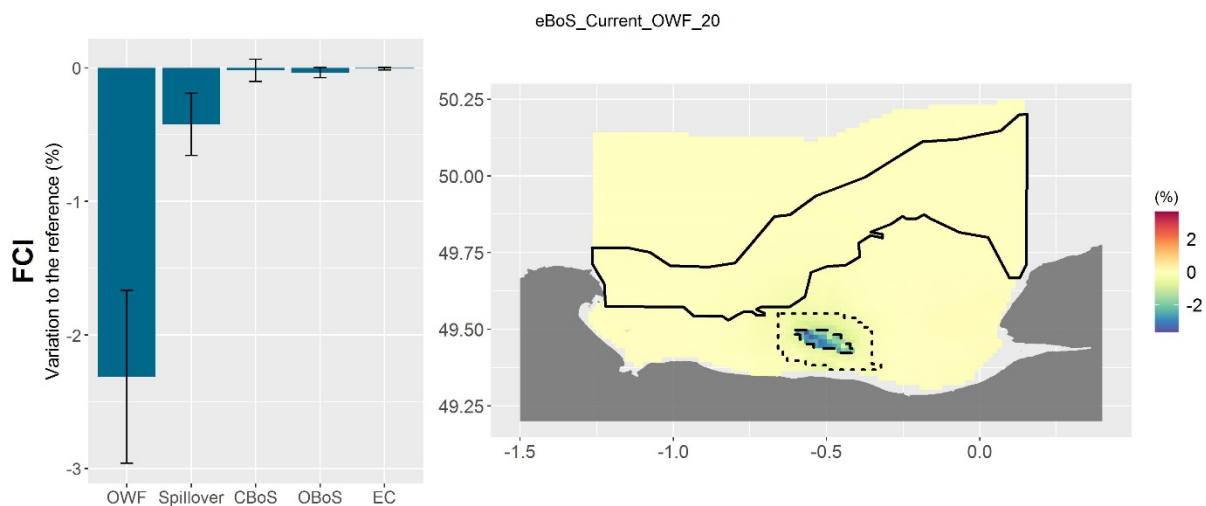


Figure SIII - 4 Offshore wind farm effect on recycling (FCI).

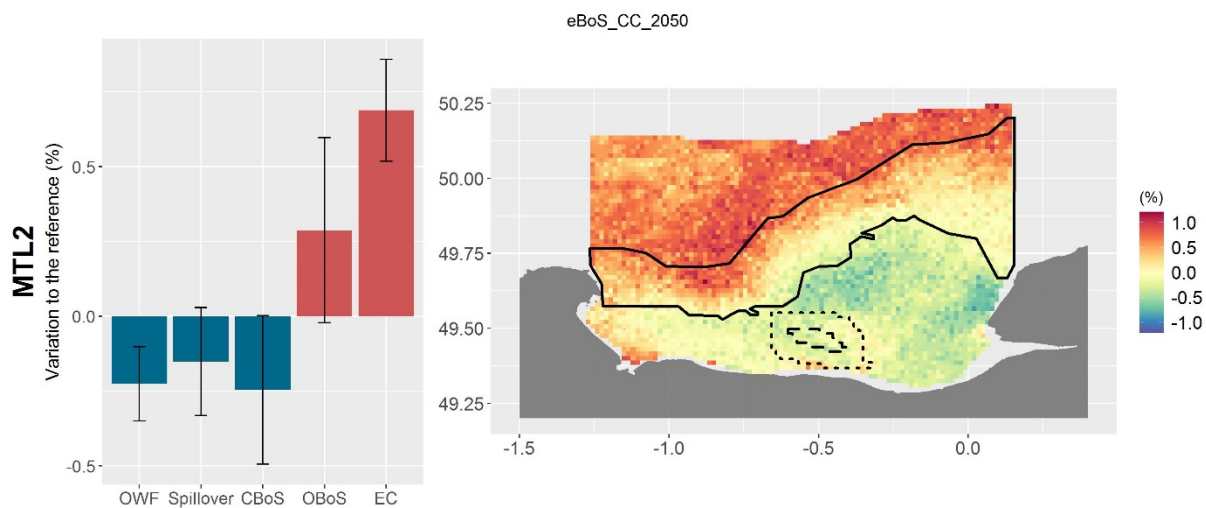


Figure SIII - 5 RCP 8.5 2050 climate change scenario effect on the mean trophic level (MTL2).

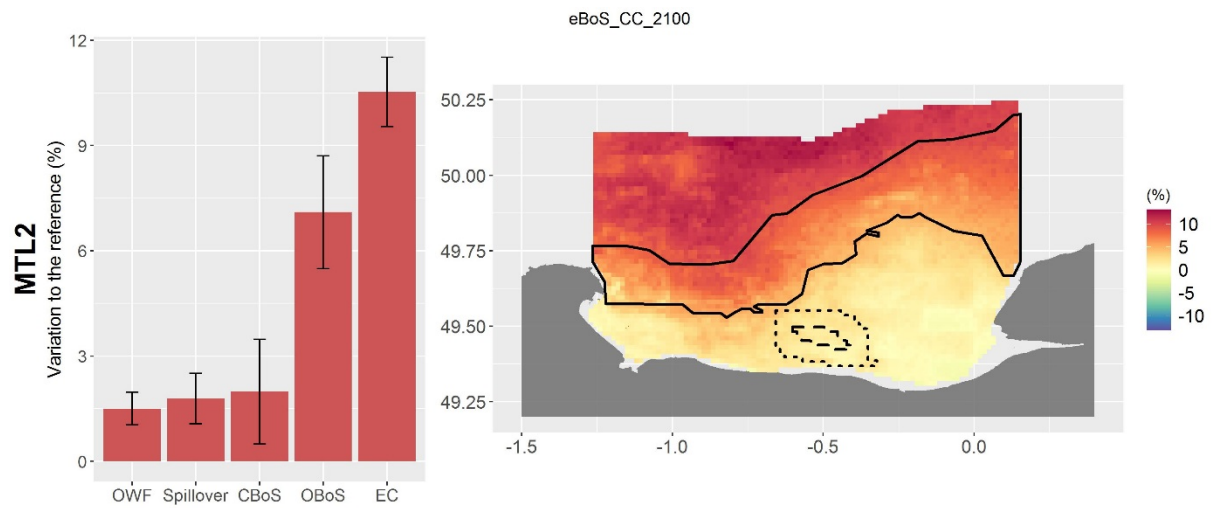


Figure SIII - 6 RCP 8.5 2100 climate change scenario effect on the mean trophic level (MTL2).

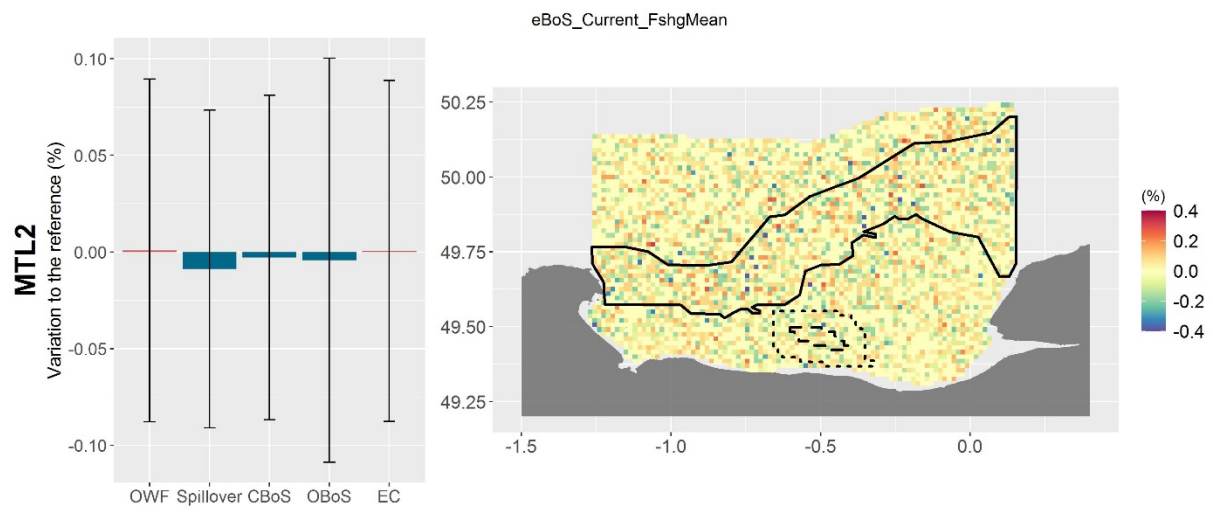


Figure SIII - 7 Averaged Brexit scenario effect on the mean trophic level (MTL2).

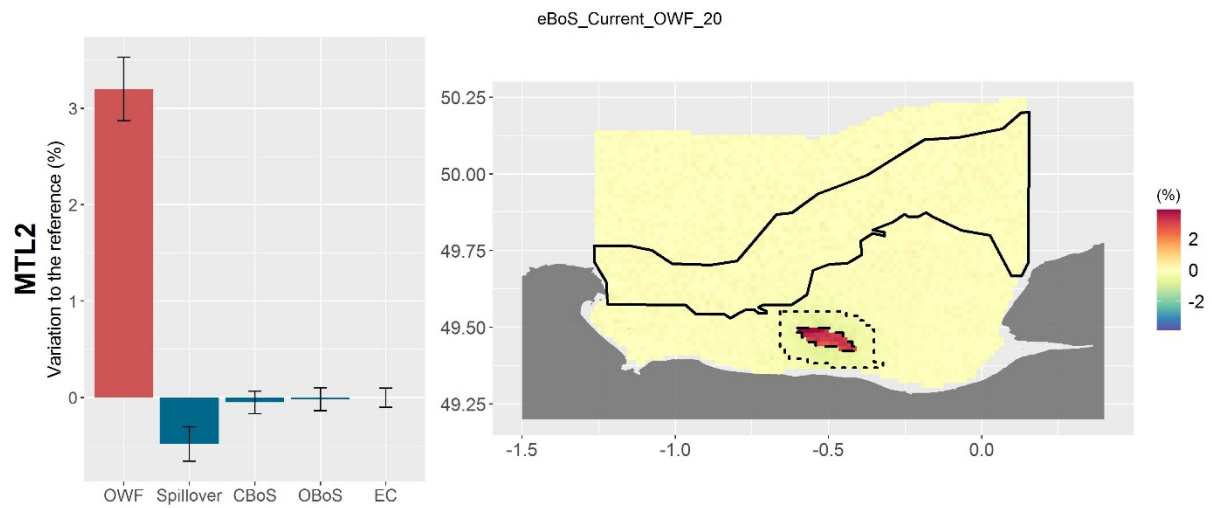


Figure SIII - 8 Offshore wind farm effect on the mean trophic level (MTL2).

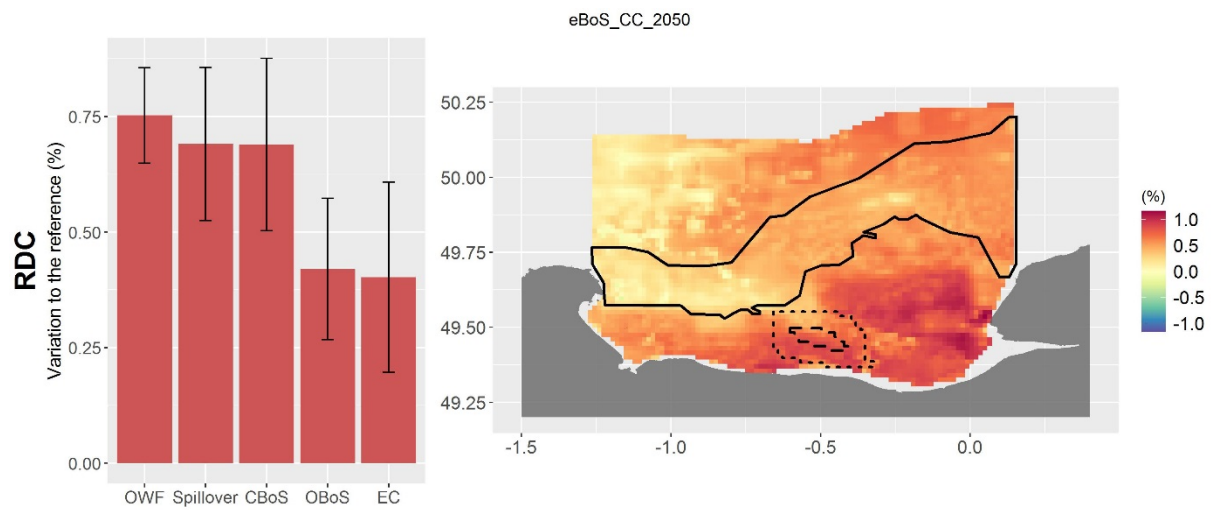


Figure SIII - 9 RCP 8.5 2050 climate change scenario effect on the relative redundancy of the flow (RDC).

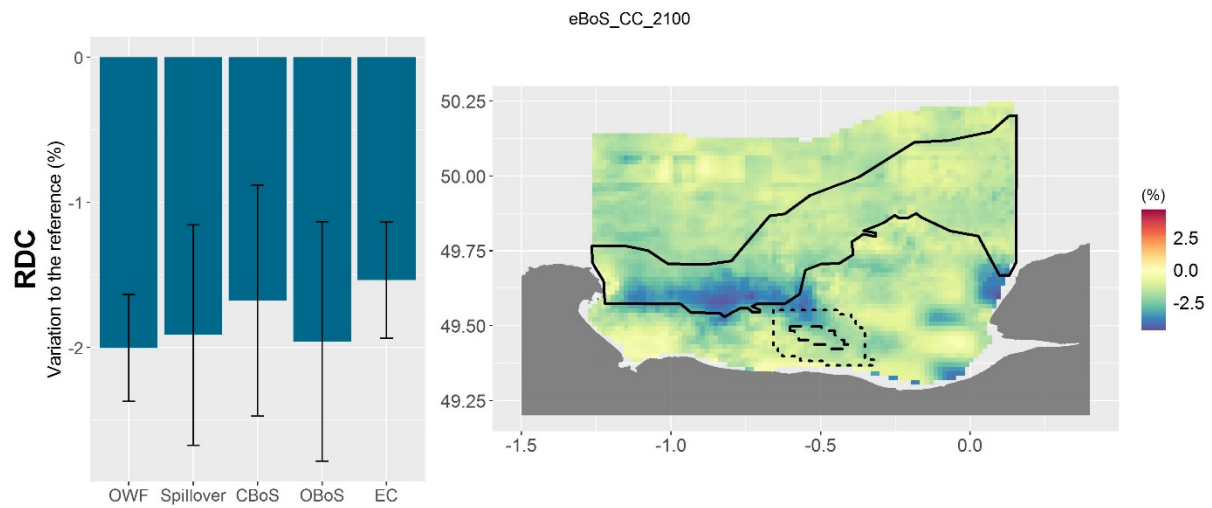


Figure SIII - 10 RCP 8.5 2100 climate change scenario effect on the relative redundancy of the flow (RDC).

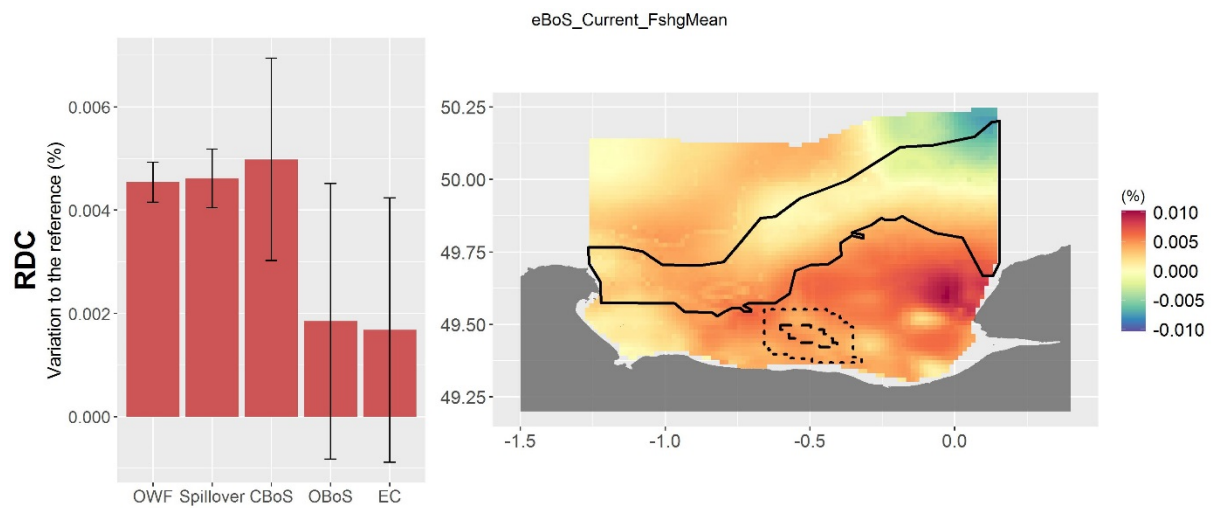


Figure SIII - 11 Averaged Brexit scenario effect on the relative redundancy of the flow (RDC).

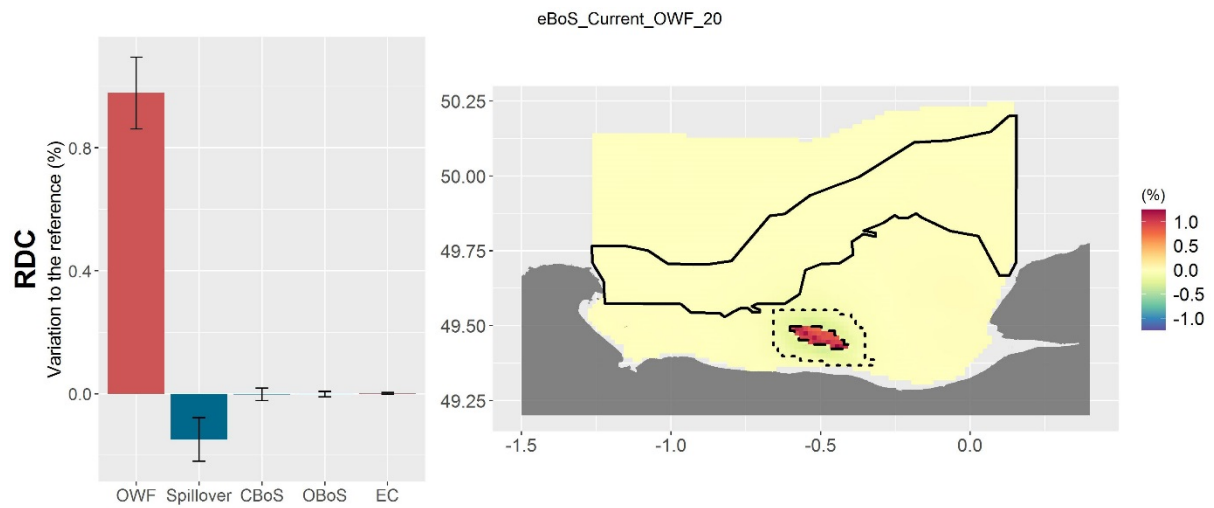


Figure SIII - 12 Offshore wind farm effect on the relative redundancy of the flow (RDC).

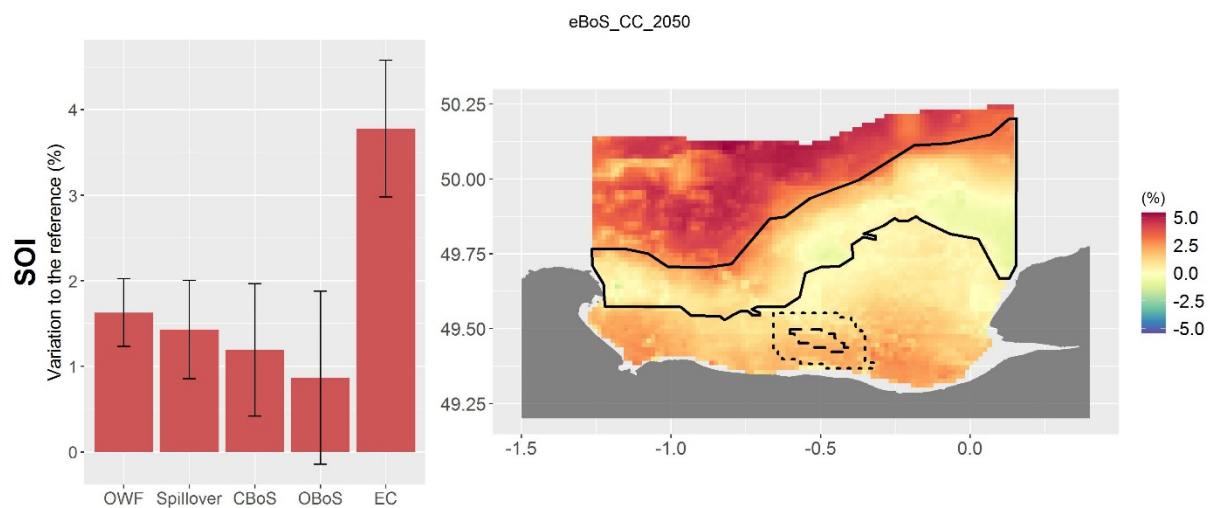


Figure SIII - 13 RCP 8.5 2050 climate change scenario effect on the system omnivory (SOI).

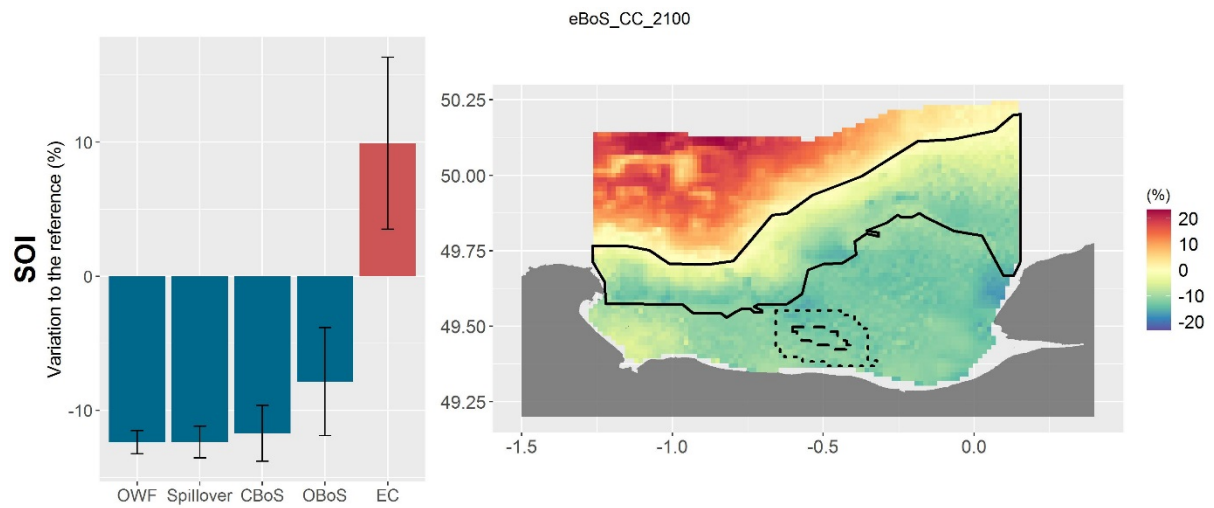


Figure SIII - 14 RCP 8.5 2100 climate change scenario effect on the system omnivory (SOI).

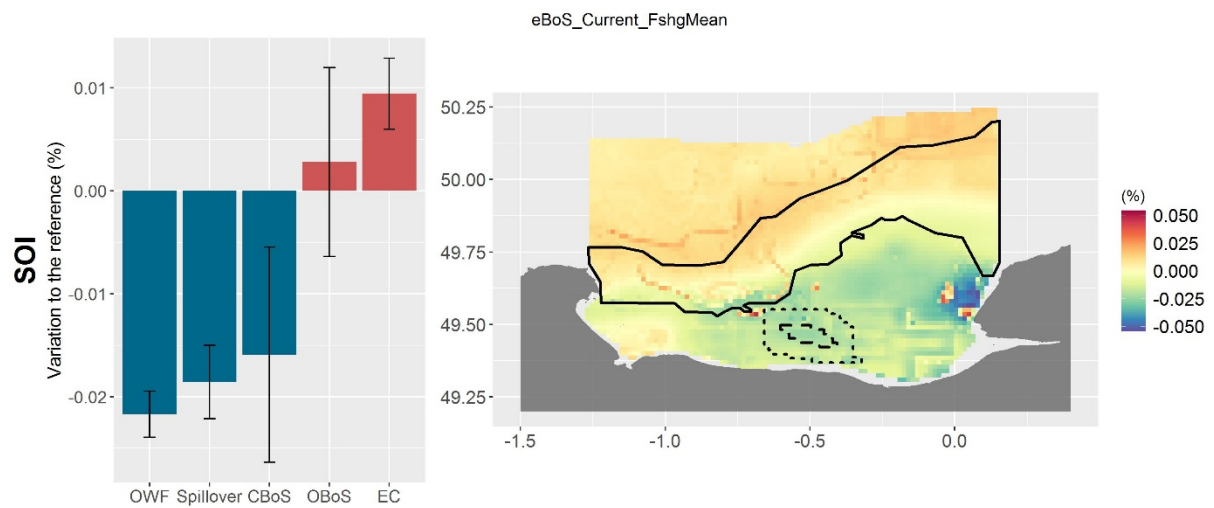


Figure SIII - 15 Averaged Brexit scenario effect on the system omnivory (SOI).

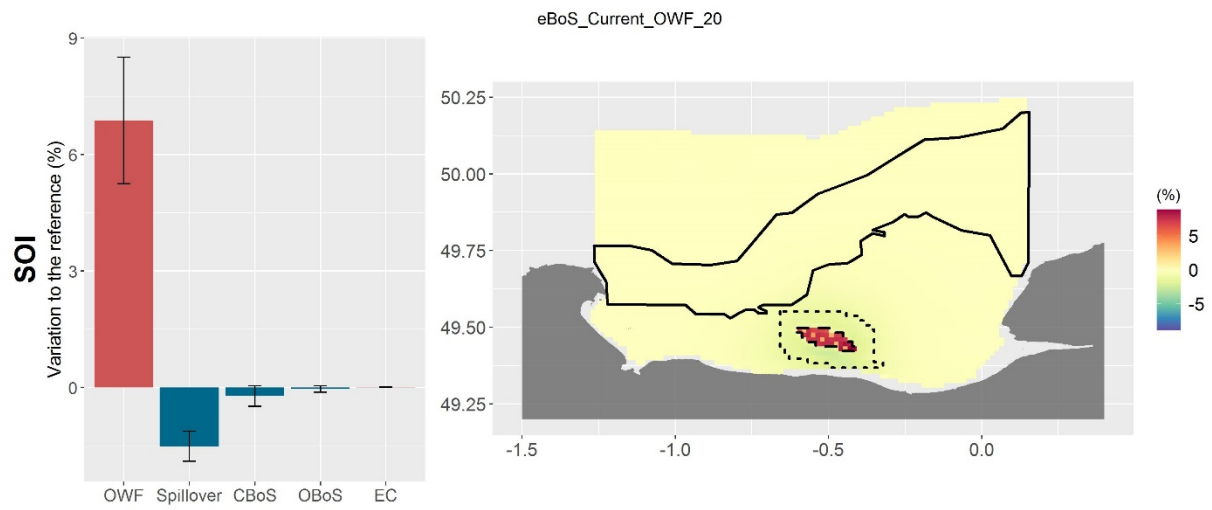


Figure SIII - 16 Offshore wind farm effect on the system omnivory (SOI).

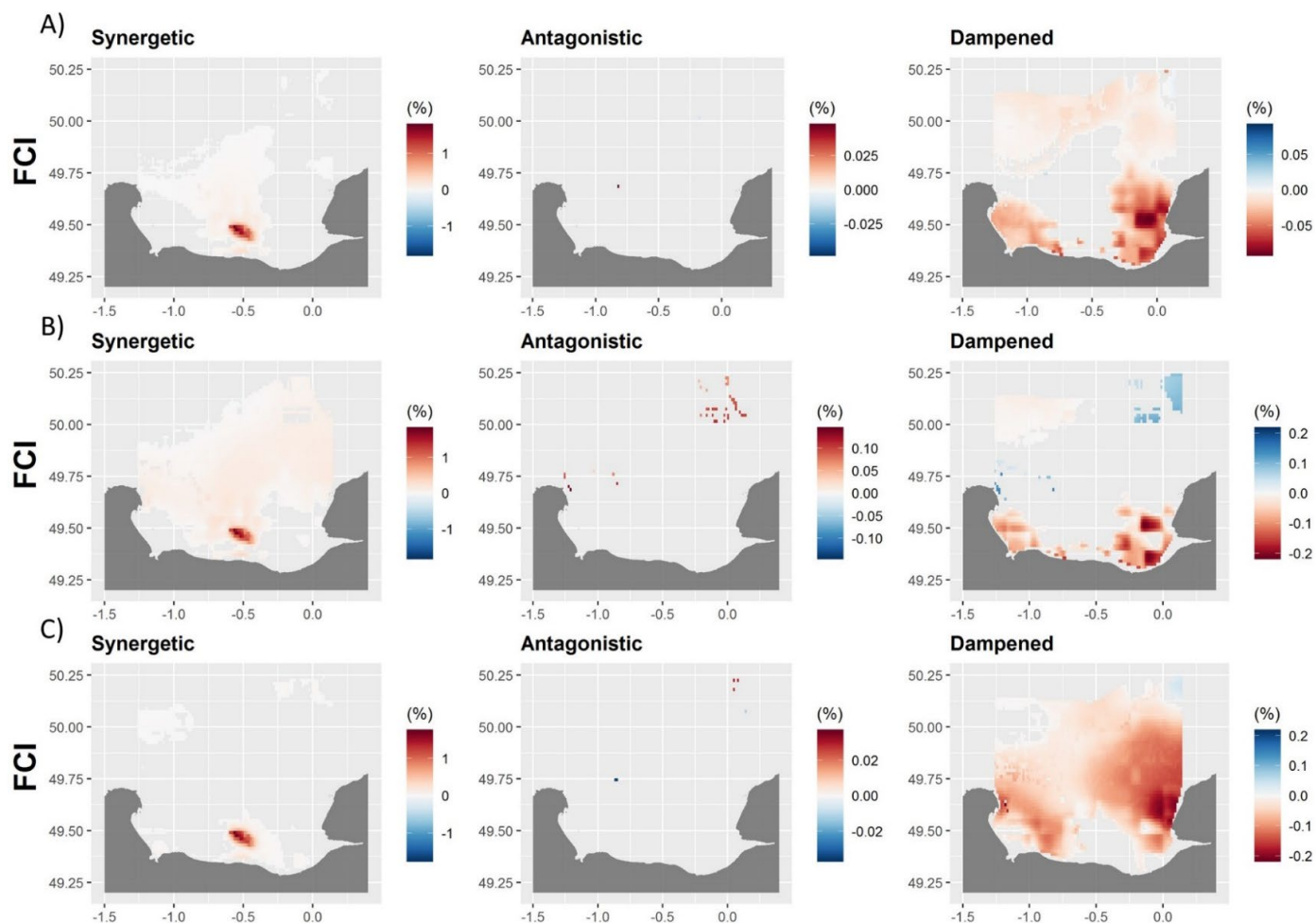


Figure SIII - 17 Cumulative effects for each Brexit scenario on recycling (FCI), with the offshore wind farm (OWF) and the 2050 RCP 8.5 climate change (2050 CC) effects on species distribution.

A), Cumulative effects of the OWF, 2050 CC and the absence of fishing variation due to Brexit (F_sam); B), Cumulative effects of the OWF, 2050 CC and increased fishing due to Brexit (F_inc); C), Cumulative effects of the OWF, 2050 CC and decreased fishing due to Brexit (F_dec). Red, positive cumulative effects compared to the reference; blue, negative cumulative effects compared to the reference.

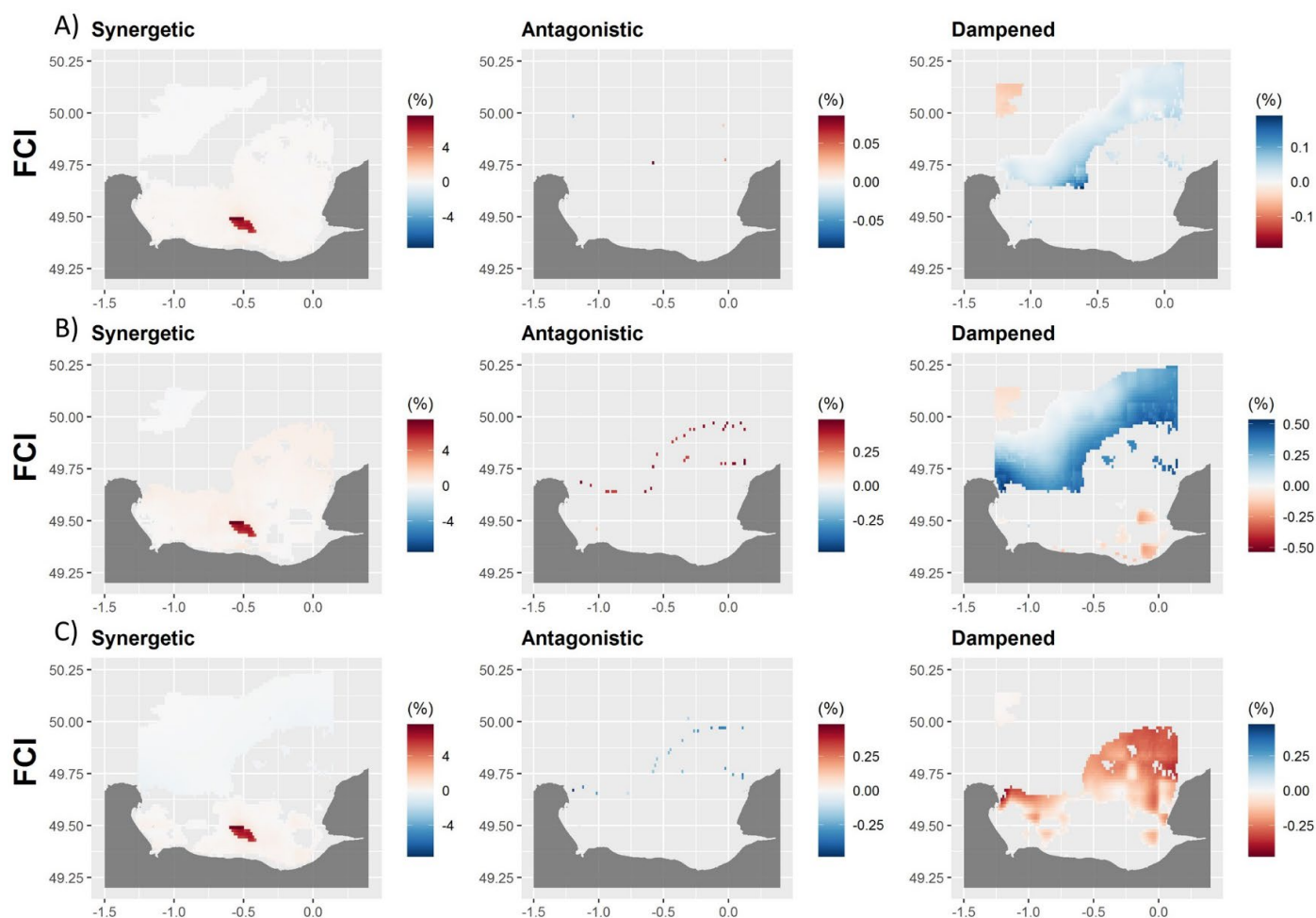


Figure SIII - 18 Cumulative effects for each Brexit scenario on recycling (FCI), with the offshore wind farm (OWF) and the 2100 RCP 8.5 climate change (2100 CC) effects on species distribution.

A), Cumulative effects of the OWF, 2100 CC and the absence of fishing variation due to Brexit (F_{sam}); B), Cumulative effects of the OWF, 2100 CC and increased fishing due to Brexit (F_{inc}); C), Cumulative effects of the OWF, 2100 CC and decreased fishing due to Brexit (F_{dec}). Red, positive cumulative effects compared to the reference; blue, negative cumulative effects compared to the reference.

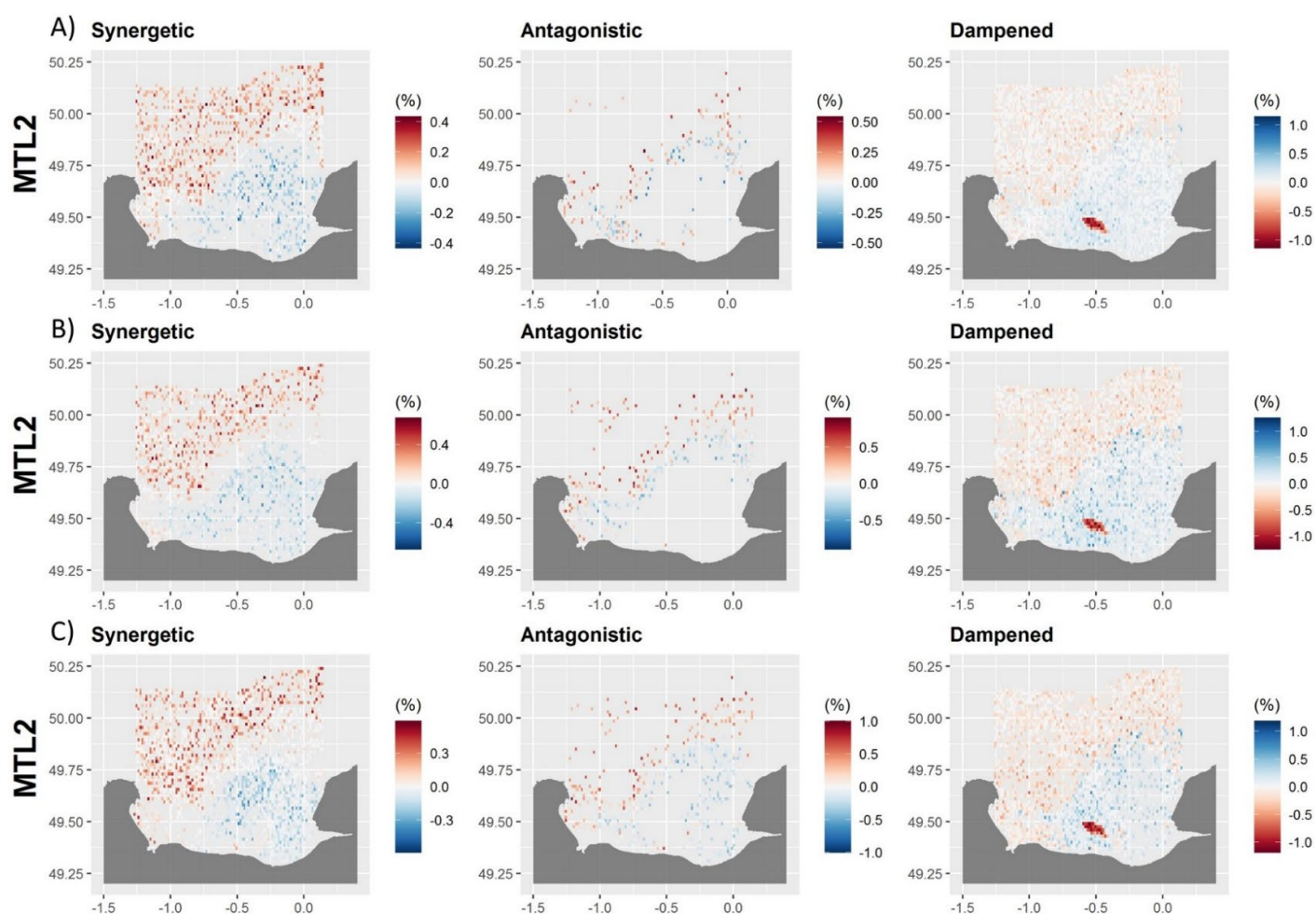


Figure SIII - 19 Cumulative effects for each Brexit scenario on the mean trophic level (MTL2), with the offshore wind farm (OWF) and the 2050 RCP 8.5 climate change (2050 CC) effects on species distribution.

A), Cumulative effects of the OWF, 2050 CC and the absence of fishing variation due to Brexit (F_{sam}); B), Cumulative effects of the OWF, 2050 CC and increased fishing due to Brexit (F_{inc}); C), Cumulative effects of the OWF, 2050 CC and decreased fishing due to Brexit (F_{dec}). Red, positive cumulative effects compared to the reference; blue, negative cumulative effects compared to the reference.

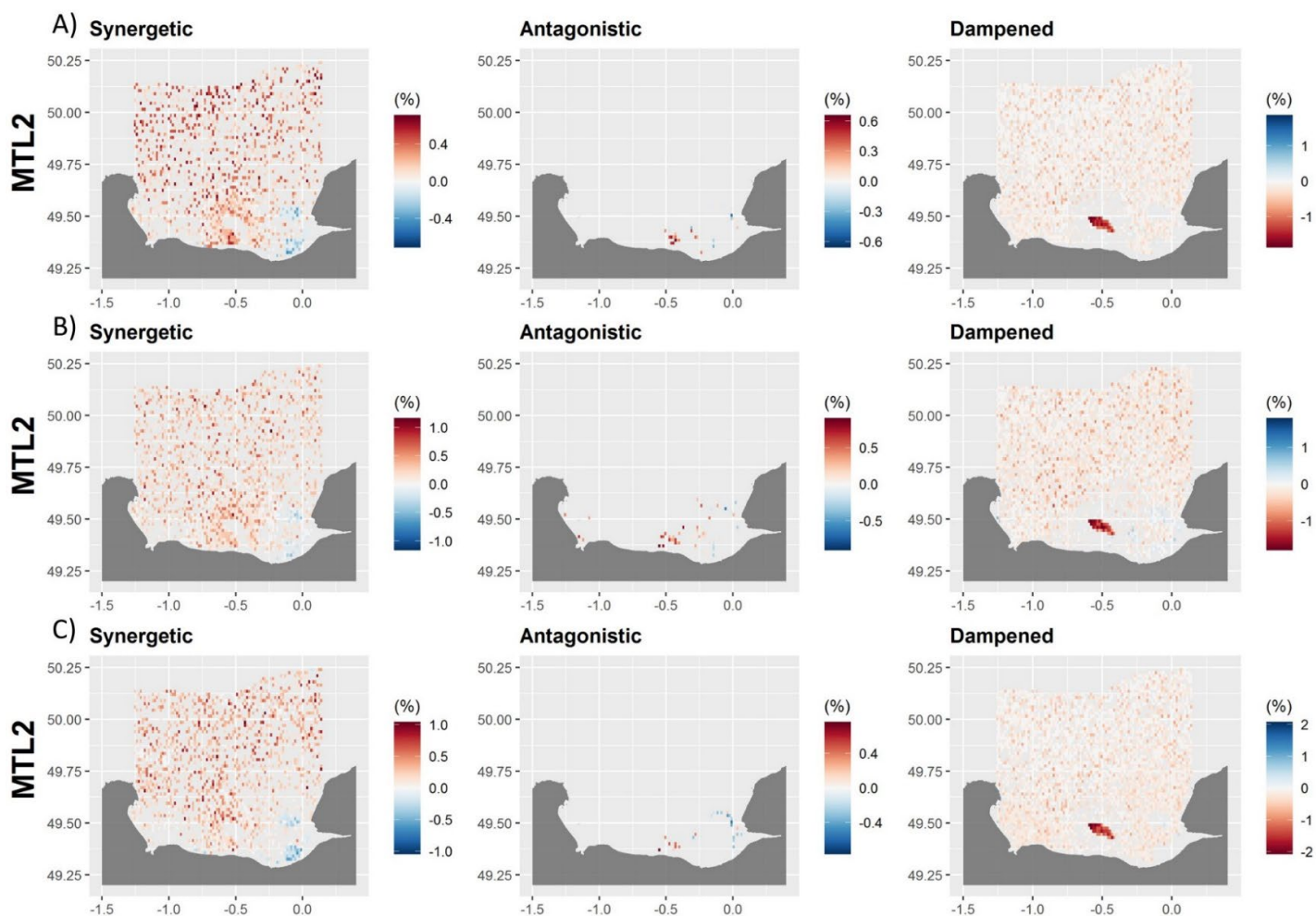


Figure SIII - 20 Cumulative effects for each Brexit scenario on the mean trophic level (MTL2), with the offshore wind farm (OWF) and the 2100 RCP 8.5 climate change (2100 CC) effects on species distribution.

A), Cumulative effects of the OWF, 2100 CC and the absence of fishing variation due to Brexit (F_{sam}); B), Cumulative effects of the OWF, 2100 CC and increased fishing due to Brexit (F_{inc}); C), Cumulative effects of the OWF, 2100 CC and decreased fishing due to Brexit (F_{dec}). Red, positive cumulative effects compared to the reference; blue, negative cumulative effects compared to the reference.

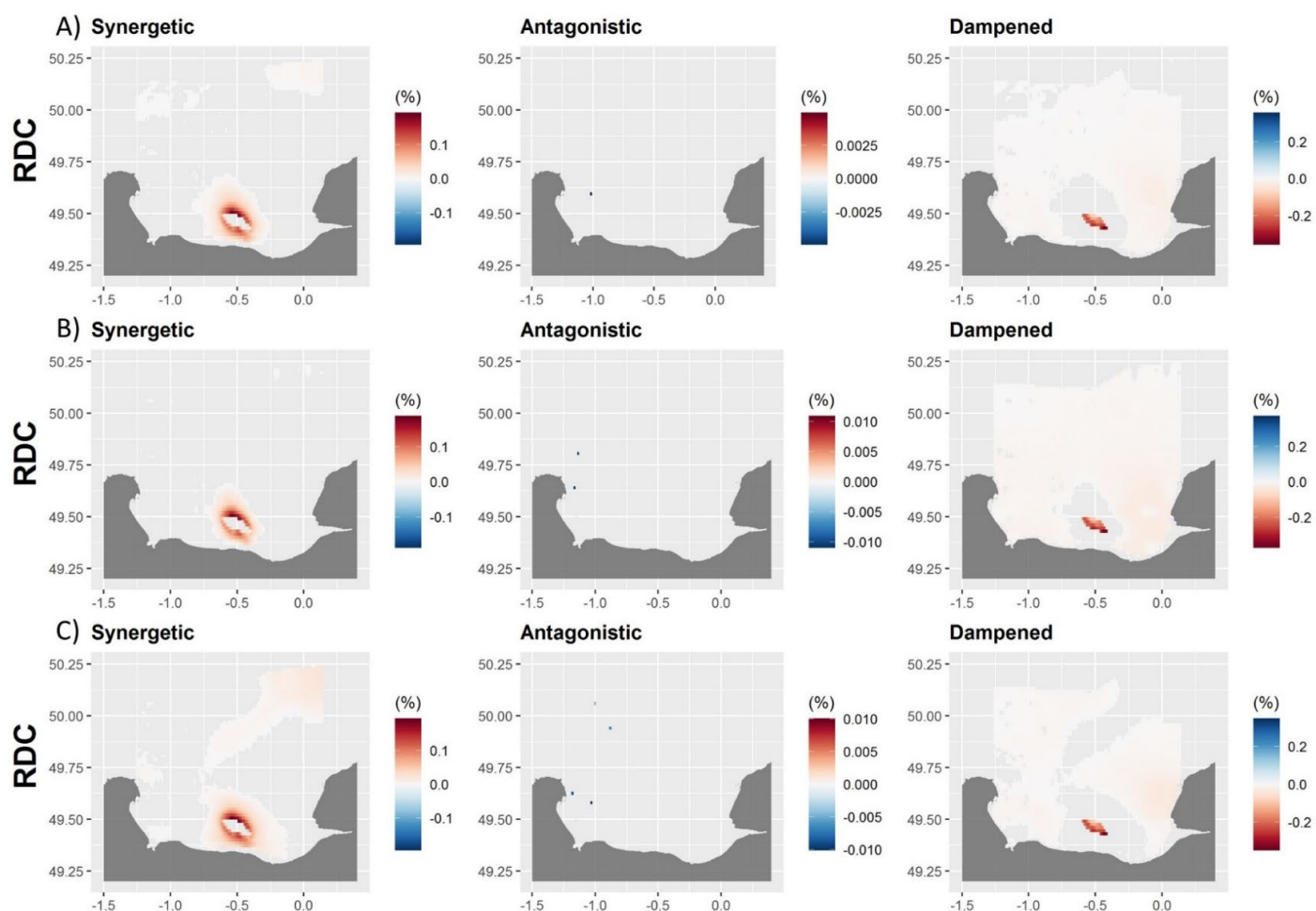


Figure SIII - 21 Cumulative effects for each Brexit scenario on the relative redundancy of the flow (RDC), with the offshore wind farm (OWF) and the 2050 RCP 8.5 climate change (2050 CC) effects on species distribution.

A), Cumulative effects of the OWF, 2050 CC and the absence of fishing variation due to Brexit (F_{sam}); B), Cumulative effects of the OWF, 2050 CC and increased fishing due to Brexit (F_{inc}); C), Cumulative effects of the OWF, 2050 CC and decreased fishing due to Brexit (F_{dec}). Red, positive cumulative effects compared to the reference; blue, negative cumulative effects compared to the reference.

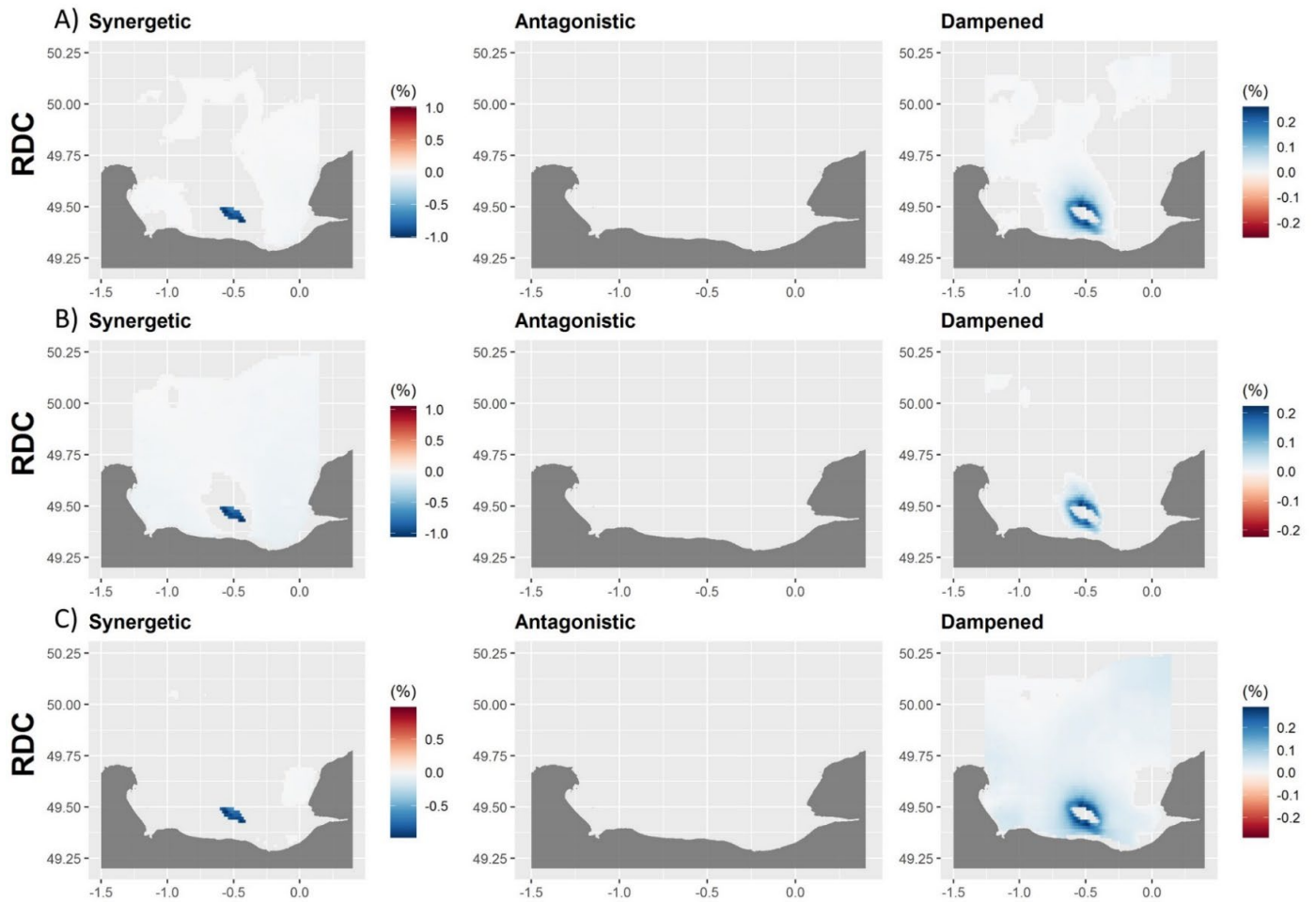


Figure SIII - 22 Cumulative effects for each Brexit scenario on the relative redundancy of the flow (RDC), with the offshore wind farm (OWF) and the 2100 RCP 8.5 climate change (2100 CC) effects on species distribution.

A), Cumulative effects of the OWF, 2100 CC and the absence of fishing variation due to Brexit (F_{same}); B), Cumulative effects of the OWF, 2100 CC and increased fishing due to Brexit (F_{inc}); C), Cumulative effects of the OWF, 2100 CC and decreased fishing due to Brexit (F_{dec}). Red, positive cumulative effects compared to the reference; blue, negative cumulative effects compared to the reference.

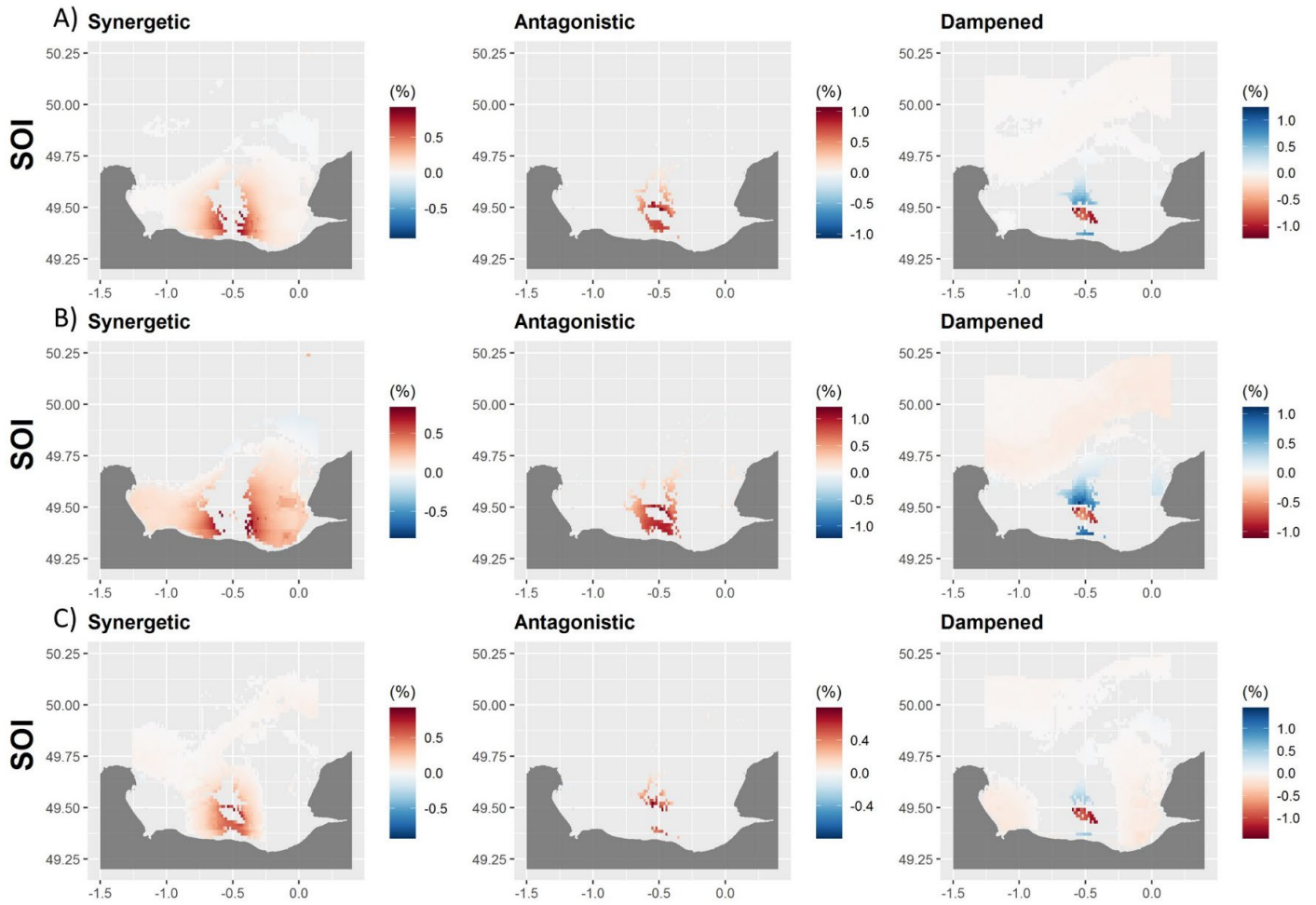


Figure SIII - 23 Cumulative effects for each Brexit scenario on the system omnivory (SOI), with the offshore wind farm (OWF) and the 2050 RCP 8.5 climate change (2050 CC) effects on species distribution.

A), Cumulative effects of the OWF, 2050 CC and the absence of fishing variation due to Brexit (F_{sam}); B), Cumulative effects of the OWF, 2050 CC and increased fishing due to Brexit (F_{inc}); C), Cumulative effects of the OWF, 2050 CC and decreased fishing due to Brexit (F_{dec}). Red, positive cumulative effects compared to the reference; blue, negative cumulative effects compared to the reference.

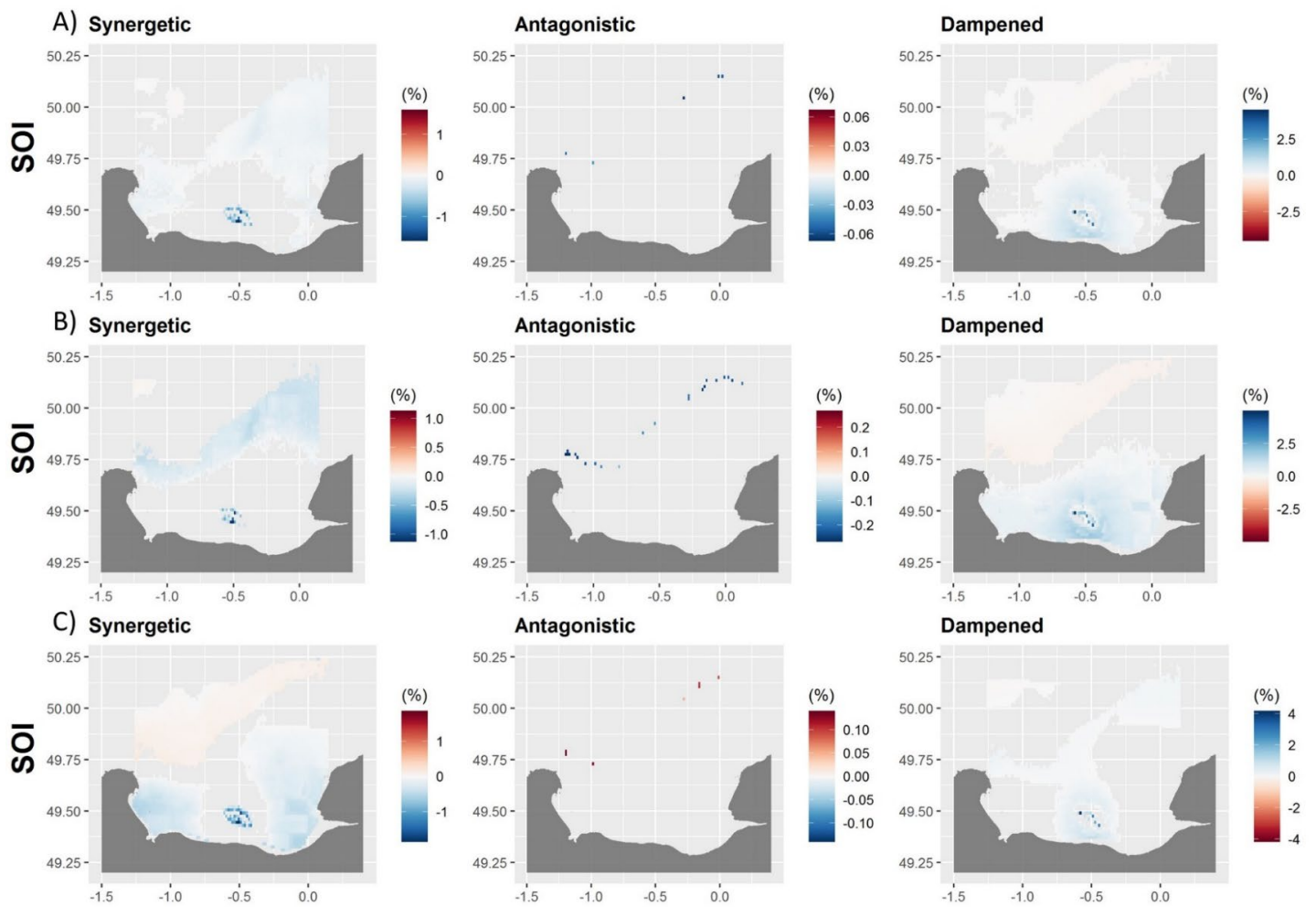


Figure SIII - 24 Cumulative effects for each Brexit scenario on the system omnivory (SOI), with the offshore wind farm (OWF) and the 2100 RCP 8.5 climate change (2100 CC) effects on species distribution.

A), Cumulative effects of the OWF, 2100 CC and the absence of fishing variation due to Brexit (F_{sam}); B), Cumulative effects of the OWF, 2100 CC and increased fishing due to Brexit (F_{inc}); C), Cumulative effects of the OWF, 2100 CC and decreased fishing due to Brexit (F_{dec}). Red, positive cumulative effects compared to the reference; blue, negative cumulative effects compared to the reference.

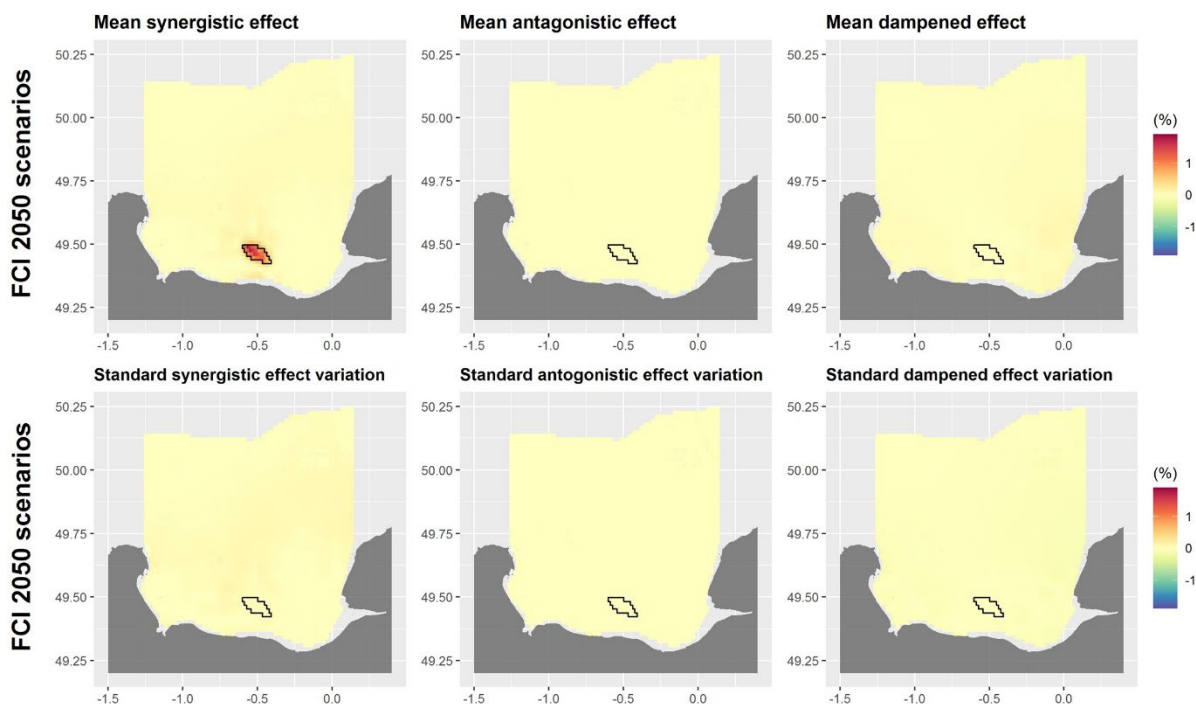


Figure SIII - 25 Mean values and standard deviations of the combined effect of the 2050 climate change scenario + the offshore wind farm on the Finn cycling index (FCI), for all Brexit fishing scenarios.

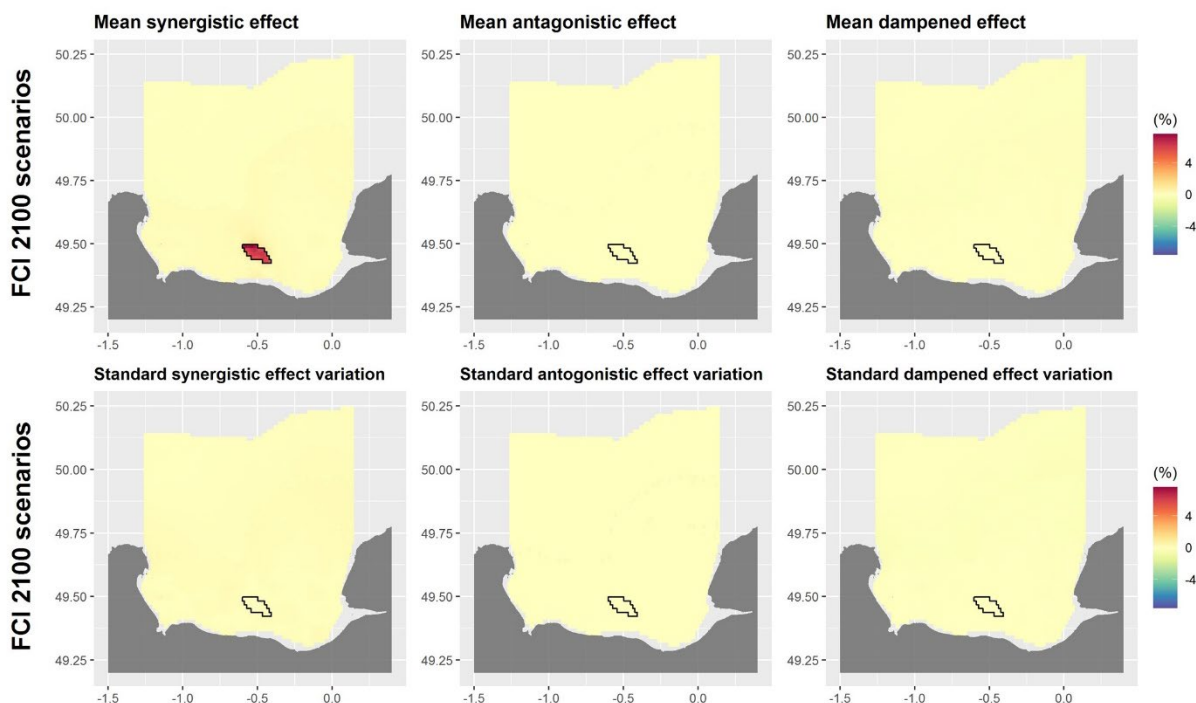


Figure SIII - 26 Mean values and standard deviations of the combined effect of the 2100 climate change scenario + the offshore wind farm on the Finn cycling index (FCI), for all Brexit fishing scenarios.

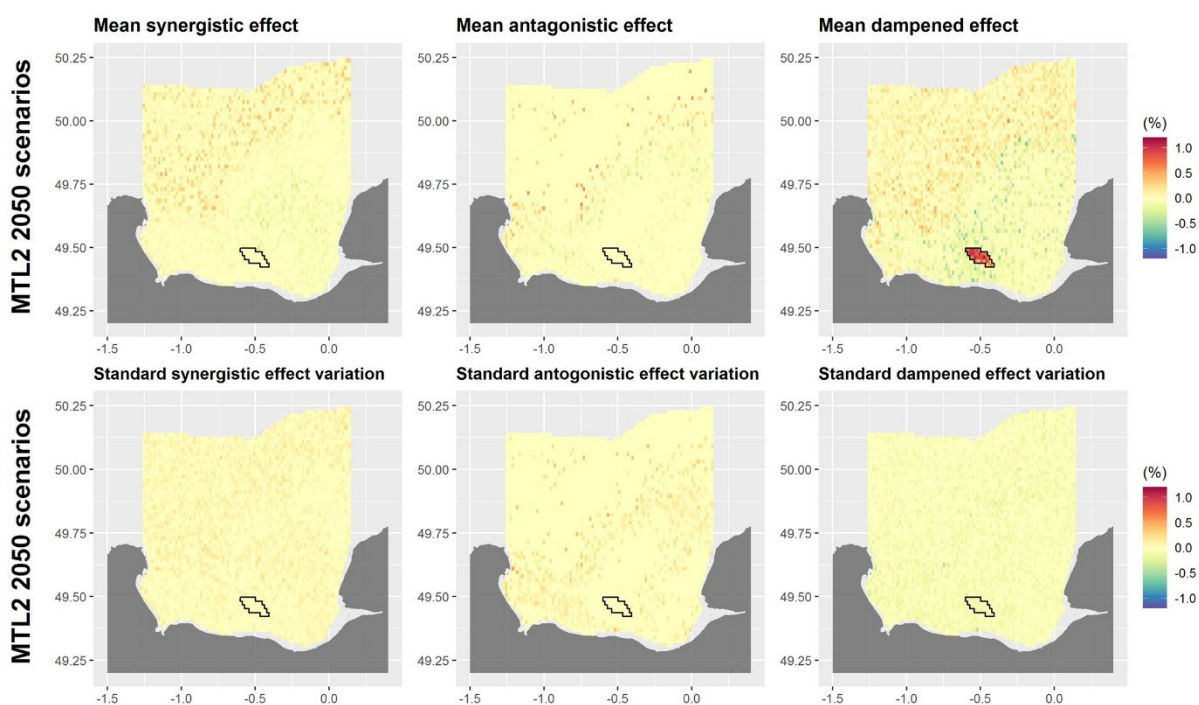


Figure SIII - 27 Mean values and standard deviations of the combined effect of the 2050 climate change scenario + the offshore wind farm on the Finn cycling index (MTL2) for all Brexit fishing scenarios.

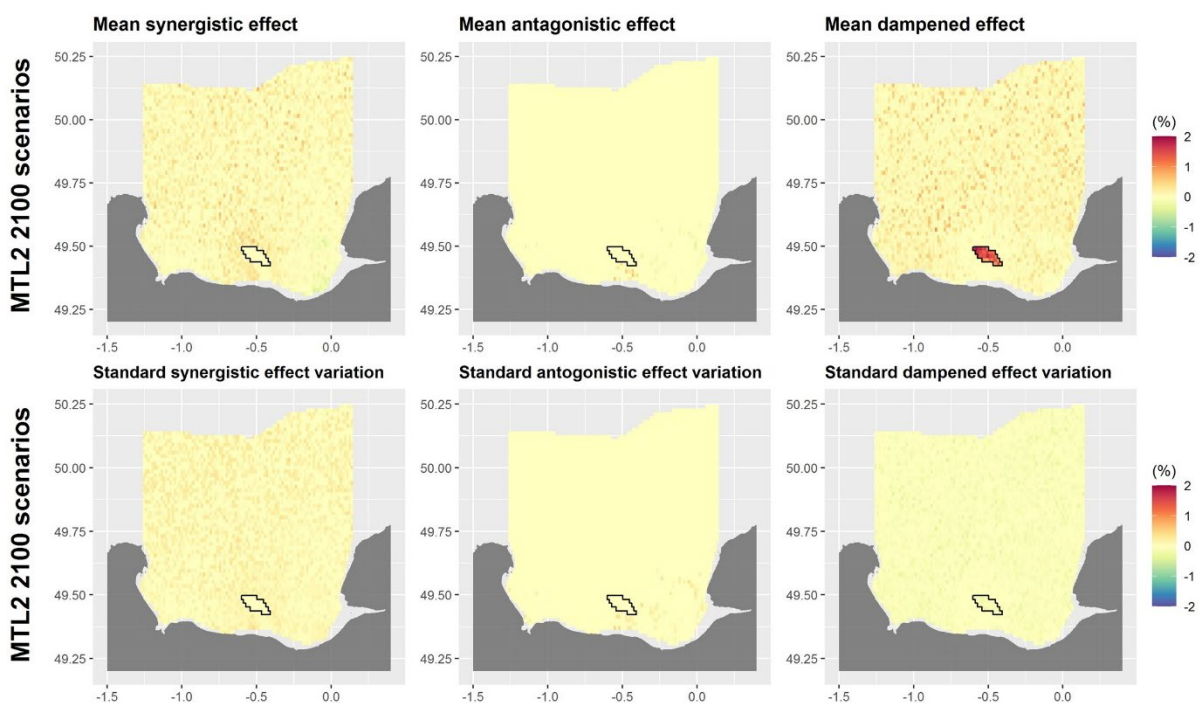


Figure SIII - 28 Mean values and standard deviations of the combined effect of the 2100 climate change scenario + the offshore wind farm on the Finn cycling index (MTL2) for all Brexit fishing scenarios.

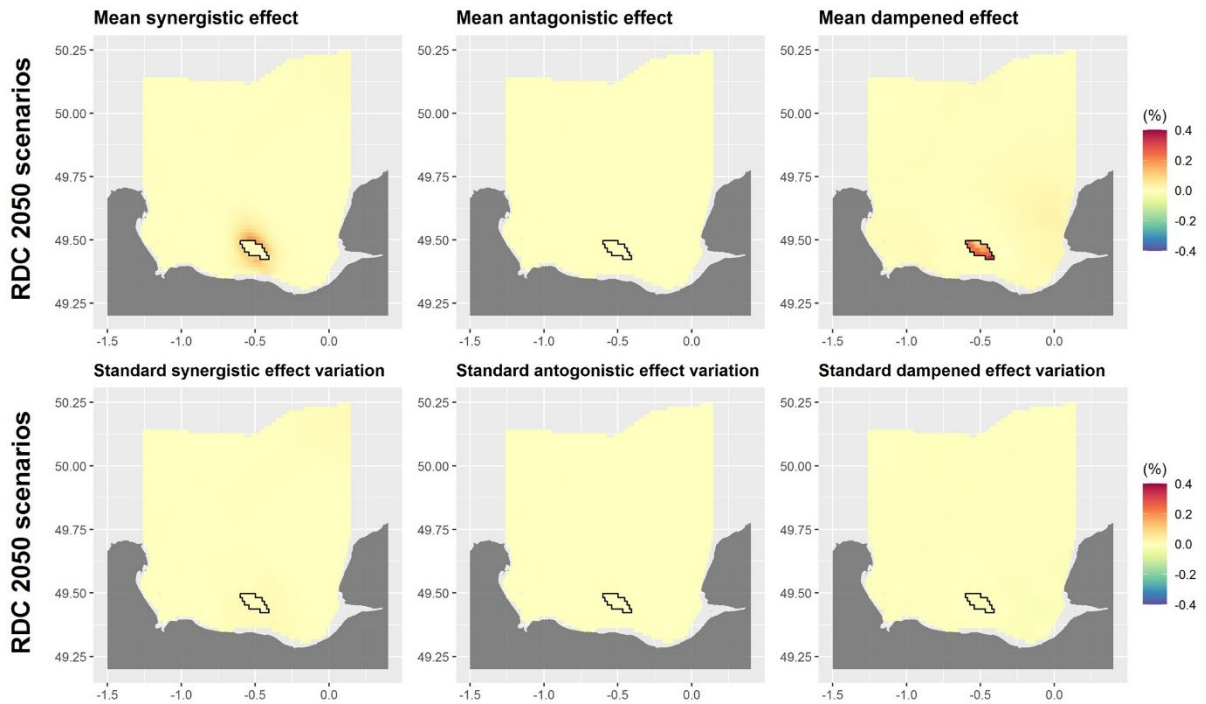


Figure SIII - 29 Mean values and standard deviations of the combined effect of the 2050 climate change scenario + the offshore wind farm on the Finn cycling index (RDC) for all Brexit fishing scenarios.

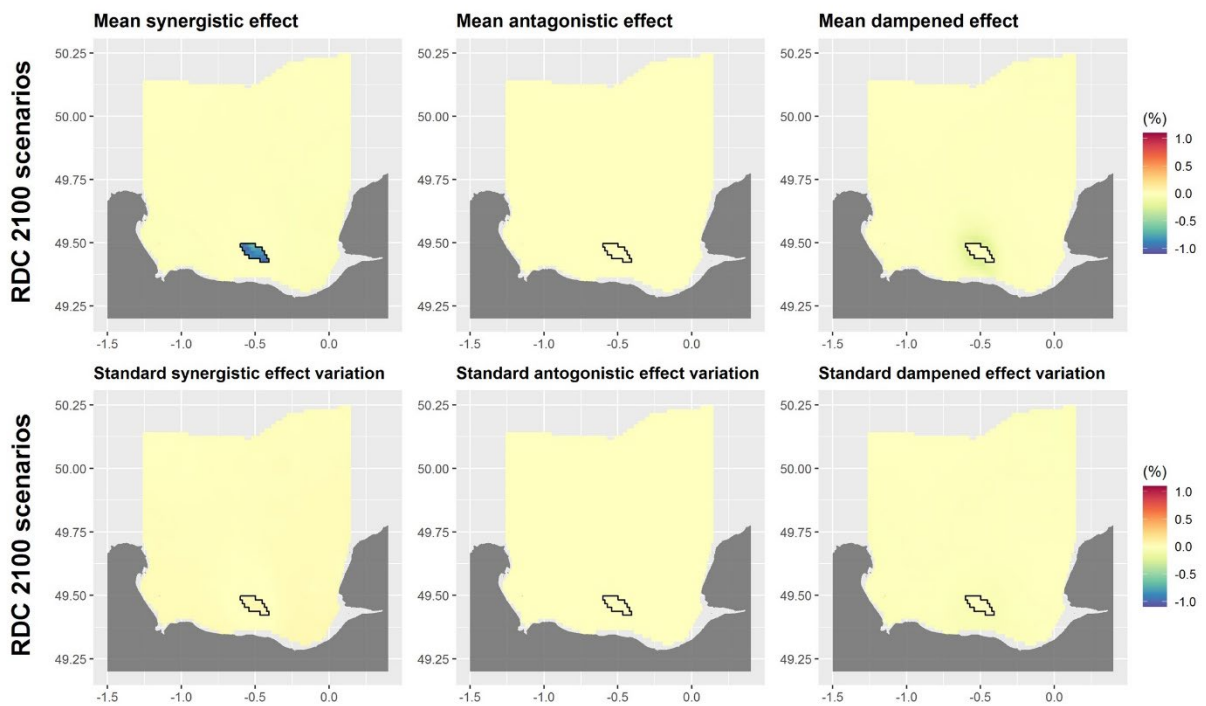


Figure SIII - 30 Mean values and standard deviations of the combined effect of the 2100 climate change scenario + the offshore wind farm on the Finn cycling index (RDC), for all Brexit fishing scenarios.

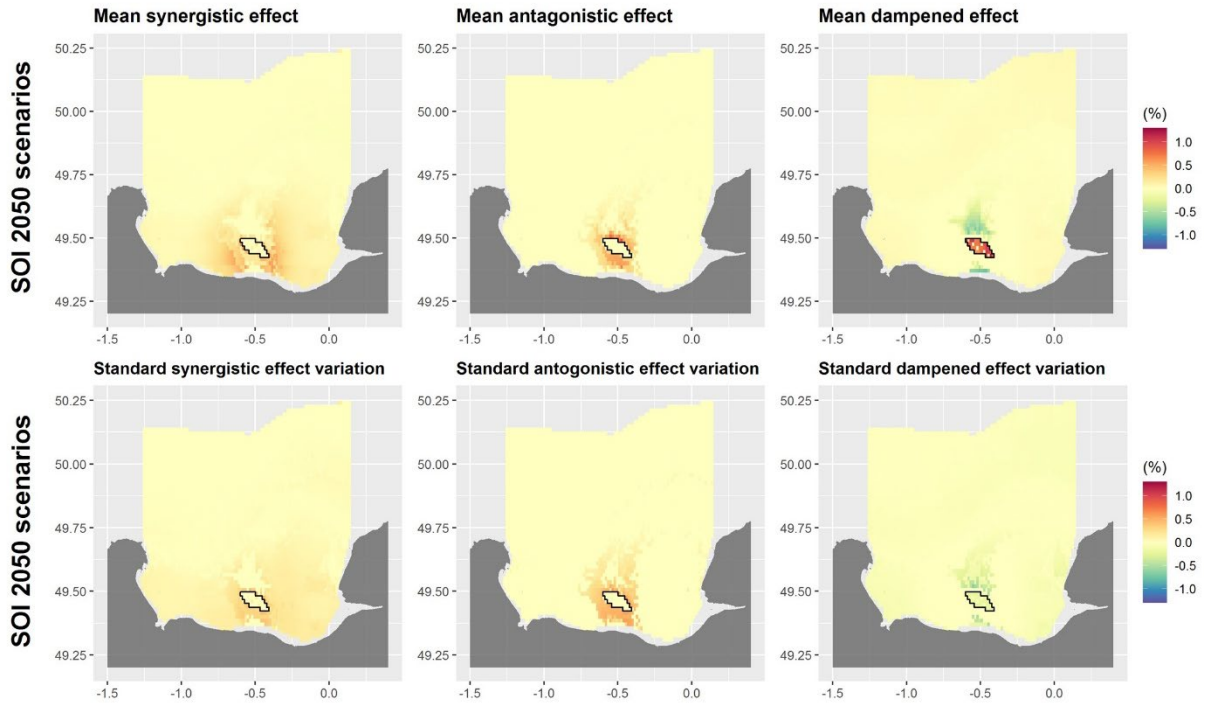


Figure SIII - 31 Mean values and standard deviations of the combined effect of the 2100 climate change scenario + the offshore wind farm on the Finn cycling index (SOI) for all Brexit fishing scenarios.

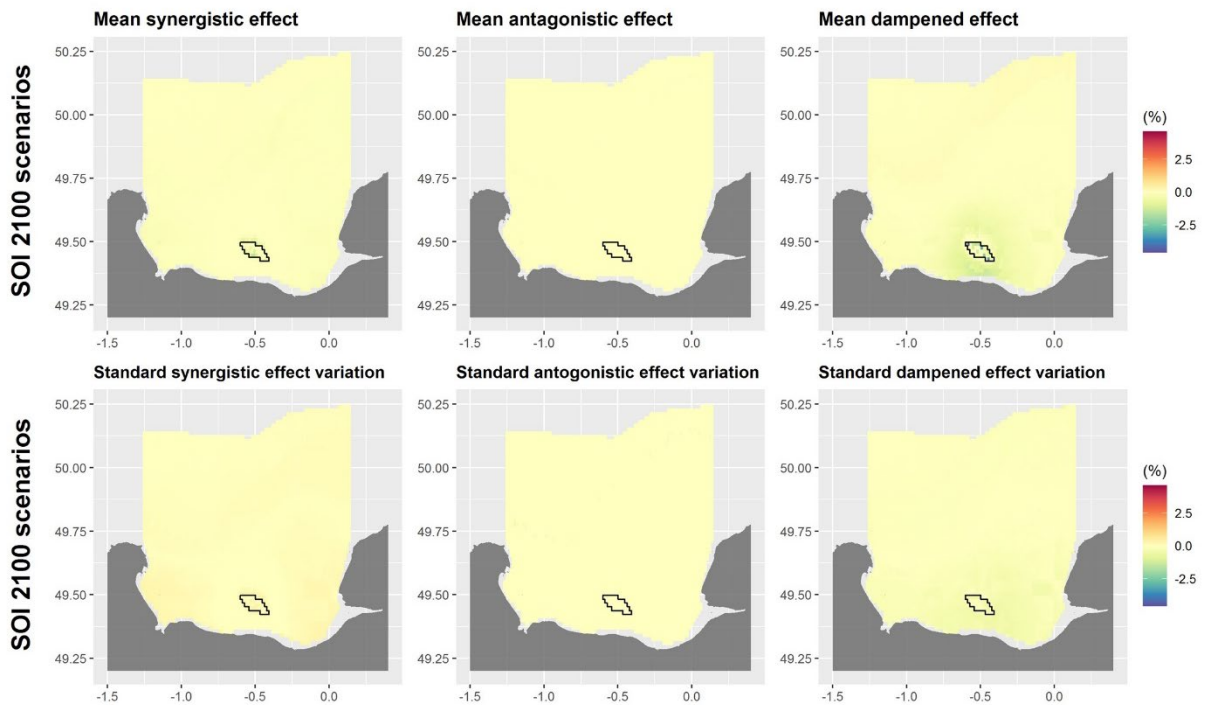


Figure SIII - 32 Mean values and standard deviations of the combined effect of the 2100 climate change scenario + the offshore wind farm on the Finn cycling index (SOI), for all Brexit fishing scenarios.

Supplementary materials IV.

Table SIVI - 1 Ecological groups of the extended bay of Seine Ecospace model with their species composition.

Ecopath functional group	Species composition
Fish Limande	<i>Limanda limanda</i>
Fish Flounder	<i>Platichthys flesus</i>
Fish european plaice	<i>Pleuronectes platessa</i>
Fish sole	<i>Solea solea</i>
Fish sea bream	<i>Spondylusoma cantharus</i>
Fish benthos feeders	<i>Callionymus</i>
	<i>Mullus surmuletus</i>
	<i>Labrus bergylta</i>
	<i>Zeus faber</i>
Fish planctivorous	<i>Clupea harengus</i>
	<i>Engraulis encrasicolus</i>
Fish piscivorous	<i>Pollachius pollachius</i>
Fish european sprat	<i>Sprattus sprattus</i>
Fish european pilchard	<i>Sardina pilchardus</i>
Fish poor cod	<i>Trisopterus minutus</i>
Fish pouting	<i>Trisopterus luscus</i>
Fish gurnard	<i>Chelidonichthys lucerna</i>
	<i>Chelidonichthys lastoviza</i>
Fish atlantic horse mackerel	<i>Trachurus trachurus</i>
Fish whiting	<i>Merlangius merlangus</i>
Fish atlantic cod	<i>Gadus morhua</i>
Fish sharks	<i>Mustelus mustelus</i>
	<i>Scyliorhinus canicula</i>
	<i>Scyliorhinus stellaris</i>
Fish rays	<i>Raja clavata</i>
	<i>Raja montagui</i>
Fish european seabass	<i>Dicentrarchus labrax</i>
Fish mackerel	<i>Scomber scombrus</i>
Benthic cephalopods	<i>Sepia officinalis</i>
Benthopelagic cephalopods	<i>Alloteuthis spp</i>
	<i>Loligo vulgaris</i>
Surface feeders seabirds	<i>Larus argentatus / Larus michahellis / Larus marinus / Larus fuscus</i>
	<i>Larus sp</i>
	<i>Larus ridibundus/ Larus melanocephalus</i>
	<i>Rissa tridactyla</i>
	<i>Sterna paradisaea/ Sterna hirundo/ Sterna albifrons/ Thalasseus sandvicensis</i>
Plunge and pursuit divers seabirds	<i>Fratercula arctica / Uria aalge / Alca torda</i>
	<i>Morus bassanus</i>
	<i>Gavia stellata/ Gavia arctica/ Gavia immer</i>
	<i>Phalacrocorax carbo / Phalacrocorax aristotelis</i>

Ecopath functional group	Species composition
	<i>Fulmarus glacialis</i>
Benthic feeders seabirds	<i>Melanitta nigra</i> / <i>Melanitta fusca</i>
Phocidae	<i>Halichoerus grypus</i>
	<i>Phoca vitulina</i>
Harbour porpoises	<i>Phocoena phocoena</i>
Bottlenose dolphins	<i>Tursiops truncatus</i>
Benthic inv bivalves filter feeders	<i>Acanthocardia echinata</i>
	<i>Angulus fabula</i>
	<i>Angulus pygmaeus</i>
	<i>Corbula gibba</i>
	<i>Ensis</i>
	<i>Ensis directus</i>
	<i>Ensis magnus</i>
	<i>Kurtiella bidentata</i>
	<i>Lanice conchilega</i>
	<i>Lutraria lutraria</i>
	<i>Mactra stultorum</i>
	<i>Moerella donacina</i>
	<i>Parvicardium scabrum</i>
	<i>Phaxas pellucidus</i>
	<i>Spisula elliptica</i>
	<i>Spisula subtruncata</i>
	<i>Tellimya ferruginosa</i>
	<i>Thracia phaseolina</i>
Benthic inv deposit feeders (Subsurface)	<i>Amphilochus neapolitanus</i>
	<i>Aphelocheata marioni</i>
	<i>Bathyporeia</i>
	<i>Bathyporeia elegans</i>
	<i>Bathyporeia guilliamsoniana</i>
	<i>Bathyporeia tenuipes</i>
	<i>Capitella capitata</i>
	<i>Capitella minima</i>
	<i>Capitellidae</i>
	<i>Caulleriella alata</i>
	<i>Caulleriella viridis</i>
	<i>Caulleriella zetlandica</i>
	<i>Chaetozone christiei</i>
	<i>Chaetozone gibber</i>
	<i>Chaetozone setosa</i>
	<i>Echinocardium cordatum</i>
	<i>Notomastus latericeus</i>
	<i>Nucula hanleyi</i>
	<i>Nucula nitidosa</i>
	<i>Phascolion (Phascolion) strombus strombus</i>
	<i>Scalibregma inflatum</i>

Ecopath functional group	Species composition
	<i>Scoloplos (Scoloplos) armiger</i>
	<i>Spio decoratus</i>
	<i>Spiophanes bombyx</i>
Benthic inv deposit feeders (Surface)	<i>Abludomelita obtusata</i>
	<i>Abra alba</i>
	<i>Acrocnida brachiata</i>
	<i>Ampharete baltica</i>
	<i>Amphicteis gunneri</i>
	<i>Amphipholis squamata</i>
	<i>Aonides oxycephala</i>
	<i>Aonides paucibranchiata</i>
	<i>Aora gracilis</i>
	<i>Apseudopsis latreillii</i>
	<i>Atylus vedlomensis</i>
	<i>Bodotria arenosa</i>
	<i>Bodotria pulchella</i>
	<i>Bodotria scorpioides</i>
	<i>Cheirocratus</i>
	<i>Cheirocratus intermedius</i>
	<i>Corophium</i>
	<i>Crassikorophium bonellii</i>
	<i>Diastylis bradyi</i>
	<i>Diastylis laevis</i>
	<i>Gastrosaccus sanctus</i>
	<i>Gastrosaccus spinifer</i>
	<i>Lagis koreni</i>
	<i>Magelona filiformis</i>
	<i>Magelona johnstoni</i>
	<i>Megaluropus agilis</i>
	<i>Megamphopus cornutus</i>
	<i>Melinna palmata</i>
	<i>Nebalia bipes</i>
	<i>Owenia fusiformis</i>
	<i>Pariambus typicus</i>
	<i>Periculodes longimanus</i>
	<i>Phtisica marina</i>
	<i>Pinnotheres pisum</i>
	<i>Poecilochaetus serpens</i>
	<i>Polycirrus medusa</i>
	<i>Pontocrates arenarius</i>
	<i>Pseudocuma (Pseudocuma) longicorne</i>
	<i>Scolelepis (Scolelepis) squamata</i>
	<i>Scolelepis bonnieri</i>
	<i>Siphonocetes (Centraloecetes) kroyeranus</i>
	<i>Synchelidium maculatum</i>

Ecopath functional group	Species composition
	<i>Urothoe elegans</i>
	<i>Urothoe poseidonis</i>
Benthic inv filter feeders	<i>Ampelisca</i>
	<i>Ampelisca brevicornis</i>
	<i>Ampelisca diadema</i>
	<i>Ampelisca spinipes</i>
	<i>Ampelisca tenuicornis</i>
	<i>Ampelisca typica</i>
	<i>Phoronis psammophila</i>
	<i>Pisidia longicornis</i>
	<i>Spirobranchus</i>
	<i>Thyone fusus</i>
Benthic inv predators	<i>Antalis vulgaris</i>
	<i>Asterias rubens</i>
	<i>Eteone longa</i>
	<i>Eualus cranchii</i>
	<i>Eulalia mustela</i>
	<i>Eumida</i>
	<i>Eumida bahusiensis</i>
	<i>Eumida sanguinea</i>
	<i>Eunereis longissima</i>
	<i>Eurydice pulchra</i>
	<i>Euspira pulchella</i>
	<i>Exogone (Parexogone) hebes</i>
	<i>Glycera gigantea</i>
	<i>Glycera lapidum</i>
	<i>Glycera tridactyla</i>
	<i>Glycinde nordmanni</i>
	<i>Haplostylus normani</i>
	<i>Harmothoe</i>
	<i>Harmothoe glabra</i>
	<i>Harmothoe pagenstecheri</i>
	<i>Malmgreniella arenicolae</i>
	<i>Myrianida</i>
	<i>Mysta picta</i>
	<i>Nemertea</i>
	<i>Nephtys assimilis</i>
	<i>Nephtys cirrosa</i>
	<i>Nephtys hombergii</i>
	<i>Nephtys kersivalensis</i>
	<i>Nymphon brevirostre</i>
	<i>Paranaitis kosteriensis</i>
	<i>Philocheras bispinosus bispinosus</i>
	<i>Pholoe baltica</i>
	<i>Phyllodoce</i>

Ecopath functional group	Species composition
	<i>Phyllodoce lineata</i>
	<i>Phyllodoce longipes</i>
	<i>Phyllodoce maculata</i>
	<i>Phyllodoce mucosa</i>
	<i>Phyllodoce rosea</i>
	<i>Processa edulis edulis</i>
	<i>Processa modica modica</i>
	<i>Protodorvillea kefersteini</i>
	<i>Sigalion mathildae</i>
	<i>Sthenelais boa</i>
	<i>Tubulanus polymorphus</i>

Étude du cumul d'impacts autour du parc éolien offshore de la Baie de Seine : quelles conséquences pour le fonctionnement trophique de l'écosystème, sa résilience et les services écosystémiques ?

Résumé :

Avec l'accroissement de la population humaine sur Terre, le nombre et l'intensité des activités humaines sur les littoraux ne cessent d'augmenter. Ces activités peuvent avoir des effets importants sur l'environnement et sur les écosystèmes. De plus, la grande diversité de ces activités sur les côtes fait que les écosystèmes côtiers sont presque toujours soumis à de multiples facteurs de changements d'origine humaine. Ces facteurs peuvent interagir entre eux, provoquant des effets dit cumulés, qui peuvent avoir des conséquences importantes, et difficilement prévisibles, sur les écosystèmes. C'est dans le cadre du développement des énergies marines renouvelables en France, que cette thèse met en place des méthodes innovantes pour quantifier les effets séparés et combinés de multiples facteurs de changements, comprenant : le futur parc éolien de Courseulles-sur-Mer, le changement climatique, et l'effet du Brexit sur les régimes de pêche. Les effets combinés de ces facteurs sur le fonctionnement et la résilience de l'écosystème de la baie de Seine ont été quantifiés avec l'aide d'approches écosystémiques holistiques.

Nos résultats indiquent que les mécanismes d'interactions des facteurs sont complexes et multiples, néanmoins les potentiels effets structurants des facteurs sur le fonctionnement des écosystèmes jouent un rôle déterminant sur la genèse des effets cumulés. Les effets cumulés apparaissent hétérogènes entre les propriétés fonctionnelles des écosystèmes et spécifiques aux écosystèmes étudiés. Il est donc important de réaliser des études fonctionnelles du cumul de multiples facteurs à des échelles locales, pour déterminer les effets de l'homme sur les écosystèmes, et *vice versa*, en prenant en compte les multiples services rendus par les écosystèmes.

Mots clés : Baie de Seine, approches écosystémiques, cumul d'impacts, écologie fonctionnelle, services écosystémiques.

Study of the cumulative impacts around the offshore wind farm of the Baie de Seine: what consequences for the trophic functioning of the ecosystem, its resilience and ecosystem services?

Abstract:

As the human population grows, the number and the intensity of anthropogenic activities increases on coastal systems. These activities can have significant effects on the environment and on ecosystems. Furthermore, the wide range of coastal activities implies that coastal ecosystems are almost always subject to multiple ecological drivers induced by humans. These drivers can interact with each other, leading to cumulative effects, which can have significant, and difficult to predict, consequences on ecosystems. In the context of the development of marine renewable energy in France, this thesis implements innovative methods to quantify the separate and combined effects of multiple ecological drivers, including: the future Courseulles-sur-Mer offshore wind farm, climate change, and the effect of Brexit on fishing regimes. We studied the combined effects of these drivers on the functioning and resilience of the Seine Bay ecosystem using holistic ecosystem approaches.

Our results indicate that interactions between drivers are numerous and complex, yet the potential structuring effects of drivers on ecosystem functioning play a determining role in the formation of cumulative effects. Cumulative effects appear to be heterogeneous between the functional properties of ecosystems and specific to the studied ecosystems. It is therefore important to carry out local functional studies of the combination of multiple drivers, to determine the effects of humans on ecosystems, as well as to evaluate the effects of combined drivers on the provisioning of ecosystem services.

Key words: Bay of Seine, ecosystem approaches, cumulative impacts, functional ecology, ecosystem services.